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Modelling work on Crozet wandering albatrosses and impact of longline fisheries in the IOTC zone

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Abstract

This paper presents a population assessment for Crozet wandering albatross using data to 2009. An age, sex, life-stage and spatially structured model is described that is conditioned upon breeding population size, breeding success, adult and juvenile survival rates and observed bycatch rate data. The model includes comprehensive data on the spatial and temporal distributions of fishing effort and foraging distributions to estimate temporal overlaps, fishery catchability and consequent bycatch. Results show that the model was not able to replicate the observed data without making some broad assumptions about seabird catchability from the pelagic longline fleets and seabird behaviour. Namely, the rapid decline in breeding pairs observed between the late 1960s and the early 1970s could not be explained without assuming that either (i) the southern Japanese pelagic longline fleet had a substantially higher rate of capture than other fleets, or (ii) that a distinct seabird behaviour exists that leads to an increased susceptibility to capture (shy-bold behavioural types). In addition, the more recent decline in breeding pairs (from the late 1990s) was not able to be explained without assuming that the Indian Ocean Taiwanese fresh longline fleet has a greater rate of capture in comparison with other pelagic longline fleets (including that of the Taiwanese deep freezing fleet). These assumptions should be given due consideration and debate in terms of their feasibility. The results may reflect a lack of comprehensive effort statistics for the pelagic longline fleets (and in particular the Taiwanese fresh longline fleet). Given the paucity of data to support some of the assumptions made during model development, caution should be taken when interpreting the results.

1. Introduction

Incidental mortality of oceanic seabirds is recognised as a key issue of conservation concern for many populations and sub-populations of seabirds throughout the world. Currently 17 of 22 albatrosses are listed as threatened or endangered, with the principal identified threat being mortality associated with fishing operations (Weimerskirch and Jouventin, 1987; Gales, 1993; Weimerskirch et al., 1997; Baker et al., 2002). Large scale oceanic pelagic longlining targetting tunas and billfish began in the 1950s and rapidly spread from south-east Asia, to equatorial latitudes and then to the Southern Ocean by the late 1960s (Tuck et al., 2003). The widespread foraging behaviour of seabirds, and albatrosses in particular, as well as their propensity to be attracted to the baited hooks and offal discarded by vessels on the high seas, can lead to fatal interactions (Weimerskirch et al., 1997; Croxall and Gales, 1998). In addition, breeding birds are susceptible to interactions with demersal longline and trawl vessels targeting continental slope and shelf fish species such as Patagonian toothfish *Dissostichus eleginoides*, ling *Genypterus blacodes* and hake *Merluccius sp* (Croxall and Prince, 1996; Favero et al., 2003).

The number of breeding pairs of Crozet wandering albatross have shown marked changes in size since census data began in the 1960s (Delord et al. 2008). An apparent stable period of around 500 breeding pairs in the late 1960s was followed by a dramatic reduction to less than 300 pairs by the mid 1970s. While the rate of decline slowed through the 1970s and into the 1980s, the population size continued to reduce, reaching 231 breeding pairs in 1985. The population then experienced a consistent recovery through the late 1980s and 1990s, to be over 400 pairs by 1997. However since then the population size has reduced yet again (Delord et al. 2008). Wandering albatross are known to be caught by industrial pelagic longline fisheries, including those of the southern Indian Ocean (Kiyota and Minami, 2001; Huang et al. 2010). Bycatch from longline vessels has been implicated in the population declines of several albatross populations, including the Crozet Islands population of wandering albatross (Gales, 1993; Weimerskirch et al. 1997; Tuck et al., 2001; Tuck, 2004; Rolland et al. 2010). Crozet wandering albatross were recently categorised as a 'High Priority' population in an Ecological Risk Assessment for Indian Ocean seabirds (Baker and Wanless, 2010). Their susceptibility to incidental capture by tuna longline fisheries was considered high as was their overlap with longline vessels fishing in the Indian Ocean.

2. Materials and Methods

2.1 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 program was undertaken (annually since 1966) between December and April. Most rings of breeding birds were checked in January and February (3-4 visits per nest), just after egg-laying, and all chicks were ringed with stainless steel rings in September and October before fledging. At fledging, breeding performance was determined. Adults were sexed from plumage characteristics and size. We used data on ringed juveniles to estimate juvenile survival and recruitment probabilities, and on breeding adults to estimate adult survival, breeding and success probabilities. Demographic parameters used in the population model (see below) were estimated as in Barbraud and Weimerskirch (2011).

Breeders of known age and sex were tracked at Crozet during incubation, brooding, and chick rearing from 1989 to 2010. Distribution data for breeders (both sexes) during incubation, brooding and chick-rearing were obtained from Argos PTT Satellite Transmitters data from 1989 to 2003, resampled global positioning system (GPS) data from 2002-2005, Argos/GPS data from 2008, and resampled GPS data from 2010. This yielded a total of 289 foraging trips (incubation: 81 male trips, 76 female trips; brooding: 49 male trips, 36 female trips; chick rearing: 38 male trips, 9 females trips). Distribution data for juvenile and immature individuals were obtained using Argos data (13 juvenile individuals and 11 immature individuals) from 2007 to 2010. Data filtering and resampling procedures are detailed elsewhere (Louzao et al. 2011). Adult non breeders were tracked using global location sensing (geolocator, GLS) tags from 2007 to 2010. All tracking data were standardized and the percentage of the total sum of time spent per square in a grid of 5 by 5 degree spatial blocks was calculated for each sex and status class (juvenile, immature, adult non breeding, incubating, brooding, rearing).

2.2 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 and the demersal longline fleets within the jurisdiction of CCAMLR (Tuck et al., 2003).

Monthly reported fishing effort data (numbers of hooks deployed) in 5 by 5 degree spatial blocks were obtained from the Indian Ocean Tuna Commission (IOTC), the Secretariat of the Pacific Community (SPC), The Commission for the Conservation of Atlantic Tunas (ICCAT), CCAMLR and the national fishing agencies of South Africa and Australia. Although the bulk of the effort data used in this study were complete, in some cases, data were clearly missing. For example, effort statistics could be missing from (i) the initial, or the most recent years, of the fishery, or (ii) the spatial and/or temporal database fields. In these circumstances, auxiliary information was used to fill in the gaps; this included catch, catch rate or numbers of vessels, or the relative spatio-temporal spread of effort from neighbouring years and months. In most cases this gap filling did not involve a substantial addition to the dataset (although, see below). In all cases, attempts were made to match known general trends in catch and/or effort for the fisheries (Tuck et al., 2003; Tuck and Thomson, 2009).

The Indian Ocean pelagic longline fleets.

This section focuses on the Indian Ocean fleets due to their relevance to the management of tunas and seabirds for the IOTC, and the fact that the Crozet wandering albatross population breeds in the southern Indian Ocean and their breeding foraging range is contained within the Indian Ocean. All fishing effort data displayed has been obtained and adapted from the IOTC public web site.

Taiwan distant water longline fleet

Deep freezing Taiwanese longliners are large (between 30m and 55m) stainless steel hulled vessels that deep freeze their catch. Numbers of hooks per set are between 2000 and 3000 with trips of 3 months or longer in duration. Target stocks include yellowfin (surface set), bigeye (deep set) or swordfish (night set). Catches are generally trans-shipped (M. Herrera pers. com.). The southern Indian Ocean Taiwanese distant water fleet largely operates between 30 and 40S and in the central southern Indian Ocean (Figure 1; Tuck et al., 2003; Huang and Liu, 2010). The magnitude of effort south of 30S gradually increased from the early 1970s reaching a peak of 60 million hooks in 2000. Reported effort to IOTC has since declined to approximately 25 million hooks between 2005 and 2008. Total hooks were estimated by scaling the reported number of hooks (to IOTC) from the logbook (monthly 5 degree catch and effort data) by the ratio of the annual total reported nominal catch (landings) for the four dominant catch species (bigeye, yellowfin, albacore and swordfish) to the logbook catches for these species (Tuck, 2004; Anon., 2007; Tuck and Thomson, 2009).

Huang et al. (2010) report that the Taiwanese tuna longline fleet operating in the southern Indian Ocean between 2004 and 2008 was estimated to have caught between 19 and 50 wandering albatross per year. The estimated bycatch of unidentified albatrosses, which could include wandering albatross, ranged between 96 and 251 birds per year.

Taiwan fresh tuna longline fleet

Taiwanese fresh tuna longliners (FLL) are composed of small (15m to 30m and <200GT) vessels that preserve their catch in ice or refrigerated sea-water. Longline sets are between 800-1600 hooks. They mostly target yellowfin and albacore tunas using surface longlines. Trips are reported to be less than one month in duration (M. Herrera, pers. comm.). Data for this fleet are poorer in extent and coverage than for the Taiwanese deep freezing fleet. Improvements to the collection of data for this fleet are expected from 2010 (Anon., 2010).

Broad assumptions have been necessary to estimate total hooks by month and 5 degree area for this fleet (Figure 2). Statistical reporting of nominal catches begins in 2001 and coverage varies between 5% and 16% (between 2007 and 2009). No catch and effort statistics at a monthly 5 degree level are available prior to 2007. The average coverage for years 2007 to 2009 was used to estimate total catches from 2001 to 2006 (Figure 2). The spatio-temporal distribution reported for 2007 was assumed for years 2001 to 2006. While predominantly an equatorial fishery, the main southern area of operation (from IOTC catch and effort statistics) was between 30-35S and 55-65E. This distance from port suggests these vessels can be at sea for extended periods of time. The fleet catches a substantial quantity of fish, with an average nominal catch of 27.5kt of the main tuna species (bigeye, yellowfin, albacore and swordfish) over 2007 to 2009, compared to 42kt over the same period from the deep freezing fleet. It is also likely that this fleet operated prior to 2001 but the magnitude of effort is unknown. Estimated hooks vary between 30 and 80 million hooks until 2007 and have since reduced. However, this reduction may be due to inconsistent or incomplete reporting, with effort perhaps moving from being reported in the fresh longline fleet to the deep-freezing fleet (see 2009 effort in Figures 1 and 2).

The level of seabird bycatch in this fleet is not known but could be substantial, as vessels move into southerly latitudes targeting albacore. The use of surface longlines in targeting yellowfin may also lead to high seabird bycatch. Information on the use of mitigation measures for this fleet was unavailable.

Japanese distant-water longline fleet

Effort deployed by the Japanese distant water longline fleet increased in magnitude within the southern Indian Ocean (south of 30S) in the late 1960s, reaching a peak of over 90 million hooks in 1985 before declining in the early 1990s to between 30 to 40 million hooks. Recent reported effort south of 30S is less than 20 million hooks. Effort is concentrated in more southerly latitudes (targeting southern bluefin tuna) than the Taiwanese fleet and to the western and eastern regions of the southern Indian Ocean (Figure 3). Japanese catch and effort statistics reported to the IOTC were not scaled to the nominal catch as they are believed to be comprehensive.

