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Studies of the Weddell seal in the Vestfold Hills, East Antarctica

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STUDIES OF THE WEDDELL SEAL
IN THE VESTFOLD HILLS, EAST ANTARCTICA

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ABSTRACT

Apart from a summary of observations of Weddell seals in the Vestfold Hills in 1966, directed research on Weddell seals did not begin until the commencement of tagging of seals, particularly pups, in 1973. Other studies of the Weddell seal in the Vestfold Hills have been directed at an understanding of their diet, vocalisations, response to anaesthesia, and their genetic make-up. Variable efforts have been made in the tagging and resighting of seals over the years. The data have been unsuitable for the calculation of some population parameters but at the same time they have provided good long-term data on other aspects such as total pup numbers. These data, along with those from aerial censuses and studies of the moult, have allowed an assessment of the methodology of seal censusing to be made. This work has supported the theory that food availability in different years affects numbers of seals censused during the moult, thus calling into question some inter-annual comparisons. In addition there are periods during the moult when aerial censuses are not comparable on an inter-annual basis, due to the composition of the population. This finding has direct relevance to seal monitoring undertaken for the CCAMLR Ecosystem Monitoring Program. Corrections of anomalies in the Weddell seal data base and a stricter sampling regime dating from the breeding season 1988–89 are expected to return results in the future that will be useful in studying population processes in an environment where the species is not being exploited and its population is regulated by natural factors.

INTRODUCTION

Long-term studies of high-level marine consumers are a useful means of monitoring the 'health' of the marine ecosystem, the effects of commercial fishing and the effects of marine pollution, as well as recording natural fluctuations. The importance of monitoring marine predators, particularly in the Southern Ocean, has been recognised by the establishment of a number of internationally coordinated programs such as the CCAMLR Ecosystem Monitoring Program (CEMP) established by the Commission for the Conservation of Antarctic Marine Living Resources. In addition, a number of census programs have been initiated by individual nations for species not covered by CEMP such as fulmarine petrels (Green and Johnstone 1986), southern elephant seals *Mirounga leonina* (Burton 1985) and leopard seals *Hydrurga leptonyx* (Rounsevell 1988). One of the longest-running of such programs is the censusing and marking of Weddell seals *(Leptonychotes weddellii)* in the Vestfold Hills, Antarctica (68°35'S, 77°58'E) (Figure 1).

Weddell seals are coastal animals of the fast ice. This allows continuing detailed scientific study without enormous logistical effort. Three long-term marking programs on Weddell seals in Antarctica have been conducted by the USA, Britain and Australia (Testa *et al.* 1990). Australia's program has been running since 1973. Although efforts in tagging and resighting have varied from year to year, the sustained 20 years of mark and resight data (to 1993) are returning valuable information. Since long-term data sets of animal numbers in Antarctica are uncommon, this program is becoming more valuable with every year that passes.

Early work on Weddell seals in the Vestfold Hills was summarised by Lugg (1966), who documented much of the basic biology of the seals in the Vestfold Hills. Between 150 and 200 seal pups were born annually to 1963 with the sex ratio of pups being close to 50:50 (53:47). Pups were first observed between 13 and 20 October from 1957 to 1963. The pups were weaned at six weeks but remained with the mothers, moving up to 5–6 km from their birth sites before separating two weeks later (Lugg 1966). Pup mortality was found to be low, about 2.5%.

Observations continued into the 1970s but directed work on Weddell seals did not recommence until 1973 with the initiation of a tagging program and occasional aerial censuses. Data from the tagging, to 1987, indicated that there might be differences in population parameters between Weddell seals at different locations around Antarctica, particularly in reproductive rate and age at first pupping (Testa *et al.* 1990). Population estimates were also obtained from aerial censuses, with infrequent censuses in 1978–79, 1982–83, 1983–84, 1984–85, 1989–90, 1990–91 and 1991–92. The data (to 1990–91) allowed an examination of the usefulness of aerial censuses in seal population studies, particularly when undertaken during the moult (Green *et al.* 1992). Dietary studies commenced on a monthly basis in 1983 and ran through 1984 into 1985. The result of this study (Green and Burton 1987a) was the first analysis of the diet of an Antarctic seal over a full twelve-month period, and this has not yet been repeated at any other location or with any other Antarctic species of seal. Work on seal vocalisations in the Vestfold Hills commenced in 1983 (Thomas *et al.* 1988) and continued through 1984 (Green and Burton 1987b, 1988). Work continued in association with the University of Tasmania in 1989–90 (Morrice 1990, Morrice *et al.* in press) and later in collaboration with international researchers in 1990–91 (Terhune *et al.* in press a and b, Terhune *et al.* submitted) and in 1991–92 in association with the University of New Brunswick (Canada). Blood samples from Weddell seals were taken for comparison of the genetic diversity of the population with that at

McMurdo Sound (Moritz *et al.* in prep). As part of this program, the anaesthetisation of Weddell seals confirmed the experience of Gales and Burton (1988) which demonstrated the difficulties of using anaesthetics with this species (Phelan and Green 1992).

Renewed interest in the Weddell seal as a major predator of fin fish in Prydz Bay has shown the importance of ongoing research on Weddell seals. This report is a summary of the data collected to date and an attempt to point the way to future research.

GENERAL BIOLOGY

Weddell seals weigh between 25 kg (Laws 1981) and 29.5 kg (Bertram 1940) at birth, double their mass in 10 days, and are weaned in six to eight weeks (Stirling 1967) at about 110 kg (Laws 1981). Pups first enter the water at 8–10 days of age (Lindsey 1937, Stirling 1969a). Adult females come into oestrus and mate on average 35–36 days post parturition (Hill 1987). This is difficult to determine as mating occurs underwater and the only mating actually observed (by underwater video) occurred 43 days post parturition (Cline *et al.* 1971). A breeding ratio of between eight and 11 females to one male was suggested by Hill (1987). Males can begin breeding at a very early age. Hill (1987) documented copulations for a four-year-old, though the only other known-age mating seals were 10 and 12 years of age. The embryo does not implant for two to three months after mating (Stirling 1967). The number of pups born to a female during her lifetime could be as high as 18 but seven is a more likely figure (Hill 1987).

The maximum age for a Weddell seal is 25 years (Testa and Siniff 1987). Elsewhere tooth wear may contribute significantly to mortality of adult seals (Stirling 1969b). Tooth wear may seriously affect the ability of a seal to abrade ice and maintain breathing holes, and after the average age in McMurdo Sound of eight to nine years (Stirling 1967) is achieved, tooth wear and necrosis showed a marked increase (Stirling 1969b). In the Vestfold Hills there are few breathing holes established in the winter because there is access to open water around nearby icebergs and off the Sørsdal Glacier. Only three holes were found by Lugg (1966) and one in 1984 (K.G. field note book) whereas in McMurdo Sound up to 150 breathing holes have been found in winter at Cape Evans (Kooyman 1981). Kooyman (1981) commented that perhaps the abundance of open water off the Vestfold Hills represents the more usual environment for Weddell seals and it is therefore fitting that one of the major studies of their population processes should continue there.

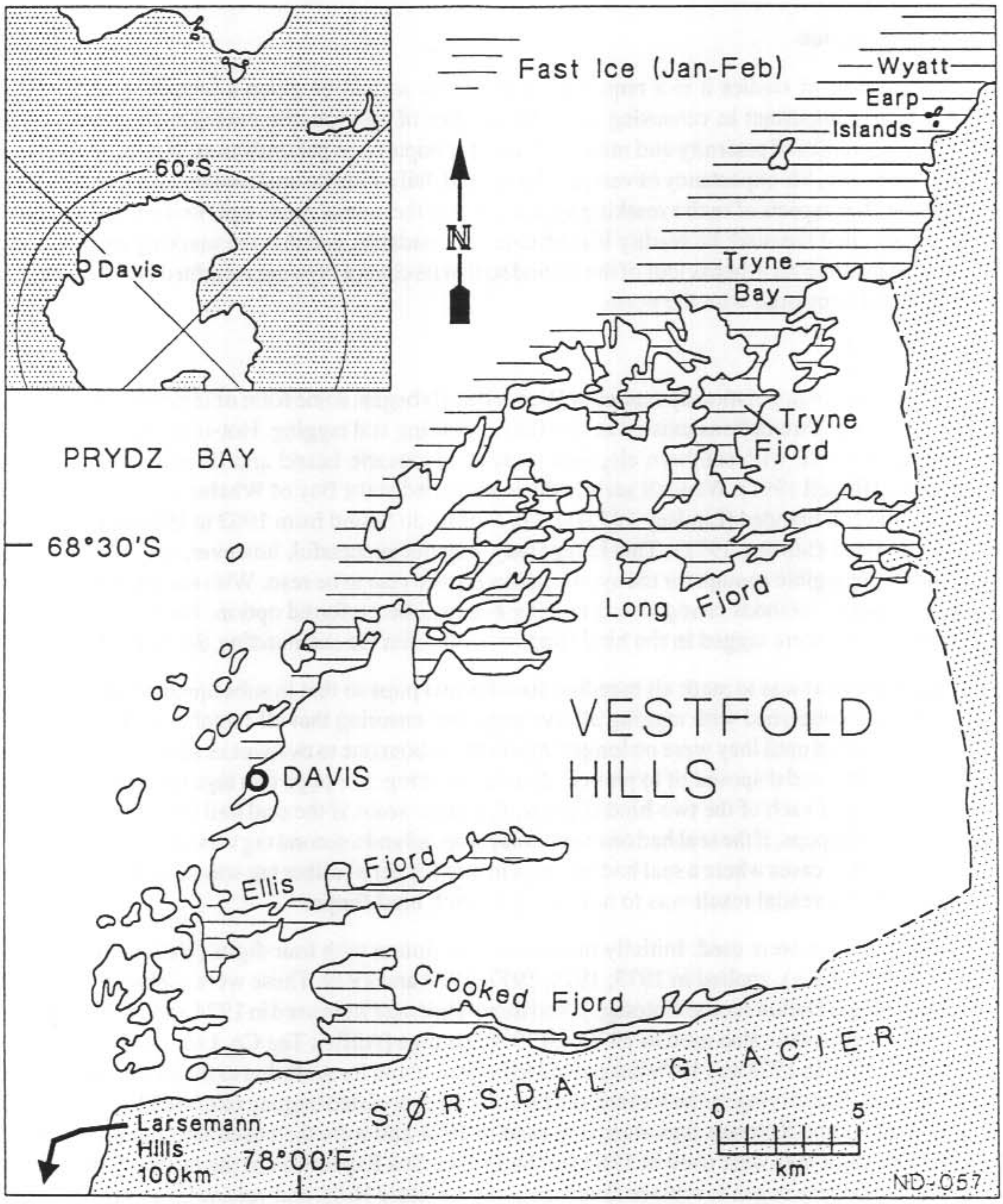

Figure 1. The Vestfold Hills, Antarctica.

1. SEAL TAGGING

1.1 Introduction

For a number of studies it is a requirement that each animal be given a unique identity. This is particularly important in censusing pups, for studies of age-specific events such as time of first breeding, studies of paternity and maternity, and for population parameters such as birth rate, death rate, longevity, life expectancy of various classes and daily and seasonal movements (Stirling 1966). The essential aspects of such a marking system are that the animal retain a permanent mark (or series of marks), that the mark be readily identifiable and readable, and that the marking method should not alter the long-term behaviour of the animal so that its chance of being resighted is either enhanced or reduced compared with the norm.

1.2 Methods

When studies of population dynamics of Weddell seals began, some form of individual marking had to be devised. Two options existed at that time: branding and tagging. Hot-iron branding had been used by ANARE with southern elephant seals at Macquarie Island and Heard Island with some success (Hindell 1991). Weddell seals had been branded at the Bay of Whales where 243 cows and pups had been branded (Lindsey 1937) and in McMurdo Sound from 1963 to 1965 when 705 pups were branded (Stirling 1971). This latter study was not successful, however, since few resighted brands were legible enough for the symbol denoting the year to be read. With the introduction of ear tags for cattle, methods changed and tagging became the preferred option. Each year from 1973, Weddell seals were tagged in the hind flippers on the fast ice surrounding the Vestfold Hills.

The initial effort was to mark all breeding females and pups so that in subsequent years the tagging was mainly concerned with tagging all live pups and ensuring that all females were tagged. Pups were not tagged until they were no longer 'newborn' (about one to two weeks after birth). Dead pups were counted, and disposed of to prevent double-counting. For pups two tags were inserted, one in the webbing of each of the two hind flippers. For other seals, if the seal had no tags two tags were inserted as for pups; if the seal had one tag it was recorded and a second tag was added to the untagged flipper. In rare cases where a seal had two tags in one flipper a further tag was added in the untagged flipper. The essential result was to have a tag in each hind flipper.

A variety of tags were used. Initially these were aluminium with four digits (National Band & Tag Co., Newport, Ky), applied in 1973, 1974, 1977, 1978 and 1979. These were replaced with plastic cattle ear tags (Dalton Jumbo Rototags). Red three-digit tags were used in 1974 and 1975, and yellow three-digit tags were also used in 1976 and 1978. Orange (Allflex Tag Co. Ltd., North Melbourne) tags were tried in 1978 and 1979 but proved to be unsuitable for seals due to their size, their loss rate (many were found lying on the ice) and the fact that the associated tagging pliers tended to bend. Blue four-digit Jumbo Rototags tags were first used in 1974 and were then used throughout this period. Pink four-digit tags were used in 1983 for the Frozen Sea Expedition in the nearby Rauer Islands. In late 1983 these began to replace blue tags in the Vestfold Hills, and yellow tags (this time of four digits) were re-introduced in 1991.

1.3 Results

The tagging program, beginning in 1973, tagged most females and pups during the breeding season. A bigger effort was made in the following year but efforts declined in 1975 and 1976 due to a shortage of tags. The tagging effort resumed fully in 1977 and, although fluctuating, it has resulted in the tagging of at least most of the pups each year since then (Table 1.1). The tagging of adults was concentrated on females during the pupping seasons. Fewer males were tagged, because they were not as commonly seen and because they were harder to tag (Table 1.2). The tagging of pups has occurred between 6 October and 9 December over the study period with the majority of pups being tagged between 22 October and 15 November (Figure 2). The majority of those pups resighted with tags were resighted in the first few years: nearly 50% were sighted within two years of tagging (all resights within the season of tagging were removed from this analysis) and 75% within about five years (Table 1.3).

1.4 Discussion

In McMurdo Sound, 68% of 252 seals tagged in January and February 1965 were resighted in the next season (Stirling 1967). The figure for non-pups in the Vestfold Hills is similar at 59% but for pups is lower at 31% (Table 1.3). The resight rate is affected by tag retention rate.

Overall tag loss rates are difficult to calculate because of the differences in types of tag used and in method of application. Loss rates of metal tags, for example, could not be calculated, as these were never used in tandem. Difficulties exist with calculations of loss rates for plastic tags because both tags have not consistently been recorded and second tags have been added to initial records in the early data base, making the initial tagging date problematical. The effectiveness of a number of different tag types was examined by Testa and Rothery (1992) who found that Dalton Jumbo Rototags showed the lowest loss rates on pups. It has been thought that tag loss rate is higher in males than females. In fact 15.9% of tagged female pups have been resighted compared with 11.3% for males. This makes the composition of resighted tagged pups 57.5% female. Considering that the adult population over the duration of the moult (tagged and untagged combined) consisted of 56.6% female in 1989–90 and 53.3% female in 1990–91, and the return rate for seals other than pups was only marginally less for males (41.3%) than for females (45.1%), the suspected loss of tags from males may in fact be attributed to the loss of males from the population. This appears to occur in the first few years with the majority of known age animals re-appearing in the population within the first five years after pupping.

The thoroughness and frequency of seal tagging has varied over the years largely because it has not been possible to have a wintering vertebrate ecologist at Davis in all years but also because (compared with access to McMurdo Sound populations) access to Davis, particularly early in the season, is more difficult, being by ship. Despite these problems the tagging program has provided a population that is increasingly of known age. If the tagging efforts of the past few years can be sustained, the population of Weddell seals in the Vestfold Hills will become important for the study of pinniped population dynamics.

Table 1.1. Number of pups and adults tagged for the period 1973–92. (Figures in brackets include total numbers tagged in the Vestfold Hills and Rauer Islands in 1983.)

Year	Pups	Adults
1973	136	151
1974	229	201
1975	32	8
1976	71	3
1977	196	3
1978	198	333
1979	245	175
1980	132	59
1981	144	140
1982	192	134
1983	218 (449)	456 (787)
1984	144	19
1985	144	22
1986	158	32
1987	168	17
1988	179	28
1989	197	26
1990	145	134
1991	193	79
1992	149	52
Total	3270 (3501)	2072 (2403)

Table 1.2. Tagging effort for adult males and females for the period 1973 –92. (Sex was not recorded for all adults tagged in some years.)

Year	Males	Females
1973	0	142
1974	7	184
1975	1	3
1976	0	2
1977	14	27
1978	26	166
1979	19	133
1980	1	51
1981	31	170
1982	74	104
1983	118 (226)	135 (415)
1984	1	0
1985	1	12
1986	6	20
1987	1	22
1988	8	46
1989	48	53
1990	39	50
1991	3	15
1992	10	59
Total	516	1674

Table 1.3. Time to resight original tags placed on seals.

Years to resight tags	Pups	Non-pups
1	136	582
2	80	187
3	57	83
4	43	44
5	30	31
6	35	22
7	27	15
8	12	6
9	14	15
10	2	1
11	1	2
15	1	–
16	1	–

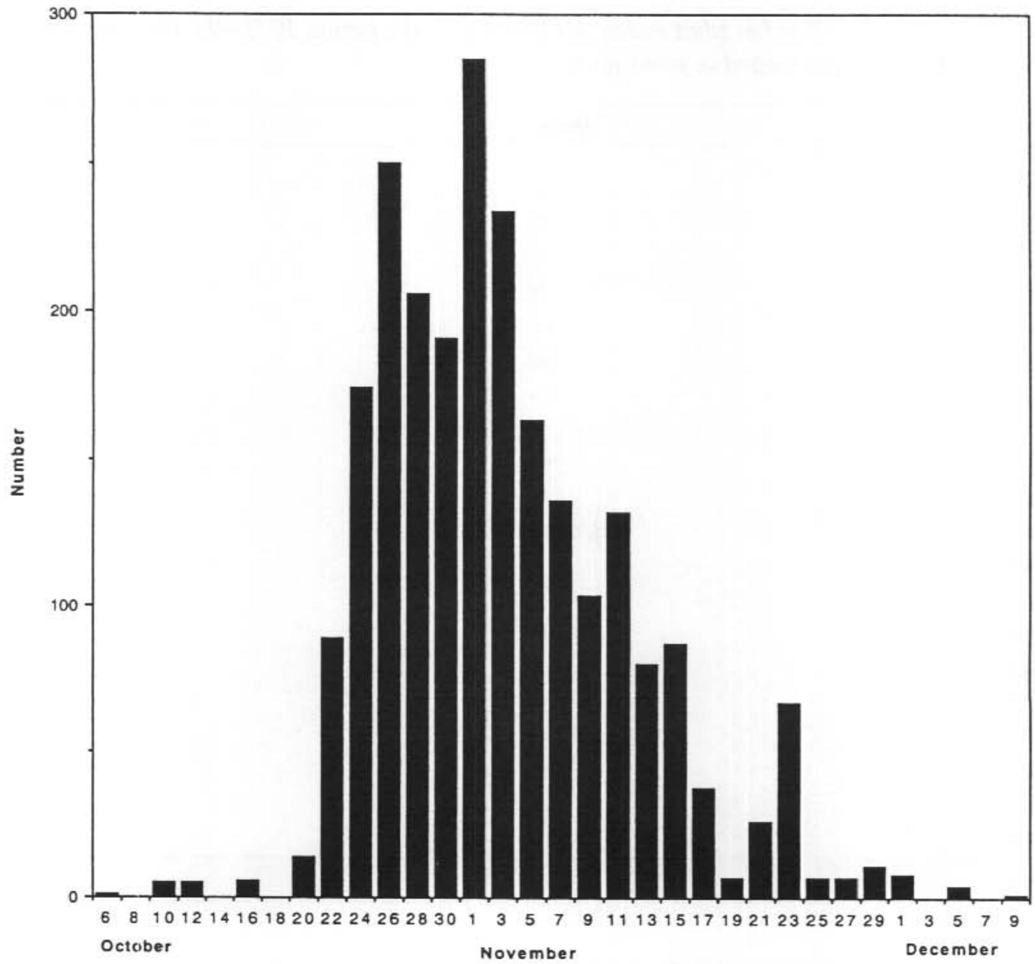

Figure 2. Frequency of initial tagging of pups for each two days from 6 October to 9 December.

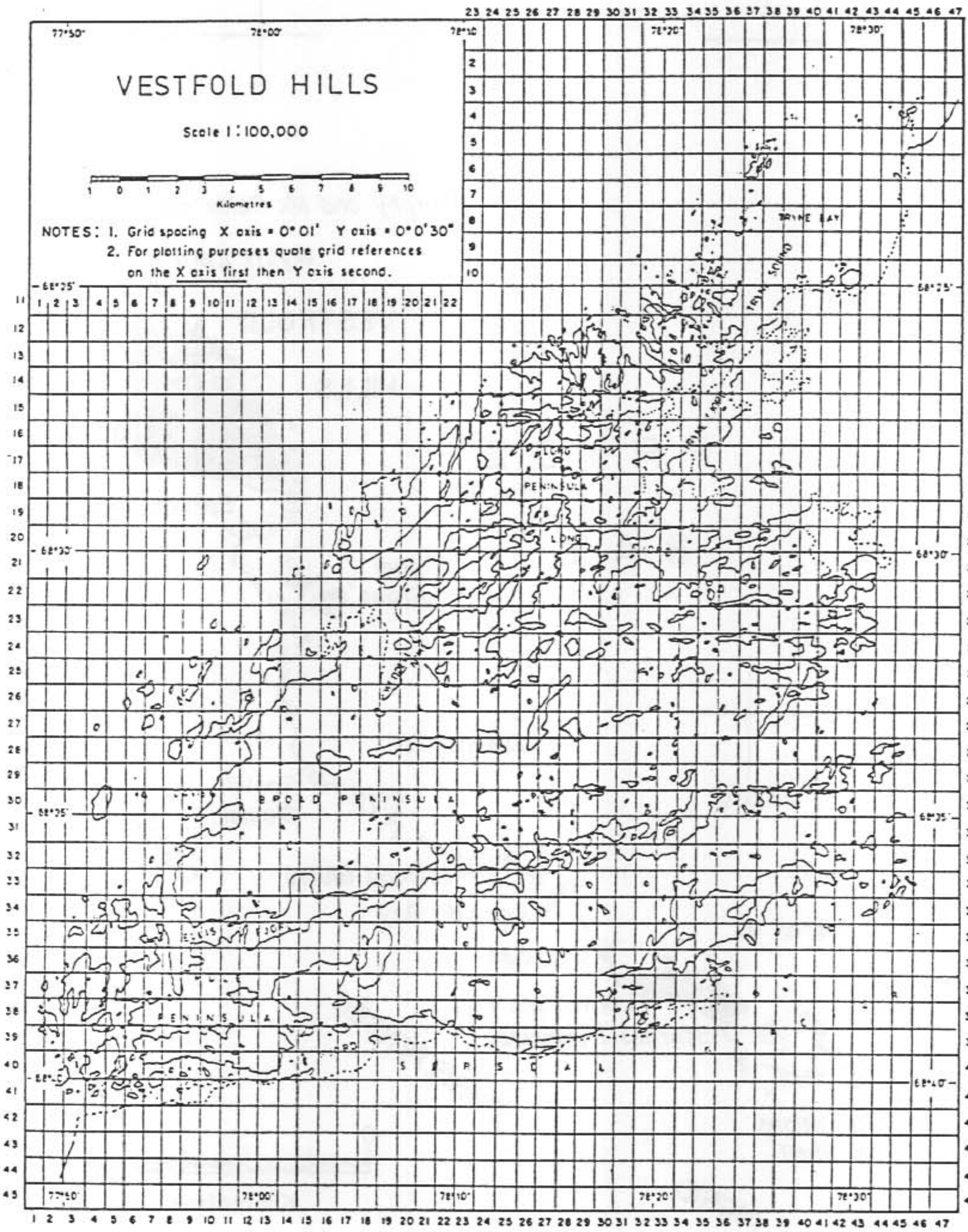

Figure 3. The 0°01' longitude and 0°0'30" latitude grid used for recording seal locations.

