

JIMAR – PFRP ANNUAL REPORT FOR FY 2006

P.I./Sponsor Name: Jean-Dominique Lebreton CNRS-CEFE/John Sibert PFRP

Project Proposal Title: Integrated modeling for Hawaiian Albatross Populations

Funding Agency: NOAA

NOAA Goal (Check those that apply):

- To protect, restore, and manage the use of coastal and ocean resources through ecosystem-base management
- To understand climate variability and change to enhance society’s ability to plan and respond
- To serve society’s needs for weather and water information
- To support the nation’s commerce with information for safe, efficient, and environmentally sound transportation

1. Purpose of the Project (one paragraph)

The purpose of the project is to analyze available information concerning Black-footed albatross (*Phoebastria nigripes*) (BFAL for the sake of brevity in what follows) and Laysan Albatros (LAAL) with the aim of assessing the status of their population in relation with the potential impact of longline fisheries.

2. Progress during FY 2006 (One-two paragraphs, including a comparison of the actual accomplishments to the objectives established for the period, and the reasons for slippage if established objectives were not met):

FY 2006 has seen decisive progress in our project: a) the capture-recapture analyses for BFAL were completed (a MS has just been submitted); b) the matrix model accounting for the effect of by-catch in presence of a delay in pair reformation after widowing has been investigated and a MS is nearly completed; c) the integrated model based on Kalman filter incorporating census and demographic information has been set up, and preliminary runs were completed. Results point to a significant impact of fishery activities on population dynamics of BFAL.

13. Plans for the next fiscal year (one paragraph):

The finalization of the various approaches above will be the main objective of the year to come. Communication with the other teams collaborating in the project, to compare various approaches to integrated modeling will be the other major theme.

4. List of papers published in refereed journals during FY 2006.

Sophie VÉRAN, Olivier GIMENEZ, Elizabeth FLINT, William L. KENDALL, Paul F. DOHERTY, Jr., Jean-Dominique LEBRETON. Quantifying the impact of longline fisheries on adult survival in the Black-footed Albatross. Journal of Applied Ecology, Submitted. (MS in appendix to this report)

5. Other papers, technical reports, meeting presentations, etc.

Combining capture-recapture data with other pieces of information in conservation ecology: the impact of longline fisheries on Black-footed Albatross (Jean-Dominique Lebreton & Sophie Véran, CEFE, Montpellier, France); Meeting « Capture », Université Laval, Québec, Canada , May 1, 2006.

Dynamique des populations exploitées, Données incomplètes et Ecologie de la conservation (exemple de l'impact de la pêche palangrière sur l'Albatros à pieds noirs) (Jean-Dominique Lebreton & Sophie Véran, CEFE, Montpellier, France) ;. Premières Rencontres scientifiques universitaires Sherbrooke-Montpellier, May 11, 2006

6. Graduates (Names of students graduating with MS or PhD degrees during FY 2006. Provide titles of their thesis or dissertation):

7. Awards (List awards given to JIMAR employees or to the project itself during the period):

8. Publication Count (Total count of publications for the reporting period and previous periods categorized by NOAA lead author and Institute (or subgrantee) lead author and whether it was peer-reviewed or non peer-reviewed (not including presentations):

	JI Lead Author			NOAA Lead Author			Other Lead Author		
	FY04	FY05	FY06	FY04	FY05	FY06	FY04	FY05	FY06
Peer-reviewed									
Non-peer reviewed									

9. Students and Post-docs (Number of students and post-docs that were associated with NOAA funded research. Please indicate if they received any NOAA funding. For institutes that award subcontracts, please include information from your subgrantees):

Viviane Hénaux, Ph.D. Student, partly funded by our subcontract, Integrated modelling
 Sophie Véran, Ph.D. Student, Albatross analyses.

10. Personnel:

- (i) Number of employees by job title and terminal degree that received more than 50% support from NOAA, including visiting scientists (this information is not required from subgrantees):

(ii) Number of employees/students that received 100% of their funding from an OAR laboratory and/or are located within that laboratory.

(iii) Number of employees/students that were hired by NOAA during the past year:

11. Images and Captions. (JIMAR will be including images in the annual report. Please send two of your best high-resolution, color images (photo, graphic, schematic) as a JPEG or TIFF with a caption for each image. Hardcopies of images can be dropped off at the JIMAR office if no electronic versions are available.

- Caption 1:

- Caption 2:

Quantifying the impact of longline fisheries on adult survival in the Black-footed Albatross

Sophie VÉРАН*, Olivier GIMENEZ†*, Elizabeth FLINT§, William L. KENDALL‡,
Paul F. DOHERTY, Jr.** , and Jean-Dominique LEBRETON*

* C.E.F.E., UMR 5175, C.N.R.S., 1919 route de Mende, 34293 Montpellier cedex 5,
France

† University of St Andrews, The Observatory, Buchanan Gardens, St Andrews, FIFE,
Scotland, KY16 9LZ

§ US Fish and Wildlife Service, Hawaiian and Pacific Islands NWR Complex, PO Box
50167, Honolulu, HI 96850, USA

‡ USGS Patuxent Wildlife Research Center, Laurel, MD 20708, USA

** Department of Fishery and Wildlife Biology, Colorado State University, CO 80523-
1474, USA

Corresponding author: Sophie Veran, C.E.F.E., UMR 5175, C.N.R.S., 1919 route de
Mende, 34293 Montpellier cedex 5, France. Tel. : +33 4 67 61 32 98 - Fax : +33 4 67 41
21 38. E-mail : veran@cefe.cnrs.fr

Word count : 7622

Summary

1. The impact of human activities on biodiversity is increasing. The interaction of man with animal populations often results in an increase in animal mortality, yet demonstrating and quantifying these increases remains difficult. 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.
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 probability for 1997-2002 was 0.92, 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 eleven years, suggesting an impact by longline fishing on albatross' survival.

4. Our analysis provides some evidence of nonlinear 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 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 the need of adequate mitigation measures.

Key-words:

bycatch, capture heterogeneity, covariates, capture-recapture, survival, compensation, exploited population.

INTRODUCTION

The impact of human activities on biodiversity is increasing (Soulé, 1987) through both direct (e.g. hunting) and indirect detrimental effects (e.g. habitat depletion). 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 (Kaplan, 2005; Lewison, Freeman & Crowder, 2004) and seabirds (Brothers, Cooper & Lokkeborg, 1999) through incidental bycatch. These large marine vertebrates have a long lifespan 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 & Ehrlén, 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*) and the Amsterdam albatross (*D. amsterdamensis*), have been subjected to significant incidental bycatch by fishery activities, notably longline fishing (Brothers, Cooper & Lokkeborg, 1999; Cherel, Weimerskirch & Duhamel, 1996; Weimerskirch, Clobert & Jouventin, 1987). 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. However, no real evidence is attributable to the effect of a specific mortality source. 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).