Wandering albatross are known to be caught by Japanese longline vessels (Kiyota and Itoh, 2007), and within southern Indian Ocean waters (Kiyota and Minami, 2001). The Japanese pelagic longline fishery operating south of 30S introduced mitigation measures in the late 1980s and early 1990s (these were voluntary until 1997) (Tuck et al., 2003). Kiyota and Takeuchi (2005) state that the use of tori-pole streamers can reduce bycatch to approximately 30% and their use on Japanese vessels is likely to have reduced seabird bycatch since 1996. Since 1996 seabird bycatch in the southern Indian Ocean is estimated to have varied between 0 birds per 1000 hooks in 2005 (with very low observer coverage) and 0.365 in 1999.

Other fleets of the southern Indian Ocean

While the Taiwanese and Japanese distant water longline fleets are the main fleets operating in the southern Indian Ocean, the fleets of Korea, South Africa, and the territories of France also operate in this area (Figure 4). The combined magnitude of effort south of 30S is substantially less than that of the Taiwanese and Japanese fleets. Reported effort from the IOTC catch and effort statistics have been raised according to the ratio of landings to logbook catches. The reliability of these effort statistics cannot be guaranteed, but given their small magnitude in comparison to the Japanese and Taiwanese fleets, they are not likely to be influential to the model outcomes.

2.3 Bycatch data

Published and unpublished data on observed fishery captures of wandering albatross were used to condition the model (Table 1). It is not always possible for observers to identify the species of a captured bird so categories such as `unknown albatross' may be presented. 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 such `unknown' categories dominated, were not used. The observed bycatch rates were treated in the same way as the time series of demographic data (e.g. breeding pairs) in that analogous estimates were calculated, and parameter values found that minimised the sum of the squared differences between these observed and estimated quantities. For each bycatch rate observation, the corresponding model estimate was the expected bycatch rates for all Crozet birds over a set of 5 by 5 degree blocks corresponding as closely as possible to the spatial coverage of the observer study, and during the same period of months or years.

Not all wandering albatross nest on Possession Island, notable colonies occur elsewhere in the Crozet Group, on Kerguelen, South Georgia and on Marion and Prince Edward Islands. From Nel et al (2002) it appears that there is a complete overlap between the at-sea distributions of Marion Island and Possession Island birds. Given geographic location and very similar population trajectories (Nel et al., 2002) it seems reasonable to assume similar at-sea distributions for Marion, Prince Edward, and Possession Island birds. Similarly, the observed latitudinal ranges for Kerguelen and Crozet show a strong overlap (Louzao et al. 2011; H. Weimerskirch unpublished data). Tracking data and demographic data are available for South Georgia wandering albatross, allowing application of our model to that population in order to calculate the numbers of South Georgia birds present in the area and at the time that each published bycatch observation was made (Thomson et al., 2011). By scaling the corresponding number of birds from Possession Island to those from other colonies assumed to have the same at-sea distribution (Table 2), and using the South Georgia estimates, we were able to calculate, for each bycatch rate observation, the proportion of the bycatch of wandering albatross likely to belong to the Possession Island population.

2.4 Population model

For wandering albatross the breeding season spans an entire year. Non-breeding birds, juveniles and immatures 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 (Figure 5). 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 distinct distribution patterns (Table 3) which we allocated to birds in each life history category on a monthly basis.

The population dynamics model is sex- and age-structured and operates on a monthly time step (Figure 6). The model ‘year’ begins at the start of December when birds arrive at the breeding colony. Any eggs that are laid are termed ‘chicks’ until the end of the first year, ‘juveniles’ until the end of the second (age 1) and immatures thereafter until they begin breeding and become ‘adults’. Adult birds are further divided into 5 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. A breeding attempt fails when either parent dies, due to natural or fishing mortality, or when the chick dies due to other natural causes.

Figure 6 shows the modelling process graphically: chicks N^0_y hatched in year *y* become juveniles $N^J_{g,a,y,m}$ (half assigned to each gender *g*) of age *a*=1 in month *m*=1 at the start of the following year. Juveniles become breeding adults $N^{bx}_{g,a,y,m}$ at age-specific annual rate λ. After a breeding attempt, individuals move into a non-breeding category according to whether their breeding attempt was successful or failed. Previously successful non-breeding birds $N^{ns}_{g,a,y,m}$ return to the breeding population at rate α and failed non-breeders $N^{nf}_{g,a,y,m}$ at rate β.

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, a substantial proportion of birds returning occasionally 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 some protection from extinction and cannot grow beyond the bounds fixed by limiting factors (such as food resources or space) for extended periods (Gedamke, 2007). This density dependent compensation also allows populations to stabilize, albeit at lower population sizes, when moderate levels of increased mortality (e.g. due to fisheries bycatch) occur. Tuck et al. (2004) found that the wandering albatross colony on Possession Island showed density dependent compensation in both juvenile survival rates and breeding success (Croxall et al., 1998; Weimerskirch et al. 1997), the ecological basis for which might be a decrease in the intra-specific competition for resources (food for example) amongst juveniles and adults foraging for their chicks (Weimerskirch, 1992). Our model also allows for both forms of density dependence.

A technical description of the model is given by Thomson et al. (2011). The implementation used here differs slightly in that for the black-browed albatross modelled by Thomson et al. (2011), the breeding season lasts only nine months, a separate immature category was not recognised, and return rates were not available on an annual basis.

Shy-bold behaviour types

A more important departure from the model of Thomson et al. (2011) is that we considered the possibility of a heterogeneous population in which some birds were behaviourally more susceptible to fisheries bycatch than others (an inheritable trait) (Wilson et al. 1994). Several studies have shown that animals (including birds) can exhibit different personality traits that have a strong influence on the survival of an individual and consequently a population's fitness (Frost et al., 2007). Referred to as the shy-bold continuum or degree of boldness, these traits express themselves in 'bold' individuals as more aggressive, risk taking, active, and they have a more rapid learning rate than 'shy' individuals (Wilson et al., 1993; Sneddon, 2003). The varying degree of aggressive behaviour exhibited by albatrosses when attempting to remove baits from longline hooks, and the mortality associated with swallowing a baited hook, could lead to substantial evolutionary pressure on a 'bold' personality type in the population. However, as no documented evidence has been found in the literature to support this type of behaviour in seabirds, due caution should be taken when interpreting the results of this paper.

To model the shy-bold behaviour, the population is divided into two reproductively distinct subpopulations, one with greater susceptibility to fishing than the other. This introduced two new parameters to the model: the proportion of the unfished population at the start of the modelling period that fell into the more susceptible category, and the degree to which the catchability parameter for this subpopulation differed from those (one for each super-fleet) of the other. This parameter was constrained so that catchability for the more susceptible population could only be equal to or greater than those estimated for the other subpopulation. This single parameter was used to modify the catchability estimates for all super-fleets. In other words, if the model estimated a 20% greater susceptibility, then birds were 20% more susceptible to capture by each super-fleet. Once fishing commenced, birds in the more susceptible subpopulation were killed at a greater rate so that the actual proportion of the population falling into that group was smaller every year.

2.5 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 super-fleets were (i) pelagic longline (targeting tunas and swordfish), (ii) demersal longline (targeting toothfish, hake, ling), (iii) IUU demersal longline fishery operating within the CCAMLR Area. Catchability coefficients were estimated for each of these super-fleets. Trawl fleets were not included as it is general accepted that wandering albatross bycatch by trawl is negligible.

In each 5 by 5 degree 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 each super-fleet is given by the product of the number of birds present, the fishing effort for that month and spatial block for a particular super-fleet *f*, and a model estimated parameter representing the super-fleet's catchability q_f. For each of the observed bycatch rates collected from the literature, the model estimates a bycatch rate for the study area (matched as closely as possible by one of more 5 by 5 degree spatial blocks) over the years and months during which the data were collected, for the observed super-fleet.

The Japanese pelagic longline fishery operating south of 30^{o}S introduced mitigation measures in the late 1980s and early 1990s (these were voluntary until 1997, Tuck et al 2003). We assume that this fleet (part of the pelagic longline super-fleet) introduced mitigation from 1992, reducing the catchability of birds by 20% (results were not overly sensitive to variations to this parameter; not shown). The model was not found to be sensitive to this choice (see Results). CCAMLR fleets introduced highly effective mitigation from 2003 (Tuck and Thomson, 2009) and consequently effort from these fleets after 2002 is not used in the model. Significant mitigatory efforts by other fleets prior to the end of the modelling period in 2009, is not known and is therefore assumed to be negligible.

2.6 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. 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, overall population size, productivity, and a density dependence parameter that minimises the sum of the squared differences between these model estimates and corresponding observed bycatch rates (Table 1) and demographic time series collected on Possession Island, Crozet (Table 4).

An adult natural mortality rate of M=0.029 was assumed, reflecting the highest adult survival rate for Amsterdam Island albatross, a closely related species that is thought to be little impacted by human activities (Rivalan et al. 2010).

Wandering albatross are biennial breeders, on average, birds return to the breeding colony at rate of α=0.797 per annum from the second year after a successful breeding attempt, or β=0.979 if unsuccessful (Barbraud and Weimerskirch, 2011). Return rates vary from year to year, probably as a function of food availability. For most of the years included in this model, it was possible to calculate that year's return rate (Table 4); otherwise the average values were used. Most Crozet wandering albatross first attempt breeding between 8 and 11 years of age although breeding could begin as early as 4 or as late as 25 years old.

Density dependence was incorporated into either through the chick natural mortality rate (and therefore breeding success) or through the juveniles natural mortality rate. Both were non-linear functions relating the size of the breeding population to natural mortality rates (Tuck et al., 2001; Thomson et al., 2011).

3. Results

Our first attempt to apply the model resulted in particularly poor fits to the observed data (Figure 7; denoted model xxx). The marked decline in breeding pairs between the late 1960s and early 1970s could not be 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 (Figure 1 and Figure 3), with the main impacting super-fleet being the pelagic longline fleet (and those of Japan and Taiwan), the continued increase in fishing effort of the pelagic longline super-fleet through the 1980s and 1990s could not be reconciled with the recovery of the population.

Alternative model structures for the super-fleets were considered in order to improve model fits to the observed data (Figure 7 and Figure 8). The Japanese (J) southern bluefin tuna longline fleet (here defined by Japanese fishing effort deployed south of 30S) and the Taiwanese fresh tuna longline fleet (F) were defined as separate super-fleets. The resulting fits are an improvement over the original model (model xxx). Including the southern Japanese fleet leads to a better fit to the decline in breeding pairs in the 1970s and the recovery from the 1990s; however, the model is not able to replicate the degree of decline in the 1980s or the decline in breeding pairs since 2000 (Figure 7; model Jxx). Separating both the southern Japanese fleet and the Taiwanese fresh 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 (Figure 7; model JFx). However, the fit to the 1980s breeding pairs remains relatively poor.

