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Relative influence of fisheries and climate on the demography of four albatross species

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Abstract

Worldwide ecosystems are modified by human activities and climate change. To be able to predict future changes, it is necessary to understand their respective role on population dynamics. Among the most threatened species are top predators because of their position in the food web. Albatross populations are potentially affected by both human activities, especially longline fisheries, and climatic fluctuations. Based on long-term data (1985–2006), we conducted through a comparative approach a demographic analysis (adult survival and breeding success) on four albatross species breeding on the Indian Ocean sub-Antarctic Islands to assess the relative impact of climate and fisheries during and outside the breeding season. The study revealed that adult survival of almost all species was not affected by climate, and therefore probably canalized against climatic variations, but was negatively affected by tuna longlining effort in three species. Breeding success was affected by climate, with contrasted effects between species, with Southern Oscillation Index having an impact on all species but one. Differences in demographic responses depended on the foraging zone and season. In order to predict population trajectories of seabirds such as albatrosses, our results show the importance of assessing the relative influence of fishing and climate impacts on demography.

Keywords: breeding success, climate, longlining, seabird, survival

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Introduction

There is increasing evidence that global climate change has affected species by modifying their phenology, physiology, distribution and abundance, thus leading to a change in interspecific interactions and consequently in the structure of ecosystems (Hughes, 2000, 2003; McCarty, 2001; Walther *et al.*, 2002). Effects of increasing climate variability/warming, human in origin, may be exaggerated by other anthropogenic stressors (Root *et al.*, 2003) such as overexploitation. Although these stressors are linked to human activities, their different effects on animal populations may or not be detectable. It is thus important to tease out these competing human effects and quantify their relative contributions in ecological scales.

Some species are more in peril than others. In particular, top predators are more vulnerable to global changes, since they integrate, through bottom-up control, all the lagged or direct effects of environmental

variations undergone by lower trophic levels (Frederiksen *et al.*, 2006). Among top predators, marine species including seabirds have been reported to be affected by human activities, more particularly by industrial fisheries (Ormerod, 2003). Effects may be negative, directly through incidental mortality (Tuck *et al.*, 2003) or indirectly through reduction in food abundance (Frederiksen *et al.*, 2004), or positive due to discards providing additional food (Oro, 1996; Bunce *et al.*, 2002). Moreover, population dynamics of seabirds may also be influenced by climate change (Croxall *et al.*, 2002; Weimerskirch *et al.*, 2003) either directly (e.g. extreme conditions causing chick mortality) or through modification of resource availability. Several long-term studies have documented, in both hemispheres, high mortality or breeding failure of seabirds associated with large-scale climatic phenomena such as El Niño Southern Oscillation and the North Atlantic Oscillation (Stenseth *et al.*, 2002; Barbraud & Weimerskirch, 2003; Sandvik *et al.*, 2005) or anomalies in oceanographic conditions such as sea surface temperatures or sea ice extent (Frederiksen *et al.*, 2004; Jenouvrier *et al.*, 2005b). Because important climate changes are expected during the next century

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(IPCC, 2007), conservation strategies need to take into account the responses of top predator populations to these expected changes and to estimate the relative role of fisheries and climate on populations.

Among seabirds, albatrosses are one of the most threatened bird family in the world with 18 of 22 species classified from vulnerable to critically endangered (IUCN, 2009). Albatrosses face a number of threats both on land and at sea (Baker et al., 2002; Cooper, 2006). Fisheries are thought to be the major cause of population declines through bycatch mortalities (Gales, 1998; Tuck et al., 2003). Indeed, tens of thousands of albatrosses are incidentally killed annually, hooked in longlines (Gales et al., 1998; Nel et al., 2002; Ryan et al., 2002), entangled or struck in trawl cables (Sullivan et al., 2006), in both the Northern and the Southern Hemisphere (Baker et al., 2007; Véran et al., 2007). Research has thus been stimulated to propose effective mitigation measures in order to reduce incidental seabird bycatch (Brothers et al., 1999; Weimerskirch et al., 2000; Bull, 2007). Most studies on albatrosses and fisheries reported mortality rates (e.g. number of birds killed per 1000 hooks) or counts of birds killed per species but few have assessed the impact of such bycatch on adult survival at the population level (e.g. Véran et al., 2007) and on the population growth rate. Yet, a substantial number of birds of a species may be killed without necessarily affecting the adult survival and its population dynamics. Therefore, it is crucial to determine the relative importance of fisheries, but also of climate impacts on survival in albatross populations in different geographical areas. This would therefore allow to quantify the potential effectiveness of mitigation measures and to implement large-scale conservation strategies such as marine protected areas.

Here, we compare the responses of four albatross species (wandering Diomedea exulans, sooty Phoebetria fusca, yellow-nosed Thalassarche carteri and black-browed T. melanophrys albatross), in terms of adult survival and breeding success, to climate variation and fishing effort. Since 2003, the three latter species are listed as Endangered whereas the wandering albatross is Vulnerable (IUCN, 2009). Effects of climate and fisheries have already been studied in annual species, the black-browed and the yellow-nosed albatrosses (Rolland et al., 2008; 2009), but not for the two biennial species. Thus, the first aim of the study was to estimate breeding success and adult survival, based on long-term mark-recapture data, of the wandering and the sooty albatrosses and test whether they were influenced by fisheries and/or climatic conditions. The second aim was to compare demographic responses of the two biennial species with those of the two annual albatross species in order to test the following a priori hypotheses (1–4).

