Assessing the impact of fisheries, climate and disease on the dynamics of the Indian yellow-nosed Albatross

Virginie Rolland *, Christophe Barbraud, Henri Weimerskirch

Centre d'Etudes Biologiques de Chizé, CNRS UPR 1934, Villiers-en-Bois, 79360 Beauvoir sur Niort, France

ABSTRACT

Many seabird populations are currently decreasing, especially albatrosses for which the primary threat is recognised to be mortality in fisheries. Introduced predators, climate change and other factors such as diseases can also have large impacts on seabirds. Here, we assessed the relative effect of three potential threats: climate, fisheries and diseases on the demography of an endangered marine predator and modelled its population dynamics to project its size under different scenarios. We based our study on a long-term monitoring of a colony of individually marked Indian yellow-nosed albatrosses at Amsterdam Island, subtropical Indian Ocean, that has declined during the past twenty years. We found no evidence for an impact of legal tuna longlining on demographic parameters. Hatching success was lower during El Niño years but survival (0.902 ± 0.011) was not affected by climatic factors. Avian cholera caused high chick mortality (0.808 ± 0.181) which in turn probably triggered the high emigration rate (0.038 ± 0.011) through dispersal of failed breeders. This colony has a high risk of extinction. However, the rest of the population at Amsterdam Island seemingly not affected to the same extent, declined but stabilised since 1998. Matrix models indicated that lowered adult survival and the very low breeding success, resulting in low recruitment, have both contributed to the decline of the yellow-nosed albatross colony until the mid-1990s, but that more recent decline was primarily caused by low fledging success. Our results highlight that potential threats such as fisheries, diseases or climate have to be considered simultaneously to disentangle their roles when assessing the conservation status of a marine predator species.

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1. Introduction

Nowadays, many marine predator species are suffering worldwide population declines (Lewison et al., 2004), particularly albatrosses and petrels, which has increasingly stimulated concerns about their status and sustainability (Croxall and Gales, 1998; Woehler et al., 2001; Cooper et al., 2006). The declines of albatrosses have been widely attributed to mortality in longline fisheries through incidental bycatch (Gales, 1998; Tuck et al., 2001; Baker et al., 2002). Indeed, as albatrosses and petrels exploit the same productive areas as longliners (Weimerskirch, 1998), they tend to be attracted to the baits as a potential food source (Brothers, 1991). Then they risk to be caught and drowned by attempting to remove bait from hooks during line setting. This bycatch has been so important in some species that adult survival has significantly decreased, resulting in population decline and in some cases endangering the population (Weimerskirch et al., 1997; Arnold et al., 2006; Baker et al., 2007).

The second most documented factor that may be the cause of reported population declines in marine top predators is climate warming (Hughes, 2000; Croxall et al., 2002; Weimerskirch et al., 2003) which influences the resource abundance and distribution. Several long-term studies have showed that population size or demographic parameters of seabirds were associated with either large-scale climatic fluctuations such as the El Nino-Southern Oscillation (Barbraud and Weimerskirch, 2003) or the North Atlantic Oscillation (Sandvik et al., 2005), or more local anomalies in sea ice extent/concentration (Jenouvrier et al., 2005) or sea surface temperature (Frederiksen et al., 2004; Nevoux et al., 2007).

However, other factors which are considered to be of lesser importance may also impact seabird populations. Apart from natural disasters (floods, fires, etc.), threats to albatrosses and petrels are all of anthropogenic origin, including introduced species, habitat degradation, human disturbance, marine pollution or plastic ingestion (Gales, 1998; Baker et al., 2002). Finally, disease outbreaks may spread rapidly and result in rapid decrease (and extinction) in avifauna (Friend et al., 2001). Diseases such as avian cholera and Lyme disease have already been reported, in seabirds, to decrease the adult survival (Williams and Ward, 2002; Österblom et al., 2004) or the breeding success (Bergström et al., 1999;

* Corresponding author. Tel.: +33 549 099 611; fax: +33 549 096 526.
E-mail addresses: rolland@cebc.cnrs.fr (V. Rolland), barbraud@cebc.cnrs.fr (C. Barbraud), henriw@cebc.cnrs.fr (H. Weimerskirch).

Weimerskirch, 2004). Thus it is important to consider, as far as possible, all the potential threats when studying population dynamics of an endangered species.

Very few studies have investigated simultaneously the effects of several threats on vital rates in seabirds (Bunce et al., 2002; Votier et al., 2005; Arnold et al., 2006) because there is generally no evidence of a causal link between these threats and observed population declines. However, it is crucial to disentangle the respective role of each potential threat and their consequences on the population dynamics to be able to make projections and to assess threats to populations. Based on long-term monitoring of a colony of the Indian yellow-nosed albatross (*Thalassarche carteri*) population of Amsterdam Island, Southern Indian Ocean, we studied the effects of different potential threats on demographic parameters and the relative role of demographic parameters including emigration/immigration on the population dynamics.

In the Southern Ocean, large numbers of seabirds, mostly albatross species, are killed each year by longline fisheries targeting the southern bluefin tuna (*Thunnus maccoyii*) and other tuna species south of 30°S (Brothers, 1991; Gales et al., 1998; Ryan et al., 2002). Several studies have demonstrated a significant impact on adult mortality of several species (Tuck et al., 2001; Rolland et al., 2008). The yellow-nosed albatross is potentially vulnerable to tuna longlining in the subtropical Indian Ocean when it forages in subtropical oceanic waters around Amsterdam where it breeds (Pinaud and Weimerskirch, 2005) and in Australasian waters where it winters (Weimerskirch et al., 1985). In these two areas, longline fisheries are very active with up to 130 million hooks set in 1984 and c. 70 million hooks set per year since 1990 (Tuck et al., 2003). Indian yellow-nosed albatrosses are the third most frequently killed albatross species in the Australian Fishing Zone (Gales et al., 1998). Thus we expect a negative impact of tuna longlining effort on survival. In addition, previous studies on yellow-nosed albatross foraging success and breeding effort showed that adult survival was not affected by sea surface temperature (SST) anomalies whereas the provisioning rate and resulting chick growth were enhanced by colder SST (Weimerskirch et al., 2001; Pinaud et al. 2005). Therefore, we expected no temperature effect on adult survival and a negative effect on breeding success. Finally, avian cholera, a disease caused by the bacterium *Pasteurella multicoda* has been shown to induce extensive chick mortality resulting in low fledging success on Amsterdam Island (Weimerskirch, 2004). Some colonies of the Amsterdam yellow-nosed albatross population are affected by avian cholera and the study colony dramatically declined since the 1980s (Weimerskirch, 2004). We thus hypothesize that this decline was at least partly caused by the disease.

In this study, our aims were twofold. First we analysed the variations of adult survival and hatching success in relation to a series of external factors that could potentially affect a population of yellow-nosed albatrosses. In a second step, we included stochasticity on demographic parameters and environmental factors in matrix population models to predict possible trajectories of the population in relation to the potential threats.

2. Materials and methods

2.1. Species and study site

Indian yellow-nosed albatrosses are subtropical seabirds inhabiting the southern Indian Ocean (Fig. 1). Population census and mark-recapture studies were carried out every year since the breeding season 1979/1980 (thereafter named 1980) on a colony of around 150 breeding pairs located at Pointe d'Entrecasteaux (37°51′S, 77°31′E), Amsterdam Island. All nests of the colony with an incubating bird or both pair members were counted directly every year in late September. This study colony is part of a larger group of neighbouring colonies (c. 7000 breeding pairs) named Entrecasteaux which is itself part of the total Amsterdam population (c. 27,000 breeding pairs in 2006) (Fig. 2). Ship-based counts for inaccessible colonies situated in steep cliffs, and land-based counts for accessible colonies and for those not entirely visible from the ship were combined to give a complete count of Amsterdam population, with no replicate.

