

Modelling impacts of long-line fishing: what are the effects of pair-bond disruption and sex-biased mortality on albatross fecundity?

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Abstract

Long-line fishing mortality poses a significant threat to many large procellariiform seabirds. To date, estimates of impacts have concentrated on lower survival rates, largely ignoring the costs to fecundity resulting from disruption of breeding pairs and skews in sex ratio. A comparative, stochastic, individual-based model was used to investigate these costs for the wandering albatross *Diomedea exulans*. Ignoring the time taken to replace a lost mate overestimates fecundity by 13–18%, resulting in annual population growth rates (λ) being 0.006–0.007 too high. Long-line mortality exacerbates this cost, which becomes more substantial with increasing demographic skew resulting from female-biased mortality. At moderate levels of long-line mortality (2–4% per year), 80% female-biased mortality reduces fecundity by 9–27% and λ by 0.003–0.010 relative to models with random mortality. Biased sex ratios accumulate and, unlike reduced survival, their impacts on albatross demography persist after long-line mortality ceases. Estimates of the demographic costs of long-line mortality should incorporate individual-level effects, especially where mortality is sex-biased.

INTRODUCTION

Accidental capture and drowning on long-line fishing hooks is a significant threat to the long-term persistence of most albatross and large petrel populations (Brothers, Cooper & Løkkeborg, 1998; Gales, 1998; BirdLife International, 2004). Extrapolation of observed rates of capture on long-line hooks indicates that long-line fisheries kill tens of thousands of seabirds annually (Brothers, 1991; Brothers *et al.*, 1998; Gales, Brothers & Reid, 1998; Tuck *et al.*, 2001; Ryan, Keith & Kroese, 2002). Decreases in seabird survival and recruitment rates measured at colonies coincide with periods of high fishing effort in areas of the ocean where birds forage (Weimerskirch & Jouventin, 1987; Croxall *et al.*, 1990; Croxall & Rothery, 1991; Nel *et al.*, 2003). This additional mortality is sufficient to have caused many of the population decreases observed at breeding colonies (Croxall & Rothery, 1991; Tuck *et al.*, 2001). Currently all 21 albatross species are listed as threatened or near-threatened (BirdLife International, 2004), making them the most threatened bird family.

Several studies have modelled the impacts of long-line mortality on seabird populations, testing population sensitivity to life-history parameters (Croxall *et al.*, 1990; Croxall & Rothery, 1991; Moloney *et al.*, 1994), assessing extinction risk (Inchausti & Weimerskirch, 2001, 2002)

and investigating the consequences of spatial overlap between albatrosses and fishing effort (Tuck *et al.*, 2001). Changes in survival rates have greater demographic impacts than changes in breeding success and frequency (Weimerskirch & Jouventin, 1987; Croxall *et al.*, 1990; Weimerskirch, Brothers & Jouventin, 1997; Nel *et al.*, 2003) and thus the impacts of long-line mortality on fecundity have been largely ignored. However, fecundity depends not only on the reproductive output per breeding adult but also on the proportion of adults that are paired and reproductively active. This parameter is not easily measured at breeding colonies and is thus often ignored. Here, we refer to fecundity as the mean number of offspring produced per adult (with or without a breeding partner) per year. This includes birds that are of reproductive age but not paired and thus not regularly present at breeding colonies. Albatrosses and large petrels rely on strong intra-pair co-operation to rear chicks successfully and typically invest much time in mate choice and pair formation (Tickell, 1968, 2000). The loss of a partner has reproductive costs beyond the immediate breeding attempt (Jouventin, Lequette & Dobson, 1999), because breeding is delayed while a new mate is sought (Pickering, 1989; Jouventin *et al.*, 1999; Nel *et al.*, 2003). As adult mortality increases, more pairs are disrupted, reducing fecundity. A skewed sex ratio among potential breeders further increases this cost, because some individuals of the more abundant sex will be unable to find a partner. Significant sex-biased long-line mortality has been reported for several seabird species

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Table 1. Model input parameters and their reported ranges for a slowly increasing wandering albatross population experiencing no long-line mortality

