

An integrated assessment model of seabird population dynamics: can individual heterogeneity in susceptibility to fishing explain abundance trends in Crozet wandering albatross?

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Summary

1. Seabirds have been incidentally caught in distant-water longline fleets operating in the Southern Ocean since at least the 1970s, and breeding numbers for some populations have shown marked trends of decline and recovery concomitant with longline fishing effort within their distributions. However, lacking is an understanding of how forms of among-individual heterogeneity may interact with fisheries bycatch and influence population dynamics.

2. We develop a model that uses comprehensive data on the spatial and temporal distributions of fishing effort and seabird foraging to estimate temporal overlaps, fishery catchability and consequent bycatch. We apply a population model that is structured by age, sex, life stage and spatially to Crozet Island wandering albatross and explore how heterogeneity in susceptibility to capture may have influenced the population's demography over time.

3. A model where some birds were assumed to be more susceptible to fisheries bycatch was able to successfully replicate the observed trend in breeding pairs. Considerably poorer fits were found without this assumption. Results suggested that the more susceptible birds may have been removed from the population by the 1990s.

4. The model was also able to highlight areas, times and fleets prone to increased bycatch. Knowledge of these factors should assist fisheries and conservation management bodies to quantify and reduce seabird bycatch through spatial management and fleet-specific mitigation efforts.

5. *Synthesis and application.* Many seabirds show complex life histories that make them highly susceptible to additional incidental mortality from fishing vessels. By applying a population model that integrates key aspects of seabird and fishery dynamics, we were able to explain the observed trends in the breeding population of Crozet wandering albatross and identify key areas and fleets where further mitigation may be required. In addition, the potential removal of a category of birds that shows increased susceptibility to capture has important implications for the conservation management of this population and other iconic species incidentally caught by large-scale commercial fisheries.

Key-words: albatross, bycatch, conservation management, Crozet Island, evolution, heterogeneity, longline fishing, personality, population model, spatial management

Introduction

Fishery-induced incidental mortality of oceanic megafauna has been identified as a major conservation issue for many wild marine populations (Weimerskirch & Jouventin 1987; Lewison *et al.* 2004; Phillips *et al.* 2006;

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Wallace *et al.* 2010). Attracted to the baited hooks and discarded offal of oceanic fishing vessels, seabirds are particularly susceptible to incidental mortality. Their wide-ranging habitat leads to considerable overlap with pelagic longline fishing operations for tunas, while breeding birds are vulnerable to interactions with demersal longline and trawl vessels targeting continental slope and shelf species (Croxall & Prince 1996; Weimerskirch, Brothers & Jouventin 1997; Favero *et al.* 2003; Tuck, Polacheck & Bulman 2003).

Wandering albatross *Diomedea exulans* (Linnaeus 1758) are known to be caught by pelagic longline fisheries, including those of the southern Indian Ocean (Kiyota & Minami 2001; Huang & Liu 2010). Bycatch from longline vessels has been implicated in the population declines of several albatross populations, including the Crozet Islands' population of wandering albatross (Weimerskirch, Brothers & Jouventin 1997; Tuck *et al.* 2001; Rolland, Weimerskirch & Barbraud 2010). The number of breeding pairs of Crozet wandering albatross has shown marked changes since census records began in the 1960s. An apparent stable period in the late 1960s was followed by a dramatic reduction by the mid-1970s. While the rate of decline slowed through the 1970s and into the 1980s, the population size continued to reduce. The population then experienced a consistent recovery through the late 1980s and 1990s, before reducing yet again in the 2000s (Delord *et al.* 2008).

The successive changes in the breeding population size suggest that a complex situation with regard to fisheries–seabird interactions may exist and that modelling the population will need to account for the various overlapping fisheries and the complex foraging distribution pattern of the species. One way of doing this is to take an alternative approach to what has been done so far with seabird–fisheries modelling through an integrated population modelling framework, whereby multiple data sources are included in a single analysis. Integrated models have several advantages, among them the ability to more appropriately balance uncertainty across many data sets (Punt & Maunder 2013). While common in the assessment of fish target species, integrated assessments are less common in evaluations of non-target species or megafauna (Tuck *et al.* 2001; Francis & Sagar 2012). Albatrosses are ideally suited to such detailed modelling because long-term demographic studies exist, there are several potential sources of fishery mortality, and account can be made of the foraging distribution of all age classes, which is fundamental for long-lived and wide-ranging species such as albatrosses.

Harvesting of species, whether targeted or incidental, can exert a substantial degree of pressure on particular traits if among-individual heterogeneity exists in the population. Such heterogeneity may be behavioural, morphological or due to individual quality (Hamel *et al.* 2008; Barbraud *et al.* 2013). For example, individuals that exhibit greater aggression or bold behaviour may be more

susceptible to capture (Law 2000; Biro & Post 2008). Recently, Patrick, Charmantier & Weimerskirch (2013) showed that distinct shy and bold personality types exist and are heritable for Crozet Island wandering albatrosses. Similarly, Patrick & Weimerskirch (2014) showed that black-browed albatross *Thalassarche melanophrys* (Temminck 1828) having a bold personality foraged closer to the colony than shy birds and consequently may experience different levels of interactions with fishing vessels. Furthermore, using individual-level sightings data, Barbraud *et al.* (2013) suggested that Crozet wandering albatrosses may exhibit differential susceptibility to capture by fishing vessels. Barbraud *et al.* (2013) modelled the effect of hidden heterogeneity in behavioural types on adult survival only, which differs from our approach that integrates all observations of demographic rates and fisheries data within a dynamic population model.