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 man-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 (Brooke, 2004; Cousins & Cooper, 2000; Cousins, Dalzell & Gilman, 2000; Hyrenbach & Dotson, 2003), as indicated by sighting records, fishery observer programmes and the recent development of telemetry. The breeding population is predominantly located in the North Western Hawaiian Islands with small breeding in colonies on Japanese islands (Brooke, 2004; Cousins & Cooper, 2000; Robertson & Gales, 1998). The population size was estimated to be about 300,000 birds from an estimate of approximately 60,000 breeding pairs (Niel & Lebreton, 2005; Robertson & Gales, 1998). Recently, concerns were raised about Black-footed albatross populations, as many birds have been killed by longline fisheries (Cousins & Cooper, 2000; Robertson & Gales, 1998). Censuses of the breeding

population indicate a decline over 12 successive years from 1992 to 2004, reinforcing these concerns (USFWS, 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 to 5% of trips for the study period (1992-2002), requiring to extrapolate bycatch rates to the entire fleet (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 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 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 relatively 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.

MATERIALS AND METHODS

Capture-recapture data

In total, 13854 Black-footed albatross chicks have been ringed (with a metal ring from the United States Fish and Wildlife Service) since 1980 on Tern Island (23°45'N, 166°15'W), in the North Western Hawaiian Islands. Regular recaptures of breeding birds started in 1992. The resulting data set consisted of 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 (GOF) 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. 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 a 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 an unobservable state to account for temporary absence (Kendall & Nichols, 2002; Lebreton, Almeras & Pradel, 1999). 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. The existence of intensive zones of capture, as well as changes in staff over time, combined with 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, pers. com.). However an ad hoc GOF test can be derived from the CJS model GOF test

(Rivalan et al., 2005), where the χ^2 statistic and the degree of freedom are modified as follows :

$$GOF_m = \chi_{CJS}^2 - \Delta dev$$

and

$$df_m = df_{CJS} - \Delta l .$$

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 fit better the data. All models were fitted using the program M-SURGE (Choquet et al., 2004). Within each type of models, 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.

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: $\varphi = \varphi_0(1-h)$ (eqn 1). 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. Such an estimate requires to have dedicated observers on fishing vessels, trained to record the number of birds caught. Although an observer program is developing, available data were insufficient to provide bycatch estimates for the whole distribution area or for the period of investigation (Lewison & Crowder, 2003; McCracken, 2001).

Assuming that 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: $\varphi = a - bE$ (eqn 2) 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 $\varphi_0 - \frac{\bar{E}}{\sigma_E}$ where \bar{E} is the mean of fishing effort and σ_E the standard deviation. Using eqn 2, we assessed the effect of longline fishing by testing the null hypothesis $H_0 b = 0$. To do so, we used F-tests based on analysis of deviance, and reported the proportion of variance explained by the covariates (Skalski, 1996).

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. To control for multiple tests, the risk of type I error was adjusted by the Bonferroni method (Rice, 1989). 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. Since fishing was conducted during the study period, we can not estimate φ_0 directly, but only a prediction $\tilde{\varphi}_0$ (Sokal & Rohlf, 2000). More precisely, using Eq [2], $\tilde{\varphi}_0$ is given by $\tilde{\varphi}_0 = a - b\tilde{E}$ with \tilde{E} being negative as fishing effort was standardized. To quantify uncertainty in the predicted $\tilde{\varphi}_0$, we calculated the associated confidence interval by accounting for both sampling and process variances (Burnham & White, 2002; Conroy, Senar & Domenech, 2002).

Fishing effort

Since many assumptions exist concerning specific fisheries, including the geographical location of fishing activities, we chose to test several alternative predictors of bycatch from fishing effort.

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 can not exclude a significant effect of bycatch mortality on the population out of the US zone.

With the development of satellite tracking, more information about albatross' foraging range is available (Hyrenbach & Dotson, 2003; Hyrenbach, Fernandez & Anderson, 2002). However, sample size is still low, consisting of 7 birds : 6 females and 1 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 characterising 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, Leatherback turtle, Laysan 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 time 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. The latter measure was necessary because the hooks used are of a variety of sizes and shapes (Bartram & Kaneko, 2005; Brothers, Cooper & Lokkeborg, 1999) and may not have the same efficiency on catch and bycatch. A natural measure of the efficiency of the hooks is the tonnage caught of the targeted species.

Data of 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 only present standardized data in appendix A.

By combining zones (Hawaii, North Pacific Ocean), species targeted (Tuna-like species, Swordfish) and measure (Hooks, Tonnage), 8 covariates potentially related to bycatch were obtained. Considering all 8 covariates separately might have hampered this analysis for the following reasons. We found correlation between fishing effort variables, which would yield bias in model selection and parameter estimation in regression analysis (Draper & Smith, 1981; Graham, 2003). Considering a large number of covariates, of the same order as the number of survival estimates, would lead to a loss of statistical power in detecting a significant effect, as well as a decrease in the precision associated with the magnitude of any effect. Furthermore, attempting to explain variation in survival with such a large number of covariates increases the probability of detecting spurious correlations merely through multiple testing (Draper & Smith, 1981). To limit the number of covariates and protect against collinearity, we first used Principal Component Analysis (PCA) to generate a few uncorrelated synthetic variables (“Principal Components” or PCs) explaining most of the variation in the covariates. The first 3 PCs were used in place of the 8 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

equal to $Z= 3.587$, $P<0.001$), and a higher capture probability for individuals captured in a previous occasion (directional test equal to $Z= -3.485$, $P<0.001$). 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 transition and capture probabilities (Temporary Age-Dependent Emigration or TADE model for short). 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 3 principal components of the 8 fishing effort time series explained 99% of the variation and we used these 3 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: mostly tonnage in the North Pacific. PC2 was correlated to covariates of fishing effort in the North Pacific zone ($R^2=0.531$, $p=0.006$). It accounted for 16% of the variability. PC3 was correlated to covariates of fishing effort in the Hawaiian zone ($R^2= 0.804$, $p<0.001$), and composed mostly by the tonnage of tuna in Hawaii. It accounted for only 6% of the variability among the variables. We can also note that fishing effort measured as number of hooks set per year was weakly correlated to fishing effort measured as Tonnage of targeted fish (Fig. 2).

