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# Fisheries risks to the population viability of Gibson's wandering albatross *Diomedea gibsoni*

New Zealand Aquatic Environment and Biodiversity Report No. 152

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#### **EXECUTIVE SUMMARY**

## Francis, R.I.C.C.; Elliott, G.; Walker, K. (2015). Fisheries risks to the population viability of Gibson's wandering albatross *Diomedea gibsoni*.

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This report attempts to assess fisheries risks to the population viability of Gibson's wandering albatross (*Diomedea gibsoni*), which is endemic to the Auckland Islands and classified as Nationally Critical under the New Zealand Threat Classification System. Three data sets covering a 21-year period (1991–2011) were analysed: mark-recapture, nest-based, and counts of breeders. There is cause for concern about the status of this population. Since 2005, the adult population has been declining at a rate of 5.7%/yr, because of sudden and substantial reductions in three demographic rates: adult survival (from 0.95 to 0.89), proportion breeding (from 0.53 to 0.37), and the proportion of breeding attempts that are successful (from 0.60 to 0.25). It is now about two-thirds of its estimated size in 1991. The breeding population dropped sharply in 2005, to 59% of its 1991 level, but has been increasing since 2005 at about 4.2% per year because of slow increases in adult survival and proportion breeding. The current (2011) breeding population is estimated to be only 54% of the average of 5831 pairs estimated by Walker & Elliott (1999) for 1991–97.

It is difficult to assess the effect of fisheries mortality on the viability of this population. There is some information about bycatch of Gibson's in New Zealand waters, and of wandering albatrosses (species unknown) in Australian waters, but little is known about the effect of fisheries in international waters. Three conclusions are possible from the available data: most fisheries mortality of this species is caused by surface longlines; mortality from fishing is now probably lower than it was; and there is no indication in the data that the sudden and substantial drops in the three above-mentioned demographic rates were caused primarily by fishing.

Forward projections showed that, of these three demographic rates, the most important to the future status of this population is adult survival.

The extent to which this species exhibits philopatry (i.e., breeds where it was born) is not known, and this compromised our ability to estimate juvenile survival. Assuming full philopatry, the annual rate of juvenile survival was estimated to be 0.88; this will be an under-estimate if philopatry is partial. The mean age of first breeding was estimated to be 12.4 y.

#### 1. INTRODUCTION

The work described in this report was carried out as part of the five-year Ministry of Fisheries project PRO200602, whose specific objectives are as follows.

- 1. Model the effects of fisheries mortality on population viability compared with other sources of mortality or trophic effects of fishing to allow an assessment of the risk posed to population viability by fishing.
- 2. Assess the ability of alternative management strategies to: a) avoid, remedy or mitigate the adverse effects of fishing on seabird population viability; and b) to reduce mortality to a negligible level, measured in population terms, for selected species.
- 3. Examine the overlap of fishing activity with species distribution at sea for different stages of the breeding and life cycle and for different sexes and provide an assessment of the risk posed to

seabird species from different fisheries (by target species fisheries, fishing methods, area and season).

4. Assess population status of selected seabird populations in relation to fisheries risks to population viability.

In NIWA's proposal for this project the above specific objectives were reworded, to better describe the proposed research, as follows.

- 1. Develop general seabird population model
- 2. Assess the status of selected seabird populations
- 3. Assess the effect of fisheries mortality on population viability
- 4. Assess the effect of alternative management strategies

The first of these objectives was addressed in year 1 of the project (Francis et al. 2007). In the succeeding years the last three objectives were addressed (where appropriate) for Southern Buller's albatross (Francis et al. 2008, Francis & Sagar 2012), black petrel (Francis & Bell 2010), and white-capped albatross (Francis 2011). In this report we describe work in the final year of this project, in which we analysed data for Gibson's wandering albatross.

#### 1.1 The species

There is no consensus about the taxonomy of the wandering albatrosses. The two taxa that are endemic to New Zealand (Gibson's wandering albatross and the Antipodean wandering albatross) are variously treated as a single species, two subspecies, and two species (Agreement on the Conservation of Albatrosses and Petrels 2009). For the purposes of this report we will follow the last treatment, using the names *Diomedea gibsoni* and *D. antipodensis*, respectively, and using *D. exulans* to refer to other wandering albatrosses that are occasionally observed in New Zealand waters but do not breed there.