Since albatrosses are typical longlived seabirds with long generation times and low maximum population growth rates (Niel & Lebreton, 2005), their populations should be very sensitive to a variation in adult survival, more than in breeding success (Saether & Bakke, 2000). Thus, mortality in fisheries through bycatch may pose a significant threat to their sustainability and given the large number of albatrosses killed in longlines, we predicted a negative impact of fisheries on adult survival of all species (1). On the other hand, canalization theory predicts a stronger buffering against environmental stochasticity in the vital rates to which the population growth rate is the most sensitive (Gaillard & Yoccoz, 2003; Morris & Doak, 2004). We thus expected adult survival to be less variable than breeding success (2) and adult survival to be less affected by climatic variability (3). However, because albatross populations have different life history traits such as different size, diets (Cherel & Klages, 1998) or foraging ecology, their demographic responses to climate and fisheries may be contrasted. In addition, albatrosses are highly migratory species foraging hundreds to thousands kilometers away from their breeding sites, so they may have to face different conditions at different time of the year. According to the tap hypothesis, climatic conditions during the breeding season should influence the production of new recruits whereas the tube hypothesis states that climate conditions during the nonbreeding season should affect the adult survival probability (Saether et al., 2004). As a result, we may expect that a given albatross species exhibits distinct responses to environmental conditions prevailing in the areas used in and outside the breeding season (4) as it was reported in the black-browed albatross (Rolland et al., 2008). More precisely, we predict identical responses to the same climatic factors, in yellow-nosed and black-browed albatrosses, because both species winter in offshore Australasian waters, and in yellow-nosed and sooty albatrosses because, during breeding, both species rely on the same oceanic water masses in the subtropical Indian Ocean.

Materials and methods

Study species and areas

The study was carried out on three sites of the French Sub-Antarctic Islands in the Southern Indian Ocean, on four albatross species which differ in several life history traits such as size, breeding frequency, foraging zones and population status (Table 1). Field procedures for banding and resighting were the same for all the four species: all birds were ringed with a stainless steel band which allowed an individual identification of both members of each pair at the time of the visits (three to four) to

Table 1 Main characteristics of the four studied albatross species

	Black-browed albatross *T. melanophrys*	Yellow-nosed albatross *T. carteri*	Wandering albatross *D. exulans*	Sooty albatross *P. fusca*
IUCN status (2009)	Endangered	Endangered	Vulnerable	Endangered
Weight (kg)*	3–5	2–3	7–12	1.8–3
Wingspan (cm)*	210–250	180–210	250–350	200
Breeding frequency	Annual	Annual	Biennial	Biennial
Colony site	Kerguelen	Amsterdam	Crozet	Crozet
Breeding population size	3150†	27000‡	579§	100§
Foraging area¶				
Breeding	East of Kerguelen shelf	West of Amsterdam	North of Crozet	North of Crozet
Nonbreeding	Tasmania	Western Australia	Circumpolar, Subtropical	Subtropical
Habitat‖	Neritic	Neritic & Oceanic	Oceanic	Oceanic
Diet**	Fish > Calmar	Fish > Calmar	Calmar > Fish	Calmar > Fish

Sources:
*Shirihai, 2002;
†Weimerskirch *et al.*, 1989;
‡Rolland *et al.*, 2009;
§Delord *et al.*, 2008;
¶See 'Materials and methods'.
‖Weimerskirch, 1998.
**Weimerkirch *et al.*, 1986.

the colony during the breeding season. At the fledging period, breeding performance was determined and chicks were ringed. Each year, new individuals (breeders or nonbreeders) found in the colony were also ringed. Foraging areas described below were provided by different satellite tracking studies and banding recoveries.

The black-browed albatross was studied at Kerguelen (49°41′S, 70°14′E) in the colony of Cañon des Sourcils Noirs (ca. 1100 breeding pairs), where ca. 200 breeding pairs were monitored annually since the season 1979/1980 (named 1980). This annual breeder forages in sub-Antarctic waters on the eastern edge of the Kerguelen shelf during the breeding season (Fig. 1a) from October to April (Pinaud & Weimerskirch, 2002) and in Tasmanian waters during the nonbreeding season (Weimerskirch *et al.*, 1985; Cherel *et al.*, 2000).

The yellow-nosed albatross was studied at Amsterdam Island (37°51S, 77°31′E) in the colony of Entrecasteaux (ca. 7000 breeding pairs) where ca. 150 breeding pairs were monitored annually since 1980. This annual breeder forages in subtropical waters west of (up to 2000 km away) and around Amsterdam Island during the breeding season (Fig. 1b) from September to April (Pinaud *et al.*, 2005), and in waters west of Australia during the non-breeding season (Weimerskirch *et al.*, 1985). In the studied colony, avian cholera caused high chick mortality (Weimerskirch, 2004) resulting in a low and variable fledging success.

The sooty albatross, a biennial breeder, was studied at Possession Island (46°25′S, 51°45′E), Crozet Islands,

where the entire colony of Pointe Basse which comprised ca. 100 breeding pairs (Delord *et al.*, 2008), i.e. only ca. 50 pairs breeding annually, was monitored every year since 1969. This species forages in subtropical waters north of Crozet (Pinaud & Weimerskirch, 2007) during the breeding season from October to June, but the nonbreeding foraging range of this population is known from limited tracking studies as extending westward and eastward from the breeding range, but limited to the oceanic part of the Indian Ocean (H. Weimerskirch, unpublished data, Fig. 1d).

The wandering albatross was studied at Possession Island, Crozet, where the entire breeding population consists ca. 580 breeding pairs (Delord *et al.*, 2008), i.e. only ca. 320 pairs breeding annually, was monitored every year since 1960. This biennial breeder forages in sub-Antarctic and subtropical waters (Fig. 1c), respectively, at the latitude and north of Possession Island (Weimerskirch *et al.*, 1993) while breeding (from December to November of the following year), and uses the whole southern Indian Ocean from South Africa to New Zealand while not breeding (Weimerskirch & Wilson, 2000).

