

Modelling the impact of fishery by-catches on albatross populations

GEOFFREY N. TUCK*, TOM POLACHECK*, JOHN P. CROXALL† and HENRI WEIMERSKIRCH‡

*CSIRO Marine Research, GPO Box 1538, Hobart, Tasmania, 7001 Australia; †British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road, Cambridge CB3 0ET, UK; and ‡CEBC-CNRS, 79360 Beauvoir, France

Summary

1. Several albatross species, including the wandering albatross *Diomedea exulans*, have shown marked declines in abundance throughout their range. These seabirds are frequently taken as by-catch in longline fisheries and this mortality has been implicated in the population declines.

2. We developed a deterministic, density-dependent, age-structured model for assessing the effects of longlining on wandering albatross populations. We used demographic data from field studies at South Georgia and the Crozet Islands, data on albatross abundance from 1960 to 1995, and reported effort data from the tuna longline fisheries south of 30° S, to model estimated by-catch levels and other population parameters in the model.

3. The model used two alternative assumptions about patterns of at-sea distribution of wandering albatross (uniform between 30° S–60° S; proportional to the distribution of longline fishing effort between these latitudes).

4. Our model was able to predict reasonably closely the observed data from the Crozet Islands wandering albatross population, but the fit to the South Georgia population was substantially poorer. This probably reflects: (i) greater overlap in the Indian Ocean than in the Atlantic Ocean between the main areas of tuna longline fishing and the foraging ranges of wandering albatrosses from the Crozet Islands and South Georgia, respectively; and (ii) greater impact of poorly documented longline fisheries, especially the tuna fisheries in the south Atlantic and the Patagonian toothfish *Dissostichus eleginoides* fishery, within the foraging range of wandering albatrosses from South Georgia.

5. The model results suggest that the marked decline in both populations, and subsequent recovery of the Crozet Islands population (but not the continued decline of the South Georgia population), can be explained by the tuna longline by-catch. They further indicate that populations may be able to sustain some level of incidental take. However, the likely under-reporting of fishing effort (especially in non-tuna longline fisheries) and the delicate balance between a sustainable and unsustainable level of by-catch for these long-lived populations suggest great caution in any application of such findings.

Key-words: Crozet Islands, longline fishing, population model, South Georgia, wandering albatross.

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Introduction

It is widely recognized that most, if not all, albatross species and populations are vulnerable to pelagic and demersal longline fisheries (Brothers 1991; Gales 1993,

1998; Weimerskirch, Brothers & Jouventin 1997; Prince *et al.* 1998). This is because albatrosses are wide ranging, highly migratory, species whose foraging ranges greatly overlap the pelagic and shelf slope habitats favoured by many longline fisheries. Moreover, many albatross species are attracted to fishing vessels as a potential source of food (bait, discharge of waste, offal or by-catch). Therefore they readily attempt to remove bait from hooks of longlines during setting

Correspondence: Geoffrey N. Tuck, CSIRO Marine Research, GPO Box 1538, Hobart, Tasmania, 7001 Australia (e-mail Geoff.Tuck@marine.csiro.au).

and, to a lesser extent, hauling operations, whereupon some birds become caught and consequently drown (Brothers 1991; Murray *et al.* 1993; Klaer & Polacheck 1997; Weimerskirch, Brothers & Jouventin 1997). Because albatrosses are long lived and have low reproductive rates (some species breeding successfully every 2 years at most), the additional mortality associated with longline fisheries can pose a significant threat to their sustainability (Croxall & Rothery 1991). Declines in many albatross populations have been observed that are concomitant with the development of longlining in the Southern Ocean. Longlining is thought to be the major source of the declines, as other anthropogenic effects are believed to be insufficient to explain the observed decreases in population size (Gales 1993).

Despite the well-documented potential significance of such interactions, there have been few studies able to compare longline fishing activities with albatross foraging distributions (Weimerskirch, Doncaster & Cuenot Chaillet 1994; Croxall & Prince 1996; Weimerskirch, Brothers & Jouventin 1997; Prince *et al.* 1998; Weimerskirch 1998). Even fewer attempts have been made to compare across-year variations in the distribution and intensity of longline fishing effort with changes in albatross populations. This is partly because of the difficulty of obtaining reliable fishing statistics in many areas, and the paucity of sufficiently detailed data on the demography of albatross populations. In addition, there is also a lack of appropriate models of both albatross population dynamics and interactions with fishing effort. Previous seabird population models have focused primarily on the demographic estimation of rates of increases or decreases (Croxall *et al.* 1990; Moloney *et al.* 1994; Weimerskirch, Brothers & Jouventin 1997). They have not explicitly attempted to model the interaction with the fishery or possible responses in the demographic parameters.

In this study we developed a discrete-time, density-dependent, age- and sex-structured model of wandering albatross population dynamics, and used alternative assumptions about the at-sea distribution of albatrosses to consider the potential impacts of interactions with Southern Ocean longline fisheries. We did this by using estimated albatross population parameters, and data on longline fishing effort, to fit the model to the best available population data sets for Bird Island, South Georgia, and Possession Island, Crozet Islands. The model is substantially different from the approach generally used to model seabird populations in that it explicitly attempts to account for the birds killed in longline fisheries and for the possibility of a density-dependent response to reduced population sizes. The model is thus analogous to those used in the assessment of fish stocks and marine mammal populations. In this modelling approach, the fitting procedure produces estimates for unknown population parameters and 'catchability coefficients' that convert fishing effort to estimates of actual by-catch. A comparison of the equilibrium population sizes at the

beginning of the simulations and the modelled population profiles thereafter provides an estimate of the impact of longlining on these populations.

Background

WANDERING ALBATROSS

Wandering albatrosses' *Diomedea exulans* (Linnaeus 1758) foraging migrations in the Southern Ocean are extensive, with documented cases of birds travelling over 800 km a day, with maximum flight speeds of approximately 80 km h⁻¹. Foraging excursions of breeding birds can cover distances of over 15 000 km and last over 30 days, while non-breeding adults and juveniles may remain at sea for several years before returning to their breeding colony (Jouventin & Weimerskirch 1990; Prince *et al.* 1992; Weimerskirch *et al.* 1993; Nicholls *et al.* 1995; Tuck *et al.* 1999).

The at-sea distribution of wandering albatrosses appears to be related to both sex and breeding status of the individual. Male wandering albatrosses tend to show a more southerly distribution during foraging (50°–60° S), whereas females forage further north (35°–45° S) (Weimerskirch & Jouventin 1987; Prince *et al.* 1992). This has important implications for mortality, as major tuna longline fisheries targeting southern bluefin tuna *Thunnus maccoyii* (Castelnau 1872) and albacore *Thunnus alalunga* (Bonnaterre 1788) are concentrated in the same latitude bands as foraging female albatrosses (Tuck & Polacheck 1997). This is reflected in the higher estimates of mortality shown for females based on returns of banded birds to breeding islands (Weimerskirch & Jouventin 1987; Croxall *et al.* 1990; Prince *et al.* 1992). Juveniles are also believed to be more susceptible to fishing than adults due to their more subtropical at-sea distribution and possibly to inexperience (Weimerskirch & Jouventin 1987). In contrast, however, juveniles may be competitively inferior to adults at longlines, and when both are present adults may be caught on baited hooks more often than juveniles (J. Croxall, personal observation).

Bird Island, South Georgia

The Bird Island population of wandering albatrosses comprises approximately 60% of the total wandering albatross population at South Georgia. Breeding birds are wide-ranging during the incubation period (December–March), regularly visiting areas 1000 km distant in the western South Atlantic, especially over the Patagonian Shelf (Prince *et al.* 1998; Croxall, Block & Wood 1999). During the brooding period (March–April), however, breeding birds are virtually restricted to areas within 500 km of South Georgia (Croxall & Prince 1996; Prince *et al.* 1998). Throughout chick-rearing (April–November) South Georgia wandering albatrosses range very widely in the south-west Atlantic sector of the Southern Ocean, particularly over

pelagic waters and along the shelf edges from southern Brazil to the Drake Passage and into the eastern Pacific Ocean. After breeding they traverse the Atlantic Ocean, past South Africa and onto Australia, where they winter. During this migration they are continually vulnerable to fishing by longline vessels (Prince *et al.* 1998). The distribution of juveniles is poorly known but they are widespread in the northern part of the Southern Ocean for at least the first 3–4 years of their life; in succeeding years they spend increasing time during the December–March period in the vicinity of South Georgia (Pickering 1989).

