

# Demographic response of a population of white-chinned petrels *Procellaria aequinoctialis* to climate and longline fishery bycatch

Christophe Barbraud<sup>1\*</sup>, Cédric Marteau<sup>1</sup>, Vincent Ridoux<sup>2</sup>, Karine Delord<sup>1</sup> and Henri Weimerskirch<sup>1</sup>

<sup>1</sup>Centre d'Etudes Biologiques de Chizé, UPR 1934 CNRS, 79360 Villiers en Bois, France; and <sup>2</sup>Centre de Recherche sur les Ecosystèmes Littoraux Anthropisés, UMR 6217 CNRS-IFREMER-Université La Rochelle, Avenue Michel Crépeau, 17042 La Rochelle, France

## Summary

1. Fisheries can affect non-target species through bycatch, and climate change may act simultaneously on their population dynamics. Estimating the relative impact of fisheries and climate on non-target species remains a challenge for many populations because the spatio-temporal distribution of individuals remains poorly known and available demographic information is incomplete.

2. We used population survey data, capture–mark–recapture methods, population modelling and the demographic invariant method to investigate the effects of climate and fisheries on the demography of a predator species affected by bycatch. These complementary approaches were used to help account for different sources of uncertainty.

3. The white-chinned petrel *Procellaria aequinoctialis* is the commonest seabird species killed by longline fisheries in the Southern Ocean. Petrel breeding success was positively related to the fishing effort for Patagonian toothfish *Dissosticus eleginoides*. El Niño events negatively affected adult survival with a time lag of 3 years. Fishing efforts for toothfish and hake (*Merluccius* spp.) were negatively related to petrel recruitment, suggesting that fisheries-induced mortality strongly impacted younger age classes. Lambda estimated from matrix population models was below replacement ( $0.964 \pm 0.026$ ), and the number of breeding pairs declined by  $\approx 37\%$  in 21 years. This decline was probably caused by low survival of both young age classes and adults.

4. The Crozet archipelago, Southern Indian Ocean, population size was estimated at  $\approx 170\,000$  individuals in the early 1980s, and would be severely affected by any additional source of mortality that approached 8000 individuals per year. The number of petrels killed by the toothfish fishery alone exceeded this threshold during the late 1990s and early 2000s, but has declined well below this since 2003.

5. *Synthesis and applications.* Complementary approaches suggest that both longline fishery bycatch and climate have a significant impact on the size of the Southern Ocean white-chinned petrel population. Stopping or reversing climate change will be a very slow process, and may be impossible. Therefore, we recommend a reduction in bycatch to help the populations recover. Further information on the status of individuals caught in longlines is required to understand the demographic processes involved.

**Key-words:** survival, demographic invariants, El Niño, longline fishing, population model, *Procellaria aequinoctialis*, recruitment

## Introduction

Increasing industrialization of fisheries and expansion into new areas have resulted in intense harvesting of fish stocks,

alteration of the structure and functioning of marine ecosystems (Jackson *et al.* 2001; Pauly *et al.* 2002), and increasing numbers of marine vertebrates becoming entangled or hooked accidentally by fishing gear intended for commercial target species (Lewison *et al.* 2004). This bycatch has been implicated in population declines of several species of

\*Correspondence author. E-mail: barbraud@cebc.cnrs.fr

marine predators (Mangel 1993; Weimerskirch, Brothers & Jouventin 1997). Conservation measures such as seasonal closure or technical improvements have been implemented to minimize bycatch in several ocean regions (Kraus *et al.* 1997; Robertson *et al.* 2006). Despite this progress, the population-level and ecosystem effects of bycatch remain poorly understood.

Several studies worldwide have documented an impact of climate on population dynamics through local weather and large-scale climatic phenomena (Stenseth *et al.* 2002; Dulvy *et al.* 2008). Both climate and fisheries can affect the dynamics of marine predators, and effective management actions rely on an understanding of the respective magnitude of the population-level effect of these threats and their respective effects on specific life-history stages. However, very few studies have disentangled the effects of fisheries and climate on vital rates of species affected by bycatch (Nel *et al.* 2003; Frederiksen *et al.* 2004; Rolland, Barbraud & Weimerskirch 2008), and the direct link between fisheries and observed population declines has been hard to establish (Guenette *et al.* 2006). Our understanding of the consequences of fisheries bycatch on non-target species has improved for marine megafauna (albatrosses, whales), but less charismatic species have received less attention, although some are caught in large numbers in fisheries, and changes in their abundance may have important ecological consequences (Lewison *et al.* 2004). Efficient mitigation measures implemented to reduce bycatch often increase costs for fishing companies, which may prevent the implementation of the mitigating technology in the fisheries of developing nations (Lewison *et al.* 2004). In addition, funds allocated to reduce mortality for some non-target species may be at the expense of other non-target species with higher conservation concerns. In this context, bycatch can be considered as exploited populations (Lebreton 2005), and the theoretical basis for harvesting renewable resources can be utilized to explore the sustainability of the dynamics and interactions between natural mechanisms and bycatch. The logic here is that it might not be necessary to reduce bycatch to zero but to reduce bycatch to a sustainable level relative to the dynamics of the population affected by bycatch (Williams, Nichols & Conroy 2002).