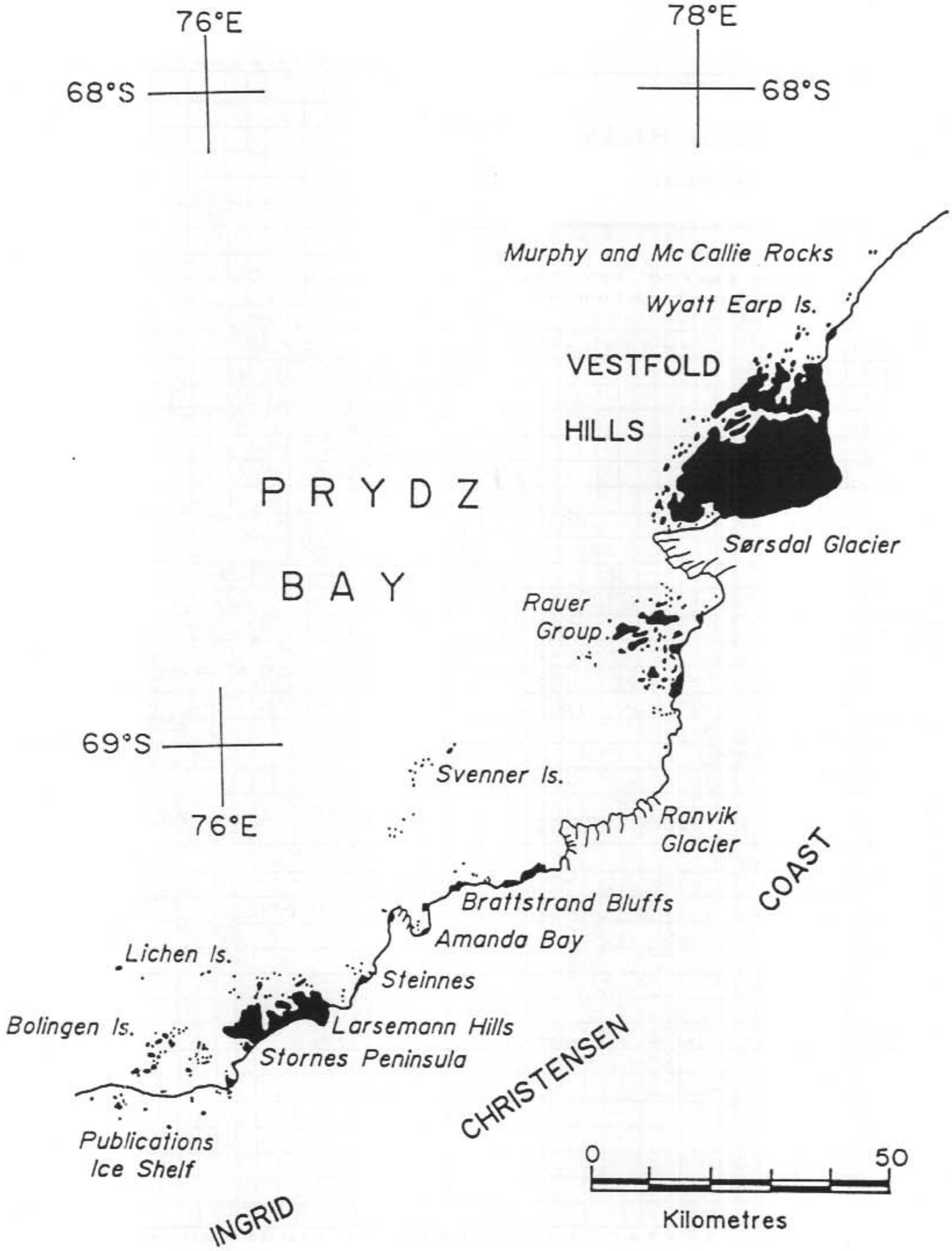

Figure 4. The eastern coast of Prydz Bay from the Vestfold Hills to the Publications Ice Shelf.

2. BREEDING

2.1 Introduction

The Weddell seal remains one of the only major seal species of the world not to have been the subject of intensive sealing, whether commercial or 'scientific'. The exception to this was the localised population in McMurdo Sound which was in fact over-harvested in the late 1950s, leading to increased recruitment and rapid growth to a level higher than that before harvesting (Testa and Siniff 1987). The major harvesting of Weddell seals in the past has been for a source of food for huskies, with the McMurdo Sound population probably being the most affected. In 1956, for example, when both New Zealand and the USA were operating dog teams there, the New Zealanders alone killed 350 seals for dog food (Stirling 1971). From 1957 through 1966 at least a further 1000 seals were killed (Stirling 1967), and until 1977 40 seals a year were still being killed by New Zealand (Kooyman 1981). Within the Australian sector most harvesting for husky food was undertaken at Mawson, with the killing ending in 1984. Huskies had been withdrawn from Davis at the end of 1964 and seal killing (mainly of southern elephant seals but also some Weddell seals) then ended there. The number of Weddell seals killed, mainly for dog food in the Vestfold Hills, were: 1957 (35), 1958 (9), 1959 (7), 1960 (2), 1961 (5), 1962 (15–16), 1963 (18) and 1964 (4). Thus Weddell seal numbers in the Vestfold Hills, unlike those at McMurdo Sound, have essentially been regulated by natural factors.

The Weddell seal population in the Vestfold Hills is, therefore, probably one of the best animal groups in which to study population processes in an environment not greatly disturbed by man. Early work suffered from both the lack of input from a specialist population biologist and the necessity for working with non-specialist field personnel. (Under the existing shipping arrangements it was impossible to get specialist seal researchers into the field in time for censusing.) Despite this, the Davis Weddell seal study provides a valuable data set for intraspecific comparisons. It has confirmed findings at McMurdo Sound that Weddell seals mature late, relative to other pinnipeds, and that there are significant fluctuations in pupping rates (Testa *et al.* 1990). These fluctuations are probably an indication of rapid, short-term changes in underlying prey populations or, perhaps, in the oceanographic regime that determines transport and circulation to coastal areas. These long-term data can serve as the background for directed, short-term studies on related ecological questions.

2.2 Methods

When seals were tagged or resighted the X and Y coordinates were recorded (Figure 3) and a written description of the site was made to allow for correction of suspect coordinates. Tags were recorded as 'new' if the seal was previously untagged or 'retag' if the seal previously had a tag. Seals were aged as pup, yearling, juvenile or adult and the sex was recorded as male, female or unknown. Tag colour and number were recorded from both flippers where possible (this is an important means of error checking). Tag numbers and sex of the seal were recorded for any related pup and the presence of the pup was recorded even if it was not tagged. These data were entered onto computer and went through a number of reorganisations until the final form was settled on in 1991.

The Vestfold Hills region was divided into seven zones. They were Ellis Fjord (Zone 1), Long Fjord (Zone 2), Tryne Fjord (Zone 3), Tryne Bay (Zone 4), Crooked Fjord (Zone 5), offshore of the Vestfold Hills (Zone 6), Murphy and McCallie Rocks (Zone 7) (Figure 4), and areas outside the Vestfold Hills.

2.3 Results

Zone 7, consisting mainly of Murphy Rocks and McCallie Rocks, has not been visited regularly over the years and not prior to 1983–84 (Table 2.2). Taking out the data for Zone 7 in these years the average annual number of pups tagged for the Vestfold Hills (excluding seasons 75–76 and 76–77 when there was a shortage of tags) was 169.8±36.6 (mean ± s.d.). The average for Murphy Rocks and McCallie Rocks was 25.8±6.2 for the six years in which these data were recorded. This makes the Vestfold Hills the major pupping site in Prydz Bay, contributing (on 1983 figures) 48.7% of pups in all its known pupping sites (Table 2.1).

The sex ratio of female to male pups was 1:1.16 (Table 2.3). The numbers of male and female pups tagged were compared for each year but were found not to be significantly different (χ^2=22.0, $p>0.05$, 17 degrees of freedom). Of 1361 male pups and 1095 female pups, 145 (10.7%) and 184 (14.4%) respectively were resighted after an elapsed period of 12 months from pupping. There are data on pre-weaning pup mortality for five years: 1963 (2.5%), 1985 (4.1%), 1986 (1.3%), 1987 (6.1%) and 1989 (3.9%).

The detailed examination of pupping rates was restricted to Long Fjord because the best and most consistent data were for that location. The majority of mothers were recorded as only having pupped once, with the frequency of pupping falling off rapidly after the second pup (Table 2.4). The pupping rate exceeded 50% for six-year-old females and was highest for ten-year-olds (Table 2.5). Post 1975 the pupping rate varied between 0.6548 in 1984 and 0.9474 in 1978. The proportion of seals that pupped in consecutive years varied between 19.6 and 60.5% (Table 2.7). The number that pupped in two out of three consecutive years varied between 34.8 and 73.5%.

2.4 Discussion

Examination of aerial photographs indicates that there is unlikely to be a major Weddell seal pupping area along the western side of Prydz Bay. The Vestfold Hills population of Weddell seals is therefore the largest in Prydz Bay, with smaller colonies occurring at the Rauer Islands and Amanda Bay. In 1983 Lewis and George (1984) found 230 pups in four colonies between the Rauer Islands and the Larsemann Hills and in 1989 a count from a Twin Otter over the same area found about 200 pups. At the Rauer Islands, the pupping sites are to the south-west of Yefremov Island, south-west of Pchelra Island and off Cape Drakon. The two former sites are inshore with islands protecting ice from breaking out. Cape Drakon is, however, relatively exposed. Amanda Bay, which has the third largest colony, is bounded by the Hovde Glacier to the north and on the south by an unnamed glacier terminating at Cowell Island which, again, would help to retain fast ice. All major sites, therefore, supporting 91.5% of the known pups born in Prydz Bay (on 1983 figures), are relatively close to each other (140 km from McCallie Rocks to Amanda Bay), have similar protection against early ice break-out and could be expected to be controlled by the same population-regulating mechanisms as operate in Prydz Bay. This makes the process of monitoring environmental change in Prydz Bay through Weddell seals possible, using the Vestfold Hills population as a reference breeding group with occasional visits to other colonies for re-censusing. The importance of monitoring this population of Weddell seals therefore makes it imperative that this be done in a way that allows inter-annual comparisons as well as comparisons of population data with those of other areas.

The quality of the population data on the Weddell seals in the Vestfold Hills varied widely between years, observers and accuracy of data entry onto the computer. Because of the different effort in different fjords and northwards to Murphy Rocks and McCallie Rocks, many population parameters such as first sighting of known-age female with pup and known-age pupping rates can be calculated only for Long Fjord. With a more directed effort to include as much as possible of the Vestfold Hills in future censuses, the data base should be broadened over future years to give a better picture of population processes.

The number of pups surviving the initial post-partum period in the Vestfold Hills from 1957 to 1964 (excluding the Murphy Rocks–McCallie Rocks area) was approximately 150–200 per annum (Lugg 1966). The number of pups tagged annually in the Vestfold Hills from 1977 to 1992 was 169.8±36.6. This is close to the actual numbers born, as there was a low pre-weaning death rate (figures varied between 1.3 and 6.1% with an annual mean of 3.6%). This mortality is of the same order as the 5% (17 of 315) for 1964 at Signy Island (Smith and Burton 1970) and at McMurdo Sound: 6.2% in the Hutton Cliffs area (Kaufman *et al.* 1975), and 4.7% in 1966 and 5.1% in 1967 on the west coast of Ross Island (Stirling 1971). It is, however, far lower than the 18% in one colony in the Bay of Whales (Lindsey 1937) and an apparently high mortality in the Windmill Island region south of Casey (M. Hovenden pers. comm. 1993).

The proportion of male pups at tagging was 51.2% (n = 2978) and is identical to the figure given for McMurdo Sound by Stirling (1971) for 1250 pups. This was also similar to the 53.3% (n = 60) recorded for 1964 (Lugg 1966). The return rate for tagged seals other than pups for males (41.3%) was only slightly less than for females (45.1%) and may be accounted for by adult males being less likely to be retagged than females. Behavioural differences make the males more difficult to find and, once found, more difficult to tag. Counts over the duration of the moult also show a preponderance of females (56.6% female in 1989–90 and 53.3% female in 1990–91). As the composition of resighted seals, tagged as pups, after one year has elapsed was 57.5% female, then much of the mortality (or emigration) leading to an imbalance in the sex ratio is likely to occur in the years before pups re-enter the observable population. Poor data on survival of subadult males, due to their rare appearance in breeding colonies, were also found by Siniff *et al.* (1977), who predicted a high mortality in the first year of life.

Estimation of population size and trends over the years was not usually possible because the second visit to the seals during pupping did not consistently involve recording seals that were tagged on the first visit. There was wide variation in the timing and number of visits to all of the sites in the Vestfold Hills, with the last visit often being as early as the first week of November. While this has been adequate to ensure that in most years virtually all of the pups have been tagged (so that the gross number of pups produced per annum is known) it does not allow accurate assessment of reproductive rates. Data up until 1987 were used by Testa *et al.* (1990) to estimate a reproductive rate of 0.80 pups per adult female (S.E. = 0.02) for the Vestfold Hills compared with 0.68 (S.E. = 0.02) for 14 years at McMurdo Sound. They suggested that the higher figure for the Vestfold Hills resulted from sampling bias because of the later and somewhat variable arrival of non-parturient females in November and December. Reproductive rates based on one or two censuses late in the season, however, provide an estimate close to that for a full season's censusing (Testa *et al.* 1990). Data from December were collected in three years prior to 1990: 1978, 1979 and 1983. The estimates from these years plus 1990–92 (0.80, S.E. = 0.01) are still higher than the highest figure recorded at McMurdo Sound (Testa *et al.* 1990). Although deficiencies exist in the data in most years up until the season 1989 when the sampling regime was changed to reflect the sampling at McMurdo, even without the three earlier years the figures for the three breeding seasons since 1989 still average 0.76 (S.E. = 0.01). This is probably a better estimate of reproductive rate and, though lower than for the six-year period, it is still higher than the figure at McMurdo Sound.

There was a strong suggestion from earlier data that the age of first reproduction (as measured by the age at which 50% of females are seen with a pup) is higher at eight years old at the Vestfold Hills than at Signy Island or McMurdo Sound where a similar sampling regime yielded a figure of seven years of age (Testa *et al.* 1990). The increased amount of data since those used by Testa *et al.* (1990), with almost eight times the available sightings, suggest that this is in fact the case and that 50% of females do breed by the age of eight (Figure 5). Testa *et al.* (1990) examined reproductive parameters at three sites to determine whether they were fluctuating in synchrony; they did not attempt to examine any physical attributes of the sites that might account for aspects such as the higher age of first reproduction or a higher reproductive rate. These can be accounted for (if in fact they are real) by differences in the sites. Signy Island has quite variable fast-ice conditions with seals possibly dispersing to pup in poor ice seasons (Croxall and Hiby 1983). At McMurdo Sound, Stirling (1969a) found a lack of constancy in pupping sites: sites were dependent upon the availability of tide cracks and, in years with few exit holes, seals were forced to pup further from shore where there was a higher risk of pup mortality if the fast ice broke up. This was not found to affect reproductive rates however (Testa and Siniff 1987). By contrast the Vestfold Hills consist of a complex coast where islands and fjords inhibit the breakout of fast ice while at the same time giving easy access to open water. It was in such stable areas that McLaren (1962) demonstrated higher reproductive success in the ecologically similar ringed seals *(Phoca hispida)* and a population skewed towards older animals.

The proportion of seals pupping in consecutive years is quite variable, ranging from 19.6 to 60.5% over all years (Table 2.7). A major effort to upgrade the quality of data collection and number of seals tagged was made in 1983. If data from this date onwards are examined, the variation is still high, ranging from 28.6% in 1985 to 60.5% in 1990. If the proportion of seals having pupped in either of the two previous years is examined from 1983 onwards there is less fluctuation with percentages ranging from 51.4% in 1986 to 72.8% in 1990. The energetic cost of reproduction is high; a Weddell seal may lose 40% of her body weight during lactation, and Siniff (1981) considered that this may contribute towards a reduction of a female's chances of pupping in consecutive seasons. The probability of pupping two years in a row is consistently lower than the probability of pupping when no pup was produced the previous year (Siniff 1981). Other factors affecting the body condition of the females, including food availability, may also be important. Trends in the proportion of seals pupping in consecutive years will be examined over the coming years as more data on diet and food availability are accumulated.

The population of Weddell seals in the Vestfold Hills appears to be driven by fundamentally different constraints from those existing at McMurdo Sound or Signy Island. It does not cycle in tune with the McMurdo Sound population and has a higher reproduction rate, although the age at first pupping is similar to that at McMurdo Sound and Signy Island. Because of the differences that exist between populations, and the importance of Weddell seals within the Prydz Bay ecosystem, it is important that the population sampling regime be kept comparable with the sampling at McMurdo Sound. This will involve addressing the problem of early access to the Vestfold Hills. Three censuses are required annually, and they must include one in late October and one in the first week of December to include late-arriving females. So far, seal researchers have seldom been able to be in the Vestfold Hills early enough to ensure the completeness of this work.

Table 2.1. Pups born and location of pupping within Prydz Bay in 1983.

Location	Pups
Vestfold Hills	185
Murphy and McCallie Rocks	33
Rauer Islands[1]	98
Larsemann Hills[1]	21
Amanda Bay/Hovdoyana Islands[1]	94
Brenesholmene Islands[1]	17

[1] Data from Lewis and George (1984)

Table 2.2. Pups born per annum and location of pupping within Vestfold Hills. Data from 1960s are from Lugg (1966). The sum of all zones will not always equal the actual number of pups born as some records did not include a location.

Zones	1 Ellis Fjord	2 Long Fjord	3 Tryne Fjord	4 Tryne Bay	5 Crooked Fjord	6 Off-Shore	7 Murphy Rocks	Total of Zones 1–7	Minus Zone 7
Season									
1962		70							
1963		79							
1973	0	124	12	0	0	0	0	136	136
1974	0	135	61	33	0	0	0	229	229
1975	0	32	0	0	0	0	0	33	33
1976	0	70	0	0	0	1	0	71	71
1977	0	132	49	1	4	10	0	196	196
1978	4	134	43	13	4	0	0	198	198
1979	1	134	91	13	0	6	0	245	245
1980	1	92	35	4	0	0	0	132	132
1981	0	83	46	14	1	1	0	144	144
1982	1	92	29	59	0	4	0	186	192
1983	0	108	36	31	0	10	33	218	185
1984	0	86	15	12	0	2	29	144	115
1985	0	75	22	20	0	0	24	141	117
1986	0	93	44	20	0	1	0	158	158
1987	1	118	43	4	0	2	0	168	168
1988	0	106	33	15	0	0	25	179	154
1989	0	107	20	62	0	7	0	197	197
1990	0	99	39	0	1	6	0	145	145
1991	0	100	33	38	0	13	15	199	184
1992	0	96	12	39	0	2	29	178	149

Table 2.3. Sex ratio of pups. Not all pups were sexed, so the total here does not equal the number of pups born.

Year	Males	Females	Ratio of males to females
73/74	82	56	1.46
74/75	108	116	0.93
75/76	8	8	1.00
76/77	30	23	1.30
77/78	104	91	1.14
78/79	96	94	1.02
79/80	118	102	1.16
80/81	72	56	1.29
81/82	55	86	0.64
82/83	75	97	0.77
83/84	243	213	1.14
84/85	67	58	1.16
85/86	39	37	1.05
86/87	77	75	1.03
87/88	30	32	0.94
88/89	84	91	0.92
89/90	5	7	0.71
90/91	71	59	1.20
91/92	86	78	1.10
92/93	74	75	0.99
Totals	1524	1454	1.05

Table 2.4. Frequency of females producing a specified number of pups during their known breeding lifetimes in the period 1974 to 1992. (This will differ from the actual reproductive success because seals tagged early in the study period may have pupped prior to 1974, while females tagged later in the period will not have completed their reproductive period.)

Number of pups	Mothers
1	766
2	191
3	109
4	68
5	38
6	36
7	32
8	15
9	13
10	10
11	5
12	5
13	3
14	1

Table 2.5. Known-age pupping rates for females in the Vestfold Hills. It is unlikely that seals of two years of age pupped, and their inclusion in the data set is most probably a result of misread tags which cannot yet be corrected.

Age	Number with pup	Number without pup	Pupping rate
1	0	15	0.0000
2	3	9	0.2500
3	1	12	0.0769
4	5	8	0.3846
5	8	18	0.3077
6	21	17	0.5526
7	34	13	0.7234
8	29	14	0.6744
9	25	13	0.6579
10	22	5	0.8148
11	14	7	0.6667
12	13	3	0.8125
13	10	2	0.8333
14	8	5	0.6154
15	7	2	0.7778
16	4	1	0.8000
17	4	1	0.8000
18	2	2	0.5000

Table 2.6. Pupping rates for females in the Vestfold Hills from 1974 to 1992.

Year	With pup	Without pup	Rate
1974	34	7	0.8293
1975	15	47	0.2419
1976	31	8	0.7949
1977	36	8	0.8182
1978	36	2	0.9474
1979	71	15	0.8256
1980	46	10	0.8214
1981	54	21	0.7200
1982	61	32	0.6559
1983	90	30	0.7500
1984	55	29	0.6548
1985	77	9	0.8953
1986	85	13	0.8673
1987	87	23	0.7909
1988	93	26	0.7815
1989	117	16	0.8797
1990	74	23	0.7629
1991	91	23	0.7982
1992	74	29	0.7184

Table 2.7. Percentage of females pupping that had pupped in the previous year and previous two years. Data are for all areas except Zone 7 (see Table 2.2).

