Antarctic Sea-Birds as Subjects for Ecological Research

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Abstract: The environment of the Antarctic and Subantarctic region is briefly described, mainly as it affects the breeding of sea-birds. The 36 species of 8 families that breed mainly in this region, and their feeding and nesting requirements, are listed.

Breeding distribution and annual cycles are analyzed in relation to these factors, and explanations of special cases and apparent anomalies are offered. Population ecology studies are summarized, including current work on the Wandering Albatross, *Diomedea exulans*, and Royal Penguin, *Eudyptes chrysolophus schlegeli*, at Macquarie Island. In the latter it is established that socially-induced deferment of maturity to 5–11 years of age is due to competition for feeding status at sea and not for nest-site or breeding status ashore.

Suggestions are made for future ecological research on Antarctic sea-birds. The necessity for better data on their foods, available and taken, is stressed, and also the unusual opportunities that some of these species offer for long-term population study.

1. Introduction

In this review the Antarctic region includes the high Antarctic and the Subantarctic. Each faunal zone grades into adjacent ones, so the empirical northern limit here set for the Subantarctic zone is the Antarctic Convergence plus those islands just north of it which have no woody vegetation, namely Marion and Prince Edward, the Crozets, Kerguelen and Macquarie (Fig. 1). This excludes islands that lie not much farther north, but which have woody plants and whose avifaunas contain many temperate zone species not found within the Subantarctic.

The review is confined to sea-birds, *i. e.* those species which obtain all or most of their food at sea or on the shore and thus form part of the marine ecosystem. It is also mainly concerned with aspects of breeding ecology, especially the factors that determine distribution, size and success of the breeding population. Critical data are lacking on the dispersion, numbers, food and mortality of most species during the non-breeding season, and investigation of the factors that regulate total population size would not be easy even if massive logistic support were available for pelagic operations in winter. Migrations and seasonal movements are not discussed in detail; during the past fifteen years banding has added useful evidence on a few species, but these results are inevitably biassed

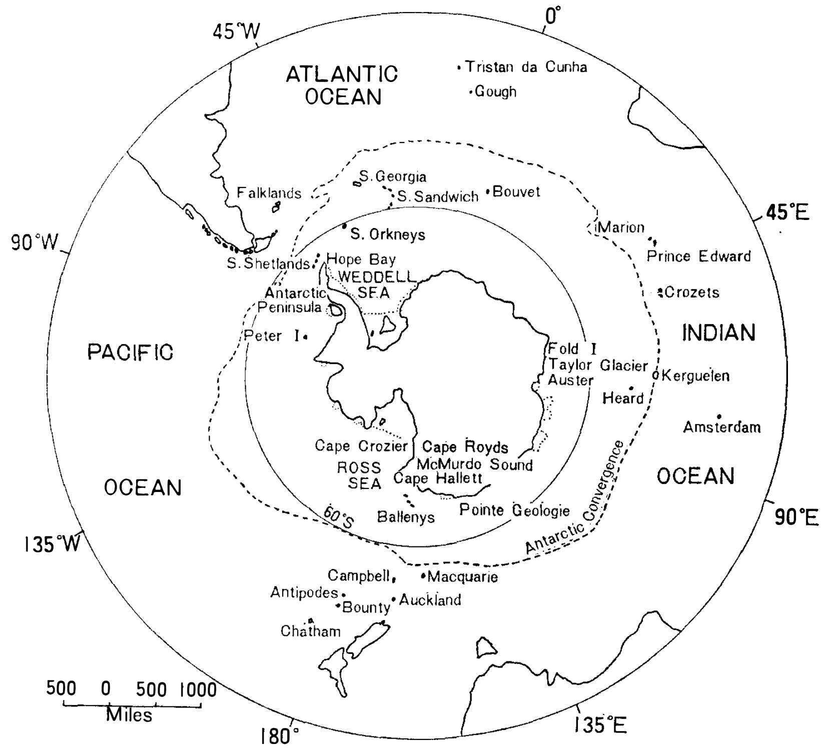


Fig. 1. Map of the Antarctic region showing place-names used in the text.

by the distribution of human populations and the difficulty of obtaining records throughout the Southern Ocean.

The considerable literature on various aspects of the ecology of Antarctic sea-birds is growing rapidly. Some important earlier papers, now superseded by several major and many minor publications, are not cited in this review. Nor are those in which the emphasis is ethological and the ecological content is limited. However, the nations now active in Antarctic research have lately prepared complete lists of their biological publications (for the First Symposium on Antarctic Biology held by the Scientific Committee for Antarctic Research at Paris in 1962). Also, their annual reports to S. C. A. R. outline current biological programmes and results. And the periodic reports of national banding schemes contain many records not yet published elsewhere.

MURPHY's (1936) classic "Oceanic Birds of South America" provides a comprehensive coverage of previous literature which has no later equivalent. FALLA (1937) deals fully with the results of two expeditions to the Australian Antarctic Territory and to Subantarctic islands in that sector, with many illustrations of breeding habitats. Recent reviews by the same authors discuss distribution of the Antarctic Procellariiformes (MURPHY, 1964) and high-Antarctic breeding birds

(FALLA, 1964) in the light of their ecological requirements. STONEHOUSE (1964) summarizes recent research, up to 1962, on all Antarctic and Subantarctic species. And VOOUS (1965), in a comprehensive ecological review of information published up to 1961, deals with breeding and pelagic distribution, breeding seasons, predation, food and migration of Antarctic and Subantarctic birds other than penguins.

Ecological-physiological studies of the Emperor Penguin, *Aptenodytes forsteri*, and Adelie Penguin, *Pygoscelis adeliae*, up to 1961 are fully reviewed by PRÉVOST and SAPIN-JALOUSTRE (1965); later French work on the Emperor Penguin is published in several short papers in *Oiseau*. BUDD (1961, 1962) has collated data on breeding biotopes and numbers of the same species. The unusual breeding cycle of the King Penguin, *Aptenodytes patagonica*, has been studied by STONEHOUSE (1960). SLADEN (1964) gives evidence for a recent increase in numbers and range of the Chinstrap Penguin, *Pygoscelis antarctica*, and Adelie Penguin, and relates this to increased food supply following depletion of whale stocks. A long-term population study of the Adelie Penguin is now under way at Cape Crozier (SLADEN), but the other species of *Pygoscelis*, the Chinstrap and the Gentoo Penguin, *P. papua*, have received little attention from ecologists. The crested genus, *Eudyptes*, has two Subantarctic species: the breeding of the Rockhopper Penguin, *E. chrysocome*, is described by WARHAM (1963), and a long-term breeding ecology and population study of the Royal Penguin, *E. chrysolophus schlegeli*, is in progress at Macquarie Island (CARRICK, 1964, p. 614). GWYNN (1953) has described the peculiar egg-laying habits of these species.

Of the four albatrosses, the Wandering Albatross, *Diomedea exulans*, is under study on its breeding grounds at Macquarie Island (CARRICK) and South Georgia (TICKELL), and its migrations between Subantarctic breeding islands and winter quarters in Australian waters have been shown by banding (GIBSON, 1963). The life-history and feeding ecology of the Black-browed Albatross, *D. melanophris*, and Grey-headed Albatross, *D. chrysostoma*, are also being studied at South Georgia (TICKELL, 1964; TICKELL and PINDER, 1966), but no similar work has been done on the Light-mantled Albatross, *Phoebetria palpebrata*. Seventeen species of petrel, and three storm-petrels, breed in the Antarctic region, and studies of breeding biology include the Giant Petrel, *Macronectes giganteus*, (WARHAM, 1962); the Cape Pigeon, *Daption capensis*, (PINDER, 1966); the Snow Petrel, *Pagodroma nivea*, (BROWN, in press); the Antarctic (Dove) Prion, *Pachyptila desolata*, (TICKELL, 1962), and Wilson's Storm-petrel, *Oceanites oceanicus*. (ROBERTS, 1940), with a full account of the extensive migrations of this species. A series of Australian and British papers on the circumpolar movements of the Giant Petrel has culminated in the account by TICKELL and SCOTLAND (1961). Little is known of the remaining species, especially those that are nocturnal and breed in burrows, but the feeding habits of several petrels are now being investigated at British bases (BECK).

Breeding and territorialism in the Brown Skua, *Stercorarius skua lonnbergi*, have been studied by STONEHOUSE (1956) at South Georgia, and at Macquarie Island PURCHASE (in preparation) has correlated its food sources, physical habitat and breeding success. YOUNG (1963a, b) carried out a similar study on McCormick's Skua, *S. s. maccormicki*. Co-operative banding of this species, initiated by EKLUND (1961), has revealed north-south as well as Antarctic coastal movements, and the project still continues. A three-year population study of the Antarctic Shag, *Phalacrocorax atriceps*, has recently been completed at Signy Island (HOWIE).

Finally, PRÉVOST (1963) has calculated the population biomass of breeding adult birds and seals, and their young, sustained by waters within reach of Pointe Géologie, Terre Adelie, in every month of the year.

At this stage a review of past and current ecological research on Antarctic sea-birds might indicate which aspects are desirable and profitable for future work. The reasons for the present emphasis on breeding ecology, with penguins the preferred subjects, are obvious. Adaptations to this extreme environment, especially by the bird forms so characteristic of the region, merit high priority. Equally, it is rewarding to choose species that are so amenable to study on land, as compared with their more mobile and cryptic counterparts in more complex habitats. A brief review of the Antarctic environment and of our ecological knowledge of the birds that inhabit it may suggest the most effective contributions that these Antarctic species can make to bird ecology in general.

2. Environment

Geography

The Antarctic Continent covers an area of about thirteen million square kilometres, extending north to between latitudes 65° S and 75° S, except for the indentations of the Weddell and Ross Seas (78° S) and the Antarctic Peninsula which reaches nearly 63° S (Fig. 1). Land free of permanent ice, either as coastal outcrops and islands or as inland mountain tops projecting through the ice, is only about 4.5 % of the whole, and some of this is too far from the coast to offer breeding sites for sea-birds.

