SHIPBOARD OBSERVATIONS OF PENGUINS AT SEA IN THE AUSTRALIAN SECTOR OF THE SOUTHERN OCEAN, 1991–1995

TIMOTHY A. REID[1], CINDY L. HULL[2], DAVID W. EADES[3], R. PAUL SCOFIELD[3] & ERIC J. WOEHLER[4]

[1]*Department of Parks and Wildlife, GPO Box 44A, Hobart, Tasmania 7001, Australia (tim.reid@dpiwe.tas.gov.au)*
[2]*Zoology Department, University of Tasmania, GPO Box 252C, Hobart, Tasmania 7001, Australia*
[3]*Birds Australia, 415 Riversdale Rd, Hawthorn East, Victoria 3123, Australia*
[4]*Australian Antarctic Division, Channel Highway, Kingston, Tasmania 7050, Australia*

SUMMARY

REID,T.A., HULL, C.L., EADES, D.W., SCOFIELD, R.P. & WOEHLER, E.J. 1999. Shipboard observations of penguins at sea in the Australian Sector of the Southern Ocean, 1991–1995. *Marine Ornithology* 27: 101–110.

Locations of penguins at sea were recorded during systematic observations carried out on voyages between Hobart, Tasmania and Antarctica during 1991–1995. Two types of voyages were undertaken: five World Ocean Circulation Experiment (WOCE) cruises along longitude 140° E; and two Antarctic and Heard Island exploratory fishing / re-supply voyages between Hobart, Heard Island and the Australian Antarctic Territory. Observations were carried out to describe the distribution of seabirds, including penguins, at sea. In this paper penguin distribution has been described, along with an analysis of environmental variables associated with the sightings, and an attempt was made to use these variables to predict penguin distribution. Ten species were observed: Emperor *Aptenodytes forsteri*, King *A. patagonicus*, Adélie *Pygoscelis adeliae*, Gentoo *P. papua*, Macaroni *Eudyptes chrysolophus*, Royal *E. schlegeli*, Rockhopper *E. chrysocome*, Snares Crested *E. robustus*, Fiordland Crested *E. pachyrhychus* and Little *Eudyptula minor* Penguins. The sightings of Snares Crested and Fiordland Crested Penguins were unique in the sector covered. Juvenile and adult Emperor, Adélie and Macaroni Penguins were found in different sectors of the Southern Ocean. Latitude, longitude, depth of water, salinity, sea surface temperature, ice cover and icebergs were recorded. Cluster analysis was used to predict penguin distribution, and compiled three groups. A discriminant function analysis revealed only moderate success in the allocation of species to these groups. This probably arose because: 1. the environmental variables measured were not good indicators of penguin distributions at sea; 2. the sightings of penguins were probably not always at foraging grounds, and penguins may have been en route to foraging zones when observed; 3. the patterns of penguin distribution are not predictable at the scale of analysis because they respond opportunistically to regions around their breeding sites; 4. penguins are not congregating at specific areas.

INTRODUCTION

Penguins, like all seabirds, spend most of their lives at sea, but research has been largely restricted to their breeding colonies (Hay 1992). Only relatively recently have attempts been made to redress the lack of information on their distribution at sea, through observations aboard ships (e.g. Bretagnolle & Thomas 1990, Woehler *et al.* 1990, Veit *et al.* 1993), and more recently using remote devices such as time-depth recorders (e.g. Hull 1997, K. Green unpubl. data), and transmitters to satellites (e.g. Davis & Miller 1990, Jouventin *et al.* 1994, Kerry *et al*. 1995, Wilson *et al.* 1995). However, the data are still scant for many species and sites, particularly during the non-breeding season.

The distribution of seabirds at sea, including penguins, is often correlated with aspects of the physical and biological environment, such as fronts (Ainley & Jacobs 1981, Abrams 1985, Hunt *et al*. 1989, Schneider 1990), eddies (Haney & McGillivary 1985, Abrams & Miller 1986, Haney 1986), ice cover (Ainley & Jacobs 1981, Hunt 1991a, Ainley *et al*. 1993), prey behaviour (Obst 1985, Ainley *et al*. 1991, Hunt 1991a,b, Veit *et al*. 1993), and the social behaviour of birds (Hunt 1988). The strength of these relationships varies with the scale at which they are examined (Hunt & Schneider 1987).

Ship-board observation of the distribution of penguins at sea fills gaps in the knowledge of foraging areas and how distribution relates to physical and biological aspects of the environment. While land-based studies can examine aspects of bird behaviour during the breeding season (or in the case of some species, the non-breeding season), few data are available outside the breeding season for species that move a long way offshore.

The purpose of this study was to describe: 1. the distribution of penguins within the Australian and south-east Indian Ocean sectors of the Southern Ocean; 2. the relationship between the distribution of penguins and environmental variables, and how effective the environmental variables were for predicting

penguin distribution, which may assist in understanding ecological specialisation of penguins; 3. the relationship between the distribution of penguins and fronts; and 4. the calculated distance the penguins travelled from assumed breeding colonies.

METHODS

Data were collected during seven cruises of the R.S.V. *Aurora Australis*, a 7000-tonne class A Super-Icebreaker supply and research vessel. Two types of cruises were undertaken (Fig. 1):

1. Exploratory fishing in the Australian Fishing Zone around Heard Island (53°S, 73°E), and re-supply of Australian Antarctic bases; and
2. Collection of oceanographic data for the World Ocean Circulation Experiment (WOCE) and re-supply of Australian Antarctic bases.

Voyages for the WOCE cruises were conducted on a transect at 140°E longitude from the south coast of Tasmania to Dumont d'Urville, Antarctica. Voyages were conducted in January–March 1992 (fishing); August–October 1993 (fishing); September–October 1991 (WOCE); March–May 1993 (WOCE); January–February 1994 (WOCE); December 1994–January 1995 (WOCE); and July–August 1995 (WOCE). WOCE transects could be used to examine aspects of penguin distribution with respect to fronts, while other transects could be used for more general distribution.

Continuous 10-minute counts were made of all seabirds during daylight hours when the ship was steaming, using the 90° forward quadrant (300-m band transect) according to the method described by BIOMASS (1982). When the ship was stationary, ten-minute 360º counts were made each hour (Tasker *et al*. 1984). From these data, penguin records were extracted. All counts were made from the internal bridge 13 m above sea level and 20 m from the bow. Environmental and oceanographic conditions were recorded concurrently (hereafter described as environmental variables).

