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Demography of cape petrels in response to environmental changes

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Abstract

Predicting the responses of populations in changing environments is an important task for ecologists. Understanding the population dynamics of high-latitude breeding species is critical given the particularly rapid environmental changes that occur in these regions. Using long-term mark–resighting data acquired over 53-years in Pointe Géologie, Terre Adélie, Antarctica, we estimated age-specific demographic parameters and evaluated the effect of the environment on survival of a poorly known species, the cape petrel *Daption capense*. We then modeled the dynamics of this population using a life-history model and performed prospective and retrospective analyses to estimate the sensitivity of the population growth rate to demographic parameters, and to quantify their relative contribution. Survival of cape petrel increased with age, being 0.610 ($\pm$0.193) for juveniles, 0.739 ($\pm$0.158) for individuals from 2 to 4, and 0.920 ($\pm$0.031) for older individuals. Minimum age at first reproduction was 3 years old, the age at which all birds were recruited was 14 years, and mean age at first reproduction was 9.05 ($\pm$2.06) years. Adult survival increased over time and was positively correlated with the southern annular mode (SAM). The stochastic population growth rate was estimated at 1.019, and adult survival over age 5 made the largest contribution to variance of the population growth rate. Sensitivity analyses revealed that population regulation was mainly driven by the SAM. Our results suggest that despite the decrease in breeding success, the population of cape petrels at Pointe Géologie increased due to the increase in immature and adult survival.

KEYWORDS

cape petrel, capture–mark–recapture, population dynamics, sea surface temperature, southern annular mode

1 | INTRODUCTION

Evidence of the effects of global changes on vertebrate populations has already been demonstrated (Jenouvrier, 2013; Lebreton, 2011; Parmesan & Yohe, 2003; Sydeman et al., 2015), especially at the poles where rapid changes have been observed (e.g., Barbraud & Weimerskirch, 2001; Descamps et al., 2017; Hansen et al., 2013; Hinke et al., 2017). Identifying and understanding how vital rates influence changes in the size of a population helps to better anticipate its responses to environmental variability. In long-lived species, population growth rate is often highly sensitive to adult survival, and a small change in survival can affect overall population dynamics (Caswell, 2000). In

this context, the demographic buffering hypothesis predicts a reduction in the variance of vital rates to which the population growth is most sensitive (Gaillard et al., 2000; Hilde et al., 2020). This has led to the expectation that vital rates strongly influencing population growth rates are buffered from environmental stochasticity (Morris & Doak, 2004). However, several studies have shown that environmental variation can affect the survival of younger individuals or indirectly the survival of adults through higher costs of reproduction (Champagnon et al., 2018; Oro et al., 2010). In addition, other vital rates (i.e., fertility) contribute to the variation of the population growth rate and these rates can also be affected by the environment (Stearns, 1992). Thus, estimating the sensitivities and contributions relative to each vital rate allows the assessment of the effects of environmental fluctuations on populations, and to understand their dynamics.

Despite the context of unprecedented climate change in polar environments, the dynamics of most polar species are nevertheless poorly studied and insufficiently understood. Deciphering the species-specific responses to environmental change is however fundamental to better understand and anticipate the impacts of global change on Antarctic ecosystems (Constable et al., 2014). Among Antarctic seabirds, the cape petrel *Daption capense* is an example of a long-lived species for which demographic processes and population dynamics have been little studied (Beck, 1969; Pinder, 1966; Sagar et al., 1996), and how environmental variation affects its vital rates remains unknown. However, the cape petrel is one of the most abundant seabirds in the Southern Ocean (Brooke & Cox, 2004), and is occasionally caught in longline fisheries as a bycatch species (Jiménez et al., 2009).

Here, we outline a comprehensive demographic study of a population of cape petrels in Terre Adélie, Antarctica. Using long-term individual monitoring, we first estimated demographic parameters including age-dependent survival, age at first breeding, and breeding success. We then investigated how environmental variation could influence vital rates. Finally, we modeled the population dynamics using a matrix population model, and carried out prospective and retrospective analyses to estimate sensitivities and contributions of demographic parameters to the population growth rate.

2 | MATERIAL AND METHODS

2.1 | Species and study site

Cape petrels are small Procellariforms (440 g, 80–91 cm wingspan) breeding on the coast of Antarctic mainland and neighboring islands, and on subantarctic islands (Marchant & Higgins, 1990). Nest sites are situated in diverse habitats, including steep rocky areas with ledges, crevices, overhangs, caves, cliffs, rock tumble, inshore rock stacks, and terraces.

Cape petrels were studied at Pointe Géologie archipelago (66°40′S, 140°01′E), Terre Adélie, Antarctica (Figure S1). Adults arrive in late October–early November at their breeding site and lay a single egg in early December that hatches in January (Mougin, 1968). The chick fledges in late February at a size similar to that of an adult. At Pointe Géologie during the breeding season cape petrels feed primarily on crustaceans (mainly Antarctic krill *Euphausia superba* and crystal krill *E. crystallorophias*) in the vicinity of the colonies (Delord et al., 2016; Ridoux & Offredo, 1989). Cape petrels mainly feed in open-water areas at the edge of the pack-ice or in the open ocean (Ainley et al., 1992; Veit & Hunt, 1991). During the non-breeding season, cape petrels also feed on cephalopods (Ainley et al., 1984; Bierman & Voous, 1950).

