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Quantifying the impact of longline fisheries on adult survival in the black-footed albatross

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Summary

1. Industrial longline fishing has been suspected to impact upon black-footed albatross populations *Phoebastria nigripes* by increasing mortality, but no precise estimates of bycatch mortality are available to ascertain this statement. We present a general framework for quantifying the relationship between albatross population and longline fishing in absence of reliable estimates of bycatch rate.

2. We analysed capture–recapture data of a population of black-footed albatross to obtain estimates of survival probability for this population using several alternative models to adequately take into account heterogeneity in the recapture process. Instead of trying to estimate the number of birds killed by using various extrapolations and unchecked assumptions, we investigate the potential relationship between annual adult survival and several measures of fishing effort. Although we considered a large number of covariates, we used principal component analysis to generate a few uncorrelated synthetic variables from the set and thus we maintained both power and robustness.

3. The average survival for 1997–2002 was 92%, a low value compared to estimates available for other albatross species. We found that one of the synthetic variables used to summarize industrial longline fishing significantly explained more than 40% of the variation in adult survival over 11 years, suggesting an impact by longline fishing on albatross' survival.

4. Our analysis provides some evidence of non-linear variation in survival with fishing effort. This could indicate that below a certain level of fishing effort, deaths due to incidental catch can be partially or totally compensated for by a decrease in natural mortality. Another possible explanation is the existence of a strong interspecific competition for accessing the baits, reducing the risk of being accidentally hooked.

5. *Synthesis and applications.* The suspicion of a significant impact of longline fishing on the black-footed albatross population was supported by the combination of a low estimate of adult survival for the study period, and a significant relationship between adult survival and a synthetic measure of fishing effort. This study highlights the sensitivity of the black-footed albatross to commercial longline fishing, and should exhort fishery management authorities to find adequate seabirds avoidance methods and to encourage their employment.

Key-words: albatross, bycatch, capture heterogeneity, capture–recapture, compensation, covariates, exploited population, survival

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Introduction

The impact of human activities on biodiversity is increasing (Soulé 1987) through both direct (e.g. hunting) and indirect (e.g. habitat depletion) detrimental effects. Often, even unexploited species suffer an increase in mortality due to human activities (Lebreton 2005). For example, ocean fishing vessels induce an indirect effect of fishing on sea turtles (Lewison, Freeman & Crowder 2004; Kaplan 2005) and seabirds (Brothers, Cooper & Lokkeborg 1999) through incidental bycatch. These large marine vertebrates have a long life span and a delayed reproduction, and as a consequence a low maximum growth rate (Niel & Lebreton 2005). Thus, their populations are highly sensitive to any decrease in adult survival (De Kroon, Groenendael & Ehrlen 2000; Saether & Bakke 2000) and even indirect exploitation can be unsustainable leading to a high extinction risk.

Several albatross species in particular, such as the wandering albatross *Diomedea exulans* (Linnaeus 1758) and the Amsterdam albatross *D. amsterdamensis* (Roux *et al.* 1983), have been subjected to significant incidental bycatch by fishery activities, notably longline fishing (Weimerskirch, Brothers & Jouventin 1997; Cherel, Weimerskirch & Duhamel 1996; Brothers, Cooper & Lokkeborg 1999). Birds are often hooked when trying to catch bait accessible on the surface when the line is set (Brothers, Cooper & Lokkeborg 1999). Nevertheless, the population-level effects of bycatch, and in turn the conservation status of these populations, are difficult to quantify. A decline in abundance may suggest a threat to the species in question. A direct estimate of the proportion of animals killed by such a mortality source is difficult to obtain because the number of animals killed and the total population size are themselves difficult to estimate reliably (Cousins & Cooper 2000; Lewison & Crowder 2003; Lewison *et al.* 2004).

As an alternative to the estimation of the number of individuals caught by longliners, or more generally subject to an anthropogenic source of mortality, one can estimate the mortality rate (or its complement, survival) using individual demographic data. Based on existing theory for the dynamics of exploited populations (Burnham & Anderson 1979; Lebreton 2005), one can represent survival as a baseline survival probability modified by the effect of human-induced mortality, and thus assess the magnitude of anthropogenic effects. This method does not require any assumption or prediction about the mortality rate imposed by human activities.

Black-footed albatross conservation is particularly sensitive to the uncertainty of the bycatch impact on the sustainability of its population. The foraging zone of black-footed albatross can be defined as encompassing the North Pacific Ocean, between Alaska, Japan and the North American coast down to California (Cousins & Cooper 2000; Cousins, Dalzell & Gilman 2000; Hyrenbach & Dotson 2003; Brooke 2004), as indicated by sighting records, fishery observer programmes, and the recent development of telemetry. The breeding population is located predominantly in the North-western Hawaiian Islands with small breeding colonies on Japanese islands (Brooke 2004; Robertson & Gales 1998; Cousins & Cooper 2000). The population size was estimated to be about 300 000 birds, from an estimate of approximately 60 000 breeding pairs (Robertson & Gales 1998; Niel & Lebreton 2005). Recently, concerns were raised about black-footed albatross populations, as many birds have been killed by longline fisheries (Robertson & Gales 1998; Cousins & Cooper 2000). Censuses of the breeding population indicate a decline over 12 successive years from 1992 to 2004, reinforcing these concerns (US Fish and Wildlife Service, unpublished data).