During the 1960s the population remained relatively stable, and perhaps increased. This was possibly facilitated by the presence of trawlers around South Georgia in the late 1960s, which may have acted as an additional food source when discarding offal. However, since then the number of breeding pairs has declined from 1600–1900 pairs in the early 1960s (Tickell 1968) to 1400–1500 pairs in the early 1970s and down to 1241 in 1996, at a rate of approximately 0.8% per annum (Croxall *et al.* 1998). During the same period, breeding success has increased from less than 60% in the late 1970s to over 70% by the late 1980s. The number of birds fledged has fluctuated but generally remained between 800 and 1000 chicks over the same period. Adult survival has also fluctuated but shown a gradually declining trend since the 1970s (Croxall *et al.* 1998). Juvenile survival to breeding age has shown a declining trend from 36% to 32% to 27% for the 1960s, 1970s and 1980s cohorts, respectively (Croxall *et al.* 1998).

Possession Island, The Crozet Islands

Wandering albatrosses from the Crozet Islands have been studied almost continuously since the early 1960s. As with South Georgia wandering albatrosses, foraging excursions are extensive across the Southern Ocean and interactions with longline vessels are likely to be frequent. Band recoveries of Crozet Island wandering albatrosses have been obtained from areas off the coast of South Africa, Australia, central Indian Ocean and the eastern south Atlantic (Weimerskirch, Brothers & Jouventin 1997).

The number of breeding pairs of wandering albatrosses at Possession Island remained relatively stable between 1960 and 1969, at about 500 pairs, before a marked decline beginning in 1970. In 1986 the number of breeding pairs reached a minimum of 231, and since then numbers have increased at approximately 4% per year. In 1995 there were 349 breeding pairs at Possession Island. Breeding success has generally remained between 70% and 80% except for a period of low breeding success in the 1970s. The number of birds fledged decreased from over 300 in the late 1960s to a low of 171 in 1986 before recovering to over 250 by 1993. Adult survival fluctuated substantially through the 1960s and 1970s. In general, annual adult survival was lower during this period than during the 1980s and 1990s, and

has been over 90% since 1979. The estimated juvenile survival to age 5 has increased markedly since the mid-1960s. For the 1967 cohort, the estimated juvenile survival to age 5 was 15.9% compared with 69.5% for the 1983 cohort (Weimerskirch, Brothers & Jouventin 1997).

SOUTHERN OCEAN TUNA LONGLINE FISHERIES

The ability to fly long distances in short periods of time, combined with their affinity for baits and offal, make albatrosses highly vulnerable to longline fisheries. The spatial distribution of tuna longline effort has been extensive across the Southern Ocean since the late 1960s, and has been predominantly targeted at southern bluefin tuna (SBT) by Japanese vessels and, more recently, at albacore, bigeye *Thunnus obesus* (Lowe 1839) and SBT by Taiwanese vessels (Tuck & Polacheck 1997).

The Japanese longline fishery for SBT in the Southern Ocean developed in the mid-1950s in waters surrounding New Zealand. Effort increased dramatically from the early 1960s, and by 1971 around 92 million hooks were set. In 1980 the fishery reached its peak in terms of number of hooks set, with 126 million hooks deployed. From the late 1980s effort declined markedly, with catch quotas at least partially responsible, and in 1994 the estimated number of hooks set was 54 million. The SBT longline fishery shows distinct spatial and temporal dynamics, with effort concentrations in certain areas in certain seasons. However, the spatial/temporal distribution of effort has not been constant. For example, strong effort concentrations off the east coast of New Zealand's South Island between April and June gradually shifted to the west coast during the mid-1980s (Tuck & Polacheck 1997).

In this study, the information on tuna longline fishing effort is based on data supplied by Australia, New Zealand and Japan and by the Secretariat of the Pacific Community (SPC), the Indian Ocean Tuna Commission (IOTC) and its predecessor the Indo-Pacific Tuna Development and Management Programme (IPTP), the International Commission for the Conservation of Atlantic Tunas (ICCAT) and the Australian Fisheries Management Authority (AFMA). Table 1 lists the fishing nations and the years of longline effort provided by the data source (obtained in 1997). Taiwanese data were only available to 1994. There has been a substantial increase in reported effort by the Taiwanese fleet south of 30° S since 1990 (Fig. 1). The 1994 Taiwanese data were used as an estimate of the effort in 1995 in order to run the models through until the end of 1995. Concerns exist about the reliability of the Taiwanese data. However, if the current large increase in reported effort is accurate and is maintained, the level of by-catch would be expected to have a substantial impact on seabird populations in the future. In terms of the results presented here, the reported large increase does not substantially affect the results as it only applies to the 2 most recent

Table 1. The source of data, nationality and years of data available. JV, joint venture; IOTC, Indian Ocean Tuna Commission; SPC, Secretariat of the Pacific Community; ICCAT, International Commission for the Conservation of Atlantic Tunas

| Data source | Nation | Years available | |
|------------------------|-------------------------------|---------------------|---------|
| IOTC | Taiwan | 1967–94 | |
| | Korea | 1975–91 | |
| SPC | Taiwan | 1967–94 | |
| | Korea | 1975–93 | |
| ICCAT | Argentina | 1967–68 | |
| | Brazil–Honduras (JV) | 1991 | |
| | Brazil–Japan (JV) | 1977–92 | |
| | Brazil–Taiwan (JV) | 1991–95 | |
| | Brazil | 1991–95 | |
| | Korea | 1967, 1969, 1976–78 | |
| | South Africa | 1979–84 | |
| | Spain | 1987, 1991–95 | |
| | Uruguay | 1981–87 | |
| | Australia, Japan, New Zealand | Japan | 1960–95 |
| | Australia–Japan (JV) | 1989–95 | |
| New Zealand–Japan (JV) | 1989–95 | | |
| Australia–Domestic | 1985–95 | | |
| New Zealand–Domestic | 1991–95 | | |

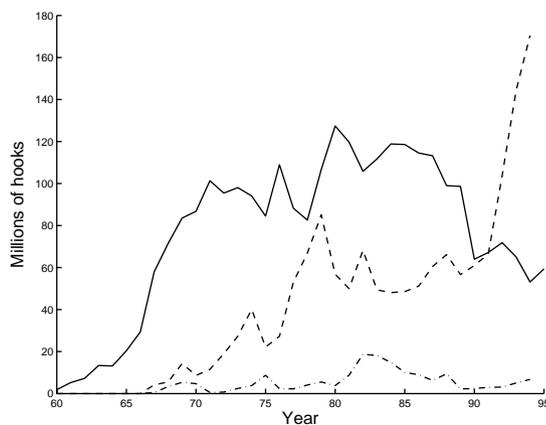


Fig. 1. The reported effort in hooks deployed in the Southern Ocean south of 30° S by Japan (solid line) and other nations (dashed line), predominantly Taiwan, fishing for tunas and tuna-like species (see Table 1). Also shown is the pelagic longline effort in the vicinity of the Crozet Islands (dotted and dashed line) (between 40° E and 75° E and south of 35° S) based on data provided to IOTC.

years in the model. Currently, there is very little information on seabird by-catch rates from this fleet (Tuck & Polacheck 1997; Ryan & Boix-Hinzen 1998). It should be noted that all effort statistics are based on reported effort. There is likely to have been under-reporting of effort by some fleets, particularly flag of convenience vessels and from the fleets off South America.

Methods

ALBATROSS SPATIAL DISTRIBUTION

Model estimates of incidental catches will depend critically on assumptions made about the spatial distribution of wandering albatrosses. To obtain an indication of the sensitivity of the model to assumptions about

their spatial/temporal dynamics, two hypothetical distributions are used for the spatial distribution of wandering albatrosses. First, the female albatross spatial distribution is assumed to mimic the effort distribution of fishing fleets in the Southern Ocean for latitudes south of 30° S. Concentrations of effort directly overlap concentrations of wandering albatross abundance. The basis for this hypothesis is that wandering albatrosses and pelagic tuna species (and thus fishers) would be attracted to areas of high productivity in order to obtain favoured prey species. The vessels themselves would also act as a direct attractor as albatrosses are known to have an affinity to fishing vessels due to the availability of food scraps and baits (Brothers 1991). The second hypothesis assumes that the wandering albatross spatial distribution is uniformly distributed across the Southern Ocean between latitudes 30° S and 60° S. The northern and southern boundaries of wandering albatross distribution are estimates taken from published distribution maps in Marchant & Higgins (1990). This assumes that the albatrosses move randomly over the Southern Ocean, and therefore some spatial cells (5 × 5-degree blocks) will have albatrosses but no fishing effort. While these two hypotheses are oversimplifications of the actual spatial distributions of wandering albatross, they provide a basis for bracketing the potential fishing mortality rates. However, there is the possibility that the distributions of albatrosses and tuna fisheries have non-overlapping areas of concentration and that the effect of longlining, in terms of incidental mortality, would be even less than that estimated by the uniform albatross distribution hypothesis.

