Antarctic Science 10 (2): 111–123 (1998)

Seabird distribution and oceanic features of the Amundsen and southern Bellingshausen seas

DAVID G. AINLEY[1], STANLEY S. JACOBS[2], CHRISTINE A. RIBIC[3] and IAN GAFFNEY[4]

[1]*H.T. Harvey and Associates, PO Box 1180, Alviso, CA 95002, USA*
Email: harveyecology@worldnet.att.net
[2]*Lamont-Doherty Earth Observatory, Columbia University, Palisades, NY 10964, USA*
[3]*USGS, Wisconsin Cooperative Wildlife Research Unit, Department of Wildlife Ecology, University of Wisconsin, Madison, WI 53706, USA*
[4]*1021 Greenwich St, San Francisco, CA 94013, USA*

Abstract: We describe the distribution and estimate the abundance of seabirdsin the Amundsen and southern Bellingshausen seas, and attempt to identify the mesoscale and larger ocean and ice features that explain the birds' discontinuous occurrence patterns. Our general objective was to assess if ocean fronts, especially near the continental shelf break, enhance feeding opportunities for top trophic-level predators. A variety of subsurface thermohaline fronts occurred on both sides of the shelf break, at shallower depths from west to east, and with warmer and saltier water on their northern sides. Pack ice overlaid some of these fronts, especially in the Amundsen Sea. Seabirds comprised either an ice group in pack ice or in polynyas, or an open-water group in waters north of the pack. In the Amundsen Sea, bird densities were near 0 birds km^{-2} in waters overlying the continental shelf, an unexplained pattern found previously in the Ross Sea but not repeated in the Bellingshausen Sea (5 birds km^{-2} over the shelf). Both groups were more abundant (densities 3–9 birds km^{-2}) near the frontal zones, the ice edge and the shelf break. In the Amundsen Sea, the distribution of ice-group species was related statistically to proximity of fronts and the pack-ice edge, thermocline slope, and depth of the chlorophyll maximum; water-group distribution was related to distance to the fronts and sea-surface temperature. In the Bellingshausen Sea, distribution of both groups was related to distance to the fronts. Many thousands of petrels, found roosting during daylight on icebergs situated near the shelf break, escaped standard census techniques and, thus, are likely to have diluted positive correlations of avian occurrence patterns with physical features of the environment. While the emperor penguin was seen in high numbers and can dive deep enough to forage within the subsurface fronts, those ocean and food-web processes that apparently affect increased food availability for surface and shallow-diving foragers in the frontal regions remain unclear.

Received 29 May 1997, accepted 24 March 1998

Key words: Antarctica, ocean fronts, pack ice edge, seabird biomass, seabird distribution, Southern Ocean

Introduction

The upwelling of Circumpolar Deep Water (CDW) near the Antarctic continental shelf break has been considered a significant feature in the natural history of certain Antarctic marine organisms, for example the Antarctic krill *Euphausia superba* Dana, which use the upward movement of water to propel planktonic larvae toward the surface (Marr 1962, Mackintosh 1973, Deacon 1984). Recent work to determine krill life cycles and age-class distributions in finer detail has expanded our understanding of why the hydrodynamics at the shelf break are biologically important (e.g. Brinton 1985, 1991, Siegel 1988, Witek *et al.* 1988).

One element of related work has been the apparent association between upper-trophic level predators, such as seabirds, and ocean fronts in the vicinity of the continental shelf break in the Southern Ocean. Ainley & Jacobs (1981) described the physical characteristics and biological importance of the Antarctic Slope Front (ASF) in the Ross Sea, referring to ocean sections that showed elevated seabird density and biomass in conjunction with upwelling CDW along the continental shelf break. Whilst the majority of seabird species present were surface foragers, trophic links were not obvious because prey were not sampled, and there was little physical manifestation of the front near the sea surface. Therefore, Ainley & Jacobs (1981) could not explain why an elevated abundance of seabirds should occur over the front. Even harder to explain was a lack of seabirds over the continental shelf, a habitat that elsewhere attracts seabirds in high densities (e.g. Abrams & Griffiths 1981, Briggs *et al.* 1987, Brown *et al.* 1975, Hunt *et al.* 1990). Marine birds are particularly good indicators of abundant food (e.g., Crawford & Shelton 1978, Glantz & Thompson 1981, Barber & Chavez 1986, Ribic *et al.* 1992, Hunt *et al.* 1991, Furness & Greenwood 1993), so there was little doubt that prey availability was elevated in some way near the ASF. Subsequently, Ainley (1985) and Ichii (1990) showed that seal and whale biomass also were elevated in the vicinity of the ASF in the Ross Sea. In addition, Ainley & Jacobs (1981) noted that the highest densities of emperor penguins *Aptenodytes forsteri* in the pack ice of the Weddell Sea, as described by Cline et al (1969), coincided approximately with the continental slope. Kirkwood & Robertson (1997) have since reported the concentration of foraging emperor penguins at the shelf break off the Indian Ocean coast of Antarctica.

On a cruise near the pack ice edge around East Antarctica and into the Weddell Sea, Veit & Hunt (1991) found a 34% elevation in bird biomass over the continental slope, but did not have access to data that would reveal oceanic fronts. The continental slope is highly variable in breadth and topography, and the ASF often occurs near its shallow end which is poorly charted in many sectors. Ocean frontal structures can be displaced from the shelf break by tens of kilometres, differing in intensity according to location (Jacobs 1991), and probably over time.

In early 1994, an opportunity arose to investigate ocean fronts in the southern Amundsen and Bellingshausen seas, and to determine the coincidence of upper-trophic level predators. Little oceanographic or ornithological work had been conducted previously in these regions, which are typically covered by perennial sea ice at high concentrations (Gloersen *et al.* 1992). At-sea ornithological studies have been completed in the northern Bellingshausen Sea (e.g. Hunt 1982, Wanless & Harris 1988), but few data have been obtained further south.

Methods

Data collection

Observations were made from the research ice-capable ship *Nathaniel B. Palmer*, from 15 February–31 March 1994. On this cruise, we completed a series of meridional sections extending from the continent outward to points well beyond the shelf break (or vice versa) beginning at King Edward VII Peninsula, Marie Byrd Land, *c.* 150°W, passing east along the coast of Ellsworth Land, and ending at Marguerite Bay, Antarctic Peninsula, *c.* 70°W (Fig. 1). Conductivity-temperature-depth (CTD) casts were made at intervals along these sections in order to investigate the ocean structure. Spacing of CTDs was determined in part by bottom depth, with closer spacing over the upper continental slope. Depths were monitored continuously along most of the track using a Precision Depth Recorder. We used the data from eight sections on which bird censuses were sufficiently continuous for analysis. The data from additional sections where shelf-break crossings were made at night are included in our analysis of community structure.

