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Unexpected effects of climate change on the predation of Antarctic petrels

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Abstract: Antarctic petrels *Thalassoica antarctica* on Ardery Island, Antarctica (66°S, 110°E), experienced major reductions in breeding success and breeder survival over four seasons between 1984/85 and 1996/97. In 1996 the reason was revealed. A large snowdrift covered part of the study colony on the cliffs. Southern giant petrels *Macronectes giganteus*, normally lacking access to this area, exploited the snow for soft 'crash landings'. After landing they waited for the disturbed birds to resettle on their nests and then used surprise to seize and kill a victim. Predation continued into the egg period, and only stopped after the snowdrift had melted. Giant petrels showed no interest in the eggs but, during the panic caused by their activities, South Polar skuas *Catharacta maccormicki* took the deserted eggs. Antarctic petrel mortality due to predation within the 1996/97 season amounted to 15.4% of experienced breeders, and breeding success was reduced to virtually zero. Weather data from the nearby Casey station over the 1980–96 period showed that a significant increase in precipitation has occurred, in combination with shifts in speed and direction of winds. We conclude that the decreases in breeding success and survival in earlier seasons were also related to increased snowfall and predation. Although similar predation behaviour by giant petrels has not been reported before, we think that it is long established and explains why nesting of the smaller fulmarine petrels is limited to steeper cliffs or sheltered sites. The complexity of the response seems unlikely to be predicted by our present understanding of how climate change affects ecosystems.

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Key words: *Catharacta maccormicki*, climate change, *Macronectes giganteus*, nesting distribution, predation pressure, snow, *Thalassoica antarctica*

Introduction

The Antarctic petrel (*Thalassoica antarctica* Gmelin) is a characteristic seabird of the high Antarctic. Its population is of the order of 10 to 20 million birds, which forage year-round in and near the marginal ice zones of the Southern Ocean. Breeding colonies are found only along the continental coast of the Antarctic or even further south (van Franeker 1996, van Franeker *et al.* 1999). Like the snow petrel (*Pagodroma nivea* Forster) (Croxall *et al.* 1995), it is found nesting on barren mountain peaks (nunataks) protruding from the Antarctic icecap, at a distance of hundreds of kilometres from the nearest open ocean waters in even mid-summer. As a representative species of the high Antarctic environment, the Antarctic petrel has been selected as one of the target organisms in the CCAMLR Ecosystem Monitoring Program CEMP (CCAMLR 1997).

A Dutch-Australian study of petrels was started in 1984/85 on Ardery Island near the Australian Casey station (Fig. 1). Investigations were continued in the 1986/87 and 1990/91 breeding seasons. The breeding success of Antarctic petrels over these three study seasons showed consecutive sharp decreases. Each time, the major reduction in breeding success was already evident in the egg phase at the start of our observations. The cause of the declining success was obscure. Timing of the breeding offered no explanation. Differences in starting dates were small and did not correlate with changes in breeding success. The composition of food, and growth of chicks indicated no shortage of food or major changes in prey species. Lacking explanations from the breeding season itself, we hypothesized that a decreasing number of birds attempted to breed, possibly because deteriorating winter foraging conditions lowered the body condition of the birds to below threshold levels required for breeding.

Therefore, in 1996/97 a new phase of the Ardery Island project began, focussing on body condition of individual birds and starting fieldwork as early as possible in the pre-breeding phase. In this season it soon became clear that less subtle factors than pre-breeding condition were affecting the breeding success of Antarctic petrels on Ardery Island. This paper reports on our observations in 1996/1997, looking back at the situation in previous years.

Methods

Antarctic petrels were studied on Ardery Island during the

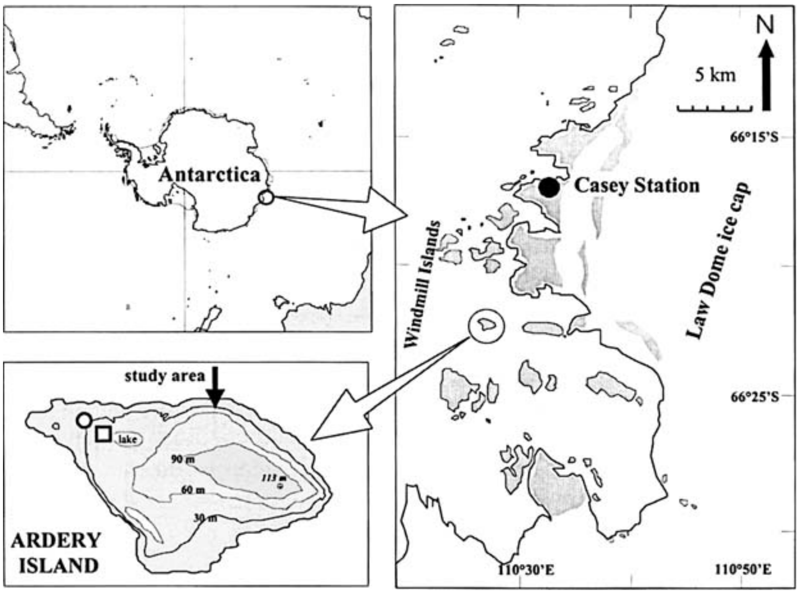

Fig. 1. Ardery Island study location. Antarctic petrels were studied on the 'Northern Plateau', a less steep section halfway down the steep northern cliffs of Ardery Island (arrow). The location of the summer field hut in 1984 and 1986 (circle) was covered by snow in 1990 and huts were placed on a new position (square).

breeding seasons of 1984/85, 1986/87, 1990/91 and 1996/97. Ardery Island (66°S–110°E) is one of the Windmill Islands, situated in Vincennes Bay, off the eastern coast of Law Dome, Wilkes Land, Antarctica (Fig. 1). The island is just over one kilometre long, 113 m high and has many steep cliffs. The Australian station 'Casey' lies about 11 km to the north. Law Dome is fully glaciated, and only a few coastal outcrops and the small islands become free of snow and ice during summer.