Ten species of penguins were observed: Emperor *Aptenodytes forsteri*, King *A. patagonicus*, Adélie *Pygoscelis adeliae*, Gentoo *P. papua*, Rockhopper *Eudyptes chrysocome*, Royal *E. schlegeli*, Macaroni *E. chrysolophus*, Snares Crested *E. robustus*, Fiordland Crested *E. pachyrynchus*, and Little *Eudyptula minor*. The low numbers of Snares Crested, Fiordland Crested and Little Penguins precluded them from some analyses. Age-related distribution (using three age categories; adult, sub-adult and juvenile) was examined for four species (Adélie, Emperor, Royal and Macaroni Penguins). Insufficient data were obtained for the remaining six species.

Distance travelled to the point of observations was estimated by measuring a great-circle course (shortest distance) to the closest breeding location. Only sub-Antarctic species were examined as there were insufficient reliable descriptions of locations of breeding colonies along the portion of the Antarctic coastline travelled (see Woehler 1993). The closest breeding sites for penguins in this sector of the Southern Ocean were Heard and Macquarie Islands.

The following oceanographic variables were recorded at the same time that penguins were seen: longitude, latitude, depth of water, sea surface temperature (in °C), salinity, ice cover (in tenths) and the presence/absence of icebergs. The association of each species to the variables was examined separately by χ^2 tests, and one-way ANOVAs and Tukey tests. In order to examine if the distribution of species could be predicted by these variables, a cluster analysis on variables was performed and the ability of these to group penguins was trialled using Discriminant Function Analysis (latitude and longitude were excluded from these analyses as they were not environmental variables and were significantly related to oceanographic variables).

To test whether penguins were observed in greater numbers in areas with oceanographic fronts, the WOCE transect was divided into blocks of 30 minutes of latitude. The total number of penguins observed in each block was calculated, and those blocks containing fronts were identified from plots of sea temperature and salinity from data collected using a Current Temperature Depth instrument. Log transformed penguin numbers were tested for the complete transect, and for data north of 60° S (north of ice-edge effects).

RESULTS

The number of sightings of each of the 10 species of penguin observed are given in Table 1. As there were observations that did not include a full complement of environmental data, these sample sizes are sometimes less than the total number of observations of penguins. The locations of all penguins are given in Figures 2 to 9. The association of each species to environmental variables is listed in Table 2.

Emperor and Adélie Penguins showed the most southerly distribution, over the shallowest water with the lowest sea surface temperature and salinity, and the highest ice cover and incidence of icebergs. Amongst the sub-Antarctic species, Gentoo Penguins occurred over the shallowest water, Royal and Rockhopper Penguins occurred over the deepest water, with Royal Penguins over warmer, but low salinity water. Fiordland Crested, Snares Crested and Little Penguins showed the most northerly distribution, over the warmest and most saline water. King and Macaroni Penguins occured in the mid-range of most variables.

Distribution of different age classes

Emperor Penguin

Juvenile Emperor Penguins were recorded farther north ($F_{3,252}$ = 46.05; $P < 0.01$), over deeper ($F_{3,225}$ = 36.83; $P < 0.01$) and warmer water ($F_{3,235}$ = 31.07; $P < 0.01$) than other age classes. They were also found farther east than adults ($F_{2,67}$ = 3.38; $P < 0.05$) and over water with less icecover than sub-adults ($F_{3,252}$ = 3.90; $P < 0.05$). All age classes were observed over seawater with differing salinity, with juveniles in the most saline water, and sub-adults in the least saline ($F_{2,41}$ = 29.87; $P < 0.01$).

Adélie Penguin

Adult Adélie Penguins were found farther south than non-adults ($F_{1,460}$ = 25.97; $P < 0.01$). Non-adult Adélie Penguins were recorded over deeper water than adults ($F_{1,460}$ = 11.79; $P < 0.01$), with less ice cover ($F_{1,460}$ = 4.87; $P < 0.05$). No differences were noted in the sea salinity ($F_{1,294}$ = 3.42; $P > 0.05$) or sea surface temperature ($F_{1,423}$ = 0.24; $P > 0.05$) (Table 3).

Macaroni Penguin

There were only records of juvenile and adult Macaroni

TABLE 1

Environmental variables for each species of penguin observed (mean ± one standard deviation)

Species of penguin (number of sightings)	Longitude (degrees)	Latitude (degrees)	Water depth (m)	Sea surface temperature (degrees)	Salinity (parts per thousand)	Ice cover (tenths)	Icebergs present (% of observations)
Adélie (1101)	78.5 ± 21.2	66.6 ± 1.2	835.8 ± 773.6	–0.6 ± 1.1	33.12 ± 0.87	3.9 ± 3.6	506 (46)
Emperor (158)	79.3 ± 21.7	66.3 ± 1.9	680.3 ± 766.6	–0.9 ± 1.1	32.95 ± 1.01	4.9 ± 3.4	72 (46)
King (13)	109.2 ± 36.0	52.2 ± 1.4	2308.0 ± 1775.7	4.3 ± 1.4	33.90 ± 0.24	0	0
Gentoo (18)	82.2 ± 22.5	52.4 ± 1.5	931.2 ± 1284.5	2.6 ± 1.9	33.94 ± 0.19	0	1 (6)
Rockhopper (11)	133.7 ± 15.3	55.7 ± 2.5	3212.8 ± 954.3	2.5 ± 1.7	33.87 ± 0.15	0	0
Royal (27)	143.4 ± 6.2	55.6 ± 3.3	3273.0 ± 865.4	4.2 ± 2.3	33.94 ± 0.19	0	0
Macaroni (36)	81.5 ± 9.0	53.8 ± 2.8	2345.8 ± 1846.9	2.5 ± 1.1	33.85 ± 0.23	0	9 (25)
Snares Crested (1)	142.4	52.7	2020	5.8	33.76	0	0
Fiordland Crested (2)	140.5 ± 7.8	49.5 ± 0.7	3577.0 ± 608.1	8.8 ± 0.4	33.98 ± 0.09	0	0
Little (1)	144.7	44.9	2796	14.6	35.10	0	0

TABLE 2

Relationship of occurrence of penguins with each individual environmental variable. Species are listed in groups (those not mentioned showed no significant relationships). Order of groups from smallest value to largest (e.g. coldest sea temperature to warmest, least icebergs to most). All *F* values with 9,1359 degrees of freedom

	Longitude	Latitude	Depth	Sea temperature	Salinity	Ice cover	Icebergs
Significance	$F = 42.93$; $P<0.01$	$F = 891.21$; $P<0.01$	$F = 54.23$; $P<0.01$	$F = 159.86$; $P<0.01$	$F = 4.45$; $P<0.01$	$F = 16.55$; $P<0.01$	$X^2_6 = 57.84$; $P<0.01$
Number of groups	3	4	3	4	2	3	3
1	Adélie, Emperor, Macaroni, Gentoo.	King, Gentoo.	Adélie, Emperor, Gentoo.	Adélie, Emperor.	Adélie, Emperor, Royal.	All others.	King, Rockhopper, Royal.
2	King, Rockhopper.	Rockhopper, Royal.	King, Macaroni, Rockhopper.	Gentoo, Rockhopper, Macaroni.	Gentoo, Macaroni.	Adélie.	Macaroni.
3	Rockhopper, Royal.	Macaroni.	Royal, Rockhopper.	King, Royal.		Emperor.	Adélie, Emperor.
4		Adélie, Emperor.		Little, Fiordland.			