Seabirds were censused and their biomass estimated

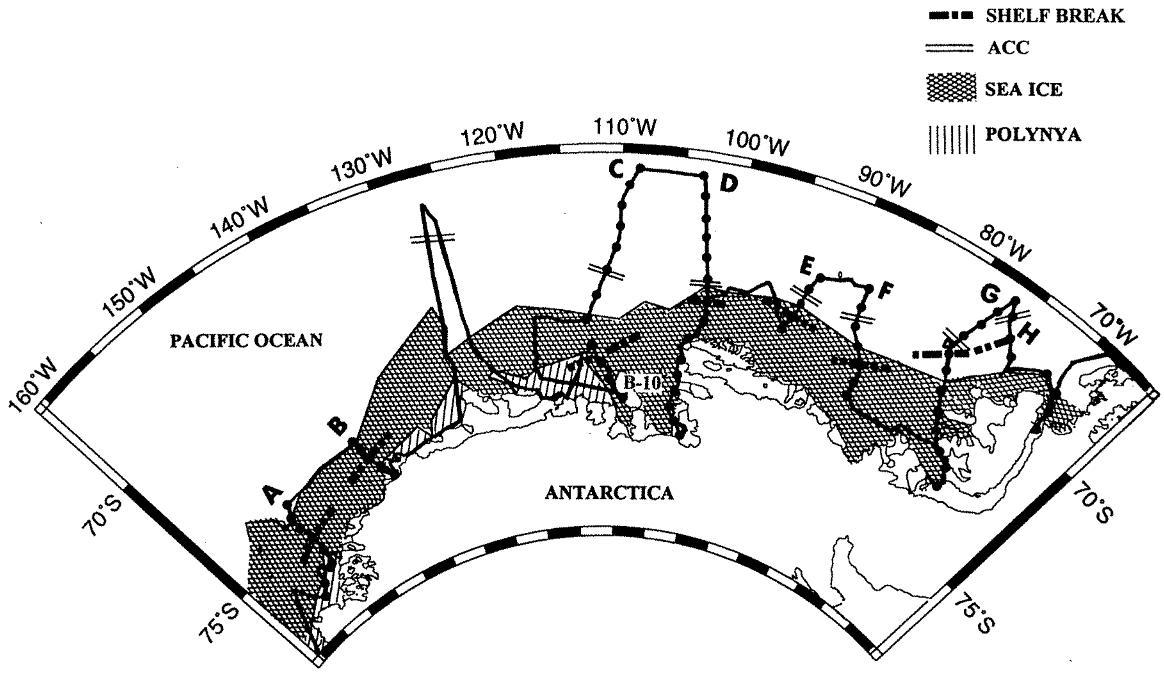

Fig. 1. The Southern Ocean between 160° and 65° W, including the Amundsen (130–100°W) and Bellingshausen (100–60°W) seas, the southern portions of which were largely covered by sea ice during this study. Cruise tracks shown by heavy lines, with dots indicating most CTD station locations for the sections shown in Figs 2 & 3. The sea-ice distribution is from satellite images, reconciled to *in situ* observations. The coastal outline includes islands, ice shelves, and the giant B-10 iceberg, which was located within the track triangle south-east of section C at the time of our survey. Along cruise tracks, the southern boundary of the Antarctic Circumpolar Current (ACC), after Orsi *et al.* (1995), is indicated by a double bar, and approximate location of shelf break is shown by heavy dashed line.

(kg km^{-2}) using the methodology employed in Ainley & Jacobs (1981) and described in detail by Ainley & Boekelheide (1983). Two observers simultaneously scanned, continuously, a 90° area 300 m forward and to the side from the bridge wing (on the side having least glare), 12 m above the sea surface, whenever the ship was underway during daylight. Bird flux, a problem with flying individuals (resulting in more or fewer individuals counted depending on relative speed and direction of bird and ship), was addressed using procedures outlined in Spear *et al.* (1992). This was an especially important correction in the pack ice where the ship frequently changed course and direction relative to wind and bird flight directions. Birds following or attending the ship were ignored unless they first approached the ship through the quadrant being censused; then they were allowed to contribute 0.1 individuals, assuming they had been attracted from at least 1 km away. No censuses were conducted when visibility was <300 m, a condition that proved to be rare. We recorded the position of any icebergs that occurred within 1 km of the ship, and counted any birds roosting on them.

Counts of birds seen over the sea or pack ice were conducted continuously, but partitioned into half-hour intervals (transects), the length of which varied as a function of ship speed and averaged 11 km. If ship speed changed dramatically (25%), we terminated a transect and started a new one.

At the start of each transect (which coincided with the end of the previous one), we logged position, ship course and speed, wind direction and speed, sea condition (Beaufort scale), distance from nearest land, and ice conditions (tenths cover, thickness, type – pack or glacial, age – new, multiyear, aging, floe size etc., see Ainley *et al.* 1993, 1994 for more details). Additional information on sea-ice conditions that existed in this sector a few weeks before our cruise appear in Haas & Viehoff (1994). Because the ship tended to follow leads when in heavy ice, ice conditions were categorized out to 800 m, rather than merely within the 300 m census strip. To examine relationships between seabird occurrence and their environment, we used the CTD, with an attached fluorometer, to determine sea-surface temperature (°C), thermocline depth (the point at which the change in temperature with depth begins to exceed 1°C 10 m^{-1}), thermocline slope (the number of degrees of temperature change in the first 20 m below the top of the thermocline), sea-surface salinity (‰), and depth of the chlorophyll maximum (m). The thermocline characteristics used herein have been used by us and others in the equatorial Pacific, Scotia–Weddell Confluence and California Current, and are explained in detail elsewhere (e.g. Ainley *et al.* 1993, 1994, Allen 1994, Ribic *et al.* 1992). When physical conditions differed between adjacent CTD stations, transects were assigned station averages weighted by linear interpolation between stations. Other variables noted were: bottom depth (m), distance to the ice edge (km), and distance to the edge of the frontal zone (km; see below). The ice edge was defined as a 30 km zone either side of the ice edge, the approximate distance over which "water sky" or "ice blink" could be seen, depending on whether the observer was in ice or open water.

Continuous underway surface and subsurface measurements are difficult to obtain in the ice-dominated environment. The ocean fronts were defined as the zone over which, on the computer-generated contour grid, the -1.0°C isotherm steepened (deepened) and then leveled off at the shelf break. The latter is the point where the relatively shallow continental shelf meets the upper continental slope, typically at 400–600 m depths around Antarctica. The fronts in our computer-generated contouring may cover a wider lateral distance than might have been found with more closely-spaced stations. However, the fronts may generally be wider in this area (e.g. Pollard *et al.* 1995), and their horizontal limits should be defined by detailed studies using horizontal profiling instruments.

Data analysis

Using results from previous studies (Ainley *et al.* 1994), seabird species were categorized into an Ice or Water group. Grouping was confirmed for this cruise for those 11 species that were seen on at least 25 transects (i.e., on 5% of the 525 transects completed) using canonical correspondence analysis (CCA; ter Braak & Prentice 1988). Analyses, using CANOCO 3.10 (ter Braak 1990), followed those of Ainley *et al.* (1994), with results presented as biplots.

Before conducting the CCA, the densities (birds km^{-2}) and biomass (kg km^{-2}) of birds in the two groups were calculated for each transect. Biomass for each transect was calculated by multiplying density by average species mass (data from our own studies, e.g. Ainley *et al.* 1994) and summing the species belonging to the two groups. To address independence of transects, the data were split sequentially into two sets (with an average of 11 km between transects, i.e. the average length of a transect) and analyses repeated. No differences were found in the results of these analyses. All subsequent analyses, therefore, were done on the entire data set. Unless specified otherwise, the standard error is given with density and biomass figures.

The relationships between species-group densities and the environmental variables were determined with regression techniques (Weisberg 1985). Data from the Amundsen and Bellingshausen seas were analysed separately and, again, attention was given only to species seen on at least 25 transects in each habitat (shelf, front, deep ocean). Density in all cases was transformed to log(density + 1) before analysis. The regression analysis was repeated using log(biomass + 1) as the dependent variable.

Analyses were conducted with and without albatrosses to see if these heavy-bodied birds might have had a disproportionate influence on biomass. Since no differences in regression models were found, with or without albatrosses, we did not consider this distinction further. We also conducted analyses with and without Adélie penguins, because many were observed moulting. When moulting, Adélies remain in place in the centre of large ice floes for three to four weeks, with piles of feathers growing around them. Thus, their observed position and the ocean conditions around them might have had less connection with the foraging conditions they sought prior to moulting. However, because results were little different between analyses with or without Adélies, it appears, perhaps, that the ice floes chosen for moulting had not moved far.

We modelled autocorrelation between transects using the semi-variogram (Cressie 1993), fitting spherical semi-variogram models using weighted nonlinear least-squares (S+SPATIALSTATS; Mathsoft 1996). Because of the potential effects of ignoring spatial autocorrelation in regression models having many significant explanatory variables (Cressie 1993), we found candidate models using independent error structures in S+ (Statistical Sciences 1995) and used SAS PROC MIXED (Littell *et al.* 1996) to determine if these variables remained significant when spatial autocorrelation was included in the error structure. Candidate models were those chosen from separate models containing sea-surface temperature, distance to the ice edge, and distance to the front. These three variables were separated into different sets because they were highly correlated ($r > 0.70$ for all pair-wise combinations). We report results only for the models that included spatial autocorrelation in the errors.

Data were analysed on the basis of both density and biomass, but patterns are illustrated only in terms of biomass, the variable used in most biological oceanography studies. Horizontal distances along sections were determined by great circle calculations between stations. The figures also show periods when no census was done due to insufficient daylight (night), less often due to fog, and because of time on oceanographic stations. These periods are referred to on the sections as "night", the duration of which also varied with ship's speed, and the rapidly waning summer light regime. Unfortunately, "night" frequently occurred during crossing of the ice edge, shelf break and oceanic fronts of primary interest.