Parameter	Input	Range	References
Adult survival	0.96	0.95–0.97	Tickell (1968); Weimerskirch & Jouventin (1987); Weimerskirch <i>et al.</i> (1987, 1997)
Juvenile survival	0.87	0.84–0.90	Weimerskirch <i>et al.</i> (1997); Nel <i>et al.</i> (2003)
Maximum age	70*	at least 45	Cooper <i>et al.</i> (2002)
Earliest breeding age	9	7–9	Weimerskirch & Jouventin (1987); Weimerskirch (1992)
Breeding success	0.70	0.64–0.76	Croxall <i>et al.</i> (1990); Weimerskirch (1992); Weimerskirch <i>et al.</i> (1997); Nel <i>et al.</i> (2003)

*When the model is run with survival and reproductive rates as given, approximately one in 1000 birds reaches 70 at stable age distribution.

(e.g. Bartle, 1990; Murray *et al.*, 1993; Gales *et al.*, 1998; Ryan & Boix-Hinzen, 1999).

Previous models of long-line mortality have not considered explicitly the impacts of pair bond disruptions or skew in population sex ratios on fecundity and population growth rate. In this study we use an individual-based model (IBM) to estimate the costs of pair bond disruptions and skew in population sex ratio to wandering albatross *Diomedea exulans* (L.) fecundity and discrete annual population growth rate (λ). IBMs trace individuals through their life cycle, making it possible to investigate such costs by incorporating population behaviours dependent on individual-specific attributes (Caswell & John, 1992). The model also allows us to infer approximate levels of long-line mortality from observed survival rates.

METHODS

Study species

The wandering albatross displays extreme life-history traits (Table 1). Individuals only start breeding from age 9, lay a single egg and pairs raise, at most, one chick every 2 years. In the absence of long-line mortality, adult survival rates are high, resulting in stable pair bonds (divorce rates < 1%: Jouventin *et al.*, 1999; Nel *et al.*, 2003). Pair formation is a lengthy process, with most birds taking at least 3 years to re-mate after the loss of a partner (Pickering, 1989; Nel *et al.*, 2003). Jouventin *et al.* (1999) estimated that losing a mate reduces lifetime chick production by 15%, based on a mean reproductive lifespan of 22.4 and 14.9 years and re-pairing lags of 3.20 and 2.27 years for males and females, respectively.

The wandering albatross is classified as Vulnerable because its population is estimated to be decreasing at a rate equivalent to >30% over 3 generations (IUCN criteria A1a, A1d: BirdLife International, 2004). Long-line mortality is regarded as the major cause of population decreases (Croxall & Gales, 1998), with an estimated 50 000 birds killed between 1960 and 1990 (Weimerskirch *et al.*, 1997). Population decreases have been documented at most large colonies, with the worst affected decreasing at > 6% per year during the 1970s and 1980s (Weimerskirch, Clobert & Jouventin, 1987; de la Mare & Kerry, 1994; Weimerskirch *et al.*, 1997).

Females have lower adult survival rates than males, apparently because they tend to forage farther north than males, in waters where pelagic long-line fisheries are most active (Weimerskirch & Jouventin, 1987; Prince *et al.*, 1992; Croxall, Black & Wood, 1999). This results in male-biased populations. At the Crozet Islands males have been estimated to outnumber females by 8:5 (Jouventin *et al.*, 1999). The shortage of adult females causes males to delay breeding and re-pairing for longer than females (Jouventin *et al.*, 1999; Nel *et al.*, 2003).

Model construction

We constructed a behaviour-explicit IBM for a wandering albatross population using Jbuilder (Borland Software Corporation, 2001; see electronic Appendix for IBM code). A post-breeding population was modelled over an annual time-step (Table 2). The age, sex and breeding-related attributes (pairing status, identity of partner, success of previous breeding attempt, time since last breeding, time since last paired) of each individual were 'monitored' at each time step. Birds were assumed to be 'adult' and potential breeders at 9 years old; younger birds were treated as immatures. For the baseline model with no long-line mortality, input parameters were based on empirical data from slowly increasing populations with no or little fishing mortality (Table 1). Starting population age structure was set to a stable age distribution, based on values derived from running the model until population growth and age structure stabilised. Because the wandering albatross is a biennial breeder, the reproductive activity of an individual in 1 year depends on its reproductive activity in the previous year. To account for this, the initial population of adults was assigned reproductive histories so that the ratio of breeders to non-breeders was correct from the first year of the model.