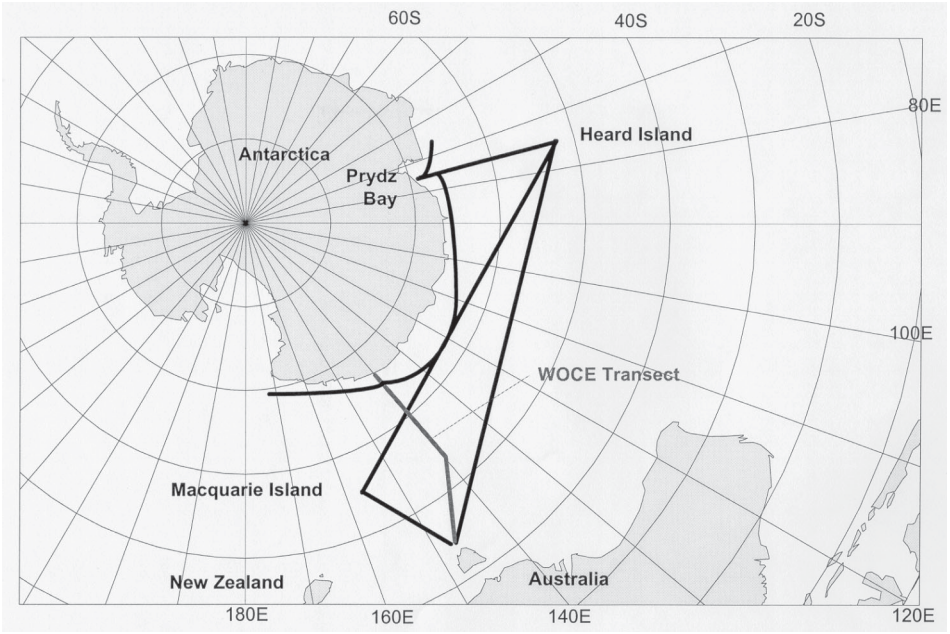

Fig. 1. *At-sea transects.*

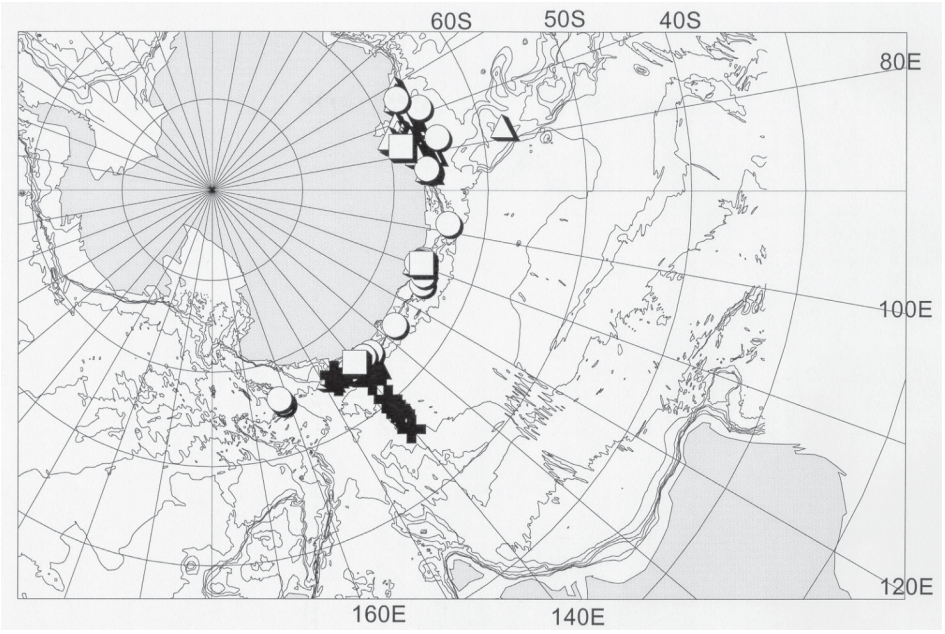

Fig. 2. *Locations of Emperor Penguins.*

❍ = *Adults*
❑ = *Sub-adults*
✚ = *Juveniles*
△ = *Unknown age*

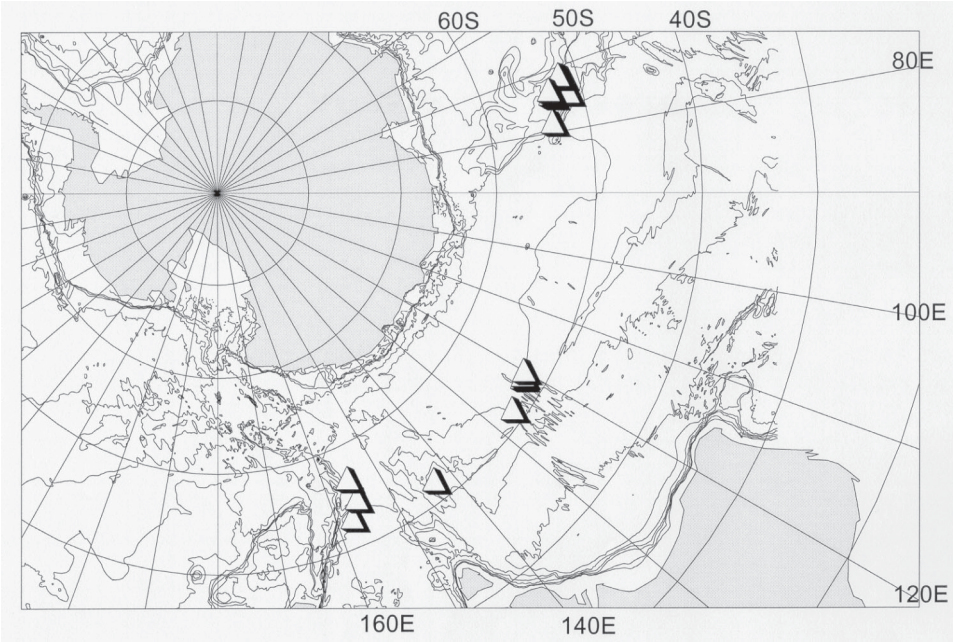

Fig. 3. *Locations of King Penguins.*

Penguins in this study. Juveniles were recorded farther south, ($F_{1,13}$ = 225.37; $P < 0.01$), in deeper ($F_{1,12}$ = 9.67; $P < 0.01$), warmer ($F_{1,13}$ = 5.54; $P < 0.05$) and less saline ($F_{1,13}$ = 9.67; $P < 0.01$) water than adults. No differences were noted in longitude ($F_{1,13}$ = 0.15; $P > 0.05$).

