Combined impacts of longline fisheries and climate on the persistence of the Amsterdam Albatross *Diomedia amsterdamensis*

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Incidental capture of seabirds in longline fishing gear is a central issue in the conservation of many long-lived marine species. Despite growing evidence of climate-induced effects on population trends of long-lived species, climate change remains generally overlooked in most risk assessments of seabirds. Because variation in climate may interact with the detrimental effects of bycatch, considering climate is of great importance, especially in the context of ongoing global warming. This paper examines the combined effects of bycatch and climate change on the persistence of one of the world's rarest birds, the Amsterdam Albatross *Diomedea amsterdamensis*, which has a single population in the upland plateau of Amsterdam Island (Southeast Indian Ocean). Using continuous monitoring from 1983 onwards, we first estimated the relationship between climate and the species' demographic parameters. We then built a stochastic matrix population model to estimate the population growth rate and the probability that the population declines below the level recorded in 1983 of nine breeding pairs under different scenarios involving the joint effects of additional mortality caused by longline fisheries and climate change. The results suggest that the demography of the Amsterdam Albatross is influenced by climate in both breeding and wintering grounds and that these relationships may to some extent compensate for the impact of additive bycatch mortality. However, these compensatory effects would be negligible if the annual additional mortality exceeds around six individuals per year, suggesting that the resumption of longline fishery in the foraging range of the Amsterdam Albatross would rapidly put this species at risk of extinction.

Keywords: *Diomedea amsterdamensis*, fishing effort, Indian Ocean Dipole, multistate capture-recapture models, stochastic matrix models.

Growing concerns have been expressed about incidental take of long-lived non-targeted marine vertebrates in global fisheries through bycatch (Lewison *et al.* 2004a). With increases in fishing effort resulting from declines in fish stocks (Myers & Worm 2003), large marine vertebrates such as marine mammals (Read *et al.* 2006), sea turtles (Lewison *et al.* 2004b) and seabirds (Brothers *et al.* 1999) have all been hooked or entangled in fishing gear deployed to catch valuable fish species. Because of their long lifespan and a deferred reproduction resulting in a low maximal population growth rate (Saether & Bakke 2000), long-lived species are particularly sensitive to the negative impact of bycatch (Lewison *et al.* 2004a). Population-specific data and stochastic matrix models have been used to investigate how interactions with fisheries impact their population persistence and to evaluate the efficiency of mitigation measures when bycatch was not sustainable (Crowder *et al.* 1994, Caswell *et al.* 1998, Lewison & Crowder 2003, Arnold *et al.* 2006, Goldsworthy & Page 2007).

It has become increasingly clear that both local (e.g. temperature, precipitation) and large-scale climatic phenomena [e.g. El Niño Southern Oscillation (SOI), North Atlantic Oscillation (NAO)]

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affect the productivity of terrestrial and oceanic ecosystems (Stenseth *et al.* 2002). Several long-term studies have documented links between climate and breeding performance of long-lived marine species, mediated probably through change in food quality and/or availability (Barbraud & Weimerskirch 2001, Forcada *et al.* 2005, Saba *et al.* 2007). Although adult survival of large-bodied vertebrates may be buffered against environmental variability (Pfister 1998, Gaillard & Yoccoz 2003), recent studies have shown that climatic variation can affect this key demographic rate, thereby threatening the persistence of populations of these long-lived species (Croxall *et al.* 2002, Jenouvrier *et al.* 2005, Le Bohec *et al.* 2008, Rolland *et al.* 2008). Although projected climate change has thus far received little attention in risk assessments of long-lived populations threatened by accidental bycatch, it is considered an important additional threat for species already threatened by local and global environmental changes (McCarty 2001). The available evidence indicates that current global warming will continue (and even accelerate) over the next 50–100 years (IPCC 2008). Therefore, it is critical to assess the impact of future climate change on the viability of populations also threatened by interactions with fisheries. This is even more critical for rare species that generally have small and fragmented populations because extreme climatic shifts could significantly reduce already small populations and thereby increase extinction risk. Risk assessments of the effect of future climate change require detailed information on the demographic parameters of the species concerned (Coulson *et al.* 2001) and knowledge of the

functional relationship between vital rates and climatic variability.

