

Respective impact of climate and fisheries on the growth of an albatross population

V. ROLLAND,¹ M. NEVOUX,² C. BARBRAUD, AND H. WEIMERSKIRCH

Centre d'Etudes Biologiques de Chizé, Centre National de la Recherche Scientifique, 79360 Villiers en Bois, France

Abstract. Climate and human activities such as fisheries impact many animal species. However, the demographic processes through which the population vital rates are affected, and the sensitivity of their growth rates, are poorly understood. The Black-browed Albatross, *Thalassarche melanophrys*, is a long-lived threatened seabird species. Previous studies have shown that the adult survival and breeding success of the population breeding at Kerguelen are affected by sea surface temperature anomalies (SSTA) during both the breeding and the nonbreeding season, and by tuna long-lining in Tasmanian waters through bycatch mortality. Here, using long-term demographic data from a Black-browed Albatross colony monitored for 26 years at Kerguelen, we estimate all demographic parameters from early to adult stages of the life cycle in order to build a fully parameterized population model and predict population growth rates under several scenarios of climate and fishing effort. The observed population growth rate (1.003) indicates that the population was stable or slightly increasing, and our population model gives a close estimate of 1.008. Population growth rate is more sensitive to survival of experienced breeders and accordingly to a change in SSTA during incubation and to tuna long-lining effort (both affecting survival of experienced breeders) than to other demographic parameters/environmental covariates. The population stability results from multiple factors and complex relationships between demographic parameters and environmental conditions, and therefore population equilibrium is precarious. If fishing effort remains stable at its current level and positive SSTA increase, or inversely if fishing effort decreases and SSTA remain similar to present values, then the population would increase. However, if fishing effort increases by 20% (i.e., to 40 million hooks) on the wintering grounds, without any change in SSTA, then the population would decrease at 0.9% per year. If fishing effort stops, the population would increase at 3.5% per year, suggesting that bycatch mortality probably currently limits the Black-browed Albatross population at Kerguelen. Our study shows how this type of model could be useful to predict trajectories of top predator populations, and eventually lower trophic web levels, in relation to climatic projections and future human activities. We highlight the need to reinforce mitigation measures.

Key words: Black-browed Albatross; bycatch; climate; Kerguelen, Southern Ocean; longline fisheries; population dynamics; population projections; sea surface temperature anomalies; Southern Oscillation Index; *Thalassarche melanophrys*.

INTRODUCTION

In the context of global warming, climate has been reported to be already profoundly affecting ecosystems through a change in species physiology, distribution, phenology, or abundance (Hughes 2000, McCarty 2001, Stenseth and Mysterud 2002). Several studies also documented a climate impact on demographic parameters such as survival, breeding success, or sex ratios in mammalian and avian species of both hemispheres (Forchhammer et al. 2001, Inchausti et al. 2003, Sandvik et al. 2005). In the Southern Ocean, correlated changes

between climate and population abundance of marine top predator species (Smith et al. 1999, Croxall et al. 2002) strongly suggest that their dynamics is at least partly influenced by oceanographic fluctuations that drive population dynamics of species in the lower levels of the trophic webs (Murphy et al. 2007).

Species have been noted to be impacted by human activities such as habitat degradation, pollution, or introduction of alien species through direct mortality or indirect effects (Wilcove et al. 1998, Baker et al. 2002, Lewison et al. 2004). Among human activities, a major threat for marine top predators is fishing (Ormerod 2003), which can affect species through reduction in food supplies (Frederiksen et al. 2004) and/or through bycatch mortality (Tuck et al. 2003).

If environmental conditions of climate or human activities affect the vital rate to which the population growth rate of a species is the most sensitive, these environmental conditions will drive the population

Manuscript received 4 June 2008; revised 9 October 2008; accepted 13 October 2008. Corresponding Editor: R. L. Knight.

¹ Present address: University of Florida, Department of Wildlife Ecology and Conservation, Gainesville, Florida 32611 USA. E-mail: vrolland@ufl.edu

² Present address: Centre for Agri-Environmental Research, School of Agriculture, Policy and Development, University of Reading, Reading RG6 6AR United Kingdom.

dynamics. In addition, synergism of climate and human activities was hypothesized to compensate for each other or alternatively amplify their effects on population dynamics (Root et al. 2003). It is thus essential to determine the respective roles of climate and human activities such as fisheries at each stage of the life cycle. Therefore, one can integrate climate and human effects on demographic parameters in population models in order to build realistic scenarios of the impact of future environmental changes on populations and species, which has seldom been done.

So far, only one study has attempted to predict the future of a seabird population under various scenarios of fisheries and oceanographic conditions by using the environmental effects found on adult breeding success and survival (Frederiksen et al. 2004). Here, we used long-term demographic data (26 years) from a Black-browed Albatross (*Thalassarche melanophrys*) colony monitored at Kerguelen. Demographic parameters of this migratory species are affected by both climate and fisheries conditions during both the breeding and the nonbreeding seasons (Nevoux et al. 2007, Rolland et al. 2008; M. Nevoux, H. Weimerskirch, and C. Barbraud, *unpublished manuscript*). In the Southern Indian Ocean, several tuna and tuna-like species are heavily fished. Tuna long-lining, which operates in Tasmanian waters where Black-browed Albatrosses winter, had a negative impact on the survival of this species, whereas warm sea surface temperatures (SST) around Kerguelen in spring favored both their survival and breeding success (Rolland et al. 2008). In addition, recent studies have shown that experienced breeders performed better than inexperienced ones in terms of breeding success and survival (Angelier et al. 2007, Nevoux et al. 2007). Therefore, we developed a deterministic population model (following Arnold et al. 2006) based on the relationships found in previous studies between climate/fisheries and some adult demographic parameters, and the differences in performances between experienced and inexperienced breeders. In this study, we estimate demographic parameters that were not estimated in previous studies for the Kerguelen Black-browed Albatross (breeding success, adult and juvenile survival, and probability to start breeding) in relation to breeding experience and environmental fluctuations, in particular, by investigating the effects of climate on the probability to breed in a given year. Second, we build and validate a fully parameterized population model that explicitly integrates the climate and fisheries effects on all demographic parameters, including juvenile survival and breeding probability. And third, we predict population growth rates under several scenarios of changes in climate and tuna long-lining effort.

MATERIAL AND METHODS

Species and study site

The Black-browed Albatross is a large (3–4 kg) procellariiform, inhabiting the Southern Ocean and

breeding on subantarctic islands during the austral summer (Marchant and Higgins 1990). At Kerguelen, this long-lived bird acquires sexual maturity on average at 9.7 years of age (Weimerskirch and Jouventin 1998) and breeds every year, arriving on colonies in September, laying only one egg, in late October. Hatching occurs in late December and fledging in April (Weimerskirch et al. 1989). Both parents share incubation and chick rearing with shifts of 3–6 days (Pinaud and Weimerskirch 2002) and 2–3 days (Cherel et al. 2000b), respectively. At Kerguelen Islands, total population size has been monitored annually at the southern colony of Cañon des Sourcils Noirs (49°41' S, 70°14' E) since the breeding season 1979–1980 (hereafter noted as 1980). In the study colony (~200 nests), which is part of a larger colony (~1000 nests), all adult breeders were banded with a stainless steel band, and every year during the breeding season three visits (during early incubation, at hatching, and before fledging) were carried out to individually identify both pair members of each nest. Incubating birds were checked while on their nest by reading the bands, and nonbreeding adults (i.e., individuals observed without egg or chick) were also identified by their bands. This check did not necessitate physical capture. Each nest was marked, and its fate was recorded during the hatching and fledging periods in order to determine breeding success. In our analysis, breeding success per individual was 1 if the egg laid produced a fledgling, and 0 in case of failure. Each year, all new individuals found in the study colony and all chicks were banded. In summer, satellite tracking of breeding birds (Weimerskirch et al. 1997, Pinaud and Weimerskirch 2002) indicated that individuals from this colony forage on the Kerguelen shelf ~250 km from the colony, feeding on fish, squid (Cherel et al. 2000b), and offal from fishing vessels (Weimerskirch et al. 1988). In winter, band recoveries (Weimerskirch et al. 1985), stable isotopes analyses (Cherel et al. 2000a), and geolocator studies (H. Weimerskirch, *unpublished data*), show that Kerguelen Black-browed Albatrosses migrate off western and southeastern Australian waters.

