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Combined effects of fisheries and climate on a migratory long-lived marine predator

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Summary

1. The impact of climate on marine ecosystems is now well documented, but remains complex. Climate change may interact with human activities to effect population dynamics. In addition, in migratory species conditions are different between the breeding and wintering grounds, resulting in more complex dynamics. All these possible effects should be considered to predict the future of endangered species, but very few studies have investigated such combined interactions.

2. As a case study, we assessed the relative impact of fisheries and of oceanographic conditions in breeding and wintering sites on adult survival and breeding success of a population of the endangered black-browed albatross *Thalassarche melanophrys* in the Kerguelen Islands, Southern Indian Ocean. This study was based on long-term monitoring of individually marked individuals (1979–2005) and identification by tracking studies and band recoveries of the oceanic feeding zones used during breeding and non-breeding seasons.

3. Breeding success was variable until 1997 and then declined gradually, from 0.88 to 0.48 chicks per egg laid. It was favoured by positive sea-surface temperature anomalies (SSTA) and trawl fishery during the breeding period, whereas it was negatively affected by positive SSTA around Tasmania, where the species winters. Adult survival was 0.918 ± 0.004 on average and increased with SSTA during incubation, but decreased significantly with high tuna longlining effort in the wintering zone.

4. Our analyses show that demographic parameters were influenced by both climate and fisheries in both breeding and wintering grounds, but with different effect size. Black-browed albatross breeding success was more favoured by trawlers' offal and discards than by any of the seasonally/spatially oceanographic conditions, whereas their survival was equally affected by tuna longline fishery through incidental by-catch and spring SSTA.

5. *Synthesis and applications.* Our work underlines that a comprehensive knowledge of the life history of a species in all the habitats used is important to disentangle the respective roles of environmental conditions and human factors on population dynamics. Identification of these effects is required when proposing effective conservation measures, because the conservation of threatened species may depend on their wintering country's exclusive economic zones.

Key-words: adult survival, black-browed albatross, breeding success, fisheries, longlining, oceanographic conditions, trawling

Introduction

A central issue today in ecology is to predict the consequences of the warming trend on populations and ecosystems, and to understand how these are affected by climatic and oceanographic changes (Hughes 2000; McCarty 2001). Several long-term studies in both hemispheres have documented an impact on population dynamics of both local climate (temper-

ature, wind, ocean currents, etc.) and large-scale climatic phenomena (El Niño Southern Oscillation, North Atlantic Oscillation, etc.) through a change in food quality and/or availability (Croxall, Trathan & Murphy 2002; Stenseth *et al.* 2002). Of particular complexity are the migratory species, which can be affected by climate within their whole distribution range, while breeding, migrating or on non-breeding grounds. According to the tap hypothesis, the strongest climatic effects on population fluctuations are expected to occur during the breeding season through recruitment, whereas according to

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the tube hypothesis, they are expected to occur during the non-breeding season through survival (Saether, Sutherland & Engen 2004). However, these hypotheses are not mutually exclusive, and climate during both periods may affect population dynamics (Saether *et al.* 2006). In addition, studies of population changes in both seasons are complicated by potential lagged responses to climate in long-lived species (Thompson & Ollason 2001; Barbraud & Weimerskirch 2003).

In addition, human impacts such as contamination from pollutants, predation by or competition with alien species, habitat loss, or transmission of parasites and diseases may cause population changes through direct mortality or indirect effects (Wilcove *et al.* 1998; Baker *et al.* 2002). This is particularly true for migratory seabirds because they have a wide spatial distribution and use different habitats (Baker *et al.* 2002). Among human activities, industrial fisheries are known to have important impacts on marine top predators (Klaer & Polacheck 1997; Ormerod 2003). Effects may be negative, directly through incidental mortality (Tuck, Polacheck & Bulman 2003) or indirectly through reduction in food abundance (Frederiksen *et al.* 2004), or positive due to a secondary food source provided by offal and discards (Bunce *et al.* 2002).

So far, very few studies have explored simultaneously the effects of human activities and climate change on vital rates of migratory long-lived marine predators (Bunce *et al.* 2002; Nel *et al.* 2003; Frederiksen *et al.* 2004; Votier *et al.* 2005) due to analytical complexity and problems of interpreting climate effects, which can be confounded with anthropogenic effects (Wilson 1991), or because of a lack of knowledge of the species' distribution range and its associated threats. However, if one wants to predict the future of endangered species, there is a crucial need to study the relative role of climate change and human disturbance on populations during both the breeding and the non-breeding seasons. Based on data for a black-browed albatross, *Thalassarche melanophrys* (Temminck 1828), colony monitored from 1979 to 2005 in the Kerguelen Islands, Southern Indian Ocean, we studied environmental effects on a marine top predator that integrates the marine environment at long-time and large spatial scales. This migratory species is potentially very vulnerable to changes in oceanography and fisheries. We expect (i) a strong and direct negative impact of longliners on survival through incidental bycatch; and (ii) a positive indirect effect of warm environmental anomalies on breeding success and survival through changes in food availability (Weimerskirch, Capdeville & Duhamel 2000; Pinaud & Weimerskirch 2002). We aimed (i) to estimate demographic parameters in relation to both oceanographic change and different fisheries during the breeding season and in the non-breeding grounds (hereafter called wintering); and (ii) to assess the relative impact of climatic and fisheries factors on both survival and breeding success in an endangered albatross species.