The main objectives of this paper are as follows: (i) to make predictions regarding the spatial distribution of bycatch and the role of each of the fisheries in the observed population dynamics and (ii) to evaluate the potential role of individual heterogeneity in susceptibility to bycatch in explaining the population dynamics of Crozet wandering albatrosses. We construct a model that explicitly accounts for the foraging distributions of different classes of individual and includes key demographic parameters, census data and the spatiotemporal distribution of fishing effort and bycatch rates. Several different fishing fleets, termed 'super-fleets', are considered, each with different potential levels of catchability (linking fishing effort to bycatch). With the aim of explaining the time series of demographic observations for Crozet Island wandering albatross, we compare models that have different assumptions regarding fleet catchabilities, and the prevalence of heterogeneity in susceptibility to bycatch. The ability to predict the relative magnitude of bycatch by spatial area allows further consideration of fishery spatial management measures to improve conservation outcomes (Hyrenbach *et al.* 2006; Hobday *et al.* 2010), while differential susceptibility to bycatch may suggest that conservation measures need to specifically incorporate characteristic heritable traits within a species. We discuss the implications of each of these factors for the conservation and management of the population.

Materials and methods

SEABIRD DEMOGRAPHIC AND DISTRIBUTION DATA

Monitoring of wandering albatross was carried out at Possession Island (46°S, 52°E), Crozet, south-western Indian Ocean. Counts of incubating birds were made in 1960, 1968, 1969, 1975, 1976, 1977 and annually since 1981. In 1960, a capture–mark–recapture programme was undertaken between December and April and this has been repeated annually since 1966. Most rings of breeding birds were checked in January and February, just after egg-laying, and all chicks were ringed with stainless steel rings in

September and October before fledging. Capture–recapture data on ringed juveniles were used to estimate juvenile survival and recruitment probabilities, and on breeding adults to estimate adult survival, breeding and success probabilities. Demographic parameters were estimated using a multi-event mark–recapture model that considers observed breeding states (successful breeders and failed breeders), unobserved individuals during their sabbatical and also accounts for uncertainty of breeding state (Barbraud & Weimerskirch 2012). Juvenile survival to age five was estimated using a multistate mark–recapture model with two states (fledging at the nest and recruited as breeder). All tracking data were standardized, and the percentage of the total sum of time spent per square in a grid of $5^\circ \times 5^\circ$ spatial blocks was calculated for each sex and status class (juvenile, immature, adult non-breeding, incubating, brooding, rearing) (Louzao *et al.* 2011; Weimerskirch *et al.* 2014).

FISHING EFFORT DATA

Numerous longline fleets operate in the Southern Ocean and are known, or suspected, to interact with Crozet wandering albatross and other seabirds. The fleets with the greatest overlap with the foraging distribution of this population are the high seas pelagic longline fleets of Japan and Taiwan, the domestic longline fleets of South Africa, Australia and New Zealand, the demersal longline fleets within the jurisdiction of the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) (Tuck, Polacheck & Bulman 2003) and, more recently, European Union fleets targeting swordfish and fresh tuna pelagic longline fleets of Taiwan, Indonesia and Malaysia.

Monthly reported fishing effort data (numbers of hooks deployed) in $5^\circ \times 5^\circ$ spatial blocks were obtained from the Indian Ocean Tuna Commission (IOTC), the Secretariat of the Pacific Community (SPC), the International Commission for the Conservation of Atlantic Tunas (ICCAT), CCAMLR and the national fishing agencies of South Africa, New Zealand and Australia.

Noting that breeding Crozet wandering albatross mainly forage within the southern Indian Ocean, the estimated annual fishing effort south of 30°S for the Indian Ocean fleets is illustrated in Fig. 1. This shows a rapid increase in effort from 1965 by Japanese distant-water vessels largely targeting Southern Bluefin Tuna *Thunnus maccoyii* (Castelnau 1872) and a gradual increase in effort from the Taiwanese distant-water fleet from

the 1970s. While effort from the Japanese fleets reduced from 1990, the Taiwanese fleet gradually increased in effort from the 1970s. Since the 2000s, the estimated effort deployed by the fresh tuna longline fleets of Taiwan, Indonesia and Malaysia has increased markedly. This fleet is composed of smaller vessels that preserve their catch in ice or refrigerated seawater. Data for this fleet are poorer in extent and coverage than for the distant-water fleets. While the fresh tuna longline vessels are believed to predominantly operate between 10°S and 30°S , a recent substantial increase in the catch levels of albacore *Thunnus alahunga* (Bonnaterre 1788) since the early 2000s may indicate a shift to southerly latitudes (Herrera & Pierre 2012; Anon, 2013; Faizal *et al.* 2014). No effort data exist for the Indonesian or Malaysian fresh tuna longline fleets, and so broad assumptions have been necessary to estimate total hooks by month and $5^\circ \times 5^\circ$ area (Appendix S1 in Supporting Information). Despite recognizing that areas of operation may differ between national fleets, fishing effort data recorded by the IOTC from the Taiwanese fresh tuna longline fleet were used as a proxy for the spatiotemporal effort trend of the combined fleets of Taiwan, Indonesia and Malaysia.

While the Taiwanese and Japanese distant-water longline fleets are the main fleets operating in the southern Indian Ocean, those of Korea, South Africa, Spain, Portugal and France-Reunion also operate in this area. The reliability of the effort statistics from these fleets cannot be guaranteed, but given their small magnitude in comparison to the Japanese and Taiwanese fleets, they are not likely to influence model outcomes (Fig. 1).