Season	Breeding seals with pup	Seals that pupped in previous year	Percentage in previous year	Percentage in previous two years
1979	219	89	40.6	41.6
1980	108	38	35.2	47.2
1981	143	28	19.6	43.4
1982	155	41	26.5	34.8
1983	178	61	34.3	53.9
1984	86	44	51.2	68.6
1985	112	32	28.6	68.8
1986	144	55	38.2	51.4
1987	152	73	48.0	63.8
1988	132	69	52.3	73.5
1989	169	82	48.5	65.7
1990	114	69	60.5	72.8
1991	132	58	43.9	65.9
1992	110	47	42.7	58.2

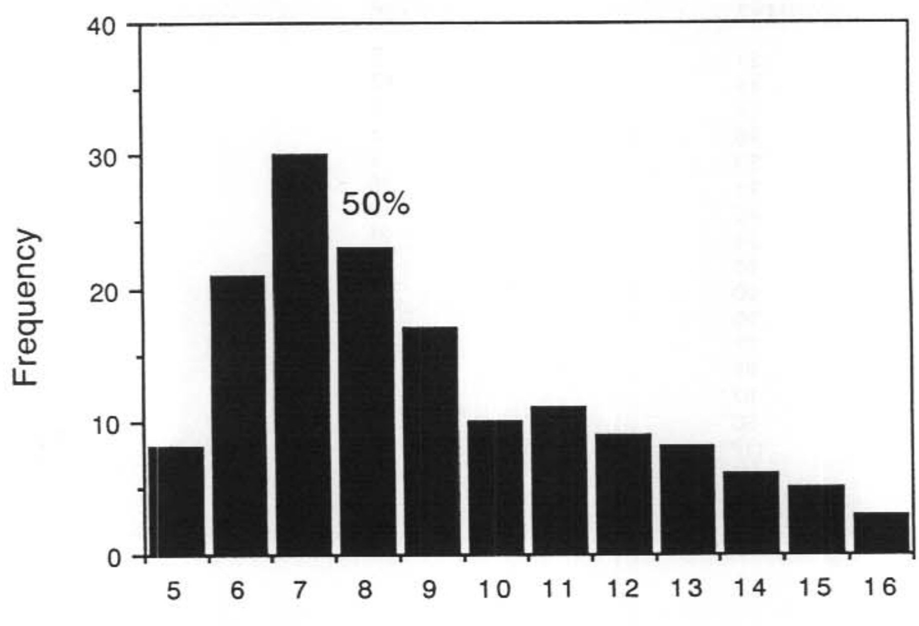

Figure 5. The age of female Weddell seals when they were first observed with pups.

3. SEAL MOVEMENTS

3.1 Methods

When tagged seals were observed and tags read the location was written down and the X and Y coordinates were recorded. To determine the seasonal movement of seals all individual seal locations were plotted onto maps. Each X/Y coordinate rectangle used for plotting was divided into 100 points and individual seal locations were plotted randomly within the confines of these 100 points. Because some rectangles included land as well as sea there was some overlap of plottings onto the land.

3.2 Results and Discussion

Location maps were produced for all months except for April to July which showed little difference and had few data; these months were amalgamated (Figures 6–14). The maps show a certain bias in recording densities as they do only record densities of sightings. For this reason areas commonly visited by people (such as just off Davis) have a higher density than would otherwise be expected. Only one site (Crooked Fjord) appeared to be under-represented in summer, due no doubt to the fact that ice was difficult to cross to the south of Davis and therefore it was visited less than is the norm. With these limitations in mind, the remainder of the plots present a useful picture of seasonal movements of seals.

From April to July there were few sightings, with most seals being found seaward of Gardner Island and in the wide mouth of Long Fjord (Figure 6). Lindsey (1937), in discussing the Bay of Whales, stated that the scarcity of Weddell seals in winter was 'more apparent than real'. He suggested that the scarcity of Weddell seals in winter was due partly to a change in their habits as a result of difficulties in reaching the ice surface, and partly to the less comfortable environment presented by the surface of the fast ice in winter when compared with summer, or the uniform water temperature in winter. The fact that this scarcity might be due to difficulty of access onto the ice was shown by seals coming to holes cut by the expedition (Lindsey 1937). Because of their ability to maintain open breathing holes, Stirling (1969a) considered that Weddell seals would not necessarily have to leave fast-ice areas. The distribution of seals during the winter is not known. Migration north in winter has been proposed in the case of McMurdo Sound; Smith (1965) suggested that 85% of the population migrated, leaving a small population of adults behind. An alternative is that there may be local movements due to ice conditions (Mansfield 1958). This may be the case in the Vestfold Hills as in 1984 only one seal maintained a hole in any fast-ice area, and then for only a short period, but when there was a major ice breakout close to land seals hauled out in high numbers (Green and Burton 1987a). In August and September seals were concentrated along the edge of the fast-ice, with a slight northern movement between the two months (Figures 7 and 8). In October there was a rapid rise in the rate of sightings as seals moved into the fjords to pup (Figure 9), with a greater emphasis on Long Fjord than Ellis Fjord and concentrations of sightings among the icebergs to the west of the mouth of Long Fjord. November was similar to October except for the greater number of sightings to the south of Davis (possibly due to more trips to visit the Sørsdal Glacier at that time). There was also deeper penetration of the two fjords used for breeding but still very little activity in either Ellis or Crooked Fjords. There was no change in overall distribution in December, but the rate of sightings fell off as the censuses undertaken during breeding came to an end (Figure 11). In January, the population was dispersed widely within the limits of the fast ice (Figure 12), with seals moving closer to shore in February with the retreat of the fast ice or expeditioners (Figure 13). At this time, the bias towards sightings at the station was accentuated. In March (Figure 14) the observed distribution is an artefact of the location of Davis and Brookes Hut in Long Fjord and the fact that in that month there is often little transport other than by foot, which restricts travel to Broad Peninsula and surrounds. Lugg (1966) did not find a build up of moulting seals following the dispersal of the young pups. He suggested that such a buildup might not have existed in the northern areas of the Vestfold Hills because as the 'areas are subject to the katabatic plateau winds, and are not well protected, the seals would not remain there.' (In fact the katabatics bring snow over the ice rather than dust off the Vestfold Hills; hence melting of the ice is later, extensive fast ice for moulting lasts longer, and seals are protected from predators for longer.) The bias due to lack of transport to the north in late summer can be demonstrated by examining the two aerial censuses for March. Both of these censuses were in the morning and were therefore not used for population estimates. They show that the seal concentrations were deep in Long Fjord or Tryne Fjord for 1990 (Figure 15) and in 1991 on the ice in Tryne Bay, along some of the outer islands and in Crooked and Ellis Fjord (Figure 16)—in fact anywhere but where the sightings of tagged seals are plotted for March. Summer movements are largely dependent on the amount of ice to the north of the Vestfold Hills, and the contraction of the summer range can be seen better in the plots of the aerial censuses (Section 5).

Work done by Morrice (1990) indicated that there may be differences in the seal vocalisations between Tryne and Long Fjords. To investigate this apparent lack of interchange, tag resight data were examined to determine whether seals sighted in one fjord appeared in another. The fjord of original tagging is here called the home fjord, and it includes those seals born in it as well as adults first tagged there. Only 77 seals (1.3% of all the seals tagged) observed in either Long Fjord or Tryne Fjord (or Sound) were subsequently sighted in Tryne Fjord (or Sound) or Long Fjord respectively. Of these 77, 32 were discounted as swapping, since they were found in their non-home fjord (usually Tryne Sound) only during the moult; another three were seen in late moult. Whereas Long Fjord is the major pupping area, Tryne Fjord and the area to its north are the main areas used for the moult, so most seals could be expected to spend some time there. Of the remaining 42 seals who could truly be said to have swapped fjords, most (35) were females. Of these, 21 did not pup in their non-home fjord. Nineteen of the 21 appeared in their non-natal fjord before they were recorded as having pupped. If they subsequently pupped they returned to the natal fjord to pup. Another two females which had pupped in previous years appeared in their non-home fjord during breeding seasons when they did not pup (one of them appeared in two seasons when it did not breed). Only eight females (1.5% of females pupping more than once) pupped in both fjords, and six others (6.9% of known-age mothers) pupped in their non-natal fjord. Of the seven males, five were seen in different fjords during different breeding seasons and the other two were born in one and appeared in the other during the breeding season, either as adult or juvenile. The lack of movement between fjords over such a short distance demonstrates an extreme conservatism in movements in the light of the greater movements that Weddell seals undertake with differing ice conditions. The degree of intermixing of these breeding populations is currently being studied using DNA fingerprinting techniques in collaboration with the University of Queensland.

One point of interest which was thought insoluble as it occurred before tagging began was the shift in pupping from Weddell Arm in the earlier days of occupation of Davis further into Long Fjord. Certainly the sightings for October from 1973 to the present show very little pupping within Weddell Arm (Figure 9). Examination of field books from early days at Davis, however, indicate that the pupping tended not to take place within Weddell Arm but only at its northern extremities.

In McMurdo Sound most breeding females were found to pup at the same place each year, which suggests fidelity to a pupping site (Stirling 1967). Lugg (1966), however, commented that 'sites of the Weddell pup concentrations for 1962 and 1963, in the Weddell Arm and Long Fjord regions, were markedly different, although the stability of the ice and the access to the water appeared to be constant.'

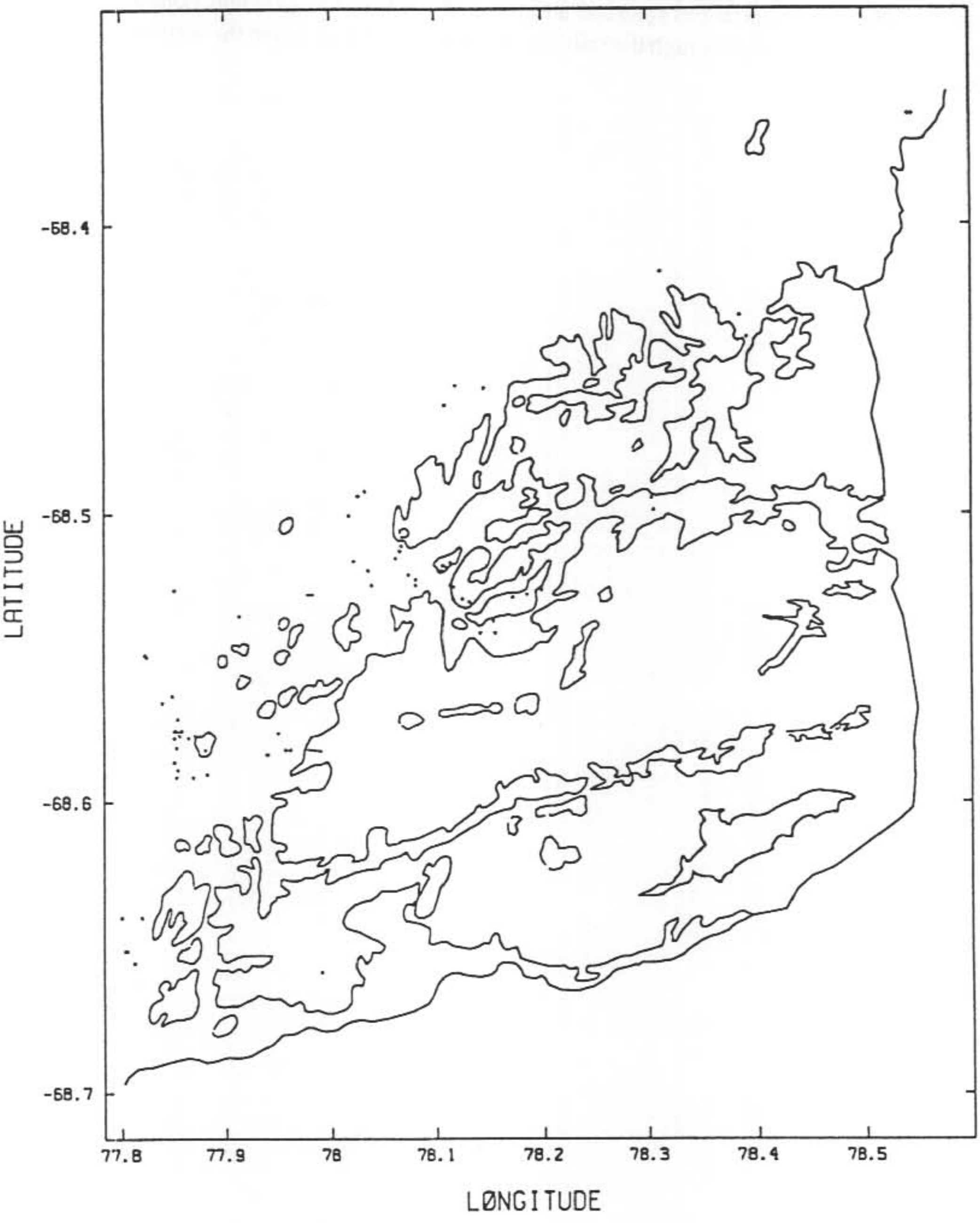

Figure 6. Sightings of tagged Weddell seals for all years from April to July.

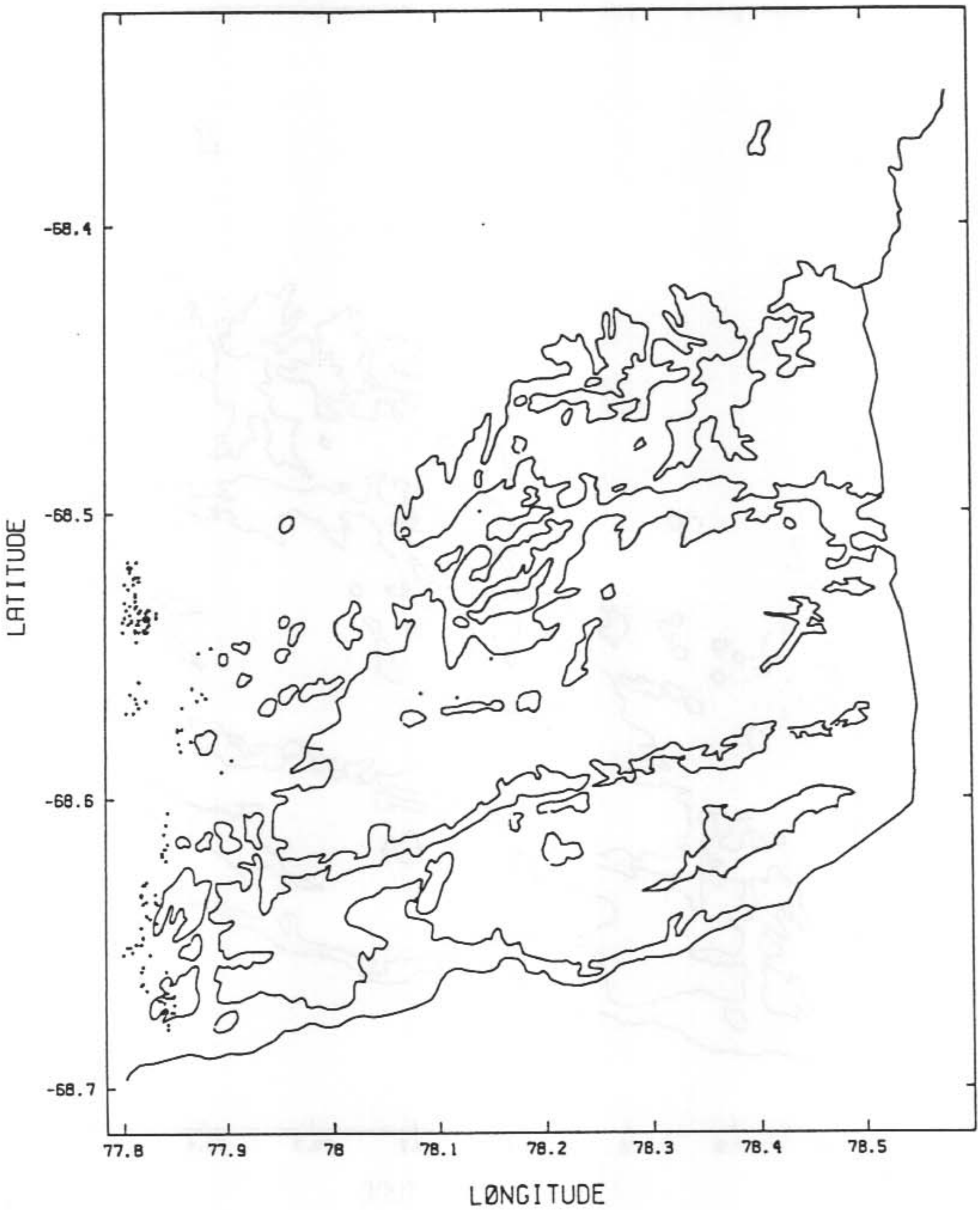

Figure 7. Sightings of tagged Weddell seals for all years for August.

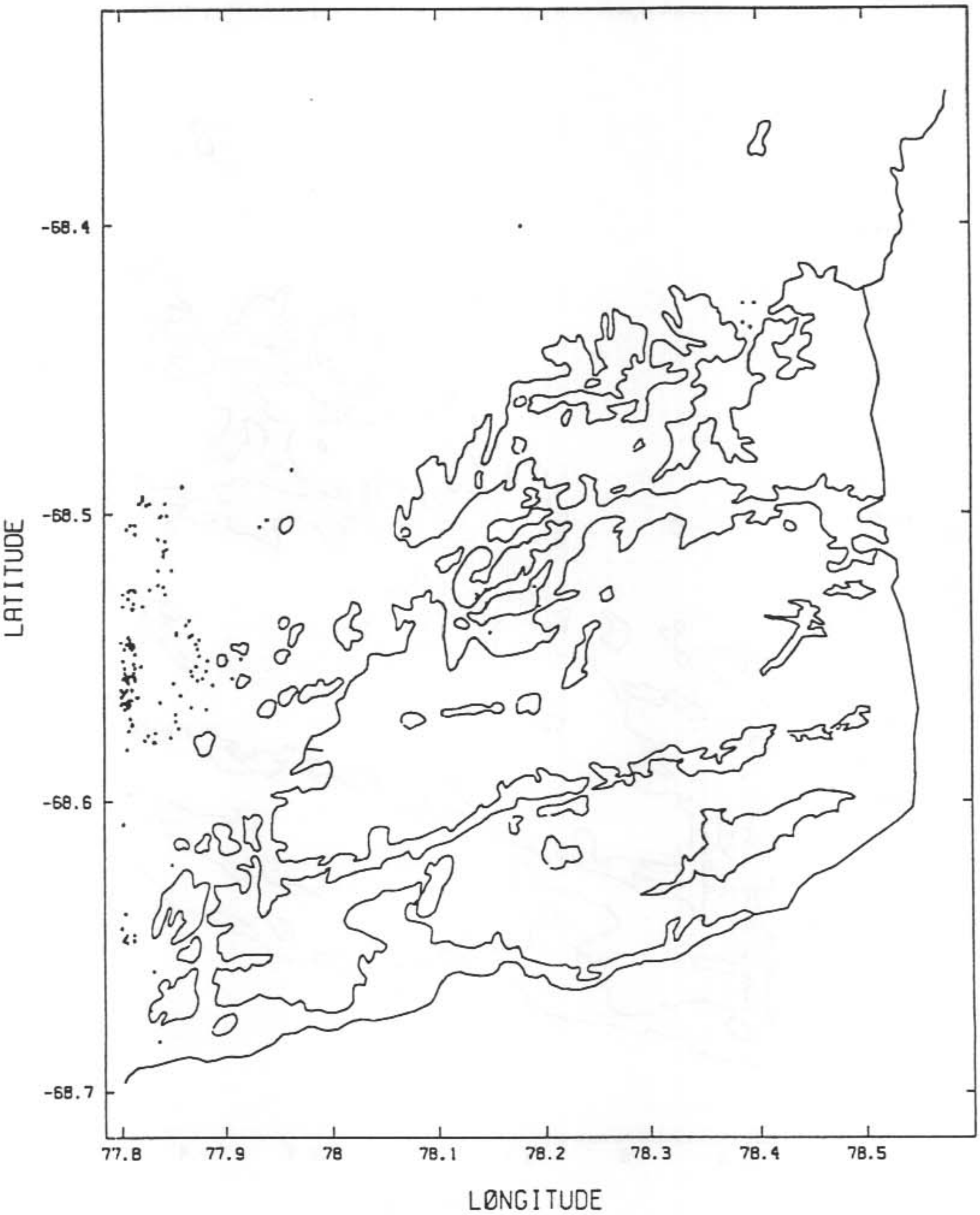

Figure 8. Sightings of tagged Weddell seals for all years for September.

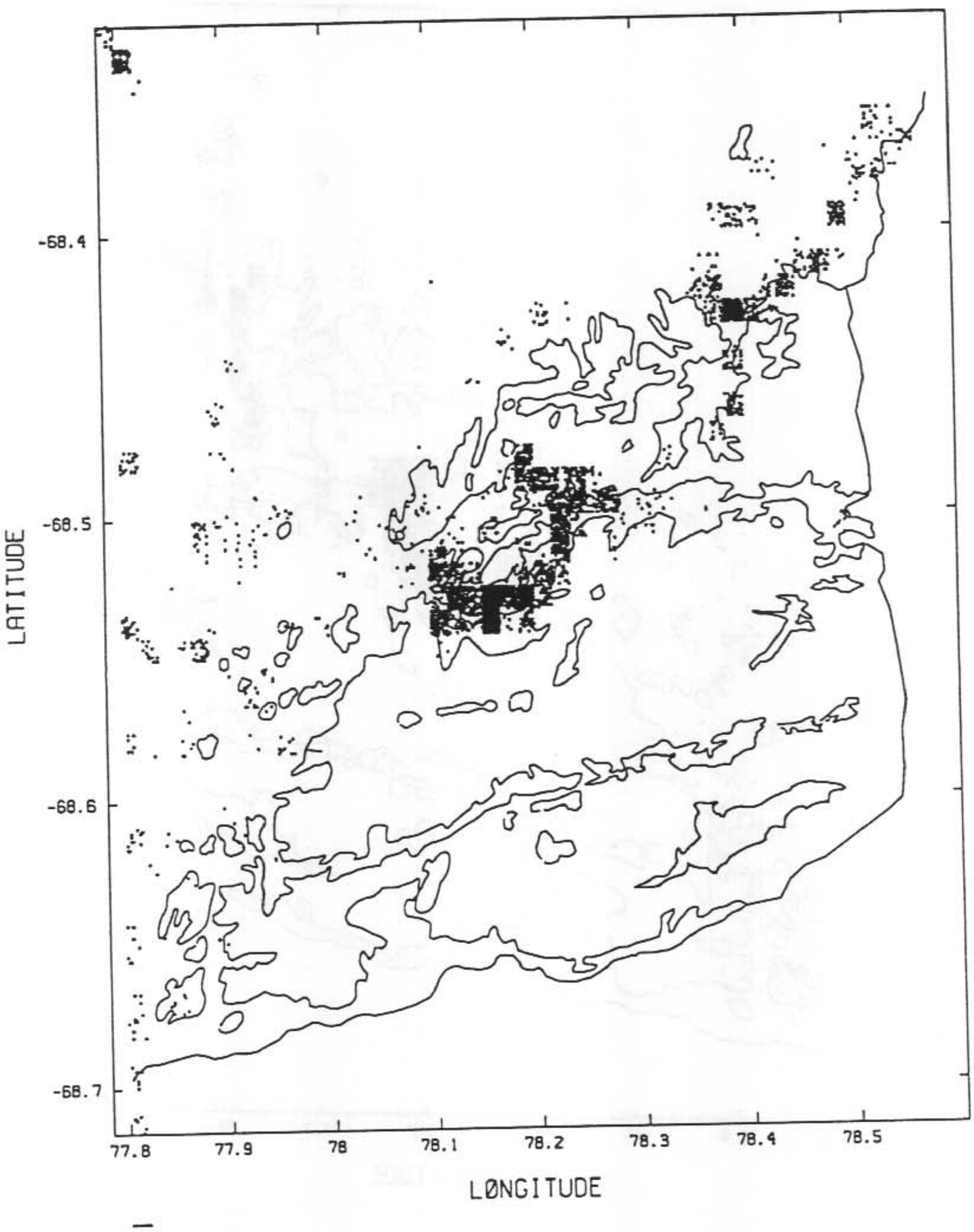

Figure 9. Sightings of tagged Weddell seals for all years for October.