BACKGROUND

Albatrosses are highly migratory and can forage hundreds to thousands kilometres away from their colonies to exploit

the same productive shelf zones as the fishing vessels (Weimerskirch 1998; Tuck *et al.* 2001). Seabirds such as albatrosses and petrels often follow longliners to feed on baits they attempt to remove from hooks during setting or hauling, and can be caught and drowned (Brothers 1991). As a consequence, albatrosses have become threatened by the development and intensification of longline fisheries (Weimerskirch, Brothers & Jouventin 1997; Gales 1998), and as albatrosses are long-lived birds with a low fecundity rate, these by-catches may cause a problem in generation renewal.

In the Southern Indian Ocean, among the main species targeted by longliners are the southern bluefin tuna *Thunnus maccoyii* (Castelnau 1872) and the Patagonian toothfish *Dissostichus eleginoides* (Smitt 1898), and by trawlers mackerel icefish *Champsocephalus gunnari* (Lönnerberg 1905) and also Patagonian toothfish (Tuck *et al.* 2003). Fishing effort has been concentrated south of 30°S since the 1980s in south-west Australia and around subantarctic islands. Black-browed albatross is one of the albatross species most frequently killed by longliners (Gales 1998; Cherel, Weimerskirch & Trouvé 2000b; Weimerskirch *et al.* 2000). This species was listed as near threatened in 1994 (Croxall & Gales 1998), became vulnerable in 2002, and finally endangered in 2003 because the global population, although the most widespread, is declining at a rate of ≈65% over three generations (BirdLife International 2005).

Materials and methods

SPECIES, STUDY SITE AND FIELD METHODS

The southern black-browed albatross colony (1200 pairs) of Cañon des Sourcils Noirs (49°41' S, 70°14' E), Kerguelen Islands has been monitored every year since the breeding season 1979–80 (hereafter noted as 1980). In the study subcolony, all birds are ringed with a stainless steel band, and every year two to three consecutive visits during early incubation (late October/early November) were made to identify individually both pair members of an average of 192 (±43) nests that were individually marked. Incubating birds were gently checked while on their nest to read the bands. Then the fate of each nest was recorded during the hatching and fledging periods to determine breeding performance. Black-browed albatrosses lay a single egg per year without clutch replacement. The breeding success is the percentage of eggs laid producing a fledging. Each year, new individuals found in the study colony and all chicks were banded.

The presence/absence of each individual in the colony was recorded every year from 1980–2005 and used for the survival analysis. The breeding success analysis was performed for the period 1986–2004, breeding success data for 1984 and 1985 being recorded for fewer than 20 nests.

ENVIRONMENTAL AND FISHING DATA DURING THE BREEDING SEASON

Black-browed albatrosses are annual breeders that return every year to Kerguelen for breeding (September–April). Potentially they can be affected by the large-scale Southern Oscillation Index (SOI), either directly like other seabirds (Stenseth *et al.* 2002; Jenouvrier *et al.* 2005) during the breeding season, or after a lag as for blue petrels, *Halobaena caerulea* (Gmelin 1789) (Barbraud & Weimerskirch 2003).

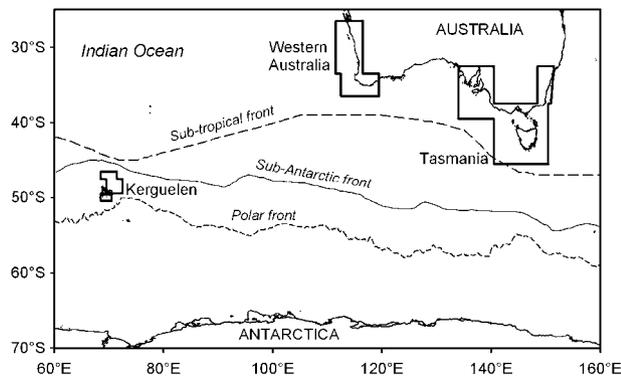


Fig. 1. Distribution area of black-browed albatrosses from the Kerguelen colony of Cañon des Sourcils Noirs, in both their breeding and wintering grounds, derived from satellite tracking and band recoveries, respectively.

As sea-surface temperature anomalies (SSTA) generated in the south Pacific Ocean take 3–4 years to reach the Kerguelen Islands by following the eastward hemispheric course of the Antarctic Circumpolar Current (Guinet *et al.* 1998; Barbraud & Weimerskirch 2003), we investigated the effects of the SOI of the current year and the SOI with a lag of 3 and 4 years (SOI_{lag3} and SOI_{lag4}) as covariates. The SOI was obtained monthly from the Australian Bureau of Meteorology, National Climate Centre, Climate Analysis Section (<http://www.bom.gov.au/climate/current/soihtm1.shtml>). Satellite tracking (Weimerskirch, Mougey & Hindermeier 1997; Pinaud & Weimerskirch 2002) and at-sea observations indicated that, during the breeding period, black-browed albatrosses of the studied colony forage over the Kerguelen Shelf edge (Fig. 1). We extracted, for this zone, monthly SSTA data on a 1° scale from the website of the Integrated Global Ocean Services System (<http://ingrid.ldeo.columbia.edu/>; Reynolds *et al.* 2002). The breeding season was divided into two biologically relevant periods: incubation (September–December) and chick rearing (January–April). Given that most breeding failures occur during incubation, breeding success is often highly correlated to hatching success. Reproductive success of black-browed albatrosses was previously found to be influenced mainly by SSTA during the incubation period (Pinaud & Weimerskirch 2002). Subsequently, the SOI of the current year and SSTA were averaged separately for incubation and rearing months. Finally, the black-browed albatross foraging area overlapped with the area frequented by fishing vessels (Cherel *et al.* 2000b). Trawling may benefit seabirds, at least in the short term, by providing a secondary food source, but longlining may affect them negatively through incidental by-catch (Weimerskirch *et al.* 2000). Thus, we tested for effects of (i) long-liners (LL_{breed}) targeting the Patagonian toothfish since the early 1990s; and (ii) trawlers (Tr_{breed}) also fishing for Patagonian toothfish, plus mackerel icefish and rockcod species (*Notothenia* sp.) between 1981 and 2001 around Kerguelen. Regarding toothfish longline fishery, an illegal unreported and unregulated (IUU) fishing effort started since 1996–97 within the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) statistical area 58-5-1 (around Kerguelen). An estimation of IUU fishing effort was calculated as (SC-CAMLR-XX 2001):