Royal Penguin

Different age classes of Royal Penguins were not distributed differently with regard to any of the variables: latitude ($F_{2,25}$ = 2.44; $P > 0.05$), longitude ($F_{2,25}$ = 0.76; $P > 0.05$), depth ($F_{2,24}$ = 1.77; $P > 0.05$), sea temperature ($F_{2,25}$ = 2.28; $P > 0.05$), or salinity ($F_{2,25}$ = 0.28; $P > 0.05$).

Cluster analysis

The cluster analysis identified three groups of environmental variables. The allocation of species to these groups is given in Table 4, and details of the associated environmental variables in Table 5. The general patterns were as follows:
Group 1. Warmer and deeper water, containing most Royal and Macaroni Penguins;
Group 2. Deep, cold water, and icebergs, with no species being strongly associated;
Group 3. Cold, shallow water, with a higher ice cover, containing Adélie, Emperor, Rockhopper and King Penguins.
Gentoo Penguins were evenly distributed between the first and last groups.

Discriminant Function Analysis

The DFA was only moderately successful at describing the distribution of species using the groups of environmental variables. It accurately assigned 34.8% of individuals to group one, 5.2% to group two, and 83.5% to group three (overall 68.1%).

Fronts

During observations while conducting the WOCE transect, 359 penguins were observed; 160 of these were north of 60° S. Penguins were found to be equally numerous in 30-minute blocks in the presence or absence of fronts, over the total length of the WOCE transect ($F_{1,97}$ = 1.04; $P > 0.05$), and in waters to the north of 60° S ($F_{1,78}$ = 0.51; $P > 0.05$).

Distance to nearest breeding sites

The minimum distance to nearest breeding sites was significantly different between the sub-Antarctic species ($F_{7,118}$ = 8.52, $P < 0.01$). Gentoo and Macaroni Penguins were found significantly closer to presumed breeding sites than were Rockhopper, Royal, King and Fiordland Crested Penguins. Rockhopper and Fiordland Crested Penguins were found the most distant from presumed breeding sites (Table 6).

DISCUSSION

Although penguins spend most of their time at sea, there are few data on their distribution at sea. Further, few studies of distribution of seabirds at sea from shipboard surveys contain records of penguins (e.g. Woehler *et al.* 1990). Therefore, much of the published information on the distribution of penguins at sea is from land-based studies (e.g. Weavers 1992, Davis & Miller 1990, Robinson & Hindell 1996, Hull *et al.* 1997). Land-based studies use radio- and satellite- tracking; these methods cannot be used for long periods. Hence there are no data on distribution during the non-breeding period. It is for these birds that studies such as this of shipboard observations of the distribution of seabirds are most useful. During this study, many birds were located by their calls while the vessel was on station.

The observations provide new records of these species at sea. Snares Crested and Fiordland Crested Penguins were observed around the sub-Tropical Convergence to the south of Tasmania (Fig. 9) for the first time. Fiordland Crested Penguins are regularly found visiting Tasmania, especially during winter, whereas Snares Crested Penguins have been recorded in small numbers around Tasmania (Woehler 1992a). The most southerly records of Little Penguins for this zone were obtained. Little Penguins generally are not thought to travel far from their breeding areas, either in the breeding or winter seasons (Gales *et al.* 1990, Weavers 1992). At least 20% of Little Penguins return to their colonies every night (Marchant & Higgins 1990), and they are thought to not travel more than 20 km from land. Adult Royal Penguins were recorded up to 1561 km west of Macquarie Island (Fig. 7), and were recorded over 1000 km from the island at all times of year. Their foraging zones change with the stage of breeding, with their maximum range found as approximately 600 km in the Polar Frontal Zone

TABLE 3

Environmental variables that had significantly different relationships with different age classes of species

Age class (n)	Latitude (mean ± sd)	Longitude (mean ± sd)	Icecover (mean ± sd)	Depth (mean ± sd)	Sea temperature	Salinity (mean ± sd)
Adélie Penguin						
Adult (342)	65.7 ± 1.6		5.2±3.7	1381.2±1133.8		
Non-adult (120)	64.9±1.1		4.4±3.2	1661.4±1080.0		
Emperor Penguin						
Adult (57)	66.4±1.6	113.3±29.9	5.5±3.5	1378.0±1174.2	–1.3±0.9	33.44±0.21
Sub-adult (5)	65.0±1.3	115.0±26.3	7.4±2.6	109.0	–1.5±0.2	32.44±0.81
Juvenile (8)	60.4±3.1	140.9±3.2	2.3±4.2	3000.0±843.1	2.0±2.5	33.88±0.03
Macaroni Penguin						
Adult (8)	52.5±0.9			2652.6±1551.6	1.4±1.2	34.11±0.18
Juvenile (7)	58.1±0.4			4485.4±155.4	2.6±0.6	33.84±0.07

(Hull *et al*. 1997). However, Woehler *et al.* (1990) recorded Royal/Macaroni Penguins at a similar distance from Macquarie Island, and Royal Penguins have also been recorded in Tasmania (mostly between February and April), approximately 1500 km north of Macquarie Island (Woehler 1992a).

Macaroni Penguins were recorded up to 1400 km east of Heard Island during the current study, greater than the 300 km found for birds late in the chick-rearing stage at Marion Island (Brown 1987). The distant records of Macaroni Penguins were either adults in late September/early October, or juveniles in late March. These periods are immediately before and after the time of breeding. Rockhopper Penguins were found to be widely distributed, and farther south (Fig. 6) than previously assumed (Scott 1994), with records of birds south to 60°53'S. Previous studies showed that breeding Rockhopper Penguins at Macquarie Island moved up to 400 km from their colonies (Hull 1997). At Marion Island, they travelled up to 157 km from the colony (Brown 1987). In the cluster analysis of the data from this study, Rockhopper Penguins were found to be associated with Antarctic penguins, which appears a spurious result. It is impossible to determine the breeding status of these birds, although all of the southerly records were between July and October, before breeding commences. This shows the necessity for at-sea distributional data to be viewed in conjunction with land-based studies.