Avian cholera is largely present in the study colony and to a lesser extent in neighbouring colonies of Entrecasteaux but its occurrence, elsewhere at Amsterdam Island, remains unknown.

During the breeding season, each nest was checked during incubation (October–November), at hatching (late November–early December) and just before fledging (late March). This enabled us to read the ring of most birds present on the colony, to identify pair members and to determine their breeding performance. Each year, new adult birds (breeders and non-breeders) and all the chicks were marked with a stainless steel band. In neighbouring colonies of Entrecasteaux, field workers also (but less regularly) searched for banded birds to detect movements between colonies.

Satellite tracking during summer breeding seasons indicated that birds from this colony foraged in pelagic waters mainly west of Amsterdam Island (Fig. 1), feeding predominantly on fish (Pinaud et al., 2005; Pinaud and Weimerskirch, 2005). Breeders foraged as far as 2000 km from the colony during the incubation period (Pinaud and Weimerskirch, 2005) whereas their foraging trips seem to be more restricted during the chick rearing period (Weimerskirch unpublished; Pinaud et al., 2005). We used band recoveries as a proxy of their wintering grounds (Weimerskirch et al., 1985). All of the 41 bands recovered (41.5% adults and 58.5%

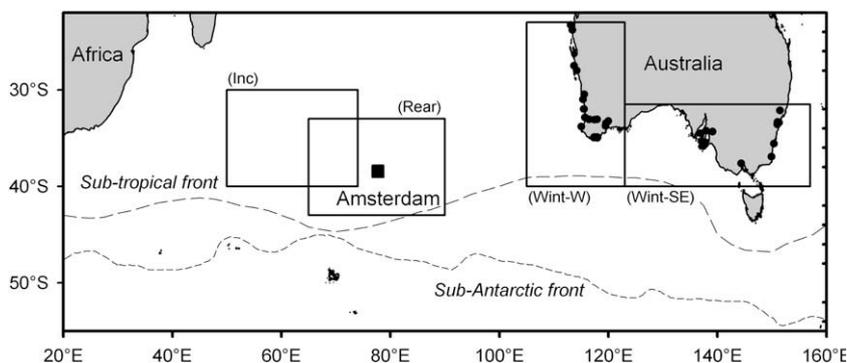**Fig. 1.** Distribution area of Indian yellow-nosed albatrosses from the Amsterdam colony of Pointe d'Entrecasteaux. Boxes (Inc) and (Rear) represent foraging areas, derived from satellite tracking, during incubation and rearing periods, respectively. Boxes (Wint-W) and (Wint-SE) refer to foraging areas, derived from band recoveries (black dots), respectively, west and southeast Australia where birds overwinter.
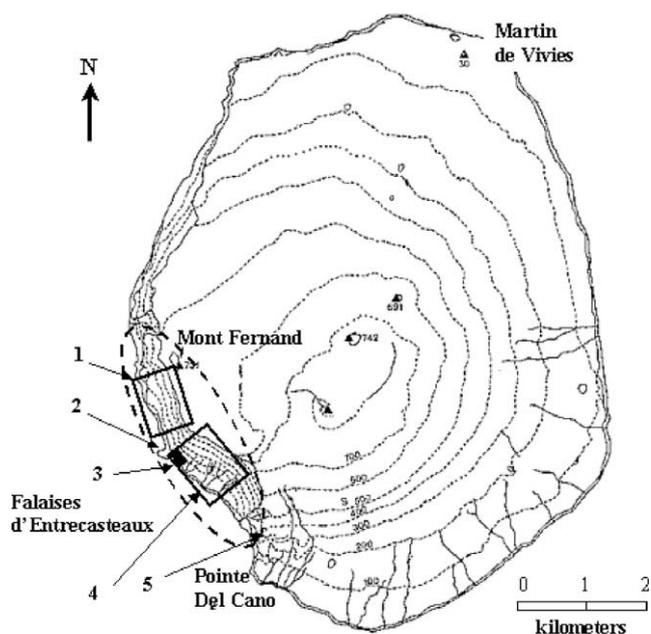
Fig. 2. Map of Amsterdam Island and repartition of colonies of Indian yellow-nosed albatross. Total area of nesting is indicated by the dotted circle. The main large colonies, represented by rectangles, are "Fernand" (1) and Entrecasteaux (4). The latter includes the study colony (3). The other small colonies are Cathédrale (2) and Del Cano (5).

immatures) outside the breeding season were on Australian coasts and indicated that yellow-nosed albatrosses migrate mainly to western (63%) and also to south-eastern (37%) Australia (Fig. 1).

2.2. Environmental covariates

The yellow-nosed albatross provisioning rate and resulting chick growth were enhanced by colder SST (Weimerskirch et al., 2001; Pinaud et al., 2005). Thus, we investigated the impact on demographic parameters of the sea surface temperature anomalies (SSTA) available monthly on a 1° scale from the Integrated Global Ocean Services System (Reynolds et al., 2002 – http://ingrid.ldeo.columbia.edu/) for different seasons (Table 1). We also used the Southern Oscillation Index (SOI) available from the Australian Bureau of Meteorology (http://www.bom.gov.au/climate/current/soihtm1.shtml). The effect of the Southern Oscillation is most pronounced in the Southern Pacific Ocean, although other

Table 1
Climatic and fisheries covariates used in the analyses of adult survival and hatching success of the Indian yellow-nosed albatross at Amsterdam Island. Season corresponds to the phenology of Indian yellow-nosed albatrosses; the corresponding calendar period is given by month. Spatial area indicates the area over which covariates were averaged, according to tracking studies in summer (Pinaud et al. 2005; Pinaud and Weimerskirch 2005) and band recoveries (Weimerskirch et al. 1985).

Covariate[a]	Season	Months	Spatial area (Fig. 1)
SOIw	Wintering	April–August	Southern Ocean
SSTAinc	Incubation	September–November	West of Amsterdam
SSTArear	Rearing	December–March	Around Amsterdam
SSTAsouth	Wintering	April–August	South-east Australia
SSTAwest	Wintering	April–August	West Australia
LLinc	Incubation	September–November	West of Amsterdam
LLrear	Rearing	December–March	Around Amsterdam
LLsouth	Wintering	April–August	South–east Australia
LLwest	Wintering	April–August	West Australia

[a] SOI, Southern oscillation index; SSTA, Sea surface temperature anomaly; LL, Longline fishing effort.

marine ecosystems are also affected, such as in the western Australian waters (e.g. Dunlop et al., 2002). Thus, albatrosses may be affected by the winter SOI (SOIw), without any lag, when they are in Australasian waters. There was no correlation between SSTA variables ($|r| < 0.37$, $P > 0.11$), nor between SSTA variables and SOIw ($|r| < 0.27$, $P > 0.26$) except the correlation almost significant found between SOIw and SSTA west of Australia ($r = 0.42$, $P = 0.07$).

In addition, yellow-nosed albatrosses forage in the same areas as tuna fishing vessels and may be caught in longlines (Gales, Brothers & Reid, 1998). Thus, its population may be considered as an overharvested population in which survival probability is proportional to the catch rate (Lebreton, 2005). However, since no accurate estimate of bycatch rate was available, we assumed following Véran et al. (2007) that the level of bycacth was proportional to fishing pressure, that is fishing effort. As covariates, we thus used longlining effort (LL) in number of hooks from the CCSBT (Commission for the Conservation of the Southern Bluefin Tuna, http://www.ccsbt.org/docs/data.html) and the IOTC (Indian Ocean Tuna Commission, http://www.iotc.org/English/data/databases.php). CCSBT data included fishing effort in the Australian Exclusive Economic Zone. Unfortunately illegal unreported and unregulated (IUU) fisheries were not taken into account because IUU catch or effort data were not publicly available.

