

DEMOGRAPHY AND POPULATION TRENDS OF THE ATLANTIC YELLOW-NOSED ALBATROSS

RICHARD CUTHBERT^{1,4}, PETER G. RYAN², JOHN COOPER³ AND GEOFF HILTON¹

¹Royal Society for the Protection of Birds, The Lodge, Sandy, Bedfordshire, UK

²Percy FitzPatrick Institute of African Ornithology, University of Cape Town, Rondebosch 7701, South Africa

³Avian Demography Unit, University of Cape Town, Rondebosch 7701, South Africa

Abstract. The Atlantic Yellow-nosed Albatross (*Thalassarche chlororhynchos*) breeds only at the Tristan da Cunha archipelago and Gough Island in the central South Atlantic Ocean, and is threatened by mortality from longline fisheries operating in the South Atlantic. Demographic data have been collected from two study colonies on Gough Island and Tristan da Cunha for 20 years. Annual variation in the number of breeding birds was strongly correlated between the two islands, and over the whole study period both study populations have trended downward at around 1.2% per year. The number of established breeders on Gough Island has declined more rapidly, and significantly, at an annual rate of 2.3%. Monitoring established breeders may be a sensitive means of detecting population trends. Average breeding success (67–69%) and breeding frequency (66–65%) were very similar on the two islands. On Gough Island immature and adult annual apparent survival averaged $88 \pm 3\%$ and $92 \pm 1\%$, respectively, and apparent survival from fledging to age 5 has averaged $31 \pm 8\%$. Apparent adult survival on Tristan da Cunha averaged only $84 \pm 2\%$. Annual survival of Tristan birds was negatively correlated with longline fishing effort in the South Atlantic Ocean. Population modeling predicts annual rates of decrease of 1.5–2.8% on Gough Island and 5.5% on Tristan da Cunha. Comparison with congeners suggests that the observed and predicted decreases are most likely to be caused by low adult and immature survival. The conservation status of Atlantic Yellow-nosed Albatrosses should be changed from Near Threatened to Endangered.

Key words: Atlantic Yellow-nosed Albatross, conservation, demography, longline mortality, survival, *Thalassarche chlororhynchos*.

Demografía y Tendencias Poblacionales del Albatros *Thalassarche chlororhynchos*

Resumen. El albatros *Thalassarche chlororhynchos* sólo se reproduce en el archipiélago Tristan da Cunha y en la isla Gough en el Océano Atlántico Sur central, y se encuentra amenazado debido a la mortalidad causada por las pesqueras de espinel que operan en el Atlántico Sur. Se colectaron datos demográficos durante 20 años en dos colonias reproductivas en el archipiélago Tristan da Cunha y en la isla Gough. La variación anual en el número de aves reproductivas se correlacionó fuertemente entre las dos islas, y durante todo el período de estudio ambas poblaciones han presentado tendencias de decrecimiento de aproximadamente un 1.2% por año. El número de reproductores establecidos en la isla Gough ha disminuido significativamente y más rápidamente, a una tasa anual de 2.3%. El monitoreo de los reproductores que se establecen puede ser un medio sensible para detectar tendencias poblacionales. El éxito reproductivo promedio (67–69%) y la frecuencia de cría (66–65%) fueron muy similares en ambas islas. En la isla Gough la sobrevivencia aparente de inmaduros y adultos fue en promedio de $88 \pm 3\%$ y $92 \pm 1\%$, respectivamente. La sobrevivencia de volantones a la edad de 5 años fue en promedio de $31 \pm 8\%$. La sobrevivencia aparente de adultos en Tristan da Cunha fue en promedio sólo de $84 \pm 2\%$. La sobrevivencia anual de las aves de Tristan se correlacionó negativamente con el esfuerzo de la pesca de espinel en el Océano Atlántico Sur. Los modelos poblacionales predicen tasas de disminución anuales de un 1.5–2.8% en la isla Gough y de un 5.5% en Tristan da Cunha. Comparaciones con congéneres sugieren que las disminuciones observadas y predichas son muy probablemente causadas por la baja sobrevivencia de adultos e inmaduros. La categoría de conservación del albatros *T. chlororhynchos* debería ser cambiada de “casi amenazada” a “en peligro.”

Manuscript received 8 October 2002; accepted 17 April 2003.

⁴Present address: The Macaulay Institute, Craigiebuckler, Aberdeen AB15 8QH, UK. E-mail: richard.cuthbert@yahoo.co.uk

INTRODUCTION

The Atlantic Yellow-nosed Albatross (*Thalasarche chlororhynchos*) breeds on the islands of Tristan da Cunha and at Gough Island in the central South Atlantic Ocean (Rowan 1951, Hagen 1952). In the 1970s its population was estimated at 27 000 to 46 000 breeding pairs (Croxall and Gales 1998). The majority of birds are found on Tristan da Cunha with an estimated population of 16–30 thousand pairs on the main island, with around 4500 and 1100 pairs on Nightingale and Inaccessible Islands, respectively (Richardson 1984, Fraser et al. 1988). In 1974 Gough Island was believed to support around 5–10 thousand pairs, although this figure is based on very limited sampling (Richardson 1984). There have been no recent estimates from either Gough Island or Tristan da Cunha, but a partial count on Inaccessible Island in 1999–2000 suggests that the population may have decreased since the late 1980s (Ryan and Moloney 2000).

This paucity of knowledge on the status of Atlantic Yellow-nosed Albatross occurs despite increasing concern about changes in the population size of albatrosses and petrels in the southern oceans. Numbers of albatrosses at several islands have shown major decreases since the 1950s; a time scale that corresponds to the dramatic increase in longline fishing throughout the foraging range of these species (Weimerskirch et al. 1997, Croxall and Gales 1998, Tuck et al. 2001). Incidental mortality on longline hooks (Brothers 1991) is the probable main cause of these population decreases (Weimerskirch and Jouventin 1987, Croxall et al. 1990, de la Mare and Kerry 1994, Gales 1998), although changes in at-sea food availability may have affected certain species (Weimerskirch and Jouventin 1998, Waugh et al. 1999). A number of long-term studies indicate that the decreases appear mainly to be a consequence of reduced adult survival (Weimerskirch and Jouventin 1987, Croxall et al. 1990) or lowered recruitment (Prince et al. 1994, Croxall et al. 1998, Waugh et al. 1999).

The only estimates of longline mortality of Atlantic Yellow-nosed Albatrosses come from the Brazilian fleet, where Olmos et al. (2001) calculated annual mortality of 568 (range 399–738) birds from the bottom longline fleet and 329 (172–486) birds from pelagic longline vessels. Mortality of Atlantic Yellow-nosed Albatrosses is also caused by other South American

fleets (Stagi et al. 1998). Seabird bycatch rates off Brazil and Uruguay are high in comparison with those reported for most other Southern Hemisphere fisheries (Vaske 1991, Neves and Olmos 1998, Stagi et al. 1998, but see Ryan et al. 2002). National and licensed foreign longline fishing fleets operating off southern Africa also kill Atlantic Yellow-nosed Albatrosses (Ryan and Boix-Hinzen 1998, Ryan et al. 2002), and along with the Brazilian and Uruguayan fleets the bycatch rates of seabirds in this area are very high, especially for Japanese vessels (Ryan et al. 2002). The South American and South African fleets are responsible for only a small proportion of the total longline fishing effort in the South Atlantic, with most fishing being undertaken by Japan and Taiwan (Tuck et al., in press). Consequently, the total number of Atlantic Yellow-nosed Albatrosses that are killed by longline fishing in the South Atlantic Ocean is likely to be far higher than the available estimates. Adding to the general problem of bycatch, the sex ratio of Atlantic Yellow-nosed Albatrosses killed is strongly female biased (Neves and Olmos 1998), which implies a greater adverse affect on the population growth rate than an unskewed sex ratio (Weimerskirch et al. 1997).