Unfortunately, no reliable estimate of the number of birds killed as a result of fisheries bycatch is available to assess the status of the species (Brothers, Cooper & Lokkeborg 1999; Gilman, Boggs & Brothers 2003). Information on seabird mortality is available only for the US fisheries (Tasker *et al.* 2000), and even this information is based on observer data covering only 3–5% of trips for the study period (1992–2002), requiring an extrapolation of bycatch rates to the entire fleet (Lewison & Crowder 2003). Depending on the method of extrapolation, the number of birds killed by the US-based fisheries in Hawaii varied between approximately 700 and approximately 3000 (Lewison & Crowder 2003). Moreover, observer estimates of bycatch cannot account for birds that have been dislodged from the line (Crowder & Myers 2001). Previous research has proposed that as many as 30% more birds are hooked but dislodged during the haul and thus not observed (Brothers 1991). Thus, an estimation of the number of birds killed in the North Pacific can only result can from a large extrapolation (Lewison & Crowder 2003), and population level effects of longline fishing can hardly be assessed robustly from bycatch estimates.

In this paper, we analysed capture–recapture data of a population of black-footed albatross to obtain estimates of survival probability for this population using several alternative models to take adequately into account heterogeneity in the recapture process. Instead of trying to estimate the number of birds killed by using various extrapolations and unchecked assumptions, we investigate the potential relationship between annual adult survival and several measures of fishing effort. Although we considered a relatively large number of covariates, we used principal component analysis to generate a few uncorrelated synthetic variables from the set, thus maintaining both power and robustness.

Materials and methods

CAPTURE–RECAPTURE DATA

In total, 13854 black-footed albatross chicks on Tern Island (23°45′ N, 166°15′ W), in the North-western

Hawaiian Islands, have been ringed (with a metal ring from the United States Fish and Wildlife Service) since 1980. Regular recaptures of breeding birds started in 1992. The resulting data set consisted of 2046 capture histories of known-age breeding birds over 12 years (1992–2003). All recaptures used in the analysis took place between November and January.

CAPTURE–RECAPTURE MODELS

Our starting point was the standard survival Cormack–Jolly–Seber (CJS) model (Lebreton *et al.* 1992), which assumes time-dependent annual survival (ϕ) and recapture probabilities (p). Goodness-of-fit of this model was assessed using the program U-CARE (Choquet *et al.* 2005). Because these tests showed that the data poorly supported the underlying assumptions of the CJS model due to a strong capture heterogeneity, we used three alternative types of multistate recapture models (Lebreton & Pradel 2002). Multistate models are a natural generalization of the single state CJS model and thus allow individuals to move between states, according to a matrix of transition probabilities ψ. States can be either geographical sites or categorical variables defined at the individual level, such as reproductive state (see Lebreton & Pradel 2002 for a review).

In the first type of multistate model we considered, the heterogeneity in the detection process could be explained by birds skipping breeding, in particular after the death of their partner, and returning to the breeding population one to four breeding seasons later (Rice & Kenyon 1962). Thus, we considered models with two states; an observable state consisting of breeding birds (B) and an unobservable state to account for temporary absence (Lebreton, Almeras & Pradel 1999; Kendall & Nichols 2002) and consisting of non-breeding birds (NB). This multistate model is parameterized by a transition matrix and vectors of survival and resighting probabilities (Nichols *et al.* 1994):

$$\begin{bmatrix} \psi_{B\to B} & 1-\psi_{B\to B} \\ \psi_{NB\to B} & 1-\psi_{NB\to B} \end{bmatrix}_t \begin{bmatrix} \phi \\ \phi \end{bmatrix}_t \begin{bmatrix} p \\ 0 \end{bmatrix}_t \qquad \text{eqn 1}$$

Capture probability in the unobservable state are constrained to 0. We also constrained survival to be equal in both states in order to have an estimable survival probability for birds in the unobservable state.

In a second type of model, we considered that the frequency of skipping breeding and the time to return to the breeding state may vary with age by decreasing with experience (see e.g. Coulson 1966; Viallefont, Cooke & Lebreton 1995). To incorporate these breeding events into our modelling study, we extended the first model type by considering age-dependence in transitions between states and capture probabilities. All birds in the analysis were ringed as chicks and seen at least once as breeding birds. Because of changes in the area of recapture, we could not include recruitment in the analysis. Thus, to account for age, all birds belonging to a same cohort were grouped. The first group consisted of birds banded as chicks in 1980, the second in 1981, etc. Age effect was a combination of time and cohort effect; for example, birds of 23 years were birds banded in 1980 and recaptured in 2002; birds of 22 years were birds banded in 1980 and recaptured in 2001 or banded in 1981 and recaptured in 2002, etc. Because recaptures started in 1992, year 2002 was time 11 for survival and time 10 for capture. We used shortcuts in M-SURGE to assign an age for each interaction between group and time (Choquet *et al.* 2004). The two examples given above were coded in M-SURGE as follows: ag21 [g(1).t(9) and g(2).t(10) and g(3).t(11)] and ag22 [g(1).t(10) and g(2).t(11)].