Breeding success and survival analysis

All species lay only one egg per breeding season without clutch replacement. Breeding success is thus '1' when the egg produced a fledgling and '0' if the egg or chick died. For the black-browed and the yellow-nosed albatrosses, estimates of breeding success and
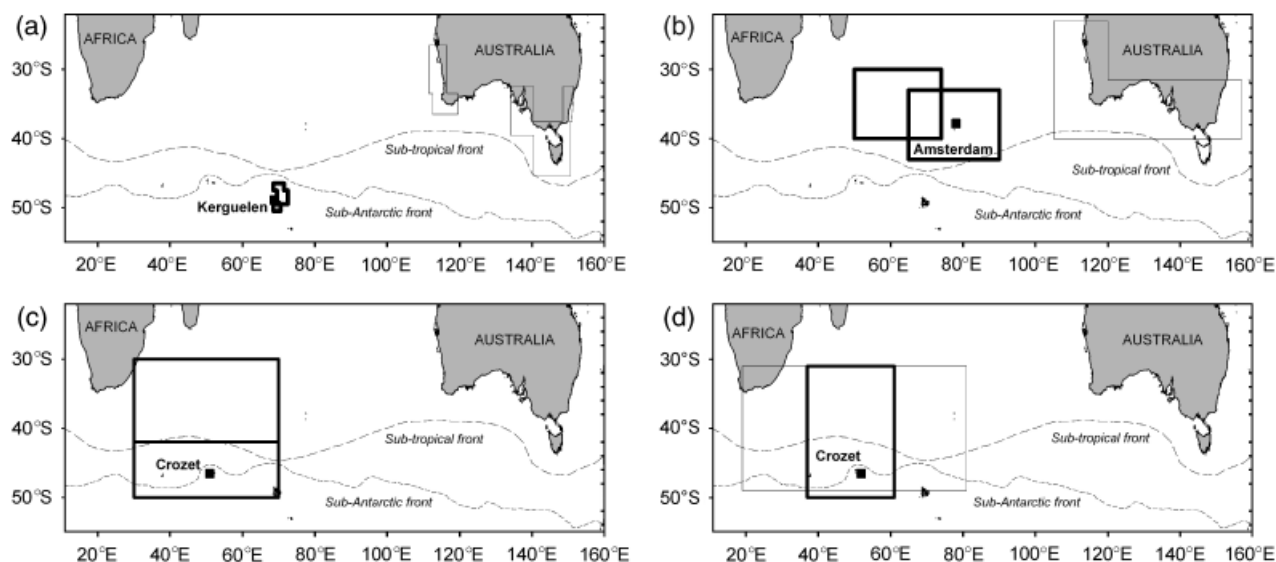
Fig. 1 Distribution area of (a) black-browed, (b) yellow-nosed, (c) wandering and (d) sooty albatrosses in both their breeding (thick rectangles) and nonbreeding (thin rectangles) grounds derived from satellite tracking and band recoveries. Breeding colonies are represented by a square.

adult survival probabilities as well as their relationships with fisheries and climate factors were synthesized from previous studies (Rolland et al., 2008, 2009). Here, we used the same modelling approach (generalized linear models with a logit link) to estimate breeding success and an analysis of deviance (Skalski, 1996) to test for relationships between this parameter and environmental covariates for the other two species. We used breeding success (and covariate) data between 1986 and 2006, which yielded 829 and 7051 breeding events from 503 and 2556 pairs for sooty and wandering albatrosses, respectively.

Adult survival probabilities of annual breeding species were estimated using monostate (i.e. a single present breeder state) mark-recapture models (Rolland et al., 2008, 2009). However, for biennial breeders, we could not use monostate models. Indeed, in sooty and wandering albatrosses, the breeding cycle is so long (8 and 12 months, respectively) that successful breeders (SB) are not able to breed two consecutive years and are consequently obligate nonbreeders the following year (noted PSB for post-SB). These birds in sabbatical year being not present on the colony are considered as temporary emigrants and this may bias survival estimates (Kendall et al., 1997). In addition, failed breeders (FB) may also attempt or decide to skip breeding the following year and be post-failed breeders (PFB). Thus, following Hunter & Caswell (2009) we used multistate models with four states, observable (SB, FB) and nonobservable (PSB, PFB), as described in details in Appendix S1.

For both species, sufficient detailed individual breeding success data were only available since 1985. Therefore, survival analyses were conducted for the 1985–2006 period on 866 and 2552 individuals for the sooty and the wandering albatrosses, respectively.

We tested whether our starting model fitted the data with a goodness-of-fit (GOF) test using U-CARE software (Choquet et al., 2005b). GOF tests were performed as if they were two instead of four states because two were unobservable (see results of GOF tests in Appendix S1).

Model selection was based on the Akaike information criterion (AIC) corrected where necessary by ĉ (QAIC) and performed with M-SURGE software (Choquet et al., 2005a). To test for an effect of fisheries and/or climate on adult survival, we used an analysis of deviance (Skalski, 1996). For both breeding success and adult survival analyses, a trend was tested for before testing for a covariate effect (Grosbois et al., 2008). For more details, see Rolland et al. (2008).

For the wandering albatross, information on individual sex was available and previous studies reported a lower survival in females than in males for the period 1966–1985 (Weimerskirch et al., 1997). Therefore, we tested again for a sex effect on adult survival.

Climate covariates

Sooty and wandering albatrosses may be affected by the large-scale Southern Oscillation Index (SOI) as other seabirds (Stenseth et al., 2002; Jenouvrier et al., 2005b). As both species forage in the Southern Indian Ocean,

we used the summer SOI from December to February (SOI_s) because El Niño events are more pronounced during these months and are thus more likely to have an influence beyond the Pacific Ocean. The monthly SOI was obtained from the Australian Bureau of Meteorology, National Climate Centre, Climate Analysis Section (http://www.bom.gov.au/climate/current/soihtm1.shtml).