Currently the Atlantic Yellow-nosed Albatross is listed as Near Threatened (BirdLife International 2000). However, if further information “confirms that the species is suffering a continuing decline or a significant overall reduction” then its conservation status would need to be altered (BirdLife International 2000: 631). In this study, we present information from a 20-year study of marked birds at Gough Island and Tristan da Cunha. We use these results to provide the first estimate of demographic parameters and population trends of the Atlantic Yellow-nosed Albatross, and to reassess its conservation status.

METHODS

STUDY SITES

The study was conducted at two small, well-defined colonies of Atlantic Yellow-nosed Albatrosses: one between the weather station and Seal Beach, southeast Gough Island (40° 21'S, 9° 53'W), the other between Hottentot and Cave Gulches on the base of Tristan da Cunha (37°S, 12°W). Adults in the Gough Island study colony were first banded in 1979, and monitoring was undertaken in each year from 1982 to 2001 by

volunteers from the South African weather station. The continuity of the project was ensured by regular visits by JC and PGR during personnel changes on the island, when volunteers from each new meteorological team were instructed on the monitoring procedure. The Tristan da Cunha study colony was established in 1984 by the schoolmaster Richard Grundy, and was continued by school children under the guidance of Jim Kerr until 1992. The study stopped after a landslide made it dangerous for the school children to access the colony via Hottentot Gulch. However, it was checked occasionally in later years for counts of breeding pairs, and these counts are used in the analysis.

FIELD METHODS

On Gough Island the study colony was checked at 3-day intervals from early September to mid-October, by which time egg laying is completed for the colony. All nests were plotted on a map of the colony and marked with a numbered pole. Thereafter each nest was checked until the single egg was laid and, where possible, the identity of both incubating birds had been recorded. All empty nests were checked for the presence of broken eggs or fragments of shell, and these were recorded as a breeding attempt. After egg laying, nests were checked at 2-week intervals until the nest failed or chicks fledged (early May). The presence or absence of an incubating bird or chick was recorded on each visit. All breeding birds and some nonbreeders were banded with a metal monel band (Mechaniska, Bankyerd, Sweden and Lambournes, Leominster, UK) on the right leg, and breeding birds were banded with a unique color combination of three bands on the left leg. Band loss was rare, with 3.3% of birds losing a colored band. These birds could still be identified either by reading the monel band or from the color combination of the two remaining bands. Where any uncertainty over the identity of birds remained, those individuals were removed from the survival analysis (3 of 353 birds excluded). Colored bands were replaced in the 1999–2000 and 2000–2001 breeding seasons with alphanumeric darvic bands (Pro-touch, Saskatoon, Saskatchewan, Canada). All fledglings were banded on the left leg with a metal band. In some years of the study, the areas surrounding the study colony were checked, to search for any banded birds breeding outside the study colony.

The monitoring protocol on Tristan da Cunha was similar to Gough Island, although checks were made less frequently for logistical reasons. All breeding birds and fledglings were banded, and eggs and chicks were checked at approximately weekly and monthly intervals, respectively. Birds were not fitted with color or darvic bands, so the metal bands had to be checked from close quarters. Consequently, these birds may have experienced more disturbance than the Gough Island study birds, although this is offset by the less frequent nest checks.

PARAMETER ESTIMATES

Hatching success was defined as the proportion of eggs that hatched. Fledging success was the proportion of hatched chicks that were presumed to have fledged from the colony (this presumption was checked by searching for dead banded fledglings around the colony at the end of each season). Total breeding success was the proportion of eggs that survived to fledging. The overall mean and standard error of each parameter were estimated following Burnham et al. (1987), which removes sampling variance from a series of estimates to obtain a better estimate of the mean (Gould and Nichols 1998).

Apparent annual adult survival was estimated from mark-recapture analysis using program MARK (White and Burnham 1999). Four different models were fitted to the data set: constant survival and constant probability of recapture [$\phi(\cdot) p(\cdot)$], time-variable survival and constant probability of recapture [$\phi(t) p(\cdot)$], constant survival and time-variable probability of recapture [$\phi(\cdot) p(t)$], and time-variable survival and variable recapture probability [$\phi(t) p(t)$]. The best model was assessed using Akaike's Information Criterion with small sample size correction (AIC_c) and significance was assessed with likelihood-ratio tests. Before accepting the results of the model we tested the goodness of fit of the data to the model using bootstrapped goodness of fit tests in program MARK. Annual adult survival was calculated for all breeding birds, and a bird was included in the recapture group if it was recorded at any stage breeding in the study colony. All birds were recorded as either present or absent for each breeding season.

On Gough Island, the oldest age at which fledglings were first recaptured was 12 years. Consequently, we estimated the average proportion of birds surviving to recapture for cohorts

of chicks banded from 1982 to 1988, because chicks from later cohorts had less chance of being recaptured. Apparent survival from fledging to age 5 years and apparent annual immature survival (birds aged 6 to 10 years) was estimated using program MARK and an age-dependent mark-recapture model. Four recapture models were run, all with a variable probability of recapture: variable survival with no age-dependence, variable survival of juveniles and immature birds, constant survival of juveniles and variable survival of immature birds, and constant survival of juveniles and immature birds. This survival analysis was restricted to the Gough study population, because the low and variable study effort on Tristan da Cunha in later years means that very few fledglings have been recaptured.

The average age at first breeding was calculated as the age at which 50% of recruiting birds were found breeding for the first time. This was estimated from the cumulative proportion of birds found breeding at each age, and could only be calculated for the Gough study colony. To estimate the frequency of breeding we used the individual breeding history of birds that were monitored for a total of 10 or more consecutive breeding seasons on Gough Island ($n = 104$ birds) and for six or more consecutive seasons on Tristan da Cunha ($n = 44$). For each individual we calculated the number of breeding attempts and number of years from the first recorded year of breeding. From all birds, we calculated the proportion breeding from the overall pooled totals of breeding attempts and years.

The numbers of established breeders and new breeders in the population each year were examined to further investigate trends in breeding numbers in the Gough study colony. To ensure that breeding birds caught for the first time were genuinely new recruits, rather than established breeders that had not previously been captured, we examined the maximum period between recaptures for all breeding birds. This period varied from 0–15 years, with 95% of birds having a maximum gap ≤ 4 years ($n = 317$ birds). Consequently, we only examined trends in new and established breeders from 1986 onwards, four years after the start of the banding program. This should ensure that over 95% of first-time captures were genuine new recruits to the population.

POPULATION MODELING

We developed an age-structured version of a Leslie matrix model, which, as usual for population models, only considered the female population (Burgman et al. 1993). Rather than just using the simple mean for each parameter, the model included parameter uncertainty by randomly selecting values for each parameter over a range of values that reflected the precision of the estimate. For each run of the model, mean values for all parameters were chosen independently and at random from a normal distribution using the estimated mean and standard error of each parameter. The upper and lower limits of each parameter were constrained to lie within the estimated lower and upper 95% confidence limits, with the exception of average age at first breeding, where we used the observed maximum and minimum ages. The model was set to run for a 30-year period. The starting population of the model was 40 000 breeding females, which approximates the total estimated population size of the Atlantic Yellow-nosed Albatross (Croxall and Gales 1998). The model estimated the population's yearly intrinsic growth rate (r) over a 30-year period. This was calculated for both the total population (adult, immature, and juvenile birds) and the breeding population of birds. The model was written on an Excel spreadsheet following the methods of Slooten et al. (2000) and Cuthbert et al. (2001). Because each run of the model used a different set of randomly selected parameters, the model was run 2500 times, and the overall mean growth rate and range of growth rates were calculated.