On average, 455 breeding pairs breed annually on five islands (Pétrels ≈ 150 pairs, Bernard ≈ 240 pairs, Lamarck ≈ 30 pairs, Rostand ≈ 35 pairs, Le Mauguen ≈ 1 pair) of the archipelago (Micol & Jouventin, 2001, Project IPEV 109 unpublished data). All nests were monitored twice annually since the breeding season 1965–1966 on Petrels Island and since 1985–1986 on the entire archipelago. Each year chicks were captured and ringed with a stainless steel ring just before fledging. At the beginning of the incubation period, the breeding status of individuals present on nests was checked, and each ringed individual was identified. Generally, adult individuals were not captured for identification and the ring was read by gently turning it around the leg with a 30-cm metal stick equipped with a piece of rubber. To minimize disturbance only one check was carried out per nest during the incubation period to allow individual identification, therefore only one partner was checked for a ring. Individuals were not sexed.

2.2 | Estimation of the demographic parameters

To estimate the vital rates and the effects of age, we used multi-state capture–mark–recapture (MSCMR) models (Brownie et al., 1993; Lebreton & Pradel, 2002) which provide unbiased demographic estimators by taking into account imperfect detectability of marked individuals. We estimated the following parameters: apparent survival probability, as the probability that an individual survives from year t to $t + 1$, the probability of first breeding, as the probability that an individual breeds for the first time, and the recapture probability. To do so, we constructed a MSCMR model with four states consisting

of one juvenile state, one immature state, one breeder state, and the dead state. Capture histories were coded considering four events corresponding to field observations: $0 =$ not observed, $1 =$ captured and marked as a chick, $2 =$ seen as a pre-breeder, and $3 =$ seen as breeder. The dead state was not observable. In this model, all parameters were age dependent. The probability of first breeding for age 1 and 2 was fixed to 0 since there was no record of an individual observed as a breeder until age 3. Individuals seen on an egg during one breeding season were considered as recruited in the breeding component of the population for the following seasons. Since the field monitoring effort varied between two periods we considered recapture probabilities in two distinct periods (1965–1985 and 1986–2018). We used individual encounter histories of 1,672 individuals for the period 1986–1985 and 7,179 for the period 1986–2018.

The first step in the CMR modeling consisted of testing the assumption of independence of fates and identity of rates among individuals using goodness-of-fit (GOF) tests. The GOF tests for multistate models (Pradel et al., 2003) were performed on our general model using the software U-Care (v.2.3.4; Choquet, Lebreton, et al., 2009).

Second, we performed a model selection, using program E-SURGE (v.2.1.4 Choquet, Rouan, & Pradel, 2009), to investigate the effects of age on vital rates and recapture probability. Using a step-down approach (Lebreton et al., 1992), we modeled the recapture probabilities first, then the probability of first breeding, and then the survival probabilities. Model selection was done using the second-order Akaike information criterion (AICc). The best model was the lowest AICc model, and we considered that two models i and j were different when the ΔAICc was greater than 2, where ΔAICc $=$ AICc$_i$ $-$ AICc$_j$ (Anderson & Burnham, 2002). If the difference in AICc values between two models was <2, the models are deemed to have equal statistical support and the simplest was preferred. However, there may be some uncertainty in the best models, related to high confidence intervals for demographic parameters. In this case, we used the "model averaging" procedure to obtain parameter estimates using all models with a delta AIC $<$ 10. To do this, we calculated the average value for the parameter by averaging over all models in the candidate model set with common elements in the parameter structure, weighted by normalized AICc model weights. To represent both conditional variation specific to the model, as well as variation resulting from model selection uncertainty (i.e., among the models in the candidate model set) we estimated the unconditional variance (Burnham & Anderson, 2004), and then the unconditional SE was given by the square root of the unconditional variance.

Since we did not have information on the breeding output at the individual level (nests were not marked and thus for each individually identified individual we did not know whether it fledged a chick or not), we estimated breeding success from time series of counts of breeding pairs during the early incubation period and of chicks just before fledging. Breeding success was estimated as the annual number of fledged chicks divided by the annual number of breeding pairs. The annual number of breeding pairs has been quantified since 1991 thus the breeding success was calculated over the period 1991–2018. Since cape petrels lay only one egg, variance and SE of breeding success estimates were calculated using the variance of a binomial distribution.

2.3 | Environmental covariates

Selection of environmental covariates was based on previous knowledge on seabirds and cape petrel ecology. To investigate effects on survival rates and breeding success, we used a large-scale climatic index, the southern annular mode (SAM). SAM is the dominant mode of atmospheric variability in the Southern Hemisphere and is characterized by the displacements of atmospheric masses between polar and mid-latitudes (Marshall, 2003; Marshall, 2007). SAM is related to changes in temperature in the Antarctic and in sea surface temperature (SST) of the Southern Ocean. In positive phase, SAM induces (i) cold SST and high chlorophyll around 60°S, that is, corresponding to the latitudinal distribution of cape petrels during the breeding season (Delord et al., 2016); and (ii) warm SST and low chlorophyll between 50°S and 40°S, that is, corresponding to the latitudinal wintering area of cape petrels (Delord et al., 2016).

We also used local oceanographic covariates on foraging areas of cape petrels on different temporal and spatial scales (Delord et al., 2016): the sea ice concentration (SIC) during the breeding season, and the SST during the breeding (SST summer, November–March) and non-breeding (SST winter, April–October) seasons. SIC and SST contribute to annual primary productivity and play an important role in the life cycle of many organisms in marine polar food webs (Carr et al., 2006; Vacchi et al., 2012). SIC and SST were extracted during summer for the sector 62°S–65°S/137°E–145°E, corresponding to the Dumont d'Urville Sea where cape petrels forage during the breeding season (Barbraud et al., unpublished data; Delord et al., 2016). SST in winter was extracted from three sectors corresponding to the areas frequented by cape petrels during the non-breeding period (157°S–160°S/50°E–57°E, 167°S–170°S/39°E–44°E, 142°S/41°E–42°E; Delord et al., 2016).