The white-chinned petrel *Procellaria aequinoctialis* Linnaeus 1758 population is an interesting case study in the context of bycatch problems since it is by far the most common seabird species killed by fishing activities in the Southern Ocean (Robertson *et al.* 2006). Large numbers are killed in longline fisheries targeting Patagonian toothfish *Dissosticus eleginoides* Smitt 1898 (Nel, Ryan & Watkins 2002; Favero *et al.* 2003) and hake *Merluccius* spp. (Barnes, Ryan & Boix-Hinzen 1997). As many as 94% of seabirds estimated killed in the Kerguelen and Crozet archipelagos toothfish longline fisheries since 1997 were white-chinned petrels (Weimerskirch, Capdeville & Duhamel 2000; Delord *et al.* 2005). Although it is estimated that hundreds of thousands of pairs are breeding worldwide (Brooke 2004), detailed and complete surveys are lacking on the major breeding grounds. The species was moved from an IUCN listing of Lower Risk/Near Threatened

to Vulnerable in 2000 (Birdlife International 2000) following recent declines observed at sea (Woehler 1996) and at a breeding colony in South Georgia (Berrow, Wood & Prince 2000), combined with tens of thousands of individuals caught in fisheries each year. These declines may be related to fishing activities around their breeding and non-breeding grounds, but changes in demographic parameters in relation to climate fluctuations have never been investigated in this species. In addition, because breeding population sizes and demographic parameters are poorly known, and because there is little information on the at-sea distribution during the non-breeding season, it has been difficult to estimate the impact of fisheries related mortality on the dynamics of the white-chinned petrel population.

Here we use population survey data, capture–mark–recapture (CMR) methods, matrix population modelling and a method based on demographic invariants to investigate the effect of climate and fisheries on the demography of white-chinned petrels at Crozet archipelago, Southern Indian Ocean. The aims of this study are: (i) to estimate the demographic parameters and to determine the relative impact of climate and fisheries on the vital rates using a 20-year data set of life history data; (ii) to develop a matrix population model allowing us to explore the impact of climate and fisheries on the population rate of increase ( $\lambda$ ); (iii) to validate this model using population survey data; (iv) to assess whether the fisheries-induced additional source of mortality is sustainable or not for this population; and (v) to conduct population projections with different levels of fishing effort and climate change.

## Methods

### SPECIES ECOLOGY, STUDY AREA AND FIELD DATA

White-chinned petrels nest in more or less aggregated burrows, forming relatively dense colonies (Brooke 2004). Visits to the colonies start before dusk and continue during the first part of the night. Birds return to colonies in September and lay their single egg in November. Chicks hatch in January and fledge in April. During breeding, males and females alternate foraging trips at sea and feed on fish, krill and squid (Ridoux 1994; Catard, Weimerskirch & Chérel 2000).

Fieldwork was conducted at Possession Island (46°25'S, 51°45'E; c. 17 × 13 km), Crozet archipelago (Supplementary Material Fig. S1), between 1983 and 2004. Since 1985, 75 burrows have been inspected annually during breeding. Every year, all adult birds captured in the study burrows were marked with a stainless steel band during egg incubation, and all chicks were marked just before fledging. Two visits during the early incubation period (December), one visit at hatching (January) and one visit just before fledging (March) allowed each marked individual to be identified and its breeding success measured.

The total number of burrows and breeding pairs on Possession Island and the Crozet archipelago were estimated in 1983 and 2004 (Supplementary Material Appendix S1).

### POPULATION MODELLING

We chose a simple age/stage structured matrix population model (Supplementary Material Appendix S2) as this allowed us to assess the importance of the basic demographic parameters without going

beyond the limits of the data. The resulting matrix model was a linear, time varying matrix  $\mathbf{A}$  that provides the parameters for projecting a vector  $\mathbf{n}$  that gives the numbers of individuals in each age/stage from time  $t$  to  $t + 1$  as  $\mathbf{n}_{t+1} = \mathbf{A}_t \mathbf{n}_t$  (Caswell 2001).