The parameters entered into the model were annual adult survival, annual immature survival, juvenile survival, age at first breeding, breeding frequency, and breeding success. Annual variation was not included in the model, and each 30-year run used the mean value of each parameter selected at random at the start of the run. The number of chicks fledging in each year of the model was divided by two so that the model only considered the female population (assuming a sex ratio of 1:1). The initial age distribution of birds for each model run (i.e., number of one-year-olds, two-year-olds, etc.) was set to a stable age distribution. This was achieved by running the model with the selected parameters for that run, until the proportions of each age class differed by ≤ 0.0001 to the proportions in the previous run (Burgman et al. 1993).

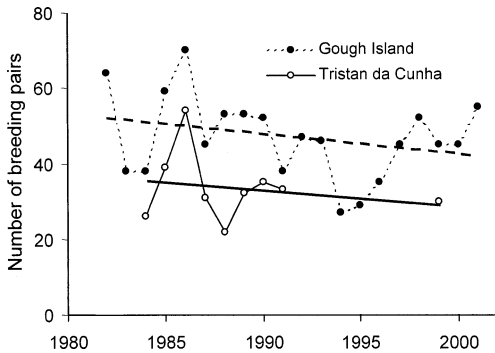


FIGURE 1. Number of incubating Atlantic Yellow-nosed Albatrosses in the study colony on Gough Island from 1982 to 2001 (filled circles and dashed lines) and on Tristan da Cunha from 1982 to 1999 (unfilled circles and solid lines). Linear regressions indicated an annual decrease of 1.1–1.2%, but were not significant.

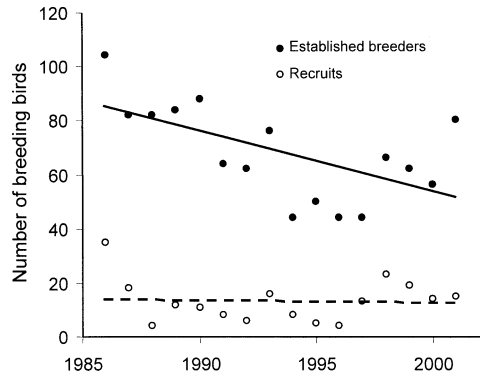


FIGURE 2. Number of established breeding Atlantic Yellow-nosed Albatrosses (filled circles) and recruits (unfilled circles) on Gough Island from 1986 to 2001. The best-fit linear regression indicates a significant decrease for established breeders (solid line, $P < 0.02$) and no significant trend for recruits (dashed line).

Information on longline fishing effort in the South Atlantic Ocean was taken from Tuck et al. (in press). The El Niño-Southern Oscillation index Niño 3 was used as an indicator of at-sea environmental variability (International Research Institute for Climate Prediction 2002). All statistical tests were two-tailed and assumed significant at $P < 0.05$. Proportions were arcsine transformed before statistical analysis. Trends in breeding numbers were calculated using least-squares regression. Data were analyzed using the program SPSS 10.0 (SPSS Inc. 1999). Values are reported as means \pm SE, with 95% confidence intervals (CI). Confidence limits for proportions were calculated after Zar (1999).

RESULTS

BREEDING NUMBERS AND RECRUITMENT

The number of breeding Atlantic Yellow-nosed Albatrosses within the Gough Island and Tristan da Cunha study colonies has varied over the study period (Fig. 1), with an average of 46.7 ± 2.4 incubating pairs (CV = 23.5%) at the Gough study area and 33.6 ± 3.0 incubating pairs (CV = 27.1%) on the Tristan da Cunha study area. Over the whole study period (1982 to 2001) breeding numbers have declined at 1.1% per year in the Gough study colony, although this is not statistically significant (regression slope = -0.5 ± 0.4 , $r^2 = 0.08$, $P = 0.22$). On Tristan da Cunha there was a similar non significant decrease at a rate of 1.2% per year from 1984 to 1999 (regression slope = -0.4 ± 0.8 , $r^2 = 0.04$, $P = 0.61$). Simulation modeling with the ob-

served variance in numbers of breeding birds, annual monitoring at one site, and a rate of decrease of 1.1% indicates that the power to detect such a trend is weak (power = 0.39, RC, unpubl. data) and that over 30 years of monitoring would be required to detect this trend with power ≥ 0.80 .

The number of new birds recruiting as breeders each year (mean 13.2 ± 1.2 birds, range 4–35) had a strong positive influence on the total number of breeding pairs in the year ($r^2 = 0.68$, $n = 16$ years, $P < 0.002$). The number of established breeders in the population decreased significantly from 1986 to 2001 (regression slope = -2.3 ± 0.8 , $r^2 = 0.37$, $P < 0.02$), at an annual rate of 2.3% (Fig. 2). There was no trend in the number of new breeders over this period (regression slope = -0.2 ± 0.5 , $r^2 = 0.01$, $P = 0.74$). With the decrease in established breeders there was an increase in the proportion of new breeders in the study population, which was significant for the period from 1988 to 2001 (regression slope = 0.9 ± 0.3 , $r^2 = 0.47$, $P < 0.01$).

BREEDING SUCCESS AND BREEDING FREQUENCY

From 1982 to 2001 breeding success in the Gough Island study colony has averaged $67 \pm 3\%$ ($n = 19$ years) and with the exception of the 1999–2000 season was relatively constant (Fig. 3). Hatching and fledging success averaged $79 \pm 2\%$ ($n = 20$ years) and $87 \pm 3\%$ ($n = 19$ years), respectively. Breeding success on Tristan da Cunha was very similar to Gough Island,

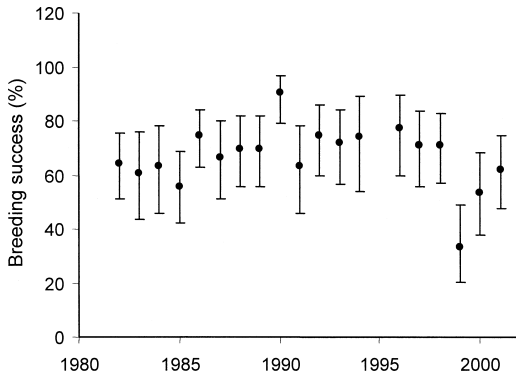


FIGURE 3. Breeding success of Atlantic Yellow-nosed Albatross on Gough Island from 1982 to 2001, mean and 95% confidence limits.

with average breeding success of $69 \pm 3\%$ ($n = 8$ years), hatching success of $79 \pm 3\%$, and fledging success of $88 \pm 3\%$. On Gough Island, the very low breeding success in 1999–2000 (33%) was mainly due to lowered fledging success (48%), rather than low hatching success (69%). Mortality of chicks (9 of 24 chicks within the study area) was observed in this season both within and outside the Gough study colony.

On Gough, birds with a breeding history of 10 or more years made a breeding attempt in 66% of years. Together with the estimated value of breeding success (67%), this indicates that breeding birds have an overall average annual breeding success of 44%. Thus the average pair fledge a chick every 2.4 years. On Tristan da Cunha 44 birds had a breeding history of 6 or more years, with 65% of these birds making a breeding attempt in each year (for comparison birds with a breeding history of ≥ 6 years on Gough Island had a breeding frequency of 66%). With average breeding success of 69%, overall annual breeding success was 45% on Tristan da Cunha.

