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Long-term population trends in seven Antarctic seabirds at Pointe Géologie (Terre Adélie)

Human impact compared with environmental change

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Abstract Antarctic seabird populations have been much studied over the last decades as bioindicators of the nature of variability in the Southern Ocean marine ecosystem, and most attention has been focused on the role of food supply and the extent of sea ice. In addition, the rapid spread of tourism and the activities of researchers since the early 1960s have raised questions related to their real and potential impact on bird populations. Our data sets start in 1952 for several species of Antarctic seabirds and this study documents the trends over a 14-year period (1985–1999) in seven species breeding on Pointe Géologie archipelago (Terre Adélie, Antarctica). This is the first study where the direct impact of destruction of breeding sites (for building of an airstrip) is examined and where such long-term populations trends have been assessed in such a number of Antarctic species at one site. Trends from 1985 show that for the whole archipelago and when excluding islands destroyed, Adélie penguins and south polar skuas were the only species to show a significant increase (> 3.5% annual change). The others species showed opposite trends, three increasing slightly (southern fulmars +0.4%, cape petrels +2.3%, snow petrels +0.9%) and two decreasing (emperor penguin –0.9%, southern giant petrel –3.9%). Three species particularly affected by the destruction of their breeding habitat (Adélie penguin, cape petrel, snow petrel) showed the capability to restore their populations. The availability of food and nesting sites is discussed in relation to environmental change. Species feeding on krill (Adélie penguins and cape petrels) increased more than other species; however, decrease of ice cover can increase availability of nesting sites. The importance of long-term studies is shown when assessing the role of human activities in Antarctica compared to larger-scale changes.

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Introduction

Antarctic seabird populations have been much studied over the last 10–20 years as bioindicators of the nature of variability in the Southern Ocean marine ecosystem (Croxall 1992; Hunt et al. 1992; Boyd 1993; Chastel et al. 1993; Guinet et al. 1994, 1998; Wilson et al. 1994). Most attention has been focused on the role of food supply, particularly in relation to commercial harvesting and its effect on the ecosystem following the removal of whales, the so-called "krill surplus" effect (Croxall and Kirkwood 1979; Laws 1985; Trathan et al. 1996). Physical factors have also been studied in relation to the change in population size of top predators, the one attracting most attention being sea-ice extent (Fraser et al. 1992; Trathan et al. 1996). In addition, the rapid spread of tourism and the activities of researchers since the early 1960s have raised questions related to their real and potential impact on bird populations (Fraser and Patterson 1997). In Antarctica, only penguins have been monitored to any extent and the status of their populations is very variable, depending on the locality and the species (Woehler and Croxall 1997). Moreover, it is not clear how applicable the findings might be to other Antarctic species, including the abundant Procellariform species. In our study, we use a broader range of species and a longer time scale to assess potential trends in Antarctica, or at least in Terre Adélie.

The Pointe Géologie archipelago (Antarctica, Terre Adélie, 140°E, 66°S) contains one of the most diverse bird communities found anywhere on the main Antarctic continent (Jouventin et al. 1984; Thomas 1986), with eight bird species breeding sympatrically. Barbraud et al. (1999) made a recent and first census of breeding seabirds along the coast of Terre Adélie, but since 1985 (Thomas 1986), no data have been presented on the population trends of the Pointe Géologie breeding species.

Along the 350-km coast of Terre Adélie, only the Pointe Géologie archipelago has been continuously inhabited since 1956, after a first survey in 1952. The scientific station, Dumont d'Urville, is located on the largest island, Ile des Pétrels, where most of the human activities take place. Thirty men overwinter each year but as many as 100 people live there during the summer season (December/March). Most of the Pointe Géologie seabirds censused in 1985 (Thomas 1986) were located in an area that we refer to in this study as the Core Area, which is composed of seven main islands and one nunatak (Fig. 1). However, the construction of an airstrip from 1984 to 1992 destroyed two of the main islands (Ile du Lion and Ile Buffon) and the current Core Area now comprises Ile des Pétrels, Ile Bernard, Ile Lamarck, Ile Rostand, Ile Le Mauguen (ex Ile Carrel) and Nunatak du Bon Docteur. All of these sites, except Ile des Pétrels, and the emperor penguin colony, are designated as an Antarctic Specially Protected Area (zone 24; ATCM Séoul 1995) and are visited only for scientific purposes.

