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BREEDING BIOLOGY OF THE NORTHERN GIANT PETREL *MACRONECTES HALLI* AND THE SOUTHERN GIANT PETREL *M. GIGANTEUS* AT ILE DE LA POSSESSION, ILES CROZET, 1966 - 1980

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SUMMARY

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Data from the ringing files of Southern Giant Petrels *M. giganteus* and Northern Giant Petrels *M. halli* at île de la Possession, îles Crozet, from 1966 to 1980 show that these birds are faithful to their breeding localities, and in particular no inter-island movement was recorded. They mate for life, and divorces occurred in only 15% of pair-bond breakup in both species. The average length of a pair-bond was 2,4 years in *M. halli* and 3,2 years in *M. g iganteus*, the surviving bird being the female in 58% of the cases in both species. The length of nonbreeding periods "sabbatical leaves" was on average 2,7 years in *M. halli* and 1,4 years in *M. giganteus*, and the interval between two of them was on average 1,7 years in *M. giganteus* and 3,1 years in *M. halli*. From 15-40% of the adult birds were on sabbatical leaves each year. The age of first breeding was between four and 11 years, and perhaps more. In the cohorts of breeders ringed in 1966, 1968 and 1969, mortality was about 8% in both species after the first year, but was more variable from year to year in *M. giganteus* than in *M. halli*. At île de la Possession, the population of *M. halli* increased 3,1 times and that of *M. giganteus* 1,8 times from 1973 to 1980. These increases are possibly related to the development of commercial fishing in the Southern Ocean as well to the general increase of human activity which provides the birds with food in the form of refuse.

INTRODUCTION

Both species of giant petrels, the northern *Macronectes halli* and the southern *M. giganteus*, breed in numbers at îles Crozet where they have been the subject of several studies (Voisin 1968 a,b, 1976, 1978, 1984, Mougin 1975). At île de la Possession (Fig. 1) they have been monitored annually since 1966 by resident biologists, who recorded their observations in ringing files of the Centre de Recherches sur la Biologie des Populations d'Oiseaux, Paris and in a special file where, besides ringing data, other observations such as the ring numbers of mates and chicks, breeding success and location of the nest were usually noted. For several reasons, ringing operations slowed down from 1978, except in 1980, at the end of which year the special file ends. In

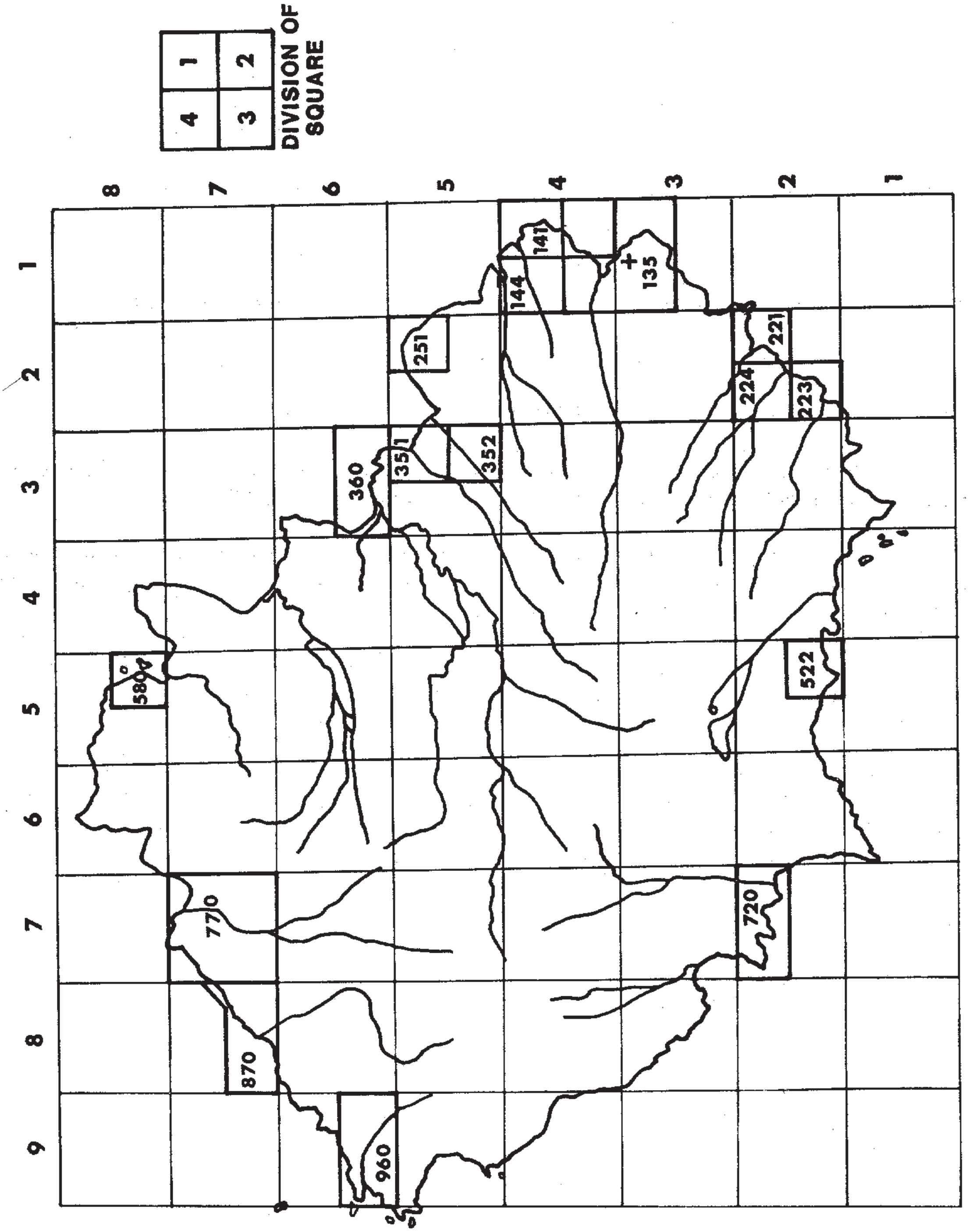

Figure 1

Ile de la Possession showing the grid system used to plot the breeding localities of giant petrels.+: station. The sides of a square are 2 km long. See Table 2 for the names of breeding localities.

spite of annual variations in the intensity of monitoring, the files contain much valuable information, an analysis of which form the basis of this paper.

METHODS

During ringing and retrapping activities, the following data were recorded as far as possible: ring number, species and sex of the bird, breeding status, ring number of its mate and, eventually, of its chick, or of its parents if it was a chick, and location of the nest. Nests were numbered annually. Some colonies were visited several times a year, whereas colonies situated farthest from the station were usually visited only once or twice a year. Some biologists surveyed colonies thoroughly, while others worked more irregularly. This has been taken into account in the data analysis.

Initially, I arranged file cards according to ring numbers, so as to compare them and to verify their data. Thus I could complete a number of cards where some data were lacking, and even reconstitute a few missing cards. I also made use of the field notes which some biologists sent to me, and of my own notes from 1966 to facilitate data checking.

The two giant petrels were not separated specifically until the mid 1960s, and their determination demands some training and attention (Warham 1962, Bourne & Warham 1966, Voisin 1968a, 1976, 1982a, Johnstone 1974, Hunter 1983a). In practice, errors in species determination were not numerous in the files, but many birds were not determined to species at all, especially in the first years from 1966. Therefore I assigned records to species using the criteria indicated in Table 1. As a result, the birds were grouped into five categories, *M. giganteus, M. halli*, probable *M. giganteus*, probable *M. halli*, and birds of uncertain status, which were only a small number. Sex determination was only made in 43% of the ringed individuals, adults and fledglings.

Data checking resulted in a computer file of 2 327 individually ringed birds. A factorial analysis of correspondence (Meyrier 1986) showed that no statistical difference could be found between individuals determined as *M. giganteus* and probable *M. giganteus*, as well as between birds determined as *M. halli* and probable *M. halli*. Therefore only three categories of birds are recognized in the following study: *M. giganteus, M. halli* and birds of undertermined species. Due to the very low numbers of adults ringed or controlled and to the overwhelming numbers of chicks ringed, data for years 1965, 1967, 1978 and 1979 deviated too much from those of other years to be kept in the analysis. If these four years are excluded, there is little variation in the parameters. The years 1974 and 1975 are characterized by a large reduction in the number of birds ringed and recaptured, probably due to disturbances, and their data are used with caution.

Breeding numbers are given as numbers of nests where either a chick or an egg has been observed. Counts made in the field, when available, are always preferred to an estimation from ringing data. I assumed an average mortality of about 60% from egg laying to chick fledging (Voisin 1968a, 1976, Mougin 1975) when calculating breeding numbers from ringing data.

Dates of death of individuals were rarely recorded. Birds were considered to be dead in biological year y+1 if recaptured for the last time in year y. Similarly, a bird was considered as a nonbreeder in year y if controlled breeding in a well-monitored colony in years y+1 and y-1, but not in year y, unless its mate from the previous year had been recaptured breeding in year y. In order to minimize imprecision, data about nonbreeders were collected only in the best monitored colonies.

A bird was considered as still mated with its original partner in year y if mated with it in years y-1 and y+1, even if it was not itself controlled in year y, and if its partner was not breeding with another bird in year y. If a pair was recorded

TABLE 1

CRITERIA USED TO DETERMINE SPECIES OF GIANT PETRELS AT ILE DE LA POSSESSION, ILES CROZET, 1966-1980

First-rank criteria (One is needed to determine to species)	Second-rank criteria (Three are needed to determine to species)	Remarks
1 - Bill tip colour 2 - determination by an experienced observer	1 - Egg-laying date 2 - Hatching date	- Period from 10-30 Sep., from 5-25 Nov. and from 1-30 Mar. excluded because of possible overlap between both species.
3 - Description of the plumage of an old bird	3 - Fledging date	
4 - Species of parents, when known	4 - Species of mate 5 - confirmation of determination by another observer	- No criterion should be in contradiction with the other ones, except second-rank 4, because of occasional inter-specific matings (Burger 1978, Hunter 1983a).

breeding one year, it was considered to have remained paired during the entire year. These assumptions are justified by the high mate fidelity of giant petrels.