Among the 3 synthetic variables used as temporal covariates in the survival analysis, only PC2 was significant (Table 3) at the α level $0.05/3 = 0.017$ according to Bonferroni adjusted one sided tests. PC2 was significantly related to survival ($F_9^1 = 7.717, p = 0.01$) 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 4 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 4 different species and they have more uncertainty than the swordfish data. So, by replicating the same significant result the control study suggests that the results were not spurious (Table 2 and 3). In the control, PC2 was again significantly related to survival ($F_9^1 = 10.583, p < 0.01$), explaining 50.9 % of the variation in adult survival.

Annual survival estimates for 1992-1994 exhibited large confidence intervals (Fig. 1), partly because the recapture effort was only conducted on 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 1995-2002) the qualitative results were the same with either 8 or 4 covariates in the PCA (respectively $F_6^1 = 16.283, p < 0.01$ and $F_6^1 = 19.887, p < 0.01$).

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 ($R^2 = 0.935, p < 0.001$) (Fig. 3). In this way, the tuna fisheries data act more like noise masking the signal than like an actual explanatory variable. Thus, for

the study period, longline fishing was negatively related to Black-footed albatross adult survival mostly through 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 (s.e 0.0051), and 0.917 (s.e 0.0054) respectively for the TADE and CJS models. The estimated slope, \hat{b} , of the relationship between PC2 and adult survival was 0.036 (s.e. 0.004). 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 (s.e 0.0051) for 1997-2002, when fishing effort was high. This survival probability was low compared to average estimates for other albatross species (Fig. 4) (Brooke, 2004; Cuthbert et al., 2003; Cuthbert et al., 2004; Jouventin & Dobson, 2002; Robertson, 1998; Weimerskirch, Brothers & Jouventin, 1997; Weimerskirch, Clobert & Jouventin, 1987). Our findings suggest that high adult mortality was acting on the Black-footed albatross population in the late 1990's. 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 following ones (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; Cuthbert et al., 2005; Inchausti & Weimerskirch, 2002; Lewison & Crowder, 2003; McCarthy, Andelman & Possingham, 2003).

Surprisingly, we found that the annual number of hooks set and the annual tonnage of caught fishes in the North Pacific Ocean were weakly correlated (Annex 1). 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 previously been done 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.

Over the 11 years studied, the swordfish tonnage varied from 11 497 to 17 181. Within this range, a variation of 1 000 metric tons 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 750 (+/- 150) breeding birds killed per additive 1 000 metric tons, if the breeding population is around 60 000 individuals, and to about 3 750 (+/- 750) individuals per additive 1 000 metric tons, for a population of 300 000 individuals (Niel & Lebreton, 2005; Robertson & Gales, 1998). The extrapolation from the breeding population to the entire population assumes there is no sex-bias or age-bias in the 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 albatrosses 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 accidental caught between male and female black-footed albatross would allow refining the estimate of the number of killed birds.

The intercept estimate of $\tilde{\phi}_0$ (corresponding to survival in the absence of fishing effort) 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 $\tilde{\phi}_0 > 1$ estimate implies that non-linear variation in survival for low values of fishing effort exists (Fig. 5), possibly resulting 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 decrease in survival with harvest less rapidly than predicted by eqn 2 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 and Anderson, 1976) 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, more sensitive to natural mortality too. 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 seems plausible. 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). However, this possible compensation can at most reduce natural mortality to 0, i.e. cannot exceed $1 - \phi_0 \approx 0.05$ (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.

Since 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 a 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 are strongly delay their reproduction if a partner dies (Cousins & Cooper, 2000; Jouventin, Lequette & Dobson, 1999).

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 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 only be provided by efficient mitigation measures.

ACKNOWLEDGEMENT

This project was funded by Cooperative Agreement NA17RJ1230 between the Joint Institute for Marine and Atmospheric Research (JIMAR) and the National Oceanic and Atmospheric Administration (NOAA). The views expressed herein are those of the authors and do not necessarily reflect the views of NOAA or any of its subdivisions. The U.S. National

Marine Fisheries Service and the U. S. Fish and Wildlife Service provided data. The field research was done on a National Wildlife Refuge by refuge staff and volunteers. We would like to thank the field workers for their hard work banding and reading bands. O. Gimenez's research was supported by a Marie-Curie Intra-European Fellowship within the Sixth European Community Framework Programme.

REFERENCES:

- Bartram, P.K. & Kaneko, J.J. (2005). *Catch to bycatch ratios: comparing Hawaii's longline fisheries with others*. SOEST 04-05, JIMAR Contribution 04-352, Honolulu, USA.
- Brooke, M.d.L. (2004) *Albatrosses and Petrels across the world*. Oxford University Press, Oxford.
- Brothers, N. (1991) Albatross mortality and associated bait loss in the Japanese longline fishery in the Southern Ocean. *Biological Conservation*, **55**(3), 255-68.
- Brothers, N., Cooper, J. & Lokkeborg, S. (1999). *The incidental catch of seabirds by longline fisheries: worldwide review and technical guidelines for mitigation*. Food and Agriculture Organisation of the United Nations, .
- Brothers, N., Gales, R. & Reid, T. (1999) The influence of environmental variables and mitigation measures on seabird catch rates in the Japanese tuna longline fishery within the Australian Fishing Zone, 1991-1995. *Biological Conservation*, **88**, 85-101.
- Buckland, S.T. (1982) A mark recapture survival analysis. *Journal of animal ecology*, **51**, 833-47.
- Burnham, K.P. & Anderson, D.R. (1979) The composite-dynamic method as evidence for age-specific waterfowl mortality. *Journal of Wildlife Management*, **43**, 356-66.
- Burnham, K.P. & White, G.C. (2002) Evaluation of some random effects methodology applicable to bird ringing data. *Journal of Applied Statistics*, **29**, 245-64.
- Cherel, Y., Weimerskirch, H. & Duhamel, G. (1996) Interactions between longline vessels and seabirds in Kerguelen waters and a method to reduce seabird mortality. *Biological Conservation*, **75**, 63-70.
- Choquet, R., Reboulet, A.-M., Pradel, R., Gimenez, O. & Lebreton, J.-D. (2004) M-SURGE: new software specifically designed for multistate capture-recapture models. *Animal Biodiversity and Conservation*, **27**(1), 207-15.
- Choquet, R., Reboulet, A.M., Lebreton, J.D., Gimenez, O. & Pradel, R. (2005). *U-CARE 2.2 User's Manual*. CEFE/CNRS, Montpellier, France.
- Conroy, M.J., Senar, J.C. & Domenech, J. (2002) Analysis of individual-and time-specific covariate effects on survival of *Serinus serinus* in north-eastern Spain. *Journal of Applied Statistics*, **29**, 125-42.
- Coulson, J.C. (1966) The influence of pair-bond and age on the breeding biology of the Kittiwake *Rissa tridactyla*. *Journal of animal ecology*, **35**, 269-79.
- Cousins, K.L. & Cooper, J. (2000). *The population biology of the black-footed albatross in relation to mortality caused by fishing*. Technical report for the Western Pacific Regional Fishery Management Council, Honolulu, Hawaii, USA.
- Cousins, K.L., Dalzell, P. & Gilman, E. (2000) Managing pelagic longline-albatross interactions in the North Pacific Ocean. *Marine ornithology*, **28**, 159-74.
- Crowder, L.B. & Myers, R.A. (2001). *A comprehensive study of the ecological impacts of the worldwide pelagic longline industry*. First Annual Report to the Pew Charitable Trusts, Philadelphia, USA.