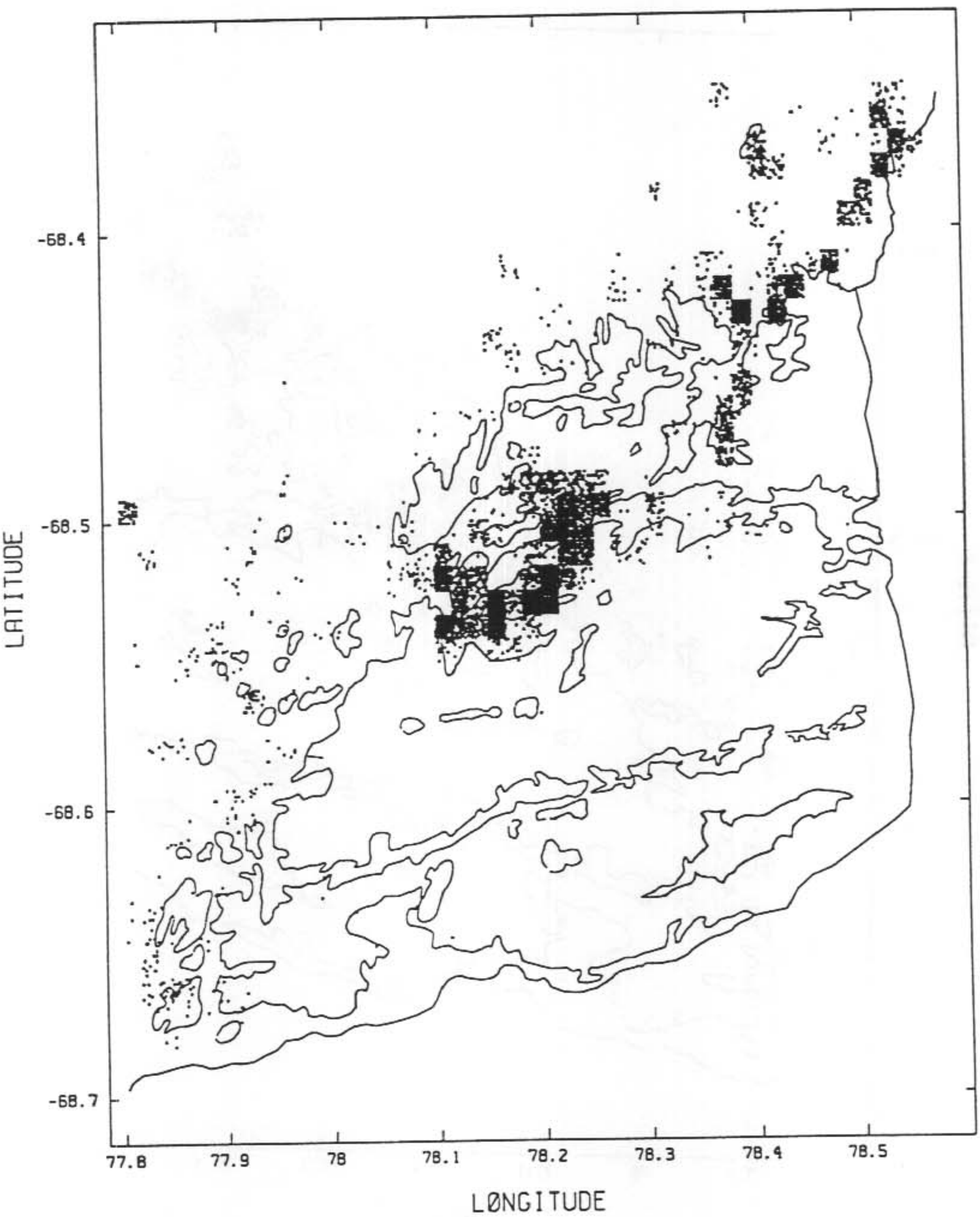

Figure 10. Sightings of tagged Weddell seals for all years for November.

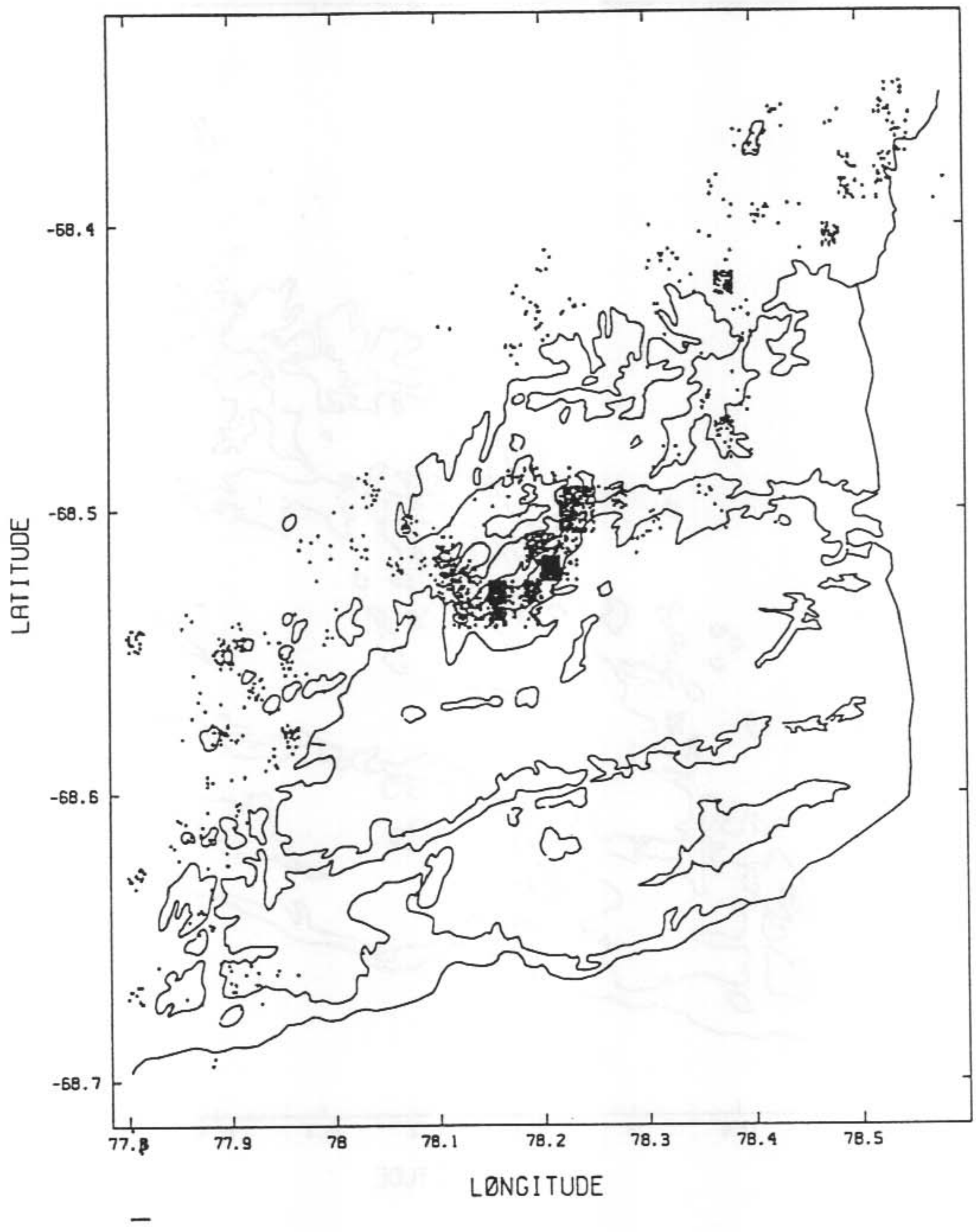

Figure 11. Sightings of tagged Weddell seals for all years for December.

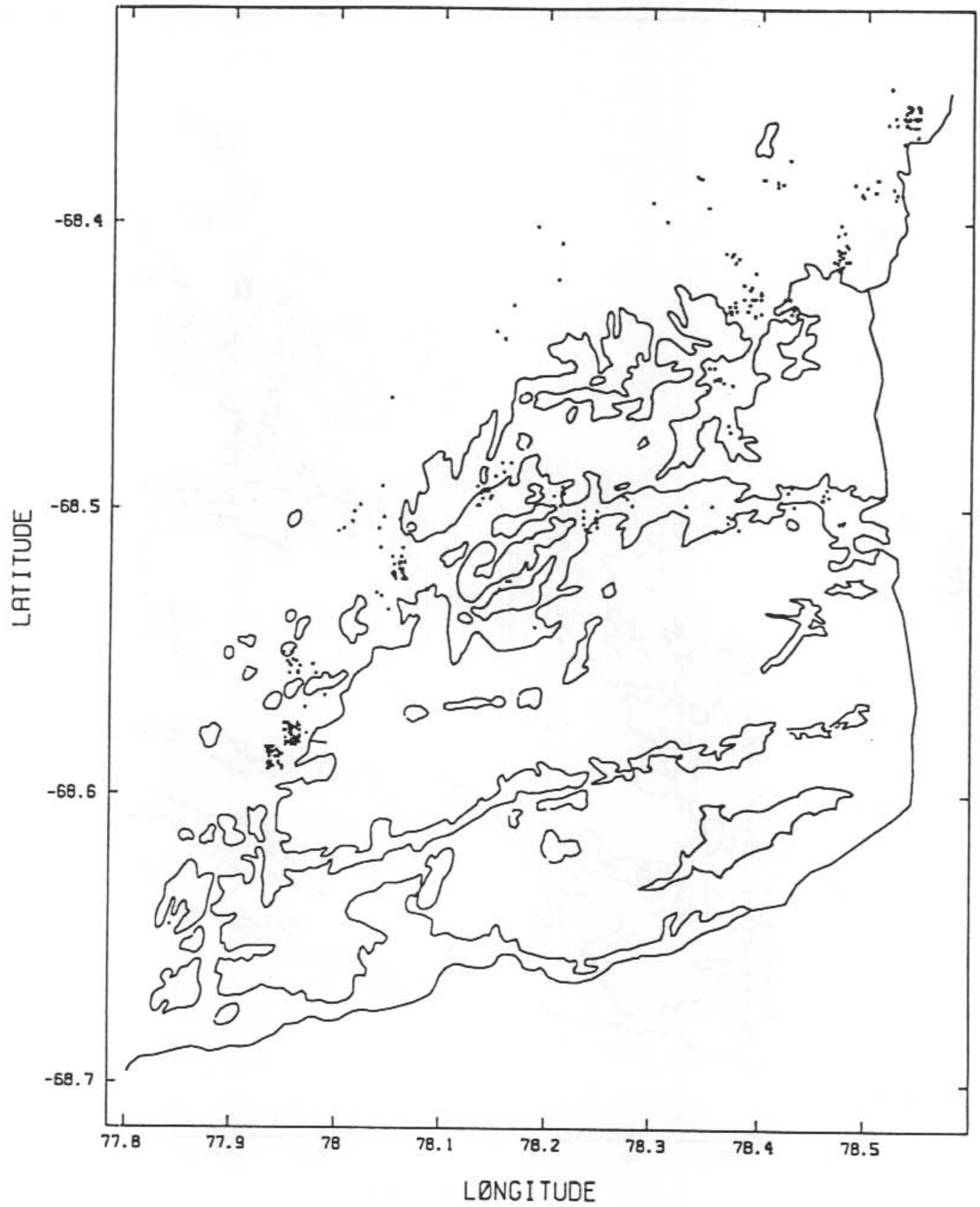

Figure 12. Sightings of tagged Weddell seals for all years for January.

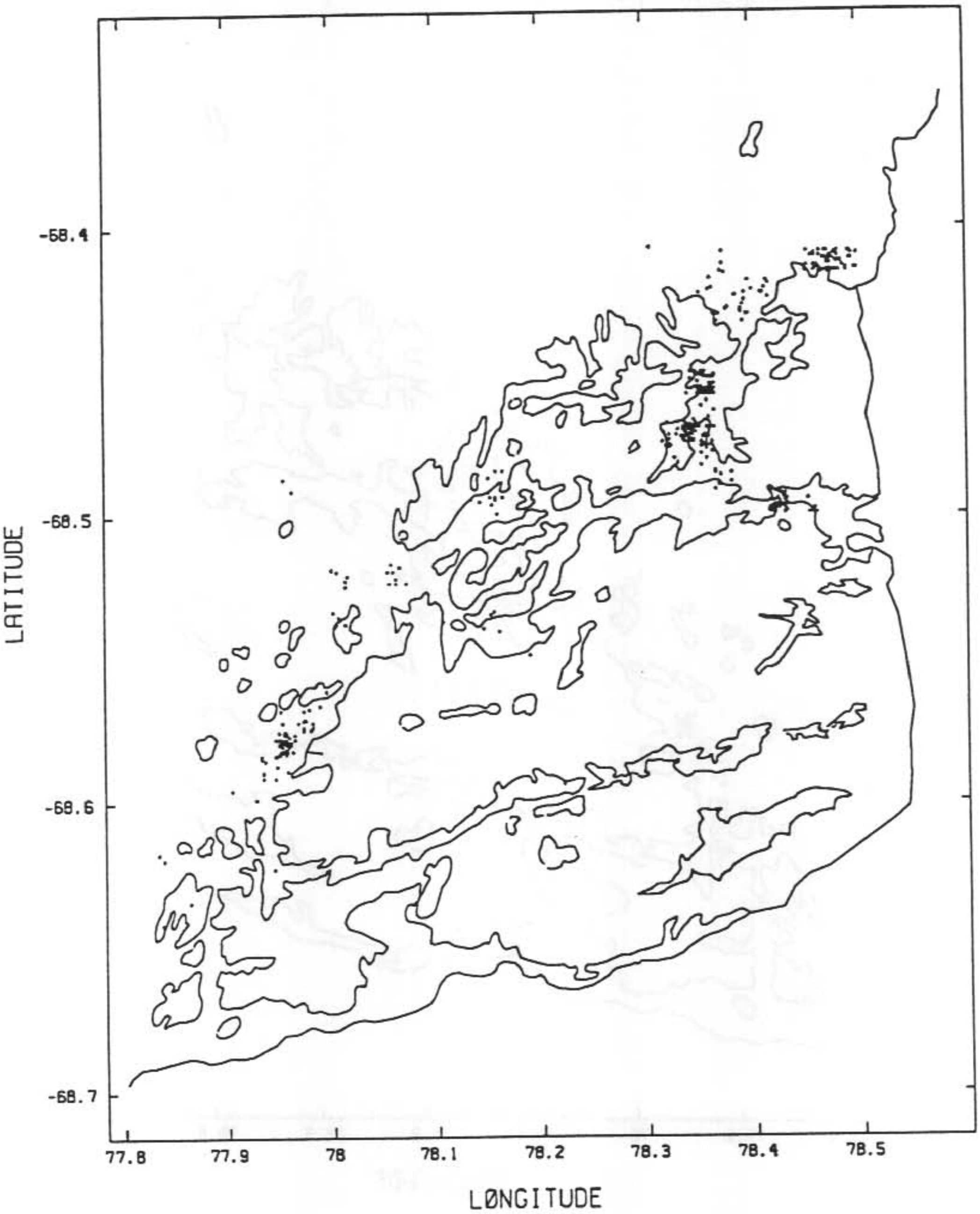

Figure 13. Sightings of tagged Weddell seals for all years for February.

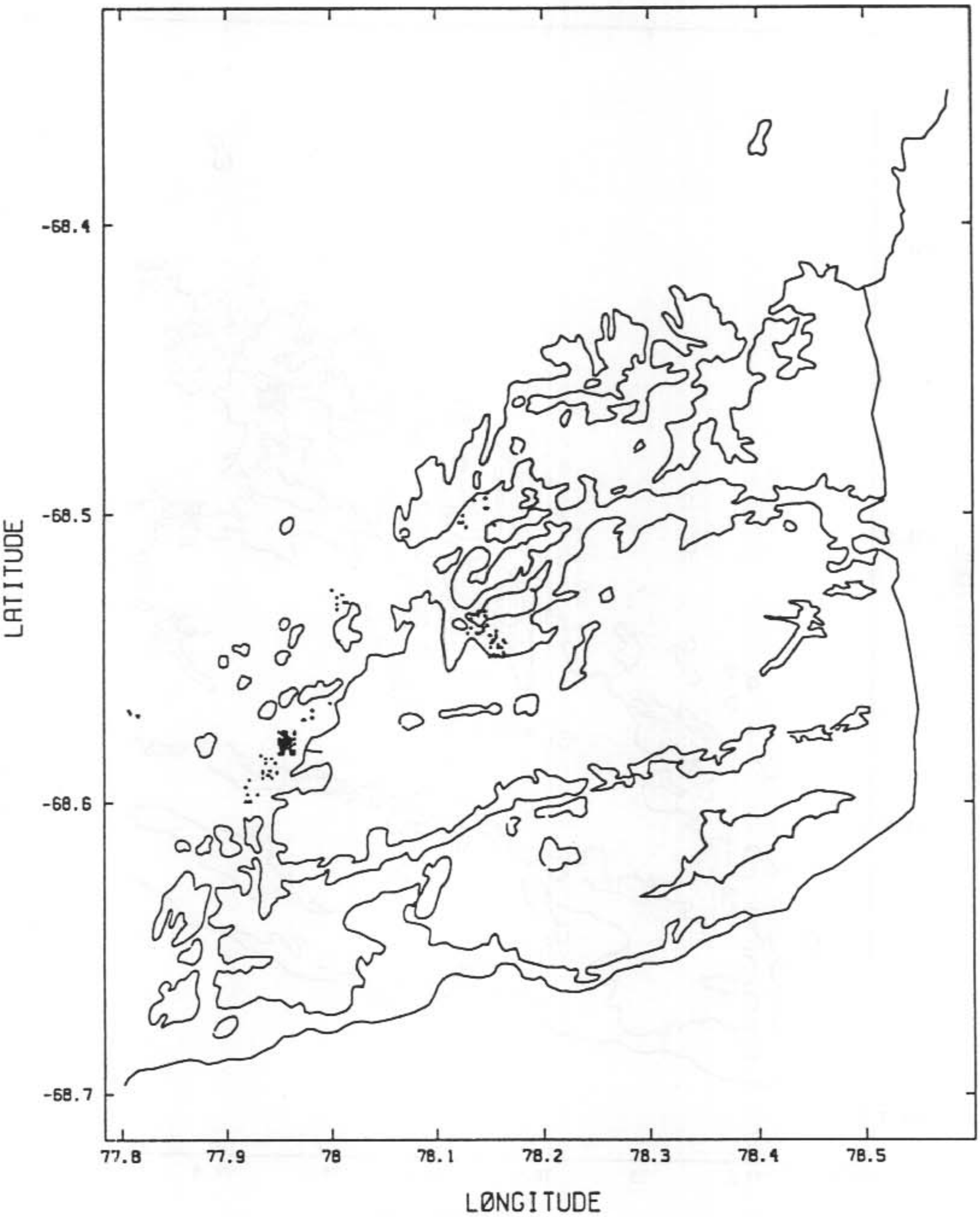

Figure 14. Sightings of tagged Weddell seals for all years for March.

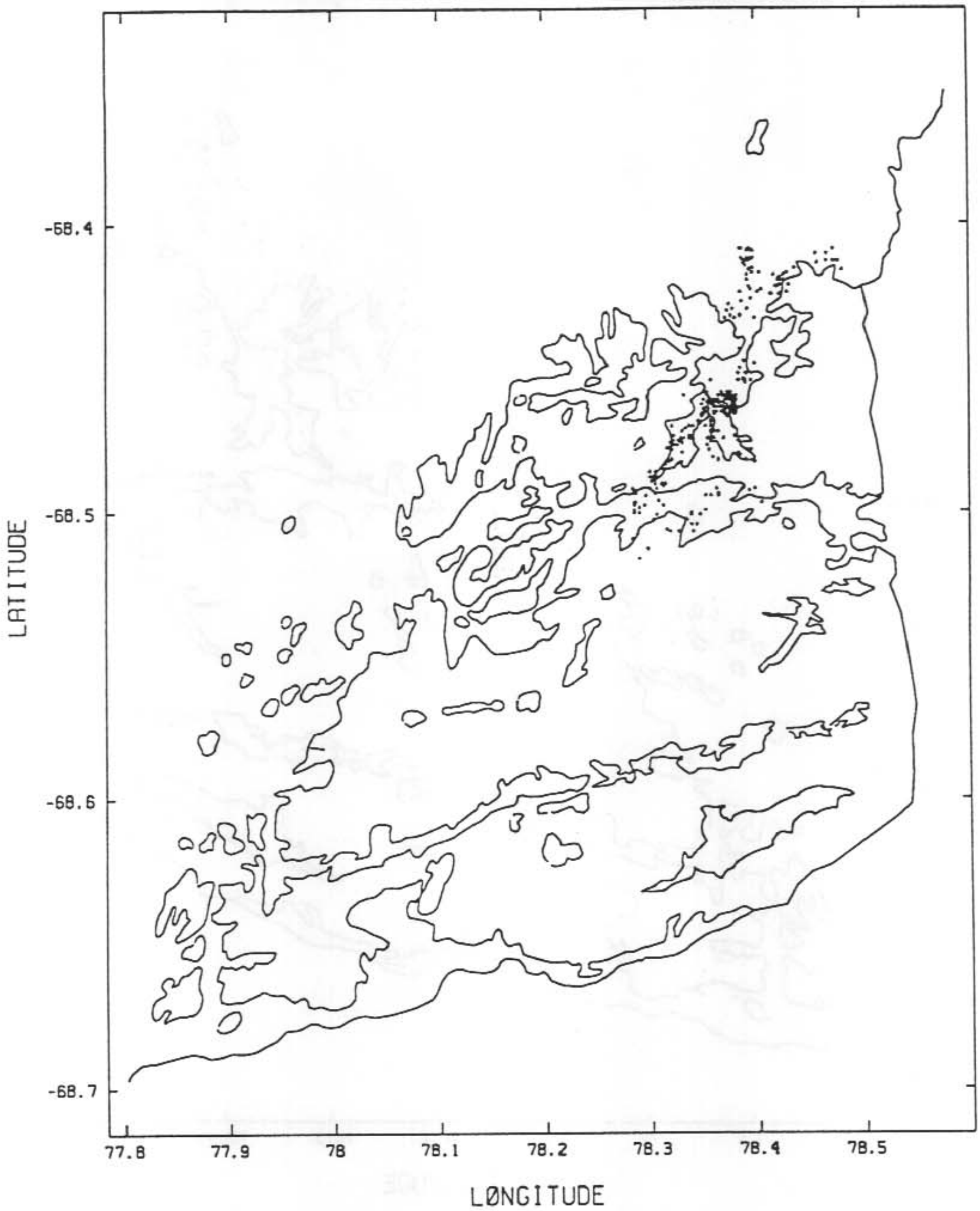

Figure 15. Sightings of all Weddell seals for the aerial census of 1 March 1990.

