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Contrasted demographic responses facing future climate change in Southern Ocean seabirds

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Summary

1. Recent climate change has affected a wide range of species, but predicting population responses to projected climate change using population dynamics theory and models remains challenging, and very few attempts have been made. The Southern Ocean sea surface temperature and sea ice extent are projected to warm and shrink as concentrations of atmospheric greenhouse gases increase, and several top predator species are affected by fluctuations in these oceanographic variables.

2. We compared and projected the population responses of three seabird species living in subtropical, sub-Antarctic and Antarctic biomes to predicted climate change over the next 50 years. Using stochastic population models we combined long-term demographic datasets and projections of sea surface temperature and sea ice extent for three different IPCC emission scenarios (from most to least severe: A1B, A2, B1) from general circulation models of Earth's climate.

3. We found that climate mostly affected the probability to breed successfully, and in one case adult survival. Interestingly, frequent nonlinear relationships in demographic responses to climate were detected. Models forced by future predicted climatic change provided contrasted population responses depending on the species considered. The northernmost distributed species was predicted to be little affected by a future warming of the Southern Ocean, whereas steep declines were projected for the more southerly distributed species due to sea surface temperature warming and decrease in sea ice extent. For the most southerly distributed species, the A1B and B1 emission scenarios were respectively the most and less damaging. For the two other species, population responses were similar for all emission scenarios.

4. This is among the first attempts to study the demographic responses for several populations with contrasted environmental conditions, which illustrates that investigating the effects of climate change on core population dynamics is feasible for different populations using a common methodological framework. Our approach was limited to single populations and have neglected population settlement in new favourable habitats or changes in inter-specific relations as a potential response to future climate change. Predictions may be enhanced by merging demographic population models and climatic envelope models.

Key-words: climate change, demography, IPCC emission scenarios, multi-state capture–recapture, population dynamics, sea ice concentration, sea surface temperature, seabirds, Southern Indian Ocean, stochastic matrix population models

Introduction

A large amount of evidence now suggests that recent global change has had impacts on a range of ecological systems

(Stenseth *et al.* 2002; Walther *et al.* 2002; IPCC 2007a) and climate impacts are apparent at several levels of biological organization (McCarty 2001). At the individual level, recent meta-analyses revealed consistent climate-related shifts, or 'fingerprints', such as an overall advancement of species phenology (Parmesan 2007) or polewards changes in geographic

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ranges (Thomas & Lennon 1999; Parmesan 2003). At the population level, changes have often been mediated through modification of local and regional environment conditions that ultimately influence life history traits such as survival and breeding performance (Saether *et al.* 2000; Sillett, Holmes & Sherry 2000; Barbraud & Weimerskirch 2001a; Croxall, Trathan & Murphy 2002). Although long-term ecological monitoring has improved our understanding of how species have coped with recent climate variability, only predictions of responses to future climate change would improve our ability to effectively assess its impact and mitigate and adapt to its effects (Berteaux *et al.* 2006).

Climate envelope models have been used to predict changes in each species' geographic range under future climatic conditions by inferring its environmental requirements from localities and habitats currently occupied (i.e. Erasmus *et al.* 2002; Thomas *et al.* 2004; Thuiller 2004; Thuiller *et al.* 2005). Recently, Guisan & Thuiller (2005) and Keith *et al.* (2008) stressed that climate envelope models could be improved by relating explicitly to population dynamics theory and models.

Predicting demographic responses to projected climate change remains challenging because one must (i) hold long-term demographic monitoring to quantify the effects of climate variation on vital rates, (ii) ascertain several scenarios of climatic conditions to consider the uncertainties of future climate change and (iii) integrate these climatic scenarios into population models that translate the effect of climate on demographic changes at least at a phenomenological level (Gotelli & Ellison 2006). To date, most demographic studies have focused on the first step since they have essentially linked recent climate change with survival rates and reproductive performances of single species in a common biome (Saether *et al.* 2000; Sillett, Holmes & Sherry 2000; Barbraud & Weimerskirch 2001a; Croxall, Trathan & Murphy 2002; Fraser & Hofmann 2003; Jenouvrier, Barbraud & Weimerskirch 2005; Le Bohec *et al.* 2008; Rolland, Barbraud & Weimerskirch 2008). To our knowledge, very few studies (Frederiksen *et al.* 2004; Jenouvrier *et al.* 2009) have attempted to forecast population level responses to long-term, future climate changes for an ensemble of ecologically similar species.

In this study, we compare and contrast the demographic responses of three southern seabird species living in different biomes in the Indian Ocean to predicted climate change. These species are the subtropical Amsterdam albatross (*Diomedea amsterdamensis*), Roux *et al.*, breeding on Amsterdam Island, a sub-Antarctic population of the black-browed albatross (*Thalassarche melanophrys*), Temminck, breeding at Kerguelen Island and the Antarctic snow petrel (*Pagodroma nivea*), Forster, breeding in Terre Adélie. We first quantified the impact of two key parameters affecting the abundance and distribution of trophic resources in the Southern Ocean such as sea surface temperature and sea ice on demographic parameters of each species over time. We then formulate stochastic population models to estimate population level responses of each species to the changes in sea surface temperature and sea ice during the next 50 years

as predicted by under different scenarios of climate change in each biome.

Materials and methods

STUDIED SPECIES

The Amsterdam albatross is a large albatross (6–7 kg) endemic of Amsterdam Island (37°49'S, 77°32'E; Fig. 1) where the unique breeding population was followed between 1983 and 2006. Breeding period lasts almost 1 year and this species is a biennial breeder that skips at least 1 year after a successful breeding season (Jouventin, Martinez & Roux 1989). With an overall population size estimated at less than 200 birds including about 80 mature individuals (Rivalan *et al.* 2010), the Amsterdam albatross is likely one of the rarest birds worldwide (Croxall & Gales 1998). Although its diet is poorly documented, it is thought to consist of fish, squid and crustaceans (Cherel & Klages 1998).

The black-browed albatross is a medium-size albatross (3–4 kg) inhabiting the Southern Ocean and breeding on sub-Antarctic islands during the austral summer (Marchant & Higgins 1990). At Kerguelen, this annual breeder forages on the northeast and southeast regions of the peri-insular Kerguelen shelf in summer (Pinaud & Weimerskirch 2002), feeding on fish and squids (Cherel, Weimerskirch & Trouvé 2000). In winter, birds migrate off southern Australia (Weimerskirch *et al.* 1985; Cherel, Weimerskirch & Trouvé 2000). Demographic data were collected from 1981 to 2006 on the colony of Cañon des Sourcils Noirs, Kerguelen Island (48°24'S, 68°218'E; Fig. 1) where *c.* 200 nests were monitored annually in a colony of *c.* 1000 breeding pairs (Rolland, Barbraud & Weimerskirch 2008).