Lastly, the existence of intensive zones of capture, as well as changes in staff over time, combined with a bird's high fidelity to their nest site, may have induced permanent differences in the probability of capture among individuals. In a third type of model, we resorted to models capable of accounting for this capture heterogeneity without assumptions on its origin (Pledger & Efford 1998; Pledger, Pollock & Norris 2003). In these models, detection probabilities are assumed to differ among two hidden classes of individuals – one having a higher capture probability than the other – and to be homogeneous within each class. Therefore, two detection probabilities have to be estimated, as well as the proportion of individuals in each class (Pradel 2005).

The multistate model with unobservable state belongs to a class of multistate models for which there are no goodness-of-fit tests currently available (Pradel, personal communication). However, an *ad hoc* goodness-of-fit test can be derived from the CJS model goodness-of-fit test (Rivalan *et al.* 2005), where the χ^2 statistic and the degree of freedom are modified as follows:

$$GOF_m = \chi^2_{CJS} - \Delta dev \qquad \text{eqn 2}$$

and

$$df_m = df_{CJS} - \Delta l \qquad \text{eqn 3}$$

where Δdev was the change of deviance between the model tested and the CJS, and Δl the change of number of parameters. It is then possible to estimate a new overdispersion coefficient $\hat{c} = GOF_m/df_m$ (Lebreton *et al.* 1992). We relied on this coefficient for comparison between the three types of models: models with the lowest overdispersion coefficient fitted the data better. All models were fitted using the program M-SURGE (Choquet *et al.* 2004), except the model incorporating permanent heterogeneity of capture, which was fitted with MATLAB. For each type of model we compared models with time-dependence in survival, models with constant survival, and models with survival related to longline fishing over time, as explained below. As we tested for a linear relationship between survival and fishing effort, we used an identity link function to fit all the models, and apply constraints to obtain estimates of capture and survival probabilities within the range 0–1.

RELATING SURVIVAL TO FISHING EFFORT

We investigated the effect of bycatch on survival based on standard results from the dynamics of exploited populations (Burnham & Anderson 1979; Lebreton 2005): for a baseline survival probability φ_0 (in the absence of bycatch) and for an annual bycatch proportion of the population h, the probability of survival approximately decreases with the proportion 'harvested' as:

$$\varphi = \varphi_0(1-h) \qquad \text{eqn 4}$$

This linear formula is only an approximation, because the risk of death from natural causes and human-induced cause compete over time. However, this approximation is quite accurate for high φ_0 and low h (Lebreton 2005).

As explained in the introduction, no reasonable estimate of the bycatch proportion h was available for the fleets concerned. To reach such an estimate, it requires dedicated observers on fishing vessels, trained to record the number of birds caught. Although an observer programme is developing, available data were insufficient to provide bycatch estimates for the whole distribution area or for the period of investigation (McCracken 2001; Lewison & Crowder 2003).

We assume that the level of bycatch h is proportional to fishing pressure is logical if mitigation measures do not exist to reduce this incidental mortality. International agreements have been established to address bycatch issues, but they are non-binding and have been implemented only within the past few years (Lewison *et al.* 2004). Thus, for our study period we can assume h is proportional to fishing effort E, which leads us to consider the regression equation:

$$\varphi = a - bE \qquad \text{eqn 5}$$

where a and b are parameters to be estimated. Note that E was standardized to avoid numerical instabilities. The intercept a was therefore equal to $\varphi_0 - \bar{E}/\sigma_E$ where $\bar{E}$ is the mean of fishing effort and σ_E the standard deviation. Assessing the effect of longline fishing can thus be based on testing the null hypothesis H_0 $b = 0$ vs. the alternative hypothesis H_1 $b \neq 0$, i.e. on the comparison of a model with constant survival [with deviance noted *Dev*(*const*)] and a model with survival function of the covariate E [with deviance *Dev*(*cov*)] (Skalski 1996). Such a test is performed using an analysis of deviance (*ANODEV*) which statistics follow under H_0 a Fisher–Snedecor distribution with 1 and n degrees of freedom, n being the difference in the number of parameters of a time-dependent model [with deviance *Dev*(*Time*)] and a model with covariates (Skalski 1996):

$$F = \frac{Dev(const) - Dev(\mathrm{cov})}{Dev(\mathrm{cov}) - Dev(Time)} \times n \qquad \text{eqn 6}$$

Because we expect albatross bycatch to increase with fishing effort, and thus to be negatively related to albatross survival, the alternative hypothesis to H_0 can be specified as H_1: $b > 0$. We therefore performed one-sided tests throughout (i.e. we divided by half the *P*-value).