The population of Antarctic petrels on Ardery Island was relatively small with approximately 275 breeding pairs (van Franeker *et al.* 1990). This estimate was based on the number of Apparently Occupied Sites (AOS; Walsh *et al.* 1995) counted from viewpoints outside the colonies during the egg period of mid-December 1984. The main colony of at least 175 AOS is located at the cliffs on the northern side of the island. We named this nesting area the 'Northern Plateau' which is somewhat misleading because it concerns a relatively small, less steep section halfway down the otherwise very steep cliffs. It has a rough surface of rock boulders and small terraces where Antarctic petrels nest closely together. They are surrounded by colonies of Southern fulmar *Fulmarus glacialoides* (Smith) and cape petrels *Daption capense* (L.) and dispersed hole nesting snow petrels and Wilson's storm petrels *Oceanites oceanicus* (Kühl).

Two pairs of South Polar skuas *Stercorarius maccormicki* (Saunders) patrol the Northern Plateau colonies. The island has a population of about 15 breeding pairs of skua with variable numbers of non-breeders around. They breed on the higher flat part of the island above the cliffs. As no penguins breed on Ardery, the skuas depend strongly on the petrels for food, and fiercely defend feeding territories against other breeders and non-residents (van Franeker *et al.* 1990, Baker & Barbraud 2001).

Southern giant petrels *Macronectes giganteus* (Gmelin) can be seen anywhere in the Casey region, but the only breeding population of ± 150 to 200 pairs in the area is on the Frazier Islands, *c.* 20 km to the north-west (Murray & Luders 1990, Woehler *et al.* 1990, personal observation).

In 1984 we established a study area for Antarctic petrels in the lower eastern quarter of the Northern Plateau colony, measuring roughly 20 by 25 m. Straightforward figures for the number of sites or birds in such an area are not easy to give. Frequent counts were made from a fixed viewpoint outside the nesting area. From subsequent detailed nest checks, the proportion of birds missed in distant counts was estimated at 10% to 20%. Instantaneous counts of individuals (maximum ever 95 birds) or the number of 'Apparently Occupied Sites' (usually 30–40 AOS; maximum ever counted 48) are repeatable measures, but do not properly reflect size of the bird population in the study area. Gradually we have identified close to a 100 sites regularly attended by two or more birds. Colony counts do not reveal this because not all birds attend the colony at the same time, in spite of what seems a high level of synchronization. Banding records indicate that at least 180 different adults are associated with our study area. Bird counts are given as mean ± s d. Sites in the study area have been marked with painted numbers.

Within the study area, we banded a large proportion of the adults and all chicks with stainless steel bands from the Australian Bird and Bat Banding Scheme (ABBBS). Additionally, in 1984/85, 90 adults were given a combination of three Darvic colourbands for easy individual recognition. From observations during the season of banding, these birds were separated in a 'breeding' category (pairs with egg or chick, or birds frequently resighted on the same site with the same partner throughout the 84/85 season; $n = 75$) and a 'non-breeding' category (not or infrequently resighted after banding, and if resighted, on different sites and/or with different partners; $n = 15$). We thus included well-established site owners with stable partner bonds in the breeder definition because observations started in the egg phase when many pairs had already failed. This initial categorization proved consistent in later years: almost all birds initially labelled as breeders were observed breeding again in later years (64 individuals out of 75), whereas of the 15 initial non-breeders only one is known to have once attempted to breed later (in 1996/97).

A new cohort of 71 adult birds was individually marked with colourbands during the October–December period of 1996. The breeder or non-breeding distinction could not be made for reasons explained in results.

Adult attendance, breeding biology and success were monitored by regular nest checks. Daily checks were made in 1986/87 and 1996/97 from egg laying until fledging. In 1984/85 and 1990/91 observations started later and were less frequent. At each visit, the breeding success was determined as the number of successful sites in the study area. A successful site is defined as 'with incubated egg or a live chick'. It needs to be emphasized that such a figure is not a measure for the number of eggs produced. Many egg losses may occur during the early laying period. Since egg laying and failure may occur in between two subsequent checks, an accurate figure for the number of breeding attempts is hard to obtain.

Annual adult survival rates between subsequent study seasons were calculated directly from resighted numbers of colourbanded birds. No correction methods for 'missed' but surviving birds were used, as in our study no bird missing in one season returned in a later one. Survival within the 1996/97 breeding season was estimated from directly observed mortality (corpses found) among colourbanded birds.

To be able to control for observer effects, the colony area outside our study plot was left undisturbed as much as possible. No observations were made in this reference area in 1984/85, except for the initial estimate of the number of AOS. In 1986/87 again the area was not entered, and the number of chicks fledging was estimated by counts from outside of the colony. As of 1990/91 the undisturbed area was entered once in each season for chick banding (around mid February).

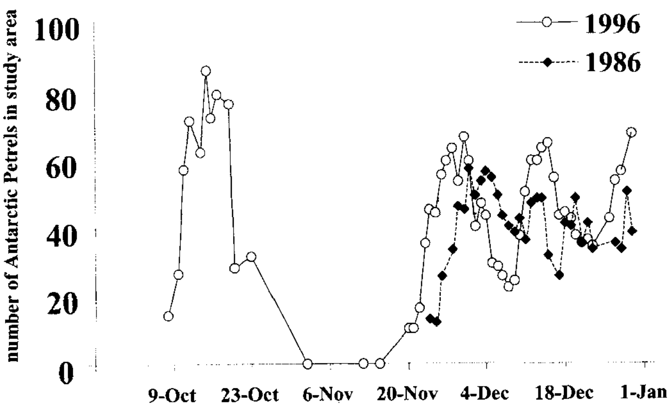

Fig. 2. Attendance patterns of Antarctic petrels in the Northern Plateau study area. Attendance is shown by daily counts of the number of individual birds in the study area during the 1986 and 1996 breeding seasons. Counts were made from the fixed viewpoint outside the colony, before entering for detailed nest checks.

