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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 Subtropical 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°52´S, 37°51´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 fledging 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 constructed 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 ith and $(i+1)$th sample ($i = 1, 2\ldots, k\text{-}1$), k being the number of recapture events, and p, the capture probability for all animals in the ith sample ($i = 1, 2\ldots, k$).

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 biennual 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*

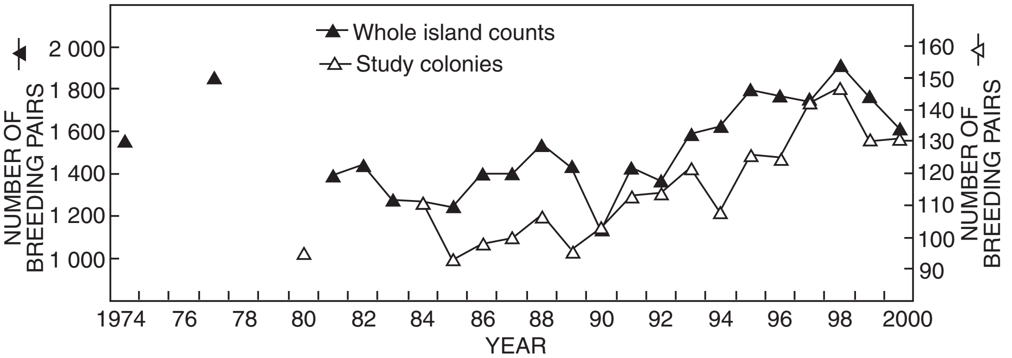

Fig. 1: Counts of breeding pairs of wandering albatrosses and within the two long-term study colonies at Marion Island that have been monitored the longest. Counts were made in January after completion of egg laying

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 5ºS, 5ºN and 150ºW, 90ºW (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).

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

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

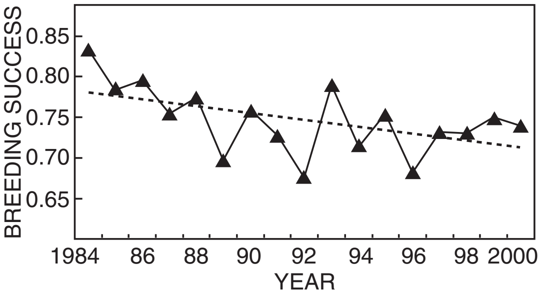

Fig. 2: Mean number of chicks fledged per pair for wandering albatrosses breeding at Marion Island, 1984–2000

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 ± 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%; $\chi^2 = 22.4$; $p < 0.001$).

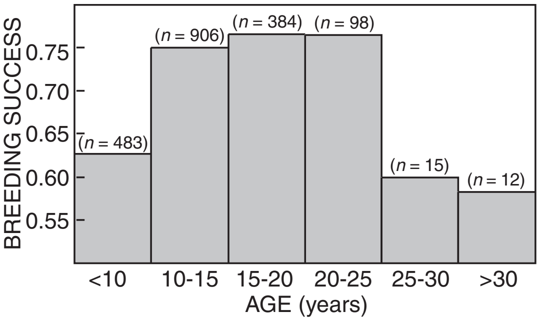

Fig. 3: Mean number of chicks fledged per pair per breeding attempt for wandering albatrosses at Marion Island of different ages, 1984–1990