Including the assumption that a proportion of the population is more susceptible to capture leads to substantial improvements to model fits to all observed data (Figure 8; model xxB). The model estimates that the initial proportion of birds of the 'bold' behaviour-type was approximately 65%. 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 of the bold behaviour type. The proportion of birds of this behaviour type reduces rapidly until none exist after approximately 1990 (Figure 9). This model alone however, is not able to account for the decline in breeding pairs from 2000. Including the Taiwanese fresh longline fleet as a separate super-fleet leads to a reasonable fit to all data sources (in combination with the shy-bold scenario) (Figure 8; model xFB). Likewise, including the southern Japanese super-fleet (with the Taiwanese fresh longline super-fleet and the shy-bold behaviour scenario) leads to fits to the data that are indistinguishable from those without this super-fleet (Figure 8; model JFB). Considering model xFB 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 (Figure 10). The estimated bycatch from the Taiwanese fresh longline fleet is concentrated in the south western Indian Ocean (Figure 10). The fits to observations of breeding success, numbers fledged, survival to age 5 and adult survival are good (Figure 11). The model (xFB) estimates that all bycatch can be attributed to the pelagic longline fleets (the aggregated pelagic super-fleet and the Taiwanese fresh longline fleet), with negligible bycatch by the demersal longline fleets (Figure 12). Estimated bycatch was greatest in the early 1970s, declined through the 1980s, before increasing again with the advent of the Taiwanese fresh longline fleet in the 2000s (Figure 12).

4. Discussion

This work raises several issues regarding the conservation management of the Crozet wandering albatross population, and seabird conservation in general, within the Indian Ocean and other oceanic regions. There is clearly a co-incident decline in the size of the Crozet wandering albatross population with an increase in reported levels of longline fishing effort within the southern Indian Ocean (Figure 1,Figure 3,Figure 7 and Figure 8). Attempts to explain the demographic observations through a population model that includes extensive data on wandering albatross dynamics and fishing effort from the Indian, Atlantic and Pacific Oceans was not successful without making additional assumptions about fleet catchability and population behaviour. In particular, extricating the southern Japanese pelagic longline fleet and the Taiwanese fresh longline fleets and including them as separate super-fleets markedly improved fits to the data. However, the justification for this needs further discussion and exploration. By separating the southern Japanese pelagic longline fleet, it is assumed that this fleet has a different catchability from other similar fleets (namely the Taiwanese longline fleet). Although these fleets may behave differently in terms of their targeting behaviour and spatial regions of concentration, evidence to justify a different catchability of seabirds for what is in essence a similar industrial distant-water longline fleet is lacking. The separation of fleets would imply that a Japanese vessel within the same spatio-temporal block would have a substantially different (and higher) level of seabird bycatch than another vessel from a different nation. Similarly, separating the Taiwanese fresh longline fleet into a super-fleet implies that these vessels have a markedly higher bycatch rate than other pelagic longline fleets. The substantial improvement in fit when this fleet is included as a super-fleet is largely due to the co-incident decrease in breeding pairs from 2000 with the advent of the Taiwanese FLL fleet (or more specifically, its data being reported to IOTC). Information on this fleet (catch and effort data) is sparse and no records of bycatch were found. However, the fleets' move into southern waters and its likely high level of effort (given the size of its reported catch of tunas and billfish) might suggest a substantial level of seabird bycatch is possible. It should be noted that a similar increased estimated catchability (and improvement to the fits) could possibly have been obtained by separating other fleets, or components thereof, over the periods of population decline (but the spatio-temporal effort trend would still need to 'fit' the data).

This paper is the first to attempt to explain major changes in population size through differential fishing impacts on specific population phenotypes. The existence of shy-bold behaviour types in populations of birds has been recognised in other studies (Wilson et al., 1994; Drent et al., 2003; Sirot, 2007). The possibility that distinct heritable behaviours exist for seabirds that influence susceptibility of capture should not be discounted. Further research into this behaviour should be conducted. In the present case, including this behaviour in the population model and estimating its initial proportion and change through time led to substantial improvements to model fits. The model was able to explain the marked decline in breeding pairs through the increased level of bycatch associated with the bold behaviour type. This behaviour type is predicted to have been removed from the population by 1990, with only shy type birds remaining (Figure 9). This clearly leads to questions about evolutionary responses to the removal of the bold behaviour type, namely whether the remaining shy birds remain 'shy' or (a proportion) adopt a bolder personality when competing for bait on longline hooks. In addition, the assumption that the population can be split into 2 distinct behaviour types, as opposed to a continuum from shy to bold behaviour types, is worth further exploration.

Projections of the Crozet wandering albatross population into the future under different scenarios regarding levels of fishing effort are not shown in this paper. Projections would provide some indication of the likely population responses under current and alternative future fishing effort scenarios. However, even in the absence of predictions of future population size, it is clearly of some concern that the number of breeding pairs has shown a consistent declining trend since 1997.

Management implications for the IOTC

The main points that arise from this paper and that require further discussion are:

1) Is it reasonable to assume that the southern Japanese pelagic longline fleet has a different (and substantially greater) catchability of seabirds than other similar pelagic longline fleets (do they and have they historically used different bait, gear, or other operational mechanisms that might lead to a high rate of bycatch)?
2) Is it reasonable to assume that the Taiwanese fresh longline (FLL) fleet has a different catchability of seabirds to other pelagic longline fleets (including that of the Taiwanese deep freezing fleet)?
3) Are the assumptions that have been made in this paper regarding the estimation of fishing effort from the Taiwanese FLL fleet reasonable?
4) Do data exist, or can assumptions be made, regarding fishing effort from the Taiwanese FLL fleet prior to 2001?
5) Given the historical lack of catch and effort statistics from the Taiwanese FLL fleet, what is the current level of reporting (coverage) for this fleet?
6) Do observations of bycatch for the Taiwanese FLL fleet (and other high seas fleets) exist that can be incorporated into the model and used to facilitate management decisions regarding seabird bycatch in the Indian Ocean?
7) What is the current understanding of use of mitigating devices by the Taiwanese FLL fleet?
8) Is it reasonable to assume that a shy-bold behaviour type exists (or existed) in wandering albatross or other large seabirds? Has there been research on seabirds that considers different levels of aggressiveness (bold behaviour) at the hook?
9) If the assumptions regarding changes in catchability and behaviour type are not reasonable, then (i) what other factor could have lead to the rapid decline in breeding pairs in the early 1970s (eg a missing fleet or component thereof; other population dynamic effects) and (ii) what other factors could be influencing the recent decline in breeding pairs (missing fleet, climate change)?

5. Acknowledgments

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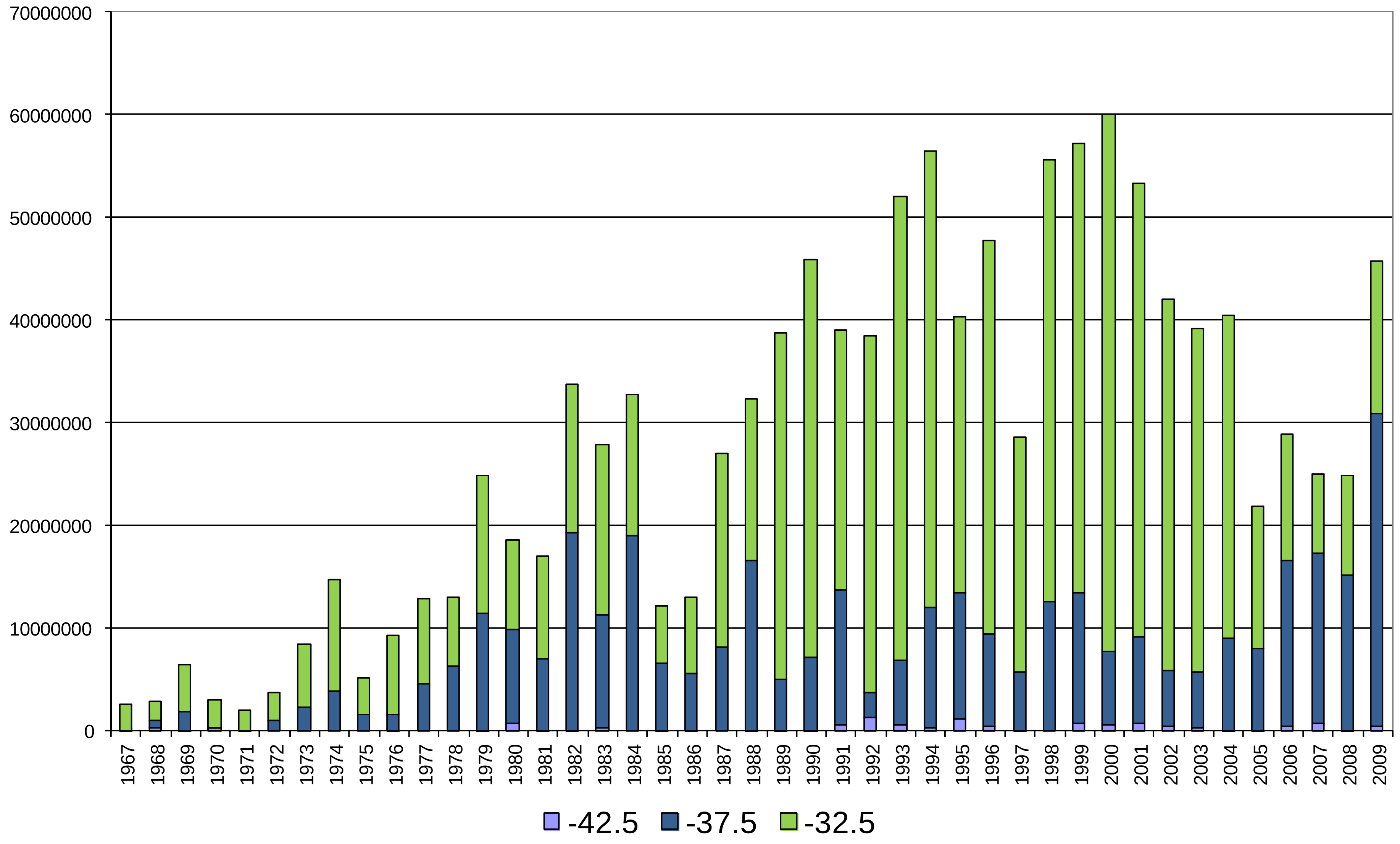


Figure 1 The estimated number of hooks deployed by the Taiwanese distant water longline fleet within the Indian Ocean (20E to 150E) south of 30S by 5 degree latitude bands centred on 32.5S, 37.5S and 42.5S.