Breeding failure was preferred to breeding success as an estimate of breeding efficiency since it became evident from the available information that it was better recorded in the field. Probably because of the timing of relief ship visits, many chicks were not followed until fledging. Breeding failure was defined as the numbers of breeding pairs known to have failed expressed as a percentage of the number of pairs recorded breeding in any one year. Due to insufficient coverage of the colonies, breeding failure was underestimated in most years. The stage at which mortality occurred was often not indicated, so I have not distinguished between egg and chick mortality. Estimates of breeding failure for *M. giganteus* were made for samples which were too small (< 10) to have any significance, except in 1966 and 1977. These uncertainties in such an important demographic parameter as breeding failure make illusory the building of any model for the giant petrel populations of île de la Possession from 1966 to 1980. When comparing results, I used Student's *t*-test.

Breeding localities were plotted on numbered 1-km^2 squares (Fig.1). When they extended without interruption through two or more adjoining squares, they were given only one number for convenience, as, for instance, at Morne Rouge (360) or in Baie du Marin (135).

Breeding seasons have been designated by the number of the year in which they commenced (e.g. the breeding seasons 1966-67 and 1967-68 are called 1966 and 1967). Since field-work commenced in January 1966, some data on the 1965 breeding season have been gathered, mainly concerning *M. giganteus*, and have been taken into consideration when of interest.

RESULTS AND DISCUSSION

Fidelity to breeding localities

Giant petrels are known for their fidelity to their breeding islands (Ingham 1959, Warham 1962, Conroy 1972, Mougin 1975, Hunter 1984). This also applies to the Crozet birds, none having been recaptured breeding on an island other than the one where it had been ringed as a breeder or chick. Observations of "strangers" always referred to nonbreeding, stray individuals.

Giant petrel colonies seem to be very unstable in the îles Crozet (Voisin 1968a, 1976, 1978, 1984, Mougin 1975). The same nest is rarely used two years in a row, and changes are the rule. The limits of the colonies, as well as the arrangement of nests within them, change from year to year, some colonies may vanish, and new ones may be founded elsewhere. However, the available data show that individuals always breed within the same general areas, here designated as "breeding localities", as opposed to breeding colonies which are the exact places where breeding occurs (Fig. 1, Tables 2 & 3). Of 2 113 observations of birds recorded breeding in two consecutive years or in two years with a nonbreeding period "sabbatical leave" in between, only 329 (15,6%) had moved to another breeding locality when recorded for the second time, with a difference between *M. halli* (16,2%, n = 1 664) and *M. giganteus* (13,3%, n = 449) which is significant (t = 1,98; $P<0,05$). About one-third of the pairs mated for two years or more moved at least once to another breeding locality.

Most moves occurred between localities 141 and 144 (Fig. 1, Table 4), which are adjacent and may be considered as one single locality. Localities 351 and 360 are also close together, and the short-lived locality 352 was an offshoot of locality 360. The easternmost localities (135, 141 & 144) make up a well defined group, most closely related to localities 221 - 223 (Fig. 1). The remaining localities show little relation to them in number of moves, and locality 720 appears very isolated. A number of

TABLE 2

BREEDING LOCALITIES OF GIANT PETRELS ON ILE DE LA POSSESSION, ILES CROZET,

1966 - 1980

Locality [a]	Name of locality	Remarks
135	Baie du Marin	- Locality extending inside squares 131, 134 and 143
141	Crique du Sphinx	- 141 and 144 may be considered as one single locality
144	Vallée de la Chaloupe	
221	Pointe du Bougainville	
223	Crique de Noël	
224	Vallée de la Malpassée	
251	Cap Chivaud	
351	Petite Manchotière	
352	Nord du Plateau Jeannel	
360	Morne Rouge	
522	Trou du Diable	
580	Baie du Petit Caporal	
720	Baie du "la Pérouse"	- sometimes called "Baie de la Pérouse"
770-870	Grande Coulée	- called "770" in the text. Information lacking to decide whether 770 and 870 are one or two separate localities
960	Pointe des Moines	

a: The eastern localities are: 135, 141, 144, 251, 351, 352 and 360. The easternmost localities are: 135, 141 and 144 and were the best monitored ones

TABLE 3

OCCUPATION OF BREEDING LOCALITIES OF GIANT PETRELS ON ILE DE LA POSSESSION, ILES CROZET, 1966 - 1980

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                                              Years
Localities    65   66   67   68   69   70   71   72   73   74   75   76   77   78   79   80
135         -----=====--------------------=====-----------=====-----===========  ?      ?
141         +++++-----   ?                  ----------======================----------  ?  ======
144         ============================================================== ------  ?  ------
221         ----------   ?    -----    ------------------
223                                    -------------------------------------  ?    ?
224                                    ---------------------
251                                         ----------------------=====  ?    ?    ?  ------
351           ?    -----   ?  ==========---------------====================-----   ?    ?  ======
352                                    ================================+++++  ?    ?
360           ?    =====   ?  ==================================================+++++   ?  ++++++
522                                                                           ------
580                                                       ?   ---------------  ?  ------
720           ?    =====   ?  =======================================================   ?  ======
770           ?    =====   ?  ==================================================   ?  ===========
960                                                                           ------
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----- : *M. halli* only; + + + + + : *M. giganteus* only; = = = = = : *M. giganteus* and *M. halli* together; ? no available data. Data for 1965 included when available.

TABLE 4

NUMBERS OF MOVEMENTS OF GIANT PETRELS BETWEEN BREEDING LOCALITIES ON ILE DE LA POSSESSION, ILES CROZET, 1966 - 1980, BOTH SPECIES COMBINED

Localities													
135	96												
141	11	84											
144	21	124	342										
221	4	1	4	17									
223	5	3		7	97								
224	9	4		2	13	36							
251							9						
351		2	6		1			72					
352	1	4					1	2	11				
360	3	7	11	1			1	44	10	166			
580	1							1		2	43		
720	1						1					277	
770			7				1		1	5	3	4	530
	135	141	144	221	223	224	251	351	352	360	580	720	770
	Localities												

moves occurred from the easternmost localities and may be related to human disturbance (see below). Such movements would likely not have occurred under normal circumstances. Natural events, such as snowstorms (Voisin 1968a, Hunter 1984) may also lead to the more or less complete desertion of colonies, but this seems to be very rare.

Of 12 birds ringed as chicks and subsequently recaptured at breeding localities, all had returned to île de la Possession (see Table 12). All three *M. giganteus*, two breeding and one nonbreeding, had moved to other localities, whereas only two *M. halli*, both breeders, had done so. The seven other *M. halli*, five breeders and two of indeterminate status, were found in their natal breeding localities or nearby. Too few observations have been carried out to know exactly to which extent breeders may visit breeding localities other than their own during the breeding season. The available evidence suggests that this happens occasionally.

The strong fidelity of giant petrels to their breeding localities should result in the species being divided into several well separated populations, and in fact differences in morphology as well as in the frequency of white-phase birds have been pointed out in *M. giganteus* (Voisin 1968a, 1982b, Shaughnessy 1971, Voisin & Bester 1981). Nevertheless, *M. giganteus* and *M. halli* from the îles Crozet do not seem different from their relatives from several other sub-Antarctic islands, such as the Prince Edward Islands or South Georgia (unpubl. data).

Since giant petrels do not apparently move between islands in the Crozets, one may think that the birds of each one make up distinct populations. To what extent this is true still remains to be determined, but, according to my observations (Voisin 1968a, 1976, 1982b, unpubl. data), the birds of the different islands are morphologically indistinguishable from each other, which suggests that sufficient gene flow exists between them. Gene flow between breeding localities at île de la Possession is documented by movements of breeders from one to the other (Table 4). Even if some of these movements have been caused by human disturbances, they must be sufficient to maintain genetic homogeneity in each species over the whole island.

In contrast to the sub-Antarctic localities of îles Crozet (this study), Macquarie and South Georgia (Warham 1962, Hunter 1984), *M. giganteus* in the South Orkneys and in Terre Adélie, Antarctica, seems to breed in colonies which are much more stable, and old nests or nest sites are reused to a large extent (Mougin 1968, 1975, Conroy 1972). This may be an adaptation to cold climates, where energy expenditure is higher, and food often more difficult to obtain : be reusing their old nest sites, the birds reduce their energy costs, not only in not searching for a new location, but also in social interactions. This explanation is nevertheless not valid for Southern Giant Petrels *M. g. solanderi* at the Falkland Islands which, although living in a sub-Antarctic environment, breed in permanent colonies (Voisin 1982b).

Nest building is a very important component of the behaviour of giant petrels at îles Crozet, even in chicks and nonbreeding birds (Voisin 1978). They only use material they can reach without leaving the nest, and, at the end of the breeding season, continued handling, as well as the effects of trampling and excreta, have considerably reduced the nest and surrounding vegetation. By changing nest-sites every season, even by only a few metres, giant petrels find a large supply of new nesting material. In this way, they behave like Gentoo Penguins *Pygoscelis papua* at the îles Crozet (pers. obs.) and apparently for the same reason.

By remaining in the same breeding locality from year to year, giant petrels do not found a new colony at the onset of each breeding season, and thus may keep most of the advantages of colonial breeding, i.e. in foraging efficiency, defence against predators and social behaviour (Furness & Monaghan 1987). Changes of nesting sites are made possible by the large area suitable for breeding at the îles Crozet. If the recent increase in numbers of both species continues (see below), these changes may become more restricted because of increased competition, not only intraspecific and between both species of giant petrels, but also between giant petrels and Wandering Albatrosses *Diomedea exulans*, as well as with Gentoo Penguins (see Voisin 1968b, 1984).

