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Pelagic distribution and numbers of the Antarctic petrel *Thalassoica antarctica* in the Weddell Sea during spring

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Abstract Estimates of the population size of the Antarctic petrel *Thalassoica antarctica* are hampered by its breeding locations in remote nunatak areas of the Antarctic continent. Studies at sea can provide additional information on numbers. Seabird censuses during spring 1992 showed few Antarctic petrels in the western part of the Weddell Sea, but high numbers east of the South Sandwich Islands. The vast majority of the birds occurred in a band of 300 km north to 150 km south of the outer ice edge. Numbers at sea fluctuated in agreement with synchronized colony attendance patterns in the pre-breeding phase and peaked shortly before egg-laying when colonies are completely deserted. In this period, densities of Antarctic petrels in the marginal ice zone suggest that at least 2.7 ± 0.5 million individuals occur in the Weddell Sea. It is likely that similar numbers occur immediately east of the study area. The distribution of the petrels matches the location, but not the size, of known breeding colonies in Dronning Maud Land and Coats Land, which suggests that important colonies in this area remain to be discovered. The observations imply that Antarctic petrels in the Weddell Sea commute over ice a surprisingly large distance of at least 2,000 km for a single pre-breeding visit to the colonies.

Introduction

The Antarctic petrel *Thalassoica antarctica* is one of the least known seabirds of the high Antarctic. Breeding colonies have been found along the coast of the Antarctic continent and in nunatak areas up to 300 km from the coast (Watson et al. 1971). The SCAR Bird Biology Subcommittee has initiated reviews of the breeding distribution and numbers of several Antarctic seabird species (SBBS 1994) as a follow-up to the penguin review of Woehler (1993). For the Antarctic petrel such a colony review (J.A. Van Franeker, F. Mehlum, R.R. Veit and E.J. Woehler, unpublished work) adds up to a breeding population of the order of half a million pairs. This estimate is contradicted by pelagic studies that reported several millions of birds in the Ross Sea (Ainley et al. 1984) as well as the Prydz Bay area (Cooper and Woehler 1993; Woehler 1995; EJ Woehler, personal communication). Off Enderby Land, Veit and Hunt (1991) even estimated a million birds in a single flock. Considering the problems in data collection in remote breeding areas, estimates of numbers at sea can be used instead to estimate population size. This paper discusses the spatial patterns and temporal changes in the distribution of Antarctic petrels in the Weddell Sea in spring and early summer and interprets these data in terms of regional population size.

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Materials and methods

Bird observations were conducted during two research cruises of the RV "Polarstern" in the Weddell Sea (Fig. 1). The European Polarstern Study (EPOS Leg 2, December 1988) included several north–south transects in the western Weddell Sea between the Scotia–Weddell Sea Confluence and closed pack ice (from 57°S to 62°S between 47°W and 49°W). Similar environmental zones, although wider spaced, were covered during "Polarstern's" Southern Ocean Joint Global Ocean Flux Study (SO-JGOFS, October/November 1992) in the eastern Weddell Sea: three return transects were made between the Antarctic Polar Front (47°S) and the pack ice interior (60°S) along the 6°W meridian. These north–south orientated study areas were connected by a single west to east transect of "Polarstern" along the ice edge in early October 1992. Full details on cruise-track, environmental conditions and studies conducted during EPOS are given by Hempel et al. (1989) and Hempel (1993), and those for SO-JGOFS by Bathmann et al. (1994).