Demographic parameters and environmental effects

Breeding adults include individuals that breed for the first time and those that have already bred at least once (hereafter named first and experienced breeders, respectively). Performance in terms of survival and breeding success are lower in first breeders than in experienced breeders (Nevoux et al. 2007), and thus we took this heterogeneity into account in our analyses.

Adult survival.—Nevoux et al. (2007) found that survival of first breeders, but not of experienced breeders, was depressed by positive phases of the global climatic Southern Oscillation Index (SOI) during the winter preceding the breeding season (SOI_{wint}). However, their analyses were restricted to the period 1992–2003, and a more recent analysis extended to the period 1981–2005 revealed that survival of experienced breeders

TABLE 1. Parameter values (mean ± SE) and their relationships with standardized environmental covariates, for Black-browed Albatross (*Thalassarche melanophrys*) breeding at Kerguelen.

Parameter	Mean	SE	Environmental relation (antilogit)	Source
S_{EB}	0.913	0.008	$2.459 + 0.252 \times SSTA_{inc} - 0.222 \times Effort_{tuna} + \epsilon_{SEB}$	1
S_{1B}	0.746	0.027	$1.550 - 1.165 \times SOI_{wint} + \epsilon_{S1B}$	2
S_{PB}	0.910	0.004	NT	3
S_0	0.281	0.021	$-1.033 + 0.505 \times BS + \epsilon_{S0}$	3
BS_{EB}	0.752	0.111	$1.126 + 0.296 \times SSTA_{spring} + 0.297 \times Effort_{trawl} - 0.139 \times SSTA_{wint} + \epsilon_{BS_{EB}}$	1, 2, 4
BS_{1B}	0.548	0.142	$0.284 + 0.296 \times SSTA_{spring} + 0.297 \times Effort_{trawl} - 0.139 \times SSTA_{wint} + \epsilon_{BS_{1B}}$	1, 2, 4
$\Psi_{1B/NB}$	0.235	0.031	NS	4
$\Psi_{EB/NB}$	0.145	0.014	NS	4
$\Psi_{NB/EB}$	0.612	0.047	NS	4
$\Psi_{5/1B}$	0.014	0.002	$-3.531 - 0.899 \times S_{1B} + \epsilon_{\Psi_5}$	3
$\Psi_{6/1B}$	0.043	0.006	$-2.504 - 0.899 \times S_{1B} + \epsilon_{\Psi_6}$	3
$\Psi_{7/1B}$	0.102	0.013	$-1.685 - 0.899 \times S_{1B} + \epsilon_{\Psi_7}$	3
$\Psi_{8/1B}$	0.188	0.019	$-1.074 - 0.899 \times S_{1B} + \epsilon_{\Psi_8}$	3
$\Psi_{9/1B}$	0.273	0.022	$-0.671 - 0.899 \times S_{1B} + \epsilon_{\Psi_9}$	3
$\Psi_{10/1B}$	0.332	0.027	$-0.476 - 0.899 \times S_{1B} + \epsilon_{\Psi_{10}}$	3
$\Psi_{11/1B}$	0.344	0.038	$-0.489 - 0.899 \times S_{1B} + \epsilon_{\Psi_{11}}$	3
$\Psi_{12/1B}$	0.308	0.051	$-0.710 - 0.899 \times S_{1B} + \epsilon_{\Psi_{12}}$	3
$\Psi_{13/1B}$	0.233	0.059	$-1.139 - 0.899 \times S_{1B} + \epsilon_{\Psi_{13}}$	3
P_{Imm}	0.044	0.038	NT	4

Notes: Definitions of variables and parameters: ϵ is the residual term. S_{EB} , S_{1B} , S_{PB} , and S_0 are survival of experienced, first, prebreeders, and juveniles, respectively. BS_{EB} and BS_{1B} are breeding success of experienced and first breeders. $\Psi_{1B/NB}$ and $\Psi_{EB/NB}$ are probabilities of skipping breeding after the first or subsequent breeding, $\Psi_{NB/EB}$ is the probability for a nonbreeder to return to breeding. $\Psi_{5/1B}$ to $\Psi_{13/1B}$ are the age-specific probabilities to begin breeding, and P_{Imm} is the immigration rate. $SSTA_{spring}$, $SSTA_{inc}$, and $SSTA_{wint}$ are, respectively, sea surface temperature anomalies during spring (September), incubation period around Kerguelen, and in winter in Tasmanian waters. SOI_{wint} is the Southern Oscillation Index in winter. $Effort_{tuna}$ and $Effort_{trawl}$ are, respectively, fishing effort of tuna long-lining in winter (Tasmania) and trawling (Kerguelen). NT indicates that effects of covariates were not tested, and NS that they were tested but not significant at the 0.05 level. Sources are: 1, Rolland et al. (2008); 2, Nevoux et al. (2007); 3, M. Nevoux, H. Weimerskirch, and C. Barbraud (*unpublished manuscript*); and 4, the present paper.

was affected by combined effects of SSTA around Kerguelen during the incubation period ($SSTA_{inc}$) and tuna long-line fishing effort ($Effort_{tuna}$) in Tasmanian waters in winter (Rolland et al. 2008). We thus tested for an effect of long-lining on survival of first breeders following the same reference model as in Nevoux et al. (2007) and used the relationships between survival, $SSTA_{inc}$, and $Effort_{tuna}$ for experienced breeders from Rolland et al. (2008) (Table 1).

Breeding success.—Nevoux et al. (2007) reported that first and experienced breeders were equally positively affected by SSTA around Kerguelen during spring. This relationship was detected with linear regressions on mean annual breeding success. On the other hand, logistic regressions on adult breeding success per nest also indicated strong associations with icefish (*Champscephalus gunnari*) trawling effort ($Effort_{trawl}$) and SSTA in the wintering grounds ($SSTA_{wint}$), and a weaker association with SOI_{wint} (Rolland et al. 2008). For the present study, we used the R software (R Development Core Team 2005) to perform a selection among generalized linear mixed models (glmmML function) with individual breeding experience (first vs. experienced), climatic covariates (SOI_{wint} , $SSTA_{wint}$, $SSTA_{inc}$), and trawling effort ($Effort_{trawl}$) as fixed effects, and individuals as a random effect for the period 1992–2003 for which experience was available.

No interaction between experience and environmental variables were tested here, as it was previously demonstrated that first and experienced breeders react similarly (Nevoux et al. 2007). Selection among models was done using a step-down selection with Akaike’s Information Criterion (AIC_c).

