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LINKING ORGANISMAL FUNCTIONS, LIFE HISTORY STRATEGIES AND POPULATION PERFORMANCE

Climate change and functional traits affect population dynamics of a long-lived seabird

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Abstract

1. Recent studies unravelled the effect of climate changes on populations through their impact on functional traits and demographic rates in terrestrial and freshwater ecosystems, but such understanding in marine ecosystems remains incomplete.
2. Here, we evaluate the impact of the combined effects of climate and functional traits on population dynamics of a long-lived migratory seabird breeding in the southern ocean: the black-browed albatross (*Thalassarche melanophris*, BBA). We address the following prospective question: "Of all the changes in the climate and functional traits, which would produce the biggest impact on the BBA population growth rate?"
3. We develop a structured matrix population model that includes the effect of climate and functional traits on the complete BBA life cycle. A detailed sensitivity analysis is conducted to understand the main pathway by which climate and functional trait changes affect the population growth rate.
4. The population growth rate of BBA is driven by the combined effects of climate over various seasons and multiple functional traits with carry-over effects across seasons on demographic processes. Changes in sea surface temperature (SST) during late winter cause the biggest changes in the population growth rate, through their effect on juvenile survival. Adults appeared to respond to changes in winter climate conditions by adapting their migratory schedule rather than by modifying their at-sea foraging activity. However, the sensitivity of the population growth rate to SST affecting BBA migratory schedule is small. BBA foraging activity during the pre-breeding period has the biggest impact on population growth rate among functional traits. Finally, changes in SST during the breeding season have little effect on the population growth rate.
5. These results highlight the importance of early life histories and carry-over effects of climate and functional traits on demographic rates across multiple seasons in population response to climate change. Robust conclusions about the roles of various phases of the life cycle and functional traits in population response to

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climate change rely on an understanding of the relationships of traits to demographic rates across the complete life cycle.

KEYWORDS
birds, climate change, foraging behaviours, non-breeding season, phenotypic traits, pre-breeding season, timing of breeding, wing length

1 | INTRODUCTION

There is now ample evidence that individual plants and animals respond to climate change with changes in their functional traits (e.g., phenology, body size and body mass, foraging behaviours) and demographic rates (e.g., survival, fecundity), which have consequences for populations and beyond (Hoegh-Guldberg & Bruno, 2010; Jenouvrier & Visser, 2011; Walther et al., 2002; Williams, Shoo, Isaac, Hoffmann, & Langham, 2008). Recent studies unravelled the effects of climatic conditions on populations through their impact on functional traits and demographic rates in terrestrial (Adler et al., 2014; Ozgul et al., 2009; Plard et al., 2014) and freshwater ecosystems (Vindenes et al., 2014). For instance, yellow-bellied marmots (*Marmota flaviventris*) were born earlier and their development rate increased in response to a longer growing season (Ozgul et al., 2010). This increase in juvenile growth led to an increase in adult body mass with a decline in adult mortality and an increase in reproductive output, ultimately resulting in an abrupt increase in population size.

However, a demographic rate or functional trait response to climate does not necessarily affect population growth, and several studies have cautioned against drawing broad conclusions about population responses to climate changes from analyses of a single functional trait, single demographic rate or single life state of a species life cycle (Adahl, Lundberg, & Jonzen, 2006; Barbraud et al., 2008; Visser et al., 2016). For example, temperature may affect the laying date of many bird species without apparent effects on population trends (McLean, Lawson, Leech, & van de Pol, 2016; Reed, Jenouvrier, & Visser, 2013; Wilson & Arcese, 2003).

Changes in climate modify population growth rate through changes in functional traits if three processes occur:

1. changes in climate affect functional traits (e.g., longer growing season → body mass),
2. changes in functional traits affect demographic rates (e.g., body mass → adult survival),
3. changes in demographic rates affect population growth rate (e.g., adult survival → population growth rate).

Thus, if a change in a functional trait has little effect on a demographic rate, and/or a change in a demographic rate has little effect on the population growth rate, then climate-induced changes in a phenotypic trait or a demographic rate will have little effect on the population dynamics (McLean et al., 2016).

Furthermore, it is crucial to combine all these processes (climate changes → functional traits → demographic rates → population growth rate) across the full life cycle because climate effects on functional traits and demographic rates may be contrasted between various states of the life cycle (Jenouvrier, 2013; Visser et al., 2016). For example, in a butterfly species (*Boloria eunomia*), higher temperatures have a positive effect on the survival of eggs, pre-diapause larvae and pupae but a negative effect on the survival of overwintering larvae (Radchuk, Turlure, & Schtickzelle, 2013). Multiple climate variables and functional traits affect populations via various pathways, which may reinforce or weaken population responses to climate (Griffith, Salguero-Gómez, Merow, & McMahon, 2016; McLean et al., 2016). In a study of 136 tropical tree species across their entire life cycle, the effects of traits on one life state or demographic rate were sometimes counteracted by opposing effects at another state (Visser et al., 2016). In a population of northern pike (*Esox lucius*), the thermal sensitivity of the population growth rate varies across demographic rates and functional trait classes (body length), resulting in complex pathways through the life cycle by which warming temperature increases the population growth rate (Vindenes et al., 2014).

In marine ecosystems, fewer studies have investigated and documented an impact of functional traits on demographic rates, and none, to our knowledge, have studied the effects of climate on population dynamics via various functional trait pathways throughout the full life cycle. Here, we integrated multiple climate–traits–demographic rates relationships across the full life cycle of a long-lived migratory seabird breeding in the southern ocean, the black-browed albatross (BBA) (*Thalassarche melanophris*), to understand the impact of the combined effects of climate and functional traits on population dynamics.

The effects of climatic conditions on seabirds generally occur indirectly. They operate primarily through effects on the availability of prey and breeding habitats potentially causing changes in transportation costs, timing of breeding and body conditions of seabirds (Barbraud et al., 2012; Grémillet & Boulinier, 2009; Jenouvrier, 2013). Thus, as for terrestrial vertebrates, phenology, body conditions and foraging behaviours are key functional traits by which individual seabirds could respond to climate changes (Frederiksen, Harris, Daunt, Rothery, & Wanless, 2004; Weimerskirch, Louzao, de Grissac, & Delord, 2012) with potential consequences for demographic rates and population dynamics.

Phenological change is an important process by which marine populations may respond to climate change because the recruitment success of organisms spanning several trophic levels is highly dependent on synchronization with pulsed planktonic production (i.e., mismatch hypothesis; Cushing, 1990; Edwards & Richardson, 2004). Several studies have detected trophic mismatches in marine ecosystems (Burthe et al., 2012; Durant, Hjermann, Ottersen, & Stenseth, 2007). For example, when their prey (capelin *Mallotus villosus*) were late, common murre (*Uria aalge*) delivered fewer fish to their chicks despite an increasing foraging effort that resulted in a lower breeding success (Regular et al., 2014).

Body condition has been shown to affect demographic rates in seabirds (Barbraud & Chastel, 1999; Chastel, Weimerskirch, & Jouventin, 1995; Harding et al., 2011). For example, male body mass affected key demographic rates of both adult and juvenile wandering albatrosses (*Diomedea exulans*) (Cornioley, Jenouvrier, Börger, Weimerskirch, & Ozgul, 2017).

Foraging behaviours affect the breeding performance of many seabirds, both directly during the breeding season (Monaghan, 1992; Pinaud & Weimerskirch, 2002) and through carry-over effects during the non-breeding season (Daunt et al., 2014; Shoji et al., 2015). European shags (*Phalacrocorax aristotelis*) performing late winter foraging trip of short duration were more likely to breed successfully during the following breeding season (Daunt et al., 2014).

