

TEMPORAL AND AGE-RELATED CHANGES IN SURVIVAL RATES OF SOUTHERN BULLER'S ALBATROSSES (*THALASSARCHE BULLERI BULLERI*) AT THE SNARES, NEW ZEALAND, 1948 TO 1997

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ABSTRACT.—We estimated survival rates of adult Southern Buller's Albatrosses (*Thalassarche bulleri bulleri*) from 1948 to 1997 based on a long-term banding and recapture program at The Snares, New Zealand. Annual survival exceeded 0.95 from 1961 to 1968 and from 1992 to 1997 but declined to between 0.913 and 0.928 from 1969 to 1991. Reduced survival may have resulted from incidental mortality associated with longline and trawl fisheries in the foraging areas of these birds, but it must have been counterbalanced by changes in other population parameters because the population increased greatly in number from 1969 to 1997. Increased trawling activity in areas where albatrosses forage may have benefited the population by providing additional food, which may have enhanced the survival rate of recently fledged birds. We found no indication that survival rates differed between males and females, but an age effect occurred in which survival of birds with at least 25 years of breeding experience was lower than that of less-experienced and presumably younger birds. Received 18 November 1998, accepted 7 December 1999.

THE SURVIVAL RATE of breeding adults is a key feature in the population ecology of long-lived species (Clutton-Brock 1988, Finch 1990). Because of delayed age of first breeding and low reproductive rate, breeding populations of albatrosses are more sensitive to changes in adult survival than to changes in breeding success or juvenile survival (Weimerskirch et al. 1987, 1997; Croxall and Rothery 1991). The relationship between generation time and relative sensitivity to fecundity and adult survival was clearly shown by Danchin et al. (1995). Estimation of survival rates has become increasingly important with the incidental mortality of large numbers of albatrosses in longline and trawl fisheries in the Southern Ocean (Bartle 1991, Brothers 1991, Murray et al. 1993, Prince et al. 1994). Increased mortality of adults and the resulting decline in the population of Wandering Albatrosses (*Diomedea exulans*) in the Crozet Islands was linked to the tuna longline fishery in the Indian Ocean (Weimerskirch and Jouventin 1997). Fishery-related declines in other albatross populations in the Southern Ocean also are suspected (Croxall and Prince

1990, de la Mare and Kerry 1994, Prince et al. 1994).

The Southern Buller's Albatross (*Thalassarche bulleri bulleri*) is an annual breeder that nests on the Solander Islands (2,625 pairs in 1996) and The Snares (8,877 pairs in 1997; Sagar et al. 1999) in New Zealand. Fisheries observers began collecting information on incidental capture of seabirds in the Japanese tuna longline fishery in southern New Zealand in 1989. Between 1989 and 1992, Southern Buller's Albatrosses made up 22% of seabird captures reported in this area (Murray et al. 1993). Numbers killed in other fisheries are unknown, but banded birds were caught by trawlers during the 1960s and 1970s (Stahl et al. 1998). Except for a banded bird caught by a longliner 2,000 km southwest of Hawaii (Warham 1982), there are no reports of mortality of Southern Buller's Albatross in fisheries outside of New Zealand waters.

Despite such incidental mortality, changes in the sizes of the two breeding populations have differed considerably. The Snares population increased greatly from 1969 to 1997 (Sagar et al. 1994, 1999), and the Solander Islands population either remained the same or decreased by as much as 18.7% from 1985 to 1996 (Sagar et

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al. 1999). Southern Buller's Albatrosses have been banded at the Solander Islands only in 1985 (fledglings only), 1996, and 1997; thus, the data are insufficient for analysis. Here, we present information on long-term survival rates of Southern Buller's Albatrosses breeding at The Snares (48°02'S, 166°36'E) from 1948 to 1997. Banding of this species at The Snares began 50 years ago, so we are able to examine survival rates over time and to evaluate whether survival varied with the age of adults. Indeed, a long-term data base is necessary to examine age-related parameters in such long-lived species (Croxall and Rothery 1991). Albatrosses have the highest known survival rates of all seabirds (Warham 1996); consequently, they provide the opportunity to test whether survival is related to age.

The main aims of our study were to (1) determine adult survival rates from 1948 to 1997; (2) identify possible fisheries-related causes for changes in survival rate with time; (3) compare male and female survival rates; and (4) determine whether age-related changes in survival occurred. In this manner, we tested the hypotheses that changes in survival over time were correlated with fishing activities, particularly effort, and that long-lived species exhibit senescence.