We also used sea surface temperature anomalies (SSTA) as local climatic conditions. Monthly SSTA data on a 1° scale were available on the website of the Integrated Global Ocean Services System (http://ingrid.ldeo.columbia.edu/, Reynolds *et al.*, 2002). We averaged SSTA for different zones and different seasons. Satellite tracking indicated that breeding wandering albatrosses foraged in a 30–50°S, 30–70°E sector during the breeding season (Pinaud & Weimerskirch, 2007). We created four SSTA variables according to two seasons, incubation (January–March) and rearing (April–November), and two zones, subtropical and sub-Antarctic (Fig. 1c): $SSTA_{incA}$, $SSTA_{incT}$, $SSTA_{rearA}$ and $SSTA_{rearT}$. We did not use SSTA as a covariate for the nonbreeding season because birds were not distributed in a restricted area. Sooty albatrosses used a subtropical 32–50°S, 37–60°E area during the breeding period (Pinaud & Weimerskirch, 2007) and we used two covariates $SSTA_{inc}$ (incubation) and $SSTA_{rear}$ (rearing). Outside the breeding season (June–August), birds of this species seem to exploit a larger area (32–48°S, 20–80°E), so we also used a SSTA variable for winter ($SSTA_{wint}$) corresponding to this area.

Fisheries covariates

Both the sooty and the wandering albatrosses are species that may be caught in longlines (Gales *et al.*, 1998; Weimerskirch *et al.*, 2000). We thus aimed to test for an effect of fishing effort on adult survival of these species. Because of this bycatch, albatross population dynamics may be considered as that of an overharvested population in which survival probability (*F*) is proportional to the catch rate (Lebreton, 2005). However, no accurate estimate of bycatch rate per species is available for these fisheries. Indeed, it would have required trained observers on every fishing vessels. Therefore, following Véran *et al.* (2007) we assumed that the level of bycatch was proportional to fishing pressure, that is fishing effort (Effort) and considered the regression equation:

$$F = \alpha - \beta \times \text{Effort}, \quad (1)$$

where α is the intercept and β the slope which should be equal to zero with the null hypothesis (i.e. no impact of fishing effort on adult survival). This equation may be applied providing that no mitigation measure exist to reduce this incidental mortality, which is the case in tuna fishery. However, some measures such as night setting have been implemented for the toothfish fishery from 1992 onwards in the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) area.

The wandering albatross foraging areas overlapped with those frequented by longliners targeting the Patagonian toothfish *Dissostichus eleginoides* in sub-Antarctic waters and tuna species in subtropical waters (Weimerskirch *et al.*, 1997). Thus, we tested for effects of (i) tuna fishing effort extracted for two zones called 'sub-Antarctic' ($Effort_{tunaA}$) and 'subtropical' ($Effort_{tunaT}$) corresponding to the wandering albatross foraging zones (45–50°S, 30–85°E and 30–45°S, 10–85°E, respectively) and (ii) toothfish fishing effort ($Effort_{tooth}$) exerted in the statistical CCAMLR areas 58.6 and 58.4.4 (i.e. around Crozet and Prince Edward Islands, respectively). For the toothfish fishery, we pooled annual legal and estimated illegal unreported and unregulated (IUU) fishing effort data. For tuna longline fisheries, no estimate of IUU is available. Data on longlining effort (number of hooks set) were obtained from the Commission for the Conservation of the Southern Bluefin Tuna (CCSBT, http://www.ccsbt.org/docs/data.html) and the Indian Ocean Tuna Commission (IOTC, http://www.iotc.org/English/data/databases.php) for tuna fisheries, and from CCAMLR (http://www.ccamlr.org/), Muséum National d'Histoire Naturelle (G. Duhamel, unpublished data) and Ryan *et al.* (2002) for toothfish fisheries. As sooty albatrosses are mostly subtropical foragers, they may interact with tuna longliners. We thus tested for an effect of tuna fishing effort on adult survival during the incubation and rearing periods ($Effort_{tuna-inc}$ and $Effort_{tuna-rear}$) and outside the breeding season ($Effort_{tuna-wint}$) in the zones 32–50°S, 37–60°E and 30–50°S, 20–80°E, respectively (Fig. 1d).

Details about environmental covariates and why they were tested on breeding success or adult survival can be found in Rolland *et al.* (2008, 2009) for the black-browed and the yellow-nosed albatrosses, respectively. All the environmental variables used in the present study are summarized in Appendix S2. All covariates were standardized on the study period which allows compare (standardized) slopes obtained for relationships between different demographic parameters and different environmental covariates (Grosbois *et al.*, 2008).

To reduce the number of climatic and fishery covariates and avoid multicollinearity, we performed two principal component analyses which were not conclusive (see Appendix S3). Therefore, we tested for a correlation among the covariates and for an effect of each described climatic and fishery covariate on breeding success and adult survival of sooty and wandering albatrosses.

Species comparison

We determined whether survival was less variable than breeding success (Hyp 2) by using V/V_{max}, a measure of variability recommended by Morris & Doak (2004).

In order to compare the magnitude of the effects of fisheries and climate on demographic parameters among species, we first averaged the standardized slopes of the significant relationships between fishery covariates and adult survival probabilities on one hand, and the standardized slopes of the significant relationships between climate and breeding success on the other hand. We used slopes from the best models for each species. We approximated the standard errors associated to the mean slopes with the delta method (Seber, 1982). Finally, we compared the mean magnitude of fisheries and climate on demographic parameters using mean slopes $\pm$ SE in a χ^2 test provided by the CONTRAST software (Hines & Sauer, 1989). All estimates are given $\pm$ SE.

In case of an impact of fisheries, we calculated the adult survival in the hypothetic condition where there would be no fishing effort from the logistic regressions that related adult survival with tuna fishing effort.

Those comparisons allowed us to conclude on Hyp 1, 3 and 4.