The pair bond

Giant petrels pair for life, or at least for a very long time (Conroy 1972, Mougin 1975, Hunter 1984). Pairs observed in this study lasted up to 11 years in *M. halli* and nine years in *M. giganteus* (Table 5). However, most pairs lasted for a shorter period, and about 80% of them were broken in the course of three years in *M. halli* and of five years in *M. giganteus*. The average duration of a pair bond was 2,24 years in the former species and 3,24 in the latter, the difference being highly significant (t = 5,13; P < 0,001). In 85,5% of the cases when one bird was found again with a new mate, the former one was never seen again and was presumed to have died. Both mates vanished at the same time in 54,9% of the widowed pairs. When known, the surviving bird was the female in 58% of the cases, and the male in 42%, with no significant difference between *M. halli* and *M. giganteus* (Table 6). Thus survival of mated females seemed to be somewhat better than that of males.

Newly paired birds usually bred in the same locality where they had bred for the last time with their previous mate, although the tendency was not as marked in *M. giganteus* as in *M. halli*. In *M. halli*, females moved much more often than did males to new breeding localities (Table 7). Seventyfive percent of the widowed *M. halli* paired again in the course of two years following the disappearance of their mate (Table 8). Movement to new localities was not related to the length of the widowed period in *M. halli*. Unfortunately, there were insufficient data to draw conclusions for *M. giganteus*. The average length of the widowed period was 2,2 years in female and 1,8 years in male *M. halli*, but the difference was not significant. These values were 1,9 years and 3,0 years, respectively for *M. giganteus*, but there were insufficient data to test for significance.

A pair was considered as divorced when both partners were retrapped subsequently and at least one of them had bred with a new mate. Divorce occurred in 16,0% of the observed *M. giganteus* pairs and in 14,1% of the *M. halli* pairs which broke up, the difference being not significant. In *M. halli*, widowed birds did not move significantly more often to new localities when breeding again with a new mate than did divorced birds, nor did they spend more time before breeding again. All four divorces observed in *M. giganteus* happened when one of the former mates moved to a new locality, and in all cases one or both partners were not retrapped during the following one to three years.

In 16 cases where the result of breeding in the last season before divorce is known with certainty in *M. halli*, nine pairs failed, and seven bred successfully. Thus, even if the sample is small, breeding success did not seem to be related to divorce in this species. In the four cases of divorce recorded in *M. giganteus*, nothing is known of the breeding success of the preceding year, except that two pairs were noted with chicks, the fates of which are unknown.

On average, established *M. halli* pairs moved to new breeding localities every 3,7 years, and *M. giganteus* pairs moved every 2,3 years. In neither species did a pair move to a new breeding locality more than three times, and about two-thirds of the mated pairs did not move at all (Table 9).

It has been shown for many species of seabirds that retention of the same mate results in improved breeding success (Furness & Monaghan 1987). The data concerning *M. halli* for îles Crozet do not support this finding : pairs breeding for the first time had a breeding failure of 68,6% (n = 70) whereas pairs established for more than one year had a breeding failure of 69,3% (n = 98), the

TABLE 5

DURATION OF PAIR-BOND IN *M. GIGANTEUS* AND *M. HALLI* AT ILE DE LA POSSESSION, ILES CROZET

		Duration of pairs in years											
		1	2	3	4	5	6	7	8	9	10	11	12
% of total numbers	*M. halli*	51,2	17,3	12,6	7,9	4,7	2,4	3,2	0	0	0	0,8	0
	M. giganteus	38,1	9,5	14,3	4,8	14,3	9,5	4,8	0	4,8	0	0	0

Total number of pairs examined : *M. halli* : 127, *M. giganteus* : 21.

TABLE 6

PERCENTAGE OF SURVIVING MALES AND FEMALES AFTER DEATH OF THEIR MATES IN BOTH SPECIES OF GIANT PETRELS AT ILE DE LA POSSESSION, ILES CROZET

	Male surviving	Female surviving
M. halli	43,4	56,6
M. giganteus	44,0	56,0

TABLE 7

MOVEMENTS TO OTHER LOCALITIES BY WIDOWED GIANT PETRELS WHICH REMATED

	In the same locality as with the previous mate	In another locality than with the previous mate
	M. halli (%)	
Males	71,4	28,6
Females	50,0	50,0
Sexes combined	59,6	40,4
Number of birds	28	19
	M. giganteus (%)	
Sexes combined	37,5	62,5
Number of birds	3	5

TABLE 8

LENGTH OF THE WIDOWED PERIOD IN GIANT PETRELS AT ILE DE LA POSSESSION, ILES CROZET

	Number of years between loss of partner and remating							
	1	2	3	4	5	6	7	8
M. halli (%)	45,8	29,2	19,4	0	2,8	1,4	1,4	0
M. giganteus (%)	30,8	38,5	15,4	15,4	0	0	0	0

TABLE 9

MOVEMENTS TO OTHER BREEDING LOCALITIES BY ESTABLISHED *M. HALLI* AND *M. GIGANTEUS* PAIRS DURING THE COURSE OF THEIR EXISTENCE

	Never having moved to another breeding locality	Having moved to another breeding locality 1 time	2 times	3 times	4 times or more
M. halli (%)	68,4	19,7	9,2	2,6	0
M. giganteus (%)	63,2	21,1	10,5	5,3	0

Total numbers of pairs examined : *M. halli* : 76; *M. giganteus* : 19.

difference being not significant. Similarly, pairs in existence for three years or less had an average breeding failure of 66,3% (n = 119), whereas in longer established pairs it was of 75,5% (n = 49), the difference being also not significant. Since breeding failure was not always thoroughly recorded, this conclusion needs confirmation. For *M. giganteus*, data are too few for such a calculation.

That giant petrels may arrive at a new locality already paired with a new mate may be an indication that at least part of the pairing takes place outside colonies, and perhaps at sea. In this case, females would be much more prone than males to follow their new mate to its breeding grounds (Table 7). The fact that both mates may turn up together at another colony, or that they may take a sabbatical leave (see below) simultaneously, may indicate that they remain together for at least some time at sea. This is supported by Mougin (1968) who noted that 55% of colony visits by *M. giganteus* at Terre Adélie during the winter of 1964 were made by pairs. That the pair-bond is very strong in giant petrels is documented by one male *M. halli*, which divorced and bred during two seasons with a new female. Then his former mate returned and the original pair reformed, and bred again for at least two successive seasons. Considering the small data set for *M. giganteus*, it seems that the pair bond is somewhat stronger in this species than in *M. halli*. Divorces in both species are most likely to occur when only one member of a pair comes back to the breeding grounds at the onset of the breeding season. Having not found its mate, it acts as if it were dead, and forms a new pair-bond.

Nonbreeding adults

Giant petrels usually breed annually, but, as in many other bird species, and especially in Procellariiformes, occasionally spend one or more years not breeding. At île de la Possession, both members of one giant petrel pair usually took a sabbatical leave at the same time, but, in several cases, only one did so, the result being a divorce.

When on a sabbatical leave, giant petrels were not reported from the island, except for 15 *M. halli* and nine *M. giganteus*. None of these birds was retrapped later, and they must have died subsequently, even if there was no information about them being sick or disabled, except for three *M. giganteus* with injured legs. Four nonbreeding *M. halli* have been recovered in South Africa, Australia and Réunion (Barré *et al.* 1976, Weimerskirch *et al.* 1985) (CF 5875, which was considered as a *M. giganteus* by Barré *et al.* (1976) was in fact a probable *M. halli*). This suggests that at least part of the nonbreeding birds spend their sabbatical leaves away from their breeding islands. In contrast, colour-banded nonbreeding sabbatical birds were regularly found around breeding sites in South Georgia (Hunter 1984, S. Hunter pers. comm.).

Most sabbatical leaves lasted one year in both species (Table 10), with an average length of 2,7 years in *M. halli* and 1,4 years in *M. giganteus*, but this difference is not significant. A few longer leaves, of up to seven years, were recorded in both species, but for the longer ones I suspect that birds which escaped retrapping were involved.

The interval between two sabbatical leaves was very variable. In the best surveyed colonies, pairs have been observed breeding each season up to five years in a row (*M. giganteus*) and even up to 10 years in a row (*M. halli*), but, on average, intervals between two sabbatical leaves were much shorter, the mean being 1,7 years in *M. giganteus* and 3,1 years in *M. halli*, the difference being significant (t = 2,05; P<0,005; Table 11). Many birds bred in more or less alternate years, especially *M. giganteus*.

In many cases, sabbatical leaves coincided with widowed periods. This was not very marked in *M. giganteus*, which bred with a new mate in only 21,4% of the cases when returning from a sabbatical leave. In this species, forming a new pair

TABLE 10

DURATION OF SABBATICAL LEAVES IN GIANT PETRELS

AT ILE DE LA POSSESSION, ILES CROZET

	Duration of sabbatical leave in years							
	1	2	3	4	5	6	7	8 and more
M. halli (%)	66,0	18,4	10,5	3,1	0,5	0,5	1,0	0
M. giganteus (%)	81,6	4,1	10,2	2,0	0	0	2,0	0

Total numbers of leaves examined : *M. halli* : 191; *M. giganteus* : 49.

TABLE 11

LENGTH OF INTERVALS BETWEEN TWO SABBATICAL LEAVES IN GIANT PETRELS

AT ILE DE LA POSSESSION, ILES CROZET

	Interval in years										
	1	2	3	4	5	6	7	8	9	10	11 and more
M. halli (%)	51,9	23,6	9,4	5,5	4,4	2,8	0,6	0,6	0,6	0,6	0
M. giganteus (%)	60,8	18,9	10,8	6,8	2,7	0	0	0	0	0	0

Total number of intervals examined : *M. halli* : 181; *M. giganteus* : 74.

occurred as often after a sabbatical leave as between two of them. In contrast, when returning from a sabbatical leave, *M. halli* bred with a new mate in about 50% of the cases, and in this species about 65% of repairings occurred at the end of a sabbatical leave, and only 35% between two of them. Sabbatical leaves of more than one year coincided with widowed periods in about 67% of the cases in both species, whereas this was the case in only 13% of the one-year leaves in *M. giganteus* (n = 28), and of 40% of them in *M. halli* (n = 71).