$$\text{effort (IUU)} = \text{catch (IUU)}/\text{CPUE (legal)}$$

where CPUE = catch per unit effort. We then pooled annual legal and estimated IUU efforts. Data were obtained from different

sources (Appendix S1, see Supplementary material) for trawling effort (in hours of trawling) and for longlining effort (in number of hooks set).

ENVIRONMENTAL AND FISHERIES DATA IN WINTERING GROUNDS

According to band recoveries (Weimerskirch *et al.* 1985), studies on feeding ecology (Cherel *et al.* 2000a) and tracking data (H.W., unpublished data), black-browed albatrosses migrate rapidly in autumn from Kerguelen to southern Australia, where they winter (May–August) (Fig. 1). They may also be exposed to the effects of the El Niño Southern Oscillation during this period. Thus we also used the SOI during this wintering phase as a covariate. SSTA during winter may determine food availability and thus influence breeding success through effects on body condition before and during breeding (Chastel, Weimerskirch & Jouventin 1995; Guinet *et al.* 1998). We distinguished two wintering areas used by Kerguelen black-browed albatrosses: the south-east ($SSTA_{winter1}$) and the western ($SSTA_{winter2}$) Australia areas (Fig. 1). On the wintering grounds, black-browed albatrosses attend longliners fishing for southern bluefin tuna and other tuna species (Gales, Brothers & Reid 1998). Longlining effort (number of hooks set) in winter (LL_{winter}) was exerted by different nations (Appendix S1, see Supplementary material).

To compare the magnitude of different covariates on demographic parameters, from the slope estimates, all the environmental variables were standardized for analyses (Abdi 2007) and are summarized in Table 1.

ADULT SURVIVAL ANALYSIS

The survival analysis was conducted on the capture histories of adults that had bred at least once in the study colony. For each individual, the first encounter was suppressed to limit inter-individual heterogeneity. Consequently, the data set included 1035 individuals for the period 1981–2005.

Adult survival probabilities were estimated with capture–mark–recapture models using M-SURGE ver. 1.7 (Choquet *et al.* 2005a), starting with the Cormack–Jolly Seber (CJS) model where survival, Φ and capture, p were time-dependent (t) and related model structures (Lebreton *et al.* 1992). The fit of our models to the data was investigated with a goodness-of-fit test using the program U-CARE ver. 2.2 (Choquet *et al.* 2005b). The CJS model did not fit the data ($\chi^2_{110} = 421.53$, $P < 0.001$). The lack of fit was mostly explained by test 2.CT ($\chi^2_{22} = 259.61$, $z = -12.7$, $P < 0.001$) indicating a trap-happiness (recapture probability is positively dependent on the first occasion of capture). Then a model with ‘two age classes’ for resighting probabilities (Φ_t, p_{mst}) accounted for trap dependence (Pradel 1993). However, as the goodness-of-fit test was still significant ($\chi^2_{88} = 161.92$, $P < 0.001$), this model with trap dependence (Φ_t, p_{mst}) was corrected with a variance inflation factor c , calculated as the χ^2 statistic over its number of degrees of freedom (Lebreton *et al.* 1992). As \hat{c} (1.84) was < 3 , the model (Φ_t, p_{mst}) was considered adequate to use as a departure model in the analysis (Lebreton *et al.* 1992).

Model selection was performed using the Akaike information criterion corrected for sample size (AICc) (Burnham & Anderson 1998). The variance inflation factor (\hat{c}) was taken into account by correcting AICc for extra-binomial variation. When comparing two models, if $\Delta\text{QAICc} > 2$, the preferred model is the one with the lowest QAICc.

To assess the effects of environmental covariates, we carried out an analysis of deviance (ANODEV) which 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:

Table 1. Climatic and fisheries covariates used in the analyses of adult survival and breeding success of black-browed albatrosses at Kerguelen

Covariate*	Season	Months	Spatial area
SOI _{inc}	Incubation	Sep–Dec	Southern Ocean
SOI _{rear}	Rearing	Jan–Apr	
SOI _{winter}	Wintering	Apr–Sep	
SSTA _{inc}	Incubation	Sep–Dec	Kerguelen (Fig. 1)
SSTA _{rear}	Rearing	Jan–Apr	Kerguelen (Fig. 1)
SSTA _{winter1}	Wintering	Apr–Sep	Tasmania/South Australia (Fig. 1)
SSTA _{winter2}	Wintering	Apr–Sep	West Australia (Fig. 1)
Tr _{breed}	Breeding	Sep–Apr	Kerguelen (CCAMLR 58-5-1)
LL _{breed}	Breeding	Sep–Apr	Kerguelen (CCAMLR 58-5-1)
LL _{winter}	Wintering	Apr–Sep	Southern Indian Ocean (25–55°S, 80–150°E)

Season corresponds to the phenology of black-browed 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 (Weimerskirch *et al.* 1997a; Pinaud & Weimerskirch 2002) and band recoveries in winter (Weimerskirch *et al.* 1985).