The Amsterdam Albatross *Diomedea amsterdamensis* is an excellent candidate for such an analysis. It is a large albatross (6–7 kg) endemic to Amsterdam Island (37°49′S, 77°32′E; Fig. 1), an isolated island in the Indian Ocean (Jouventin & Roux 1983). This obligate biennial breeder (Jouventin *et al.* 1989) returns to its breeding grounds in late January, and lays one egg in late February, which hatches in May, the chick usually fledging from mid-January to early February of the following year (Jouventin *et al.* 1989). After fledging, birds stay at sea for several years before returning to the breeding colony as non-breeders and eventually recruiting into the breeding population. Satellite tracking has shown that Amsterdam Albatrosses forage over a large zone around Amsterdam Island when breeding (i.e. 50–95°E/30–42°S, Fig. 1, Waugh & Weimerskirch 2003) and that the range of non-breeding birds during 'sabbatical' years (i.e. after the successful raising of a chick) ranges from southeastern Africa to waters off southwestern Australia (i.e. 20–120°E/29–43°S; Fig. 1). With an overall population size estimated at fewer than 200 birds, including about 50 mature individuals (Weimerskirch & Jouventin 1998), this is one of the world's rarest birds (Croxall & Gales 1998) and is listed as Critically Endangered (BirdLife_International 2009). Weimerskirch *et al.* (1997) have suggested that the incidental bycatch due to the overlap between the Amsterdam Albatross's foraging zone (Fig. 1, Waugh & Weimerskirch 2003) and the longline fisheries for the Southern Bluefin Tuna *Tunnus maccoyii* during
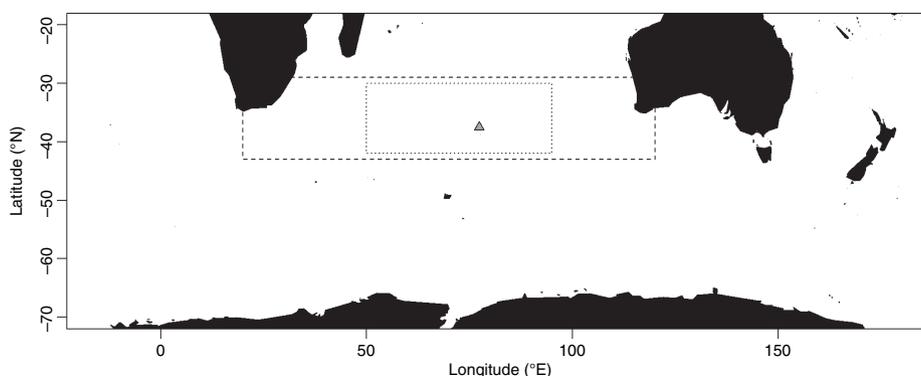

Figure 1. Foraging areas of the Amsterdam Albatross in the Indian Ocean during breeding periods (dotted line) and during non-breeding sabbatical years (dashed line, Waugh & Weimerskirch 2003). Amsterdam Island is represented by the grey triangle (37°50′S, 77°31′E).

the 1960s and 1970s (Tuck *et al.* 2003) could explain the small number of adults when the species was first described in 1983. Although longline fishing effort targeting the tuna has declined in most of the foraging range of the Amsterdam Albatross (Klaer & Polacheck 1997) and there is no record of accidental take by commercial fishery, this species remains sensitive to the resumption of any longline fishery in its foraging range (Inchausti & Weimerskirch 2001). Because fishing effort has been extremely dynamic over space and time in the subtropical Indian Ocean (Klaer & Polacheck 1997, Tuck *et al.* 2001), the re-establishment of longline fisheries around Amsterdam Island constitutes a very realistic possibility and could increase the level of threat faced by this species.

In this paper, we investigated the joint effect of additional adult mortality due to incidental bycatch and of climate change on the population dynamics of the Amsterdam Albatross. Here, our goal was to determine whether climate change is likely to aggravate or to compensate for the detrimental effect of bycatch and to estimate the relative role of climate in the dynamics of the Amsterdam Albatross. We used the opportunity of a unique long-term monitoring programme to estimate the demographic parameters of the species and investigate the relationships between demography and environmental covariates (i.e. fishery effort and climatic indices). Relying on these relationships, we constructed a stochastic demographic model that allowed us to investigate the joint effects of continuing climate change and of the removal of varying number of adults due to bycatch in its foraging and wintering ranges and to estimate the probability of decline of the Amsterdam Albatross.

METHODS

Study area and data collection

The Amsterdam Albatross has been monitored annually since 1983 when it was first identified as a species (Fig. 2), and all individuals attending the island have been individually marked. Starting in early March in each year, the entire population has been screened once a week for breeding pairs and non-breeders. The identity of individuals already marked has been recorded and new birds and chicks marked with numbered stainless steel and plastic colour bands. From April to January,
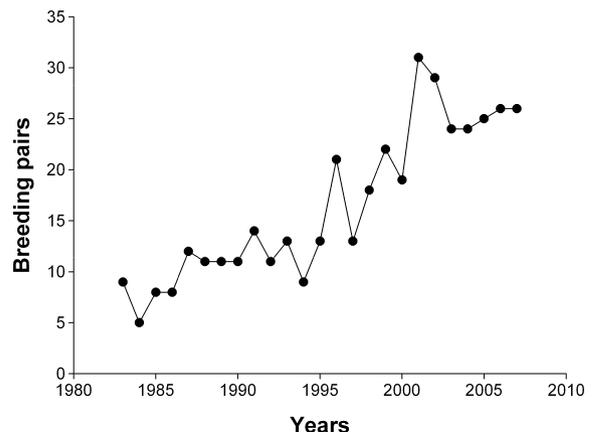

Figure 2. Changes in the population size of Amsterdam Albatross on Amsterdam Island from 1983 to 2007.

nests have been visually checked once a month to determine breeding status of adults and their breeding performance. From these records, three breeding states were attributed: (i) breeders that produced a fledging (hereafter successful breeders, *SB*), (ii) breeders that lay an egg but failed to produce a fledging (failed breeders, *FB*) and (iii) adult non-breeders (*NB*).

