

ABSENCE OF HAEMATOZOA IN BREEDING MACARONI *EUDYPTES CHRYSOLOPHUS* AND ROCKHOPPER *E. CHRYSOCOME* PENGUINS AT MARION ISLAND

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Haematozoan infections cause the death of penguins in captivity, but seldom in the wild. No haematozoa were found in 89 blood smears taken from macaroni penguins *Eudyptes chrysolophus* or 80 smears from eastern rockhopper penguins *E. chrysocome filholi* at subantarctic Marion Island between October and November 2001. Discussion centres on the possibility of vector introduction and establishment under conditions of climatic and/or anthropogenic change.

Key words: *Eudyptes*, haematazoa, Marion Island, penguins, Subantarctic

Blood parasitism is a subject of increasing interest (Hamilton and Zuk 1982, Earlé *et al.* 1991, Bennet *et al.* 1995, Jovani *et al.* 2002), resulting in extensive documentation of both host and parasite species throughout the world. Five species of haematozoa have been reported in penguins in the wild: *Leucocytozoon tawaki*, *Plasmodium relictum*, *P. elongatum*, *P. cathemerium* and *Babesia peircei* (Jones and Shellam 1999a). Haematozoan infections have been implicated as a cause of mortality in captive penguins and could therefore have an effect on the health of wild populations (Brossy 1992, Jones and Shellam 1999b). This study evaluates the occurrence of haematozoa in breeding macaroni *Eudyptes chrysolophus* and eastern rockhopper *E. chrysocome filholi* penguins at subantarctic Marion Island in the southern Indian Ocean. The Antarctic and Subantarctic have been inadequately studied in terms of blood parasites. The environment is thought to lack suitable vector populations, but various factors could act to increase the suitability of these habitats to the vectors of blood parasites.

MATERIAL AND METHODS

Totals of 356 000 pairs of macaroni penguins and 67 000 pairs of rockhopper penguins (Crawford *et al.* 2003) breed on Marion Island (290 km²; 46°52'S, 37°51'E). Fieldwork was conducted at the Bullard Beach and Rockhopper Bay penguin colonies on the eastern side of the island between 3 October and 9

November 2001. Totals of 89 adult macaroni penguins (50 males, 39 females) and 80 adult rockhopper penguins (53 males, 27 females) were captured on return to their breeding colonies after the non-breeding winter period, and sampled for haematozoa.

Blood was obtained from the jugular vein and thinly smeared. Upon drying, Kyroquick (100% analytic-grade methanol) was applied for five seconds. Smears were transported to South Africa where, during August 2002, they were fixed with May Grunwald's Giemsa and stained with 4% Giemsa solution buffered to pH 7.3 (1/25 v/v) for 30 minutes, rinsed with 7.3 pH buffer and dried overnight. Blood smears were examined by light microscopy, for 15–20 minutes for each smear, with a minimum of 1 100 fields (c. 122 red cells per field) under 100× magnification oil-immersion objective for haematozoa.

During blood collection, ticks were opportunistically collected from the head of the penguins and preserved in 70% ethanol.

RESULTS

No haematozoa were found in any of the 89 blood smears from macaroni penguins or the 80 smears from rockhopper penguins. Six ticks were found and identified as *Ixodes (Ceratixodes) uriae*. All were found on rockhopper penguins, four around the eyes and two around the base of the culmen. Tick burdens were low (6.7% of individual rockhopper penguins).

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DISCUSSION

The lack of avian haematozoa in blood smears cannot be explained in terms of temporal or inappropriate sampling or methods used. Once infected, avian malaria infections remain with adult penguins throughout their lives, although they are not always detectable in blood smears (Cranfield *et al.* 1994). Chicks receive natural resistance of "anti-*Plasmodium* species" through maternal transfer for up to eight weeks after hatching (Graczyk *et al.* 1994). Therefore, only adult penguins were sampled. Justified concern has been expressed by Cooper and Anwar (2001) and Jones and Shellam (1999a) regarding procedures, methods and findings in reports interpreting parasitological examinations of blood smears as negative. Ideally, definitive assessment for malaria should be determined using a serum antibody ELISA test or polymerase chain reaction (Graczyk *et al.* 1995).

In captivity, avian malaria caused by the haematozoan *Plasmodium* spp. is the largest cause of mortality among penguins in American zoos (Cranfield *et al.* 1994). The same applies at the South African Foundation for the Conservation of Coastal Birds rehabilitation centre in Cape Town, in years when a major oil spill event affecting African penguins *Spheniscus demersus* does not occur (SLP pers. obs.).

There have been a few reports of haematozoa-induced mortality in the wild, but the intensity and the prevalence of these infections have been low (Jones and Shellam 1999a). *Leucocytozoon tawaki* (vector: simuliid flies) has been reported in Fiordland *E. pachyrhynchus* and African penguins; *Plasmodium* spp. (vector: mosquitoes and midges) in Fiordland, yellow-eyed *Megadyptes antipodes* and African penguins (Clarke and Kerry 1993, Jones and Shellam 1999a); and *Babesia peircei* (vector: ticks) in African penguins (Earlé *et al.* 1993). It is interesting that species where haematozoa have been identified in the wild are essentially "mainland" species breeding among vegetation where the environment is suitable for the establishment of vector species. There have been reports of negative blood examinations of 12 penguin species in their natural environment (700 birds from 14 localities, Jones and Shellam 1999a). No avian malaria was found in Galapagos penguins *S. mendiculus* (Miller *et al.* 2001).

Blood samples from penguins have been examined for haematozoa from several Subantarctic localities: Macquarie Island (Laird 1952, Jones 1988), Heard Island (Jones 1988) and South Georgia (Pierce and Prince 1980). All of these were negative. A northern rockhopper penguin *E. c. moseleyi* from cold-temperate Gough Island, South Atlantic, was reported positive

for *Plasmodium relictum* (Fanthon and Porter 1944). However, no mention was made of where sampling took place, in the wild or in transit. Because no malaria vector species are present on Gough Island (Jones *et al.* in press), it is presumed that infection took place in transit.

The absence of blood parasites in penguins at Marion Island is attributed to the lack of established vector populations there. Similarly, the lack of haematozoa in birds living in the Arctic tundra has been attributed to the lack of appropriate vectors (Bennett *et al.* 1992, Earlé and Underhill 1993). Vectors commonly associated with genera of avian blood parasites include biting midges *Culicoides* spp., blood-sucking flies *Simulium* spp., mosquitoes *Culex* spp. and ticks *Ixodes* spp. All except the tick *I. uriae* are absent from Marion Island (Chown *et al.* 2002). Island habitats are, however, suitable for these genera in terms of physical environment and nutritional requirements. Dispersion to the island is possible through movement in the upper air column or through anthropocentric or avian introductions. Based on a few band recoveries (Gartshore *et al.* 1988), Subantarctic skuas *Catharacta antarctica* can reach the coast of Africa, where they are potentially exposed to avian malaria and *Babesia* through their vectors. These birds could then introduce infected vectors or infect vectors already established on Marion Island or on other subantarctic islands. No blood parasites were, however, found in a survey of south polar skuas *C. maccormicki* (Jones *et al.* 2002). Strong winds, cold temperatures and the absence of freshwater inhibit the establishment of vector species. Although there is an abundance of freshwater, Marion Island experiences winds exceeding 55 km h⁻¹ on c. 107 days per year. Atmospheric temperatures are usually between -2.8 and 13.9°C with an annual mean of 5.7°C (Hänel and Chown 1998). *Limnophyes pusillus*, an invasive chironomid midge, has established itself on Marion Island (Crafford 1986). Its success has been attributed to the suitability of its life history: short reproductive phase and loss of swarming behaviour (Crafford 1986). Future success of avian blood parasites and/or vector species introduced to Marion Island depends on their ability to adapt to prevailing environmental conditions. *L. pusillus* has been capable of overcoming such obstacles (Crafford 1986). Changing climate has impacted Marion Island. The mean annual temperature has increased by 1°C over the past 50 years and annual precipitation has decreased by 600 mm (Smith and Steenkamp 1990, Smith 2002). Climatic changes within the Antarctic and Subantarctic may increase the likelihood of establishment of alien insect species (Chown *et al.* 1998), including parasitic vectors.

Low tick infestation observed on rockhopper pen-

guins and the absence of ticks on macaroni penguins in this study may be attributed to the fact that these penguins were returning from six months at sea when sampled. In a previous study conducted at Marion Island, moderate tick infestations of rockhopper and macaroni penguins were observed (Brooke 1985). Moderate infestations of rockhopper penguins and massive infestations of royal penguins *E. schlegeli* were found on Macquarie Island (Murray and Vestjens 1967). Heavy infestations on king penguin *Aptenodytes patagonicus* chicks have been seen at Marion Island (J. Cooper, Avian Demography Unit, University of Cape Town, pers. comm.). Differences in severity of tick infestations between penguin species are determined by the duration of contact with plants and differences in breeding and moulting behaviours (Murray and Vestjens 1967). Acquired natural resistance to ticks is also a possible explanation for low infestation rates (Trager 1939, Roberts 1968), but this does not happen in all species (Randolph 1975). Serological studies could determine this relationship. *Ixodes uriae* is a vector for *Babesia peircei* (Earlé *et al.* 1993). *B. peircei* could therefore parasitize *Ixodes* spp. already established on Marion Island, potentially leading to deleterious consequences for penguin populations.

Hepatozoon albatrossi, also considered to be transmitted by *I. uriae*, has been recorded in wandering *Diomedea eulans*, grey-headed *Thalassarche chrysostoma* and black-browed *T. melanophris* albatrosses at South Georgia (Jones 1988). Wandering and grey-headed albatrosses both breed at Marion Island (Crawford *et al.* 2003). It is possible that this haematozoan is present in these species at Marion Island. *H. albatrossi* is considered non-pathogenic.

Subantarctic penguins are adapted to an environment free of haematozoan vectors (Laird 1961). Therefore, they have not developed an immune system to deal with these pathogens. If, as a result of global climate change or because of anthropogenic or avian introductions vectors become established on subantarctic islands, acute infections and mass mortality could occur, as has happened to birds on the oceanic island of Hawaii (van Riper *et al.* 1986). This underlines the need to prevent introduction of haematozoa and vectors to Marion Island.

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A view of the colony of macaroni penguins at Kildalkey Bay, Marion Island (photo B. M. Dyer)

POPULATION DYNAMICS OF THE WANDERING ALBATROSS *DIOMEDEA EXULANS* AT MARION ISLAND: LONGLINE FISHING AND ENVIRONMENTAL INFLUENCES

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The subantarctic Prince Edward Islands (Marion and Prince Edward) support the largest breeding population of the Vulnerable wandering albatross *Diomedea exulans*. The number of birds breeding at Marion Island has fluctuated over the past three decades apparently as a result of both real changes in the size of the population and changes in the proportion of the population that attempts to breed in a given year. Changes in several demographic parameters that appear to be influenced by both environmental and anthropogenic effects are described. From 1994–2001, the proportion of first-time breeders in the population was positively correlated with the maximum ENSO (Niño 3) index, whereas from 1984–2000 the annual survival rates of breeding adults were negatively correlated with Japanese pelagic longline fishing effort in the southern Indian Ocean. Adult survival rates were significantly correlated with those on neighbouring Possession Island, Crozet Islands, but differed from those at South Georgia, suggesting common factors operating at an ocean-basin scale. The average survival rate of adult females was lower than that of males. Males who lost partners took 40% longer than females to find a new mate, suggesting a male-biased population. Survival rates of juvenile males and females did not differ. The age distribution of first-time breeders shifted progressively towards younger birds during the 1990s. Higher than expected survival rates of breeding adults during the late 1990s may be linked to large amounts of supplementary food being made available by the initiation of a longline fishery for Patagonian toothfish *Dissostichus eleginoides* close to the islands at this time. Overall, breeding success was better than recorded at other localities, indicating that breeding conditions at Marion Island were comparatively favourable. The early implementation of both international and national conservation initiatives to reduce the impact of longline fishing on this species and improve its conservation status is encouraged.

Key words: *Diomedea exulans*, longline fishing, Marion Island, population dynamics, Prince Edward Islands, Subantarctic, wandering albatross

The wandering albatross *Diomedea exulans* is classified as Vulnerable on the basis of population reductions in excess of 20% over most of its range within the last three generations (BirdLife International 2000). The main cause of this population decrease has been identified as mortality associated with longline fishing operations (Gales 1998). The subantarctic Prince Edward Islands (comprising of Marion and Prince Edward islands, 21 km apart) in the southern Indian Ocean are the most important breeding site for wandering albatrosses, hosting 44% of the species' global population (Gales 1998, Crawford and Cooper 2003). Information on the dynamics of the population at the Prince Edward Islands is therefore of great importance for the conservation of the species.

Wandering albatrosses are highly efficient flyers (Weimerskirch *et al.* 2000) that are able to move vast distances from their breeding islands. Tracking studies (Nel *et al.* 2002a) as well as band recoveries (Gales *et al.* 1998) indicate that wandering albatrosses breeding on Marion Island interact with a range of longline

fisheries close to their breeding site, on the high seas, as well as in continental waters surrounding southern Africa and Australia. Of particular concern for the birds breeding on Marion Island is the time that tracked birds (notably females) spend in the region of the Sub-tropical Front south of Africa (Nel *et al.* 2002a). This area is utilized intensively by pelagic longline fishing vessels targeting tuna *Thunnus* spp. (Tuck and Bulman 2001). Wandering albatrosses are vulnerable to being killed by pelagic longlines (Brothers 1991, Gales *et al.* 1998, Ryan and Boix-Hinzen 1998) because these lines are only lightly weighted and sink slowly, thereby allowing the large and shallow-diving wandering albatrosses to access the baited hooks (Brothers *et al.* 1999). In contrast, wandering albatrosses are seldom killed in the demersal longline fishery for Patagonian toothfish *Dissostichus eleginoides* around Marion Island (Nel *et al.* 2002b). However, they did appear to obtain a substantial amount of the food that they fed their chicks from scavenging offal disposed by these vessels (Nel and Nel 1999, Nel *et al.* 2002a).

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Long-term demographic studies of wandering albatrosses (and the closely related Amsterdam albatross *D. amsterdamensis*) in the Indian Ocean show strong evidence that spatio-temporal changes in longline fishing effort for pelagic tuna in the southern Indian Ocean may be the primary driving force behind the observed population changes (de la Mare and Kerry 1994, Weimerskirch *et al.* 1997). This paper describes long-term changes in population parameters of wandering albatrosses at Marion Island in relation to possible anthropogenic and environmental influences.

MATERIAL AND METHODS

Long-term study colonies

Studies were conducted in three separate colonies located on the north-eastern coast of Marion Island (240 km^2 ; $46^\circ 52' \text{S}$, $37^\circ 51' \text{E}$). Two of the study colonies have been monitored continuously since 1984, whereas the third was established in 1987. However, birds have been metal-banded opportunistically in the study colonies since 1976 (Appendix 1).

On average c. 230 pairs breed in the three study colonies each year (c. 14% of the Marion Island breeding population). Since their establishment, all fledgling chicks and adults breeding within the colonies have been banded with metal identification bands. Breeding birds also received unique colour alpha-numeric bands for quick identification and reduced disturbance. Nest sites are marked with numbered stakes once an egg has been noted in the nest. Both partners are then checked for metal and colour identification bands, and chicks are banded five months after hatching. Nests were checked weekly from egg-laying until the completion of the brood/guard phase (c. two months after hatching). After this, the fate of chicks was followed by monthly checks.

Once a year during peak incubation, every incubating bird on Marion Island (i.e. half of the annual breeding population) was checked for identification bands. For three seasons (1992, 1993, 1994), both mates in all the areas surrounding and between the three study colonies were checked for bands and banded if they were not already banded. Those studies were conducted in order to determine the level of emigration out of the study colonies.

Survival data analysis

Encounter history matrices, which are required for capture-mark-recapture (CMR) analysis, were con-

structed from the resighting data, treating multiple sightings in a year as a single sighting. Two matrices were constructed: the first included the sightings of all known-age birds (i.e. birds banded as chicks) in the monitoring colonies; the second included all adult birds that had been recorded breeding at least once in the colonies. Birds were assumed to age by one year at the beginning of January, which is the peak laying month on Marion Island (Percy FitzPatrick Institute unpublished data). Juvenile survival was estimated using birds from age 1 to 9 years in the first matrix (i.e. known age birds), whereas adult survival was estimated using the second matrix (i.e. birds known to have bred).

The software program MARK (G. White, University of Colorado, USA), was used to obtain estimates of survival and of the probability of capture using primarily the Cormack-Jolly-Seber (CJS) model (Cormack 1964, Jolly 1965, Seber 1965). Because it was impossible to distinguish mortality from permanent emigration in the study colonies, reference is made to apparent rather than absolute survival. However, no bird that was recorded breeding within a study colony was recorded breeding elsewhere afterwards, so the effect of permanent emigration will likely be negligible.

The two fundamental parameters in the models are ϕ , the survival probability for all animals between the i th and $(i+1)$ th sample ($i = 1, 2, \dots, k-1$), k being the number of recapture events, and p , the capture probability for all animals in the i th sample ($i = 1, 2, \dots, k$).

A Goodness of Fit (GOF) test (Appendix 2) suggested that there was underlying heterogeneity in the recapture probabilities. Estimates produced by CJS models can be biased for biennial breeding birds (Rothery and Prince 1990), because very few birds that breed successfully in a particular year will attempt to breed the following year. This behaviour introduces heterogeneity into the probability of recapture and leads to a bias in estimates. However, departures from the CJS model in general do not affect point estimates of survival (Carothers 1979), although they cause underestimation of standard errors of survival estimates (Burnham *et al.* 1987). Rothery and Prince (1990) analysed the problem by simulating data using a model of biennial breeders and showed that the bias was most marked in the first and last two years of the series. Accordingly, the estimates at the ends of the series were ignored for analysis of annual variation.

Evaluation of the relative fit of the models was accomplished using the Akaike Information Criterion (AIC; Anderson *et al.* 1994; Appendix 3). AIC is a standard procedure for model selection in a CMR context, and it weighs the quality of fit (deviance) and the precision (via the number of parameters), so as to select the most parsimonious model that adequately describes the data (Lebreton *et al.* 1993, Anderson *et*

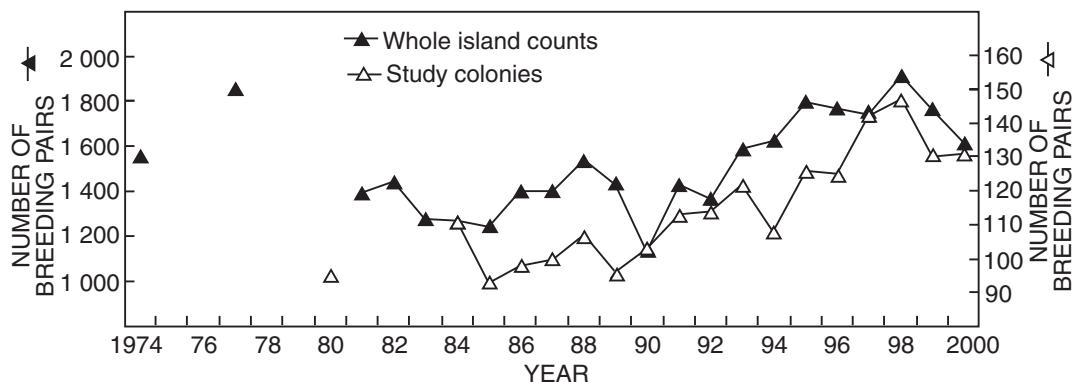


Fig. 1: Counts of breeding pairs of wandering albatrosses and within the two long-term study colonies at Marion Island that have been monitored the longest. Counts were made in January after completion of egg laying

al. 1994). It was used to select between the full time-, age- and sex-dependent model and various models assuming no differences in survival and capture probability between the sexes, between different-aged birds (for the combined cohort data), and between years. The likelihood ratio test, which provides a means to test between two nested models, was used to test the null hypothesis that the survival rates were constant between sexes, versus the alternative hypothesis that the survival rates varied between the sexes.

Fishery and environmental parameters

Pelagic longline fishing effort in the Southern Ocean was taken with permission from Tuck and Bulman (2001). The *El Niño*-Southern Oscillation (ENSO) index *Niño* 3 was used as an indicator of environmental variability. This index is the sea surface temperature anomaly averaged over 5°S, 5°N and 150°W, 90°W (i.e. the eastern equatorial Pacific). *Niño* 3 data were obtained from the International Research Institute

for Climate Prediction website (<http://ingrid.ldgo.columbia.edu/SOURCES/Indices/ensomonitor>).

Population modelling

A simple age-structured model (similar to that used by Weimerskirch *et al.* 1997 and Waugh *et al.* 1999) was constructed to test if the measured demographic parameters could broadly explain the observed changes in the number of breeding birds in the long-term study colonies. The model was run for breeding females, because the expectation was that the populations were male-biased, and therefore that females would be limiting. In terms of survival, age-classes 1–9 years were classed as juveniles and >10 years as adults. The proportion of birds of each age-class that attempted to breed was estimated using the average ages at which birds recruited into the breeding population. The proportion of the potential breeding population that actually bred in a given year was calculated from the time that it took birds to breed again after either a failed or a successful breeding attempt (see Table I). Except for the final model, this parameter was kept constant.

RESULTS

Population trend and breeding success

Although only two whole-island counts were conducted during the 1970s, it appears that the breeding population was considerably higher than during the 1980s (Fig. 1). During the 1980s the population remained relatively

Table I: Percentage of wandering albatrosses breeding in a specified number of years after a breeding attempt that was either suggested or failed

Years after breeding attempt	% outcome of breeding attempt	
	Successful	Failed
1	0.7	81.0
2	87.0	13.4
3	7.2	3.2
4	3.0	1.2
>4	2.1	1.2

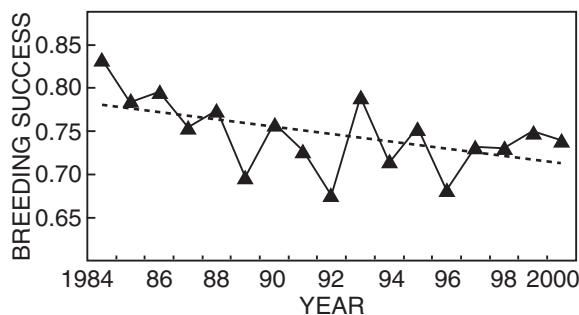


Fig. 2: Mean number of chicks fledged per pair for wandering albatrosses breeding at Marion Island, 1984–2000

constant, before increasing during the early to mid 1990s at a rate of c. 5% per year (Nel *et al.* 2002c). During the late 1990s the population once again stabilized or started to decrease. Counts of birds breeding in the long-term study colonies showed similar trends to the whole island population.