*SOI, Southern Oscillation Index; SSTA, Sea Surface Temperature Anomaly; Tr, Trawling; LL, Longlining; CCAMLR, Commission for the Conservation of Antarctic Marine Living Resources.

$$\frac{[\text{DEV}(M_{\cdot}) - \text{DEV}(M_{\text{cov}})] / (n_{\text{cov}})}{[\text{DEV}(M_{\text{cov}}) - \text{DEV}(M_{\cdot})] / (n - n_{\text{cov}} - 1)}$$

where DEV was the deviance of the models with constant (M_{\cdot}), 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 an F -test statistic with n_{cov} and $(n - n_{\text{cov}} - 1)$ df. The proportion of variation explained by covariates (analogous to R^2 in regression) was calculated as (Schemper 1990):

$$R^2 \approx \frac{\text{DEV}(M_{\text{cov}}) - \text{DEV}(M_{\cdot})}{\text{DEV}(M_t) - \text{DEV}(M_{\cdot})}$$

Finally, we checked the significance of the slope of each covariate by examining if zero was not included in the slope's 95% confidence interval.

Adult survival rates were modelled as a function of all the covariates we cited above. However, the three types of fishing effort (LL_{winter}, LL_{breed}, Tr_{breed}) (Fig. 2) were correlated ($|r| = 0.4$, $P = 0.03$), and to avoid possible multicollinearity effects we analysed independently each of these covariates on survival. All estimates are given ± 1 SE.

BREEDING SUCCESS ANALYSIS

Breeding success was studied from 1986 to 2004 in the subcolony for an annual mean of 192 (114–265) nests. Only nests with an egg were included in this analysis. As black-browed albatrosses lay a single egg per breeding attempt, breeding success per nest was defined as a binomial variable where 1 indicated that the egg produced a fledgling and 0 a failure at either egg or chick stage.

To test for environmental effects on breeding success, we used generalized linear models for logistic regression with the glm function of software R (Crawley 2002; R Development Core Team 2005). Model selection was based on AICc.

To assess the fit of the selected model, we checked for the significance of each covariate slope and calculated a Pearson correlation coefficient between the annual predicted and observed breeding

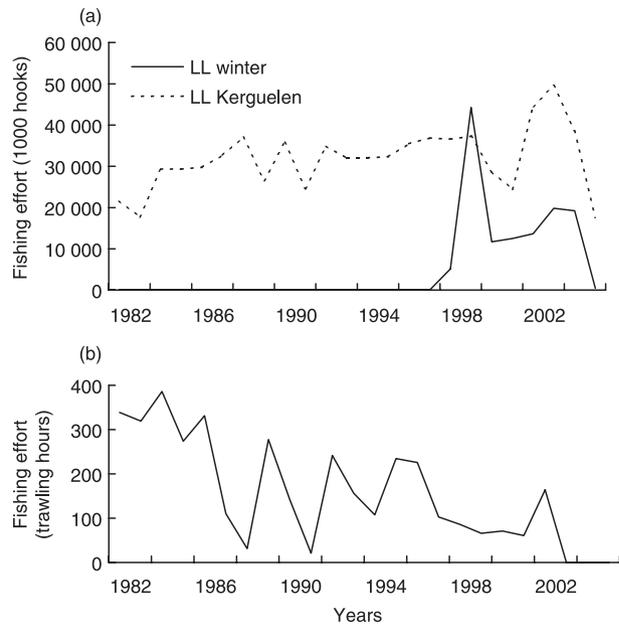


Fig. 2. Annual fishing effort of fisheries from (a) longlining efforts exerted in both Kerguelen and Australasian waters; (b) the trawling effort around Kerguelen.

success for a measure of R^2 . Breeding success was modelled as a function of the defined SOI and SSTA (Appendix S1, see Supplementary material). As longline fishing is known to have a direct impact on albatrosses survival only through incidental by-catch (Brothers 1991), we kept only fisheries that took place during breeding (trawl and longline fishing effort) in the Kerguelen Exclusive Economic Zone, but two fishing variables were insufficient to use a principal components analysis (PCA). We found three significant correlations between the different SOI and SSTA covariates ($|r| = 0.6$, $P < 0.03$), but as the results of the PCA on these climatic parameters did not explain sufficient variation, we started with the full model including all of them. We checked for the significance of each of estimated parameter before performing model selection.

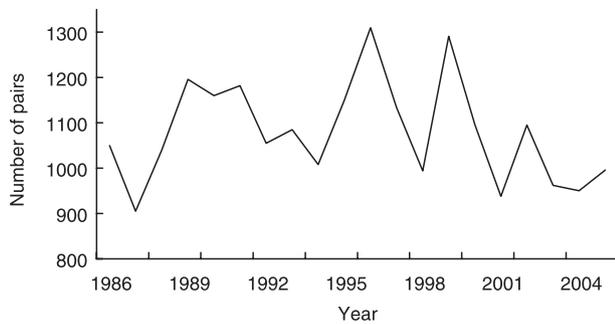


Fig. 3. Annual variation in the number of breeding pairs of black-browed albatrosses at Kerguelen (Cañon des Sourcils Noirs) between 1986 and 2005.