Estimation of demographic parameters

Survival and breeding probabilities
Demographic parameters were estimated with multistate capture-recapture models (Brownie *et al.* 1993). These models include three kinds of parameters: the probability that a marked animal in state r has survived from time i to $i+1$ (S_i^r), the conditional transition probability that an animal in state r at time i is in state s at time $i+1$, given that the animal survived until $i+1$ ($\psi_i^{r \to s}$), and the probability that an animal is captured at time i in state r, given that it is alive and present at time i (p_i^r).

Adult survival rate and transition probabilities between breeding states were estimated first in a multistate capture-recapture model. Because the Amsterdam Albatross is an obligate biennial breeder, successful breeders skip the next breeding season and are therefore unavailable for detection on breeding grounds. We therefore selected a model that considers two observable breeding states (*SB* and *FB*) and one unobservable breeding state (*NB*) (Kendall & Nichols 2002), the latter having by definition a capture probability equal to zero. We also assumed that there was no age or

experience effect on vital rates amongst adults, and assumed an equal adult survival rate regardless of breeding state. Due to the small population size of the species, we had to assume that the probability of breeding transitions was constant over time. Our starting model for the estimation of these two parameters therefore included time-dependent survival probabilities, time- and state-dependent capture probabilities, and constant state-dependent transition probabilities. Data consisted of all birds marked from 1983 to 2006 and resighted or recaptured from 1984 to 2007.

Juvenile survival rate and recruitment probabilities were estimated with a second multistate capture-recapture model considering two states: juvenile birds (*J*) that remain unobservable until recruiting into the breeding population, and birds that have recruited into the breeding population (*B*) (Pradel & Lebreton 1999). Separating the estimation of these two vital rates from adult and breeding probabilities was necessary due to the small size of the dataset. Recruitment into the breeding population is irreversible and the transition probability between *B* and *J* was thus set to zero (and its complement was set to one) and recapture probabilities of juveniles were also set to zero. Given that the observed age at first reproduction ranged from 7 to 17 years (mean = 9.39, sd = 2.02; supplementary Fig. S1), recruitment probability ($\psi_i^{J \to B}$) was estimated from age 7 to 17 years (where age 0 = fledging). Accordingly, juvenile survival was estimated as the cumulate survival probability over the age interval 0–7 years (Reed *et al.* 2003). Our starting model included time- and state-dependent survival rates, time-dependent capture rates and constant state-dependent transition probabilities. This second analysis considered only birds marked as chicks from 1983 to 1994 and recaptured from 1991 to 2007 to ensure that all birds had recruited.

There are no formal goodness-of-fit (GOF) tests available for multistate mark–recapture models with unobservable states. However, one way of verifying whether our starting models reasonably fitted the data in the first multistate model was to perform GOF tests for multistate models with the two observables states (*SB* and *FB*) (Pradel *et al.* 2003) using the programme U-Care (Choquet *et al.* 2003). We simplified each of the two starting models to obtain two minimal models that were used to investigate the effect of explanatory variables (fisheries and climate change) on each vital

rate. Model selection, performed using the program MSURGE (Choquet *et al.* 2004), was based on Akaike's Information Criterion adjusted for small sample size (AICc, Burnham & Anderson 2002), and AIC weights (w_i) were used to indicate the strength of evidence among a set of candidate models (Burnham & Anderson 2002).

We considered the selected models to explain the yearly variations in adult and juvenile survival probabilities in terms of environmental covariates. We used ANODEV (Skalski *et al.* 1993) to estimate the significance of each covariate in explaining the temporal variation of the parameter of interest and estimated the proportion of the total temporal variation of a vital rate explained by environmental covariates using deviance ratios (Schemper 1990). A sequential Bonferroni correction (Rice 1995, Graham 2003) was used to adjust for the number of candidate environmental covariates tested.

Environmental covariates

We considered a first set of covariates related to longline fishery effort over the foraging and wintering areas of the Amsterdam Albatross. These areas were delimited by data from 15 individuals that were equipped with ARGOS satellite tags and five individuals with geolocating devices between 1996 and 2007 (Waugh & Weimerskirch 2003, Weimerskirch unpubl. data), and whose movements constitute the only available evidence of habitat use for the species to date. We used the total number of hooks deployed annually by tuna longliners each year in the foraging area used during breeding (i.e. 50–95°E/30–42°S, hereafter called '*hooks^B*') and in wintering grounds (i.e. 20–110°E/29–43°S, hereafter called '*hooks^NB*'; Table 1) as a proxy of the fishing effort in each area (Véran *et al.* 2007).

A second set of covariates included climatic variables that could indirectly affect seabirds through their effect on the primary production and subsequently cascade through the food chain to influence the abundance of food resources used by top predators (Aebischer *et al.* 1990, Bertram *et al.* 2001). We considered the sea surface temperature anomaly ('*SST*'; see Table 1) that is linked to the vertical mixing of the water masses and that controls the quality of the physico-chemical environment and ultimately pelagic primary production (Wilson & Adamec 2002). Annual values of SST were averaged over the foraging zone during

Table 1. Environmental covariates used in the analyses of adult survival of Amsterdam Albatrosses at Amsterdam Island.