SSTA and fishing efforts were both extracted and averaged over summer and winter grounds used by the yellow-nosed albatross (Fig. 1). All indices, summarized in Table 1, were standardized so that the mean and variance over the study period were set to 0 and 1, respectively. This allows comparisons of the magnitude of the impact of distinct (climate or fishery) covariate on survival or breeding success (Grosbois et al., 2008). Time series of covariates are given in Appendix A.

2.3. Estimation of demographic parameters

Adult survival probabilities were estimated with capture-mark-recapture models using M-Surge software (Choquet et al., 2005a). We removed the first capture to limit heterogeneity in survival probability. Analyses were thus conducted for the period 1982–2005 on 1234 breeding individuals, banded as chicks and adults. All cohorts were mixed up because all cohorts were assumed to have the same demographic parameters. To obtain unbiased estimates of survival probabilities, we used the Cormack–Jolly–Seber (CJS) model (Φ_t, p_t) where both survival (Φ) and capture (p) probabilities were time-dependent (t). To test whether this model fitted the data, we performed a goodness-of-fit (GOF) test with U-Care software (Choquet et al., 2005b). The CJS model did not fit the data ($\chi^2_{108} = 748.95$, $P < 0.001$) because of a positive trap-dependent effect ($\chi^2_{21} = 610.13$, $P < 0.001$) indicating that individuals were more likely to be resighted if they had been resighted again on the previous occasion. This is a common effect detected in seabirds because of their faithfulness to their breeding colonies. We thus built a model with "two age-classes" for recapture probabilities (Φ_t, $p_{m \times t}$) to account for trap dependence (Pradel, 1993). However, as the GOF test of this model was still significant ($\chi^2_{87} = 138.81$, $P < 0.001$), we followed Lebreton et al. (1992) by using a variance inflation factor $\hat{c}$ calculated as the χ^2 statistic over its number of degrees of freedom to account for overdispersion. As $\hat{c}$ (1.59) was below three, the model (Φ_t, $p_{m \times t}$) was considered as adequate to be used as a departure model in the model selection (Lebreton et al., 1992). The selection among time-dependent models was performed using a second-order Akaike Information Criterion (AICc) corrected for $\hat{c}$ (QAICc). The model with the lowest QAICc was considered as the best model. When ΔQAICc was below two, models are assumed to be not different. To assess the effects of environmental covariates, an analysis of deviance (anodev) was carried out. It compares the amount of deviance explained against

the amount of deviance not explained by the covariate (Skalski et al., 1993; Skalski, 1996). It is calculated as

$$\frac{[\mathrm{DEV}(M.) - \mathrm{DEV}(M\mathrm{cov})]/[n\mathrm{cov}]}{[\mathrm{DEV}(M\mathrm{cov}) - \mathrm{DEV}(M_t)]/[n - n\mathrm{cov} - 1]},$$

where DEV was the deviance of the models with constant ($M.$), covariate (M_{cov}) and time-dependent (M_t) effects; n was the number of parameters of the time-dependent model and n_{cov} the number of covariates included in M_{cov}. This anodev is a F-test statistic with n_{cov} and $(n - n_{\mathrm{cov}} - 1)$ degrees of freedom. Before testing for environmental effects on both capture and survival probabilities, we examined whether there was a general trend to avoid spurious environmental effects caused by co-occurrence of trends in the vital rate and covariate time series (Grosbois et al., 2008).

In the yellow-nosed albatross study colony, fledging success was highly variable (CV = 96.4%) and overall low (0.192 ± 0.181) for the period 1987–2005 (Fig. 3). Avian cholera was responsible for this high chick mortality (Weimerskirch, 2004). Variability in fledging success was assumed to mostly reflect the strength of the disease although a part of this variability was probably explained by other environmental factors.

Since breeding success is the product of fledging success by hatching success, the major part of the variability in breeding success was due to the high variability in fledging success. Thus, we did not test for environmental effects on the overall breeding success and we only investigated the relationships between climate covariates (SSTA and SOI_w) and hatching success. Hatching success was defined as a binomial variable with "1" if the egg produced a chick and "0" if parents failed during the incubation. Data for each nest were available since 1987. We tested for environmental effects on the hatching success during the period 1986–2004, for an average of 91 (±40) nests, using generalized linear models for logistic regression with the "glm" function of software R (R Development Core Team, 2005). Model selection was performed with likelihood ratio tests (LRT) which are F-tests of the difference in deviances between constant model and models with a trend or a covariate.

2.4. Population modelling

To determine the vital rate(s) of which a change had the greatest impact on the population growth rate in the yellow-nosed albatross, we performed sensitivity and elasticity analyses from a deterministic matrix population model which also provided the stable age distribution (Caswell, 2001). Sensitivity or elasticity is negative when a parameter increase induces a decrease in population growth rate. Analyses and modelling was conducted using a pre-breeding matrix with the software ulm (Legendre and Clobert, 1995).
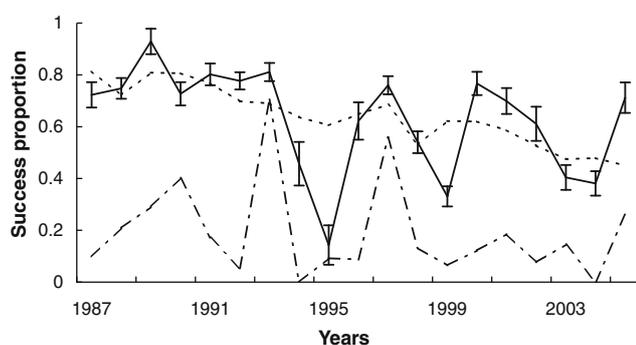
Fig. 3. Annual variations of observed hatching success (solid line) and fledging success (dashed line), and hatching success predicted from the best model (dotted line), in the yellow-nosed albatross at Amsterdam Island.

The life cycle of the yellow-nosed albatrosses was structured by age and reproductive status classes (Fig. 4). Modelling was conducted using a pre-breeding matrix with the software ulm (Legendre and Clobert, 1995). Individuals aged from 1 to 3 years-old are immature. Between 4 and 15 years-old, individuals are able to start breeding the year after and are thus considered as pre-breeders. Then, a pre-breeder can either become a breeder (B) with the probability $S_{\mathrm{PB}} \times T_{a/B}$ or stay in this class with probability $S_{\mathrm{PB}} \times (1 - T_{a/B})$. Pre-breeder survival ($S_{\mathrm{PB}}$) and probabilities to breed for the first time at age $a + 1$ ($T_{a/B}$) were estimated from a multistate model. Once recruited, birds reproduce almost every year with the probability $S_B \times (1 - T_{B/NB})$ where S_B is the adult survival. Indeed, they are able to skip reproduction with probability ($S_B \times T_{B/NB}$) i.e. become a non-breeder (NB). Non-breeders can breed ($S_B \times T_{NB/B}$) or skip another breeding ($S_B \times (1 - T_{NB/B})$). These probabilities $T_{B/NB}$ and $T_{NB/B}$ are transitions between two observable states "breeder" and "non-breeder" seen on the colony and were estimated using multistate capture-mark-recapture models. The pool of breeders produces female juveniles of 1 year old with the probability BS $\times S_j \times$ SR, where BS is the breeding success, S_j the juvenile survival and SR the sex ratio. Here, we considered a population of females and thus sex ratio was assumed to be balanced (SR = 0.5). The breeding success is the product of the hatching success (HS) by the fledging success (FS). Hatching success is the proportion of eggs that produced a newly born chick whereas the fledging success is the proportion of newly born chicks that produced a fledgling. Juvenile survival, defined as the probability that fledglings survive during their first year at sea, was estimated from the same multistate models as age-specific probabilities to breed for the first time. Some studies highlighted the importance of immigration in seabird populations (Jenouvrier et al., 2003; Jenouvrier et al., 2005). In the study colony, breeders are resident individuals, emigrants or immigrants. The probability of emigration (P_{Em}) was estimated from a multistate model, using marked birds breeding in the study colony or other neighbouring colonies. This model allowed us to obtain independent estimates of emigration probability and survival in adult breeders which was then used as real adult survival (S_B). We tested for external factors on adult survival by using a monostate model (see previous section) instead of this multistate model, only used to estimate emigration rates on a limited period. The number of immigrants in year t in our study colony was the number of adults found breeding for the first time in the study colony. The rate of immigration (P_{Im}) was thus estimated as the number of immigrants on the total number of breeders.