Survival in the absence of fishing effort φ_0, corresponding to natural survival, is an important demographic parameter especially in assessing population dynamics and calculating extinction probabilities using population viability analysis. Because fishing was conducted during the study period we cannot estimate φ_0 directly, but only make a prediction $\tilde{\phi}_0$ (Sokal & Rohlf 2000). More precisely, using eqn 5, $\tilde{\phi}_0$ is given by $\tilde{\phi}_0 = a - b\tilde{E}$ with $\tilde{E}$ being negative as fishing effort was standardized. To quantify uncertainty in the predicted $\tilde{\phi}_0$, we calculated the associated confidence interval by accounting for both sampling and process variances (Burnham & White 2002; Conroy, Senar & Domenech 2002).

FISHING EFFORT

Several alternative predictors of bycatch from fishing effort could be tested, including the geographical location of fishing activities and the type of fishing activities. Based on the biological knowledge of the system, we formulated a priori hypotheses about which factors were suspected to be important.

The hypothesis of an increased impact of bycatch close to albatross nests has been formulated (Crowder & Myers 2001) but based on US fleet data only. We cannot exclude a significant effect of bycatch mortality on the population outside of the US zone. With the development of satellite tracking, more information about albatross' foraging range is available (Hyrenbach, Fernandez & Anderson 2002; Hyrenbach & Dotson 2003). However, sample size is still low, consisting of seven birds: six females and one male (Hyrenbach, Fernandez & Anderson 2002), and thus a precise overlap of fishing fleet and albatross foraging range for the study period is not feasible. Consequently, we considered two covariates characterizing fishing close to nesting sites and fishing over the entire foraging range. The former was given by the fishing effort of the Hawaiian fleet and the latter by the aggregated fishing effort for the whole North Pacific Ocean.

We focused on the two major types of fishes targeted: tuna and tuna-like species (*Thunnus thynnus orientalis*, *T. obesus*, *T. albacares* and *T. alalunga*), and swordfish (*Xiphias gladius*), which require different fishing techniques, and to which albatross may be differentially susceptible (Lewison & Crowder 2003). Indeed, several bycatch species, whether loggerhead turtle (*Caretta caretta*), leatherback turtle (*Dermochelys coriacea*), laysan (*Phoebastria immutabilis*), or black-footed albatross, appear to be more often caught by longlines targeting swordfish than those targeting tunas. Swordfish sets are particularly shallow, with slowly sinking baited hooks that are generally deployed at the same

Table 1. Comparison of the different structures of capture–recapture models. The Cormack–Jolly–Seber (CJS) model accounts for time-dependent annual survival and recapture probabilities. The multistate with one unobservable state (unobservable state) accounts for temporary absence (birds skipping breeding). The same multistate model with age-dependence in transition and capture probabilities accounts for increasing experience with age of birds as breeders (TADE model). Models incorporating capture heterogeneity among individuals (capture heterogeneity) are relevant for handling with permanent capture heterogeneity associated with sampling design. Models were compared using QAIC within a class of models. Only the results regarding the family of models best supported by the data, corresponding to the lowest overdispersion coefficient, are provided (the TADE). Φ refers to the survival probability, p to capture probability and ψ to the transitions probabilities. The indices *t*, *i*, A and PC refer to, respectively, time-varying, constant, age-varying and covariate-dependent probabilities. H refers to a model with two classes of individuals having a permanent different capture probability; +: additive effects

Model	Deviance	No. of parameters	QAIC	$\hat{c}$ (overdispersion coefficient)
CJS				3·02
Φ_t, p_t	7845·85	23		
Unobservable state				2·53
Φ_t, p_t, ψ_i	7831·24	26		
Capture heterogeneity				1·89
Φ_t, p_{t+H}	7804·70	26		
Age effect on capture and unobservable state (TADE)				< 1
Φ_t, p_{t+A}, ψ_A	7756·63	27	7810·63	
Φ_i, p_{t+A}, ψ_A	7822·80	17	7856·8	
$\Phi_{PC1(8cov)}$, p_{t+A}, ψ_A	7820·09	18	7856·09	
$\Phi_{PC2(8cov)}$, p_{t+A}, ψ_A	7793·45	18	7829·45	
$\Phi_{PC3(8cov)}$, p_{t+A}, ψ_A	7822·51	18	7858·51	
$\Phi_{PC1(4cov)}$, p_{t+A}, ψ_A	7821·01	18	7857·01	
$\Phi_{PC2(4cov)}$, p_{t+A}, ψ_A	7789·12	18	7825·12	
$\Phi_{PC3(4cov)}$, p_{t+A}, ψ_A	7822·53	18	7858·53	

time that birds are feeding most actively (Cousins, Dalzell & Gilman 2000; Crowder & Myers 2001).

We also used two measures of fishing effort: the annual number of hooks set and the annual tonnage of fish caught for each of the two fish species. For the same fleet, we expect annual tonnage of fish caught and the number of hooks set to be highly correlated and related by a relatively constant catch per unit effort. Nevertheless, when considering several fleets we expect the use of different techniques to be applied, for example hooks with a variety of sizes and shapes (Brothers, Cooper & Lokkeborg 1999), we do not expect, however, to obtain the same efficiency on catch and bycatch (Tuck *et al.* 2001). We thus tested the two measures of fishing effort separately.

