BANDING RECOVERIES AND THE DISPERSAL OF SEABIRDS BREEDING IN FRENCH AUSTRAL AND ANTARCTIC TERRITORIES

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SUMMARY

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The paper summarises banding activities on French Austral and Antarctic Territories and recoveries between 1951 and 1982. Out of 61,807 birds banded, 192 were recovered elsewhere. Maps give the location of all these recoveries. Variations in the recovery rates are discussed. The fidelity rate to the hatching grounds is close to 100% for breeding birds. Spatial segregation in winter is established between different populations or species nesting on antarctic or sub-antarctic localities. From recoveries and observations at sea, four methods of oceanic resource utilization during the non-breeding season are defined for 22 species: sedentariness, migration and the concentration over rich zones of food availability, dispersion throughout the Southern Ocean and a combination of the second and third methods. The importance of food availability the ecology of albatrosses during the non-breeding season is discussed.

INTRODUCTION

Seabirds banded in the French Austral and Antarctic Territories have been recovered throughout the southern hemisphere, from the antarctic continent to 9°S. There are two aims of this bird banding: long term population studies, and information on the dispersal and migration of the different species. The second aspect has already been discussed (Prevost 1965; Lacan *et al.* 1969; Mougin *et al.* 1969; Isenman *et al.* 1971; Barrat *et al.* 1973; Derenne *et al.* 1972; Barre *et al.* 1976). These authors reviewed recoveries of birds that were banded within the four localities of banding as well those birds reported there but banded elsewhere. Since 1968 for Adelie Land, and 1976 for the other three localities, 107 new recoveries have been obtained. This paper is a synthesis of all the information on recoveries of birds banded in French Austral and Antarctic Territories between 1951 and 1982.

We try to interpret how each species is distributed at sea, what their patterns of dispersal are and why recovery rates are so different between species. We need to know dispersal patterns to understand the ecology of antarctic and sub-antarctic seabirds during the non-breeding season, a crucial period where few data are available.

METHODS AND MATERIALS

Banding programmes have been carried out in the four localities of the French Austral and Antarctic Territories: Adelie Land, which is on the antarctic continent (Pointe Géologie archipelago, 67°S, 140°E) and on three island groups in the south Indian Ocean, the Kerguelen Islands (49°S, 70°E), the Crozet Islands (46°S, 50-52°E) including Ile de la Possession, Ile de l'Est and Ile aux Cochons, and Amsterdam Island (37°S, 77°E).

A total of 61,807 seabirds of 38 species have been banded, including adults, immatures and juveniles. Procellariiforms, Phalacrocoracidae and Lariforms were banded with monel bands placed on the tarsometatarsus. The rate of loss for this type of band appears to be close to zero. Penguins were marked with monel tags placed on their flippers. The annual rate of loss here is higher and differs according to the species. Being low for the *Pygoscelis* and *Eudyptes* genera, it could reach 20 to 30% for the genus *Aptenodytes*.

Banding started in 1951 on Kerguelen, 1952 on Adelie Land, 1957 on Amsterdam Island and 1960 on the Crozet Islands. In calculating recovery rates, we used the total number of birds recovered at least once; when the same bird is recovered again, this second report is disregarded (this being particularly the case for Wandering Albatrosses *Diomedea exulans*).

All information on birds recaptured in foreign countries is centred at "Centre de Recherche sur la Biologie des Populations d'Oiseaux" (C.R.B.P.O.) at the National Museum of Natural History in Paris.

RESULTS

The banding date, bird status, location and date of each recovery, are given in the Appendix for the data available since 1968 for Adelie Land and since 1976 for the other three localities. Previous information is available in the papers cited in the introduction.

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Differences in recovery rates between species

Table I shows the number of birds banded, the number of birds recovered and the recovery rate for each species of which at least 200 individuals have been banded. Out of 61,807 seabirds banded around French bases, 192 have been recovered away from their breeding stations — a recovery rate of 0.31%, varying from 0 to 1.07%. This rate depends on the recapture effort, according to the locality and the species. Certain species are reported more often than others. This is particularly noticeable for the Wandering Albatross in Australia where this

TABLE I

Number of birds banded, number recovered and recovery rate, between 1951 and 1982, of 38 antarctic and sub-antarctic seabirds breeding in the French Austral and Antarctic Territories (C = Crozet Islands, K = Kerguelen Islands, A = Amsterdam Island, G = Pointe Geologie Archipelago).

Species	Banding location	Numbers banded	Number of recoveries	Recovery rate (%)
Emperor Penguin *Aptenodytes forsteri*	G	6,402	0	0
King Penguin *Aptenodytes patagonicus*	C, (K)	9,602	24	0.25
Gentoo Penguin *Pygoscelis papua*	C, (K)	1,567	0	0
Adelie Penguin *Pygoscelis adeliae*	G	5,312	0	0
Macaroni Penguin *Eudyptes chrysolophus*	C, (K)	2,551	0	0
Rockhopper Penguin *Eudyptes chrysocome*	C, K, (A)	2,321	0	0
PENGUINS		27,755	24	0.09
Wandering Albatross *Diomedea exulans*	C, K	8,617	76	0.88
Black-browed Albatross *Diomedea melanophris*	K	1,408	11	0.78
Yellow-nosed Albatross *Diomedea chlororhynchos*	A	2,608	11	0.42
Grey-headed Albatross *Diomedea chrysostoma*	C	719	0	0
Sooty Albatross *Phoebetria fusca*	C, (A)	1,630	0	0
Light-mantled Sooty Albatross *Phoebetria palpebrata*	C, K	1,145	1	0.09
ALBATROSSES		16,127	99	0.61
Giant Petrels *Macronectes giganteus* and *M. halli*	C, K, G	4,869	40	0.82
Cape Petrel *Daption capense*	G, (C)	2,840	5	0.18
Southern Fulmar *Fulmarus glacialoides*	G	558	0	0
Snow Petrel *Pagodroma nivea*	G	2,438	0	0
White-chinned Petrel *Procellaria aequinoctialis*	C, (K)	972	3	0.31
Kerguelen Petrel *Pterodroma brevirostris*	C	248	0	0
Salvin's Prion *Pachyptila salvini*	C	1,364	1	0.07
Wilson's Storm Petrel *Oceanites oceanicus*	G	335	0	0
South Georgian Diving Petrel *Pelecanoides georgicus*	C, K	446	0	0
other Petrels	C, K, A	1,010	0	0
PETRELS		15,080	49	0.32
Sub-antarctic Great Skua *Stercorarius skua lonnbergi*	C, K	1,040	11	1.06
South Polar Skua *Stercorarius maccormicki*	G	971	9	0.93
Kelp Gull *Larus dominicanus*	C, K	310	0	0
Terns *Sterna virgata* and *S. vittata*	C, K	111	0	0
LARIFORMS		2,432	20	0.82
Blue-eyed Shag *Phalacrocorax albiventer*	C	351	0	0
Kerguelen Shag *Phalacrocorax verrucosus*	K	62	0	0
CORMORANTS		413	0	0
TOTAL SEABIRDS		61,807	192	0.31

