



## Biological Sciences

# Population growth of the grey-headed albatross population on Marion Island inferred using three analysis methods

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### Abstract

Globally, the grey-headed albatross *Thalassarche chrysostoma* is listed as Endangered due to decreasing populations at its major breeding colonies. We analysed the population trend at Marion Island using annual counts of incubating pairs and fledglings from 1984 to 2021 and three methods: TRends and Indices for Monitoring data (TRIM), a generalized additive model and a state-space model. In contrast to rapid decreases at most other colonies, all three methods indicated a local population increase at an average annual rate of 1.3%. The latter two models indicated a decreasing trend from 1997 to 2002, presumably related to mortality on longlines set for Patagonian toothfish *Dissostichus eleginoides* around the island, which peaked from 1996 to 1998. Grey-headed albatrosses exhibit greater variation in annual counts than other seabird species at Marion Island, possibly linked to interannual variation in breeding success because they are biennial breeders. However, breeding success alone was not significant in any of the models, presumably because it cannot capture the complexities of both population processes and environmental variation. Although all three models predicted the overall trends well, integrated population models, which can account for demographic processes, might be more appropriate to model long-term population trends.

**Key words:** generalized additive model, population trend, Prince Edward Islands, state-space model, *Thalassarche chrysostoma*, TRIM

(Received 24 October 2023; revised 5 July 2024; accepted 19 July 2024)

### Introduction

Albatrosses are the most threatened group of seabirds, with 21 of the 22 species being listed as Threatened or Near Threatened (Phillips *et al.* 2022, BirdLife International 2023). One of these threatened species is the grey-headed albatross *Thalassarche chrysostoma*, which is listed as Endangered (BirdLife International 2023) due to a > 50% decrease in the population over three generations at South Georgia and Campbell Island (Sagar 2014, Poncet *et al.* 2017). Together, these islands hold ~49 500 breeding pairs annually, just over half of the total population (~92 800 pairs; BirdLife International 2023). Fishery bycatch at sea and environmental variability are probable major drivers of population change affecting the grey-headed albatross population globally (Pardo *et al.* 2017).

The Prince Edward Islands are one of seven island groups where grey-headed albatrosses breed, with some 7800 pairs breeding each year on Marion Island and 2000 pairs breeding on the smaller Prince Edward Island (Ryan *et al.* 2009). The main fishery impact on albatrosses around the Prince Edward Islands occurred in the mid-1990s when large numbers of adult grey-headed albatrosses were caught as bycatch in the Patagonian toothfish *Dissostichus eleginoides* fishery. This fishery killed an estimated 5000–20 000 seabirds in 1 year, of which 20% were grey-headed

albatrosses (Ryan *et al.* 1997, Ryan & Boix-Hinzen 1999, Nel *et al.* 2002a). Fortunately for seabirds, fishing effort soon dwindled as fish stocks were exhausted, and mitigation measures greatly reduced albatross bycatch rates (Brandão & Butterworth 2002). More recently, introduced house mice *Mus musculus* have started preying on grey-headed albatross chicks at Marion Island (Dilley *et al.* 2016), but the effect at the population level is still unknown. The overall effects of environmental variability are also unclear, but changes in demographic rates at Marion Island have been related to indices such as the Southern Oscillation Index (SOI) and single El Niño events (Nel *et al.* 2002b, Crawford *et al.* 2003, Ryan & Bester 2008).

As with all threatened species, it is important to understand their long-term population trends to protect and conserve them. Albatrosses spend most of their lives at sea, only returning to land to breed. The best index of population size is the number of breeding pairs at the start of incubation. Each pair produces one egg per season and does not lay again in the same season if they fail. Most pairs that fail early in the season return to lay again in the next breeding season, whereas pairs that successfully raise a chick generally only attempt to breed every second year (Tickell 1968, Prince *et al.* 1994). However, at Marion Island some 5% of successful pairs breed annually (Ryan *et al.* 2007). Annual counts of breeding pairs thus consist of a mix of successful and failed breeders from previous years (Prince *et al.* 1994, Nel *et al.* 2002b), and fluctuations in breeding success could cause marked interannual changes in breeding numbers because the

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**Cite this article:** Stevens KL, Altwegg R, Connan M, Ryan PG (2024). Population growth of the grey-headed albatross population on Marion Island inferred using three analysis methods. *Antarctic Science* 1–11. <https://doi.org/10.1017/S0954102024000336>

proportion that breeds each year (the re-breeder rate, *sensu* Bonnevie *et al.* 2012) is largely determined by breeding success in the preceding year.

Various methods can be used to infer population trends from counts of breeding pairs. One option is to look at linear trends (Ryan *et al.* 2009, Poncet *et al.* 2017), but since population change is seldom linear for extended periods, using linear trend models alone has its limitations, and models cannot identify factors that might cause natural annual fluctuations in population size (Storch *et al.* 2023). For long-lived species such as albatrosses with large annual fluctuations, a linear trend model will only work after 2 decades of data have been gathered (Wauchope *et al.* 2019). To determine the trend earlier than that would require explaining what causes the annual fluctuations so as to infer what the underlying trend might be. To overcome this limitation, linear trend models could be used to identify when growth rates change and then to analyse the trends within these time periods (e.g. piecewise regression; Toms & Lesperance 2003). TRends and Indices for Monitoring data (TRIM) uses linear models with the option to assign changepoints. However, the changepoints may not be easy to identify if the count data are highly variable, and, statistically, fitting linear trends might be problematic if there is strong autocorrelation in the data (Fewster *et al.* 2000). Another approach is to use time-series models where the trends can be non-linear and change flexibly over time, such as generalized additive models (GAMs) or state-space models (SSMs; Fewster *et al.* 2000).

This study estimates the population trend of grey-headed albatrosses at Marion Island from 1984 to 2021 using three statistical methods: TRIM, GAMs and SSMs. We assess the advantages and disadvantages of each of these methods for a biennially breeding seabird species and test whether including breeding success as a covariate improves our understanding of the population trend.

## Methods

### Scan counts

Grey-headed albatrosses breed during the summer. Adults return to Marion Island from early September and lay in the first 3 weeks of October. The chicks hatch in December, after an incubation period of 72–74 days, and fledge ~4 months later in late April and May (Agreement on the Conservation of Albatrosses and Petrels 2010).

Since the 1980s, two counts of grey-headed albatrosses in all breeding colonies have been conducted each year at Marion Island: one during incubation (October) and the second just prior to fledging (April). The second count allows a crude estimate of island-wide breeding success. The albatrosses breed in dense cliff-side colonies, so counts are made by scanning with binoculars from vantage points either above or below each colony and using a tally counter to record the number of birds sitting on nests. Individuals from breeding pairs take turns incubating the egg, with one partner sitting on the nest while the other forages at sea. Thus, the number of birds sitting on nests represents the crude count of the number of breeding pairs attempting to breed.