METHODS

Banding and recapture of Southern Buller's Albatrosses at The Snares occurred from 1948 to 1997 during five discrete periods: 1948, 1961, 1967 to 1977, 1983 to 1986, and 1992 to 1997. Birds in the Punui Bay area and a colony at Mollymawk Bay were used in this analysis, but searches for banded birds were also made in other areas (see Richdale 1949 for colony locations). Nest-site fidelity is well documented in albatrosses, and the Southern Buller's is no exception (Sagar and Warham 1998). During each visit to the island subsequent to banding (1961 to 1997), regular searches were made of the areas where these birds were known to nest to record the identity of banded birds regardless of whether they were breeding. Numbers of birds banded and recaptured each year are given in Table 1.

Data collection in 1948.—In 1948, birds were banded as soon as the eggs were laid, and sex was determined by prelaying attendance at the nest, position during copulation, which bird undertook the first incubation shift, or a combination of these factors (Richdale 1949). Bands were made from an aluminum strip, 19 mm wide and 1.4 mm thick, with a known durability of 15 to 20 years (Richdale 1949),

but they lasted longer than this and were still legible and secure after 22 years (Richdale and Warham 1973). However, the original bands were replaced with monel bands as birds were recaptured from 1967 to 1972. Thus, band loss was unlikely.

Data collection in 1961.—The sex of most of the birds banded at Mollymawk Bay was not determined at banding, so analyses of this cohort were conducted only on their 1961 unsexed status to avoid overestimating survival rates (Lebreton et al. 1992). During 1961, all new banded birds were fitted with aluminum bands of a different grade than those used by Richdale (1949); these bands showed considerable wear, and some began to open within 10 years (Richdale and Warham 1973). Several of these birds were fitted with monel or stainless steel bands beginning in 1970, but most of these bands were not replaced, and we assumed that band loss occurred.

Data collection from 1969 to 1997.—Beginning January 1969, studies of demography and breeding biology were conducted at Mollymawk Bay, and breeding birds were fitted with aluminum or monel bands. Sex was determined (79 males and 89 females) by observation of behavior, as described above. Some of the aluminum bands fitted in 1969 began to open by 1977, so these were replaced with stainless steel bands. The latter showed no signs of wear or opening after 20 years; therefore, we assumed that no band loss occurred. The sex of birds banded in 1970, 1975, and 1977 was not determined. In each year from 1992 to 1997, we checked colonies adjacent to the study colony for banded birds, but none was found.

Data analysis.—Capture-recapture data were analyzed with a Cormack-Jolly-Seber model (Cormack 1964, Jolly 1965, Seber 1965) and its developments (Lebreton et al. 1992). We used RELEASE goodness-of-fit tests (Burnham et al. 1987) and SURGE 4.2 software for model fitting and computation of likelihood-ratio tests (Clobert et al. 1987, Pradel et al. 1990, Lebreton et al. 1992). Changes in survival (ϕ) and recapture rates (p) as a function of sex and time were analyzed, and the best model was selected using Akaike's Information Criterion (AIC; Lebreton et al. 1992). In cases with similar AIC values, the model with the smaller number of parameters was preferred. For SURGE, years with no recaptures were fixed to $p = 0$.

Because of differences in band types among cohorts and because there were periods of several years with no recaptures, the RELEASE test showed that the data were not homogeneous. Therefore, the analysis was conducted for birds banded in three separate periods: 1948, 1961, and 1969 to 1997. Within each period, we tested first for age and band effects. If band-loss effects were indicated (by heterogeneity in the data), we truncated the analysis to a year before the effect was detected. For birds banded in 1961 and 1969 to 1997, the analysis was conducted only for birds that nested in the Mollymawk Bay study

TABLE 1. Capture-recapture data for breeding adult Southern Buller's Albatross at The Snares, New Zealand, 1948 to 1997.