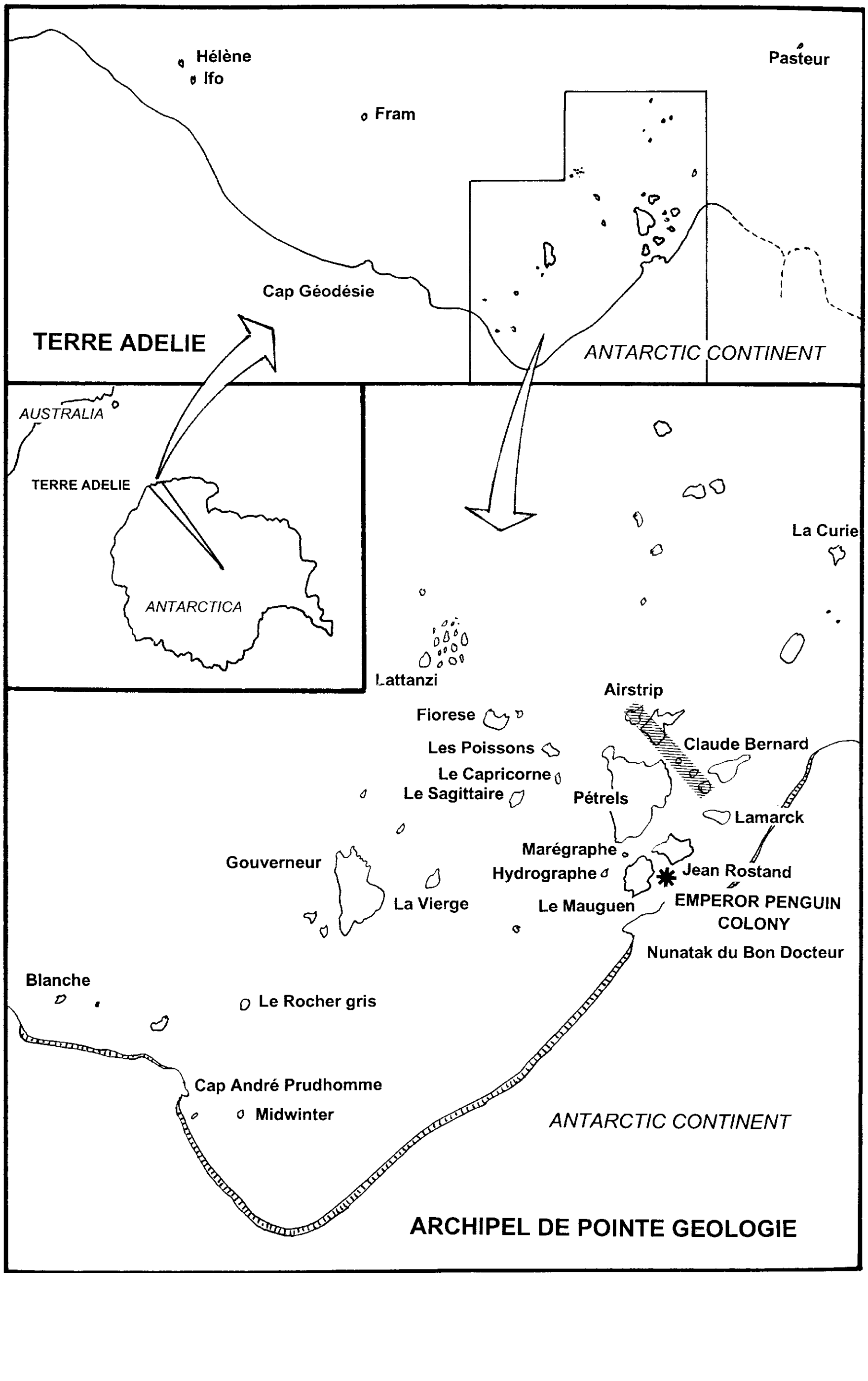

Fig. 1 Map of Pointe Géologie archipelago showing the reduced Core Area with the airstrip previously included in the Core Area. Far islands are also shown as they support breeding species

Our data sets start in 1952 for some species and this study documents the trends over the 14-year period 1985–1999 for seven species [emperor penguin (*Aptenodytes forsteri*), Adélie penguin (*Pygoscelis adeliae*), cape petrel (*Daption capense*), snow petrel (*Pagodroma nivea*), southern fulmar (*Fulmarus glacialoides*), southern giant petrel (*Macronectes giganteus*), south polar skua (*Catharacta maccormicki*)] breeding on Pointe Géologie archipelago. Wilson's storm petrel (*Oceanites oceanicus*) was the single breeding species not to be included in the study as it is almost impossible to obtain counts of colonies (Thomas 1986). These data sets are amongst the longest in Antarctica and trends before 1985 are also shown and discussed. This is the first study where the direct impact of the destruction of breeding sites (for building of an airstrip) is examined and where long-term population trends at one site have been assessed in such a number of Antarctic species.

Materials and methods

In our study, the same protocol was used each year to count visually the breeding pairs (census of the population) and the fledging chicks (breeding success of the population) of all species. The timing of counts was planned according to the biology of each species and they were carried out just after laying for most of the species. All the species breed in summer on islands except for emperor penguins, which lay in winter on the ice-shelf. Regular counts (see below for periodicity) of the seven seabird species were carried out in the Core Area (82% of the archipelago population) whereas some distant islands were counted less regularly depending on the access (ice walking or sea shipping). Thus changes in population size are given for the Core Area although the numbers of breeding pairs in 1999 are given for all the Pointe Géologie islands. Breeding success is calculated as the ratio of fledging chicks/breeding pairs counted in the same breeding season. Count accuracy for each species was estimated following Woehler (1993). Counts for emperor penguins were accurate to better than $\pm 5\%$ and count accuracy of Adélie penguins was estimated to ± 5 to 10%. Pairs of petrels and skuas were individually counted, giving an accuracy likely better than $\pm 5\%$. Changes in population size with time were examined using linear regression.

Building of the airstrip started in 1985 and ended in 1993, after destruction of two islands. During this time, nests of 2,964 Adélie penguins, 211 snow petrels and 168 cape petrels were destroyed, and birds were obliged to move elsewhere.

For a better understanding, breeding seasons of birds are given as years where chicks fledged, i.e. 1985 means the 1984/1985 breeding season. The only exception is for emperor penguins, which breed in winter.

Emperor penguin

The proximity of the emperor penguin colony to Dumont d'Urville allowed us to monitor the population yearly. No direct count of incubating males was used but breeding failure was assessed from May to November by daily checks for lost eggs and then by weekly checks of lost eggs and dead chicks. The estimated number of breeding pairs was calculated subsequently from the numbers of eggs and chicks lost, which were then added to the number of live chicks in late November before departure. Counts were carried out for each breeding year from 1952 to 1998.

Adélie penguin

In some Antarctic localities, long-term studies were based on counts of only small colonies and correcting for the largest ones from a first overall count (Trivelpiece et al. 1990). Other studies have suggested, however, that small sub-colonies may be more vulnerable to extinction (Fraser and Patterson 1997), making this census method doubtful. This is why, in our study, all the breeding pairs were counted visually between 15 and 18 November at the end of the laying period, i.e. the onset of incubation. Whereas the first counts on some islands were carried out in 1958 (Prévost 1963), the first complete census of Pointe Géologie was made in 1985 (Thomas 1986). From 1989, except in 1993, the breeding pairs of the Core Area were counted every year. Chicks at fledging were counted between 3 and 6 February every year from 1993.

Southern fulmar

The only colony of southern fulmar at Pointe Géologie is located on a cliff 20 m from the nearest buildings of the station. Breeding pairs were censused around 20 December, after egg laying. Hatched eggs were checked in late January and counts of live chicks before fledging were carried out from mid- to late-February. These counts were carried out in this species every year from 1964 to 1999.

Cape petrel and snow petrel

Breeding pairs were counted in mid-December, after laying. Counts were carried out in 1985 (Thomas 1986), 1989, 1990 and 1992. From 1994, counts were carried out for cape petrels every 2nd year, alternating with snow petrels, except in 1999 when both species were censused. From 1991 for snow petrels, and from 1992 for cape petrels, all chicks were banded every year before fledging in late January/early February, on all the accessible islands (at least the Core Area), which represent more than 99.5% of the archipelago's nests.