All multistate models, summarised and detailed in Appendix B, were performed with the M-SURGE software and all estimates are given ±SE.

Thus, the resulting population matrix model was the following time-invariant equation:

$$n_t + 1 = An_t, \tag{1}$$

where A is the population projection matrix and n_t a vector giving the number of individuals in each class of the population at any one time (t). We started with a deterministic model where demographic parameters were constant. Then, we ran a stochastic model by including temporal variability in the elements of the transition matrix which thus became:

$$n_{t+1} = A_t n_t. \tag{2}$$

A modified beta distribution was used to make parameters vary according to their mean and standard deviation. All the relationships that will have been found between environmental variables and adult survival or hatching success were also included into the stochastic model.

First, we assessed the fit of this model by comparing the number of breeding pairs observed and predicted by the model. Then
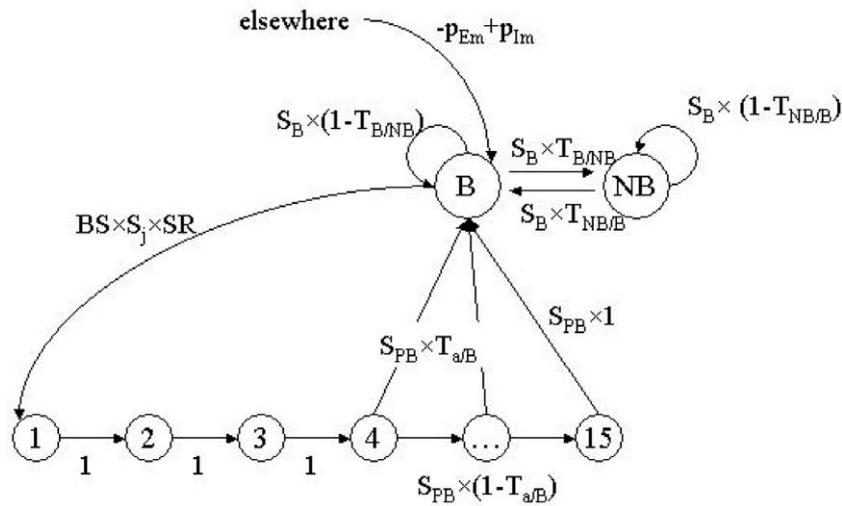
Fig. 4. Life cycle graph of the Indian yellow-nosed albatross at Amsterdam Island. Since age at first breeding ranges from 5 to 16 years, birds are immatures between 1 and 3 years and pre-breeders between 4 and 15 years. $T_{a/B}$ are the probabilities to breed for the first time at age $a + 1$, S_B and S_{PB} are adult and pre-breeder survivals. Once they have started to reproduce, birds are in a breeder (B) stage. They produce fledglings with the probability $BS * SR * S_j$ where BS is the breeding success, SR the sex ratio (0.5) and S_j the juvenile survival. Breeders can become non-breeders (NB) with the proportion $T_{B/NB}$ and non-breeders can return breeder with the proportion $T_{NB/B}$. Some breeders emigrate with the probability P_{Em} whereas some breeders from other colonies immigrate with the probability P_{Im}.

we constructed a stochastic population model to predict the population growth rate and time to extinction under a change in mean estimates of fledging success, immigration and emigration rates for the following reasons. First, the low fledging success is caused by avian cholera while it is commonly above 80% in other albatross populations (see Schreiber and Burger, 2001). Therefore, population growth rate was modelled with values of fledging success ranging from 0 to 0.8 to assess how the population would behave with different levels of disease. Second, immigration may greatly lower population decline and making it vary from 0 to the observed rate would allow us to assess its role in the yellow-nosed albatross declining colony. Inversely, emigration may accelerate population decline, and making it vary from 0 to the observed rate would also give an indication of its role in the colony. Preliminarily, we also investigated the effects of a change in variance (i.e. amplitude) of these parameters but results were not given here because the population growth rate only varied at the fourth or fifth decimal point, even with a change in variance (from 0.05 to 0.4) of fledging success.

3. Results

3.1. Population change

3.1.1. Study colony

The study colony has decreased in numbers continuously from 233 pairs in 1987 to 113 pairs in 2005 (Fig. 5). The corresponding observed geometric growth rate (λ_{87-05}) was 0.961 indicating an overall decline of 3.9% per year. It seems that the colony size declined more abruptly between 1987 and 1995 ($\lambda_{87-95} = 0.931$) and experienced higher variability ($CV_{87-95} = 20.17\%$) than during the period 1997–2005 ($\lambda_{97-05} = 0.972$, $CV_{97-05} = 13.93\%$).

3.1.2. Amsterdam population

Between 1982 and 2006, Amsterdam population declined at a rate of 1.4% per year. However, there was a steeper decline of 4.9% per year between 1982 and 1995. Population seems to have stabilized since 1998 (Fig. 6). The lowest numbers were recorded in 1995, with higher numbers between 1996 and 2006, when the population was stable.
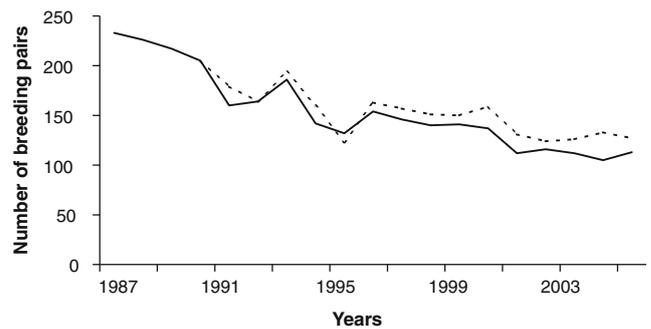

Fig. 5. Annual variation of the numbers of breeding pairs of yellow-nosed albatross observed in the study colony between 1987 and 2005 (solid line with error bars) and the number predicted by the matrix model (dotted line).
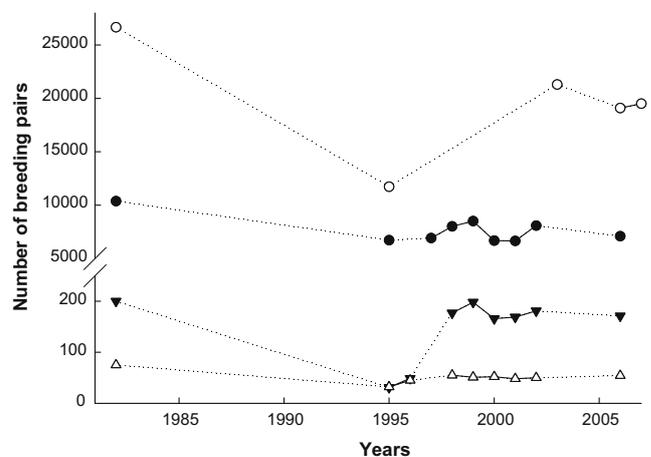

Fig. 6. Annual variation of the number of breeding pairs of Indian yellow-nosed albatross at Amsterdam since 1982. Counts for large colonies of "Fernand" and Entrecasteaux are represented by blank and filled circles, respectively, whereas counts for small colonies of Del Cano and Cathédrale are indicated by blank and filled triangles.