Fishing effort of illegal, unreported and unregulated (IUU) demersal longline fleets operating in the CCAMLR region was estimated from IUU catch estimates of Patagonian toothfish *Dissostichus eleginoides* (Smitt 1898) and an annual toothfish catch rate from the regulated fishery. The spatial distribution of effort was apportioned according to the regulated fishery (Appendix S1).

BYCATCH DATA

Bycatch of wandering albatross is known to have occurred on Japanese and Taiwanese distant-water vessels (Kiyota & Minami 2001; Huang & Liu 2010). The level of seabird bycatch in the fresh tuna longline fleets is not known but could be substantial, in particular as vessels move into southerly latitudes.

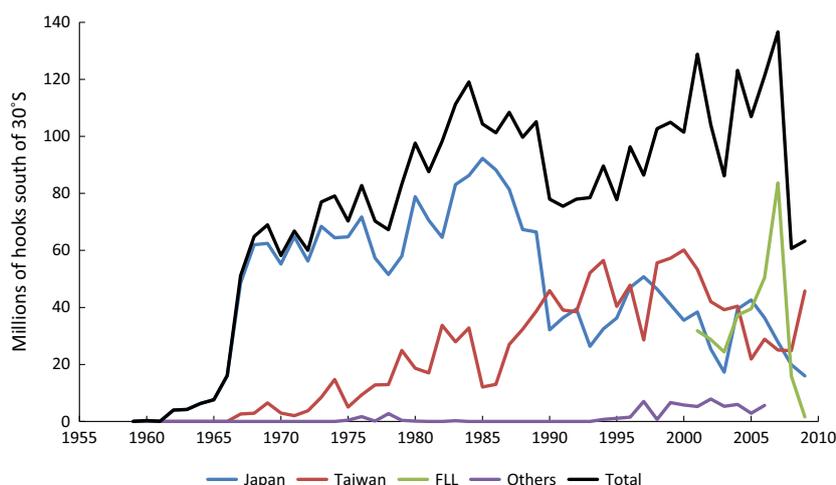


Fig. 1. The estimated number of hooks deployed by the Japanese and Taiwanese distant-water deep freezing longline fleets and the fresh tuna longline fleets (FLL) and by Korea, Spain, South Africa, Mauritius and the Seychelles (Others) within the Indian Ocean (20°E to 150°E) and south of 30°S (source: IOTC, 2011).

Published and unpublished data on observed fishery captures of wandering albatross were used to condition the model (Table S1 and Appendix S2). It is not always possible for observers to identify the species of a captured bird, so categories such as 'unknown albatross' may be present. Such captures were allocated among the remaining species categories in proportion to the observations reported for those categories. As this could introduce a bias towards more easily identified bird species, studies in which 'unknown' categories dominated were not used. Each observed bycatch figure related to a place (i.e. one or more $5^\circ \times 5^\circ$ blocks) and a time (1 month or several consecutive months) for which the model was able to calculate an estimated bycatch rate. These were compared with the observed bycatch rates using the sum of the squared differences.

POPULATION MODEL

For wandering albatross, the breeding season spans an entire year. Non-breeding birds, juveniles and immature birds forage widely across the Southern Ocean, whereas breeding birds are relatively restricted in their distributions, particularly during the incubation and brood-guard stages; females show a more northerly distribution than males during this time (Fig. S1). Failed breeders show a relatively restricted distribution that was assumed to be the same as that for incubating birds. We used time of year, sex and life stage to distinguish nine distribution patterns that we allocated to birds in each life-history category on a monthly basis (Table S2).

The population dynamics model is structured by sex and age and operates on a monthly time-scale (Fig. 2 and Appendix S2). The model 'year' begins at the start of December when birds arrive at the breeding colony. Any eggs that are laid are termed

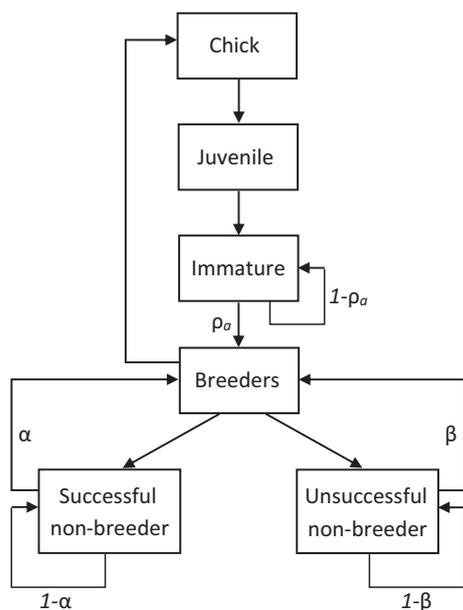


Fig. 2. Schematic representation showing the organization of bird life-history stages in the model. Chicks become juveniles at age one and immatures at age 2, which mature at rate ρ_a . After a breeding attempt, birds become non-breeders, returning to the breeding colony at rates α or β if previously successful or unsuccessful (respectively) in their breeding attempt.

'chicks' until the end of the first year, 'juveniles' until the end of the second (age one) and 'immatures' thereafter until they begin breeding and become 'adults' (breeding proportions at age are given in Appendix S2). Adult birds are further divided into four categories: during a particular breeding season, they will be active breeders, failed breeders (birds that made a breeding attempt that season) or sabbatical (deferring) birds that were either successful or unsuccessful at their previous breeding attempt the preceding year. A breeding attempt fails when either parent dies, due to natural or fishing mortality, or when the chick dies due to other natural causes.