The Southern Ocean extends north from Antarctica to South America, South Africa and Australia, a distance of 2500–3500 km. Most of it is 3500–5500 m deep and the continental shelf is narrow. Hydrologically and biologically it is divided into two by the Antarctic Convergence at 50°–55° S. The few small, isolated oceanic islands available as breeding places for birds are surrounded by a vast and rich feeding area in summer. During winter and spring the area of sea south of the Convergence is roughly halved by sea-ice which extends north from the Continent; it reaches its maximum extent in September, retreats to form a narrow belt around the coast in summer, and again extends from March onwards (Fig. 2). Unbroken "fast-ice" forms on the coast and persists throughout the year only in well-sheltered places such as deep narrow bays and among offshore islands. Farther out is the pack-ice zone, in constant movement with open water appearing and disappearing between the ice-floes. In a few places open water persists throughout the year within several miles of the coast.

Climate

On the coast of Antarctica the mean annual air temperature is –5° C or less; the winter minimum can be as low as -40° C, while in ice-free areas on still days it may rise to +9° C. At the Convergence the mean annual air temperature is about +5° C, and the annual range is small. Sea temperatures are very constant, about 0° C near the Continent and 3° C at the Convergence.

The long dark polar winter and continuous daylight in summer are well known. At McMurdo Sound (78° S), the sun is below the horizon for four months in winter and above it for the same period in summer. Along the east coast of the Continent (66° S) there are two hours of daylight and two of twilight even in midwinter.

Precipitation is fairly low over the whole area. On the coast it is about 20–25 cm of water equivalent, but this is augmented by snow blown from the inland. At Subantarctic islands rainfall is higher, *e. g.* 103 cm at Macquarie Island, and is evenly distributed throughout the year.

The mean annual wind speed at 60° S is over 40 knots, higher in winter than in summer. West winds predominate over a wide belt north of 65° S, and easterlies south of this. Katabatic winds blow down the slope of the ice plateau and up to 20 km out to sea; where the surface topography permits they are both strong and constant, they carry large quantities of snow to the coast, and they may disperse the pack-ice to form an inshore belt of open water.

Marine Productivity

The surface water of the Southern Ocean moves with the wind, westward south of 65° S and eastward north of it. It also flows northward, and at the Convergence this cold, poorly saline water (diluted by ice-melt) meets and sinks below warmer northern water. At a deeper level, warmer and more saline water carries nutrients southward. Wind-induced turbulence ensures continual mixing of the nutrient-rich deeper waters with the surface layer.

Marine photosynthesis is limited in winter by lack of light, and almost inhibited under ice, but in the open sea it never suffers from lack of nutrient salts. In ice-free water south of the Convergence, photosynthesis is low in winter, increases rapidly from September to December, and then falls more slowly until April. In the sea-ice zone it remains low until the ice breaks out, which is not until December or January near the coast. It is very high during the season of almost continuous daylight, and ceases when ice re-forms in autumn.

Zooplankton is densest in the surface 100 m during summer—January at the Convergence and January-March near the Continent. In winter there is little at the surface, but below 500 m there is a high concentration. Both zooplankton and the nekton which feed on it are extremely abundant, though not always evenly distributed.

The most important organisms as food for sea-birds are euphausiids, squids, and to a lesser degree fish. There is a north-south zonation, with smaller species of *Euphausia*, *e. g. E. vallentini*, north of the Convergence, large ones such as *E. frigida* and *E. superba* south of it, and the small *E. crystallorophias* in the ice belt. These crustacea can occur in extremely dense patches, but seasonal vertical migration has not been demonstrated. Study of the squids is just beginning, and they are also very abundant and occur in a wide range of sizes. Fish may be important near land, less so pelagically. It may be assumed that the nekton, such as squids, follows the zooplankton, so in winter less live food is available to surface-feeding birds than to diving species such as penguins.

Land Surface

The ice-free areas of the Antarctic Continent are bare rock with a sparse growth of lichens and mosses, offering as nest-sites only crevices, ledges and stony open spaces. These are all snow-covered in winter and liable to intermittent blockage by snow in summer. At the northern end of the Antarctic Peninsula, and in the South Shetland and South Orkney Islands, the mosses form extensive deep banks, and there are a few scattered vascular plants.

Islands on and just north of the Convergence have deep peaty soils with an extensive cover of grasses and herbs at lower levels, mosses and lichens on stony soil in the higher and more exposed places, and permanent snow at high altitudes (1200 m at Marion Island). South of the Convergence, islands such as Heard and Bouvet are intermediate in character. The larger islands, South Georgia and Kerguelen, offer a greater variety of altitude, climate and terrain than smaller ones in the same position relative to the Convergence. For instance, Heard Island lacks the extensive areas of tussock grass found on South Georgia, and the latter offers nesting habitats ranging from coastal rocks, cliffs and mountains with rocky ledges, to hill slopes and grassy ledges with deep soil for burrows and vegetation for nest-building, as well as flat open areas of grass.

The essential features of the Antarctic and Subantarctic environment as they affect sea-birds are the extremes of temperature, wind and day-length, with small annual variations; the abundant food supply over vast areas of ocean, which varies seasonally in availability to all but the deep divers, but little from year to year; and terrestrial breeding-places limited in area on the Continent and severely so in the Subantarctic, with the variety of nesting habitats decreasing southward.

3. Breeding Species

Though there is little doubt that all the breeding species of sea-birds, and most varieties, that occur in the Antarctic region are now on record, problems of systematics and taxonomy still remain. FALLA (1964) has illustrated and stressed the need for more adequate and critically-collected material, especially skuas.

Eight families and at least thirty-six species are represented, excluding another five species whose main range lies to the north and each of which breeds in small numbers at only one of the Subantarctic islands north of the Convergence (Table 1). These are the Sooty Albatross, *Phoebetria fusca*; the Fairy Prion, *Pachyptila turtur*; the Thin-billed Prion, *P. belcheri*; the Sooty Shearwater, *Puffinus griseus*; and Soft-plumaged Petrel, *Pterodroma mollis*. Among the other thirty-six, some closely-related forms with recognizable morphological (and doubtless physiological, ethological and ecological) differences are lumped here under one species, pending clearer proof of specific distinction. *Stercorarius skua* is the case that will probably find least acceptance, though VOOUS (1965) does not even separate the

Table 1. Breeding sea-birds of Antarctica and Subantarctic islands.

Families and species	Antarctic Continent	Peninsula and Subantarctic islands							
		South of Convergence					North of Convergence		
	Coast and offshore islands, including Balleny and Peter I (1)	Peninsula (2)	S. Shetlands S. Orkneys S. Sandwich (3)	Bouvet I. (4)	Heard I. (5)	S. Georgia (6)	Kerguelen (7)	Macquarie I. (8)	Marion I. Prince Edward I. (9)
SPHENISCIDAE									
Emperor Penguin *Aptenodytes forsteri*	B	68°S b]							
King Penguin *Aptenodytes patagonica*			S. Sa. [b	N. S.	b	B→	B	B]	B]
Adelie Penguin *Pygoscelis adeliae*	B B b	B	B	b]					
Chinstrap Penguin *Pygoscelis antarctica*	(b) b	B	B	B	(b)]	B]			
Gentoo Penguin *Pygoscelis papua*		[B	B	N. S.	B	B→	B	B]	B
Macaroni/Royal Penguin *Eudyptes chrysolophus*			[b	b	B	B→	B	Royal B]	B]
Rockhopper Penguin *Eudyptes chrysocome*					[B	? →	B→	B→	B→
DIOMEDEIDAE									
Wandering Albatross *Diomedea exulans*					? N.S.	[B→	B	B→	B→
Black-browed Albatross *Diomedea melanophris*					[b	B→	B	b →	(Prince Edward I)
Grey-headed Albatross *Diomedea chrysostoma*					?	[B	B	B→	B
Light-mantled Albatross *Phoebetria palpebrata*					[b	[B	B	B→	b]
Sooty Albatross *Phoebetria fusca*									[B→
PROCELLARIIDAE									
		M. giganteus					*M. halli*		
Giant Petrel *Macronectes giganteus* and/or *M. Halli*	b	b	B	N. S.	B	B→	B	B→	B→
Cape Pigeon *Daption capensis*	B B	B	B	B	B	b	b	b→	b→

	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	
Antarctic Fulmar *Fulmarus glacialoides*	b **B** **B**	**B**	**B**	**B**		b]				
Snow Petrel *Pagodroma nivea*	**B**←**B** p	**B**	**B**	b		b]				
Antarctic Petrel *Thalassoica antarctica*	←**B**]									
Blue Petrel *Halobaena caerulea*			p				**B**	b	**B**	
Antarctic (Dove) Prion *Pachyptila desolata*	b	p	**B**	p	**B**	**B**	**B**	**B**→	p	
Fulmar Prion *Pachyptila crassirostris*					**B**					also Antipodes, Bounty
Fairy Prion *Pachyptila turtur*								b→		also S. Aust., N. Z.
Thin-billed Prion *Pachyptila belcheri*							b			also Falkland
Medium-billed Prion *Pachyptila salvini*									**B**	also Crozets
Sooty Shearwater *Puffinus griseus*								[b →		
White-chinned Petrel *Procellaria aequinoctialis*						[**B**→	**B**		**B**→	
Grey Petrel *Procellaria cinerea*							[**B**	b	b→	
Great-winged Petrel *Pterodroma macroptera*							[**B**		**B**→	
White-headed Petrel *Pterodroma lessoni*							[**B**	**B**		
Kerguelen Petrel *Pterodroma brevirostris*							[**B**		**B**	
Soft-plumaged Petrel *Pterodroma mollis*									[b →	
HYDROBATIDAE										
Wilson's Storm-petrel *Oceanites oceanicus*	p←**B** b	**B**	**B**	(b)	**B**	**B**→	b]			
Black-bellied Storm-petrel *Fregetta tropica*			[b	(b)		b	b]			
Grey-backed Storm-petrel *Garrodia nereis*						[b →	b	b →		