The primary goal of this study was to compare the performance of populations subject to different long-line mortality rates, rather than to predict absolute population growth rates. Comparative models probably provide more robust results and allow simplifying assumptions (Starfield, 1997; Bessinger & Westphal, 1998). We assumed uniform breeding success with age, despite some empirical evidence of age-dependent breeding success (Nel *et al.*, 2003) and only differentiated survival rates between adults and immatures, given few detailed

Table 2. The main components of model behaviour (Activity) that each albatross (A_1) goes through at each time step, listing the questions (Q) asked and the rationale followed to decide the outcome of an activity

Activity	Question	Rationale and outcome
Ageing	–	Age by 1 year
Mortality	1. Has A_1 reached max. age? 2. Does A_1 die?	If $ \text{age} = 70 $, remove from population and unpair partner (if paired). If not, go to Q2 If $ \text{RN} > (1 - \text{natural mortality}) \times (1 - \text{long-line mortality}) $, remove from population and unpair partner (if paired). If not, go to Q3. Dependent on the age and sex of A_1 .
Pairing	3. Can A_1 pair? 4. Is A_1 ready to pair? 5. Is a partner available?	If $ \text{age} > (\text{age of earliest breeding} - 1) $ and A_1 is not paired, go to Q4; if not, go to Q6. If $ \text{RN} < \text{probability of pairing} $ (given time since last paired; see Table 3), go to Q5 If an individual of the opposite sex is available and ready to pair, then A_1 pairs
Breeding	6. Can A_1 reproduce? 7. Is A_1 ready to breed? 8. Is breeding successful?	If A_1 is paired and female, go to Q7; if not, cycle is complete If A_1 did not breed successfully last year, go to Q8; if not, cycle is complete If $ \text{RN} < \text{breeding success} $, create a new individual with $\text{age} = 0$ and of random sex

Every A_1 completes an activity before the entire population moves on to the next activity.
RN, randomly generated number between 0 and 1.

survivorship data (e.g. Weimerskirch & Jouventin, 1987; Weimerskirch, 1992). The model was run for only 20 years to reduce the impact of unknown factors such as density dependence (e.g. Croxall *et al.*, 1990). However, it is unlikely that density dependence is a significant factor, because populations are probably below carrying capacity due to long-line mortality and most projections result in shrinking rather than growing populations.

To select an appropriate starting population size (P_0) we ran 10 simulations for each of seven different P_0 values (range 100–10 000) to monitor population growth rate and random deviation in adult sex ratio with increasing P_0 , where:

$$\text{Deviation in Sex Ratio} = \text{Males/Females} - 1.$$

Because of demographic stochasticity, deviation in sex ratio decreased logarithmically with increasing population size (Spearman $r^2 = 0.758$, $P < 5 \times 10^{-7}$), tending to zero with increasing P_0 . Population growth rate mirrored this effect (Spearman $r^2 = 0.217$, $P < 0.001$), with the costs of random demographic stochasticity being reduced to almost zero for a starting population of >1000 . Consequently, we selected a starting population of 5000 and excluded data if the average population size after 20 years fell below 1000. This occurred only for the highest levels of long-line mortality. A population of 5000 has approximately 1275 breeding pairs, with an annual breeding cohort of some 700 pairs, which is typical for many wandering albatross colonies (Tickell, 2000).

There are no empirical data to assess the relationship between population size and the number of individuals killed on long-lines. Long-line mortality was simulated on the basis of a fixed proportion of the population rather than on absolute numbers, resulting in smaller actual numbers of birds killed with decreasing population size. This results in conservative estimates of long-line impacts for decreasing populations.

Model output included information on population size, structure and breeding activity. We focussed on: (1) adult sex ratio (males/females), (2) the proportion of unpaired adults, (3) the proportion of pairs disrupted each year,

(4) fecundity (the mean number of offspring produced per year per adult in the population) and (5) annual population growth rate (λ). Values of these parameters were calculated for each model year and averaged for each simulation ($n = 20$ years). In all experiments, 10 simulations were run for each scenario. Given low model stochasticity, this sample size was sufficient to assess the range of probable outcomes (see Results).