Confidence in the counts is fairly high; grey-headed albatrosses are easily visible during scan counts using binoculars because their pale grey and white colouration stands out against the dark green vegetation, and most nests are visible from the vantage points used. Until 1997, only a single count was made by one person without any control counts, yielding only a single estimate for

the entire island population. Since 1997, multiple counts have been made of each colony and, where possible, by at least two people. If individual counts differ by more than 5% then counts are repeated until they agree within 5%, and then the average count is used as the best estimate. Counts are separated into six zones: Rook's Hut, Rook's Peninsula West, Rook's Peninsula East, Good Hope Bay, Grey-Headed Albatross Ridge and Crawford Bay (Fig. 1).

### Historical counts

For this study, the breeding season is referred to by the year in which it commenced (i.e. 2020–2021 is breeding season 2020). Counts of incubating albatrosses on Marion Island were made in late October or early November in 1974, 1976 and 1984 and in each year from 1987 to 2021 (Fig. 2). However, the two 1970s counts are not well documented (Nel *et al.* 2002b) and so were omitted from the formal analysis. The Crawford Bay colony was not counted in 2000 and 2001, and this tiny colony (< 1% of total count; mean  $42 \pm 12$  pairs, range 21–70,  $n = 24$ ), which is not easy to find, may also have been missed in some counts prior to 1997.

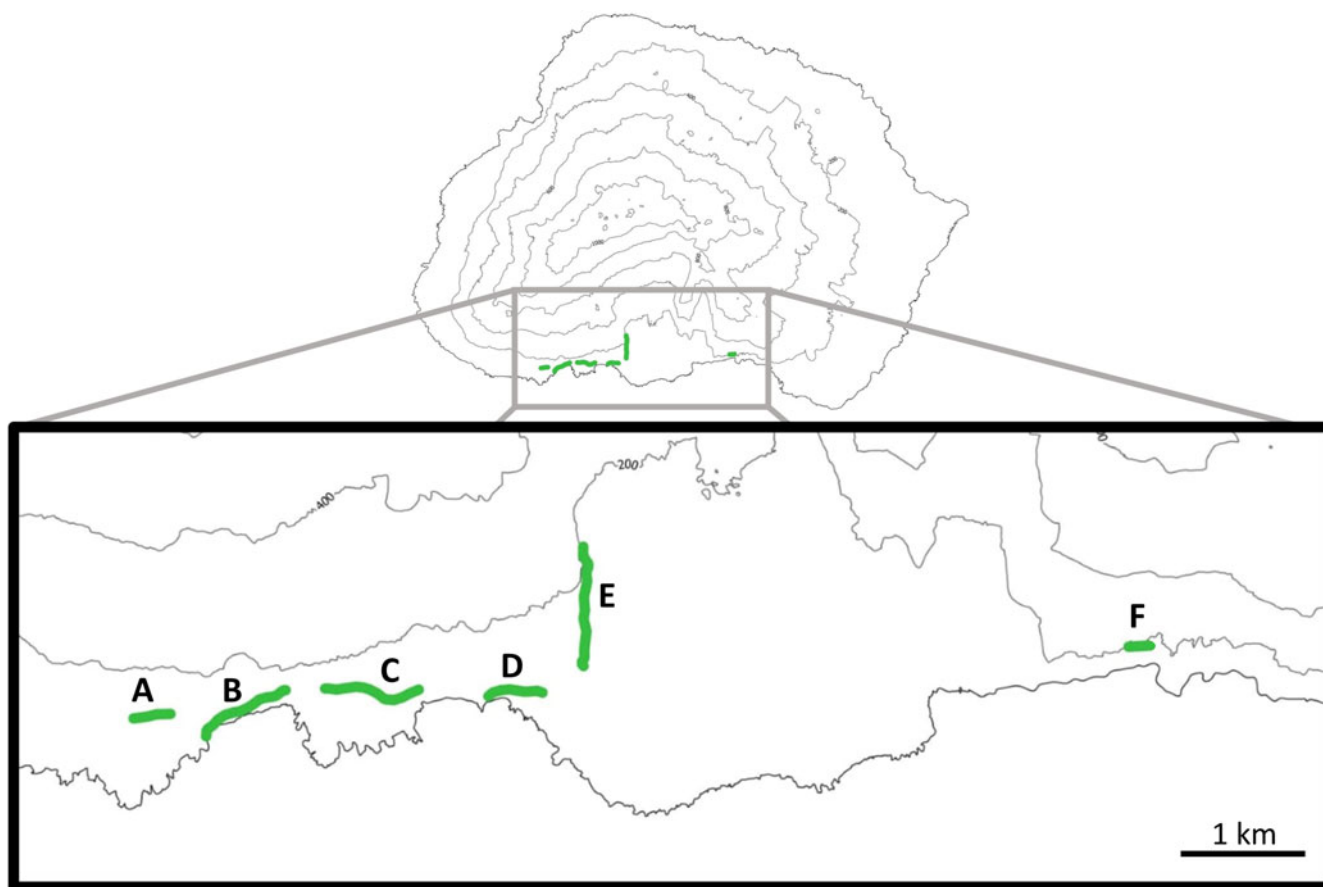
In 1990, the incubator count was unusually low compared to the 1989 (48% lower) and 1991 counts (53% lower), and inferred breeding success (fledgling count/incubator count) was the highest of all years (77%). Although this high breeding success could relate to lower competition between fewer adults, it is more likely that the incubator count in 1990 was a substantial underestimate, with the breeding success therefore being an overestimate (Nel *et al.* 2002b). Thus, we analysed the data both with and without the 1990 count.

Scan counts of all birds sitting on nests inevitably include some non-breeding 'loafers' (birds sitting on nests but with no egg). To account for this, an incubation correction factor was calculated as the proportion of nests with eggs found when visiting a minimum of 300 nests on Grey-Headed Albatross Ridge on the same day as the incubation scan count each year, and this could then be applied to the scan counts from all six count zones. These nest-occupancy checks were done from 1997 to 2021, except in 2002, with an average correction factor of  $0.869 \pm 0.065$  (range: +0.679 to +0.945,  $n = 24$ ). However, because there were no correction factors from 1984 to 1996, we used the uncorrected scan counts for all years for the analyses. Fledgling counts were completed for 33 of the 36 years (no fledgling counts in 1984, 1987 and 1995).

Because some fledgling counts were missing, breeding success data were not available for all years, and neither TRIM nor the GAM modelled within a frequentist framework was able to estimate the missing breeding success data, so we used values estimated by the SSM to inform missing breeding success data in all models.