AGE OF FIRST BREEDING AND SURVIVAL

Fledglings first returned to Gough Island at 5–12 years of age and started breeding between ages 6 and 13 years. Forty-five known-age birds were found breeding within the study colony, including some birds originally banded outside the study area. The cumulative proportion of birds breeding for the first time in each year followed a sigmoidal curve (Fig. 4), with an average age of first breeding of 9.7 ± 1.5 years.

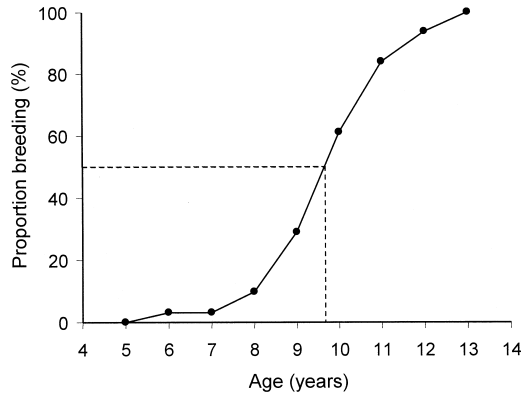


FIGURE 4. Cumulative proportion of ages at first breeding for Atlantic Yellow-nosed Albatrosses, from a sample of 45 known-aged birds captured at first breeding on Gough Island. The dashed line indicates the sample mean.

For chicks on Gough Island banded from 1982 to 1988 (cohorts of birds older than 12 years in 2000), an average of $18 \pm 3\%$ survived until recapture. The overall best-fit mark-recapture model was one with variable detection probability and constant survival in both the juvenile and immature age classes. Survival from fledging to age 5 years averaged $31 \pm 8\%$ (CI 18–49%). Annual survival of immature birds aged 6–10 years was $88 \pm 1\%$ (CI: 80–93%).

For Gough Island, the overall best-fit mark-recapture model of breeding adults for the period 1982–2001 was one with variable survival and variable detection probability (Table 1). There was no significant lack of fit of the data in the model (bootstrapped goodness of fit, $P = 0.37$). Examination of these results indicated that apparent survival was very low in the 1995–1996 breeding season (Fig. 5). The model was re-run with the 1995–1996 season omitted and with a specified gap of 2 years in recapture frequency for this period. The best-fit model was again one with variable survival and variable detection probability, with a low estimate of survival from 1994 to 1997, indicating that the low survival estimate was genuine and not a consequence of poor survey effort in this season. Average adult survival over the entire study (1982–2001) was $92 \pm 1\%$ (CI: 91–93%), and the detection probability over this period was 0.77 ± 0.01 (CI: 0.75–0.79). With this survival estimate, birds on Gough Island have an average breeding life of 12 years (breeding life = [2 –

TABLE 1. Models fitted in MARK to determine the survival and resighting probabilities of adults breeding on Gough Island and Tristan da Cunha, indicating the model deviance, number of parameters, Akaike's Information Criterion (AIC_c), ΔAIC_c and the model weight. There was no significant lack of fit for either the Gough or Tristan da Cunha data, with estimated overdispersion in the datasets of 1.02 and 0.98, respectively. For both sites the models with the lowest AIC_c values were ones with variable survival and variable recapture effort ($\phi(t)$, $p(t)$), indicating this is the best fit model for the data.

Model	Deviance	No. of parameters	AIC_c	ΔAIC_c	Model weight
Gough Island (1982–2001)					
$\phi(t), p(t)$	1853.44	37	3942.94	0.00	0.78
$\phi(\cdot), p(t)$	1890.85	20	3945.41	2.47	0.22
$\phi(t), p(\cdot)$	2105.07	20	4159.63	216.69	0.00
$\phi(\cdot), p(\cdot)$	2145.24	2	4163.41	220.41	0.00
Tristan da Cunha (1982–1991)					
$\phi(t), p(t)$	231.90	16	1182.06	0.00	0.94
$\phi(\cdot), p(t)$	250.06	10	1187.53	5.47	0.06
$\phi(t), p(\cdot)$	257.77	10	1195.23	13.17	0.00
$\phi(\cdot), p(\cdot)$	285.98	2	1207.01	24.95	0.00

$m]/2m$, where m = annual mortality; Prince et al. 1994).

For the Tristan study colony, adult survival could only be estimated for the period 1982 to 1991, as recapture effort was poor or nonexistent in later seasons. The best-fit mark-recapture model for this period was one with variable survival and variable detection probability (Table 1), and there was no significant lack of fit of the data (bootstrapped goodness of fit, $P = 0.47$). Average adult survival over this period was $84 \pm 2\%$ (CI: 80–87%), with an overall detection probability of 0.52 ± 0.03 (CI: 0.47–0.56). For birds on Gough Island, average adult survival was $92 \pm 1\%$ (CI: 90–93%) over the same period.

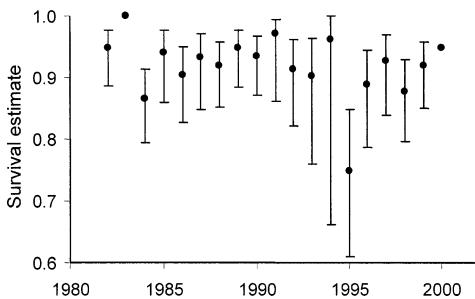


FIGURE 5. Annual adult apparent survival of Atlantic Yellow-nosed Albatrosses on Gough Island from 1982 to 2000, estimated from the best-fit model with variable survival and variable detection probability using program MARK. Values represent the annual survival estimate and upper and lower 95% confidence limits.

EMIGRATION

Fifty-six banded fledglings have been recaptured on Gough Island, with 46 of these captured within the study area and 10 within 100 m of the boundary of the study colony. These results crudely indicate a fledgling emigration rate of around 18% (CI: 9–30%). Movements of breeding adults outside of the Gough study colony were very rare, with only four birds known to have moved out of 355 birds followed over the 20-year study. The observed emigration rate of breeding adults is 1.1% (CI: 0.3–2.9%). If the estimated emigration rates for fledglings and adults are accurate, then juvenile survival of Gough birds may be closer to 37% (estimated juvenile survival [0.31] \times estimated emigration rate [1.18]), and adult survival of Gough birds is estimated to be 93%.

RELATIONSHIP BETWEEN DEMOGRAPHY AND AT-SEA CONDITIONS

The number of breeding birds at the Gough Island and Tristan da Cunha study colonies were strongly correlated across years ($r = 0.74$, $n = 9$, $P < 0.01$, Fig. 1). There were no significant correlations between the Gough and Tristan da Cunha colonies in hatching, fledging, and total breeding success. There were no significant relationships between the Niño 3 index and the number of breeding birds, recruitment, or adult survival of either the Gough or Tristan study populations.

For birds on Gough Island, there was no correlation between adult survival and longline

TABLE 2. Demographic parameters of Atlantic Yellow-nosed Albatrosses from Gough Island and Tristan da Cunha used to construct population models. Unmeasured parameters at Tristan da Cunha used values from Gough Island. Sampling error was incorporated into these parameters by using the methods of Burnham et al. (1987) for the estimate of breeding success and program MARK for the survival estimates. For breeding frequency and emigration, the SE and 95% confidence limits were estimated using a binomial standard deviation and confidence limits (Zar 1999). All values are percentages, except for age at first breeding.