We tested model sensitivity to the time taken to re-pair (pairing lag), using four different lag scenarios (Table 3). The ‘zero lag’ scenario assumed that birds re-pair the season after losing a partner (actual lag = 1 year), effectively behaving as though they had not lost a partner. This was compared with three sets of empirical data: the ‘Bird Island female’ scenario is based on female lag times at Bird Island, South Georgia (Pickering, 1989) and the ‘Marion’ scenarios on data from Marion Island (Nel *et al.*, 2003). ‘Marion female’ values are from females only, whereas ‘Marion mean’ values are average lags of males and females combined. The ‘Marion female’ lag is close to the average of the three empirical data sets and was used as the standard lag in all subsequent trials.

To test the impact of long-line fishing, five levels of long-line mortality, spanning the probable range experienced by the species (Croxall *et al.*, 1990; Weimerskirch *et al.*, 1997; Nel *et al.*, 2003) were simulated: 1, 2, 4, 6 and 8% of birds killed per year, applied across all age classes. We also tested the effect of changes in the proportion of adults killed by comparing four levels of age bias (20, 35, 65 and 80% of the birds killed being adults) to the null model of random mortality (51% being adults at stable age distribution). The impact of increasing sex-biased mortality was tested for four levels of female bias, with 60, 70, 80 and 90% of adults killed being females.

Output ($n = 10$ runs) for all scenarios was tested for normality (Kolmogorov–Smirnov Normality Test; $P > 0.20$ assumed to be normal), and for homoscedasticity (Levene test) using Statistica (StatSoft Inc., 2000), to verify the suitability of parametric statistical tests. To compare population performance between different scenarios we used non-parametric tests where transformation was

Table 3. Probabilities of wandering albatrosses pairing 1–6 years after having lost a mate for the four lag scenarios and model output showing mean pairing lag (years), the proportion of unpaired adults, fecundity (offspring per adult per year) and population growth rate in the absence of long-line mortality

Lag scenario	Probability of pairing during year						Pairing lag (years)	% unpaired	Fecundity	Growth rate (λ)
	1	2	3	4	5	6				
Zero lag	1.00	1.00	1.00	1.00	1.00	1.00	1.14 (1.01–1.23)	2.4 (1.6–3.6)	0.202 (0.201–0.204)	1.0150 (1.0139–1.0164)
Bird Island female	0.00	0.49	0.48	0.92	1.00	1.00	2.54 (2.39–2.84)	16.5 (15.0–18.3)	0.178 (0.175–0.182)	1.0094 (1.0080–1.0103)
Marion female	0.03	0.16	0.85	0.75	1.00	1.00	2.62 (2.58–2.83)	16.8 (16.3–18.1)	0.177 (0.174–0.179)	1.0091 (1.0069–1.0106)
Marion mean	0.02	0.12	0.64	0.62	0.85	1.00	2.87 (2.78–3.11)	20.3 (18.0–22.0)	0.171 (0.167–0.173)	1.0076 (1.0062–1.0088)

Values are means followed by ranges in parentheses.

ineffective. Differences between scenarios were highly significant. Consequently we report only means (as single values) or ranges (as 2 values) and not test results.

RESULTS

In the absence of long-line mortality, model populations grew slowly, with all output parameters being realistic over the 20-year simulation period (Table 4). Given a natural adult mortality of 4%, 6–7% of pairs lost a partner each year. With no explicit pairing lag, only 2–4% of adults were unpaired (i.e. had no partner: Table 3), giving an average lag time of 1.1 years, average fecundity of 0.20 offspring per adult per year and average population growth rate (λ) of 1.0150 (Table 3). When explicit lags were incorporated into the model, a greater proportion of adult birds was unpaired (in the ‘Marion female’ lag scenario, 16–18%), reducing fecundity to 0.17–0.18 and population growth rate by 0.006–0.007 (Table 3). This resulted in a population 12–15% smaller after 20 years.

Adding long-line mortality exaggerated the differences between ‘zero lag’ and other lag scenarios, because the frequency of pair disruption increased, being almost double by 4% long-line mortality (Table 4). Consequently, the proportion of unpaired adults also increased, although not as rapidly as the frequency of pair disruption. This reduced fecundity, although only modestly relative to the marked changes in population growth rate. Given the direct cost of long-line mortality on population growth rate, reduced fecundity accounts for only 4–8% (calculated by comparing the model to the corresponding zero lag scenario) of the decreases in model population growth. This confirms that the impacts of random long-line mortality on population growth rate operate primarily through reduced survival rather than lower fecundity, especially where sex skews do not occur.