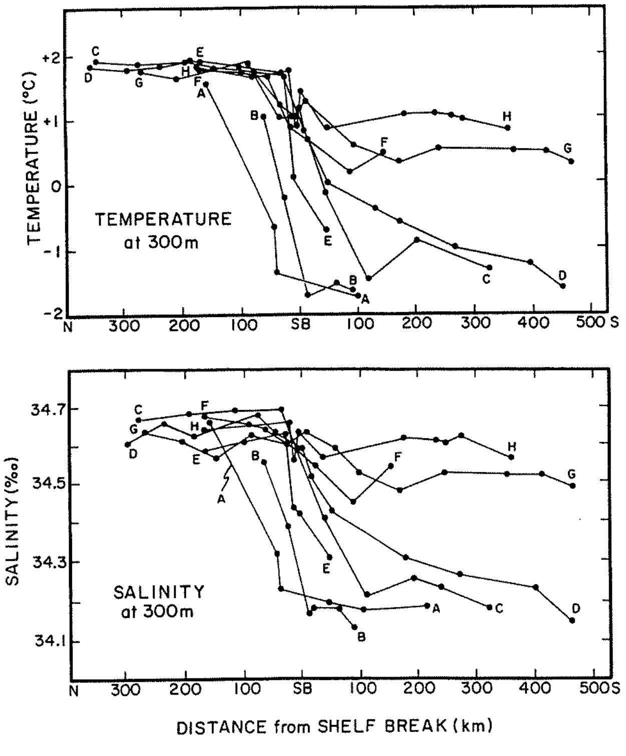

Fig. 2. The temperature and salinity at 300 m on the 8 sections investigated during the cruise. Distances are kilometres from the Continental Shelf Break (SB). Letters refer to the sections in Fig. 1.

Scientific names of birds are given in Appendix 1.

Results

Hydrography

The continental shelf in the Amundsen and Bellingshausen seas is relatively wide, compared to much of Antarctica, but displays a more varied topography than the wide shelves of the Ross and Weddell seas. Station spacing was compromised at times by the unanticipated bathymetry encountered, and by the difficulty of obtaining good-quality soundings while the ship was underway in the pack ice. Nonetheless, on most meridional sections, it was possible to identify the shelf break separating the 500–1000 m depths of the upper continental slope from the generally shallower outer continental shelf. Several stations to the south of the shelf break were occupied in depressions or canyons that were deeper than the outer shelf.

The thermohaline structure of this region is also unusual in comparison to most of the remaining Antarctic continental margin. Aside from the typically perennial sea-ice cover, near-surface summer salinities are relatively fresh, CDW invades the deeper regions of the shelf, and there is little evidence of high-salinity shelf water or bottom water formation (Jacobs & Comiso 1997; see Fig. 2). At some distance off the continental shelf, a divergence occurs between light and variable easterly winds to the south and stronger, more-coherent westerlies to the north. South-east of 140°W, the southern boundary of the Antarctic Circumpolar Current (ACC) swings far to the south (Orsi *et al.* 1995), crossing our sections at the approximate locations shown in Fig. 1.

We referred earlier to an oceanic feature, the Antarctic Slope Front, associated with the upper continental slope and manifested beneath the surface mixed layer along portions of the Antarctic continental margin. The ASF is particularly sharp in the Ross Sea, where it is typically found within 25 km of the shelf break (Jacobs 1991), but ranged from 10–55 km in the sections shown by Ainley & Jacobs (1981). A variety of frontal zones appear in the Fig. 3 sections, more restricted in the vertical and with apparently weaker horizontal thermal gradients (Fig. 2) than in the Ross or Weddell seas. Some of these fronts appear on the outer shelf or extend well north of the shelf break, on occasion coinciding with the southern ACC boundary. In most cases, frontal structure was primarily subsurface, with the warmer and saltier water to the north. Most net flow to the south of these fronts will be toward the west, accompanied by cooling and freshening in that direction (Jacobs & Comiso 1997), as evidenced by the westward deepening of isotherms and isohalines (Fig. 3). We will refer to these frontal zones collectively as "the front."

Species distributions: Amundsen Sea

Section A: along *c.* 150°W, 17–19 February (Fig. 3). Emperor penguins, Adélie penguins and snow petrels were the dominant species, in that order; with only one other individual of another species (a southern giant petrel). No birds were seen in the coastal region of open water, which apparently is maintained by strong, offshore winds. Emperor penguins and snow petrel occurrence peaked at the inner ice edge; Adélie penguins replaced emperor penguins in the outer part of the section. The ice edge was close to the shelf break, with the front extending 100 km to the north.

A large emperor penguin colony occurs to the south-east of this area (77°40'S, 158°30'W; Woehler 1993) and snow petrels and Antarctic petrels nest on nunataks inland from the coast (Watson *et al.* 1971). Since none of these species were breeding at the time of the survey, their presence in the region was not likely to be governed by breeding duties.

Section B: along *c.* 140°W, 20–22 February (Fig. 3). The same species that dominated Section A also dominated this one. Pack ice was densely concentrated all along the section. All species' abundances peaked in the middle of the section, over the shelf break. A relatively sharp front occurred within 50 km north of the shelf break over water depths between 1760 and 2330 m. Nightfall interfered with censusing over the innermost portion of the section, but we saw no birds while cruising along shore east of this section (Fig. 1). A small Adélie penguin colony (100 pairs) exists in this area at Cruzen Island, 64 km from the coast (74°45'S, 140°00'W; Woehler 1993), but no penguins were evident (nor expected at this season).

Between sections B and C, observations along *c.* 127°W (Fig. 1) revealed biomass peaks near and north of the shelf break and, again, few birds over the continental shelf (Ainley 1994).

Section C: along *c.* 110°W, 3–9 February (Fig. 3). This section extended to a point 500 km seaward of the shelf break, unfortunately with a join between two shorter sections over the primary front. Pack ice occurred over the inner 250 km of the section; much of it was new ice that had recently formed over the coastal polynya. "Night" precluded any census over the continental slope, but the section illustrates the typical paucity of birds over the inner continental shelf (inner 150 km of the section). A peak in biomass near station 53, composed of emperor and Adélie penguins and snow petrels, occurred near the landward edge of a depression on the continental shelf. In the middle of the section, about 150 km north of the shelf break, an elevated biomass of seabirds corresponded to the edge of a surface layer, slightly warmer to the north, and more saline to the south. The composition here was dominated numerically by blue petrels and Antarctic prions, which are surface-foraging species.

Section D: along *c.* 104°W, 9–13 March (Fig. 3). Much of this section was covered by new ice, although very heavy multiyear pack existed over the outer shelf and immediately to the west. The continental shelf portion of the track was near the coastline. Unlike sections to the west, Adélie penguins and snow petrels, but also high numbers of Antarctic petrels with a few emperor penguins, occurred along the inner portion of the section. Densities of all four species peaked near the shelf break, located at the southern end of the front. Among open-water species – blue petrels and Antarctic prion mostly – a peak in biomass occurred seaward of the ice edge, at the northern edge of a low-salinity surface feature overlying the front.

Species distributions: Bellingshausen Sea

Section E: along *c.* 95°W, 18–19 March (Fig. 3). This short section showed a high peak in bird biomass (emperor penguins and snow petrels) over the outer shelf. The inner shelf was not accessible due to heavy ice cover (Fig. 1), and the ice edge was crossed in the dark. A slight biomass peak (snow petrels) was most closely aligned with the centre of a two-step front, and with the ice edge. Correspondence with the ice edge, however, might have been an artifact of coincident correspondence with nightfall (the high biomass might have extended well into the front).

Section F: along *c.* 90°W, 20–21 March (Fig. 3). Although perception of the pattern, again, was degraded by occurrence of nightfall (see section E), bird biomass decreased between the ice edge and the shelf break. There were no bird observations made above a weak front about 75 km north of the ice edge. The dominant species on this section was the Adélie penguin, followed by high numbers of emperor penguins, snow petrels and Antarctic petrels. As with section D, some birds occurred over the inner portion of the shelf.

Over open waters there was little evidence of a biological signal, but species composition was altered from that of sections to the west. Here there were many more Antarctic fulmars and cape petrels, more characteristic of the subantarctic. These species breed in low numbers at Peter I Island (Watson *et al.* 1971), near the north end of the section, although they would not have been breeding at the time of the survey. A very small colony of Adélie penguins (50 pairs) exists at that island as well (Woehler 1993).