South polar skua

The number of occupied territories by pairs was determined before laying in early November and fledging chicks were counted in January. Bi-monthly checks were done to assess lost eggs and chicks. These counts were carried out yearly from 1966.

Southern giant petrel

Scientific activity started in 1952 on Ile des Pétrels, on which the only breeding colony of southern giant petrels in Terre Adélie was located. The first counts of departing chicks were carried out in 1952, 1956 and 1961, and then annual censuses of chicks were made in late March from 1965 to 1999. In order to reduce the disturbance to the breeding population, banding of breeding birds was stopped in 1996, and only fledging chicks are now banded before departure. Thus only the number of fledging chicks is given in this study.

Results

Emperor penguin

The emperor penguin colony is mainly located in Baie des Empereurs between Ile Rostand, Ile Le Mauguen and Nunatak du Bon Docteur (Fig. 1). From 1952 to 1975, the colony of emperor penguins numbered ca. 6,000 pairs (Fig. 2). From 1975 the population decreased rapidly and stabilised from 1982 at around 2,800 pairs (2,848 ± 345), ranging from 2,303 in 1987 to 3,338 in 1994. There were 2,740 pairs in 1998 (Table 1). The linear regression model gives a non-significant slight decrease since 1984 (Table 2). From 1962 to 1971, just before the failure of 1972 (see Thomas 1986), the breeding success averaged 72 ± 8%. From 1974 to 1989, the breeding success decreased to 57 ± 16%, and then fell to an average of 38 ± 29% from 1990 to 1998, including 4 years where the success was lower than 16%. Since the decrease of the population, the breeding success has been highly variable, ranging from 2.4% in 1994 to 81% in 1993. However, since the very bad year of 1994 with only 80 chicks, the number of chicks is now generally increasing (2,110 in 1998).

Adélie penguin

The Adélie penguin breeds on nearly all the islands and islets of the archipelago. The 1999 population numbered 43,901 pairs, of which 82% was in the Core Area (Table 1). Since 1985, the Core Area population has showed a significant 49% linear increase ($P = 0.011$; Fig. 2; Table 2). On some sites, the increase was much more substantial, being 154% on Ile des Pétrels (+6.9% annual change) and up to 826% on Cap Géodésie (+17.2% annual change). The only decrease (−14%) was observed on Cap Prud'Homme, where building activities led to the forced removal of only 15 of 400 pairs (3.7%) from 1992 to 1994. The breeding success of Adélie penguins in the Core Area since 1994 averaged 68 ± 32% ($n = 6$) but was highly variable (CV = 0.47).

Southern fulmar

The number of breeding pairs of southern fulmar increased significantly from 31 in 1964 to 54 in 1999 (1.5% annual change; Fig. 2), although fluctuating every 2–4 years. Since 1985, the rate of increase has been lower and non-significant (0.4% annual change; Table 2). During the study period, the overall breeding success varied from 32% to 94%, except for an exceptionally bad year of 18% in 1977. From 1985 to 1999, the breeding success averaged 71 ± 18% (CV = 0.31), ranging from 41% in 1997 to 90% in 1999.

Cape petrel and snow petrel

Breeding colonies of cape petrel occur only in the Core Area of Pointe Géologie (Table 1). Other distant islands seem to have no substantial nesting sites, except for occasional breeding (e.g. Ile Fram and Ile Poisson). The Core Area hosted 453 pairs in 1999, but up to 533 in 1996. From 1985 to 1999, the Core Area population decreased, but not significantly, by 9% (Fig. 2; Table 2), the decrease in the late 1980s being related to the destruction of 168 breeding sites for the building of the airstrip. However, when considering the islands separately, a 38% increase, not related to movements of displaced birds, occurred on the remaining islands and varied from 29% on Ile Bernard to 140% on Ile Lamarck. During the 1985–1999 period, the breeding success varied from 54% to 87%, with a mean of 68 ± 15%.

There were breeding colonies of snow petrel on all islands of the Core Area and a few individual pairs on other islands (Table 1). Snow petrels numbered 897 pairs in 1999 (but up to 1,050 pairs in 1995). The destruction of 211 breeding sites for the building of the airstrip did not result in a subsequent significant decrease in the breeding population, and from 1985 to 1999 the population decreased by 11%, but non-significantly (Fig. 2; Table 2), ranging from a 8% decrease on Ile Lamarck to a 85% increase on Ile Rostand. Breeding success was 57 ± 15% (CV = 0.26), with an exceptionally low value of 35% in 1999.

▶

Fig. 2a–g Changes in breeding pairs (*solid lines* and *black circles*) and fledging chicks (*dotted lines* and *white circles*) of seven seabird species at Pointe Géologie archipelago from 1985 to 1999 (emperor penguin, Adélie penguin, southern fulmar, cape petrel, snow petrel, south polar skua, southern giant petrel). The *lines* in the southern giant petrel graph represent cumulated number of fledged chicks for Ile des Pétrels (*dashed line*), Ile Gouverneur (*dotted line*) and Ile Rostand (*solid line*)

South polar skua

The number of south polar skuas' territories increased from 29 in 1966 to 58 in 1998 (Fig. 2), and then decreased to 46 in 1999, while the number of fledged chicks varied from a minimum of 12 (in 1999) to a maximum of 46 (in 1996). During the recent study period (1985–1998), the number of occupied territories increased significantly by 57% (+3.5% annual change; Table 2), with most of the increase occurring since 1996 (61%, +12.7% annual change). The same result is apparent in breeding pairs, which increased by 39% in 4 years. However, the last count in 1999 gave only 46 territories and 41 breeding pairs. Because skuas can raise more than one chick, the hatching success can be higher than 100% and during the last 14 years it ranged from 29% in 1999 to 125% in 1986.

Southern giant petrel

In 1957, 69 chicks fledged on Ile des Pétrels (Prevost 1963), decreasing to 16 in 1961 and 8 in 1965 (Fig. 2). Concurrent with the extension of the base in 1957, breeding pairs attempted to colonise two nearby islands.