The overall breeding success in study colonies was $74.6 \pm 4.2\%$ ($n = 17$ seasons). It decreased from 1984 to 1996 (Fig. 2, $F = 5.386$; $p = 0.035$) and then stabilized. Breeding success also varied with age (Fig. 3). Breeding success of birds younger than 10 years (63%) was significantly lower than for birds between 10 and 25 years (76%; $\chi^2 = 28.8$; $p < 0.001$). Breeding success of birds older than 25 years was once again lower (60%). Breeding success of first-time breeders (66%) was also lower than that of more experienced birds (75%; $\chi^2 = 15.1$; $p < 0.001$). This was mainly due to hatching success, which was much lower for first-time breeders (79%) than for more experienced birds (87%;

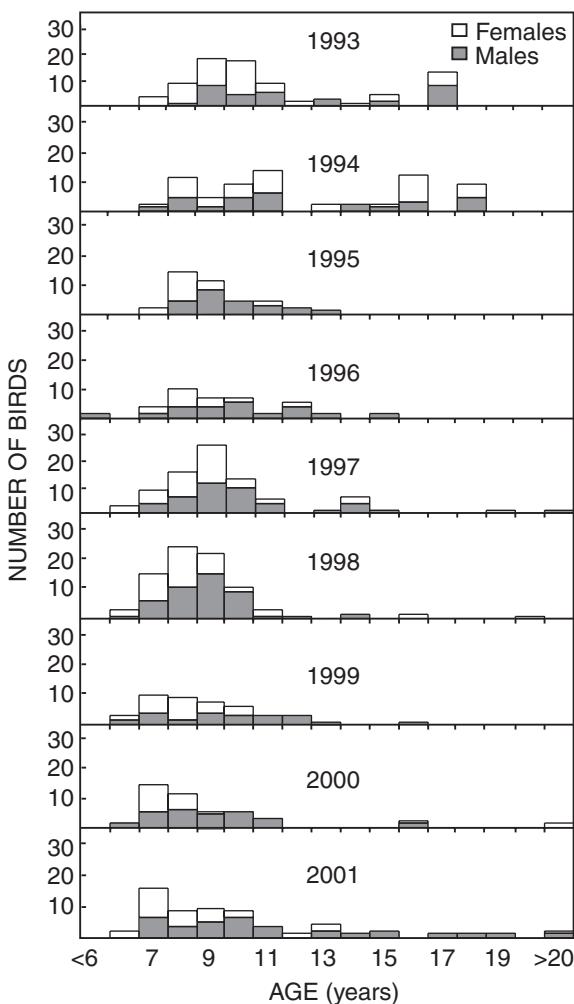


Fig. 4: Numbers of wandering albatrosses of different ages recorded breeding for the first time at Marion Island, 1993–2001

$$\chi^2 = 22.4; p < 0.001.$$

Most birds (81%) that failed in a breeding attempt in a given year attempted to breed the following year, whereas most birds (87%) that fledged a chick in a given year attempted to breed only after a full year's "sabbatical" (Table I). These parameters did not vary significantly over the duration of the study.

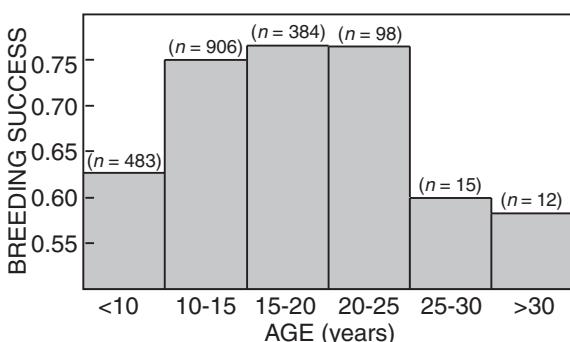


Fig. 3: Mean number of chicks fledged per pair per breeding attempt for wandering albatrosses at Marion Island of different ages, 1984–1990

Mate fidelity and mate loss

Analyses were limited to all breeding attempts during

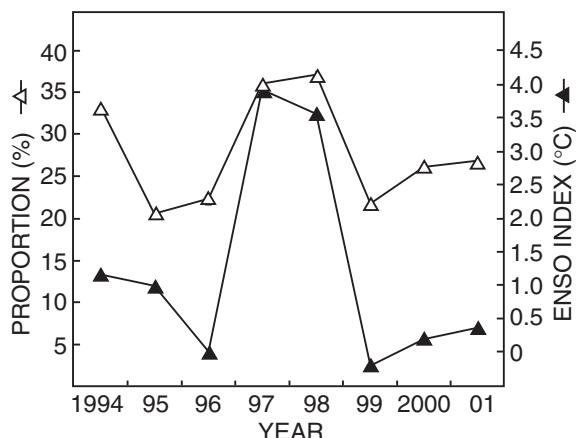


Fig. 5: Proportion of wandering albatrosses in the breeding population at Marion Island that were breeding for the first time and the annual maximum Niño 3 (ENSO) index, 1984–2000

or before 1995, thus giving sufficient time for a “lost” mate to be resighted. Individuals recorded breeding once only were ignored. Of the remaining 3 984 breeding attempts, 5.3% ($n = 210$) recorded a mate change.

However, only 0.7% ($n = 30$ breeding events) of breeding attempts were true “divorces” (i.e. the lost mate was resighted alive or breeding after the mate change). In the remainder of the cases the “lost” mate was never resighted again and had presumably died. Following a mate loss, males took significantly longer than females to find a new mate (males = 4.1 ± 1.7 years; females = 2.9 ± 0.7 years; $t = 5.6$, $p < 0.0001$).

Age of first-time breeders

The average age at first breeding for all birds was 9.9 ± 2.9 years. On average, males bred at a slightly older age (10.2 ± 2.8 years) than females (9.6 ± 2.9 years; $t = 2.59$; $p = 0.01$). The average age of first-time breeders for the period 1997–2001 (10.0 years) was significantly younger than from 1991 to 1996 (10.7 years; $t = 12.2$; $p = 0.005$). This is reflected in the age distribution of first-time breeders, which shifted towards younger age-classes during the later part of the 1990s (Fig. 4). Between 1991 and 1996 the proportion of first-time breeders younger than eight years was only 5%, but from 1997–2001 this increased to 26%. From 1999–2001, the modal age group of first-time breeders was seven years (Fig. 4). The proportion of first-time breeders in the breeding population was significantly correlated with the maximum Niño 3 index of the same

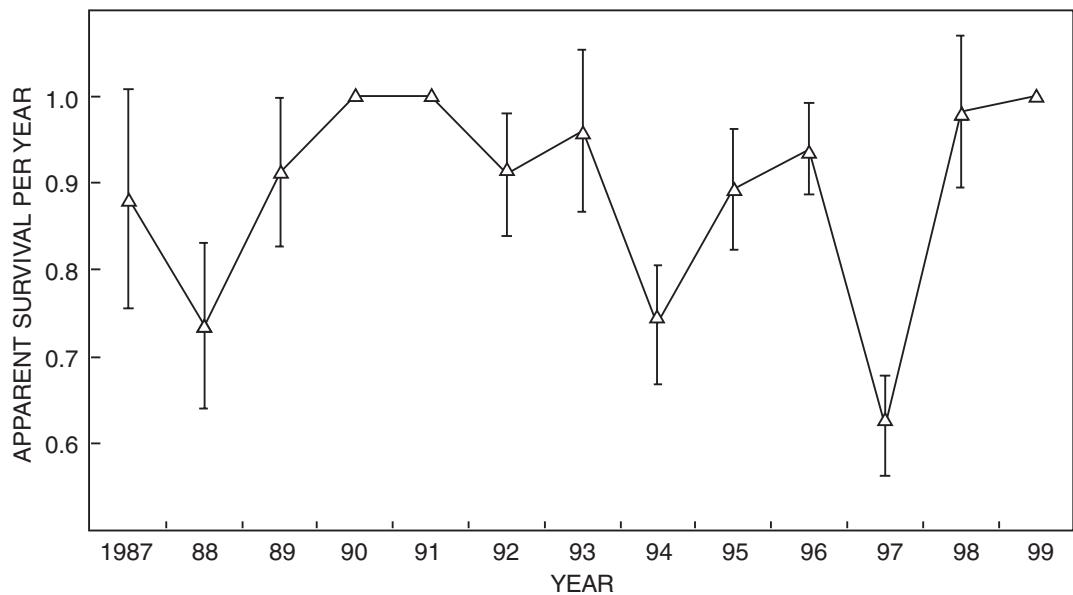


Fig. 6: Annual survival rate of juvenile wandering albatrosses (both sex combined) at Marion Island, 1987–1999

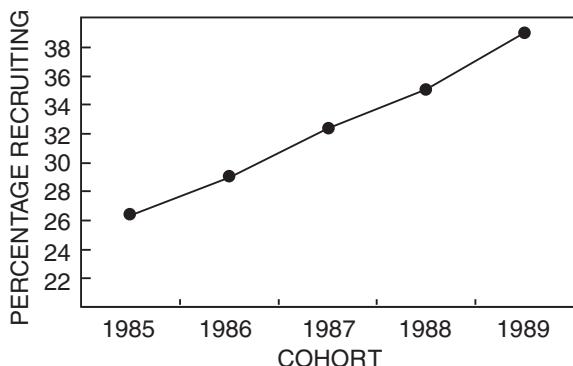


Fig. 7: Percentage of birds from the 1985–1989 cohorts of wandering albatrosses at Marion Island that recruited to the breeding population

year ($n = 8$; $r = 0.85$; $p = 0.007$; Fig. 5). This correlation was especially apparent during the large ENSO event of 1997/98.

Juvenile survival and recruitment

The average annual survival of juvenile birds (i.e. <10 year olds) was $89.9 \pm 0.004\%$. Male juvenile survival ($90.1 \pm 0.006\%$) was similar to that of females ($89.8 \pm 0.006\%$). The annual survival of juveniles varied considerably between 1987 and 1999 (Fig. 6), with the highest survival rates being recorded during the early and late 1990s and lower rates during the mid 1980s and mid 1990s.

Recruitment could only be calculated for five cohorts (allowing sufficient time for juveniles to recruit). The average recruitment rate for these cohorts was 32.9% and did not differ between males and females. Recruitment increased consistently between the 1985 and 1989 cohorts (Fig. 7).

Adult survival

Overall, the annual survival rate of birds older than 10 years was $94.2 \pm 0.008\%$. Male and female adult survival was 95.7 ± 0.009 and $92.6 \pm 0.01\%$ respectively. A sex-dependent model provided a significantly better fit than a sex-independent model ($\chi^2 = 12.37$; $p = 0.015$). Annual survival of adult breeding birds varied considerably from 1984–2000 (Fig. 8). It increased between 1984 and 1991 ($F = 5.859$; $p = 0.052$). It then fluctuated substantially, but was consistently low between 1994 and 1996 and high from 1997–2000.

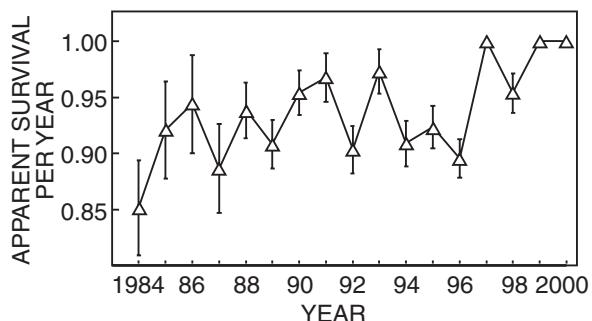


Fig. 8: Annual survival rate of adult wandering albatrosses (both sex combined) at Marion Island, 1984–2000

Correlations with other populations and longline fishing effort

Pelagic longline fishing effort in the southern Indian Ocean (south of 30°S , $20^\circ\text{--}141^\circ\text{E}$) and in the vicinity of the Prince Edward Islands ($35^\circ\text{--}60^\circ\text{S}$, $25^\circ\text{--}50^\circ\text{E}$), has fluctuated considerably over time (Fig. 9). Fishing effort in the southern Indian Ocean peaked in the mid 1980s, before decreasing to the lowest levels in more than a decade in the early 1990s. During the mid 1990s effort once again increased, before decreasing rapidly near the end of the 1990s. Effort in the vicinity of the Prince Edward Islands followed a similar pattern to that of the entire southern Indian Ocean, except that the decrease in effort at the end of the 1990s commenced earlier close to the islands. Japanese longline fishing effort in the southern Indian Ocean followed a similar trend, except that effort declined earlier after the peaks in both the 1980s and 1990s. Annual survival rates of breeding adult wandering albatrosses at Marion Island were most strongly correlated (negatively) with the annual effort of the Japanese pelagic longline fleet in the entire Southern Ocean (Table II).

Table II: Correlations of annual survival rates of wandering albatrosses from Marion Island with annual longline fishing effort in the southern Indian Ocean, 1984–2000 (after Tuck and Bulman 2001)

Parameter	Correlations		
	Prince Edward Islands ¹	Indian Ocean ² (Taiwanese)	Indian Ocean ² (Japanese)
r	0.368	0.199	-0.534
p	0.146	0.460	0.027

¹ $35^\circ\text{--}60^\circ\text{S}$, $25^\circ\text{--}50^\circ\text{E}$

² South of 30°S , $20^\circ\text{--}141^\circ\text{E}$

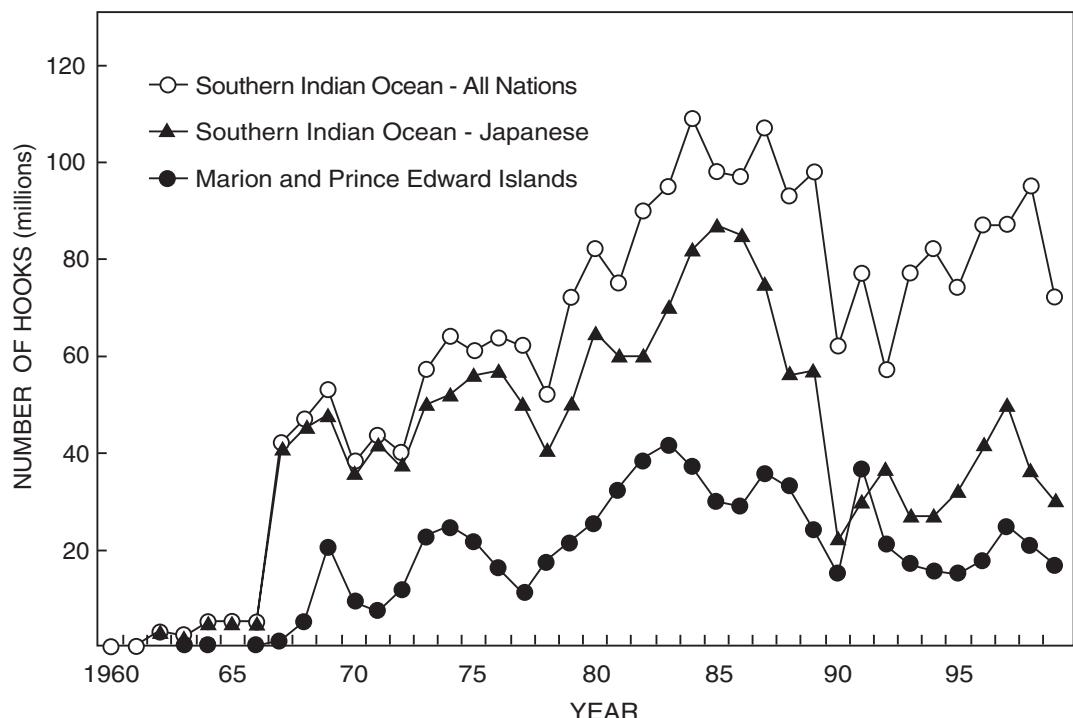


Fig. 9: Trends in the pelagic longline fishing effort of Japanese vessels and overall in the southern Indian Ocean (south of 30°S; 20–141°E) and in the vicinity of the Prince Edward Islands (35–60°S; 25–50°E), 1960–1999

Annual survival rates of breeding adults were not significantly correlated with pelagic longline fishing effort closer to the Prince Edward Islands (Table II).

Annual survival rates of adult wandering albatrosses on Marion Island were significantly correlated with adult survival rates on the Crozet Islands between 1984 and 1991 (the period of overlap between the Marion data and those presented in Weimerskirch and Jouventin [1998] for the Crozets, Fig. 10). Survival rates of adult birds on Marion Island were not correlated with those recorded for the South Georgia population (Croxall *et al.* 1998; $n = 11$, $r = -0.505$, $p = 0.113$).

Population modelling

When all parameters of the model were set at the means measured for the study period (1984–2000), the population increased at 0.43% per year, indicating that the population was stable or increasing slightly over the study period as a whole. However, as discussed in Nel

et al. (2002c), this probably represents a recovery of the population from a low point during the mid 1980s. The population appears to have been much higher during the mid 1970s.

When the year-specific annual adult female survival rates were added to the model, the predicted population showed a steady increase over most of the study period, although for the period 1993–1996 the population decreased slightly (Fig. 11a). Adding year-specific juvenile survival caused the predicted population to increase more rapidly from 1989 to 1993, mimicking the observed population (Fig. 11b). However, after 1994 the observed population increased steeply to 1998, whereas the predicted population remained relatively constant until 1997, only increasing slowly again at the end of the 1990s. As expected, adding the measured breeding success to the model did not cause the predicted population to change much. Survival and productivity parameters (and therefore changes in the whole population) only appear able to explain the observed changes in numbers of breeding pairs up to

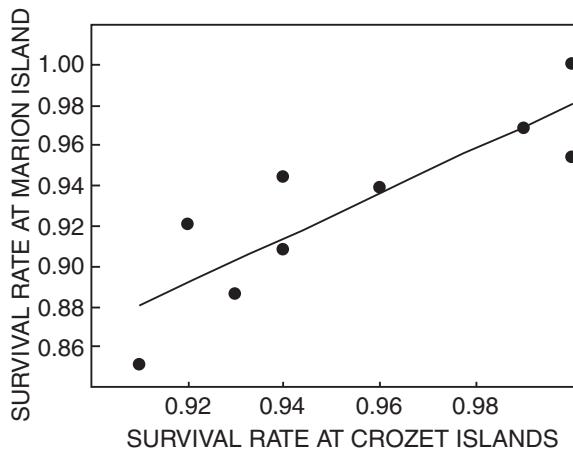


Fig 10: Relationship between annual survival rates of adult wandering albatrosses breeding on Marion Island and the Crozet Islands between 1984 and 1991 ($r = 0.818$; $p = 0.013$)

1994. However, the observed population is only the proportion of the whole population that attempts to breed in a given year. As demonstrated in this study, this proportion does not remain constant and can be affected by several factors, including: the age of first-time breeders, the number of juvenile birds that recruit into the population in a given year, and the breeding frequency of adults.

If the proportion of each age-class that attempts to breed is allowed to vary according to the measured frequency distribution of the age of first-time breeders for each year (Fig. 4), a closer fit is obtained (Fig. 11c). Adding this variable causes the trends in the predicted population to match the observed population for most of the study period, and it is only during 1997 and 1998 that the predicted population differs markedly from the observed population. These two years were the strongest ENSO years during the study, and they were also the first two years when there were large quantities of supplementary food available from toothfish longliners (Nel *et al.* 2002a, b).

Variation in the age of first-time breeders, however, does not take into account the actual numbers of first-time breeders that will recruit in a given year. As shown in Figure 5, this parameter varied substantially and was correlated with the annual maximum ENSO index, suggesting that environmental factors may cause the variation. The number of birds recruiting to the breeding population was approximated by changing the proportion of birds that breed each year by the residuals of the mean proportion of the breeding population that is made up by first-time breeders. Adding

this parameter to the model caused the predicted population to increase for 1997 and 1998 and to follow that of the observed population for the entire study period (Fig. 11d).

DISCUSSION

The size of the population of wandering albatrosses breeding on Marion Island has fluctuated considerably over the past three decades. These fluctuations are similar to those recorded on other southern Indian Ocean islands (Weimerskirch *et al.* 1997), but differ from the trend on South Georgia, South Atlantic Ocean (Croxall *et al.* 1998). These trends are compared in more detail in Nel *et al.* (2002c).

The simple modelling exercise undertaken in this study allows significant insights into the observed trends in numbers of wandering albatrosses breeding on Marion Island. First, it appears that the population was stable during the 1980s and then increased between 1989 and 1993. This increase probably resulted from improved adult and juvenile survival during the early 1990s. Arguments presented in this study suggest that the increased survival rate resulted from decreased tuna longline fishing effort (particularly by Japanese vessels) during the early 1990s. However, subsequent to 1994, observed changes in numbers of breeding birds can no longer be explained solely by changes in survival rate (and therefore the changes in the whole population size). Rather they appear to result from changes in the proportion of the population attempting to breed in a given year.

The population size and the proportion that attempts to breed on Marion Island appear to be products of both environmental and anthropogenic effects. First, the proportion of first-time breeders breeding in the study colonies was correlated with the maximum ENSO index. Improved foraging attributable to changes in environmental variables could enable more young birds to attain a body condition that will allow them to breed for the first time. The physical mechanism behind a possible link between ENSO (as measured in the eastern equatorial Pacific Ocean) and foraging conditions in the southern Indian Ocean is unknown, but ENSO events are known to affect climate patterns at a global scale. White and Peterson (1996) described an Antarctic Circumpolar Wave of surface air pressure, sea surface temperature and wind stress, which appeared to be linked to *El Niño*. Such mechanisms could affect the availability of food resources as well as the ability of birds to find food. For instance, increased wind stress may allow large procellariiforms (which are reliant on wind for flight) to forage more efficiently, and thus increase net body condition more

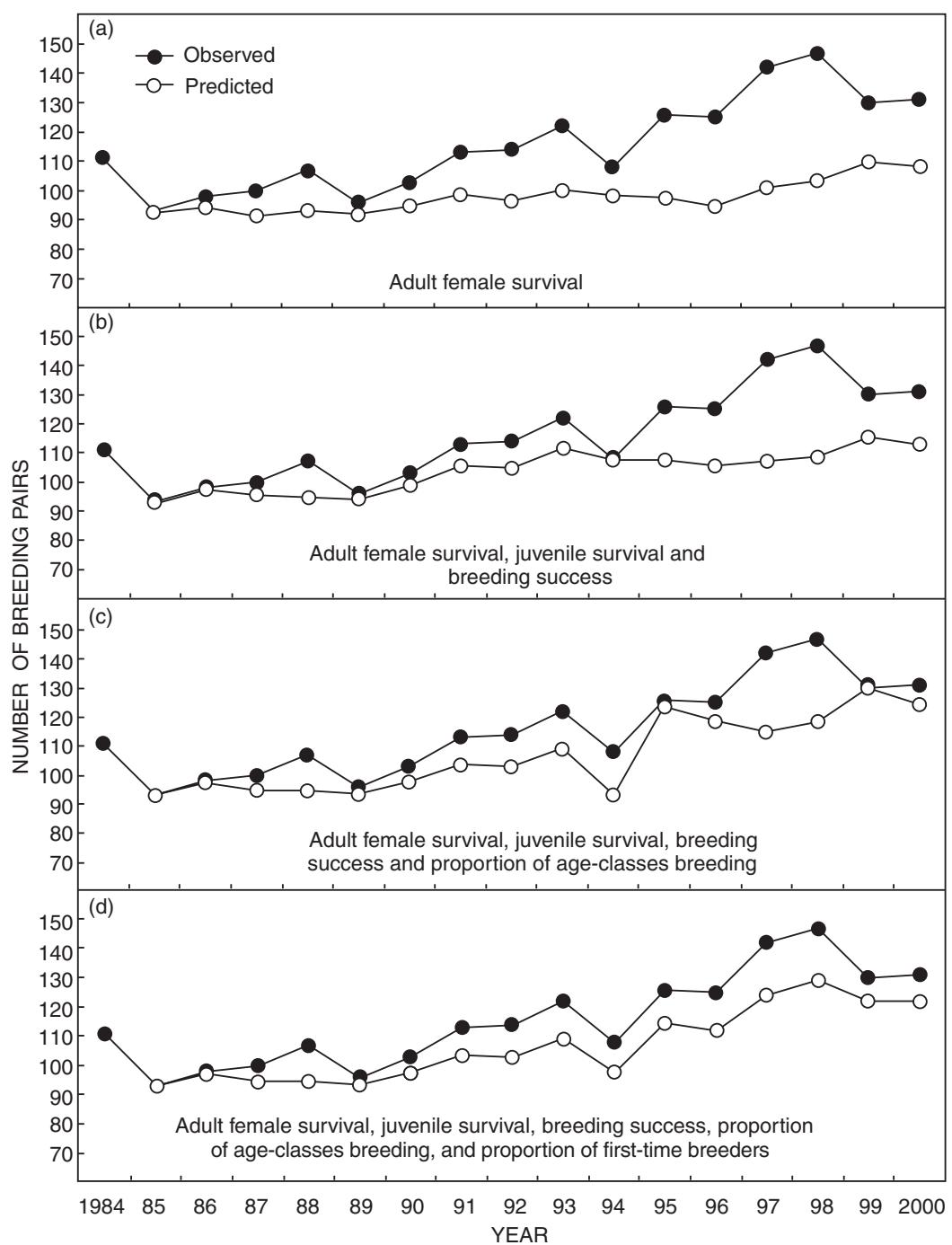


Fig. 11: Comparison between observed and predicted (using age-structured models) numbers of breeding pairs of wandering albatrosses in study colonies on Marion Island. Annual parameters that were varied according to measured data are indicated for each model (a–d). Means for the study period were used for all other parameters

quickly. Cooper and Lutjeharms (1992) found a positive correlation between breeding success of Atlantic yellow-nosed albatrosses *Thalassarche chlororhynchos* and a seasonal "windiness" index at Gough Island, suggesting that wind stress can be an important factor in foraging ecology of albatrosses. Nel *et al.* (2002c) showed that the residuals of the smoothed population trends of wandering albatrosses and northern giant petrels *Macronectes halli* breeding at Marion Island also were correlated with the maximum ENSO index. The ENSO effects recorded in this study and in Nel *et al.* (2002c) were dominated by the large 1997/98 event. Further to these studies, Crawford *et al.* (2003) recorded anomalous breeding for a range of seabird species on Marion Island during the 1997/98 ENSO event, indicating that the effects were in fact widespread.