The matrix model was run with various values of first year survival, starting with the one estimated from return rates, to find the value that provided the best fit to the data. Secondly, we performed a sensitivity analysis of the population growth rate,  $\lambda$ , to changes in the lower level demographic parameters using arcsin-scaled variance-stabilized sensitivities (Link & Doherty 2002). Thirdly, a life-table response experiment (Caswell 2001) was performed to quantify the contribution of the vital rates for which we had enough data to estimate their temporal variation to variability in  $\lambda$  (Supplementary Material Appendix S3). Finally, a stochastic matrix model was built using the relationships between vital rates and covariates to predict population growth under various scenarios of environmental change.

#### ESTIMATING BREEDING PARAMETERS AND JUVENILE SURVIVAL

Annual breeding success was estimated from the sample of 75 marked burrows as the proportion of eggs that fledged a chick. Age at first breeding was estimated from known aged individuals ringed as chicks that were observed breeding at the colony for the first time. Because petrels stay at sea during their first years of life, no CMR data is available for estimating juvenile and immature survival. The annual survival during the first years at sea was calculated to give the mean return rate observed in the study colony to 4 years, the minimum age at first breeding observed (Supplementary Material Appendix S2; Results).

#### ESTIMATING ADULT SURVIVAL AND RECRUITMENT

Field observations indicate that very few non-breeders were observed at the colony and that some individuals absent on the colony during a given year were seen again during the next or following breeding seasons. This is equivalent to temporary emigration from the study area which can be modelled using an unobservable state (Kendall & Nichols 2002). We thus defined two states: B, breeder and NB, non-breeder, and estimated adult annual survival, transition and recapture probabilities with multistate CMR models (Supplementary Material Appendix S4).

The recruitment probability was estimated using the CMR methodology developed by Pradel (1996) (Supplementary Material Appendix S4). The same recapture histories were used as for estimating survival but with only one state (B), as these models have not been developed for a multistate approach. Consequently, the parameters estimated were the probability that an individual breeding in a given year had not bred previously, and the recapture probability.

Survival and recruitment were estimated from a sample size of 248 individual capture histories. Recruitment was not estimated during the first 2 years of the study when the study colony was settled.

#### CLIMATE AND FISHERIES COVARIATES

Climatic fluctuations are often suspected of affecting populations through an indirect mechanism, where climate first affects primary production, this disturbance then being integrated along the trophic web up to predators (Frederiksen *et al.* 2004). In marine ecosystems, abundance data of prey consumed by predators are seldom available due to logistic constraints for sampling. We used proxies of the biotic production in the foraging zones which are strongly involved in controlling the quality of the physico-chemical environment available for the

primary production (Wilson & Adamec 2002). Two factors believed to have consequences for the white-chinned petrel demographic parameters were fitted as covariates: (i) sea surface temperature anomalies (SSTA); and (ii) southern oscillation index (SOI). SOI is closely associated to El Niño and provides an index of oceanographic and climatic conditions over a large spatial scale, which is associated with changes in marine food webs (Comiso *et al.* 1993) and population dynamics (Barbraud & Weimerskirch 2003). SSTA influences seabird breeding ecology but at a smaller spatial scale than SOI (Croxall, Trathan & Murphy 2002). Using ring recoveries, diet and radio-tracking data on white-chinned petrels from Possession Island (Ridoux 1994; Weimerskirch *et al.* 1999; Catard *et al.* 2000), we restricted SSTA to the geographical regions frequented by petrels during specific time periods of the year (Supplementary Material Appendix S5 and Fig. S1). Since portions of the oceanographic anomalies associated with the SOI follow the eastward hemispheric course of the Antarctic Circumpolar Current and reach the western South Indian Ocean 3–4 years later (Xie *et al.* 2002), we investigated the effects of the SOI of the current year and the SOI with a lag of 3 and 4 years (SOI<sub>-3</sub> and SOI<sub>-4</sub>) as covariates.

White-chinned petrels are potentially vulnerable to encounters with longline vessels fishing for toothfish in the immediate vicinity of their breeding sites at Crozet, and for hake around coastal shelf-edge habitats of South Africa (Weimerskirch *et al.* 1999). We tested for effects of longline fishing efforts targeting toothfish and hake on demographic parameters. Effort data were extracted from several sources (Supplementary Material Appendix S5 and Fig. S1.) and were expressed as numbers of hooks set. We also tested for the effect of the minimum bycatch estimate (Supplementary Material Appendix S5) on survival and recruitment. Recruitment of breeders at the colony being an age-dependent process, we tested the effect of fisheries covariates on recruitment with a lag of 1 and 2 years (*i.e.* for each covariate, we tested the effect of the covariate in year  $t - 1$  and  $t - 2$  on recruitment in year  $t$ ).