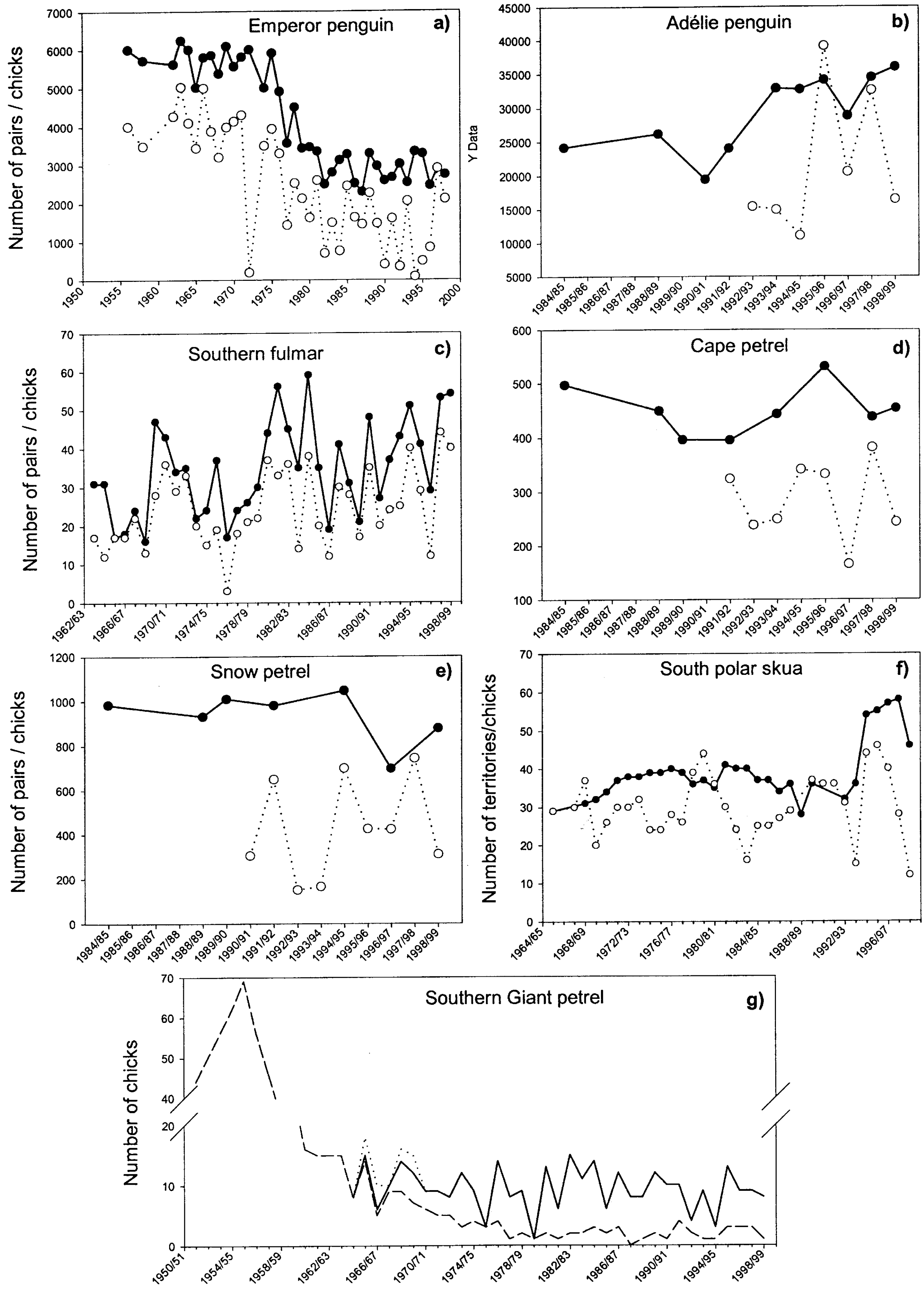
Emperor penguin
a)
Number of pairs / chicks
0
1000
2000
3000
4000
5000
6000
7000
1950
1955
1960
1965
1970
1975
1980
1985
1990
1995
2000
Adélie penguin
b)
Y Data
5000
10000
15000
20000
25000
30000
35000
40000
45000
1984/85
1985/86
1986/87
1987/88
1988/89
1989/90
1990/91
1991/92
1992/93
1993/94
1994/95
1995/96
1996/97
1997/98
1998/99
Southern fulmar
c)
Number of pairs / chicks
0
10
20
30
40
50
60
70
1962/63
1966/67
1970/71
1974/75
1978/79
1982/83
1986/87
1990/91
1994/95
1998/99
Cape petrel
d)
100
200
300
400
500
600
1984/85
1985/86
1986/87
1987/88
1988/89
1989/90
1990/91
1991/92
1992/93
1993/94
1994/95
1995/96
1996/97
1997/98
1998/99
Snow petrel
e)
Number of pairs / chicks
0
200
400
600
800
1000
1200
1984/85
1985/86
1986/87
1987/88
1988/89
1989/90
1990/91
1991/92
1992/93
1993/94
1994/95
1995/96
1996/97
1997/98
1998/99
South polar skua
f)
Number of territories/chicks
0
10
20
30
40
50
60
70
1964/65
1968/69
1972/73
1976/77
1980/81
1984/85
1988/89
1992/93
1996/97
Southern Giant petrel
g)
Number of chicks
0
10
20
40
50
60
70
1950/51
1954/55
1958/59
1962/63
1966/67
1970/71
1974/75
1978/79
1982/83
1986/87
1990/91
1994/95
1998/99

Table 1 Population size of breeding pairs censused in 1998/1999 in Pointe Géologie archipelago (Terre Adélie, Antarctica) except for southern giant petrels whose fledging chicks are given. The trend for 1985–1999 is given considering for 1985 only islands not destroyed by the airstrip (*X* indicates that breeding of a few pairs was known to occur in previous years but not the census year; * indicates that censuses were conducted in 1998 and not in 1999)

Species	Emperor penguin	Adélie penguin	Southern fulmar	Cape petrel	Snow petrel	Southern giant petrel	South polar skua
Core area							
Pétrels		15035	54	135	541	2	14
Lamarck		1479		36	34		1
Bernard		5033		248	169		5
Rostand		6825		32	98	6	5
Le Mauguen	2740	4991		2	23		10
Nunatak		2520			7		2
Total	2740	35883	54	453	872	8	37
Trend 1985–1999	−12%	+69%	+6%	+38%	+13%	−43%	+61%
Annual change	−0.9%	+3.8%	+0.4%	+2.3%	+0.9%	−3.9%	+3.5%
Other islands							
Gouverneur		2820					X
Marégraphe		102					
Hydrographes		148					X
Curie		69					X
Pasteur		173			16		1
Fiorèse (ex Taureau)		278					
Vierge		402			X		
Midwinter		62					
Ste Blanche		21					
Cap Prud'homme		722					X
Cap Géodésie		1481					1
Fram		801		X	10		1
Ifo		(778*)			4		1
Hélène		(56*)					
Rocher Gris		(5*)					
Poisson				X			
Sagittaire					X		
Capricorne							X
Airstrip					5		
Total	2740	43901	54	453	902	8	41