Notation	Meaning	Time period	Source
$hooks^B$	Number of hooks in breeding zone (cf. Fig. 1)	Annual	CCSBT[a] and IOTC[b]
$hooks^{NB}$	Number of hooks in sabbatical zone (cf. Fig. 1)	Annual	CCSBT[a] and IOTC[b]
SST^B_{hatch}	Mean sea surface temperature (SST) in breeding zone	March to May	http://iridl.ldeo.columbia.edu/SOURCES/.IGOSS/nmc/
SST^{NB}_{yr}	Mean SST in sabbatical zone	Annual	http://iridl.ldeo.columbia.edu/SOURCES/.IGOSS/nmc
DMI	Dipole Mode Index	June to November	http://www.jamstec.go.jp/frcgc/research/d1/iod/
SOID	Southern Indian Ocean Dipole	December to March	

[a]Commission for the Conservation of Southern Bluefin Tuna; [b]Indian Ocean Tuna Commission.

incubation ('SST^B_{hatch}') and over the non-breeding zone during the current year (SST^{NB}_{yr}). Temporal trends in SST during the studied period (i.e. 1983–2006) were not significant (SST^B_{hatch}: $r = 0.009$, $P = 0.389$; SST^{NB}_{yr}: $r = 0.003$, $P = 0.575$; Fig. 3a).

We also assessed the influence of large-scale climatic indices that reflect climate variability across the Indian Ocean (Fig. 3b). We considered the Subtropical Indian Ocean Dipole index (SIOD), which measures the intensity of the east (90–100°E, 0–10°S)–west (55–65°E, 27–37°S) dipole in the SST anomalies (Behera & Yamagata 2001) in the eastern subtropical Indian Ocean. Positive values of SIOD are associated with a warm SST anomaly over the western subtropical Indian Ocean and a cold SST anomaly over the eastern subtropical Indian Ocean (Behera & Yamagata 2001). We also considered the dipole mode index (DMI), which quantifies the tropical Indian Ocean Dipole (IOD) and is known to be independent from SIOD (Behera & Yamagata 2001). IOD is related to wind stress, sea surface temperature and precipitation anomalies over the Indian Ocean (Saji *et al.* 1999). DMI is defined as the difference in SST anomaly between the western (50–70°E, 10°N–10°S) and eastern (90–110°E, 0–10°S) tropical Indian Ocean (Saji *et al.* 1999). Positive values of DMI (see Table 1 for sources of data) are associated with a warm SST anomaly over the western Indian Ocean and a cold SST anomaly over the eastern tropical Indian Ocean (Saji *et al.* 1999). Although measured in the northern Indian Ocean, IOD also affects SST over foraging areas used by the Amsterdam Albatross: negative DMI values are associated with an increase of SST in the southern Indian Ocean (i.e. < 35°S, Saji *et al.* 1999). For both indices, the sign of the index reverses when SST anomalies swing over to the opposite phase. Neither index increased during the studied period (DMI: $r = 0.009$, $P = 0.401$; SIOD: $r = 0.040$, $P = 0.110$; Fig. 3a). None of the climatic covariates was correlated with each other (Table S1).
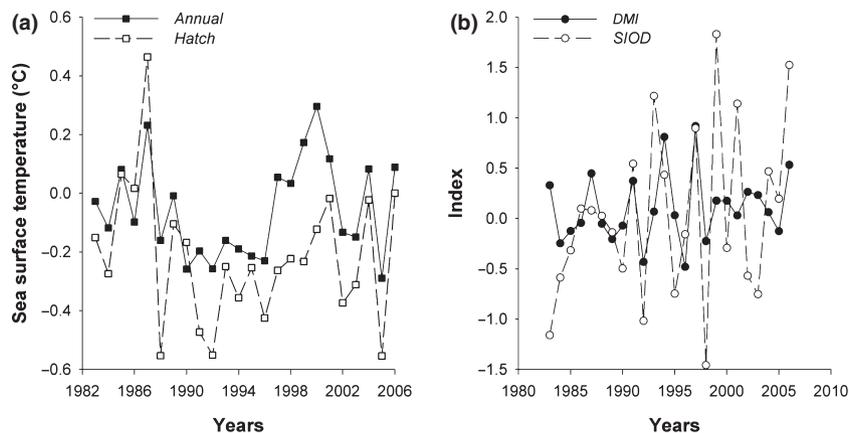

Figure 3. Sea surface temperature (*annual*: annual mean; *hatch*: mean during hatching period) from 1983 to 2006 (a), and Dipole Mode Index (DMI) and Southern Indian Ocean Dipole (SIOD) from 1983 to 2006 (b).