3.2. Demographic parameters

3.2.1. Adult survival

Because parameters were not all estimable, the departure model (Φ_t, $p_{m \times t}$) was reduced to an additive model (Φ_t, $p_{m + t}$) (Pradel, 1993) that had the lowest QAICc (Table 2). However, according to the parsimony principle, the model with the lowest number of parameters should be selected when ΔQAICc < 2, so model 3 (Φ, $p_{m + t}$) where survival was constant was the best model.

The best model was the model with a positive linear trend on capture probability ($P_{ANODEV} = 0.011$). After having accounted for this trend, SSTA and fisheries covariates (whichever the period, incubation, rearing or wintering) and SOI_w had no significant effect on capture probability ($P_{ANODEV} > 0.1$) except $SSTA_{west}$ of Australia ($P_{ANODEV} = 0.001$). Mean capture probability was estimated at 0.565 (±0.166) and tended to increase (Appendix C). Warm anomalies during winter in waters west of Australia increased capture probability ($\beta = 0.600$, SE = 0.038).

Starting from the latter model, we investigated environmental effects on survival probability which showed a quadratic trend ($P_{ANODEV} = 0.015$) which was accounted for thereafter. A preliminary analysis indicated no impact of fisheries ($P_{ANODEV} > 0.103$) either in the IOTC or the CCSBT regions and either during incubation, rearing or winter (in western or south-eastern Australia). Thus, fishing data from IOTC and CCSBT were pooled together in order to reduce the number of fishery covariates (from 8 to 4). However, no environmental (SSTA, SOI or fishery) effect was detected on adult survival ($P_{ANODEV} > 0.2$). Adult survival probability decreased until 1990, remained relatively low (0.849, SE = 0.027) until 1996 before increasing again (Fig. 7).

3.2.2. Hatching success

Hatching success of yellow-nosed albatrosses was on average 0.629 (±0.201) for the whole study period 1987–2005 (Fig. 3). It was more variable in the second than in the first part of the study period ($CV_{87–93} = 9.01\%$ vs. $CV_{96–05} = 27.78\%$) with a very low value in 1995. Hatching success showed a significant decrease over the study period ($P_{LRT} < 0.001$, $\beta = -0.825$). However, no significant linear trend was detected in SOI_w or SSTA variables ($P > 0.196$), which could have explained the decrease in hatching success. Then, to assess effects of environmental covariates, we first accounted for the overall decreasing trend in hatching success. Hatching success was found to be significantly positively related to SOI_w preceding the breeding season ($P_{LRT} < 0.001$). The correlation between observations and predictions of the hatching success was significant ($r = 0.549$, $P = 0.015$) and showed that SOI_w together with the decreasing trend explained 30% of the variations in hatching success (Fig. 3). Positive anomalies of the SOI_w improved the hatching success ($\beta = 0.186 \pm 0.049$). No significant relationship with any other environmental variables was detected.

3.3. Population modelling

Parameters used for modelling population dynamics of the study colony are given in Table 3. Both components (fledging and ha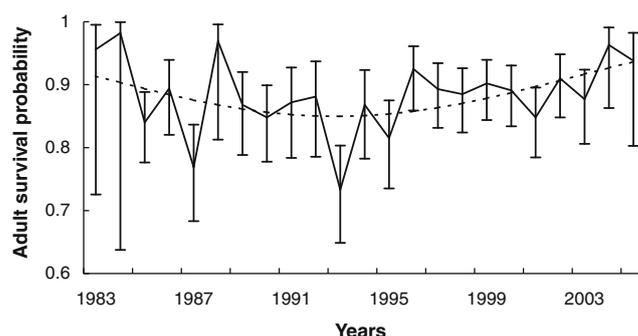tching success) of the breeding success were separated to include hatching success as the following function of SOI_w into the stochastic model: logit (HS) = $0.656+0.018 \times SOI_w$. We used a Gaussian distribution for SOI_w.

The deterministic model predicted a long-term annual growth rate of 0.968, indicating that the population would be decreasing at an average rate of 3.2% per year. The sensitivity and elasticity analyses showed that the growth rate is mainly sensitive to adult survival but also to emigration or immigration (Table 3). However, proportionally, adult survival contributes to the growth rate more than either the immigration or the emigration rate. The other parameters have low elasticities (Table 3).

Fig. 7. Annual variations of adult survival probabilities estimated from the time-dependent model (Φ_t, $p_{m + T + SSTAwest}$) in solid line, and from the selected model ($\Phi_{T + T2}$, $p_{m + T + SSTAwest}$) in dashed line. Error bars indicate standard errors.

Table 3

Mean and its standard error (SE) for the Southern Oscillation Index in winter (SOI_w) during the period 1981–2004 as well as sensitivities and elasticities (estimate from the deterministic model) for the yellow-nosed albatross demographic parameters: survival of adults (S_B), pre-breeders (S_{PB}) and juveniles (S_j), immigration (P_{Im}) and emigration (P_{Em}) rates, age-specific probabilities to breed for the first time ($T_{a/B}$), hatching (HS) and fledging success (FS), probability to become breeder ($T_{NB/B}$) or non-breeder ($T_{B/NB}$).

	Mean	SE	Sensitivity	Elasticity
S_B	0.902	0.011	*0.863*	*0.804*
S_{PB}	0.869	0.013	0.098	0.088
S_j	0.645	0.086	0.023	0.016
$T_{4/B}$	0.009	0.006	0.011	0.000
$T_{5/B}$	0.033	0.014	0.009	0.000
$T_{6/B}$	0.098	0.026	0.007	0.001
$T_{7/B}$	0.238	0.048	0.006	0.001
$T_{8/B}$	0.165	0.053	0.004	0.001
$T_{9/B}$	0.283	0.076	0.003	0.001
$T_{10/B}$	0.124	0.076	0.002	0.000
$T_{11/B}$	0.176	0.088	0.001	0.000
$T_{12/B}$	0.201	0.125	0.001	0.000
$T_{13/B}$	0.399	0.193	0.000	0.000
$T_{14/B}$	0.013	0.193	0.000	0.000
P_{Im}	0.103	0.085	0.678	0.072
P_{Em}	0.038	0.011	−0.678	−0.027
$T_{B/NB}$	0.160	0.008	−0.091	−0.015
$T_{NB/B}$	0.419	0.019	0.030	0.013
HS	0.629	0.201	0.024	0.016
FS	0.192	0.181	0.079	0.016
SOI_w	−4.082	8.888	–	–

Table 2

Modelling capture (p) and survival (Φ) probabilities for yellow-nosed albatrosses between 1982 and 2005 at Amsterdam Island. The selected model is in bold type. Np is the number of estimated parameters and ΔQAICc is the difference in the corrected second-order Akaike's information criterion for the model.