Data for fishing effort were provided by the NMFS and the Interim Scientific Committee for tuna and tuna-like species in the North Pacific Ocean. Because several data are confidential, we present only standardized data in the Appendix (see Appendix S1 in Supplementary material).

By combining zones (Hawaii, North Pacific Ocean), species targeted (tuna-like species, swordfish) and measure (hooks, tonnage), eight covariates potentially related to bycatch were obtained.

Considering all covariates separately might have hampered this analysis. First, the large number of candidate covariates raises the classical multiple test issue: the inflation of the probability of detecting spurious correlations (Type I error) (Rice 1989; Roback & Askins 2005). The sequential Bonferroni method (Rice 1989; Graham 2003) used to avoid Type I error results in a substantial loss of statistical power (Roback & Askins 2005).

Secondly, we expected high correlations among fishing effort variables, particularly among locations and measures of fishing effort. Interdependence among explanatory covariates is referred to as multicollinearity (Graham 2003), which hampers model selection and parameter estimation in regression analysis by inducing instability of regression coefficient estimates (Graham 2003).

To limit the number of covariates and protect against collinearity, we first used principal component analysis (PCA) to generate a small number of uncorrelated synthetic variables (principal components: PCs). PCs are uncorrelated linear combinations of the original variables explaining most of the variation in the covariates. The first three PCs were used in place of the eight original variables in the capture–recapture models described above.

Results

The goodness-of-fit test indicated the CJS model fitted the data poorly (Table 1). More precisely, we detected an excess of tagged individuals never seen again (directional test for transience equal to $Z = 3{\cdot}587$, $P < 0{\cdot}001$), and a higher capture probability for individuals captured in a previous occasion (directional test for trap-dependence equal to $Z = -3{\cdot}485$, $P < 0{\cdot}001$). These tests indicate an excess of runs of 0s (non-captures) and 1s (captures) in our data, indicating strong heterogeneity in capture probabilities. Based on the lack-of-fit criteria (Table 1), this heterogeneity was best accounted for by considering the family of models with age-dependent

Table 2. Contribution of the eight fishing variables to the first three principal components (PC) of the principal component analysis (PCA) (a-) and contribution of the four swordfish fishing effort variables (b-). Fishing variables are functions of fishing effort (number of hooks per year vs. tonnage of fish species targeted per year), geographical location (North Pacific – NP, vs. Hawaiian Exclusive Economic Zone) and fish species targeted (swordfish vs. tuna)

PC axis	Tonnage NP swd	Tonnage Hawaii swd	Hooks NP swd	Hooks Hawaii swd	Hooks NP tuna	Hooks Hawaii tuna	Tonnage Hawaii tuna	Tonnage NP tuna
a-								
Axis 1	0·577	0·9464	0·983	0·790	–0·956	–0·972	–0·783	0·730
Axis 2	0·777	0·157	–0·094	–0·491	0·247	0·061	0·238	0·501
Axis 3	0·196	0·042	0·100	0·283	–0·020	–0·093	0·547	–0·273
b-								
Axis 1	0·649	0·970	0·980	0·781				
Axis 2	0·737	0·129	–0·149	–0·585				
Axis 3	0·187	–0·202	–0·097	0·216				

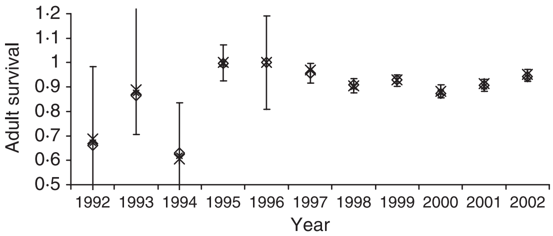

Fig. 1. Adult black-footed albatross survival from 1992 to 2002 for three types of model: Cormack–Jolly–Seber model (Δ), model with capture heterogeneity (×), and model with age effect on capture and transition (◇). Confidence intervals are from the model with age effect on capture and transition. As all models were fitted with an identity link, the confidence intervals can exceed one, but not the estimates.

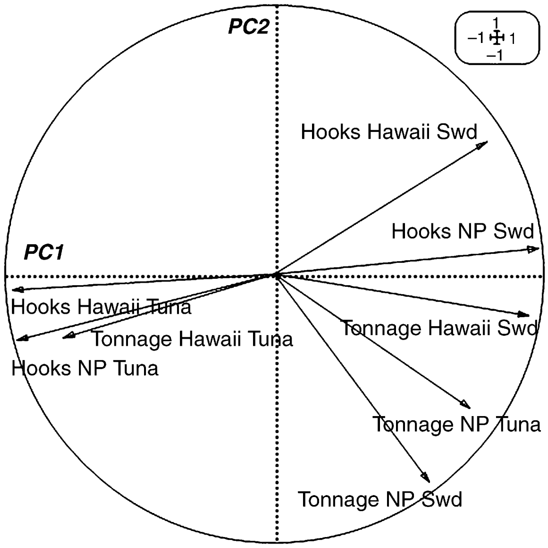

Fig. 2. Correlation circle of the eight fishing variables. Fishing effort variables are functions of fishing effort (number of hooks per year vs. tonnage of fish species targeted per year), geographical location (North Pacific – NP, vs. Hawaiian Exclusive Economic Zone) and fish species targeted (swordfish vs. tuna).

transition and capture probabilities (temporary age-dependent emigration: TADE model). Hence all the results presented thereafter were based on the TADE model. Nevertheless, we note that survival estimates from all models were very similar (Fig. 1).