species is systematically captured by the "Albatross Study Group" (see Tickell & Gibson 1968). Nowhere else are albatrosses caught in large numbers away from the breeding place. The probability of a recovery in sparsely inhabited areas like the west coast of South America is certainly lower than that in areas like the Australian or South African coast.

Spheniscidae and Phalacrocoracidae have very low recovery rates in comparison to other groups (Table I). Cormorants are known to be inshore feeders around the Crozet Islands (Jouventin *et al.* 1982a) and are limited to the continental shelf around Kerguelen. Neither species has been observed in the pelagic zone (Jouventin *et al.* in press). Although few birds have been banded, it is not surprising that none of these sedentary species has been recovered. Many penguins have been banded but few recovered, as might be expected from their mode of dispersal. Sub-antarctic penguins are known to be pelagic feeders (Stahl *et al.* in press), ranging to more than 500 km offshore during the breeding season. The isolation of the breeding grounds makes recovery unlikely. The King Penguin with 24 individuals recovered is an exception. The recovery on Macquarie Island and regular exchanges between Crozet and Marion Island denotes important dispersal abilities of this species. However banded Macaroni and Adelie Penguins might pass unnoticed in the enormous colonies of these species.

Albatrosses are recognized as long-distance travellers. The high recovery rate for Wandering Albatross is exceptional as discussed before. However the albatrosses can be divided into two groups: one with a high recovery rate - 0.78% for 12,633 banded birds (Wandering, Yellow-nosed and Black-browed Albatrosses), and the others with a recovery rate close to zero - 0.03% for 3,494 banded birds (the two Sooties and Grey-headed Albatrosses). The former group concerns albatrosses that move to coastal waters outside their breeding season, such as along the coasts of Australia, South Africa or South America. The second group corresponds to species remaining in pelagic waters, where they are unlikely to be recaptured.

For the other three families of Procellariiforms, the recovery rate is close to the mean value of all seabirds studied. Giant Petrels, which have a recovery rate of 0.82%, distort the value for all petrels. If we disregarded this genus, the other petrel species show a recapture rate of 0.09%.

Finally the skuas show the highest recovery rate of all seabirds from this zone. They are often attracted to human settlements and this is certainly one of the reasons for such a high recapture rate. Kelp Gulls and Kerguelen Terns are known to be sedentary (Watson 1975; Stahl & Weimerskirch 1982) and so recoveries away from the nesting area are unlikely.

Recovery rate and age

While the percentage of all the birds banded as chicks (n = 11,875) and recaptured afterwards away from their hatching places, is 0.85%, only 0.39% of the birds banded as adults (n = 20,549) have been recaptured ($p < 0.001$). This difference is even greater for species like King Penguin, Yellow-nosed Albatross or Giant Petrels (Table II). For the Wandering Albatross and South Polar Skua adults are more often recaptured but not significantly so.

TABLE II

Differences between adult and juvenile birds in the recovery rate of 9 species of seabirds banded in the French antarctic and sub-antarctic stations.

Species	Adults		Juveniles		Comparison of 2 percentages test	
	Numbers ringed	Recovery rate (%)	Numbers ringed	Recovery rate (%)	t	Prob.
King Penguin	7,737	0.14	1,803	0.67	4.07	P < 0.001
Wandering Albatross	5,638	0.92	2,979	0.64	1.40	N.S.
Black-browed Albatross	500	0.40	908	0.99	1.20	N.S.
Yellow-nosed Albatross	1,870	0.11	738	1.22	3.96	P < 0.001
Giant Petrels	2,095	0.09	2,774	1.37	4.9	P < 0.001
White-chinned Petrel	588	0	168	1.79	—	
Cape Petrel	1,167	0.08	1,603	0.25	1.12	N.S.
Sub-antarctic Great Skua	395	1.01	490	1.02	0.22	N.S.
South Polar Skua	559	1.25	412	0.48	1.24	N.S.

The location of recoveries

The recapture localities are shown in Figures 1 to 11 for twelve species.

King Penguin - Although the recovery rate is rather low, King Penguins regularly move between Marion and Crozet Islands, 900 km apart. The only two recoveries of Crozet birds on Kerguelen (1,500 km apart) and Macquarie Island (5,600 km apart) may concern vagrants rather than individuals in their normal dispersal areas. Most King Penguins were observed on Marion Island between November and January, i.e. during the moulting period. During this time a large section of the population is breeding and Stahl *et al.* (in press) showed that birds forage principally over the shelf and slope areas of the Crozet Islands. They also recovered some individuals as far as 400 km from these islands. In view of our recoveries, we can assess that the dispersal range of the Crozet population could exceed 900 km, though this would concern mainly immature and moulting non-breeding birds. No individual hatched or bred on the Crozet Islands has ever been observed breeding elsewhere.