Changes in population breeding success in the study area were tested by GLM regression using binomial distribution (GENSTAT: Payne *et al.* 1993, p. 418), fitting 'year' on response variates 'egg on 31 December' or 'chick fledged'. Chi-square tests were used to compare frequencies in e.g. comparisons to the reference area and in resighting data for survival analysis.

Weather data on snowfall, temperature and wind over the period from January 1980 to December 1996 were obtained from the Australian Bureau of Meteorology. We analysed snowfall patterns for 'monthly total precipitation', recognizing the potential for some uncertainty under conditions of 'blowing snow'. We used the mean maximum monthly air temperature. Wind speeds and direction were analysed from annual frequency tables containing the number of records per 10 km h^{-1} wind speed category for each of 16 wind directions. Frequencies were recalculated to percentages of the annual total of observations. Trends in weather data were explored by simple regression analysis (GENSTAT: Payne *et al.* 1993). Anemometers and thermometers at Casey changed location in 1989, but simultaneous records at both locations during the whole of 1989 revealed no significant differences in any of the measurements (Chi-square tests on frequencies of wind speeds $P = 0.996$; wind directions $P = 0.18$; and t-test on all temperatures $P = 0.80$).

Results

In 1996, observations began on 5 October when the first Antarctic petrels started to arrive (8 birds over the whole Northern Plateau). A large snowdrift, one to two metres thick, blanketed a considerable proportion of the study area. This snowdrift had never been observed before, but previous observations had not started before 23 November in 1986 and mid-December in other years. The number of pre-breeding attendants in the study area increased from 14 on 8 October, to a maximum of 86 birds simultaneously present on 15 October. Numbers decreased after 20 October, and the colony was virtually deserted by early November (Fig. 2).

During the mid-October attendance period, extensive snow digging, courtship display and copulations took place. Some pairs were digging out impressive snow caves, but few of those with nest sites in the snowdrift managed to clear the snow down to the rock below. The behaviour of Antarctic petrels in this period was more nervous than in earlier years. Birds that previously were easily inspected for colourbands appeared shy when more closely approached.

Southern giant petrel predation

The reason behind the nervousness of Antarctic petrels became apparent when on 14 October we observed a giant petrel hovering over the colony. It caused panic among the Antarctic petrels, with many flying off. No similar event had been observed in any of the previous seasons.

However, in 1996, after the first bird on 14 October, the next day another giant petrel crash-landed in the snowdrift. Its body left a deep impression in the snow, indicating that 'normal' landing in this cliff area was difficult, with a high risk of injury if no snow had been present. All Antarctic petrels in the vicinity had taken off, but the giant petrel sat quietly, and after a few minutes birds gradually started to resettle on their nest sites. Some of these could not see the giant petrel because they were inside snow caves or behind rocks. At this stage, the giant petrel took a sudden run to one site, and grabbed the Antarctic petrel. The victim was killed by biting in the head and neck and shaking. After the kill, breast and belly area were plucked and ripped open. The carcass was cleaned in about half an hour.

Similar events were witnessed several times during October. Giant petrels occasionally attempted to chase Antarctic petrels during the panic directly after landing, but only the surprise attack strategy was successful. Remarkably, Antarctic petrels always fled during attacks and never responded by spitting stomach oil, a successful defence strategy in the fulmarine petrels (Warham 1990). From diet sampling we know that they do accumulate stomach oils like the other species. On rare occasions we observed that chicks are well able to use oil spitting and vomiting in defence and fear. Why this defensive behaviour is so rarely shown by the adult Antarctic petrel is unclear.

A considerable number of different giant petrels, recognized by their plumage, were involved in the attacks on Northern Plateau. When wind conditions were suitable for soaring along the cliffs, several giant petrels were checking out the colony each day. However, they did not always land, and not all visits resulted in successful kills. Nevertheless, by 25 October, when pre-breeding attendance dwindled (Fig. 2), ten fresh corpses of Antarctic petrel victims had been found in and around the study area. This is no doubt a minimum figure as corpses in the reference colony may have been missed and others may have been blown away in strong winds or were removed by skuas.

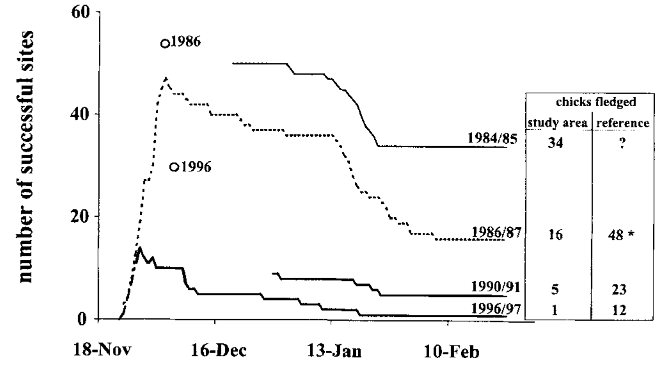

Fig. 3. Antarctic petrel breeding success in the Northern Plateau study area. Line graphs show numbers of successful sites (see methods) in the study area for all four seasons. For years with full seasonal coverage (1986 and 1996), the minimum number of eggs laid is shown by circles (note that these are underestimates since laying and loss may occur in between two subsequent checks). The box on the right compares final breeding success from the study area with that of the reference area. See text for details.

