



Additive effects of climate and fisheries drive ongoing declines in multiple albatross species

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Environmental and anthropogenic factors often drive population declines in top predators, but how their influences may combine remains unclear. Albatrosses are particularly threatened. They breed in fast-changing environments, and their extensive foraging ranges expose them to incidental mortality (bycatch) in multiple fisheries. The albatross community at South Georgia includes globally important populations of three species that have declined by 40–60% over the last 35 years. We used three steps to deeply understand the drivers of such dramatic changes: (i) describe fundamental demographic rates using multievent models, (ii) determine demographic drivers of population growth using matrix models, and (iii) identify environmental and anthropogenic drivers using ANOVAs. Each species was affected by different processes and threats in their foraging areas during the breeding and nonbreeding seasons. There was evidence for two kinds of combined environmental and anthropogenic effects. The first was sequential; in wandering and black-browed albatrosses, high levels of bycatch have reduced juvenile and adult survival, then increased temperature, reduced sea-ice cover, and stronger winds are affecting the population recovery potential. The second was additive; in gray-headed albatrosses, not only did bycatch impact adult survival but also this impact was exacerbated by lower food availability in years following El Niño events. This emphasizes the need for much improved implementation of mitigation measures in fisheries and better enforcement of compliance. We hope our results not only help focus future management actions for these populations but also demonstrate the power of the modelling approach for assessing impacts of environmental and anthropogenic drivers in wild animal populations.

seabird demography | climate | fisheries | conservation | population dynamics

Top predators are usually long-lived, with population growth rates that are sensitive to small changes in survival, and to a lesser extent to changes in reproductive traits. In the marine environment, climate can affect both survival and reproduction (1–3). This generally reflects bottom-up processes, whereby climate effects propagate through trophic levels, affecting food availability, foraging success, provisioning rates, and survival (1). Although most analyses focus on mean conditions, recent studies demonstrate that extreme climate and weather events can cause widespread breeding failure (4, 5) or reduce survival rates (6) on very short time scales. Impacts of climate can be compounded by other factors. Incidental mortality in fisheries (bycatch) is a major threat to seabirds (7, 8), yet very few studies have examined the combined impacts of climate and fisheries on demography (9–13). In this study, we predict that populations threatened by fisheries bycatch may be more sensitive to climate variability. As bycatch is heterogeneous, unbalanced losses according to age (14), sex (14), or behavior (15) reduce resilience to environmental change (16). Additionally, as the environment becomes unfavorable and prey less abundant or predictable, birds may increasingly seek feeding opportunities behind vessels, entailing a greater bycatch risk or a re-

duction in reproductive output by overreliance on poor-quality prey (17).

In long-lived seabirds, major gaps exist in our knowledge of young age classes (prerecruits) and adult nonbreeders, which are usually unobservable because they spend extensive periods at sea. Filling these gaps requires data on at-sea distributions from tracking devices, intensive and long time series of individual monitoring data at colonies, and advanced modeling tools. Prerecruits can represent half the population; they contribute ultimately to the total reproductive value and also influence demographic stochasticity (18). Although juveniles are potentially the age class that is most vulnerable to climatic and anthropogenic threats, few studies have identified the key drivers of their survival (19). Flexibility in recruitment age and breeding frequency can buffer populations of long-lived species when environmental conditions are poor (20). Modeling temporal variation in these processes is challenging, but our study exploits an unprecedented opportunity to explore drivers at the community level, contrasting the responses of related species to common environmental conditions according to their specific ecological and life-history traits.

The Diomedidae (albatrosses) are one of the most threatened of all bird families, with 18 of the 22 species classified as Near-Threatened (3 species), Vulnerable (7 species), Endangered (5 species), or Critically Endangered (3 species) by the International Union for the Conservation of Nature in 2016. Disproportionate

Significance

Three high-conservation priority populations were studied: the wandering, grey-headed, and black-browed albatrosses from Bird Island, South Georgia. They represent 12–50% of global numbers and have declined by 40–60% in 35 years. As temperatures and environmental stochasticity increase, polar species are particularly at risk, while fisheries accidentally kill hundreds of thousands individuals each year. Longitudinal monitoring of >40,000 individuals ringed since 1972 was used with detailed at-sea distributions, environmental data, and fisheries effort spanning the Southern Ocean to explore the factors driving population change and how they may combine. The powerful comparative framework used here is one of the most extensive to date and could be used to understand and better mitigate the fate of many threatened wild populations.

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numbers of albatross populations in the South Atlantic are in steep decline, including wandering (*Diomedea exulans*), gray-headed (*Thalassarche chrysostoma*), and black-browed (*Thalassarche melanophris*) albatrosses breeding at South Georgia (a UK Overseas Territory that is located southeast of South America), which currently represent 18%, 50%, and 12% of global numbers, respectively. Here we studied the demography of those three albatross species breeding sympatrically at Bird Island (a small island off the northwestern tip of South Georgia); total numbers at Bird Island represented 61.0%, 11.1%, and 10.7%, respectively, of those breeding at South Georgia in 2003–2004, based on the all-islands surveys (21) (*SI Appendix, Fig. S1*). All three populations were included among the eight populations considered by the Agreement for the Conservation of Albatrosses and Petrels in 2016 to be global conservation priorities in 20 (22). The monitored portion in Bird Island has decreased by 40%, 60%, and 60%, respectively, in the last 35 y and there is evidence that those trends reflect those in the remainder of the island group (23). Therefore, the aims of our study were as follows: *i*) describe fundamental demographic rates for juveniles and adults over time in the three sympatric species using multievent models, *ii*) determine which changes in demographic rates were responsible for low population growth rates using matrix models, and *iii*) identify the environmental drivers (climate, fisheries, and population variables) alone and combined that were influencing the populations using ANOVA.