- Cuthbert, R., Hilton, G., Ryan, P. & Tuck, G.N. (2005) At-sea distribution of breeding Tristan albatross *Diomedea dabbenena* and potential interactions with pelagic longline fishing in the South Atlantic Ocean. *Biological Conservation*, **121**, 345-55.
- Cuthbert, R., Ryan, P., Cooper, J. & Hilton, G. (2003) Demography and population trends of the Atlantic yellow-nosed albatross. *The Condor*, **105**, 439-52.
- Cuthbert, R., Sommer, E., Ryan, P., Cooper, J. & Hilton, G. (2004) Demography and conservation of the Tristan Albatross *Diomedea [exulans] dabbenena*. *Biological Conservation*, **117**(4), 471-81.
- De Kroon, H., Groenendaal, J.V. & Ehrlén, J. (2000) Elasticities: a review of methods and model limitations. *Ecology*, **81**(3), 607-18.
- Draper, N.R. & Smith, H. (1981) *Applied Regression Analysis*. 2nd edn. Wiley, New York.
- Fisher, H.I. (1976) Some dynamics of a breeding colony of Laysan Albatrosses. *The Wilson Bulletin*, **88**, 121-42.
- Furness, R.W. & Birkhead, T.R. (1984) Seabird colony distributions suggest competition for food supplies during the breeding season. *Nature*, **311**, 655-56.
- Gilman, E., Boggs, C. & Brothers, N. (2003) Performance assessment of an underwater setting chute to mitigate seabird bycatch in the Hawaii pelagic tuna fishery. *Ocean and Coastal Management*, **46**, 985-1010.
- Graham, M.H. (2003) Confronting multicollinearity in ecological multiple regression. *Ecology*, **84**(11), 2809-15.
- Hyrenbach, K.D. & Dotson, R.C. (2003) Assessing the susceptibility of female black-footed albatross (*Phoebastria nigripes*) to longline fisheries during their post-breeding dispersal: an integrated approach. *Biological Conservation*, **112**, 391-404.
- Hyrenbach, K.D., Fernandez, P. & Anderson, D.J. (2002) Oceanographic habitats of two sympatric North Pacific albatrosses during the breeding season. *Marine Ecology Progress Series*, **233**, 283-301.
- Inchausti, P. & Weimerskirch, H. (2002) Dispersal and Metapopulation dynamics of an oceanic seabird, the wandering albatross, and its consequences for its response to long-line fisheries. *Journal of animal ecology*, **71**, 765-70.
- Jouventin, P. & Dobson, S. (2002) Why breed every other year? The case of albatrosses. *Proceedings of the Royal Society of London*, **269**, 1955-61.
- Jouventin, P., Lequette, B. & Dobson, S. (1999) Age-related mate choice in the wandering albatross. *Animal Behavior*, **57**, 1099-106.
- Kaplan, I.C. (2005) A risk assessment for Pacific leatherback turtles (*Dermochelys coriacea*). *Canadian Journal of fisheries and aquatic sciences*, **62**(8), 1710-19.
- Kendall, W.L. & Nichols, J.D. (2002) Estimating state-transition probabilities for unobservable states using capture-recapture/resighting data. *Ecology*, **83**(12), 3276-84.
- Lebreton, J.-D. (2005) Dynamical and statistical models for exploited populations. *Aust. N. Z. Stat.*, **47**(1), 49-63.
- Lebreton, J.-D., Almeras, T. & Pradel, R. (1999) Competing events, mixtures of information and multistrata recapture models. *Bird Study*, **46**(suppl.), 39-46.
- Lebreton, J.-D., Burnham, K.P., Clobert, J. & Anderson, D.R. (1992) Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs*, **62**, 67-118.

- Lebreton, J.-D. & Clobert, J. (1991). Bird population dynamics, management, and conservation: the role of mathematical modelling. In *Bird population studies: their relevance to conservation and management* (eds C. M. Perrins, J.-D. Lebreton & G. J. M. Hiron), pp. 105-125. Oxford University Press, Oxford.
- Lebreton, J.D. & Pradel, R. (2002) Multistate recapture models: modelling incomplete individual histories. *Journal of Applied Statistics*, **29**, 353-69.
- Lewis, S., Sherratt, T.N., Hamer, K.C. & Wanless, S. (2001) Evidence of intra-specific competition for food in a pelagic seabird. *Nature*, **412**, 816-19.
- Lewison, R.L. & Crowder, L.B. (2003) Estimating fishery bycatch and effects on a vulnerable seabird population. *Ecological applications*, **13**, 743-53.
- Lewison, R.L., Crowder, L.B., Read, A.J. & Freeman, S.A. (2004) Understanding impacts of fisheries bycatch on marine megafauna. *Trends in Ecology and Evolution*, **19**(11), 598-604.
- Lewison, R.L., Freeman, S.A. & Crowder, L.B. (2004) Quantifying the effects of fisheries on threatened species: the impact of pelagic longlines on loggerhead and leatherback sea turtles. *Ecology Letters*, **7**.
- McCarthy, M.A., Andelman, S.J. & Possingham, H.P. (2003) Reliability of relative predictions in Population Viability Analysis. *Conservation Biology*, **17**(4), 982-89.
- McCracken, M. (2001). *Estimation of albatross take in the hawaiian longline fisheries*. National Marine Fisheries Service, NOAA, Honolulu, USA.
- Mills, L.S. & Ryan, P. (2005) Modelling impacts of long-line fishing: what are the effects of pair-bond disruption and sex-biased mortality on albatross fecundity? *Animal Conservation*, **8**, 359-67.
- Nichols, J.D., Conroy, M.J., Anderson, D.R. & Burnham, K.P. (1984) Compensatory mortality in waterfowl populations: A review of the evidence and implications for research and management. *Trans. N. Amer. Wildl. Nat. Resour. Conf.*, **49**, 535-54.
- Niel, C. & Lebreton, J.-D. (2005) Using demographic invariant to detect overhaversted bird populations from incomplete data. *Conservation Biology*, **19**(3), 826-35.
- Phillips, R.A., Silk, J.R.D., Phalan, P., Catry, P. & Croxall, J.P. (2004) Seasonal sexual segregation in two *Thalassarche* albatross species: competitive exclusion, reproductive role specialization or foraging niche divergence? *Proceedings of the Royal Society of London*, **271**, 1283-91.
- Pledger, S. & Efford, M. (1998) Correction of bias due to heterogeneous capture probability in capture-recapture studies of open populations. *biometrics*, **54**, 888-98.
- Pledger, S., Pollock, K.H. & Norris, J.L. (2003) Open capture-recapture models with heterogeneity: I. Cormack-Jolly-Seber Model. *biometrics*, **59**, 786-94.
- Pradel, R. (2005) Multievent: an extension of multistate capture-recapture models to uncertain states. *biometrics*, **61**, 442-47.
- Prevot-Julliard, A.-C., Lebreton, J.-D. & Pradel, R. (1998) Re-evaluation of adult survival of Black-headed gulls (*Larus ridibundus*) in presence of recapture heterogeneity. *The Auk*, **115**(1), 85-95.
- Rice, D.W. & Kenyon, K.W. (1962) Breeding cycles and behavior of laysan and black-footed albatrosses. *The Auk*, **79**, 517-67.
- Rice, W.R. (1989) Analyzing tables of statistical tests. *Evolution*, **43**, 223-25.