Results

COLONY SIZE

Variability in breeding colony size increased after 1995 ($CV_{87-95} = 8.14\%$, $CV_{96-05} = 12.14\%$), showing peaks and strong decreases approximately every 3 years (Fig. 3). A quadratic trend suggested an inflection point in 1995 ($R^2 = 0.31$, $P = 0.052$), although a linear regression showed that the size of the breeding colony was constant overall throughout the period 1987–2005 ($r = -0.149$, $P = 0.542$, $n = 19$) and the number of pairs was $1080.6 (\pm 26.7)$ on average.

Model	Equation	N_p	QAICc	QDEV
1 Fully time-dependent	$\Phi t, pt \times m$	69	5453.5	9762.12
2 Additive trap effect on p	$\Phi t, pt + m$	48	5451.8	9845.91
3 Constant trap effect on p	$\Phi t, pm$	26	5490.5	10004.33
4 Constant survival and additive trap effect on p	$\Phi, pt + m$	26	5426.1	9885.75

Table 3. Modelling capture probabilities as a function of climatic covariates (selected model in bold type)

No.	Model	np	QDEV	P_{ANODEV}	R^2	Slope (\pm SE)
4	$t + m$	26	9885.75			
5	m	3	10067.77			
6	T	4	10054.12	0.176		NS
7	T	5	10004.96	0.008	0.345	+1.918 (0.244) −0.639 (0.089)
8	$T + T^2 + SOI_{inc}$	6	10004.77	0.023		NS
9	$T + T^2 + SOI_{rear}$	6	10004.74	0.023		NS
10	$T + T^2 + SOI_{winter}$	6	10004.19	0.022		NS
11	$T + T^2 + SOI_{lag3}$	6	10001.49	0.016		NS
12	$T + T^2 + SOI_{lag4}$	6	10003.71	0.021		NS
13	T	6	9981.72	0.002	0.473	+1.705 (0.249) −0.604 (0.089) +0.162 (0.034)
	+T^2					
	+$SSTA_{inc}$					
14	$T + T^2 + SSTA_{rear}$	6	10002.57	0.019		NS
15	$T + T^2 + SSTA_{winter}^1$	6	10003.48	0.020		NS
16	$T + T^2 + SSTA_{winter}^2$	6	9999.51	0.014		NS

Survival was taken constant. np, Number of estimated parameters. T and $T + T^2$ represent linear and quadratic trends, respectively.

ADULT SURVIVAL

Model selection from the time-dependent model (Φ_t, p_{m+t}) is presented in Table 2. An additive trap effect was selected on capture probabilities (model 2 vs. models 1 and 3), and a model with constant survival was preferred over a time-dependent survival (model 4 vs. model 2). Survival probability from model (Φ, p_{m+t}) was estimated as $0.917 (\pm 0.005)$. Capture probability was higher for the first age-class, 'trap-happy' individuals (≈ 0.8) than for the second age-class (≈ 0.6).

We then assessed for effect of covariates on capture probability (Table 3). We detected a significant quadratic trend in capture probability (model 7), but model fit improved when SSTA during incubation was included (model 13, $ANODEV = 6.575$, $P_{ANODEV} = 0.002$). SSTA, when accounted for the quadratic trend, explained 47.3% of between-year variation in capture probability. Capture probability increased with increasing SSTA during incubation. The other covariates did not show any significant effect on capture probability.

Starting from the model ($\Phi, p_{m+T+T^2+SSTA_{inc}}$), we first searched for climate effects on adult survival and then tested for potential additive effects of fisheries (Table 4). An effect of SSTA during incubation on survival was detected (model 25, $ANODEV = 5.196$, $P_{ANODEV} = 0.031$) but explained only 16% of the variation. A model with additive effects of $SSTA_{inc}$ and LL_{winter} (model 30) was the best to explain year-to-year variations in survival ($P_{ANODEV} < 0.0001$; $R^2 = 35.4\%$). It indicated that $SSTA_{inc}$ had a significant positive effect on survival

Table 2. Modelling capture and survival probabilities for black-browed albatrosses between 1982 and 2005 at Kerguelen (selected model in bold type)

Table 4. Modelling survival probabilities as a function of climatic and fisheries covariates

No.	Model	<i>np</i>	QDEV	<i>P</i> ANODEV	<i>R</i> ²	Slope (±SE)
13		6	9981.72			
17	<i>t</i>	29	9935.37			
18	<i>T</i>	7	9980.85	0.478		
19	<i>T + T</i> ²	8	9979.41	0.374		
One covariate						
20	SOI _{inc}	7	9981.65	0.841		NS
21	SOI _{rear}	7	9980.20	0.347		NS
22	SOI _{winter}	7	9979.71	0.278		NS
23	SOI _{lag3}	7	9981.54	0.748		NS
24	SOI _{lag4}	7	9981.15	0.567		NS
25	SSTA _{inc}	7	9974.24	0.031	0.161	+0.156 (0.058)
26	SSTA _{rear}	7	9981.17	0.574		NS
27	SSTA _{winter1}	7	9980.55	0.411		NS
28	SSTA _{winter2}	7	9981.70	0.914		NS
Two covariates						
30	SSTA _{inc}	8	9965.29	<0.0001	0.354	+0.252 (0.064)
31	LL _{winter}	8	9973.00	0.007		-0.222 (0.071)
32	LL _{breed}	8	9971.60	0.003		NS

Capture was modelled with a trap effect additive to a quadratic trend and SSTA_{inc} effects. NS, non-significant slope. *T* and *T + T*² represent linear and quadratic trends, respectively.