During incubation and the brood-guard stage (December to April), one parent remains on the nest at all times so that only half the population is vulnerable to fishing mortality. During the rest of the year, all birds are considered to be, effectively, at sea at all times, except that previously successful non-breeders are assumed to spend only 80% of their time at sea, as these birds occasionally return to visit the colony.

At least some life-history traits must be pliable and able to respond to changes in population size so that populations have protection from extinction and cannot grow beyond the bounds fixed by limiting factors (such as food resources or space) for extended periods. The model developed here allows density-dependent compensation in both juvenile survival rates and breeding success (Appendix S2; Weimerskirch, Brothers & Jouventin 1997).

HETEROGENEITY IN FISHERY SUSCEPTIBILITY

Our model considers the possibility of a heterogeneous population in which some birds, for any number of reasons, are more susceptible to fisheries bycatch than others. We refer to the more and less susceptible groups as subpopulations to emphasize the assumption of heritability. The entire population is divided into two distinct hypothetical subpopulations, one with greater (or equal) susceptibility to fishing than the other. This adds two estimated parameters to the model: (i) the proportion of the population at the start of the modelling period that falls into the more susceptible subpopulation and (ii) a parameter that specifies how much more susceptible one subpopulation is to capture. These parameters are freely estimated, and if the first parameter is equal to one, there is no heterogeneity across subpopulations. The second parameter was used to modify the catchability estimates for all super-fleets. In other words, if the model estimated a 20% greater catchability for the susceptible subpopulation, then birds were 20% more susceptible to capture by every super-fleet. Once fishing commences, birds in the more susceptible subpopulation are killed at a greater rate so that the actual proportion of the population falling into that group becomes smaller every year. This assumes that susceptibility breeds true, that is if 30% of breeding adults fall into a subpopulation, then 30% of that year's chicks also fall into this category. This structure is equivalent to a genetic model that assumes a single gene with two alleles, a recessive allele for the less susceptible phenotype and a dominant one for the more susceptible phenotype, and where alleles are passed from parents to chicks in Hardy-Weinberg proportions.

FISHING MODEL

Individual fleets were collated into 'super-fleets' based on similarity in operational characteristics, including type of gear used,

target species and depth. The basic super-fleets were as follows: (i) pelagic longline (targeting tunas), (ii) demersal longline (targeting toothfish, hake, ling) and (iii) IUU demersal longline fishery operating within the CCAMLR Area. Catchability coefficients, q^f , relating population size to bycatch were estimated for each super-fleet, f , and alternative super-fleet scenarios. Trawl fleets were not included as it is generally accepted that wandering albatross bycatch by trawl is negligible. With regard to the alternative pelagic super-fleet scenarios, the southern Japanese fleet is distinguished due to its concomitant increase in operations within the Indian Ocean with the observed decline in breeding pairs. In addition, this essentially allows separate catchabilities to be estimated for the Japanese and Taiwanese distant-water fleets, as the remaining pelagic super-fleet is dominated by effort from the Taiwanese fleet. The fresh tuna longline fleets are distinguished as these fleets are less well regulated and consequently may have less mitigation and higher bycatch (compared to the regulated fleets).

Recent mitigation measures adopted by fleets will also influence estimates of bycatch. The Japanese pelagic longline fishery operating south of 30°S introduced mitigation measures in the late 1980s and early 1990s (these were voluntary until 1997). It is assumed that the Japanese fleet (part of the pelagic longline super-fleet) introduced mitigation from 1992, reducing the catchability of birds by 20%. The model was not sensitive to this choice. CCAMLR fleets introduced highly effective mitigation from 2003, and consequently, effort from these fleets after 2002 is not used in the model. The IOTC have made specific resolutions regarding mitigation, including, from 2010, the use of mitigation measures for vessels operating south of 25°S (Resolutions 10/06 and 12/06) (Anon 2012). While bycatch rates are likely to be lower in recent years as a result of these measures, the modelling period finished in 2009, before the IOTC Resolutions 10/06 and 12/06 were in place. Significant mitigation efforts by other fleets prior to 2009 are also not known and are assumed to be negligible.

In each 5° × 5° spatial block, in each month of each year, the model estimates the number of Crozet wandering albatross present, using the product of the 'at sea' spatial distributions for all categories of bird, the proportion likely to be at sea (some birds may be attending their nests) and the estimated numbers of birds in each category. The estimated bycatch for a super-fleet within a specific month and spatial block is given by the product of the number of birds present, the fishing effort and the model estimate of that super-fleet's catchability. The overall catchability is also related to the proportion of birds in each subpopulation.

PARAMETER ESTIMATION

The model estimates the numbers of albatross of each sex in each month, year and category (chick, juvenile, immature, active or failed breeding adult, non-breeding adult). Both natural and fishing-related mortality rates are modelled, as well as breeding failure due to the death of the chick or of either parent (Appendix S2). Bycatch rates at times and in regions where observer data were collected are estimated, as are the number of breeding pairs in the colony, annual breeding success, the annual adult survival rates and juvenile survival rates (to age 5). The model estimates values for a catchability parameter for each super-fleet, pre-fishing population size (carrying capacity), productivity (breeding success of the pre-fishing population) and a density-dependent parameter. Parameter values are chosen that minimize the sum of the squared residuals (SSR), where the residuals are

the differences between the model estimates and the corresponding observed bycatch rates (Table S1) and demographic time series (Table S3) (Pawitan 2001).