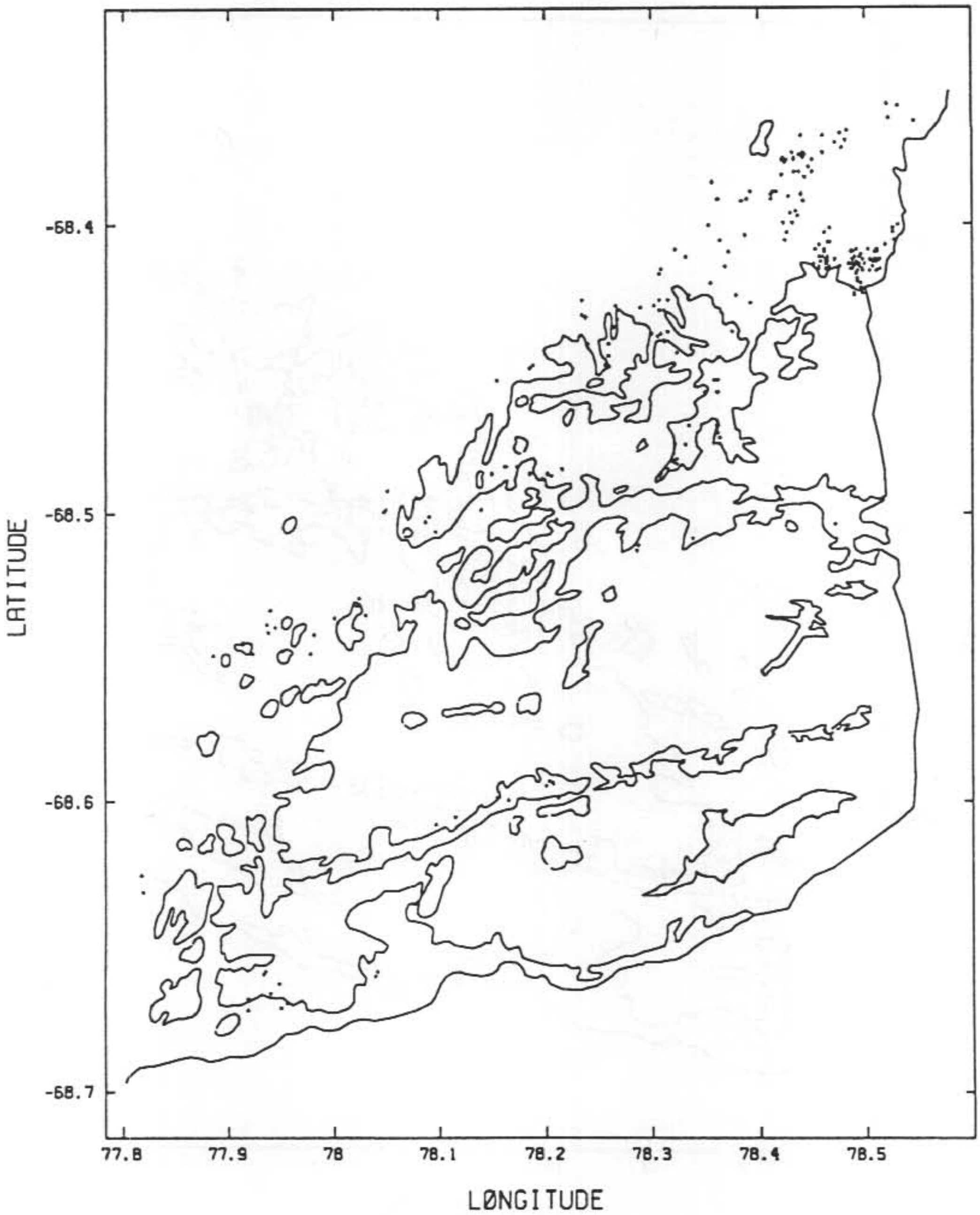

Figure 16. Sightings of all Weddell seals for the aerial census of 5 March 1991.

4. THE MOULT

4.1 Introduction

Weddell seals are available for study in high numbers only twice during their annual cycle. The first period is during the breeding season, the second during the moult. During the breeding season only females and their pups are commonly seen, whereas the whole population—breeders, non-breeding adults, juveniles and pups—must haul out to undergo a moult. This period is the one most used for censusing of seal populations. Little work, however, has been done to examine the period of the moult in the Weddell seal, or in fact in any of the ice-breeding seals in the Antarctic. By contrast, the moulting of the southern elephant seal has been studied intensely (Hindell and Burton 1988 and references therein). A summary of moulting in the Weddell seal was presented by Ling (1970), who relied on notes compiled by Wilson (1907) and Bertram (1940). Ling's (1970) synthesis was essentially limited to the approximate time of the moult and the fact that the Weddell seal, like the southern elephant seal, usually undergoes a postnatal moult at two to four weeks, before swimming for the first time.

The field component of the present study was undertaken in the belief that there was a period when all animals hauled out to moult with little difference in age groupings. During the analysis phase, however, attempts were made using the limited data to discover whether there were changes to the composition of the moulting population.

4.2 Methods

In the summers of 1989–90 and 1990–91 assessments were made of the state of moult of a number of seals. In 1989–90 this was done by visiting the largest groups of seals and checking these and any other seals in the vicinity. The first check in that summer was made on 20 January and the last on 20 February. In 1990–91 an assessment was made of the state of moult between 4 December and 3 March, during the course of ground counts. In both years, the sites checked were located at Long Fjord, Tryne Fjord, Tryne Bay and the Wyatt Earp Islands. In 1989–90 908 checks (417 males and 491 females) were made in eight groups of seals; in 1990–91 302 seals (194 males and 108 females) were checked.

Stages of the moult were determined on 3 January 1990 by the senior author, with Jim Phelan and Vera Wong (who completed the 1989–90 study). Seven stages of moult were originally defined but two stages which were difficult to distinguish in the field were later amalgamated to form Stage III. In addition, the original stage II (when rolls of black skin appeared to be coming off the animal's body from between its old fur) was found to be an unusual stage observed in relatively few animals, so it was amalgamated with stage I. The stages of the moult were therefore defined as:

0 Moult has not begun.

I Fur is dark brown in colour, bristly looking, with the odd loose hair on the seal or on the ground, together with black flecks of skin on the ground. Rolls of black skin may appear to be coming off the animal's body from between its old fur.

II Small tufts of fur are observed on the animal or on the ground or the seal is profusely moulting, losing sizeable chunks of fur.

III Distinct hair loss visible, with the new silky-looking grey coat distinctly visible on head, flippers and on a central narrow strip on the animal's dorsal and ventral sides.

IV The coat is mostly moulted at this stage, with only small patches of fur remaining on both sides of the animal between its front and rear flippers.

V Moulted—grey smooth coat present all over animal.

4.3 Results

The moult began in early December, having reached stage I in 11 seals of the 41 investigated. From this point it appeared to progress evenly, with the peak frequency moving through to stage V by mid to late February. In 1990–91 this progression appeared to be slow (or the changeover in individuals was more complete). Most of the animals seen were still in the 0 to I category until late January, even though the majority seen in 1989–90 had passed this stage by the same time (Figures 17 and 18).

The moult began in early December at the latter part of lactation, the majority of moulting seals hauled out being female. Between 4 and 6 December 1990, of 41 animals assessed for moult 39 were female. In early December 1992 114 of 184 seals were female. Males then entered the moulting population with increased frequency. The mean ratio of males to females over the moult from January onwards was 1:1.24. However, the ratios over eight censuses between 20 January and 20 February 1990 were not stable and decreased more or less steadily from 1:1.09 to 1:0.89, 1:0.93, 1:1.19, 1:1.15, 1:1.20, 1:1.21 and 1:1.42. In 1991, with smaller sample sizes than in 1990, the ratios were more in favour of males over about the same period, being 1:0.70, 1:0.74, 1:0.30 to 1:0.38, but they also fell to a low point of 1:1.16 towards the end of the moult in early March.

Moulting groups in 1989–90 commonly consisted of as many as a hundred seals. In 1990–91, on the other hand, sites and numbers changed rapidly with changing ice conditions: 'popular' sites lasted only for a week or two. In addition, the composition of these groups varied. Despite tagging all seals at particular popular sites, it was common to find a different group composition on the next visit.

Data from tagging files indicated that the age of animals moulting may have varied throughout the period December to March. Females that had recently pupped began to moult in early December, but during this period 5 of 11 tagged females, which had pupped in the past, had not recently pupped. The pups then moulted until the end of December. Breeding females continued to moult through to March, with immature females beginning to moult in late December.

The two seasons examined were quite different in respect of the numerical dominance of younger animals and breeding females. In 1989–90 the proportion of females that had not pupped rose from mid-January to be about 50% of the female population in mid-February (Figure 19). In 1990–91, however, the proportion fell from 83% to be about 50% in mid-February. Adult males appeared to moult from mid-January to late February, with immature males appearing in February. For animals of known age there was a decrease in mean age in both 1989–90 and 1990–91 from peaks in early to mid February. This was supported by the observation made by the counters in 1990–91 that there were far more younger animals after mid-February. These data are summarised in Figure 19.

4.4 Discussion

The moult in southern elephant seals, as with the northern elephant seal *(Mirounga angustirostris)*, hooded seal *(Cystophora cristata)* and Hawaiian monk seal *(Monachus schauinslandi)*, is hastened by the hair being shed with large pieces of cornified epidermis (Ling 1970). This makes the process of the moult more obvious than in the simple shedding of hairs by Weddell seals. The latter has therefore attracted less attention. The moult in Weddell seals was studied by Wilson (1907) and Lindsey (1937) and summarised by Bertram (1940). Wilson (1907) was concerned with describing the sequence of the moult in individual animals, whereas Lindsey (1937) concentrated more on pups and calculated the average duration of the moult at 30.2 days. In contrast to the accuracy with which pups were examined, little was written about the time taken by adults to moult, other than noting the fact that Weddell seals may be found moulting from the third week in November to the end of March (Wilson 1907), and that 'it is not possible to state at all precisely the time taken by the average Weddell seal to complete the moult. Probably it is variable' (Bertram 1940). The present authors agree with the latter statement. Because Weddell seals can return to the water at any time during the moult, and frequently do so, it is difficult to make serial observations on the same animal. The present study attempted to overcome this by examining a high number of seals and following the progression through a number of moult stages. This approach did result in a sequence of histograms (Figures 17 and 18) which appeared to show a natural progression over the course of a month or so. The neatness of this was, however, contradicted by the apparent change in age and sex of individuals.

The sexes and gross age groups of southern elephant seals can be differentiated quite easily, and simple observation indicates that there are differences in composition of the hauled-out moulting population. Such cues are not obvious in the ice-breeding seals and it appears that this aspect of the moult has not been investigated in the past. In southern elephant seals the animals moulting tend to ascend in age, with numbers of juveniles peaking slightly before sub-adult males. These in turn peak before females and later adult males (see Hindell and Burton 1988). In the Weddell seal this process is not as clear but does seem to be reversed: older animals (apart from pups) moult before younger ones (Figure 17).

The importance of determining the course of the moult in different age groups and sexes cannot be underestimated. An understanding of the moult is essential both for practical reasons (e.g. to decide when to attach dive recorders or transmitters) and from a theoretical perspective in answering the questions when to census and when to take samples to examine age structure of a population. Comparison of aerial censuses of Weddell seals in the past has been done under the assumption that there was little difference between a sample early in the moult and one in mid or late moult. While this may be true of numbers in some years, the question of what is being counted is an important one. A dip in the serial aerial censuses in mid-February 1991 and a little later in 1992 (see next section) may indicate that numbers that look similar from one year to the next, but are taken from different dates, may in fact have occurred only by chance and are actually of different age groups within the population. The apparent slower progression through the moult in 1990–91 may have derived from a greater turnover in animals in the less stable ice conditions, so that even at the same time of year the composition of animals moulting may vary from year to year. These problems mean that a full investigation, in the field, of the moult and the age groups involved at different times is of great importance. This is not only relevant to population studies of Weddell seals but extends to any seal for which the moult is an important time for sampling.

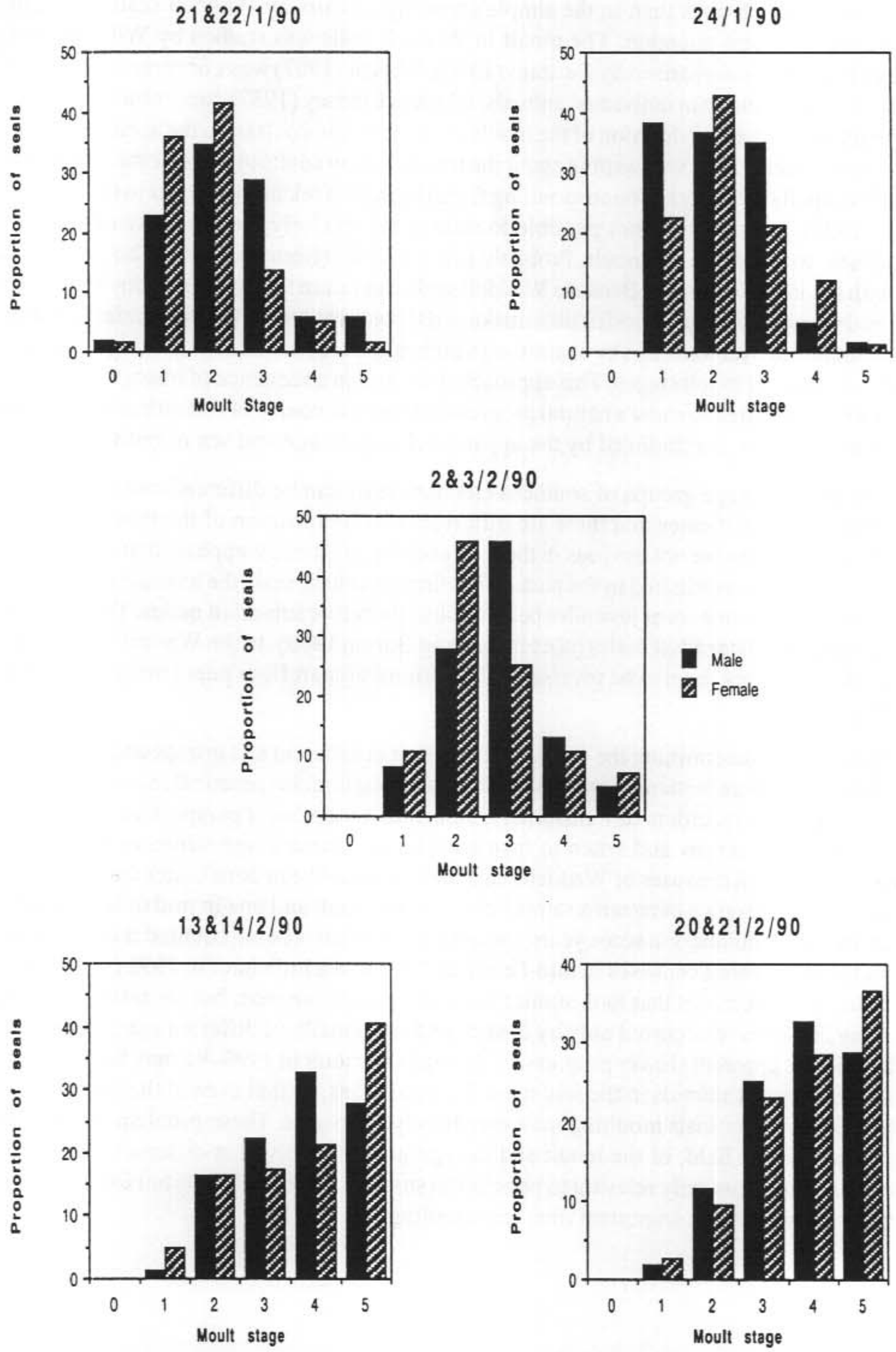

Figure 17. Frequency of seals at different stages of the moult between late January and late February 1990.

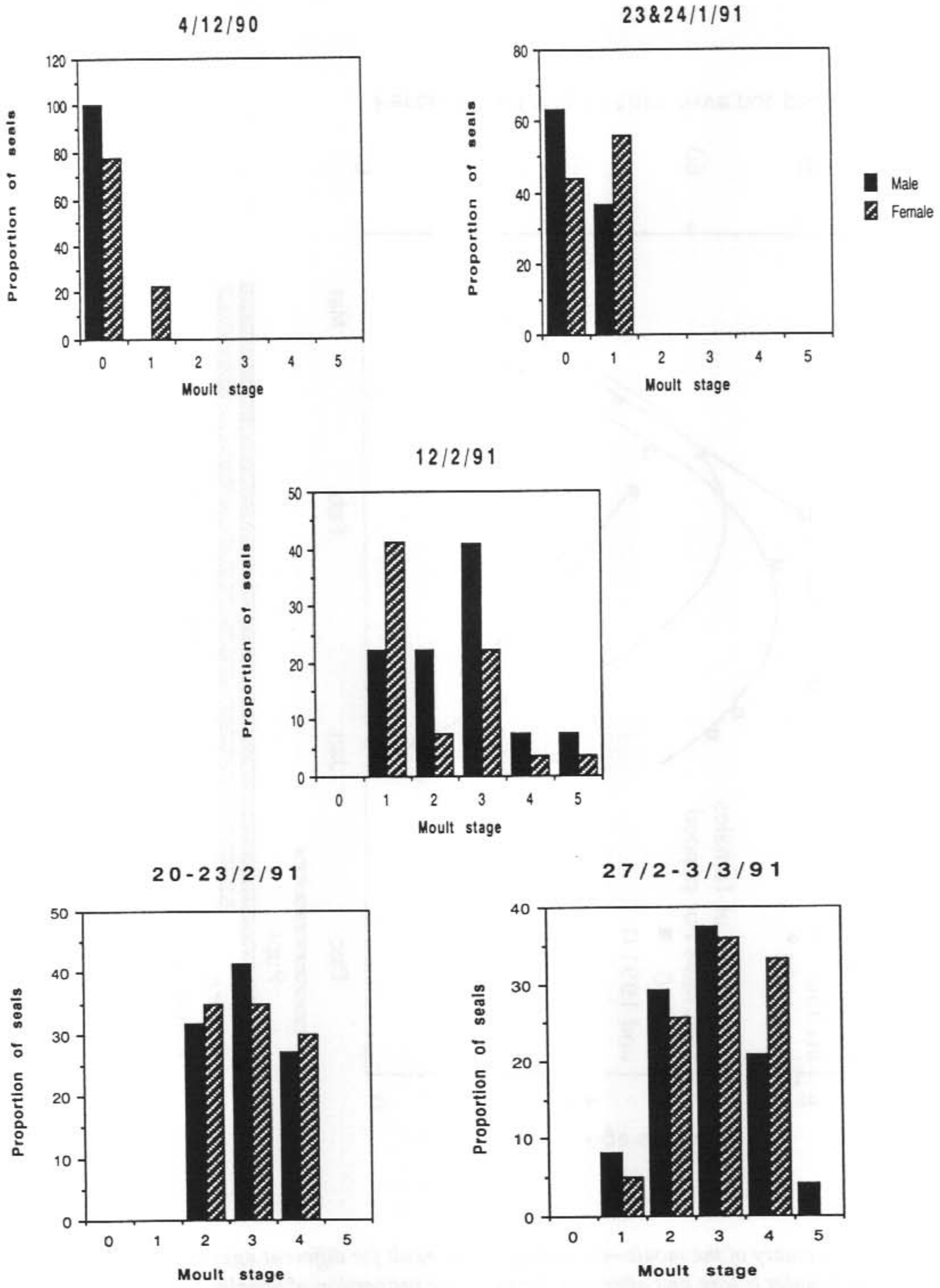

Figure 18. Frequency of seals at different stages of the moult between early December 1990 and early March 1991.