Since breeding individuals are known to catch bait while following vessels targeting toothfish (Catard *et al.* 2000), we predicted a positive effect of fishing effort for toothfish on breeding success. Given the large numbers of white-chinned petrels killed in fisheries, and the mean age of individuals found dead in longline vessels from both hake and toothfish fisheries (~4 years,  $n = 6$ , H. Weimerskirch and D. Besson, unpublished data), we predicted a negative effect of fishing effort and bycatch estimate on adult survival and recruitment. We had no a priori prediction on the effect of climatic covariates on demographic parameters.

#### DEMOGRAPHIC INVARIANT METHOD

Although matrix population models are useful to assess the importance of covariates on the population dynamics, it is seldom possible to account for all possible sources of uncertainty. We therefore used the demographic invariant method (Niel & Lebreton 2005) as an alternative modelling approach to assess the impact of bycatch (Supplementary Material Appendix S6).

All estimates reported in the text are  $\pm 1$  standard error (SE).

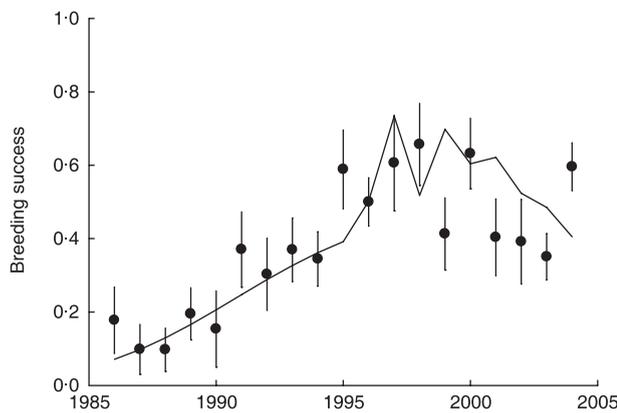
## Results

#### BREEDING POPULATION SIZE

In 1983, 9582 burrows were counted, giving an estimated number of 7707 breeding pairs. In 2004, the number of burrows counted

**Table 1.** Results of the final reduced mixed model showing variables with significant effects on annual breeding success of white-chinned petrels at Possession Island between 1986 and 2004. Test statistics ( $F$  and  $P$  values) are type III, and  $df$  (numerator, denominator) for fixed effects were estimated using the Satterthwaite approximation. Goodness-of-fit:  $\chi^2/df = 0.91$ . Variance components plus their SE are shown for random effects

Effect	$F$	$df$	$P$	Estimate	SE
<b>Fixed effects</b>					
Intercept	15.76	1, 27.35	< 0.001	-2.657	0.669
Trend	8.92	1, 18.28	0.008	0.387	0.130
Trend <sup>2</sup>	5.99	1, 14.01	0.028	-0.014	0.006
TOOTH	4.69	1, 14.68	0.047	0.387	0.179
<b>Random effects</b>					
Burrow				0.155	0.134
Year				0.248	0.189
Residual variance				0.909	0.066



**Fig. 1.** White-chinned petrel breeding success at Possession Island as a function of year. Regression line is estimated from the statistical model in Table 1. Error bars indicate SE.

was 7531, and the number of breeding pairs was estimated at 5321. Burrow detection probability (Supplementary Material Appendix S1) was estimated in 2004 at  $0.92 \pm 0.02$  ( $CI_{95}$ : 0.88–0.95). Assuming a constant detection probability, the number of breeding pairs was estimated at 8377 ( $CI_{95}$ : 8020–8733) and 5783 ( $CI_{95}$ : 5538–6028) in 1983 and 2004, respectively. The number of breeding pairs declined by 37.1% in 21 years, corresponding to a  $\lambda$  of  $0.983 \pm 0.001$  (i.e. an average rate of decline of 1.76% per year), lower than 1 ( $z = 12.16$ ,  $P < 0.001$ ).

#### BREEDING SUCCESS

The mean breeding success during the period 1986–2004 was 38.2% ( $\pm 4.2$ ). Breeding success increased nonlinearly during the study period (Table 1), varying around an average of 51.4% since 1995 (Fig. 1). None of the climate covariates were found to affect breeding success (Table 1). Fishing effort for toothfish had a positive effect on breeding success (Table 1). The generalized linear mixed effect model including the effects of these significant variables explained 68.5% of the variance in breeding success. The random effect for burrow

**Table 2.** Modelling the impact of climatic and fishery covariates on survival.  $T$  and  $T^2$  respectively indicate linear and quadratic trends;  $df$  (numerator, denominator)

Model	$F$	$df$	$P$	Slope	$CI_{95}$
$S_T$	2.432	1, 16	0.138		
$S_{T+T^2}$	4.262	2, 15	0.034		
$S_{SOI}$	0.073	1, 16	0.792		
$S_{SOI-3}$	60.39	1, 16	< 0.001	2.640	0.631–4.650
$S_{SOI-4}$	0.870	1, 16	0.365		
$S_{SSTALT}$	0.628	1, 16	0.439		
$S_{SSTAST}$	0.001	1, 16	1		
$S_{SSTAW}$	0.143	1, 16	0.710		
$S_{TOOTH}$	0.005	1, 16	0.500		
$S_{HAKF}$	0.983	1, 16	0.168		
$S_{NKILL}$	0.369	1, 16	0.276		

identity accounted for 11.8% of the total variance in breeding success (calculated as the sum of the burrow identity, year and residual variance components).