Despite relatively short datasets, the annual survival rates of adult and juvenile wandering albatrosses at Marion Island were negatively correlated with Japanese pelagic longline fishing effort in the southern Indian Ocean. The lack of a correlation with pelagic longline fishing effort closer to the Prince Edward Islands suggests that a significant proportion of the mortality being suffered by the Marion Island population occurs when birds move farther from the islands. This takes place mainly during the non-breeding (sabbatical) year of breeding adults, or during the pre-breeding juvenile years. Tracking studies have shown that non-breeding birds move farther from the islands and spend more time on the warmer pelagic tuna fishing grounds to the north of the islands (Weimerskirch and Wilson 2000, Nel *et al.* 2002a). At-sea observations suggest that juveniles also make extensive use of these warmer waters (Weimerskirch and Jouventin 1987). Juvenile wandering albatrosses were also killed more frequently than adults in the pelagic longline fisheries along the coast of Australia (Gales *et al.* 1998). In fact, four metal-banded wandering albatrosses from Marion Island have been recorded killed in pelagic longline fishing operations around Australia (Gales *et al.* 1998), an area that is only likely to be used by non-breeding birds (Nel *et al.* 2002a) or juveniles from Marion Island. However, little is known of the age and sex of birds killed in the vicinity of the Subtropical Convergence, south of Africa (Ryan and Boix-Hinzen 1998). These foraging areas are closer to Marion Island and are consequently more accessible to adult wandering albatrosses breeding on Marion Island (Nel *et al.* 2002a).

The fact that survival rates were more strongly correlated with Japanese pelagic longline fishing in the southern Indian Ocean than that of Taiwanese fleets can also be explained. Japanese longliners fish farther south (i.e. in the belt 40–45°S) than other nations, targeting more profitable southern bluefin tuna *Thunnus maccoyii* and bigeye tuna *T. obesus* (Tuck and Bulman

2001). Taiwanese pelagic longliners (the other major longline fishing entity in the Southern Ocean) mainly target albacore *T. alalunga* and fish mostly north of 40°S (Tuck and Bulman 2001).

The high survival rates observed for breeding adults from 1997 onwards are interesting, because two factors may be at play here. First, Japanese longline fishing effort started to decrease at the end of the 1990s. However, this decrease only started during 1998. More important perhaps was the development of a demersal longline fishery for Patagonian toothfish close to Marion Island during late 1996. The legal fishery for toothfish around Marion Island developed after large-scale Illegal, Unreported and Unregulated (IUU) fishing during the austral spring of 1996 (Nel *et al.* 2002b). Only one wandering albatross is known to have been killed in the legal fishery since its commencement (Nel *et al.* 2002b). However, this fishery produces large amounts of offal in the way of bycatch fish and Patagonian toothfish heads. During the 1997 season, fishery-derived items (i.e. by-catch species, toothfish heads, or fisheries litter) were recorded in 58% of all diet samples obtained from chicks, and in 76% of samples collected during the early chick-rearing period (Nel *et al.* 2002a). A large supplementary source of food close to their breeding island would not only allow breeding birds to maintain a better body condition throughout the breeding season, but could also cause birds to spend more time close to the islands and less time in the waters of the Subtropical Front, where the risk of mortality on pelagic longlines is far greater (Ryan and Boix-Hinzen 1998). These combined effects could result in the higher survival rates of adults observed since 1997. The negative trend in breeding success recorded since 1984 also appears to halt at the end of 1996, and may have even increased slightly since 1997 (Fig. 2). This could also be a result of a supplementary source of food closer to the island. However, the advantages of this supplementary source of food for chicks may have been offset in part by the large amount of fisheries litter (i.e. ropes and hooks) that the chicks accumulated (Nel and Nel 1999).

The increase in the number of younger birds that attempted to breed since 1997 may also be the result of supplementary sources of food (in the form of offal from toothfish longliners) being available close to the island. This would allow younger birds to attain breeding condition, which they might not have been able to do under natural conditions. A decrease in the age of first-time breeders will result in a higher proportion of the whole population that is breeding. Counts of breeding birds (the most frequently used indicator of population trends) would therefore give the mistaken impression that the population had increased, when in fact it was just the proportion of birds breeding that

Table III: Comparison of demographic parameters recorded for the three largest populations of wandering albatrosses

Population	Frequency (%)		
	Adult annual survival (post 1980)	Juvenile recruitment (cohorts)	Breeding success
South Georgia ¹	92.0	27.5	65.6
Crozet Islands ²	95.6	38.2	68.5
Marion Island	94.2	32.9	74.6

¹ Croxall *et al.* (1998)

² Weimerskirch *et al.* (1997), Weimerskirch and Jouventin (1998)

had changed.

Survival rates of juvenile males and females did not differ, indicating that longline fishing impacts are probably similar for both sexes in this age group. This could also indicate that juveniles from both sexes forage in similar areas, so experiencing similar environmental conditions and human impacts. However, adult females suffered higher mortality than adult males. Female wandering albatrosses breeding at Marion Island foraged farther from the island and spent more time in warmer waters of the Subtropical Convergence than did males (Nel *et al.* 2002a). Females were therefore at higher risk of being killed by pelagic longline fishing vessels concentrated at the Subtropical Front, south of Africa. Males spent more time within the main toothfish longlining areas and would therefore derive the greatest benefits from feeding on offal (Nel *et al.* 2002a). The fact that males took longer to re-mate following a mate loss is also indicative of a male-biased population. The time taken for these birds to find new mates results in a significant decrease in their lifetime productivity (Jouventin *et al.* 1999), so decreasing the fecundity of the population. Unmated males have been seen to harass mated females holding nests or incubating on the Prince Edward Islands (DCN, PGR and JC pers. obs.). Such disturbance could possibly lead to females deserting nests or eggs being broken.

The correlation between adult survival rates recorded on Marion and Crozet islands and their lack of correlation with survival rates on South Georgia suggests that the two Indian Ocean populations are affected by a common underlying cause while foraging at sea. Tuck *et al.* (2001) were able to match observed trends in wandering albatrosses at the Crozet Islands using a model that predicted by-catch levels from tuna longline fishing effort. However, they were unable to match trends in the South Georgia population using this model. They concluded that the population trends on the Crozet Islands were influenced primarily by tuna longline effort, whereas the situation at South

Georgia was more complex owing to its proximity to the Patagonian Shelf of South America and the range of longline fisheries present within the foraging range of that population (Neves and Olmos 1998, Schiavini *et al.* 1998, Stagi *et al.* 1998). The similarity of population parameters recorded for the Prince Edward Islands population with those recorded at the Crozet Islands suggests that population trends on the Prince Edward Islands are also influenced primarily by pelagic tuna longline fishing effort. Average adult survival on Marion Island was similar to that on the Crozets, both being substantially higher than adult survival recorded on South Georgia since the 1980s (Table III), which suggests that South Georgia birds experience higher levels of incidental mortality. Juvenile recruitment was higher at the Crozets than at Marion and South Georgia (Table III). However, the Marion data only represent five cohorts and therefore are probably not very accurate.

Despite these apparent effects on the population, breeding conditions at the Prince Edward Islands appear to be favourable. Not only do the Prince Edward Islands maintain the largest breeding population of wandering albatrosses (Crawford and Cooper 2003), but mean breeding success is also higher than at the Crozet Islands and South Georgia (Table III). The intensity of mesoscale variability at the Subtropical Front diminishes from a peak south of Africa to a low point at about 70°E (Lutjeharms and Ansorge 2001), suggesting that the prevalence and intensity of eddies at this front would also decrease. Froneman *et al.* (1999) demonstrated higher primary productivity at the edges of warm-core eddies in this region, and Nel *et al.* (2001) showed that grey-headed albatrosses *Thalassarche chrysostoma* concentrated foraging effort around such mesoscale eddies. Marion Island's location relatively close to this highly variable part of the Subtropical Front could allow wandering albatrosses breeding on Marion Island to experience comparatively favourable foraging conditions.

Conservation of the population of wandering albatrosses breeding on the Prince Edward Islands is of great importance for the species as a whole. Improved conservation status for the species will require both concerted international and national efforts. In this regard, the signing, ratification and implementation of the Agreement on the Conservation of Albatrosses and Petrels (ACAP; Cooper and Ryan 2001) by all range states (including those countries whose vessels and/or nationals are engaged in longline fishing operations in the Southern Ocean) is strongly encouraged. South Africa acceded to this Agreement in April 2003. ACAP is expected to come into force by the end of 2003. A significant national initiative by South Africa is the production during 2003 of a draft National Plan

of Action for Reducing Incidental Catch of Seabirds in Longline Fisheries (NPOA-Seabirds), in accordance with guidelines adopted by the Committee on Fisheries of the Food and Agriculture Organization of the United Nations (FAO 1999, Cooper and Ryan 2003, Crawford and Cooper 2003). Continued monitoring of wandering albatrosses breeding at the Prince Edward Islands should also receive high national priority (Cooper and Ryan 2001, Crawford and Cooper 2003).

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A wandering albatross at Marion Island (photo B. M. Dyer)

APPENDIX 1**Numbers of wandering albatrosses banded in study colonies on Marion Island**

Year	Adults	Chicks	Total
*1976	32	357	389
*1977	1		1
*1978	4	289	293
*1979	186	109	295
*1980		61	61
*1981		15	15
*1982		84	84
*1983	6	250	256
1984	124	101	225
1985	109	72	181
1986	30	312	342
1987	209	286	495
1988	194	157	351
1989	78	135	213
1990	133	190	323
1991	80	191	271
1992	88	237	325
1993	87	195	282
1994	90	160	250
1995	66	192	258
1996	13	181	194
1997	32	193	225
1998	14	215	229
1999	9	197	206
2000	16	185	201
Total	1 601	4 364	5 965

* Denotes birds that were banded within and in the vicinity of the study colonies prior to study colonies being monitored. These birds were treated as known-history birds if they were resighted in the study colonies, but no survival or recruitment estimates were calculated prior to 1984

APPENDIX 2**Goodness-of-fit tests of the Cormack-Jolly-Seber model by wandering albatross cohort and all adult birds for the Marion Island population**

Cohort	p	Observed deviance	Expected deviance	\hat{c}
1976	0.40	277	431	0.643
1979	0.18	179	146	1.229
1980	0.11	215	189	1.136
1982	0.19	373	343	1.089
1983	0.16	222	191	1.163
1984	0.09	393	340	1.155
1985	0.02	114	79	1.434
1986	0.14	319	285	1.120
1987	0.08	268	235	1.143
1988	0.09	267	238	1.123
1989	0.10	194	167	1.166
1990	0.04	140	115	1.214
1991	0.13	83	74	1.120
1992	0.03	68	48	1.416
1993	0.01	66	41	1.592
1994	0.11	10	5	1.914
1995	—	0	0	—
All adults	0.00	9 808	8 608	1.139

p = Probability of a deviance as large or greater than the observed value

\hat{c} = Estimate of over-dispersion quasi-likelihood parameter, obtained by dividing the observed deviance by the mean of the simulated deviances (a \hat{c} of 1 denotes a perfect fit)

APPENDIX 3

Elimination of non-significant effects from the full CJS model in estimating survival probability in wandering albatrosses at Marion Island

516	Model	Akaike Information Criterion	Number of estimable parameters	Deviance
<i>Combined cohorts</i>				
(1)	$[(\phi(gt), p(at))]$	10 497	562	3 060
(2)	$[(\phi(at), p(at))]$	10 143	389	3 198
(3)	$[(\phi(t), p(t))]$	12 644	42	6 402
(4)	$[(\phi(ga), p(ga))]$	10 293	85	3 962
(5)	$[(\phi(a), p(a))]$	10 290	43	4 046
(6)	$[(\phi_{1-9}(g), \phi_{10-}(ga), p_{1-9}(g), p_{10-}(ga))]$	11 995	53	5 730
(7)	$[(\phi_{1-9}(g), \phi_{10-}(g), p_{1-9}(g), p_{10-}(g))]$	12 019	8	5 846
(8)	$[(\phi_{1-9}(c), \phi_{10-}(g), p_{1-9}(c), p_{10-}(g))]$	12 021	6	5 852
(9)	$[(\phi_{1-9}(c), \phi_{10-}(c), p_{1-9}(c), p_{10-}(c))]$	12 023	4	5 859
<i>Adult breeders only</i>				
(1)	$[(\phi(gt), p(gt))]$	21 438	84	9 808
(2)	$[(\phi(t), p(t))]$	21 414	44	9 866
(3)	$[(\phi(c), p(c))]$	22 178	2	10 715

ϕ = Apparent survival rate

ϕ_{1-9} = Apparent survival rate for Ages 1–9

ϕ_{10-} = Apparent survival rate for Ages 10 and older

p = Recapture probability

p_{1-9} = Recapture probability for Ages 1–9

p_{10-} = Recapture probability for Ages 10 and older

g = Sex

a = Age

t = Time

c = Constant

EXCHANGE OF THE WANDERING ALBATROSS *DIOMEDEA EXULANS* BETWEEN THE PRINCE EDWARD AND CROZET ISLANDS: IMPLICATIONS FOR CONSERVATION

J. COOPER* and H. WEIMERSKIRCH†

Exchange of 61 wandering albatrosses *Diomedea exulans* has been recorded between the French Crozet Islands and the South African Prince Edward Islands, 1 068 km apart in the Southern Ocean. Most movements of banded birds (57) have been westwards, from the Crozets to the Prince Edwards. In all, 18 fledglings banded at Possession Island, Crozets, have bred at Marion Island, Prince Edwards, but only one fledgling from Marion Island has been recorded breeding on Possession. The wandering albatrosses of the two island groups form a metapopulation that ideally should be conserved as a single unit. It is suggested that France and South Africa collaborate through the Agreement on the Conservation of Albatrosses and Petrels to effect an improved conservation status for the wandering albatrosses of the two island groups.

Key words: conservation, *Diomedea exulans*, metapopulation, movements, Prince Edward and Crozet islands, Subantarctic

Banding of seabirds in the Southern Ocean has been undertaken both for demographic purposes and to elucidate movements away from breeding sites (e.g. Weimerskirch *et al.* 1985, 1997). With the advent of satellite-tracking and other data-acquisition devices (e.g. Jouventin and Weimerskirch 1990, Prince *et al.* 1992, Nicholls *et al.* 1995, Nel *et al.* 2002b), banding recoveries have become less important for understanding where seabirds (at least those large enough to carry devices) go when not at their breeding islands. However, recapturing banded birds is probably still the best way to study movements of birds (and thus immigration and emigration) between breeding populations (Weimerskirch *et al.* 1997).

The population dynamics of the wandering albatross *Diomedea exulans* have been studied at Marion Island, Prince Edward Islands, southern Indian Ocean, since 1984, by way of following banded individuals in study colonies (Nel *et al.* 2003). A similar study (commencing in the 1960s) is carried out at Possession Island, Crozet Islands (Weimerskirch *et al.* 1997). These studies show that the two populations have similar population dynamics and trends, thought due to being exposed to similar levels of mortality from longline fisheries in the Southern Ocean (Weimerskirch and Jouventin 1987, Weimerskirch *et al.* 1997, Nel *et al.* 2002a, b, 2003).

The two island groups are 1 068 km (great circle distance) apart and movements of wandering albatrosses between them have been reported for more than a quarter of a century (Mougin 1977, Gartshore

et al. 1988). Weimerskirch *et al.* (1997) analysed records of 27 French-banded birds recaptured at Marion Island and showed that most were females, and that they included eight chicks banded at Possession which bred at Marion, showing true immigration. In contrast, they reported no Marion-fledged birds breeding at Possession. Since this analysis, the number of recorded movements between the two islands has more than doubled and, for the first time, a Marion Island fledgling has been recorded breeding at Possession Island. This paper updates the known information on inter-island movements of the wandering albatross metapopulation (Inchausti and Weimerskirch 2002) between the two island groups and considers how best to improve the species' conservation status at both.

METHODS

On an annual basis, breeding and non-breeding adult and fledgling wandering albatrosses at Marion Island (290 km²; 46°54'S, 37°45'E) from 1976 and at Possession Island (146 km²; 46°25'S, 51°45'E) from 1960 have been banded and checked for bands at various levels of intensity, as described by Weimerskirch *et al.* (1997) and Nel *et al.* (2003). A total of 5 965 wandering albatrosses (1 601 adults, 4 364 fledgelings) was banded at Marion Island over the period 1976–2000 (Nel *et al.* 2003). No wandering albatrosses

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have been banded at Prince Edward Island (44 km^2 ; $46^\circ 38' \text{S}$, $37^\circ 57' \text{E}$). At both Marion and Possession islands, annual counts of all incubating birds are undertaken. A survey of the wandering albatross population of little-visited Prince Edward Island was undertaken in December 2001 (Ryan *et al.* 2003), during which most of the birds occupying a total of 1 687 nests were checked for bands.

All foreign bands found were carefully recorded and information exchanged via the South African and French banding schemes and by direct correspondence between the authors, creating a single, validated dataset, which was further checked against and augmented by published records (Berruti *et al.* 1975, Barré *et al.* 1976, Burger and Morant 1977, Mougin 1977, Brown and Oatley 1982, Weimerskirch *et al.* 1985, Gartshore *et al.* 1988).

RESULTS

Since banding commenced at the two islands, a total of 57 Possession-banded wandering albatrosses (28 sexed as females, 15 as males) has been recaptured at the Prince Edward Islands (55 at Marion Island and two, one of which was dead, at Prince Edward Island). Age-class at banding is unknown for one French-banded bird recaptured as a breeding male at Marion Island. This bird has therefore been left out of the following analyses.

A total of 29 birds (14 females, 8 males, 7 unsexed) banded as chicks at Possession Island has been recaptured at Marion Island. Of these, 18 (7 identified as females, 6 as males) have been recorded breeding. A few birds that bred within study colonies have been recorded breeding up to seven times, but most have been recorded breeding only once or twice. Years elapsed to first breeding records range from 7 to 28 years (average 12.7 ± 5.3 years), with no significant difference between the sexes. A temporal analysis grouping first-breeding records into five-year periods showed no discernible difference between the sexes, although the sample was small. Most first-breeding records date from the 1990s, with only one earlier, a female, in 1975 (Mougin 1977). Five Possession fledglings (4 females, 1 male) recaptured at Marion as non-breeders have been subsequently recorded at Possession Island, four as breeding birds.

A further 27 birds (14 females, 5 males) banded as adults at Possession Island (26 as non-breeders and presumed to be immatures) have been recorded at the Prince Edward Islands (25 at Marion, 2 at Prince Edward). Of these, 17 (9 identified as females, 4 as males) have been recorded subsequently breeding at

Marion Island. Two of these birds had previously been recorded breeding at Possession Island, one male with an intervening gap of 31 years, the second a female with an interval of 17 years.

Overall, 35 (61%) of the 57 birds banded at Possession have been recorded breeding (incubating or attending a chick) at Marion Island. This total, which includes 16 females and 10 males, does not include a number of birds variously reported as displaying, with a partner or attending an empty nest, so the actual percentage that has bred is likely to be somewhat higher.

Nine (0.63%) of 1 426 incubating wandering albatrosses checked at Marion Island in January 2003 carried bands attached at Possession Island.

In contrast, only four wandering albatrosses banded at Marion Island have subsequently been recorded at Possession Island. Three Marion fledglings were recaptured (two once each, the third twice) as non-breeders aged 5–7 years in the mid-1980s (Gartshore *et al.* 1988). A fourth bird, a female, banded as a chick at Marion was found breeding on Possession aged 7 years in 2002. No birds banded as non-breeders at Marion Island have yet been recaptured at Possession Island.

DISCUSSION

The annual breeding populations of wandering albatrosses at Marion and Possession Islands have fluctuated over the periods of their study (Weimerskirch *et al.* 1997, Woehler *et al.* 2001, Nel *et al.* 2002a). The most recent counts made in the 2001/02 and 2002/03 breeding seasons give annual populations at Marion of 1 869 and 1 593 pairs respectively (Crawford *et al.* 2003), and at Possession of 394 pairs in 2002/03 (HW unpublished data), only a quarter of that at Marion in the same season. The annual breeding population at Prince Edward Island was estimated as 1 850 pairs for the 2001/02 season (Ryan *et al.* 2003). The total annual breeding population of the Crozet Islands is 1 734 pairs (Weimerskirch and Jouventin 1987), approximately half that of the Prince Edward Islands.

Movements of wandering albatrosses between the two island groups are not easy to interpret. For example, it cannot be assumed that all Possession-banded non-breeders fledged from that island; their numbers may include Marion fledglings that visited Possession as non-breeders, when they were caught and banded. However, given that 57 Possession birds have been recorded as making the westward journey to the Prince Edward Islands, compared with the four from Marion that moved east to Possession, it is reasonable to assume that the majority of the Possession-

banded birds did indeed fledge from that island. This fits the fact that some of these birds commenced breeding at Possession (and thus their assumed natal island) after visiting Marion without being recorded breeding there. This assumption is partially confounded by known or likely differences in banding effort (few non-breeding wandering albatrosses are banded at Marion Island) and search intensity, and by the important fact that, whereas Marion Island supports approximately half the wandering albatrosses of the Prince Edward Island group, Possession Island supports only 20% of the total Crozet wandering albatross population. This means that, even at similar search intensities at the two islands where research programmes exist, the chances of finding west-moving birds is far higher than the reverse. If birds prefer to recruit to islands with larger colonies (as the preponderance of movements from Possession to Marion might suggest), then it may be that more Marion-banded birds have also visited, and perhaps recruited to, Ile au Cochons in the Crozet group, which supported 1 060 wandering albatross pairs in 1981 (Weimerskirch and Jouventin 1987), than have done so to Possession, with its markedly smaller population.