Gibson's wandering albatross (sometimes called Gibson's albatross) is endemic to the Auckland Islands, with about 95% of the population breeding on Adams Island, the southernmost island in the group (Walker & Elliott 2009). The population is relatively small (ranking 11th most abundant of 14 albatross taxa that breed in New Zealand, Scofield & Sagar 2006) and declining.

The population is classified under the New Zealand Threat Classification System as a 'Nationally Critical' threatened species (Robertson et al. 2013). Internationally, the two New Zealand wandering albatrosses are collectively classified as Vulnerable, with the comment "Recent data ... indicate declines in adult survival, productivity, and recruitment which, if confirmed ..., could result in a reclassification of Endangered or Critically Endangered" (IUCN 2010).

#### **1.2 Range of Gibson's wandering albatross**

Between 1994 and 2003 Walker & Elliott (2006) used satellite telemetry to track the movements of 46 Gibson's Wandering albatrosses from Adams Island. They tracked adult birds of both sexes at all stages in the breeding cycle with a total of 2474 bird-days tracked and 13 394 satellite fixes. Gibson's albatross spent most time in the Tasman Sea between 35° and 45°S but a few birds went to the east of New Zealand, and a few south of Australia. Birds also spent a lot of time in an area between the Auckland Islands and their apparently preferred foraging area in the Tasman Sea (Figure 1). Overall, 53% of observations were inside EEZs (37% New Zealand, 16% Australian) and 47% were outside. There were

some seasonal and breeding stage related changes in foraging distribution. While incubating and raising chicks the foraging ranges of birds was smaller than at other times. On average, males foraged slightly further south than females although there was substantial overlap. During the colder months birds on average foraged further north.

Walker & Elliott (2006) examined overlap with fishing effort and found that the foraging range of Gibson's wandering albatross between 1994 and 2003 overlapped almost entirely with the reported range of long-line fishing fleets. Areas where the interaction between Gibson's wandering albatrosses and long-line fishing fleets was greatest were in the Tasman Sea about 500 km east of Australia and just to the south and west of the South Island.

Since 2009 Gibson's wandering albatrosses have been tracked again, this time using geolocator datalogger technology (Fox 2010). Geolocator loggers are small devices (2.5 g) that are attached to bands on the legs of birds. They record light levels, and sea-surface temperatures (when they are in the water) and this information is used to calculate position. Geolocator loggers are much smaller and less expensive than satellite transmitters, but they have to be recovered from the birds to get any data and the estimates of position they produce are much less accurate. The aim of this second set of tracking is to determine whether the patterns of movement of the birds changed between 2003 when the population was stable and 2009 when the population was declining. These data are still being collected and have yet to be analysed.



Figure 1. Kernel density plot of Gibson's wandering albatrosses satellite-tracked between 1994 and 2003. Black indicates the 50% contour, dark grey the 75% contour, and light grey the 95% contour. Data from Walker & Elliott (2006).

#### 1.3 The study population

The population studied breeds on Adams Island, with mark-recapture data coming from a 61 ha Study Area and counts of breeders from three larger areas (Figure 2).

#### 2. BYCATCH

The at-sea distribution of Gibson's wandering albatross falls into four areas: two in international waters (in the Tasman Sea and the southwest Pacific east of New Zealand), and two in national exclusive economic zones (EEZs) (of New Zealand and Australia) (Nicholls et al. 2002, Walker & Elliott 2006). Nothing is known of the bycatch of Gibson's in international waters, but there is some limited information concerning the two EEZs.

#### 2.1 New Zealand bycatch

The earliest information for New Zealand waters was provided by Murray et al. (1993), who estimated that the total seabird bycatch from Japanese surface longliners (SLLs) fishing for southern bluefin tuna (SBT) dropped sharply from 3650 in 1988 to 360 in 1992. This drop was primarily because of a reduction in catch rates (from 0.30 to 0.04 birds/1000 hooks) which they said was "probably as a result of mitigation measures introduced progressively by the industry and by government regulation". Of the 135 birds reliably identified, 26 were wandering albatrosses; of these, 13 were identified to species level and 8 were found to be Gibson's wandering albatross. Thus, approximately 12% of the bycatch (i.e. 100 ×  $(26/135) \times (8/13)$ ) was Gibson's wandering albatross, and the estimated bycatch for this species in this fishery dropped from about 433 in 1988 to 43 in 1992.