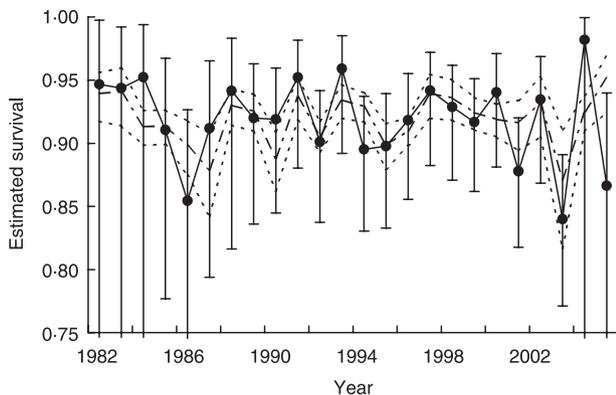


Fig. 4. Annual variations of adult survival probabilities estimated from the time-dependent model (Φ_t , $p_{m+T+T^2+SSTA_{inc}}$) (●, solid line with error bars) and from the selected model ($\Phi_{LL_{winter}+SSTA_{inc}}$, $p_{m+T+T^2+SSTA_{inc}}$) (dashed lines with CI). Error bars, SE.

(+0.252 ± 0.064) whereas LL_{winter} had a significant negative impact (-0.222 ± 0.071), which means that birds survived better when SST_{inc} were warmer around breeding grounds and longline fishing effort in Australasian waters were reduced. Estimates from this model overlapped those from the time-dependent model (Φ_t , $p_{m+T+T^2+SSTA_{inc}}$) except when estimates were at the boundaries (close to 0 or 1) (Fig. 4). To assess the relative importance of each covariate, we used the general procedure for the comparison of several normally distributed parameter estimates that incorporates their associated variance with the software CONTRAST (Hines & Sauer 1989). The effect size of longlining was non-significantly dif-

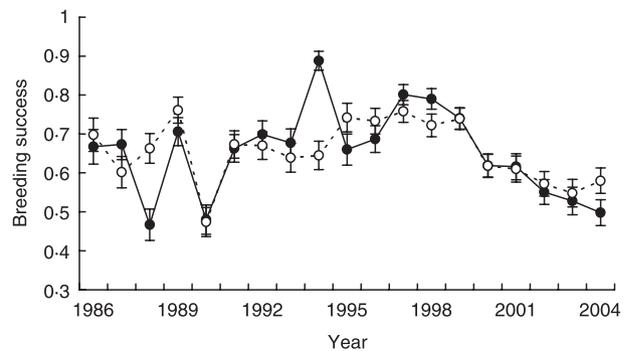


Fig. 5. Annual variations of observed breeding success (●) and breeding success estimated from the best model (○) of black-browed albatrosses at Kerguelen. Error bars, SE.

ferent from that of SSTA_{inc} ($\chi^2 = 0.10$, $P = 0.754$). According to their non-significant slopes (models 31 and 32), the trawling and longlining fishing effort during the breeding season were weak, whereas there was a strong effect of the tuna fishery (LL_{winter}).

BREEDING SUCCESS

Annual breeding success during 1986–94 varied from 47.5 to 88.3% (mean of 65.9 ± 10.3%) and then decreased continuously since 1997 (Fig. 5). We analysed the effect of SOI with different lags on breeding success and then compared AICc values. The SOI with a lag of 3 years (lowest AICc) had the strongest potential impact (Appendix S2, see Supplementary material), so we only included this variable in the complete

Model	AICc	Δ AICc
$Tr_{\text{breed}} + SSTA_{\text{winter}1} + SSTA_{\text{inc}} + SSTA_{\text{rear}} + SOI_{\text{winter}}$	4622.2	0
$Tr_{\text{breed}} + SSTA_{\text{winter}1} + SSTA_{\text{inc}} + SSTA_{\text{rear}}$	4625.1	2.9
$Tr_{\text{breed}} + SSTA_{\text{winter}1} + SSTA_{\text{inc}} + SOI_{\text{winter}}$	4631.9	9.7
$Tr_{\text{breed}} + SSTA_{\text{winter}1} + SSTA_{\text{inc}} + SOI_{\text{winter}}$	4632.1	9.9
$Tr_{\text{breed}} + SSTA_{\text{inc}} + SSTA_{\text{rear}} + SOI_{\text{winter}}$	4661.4	39.2
$SSTA_{\text{winter}1} + SSTA_{\text{inc}} + SSTA_{\text{rear}} + SOI_{\text{winter}}$	4677.4	55.2

Table 5. Modelling breeding success as a function of climatic and fisheries covariates

Table 6. Maximum likelihood of intercept and slope estimates from the full model for the effect of covariates on breeding success