We used meteorological data recorded at the study site to investigate the effect of local weather on breeding success. Low temperatures and strong winds during incubation can increase the energy needs of parents incubating the egg. This can increase the frequency of egg neglect (i.e., interruption of incubation during a day or more) if parents have to leave the nest unattended to forage at sea, and suboptimal nest temperatures during incubation may have a negative impact on embryonic development in birds, potentially resulting in breeding failure (Ardia et al., 2009). In addition, snowfalls during the breeding season may be a major cause of death of eggs and chicks in seabirds, with also negative impacts on the body condition of chicks or incubating parents (Kuepper et al., 2018; Martin & Wiebe, 2004). To test for these weather effects on breeding success, we used the number of days of wind above 100 km/h (windy days), the number of days with snowfall (snowfall days), and the average maximum air temperature (air temperature) during the breeding period (November–March) as covariates over the period 1991–2018. Meteorological data were obtained from the Dumont d'Urville station weather station of Météo France public administrative institution.

To test for predation effects we used the annual number of breeding pairs of south polar skuas *Catharacta maccormicki* on Ile des Pétrels from 1981 to 2018 (skua pairs). Each year, as part of a long-term demographic monitoring program, the number of pairs of skuas breeding on Ile des Pétrels was recorded and monitored throughout the breeding season. More details on the monitoring methodology are provided in Pacoureau et al. (2018).

2.4 | Modeling the effects of environmental covariates

For survival probability, we used the structure of the selected MSCMR model that best described the age-dependent variation to which each covariate was added in interaction with age. Relationships between covariates and survival were fitted using a logit link function: logit $(\theta) = B0 + B1 \times X_n$ where θ is the demographic trait, $B1$ is an intercept parameter, $B1$ is a slope parameter, and X_n is the value of the covariate at year n.

We performed an analysis of deviance (ANODEV; Grosbois et al., 2008) to assess the fit of a covariate model relative to that of the constant and the time-dependent models, and to test the significance of each relationship. ANODEV was calculated as:

$$ANODEV = \frac{\frac{\text{Deviance (Mcst)} - \text{Deviance (Mcov)}}{J-1}}{\frac{\text{Deviance (Mcov)} - \text{Deviance (Mt)}}{n-J}}, \quad (1)$$

where J is the number of parameters required to model the relationship between the demographic parameter θ and the covariate, n is the number of parameters estimated by the time-dependent model for the vital rate θ, Mcov is the covariate model, Mt is the time-dependent model, and Mcst is the constant model. The proportion of deviance explained by covariates (R^2; Skalski, 1996) was estimated as:

$$r^2 = \frac{\text{Deviance (Mcst)} - \text{Deviance (Mcov)}}{\text{Deviance (Mcst)} - \text{Deviance (Mt)}}. \quad (2)$$

In order to avoid a spurious correlation with covariates in the presence of temporal trends, linear trends in demographic parameters were investigated using ANODEV tests, and in environmental covariates in R with linear regression. If temporal trends were detected, we followed the procedure in Grosbois et al. (2008), that is, using residuals of the linear regression of the covariates, to test whether the covariates accounted for a significant fraction of the variation in survival about the trend.

For breeding success, we also tested for a temporal trend in breeding success and covariates using linear models. To examine the relationship between environmental covariates and breeding success, we used a generalized additive model (GAM) explaining the variation in breeding success according to covariates, whose predictors depended on a smoothing function and breeding success was a function of covariates. To account for possible temporal autocorrelation we built an optimal error structure (ARMA) in the GAM models (Zuur, 2009). The comparison was based on the AIC of the concurrent models. We applied the ARMA structure to the model. Residual normality was visually verified. We used a GAM with a Gaussian family and identity link function. Models were fitted with R 3.6.2 R Core Team (2019). To detect collinearity between covariates, we used variance inflation factors with a threshold value of 3, above which covariates showing a value above such threshold should be discarded (Zuur, 2009).

2.5 | Population modeling

To model the dynamics of the population we built a female-only, age-classified prebreeding census matrix population model (Caswell, 2001). The life cycle of cape petrel was structured by age (Figure S2 and Table S1).

Survival varied according to three age-classes (first-year survival, survival from age 2 to 4, adult survival from age 5 and older). Between 1 and 2 years old, individuals are immature, and then, between 3 and 13, they are able to start breeding and are thus considered as prebreeders. We thus constructed a matrix population model with 13 age-classes. The age-specific survival probability and probability of first breeding was taken from the selected MSCMR model. We assumed equal survival between sexes and a sex ratio 1:1. The number of breeding attempts per year is limited to one.

We constructed a deterministic model based on the mean values of the estimated vital rates to obtain the deterministic population growth rate (λ). We used this deterministic model to estimate the stable age distribution, the generation time, the reproductive value, and the sensitivities and elasticities of the growth rate to each demographic parameter. We then estimated the contribution of temporal variations of survival and breeding success (θ) to the variability of λ using the first-order Taylor expansion as $V(\lambda) = s(\theta)^2 \text{var}(\theta)$, where $s(\theta)$ is the sensitivity of λ to parameter θ, and we assumed that vital rates varied independently (Caswell, 2001).