Among climate variables, sea surface temperature (SST) is known to influence primary and secondary production in several marine ecosystems (Behrenfeld et al., 2006) and has been linked to various demographic rates in several seabird species (Barbraud et al., 2012). In BBAs breeding at Kerguelen Island, SST during various phases of the life cycle influences their migratory schedule, survival, breeding and success probabilities (Desprez, Jenouvrier, Barbraud, Delord, & Weimerskirch, 2018; Nevoux, Weimerskirch, & Barbraud, 2007; Pinaud & Weimerskirch, 2002; Rolland, Barbraud, & Weimerskirch, 2008). Juvenile BBA migrates from Kerguelen to the coasts of Australia, moving progressively from the south-western coasts along to the south-eastern coasts (De Grissac, Börger, Guitteaud, & Weimerskirch, 2016). Adults from Kerguelen migrate in this sector as well during the non-breeding season (Desprez et al., 2018). Consequently, the SST in this wintering sector affects demographic rates and functional traits of both juveniles and adults. Furthermore, higher SST during the breeding season over the eastern Kerguelen shelf—the main foraging area of this BBA population—positively influenced breeding success (Nevoux et al., 2007; Pinaud & Weimerskirch, 2002; Rolland, Barbraud, & Weimerskirch, 2008). Finally, larger fledging body size positively affected both juvenile survival and recruitment probabilities (Supporting Information, R. Fay, M. Desprez, S. Jenouvrier, C. Barbraud, K. Delord, & H. Weimerskirch, unpublished data), and both timing of arrival on the pre-breeding grounds and foraging behaviours in the pre-breeding grounds affected future breeding success (Desprez et al., 2018).

The effects of SST and foraging behaviours depend on individual breeding experience and status at the previous breeding season (Desprez et al., 2018; Nevoux et al., 2007; Rolland, Barbraud, & Weimerskirch, 2008). In BBA, like in many seabirds, individuals breeding successfully in a given year have a higher probability of reproducing and successfully raising a chick in the following year compared to failed breeders and non-breeders (individuals that skipped reproduction in a given year; Cam & Monnat, 2000; Jenouvrier, Péron, & Weimerskirch, 2015). In addition, failed breeders return earlier to pre-breeding grounds and have extended winter and pre-breeding periods, suggesting that they require longer foraging periods to build the energetic reserves necessary to reproduce compared to successful breeders (Desprez et al., 2018). These differences in functional traits and demographic rates between failed and successful breeders may indicate a lower intrinsic quality of failed breeders (sensu Wilson & Nussey, 2010). Finally, first-time breeders have lower reproductive success and survival than experienced breeders probably because they are less experienced in foraging and breeding activities (Nevoux et al., 2007). Consequently, it is important to consider breeding experience and breeding states (successful breeders, failed breeders and non-breeders) in seabirds' life cycles to comprehend the effects of climate on their population dynamics (Jenouvrier, Barbraud, Cazelles, & Weimerskirch, 2005; Jenouvrier, Barbraud, & Weimerskirch, 2005).

Here, we investigate the functional dependence of population growth rate on demographic rates, functional traits and climate variables to address the following prospective question (Caswell, 2000): "Of all the changes in the climate and functional traits, which would produce the biggest impact on the population growth rate of the black-browed albatross?" We explicitly link the following processes: climate changes → functional traits → demographic rates → population growth rate, across the full life cycle by developing a life cycle structured by age classes, breeding experience and breeding states. Our analysis is based on a 35-year longitudinal demographic dataset combined with data on fledging body condition (29 years) and adult foraging behaviour and migratory schedule inferred from tracking devices (8 years). We use sensitivity analysis to predict the changes in the population growth rate that would result from any specified change in the demographic rates, functional traits and climate variables and characterize pathways by which climate, functional traits and demographic rates produce the biggest impact on the population growth rate.

2 | MATERIALS AND METHODS

The key to studying population response to climate variability is to define the demographic rates ($\boldsymbol{\theta}$) as a function of climate variables ($\mathbf{c}$) (Jenouvrier, 2013). These relationships may be mediated through the effect of climate on functional traits ($\mathbf{f}$) (Jenouvrier & Visser, 2011). First, we describe the study species (Section 2.1), climate variables and functional traits (Section 2.2). Second, we develop a structured matrix population model (Section 2.4) that includes the effect of climate and functional traits on the entire BBA life cycle (Section 2.3) to understand their respective effects on the long-term deterministic population growth rate λ. Finally, to understand the main pathway by which climate and functional trait changes affect the population growth rate, we conducted a detailed sensitivity analysis (Section 2.5).

2.1 | Study species: the BBA

Black-browed albatrosses are large Procellariiformes (3–4 kg, 2–2.5 m wingspan) breeding on sub-Antarctic islands during the austral summer. Adults arrive in September at their breeding site and lay a single egg in October that will hatch in December. The chick fledges in late March at a size similar to that of an adult.

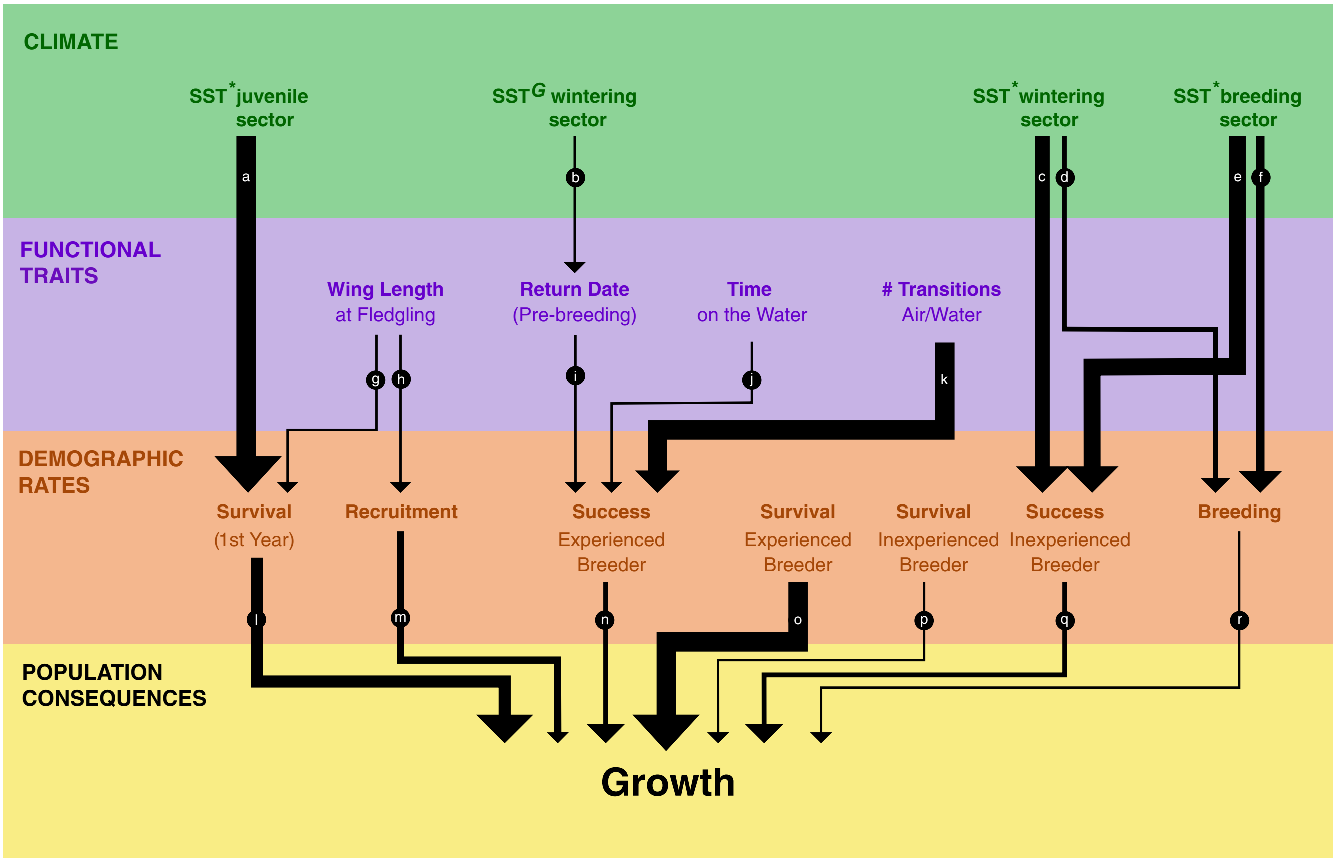
Our BBA study population is located at Kerguelen Island (49°41′S, 70°14′E), in the colony of Cañon des Sourcils Noirs (≃1,100 breeding pairs), where ca. 200 breeding pairs were monitored annually since the season 1979/1980. BBAs forage over sub-Antarctic waters on the north-eastern edge of the Kerguelen shelf during the breeding season from October to April (Pinaud & Weimerskirch, 2002) and in Tasmanian waters during winter (Desprez et al., 2018). Their diet is composed of fish (73%), penguin carrion (14%) and squids (10%) (Cherel, Weimerskirch, & Trouvé, 2000).