Materials and Methods

We studied four fundamental demographic rates—probabilities of survival, return, breeding (laying the single-egg clutch), and breeding successfully (fledging the chick; hereafter termed “success”)—of juveniles (aged 0–3 y), immatures (from first return at age 4 until recruitment at age ≤ 20), and adults. In this, the most extensive set of analyses for any albatross species to date, we developed a powerful method that can be used on any taxa with sufficient individual-based information. The models integrated the following:

- i*) Totals of 21,887, 7,913, and 6,651 individual capture histories for wandering, gray-headed, and black-browed albatrosses, respectively, spanning five decades (1972–2012). Individuals in each population were monitored intensively on a daily to weekly basis, and particular effort was targeted at detecting nonbreeding individuals. All chicks were ringed each year.
- ii*) A capture-mark-recapture multievent framework encompassing imperfect detection (*SI Appendix, Fig. S3*), intermittent breeding, and delayed recruitment. This incorporated nine events (observed in the field) corresponding to 13 possible states: chick, unobservable/observable prebreeder, inexperienced failed/successful breeder (first breeding attempt), experienced failed/successful breeder (subsequent breeding occasions), experienced nonbreeder observed on breeding colonies, post-failed/successful/nonbreeding states that are unobservable because the birds do not attend the colony, recovered dead in a fishery, and dead (*SI Appendix, Fig. S2 and Table S1*).
- iii*) An age- and stage-structured matrix population model with results entered from the multievent model to calculate the deterministic population growth rate of each population for each year of the study period (*SI Appendix, Fig. S4*). Furthermore, a Life-Time Response Experiment (LTRE) analysis was conducted to measure the retrospective contribution of each demographic rate to the observed changes in population growth rate.
- iv*) Eight climatic and prey variables to investigate the effects of wind [meridional north-south (*wm*) and zonal west-east (*wz*) components, and speed (*ws*)], proxies of food availability [sea surface temperature (*SST*), sea ice extent (*SIE*), and krill density], and global oceanographic indices [Southern Annular Mode (*SAM*) and Southern Oscillation Index (*SOI*)], as well as two population variables to measure the influence of density dependence (*SI Appendix, Detailed Material and Methods*).
- v*) The most complete dataset available on effort in demersal longline, pelagic longline, and trawl fisheries across the Southern Ocean (*SI Appendix, Table S2*).

All environmental variables were extracted from well-mapped foraging areas during the corresponding time periods for each species, based on extensive tracking [399 tracks from 1991 to 2012, 363 tracks from 1993 to 2012, and 447 tracks from 1993 to 2010 for wandering, gray-headed, and black-browed albatrosses, respectively, during the breeding season (B) and 18 tracks from 2003 to 2005, 22 tracks from 1999 to 2000, and 25 tracks from 2002 for wandering, gray-headed, and black-browed albatrosses, respectively, during the

nonbreeding season (NB)]. Juvenile birds were assumed to follow the nonbreeding adult distribution.

Model selection was conducted on detection probability based on Akaike Information Criterion (24) for each species. Then, for all demographic rates, four types of models were run: constant, time-dependent, linear trend, and with each environmental variable. The contributions of environmental variables in explaining variation in demographic rates over time were measured with two metrics based on the differences in deviance between the four types of models tested above (ANODEV) (25): R^2_{basic} (R^2_{b}) is the usual long-term variability indicator but can be sensitive to temporal trends if present in both the demographic rate and the environmental variable, and $R^2_{\text{detrended}}$ (R^2_{d}) is more conservative and better for assessing fine-scale (interannual) variability. When R^2 was $\geq 10\%$ (25–27), the environmental variable was considered to have a significant effect, the sign (+ or –) and period (B or NB) of the relationship was investigated and the variable was included with all other significant variables in a general model (*SI Appendix, Detailed Material and Methods*).

Results

Comparative Description of Fundamental Demographic Rates (Fig. 1 A–G).

Counts of wandering albatrosses were stable at $\sim 1,400$ breeding pairs from the 1980s until the late 1990s, decreased by almost half in the subsequent decade, and then stabilized between 2007 and 2012 at ~ 800 breeding pairs (Fig. 1A, *Upper*). Adult survival declined markedly from 0.952 ± 0.012 in 1995 to 0.879 ± 0.015 in 2006 (Fig. 1G). Juvenile survival declined from 0.949 ± 0.011 in 1989 to 0.680 ± 0.018 in 1998 (Fig. 1D); and breeding success probability (Fig. 1P) increased during the study period (1981–2012) from 0.583 ± 0.052 in 1986 to 0.808 ± 0.014 in 2008, at the expense of return probability, which declined from 0.844 ± 0.054 in 1986 to 0.561 ± 0.019 in 2012, because this is a biennial species that defers breeding if successful (Fig. 1J).

The number of gray-headed albatrosses in the study colonies declined gradually after 1989 from 1150 to ~ 400 breeding pairs, with high annual variability particularly until 2000 (Fig. 1B); however, there were no significant negative temporal trends in any demographic rate. However, over the study period, average juvenile survival was 0.764 ± 0.076 (Fig. 1E), and other rates (means of 0.573 ± 0.108 , 0.642 ± 0.110 , and 0.365 ± 0.197 for return, breeding, and success probabilities, respectively; Fig. 1K, N, and Q) were highly variable and lower than expected for a biennially breeding species. Adult survival was quite stable at 0.952 ± 0.029 , with a substantial drop in 2000 to 0.828 ± 0.018 , and an apparent period of very low survival from 2005 to 2010 of 0.931 ± 0.018 .

The number of black-browed albatrosses in the study colonies also declined gradually from 607 breeding pairs in 1990 to 202 breeding pairs in 2012, with an anomalously low count in 1995 of 108 pairs (Fig. 1C) but with less annual variability than in gray-headed albatrosses. Juvenile and adult survival decreased significantly over the study period from 0.910 ± 0.029 in 1985 to 0.653 ± 0.028 in 1997, and from 0.979 ± 0.011 in 1989 to 0.875 ± 0.013 in 2008, respectively (Fig. 1F and J). Similarly to gray-headed albatrosses, adult survival of black-browed albatross was particularly low in 2006–2011, at 0.893 ± 0.012 . Return and breeding probabilities were 0.846 ± 0.098 and 0.693 ± 0.175 , on average, and particularly low in 1987–1995, at 0.578 ± 0.025 and 0.103 ± 0.017 , respectively. Success probability was even lower than for gray-headed albatrosses at 0.300 ± 0.174 , with no significant trend over time but with more years of complete breeding failure (Fig. 1L, O, and R).

Contribution of Demographic Rates to Observed Declines (Fig. 1 S–X).

The population growth rate of all three species was negative for most of the study period (Fig. 1S–U). The LTRE analysis showed that, as expected in such long-lived species, adult survival was the main driver of population decline; however, a comparison of species- and year-specific variation provided additional insights (Fig. 1V–X). For wandering albatrosses, the population growth rate changed from a positive phase in 1984–1995 to a negative phase in which the population declined, on average, by 3% per year (Fig. 1S).