Table 2 Parameters of the linear regression for the population size of seabirds in the "core area" of Pointe Géologie archipelago (Terre Adélie, Antarctica) from 1985 to 1999 ($f = y0 + a*x$)

Species	Emperor penguin	Adélie penguin	Southern fulmar	Cape petrel	Snow petrel	Southern giant petrel	South polar skua
$y0$	2910	19939	33.09	448	1033	10	22.14
a	−5.44	966.66	0.77	0.21	−12.01	−0.16	1.11
r	0.07	0.76	0.28	0.02	0.50	0.24	0.76
P	NS	0.011	NS	NS	NS	NS	0.001
F	0.06	10.99	1.11	0.01	1.69	0.78	17.24

Ile Gouverneur, located 2 km west from Ile des Pétrels, was occupied by four/five pairs, with a maximum of four chicks fledged in 1967, but this colony was abandoned in 1970. On Ile Rostand, located 150 m off Ile des Pétrels, the colonisation was more successful, and in 1966 the first chick fledged. This site rapidly became the major part of the Pointe Géologie breeding population of southern giant petrels. During the 1985–1999 period, the overall chick production showed a slight decrease, with up to 14 chicks (in 1985) fledging on Ile Rostand (7 on average) although only a maximum of 4 fledged (in 1992) on Ile des Pétrels (2 on average). In 1999, six fledged on Ile Rostand and two on Ile des Pétrels.

Discussion

Emperor penguin

Based on the previous drastic decrease of the breeding population and on the low breeding successes in winters 1980, 1982 and 1984, Thomas (1986) predicted a new decrease in the following years. However, this trend was not apparent as the population has been fairly stable since the early 1980s (Fig. 2). Nevertheless, since 1991, the emperor penguin colony suffered 4 years with a very low breeding success and it seems likely that we will observe a significant decrease of the population in the future. Change in demographic parameters, such as an increase of adult or immature survival, or supposed immigration from a close colony, would be able to counterbalance this lost of intra-population recruitment possibilities.

Thomas (1986) proposed several causes (bad winter sea conditions causing higher adult mortality, emigration of adults to other localities, low recruitment due to chick loss during bad years) of the decrease in the 1970s. Although the rapidity of the decrease suggests that a decrease in adult survival is implicated, none of these explanations are satisfactory nor are recent studies that intend to show relationships between the demography of penguins and physical factors such as sea-ice extent or mean air temperature. However, breeding success becomes more variable as the population decreases, the result being low numbers of fledging chicks, and this would imply that the recruitment cannot offset the mortality rate. A more complete analysis of the demographic parameters linked with long-term data on environmental change should allow us to understand better the causes of the population decrease.

Data on trends of emperor penguins at other colonies in Antarctica are scarce (Woehler and Croxall 1997) and their accuracy is probably debatable according to our long-term results. Thus, based only on counts of live and dead chicks once in the breeding season, Woehler and Johnstone (1991) indicated two possible short-term increases and one short-term decrease at three colonies in the Antarctic Australian Territories. From 1981, in our study, the number of departing live chicks varied between 80 and 2,600, without any correlation with colony size. This clearly indicates that interpretations of trends without data on the number of eggs laid should be avoided for emperor penguins.

Adélie penguin

Despite the construction of the airstrip which caused from 1987 to 1992 the destruction of 10% of the archipelago's nesting sites, Adélie penguins have increased dramatically by 50% in the archipelago. This increase cannot be due to movements of delocated birds as only 18% of them were back as breeders 4 years later on another island of the Core Area (T. Micol, unpublished data). We have no clear data to assess if the causes of this increase are immigration, an increase in survival or fecundity, or a combination of these parameters.

Adélie penguin populations have fluctuated substantially in Antarctica over the last 20 years. Some local populations have decreased and it has been suggested that this may be due to human disturbance (Culik et al. 1990; Aguirre 1995). The observed increase (+3.8% mean annual change) since 1985 in the Core Area of Pointe Géologie is incompatible with this hypothesis. On Ile des Pétrels where the base is located and where engines and helicopters operate every summer season from December to late February, the Adélie penguin population has increased by a factor of 2.5 (from 6,000 to 15,000 pairs) since 1985. This increase also occurred on other islands of the Pointe Géologie archipelago. The only decrease occurred in the Cap Prud'homme population (−14% of 838 pairs), where building activities started in 1992 and caused the destruction of breeding sites. Buildings are now completed and even if this base is inhabited by ten people every summer, we can extrapolate from the experience of Ile des Pétrels that this population, located at the periphery of the archipelago and of main colonies, will soon recover to its previous numbers.

It has been suggested that in the northern portions of the Southern Ocean, extensive cover of pack ice leads to greater reproductive success and/or breeding population size in Adélie penguins (Ainley et al. 1998). With only 9 years censused of the 13-year period, our data set did not allow us to find any relationship between the extent of sea ice and the size of populations (National Snow and Ice Data Center, University of Colorado, Boulder, http://nsidc.org).The cause of the observed increase may be in the food availability hypothesis (but quantitative data are needed) or/and in the appearance of breeding sites due to the decrease in ice cover. This last hypothesis is suggested by observations in several places, such as the Cap Géodésie population, which increased 17.2% per year for 14 years concurrently, with a noticeable ice decrease as revealed when comparing photographs. This would suggest that Adélie penguin population sizes are limited, at least in part, by the availability of nesting sites.

When considering trends of Adélie penguin populations in Antarctica, it is thus necessary to distinguish the short-term effects of human disturbance (or disruption), i.e. the building of an airstrip and a base, from the long-term effects of environmental conditions (or disturbance), i.e. the increase of food resources possibly, and/or nest sites certainly. In Terre Adélie, the combined result of these two long-term factors is strongly positive for this species compared to apparently non-negligible short-term human impacts.