No.	Year of recapture																				Not recaptured
	1948	1961	1967	1969	1970	1971	1972	1973	1975	1977	1983	1984	1985	1986	1992	1993	1994	1995	1996	1997	
127	27	16	16	16	11	4	5	0	2	1	0	0	0	0	1	1	0	0	0	0	98
164	—	59	81	81	80	65	78	35	47	39	8	1	3	5	0	0	0	0	0	0	47
1967	0	—	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	—
1969	179	—	—	—	148	113	136	52	102	91	36	2	14	25	17	16	14	12	10	10	7
1970	4	—	—	—	—	4	4	1	3	4	2	0	0	2	1	1	1	0	1	1	0
1971	0	—	—	—	—	—	0	0	0	0	0	0	0	0	0	0	0	0	0	0	—
1972	0	—	—	—	—	—	—	0	0	0	0	0	0	0	0	0	0	0	0	0	—
1973	0	—	—	—	—	—	—	—	0	0	0	0	0	0	0	0	0	0	0	0	—
1975	38	—	—	—	—	—	—	—	—	33	19	0	8	15	11	13	13	11	11	11	5
1977	40	—	—	—	—	—	—	—	—	—	16	1	8	17	7	8	8	6	6	6	17
1983	0	—	—	—	—	—	—	—	—	—	—	0	0	0	0	0	0	0	0	0	—
1984	0	—	—	—	—	—	—	—	—	—	—	—	0	0	0	0	0	0	0	0	—
1985	0	—	—	—	—	—	—	—	—	—	—	—	0	0	0	0	0	0	0	0	—
1986	0	—	—	—	—	—	—	—	—	—	—	—	—	0	0	0	0	0	0	0	—
1992	120	—	—	—	—	—	—	—	—	—	—	—	—	—	0	106	93	93	95	89	4
1993	85	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	60	68	73	68	2
1994	13	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	7	9	10	2
1995	15	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	10	8	3
1996	20	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	16	4	4

TABLE 2. Recapture probabilities (p) of Southern Buller's Albatrosses at The Snares, New Zealand, for cohorts banded from 1948 to 1996. Estimates were calculated for the best models specified in the text. CI = 95% confidence interval.

Year	1948		1961		1969 to 1996	
	p	CI	p	CI	p	CI
1961	0.948	0.716–0.992	—	—	—	—
1967	0.872	0.615–0.967	0.409	0.334–0.488	—	—
1969	0.928	0.647–0.989	0.680	0.598–0.752	—	—
1970	0.876	0.497–0.980	0.747	0.667–0.813	0.797	0.691–0.873
1971	0.467	0.167–0.794	0.623	0.538–0.702	0.727	0.611–0.818
1972	0.971	0.786–1.000	0.839	0.747–0.902	0.893	0.783–0.950
1973	0.000	0.000–1.000	0.449	0.351–0.550	0.348	0.241–0.472
1975	1.000	0.000–1.000	0.888	0.769–0.950	0.915	0.795–0.967
1977	1.000	0.000–1.000	1.000	0.000–1.000	0.984	0.894–0.998
1983	—	—	—	—	0.800	0.680–0.878
1984	—	—	—	—	0.029	0.007–0.108
1985	—	—	—	—	0.422	0.305–0.548
1986	—	—	—	—	0.862	0.724–0.937
1992	—	—	—	—	0.797	0.632–0.900
1993	—	—	—	—	0.936	0.889–0.964
1994	—	—	—	—	0.881	0.822–0.923
1995	—	—	—	—	0.843	0.765–0.899
1996	—	—	—	—	0.912	0.837–0.935
1997	—	—	—	—	0.898	0.667–0.973

colony. Heterogeneity in the data was assumed to indicate age-related effects and was considered in subsequent analysis.

Following identification of age or band-loss effects, various models were tested to determine which one gave the best fit for the data. After modeling of survival and recapture rates for males and females separately (the 1948 and 1969 cohorts only), the analysis was carried out for both sexes jointly, with the addition of breeding birds of unknown sex.

RESULTS

From 1948 to 1997, 805 different breeding adult Southern Buller's Albatrosses were banded on The Snares in the study areas associated with the present analysis. The number of birds

banded and recaptured in each year is summarized in Table 1. Recapture probabilities (Table 2) indicated lower efficiencies for the 1948 cohort in 1971 and 1973; the 1961 cohort in 1967, 1969, 1971, and 1973; and for the 1969 to 1997 cohorts in 1971, 1973, 1984, and 1985.