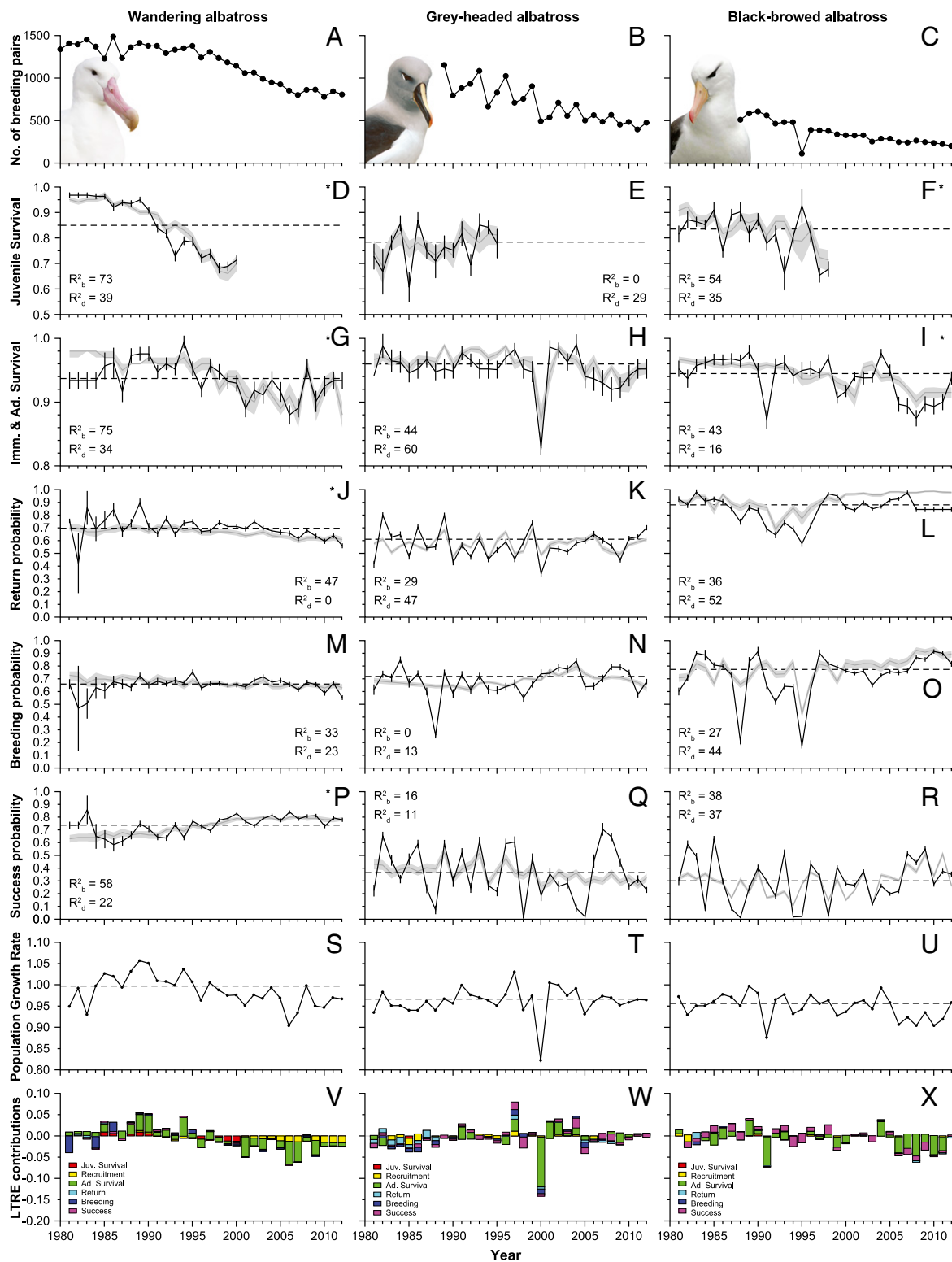


Fig. 1. Number of breeding pairs counted in the field (A–C), estimated demographic rates (D–R), and results of matrix population retrospective analysis (LTRE; S–X) for wandering, gray-headed, and black-browed albatrosses breeding in long-term study colonies at Bird Island, South Georgia, from 1981 to 2012. (D–R) Black lines represent means \pm SEs. Gray dashed horizontal lines represent the average values estimated for the time series over the same period. The asterisks (*) at the top right of D, F, G, I, J, and P indicate if the demographic rate increased or decreased significantly. Gray lines (with 95% CI shaded areas) indicate the estimates from a model encompassing all significant climatic, population, and fisheries covariates (average results from the basic and detrended model) for each demographic rate. The percentages of variance explained for the best models with either the basic R^2_b or detrended R^2_d framework are given for each demographic rate. Ad., adult; Imm., immature; Juv., juvenile.