- Rivalan, P., Prevot-Julliard, A.-C., Choquet, R., Pradel, R., Jacquemin, B. & Girondot, M. (2005) Trade-off between current reproductive effort and delay to next reproduction in the leatherback sea turtle. *Oecologia*.
- Robertson, C.J.R. (1998). Factors influencing the breeding performance of the Northern Royal Albatross. In *Albatross Biology and Conservation* (eds G. Robertson & R. Gales), pp. 99-104. Surrey Beatty and Sons, Chipping Norton.
- Robertson, G. & Gales, R. (1998) *Albatross: Biology and Conservation*, Surrey Beatty & Sons, Chipping Norton.
- Saether, B.-E. & Bakke, O. (2000) Avian life history variation and contribution of demographic traits to the population growth rate. *Ecology*, **81**(3), 642-53.
- Skalski, J.R. (1996) Regression of abundance estimates from mark-recapture surveys against environmental covariates. *Can. J. Aquat. Sci.*, **53**, 196-204.
- Sokal, R. & Rohlf, F.J. (2000) *Biometry: the principles and practice of statistics in biological research*. 3rd edn. W. H. Freeman and company, New York.
- Soulé, M.E. (1987) *Viable population for conservation*. Cambridge University Press, Cambridge.
- Tasker, M.L., Camphuysen, C.J., Cooper, J., Garthe, S., Montevecchi, W.A. & Blaber, S.J.M. (2000) The impacts of fishing on marine birds. *Journal of marine science*, **57**, 531-47.
- Viallefont, A., Cooke, F. & Lebreton, J.-D. (1995) Age-specific costs of first-time breeding in the snow goose *Anser caerulescens*. *The Auk*, **112**(1), 67-76.
- Weimerskirch, H. (1992) Reproductive effort in long-lived birds: age specific patterns of condition, reproduction and survival in the wandering albatross. *Oikos*, **64**, 464-73.
- Weimerskirch, H., Brothers, N. & Jouventin, P. (1997) Population dynamics of wandering albatross *Diomedea exulans* and amsterdam albatross *D. amsterdamensis* in the indian ocean and their relationship with long-line fisheries: conservation implications. *Biological Conservation*, **79**, 257-70.
- Weimerskirch, H., Clobert, J. & Jouventin, P. (1987) Survival in five southern albatrosses and its relationship with their life history. *Journal of animal ecology*, **56**, 1043-55.
- Weimerskirch, H. & Jouventin, P. (1987) Population dynamics of the wandering albatross, *Diomedea exulans*, of the Crozet islands: causes and consequences of the population decline. *Oikos*, **49**, 315-22.
- Weimerskirch, H., Salamolard, M., Sarrazin, F. & Jouventin, P. (1993) Foraging strategy of wandering albatrosses through the breeding season: a study using satellite telemetry. *The Auk*, **110**(2), 325-42.

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 unobservable state model accounts for temporary absence (birds skipping breeding), the same model with age-dependence in transition and capture probabilities accounts for increasing experience with age of birds as breeders. Capture heterogeneity among individuals are relevant for permanent capture heterogeneity (sampling design).

Model	Deviance	Number of parameters	\hat{c} (overdispersion coefficient)
CJS	7845.85	23	3.02
Unobservable state	7831.24	26	2.53
Capture heterogeneity	7804.70	26	1.89
Age effect on capture and unobservable state	7756.63	27	<1

Table 2 Contribution of the 8 fishing variables to the first 3 principal components (PC) of the Principal Component Analysis (PCA) (a-) and contribution of the 4 swordfish fishing effort variables (b-). Fishing variables are functions of fishing effort (number of hooks per year versus tonnage of fish species targeted per year), geographical location (North Pacific –NP, versus Hawaiian Exclusive Economic Zone) and fish species targeted (swordfish versus tuna).

a-

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
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-

PC axis	Tonnage NP swd	Tonnage Hawaii swd	Hooks NP swd	Hooks Hawaii swd
Axis 1	0.742	0.983	0.987	0.753
Axis 2	-0.662	-0.143	0.143	0.651
Axis 3	-0.101	0.109	0.033	-0.086

Table 3 Tests of linear relationship between adult black-footed albatross survival and synthetic variables of fishing effort (PC1, PC2 and PC3) for a model with 8 fishing variables (a-) and for a model with 4 fishing variables (b-).

The P-level is of a one-sided test ($\alpha=0.017$ with Bonferroni correction)

a-

Fishing Effort Covariate	deviance	R²	F	df1	df2	P-value
TIME-DEPENDENT MODEL	7756.63					
PC2	7793.45	0.444	7.174	1	9	0.012
PC1	7820.09	0.028	0.26	1	9	>0.5
PC3	7822.51	0.005	0.04	1	9	>0.5
CONSTANT	7822.80					

b-

Fishing Effort Covariate	deviance	R²	F	df1	df2	P-value
TIME-DEPENDENT MODEL	7756.63					
PC2	7789.12	0.509	9.329	1	9	0.007
PC1	7821.01	0.027	0.25	1	9	>0.5
PC3	7822.53	0.005	0.04	1	9	>0.5
CONSTANT	7822.80					

Figures legend

Fig. 1 Adult black-footed albatross survival from 1992 to 2002 for 3 types of model: CJS model (Δ), model with capture heterogeneity (\times), and model with age effect on capture and transition (\diamond). 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.