Southern fulmar

Yearly variations of the breeding populations are mainly due to the effects of environmental parameters such as snow cover early in the season affecting the availability of nesting sites. Although non-significant, the trend showed a slight but constant increase for 36 years. One explanation of this trend is related to the recent discovery in 1998 of a large fulmar colony of 3,807 pairs at Cape Hunter, 100 km away from Pointe Géologie (Barbraud et al. 1999). This large colony would play the role of a reservoir for the Pointe Géologie colony, which in turn would be used as a peripheral colony. However, preliminary data also indicate that the intra-colony recruitment rate is very high (H. Weimerskirch, unpublished data).

Another hypothesis would be, as suggested for Adélie penguins, the decrease of ice cover leading to an increase in availability of nest sites. The food increase hypothesis is later discussed, in conjunction with trends in other species.

Cape petrel and snow petrel

The loss of 34% of the 1984 breeding sites of cape petrels due to the building of the airstrip was partially offset by an increase of the overall population. Studies on the fate of delocated birds indicate that this increase was not uniquely due to birds returning after destruction of their breeding sites, because only 16% of these delocated birds were found back as breeders in the Core Area (T. Micol, unpublished data).

The 9% decrease of the whole snow petrel population of the archipelago is the result of the loss of 21% of their breeding sites, following the airstrip building, offset by an overall increase of the snow petrel population. However, this trend appears more substantial if we consider the change on remaining islands of the Core Area where there was a 13% increase (+0.9% annual change). The breeding success variation (mean $57 \pm 15\%$) can be explained by the climatic conditions found during brooding (Chastel et al. 1993). These authors showed that, from known demographic parameters, the snow petrel population decreases at 5.2% per year and that this is compensated for by an annual recruitment of 5.7%. This should give an annual increase of 0.5%, which is comparable to the 0.9% of our study.

Ile Lamarck, which supported the largest cape petrel increase on the archipelago (140%), was paradoxically subject to an 11% decrease for snow petrels. This different trend for the two species can be explained by the differential availability of breeding sites, as cape petrel are cliff-nesting species and snow petrel are rock-burrowed nesting species. The concomitant increase of Adélie penguin colonies (47% on Ile Lamarck) can explain part of this trend, as on some small islands they can cover most of the island and thus can block some breeding sites of snow Petrels, whereas cliff-nesting cape petrels would not be affected. The possible role of the differential diet of the two species (Ridoux and Offredo 1989) is discussed later with other species.

South polar skua

The population increase of this species on Ile des Pétrels is closely correlated ($r = 0.674$, $n = 11$, $P = 0.023$) with the number of Adélie penguin breeding pairs. The same trend exists for the whole archipelago. Although south polar skuas feed mainly on fish in some localities (Ainley et al. 1990), they often breed near Adélie penguin colonies around the coast of Antarctica. They do not use marine resources in Pointe Géologie archipelago (P. Jouventin, unpublished data.). It is known that south polar skuas do not require association with penguins for successful reproduction (e.g. Pietz 1987), but predation on penguin eggs and chicks provides a substantial food resource for adult skuas and their chicks (Young 1963, 1994; Mund and Miller 1995). Young (1994) suggested that south polar skuas benefit little by nesting near Adélie penguins, and that the association of penguins and skuas is driven more by abiotic factors (i.e. nest microclimate). Hagelin and Miller (1997) assumed that skuas must benefit from nesting near penguins in order to balance a measurable cost to their reproductive success. In Terre Adélie, following the important population increase from 1996, the breeding success of south polar skuas decreased from 121% in 1996 to 29% in 1999. Although density-independent factors may cause such large changes in numbers that they mask the effects of density-dependent factors (Newton 1998), one can explain this decrease with density-dependence phenomena. One hypothesis could be that the breeding south polar skua population increased too quickly, following that of the Adélie penguin, and became too numerous for sustainable dependence on penguins. Because most of the breeding failure occurred before hatching, we should consider the model developed by Hagelin and Miller (1997), where up to 29% and 71% of all skua egg loss can be due, respectively, to penguins' activity and intraspecific predation by skuas.

From the onset of the station based on Ile des Pétrels base, the dumpsite was believed to be an important foraging site for skuas around Pointe Géologie (Jouventin and Guillotin 1979). It was closed and capped by the end of the 1988 season so the source of human refuse is now much smaller. In our study on Ile des Pétrels, the number of south polar skua breeding pairs increased from 9 in 1988 to 16 in 1998, which is the reverse to that expected following the closure of the dumpsite; this is probably because the dumpsite was used mainly by non-territorial skuas. In fact, the increase of breeders should have been facilitated by recruitment among the important numbers of non-breeding birds living in the area (up to 115 per season).

Our study shows that, at least in some localities, south polar skuas do depend mainly on penguins for successful reproduction, and that this relationship was possibly counterbalanced by density-dependent factors. It seems likely that in future years the number of south polar skua breeding pairs will decrease enough to fit its population size to the number of Adélie penguins.

Southern giant petrel

The movement of breeding birds to nearby Ile Rostand in the late 1960s only concerned a few individuals of the original population. The breeding population then stabilised at three to seven pairs. We believe that human activities close to southern giant petrels limit the establishment of breeding. Southern giant petrels are only present at four breeding localities around the Antarctic continent. Three of these sites are in the Australian Antarctic Territory (AAT); the other is at Pointe Géologie (Woehler et al. 1990). Breeding populations decreased at all localities on the Antarctic continent since their discoveries. The sizes of the population in the AAT have declined 55–73% from 1956 to the mid-1980s (Woehler and Johnstone 1991), which is less than the 87% decrease observed at Pointe Géologie. In the AAT, the activities associated with the construction and operation of stations are known to have directly affected only snow petrels and Wilson's storm petrels (Woehler and Johnstone 1991). Thus the higher decrease in the southern giant petrel population at Pointe Géologie can be mostly attributed to the higher human disturbance, the most important factor being the helicopter landing zone, only 40 m from the traditional main breeding area of southern giant petrels.