Adults and chicks are leg-banded with stainless steel rings and a capture–mark–recapture programme is ongoing annually during the breeding season. The rings of breeding birds are checked just after egg laying, and all chicks are ringed just before fledging and body condition measurements (e.g., mass [g], wing length [mm]) are recorded.

2.2 | Climate variables and functional traits

We have a reasonable knowledge of the links between climate variables (**c**) and functional traits (**f**), and how those traits affect the demographic rates (**θ**[**f**(**c**), **c**]) from previous studies (R. Fay, M. Desprez, S. Jenouvrier, C. Barbraud, K. Delord, & H. Weimerskirch, unpublished data; Desprez et al., 2018; Nevoux et al., 2007; Rolland, Barbraud, & Weimerskirch, 2008; Pinaud & Weimerskirch, 2002). Figure 1 summarizes the *statistically significant* relationships and hereafter, we will refer to the various pathways on Figure 1 by their letter [**x**]. Desprez et al. (2018) estimated pathways [**b**, **g**, **h**, **i**, **j**, **k**, **n**], and Supporting Information Methods and Results detail the estimation of other pathways.

Sea surface temperatures (SSTs) were extracted from satellite data from 1982 to 2015 in several spatial sectors that correspond to the different foraging areas during various seasons of the BBA life cycle (hereafter SST*, Supporting Methods 1.1, Figure S1a). In addition, we used SST during the wintering season (July to September)



SST*= Sea Surface Temp. (Satelite measured) SST^G = Sea Surface Temp. (GLS measured)

FIGURE 1 Diagram summarizing the relationships between the different hierarchical levels through which climate variables affect population growth rate. A change in climate can impact functional traits, which in turn can affect demographic rates, and subsequently population dynamics. Letter shows specific pathway we refer to in the main text, and the thickness of the line refers to the magnitude of the sensitivity of an output variable (y) to an input variable (x) of the model: $\frac{d_y}{d_x}$ (Table 1). The relationships that were not statistically significant are not shown. For example, no relationship between climate and the following functional traits has been detected: wing length, proportion of time on the water, the number of air/water transition (Desprez et al., 2018, Supporting Information). Note these relationships may vary with the breeding status of the individuals during the previous breeding season

TABLE 1 Outputs of the climate- and trait-dependent matrix population model and sensitivity analysis

Variable	Notation	Calculation
Population growth rate	λ	Dominant eigenvalue of **A**
Stable state distribution	**w**	Right eigenvector corresponding to λ
Reproductive value	**v**	Left eigenvector corresponding to λ
Sensitivity of λ to population matrix **A**	$\frac{d\lambda}{d\mathrm{vec}^{\mathsf{T}}\mathbf{A}}$	$\frac{\mathbf{w}^{\mathsf{T}} \otimes \mathbf{v}^{\mathsf{T}}}{\mathbf{w}^{\mathsf{T}}\mathbf{v}}$
Sensitivity of λ to vital rate $\boldsymbol{\theta}$	$\frac{d\lambda}{d\boldsymbol{\theta}^{\mathsf{T}}}$	$\frac{d\lambda}{d\mathrm{vec}^{\mathsf{T}}\mathbf{A}} \frac{d\mathrm{vec}\mathbf{A}}{d\boldsymbol{\theta}^{\mathsf{T}}}$
Sensitivity of λ to functional traits **f**	$\frac{d\lambda}{d\mathbf{f}^{\mathsf{T}}}$	$\frac{d\lambda}{d\mathrm{vec}^{\mathsf{T}}\mathbf{A}} \frac{d\mathrm{vec}\mathbf{A}}{d\boldsymbol{\theta}^{\mathsf{T}}} \frac{d\boldsymbol{\theta}}{d\mathbf{f}^{\mathsf{T}}}$
Sensitivity of λ to climate variables **c**	$\frac{d\lambda}{d\mathbf{c}^{\mathsf{T}}}$	$\frac{d\lambda}{d\mathrm{vec}^{\mathsf{T}}\mathbf{A}} \frac{d\mathrm{vec}\mathbf{A}}{d\boldsymbol{\theta}^{\mathsf{T}}} \left(\frac{d\boldsymbol{\theta}}{d\mathbf{f}^{\mathsf{T}}} \frac{d\mathbf{f}}{d\mathbf{c}^{\mathsf{T}}} + \frac{d\boldsymbol{\theta}}{d\mathbf{c}^{\mathsf{T}}} \right)$

For the calculation of the sensitivity of the population growth rate λ with respect to the climate variables **c**, the term $\frac{d\theta}{d\mathbf{c}^{\mathsf{T}}}$ represents the direct measured effect of climate variables on $\boldsymbol{\theta}$; that is, that does not occur through an indirect impact of climate on body size and foraging processes. Notation as in Caswell (2008) with vec is the vec operator, which transforms a matrix to a column vector by stacking each column on top of the next.

recorded by Global Location Sensor (GLS) fitted on birds (thereafter SST^{G}, Figure S1b; Desprez et al., 2018).

The functional traits measured are body condition standardized at a reference date during the breeding season and foraging variables (Supporting Methods 1.2 and Figure S2). We focus on wing length in our analysis, as this was the body condition measurement most strongly associated with demographic rates (Supporting Results 2). Two foraging variables during the pre-breeding period were calculated from GLS data (see Desprez et al., 2018): (1) the percentage of daily time spent sitting on the water (Time_{w}), and (2) the minimal number of daily transitions between air and water ($\#T_{a/w}$) (Supporting Methods 1.3, Figure S2). The last functional trait is the date of return on the pre-breeding ground calculated from GLS data.

All our variables are expressed as standard score, which is a dimensionless quantity obtained by subtracting the population mean from an individual raw value and then dividing the difference by the population standard deviation. For the climate variables, we used the 2006–2013 (excluding 2008), which is the overlapping period of the SST measurements between GLS and satellite.

2.3 | The BBA life cycle

Our analysis is based on a life cycle that includes 25 states ($s = 25$), based on breeding states and age defined at the end of the breeding season in March of year t (Figure 2). Note that while the demographic rates may, in general, vary with state j and time t, we include only the state subscript in the following notation for clarity, where j corresponds to the life cycle state ($j = 1,\ldots,s$).

The breeding states are defined as follows:

1. Pre-breeders: individuals that have yet to breed; this state includes fledged chicks produced during the current season (from October of year $t-1$ to March of year t).
2. Successful inexperienced breeders: individuals that breed for the first time and successfully raised a chick during the current season.
3. Failed inexperienced breeders: individuals that breed for the first time and either failed to hatch an egg or failed to raise a chick during the current season.
4. Successful experienced breeders: individuals that have bred at least once before and successfully raised a chick during the current season.
5. Failed experienced breeders: individuals that have bred at least once before and either failed to hatch an egg or failed to raise a chick during the current season.
6. Non-breeders: individuals that have bred at least once before, but did not breed in the current season.

From 1 to 10 years of age, individuals can be pre-breeders or successful or failed inexperienced breeders. However, there is no age class once individuals have bred at least once in their lifetime (i.e., experienced individuals, states 23–25).