Model scenarios were named according to three alternative assumptions: the separation into its own distinct super-fleet of (i) the Japanese (J) southern bluefin tuna longline fleet (here defined by Japanese fishing effort deployed south of 30°S); (ii) the fresh tuna longline fleet (F); and (iii) the inclusion of two subpopulations that differ in susceptibility to bycatch (B). If any of these assumptions are not included in the model, then an 'x' is included in the model name. For example, a model with none of the aforementioned assumptions is named model xxx, and the model that uses all three is named JFB. Specifying a separate super-fleet, such as J or F, does not imply that effort data from other fleets, such as the broader pelagic super-fleet, are removed. Instead, it simply allows each super-fleet to have its own relationship between effort and consequent bycatch (through catchability).

Results

Applying the full model JFB or the model xFB led to reasonable fits to all data sources (Figs 3 and 4, Table 1). While there is some interannual variation of the observed data about the model expected values, generally the mean behaviour of the observations has been captured well (Fig. 4). The model underestimates breeding success in recent years, which might suggest that we have imperfectly captured all the drivers affecting the population during the most recent decade. The JFB and xFB models estimate that the initial proportion of birds of the susceptible subpopulation was approximately 65%. This proportion reduces rapidly until none exist after the late 1980s (Fig. 5). Distinguishing the southern Japanese fleet as a separate super-fleet (model JFB; not shown) makes little difference to the fits (Table 1), and so the more parsimonious xFB model is therefore preferred in further discussion.

Considering the xFB model in more detail, the spatial distribution of estimated bycatch across all years shows regions of high bycatch to the south-east of South Africa, with additional historical estimates of high bycatch off eastern Australia and New Zealand (Fig. 6). The estimated bycatch from the fresh tuna longline fleet is concentrated in the south-western Indian Ocean. Model xFB concludes that all bycatch can be attributed to the pelagic longline fleets, with negligible bycatch by the demersal longline fleets (Fig. 7). Estimated bycatch was greatest in the early 1970s, and declined through the 1980s, before increasing again with the advent of the fresh tuna longline fleets in the 2000s.

It is worth considering how well the model fits if assumptions regarding fleet catchabilities and behaviour are removed. Consideration of model xxx, which does not distinguish specific fleets or include heterogeneity in bycatch susceptibility, resulted in poor fits to the observed data (Fig. 3 and Table 1). The marked decline in breeding pairs between the late 1960s and early 1970s could not be

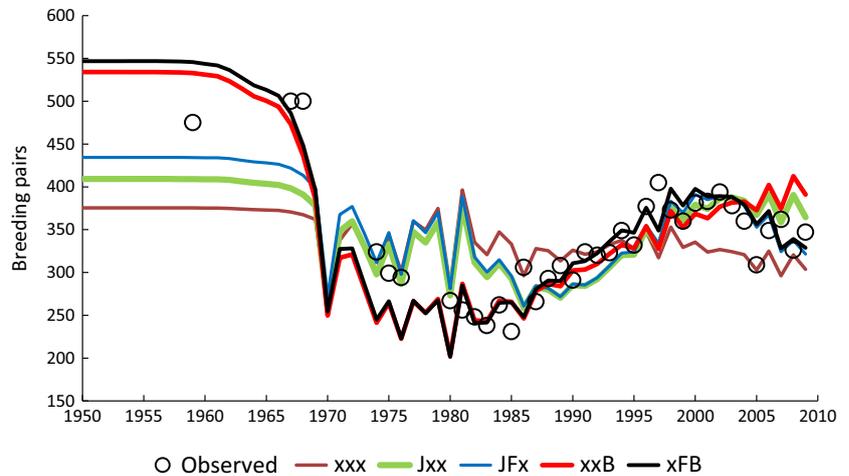


Fig. 3. The observed and predicted numbers of breeding pairs for selected model scenarios: the base model structure xxx; a separate southern Japanese (J) super-fleet (<30°S) Jxx; a separate southern Japanese super-fleet and a separate fresh tuna longline fleet (F) JFx; heterogeneity to capture (B) xxB; and a separate fresh tuna longline super-fleet and heterogeneity to capture xFB.

replicated by the model, given the distribution of effort for the super-fleets and the corresponding foraging distributions of Crozet wandering albatross. While a clear increase in fishing effort occurs from the late 1960s (Fig. 1), the continued high levels of fishing effort of the pelagic longline super-fleet through the 1980s and 1990s could not be reconciled with the recovery of the population.

Better fits to the decline in breeding pairs in the 1970s and the recovery from the 1990s were found if the southern Japanese longline fleet (model Jxx) is considered a distinct super-fleet; however, the model is unable to replicate the degree of decline in the 1980s or the decline in breeding pairs since 2000. Separating both the southern Japanese fleet and the fresh tuna longline fleet from the aggregated pelagic longline super-fleet, as distinct super-fleets, leads to a substantially improved fit to the decline in breeding pairs from 2000 (model JFx). However, the fit to the breeding pairs from the 1980s remains relatively poor.

Including subpopulations with heterogeneity in susceptibility to capture leads to substantial improvements to model-fits to all observed data (model xxB). The model is able to replicate the marked decline in breeding pairs from the late 1960s to early 1970s by estimating that a large proportion of the birds captured were from the susceptible subpopulation. This model alone, however, is not able to account for the decline in breeding pairs from 2000. Including the fresh tuna longline fleet as a separate super-fleet, in combination with heterogeneity to capture, leads to a reasonable fit to all demographic data (model xFB).