	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)
PELECANOIDIDAE									
South Georgian Diving-petrel *Pelecanoides georgicus*					[**B**	**B**	**B**		**B**]
Common Diving-petrel *Pelecanoides urinatrix*					[**B**	**B**→	**B**→	b→	**B**→
PHALACROCORACIDAE									
Antarctic Shag *Phalacrocorax atriceps*		[b	(b)		b	**B**]			
Kerguelen Shag *Phalacrocorax albiventer*							[**B**	**B**	**B**
STERCORARIIDAE									
Great Skua *Stercorarius skua*	*S. s. maccormicki*			*S. s. lonnbergi*					
	p←**B** p	**B**	**B**	**B**	**B**	**B**→	**B**	**B**→	**B**→
LARIDAE									
Dominican Gull *Larus dominicanus*		[**B**	**B**		**B**	**B**→	**B**	**B**→	**B**
Antarctic Tern *Sterna vittata*		[b	b	b	b	**B**	**B**→	b→	(b)→
Kerguelen Tern *Sterna virgata*							[**B**		**B**]

	Total	Continent	South of Convergence	North of Convergence	
SPHENISCIDAE	7	2	6+1	4	a
DIOMEDEIDAE	4+1[a]	0	4	4+1[a]	*P. fusca*
PROCELLARIIDAE	14+4[b]	6	7	10+4[b]	b
HYDROBATIDAE	3	1	2+1[c]	1+2[d]	*P. turtur* *P. belcheri*
PELECANOIDIDAE	2	0	2	2	*P. griseus* *P. mollis*
PHALACROCORACIDAE	2	0	1	1	c
STERCORARIIDAE	1	1	1	1	*G. nereis*
LARIDAE	3	0	2	3	d
	36(+5)	10	25 (+2)	26 (+7)	*F. tropica* *O. oceanicus*

B: Breeding—numerous.
b : Breeding—few.
(b): Breeding recorded.
p : Breeding possible, but not certain.
N. S.: Not breeding because unsuitable terrain.
? : Not breeding, reason unknown.
[: Southern limit.
]: Northern limit.
←→: Breeding also to north or south in this sector.

northern hemisphere Great Skua, *S. s. skua*, specifically from the southern forms.

The first five families in Table 1, comprising thirty species of penguins and Procellariiformes, are pelagic feeders, with the partial exception of the Giant Petrel, *Macronectes giganteus*. Although the petrels outnumber the others, the Antarctic region has a much larger share, in biomass as well as species, of the world's penguins than it has of any other family. The adaptations to aquatic life that enable penguins to reach their plankton and nekton food throughout the year, without dispersing anything like so far as the surface feeders, are possible in the absence of serious mammal and bird predators on land. The other three families and six species are less specialized, feeding around the coasts and offshore waters, also on land in the case of the Skua and Dominican Gull, *Larus dominicanus*. Apart from the skuas, they are sedentary.

The wide range of food types on or at varying depths under the surface of the sea is reflected in the adaptations of size, structure and habit of this relatively small group of birds. The Wandering Albatross weighs 10 kg, 300 times as much as the 35 g Wilson's Storm-petrel. The specializations, particularly of wings, legs and fat-storage capacity, that enable birds to forage over and under vast areas of ocean and to starve for lengthy periods, impose corresponding restrictions on their terrestrial life. The penguin's flippers are powerful oars, and its short webbed feet are an effective rudder, that enable it to fly at speed under water and to catch fast-swimming fish at considerable depths as well as to evade its pinniped predators; but on land it is right out of its element. The long narrow wings of the albatrosses and petrels are well suited to effortless gliding for hours and many miles low over the waves, but their overloading by a relatively heavy body poses serious problems of landing and take-off, especially when terrain and wind are unfavourable.

The terrestrial inefficiencies of these sea-birds make them unusually approachable at their breeding-places, and even the skuas, that can avoid man, are often remarkably tame. Many species can be caught with ease, and large samples or even entire breeding groups can be marked for the individual identification which is essential for most field studies. Any difficulties of observation usually relate more to weather and terrain than to the birds. Their suitability is often further enhanced by a high degree of constancy of seasonal cycle in time, place and mate, and frequently by synchrony of seasonal activities.

4. Annual Cycles

The seasonal activities of birds are highly adaptive, selected for their contribution toward the ultimate result perpetuation of the genotype. It would be surprising if an environment with the physical extremes and regional differences of the Antarctic and Subantarctic did not evoke some unique features and diversity of avian annual cycles. But the rich and dependable seasonal food supply must ultimately dictate the pattern, however exacting the adaptations of any species to limitations of climate and nest-site must be to enable it to make the best use of its own particular food. In addition to surviving, the individual

Table 2. Annual cycles of Antarctic sea-birds.

Species	Cycle: Type	Cycle: Synchrony	Locality	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May
A. forsteri	W	S	66°	E →	→	H →	→	→	→	→	→ F		M	d	r	
			78°	r	E →	→	H →	→	→	→	→	→ F	(M)	d	d	
A. patagonica	W 1/2	O	All					M	M	ME	ME	MEH	MEH	EH	H	
				→	→	→	→	→	→	→	→ F	F	F	F	s	
P. adeliae	N	S	SO	d	d	d	d	d	r	E →	H →	→	→ F	M	d	
			78°	d	d	d	d	d	r		E → H	→	→ F	M	d	
P. antarctica	N	S	P	d	d	d	d	d	d	r E →	→	H →	→ F	M	d	
P. papua	N	O	Mq	s	s	s	s	E →	EH	EH	EHF	HF	F	FM	M	
			P	sd	sd	sd	s	s	s	s	E →	EH	HF	FM	M	
E. chrysolophus	N	S	Mq	d	d	d	d	r	E →	H →	→	→	→ F	M	M	
			H	d	d	d	d	d	r	E →	H →	→	→ F	M	M	
E. chrysocome	N	S	Gough	d	d	d	d	r	E →	H →	→	→	→ F		M	
			H	d	d	d	d	d	dr	E →	→	H →	→	→ F	M	
D. exulans	W 2	S	All								r	E →	→	H →	→	
				→	→	→	→	→	→	→	→ F	F	m	m	m	
				m	m	m	m	m	m	m						
D. melanophris	N	S	All	m	m	m	m	r	E →	→	H →	→	→	→	→ F	
D. chrysostoma	N	S	All	m	m	m	m	r	E →	→	H →	→	→	→	→ F	
P. palpebrata	N	S	All						r	E →	→ H	→	→	→	→	F
M. halli	N	S	K, Mq	s	s	s	s E →	→	→ H	→	→	→	→ F	F		
M. giganteus	N	S	Mq, H SG, C		s	s	s	s	E →	→	H →	→	→	→ F	F	
D. capensis	N	S	All						r		E →	H →	→	→ F		
F. glacialoides	N	S	C	d	d	d	d	d	r		E →	H →	→	→ F		
P. nivea	N	S	C	d	d	d	d	r			E →	H →	→	→ F		
T. antarctica	N	S	C						r	E →	→	H →	→	→ F		
H. caerulea	N	S	K	s				r		E →	→	H →	→	→ F		
P. desolata	N	S	Mq					r	r		(E) →	H →	→	→ F		
			SO							r	E →	→ H	→	→ F		
P. crassirostris	N		H	s	s	s	s	s	s	E →	→	H →	→ F	s	s	
P. salvini	N		Mn											F		
P. aequinoctialis	N	+	SG						r	E	E	H	H →	→	→	F
P. cinerea	W		K	(H) →	→	→	→	(F)						(E) →	→	
P. macroptera	W	+	K	E	E					F	F					
P. lessoni	N	S	K, Mq					r			E →	H →	→	→	→	F
P. brevirostris	N	S	K					E →	→	H						
O. oceanicus	N	S	K	m	m	m	m	m	m	r	r	E →	H →	→	→ F	
			66°	m	m	m	m	m	m	r	E →	→ H	→	→ F	m	
F. tropica	N		K SO								E	H				
G. nereis	N		K SG							(E)	(E)				F	

Species	Cycle: Type	Cycle: Synchrony	Locality	Seasonal events: May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May
P. georgicus	N	+	K SG					r	r	E→ r	→H E→	 →H→	 →	 →F		
P. urinatrix	N	+	K, H	s	s	s	s	s	s	E	E	H	(H)			
P. atriceps	N	O	SG P	s d	s d	s d	s d	s	E E	EH H→	EH →	EHF →	HF →	F →F	F d*	
P. albiventer	N	O	Mq	s	s	s	s	s	E	EH	EH	EH	HF	F	s	
S. s. lonnbergi	N	+	Mq	m	m	m	r	r	E	EH	H	F	F	s	sm	
S. s. maccormicki		S	78°	m	m	m	m	m	r	r	E	H→	→	→F	m	
L. dominicanus	N	+	All	s	s	s	s	s	s	E→	→H→	→	→F	M	s	
S. vittata	N	S O O	K, H SG, Mq P	 d	d M d	d s d	d s d	d s d	d E r	d EH E	r EH E	E→ EHF E	H→ HF	→ FM	→F FM F	FM FM
S. virgata	N	S	K	s	s	s	s	s	s	EH→	→	→F	(M)	s	s	

KEY   * to ice edge

Cycle Type—N : Normal spring to autumn breeding.
W : Chick tended through winter.
1/2 : 1 or 2-year cycle.
2 : 2-year cycle.
Synchrony—S : Highly synchronized, eggs laid during about 3 weeks.
+ : Intermediate, eggs laid during about 6 weeks.
O : Not synchronized, eggs laid during 3–4 months.
Seasonal Events— r : Return.
E : Egg-laying.
→ : Incubation.
H : Hatch.
➡ : Feeding young.
F : Fledging.
M : Moult.
s : Breeding adults sedentary (immatures may migrate, *e. g. M. giganteus*).
d : Dispersal around breeding-place.
m : Adults migrate outside Antarctic region.

has to breed and moult successfully, and the primary determinant of the annual cycle is the necessity to launch well-nourished but inexperienced young into the most favourable food situation possible. The timing and duration of the other seasonal activities hinge around this event, and are also adapted to spread the energy load throughout the year. This factor is of the utmost importance to species that have to lay down large reserves of fat to tide them over lengthy periods of starvation ashore, as in the penguins, albatrosses and petrels that forage far afield and are ill-adapted to land. The efficiency of some events in the cycle may be compromised, sometimes severely, in the interest of achieving the overall aim; the classic example of this is incubation by the Emperor Penguin on ice throughout the Antarctic winter.