Results

Wandering albatross, demographic parameters and environmental effects

In the wandering albatross, annual breeding success was on average 0.728 ± 0.039, with little year-to-year variations (Table 2) and increased regularly over the 1986–2006 period (Appendix S4, Fig. S1). This linear trend was significant ($P_{ANODEV} = 0.032$, $\beta = 0.155 \pm 0.046$). However, there was no significant linear trend in SOI_s or SSTA variables ($P > 0.139$). We thus accounted for this linear trend to assess the effect of environmental covariates. No significant relationship was detected with any environmental variables ($P_{ANODEV} > 0.400$, Appendix S4, Table S1).

Adult survival was not time dependent and was estimated at 0.938 ± 0.002, and sex had not a significant effect. We did not detect any significant trend in adult survival probability ($P_{ANODEV} > 0.744$, Appendix S4, Table S3). The analysis of deviance indicated that none of environmental covariates affected survival probability ($P_{ANODEV} > 0.146$) except $Effort_{tunaA}$ ($\beta = -0.241 \pm 0.070$, $P_{ANODEV} = 0.010$). Fishing effort for tuna in the sub-Antarctic zone had a negative impact on adult survival and this model explained 25% of the variation in adult survival probability (Appendix S4, Fig. S2).

Sooty albatross, demographic parameters and environmental effects

In the sooty albatross, annual breeding success was on average 0.689 ± 0.099 and was stable over the 1986–2006 period (Appendix S5, Fig. S3). Indeed, we found no linear or quadratic trend in breeding success ($P_{ANODEV} > 0.745$). There was no significant linear trend in SOI_s or SSTA variables ($P > 0.297$). There was no correlation between SSTA variables and SOI_s ($r < |0.302|$, $P > 0.184$). $SSTA_{inc}$ and $SSTA_{rear}$ were correlated ($r = 0.453$, $P = 0.039$), but we did not detect a significant effect of one or the other ($P_{ANODEV} > 0.191$) on breeding success. The best model ($P_{ANODEV} = 0.037$, Appendix S5, Table S4) indicated a negative effect of SOI_s ($\beta = -0.181 \pm 0.078$) and a positive effect of $SSTA_{wint}$ ($\beta = 0.197 \pm 0.068$) on breeding success. The correlation between the observed and predicted breeding success was significant ($r = 0.665$, $P = 0.001$, $n = 21$) and indicated that SOI_s together with $SSTA_{wint}$ explained 44.2% of the variations in breeding success (Appendix S5, Fig. S3). Negative anomalies of the SOI_s and warm anomalies during the winter preceding the reproduction favoured the breeding success.

Adult survival was best modelled as time-dependent, and was estimated at 0.884 ± 0.006 on average. Adult survival probability significantly decreased over time ($P_{ANODEV} = 0.017$, Appendix S5, Table S6) but a better fit was obtained when tuna fishing effort during incubation was included as an additional covariate ($P_{ANODEV} = 0.024$). Tuna fishing effort had a negative impact on survival ($\beta = -0.248 \pm 0.075$). This model explained 33.5% of adult survival variations (Appendix S5, Fig. S4), of which 17.4% was attributed to tuna fishing effort which did not decrease or increase over the study period ($F = 1.498$, $P = 0.237$).

Interspecific comparison

The studied colony of black-browed albatrosses remained stable along the study period (population growth rate: $\lambda = 1.003$) with large interannual variations. The wandering albatross population of Crozet overall increased ($\lambda = 1.012$). The sooty albatross colony continuously declined ($\lambda = 0.956$) (Fig. 2) as well as the yellow-nosed albatross studied colony ($\lambda = 0.962$).

We synthesized breeding success and adult survival estimates and their relationships with environmental covariates for each species in Table 2. In each species except the sooty albatross, adult survival was less variable than breeding success. All species had a high breeding success except the yellow-nosed albatross which also had the most variable one. Inversely, the wandering albatross was the only species for which the
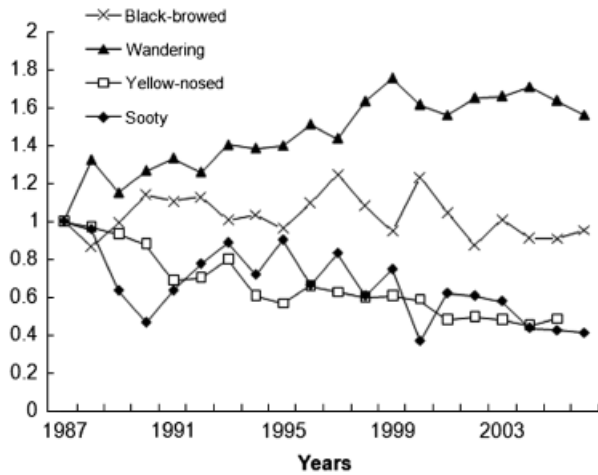
Fig. 2 Annual variation in the relative number of breeding pairs, calculated as the number of breeding pairs in year t divided by that in 1987 which was 233 for the yellow-nosed albatross (black dots) studied colony at Amsterdam Island; 71 and 231 for the sooty albatross (blank dots) colony and the wandering albatross (blank triangles) population at Possession Island, Crozet; and 1050 for the black-browed albatross (black triangles) colony at Kerguelen.

breeding success varied weakly and was increasing. Adult survival variability was also very low in the wandering albatross as well as in the black-browed albatross.

All species except the wandering albatross showed a response of breeding success to climatic anomalies, in particular with the SOI. The comparison of the slopes of the effect of SOI on breeding success indicated that this factor had an effect of similar importance ($\chi^2 = 2.632$, df = 2, $P = 0.262$) on the three species. Regarding the relative effect of SSTA on breeding success, we first estimated an average effect of SSTA for the black-browed albatross. Since the three SSTA covariates were not correlated (see Rolland *et al.*, 2008), we assumed the covariance to be null and we found an average slope of 0.160 ± 0.021. The comparison of this average slope of SSTA on black-browed albatross breeding success with the slope of the effect of $SSTA_{wint}$ on sooty albatross breeding success indicated that SSTA had a similar impact ($\chi^2 = 0.287$, df = 1, $P = 0.592$) on breeding success of these two species.