### Trend analysis methods

We used three methods to analyse the data, as described below. The final models selected for each method used the total uncorrected annual population count data with missing data in 3 years (1985, 1986 and 1990) and partial annual counts in 2000 and 2001 (when Crawford Bay site counts were missing). For each method we tested the impact of including the 1990 count or not, and we used the TRIM method to test whether



**Figure 1.** Map of grey-headed albatross census colonies at Marion Island. A = Rook's Hut, B = Rook's Peninsula West, C = Rook's Peninsula East, D = Good Hope Bay, E = Grey-Headed Albatross Ridge, F = Crawford Bay.

including imputed data for the missing Crawford Bay site counts in 2000 and 2001 would produce better-fitting models.

#### *Trends and Indices for Monitoring data*

TRIM uses log-linear Poisson regression models in which missing values, overdispersion and serial autocorrelation can be accounted for, as well as counts at different colonies (Pannekoek & van Strien 2005). We used the 'rtrim' package (Bogaart *et al.* 2020) in R 4.1.0 (R Core Team 2021) to analyse the data. We fitted several TRIM models to accommodate variations in the data used or the model applied. The adjustments to the data included 1) using the 1990 count or not and 2) using the total uncorrected, annual population count data or allowing TRIM to impute the missing values for the Crawford Bay colony in 2000 and 2001. The latter was used to test whether the missing values for Crawford Bay counts in some years would make a significant difference to the trend estimate or not. The adjustments to the model included 1) using the stepwise approach, which allows the slope to vary or not, and 2) including breeding success as a covariate or not. TRIM only allows covariates to be included as categorical variables, so we assigned breeding success to five categories (10% intervals from 15% to 65%). Twelve models were tested, and the best was selected according to goodness of fit. The 12 models were all possible combinations of stepwise or linear; with or without site values imputed; or with or without covariate and 1990 data. Goodness of fit was assessed by Pearson's  $\chi^2$  statistic,

where the best-fitting models have the smallest  $\chi^2$  value and a large  $P$ -value ( $P > 0.05$ ; see Table S2).

We used TRIM model 2, which accounts for missing data, overdispersion and serial autocorrelation and allows the slope to vary (stepwise approach). Imputed expected counts ( $\mu_{ij}$ ) are modelled on the log scale as:

$$\log(\mu_{ij}) = \alpha_i + \beta(j - 1)$$

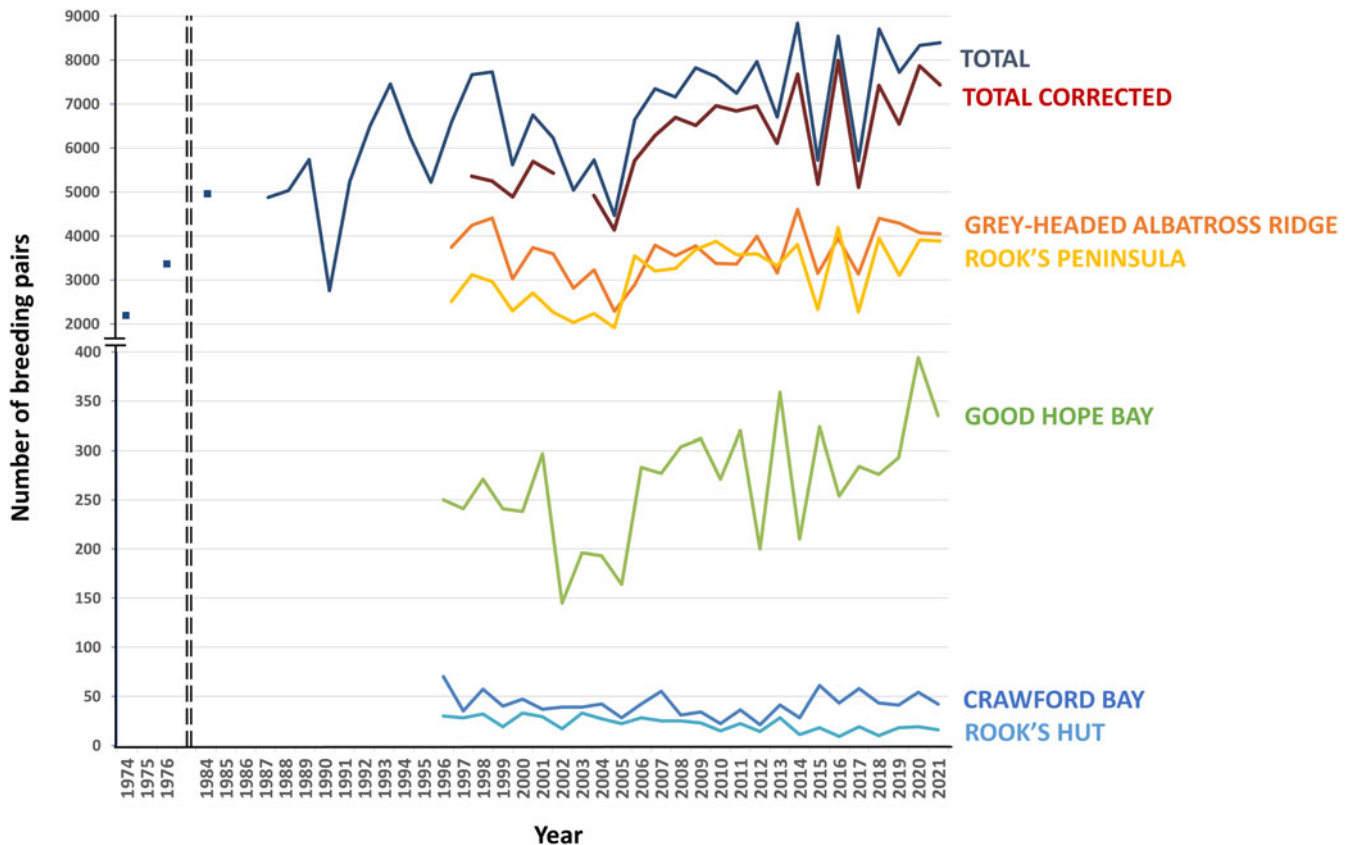
where  $\alpha_i$  is the colony effect of colonies  $i$ ,  $\beta$  is the mean growth over time  $j$  and observed counts in colony  $i$  at time  $j$  ( $y_{ij}$ ) are assumed to be Poisson distributed:

$$y_{ij} \sim \text{Poisson}(\mu_{ij})$$

For the non-stepwise approach,  $\beta$  is the growth rate. However, TRIM can also allow the slope to change at significant time points (change points) using a 'stepwise' model. In this case, growth rates are compared using a Wald test, and if a significant difference is found, it indicates a change point. The trend is then calculated as the ordinary least squares estimator  $\hat{\beta}_0$  of  $\beta_0$  using the equation:

$$\log(\hat{\mu}_{+j}) = \alpha + \beta_0(j - 1) + \epsilon_j$$

where  $\hat{\mu}_{+j}$  is the ordinary least squares estimate of the count at



**Figure 2.** Crude counts of grey-headed albatross breeding pairs at Marion Island from 1974 to 2021. From 1996 to 2021 counts were split into six count zones. The corrected totals account for loafing birds and the two missing Crawford Bay counts in 2002 and 2003 but exclude the missing correction factor data in 2002.

time  $j$ ,  $\beta_0$  is the slope and  $\epsilon_j$  is the difference between the natural log of the expected counts and the linear trend.