Methods for bird counts were described in detail by van Franeker (1992, 1994a) and are summarized here. Bird densities were derived from counts according to the "snapshot method" (Tasker et al. 1984) and not according to the BIOMASS standard (BIOMASS 1992). Differences between the methods need some explanation because they are important in quantitative applications such as population

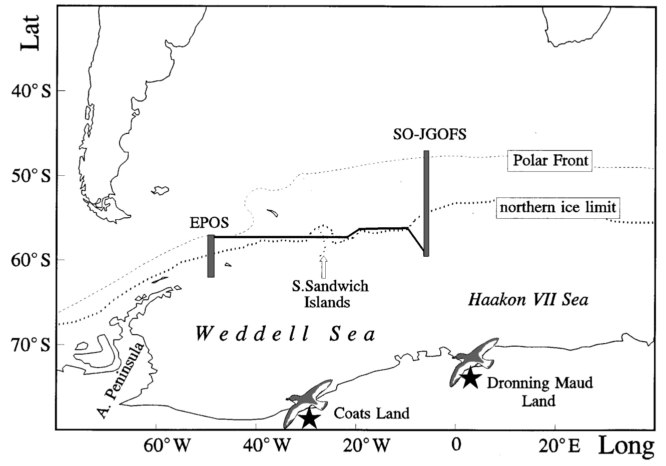


Fig. 1 Western (EPOS) and eastern (SO-JGOFS) study areas in the Weddell Sea and connecting ice-edge transect. *Bird silhouettes* indicate known breeding localities of the Antarctic petrel. In Dronning Maud Land the large Svarthamaren colony and various smaller ones are found between 2°E and 5°E in the Mühlig Hofmann Mountains and Gjelviksfjella. Coats Land has two smaller colonies in the Shackleton Mountains and Theron Mountains

estimates. The methods are the same for stationary birds (sitting on water or on ice): during time-blocks of 10 min birds are counted from a moving ship within a transect band of usually 300-m width. As ship speed is known, a density estimate may be calculated for each 10-min period from the number of birds observed and the area surveyed. The important difference between the methods concerns the method of counting birds in flight. In BIOMASS, the inclusion of all birds that cross the transect in flight results in over-estimated densities because more birds move through the transect during the time of observation than there are present at any particular moment. The snapshot method avoids this bias from movement by including birds in flight only if seen in instantaneous counts of consecutive subsectors of the transect band: a series of snapshots at specific time intervals covers the whole transect area in a photographic manner. Comparative study in the western Weddell Sea in 1988 showed that average density estimates for procellariiform seabirds by snapshot methods were about 45% lower than BIOMASS density estimates (Van Franeker 1994a).

Results of bird counts were grouped into latitudinal zones of half a degree of latitude (30 nautical miles) or according to distances from the ice edge. Average density in a particular zone was generally calculated as the total number of birds divided by the total area surveyed, so without an index of variance. For population estimates, mean densities in latitudinal zones were calculated from densities of individual 10-min counts to supply the standard error of the mean.

Sea-ice cover within the transect area and numbers of icebergs within horizon distance were monitored in association with bird observations (Van Franeker 1989, 1994b). The local position of the ice edge was assessed by a combination of direct observations, satellite pictures, and weekly Navy-NOAA ice maps. Temperature of the surface water was measured continuously from the ship's bow inlet.

Results

In the western Weddell Sea (EPOS) Antarctic petrels occurred in low numbers only: in December 1988 the average density during all 10-min counts ($n = 704$) between 56°S and 62°S was 0.02 individuals per km^2. The species was concentrated in the marginal ice zone with average densities of up to 0.07 birds per km^2 (Fig. 2A) and a tendency for somewhat higher numbers during the transect along 47°W (maximum density of 0.74 birds per km^2 at 61°30′S).

Much higher densities of Antarctic petrels were observed in the eastern Weddell Sea (SO-JGOFS; Fig. 2B). During the repeated north–south transects along 6°W in October and November 1992, the average density for all 10-min counts ($n = 960$) was 1.01 birds per km^2 again with the higher densities concentrated around the marginal ice zone.

The eastward transect between both study areas went along the marginal ice zone, and thus followed the main zone of occurrence of Antarctic petrels (Fig. 3). Counts showed that in early October also, low numbers of Antarctic petrels were characteristic for the western Weddell Sea. West of the South Sandwich Islands (26°30′W) the average density during 115 counts was 0.05 birds per km^2 and even close to the ice edge densities never exceeded 0.26 birds per km^2. East of the South Sandwich Islands, however, Antarctic petrels were always abundant in this zone, with densities ranging from 1 to 7 birds per km^2 (average 3.89 per km^2; 118 counts).