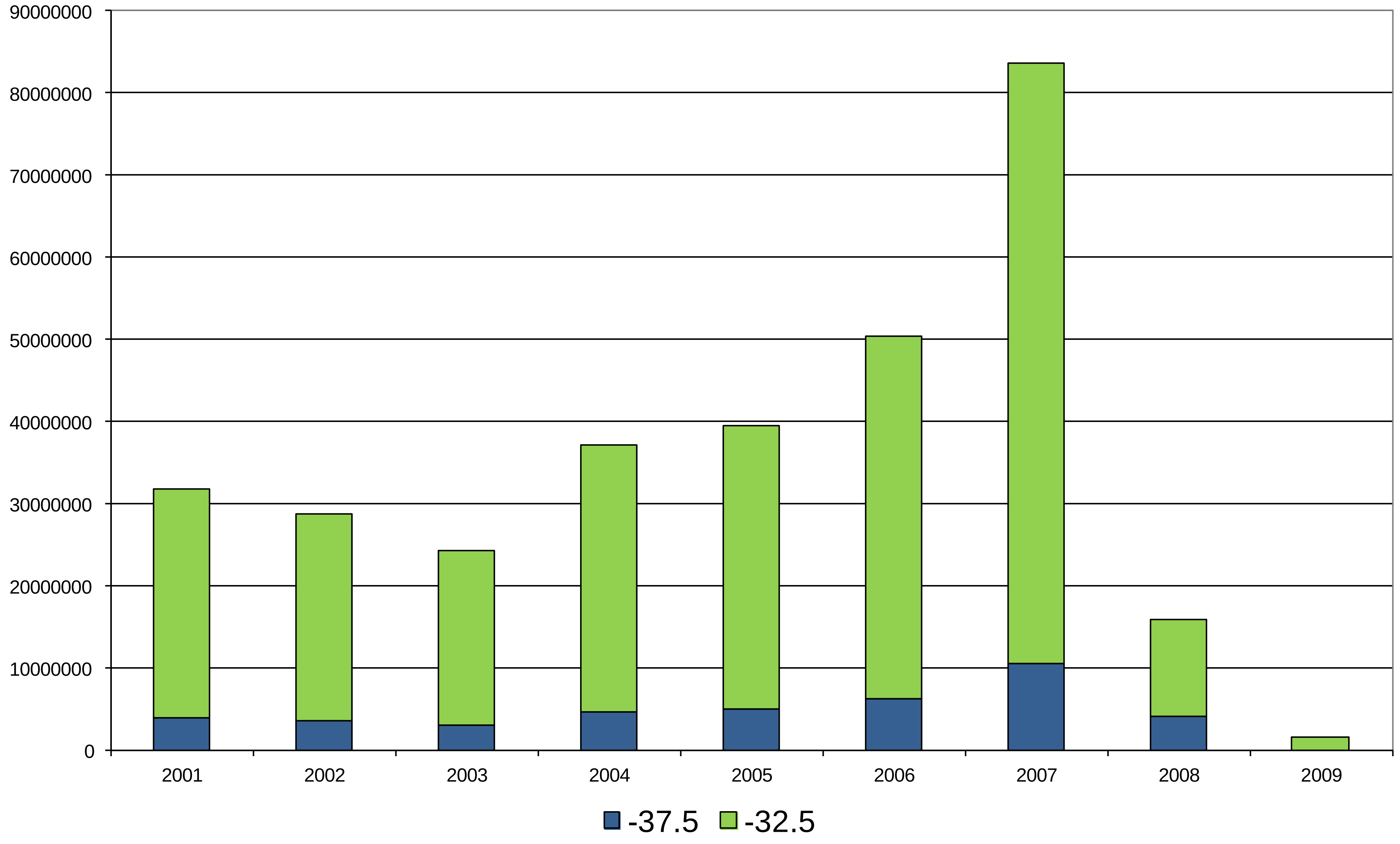


Figure 2. The estimated number of hooks deployed by the Taiwanese fresh longline fleet within the Indian Ocean (20E to 150E) south of 30S by 5 degree latitude bands centred on 32.5S and 37.5S.

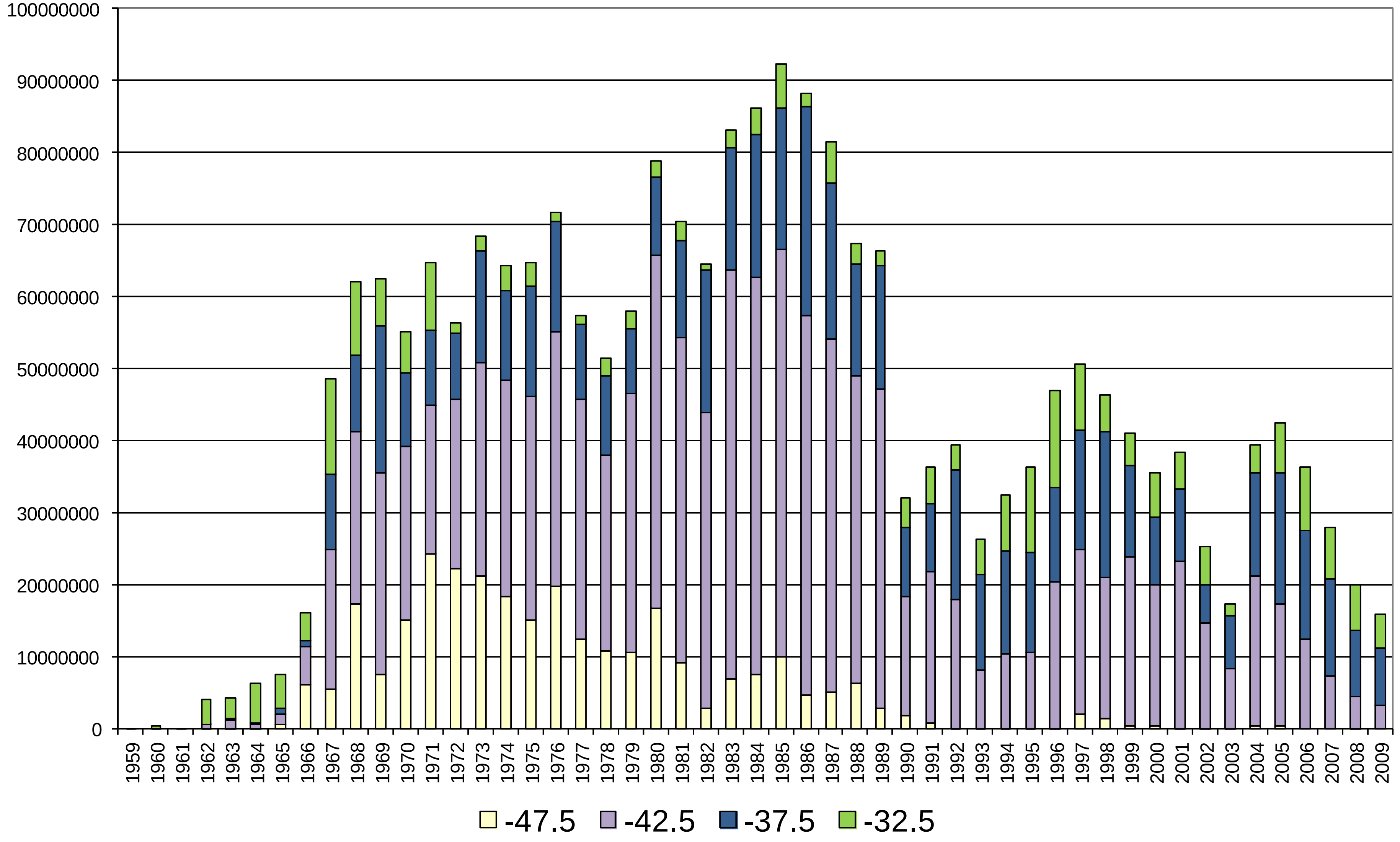


Figure 3. The reported number of hooks deployed by the Japanese distant water longline fleet within the Indian Ocean (20E to 150E) south of 30S by 5 degree latitude bands centred on 32.5S, 37.5S, 42.5S and 47.5S.

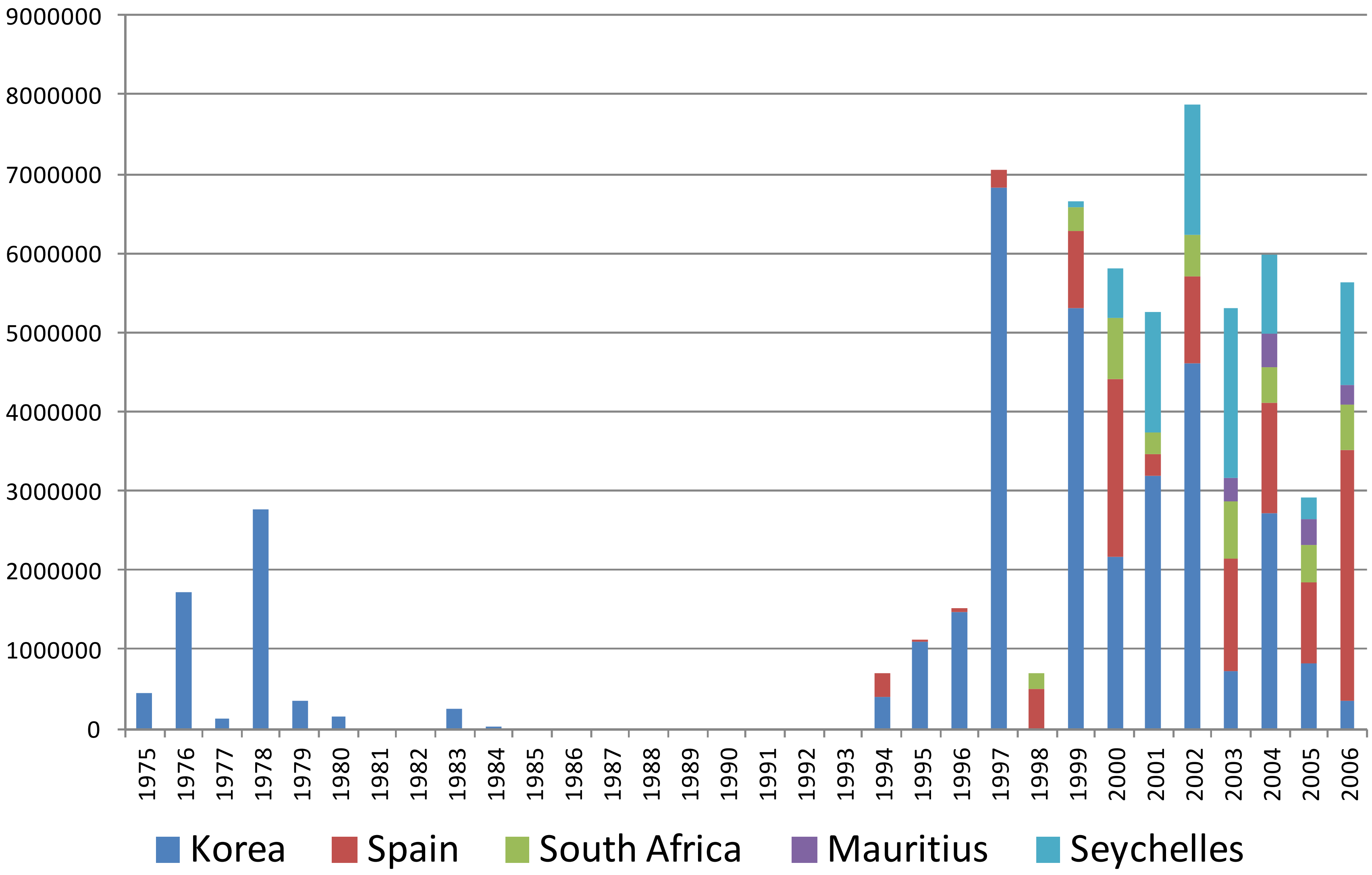


Figure 4 The estimated number of hooks deployed in the southern Indian Ocean (20E to 150E) south of 30S by Korea, Spain, South Africa, Mauritius and the Seychelles.