Figure 2: Adams Island, showing the Study Area (black) and the three larger areas in which annual counts of breeders have been made (shaded): Amherst to Astrolabe (162 ha, including the Study Area); Rhys's Ridge (67 ha); and Fly Square (25 ha).

To estimate the total Gibson's bycatch from New Zealand fisheries over these years we would need to allow both for bycatch from other SLL fisheries and other fishing methods. It might be reasonable to allow an additional 17% for other SLL fisheries because the total tuna SLL effort in New Zealand waters between 1998 and 1992 was 59.4 million hooks (F. Wei, NIWA, pers. comm.; data from the tuna database) which is 17% higher than the effort on which the estimates of Murray et al. (1993) were based (50.6 million hooks - see their table 1). Any allowance for other fishing methods is likely to be small since Gibson's is caught primarily by SLL (see below).

Abraham & Thompson (2011) provided more comprehensive information about seabird by catch from all New Zealand fisheries over the 11-year period from 1998–99 to 2008–09. Looking first at the SLL SBT fishery, they estimated an average annual by catch of 211 seabirds (see their table 119). Of the 589 birds observed caught in this fishery, 26 were wandering albatrosses; and of the 37 wandering albatrosses caught across all fisheries and identified to species level, 22 were Gibson's. Thus the average annual by catch of Gibson's in the SBT SLL fishery over these years was approximately 6 (i.e. 211 ×  $(26/589) \times (22/37)$ ), which is a substantial reduction from the above estimate of 43 for 1992. This reduction was caused partly by a decrease in effort (from 9.0 million hooks in 1992 to 2.1 million hooks per year from 1998–99 to 2008–09) and partly by a drop in the estimated percentage of the seabird by catch that was Gibson's (from 12% in 1992 to 2.6% in recent years).

In order to estimate the Gibson's bycatch from all New Zealand fisheries, the calculations in the previous paragraph, which were based on table 119 of Abraham & Thompson (2011), were repeated for other tables from that report (Table 1) (the values in the last row of this table were inferred from the differences between the fourth row and the fifth to seventh rows). This provided three alternative estimates of the average Gibson's bycatch from SLL fisheries from 1998–99 to 2008–09: 31, 61, or 51 birds/yr (from row 2, row 4, or the sum of rows 5–8, respectively). After adding the estimates for the

trawl and BLL fisheries, we obtain estimates of the New Zealand bycatch of Gibson's from all fisheries between 35 and 65 birds/yr, with between 89% and 94% of this bycatch coming from SLL fisheries.

These estimates of Gibson's bycatch should be treated as indicative, rather than definitive, because of some major uncertainties which are difficult to quantify. For example, the annual bycatch from the swordfish SLL fishery is very uncertain because 71 of the 76 birds observed caught in this fishery over the 11-year period were caught in a single year (2006-07). Bycatch from the bigeye tuna fleet (predominantly domestic vessels) is more uncertain than that from the southern bluefin tuna fleet (predominantly foreign charter vessels) because of much lower observer coverage (2.8%, compared to 41%). Another source of uncertainty is the species composition of the wandering albatross bycatch, which was quite variable (Table 2). Note that most observer records identify wandering albatrosses only to the species level (170 of the 176 wandering albatrosses recorded in the *l line* database were coded as "wandering albatross (unidentified)", which is species code XWA) so the identifications in Table 2 were mostly based on autopsied birds (for the 11 years covered by Abraham & Thompson (2011), about half (37/79) of the observed wandering albatross bycatch was autopsied). Our estimates of Gibson's by catch could be biased if the species composition of necropsied birds was not representative of the total bycatch. Finally, these estimates of bycatch exclude any "cryptic" fishing-related mortality whereby birds are drowned on a hook but are not subsequently recovered on board the fishing vessel and, thus, cannot be observed (Brothers et al. 2010).