The deterministic growth rate describes the population trend for constant, invariant vital rates, so we constructed a stochastic model to account for variability in those rates. To do so, we chose random values of fertility rates from beta distributions using the mean and process variance values obtained from the breeding success analysis. For survival, we chose random values from normal distributions using the mean and process variance on logit scale from our MSCMR model to account for covariation among survival and then we transform the survival to the real scale.

The deterministic and stochastic matrix population models were analyzed by Monte Carlo simulations (1,000 iterations) using the package popbio (Stubben & Milligan, 2007) implemented in program R (R Core Team, 2019).

2.6 | Sensitivity analysis

To assess the sensitivity of the population growth rate (λ) to environmental variables, we performed a sensitivity analysis considering the sensitivity of λ to demographic parameters (estimated from the deterministic matrix model) and the sensitivity of demographic parameters to covariates (estimated from the partial derivative of the parameter with respect to each covariate, Text S1). The sensitivity of λ to a climate covariate c was calculated as:

$$\frac{d\lambda}{dc^T} = \frac{d\lambda}{d\theta^T}\frac{d\theta}{dc^T}, \quad (3)$$

where the first term $\left(d\lambda/d\theta^T\right)$ describes the sensitivity of λ to demographic parameter θ, and the second term $\left(d\theta/dc^T\right)$ describes the sensitivity of demographic parameter (θ) to covariate c.

The sensitivity of λ to changes in a covariate X can be difficult to compare with sensitivities to a covariate Y, because demographic parameters can be measured at different scales and environmental covariates are measured in different units. We therefore performed an elasticity analysis to estimate the effect of a proportional change in covariates on λ. We estimated elasticity of λ to environmental covariate c as:

$$\frac{d\lambda}{dc^T}\frac{c}{\lambda}, \quad (4)$$

and scaling covariates between 0 and 1.

3 | RESULTS

The GOF test for the MSCMR model was overall not significant (Table S2), indicating that our model fitted the data satisfactorily. Although a minor trap-dependence effect was detected by the GOF test, parameter estimates obtained by a model taking into account trap-dependence did not differ from a model without trap-dependence (Text S2).

3.1 | Demographic parameters

The model selection procedure on the recapture probability retained two distinct periods, 1966–1985 and 1986–2018, 6 age-classes for individuals never seen as breeders and 16 age-classes for individuals seen as breeders at least once during the study (Table S3). Overall recapture probability was relatively low (Table S4). It was lower during the period 1966–1985 than during the period 1986–2018 and increased with age.

Eleven age-classes best described age variation in probability of first breeding. The probability increased from age 3 to age 8 from 0.004 (0.003) to 0.200 (0.056). From age 9 to 13, estimates varied between 0.102 (0.059) and 0.335 (0.072).

The best model structure for the annual survival probability had three age-classes: first-year survival, survival from age 2 to 4, and survival from age 5 and older.

However, several models had similar AICc, leading to high uncertainty in model selection. Apparent survival was thus estimated from the models with ΔAICc < 10 using model averaging on the three age-classes. Model averaged apparent survival increased from 0.61 ± 0.19 during the first year to 0.92 ± 0.03 at 5 years and older (Table 1).

The average breeding success was 0.62 ± 0.05. The breeding success estimated each year over the period 1991–2018 showed a negative linear temporal trend (slope $= -0.012 \pm 0.004$, t test $= -2.859$, $p = 0.009$, $r^2 = 0.24$, Figure 1).

3.2 | Effect of environmental covariates

SST during the breeding and non-breeding periods respectively tended to decrease and increase over time but trends were not significant (slope $= -10.09 \pm 6.92$,

t value $= -1.46$, $p = 0.15$; slope $= 9.40 \pm 5.02$, t value $= 1.87$, $p = 0.06$, Figure 2). There was no effect of SST during the breeding or non-breeding periods on survival from t to $t + 1$ (Table 2). The SAM showed a positive trend over the time (slope $= 13.75 \pm 2.64$, t value $= 5.21$, $p < 0.001$, Figure 2), and had a positive effect on survival (Table 2, Figure 3). The survival probability also showed a positive linear trend over time for individuals aged 2–4 and for individuals older than five, but not for juveniles, for which a negative trend was detected (Table 2, Figure S3). However, time-dependent survival estimates for juveniles were poorly estimated and had large variances. Thus, the temporal trend in juvenile survival and the relationship between SAM and juvenile survival were considered as unreliable. After accounting for linear trends in both survival and SAM, de-trended SAM accounted for a significant fraction of the variation in survival about the trend (ANODEV: F-statistic $= 2.76$, $p = 0.007$, $r^2 = 0.09$), although this fraction was lower than the one explained by the trend.

The covariates used to test the effect of environmental variations on breeding success showed no collinearity (variance inflation factors <3). The model detected a negative impact of the percentage of days with snowfall and of the number of breeding pairs of skuas on breeding success of cape petrels (Table 3, Figure 4). The model also detected a positive influence of SST during the breeding season on breeding success (Table 3, Figure 4).

3.3 | Population modeling

The deterministic model, using the mean parameter values in Table 4, yielded a long-term annual population growth rate of 1.0039, indicating that the population is stable or increasing slightly, and a generation time of 14.0 years. The stochastic population growth rate was 1.0069 [95% CI $= 1.0063$, 1.0075]. The prospective analysis indicated that the population growth rate showed the highest sensitivity to survival of individuals of age 5 and older, followed by survival from year 2 to 4, first-year survival, and breeding success (Table 4). The retrospective analysis suggested a large contribution of survival of older individuals to the population growth rate. Survival from year 2 to 4 had an intermediate contribution. First-year survival and breeding success had small contributions (Table 4). However, should the decrease in breeding success in recent years persist, the asymptotic stochastic population growth (0.9913 [95% CI $= 0.9908$, 0.9918]) would indicate a slightly decreasing population given the average breeding success and survival estimated since 2010.