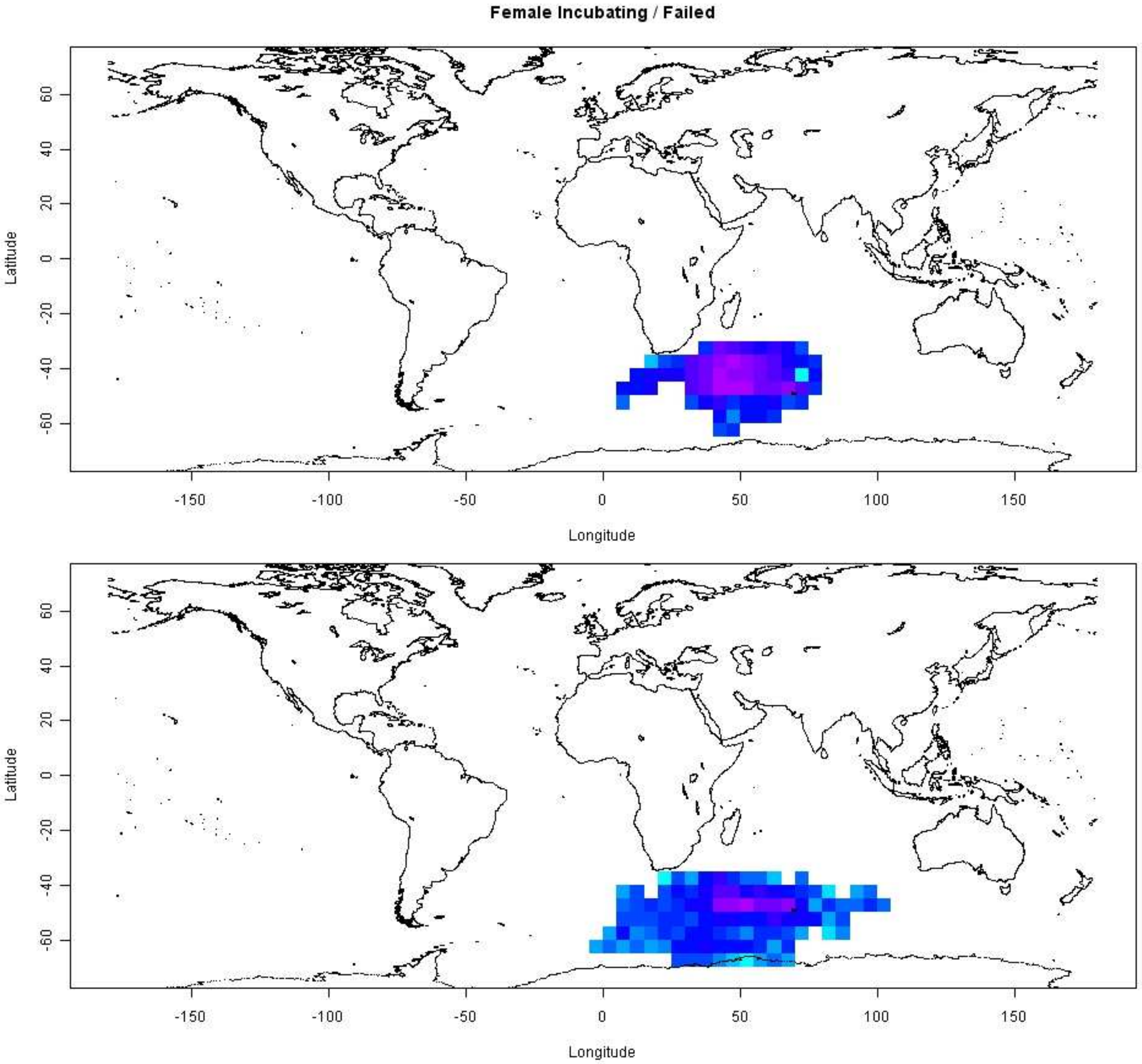


Figure 5. The density of Crozet wandering albatross for the incubating life-stage of females (top) and males (bottom). Purple indicates high density areas, light blue lower density.

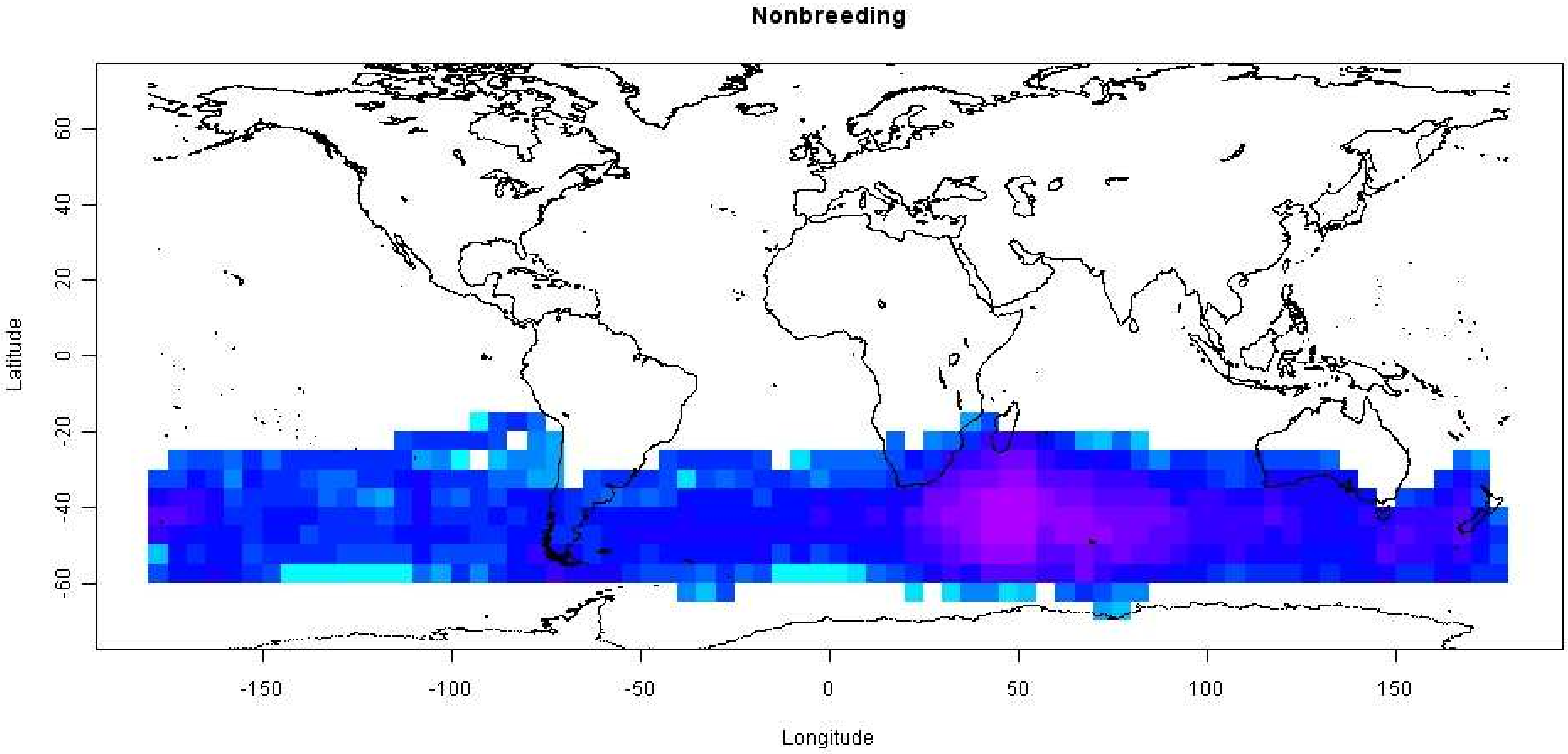


Figure 5 (cont). The density of Crozet wandering albatross for the non-breeding life-stage. Purple indicates high density areas, light blue lower density.

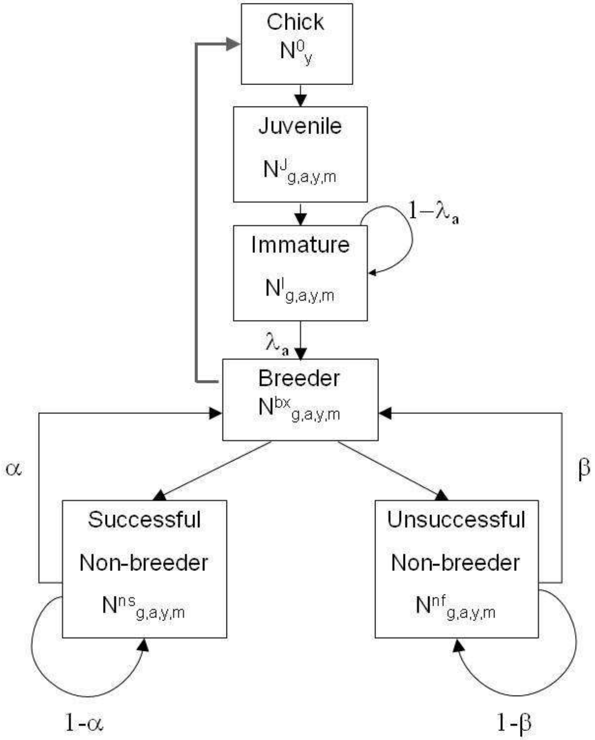


Figure 6. Schematic representation showing the organisation of bird life history stages in the model. Chicks become juveniles at age 1 and at age 2 become immatures, which mature (become breeding adults) at rate λ. After a breeding attempt birds become non-breeders, returning to the breeding colony at rates α or β if previously successful or unsuccessful (respectively) in their breeding attempt.