In all species except the yellow-nosed albatross, a decrease in adult survival was associated with an

Table 2 Mean breeding success ($\pm$ SD) and survival ($\pm$ SE) and relationships (slopes $\pm$ SE) with climate and fisheries for each studied albatross species

	Wandering Albatross	Sooty Albatross	Yellow-nosed* Albatross	Black-browed Albatross
Breeding success				
Mean	0.728 ± 0.039	0.689 ± 0.099	0.139 ± 0.149	0.659 ± 0.103
Period	86–06	86–06	87–05	86–04
V/V_{max}	0.007	0.031	0.378	0.061
$Effort_{trawl}$	–	–	–	0.390 ± 0.053
$SSTA_{inc}$	ns	ns	ns	0.119 ± 0.035
$SSTA_{rear}$	ns	ns	–	0.133 ± 0.039
$SSTA_{wint}$	–	0.197 ± 0.068	ns	-0.228 ± 0.036
SOI_s	ns	-0.181 ± 0.078	–	–
SOI_w†	–	–	0.186 ± 0.049	0.09 ± 0.041
Adult survival				
Mean	0.938 ± 0.002	0.884 ± 0.006	0.874 ± 0.005	0.918 ± 0.004
Period	85–06	85–06	82–05	81–05
V/V_{max}	0.005	0.033	0.013	0.003
$Effort_{tuna}$	-0.241 ± 0.070	-0.248 ± 0.075	ns	-0.222 ± 0.064
$Effort_{tooth}$	ns	–	–	ns
$SSTA_{inc}$	ns	ns	ns	0.252 ± 0.071
$SSTA_{rear}$	ns	ns	ns	ns
$SSTA_{wint}$	–	ns	ns	ns
SOI_s	ns	ns	–	–
SOI_w†	–	–	ns	ns

*For the yellow-nosed albatross, environmental effects were only tested on hatching success, fledging success variations being mainly caused by avian cholera (Rolland *et al.*, 2009).

†Southern Oscillation Index during winter was tested on breeding success and adult survival of the two annual species that spend the winter in Australasian waters (Rolland *et al.*, 2008; 2009).

V/V_{max} is a measure of variability. ns indicates a nonsignificant (at 0.05 level) slope whereas '–' corresponds to a nontested relationship.

increase in tuna fishing effort. Slopes indicate that this fishery had a similar impact on adult survival of the three species ($\chi^2 = 0.078$, df = 2, $P = 0.962$).

With values of adult survival estimated in the absence of fishing, adult survival probabilities of 0.938, 0.884 and 0.918 would be 0.939, 0.902 and 0.968 for the wandering, sooty and black-browed albatross, respectively. Note that adult survival of wandering albatrosses would not change. This is because fishing effort was low in their foraging area. Thus, slopes provide general information on the potential magnitude of effects but not on current impact. Therefore, for a more straightforward interspecific comparison of the actual current effects of fisheries and climate on demographic parameters, we calculated the Wald P-value (i.e. χ^2 test on the square of the mean estimate divided by its associated standard error) for the slope of each relationship between vital rates and climatic or fisheries covariate. The level of significance of these P-values was then used to arbitrarily define the intensity of each effect as high, medium or low. Intensities of each effect are summarized in Table 3, which suggests that the black-browed albatross was the most affected species.

Discussion

Our results show contrasted demographic responses of the four albatross species to fluctuations in climate and fishing conditions and underline the complexity of their interactions. However, some general rules on the impact of climate and anthropogenic effects such as fisheries on top predator demography can be inferred from this study, in particular the sensitivity of breeding parameters to climate and of survival to fisheries.

Effect of fisheries

As expected overall longline fishing for tunas had a major impact, by negatively affecting adult survival of three out of four southern albatross species. Slopes relative to tuna fishing effort indicated similar magnitude on the three species. Similarly, decrease in survival was previously linked to tuna longlining for the wandering albatross from this colony (Weimerskirch et al., 1997) and other colonies (Tuck et al., 2001; Nel et al., 2003; Terauds et al., 2006) and for the Tristan yellow-nosed albatross T. chlororynchos (Cuthbert et al., 2003). Even in the North Pacific, tuna longline fishing was reported to have caused the low adult survival of the black-footed albatross Phoebastria nigripes declining population (Véran et al., 2007).

Although black-browed and wandering albatrosses were observed to interact with Patagonian toothfish longliners (Weimerskirch et al., 2000; Nel et al., 2002),

toothfish fishing effort had apparently no impact on their adult survival probability over the 1985–2006 period. This result is in accordance with at sea observations from fisheries observers that reported low numbers of black-browed albatrosses and few or even no (since 2000) wandering albatrosses caught in this longline fishery (Delord et al., 2005). This suggests that mitigation measures have become efficient for albatrosses in the CCAMLR convention area, especially night setting (Weimerskirch et al., 2000). According to a study on the Prince Edward Islands population, the wandering albatross could even potentially benefit from the toothfish fishery by providing additional food (Nel et al., 2003).

In addition to having a positive effect on the breeding success of the Kerguelen black-browed albatross population, trawling had no negative impact on its adult survival (Rolland et al., 2008) which contrasts with the high level of mortality caused by trawl fisheries in the Falkland Islands population (Sullivan et al., 2006).