Table 1: Estimates of the average annual bycatch of Gibson's wandering albatross in various New Zealand fisheries for fishing years 1998–99 to 2008–09, inclusive. Each estimate (last column) was derived from the named table in Abraham & Thompson (2011). The values in columns 3, 4, and 6 come directly from those tables; see text for details of the calculation of columns 5 and 7. SLL, surface longline; BLL, bottom longline; SBT, southern bluefin tuna (*Thunnus maccoyii*); BIG, bigeye tuna (*T. obseus*); SWO, swordfish (*Xiphia gladius*).

		Observed byc			
oraham & Thompson 2011		Wandering	Percentage	Estimated byca	tch (no./yr)
Description	$All^1$	albatrosses <sup>2</sup>	Gibson's	All <sup>3</sup>	Gibson's
Other albatrosses in trawl	487	4	0.49	360	2
Other albatrosses in SLL	533	69	7.70	399	31
Other albatrosses in BLL	242	6	1.47	150	2
All birds in SLL	932	69	4.40	1384	61
All birds in SBT SLL	589	26	2.62	211	6
All birds in BIG SLL	191	8	2.49	990	25
All birds in SWO SLL	76	25	19.56	50	10
All birds in other SLL	76	10	7.82	133	10
	Description Other albatrosses in trawl Other albatrosses in SLL Other albatrosses in BLL All birds in SLL All birds in SBT SLL All birds in SBT SLL All birds in SWO SLL All birds in other SLL	DescriptionAll1DescriptionAll1Other albatrosses in trawl487Other albatrosses in SLL533Other albatrosses in BLL242All birds in SLL932All birds in SBT SLL589All birds in BIG SLL191All birds in SWO SLL76All birds in other SLL76	Observed bycoraham & Thompson 2011WanderingDescriptionAll <sup>1</sup> albatrosses <sup>2</sup> Other albatrosses in trawl4874Other albatrosses in SLL53369Other albatrosses in BLL2426All birds in SLL93269All birds in SBT SLL58926All birds in BIG SLL1918All birds in SWO SLL7625All birds in other SLL7610	Observed bycatch (all years)praham & Thompson 2011WanderingPercentageDescriptionAll <sup>1</sup> albatrosses <sup>2</sup> Gibson'sOther albatrosses in trawl48740.49Other albatrosses in SLL533697.70Other albatrosses in BLL24261.47All birds in SLL932694.40All birds in SBT SLL589262.62All birds in BIG SLL19182.49All birds in SWO SLL762519.56All birds in other SLL76107.82	$\begin{array}{c c c c c c c c c c c c c c c c c c c $

<sup>1</sup>Sum of column 'Capt.'

<sup>2</sup>Birds recorded as wandering albatross (unidentified), Gibson's albatross, or antipodean albatross <sup>3</sup>Mean across all years of column 'Est. captures'

Overall, seabird bycatch in New Zealand waters is showing a downwards trend. For all but one of the tables from Abraham & Thompson (2011) that were used in Table 1, the estimated annual bycatch (of 'all birds' or 'other albatrosses') was 24% to 69% lower on average in the last 6 years than in the preceding 5 years. The exception was for the swordfish fishery, which was established during this period (average annual effort increased from 6750 hooks for the first 5 years to 147 819 hooks for the last 6 years). The downward trend in bycatch is also seen in estimates of all birds caught in trawls and bottom longlines (tables 15 and 19 of Abraham & Thompson 2011). We cannot be sure whether this downward trend also applies to Gibson's, because there are no reliable annual data on what proportion this species contributes to the total bycatch.

				Species
Source	Period covered	Gibson's	Antipodean	Other
Murray et al. (1993)	1988 to 1992	8	3	$2^{2}$
Anonymous (2008) <sup>1</sup>	1996–97 to 2004–05	40	93	2 <sup>3</sup>
Thompson (2009, 2010b, 2010c, 2010a) <sup>1</sup>	2005–05 to 2008–09	11	9	$2^{4}$
Abraham & Thompson (2011)	1998–99 to 2008–09	22	15	0
<sup>1</sup> Autopsy reports				

 Table 2: Numbers of wandering albatrosses caught in New Zealand fisheries and identified to species level in four data sets.

<sup>2</sup>Wandering (Snowy) albatross "*Diomedea exulans exulans*" <sup>3</sup>Snowy (wandering) albatross "*D. chionoptera*"

<sup>4</sup>D. exulans (one bird was banded as an adult at Kerguelen Island in the southern Indian Ocean)

Of the 51 necropsied Gibson's wandering albatrosses over a 13-year period (1996–97 to 2008–09), all but 1 were adults, and the sex ratio was even (there were 24 males, 25 females, and 2 unsexed) (Anonymous 2008, Thompson 2009, 2010b, 2010c, 2010a).