Snow Petrels are annual breeders that forage over Antarctic pack-ice for krill and fish in summer and for a wider spectrum of prey in winter in close association with sea ice (Ainley, O'Connor & Boekelheide 1984; Ridoux & Offredo 1989). Demographic data were obtained from a 40-year study (1968–2006) carried out on Pointe Géologie, Terre Adélie, Antarctica (66°40'S, 140°01'E; Fig. 1) This colony hosts about 800–1000 breeding pairs (Micol & Jouventin 2001), among which *c.* 200 were monitored annually. All three species were annually monitored through census and individual identification by capture-recapture sampling [see details about the monitoring methodology in Weimerskirch, Brothers & Jouventin (1997) and Rivalan *et al.* (2010) for Amsterdam albatross, Nevoux, Weimerskirch & Barbraud (2007) and Rolland, Barbraud & Weimerskirch (2008) for black-browed albatross, and Chastel, Weimerskirch & Jouventin (1993) and Barbraud & Weimerskirch (2001b) for snow petrels].

ENVIRONMENTAL COVARIATES: PAST TO PRESENT CLIMATIC DATA

Based on previous studies (Barbraud & Weimerskirch 2001a,b; Jenouvrier, Barbraud & Weimerskirch 2005; Nevoux, Weimerskirch & Barbraud 2007; Rolland, Barbraud & Weimerskirch 2008), we tested the effect of climatic covariates on the demographic parameters. For Amsterdam and black-browed albatrosses, we considered the sea surface temperature (SST) because it is known to be linked to the vertical mixing of the water masses, controls the quality of the physico-chemical environment available for the primary production (Wilson & Adamec 2002), and has been used in many studies (e.g. Inchausti *et al.* 2003). For the snow petrel, we considered instead sea ice concentration (SIC; Jenouvrier, Barbraud & Weimerskirch 2005)

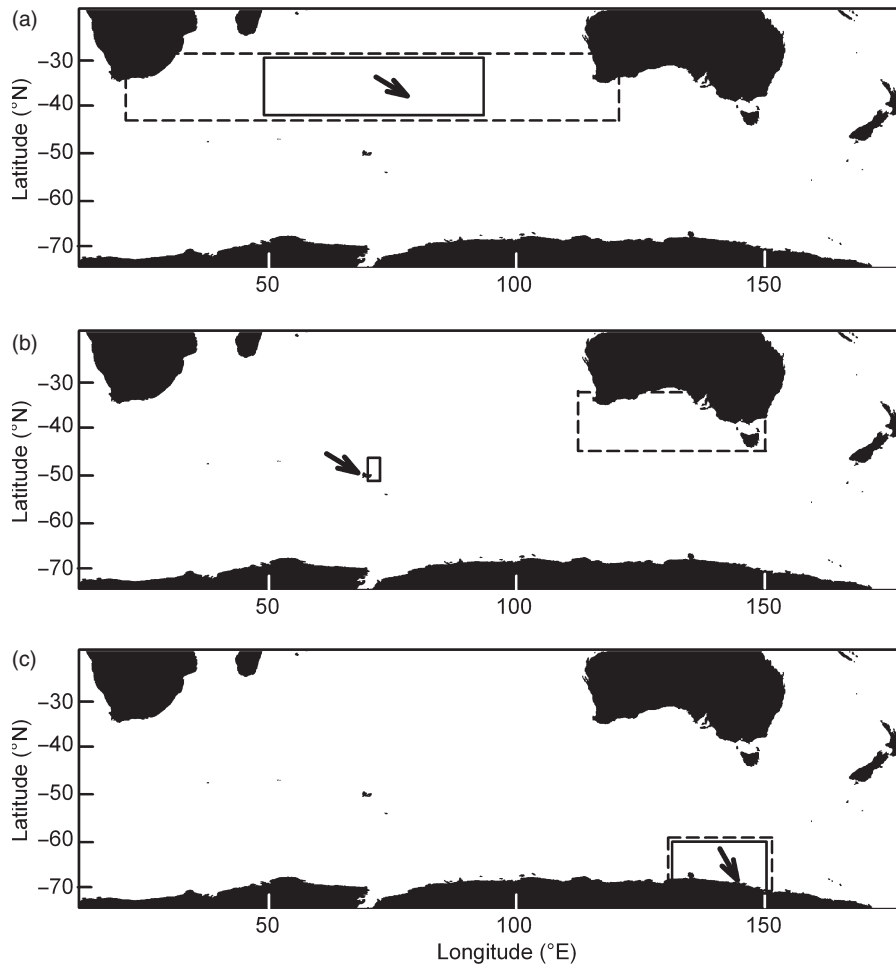


Fig. 1. Distribution area of (a) the Amsterdam albatross, (b) the black-browed albatross and (c) the snow petrel in both their breeding (solid lines) and wintering grounds (dashed lines), derived from satellite tracking, band recoveries and at sea observations. Arrows indicate the breeding colonies where the demographic studies were conducted. For the snow petrel breeding and wintering grounds entirely overlap.

because its foraging largely depends on sea ice cover (Ainley, O'Connor & Boekelheide 1984). We did not consider large-scale climatic indices such as the Southern Oscillation Index or the Indian Ocean Dipole because of the difficulties in predicting their future values from atmosphere-ocean coupled models (Saji, Xie & Yamagata 2006; IPCC 2007b; Leloup, Lengaigne & Boulanger 2008). All the selected covariates were averaged over areas exploited during the breeding period and non-breeding periods (Table 1) and expressed as annual anomalies (SSTa and SICa) from their seasonal averages of 1982–2006. For the Amsterdam albatross, we used the winter SSTa of the previous year to investigate breeding transition from breeding states, and the winter SSTa in the wintering ground of the current year to investigate breeding transition from non-breeding states. Climatic data were available at the International Research for Climate and Society (<http://iridl.ldeo.columbia.edu>) from 1982 onwards. Seasonal SIC data were averaged over the area covered by ice, excluding regions with < 15% ice concentration, for the sector 130–150°E.

ENVIRONMENTAL COVARIATES: PROJECTED CLIMATIC DATA

Projected climatic data from 2007 to 2057 were obtained from the atmosphere ocean General Circulation Models (GCMs) of the 4th

Assessment Report of the IPCC (2007b). These climatic models provide credible simulations of climate down to continental scales and over seasonal to decadal time scales (Randall *et al.* 2007). These GCMs are used to simulate future climatic conditions under different IPCC emission scenarios (A1, A2, B1 and B2) of greenhouse gases emission. The projected data for SST and SIC were available at <http://www-pcmdi.llnl.gov/>. We selected GCMs with monthly simulations under emission scenarios A1B, A2 and B1 (simulations under emission scenario B2 were not available), leading to a total of 18 climatic models per emission scenario (see Table S1), yielding 54 climatic scenarios.