TABLE 4

Allocation (%) of species to the three environmental groups derived from cluster analysis

Species of penguin	Group 1	Group 2	Group 3
Emperor	7.6	5.0	87.4
King	7.2	7.1	85.7
Adélie	9.8	12.1	78.1
Gentoo	52.6	0.0	47.4
Rockhopper	8.3	16.7	75.0
Royal	85.7	10.7	3.6
Macaroni	77.8	22.2	0.0

TABLE 5

Environmental variables associated with each category derived from the cluster analysis (mean ± standard deviation)

Variables	Group 1	Group 2	Group 3
Sea temperature	1.1±2.8	–0.5±1.6	–0.5±1.2
Salinity	33.1±4.3	33.1±0.8	33.1±0.9
Depth	3164.6±649.8	1468.4±336.8	474.1±196.1
Icebergs	0.6±0.7	1.6±0.7	0.6±0.8
Ice cover	2.2±3.3	2.8±3.2	4.2±3.7

TABLE 6

Distances of penguins to their closest presumed breeding sites

Species	Mean ± s.d. (km)	Number	Range (km)
King Penguin	752.9±905.5	15	16–2257
Gentoo Penguin	215.3±325.5	17	17–972
Macaroni Penguin	573.0±488.2	38	16–1366
Rockhopper Penguin	1152.1±297.6	15	805–2142
Royal Penguin	913.2±292.0	36	274–1562
Snares Crested Penguin	1528.9	1	1529
Fiordland Crested Penguin	2052.0±398.3	2	1770–2334
Little Penguin	133.0	1	133

King Penguins had the greatest recorded range of distances from breeding islands, with birds observed up to 2300 km from the closest breeding island, south of Western Australia. They were recorded over warmer water than most species. They are considered the most pelagic of the penguins, foraging in the Polar Frontal Zone 300–500 km from their colonies (Adams 1987, Jouventin *et al.* 1994). Gentoo Penguins had the least mean distance from their presumed breeding location, but were recorded up to 972 km away. The distant sightings were of one sub-adult during January, and unaged birds in March and April. Most sightings were near or over the shelf around Heard Island, with only two sightings in the deep water to the east. Gentoo Penguins are generally considered to be inshore foragers, feeding within 40 km of colonies (Adams & Wilson 1987), and on average foraging 5 km away (Robinson & Hindell 1996). Juvenile Emperor Penguins were sighted well north of the ice edge (at 56° 26'S) between late January and late March, over deeper and warmer water (up to 4.2ºC), suggesting they were dispersing some distance from natal colonies (Figure 2). Satellite-tracking of juveniles has shown similar dispersal patterns (Kooyman *et al*. 1996). These records are farther north than has been recorded in this sector previously (e.g. Woehler *et al*. 1990), and accord with land-based sightings listed in Woehler (1992a). Female Emperor Penguins forage over open water over the continental shelf about 100 km from colonies during winter (Kirkwood & Robertson 1997). Only one Adélie Penguin was observed north of 63°S in this study. During breeding, Adélie Penguins are generally recorded as foraging close to their colonies over the continental shelf and within 25 km of colonies, but females can range up to 272 km during incubation (Davis & Miller 1990, Kerry *et al.* 1995). During winter they travelled 1500 km north from colonies, possibly to common over-wintering grounds (Davis *et al.* 1996).

Several interesting observations were made during this study. Pre-breeding birds of both Antarctic species, but especially the Emperor Penguin, moved much farther north than did adults; juvenile Macaroni Penguins rapidly dispersed well to the east of Heard Island after fledging; Rockhopper, Royal and Gentoo Penguins were all observed much farther from land than land-based studies had indicated; while Fiordland Crested and Snares Crested Penguins were observed near the Sub-tropical Convergence Zone to the south-west of Tasmania.

The locations of different age classes of some species suggested that juveniles and sub-adults were dispersing