The annual cycles, in so far as they are known, of the 36 species of Antarctic sea-birds are outlined in Table 2, and some idea of their food preferences, on which data are far from adequate, is given in Table 3. Three recent reviews have exposed the paucity of ecological information, relative to ornithology, on the marine life of the Southern Ocean. FOXTON (1956, 1964) had to base his account of seasonal variation in the plankton of Antarctic waters on the small-to-medium salps, copepods and chaetognaths sampled by one type of net that failed to catch important fauna certainly present, though he suggests that inclusion of *Euphausia superba* and other larger forms would not be likely to alter the picture. A review of the work of marine biologists on Southern Ocean crustacea, and of the food of sea-birds there, gives the impression that man can catch copepods (*Calanus*) while birds take amphipods. In a comprehensive review (POWELL, 1965) of the mollusca of Antarctic and Subantarctic seas, the scanty information on cephalopods is contained in a brief tail-piece. ANDRIASHEV (1965) reviews the Antarctic fish fauna and gives some facts on life-histories and planktonic distribution of young stages of some species of interest to sea-birds.

Five Subantarctic species, which cannot usefully be included in an assessment of the factors that determine seasonal cycle because information on breeding dates is too vague, are the Fulmar and Medium-billed Prions, Grey Petrel, and Black-bellied and Grey-backed Storm-petrels. Thirty-one species follow the normal routine of egg-laying in spring or summer, fledging of young in summer or autumn, moult in autumn, and dispersal or migration, if any, during winter. The other five rear their young throughout winter.

Of the 31 annual cycles that are known, 22 are well synchronized, laying being confined to three weeks or less and re-laying being physiologically impossible except in the Skua and the two terns. This group contains all the birds that breed on or near the Continent, including McCormick's Skua, where the short summer alone would impose considerable synchrony on species with such long incubation and fledging periods as penguins and petrels. However, two winter breeders, Emperor Penguin and Wandering Albatross, also have synchronized cycles. The four stout-billed euphausiid-feeding penguins—Adelie, Chinstrap, Macaroni/Royal, and Rockhopper—are in this group, with 13 Procellariiformes—Black-browed, Grey-headed and Light-mantled Albatrosses; Giant Petrel, Cape Pigeon and Antarctic Fulmar; Snow, Antarctic and Blue Petrels; Antarctic Prion; White-headed and Kerguelen Petrels; and Wilson's Storm-petrel. It also contains McCormick's Skua (but not the Brown Skua), the Antarctic Tern at Kerguelen and Heard Islands only (but not elsewhere), and the Kerguelen Tern.

The food types most frequently recorded from these synchronized breeders are cephalopods from 18, fish from 15, and euphausiids from 15, with carrion, birds and eggs, and other molluscs and crustacea less important (Table 3). Fish, cephalopods and euphausiids are taken by birds breeding throughout the entire region; but while the first two of these are important to species whose young fledge any time between December and May, the euphausiid-feeders all fledge their young in February-March. Also, the more southerly populations of the latter, *e. g.* Antarctic Prion and Adelie Penguin, feeding on the very rich plankton of high latitudes, can rear their young more quickly than their northern counterparts. In the fish-feeding Emperor Penguin, however, the young at Cape Crozier (78° S) fledge proportionately later than those at Pointe Géologie (66° S). Several other species show this latitudinal trend that is characteristic of North Temperate Zone birds, but Wilson's and the Grey-backed Storm-petrel appear to reverse it. The Giant Petrel, on the other hand, has two almost allopatric forms (BOURNE and WARHAM, 1966), overlapping at Macquarie Island; the colonial-nesters lay in October throughout their range right to the Continent, and the non-gregarious northern ones lay in August. The reasons for high synchronization in a species with such a wide range of terrestrial and pelagic food are not yet apparent, nor has the ecological basis of coexistence of the two forms been fully investigated. The highly-specialized Kerguelen Tern, feeding on flies, caterpillars, spiders and intertidal crustacea, completes its breeding cycle by January; and it is intriguing that the Antarctic Tern, with more catholic feeding habits, has a synchronized cycle from January to April at Kerguelen and Heard only, though the Kerguelen Tern does not occur on Heard. The general relationship between the breeding cycles of these sea-birds and the plankton and nekton on which they principally depend is obvious, but it would be straining present evidence too far to seek closer specific correlations. More detailed information is required on food species, and their seasonal availability and importance to birds with different capacities to obtain them. Accurate as the timing of these avian events are, the control of them may yet prove to be more complex than the relative simplicity of the Antarctic ecosystem might lead one to expect.

Six Subantarctic birds have laying periods of about six weeks—White-chinned Petrel, Great-winged Petrel (a winter breeder), South Georgian and Common Diving-petrels, Brown Skua, and Dominican Gull. None of these are known to feed on *Euphausia*; the species of cephalopods and fish taken by the two petrels are not on record; the diving-petrels are a typical case of closely-related species selecting different amphipod food (Table 3) and preferring different nest-habitats (Table 4) (EALEY, 1954); the Brown Skua takes a succession of seasonal foods, and the varied intertidal fauna on which the Dominican Gull relies is supplemented by carrion and soil invertebrates.

Five sedentary coastal species—King and Gentoo Penguins, Antarctic and Kerguelen Shags, and Antarctic Tern—have extended laying periods of three or four months. Fish is the major item in the diet of shags, it is important along with cephalopods to the slender-billed penguins, and is taken along with crustacea and intertidal organisms by the tern. Thus these five birds are sustained by food species that are available to them throughout the year, though probably more abundant and accessible in summer. It would be interesting to know why the shags manage to rear broods of three or four, and the Gentoo Penguin two or even three young, while the King Penguin takes a year to fledge its single chick, which may actually lose weight during winter (STONEHOUSE, 1960).

Egg-laying by Emperor Penguin, Grey Petrel and Great-winged Petrel before the winter solstice is a phenomenon not unknown elsewhere, but it is remarkable indeed in the winter darkness of Cape Crozier at 78° S. The Emperor Penguin

Table 3. Feeding requirements of Antarctic sea-birds.

Species	Locality	Feeding habitat						Food										Ref.
		Sea surface	Sea (diving)	Pack-ice surface	Pack-ice (diving)	Beach	Land	Birds	Eggs, chicks	Carrion	Fish	Cephalopods	Other molluscs	Euphausiids	Other crustacea	Intertidal organisms		
A. forsteri					+						+	+		+				5, 9
A. patagonica			+								+	+						13, M
P. adeliae					+							+	+	+	+			11
P. antarctica			+		+						+			+				1, 6
P. papua	Mq, H, K		+								+	+			+			3, 4, 5, 8, M
	P		+		+						+			+				1
E. chrysolophus			+									+		+	+			5, 7, M
E. chrysocome			+								+			+	+			4, 5, 8, M
D. exulans		+								+	+	+						5, 6, 8, M
D. melanophris	SG	+								+	+	+		+	+		Salps	14
D. chrysostoma	SG	+								+	+	+		+	+		Lampreys, Salps	14
P. palpebrata		+								+	+	+			+			3, 6, 8, M
M. giganteus		+				+	+	+	+	+		+	+	+				3, 8, 16, 18
D. capensis		+								+	+	+		+	+			2, 3, 8, M
F. glacialoides		+		+							+	+	+	+	+			2, 5
P. nivea				+							+	+	+	+	+			2, 5
T. antarctica		+	(+)								+	+		+	+			2, 5, 16
H. caerulea	K, Mq	+									+	+						7, M
	Sea	+												+				2
P. desolata		+										+	+	+	+			4, 8, 14, M
P. crassirostris		+									+		+		+			3, 4
P. salvini		+											+	+				2
P. aequinoctialis		+									+	+		+	+			6, 8, 16
P. cinerea		+									+	+						5, 8
P. macroptera		+									+	+						5, 8, 16
P. lessoni		+									+	+			+			8, M
P. brevirostris		+										+						8
O. oceanicus	K	+										+						8
	Sea	+										+		+	+			5, 16
	P	+												+				10
F. tropica		+									+	+						2, 8
G. nereis	Mq	+											+					M
P. georgicus	H		+												+*		**Euchaeta Euthemisto*	4
P. urinatrix	H		+												+*		**Hyperiella*	4
P. atriceps			+								+			+	+			3, 6, 16

Species	Locality	Feeding habitat						Food										Ref.
		Sea surface	Sea (diving)	Pack-ice surface	Pack-ice (diving)	Beach	Land	Birds	Eggs, chicks	Carrion	Fish	Cephalopods	Other molluscs	Euphausiids	Other crustacea	Intertidal organisms		
P. albiventer	Mq K		+ +								+ +				+		 Echinoids	M 8
S. skua	SG,Mq 78°	+ +				+	+ +	+	+ +	+	 +	+					Rabbits, etc.	12, M 18
L. dominicanus						+	+			+	+					+	Soil invertebrates	4, 6, 8, M
S. vittata	K,H,Mq SG,SO		+ +			+ +					+ +			 +	+ +	+		3, 4, 8, M 6
S. virgata						+	+									+	Insects, Spiders	8

KEY

+ : Important food item.
+ : Common food item.
+ : Minor food item.

For key to numbers under "Ref", see Reference List at end of this paper.
M : unpublished data from Macquarie I.

that fledges a young one in December and moults in February, has barely two months' respite if it is to breed each year, a fact that, most surprisingly, has not yet been proved with banded birds. To the enigma of what proximate stimulus leads to the Emperor Penguin laying its egg in the dark, can be added the question why a bird that feeds on fish, with some squids and euphausiids, should be so highly synchronized. One of the rigorous adaptations of this species, the necessity for breeding adults and chicks to huddle during blizzards, means that those out of step would succumb (PRÉVOST and SAPIN-JALOUSTRE, 1965).