Even with the above imponderables, it seems clear that most inter-island group movements, and importantly breeding interchanges, have been in a westerly direction to Marion Island. Further, most movements have been by females, as shown by Weimerskirch *et al.* (1997) for a smaller sample. However, given that males are more faithful to natal sites when recruiting to breed than are females (Weimerskirch *et al.* 1997 for Possession Island, unpublished data for Marion Island), the fact that 35% (15/43) of sexed Possession-banded birds recaptured at Marion Island were males is notable, as are the essentially equal numbers (7 females, 6 males) of Possession fledglings that moved to breed at Marion. With the exception of the 1970s female that made this movement in the 1970s (Mougin 1977), all breeding interchanges have taken place from the 1990s onwards. It might be postulated that an unequal sex-bias in longline-fishing mortality, which is assumed to have caused a preponderance of males in the population in the past few decades (Weimerskirch and Jouventin 1987, Nel *et al.* 2002a, 2003), has led to an increasing number of pre-breeding males in recent years being unable to find partners at their natal island, in turn causing them to emigrate to another island, where its larger population makes it more likely that a partner will be found. However, an increased search effort at Marion Island in the 1990s than earlier confounds this assumption to a degree.

Records of individual birds breeding at both island groups are unexpected for a species that shows high fidelity to its first breeding site (Weimerskirch *et al.*

1997 for Possession, unpublished data for Marion Island). Weimerskirch *et al.* (1997) report three females that bred on two different islands in the Crozet Islands, but the two birds reported here appear to be the first records of individual wandering albatrosses breeding at two different island groups, in this case a little over 1 000 km apart.

The average age of known first breeding of 12.7 years is more than the overall 9.9 years recorded at Marion Island (Nel *et al.* 2003), but closer to the overall 11.4 years reported for Possession Island (Weimerskirch and Jouventin 1987). Because few Possession fledglings recruited to study colonies at Marion Island, some may have been overlooked as breeding birds prior to their first recapture, leading to an increased figure.

Based on the level of breeding interchange, the wandering albatrosses of the Prince Edward and Crozet Island groups may be regarded as forming a metapopulation (Inchausti and Weimerskirch 2002). On the evidence presented, there appears to be an ongoing net movement of wandering albatrosses from Possession to Marion, although it is as yet not known if this applies to the two island groups as a whole. Given the Vulnerable status of the species (BirdLife International 2000), it is recommended that this metapopulation should be conserved as single unit. This will require collaboration between the French and South African authorities holding responsibility for managing the islands and their biota, including the wandering albatross, as well as between the scientists studying the species at the two island groups. Some level of sharing of research and management information between France and South Africa already takes place within several international fora, notably the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR), mainly through its *ad hoc* Working Group on Incidental Mortality Arising from Fishing (WG-IMAF; SC-CAMLR 2002) and through the Scientific Committee on Antarctic Research's now-named Group of Experts on Birds (Woehler *et al.* 2001, SCAR-BBS 2002). Scope for further collaboration exists via the Food and Agriculture Organization of the United Nations' International Plan of Action for Reducing Incidental Catch of Seabirds in Longline Fisheries, which recommends the production of National Plans of Action (NPOA-Seabirds; FAO 1999, Cooper *et al.* 2001).

However, perhaps the most promising forum for coordinating research and management of wandering albatrosses at the Crozet and Prince Edward islands is via the Agreement on the Conservation of Albatrosses and Petrels (ACAP) of the Bonn Convention on Migratory Species (Cooper and Ryan 2001, www.ea.gov.au/coasts/species/seabirds/albatross). South Africa has

ratified the Agreement (Crawford and Cooper 2003), but France has not yet ratified (Anon. 2001, 2003). ACAP is expected to come into force during the course of 2003, three months after five countries have ratified it. It is suggested that France and South Africa could produce a joint background paper for the first Meeting of Parties of ACAP, expected to be held in 2004, that sets out how they may work together to improve the conservation status of their shared metapopulation of wandering albatrosses. This paper could also consider the other species of procellariiform seabirds included within ACAP, some of which may also form metapopulations shared by the two island groups, based on observations of interchange of banded individuals, such as of the southern giant petrel *Macronectes giganteus* (Crawford and Cooper 2003). The paper could cover such matters as joint and/or shared sea patrols to detect and deter Illegal, Unreported and Unregulated (IUU) fishing by longline vessels within the island groups' Exclusive Economic Zones (EEZs), perhaps by way of a joint Plan of Action (FAO 2001); developing and adopting NPOA-Seabirds with similar regulations to enforce the use of mitigation measures by longline fisheries; sharing information and ideas in relation to producing management plans for the island groups; considering the feasibility and value of declaring marine protected areas surrounding the two island groups; and the exchange of ornithologists and managers between the two countries.

South Africa has produced a draft NPOA-Seabirds and is in the process of reviewing its management plan for the Prince Edward Islands (Cooper and Ryan 2002, Crawford and Cooper 2003). Of course, such collaboration as mooted here could lead to improvements in the conservation status of the other species of co-occurring albatrosses, as well as all the seabirds that breed at both island groups. All such activities would be more likely to bear fruit once the Agreement on the Conservation of Albatrosses and Petrels comes into force.

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A wandering albatross with its chick at Marion Island (photo L. Upfold)

THE OLDEST KNOWN BANDED WANDERING ALBATROSS *DIOMEDEA EXULANS* AT THE PRINCE EDWARD ISLANDS

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The oldest known wandering albatross *Diomedea exulans* at the Prince Edward Islands is estimated to have been approximately half a century old when last recaptured in 2001. Demographic studies need to continue for several more decades before the true maximum longevity of the species becomes evident.

Key words: banding, *Diomedea exulans*, maximum longevity, Prince Edward Islands, Subantarctic, wandering albatross

How long animals are able to live in the wild has always been a matter of some fascination to biologists and non-biologists alike, especially for those few species that are known or are thought to have the ability to live longer than humans. Bird banding, or ringing, has long been used to obtain maximum longevity records for birds (e.g. Rydzewski 1978, Staav 1998, 2001), but for some extremely long-lived species, most banding schemes have not been operating long enough with hard-wearing bands to be certain that reliable information on maximum longevity has been obtained.

The first wandering albatrosses *Diomedea exulans* to carry modern metal numbered bands carrying a return address, 27 in number and including both adults and fledglings, were banded at subantarctic Marion Island in the Prince Edward Islands group, southern Indian Ocean in 1951 by R. W. Rand, a pioneer South African marine biologist (Rand 1952). His early efforts were followed in 1954, when a further 114 birds were banded at Marion Island (Berruti *et al.* 1975, South African Bird Ringing Unit [SAFRING] records). Banding of wandering albatrosses followed at Kerguelen Island (1952), Macquarie Island (1954), Bird Island, South Georgia (1958) and Iles Crozet (1960; Sladen *et al.* 1968, Tickell and Gibson 1968, Battam and Smith 1983, de la Mare and Kerry 1994). In July 1956, banding of birds caught at sea commenced off the coast of New South Wales, Australia (Gibson and Sefton 1959). These early banding efforts used aluminium bands, which wore easily and so relatively few long-term recoveries ensued. For example, only one of the 1950s-banded wandering albatrosses from Marion Island was subsequently reported, after having been caught alive (and released) five years later off Australia (McLachlan 1964, Berruti *et al.* 1975, Anon. 1977).

Research on wandering albatrosses recommenced at Marion Island in 1960/65, when 650 birds were marked with aluminium US Fish & Wildlife bands (Sladen *et al.* 1968). A number of these birds has been subsequently reported (Berruti *et al.* 1975, Brown and Oatley 1982, Gartshore *et al.* 1988, SAFRING records). A few birds were marked with monel bands in the early 1970s. In 1975, marking of wandering albatrosses continued at Marion Island with stainless steel bands, followed with the addition of plastic alphanumeric bands from 1984 as part of an ongoing demographic study (Nel *et al.* 2003). By 2000, more than 8 000 had been marked with stainless steel bands. During this time, banding of wandering albatrosses has continued off the coast of Australia and a number of these birds has now been recaptured at Marion Island and at nearby Prince Edward Island, as have birds banded at Possession Island, Crozet Islands (Gartshore *et al.* 1988, Cooper and Weimerskirch 2003, SAFRING records).

Based on the above datasets, the oldest known wandering albatross at the Prince Edward Islands is reported and the bird's age is compared with what is known of maximum longevity of the species from studies conducted elsewhere and of albatrosses in general.

MATERIAL AND METHODS

On an annual basis, breeding wandering albatrosses are checked for bands at Marion Island (290 km^2 ; $46^{\circ}52'S$, $37^{\circ}51'E$) as part of a complete count of incubating pairs (Nel *et al.* 2003). The island's annual populations were 1 869 pairs in 2001 and 1 593 in 2002

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(Crawford *et al.* 2003). In December 2001, an expedition to uninhabited Prince Edward Island (44 km²; 46°38'S, 37°57'E) surveyed its population of wandering albatrosses, and many birds occupying nest sites prior to egg-laying of an estimated population of 1 850 pairs were checked for bands (Ryan *et al.* 2003). All "foreign-banded" birds were reported to their respective banding schemes by direct contact with researchers and through SAFRING, Avian Demography Unit, University of Cape Town, to obtain primary banding data and elapsed times and thus information on maximum longevity.

RESULTS

The oldest banded wandering albatross recaptured at the Prince Edward Islands to date is a male, observed on 18 and 19 December 2001 bearing Australian Bird and Bat Banding Scheme band number 140-25350, while occupying a fresh but empty nest on the east side of Albatross Valley, Prince Edward Island, near the edge of the sea cliff. The bird was originally banded (as 140-03339) on 24 July 1960, 41 years and four months previously off Austinmer, New South Wales, Australia (34°18'S, 150°58'E) by D. Gibson of the then New South Wales Albatross Group (now the Southern Oceans Seabird Study Association – SOSSA) as an adult male (culmen 177 mm) of unknown age with a Gibson Code Index (Gibson 1967) of 14, corresponding to an age of 5–10 years. Thus, the bird, when recaptured in 2001, was aged an estimated 46–51 years. 140-25350 is currently the oldest banded bird in the records of both the Australian and South African banding schemes.

Between the above two dates, the bird has been recaptured five times in New South Wales waters – in August 1966 (when its band was replaced), July 1970, August 1985, August 1989 and July 1994 (SOSSA records) and once with a chick in Albatross Valley, Prince Edward Island, in April 1973 (Anon. 1973, Berruti *et al.* 1975, Grindley 1981). During this time, its Gibson Code increased from 14 in 1960, to 19 in 1966, 20 in 1970 and 21 (the highest score possible; Gibson 1967) in 1985, 1989 and 1994.

DISCUSSION

Because of the problem of band loss from birds marked in the early years, no wandering albatross originally banded at the Prince Edward Islands has as yet attained

a known age of >40 years. However, such birds are likely to be recorded in future because stainless steel bands placed on birds from the 1970s show very little sign of wear and therefore should be able to last for many more decades. A wandering albatross, known to have bred at the Crozet Islands, was recovered 39 years after banding as an adult in 1960 and was estimated to be at least 50 years old when it died (Weimerskirch and Wilson 2000). Wandering albatrosses banded as adults in the early 1960s are still being recaptured on Bird Island, South Georgia, and are therefore also likely to have reached a half-century (J. P. Croxall, British Antarctic Survey, UK *in litt.*).

Other albatross species have been recorded as reaching more than a half-century in age. A Laysan albatross *Phoebastria immutabilis* banded as a breeding adult in 1956 (at at least five years old) was recaptured, still breeding, in February 2002 at an estimated age of at least 51 years (Robbins 2002). This bird, which has been re-banded no less than four times over the years, is now the oldest banded bird in the records of the North American banding scheme. However, the oldest known albatross is a northern royal albatross *Diomedea sanfordi*, which bred at Taiaroa Head, New Zealand, and reached an estimated age of at least 61 years by the last time it was recorded (rearing a chick) in 1989, 51.5 years after being originally colour-banded as a breeding adult at an estimated minimum age of 10 years by L. E. Richdale in 1937 (Robertson 1993). Indeed, that author conjectured that maximum age for this species may approach 100 years, with 1% of the population estimated to survive to 80 years.

It seems clear that albatrosses are among the oldest, if not the oldest, lived birds. However, the long-term demographic studies underway on the wandering albatross at several localities will need to continue for a few more decades before we can safely answer with authority the question posed by D. Gibson in 1967: how long do wandering albatrosses live?

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Wandering albatrosses at Prince Edward Island (photo R. J. M. Crawford)

NEST DENSITIES OF THE WANDERING ALBATROSS *DIOMEDEA EXULANS* AT THE PRINCE EDWARD ISLANDS, ESTIMATED USING GPS

L. G. UNDERHILL*, S. L. PETERSEN*† and J. COOPER*

Hand-held Global Positioning System (GPS) receivers provide opportunities for detailed and rapid mapping of features, including biological ones, further enhanced by the removal during 2000 of “selective availability”. GPS was used to map, describe and compare nest densities within wandering albatross *Diomedea exulans* colonies at subantarctic Marion and Prince Edward islands. On Prince Edward Island, the coordinates of 1 061 wandering albatross nests were determined and, on Marion Island, 1 779 nests. For describing nest densities of wandering albatrosses, a 50-m grid is recommended, at which scale, the densest area of Prince Edward Island was in Albatross Valley, where the area of the colony was 46 ha and nest density was 22.3 nests ha⁻¹. For Marion Island, the total area of the wandering albatross colonies was 306 ha and the nest density was 5.8 nests ha⁻¹. In the three study colonies there (Macaroni Bay, 28 nests; Sealer's Beach, 117 nests; Goney Plain, 140 nests), the density statistics did not differ greatly from the overall densities on the island, with overall mean densities of 4.9, 5.7 and 8.0 birds ha⁻¹ respectively. Although comparisons with nest densities at other breeding colonies are uncertain because of differing methods of computing them, the nest densities in Albatross Valley lie within the reported ranges for other colonies of great albatrosses.

Key words: *Diomedea exulans*, GPS, nest density, Prince Edward Island, Subantarctic, wandering albatross

The availability of relatively cheap hand-held Global Positioning System (GPS) receivers from the 1990s opened new opportunities for detailed and rapid mapping of features, including biological ones. These opportunities were further enhanced by the removal, on 2 May 2000, of “selective availability” by the United States Department of Defense, whereby position fixes had been substantially degraded.

Most species of seabirds breed in colonies. For some ground-nesting species, nests may be so closely packed that breeding birds are within pecking distance of their nearest neighbours. In such cases, maximum density is achieved by hexagonal packing, as shown for royal terns *Sterna maxima* and African penguins *Spheniscus demersus* (Buckley and Buckley 1977, Siegfried 1977). In contrast, other ground-nesting seabirds breed at much greater inter-nest distances, in what might be called loose colonies. Examples of such species include the great albatrosses of the genus *Diomedea* (Warham 1990, Tickell 2000).

Scott (1993) analysed the distribution of nest sites of the wandering albatross *D. exulans* using triangulation data collected with a Vickers Instruments prismatic compass in three long-term study colonies at subantarctic Marion Island, Prince Edward Islands, in the southern Indian Ocean, whose boundaries had been previously surveyed trigonometrically. The error ellipses of nest positions were unsatisfactorily large,

probably on account of the difficulties of obtaining accurate data with a hand-held compass in often windy conditions, so the approach failed to produce results considered useful.

Albatross Valley, on the east coast of Prince Edward Island, 21 km from Marion Island, supported 1 182 pairs of wandering albatrosses in December 2001 (Ryan *et al.* 2003). It is reputed to have the largest nest density of any colony of wandering albatrosses in the world, but hitherto, no density data have been available for this little-visited island. The main objective of this study is to describe and compare nest densities within wandering albatross colonies at Marion and Prince Edward islands obtained by use of a GPS receiver. The aim is also to provide guidelines for the use of GPS receivers for measuring densities of birds in loose colonies.

MATERIAL AND METHODS

Prince Edward Island (44 km²; 46°38'S, 37°57'E) was visited under special entry permit from 17 to 22 December 2001 (Ryan *et al.* 2003). Among other objectives, all wandering albatross nests in Albatross Valley belonging to the 2001/02 breeding cohort were counted; the handful of remaining chicks from

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Table I: Densities and other statistics relating to the nest densities of wandering albatrosses at the Prince Edward Islands in the 2000/01 breeding season

Parameter	Albatross Valley 1 030 nests			Albatross Valley (offset) 1 030 nests			Colony near R.S.A. Point 28 nests		
	25 m 16	50 m 4	100 m 1	25 m 16	50 m 4	100 m 1	25 m 16	50 m 4	100 m 1
<i>Density (nests ha⁻¹)</i>									
Lower quartile	16	8	3	16	4	3	16	6	2.2
Median	32	16	7.5	32	12	8	16	8	4
Upper quartile	48	28	19.5	48	32	20	32	12	5.8
Maximum 1	176	124	60	192	92	61	48	24	10
Maximum 2	176	96	59	176	92	50	48	24	6
Maximum 3	160	88	51	176	88	49	32	12	5
Maximum 4	160	88	50	176	80	44	32	12	4
Maximum 5	160	84	44	160	72	38	32	8	3
Maximum 6	160	84	43	160	68	36	32	8	2
Maximum 7	160	80	36	160	68	34	32	8	1
Maximum 8	144	80	34	144	68	34	32	8	
Maximum 9	144	72	34	144	68	30	16	8	
Maximum 10	144	72	29	128	68	30	16	4	
<i>Other statistics</i>									
Number of occupied quadrats	399	185	76	394	191	75	21	12	7
Area (ha)	24.9	46.2	76	24.6	47.8	75	1.3	3	7
Mean density	41.4	22.3	13.6	41.9	21.6	13.7	23.6	10.3	4.4
Smallest number of quadrats containing 50% of the total for colony	88	33	14	91	35	15	8	5	3
Area of these quadrats (ha)	5.5	8.2	14	5.7	8.5	15	0.5	1.2	3
Density within these quadrats	93.6	62.4	36.8	90.6	60.6	34.4	31.0	12.4	5.2

the 2000/01 cohort that had not yet fledged were ignored (Ryan *et al.* 2003). On 20 and 21 December 2001, 18 months after the removal of selective availability, a stand-alone handheld GPS receiver (Garmin II+) was used by LGU to record the position of the nests of as many of the 2001/02 cohort of wandering albatrosses in Albatross Valley as could be visited in the time available. To avoid unnecessary disturbance to the birds, observations were offset by 2 m to the east of the actual nest sites. Each nest was marked as having had its position recorded by making a small hole in the ground at this point with a pole. Two small clusters of nests, isolated from the remainder of the colony, could not be reached, and two clusters of nests in the valley west of R.S.A. Point were also recorded.

Coordinates were recorded to a thousandth of a minute; at the latitude of the Prince Edward Islands, these represent 1.8 m of latitude and 1.3 m of longitude. However, the accuracy is not as fine as this, and, even with the removal of selective availability, errors in coordinates with handheld GPS units are approximately an order of magnitude larger (Merry 2000; see Discussion).

On Marion Island (290 km²; 46°38'S, 37°57'E), SLP similarly recorded the positions of wandering albatross nests between 27 December 2001 and 12 April 2002 using a GPS receiver (Garmin 12XL) as part of a complete round-island count of nesting birds and other fieldwork.

The geographical coordinates were transformed into rectangular coordinates in metres, using the relationship that one minute of latitude is 1 852.3 m and one minute of longitude is 1 271.8 m at the latitude (46°37'S) of Albatross Valley; these distances were computed using the algorithm of Imboden and Imboden (1972). On Marion Island, one minute of longitude averaged 1 265.3 m.

A rectangular grid, in metres, was used to map the colonies. Nest counts per quadrat were computed using quadrats with sides 25, 50 and 100 m. To make the counts independent of quadrat size, counts were expressed as nests per hectare (ha) by multiplying by 16, 4 and 1, for the quadrats with sides 25 m (area 0.0625 ha), 50 m (0.25 ha) and 100 m (1 ha) respectively. For those quadrats that contained at least one nest, summary statistics (mean, median, quartiles)

were computed. For Albatross Valley alone, for the colony near R.S.A. Point, for Marion Island as a whole and, for each of the three study colonies on Marion Island, Macaroni Bay, Sealer's Beach and Goney Plain, the 10 largest densities for each quadrat were determined. In addition, colony size was estimated as the area of the quadrats containing at least one nest (the "area of occupancy"). The minimum number of quadrats that held 50% of the nests was computed, so the density within the densest part of the colony could be estimated.

Clearly, a different placement of the grid would generate slightly differing values. To obtain an idea of the extent to which this is an important consideration, the analyses for Albatross Valley were repeated with the grid offset by 50 m for the 100-m grid, 25 m for the 50-m grid, and by 12.5 m for the 25-m grid.

RESULTS

The coordinates of 1 059 wandering albatross nests on Prince Edward Island were determined, of which 1 030 were in Albatross Valley (87% of the 1 182 counted during the December 2001 survey, Ryan *et al.* 2003), 28 near R.S.A. Point and one near Cave Bay. On Marion Island, 1 779 nest positions were determined, 95% of the total population of 1 869 occupied nests (Crawford *et al.* 2003), spaced around the whole island.

At the three grid scales examined, the largest densities were obtained in Albatross Valley (Table I). When a 100-m grid, generating 1-ha quadrats, was placed over Albatross Valley (Fig. 1), 76 of the quadrats contained at least one nest, and the maximum density in any single quadrat was 60 nests ha⁻¹. With 50- and 25-m grids (0.25-ha and 0.0625-ha quadrats), the maximum nest counts per quadrat were 31 and 11 respectively, equivalent to maximum densities of 124 and 176 nests ha⁻¹ respectively (Table I).

In all, 71 of the 1-ha quadrats in Albatross Valley contained at least one nest, yielding a total colony area of 76 ha. At this grid scale, there were no quadrats without nests that were entirely surrounded by quadrats with nests (Fig. 1). With 50- and 25-m grids, 185 and 399 quadrats contained nests, and the colony areas were 46.2 and 24.9 ha respectively. For those quadrats that contained at least one nest, the overall average nest densities were 13.6, 22.3 and 41.4 nests ha⁻¹ for the 1-, 0.25- and 0.0625-ha quadrats respectively (Table I).

The results obtained when the grids were offset by half the length of the quadrat were similar to the ori-

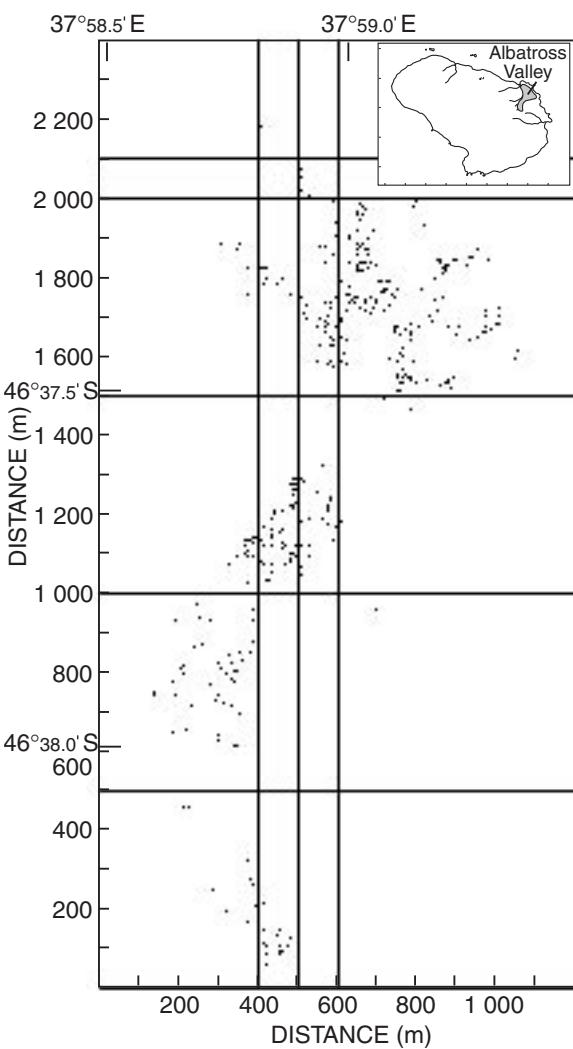


Fig. 1: Location of wandering albatross nests in Albatross Valley on Prince Edward Island, overlaid with a 100-m grid. The line $y = 0$ corresponds to $46^{\circ}38.3101^{\circ}\text{S}$, the line $y = 2\ 400$ to $46^{\circ}37.0151^{\circ}\text{S}$, the line $x = 0$ to $37^{\circ}58.4952^{\circ}\text{E}$ and the line $x = 1\ 200$ to $37^{\circ}59.4386^{\circ}\text{E}$. No digital map is available to insert coastline or rivers

nal results for Albatross Valley (Table I). These offset results are not considered further.