RESOURCE DYNAMICS

The age structure of the population is modelled by classifying albatrosses into fledglings, juveniles, breeding

adults and non-breeding adults. The number of birds fledged is dependent on both chick and adult mortality. Wandering albatrosses that successfully breed produce one chick per breeding attempt. Those birds that are successful do not breed the following year, and thus breed successfully at most every second year (Tickell 1968; Croxall, Block & Wood 1999). Those birds that are unsuccessful, due to the loss of an egg or chick (whether due to environmental or physiological causes, or the death of a partner), are able to breed the following year. Rates of return from the non-breeding adult population depend on the number of years since the last breeding attempt and whether or not the bird successfully bred (Croxall *et al.* 1990). The population model is a discrete-time, age-structured, model of the number of female birds. It is assumed that there is no emigration from or immigration to the albatross colony, as exchanges between the populations modelled here and other colonies has been small based on extensive observations (Weimerskirch, Brothers & Jouventin 1997). Numbers at age are recorded at the beginning of the season. Female birds of age $a > 1$ have dynamics given by:

$$N_{y+1,a}^J = e^{-Z_n^J} N_{y,a-1}^J (1 - \lambda_{y-a+1,a-1}) \quad \text{eqn 1}$$

$$N_{y+1,a}^{ns} = e^{-Z_n^f - Z_b^m - M_c} N_{y,a-1}^b + e^{-Z_n^f} (1 - \alpha) N_{y,a-1}^{ns} \quad \text{eqn 2}$$

$$N_{y+1,a}^{nf} = e^{-Z_n^f} (1 - p_f) (1 - e^{-M_c - Z_b^m}) N_{y,a-1}^b + e^{-Z_n^f} (1 - \beta) N_{y,a-1}^{nf} \quad \text{eqn 3}$$

$$N_{y+1,a}^b = e^{-Z_n^f} \lambda_{y-a+1,a-1} N_{y,a-1}^J + e^{-Z_b^m} p_f (1 - e^{-M_c - Z_b^m}) N_{y,a-1}^b + e^{-Z_n^f} (\alpha N_{y,a-1}^{ns} + \beta N_{y,a-1}^{nf}), \quad \text{eqn 4}$$

$N_{y,a}^J$, $N_{y,a}^{ns}$, $N_{y,a}^{nf}$ and $N_{y,a}^b$ = the number of female juveniles, non-breeding adults that were either successful (ns) or failed (nf) at their last breeding attempt, and the number of breeding adults (b) that are of age a at the beginning of year y , respectively (Fig. 2). Z_n^f , Z_n^m , Z_b^f and Z_b^m = the instantaneous rate of mortality (natural and fishing) for juveniles, non-breeding adults and breeding adults (for females f and males m), respectively. $\lambda_{y-a,a}$ = the proportion of juveniles born in year $y - a$ that are mature at age a in year y . M_c = the instantaneous rate of chick mortality. α and β = the proportion of non-breeding adults that join the breeding population after successfully or unsuccessfully breeding at the last attempt, respectively. And p_f = the proportion of unsuccessful birds that attempt to breed in the following year.

Equation 1 states that the number of female juveniles in year $y + 1$ of age a is equal to the number that survived the previous year of age $a - 1$ less those that reached sexual maturity. Equation 2 states that the number of non-breeding females in year $y + 1$ that were successful at their last breeding attempt is composed of the successful breeding birds in year y that survived to year $y + 1$ and the surviving successful non-breeders that do not breed in year $y + 1$. Equation 3 states that in

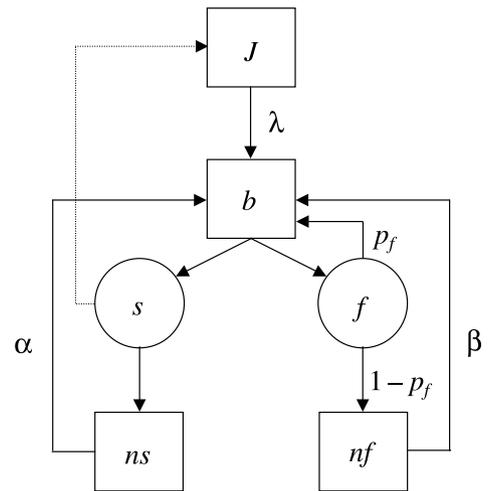


Fig. 2. A diagrammatic representation of the population model. Juveniles (J) become breeding adults according to the parameter λ . Breeding adults (b) are either successful (s) or fail (f). If chicks are successfully reared all adults become non-breeders the following year (ns). If unsuccessful, adults either breed the following year (with rate p_f) or join the non-breeding population (nf). The rates of return from the non-breeding populations are given by α and β for successful and failed breeders, respectively.

year $y + 1$ the number of non-breeders that were unsuccessful at their last breeding attempt is equal to the number of surviving breeders in year y that were unsuccessful and do not breed in year $y + 1$ plus the number of unsuccessful non-breeders that survived that do not breed in year $y + 1$. The number of breeding birds in year $y + 1$ is then equal to the number of juveniles in year y that become mature in year $y + 1$, plus the number of surviving breeding female birds that were unsuccessful but return to breed in year $y + 1$, plus the number of surviving successful and unsuccessful non-breeding birds that return to the breeding population in year $y + 1$.

Note that the chick mortality rate, along with adult mortality, determines the success or failure of a breeding pair. The total mortality rate terms, Z , are the sum of natural, M , and fishing, F , mortalities. Mortality rates may depend on the year, age, sex and breeding status of the birds. The inclusion of male and female mortality terms is due to the possibility of either parent dying leading to the death of the chick. This mortality affects whether the breeding adult is a successful or failed breeder. Fishing mortality rates were estimated using the standard Baranov catch equation (Quinn & Deriso 1999) and the model-predicted incidental catches (see below).

BIRTHS

The breeding period for the wandering albatross is essentially the whole year, with those birds that are successful rearing a single chick. Chick mortality may occur directly through natural causes (e.g. environmental, physiological, and expressed in the model by M_c) or indirectly due to the death of a parent by either natural

or fishing mortality. It is assumed that the death of a parent leads to chick mortality due to the intensive nature of feeding required for the chick to survive (Tickell 1968). This leads to the inclusion of both male and female mortality terms in the formulation of the number of fledglings.

Assuming a 1 : 1 sex ratio at birth, the number of female fledglings (age 1) at the beginning of year $y + 1$ is:

$$N_{y+1,1}^J = \frac{1}{2} e^{-M_c - Z_b^f - Z_b^m} \sum_a N_{y,a}^b \quad \text{eqn 5}$$

The number of eggs produced is $\sum_a N_{y,a}^b = B_y$, i.e. the total number of breeding pairs at the beginning of year y , as each breeding pair produces a single egg.

INCIDENTAL CATCH

The incidental catch of wandering albatrosses is likely to depend on the space and time overlap of the albatross population and fishing effort. This will be a function of the sex of the birds (females tend to feed in more northerly latitudes; Weimerskirch & Jouventin 1987), age (juveniles may be more susceptible to capture due to their more subtropical distribution overlapping with that of longline vessels), breeding status (breeding individuals forage in different areas than non-breeding birds) and the particular population under consideration (Crozet Island and South Georgia birds show differing foraging areas; Prince *et al.* 1998).