Demographic parameter	Mean \pm SE	95% CI
Gough Island		
Breeding success	67 \pm 3	62–72
Breeding frequency	66 \pm 1	63–68
Age at first breeding (years)	9.7 \pm 1.5	6–13 ^a
Juvenile survival (from 0–5 years)	31 \pm 8	18–49
Annual immature survival	88 \pm 3	80–93
Annual adult survival	92 \pm 1	91–93
Juvenile emigration rate	18 \pm 5	9–30
Adult emigration rate	1.1 \pm 0.6	0.3–2.9
Tristan da Cunha		
Breeding success	69 \pm 3	62–76
Breeding frequency	65 \pm 3	60–71
Annual adult survival	84 \pm 2	80–87

^a Minimum and maximum age at first breeding.

fishing effort in the South Atlantic Ocean ($r = 0.24$, $n = 19$, $P = 0.38$). However, fishing effort was strongly and negatively correlated with annual survival for birds on Tristan da Cunha from 1982 to 1991 ($r = -0.62$, $n = 9$, $P < 0.05$). This relationship appears to be driven by Taiwanese fishing effort ($r = -0.68$, $P < 0.02$), rather than the Japanese fleet ($r = -0.25$, $P = 0.24$). Annual adult survival on Tristan and Gough were not significantly correlated ($r = 0.41$, $n = 9$, $P = 0.18$), nor was there any correlation between recruitment and longline fishing effort for either colony.

POPULATION MODELING

We ran four different population models (Table 2). Model 1 used all the estimated breeding and survival values from Gough Island. Model 2

used all estimated parameters from the Tristan da Cunha study population and where these were unavailable used values from Gough Island. Models 3 and 4 used the same breeding and survival parameters as Models 1 and 2, respectively, but included an emigration rate of 18% for the juvenile age class and an emigration rate of 1.1% for the immature and adult age classes.

The average population growth rates predicted by the four population models are all negative (Table 3), with annual rates of decrease ranging from 1.5% to 6.7% for the total population. The addition of emigration into the models reduced the absolute annual rate of population decrease by 1.1–1.2 percentage points (Table 3), indicating the sensitivity of the model to the inclusion and estimation of this parameter. The absolute

TABLE 3. Projected population growth rates from 2500 model runs simulating 30-year periods of Atlantic Yellow-nosed Albatrosses breeding on Gough Island and Tristan da Cunha. The models produced a mean population growth rate and a range, calculated in terms of the total population and in terms of the breeding population only. See Table 2 for parameter values used in the models.

Model	Total population		Breeding population	
	Mean annual increase (%)	Range (%)	Mean annual increase (%)	Range (%)
1: Gough parameters	-2.6	-4.7 to -0.3	-4.4	-7.4 to -1.1
2: Tristan parameters	-6.7	-11.2 to -2.6	-8.7	-13.2 to -3.6
3: Gough parameters + emigration	-1.5	-3.8 to +0.9	-2.8	-6.2 to +0.5
4: Tristan parameters + emigration	-5.5	-10.0 to -1.1	-7.3	-12.1 to -2.2

rate of decrease was 1.3–1.8 percentage points greater for the breeding population than for the total population. The average predicted annual population growth rate for the Gough Island population with emigration included was -1.5% for the total population and -2.8% for the breeding population. Both models using data from Tristan da Cunha predicted a rapidly decreasing population (Table 3), with the emigration model predicting annual rates of decrease of 5.5% and 7.3% for the total and breeding populations respectively.

DISCUSSION

POPULATION TRENDS

This study provides the first estimates of population trends and demographic parameters of the Atlantic Yellow-nosed Albatross. Over the 20 years of this study both the Gough Island and Tristan da Cunha study colonies have decreased at annual rates of 1.1–1.2%. Neither of these trends is statistically significant, but the power to detect such a trend is poor. Examining the number of established breeders at Gough Island (birds that had made at least one previous breeding attempt) indicated a significant decrease from 1986 to 2001, at an annual rate of 2.3%. The number of new recruits in the Gough Island study colony has remained relatively constant from 1986–2001, and with the decline in established breeders new recruits have made up an increasing proportion of breeding numbers since 1988. These results suggest that there has been a genuine decrease in the numbers of breeding birds over the last 20 years, but that this trend is being masked by annual fluctuations in breeding numbers and an increase in the proportion of birds recruited into the population. Such a pattern is consistent with the results from population modeling using the estimated demographic parameters for the Gough Island population, which predicted an average annual rate of decrease of 1.5% for the total population and 2.8% for the breeding population.

Similar results have been found for Wandering Albatrosses (*Diomedea exulans*), where the proportion of recruits has increased at the same time as there has been an overall decrease in the population (Weimerskirch et al. 1997), and where there has also been a general reduction in age at first breeding (Weimerskirch and Jouventin 1987, Croxall et al. 1990). Empirical evi-

dence for the importance of immature or nonbreeding birds in the population dynamics of seabirds has been reported for Cassin's Auklet (*Ptychoramphus aleuticus*; Manuwal 1974), Black-legged Kittiwake (*Rissa tridactyla*; Porter and Coulson 1987), Sub-Antarctic Skua (*Catharacta antarctica*; Furness 1987) and Great Skua (*Stercorarius skua*; Klomp and Furness 1992). Klomp and Furness (1992) discuss the potential role of nonbreeders as a buffer for a population subject to environmental stress, whereby increased recruitment of birds maintains the population at a stable level despite adverse conditions affecting the population. Klomp and Furness (1992) also suggest that monitoring numbers of nonbreeders may be a sensitive way of monitoring populations of seabirds, as environmental or anthropogenic changes will impact more rapidly and to a greater extent on the population of nonbreeding birds. Providing that recapture effort is quantified, counts of nonbreeding albatrosses attending breeding colonies may give an early indication of population trends. Alternatively, monitoring a marked population of breeding birds, such as in this study, may make it possible to separate the effects of recruitment from the underlying trend affecting established breeders.

TEMPORAL VARIATION AND RELATIONSHIP TO AT-SEA CONDITIONS

The numbers of birds breeding in each year in the two study populations were strongly correlated, suggesting that similar at-sea processes affected both populations. At-sea conditions could affect the body condition of birds and consequently the number of birds that attempt to breed in each season (Weimerskirch 1992, Chastel et al. 1995), or they could influence the survival of juveniles and immature birds and subsequently the number of individuals recruiting into the population. In contrast, there was relatively little annual variation in breeding success for both populations over the study period, and there was no correlation between the two populations in hatching, fledging, or total breeding success. These results suggest that for the Atlantic Yellow-nosed Albatross, at-sea feeding conditions are important in determining the number of birds attempting to breed, rather than affecting breeding success of birds that do choose to breed. At-sea conditions are only likely to affect breeding success in exceptional years (see below).

Breeding success was substantially lower in the 1999–2000 breeding season on Gough Island in comparison to all previous years. Low breeding success in 1999–2000 was also observed in populations of Grey-headed (*T. chrysostoma*) and Black-browed Albatrosses (*T. melanophris*) breeding on South Georgia (2500 km southwest of Gough Island). The poor breeding success of these two species was linked to a substantial fall-off in the abundance of cephalopods, which are a major part of the diet (Xavier et al., in press). It therefore seems possible that changes in at-sea food availability may be responsible for the low breeding success observed on Gough Island in 1999–2000. No demographic parameters were correlated with the El Niño–Southern Oscillation index, suggesting either that Atlantic Yellow-nosed Albatrosses are unaffected by El Niño events, or that the Niño 3 index is a poor indicator of changes in sea conditions that affect this species.