Using 100-, 50- and 25-m grids, the numbers of occupied grid cells (and their areas) on Marion Island were 757 (757 ha), 1 224 (306 ha) and 1 531 (95.7 ha)

respectively. The respective overall densities (nests ha⁻¹) were 2.43, 5.81 and 18.6 (Table II). In the three study colonies on Marion Island, at Macaroni Bay, Sealer's Beach and Goney Plain, the density statistics did not differ greatly from the overall densities on the island (Tables II and III). Nest densities in the small colony near R.S.A. Point on Prince Edward Island were larger than in these study colonies (Table I).

DISCUSSION

Accuracy of GPS coordinates

The main sources of error (and their approximate standard deviations, *SD*) of the accuracy of horizontal GPS coordinates are satellite orbit (5 m), satellite clock (5 m), ionospheric refraction (5–15 m), tropospheric refraction (0.5–2 m), multipath reflection (0–10 m) and receiver resolution (0.1–2 m; Merry 2000). Assuming no correlation between these error sources, the anticipated minimum and maximum overall *SDs* are 8.7 and 18.9 m respectively (computed from the square root of the sum of squares of the *SDs*). Assuming a normal distribution, this is interpreted as meaning that, at best, a circle with radius 8.7 m centred on the GPS reading will be 68% certain of containing the true horizontal coordinates of the point, and that a circle of diameter 17.1 m ($=1.96 \times 8.7$) will be 95% certain of containing the true coordinates. In practice, however, smaller *SDs* are frequently experienced, especially when satellite geometry is good and there are no multipath effects. For example, Merry (2000), in an experiment in which the horizontal coordinates had been predetermined to within 0.15 m, found that a Garmin 2+ GPS receiver, similar to that used on Prince Edward Island, yielded an *SD* of 2.8 m, based on 120 recordings made over a period of three days. Given the lack of reflective surfaces in the wandering albatross colonies on the Prince Edward Islands, multipath reflection effects were probably small.

Assuming that the position of each nest is determined independently, the *SD* of the inter-nest distances is given by the square root of twice the squared *SD* of the position fixes. For an optimistic *SD* of 2.8 m, the standard deviation of an inter-nest distance would be 4.0 m ($= 2 \times 2.8^2)^{0.5}$). For the theoretical anticipated minimum and maximum *SD* of 8.7 and 18.9 m, the inter-nest distance *SDs* would be 12.3 and 26.7 m respectively. These are greater than the observed distances between most neighbouring nests in Albatross Valley. Therefore, it was deemed unwise to calculate

statistics based on inter-nest distances from the coordinates obtained during this study. Consequently, the analysis was focused on statistics based on nest densities within quadrats; the quadrats based on a 25-m grid probably represent the finest grid at which meaningful results can be obtained.

However, there is autocorrelation in time between errors (C. L. Merry, University of Cape Town, pers. comm.). In the context of this analysis, this means that the positions of nests determined over a short period of time are all likely to have a similar shift relative to their true coordinates. Inter-nest distances calculated from these positions are likely to be more accurate than the above analysis suggests. Observational experiments, using a configuration of points at known distances apart, with a careful record of the time at which each position fix was made, would be valuable in assessing this. The objective of the experiment would be to produce guideline times during which position fixes for all the nests in quadrats of various sizes need to be determined.

Differential GPS could potentially reduce errors to <1 m. Besides the equipment being cumbersome rela-

Table II: Densities and other statistics relating to the nest densities of wandering albatrosses at Marion Island in the 2000/01 breeding season

Parameter	Marion Island 1 779 nests		
	25 m	50 m	100 m
<i>Density (nests ha⁻¹)</i>			
Quadrat grid	16	4	1
Quadrats per ha	16	4	1
Lower quartile	16	4	1
Median	16	4	2
Upper quartile	16	8	3
Maximum 1	128	36	18
Maximum 2	96	36	15
Maximum 3	80	32	14
Maximum 4	80	32	13
Maximum 5	80	32	13
Maximum 6	64	28	11
Maximum 7	64	28	10
Maximum 8	64	24	10
Maximum 9	64	24	9
Maximum 10	64	24	9
<i>Other statistics</i>			
Number of occupied quadrats	1 531	1 224	757
Area (ha)	95.7	306	757
Mean density	18.6	5.8	2.4
Smallest number of quadrats containing 50% of the total for colony	643	348	151
Area of these quadrats (ha)	40.2	87.0	151
Density within these quadrats	22.1	10.2	5.9

Table III: Densities and other statistics relating to nest densities of wandering albatrosses at the three study colonies on Marion Island in the 2000/01 breeding season

Parameter	Macaroni Bay 28 nests			Sealers Beach 117 nests			Goney Plain 140 nests		
	25 m 16	50 m 4	100 m 1	25 m 16	50 m 4	100 m 1	25 m 16	50 m 4	100 m 1
<i>Density (nests ha⁻¹)</i>									
Lower quartile	16	4	1	16	4	1	16	4	2
Median	16	4	1	16	4	2	16	8	4
Upper quartile	16	4	2	16	8	3	16	8	6
Maximum 1	32	8	4	32	12	9	80	24	13
Maximum 2	32	8	2	32	12	7	64	20	9
Maximum 3	16	8	2	32	12	6	64	20	9
Maximum 4	16	8	2	32	12	6	48	20	8
Maximum 5	16	8	2	32	12	5	48	20	8
Maximum 6	16	4	2	32	12	5	48	16	7
Maximum 7	16	4	2	32	12	5	32	16	7
Maximum 8	16	4	1	32	12	5	32	16	6
Maximum 9	16	4	1	16	12	4	32	16	6
Maximum 10	16	4	1	16	8	4	32	12	6
<i>Other statistics</i>									
Number of occupied quadrats	26	23	19	109	82	46	105	70	32
Area (ha)	1.6	5.8	19	6.8	20.5	46	6.6	17.5	32
Mean density	17.2	4.9	1.5	17.2	5.7	2.5	21.2	8.0	4.4
Smallest number of quadrats containing 50% of the total for colony	13	10	7	52	26	13	36	20	10
Area of these quadrats (ha)	0.8	2.5	7	3.3	6.5	13	2.3	5.0	10
Density within these quadrats	17.2	5.6	2.0	18.0	9.1	4.5	31.1	14.0	7.0

tive to a 150 g hand-held GPS receiver, these depend on regional monitoring stations on the ground to provide correction signals, and the nearest such stations to the Prince Edward Islands are in South Africa, and would be unlikely to improve accuracy over that achieved by the stand-alone GPS receiver as used in this study (C. L. Merry, pers. comm.).

A comparison of nest density and nearest-neighbour distance in great albatrosses

Great albatrosses breed at Subantarctic and southern cool-temperate islands in loose colonies on coastal and inland plains and gentle slopes with short vegetation, often in mires (Marchant and Higgins 1990, Tickell 2000), but information on nest densities for the genus is limited. At Bird Island, South Georgia, Tickell (1968) reported wandering albatross nest densities of 40–106 nests ha⁻¹ in “most favoured” areas. At Possession Island, Crozet Islands, nest densities in three areas were 0.35, 0.82 and 1.01 nests ha⁻¹ (Weimerskirch and Jouventin 1987), more than two orders of magnitude less dense than at Bird Island. This difference is prob-

ably partly because densities were measured in small (0.85–2.5-ha) study plots on Bird Island, but over areas ranging from 1.6 to 5.1 km² in size on Possession Island, and probably containing some areas unsuitable for breeding.

Nest densities for the Antipodean albatross *D. antipodensis* and Gibson’s albatross *D. gibsoni* have been reported as 20 and 26 nests ha⁻¹ respectively (Warham and Bell 1979, Warham 1990). Ryan *et al.* (2001) gave nearest-neighbour distance for the Tristan albatross *D. dabbenena* as “as little as 3 m”, but noted that nests were as far as 500 m apart. No nest density data are available for this species of great albatross.

Westerskov (1963) and Warham (1990) reported 153 and 20 nests ha⁻¹ respectively for the southern royal albatross *D. epomophora* at Campbell Island, where the species breeds in broadly similar habitat to that of wandering albatrosses (JC pers. obs.). In contrast, the northern royal albatross *D. sanfordi* breeds at a density as large as 520 nests ha⁻¹ and approaching 800 nests ha⁻¹ on The Forty-Fours and The Big Sister, Chatham Islands, respectively (Robertson 1974).

Because of the wide variety of approaches to computing nest densities, it is difficult to make strong

comparisons between these studies. However, knowing the coordinates of each nest as accurately as can be achieved, even with stand-alone hand-held GPS receivers, enables alternative approaches to be explored and compared. The concept of applying a grid of an appropriate dimension, as done here, enables an "area of occupancy" to be calculated in an objective way. The scale of this grid makes a considerable difference to the results, as demonstrated in Tables I–III. Of the three grid scales considered in this study, the 100-m grid reveals large areas that do not contain nests (Fig. 1), and which may therefore be unsuitable habitat. This biases nest densities downwards. The 25-m grid, especially on Marion Island where nest densities are relatively low, resulted in a large proportion of quadrats with only a single nest (1 779 nests in 1 531 quadrats, Table II); intuitively, choosing too fine a grid can generate unrealistically high densities. It is believed that the 50-m grid, because of the small area with no nests and relatively small proportion of quadrats with only one nest, is sensible and appropriate for wandering albatrosses. Its adoption is therefore proposed when comparing nest densities between breeding colonies for this species. It might also be appropriate for other loosely colonial species.

It is clearly desirable that areas selected as study colonies for birds should be representative of the population being sampled. Using the 50-m grid as the basis of comparison, the colony at Sealers Beach has a mean density similar to the mean for Marion Island (5.7 v 5.8 nests ha⁻¹); the colonies at Macaroni Bay and Goney Plain have densities 16% below and 38% above the average respectively, and close to the lower and upper quartiles of nest density on the islands respectively (Tables II and III). From the viewpoint of nest densities in the three study colonies being representative of the range of densities on Marion Island, they were well chosen.

It would seem that the wandering albatross does not breed at exceptional densities for a great albatross in Albatross Valley on Prince Edward Island, with this study reporting overall mean and median densities, using a 50-m grid, of 22 and 16 nests ha⁻¹ respectively (Table I). Although the comparisons are uncertain because of the differing methods of computing densities, these densities within Albatross Valley lie within the reported ranges for other colonies of great albatrosses. What does seem to be exceptional is that more than a thousand pairs breed annually in this valley in what may be considered a single colony (Fig. 1). This affords the privileged visitor to this specially protected island one of the most spectacular ornithological sights in the world.

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Albatross Valley, Prince Edward Island (photo R. J. M. Crawford)

**POPULATION, BREEDING, DIET AND CONSERVATION OF THE CROZET SHAG
PHALACROCORAX [ATRICEPS] MELANOGENIS AT MARION ISLAND,
1994/95–2002/03**

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The number of Crozet shags or cormorants *Phalacrocorax [atriceps] melanogenis* breeding at subantarctic Marion Island decreased by 68% from 841 pairs in 1994/95 to 272 pairs in 2002/03. The mean number of pairs at colonies also decreased and was significantly related to the overall number of birds breeding in any given season. The decreases coincided with a period of warming and reduced precipitation at Marion Island and with a decrease in the number of gentoo penguins *Pygoscelis papua* breeding there. Both these seabird species forage inshore and there is considerable overlap in their diets. Nototheniid fish and the decapod *Nauticaris marionis* continued to be important in the diet of Crozet shags, but a change in dominance among nototheniid prey suggests availability of prey to shags changed after the mid 1980s. Crozet shags breed for the first time when aged three years. It is probable that about 25% of the mature population did not breed in 1997/98, coincident with a strong *El Niño* Southern Oscillation event. In four seasons, breeding pairs on average fledged 0.30 chicks from first clutches, an amount thought inadequate to sustain the population. Crozet shags at the Prince Edward Islands should now be regarded as Endangered. Placing breeding colonies in the most highly protected zone on Marion Island, considering the establishment of an *ex situ* population and undertaking a genetic study of the specific status of the Crozet shag are recommended conservation measures.

Key words: age at breeding, breeding success, conservation, Crozet shag, diet, Marion Island, *Phalacrocorax [atriceps] melanogenis*, population decrease, Subantarctic

The Crozet shag or cormorant *Phalacrocorax [atriceps] melanogenis* is found only at the subantarctic Crozet Islands and Prince Edward Islands (Prince Edward Island and Marion Island) in the southern Indian Ocean. Together with several other taxa of shags in the Southern Ocean, including the Antarctic shag *P. [a.] bransfieldensis*, South Georgian shag *P. [a.] georgianus*, Heard shag *P. [a.] nivalis* and Macquarie shag *P. [a.] purpurascens*, the Crozet shag is considered to be a member of the imperial cormorant *P. atriceps* complex (Rand 1954, Marchant and Higgins 1990). However, the classification of the shags of the Prince Edward Islands is provisional (Marchant and Higgins 1990) and is not based on a genetic study. An investigation into the specific status of shags at the Prince Edward Islands is therefore urgently required (Barnes 2000). The population at the Crozet Islands was 815–835 pairs in 1981/82 (Jouventin *et al.* 1984), whereas in

1984/85 that at Prince Edward Island was about 120 pairs (Ryan and Hunter 1985) and in 1987/88 that at Marion Island was 589 pairs (Cooper and Brown 1990). Therefore, in the 1980s, the total population of the taxon was of the order of 1 500 pairs. The Crozet shag is listed as Vulnerable in *The Eskom Red Data Book of Birds of South Africa, Lesotho and Swaziland* (Barnes 2000).

The number of Crozet shags breeding at Marion Island has been monitored annually since 1994/95. Additionally, information has been gathered on the ages at which birds breed, on their breeding success and on their diet. This paper reports the results of these studies. It draws attention to a decrease in the number breeding at Marion Island during the 1990s, discusses factors that may have influenced this trend and re-considers the conservation status of the species at the Prince Edward Islands.

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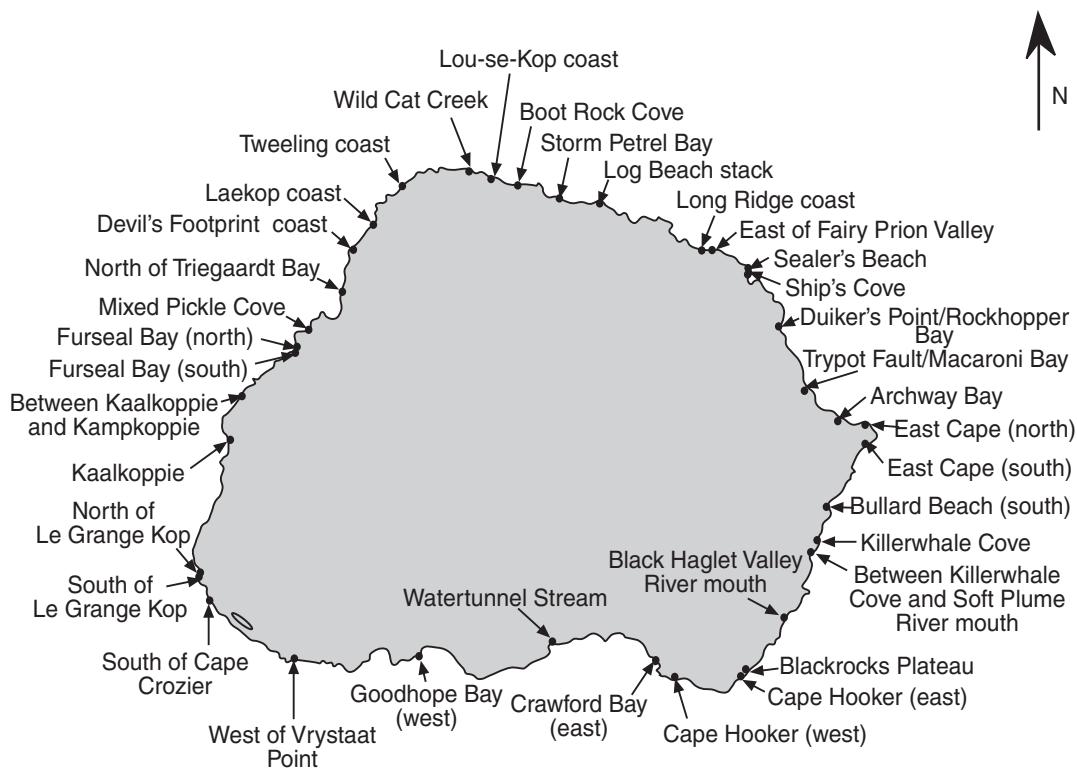


Fig. 1: Localities of breeding colonies of Crozet shags at Marion Island, 1987/88–2001/02

MATERIAL AND METHODS

Population

Numbers of active nests of Crozet shags around the whole coastline of Marion Island (290 km^2 ; $46^{\circ}52'S$, $37^{\circ}51'E$; Fig. 1) were counted in each season from 1994/95 to 2002/03. Additionally, detailed information was available for a count made in October 1987 (Cooper and Brown 1990, JC unpublished data). A nest was defined as being active if it consisted of nest material and an adult or a chick was occupying it. The locations of breeding colonies were recorded and, except in 2002/03, counts were assigned to localities. Counts were undertaken from 21 November to 6 December 1994, from 20 November to 2 December 1995, from 19 November to 6 December 1996, from 20 November to 12 December 1997, from 25 November to 9 December 1998, from 25 November to 13 December

1999, from 23 November to 7 December 2000, from 18 to 23 December 2001 and from 28 November to 8 December 2002. At Marion Island, breeding is seasonal, eggs are normally laid between October and January, and 50% of eggs of first clutches are laid by 11 November. Eggs laid after November are mostly replacements (Williams and Burger 1979).

The census in 2001 was undertaken later in the breeding season than were counts in other years. This may have resulted in additional nest failure before active nests were counted. In 2001, the numbers of pairs at three colonies were counted each week during November and December. The proportional decrease in nests between 29 November, close to the midpoint of surveys for the years 1994–2000 and 2002, and 20 December, the mid point of the 2001 census, was calculated and used to adjust the 2001 count to make it comparable with those for the other surveys. In 2000, repeat counts were undertaken at several colonies in order to determine the coefficient of variation (CV) for counts.

Table I: Minimum numbers of Crozet shags from different cohorts present (P) and breeding (B) at Marion Island, at approximate ages. Numbers of chicks banded for each cohort are shown

Cohort	Number banded	Numbers per approximate age (years)													
		1		2		3		4		5		6		7	
		P	B	P	B	P	B	P	B	P	B	P	B	P	B
1994/95	200	22	0	1	0	3	3	8	4	1	1	0	0	1	1
1995/96	49	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1996/97	39	0	0	0	0	1	1	0	0	1	1				
1997/98	11	0	0	0	0	0	0	0	0						
1998/99	28	1	0	0	0	1	0								
1999/00	56	0	0	0	0										
Overall	383	23	0	1	0	5	4	8	4	2	2	0	0	1	1

Age at breeding

From 1994/95 to 1999/00, cohorts of Crozet shag chicks were banded in such a way that each cohort could be distinguished. Until January 1998, the chicks were banded with individually numbered 16-mm stainless steel bands and with 16.5-mm (internal diameter) coiled, coloured plastic bands of depth 16 mm. Subsequently, the stainless steel bands were coloured (powder coated) and only this band was applied. Numbers of chicks banded in each season are shown in Table I.

From December 1994 to May 2002, research assistants stationed at Marion Island conducted observations on the presence of known-age Crozet shags at breeding colonies. If a bird was observed at a nest containing nest material, it was assumed to be breeding. Chicks fledge during summer, so information on resightings of birds was summarized for the 12-month periods July–June. In these periods, the maximum number of banded birds from a cohort observed at any colony was assumed to represent the minimum number of birds of known age at that colony. Generally it was not possible to distinguish birds of the same cohort, but on a few occasions the unique numbers on the metal bands were read.

Breeding success

The breeding success of Crozet shags was estimated in 1998/99, 1999/00, 2001/02 and 2002/03. In 1998/99, 33 nests were monitored at Duiker's Point/Rockhopper Bay and 22 at Trypot Fault/Macaroni Bay (Fig. 1). In 1999/00, 74 nests were monitored at Trypot Fault/Macaroni Bay. In 2001/02, 35 nests were monitored at Duiker's Point/Rockhopper Bay and 45 at Trypot

Fault/Macaroni Bay. In 2002/03, 20 nests were monitored at Duiker's Point/Rockhopper Bay, 55 at Trypot Fault/Macaroni Bay and 14 at Archway Bay. Positions of nests in these colonies were mapped so that progress at each nest could be followed.

The colonies were visited at intervals of 2–17 days: in 1998/99 from 9 November to 31 January (19 visits); in 1999/00 from 11 October to 26 January (10 visits); in 2001/02 from 1 November to 19 February (16 visits); in 2002/03 from 1 November to 27 December (eight visits). Nests were examined with binoculars, and the content of each was noted, except if a nest had an adult in a prone position, when eggs or small chicks were not visible.

All large post-brooded chicks at nests were assumed to have fledged and, for each season, the mean number of chicks fledged per nest was calculated. Nests for which breeding was still in progress at the conclusion of observations were excluded from the analysis: three in 1998/99; five in 1999/00; none in 2001/02; eight in 2002/03.