Wandering Albatross - With 8,617 birds banded and 76 recoveries, movements of this albatross are now becoming well documented though they appear complex. Recoveries present a circumpolar distribution (Figure 2), but most of them take place around Australia, particularly along the New South Wales coast where the species occurs throughout the year, though more so during spring and early summer (Barton 1979). Some birds breeding on the Crozet Islands are regular visitors to Australia (Figure 12). Sixteen birds have been reported twice there, ten birds three times, two five times and one

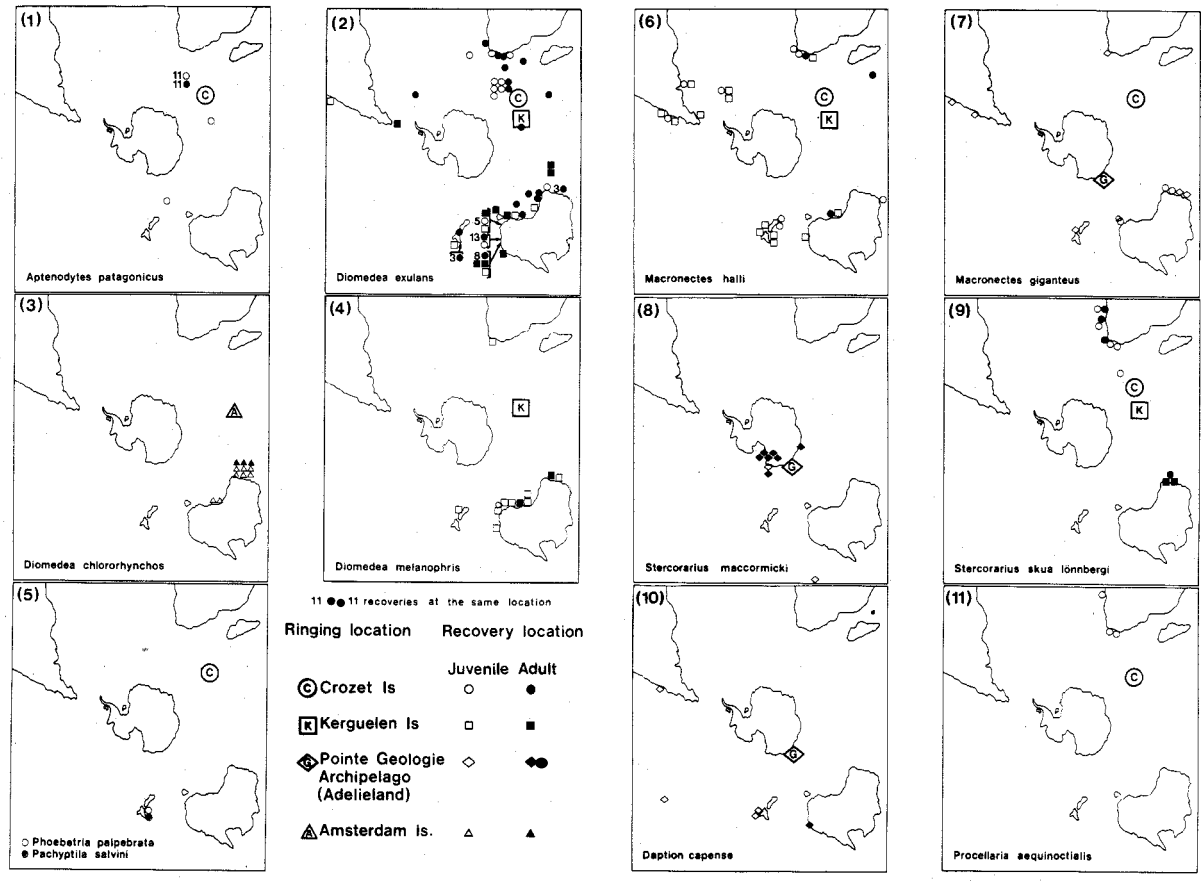

Figure 1 to 11. Location of the recoveries for 12 seabirds species banded at Amsterdam, Crozet and Kerguelen Islands and at Pointe Géologie (Adélie Land) between 1951 to 1982.

bird seven times in this particular area.

Tickell (1968) showed that Wandering Albatrosses are biennial breeders if a chick is successfully reared. The adult population is thus divided into two halves with each part breeding every alternate year, some birds moving between halves if they fail. Monitoring of adults is carried out every year on Crozet Islands and shows that the recapture of Wandering Albatrosses in Australia occurs either during the non-breeding year after a chick has been reared and before the next breeding year or during the same season when the egg has been lost. Part of the population appears to prefer the Australian sector during its non-breeding season and therefore a true migration exists for these birds between the Crozet and Kerguelen Islands and Australia. One bird banded on Ile de I'Est as incubating was reported four years later off the New South Wales coast and eight years later in South Africa. This observation could reflect circumpolar migration. Many Wandering Albatrosses (adults and immatures) are observed all through the year in pelagic waters throughout the Southern Ocean and Jouventin *et al.* (1982b) also stated that at least in the Indian Ocean adult and immature birds have a distinct distribution. Thus, for one species there appear to be two types of dispersal. Some birds migrate regularly between coastal waters (especially Australia) and the nesting site, whereas the rest of the population remains in pelagic waters all year and possibly circumnavigates