RELATIONSHIP TO LONGLINE FISHING EFFORT

For both study populations, the best-fit mark-recapture model of adult survival was one with variable survival. Temporal variation in adult survival has been observed in several albatross populations, and in some species is correlated with longline fishing effort in foraging areas (e.g., Weimerskirch et al. 1997, Sagar et al. 2000, Nel et al., in press). Since the early 1980s, numbers of longline hooks set in the South Atlantic Ocean each year have remained relatively stable (Tuck et al., in press), and changes in total fishing effort did not easily explain the temporal trends in survival observed in the Gough study population. In contrast, annual survival of birds on Tristan da Cunha was negatively correlated with fishing effort, particularly that of the Taiwanese fleet.

Why longline fishing fleets in the South Atlantic should affect these two populations differently is unknown, but the lack of any correlation between adult survival in the two populations suggests that this is indeed the case. Band returns from the 1960s indicate that many birds from Nightingale Island (Tristan group) visited areas off Angola and Namibia (Morant 1977), and few birds from Gough Island have been captured there (Cooper 1983, Ryan et al. 2002). Longline mortality of Atlantic Yellow-nosed Albatrosses is known to occur in waters off the west coast of southern Africa (Ryan et al. 2002). If Tristan birds were using these sea

areas more frequently than Gough birds, this could explain the colony differences. Alternatively, these band returns may just represent long-term differences in fishing and banding effort, because few Atlantic Yellow-nosed Albatrosses from Gough Island were banded before the early 1980s, and there have been very few recoveries of the more than 1000 Atlantic Yellow-nosed Albatrosses banded on Inaccessible Island (Tristan group) in 1982–1983 (Fraser et al. 1988). Colony-specific differences in the at-sea distribution of albatrosses are known to occur (Brothers et al. 1998, Huin 2002) and clarification of this issue for the Atlantic Yellow-nosed Albatross would aid our understanding of this species' conflicts with longline fisheries.

COMPARISON WITH OTHER *THALASSARCHE* ALBATROSSES

Breeding success, juvenile survival, and average breeding age of Atlantic Yellow-nosed Albatrosses are within the observed ranges for congeners (Table 4). Breeding success of the Gough and Tristan da Cunha populations averaged 67–69% over the study period, similar to that found in the Campbell Albatross (*T. impavida*; 66%, Waugh et al. 1999) and Black-browed Albatross breeding on Kerguelen Island (63%, Weimerskirch and Jouventin 1998). Our mark-recapture analysis indicated that juvenile survival averages 31%. This estimate is similar to those observed for Black-browed and Grey-headed Albatrosses at Campbell Island, where juvenile survival averaged 29% and 24% respectively (Waugh et al. 1999). Average age at first breeding varies between 9 and 10 years for annual-breeding *Thalassarche* species (Table 4), and our species' observed age of 9.7 years is in the middle of this range.

In contrast, values of annual apparent survival for immatures and adults (particularly for the Tristan da Cunha population) were lower than those observed in most other *Thalassarche* species (Table 4). At 88%, immature survival of Gough Island birds was substantially lower than the estimates for Campbell and Grey-headed Albatrosses (96% and 94% respectively). Adult survival of Gough birds was also lower than most other species, and the only exception to this is the Indian Yellow-nosed Albatross (*T. carteri*) at Amsterdam Island, which has an adult survival estimate of 86% and has decreased at 3.6% per year since 1978 (Weimerskirch and Jouventin 1998). The very low survival estimate

TABLE 4. Mean reproductive parameters and observed population growth rates for Atlantic Yellow-nosed Albatrosses compared with published data for other *Thalassarche* albatrosses. Species listed are the annual-breeding Atlantic Yellow-nosed Albatross (*T. chlororhynchos*) on Gough Island and Tristan da Cunha, Indian Yellow-nosed Albatross (*T. carteri*), Campbell Albatross (*T. impavida*), Black-browed Albatross (*T. melanophris*), Southern Buller's Albatross (*T. bulleri*), and the biannual-breeding Grey-headed Albatross (*T. chrysostrama*). Annual apparent survival data for Buller's Albatross are from 1961 to 1968, when longline fishing effort was unlikely to be affecting this species (Sagar et al. 2000). Data from Prince et al. (1994) show the modal age of first breeding.

Species	Adult apparent survival (%)	Immature apparent survival (%)	Apparent survival 0–5 years (%)	Age of first breeding (years)	Breeding frequency (%)	Breeding success (%)	Annual population growth rate (%)
<i>T. chlororhynchos</i> ^a	92	88	31	9.7	63	67	-1.1
<i>T. chlororhynchos</i> ^b	84				65	69	
<i>T. carteri</i> ^c	86		15.4	8.7		25	-3.6
<i>T. impavida</i> ^d	95	96	29	10.0	82	66	1.1
<i>T. melanophris</i> ^e	93			10		29	0.8
<i>T. melanophris</i> ^f	16		14	9.7		63	-0.2
<i>T. bulleri</i> ^g	95		—	—	90	57	2.4
<i>T. chrysostrama</i> ^d	56	94	24	13.5	37	40	-2.8
<i>T. chrysostrama</i> ^e	65			12		39	-1.8

^a Gough Island, this study.

^b Tristan da Cunha, this study.

^c Amsterdam Island, Weimerskirch and Jouventin 1998.

^d Campbell Island, Waugh et al. 1999.

^e South Georgia, Prince et al. 1994.

^f Iles Kerguelen, Weimerskirch and Jouventin 1998.

^g Snares Island, Sagar and Warham 1998, Sagar et al. 2000.

found at Tristan da Cunha in comparison to Gough Island may be a consequence of higher levels of observer disturbance, which may have caused some birds to leave the area, a result that would lower the apparent survival estimate. While the survival estimate from Tristan da Cunha must be treated with some caution, the estimates from Gough Island are still lower than most other *Thalassarche* species.

CONCLUSIONS

The results from population modeling and counts on Gough Island and Tristan da Cunha suggest that populations of Atlantic Yellow-nosed Albatrosses are decreasing. Trends in the number of breeding birds are partially masked by annual variation in breeding numbers and the relatively stable levels of recruitment. For a marked population, monitoring numbers of established breeders may be a sensitive means of detecting trends. Monitoring established breeders is also biologically sensible, as recruitment is only a temporary buffer against an eventual decrease. The observed and predicted declines in Atlantic Yellow-nosed Albatrosses are consistent with the trends observed in many albatross species (e.g., Weimerskirch et al. 1997, Croxall et al. 1998, Waugh et al. 1999, Nel et al. 2002), including decreases at some colonies of the closely related Indian Yellow-nosed Albatross (*T. carteri*; Weimerskirch and Jouventin 1998), although there is no evidence of a decrease for this species at the Prince Edward Islands (Ryan et al., in press). Continued monitoring of breeding and survival parameters and long-term counts of Atlantic Yellow-nosed Albatrosses from both Gough Island and the Tristan da Cunha group are clearly needed to provide better estimates of population trends. The Atlantic Yellow-nosed Albatross is currently classified as Near Threatened in the most recent review of its conservation status (BirdLife International 2000). Given the evidence for a decrease in numbers over the last 20 years and a continued predicted decrease from estimates of demographic parameters and population modeling, the status of the species should be reassessed. With an average generation length of 22 years (10 years to colony return and 12 years of breeding life) and an observed or modeled annual rate of decrease of between 1.1% and 1.5%, we predict the Atlantic Yellow-nosed Albatross will decline by 54–63% over three generations. Under these

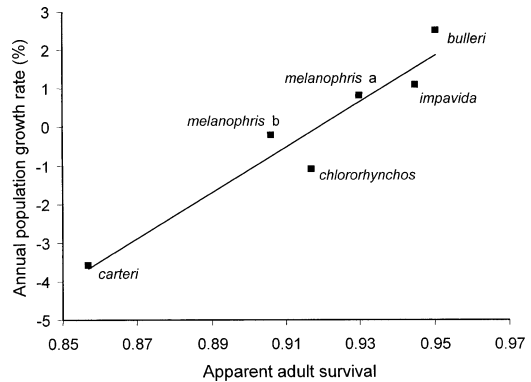


FIGURE 6. Apparent adult survival of the Atlantic Yellow-nosed Albatross (*T. chlororhynchos*) breeding on Gough Island, Indian Yellow-nosed Albatross (*T. carteri*), Black-browed Albatross (*T. melanophris*) breeding on (a) South Georgia and (b) Kerguelen Islands, Southern Buller's Albatross (*T. bulleri*), and Campbell Albatross (*T. impavida*). The regression of survival on measured population growth rate for these six populations is highly significant ($r^2 = 0.91$, $P < 0.005$). See Table 4 for sources of data.

conditions the species should be classified as Endangered (BirdLife International 2000).