The annual life cycle starts in March of year t, immediately after the fledging period. The demographic rates associated with the life cycle transitions among states are defined as follows:

1. State-specific survival probability ϕ_j: the probability of surviving and not permanently emigrating to a different colony from the end of the breeding season in 1 year t (i.e., March t) to the end of the breeding season in the next year (i.e., March $t+1$).
2. State-specific breeding probability β_j: the conditional probability of returning to the colony and breeding in the next breeding season (i.e., October t), given survival.
3. State-specific success probability γ_j: the conditional probability of successfully raising a chick to fledging in the next breeding season (i.e., March $t+1$), given survival and breeding.

For example, pre-breeders older than 5 years old at year t may produce offspring the following year at $t+1$, if they survive from March t to $t+1$ with probability ϕ_j ($j \in [5\ 10]$), and return to the colony and breed in October of year t with probability β_j, and raise successfully a chick to fledging in March $t+1$ with probability γ_j. These transitions appear on Figure 2 (dashed lines from nodes $j \in [5\ 10]$ to node 1).

These state-specific survival, breeding and success probabilities were estimated using a multi-event capture–recapture model (Pradel, 2005) (Supporting Methods 1.4). We performed goodness-of-fit tests (Supporting Methods 1.5) and a model selection according to the parsimony criteria Akaike information criterion ([AIC]; Burnham & Anderson, 2002) (Supporting Methods 1.6).

2.4 | The matrix population model

Based on this life cycle, we construct a climate- and trait-dependent matrix population model (Caswell, 2001). The matrix population model predicts the population from time t to $t+1$ by $\mathbf{n}_{t+1} = \mathbf{A}_t\mathbf{n}_t$

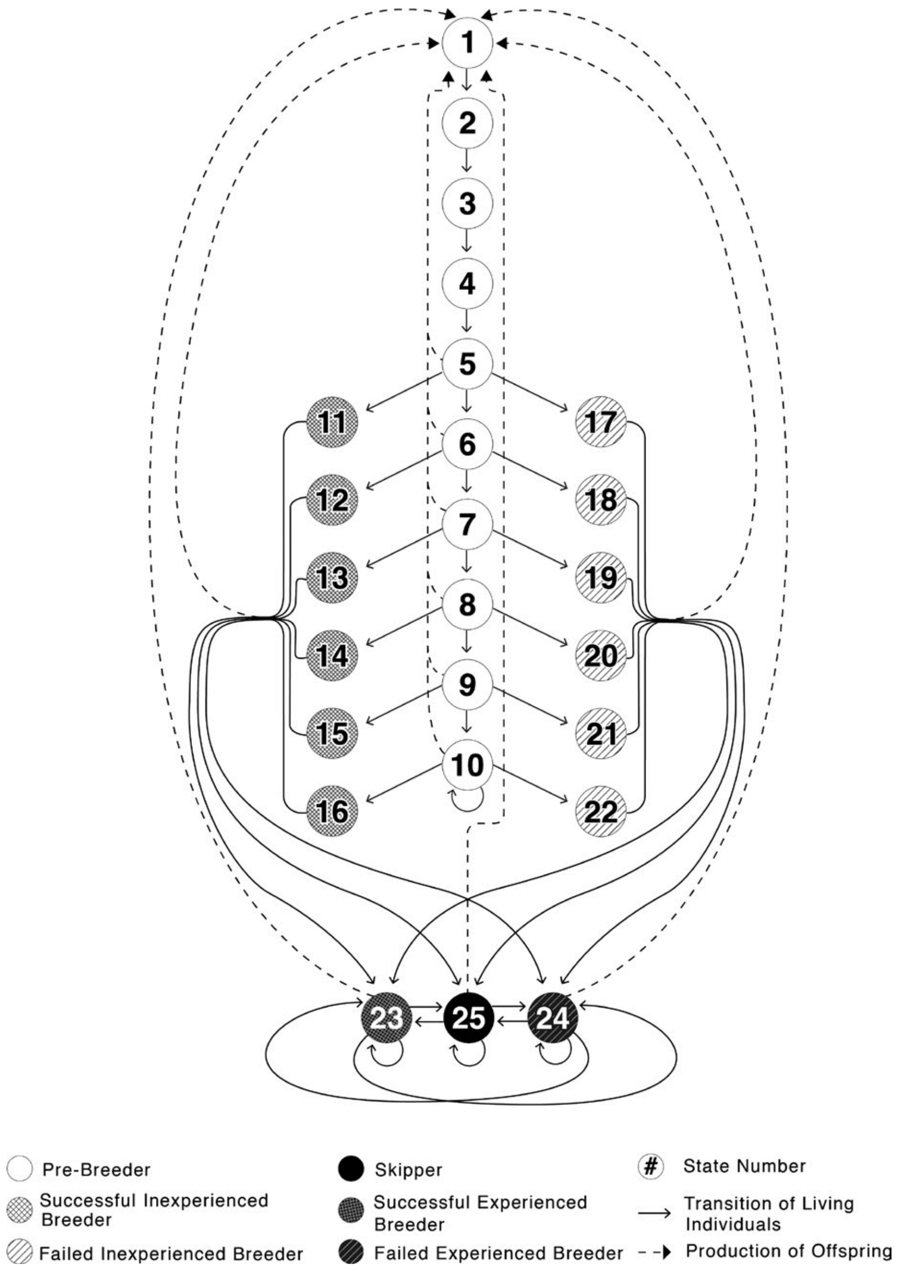


FIGURE 2 Life cycle of the black-browed albatross. It includes 25 states based on breeding states and age defined at the end of the breeding season in March *t*. The numbering of the nodes corresponds to the rows of the population vector **n**. Colours and patterns refer to specific breeding states (see Section 2.3). Fertilities are represented by dashed lines, and the transitions between states of individuals already present in the population are represented by solid lines

where n_j is the abundance of state *j* and $\mathbf{A}_t$ is the population projection matrix at time *t*, which contains the demographic rates ($\boldsymbol{\theta}_t$, a vector of 68 entries) (Supporting Method 1.7). The population matrix at time *t* depends on the vectors of functional traits **f** and climate variables **c**: $\mathbf{A}\left\{\boldsymbol{\theta}[\mathbf{f_t}, \mathbf{c_t}, \mathbf{f}(\mathbf{c_t})]\right\}$ (Figure 1). From this model, we calculate the asymptotic deterministic population growth rate λ (maximum eigenvalue of **A**; Caswell, 2001) as a function of functional traits and climate variables. This analysis provides information under the hypothetical scenario in which individuals experience a constant set of climate conditions or persistent functional traits over their entire life.

2.5 | Sensitivity analysis

Sensitivity analysis allows us to understand the respective role of demographic and functional traits underlying population responses to climate change (McLean et al., 2016) and address the question “To which climate variables and traits is λ most sensitive, when the climate variables and traits are scaled relative to their variation?” (Supporting Methods 1.8). It measures the effects of absolute, or unit change in an input parameter **x** on an output **y**. Sensitivity of λ can be calculated with respect to any parameters: demographic rates or functional traits (e.g., body size or foraging behaviours) of the model: $\frac{d\lambda}{d\mathbf{x}}$ using derivative chain rule (Caswell, 2008; Table 1).

Because multiple climate variables and various functional traits affect the population growth rate with various interactive effects, we conducted our analysis over all possible combinations of **c** and **f** over their observed range. Specifically, we used 10 values per variable distributed evenly over the minimum and maximum values observed (except for the number of transition air/water for which we restricted the range, see Supporting Methods 1.3, Figure S3).

Furthermore, we set SST* in the juvenile and adult sector during the wintering period to be equal because they were calculated over similar seasons and sectors and are highly correlated (Pearson's correlation coefficient of 0.77, *p*-value <.0001, Figure S1). Thus, we vary seven variables (three climate variables and four functional traits), that is study 10^7 samples of the parameter space.

3 | RESULTS

Changes in climate and functional traits cause changes in the demographic rates (Section 3.1) and population growth rate (Section 3.2). The sensitivity analysis determines how much change in the population growth rate is caused by a change in a parameter (climate or a functional trait or a demographic rate, Section 3.3).