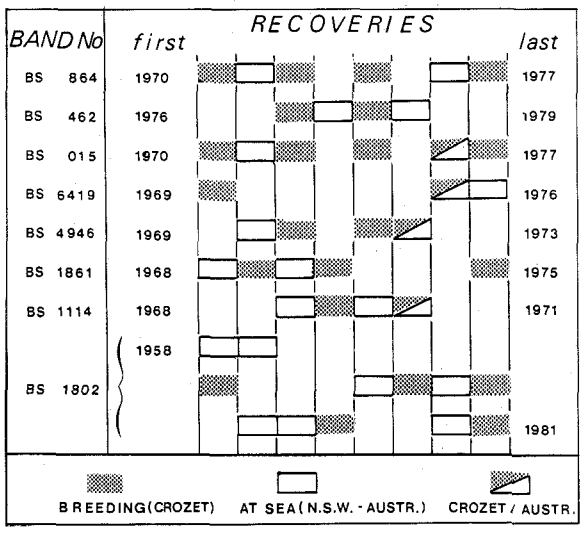

Figure 12. Year to year movements of Wandering Albatrosses between New South Wales (N.S.W.) and Crozet Islands. Each rectangle denotes one or two recoveries during one year.

in the west wind zone. Eleven of the recoveries concern birds banded on the Crozet Islands and reported on other breeding grounds of the species. One of them, the only case known for this species, hatched on Crozet and bred nine years later on Marion Island (Mougin 1977).

Black-browed Albatross - Swanson (1973) reported that *Diomedea melanophris* represented 90% of all albatrosses seen within 30 km of Kangaroo Island. Nine birds banded on Kerguelen were recorded along the Australian coast, two of them near Kangaroo Island. This species moves to coastal waters during the non-breeding season with a specific distribution. Each population of the subspecies *D. m. melanophris* winters in a distinct zone. Tickell (1967) stated that the bulk of recoveries (87.8%; n = 66) of Black-browed Albatrosses originating from the Falkland Islands were obtained off the eastern coast of South America, and those originating from South Georgia were off the west coast of South Africa (94.6%; n = 186). Both subspecies occur off South Australia . *D. m. impavida* originating from Campbell or Antipodes Islands is observed along the New South Wales coasts (Milledge 1977), and a juvenile banded on Campbell Island was also found dead on the coast of New Zealand (Robertson 1979). *D. m. melanophris* originating from Heard Island (1 recovery: Howard 1954), Macquarie Island (4 recoveries: Hindwood 1955; Purchase 1969, 1970, 1971) and Kerguelen (this paper) have been recovered from the southern coast of Australia. Therefore during winter the feeding zones for this species appear to be located always over coastal waters (on continental shelves or over oceanic currents). The remaining two recoveries from the Kerguelen banded birds were made in New Zealand and South Africa respectively, indicating that wintering areas of the different Black-browed populations are not absolutely segregated (see also Tickell 1967).

Yellow-nosed Albatross - Brooke *et al.* (1980) distinguished two subspecies: *D. chlororhynchos bassi* breeding on on Amsterdam, Crozet and Marion Islands and the nominate subspecies *D. c. c.* breeding on Tristan da Cunha and Gough Islands. The different populations of Yellow-nosed Albatross also show a specific distribution during winter. *D. c. chlororhynchos* moves from the the Tristan da Cunha Group to the South African coast over the Benguela current (Hagen 1980). Our recoveries show that *D. c. bassi* moves from Amsterdam Is to the east coast of Australia but away from Black-browed wintering zones. In effect the Yellow-nosed Albatross moves to more northern inshore waters of Australia (Barton 1979). Observations of *D. c. bassi* on the south-eastern coast of Africa (Morant *et al.* in press) probably concern birds from Marion or Crozet Islands, but further information is needed.

Light-mantled Sooty Albatross - One bird banded as a chick on Crozet Islands was found dead 15 months later in New Zealand (Barrat *et al.* 1973). This species generally avoids coastal waters during the non-breeding season (see Morant *et al.* in press for South Africa, Barton 1979 for South Australia, J.A. Bartle pers. com. for New Zealand). In New Zealand *c* 80% of Light-mantled Sooty Albatrosses found dead on beaches are first year birds, generally emaciated (J.A. Bartle pers. com.).

Giant Petrels - For both species the distribution of recoveries is circumpolar (Figure 6 and 7). Dominant west winds seem to have a great influence on the dispersal of juvenile birds. For the Northern Giant Petrel the time between departure from the colony to recapture increases in an easterly direction from the fledging site. This phenomenon was also observed by Conroy (1972) for the Southern Giant Petrel. Some movements of these juvenile birds can be rather rapid just after leaving the colony e.g. taking three months from Kerguelen to the coast of Chile (distant of *c* 14,000 km, or *c* 21,000 km in a westerly direction) two months from Kerguelen to Argentina or from Crozet to New Zealand. The first two recoveries indicate possible movements against the west winds. In adult birds little information is available although three adult Northern Giant Petrels were recovered on Reunion Island (31°S-55°E), in South Africa and in Australia respectively.

Giant Petrels seem to prefer to move over certain coastal waters according to their banding site (Table III). Most of the birds native to the South Atlantic sector (South Georgia, Signy, Shetland and Anvers Islands) move to Australia, whereas Giants Petrels native of Crozet, Kerguelen, Heard and Macquarie Islands do not show this preference. Most recoveries were made before the two species of Giant Petrels were separated by Bourne & Warham (1966). Afterwards each can now be considered separately and the differences are greater between two populations of the southern species (Signy compared with Crozet-Heard) than between the Northern (Crozet-Kerguelen) and the Southern Giant Petrel (Heard). As for the Wandering Albatross, Giant Petrels are observed over coastal waters as well as over pelagic waters (Jouventin *et al.* in press).

Cape Petrel - This species shows important seasonal changes in its distribution (Cheshire *et al.* 1979; Jouventin *et al.* 1982b). During winter, it ranges as far as 20°S and a chick banded on Pointe Geologie and recaptured on Pitcairn Island need not be considered a vagrant. For the moment data are not reliable as far as the number of birds recaptured is concerned, but the species shows a circumpolar dispersal. Particularly interesting are a recapture at the same place (Aerial Reef, New Zealand) and recaptures within four days of each other, of two birds banded as chicks in the same season in the same colony of Adelie Land. From this we can infer that either immature birds disperse in flocks or each population visits the same wintering zones every year.