Recruitment.—Recruitment was defined as the product of survival by the probability of starting breeding. Age at first breeding ranges from 6 to 15 years old. Juvenile survival, survival between fledging in year t and one year old, was estimated using multistate mark–recapture models, and was positively linked to the breeding success in year t (M. Nevoux, H. Weimerskirch, and C. Barbraud, *unpublished manuscript*). The probability of the beginning of breeding, also estimated with multistate mark–recapture models, depended on both age at first reproduction and survival of first breeders (M. Nevoux, H. Weimerskirch, and C. Barbraud, *unpublished manuscript*). In addition to these findings, we tested whether there was also an effect of $Effort_{tuna}$ on juvenile survival, based on the hypothesis that juveniles forage in Australian waters, as do adult nonbreeders, by using the same reference model as in M. Nevoux, H. Weimerskirch, and C. Barbraud (*unpublished manuscript*), based on a multistate model used in previous bird studies (Reed et al. 2003, Crespín et al. 2006). This reference model was characterized by a time-

dependent capture and adult survival probabilities and a constant juvenile survival. All the mortality was assumed to occur during the first year of life, because immatures are unobservable, spending their time at sea. Therefore, immature capture probability was fixed to zero and their survival was constrained to one, and juvenile survival thus corresponds to the mean survival over the whole immature period. Probability of starting breeding was constant, with a quadratic age effect, increasing from 5 to 11 and decreasing in older individuals.

Breeding probability.—The probability of breeding or skipping a breeding event given that birds were first or experienced breeders was estimated with multistate capture–mark–recapture models using the M-SURGE software (Choquet et al. 2005a). Two kinds of analyses were performed in order (1) to estimate the probability of breeding in relation to breeding experience, and (2) to test for environmental effects on transitions between the breeding and nonbreeding states.

The first breeding event could only be determined for birds ringed as fledglings. Because of a long-lasting immature period, there were not enough individuals to consider the first breeding state before 1990. Therefore, analyses of the breeding probability in relation to breeding experience were realized only for the period 1990–2005. However, for environmental effects we used a longer period (1980–2005), which was made possible by using only experienced and nonbreeders.

First, we used models with two observable states: nonbreeders (NB) that have already reproduced at least once and breeders (B). The breeder state was divided into two age classes. The first and second age classes corresponded respectively to first (1B) and experienced breeders (EB). As birds are first breeders only once in their lives, we constrained to zero the following transitions: from EB to 1B and from NB to 1B. A goodness-of-fit (GOF) test was performed using the U-CARE software (Choquet et al. 2005b) to test whether the data fitted the more complex model $p(s,t) \psi(s,t) F(s,t)$ where capture (p) transitions (ψ) and survival (F) probabilities were state (s) and time (t) dependent. The GOF indicated a transient effect (survival probability depended on the first occasion of capture) and was overall nearly significant at the 5% level ($\chi_{86}^2 = 108.41$, $P = 0.052$). The transient effect was thus subsequently taken into account into our models using the two age classes on breeders survival (Lebreton et al. 1992). The departure model was thus $p(s,t) \psi(s_{NB,t} + s_{B,a_2,t}) F(s_{NB,t} + s_{B,a_2,t})$, where a_2 represented the two breeding experience classes, and fitted the data ($\chi_{72}^2 = 52.79$, $P = 0.957$).

For the period 1980–2005, the GOF for the model $p(s,t) \psi(s,t) F(s,t)$ was overall not significant ($\chi_{242}^2 = 241.96$, $P = 0.489$), but revealed a trap-dependence effect. (Capture probability was not independent of the first occasion of capture.) We thus built a departure model $p(s,m,t) \psi(s,t) F(s,t)$ where m represents “two age

classes” for recapture probabilities to account for trap dependence (Pradel 1993), which fitted to the data ($\chi_{221}^2 = 191.2$, $P = 0.927$). After having selected for the best time-dependent model, we used it as a reference model to test for climatic effects on the probability to breed or skip a breeding event. As in other procellariiform species, the breeding status of individual Black-browed Albatrosses is closely associated with their body condition (Weimerskirch 1999, Pinaud and Weimerskirch 2002), which depends indirectly on climatic conditions through its impact on the trophic web (Pinaud and Weimerskirch 2002). We thus tested for an effect of SSTA on the Kerguelen zone before and during early incubation (June–October) and around Tasmania in winter (June–August) on the probability of breeding in the present year.

For both analyses, selection among time-dependent models was done with a second-order Akaike’s Information Criterion (AIC_c), and the effect of climatic covariates on the probability of breeding was tested using the analysis of deviance (AnODEV) with a Fisher-Snedecor distribution (Grosbois et al. 2008). More details on the way we used these methods can be found in Nevoux et al. (2007) and Rolland et al. (2008).

Immigration rate.—Immigration may play an important role in seabird population dynamics (Danchin and Monnat 1992, Jenouvrier et al. 2003). Since all chicks were banded each year, the proportion of immigration was calculated as the number of newly banded adults at year t (i.e., adults, born elsewhere and not banded, found breeding for the first time in the colony) on the total number of breeders at year $t - 1$. The frontiers of the study colony regularly expanded during the study period, leading to an increase in the number of nests monitored, particularly in the first half of the study period. These frontiers stopped expanding after 2000. Therefore the immigration rate was estimated from the period 2000–2005.

Emigration rate.—By definition, the emigration rate was included in the apparent survival probabilities estimated for breeders.

Density dependence.—In a preliminary step, we searched for density effects on breeding success and adult survival in year t by using the whole colony size in year t as a covariate. Colony size did not affect survival of experienced ($\beta = -0.0038 \pm 0.0029$, $P_{Wald} = 0.190$) or first-time breeders ($\beta = 0.0036 \pm 0.0032$, $P_{Wald} = 0.261$), nor the breeding success of first-time breeders ($\beta = 0.003 \pm 0.002$, $P_{Wald} = 0.134$). However, we found a surprising positive effect of colony size on breeding success of experienced breeders ($\beta = 0.0014 \pm 0.0003$, $P_{Wald} < 0.001$). Given the relatively large size of the colony, this is unlikely to be an Allee effect, but rather a common environmental effect, i.e., a factor that favored the return of breeders on the colony may also have favored their breeding success. Therefore, as we did not detect a density-depressing effect, we did not include density in our population model.