Rather than focusing on a single climatic model or a single greenhouse gases emission scenario, we used the average of an ensemble of different models under a climate scenario (Beaumont, Hughes & Pitman 2008). This approach filters out biases of individual models, retaining only those errors that are generally pervasive, and it is thought to compare better with the observed climatology than individual models (Randall *et al.* 2007). Climate models widely differ in their ability to simulate current conditions, and when projecting species distribution or abundance under future climates is it important to identify the most appropriate climate models to be used (Beaumont, Hughes & Pitman 2008). Climatologists agree that no single best climate model exists and recognize that if a climate model is unable to simulate current

Table 1. Specification of the seasonal periods, seasonal activities (A: arrival on colonies; L: laying; I: incubating; R: rearing; F: fledging; W: wintering) and the associated climatic covariates used in this study for Amsterdam (AA) and black-browed albatrosses (BBA), and snow petrels (SP). Anomaly^a_b refers to the anomaly (SST for AA and BBA, and SIC for SP) in foraging zone *a* (NB: non-breeding; B: breeding) during season *b* (w: winter; sp: spring; su: summer; au: autumn). Note that breeding failure can occur at each stage I, R or F

Year	Months	Season	Seasonal activities			Foraging	
			AA	BBA	SP	Zone	Covariates
<i>t</i> - 1	Jul-Sep	Winter	R	W-A	W-A	Non-breeding	Anomaly ^{NB} _{w-}
<i>t</i> - 1	Oct-Dec	Spring	R-F	L-I	L-I	Breeding	Anomaly ^B _{sp-}
<i>t</i>	Jan-Mar	Summer	A-L	R-F	R-F	Breeding	Anomaly ^B _{su}
<i>t</i>	Apr-Jun	Autumn	I	W	W	Non-breeding	Anomaly ^{NB} _{au}
<i>t</i>	Jul-Sep	Winter	R	W-A	W-A	Non-breeding	Anomaly ^{NB} _w
<i>t</i>	Oct-Dec	Spring	R-F	L-I	L-I	Breeding	Anomaly ^B _{sp}

In AA, wintering is year-round after a successful breeding attempt or until the next January for failed breeders.

conditions, less confidence can be placed in its ability to simulate future conditions (Giorgi 2005). Testing current simulated climate variables against current observed climate variables is an important part of climate model evaluation (Randall *et al.* 2007; Beaumont, Hughes & Pitman 2008). In order to identify the most appropriate climate models in the regions of interest for each species, we thus compared the mean of the current with the simulated SSTa and SICa from 1982 to 1999 in each region of interest (Beaumont, Hughes & Pitman 2008). It is known that there are systematic biases in most models' simulations of the Southern Ocean where our study takes place. More precisely, there is a warm bias in sea surface temperatures, there are wide differences among the single models for sea ice extent projections, and simulated sea ice extent may strongly deviate from observed values for individual climate models (Randall *et al.* 2007). However, there is strong evidence that the multi-model average outputs are often in better agreement with observations than any of the outputs simulated by the individual models (Randall *et al.* 2007). Consequently, models that provided a difference greater or smaller than 5% compared with the current mean were discarded from further analyses. We used the observed SST and SIC for the period 1982–1999 as a reference climate, available at the International Research for Climate and Society (<http://iridl.ldeo.columbia.edu>). By using a multi-model average approach and selecting climate models that best match current conditions we therefore removed biases caused by poor climate models.

ESTIMATION OF DEMOGRAPHIC PARAMETERS

Previous studies have already estimated several demographic parameters in our three species (Weimerskirch, Brothers & Jouventin 1997; Jenouvrier, Barbraud & Weimerskirch 2005; Rolland, Barbraud & Weimerskirch 2008; Rivalan *et al.* 2010). We used these estimates and updated the time series with the most recent years when necessary. Breeding success, defined as the proportion of eggs that fledged a chick, was analysed using Generalized Linear Mixed Models (GLMM) with binomial error distribution (macro Glimmix SAS Institute; Littell *et al.* 2006). Environmental covariates were included as fixed effects and individual identity (i.e. ring number) was introduced as a random effect.

We used multistate capture–recapture (MS CR) modelling with unobservable states (Kendall & Nichols 2002) to estimate probabilities of adult survival, juvenile survival, breeding and recruitment for the three species (see Appendix S1, Table S2).

MODELLING THE POPULATION DYNAMICS

We formulated a pre-breeding census matrix population model that mixed age and stage classes and assumes equal survival probabilities for males and females (Caswell 2001; Arnold, Brault & Croxall 2006). Males and females approximately share equally the breeding duties in these three species as in many Procellariiformes species (Warham 1990) and thus we did not expect major differences in vital rates between both sexes. Each matrix population model consisted in *n* juvenile age-classes (*n* = age at recruitment - 2), one pre-breeding stage-class and two state-classes according to breeding status (Fig. 2, see also Appendix S2). Given the small population size of the Amsterdam albatross, we included demographic stochasticity by sampling the number of individuals in each age-stage class from a binomial distribution (Akçakaya 1991). We did not include demographic stochasticity for the populations of the other two species because of their large sizes. Environmental stochasticity was included differently depending on whether there was a statistically significant effect of climatic covariates (Appendix S2).

The matrix population models were analysed by Monte Carlo simulations (1000 iterations) using package *popbio* (Stubben & Milligan 2007) implemented in program R (R Development Core Team 2007). Initial stage abundances corresponded to the stable age distribution based on the number of breeders actually observed in 2007. From these simulations, we estimated future population changes in abundance and probabilities of decline over the next 50 years.

Results

BREEDING PARAMETERS

Breeding success in the three populations showed significant variation over time in the most recent years (Fig. 3). The mean breeding successes over the monitoring periods were 0.610 (SD = 0.098), 0.673 (SD = 0.010) and 0.540 (SD = 0.08) for the Amsterdam, black-browed albatrosses and snow petrels respectively.

Analyses of climatic and individual effects on the annual breeding success are provided in Table 2. In Amsterdam albatrosses, SSTa averaged over the breeding zone during the previous spring and during the current summer and