White-chinned Petrel - In the Indian Ocean, this species shows a specific migration as is the case with Black-

TABLE III

Distribution of recoveries of Giant Petrels banded in different Antarctic and sub-Antarctic stations. Species are not separated.

Ringing station \ Locality recovered	South America (+ South Georgia)	South Africa	Australia	New Zealand	Elsewhere	Total recovered	References
Crozet-Kerguelen	9 (33.3%)	4 (14.8%)	7 (25.9%)	6 (22.2%)	1 (3.7%)	27	This paper
Heard	9 (25.8%)	6 (17.1%)	10 (28.6%)	8 (22.9%)	2 (5.8%)	35	Downes *et al.* (1954), Howard (1956), Ingham (1959)
Macquarie	12 (46.1%)	4 (15.3%)	5 (19.2%)	5 (19.2%)	—	26	Downes *et al.* (1954), Howard (1956), Ingham (1959)
South Georgia	17 (14.9%)	15 (13.2%)	64 (56.2%)	17 (14.9%)	1 (0.9%)	114	Sladen *et al.* (1968)
Signy	22 (6.0%)	61 (16.5%)	227 (61.5%)	59 (16.0%)	—	369	Conroy (1972)
Anvers-Shetland	1 (7.7%)	2 (15.4%)	8 (61.5%)	2 (15.4%)	—	13	Sladen & Tickell (1958), Stonehouse (1958), Tickell & Scotland (1961), Sladen *et al.* (1968)
Antarctic Continent (90°-180°E)	5 (35.7%)	2 (14.3%)	3 (21.4%)	3 (21.4%)	1 (7.2%)	13	Orton (1963), Sladen *et al.* (1968), this paper

browed or Yellow-nosed Albatrosses. Immature birds migrate to the Benguela current. Between June and August White-chinned Petrels completely disappear from the pelagic and peri-insular zones of the south-western Indian Ocean (Rand 1962, 1963; Jouventin *et al.* in press) and were only restricted to the south-eastern African coastal vicinity (Rand 1962, 1963).

Salvin's Prion - One chick banded on Crozet Islands was found dead three months later on a beach in New Zealand (Howell 1974). From May to July Salvin's Prions are commonly found dead on beaches in New Zealand (Harper 1980). Most of them are severely emaciated immatures. Actually no information is available on the winter feeding zones of this species.

Sub-antarctic Great Skua - The recoveries of the Crozet birds show that at least part of the population migrates in winter along the south and west coast of Africa. All the birds captured in this area originate from Crozet or Marion Islands (Brooke 1978). On the other hand the Kerguelen population could move to Australia but further information is needed. Some individuals have also been observed around Reunion and Seychelles Islands and across the Equator as far as the Indian coast (Ali & Ripley 1969). Thus this skua presents a specific dispersal in winter with most of the population moving to zones where seabirds that they may predate or parasitize, e.g. boobies or terns, are concentrated.

South Polar Skua - Salomonsen (1976) and Devillers (1977) based on museum specimens, observations at sea and band recoveries stated that this species effects a long distance migration as far as the Arctic waters e.g. Greenland. All our recoveries except a chick, banded in Adelie Land and recaptured 11 months later on Solomon Islands, took place just on the edge of the antarctic continent (Figure 8). Such movements have already been pointed out by Pryor (1968) and Lereshe *et al.* (1970). Birds of Adelie Land periodically visit other breeding localities and one chick that hatched on Pointe Geologie archipelago was found breeding on Possession Island (71°S, 171°E).

DISCUSSION

In the past 20 years nearly 200 birds banded in the French Austral and Antarctic Territories have been recorded from a great number of locations in the southern hemisphere. There is now enough evidence to allow tentative conclusions on three interesting problems concerning antarctic and sub-antarctic seabirds:

fidelity rate to the hatching grounds,

spatial segregation between species or populations outside the breeding season,

strategy of exploitation of oceanic resources during the non-breeding season.

Recoveries also show that the presence of continuous west winds is an important factor in the dispersal of seabirds in the southern ocean. The higher recovery rate for juvenile birds may be explained by the mortality rate for immature birds being generally higher than that for adults, especially during their first year at sea after fledging (see e.g. Harper 1980 for prions or more generally Croxall 1982). Indeed a great number of the recoveries consist of birds found dead on beaches. Also young inexperienced birds are more easily caught than older ones. For some species young birds disperse to areas outside the usual range of the species, for instance to more northern inhabited areas.

Fidelity rate to the hatching grounds

In spite of their great dispersal abilities, antarctic and sub-antarctic seabirds show a fidelity rate close to 100% to the hatching grounds. Even in the South Polar Skua, which shows important exchanges of immature birds between populations, few birds breed outside their hatching place. The case of one Wandering Albatross which hatched on Crozet and was found breeding on Marion Island must be considered an exception in view of the great number of birds banded and monitored every year on all breeding grounds for the species.

Thus population exchange is almost absent and this fact must be taken into account if one considers the significant speciation and sub-speciation rate for such an open area as the Southern Ocean which is without landmasses that would act as barriers to seabird dispersal. This applies of course to sedentary species like Sheathbills, shags or terns, but even to albatrosses if one consider the two subspecies of Wandering, Royal, Yellow-nosed, Black-browed and Buller's Albatrosses and the three subspecies of *Diomedea cauta*.

At least in the Wandering Albatross, birds return each non-breeding season to the same feeding area. It could be expected that other species frequent specific areas just as regularly.