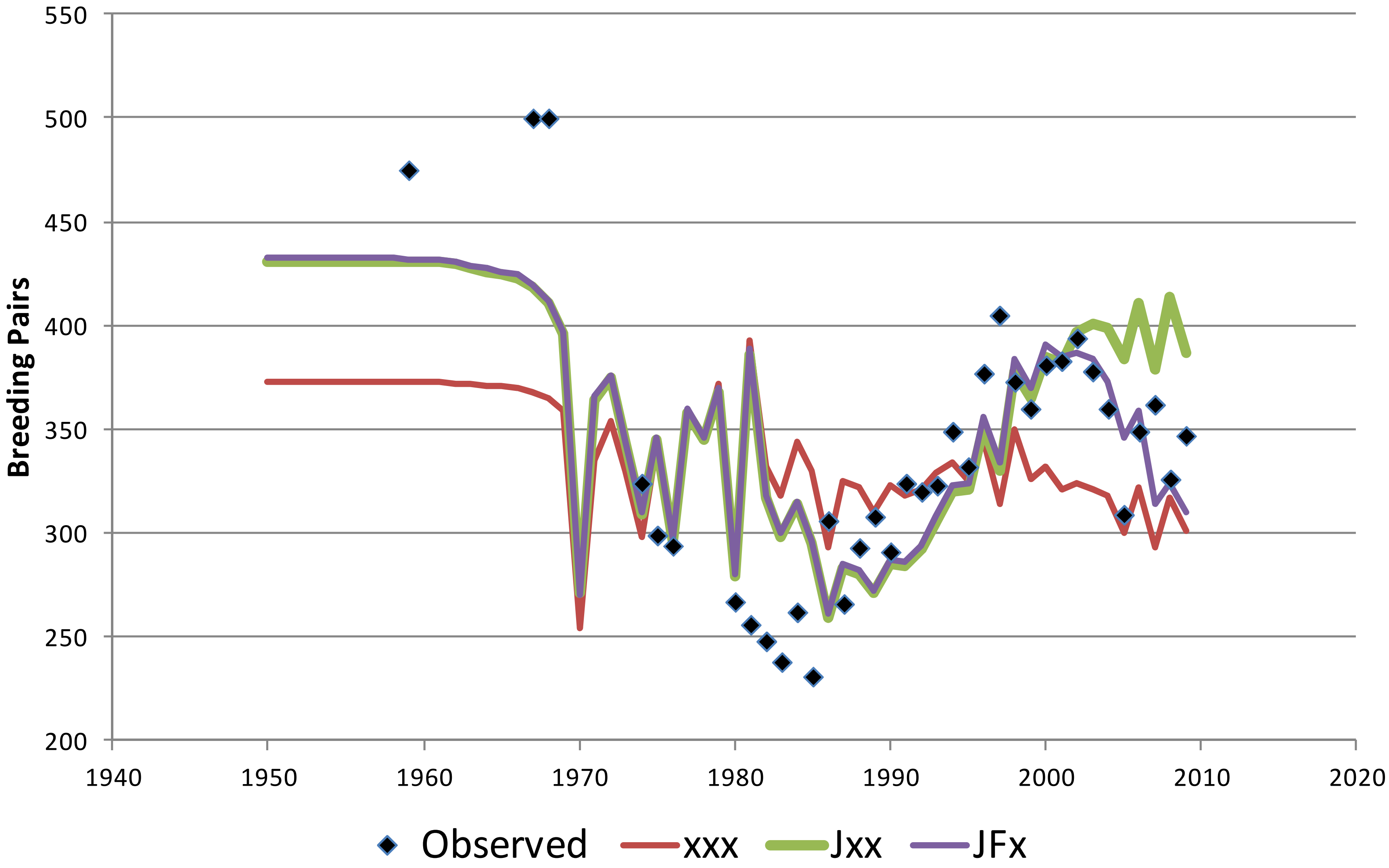


Figure 7. The observed and predicted numbers of breeding pairs for three models: xxx The original model structure. Jxx The original model structure but with the southern Japanese fleet (<30S) as a separate super-fleet (J). JFx The original model structure with the southern Japanese fleet (J) and the Taiwanese fresh longline fleet (F) as separate super-fleets.

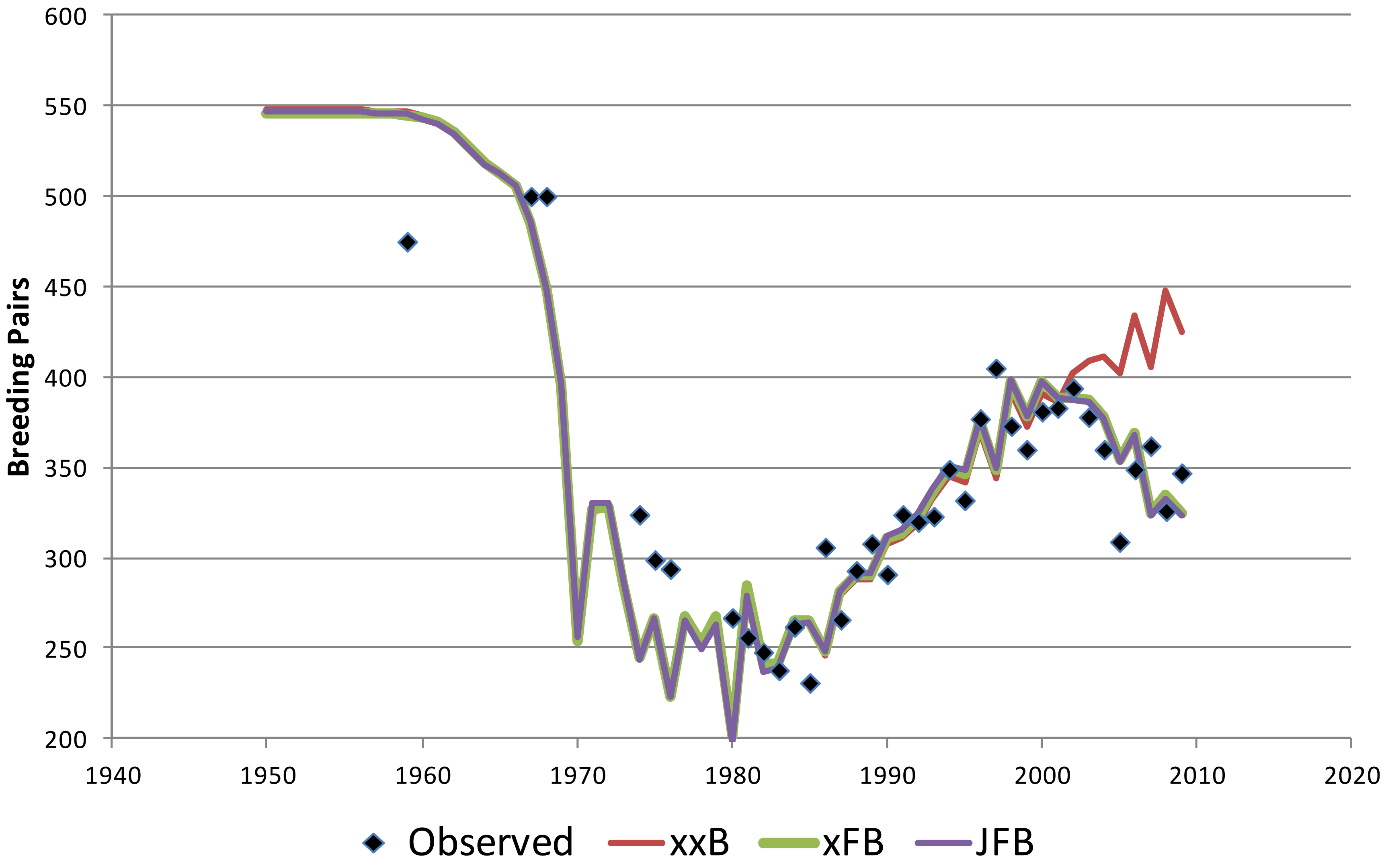


Figure 8. The observed and predicted numbers of breeding pairs for three models: xxB The original model structure with shy-bold (B) behaviour. xFB The original model structure but with the Taiwanese fresh longline fleet as a super-fleet (F) and shy-bold behaviour (B). JFB The original model structure with shy-bold behaviour (B), the southern Japanese fleet (J) and the Taiwanese fresh longline fleet as super-fleets (F).

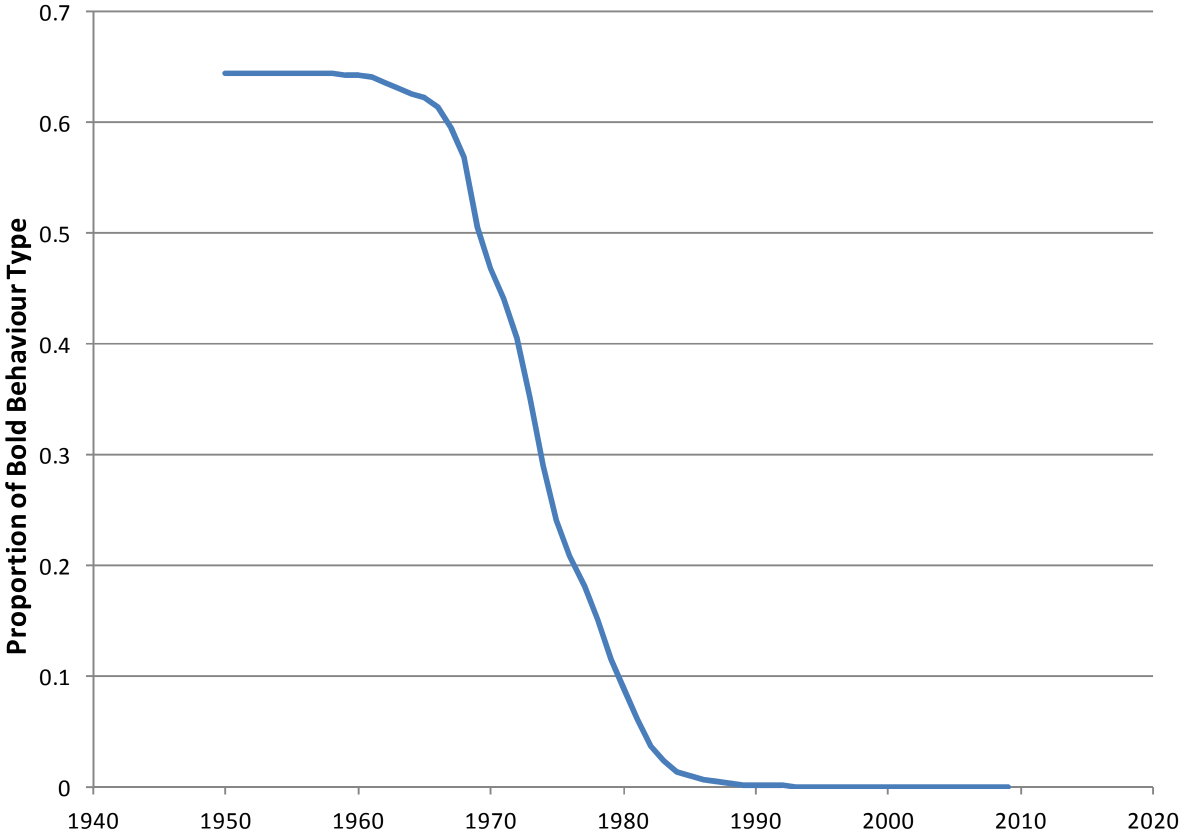


Figure 9. The estimated proportion of the population that is made up of the 'bold' behaviour type for the xFB model.