The percentage of birds on sabbatical leaves each year was similar for both species, varying from 15-40% (Fig. 2), and was on average 26,7% in *M. halli* and 30,1% in *M. giganteus*. Only for the latter species do these data fit well with those for South Georgia in 1979 and 1980 (26,9 and 33,8%, Hunter 1984, 1985). My values for *M. halli* are much lower than the ones for South Georgia in 1979 and 1980 (37,7 and 57,5%, Hunter 1984, 1985), except in the years 1974 and 1975, when breeding by *M. halli* was disturbed at île de la Possession.

Several causes may play a role in making giant petrels take sabbatical leaves. It is possible that some widely dispersed birds may be unable to return to their breeding grounds in time, and widowed birds may need some time to find a new mate, and thus their sabbatical leave is not equivalent to that of established pairs. One of the main reasons may be that some birds may not recover completely from chick-rearing the previous breeding season and thus may miss a season. Here several factors may be involved, such as disease, age, and above all food availability in winter. Postbreeding body condition would then be the key, in a way similar to that of the Greyheaded Albatross *Diomedea chrysostoma* (Hector *et al.* 1986).

For slow-reproducing species such as giant petrels, it is surely an advantage to have each year a large part of the adult population not breeding. It constitutes a kind of "security stock" in case of abnormally large mortality of adults on the breeding grounds. Then, in following years, if conditions, and above all food conditions are good again, breeding numbers would be more or less restored when there would be fewer birds on sabbatical leaves. In fact, the percentage of birds on sabbatical leaves was often low when the yearly mortality of adults was high during this study (see below). Moreover, any unforseen increase in food supplies may be turned into profit by pairs breeding in larger numbers, and giant petrels are largely scavengers which rely upon food supplies which are very variable. In this case, food availability during the late postbreeding season and at the onset of the breeding season would be a decisive factor. Supplementary breeders could hardly be recruited among immatures, since these need a long time to reach maturity and only come back to breeding grounds after several years (see below).

Age of first breeding and mortality of immatures

Only nine *M. halli* ringed as chicks at île de la Possession have been recaptured on the island (Table 12). Seven were breeding when controlled, and were 5-11 years old. The remaining two were the youngest (three years old) and were of unknown status. Since retrapping activities were less intense in 1978 and 1979, it is possible that the three 11-year old birds controlled in 1980 had bred once or twice previously, but had escaped detection. Three *M. giganteus* ringed as chicks were subsequently recovered on île de la Possession. Two of them were breeding, and were four and 10 years old (Table 12).

These data on the age of first breeding of giant petrels at the îles Crozet are in accord with those for *M. giganteus* at Terre Adélie (Lacan *et al.* 1969, Mougin 1968, 1975), Signy Island (Conroy 1972) and for both species at Bird Island, South Georgia (Hunter 1984). According to Lacan *et al.* (1969), as well as Carrick & Ingham (1970), *M. giganteus* may breed for the first time at an age older than 11 years, and my data for the ten last cohorts of chicks may be thus incomplete. However, the number of recaptures of chicks of cohorts 1966 to 1970 is low,

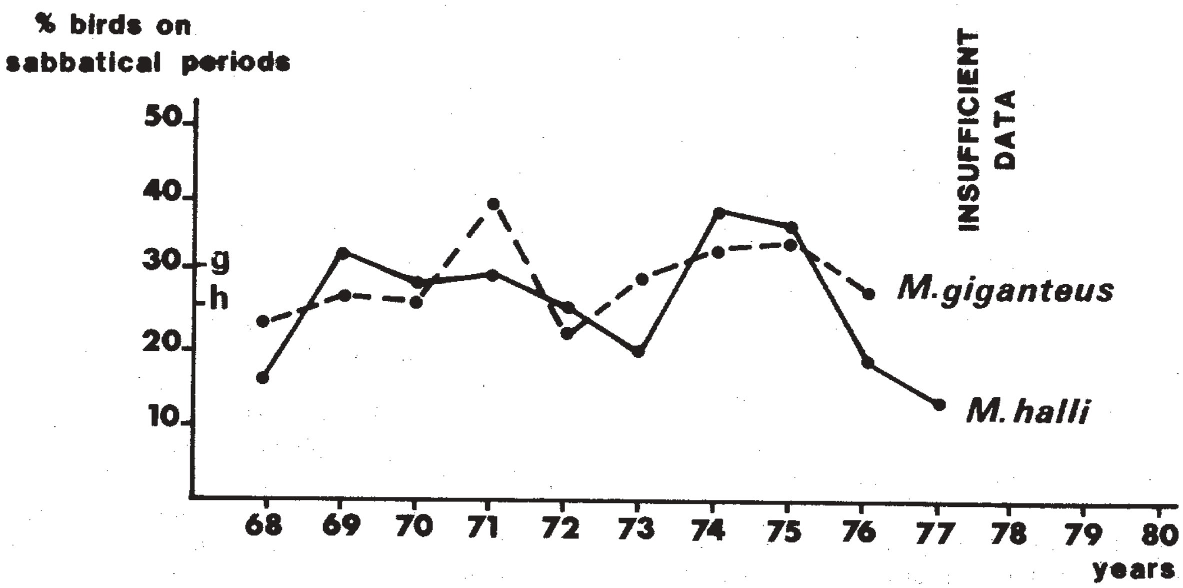

Figure 2

Annual percentages of adult giant petrels on sabbatical leaves at île de la Possession. g: mean percentage for *M. giganteus*; h: mean percentage for *M. halli* during the period of study.

TABLE 12

FIRST RECOVERIES ON BREEDING GROUNDS OF GIANT PETRELS RINGED AS CHICKS ON ILE DE LA POSSESSION, ILES CROZET

Species	Status	Age (years)	No. in the same locality as where ringed	No. in another locality than where ringed
M. halli	B	11	2	1
	B	9	2	-
	B	8	-	1
	B	5	1	-
	I	3	2	-
M. giganteus	B	10	-	1
	B	4	-	1
	I	4	-	1

B : breeding, I : definitely not breeding or breeding not certain when recovered.

and may be related to a high mortality of immatures at sea (Table 13). Nevertheless, data are still too few to allow for firm conclusions on the demography of immatures.

If the mortality of immatures is high, then the "reserve stock" of them from which the population may recover in case of a dramatic mortality of breeders (e.g. Jouventin & Weimerskirch 1984) is very low, and its role may be overtaken by the numerous adults on sabbatical leaves.

Mortality of adults

Because of the duration of this study (15 years) and the longevity of giant petrels, it was only possible to follow the fate of the three cohorts of adults ringed in 1966, 1968 and 1969 (Table 14, Figs. 3 & 4). These cohorts were composed of birds of various ages, although, similar to those of the whole adult population (Voisin 1968a, 1982b), young breeders in dark plumage with light faces and upper throats dominated. In both species, the survival curves were similar, with a steep decrease of about 34% in the first years, followed by a rather regular decrease, implying a more or less constant, and low, mortality rate. This decrease was markedly more irregular in *M. giganteus* than in *M. halli*, even though sample sizes (respectively 89 and 189) were large. The mean annual mortality rate was 7,7% in *M. halli* and 8,3% in *M. giganteus*.

No bird in these cohorts survived for more than 11 (*M. giganteus*) or 12 years (*M. halli*). Life expectancy of adults from the year of ringing was estimated to be 12,5 years in *M. halli* and 11,6 years in *M. giganteus*, using the formulas of Barrat *et al.* (1976) and Pascal (1979). Since giant petrels breed for the first time between five and 11 years of age, their longevity at île de la Possession is in the order of 18-24 years. The sudden dip in survival in the year after ringing is certainly related to the mortality of birds breeding for the first time, since mortality of older adults varies little.

The mortality of adults from year to year was variable, but of the same order of magnitude in both species (Fig. 5), and similar to that noted at South Georgia (Hunter 1984). It went through a minimum in the years 1969-1972, and was consistently higher in *M. giganteus* until 1973. Then differences between both species were small. Mortality from year to year was usually slightly lower in females (Fig. 6).

Mortality from year to year is more likely related to the one of young breeeders, since the mortality of adults varies little. In *M. halli*, it shows a peak in 1974, probably following disturbance in colonies (see below). At the beginning of this study, it was high in both species. We do not know what happened in 1967, but in 1966 colonies suffered from adverse weather, and a few even disappeared after a snowstorm (Voisin 1968). Thus it is possible that the low mortality during years 1969 to 1972 was at least partially due to improved weather conditions. The lower mortality in females is consistent with the fact that the surviving bird of a pair is usually the female. Hunter (1984) in contrast observed a slightly higher mortality of females at South Georgia.

Mortality of eggs and chicks

In *M. halli*, breeding failure from 1966 to 1977 varied from 29,4 to 87,8% (Fig. 7), but it is not possible to know how accurately it was recorded every year. It varied in much the same way as did mortality of adults from 1966 to 1974, but differently during 1974-1977. This is certainly a consequence of disturbance in colonies during the latter period, as suggested by the level of breeding failure in the easternmost, and most frequented colonies, during 1975-1977 (Fig. 7).