Fig. 2 Correlation circle of the 8 fishing variables. Fishing effort variables are functions of fishing effort (number of hooks per year versus tonnage of fish species targeted per year), geographical location (North Pacific –NP, versus Hawaiian Exclusive Economic Zone) and fish species targeted (swordfish versus tuna).

Fig. 3 Time series of the 2nd synthetic variable from the PCA (PC2) with 8 fishing effort variables of tuna and swordfish fishing (a-) and with only 4 fishing effort variables of swordfish fishing (b-)

Fig. 4 Distribution of average estimates of adult survival for 17 albatross's species (a-) and for 9 annual albatross's species (b-) (Brooke, 2004; Cuthbert et al., 2003; Cuthbert et al., 2004; Jouventin & Dobson, 2002; Robertson, 1998; Weimerskirch, Brothers & Jouventin, 1997; Weimerskirch, Clobert & Jouventin, 1987). Some species have several survival estimates, either sex dependent, colony dependent or from two distinct time period (high fishing pressure/ low fishing pressure). Vertical lines represent low survival

related to fishing pressure, no lines for suspected impact of fishing on survival, and horizontal lines no impact or no significant impact of fishing on survival.

Fig. 5 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 2). In dotted line (....), prolongation of the linear model, corresponding to additive bycatch mortality. In dash-dot line (.-.-), non-linear model, 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.

Fig. 1

Adult survival

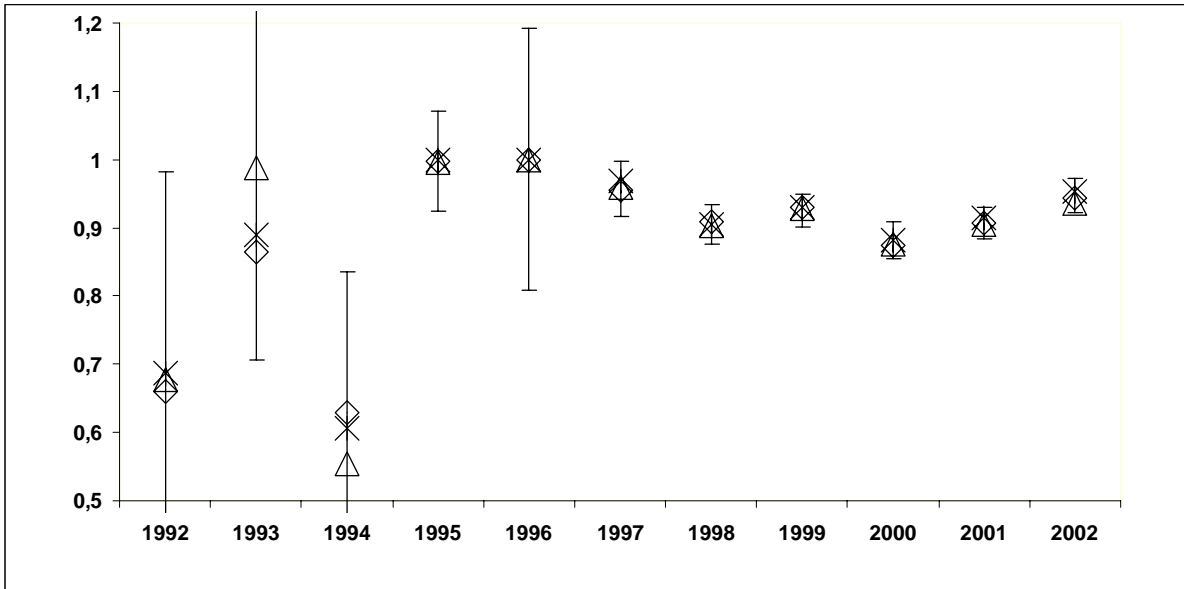


Fig. 2

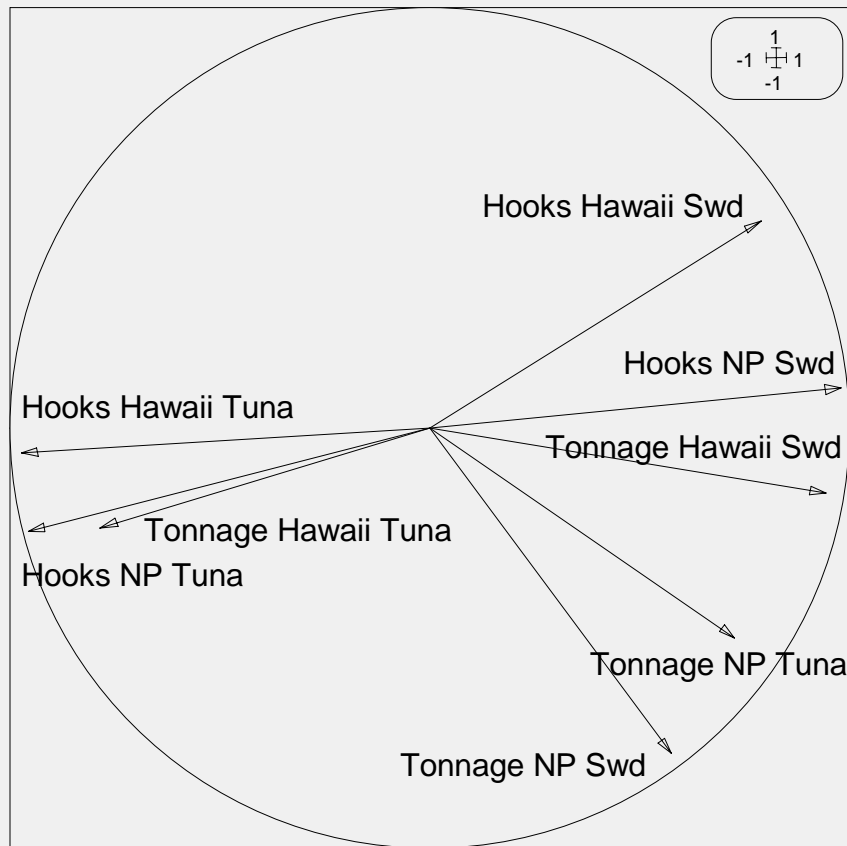
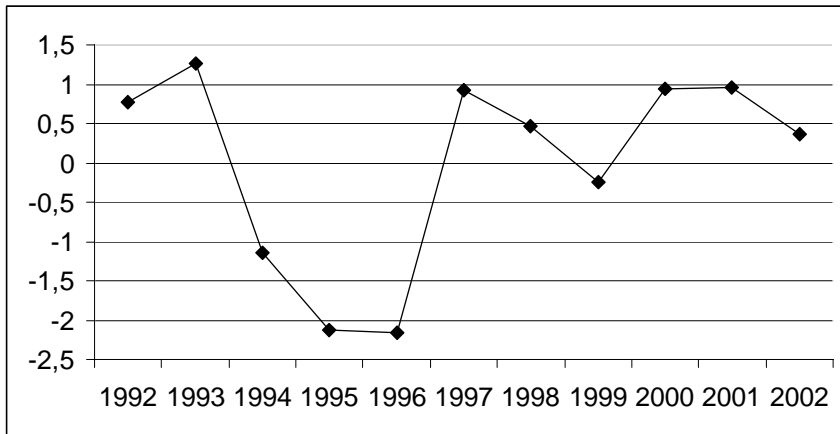