3.1 | Effect of climate and functional traits on demographic rates

SST* during winter in the juvenile sector (Figure 1 pathway [**a**]) and wing length [**g**] both affect survival during the first year at sea (ϕ_1), but wing length is not related to the climate variables studied. ϕ_1 is maximized at SST* standard scores ~−0.4 (hereafter optimal SST* that are slightly cooler than the 2006–2013 average) and declines at higher or lower values (Supporting Results 2, Figure S4). This non-linear relationship is stronger for individuals with larger wing length. Wing length but not climate affects recruitment probabilities [**h**]: the probability to recruit increases for individuals with a longer wing length, especially for younger individuals (Figure S5).

Foraging and phenology variables during the pre-breeding period (Time$_w$, #$T_{a/w}$ and the date of return) influence the success probability of experienced breeders (Desprez et al., 2018), [**i**, **j**, **k**]. During the pre-breeding period, individuals that spent less time on water and did more take-offs and landings (i.e., likely having a higher foraging effort) were more likely to breed successfully during the subsequent breeding season (Figure S6a). Earlier return date to the pre-breeding grounds was associated with higher SST^G in the wintering sector and lower breeding success (Desprez et al., 2018) (Figure S6b). This is the only relationship through which the effect of climate is mediated by a functional trait [**bin**].

SST* during winter and during the breeding season both affect the probability to successfully raise a chick for inexperienced breeders

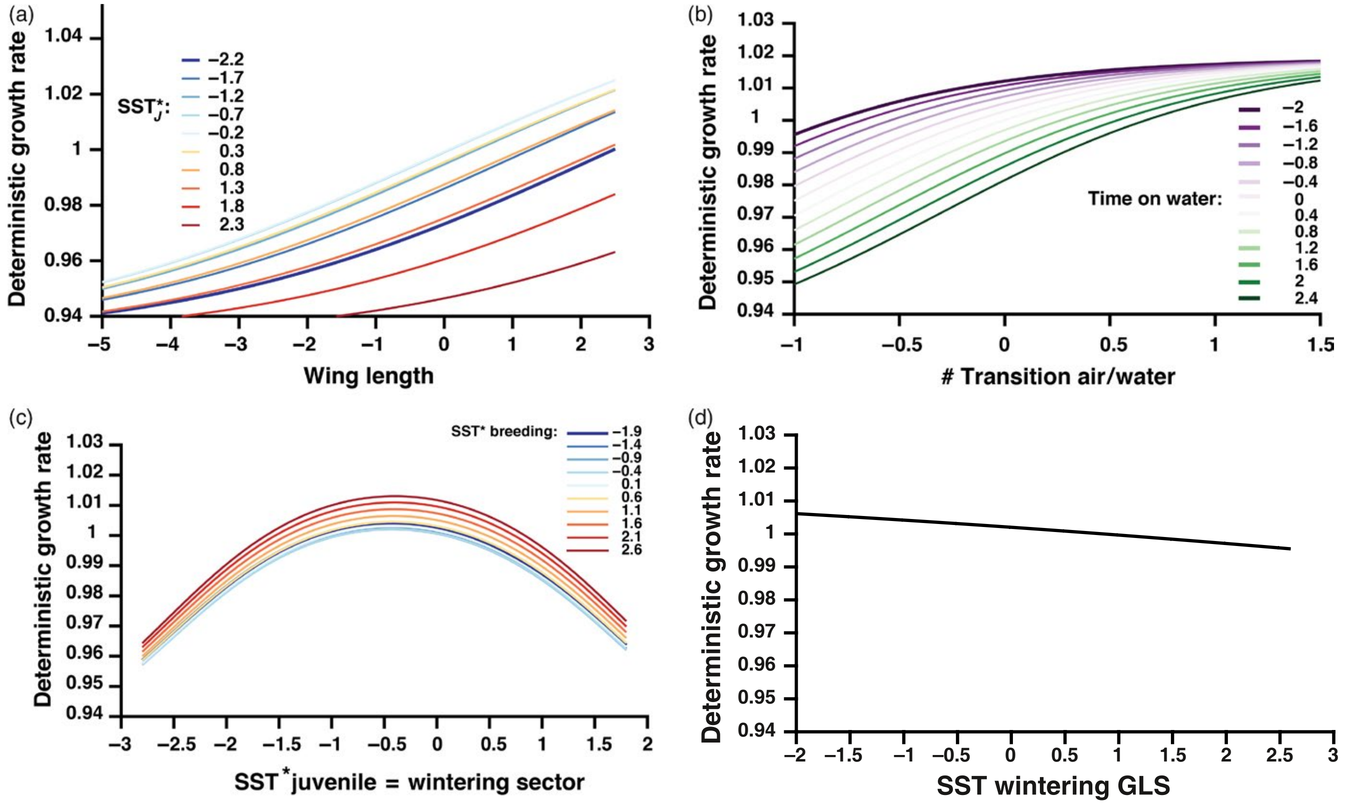


FIGURE 3 Impact of sea surface temperatures (SST) and functional traits on the deterministic population growth rate of black-browed albatross breeding at Kerguelen Island. SST is expressed as a standard score relative to the time period 2006–2013. Each figure shows a combination of variables varying over their observed range, while the other variables not shown are set to their mean. (a) Is the effect of wing length (*x*-axis) and SST* in the juvenile sector (colour lines). (b) Is the impact of the number of daily transitions between air and water (#$T_{a/w}$ *x*-axis) and the percentage of daily time spent sitting on the water Time$_w$ (colour lines). (c) Is the effect of SST* in the juvenile sector equal to SST* in the adult non-breeding sector during the wintering period (*x*-axis) and SST* during the breeding season (colour lines). (d) Is the impact of SST^G during the wintering season

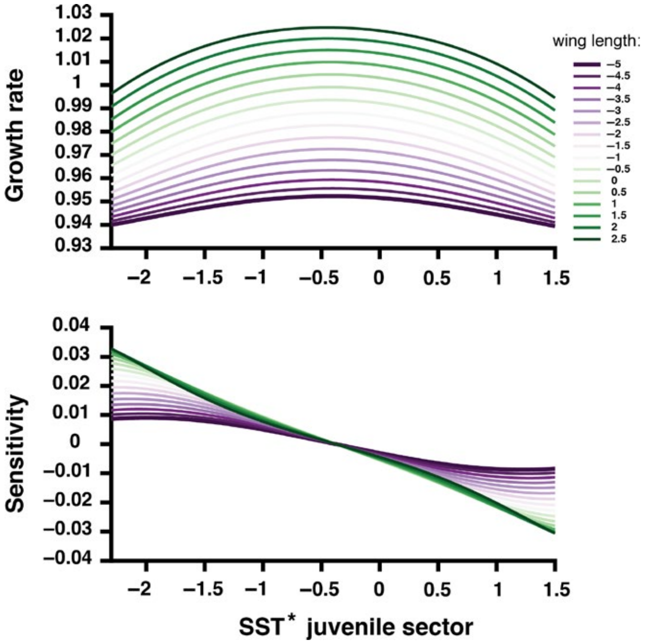


FIGURE 4 (Top panel) Impact of sea surface temperatures in the juvenile sector (SST^*_J, *x*-axis) and wing length (coloured lines) on the deterministic population growth rate of black-browed albatross breeding at Kerguelen Island. SST^*_J and wing length are standard scores. (Lower panel) The sensitivity of the population growth rate λ with respect to SST^*_J in the juvenile sector. Other climate variables and functional traits are fixed to their mean value, except the SST* during winter which is equal to SST^*_J

(γ_5, [**c**] and [**e**], Figure S6c) and the probability to breed for experienced breeders (β, [**d**] and [**f**], Figure S7). γ_5 are maximized at cold SST* in the wintering sector and decline at warmer values. β are maximized at SST* in the wintering sector cooler than the 2006–2013 average and decline at warmer or lower values. Although the relationships are nonlinear, overall warmer SST* in the breeding sector increase γ_5 and β.