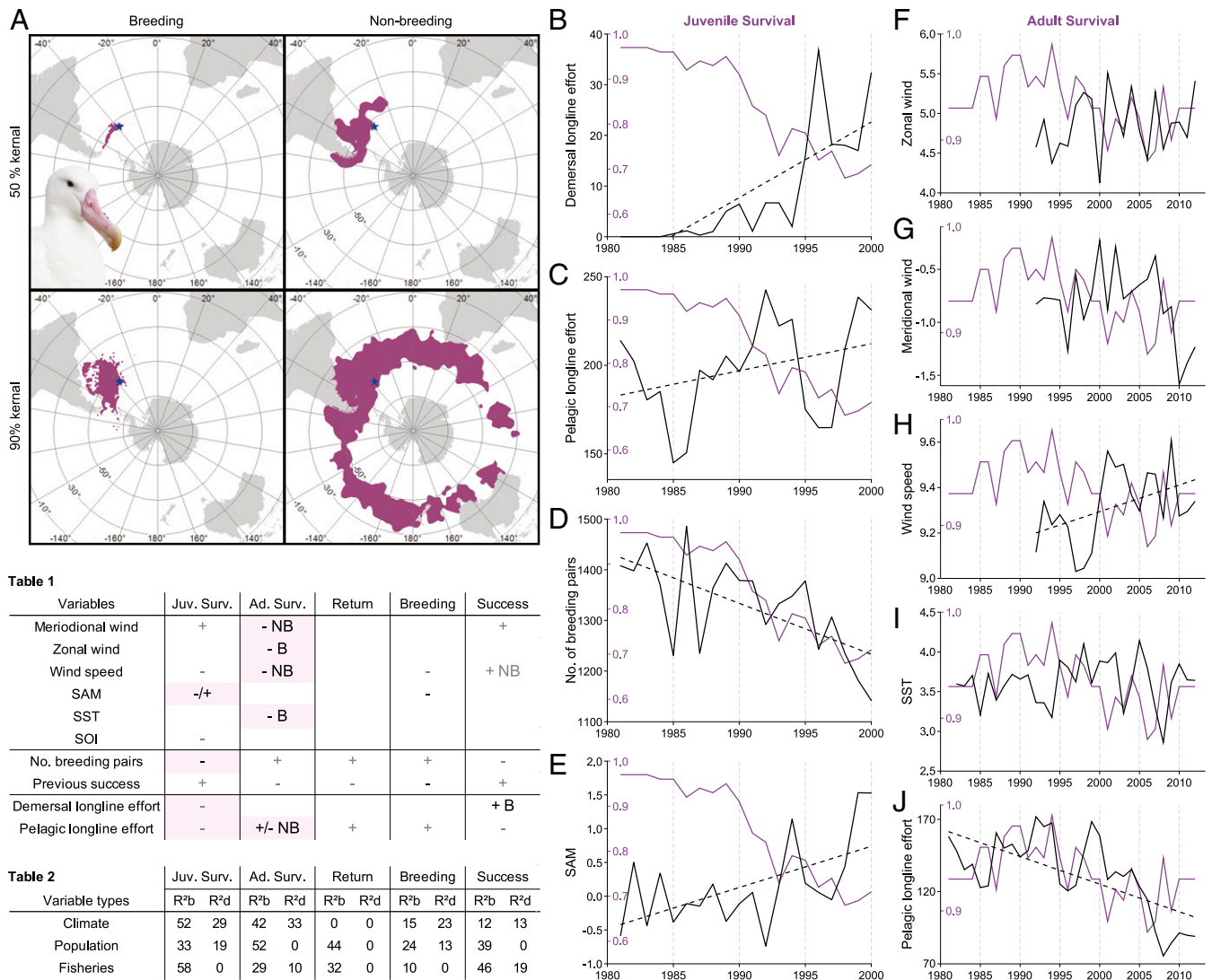


Fig. 2. (A, Upper) Breeding (B) and nonbreeding (NB) 50% and 90% kernel distribution of wandering albatrosses from Bird Island (blue star in A). A, Middle indicates the sign and main season of the relationships found between a demographic rate and an environmental covariate (in gray when R^2_b or R^2_d was $>10\%$, in black when both were $>10\%$, highlighted when plotted on the right part of the figure). A, Lower summarizes the total variance explained by groups of variables. B–J represent the temporal variations in environmental variables (black lines) with a linear trend (dashed black lines) when significantly increasing or decreasing over time compared with juvenile survival (purple lines in B–E) and adult survival (purple lines in F–J). The unit for longline effort is millions of hooks deployed, wind components are in $m \cdot s^{-1}$, and SST is shown in $^{\circ}C$. Ad., adult; Juv., juvenile; Surv., survival.

The LTRE analyses showed that the increase in success did not result in population growth (Fig. 1*V*). The decline in juvenile survival played an increasing role in the population decrease, although for methodological reasons (*SI Appendix, Detailed Material and Methods*), this could not be quantified after year 2000. We nevertheless detected a growing influence of poor recruitment, which reflects the impact of juvenile mortality over the long-term.

For gray-headed albatrosses, the population growth rate has been negative (on average, -2.5% per year) since the start of the monitoring, except during a few years when it was stable and 1 y when it was positive (1997; Fig. 1*T*). Therefore, it is difficult to determine the ultimate demographic driver of the decline. Regardless, the results indicate that the population could reach stable or increasing population growth only in years when survival, breeding, or success probabilities were all close to or higher than the long-term means (e.g., 1997, 2001, 2002, 2004) (Fig. 1*H, N, Q, T, and W*). The LTRE analysis confirmed that adult survival was the main driver of population growth but showed the relatively high contribution of

return, breeding, and success probabilities, and to a lesser extent of juvenile survival, in driving population trends. In 2000, the steep decrease in population growth rate appeared principally to reflect the observed decline in adult survival.

The breeding population of black-browed albatrosses has declined, on average, by almost 4% per year since the study began (Fig. 1*U*). The two exceptions were in 1989 and 2004 when population growth reached 1 (was stable) (Fig. 1*I and R*). Variability in success allowed a higher than average population growth rate by compensating for average adult survival in 1985, 1987, 1992, 1993, 1996, and 1998. However, since the mid-2000s and in 1991, adult survival has been very low and the main driver of the low population growth rate according to the LTRE analysis (Fig. 1*X*). In all species, the apparent influences of return and breeding probabilities in the first few years of the analyses reflect estimation uncertainties.

Relationships with Climate and Prey Variables (Figs. 2–4 for Each Species). There was no effect of krill density in wandering albatrosses; however, many climatic variables had a significant effect