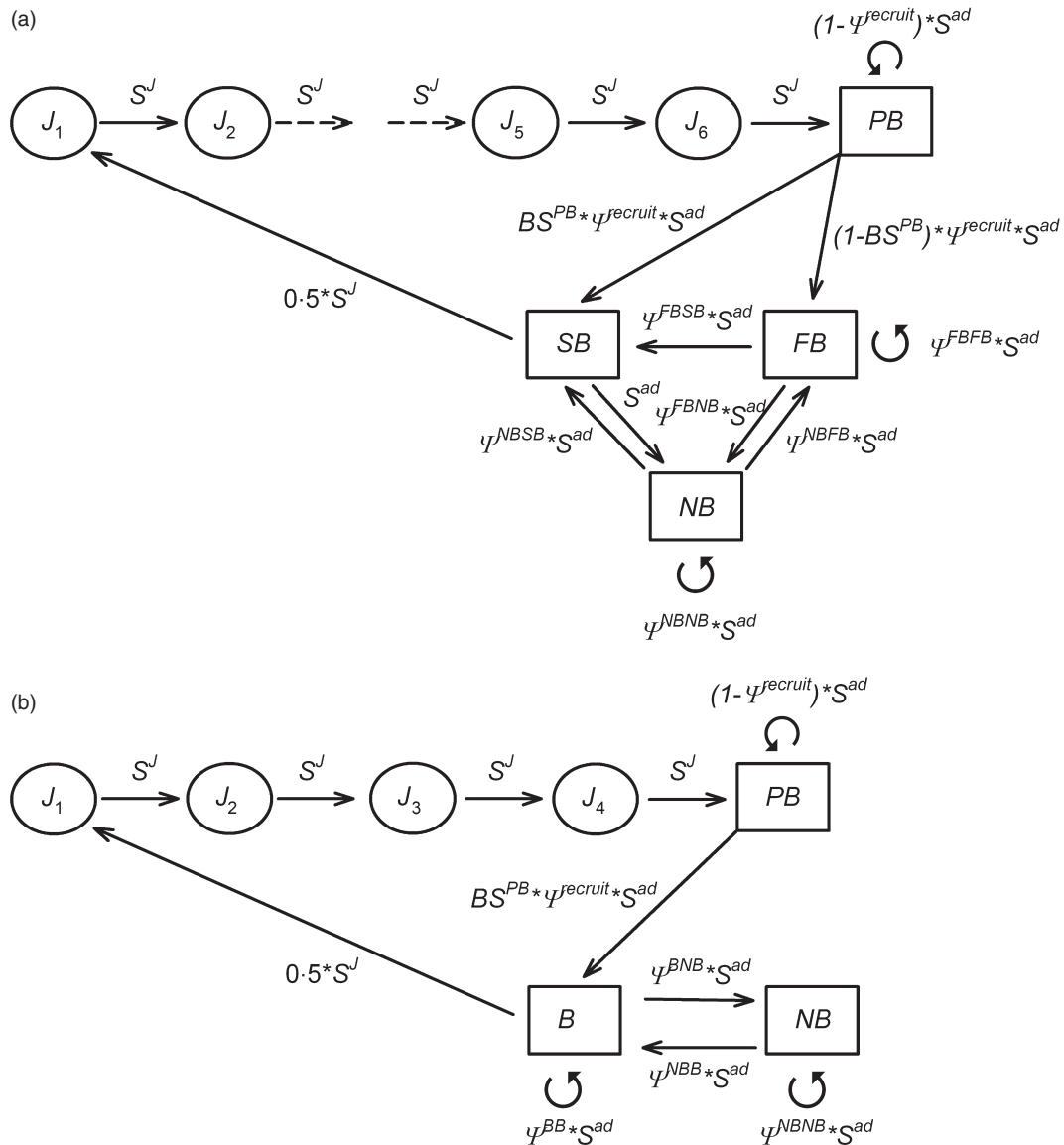


Fig. 2. Lifetime cycle graph for (a) the Amsterdam albatross, (b) the black-browed albatross and the snow petrel. J^i : juvenile of age class i ; PB: pre-breeder; SB: adult successful breeder; FB: adult failed breeder; NB: adult non-breeder; B: adult breeder; S^j : juvenile survival probability; S^{ad} : adult survival probability; $\psi^{recruit}$: recruitment probability into the breeding population; ψ^{rs} : transition probability from state r to state s .

spring were linked to breeding success variations (Table 2). All these three relationships were quadratic thus suggesting that breeding success presented an optimum that decreased for extreme values of SSTa. We also detected a significant individual effect ($Z = 3.823$, $P < 0.001$) that accounted for more than 50% of the total variance in breeding success. For the black browed albatross, we detected a quadratic relationship between breeding success and SSTa averaged over the previous winter and the current summer (Table 2), with individual identity explaining only 21% of the total variance in breeding success ($Z = 4.902$, $P < 0.001$). For the snow petrel, we detected a quadratic relationship between SICa during the summer and breeding success (Table 2), and again a moderate individual effect ($Z = 5.833$, $P < 0.001$) that explained 20% of the total variance in breeding success.

SURVIVAL PROBABILITIES AND BREEDING TRANSITIONS

In Amsterdam albatross, model selection favoured an additive (models 2 vs. 1, see Table S3) time-dependent effect (models 3 vs. 5, Table S3) on capture probabilities and a constant adult survival (Anodev for a temporal trend in adult survival: $F_{1,22} = 1.511$, $P = 0.232$). Breeding probabilities are given in Table S4. For the black-browed albatross and the snow petrel, model selection favoured an additive (models 2 vs. 1, Table S5) time-dependent (models 2 vs. 3, Table S5) trap effect on capture probabilities. Average capture probabilities were 0.681 (SE = 0.035) and 0.615 (SE = 0.009) for black-browed albatross and snow petrel respectively. Model selection led to a constant adult survival probability and a time-dependent survival probability for the

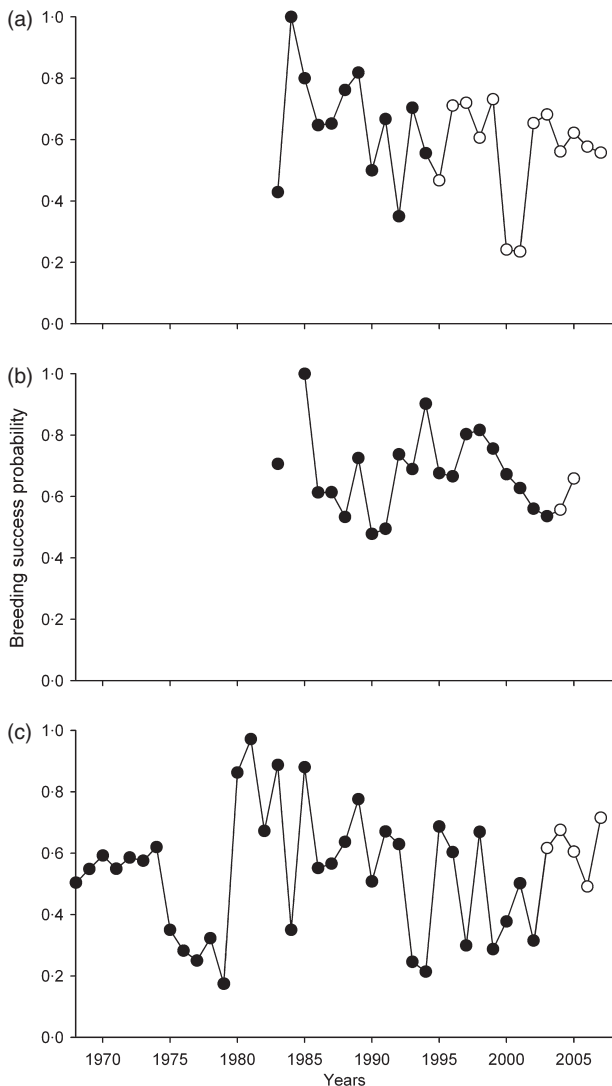


Fig. 3. Breeding success for (a) the Amsterdam albatross, (b) the black-browed albatross and (c) the snow petrel. The most recent years (open circle) complete the historical data (solid circle) provided in Weimerskirch, Brothers & Jouventin (1997), Nevoux, Weimerskirch & Barbraud (2007) and Jenouvrier, Barbraud & Weimerskirch (2005) for Amsterdam, black-browed albatrosses and snow petrels respectively.

black-browed albatross and the snow petrel respectively (models 4 vs. 3, models 2 vs. 4, Table S5). Adult survival probabilities were high and slightly larger for the snow petrel than for black-browed albatross (0.939, SE = 0.002 vs. 0.921, SE = 0.007), and no temporal trend was detected in adult survival probability for either species (Anodev: $F_{1,21} = 0.218$, $P = 0.645$ and $F_{1,37} = 1.576$, $P = 0.217$ respectively). Breeding transitions exhibited a similar pattern in the latter two species, with a higher probability of remaining in the same state between consecutive years (Table S4).