TABLE 1 Model averaged estimates of apparent survival according to age-classes for cape petrels breeding at Pointe Géologie archipelago, Terre Adélie, Antarctica during the period 1965–2018

Age-class	Weighted estimate	Unconditional *SE*
1	0.61	0.19
2–4	0.74	0.16
5+	0.92	0.03

Note: Estimates were obtained from the model averaging of models select with ΔAICc < 10.
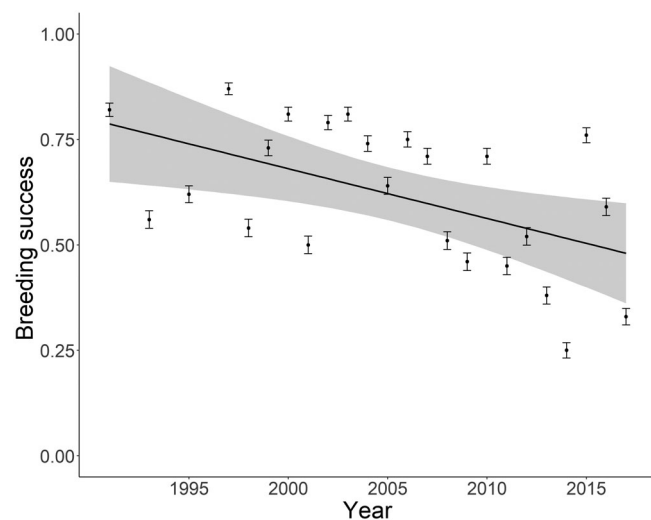

FIGURE 1 Time series of breeding success for cape petrels breeding at Pointe Géologie archipelago, Terre Adélie, Antarctica, 1991–2018. Plain line corresponds to estimate from linear regression with the *SE*. Filled circles correspond to the values of breeding success by year. Error bars are ±*SE*.

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FIGURE 2 Time series of sea surface temperature (SST) during the non-breeding period (April–October) (a), sea surface temperature during the breeding period (November–March) (b) during the period 1980–2018 and of the southern annular mode (c) during the period 1970–2018. Filled circles indicate observed values, plain line indicates modeled relationship, and gray area indicates 95% confidence intervals.
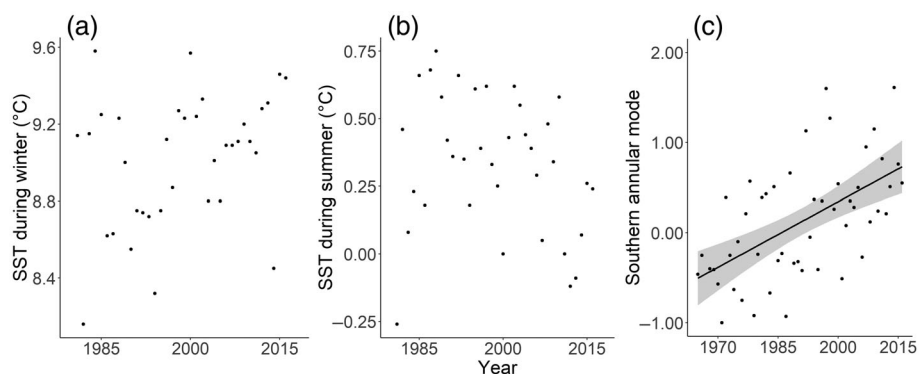

TABLE 2 Testing for the effects of covariates and linear trend on survival probability of cape petrels breeding at Pointe Géologie, Terre Adélie, Antarctica during the period 1965–2018

Models	Dev	J	F-statistic	p	r²	Age-class	Slope (SE)
SAM	**21,010.33**	**6**	**12.42**	**<0.001**	**0.29**	1	0.75 (0.25)
						2–4	0.63 (0.08)
						5+	0.48 (0.10)
De-trended SAM	**20,942.93**		**2.76**	**0.007**	**0.09**	1	NS
						2–4	1.16 (0.17)
						5+	1.71 (0.27)
SST winter	20,905.11	6	1.34	0.255	0.06		
SST summer	20,912.98	6	0.85	0.518	0.03		
Linear	**20,999.03**	**6**	**13.52**	**<0.001**	**0.31**	1	−0.83 (0.27)
						2–4	0.71 (0.16)
						5+	0.48 (0.10)

Note: J is the number of parameters describing the relationship between the demographic trait and the covariate. ANODEV is the F-statistic testing the null hypothesis that the focal covariate has no effect on demographic parameters. r² is the proportion of deviance explained by the covariate. Slopes are on the logit scale. All covariates were standardized. In bold characters models for which the specific ANODEV was statistically significant at the level of 5%. Abbreviations: Dev, deviance; NS, not significant; SAM, southern annular mode; SST summer, sea surface temperature during the breeding period (November–March); SST winter, sea surface temperature during the non-breeding period (April–October).