Diet

Freshly regurgitated pellets were collected at breeding colonies in 1997/98 ($n = 1$, 28 January), 1998/99 ($n = 51$, 1 December–1 March), 2000/01 ($n = 44$, 4 December–27 January) and 2001/02 ($n = 3$, 24 December). Prey remains were removed from pellets using forceps and sorted into polychaete, crustacean, cephalopod and fish components. Crustaceans were identified by reference to Baker *et al.* (1990) and Branch *et al.* (1991), cephalopod beaks by reference to Clarke (1986) and fish otoliths by reference to Hecht (1987), Williams and McEldowney (1990) and Reid (1996). For each pellet, the number of polychaetes represented was taken

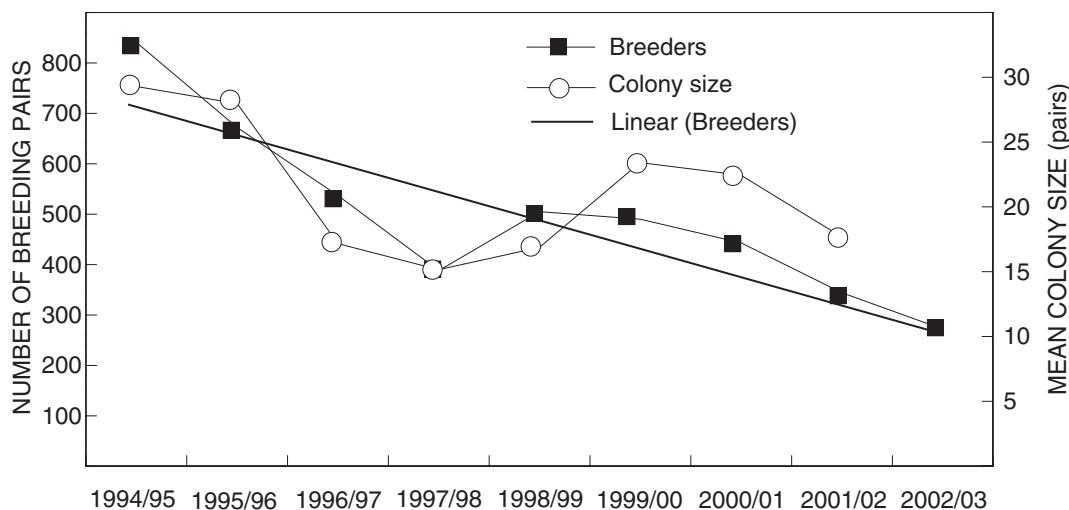


Fig. 2: Numbers of breeding pairs and mean size of colonies of Crozet shags at Marion Island, 1994/95–2002/03. The linear regression for the number of breeding pairs is shown

to be the number of mandibles present. The number of cephalopods present was taken to be the higher number of either upper or lower rostra found. The number of each fish species present was estimated by dividing the number of otoliths for that species by two and regarding any remainder as representing one fish. The contribution to the diet was estimated by percentage frequency of occurrence and, except for crustacean components for which numbers could not be determined, by percentage of the overall number of prey items found. Both these methods may overestimate the contribution to the diet of fish and cephalopods, whose harder otoliths and beaks take longer to digest, but the method nevertheless provides useful information for largely piscivorous birds (Espitalier-Noel *et al.* 1988).

RESULTS

Population

From 1994/95 to 2001/02, Crozet shags at Marion Island bred at 37 localities, all in close proximity to the coast (Fig. 1). In any one season they bred at between 19 and 25 localities. The mean size of colonies varied between 15 pairs in 1997/98 and 29 in 1994/95 (Fig. 2). In the eight seasons, the overall mean size of colonies was 24 pairs ($n = 179$, $SD = 22$ pairs). Solitary pairs

were seen on seven occasions. The largest breeding colony encountered was 94 pairs at Trypot Fault/Macaroni Bay in 1994/95. The small size of colonies facilitated accurate counts and, in 2000, the CV on the overall count was 1%.

In 2001, the count of active nests at three colonies decreased from 67 on 29 November to 58 on 20 December. Therefore, counts made during the period 18–23 December were multiplied by a factor of 1.156 to account for nest failure prior to the survey.

The breeding population at Marion Island decreased by 68% from 841 pairs in 1994/95 to 272 pairs in 2002/03 (Table II). There was a steep decrease to 388 pairs in 1997/98, an increase to about 500 pairs in both 1998/99 and 1999/00 and then a decrease from 2000/01 to 2002/03 (Fig. 2). The decrease from 1994/95 to 2002/03 was approximately linear and significantly related to time ($n = 9$, $r = -0.883$, $p < 0.002$). There was also a significant correlation between numbers breeding and the mean size of breeding colonies ($n = 8$, $r = 0.806$, $p < 0.02$).

There was considerable fluctuation in numbers breeding at some localities, e.g. Trypot Fault/Macaroni Bay, but a steady decrease at others, e.g. between Killerwhale Cove and Soft Plume River mouth between 1995/96 and 1999/00. Breeding stopped altogether at Goodhope Bay (west) after 1995/96 and at Bullard Beach (south), Watertunnel Stream and Storm Petrel Bay after 2000/01. At some localities, e.g. Killerwhale Cove and south of La Grange Kop, Crozet shags bred sporadi-

Table II: Counts of active nests of Crozet shags at different localities or sections of Marion Island, 1987/88 and 1994/95–2001/02. The counts in 2001/02 were adjusted to account for failed breeding prior to the survey using information from three monitored colonies (see text). In 2002/03, counts were not assigned to equivalent localities and sections, but totalled
272 active nests

Locality or section	Counts									
	1987/88	1994/95	1995/96	1996/97	1997/98	1998/99	1999/00	2000/01	2001/02	2001/02 adjusted
Trypot Fault	16	94	90	38	25	18	87	30	45	52
Archway Bay to East Cape	43	50	52	23	38	30	21	13	11	13
Bullard Beach (south)	42	60	42	40	44	47	54	48	0	0
Killerwhale Cove	0	0	0	0	2	0	0	0	3	3
Between Killerwhale Cove and Soft										
Plume River mouth	45	53	56	39	28	25	12	6	11	13
Black Haglet Valley River mouth	0	8	3	8	0	17	13	5	0	0
Blackrocks Plateau	0	0	0	25	0	38	52	57	53	61
Cape Hooker	0	78	72	50	45	11	0	0	0	0
Crawford Bay (east) 15	0	0	11	20	0	2	0	0	0	0
Watertunnel Stream	0	31	31	15	6	29	16	35	0	0
Goodhope Bay (west)	23	53	54	0	0	0	0	0	0	0
West of Vrystaat Point	0	5	0	9	0	0	1	1	0	0
South of La Grange Kop	0	0	6	0	5	3	0	13	3	3
North of La Grange Kop	0	15	5	0	0	7	7	0	13	15
Kaalkoppie	0	14	12	0	0	13	0	0	0	0
Between Kaalkoppie and Kampkoppie	18	10	0	10	5	0	0	8	5	6
Furseal Bay (south)	0	35	9	10	6	5	46	26	6	7
Furseal Bay (north)	51	0	10	8	0	0	0	0	5	6
Mixed Pickle Cove	0	23	9	0	4	46	0	1	7	8
North of Triegaardt Bay	24	5	1	0	0	4	4	0	10	12
Devil's Footprint coast	0	0	6	2	6	4	1	0	0	0
Laekop coast	0	16	5	4	0	4	3	0	17	20
Tweeling coast	38	0	0	7	0	12	0	0	0	0
Wild Cat Creek	0	0	0	5	6	7	7	1	9	10
Lou-se-Kop coast	5	63	30	22	7	16	21	8	12	14
Boot Rock Cove	12	0	5	15	9	6	9	0	6	7
Storm Petrel Bay	26	73	82	46	31	29	31	64	0	0
Log Beach stack	55	7	9	13	32	38	24	16	4	5
Long Ridge coast	25	1	0	3	3	0	0	0	0	0
East of Fairy Prion Valley	0	52	59	0	0	66	18	30	16	18
Sealer's Beach	25	85	0	43	37	0	60	72	49	57
Ship's Cove	35	0	13	62	0	3	1	0	0	0
Duiker's Point/Rockhopper Bay	91	10	11	29	29	27	0	9	13	15
Total	589	841	672	537	388	505	490	443	298	344

cally in small numbers. Fluctuations at the adjacent colonies east of Fairy Prion Valley and at Sealer's Beach were often out of phase, suggesting some movement between these localities (Table II).

Age at first breeding

Minimum numbers of banded Crozet shags from the 1994/95–1999/00 cohorts that were present and breeding at colonies at Marion Island are shown in Table I. No birds aged two years or younger were observed at nest sites, whereas 80% of three-year-old birds and substantial proportions of older age-classes were breeding. Therefore, the age at which Crozet shags

commence breeding can be assumed to be three years.

First-time breeders did not necessarily recruit to natal colonies. A chick banded at Trypot Fault/Macaroni Bay on 28 December 1994 was at the colony at Archway Bay on 21 January and 25 November 1999, on the last occasion with an incubating mate. One chick banded at Cape Hooker on 13 January 1995 was breeding at Bullard Beach South in December 1998, another at Killerwhale Cove in January 1999.

Breeding success

In 1998/99, 11 of 52 monitored nests were successful: 10 pairs fledged one chick and one pair fledged

Table III: Contribution of different prey items to the diet of Crozet shags at Marion Island by frequency of occurrence and by number, 1998/99–2001/02

Prey species	Frequency of occurrence (%)	Contribution by number (%)
Polychaeta	2	0.69
Crustacea		
Euphausiaceae		
<i>Euphausia lucens</i>	1	
<i>Thysanoëssa vicina</i>	1	
Isopoda	1	
Amphipoda	1	
Decapoda		
<i>Nauticaris marionis</i>	42	
Cephalopoda		
<i>Octopus magnificus</i>	33	1.04
Unidentified octopus	2	0.03
Fish		
Muraenolepididae		
<i>Muraenolepis marmoratus</i>	1	0.02
<i>M. microps</i>	50	0.09
Moridae		
<i>Antimora rostrata</i>	2	0.03
Congiopodidae		
<i>Zanclorhynchus spinifer</i>	2	0.07
Nototheniidae		
<i>Dissostichus eleginoides</i>	7	0.17
<i>Gobionotothen marionensis</i>	57	10.23
<i>G. gibberifrons</i>	1	0.02
<i>Lepidonotothen squamifrons</i>	4	0.12
<i>L. larseni</i>	55	7.04
<i>Notothenia acuta</i>	5	0.71
<i>N. coriiceps</i>	24	0.92
<i>N. neglecta</i>	1	0.02
<i>N. rossii</i>	1	0.02
<i>Paranotothenia magellanica</i>	39	1.79
<i>Pagothenia bernacchii</i>	3	0.07
<i>Trematomus</i> sp.	1	0.02
Unidentified nototheniid	65	75.16
Harpagiferidae		
<i>Harpagifer georgianus</i>	23	1.42
Unidentified fish	4	0.33
Total		100.00

two chicks. On average, pairs fledged 0.23 chicks. Of the 41 failed nests, 15 failed at an early stage (prior to the first egg being laid) and 26 during incubation. In 1999/00, 32 of 69 nests were successful: 29 pairs fledged one chick and three pairs fledged two chicks. On average, pairs fledged 0.51 chicks. Of the 37 failed nests, four failed at an early stage, 24 during incubation and nine during chick rearing. Laying after nest failure was observed at three nests. Laying was also observed at three nests that had successfully fledged chicks. However, because parents were not marked in any of these instances, it is not certain that these were second clutches. In 2001/02, seven of 80 nests were successful:

six pairs fledged one chick and one pair two chicks. On average, pairs fledged 0.09 chicks. Of the 73 failed nests, six failed at an early stage, 56 during incubation and 11 during chick rearing. In 2002/03, 17 of 81 nests were successful: five pairs fledged one chick and 12 pairs fledged two chicks. On average, pairs fledged 0.36 chicks. Of the 64 failed nests, 56 failed during incubation and eight during chick rearing.

If each of the four seasons is given equal weighting, pairs fledged an average of 0.30 chicks per season ($SD = 0.21$ chicks, $n = 4$).

Diet

From 1998/99 to 2001/02, nototheniid fish dominated the diet of Crozet shags breeding at Marion Island (Table III). *Gobionotothen marionensis* was in 57% of the 99 regurgitated pellets investigated and *Lepidonotothen larseni* in 55%. By number, these two fish species were also the dominant contributors to prey that could be identified. Other nototheniids frequently found were *Paranotothenia magellanica* and *Notothenia coriiceps*. Eight other nototheniids were encountered, as well as four species of fish from three other families. Of these *Harpagifer georgianus* was found in 23% of the pellets. The decapod benthic shrimp *Nauticaris marionis* was in 42% of the pellets and the cephalopod *Octopus magnificus* in 33%. Other prey items found occasionally were euphausiids, polychaetes, isopods and amphipods (Table III).

DISCUSSION

Population

In 1951/52, the population of Crozet shags at Marion Island was estimated to be 250–400 adults. However, there were at least 172 active nests at eight colonies, reading Rand (1954) and Rand (1956) together, making the upper estimate the more likely one. No breeding birds were found between Goodhope Bay and Furseal Bay on the west coast (Rand 1954, 1956). The upper estimate of 400 adults for 1952 was repeated by Williams *et al.* (1975), who gave their own count of 647 birds for the period January–March 1974 over 75% of the island's coastline. Based on counts made between January 1974 and April 1975 and from April 1976–May 1977, Siegfried *et al.* (1978) and Williams *et al.* (1979) estimated the population to be 285 breeding pairs distributed in 16 kilometre squares (and thus representing a minimum of 16 colonies),

mostly on the island's eastern coast. This estimate is lower than any of the nine made between 1987/88 and 2001/02 but similar to that for 2002/03 (Table II). However, uncertainty regarding the methods used by Siegfried *et al.* (1978) and Williams *et al.* (1979) precludes strict comparison. The breeding population may have increased from 587 pairs in 1987/88 (Cooper and Brown 1990) to 841 pairs in 1994/95. However, the count in 1987/88 was undertaken about one month earlier than those from 1994/95 to 2002/03 and before most eggs would have been laid (Williams and Burger 1979).

There was a 68% decrease in numbers of Crozet shags breeding at Marion Island between 1994/95 and 2002/03 (see also Woehler *et al.* 2001). There was a large (40%) decrease in numbers of gentoo penguins *Pygoscelis papua* breeding at Marion Island over the same period (Crawford *et al.* 2003a) and the two trends are significantly correlated ($n = 9$, $r = 0.889$, $p < 0.002$). At Marion Island there is considerable overlap in the diets of these two species, which forage close to the island (Cooper 1985, Adams and Wilson 1987, Espitalier-Noel *et al.* 1988, Adams and Klages 1989).

Mean annual surface air temperature at Marion Island increased by 1.2°C between 1969 and 1999 and was higher in the years 1996–1999 than in any year between 1950 and 1995. Precipitation at the island decreased after the mid 1960s and the 1990s were the driest of five decades for which this parameter has been measured at the island (1950s–1990s, Smith 2002). Over a 43-year period (1956–1998), sea surface temperature increased at Marion Island by 1.55°C (Mélice *et al.* in press). Such long-term changes in climate may have influenced oceanic processes near Marion Island. A large decrease in the number of rockhopper penguins *Eudyptes chrysocome* at Campbell Island south of New Zealand between the early 1940s and 1985 was attributed to rising sea surface temperatures causing euphausiids to move offshore, thereby affecting availability of prey to the penguins and the growth and survival of chicks (Moors 1986, Cunningham and Moors 1994). A decrease of rockhopper penguins at Amsterdam Island in the south-western Indian Ocean between 1971 and 1993 may have been caused by a drop in sea surface temperature affecting the distribution and abundance of prey (Guinard *et al.* 1998).

Off South Africa, the size of breeding colonies of swift terns *Sterna bergii* decreases when food is scarce, presumably because the density of prey within the foraging range of colonies is reduced (Crawford 2003). The trend to smaller colony sizes of Crozet shags recorded in this study may indicate a reduced density of prey around Marion Island.

The few Crozet shags breeding in 1997/98 coincided with a strong *El Niño* Southern Oscillation (ENSO) event. In the same season, breeding at Marion Island by five seabird species able to forage far from the island was exceptionally good, whereas for gentoo penguins it was noticeably poor (Crawford *et al.* 2003b).

Age at breeding and proportion breeding

Similarly to Crozet shags, South Georgian shags are able to breed when three years old but their average age at first breeding is about five years (Shaw 1986).

The trough in the numbers of Crozet shags breeding in 1997/98, when counts of active nests decreased to 72–77% of those in the immediately preceding and following seasons, may have resulted from strong recruitment of first-time breeders to the breeding population in 1998/99. However, it more probably arose from about 25% of mature birds choosing not to breed in 1997/98. In periods of food scarcity off southern Africa, Cape cormorants *Phalacrocorax capensis* and swift terns may defer the age at which they first breed by 1–3 years (Crawford *et al.* 2001, 2002). It is quite possible that the Crozet shag also does so, which would contribute to decreased numbers of mature birds breeding in certain years.

Breeding success

Williams and Burger (1979) reported that the average clutch of Crozet shags at Marion Island was 2.6 eggs and that, in 1976/77, 54.8% of eggs failed to hatch and 78% of chicks died. This means that pairs on average fledged 0.26 chicks from first clutches in that season. The value is similar to the mean of 0.30 chicks per pair obtained for the four seasons reported here. At the Crozet Islands, clutch size was 2.9 eggs, of which 31–39% produced fledged young, equivalent to 0.90–1.13 chicks per pair (Derenne *et al.* 1976). At Heard Island in 1986/87, Heard shags fledged a maximum of seven chicks from 27 nests, i.e. 0.26 chicks per pair (Pemberton and Gales 1987). For Antarctic shags, food availability is considered an important determinant of breeding success. Many pairs fledged three chicks in 1978/79 when food was plentiful, but in 1979/80 when food was limited, many pairs failed to fledge chicks or fledged just one chick (Marchant and Higgins 1990). At Signy Island, South Orkney Islands, South Georgian shags fledged 1.9–2.0 chicks per pair on average during 1980/81 and 1981/82 (Shaw 1986).

At Marion Island in 1974–1977, Williams and Burger (1979) noted that 39% of egg mortality resulted from

high seas washing away nests, 37% from failure to hatch and the remainder from disappearance of single eggs. Most mortality (78%) of chicks was attributed to starvation. Storms often prevented adults foraging at sea and chicks starved as a result. In the present study, 187 (87%) of unsuccessful breeding attempts failed before hatching and 28 (13%) during chick rearing. Some cormorants may stop breeding at an early stage when food is scarce (e.g. Cape cormorant *P. capensis*, Crawford *et al.* 1992).

There are no published estimates of post-fledging survival of Crozet shags. Information for other cormorants suggests that survival may be 80–90% per year, except in the first year when it is likely to be lower (Cramp and Simmons 1977, Crawford *et al.* 1991, 1992, Orta 1992). If no new breeders recruited to colonies at Marion Island during the period 1995/96–2002/03, so that the decrease in the number of breeders from 1994/95–2002/03 was solely attributable to mortality, the annual mortality rate of adults would have been 14%. This is an underestimate because observations of known-age birds showed that some young birds did recruit to the breeding population. Therefore, the maximum survival rate is probably 85% per year.

If all birds breed for the first time when aged three years, all mature birds breed each year and survival of birds of all ages is 85% per year, it would be necessary for pairs, on average to fledge 0.49 chicks per year to maintain the population in equilibrium. If 50% of fledged chicks survive their first year, pairs would need to fledge 0.83 chicks per year to achieve the equilibrium situation. If annual survival of adults is <85%, a higher production of fledged chicks would be required. The average breeding success at Marion Island is much lower than the value required to maintain the population, even assuming high levels of survival for both adults and first-year birds and that all mature birds breed every year. Inadequate reproduction is probably a major cause of the decrease in numbers of Crozet shags at the Prince Edward Islands. By contrast, breeding success at the Crozet Islands was likely to have been sufficient to maintain the population there.

Cape cormorants may lengthen their breeding season when food is plentiful (Crawford *et al.* 1999). The breeding season of Crozet shags also may be lengthened in periods of abundant food. Winter breeding of Crozet shags at Prince Edward Island was recorded in 1984, suggesting the possibility of double brooding (Ryan and Hunter 1985). Replacement laying following failed clutches is probable (Williams and Burger 1979). Double brooding and replacement laying will serve to increase the output of fledged chicks in conditions that are favourable for breeding.

Diet

Cooper (1985) noted that, in their non-breeding season, Crozet shags at Marion Island usually foraged within 400 m of the island and that they appeared to feed mainly on the seabed. The benthic nature of feeding was also noted by Blankley (1981) and Espitalier-Noel *et al.* (1988). Blankley and Grindley (1985) thought that Crozet shags foraged within 50 m of the island at depths of 1–15 m. The taxon is similarly regarded as an inshore, benthic feeder at the Crozet Islands (Stahl *et al.* 1985, Ridoux 1994).

At Marion Island in 1951/52, stomachs of both adult and immature Crozet shags contained partly digested fish (Rand 1956). In 1979/80, fish formed the largest part of three diet samples collected (Blankley 1981). In 1984/85, fish, the shrimp *Nauticaris marionis* and octopods contributed 71, 19 and 7% respectively of the overall mass of 47 diet samples collected using a stomach-flushing technique. Fish and octopods contributed 93 and 6% respectively of numbers of prey items found in 38 regurgitated pellets. *Lepidonotothen (Notothenia) squamifrons* was the most abundant fish in the diet. *Paranotothenia magellonica* contributed <1% by number (Espitalier-Noel *et al.* 1988), although regarded as the most abundant inshore nototheniid at the Prince Edward Islands by Gon and Klages (1988).

Octopods were less important by number in the years 1998/99–2001/02, constituting just 1% of prey items, whereas fish contributed 98% of those that could be recognized. *N. marionis* remained an important component of the diet. However, *L. squamifrons* was only the seventh most numerous of the 12 nototheniids encountered and occurred in just 4% of pellets. *P. magellonica* was present in almost 40% of pellets and both *Gobionotothen marionensis* and *L. larseni* in more than 50% (Table III). The last two species were not recorded in Crozet shag diet by Espitalier-Noel *et al.* (1988). *G. marionensis* larvae dominated the catch made by neuston nets around the Prince Edward Islands in May and June 1980 (Miller 1982). However, Gon and Klages (1988, p. 41) noted that "... several marine biological studies around PEI [Prince Edward Islands] during the last 7–8 years failed to collect substantial numbers of *G. marionensis*." *Harpagifer bispinus* identified in the diet of Crozet shag by Blankley (1981) may have been *H. georgianus* (Fischer and Hureau 1985).

It is apparent that the relative importance of nototheniid species in the diet of Crozet shags at Marion Island changed between 1984/85 and 1998/99–2001/02. By contrast, there was little difference in the species of fish eaten by Heard shags at Heard Island in three

seasons between 1979/80 and 1987/88, although there was a significant reduction in numbers of polychaetes found in pellets collected at a roosting site between 1985/86 and 1987/88 (Green *et al.* 1990b).

At the Crozet Islands during 1982–1983, fish accounted for 62% of the number of prey items and 82% of the reconstituted mass of the diet of Crozet shags. Two fish species, *L. larseni* and *P. magellanica*, together contributed 45% of the reconstituted mass. *N. marionis* was found in 33% of diet samples (Ridoux 1994). Fish, including nototheniids and often *Harpagifer* spp., dominates the diet of Macquarie shags (Brothers 1985, Green *et al.* 1990a), breeding Heard shags (Green *et al.* 1990b), South Georgian shags (Wanless *et al.* 1992) and Antarctic shags (Casaux *et al.* 1998), all members of the *P. atriceps* complex.

It is not certain that the poor breeding success of Crozet shags at Marion Island can be attributed to a reduced availability of food. However, the similar downward trend between 1994/95 and 2002/03 in numbers of gentoo penguins, whose diet overlaps considerably with that of Crozet shags (Espitalier-Noel *et al.* 1988, Adams and Klages 1989), suggests this may be the case. The changed composition of the diet of Crozet shags between 1984/85 and 1998/99–2001/02 is indicative of an altered availability of prey species between these two periods.

Conservation

The number of Crozet shags breeding at Prince Edward Island decreased from 120 pairs in September 1984 to an estimated 50 pairs in December 2001, i.e. by about 58% (Ryan *et al.* 2003). This is similar to the decrease at Marion Island of 68% between 1994/95 and 2002/03. The combined population of Crozet shags at the Prince Edward Islands for 2001/02 was about 400 pairs. Assuming that the population at Crozet Islands has remained stable since the early 1980s, the overall population of this species in 2001/02 would have been about 1 200 pairs.

Although some movement of shags between breeding colonies at Marion Island has been observed, the species is mainly sedentary (Marchant and Higgins 1990). Movements between the Prince Edward Islands and the Crozet Islands (950 km to the east) are not expected and there have been no such movements shown by banding. The populations at the two island groups should be managed separately.