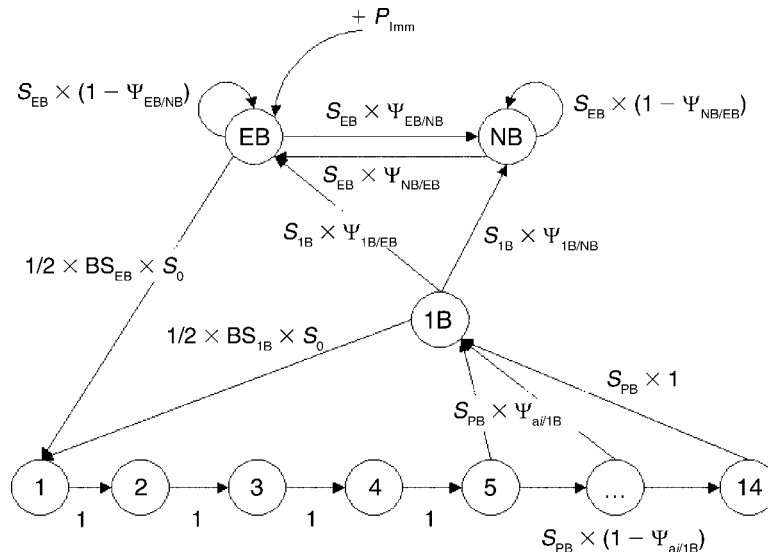


FIG. 1. Life cycle graph of the Black-browed Albatross (*Thalassarche melanophrys*) breeding at Kerguelen. Since minimum age at first breeding is 6 years, birds enter into a prebreeder (PB) stage at 5 years. At 15 years, 95% of them have started to breed. $\Psi_{a/1B}$ is the age-specific (*a*) recruitment rate, and S_{PB} is the survival of prebreeders. Birds start to reproduce as first-time breeders (1B). They may then return to breed the following year with the probability $\Psi_{1B/EB}$ and survival S_{1B} and enter the stage of experienced breeders (EB). Breeding success (BS) is stage-specific, and fledgings have the probability S_0 to survive during their first year. Breeders can become nonbreeders (NB) with a stage-specific transition probability ($\Psi_{1B/NB}$ and $\Psi_{EB/NB}$), and nonbreeders can return as breeders with the transition probability $\Psi_{NB/EB}$. Some breeders immigrate with the probability P_{Imm} .

Population modeling

A life cycle of the Black-browed Albatross was structured by age and reproductive status classes (Fig. 1). Between 1 and 4 years old, individuals are immature, and then, between 5 and 14, they are able to start breeding and are thus considered as prebreeders. As Black-browed Albatrosses are not biennial breeders, it was not necessary to differentiate three nonbreeder states as proposed by Arnold et al. (2006) in their generalization of albatross population models.

Using this prebreeding population model, we determined to which vital rate the population growth rate was the most sensitive. Sensitivities of the population growth rate as well as the stable age distribution were estimated from the deterministic model (Caswell 2001). Mean estimates of the demographic parameters used in this model are summarized in Table 1.

A stochastic model was then built, in which the relationships between covariates and demographic parameters were included with an antilogit function. To take into account the fact that covariates only explained a part of the yearly variation in demographic parameters, we included the residuals between the observed annual estimates and the predicted estimates from models with the covariates into the covariate–demographic parameter relationships using the equation, $\theta = \text{antilogit} (i + \sum_{K=1}^n \beta_K \times \text{cov}_K + \epsilon)$, where θ is the demographic parameter, i is the intercept, β_K are slopes, and cov_K are standardized covariates. The residual term ϵ has a Gaussian distribution with specific mean μ and variance σ^2 for each covariate–demographic parameter

equation. The relationships between demographic parameters and their associated environmental covariate are summarized in Table 1. We calculated the process variance for all parameters (except immigration rate) that were not related to another factor (i.e., probability of skipping breeding and prebreeders survival).

First, we assessed the fit of our stochastic population model by comparing observed annual counts with the number of breeding pairs estimated by the model in which we used annual standardized values of each covariate or annual estimates of parameters between 1992 and 2003.

Second, to predict the population growth rate under various scenarios of fisheries and oceanographic changes, we started from 2003 (1057 pairs) and ran 1000 Monte Carlo simulations over 100 years. Standardized covariates were extracted from a Gaussian distribution with mean 0 and variance 1, and we used a modified beta distribution with specific mean and variance for those demographic parameters which were not associated with an environmental variable. We tested the effects on population growth rate of a change (from -1 to $+1$) in mean of standardized fishing effort and climatic variables in order to compare the effect of each covariate. However, from 2001, trawl fishing has ceased in the summer foraging zone of Black-browed Albatrosses breeding at Kerguelen. Thus, in our scenarios, trawling effort was fixed to zero. Then, we predicted possible trajectories for the Kerguelen population of Black-browed Albatrosses using scenarios of changes in oceanic surface temperature (up to $+2^\circ\text{C}$) in the 30°--

TABLE 2. Step-down selection among breeding success models

Models	AIC _c	ΔAIC _c
Exp + SSTA _{wint} + SSTA _{spring} + SOI _{wint} + Effort _{trawl}	4816	2
Exp + SSTA_{wint} + SSTA_{spring} + Effort_{trawl}	4814	0
Exp + SSTA _{spring} + SOI _{wint} + Effort _{trawl}	4827	13
Exp + SSTA _{wint} + SOI _{wint} + Effort _{trawl}	4864	50
Exp + SSTA _{wint} + SSTA _{spring} + SOI _{wint}	4829	15
Exp + SSTA _{spring} + Effort _{trawl}	4825	11
Exp + SSTA _{wint} + Effort _{trawl}	4866	52
Exp + SSTA _{wint} + SSTA _{spring}	4831	17

Notes: The best model is in boldface type (lowest AIC_c) and detailed in Appendix A. Tested covariates were breeding experience (Exp), sea surface temperature anomalies in spring (September), incubation, and winter (SSTA_{spring}, SSTA_{inc}, SSTA_{wint}), the Southern Oscillation Index in winter (SOI_{wint}), and trawling effort (Effort_{trawl}).

50° S latitude range (IPCC 2007), and hypothetical scenarios of tuna long-lining effort from a total suspension and up to a mean of 50 millions of hooks (maximum observed in 2002). However, because climate models were inconsistent in terms of amplitude and frequency of projected SOI (IPCC 2007), we preferred to keep the same variability of SOI in our projection analyses.

Modeling was conducted with the software ULM 4.1 (Legendre and Clobert 1995).

RESULTS

Breeding success, experience, and environmental parameters

Model selection indicated that the lowest AIC_c model was a model with all the covariates but the SOI_{wint} (Table 2), which matches previous results (Nevoux et al. 2007, Rolland et al. 2008). In this model, breeding success (BS) was higher in experienced breeders than in first breeders (odds ratio = 2.321, *P* < 0.001, Table 1), increased with warm SSTA_{spring} (slope = 0.296 ± 0.040 [mean ± SE], *P* < 0.001) and trawl fishing effort (slope = 0.297 ± 0.068, *P* < 0.001), but decreased with warm SSTA_{wint} (slope = -0.139 ± 0.038, *P* < 0.001). More details on this model are given in Appendix A.

Survival probabilities and fishing effort

No effect of tuna long-lining effort on survival of first breeders or juveniles (*P*-Anodev > 0.285) was found. Therefore, relationships between juvenile, first breeder survival, and climate parameters found in previous studies were used in our population model (Table 1).

Breeding probabilities, experience, and SSTA

Model selection indicated that breeding and survival probabilities were constant and that capture probability was time dependent for breeders and constant for nonbreeders. Survival of nonbreeders was equal to that of experienced breeders (0.913 ± 0.008 [mean ± SE]) but higher and less variable than survival of first breeders (0.746 ± 0.027). First breeders were more likely to skip

the next breeding opportunity (0.235 ± 0.031) than experienced breeders (0.145 ± 0.014), and more than half of nonbreeders return to breed the following year (0.612 ± 0.047).

Selection among models where we distinguished only between experienced breeders and nonbreeders indicated that an additive trap and time dependence on capture probabilities, constant survival probabilities, and an additive time-dependent effect on transition probabilities had the lowest AIC_c. No effect of SSTA around Kerguelen on these transitions probabilities, whatever the SSTA covariate (June to October, Kerguelen or Tasmania), was detected (*P*-Anodev > 0.061). This suggests that the decision to breed was only weakly affected by SSTA.