Data are insufficient for estimating breeding failure in *M. giganteus*, except for the years 1966 and 1977, when it was 54,5 and 39,4%, respectively (Fig. 7). As a whole, these data on breeding failure at île de la Possession are consistent with those of Warham (1962) for both species combined at Macquarie

TABLE 13

ESTIMATED MORTALITY IN COHORTS OF GIANT PETREL CHICKS RINGED AT ILE DE LA POSSESSION, ILES CROZET, 1966-1980

Cohort (Year of birth)	Number of ringed chicks		Number recovered		Mortality (%)	
	H	G	H	G	H	G
1966	10	3	1	0	90	100
1967	8	20	0	2	100	90
1968	25	3	1	0	96	100
1969	86	5	3	0	96,5	100
1970	80	4	1	0	98,7	100

H : *M. halli*, G : *M. giganteus*

TABLE 14

SURVIVAL (%) IN THREE COHORTS OF ADULT GIANT PETRELS RINGED IN 1966, 1968 AND 1969 AT ILE DE LA POSSESSION, ILES CROZET

	Years after ringing													
	0	1	2	3	4	5	6	7	8	9	10	11	12	13
M. halli	100	66,1	64,0	57,1	53,4	45,5	40,2	35,4	27,0	19,0	13,0	8,5	3,1	0
M. giganteus	100	65,0	60,6	54,9	50,5	39,4	36,0	26,9	24,6	20,2	10,1	10,1	0	0

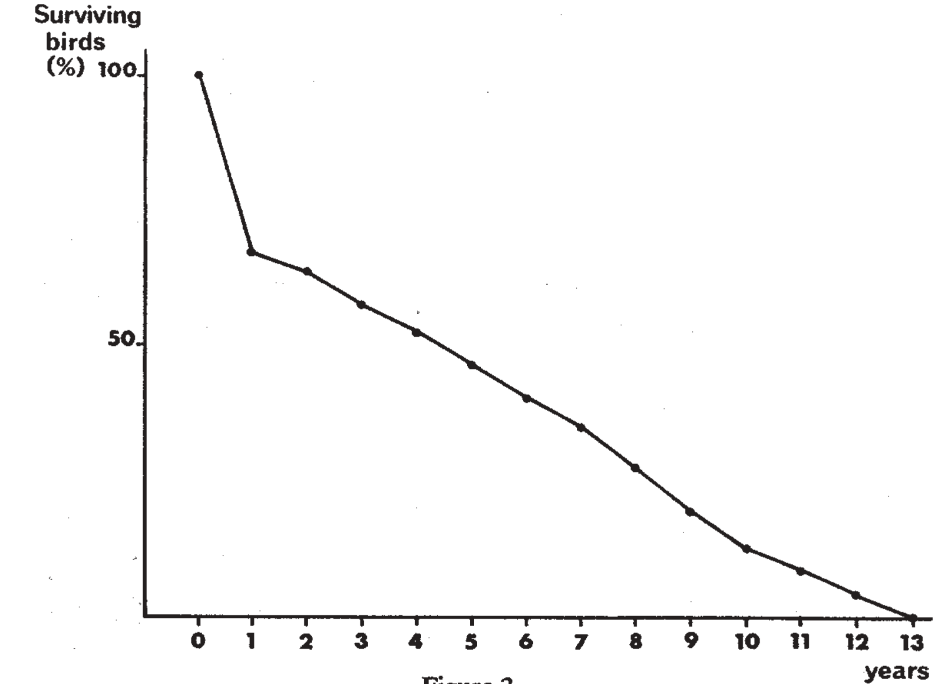

Figure 3
Mortality in three cohorts of *M. halli* ringed as breeders.

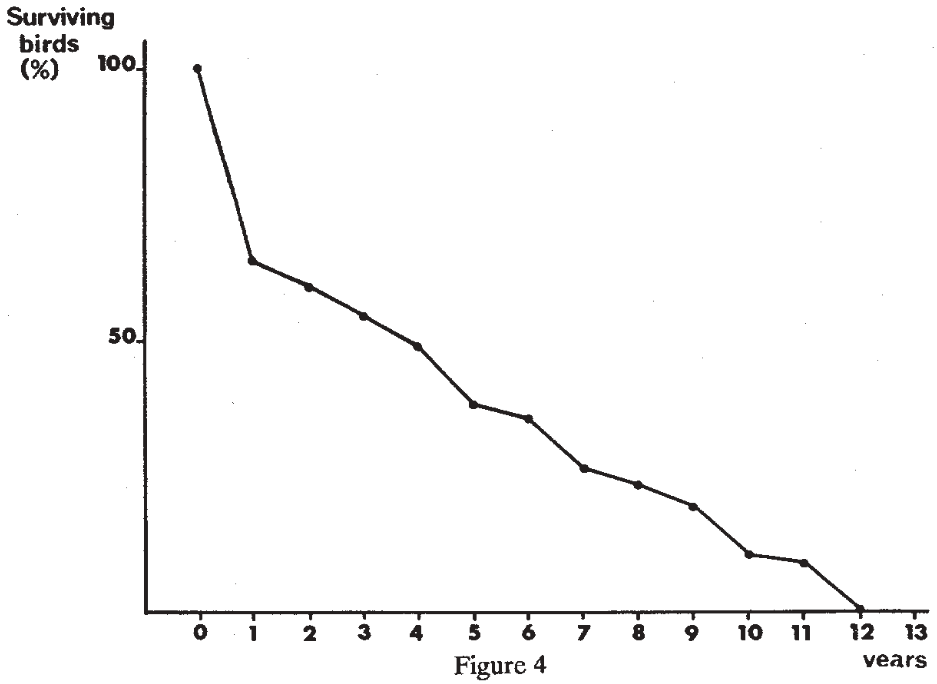

Figure 4
Mortality in three cohorts of *M. giganteus* ringed as breeders.

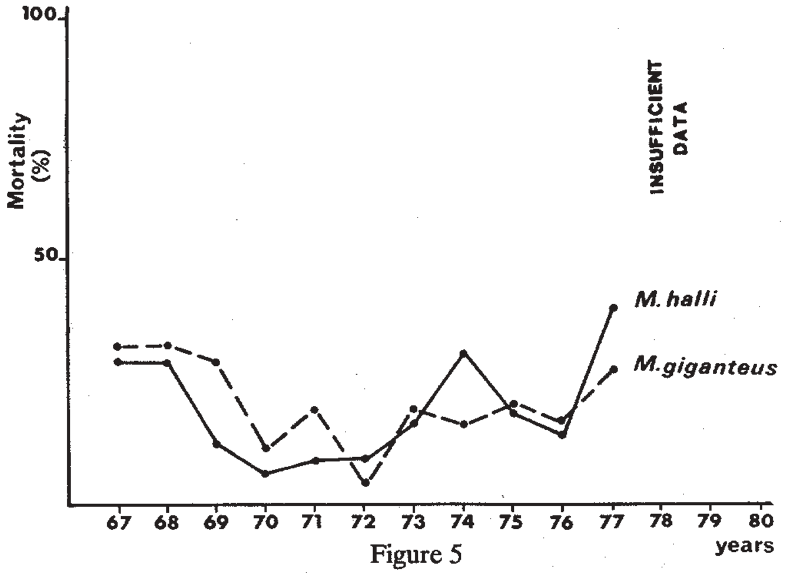

Figure 5

Variation in annual mortality of adult *M. halli* and *M. giganteus*, both sexes combined.

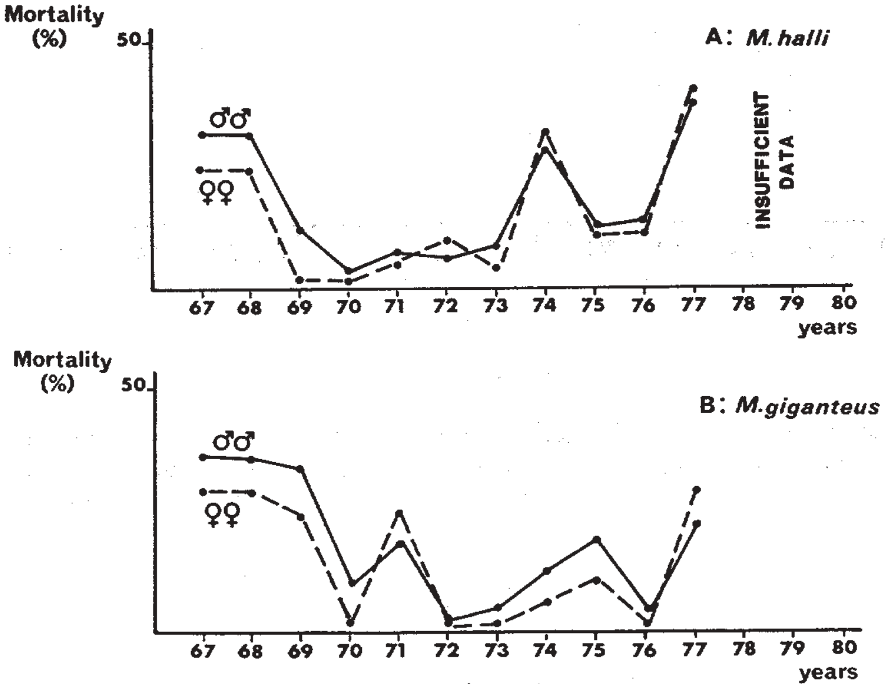

Figure 6

Variation in annual mortality of male and female *M. halli* and *M. giganteus* (based on a smaller sample than on Fig. 5, because only 43% of the birds have been sexed).