Fig. 3

a-



b-

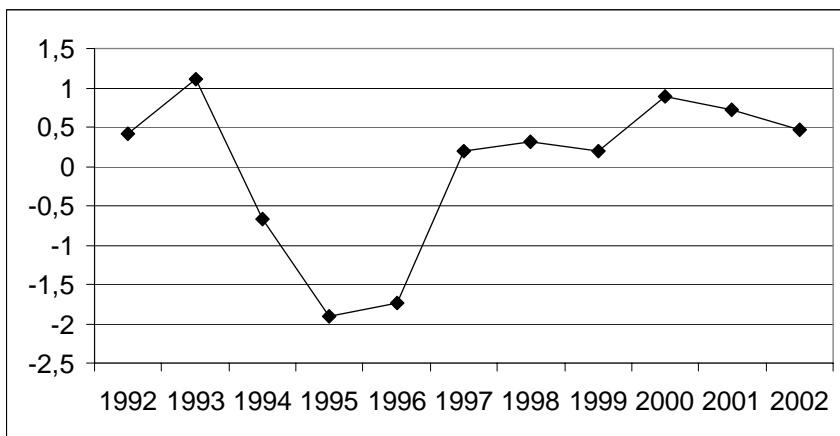
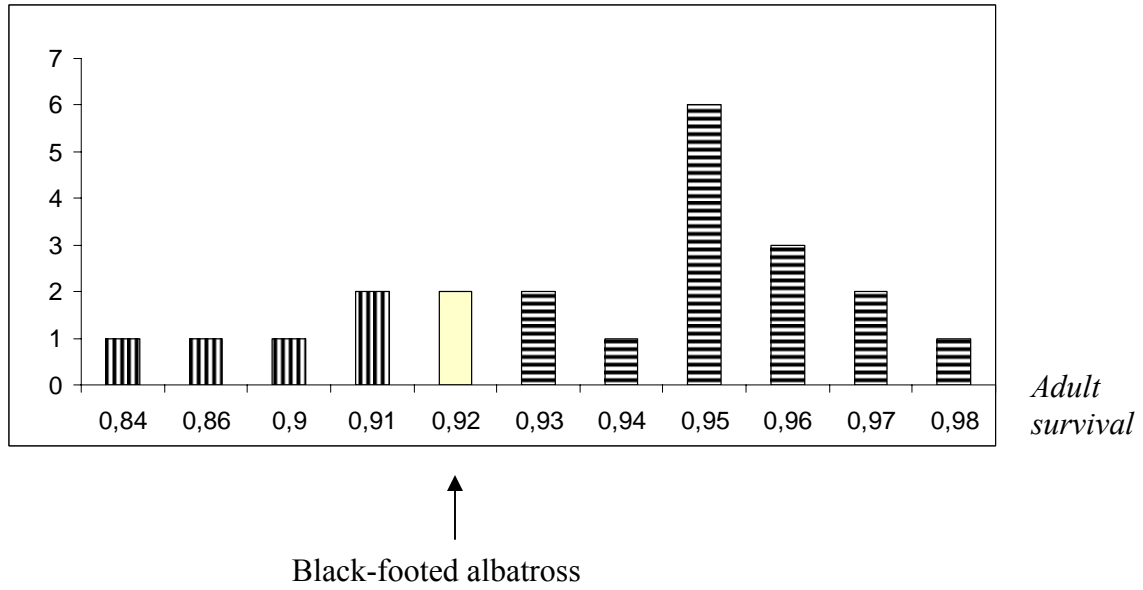