Observed population size and population models

The number of breeding pairs of Black-browed Albatross in the southern colony of Cañon des Sourcils Noirs remained fairly stable between 1988 and 2005, with high year-to-year fluctuations (Fig. 2). The annual geometric mean population growth rate, estimated from counts, was 1.003, indicating a slightly increasing trend.

For the deterministic model, we used the mean parameter values (Table 1) and obtained the age distribution at the equilibrium from the matrix properties. Estimated population growth rate was 0.995, close to that observed in the colony.

Sensitivity analyses suggest that the population growth rate is more sensitive to a change in survival of experienced breeders (sensitivity = 0.666) and immigration rate (sensitivity = 0.557) than to a change in survival of prebreeders (sensitivity = 0.188) and juveniles (sensitivity = 0.114). Weaker effects would be from a change in survival of first breeders or breeding success of experienced breeders (sensitivity = 0.041). Breeding probabilities (sensitivity = 0.015–0.025), age-dependent recruitment rate (sensitivity = 0–0.016), and breeding success of first breeders (sensitivity = 0.003) would have the lowest effects on lambda.

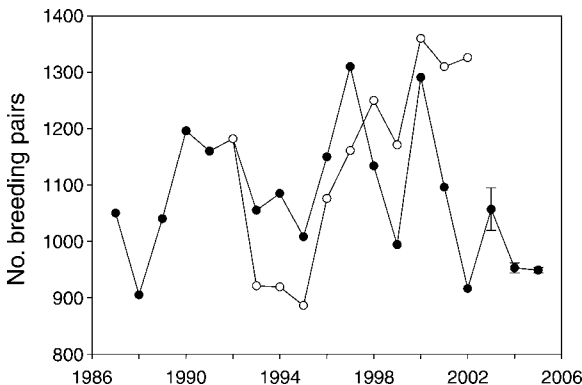


FIG. 2. Annual variation of the observed (solid dots) and estimated (open dots) number of breeding pairs of Black-browed Albatross from the population model with covariates between 1992 and 2002 in the study colony at Kerguelen.

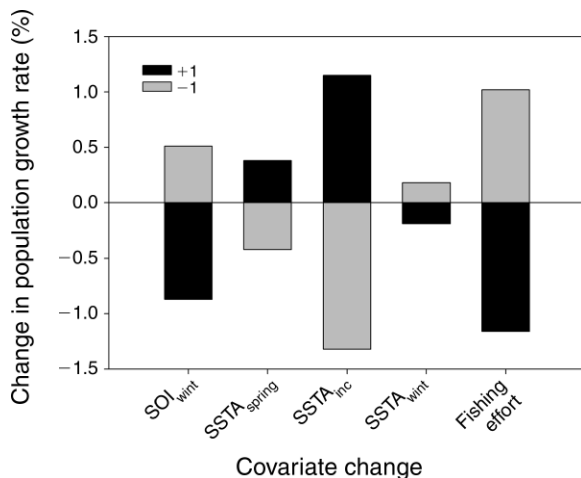


FIG. 3. Change in population growth rate (as a percentage of increase) of Black-browed Albatross at Kerguelen with a change in each of the standardized covariates from a mean of 0 to +1 (solid bars) or -1 (gray bars). For instance, a change of +1 in mean SOI leads to a decrease of 0.8% in population growth rate (i.e., from 1.003 to 0.995). Covariates are: SOI_{wint}, Southern Oscillation Index in winter; SSTA_{spring}, SSTA_{inc}, and SSTA_{wint}, sea surface temperature anomalies during spring, incubation, and winter; and fishing effort in tuna fisheries.

The stochastic model with environmental covariates overall reproduced well the trend in observed counts between 1992 and 2003 in the colony, but the fit was poor when considering year-to-year fluctuations (Pearson's $r = 0.235$, $P = 0.486$). However, the population growth rate estimated from this model (1.008) was close to the observed one and indicated a similar slightly increasing trend of <1% per year.

Scenarios of climate and fisheries changes

When trawling effort was fixed to zero, our population model where all the covariates were included except trawling effort indicated a growth rate of 1.003. If the colony no longer benefits from an annual pool of immigrants, it would decline at a rate of 1.9% per year.

For a similar change in the mean values of covariates, the population growth rate would not be similarly affected (Fig. 3). The most important change in lambda would occur with a change in SSTA_{inc} or tuna long-lining effort; both of these factors affect survival of experienced breeders.

The results of all the scenarios of SSTA and tuna long-lining effort are summarized in Fig. 4. If the impact of fishing effort remains identical and sea surface temperatures warm, or inversely if fishing effort decreases and sea surface temperatures remain the same, then the population would increase at a higher rate. However, if fishing effort increases up to an average of 40 million hooks per year without any change in SSTA, then the population would decrease at an estimated growth rate of 0.991.

DISCUSSION

Demographic parameters and environmental conditions

Our results on breeding success of Black-browed Albatross confirm that first-time breeders had a lower breeding success than experienced ones (Nevoux et al. 2007), and that breeding success was negatively influenced by warm sea surface temperatures in Tasmanian waters during the austral winter, and positively associated with trawling effort around Kerguelen (Rolland et al. 2008). The positive effect of SSTA in September on breeding success is in agreement with previous results (Rolland et al. 2008), as September was included in the incubation period. However, no impact of the SOI in the winter preceding the breeding season was found. Rolland et al. (2008) had found a weak positive effect of this index and hypothesized that it might be a by-product of its correlation with SSTA during rearing. Our results tend to confirm this hypothesis. Interestingly, we found that SSTA and trawl fishing affect experienced breeders but also first breeders. This might be because most Black-browed Albatrosses breeding for the first time (76.3%) paired with an experienced breeder, and the resulting breeding success was common to both pair members. However, SSTA and trawl fishing effort might also affect first breeders.

As expected from poor performers, first breeders were more likely to skip breeding the following year than experienced breeders, which is in agreement with other studies on mammalian and avian species (Weimerskirch

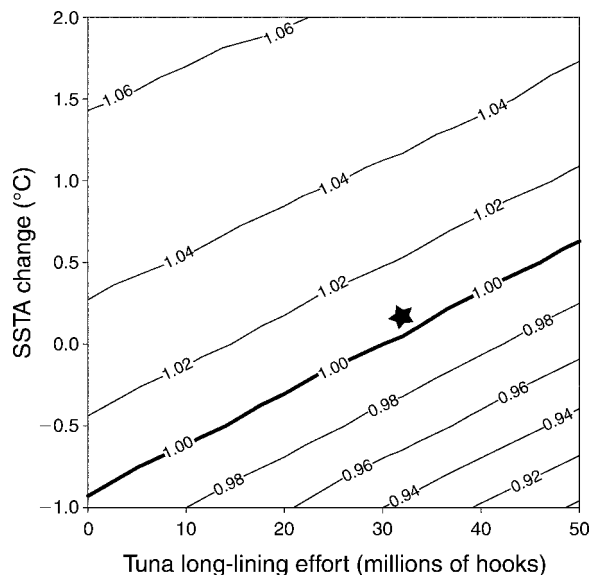


FIG. 4. Black-browed Albatross population growth rate under different scenarios of sea surface temperature anomalies (SSTA) change ($^{\circ}\text{C}$) and tuna fishing effort (millions of hooks) set during the wintering period in Tasmanian waters). The star represents the current conditions of fisheries and SSTA (population growth rate of 1.001), and lines are isoclines where population growth rate is constant for different parameter values.