It appears from our estimates of adult survival in case of no fishing that the black-browed albatross survival probability would be much higher (0.968) than those of the wandering (0.939) and the sooty (0.902) albatrosses, which in the latter species, would probably not guarantee an increasing or at least stable population. This result is surprising, particularly for the wandering albatross for which population size is increasing. We propose the following nonexclusive explanations. First, we assumed a linear relationship between adult survival and fishing effort, while mortality might be non-linearly related to fishing effort. In other words, mortality due to fisheries might be compensated at low levels (i.e. confounded with mortality not caused by fisheries) whereas at high levels, i.e. above a certain threshold, survival would substantially decrease as suggested by the example of the wandering albatross in which survival was only very low in 2004, year of the highest tuna longlining effort in the breeding foraging range of the species. With this kind of relationship, we would have found a lower survival estimate for black-browed albatrosses in case of no fishing. Unfortunately, we could not test for non linear relationships because during the study period, the lowest fishing effort in the foraging Tasmanian zone of the black-browed albatross was already very high with 17.7 million hooks set in 1982 and 2004 winters, compared with the maximum of 400 thousand hooks set in the 2004 breeding season in the wandering albatross foraging range.

Second, fishing efforts in the Southern Indian Ocean were likely to be underestimated because of substantial IUU fisheries (Tuck et al., 2003) for which we had no estimates. As a result, slopes of the regression [Eqn. (1)] might have been underestimated. Thus, we cannot

Table 3 Intensity of the effect of each climate and fishery variable on breeding success and survival for the studied albatross species

	Wandering Albatross	Sooty Albatross	Yellow-nosed Albatross	Black-browed Albatross
Breeding success				
Effort$_{trawl}$	–	–	–	High
SSTA$_{inc}$	None	None	None	Medium
SSTA$_{rear}$	None	None	–	Medium
SSTA$_{wint}$	–	Low	None	High
SOI$_s$	None	Low	–	–
SOI$_w$	–	–	High	Low
Adult survival				
Effort$_{tuna}$	Medium	Medium	None	High
Effort$_{tooth}$	None	–	–	None
SSTA$_{inc}$	None	None	None	High
SSTA$_{rear}$	None	None	None	None
SSTA$_{wint}$	–	None	None	None
SOI$_s$	None	None	–	–
SOI$_w$	–	–	None	None

Based on each slope *P*-value, intensity of each effect was arbitrarily categorized into four groups: none (>0.05), low ($0.05–0.005$), medium ($0.005–0.0005$) and high (<0.0005) whereas '–' corresponds to a nontested relationship.

exclude that yellow-nosed albatross survival may have been affected by tuna fisheries. In addition, if slopes were indeed higher for the sooty and wandering albatrosses, their survival in case of no fishing would have been higher.

Third, survival probabilities we estimated were apparent survival estimates. Thus, true survival probability could have been slightly underestimated due to some emigration, as dispersal have been reported in wandering albatross (Inchausti & Weimerskirch, 2002) and yellow-nosed albatross (Rolland *et al.*, 2009) colonies.

Fourth, survival of sooty albatrosses estimated in the absence of fishing seems to be an underestimation of their survival under optimal conditions. Thus, if tuna fishing effort does not fully explain the low survival of the subtropical sooty and yellow-nosed albatrosses, another factor in their similar breeding foraging range, that we did not test here, could have been detrimental to their survival leading to their parallel population decline.

Finally, we are convinced that the use of the equation [Eqn. (1)] was reliable for testing the effect of tuna fishing effort on adult survival because international waters of the Southern Indian Ocean did not benefit from mitigation measures that could have masked an important impact of fishery.

Effect of climate

In all our studied species except the wandering albatross, we detected a climate effect on breeding success,

with contrasted responses between species. However, there was a common impact of the SOI with similar magnitude on breeding success of the three species although it was positive for the yellow-nosed and the black-browed albatross which migrate to Australian waters during winter; and negative for the sooty albatross which remains in a subtropical zone north of Crozet during summer. This suggests that the SOI has a global effect on oceanic ecosystems in the Southern Hemisphere. Indeed, although El Niño occurs in the Pacific Ocean, many marine predator species are influenced by the SOI in the whole Southern Ocean (Barbraud & Weimerskirch, 2003; Nel *et al.*, 2003; Murphy *et al.*, 2007). Regarding the wandering albatross in which we found no climate effect on breeding success, it might be a species less susceptible to environmental variations than the three other studied species because its larger size by conferring a greater safety margin allows a buffer to environmental variability (Weimerskirch, 1999). In addition, its breeding success was the least variable, and was very high. However, over a shorter study period, Inchausti *et al.* (2003) found a positive impact of SSTA during rearing on its breeding success. Other climate factors such as the wind conditions that we did not test here may also affect breeding success of the wandering albatross. Finally, climate effects may not be easily detectable because this species uses very large areas over the whole year. Contrary to the breeding success, adult survival for all species was not associated with any of the climate variables investigated in any of the studied species except for the black-browed albatross. In addition, adult survival

was less variable than breeding success for every studied species except the sooty albatross. This suggests that adult survival could be canalized against environmental variation as found in other longlived species such as herbivores (Gaillard & Yoccoz, 2003). The sooty albatross had a low and the most variable adult survival which is very likely the cause of their decline.

Patterns of demographic responses

Despite a similar magnitude, the nature of environmental impacts on demography is clearly contrasted between annual and biennial species. We did not find the same impacts among biennial breeders. Indeed, contrary to the wandering albatross, the sooty albatross was affected by climatic conditions. Among annual breeders, there was only a common influence of SOI on breeding success.

Season and area in which fishing activities that had the strongest impact on demography differed among species. Black-browed albatrosses had higher mortalities associated with tuna fishing effort in Tasmanian waters the winter preceding the reproduction whereas the adult survival of the other two species (sooty and wandering albatross) was sensitive to tuna fishing effort in the southern Indian Ocean; the former in subtropical waters during the incubation period and the latter in sub-Antarctic waters during the total breeding season, i.e. in their main foraging zones.