Discussion

This paper is the first to use integrated modelling to understand the possible links between seabird population dynamics, fishery incidental mortality and differential susceptibility to capture. Our model was able to successfully match demographic observations through an integrated assessment model that includes extensive data on

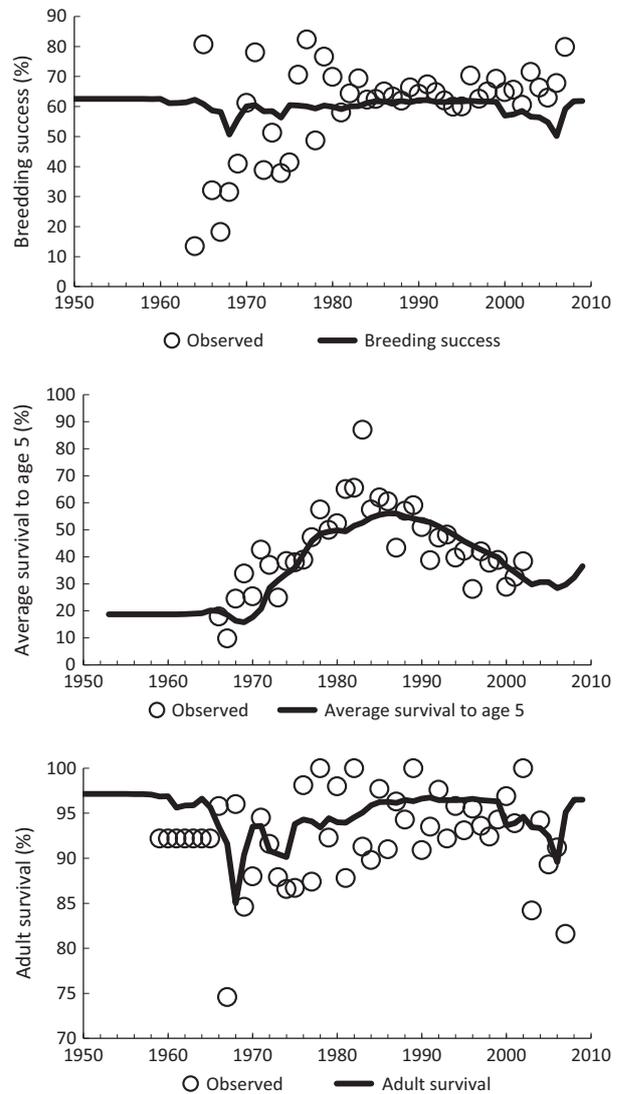


Fig. 4. The time series of model-fits (lines) to observations (circles) for the xFB model. Breeding success (top), survival to age five (middle) and adult survival (bottom).

Table 1. The parameter estimates and the weighted sum of squared residuals (SSR) for each component of the objective function and for each of the model scenarios considered: the base model structure xxx; a separate southern Japanese (J) super-fleet (<30°S) Jxx; a separate southern Japanese super-fleet and a separate fresh tuna longline fleet (F) JFx; heterogeneity to capture (B) xxB; a separate fresh tuna longline super-fleet and heterogeneity to capture xFB; and a scenario with all three model components JFB

	Model					
	xxx	Jxx	JFx	xxB	xFB	JFB
Population parameters						
Initial breeding pairs	376	409	434	534	547	547
Productivity	0.58	0.61	0.62	0.61	0.63	0.63
Juvenile density dependence	10.5	8.6	7.3	2.0	2.3	2.2
Super-fleet catchability parameters, q^f ($\times 10^{-8}$)						
Pelagic longline	3.9	1.7	1.3	2.0	1.6	1.6
Demersal longline	0	0	0	0	0	0
Japanese longline	–	10	11	–	–	1
Fresh tuna longline	–	–	9	–	12	12
IUU	0	0	0	0	0	0
Subpopulation parameters						
Initial proportion more susceptible	–	–	–	0.61	0.65	0.65
Multiplier on q^f	–	–	–	31	35	49
Sum of squared residuals						
Breeding pairs	31.3	18.7	15.9	13.1	9.3	9.4
Breeding success	47.0	43.7	45.7	38.2	40.8	40.6
Juvenile survival	20.0	15.0	16.0	7.3	6.3	6.1
Adult survival	74.1	71.1	66.7	60.7	55.6	55.9
Bycatch rate	81.1	69.4	68.8	70.9	69.3	69.3
Total SSR	253.5	217.8	213.1	190.3	181.3	181.3

wandering albatross life history and fishing effort using assumptions about fleet catchability and population heterogeneity. The paper raises several issues regarding the conservation management of the Crozet wandering albatross population, and seabird conservation in general. These include the ability to manage bycatch at reasonable spatial scales, the relative attribution of bycatch to fleets and the consequences of heritable traits that effect susceptibility to fishery mortality.

Integrated assessments that explicitly include spatiotemporal aspects of the fishing fleets and foraging distributions of the seabirds have the additional benefit of being able to estimate regions (and times) of high bycatch. This is particularly useful if managing bodies wish to include spatial elements in their mitigation regimes. Regions can be identified where seabird bycatch is predicted to be excessive (for the population as a whole or for particular key breeding stages) and provide candidate areas for high seas marine protected areas or, more simply, where increasing monitoring and mitigation within these 'hot spots' will benefit conservation outcomes (Hyrenbach *et al.* 2006). The estimated spatial distribution of bycatch

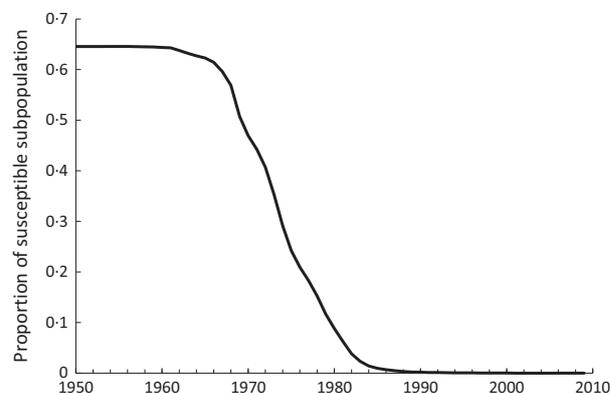


Figure 5. The estimated proportion of the population composed of the susceptible subpopulation for model xFB.

for Crozet wandering albatross shows elevated bycatch in the south-western Indian Ocean and the Tasman Sea (Fig. 6). These potentially high-risk areas could be provided additional attention by management agencies responsible for reducing the impacts of seabird–fishery interactions (Tuck *et al.* 2011; Waugh *et al.* 2012).