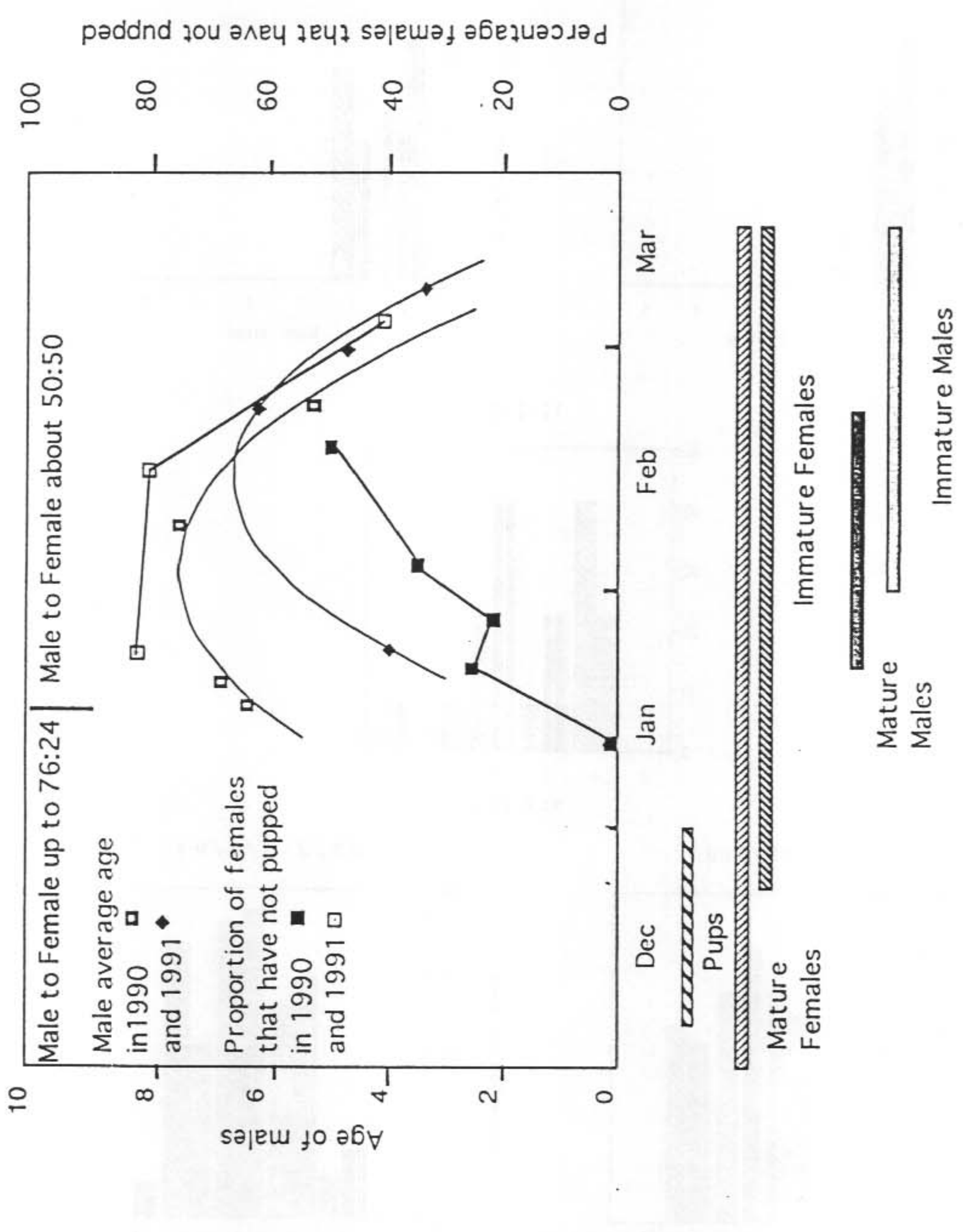

Figure 19. Summary of the moult—the timing of the moult for different ages and sexes; the ratio of males to females before and after mid-January; the proportion of females that haven't pupped and the male average age through the moult.

5. AERIAL CENSUSES

5.1 Introduction

Usually seal censuses are undertaken at only one time of the annual cycle, such as the moult (Gales and Burton 1989; Erickson and Hanson 1990) or the breeding season (Hindell and Burton 1987), but rarely at both (Pitcher 1990). The size of a population of seals is usually estimated from pup numbers, using a scaling factor obtained by modelling the whole population with a variety of demographic parameters as input (Wickens and Shelton 1992). Pitcher (1990) demonstrated a decrease in numbers of harbour seals *Phoca vitulina*, based on numbers hauled out to pup (72% decrease) and on numbers hauled out to moult (85% decrease). Counts of breeding cows and bulls (Hindell and Burton 1987) and seals moulting on land (Burton 1985, Gales and Burton 1989) have demonstrated clear falls in population numbers of southern elephant seals. This is confirmed by evidence of a general fall in numbers of southern elephant seals throughout the Indian and Pacific sectors of the Southern Ocean (Burton 1986, Barrat and Mouglin 1978, Condy 1979, Skinner and van Aarde 1983). These counts were made on land, where alternative haul-out sites could be examined, and the conclusion that this decline was real is unequivocal. Counts of animals moulting on shifting sea ice, however, do not necessarily have the advantage that all sites can be checked, and as access is generally not easy most such counts are, of necessity, made from the air.

There are, however, potential problems with aerial censusing of marine mammals, and three major difficulties were highlighted by Gilbert (1989). Individuals may abandon ice floes when being flown over; the counter may be unable to obtain a sufficient sample size in any one day; and an unknown fraction of animals may be in the water at any one time. Another consideration that might apply is different dispersion of animals in different years.

The Weddell seal population in the Vestfold Hills is a suitable population on which to examine the assumptions of aerial censusing in that some of these problems are negated by the tractable nature of these seals: they do not abandon the ice as easily as Gilbert found with walruses *Odobenus rosmarus*; they are restricted to close inshore areas for breeding (so checks independent of aerial censuses can be made on the population); and the whole area used for moulting can be flown over in a matter of a few hours to conduct the census.

5.2 Methods

Aerial counts were conducted during the moult (late December through to early March) in 1978–79 (two counts), 1982–83 (three), 1983–84 (two), 1984–85 (three) 1989–90 (five), 1990–91 (nine) and 1991–92 (ten). Censuses were conducted on warm,calm days between 10 am and 2 pm local solar time. Helicopters flew over all areas of fast-ice in the Vestfold Hills, an area containing a maximum of about 136 km^2 of fast ice. The coverage each year extended from the Sørsdal Glacier in the south to the Wyatt Earp Islands in the north (Figure 1). Flying height varied between 100 m and 200 m depending on ice conditions, with a variable transect width, but generally seals were not counted much beyond 100 m laterally from the helicopter. The numbers of seals seen in grid squares of one minute longitude by 30 seconds latitude were recorded directly onto a map (Figure 3) and summed to give a total count. From December to February 1991–92 three censuses were conducted in the Larsemann Hills (100 km to the south-east of the Vestfold Hills—see Figure 4).

In the summer of 1989–90, an assessment was made of the proportion of the counted seals that had previously been tagged. Six groups totalling 820 seals were checked, the minimum group size used for this study being 95. A further 221 seals were checked in smaller groups. Seals were also examined for tags at major haul-out sites for 100 km along the coast south of the Vestfold Hills.

5.3 Results

Mean population counts from aerial censuses of Weddell seals in the Vestfold Hills fell from approximately 1300 seals in 1978 to 307 in 1984 (a 75.3% reduction), increased to 815 in 1989–90, fell slightly to 599 in 1990–91 and fell again to 352 in 1991–92 (Figure 20). Serial aerial censuses were undertaken only in 1989–90, 1990–91 and 1991–92. No predictable seasonal trend in numbers from December to March has yet been established but there are indications that a real drop in numbers may have occurred in mid-February 1991 and 1992 in the Vestfold Hills and in 1992 in the Larsemann Hills (Figure 21).

In all years when serial aerial censuses were conducted the distribution of moulting seals contracted with the loss of fast ice to the north of the Vestfold Hills. On 10 January 1990 seals were distributed along the Zashchitnyye Islands and Tryne Islands to the Wyatt Earp Islands (Figure 23). By 18 January the seal distribution had contracted closer to the coast, with seals moving into the vicinity of Walkabout Rocks, Tryne Sound, Tryne Bay and Tryne Fjord (Figure 24). By 1 February the seals were mainly in the two northern fjords, with only a few occupying ice in Tryne Bay (Figure 25). By 22 February the seals were mainly in Tryne Fjord and Tryne Bay, and had retreated deep into Long Fjord (Figure 26). The details of this situation varied from year to year. On 26 February 1991, for example, very few occupied Tryne Fjord, and seals in Long Fjord were closer to the mouth of the fjord (Figure 27). By contrast, in 1992, seals were deep in the western horn of Tryne Fjord and there were large concentrations south of Davis around Warriner Island and Hawker Island (Figure 28).

Differences between censuses did not, however, result from differences in distribution and during the drop in numbers on 9 February 1991 (Figure 29) the distribution of seals was similar to that on 13 February when the numbers were almost back to normal (Figure 30). Similarly, in 1992 there was no great difference in distribution between high and low counts. The differences between years also could not be attributed to differences in distribution, with distribution in 1984, the year with the lowest count (Figure 31), being similar to that in 1991 (Figure 32).

The proportion of seals in six groups, each with over 95 individuals that had been tagged previously, ranged between 5.4 and 19.4% (mean 12.5%). Of 120 animals seen in the 1989–90 summer at the Rauer Islands, 20 km south of the Vestfold Hills, only nine had been tagged previously, and of these only two had been tagged in the Vestfold Hills. Similarly, between February 1983 and January 1984, of about 2500 Weddell seals examined from the Rauer Islands to the Larsemann Hills, 100 km to the south of the Vestfold Hills, only 23 had been tagged in the Vestfold Hills (Schou and Cracknell 1984). None of about 300 seals checked in 1989/90 at the Larsemann Hills had been tagged. An aerial census of the Larsemann Hills on 12 January 1991 resulted in a total of 428 seals being counted, but because of ice condition and time restraints only 18 could be checked on the ice for tags. None of those seals were tagged. Six of the 18 were pups.

5.4 Discussion

The aerial censuses conducted in this study clearly did not provide a reliable index of population changes in Weddell seals in the Vestfold Hills. There was a lack of any evidence of unusually high mortality other than from the aerial censuses themselves. There was no major perturbation in pup numbers in the Vestfold Hills over the years since 1957. At McMurdo Sound, by contrast, the number of Weddell seal pups born between 1963 and 1979 varied by a factor of greater than three (Siniff 1981). There was no evidence that mortality of breeding females was high in the Vestfold Hills, a situation that would be unlikely with a decline in population numbers of the order of 80%. DeMaster (1978) stated that 'regulating factors associated with stable environments tend to produce population changes that are relatively small and take many years to reach an equilibrium once the population is perturbed.' However, if the aerial census figures are to be believed, there was a greater than 100% increase in numbers from 1983–84 to 1984–85 (from 307 to 687). Such a wide swing in numbers in the fast ice of the Vestfold Hills (a very stable environment), together with lack of evidence of a decrease in numbers from the monitored breeding population, argue against a real decrease in population size (Green *et al.* 1992).

There was no major movement of seals to areas of fast ice away from the Vestfold Hills (as tagged seals became rarer with increasing distance) and they did not disperse outwards into the pack ice to moult. (Sightings of Weddell seals in hourly ten-minute counts in the pack ice were not lower in 1983–84 than in 1989–90 (Green unpublished data). Green *et al.* (1992) suggested that the most likely major cause of variation in the aerial censuses was the varying proportion of animals in the water due to differences in food availability. There were 'good' years when there was an abundance of easily available inshore-benthic food and 'bad' years when seals had to travel further to take pelagic species, resulting in their spending less time on the ice to be counted. Additional data on numbers and diet since that paper seem to confirm those conclusions. There is a significant negative relationship between the occurrence of pelagic prey in the diet and the number of seals on the fast ice (Figure 22).

Possible changes in numbers of moulting seals during the census period due to the different composition of the population over time have not been examined in previous work on aerial censusing of ice-breeding seals (e.g. Erickson and Hanson 1990, Green *et al.* 1992). However, work by Hindell and Burton (1988) has shown that there are different haulout patterns for differing ages of southern elephant seals during the moult. This pattern has been studied because of the ease in differentiating in size between males and females and between breeding males and subadults. The differences are not so obvious with ice-breeding seals, in which sexual dimorphism is minimal. As a consequence, aerial surveys (as distinct from the ground surveys of southern elephant seals) have tended to just record numbers, without attempting to characterise the animals by sex or age.

The serial census in 1990–91 showed a dip in mid–February, with a similar dip occurring somewhat later in 1991–92. There was also a decline in numbers at the Larsemann Hills at about the same time, although the lack of a follow-up census makes it difficult to differentiate between a trough and a tailing off in numbers as the moult is completed (Figure 21). The cause of this dip is difficult to ascertain. The changes in ratio of males to females over the course of the moult, and the influx of juveniles, especially juvenile males, in mid-February 1991, resulting in a lowering of the mean age of males in late February and March, both point to the possibility that there is a real age pattern to the composition of the moulting population as there is with southern elephant seals. Such a pattern is likely to result in peaks and troughs in numbers of seals (see Hindell and Burton 1988), and these may be either constant or variable from year to year. Smith (1966) presented a smoothed graph (his Figure 3.7) of numbers of Weddell seals in a study area in McMurdo Sound for a three-year period in the early 1960s. Examination of his annual data (his Figure 3.6), however, shows that in only one of the three years was the graph of the raw data anywhere near being as smooth as his Figure 3.7. The more common sequence was a series of peaks and troughs, with the deepest troughs appearing on about 11 February in 1964 and about 17 February 1963, but with no trough at all in 1962. The data from McMurdo Sound are complicated by a number of factors, the effects of which are hard to disentangle. Smith (1966) suggests that the fluctuations in 1963 were due to weather differences, but details are not given; and no cause is given for fluctuations in 1964. In McMurdo Sound the situation differs from that at the Vestfold Hills due to the lesser access to open water throughout the year. Wintering seals at McMurdo Sound are dependent upon access to the few (150–200) ice holes, and juvenile animals are forced northwards to more open water (Kooyman 1981). There are, then, three major influxes of seals during the spring and summer months—pregnant females arrive first and, later in November, the breeding bulls arrive; juveniles first appearing in December (Kooyman 1968); and yearlings and two-year-olds remaining quite uncommon until middle to late summer (Kooyman 1981). An initial buildup of numbers of moulting seals in early January was followed by a secondary buildup in late January that had a higher proportion of subadult seals (Smith 1966). This means that age-class segregation is present in all months of the summer at McMurdo (November–February) (Testa *et al.* 1985). In the absence of a good age comparison (because ofthe different availability of access) there is still some evidence for at least changes in the sex ratio. In McMurdo Sound in 1967 the ratios of males to females were: 28 January 1:2.6, 6 February 1:2.8, 12 February 1:2.8, 19 February and 21 February 1:1.6. In 1968 the radios were: 9 January to 3 February between 2.2 and 2.4 to one; 7, 9 and 10 February combined 1:2.0 (Stirling 1969). These results were due to the numbers of females dropping in about mid-February (Stirling 1969), a situation similar to that in the Vestfold Hills. Further work to determine whether or not the dip in mid-February is real or an artefact will continue, but if there are differences between groups making up the moulting population then inter-annual comparisons in censuses must take this into account.

This study of Weddell seals in the Vestfold Hills has therefore suggested two areas of potential error in the censusing of seals on ice, and it points at two questions that must be answered if the data from censusing of ice seals are to be of use in making inter-annual comparisons.

1. Are there different haulout patterns in different years that are determined by food availability? This raises the testable hypothesis that seal distribution during the moult is determined by prey availability and that ice may be classed as a necessary but not sufficient determinant. This hypothesis has important implications for the conduct of inter-annual comparisons where there are changes in prey distribution and/or ice cover.

2. Due to the biology of moulting in seals, which appears at least to cross the boundary between Weddell and southern elephant seals, there is a difference between the composition of moulting groups over the course of the moult, and if each sex/age class is not equally represented in the population then this will result in periods of low counts. The timing of these counts, however, may be difficult to elucidate. This suggests a second hypothesis which must be tested in ice seals before confidence can be placed in inter-annual counts made during the moult: that because the age, sex, physical or reproductive condition of seals has an effect upon the physiological conditions necessary to initiate the moult, there will be temporal differences in the composition of the population hauled out to moult.

Because of the ease of conducting many studies on easily accessible Weddell seals, because they inhabit the conservative habitat of the fast-ice, and because whole population processes can be examined in detail by a number of methods, they can be envisaged as 'laboratory' animals upon which hypotheses can be tested in order to pose questions about processes occurring in the 'field' situation occurring in the far less accessible pack ice. Further studies of these questions will continue and are expected to yield useful and far-reaching results for ecosystem monitoring.

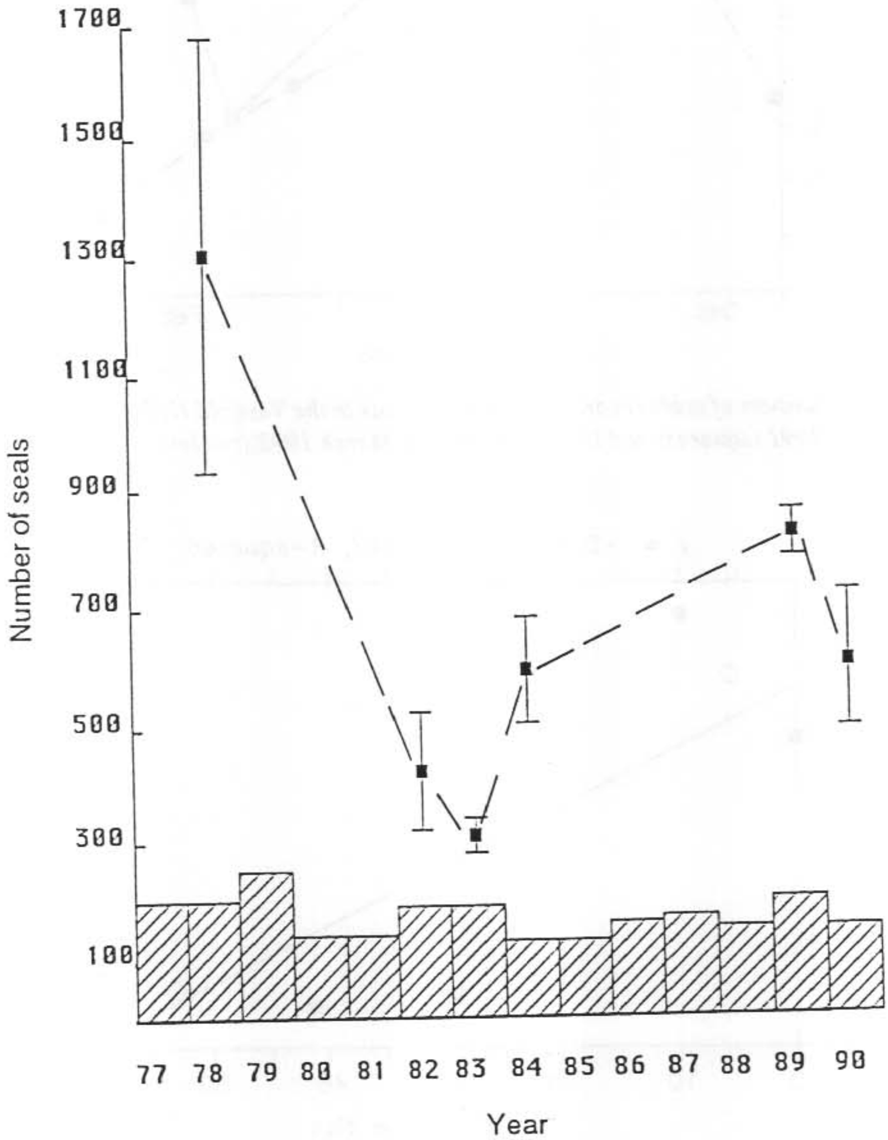

Figure 20. Aerial census (lines) and pup numbers (histograms) for Weddell seals in the Vestfold Hills between the spring/summer seasons of 1977–78 and 1992–93. Aerial census counts are mean ± one standard deviation. The year referred to on the X axis is the year in which the season began (e.g 77 refers to 1977–78).

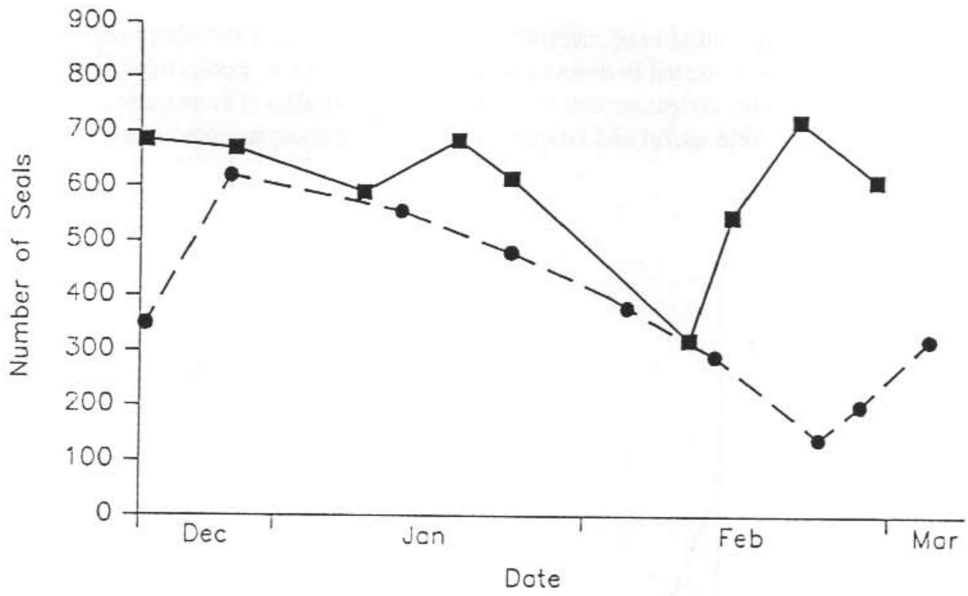

Figure 21. Numbers of seals recorded by aerial census in the Vestfold Hills from December 1990 to February 1991 (squares) and December 1991 to March 1992 (circles).

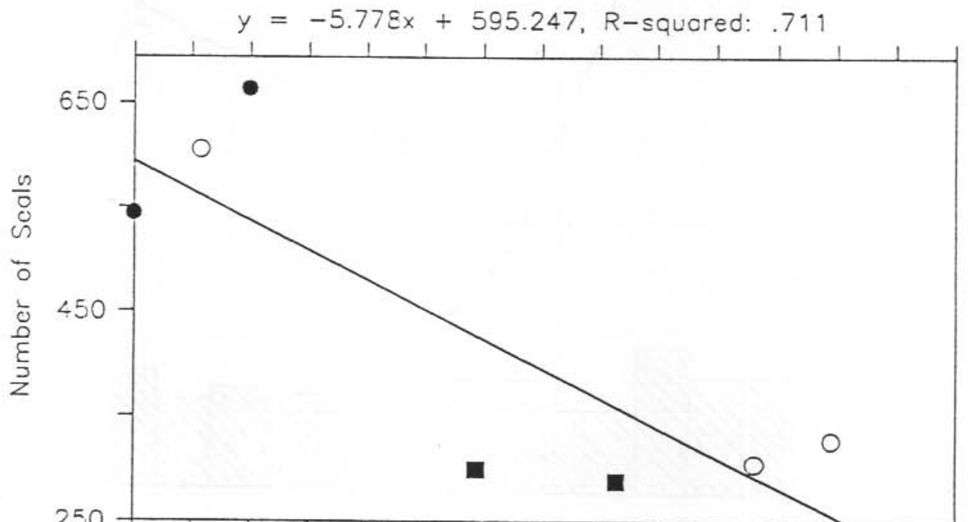

Figure 22. Regression of numbers of seals counted during aerial surveys on the percentage occurrence of pelagic remains in scats containing fish remains. Squares are from January and February 1984, closed circles are from February 1991 and open circles are from December to February 1991–92.