The method used to model catch is to model the proportion of the wandering albatross population found in a particular grid reference (say 5×5 -degree square) at a particular time, and multiply this by the number of birds in the population at that time. This results in an estimate of the spread of wandering albatrosses over the Southern Ocean. To determine the total incidental catch of females, the seabird distribution is multiplied by the effort and a catchability coefficient, giving the familiar catch equation used in fisheries science:

$$C_{y,i} = q_i \sum_{s,t} N_{t,i} P_{s,t} E_{s,t} \quad \text{eqn 6}$$

Here q_i is the catchability coefficient of birds of life stage i ($i = J$, juveniles, or $i = A$, adults), $P_{s,t}$ is the proportional spread of albatrosses in square s at time t (where t may be months or quarters in year y), $N_{t,i}$ is the total number of female albatrosses of life stage i in the population in period t , and $E_{s,t}$ is the number of hooks set in square s at time t .

The susceptibility to capture of juvenile albatrosses may differ from that of adults, due to either inexperience or competition. As such, the catchability of adults, q_A , is assumed to be a fraction of that of juveniles, q_J , such that $q_A = q_J q_A$. Varying the value of the parameter q_J allows a range of different catchabilities to be explored.

Due to the introduction of catch mitigating devices by the Japanese longline fleet in the late 1980s and early

1990s, the catch rate of seabirds is likely to be less than that historically in the fishery (Klaer & Polacheck 1998). Mitigation measures implemented include setting lines at night, tori lines, bait-throwing devices, bait thawing and line weighting (Brothers 1991; Klaer & Polacheck 1998). The decrease in catch due to mitigation since 1990 is modelled as a constant proportion of the rate prior to this period, q_m , where $0.1 \leq q_m \leq 1$. The lower limit suggesting a 90% reduction in albatross by-catch is indicative of the maximum potential of mitigation measures to reduce by-catch, as observed in the Japanese longline fishery (Takeuchi, Uozumi & Tanaka 1997; Klaer & Polacheck 1998). The Japanese longlining fleet is the best documented and is also the fleet with greatest application of mitigation devices, with tori lines now mandatory within the Australian and New Zealand EEZs (Exclusive Economic Zones) and on the high seas. It is unlikely that a similar reduction in by-catch has occurred for fisheries other than for the Japanese fishery, and so q_m is only applied to effort data from the Japanese fleet.

The catchability of seabirds may possibly differ between tuna longline fleets from different nationalities due to factors such as differences in gears and the differing application of mitigation measures among fleets (Tuck & Polacheck 1997). However, there is no information available that would allow an estimate of the differences in gear or their potential effects on by-catch rates. Moreover, the gear for the Taiwanese fleet (which is the main other longline fleet in the model) is similar to that of the Japanese fleet. Thus, the model assumes that the catchability for all fleets is the same prior to the introduction of mitigation measures in the Japanese fleet.

DEMOGRAPHIC DATA

A description of the demographics of these populations can be found in Croxall *et al.* (1990, 1998) for the Bird Island population and Weimerskirch, Brothers & Jouventin (1997) for the Possession Island population. Data used are a combination of the demographic parameters from these papers and unpublished data provided by J. Croxall and H. Weimerskirch.

For the simulations that follow, adult natural mortality is set to $M = 0.02$, giving an annual finite survival rate of 0.961. This reflects observations of high survival rates for known individuals. The adult natural mortality rate needs to be less than the rate that yields the observed survival rates in the field in order to take into account fishing mortalities. The value of M is confounded to some extent with the catchability parameters, and as such the model has poor power to estimate it. A range of values for M was explored. Although the general behaviour of the model was similar over a range of values for M , the sums of squares for the Possession and Bird Island data responded differently to changes in the value of M . The reasons for this are outlined in the Discussion. For simplicity, it is assumed

that adult female and male mortality rates are equal, $Z^f = Z^m$. Further refinement of the model could consider the possibility that fishing mortality is sex dependent due to differences in foraging behaviour of the sexes. Note that male mortality rates only enter the present model in determining the chick survival rate.

The maximum attainable age is set to $A_m = 70$ years of age. The maximum age is based on an extrapolation of observations of known animals. The results are insensitive to increasing the maximum age, as the potential overall reproductive contribution from animals beyond this age is relatively small, given values used for the natural survival rate of adults.

Chick natural mortality is set to $M_c = 0.4$ for the Bird Island population and $M_c = 0.2$ for the Possession Island population. We have used different values for the chick mortality parameters for the two populations because observed data on breeding success suggest a difference existed prior to significant longline fisheries in the area of breeding colonies (Weimerskirch, Brothers & Jouventin 1997; Croxall *et al.* 1998). Breeding success will be lower than chick natural survival rates because some adult breeding birds are estimated to die within the model as the result of fishing and natural mortality. The difference in the level of chick mortality rates does not have a substantive effect on the model results because any increase in M_c would be compensated for by a decrease in juvenile mortality (and vice versa). As such, the estimated total number of recruits to the breeding stock from a cohort of chicks would remain similar.

Juveniles are assumed to reach sexual maturity at age 10 (Croxall *et al.* 1990; Weimerskirch, Brothers & Jouventin 1997). Thus, the proportion of those albatrosses born in year $y - a$ that are mature at age a in year y is:

$$\lambda_{y-a,a} = \begin{cases} 0 & a < 10 \\ 1 & a \geq 10 \end{cases} \quad \text{eqn 7}$$

for all years.

The proportion of non-breeding adults that join the breeding population after successfully breeding at the last attempt is $\alpha = 0.741$, while the proportion of non-breeding adults that join the breeding population after unsuccessfully breeding is $\beta = 0.8$. These parameters were derived by collapsing the year-specific parameters of Croxall *et al.* (1990) into two parameters (α and β) that produce very similar dynamics and greatly simplifies the model structure and programming (Tuck 1999). The proportion of unsuccessful breeding birds that attempt to breed in the next season is $p_f = 0.8$ (Croxall *et al.* 1990).

DENSITY DEPENDENCE

There is some evidence that populations of wandering albatrosses show a density-dependent response to declines in the breeding population size (Croxall *et al.*

1990; Weimerskirch 1992; Weimerskirch, Brothers & Jouventin 1997). At Bird Island, breeding success (defined as the number of chicks fledged per eggs laid) shows an increasing trend over time from approximately 0.57 in 1976, to 0.70 in 1988 (Croxall *et al.* 1990; Fig. 2). This is in contrast to the estimated 1% per annum decline shown by breeding pairs. Likewise, the age at first breeding has decreased at South Georgia from 10.9 to 9.9 years (females) and 11.6 to 10.3 years (males), based on recruitment of the 1972 and 1980 cohorts (Croxall *et al.* 1998). Once fledged, wandering albatross chicks do not return to their breeding colony for approximately 5 years (Croxall *et al.* 1990, 1998). The juvenile survival to age 5 of wandering albatross populations of the Crozet Islands has shown a steady increase from approximately 0.2 for the 1966 cohort to above 0.6 for the 1983 cohort (Weimerskirch, Brothers & Jouventin 1997). During this period, the breeding population size on Possession Island halved.

Juvenile natural mortality rate was selected as the density-dependent demographic component because of the strong indication that juvenile survival rates increase when the numbers of breeding pairs decrease for the Possession Island population, as discussed above. While observations of juvenile survival rates for the Bird Island population do not indicate an increase, the observed increase at Possession Island occurred prior to most observations from South Georgia. More recently, there has been a decrease in the juvenile survival estimates from South Georgia. However, this decrease is a combination of both natural and fishing mortality rates and is not inconsistent with a density-dependent response in the juvenile natural mortality rate. Although there is an indication of a decrease in the age of first breeding for the Bird Island population, changes in the age of maturity have only a small effect on the potential rates of increase (particularly for the 1-year change that has been observed). As such, density dependence is modelled by allowing juvenile natural mortality to age 5 for a cohort, M_j^5 , to be a function of the breeding population size. The ecological basis for this would be a decrease in the intraspecific competition for resources (food for example) (Weimerskirch 1992).

Current data would not allow independent estimation of density-dependent functions for two different demographic components. The overall recruitment of a cohort to the breeding population is the critical component in the model. As such, results would not be expected to be sensitive to having density dependence act on both age of first breeding and juvenile natural mortality rates.