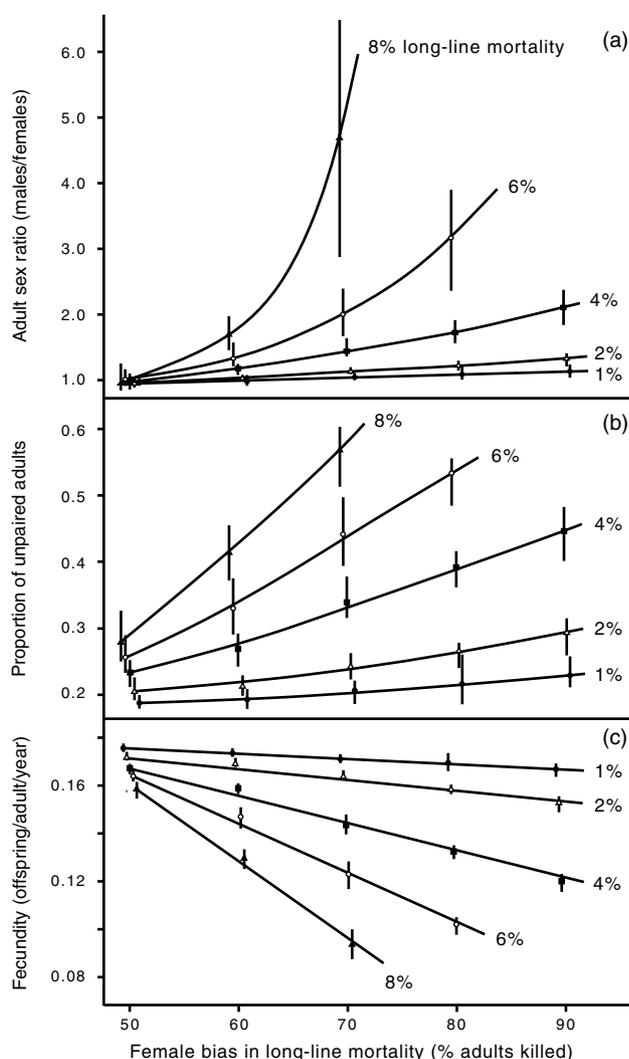
Sex- and age-biased mortality

In the absence of sex-biased mortality, adult sex ratios ranged from 0.98–1.04. Sex ratios increased with increasing female bias in long-line mortality. At higher levels of mortality, increase was more rapid, becoming exponential at 6–8% (Fig. 1(a)). The frequency of pair disruption showed similar effects. Combined with the reduced effective population size resulting from sex skew, this caused large increases in the proportion of unpaired adults (Fig. 1(b)) and decreases in fecundity (Fig. 1(c)). The failure to explicitly consider the effects of sex-biased mortality overestimated population performance, even for combinations of moderate levels of long-line mortality and bias (Table 5). For example, if 80% of adults killed are female, at 2% long-line mortality, fecundity is overestimated by 9%. This results in a population growth rate that is 0.003 too high. An increase to 4% mortality reduces fecundity by 27% and population growth rate by almost 0.01.

These results were derived using random long-line mortality with respect to age. Predictably, increasing

Table 4. Means and ranges ($n = 10$) of the proportion of pairs disrupted, the proportion of unpaired adults, fecundity (offspring per adult per year) and population growth rates for the 'Marion female' lag scenario under different levels of long-line mortality

Long-line mortality	% pairs disrupted	% unpaired	Fecundity	Growth rate (λ)
0%	6.5 (6.2–6.7)	16.8 (16.3–18.1)	0.177 (0.174–0.179)	1.0091 (1.0069–1.0104)
1%	7.9 (7.5–8.2)	18.5 (17.6–19.7)	0.175 (0.172–0.177)	0.9982 (0.9963–1.0000)
2%	9.3 (8.9–9.7)	20.2 (19.0–22.2)	0.172 (0.168–0.174)	0.9875 (0.9853–0.9896)
4%	12.5 (11.1–12.4)	22.7 (21.0–25.0)	0.167 (0.166–0.170)	0.9669 (0.9651–0.9691)
6%	16.9 (13.5–15.5)	24.9 (23.3–28.8)	0.164 (0.155–0.167)	0.9468 (0.9445–0.9497)
8%	18.0 (16.2–18.6)	27.6 (24.8–32.3)	0.158 (0.146–0.165)	0.9252 (0.9214–0.9291)