1990, Viallefont et al. 1995). However, no effect of SSTA on breeding decisions was detected. Environmental parameters other than those tested here could have affected this probability. Another explanation might be that we tested for SSTA effects on breeding probability only among experienced breeders, but that only first breeders may be affected by SSTA.

The population model

Our stochastic population model accurately reproduced the long-term trend observed at the colony. This suggests that interannual fluctuations in population size may be partly explained by environmental influences on several demographic parameters. However, the fit between annual counts and annual predictions was poor, indicating our poor ability to reproduce the very high interannual variability in the number of breeding pairs.

Black-browed Albatross population growth rate was very sensitive to survival of experienced breeders, as was also found for the South Georgia population (Arnold et al. 2006), and as expected for a long-lived species (Sæther and Bakke 2000). Accordingly, survival of experienced breeders varied little compared to survival of inexperienced ones (Nevoux et al. 2007). This observation fits with theoretical predictions that the mean population growth rate should be the most sensitive to the least variable vital rate, but also that the most variable parameter should contribute the most to the variance in population growth rate (Sæther and Bakke 2000).

Predictions and future population growth

Our population model provides information about possible trajectories of the Black-browed Albatross population from Kerguelen according to different demographic/environmental scenarios. First, our results suggest that an absence of immigration would lead the population to decline. Immigration rate estimated in the study colony was 4.4%, which was relatively similar to those found for other procellariiform species (Jenouvrier et al. 2003, 2005). Nevertheless, despite the relatively high nest fidelity of this species, because immigration rate was estimated from a study colony that is a subset of the larger adjacent colony, we cannot exclude that the immigration rate was overestimated due to birds from the larger colony moving into the study colony. Immigration may, however, be an important parameter affecting the population dynamics of seabirds, and studies investigating factors affecting immigration rate are needed. Future studies, when possible, should also take senescence into account. Indeed, onset of senescence was suggested in very old, experienced Black-browed Albatrosses (Angelier et al. 2007), but the small sample sizes for older age classes (51 individuals older than 20 years from which a decline in breeding success was observed) did not allow us to properly model survival and breeding success for older age classes.

Second, if environmental conditions do not change, the population would remain stable. However, it is likely that the frequency and intensity of positive SSTA will increase in the future (IPCC 2007), and our results suggest that this may cause the Black-browed Albatross population to increase. Surface oceanic temperatures south of 30° S are predicted to increase from 0.5° to 1.5°C by 2050 and from 1° to 2°C by the end of the 21st century (IPCC 2007). Our model predictions indicate that with only a 0.62°C increase, the Kerguelen Black-browed Albatross population would increase, and that with the current level of fishing effort, a predicted warming of 0.5°–1.5°C could enhance the population growth with an increase of 82.4–93.3% in growth rate (Fig. 4). This suggests that climate warming could compensate for any increase in fishing effort.

Interactions between top predators and lower levels in the trophic web are unknown, but the positive relation between SSTA around Kerguelen and vital rates of the Black-browed Albatross suggest that an increase in SSTA would favor their prey. A similar increase in SSTA in Tasmanian waters does not prevent this population from increasing because the population growth rate is not very sensitive to variations in breeding success. In the case where SSTA in Tasmanian waters would affect the prey of Black-browed Albatrosses, it is difficult to predict consequences, as their diet in winter is unknown.

Regarding fisheries, an increase in fishing effort from 32 to 40 million hooks per year would be enough for the population to decline. However, interactions between climate, fisheries, and tuna populations are complex and unknown, although changes in tuna abundance and distribution are expected with climate warming (Hobday and Poloczanska 2008). Tuna populations may be highly affected by climate change, which may in turn affect fishing effort. Indeed, studies have reported a climate effect on catches of tuna species (Le Blanc and Marsac 1999, Catarci 2005, Ménard et al. 2007). Nevertheless, adult stocks such as those of southern bluefin tuna (*Thunnus maccoyii*) are presently at very low levels (Hunt 2006). In addition, the increase in fuel costs is currently considered as one of the most important factors driving changes in fishing effort (SC-WCPFC 2008). Therefore, however the climate may change in future, fishing pressure in Australian waters is likely to decline by 10% to 50% in the next 30 years (A. Hobday, *personal communication*). With a 10% decline in fishing effort (e.g., 28.8 million hooks) and an increase of 0.62°C, this Black-browed Albatross population would increase at 2.7% per year.

Climate and long-lining effort had an overall similar effect size on Black-browed Albatross adult survival (Rolland et al. 2008). However, the range and speed of variation are likely to be higher for fishing effort than for SST, which might differentially affect the demographic responses. Even in the case of an exponential increase of the SST, warming is a progressive process.

Changes in fishing effort, on the contrary, may be abrupt, reaching unprecedented low or high levels. Moreover, as no estimate of annual bycatch was available for this species in that period and area, we assumed that mortality was proportional to fishing effort. However, the level of bycatch may change without any change in fishing effort as a result of mitigation measures.

Here, we would expect at least a 3.5% annual increase of the population if there was no mortality associated with longline fishing in Australian waters. Given that the population is stable today, this suggests that it could currently be limited by the negative effect of tuna fisheries on adult survival, unless there are other limiting factors that we did not identify. Here, we used linear regressions, but nonlinearities may be expected between demographic parameters and climate (Stenseth and Mysterud 2002). In addition, we can easily imagine a threshold of temperature or fishing effort above or below which the population would be substantially positively or negatively affected. The effects of bycatch can be seen as a harvesting problem, with harvest rate affecting survival. Three hypotheses relate survival and harvest: (1) the additive mortality hypothesis (AMH) where survival is negatively linearly correlated to the harvest rate; (2) the compensatory mortality hypothesis (CMH), where survival is regulated by density dependence up to a harvest threshold, above which survival decreases; and (3) the partial compensatory mortality hypothesis (PMH), where survival decreases with increasing harvest more rapidly above than below the harvest threshold (Williams et al. 2002). Without tuna fishing effort, the survival of experienced breeders would be 0.968 according to our population model, which means either a 5.7% mortality due to fisheries under the AMH, or 5.5% mortality due to fisheries and a threshold of 3.2% mortality below which mortality is compensated under the CMH (see formulas in Appendix B). Compensatory or additive mortality depends on the strength of density dependence. Given that we did not find strong evidence for density dependence on adult survival and breeding success, we suspect that additive bycatch mortality is more likely to limit the population of Kerguelen Black-browed Albatrosses. Therefore, from a conservation perspective, our results suggest that either longline fishing effort in Tasmanian waters should be reduced, or that mitigation measures should be reinforced so as to decrease adult mortality caused by this fishery.