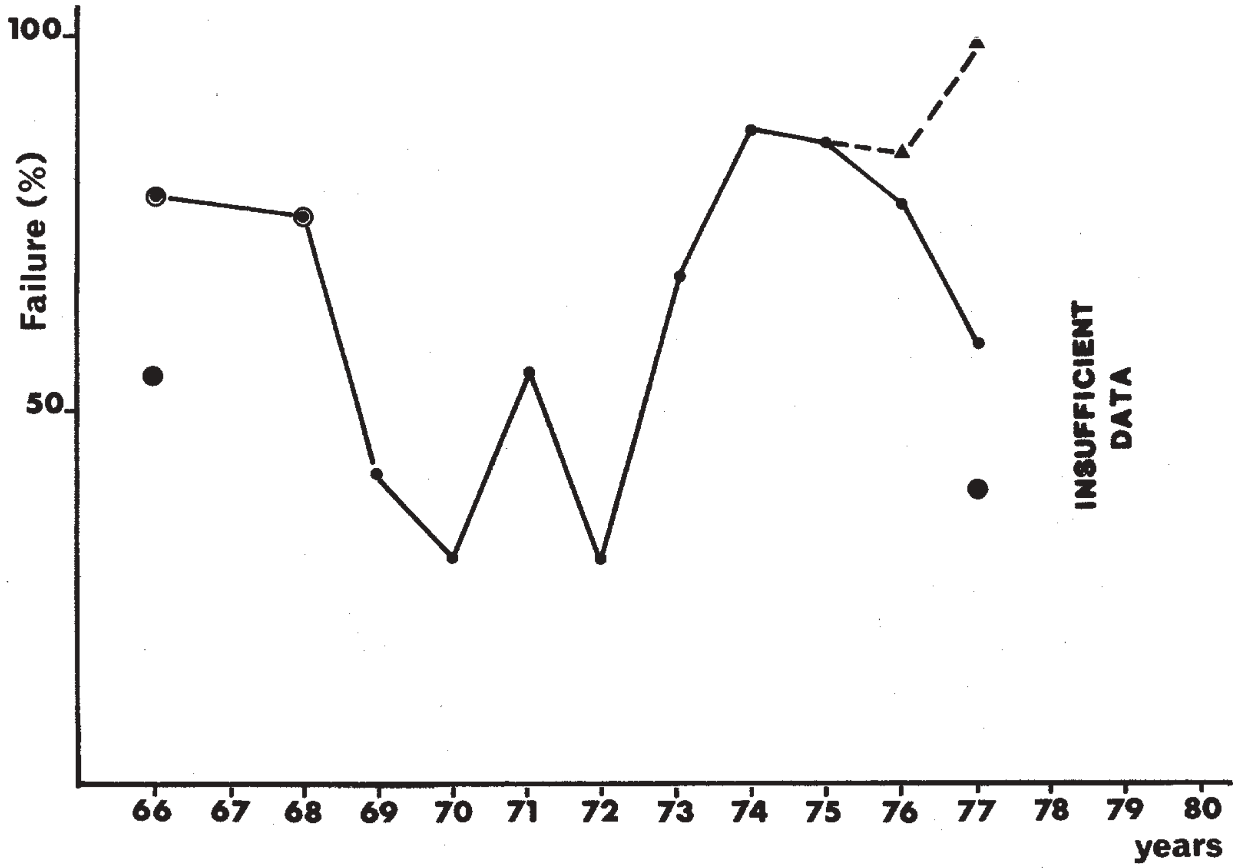

Figure 7

Breeding failure of giant petrels at île de la Possession from 1966 to 1977. *M. halli*: ● all data combined, ▲ : in the easternmost colonies, 1976-77. ◉ results based on field notes. *M. giganteus*: ● : the only two reliable data.

Island, of Mougin (1968, 1975) for *M. giganteus* in Terre Adélie and for both species at île de la Possession, and of Conroy (1972) for *M. giganteus* at Signy Island. Breeding success is on average higher in both species at South Georgia (Hunter 1984, 1985).

Changes in population size of giant petrels at île de la Possession, 1966-1980

The change in population size of giant petrels breeding at île de la Possession from 1966 to 1980 is shown in Table 15 and Figs. 8, 9 and 10. Apart for the years 1974 and 1975, there has been a consistent increase in population size from 1966 to 1980. From 1966 to 1969, the total number of breeding pairs, both species combined, decreased from at least 220 to 200. It then increased, first to 240 pairs in 1973, then to about 650 pairs in 1980. From 1973 to 1980, population size increased 2,7 times. The low values for 1974 and 1975 are certainly due to disturbances in colonies. This is supported by the fact that the reduction in nest numbers in the easternmost localities, nearest the station, accounted for most of the decrease over the whole island (Fig. 8).

The change in numbers of breeding *M. giganteus* and *M. halli*, when considered separately, showed clear differences (Table 15, Fig. 9). *M. halli* has always been the most numerous species, and increased 3,1 times from 1973 to 1980, compared to the 1,8 times of *M. giganteus*. The proportion of the latter species in the whole giant petrel population of île de la Possession decreased from 27 to 14% during the period of study. Lastly, the decrease in 1974 and 1975 was much less marked in *M. giganteus*, except in the easternmost breeding localities (Fig. 10).

This increase in the giant petrel population of île de la Possession exceeded that at île aux Cochons, îles Crozet, from 1974 to 1982, which doubled (Voisin 1984). During the same period, numbers of *M. halli* also more or less doubled in South Georgia (Hunter 1984), and *M. giganteus* colonized Bouvet Island (Haftorn & Voisin 1982). The increase in giant petrel numbers seems to have been a general phenomenon in the late seventies. Where both species occur together, numbers of *M. halli* increased markedly whereas those of *M. giganteus* grew only slightly, and even returned to their level of 1972-73 after a peak in 1978 at South Georgia (Hunter 1984).

The number of breeding localities (Tables 3 & 16) increased with the number of breeding pairs up to 1972. Thereafter, it decreased, in spite of an increase in the number of breeding pairs. This decrease was essentially due to the loss of some eastern breeding localities. Even if *M. giganteus* is more readily disturbed by humans than is *M. halli* in the îles Crozets, and seems to have more difficulty in rearing chicks (Voisin 1968a, 1976, 1978), it was much less affected than *M. halli* by human disturbances during the years 1974 and 1975. Disturbances also occurred in other years, without dramatic effects. It is thus possible that the 1974-1975 disturbances were not the only factor leading to the more or less complete desertion of giant petrel colonies during this period. Other causes, such as local weather conditions, may also have played a role.

During the period of study, the numbers of breeding Wandering Albatrosses decreased from *c.* 500 in 1968 to 267 in 1981 on the whole île de la Possession. On the eastern part of the island, they decreased from 248 in 1966 to 130 in 1981 (Weimerskirch & Jouventin 1987, H. Weimerskirch pers. comm., pers. obs.). However, the data for this species are not detailed enough to test for a correlation between its numbers and those of giant petrels, such as the one found by Voisin (1984) at île aux Cochons. Fairly good information exists for the Baie du Marin, but this area is too near the station for such a test being of any significance.

TABLE 15

NUMBERS OF GIANT PETREL PAIRS AT ILE DE LA POSSESSION, ILES CROZET, 1966 - 1980

	Whole island				Eastern localities		
Years	*M. halli*	*M. giganteus*	Undetermined species	Total	*M. halli*	*M. giganteus*	Total
1965	-	-	-	-	-	20	-
1966	150	60	10	220[a,b]	51t	18	69
1967	-	-	-	-	-	20	-
1968	150	50	10	210[b]	45	12	57
1969	140	50	10	200[b]	31	12	43
1970	160	40	10	210	34	6	40
1971	180	50	-	230	51	5	56
1972	170	60	10	240	56	10	66
1973	180	50	10	240[b]	93	8	101
1974	130	50	20	(200)	44	9	53
1975	120	50	20	(190)[b]	47	3	50
1976	250	60	10	320[b]	46	6	52
1977	220	80	10	310	37	1	38
1978	-	-	-	-	-	-	-
1979	-	-	-	-	-	-	-
1980	560	90	-	650[b]	43	5	48
	Results rounded to the above 10				Nests counted in the field		

a : minimum estimate, b : estimated through ringing files and field notes, () years with disturbances in colonies.