3.2 | Effect of climate and functional traits on population growth rate

The population growth rate increases when the wing length of individuals is larger (Figure 3a). This effect is mediated by SST* in the juvenile sector, with a larger wing length effect observed for optimal SST* values (Figure 3a). For example, a population of individuals with small wing length living in an environment characterized by the coolest or warmest $\mathrm{SST}^*_J = \mathrm{SST}^*_W$ is predicted to decline dramatically by ~6.3% per year). A population of individuals with large wing length living in an environment characterized by optimal SST* is predicted to increase up to 2.5% per year.

The population growth rate decreases when the percentage of daily time spent sitting on the water increases, and it increases when the number of daily transitions between air and water increases (Figure 3b). These relationships are nonlinear, and for high values of the number of transition air/water and low values of time sitting on the water, the effect of these foraging variables is smaller. For a population of individuals spending a high proportion of their time on the water, with few take-offs and landings (i.e., low foraging activity), the population growth rate is predicted to decline up to 5.3% per year. However, for a population of individuals with high foraging activity (high $\#T_{a/w}$ low Time_w), the population growth rate is predicted to increase by up to 1.8% per year.

The population growth rate is maximized at optimal $\mathrm{SST}^*_J = \mathrm{SST}^*_W \simeq -0.4$ in the wintering season and declines at higher or lower values (Figure 3c). For example, for warm SST* during the breeding season (SST* = 2.6), the population growth rate is predicted to increase by ~1.3% per year for a range of winter $\mathrm{SST}^*_J = \mathrm{SST}^*_W$ of [−0.6 −0.2]. Although the relationship is nonlinear, overall warmer SST* in the breeding season slightly increases the population growth rate. The effect of SST^G during the wintering season on the population growth rate is small (Figure 3d).

3.3 | Sensitivity analysis

The sensitivity of λ to any variable (climate, functional trait or demographic rate) is a local result that depends on specific values of all the other parameters (climate variables and functional traits) that determine the demographic rates. For example, Figure 4 details the sensitivity of λ to SST^*_J in the juvenile sector as function of two influential variables: wing length and SST^*_J. The population growth rate is maximized at $\mathrm{SST}^*_J \simeq -0.4$ with a wide range of values almost equal to this optimum. Hence, the sensitivity of λ to SST^*_J is close to zero at these optimal SST^*_J. From coolest SST^*_J to the optimum, λ increases while the opposite pattern occurs from the optimum to warmest SST^*_J. Thus, the sensitivity of λ to SST^*_J is positive for cooler SST^*_J, while it is negative for warmer SST^*_J. The concavity of this relationship increases when the wing length of individuals is larger, and as a result, the sensitivities are larger in a population of larger individuals (green lines on Figure 4). The same pattern is observed qualitatively regardless of the values of other climate variables and functional traits: SST^G (Figure S8); SST* during breeding (Figure S9); and foraging activity (Figure S10).

Confronted with such a range of interacting parameter values, we calculated results for a set of 10^7 samples of the parameter space, calculating the sensitivity of λ for each. We summarize the results with bar figures showing the 90% and 50% envelopes of absolute sensitivity of λ to each parameter. The distribution of these sensitivities is detailed in Figures S11–S15. To infer general pattern on which traits the population growth rate is mostly sensitive, we compare the distribution of the absolute sensitivity of λ to a variable. For clarity, we refer to the sensitivity of λ to a variable instead of detailing its distribution in the following paragraphs.

As expected for a long-lived species, λ is mostly sensitive to adult survival of experienced breeders (Figures 5 and 1: pathway [**o**]). The sensitivity of λ to the first-year survival [**l**] is larger than the sensitivity of λ to survival of inexperienced [**p**], and breeding and success probabilities [**r**,**n**,**q**]. The sensitivity of λ to breeding and success probabilities are larger for experienced breeders than pre-breeders or inexperienced breeders.

The sensitivity of λ to the number of air/water transitions is larger than the sensitivity of λ to other functional traits (Figures 6 and S14).

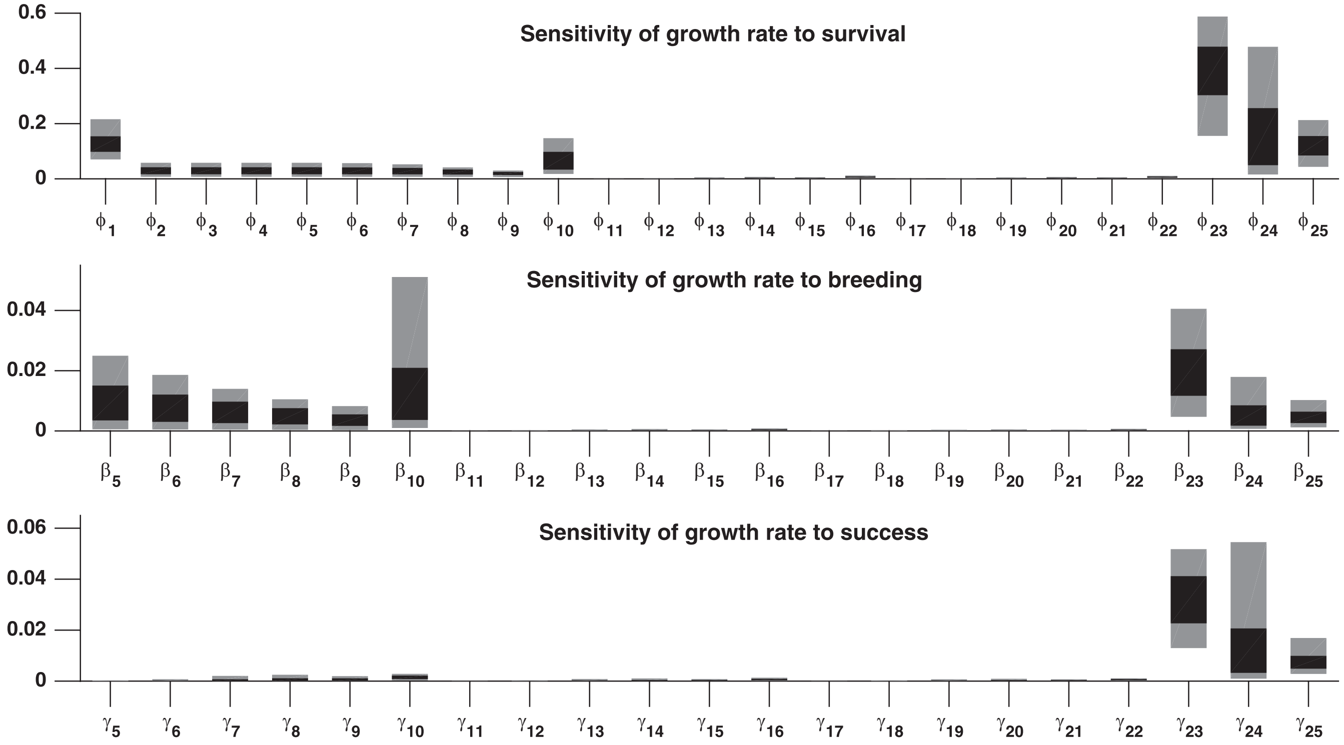


FIGURE 5 The sensitivity of the population growth rate λ with respect to demographic rates. Panels show, respectively, the following: (higher)—the sensitivity of λ to survival probabilities ϕ_j for the 25 states *j* of the life cycle (Figure 2); (intermediate)—the sensitivity of λ to breeding probabilities β_j; and (lower)—the sensitivity of λ to breeding success probabilities γ_j. The bar shows the range of sensitivity values to each demographic parameter, with the grey and black areas representing the 90% and 50% envelope of the 10^7 samples of the parameter space. Figures S11–S13 detail the distribution of these sensitivities

