Changes in seabird species abundance near South Georgia during a period of rapid change in sea surface temperature

G.L. HUNT Jr 1, J. PRIDDLE 2, M.J. WHITEHOUSE 2, R.R. VEIT 1,2 and R.B. HEYWOOD 2

1Department of Ecology and Evolutionary Biology, University of California, Irvine, CA 92717, USA
2British Antarctic Survey, NERC, High Cross, Madingley Road, Cambridge CB3 0ET, UK

Abstract: During a three month research cruise near the island of South Georgia, sea surface temperature (SST) increased from c. 2°C to over 4°C. Satellite derived SST show that this corresponded to a rapid southward and eastward shift of isotherms in the northern Scotia Sea, which could have resulted from changes in the wind field. At the same time, observation from the ship of seabirds close to the island indicated changes in the abundance of some non-resident species, whereas resident breeders from South Georgia, such as black-browed albatrosses (Diomedea melanophris) and prions (Pachyptila spp.) which were foraging locally, were present at consistent density in both halves of the survey. Blue petrels (Halobaena caerulea) left the area after breeding, so were associated only with the low water temperatures during the first part of the cruise. In contrast, great shearwaters (Puffinus gravis) and soft-plumaged petrels (Pterodroma mollis) migrated into the area later in the survey. These birds were almost certainly non-breeders which were feeding in the warmer water which had moved towards the island.

Received 14 November 1990, accepted 21 March 1991

Key words: albatross, petrel, sea surface temperature, seabird distribution, South Georgia

Introduction

The spatial distribution of marine birds at sea is influenced over a variety of scales by the distribution of water masses and other hydrographic features (see Brown 1980, Hunt & Schneider 1987, and Hunt 1990 for reviews). Temporal variation in the use of specific areas by marine birds is less well documented due to inadequate sampling. Available data show that variation in seabird distribution between seasons is substantial (e.g. Bering Sea: Hunt et al. 1981, California Current: Briggs & Chu 1986, Briggs et al. 1987), as is variation between different stages of tidal cycles (e.g. Vermeer et al. 1987, Brown & Gaskin 1988). However, evidence for responses by marine birds to changes in oceanographic conditions at the scale of days to weeks is largely undocumented (but see Hunt & Harrison 1990). In this paper we examine variation in the abundance of marine birds in the vicinity of the island of South Georgia during a three month oceanographic study. Within this period, sea surface temperature changed by 2°C, and abundances of various seabird species were correlated with changes in water temperature.

Methods

Study Area

Data are derived from a survey undertaken close to South Georgia (54°20'S, 36°40'W), situated in the northern Scotia Sea. The island lies well to the south of the mean position of the Antarctic Polar Front, and is thus located in the Antarctic Circumpolar Current. In summer, sea-surface temperatures usually rise to 3.5–6°C from their average winter values of 0–1°C. Meanders in the surface features of the frontal structure of the Antarctic Circumpolar Current are well documented for the Scotia Sea and for the Drake Passage to the west (Legeckis 1977, Gordon 1988). These meanders may result in comparatively rapid changes in the sea-surface temperature around an island like South Georgia.

South Georgia and its associated islands are the breeding site for 25 species of seabird, most of which feed in the waters close to the island during the breeding season (Croxall & Prince 1980). These waters may also be visited by birds which breed at locations far from South Georgia, such as Tristan da Cunha and islands in the subantarctic Indian Ocean (Prince & Croxall 1983).

Spatial coverage

Observations were made during a research cruise from 27 December 1985 to 22 February 1986. The cruise consisted of two parts which differed markedly in their character, although systematic bird observations and oceanographic measurements are available for both parts. The first was a study of marine microbial dynamics and was conducted along a small number of short transects across the shelf-slope-break to the northeast of Bird Island, at the western end of the main island of South Georgia (Fig. 1a). The second part formed the seaborne component of a study of the relationship between seabirds breeding at Bird Island, and their principal prey, Antarctic krill Euphausia superba. A larger area was covered
during which we conducted a series of transects radiating from Bird Island (Fig. 1b). Some of the radial transects visited areas covered during the first part of the cruise.