**Fig. 1.** The effects of female-biased adult mortality on the average sex ratio (a), the proportion of unpaired adults (b) and fecundity (c) of a wandering albatross population subject to different levels of long-line mortality. Data were excluded if $N_{20} < 1000$.

the proportion of adults among long-line mortalities exacerbated the impacts of pairing lags, resulting in lower fecundity and lower population growth rates (Table 6). However, for age-biased mortality the change in fecundity

was relatively minor and the impact on survival greatly outweighed the reduced fecundity.

Different levels of age-bias and long-line mortality resulted in different combinations of adult and immature survival rates (Fig. 2). Similarly, varying the degree of sex-bias and long-line mortality resulted in different combinations of adult male and female survival rates (Fig. 3). Thus levels of fishing mortality can be inferred, albeit crudely, from empirical estimates of survival data and the associated reductions in fecundity estimated (Table 7).

DISCUSSION

IBMs use the attributes of individuals to model population processes, allowing insights into interactions between factors operating at a variety of scales (Caswell & John, 1992; Gross *et al.*, 1992). Such bottom-up approaches have been criticised for incorporating unnecessary detail (e.g. Starfield & Bleloch, 1991), because model error increases with the number of parameters estimated. This happens particularly when parameter values are poorly known or highly variable (Bessinger & Westphal, 1998). However, the level of detail required should depend on the aims of the investigation and the quality and type of data available (Starfield, 1997). We based our model on robust empirical data for wandering albatrosses and used it primarily to assess relative impacts rather than predict absolute changes (Bessinger & Westphal, 1998). However, the model produced realistic output parameters where these could be tested. For example, model fecundity (0.17–0.18) is similar to empirical estimates (0.16–0.19), given 0.33–0.37 offspring produced per pair per year (Weimerskirch *et al.*, 1987; Jouventin & Weimerskirch, 1988; Nel *et al.*, 2003), 59% of pairs attempting to breed each year (Weimerskirch, Jouventin & Stahl, 1986) and c. 16% of adults being unpaired (our model).

What have we learned from the model? Not surprisingly, the time lost in finding a new mate significantly impacts fecundity and population growth rate. Jouventin *et al.* (1999) estimated a 15% reduction in lifetime chick production each time re-pairing occurs. However, the significance of this cost was not assessed in relation to more frequent pair disruptions resulting from long-line mortality. We did not use the model to estimate lifetime reproductive success, because the model was not designed

Table 5. The overestimation of fecundity and reduction in population growth rate associated with different degrees of sex-bias in long-line mortality (female bias) for different levels of fishery mortality (mortality)

Mortality	Overestimate of fecundity (%)				Reduction in growth rate (λ)			
	Female bias				Female bias			
	60%	70%	80%	90%	60%	70%	80%	90%
1%	0.9	2.2	3.6	5.6	0.0003	0.0010	0.0018	0.0025
2%	1.1	4.9	9.0	13.2	0.0004	0.0022	0.0034	0.0051
4%	5.4	16.6	26.7	40.1	0.0022	0.0059	0.0098	0.0142
6%	12.4	34.7	61.9	–	0.0054	0.0118	0.0177	–
8%	22.7	68.8	–	–	0.0069	0.0180	–	–

These values are followed by the associated reduction in population growth rate. No data are given for models where $N_{20} < 1000$.