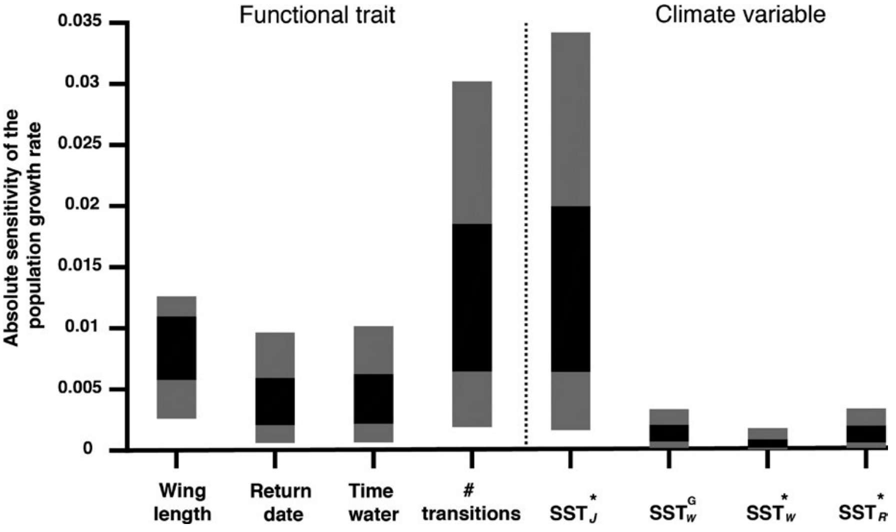


FIGURE 6 The sensitivity of the population growth rate λ with respect to climate and to functional trait. The bar shows the range of absolute sensitivity values to each parameter, with the grey and black areas representing the 90% and 50% envelope of the 10^7 samples of the parameter space. Figures S14 and S15 detail the distribution of these sensitivities

Among foraging variables, the sensitivity of λ to the number of air/water transitions is larger because the sensitivity of the success probabilities to this trait (pathway [**k**] on Figure 1) is larger than the sensitivity of the success probabilities to other foraging traits ([**i**] and [**j**], Figure S16).

The sensitivity of λ to the number of transitions air/water is larger than the sensitivity of λ to wing length (Figure 6), despite the fact that the sensitivity of λ to the breeding success is smaller than the sensitivity of λ to first-year survival ([**n**] < [**l**], Figure 5). Indeed, the sensitivity of the breeding success probabilities γ_i to the number of air/water transitions [**k**] is much larger than the sensitivity of ϕ_1 to wing length ([**g**], Figure S16).

The sensitivity of λ to the SST in the juvenile sector is potentially much larger than the sensitivity of λ to other climate variables (Figure 6), despite the sensitivity of the demographic rates to SST during the breeding season being relatively comparable to the sensitivity of the first-year survival to the SST in the juvenile sector ([**a**] vs. [**e,f**], Figure S17). This pattern occurs because the sensitivity of λ to the first-year survival is much larger than the sensitivity of λ to the breeding and success probabilities ([**l**] > [**q**,**r**], Figure 5).

The sensitivity of λ to the SST recorded by GLS is small because both the sensitivity of the breeding success probabilities to the SST recorded by GLS ([**ib**], Figure S17) and the sensitivity of λ to the breeding success [**n**] are small.

4 | DISCUSSION

Our results suggest that the population dynamics of BBA are driven by the combined effects of climate over various seasons, multiple functional traits and demographic processes across the full life cycle. Sensitivity analyses indicate that changes in sea surface temperature (SST) during late winter cause the biggest changes in the population growth rate through their effect on juvenile survival, except if winter environmental conditions are close to the SST optimum. Among functional traits, adult foraging activity during the pre-breeding period has the biggest impact on population growth rate, but this trait was not influenced by the studied climate variables. Adults appeared to respond primarily to changes in winter climate conditions by modifying their migratory schedule rather than by changing their at-sea foraging activity (Desprez et al., 2018). Indeed, BBA tended to advance their spring migration to pre-breeding grounds when SST^G during winter were warmer, which had a negative impact on their breeding success the following breeding season. However, changes in SST^G affecting their migratory schedule have little impact on the population growth rate. Our analysis illuminated the population consequences of climate changes on demographic rates and functional traits through complex carry-over effects. In addition, it unravelled the important role of the wintering season and juvenile phase of the life cycle, two understudied parts of the life cycle in migratory species.

4.1 | Population response to climate

Juvenile survival, breeding and success probabilities showed nonlinear relationships with SST^* during various seasons, and return date to the pre-breeding grounds was negatively correlated with SST^G during late winter. SST is widely used as an indicator of food availability for marine predators because warmer SST usually results in lower primary productivity in several water masses and oceanographic systems, ultimately reducing prey availability (Constable et al., 2014; Sydeman, Thompson, & Kitaysky, 2012). The relationships between SST and BBA demographic rates are strongly bell-curve-shaped (i.e., concave), which could result from contrasted relationship between SST and primary productivity among areas of the Southern Ocean (Arrigo, van Dijken, & Bushinsky, 2008; Behrenfeld et al., 2006). Alternatively, this bell-curve suggests that the optimal SST for various demographic rates is a balance of trade-offs in the underlying unobserved functional traits and their response to climate (Cornioley et al., 2017).

Black-browed albatross breed at the colony in Kerguelen Islands during October–April and are at sea off Australia in austral winter (May–September). During the breeding season, higher SST over BBA's main foraging grounds around Kerguelen Islands positively affects BBA demographic rates (Nevoux et al., 2007; Pinaud & Weimerskirch, 2002) and thus the population growth rate. Warmer SST during breeding may reflect a change in water masses distribution and an increase in primary productivity in this naturally fertilized region off the Kerguelen Islands, resulting in higher food availability during the breeding season and a higher breeding probability and breeding success (Blain et al., 2007; Nevoux et al., 2007). However, potential changes in SST during the breeding season have little effect on the population growth rate compared to the impact of changes in SST during the wintering season.

The optimal population growth rate predicts a population increase of 5.5% per year for a population of individuals with the largest observed wing length and maximal foraging activity (i.e., large number of landings and take-offs but little time resting on the water) in an environment characterized by warm SST during breeding but intermediate SST during winter. The minimal growth rate (a population decline of 7.8% per year) is predicted for a population of individuals with the smallest observed wing length and minimal foraging activity in an environment characterized by warm SST during winter and cold SST during breeding.

The concave population response to SST during winter (SST_J^*) has important implications for BBA population response to future climate change. Indeed, Pardo, Jenouvrier, Weimerskirch, and Barbraud (2017) found that the historical mean SST (1982–2015) was lower than the optimal SST for this species providing a "climate safety margin" (i.e., difference between optimal and historical climatic conditions). If the mean SST increases, BBA will thus first experience SST that will be more often at or near the optimum range for the species that buffer the negative effects of the extreme warming SST. Here, we found a negative optimal SST and thus no climate safety margin. This pattern occurs because our standard scores are calculated relative to the SST mean over period 2006–2013, which is warmer than the historical SST mean. Furthermore, our results show that the population growth rate will become more sensitive to change in SST_J^* for warmer SST than the recent period 2006–2013 (Figure 4). Hence, if SST increases relative to the recent period, the BBA population is predicted to decline and will do so at a faster rate as the climate warms.

4.2 | Population response to functional traits

The effect of climate changes on BBA population growth rate mediated by their impacts on a functional trait (date of return on pre-breeding ground) are small. Several studies did not identify an effect of phenological changes on population dynamics, despite the strong responses of the timing of life cycle events to climate changes (Reed, Grøtan, Jenouvrier, Sæther, & Visser, 2013; Reed, Jenouvrier et al., 2013; Wilson & Arcese, 2003). However, the direct effects of other BBA functional traits (body size at fledging and adult foraging activity during pre-breeding) on demographic rates exhibit a larger influence on the population growth rate.

In an environment characterized by favourable climate conditions, the BBA growth rate of a population comprising smaller fledging and foragers with low activity is predicted to decline by 7.2% per year, while the growth rate of a population with larger fledging and foragers with intense activity is predicted to increase by 5.5% per year. Interestingly, in an environment characterized by unfavourable climate conditions, a population with larger fledging and foragers with intense activity is still viable (increase of ~1% per year) despite extremely poor environmental conditions. Thus, a population of individuals with the optimal functional traits (large structural size and intense foraging activity) could buffer the negative impact of unfavourable climate conditions.