Breeding success was incorporated into the model by replacing  $\beta_0$  with  $\beta_0 + \beta_k(j-1)$ :

$$\log(\mu_{ij}) = \alpha_i + (\beta_0 + \beta_k(j-1))$$

where  $\beta_0$  is the slope parameter of the first category of the covariate and  $\beta_k$  is the breeding success at time  $j-1$ . We assume that breeding success at time  $j$  affects the magnitude of the change in the number of birds present from time  $j$  to  $j+1$ .

### Generalized additive models

GAMs are extensions of generalized linear models, which allow the change in population count over time to follow a smoothed curve (Fewster *et al.* 2000). We analysed the total uncorrected, annual population count data using the package ‘mgcv’ (Wood 2011), which also accounted for the 3 years with missing data, in R 4.1.0 (R Core Team 2021). Because we used the total island counts for the analysis, there was no colony effect, only a time effect, and the equation for the model on the log scale was:

$$\log(\mu_j) = s(j)$$

where  $\mu_j$  is the expected count in year  $j$  and  $s(j)$  is the smoothing function in year  $j$  using a fixed degrees of freedom regression spline. To account for overdispersion, we assumed that the

observed counts in year  $j$  ( $y_j$ ) follow a negative binomial distribution  $y_j \sim \text{NegBinom}(\mu_j)$  and used a log link function. Based on the model checking function `gam.check()` in R, the model converged and was a good fit. We then followed Fewster *et al.* (2000) and used their R code (<https://www.stat.auckland.ac.nz/~fewster/gams/R/>) to calculate changepoints (significant ‘upturns’ and ‘downturns’).

To assess the effect of breeding success, we added it as a term to the model:

$$\log(\mu_j) = s(j) + s(b_{j-1})$$

where  $s(b_{j-1})$  is the smoothing function for breeding success  $b$  using a fixed degrees of freedom regression spline. The counts  $\log(\mu_j)$  in year  $j$  are dependent on breeding success  $b$  in year  $j-1$ . The best model was selected by comparing the deviance explained between models with significant smooth terms only. The model with the highest percentage deviance explained was chosen.

### State-space models

Bayesian SSMs (Kéry & Schaub 2012) are time-series models with numerous ecological applications that include population dynamics (Auger-Méthé *et al.* 2021). They are hierarchical models with a hidden state and an observed state, which allow for the natural variation in population processes to be modelled separately from the observation error, and they can also account for missing data (Clark & Bjørnstad 2004). In our case, the actual size of the

breeding population is the hidden state, and the observed state is the annual population count. We used total uncorrected, annual population counts, and we log-transformed the data. Missing annual counts in 1985, 1986 and 1990 were imputed by the model.

We analysed the counts using 'rjags' (Plummer 2019) in R 4.1.0. The model equations for the state process were:

$$\log(N_{t+1}) = \log(N_t) + \lambda_t$$

$$\lambda_t \sim \text{Normal}(\bar{\lambda}, \sigma_\lambda^2)$$

where  $\log(N_{t+1})$  is the actual population size on the log scale at time  $t + 1$ ,  $\log(N_t)$  is the actual population size on the log scale at time  $t$  and  $\lambda_t$  is the growth rate at time  $t$  and is modelled as a normal distribution with a mean of  $\bar{\lambda}$  and variance of  $\sigma_\lambda^2$ . The model for the observation process was:

$$y_t = N_t + \epsilon_t$$

$$\epsilon_t \sim \text{Normal}(0, \sigma_y^2)$$

where  $y_t$  are the observed counts,  $N_t$  is the actual population size and  $\epsilon_t$  is the observation error at time  $t$  and is modelled as a normal distribution with a mean of 0 and a variance of  $\sigma_y^2$ . Breeding success was included as a covariate:

$$\lambda_t \sim \text{Normal}(\bar{\lambda} + \beta_p p_t, \sigma_\lambda^2)$$

where  $\lambda_t$  is the growth rate at time  $t$  and is modelled as a normal distribution with a mean of  $\bar{\lambda} + \beta_p p_t$  and a variance of  $\sigma_\lambda^2$  and  $\beta_p$  is the beta coefficient of the breeding success covariate  $p$ , the probability of breeding successfully, at time  $t$ . In years when covariate data were not available, the values were estimated by the model.

Vague priors were chosen with normal distributions for  $\log(N_{est}[1])$  (mean = 8.5, precision = 0.35),  $\bar{\lambda}$  (mean = 0.0, precision = 0.50) and  $\beta_p$  (mean = 0.0, precision = 0.10) and uninformative priors were chosen with uniform distributions for  $\sigma_\lambda^2$  and  $\sigma_y^2$  (range = 0–1; Banner *et al.* 2020). A sensitivity analysis was performed by changing the parameters of these prior distributions to ensure that the choice of prior did not affect the posterior (see Analysis S1). Informative priors were chosen using beta distributions (with alpha = 2, beta = 2) to encourage the missing breeding success values to follow a similar distribution to those values observed in the global population (Agreement on the Conservation of Albatrosses and Petrels 2010).

The values chosen for the Markov chain Monte Carlo (MCMC) sampling procedure were 300 000 iterations and 3 chains, with a thinning rate of 15 and a burn-in of 150 000 iterations. Chains were considered to have converged if the R-hat values were < 1.1. The parameter of mean growth rate ( $\bar{\lambda}$ ) was monitored and the confidence interval (CI) was extracted using the 2.5% and 97.5% quantiles of all simulations.

## Results

The number of breeding pairs of grey-headed albatrosses at Marion Island increased by ~60% between 1984 and 2021 (Figs 2 & 3 & Table S1), and this trend probably extends back to the

1970s (Fig. 2). All three model approaches estimated the overall growth rate to be 1.3% per annum (see Table S1). In 2021, the estimated number of pairs was ~8060, with an average of ~8180 from 2019 to 2021 (see Table S1). Both non-linear models detected negative growth rates from 1997 to 2002 (Fig. 3b,c). All models smoothed out the strong fluctuations in the number of annual breeding pairs present during the mid-2010s compared to other periods (Fig. 3). These overall patterns were evident whether the correction factor was applied or not and were similar across count zones (Fig. 2).