**Physical oceanographic measurements**

Physical data were obtained on board ship from two sources. Vertical temperature profiles were measured underway using expendable bathythermographs (XBT, T-4 and T-7, Sippican Corporation). Temperatures from a platinum resistance thermometer, situated in the ship's pumped seawater system close to the hull intake (nominally 3 m depth), were logged continuously on a microcomputer. During the first part of the cruise, detailed vertical profile data were obtained on station with a Neil Brown Mk 3 CTD probe, which was used to calibrate both the XBTs and surface temperature sensor.

A larger-scale view of the physical environment was obtained from satellite remotely-sensed images of sea-surface temperature. These were obtained as charts of weekly mean temperature distribution for the world ocean, published by NOAA-NESDIS and derived from data from the Advanced Very High Resolution Radiometer (AVHRR) on the TIROS satellites. These data have a temperature resolution of better than 0.5°C, and are plotted as surface isotherms of weekly mean temperature. The raw data, with a spatial resolution of 2 x 2 km, are gridded on 1 x 1 degree latitude-longitude. We compared the NOAA satellite data with our shipborne measurements, and found there to be good correspondence between the two. The resemblance between bulk temperature in the upper mixed layer and radiometric skin temperature depends on the surface skin effect, which is affected by humidity and the temperature gradient between sea and atmosphere (see discussion in Hepplewhite 1989).

**Observation methods**

We conducted a continuous survey of seabirds from the ship, with the observer being positioned on one wing of the bridge, c. 10 m above the sea-surface and on whichever side of the ship offered the better visibility. Ship speed was generally 8–11 knots (15–20 km h⁻¹) All birds in a 90° arc from the bow to the beam, and to a distance of 300 m from the observer, were counted. Data on species, numbers and behaviour were entered directly onto a portable microcomputer, timed to the nearest six seconds (Updegraff & Hunt 1985).

**Species selected for study**

We have focused on five species of birds. Two, the great shearwater (*Puffinus gravis*) and the soft-plumaged petrel (*Pterodroma mollis*), are species which breed elsewhere and were not commonly seen at South Georgia during the time of our study. These were the only non-resident species which were sufficiently abundant to allow statistical comparisons to be made. The closest breeding colonies of great shearwaters are at Tristan da Cunha (c. 3000 km from South Georgia) and a smaller site on the Falkland Islands (c. 1700 km from South Georgia) (Elliot 1957, Swales 1965, Woods 1970). Soft-plumaged petrels breed both on Gough Island and Tristan da Cunha (Swales 1965) as well as on islands in the southern Indian Ocean and on the Cape Verde and Canary Islands. Both species become moderately common in autumn over the continental shelf waters near South Georgia (Prince & Croxall 1983).

The other three species, black-browed albatross (*Diomedea melanophris*), blue petrel (*Halobaena caerulea*) and prions (overwhelmingly dove prion, *Pachyptila desolata* - see Prince & Croxall 1983) all nest on South Georgia (Croxall & Prince 1980). Prions observed from the ship during this study would have been almost exclusively birds breeding in the locality, but definite identification to species for all individuals seen was not always possible. The three resident species were selected to provide distributions which could be predicted reliably, providing a test of the observations and their implications. Overall, this selection of species gave us the opportunity to compare responses to a change in sea surface temperatures both by species resident in the area, and by species which travel to the area and therefore forage less
frequently in the vicinity of South Georgia.

Numerical analyses

The more restricted spatial coverage of the first part of the cruise limits statistical comparison between the two parts of the cruise to the area to the northeast of Bird Island. We selected as a sampling unit for seabird abundance the presence or absence of a species during observation segments of >10 nautical miles (n mi) completed in a single day. Segments of this length were available on 20 days of the first part of the cruise. In the second part of the cruise, 16 segments of suitable length were available on portions of transects, more than 30 n mi from Bird Island, that were over shelf-slope waters similar to those sampled in Part I of the cruise (Fig. 1). The use of these large sample units reduces the potential problem of autocorrelation between samples (Schneider 1990). Since the distribution of data did not conform to a normal sample distribution, $\chi^2$ contingency tables were used to compare species occurrence between parts of the cruise. We used $\chi^2$ analysis with Yates correction (Sokal & Rohlf 1981) to determine the statistical significance of the differences. We also present data standardized to distance travelled as ‘number of birds observed per n mi travelled’. These data are used to compare for Parts I and II the number of birds per n mi, excluding zero-occurrences, using a Mann-Whitney $U$ test.