FIGURE 3 Survival estimates of cape petrels breeding at Pointe Géologie archipelago, Terre Adélie, Antarctica, 1965–2018 for two age-classes, age-class 2–4 (a), older than age 5 (b), as function of southern annular mode. Plain line indicates modeled relationship, gray areas indicate 95% confidence intervals, filled circles indicate annual estimates obtained from the time-dependent model. Error bars are ±SE.
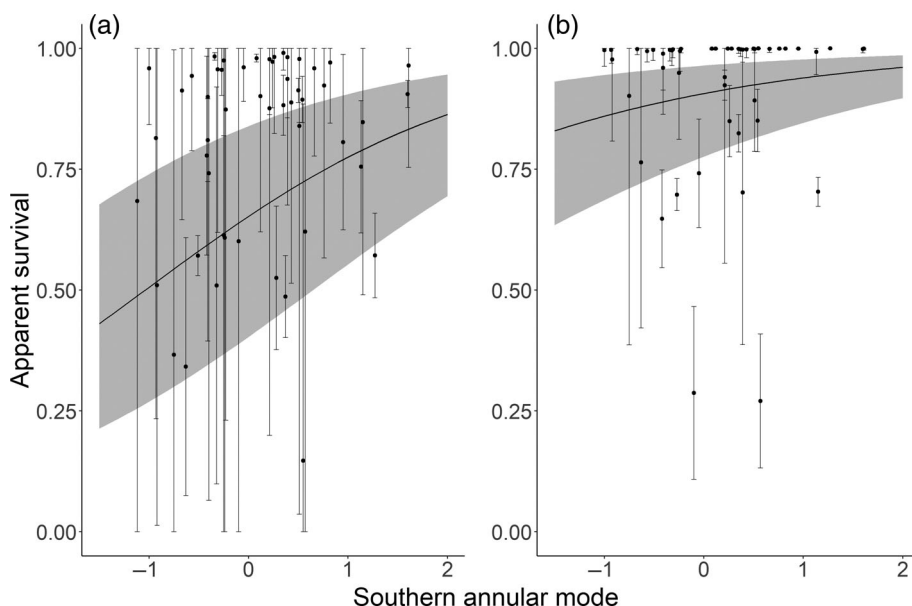
3.4 | Sensitivity of the population growth rate to environmental covariates

Sensitivity analysis (Figure 5, Table S5) revealed that breeding success was most sensitive to the number of breeding pairs of skuas and to the number of snow days on the breeding site while SST showed lower sensitivity. On the other hand, population growth rate was most sensitive (in proportional change in covariates on population growth rate) to SAM (through the positive effect of SAM on survival) and showed lower sensitivity to the number of breeding pairs of skuas, the number of snow days and SST, which affected breeding success.

4 | DISCUSSION

Results from this long-term demographic study showed that despite opposite trends in survival and breeding success, the growth rate of this Antarctic cape petrel population increased, mainly driven by an increase in adult survival, with contrasting effects of environmental variations on different vital rates. However, if the breeding success of the population continues to decrease, the population may decline in the future.

4.1 | Demography and population dynamics of cape petrels

This long-term study demonstrated a gradual increase in survival of cape petrels which was categorized by age-classes. Our estimate of first-year survival (0.610) is consistent with those obtained on other procellariforms

TABLE 3 Results of the general additive model for breeding success of cape petrels breeding at Pointe Géologie, Terre Adélie, Antarctica, 1965–2018

Covariates	Edf	F	p-value
SST summer	1	34.31	<0.001
Skua pairs	1	36.56	<0.001
Windy days	1	2.83	0.112
Snowfall days	1	27.98	<0.001
Air temperature	1	0.01	0.934
SAM	1	0.19	0.672
SIC	1	0.45	0.511

Note: The proportion of deviance explained by the model was 35%. Abbreviations: Edf, estimated degree of freedom; SAM, southern annular mode; SIC, sea ice concentration; SST summer, sea surface temperature during the breeding period (November–March).
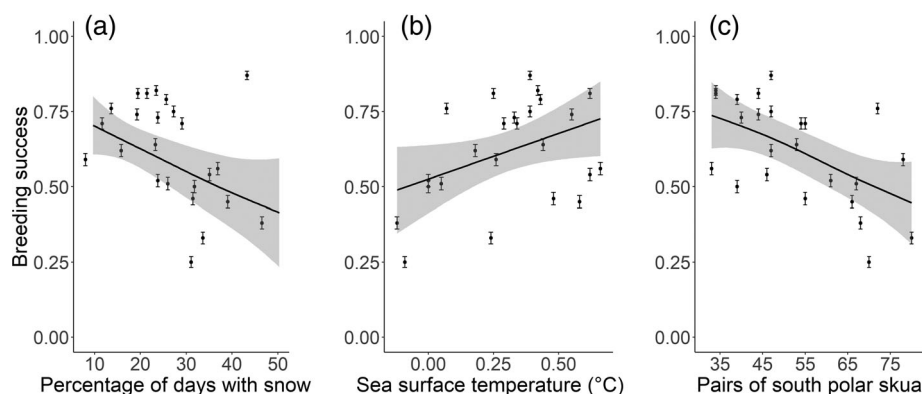

FIGURE 4 Relationships between percentage of days with snowfall (a), sea surface temperature during the breeding period in the summer foraging area (November–March) (b), number of breeding pairs of south polar skua (c), and breeding success of cape petrels breeding at Pointe Géologie, Terre Adélie, Antarctica, 1965–2018. Plain line corresponds to the estimated smoother from the general additive models with the *SE*. Filled circles indicate observed values. Errors bars are ±*SE*.