The estimated demography of Atlantic Yellow-nosed Albatrosses in comparison to other congeners suggest that the low values of adult and immature survival found in this study are causing the observed and predicted decrease in breeding numbers. Long-lived seabird populations are highly sensitive to changes in adult survival (Croxall and Rothery 1991, Lebreton and Clobert 1991, Russel 1999, Cuthbert et al. 2001), and this relationship is demonstrated by the significant trend between adult apparent survival and observed population growth rates of six annual-breeding *Thalassarche* species (Fig. 6). Population modeling indicates that immature survival is the second most important parameter (next to adult survival) influencing the population growth rate of long-lived species (Croxall and Rothery 1991, Russel 1999, Cuthbert et al. 2001), and the low value of immature survival found for Gough birds will also affect the population growth rate of the species. Decreases in adult survival or recruitment are responsible for the observed declines in several albatross species (Weimerskirch and Jouventin 1987, Croxall et al. 1990, 1998, Prince et al. 1994, Waugh et al. 1999) and can for some populations be linked to temporal changes in longline fishing effort (Weimerskirch et al. 1997, Nel et al., in press).

Given the levels of longline fishing effort in the South Atlantic Ocean (Tuck et al., in press) and known at-sea mortality of Atlantic Yellow-nosed Albatrosses (Ryan and Boix-Hinzen 1998, Stagi et al. 1998, Olmos et al. 2001, Ryan et al. 2002), effective mitigation measures are imperative to protect populations of Atlantic Yellow-nosed Albatrosses in the South Atlantic Ocean.

ACKNOWLEDGMENTS

We are very grateful for the succession of volunteers from the Gough Island meteorological base who have collected data over the last 20 breeding seasons, and in particular Erica Sommer, who helped gather much of the data during the 2000–2001 breeding season. We are also grateful to J. Kerr, R. Grundy, C. McKenzie, L. Swain, T. Andrew, and I. Laverello on Tristan da Cunha, for their efforts in collecting data. We would like to thank the South African Department of Environmental Affairs and Tourism and the South African National Antarctic Program for logistical support on Gough Island, and the University of Cape Town for assistance with field equipment and support during writing. We thank Paul Sagar for detailed comments that improved an earlier version of the paper. This study was made possible by a grant from the UK Foreign and Commonwealth Office to the Royal Society for the Protection of Birds and the Percy FitzPatrick Institute of African Ornithology.

LITERATURE CITED

- BIRDLIFE INTERNATIONAL. 2000. Threatened birds of the world. Lynx Edicions, Barcelona, and BirdLife International, Cambridge, UK.
- BROTHERS, N. 1991. Albatross mortality and associated bait loss in the Japanese long-line fishery in the Southern Ocean. *Biological Conservation* 55:255–268.
- BROTHERS, N., R. GALES, A. HEDD, AND G. ROBERTSON. 1998. Foraging movements of the Shy Albatross *Diomedea cauta* breeding in Australia; implications for interactions with longline fisheries. *Ibis* 140:446–457.
- BURGMAN, M. A., S. FERSON, AND H. R. AKÇAKAYA. 1993. Risk assessment in conservation biology. Chapman & Hall, New York.
- BURNHAM, K. P., D. R. ANDERSON, G. C. WHITE, C. BROWNIE, AND K. H. POLLOCK. 1987. Design and analysis methods for fish survival experiments based on release-recapture. American Fisheries Society Monograph 5.
- CHASTEL, O., H. WEIMERSKIRCH, AND P. JOUVENTIN. 1995. Influence of body condition on reproductive decision and reproductive success in the Blue Petrel. *Auk* 112:964–972.
- COOPER, J. 1983. Bird ringing at Gough Island, 1977–1982. *South African Journal of Antarctic Research* 13:47–48.
- CROXALL, J. P., AND P. ROTHERY. 1991. Population regulation of seabirds: implications of their demography for conservation, p. 272–296. *In* C. M. Perrins, J. D. LeBreton, and G. M. Hirons [EDS.], *Bird population studies: relevance to conservation and management*. Oxford University Press, Oxford, UK.
- CROXALL, J. P., AND R. GALES. 1998. An assessment of the conservation status of albatrosses, p. 46–65. *In* G. Robertson and R. Gales [EDS.], *Albatross biology and conservation*. Surrey Beatty and Sons, Chipping Norton, NSW, Australia.
- CROXALL, J. P., P. A. PRINCE, P. ROTHERY, A. G. WOOD, AND R. GALES. 1998. Population changes in albatrosses at South Georgia, p. 69–83. *In* G. Robertson and R. Gales [EDS.], *Albatross biology and conservation*. Surrey Beatty and Sons, Chipping Norton, NSW, Australia.
- CROXALL, J. P., P. ROTHERY, S. P. C. PICKERING, AND P. A. PRINCE. 1990. Reproductive performance, recruitment and survival of Wandering Albatrosses *Diomedea exulans* at Bird Island, South Georgia. *Journal of Animal Ecology* 59:775–796.
- CUTHBERT, R. J., D. FLETCHER, AND L. S. DAVIS. 2001. A sensitivity analysis of Hutton's Shearwater: prioritizing conservation research and management. *Biological Conservation* 100:163–172.
- DE LA MARE, W. K., AND K. R. KERRY. 1994. Population dynamics of the Wandering Albatross (*Diomedea exulans*) on Macquarie Island and the effect of mortality from long-line fishing. *Polar Biology* 14:231–241.
- FRASER, M. W., P. G. RYAN, AND B. P. WATKINS. 1988. The seabirds of Inaccessible Island, South Atlantic Ocean. *Cormorant* 16:7–33.
- FURNESS, R. W. 1987. The skuas. T & AD Poyser, Calton, UK.
- GALES, R. 1998. Albatross populations: status and threats, p. 20–45. *In* G. Robertson and R. Gales [EDS.], *Albatross biology and conservation*. Surrey Beatty and Sons, Chipping Norton, NSW, Australia.
- GOULD, W. R., AND J. D. NICHOLS. 1998. Estimation of temporal variability of survival in animal populations. *Ecology* 79:2531–2538.
- HAGEN, Y. 1952. Birds of Tristan da Cunha. Results of the Norwegian Scientific Expedition to Tristan da Cunha. 1937–1938. No 20. Oslo Norske Videnskaps-Akademi, Oslo.
- HUIN, N. 2002. Foraging distribution of the Black-browed Albatross, *Thalassarche melanophris*, breeding in the Falkland Islands. *Aquatic Conservation* 12:89–99.
- INTERNATIONAL RESEARCH INSTITUTE FOR CLIMATE PREDICTION [ONLINE]. 2002. Niño 3. <<http://ingrid.ldeo.columbia.edu/SOURCES/Indices/.nino/.KAPLAN/NINO3/>> (25 June 2002).
- KLOMP, N. I., AND R. W. FURNESS. 1992. Non-breeders as a buffer against environmental stress: declines in numbers of Great Skua on Foula, Shetland, and prediction of future recruitment. *Journal of Applied Biology* 29:341–348.
- LEBRETON, J.-D., AND J. CLOBERT. 1991. Bird population dynamics, management, and conservation: the role of mathematical modelling, p. 272–296. *In* C. M. Perrins, J. D. LeBreton, and G. M. Hirons [EDS.], *Bird population studies: relevance to conservation and management*. Oxford University Press, Oxford, UK.