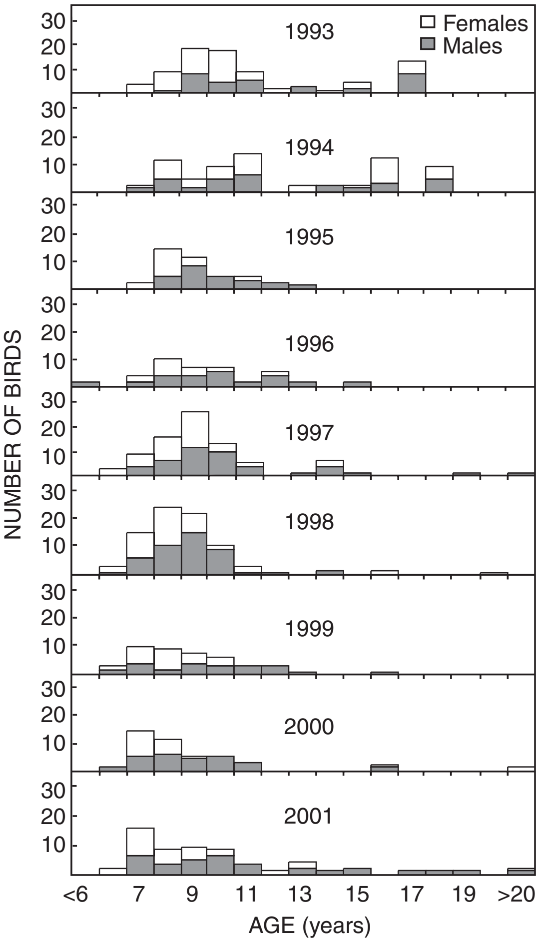

Fig. 4: Numbers of wandering albatrosses of different ages recorded breeding for the first time at Marion Island, 1993–2001

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.

Mate fidelity and mate loss

Analyses were limited to all breeding attempts during

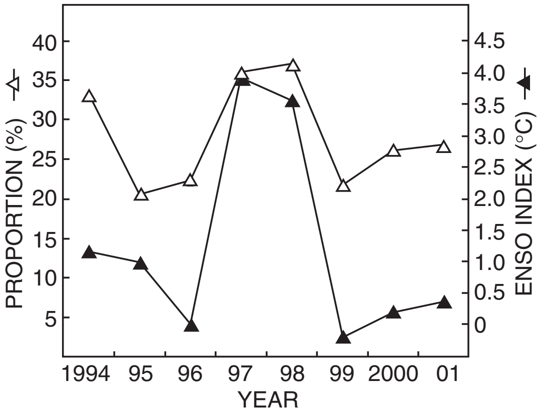

Fig. 5: Proportion of wandering albatrosses in the breeding population at Marion Island that were breeding for the first time and the annual maximum *Niño* 3 (ENSO) index,1984–2000

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

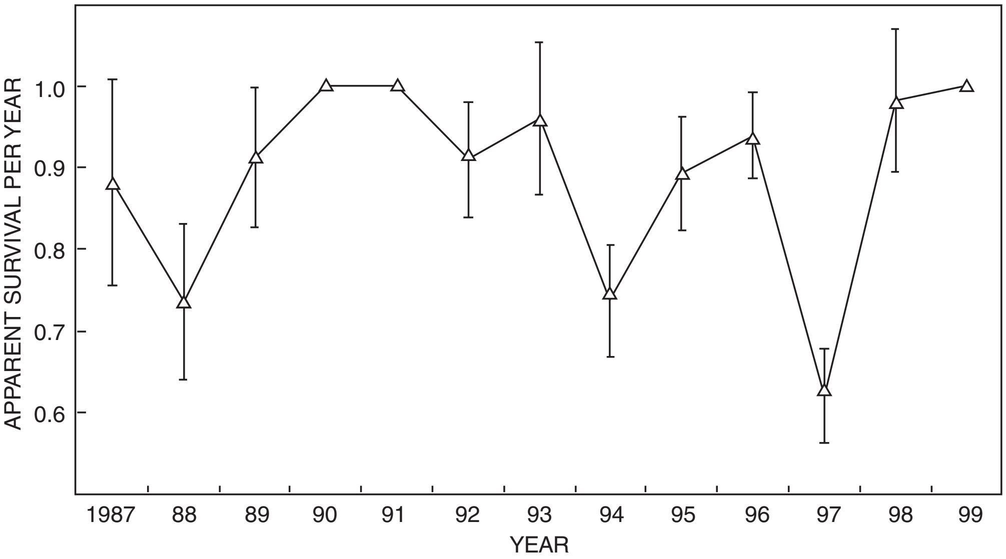

Fig. 6: Annual survival rate of juvenile wandering albatrosses (both sex combined) at Marion Island, 1987–1999