Since a fundamental aspect of this study was to identify correlation between the abundance of individual species and water temperature, we needed to ensure that a false relationship was not generated through the unequal representation of temperature observations in the dataset. To determine if the various species of birds showed a preference for warmer or cooler sea surface temperatures, we compared the distribution of surface temperatures, for hours in which bird observations were made, with the distribution of surface temperatures in which a particular species was observed using a $2 \times N$ contingency table and a $\chi^2$ test. Mean temperatures were calculated for each hour using data from the hull intake temperature sensor. For this analysis of temperature preference we used 585 hours of bird observations obtained between 21 December 1985 and 27 February 1986 in the vicinity of South Georgia, and on those portions of the route between South Georgia and the Falkland Islands where water temperatures were similar to those encountered near South Georgia.

Results and Discussion

Environmental conditions in the research area —the large-scale picture

The satellite-derived maps of sea-surface temperature indicated a marked difference in temperature between the first and second parts of the cruise (Fig. 2). In the first part, the island was surrounded by water with a surface temperature of 2°C.

Fig. 2. Maps of weekly mean sea surface temperatures during the course of the study. Data derived from satellite measurements supplied by NOAA-NESDIS. Arrows indicates the position of South Georgia (SG) and the Falkland Islands (FI).
Whereas temperatures around South Georgia were relatively constant for this period, it appears that there was more variation in sea-surface temperature to the west in Drake Passage, with rapid shifts in the positions of surface isotherms. During the second part of the cruise, surface temperatures increased to 3–4°C around South Georgia (Fig. 2).

A gradual increase in temperature is to be expected as summer warming gives rise to a southerly shift of surface isotherms. What is noteworthy in these maps for 1986 is the highly dynamic nature of the pattern and the apparent rapidity of the change in surface temperature around South Georgia, with a rise of almost 1°C per week in the first half of February.

Environmental conditions in the research area — the local picture

Our shipboard measure of sea-surface temperature paralleled closely the temperatures estimated by the satellite sensor (Fig. 3). Temperature profiles obtained from XBT casts showed that the surface temperatures were representative of the upper 50+ m of the water column. These depths are within or exceed the diving depths of the seabird species we studied (Prince 1980a,b, Croxall & Prince 1980, 1982, Croxall et al. 1984), although the prey of the birds have diurnal migrations that are frequently greater than this.

The XBT profiles indicate that changes in temperature were restricted to shallow depths (Fig. 3). Comparison of the vertical profiles from around South Georgia during the first and second parts of the cruise shows that the upper 50 m had warmed uniformly by approximately 2°C, but temperatures at depths greater than 150 m remained more-or-less uniform. By contrast, representative profiles taken in water to the west of the study area show an entirely different character. Thus, although the surface temperature in the second part of the cruise was similar to that of water closer to the Falkland Islands, vertical profiles indicate that the change was consistent with a movement of warm surface water to South Georgia, rather than an alteration in the position of oceanic fronts.