We did not detect any relationship between SSTa, SICa and adult survival probability for either the Amsterdam albatross or the snow petrel (Tables S6 and S7). For the

black-browed albatross, adult survival was quadratically related to spring SSTa in the vicinity of Kerguelen Islands [$\text{logit}(S^{\text{ad}}) = 2.567 + 0.706 \times \text{SSTa} - 1.063 \times \text{SSTa}^2$, quadratic $P = 0.023$, Table S7]. In contrast, we found at least one significant relationship between climatic covariates and breeding probabilities of the three species (Tables S6 and S7). For the Amsterdam albatross, summer SSTa explained a significant part of ψ^{NBSB} variation, whereas the current year's non-breeding SSTa explained a significant part of both ψ^{NBSB} and ψ^{NFBF} (Table S6). SSTa had a significant linear and quadratic relation with the breeding and the current year non-breeding transitions: ψ^{NBSB} linear $P = 9.10^{-4}$, quadratic $P = 0.004$; ψ^{NFBF} linear $P = 8.10^{-4}$, quadratic $P = 0.004$. However, quadratic functions did not explain a significantly greater part of variance than the linear ones (Anodev ψ^{NBSB} $P = 0.895$, ψ^{NBNB} $P = 0.575$). The probability for a non-breeder to become a successful breeder was greater when the current winter SSTa was low ($\text{logit}(\psi^{\text{NBSB}}) = 2.698 - 3.623 \times \text{SSTa}$). On the contrary, the probability for a non-breeder to become a failed breeder decreased with decreasing current winter SSTa [$\text{logit}(\psi^{\text{NFBF}}) = 3.029 + 3.762 \times \text{SSTa}$, Fig. S1]. For the snow petrel and black-browed albatross, breeding transitions were related to wintering conditions (Tables S1 and S7). For the black-browed albatross, the probability of becoming a breeder was quadratically related to the winter SSTa in waters off southern Australia [$P = 0.007$, $\text{logit}(\psi^{\text{NBB}}) = 0.802 + 0.143 \times \text{SSTa} - 4.623 \times \text{SSTa}^2$ and centred on a SSTa = 0.015 or SST = 3.6 °C, Fig. S1]. The probability for black-browed albatross to remain non-breeder was about the unity for extreme values of SSTa in their foraging area (i.e. $|\text{SSTa}| > 1$). For the snow petrel the relationship between the probability to remain breeder and the winter SICa was also quadratic [$P = 0.007$, $\text{logit}(\psi^{\text{BB}}) = 5.517 - 4.093 \times \text{SICa} - 25.408 \times \text{SICa}^2$] and centred on SICa = -1 and with a plateau (i.e. $\psi^{\text{BB}} \geq 90\%$) for SICa ranging from -4.5 to 2.8 (i.e. $67.870^{\circ}\text{S} \leq \text{SIC} \leq 75.100^{\circ}\text{S}$, Fig. S1). For both species, quadratic winter covariates explained almost 40% of the total temporal variation in breeding probability (Table S7).

Regarding the Amsterdam albatross, model selection favoured a model with constant juvenile survival probability, constant capture probability of breeders and constant recruitment probability (model 5, Table S8). Juvenile survival probability was 0.672 (SE = 0.057), i.e. an annual survival of 0.936 from fledging to 7 years of age. Annual recruitment probability, constrained to be constant over years (cf. section Methods), was estimated to 0.370 (SE = 0.056) from 1990 to 2007. For both black-browed albatross and snow petrel, model selection favoured time-dependent capture probabilities and time-dependent juvenile survival probabilities (model 4, Table S8). In the case of the black-browed albatross, cumulative juvenile survival from fledging to 4 years of age ranged from 0.032 to 0.664, i.e. annual survival ranged from 0.564 to 0.934, and annual recruitment probability was 0.122. Cumulative juvenile survival of the snow petrel from fledging to 5 years of age ranged

Table 2. Climatic and individual effects on the annual breeding success for Amsterdam (AA, 1983–2006) and black-browed albatrosses (BBA), and snow petrels (SP) from 1982 to 2006. Test statistics (F - and P -values) are type III, and d.f. (numerator, denominator) for fixed effects were estimated using the Satterthwaite approximation. Variance components plus their SE are shown for random effects. Covariables not tested (–)

Effects	AA			BBA			SP		
	d.f.	F	Slope estimate (SE)	d.f.	F	Slope estimate (SE)	d.f.	F	Slope estimate (SE)
Fixed									
Anomaly ^{NB} _{w-}	1, 618.3	0.38	2.957 (0.711)	1, 5066	0.36	-0.102 (0.168)	1, 5773	2.19	-0.191 (0.129)
Squared anomaly ^{NB} _{w-}	1, 583.5	1.00	-0.548 (0.884)	1, 4909	4.32	-1.395 (0.671)*	1, 5824	0.35	0.276 (0.470)
Anomaly ^B _{sp-}	1, 642.4	2.91	7.179 (7.191)	1, 5083	0.15	0.099 (0.253)	1, 5871	0.33	0.061 (0.106)
Squared anomaly ^B _{sp-}	1, 606.4	29.77	0.439 (0.257)*	1, 4999	0	-0.04 (0.62)	1, 5930	3.10	0.109 (0.157)
Anomaly ^B _{su}	1, 641	0.95	-0.388 (0.071)	1, 4968	5.87	0.31 (0.128)*	1, 6135	0.98	-0.06 (0.061)
Squared anomaly ^B _{su}	1, 597	2.69	0.276 (0.284)	1, 4876	2.98	-0.253 (0.147)*	1, 5900	10.01	-0.233 (0.073)**
Anomaly ^{NB} _{au}	1, 588	9.35	-0.151 (0.092)**	–	–	–	–	–	–
Squared anomaly ^{NB} _{au}	1, 588.2	13.18	-0.89 (0.291)**	–	–	–	–	–	–
Anomaly ^B _{sp}	1, 594	18.37	-0.432 (0.119)**	–	–	–	–	–	–
Squared anomaly ^B _{sp}	1, 619.5	4.88	-1.127 (0.263)*	–	–	–	–	–	–
Random									
Individual identity			1.118 (0.292)			0.250 (0.051)			0.245 (0.042)
Residual			0.851 (0.052)			0.942 (0.020)			0.957 (0.019)

**0.001 ≤ P -value < 0.01, *0.01 < P -value ≤ 0.05.

from 0.030 to 0.870, i.e. annual survival ranged from 0.557 to 0.977. Annual recruitment probability in snow petrels was 0.081 (SE = 0.0095).

CLIMATIC DATA

Annual observed SST in the wintering foraging area of Amsterdam albatrosses (Fig. 4a) ranged from 17.4 °C in 1992 to 17.9 °C in 2000 (mean = 17.6 °C). Foraging waters

used by black-browed albatrosses in the vicinity of Kerguelen Island during spring had high inter-annual variations (Fig. 4b). Spring SST varied from 4.1 °C in 1994 to 5.7 °C in 2001 (mean = 4.7 °C). SST recorded in wintering waters off southern Australia (Fig. 4c) ranged from 12.9 °C in 1996 to 13.9 °C in 2001 (mean = 13.3 °C). All these three areas had similar trends from 1982 to 2006 with mean annual increasing rates equal to 0.091%, 0.100% and 0.131% respectively (Fig. 4a–c).