The first three PCs of the eight fishing effort time-series explained 99% of the variation and we used these three synthetic variables (PC1, PC2 and PC3) as temporal covariates in the survival analysis (Table 2).

PC1 accounted for 72% of the variability among the variables. From the correlation circle (Fig. 2), PC1 could be interpreted as a synthetic variable representing the general trend of fishing effort through the study period: an overall decline of swordfish fishing and an overall increase of tuna-like species fishing. PC2 represented short-term variations over this general trend, with a strong role of covariates having the least pronounced trend: mainly tonnage in the North Pacific. PC2 was correlated with covariates of fishing effort in the North Pacific zone ($R^2 = 0\cdot531$, $P = 0\cdot006$), and accounted for 16% of the variability. PC3 was correlated with covariates of fishing effort in the Hawaiian zone ($R^2 = 0\cdot804$, $P < 0\cdot001$), and comprised mainly the tonnage of tuna in Hawaii. It accounted for only 6% of the variability among the variables. We also note that fishing effort measured as number of hooks set per year was correlated weakly with fishing effort measured as tonnage of targeted fish (Fig. 2).

Among the three synthetic variables used as temporal covariates in the survival analysis, only PC2 was significant at the α level $0\cdot05/3 = 0\cdot017$, according to Bonferroni-adjusted one-sided tests. PC2 was related significantly to survival ($F_9^1 = 7\cdot717$, $P = 0\cdot01$) and explained 44·4% of the variation in adult survival, whereas PC1 and PC3 explained less than 5% of the observed variability in this demographic parameter. As a control, we conducted the same analysis using only the four fishing effort variables concerning swordfish, because swordfish fishing was suspected to catch more birds than tuna fishing. In addition, the tuna data were compiled from four different species and they have more uncertainty than the swordfish data. Therefore, by replicating the same significant result, the control study suggests that the

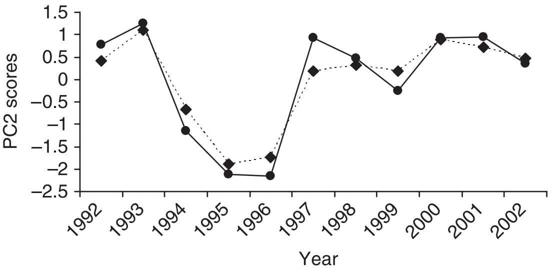

Fig. 3. Time-series of the second synthetic variable from the PCA (PC2) with eight fishing effort variables of tuna and swordfish fishing (plain line) and with only four fishing effort variables of swordfish fishing (dotted line).

results were not spurious. In the control, PC2 was again related significantly to survival ($F_9^1 = 10{\cdot}583$, $P < 0{\cdot}01$), explaining 50·9% of the variation in adult survival.

Annual survival estimates for 1992–94 exhibited large confidence intervals (Fig. 1), partly because the recapture effort was conducted on only a small plot on the island, with few recaptured birds each year. When we conducted an analysis without the data collected during these years (i.e. only using data from 1995 to 2002) the qualitative results were the same with either eight or four covariates in the PCA (respectively $F_6^1 = 16{\cdot}283$, $P < 0{\cdot}01$ and $F_6^1 = 19{\cdot}887$, $P < 0{\cdot}01$).

The PC2 synthetic variable based on swordfish covariates explained more variation of survival than the PC2 synthetic variable based on tuna and swordfish covariates, although they were very similar ($R^2 = 0{\cdot}935$, $P < 0{\cdot}001$) (Fig. 3). In this way, the tuna fisheries variables act more as a noise than as an actual explanatory variable. Thus, for the study period, the variation of longline fishing effort was related negatively to the variation of black-footed albatross adult survival due mainly to the variation of swordfish fishing effort in the North Pacific Ocean.

The estimated average survival probability for years 1997–2002, when fishing effort was higher than average (i.e. values of PC2 > 0), was 0·920 [CI = (0·910; 0·930)], and 0·917 [CI = (0·906; 0·927)], respectively, for the TADE and CJS models. The estimated slope, $\hat{b}$, of the relationship between PC2 and adult survival was 0·036 [CI = (0028; 0·044)]. Survival in the absence of fishing effort $\tilde{\phi}_0$ was predicted to be 1·099 [CI = (1·026; 1·181)], the interpretation of this value, which is higher than 1, is discussed below.