For a particular cohort, the juvenile natural mortality rate to age 5 is modelled using the following non-linear function:

$$M_j^5 = 4M - (4M - \bar{J}_M)(B_y/\bar{B})^\gamma \quad \text{eqn 8}$$

where B_y is the current year's number of breeding pairs. Equation 8 provides a non-linear function joining the

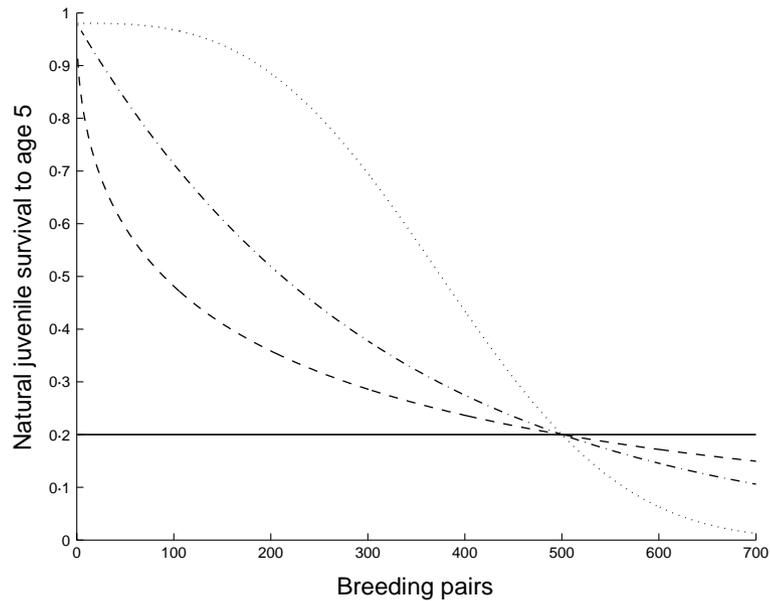


Fig. 3. The non-linear function specifying the relationship between juvenile survival to age 5 (excluding fishing mortality) and the number of albatross breeding pairs as a function of the control parameter γ . This example assumes an equilibrium number of breeding pairs of 500. Solid line, $\gamma = 0$; dashed line, $\gamma = 0.5$; dotted and dashed line, $\gamma = 1$; dotted line, $\gamma = 3$.

point (\bar{B}, \bar{J}_M) , i.e. the equilibrium number of breeding pairs and equilibrium juvenile natural mortality rate to age 5, to the minimum juvenile mortality rate to age 5 at zero breeding pairs. The minimum juvenile mortality rate to age 5 is set to that which would be attained if juveniles' dynamics mimicked that of adults, $4M$. The γ term controls the level of compensation (e.g. $\gamma = 0$ implies density-independent juvenile survival to age 5). The annual instantaneous juvenile mortality rate for the cohort is $M_J^5/4$, assuming 4 years as a juvenile after 1 year as a chick. Total juvenile survival to age 5 for a cohort is $\exp(-M_J^5)$ less the cumulative effects of fishing on the juveniles over 4 years. Figure 3 gives examples of juvenile survival to age 5 (excluding fishing mortality) for different levels of the control parameter γ .

INITIAL CONDITIONS

The initial numbers at age in deterministic equilibrium are found by iterating the resource dynamics equations from a unit number of fledglings, and adjusting a free parameter, e.g. juvenile mortality M_J , so as to equate the output number of fledglings to the initial number of fledglings. To obtain a particular equilibrium number of breeding pairs, \bar{B} say, the unit number of juveniles is multiplied by \bar{B}/\hat{B} , where \hat{B} is the equilibrium number of breeding pairs found when iterating from the unit number of fledglings.

FITTING PROCEDURE

The objective function minimizes the sum of squared residuals across four time-series of response variables. In doing this, it is necessary to specify the relative weights given to each series. A sequential procedure

was used to assign the relative weights. This was done by fitting to an individual response variable only and recording the resulting sum of squared residuals:

$$S_i = \sum_{j=1}^{n_i} (Y_{i,j} - \tilde{Y}_{i,j})^2, \quad \text{eqn 9}$$

for $i = 1, \dots, n$, where n is the number of response variables. The number of observations for response variable i is n_i . The j^{th} observed record is given by $Y_{i,j}$ and $\tilde{Y}_{i,j}$ is the j^{th} model-predicted value from fitting to response variable i only.

The reciprocal value of S_i was then used to weight that response variable. Thus, the relative weight given to the different response variables becomes approximately equivalent. In other words, the following equation is minimized for a particular parameter set:

$$\sum_{i=1}^n \frac{1}{S_i} \sum_{j=1}^{n_i} (Y_{i,j} - \hat{Y}_{i,j})^2, \quad \text{eqn 10}$$

where $\hat{Y}_{i,j}$ is the j^{th} model-predicted value when all response variables are used in the minimization.

The response variables considered are the annual (i) number of breeding pairs, (ii) number of birds fledged, (iii) estimated juvenile survival to age 5 and (iv) estimated total adult survival. The sum of squared residuals is used to fit the model to the observations. The parameters adjusted to achieve the minimization are (i) the catchability coefficient, q_J , (ii) the density-dependence parameter, γ , (iii) the equilibrium number of breeding pairs, \bar{B} and (iv) the fractional decrease in catch due to the introduction of catch mitigating measures, q_m , since 1990. All other parameters are input to the model as constants (Table 2).

To examine the sensitivity of the model results to differences in vulnerability of adults and juveniles to

Table 2. The fixed and estimated parameters of the model

| Parameter | Value | Reference |
|---|---|---|
| Age at first breeding | 10 | Weimerskirch, Brothers & Jouventin (1997) Croxall <i>et al.</i> (1990, 1998) |
| Maximum age | $A_m = 70$ | J. Croxall, personal communication |
| Adult natural mortality | $M = 0.02$ | Tuck (1999) |
| Chick natural mortality | $M_c = 0.2$ (Crozet Islands) $M_c = 0.4$ (South Georgia) | Weimerskirch, Brothers & Jouventin (1997) Croxall <i>et al.</i> (1990, 1998) |
| Juvenile catchability coefficient | $q_j = 1.5$ | Tuck (1999) |
| Return rates | $\alpha = 0.741$ $\beta = 0.80$ $p_f = 0.80$ | Croxall <i>et al.</i> (1990) Tuck (1999) |
| Introduction of mitigation | 1990 | Klaer & Polacheck (1998) |
| Equilibrium breeding pairs | \bar{B} | Estimated |
| Density dependence control | γ | Estimated |
| Mitigation response variable | q_m | Estimated |
| Equilibrium juvenile natural mortality to age 5 | \bar{J}_M | Estimated |

longlining, separate parameters for adults and juvenile catchability were included in the model specification. However, it was found that there is insufficient information in the response variables to provide meaningful estimates of their relative vulnerability, q_j . This parameter, the juvenile catchability coefficient, q_j , the density-dependent response parameter, γ , and the weights, S_i , are confounded. The procedure for selecting the weights is discussed in detail in Tuck (1999), where it is shown that the overall results are insensitive to the choice of weights and the value for q_j . Similar model responses are achievable for different combinations of adult and juvenile catches. The main determinant of the population trajectories is the overall number of removals (when discounting for the lower contribution to future generations because of higher juvenile natural mortality rates). Thus, given the current data, the model cannot discriminate among values for q_j . However, very low values for q_j resulted in a very strong density-dependent response, which was considered less realistic (Tuck 1999). Overall, the model results are robust to possible differences in catchabilities and this means that results only need to be provided for a single set of parameters for the catchabilities. We have selected a value of $q_j = 1.5$ for presentation.

Results

Model results are classified according to the particular wandering albatross population being considered and assumptions made about the spatial distribution of wandering albatrosses across the Southern Ocean. Two hypotheses are considered regarding the spatial distribution of wandering albatrosses, namely that they are distributed uniformly across the Southern Ocean, or that their spatial distribution is proportional to the longline fishery distribution. Both of these hypotheses constrain the spatial extent of the distribution in the Southern Ocean to latitudes between 30° S and 60° S.

CROZET ISLANDS

Albatross spatial distribution proportional to effort

Applying the proportional to effort model to the Possession Island population yielded point estimates for the parameters of $q_j = 3.97 \times 10^{-9}$, $\gamma = 2.67$, $\bar{B} = 477$ and $q_m = 0.1$, with a weighted sum of squared residuals of 3.63. Figure 4a shows the time-series of predicted female abundances for adults (breeding and non-breeding combined) and juveniles. The model predicts a gradual decline in the numbers of adult female birds from 997 in 1960 through to the early 1980s. Thereafter abundances stabilized and then increased from a low of 557 adult females in 1987 to 605 in 1995. The model estimates that the abundance of female juveniles declined initially from 617 to approximately 570 in 1969. Juvenile abundance then stabilized and increased to pre-exploitation levels by the early 1980s. From 1989 juvenile abundance is estimated to have increased further to approximately 646 female birds by 1995. This model predicts that tuna longlining could have resulted in a net decline of approximately 39% in the number of adult females over the period 1960–95 (Fig. 4a).