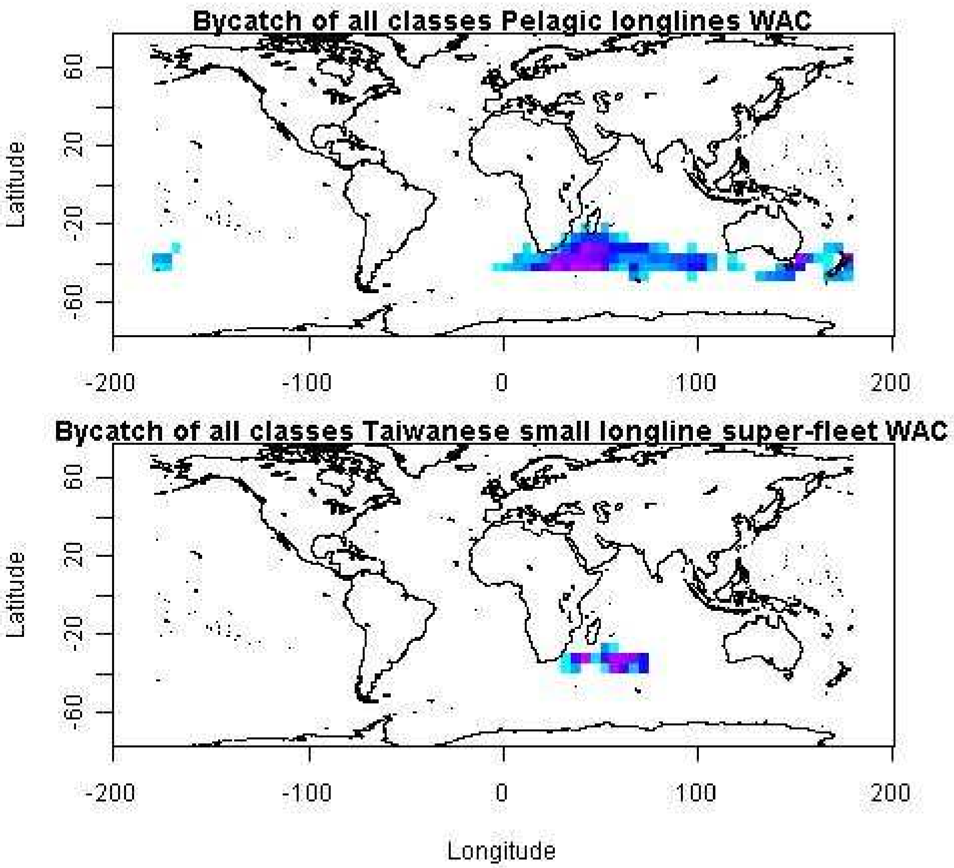


Figure 10. The density of estimated bycatch across all years for the xFB model. Top: the pelagic longline super-fleet. Bottom: The Taiwanese fresh longline super-fleet. Purple indicates high bycatch areas, light blue lower bycatch.

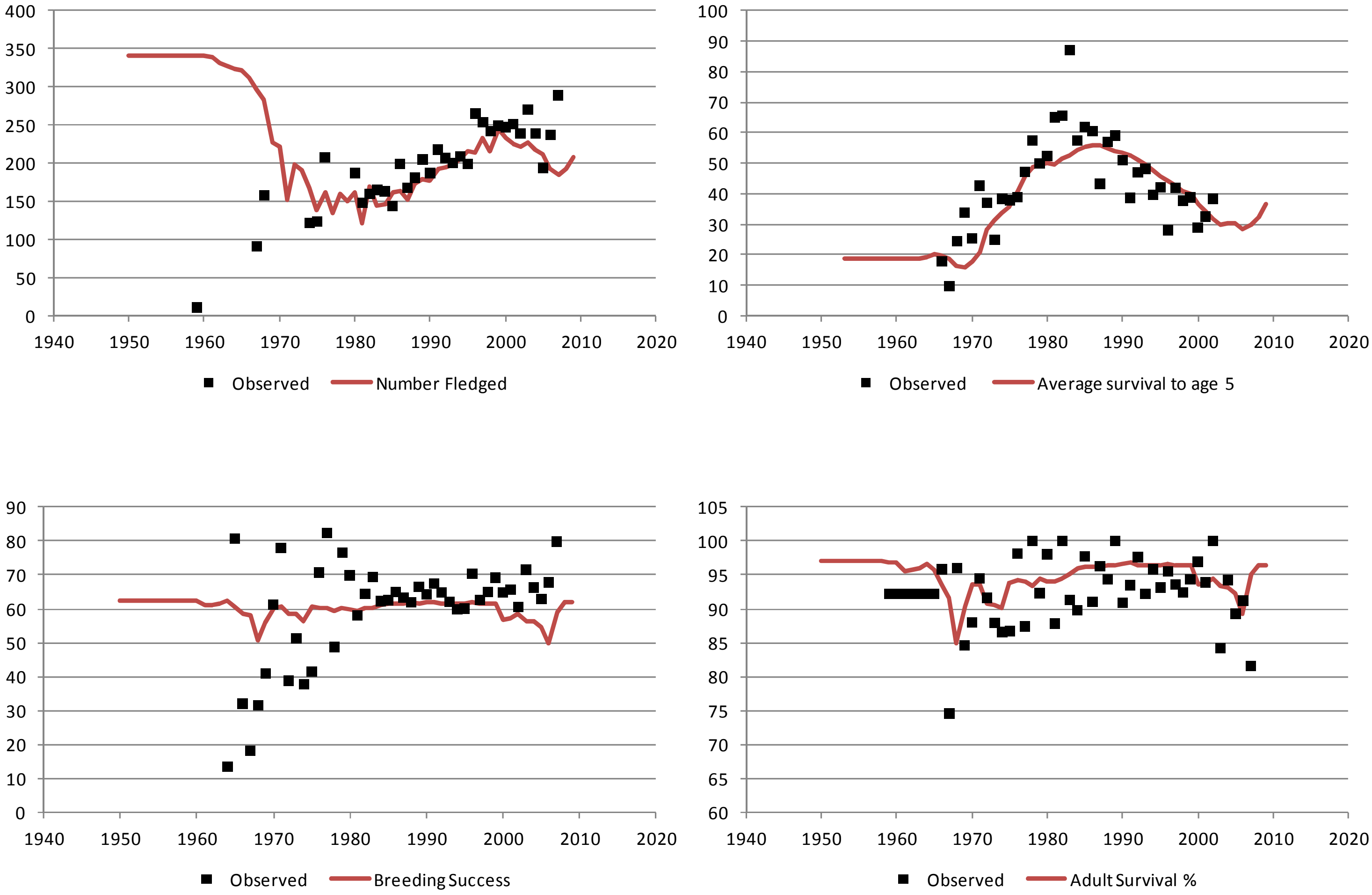
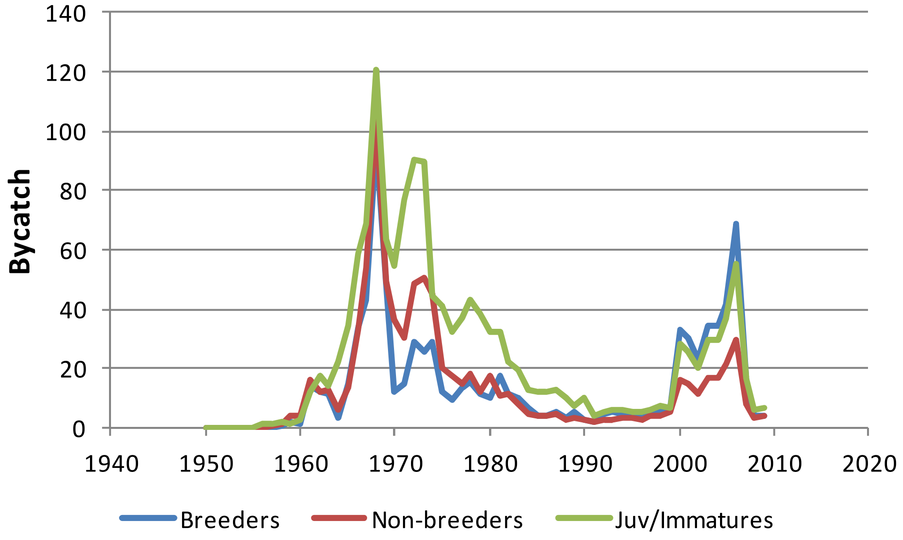


Figure 11. The time-series of model fits (line) to observations (black squares) for the xFB model. Shown are fits to the number of fledged birds (top left), survival to age 5 (top right), breeding success (bottom left) and adult survival (bottom right).



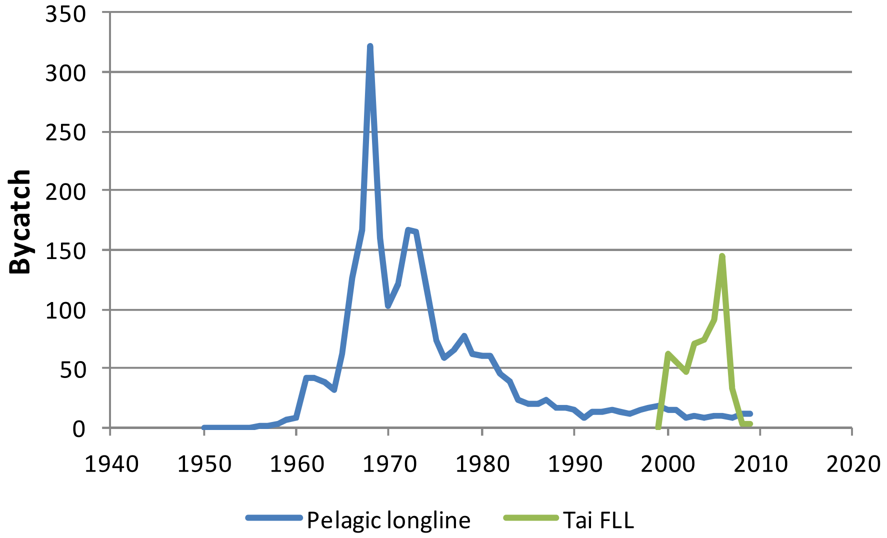


Figure 12. The time-series of model predicted bycatch by breeding status (top) and by super-fleet (bottom) for the xFB model.

TABLES

Table 1 Published and unpublished observations of wandering albatross bycatch rates Byc classified by super-fleet (Japanese pelagic longline south of 30oS JapS, demersal longline Dem, pelagic longline Pel, and IUU demersal longline in CCAMLR waters IUU). The timing (from firs month m1 and year Year1 to last month m2 and year Year2) and location (centre point of bounding 5 by 5 degree blocks given as LatS, LatN, LonW and LonE) of the studies is shown (to the nearest month and 5 by 5 degree block). The proportion of wandering albatross calculated as likely to belong to the Possession population is shown Ratio.