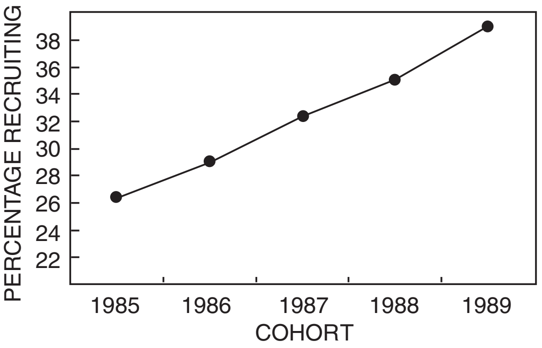

Fig. 7: Percentage of birds from the 1985–1989 cohorts of wandering albatrosses at Marion Island that recruited to the breeding population

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 ± 0.004%. Male juvenile survival (90.1 ± 0.006%) was similar to that of females (89.8 ± 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 ± 0.008%. Male and female adult survival was 95.7 ± 0.009 and 92.6 ± 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.

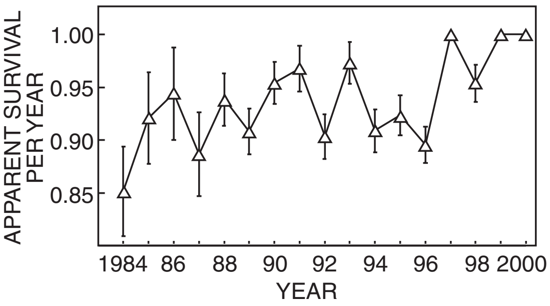

Fig. 8: Annual survival rate of adult wandering albatrosses (both sex combined) at Marion Island, 1984–2000

Correlations with other populations and longline fishing effort

Pelagic longline fishing effort in the southern Indian Ocean (south of 30ºS, 20º–141ºE) and in the vicinity of the Prince Edward Islands (35º–60ºS, 25º–50ºE), 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°–60°S, 25°–50°E

[2] South of 30°S, 20°–141°E

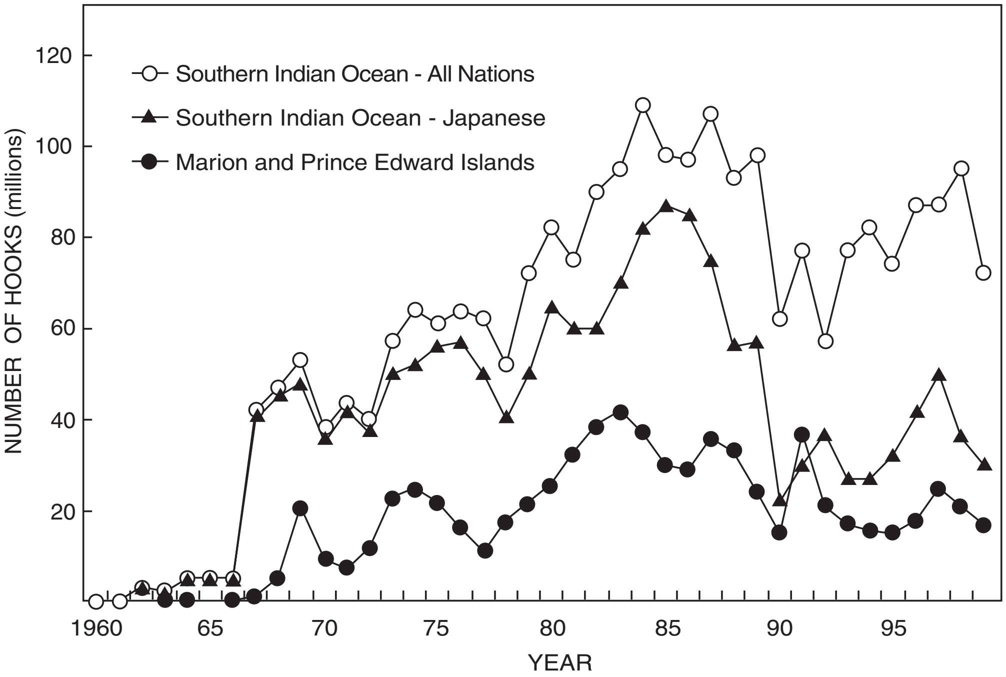

Fig. 9: Trends in the pelagic longline fishing effort of Japanese vessels and overall in the southern Indian Ocean (south of 30°S; 20–141°E) and in the vicinity of the Prince Edward Islands (35–60°S; 25–50°E), 1960–1999