Parameter	Estimate	SE	P
Intercept	0.807	0.042	<0.001
Tr_{breed}	0.390	0.053	<0.001
$SSTA_{\text{winter}1}$	-0.228	0.036	<0.001
$SSTA_{\text{inc}}$	0.119	0.035	<0.001
$SSTA_{\text{rear}}$	0.133	0.039	<0.001
SOI_{winter}	0.090	0.041	<0.05

model. The model including all the covariates showed that covariates LL_{breed} , SOI_{inc} , SOI_{rear} , $SOI_{\text{lag}3}$ and $SSTA_{\text{winter}2}$ did not contribute significantly to explain variation in breeding success ($P > 0.1$). We thus used a model with the remaining covariates SOI_{winter} , $SSTA_{\text{inc}}$, $SSTA_{\text{rear}}$, $SSTA_{\text{winter}1}$ and Tr_{breed} as a starting point for model selection (Table 5). In this latter model, the three correlations between covariates from the complete model were all removed. The model with lowest AICc was found for the initial model in which trawl fishery had a significant positive effect on breeding success as well as SSTA in the Kerguelen sector, whereas SSTA during wintering before the breeding season had a significant negative impact (Table 6). Modelled breeding success fitted the data well ($r_{\text{Pearson}} = 0.651$, $P = 0.003$; Fig. 5). Using the software CONTRAST, we found that the effect of trawling was significantly higher than the effect of SSTA during wintering ($\chi^2 = 6.39$, $P = 0.012$), the latter also being significantly higher than SSTA during breeding ($\chi^2 = 4.71$, $P = 0.03$). However, the effects of SSTA during incubation and rearing were similar ($\chi^2 = 0.07$, $P = 0.789$), and SOI_{winter} did not differ significantly ($\chi^2 = 0.29$, $P = 0.591$) from any of the SSTA during breeding.

Discussion

Our results are the first to demonstrate that demographic parameters of a population of a migratory long-lived predator may be affected by a combined effect of climatic conditions and fisheries on both breeding and wintering grounds.

Climate impacts were associated with both annual survival and breeding success of the black-browed albatross. Warm SST around Kerguelen during the incubation period favoured adult survival of breeding birds, contrary to what was found in several other seabirds (Jenouvrier, Barbraud & Weimerskirch 2003; Sandvik *et al.* 2005). Breeding success also increased with SSTA around Kerguelen during both periods of the

breeding season (for the opposite case see Guinet *et al.* 1998) and with winter SOI, but decreased with SSTA in Tasmania during the wintering period. In addition, the probability of capturing breeding birds at the colony increased with SSTA around Kerguelen. The mechanisms behind all these environmental factors influencing demographic traits are not clear, but may be as follows. Oceanographic conditions such as SSTA seem to be related to water mass dynamic (Park *et al.* 1998) and the position of frontal zones (Kostianoy *et al.* 2004). Therefore it affects the abundance and distribution of plankton, fish and squid (Hunt *et al.* 1981), and consequently their availability to predators (Montevecchi & Myers 1996; Pinaud, Chérel & Weimerskirch 2005). Warm SST during the breeding period (mostly during incubation) was associated with favourable breeding by black-browed albatross. This corroborates Pinaud & Weimerskirch (2002), who showed that warm spring SST allowed a better foraging success and subsequently improved body condition of birds, which resulted in higher incubation and rearing success. In addition, we can expect that when their body condition is not altered, their survival is increased. The positive effect of warm SST around Kerguelen is balanced by the negative effect of warm SST around Tasmania. These opposite responses to SSTA are likely to be system-specific. Black-browed albatrosses feed in different water masses and at different trophic levels in summer when foraging south of the Subantarctic Front at Kerguelen and in winter north of Subtropical Front in southern Australia (Chérel *et al.* 2000a). Finally, it seems that foraging conditions associated with warm SST events enhanced breeding success of seabird species foraging north of the Polar Front, contrary to species feeding south of the Polar Front (Inchausti *et al.* 2003). This phenomenon might also be reversed north of the Subtropical Front. Indeed, foraging and rearing success of the Indian yellow-nosed albatross *Thalassarche carteri* (Rothschild 1903), exploiting the subtropical waters, were reported to be higher in years of colder oceanic conditions (Weimerskirch, Zimmermann & Prince 2001; Pinaud *et al.* 2005).

The quadratic trend found in capture probability probably reflected the increasing (and then stabilizing) effort exerted by fieldworkers in capturing individuals. Interestingly, capture probability was also found to fluctuate significantly with SSTA during incubation. As the incubation season was defined as starting in September (a little before laying, which starts in mid-October), this result suggests that SSTA probably played a role in the decision to breed. It seems that when SSTA increased at Kerguelen, black-browed albatrosses were more likely to be detected at the colony, indicating that they were more likely to breed.