The justification for the changes in fleet catchability requires further discussion. Separating the southern Japanese pelagic longline fleet assumes that this fleet has a different catchability from other similar fleets. Under this model scenario, nearly all of the bycatch was attributed to the Japanese pelagic super-fleet. This implies that a Japanese vessel within the same spatiotemporal region has a substantially higher level of seabird bycatch than another vessel from a different nation, such as a Taiwanese vessel. Although Japanese and Taiwanese fleets may differ in terms of targeting behaviour and spatial regions of concentration, evidence to justify a different catchability of seabirds for what is in essence a similar industrial longline fleet is lacking. In addition, under this model scenario, fits to the numbers of breeding pairs during the 1980s were poor (Fig. 3). Allowing the fresh tuna longline fleets, a distinct catchability parameter means that these vessels could have a different bycatch rate than the other pelagic longline fleets. The resulting improvement in fit is due to the co-incident decrease in breeding pairs from 2000 with the advent of the Taiwanese fresh tuna longline (FLL) fleet (more specifically, its data being reported to and included as a separate fleet by IOTC), which was used as a proxy for all southern Indian Ocean fresh tuna longline fleets. A similar greater-estimated catchability, and improvement to the fits, could possibly have been obtained by separating other fleets, or components thereof, over the period of population decline, but the spatiotemporal effort trend would still need to fit the data. Caution should be taken when interpreting this result and attributing bycatch to this fleet, as information is sparse and no records of bycatch are available. However, it is worth noting that the fleet's move into southern waters and its likely high level of effort (given the size of

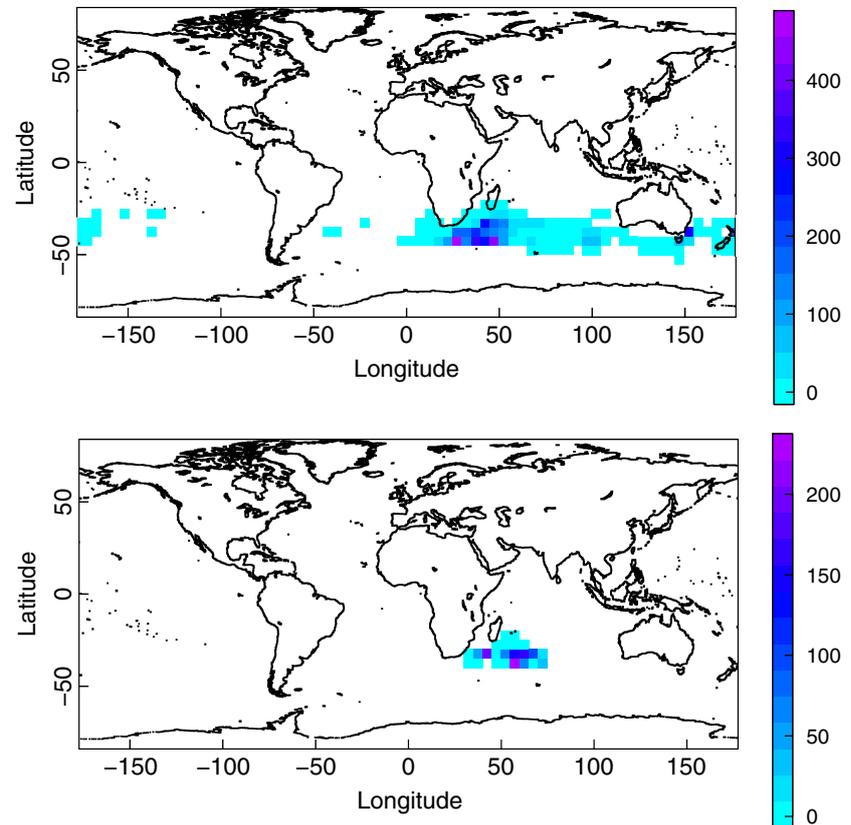


Fig. 6. Estimated bycatch in number of birds caught per spatial cell across all years for the xFB model. Top: the pelagic longline super-fleet. Bottom: the fresh tuna longline super-fleet.

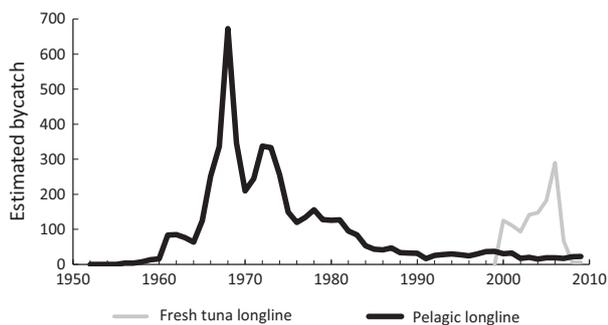


Fig. 7. The time series of model-predicted bycatch by super-fleet for the xFB model. Pelagic longline is an aggregation of all pelagic longline fleets except the Indian Ocean fresh tuna longline fleets.

its reported catch of albacore) might suggest a substantial level of seabird bycatch (Herrera & Pierre 2012).