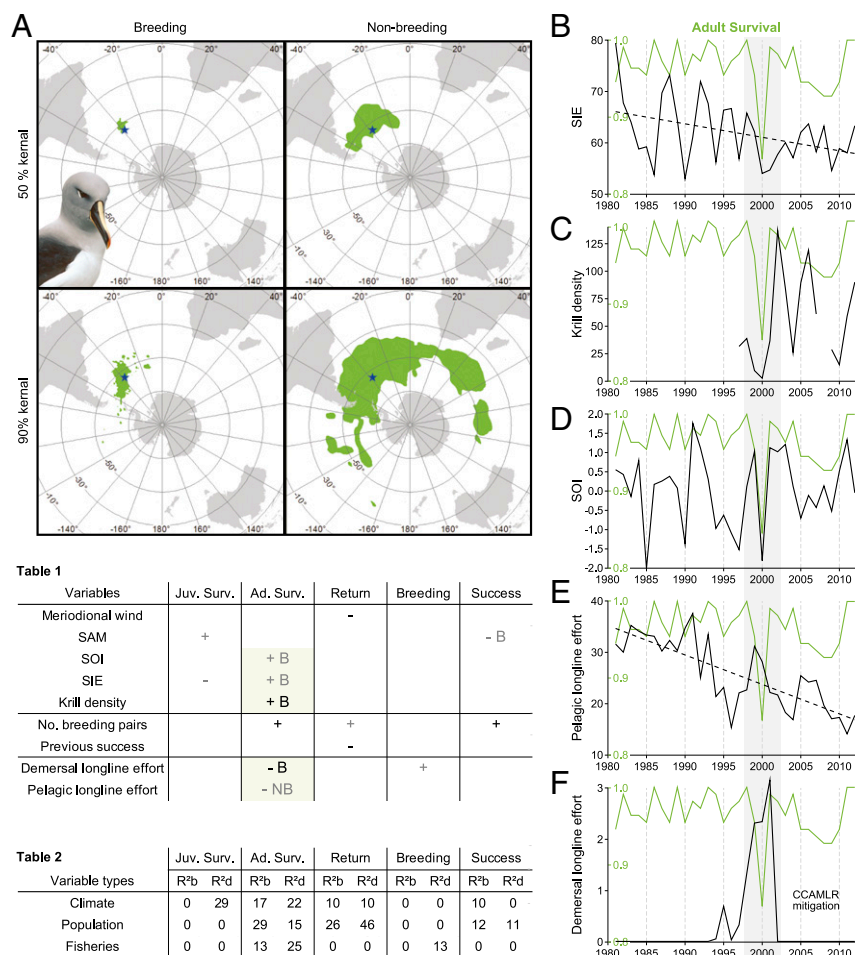


Fig. 3. (A, Upper) Breeding (B) and nonbreeding (NB) 50% and 90% kernel distribution of gray-headed albatrosses from Bird Island (blue star in A). A, Middle indicates the sign and main season of the relationships found between a demographic rate and an environmental covariate (in gray when R_b^2 or R_d^2 was >10%, in black when both were >10%, highlighted when plotted on the right part of the figure). A, Lower summarizes the total variance explained by groups of variables. B–F represent the temporal variation in environmental variables (black lines) with a linear trend (dashed black lines) when significantly increasing or decreasing over time compared with adult survival (green lines in B–F). Units for longline effort is millions of hooks deployed, SIE is measured as the percentage of ice cover in a polygon around the Antarctic peninsula, krill density was measured in the western core box in $g \cdot m^{-2}$, and a negative SOI represents El Niño events. Ad., adult; CCAMLR, Convention on the Conservation of Antarctic Marine Living Resources; Juv., juvenile; Surv., survival.

according to both basic and detrended models (black letters and symbols in Fig. 2, Middle). Wind components appeared to play a major role in adult survival, which declined with more poleward (wm: $R_b^2 = 26\%$, $R_d^2 = 21\%$; Fig. 2G and SI Appendix, Table S3) and stronger (ws: $R_b^2 = 26\%$, $R_d^2 = 21\%$; Fig. 2H) winds during the nonbreeding period. During the breeding period, adult survival was favored by westerly winds (wz: $R_b^2 = 23\%$, $R_d^2 = 11\%$; Fig. 2F) and lower SST ($R_b^2 = 15\%$, $R_d^2 = 10\%$; Fig. 2I). An opposite effect of winds was found on breeding success; more poleward winds before (wm: $R_d^2 = 13\%$) and during (wm: $R_d^2 = 11\%$) the breeding season increased breeding success, as did stronger winds (ws NB: $R_b^2 = 12\%$). Climatic effects on juvenile survival were more difficult to interpret: first, because SAM had a significant effect according to both basic and detrended models ($R_b^2 = 27\%$, $R_d^2 = 14\%$; Fig. 2E) but in opposite directions [a long-term negative (R_b^2) but short-term positive (R_d^2) effect]; second, because effects of other climatic variables were apparent only in the basic or the detrended models (gray letters and symbols in Fig. 2, Middle). In contrast to adult survival, juvenile survival was positively affected by more poleward winds (wm: $R_d^2 = 18\%$) but, as with adult survival, was negatively affected by stronger winds (ws: $R_b^2 = 34\%$). Additionally, there was a slight

positive effect of El Niño events (SOI: $R_d^2 = 11\%$). Breeding probability was reduced by stronger wind conditions (SAM: $R_b^2 = 15\%$, $R_d^2 = 15\%$; ws: $R_d^2 = 13\%$). The combination of all significant climatic variables explained substantial amounts of total variability over time in demographic rates of wandering albatrosses, including up to $R_b^2 = 54\%$ in juvenile survival (Fig. 2, Lower).

Effects of climatic and prey conditions were only apparent in gray-headed albatrosses during the breeding season (Fig. 3, Middle and SI Appendix, Table S3). Only two variables had a significant effect in both basic and detrended models: a positive influence of krill density on adult survival ($R_b^2 = 10\%$, $R_d^2 = 12\%$; Fig. 3C) and a negative influence of more poleward winds on return probability ($R_b^2 = 10\%$, $R_d^2 = 10\%$). SIE ($R_b^2 = 10\%$; Fig. 3B) and SOI ($R_d^2 = 13\%$; Fig. 3D) also had a positive influence on adult survival; more sea ice was beneficial and El Niño events were detrimental. SAM during the breeding period had a negative effect on success ($R_b^2 = 10\%$). In contrast to adults, survival of juveniles was influenced negatively by SIE ($R_d^2 = 10\%$) and positively by SAM ($R_d^2 = 10\%$).

Only two variables had a significant effect in both basic and detrended models for black-browed albatrosses (Fig. 4, Middle and