#### AGE AT FIRST BREEDING AND JUVENILE SURVIVAL

The mean observed age at first breeding was 6.1 years ( $\pm 0.3$ ,  $n = 16$ , min = 4, max = 9). Most (87.5%) individuals were observed breeding for the first time between 4 and 7 years of age. Only 16 (4%) of the 401 chicks ringed since 1986 were observed as breeding recruits in the colony. Excluding the last 7 years of the study for which the recruitment process was not terminated, the average return rate was 9%, and the average annual juvenile survival was low and estimated at 39.3% with a low precision ( $SE = 29.2\%$ ).

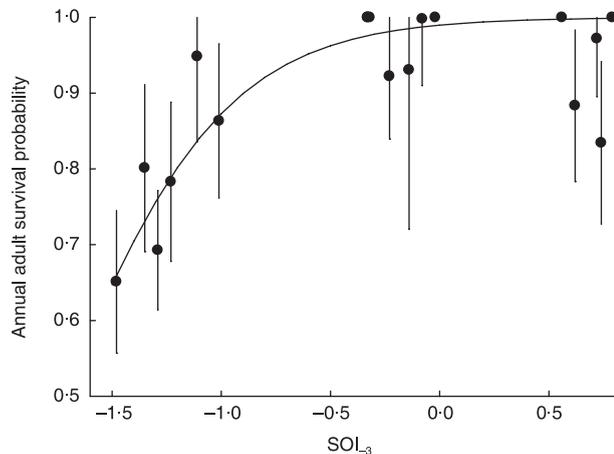
#### ADULT SURVIVAL

The GOF test indicated that the Jolly–Move model fitted the data satisfactorily ( $\chi^2_{63} = 136.33$ ,  $P = 0.97$ ). Modelling the recapture probability indicated that it was constant across years (Supplementary Material Table S1), and high ( $0.826 \pm 0.057$ ,  $CI_{95}$ : 0.686–0.911). Transition probabilities varied according to state but not year. Local survival of adults was estimated at  $0.895 \pm 0.019$  ( $CI_{95}$ : 0.851–0.928). Transitions between states were not random. Non-breeders in year  $t$  were less likely to become breeders in year  $t + 1$  ( $0.178 \pm 0.058$ ) than breeders in year  $t$  ( $0.766 \pm 0.042$ ).

Only  $SOI_{-3}$  was related to the probability of adult survival (Table 2), and explained 73.3% of its variability. Adult survival was positively related to  $SOI_{-3}$  (Fig. 2), indicating that adult survival decreased 3 years after El Niño events. The effect of  $SOI_{-3}$  was strong, the  $F$ -test remaining significant after correction of the  $P$  value using the Bonferroni method.

#### RECRUITMENT

The GOF test of the more general model  $p_i \gamma_i$ , where  $p$  and  $\gamma$  are respectively the capture and seniority (1-recruitment) probabilities, was significant ( $\chi^2_{63} = 136.33$ ,  $P < 0.001$ ). The lack of fit was due to Test 2.Ct ( $\chi^2_{16} = 83.15$ ,  $P < 0.001$ ), indicating



**Fig. 2.** White-chinned petrel adult survival at Possession Island as a function of  $SOI_{-3}$ . Regression line is estimated from a statistical model on a logit scale, and point estimates are with full variation over time. Error bars indicate SE.