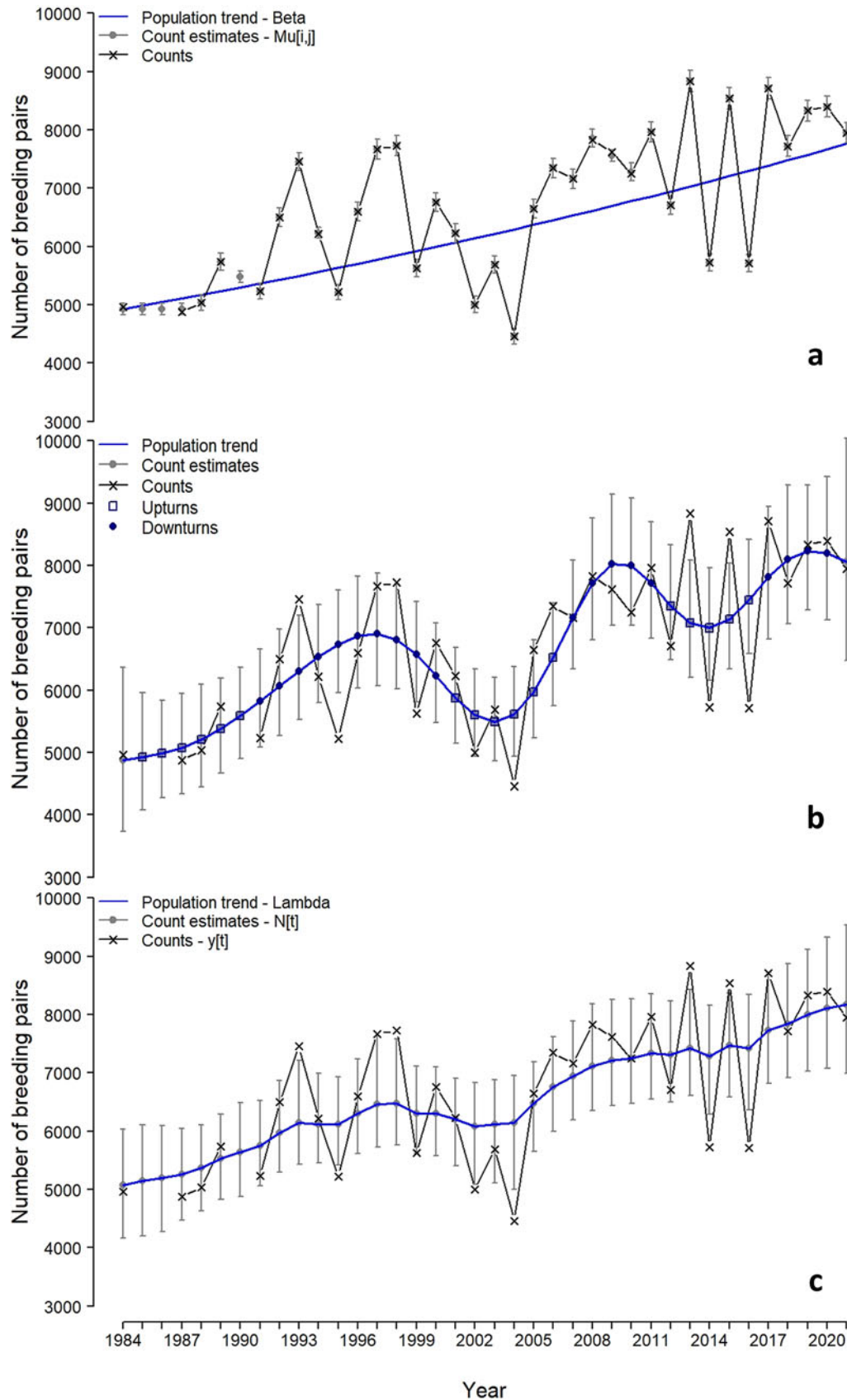
## Model selection and comparison of methods

For all three methods, the best-fitting models did not include the 1990 count or breeding success as a covariate. Of the 12 TRIM models tested, TRIM without a covariate using a stepwise approach and with the 1990 count excluded had the best fit ( $\chi^2 = 1.44$ ,  $df = 3$ ,  $P = 0.70$ ). The fit was the same using total values and imputed values for missing data, so we chose the former, simpler model (see Table S2). For both of these models, TRIM reported that overdispersion and serial correlation were not significant. None of the other 10 models was a good fit (see Table S2). The GAM with only a year term and without the 1990 count explained more deviance (60.4%) than the model including the 1990 count (54.6%), and including breeding success the previous year as a covariate was not significant ( $\chi^2 = 6.46$ ,  $df = 9$ ,  $P = 0.69$ ). The SSM with breeding success as a covariate converged with R-hat values of < 1.1, but beta, the coefficient of the effect of breeding success on the trend, showed no effect based on the mean posterior values (mean: +0.09, range: -1.24 to +1.31, 95% CI: -0.38 to +0.53; Fig. 4), and a plot of the change in the number of breeding pairs from year  $t$  to  $t + 1$  against breeding success in year  $t$  showed no clear relationship (see Fig. S1). Thus, the SSM without breeding success was chosen, and it also converged.

Neither TRIM nor GAM detected change points for data with such high annual variability. Of the 37 potential change points using the stepwise approach by TRIM, 31 were found to be significant by TRIM (all years from 1987 to 1989, from 1991 to 1993, from 1995 to 2008 and from 2010 to 2020). Regarding the GAM, all change points were significant, with upturns identified from 1985 to 1990, from 2001 to 2006 and from 2012 to 2016, and downturns from 1991 to 2000, from 2007 to 2011 and from 2017 to 2020 (Fig. 3b). The SSM estimated a potential decline in annual growth rates between 1998 and 2002.

## Discussion

All three methods estimated an overall increase in the grey-headed albatross annual breeding population at Marion Island from 1984 to 2021, and this increasing trend probably extends back to the 1970s. The counts fluctuated greatly among years, especially in the mid-2010s. Inferring overall population trends based on models that use counts of a subset of the population (which is true for most seabirds) is inherently flawed, but in the case of biennial breeders, where the proportion of adults breeding is potentially more variable than in annual breeders (such as in the mid-2010s), the scope for error is substantially worse. This problem is common to all of the models used in this study, but the SSM is capable of modelling these annual fluctuations as potential changes in the annual population growth rate. It is clear that the increases at least cannot be occurring in the



**Figure 3.** The overall trend and fitted estimates for numbers of grey-headed albatrosses breeding each year at Marion Island from 1984 to 2021 estimated by (a) TRIMs and Indices for Monitoring data (TRIM), (b) the generalized additive model (GAM) and (c) the state-space model (SSM). The mean (error bars represent the 95% confidence intervals) annual growth rates from 1984 to 2021 were estimated at 1.31% (1.30–1.31%) by TRIM, 1.37% (1.24–1.50%) by the GAM, and 1.29% (-0.77–3.58%) by the SSM.