Table 6. Change in fecundity and difference in population growth rate as a function of age-bias in long-line mortality (mortality), compared with the performance of a population with no age-biased mortality and the same level of long-line mortality

Mortality	% change in fecundity				Difference in growth rate (λ)			
	Proportion of adults killed				Proportion of adults killed			
	20%	35%	65%	80%	20%	35%	65%	80%
1%	0.9	0.3	-0.5	-1.5	0.0027	0.0016	-0.0009	-0.0031
2%	2.2	2.0	-1.2	-1.4	0.0062	0.0035	-0.0029	-0.0042
4%	6.1	3.5	-1.9	-2.7	0.0116	0.0063	-0.0058	-0.0100
6%	7.0	3.7	-4.6	-6.9	0.0174	0.0084	-0.0092	-0.0170
8%	11.1	5.4	-6.1	-10.0	0.0250	0.0127	-0.0129	-0.0229

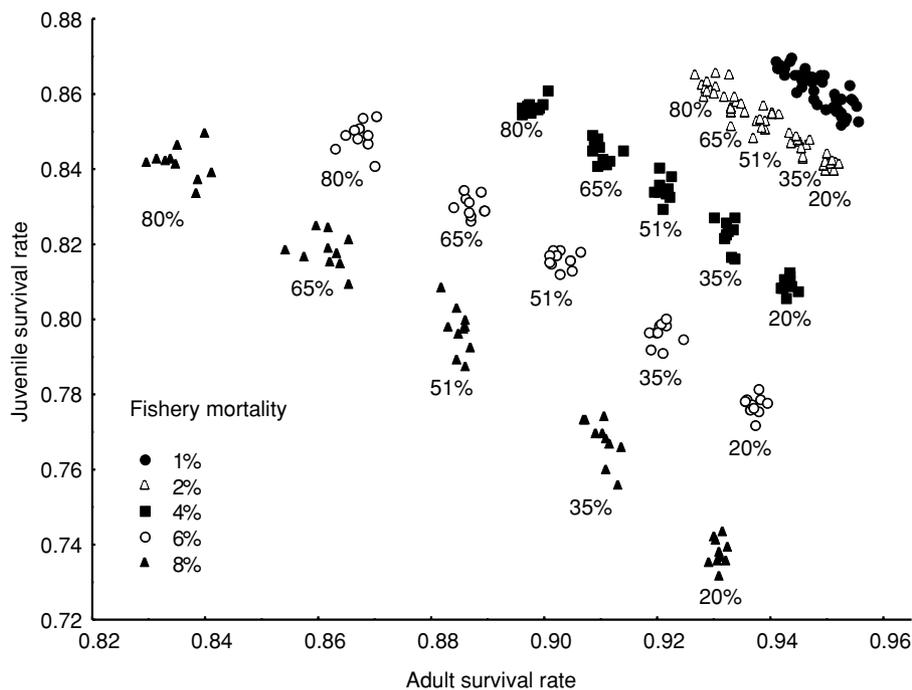


Fig. 2. The effects of different levels of age-biased long-line mortality on adult and immature survival in wandering albatross populations.

to be predictive. However, it is clear that any assessment of the impacts of long-line mortality on seabirds needs to incorporate the cost of lags resulting from pair bond

disruptions. The magnitude of these costs are directly related to the duration of the pairing lag and probably are most marked in large albatrosses like the wandering