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

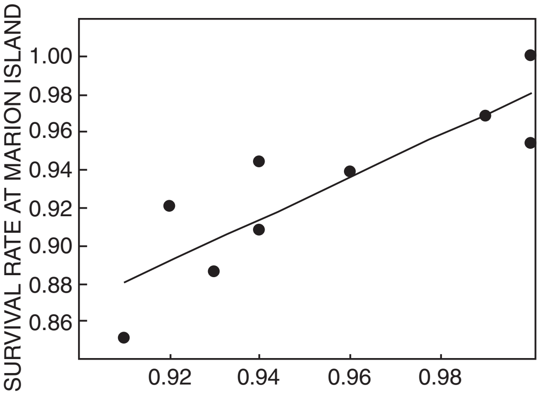

Fig 10: Relationship between annual survival rates of adult wandering albatrosses breeding on Marion Island and the Crozet Islands between 1984 and 1991 (r = 0.818; p = 0.013)

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

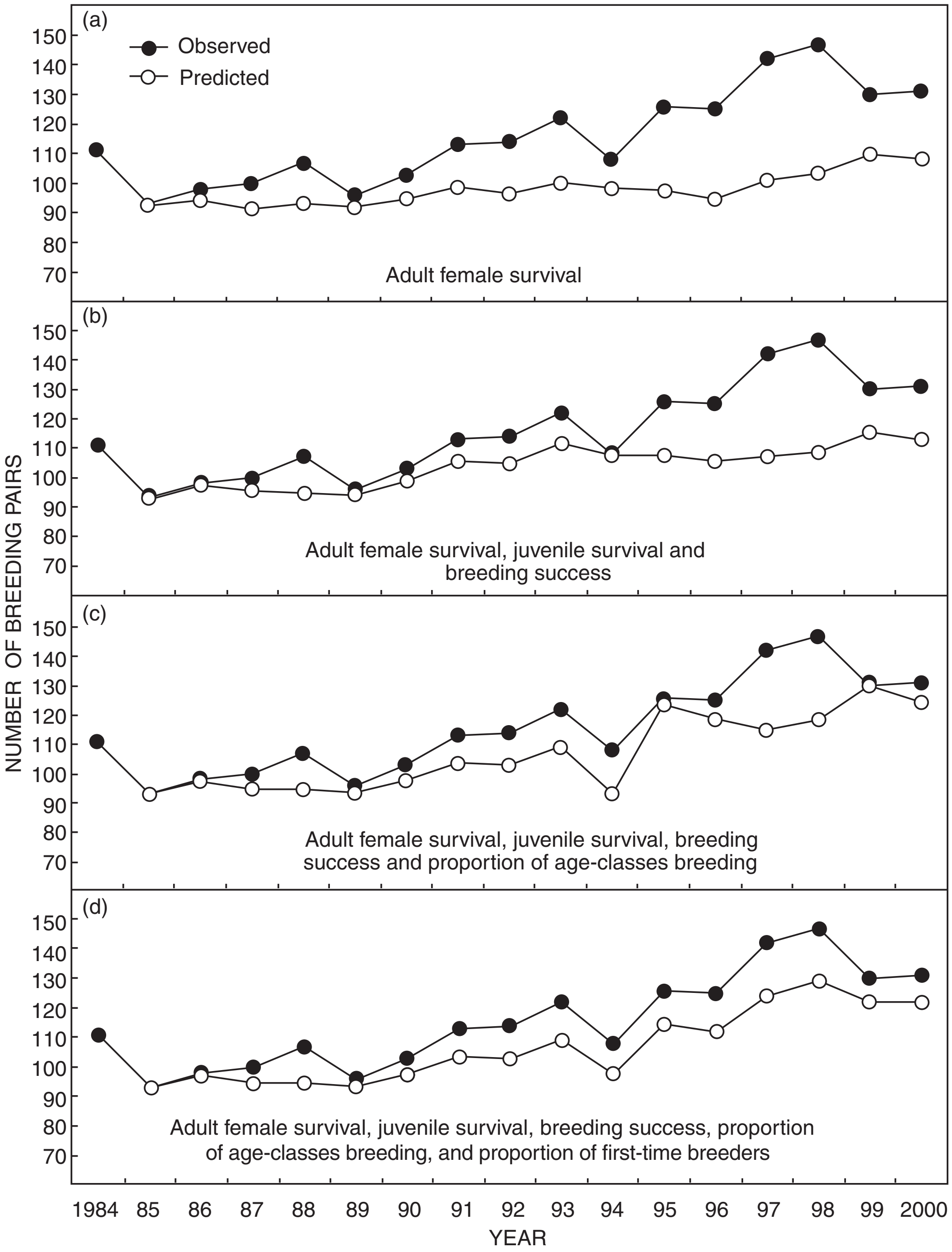

Fig. 11: Comparison between observed and predicted (using age-structured models) numbers of breeding pairs of wandering albatrosses in study colonies on Marion Island. Annual parameters that were varied according to measured data are indicated for each model (a–d). Means for the study period were used 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 40–45ºS) 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 40ºS (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 70ºE (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
	Combined cohorts			
(1)	$[(\phi(\mathrm{gat}), p(\mathrm{at}))]$	10 497	562	3 060
(2)	$[(\phi(\mathrm{at}), p(\mathrm{at}))]$	10 143	389	3 198
(3)	$[(\phi(\mathrm{t}), p(\mathrm{t}))]$	12 644	42	6 402
(4)	$[(\phi(\mathrm{ga}), p(\mathrm{ga}))]$	10 293	85	3 962