Using an age at first breeding of three years and an adult survival rate of 85% per year, the average life expectancy of Crozet shags that attain breeding age is

about seven years. Therefore, the decrease of 68% at Marion Island between 1994/95 and 2002/03 occurred in just more than a single generation. In terms of the criteria of the World Conservation Union (IUCN 2001), the population at Prince Edward Islands should now be regarded as Endangered, rather than Vulnerable (Barnes 2000).

Crozet shags at the Prince Edward Islands are susceptible to human disturbance when breeding, with Subantarctic skuas *Catharacta antarctica* being quick to take exposed eggs (Rand 1956, Barnes 2000, pers. obs.). In the mid 1980s, a gillnet set from the shore to catch fish for scientific purposes at Transvaal Bay resulted in the death of at least one shag because of entanglement and subsequent drowning (Barnes 2000, JC pers. obs.). Use of such nets at the Prince Edward Islands has not been allowed since this event.

In view of the current poor conservation status of the Crozet shag at the Prince Edward Islands, three conservation measures are proposed for consideration by the Prince Edward Islands Management Committee in terms of the island's management plan (Prince Edward Islands Management Plan Working Group 1996):

1. Placing all breeding colonies at Marion Island within the most-protected Zone 4 category (along with gentoo penguins *Pygoscelis papua* and southern giant petrels *Macronectes giganteus*, which are currently so treated with a 100-m perimeter around their colonies) so that access will be strictly limited under special entry permit for approved conservation and research purposes only.
2. Investigating the desirability and feasibility of establishing an *ex situ* captive population.
3. Undertaking a genetic study of the specific status of the Crozet shag.

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Crozet shag at Marion Island (photos R. J. M. Crawford)

POPULATION NUMBERS OF FUR SEALS AT PRINCE EDWARD ISLAND, SOUTHERN OCEAN

M. N. BESTER*, P. G. RYAN† and B. M. DYER‡

During the period 17–22 December 2001, the onshore distribution and the abundance of Antarctic fur seals *Arctocephalus gazella* and Subantarctic fur seals *A. tropicalis* were determined for Prince Edward Island. Two breeding colonies of Antarctic fur seals were located on the south-east coast of the island; the first a mixed (with Subantarctic fur seals) breeding colony with an estimated 24 pups on a vegetated promontory on the northern section of Boggel Beach, and the second, a presumably pure Antarctic fur seal breeding colony with an estimated 380 pups, at Penguin Beach. At a mean intrinsic rate of natural increase of 16.2% per year, Antarctic fur seals appear to be in the rapid recolonization phase of population growth. Breeding colonies of Subantarctic fur seals, largely found on the entire east coast, produced an estimated 15 000 pups, and the population had maintained a mean intrinsic rate of natural increase of some 9.5% per year since 1987/88.

Key words: *Arctocephalus*, distribution, fur seals, population increase, Prince Edward Island, Subantarctic

Both the Antarctic fur seal *Arctocephalus gazella* and the Subantarctic fur seal *A. tropicalis* breed on the Prince Edward Islands in the southern Indian Ocean (Condy 1978), which comprise Marion Island and Prince Edward Island (21 km apart). Sealing began shortly after the discovery of the islands in 1772, and continued intermittently until 1931 (Marsh 1948, Kerley 1987). Population counts were first conducted in 1952 on Marion Island (Rand 1956), and although it was thought that only Subantarctic fur seals were present, one of the skulls collected at the time was that of an Antarctic fur seal (King 1959). On Marion Island more recent censuses of both species have been conducted in 1974/1975, 1981/1982, 1988/1989 and 1994/1995 during and/or at the end of the breeding/pupping season (Condy 1978, Kerley 1983a, Wilkinson and Bester 1990, Hofmeyr *et al.* 1997). However, the three censuses of *A. tropicalis* at Prince Edward Island (1981, 1982 and 1988), subsequent to the partial count in April 1973 (de Villiers and Ross 1976), were sporadic and always took place during March/April (Condy 1978, Kerley 1983a, Wilkinson and Bester 1990), well after the breeding (pupping) season (Kerley 1983b). The estimated number of births was therefore derived from the pup counts, adjusted for undercounting, and a mortality figure to compensate for the later census date (Kerley 1987, Wilkinson and Bester 1990).

Breeding of Antarctic fur seals at Prince Edward Island was first confirmed in 1975 (Condy 1978), but

the late census dates allowed neither an acceptable estimate of the number of births nor the breeding population size (Condy 1978, Wilkinson and Bester 1990), despite an attempt to calculate it indirectly (Kerley 1983a).

This study determines, for the first time, the breeding population size and pup production of Antarctic fur seals at Prince Edward Island. It also updates the available census figures for the Subantarctic fur seal, as an objective of the Prince Edward Islands Management Plan (Prince Edward Islands Management Plan Working Group 1996).

MATERIAL AND METHODS

The survey of fur seals was conducted from 17 to 18 December 2001 on the northern section (Kent Crater to Ross Rocks Peninsula) and from 20 to 22 December 2001 on the south-eastern section (McNish Bay to Albatross Valley Beach) of Prince Edward Island (44 km²; 46°38'S, 37°57'E; Fig. 1). Two inaccessible sections of coastline were not surveyed: a talus strip at the foot of the high bluffs from McNish Bay to Kent Crater, and a stretch of jumbled rocky to intermediate type beaches (terminology after Bester 1982) from Albatross Valley Beach to Ross Rocks (Fig. 1). The census periods represent the height of the breeding season haulout for the Subantarctic fur seal population (pupping only

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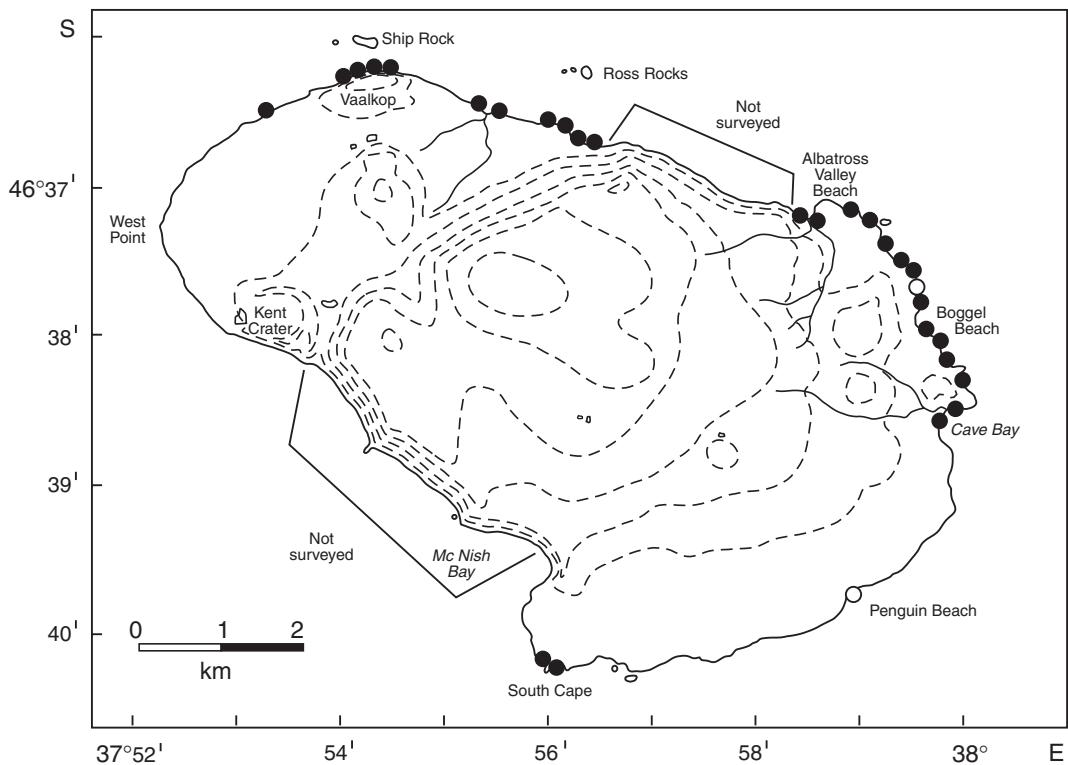


Fig. 1: Prince Edward Island, showing the localities mentioned in the text, the main topographical features and the distribution of breeding colonies of *A. tropicalis* (closed circles) and *A. gazella* (open circles). The distribution of the numerous nonbreeding and idle colonies of *A. tropicalis* are not shown because they occurred virtually everywhere along the coastline

half complete) and the end of the breeding/pupping season for the Antarctic fur seal (Condy 1978, Kerley 1983a). Aggregations of seals were assigned to breeding, nonbreeding and idle colonies following Bester (1982). Identification of the species and assumed hybrids followed descriptions given by Bonner (1968), Condy (1978) and Bester and Wilkinson (1989). The following age-sex-classes of seals were recognized: adult males, adult females, subadults and black pups (after Bester 1977, Condy 1978). Most counts were done by MNB, whereas PGR surveyed the beaches at West Point (Fig. 1), by moving on foot between and at sites, using binoculars when required (Table I). The large area involved in the count, and the time constraint (six days on the island) prohibited repeated counting of all beaches to calculate errors of the estimates. Breeding colonies in particular had to be viewed from raised areas or cliffs (3–200 m) at the back and/or sides of beaches, because of their inaccessibility and

the presence of aggressive territorial males. Similar constraints applied to previous counts at the island (Condy 1978, Kerley 1983a, Wilkinson and Bester 1990). The intrinsic rate of population change was calculated using estimated pup numbers for the various years and the exponential function $N_t = N_0 e^{rt}$, following Caughley (1977) as applied to fur seal populations by, for example, Bester (1980), Kerley (1983a) and Hofmeyr *et al.* (1997). The intrinsic rate of population change (r) was converted to a mean annual percentage change [$\% = (e^r - 1) \times 100$] following Caughley (1977).

A. gazella

All adult males (territorial and idle males scored separately), adult females, subadults and black pups were counted directly. No correction for undercounting

Table I: Counts of *A. gazella* and *A. tropicalis* at Prince Edward Island, 17–22 December 2001. Estimated pup numbers for *A. tropicalis* are derived from counts of territorial males (following Bester 1980)

Locality	<i>A. gazella</i>					<i>A. tropicalis</i>	
	TM	IM	AF	SA	P	TM	P
Vaalkop	0	0	0	0	0	129	852
Vaalkop West – Kent Crater	0	0	0	0	0	54	357
McNish Bay – Cave Bay	38	36	163*	30	163	3	20
Cave Bay	0	2	0	0	0	106	700
RSA Point – Boggel Beach	0	0	0	0	0	148	977
Boggel Beach	15	0	24	0	24	463	3 056
Boggel Beach – Albatross Beach	0	0	0	0	0	383	2 528
Albatross Beach	0	0	0	4	0	111	733
Ross Rocks Peninsula	0	0	0	2	0	582	3 842
Ross Rocks – Hope Stream	0	0	0	0	0	93	614
Hope Stream Beach	0	0	0	0	0	119	786
Hope Stream Beach - Vaalkop	0	0	0	0	0	0	0
Total	53	38	187	36	187	2 191	14 465

* Number of adult females derived from the pup count

TM = Territorial males
 IM = Idle males
 AF = Adult females
 SA = Subadults
 P = Pups

was made. Only older black pups in the white-faced stage (Bonner 1968, Bester and Wilkinson 1989) and younger black pups with their mothers in attendance were assigned to this species. All other black pups were assigned to *A. tropicalis* because no morphometric confirmation of the species (Bester and Wilkinson 1989) was possible with lone observers.

A. tropicalis

On rocky beaches, only adult, territorial males were counted directly; adult females and black pups were simply recorded as being either present or absent, because the pupping season continues into the second week of January (Kerley 1983b). On the open vegetated areas behind landing beaches, all fur seals were counted and classified. Pup numbers were derived from three sources: first, an estimate of the degree of polygyny (2.4 pups per adult male) calculated for a Marion Island breeding colony (Kerley 1987) and applied to all beaches where breeding (pupping) took place; second, an estimate based on a conversion factor (1:6.6) of territorial males:numbers of births (corrected for undercounting) at established breeding colonies at Gough Island, following Bester (1980); and third, a conversion factor (1:1.22) using the ratio between adult male numbers (irrespective of social status) and the numbers of pups (corrected for undercounting), which was derived from Marion Island-wide counts

(excluding the Furseal Peninsula and Furseal Bay established breeding colonies, for which no counts of adult males are available) presented by Hofmeyr *et al.* (1997). Total population size was estimated from the pup number:total population size ratio (1:4.8), following Kerley (1987).

Hybrids

Hybrids other than adult males are very difficult to distinguish from individuals of the two species, so likely hybrid males were noted only.

RESULTS AND DISCUSSION

A. gazella

The Antarctic fur seal breeding (pupping and mating) season had drawn to a close (median birthdate = 6 December, with all pups born by mid-December – Kerley 1983b), and only two breeding colony sites were found (Fig. 1). The first, on the northernmost part of Boggel Beach, was a small mixed (with Subantarctic fur seals of both sexes and two hybrid males) colony consisting of *A. gazella* males ($n = 6$) on vegetated areas holding aggregations of *A. gazella* ($n = 24$) and/or *A. tropicalis* females. Only 13 positively iden-

Table II: Numbers of *A. tropicalis* pups and their mean annual percentage increase (see text) for beaches on Prince Edward Island between 1980/81 or 1981/82, 1987/88 and 2001/02. Estimated pup numbers for 2001/02 are derived from counts of territorial males (following Bester 1980)

Locality	Pup numbers			Mean annual percentage increase	
	Unadjusted for 1981 and 1982	Unadjusted for 1987/1988	Estimated for 2001 (Method 2)	1982–1987 (%)	1987–2001 (%)
Vaalkop	—	—	852		
Vaalkop West – Kent Crater	5**	12	357	15.7	27.4
McNish Bay – Cave Bay	2**	0	20		
Cave Bay	7*	0	700		
RSA Point – Boggel Beach	90**	155	977	9.5	14.1
Boggel Beach	561**	1 145	3 056	12.7	7.3
Boggel Beach – Albatross Beach	559**	430	2 528	-4.5	13.5
Albatross Beach	125**	155	733	3.7	11.7
Ross Rocks Peninsula	412*	1 643	3 842	21.9	6.3
Ross Rocks – Hope Stream	36*	85	614	13.1	15.2
Hope Stream Beach	503*	561	786	1.6	2.4
Total	2 300	4 186	14 465	12.7	9.3

* 1981

** 1982

tified “white-faced” *A. gazella* pups were found there, and one black pup that suckled from its *A. gazella* mother. An additional 10 black pups were found in the immediate proximity of *A. gazella* females, and although it could not be ascertained whether they formed mother-pup pairs, the pups were assumed to be *A. gazella*, giving a total of 24 pups for this locality (Table I). The second site contained a large, presumably pure breeding colony of *A. gazella* on a cobble/boulder beach in front, and to the sides of, the king penguin *Aptenodytes patagonicus* breeding colony at Penguin Beach. A total of 163 pups was counted there (Table I), and given the extent of the front part of the beach that could not be viewed close up, another 130–140 pups might have been present. However, seen from a low hillock at some distance that defied pup counts, an estimated 38 territorial males were on site in the Penguin Beach colony. Such a number of territorial males translates into a total of 380 pups, given a male:female ratio of 1:10 on crowded beaches at the peak of female numbers for this species at South Georgia (McCann and Doidge 1987). A total count of 380 pups is probably realistic, given the likelihood of pup undercounting that reaches 14.2–34.3% in the Subantarctic fur seal (Condy 1978, Bester 1980, Kerley 1983a, Hofmeyr *et al.* 1997) and the fact that the ratio of “harem” male:final pup number could be as high as 1:15 (Bonner 1968). Adult female numbers are not given because most were absent on foraging trips (see Bester and Bartlett 1990), but each live pup was assumed to represent a mother. Single Antarctic

fur seal males ($n = 9$) and an assumed male hybrid were present (and presumably held territories) among Subantarctic fur seals on Boggel Beach, with idle adult ($n = 36$) and subadult ($n = 36$) males found singly or in small scattered groups on vegetated areas in the other parts of the south-eastern sector of Prince Edward Island (Table I). The total of 501 is undoubtedly an underestimate, and the population is probably approximately 2 000 individuals, after converting estimated pup numbers to total population size, following Kerley (1983a). Growing at a mean annual intrinsic rate of 16.2% (this study) from the estimated population of about 100 in 1981/1982 (Kerley 1983a), the population appears to be in the rapid recolonization phase (Roux 1987) of population growth similar to its Marion Island counterpart (Hofmeyr *et al.* 1997). However, this increase is possibly augmented by individuals from elsewhere, as postulated by Wilkinson and Bester (1990), most likely from South Georgia (see Wynen *et al.* 2000).

A. tropicalis

Established breeding colony sites of Subantarctic fur seals were found primarily in the eastern sector of the island from Vaalkop to Cave Bay (Fig. 1). A few small breeding colony beaches were on the southern and western side of the island, mainly around South Cape, and one larger one west of Vaalkop. Large numbers of idle males, mostly adult ($n = 11 003$), were found in

idle colonies, e.g. McNish Bay, but primarily on vegetated areas behind access points from the sea as well as behind breeding colony beaches. Because of (i) the *A. tropicalis* breeding season being only half complete (median birthdate = 17 December; Kerley 1983b), (ii) aggressive territorial males preventing access to beaches for searches of pups and (iii) the broken nature of the terrain (largely jumbled rocky and intermediate type beaches; see Bester 1982), major undercounts of pups and females would have resulted (Bester 1980, Kerley 1983a, Hofmeyr *et al.* 1997). Therefore, the presence/absence of pups and adult females was scored on all beaches to establish their status (breeding, nonbreeding and idle colony beaches following Bester 1982) and only territorial males on breeding colony beaches were counted (Table II). The three estimates of the number of births over the 2001/2002 pupping season amounted 5 260, 14 465 and 16 097 for Methods 1, 2 and 3 respectively. This realistically suggests a pup population of about 15 000 (Methods 2 and 3).

The estimated minimum pup number, excluding the inaccessible coastline (Kent Crater to McNish Bay and Ross Rocks Peninsula to Albatross Valley Beach; Fig. 1), amounted to approximately 15 000 pups (Table II), representing an estimated minimum total population of 72 000 Subantarctic fur seals. This translates into a mean intrinsic rate of natural increase of some 9.5% annually for the population over the 14 years since 1987/1988, when the last pup counts were made. This is similar to the rate of increase (9.7%) over the preceding six-year (1981/1982–1987/1988) period (Wilkinson and Bester 1990). It suggests that the Prince Edward Island population of Subantarctic fur seals is still in a relatively rapid recolonization phase (Bester 1980, Roux 1987), whereas the neighbouring Marion Island population (increasing at a mean annual rate of 2.0%) had entered the maturation phase (Hofmeyr *et al.* 1997).

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Populations of Antarctic (left) and Subantarctic (right) fur seals have increased at Prince Edward Island (photos B. M. Dyer)

THE DISTRIBUTION AND SPREAD OF ALIEN VASCULAR PLANTS ON PRINCE EDWARD ISLAND

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Surveys of alien plants at subantarctic Prince Edward Island in 2001 show that the ranges of all three introduced species have increased since the last survey in 1998. *Poa annua*, the longest-established species, increased its range substantially after 1987, prior to which it was confined to a single site for more than 20 years. It remains largely restricted to sites characterized by intense disturbance by seals and seabirds. *Sagina procumbens*, the most recently discovered alien plant, has spread even more rapidly (up to 800 m year⁻¹) and has colonized the west coast of the island (a leap of at least 3 km). Unlike *Poa annua*, it is not restricted to animal-disturbed areas, although its seeds probably are dispersed by both birds and fur seals. *Cerastium fontanum* also continues to spread at the island, but remains confined to the western coastal plain, where it occurs mostly on dry feldmark slopes or erosion scars. All three species have expanded their ranges faster than at Marion Island, possibly because of a warmer recent climate and higher densities of seabirds and seals at Prince Edward Island. The ranges of alien plants are likely to continue to expand, with *S. procumbens* causing considerable changes in the island's terrestrial ecology.

Key words: *Cerastium fontanum*, invasive plants, Prince Edward Island, *Poa annua*, *Sagina procumbens*, Subantarctic

Introduced organisms pose the most significant threat to the conservation status of oceanic islands (e.g. Williamson 1996). Subantarctic Prince Edward Island, the smaller of the two islands in the Prince Edward Island group, has few introduced organisms; it is currently known to support only three introduced animals (all invertebrates; Chown *et al.* 1998) and three introduced vascular plants (Gremmen and Smith 1999). By comparison, nearby Marion Island has supported naturalized populations of two introduced mammals, one fish, 16 invertebrates and at least 12 vascular plant species (Watkins and Cooper 1986, Chown *et al.* 1998, Gremmen and Smith 1999). The paucity of introduced species at Prince Edward Island is the main factor determining the island's high conservation ranking among subantarctic islands (Chown *et al.* 2001).

The near-pristine status of Prince Edward Island has been degraded by the recent arrival of two new alien plants. Prior to the 1980s, the almost ubiquitous weed *Poa annua* was the only introduced vascular plant at the island (Huntley 1971, Gremmen 1975). In 1987, a well-established population of *Cerastium fontanum* was discovered growing on the northern slope of Kent Crater (Bergstrom and Smith 1990) and in 1997 *Sagina procumbens* was found at two sites on the east coast (Gremmen and Smith 1999). All three species are widespread at Marion Island, where they

produce small, easily dispersed seeds that form a persistent seedbank (Gremmen 1997). With the exception of *Cerastium*, they also become locally dominant, displacing native species (Gremmen 1997). The occurrence of *Sagina* is especially worrying, because of its marked impact on a wide range of terrestrial communities (Gremmen 1997, Gremmen and Smith 1999). It is also an extremely difficult alien plant to eradicate, because it produces exceptionally large numbers of long-lived seeds; up to 200 000 *Sagina* seeds m⁻² were recorded in infested areas at Gough Island (NJMG unpubl. data).

This study reports the current distribution of alien plants on Prince Edward Island, based on surveys made in 2001, updating the last survey of alien plants made in 1998 (Gremmen and Smith 1999). Its aim is partly to document the rates of spread of alien species, but it also provides information for making informed decisions about possible attempts to eradicate one or more of the introduced species, as called for in terms of the Prince Edward Islands Management Plan (Prince Edward Islands Management Plan Working Group 1996). Of particular interest is the feasibility of controlling *S. procumbens* on Prince Edward Island, given the rapid habitat transformation it has caused on Marion Island (Gremmen 1997, Gremmen and Smith 1999).