Changes in the distribution and abundances of Antarctic petrels during retreat of the sea ice could be

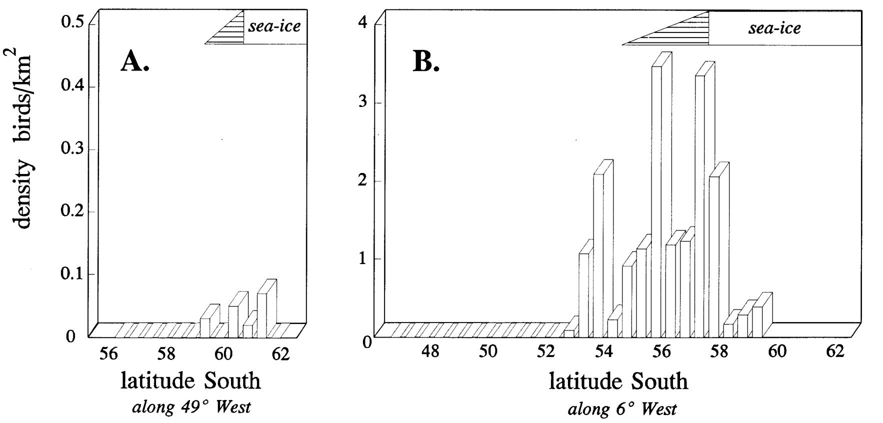
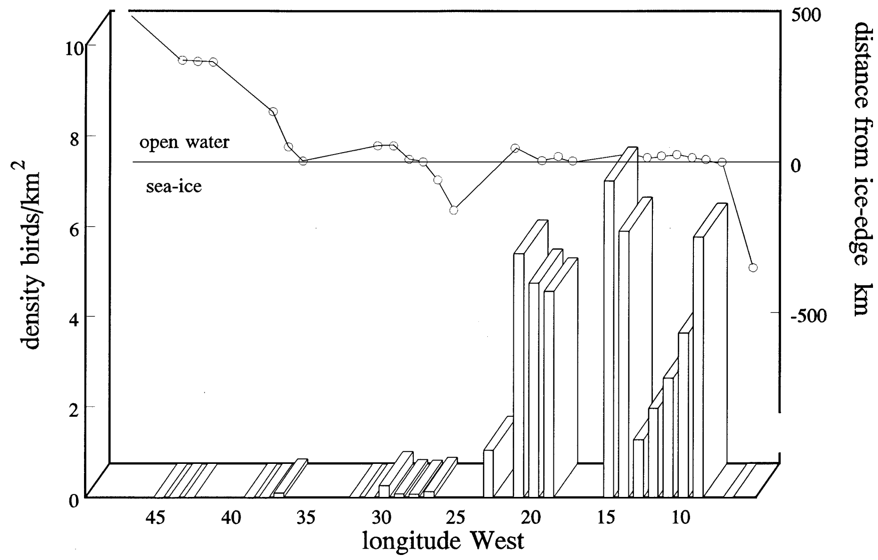


Fig. 2A, B Antarctic petrel average densities along multiple latitudinal transects in the western (**A**: EPOS Leg 2, December 1988; 704 counts) and eastern Weddell Sea (**B**: SO-JGOFS, October/November 1992; 960 counts). Note different *density scales*. Zero density indicated by *contour of bar position on x-axis*; omitted when no data available (e.g. south of 60°S in **B**). Extent of sea ice shown by *horizontal bar in top of graph*, with *hatched part* indicating the retreat of the ice edge during study periods

Fig. 3 Antarctic petrel average densities during single eastward transect along the Weddell Sea ice edge (2–10 October 1992; 233 counts). Zero density indicated by *contour of bar position on x axis*; omitted when no data available. The *line with unfilled circles* shows average distance from the ice edge during counts