#### 2.2 Australian bycatch

For the Japanese SLL fishery in Australian waters, there are two estimates of the annual bycatch of wandering albatrosses: 393 birds/year for fishing years 1992–93 to 1994–95 (Klaer & Polacheck 1997); and 'over 500' birds/year for years 1988 to 1995 (Gales et al. 1998). Most of these birds were caught in waters off Tasmania and south-eastern Australia; and Gales et al. (1998) said that most were immature males, and that they originated from at least five island locations. This would include Gibson's from the Auckland Islands, but there is no information about what proportion of the bycatch would be from this population.

Since the exclusion of the Japanese tuna fishery from Australian waters in 1998, a domestic longline fishery has formed and expanded, and the bycatch of wandering albatrosses seems to have decreased substantially. Trebilco et al. (2010) characterized seabird bycatch in the eastern Australian tuna and billfish pelagic longline fishery (which includes waters off Tasmania and south-eastern Australia) between September 2001 and June 2006. Of the 280 seabirds observed caught and necropsied, the great majority (85%) were flesh-footed shearwaters, *Puffinus carneipes*, and only 8 (2.9%) were wandering albatrosses (corresponding figures from Klaer & Polacheck (1997) were 6.8% and 7.8%, respectively). Further, the observed bycatch rate (for all birds) decreased substantially over this period, from 1.88 to 0.02 birds/1000 hook. Applying these bycatch rates to the total effort in this fishery (both from table 1 of Trebilco et al. 2010), and assuming that a constant 2.9% were wandering albatrosses, the estimated bycatch of wandering albatrosses in this fishery fell from 168 in 2002 to 5 in 2005 (data for 2001 and 2006 were incomplete).

#### 3. DATA

Three sets of data (all belonging to Albatross Research) are analysed in this report. The first was markrecapture data from the Study Area in 1991, and then annually since 1993 (Figure 3) (throughout this report, observations associated with the breeding season in the summer of 1990–91, are labelled 1991 and so forth). Each year from the year of banding, the status of each banded bird was recorded using one of 14 status codes (Table 3). Code U was needed for some birds breeding in 2011 because the success or failure of breeding in any year is not usually known until the colony is visited in the following year. For the purposes of this report, all observations of status B for birds banded as fledglings (at age about 1 y) were assigned code P (pre-breeder) if they occurred before that bird was first observed breeding. There are several patterns of interest in Figure 3. It is to be expected that, as the banding program becomes established over the initial 5–10 years, the number of breeders banded each year will gradually decrease, and the number of breeders seen will increase. However, the subsequent sudden decrease in numbers banded (from 2005 for breeders, and from 2006 for fledglings) was not expected, and is cause for concern. Note also how the low number of breeders seen in 2000 is reflected in the low number of fledglings banded the following year.

The second data type was nest-based. Each year, the location of all breeding nests in the Study Area was recorded. For those nests where the success of breeding was known (almost all nests, except in the first few years, and in 2011 [the success of breeding in any year is not known until a fledgling is observed the next year]), a record was kept as to whether both breeders were observed, or just one or none (the last category was rare). These data were used to estimate resighting probabilities for breeding birds.

The third data type was annual counts since 1998 of breeders from three larger areas. Although these areas were chosen to represent a wide range of nest densities (the average number of nests per hectare was 0.7, 2.1, and 6.7 in Rhys's Ridge, Amherst to Astrolabe, and Fly Square, respectively), the counts show remarkably similar trends over time (Figure 4). Both the low counts in 2000 and the substantial drop in counts from 2005 are consistent with analogous patterns noted above in the banding data.



Figure 3: Summary of mark-recapture data, showing the numbers of breeders and fledglings banded each year and the number of banded breeders seen each year.

### Table 3: Codes used to describe the status of banded birds each year (unless otherwise stated, all observations were within the study area).