We highlighted the important impact of different types of fisheries in different seasons on both survival and breeding success. First, adult survival did not fluctuate in relation to trawling effort. Conversely, when the trawl fishery was active, breeding success was higher. Black-browed albatross breeding success was already reported to fluctuate with CPUE of trawl fishery during the 1980s (Weimerskirch & Jouventin 1998). Moreover, this result is consistent with the at-sea observations of black-browed albatrosses attending trawlers (Weimerskirch *et al.* 2000), scavenging on offal and discards discharged by trawlers (Thompson 1992), and the significant amount of offal remains found in the stomachs of black-browed albatross chicks (Cherel *et al.* 2000b). Our results also confirm what was previously proposed for other colonies of black-browed albatross (Woehler, Auman & Riddle 2002) and other seabird species (Tuck *et al.* 2001): that trawling had a positive indirect effect on demographic traits through offal and discards as an additional food source. Second, contrary to the trawling effect, adult survival was depressed when the longline tuna fishing effort around Tasmania was high. This is in agreement with the large effort exerted by the Japanese and Taiwanese fleets (on average 20 million and 8 million hooks set, respectively, between 1981 and 2004). Japanese longline fishing in the Southern Indian Ocean has already been shown to have a negative effect on albatross survival (Weimerskirch *et al.* 1997a; Nel *et al.* 2003). Indeed, longline fishing constitutes a direct negative impact on survival through incidental by-catch. On the other hand, longline fishery in the Kerguelen Exclusive Economic Zone did not appear to affect either adult survival or breeding success of black-browed albatrosses. This result is consistent with satellite-tracking data showing that black-browed albatross foraging areas overlapped little with toothfish longline fishing grounds (Cherel *et al.* 2000b). In addition, as longline fishing effort in the Kerguelen Exclusive Economic Zone started to be high only in the mid-1990s, its effect may have been unnoticed compared with that of the sustained longlining around Australia since the beginning of this study. In addition, even though black-browed albatrosses are observed to be killed by longliners around Kerguelen, the number of individuals caught incidentally remained low relative to population size (Delord *et al.* 2005). Thus this mortality on the Kerguelen shelf probably did not represent an additive mortality, but might possibly be included in the compensatory mortality of the population.

Spatio-temporal interactions of oceanographic conditions and fisheries affected survival and breeding success of black-browed albatrosses. Overall, the annual survival rate was estimated between 91.6 and 91.8%, which is similar to the Bird Island colony, South Georgia (Croxall *et al.* 1998), and relatively low compared with other albatross species (Weimerskirch & Jouventin 1998; Nel *et al.* 2003). It appeared from the best model that adult survival was affected by a combination of SSTA during incubation and fisheries. However, this model accounted for more than a quarter of the variation in survival. Breeding success was best explained by additive effects of trawl fishery, SSTA and winter SOI. The 1986–94 period of variable breeding success coincided with important varia-

tions in both trawl fishery and SSTA during breeding, and the continuous decline since 1997 corresponded to (i) the progressive reduction (down to suspension in 2001) in trawling effort around Kerguelen; (ii) the decrease of SSTA during breeding at Kerguelen (from 1986 to 2002); and (iii) the increase of SSTA in Tasmania during the black-browed albatross wintering period. With regard to the winter SOI effect, the slope was weak compared with the other covariates, and winter SOI was correlated with SSTA during rearing ($r = -0.444$, $P = 0.052$). Thus the effect of winter SOI may be linked to that of SSTA.

We underlined the importance of standardizing environmental variables that allowed us to compare the relative magnitude of the different effects on demographic parameters. Interestingly, the effect of trawling effort on breeding success was more important than oceanographic conditions, whereas the effect size of longlining and SSTA on survival were similar. However, the effect size of longlining on survival is probably a minimum estimate, as figures available for longline fishing effort are often underestimated (Tuck *et al.* 2003). So far, mitigation measures used in the CCAMLR zone, such as night setting and weighting lines, must be maintained as they have been proven efficient in reducing mortality (Cherel, Weimerskirch & Duhamel 1996; Weimerskirch *et al.* 2000; Reid & Sullivan 2004). The impact of trawling on breeding success was significantly higher relative to other environmental variables (about two- and fourfold relative to SSTA during wintering and breeding, respectively, in absolute values). However, the positive effect of trawling must be viewed with caution: it certainly represented a short-term benefit by an easily foraged food source for black-browed albatross reproduction, but its long-term impacts on the trophic web through the drastic depletion in *C. gummari* stock is unknown (Duhamel & Agnew 1990).

Although further population modelling will be carried out to predict the future of this population, accounting for the effects of fisheries and climate on demographic parameters, our study already shows for the first time a clear effect of combined fisheries and climate. The black-browed albatross population from Cañon des Sourcils Noirs, Kerguelen, has remained quite stable since the 1980s. However, the gradual decline in breeding success since 1997 is alarming for the future recruitment rate and population size. Climate has already been reported to act on breeding, as well as on wintering grounds of migratory species (Saether *et al.* 2006), validating both the tap and tube hypotheses. However, in our case, effects of environmental conditions on the wintering grounds appeared to be stronger on the breeding success. Thus a change in climate around Kerguelen and/or Australia would affect the population. Similarly, even though fisheries during both seasons influenced the demography of black-browed albatross, longlining in the wintering foraging area appeared to have had a greater impact on the population. In long-lived species such as the black-browed albatross, adult survival should be the least variable parameter according to the canalization theory (Gaillard & Yoccoz 2003). Thus a significant negative effect of longlining on adult survival may decrease the population growth rate dramatically. In this respect, conservation of this species depends on jurisdiction in countries

other than the expected Kerguelen breeding site. These results underline the complexity of interactions between climate and human activities, which must be taken into account in future population trajectories or viability analyses.

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Supplementary material

The following supplementary material is available for this article.

Appendix S1. Trawl and longline fisheries: source of data, nationality and period used.

Appendix S2. Results, in terms of AICc, of breeding success explained by the Southern Oscillation Index with time lag of 0–6 years.

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Cover image: Restoring wet grasslands by reinstating managed wet features can attract breeding lapwing *Vanellus vanellus*, and be compatible with commercial grazing marsh management (see p. 315). Photo by Kevin Simmonds.