- MANUWAL, D. A. 1974. Effects of territoriality on breeding in a population of Cassin's Auklet. *Ecology* 55:1399–1406.
- MORANT, P. D. 1977. Bird ringing at Tristan da Cunha and Gough islands, 1937–1977. *South African Journal of Antarctic Research* 7:23–26.
- NEL, D. C., P. G. RYAN, R. J. M. CRAWFORD, J. COOPER, AND O. HUYSER. 2002. Population trends of albatrosses and petrels at sub-Antarctic Marion Island. *Polar Biology* 25:81–89.
- NEL, D. C., F. TAYLOR, P. G. RYAN, AND J. COOPER. In press. Population dynamics of Wandering Albatrosses *Diomedea exulans* breeding on the Prince Edward Islands. *African Journal of Marine Science*.
- NEVES, T. S., AND F. OLMOS. 1998. Albatross mortality in fisheries off the coast of Brazil, p. 214–219. In G. Robertson and R. Gales [EDS.], *Albatross biology and conservation*. Surrey Beatty and Sons, Chipping Norton, NSW, Australia.
- OLMOS, F. C. N., G. C. C. BASTOS, AND T. S. NEVES. 2001. Pesca no Céu—A morte de aves em espinhéis no Brasil. *Ciência Hoje* 29:28–32.
- PORTER, J. M., AND J. C. COULSON. 1987. Long-term changes in recruitment to the breeding group, and the quality of recruits at a Kittiwake *Rissa tridactyla* colony. *Journal of Animal Ecology* 56:675–689.
- PRINCE, P. A., P. ROTHERY, J. P. CROXALL, AND A. G. WOOD. 1994. Population dynamics of Black-browed and Grey-headed Albatrosses *Diomedea melanophrys* and *D. chrysostoma* at Bird Island, South Georgia. *Ibis* 136:50–71.
- RICHARDSON, M. E. 1984. Aspects of the ornithology of the Tristan da Cunha Group and Gough Island, 1972–1974. *Cormorant* 12:122–201.
- ROWAN, M. K. 1951. The Yellow-nosed Albatross *Diomedea chlororhynchus* Gmelin, at its breeding grounds in the Tristan da Cunha group. *Ostrich* 22:139–155.
- RUSSEL, R. W. 1999. Comparative demography and life history tactics of seabirds: implications for conservation and marine monitoring. *Proceedings of the American Fisheries Society Symposium* 23: 51–76.
- RYAN, P. G., AND C. BOIX-HINZEN. 1998. Tuna longline fisheries off southern Africa: the need to limit seabird bycatch. *South African Journal of Science* 94: 179–182.
- RYAN, P. G., J. COOPER, B. M. DYER, L. G. UNDERHILL, AND R. J. M. CRAWFORD. In press. Counts of surface-nesting seabirds breeding at subantarctic Prince Edward Island, summer 2001/02. *South African Journal of Marine Science*.
- RYAN, P. G., D. G. KEITH, AND M. KROESE. 2002. Seabird bycatch by tuna longline fisheries off southern Africa 1998–2000. *South African Journal of Marine Science* 24:103–110.
- RYAN, P. G., AND C. L. MOLONEY. 2000. The status of Spectacled Petrels *Procellaria conspicillata* and other seabirds at Inaccessible Island. *Marine Ornithology* 28:93–100.
- SAGAR, P. M., J. MOLLOY, H. WEIMERSKIRCH, AND J. WARHAM. 2000. Temporal and age-related changes in survival rates of Southern Buller's Albatrosses (*Thalassarche bulleri bulleri*) at the Snares, New Zealand, 1948 to 1997. *Auk* 117:699–708.
- SAGAR, P. M., AND J. WARHAM. 1998. Breeding biology of southern Buller's Albatross *Diomedea bulleri bulleri* at the Snares, New Zealand, p. 107–112. In G. Robertson and R. Gales [EDS.], *Albatross biology and conservation*. Surrey Beatty and Sons, Chipping Norton, NSW, Australia.
- SLOOTEN, E., D. FLETCHER, AND B. TAYLOR. 2000. Taking account of uncertainty in the management of animal populations: is Hector's dolphin at risk from bycatch? *Conservation Biology* 14:1264–1270.
- SPSS INC. 1999. *Advanced statistics user's guide*. Version 10.0. SPSS Inc., Chicago.
- STAGI, A., R. VAZ-FERREIRA, Y. MARIN, AND L. JOSEPH. 1998. The conservation of albatrosses in Uruguayan waters, p. 220–224. In G. Robertson and R. Gales [EDS.], *Albatross biology and conservation*. Surrey Beatty and Sons, Chipping Norton, NSW, Australia.
- TUCK, G., T. POLACHEK, AND C. BULMAN. In press. Spatio-temporal trends in longline fishing effort in the Southern Ocean and implications for seabird bycatch. *Biological Conservation*.
- TUCK, G. N., T. POLACHEK, J. P. CROXALL, AND H. WEIMERSKIRCH. 2001. Modelling the impact of fishery by-catches on albatross populations. *Journal of Applied Ecology* 38:1182–1196.
- VASKE, T., JR. 1991. Seabird mortality on longline fishing for tuna in Southern Brazil. *Ciência e Cultura* 43:388.
- WAUGH, S. M., H. WEIMERSKIRCH, P. J. MOORE, AND P. M. SAGAR. 1999. Population dynamics of Black-browed and Grey-headed Albatrosses *Diomedea melanophrys* and *D. chrysostoma* at Campbell Island, New Zealand. *Ibis* 141:216–225.
- WEIMERSKIRCH, H. 1992. Reproductive effort in long-lived birds: age-specific patterns of condition, reproduction and survival in the Wandering Albatross. *Oikos* 64:464–473.
- WEIMERSKIRCH, H., N. BROTHERS, AND P. JOUVENTIN. 1997. Population dynamics of Wandering Albatross *Diomedea exulans* and Amsterdam Albatross *D. amsterdamensis* in the Indian Ocean and their relationships with long-line fisheries: conservation implications. *Biological Conservation* 79:257–270.
- WEIMERSKIRCH, H., AND P. JOUVENTIN. 1987. Population dynamics of the Wandering Albatross, *Diomedea exulans*, of the Crozet Islands: causes and consequences of the population decline. *Oikos* 49:315–322.
- WEIMERSKIRCH, H., AND P. JOUVENTIN. 1998. Changes in population size and demographic parameters of six albatross species breeding in the French sub-Antarctic islands, p. 84–91. In G. Robertson and R. Gales [EDS.], *Albatross biology and conservation*. Surrey Beatty and Sons, Chipping Norton, NSW, Australia.
- WHITE, G. C., AND K. P. BURNHAM. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46(S):120–139.
- XAVIER, J. C., J. P. CROXALL, AND K. REID. In press. Inter-annual variation in the diet of albatrosses breeding at South Georgia: influence of breeding performance. *Ibis*.
- ZAR, J. H. 1999. *Biostatistical analysis*. Prentice Hall International, Englewood Cliffs, NJ.