Fig. 4

a-

Numbers of estimates



b-

Numbers of estimates

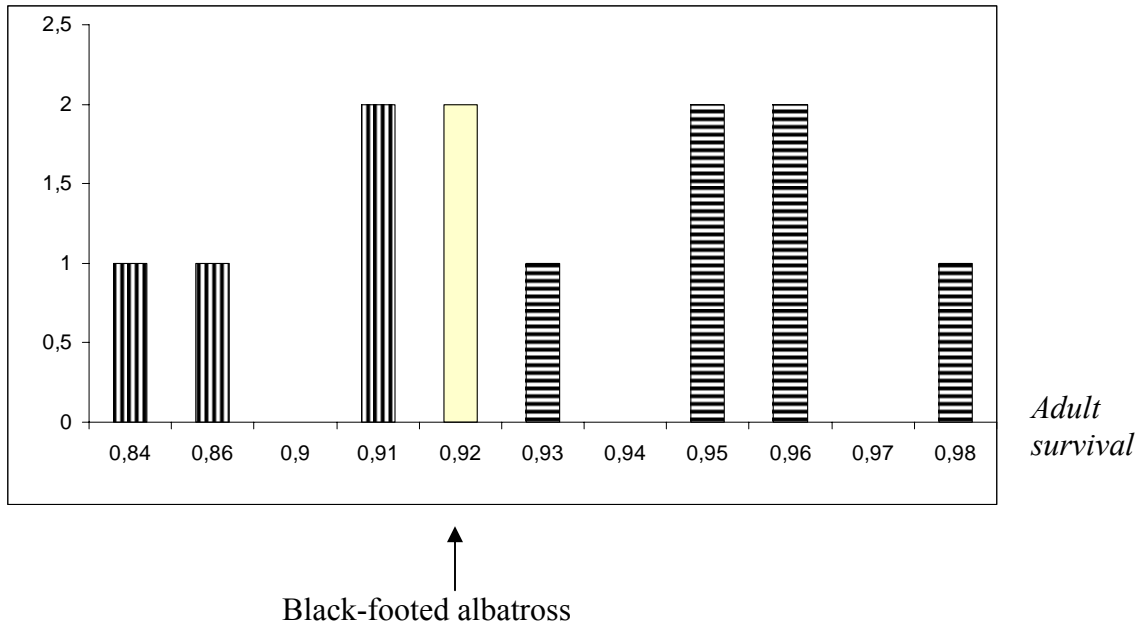
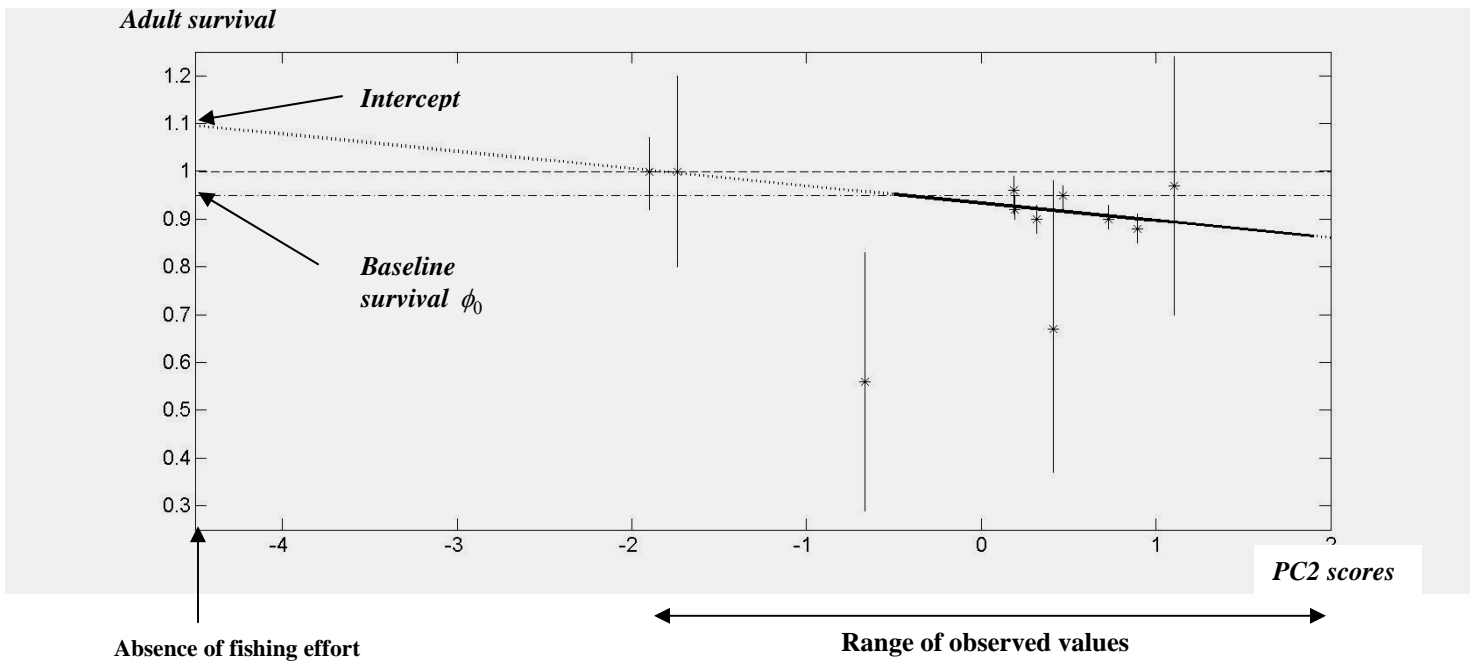


Fig. 5



Appendix A :

Time series of the 8 fishing effort variables. All variables are standardized. Plain lines represent variation of fishing effort in the Hawaiian Exclusive Economic Zone (EEZ), dotted line variation of fishing effort in the North Pacific Ocean. Fishing effort measured as number of hooks set per year is represented in circles (●), and fishing effort measured as tonnage of targeted fish species in diamond (■).

Figure a- are the time series for swordfish fishing effort in the Hawaiian EEZ, figure b- time series for tuna fishing effort in the Hawaiian EEZ, figure c- and d- respectively for swordfish and tuna fishing effort in the North Pacific Ocean.

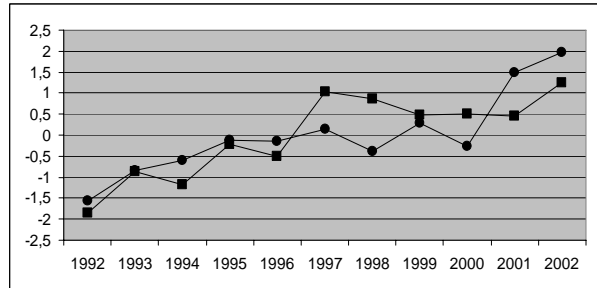
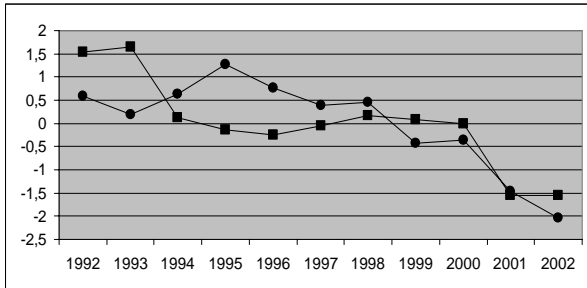


Figure a-

Figure b-

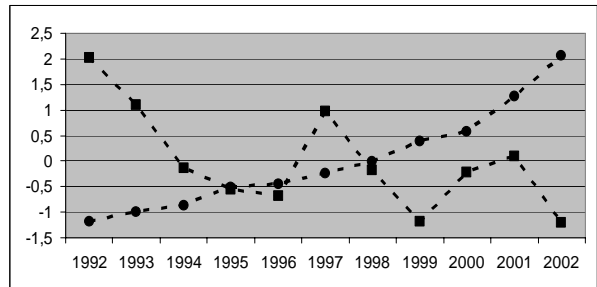
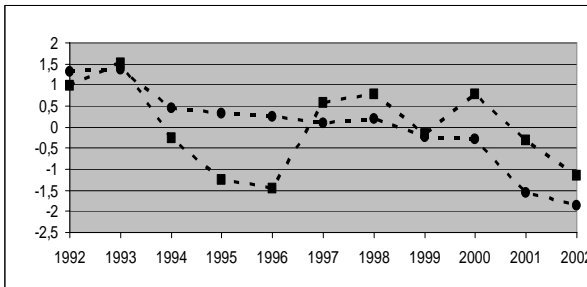


Figure c-

Figure d-