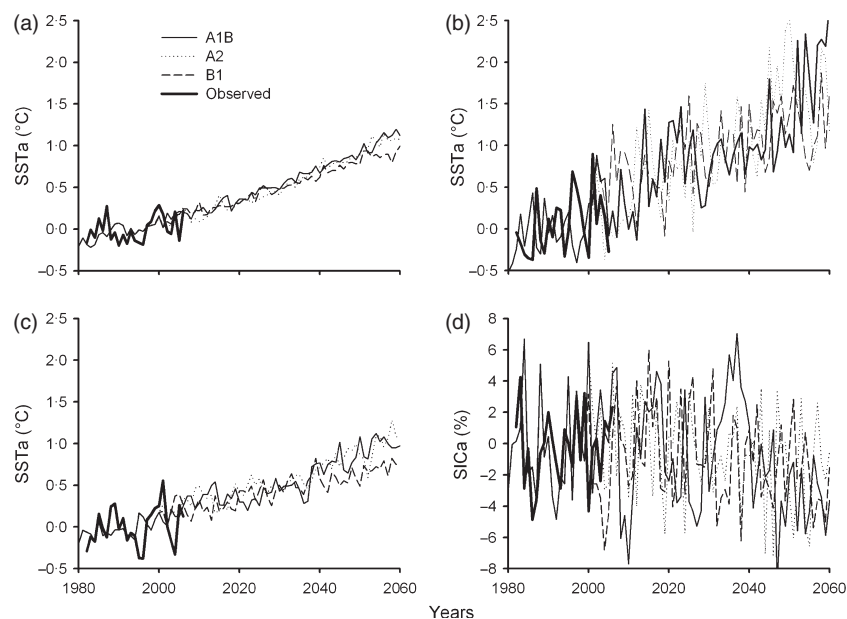


Fig. 4. Observed and predicted oceanographic conditions over foraging grounds of (a) Amsterdam albatrosses during the non-breeding season, (b) black-browed albatrosses in the vicinity of Kerguelen during the breeding season, (c) black-browed albatrosses in the vicinity of southern Australia during the non-breeding season and (d) snow petrels during the non-breeding season. Thick line: observed conditions; thin lines: predicted conditions from emission scenarios A1B, A2 and B1.

Eleven of the 18 GCMs produced an error lower than 5% on the mean SST recorded from 1982 to 1999 over the wintering areas used by Amsterdam albatrosses (Table S9). Considering these 11 GCMs, simulated SST from 2007 to 2058 exhibited a mean annual increasing rate of 0.114%, 0.109% and 0.079% for emission scenarios A1B, A2 and B1 respectively (Fig. 4a). GCMs appeared less precise over the wintering region of black-browed albatrosses with only 5 and 8 out of 18 models producing an error smaller than 5% in the spring and wintering areas used by the black-browed albatross respectively (Table S9). According to the 'climatic scenario ensemble average' approach, the simulated mean annual increasing rates of winter SSTa were greater than those estimated for Amsterdam albatrosses (i.e. 0.120%, 0.115% and 0.095% for emission scenarios A1B, A2 and B1 respectively, Fig. 4c). The greatest annual increasing rates were predicted for the waters used by the black-browed albatross during spring (i.e. 0.253%, 0.161% and 0.171% for emission scenarios A1B, A2 and B1 respectively Fig. 4b).

SIC over the winter foraging area of snow petrels (Fig. 4d) showed a slightly negative trend from 1980 to 2006 with a

mean annual rate of -0.014% . Extreme values of SIC were recorded in 1983 with 76.6% and in 1985 with 67.5%. Four out of the 18 GCMs presented an error lower than 5% (Table S9). These four models provided mean annual rates of -0.166% , -0.057% and -0.063% per year from 2007 to 2058 for emission scenario A1B, A2 and B1 respectively. In contrast to the projected SSTa, predicted SICa had a higher inter-annual variability (Fig. 4).

MODELLING THE POPULATION DYNAMICS FACING CLIMATE CHANGE

Our population model predicted that the number of breeding pairs of Amsterdam albatross was expected to increase in the near future (Fig. 5). Considering a purely stochastic model, the predicted population growth rate ($\lambda_{\text{mod}}^{\text{sp}}$ where sp = AA, BBA or SP for Amsterdam albatross, black-browed albatross and snow petrel, respectively, and mod = stoch, A1B, A2 or B1 for purely stochastic, or considering climatic scenario A1B, A2 and B1 respectively) for the next 50 years ($\lambda_{\text{stoch}}^{\text{AA}} = 1.0480$) was very similar to the mean annual population growth rate observed from 1983 to 2006