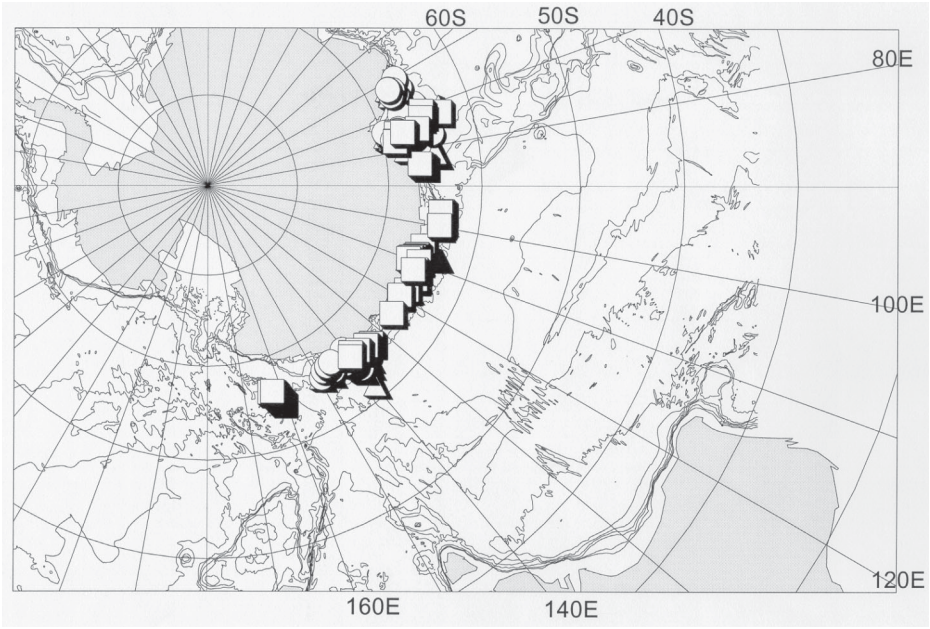

Fig. 4. *Locations of Adélie Penguins.*

❍ = *Adults*
❑ = *Non-adults*
△ = *Unknown age.*

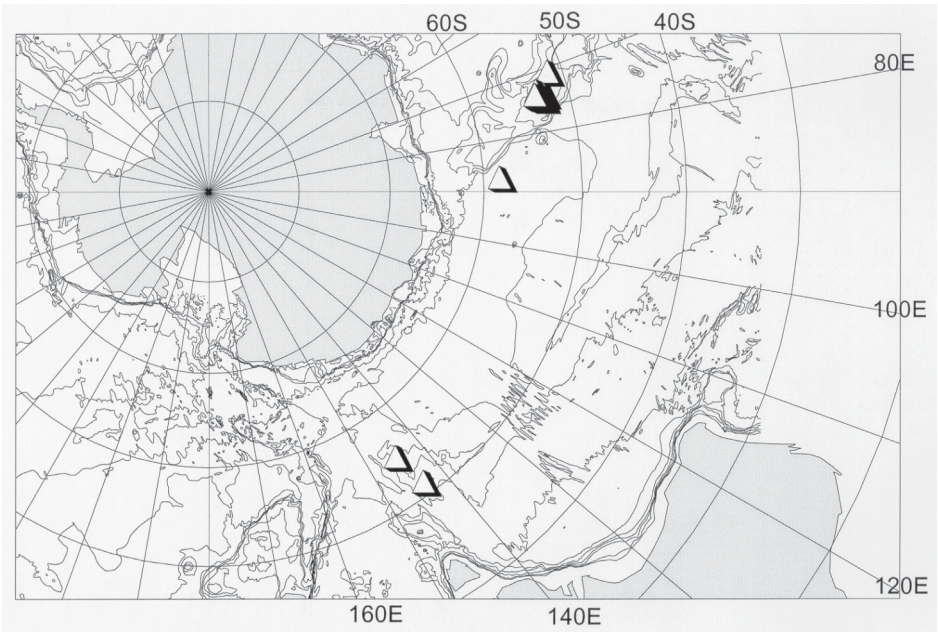

Fig. 5. *Locations of Gentoo Penguins.*

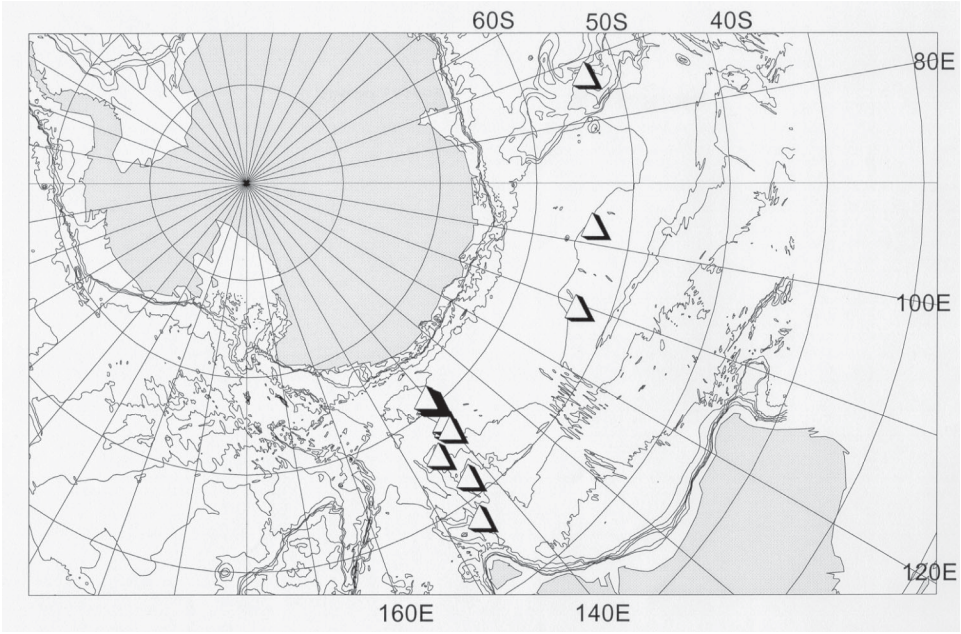

Fig. 6. *Locations of Rockhopper Penguins.*

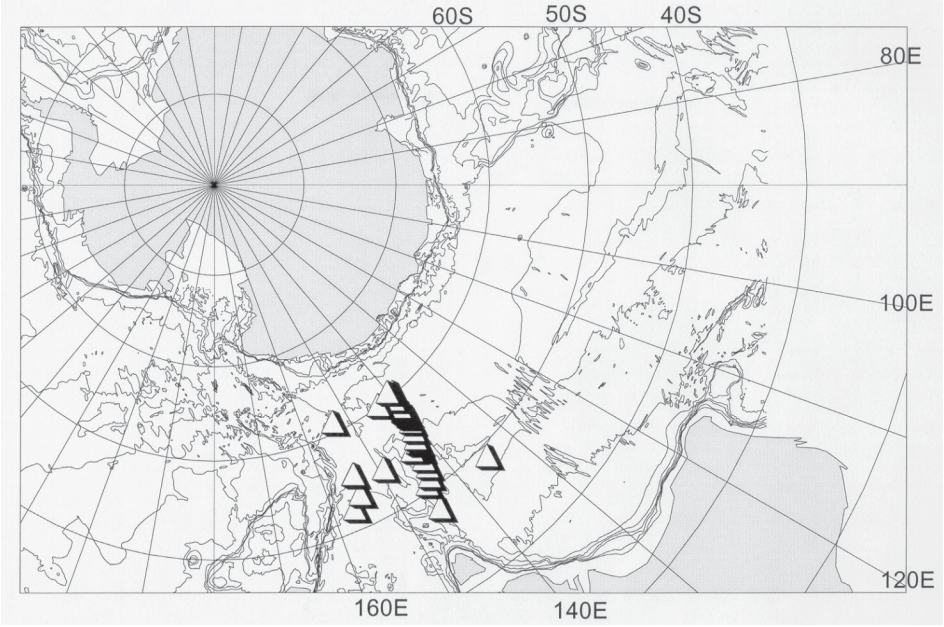

Fig. 7. *Locations of Royal Penguins.*

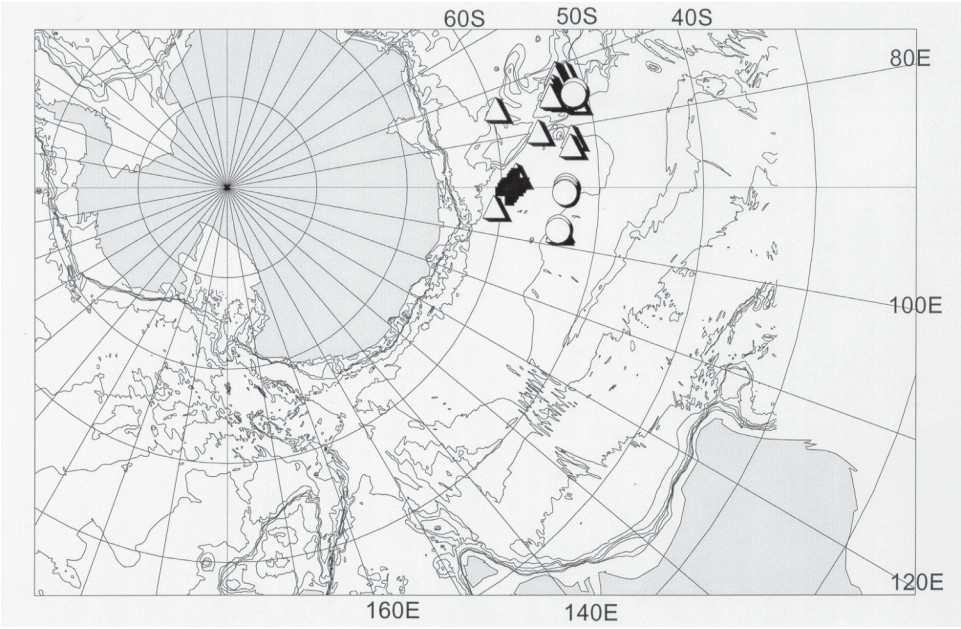

Fig. 8. *Locations of Macaroni Penguins.*

❍ = *Adults*
❑ = *Sub-adults*
✚ = *Juveniles*
△ = *Unknown age*

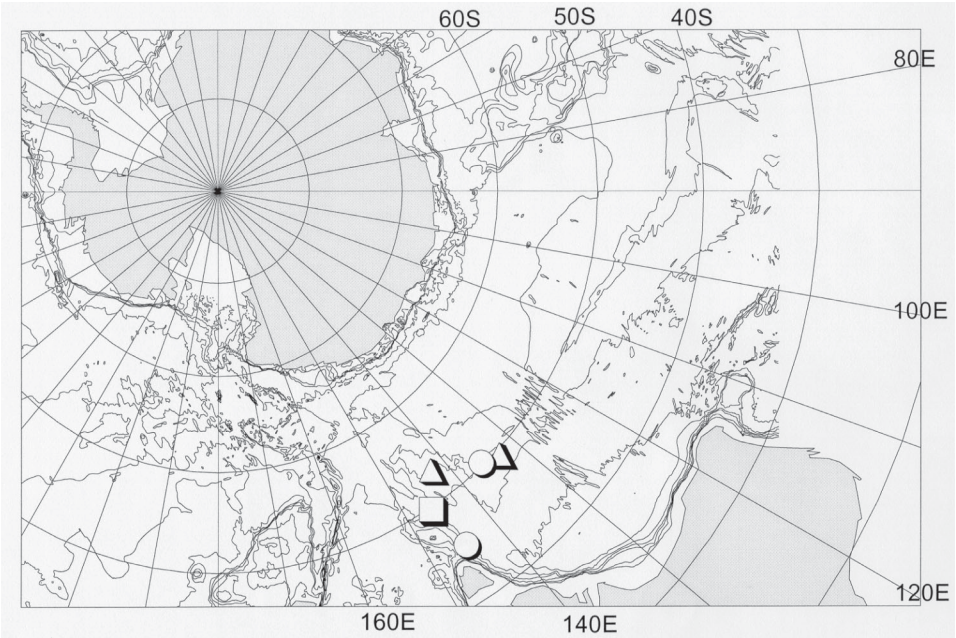

Fig. 9. *Locations of Penguins: Fiordland Crested* (△), *Snares Crested* (❑) *and Little* (❍).

into different regions than the adults. The northerly records of juvenile Emperor Penguins indicate that pre-breeding birds disperse more widely than previously supposed, thereby leading them to interact with a greater number of ecosystems (Kooyman *et al.* 1996). Juvenile and sub-adult Adélie Penguins were observed farther north than adults, with juveniles in water with less ice cover. Nevertheless, in this study they did not move as far north as Emperor Penguins. Although adult Macaroni Penguins have been previously recorded several hundred kilometres from breeding sites (Stahl *et al.* 1985, Woehler *et al.* 1990, Woehler 1992b), the distribution of juveniles at sea has not been described. In this study, juveniles were observed 1314 km east of Heard Island over the Kerguelen Plateau during March, in deeper, warmer and less saline water than adults.

Gentoo and Macaroni Penguins were recorded closer than Royal and Rockhopper Penguins to breeding grounds. Gentoo Penguins are recognised as inshore feeders (Adams & Wilson 1987, Robinson & Hindell 1996), whereas Royal, Macaroni and Rockhopper Penguins are offshore feeders (Horne 1985, Cooper & Brown 1990, Sadlier & Lay 1990, Scott 1994). In addition, there were differences in the distance birds moved to foraging grounds between different breeding islands. This most likely reflects differences in oceanographic conditions at different breeding sites, and probably differences in the distribution of their prey species (Hindell 1988). Some of the species disperse during the non-breeding season (Macaroni, Royal and Rockhopper Penguins), whereas others remain at their breeding sites (e.g. Gentoo Penguins). Therefore, there is probably a seasonal component to the location of foraging grounds that differs between species.

The species have been associated with different combinations of environmental variables. Longitude and latitude resulted in fairly predictable associations. There were three main groups:

1. Antarctic penguins – being the most southerly and in the area of Prydz Bay, comprising Adélie and Emperor Penguins;
2. Heard Island, comprising Macaroni and Gentoo Penguins; and
3. Macquarie Island penguins, consisting of Royal and Rockhopper Penguins. King Penguins were observed in equal proportions at Heard and Macquarie islands.

The inability to split the species of penguins from these environmental variables indicates that species are not responding to the measured variables in a predictable manner. The three groups distinguished by the cluster analysis consisted of one group dominated by the Antarctic penguins, and the other two with a spread of species. The DFA was quite successful in assigning species to group three, but was not very successful in assigning species to groups one and two. There were also some inaccuracies with King and Rockhopper Penguins being assigned to the Antarctic group. This inability to predict the distribution of species of penguins from environmental variables may have arisen from small sample sizes (especially of sub-Antarctic species). Therefore, while the data can reasonably separate the Antarctic penguins, the others fall into unsatisfactory groupings. Other problems that may decrease the ability to predict the distribution of penguins include factors such as the different observability of some species (e.g. Antarctic vs non-Antarctic species; also Mochizuki & Kasuga 1985), whether penguins observed were foraging or in transit (Veit *et al.* 1993), and, for breeding adults, the oceanic habitats around their breeding colonies. For example, Heard Island has a wide shelf to the north-east (where many shipboard observations were carried out), whereas Macquarie Island is on a narrow ridge, hence the feeding opportunities could be expected to differ between sites.

Penguins were not observed to be more numerous in areas with oceanographic fronts, despite several studies indicating that penguins forage in frontal areas (e.g. Jouventin *et al.* 1994, Hull *et al.* 1997). This suggests that either penguins observed were not responding to oceanographic fronts, or, more likely, there were insufficient data to determine correlations with fronts.

ACKNOWLEDGEMENTS

Observations used in this study were also carried out by Kevin Bartram, Mark Hindell, Dion Hobcroft and David James, who we thank. Steve Rintoul (CSIRO Division of Marine Research) gave details of oceanography during the WOCE transects. Thanks also to Mark Hindell, Leon Barmuta, Jan van Franeker and Robert Crawford for comments on a draft of the manuscript.