Also the geographical and seasonal characteristics of influential climatic factors varied among species. We detected no environmental effects in the wandering albatross, yet it exploited both the subtropical and the sub-Antarctic ecosystems but over extensive areas. We could not test for climate or fishery effects during the sabbatical year of the wandering albatross because its range extends to Tasman Sea and Pacific Ocean. Although they are both subtropical species, effects found in the sooty albatross were not significant for yellow-nosed albatross. However, both species had a similar adult survival and both colonies are declining. Thus, there may have been a common factor, not tested here because of lack of information on the causes, in subtropical waters of the southern Indian Ocean that affected both species.

In addition to differences in demographic responses between species, there are some evidences that differences also exist between populations of the same species. For example, black-browed albatrosses from Kerguelen and from South Georgia have, respectively overall high (65%) and low (29%) breeding success but the formers feed on fish on the Kerguelen shelf whereas the latter are dependent upon krill of which abundance

and availability depends on sea ice extent and concentration (Weimerskirch, 2001; Xavier *et al.*, 2003).

Finally, from a methodological point of view, it might be interesting in the future to model the effects of climate and fisheries covariates on vital rates in a different framework, where unexplained variance is modelled as a random effect (Grosbois *et al.*, 2008).

Conclusion

Although a common impact of SOI on breeding success and of tuna fishery on adult survival of these four albatross species was clearly detected, results also highlighted contrasted responses possibly due to different life history traits, different foraging zones and different interactions with different types of fisheries. Contrasted demographic responses to environmental fluctuations have also been documented between closely related species in other marine ecosystems such as Pygoscelid penguins in the Antarctic (Forcada *et al.*, 2006) or guillemots in the Arctic (Irons *et al.*, 2008); and between different populations of the same species such as black-legged kittiwakes from the North Sea (Frederiksen *et al.*, 2005).

Despite an increasing concern about the consequences of climate warming on ecosystems, very few studies have been conducted on the potential effects of climate change on demographic parameters of albatross species. The lack of such studies possibly originates from the assumption that in longlived species, population growth rate is weakly sensitive to breeding success and adult survival is environmentally canalized. Thus, one may have rightly thought that albatross population declines were more likely caused by fisheries than climate change. However, climate variability/warming are likely to increase (IPCC, 2007) and this might have profound impact on albatross demography, particularly on breeding success and recruitment. Indeed, although albatross adult survival was canalized against climate variation, breeding success was sensitive to climate change. This should not be neglected because breeding success may significantly contribute to the population dynamics (Jenouvrier *et al.*, 2005a) and limit population recovery (Jenouvrier *et al.*, 2009). We also showed that above a certain level of fishing effort, mortality due to bycatch can no longer be compensated by a decrease in natural mortality. Therefore, it is important to determine the relative contribution to the demography of driving environmental factors, including climate, especially in the context of climate change. In addition, interactions between climate and fisheries could exacerbate the effects of fisheries and this need to be investigated.

Because our results suggest that population responses were dependent upon location, species, type

of fisheries, etc. more studies are needed on the effects of climatic and oceanographic conditions on demographic parameters on top predators species to predict the consequences of climate and fisheries scenarios on their populations according to their foraging habitats, behaviours and life history traits.

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Supporting Information

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

Figure S1. Annual variations of breeding success of the wandering albatross observed (solid line) at Possession Island, Crozet and the modelled breeding success (dashed line) with a linear trend.

Figure S2. Annual variations of the adult survival estimated (solid line) in the wandering albatross population of Possession Island, Crozet and modelled adult survival with tuna fishing effort in the sub-Antarctic foraging range of wandering albatrosses during breeding.

Figure S3. Annual variations of breeding success of the sooty albatross observed (solid line) at Possession Island, Crozet and the modelled breeding success (dashed line) with the summer Southern Oscillation Index and winter sea surface temperature anomalies.

Figure S4. Annual variations of the adult survival estimated (solid line) in the sooty albatross colony at Pointe Basse, Possession Island, Crozet and modelled adult survival with tuna fishing effort during the incubation period.

Table S1. Model selection for the breeding success of the wandering albatross. Dev is the deviance of the model and P_{ANODEV} the p-value of the analysis of deviance (test $F_{1,19}$). The best model is in italics. T and $T + T^2$ respectively indicate linear and quadratic trends.

Table S2. Selection of the reference model for the wandering albatross. Capture (p), transitions (ø) and survival (F) may be constant (.), time (t), state (s) or group (g) dependent and np is the number of parameters of the model. The best model is in italics.

Table S3. Model selection for capture (p) and adult survival (F) of the wandering albatross. Dev is the deviance of the model and np its number of parameters.

Table S4. Model selection for the breeding success of the sooty albatross. Dev is the deviance of the model and P_{ANODEV} the p-value of the analysis of deviance (test $F_{1,19}$). The best model is in italics. T indicates a trend.

Table S5. Selection of the reference model for the sooty albatross. Capture (p), transitions (ø) and survival (F) may be constant (.), time (t) or state (s) dependent and np is the number of parameters of the model. The best model is in italics.

Table S6. Model selection for capture (p) and adult survival (F) of the sooty albatross. Dev is the deviance of the model and np its number of parameters.

Appendix S1. Multistate model structure used for analysis of adult survival in biennial breeders.

Appendix S2. Summary of the variables used for the breeding success and the survival analyses of the wandering and the sooty albatrosses. SSTA are sea surface temperatures anomalies, SOI is the Southern Oscillation Index. For the wandering albatross, subtropical and sub-Antarctic zones are distinguished with indices T and A respectively.

Appendix S3. Principal Component Analyses on climate and fishery covariates.

Appendix S4. Wandering albatross, demographic parameters and environmental effects.

Appendix S5. Sooty albatross, demographic parameters and environmental effects

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