Parameter	Mean (*SE*)	Sensitivity	Elasticity	Contribution
First-year survival	0.610 (0.193)	0.120	0.073	0.0012
Survival age 2–4	0.739 (0.158)	0.286	0.211	0.0034
Survival age 5+	0.920 (0.031)	0.782	0.717	0.0169
Breeding success	0.618 (0.052)	0.118	0.073	0.0002

TABLE 4 Mean demographic parameter values, sensitivities, and elasticities of population growth rate, and contributions to variance of the population growth rate for the cape petrel from 1965 to 2018
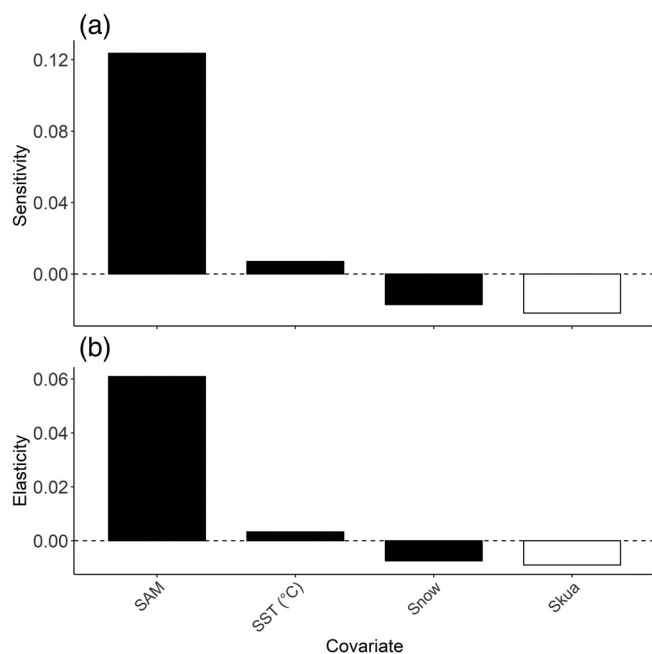
Note: Sensitivities, elasticities, and contributions to variance were calculated on the basis of a deterministic model.

FIGURE 5 Sensitivities (a) and elasticities (b) of population growth rate to environmental covariates for the cape petrel breeding in Terre Adélie, Antarctica, 1965–2018. SAM: southern annular mode. SST: sea surface temperature during breeding period in the summer foraging areas (November–March). Skua: number of breeding pairs of skuas. Snow: number of snowy days on the breeding site during the breeding period. Black bar indicates climate-related covariate. White bar indicates covariate not related to climate.

(e.g., Fay et al., 2015; Nicoll et al., 2017; VanderWerf & Young, 2016). As well for adult survival, our estimate (0.920) approximates those obtained on other procellariidae (e.g., Cuthbert & Davis, 2002; Jenouvrier et al., 2003; Waugh et al., 2006). Survival of young individuals in long-lived species is often lower than survival of adults (Jones et al., 2011), and our results showed this is also true for cape petrels. Improving demographic performance (here survival) with age is a pattern reported in many wild animal populations (Forslund & Pärt, 1995; Gaillard & Yoccoz, 2003). This may be a consequence of selective disappearance of phenotypes and/or of an improvement of foraging or migration skills required to cope with environmental constraints (Curio, 1983; Rebke et al., 2010; Williams, 1957). Our estimate of adult survival is also consistent with the literature on cape petrels. Hudson (1966) estimated an average annual survival rate for adult cape petrels of 94%–95% on Signy Island. Subsequently, using simple binomial models, Sagar et al. (1996) estimated adult survival of male and female cape petrels in the Snares Islands (New Zealand) at 0.939 and 0.844, respectively.

Cape petrels from Pointe Géologie started breeding at 3 years old. This minimum age at first reproduction

obtained from observations is consistent with observations made at other sites. Pinder (1966) observed a 4-year-old breeding bird, Beck (1969) observed a 3-year-old breeding bird despite a low sampling effort and a low recapture rate of birds banded as chicks. Average breeding success at Pointe Géologie (0.62) was close to those obtained by Prévost (1964) on the same study site (between 0.60 and 0.65) despite the negative trend that we observed since the beginning of our time series (1990–2018). However, estimates obtained on other study sites are lower (0.33 at Signy, Pinder, 1966; 0.54 at Snares, Sagar et al., 1996). This could be due to sampling bias: relatively few years were monitored for breeding success at Signy and Snares and our results indicate that breeding success can vary importantly from year to year. In addition, Pinder's study (1966) monitored a small number of nests. However, these regional differences in adult survival and breeding success may also reflect different breeding tactics and underlying changes in life history traits as an adaptive response to environmental variability, as observed in a handful of seabird species (black-browed albatross *Thalassarche melanophris* [Nevoux et al., 2010]; European shag *Phalacrocorax aristotelis* [Fortin et al., 2013]). Indeed, the population with the lowest breeding success (Signy) was the one with the highest adult survival, the Pointe Géologie population had the highest breeding success but lowest survival and the Snares population was intermediate. Thus, we cannot exclude that these intraspecific differences in life history traits in cape petrels constitute an adaptation to differences in environmental variability between breeding sites.

Population modeling showed that the growth rate was mainly sensitive to adult survival, as expected for a long-lived species (Lebreton & Clobert, 1991). Our findings suggest that the cape petrel population should be slightly increasing at a rate of 0.38% per year in Terre Adélie. Our estimation is consistent with the observed population growth rate estimated from counts of breeding pairs between 1984 and 2018 which was 1.0147. Our retrospective analysis suggests that the slight increase in the population size may be explained by the increase in adult and immature survival despite the decrease in breeding success which had a lower contribution. Dispersal from Petrels Island, which was the only site where nests were monitored during the first time period, may have biased our survival estimates and therefore the trend detected in survival. The raw proportion of breeding adults marked at Petrels Island and recaptured at other islands of the archipelago as breeding adults was 8%. However, a model where survival was estimated separately for the two time periods was not supported using our model selection criteria.