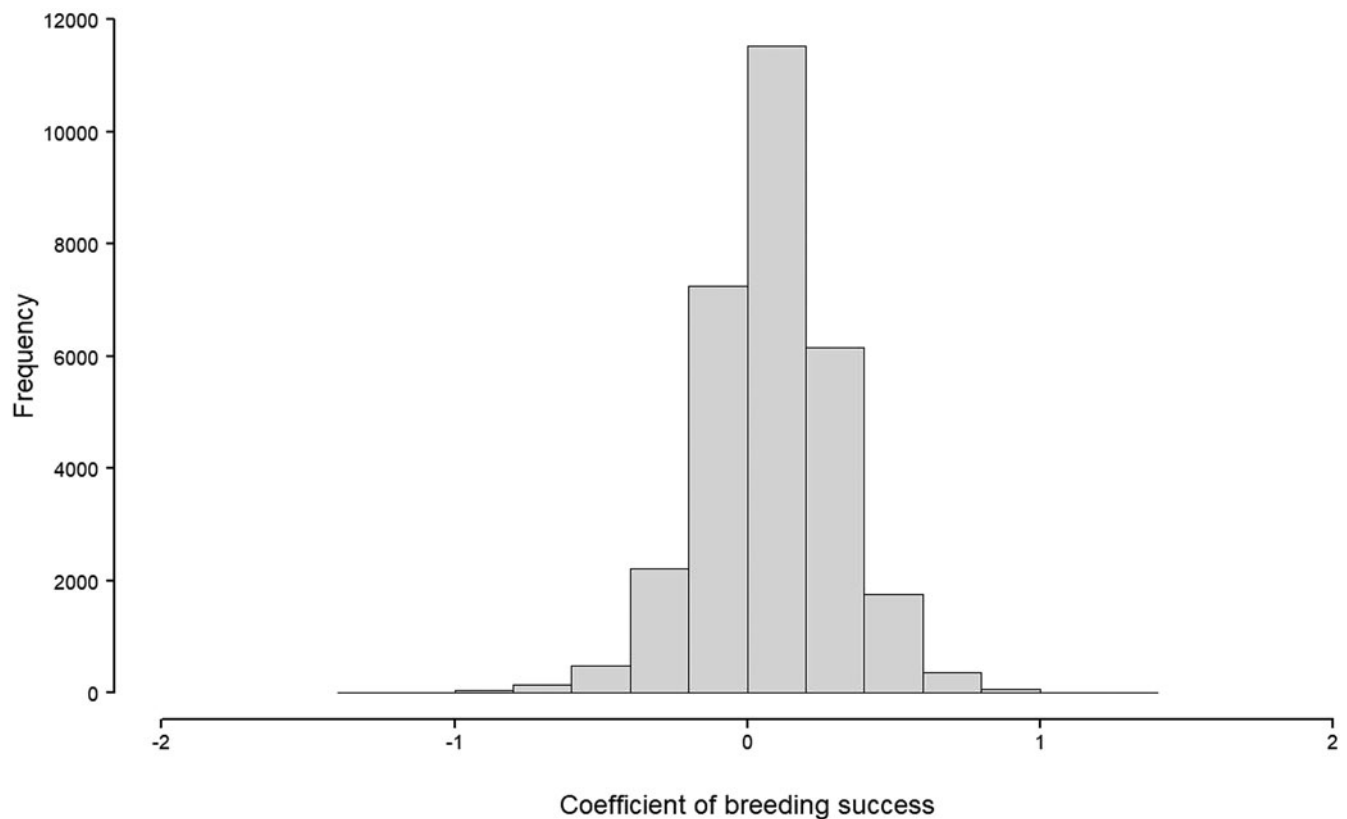


Figure 4. Posterior distribution of the beta coefficient of the breeding success covariate in the state-space model.

underlying population - some of the annual increases are so large that they could not reflect a genuine population increase and must therefore have been caused by either massive immigration or a changing proportion of adults returning to breed. In this study, we interpret the overall trends here with this in mind, but one possible option to overcome this in future studies might be to fit a model that explicitly includes the underlying demographic processes, such as an integrated population model (IPM; Schaub & Kéry 2022), which would be much better than a purely phenomenological model.

The only period when there was not an overall increase was from 1997 to 2002, probably due to high adult mortality in the Patagonian toothfish longline fishery around the Prince Edward Islands (Ryan & Boix-Hinzen 1999, Nel *et al.* 2002a). High levels of illegal, unregulated and unreported (IUU) fishing for Patagonian toothfish occurred in 1995, prompting the licensing of a sanctioned fishery in 1996 (Ryan *et al.* 1997). Observers on board sanctioned vessels provided the first estimates of seabird bycatch, which extrapolated to 1000–4000 grey-headed albatrosses killed in 1996 by both IUU and sanctioned vessels (Ryan *et al.* 1997). Most of these (85%) were breeding adult males (Ryan & Boix-Hinzen 1999), probably because males tend to feed closer to the island during the breeding season than females (Nel *et al.* 2002a), increasing their risk of being caught.

Mitigation measures instituted to reduce seabird bycatch by sanctioned vessels included setting lines at night, the use of bird-scaring (*tori*) lines and limiting fishing to more than 200 km from the Prince Edward Islands, especially during summer, when most seabirds breed. These measures greatly reduced the number of albatrosses killed by this fishery (Nel *et al.* 2002a). By 2000,

toothfish catches had decreased around the Prince Edward Islands to the point where fishing effort became negligible (Brandão & Butterworth 2002, Nel *et al.* 2002a). However, between 1996 and 2000, an estimated 5–12% of the grey-headed albatross breeding population was killed (Nel *et al.* 2002a). Such a high mortality of breeding adults can have complex, long-lasting effects on the demography of monogamous, long-lived seabirds, especially when mortality is sex-biased (Ryan & Boix-Hinzen 1999, Mills & Ryan 2005). Fortunately, the annual breeding population began to grow again from 2002, but grey-headed albatrosses are still at risk to fisheries outside the Prince Edward Islands Exclusive Economic Zone during both the breeding and non-breeding seasons (Reid *et al.* 2023).