Human impact and environmental change

Where habitats are not disturbed either by human activities or by environmental variability, most bird species remain relatively stable in abundance around a long-term mean over many years. Their numbers may fluctuate from year to year, but between limits that are determined by reproductive and mortality rates (Lack 1954). Among the factors that regulate the number of seabirds breeding in a region, the most important appears to be food availability (Furness and Birkhead 1984; Cairns 1989) and/or nesting sites (Ainley and Boekelheide 1990). When taking into account the destruction of some islands for building the airstrip in Pointe Géologie, of the seven species studied from 1984 to 1999, only two showed a significant increase (> 3.5% annual change), the others showing diverse trends with one consistent increase (> 2% annual change), two slight increases and two decreases. The clearest fact in terms of conservation is that the two species that decreased are already the least numerous in Antarctica, these being the emperor penguins – 220,000 pairs – and the southern giant petrels – less than 300 pairs (Table 1). It is nevertheless noticeable that these decreases appear to have stabilised recently (Woehler and Croxall 1997).

Few studies have so far been able to address the long-term impact of bases on Antarctic wildlife, except for the case of Cape Hallett, which is perhaps the best-documented for long-term effects (Taylor and Wilson 1990). Seasonal short-term studies have demonstrated the impact of human activity on physiological, behavioural and reproductive parameters of individual penguins (Culik et al. 1990; Giese 1996). Human visitors are believed to be responsible for the observed changes in the distribution and the abundance of breeding pairs of penguins, and for maintaining the stable population by reducing overall breeding success through the disturbance associated with visits (Woehler et al. 1994). Some studies suggest that the potentially adverse effects of tourism and research on Antarctic wildlife populations may be negligible relative to the effects imposed by long-term changes in other environmental variables (Taylor and Wilson 1990; Fraser and Patterson 1997). Although our 14-year study can be considered as a medium-term study, it suggests that for most of the species, southern giant petrels being the exception, long-term rather than temporary impacts should be considered. In addition, it is conceivable that continuous disturbance linked with daily base activities, including lorries and helicopter runs, are perhaps less disruptive than some occasional visits of tourists to some remote colonies, at least for penguins and small petrels. More long-term studies of population processes related to human activities are thus desirable.

The "krill surplus" hypothesis related to whale reduction was also considered as an important explanation of observed trends in the Southern Ocean several decades ago but its relevance is now debatable (Blackburn et al. 1991; Croxall 1992). However, our findings on diverse trends shown by Adélie penguins and cape petrels on one hand and snow petrels on the other may be related to the differential diets of these species. The first two species feed mainly on krill in open sea (64–79% by mass of their diet; Ridoux and Offredo 1989) whereas snow petrels are more likely to feed on fish at the sea-ice margins (95% by mass of their diet; Ridoux and Offredo 1989). The greater increase in population size of the krill-eating species can be related to the "krill surplus" hypothesis argued for some penguin populations' increases (Trathan et al. 1996) and it would be useful to reassess the importance of krill per se for other species, if not for penguins.

Most of the explanations of recent trends in Antarctic species refer to environmental change, i.e. sea-ice extent or global warming acting as a cause of increased availability of winter food (Taylor and Wilson 1990), but none explain all the observed trends. Thus, chinstrap penguins (*Pygoscelis antarctica*) are increasing on the Antarctic peninsula (Fraser et al. 1992) while slightly decreasing on the South Orkney Islands (Weddel Sea, Trathan et al. 1996). Adélie penguin (*Pygoscelis adeliae*) populations have either remained stable (South Orkney Islands, Trathan et al. 1996; Admiralty Bay, King George Island, Fraser et al. 1992), declined noticeably (at several localities on the Antarctic Peninsula, Poncet and Poncet 1987; Fraser and Patterson 1997), or have increased (Ross Sea region, Taylor and Wilson 1990). The opposite trends that we observe between species, here chinstrap and Adélie, and populations, here Adélie penguins, may be explained by a combination of factors. Thus, global change of water masses can alter the species' range through modification of food chains but also through increasing availability of breeding sites due a decrease in ice cover, which has been observed in Terre Adélie for Adélie penguins (this paper) and suggested for snow petrels (Jouventin and Viot 1985; Barbraud and Jouventin 1998).

To conclude, there is no apparent general trend among the seven species of seabirds between 1985 and 1999 at Terre Adélie (see Fig. 2). This is the first instance that such a huge human impact on seabird populations, from the disappearance of 10–35% of their breeding sites, has been studied, and it appears to be relatively small in terms of observed long-term population trends. Interactions between seabirds, human activities and environmental change are complex and multidisciplinary studies are required to identify the linkages. Moreover, because published data on the breeding distribution of petrels from the Antarctic continent are very sparse (Croxall et al. 1995), new data are important and will add to our ability to ensure appropriate protection of Antarctic species and monitor future changes.

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References

Aguirre CA (1995) Distribution and abundance of birds at Potter peninsula, 25 de Mayo, King George Island, South Shetland Islands, Antarctica. Mar Ornithol 23: 23–31

Ainley DG, Boekelheide RJ (1990) Seabirds of the Farallon Islands: ecology, structure and dynamics of an upwelling-system community. Stanford University Press, Stanford, Calif

Ainley DG, Ribic CA, Wood RC (1990) A demographic study of the south polar skua *Catharacta maccormicki* at Cape Crozier. J Anim Ecol 59: 1–20

Ainley DG, Wilson PR, Barton KJ, Ballard G, Nur N, Kark B (1998) Diet and foraging effort of Adélie penguins in relation to pack-ice conditions in the Southern Ross Sea. Polar Biol 20: 311–319

Barbraud C, Jouventin P (1998) What causes body size variation in the snow petrel *Pagodroma nivea?* J Avian Biol 29: 161–171

Barbraud C, Delord KC, Micol T, Jouventin P (1999) First census of breeding seabirds between Cap Bienvenue (Terre-Adélie) and Moyes Islands (King George V Land), Antarctica: new records for Antarctic seabird populations. Polar Biol 21: 146–150

Blackburn N, Taylor RH, Wilson PR (1991) An interpretation of the growth of the Adélie penguin rookery at Cape Royds, 1955–1990. NZ J Ecol 15: 117–121

Boyd IL (1993) Tooth growth in male Antarctic fur seals (*Arctocephalus gazella*) from South Georgia: an indicator of long term growth history. J Zool Lond 229: 177–190

Cairns DK (1989) The regulation of seabird colony size: a hinterland model. Am Nat 134: 141–146

Chastel O, Weimerskirch H, Jouventin P (1993) High annual variability in reproductive success and survival of an Antarctic seabird, the snow petrel *Pagodroma nivea*. Oecologia 94: 278–285