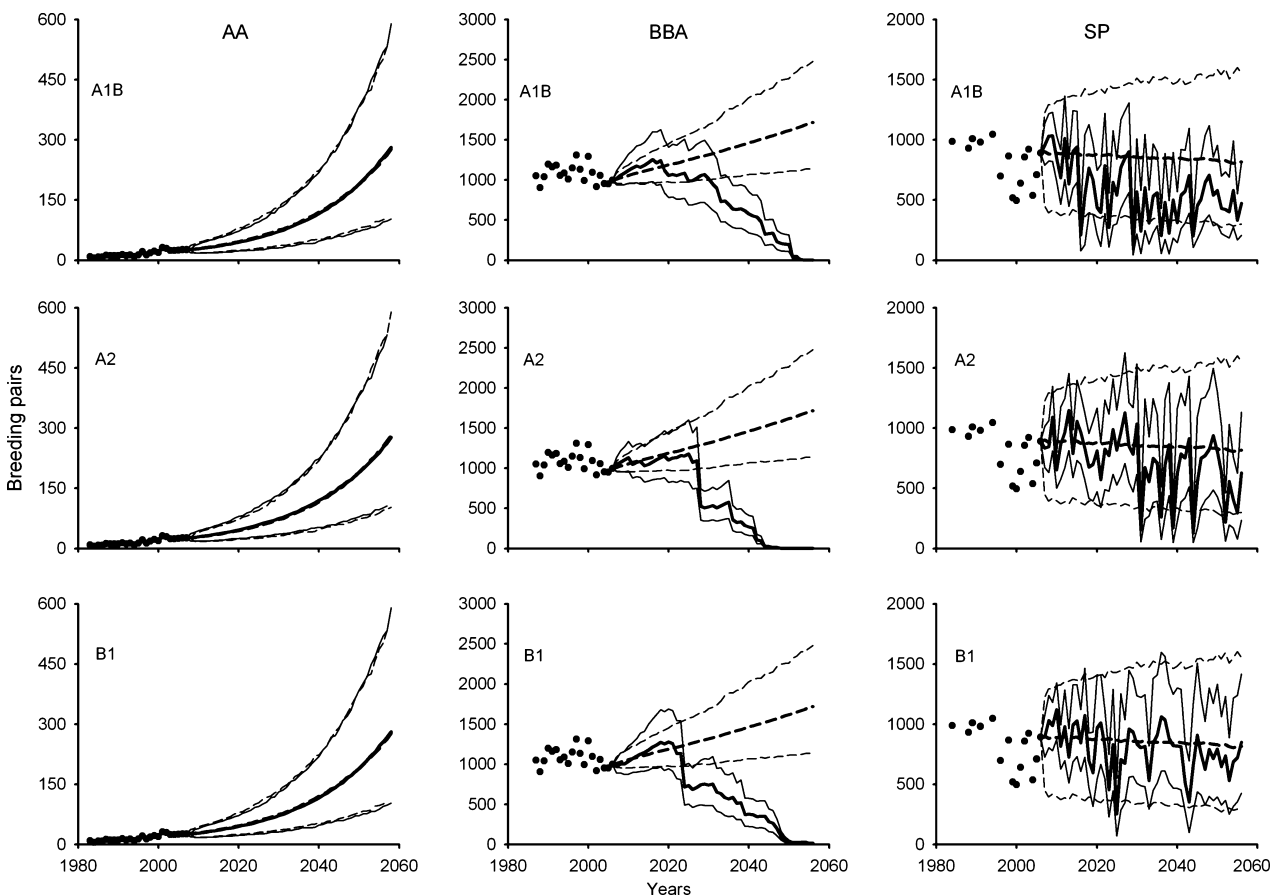


Fig. 5. Observed and predicted number of breeding pairs for the Amsterdam albatross (AA) in Amsterdam Island (left panels), the black-browed albatross (BBA) in Kerguelen Island (centre panels) and the snow petrel (SP) in Terre Adélie (right panels). Observed population size is represented by solid circles, predicted trajectories are represented by bold lines and 95% confidence intervals on predicted population trajectories are represented by thin lines. Predicted population trajectories obtained from purely stochastic models (dashed lines) are shown with predicted population trajectories obtained from stochastic models accounting for future climate changes (solid lines). Three emission scenarios are presented: A1B (top panels), A2 (middle panels) and B1 (bottom panels).

(i.e. 1.0472). Population growth rate accounting for future climate change was very similar to the purely stochastic growth rate regardless of the climatic scenarios ($\lambda_{A1B}^{AA} = 1.0487$, $\lambda_{A2}^{AA} = \lambda_{B1}^{AA} = 1.0483$) considered. This is despite of the increase of breeding probabilities forced by climate change (ψ^{NBSB} : 0.692–0.748) compared to stochastic values (Table S4).

According to the purely stochastic model, the number of breeding pairs of black-browed albatross in Kerguelen Island would moderately increase for the next 50 years (Fig. 5), with a stochastic growth rate slightly greater ($\lambda_{stoch}^{BBA} = 1.0057$) than the one observed from 1987 to 2006 (0.9907). However, population trajectories were very different when predicted increase of SST from GCMs was included into population modelling (Fig. 5). In all these three climatic simulations, population trajectories remained close to the purely stochastic simulations for a few decades and then declined very rapidly. Population decline started earlier under emission scenario A2 (i.e. 2013) and predictions under emission scenario A2 provided the shortest mean time to quasi-extinction equal to 2045 (vs. 2052 and 2050 under emission scenario A1B and B1). The annual population growth rate became smaller than one ($\lambda_{A1B}^{BBA} = 0.917$, $\lambda_{A2}^{BBA} = 0.906$, $\lambda_{B1}^{BBA} = 0.934$) and quasi-extinction probability reached 100% for the three emission scenarios. From 2006 to 2058, the predicted adult survival probability would average 0.857 (range: 0.389–1.000), 0.815 (range: 0.385–0.998) and 0.825 (range 0.421–0.981) under emission scenarios A1B, A2 and B1 respectively. Note that these predicted survival probabilities occurred towards the end of the forecasting period (i.e. years 2054, 2052 and 2048). In all the three climatic simulations, the population decline occurred when adult survival probability dropped for the first time below 0.850 (i.e. 0.841 in 2016, 0.855 in 2011 and 0.828 in 2019). Breeding transition ψ^{NBB} accounting for climate was hardly affected by climate and averaged 0.440 (range: 0.000–1.000), 0.502 (range: 0.000–1.000) and 0.429 (range: 0.000–1.000) from 2007 to 2058 under emission scenarios A1B, A2 and B1 respectively. Note that large and extreme values of ψ^{NBB} occurred during the last 20 years of the simulations (i.e. 2046, 2041 and 2050 for emission scenario A1B, A2 and B1).

Finally, the stochastic population growth rate of $\lambda_{stoch}^{SP} = 0.9980$ predicted for the snow petrel population of Terre Adélie agreed well with the population stability observed from 1983 to 2006 (i.e. 0.9997, Fig. 5). In models accounting for future climate changes, population abundance of the snow petrel declined during the next 50 years, but the rate of decline varied depending on the emission scenario. Simulations under scenario B1 predicted a population growth rate very similar to the one observed from 1983 to 2007 ($\lambda_{B1}^{SP} = 0.9991$), though with the lower inter-annual variability. Simulations under scenario A2 projected greater inter-annual variations and a greater decline ($\lambda_{A2}^{SP} = 0.9942$) during the last 25 years of the simulations than the other climatic scenarios (Fig. 5). Simulations carried

out under scenario A1B produced the greatest inter-annual variation in the number of breeding pairs and the largest population decline ($\lambda_{A1B}^{SP} = 0.9857$) of all scenarios considered.

For both the Amsterdam albatross and the black-browed albatross the predicted population trajectories of the average of the numbers of breeding pairs and of mature birds (i.e. breeders and non-breeders) were similar (data not shown). In contrast, the average number of breeding pairs of the snow petrel, considering climate variation, was higher than the one predicted by the purely stochastic model at the very beginning of the simulations. This could reflect that due to increasing moderate values of SICa, the total number of mature birds responded with a delay and remained very similar to purely stochastic values for few years before increasing.

Discussion

This study investigates how populations of three marine top predators would respond to projected future climate change. We developed stochastic, stage-classified population models for each species whose vital rates were forced by climate to determine the impact of three IPCC emission scenarios on their population trajectories and projected growth rates. To our knowledge, this is the first attempt to study the demographic responses for several populations with contrasted environmental conditions. This required quantifying the functional relationships between demographic parameters and two key climatic variables, SSTa and SICa.

Whereas previous studies of the effect of climate on the vital rates of these species only considered linear relationships (Jenouvrier, Barbraud & Weimerskirch 2005; Rolland, Barbraud & Weimerskirch 2008), our results suggested that non-linear relationships might be the rule in demographic responses to climate. Generally considered as biologically more relevant (Myserud *et al.* 2001), our quadratic function – in logit space – enabled more complex responses with thresholds for extreme values. For instance, the probability for a snow petrel to remain breeder 2 years in a row declined for both high and low anomalies (Fig. S1), and the existence of optimal conditions for moderate SICa was coherent with snow petrel foraging, since this species generally forages whenever there is open or broken sea-ice (Ainley, O'Connor & Boekelheide 1984). Moreover, sea ice dynamics strongly influences overall phytoplankton productivity, which, in turn, fuels higher trophic levels in a relatively short food web where Antarctic Krill, *Euphausia superba*, Dana, is a keystone species (Moline *et al.* 2004). When SICa is too low, so is krill abundance (Loeb *et al.* 1997; Nicol *et al.* 2000), but when SICa is high, there is hardly any open or broken sea-ice, therefore reducing the favourable foraging areas for snow petrels. Because breeding decision in long-lived species is conditional to body condition and therefore foraging success (Chastel, Weimerskirch & Jouventin 1995), moderate SICa therefore provides the best foraging conditions and leads to the highest probability to remain in the breeder state. The mechanisms underlying the quadratic relationship between