Population matrix model

Population growth rate, sensitivity analyses and contribution

We formulated a matrix population model that mixed age and stage classes and assumed equal survival probabilities for males and females (Arnold *et al.* 2006). This pre-breeding census model (Caswell 2001) consists of five juvenile age-classes, one pre-breeding stage-class and three stage-classes according to breeding status (Fig. S2). Model parameters were the recruitment probability $\psi^{Im \to B}$, adult survival rates (S^{ad}), transitions between breeding states ($\psi^{FB \to SB}$, $\psi^{FB \to NB}$, $\psi^{NB \to SB}$ and $\psi^{NB \to FB}$) and the breeding success of first-time breeders (BS^{PB}: proportion of eggs that fledged a chick in first-time breeders). Fecundity was modelled as the product of breeding success for successful breeders (by definition equal to one) and the juvenile survival rate estimated from the capture-recapture methods (S^J). We first focused on a deterministic, time-independent and density-independent model to calculate the population growth rate, λ_{mod}, the stable age distribution, and the sensitivities of the growth rate to variations in changes in each demographic parameter (Caswell 2001). We then estimated the contribution of temporal variations of each demographic parameter θ to the variability of λ using the first-order Taylor expansion:

$$V(\lambda) = s(\theta)^2 \text{var}(\theta) \qquad (1)$$

where $s(\theta)$ is the sensitivity of λ to parameter θ (Caswell 2001).

Scenarios of additional mortality and climate changes

A stochastic matrix population model was used to predict the population growth rate of the Amsterdam Albatross under various scenarios of fishery-induced mortality and climate change. In this model, demographic stochasticity was incorporated by sampling the number of individuals in each age-stage class from a binomial distribution (Akçakaya 1991). We partitioned the variance of the survival estimates into sampling variance and process variance (Link & Nichols 1994). Environmental stochasticity (i.e. the random temporal variation of each demographic rate) was included differently depending on whether there was a statistically significant effect of the fishery and climatic covariates. When a vital rate had no significant relationship

with climatic covariates, its yearly values were sampled from a beta distribution (Morris & Doak 2002) whose mean and variance were set equal to those estimated from the minimal multistate model selected. Whenever a relationship between parameter θ and k climatic covariates ($k = 1, \dots n$) was detected, the value of parameter θ at year i was modelled as:

$$\theta_i = logit^{-1}\left(\alpha + \sum_{k=1}^{n} \beta(k) \times cov(k)_i\right) + \varepsilon_i \qquad (2)$$

where α and $\beta(k)$ respectively represent the intercept and slope of the relation between θ and the kth climatic covariate, the error term ε_i is the residuals denoting the variation in $logit(\theta)$ unexplained by climatic covariates and $logit^{-1}$ is the inverse logit function. When modelling the effect of future changes in the climatic covariates, we drew the ε_i from a Gaussian distribution whose mean and standard deviation corresponded to those of the residuals of the multistate model including the climatic covariates. We assessed the combined effects on population growth rate of an additional adult mortality due to incidental capture by longline fisheries (from 0 to 20 individuals per year) and a change (from −2 to +2 units) in the mean value of the climatic covariates over the next 50 years. Regarding climatic covariates, a change of ± x units over the next 50 years corresponded to a constant annual change of $(x/50)\%$ per year. For each combination of additional mortality (considering incremental steps of one individual) and changes in climatic covariates (by step of ± 0.01 units), the matrix population model was analysed by Monte Carlo simulations (2000 iterations per combination) using package POPBIO (Stubben *et al.* 2007) implemented in program R (R_Development_Core_Team 2007). Initial stage abundances were set equal to the stable age distribution based on the total number of breeders of 2007.

RESULTS

Breeding population size

The number of breeding birds observed on Amsterdam Island has gradually increased since the 1980s (Fig. 2), reaching a maximum of 31 breeding pairs in 2001. In 2007, 26 breeding pairs were monitored, of which 14 were successful and

12 failed. Based on the breeding birds observed from 1983 to 2007, the observed population growth rate (i.e. geometric mean of the ratio N_{t+1}/N_t) was equal to 1.049.

Breeding success

Breeding success of first-time breeders was lower (0.481, se = 0.038) than breeding success of experienced breeders (0.639, se = 0.028). From 1983 to 2007, the mean annual breeding success was 0.610 (se = 0.026). Compared with the other years, breeding success was rather low in 2000 (24.1%; $n = 19$ pairs) and 2001. Excluding these 2 years, breeding success was 0.653 (se = 0.026).

Adult survival rates and transition probabilities between breeding states

Since 1983, 301 Amsterdam Albatrosses (57 adults and 244 chicks) have been marked. The GOF test of our general model did not detect any lack of fit ($\chi^2_{157} = 177.97$, $P = 0.121$). The model with constant survival, additive time- and state-dependent capture probabilities and state-dependent transition probabilities was the best supported (Model 7: $S_{cst}\,\psi^s\,p^s_{t+}$; AICC = 1970.32; Table S2a). This model was over 2.5 times better supported than that having a time-dependent and state-independent capture rate ($w_7/w_8 = 2.606$; Table S2a). In Model 7, adult survival rate was high ($S = 0.971$, se = 0.005; Table 2) and mean capture probabilities were 0.744 and 0.910 for successful and failed breeders, respectively. Transition probabilities between breeding states are given

in Table 2. No temporal trend was detected in adult survival rate (ANODEV: $F_{1,22} = 1.511$; $P = 0.232$).