It is probably no accident that it is the two largest penguins and the largest albatross that require most time to raise a single chick (Table 2). The two species, King Penguin and Wandering Albatross, that lay in one summer and fledge their young in the next, each take fifteen months for successful completion of breeding and moulting. The extended four-month laying period of the former would enable an early breeder of one season to lay late in the next, and then miss a season; the existence of such an unusual cycle still awaits proof from banded individuals. It is now well established at Macquarie Island that successful Wandering Albatrosses breed every second year. This small population of about 25 nests each year is widely scattered, yet even birds breeding for the first time conform to the short laying period in late December, which is uniform throughout the range (VOOUS, 1965). King Penguin and Wandering Albatross show that there is no essential relationship between synchrony of breeding and degree of gregariousness or size of colony. It is not obvious what the latter would lose by being less synchronized, for it feeds on cephalopods, carrion and fish. Pairs remain very faithful indeed to their site and mate, and groups of breeding and adolescent birds indulge in much communal display, so return of individuals to the breeding-place at the same time would help to maintain these bonds and also shorten the period of hazardous visits to land.

What is the advantage of winter breeding? VOOUS (1965), referring to the Grey and Great-winged Petrels, suggests that it avoids inter-specific competition for nesting-holes, and fledges the young into a rich food supply in early spring. It would have to be shown that the species of fish and cephalopods on which these petrels feed are most available at that time. The winter-breeding penguins and albatross are not only the largest Antarctic sea-birds, but their main foods, fish and cephalopods, are available throughout the year without undergoing a high seasonal flush. Breeding-space on land or ice is not a limiting factor, and in any case all three species require the site throughout the year. The limited capacity of the parents to supply these particular foods to the chick seems a likely explanation of its slower growth; the young Emperor Penguin, nourished from the rich off-shore waters of Antarctica, actually grows faster than its close relative the King Penguin.

After breeding, the event in the annual cycle that makes a heavy demand on the bird's energy is the moult, and in some cases migration. The penguin has to come ashore to moult, with stored fat to sustain it during several weeks of starvation. Penguins moult in the breeding area, often at their own nest-site, and in winter they appear to remain sedentary or disperse throughout adjacent feeding areas. Albatrosses and petrels moult slowly at sea, and other birds remain active while they do so ashore. The variety of migration patterns reflects the reduced carrying capacity of the breeding areas outside the favourable season. Recoveries of banded birds are steadily providing data on, for example, the global movements of Wandering Albatross (GIBSON, 1963), the similar partial migration of Giant Petrels (TICKELL and SCOTLAND, 1961), and the Antarctic coastal and northern journeys of Skuas. Much remains to be found out.

Nearly all of these Antarctic sea-birds are out of the ornithologist's reach when the factors that determine overall population size are operating. No direct studies of population regulation have been attempted, but a few long-term projects at breeding-places are obtaining good data on annual survival and breeding population size. Results on the Royal Penguin at Macquarie Island (CARRICK, in preparation), where the progeny of a study colony have been banded since 1956, show that the breeding population (measured by the occupied area, density being uniform) has remained constant, that only about 10 per cent of the fledged chicks survive to six years old (first laying occurs at 5–11 years of age), and that the annual survival rate of breeding birds is around 80–90 per cent.

5. Breeding Distribution

The breeding areas occupied by Antarctic sea-birds range from a single oceanic island to the entire region plus part of the Temperate Zone (Table 1). Three main factors determine the breeding distribution of each species:

a) the appropriate food within such effective range of a suitable nest-site that at least one chick can be reared successfully in most seasons;

b) the propensity for speciation, which has been high in the prions so that four species each occur on one island only in this region, but low in the widespread Skua, Dominican Gull, Gentoo Penguin, Giant Petrel and Cape Pigeon, the regional forms of which attain only subspecific rank, as do the allopatric Macaroni and Royal Penguins;

c) population pressure, due to high survival or productivity, leading to colonization of new breeding-places.

The known breeding distribution of each species is shown in Table 1. Data are not complete for the less frequented coasts, the more inaccessible islands, and the more cryptic species, *e. g.* smaller burrowing or crevice-nesting petrels of nocturnal habit. But, with good information available on the relevant physical factors of terrain and climate, present knowledge of birds and breeding-sites compares more than favourably with that of food supplies and specific feeding habits (Tables 3 and 4). Several recent writers (FALLA, 1964; MURPHY, 1964; SLADEN, 1964; VOOUS, 1965) have drawn attention to the need for more extensive, critical and quantitative studies of the pelagic invertebrates of the Southern Ocean, and of avian use of them, before meaningful correlations with bird distribution can be made. These reviewers, and MACKINTOSH (1960) have stressed the circumpolar zonation of many Antarctic birds, reflecting the latitudinal gradation of ecological conditions outward from the Continent to the Convergence. The polar ice mass is the basic factor, and as oceanographic and climatic conditions ameliorate and habitats become more complex with decreasing latitude, the variety of breeding species increases. There are 10 around the Continent, 25 on the Antarctic Peninsula and six islands south of the Convergence, and 26 (plus 5 that really belong to the South Temperate Zone) on the three island groups just north of the Convergence (Table 1). The discontinuity due to wide distances between the isolated Subantarctic breeding-places does not affect the zonal distribution of penguins and many petrels, for their pelagic foods show marked circumpolar continuity (ANDRIASHEV, 1965; DAVID, 1964; VERVOORT, 1965).

Antarctic breeding birds fall into several distributional categories, with some species rather uncertainly placed on account of marginal populations and incomplete data. The west Pacific sector, with only the little-known Peter I Island (70° S), presents an inevitable gap, and in the following list species that breed in any substantial part of the sector from South America eastwards to New Zealand are regarded as circumpolar (C); other letters indicate the Atlantic (A) and Indian (I) Ocean sectors and the islands of South Georgia (SG), Heard (H), Kerguelen (K), Marion (Mn) and Macquarie (Mq).

Zonal Distribution

ANTARCTIC CONTINENT

C Emperor Penguin (also marginal on Peninsula at 68° S) (Fig. 2)
C Antarctic Petrel
[C McCormick's Skua: also on Peninsula]

CONTINENT AND ISLANDS SOUTH OF CONVERGENCE

C Adelie Penguin

C Cape Pigeon (also marginal on Kerguelen, Macquarie, etc.)
C Antarctic Fulmar
C Snow Petrel
C Wilson's Storm-petrel (also marginal on Kerguelen, Falklands, etc.)

CONTINENT TO TEMPERATE ZONE

C Great Skua, all regional forms

PENINSULA AND ISLANDS SOUTH OF CONVERGENCE

A Chinstrap Penguin (also breeds on Peter I and possibly Balleny and Heard)
[C Giant Petrel, southern form: marginal on Continent, Peninsula, Macquarie and possibly Marion and Crozets]

PENINSULA AND ALL SUBANTARCTIC ISLANDS

C Antarctic (Dove) Prion (also marginal on Continent and Aucklands)

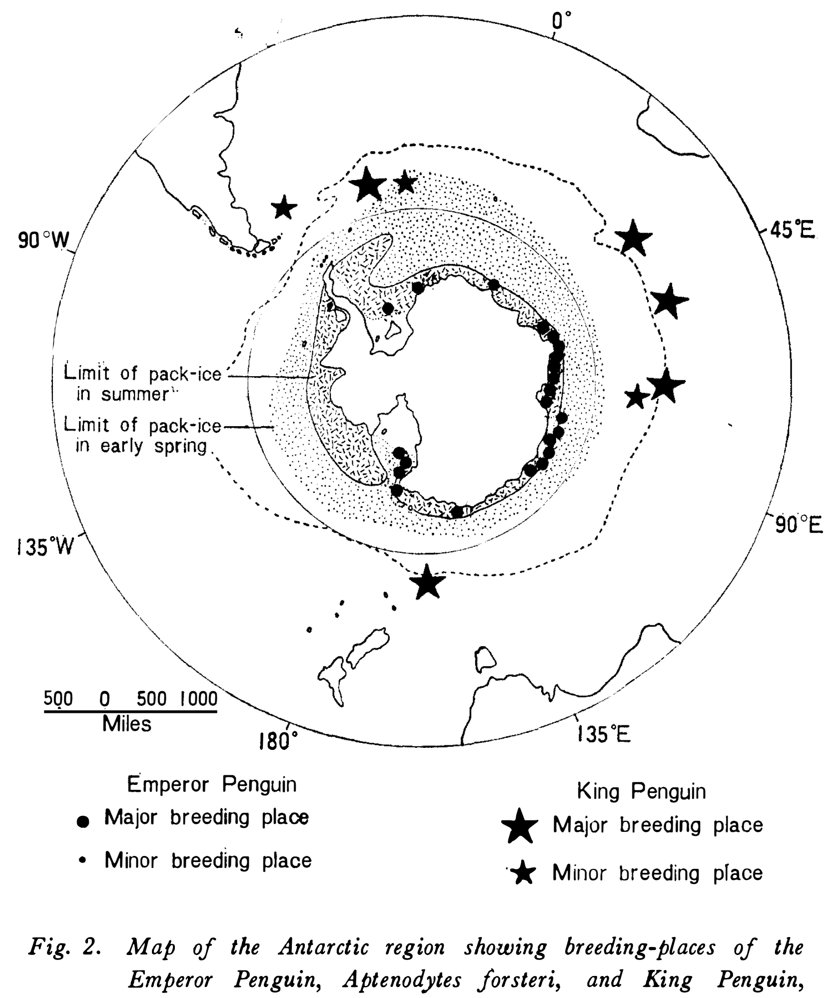


Fig. 2. Map of the Antarctic region showing breeding-places of the Emperor Penguin, Aptenodytes forsteri, and King Penguin, Aptenodytes patagonica.