Breeding success

From late October to 20 November 1996, the Antarctic petrel colony was completely deserted (Fig. 2), all birds being away on the 'pre-laying exodus'. First eggs in the study area were laid on 24 November (Fig. 3). In spite of some melt, the snowdrift covering part of the nesting area was still largely intact. Some eggs were laid on 'snow nests'. Usually, such eggs melt into the snow and subsequently freeze. Proper records of such causes of failure were impossible because events during the egg laying period were totally chaotic. Giant petrels were regularly crash landing and strongly disturbed the breeding process. The giant petrels showed no interest in the eggs, but only went for the adults. However, the skuas were now constantly patrolling their territories in the petrel colonies and were taking advantage of the disturbance by stealing the temporarily deserted eggs. During a giant petrel attack on 26 November, a single skua was seen to take three eggs. Other eggs were deserted for over an hour, and just when adults resumed incubation, a second giant petrel landed and created a new panic. By 6 December, when the last egg laying was observed, only 10 of 30 pairs observed to have laid still had eggs. Considerably more than 30 eggs were undoubtedly produced within the study area, but many must have immediately been lost in between our daily checks. By 12 December, only five eggs remained. During the remainder of December, the snowdrift gradually melted and after 12 December no further giant petrel landings were seen. In the late egg phase and early chick phase some further 'normal' losses occurred in the study area. Of the five remaining eggs, one was lost due to nest flooding, one 'rolled out' of the site, and a third disappeared for no apparent reason. Of the two chicks hatched, one disappeared probably due to skua predation, apparently unrelated to giant petrel disturbance.

The end result was that the 1996/97 breeding season was the poorest on record, with only one chick fledged from the study area and only 12 from the remainder of the Northern Plateau colony. The trend of declining success of earlier years was thus continued. Compared to fledging numbers in 1984/85, success in the study area fell to 47% in 1986/87, 15% in 1990/91 and 3% in 1996/97.

It is difficult to express such figures in terms of 'population success'. Breeding success is usually defined as the proportion of 'egg producing pairs' that succeeds in fledging a chick, but it is extremely hard to determine accurately the numbers of eggs laid. The best estimate for numbers of eggs produced in our study area is from 1986/87. Daily nest observations indicated that at least 54 eggs were produced in 1986, although

Table I. Colourbanding and resightings of Antarctic petrels on Northern Plateau study area. Numbers of birds colourbanded in 1984/85 and in October–December 1996 and their subsequent resightings. See methods for the breeder vs non-breeder distinction. Resightings were used to calculate survival rates shown in Fig. 4.

	numbers (*banded*)/resighted			
	84/85 cohort			96 cohort
	all	breed	nonbreed	
banded 1984/85	*90*	*75*	*15*	
resighted 1986/87	80	69	11	
resighted 1990/91	64	54	10	
resighted start 96/97	34	26	8	*71 banded*
end 96/97*	30	22	8	64

*'Resighted' figures for the end of the 1996/97 breeding season have been calculated from numbers of colourbanded birds found dead, assuming that others were still alive.

at no time were there more than 47 eggs present (Fig. 3). During egg laying, some eggs are rapidly lost, even in the absence of giant petrel disturbance like in 1996/97. Poor nest site quality (covered with snow, flooding with melt water, or eggs easily rolling out) or improper coordination of incubation duties between partners are common reasons for immediate egg loss. The skuas quickly remove any trace of these events. Observations once a day will definitely miss a number of such immediate losses, and thus underestimate both egg numbers and the breeding population. Initial loss rates as commonly seen in fulmarine petrels, suggest that the 50 eggs in the Antarctic petrel study area on 18 December 1984 represented a much higher number of egg producing pairs. Some of the sites in which we never observed an egg, are definitely used by adults capable of breeding. From data in our first two seasons our best estimate of the 'potential breeding population' in our study area is 75 pairs. From numbers of birds attending the study area in 1986/87 and ten years later in 1996/97 (Fig. 2) there is no indication that the population significantly changed over that period: counts over the December egg period averaged 42 ± 8 birds in 1986, and 44 ± 13 in 1996 (*t*-test: $P = 0.66$, n.s.). In terms of an initial breeding population of 75 pairs, the population breeding success in fledging chicks was 45% in 1984/85, 21% in 1986/87, 7% in 1990/91 and 1% in 1996/97. The decrease over the years is highly significant ($t_{(298)} = -6.20$; $P < 0.001$) and largely due to egg losses before 31 December ($t_{(298)} = -7.43$; $P < 0.001$) with no clear effect of further egg or chick losses after that date ($t_{(98)} = -1.49$; $P = 0.139$).

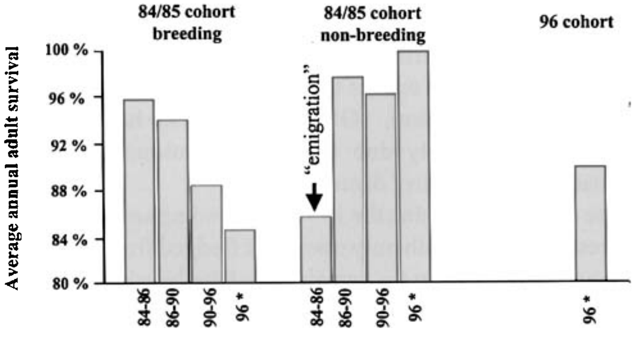

Fig. 4. Survival rates of adult Antarctic petrels. Average annual survival rates in between study years were calculated from live resightings of birds colourbanded as adults in 1984/85. The breeding and non-breeding categories refer to the status of the birds in 1984/85 (see methods). Survival within the 1996/97 breeding season (96*) was derived from dead recoveries of banded birds. Within season survival is also given for a new cohort of birds first colourbanded in October–December 1996. As not all killed birds may have been recovered, the 96* survival figures are maximum values. See Table 1 and text.