Croxall JP (1992) Southern Ocean environmental changes: effects on seabirds, seal and whales populations. Philos Trans R Soc Lond B 338: 319–328

Croxall JP, Kirkwood ED (1979) The distribution of penguins on the Antarctic peninsula and islands of the Scotia sea. British Antarctic Survey, Cambridge

Croxall JP, Steele WK, McInnes SJ, Prince P (1995) Breeding distribution of the snow petrel *Pagodroma nivea*. Mar Ornithol 23: 69–99

Culik BM, Adelung D, Woakes AJ (1990) The effects of disturbance on the heart rate and behaviour of Adélie penguins (*Pygoscelis adeliae*) during the breeding season. In: Kerry KR, Hempel G (eds) Antarctic ecosystems, ecological change and conservation. Springer, Berlin Heidelberg New York, pp 177–182

Fraser WR, Patterson DL (1997) Human disturbance and long-term changes in Adélie penguin populations: a natural experiment at Palmer Station, Antarctic peninsula. In: Battaglia B, Valencia J, Walton DWH (eds) Antarctic communities: species, structure, and survival. Cambridge University Press, Cambridge, pp 445–452

Fraser WR, Trivelpiece WZ, Ainley DG, Trivelpiece SG (1992) Increases in Antarctic penguin populations: reduced competition with whales or a loss of sea ice due to environmental warming. Polar Biol 11: 525–531

Furness RW, Birkhead TR (1984) Seabird colony distributions suggest competition for food supplies during the breeding season. Nature 311: 655–656

Giese M (1996) Effects of human activity on Adélie penguin *Pygoscelis adeliae* breeding success. Biol Conserv 75: 157–164

Guinet C, Jouventin P, Georges JY (1994) Long term population changes of fur seals *Arctocephalus gazella* and *A. tropicalis* on subantarctic (Crozet) and subtropical (Saint Paul and Amsterdam) islands and their possible relationship to El Niño Southern Oscillation. Antarct Sci 6: 473–478

Guinet C, Chastel O, Koudil M, Durbec JP, Jouventin P (1998) Effects of warm sea-surface temperature anomalies on the blue petrel at the Kerguelen Islands. Proc R Soc Lond B 265: 1001–1006

Hagelin JC, Miller GD (1997) Nest-site selection in south polar skuas: balancing nest safety and access to resources. Auk 114: 638–645

Hunt GL Jr, Priddle J, Whitehouse MJ, Veit RR, Heywood RB (1992) Changes in seabird species abundance near South Georgia during a period of rapid change in sea surface temperature. Antarct Sci 4: 15–22

Jouventin P, Guillotin M (1979) Socio-écologie du Skua antarctique à Pointe Géologie. Terre Vie 33: 109–127

Jouventin P, Stahl JC, Weimerskirch H, Mougin JL (1984) The seabirds of the French subantarctic islands and Adélie Land. In: Croxall JP, Evans PGH, Schreiber RW (eds) Status and conservation of world's seabirds. ICBP Tech Publ 2: 603–625

Jouventin P, Viot CR (1985) Morphological and genetic variability of snow petrels. Ibis 127: 430–441

Lack D (1954) The natural regulation of animal numbers. Clarendon Press, Oxford

Laws RM (1985) The ecology of the Southern Ocean. Am Sci 73: 26–40

Mund MJ, Miller GD (1995) Diet of the south polar skua *Catharacta maccormicki* at Cape Bird, Ross island, Antarctica. Polar Biol 15: 453–455

Newton I (1998) Population limitation in birds. Academic Press, London

Pietz PJ (1987) Feeding and nesting ecology of sympatric south polar and brown skuas. Auk 104: 617–627

Poncet S, Poncet J (1987) Censuses of penguin populations on the Antarctic Peninsula, 1983–87. Br Antarct Surv Bull 77: 109–129

Prévost J (1963) Densités de peuplement et biomasses des vertébrés terrestres de l'Archipel de Pointe Géologie. Terre Vie 17: 35–49

Ridoux V, Offredo C (1989) The diets of five summer breeding seabirds in Adélie land, Antarctica. Polar Biol 9: 137–145

Taylor RH, Wilson PR (1990) Recent increase and southern expansion of Adélie penguin populations in the Ross Sea, Antarctica, related to climate warming. NZ J Ecol 14: 25–29

Thomas T (1986) L'effectif des oiseaux nicheurs de l'archipel de Pointe Géologie (Terre Adélie) et son évolution au cours des trente dernières années. L'Oiseau RFO 56: 349–368

Trathan PN, Croxall JP, Murphy EJ (1996) Dynamics of Antarctic penguin populations in relation to inter-annual variability in sea ice distribution. Polar Biol 16: 321–330

Trivelpiece WZ, Trivelpiece SG, Geupel GR, Kjelmyr J, Volkman NJ (1990) Adélie and chinstrap penguins: their potential as monitors of the Southern Ocean marine ecosystem. In: Kerry KR, Hempel G (eds) Antarctic ecosystems, ecological change and conservation. Springer, Berlin Heidelberg New York, pp 191–202

Wilson RP, Culik BM, Bannasch R, Lage J (1994) Monitoring Antarctic environmental variables using penguins. Mar Ecol Prog Ser 106: 199–202

Woehler EJ (1993) The distribution and abundance of Antarctic and subantarctic penguins. SCAR, Cambridge

Woehler EJ, Croxall J (1997) The status and trends of antarctic and sub-antarctic seabirds. Mar Ornithol 25: 43–66

Woehler EJ, Johnstone GW (1991) Status and conservation of the seabirds of the Australian Antarctic Territories. ICBP Tech Publ 11: 279–297

Woehler EJ, Martin MR, Johnstone GW (1990) The status of southern giant petrels, *Macronectes giganteus*, at the Frazier Islands, Wilkes land, East Antarctica. Corella 14: 101–106

Woehler EJ, Penney RL, Creet SM, Burton HR (1994) Impacts of visitors on breeding success and long-term population trends in Adélie penguins at Casey, Antarctica. Polar Biol 14: 269–274

Young EC (1963) Feeding habits of the south polar skua *Catharacta maccormicki*. Ibis 105: 301–318

Young E (1994) Skua and penguin: predator and prey. Cambridge University Press, Cambridge