Section G: along *c.* 80°W, 24–28 March (Fig. 3). The section, most of it near the coastline, traversed a wide continental

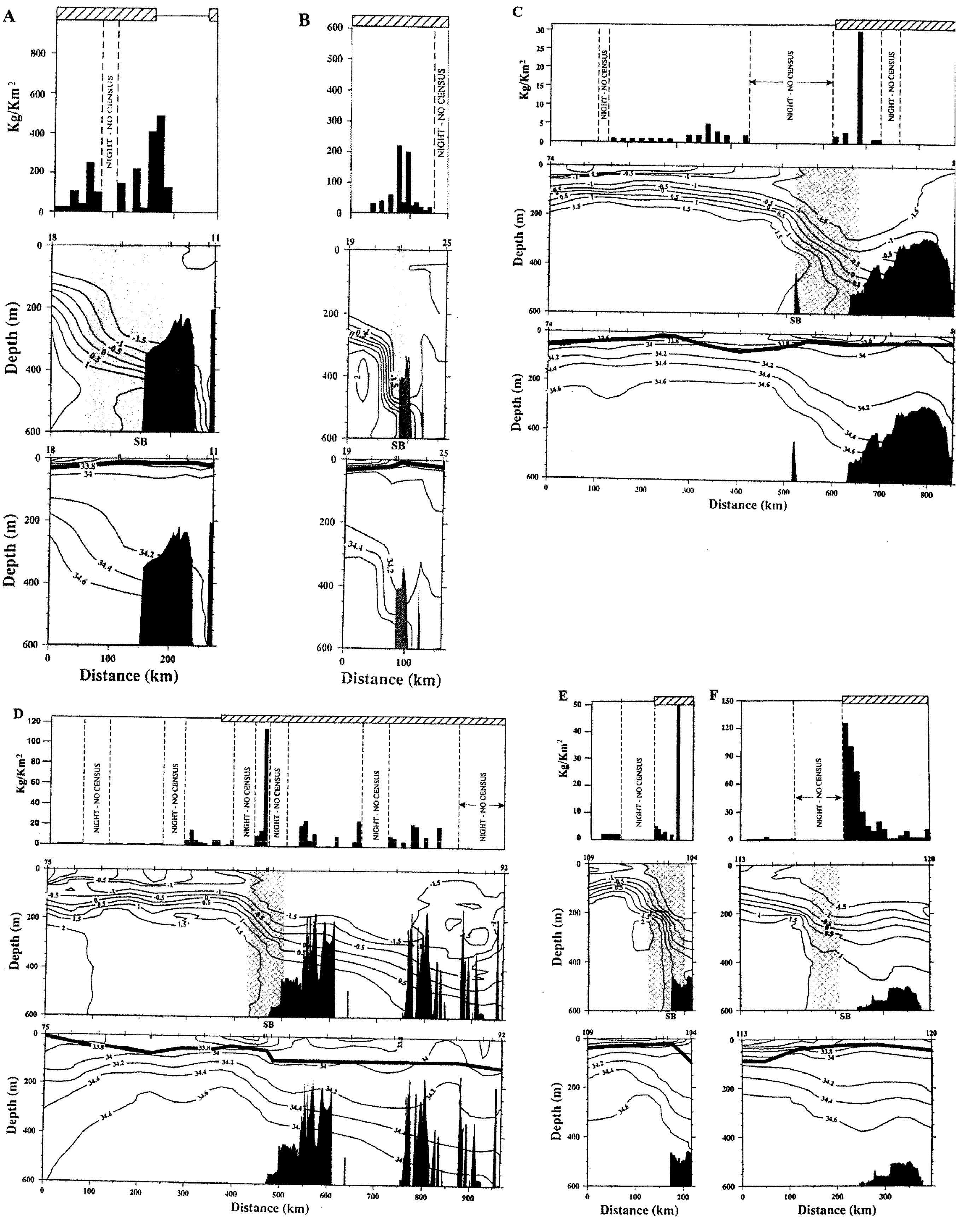

Fig. 3A–F. For caption see opposite.

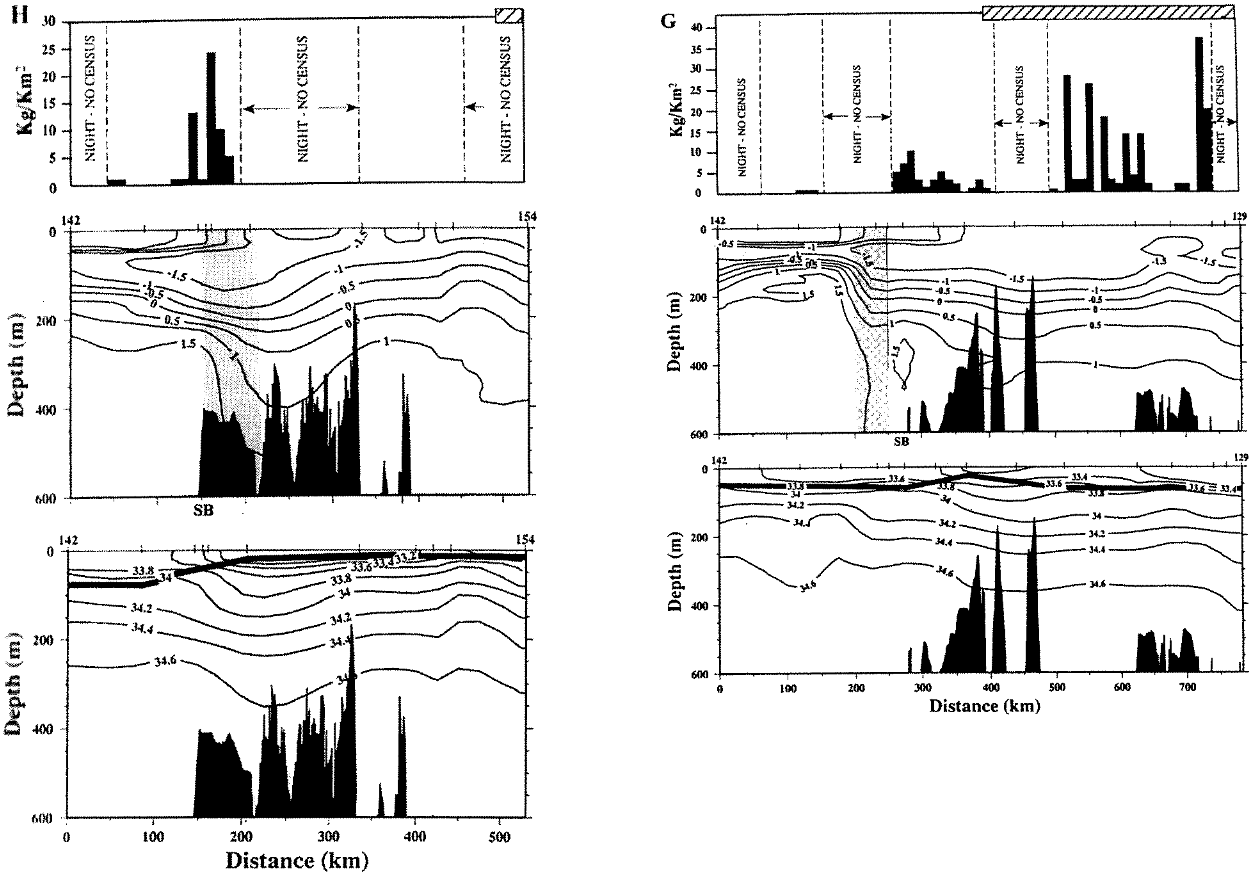

Fig. 3A–~~H~~G. Sections roughly perpendicular to the Antarctic coast (Fig. 1) showing shallow bathymetry (≤ 600 m), temperature (°C) and salinity (‰) structure, depth of the chlorophyll maximum, pack ice extent, and avian biomass. North is to the left; the depth of the chlorophyll maximum is shown by the thick dark line in the salinity sections (bottom); the frontal zone, defined by behaviour of the -1°C isotherm (see Methods), is indicated by light shading in the temperature sections (middle); the sea bottom is shown by black shading in both sections; and pack ice extent is shown by cross-hatching at the top of the biomass section. Positions of the ocean stations are indicated by tick-marks along the top of temperature and salinity section, with inclusive CTD station numbers at left and right. SB, in the middle panel, indicates position of the shelf break.

shelf. Large populations of Adélie penguins breed on islands in the Bellingshausen Sea (although not at the time of this survey; Woehler 1993). The inner portion of the section was heavily populated with these penguins and other birds, but at higher biomass levels than on the southern end of section D. No increased biomass was associated with the pack ice edge. Among the open-water species, elevated biomass occurred near the shelf break. The weak, shallow front 75 km to its north was crossed in darkness.

Section H: along *c.* 75°W, into Marguerite Bay, 28–31 March (Fig. 3). The southern end of this disjointed section lies over the continental shelf and near the coastline. A high biomass peak, composed mainly of Antarctic petrels, occurred near the shelf break and the front, and any subsurface front was weaker or deeper than on sections to the west. However, the shelf was again overlain by well-stratified water in the upper 300 m, and relatively high thermohaline gradients occurred in surface waters just south of the shelf break. Birds were common over these waters.