#### Factors affecting the interannual count fluctuations

Confidence in the counts is fairly high at Marion Island (see the 'Methods' section), and the main source of observation error is that some birds counted on nests were not actually incubating (although they could include some pairs that failed before the count took place). Correction factors from nest-occupancy checks were not applied as they were not available for all years; therefore, the total count data used in this study represent a slight overestimate of the size of the annual breeding population (even though they probably represent a good estimate of the number of birds that were present). However, the same patterns in corrected and uncorrected counts were observed, and therefore the overall growth rates and population trend should not be affected. The missing Crawford Bay count data in 2000 and 2001 accounted for such a small proportion of the overall counts (< 1%) that

they had no effect on the estimated population trends. This was tested using TRIM models with and without site-imputed data, and no difference was found. Overall, there is certainly some observation error, but there is a higher degree of confidence compared to other cliff-nesting species, such as sooty albatrosses *Phoebastria* spp., which are less colonial and much less conspicuous (Schoombie *et al.* 2016).

Natural variation in population-level processes could explain the strong interannual fluctuations in counts. The most likely mechanism for this is variation in the proportion of the population that breeds each year (Bonnievie *et al.* 2012). Because grey-headed albatrosses are mostly biennial breeders, the breeding cohort is a mix of birds that bred but failed in the previous season and those that were successful two seasons prior. If one cohort suddenly decreases or increases in size due to a change in the re-breeder rate, the breeding cohort in the following year should increase or decrease proportionally, leading to 2 year fluctuations in the annual count for several years (Prince *et al.* 1994, Bonnievie *et al.* 2012). This is probably the cause of the variation observed in the mid-2010s - in 2010, the breeding success was the second lowest ever recorded (29%, mean of all years =  $44\% \pm 8\%$ , range = 21–58%,  $n = 32$ ) and was followed by above-average breeding success (50%) in 2011 - as opposed to true fluctuations in the number of breeding pairs.

Environmental variability can also have complex effects on population dynamics by altering vital rates (Jenouvrier 2013). Isolating and understanding the magnitude of these effects is not straightforward as they could be indirect, direct or time-lagged (Jenouvrier 2013). For example, grey-headed albatrosses at Marion Island have strong associations with ocean frontal systems when foraging (Carpenter-Kling *et al.* 2020), which are also prime fishing grounds (Nel *et al.* 2000). Changing climatic conditions may cause changes to the distribution of fish stocks, which could alter the risk of incidental mortality of seabirds in fisheries and therefore impact adult and juvenile survival. These same changes in environmental conditions could directly affect food availability, which would probably affect both adult survival and breeding success (Pardo *et al.* 2017). The strong El Niño event in 1997 has been linked to exceptionally high breeding success in five wide-ranging seabird species at Marion Island, including the grey-headed albatross (Nel *et al.* 2002b, Crawford *et al.* 2003). A strong correlation between breeding success and the SOI was also found from 1997 to 2004 (Ryan & Bester 2008).

Considering the potential link between breeding success and environmental change, and that breeding success is inherently linked to the re-breeder rate (Bonnievie *et al.* 2012), we expected that breeding success would explain some of the interannual variation in counts. However, none of the models found breeding success to be a significant covariate. This is probably because the relationships between population dynamics and environmental variation are complex and not captured adequately by breeding success alone. One potential option would be to lag breeding success by several years to account for the influx of new recruits; however, from ringing records it is known that the recruitment age follows a bell curve from age 6 to 22 (age first seen, peak at age 8 and 11) or from 9 to 19 (age first seen breeding, peak at age 12; FIAO, unpublished data 1978–2021), and therefore it would be difficult to detect changes of the effects of breeding success on population size via recruitment. One other factor to consider is the timing of the nest failure - this may also have an impact on the re-breeder rate, which we did not account for in this study. Vital rates such as the re-breeder rate or adult survival

may be better suited to explaining such complex relationships, but unlike breeding success, these demographic rates cannot be easily extracted from population count data. IPMs could be used to calculate these rates. IPMs would also incorporate the recruitment lag by tracking the survival of fledglings from years ago. Even so, the difference in the number of recruits joining in a given year is probably very small compared to the massive fluctuations that result from breeding propensity. By utilizing multiple sources of data, not just count data as in this study, IPMs would be able to assess which combinations of environmental and demographic processes drive an increase in the number of breeding pairs.

#### *Advantages and disadvantages of each method*

The three statistical models used to determine population trends each have advantages and disadvantages. The fundamental difference between the three approaches is the type of trend fitted: TRIM estimates linear trends, a GAM is a smoothing technique that helps to visualize the trend over time, whereas a SSM separates the state (annual breeding population size) process from the observation process and then estimates the rate at which the state process changes over time. When applied to population counts, SSMs estimate population growth rate directly and can therefore give a more biologically intuitive explanation than methods that estimate an overall slope parameter. SSMs also allow the population growth rate to be modelled as a function of covariates, which can add biologically meaningful parameters. GAMs can also incorporate covariates, but because GAMs are essentially a smoothing technique, there is no easy way to examine the effect of covariates on the annual fluctuations. TRIM only allows categorical covariates, but this is more likely to be a limitation of the software than the model itself, as continuous covariates can be included in linear regression models.

The various frameworks within which a model can be fitted also have advantages and disadvantages. In this study, we fitted the GAM in a frequentist framework and the SSM in a Bayesian framework. The latter requires the careful choice and testing of priors, and the coding of the model takes more time. By comparison, the frequentist approach is comparatively quick to run. Model assumptions such as overdispersion and serial autocorrelation are also accounted for slightly differently depending on the framework and the type of model. Imputing missing data is straightforward in all three models. Using TRIM, one can easily account for overdispersion and serial autocorrelation, and it is also very quick to run compared to fitting a SSM in a Bayesian framework. SSMs naturally account for serial autocorrelation due to the separation of the state and observation processes, and overdispersion was not a concern in our case because we modelled the means with a log-normal distribution, which is more flexible than the Poisson distribution assumed in TRIM. In a frequentist framework, GAMs can account for overdispersion using a negative binomial distribution and log link function. Overdispersion can also be accounted for by fitting a GAM to the log counts with normally distributed errors, in both a frequentist and a Bayesian framework. In this study, serial autocorrelation was not detected, but if it were present, accounting for serial autocorrelation in a GAM would be complex.

#### *Implications for global population trends*

Despite their differences, all three models gave similar results, which gives confidence that the grey-headed albatross population



**Table 1.** The most recent estimates of the number of grey-headed albatross breeding pairs (annual counts) at all breeding sites ordered by geographical location from west (Islas Diego Ramirez) to east (Campbell Island).