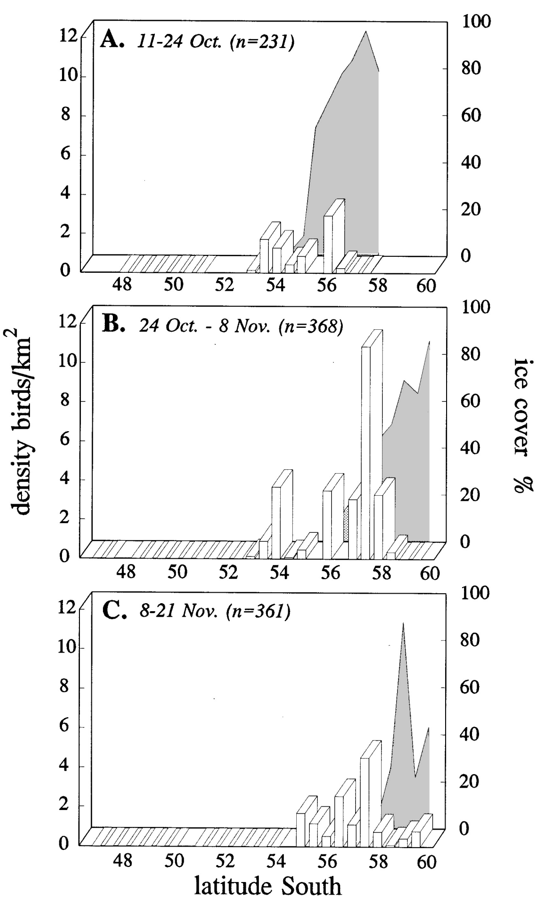


Fig. 4A–C Changes in latitudinal distribution of Antarctic petrels during consecutive transects in the eastern Weddell Sea (along 6°W). Zero density indicated by *contour of bar position on x-axis*; omitted when no data available. *Shaded areas* in background show the average ice cover during counts

analysed for the eastern Weddell Sea. Data were separated into three subsequent time periods (Fig. 4), each containing a full northward and southward voyage along 6°W (only northward in third period). Major concentrations of birds shifted south with the retreating ice edge, with no birds dispersing farther north than 2–3° latitude away from the ice, but there was also a virtual absence in closed pack-ice areas to the south. Average abundance over the whole study area was highest in the middle period (1.80 birds per km^2; 368 counts) and considerably lower in the first (0.55; 231 counts) and last period (0.51; 361 counts).

The association between Antarctic petrels and sea ice in the eastern Weddell Sea is clearly illustrated if 10-min counts are grouped according to the distance from the ice edge at the time of observation (Fig. 5). Peak densities of Antarctic petrels were found close along the ice edge, though considerable changes occurred at relatively short distances. The vast majority of birds occurred in a band of 300 km north to about 150 km south of the ice edge: they thus avoided areas with water temperatures above -1°C as well as closed pack-ice zones.

Discussion

General distribution and abundance

Two series of north–south transects in the western and eastern Weddell Sea plus a single connecting transect are not the ideal survey design to study the distributional pattern of a bird species in this huge area. However, a favourable condition in the case of the Antarctic petrel is that the connecting transect followed its favoured habitat along the ice edge and the literature confirms a more general validity of the observed patterns. Low densities of Antarctic petrels in the western Weddell Sea have been reported by a number of other observers. Joiris (1991) recorded 0.2 birds/km^2 in