Effect of icebergs on bird densities

Many icebergs occurred in the study area; 140 were logged within 1 km of the ship during our surveys, mainly west of 90°W. About half of these bergs occurred over the continental shelf and upper continental slope, where many appeared to be grounded, especially near the shallower shelf breaks. Antarctic and snow petrels roosted on a few of these bergs, but rarely in numbers greater than a few dozen (Fig. 4). Similarly, birds roosted on only a small proportion of bergs over the deep ocean, i.e. waters overlying depths >3000 m. In sharp contrast, about a quarter of bergs in waters over the deep continental slope possessed high numbers of roosting petrels (often several thousand per berg). In these areas, these petrels were not abundant on our censuses. Antarctic and snow petrels are known to feed mainly at night (Ainley *et al.* 1992) and, not surprisingly, they inundated the area lighted by the ship's flood-lights when on station. By roosting during the day, these birds escaped our census strip, biased our assessment of densities and relative species composition, and probably diluted stronger connections between birds and the frontal zones. Not surprisingly, Japanese krill trawlers seek and work areas where high numbers of petrels are noted to be roosting on icebergs (Ichii 1990).

Overall density and biomass of seabirds

In the Amundsen Sea, average seabird density and biomass, respectively, was 3.01±0.40 birds and 20.67±4.07 kg km^{-2} ($n = 356$ transects). Density and biomass in waters overlying the shelf was 2.02±0.59 birds and 9.40±3.30 kg km^{-2} (n = 141); overlying the shelf break front, 2.92±0.56 and 43.10±12.40 kg km^{-2} ($n = 101$); and overlying the deep ocean, 4.31±0.88 birds and 14.70±4.45 kg km^{-2} (n = 114).

In the Bellingshausen Sea, average seabird density and biomass, respectively, was 5.68±0.82 birds and 6.15±1.16 kg km^{-2} (n = 169 transects). Density and biomass in waters overlying the shelf was 4.85±1.00 birds and 8.29±1.92 kg km^{-2} ($n = 94$); overlying the shelf break front, 8.88±2.05 birds and 4.66±1.48 kg km^{-2} ($n = 47$); and overlying the deep ocean, 3.11±0.96 birds and 1.48±0.59 kg km^{-2} (n = 28).

Species-group/environmental gradient relationships

The species seen were classified into one of two groups, the Ice- or the Water-Group (Appendix 1). Two environmental axes separated the two groups, with 68.7% and 69.9% of the species-environmental variability explained (Fig. 5). The first axis was composed of ice type (in particular, the contrast between open water and new/old ice), distance to the ice edge, and sea-surface temperature (SST); the second axis was composed of brash ice, distance to the front (defined in Fig. 3), and thermocline depth. In particular, snow petrel and Adélie and emperor penguins were found in new and old ice (all floe sizes), while blue petrel and Antarctic and narrow-billed prions were found over the deep, ice-free ocean. Arctic tern, Antarctic petrel, Antarctic fulmar, and cape petrel were found in brash ice or open water where thermoclines were relatively shallow.

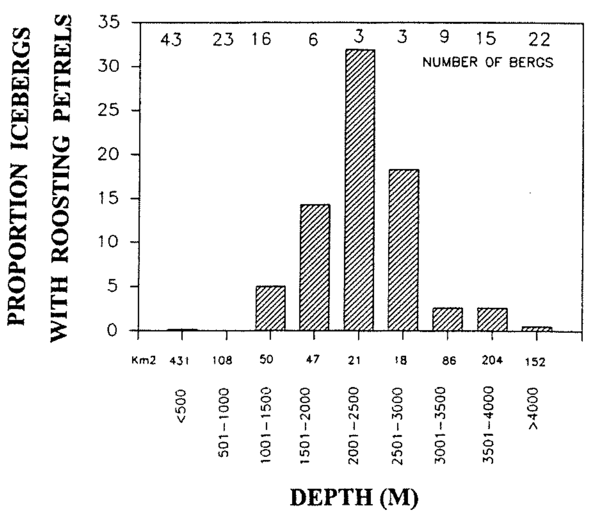

Fig. 4. Percentage of icebergs on which seabirds were roosting as a function of ocean depth (m) and ocean area, weighted by the number of bergs available within each depth category. Many hundreds of additional icebergs were observed beyond the 1 km range included here. A similar compilation of the distribution of minke whales (Ainley 1994) showed a maximum higher on the slope, in the 1000–1500 m band.

Amundsen Sea. The density of Ice-Group species in the Amundsen Sea was related to thermocline slope, depth of the chlorophyll maximum, and distance to the ice edge ($P<0.001$; Table I). Specifically, the Ice-Group was seen at 2.94±0.40 birds km^{-2} within the pack ice ($n = 273$ transects) compared to only 0.03±0.02 birds km^{-2} in open water ($n = 68$ transects; see Fig. 6). Particularly important for explaining occurrence patterns were ice areas having a shallow chlorophyll maximum and steep thermocline slope. These were characteristics of ice-edge waters near to or within the front.

The density of Water-Group species in the Amundsen Sea was related to distance to the front, depth of the chlorophyll maximum, and SST (P < 0.001; Table I). Water-Group species were seen at 2.2±0.8 birds km^{-2} over the deep ocean ($n = 114$), compared to 0.012±0.007 birds km^{-2} ($n = 101$) over

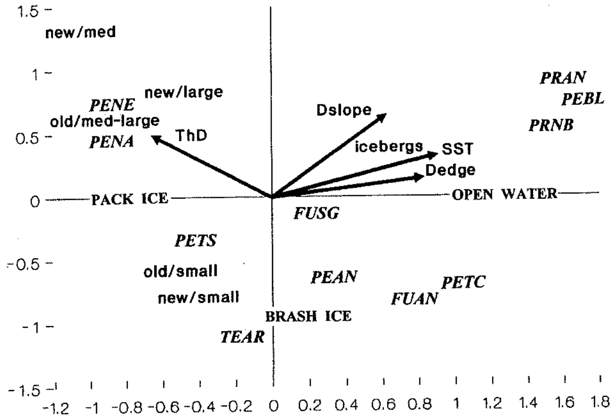

Fig. 5. Biplot from canonical correspondence analysis showing the most common species and significant environmental variables that explained their occurrence patterns, Amundsen and Bellingshausen seas combined. The graph shows positions of species relative to one another as explained by the environmental gradients: ThD = thermocline depth, SST = sea-surface temperature, Dslope = distance to the slope frontal zone, Dedge = distance to the ice edge, and types of ice – new or old refers to new or old ice and small, medium, and large refers to the size of the floes. The vertical axis is positioned according to the relative effect of ThD (a negative relationship to species) and Dslope, SST and Dedge (positive relationships), as well as relationship to ice-to-open water continuum. The horizontal axis is positioned according to how strict are species' relationships to ice or open water; those below the axis are occasionally found in both, with those to the left more so in ice.

the slope, and 0.001±0.001 birds km^{-2} (n = 141) over the continental shelf (Fig. 6). Densities were higher where surface waters were warmer and the chlorophyll maximum was deeper.

The total biomass of Ice-Group species was related to depth of the chlorophyll maximum, thermocline slope, and SST (P <0.001; Table II). Most biomass occurred in cooler waters having a shallow chlorophyll maximum and where the thermocline slope was steep. For the biomass of Water-Group species, the significant variables in the regression model were the same as for density (P <0.001; Table II). The biomass was 0.54±0.17 kg km^{-2} over the deep ocean (n = 114) compared to 0.02±0.01 kg km^{-2} (n = 101) over the slope (Fig. 6). Over the deep ocean, biomass was highest over warmer waters with deeper depths to the chlorophyll maximum.

Bellingshausen Sea. The density of Ice-Group species in the Bellingshausen Sea was related to distance to the front and depth of the chlorophyll maximum (P <0.001). Densities over the continental shelf were 4.70±1.0 birds km^{-2} (n = 94), [illegible]1.31 birds km^{-2} (n = 47) over the front, and 0.65±0.27 birds km^{-2} (n = 28) over the deep ocean (Fig. 6). Densities were higher in areas where the chlorophyll maximum was shallower (Table I). The density of Water-Group species was related to distance to the front and to thermocline slope (P <0.001). Densities were 3.76±1.68 birds km^{-2} (n = 47) within the frontal zone, 0.14±0.06 birds km^{-2} over the continental shelf (n = 94), and 2.46±0.78 birds km^{-2} over the deep ocean (n = 28; Table I, Fig. 6).

For Ice-Group biomass, the significant variable in the regression model, whether or not Adélie penguin was included, was distance to the front (P <0.001; Table II). Most of the biomass occurred over the continental shelf when Adélie penguin was included in the total (mean = 8.15±1.92 kg km^{-2}, n = 94), with a lower second peak within the front (3.24±1.31 kg km^{-2}, n = 47; Fig. 6). When Adélie penguin was removed, biomass over the continental shelf was halved (4.42±0.91 kg km^{-2}), but elsewhere it was little affected. Ice-Group biomass over the deep ocean was low (0.39±0.20 kg km^{-2}, n = 28). For Water-Group biomass, the significant variable in the regression model was thermocline slope (P <0.001).