Figure 4b shows the time-series of predicted female by-catch for juveniles and adults. By-catch gradually increased from relatively low levels in the early 1960s to between 30 and 50 females per year in total through the 1970s and 1980s. From 1990, when modelled mitigation measures are introduced, the level of predicted by-catch initially declines, but then increases to about 40 female birds by 1995. While mitigation measures are predicted to have decreased by-catch from the Japanese fleet since 1990, the increase in predicted by-catch is due to the large increase in non-Japanese effort from 1993 (Fig. 1).

The predicted trajectories and the observed data for the number of breeding pairs, number fledged, juvenile survival to age 5 and total adult survival are given in Fig. 5a–d. These figures generally show good correspondence between the predicted values and

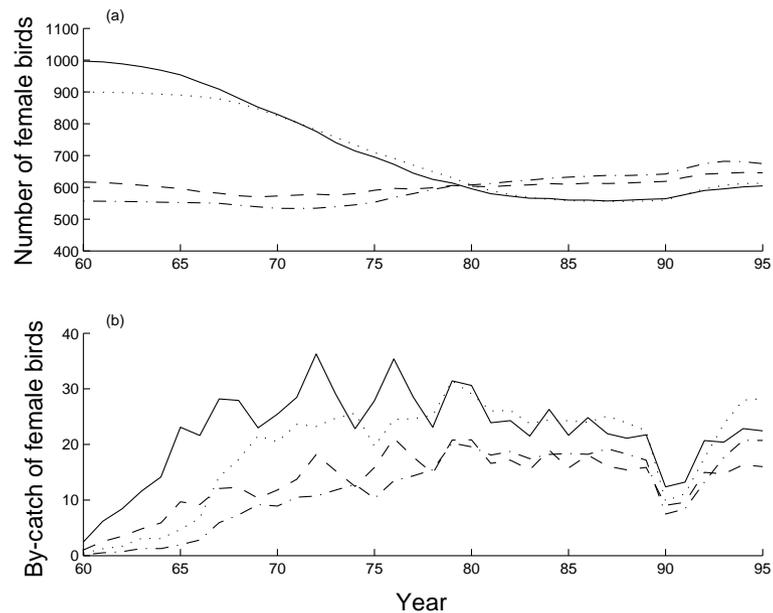


Fig. 4. (a) The predicted time-series of female adult and juvenile abundance as applied to the Possession Island population of wandering albatross. (b) The predicted time-series of female by-catch for juvenile and adult Possession Island wandering albatrosses. Trajectories with label (E) assume that the albatrosses' spatial distribution is proportional to the Southern Ocean longline effort, while (U) assumes that the albatrosses' spatial distribution is uniformly distributed across the Southern Ocean. Solid line, adults (E); dashed line, juveniles (E); dotted line, adults (U); dotted and dashed line, juveniles (U).

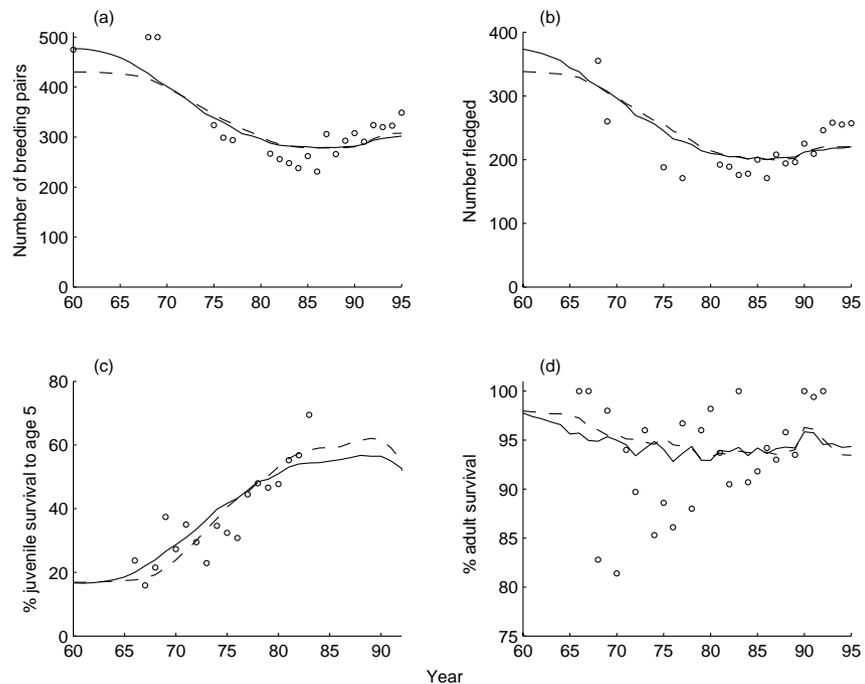


Fig. 5. The predicted (line) and observed (circle) values for (a) breeding pairs, (b) numbers fledged, (c) juvenile survival to age 5 and (d) adult survival for the Possession Island wandering albatross population. The solid line shows predicted trajectories when it is assumed that the albatrosses' spatial distribution is proportional to the Southern Ocean longline effort, while the dashed trajectories make the assumption that the albatrosses' spatial distribution is uniformly distributed across the Southern Ocean.

observed values across all years of the study, with the exception of the most recent years (see the Discussion). The values for total adult survival calculated from the observed data are quite variable from one year to the next, especially in the early years of the census, and so the predicted values do not match the observations as well as those for the other fitted variables.

Uniform albatross spatial distribution

The point estimates for parameters as estimated by the uniform spatial distribution model are $q_J = 74.9 \times 10^{-9}$, $\gamma = 3.81$, $\bar{B} = 431$ and $q_m = 0.1$, with a weighted sum of squared residuals of 3.85. Figure 4a shows the time-series of predicted female abundances for adults

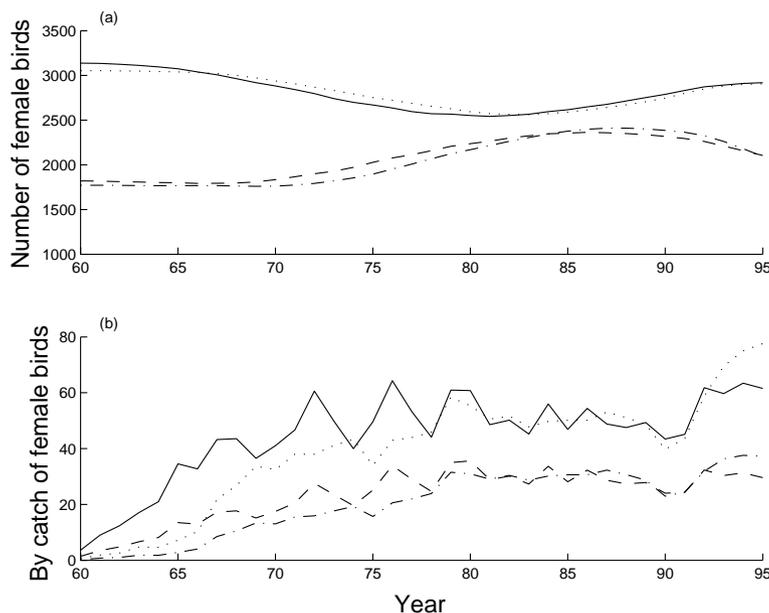


Fig. 6. (a) The predicted time-series of female adult and juvenile abundance as applied to the Bird Island population of wandering albatross. (b) The predicted time-series of female by-catch for juvenile and adult Bird Island wandering albatrosses. Trajectories with label (E) assume that the albatrosses' spatial distribution is proportional to the Southern Ocean longline effort, while (U) assumes that the albatrosses' spatial distribution is uniformly distributed across the Southern Ocean. Solid line, adults (E); dashed line, juveniles (E); dotted line, adults (U); dotted and dashed line, juveniles (U).

and juveniles. These results are generally similar to those for the proportional to effort model. Estimated adult female abundance in 1960 was 900 birds. Abundance remained stable until the early 1970s, when a gradual decline in abundance occurred through to the mid-1980s. From 1988 the estimated numbers of adult females increased from a low of 556 birds and was equal to 613 birds by 1995.