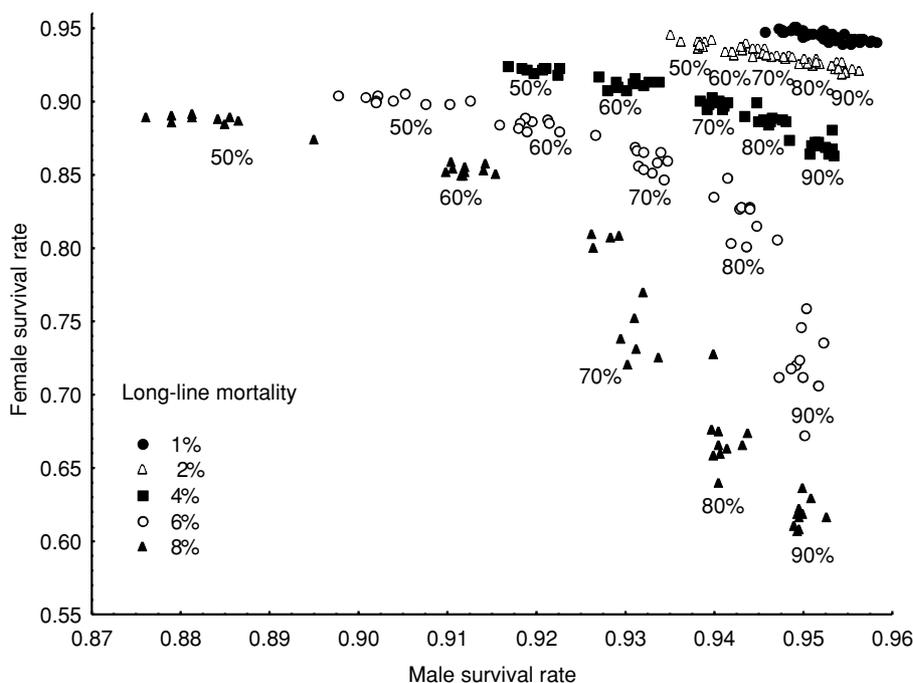


Fig. 3. The effects of different levels of female-biased long-line mortality on male and female survival in wandering albatross populations.

Table 7. The impact of age- and sex-biased mortality on mean fecundity (offspring per adult per year) expressed as the % reduction relative to the scenario with no long-line mortality (mortality) (fecundity = 0.177). No data are given for models where $N_{20} < 1000$

Mortality	% females killed					% adults killed				
	50	60	70	80	90	20	35	51	65	80
1%	1.1	2.4	3.6	4.9	6.7	0.6	1.2	1.1	2.0	3.0
2%	2.8	4.3	7.7	11.2	14.5	1.1	1.3	2.8	4.4	4.6
4%	5.6	10.9	19.5	25.9	33.0	0.4	2.8	5.6	7.9	8.6
6%	7.3	17.9	31.5	43.0	–	1.2	4.3	7.3	11.9	14.1
8%	10.7	27.4	47.2	–	–	1.0	6.1	10.7	16.3	19.8

No data are given for models where $N_{20} < 1000$.

albatross (Tickell, 2000). The effects of pairing lags can be incorporated into fecundity estimates for traditional state-variable models, but this needs to be done with care, because the impact changes relative to the level of long-line mortality.

Even more critical is the need to incorporate sex-biased long-line mortality where it occurs. This results in skewed sex ratios, impacting on fecundity by reducing the effective population size. The demographic costs to fecundity can be profound (Table 5). An additional problem is that the impacts of sex-biased mortality persist once long-line mortality is managed through mitigation. Populations remain skewed for a complete generation. Fortunately the effects of increased frequency of pair disruption disappear as soon as long-line mortality abates.

Finally, the model gives insights into the reduction in fecundity experienced by populations. For example, Weimerskirch *et al.* (1997) estimated adult and immature survival rates to be 0.895 and 0.780, respectively, for the Possession Island population from 1970–1976. Figure 2

suggests that 8% long-line mortality with 35–51% adult bias occurred during this period. This would result in a reduction in fecundity of 6–11% (Table 7). Running the model with these parameters predicts a population growth rate of 0.93, equal to that observed (Weimerskirch *et al.*, 1997). Male and female survival rates have been estimated for three populations: 0.948 and 0.931 at Bird Island (Croxall *et al.*, 1990), 0.957 and 0.926 at Marion Island (Nel *et al.*, 2003), and 0.924 and 0.882 at the Crozet Islands during 1968–1976 (Weimerskirch & Jouventin, 1987). These values suggest a 2% long-line mortality with a 70–80% female bias, a 2% long-line mortality with *c.* 80% female bias and a 6% long-line mortality with 60–70% female bias, for the three studies, respectively (Fig. 2). These populations have thus experienced decreases in fecundity of 10–20%, but possibly up to 30% (Table 7).

Population level sex-biases in long-line mortality are poorly known for wandering albatrosses, although lower female survival rates relative to males, male-biased sex ratios and longer male pairing lags give cause for concern

(Croxall & Prince, 1990). The difficulty with inferring degree of sex-bias in long-line mortality from sex ratios is that skew in sex ratio accumulates with time and the rate of accumulation depends on the level of long-line mortality. Differences between male and female pairing lags also cannot be used to make quantitative predictions of sex-biased mortality, because differences depend on sex ratio. However, estimates of age- and sex-specific survival rates can give an indication of both long-line mortality and sex bias (Figs 2 and 3). This assumes that both long-line and natural mortality are constant and that natural mortality is the same for both sexes. Both these assumptions are simplistic, but Figs 2 and 3 will be useful for tracking the relative recovery of populations as mitigation measures are increasingly implemented to avoid bird bycatch on long-lines.

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