Discussion

We estimated an average adult survival probability of 0·92 [CI = (0·910; 0·930)] for 1997–2002, when fishing effort was high. This survival probability was low compared to average estimates for 17 other albatross species (see Appendix S2 in Supplementary material for references and details on species). Our findings suggest that high adult mortality was acting on the black-footed albatross population in the late 1990s. It should be emphasized that we formally accounted for potential sources of heterogeneity in the detection process, which could have led to underestimation in adult survival and/or detection of spurious effects of the covariates (Buckland 1982; Prevot-Julliard, Lebreton & Pradel 1998). The heterogeneity of capture was best explained by the skipping of reproduction of some adults, which was more frequent in younger birds. The first reproduction tend to have a higher cost than the those that follow (Weimerskirch 1992), thus the proportion of birds skipping the next reproduction is higher for inexperienced birds (Fisher 1976). The key question is whether the high mortality rates that we detected were induced by human activity – notably longline fishing.

The number of hooks set from vessels has traditionally been used as a measure of fishing effort (Brothers, Gales & Reid 1999; Inchausti & Weimerskirch 2002; Lewison & Crowder 2003; McCarthy, Andelman & Possingham 2003; Cuthbert *et al.* 2005). Surprisingly, we found that the annual number of hooks set and the annual tonnage of fish caught in the North Pacific Ocean were weakly correlated (Appendix S1 in Supplementary material). This result might be explained by the high variability in catch-per-hook ratios due to weather conditions, time of the day when the line is set, type of hooks used, etc. (Brothers, Cooper & Lokkeborg 1999), and suggests that the same amount of fish caught requires a different number of hooks set depending on various environmental parameters. Alternatively, the lack of correlation can result from the difficulty in compiling politically and economically sensitive data, with regard to fishing effort. Consequently, checking the relevance of fishing effort measures was a key step prior to our analysis. Using the number of hooks set as the sole variable of fishing effort, as has been conducted previously, would have led us to overlook the impact of longline fishing on adult black-footed albatross survival. Instead, by using PCA to integrate every relevant fishing effort measurement, we were able to explain more than 40% of the variation in annual adult survival and suggest that most of this impact is due to swordfish fishing in the North Pacific Ocean. Of course, the use of PCA should not be substituted to a first step consisting of formulating a priori hypotheses, and we included in our analysis only those fishing effort variables that we considered relevant.

Over the 11 years studied, the swordfish tonnage varied from 11 497 to 17 181. Within this range, a variation of 1000 metric tonnes corresponded to a variation in survival of 1·25%, based on the estimated slope of the regression. In terms of harvesting, this corresponds to about 1500 (± 300) breeding birds killed per additive 1000 metric tonnes if the breeding population is approximately 60 000 individuals, and to approximately 3750 (± 750) individuals per additive 1000 metric tonnes for a population of 300 000 individuals (Robertson & Gales 1998; Niel & Lebreton 2005). The extrapolation from the breeding population to the entire population assumes there is no sex- or age-bias in the

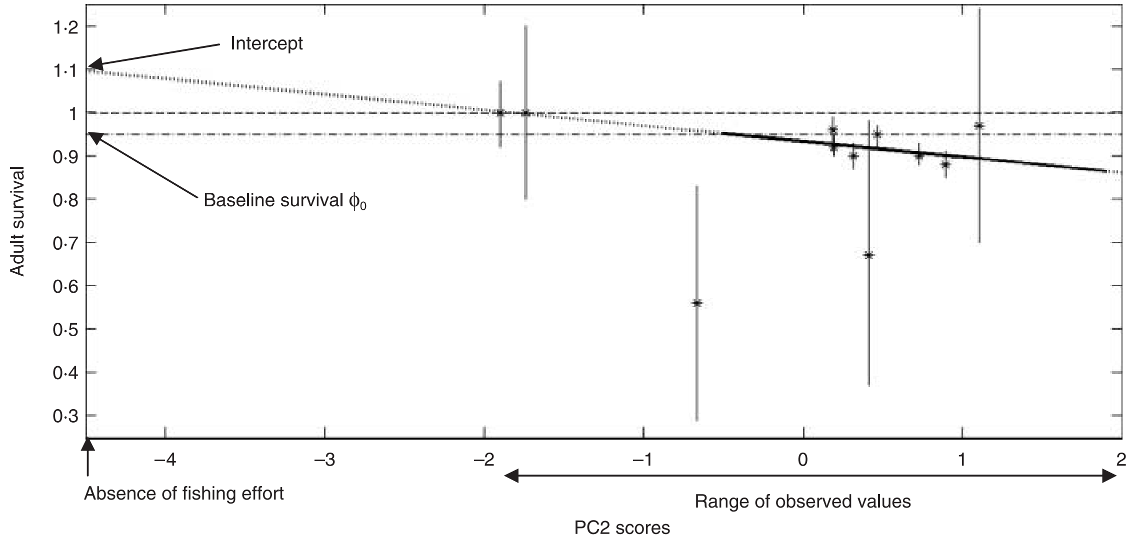

Fig. 4. Relationship between PC2 as a measure of fishing effort (E) and adult survival φ. In full line, linear regression from the model $\varphi = a – bE$ (eqn 5). Dotted line (····): prolongation of the linear model, corresponding to additive bycatch mortality. Dash-dot line (·—·) suggests that the relationship between fishing effort and adult survival is not linear, corresponding to compensation of bycatch by a decreasing in natural mortality or a non linear relationship between bycatch and fishing effort. *Time-dependent estimates of adult survival probabilities based on the temporary age-dependent emigration model, with 95% confidence interval.

probability of being caught. As yet, too few black-footed albatrosses have been studied for it to be possible to check for a significant gender effect on foraging area (Hyrenbach, Fernandez & Anderson 2002), although a gender affect has been demonstrated for other albatross species, such as the wandering albatross (Weimerskirch & Jouventin 1987; Weimerskirch *et al.* 1993), the black-browed albatross and the grey-headed albatross (Phillips *et al.* 2004). Knowledge of a differing susceptibility to being caught accidentally between male and female black-footed albatross would allow for refining the estimate of the number of killed birds.