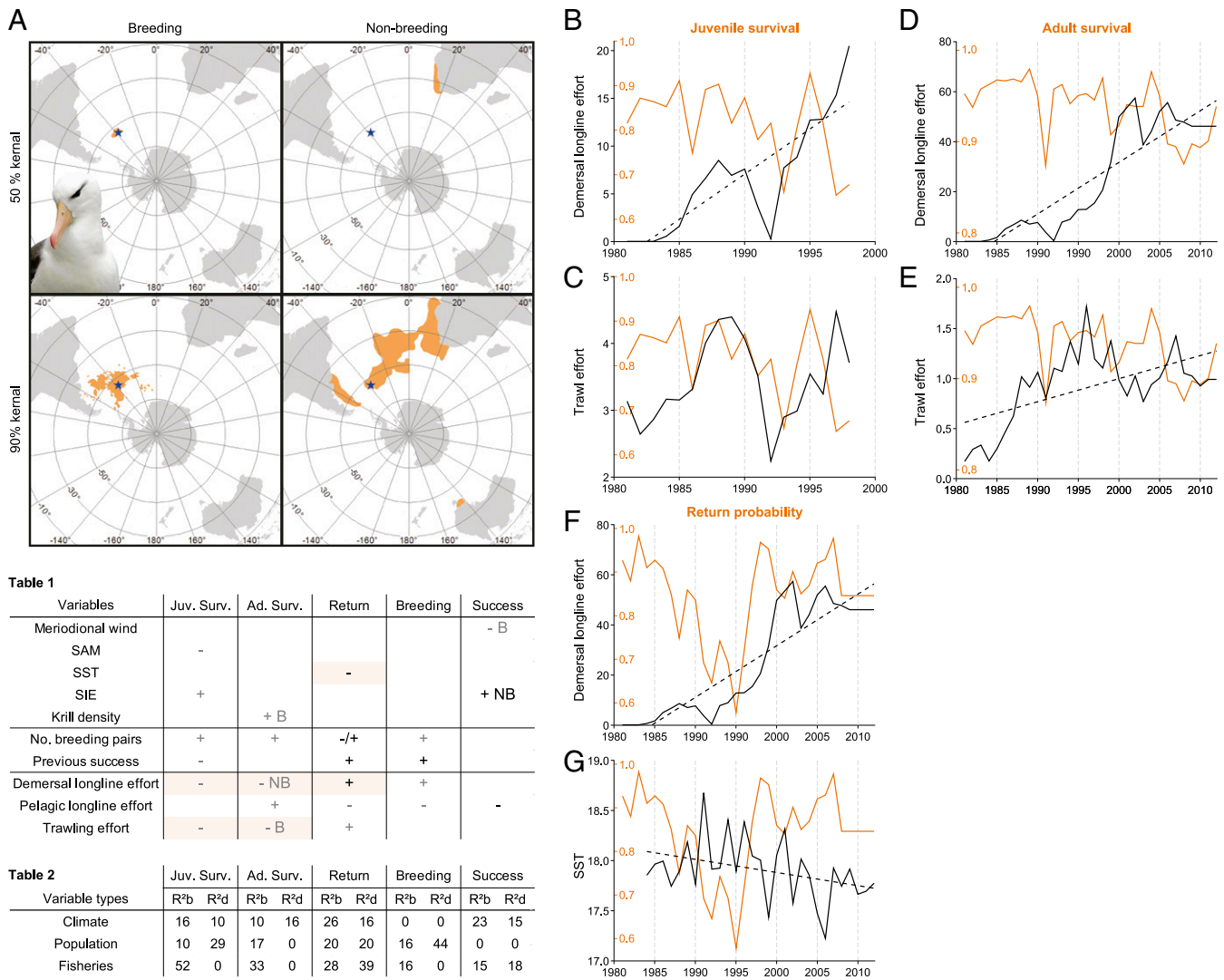


Fig. 4. (A, Upper) Breeding (B) and nonbreeding (NB) 50% and 90% kernel distribution of black-browed albatrosses from Bird Island (blue star in A). A, Middle indicates the sign and main season of the relationships found between a demographic rate and an environmental covariate (in gray when R_b^2 or R_d^2 was $>10\%$, in black when both were $>10\%$, highlighted when plotted on the right part of the figure). A, Lower summarizes the total variance explained by groups of variables. B–G represent the temporal variations in environmental variables (black lines) with a linear trend (dashed black lines) when there was a significant increase or decrease over time in juvenile survival (orange lines in B and C), adult survival (orange lines in D and E), and return probability (orange lines in F and G). The unit for longline effort is millions of hooks deployed and for trawling effort is numbers of hours trawled. SST is shown in $^{\circ}\text{C}$. Ad., adult; Juv., juvenile; Surv., survival.

(SI Appendix, Table S3): a positive influence of SIE during the preceding nonbreeding period on success ($R_b^2 = 13\%$, $R_d^2 = 15\%$) and a negative influence of SST on return probability ($R_b^2 = 26\%$, $R_d^2 = 16\%$; Fig. 4G). Recent changes in wind regime appeared to be detrimental, as more poleward winds during the breeding period reduced breeding success ($R_b^2 = 12\%$) and SAM had a negative influence on juvenile survival ($R_d^2 = 10\%$). The direct and indirect indices of krill availability both appeared to have positive effects, as juvenile survival was improved by higher SIE ($R_b^2 = 16\%$) and adult survival by greater krill density during the breeding period ($R_d^2 = 10\%$).

Role of Fisheries in Population Changes (Figs. 2–4 for Each Species).

There was a strong response to longline fisheries apparent in all demographic rates of wandering albatrosses (Fig. 2, Middle and Lower). Higher demersal and pelagic longline effort was associated with reduced juvenile survival ($R_b^2 = 49\%$ and $R_b^2 = 10\%$ in Fig. 2 B and C, respectively) and higher pelagic longline effort with

reduced adult survival ($R_b^2 = 26\%$, $R_d^2 = 10\%$; Fig. 2J). Conversely, the effects of fisheries on reproductive rates (return, breeding, success) were mostly positive. Higher return and breeding probabilities were associated with greater pelagic longline effort ($R_b^2 = 32\%$ and $R_b^2 = 10\%$, respectively). Demersal longline effort, particularly during the breeding period, had a strong positive effect on success ($R_b^2 = 23\%$, $R_b^2 = 19\%$). Finally, there was a negative relationship between year-round pelagic longline effort and success (up to $R_b^2 = 23\%$).

In gray-headed albatrosses, the greatest impact of fisheries was on adult survival, with negative effects of higher demersal longline effort during the breeding period ($R_b^2 = 13\%$, $R_d^2 = 12\%$; Fig. 3F) and of higher pelagic longline effort during the nonbreeding period ($R_d^2 = 16\%$; Fig. 3E). As for wandering albatrosses, there was a positive influence of demersal longline effort preceding the breeding season on breeding probability ($R_d^2 = 13\%$; Fig. 3, Middle and Lower).