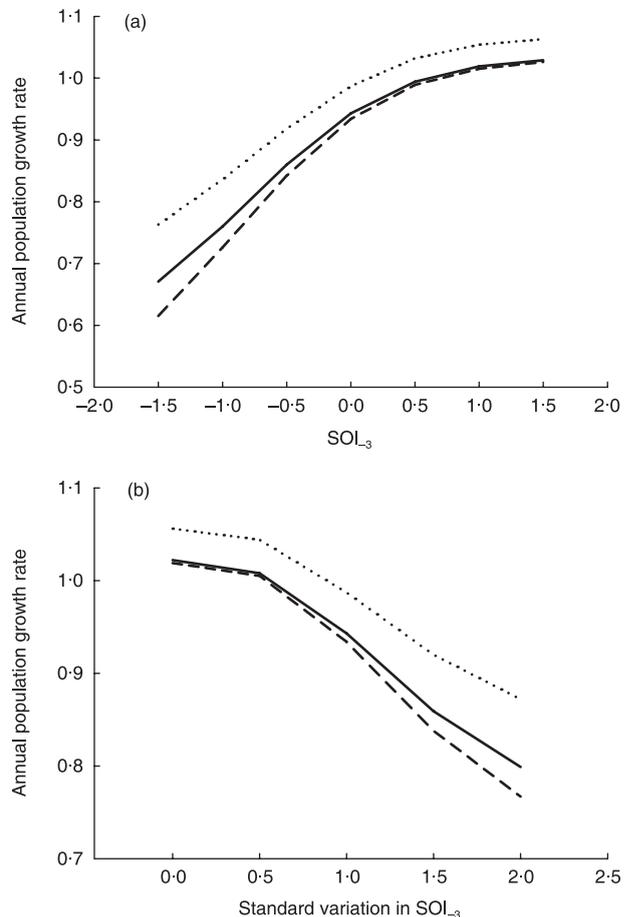
that individuals captured in year  $t$  were more likely to be captured in year  $t + 1$  than those not captured in year  $t$ . Following Lebreton *et al.* (1992), we made use of the overdispersion factor ( $\hat{c} = 2.164$ ).

Model selection indicated that recapture probability was constant and recruitment time-dependent. As expected, fisheries covariates negatively affected recruitment probability in year  $t$ , but also in year  $t + 1$  and  $t + 2$  (Supplementary Material Table S2). Most important was the effect of the toothfish fishery with a lag of 1 year, which remained significant using a Bonferroni corrected  $P$  value, and which explained 53.2% of the variability in recruitment. The number of individuals killed also negatively affected the recruitment probability in year  $t + 1$  and  $t + 2$  (Supplementary Material Table S2), and this effect remained nearly significant after using the Bonferroni method.

#### POPULATION MODELLING

The asymptotic properties of the matrix model with time-varying parameters were used for the starting age distribution of the simulation model. With a juvenile survival of 0.393, the predicted  $\lambda$  over the study period was  $0.907 \pm 0.026$ , lower than 1 ( $z = 3.58$ ,  $P < 0.001$ ). True juvenile survival must be much higher since we did not take into account the probability of detecting returning birds and of permanent emigration, and only a small part of the entire population was monitored. The best fit to the observed  $\lambda$  was obtained for a value of juvenile survival of 0.7. The sensitivity analysis of  $\lambda$  to demographic parameters showed that it is mainly sensitive to adult survival which showed the most important contribution to the variance of  $\lambda$  (Supplementary Material Table S3).

Incorporating the improvement in breeding success observed since 1995 in the population model and keeping other parameter values and their variance constant, achieved  $\lambda \approx 1$ . Using the mean values of SOI, toothfish and hake fishing efforts during the last 3 years of the study achieved  $\lambda = 0.99$ ,

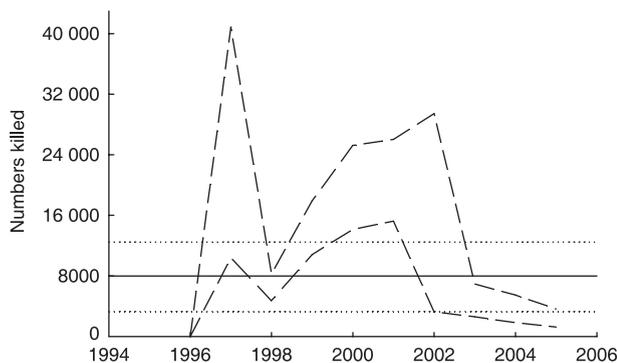


**Fig. 3.** Mean projected growth rate of the white-chinned petrel population of Possession Island from a stochastic matrix model as a function of a change in (a) mean  $SOI_{-3}$ , and (b) standard deviation of  $SOI_{-3}$ . Plain line indicates the current effect of fisheries, dashed line a doubling of fishing effort of both toothfish and hake fisheries, and dotted line no effect of fisheries.

indicating that the population is still declining at a slow rate of 1% per year. The stochastic model indicated that the projected mean  $\lambda$  was strongly dependent both on variations in the mean and variability of  $SOI_{-3}$  and fisheries activities (Fig. 3). When fisheries are operating,  $\lambda$  is more sensitive to a decrease of the mean or to an increase of the variance of  $SOI_{-3}$ . It is likely that if the fisheries continue to operate at current levels the population will probably not recover unless  $SOI_{-3}$  increases importantly. If the fisheries continue to operate and  $SOI_{-3}$  decreases, it is likely that the population will decrease dramatically. A doubling of fishing efforts would strongly impact  $\lambda$  for decreasing, but not increasing, values of  $SOI_{-3}$ .