Sex-related survival.—When we tested for interactions between sex and time for the cohorts banded during 1948 and 1969, survival of males and females was similar (Table 3). Thus, for each cohort of banded birds, all subsequent analyses were conducted on the entire sample, regardless of whether the sex of the birds had been determined.

Time-dependent survival: 1948.—Data from 1948 were highly heterogeneous ($\chi^2 = 36.97$, df

TABLE 3. Estimated mean annual survival rate (\pm SD) by cohort (centered in bold) of adult male and female Southern Buller's Albatrosses at The Snares, New Zealand, relative to number of years of breeding experience.

Period	Minimum breeding experience (years)	Survival rate	
		Males	Females
1948			
1948 to 1968	1 to 21	0.901 \pm 0.012	0.900 \pm 0.086
1969 to 1977	22 to 30	0.691 \pm 0.103	0.702 \pm 0.068
1969			
1969 to 1977	1 to 9	0.923 \pm 0.009	0.940 \pm 0.084
1978 to 1986	10 to 18	0.893 \pm 0.021	0.863 \pm 0.019

TABLE 4. Estimates of survival (ϕ) of Southern Buller's Albatrosses (sexes pooled) at The Snares, New Zealand. Estimates for each period are based on models^a with the lowest AIC value (95% confidence interval in parentheses).

Period	1948	1961	1948 and 1961	1969 to 1997
1948 to 1960	0.891 (0.868–0.910)	—	—	—
1961 to 1968	0.947 (0.902–0.972)	0.954 (0.942–0.964)	0.951 (0.932–0.965)	—
1969 to 1977	0.695 (0.548–0.811)	0.890 (0.861–0.914)	0.940 (0.899–0.964)	—
1969 to 1974	—	—	—	0.913 (0.896–0.927)
1975 to 1982	—	—	—	0.928 (0.907–0.944)
1983 to 1985	—	—	—	0.920 (0.882–0.949)
1986 to 1991	—	—	—	0.922 (0.882–0.949)
1992 to 1997	—	—	—	0.955 (0.926–0.974)

^a Models with best fit are ϕ_3, p_i for 1948; ϕ_2, p_i for 1961; ϕ_2, p_i for 1948 and 1961; and ϕ_3, p_i for 1969 to 1997.

= 5, $P = 0.001$), and we were unable to correct for this. This may have resulted from the lack of information between banding and first recapture (a 13-year period), heterogeneity in the life of the bands (given that they were hand made), and/or variable recapture probabilities, with noticeably lower recaptures in 1971 and 1973 (Table 2). Because we were dealing with a single cohort, we could not separate between age- and time-dependent effects. The model

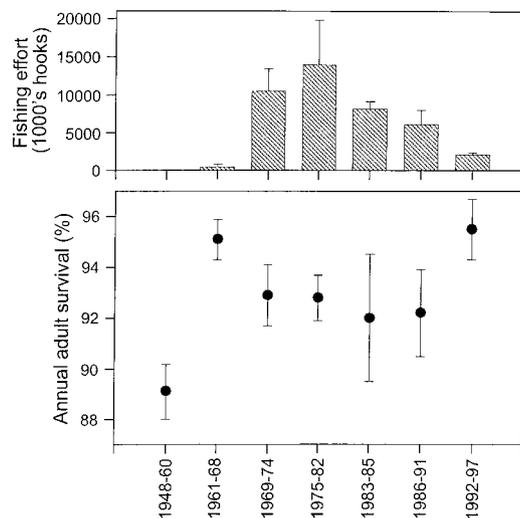


FIG. 1. Changes in (upper) the numbers of hooks set in southern New Zealand waters by the Japanese tuna longline fishery and (lower) estimated mean annual survival (\pm SD) of adult Southern Buller's Albatrosses breeding at The Snares during seven periods from 1948 to 1997. Survival figures 1948 to 1960 and 1986 to 1991 are based on one recapture period. Information on the Japanese tuna long-lining fishery was obtained from the 13th Southern Bluefin Tuna Trilateral Scientific Meeting Report (CSIRO-MAF) and Polacheck and Tuck (1995).

with the best fit (Table 4, Fig. 1) indicated that survival was different between groups of years (or age classes) and that survival was significantly lower for the latest period (or older ages; Table 4, Fig. 2). One bird banded as an adult in 1948 was still alive in 1993 and so was at least 51 years old (at least 45 years as a breeder, plus at least six years as a prebreeder), but it disappeared thereafter.