(5)	$[(\phi(\mathrm{a}), p(\mathrm{a}))]$	10 290	43	4 046
(6)	$[(\phi_{1\text{-}9}(\mathrm{g}), \phi_{10\text{-}}(\mathrm{ga}), p_{1\text{-}9}(\mathrm{g}), p_{10\text{-}}(\mathrm{ga}))]$	11 995	53	5 730
(7)	$[(\phi_{1\text{-}9}(\mathrm{g}), \phi_{10\text{-}}(\mathrm{g}), p_{1\text{-}9}(\mathrm{g}), p_{10\text{-}}(\mathrm{g}))]$	12 019	8	5 846
(8)	$[(\phi_{1\text{-}9}(\mathrm{c}), \phi_{10\text{-}}(\mathrm{g}), p_{1\text{-}9}(\mathrm{c}), p_{10\text{-}}(\mathrm{g}))]$	12 021	6	5 852
(9)	$[(\phi_{1\text{-}9}(\mathrm{c}), \phi_{10\text{-}}(\mathrm{c}), p_{1\text{-}9}(\mathrm{c}), p_{10\text{-}}(\mathrm{c}))]$	12 023	4	5 859
	Adult breeders only			
(1)	$[(\phi(\mathrm{gt}), p(\mathrm{gt}))]$	21 438	84	9 808
(2)	$[(\phi(\mathrm{t}), p(\mathrm{t}))]$	21 414	44	9 866
(3)	$[(\phi(\mathrm{c}), p(\mathrm{c}))]$	22 178	2	10 715

ϕ = Apparent survival rate
$\phi_{1\text{-}9}$ = Apparent survival rate for Ages 1–9
$\phi_{10\text{-}}$ = Apparent survival rate for Ages 10 and older
p = Recapture probability
$p_{1\text{-}9}$ = Recapture probability for Ages 1–9
$p_{10\text{-}}$ = Recapture probability for Ages 10 and older
g = Sex
a = Age
t = Time
c = Constant