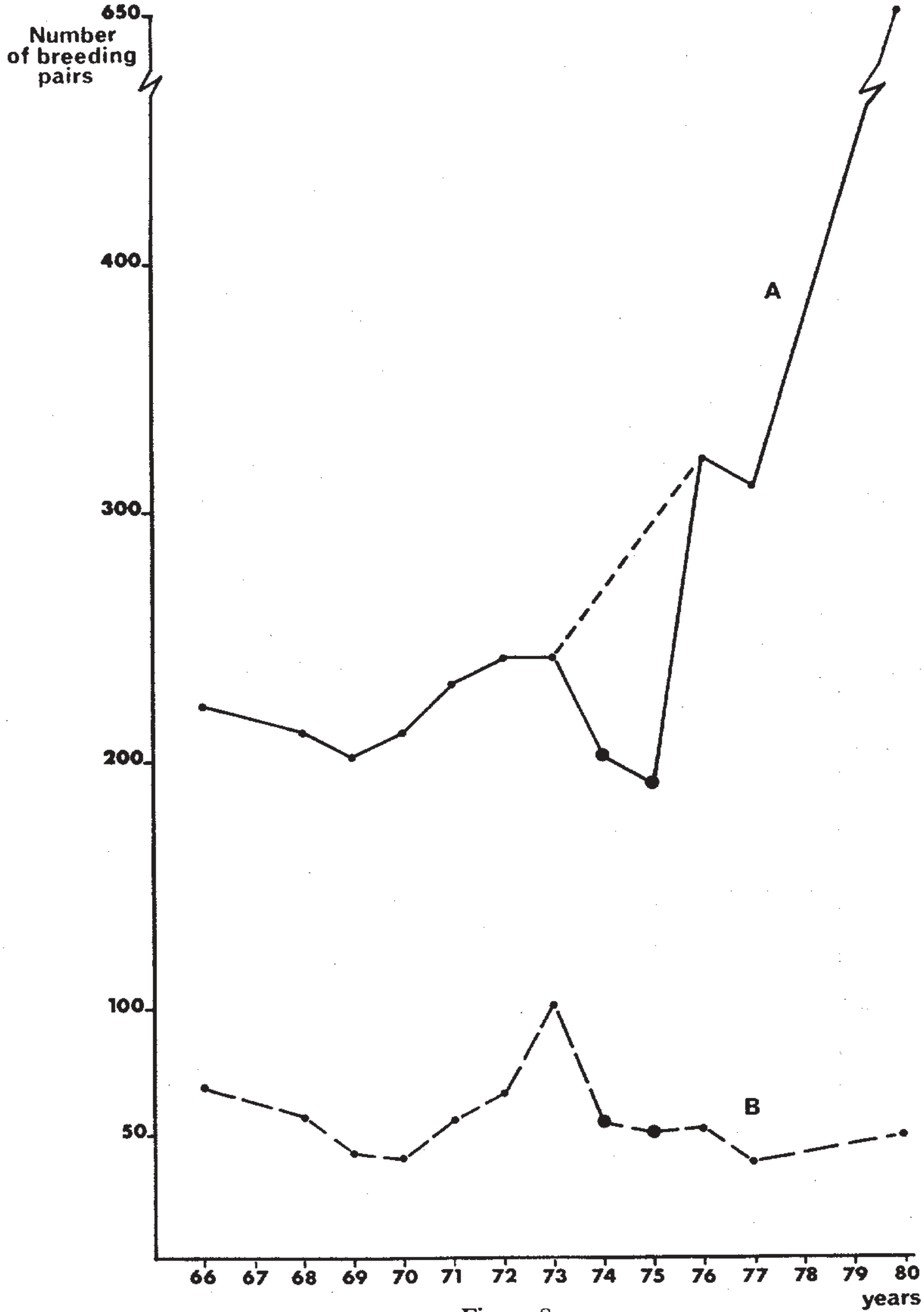

Figure 8

Total numbers of breeding giant petrel pairs on île de la Possession from 1966 to 1980, both species combined. A: on the whole island, B: in the eastern colonies

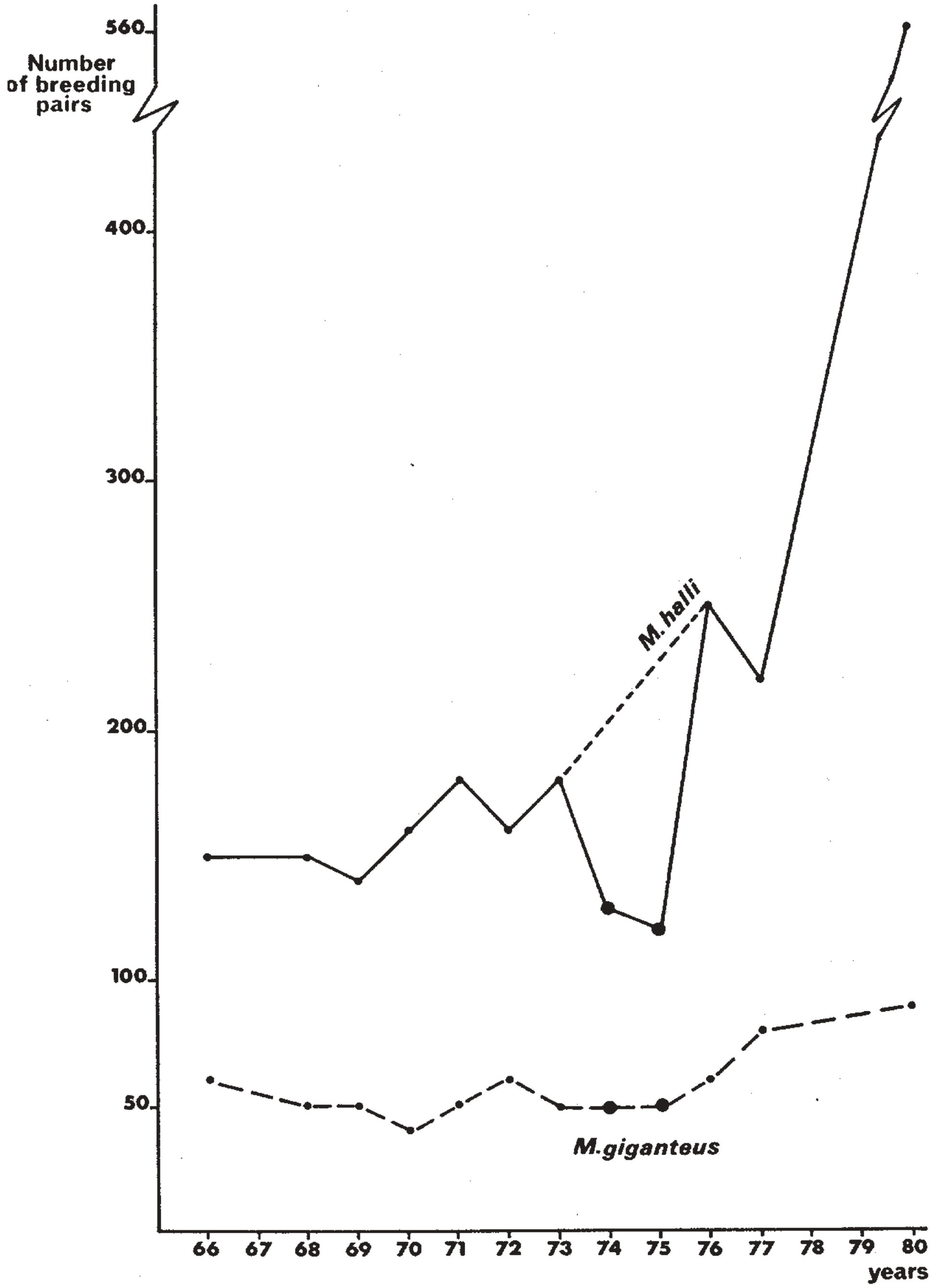

Figure 9

Total numbers of breeding *M. halli* and *M. giganteus* pairs on île de la Possession from 1966 to 1980.

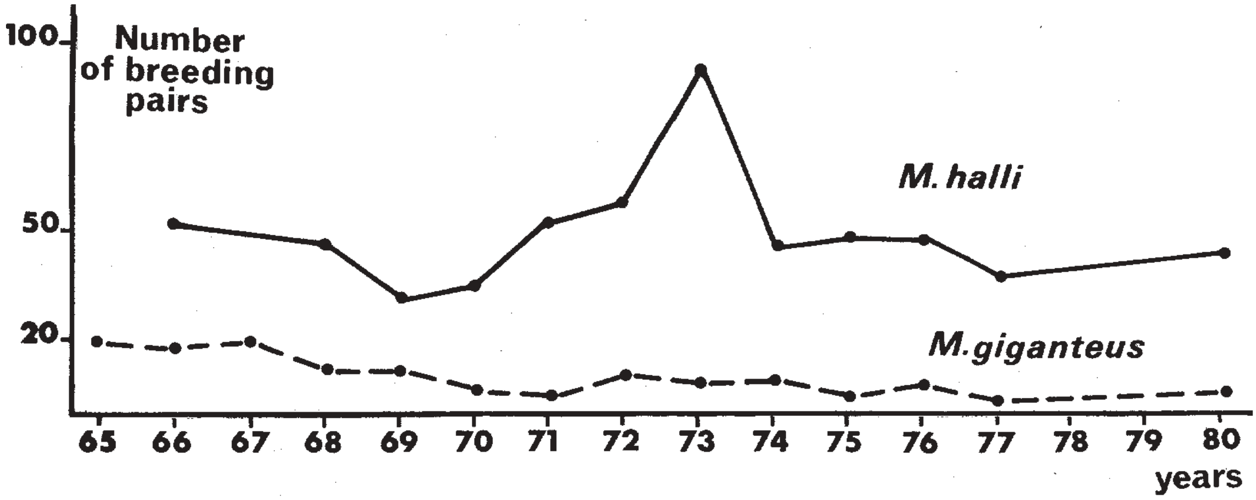

Figure 10

Numbers of breeding *M. halli* and *M. giganteus* pairs in the eastern localities of île de la Possession from 1965 to 1980.

TABLE 16

NUMBER OF BREEDING LOCALITIES OF GIANT PETRELS ON

ILE DE LA POSSESSION, ILES CROZET, 1966-1980

Years	Whole island	Eastern localities[a]
1966	8	4
1968	7	3
1969	6	2
1970	7	3
1971	11	6
1972	12	7
1973	11	6
1974	11	6
1975	10	5
1976	10	4
1977	10	4
1980	10	2

a : localities 135, 141, 144, 221, 223, 224, and 251.

Possible factors affecting numbers of giant petrels at île de la Possession.

Because giant petrels are very faithful to their breeding localities, and since their numbers have increased simultaneously at several of their breeding islands in the late seventies, inter-island movements are unlikely to be the cause of population changes at île de la Possession during the years 1966-1980. Earlier recruitment of breeders from the immature population, and a reduced number of birds on sabbatical leaves are possible explanations.

The annual numbers of newly ringed breeders decreased to a minimum in 1970. Since ringing efforts were intensive during the first eight years of this study, except in 1967, it can be considered that the bulk of the "old" breeders had been ringed by then, and that after 1970 almost all newly ringed breeders were individuals breeding for the first or second time. Consequently, an idea of the importance of recruitment in giant petrel populations of île de la Possession from 1970 can be obtained from the yearly percentage of newly ringed breeders of the total number of ringed and recaptured birds (Fig. 11). In *M. halli*, this percentage increased until 1973, and during this period was higher than annual adult mortality, except in 1970 when it was similar. Recruitment was low, and less than annual adult mortality, in 1974 and 1975, probably as a result of disturbance. High values were once again obtained in 1976, 1977 and 1980. Ringing effort was too low in 1978 and 1979 to draw conclusions.

In *M. giganteus*, which seemed to have suffered less from human disturbances than did *M. halli* in 1974 and 1975, recruitment was only markedly higher than mortality in 1972, 1975 and 1976. It was similar in 1973, 1974 and 1977, and lower in 1970 and 1971. Therefore, recruitment paralleled reasonably well the changes in the numbers of both species of giant petrels at île de la Possession from 1970 to 1977.