Discussion

Due to lateness of the survey (after most adults were free of nesting duties) and a paucity of seabird breeding sites along the Marie Byrd Land and Ellsworth Land coasts bordering our study area, we were able to investigate seabird concentrations without the confounding effects of birds commuting between feeding and breeding sites. Therefore, it is more probable that the location of most birds (other than moulting penguins) was where they were finding food, although some might have been resting or prospecting for food. In coastal areas elsewhere, commuting individuals can muddle any perceived tie between environmental variables and related seabird patterns. Only a few at-sea seabird studies of seabird habitat have directly addressed or statistically controlled for locations of breeding colonies (e.g. Briggs *et al.* 1987, Allen 1994, Spear *et al.* 1995), or have been specifically located in areas where breeding colonies are few (e.g. the eastern Weddell–Scotia Confluence: Ainley *et al.* 1993, 1994,

Table I. Seabird densities (birds km^{-2}) as a function of those habitat features that best explained the occurrence patterns of Ice-group and Water-Group species in the Amundsen and Bellingshausen seas. Sample size (number of transects) is shown in parentheses.

Species group	Amundsen Sea			Bellingshausen Sea		
Ice group						
Depth of chlorophyll maximum (m):	0–30	>60		0–40	>40	
	4.8±0.8	0.4±0.1		7.1±0.3	1.3±0.2	
	(131)	(62)		(28)	(86)	
Habitat with respect to ice*:	open water	edge	pack ice			
	0.03±0.02	0.8±0.4	2.9±0.4			
	(68)	(15)	(273)			
Habitat with respect to front*:				shelf	front	ocean
				4.7±1.0	5.1±1.3	0.6±0.3
				(94)	(47)	(28)
Thermocline slope (°C 20 m^{-1}):	1.0–2.0	>2.0				
	0.8±0.3	5.4±0.8				
	(139)	(57)				
Water Group						
Habitat with respect to front*:	shelf	front	ocean	shelf	front	ocean
	0.001±0.001	0.01±0.01	2.2±0.8	0.1±0.1	3.8±1.7	2.5±0.8
	(141)	(47)	(28)	(94)	(47)	(28)
Thermocline slope (°C 20 m^{-1}):				1.0–2.0	>2.0	
				3.1±1.1	0.3±0.1	
				(76)	(93)	

*See Fig. 6 for a more detailed analysis.

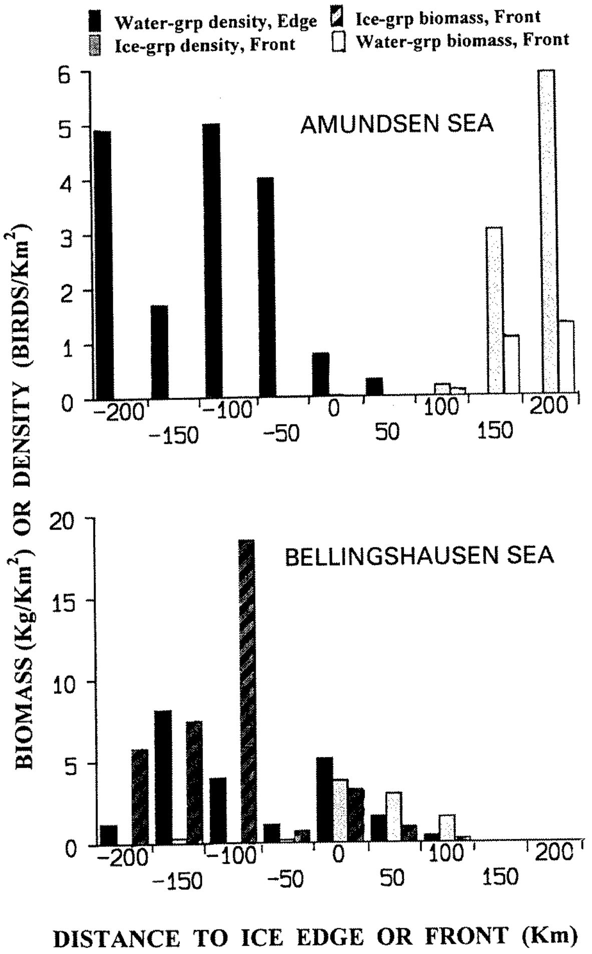

Fig. 6. Seabird density and biomass in the Amundsen and Bellingshausen seas, depending on classification of Ice-Group or Water-Group species, at incremental distance (in kilometres) to either the ice edge or the frontal zone, each designated as 0 on the horizontal axis. Along the horizontal axis (depending on the variable is being measured, i.e. either distance to the front or edge of pack ice), density or biomass is partitioned into smaller spatial units than those presented in Tables I and II. A minus sign on the horizontal axis indicates distances over the shelf or in the pack ice and, accordingly, a positive number indicates distances over the deep ocean or in ice-free waters to the North.

or the eastern equatorial Pacific Ocean: Ribic *et al.* 1992).

Ainley & Jacobs (1981) described an absence of marine birds over the continental shelf of the Ross Sea (<4.0 kg km^{-2}; Ainley 1985) in contrast to high concentrations near the shelf break and slope front (50 to >150 kg km^{-2}; Ainley 1985), a pattern observed also for other upper-trophic level predators (Ainley 1985, Ichii 1990). The degree of contrast differs from the seabird distribution over continental shelves other than Antarctica, where seabird densities are characteristically high, e.g. off northeastern North America (Brown *et al.* 1975), South Africa and Namibia (Abrams & Griffiths 1981), California (Briggs *et al.* 1987, Allen 1994), and the eastern Bering Sea (Schneider 1982, Schneider *et al.* 1986). Ainley & Jacobs (1981) speculated that the lack of upper-trophic level predators over the central Ross Sea continental shelf might be related to its depths, which typically range from 400 to >700 m (i.e. deeper than continental shelves elsewhere). Penguins can dive to appreciable depths (>100 m), and commonly forage in the shallower areas along the Victoria Land coast in the western Ross Sea (Ainley *et al.* 1984). Emperor penguins could reach the subsurface fronts, if not the sea floor near the continental shelf break (e.g. Kooyman & Kooyman 1995). In addition, stronger or convergent currents near the shelf break may help to concentrate ice and zooplankton in the near surface layers (Ichii 1990, Keys *et al.* 1990).

We now have studied bird abundance and occurrence patterns along ocean sections, perpendicular to the coast, around one third of the Antarctic continent, from *c.* 160°E in the western Ross Sea to 70°W in the southern Bellingshausen Sea. In the Ross Sea, breeding populations of seabirds are enormous (several million birds; Ainley *et al.* 1984, Woehler 1993), but in the Amundsen Sea they are small perhaps due to the nearly perennial sea ice and lack of ice-free coastal terrain. Nevertheless, the at-sea distribution of the avifauna of the Amundsen Sea roughly duplicated the Ross Sea pattern, with higher density and biomass (3 birds or 43 kg km^{-2}) near the shelf break and frontal zones, compared to low density and biomass over the shelf (2 birds or 9 kg km^{-2}). Average bird density overall in the Amundsen Sea (3 birds km^{-2}) was five times or two orders of magnitude lower than in the Ross Sea (16 birds km^{-2}; Ainley 1985); average biomass in the Amundsen Sea (21 kg km^{-2}) was half that of the Ross Sea (40 kg km^{-2}; Ainley 1985).

In the Bellingshausen Sea, the average density of seabirds overall was similar to the Amundsen Sea (6 vs 3 birds km^{-2}, respectively), but biomass was a third less than in the Amundsen Sea (6 vs 21 kg km^{-2}). In the Bellingshausen, unlike the Amundsen and Ross seas, density and biomass of birds over the front were not different from values over the continental shelf. Aside from the statistical parameters investigated, this difference may have been related to the proximity of more favorable coastal resources (breeding sites, shallow bays etc.), or to the greater near-surface stratification of the water column over the shelf (Fig. 3). The latter factors could result in a greater concentration of prey. Another factor involved might have been the large numbers of petrels that roosted on icebergs positioned near the shelf break, especially in the Bellingshausen Sea; these birds could not be included in our census totals but, presumably, without the icebergs, we would have encountered them on the sea or sea ice in waters overlying the slope and within the fronts. Overall, seabird density and biomass in both the Amundsen and the southern Bellingshausen Sea were much lower than in the Ross Sea, but were similar to continental shelves elsewhere in the Antarctic, e.g. the Prydz Bay region of the Southern Ocean

Table II. Seabird biomass (kg km^{-2}) as a function of those habitat features that best explained the occurrence patterns of Ice-Group and Water-Group species in the Amundsen and Bellingshausen seas. Sample size (number of transects) is shown in parentheses.