#### POTENTIAL EXCESS GROWTH

Using the estimated average age at first breeding (6.1) and adult annual survival (0.895), we obtained  $\lambda_{\max} = 1.094$ . On Possession Island, burrows were only found on 5° to 30° vegetated slopes at a maximum altitude of 200 m above sea level, and average density was 0.0714 breeding pairs 100 m<sup>-2</sup>. The estimated surface area favourable for petrels on the other



**Fig. 4.** Numbers of white-chinned petrels killed by the longline toothfish fishery in the CCAMLR areas 58.6 and 58.4.4 (dashed lines). Upper and lower dashed lines indicate maximum and minimum estimates, respectively. Horizontal lines indicate the potential excess growth. Solid line represents the mean estimate and pointed lines represent minimum and maximum estimates.

islands of the Crozet archipelago was about  $25 \cdot 10^6$  m<sup>2</sup>, yielding 23 600 (min 9800; max 36 800) breeding pairs. Based on the matrix population model, the population size of the entire archipelago was estimated at 106 700 individuals (min 44 300; max 166 300). Taking into account the decline of the population of 37% in 21 years, the population size in the early 1980s was 169 300 individuals (min 70 300; max 264 000). Given these numbers, any additional source of mortality that approaches 8000 (min 3300; max 12 500) individuals will be a source of serious concern for this population.

The minimum estimates of the numbers of white-chinned petrels killed by the toothfish fishery around the Crozet archipelago exceeded 8000 individuals in 1997, 1999, 2000 and 2001 (Fig. 4), but numbers killed have declined below 8000 since 2003. Using the most conservative approach, the numbers killed still exceeded 12 500 in 2000 and 2001.

## Discussion

This study is among the first to use simultaneously several modelling approaches to examine the effects of climate and fisheries on the population dynamics of a marine vertebrate. Results suggest that the breeding population size of the most frequently accidentally killed seabird species in the Southern Ocean has decreased by  $\approx 37\%$  in 21 years at one of its main breeding localities. This adds to a growing body of evidence for declining populations of white-chinned petrels with a 28% decline of occupied burrows at Bird Island, South Georgia between 1978 and 1998 (Berrow *et al.* 2000), and a 86% decline of at-sea densities in the Prydz Bay area between 1980 and 1992 (Woehler 1996). There is strong inference for this decreasing trend at Crozet since both approaches used to estimate  $\lambda$  (direct survey, matrix modelling) led to a  $\lambda$  lower than 1. Climate and longline fisheries probably contributed to the population decline, highlighting the complexity of the impact of global changes on animal populations and the fact that fishery, oceanographic and climate conditions act in combination to influence seabird demography.

The negative effects of fishing effort and bycatch estimates on recruitment probability suggest a negative effect on the number of recruits through juvenile and immature survival. This coincides well with the mean age of birds found dead in longline vessels targeting toothfish ( $\sim 4$  years), and by the very low numbers of ringed chicks recruited in the study population, although this could partly reflect some immigration to other areas. Higher vulnerability of younger individuals to fishing gear has been observed in other seabird species (Murray *et al.* 1993; Gales, Brothers & Reid 1998; Bregnballe & Frederiksen 2006). Younger birds may (i) spend more time in areas with high longlining efforts than adult birds, (ii) be less efficient foragers than adults and may therefore attempt to fish behind vessels more frequently, (iii) be more hungry than adults and take more risks behind vessels, and (iv) be less experienced than adults in foraging behind vessels without getting hooked.

Adult survival was relatively lower than in the closely related Cory's shearwater *Calonectris diomedea* Scopoli 1769 (0.927, Mougouin, Jouanin & Roux 2000) and Westland petrel *Procellaria westlandica* Falla 1946 (0.965, Waugh *et al.* 2006). This may reflect permanent emigration from the study colony (which we were not able to estimate), or species to species variation. Contrary to our prediction, we did not detect an effect of fishing effort on adult survival. It is possible that our assumption of a fishing effort proportional to the bycatch proportion of the population was false. This may be the case if mitigation measures to reduce incidental mortality exist, or if the relationship between fishing effort and bycatch mortality is not linear with a threshold value attained at high fishing efforts. However, we did not find a significant relationship between numbers caught and adult survival, mitigation measures have only been systematically implemented since 2001 (Delord *et al.* 2005), and as explained above and coherent with this finding, few adults died by getting caught in longlines.