Fleet	m1	Year1	m2	Year2	LatS	LatN	LonW	LonE	Byc	Reference	Ratio
Dem	1	1999	12	1999	-57.5	-37.5	-67.5	-52.5	0	Favero et al. (2003)	194
Dem	1	2000	12	2000	-57.5	-37.5	-67.5	-52.5	0	Favero et al. (2003)	194
Dem	1	2001	12	2001	-57.5	-37.5	-67.5	-52.5	0	Favero et al. (2003)	194
Pel	1	2004	12	2007	-42.5	-17.5	-52.5	-17.5	0.0029	Jiménez et al. (2008)	93
Pel	1	2007	12	2007	-42.5	-32.5	7.5	32.5	0.0012	Ryan et al (2009a, b)	22
Pel	1	2008	12	2008	-42.5	-32.5	7.5	32.5	0	Ryan et al (2009a, b)	22
Dem	10	1994	12	1994	-37.5	-37.5	17.5	22.5	0	Barnes et al (1997)	25
Pel	1	2002	5	2002	-32.5	-27.5	312.5	312.5	0.0033	Mancini et al (2009)	275
Pel	6	2002	10	2002	-32.5	-27.5	312.5	312.5	0.0027	Mancini et al (2009)	275
Pel	6	2003	10	2003	-32.5	-27.5	312.5	312.5	0.0019	Mancini et al (2009)	275
Pel	1	2004	5	2004	-32.5	-27.5	312.5	312.5	0	Mancini et al (2009)	275
Pel	6	2004	10	2004	-32.5	-27.5	312.5	312.5	0.0006	Mancini et al (2009)	275
Pel	1	2005	5	2005	-32.5	-27.5	312.5	312.5	0	Mancini et al (2009)	275
Pel	6	2005	10	2005	-32.5	-27.5	312.5	312.5	0.002	Mancini et al (2009)	275
Pel	1	2006	5	2006	-32.5	-27.5	312.5	312.5	0.0011	Mancini et al (2009)	275
Pel	6	2006	10	2006	-32.5	-27.5	312.5	312.5	0.0063	Mancini et al (2009)	275
Pel	1	2007	5	2007	-32.5	-27.5	312.5	312.5	0.0022	Mancini et al (2009)	275
Pel	6	2007	10	2007	-32.5	-27.5	312.5	312.5	0.0083	Mancini et al (2009)	275
Pel	1	2008	5	2008	-32.5	-27.5	312.5	312.5	0	Mancini et al (2009)	275
Pel	6	2008	10	2008	-32.5	-27.5	312.5	312.5	0.0092	Mancini et al (2009)	275
JapS	4	1992	3	1993	-32.5	-47.5	112.5	152.5	0.0254	Klaer & Polacheck (1997)	22
JapS	4	1993	3	1994	-32.5	-47.5	112.5	152.5	0.0201	Klaer & Polacheck (1997)	22
JapS	4	1994	3	1995	-32.5	-47.5	112.5	152.5	0.0287	Klaer & Polacheck (1997)	22
JapS	5	1998	6	1998	-42.5	-42.5	142.5	142.5	0.0644	Brothers (1991)	22
Dem	3	1996	7	1996	-57.5	-52.5	317.5	327.5	0.0092	CCAMLR	1774
Dem	3	1997	4	1997	-57.5	-52.5	317.5	327.5	0.0035	CCAMLR	1774
Dem	5	1997	8	1997	-57.5	-52.5	317.5	327.5	0	CCAMLR	1774
Dem	4	1998	4	1998	-57.5	-52.5	317.5	327.5	0.0003	CCAMLR	1774
Dem	5	1998	5	1998	-57.5	-52.5	317.5	327.5	0	CCAMLR	1774
Dem	5	1999	7	1999	-57.5	-52.5	317.5	327.5	0	CCAMLR	1774
IUU	9	1995	4	1996	-57.5	-52.5	317.5	327.5	0.014	CCAMLR	1774
IUU	5	1996	8	1996	-57.5	-52.5	317.5	327.5	0	CCAMLR	1774
Dem	10	2001	9	2007	-52.5	-27.5	162.5	187.5	0.0001	Abraham & Thompson (2009)	25
Pel	10	2006	9	2007	-52.5	-27.5	162.5	187.5	0.0021	Abraham & Thompson (2009)	25

Pel	10	2005	9	2006	-52.5	-27.5	162.5	187.5	0.0016	Abraham & Thompson (2009)	25
Pel	10	2004	9	2005	-52.5	-27.5	162.5	187.5	0	Abraham & Thompson (2009)	25
Pel	10	2003	9	2004	-52.5	-27.5	162.5	187.5	0	Abraham & Thompson (2009)	25
Pel	10	2002	9	2003	-52.5	-27.5	162.5	187.5	0.0021	Abraham & Thompson (2009)	25
Pel	10	1998	9	2002	-52.5	-27.5	162.5	187.5	0	Abraham & Thompson (2009)	25
Dem	11	1994	3	1995	-45	-53.1	80	60	9.5e-7	Williams & Capdeville (1996)	23
Dem	2	1994	2	1994	-48	-48.3	68	66	0	Cherel et al. (1996)	38
Dem	10	1993	4	1994	-48	-50	68	67	0	Weimerskirch et al. (2000)	38
Dem	10	1994	4	1995	-48	-50	68	67	0	Weimerskirch et al. (2000)	38
Dem	10	1995	4	1996	-48	-50	68	67	0.028	Weimerskirch et al. (2000)	38
Dem	10	1996	4	1997	-48	-50	68	67	0	Weimerskirch et al. (2000)	38
Dem	2	1996	4	1997	-46.5	-51	72	66	0.003	Weimerskirch et al. (2000)	23
Dem	9	2001	7	2002	-45	-50	60	40	0	Delord et al. (2005)	26
Dem	9	2001	7	2002	-45	-53.1	80	60	0	Delord et al. (2005)	23
Dem	9	2002	8	2003	-45	-50	60	40	0	Delord et al. (2005)	26
Dem	9	2002	8	2003	-45	-53.1	80	60	0	Delord et al. (2005)	23
Dem	9	2003	8	2006	-45	-50	60	40	0	Delord et al. (2010)	26
Dem	9	2003	8	2006	-45	-53.1	80	60	0	Delord et al. (2010)	23

Table 2. Number of breeding pairs during 2001 from each major wandering albatross breeding location, the published source of this information, and the at-sea distribution assumed for each group of birds.

Population	Breeding pairs (Year)	Distribution	Source
Possession Island	381	Possession Island	This study
Crozet group (*Possession, Cochon, Est and Apôtres Islands*)	2337	Possession Island	Jouventin & Weimerskirch (1987),
Kerguelen (*Courbet Peninsula, Rallier du Baty Peninsula, Joffre, Howe, Nuageuses and Leygues Islands, and Baie Larose*)	1695	Possession Island	
Marion and Prince Edward Islands	3719	Possession Island	Crawford & Cooper (2003)
South Georgia	1736	South Georgia	Richard Phillips, BAS unpublished data

Table 3. Showing which of nine district at-sea distribution patterns was allocated each month to birds falling into specified life categories: breeding adults (breeder), breeders whose attempt failed (failed), non-breeders who failed (Nb failed) or succeeded (Nb success) in their previous breeding attempt, and juvenile or immature birds. Note that the model year and wandering albatross breeding season) begins in December. Italics indicate distributions that differ for males and females.

Month	Breeder	Failed	Nb failed	Nb success	Juvenile	Immature
Dec	*Incubating*	*Incubating*	*Incubating*	*Incubating*	Juvenile	Immature
Jan	*Incubating*	*Incubating*	*Incubating*	*Incubating*	Juvenile	Immature
Feb	*Incubating*	*Incubating*	*Incubating*	*Incubating*	Juvenile	Immature
Mar	*Brooding*	*Incubating*	Non-breeder	Non-breeder	Juvenile	Immature
Apr	*Brooding*	*Incubating*	Non-breeder	Non-breeder	Juvenile	Immature
May	Rearing	Non-breeder	Non-breeder	Non-breeder	Juvenile	Immature
June	Rearing	Non-breeder	Non-breeder	Non-breeder	Juvenile	Immature
July	Rearing	Non-breeder	Non-breeder	Non-breeder	Juvenile	Immature
Aug	Rearing	Non-breeder	Non-breeder	Non-breeder	Juvenile	Immature
Sept	Rearing	Non-breeder	Non-breeder	Non-breeder	Juvenile	Immature
Oct	Rearing	Non-breeder	Non-breeder	Non-breeder	Juvenile	Immature
Nov	Rearing	*Incubating*	*Incubating*	*Incubating*	Juvenile	Immature

Table 4. Demographic time series collected on Possession Island, Crozet: number of breeding pairs BP, numbers fledged N1, breeding success BS, adult survival Sa, juveniles survival to age 5 Sj5, return rates for successful α, and unsuccessful non-breeders β. Note that average return rates of 0.797 and 0.979 are used where annual rates could not be calculated, and that 1960 indicates the model year Dec 1960 to Nov 1961.

Year	BP	N1	BS	Sa	Sj5	α	β
1959	475	11	-	0.922	-	0.797	0.979
1960	-	-	-	0.922	-	0.797	0.979
1961	-	-	-	0.922	-	0.797	0.979
1962	-	-	-	0.922	-	0.797	0.979
1963	-	-	-	0.922	-	0.797	0.979
1964	-	-	0.135	0.922	-	0.797	0.979
1965	-	-	0.807	0.922	-	0.797	0.979
1966	-	-	0.321	0.958	0.179	0.797	0.979
1967	500	91	0.182	0.746	0.098	0.797	0.979
1968	500	158	0.315	0.96	0.245	0.797	0.979
1969	-	-	0.41	0.846	0.338	0.383	1
1970	-	-	0.612	0.88	0.254	0.72	0.686
1971	-	-	0.78	0.945	0.426	0.86	0.838
1972	-	-	0.388	0.916	0.37	0.699	1
1973	-	-	0.513	0.879	0.249	0.706	0.785
1974	324	122	0.378	0.866	0.384	0.802	0.854
1975	299	124	0.414	0.867	0.379	0.781	0.762
1976	294	208	0.706	0.981	0.389	0.903	0.839
1977	-	-	0.823	0.874	0.472	1	0.864
1978	-	-	0.487	1	0.575	1	1
1979	-	-	0.766	0.923	0.499	0.769	0.801
1980	267	187	0.699	0.98	0.524	1	0.938
1981	256	148	0.58	0.878	0.65	1	1
1982	248	160	0.644	1	0.655	0.928	0.828
1983	238	165	0.694	0.913	0.87	0.95	1
1984	262	163	0.623	0.898	0.575	1	1
1985	231	144	0.625	0.977	0.619	1	0.695
1986	306	199	0.65	0.91	0.605	0.951	0.893
1987	266	168	0.633	0.963	0.433	1	0.97
1988	293	181	0.619	0.943	0.57	0.966	0.944
1989	308	205	0.664	1	0.591	1	0.939
1990	291	187	0.642	0.909	0.51	0.967	1
1991	324	218	0.674	0.935	0.387	0.992	0.896
1992	320	207	0.648	0.976	0.471	1	0.91
1993	323	200	0.62	0.922	0.482	1	0.962
1994	349	209	0.599	0.958	0.397	0.958	0.955
1995	332	199	0.6	0.931	0.422	1	0.987
1996	377	265	0.703	0.955	0.281	0.931	0.911
1997	405	254	0.626	0.936	0.42	1	0.926
1998	373	242	0.65	0.924	0.378	0.985	0.931
1999	360	249	0.692	0.943	0.388	0.963	0.926
2000	381	247	0.648	0.969	0.289	0.958	0.901

2001	383	251	0.656	0.939	0.325	0.946	0.951
2002	394	239	0.606	1	0.383	0.981	0.937
2003	378	270	0.715	0.842	-	0.936	0.974
2004	360	239	0.663	0.942	-	1	0.754
2005	309	194	0.629	0.893	-	1	0.894
2006	349	237	0.678	0.912	-	0.921	0.911
2007	362	289	0.798	0.816	-	0.959	0.991
2008	326	-	-	-	-	0.97	0.931
2009	347	-	-	-	-	0.97	0.931