A, I Black-bellied Storm-petrel (very inadequate data)

PENINSULA TO TEMPERATE ZONE

C Gentoo Penguin (fairly common on Falklands)
C Giant Petrel, all forms (marginal on Peninsula and Continent)
[C Brown Skua]
C Dominican Gull
C Antarctic Tern (most numerous on South Georgia and Kerguelen) (Fig. 3)

ISLANDS NEAR CONVERGENCE (NORTH AND SOUTH)

C King Penguin (also marginal at Falklands, South Sandwich and Heard) (Fig. 2)
C Macaroni/Royal Penguin (also marginal at South Shetlands)
A, I South Georgian Diving-petrel

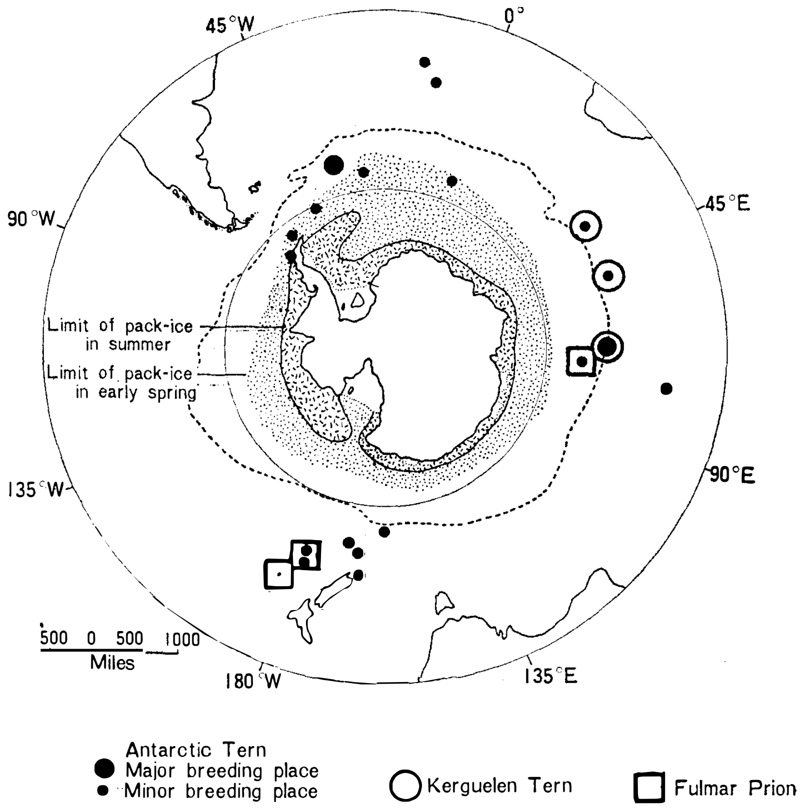


Fig. 3. Map of the Antarctic region showing breeding-places of the Fulmar Prion, Pachyptila crassirostris, Antarctic Tern, Sterna vittata, and Kerguelen Tern, Sterna virgata.

ISLANDS NEAR CONVERGENCE TO TEMPERATE ZONE

C Rockhopper Penguin (absent from South Georgia)
C Wandering Albatross (absent from Heard)
C Black-browed Albatross (marginal on Heard and Macquarie)
C Grey-headed Albatross (absent from Heard)
C Light-mantled Albatross (marginal on Heard)
A, I White-chinned Petrel
C Grey-backed Storm-petrel (mainly Temperate Zone)
C Common Diving-petrel

ISLANDS NORTH OF CONVERGENCE

I, Mq White-headed Petrel (also at Aucklands)
I Kerguelen Petrel
I, Mq Kerguelen Shag

ISLANDS NORTH OF CONVERGENCE TO TEMPERATE ZONE

[I, Mq Giant Petrel, northern form: on Kerguelen, etc.; smaller numbers on Macquarie and perhaps Falklands]
I Blue Petrel (marginal on Macquarie; perhaps on South Orkneys)
I Great-winged Petrel

Restricted Distribution

ISLANDS SOUTH OF CONVERGENCE

H Fulmar Prion (also on Antipodes, Bounty and Chathams) (Fig. 3)
SG Antarctic Shag (also marginal on Heard and Peninsula)

ISLANDS NORTH OF CONVERGENCE

[Mq Royal Penguin, subspecies of Macaroni]
Mn Medium-billed Prion (also on Crozets)
K Grey Petrel (also marginal on Marion, etc. and Macquarie)
K,Mn Kerguelen Tern (also on Crozets) (Fig. 3)

Thus 22 species have a circumpolar breeding distribution and 5 a partial one; 3 are limited to the Indian and 1 to the Atlantic Ocean sectors; and 5 are more-or-less restricted to one Subantarctic island. The contrasts of latitudinal range are equally great, from the Antarctic Petrel, confined to the coast of the Continent, to the Skua, Cape Pigeon, Giant Petrel and Antarctic Prion that breed throughout the whole region and even penetrate the South Temperate Zone. The Dominican Gull and Gentoo Penguin are almost as cosmopolitan. These differences between species, and some apparent anomalies of breeding distribution, should be explicable mainly in terms of the feeding and nesting requirements that jointly determine where successful breeding is possible (Tables 3 and 4). Analysis of nest-site preferences reveals that 9 of these sea-birds require open, fairly level, areas of ice, beach, grass or bare ground; 7 require

Table 4. Nesting requirements of Antarctic sea-birds.

Species	Social habit	Type of site	Material
A. forsteri	Large, dense colony, non-territorial	Level sea-ice, stable May to December; shelter	None
A. patagonica	Large dense colony	Level area behind beach; shelter	None
P. adeliae	Large, more open colony	Sheltered, well-drained rocky area	Stones
P. antarctica	Large, more open colony	Sheltered, well-drained rocky area	Stones
P. papua	Small open colony	Sloping or flat ground	Grass; stones
E. chrysolophus	Large dense colony	Level or gently sloping ground; shelter	Stones
E. chrysocome	Large to small open colony	Rock or sloping ground	Grass; stones
D. exulans	Large open colony to single nest	Wide ledge or flat ground; exposed to wind	Grass and moss
D. melanophris	Large open colony	Hillside or ledge	Grass and moss
D. chrysostoma	Large open colony	Hillside or ledge	Grass and moss
P. palpebrata	Single nest to small open group	Hillside ledge	Grass and moss
M. giganteus	Medium-sized open colony to solitary	Flat or gently sloping area; exposed to wind, or sheltered	Grass; stones
M. halli	Solitary, or small dispersed group	Sheltered by rock stack or long vegetation	Vegetation
D. capensis	Large to small colony	Rock ledge or shallow crevice; exposed to wind	Few stones
F. glacialoides	Large colony	Rock ledge or shallow crevice; sheltered	Few stones
P. nivea	Large to small colony	Deep rock crevice	None
T. antarctica	Large colony	Rock ledge or shallow crevice; exposed to wind	Stones
H. caerulea	Large colony	Burrow under *Azorella* or grass	Little vegetation
P. desolata	Large colony	Burrow under *Azorella* or *Acaena*; shallow rock crevice	Little vegetation
P. crassirostris	Large colony	Deep rock crevice	Few stones
P. salvini	Colony	Burrow under *Azorella*	Little vegetation
P. aequinoctialis	Colony	Burrow in soft damp soil; sheltered	Vegetation
P. cinerea	Colony	Burrow under *Azorella* or *Acaena*	Vegetation
P. macroptera	Small colony or isolated burrow	Burrow under *Azorella* or *Acaena*	Vegetation
P. lessoni	Medium-sized to large colony	Burrow under *Azorella* or in bare soil	Little vegetation
P. brevirostris	Colony	Burrow in soft deep soil	Vegetation

Species	Social habit	Type of site	Material
O. oceanicus	Medium-sized to large colony	Deep narrow rock crevice; burrow in moss bank	None
F. tropica	Colony	Rock crevice; burrow in bare soil	None
G. nereis	Colony	Base of tussock grass	Little vegetation
P. georgicus	Large colony	Burrow in bare soil on flat or gently sloping ground	Few stones
P. urinatrix	Large colony	Burrow under tussock or moss on steep slope	Little vegetation
P. atriceps	Medium-sized open colony	Coastal rocks	Grass and algae
P. albiventer	Medium-sized open colony	Coastal rocks	Grass and algae
S. skua	Isolated nest territory	Short vegetation; rock	Little vegetation; none
L. dominicanus	Isolated nest territory	Ledge on rock or hillside near beach	Little vegetation
S. vittata	Isolated nest territory	Bare soil or short vegetation	Little vegetation
S. virgata	Isolated nest territory	Bare soil or short vegetation	Little vegetation

rocky or rough ground, sometimes with vegetation; 3 need grass-covered slopes; 3 use cliff ledges; 4 seek the safety of deep crevices in cliffs or rocks; and 12 burrow into soil or dense vegetation.

The distribution of land places the first broad limit on breeding possibilities, and this is further reduced by the unsuitability of large stretches of the ice-covered Antarctic coast, and even of some oceanic islands such as Bouvet with few beaches. No doubt the uneven distribution of pelagic food species, or their inaccessibility, further reduces the number of potential breeding-places, an obvious example being the pack-ice which is the special feeding habitat of the Snow Petrel.

The widespread species listed above are relatively unspecialized in both food and nest-site requirements. The Giant Petrel and Skua are generalized scavengers and predators on land, and also take squid, fish and crustacea at sea; both can use stones or vegetation for their shallow surface nests. The Antarctic Prion feeds on a wide range of small euphausians, amphipods, pteropods and even squid (Ealey, 1954; Tickell, 1962); it burrows into soil but can use rock crevices in the southern part of its range. The Cape Pigeon feeds at sea on fish, squid, crustacea and carrion, including the by-products of whaling; it nests on cliff ledges but does not require a crevice, and the comparatively small numbers reported breeding in lower latitudes, even where it is plentiful at sea, may be due to the difficulty of searching coastal and off-shore cliffs, at Macquarie and Kerguelen for example. The Gentoo Penguin feeds on fish, squid and amphipods, and it can use either vegetation or stones to make its large nest. The Dominican Gull is a general shore-feeder and scavenger, the Antarctic Tern a shore and shallow-water feeder, and both nest in shallow scrapes on moss, grass or bare ground, or among rocks. Wilson's Storm-petrel breeds from the Continent to Kerguelen, though not on Marion or Macquarie; its crustacean diet varies with locality, it also takes squid, and its versatility is shown by the inclusion of North Atlantic fish in winter; it breeds in deep rock crevices or in burrows in thick moss (ROBERTS, 1940), but it may be unable to burrow in soil for at Kerguelen it nests on the mountains.