The intercept estimate of φ_0 (corresponding to survival in the absence of fishing effort) is an extrapolation of the regression analysis far outside the limit of observed data, and thus interpretation has to be cautious. However, it was found to exceed 1 and therefore cannot be interpreted as an estimate of survival in absence of fishing. A plausible natural survival rate, as determined from data on other albatross species with similar breeding frequency and body mass (Jouventin & Dobson 2002), would be around 0·95. The $\varphi_0 > 1$ estimate implies that non-linear variation in survival for low values of fishing effort exists (Fig. 4), resulting possibly from a non-linear relationship either between survival and bycatch or between bycatch and fishing effort.

A non-linear relationship between survival and bycatch implies a less rapid decrease in survival with harvest than predicted by eqn 4, or that mortality induced by longline fishery is partially compensated. The most common mechanism invoked to induce compensatory mortality are density-dependence in survival (Burnham & Anderson 1979) and heterogeneity in survival among individuals (Lebreton 2005). Density-dependence affects the population by the limitation of food supplies (Furness & Birkhead 1984; Lewis *et al.* 2001). Because albatrosses are pelagic species, distributed at very low densities over a large foraging area, density-dependence on survival is unlikely. Heterogeneity in survival as a mechanism of compensation is based on the assumption that the population is made up of vulnerable and non-vulnerable individuals, where vulnerable individuals have low survival and high probability to be harvested (Lebreton 2005). Heterogeneity in survival would imply here that albatrosses caught by hooks would be vulnerable individuals, and more sensitive to natural mortality. Given the accidental nature of bycatch, as well as a high competition for accessing to the baits (Brothers, Cooper & Lokkeborg 1999; Lewison & Crowder 2003), this assumption is hardly plausible. Another unrelated compensation mechanism that seems more plausible is that fisheries activities may increase the survival of some individuals by providing a considerable additional source of food through discards of offal (Tasker *et al.* 2000; Nel *et al.* 2003). However, this possible compensation can, at most, reduce natural mortality to 0, i.e. cannot exceed $1 - \varphi_0 \sim 0{\cdot}05$ (Nichols *et al.* 1984), if the average survival φ_0 is taken to be 0·95.

Alternatively, the non-linear variation in survival for low values of fishing effort could arise from a non-linear relationship between fishing effort and bycatch at low values of fishing effort. Indeed, many marine bird species aggregate around fishing boats and compete for accessing baits and discards (Brothers, Cooper & Lokkeborg 1999; Lewison & Crowder 2003). If competition between species decreases with increasing fishing effort, then the probability of a black-footed albatross being caught on a hook would increase. Below a certain threshold, this probability may remain constant and low.

Because population growth is most sensitive to adult survival in long-lived species, such as the black-footed albatross (Lebreton & Clobert 1991), a decrease in adult survival can translate into a dramatic impact on the growth rate of the population and threaten its sustainability. Our estimate of low adult survival probability during the study period, combined with a significant correlation with longline fishing, suggests an anthropogenically induced decline of the black-footed albatross population. Furthermore, the population impact of human-induced mortality, such as longline fishing bycatch (Mills & Ryan 2005), can be worsened by 'widowing', whereby adults strongly delay reproduction if a partner dies (Jouventin, Lequette & Dobson 1999; Cousins & Cooper 2000).

The method used in this study to model the impact of longline fishing on the black-footed albatross population underlines the need of mitigation measures. Indeed, to maintain a sustainable population through a limited bycatch, only two ways are possible: either the longline fishing pressure should be decreased in order to maintain a sustainable survival probability for the birds or the relationship between fishing effort and bycatch rate should be broken, which can be provided only by efficient mitigation measures. Incidental mortality of albatrosses results from vessels fishing in the whole foraging area of birds. Local management policies can provide an immediate solution (Lewison, Freeman & Crowder 2004), but international agreements are necessary to solve the problem of bycatch. However, most agreements are non-binding; they mostly establish a common expectation and understanding among fishing nations. Hence, as many mitigation methods exist, it is critical to identify seabird avoidance strategies that are not only highly effective, but are also economically viable and commercially practical (Brothers, Cooper & Lokkeborg 1999; Gilman, Boggs & Brothers 2003).

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Supplementary material

The following supplementary material is available for this article.

Appendix S1. Time-series of the eight fishing effort variables used for the principal component analysis.

Appendix S2. Estimates of survival of 17 albatross species from literature and their references.

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/full/10.1111/j.1365-2664.2007.01346.x

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