Adult mortality decreased 3 years after El Niño events. This result adds to a growing body of evidence that large-scale environmental conditions influence the demography of marine predators (e.g. Thompson & Ollason 2001; Votier *et al.* 2005). El Niño conditions are frequently associated with warmer sea surface temperature in the Crozet basin with a lag (Xie *et al.* 2002), which negatively affect primary production through a limitation of surface-mixing reducing the upward nutrient supply (Sedwick *et al.* 2002; Behrenfeld *et al.* 2006), and may therefore affect petrels indirectly by altering food availability. There is recent evidence for a propagating mode of SOI evolving eastward from the eastern Pacific into the southern Atlantic basin (Tourre & White 2005), with warm sea surface temperature occurring in the South Atlantic about 2.5 years after El Niño events and affecting the demographic performances of Antarctic fur seals *Arctocephalus gazella* Peters 1875 at South Georgia (Forcada *et al.* 2005). Some climate models forced by future greenhouse warming suggest an increased El Niño frequency and intensity (Merryfield 2006), and our prospective study suggests that an increase in the intensity or the variability of El Niño events may have negative impacts on the populations of white-chinned petrels.

Breeding success increased during the study period, but this increase may only concern the study colony where a rat control programme has been conducted since the late 1980s (Jouventin, Bried & Micol 2003). Breeding success is still probably low elsewhere where no rat control has been undertaken. Residual variations of breeding success around the increasing trend were due to fluctuations in fishery activities, which positively affected breeding success. This is in accordance with studies on the foraging ecology of breeding white-chinned petrels at Possession Island. In 1997, remains of Patagonian toothfish were recorded in 40% of stomach samples collected after foraging trips, and preys associated with fisheries (bait, toothfish) were present in 70% of the chick's food samples (Catard *et al.* 2000). No fishery waste was found between 1981 and 1983 within the same population (Ridoux 1994) when no longline fishery was active. Positive relationships between breeding success and fishery activities are known from other seabird species (e.g. Oro 1999; Tuck *et al.* 2001). This may indicate that some species directly benefit from offal resulting from increased fishing activities, although a purely correlative pattern cannot be excluded. Nevertheless, given the small contribution of breeding success to  $\lambda$ , the effect of fisheries through breeding success is small, and might even be negative on a long-term scale if fish stocks are overexploited and the structure of food webs is affected.

Although our results suggest an effect of climate on the dynamics of this petrel population, there was still some uncertainty for an effect of fisheries originating from the fact that immature survival could not be estimated from CMR data and the effect of fishing effort on this parameter could not be directly tested. Further evidence for a negative effect of mortality in fisheries on the population dynamics comes from the demographic invariant method. Numbers killed by just the toothfish fishery exceeded the potential excess growth during several years, indicating that this fishery negatively impacted the population. These are conservative figures since we could only estimate the numbers killed by the toothfish fishery, the total numbers killed being underestimated. The potential excess growth is very sensitive to the value of  $\beta$  which was not estimated in our study but taken from Wade (1998). In the future, the value of  $\beta$  could be increased (decreased) to adjust the potential excess growth if the population increases (decreases) while still experiencing a known level of incidental mortality. The decrease in the numbers killed since 2002 probably reflects the effect and improvement of recent conservation measures including seasonal closure, streamer lines and line weighting (Delord *et al.* 2005).

To conclude, our results suggest that both climate fluctuations and fisheries affected the population dynamics of white-chinned petrels. Because of the diversity and plasticity of the foraging strategies of marine top predators at the species and population levels (Weimerskirch 2007), more studies disentangling the effects of climate and fisheries on their dynamics are needed to understand the underlying processes. Better knowledge on the status (e.g. sex, age) and at-sea distribution of individuals caught in longlines is needed to facilitate our understanding of the demographic processes involved. This

additional information could be modelled together with demographic and bycatch data using Bayesian integrated population modelling that would allow efficient use of information in the data and description of uncertainty (Punt *et al.* 2001, Maunder 2004). For white-chinned petrels, our and previous studies suggest that several actions (eradication of introduced predators, reducing bycatch) may help the populations to recover in the long term, depending on the future impact of climate.

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## Supporting Information

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

**Fig. S1.** Map of the study area.

**Table S1.** Modelling probabilities of recapture, transition and survival

**Table S2.** Modelling the impact of covariates on recruitment

**Table S3.** Sensitivity of  $\lambda$  to demographic parameters

**Appendix S1.** Estimating the number of breeding pairs

**Appendix S2.** Life-cycle diagram and matrix population model

**Appendix S3.** Estimating the contribution of the vital rates to variability in  $\lambda$

**Appendix S4.** Estimating adult survival and recruitment

**Appendix S5.** Climatic and fisheries covariates

**Appendix S6.** Estimating the maximum annual growth rate

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