This paper is the first to attempt to explain major changes in seabird population abundance and demographic parameters through fishing impacts on heterogeneous population traits. We have not attempted to identify the mechanism, for example whether behavioural or morphological, that may lead to differences in incidental mortality. Instead, as studies have shown heterogeneity exists in this population and individual albatross can show a propensity towards fishing vessels (Votier *et al.* 2010; Granadeiro *et al.* 2011; Patrick, Charmantier & Weimerskirch 2013), we suggest that there is an increased

likelihood of fishery-related mortality for these birds. The mechanisms driving differing susceptibility may be related to relative fishery overlap, attraction to vessels, competition at the vessel (e.g. diving ability) or perhaps ability to avoid hooks. While these traits may or may not be behavioural, the existence of different behaviour types in populations of birds has been recognized (Wilson *et al.* 1994; Drent, van Oers & Noordwijk 2003) and distinct heritable behaviours that influence susceptibility to capture may exist for Crozet wandering albatross (Patrick, Charmantier & Weimerskirch 2013). Our study encourages further exploration of the individual-level mechanisms that can lead to increased susceptibility of particular subpopulations.

Including heterogeneity in the population model through a parameter reflecting differential catchability led to substantially better model-fits than those that ignored differential susceptibility. The model was able to explain the marked decline in breeding pairs through the increased level of bycatch associated with the more susceptible category of birds, which is predicted to have been removed from the population by 1990 (Fig. 5). This is consistent with the predictions of the capture–mark–recapture model of Barbraud *et al.* (2013) that only used disaggregated adult survival. Unlike Barbraud *et al.* (2013), our study uses estimates of annual survival rates that were calculated by pooling across any heterogeneity in survival that might exist, and we explicitly include all fishery and demographic data within the population model.

To match the observed data, catchability for the more susceptible birds – roughly 35 times higher than that for less susceptible birds – was estimated. While a substantial difference in catchability, this may reflect a lower propensity for the less susceptible birds to follow vessels or to pursue baited hooks. We assumed a simple one-gene model with two alleles, with the more susceptible phenotype dominant over the other. Incomplete dominance or a more complicated genetic model involving more than one gene might not allow the rapid depletion of the more susceptible phenotype needed to match the observed data. If these assumptions are not reasonable, then other factors that could lead to the rapid decline in breeding pairs in the early 1970s need to be considered. For example, changes in fishing practices may have caused catchability to markedly decline from the 1960s to the 1980s. Alternatively, there may be a fleet or component thereof that has had a substantial impact on the population, particularly prior to 1990, but whose data are missing from fishing agency data bases. However, statistics from the tuna long-line fleets were obtained from each of the major Southern Ocean tuna regional fisheries management organisations (RFMOs), and the dominant fleets over the late 1960–1970s were those of the Japanese and, later, the Taiwanese distant-water fleets. Fishing effort data from these nations are generally considered comprehensive (Tuck, Polacheck & Bulman 2003).

The potential extirpation of the more susceptible subpopulation clearly leads to questions about evolutionary responses to its removal, namely whether the remaining less susceptible birds remain so, or become more susceptible (Patrick, Charmantier & Weimerskirch 2013). In addition, further refinements to the model should examine the assumption that the population can be considered a continuum from more to less susceptible, as opposed to being split into two distinct subpopulations. The evolutionary and population-level significance of removing the more susceptible phenotype from the population requires further exploration. Barbraud *et al.* (2013) showed that the remaining non-attracted birds have a lower generation time than the attracted birds and the population as a whole. This has implications for the ability and time for the population to recover from major unsustainable mortality. Barbraud *et al.* (2013) argue that removal of birds susceptible to fishing mortality may have allowed the severely depleted population of Amsterdam Albatross *Diomedea amsterdamensis* to recover, even though their foraging overlap with longline fisheries has remained high (Thiebot *et al.* 2014).

This paper has highlighted the potential for integrated models to improve our understanding of the impact of fisheries on seabird populations when a good knowledge of the dynamics and distribution of the population and fisheries exist. It also stresses that management bodies need to consider the possibility that, without adequate mitigation measures that prevent bycatch across phenotypes, additional fishing pressure may be forcing changes to the

genetic constituency of bycatch species. The consequent removal of individuals with susceptible behaviours could have substantial implications for the affected populations (such as slower intrinsic reproductive rates) and these should be considered in their management. Without properly accounting for heterogeneity within incidentally caught populations, sustainable fishery objectives and conservation goals may be compromised.

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Data accessibility

Publicly available fishery effort data are listed here: DRYAD entry: doi: 10.5061/dryad.7f63m (Tuck *et al.* 2015). Data that are not publicly available can be requested through the various agency data managers via the following web-links: New Zealand (www.mpi.govt.nz/); Australia (www.afma.gov.au/); CCAMLR (www.ccamlr.org/); SPC (www.spc.int/oceanfish/) Seabird foraging distribution data (H. Weimerskirch, CNRS-CEBC).

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Supporting Information

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

Appendix S1. Fishing fleets of the Southern Indian Ocean.

Appendix S2. The model of albatross population dynamics.

Table S1. Observations of wandering albatross bycatch rates.

Table S2. The 'at sea' distribution patterns according to month and breeding stage.

Table S3. The time series of demographic data for Crozet wandering albatross.

Figure S1. Utility distributions for Crozet wandering albatross.