4.2 | Environmental drivers

Some studies have shown an influence of environmental covariates on juvenile seabird survival (e.g., Oro et al., 2010) or on adult seabird survival through a higher reproductive cost (e.g., Lescroël et al., 2009). Our results showed a positive relationship between SAM and the probability of survival of cape petrels, and this relationship remained effective on the de-trended series of SAM, suggesting that SAM affected the interannual variations of survival probability. Migration data on cape petrels during the non-breeding period indicate that they stay mainly below 50°S (Delord et al., 2016). In this area, a positive phase of SAM leads to an increase in the abundance of phytoplankton (Lovenduski & Gruber, 2005). We therefore suggest that SAM in the positive phase allows an increase in the abundance of resources for cape petrels, thus increasing their probability of survival during the non-breeding period, which is the period during which most mortality seems to occur in seabirds (Barbraud & Weimerskirch, 2003). These results provide support for the tub hypothesis which proposes fluctuations in population size to be closely related to climate variation during the non-breeding season as weather conditions determine the number of birds surviving during this critical period of the year (Lack, 1954; Sæther et al., 2016). Changes in climate and oceanographic conditions in this part of the Southern Ocean (i.e., increasing SAM) therefore seem favorable to the survival and populations of cape petrels. Although little information is available to understand the underlying mechanisms linking SAM to the demography of southern seabird populations, the effects of this climate index have been reported for several species. Previous studies in Antarctica have shown an influence of SAM on the survival of snow petrels *Pagodroma nivea* (Sauser et al., 2018) and on the juvenile survival of emperor penguins *Aptenodytes forsteri* (Abadi et al., 2017). SAM is also known to affect seabird species living in the subantarctic environment. For example, a positive relationship between the age of recruitment of wandering albatrosses *Diomedea exulans* breeding at Crozet (southern Indian Ocean) and SAM has been shown (Fay et al., 2017). Fay et al. (2017) suggested that the climatic conditions induced by SAM influence food availability several years before the first breeding attempt of individuals, affecting the time at which an individual reaches the body condition required for breeding. Another study showed that the survival of male southern giant petrels *Macronectes giganteus* breeding at South Georgia was positively affected by SAM (Gianuca et al., 2019). In this region, a positive phase of SAM is linked to warmer sea conditions, thus the positive effect of SAM on the survival suggests that the survival of this species was higher in the relatively warmer years.

Breeding success was influenced by several environmental covariates. Locally, on the breeding colony, the percentage of snow days had a negative effect on breeding success. As documented for snow petrels (Chastel et al., 1993), we suggest that in years with a high percentage of snow days during the breeding season, eggs and/or chicks of cape petrel were more affected by flooding in nests following snowmelt, resulting in higher proportion of failures during incubation and chick rearing. Interestingly, we found that the number of breeding pairs of south polar skuas had a negative effect on breeding success. Cape petrels breed in open nests and therefore may be exposed and sensitive to predation of eggs or chicks by skuas. Although cape petrels defend their nest against predators by spitting stomach oil toward intruders, diet studies of south polar skuas and brown skuas (*C. lonnbergi*) documented a significant proportion of cape petrel eggs and chicks in their diet (Baker & Barbraud, 2001; Pinder, 1966). Skuas probably take unguarded eggs and chicks, a behavior that we observed at Pointe Géologie (Barbraud, personal observation). The relationship between cape petrel breeding success and skuas pairs suggests that predation is rather common and that there is a top-down control of the cape petrel population dynamics. SST had a positive influence on the breeding success of cape petrels. This result appears surprising as warm SST anomalies are generally negatively related to demographic parameters in seabirds (Barbraud et al., 2012). However, given the observed range of SST values [−0.12, 0.66] we strongly suspect that low values of SST in the studied area corresponded to more sea ice in the foraging areas. Since cape petrels avoid sea ice (both fast ice and pack ice) and prefer to feed in open waters (Ainley et al., 1992; Barbraud & Delord, unpublished data; Veit & Hunt, 1991), this suggests that foraging habitat may be limited when SST were low (corresponding to more sea ice), limiting the availability of resources for cape petrels. In the light of these results, the negative temporal trend in breeding success of cape petrels at Pointe Géologie could be partly driven by (i) the increasing breeding population size of south polar skuas (Pacoureau et al., 2019), and (ii) more frequent occurrence of sea ice during the summer (Barbraud et al., 2015).

To conclude, this work constitutes the most comprehensive study on the demography of cape petrels and identified important environmental drivers of its population dynamics in East Antarctica. Our results showed that environmental variation had contrasting effects on different vital rates, but indicated that increasing survival, linked to a positive trend in SAM, mainly

contributed to the growth of the population over the past decades, despite a negative trend in breeding success mainly due to increased predation pressure and perhaps sea ice changes. At a broader scale, since SAM affects the climate across the Southern Ocean to Antarctica, it is possible that other breeding populations of cape petrels around Antarctica were also positively affected by the increasing trend in SAM. As the positive trend in SAM is primarily due to stratospheric ozone depletion and increases in greenhouse gases as a consequence of human activities (Fogt & Marshall, 2020; Shindell & Schmidt, 2004; Solomon & Polvani, 2016), our results suggest an unexpected and unpredicted positive consequence of these global changes for populations of an Antarctic seabird. However, as these global changes in the study area have been relatively limited to date, it can be assumed that climate conditions, which became more optimal for the cape petrel, may become detrimental if these changes become more pronounced in the future.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

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