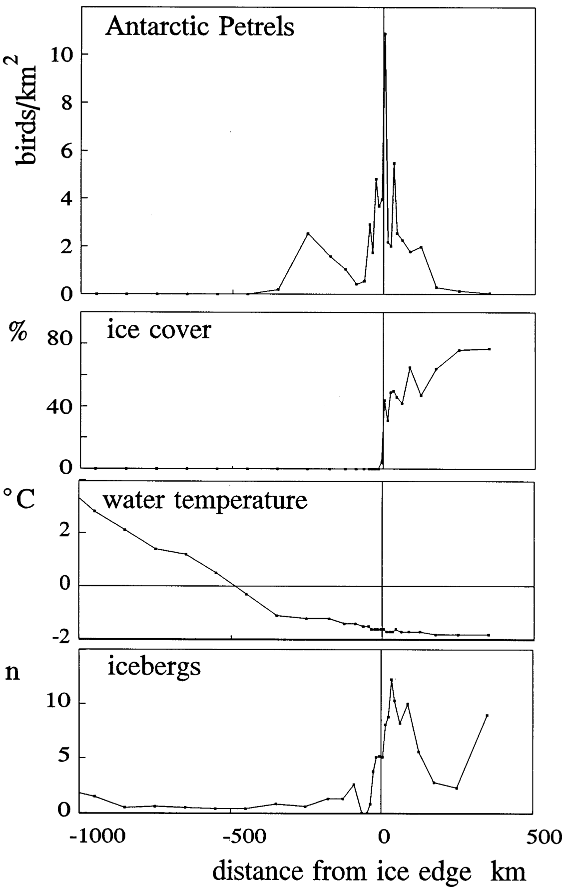


Fig. 5 Antarctic petrel densities and environmental conditions in relation to distance from ice edge during transects along 6°W in October/November 1992 (960 counts). Distance categories were determined on a finer scale when close to the ice edge

October/November in the EPOS study area. Cline et al. (1969) reported an average of 0.3 birds/km^2 during extensive transects over the whole western Weddell Sea in February/March. Similarly, counts by Veit and Hunt (1991) in the central and western Weddell Sea in February resulted in an average density of 0.11 birds/km^2 (RR Veit, personal communication). Near the tip of the Antarctic Peninsula, BIOMASS data yielded too few records of Antarctic petrels to express figures as density estimates (Hunt et al. 1993). All these densities may be considered as upper limits, because no correction for movement of birds was applied (see Introduction). The same may apply to the 3 birds/km^2 recorded in the northwest in February by Zink (1978). However, Ainley et al. (1994) did correct for flux (Spear et al. 1992) but nevertheless reported for the northwestern Weddell Sea (36°W to 50°W) 6–9 Antarctic petrels per km^2 in preferred zones during spring (ice edge), autumn (open water) and winter ($>3/8$ ice cover). The overall conclusion that Antarctic petrels are uncommon in the western Weddell Sea is therefore tentative, as there may be locations or times when more birds do occur.

Comparative data for the eastern Weddell Sea are scarce, but support the evidence for high densities of Antarctic petrels. Plötz et al. (1991) observed large numbers in the marginal ice zone at 56°S–8°E in July and September and Griffiths (1983) noted 4 birds per km^2 in winter near 57°S–10°W. Later in summer, birds concentrated near the continent (Veit and Hunt 1991; Griffiths 1983). The increase in numbers of Antarctic petrels when moving eastward across the South Sandwich Islands is mentioned by Kock and Reinsch (1978) and Thurston (1982), but without quantitative information.

Association with sea ice and icebergs

A close association between Antarctic petrels and sea ice or icebergs has been frequently demonstrated (for example, Falla 1937; Watson et al. 1971; Ainley et al. 1984). According to Griffiths (1983) Antarctic petrels (and snow petrels *Pagodroma nivea*) have adapted to the use of an active flapping flight to exploit ice-covered waters not accessible through soaring flight: the higher energetic costs of flapping would restrict their foraging ranges to within the distribution of sea ice or icebergs. However, from Fig. 5 it is clear that more factors are involved. Icebergs were present all the way north to the Polar Front but Antarctic petrels did not enter an area with surface water warmer than -1°C. In summer in the Ross Sea, Ainley et al. (1984) noted that Antarctic petrels were limited to waters colder than 0.5°C. In all transects, peak numbers of birds were found close along the ice edge, with a dip in numbers 50–100 km to the north, but again with higher numbers farther off (Figs. 4, 5). The pattern cannot be explained by changes in water masses or frontal zones (cf. Fraser and Ainley 1986; Van Franeker 1992). Also, the absence of icebergs in a zone north of the edge only partly coincides with the dip in bird numbers. A possible explanation is that birds within easy flying range of the edge prefer to roost on sea ice, whereas birds farther out do not commute to the ice. Such an explanation is supported by the proportions of stationary birds in different zones: in the outer 50 km of sea ice, 61% of Antarctic petrels roosted on floes, bergs or water; in the first 100 km of open water north of the ice edge this percentage fell to 35%, but farther north it increased to 46% in the 100- to 200-km zone and 62% in the 200- to 300-km zone. So, peak densities of Antarctic petrels in the outer ice zone and a dip in numbers just north of the ice may reflect roosting habits rather than the different suitability of these zones as foraging areas.