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Table I: *Poa annua* populations on Prince Edward Island in 2001 and 2003. The locations of numbered sites are shown in Figure 1

Site	Status and habitat
1	Widespread, but with few dense stands in an area dominated by fur seals and southern elephant seals <i>Mirounga leonina</i> . First recorded at this site in the 1990s ¹
2	Penguin Beach: very abundant in the elephant seal wallows and adjacent areas affected by fur seals and king penguins <i>Aptenodytes patagonicus</i> . Some dense stands of up to 100 m ² . First recorded in the 1990s ¹
3	Fairly abundant in a localized area dominated by fur seals. First recorded in the 1990s ¹
4	Cave Bay: very abundant in the areas dominated by fur seals both north and south of the main landing beach. Also occurs along the edge of the rockhopper penguin <i>Eudyptes chrysocome</i> colony and along the lower reaches of the stream. NJMG recorded a few plants in <i>Acaena-Azorella</i> vegetation between the two Golden Gate outcrops in 1994. It does not extend inland to above Golden Gate, despite the presence of fur-seals and gentoo penguins <i>Pygoscelis papua</i> breeding there. The affected area has increased considerably since first recorded here in 1965 ²
5*	Abundant with some dense stands on a fur seal-dominated area, with scattered plants extending up an erosion slip to the south and around the inland fringe of a rockhopper penguin colony to the north
6*	Scattered plants around white-chinned petrel burrows on a denuded area of <i>Blechnum penna-marina</i> slope between two mire areas
7*	Locally abundant in a fur-seal-dominated area immediately south of Boggel Beach, with scattered plants at white-chinned petrel burrows at the top of the coastal cliffs
8*	As Site 7, but north of Boggel Beach, and extending north along the coast to the end of the area occupied by fur seals (the extent of coastal lowlands); sparse above the small, boulder beach midway through this area
9*	A few plants were found along the stream in the upper reaches of Albatross Valley in 2003
10*	Albatross Valley: abundant along the lower stream course and on adjacent slopes dominated by fur seals. Scattered plants extend up some of the stream beds and widely through the grey-headed <i>Thalassarche chrysostoma</i> and yellow-nosed albatross <i>T. [chlororhynchos] carteri</i> colonies
11*	A few plants on a small stream course among dense <i>Acaena</i> vegetation
12*	Fairly common, but mostly scattered plants in a fur-seal-dominated area, with small numbers of plants extending patchily inland along a small stream through mire vegetation
13*	Hope Stream: locally abundant in seal-dominated areas, with scattered plants extending c. 300 m inland along all four tributaries
14	Apparently restricted to the bottom of two small ponds; first recorded in 1990s ¹
15*	A few plants recorded in vegetation quadrats in an area of jumbled black lava where there is a high density of grey petrels <i>Procellaria cinerea</i>

¹Gremmen and Smith (1999)²Huntley (1971)

* New sites

STUDY AREA AND METHODS

The Prince Edward Islands lie in the Indian Ocean sector of the Southern Ocean. They have depauperate native floras, because of their relatively recent volcanic origin, isolation from other land masses, and possibly their cold, wet and extremely windy climate (Gremmen 1981). The recent origin and depauperate nature of the native flora renders it susceptible to introductions of non-native species by human visitors.

Prince Edward Island (44 km²; 46°38'S, 37°57'E) was visited from 17 to 22 December 2001. During this period, PGR conducted surveys of surface-nesting seabirds at the island and also made notes on all alien plants encountered. Coverage included all readily accessible coastlines, as well as much of the adjacent interior of the island (see Fig. 1 of Ryan *et al.* 2003). In view of the association between most alien plants and seabird and seal colonies, coverage is thought to have been reasonably comprehensive, especially given the localized ranges of most species. However, some aliens may have been missed in areas where access was impossible owing to high densities of fur seal

Arctocephalus spp. bulls defending harems. December is the period of peak territory defense by fur seal bulls.

Additional observations were made by VRS during a nine-day visit to Prince Edward Island in April 2001 and by NJMG and VRS during a five-day visit in April 2003. The whole island was inspected for alien plants in 2001; only the eastern part was visited in 2003. GPS fixes were made for most sites, and distributions were plotted on a revised map of the island. The mapped distributions are only approximate, and are intended to show the extent of affected areas. A revised map with names of localities is given in Figure 1 of Ryan *et al.* (2003).

RESULTS

No new alien vascular plants were found during the surveys of Prince Edward Island in 2001, but the ranges of all three alien species known at the island were substantially larger than the ranges observed in 1998 (Gremmen and Smith 1999). All three species were flowering during December, but it was too early to ascertain the proportion of flowers setting seed.

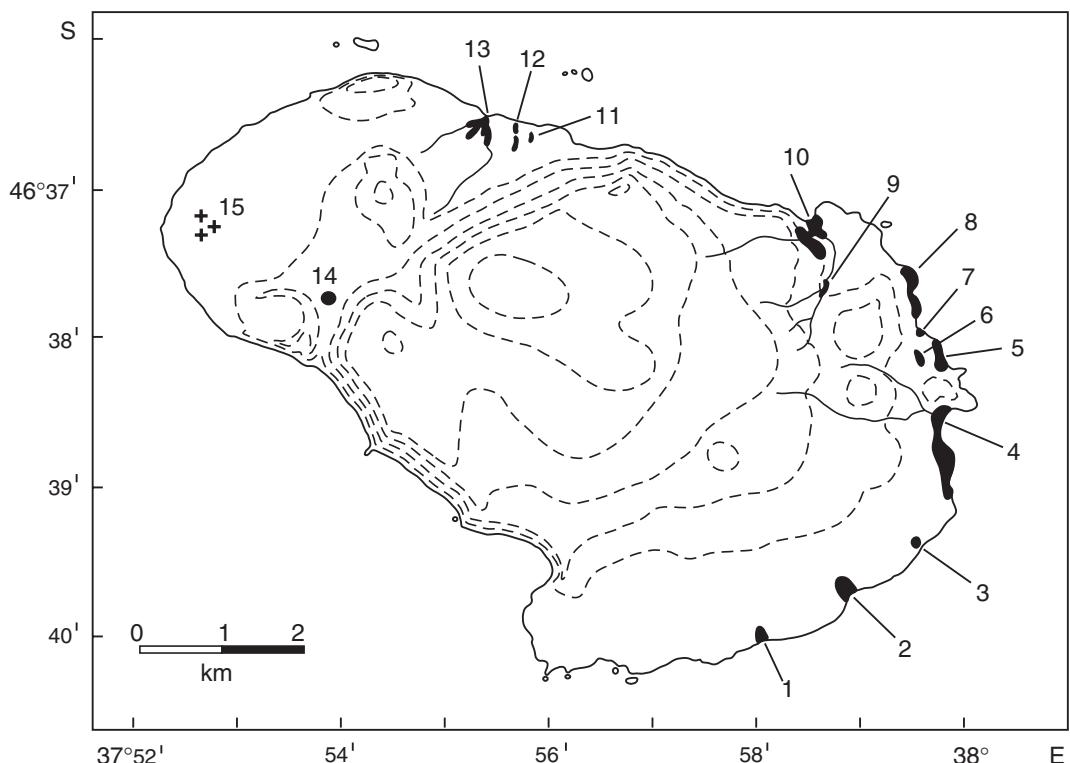


Fig. 1: Distribution of *Poa annua* on Prince Edward Island in 2001 and 2003. The symbol + denotes scattered plants (see Table I)

Poa annua

This species was found at 15 sites, 10 of which are new records (Table I). It is widely distributed along the east, north and west coasts (Fig. 1) and is the most abundant alien plant on the island. Most sites where it occurs are characterized by trampling and manuring by seals or, to a lesser extent, penguins and other seabirds (Table I). At most seal-affected sites it forms dense stands, especially in old wallows, entirely dominating the vegetation for areas of up to 100 m². It tends to be more scattered when associated with seabird colonies, typically occurring singly or in small clumps in disturbed areas (e.g. around albatross *Thalassarche* nests or petrel burrows), or forming a narrow fringe around the edge of *Eudyptes* penguin colonies. It is possible that the species is even more widespread than shown in Figure 1, because single plants are easily overlooked (e.g. Site 15). It is probably also more widespread in the albatross colonies that extend westwards along the cliffs from Site 10 (these steep cliffs were not visited

during 2001).

P. annua was first reported from the island in 1965, when it was found at Cave Bay (Site 4 in Fig. 1; Huntley 1971). It may have been on the island for some time prior to this (possibly even dating back to early visits by sealers), but Cave Bay was the only known site for the species through at least 1987 (Bergstrom and Smith 1990). In the 1990s, it was discovered at three sites frequented by fur seals south of Cave Bay on the east coast (Sites 1–3 in Fig. 1) as well as in ponds north of Kent Crater, the first record from the west coast (Site 13; Gremmen and Smith 1999). Its initial spread from Cave Bay has averaged approximately 280 m year⁻¹ on the east coast, with larger movements involved in the colonization of the west coast. Once established in a suitable site, it seems to spread rapidly. The stands at Penguin Beach (Site 2) are at least as extensive as those at Cave Bay, and fairly large, dense stands have already formed at several seal-dominated sites where the species was not found in 1998 (e.g. Sites 5, 8, 10 and 13).

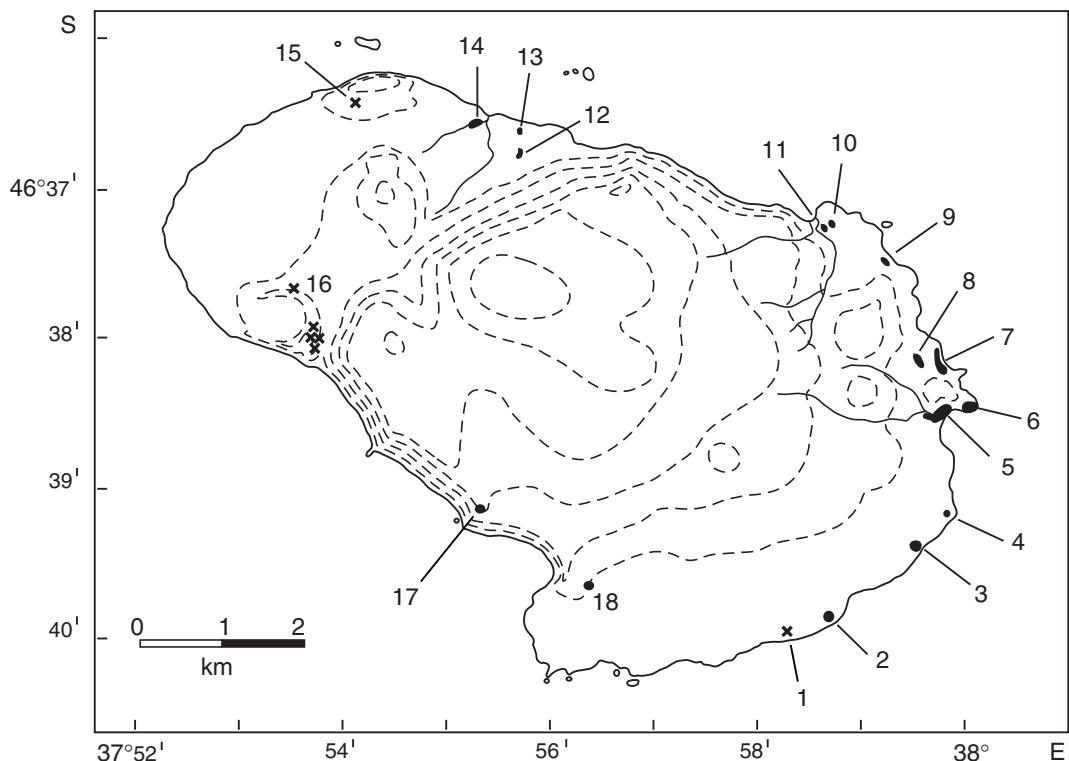


Fig. 2: Distribution of *Sagina procumbens* on Prince Edward Island in 2001 and 2003. The symbol x denotes small plants removed in April 2001 (see Table II)

Sagina procumbens

This species was first recorded at Prince Edward Island in 1997 at two east coast localities (Sites 2 and 5 in Table II and Fig. 2), and then at two further localities in 1998 (Sites 3 and 4; Gremmen and Smith 1999). In 2001 it was found at another seven localities on the eastern side of the island, suggesting an average spread of c. 800 m year⁻¹. It was recorded for the first time on the west side of the island in April 2001, but some of the localities discovered there in December 2001 (e.g. Site 14, Hope Stream, Table II) were heavily infested with some very large plants (cushions in excess of 1 m²), suggesting that they were colonized several years previously. VRS did not visit Hope Stream in April 2001, but it was inspected in 1998 (by NJMG and D. C. Nel, Percy FitzPatrick Institute, University of Cape Town) and it is unlikely that the species was overlooked there then. VRS removed all *S. procumbens* plants he found on the west coast in April 2001 (Sites 15 and 16 in Fig. 2). None was recorded at these sites

in December 2001, but had PGR been aware of the April findings the two sites would have been inspected more closely.

In 2001, *S. procumbens* was less abundant than *P. annua* at Prince Edward Island, but it was equally widely dispersed (Figs 1, 2). It co-occurred with *P. annua* at seven of 18 sites and tended to be more abundant at these sites. Most sites with *S. procumbens* were influenced by seabirds or seals, but it was also at sites with little or no animal influence, e.g. *Crassula* and *Cotula* salt-spray communities along cliff tops on the east coast (Sites 1 and 2), inland mires (sites 12 and 18), and dry feldmark slopes on Kent Crater, Vaalkop and above McNish Bay (sites 15–17).

Cerastium fontanum

This species is locally abundant, but remains the most restricted of the three alien plants found on Prince Edward Island, only occurring on the west coast (Fig. 3).

Table II: *Sagina procumbens* populations on Prince Edward Island in 2001 and 2003. The locations of numbered sites are shown in Figure 2

Site	Status and habitat
1*	A single, small plant removed in April 2001 from <i>Crassula</i> cliff-top vegetation; none seen in December 2001
2	Fairly common in <i>Crassula</i> cliff-top vegetation; seven large plants found in May 1997 ¹ . Possibly spreading farther inland in 2001
3	Extensive mats >200 m ² , concentrated in an area where fur seals haul out. Large cushions (total extent >100 m ²) were already present in May 1998 ¹
4	Near East Cape: scattered, fairly small plants in a coastal area of <i>Cotula</i> and <i>Crassula</i> with moderate seabird activity, but no seals. This is in the same area where well-established plants were present in May 1998 ¹ , but no large plants were found in 2001
5	Cave Bay: quite common on the fur-seal-dominated slope area north of the beach, with a concentration in the disturbed area where the old hut was situated. Two plants were found here in May 1997 ¹ . A few plants occur high up the slope along the route to the interior, but none was found above the level of the inland cliffs (Golden Gate)
6*	RSA Point: abundant on the southern part of the point, with total cover >50% in some areas, becoming less frequent closer to the macaroni penguin <i>Eudyptes chrysophrys</i> colony (where <i>Poa cookii</i> predominates)
7*	A few plants on the slope south of the fur seal-dominated area, but many more forming large cushions on the north slope, with scattered plants extending north along the inner edge of a rockhopper penguin colony
8*	Scattered plants around white-chinned petrel burrows on a denuded area of <i>Blechnum penna-marina</i> slope between two mire areas
9*	Scattered plants around white-chinned petrel burrows on the cliff top
10*	Albatross Valley: a few small plants on mire vegetation, at the edge of the areas influenced by fur seals and wandering albatrosses <i>Diomedea exulans</i>
11*	As Site 10; the two sites are separated by a deep stream valley
12*	A few small plants at the edge of a small pool (stream) in an area of level mire, inland of the area where most fur seals penetrate
13*	Several small and medium-sized plants on a stream bank used as a commuting route by fur seals
14*	Western tributary of Hope Stream: quite common in the fur-seal-dominated area; some large cushions >1 m ² , with the total affected area >10 m ²
15*	Vaalkop: seven small plants removed in April 2001 from c. 20 m diameter area on southern slope; none seen in December 2001
16*	Kent Crater: scattered small plants (<6 cm diameter) on dry feldmark along 80 m crest of eastern crater rim (288 plants), plus a single plant on north side. All plants found in April 2001 were removed; none seen in December 2001
17*	Small plants (<10-cm diameter) in open, high-altitude feldmark in 2003
18*	Large, coalescing cushions in mire vegetation around a small lake found in 2003, possibly overlooked in 2001

¹ Gremmen and Smith (1999)

* New sites

In 2001 it was found at five sites, two of which are new records (Table III). It colonizes open areas on dry feldmark and scoria slopes, as well as erosion slips and slumps. The average rate of spread since 1998 has been approximately 370 m year⁻¹, with a leap of at least 1 km to reach Vaalkop (Site 4). Its current range is consistent with gradual spread from its initial colonization site at Kent Crater.

DISCUSSION

All three alien plants found at Prince Edward Island are widespread, naturalized species at adjacent Marion Island (Gremmen 1975, Bergstrom and Smith 1990, Gremmen and Smith 1999). Two of the three alien plants have arrived at the island during the past 20 years, despite strict controls on human visits to the island (Prince Edward Islands Management Plan Working Group 1996). It is not known whether the two recent arrivals colonized Prince Edward Island naturally from Marion Island (i.e. seeds carried by

seabirds or the wind), or were carried there by people (Bergstrom and Smith 1990, Gremmen and Smith 1999). The distributional data presented here, coupled with the virtual lack of human traffic on the island, argues strongly that dispersal around Prince Edward Island is primarily by natural means. For example, the presence of *Sagina* and *P. annua* at remote, isolated petrel colonies suggests that propagules are dispersed either by birds or the wind. Ryan et al. (2003) show the first definite movements of birds from Marion to Prince Edward Island, with three southern giant petrels *Macronectes giganteus* banded as chicks at Marion being found breeding on Prince Edward during the December 2001 survey.

In general, the dispersal rates estimated for the alien species at Prince Edward Island are 2–3 times higher than those calculated for the same species at Marion Island (Gremmen and Smith 1999). The more rapid dispersal on Prince Edward Island has taken place despite the virtual absence of humans there. One plausible explanation for the faster spread is the much higher densities of seabirds and, to a lesser extent, fur seals at Prince Edward Island, which appear to be

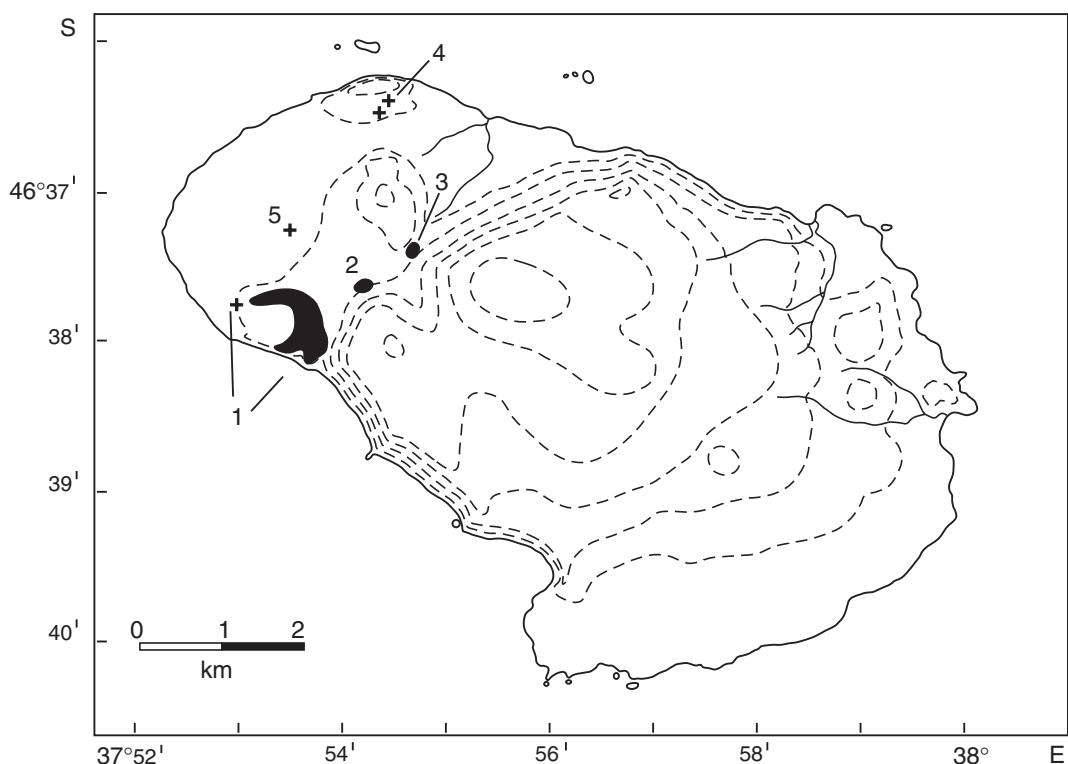


Fig. 3: Distribution of *Cerastium fontanum* on Prince Edward Island in 2001. The symbol + denotes single or small groups of plants (see Table III)

important vectors in spreading propagules. The rapid increase in numbers of fur seals (Bester *et al.* 2003) may have aided the recent spread of *P. annua* by creating more suitable habitat for it. Climate amelioration

or a succession of warm summers, resulting in the production of more viable seeds, might also have aided the spread of alien plants during the last few years (Smith 2002). Climate change is predicted to facilitate

Table III: *Cerastium fontanum* populations on Prince Edward Island in 2001. The locations of numbered sites are shown in Figure 3

Site	Status and habitat
1	Kent Crater: abundant on dry feldmark slopes (mostly outer slope and crest, but also on the inner slopes). A few plants occur off the crater walls, mostly in the exposed margins around the lake shores at the crater entrance. Its range has increased considerably since it was first found in 1987 ¹ , but appears to be little changed since 1994 ²
2	Foot of the western scarp: locally common on a slump area, where individual plants grew much larger and more luxuriantly than at more exposed sites on Kent Crater. First reported from this area in 1998 ²
3	Neck between Moeder-en-Kind and the western scarp: only one large plant was found on loose scoria; it was reported to be numerous in this area in 1998 ² , but it may have been overlooked because observers walked farther from the foot of the western scarp
4*	Vaalkop: several groups of plants on the southern and eastern slopes, each containing 5–10 individuals
5*	Black lava flow east of West Point: one medium-sized plant on flat expanse of lava in April 2001

¹ Bergstrom and Smith (1990)

² Gremmen and Smith (1999)

* New sites

the establishment and spread of alien species in the Antarctic (Kennedy 1995).

Gremmen and Smith (1999) suggested that the rapid spread of *Sagina* on Marion Island during the 1990s could be linked to the exponential increase of the plant around the base area (Gremmen 1997), resulting in a massive increase in the production of seeds. This mechanism does not appear to account for the fast spread of the plant on Prince Edward Island, where it has dispersed before building up a significant population around the initial sites of infestation. However, given that colonization of Prince Edward Island by this species may well have been "natural", it is possible that the widespread, small populations on Prince Edward Island are the result of multiple invasions from Marion Island. Many of the long-distance dispersal events of *Sagina* at Marion appear to be linked to human activities, with focal infestations at huts around the island (Gremmen and Smith 1999). This is unlikely to account for its spread at Prince Edward Island, where the greater densities of seabirds are a more plausible vector (cf. its occurrence at colonies of white-chinned petrels *Procellaria aequinoctialis*).

Gremmen and Smith (1999) argued that alien plants have a negligible impact on the terrestrial ecosystems at Prince Edward Island, although they did suggest that *S. procumbens* has the potential for a significant impact. The situation on Marion Island, where alien plants (especially *S. procumbens* and *Agrostis stolonifera*) are influencing the island's biota and ecosystem severely (Gremmen et al. 1998), suggests that Prince Edward Island will be similarly susceptible to invasive exotic plant species. Our surveys show that the abundance and distribution of *Sagina* has increased much faster than on Marion Island. Control was deemed "very difficult" based on the species' range in 1998 (Gremmen and Smith 1999), and it is now probably too late to instigate control measures. In any case, given the huge source of *Sagina* on Marion Island, and the likelihood that it arrived (possibly several times) "naturally" at Prince Edward Island, control measures are likely to be futile. Judging from what we know about the ecological preferences of *Sagina* on Marion Island, areas offering ideal habitats for the species are numerous, large and widespread on Prince Edward Island. It is inevitable, therefore, that *Sagina* is going to markedly influence the island's biota and ecology.

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A view over the camp at Cave Bay that was used for the 2001 survey of seabirds and seals at Prince Edward Island (photo R. J. M. Crawford)