Fig. 3. Temporal variation of sea temperature during the study. The upper panel shows the time-course of sea-surface temperature measured at the ship's hull throughout the period of observations. The first and second parts of the cruise near South Georgia are separated by a period on passage to and from the Falkland Islands. The lower panels show three representative vertical profiles obtained with XBTs. Note warming of surface temperatures between the two South Georgia profiles (left and right) but consistently cold temperature in deep water, whilst the profile made close to the Falkland Islands (central panel) has different characteristics.
SEABIRD SPECIES ABUNDANCE NEAR SOUTH GEORGIA

A plot of calculated geostrophic winds for South Georgia shows that changes in wind forcing could have been responsible for the change in surface water distribution. There was a dramatic change in mean wind direction between the two parts of the cruise (Fig. 4). Prior to the cruise, during the period 1 October to 25 December 1985, mean wind speed was 17 knots (8.8 m s\(^{-1}\)) (range 3–26 but 83% >10 knots) and direction ranged from 190–315\(^\circ\), with 60% of observations lying within the sector 240–300\(^\circ\). During the first part of the cruise, this pattern was maintained, with continued high winds blowing predominantly from the south-west (mean wind speed 20 knots, range 15–24, and direction 248–321\(^\circ\)). During the second part of the cruise, the wind field was more variable (Fig. 4). Average wind speed was lower (mean value 12 knots, range 4–18) and direction varied widely from 005–323\(^\circ\). Thus, we hypothesize that the change in wind-forcing altered the distribution of surface water, in a manner consistent with the change in distribution of sea surface temperatures. The more or less constant wind direction during October 1985–January 1986 may have forced colder surface water from the southwest into the vicinity of South Georgia. The relaxation of this forcing may have then allowed warmer water to flow into the area.

Changes in bird abundances in the study area during the cruise

Between the two parts of the cruise the occurrence or abundance of several bird species changed, while those of others did not. The abundance and frequency of occurrence of great shearwaters increased between the first and second parts of the cruise, both in terms of number of survey segments in which they were seen (\(\chi^2 = 10.4, P < 0.001\)) and in total numbers of individuals seen per n mi (Table I). In contrast, the encounter rate and abundance of blue petrels decreased, as might be expected as a result of post-breeding dispersal (\(\chi^2 = 16.4, P < 0.001\)). Soft-plumaged petrels were more abundant during Part II (Mann Whitney \(U = 12, P = 0.055\)), even though the frequency of transects in which they were sighted did not change significantly between Parts I and II (\(\chi^2 = 1.12, P = 0.29\)). For the two species which were resident in the study area for the entire survey — black-browed albatrosses and prions — there was no significant change in either the number of segments in which they were seen, or in the number of individuals counted per n mi of survey (Table I). Changes in the species composition of the prions, correlated with environmental change, cannot be excluded absolutely. However, with an estimated breeding population of 22 million pairs of dove prions on South Georgia and its associated islands, and only few records of other species (Prince & Croxall 1983), it is assumed that nearly all birds observed were local breeders and of one species.

We examined the possibility that the five species of birds for which we had adequate samples in both parts of the study showed a response to the incursion of warmer surface waters into the study area (Fig. 5). We found statistically significant differences between the distribution of all observation hours with respect to temperature and the distributions of hours in which great shearwaters were seen (\(\chi^2 = 108, df = 29, P < 0.001\)) and a weaker difference for soft-plumaged petrels.

Changes in bird abundances in the study area during the cruise

| Date | PRE-CRUISE | PART 1 | PART 2 |
|------|------------|--------|--------|
| 1 Oct | 31 Oct | 30 Nov | 25 Dec |
| 24 Jan | 8 Feb | 22 Feb | 10 March |

Table I. Presence of five seabird species in South Georgia study area in mid summer and late summer, 1985–86.

| Species | 27 December–23 January | 6–22 February |
|---------|-------------------------|--------------|
|          | Segments in which observed | Mean individuals n mi\(^{-1}\) surveyed | Segments in which observed | Mean individuals n mi\(^{-1}\) surveyed |
| Sample size | 21 | 886 n mi | 16 | 387 n mi |
| Species | 21 | 2.55 | 16 | 2.97 |
| black-browed albatross | 21 | 7.24 | 16 | 8.93 |
| prion spp. | 15 | 0.21 | 0 | 0.0 |
| blue petrel | 6 | 0.02 | 14 | 0.68 |
| great shearwater | 7 | 0.03 | 9 | 0.05 |
| soft-plumaged petrel | 7 | 0.03 | 9 | 0.05 |
Fig. 5. Relationship between the abundance of different seabird species and sea-surface temperature around South Georgia and on passage to the Falkland Islands.