Spatial segregation

Pelagic distribution, observations at sea on the continental shelves and recoveries of seabirds banded on their breeding grounds, show evidence of spatial segregation. This in turn limits intra- and inter-specific competition during the non-breeding season. This concerns segregation between:

(i) adult and immature birds of the same species. This is particularly so for albatrosses, immatures not being observed around their hatching grounds before they are 3 to 5 years old. For example, spatial segregation between adult and immature birds is known to occur for the

Wandering and the two Sooty Albatrosses (Falla 1937; Jouventin *et al.* 1982b; Jouventin & Weimerskirch 1984).

(ii) the two half populations of adult birds in the case of biennial breeding species. This is obvious for the Wandering Albatross, where a part of the non-breeding population each year concentrates around Australia which is far from the foraging range of the breeding birds. This is certainly also the case for Royal Albatrosses moving to the coasts of South America (Robertson & Kinsky 1972) and might be true for Grey-headed and the two Sooty Albatrosses, but this has not been proven yet.

(iii) populations or subspecies, as shown for the Black-browed or Yellow-nosed Albatrosses respectively.

(iv) species of comparable size. Segregation appears clearly between Yellow-nosed and Black-browed Albatrosses, both wintering along the Australian coast. The former species winters in more northern or warmer waters, especially the western coast of Australia (Serventy *et al.* 1971), than the second one. The same situation appears in the two species occuring along the coast of South Africa. In winter *D. c. chlororhynchos* moves to more northerly places than *D. melanophris* (Morant *et al.* in press). The non-breeding halves of the population of the two similar-sized great albatrosses are also separated. Royal Albatrosses concentrate more particularly around the South American coasts or over pelagic waters.

The exploitation of oceanic resources during the non-breeding season

Most of sub-antarctic and especially antarctic seabirds breed in summer, the time of greatest availability of food. In winter primary production falls because of the decrease in illumination, particularly at high latitudes (see Ashmole 1971 for discussion on the topic). During this period most of the southern seabird species have to change the feeding habits displayed during their breeding season: most of the species migrate to more favourable waters than those around their nesting place. In zones of upwelling or at the boundaries of currents, primary production, and thus food for seabirds, remains higher than in antarctic and sub-antarctic pelagic waters (Ashmole 1971). Because of the occurrence of upwelling or cold currents in their vicinity, the coasts of South Africa, Australia and South America provide zones of high food availability to seabirds.

Recoveries and observations of seabirds in pelagic and coastal waters permit us to distinguish four ways of exploiting oceanic resources outside the breeding season for the different species of antarctic and sub-antarctic seabirds.

(i) Some species are sedentary (Kelp Gull, Shags, Gentoo Penguin and Kerguelen Tern) or remain close to the breeding grounds, not dispersing further than 1,000 km (King Penguin, Macaroni Penguin). Penguins, shags and terns start their moult just after or even during the breeding cycle and thus take advantage of the short productive season. After moult, they spend winter near the marine zone where they breed.

(ii) Other species show a specific migration (Yellow-nosed and Black-browed Albatrosses, White-chinned Petrel, Sub-antarctic Great Skua and Antarctic Tern). Apparently these species respond to permanently profitable foraging areas where the population returns to every year. These areas, mostly the coastal waters of South Africa, South America and Australia, are limited in size but the food there is more adequate, accessible and predictable than elsewhere.

(iii) Three species (the Wandering Albatross and both Giant Petrels) concentrate over localized offshore areas, although part of the population remains in pelagic waters.

(iv) The last group concerns species dispersing over the pelagic waters of the Southern Ocean (Grey-headed and the two Sooty Albatrosses, Cape Petrel and the four *Pterodroma* species). In contrast to the species that effect a specific migration, these species avoid coastal waters. They seem to disperse completely over a vast surface of ocean. The food here is certainly less accessible and less concentrated but intra-specific competition would be less intense. Immature birds of this group often forage in different areas from adults.

Among the small species of albatrosses some are biennial breeders (the Grey-headed Albatross — Tickell & Pinder 1967; the Sooty Albatross — Weimerskirch 1982; the Light-mantled Albatross, unpublished data), others are annual breeders (the Black-browed Albatross — Tickell & Pinder 1967; the Yellow-nosed Albatross — Jouventin *et al.* 1983). It is interesting to note that biennial species remain in pelagic waters in winter while annual ones concentrate over specific areas of high food availability. In contrast with penguins or Giant Petrels, albatrosses do not start their moult when breeding (Hunter 1984). The completion of moult has to take place in winter when these species also have to reconstitute fat reserves for the next nesting season. Both annual breeding species have a longer non-breeding period than biennial species (Tickell & Pinder 1975; Jouventin *et al.* 1983; Jouventin & Weimerskirch 1984). So the conjection of a non-breeding time of at least five months and a high food availability in wintering zones permits the Black-browed and Yellow-nosed Albatrosses to breed every year. But albatrosses foraging

over pelagic waters during winter can only breed every alternate year if a chick is successfully raised. They complete their moult and reattain breeding condition after more than one year.

Thus the knowledge of the dispersal patterns during the non-breeding is essential to the comprehension of southern seabird's ecology.

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APPENDIX

1968–1982 recoveries of seabirds banded at Pointe Geologie Archipelago (Adelie Land) and 1976–1982 recoveries of seabirds banded at Crozet, Amsterdam and Kerguelen Islands.