Towards the south, Antarctic petrels avoided closed pack-ice conditions in spite of the fact that small leads and open water areas were available (Figs. 4A, B, 5). Because these small open patches were constantly re-freezing, the pattern of open water may have been too unpredictable for the birds. Plötz et al. (1991) observed very few Antarctic petrels in the closed pack ice in this area during winter (July/September): observed numbers only increased in the Maud Rise area where upwelling of warm water induces regular melting of the local pack ice. However, numbers of birds in this area were still very low when compared to those in the marginal ice zone. During the third transect (Fig. 4C), when heavy melting occurred and large open water areas became available thoughout the ice zone, Antarctic petrels were also distributed farther south. Thurston (1982) observed that birds avoided dense pack ice later in summer also.

Fluctuating numbers

The densities of Antarctic petrels along the marginal ice zone in the eastern Weddell Sea fluctuated considerably. Birds that were present at the end of the eastward transect (Fig. 3) had largely disappeared during the first north–south transect from 11 to 24 October (Fig. 4A) with particularly low numbers during the start. During the next transect, from 24 October to 8 November, densities of Antarctic petrels increased threefold (Fig. 4B), only to fall again in the middle of November (Fig. 4C). Although seemingly erratic, these observations conform to the consistent and highly synchronized breeding behaviour of Antarctic petrels (Pryor 1968; Luders 1977; Kamenev 1979). After winter, all potential breeders return to the colonies between 7 and 14 October for site-reclamation, courtship and copulation. Observations by Konovalov (1964) suggest that this is also the case in nunatak colonies far inland. Birds stay at the colony for 2–3 weeks. Around 26 October virtually all have left to return to sea for a pre-laying exodus of about 3 weeks. Colonies remain deserted until 15–20 November when birds return to lay eggs. Low numbers of birds during our third transect can be attributed to a combination of a return to the colonies and the opening up of sea ice to the south of the study area. The good fit between bird numbers at sea and the timing of colony attendance allows further interpretation of the data. Because peak numbers of birds during the second transect coincide with the pre-laying exodus and because relatively few birds stayed in closed pack ice at that time, Antarctic petrel numbers in the marginal ice zone in this period probably represent the distribution of the bulk of the population of nearby breeding colonies.

Weddell Sea population size

A minimum estimate for the Weddell Sea population of Antarctic petrels may thus be derived from densities encountered along the marginal ice zone during the period of the pre-laying exodus. Table 1 gives mean bird densities and standard errors in surface blocks of half a degree latitude by one degree of longitude for both the study areas. From these figures it can be calculated that in the eastern study area, per one-degree longitude sector, about 106,000 $\pm$ 18,000 Antarctic petrels were present during the pre-laying exodus (second transect, Fig. 4B). Numbers were considerably lower during the pre-breeding colony visits (38,000 $\pm$ 10,000; Fig. 4A) and towards the time of egg-laying (46,000 $\pm$ 9,000; Fig. 4C) and averaged at 71,000 $\pm$ 8,000 for the whole study period (Fig. 2B). Compared to these figures, almost negligible numbers were present in the western study area in December 1988: on average less than 600 $\pm$ 200 birds per one-degree longitude sector (Fig. 2A), with a maximum of 2,700 $\pm$ 1,300 on the transect during which Antarctic petrels were most frequently seen. Data from the eastward transect and most of the literature show that these December densities are similar to those in the pre-breeding periods.