The timing of great shearwater movement to South Georgia during Part II of our cruise corresponded to their previously documented seasonal occurrence there (Prince & Croxall 1983), but the numbers in 1986 were unusually large. Our observations suggest that these birds appear at South Georgia only when the sea surface temperature exceeds 3.5°C. This temperature is considerably below 7.0°C, the lowest sea surface temperature at which Brown et al. (1975 table 1) found great shearwaters over the Patagonian shelf in the South Atlantic. Although Brown et al. reported an isolated great shearwater in Lemaire Channel, Antarctic Peninsula, the species is rare south of the Antarctic Polar Front. Similarly Tickell & Woods (1972) found that great shearwaters were abundant near the South American coast in summer, where the species was seen in all reported months of observation (November-January and April-May). However, these authors observed only one flock of great shearwaters south of East Falkland Island, and saw none between the Falklands and South Georgia.

Our observations were probably too early in the season to detect birds that had dispersed after successful breeding, which should not occur until late April or early May (Swales 1965). Brown et al. (1975) and Veit (1988) reported great shearwaters as abundant off the Argentine coast in January and February where there are large numbers of what Tickell & Woods (1972) surmized were foraging, non-breeding birds. Similarly, it is most likely that the birds we observed were non-breeders.

The exact reason why observations of great shearwaters and soft-plumaged petrels near South Georgia coincided with the presence of warmer water is uncertain. It seems unlikely that this phenomenon occurred by chance, given the striking parallel changes in the distribution of two species of birds with similar diets. Furthermore, both species were present relatively close to the island and seen between South Georgia and the

$(\chi^2 = 39.4, \text{df} = 29, \ 0.10 > P > 0.05)$. In both cases, the distributions of bird observations were skewed towards higher temperatures (Fig. 5). In contrast, the distributions for black-browed albatross and prions showed no statistically significant relationship that would suggest a preference for- or avoidance of the warmer waters encountered in the second part of the study.

These results suggest that great shearwaters moved south to the vicinity of South Georgia at the same time as the warming of the surface water. Observations made on passage between the Falkland Islands and South Georgia show that this species, and soft-plumaged petrels, were abundant in waters adjacent to the study area. During three days of observation prior to Part II of the cruise (24–26 January 1986), 293 great shearwaters and 278 soft-plumaged petrels were seen to the northwest of the study area where the water was warmer. The largest counts of great shearwaters in the study area, 155 and 57, were made on 6 and 19 February, respectively. These large counts occurred when winds were northeasterly, and the majority of these birds were flying in a westerly direction.

The timing of great shearwater movement to South Georgia during Part II of our cruise corresponded to their previously documented seasonal occurrence there (Prince & Croxall 1983), but the numbers in 1986 were unusually large. Our observations suggest that these birds appear at South Georgia only when the sea surface temperature exceeds 3.5°C. This temperature is considerably below 7.0°C, the lowest sea surface temperature at which Brown et al. (1975 table 1) found great shearwaters over the Patagonian shelf in the South Atlantic. Although Brown et al. reported an isolated great shearwater in Lemaire Channel, Antarctic Peninsula, the species is rare south of the Antarctic Polar Front. Similarly Tickell & Woods (1972) found that great shearwaters were abundant near the South American coast in summer, where the species was seen in all reported months of observation (November–January and April–May). However, these authors observed only one flock of great shearwaters south of East Falkland Island, and saw none between the Falklands and South Georgia.

Our observations were probably too early in the season to detect birds that had dispersed after successful breeding, which should not occur until late April or early May (Swales 1965). Brown et al. (1975) and Veit (1988) reported great shearwaters as abundant off the Argentine coast in January and February where there are large numbers of what Tickell & Woods (1972) surmized were foraging, non-breeding birds. Similarly, it is most likely that the birds we observed were non-breeders.