A strong decrease in number of chicks fledged was also observed in the reference area (Fig. 3 inset). Chick numbers were not counted in 1984/85, but were definitely in the range of 100 to 150 chicks. The 1986/87 figure of 48 chicks in the reference area is from a count made from distance: a tentative correction for 10% to 20% 'hidden' sites suggests that around 55 chicks could have fledged. The decrease in fledgling numbers in the study area after 1986/87 was stronger than that in the control area. According to the 1986 to 1996 trend in the reference area, expected numbers to fledge from the study area would have been 7 chicks in 1990/91, and 3 in 1996/97 (5 and 1 respectively were observed; Chi-square test n.s., but observed frequencies too low for proper testing).

Survival/mortality

Survival and mortality were analysed from cohorts of adult birds banded in 1984/85 and in 1996/97 and their live resightings or dead recoveries (Table I). From these, average annual survival rates were calculated (Fig. 4). The fulmarine petrels have high loyalty to established sites and apparently attend the colony annually (whether breeding or not). We interpret 'resighting' data directly as survival data. However, four out of eight 'non-breeding' females in 1984/85 disappeared immediately after banding and were never resighted. As survival of non-breeding males was 100% from 1984 to 1986, it seems likely that the disappeared females were only visitors, prospecting for a male partner with a site, and that they 'emigrated' to another part of the colony or another area after banding. This biases the 1984–86 survival figure for non-breeders in Fig. 4 and represents the only instance where resightings are inappropriate to calculate 'survival'. Otherwise we have found no significant differences in survival between the sexes (overall breeder survival over 12 years: 13 out of 38 males, and 13 out of 37 females).

No distinction between breeders and non-breeders could be made in the new '96 cohort' of birds first banded in October–December 1996. The chaotic predation events and snowdrift complicated records of individual site locations, pair bonds and breeding.

Survival of breeders in the 1984/85 cohort started with an average annual survival of 95.9% over the 1984–86 period, but decreased to 94.1% between 1986 and 1990, and 88.5% over the 1990–96 period. Within the 1996/97 summer, observed breeder mortality due to giant petrel predation was at least 15.4%! Very different results were obtained for the non-breeding component of the 1984/85 cohort. As indicated, the low average 'survival' for non-breeders over the 1984 to 1986 period in Fig. 4 (females 71%; males 100%) probably reflects 'emigration' of prospecting females. Over later periods, mean annual survival in this group was consistently high (97.7% and 96.3%). Within the 1996/97 breeding season, no mortality from giant petrel predation was observed among the non-breeder survivors of the 1984/85 cohort.

Using 96% as an expected survival figure for Antarctic petrels (Warham 1996) for all periods, Chi-square tests show highly significant lowered survival for breeders of the 84/85 cohort ($P < 0.001$), but not for the non-breeders ($P = 0.89$ if 1984–86 period included; $P = 0.72$ if excluded).

The within season survival figure for the 1996 cohort is merely indicative. Birds were banded gradually over time, and thus could only be detected as victims of giant petrels after the date of banding. Furthermore, the sample contained a mix of breeders and non-breeders. Out of 71 new birds banded from October to December 1996, seven were recovered dead the same season demonstrating at least 9.9% mortality within a few months due to giant petrel predation.

Climate data

The large snowdrift on Northern Plateau in 1996 that persisted well into December had not been observed in previous years. However, only in 1986 had observations started early enough (24 November) for a comparison. It is known that not much snow was present and none of the nest sites was snow-covered that year. Snowdrifts on several other places on the northern side of the island were also larger in 1996 than in any of the previous years, and persisted well into December and January.

Snowfall showed a strong increase over the observed period. Total annual precipitation over the 17 years significantly increased (Fig. 5a; linear regression $P = 0.01$) in spite of considerable interannual variation. The increase was not evenly distributed over the year. A comparison of average monthly precipitation figures during the 1980s to those in the 1990s (Fig. 5b) shows that summer snowfall had not much changed, it may have even slightly decreased in December and January in later years. For the separate months, increases over 17 years were only significant for August ($P = 0.008$) and November ($P = 0.036$). Seasonal precipitation totals significantly increased in winter (June–August: $P = 0.023$) and especially spring (September–November: $P = 0.005$), but not in summer (December–February; $P = 0.760$) and autumn (March–May: $P = 0.212$). The four-month period prior to egg laying showed a highly significant increase (August–November: $P < 0.001$).

Air temperatures in the Casey area showed no clear changes over the 1980–1996 period. Trends over 17 years for the annual mean maximum ($P = 0.09$) or the mean minimum ($P = 0.08$) were not significant (Fig. 6a). Monthly mean maximum air temperatures during the 1980s are compared to those 1990s in Fig. 6b. Except for an apparent cooling of May temperatures (linear regression over 17 years $P = 0.016$) none of the months showed a significant increase or decrease. We also tested annual and monthly temperature trends over the longer period 1970–96, and these confirmed the absence of significant trends in mean, minimum or maximum air temperatures. The drop in mean maximum May temperatures remained the only significant finding (over 27 years $P = 0.002$).