The suggestion of a sudden change in bird densities around the South Sandwich Islands (Fig. 3) with low densities to the west and high ones to the east, was confirmed by Kruskal Wallis tests using all counts within a band of half a degree north of the ice edge. A highly significant longitudinal difference exists among the whole Weddell Sea data set ($n = 247$; $\chi^2 = 102$; $P = 0.000$; corrected for ties) but there were no differences within the counts west of 25°W ($n = 95$; $\chi^2 = 0.34$; $P = 0.95$) nor significant differences within the counts east of 25°W ($n = 152$; $\chi^2 = 6.14$; $P = 0.19$). So, an estimate of bird numbers in the whole Weddell Sea (between 0 and 60°W) can be based on the assumption that bird numbers everywhere west or east of 25°W are similar to those encountered in, respectively, the EPOS and SO-JGOFS study areas. Extrapolation of the one-degree longitude estimates in Table 1 then suggests a total population of 2.7 $\pm$ 0.5 million Antarctic petrels in the Weddell Sea between 0 and 60°W. With 95% confidence limits, this population may be estimated at between 1.6 and 3.8 million individuals. Assuming a more gradual east–west decrease in densities would not seriously alter the overall figure. The western Weddell Sea represents less than one percent of the total figure but this could be an underestimate. Since it is also assumed that there are no significant bird numbers within the Weddell Sea pack ice, this estimate must be considered as a minimum.

Breeding colonies

The concentration of Antarctic petrels in the eastern Weddell Sea is in agreement with the locality of known breeding colonies (Fig. 1). No colonies have been discovered on the Antarctic Peninsula or to the south of the Weddell Sea, but several are present along the eastern shore. In Dronning Maud Land there are various colonies on nunataks in Gjelviksfjella (72°S–3°E)

Table 1 Calculations for population estimates of the Antarctic petrel in the Weddell Sea (*Area* the surface area of a 0.5°Lat*1°Long block in km^2; *Counts* the number of 10-min counts; *Dens* ± *SE* mean number of Antarctic petrels per km^2 with standard error. Western data based on all EPOS Leg 2 transects along 47–49°W ($n = 704$; Fig. 2A); eastern data based on the second SO-JGOFS transect along 6°W during the pre-laying exodus ($n = 368$; Fig. 4B). *Sector-density* for a one-degree longitude sector is the average of the mean densities in the latitudinal zones where the species occurred, with standard error derived from the summed variances. Estimates for bird numbers within a one-degree longitude sector obtained by multiplication of *Sector-density* ± *SE* with the sum of surface areas where the species occurred)

		WEST (49°W)		EAST (6°W)	
Lat-S	Area (km^2)	Counts (n)	Dens ± SE (birds/km^2)	Counts (n)	Dens ± SE (birds/km^2)
< 51				100	0
51.5	3843			15	0
52.0	3801			16	0
52.5	3758			8	0
53.0	3716			8	0.12 ± 0.12
53.5	3672			16	0.89 ± 0.24
54.0	3629			17	2.92 ± 2.42
54.5	3585			14	0.07 ± 0.07
55.0	3543			7	0.54 ± 0.36
55.5	3497			0	
56.0	3452			37	3.55 ± 0.47
56.5	3408	41	0	0	
57.0	3363	39	0	9	2.80 ± 0.74
57.5	3317	29	0	41	10.25 ± 3.20
58.0	3272	37	0	42	3.91 ± 1.18
58.5	3226	47	0	18	0.36 ± 0.16
59.0	3180	67	0	8	0
59.5	3134	71	0.04 ± 0.02	12	0
60.0	3086	48	0		
60.5	3040	46	0.04 ± 0.03		
61.0	2993	129	0.02 ± 0.01		
61.5	2954	115	0.09 ± 0.05		
62.0	2899	35	0		
Per one-degree longitude sector:					
Sector-density ± SE			0.04 ± 0.01		2.54 ± 0.43
Σ Area		15200		41679	
Number of birds		578 ± 190		105906 ± 17922	