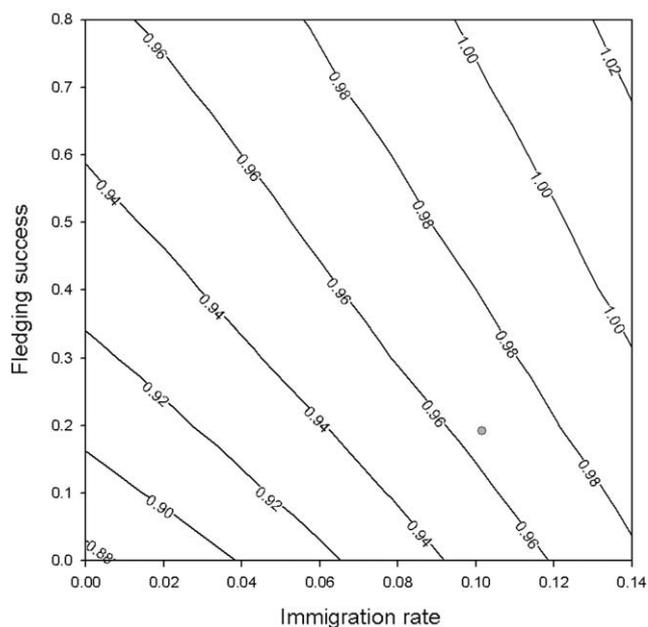| No.	Definition	Model	Np	QAICc	ΔQAICc
1	Fully time-dependent	Φ_t, $p_{m + t}$	47	5892.84	0
2	Constant trap effect on p	Φ_t, p_m	25	6299.57	406.73
3	**Constant Φ and additive trap effect on p**	**Φ, $p_{m + t}$**	**25**	**5894.41**	**1.57**
4	Constant Φ and trap effect on p	Φ, p_m	3	6361.62	468.78

Fig. 8. Yellow-nosed albatross population growth rate (λ) under different scenarios of fledging success and immigration rate in the study colony if emigration rate remains at 3.8% per year, the grey dot representing the current conditions of fledging success and immigration ($\lambda = 0.966$).

When accounting for annual variability in demographic parameters and SOI_w, the number of breeding pairs predicted by the matrix model was close to the observed values ($R^2 = 0.893$, $P < 0.001$; Fig. 5). The stochastic model indicated a growth rate (λ) of 0.966. When the mean of the SOI_w (-4.08) was modified (4 and -12), mean growth rate did not change significantly (0.967 and 0.966, respectively).

If all climate conditions, fishing effort and distribution and disease intensity remain constant, the study colony should become extinct in 148 years ($P = 0.971$). If the emigration of adult breeders stops, the colony would be nearly stable ($\lambda = 0.993$). Nevertheless, if emigration and immigration together stop, it would become extinct by the end of the century (69 years, $P = 1$, $\lambda = 0.926$).

All other parameters (included emigration) being unchanged, if the fledging success was on average 72%, the colony could be stable ($\lambda = 1.001$, Fig. 8). With a decreasing immigration rate, the colony would decline at an increasing rate (Fig. 8) and time to extinction would be short (53 years, $P = 1$, $\lambda = 0.904$) in absence of immigration. However, if emigration rate was 2% corresponding to a rate comprised between those of the wandering albatross (Inchausti and Weimerskirch, 2002) and the Atlantic yellow-nosed albatross (Cuthbert et al., 2003), growth rates would be higher and a fledging success of only 51% would be enough for the colony to be stable.

4. Discussion

4.1. Interaction with tuna fisheries

Unexpectedly, we found no evidence that yellow-nosed albatross adult survival was affected by legal tuna longlining effort, whichever the stage (incubation, rearing or wintering) and the area (west of or around Amsterdam or around Australia) where tuna fisheries and yellow-nosed albatrosses may have interacted. These results must be interpreted with care because our understanding of bycatch rates in IOTC and CCSBT fisheries is poor. Indeed, there are few observers on most (particularly in high seas) tuna fleets so the number of birds killed is generally not recorded or underesti-

mated (CCSBT, 2006; IOTC, 2007). However, it is possible that the population trend of this colony of yellow-nosed albatrosses is not related to bycatch in longline fisheries. Indeed, the closely related Atlantic yellow-nosed albatross (*Thalassarche chlororynchos*) from Gough Island does not seem to be affected by fisheries (Cuthbert et al., 2003). In addition, the apparent survival of 0.903 in our study colony when it was relatively stable (1996–2001) is more similar to the survival estimated for the Gough Island population (0.92), than to the fishery-affected survival (0.84) of the Tristan Island population (Cuthbert et al., 2003). Similarly, regarding the Indian yellow-nosed albatrosses from Prince Edward Island, despite a significant number of birds killed in longlines targeting both Patagonian toothfish around the Prince Edward Islands (Nel et al., 2002) and tunas around South Africa (Ryan et al., 2002), the population has remained stable for twenty years (Ryan et al., 2003). However, since we could not take IUU fishery into account, while it may have an important effect, the effect size of the fisheries impact on adult survival was probably underestimated. Thus, fisheries should not be totally dismissed as a potential threat to the Amsterdam yellow-nosed albatross population. More information on the at-sea distribution of the non breeding part of the population is required to clarify the interactions between birds and fleets, and observers are needed onboard vessels targeting tuna to record bycatches.

4.2. Effect of climate

The quadratic trend in adult survival was not explained either by SSTA (during the breeding period around Amsterdam or during the wintering period west of Australia) or by SOI the winter preceding the reproduction. This is in agreement with Weimerskirch et al. (2001) which have already reported that adult survival was not affected by SSTA during the chick rearing period. However, other environmental factors, not tested here, could have had an influence on adult survival.

Increase in capture probability of breeding individuals may result from increasing recapture effort in the field study. This probability has two components: real detection and breeding abstention probabilities. Thus, the relationship between SSTA in Australian waters and capture probability might reflect that SSTA before incubation probably played a role in the decision to breed through acquisition of body condition.

We detected no effect of SSTA on the hatching success. Previous studies on a neighbouring colony at Amsterdam Island found similar results. Despite the existence of an effect of SSTA on the provisioning rates to the chicks, fledging success was not affected (Weimerskirch et al., 2001; Pinaud et al., 2005). However, the yellow-nosed albatross hatching success was favoured during positive phases of winter SOI, characteristic of a La Niña year. Likewise, a better breeding success of black-browed albatrosses (*Thalassarche melanophrys*) from Kerguelen which also winter in Australasian waters, was associated with positive SOI_w (Rolland et al., 2008). This relationship could not be explained by SSTA because there was not a strong correlation between SOI_w and SSTA in the wintering area. This suggests that the foraging strategy of yellow-nosed albatrosses was influenced by another factor related to the SOI_w, such as the Leeuwin current. This warm current flowing southward off western Australia and extending as far as Tasmania is stronger during winter and during La Niña years (Feng et al., 2003). It was reported to affect abundance and distribution of several marine species from krill and fish to seabirds (Wooller et al., 1991; Wilson et al., 2001, 2003). In addition, the Leeuwin current can also generate eddies away from the coast (Heywood and Somayajulu, 1997). Given that foraging yellow-nosed albatrosses are known to exploit such eddies that form in the Agulhas Current during the summer season (Pinaud and Weimerskirch, 2005), they may be affected by this current during the wintering season.