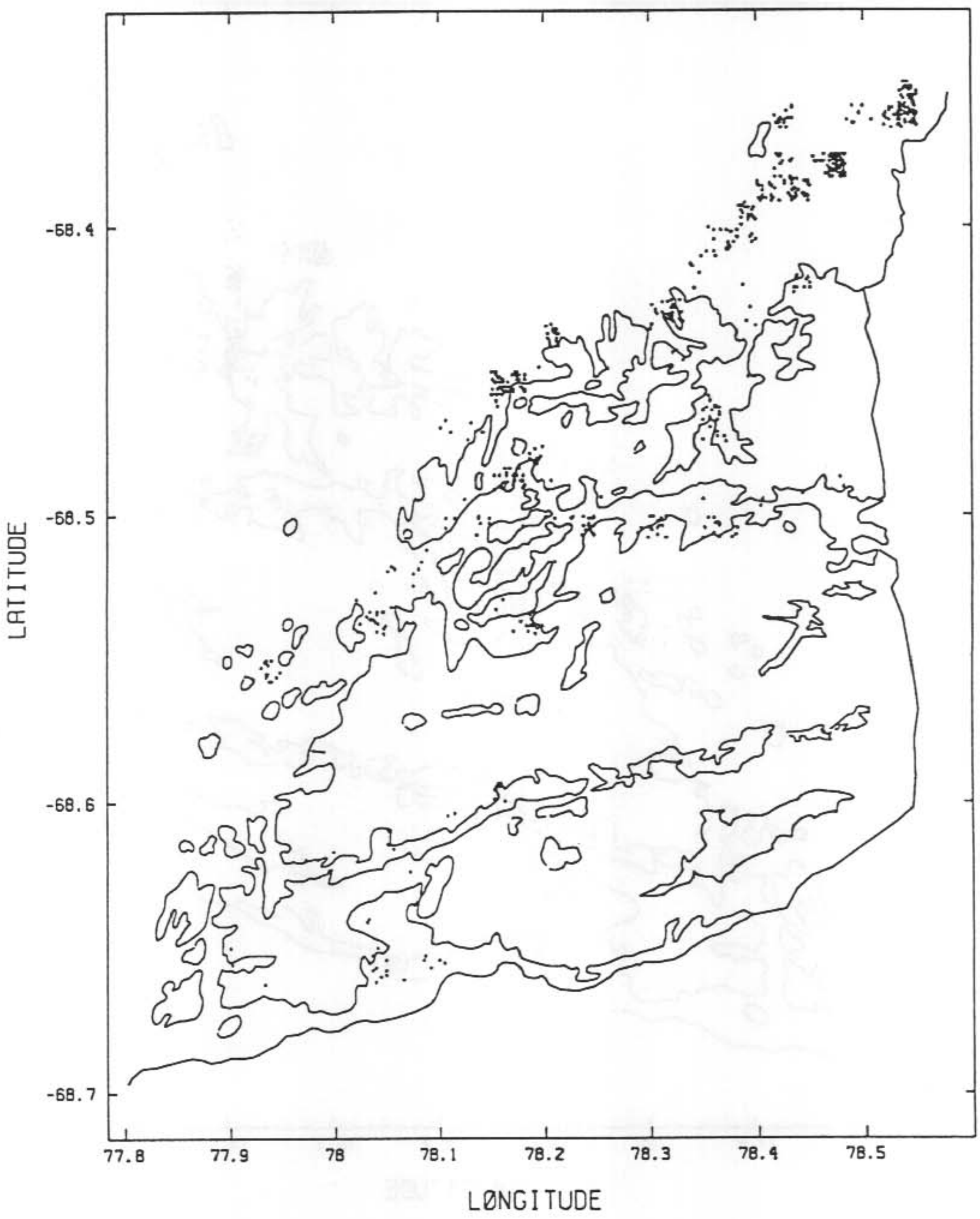

Figure 23. Sightings of all Weddell seals for the aerial census of 10 January 1990.

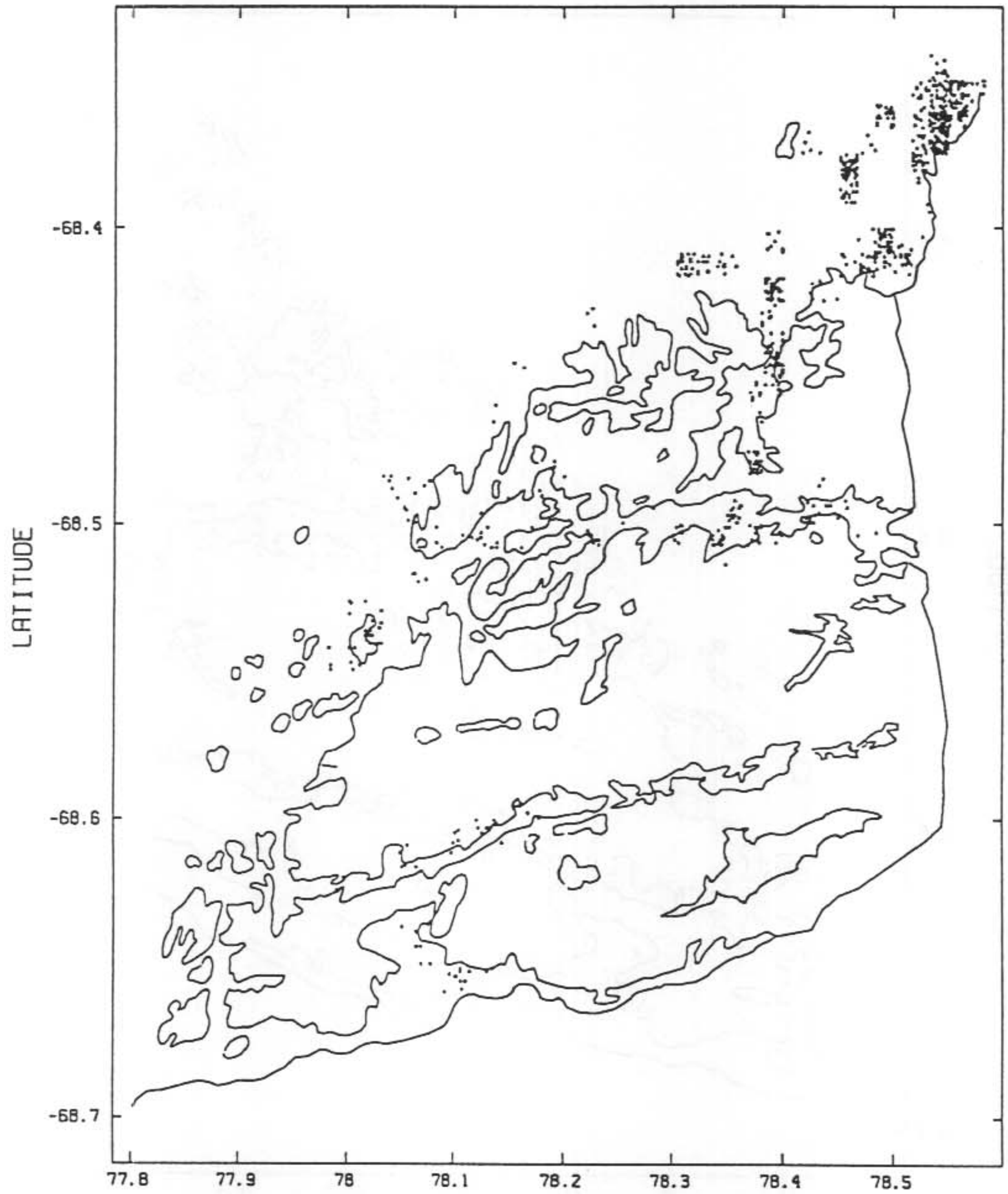

Figure 24. Sightings of all Weddell seals for the aerial census of 18 January 1990.

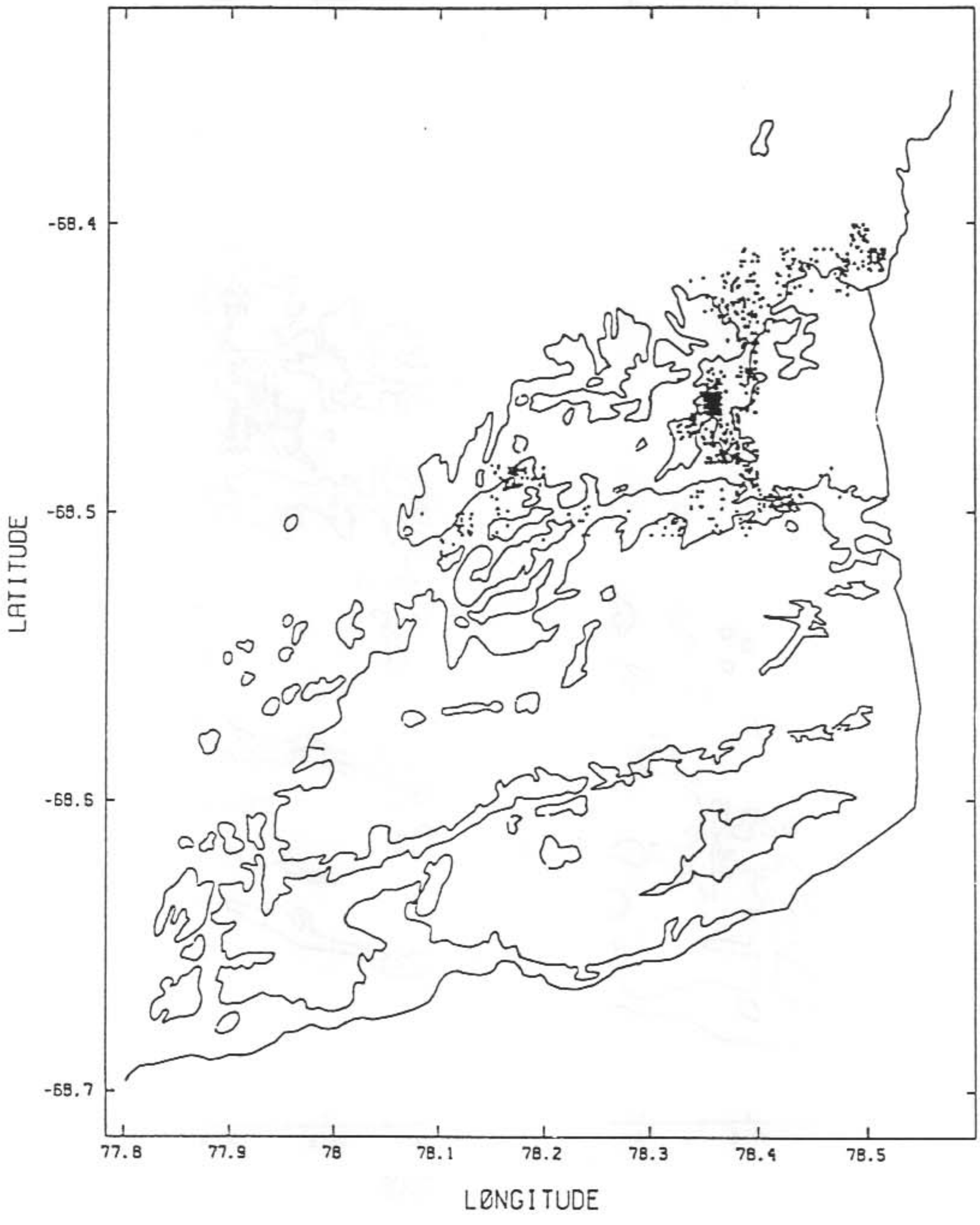

Figure 25. Sightings of all Weddell seals for the aerial census of 1 February 1990.

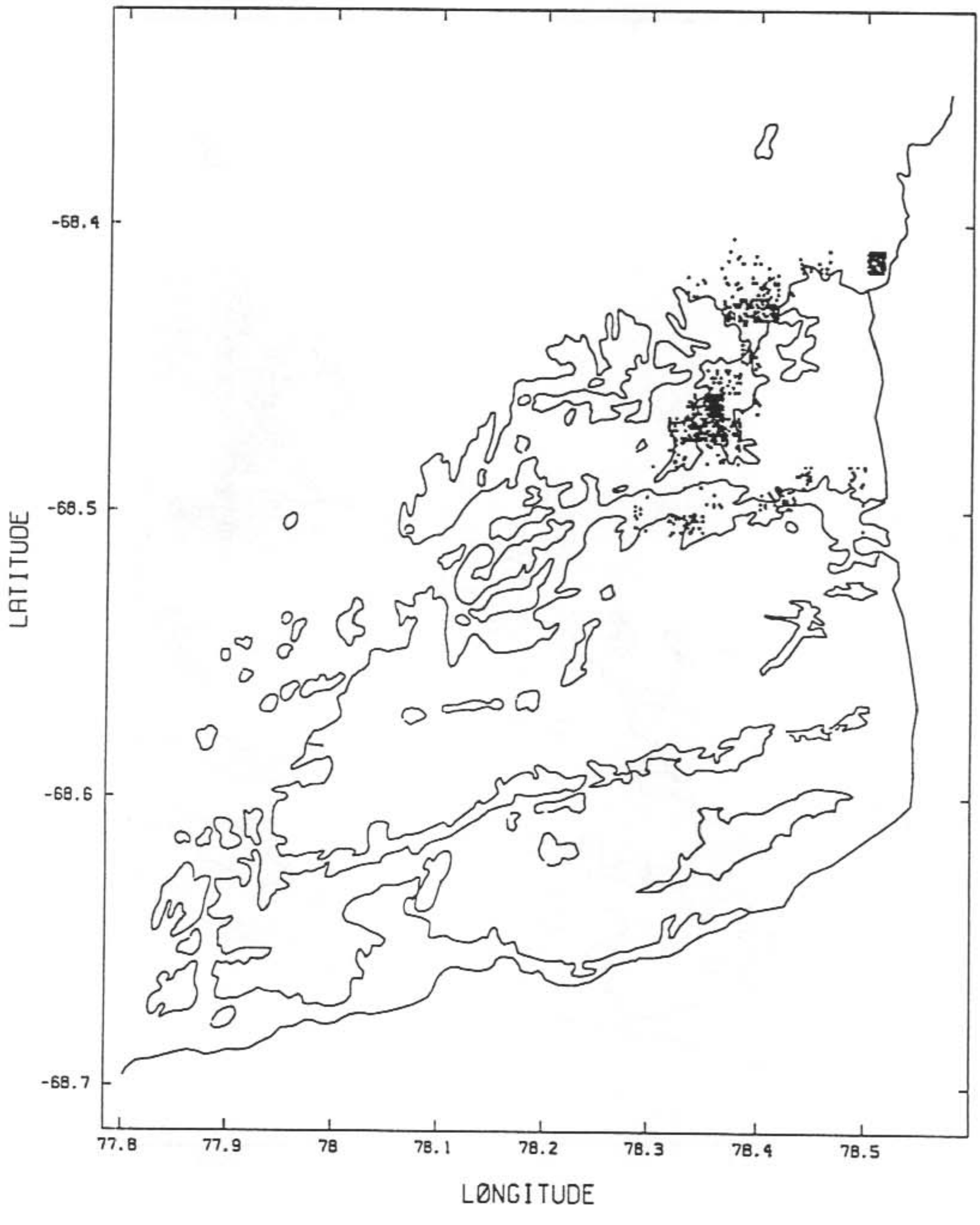

Figure 26. Sightings of all Weddell seals for the aerial census of 22 February 1990.

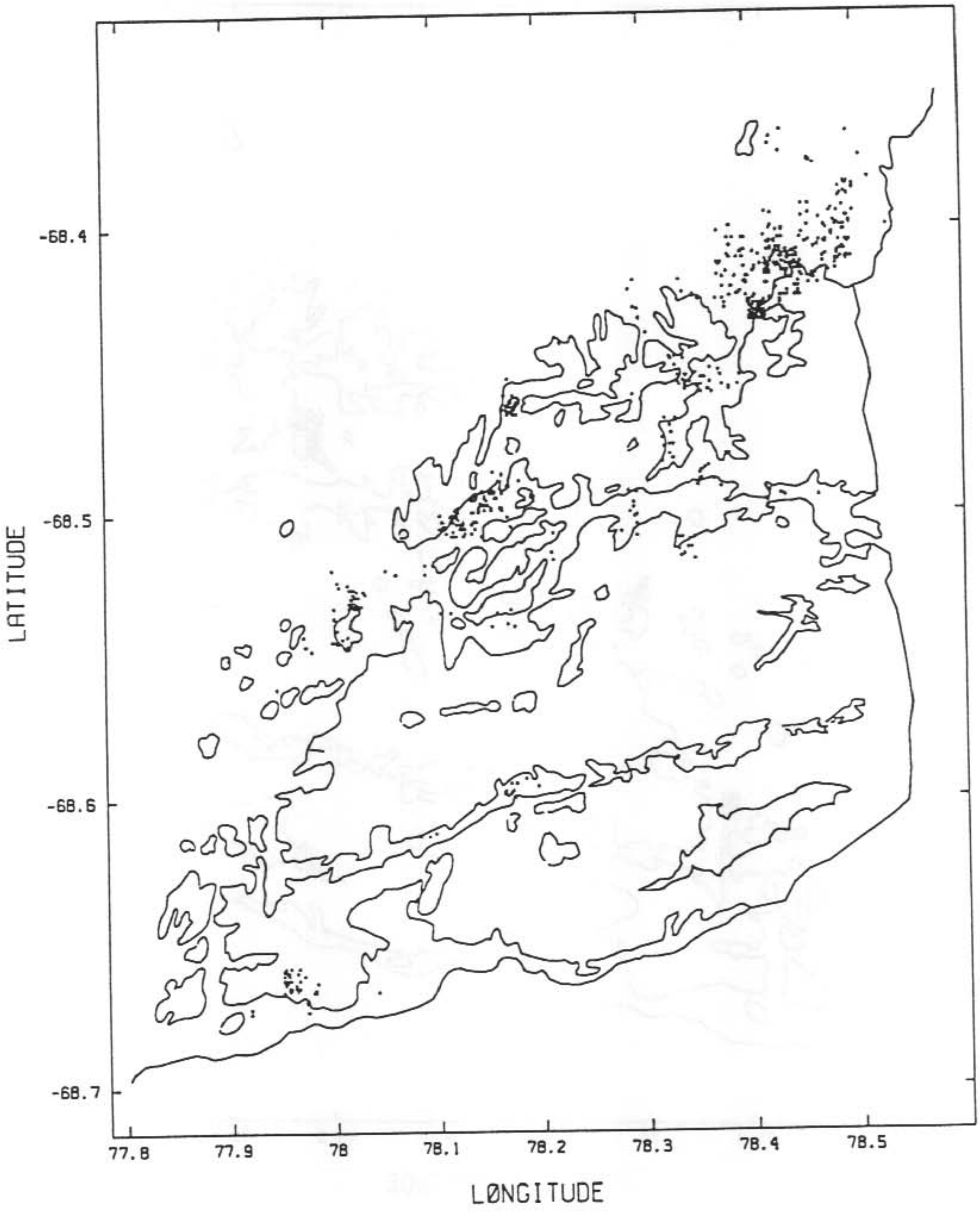

Figure 27. Sightings of all Weddell seals for the aerial census of 26 February 1991.

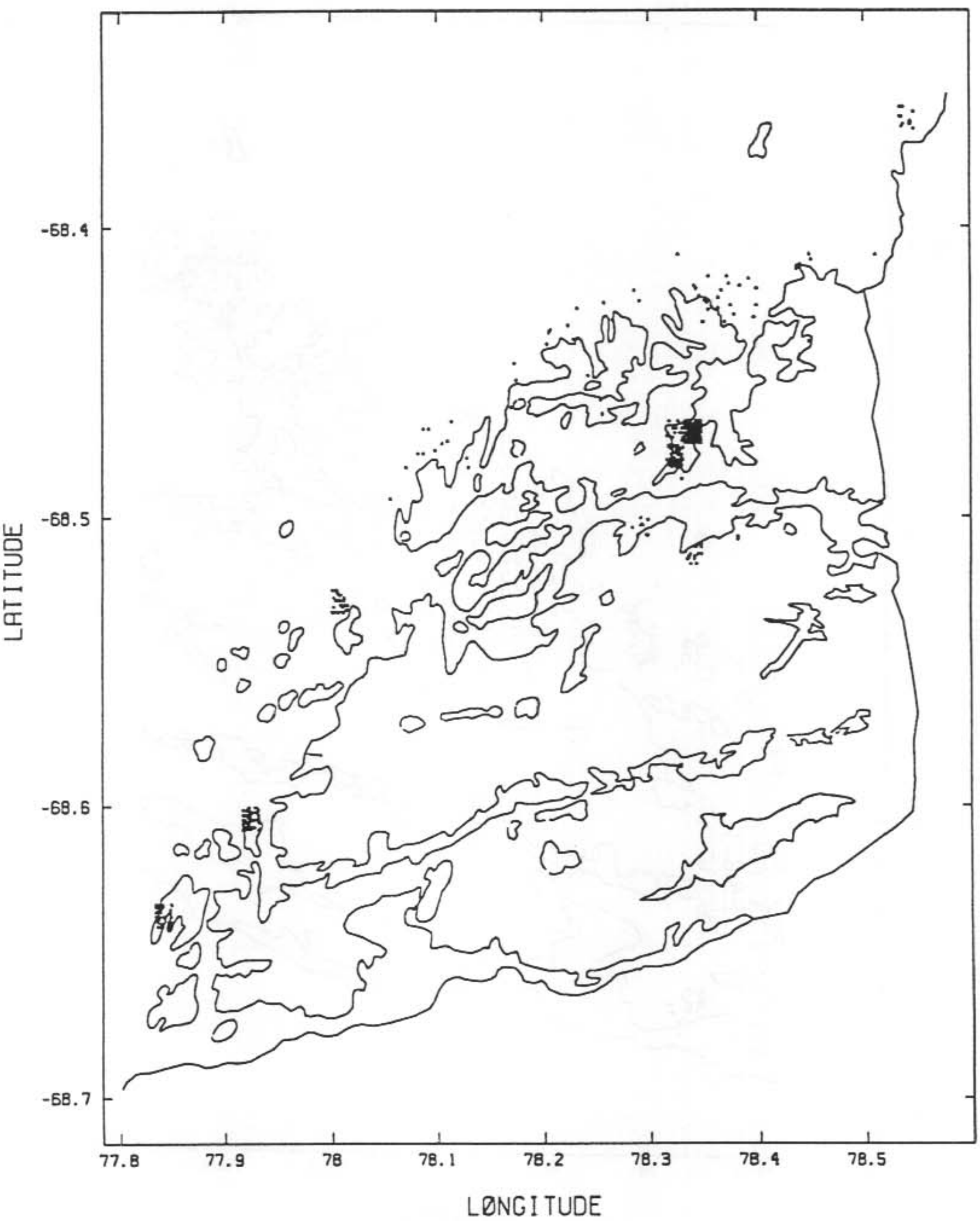

Figure 28. Sightings of all Weddell seals for the aerial census of 25 February 1992.