In black-browed albatrosses, trawl and demersal longline effort influenced demographic rates, with negative effects on survival but positive effects on reproductive traits. Surprisingly, the influences of pelagic longline effort were in the opposite directions. There were negative effects of trawl effort on juvenile survival ($R_b^2 = 16\%$ and $R_b^2 = 51\%$ in Fig. 4C and B, respectively) and of demersal longline effort on adult survival ($R_b^2 = 10\%$ and $R_b^2 = 21\%$ in Fig. 4E and D, respectively), year-round, but mostly during the nonbreeding period. Return probability was greatly improved by higher demersal longline effort ($R_b^2 = 22\%$, $R_d^2 = 39\%$; Fig. 4F) as was breeding probability ($R_b^2 = 11\%$); the latter also showed a positive relationship with trawl effort ($R_b^2 = 12\%$). Higher pelagic longline effort, year-round, showed a strong negative relationship with success (up to $R_b^2 = 13\%$, $R_b^2 = 15\%$), return ($R_b^2 = 21\%$), and breeding ($R_b^2 = 14\%$) probabilities. In contrast, pelagic longline effort had a positive relationship with adult survival ($R_b^2 = 21\%$).

Discussion

Comparative Demography and Population Dynamics. The populations of gray-headed and black-browed albatrosses at Bird Island have been declining since monitoring began in the 1970s. In the gray-headed albatross, we did not detect a significant decline over time in any demographic rate, whereas for the black-browed albatross, both juvenile and adult survival declined significantly during the study. This suggests that the population sizes of both these species were unsustainable based on their demography. In contrast, the wandering albatross population was stable in the 1980s, but, like the other species, declined steeply thereafter, driven by significant declines in juvenile and adult survival, and despite a significant increase in breeding success over the study period.

If these demographic rates are compared with results for breeding populations elsewhere, two clear patterns emerge. First, breeding propensity (the product of return and breeding probability) and success were consistently lower (strikingly so for gray-headed and black-browed albatrosses) at South Georgia compared with wandering, gray-headed, and black-browed albatrosses at Crozet (28), Marion (29), and Kerguelen (30), respectively. Second, and probably as a consequence of reduced costs of reproduction (related to frequent early breeding failure), adult survival was significantly higher at South Georgia than at other locations (31), except for the wandering albatross, large numbers of which are killed by fisheries in the South Atlantic. Estimates using similar multievent models indicate that juvenile survival of wandering albatrosses was higher at South Georgia than at Crozet (0.614 ± 0.014 vs. 0.589 ± 0.013) (19).

The retrospective analysis was very informative in identifying which demographic rates explained the variation in past population growth rates (32). This is a key step forward from our previous understanding of population dynamics of marine species (9, 19, 31, 33, 34). As expected for such long-lived species (20, 35), the LTRE analysis indicated that adult survival was the dominant driver of population growth rate, and depending on the species, showed a gradual decline over time or steep decreases in some years. Nevertheless, other demographic rates were also important drivers of population changes at different times for each species. For wandering albatrosses, the decline in juvenile survival became increasingly important, later reflected in much reduced recruitment, which continues to be a major problem for this population. For gray-headed albatrosses, the combination of low and highly variable rates for the different reproductive parameters, especially breeding success, was a major driver explaining past population declines. Similarly, poor breeding success was a key driver of the decline in the black-browed albatross. When reproductive parameters are so low, demographic buffering mechanisms involving prerecruits recruit-

ing earlier and adult nonbreeders attempting to breed more often can lead the population to rebound (36). Such changes were clearly detected in gray-headed albatrosses.

For all three species, positive effects of the number of breeding pairs on survival and reproductive rates suggest positive density dependence, and that birds benefit from social information for locating prey (37) or suffer from increased predation rates of eggs and chicks as subcolony size declines in black-browed and gray-headed albatrosses; this increases the proportion of nests at the periphery, which are targeted by predatory brown skuas (*Stercorarius antarcticus*) and giant petrels (*Macronectes* spp.) (38). Juvenile survival and success of the wandering albatross, however, were lower when the population size was higher, perhaps related to greater interference competition for food at sea (39). In the two biennially breeding species (wandering and gray-headed albatrosses), previous success had a negative effect on subsequent reproduction, as expected, and in wandering albatrosses also on adult survival, which might indicate a cost of reproduction (28). In contrast, in black-browed albatrosses, the only annual species, previous success had a positive effect, suggesting consistent long-term differences in individual performance.

Environmental and Anthropogenic Drivers of Declines. Although wandering, gray-headed, and black-browed albatrosses breed in sympatry at South Georgia, there were major differences between species in the relationships between demographic rates and environmental variables. We observed high synchrony (*SI Appendix, Table S4*) between success probabilities of gray-headed and black-browed albatrosses, suggesting similar environmental forcing. This presumably reflects the moderate dietary overlap (40, 41) and broadly similar overall distributions during breeding (42) (Figs. 3A, Upper and 4A, Upper). However, although we tested an extensive suite of climate, prey, population, and fishery variables specifically extracted from foraging areas at specific periods of the breeding cycle, our models struggled to explain a substantial proportion of temporal variability in their reproductive rates. Two variables were significant—krill density and SIE in one of the main krill nursery grounds in the region—underlining the sensitivity of these populations to the availability of one of their main food sources, as demonstrated previously for other krill-dependent species at South Georgia (43, 44). Other global changes that are ongoing (increasing temperature and changing wind patterns) seem likely to have increasing impacts on breeding success. Krill density also affected survival. Both gray-headed and black-browed albatrosses feed mainly in sub-Antarctic and Antarctic waters during breeding (42), and greater SIE around the Antarctic Peninsula in the austral summer improved survival of adult gray-headed and juvenile black-browed albatrosses but reduced survival of juvenile gray-headed albatrosses. Black-browed albatrosses appeared to benefit from fisheries discards (from trawlers and demersal longliners) in their nonbreeding grounds in the Benguela Upwelling. Until recently, scavenging behind vessels in that region would have put birds at high risk of bycatch, but the risk has been much reduced by the introduction of improved bycatch mitigation measures and close monitoring of compliance (45). Adult survival of gray-headed albatrosses responded strongly to El Niño events, which are expected to increase in intensity and frequency (46) and seem likely to further impact the population.