4.3. Effect of avian cholera

Avian cholera was reported to cause the low breeding success in the yellow-nosed albatross by killing young chicks just after hatching (Weimerskirch, 2004). Indeed, average fledging success (0.19) was very low compared to other yellow-nosed albatross colonies from Amsterdam (Weimerskirch et al., 2001) resulting in the low breeding success. This is comparable to the black-browed albatross fledging success at Bird Island, South Georgia, which was very low (0.18) in a colony infested with ticks and high (0.88) in a non-infested colony (Bergström et al., 1999). Weimerskirch (2004) suggested that the disease could be the cause of the low adult survival in the 1990s. We could not have a direct measure of the virulence or prevalence of the disease that could permit to test explicitly whether the disease affected adult survival. However, in the colony, very few adults were found killed by this disease (Weimerskirch, 2004). In addition, adult survival increased after 1996 despite the persistence of the disease affecting chicks, so adults may have become resistant.

4.4. Population dynamics

Population growth rate of the study colony was below replacement and in accordance with its decreasing trend in numbers observed over the past few decades. According to our analyses on the demographic parameters, this decline was not caused by anomalies of the sea surface temperatures. Likewise, the winter SOI had an impact on the hatching success but a simulated change in winter SOI did not significantly affect the population growth rate, because variations in hatching success contribute little to the variation of growth rate. We suggest that the decline was mainly caused by the avian cholera affecting fledging success. Indeed, a decrease in breeding success due to a disease may have an impact on population dynamics by three ways (Boulinier and Danchin, 1996): (1) a low local recruitment and so a delayed decrease in the number of breeders, (2) an increase in the proportion of breeders skipping reproduction the year after, or (3) a low breeding site-fidelity. On the total number of birds banded as fledglings between 1980 and 1993, only 18.9% have recruited in the study colony. The probability to skip breeding was not high (16%) but the probability to move from non-breeders to breeders is low (41.9%) compared to other species such as the black-browed albatross where these probabilities were, respectively, 19.6% and 57–71% (Arnold et al., 2006). Our study reveals that c. 4% of breeders emigrated each year, which is a higher proportion than in the wandering albatross (*Diomedea exulans*) (2.9%; Inchausti and Weimerskirch, 2002) or in the Atlantic yellow-nosed albatross (1.1%; Cuthbert et al., 2003). Avian cholera could be the cause of emigration through breeding failure since 71% of emigrating breeders have failed their last breeding in the study colony and once they have emigrated to a neighbouring colony, they never returned to the study colony. In addition, the proportion of new breeders immigrating was high (10.1%) compared to other seabirds such as southern fulmars (*Fulmarus glacialoides*) (3%; Jenouvrier et al., 2003) or the black-browed albatross (6.2%; Rolland et al., in press). This indicates important movements between colonies, which seems different from what is known for other albatross species.

Finally, we predict that the study colony should go extinct within 150 years if the demographic parameters do not change. If immigration of new breeders stops, the decline will be more rapid and the study colony should go extinct by 2055. However, if emigration of breeders stops, the colony should become stable. On the other hand, a fledging success of 72% would be sufficient for the population growth rate to stabilise. This value might correspond for example to a decrease in avian cholera prevalence/virulence, since fledging success observed in other albatross species are commonly above 80% (Bergström et al., 1999; Cuthbert et al., 2003). This result highlights the large potential effects of a disease and the important contribution of emigration/immigration in population dynamics. Nevertheless, in the future, an index of the disease should be found to properly model the frequency of disease appearance and its intensity, for instance, by determining the disease prevalence in newly born chicks and their parents few days after hatching. This could also provide information on whether parents are disease carriers and the part of variability of fledging success attributable to the disease prevalence.

To summarize, the study colony and the rest of the population of yellow-nosed albatross at Amsterdam Island declined simultaneously until 1995. Then, the population stabilised whereas the study colony continued to decrease. Interestingly, adult survival followed a quadratic trend with lower values between 1991 and 1996. Similarly, hatching and fledging success were at their lowest levels in 1994–1995. Thus, we hypothesized that the common phase of decline in colonies was due to a decrease in adult survival which may have been affected by climatic factors not tested here, or by IUU fisheries, or even by the disease at the beginning of the study period. During the second phase, adult survival increased but the study colony continued decreasing unlike the rest of the population because of the very low fledging success in the colony, caused by the disease and resulting in low recruitment and high emigration.

To conclude, although the study colony may not be an entirely representative sample of the Amsterdam yellow-nosed albatross population because all the neighbouring colonies are probably not infected to the same extent by the avian cholera (Weimerskirch, 2004), we draw attention to the potential of such a disease to lead the whole population to extinction. Indeed, our results show that the study colony is threatened with extinction, mainly because of this disease, and breeders emigrating from this colony might possibly become vectors of the disease to other colonies of Amsterdam Island. In addition, we do not know the biology of *P. multicoda* in relation to albatrosses and whether this bacterium is able to spread out to other colonies as documented for other species such as Anseriformes (Friend, 1999). Although today the Amsterdam Island population of yellow-nosed albatrosses seems to have stabilised since 1997 after the initial decline occurring before 1995 (Fig. 6) (Weimerskirch and Jouventin, 1998), its size should be more regularly censused and the total breeding success should be estimated in order to assess whether the disease spreads. Finally, the present study underlines the complex interactions between potential threats such as disease, climate and fisheries in albatross demography.
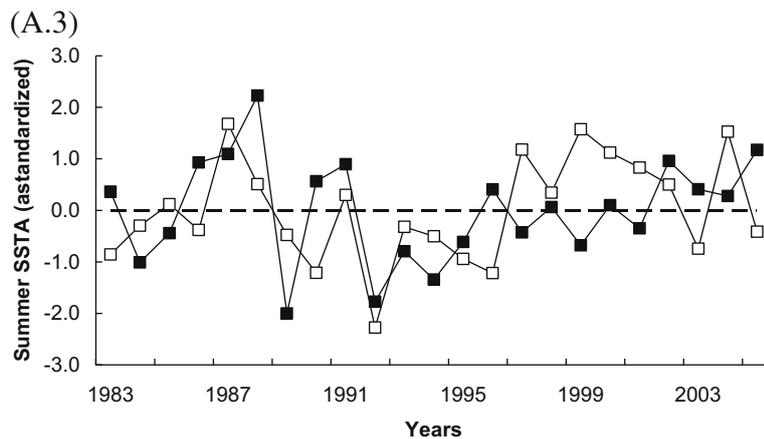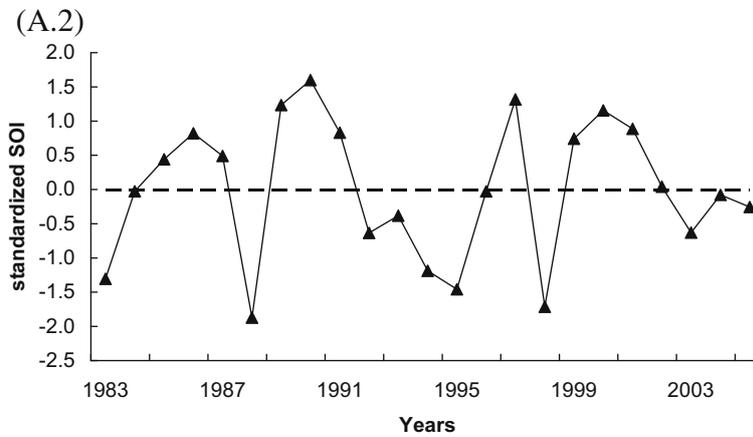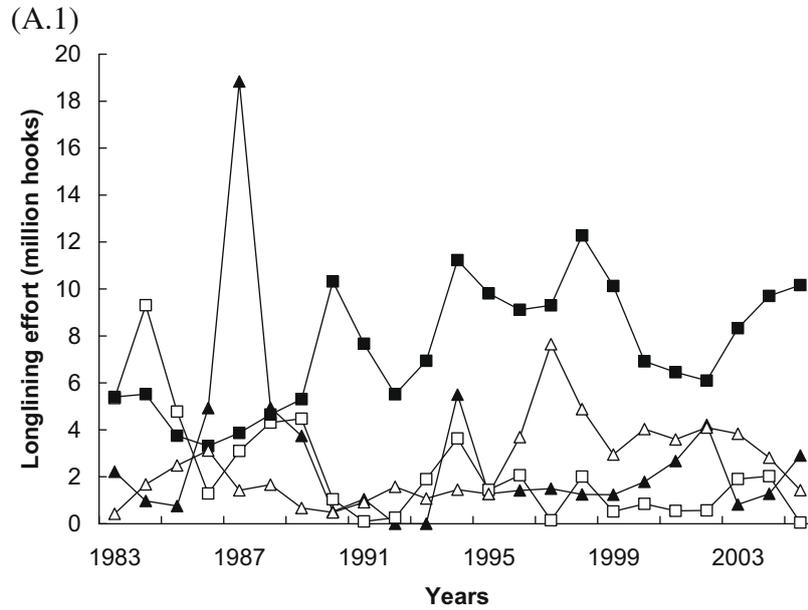
Appendix A