The exact reason why observations of great shearwaters and soft-plumaged petrels near South Georgia coincided with the presence of warmer water is uncertain. It seems unlikely that this phenomenon occurred by chance, given the striking parallel changes in the distribution of two species of birds with similar diets. Furthermore, both species were present relatively close to the island and seen between South Georgia and the
Falkland Islands; chance dispersal would have lead to a random pattern of observations at South Georgia. Likewise, we do not believe that the change in wind-forcing, which resulted in warm water reaching the island, was the principal influence on the distribution of the birds.

It seems to be more likely that the birds were following a particular water mass out of choice, probably because of the quality or quantity of food available in the warmer water (cf. Pocklington 1979). The large number of birds, of other species but with broadly similar feeding ecology (Croxall & Prince 1980), which breed on South Georgia and its associated islands suggests that there is sufficient quantity of food available in the area. It seems more likely that it is particular types of food associated with individual water masses which determine the foraging areas for these birds. Information on the diet of adult and nestling great shearwaters at Tristan da Cunha indicate that squid form the main bulk of the diet, with occasional fish and crustaceans (Cram & Simmons 1977, p. 142). In their northern wintering grounds off Nova Scotia, Canada, great shearwaters eat squid, fish and euphausiids (Brown et al. 1981). R. R. Veit (unpublished) has observed soft-plumaged petrels eating small squid in the southwest Atlantic Ocean. However, the data for neither species are specific enough to identify the cause of the correlations described here.

Our data support the proposition that foraging seabirds respond to relatively rapid changes in the location of important oceanographic features by changes in foraging area. Although this behaviour is obviously systematic and likely to be linked to the distribution of preferred prey species, further work is needed before either the underlying cause for the distribution or the cues used by the birds can be identified.

Acknowledgements

We thank D. Heinemann and N. M. Harrison for help with the ornithological observations, D. Heinemann and A. G. Wood for aid with data management, and A. W. A. Murray and P. Rothery for statistical assistance. Lynette Allen-Elbourn and John King provided the geostrophic wind data. Comments from two referees are gratefully acknowledged. The captains and crew of the RRS John Biscoe provided valuable cooperation and help during the cruise. Financial support for this project was provided by the Natural Environment Research Council to the British Antarctic Survey and by grant DPP-83-18464 from the National Science Foundation.

References

BRIGGS, K. T. & CHU, E. W. 1986. Sooty Shearwaters off California: distribution, abundance and habitat use. Condor, 88, 355-364.

BRIGGS, K. T., TYLER, W. B., LEWIS, D. B. & CARLSON, D. R. 1987. Bird communities at sea off California: 1975-1983. Studies in Avian Biology, 11, 1-74.

BROWN, R. G. B. 1980. Seabirds as marine animals. In BURGER, J., OLLA, B. L. & WINN, H. E., eds, Behavior of Marine Animals, Vol. 4. New York: Plenum Press, 1-39.

BROWN, R. G. B. & GASKIN, D. E. 1988. The pelagic ecology of the Grey and Red-necked Phalaropes Phalaropus fulicarius and P. lobatus in the Bay of Fundy, eastern Canada. Ibis, 130, 234-250.

BROWN, R. G. B., BARBER, S. P., GASKIN, D. E. & SANDDEMANN, M. R. 1981. The foods of Great and Sooty Shearwaters Puffinus gravis and P. griseus in eastern Canadian waters. Ibis, 123, 19-30.

BROWN, R. G. B., COOKE, F., KINNEAR, P. K., & MILLS, E. L. 1975. Summer seabird distribution in Drake Passage, the Chilean fjords and off southern South America. Ibis, 117, 339-356.

CRAMP, S. & SIMMONS, K. E. L. 1977. The birds of the western Palearctic. Volume 1. Oxford: Oxford University Press, 722 pp.

CROXALL, J. P. & PRINCE, P. A. 1980. Food, feeding ecology and ecological segregation of seabirds at South Georgia. Biological Journal of the Linnean Society, 14, 103-131.

CROXALL, J. P. & PRINCE, P. A. 1982. A preliminary assessment of the impact of seabirds on marine resources at South Georgia. Comité National Français des Recherches Antarctiques, 51, 501-509.