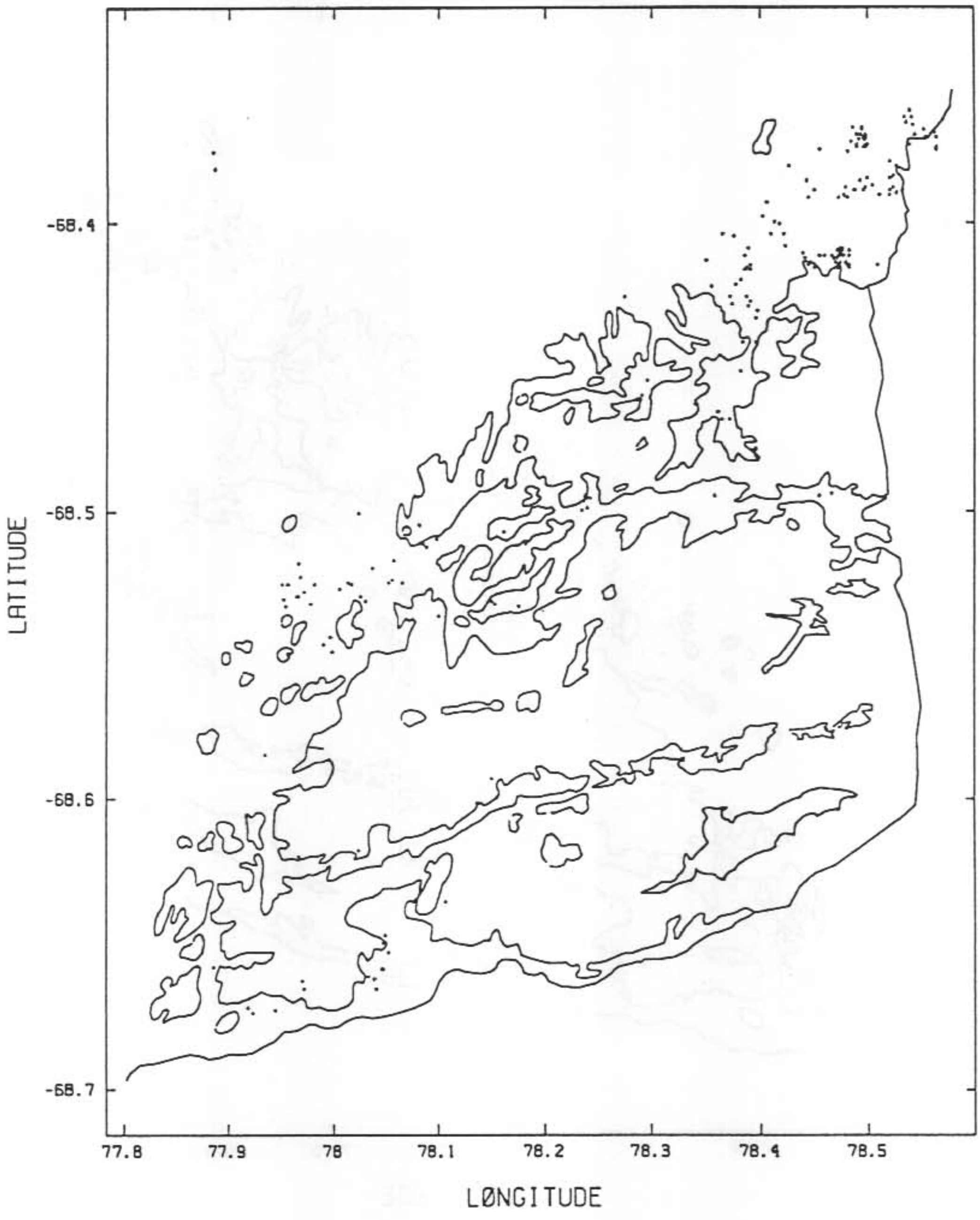

Figure 29. Sightings of all Weddell seals for the aerial census of 9 February 1991.

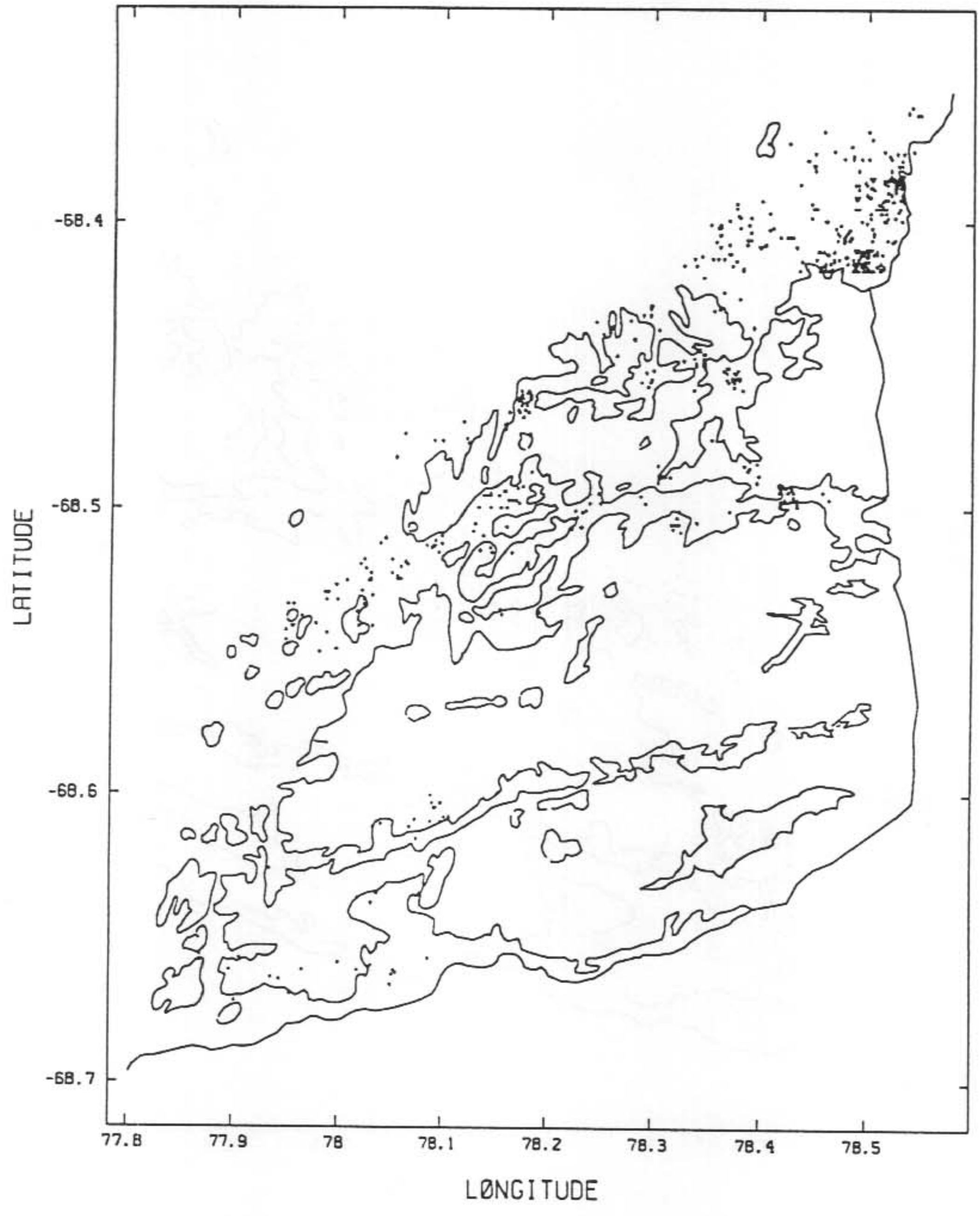

Figure 30. Sightings of all Weddell seals for the aerial census of 13 February 1991.

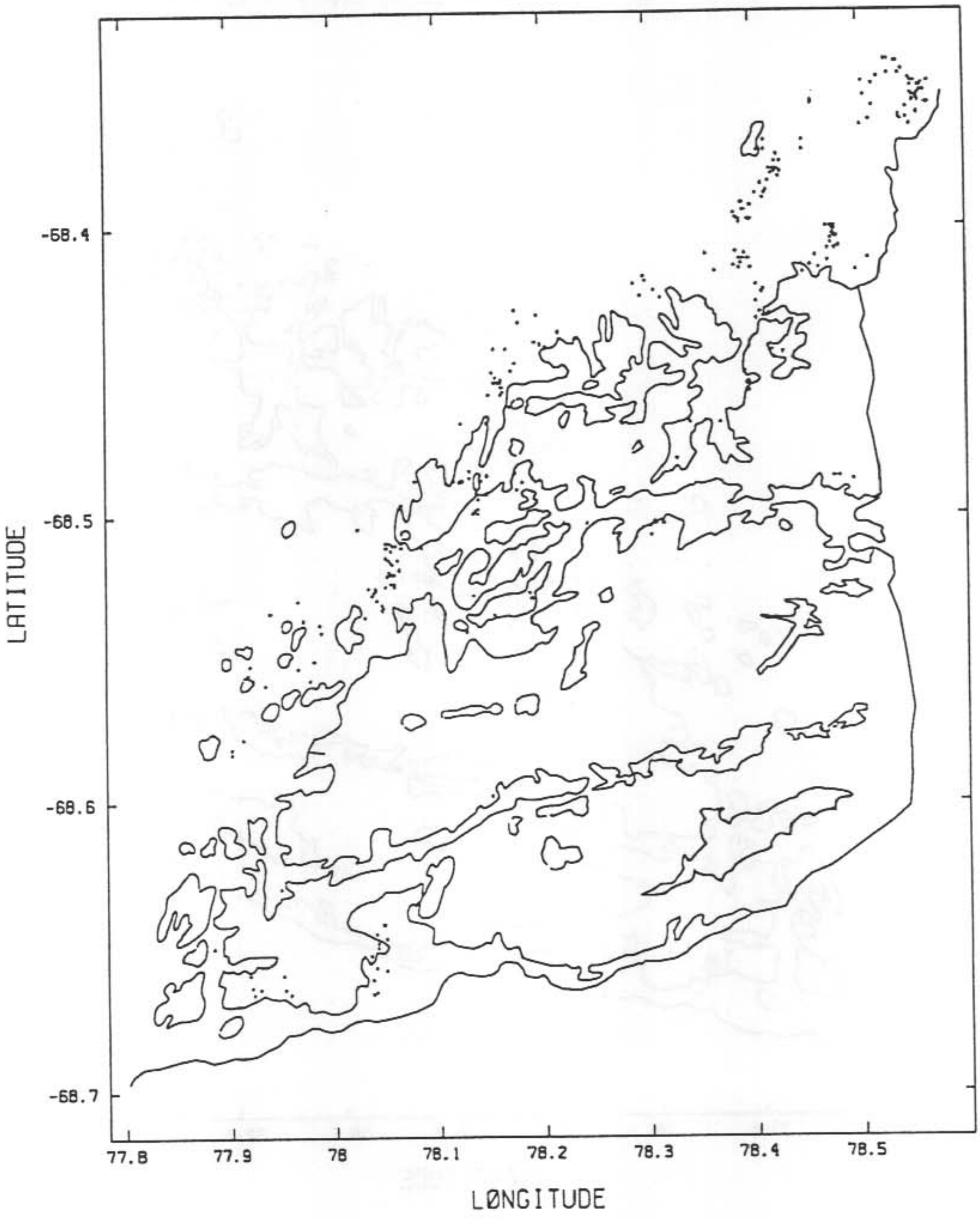

Figure 31. Sightings of all Weddell seals for the aerial census of 19 January 1984.

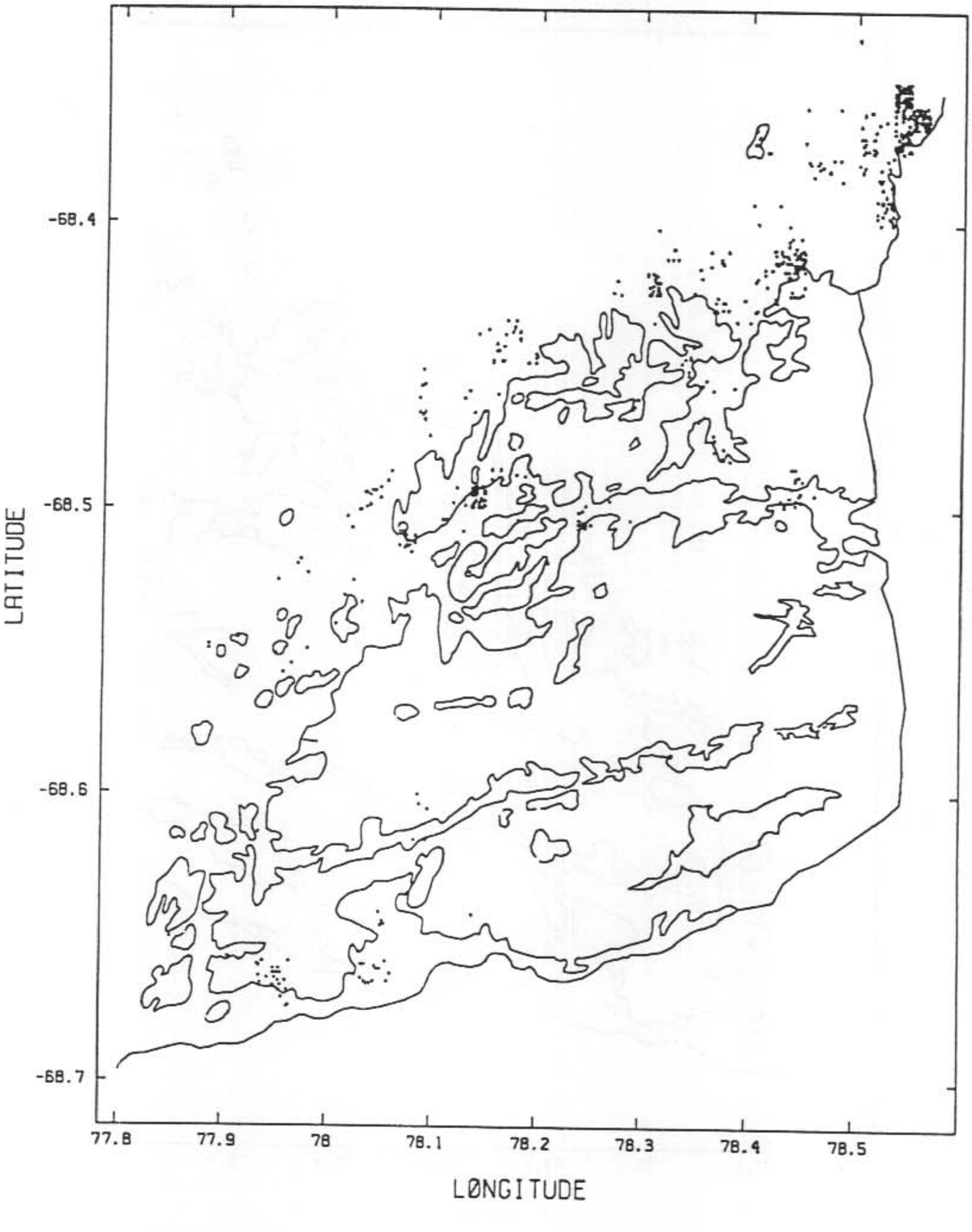

Figure 32. Sightings of all Weddell seals for the aerial census of 23 January 1991.

6. DIET

6.1 Introduction

The major work on Weddell seal diet conducted at the Vestfold Hills (Green and Burton 1987a) sampled a period from late 1983 to early 1985. While this was, and still is, the only dietary study of Antarctic seals to examine the diet over a full twelve months, the question remained—was a single year's data representative of the whole diet? Green and Burton (1987a) demonstrated geographical differences in the diet by examining samples from three sites: Mawson and McMurdo Sound were compared to the main Vestfold Hills sampling. Temporal differences were also demonstrated for seasons, but only one month (January) was sampled in consecutive years. Since then a number of small collections of dietary material have been made in the Vestfold Hills, only one of which has been published (Gales and Burton 1988). This section, therefore, draws together the dietary work that has been conducted in the Vestfold Hills for a re-assessment.

6.2 Methods

Individual faecal samples collected from the fast ice were kept separate and were returned frozen to the laboratory for analysis. Faecal samples were broken open in water in a sieve of 1.0 or 0.5 mm mesh and the residue was sorted beneath a dissecting microscope. Fish otoliths, vertebrae, crustacean remains and cephalopod beaks were removed for further identification and measurement.

Most fish remains were assigned specific identities on the basis of otoliths. In the absence of remains sufficient for specific identification, bony fish remains were classified for estimation of frequency of occurrence into pelagic types and nearshore-benthic types, according to the characteristics of the vertebrae (degree of ribbing, the length–width ratio and the diameter of the lumen) compared to reference skeletons of known species. Standard lengths of fish prey were estimated from measurements of the length and width of otoliths. Only otoliths showing very little or no sign of erosion were used for this purpose. Formulae derived from fish of known size were used to calculate standard lengths from the otolith measurements.

6.3 Results

In 1990–91 a total of 30 scats was collected between December and early March, and between December and February 1991–92 the total was 122.

Fish occurred in all scats in 1990–91 and 82% in 1991–92, compared with a range of 58.1 to 64.6% reported for similar months in 1984–85 (Green and Burton 1987a). Fish species identified from otoliths were *Pleuragramma antarcticum* and Nototheniids, possibly *Trematomus* sp and occasionally possibly *T. newnesy* (R. Williams pers. comm. 1993). Fish standard length calculated from three otoliths of *P. antarcticum* averaged 164±22 mm and were well within the range of sizes found in 1984 and 1986.

Prawns occurred in 27.6% and 31.1% of scats in 1990–91 and 1991–92 respectively compared with 67.4 to 74.2% for summer 1983–84 (January to March) and 37.5 to 70.6% for 1984–85 (December and January). The carapace length of *Chorismus antarcticus* found in scats between December 1991 and February 1992 was 13.1±1.2 mm (n = 78) and in 1990–91 was 13.6±1.5 mm (n = 18) compared with 13.2±0.8 mm (n = 12) for December 1989 and 13.3±1.5 mm in December 1984 (n = 25). In 1991–92 the carapace length of *Notocrangon* was 13.3±1.5 (n = 38) compared with 14.1±2.7 mm (n = 6) for January and February 1990. The latter is within the range of 14.0 to 14.4 found in January and February 1984 (Green and Burton 1987a). The ratio of *Chorismus* to *Notocrangon* in 1990–91 was 3:1 compared to 2.2:1 in 1983, 1.4:1 over the same months in 1984 and 3.2:1 in January 1985. In 1991–92 *Chorismus* appeared in 17 scats by itself and *Notocrangon* in 3. Where the two occurred together, *Chorismus* just outnumbered *Notocrangon* by 1.15:1.

6.4 Discussion

Differences in the diet of Weddell seals in the Vestfold Hills between years have been commented on by Gales and Burton (1988). They found similar fish sizes (but two previously unreported species) and cephalopod types, but reported no prawns or, in fact, any evidence of predation on crustaceans. While their sample was both small (n = 6) and taken in spring, larger samples collected in summer 1990–91 and 1991–92 still found a lower occurrence of prawns (in 31% of scats in each season) compared with over 50% in both 1983–84 and 1984–85. This lower occurrence of prawns was negatively correlated with a greater amount of fish, as might be expected. However, if, as hypothesised by Green and Burton (1987a), predation on prawns is linked to predation on benthic fish, then a positive correlation between consumption of the two would be expected. This was in fact the case seasonally in 1984 ($r = 0.77$, $P < 0.05$) for the outer zone of their study only (the fast-ice edge and the islands and icebergs with access to open water), but it was not the case in inter-annual comparisons, where there was instead a significant negative correlation ($p < .05$) and a positive correlation between consumption of prawns and pelagic fish (which at $p = .08$ was not statistically significant). The seasonal correlation can be explained by seals moving out of the fjords in winter. This effectively means that they move away from shallow waters into deeper waters and hence away from high densities of *Chorismus* and easily available benthic fish at shallow depths in the Vestfold Hills into lower densities of prawns in the open ocean (Arntz and Gorny 1991) and benthic fish available only at greater depths. To examine the reasons for the negative correlation between prawns and benthic fish between summer seasons requires some interpretation from population data.

The changes in diet of Weddell seals in the Vestfold Hills between years is an important indication that there are fundamental changes occurring in the food resource base that, without directed dietary studies, might otherwise be undetected. The causes of these changes in prey type can be explained in terms of seasonal movements of the seals (Green and Burton 1987a), but explanations for inter-annual differences in movements of the seals within seasons are probably more a reflection of prey ecology than predator ecology.

Green *et al.* (1992) suggested that the difficulties in getting representative counts of Weddell seals from aerial censuses during the moult was due to the different time spent in the water foraging in 'good' and 'bad' food years. Their argument was that, in a good year, locally abundant food could be taken quickly and the animals would return to the ice where they were more likely to be counted. In a bad year the seals spent more time searching for less abundant food and had to travel further out to sea to collect it, resulting in less time on the ice and, therefore, a lower chance of being counted. Green *et al.* (1992) documented an 80% reduction in numbers from aerial seal censuses but suggested that the fall could be attributed to different food status.

Their speculations were based largely on inference from other species. A decrease in the number of chicks of Adélie penguins *Pygoscelis adeliae* at reference breeding groups in the Vestfold Hills between January 1983 and January 1986 was accompanied by a change in the diet of Adélie penguins, with a shift from nearshore euphausiids and benthic/inshore fish to food of pelagic origin (Green and Johnstone 1988). It appeared that Adélie penguins were having to forage further offshore, leading to a decline in reproductive success due to longer foraging times (Green and Johnstone 1988). Throughout the moult in 1983–84, seals occupying inshore ice in the Vestfold Hills also had a high content of pelagic prey in their diet (Green and Burton 1987a). Green *et al.* (1992) therefore postulated that if the foraging times for Weddell seals were also increased, then the amount of time spent on the ice, and therefore the proportion of the population on the ice at any one time, would be less than in a year of high local availability of food.

The present study has added greater weight to that argument. When aerial census counts were low the frequency of pelagic fish in the diet has tended to be high (Figure 22). This relationship was statistically significant ($p < .05$). In addition to pelagic fish being less common in the diet at the time of high counts, prawns also tended to be less common, and they occurred more frequently in the diet when pelagic fish were most important. This suggests that prawns may not be a preferred food item and may not be taken as a by-catch of taking benthic fish, but are instead only taken commonly in bad years, when they are taken opportunistically on the way to and from more distant foraging grounds.

More data are required to detail the relationship between aerial censuses, diet and foraging time. This question has important ramifications for ecosystem monitoring, not only in regard to this major fish predator, but also as a model for estimating the abundance of other ice-breeding seals, particularly the Crabeater seal. This is one area where future research is planned.

Table 6.1. Frequency of occurrence (%) of contents of Weddell seal faecal samples for four summer seasons.

	1983–84 Jan–Mar	1984–85 Nov–Jan	1990–91 Dec–Mar	1991–92 Nov–Feb
Fish	58	69	100	82
(Benthic)			77	45
(Pelagic)			16	28
Crustacean	-	-	53	84
Prawn	72	60	31	31
(*Chorismus*)	39	43	27	20
(*Notocrangon*)	20	20	10	10
Amphipod	11	10	10	19
Isopod	18	14	0	13
Cephalopod*	6	7	3	6
Gastropod	7	10	10	4
Bivalve	-	0	0	2
Polychaete**	-	-	3	16
Sample size	169	82	30	121

*Only octopods were actually identified

**Polychaetes were present but not recognised in 1983–85

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