In Continental species, such as the Emperor and Adelie Penguins and the Snow Petrel, with coastal circumpolar breeding ranges, the problem of bringing adequate feeding and nesting resources together is intensified by the extreme weather that freezes up the former and often severely limits the availability of the latter. Despite the most unusual physiological and behavioural adaptations (PRÉVOST and SAPIN-JALOUSTRE, 1965), these birds do not always succeed in overcoming adversity. The embayed or otherwise sheltered sea-ice on which 21 of the 23 Emperor Penguin colonies occur (Fig. 2; Plate 1) represents a compromise site with no margin for the exceptional season. Apart from the fact that sea-ice is the only Continental landfall available and suitable for a swimmer with the build of the Emperor Penguin, the level surface is necessary for huddling behaviour with egg or chick on foot. But years vary, and the more stable ice may sometimes be too far from open water when the young are due to depart in January, and in less protected sites it may break away too soon and cause catastrophic losses of chicks not ready for independence (BUDD, 1961). Breeding-space is superabundant at all Emperor Penguin sites, but the known colonies are distributed around the Continent in a manner that would enable the estimated total of over 250,000 birds to make the most effective use of their fishing-grounds (Fig. 2).

The enormous colonies of Adelie Penguins are similarly distributed, but this euphausiid-eating species can rear its young in the short summer and requires exposed rocky ground, sheltered from wind and snow, with stones to raise the eggs and small chicks above ground level to prevent burial during snowstorms or flooding during thaws (Plate 1). The Snow Petrel feeds in the pack-ice on particles of fish and plankton crushed by the floes. For nesting it requires the safety (from Skuas) of a deep rock crevice; its problem is to find a site not filled by fine moraine debris, for it does not excavate, nor continually blocked by wind-blown snow (BROWN, in press). Some escape the latter on offshore islands beyond the influence of the katabatic winds, or on inland mountains above the level of blown snow (SIPLE and LINDSEY, 1937), and the advantage of a good site offsets a flight over even 300 km to the sea (LØVENSKIOLD, 1960).

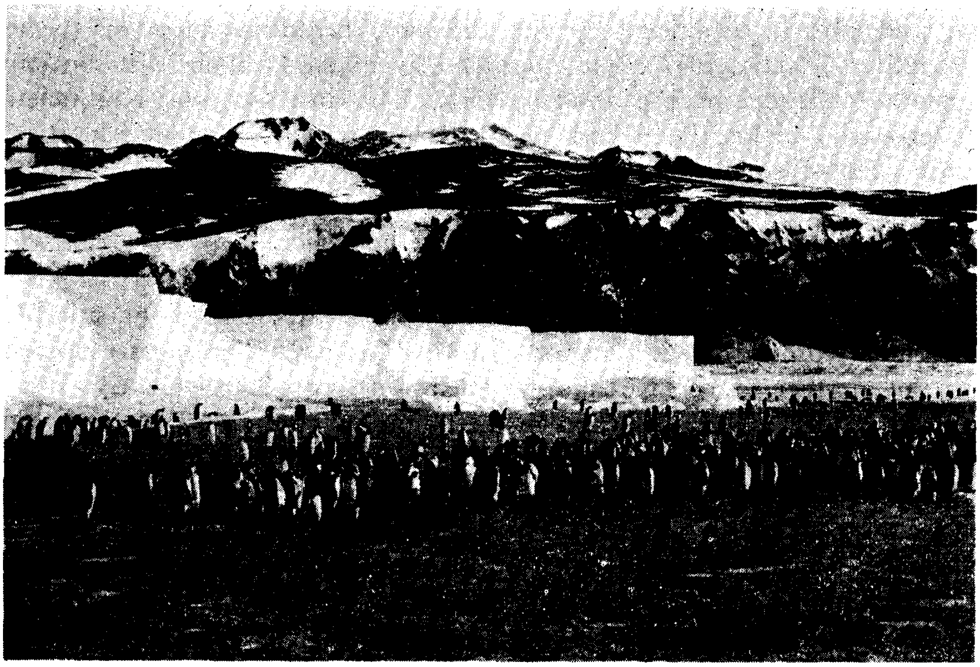
Five valid species of Antarctic sea-birds have breeding ranges restricted mainly to one Subantarctic island, with subsidiary populations on other islands, adjacent or distant. The Fulmar Prion on Heard Island and Antipodes-Bounty (FALLA, 1940; FLEMING, 1941) shows surprising discontinuity. The variations of bill size and shape by which prions are classified suggest significant food specialization, and this is supported by the different breeding dates of species that occur together (FALLA, 1937), but whether this explains their distribution must await more evidence on the food species. The insectivorous Kerguelen Tern fills a terrestrial niche there and on the Crozets and Marion Island, distinct from the shore-frequenting Antarctic Tern; its absence from colder Heard Island is understandable. Its sedentary habit may prevent it from bridging the foodless gap to other potentially suitable islands such as Macquarie, where its introduction would be an experiment of some scientific interest.

The failure of some widespread species to occupy apparently suitable parts of their range could throw light on limiting factors. The most unexpected of these is the absence of the Rockhopper Penguin from South Georgia, an island well suited to it, especially when it is abundant on Heard Island, similarly distant from the Convergence. It feeds on *Euphausia* and other crustacea; the large *E. superba*, the 9.0 cm adults of which are the dominant euphausiids around South Georgia at some seasons, is replaced by smaller species at Heard and lower-latitude breeding-places. The bill of the Macaroni Penguin is 6.5 cm long, but the Rockhopper Penguin's is only 4.5 cm, so study of the food of the latter should take into account the possibility that species and stages of appropriate size may be lacking at South Georgia during an important part of the Rockhopper Penguin's breeding-moult cycle. Heard Island also has its deficiencies, notably the Wandering Albatross but also the Grey-headed Albatross, while Black-browed and Light-mantled Albatrosses, and King Penguin, are marginal (DOWNES *et al.*, 1959). These birds are well represented on nearby Kerguelen, and on South Georgia. They are large species, but it would be surprising if their food were in short supply around Heard, south of the Convergence, compared to Kerguelen. Squid, crustacea and fish are reported from the Light-mantled Albatross at Heard, and elsewhere the albatrosses eat mainly cephalopods, fish and carrion at sea, while the King Penguin takes fish and cephalopods. The albatrosses nest on the wind-swept west sides of other islands, and the clumsy Wandering Albatross needs an open fairly flat area for landing and take-off; all three need good vegetation for the large nest that keeps the egg and chick dry. These requirements are inadequate on Heard Island.

Evidence for an increase in range and numbers of the pygoscelid penguins, the Chinstrap Penguin in particular, has been given by SLADEN (1964). He advances the hypothesis that the removal of whales equal to 300,000,000 penguins every year must affect their numbers through the common food supply. The opportunity should be taken to document this process, and once again proof of the causes will rest on the relevant information on plankton, which itself may yet be subject to economic exploitation that will further complicate the issue.

The broader aspects of the distribution of Antarctic birds can be related to their feeding and nesting habits, and in some species particular requirements evidently limit occurrence. There is scope, however, for more complete information on the distribution of some species, including assessment of abundance and definitive

Plate 1

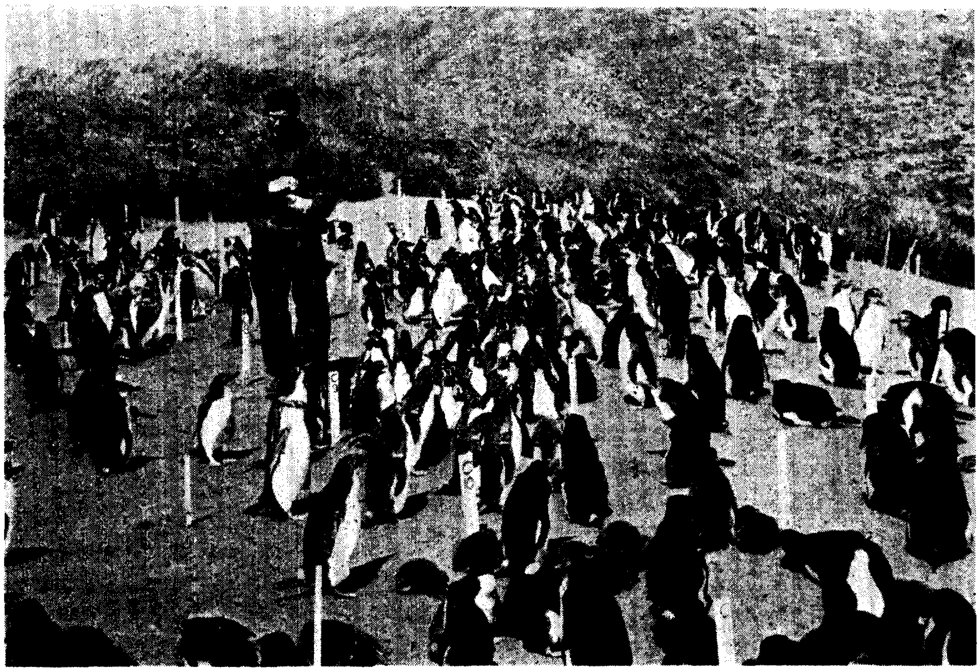


Emperor Penguin, Aptenodytes forsteri, colony on frozen sea-ice at Cape Crozier (78° S), October 1961. This breeding-site is sheltered by the Ross Ice Barrier and Ross Island.

Adelie Penguin, Pygoscelis adeliae, placing a stone during nest-building at Cape Crozier (78° S), October 1961. The nest of stones ensures drainage of snow-melt and keeps the egg and chick dry.

Plate 2

Wandering Albatross, Diomedea exulans, at Caroline Cove, Macquarie Island, January 1966. The adolescent male at an empty nest is displaying and calling to a similar female flying overhead. The pair frequently displayed at this nest-site, where they will probably nest in future.



Royal Penguin, Eudyptes chrysolophus schlegeli, study colony at Bauer Bay, Macquarie Island, January 1966. The grid of stakes enables nest-sites to be identified, and observers can move slowly among the birds without disturbing them. *(Photographs taken by R. Carrick)* analysis of nest-sites. Observations on feeding behaviour and foraging ranges, which are little known, and specific regional and seasonal data on food taken, especially fed to the young, are needed. It is felt that a good deal of information exists, in records and collections, that is not readily available at present, and it would seem well worth while to take stock of this before proceeding with the much-needed task of surveying the plankton, nekton and other foods that sustain Antarctic sea-birds.