Time-dependent survival: 1961.—Again, the entire data set was heterogeneous ($\chi^2 = 76.86$, $df = 23$, $P = 0.001$), and the results suggested an effect of age and/or band loss. Consequently, survival probability was tested against age (years since banding) and time. The model with the best fit indicated a significant decline in survival rate during the period 1973 to 1977, 12 to 16 years after banding (Table 4, Fig. 2). Because an age effect was not discernible until 25 years after banding in the 1948 cohort, and the bands used in 1961 were aluminum, we concluded that the heterogeneity resulted from band loss. Therefore, capture-recapture data for birds banded in 1961 were used only to estimate survival rates for the period 1961 to 1968. These data were pooled with those for birds banded during 1948 ($\chi^2 = 30.23$, $df = 14$, $P = 0.007$) to increase sample size and thus reduce confidence intervals. The model with the best fit indicated that survival was constant from 1961 to 1968 and gave an estimated survival rate of 0.951 (Table 4).

Time-dependent survival: 1969 to 1997.—All data obtained during this period were from birds that bred at the Mollymawk Bay study colony. Capture-recapture data for all birds banded during this period were pooled and found to be homogeneous ($\chi^2 = 29.25$, $df = 35$, $P = 0.74$). Although the model with the best fit

indicated that survival rates differed over two time periods (1969 to 1991, $\phi = 0.926$; 1992 to 1997 $\phi = 0.955$), we split the data into five periods to examine changes in survival over time in finer detail. Again, the analysis indicated that survival rates were relatively constant from 1969 to 1992 at 0.913 to 0.928 before increasing to 0.955 from 1993 to 1997 (Table 4, Fig. 1).

Age-related survival.—Survival of birds with more than 25 years of breeding experience was significantly lower than that of less-experienced birds, as indicated by the nonoverlapping confidence intervals (Table 4). Plots of the percentage of birds surviving against years since banding for each cohort confirmed a relatively constant survival rate until about 25 years after banding (Fig. 2). Subsequently, survival decreased in all three cohorts (1948, 1961, 1969) for which we had recapture data beyond these time periods.

DISCUSSION

Time-dependent survival.—Survival rates of breeding adult Southern Buller's Albatrosses at The Snares showed marked variations with time. Our estimated survival rate of 0.891 for the period 1948 to 1960 is similar to that based on a simple ratio for the period from 1948 to 1971 (Richdale and Warham 1973). For the period from 1962 to 1968, modeling recaptures of birds banded in 1948 and 1961 provided independent survival estimates of 0.947 and 0.954. Survival was consistently lower, ranging from 0.913 to 0.928, from 1969 to 1991, followed by an increase to 0.955 for the period from 1992 to 1997.

Detailed demographic information for Southern Buller's Albatrosses is not available. The population size has been estimated in detail on The Snares three times: in 1969 (Warham and Bennington 1983), 1992 (Sagar et al. 1994), and 1997 (Sagar et al. 1999). The population increased by an estimated 78% between 1969 and 1992 (Sagar et al. 1994) and by a further 8% between 1992 and 1997 (Sagar et al. 1999), suggesting high adult survival and/or high recruitment. Breeding success was determined only in 1972, when 57% of eggs laid produced fledglings (Sagar and Warham 1998). Among albatrosses, however, this demographic parameter has a relatively small effect on population

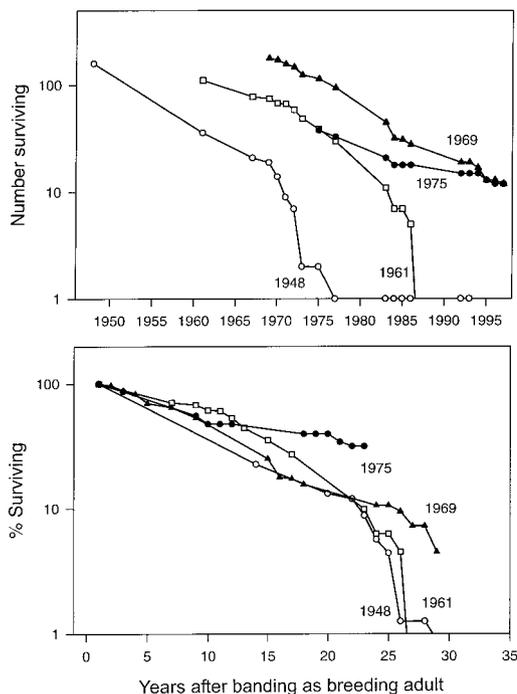


FIG. 2. Changes in numbers surviving (by year) and percentage surviving (by years after banding) of four cohorts of Southern Buller's Albatrosses banded as breeding adults at The Snares, New Zealand.