REFERENCES

ADAMS, N.J. & WILSON, M.-P. 1987. Foraging parameters of Gentoo Penguins *Pygoscelis papua* at Marion Island. *Polar Biol.* 7: 51–56.

BIOMASS 1982. Methods for counting seabirds at sea. *BIOMASS Rep.* 14: 1–22.

BRETAGNOLLE, V. & THOMAS, T. 1990. Seabird distribution between Tasmania and Adélie Land (Antarctica), and comparison with nearby Antarctic sectors. *Emu* 90: 97–107.

BROWN, C.R. 1987. Traveling speed and foraging range of Macaroni and Rockhopper Penguins at Marion Island. *J. Field Orn.* 58: 118–125.

COOPER, J. & BROWN, C.R. 1990. Ornithological research at the sub-Antarctic Prince Edward Islands: a review of achievements. *S. Afr. J. Antarct. Res.* 20: 40–57.

DAVIS, L.S., BOERSMA, P.D. & COURT, G.S. 1996. Satellite telemetry of the winter migration of Adélie Penguins (*Pygoscelis adeliae*). *Polar Biol.* 16: 221–225.

DAVIS, L.S. & MILLER, G.D. 1990. Foraging patterns of Adélie Penguins during the incubation period. In: Kerry, K.R. & Hempel, G. (Eds). Antarctic ecosystems. Ecological changes and conservation. Berlin: Springer-Verlag. pp. 203–207.

GALES, R., WILLIAMS, C. & RITZ, D. 1990. Foraging behaviour of the Little Penguin, *Eudyptula minor*: initial results and assessment of instrument effect. *J. Zool., Lond.* 220: 61–85.

HAY, R.B. 1992. The oceanic habitats of seabirds: their zonal distribution off Vancouver Island, British Columbia, Canada. *J. Biogeog.* 19: 67–85.

HINDELL, M.A. 1988. The diet of the Royal Penguin *Eudyptes schlegeli* at Macquarie Island. *Emu* 88: 219–226.

HORNE, R.S.C. 1985. Diet of Royal and Rockhopper Penguins at Macquarie Island. *Emu* 85: 150–156.

HULL, C.L. 1997. The comparative foraging ecology of Royal *Eudyptes schlegeli* and Rockhopper *E. chrysocome* Penguins. PhD thesis. University of Tasmania, Hobart.

HULL, C.L., HINDELL, M.A. & MICHAEL, K. 1997. Foraging zones of Royal Penguins during the breeding season and their association with oceanographic features. *Mar. Ecol. Prog. Ser.* 153: 217–28.

JOUVENTIN, P., CAPDEVILLE, D., CUENOT-CHAILLET, F. & BIOTEAU, C. 1994. Exploitation of pelagic resources by a non-flying seabird: satellite tracking of the King Penguin throughout the breeding cycle. *Mar. Ecol. Prog. Ser.* 106: 11–19.

KERRY, K.R., CLARKE, J.R. & ELSE, G.D. 1995. The foraging range of Adélie Penguins at Bechervaise Island, Mac.Robertson Land, Antarctica as determined by satellite telemetry. In: Dann, P., Norman, I. & Reilly, P. (Eds). The penguins: ecology and management. Chipping Norton: Surrey Beatty & Sons. pp. 216–243.

KIRKWOOD, R. & ROBERTSON, G. 1997. The foraging ecology of female Emperor Penguins during winter. *Ecol. Monogr.* 67: 155–176.

KOOYMAN, G.L, KOOYMAN, T.G., HORNING, M. & KOOYMAN, C.A. 1996. Penguin dispersal after fledging. *Nature* 383: 397.

MARCHANT, S. & HIGGINS, P.J. 1990. The handbook of Australian, New Zealand and Antarctic birds. Vol. 1. Melbourne: Oxford University Press.

MOCHIZUKI, H. & KASUGA, I. 1985. Seabirds in the Australian sector of the Southern Ocean, January and February 1984. *Trans. Tokyo Univ. Fish.* 6: 155–165.

ROBINSON, S.A. & HINDELL, M.A. 1996. Foraging ecology of Gentoo Penguins *Pygoscelis papua* at Macquarie Island during the period of chick care. *Ibis* 138: 722–731.

SADLIER, R.M.F.S. & LAY, K.M. 1990. Foraging movements of Adélie Penguins (*Pygoscelis adeliae*) in McMurdo Sound. In: Davis, L.S. & Darby, J.T. (Eds). Penguin biology. San Diego: Academic Press. pp. 157–179.

SCOTT, J. 1994. Marine conservation at Macquarie Island. A marine conservation strategy and an account of the marine environment. Hobart: Parks and Wildlife Service, Tasmania.

STAHL, J.-C., JOUVENTIN, P., MOUGIN, J.-L., ROUX, J.-P. & WEIMERSKIRCH, H. 1985. The foraging zones of seabirds in the Crozet Islands sector of the Southern Ocean. In: Siegfried, W.R., Condy, P.R. & Laws, R.M. (Eds). Antarctic nutrient cycles and food webs. Berlin: Springer-Verlag. pp. 478–486.

TASKER, M.L., JONES, P.H., DIXON, T.J. & BLAKE, B.F. 1984. Counting seabirds at sea from ships: a review of methods employed and a suggestion for a standardised approach. *Auk* 101: 676–677.

VEIT, R.R., SILVERMAN, E.D. & EVERSON, I. 1993. Aggregation patterns of pelagic predators and their principle prey, Antarctic Krill, near South Georgia. *J. Anim. Ecol.* 62: 551–564.

WEAVERS, B.W. 1992. Seasonal foraging ranges and travels at sea of Little Penguin *Eudyptula minor*, determined by radiotracking. *Emu* 91: 302–317.

WILSON, R.P., SCOLARO, J.A., PETERS, G., LAURENTI, S., KIERSPEL, M., GALLELLI, H. & UPTON, J. 1995. Foraging areas of Magellanic Penguins *Spheniscus magellanicus* breeding at San Lorenzo, Argentina, during the incubation period. *Mar. Ecol. Prog. Ser.* 129: 1–6.

WOEHLER, E.J. 1992a. Records of vagrant penguins from Tasmania. *Mar. Orn.* 20: 61–74.

WOEHLER, E.J. 1992b. Records of nonbreeding seabirds from the Australian Antarctic Territory, 1954–1988. *Mar. Orn.* 20: 84–90.

WOEHLER, E.J. 1993. The distribution and abundance of Antarctic and sub-Antarctic penguins. Cambridge: Scientific Committee on Antarctic Research.

WOEHLER, E.J., HODGES, C.L. & WATTS, D.J. 1990. An atlas of the pelagic distribution of seabirds in the southern Indian Ocean, 1981 to 1990. *ANARE Res. Notes* 77: 1–406.