Covariates extracted for the period 1983–2005: (A.1) effort in tuna longlining; (A.2) standardized Southern Oscillation Index (SOI) during winter; and standardized seas surface temperature anomalies (SSTA) during the breeding (A.3) and wintering (A.4) seasons of the yellow-nosed albatross. Squares correspond to breeding periods of incubation (filled) and chick rearing (blank) whereas triangles correspond to winter foraging areas, south (filled) and west (blank) Australia.

(A.1)

(A.2)

(A.3)

(A.4)
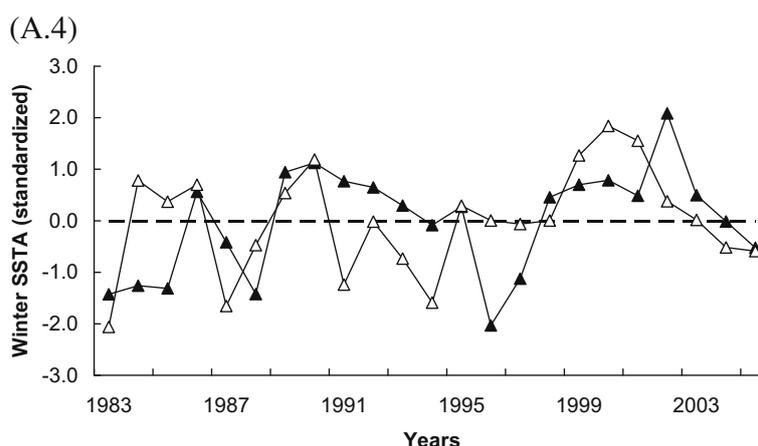
Appendix B

Summary of the multistate models used in the population modelling.

No selection was performed on these multistate models as only the mean parameter of interest was needed and estimated from constant models. Survival (F), transition between states (ψ) and capture probabilities (p) were constant (.), modelled with age (a) and/or states (s) depending on the model.

Model	States	Parameter(s) of interest
$(F., \psi_s, p_s)$	"Breeder"	Probability to skip a reproduction ($T_{B/NB}$)
	"Non-breeder"	Probability of returning breeder ($T_{NB/B}$)
(F_s, ψ_s, p_s)	"Study colony"	Probability of emigration (P_{Em})
	"Other colonies"	Real survival (S_B)
$(F_{a \times s}, \psi_{a \times s}, p_{a \times s})$	"Fledgling"	First-year survival (S_j)
	"Breeder"	Probability to breed for the first time ($T_{a/B}$)

Model ($F_{a \times s}$, $\psi_{a \times s}$, $p_{a \times s}$)

To estimate juvenile survival (S_j) and age-specific probabilities to breed for the first time ($T_{a/B}$), we needed birds known as fledglings and potentially observable as first breeders on the colony. Because most birds (95%) first reproduce before 10 years-old, we used capture histories of 418 individuals banded as fledglings from the cohorts 1980–1993. We used an age-dependent multistate model ($F_{a \times s}$, $\psi_{a \times s}$, $p_{a \times s}$), where a was age and s represented the states "fledgling" or "breeder". Yellow-nosed albatrosses have delayed maturity and stay at sea between fledging and recruitment, period during which they are unobservable.

Therefore, the model can only provide a probability of surviving to the breeding age and to estimate juvenile survival, we need to fix survival of immatures of 1–4 years-old to 1, since the minimum age of first breeding was five. Similarly, capture probability of fledglings and immatures was fixed to zero. Probability to start breeding (i.e. transition from fledging to breeder) was age-dependent. We assumed that all birds aged 16 or more have started to breed so $T_{15/B}$ must be forced to 1. As pre-breeders are unobservable, we assumed their survival (S_{PB}) be equal to adult survival in this model.

Model ($F.$, ψ_s, p_s)

To estimate probability to skip a breeding event, we used 1228 birds banded as chicks and adults, all cohorts mixed up. Individuals could be in two states, breeder or non-breeder seen on the colony. The analysis was conducted for the period 1981–2005. We first performed a goodness-of-fit test on the multistate model ($F.$, ψ_s, p_s) and it revealed a trap-dependent effect ($\chi^2_{24} = 89.9$, $P < 0.001$). We thus built a model with two age classes for recapture probabilities to account for trap-dependence (Pradel, 1993). However, the GOF test was still significant ($\chi^2_{211} = 273.2$, $P < 0.001$), we thus calculated a variance inflation factor ($\hat{c} = 1.29$) to account for overdispersion. Capture probability was higher for breeders (0.9) than for non-breeders (0.24). It is not surprising since breeders are systematically checked on their nests whereas for non-breeders, it is more opportunistic.

Model (F_s, ψ_s, p_s)

The multistate model (F_c, ψ_c, p_c) was used for the period 1990–2005 on 1126 individuals where c represented two sites "the study colony" or "other neighbouring colonies at Amsterdam Island". The GOF test of this model ($\chi^2_{45} = 55.73$, $P = 0.131$) indicated that the model fitted the data. The transition corresponding to the immigration was fixed to zero because banded individuals breeding on other colonies were not sufficiently numerous.
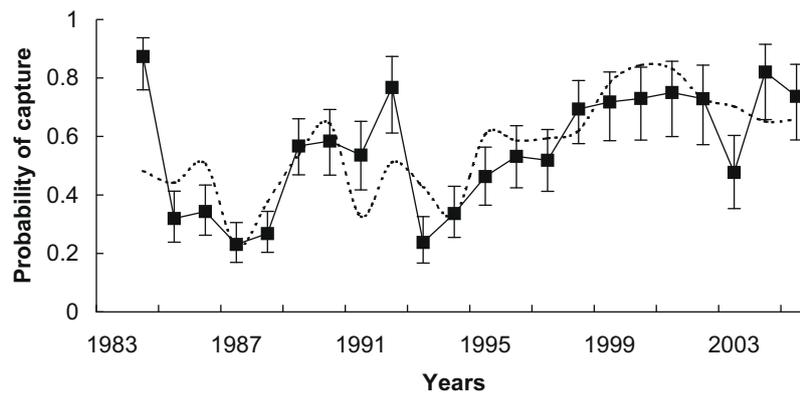
Appendix C

Annual probability of capture of Indian yellow-nosed albatross estimated from the model with additive trap-dependence (solid line with squares and standard errors) and from the selected model with a linear trend and an effect of SSTA$_{west}$ (dotted line). Survival was time-dependent in both models.

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