and the Mühlig Hofmann Mountains (72°S–5°E) (Ohta 1993). The latter area holds by far the largest of all known colonies of the Antarctic petrel: 250,000 pairs breed at Svarthamaren, with non-breeding attendants pushing the total figure to about 820,000 colony-associated birds (Konovalov 1964; Mehlum et al. 1988; Røv et al. 1994; Lorentsen and Røv 1995). Small populations are known to breed even further south in Coats Land on the Theron Mountains (79°S–29°W; Brook and Beck 1972) and the Shackleton Mountains (80°S–30°W; Wright and Wyeth 1971). The nearest known next breeding area is in Enderby Land (51°E), almost 2,000 km further east (Watson et al. 1971). Census figures for all known colonies along the eastern Weddell Sea add up to about 300,000 breeding pairs. Information for the Svarthamaren colony suggests that such a figure represents about 1 million colony-attending individuals (breeding and non-breeding) for the whole area.

The pelagic region covered by this study is actually still west of the main (known) centre of breeding of these birds (Fig. 1). Hunt and Veit (1983) noted that Antarctic petrels were numerous just north of the ice all the way from Enderby Land to the Weddell Sea. It is therefore not unreasonable to assume that the Weddell Sea estimate of 2.7 million birds represents about half of the Dronning Maud Land and Coats Land populations. When similar numbers of birds occur immediately east of the study area in the Haakon VII Sea, the total population then is of the order of 5 million birds.

Because the Antarctic petrel is a long-lived seabird with delayed maturity, not all of the birds at sea will also attend colonies. Differences in estimated bird numbers in the Weddell Sea during the pre-breeding colony visit (1.0 ± 0.3 million birds at sea) and the pre-laying exodus (2.7 ± 0.5 million birds at sea) suggest that about 1.7 million birds (60%) from this area had visited the colonies, whereas approximately 40% of the birds were probably immatures not participating in colony activities. The assumption of similar bird numbers in the Haakon VII Sea leads to an estimate of well over 3 million birds attending colonies in Dronning Maud Land and Coats Land. Thus, there is a clear discrepancy between extrapolations of bird numbers observed at sea and population estimates from known colonies in the area. The figures indicate that there is still an opportunity for some exciting discoveries of colonies in Dronning Maud land and Coats Land.

Long-distance flights

The sheer numbers of Antarctic petrels around the marginal ice zone make it indeed likely that most birds spend the pre-breeding season here rather than in the closed pack ice farther south. The most northerly coasts along the eastern Weddell Sea are all south of 71°S. The combination of the known or possible breeding locations of Antarctic petrels with their spring attendance patterns and main marine foraging areas leads to surprising conclusions on the flying capacities and endurance of these animals. In early October, birds of the eastern Weddell Sea must fly at least 2,000 km (54 → 72°S) over ice to reach their breeding colonies. Here they starve for about 2 weeks to claim sites, court and copulate before flying another 1,800 km (72 → 56°S) back to the marginal ice zone to feed. After mid-November, birds again travel about 1,700 km (57 → 72°S) to breed: females return immediately to the sea after egg-laying and males stay behind for the first incubation shift of about 2 weeks (Van Franeker 1994c; Lorentsen and Røv 1995). Ice retreat during the incubation period gradually reduces the minimum foraging distance to about 200 km in the chick-rearing period (Lorentsen and Røv 1995).

For the Antarctic petrels of Coats Land the situation is even more extreme: in October, flying distances to the marginal ice zone anywhere in the Weddell Sea are in excess of 2,600 km. Unless predictable open water suitable for foraging is available in the Weddell Sea interior, it could be advantageous for these birds at this time of year, to fly about 2,500 km in a westernly direction across the base of the Antarctic Peninsula towards the Bellingshausen Sea. This could be a speculative explanation for the fact that flocks of Antarctic petrels do occur in the Bellingshausen Sea (Tomo 1973) even though no breeding colonies are known anywhere near the area (Watson et al. 1971). In any case, such a potential range of distribution illustrates the great adaptation of Antarctic petrels to life in the Antarctic environment and invites studies into the energetic implications of such a lifestyle on the individual and its breeding performance.

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