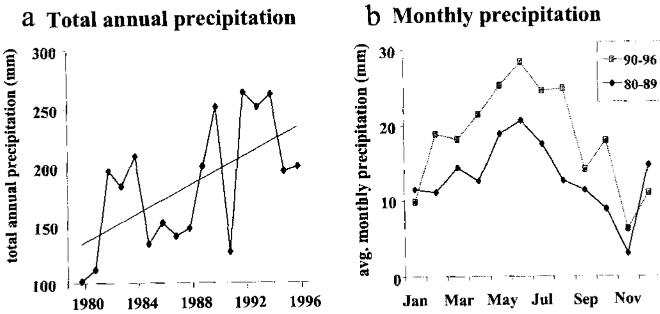

Fig. 5. Increased precipitation in the Casey area over the period 1980–96.

Analysis of the annual tables for wind speed and direction (Fig. 7) revealed a significant shift in wind direction from a predominantly south-eastern quarter during the 1980s to a more north-easterly one in later years (Fig. 7a: linear regression on 17 year trend in E–SSE winds $P < 0.001$; on N–ENE winds $P = 0.004$; other directions n.s.). At the same time, the frequency of moderate wind speeds in the range of 10 to 30 km h^{-1} increased ($P < 0.001$), whereas those of calm weather decreased ($P < 0.001$). No significant change occurred in the frequency of high wind speeds (Fig. 7b).

Discussion

Our observations in 1996 showed that Antarctic petrel breeding success and survival on Ardery Island were dramatically

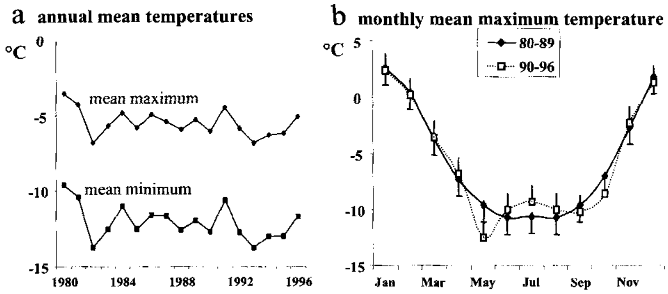

Fig. 6. Temperatures at Casey station over the period 1980–96. Monthly data in Fig. 6b are pooled for the 1980s (standard deviation in downward bars) and 1990s (standard deviation in upward bars).

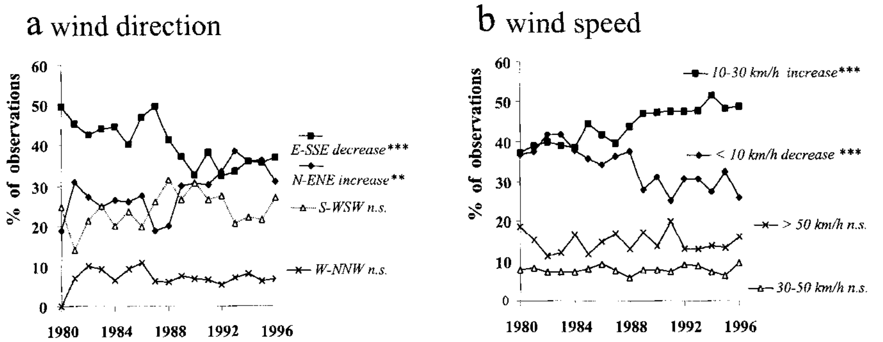

Fig. 7. Wind-directions and speeds at Casey station over the period 1980–96. Data expressed as percentage contribution to the total of observations. Original data for directions and speeds have been pooled in smaller number of categories which are described alongside the respective data. The significances of linear regressions over 17 years of data are alongside each category (n.s.= not significant; $**=P < 0.01$; $***=P < 0.001$).

lowered as a consequence of predation by the southern giant petrel during the prelaying and egg laying periods.

Survival/mortality

Survival was directly affected by giant petrel predation, most seriously so among experienced breeders. Within the 1996/97 summer, observed mortality among breeders was 15.4%. Average annual mortality of such birds had been 11.5% from 1990/91 until October 1996, a significant increase in comparison to earlier periods. "Normal" mortality of adult petrels with life strategies like the Antarctic petrel is in the order of 4% (Warham 1996), a level only observed over the initial two years of our study.

Remarkably different mortality was recorded for non-breeding birds, whose numbers seemed unaffected throughout the period of observation (1984–86 emigration period not considered). Overall mortality levels among non-breeders remained at a "normal" level for the 1986–96 period, and no mortality from predation was observed within the 1996/97 breeding season. The differences between breeding and non-breeding Antarctic petrels can be explained by the observed hunting technique of the giant petrels. Successful kills were only made when they followed the 'surprise attack' strategy. As a consequence, the Antarctic petrels with the strongest site tenacity became the victims.

In the newly banded cohort of birds, 10% mortality within the 1996 season is in between the figures for the 'old' breeder and non-breeder groups. The similarity shows that high mortality in our older cohort is not a matter of birds dying of old age. Furthermore, the change in mortality rate is much stronger than could be expected from published examples of old age in petrels (Warham 1996).

Breeding success

The almost total breeding failure of Antarctic petrels in 1996/97 was an indirect result of giant petrel predation. Disturbance during their attacks caused intense predation on deserted eggs by skuas. Most eggs had already disappeared by the end of the 2-week laying period, and this determined the final breeding success. The decline in breeding success in our study area appeared sharper than that in the reference area probably due to local topography. The study area at Northern Plateau was situated in between the snowdrift and the remainder of the colony, which means that the giant petrels had to walk through or closely past the study area at every approach to the reference area.