Recruitment of new breeders depends on two important factors: breeding success and survival of immature birds. In *M. halli*, the only giant petrel at île de la Possession for which usable information exists, breeding failure was low when numbers of breeding pairs were lowest, and when they began to increase from 1969 to 1973. This higher production of fledglings could have influenced the demography of the species from 1974 or 1975 onwards. However, recapture data do not reflect this.

The recapture data suggests low immature survival, in complete contradiction with a high recruitment of breeding birds and the spectacular growth of *M. halli* populations at île de la Possession since 1973. Losses of rings by fledglings and immatures could have occurred, but this seems unlikely to have happened on such a scale. Insufficient recapture effort may be ruled out for at least the first eight years, except 1967, for 1976, 1977 and 1980, and for the moment I have no real explanation for the contradiction, which is also valid, to a lesser degree, for *M. giganteus*.

In *M. halli*, the percentage of birds on sabbatical leaves was highest when the number of breeding birds was lowest: in 1969, 1974 and 1975, and lowest in 1973, 1976 and 1977, at the start of the increase in population size. So a better mobilization of breeders from the stock of nonbreeding adults seems to have played an important role in this increase. For *M. giganteus*, the pattern is less clear. The numbers of birds on sabbatical leaves were low when breeding numbers were high, but they showed an unexpected peak in 1971. Mobilization of breeders from the nonbreeding stock seems thus to have played a less important role in the case of *M. giganteus*.

Adult mortality from year to year was highest until 1970 in both species, and in 1974 in *M. halli*, when numbers of breeders decreased. It tended to be low, but slowly increasing, when population size increased. In *M. halli*, adult mortality changed mostly in opposition to the percentage of birds on sabbatical leaves, which tended to counteract its

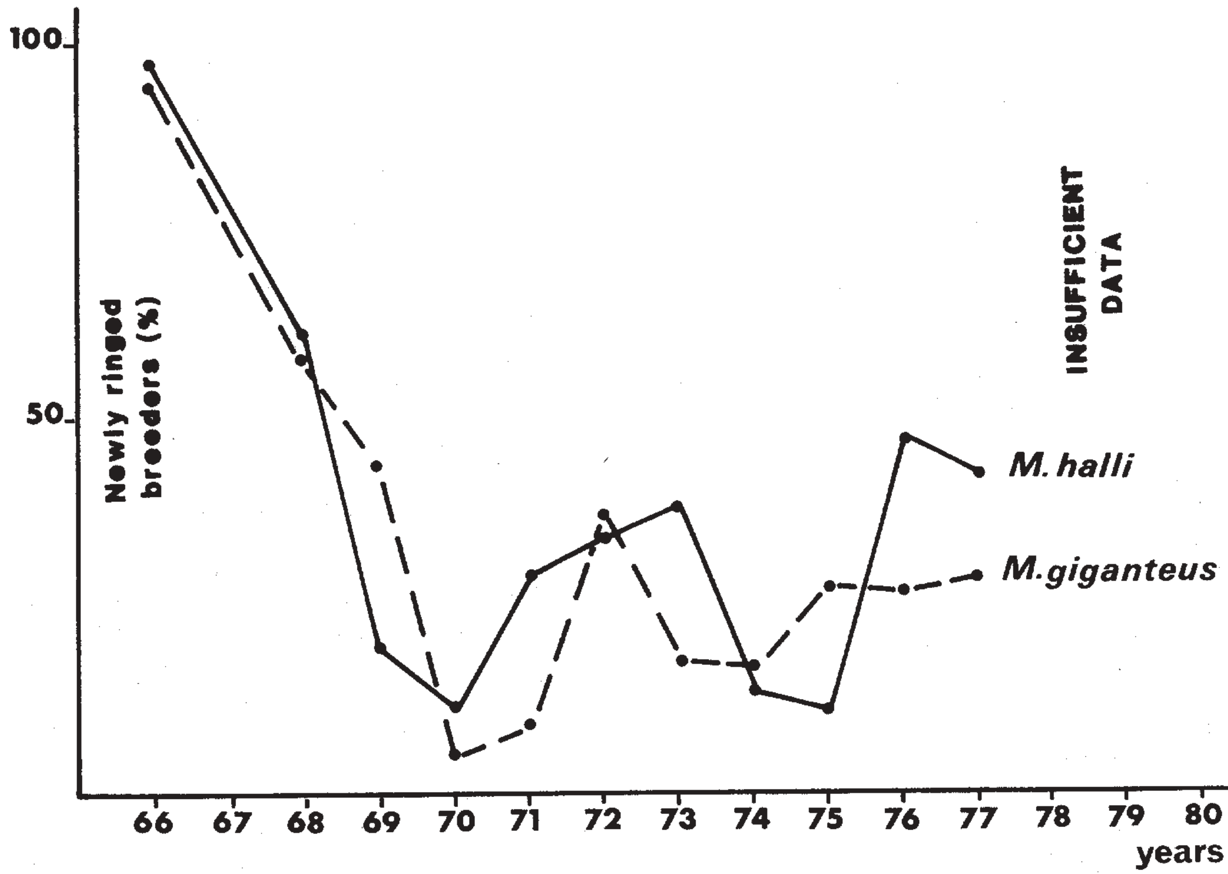

Figure 11

Annual percentage of newly ringed breeding *M. halli* and *M. giganteus* from 1966 to 1977 on île de la Possession.

effects on the number of effectively breeding birds. In 1974 however, both mortality and percentage of birds on sabbatical leaves were high, and the species may have suffered losses. Mortality of adults was much more irregular in *M. giganteus*, and changed in the same way as the percentage of adults on sabbatical leaves in 1971-1973. Thus the peak in breeding *M. giganteus* in 1972 appears as the result of the combined action of a low mortality and of a good mobilization of breeders from the stock of birds on sabbatical leaves. Since adult mortality and the percentage of birds on sabbatical leaves varied contrary to one another in 1976 and 1977, I think that the increase in numbers of *M. giganteus* was a real one, even if it was small.

The causes of population changes of giant petrels at île de la Possession are not well understood. An increase in food resources in the form of seal carrion, as suggested by Hunter (1983) for *M. halli* in south Georgia, can be ruled out at the îles Crozet because fur seals *Arctocephalus tropicalis* and *A. gazella*, although increasing, were still very few at the time of this study, and because the numbers of Southern Elephant Seals *Mirounga leonina* were decreasing rapidly (Jouventin *et al.* 1982, Barrat & Mougin 1978, pers. obs.). No apparent changes were detected in penguin colonies during this period (Jouventin *et al.* 1984), so that the increase of giant petrels at the îles Crozet is most likely related to changes in pelagic food resources (Voisin 1984). It is possible that the recent development of commercial fishing in the Southern Ocean may have contributed to the recent increase in numbers of giant petrels by providing them with quantities of garbage. The increase in the number of Antarctic and sub-Antarctic bases and expeditions may have played a similar, but less important role.

Whatever these causes may be, it is obvious that *M. halli* readily took advantage of them, and is now increasing in numbers in several localities. At the îles Crozet at least, *M. giganteus* has a higher breeding failure (Voisin 1976), has a much more irregular, and often higher, mortality of adults, and has increased only slightly in numbers. This may be related to different feeding habits. This species rarely follows ships (Johnstone 1974, Voisin & Bester 1981), and may travel farther from the islands when breeding than does *M. halli* (Voisin 1984).

Since adult mortality and breeding failure tended to be high in both species when the number of breeders was also high, there is some indication that the giant petrel populations of île de la Possession have reached a level at which density-dependent regulation factors act markedly (Ashmole 1963, Furness & Monaghan 1987).

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RÉSUMÉ

De 1966 à 1980, 2 327 pétrels géants des deux espèces, *Macronectes halli* et *M. giganteus* ont été bagués à l'île de la Possession, archipel Crozet. Le dépouillement des fichiers de baguage a montré que ces oiseaux sont très fidèles à leurs localités de reproduction, même à l'intérieur de l'île, et les deux-tiers des couples n'en changent jamais. Les couples sont en règle générale unis pour la vie, et

les divorces ne comptent que pour 16% des cas de dissolution. Chaque année, de 30 à 50% des couples ne se reproduisent pas, mais prennent une période sabbatique qui peut durer deux ans et plus, et est en général un peu plus longue chez *M. giganteus* que chez *M. halli*. La mortalité des adultes, qui a pu être suivie sur trois cohortes dans chaque espèce, est faible (de 5 à 15% chaque année), extrêmement constante chez *M. halli*, et assez irrégulière chez *M. giganteus*. La mortalité des immatures en mer semble très élevée, et l'âge de la première reproduction se situe entre 5 et 11 ans. La mortalité des oeufs et des poussins n'a malheureusement pas été enregistrée avec suffisamment d'exactitude pour apporter des renseignements utilisables.

De 1966 à 1970, les effectifs de pétréls géants de l'île de la Possession ont lentement diminué. Ensuite, ils ont lentement progressé pour atteindre environ 220 couples en 1973. Après deux années difficiles, la croissance reprend ensuite à vive allure, et en 1980 on comptait 560 couples de *M. halli* et 90 de *M. giganteus* à l'île de la Possession (Fig. 1). Les raisons de cet accroissement démographique spectaculaire, qui s'est aussi produit dans d'autres localités subantarctiques, comme l'île aux Cochons, dans l'archipel Crozet, ou en Géorgie du Sud, ne sont pas très claires. Il y a certainement eu une dimimution du nombre des oiseaux en période sabbatique certaines années, et un important recrutement de nouveaux reproducteurs, mais ce dernier point semble en contradiction avec le très faible nombre d'oiseaux bagués comme poussins et contrôlés comme reproducteurs ensuite. De toutes façons, il semble que les ressources en nourriture utilisables par *M. halli* se soient beaucoup accrues, alors que *M. giganteus*, qui ne se nourrit pas dans les mêmes zones en mer, n'en ait que très peu profité.

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