Species group	Amundsen Sea			Bellingshausen Sea		
Ice-Group						
depth of chlorophyll maximum (m):	0–40	>40				
	30.0±6.1	0.4±0.1				
	(231)	(62)				
habitat with respect to front*:				shelf	front	ocean
				8.2±1.9	3.2±1.3	0.4±0.2
				(94)	(47)	(28)
sea-surface temperature (°C):	<-1.0	-1.0–0.5	>0.5			
	27.9±5.5	1.0±0.4	0.01±0.0			
	(260)	(36)	(60)			
thermocline slope (°C 20 m^{-1}):	<1.5	1.5–2.5	>2.5			
	6.8±2.8	3.0±1.05	5.0±12.1			
	(133)	(113)	(110)			
Water-Group						
depth of chlorophyll maximum (m):	0–40	>40				
	0.05±0.01	0.4±0.1				
	(231)	(125)				
habitat with respect to front*:	shelf	front	ocean			
	0.01±0.004	0.02±0.01	0.5±0.2			
	(141)	(101)	(114)			
sea-surface temperature (°C):	<0.1	>0.0				
	0.1±0.01	0.7±0.4				
	(315)	(41)				
thermocline slope (°C 20 m^{-1}):				<1.9	>1.8	
				1.3±0.5	0.2±0.1	
				(74)	(95)	

(Woehler 1997).

Even with the presence of the ice edge, which had a small but measurable effect on the distribution of species' densities in the study area, it was apparent that the presence of fronts influenced seabird distributions the most, both for species that tend to stay in the ice and those that prefer ice-free waters. The frontal effect of the ice edge on seabird densities may have had more to do with it being a habitat boundary, where the Ice- and Water-groups of species reached the edge of their respective habitat and lingered (and accumulated) for a while. Such a phenomenon was apparent in the Bering Sea (Schneider *et al.* 1986) and the Scotia–Weddell Confluence region of the Southern Ocean (Ainley *et al.* 1993, 1994).

To be sure, the oceanic frontal features and the shelf break sometimes covered 130 km of our transect (average gray zone in Fig. 3 is about 80 km), and surface waters were mixed to greater depths than elsewhere where surface frontal features attract seabirds (e.g. Bering Sea; Schneider 1982, Schneider *et al.* 1986). Thus, the elevation in bird densities and biomass was more diffuse as well. In the Amundsen Sea, besides distance to the ice edge, other environmental variables that influenced seabird distributions (shallow chlorophyll maximum and strong thermocline slope) were characteristic of the frontal zone. Owing to our attention to autocorrelation in the statistical analysis, however, distance to the ice edge masked the distance-to-the-front variable.

Individual species responded differently to the front. For example, Adélie penguins preferred to be farther into the pack ice than other Ice-Group species. This preference has been noted in other studies (e.g. Ainley *et al.* 1994 , and references therein), but in the present data set, the fact that the majority of Adélie penguins were moulting, thereby precluding free movement, perhaps diluted the importance of the front to them.

A problematic aspect of the apparent influence of the oceanic front(s) and shelf break on the distributions of surface or near-to-surface predators is the lack of an obvious surface manifestation, as noted also by Ainley & Jacobs (1981) for the Ross Sea. Abundant food must be available at the shelf break. Supporting this contention, and summarizing two decades of catch data, Ichii (1990) noted that Antarctic "krill trawlers target only fishable concentrations" and that most krill trawlers, and whaling vessels, have conducted their operations mainly near the shelf break (see also references cited in the Introduction). Unfortunately, a thorough investigation of trophic links, including organisms other than krill, remains to be undertaken near the Antarctic continental shelf break. Recent work on emperor penguins sheds some light on why a more complete trophic study would be of interest. Using satellite transmitters and time-depth recorders, Kirkwood & Robertson (1997) found that these birds could reach close to the bottom at the shelf break, which in the

Southern Ocean tends to have depths shallower than at points further landward or seaward. By far the deepest diving birds (to depths of 500 m), these penguins are not known as krill predators (e.g. Klages 1989, Ainley *et al.* 1992). Therefore, shelf-break processes must concentrate other zooplankton, as well as the fish and squid eaten by emperor penguins and other Antarctic seabirds.

Acknowledgements

Logistical support was provided by the crew of the *Nathaniel B. Palmer* and personnel of Antarctic Support Associates. Several shipboard colleagues were instrumental in obtaining the CTD and bathymetric data. The manuscript benefited from critical comments by N. Harrison, G. Hunt Jr., H. Keys, F. Mehlum, L. Spear, R. Veit and E. Woehler. Our research was supported by NSF/DPP grants 94-00809 (DGA) and 94-18151 (SJ). Contribution 5781 of the Lamont-Doherty Earth Observatory of Columbia University.

References

ABRAMS, R.W. & GRIFFITHS, A.M. 1981. Ecological structure of the pelagic seabird community in the Benguela Current region. *Marine Ecology-Progress Series*, **5**, 269-277.

AINLEY, D.G. 1985. The biomass of birds and mammals in the Ross Sea, Antarctica. *In* SIEGFRIED, W.R., CONDY, P.R. & LAWS, R.M., *eds. Antarctic nutrient cycles and food webs*. Berlin: Springer-Verlag, 498-515.

AINLEY, D.G. 1994. Autumn distribution of marine birds and mammals in the Amundsen and Bellingshausen seas. *Antarctic Journal of the United States*, **29**(5), 118-119.

AINLEY, D.G. & R.J. BOEKELHEIDE. 1983. An ecological comparison of oceanic seabird communities of the South Pacific Ocean. *In* SCHREIBER, R.W., *ed. Tropical seabird biology. Studies in Avian Biology*, **8**, 2-23.

AINLEY, D.G. & JACOBS, S.S. 1981. Affinity of seabirds for ocean and ice boundaries in the Antarctic. *Deep-Sea Research*, **28A**, 1173-1185.

AINLEY, D.G., O'CONNOR, E.F. & BOEKELHEIDE, R.J. 1984. Ecology of seabirds in the Ross Sea, Antarctica. *American Ornithologists' Union, Monograph*, No. 32, 79 pp.

AINLEY, D.G., RIBIC, C.A. & SPEAR, L.B. 1993. Species-habitat relationships among Antarctic seabirds: a function of physical and biological factors? *Condor*, **95**, 806-816.

AINLEY, D.G., RIBIC, C.A. & FRASER, W.R. 1992. Does prey preference affect habitat choice in Antarctic seabirds? *Marine Ecology-Progress Series*, **90**, 207-221.

AINLEY, D.G., RIBIC, C.A. & FRASER, W.R. 1994. Ecological structure among migrant and resident seabirds of the Scotia–Weddell Confluence region. *Journal of Animal Ecology*, **63**, 347-364.

ALLEN, S.G. 1994. *The distribution and abundance of marine birds and mammals in the Gulf of the Farallones and adjacent waters, 1985–1992*. PhD thesis, University of California, Berkeley. 300 pp. [Unpublished.]

BARBER, R. & CHAVEZ, F.P. 1986. Ocean variability in relation to living resources during the 1982–1983 El Niño. *Nature*, **319**, 279-285.

BRIGGS, K.T., TYLER, W. B., LEWIS, D.B. & CARLSON, D.R. 1987. Bird communities at sea off California: 1975 to 1983. *Studies in Avian Biology*, No. 11. 74 pp.

BRINTON, E. 1985. The oceanographic structure of the eastern Scotia Sea. III. Distributions of euphausiid species and their developmental stages in 1981 in relation to hydrography. *Deep-Sea Research*, **32**, 1153-1180.

BRINTON, E. 1991. Distribution and population structures of immature and adult *Euphausia superba* in the western Bransfield Strait region during the 1986–87 summer. *Deep-Sea Research*, **38**, 1169-1193.

BROWN, R.G.B., NETTLESHIP, D.N., GERMAIN, P., TULL, C.E. & DAVIS, T. 1975. *Atlas of eastern Canadian seabirds*. Ottawa: Canadian Wildlife Service, 220 pp.

CLINE, D.R., SINIFF, D.B. & ERICKSON, A.W. 1969. Summer birds of the pack ice in the Weddell Sea, Antarctica. *Auk*, **86**, 701-716.

CRAWFORD, R.J.M. & SHELTON, P.A. 1978. Pelagic fish and seabird interrelationships off the coasts of Southwest and South Africa. *Biological Conservation*, **14**, 85-109.

DEACON, G.E.R. 1984. Water movements and Antarctic krill. *Journal of Crustacean Biology*, **4** (Special Number 1), 13-15.

FIENBERG, S.E. 1980. *The analysis of cross-classified categorical data*. 2nd edition. Cambridge, MA: The MIT Press, 198 pp.

FRASER, W.R . & AINLEY, D.G. 1986. Ice edges and seabird occurrence in Antarctica. *BioScience*, **36**, 258-263.