We then assessed whether any of the six environmental covariates influenced the survival of adult breeders (Table S2b–c; Models 9–14). Fishing effort did not explain any significant part of the total variance in adult survival rate (Table S2b; Models 9–10). Among the five climatic covariates, only the *DMI* was statistically significant after Bonferroni correction (significant at the α-level $0.05/6 = 0.008$; $F_{1,22} = 11.829$; $P = 0.002$), explaining 35% of the total temporal variance in adult survival. We observed a positive relationship between the *DMI* and adult survival (slope = 2.834, se = 0.891), with the latter being higher during positive IOD events that indicate lower sea surface temperature anomalies in the south and southwestern Indian Ocean.

Juvenile survival rates and recruitment probability

Model selection favoured a model with constant juvenile survival rate, constant capture rate of breeders and constant recruitment probability (Model 5: $S^s\,\psi^s\,p_{cst}$; AICC = 693.93; Table S3a). Juvenile survival rate was 0.672 (se = 0.057), in other words an annual survival rate of 0.936 from fledging to 7 years of age. Annual recruitment probability was estimated at 0.370 (se = 0.056) from 1990 to 2007. No temporal trend was detected in juvenile survival rate (ANODEV: $F_{1,8} = 0.753$; $P = 0.411$). None of the six environmental covariates explained a significant part of the total variance in juvenile survival (Table S3b–c; Models 6–11).

Table 2. Demographic parameter mean value, sensitivity of population growth rate to change in demographic parameters and their contribution to variance of the population growth rate for the Amsterdam Albatross from 1983 to 2007.

Parameter		Mean value (se)	Sensitivity	Contribution
Survival rate				
Juvenile	S^J	0.672 (0.057)	0.306	0.0009
Adult	S^{ad}	0.971 (0.005)	0.734	0.0013
Breeding transition				
From failure to success	ψ^{FBSB}	0.494 (0.033)	0.154	0.0002
Remaining failure	ψ^{FBFB}	0.402 (0.041)	0.133	0.0001
From failure to non-breeder	ψ^{FBNB}	0.104 (0.033)	0.136	0.0001
From non-breeder to success	ψ^{NBSB}	0.656 (0.024)	0.234	0.0003
From non-breeder to failure	ψ^{NBFB}	0.272 (0.026)	0.195	0.0001
Remaining non-breeder	ψ^{NBNB}	0.072 (0.025)	0.004	< 0.0001
Recruitment probability	ψ^{recrut}	0.452 (0.025)	0.263	0.0008
Breeding success	BS	0.610 (0.020)	0.078	0.0009

Matrix population model

Population growth rate, sensitivity analyses and contribution

The deterministic population matrix model included the mean values of demographic parameters from 1983 to 2007 (Table 2). The population growth rate λ_{mod} of this deterministic model was estimated as 1.048. Using the proportional stable stage distribution scaled by the number of breeding pairs in 2007, the total population size in that year was estimated at 167 individuals, of which 86 were mature birds. Sensitivity analysis suggested that changes in adult survival will have the greatest effect on the population growth rate, followed by changes in the juvenile survival rate. Recruitment probability and transitions between breeding states were intermediate (Table 2). Adult survival rate made the largest contribution to variance of the population growth rate (Table 2), followed by juvenile survival, breeding success and recruitment probability. Breeding transition probability had the smallest contribution to λ_{mod}.

Scenarios of additional mortality and climate changes

As expected, given the positive relationship between adult survival rate and DMI, the population growth rate predicted for the next 50 years increased with increasing mean DMI. When additional bycatch mortality was set to zero, the population growth rate varied from 1.028 to 1.054 depending on the value of the climatic covariate (Fig. 4). Considering an additional mortality of five individuals per year, population growth rate declined from 1.002 without any climate change to 0.967 whenever the mean DMI decreased by −2 units over the next 50 years (−3.486%), whereas it only increased to 1.007 if the mean DMI increased by 2 units (+0.596%). Although this difference in predicted population growth rate considering extreme values of climate change was relatively small, it was more striking when expressed through probability of decline below the historical level of 1983 (i.e. nine breeding pairs) within the next 50 years. Indeed, this probability decreased from 64% to 57% (i.e. −7%) if the mean DMI increased from 0 to +2 units, whereas it increased up to 96% when the mean DMI decreased from 0 to −2 units. Regardless of the magnitude of the predicted change in the climatic covariates, population decline was predicted when bycatch mortality exceeded six adult individuals per year. With
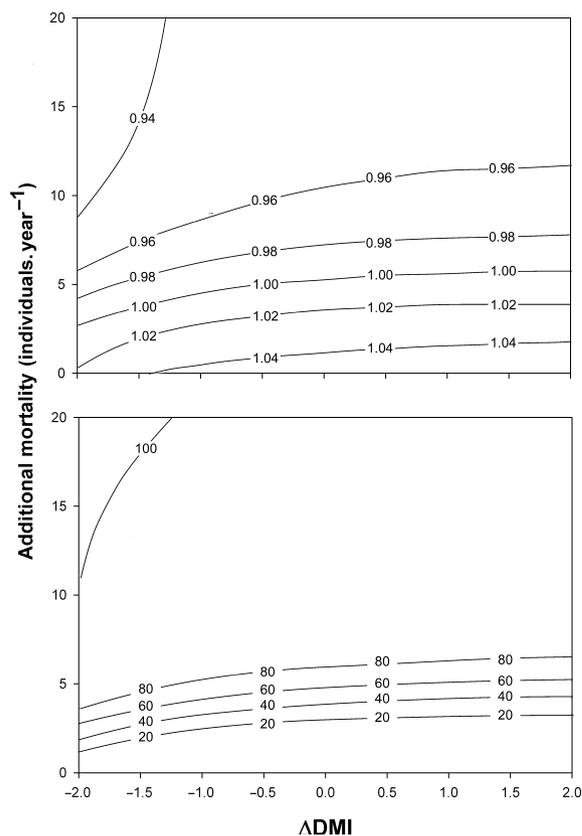