CROXALL, J. P., RICKETTS, C. & PRINCE, P. A. 1984. Impact of seabirds on marine resources, especially krill, of South Georgia waters. In WHITTO, G. C. & RASH, H. eds. Seabird energetics. New York: Plenum Press, 285-318.

ELLIOTT, H. F. I. 1957. A contribution to the ornithology of the Tristan da Cunha group. Ibis, 99, 545-586.

GORDON, A. L. 1988. Spatial and temporal variability within the Southern Ocean. In SAINSHAGE, D. ed. Antarctic ocean and resources variability. Berlin: Springer Verlag, 41-56.

HEPPNER, W. L. 1989. Remote observation of the sea surface and atmosphere. The ocean skin effect. International Journal of Remote Sensing, 10, 801-810.

HUNT, G. L. Jr. 1990. The pelagic distribution of marine birds in an heterogeneous environment. Polar Research, 8, 43-54.

HUNT, G. L. Jr. & HARRISON, N. M. 1990. Foraging habitat and prey selection by Least Auklets off King Island, Alaska. Marine Ecology Progress Series, 65, 141-150.

HUNT, G. L. Jr. & SCHNEIDER, D. C. 1987. Scale-dependent processes in the physical and biological environment of marine birds. In CROXALL, J. P., ed., Seabirds: feeding biology and role in marine ecosystems. Cambridge: Cambridge University Press, 7-41.

HUNT, G. L. Jr., GOULD, P., FORSELL, D., & PETTERSON, H. 1981. Pelagic distribution of marine birds in the eastern Bering Sea. In HOOO, D. W. & CAULDER, J. A., eds, The eastern Bering Sea Shelf: oceanography and resources. Vol. 2. Washington, DC: National Oceanographic and Atmospheric Administration, 689-717.

LEGENDRE, R. 1977. Ocean polar front in the Drake Passage - satellite observations during 1976. Deep-Sea Research, 24, 701-704.

POCKLINGTON, R. 1979. An oceanographic interpretation of seabird distributions in the Indian Ocean. Marine Biology, 51, 9-21.

PRINCE, P. A. 1980a. The food and feeding ecology of the Blue Petrel Halobaena caerulea and Dove Prion Pachyptila desolata. Journal of Zoology, 190, 59-76.

PRINCE, P. A. 1980b. The food and feeding ecology of Grey-headed Albatross Diomedea chrysostoma and Black-browed Albatross D. melanophris. Ibis, 122, 476-488.

PRINCE, P. A. & CROXALL, J. P. 1983. Birds of South Georgia: new records and re-evaluations of status. British Antarctic Survey Bulletin, No. 59, 15-27.

SCHNEIDER, D. C. 1990. Spatial autocorrelation in marine birds. Polar Research, 8, 89-97.

SOKAL, R. R. & ROHLF, F. J. 1981. Biometry. The principles and practice of statistics in biological research. Second edition. New York: W. H. Freeman, 859 pp.

SWALES, M. K. 1965. The sea-birds of Gough Island. Ibis, 107, 17-42.

TICKELL, W. L. N. & WOODS, R. W. 1972. Ornithological observations at sea in the South Atlantic Ocean, 1954-64. British Antarctic Survey Bulletin, No. 31, 63-84.
UPDEGRAFF, G.E. & HUNT, G.L. 1985. Field use of microcomputers for the collection of seabird data. Pacific Seabird Group Bulletin, 12, 19.

Veit, R.R. 1988. Spatial dispersion patterns of Antarctic seabirds. Ph.D. thesis, Irvine, University of California, 175pp [Unpublished].

VERMEER, K., SZABO, I. & GREISMAN, P. 1987. The relationship between plankton-feeding Bonaparte’s and Mew Gulls and tidal upwellings at Active Pass, British Columbia. Journal of Plankton Research, 9, 483-501.

WOODS, R.W. 1970. Great Shearwater Puffinus gravis breeding in the Falkland Islands. Ibis, 112, 259-260.