To conclude, overall, the population of Black-browed Albatross breeding at Kerguelen has remained fairly stable throughout the study period, and might increase with further climate warming, potentially compensating for fishery bycatch. However, the major populations worldwide are in decline (Croxall et al. 1998, Huin 2001), resulting in the alarming "endangered" conservation status of this species from 2003 (BirdLife International 2005). Environmental conditions that

drive the Kerguelen population are thus likely to be different from those of other populations. Indeed, trawl fisheries have a negative impact on other populations in some particular regions such as the Falkland Islands (Sullivan et al. 2006), Golfo San Jorge (González-Zevallos et al. 2007), and South African coasts (Watkins et al. 2008), and longline fisheries may have caused the recent steep decline in the South Georgia population (Arnold et al. 2006). Moreover, climate warming could have opposite effects on Black-browed Albatrosses from South Georgia because they feed mainly on krill (Croxall et al. 1997), the availability of which depends strongly on sea ice (Croxall 1992), and which has decreased over the past decade (Atkinson et al. 2004). The very low breeding success (13.6%) of this population is thought to be related to low krill production (Arnold et al. 2006). This is the reason why we highlighted how crucial it is to quantify the impact of both fisheries and climate on demographic parameters, and use these findings to help predict the possible trajectories of a population according to predicted climate change and possible modifications in human activities. In the context of global warming and loss of biodiversity due to human activities, this type of model allows us to include predictions from climatologists among others to determine the future of top predator populations.

ACKNOWLEDGMENTS

We gratefully acknowledge all the wintering field workers involved in the long-term monitoring of Black-browed Albatrosses at Kerguelen, and Dominique Besson and Karine Delord for support and help in data management. This study was supported by Institut Paul Emile Victor (Program IPEV No. 109) and by Terres Australes et Antarctiques Françaises, and is a part of program REMIGE funded by ANR Biodiversity. The Région Poitou-Charentes (grant to M. Nevoux) also supported this study.

LITERATURE CITED

- Angelier, F., H. Weimerskirch, S. Dano, and O. Chastel. 2007. Age, experience and reproductive performance in a long-lived bird: a hormonal perspective. *Behavioral Ecology and Sociobiology* 61:611–621.
- Arnold, J. M., S. Brault, and J. P. Croxall. 2006. Albatross populations in peril: a population trajectory for Black-browed Albatrosses at South Georgia. *Ecological Applications* 16:419–432.
- Atkinson, A., V. Siegel, E. Pakhomov, and P. Rothery. 2004. Long-term decline in krill stock and increase in salps within the Southern Ocean. *Nature* 432:100–103.
- Baker, G. B., R. Gales, S. Hamilton, and V. Wilkinson. 2002. Albatrosses and petrels in Australia: a review of their conservation and management. *Emu* 102:71–97.
- BirdLife International. 2005. *Thalassarche melanophrys*. In 2007 IUCN Red List of Threatened Species. International Union for the Conservation of Nature, Gland, Switzerland.
- Caswell, H. 2001. Matrix population models: constructions, analysis and interpretation. Second edition. Sinauer Associates, Sunderland, Massachusetts, USA.
- Catarci, C. 2005. The world tuna industry: an analysis of imports and prices, and of their combined impact on catches and tuna fishing capacity. Pages 235–278 in W. H. Bayliff, J. I. de Leiva Moreno, and J. Majkowski, editors. Meeting of the Technical Advisory Committee of the FAO Project

- Management of Tuna Fishing Capacity: Conservation and Socio-economics, 15–18 March 2004, Madrid, Spain. FAO, Rome Italy.
- Cherel, Y., K. A. Hobson, and H. Weimerskirch. 2000a. Using stable-isotope analysis of feathers to distinguish moulting and breeding origins of seabirds. *Oecologia* 122:155–162.
- Cherel, Y., H. Weimerskirch, and C. Trouvé. 2000b. Food and feeding ecology of the neritic-slope forager black-browed albatross and its relationships with commercial fisheries in Kerguelen waters. *Marine Ecology Progress Series* 207:183–199.
- Choquet, R., A.-M. Reboulet, J.-D. Lebreton, O. Gimenez, and R. Pradel. 2005b. U-CARE 2.2 User's Manual. CEFE, Montpellier, France.
- Choquet, R., A.-M. Reboulet, R. Pradel, O. Gimenez, and J.-D. Lebreton. 2005a. M-SURGE 1-7 User's Manual. Mimeographed document. CEFE/CNRS, Montpellier, France.
- Crespin, L., M. P. Harris, J.-D. Lebreton, M. Frederiksen, and S. Wanless. 2006. Recruitment to a seabird population depends on environmental factors and on population size. *Journal of Animal Ecology* 75:228–238.
- Croxall, J. P. 1992. Southern Ocean environmental changes: effects on seabird, seal and whale populations. *Philosophical Transactions of the Royal Society B* 338:319–328.
- Croxall, J. P., P. A. Prince, and K. Reid. 1997. Dietary segregation of krill-eating South Georgia seabirds. *Journal of Zoology* 242:531–556.
- Croxall, J. P., P. A. Prince, P. Rothery, and A. G. Wood. 1998. Population changes in albatrosses at South Georgia. Pages 69–83 in G. Robertson and R. Gales, *Albatross biology and conservation*. Surrey Beatty and Sons, Chipping Norton, New South Wales, Australia.
- Croxall, J. P., P. N. Trathan, and E. J. Murphy. 2002. Environmental change and Antarctic seabird populations. *Science* 297:1510–1514.
- Danchin, E., and J. Y. Monnat. 1992. Population-dynamics modeling of two neighboring Kittiwake *Rissa tridactyla* colonies. *Ardea* 80:170–180.
- Forchhammer, M. C., T. H. Clutton-Brock, J. Lindstrom, and S. D. Albon. 2001. Climate and population density induce long-term cohort variation in a northern ungulate. *Journal of Animal Ecology* 70:721–729.
- Frederiksen, M., S. Wanless, M. P. Harris, P. Rothery, and L. J. Wilson. 2004. The role of industrial fisheries and oceanographic change in the decline of North Sea black-legged kittiwakes. *Journal of Applied Ecology* 41:1129–1139.
- González-Zevallos, D., P. Yorio, and G. Caille. 2007. Seabird mortality at trawler warp cables and a proposed mitigation measure: a case study in Golfo San Jorge, Patagonia, Argentina. *Biological Conservation* 136:108–116.
- Grosbois, V., O. Gimenez, J.-M. Gaillard, R. Pradel, C. Barbraud, J. Clobert, A. P. Møller, and H. Weimerskirch. 2008. Assessing the impact of climate variation on survival in vertebrate populations. *Biological Reviews* 83:357–399.
- Hobday, A. J., and E. S. Poloczanska. 2008. Marine fisheries and aquaculture. In C. J. Stokes and S. M. Howden, editors. *An overview of climate change adaptation in Australian primary industries—impacts, options and priorities*. CSIRO, Canberra, Australia.
- Hughes, L. 2000. Biological consequences of global warming: is the signal already apparent? *Trends in Ecology and Evolution* 15:56–61.
- Huin, N. 2001. Census of the black-browed albatross population of the Falkland Islands 2000/2001. Falkland Conservation, Stanley, Falkland Islands.
- Hunt, C. 2006. Concern for Southern Ocean fish stocks and bird populations. *Marine Policy* 30:357–359.
- Inchausti, P., C. Guinet, M. Koudil, J.-P. Durbec, C. Barbraud, H. Weimerskirch, Y. Cherel, and P. Jouventin. 2003. Inter-annual variability in the breeding performance of seabirds in relation to oceanographic anomalies that affect the Crozet and the Kerguelen sectors of the Southern Ocean. *Journal of Avian Biology* 34:170–176.
- IPCC. 2007. Global climate projections. In *Climate Change 2007—The physical science basis*. Working Group I Contribution to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.
- Jenouvrier, S., C. Barbraud, and H. Weimerskirch. 2003. Effects of climate variability on the temporal population dynamics of southern fulmars. *Journal of Animal Ecology* 72:576–587.
- Jenouvrier, S., C. Barbraud, and H. Weimerskirch. 2005. Long-term contrasted responses to climate of two Antarctic seabirds species. *Ecology* 86:2889–2903.
- Le Blanc, J.-L., and F. Marsac. 1999. Climate information and prediction services for fisheries: the case of tuna fisheries. CLIMAR 99–WMO Workshop on advances in Marine Climatology, Vancouver, Canada.
- Lebreton, J.-D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* 62:67–118.
- Legendre, S., and J. Clobert. 1995. ULM, a software for conservation and evolutionary biologists. *Journal of Applied Statistics* 22:817–834.
- Lewison, R. L., L. B. Crowder, A. J. Read, and S. A. Freeman. 2004. Understanding impacts of fisheries bycatch on marine megafauna. *Trends in Ecology and Evolution* 19:598–604.
- Marchant, S., and P. J. Higgins. 1990. Procellariiformes; Diomedidae. Pages 263–354 in *Handbook of Australian, New Zealand and Antarctic birds—ratites to ducks*. Oxford University Press, Oxford, UK.
- McCarty, J. P. 2001. Ecological consequences of recent climate change. *Biological Conservation* 15:320–331.
- Ménard, F., F. Marsac, E. Bellier, and B. Cazelles. 2007. Climatic oscillations and tuna catch rates in the Indian Ocean; a wavelet approach to time series analysis. *Fisheries Oceanography* 16:95–104.
- Murphy, E. J., P. N. Trathan, J. L. Watkins, K. Reid, M. P. Meredith, J. Forcada, S. E. Thorpe, N. M. Johnston, and P. Rothery. 2007. Climatically driven fluctuations in Southern Ocean ecosystems. *Proceedings of the Royal Society B* 274:3057–3067.
- Nevoux, M., H. Weimerskirch, and C. Barbraud. 2007. Environmental variation and experience-related differences in the demography of the long-lived black-browed albatross. *Journal of Animal Ecology* 76:159–167.
- Ormerod, S. J. 2003. Current issues with fish and fisheries: editor's overview and introduction. *Journal of Applied Ecology* 40:204–213.
- Pinaud, D., and H. Weimerskirch. 2002. Ultimate and proximate factors affecting the breeding performance of a marine top-predator. *Oikos* 99:141–150.
- Pradel, R. 1993. Flexibility in survival analysis from recapture data: handling trap-dependence. Pages 29–37 in J.-D. Lebreton and P. M. North, editors. *Marked individuals in the study of bird populations*. Birkhauser Verlag, Basel, Switzerland.
- R Development Core Team. 2005. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Reed, E. T., G. Gauthier, R. Pradel, and J.-D. Lebreton. 2003. Age and environmental conditions affect recruitment in Greater Snow Geese. *Ecology* 84:219–230.
- Rolland, V., C. Barbraud, and H. Weimerskirch. 2008. Combined effects of fisheries and climate on a migratory long-lived marine predator. *Journal of Applied Ecology* 45:4–13.