Figure 4. Amsterdam Albatross population growth rate (*upper panel*) and decline probability (*lower panel*) under different scenarios of change in mean DMI and additional mortality. Lines are isoclines of constant population growth rate (or decline probability) for different parameter values. Decline probability represents the probability that the Amsterdam Albatross population decreases below its historical level recorded in 1983 (i.e. nine breeding pairs).

this annual additional mortality, the probability that the Amsterdam Albatross population will decrease below the historical level reached in 1983 (i.e. nine breeding pairs) within the next 50 years was greater than 75% (Fig. 4). Finally, the predicted positive effects of DMI on population growth were cancelled for large values of bycatch mortality so that the probability that the population declined below nine breeding pairs reached 100% when the additional mortality exceeded 12 individuals per year (Fig. 4).

DISCUSSION

With fewer than 10 breeding pairs when it was described as a new species in 1983 (Jouventin & Roux 1983), the population of Amsterdam

Albatross still has one of the smallest populations of all Procellariiformes (Brooke 2004) and it is one of the rarest bird species worldwide. Since 1983, the population has increased at an annual rate of almost 5%. This positive population trend stands in contrast to those of most albatross species, which have suffered steady to steep declines over a similar period (Croxall & Gales 1998). However, comparable population growth rates have been recorded for the few increasing populations of great albatrosses, such the Gibson's Albatross *Diomedea gibsoni* on Auckland Island, New Zealand (Walker & Elliot 1999), the Antipodean Wandering Albatross *Diomedea antipodensis* on Antipodes Island, Antarctica, (Walker & Elliot 2005), and the Short-tailed Albatross *Phoebastria albatrus* on Torishima Island, Japan (Zador *et al.* 2008). According to our sensitivity analysis, adult survival has made the highest contribution to the variance of the Amsterdam Albatross population growth rate from 1983 to 2007. This suggests that oceanographic conditions have been very favourable to Amsterdam Albatrosses during the past 24 years, and the control of feral cattle on the island may have had a positive effect (Micol & Jouventin 1995).

Impacts of climate on the demography of the Amsterdam Albatross

In accordance with the 'slow-fast continuum' theory (Saether & Bakke 2000), we found that adult survival rate was very high and its temporal variation very low. Just as for the juvenile rate, the estimated adult survival for the Amsterdam Albatross was the highest ever found for an albatross (Cuthbert *et al.* 2004), and is likely to be the largest ever estimated for a long-lived vertebrate. Although adult survival was expected to be buffered against environmental variations (Pfister 1998, Gaillard & Yoccoz 2003), we found that it was significantly related to temporal variation in climate. In particular, our analysis suggested a positive relationship between adult survival of the Amsterdam Albatross and the Indian Ocean Dipole (IOD). During dipole mode events, the surface wind field over the Indian Ocean experiences large changes (Saji *et al.* 1999). Negative IOD events are associated with a weakening of the wind speed in the southern Indian Ocean (i.e. around 40°S) that reduces vertical mixing of the water masses and leads to increases in the SST (Saji *et al.* 1999, Meyers *et al.* 2007). Reduction in the verti-

cal mixing layer and high SST are generally poor growing conditions for zooplankton (Sarmiento *et al.* 1998, Gregg *et al.* 2003). Pelagic systems mostly have bottom-up regulation, so that the effect of climate forcing on zooplankton would cascade upwards through the food web (Aebischer *et al.* 1990). Similar negative relationships between SST and adult survival have been documented in several seabird species in the Southern Ocean (Barbraud & Weimerskirch 2003, Jenouvrier *et al.* 2005, Nevoux *et al.* 2007, Le Bohec *et al.* 2008). Moreover, the weakening of prevailing winds during a negative IOD could induce higher energetic costs of flight, with possible negative impact on survival rate and breeding success because large albatrosses generally use wind to reduce flight cost (Weimerskirch *et al.* 2000).

Although we considered linear relationships between climatic variables and demographic parameters, non-linear responses might be expected (Mysterud *et al.* 2001). However, when testing the effect of a quadratic relationship between adult survival and climatic covariates (i.e. DMI, SIOD and SST), these non-linear terms did not explain a significantly greater part of variance compared with linear ones (results not shown). Because a decline in IOD would result in weaker winds in the southern Indian Ocean (Meyers *et al.* 2007) and a decline in primary production (Sarmiento *et al.* 1998) and of biomass at higher trophic levels (Aebischer *et al.* 1990), fishing effort could be expected to remain low and interactions between fisheries and seabirds reduced when IOD was low. On the other hand, positive IOD events would result in higher primary production that could induce the resumption of longline fishing in the southern part of the Amsterdam Albatross's foraging range. However, these predictions raise the complex issue of the time invariance of links between a climatic index such as the IOD and the local climatic conditions under climate change. Only by considering a large set of Global Circulation Models differing in their representation of climatic variability (AchutaRao & Sperber 2006) can one hope to address this problem.