change (Weimerskirch et al. 1997). No information exists on recruitment rates and age of first breeding. As indicated below, survival of Southern Buller's Albatrosses is high compared with other albatrosses that breed annually, but this alone may not have resulted in the population increase estimated during the period from 1969 to 1997. Therefore, changes in other parameters such as age of first breeding or increased survival of juveniles are likely to have been involved in the population increase. Immigration is unlikely to have influenced population size because once an albatross has bred in a particular colony it seldom shifts to another (Warham 1990). However, although no movement of banded breeders between the Solander Islands and The Snares has been recorded, few Buller's Albatrosses were banded at the Solanders before 1996, so any immigration to The Snares from 1969 to 1997 would have gone undetected.

In southern New Zealand waters, incidental mortality of Buller's Albatrosses has been reported on longliners and trawlers and in set

nets (Stahl et al. 1998). For example, of 11 breeding birds banded on The Snares and recovered in southern New Zealand waters, at least four succumbed to incidental mortality associated with trawl fisheries (Stahl et al. 1998). From 1989 to 1992, it was estimated that up to 350 adult Southern Buller's Albatrosses were killed annually in the Japanese tuna longline fishery. All of these birds were caught off southwestern New Zealand (Murray et al. 1993, Stahl et al. 1998) in areas closest to the two breeding locations. This represents a decrease of about 1.4% per year in the estimated population size of adult Southern Buller's Albatrosses in 1992 (Sagar et al. 1994, Baird 1996). However, fishing effort was two to three times higher during the 1970s (Fig. 1; Murray et al. 1993), so incidental mortality was likely to have been proportionally higher, with up to 1,050 birds (3.8% of the adult population) being killed annually. This assumes that the birds involved in incidental mortality came from the Solander Islands and The Snares.

Our study indicated a decline of 0.025 in the survival rate of adults at The Snares, yet the population increased between 1969 and 1992 (Sagar et al. 1994). The decrease in survival during the late 1960s or early 1970s was contemporaneous with an increase in longline fishing effort in the southern New Zealand region (Fig. 1), where Southern Buller's Albatrosses mainly forage (Sagar and Weimerskirch 1996, Stahl et al. 1998). This was followed by an increase in survival during the 1990s that corresponded with a decrease in longlining effort (Fig. 1) and the use of mitigation devices by fishing vessels. A similar relationship between fishing effort and decreased survivorship of adults was found for Wandering Albatrosses from the Crozet Islands (Weimerskirch et al. 1997). However, the decrease of 0.061 in adult survivorship associated with the period of greatest fishing effort near the Crozet Islands was higher than that estimated for Southern Buller's Albatrosses.

A decline in adult survival of 0.025 would lead to a decrease of about 2% in the rate of change of population size (H. Weimerskirch unpubl. data) and thus would have a significant influence on population size. Yet, despite this reduction in adult survival during the period of highest longlining effort (plus mortality associated with trawl and set-net fisheries), the al-

batross population increased by 78% over the 23 years during which survival was estimated. This increase is possible only if natural adult survival and/or juvenile survival and recruitment were very high.

Large numbers of Southern Buller's Albatrosses congregate around trawlers to scavenge discards and offal (Petyt 1995). Therefore, the rise in trawl fisheries since 1968 (Fenaughty and Bagley 1981) may have led to increased juvenile survival and breeding success, thus offsetting at least part of the negative influence of fisheries-related incidental bycatch. However, the situation is complex, and the effects of longlining and trawling are difficult to disentangle. The large numbers of Southern Buller's Albatrosses estimated to have been killed by Japanese tuna longliners operating off southern New Zealand (Murray et al. 1993) raise the question of the provenance of Southern Buller's Albatrosses killed since 1988. The most likely explanation is that these birds came from the less well-studied breeding population on the Solander Islands, where the population size has remained similar or decreased by as much as 18.7% in the period from 1985 to 1996 (Sagar et al. 1999).