6. Population Ecology

Antarctic sea-birds have low reproductive rates. Procellariiformes lay one egg, some penguins and other birds lay two or three, and losses during breeding are often heavy. Taking into account the period of immaturity and other factors, the proportion of young that eventually breed must be very low in many species. Their correspondingly high longevity can be inferred, for the numbers of most species remain stable. The population turn-over of the Wandering Albatross, with its two-year cycle, and other Subantarctic petrels and penguins, must be among the slowest of any animals. Constancy of return of individuals year after year to breed at the same place makes these species ideal subjects for the study of reproductive ecology and associated physiology and behaviour, but the other side of the population equation, mortality and its causes, can only be inferred from survival data obtained on land.

Quantitative studies of breeding performance fall into two classes: short-term, for one or two seasons, on adults of unknown age; and long-term, on population samples of known age/sex structure. Data from eight Antarctic studies are available, and six of them, on four Continental species, are short-term because the turn-over of biologists seldom matches the longevity, and sometimes not even the adolescent period, of their subjects. The long-term studies are on two Macquarie Island birds in which the return of marked individuals to their birth-place virtually eliminates the emigration-immigration factor so difficult to assess in field population work on homeotherms.

In the Emperor Penguin colony at Pointe Géologie, from 6081 eggs there were 4664 chicks in December 1952, equal to 77 per cent, and in 1956 the figure was 76 per cent (PRÉVOST and SAPIN-JALOUSTRE, 1965). However, blizzards in the spring of 1952 caused heavy chick losses after a good hatch, whereas in 1956 nearly three times as many eggs failed as in 1952. The variable effects of weather in different seasons, years and places in this risky environment are further demonstrated by the survival of Emperor Penguin chicks to October at three other colonies (BUDD, 1962):

	Taylor, 3000 pairs	Fold Island, 1000 pairs	Auster, 12000 pairs
1957	71 per cent	24 per cent	—
1959	32 per cent	27 per cent	57 per cent
1960	26+ per cent	—	—

At Hope Bay, SLADEN (1958) estimated 82 per cent survival of Adelie Penguin chicks to the creche stage, compared with 60 per cent at Signy Island. In a detailed study that revealed differential success according to site in the colony, TAYLOR (1962) recorded an overall success of 50 per cent at Cape Royds, Ross Island. Also on the Continent, YOUNG (1963a) found 23 per cent fledging success of McCormick's Skua at Cape Royds and 21 per cent at Cape Hallett. Again, egg and chick losses differed, being 20 and 57 per cent respectively at Cape Royds; at Cape Hallett eggs were often left unattended and incurred 50 per cent loss, but plentiful food in the large Adelie Penguin colonies reduced chick losses to 28 per cent.

The Snow Petrel chick, protected from predators in a deep rock crevice, runs another hazard. BROWN (in press) found that only 23 per cent reared their chick successfully in an area where blown snow frequently blocked the sites, but outside the limit of this effect the figure was 63 per cent.

At Macquarie Island, the Wandering Albatross is increasing as it re-establishes after extermination last century. Offspring, banded since 1955, are now returning to breed, the youngest at 9 years old and others at 10 and 11; adolescents visit the island from 5 years of age onwards (Plate 2). The recent occupation of many sites, and the high failure rate—only 9 of the 26 nests had a chick by August in 1966—both indicate young inexperienced birds. It is a long-lived species, in which the full adult plumage has not been attained at 11 years old, yet the delayed onset of sexual maturity in a small expanding population requires an explanation. There is no shortage of nest-sites, but it is conceivable that the foraging range brings these Macquarie birds into competition with the old-established populations based on the Auckland and Campbell Islands. Or the task of feeding a young one, in addition to itself, throughout the Subantarctic winter may call for food-finding skill and experience that take a decade to acquire; premature attempts by individuals not fully efficient would increase the very real hazards that terrestrial life holds for this large albatross.

The Royal Penguin breeds only at Macquarie Island and has a highly-synchronized breeding cycle from late September to early February. The moult follows, and the entire population is dispersed at sea during May to August. At the study colony of two "nurseries" of about 1000 breeding (*i. e.* laying) pairs each (Plate 2), 7403 chicks of 11 successive age-groups have been banded since 1955–56, and their life-histories recorded since 1962. About 750 young are fledged each year from the colony of fully 5000 birds of all ages. One-year-old birds come ashore briefly in December. Those of each older age-group arrive earlier, stay longer, and progressively improve their status at the colony, becoming attached first to a particular area and later to a nest-site and mate. Individuals vary in precocity: a few 4-year-olds are ashore at egg-laying late in October, a few 5-year-olds lay, nearly all 7-year-olds are present at laying, but some birds are 11 years old before they first breed. No 5-year-old has succeeded in fledging a chick, and in 1965–66 only 7 out of the 27 chicks hatched by known-age parents 6–10 years old were reared successfully.

The successful breeders return earliest, are older birds, and weigh most on arrival. This is particularly true of females, which not only have to produce the eggs but starve for nearly five weeks, for they undertake the first incubation spell of about 19 days. The minimum arrival weight of a hen is 4.2 kg and better fat reserves may bring it to 6.3 kg; cocks go up to 7.0 kg. Hens lighter than 4.8 kg rarely lay, and most do not settle or stay ashore long; those weighing 4.8 kg and over usually lay, but their incubation performance is related to age and previous experience rather than to weight above the 4.8 kg threshold. First breeders, whatever their age, are less successful than older birds, and 5- or 6-year-olds compare unfavourably with those that defer the attempt to a later age.

The breeding performance of a Royal Penguin is a function of its social status, in which feeding status is most important for that is what determines the date and weight at which it comes ashore, which in turn determine how soon it acquires the experience and good nest-site and mate that lead to success. The best sites are away from the edge of the nursery, *i. e.* safer from predators, and are not subject to flooding, but there is ample good ground for each colony to expand, and nothing apart from their own inability prevents site-holding pairs in the outer area from laying. When the dispersed population of over two million breeding birds plus adolescents converges on Macquarie Island in spring the plankton, including the euphausiids on which the Royal Penguin feeds, is just beginning to increase. Those birds that can feed nearest the island have the most efficient time-and-energy budget, so competition between individuals for feeding rights must be most intense in the nearest off-shore areas of plentiful food. The individuals that are dominant at sea will be first to acquire the adequate fat reserves and attain the gonad development that enable them to come ashore early and secure an equally dominant breeding status. Some birds come ashore in time to lay, *i. e.* by October 23, but are underweight and do not stay long; others are heavy enough but arrive late, having taken too long to make the weight.

This explanation accounts for the facts observed at the colony in spring. The long spells of enforced starvation ashore undertaken first by the female and then by the male (who incubates the egg during the second 19 days or so, and continues to guard the chick for about three weeks), may be similarly explained. The foraging distance is not known, but it is evidently more efficient for the birds to minimize travelling time and energy than to attempt frequent visits. By December, when the chicks are being fed, and late January when they go to sea, plankton production is maximal (FOXTON, 1956) and competition presumably relaxes, for even the youngest and most subordinate birds are able to visit the colony.

These few quantitative studies in breeding ecology show the potential of Antarctic sea-birds for research in this field. In time, as more long-term studies develop, the interest of individual species will be enhanced by comparison of the population dynamics of Subantarctic and Antarctic birds. The intraspecific pressures among the former, that stem from the isolation and inadequacy of breeding-places compared to the extensive food supply, can be expected to be less evident around the Continent, where suitable landfalls at intervals should enable a higher proportion of the total bird population to breed each year by reducing socially-induced deferment of maturity.

7. Future Research

From this review of ecological studies on Antarctic sea-birds it is evident where most of the present weaknesses and gaps lie, and where opportunities for future work are to be found. It is equally clear that resources such as more biologists, research vessels—for offshore as well as pelagic work — and security for planned continuing programmes will be required.

In some respects Antarctic biology has not yet emerged from the survey stage that should precede more specialized ecological work. The international cooperation that is a feature of this region favours the biogeographical coverage necessary for systematic studies and collection of comparative basic data on distribution, abundance and annual cycles. The consultation that exists on bird-banding activities might well be extended to cover collection of bird specimens and food samples as well as breeding data (including habitat and nest-site analysis) on the lines followed elsewhere by several national ornithological organizations. Critical collecting is important; specimens of known breeding status, and age if possible, are most valuable, and food from large chicks or parents would indicate the feeding situation at the all-important time of fledging. An extensive survey of the food taken by Antarctic sea-birds would be rewarding; use of emetics might minimize the cost in birds, but provision has to be made for analysis and identification of samples, which would depend on prior marine collecting and on the availability of specialist systematists.

In marine biology there is a need for collecting equipment with more "ornithological" properties that will catch the squids, fish and amphipods taken by birds. Collection of birds at sea, live and dead, for ecological data, is well overdue. Seasonal plankton maps, to be meaningful in terms of bird distribution and breeding, would have to show not only the species present and their biomass and vertical distribution, but also the range of sizes and stages. Food relationships can be highly specific. The trend toward greater accuracy and detail is equally important in study of the birds themselves. It means, for example, telemetric methods to define foraging ranges and diving depths; use of individual and versatile marking methods, even at the chick stage, with readable numbers that permit identification without recapture when desired; preparatory marking of young for years to enable the variables of origin, age, experience and social status to be taken into account and to make full use of constancy of breeding groups; and automatic trapping of birds like penguins and burrowing petrels to ensure that large representative samples can be examined.

Long-term population studies are worth consideration in the case of species that are sedentary and available from a land base throughout the year, and thus lend themselves to direct study of the factors that regulate their numbers.

The Gentoo Penguin appears to be the only penguin in this category; the shags are potentially suitable, and individual or group marking with coloured plastic collars would be feasible; the terns might prove more difficult subjects, but the Dominican Gull has good attributes for quantitative field study.

Experimental bird ecology, such as local manipulation of numbers or distribution, may have a future place in research on Antarctic sea-birds. Even at this stage, though perhaps just beyond the scope of this paper, it is tempting to suggest investigation of some aspects of physiology and behaviour that contribute to ecological results. The sensory basis of social behaviour and homing ability are examples; the study of food-finding capacities could be revealing. The proximate stimuli for gonad development in winter layers would be a challenging subject. And to establish, under favourable controlled conditions, the earliest age at which sexual maturity is physiologically possible in a species such as the Royal Penguin, would be a useful complement to field results.

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