Impact of additional mortality on the Amsterdam Albatross population

Fishery-induced mortality is likely to be the key factor explaining the discrepancy in survival rates between populations of similar species of great albatrosses. Many populations of albatrosses are

currently vulnerable to capture and drowning in longline fishing gear set for tunas *Thunnus maccoyii*, *Thunnus albacares* and *Thunnus obesus* over a very large area of the Southern Ocean (Tuck *et al.* 2001). However, using the number of hooks set annually from 1983 to 2007 by the tuna longline fishery operating in the entire Indian Ocean south to 29°S, we did not detect any effect of longline fisheries either on juvenile or on adult survival rate, despite the extensive overlap between foraging zones exploited by foraging Amsterdam Albatrosses and fishing areas. This lack of relationship is somewhat surprising given the magnitude and extent of fishing effort for the Southern Bluefin Tuna in the Indian Ocean. It is consistent with high adult and juvenile survival rates and with the absence of records of accidental captures of Amsterdam Albatrosses (Brothers *et al.* 1999). Nevertheless, because tuna fisheries are outside the exclusive economic zone, they are not required to declare bycatch or band recoveries.

Future population growth rate and environmental changes

Our stochastic model predicts the expected dynamics of the Amsterdam Albatross population under several scenarios of environmental change, specifically climate and additional fishing-induced mortality. If environmental conditions remain similar to those experienced from 1983 to 2007 and without any additional mortality due to fishery bycatch, our model suggests that the population size could increase 10-fold over the next 50 years. However, both climate and fishing pressure are likely to change in the near future. Although SST is likely to increase from 0.5 to 1 °C by 2100 in the whole Indian Ocean (IPCC 2008), much less is known about the future changes of large-scale climatic patterns such as IOD, SIOD or SOI (Suzuki *et al.* 2004, Saji *et al.* 2006, Leloup *et al.* 2008). Assuming that most coupled ocean–atmosphere Global Circulation Models used by IPCC are successful in simulating the inter-annual variability of IOD, a trend in IOD from 2008 to 2058 is predicted to range from −0.832 to +1.924 (Saji *et al.* 2006). Provided there is no additional bycatch mortality, the population growth rate can be expected to remain close to its current value if future IOD values remain within this range (Fig. 4). Although adult survival, the parameter that has the largest influence on population growth

rate, was positively linked to IOD, climate change is likely to compensate for small additional bycatch mortality within this projected range of climate change. Population growth rate is predicted to decrease below unity whenever bycatch mortality exceeds six individuals per year (Fig. 4). Given that fishing efforts have been extremely dynamic in the Southern Ocean recently (Klaer & Polacheck 1997, Tuck *et al.* 2003), waters around Amsterdam Island might be searched again for tuna. The resumption of longline fisheries is a very realistic possibility and would represent a real threat to the persistence of the Amsterdam Albatross given its current small population size. We therefore stress that preventative mitigating measures need to be applied by all vessels targeting the Southern Bluefin Tuna and other tunas in the tropical Indian Ocean, especially in the foraging range of this species. These measures include appropriate treatment of waste and offal, streamer lines to prevent birds from eating the baited hooks before they sink, additional weighting on the line so that hooks sink faster, and line setting at night or outside the Albatross's albatross breeding season (Croxall & Nicol 2004). We would encourage the Indian Ocean Tuna Commission (IOTC) to put in action the resolutions adopted during the last two IOTC sessions that are intended to promote the collection and reporting of bycatch data to increase the amount of information available in the early future (IOTC 2005).

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SUPPORTING INFORMATION

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

Figure S1. Observed age at first reproduction in Amsterdam Albatross from birds tagged as chicks from 1983 to 1994.

Figure S2. *Upper figure*: Lifetime cycle graph for the Amsterdam Albatross population. Circles and boxes respectively represent age- and stage-classes. J_i, juvenile of age i; PB, pre-breeding birds; SB, successful breeders; FB, failure breeders; NB, non-breeders; S^J, juvenile annual survival rate; S^{ad}, adult annual survival rate; ψ^{rec}, annual recruitment probability; ψ^{rs}, transition from breeding state r to breeding state s; BS^{PB}, 1 year breeding success. *Lower figure*: Population projection matrix A is multiplied by $n(t)$, a vector describing the state of the population at time t, to obtain the state of the population at $t+1$.

Table S1. Partial correlation coefficients between the five climatic covariates. None of the correlations was significant.

Table S2. Modelling variations in survival (S), transition probabilities (ψ) and recapture rate (p) of adult Amsterdam Albatrosses marked from 1983 to 2007 and recaptured from 1984.

Table S3. Modelling variations in immature survival (S), transition (ψ) and recapture rates (p) of Amsterdam Albatrosses tagged as chicks from 1983 to 1994 and recaptured from 1984 to 2007.

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