- Root, T. L., J. T. Price, K. R. Hall, S. H. Schneider, C. Rosenzweig, and J. A. Pounds. 2003. Fingerprints of global warming on wild animals and plants. *Nature* 421:57–60.
- Sæther, B.-E., and O. Bakke. 2000. Avian life history variation and contribution of demographic traits to the population growth rate. *Ecology* 81:642–653.
- Sandvik, H., K. E. Erikstad, R. T. Barbett, and N. G. Yoccoz. 2005. The effect of climate on adult survival in five species of North Atlantic seabirds. *Journal of Animal Ecology* 74:817–831.
- SC-WCPFC. 2008. Fourth Scientific Committee regular session of the Western and Central Pacific Fisheries Commission, Port Moresby, Papua New Guinea.
- Smith, R. C., D. Ainley, K. Baker, E. Domack, S. Emslie, B. Fraser, J. Kennett, A. Leventer, E. Mosley-Thompson, S. Stammerjohn, and M. Vernet. 1999. Marine ecosystem sensitivity to climate change. *BioScience* 49:393–404.
- Stenseth, N., and A. Mysterud. 2002. Climate, changing phenology, and other life history traits: nonlinearity and match-mismatch to the environment. *Proceedings of the National Academy of Sciences (USA)* 99:13379–13381.
- Sullivan, B. J., T. A. Reid, and L. Bugoni. 2006. Seabird mortality on factory trawlers in the Falkland Islands and beyond. *Biological Conservation* 131:495–504.
- Tuck, G. N., T. Polacheck, and C. M. Bulman. 2003. Spatio-temporal trends of longline fishing effort in the Southern Ocean and implications for seabird bycatch. *Biological Conservation* 114:1–27.
- Viallefont, A., F. Cooke, and J.-D. Lebreton. 1995. Age-specific costs of first-time breeding. *Auk* 112:67–76.
- Watkins, B. P., S. L. Petersen, and P. G. Ryan. 2008. Interactions between seabirds and deep-water hake trawl gear: an assessment of impacts in South African waters. *Animal Conservation* 11:247–254.
- Weimerskirch, H. 1990. The influence of age and experience on breeding performance of the Antarctic fulmar, *Fulmarus glacialisoides*. *Journal of Animal Ecology* 59:867–875.
- Weimerskirch, H. 1999. The role of body condition in breeding and foraging decision in albatrosses and petrels. Pages 1178–1189 in N. J. Adams and R. H. Slotow, editors. *Proceedings of the 22nd International Ornithological Congress*. BirdLife South Africa, Durban, South Africa.
- Weimerskirch, H., J. A. Bartle, P. Jouventin, and J.-C. Stahl. 1988. Foraging ranges and partitioning of feeding zones in three species of southern albatrosses. *Condor* 90:214–219.
- Weimerskirch, H., and P. Jouventin. 1998. Changes in population sizes and demographic parameters of six albatross species breeding on the French sub-Antarctic islands. Pages 84–91 in G. Robertson and R. Gales, editors. *Albatross biology and conservation*. Surrey Beatty and Sons, Chipping Norton, New South Wales, Australia.
- Weimerskirch, H., P. Jouventin, J. L. Mougouin, J.-C. Stahl, and M. Van Beveren. 1985. Banding recoveries and the dispersal of seabirds breeding in French Austral and Antarctic Territories. *Emu* 85:22–33.
- Weimerskirch, H., T. Mougey, and X. Hindermeyer. 1997. Foraging and provisioning strategies of black-browed albatrosses in relation to the requirements of the chick: natural variation and experimental study. *Behavioral Ecology* 8:635–643.
- Weimerskirch, H., R. Zotier, and P. Jouventin. 1989. The avifauna of the Kerguelen Islands. *Emu* 89:15–29.
- Wilcove, D. S., D. Rothstein, J. Dubow, A. Phillips, and E. Losos. 1998. Quantifying threats to imperiled species in the United States. *BioScience* 48:607–615.
- Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. *Analysis and management of animal populations*. Academic Press, Elsevier, Burlington, Massachusetts, USA.

APPENDIX A

Output of the best generalized linear mixed model for individual Black-browed Albatross breeding success at Kerguelen (*Ecological Archives* A019-054-A1).

APPENDIX B

Formulas relating nonharvest mortality $m(t)$ in the presence of harvest with mortality due to harvest $h(t)$ and natural mortality m_0 (*Ecological Archives* A019-054-A2).