For BBA, fledglings with longer wings are more likely to survive the first year at sea and to recruit into the population. This result supports the size advantage hypothesis, whereby larger body size confers an advantage in physical competition for resources (Garnett, 1981), with consequently higher juvenile survival and recruitment probabilities (Maness & Anderson, 2013; Rodríguez, van Noordwijk, Álvarez, & Barba, 2016) hence fitness (Marshall, Pettersen, & Cameron, 2018). Seabirds should also maximize the length of flight feathers as opposed to that of weight or other body size structure because flight is required to forage when they reach independence after fledging. Structural size may also be related to an individual's physiology, foraging behaviour, competitive abilities and cognitive capabilities that will influence its performance after fledging (Maness & Anderson, 2013). In addition, wing length may be a proxy of age at fledging as this measure attains an asymptote only at fledging (Ricketts & Prince, 1981; Warham, 1990). In that case, our results are consistent with the timing effect hypothesis; that is, chicks hatching earlier in the season have a longer wing length and thus a greater fitness (Perrins, 1970) and population growth rate. Obviously, the size advantage hypothesis and the timing hypotheses are not mutually exclusive (Maness & Anderson, 2013), and more work is needed to understand the processes by which wing length affects BBA juvenile survival and recruitment, with consequences for the population growth rate.

The population growth rate of BBA is mostly sensitive to the adult foraging activity of individuals, specifically the number of take-offs and landings during the pre-breeding period. More active individuals are likely able to accumulate more energetic reserves in preparation for the breeding season and to raise a chick until fledging during the following breeding season (Desprez et al., 2018). At the population level, only one study, to our knowledge, related population growth to foraging effort (Lewis et al., 2006) and found correlations between population growth rates of several colonies of Cape Gannet (*Morus capensis*) and foraging trip duration, energy gain and body condition during a single breeding season. Making general inferences about the importance of foraging activity for population dynamics requires further studies across a broader range of species and ecosystems.

4.3 | Importance of studying the full life cycle

For long-lived migratory species, population responses to climate are constrained by different climate conditions during the breeding and non-breeding seasons (Small-Lorenz, Culp, Ryder, Will, & Marra, 2013; Thaxter, Joys, Gregory, Baillie, & Noble, 2010). Our results showed that the population dynamic of BBA is driven by processes occurring during multiple seasons (the wintering, pre-breeding and breeding season) through carry-over effects, whereby climate or functional traits that affect an individual in one season also affect its demographic rates during a subsequent season (Harrison, Blount, Inger, Norris, & Bearhop, 2011; Norris & Marra, 2007). Changes in SST during the breeding season have little impact on the population growth rate. However, the population growth rate is highly sensitive to both winter climate conditions and foraging activity during pre-breeding season. For adults, winter climate conditions and foraging activity during pre-breeding season have large carry-over effects on the breeding and success probabilities during the next breeding season. Carry-over effects of winter climate conditions on functional traits (e.g., body conditions) and reproductive performance during the successive breeding season have been reported in several species (Barbraud & Weimerskirch, 2001; Inger et al., 2010). Carry-over effects have potentially large impacts on populations (Harrison et al., 2011), and it is thus very difficult to draw general conclusions about which season of the life cycle is the most critical for population dynamics without analyses integrating the complete life cycle (Sæther & Engen, 2010).

While changes in adult survival cause the largest effects on BBA population growth rates, our model selection results indicated that adult survival was relatively constant through time (Supporting Results). For long-lived species, it is well established that temporal variation in adult survival is buffered against environmental variations (Gaillard & Yoccoz, 2003; Sæther & Bakke, 2000). For these species, the demographic rates of young individuals are usually highly variable and more likely influenced by climate variations than the one of adults (Fay, Weimerskirch, Delord, & Barbraud, 2015; Oro, Torres, Rodríguez, & Drummond, 2010). We found that BBA population growth rate is mostly sensitive to a change in winter SST that impacts juvenile survival. There is increasing evidence that during the first year at sea, juvenile seabirds experience a high mortality (Fay et al., 2015; Oro et al., 2010), as documented in other taxa (Baron, Le Galliard, Tully, & Ferrière, 2010; Gaillard et al., 1997; Ozgul, Armitage, Blumstein, & Oli, 2006). Due to their inexperience and potentially incomplete growth, young individuals may exhibit lower foraging efficiency relative to that of adults (Enstipp et al., 2017; Orgeret, Weimerskirch, & Bost, 2016). Indeed, in other seabirds, the development of tracking technology has revealed lower performance of young individual in flying and diver activity during foraging or migration trips (Harel, Horvitz, & Nathan, 2016; Orgeret et al., 2016; Rotics et al., 2016). The important direct effect of SST on juvenile survival is probably mediated by unknown/unmeasured functional traits, and perhaps foraging efficiency since adult foraging activity is the trait to which the population growth rate is mostly sensitive.

4.4 | Model considerations

Our analysis is based on a set of traits, which define a set of vital rates, which in turn define a population growth rate (among other things). This makes the traits equivalent to what are often referred to as "lower-level" parameters in a demographic model: quantities that determine the transition and fertility terms that appear in the population projection matrix.

An extension of these results would incorporate the trait values themselves into the state space of the population model, to create a stage × trait- or age × trait-structured model. The population at any time would then be composed of a mixture of individuals with different trait values, experiencing the vital rates associated with their traits in the environment of the moment (e.g., Caswell, 2014; Hartemink, Missov, & Caswell, 2017, in which the trait is frailty).

In such an analysis, traits might be fixed over the lifetime of the individual, as wing length at fledging clearly is. Or, they might be dynamic, changing over the individuals lifetime according to a set of age- or stage-dependent transition matrices (e.g., Caswell, 2012; Caswell & Salguero-Gómez, 2013; for a general methodology see Caswell, de Vries, Hartemink, Roth, & van Daalen, 2018). Foraging behaviours, for example, are not necessary static traits and may change over the lifetime of an individual. Generally, seabirds are spatially consistent in their foraging behaviour, returning to the same site from one foraging trip to another (Patrick et al., 2014; Weimerskirch, 2007). However, they show a certain amount of plasticity over time as an adaptive response to energetic requirements that differ over the breeding cycle and to changes in oceanic variability. In BBA within a year, individuals, especially males, show a high degree of repeatability in their foraging trips, with important fitness consequences: individuals that are more consistent in their foraging behaviours have a higher breeding success (Patrick & Weimerskirch, 2014a). Between years, there is little information on repeatability in foraging behaviour, but BBA has the ability to adjust their foraging behaviour by increasing foraging range when condition are poorer (Patrick & Weimerskirch, 2014b).

Incorporating the dynamics of individual transitions among trait categories would require a great deal of very detailed longitudinal individual data, which are not available yet for the BBA.

5 | CONCLUSIONS

This study simultaneously quantified the relative effects of climate variables, functional traits and demographic rates on the population dynamics of a long-lived species and unravelled complex underlying mechanisms of a population response to climate change. Each population response to climate effects reflects the unique combination of meaningful climate factors and species life-history traits (demographic rates and functional traits) across different seasons and phases of the life cycle. Several studies have proposed some general biological traits or characteristics inherent to vulnerability of particular species to climate change. Notwithstanding, a robust conclusion requires the consideration of the complete life cycle and assessing the sensitivity of multiple pathways by which climate affects population.

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AUTHORS' CONTRIBUTIONS

S.J., C.B. and H.W. conceived the ideas; S.J. and H.C. conceived the methodologies; C.B. and H.W. obtained the funding for fieldwork; C.B., H.W. and K.D. collected the data; K.D. managed the demographic database and managed and analysed the GLS data; S.J. and H.C. obtained the funding for the demographic analyses; S.J. and M.D. designed the life cycle; M.D. performed the statistical analysis to parametrize the life cycle with input from R.F. and S.J.; S.J. developed and analysed the matrix model and performed the sensitivity analysis; S.J. led the writing of the manuscript; and S.J. and M.D. wrote the Supporting Information. All authors contributed to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data for this publication are available online at the Dryad Digital Repository: https://doi.org/10.5061/dryad.h5vk5 (Jenouvrier et al., 2018).

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