From a pre-exploitation abundance of 556, the predicted number of juvenile females gradually decreased through the late 1960s and early 1970s before increasing in the late 1970s. Estimated juvenile abundance remained stable at approximately 630 birds through the 1980s before rising once again to be 674 juvenile females in 1995. Over the period 1960–95, this model predicts a net decline of approximately 32% in the number of adult females as a potential consequence of Southern Ocean tuna longlining (Fig. 4a).

The predicted female by-catch for adults and juveniles is shown in Fig. 4b. The uniform distribution model predicts an initially smaller and overall less fluctuating by-catch than that predicted by the model assuming the spatial distribution of the birds is proportional to longline effort. The total by-catch across both juveniles and adults was between 40 and 50 females per year during the peak catch period in the 1980s.

The observed and predicted numbers of breeding pairs, number fledged, juvenile survival to age 5 and total adult survival are given in Fig. 5a–d. During the initial years of the study, the predicted numbers of breeding pairs do not appear to fit the observed data as well as for the proportional to effort model.

SOUTH GEORGIA

Albatross spatial distribution proportional to effort

Applying the proportional to effort model to the Bird Island population of wandering albatrosses yields the following point estimates for the parameters $q_J = 1.84 \times 10^{-9}$, $\gamma = 5.1$, $\bar{B} = 1621$ and $q_m = 1.0$, with a weighted sum of squared residuals of 9.25. Figure 6a shows the time-series of predicted adult and juvenile female abundance. Abundance remained at approximately pre-exploitation levels until the late 1960s, whereupon juvenile abundance increased and adult abundance declined. The abundance of adult females declined from a pre-exploitation level of 3138 to a low of 2542 in 1981 (a net decline of approximately 19%), after which the predicted female adult abundance gradually increased to approximately 2919 birds in 1995 (but note that this model does not provide a good prediction of the observed number of breeding pairs). Juvenile female abundance increased to a peak of 2364 birds in 1986 and then steadily declined to 2105 birds in 1995.

The predicted by-catch of juvenile and adult birds is shown in Fig. 6b. By-catch gradually increases through the 1960s to a peak of approximately 100 female birds in 1976. Catch then declined before increasing markedly in the 1990s. The total predicted female by-catch in 1995 was 91 female birds.

Figure 7a–d shows the predicted values against observations for the number of breeding pairs, number fledged, juvenile survival to age 5 and total adult survival. A poor fit to the observed number of breeding

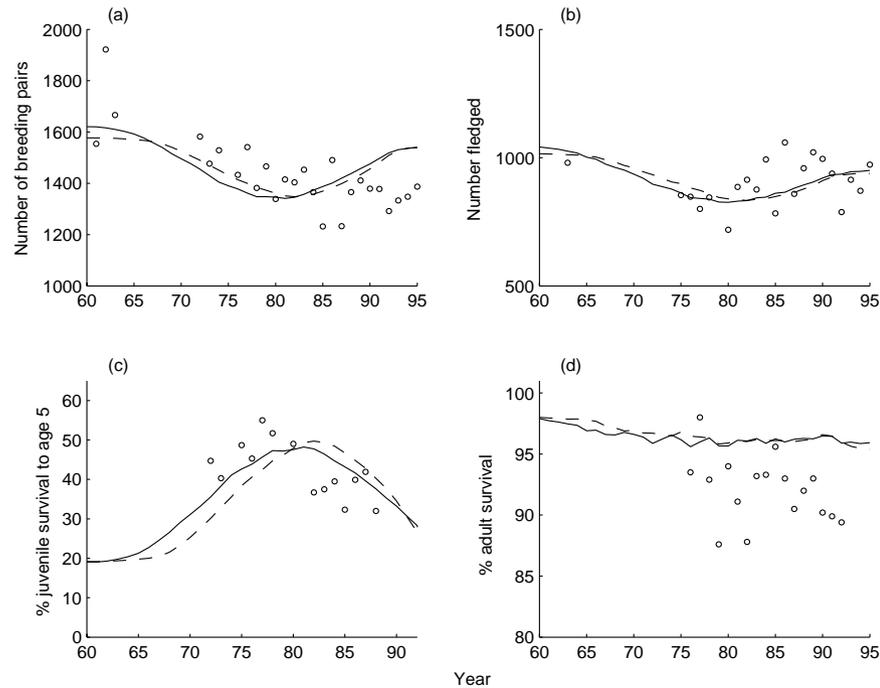


Fig. 7. The predicted (line) and observed (circle) values for (a) breeding pairs, (b) numbers fledged, (c) juvenile survival to age 5 and (d) adult survival for the Bird Island wandering albatross population. The solid line shows predicted trajectories when it is assumed that the albatrosses' spatial distribution is proportional to the Southern Ocean longline effort, while the dashed trajectories make the assumption that the albatrosses' spatial distribution is uniformly distributed across the Southern Ocean.

pairs is evident in Fig. 7a. The model underestimates the number of breeding pairs up to approximately 1984 and then overestimates breeding pairs. The predicted number of birds fledged and the survival to age 5 show a reasonable fit to the observed data; however, total adult survival appears to be overestimated.

Uniform albatross spatial distribution

If the spatial distribution of albatrosses is assumed to be evenly distributed across the Southern Ocean, then the model parameters estimated for the Bird Island population are $q_j = 33.3 \times 10^{-9}$, $\gamma = 6.5$, $\bar{B} = 1577$ and $q_m = 1.0$, with a weighted sum of squared residuals of 10.49. Figure 6a shows the time-series of predicted female adult and juvenile abundances. As with the previous spatial model, predicted abundances showed only marginal changes until the early 1970s, when juvenile abundance increased and adults declined in abundance. The number of adult females reached a low of 2563 birds in 1983 from a pre-exploitation level of 3054 birds (a net decline of 16%), before increasing to 2906 birds in 1995 (as before, it should be noted that this model does not provide a good prediction of the observed number of breeding pairs). The number of female juveniles increased from a pre-exploitation level of 1771, to a high of 2411 in 1987.

The predicted by-catch of juvenile and adult females is shown in Fig. 6b. Catch increased markedly from 1966 before stabilizing at approximately 80 female birds per year during the 1980s. During the 1990s by-

catch decreased due to mitigation before increasing once again with the increase in non-Japanese effort (Fig. 1).

As with the previous spatial model, the model predictions appear to under- then overestimate the observed number of breeding pairs (Fig. 7a). The fit to the number of birds fledged appears reasonable; however, fits to the juvenile survival to age 5 and total adult survival are poor (Fig. 7b–d).

Discussion

The models presented in this paper are a first attempt at modelling the potential interactions between two well-studied populations of wandering albatrosses and Southern Ocean longline fisheries. The model predicts that the impact of the longline catches on these populations is substantial, as without any longline by-catch the modelled population trajectories would have remained at their equilibrium levels. The results illustrate the potential of using a fisheries modelling approach, which incorporates density dependence and explicitly models the catch, in the context of modelling the fishery interaction problems currently facing seabirds. The simulations of wandering albatross population dynamics appear to fit the published data for the Possession Island population in a reasonably consistent fashion (Fig. 5). However, the fit to observations from South Georgia is generally much poorer (Fig. 7). The results also suggest different implications about each population's behaviour (spatial dynamics and life history)

and their response to the interaction with longline fisheries. It should be noted that the models were explored over a wide range of different parameterizations and the general pattern of results was similar (Tuck 1999).

The two albatross–fishery spatial distribution hypotheses presented here are used to model the potential overlap in distributions of the albatross populations and Southern Ocean longline fisheries. These hypotheses make quite different predictions about the most recent trends in abundance and particularly the trends in the number of albatrosses incidentally caught. Total by-catch is predicted to be lower (for similar predicted abundance trends) under the uniform hypothesis. The estimated catchability coefficient, assuming the albatrosses' spatial distribution is proportional to effort, is markedly lower than if it is assumed that the albatrosses have a uniform spatial distribution. This is due to the greater catches required when assuming a uniform distribution to compensate for albatrosses not being in cells of high fishing effort. The 'true' catchability is likely to be greater than that from assuming that the albatrosses' distribution is proportional to that of fishing effort.