Population trend

As yet, no significant change in bird numbers attending the study area was detected between 1986 and 1996 (Fig. 2). Seabird life strategies are able to withstand many years of unfavourable conditions but complicate early detection of population change (Anker-Nilssen & Röstad 1993, Anker-Nilssen *et al.* 1996). Large 'backup' populations of immatures and non-breeding adults form 'strategic reserves' (Warham 1996) that may obscure adverse effects, especially if the species' loyalty to the natal colony is low. Indeed, in the study area of the roughly 200 regularly attending birds there are three immigrants banded as chicks on Haswell Island and the Rauer Islands, thousands of kilometres to the west. Nevertheless, if adult mortality and breeding failure in the Northern Plateau colony continue at the 1996 level, there seems little doubt that the colony will gradually disappear.

Southern giant petrel as predator

The hunting technique of giant petrels on Ardery Island is that of an efficient predator capturing healthy adult prey on land. We know of no earlier reports of such behaviour. Both *Macronectes* species are considered to be scavengers (e.g. Conroy 1972, Johnstone 1977, Hunter 1983, 1985, Voisin 1991, Emslie *et al.* 1995, Warham 1996) taking dead, injured, and weak or defenceless prey among marine mammals and birds, and are persistent ship followers. They do take apparently healthy penguin chicks too, but the taking of chicks that can neither escape nor defend themselves is very different from the predatory behaviour witnessed on Ardery Island. Few records have been made of predation on smaller petrels at sea, e.g. of burrowing petrels (Johnstone 1977, Hunter 1990) although most refer to the taking of birds that were somehow impaired. Observations most similar to ours were described by Punta & Herrera (1995) on Isabel Island where southern giant petrels scared imperial cormorants *Phalacrocorax atriceps* (King) off their nests by low flights over the colony. They did not land but chased and attacked cormorants when flying over sea or on the water. The success rate was relatively low (two kills in 85 attacks). As on Ardery Island, other birds, in this case gulls and sheathbills, took advantage of the disturbance by taking the cormorant eggs from the deserted nests.

Predation and petrel breeding distribution

We have no indications that either our presence in the colony or food shortage has led to this predatory behaviour as a newly acquired technique. If the behaviour was due to our activities, similar predation events would have been expected in earlier years, and not only in, and immediately at the start of the 1996 season. In addition, there is no evidence of food scarcity for the giant petrels. Expected local food sources have either been growing (Adélie penguin *Pygoscelis adeliae* (Hombron & Jacquinot): Woehler *et al.* 1994; elephant seal *Mirounga leonina* (L.): Murray & Luders 1990) or not known to have undergone major changes (e.g. Weddell seal *Leptonychotes weddellii* Lesson). In our opinion the predatory behaviour is an 'old' and normal event, which is simply rarely observed.

This view is based on the knowledge that the colonies of all four smaller fulmarine petrels (fulmar and Antarctic, cape and snow petrels) are largely, but not completely, restricted to steep slopes and cliffs. We believe that the nesting distribution of petrels shows all the signs of long-term adaptation to the presence of predators that approach from land. In the schematic cross section of Ardery Island (Fig. 8) three types of terrain may be distinguished:

Type A: steep cliffs;

Type B: moderately sloping boulder terrain found in inland slopes (B1), along cliff tops (B2), and subsections in the cliffs (B3); and

Type C: flat areas.

Dense nesting of all petrel species breeding on Ardery Island occurs on the cliffs (terrain type A) and on slope sections within the cliffs (type B3). This is especially true for the Antarctic petrels and fulmars. Cape petrels and particularly snow petrels also occur on some of the inland slopes (B1) and the higher cliff edges (B2) but usually more scattered and in lower numbers.

We reject the idea that such nesting distributions are determined by limited flying skills of the smaller petrels, necessitating a strong vertical drop for nest access or departure. Antarctic petrels have little problems in taking off from relatively flat ground (Cowan 1979; personal observation). Also snow petrels and cape petrels nest on more level surfaces. None of the species seems to have problems at locations like the Northern Plateau. If flying skills were the major factor, similar dense nesting of all petrels would be seen on all type B locations and not just on type B3.

Two land predators, skuas and giant petrels, have to be considered as potentially limiting nesting distributions of petrels. From our observations, skuas are unlikely to exert such a predation pressure. Skuas were never seen to attack adult petrels at nests, but only in air. Even hovering over nest sites, a common skua threatening behaviour in penguin colonies for stealing eggs or chicks (e.g. Emslie *et al.* 1995), is infrequent in petrel colonies (personal observation; Haftorn *et al.* 1991). Weidinger (1998) showed that cape petrel eggs and chicks were more frequently taken if skuas could attack from the ground. Many spots on Ardery do allow 'ground attacks' by skuas, but are nevertheless densely populated with nesting petrels. Northern fulmars (*Fulmarus glacialis* (L.)) can also be found nesting on flat ground in the presence of skuas, but usually only in places where access for other land predators is impossible. Thus, in our view, skua predation pressure does not explain the current limits of petrel nesting areas.

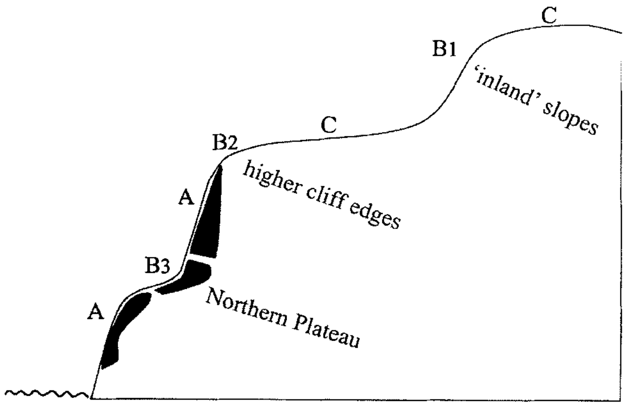

Fig. 8. Schematic cross section of Ardery Island showing main petrel nesting areas (dark) in relation to the type of terrain (A = steep cliffs; B = boulder slopes; C = level terrain). Normally, giant petrels can only land in the flat areas (C) from where adjacent slopes (B1, B2) can be reached by foot.