If the survival rate from 1948 to 1960 (that which is most likely to be underestimated) is omitted, the overall survival rate from 1961 to 1997 is 0.934. Considering other species of albatross that breed annually in the subantarctic, this value is similar to that (0.935) calculated for Black-browed Albatrosses (*T. melanophris*) on South Georgia from 1976 to 1988 (Prince et al. 1994) but is higher than that (0.906) recorded for this species in a declining population on Kerguelen from 1979 to 1995 (Weimerskirch and Jouventin 1998). However, because birds from this population were at high risk from fisheries (Weimerskirch and Jouventin 1998), this factor would have had a negative effect on survival rates. The estimated survival rate of Yellow-nosed Albatrosses (*T. chlororhynchos*) on Amsterdam Island from 1978 to 1995 was 0.857 (Weimerskirch and Jouventin 1998), but the population appeared to be sustained by the recruitment of extremely young birds (Prince et al. 1994). Within the New Zealand region, annual survival of adult New Zealand Black-browed Albatrosses (*T. m. impavida*) breeding on Campbell Island was constant at 0.945 from 1984 to 1995 (Vaughn et al. 1999), whereas an-

nual survival of Southern Buller's Albatrosses varied with time during this same period. Indeed, survival of Southern Buller's Albatrosses from 1992 to 1997 was similar to the 0.953 recorded for the biennially breeding Gray-headed Albatross (*T. chrysostris*) at Campbell Island (Waugh et al. 1999) but lower than the 0.98 reported for the Northern Royal Albatross (*D. epomophora sanfordi*) at Taiaroa Head, New Zealand (Robertson 1993).

Age-related survival.—Because of the long generation times of most seabirds and the relatively recent use of reliable means with which to identify individuals over many years, few studies have examined age-related differences in local apparent survival. A strong negative relationship occurred between annual adult survival and number of years since first breeding in Northern Fulmars (*Fulmarus glacialis*; Dunnet and Ollason 1978) and Atlantic Puffins (*Fratercula arctica*; Harris et al. 1997), and in a Black-legged Kittiwake (*Rissa tridactyla*) population, annual adult survival decreased by 11% for birds with more than 12 years of breeding experience (Aebischer and Coulson 1990). Similarly, the mortality rate of older birds was substantially higher than that of younger adults in a population of Short-tailed Shearwaters (*Puffinus tenuirostris*; Bradley et al. 1989), and survival of Wandering Albatrosses older than 27 years (Weimerskirch 1992) and of Northern Royal Albatrosses older than 25 years (Robertson 1993) was significantly lower than that of younger breeding adults. Thus, in general, local apparent survival rates of seabirds support the concept of age-dependent mortality assumed by Botkin and Miller (1974), but more long-term data are needed to support this contention.

In a previous analysis of capture-recapture data for Southern Buller's Albatrosses banded at The Snares during 1948 and 1961, Richdale and Warham (1973) found no evidence that survival varied with age. They attributed a marked decline in the recapture of birds in 1970 and 1971, the final years of the analysis, to decreased search effort rather than increased mortality. Our analysis supported this for 1971, but not for subsequent years, and it identified a marked decline in survival of birds banded for each of the 1948, 1961, and 1969 cohorts after about 25 years of breeding. For the 1969 cohort, this decline was detected during a

period of intense research at a well-defined study colony and so was not related to reduced recapture effort. Loss of bands appeared unlikely because of the nature of the bands applied in 1948 and the subsequent rebanding of birds captured in 1961 and 1969. Because we recaptured breeders and nonbreeders, it is unlikely that our results were confounded by a decline in the propensity to breed with age. Furthermore, reduced recapture probability with age was not indicated because 90% of the intact pairs returned to breed each year (Sagar and Warham 1998), and no banded adults that were absent from the colony for more than three years were recaptured subsequently (P. M. Sagar and J. Molloy unpubl. data), which suggests that these birds had died. Therefore, our results suggest that survival rate declines with age in Southern Buller's Albatrosses.

Age of first return to breeding colonies is 5 years, and average age of first breeding is about 10 years in Southern Buller's Albatrosses. Thus, the minimum age at which survival begins to decline is 35 years. However, the birds in our sample were banded as breeders of unknown age, so the average age at which survival begins to decline is more likely to be higher than 35 years.

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