Site	Population estimate (n pairs per year)	% of total population	% annual growth	References
Islas Diego Ramirez and Ildefonso	20 970 (2014) <sup>a</sup>	22.6	-0.1 (2002–2011) +7.7 (2011–2014)	Robertson <i>et al.</i> (2017)
South Georgia	40 890 (2014) <sup>b</sup>	44.2	-3.9 (2003–2014)	Poncet <i>et al.</i> (2017)
Prince Edward Islands	10 200 (2019–2021) <sup>c</sup>	11.0	+1.3 (1984–2021) -2.9? (2001–2008) <sup>d</sup>	This study Ryan <i>et al.</i> (2009)
Iles Crozet	5320 (2016)	5.8	+1.4 (1985–2016) <sup>e</sup> +0.5 (1985–2016) <sup>f</sup>	Weimerskirch <i>et al.</i> (2018)
Iles Kerguelen	6680 (2016)	6.9	-0.5 (1985–2014)	Weimerskirch <i>et al.</i> (2018)
Macquarie Island	110 (2019)	0.1	+? (< 5.0) <sup>g</sup> (2009–2019)	DPIPWE (2021)
Campbell Island	8610 (2006–2012) <sup>h</sup>	9.3	-0.3 (1940s–2012) -0.1 (1980–2012) +0.8 (1995–2012)	Sagar (2014)
<i>Total</i>	92 780			

<sup>a</sup>Almost all on Diego Ramirez.

<sup>b</sup>Estimated the missing colony totals for Main, Trinity and Hall as  $(5177 + 3309 + 2686) \times (1 - 0.434)$  and added to 34 571 to get total island estimate (Poncet *et al.* 2017).

<sup>c</sup>Total of 2000 at Prince Edward Island from 2008 (Ryan *et al.* 2009) and 8200 on Marion Island (this study).

<sup>d</sup>Only two counts conducted at Prince Edward Island with -2.9% annual growth rate (Ryan *et al.* 2009), but unreliable given biennial breeding.

<sup>e</sup>Annual growth rate for Ile des Apôtres population.

<sup>f</sup>Annual growth rate for Ile des Pingouins population.

<sup>g</sup>Reported as a 'moderate increase over the past ten years using TRIM', but no rate specified.

<sup>h</sup>The most recent counts were in 2019 but are not yet reported (Rexer-Huber *et al.* 2020).

at Marion Island increased by 1.3% per year from 1984 to 2021, and this increasing trend probably extends back to the 1970s. This is in stark contrast to the estimated declines at Bird Island, South Georgia (43% from 2003 to 2014; Poncet *et al.* 2017) and Campbell Island (82–88% from the 1940s to 1990s; Table 1; Moore 2004, BirdLife International 2023). Fortunately, the population at Campbell Island appears to have increased in more recent years (0.8% per annum from 1995 to 2012; Table 1; Sagar 2014). The populations at South Georgia and Campbell Island account for ~53% of the global number of annual breeding pairs (Table 1). The other population in decline is that at Iles Kerguelen (Table 1). At Prince Edward Island the trend is unknown, as only two counts have been conducted (Ryan *et al.* 2009). For the remaining populations, the trend is either stable or increasing. At Islas Diego Ramirez, where the second largest population breeds, the population remained stable from 2002 to 2011 and increased from 2011 to 2014 - averaged over the entire period, the trend is an increase of 1.8% per annum. However, due to the infrequency of surveys, this apparent increase should be viewed with caution (Robertson *et al.* 2017), as it should be for all colonies with sparse counts. At Iles Crozet the population increased from 1985 to 2016, but the rate of increase varied depending on the colony; and at Macquarie Island, the small population of ~110 pairs also appears to be increasing (Table 1). Interestingly, there was a similar increasing population trend at Iles Crozet and Marion Island over the same period (Table 1), suggesting that their geographical location might favour these populations (Nel *et al.* 2000, Ryan *et al.* 2007).

Albatrosses have a complicated life-history, breed in remote, hard-to-access locations and, especially in the case of biennially breeding species, undergo significant annual fluctuations in their populations (Weimerskirch *et al.* 2018, this study). These factors make it difficult to reliably estimate long-term population trends due to varying sampling intervals, often with large gaps

between surveys. In a study to determine effective sampling intervals, Wauchope *et al.* (2019) found that less frequent but regular sampling intervals will often reliably give a similar significant trend (i.e. positive or negative) to that of a significant trend estimated from continuous count data, but in doing so will make the rate of this trend difficult to determine. They also found that for bird species with longer generation lengths (10–15 years), accurately estimating population trends became more difficult as the sampling interval increased. For grey-headed albatrosses, which have a generation length of 30 years and are biennially breeding species, the sampling interval would therefore need to be low (i.e. every year) to determine a trend accurately and reliably. For other albatrosses that breed on an annual basis, this could perhaps be increased to every second year; however, more in-depth calculation could be done on an individual-species basis following the methods in Wauchope *et al.* (2019).

The trends presented here are of the annual breeding population and might not necessarily reflect the underlying trends of the entire Marion Island population in a given year, including all age classes, which could have important implications for the conservation of the species (Oppel *et al.* 2022). Notably, the demographic effects of mouse predation on the grey-headed albatross chicks at Marion Island since 2015 (Dilley *et al.* 2016) are unknown. The first year in which a portion of this cohort would be attempting to breed would have been 2024 (assuming the minimum age at first breeding for grey-headed albatrosses as 9 years; FIAO, unpublished data 1978–2021). It is therefore essential that monitoring of the Marion Island grey-headed albatross population continues because their longevity, delayed age at first breeding and low productivity mean that the lagged effects of threats such as predation by mice on their populations cannot be assessed immediately. In addition, if the data are available, the use of more complex models such as IPMs, which can incorporate different age classes and calculate

demographic rates over time, will help to predict the effects of such phenomena.

In conclusion, the grey-headed albatross population at Marion Island, which comprises approximately one-tenth of the global population, increased from 1984 to 2021. This is in stark contrast to global populations elsewhere in the Southern Ocean, which are estimated to be decreasing drastically. Multiple statistical methods, each with their own advantages and disadvantages, can be used to assess these trends using data from population counts. Future work could include IPMs that can utilize multiple sources of data, which may help disentangle the environmental and demographic factors influencing the population trends and therefore which of these factors we could focus on to conserve grey-headed albatross populations in the future.

**Acknowledgements.** We thank all field workers who counted grey-headed albatrosses at Marion Island. Logistical and financial support was provided by the South African Department of Forestry, Fisheries and the Environment through the South African National Antarctic Programme, the National Research Foundation and the University of Cape Town under permit from the PEIAC/DFFE. We also thank Birgit Erni for discussions on statistical methodology, Ben Dilley for his comments on early drafts and Janine Schoombie for creating the colony map used in Fig. 1. We thank the editor and reviewers for their comments.

**Author contributions.** KLS analysed the data and wrote the draft. MC and PGR supported the collection of counts on Marion Island. RA supervised the research and advised on manuscript preparation. All authors contributed critically to the drafts and gave final approval for the manuscript.

**Supplemental material.** A supplemental analysis, two supplemental tables and a supplemental figure will be found at <https://doi.org/10.1017/S0954102024000336>.

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