The model fit to the Bird Island population is poorer than might have been anticipated, particularly in contrast to the fit to the data for the Possession Island population. This may be a consequence of the sole use of pelagic tuna longline data in the simulations. Since the late 1980s demersal longline fisheries for Patagonian toothfish *Dissostichus eleginoides* have developed rapidly in the Southern Ocean (Croxall & Prince 1996). Data from the demersal fishery for Patagonian toothfish were not available at the time of this study. This fishery was initially concentrated in waters off Patagonia and South Georgia and effort has only recently spread to other regions. The reported number of hooks deployed in waters surrounding South Georgia has increased from approximately 5 million hooks in 1989 to nearly 15 million in 1997 (data provided by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR)). Seabirds are a significant by-catch of the Patagonian toothfish longline fishery in CCAMLR waters, with an estimated 0.215 birds caught per 1000 hooks in 1996. Nearly 100 wandering albatrosses were estimated to have been killed on longline hooks directed at Patagonian toothfish during this season alone (SC-CAMLR 1996).

The continued decline in abundance of Bird Island breeding pairs may, to some extent, be due to the increased presence of the fishery for Patagonian toothfish. As such, the model is not able to impart the appropriate level of effort in the latter years of the study in order to continue the declining abundance trend. Instead, the model compensates for this by choosing a high estimate for the mitigation parameter, $q_m = 1.0$, for both spatial models. This essentially puts greater weight on latter years' effort, thereby increasing by-catch. However, the compensation is clearly not substantial enough to allow a good fit to the observed data.

The best fit is then one that underestimates abundance in the initial years and then overestimates abundance in the latter years, as seen in Fig. 7a.

The estimated tuna longline effort used in fitting the model is based on reported effort. There is likely to have been effort that has not been accounted for in the available data. If this has been constant spatially and temporally, such under-reporting would have no effect on the results (i.e. the estimated catchability would be lower). However, a systematic temporal and/or spatial shift in where unreported effort occurred could induce a lack of fit into the model. The Japanese longline effort data are generally considered the most reliable. Since the Japanese longline fishery has traditionally been the dominant longline fishery in the Indian Ocean south of 30° S, this could explain the better fit to the Crozet Islands data. In the South Atlantic, the Japanese longline fleet has not been the dominant tuna fishery. Instead, fleets from South America and Taiwan have played an important role. The size of these fisheries has varied over the years and the data from them are less reliable. As such, this may be contributing to the lack of fit to the South Georgia data.

Weimerskirch, Brothers & Jouventin (1997) and Prince *et al.* (1998) suggest that a strong link has existed between the pelagic tuna fishery and the Crozet Islands wandering albatross population. This conclusion is supported by the results in this paper. During the 1970s and early 1980s the distribution of pelagic longline effort was in close proximity to the Crozet Islands, and corresponded to a period of rapid decline in the breeding population (Weimerskirch, Brothers & Jouventin 1997). During the same period, the South Georgia populations declined at a much slower rate (Croxall *et al.* 1990; Prince *et al.* 1998). However, since the mid-1980s pelagic longline effort has decreased around the Crozet Islands (Fig. 1) and the spatial distribution of effort has been further from the islands and more concentrated (Weimerskirch, Brothers & Jouventin 1997).

The decline in pelagic longline effort, minimal demersal longlining and the influence of mitigating devices may, to some extent, explain the recovery in Crozet Island breeding pairs seen in Fig. 5a. Until recently the level of effort targeting Patagonian toothfish has been much greater near the breeding colonies on South Georgia than the Crozet Islands. As such, it is not surprising that the two populations show a different response to the development of the fishery. Very little effort was directed toward Patagonian toothfish in the waters surrounding the Crozet Islands until 1995. However, fishing effort was substantial near the Crozet Islands in 1996. The estimated combined reported and unreported catch of Patagonian toothfish from this area was about 25% of the predicted median pre-exploitation spawning biomass (CCAMLR 1996). Given the known seabird by-catch problem in this fishery, the potential impact of the recent increase in demersal longline effort in the region of the Crozet

Islands is cause for considerable concern. Likewise, the recent substantial increase in longlining off South America, a key foraging area for South Georgia wandering albatrosses (Croxall & Prince 1996; Tuck *et al.* 1999), may be contributing to their continued decline (Prince *et al.* 1998).

As noted in the Methods, the sums of squares for the Crozet Islands and South Georgia data responded differently to changes in the value of M . For the Crozet Islands' data, the best fit in terms of the sums of squares occurs with very low values of M , while for the South Georgia data the fit improved with higher values of M . The reason for this has to do with differences in the trajectories of the number of breeding pairs in the most recent years. In order to obtain the rapid increase in breeding pairs seen in the Crozet Islands' data, the estimates of M are low to enable a very rapid recovery. For the South Georgia population a higher value of M is estimated to keep the population from recovering due to the decline in effort that occurred in the late 1980s and early 1990s. In both cases, the M -value becomes unrealistic. As already discussed, the most likely explanation for this behaviour in the South Georgia population is that Patagonian toothfish longline data are not accounted for in the model. For the Crozet Islands' data, the model cannot achieve quite as fast a recovery as is seen in the data. The discrepancy in this case may be due to limitations in the modelling of the overlap in distributions of the birds and longline effort. The decline in effort in the late 1980s and early 1990s appears to have been disproportionately greater around the Crozet Islands than the overall decline. Because, during breeding, adult birds spend more time near the islands, the decrease in their vulnerability to longlining may have been greater than the overall decline in longline effort. These problems in fitting the most recent data were also seen in variants to the model in which a separate parameter for the catchability of non-Japanese vessels was included. In these variants, improved fits were obtained. However, the catchability parameter in the Crozet Islands case was zero and a high catchability was obtained for the South Georgia data. This reflects the fact that non-Japanese effort increased in the late 1980s (Fig. 1). There is a need for improved models for the overlap of the birds and the fishing fleets in future applications of the model.

While the declines in the observed number of breeding pairs for both populations have been quite substantial, it is interesting to note the corresponding compensation in the number of juveniles. Wandering albatrosses have a relatively low reproductive output, which one would not normally associate with a strong compensatory effect. However, it is clear from Figs 4a and 6a that the predicted number of juveniles increases markedly as the number of breeding females declines. The compensation can be seen implicitly from the observed temporal changes in juvenile survival to age 5 (Figs 5c and 7c). While the predicted increase in juvenile abundance may sustain the population through

periods of increased mortality, one should be careful not to overstate the sustainability of the population. It is apparent that there is only a small difference in magnitude between a sustainable and unsustainable take. The continuing decline of the Bird Island population in contrast to the Possession Island population reflects the delicate nature of this balance. The low levels of absolute incidental catches that are required to explain the observed declines means that direct monitoring of the incidental catches to determine if the estimates of the absolute catches from a given population are above or below a sustainable level would be extremely difficult (e.g. requiring very high levels of at-sea observer coverage).

Obviously, model results will benefit from more precise information on albatross spatial distribution, as the two hypotheses used are simplifications made to bracket the populations' possible spatial distributions. Every effort should be made to continue research into the foraging distributions of these birds using satellite tracking, archival tagging, bird banding and by-catch data (Jouventin & Weimerskirch 1990; Prince *et al.* 1998; Tuck *et al.* 1999). In particular, there is a need for data on at-sea distributions of juveniles, non-breeding adults and at times outside of the breeding season. In addition, a high priority should be placed on the collection of accurate (and in many cases any) effort data from fisheries that target species within wandering albatross foraging ranges. In particular, greater monitoring is required on the substantial and increasing Southern Ocean Taiwanese tuna fishery and many fisheries for Patagonian toothfish, as these have potentially large interactions with albatross populations.

The results presented here are not meant to be a definitive assessment. They do, however, provide valuable insights into the likely impact of incidental takes on these populations and their demographic responses to such impacts. They demonstrate the importance of integrating the demographic and fishery data in order to be able to assess fully the populations and effects of the incidental takes. They also identify critical areas where more information is required in order to improve any quantitative predictions of the model. In particular, given the developmental stage of the modelling work and the existing gaps in available data, it would be inappropriate to use the model results to estimate or predict whether the populations are recovering or declining further. Such assessments should be based on the continuation of the direct observations and monitoring of these populations.

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