Ring number	Banding			Recovery	
	Age	Date	Location	Date	Location
King Penguin *Aptenodytes patagonicus*					
TA 1680	Pull	14-11-74	Possession	17-01-76	Macquarie Is., 54°30′S, 158°57′E
TA 2521	Pull	08-12-75	"	11-01-77	Marion Is., 46°54′S, 37°45′E
TA 2381	Pull	17-12-75	"	07-01-77	" " "
TA 2575	Pull	17-12-75	"	19-12-76	" " "
TA 4793	Pull	12-11-77	"	16-01-80	" " "
TA 8267	Pull	03-12-78	"	25-01-80	" " "
TA 10732	Pull	29-11-80	"	14-12-81	" " "
TA 2163	Ad	09-02-75	"	30-11-76	" " "
TA 2557	Ad	16-12-75	"	10-09-81	" " "
TA 2637	Ad	21-12-75	"	07-01-77	" " "
TA 2951	Ad	25-01-76	"	11-01-77	" " "
TA 4465	Ad	17-11-76	"	15-07-77	" " "
TA 8748	Ad	10-01-79	"	03-12-79	" " "
TA 10402	Ad	18-11-79	"	14-10-82	" " "
TA 10231	Ad	25-11-80	"	?-01-82	" " "
TA 10490	Ad	28-11-80	"	?-01-82	" " "
TA 11670	Ad	18-12-80	"	11-11-82	" " "
Wandering Albatross *Diomedea exulans*					
BS 7635	Pull	27-09-79	Possession	04-07-80	Bass Strait, 39°56′S, 143°52′E, Tasmania, Australia
BS 6141	Ad	25-01-74	"	23-07-77	Wollongong, 34°24′S, 151°00′E, N.S.W., Australia
BS 4762	Im	30-12-71	"	05-08-78	" " " " "
BS 0462	Ad	18-03-68	"	03-07-77	" " " " "
BS 5890	Pull	15-10-73	"	27-07-77	Rutledge Cutting, 38°21′S, 142°22′E, Victoria, Australia
BS 4679	Pull	30-09-71	"	01-05-76	Narrawong, 38°21′S, 141°38′E, Victoria, Australia

APPENDIX *Continued*

Ring number	Banding			Recovery	
	Age	Date	Location	Date	Location
Wandering Albatross *Diomedea exulans*					
BS 039	Ad	12-01-67	Possession	01-01-69	Stenhouse Bay, 35°02′S, 137°35′ E, South Australia
BS 1844	Ad	05-03-71	"	?-05-76	Kangaroo Island, 35°54′S, 136°32′E, South Australia
BS 1380	Ad	06-04-70	"	13-10-78	At sea, 41°55′S, 133°47′E
BS 1686	Ad	13-12-70	"	07-03-76	Albany, 35°13′S, 118°01′E, Western Australia
BS 6654	Ad	25-01-76	"	12-02-77	Marion Is., 46°54′S, 37°45′E
BS 6578	Pull	11-11-75	"	10-03-80	" " "
BS 6494	Pull	26-09-75	"	10-03-80	" " "
BS 6164	Ad	25-01-74	"	01-12-79	" " "
BS 5802	Im	26-02-73	"	22-02-77	" " "
BS 6565	Pull	11-11-75	"	?-10-77	Treasure Beach, 31°10′S, 26°60′E, Natal, South Africa
BS 6472	Ad	01-04-75	"	21-02-77	Bird Island, 54°00′S, 38°02′W, South Georgia
BS 1286	Ad	08-01-71	Est	11-08-81	Bellambi, 34°22′S, 150°56′E, N.S.W., Australia
BS 7563	Ad	30-01-77	"	30-07-78	Wollongong, 34°24′S, 151°00′E, N.S.W., Australia
BS 4187	Ad	10-01-71	"	16-08-75	" " " " "
				23-02-80	Yserfontein, 33°16′S, 18°07′E, South Africa
BS 4474	Ad	30-01-71	"	02-11-76	At sea 40°35′S, 122°10′E
BS 2685	Ad	07-03-74	Cochons	17-08-80	Bellambi, 34°22′S, 150°56′E, N.S.W., Australia
BS 2606	Ad	07-03-74	"	12-08-79	Wollongong, 34°24′S, 151°00′E, N.S.W., Australia
BS 2923	Ad	07-03-74	"	30-08-78	" " " " "
BS 2637	Ad	07-03-74	"	14-11-76	Esperance, 33°49′S, 121°52′E, Western Australia
BS 3194	Ad	11-04-74	"	18-12-77	Kerguelen Is., 49°20′S, 70°15′E
BS 3875	Ad	29-01-74	Kerguelen	06-09-75	Kaitaia, 35°08′S, 173°18′E, New Zealand
BS 3631	Ad	15-02-72	"	20-08-77	Wollongong, 34°24′S, 151°00′E, N.S.W., Australia
BS 3811	Pull	19-12-73	"	09-04-77	Queenstown, 42°07′ S, 145°33′E, Tasmania, Australia
BS 3978	Pull	16-10-76	"	10-07-77	Point Duquesne, 38°23′S, 141°22′E, Victoria, Australia
Black-browed Albatross *Diomedea melanophrys*					
CF 15105	Pull	17-02-76	Kerguelen	?-04-78	Mossel Bay, 34°11′S, 22°08′E, South Africa
CF 16286	Ad	12-11-79	"	14-01-82	Breton Bay, 31°13′S, 115°25′E, Western Australia
CF 12019	Ad	20-01-73	"	03-05-81	Kangaroo Island, 35°46′S, 137°53′E, South Australia
CF 15444	Pull	17-02-76	"	26-10-76	" " " "
CF 19162	Pull	27-02-82	"	06-06-82	Goolwa, 35°31′S, 138°45′E, South Australia
CF 7874	Pull	13-02-71	"	15-05-78	Kingston, 36°50′S, 139°20′E, South Australia
CF 15277	Pull	18-02-76	"	21-02-78	West Point, 40°55′S, 144°00′E, Tasmania, Australia
CF 15479	Pull	18-02-76	"	09-06-82	Wilson's Promontory, 39°36′S, 146°56′E, Victoria, Australia
CF 15267	Pull	18-02-76	"	01-09-76	Bungaree Norah Point, 33°19′S, 151°08′E, N.S.W., Australia
CF 15481	Pull	18-02-76	"	16-01-77	Auckland, 36°55′S, 174°45′E, New Zealand
Yellow-nosed Albatross *Diomedea chlororhynchos*					
CF 18299	Pull	21-02-82	Amsterdam	28-08-82	Pelsart Id., Abrolhos Ids., 28°48′S, 114°05′E, W. Australia
CF 9049	Ad	01-03-70	"	26-06-76	Rottnest Island, 32°01′S, 115°28′E, Western Australia
CF 11419	Ad	07-10-72	"	16-04-79	Denmark, 34°54′S, 117°25′E, Western Australia
CF 14500	Pull	08-02-81	"	30-04-81	Albany, 34°57′S, 117°54′E, Western Australia
CF 16928	Pull	20-02-78	"	25-01-79	Bremer Bay, 34°16′S, 119°30′E, Western Australia
CF 18206	Pull	21-02-82	"	11-08-82	Kangaroo Island, 35°46′S, 137°53′E, South Australia
Southern Giant Petrel *Macronectes giganteus*					
CF 6818	Pull	16-02-72	Pointe Géologie	16-07-72	Carnarvon, 24°51′S, 113°45′E, Western Australia
CF 8160	Pull	10-02-73	"	09-06-73	South Beach, 28°55′S, 153°28′E, N.S.W., Australia
CF 6851	Pull	02-04-74	"	13-04-75	West Shore, 39°28′S, 176°53′E, New Zealand
CF 14787	Pull	18-01-75	Possession	05-06-76	Bicheno, 41°51′S, 148°17′E, Tasmania, Australia
Northern Giant Petrel *Macronectes halli*					
BS 6399	Pull	16-01-79	Possession	?-02-80	Arauco, 37°15′S, 73°22′W, Chile
BS 6639	Pull	08-01-76	"	25-01-80	Bird Island, 54°00′S, 38°03′W, South Georgia
BS 8082	Pull	25-01-80	"	20-11-81	Mossel Bay, 34°12′S, 22°08′E, South Africa
CF 5879	Ad	06-09-68	"	10-09-76	" " " "
BS 8099	Pull	25-01-80	"	10-11-80	Heretaniwha Point, 43°35′S, 169°35′E, New Zealand
CF 13105	Pull	12-02-74	Cochons	10-09-76	Mossel Bay, 34°12′S, 22°08′E, South Africa
CF 13369	Ad	30-01-74	"	12-09-76	Kangaroo Island, 35°54′S, 136°32′E, South Australia
CF 12455	Pull	18-01-74	Kerguelen	?-04-75	Bahia Coliumo, 36°33′S, 72°56′W, Chile
CF 12159	Pull	28-01-73	"	30-12-79	Bird Island, 54°00′S, 38°03′W, South Georgia
CF 12539	Pull	19-01-74	"	19-01-80	" " " "
CF 12514	Pull	18-01-74	"	?-01-76	Ohawe, 39°35′S, 174°13′E, New Zealand