SSTa in waters off southern Australia and ψ^{NBB} , and between SSTa in waters off Kerguelen in spring and adult survival probability in black-browed albatross, are not known. However, cooler waters in the western part of the tropical Pacific and southern Australia seem to favour enhanced productivity in this oligotrophic area (Wilson & Adamec 2002). Moreover, high SST generally reduces vertical mixing and provides poor growing conditions for zooplankton communities (Sarmiento *et al.* 1998; Gregg, Sanford & Winkel 2003). Considering that pelagic systems largely have bottom-up regulations, the effect of climate forcing on zooplankton could affect the food chain in an upward cascading effect, including seabirds (Aebischer, Coulson & Colebrook 1990). These two phenomena, previously proposed independently to explain the relationship between breeding success and SSTa in the black-browed albatross (Nevoux, Weimerskirch & Barbraud 2007; Rolland, Barbraud & Weimerskirch 2008) could together explain the nonlinear relationship between SSTa and breeding transitions in this species. Finally, the only exception to the nonlinear relationships between vital rates and climate was for the Amsterdam albatross. This could be due to the small population size (i.e. about 25 pairs per year) that prevented detecting nonlinear relationships. In addition, the linear relationship between winter SSTa and the probability to move from non-breeder to breeder (regardless success) is difficult to explain because of the very large wintering range of the Amsterdam albatross and the paucity of information on food webs and oceanographic functioning within its foraging range.

Our stochastic models forced by future predicted climatic change provided contrasting population responses depending on the species considered. The northernmost distributed species, the Amsterdam albatross, was predicted to be little affected by the expected increase in SST over its wintering area. Although these winter SSTa would increase from 0.9 to 1.1 °C between 2008 and 2058, climate forced models and purely stochastic models provided very similar population growth rates. Climatic impact in Amsterdam albatross was moderate because climate forcing only affected breeding transitions from non-breeding states, which has a relatively small effect on the overall population growth rate (i.e. 3rd largest elasticity, Table S4). In contrast, trajectories using purely stochastic and climate-forced models exhibited large discrepancies for black-browed albatrosses and snow petrels. Regarding the black-browed albatross, the purely stochastic model projected a slight population increase in accordance with the one observed over the past 20 years. However, climate-forced simulations predicted a steep decline resulting from low predicted values of survival probabilities. Actually, climate had an important effect on population of black-browed albatross because it affected adult survival probability, whose variations have the greatest impact on population growth rate (1st elasticity, Table 1). Overall, mean predicted adult annual survival probability was 0.895, 0.887 and 0.878 for scenarios A1B, A2 and B1 respectively. Although these predictors were low, they were in agreement with previous estimates obtained on the same population (Rolland, Barb-

raud & Weimerskirch 2008) when there were two consecutive, high positive SSTa events in the vicinity of Kerguelen Island (0.47 and 0.89 °C, Fig. 4b). According to climatic predictions, the maximum observed spring SSTa (i.e. 0.89 °C in 2001) would be quickly exceeded under scenario B1 (i.e. 1.14 °C in 2020), but was only reached in 2033 and 2025 under scenario A1B and A2. We were therefore confident about the population predictions for the next 20 years, at least for these two latter climatic scenarios. The discrepancy between purely stochastic and climate-forced models for the snow petrel originated from the very important inter-annual variations of SICa that subsequently affected the probability to remain a breeder. However, this discrepancy appeared to be delayed when considering the total number of mature birds. Interestingly, this decline occurred 7–9 years after extreme anomalies, a delay that corresponds to the mean age at first breeding (Chastel, Weimerskirch & Jouventin 1993). This suggests that the population decline occurred through a decline in recruitment. The impact of climate was slower than in black-browed albatross because climate affected the probability to remain a breeder, which has a lower relative impact on population growth rate than adult survival probability (2nd elasticity, Table S4).

Finally, this study suggests that investigating the effects of climate change on core population dynamics is feasible for different populations using a common methodological framework (see also Ådahl, Lundberg & Jonzén 2006). Our approach was limited to single populations and have neglected population settlement in new favourable habitats, or changes in species interactions due to climate change such as exposure to new parasites, new competitors or new preys. Actually, considering the projected increase of SST and air temperature, unfavourable habitats might become favourable for breeding. In this perspective, there is a need to merge demographic population models and climatic envelope models, focusing especially on margins of the current geographic ranges of species (Keith *et al.* 2008).

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Supporting information

Additional Supporting Information may be found in the online version of this article.

Fig. S1. Relationships between climatic covariates and demographic parameters. (a) Relationship between adult survival probability and spring SSTa in black-browed albatross, (b) relationship between probability to move from non-breeder to successful breeder (solid line) or to failed breeder (dash line) and winter SSTa in Amsterdam albatross, (c) relationship between probability of remaining breeder and winter SSTa in black-browed albatross and (d) relationship

between probability of remaining non-breeder and winter SICa in snow petrel. Observed values of environmental covariates are reported on the *x*-axis (solid circles, triangles and diamonds).

Table S1. Eighteen IPCC general circulation models submitted to the 4th Assessment Report from which sea surface temperature and sea ice concentration projections were extracted.

Table S2. Detailed goodness-of-fit statistics for black-browed albatross and snow petrel.

Table S3. Modelling variations in survival (*S*), breeding transition (ψ) and recapture probabilities (*p*) of Amsterdam albatross breeding in Amsterdam Island and marked from 1983 to 2006 and recaptured from 1984 (best model in boldface).

Table S4. Mean parameter estimates and elasticity of population growth rate to change in demographic parameters for the Amsterdam albatross breeding in Amsterdam Island (1983–2006), for the black-browed albatross breeding in Kerguelen Island (1981–2006) and for the snow petrel breeding in Terre Adélie (1968–2006).

Table S5. Modelling variations in survival (*S*), breeding transition (ψ) and recapture probabilities (*p*) of adult black-browed albatrosses marked from 1981 to 2006 and recaptured from 1982, and of adult snow petrels marked from 1968 to 2006 and recaptured from 1969 (best models in boldface).

Table S6. Testing for the effects of climatic covariates on survival and breeding transition probabilities of Amsterdam albatrosses breeding in Amsterdam Island (1983–2006).

Table S7. Testing for the effects of climatic covariates on survival and breeding transitions probabilities of black-browed albatrosses breeding in Kerguelen Island (1981–2006) and snow petrels breeding in Terre Adélie (1968–2006).

Table S8. Modelling variations in juvenile survival (*S*) and recapture probabilities of recruited birds (*p*) for Amsterdam albatrosses, black-browed albatrosses and snow petrels (best models in boldface).

Table S9. IPCC models that produced error $\leq 5\%$ on the observed variation of environmental covariates. Geographical range of the covariates is indicated in brackets. SSTa, sea surface temperature anomaly; SIC, sea ice concentration.

Appendix S1. Estimating adult survival probabilities, breeding probabilities, juvenile survival probabilities and recruitment probabilities of Amsterdam albatross, black-browed albatross and snow petrel.

Appendix S2. Modelling the population dynamics of Amsterdam albatross, black-browed albatross and snow petrel.

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