FURNESS, R.W. & GREENWOOD, J.J.D. *eds*. 1993. *Birds as monitors of environmental change*. London: Chapman Hall. 356 pp.

GLANTZ, M.H. & THOMPSON, J.D. *eds*. 1981. *Resource management and environmental uncertainty: lessons from coastal upwelling fisheries*. New York: Wiley, 491pp.

GLOERSEN, P., CAMPBELL, W. J., CAVALIERI, D.J., COMISO, J.C., PARKINSON, C.L. & ZWALLY, H.J. 1992. *Arctic and Antarctic sea ice, 1978–1987: satellite passive-microwave observations and analysis*. NASA SP-511. Washington, DC: National Aeronautics & Space Administration, 206 pp

HANEY, J.C. 1986. Seabird aggregation at Gulf Stream frontal eddies. *Marine Ecology-Progress Series*, **28**, 279-285.

HUNT JR, G.L. 1982. Distribution and abundance of marine birds in the Ross and Bellingshausen seas. *Antarctic Journal of the United States*, **17**(5), 179.

HUNT JR, G.L., HEINEMANN, D., VEIT, R.R., HEYWOOD, R.B. & EVERSON, I. 1990. The distribution, abundance and community structure of marine birds in southern Drake Passage and Bransfield Strait, Antarctica. *Continental Shelf Research*, **10**, 243-257.

HUNT JR, G.L., PIATT, J.F. & ERIKSTAD, K.F. 1991. How do foraging seabirds sample the environment? *Congressus Internationalis Ornithologica*, **Acta XX**, 2272-2279.

ICHII, T. 1990. Distribution of Antarctic krill concentrations exploited by Japanese krill trawlers and minke whales. *Proceedings NIPR Symposium on Polar Biology*, **3**, 36-56.

JACOBS, S. 1991. On the nature and significance of the Antarctic Slope Front. *Marine Chemistry*, **35**, 9-24.

JACOBS, S. & COMISO, J.C. 1997. Climate variability in the Amundsen and Bellingshausen seas. *Journal of Climate*, **10**, 697-709.

JEHL JR, J.R. 1974. The distribution and ecology of marine birds over the continental shelf of Argentina in winter. *Transactions of the San Diego Society of Natural History*, **17**(16), 217-234.

KEYS, H.J.R., JACOBS, S.S. & BARNETT, D. 1990. The calving and drift of iceberg B-9 in the Ross Sea, Antarctica. *Antarctic Science*, **2**, 243-257.

KIRKWOOD, R. & ROBERTSON, G. 1997. The foraging ecology of female emperor penguins in winter. *Ecological Monographs*, **67**, 155-176.

KLAGES, N.T.W. 1989. Food and feeding ecology of emperor penguins in the eastern Weddell Sea. *Polar Biology*, **9**, 385-390.

KOOYMAN, G.L. & KOOYMAN, T.G. 1995. Diving behavior of emperor penguins nurturing chicks at Coulman Island, Antarctica. *Condor*, **97**, 536-549.

Marr, J.S.W. 1962 The natural history and geography of the Antarctic krill (*Euphausia superba* Dana). *Discovery Reports*, **32**, 33-464.

Mackintosh, N.A. 1973. Distribution of post-larval krill in the Antarctic. *Discovery Reports*, **36**, 95-156.

Orsi, A.H., Whitworth iii, T. & Nowlin Jr, W.D. 1995. On the meridional extent and fronts of the Antarctic Circumpolar Current. *Deep-Sea Research*, **42**, 641-673.

Pollard, R.T., Read, J.F., Allen, J.T., Griffiths, G. & Morrison, A.I. 1995. On the physical structure of a front in the Bellingshausen Sea. *Deep-Sea Research*, **42**, 955-982.

Ribic, C.A., Ainley, D.G. & Spear, L.B. 1992. Effects of El Niño and La Niña on seabird assemblages in the Equatorial Pacific. *Marine Ecology-Progress Series*, **80**, 109-124.

Rumboll, M.A.E & Jehl Jr, J.R. 1977. Observations on pelagic birds in the South Atlantic Ocean in austral spring. *Transactions of the San Diego Society of Natural History*, **19**(1), 1-16.

Schneider, D.C. 1982. Fronts and seabird aggregations in the southeastern Bering Sea. *Marine Ecology-Progress Series*, **10**, 101-103.

Schneider, D.C., Hunt Jr, G.L. & Harrison, N.M. 1986. Mass and energy transfer to seabirds in the southeastern Bering Sea. *Continental Shelf Research*, **5**, 241–257.

Siegel, V. 1988. A concept of seasonal variation of krill (*Euphausia superba*) distribution and abundance west of the Antarctic Peninsula. *In* Sahrhage, D., *ed. Antarctic ocean and resources variability.* Heidelberg Berlin: Springer-Verlag, 219-230.

Smith Jr, W.O. & Nelson, D.M. 1985. Phytoplankton bloom produced by a receding ice edge in the Ross Sea: spatial coherence with the density field. *Science,* **227**, 163-166.

Spear, L., Nur, N. & Ainley, D.G. 1992. Estimating absolute densities of flying seabirds using analysis of relative movement. *Auk*, **109**, 385-389.

Spear, L.B., Ainley, D.G., Nur, N. & Howell, S.N.G. 1995. Population size and factors affecting at-sea distribution of four endangered procellarids in the tropical Pacific. *Condor*, **97**, 613-638.

Statistical Sciences. 1995. *S-PLUS, guide to statistical and mathematical analysis, version 3.3*. Seattle, WA: StatSci.

ter Braak, C.J.F. 1990. *Update notes: CANOCO Version 3.10.* Wageningen: Agricultural Mathematics Group.

Ter Braak, C.J.F. & Prentice, I.C. 1988. A theory of gradient analysis. *Advances in Ecological Research*, **18**, 271-317.

Veit, R.R. & Hunt Jr, G.L. 1991. Broadscale density and aggregation of pelagic birds from a circumnavigational survey of the Antarctic ocean. *Auk*, **108**, 790-800.

Wanless, S. & Harris, M.P. 1988. Seabird records from the Bellingshausen, Amundsen and Ross seas. *British Antarctic Survey Bulletin*, No. 81, 87-92.

Watson, G.E, Angle, J.P., Harper, P.C., Bridge, M.A., Schlatter, R.P., Tickell, W.L.N., Boyd, J.C. & Boyd, M.M. 1971. Birds of the Antarctic and subantarctic. *Antarctic Map Folio Series*, Folio 14. Washington, DC: American Geographical Society.

Weisberg, S. 1985. *Applied linear regression.* 2nd edition. New York: Wiley, 324 pp.

Witek, Z., Kalinowski, J. & Grelowski, A. 1988. Formation of Antarctic krill concentrations in relation to hydrodynamic processes and social behaviour. *In* Sahrhage, D., *ed. Antarctic ocean and resources variability.* Berlin: Springer-Verlag, 237-244.

Woehler, E.J. 1993. *The distribution and abundance of Antarctic and subantarctic penguins*. Cambridge: Scientific Committee for Antarctic Research, 76 pp.

Woehler, E.J. 1997. Seabird abundance, biomass and prey consumption within Prydz Bay, Antarctica, 1980/1981–1992/1993. *Polar Biology*, **17**, 371-383.

Appendix 1. Species of birds seen in the ice and water groups, with abbreviations used in various figures.

Common name	Latin name	Abbreviation
Ice-Group		
emperor penguin	*Aptenodytes forsteri*	PENE
Adélie penguin	*Pygoscelis adeliae*	PENA
Antarctic fulmar	*Fulmarus glacialoides*	FUAN
snow petrel	*Pagodroma nivea*	PETS
Antarctic petrel	*Thalassoica antarctica*	PEAN
Antarctic tern	*Sterna vittata*	TEAN
Arctic tern	*S. paradisaea*	TEAR
South Polar (McCormick's) skua	*Catharacta maccormicki*	SKMA
Water-Group		
chinstrap penguin	*Pygoscelis antarctica*	PENC
gray-headed albatross	*Diomedea chrysostoma*	ALGH
black-browed albatross	*D. melanophris*	ALBB
light-mantled sooty albatross	*Phoebetria palpebrata*	ALLS
southern giant fulmar	*Macronectes giganteus*	FUSG
white-chinned petrel	*Procellaria aequinoctialis*	PETW
cape petrel	*Daption capense*	PETC
white-headed petrel	*Pterodroma lessoni*	PETH
Kerguelen petrel	*P. brevirostris*	PETK
blue petrel	*Halobaena coerulea*	PETB
Antarctic prion	*Pachyptila desolata*	PRAN
narrow-billed prion	*P. belcheri*	PRNB
Wilson's storm-petrel	*Oceanites oceanicus*	STWI
kelp (Dominican) gull	*Larus dominicanus*	GUDO