APPENDIX *Continued*

Ring number	Banding			Recovery	
	Age	Date	Location	Date	Location
Cape Petrel *Daption capense*					
FL 12422	Pull	18-02-74	Pointe Géologie	16-07-74	Pitcairn Is., 25°04′S, 130°06′W
FL 12425	Pull	18-02-74	"	04-09-74	Concon, 32°55′S, 71°32′W, Chile
FL 4867	Ad	23-02-66	"	12-09-68	Cape Byron, 28°26′S, 153°33′E, N.S.W., Australia
FL 14439	Pull	16-02-78	"	16-09-79	Aerial Reef, 38°40′S, 178°10′E, New Zealand
FL 14408	Pull	16-02-78	"	20-09-79	" " " "
Sub-antarctic Great Skua *Stercorarius skua lonnbergi*					
DZ 15408	Pull	02-01-79	Possession	24-09-79	At sea 27°39′S, 14°34′E, off Bogenfels, Namibia
DZ 14313	Ad	13-11-73	"	18-10-79	At sea, 29°23′S, 14°39′E, off Porth Nolloth, South Africa
DZ 13785	Ad	23-10-73	"	21-05-80	Cap Infanta, 34°27′S, 20°51′E, South Africa
DZ 15454	Pull	27-01-79	"	?-04-81	Mossel Bay, 34°12′S, 22°08′E, "
DZ 15424	Pull	23-01-78	"	?-01-82	Marion Is., 46°54′S, 37°45′E.
DZ 12972	Ad	20-12-75	Kerguelen	11-07-76	Rockingham, 32°16′S, 115°21′E, Western Australia
DZ 14144	Ad	23-01-77	"	10-07-77	Quinns Rocks, 31°41′S, 115°28′E, "
South Polar Skua *Stercorarius maccormicki*					
DZ 16078	Ad	?-02-79	Pointe Géologie	08-12-81	Dailey Islands, 77°53′S, 165°06′E, Antarctica
DZ 16090	Ad	?-02-81	"	20-12-81	Cap Crozier, Ross Is., 77°31′S, 169°23′E, Antarctica
DZ 18507	Ad	02-02-78	"	14-01-82	Franklin Island, 76°05′S, 168°11′E, Antarctica
DZ 16110	Ad	08-03-79	"	14-01-82	" " " "
DZ 16064	Ad	14-02-79	"	14-01-82	" " " "
DZ 13066	Pull	12-01-69	"	09-01-82	Possession Island, 71°27′S, 171°08′E, Antarctica
DZ 12078	Ad	11-01-69	"	09-01-82	" " " "
DZ 13094	Ad	28-02-69	"	02-12-71	Casey, 66°17′S, 110°32′E, Antarctica
DZ 14919	Pull	28-01-76	"	10-12-76	At sea, between Tulagi (Florida Is.) and Honiara (Guadalcanal Is.), 09°17′S, 160°00′E, Solomon Is.