Albatrosses rely heavily on winds for efficient flight and foraging, and there is evidence that climate change has benefited wandering albatrosses in the Indian Ocean by increasing the frequency of favorable wind conditions (33). A shift in the SAM in the 1990s changed the wind patterns in the Southern Ocean to more poleward (wm), westerly (wz), and faster (33). Here we also found mostly positive effects of changing wind regimes (SAM, meridional, zonal, and speed) on success probabilities, particularly in the wandering albatross, which may relate to its larger size, higher wing loading (47), much longer breeding season (12 mo

compared with 8 mo), and more extensive circumpolar distribution (48). However, we also found that increased wind speed reduces breeding propensity and, more importantly, that it had negative impacts on juvenile and adult survival. Given that wind regimes are predicted to change further (46), these relationships suggest there will be major and, overall, negative consequences for the wandering albatross population at South Georgia.

There was a high synchrony in annual juvenile and adult survival rates of wandering and black-browed albatrosses (*SI Appendix, Table S4*). The explanation for this is not entirely clear, as there are few data on fine-scale distributions of juveniles from South Georgia (49). However, it could demonstrate similar influences of bycatch on these two species, which both interact a great deal with fishing vessels (14). Indeed, we detected strong relationships between survival and fishing effort in each species, in particular during the nonbreeding periods (48). There were also other direct anthropogenic impacts of fisheries (*SI Appendix, Table S2*). Despite concerns about unsustainable levels of seabird bycatch since the 1990s, mitigation measures (e.g., heavier line-weighting, night-setting, use of streamer lines) have been introduced only in a minority of fisheries and, in many cases, only in recent years (8, 47, 50). Black-browed albatrosses interact with a range of trawl, pelagic, and demersal longline fleets, and this is the most common albatross recorded as bycatch worldwide (14). The positive relationships between effort in some fisheries and reproductive traits may indicate the benefits provided by discards (14); moreover, we cannot rule out a common environmental effect that is beneficial for both fisheries and albatrosses. The strongest relationships were with trawling activity, but demersal longline fishing effort in the Benguela Upwelling also had a negative impact on the probability of survival, return, and breeding in the black-browed albatross. Wandering albatrosses often out-compete other species while feeding behind pelagic vessels (51), and our results indicate that pelagic longline fishing effort is associated with reduced survival of both juveniles and adults. In addition, a 20% drop in juvenile survival coincided with the onset of large-scale demersal longline fishing around sub-Antarctic islands in the mid-1990s. The pelagic tuna fleets in the Atlantic and Indian oceans, dominated by Taiwan and Japan, are likely to have the greatest impacts because of their high fishing effort and spatiotemporal overlap with wandering albatrosses (8, 48). Bird bycatch mitigation was not mandatory in these fisheries until the late 2000s and did not reflect best-practice until even more recently, and observer coverage remains far below the level necessary for effective monitoring of compliance (52). However, mitigation has reduced seabird bycatch by some fleets (48) and the overlap between wandering albatrosses and vessels has declined as these fisheries have moved north and effort reduced in the last 5 y, which might explain the recent stabilization in adult survival rates. Given the time between fledging and recruitment, the expected improvements in juvenile and immature survival may not be apparent until the next decade.

Combined Effect of Environmental and Anthropogenic Variables.

There are a few ways in which environmental variables can act together to affect albatross demography. Although our approach used the latest multievent modeling techniques (29, 53) and the most advanced ANODEV interpretation (25, 54), it remains correlative. However, we have evidence for two kinds of combined effects: additive and sequential. Gray-headed albatrosses were recorded infrequently as bycatch in demersal longline fisheries around sub-Antarctic islands and pelagic longline fisheries off Australia and South Africa in the last one to two decades (*SI Appendix, Table S2*); nevertheless, we detected an effect of these fisheries in some years. In 2000, the population crashed, an event that reflected a sudden drop in adult survival, attributed by the models to a combination of environmental conditions indicative of poor food avail-

ability and to a peak in fishing effort. In this year, the lagged effect of a strong El Niño reached the Scotia Sea, greatly reducing krill abundance during the breeding season according to acoustic surveys and suggested by low SIE. Simultaneously, pelagic and demersal longline effort peaked during the nonbreeding and breeding seasons, respectively. The following year, use of seabird bycatch mitigation became mandatory in the demersal fishery (47), and annual adult survival rates returned to previous levels.

We have demonstrated that fisheries bycatch had a very important role in the population declines, especially of wandering and black-browed albatrosses since the 1990s. Its influence might now be lower; overall effort is diminishing, the overlap during the breeding season is decreasing, and bycatch mitigation measures are gradually becoming more widespread (55, 56). Moreover, studies suggest that the influence of fisheries may also change as a result of selection on individual traits (e.g., in favor of less bold individuals) (15) or a sex or age bias in bycatch rates (57). In the meantime, the climate is changing, with temperatures rising in many regions, the wind regime is altering, and more frequent and extreme climatic events are predicted. Therefore, although the populations may benefit from the reduced influence of fisheries bycatch, indirect anthropogenic activities that are changing the global climate may have increasing impacts on foraging efficiency or prey availability, and hence on survival, breeding probability, and success, and thus prevent future recovery.

Conclusions. This study gathered together diverse data types (tracking, ringing, monitoring, climatic, and fisheries) and analyzed the resighting histories of >40,000 individuals of three albatross species over three decades. It is therefore one of the most extensive demographic studies to date. In a series of steps strengthened by specific methodologies, we described the direction of temporal trends as well as the extent of annual variability in fundamental demographic rates for both juveniles and adults in a comparative manner for the three sympatric albatross species. Then we were able to determine which of those demographic rates were most influential for population growth in different phases over time, highlighting the impact of lagged juvenile mortality on recruitment in wandering albatrosses, and poor breeding propensity and success in gray-headed and black-browed albatrosses. Finally, a series of carefully selected climate, prey, and fisheries variables were identified as correlates of population changes. Each species responded in its way, revealing the specific environmental and anthropogenic threats facing those high-priority conservation populations. Furthermore, combined effects of environmental and anthropogenic variables were detected. One of them was the exacerbated impact of fisheries bycatch on adult survival when lagged El Niño events generate particularly poor environmental conditions. This emphasizes the need for much improved implementation of bird bycatch mitigation in fisheries, and better enforcement of compliance, particularly in the second and third year following a strong El Niño. Mitigating the effects of ongoing changes in climate (SST, wind, extreme events), which depress reproductive rates (return, breeding, and success probabilities) in these populations, will be even more challenging without much-improved political and societal efforts at a global scale. Until that takes effect, the future for gray-headed and black-browed albatrosses, in particular, appears to be bleak.

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