The behavioural pattern of the only other predator, the giant petrel, does explain the nesting distributions of the smaller petrels. Unlike the skuas, giant petrels need relatively large, flat and smooth surfaces for landing, occurring only on the type C locations in Fig. 8. Potential petrel nesting slopes that border these are accessible for giant petrels by foot (type B1 and B2) and are void of colonies of Antarctic petrels and fulmars. Snow and cape petrels can only extend some of their nesting to such areas by breeding in inaccessible holes in between rocks or scattered in otherwise sheltered sites (Green 1986). In addition, both species have a particularly well-developed defensive oil-spitting behaviour that would discourage predators from preying on them on the nest (Johnstone 1977). Only where type B locations are surrounded by steep cliffs and have a rough surface, is access for giant petrels (not for skuas) impossible, as they can not land nor approach on foot. In such areas all smaller petrels are nesting in high densities. We conclude that nest locations of the fulmarine petrels in the area are determined by long-term predation pressure from giant petrels. Under stable conditions, predatory actions will be infrequent, and restricted to the margins of areas where giant petrels can land (type C). Our

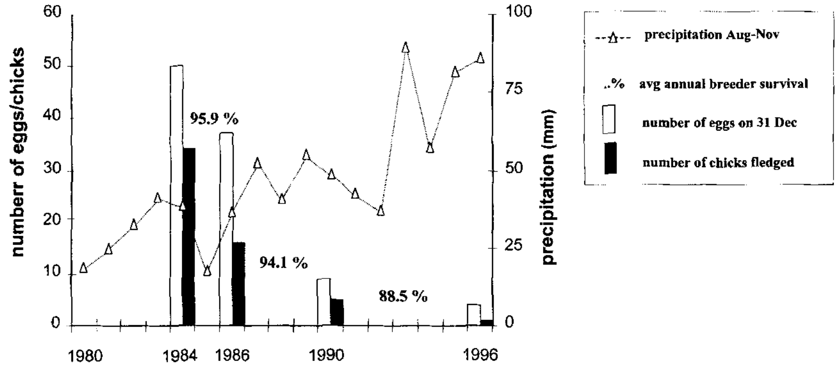

Fig. 9. Snowfall in relation to breeding success and survival of Antarctic petrels. Annual data for precipitation at Casey during the prelaying period (August–November) since 1980 plotted in relation to changes in breeding success and average annual survival of Antarctic petrels in the Northern Plateau study area.

very few observations of giant petrels along the cliff tops in earlier years, might in retrospect be interpreted in such a way. Only when changed conditions create new landing sites in previously inaccessible locations, does predation become frequent enough to be regularly witnessed.

Climate change

Our analysis showed important changes in the *local* climate in the Casey region since 1980. For the Wilkes Land coast, Morgan *et al.* (1991) used ice-cores to look at longer-term changes over a wider area. They concluded that snow accumulation rates had significantly increased from 1960 to the mid 1980s, to 20% above the average long-term level. Apparently, this trend is still in progress. They also noted that increases were due to 'winter' precipitation (c.f. Fig. 5b) and linked this to intensified cyclonic activity and a more oceanic type of climate (c.f. Fig. 6). Morgan *et al.* (1991) suggest that increased precipitation occurs over a wide Antarctic region and Jacobs (1992) links such increased precipitation to global atmospheric warming.

The key factor for predation in 1996 was the presence of a large snowdrift adjacent to, and partly over our study area. The snow provided a new landing area for giant petrels in an area that was previously inaccessible. The reduction in the giant petrel visits during melt of the drift in December confirmed the crucial role of the snow in providing access. Visits did not stop because of lack of prey, because Antarctic petrels continue to attend their nest sites until late January irrespective of earlier breeding failure. Critical for the effects on Antarctic petrels in 1996 was persistence of the snowdrift into the egg laying period. This totally influenced the year's breeding success in the population, and aggravated adult mortality.

Because of the lack of data on the annual persistence of the snowdrift and our small sample of only four study seasons, no statistical significance can be demonstrated for correlations between Casey snowfall and the number of remaining eggs or fledged chicks in study years, nor for the survival rates in between those periods (Fig. 9). Nevertheless, the significant trend in local climate and our observations of predation events suggest strongly that giant petrel predation has increased in response to snow conditions and is the background to steadily decreasing survival and breeding success among the Antarctic petrels.

Concluding remarks

The effects of increased snowfall on a local population of Antarctic petrels should not be interpreted as a general consequence of global warming for Antarctic seabirds. General increases in snowfall are not necessarily followed by proportional increases in local snow accumulation. Snow petrels are known to have used the same nunatak nesting areas over periods up to 35 000 years (Hiller *et al.* 1988, Ryan *et al.* 1992) in spite of the many climatic variations that must have occurred over such a period. On the other hand, part of the Adélie penguin colonies near Palmer station was abandoned because of increased snowfall (Fraser & Patterson 1997).

Our concern from the Ardery Island events is not so much the changes faced by the local population of Antarctic petrels. Natural climatic changes, both short- and long-term, will continuously alter suitability of bird nesting areas in many ways. It was the extreme complexity and unpredictability of ecosystem response to such change, that surprised us. The predictable effect of increased snowfall would have been a relatively minor reduction in breeding success by the freezing of eggs laid in snow. It is the unpredictable chain of secondary events that followed (access for bird predator, mortality, disturbance, egg predation and total breeding failure) that leaves us uncomfortably aware of limitations in predicting the effects of environmental change on ecosystems.

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