Code	Interpretation
0	Not seen
С	Fledgling (age approximately 1 yr)
3-7	Age (to nearest year)
В	Non-breeder
F	Failed breeder (bred, but no fledgling produced)
G	Failed breeder (just) outside the Study Area
S	Successful breeder (bred and produced fledgling)
Т	Successful breeder (just) outside the Study Area
T	Duad but manage of busiding unlinger (and una

- U Bred, but success of breeding unknown (only recorded for 2011 observations)
- A Not breeding, but bred successfully last year



Figure 4: Counts of breeding pairs in three areas on Adams Island: A, the original counts; and B, the counts scaled to have the same averages as in area Amherst to Astrolabe, showing the strong correlation between areas.

#### 4. MODELLING OF THE DATA

We describe results from a series of models of increasing complexity, all implemented in SeaBird (Francis et al. 2008). The initial models used just part of the mark-recapture data, but all the data were used in the final models. For all but one model, only point estimates were obtained (such estimates are sometimes known as MPD estimates, because they represent the <u>mode</u> of the <u>posterior distribution</u> of the parameter vector). Full Bayesian estimates were also obtained for one model (model GIB5 – see Section 4.5.2).

#### 4.1 Model GIB0 - juveniles only, ignoring pre-breeders

The first model, GIB0, dealt only with the juvenile period (up to first breeding). Thus it included only birds banded as fledglings (excluding those banded after 2004, which were too young to have bred before 2012) and, for those birds that were observed breeding, all observations after that observation were ignored. For reasons discussed under model GIB1, pre-breeding observations were also ignored.

Since the observed ages at first breeding have all been between 8 y and 16 y, birds were assumed not to breed before age 8, and all birds that reached age 18 without breeding were assumed to breed at that age. Thus, if we define P1stbr*a* to be the probability that a bird breeds at age *a*, given that it survives to that age and hasn't already bred, we are assuming that P1stbr*a* = 0 for a < 8, and P1stbr*a* = 1 for a = 18. For ages between 8 and 17, P1stbr*a* is assumed to increase linearly in logit space, i.e.,

$$logit(P1strbra) = logit(P1stbr10) + (a-10)*log(M1stbr)$$

GIB0 has 18 states (ages 1–17 and adult) and 3 estimable parameters (Table 4). There are no resighting probabilities to be estimated because these are assumed to be 0 for juveniles and 1 for adults. (Note that the rows of the transition matrix must sum to 1, so Pjva = 1-P1stbra).

The mean age of first breeding was estimated to be 12.4 y, with more than 90% of birds breeding between ages 9 and 16, inclusive (Figure 5). Annual survival for juveniles was estimated to be 0.88

Table 4: Details of model GIB0: A, model states; B, transition matrix; and C, parameters.

A. States: age1, age2, ..., age17, ad

B. Tran	sition n	natrix				
	agel	age2	age3	 age8	 age17	ad
agel	0	1	0	 0	 0	0
age2	0	0	1	 0	 0	0
age7	0	0	0	 Pjv8	 0	P1stbr8
•••				 	 	
age16	0	0	0	 0	 Pjv17	P1stbr17
age17	0	0	0	 0	 0	1
ad	0	0	0	 0	 0	1
C D						

C. Parameters:

juvsurv annual probability of survival for juveniles

used to calculate probabilities of first breeding, Pr1stbra P1stbr10, M1stbr



Figure 5: Estimated distribution of ages at first breeding from model GIB0.

We considered two variants of GIB0 which allowed more parameters to estimate the P1strbra. In the first variant (GIB0a), rather than assuming that logit(P1stbra) was linear with age, there were separate parameters for P1stbr8, P1stbr9, ..., P1stbr17; in the second variant (GIB0b), logit(P1stbra) was assumed to be linear from ages 8 to 13, and (independently) linear from ages 14 to 17. Both of these variants were inferior to GIB0 according to AIC (Table 5).

Table 5:	Comparison of	GIB0 wi	ith three of its vai	riants.	
	Number of			Mean age of	
Model	parameters	AIC	juvsurv	1st breeding	Description
GIB0	3	1187	0.878	12.40	
GIB0a	11	1195	0.875	12.28	GIB0 plus 8 pars for P1stbra
GIB0b	5	1191	0.875	12.31	GIB0 plus 2 pars for P1stbra
GIB0c	6	1139	$1, 0.67, 0.25, 1^{1}$		GIB0 plus 3 juvsurv pars
<sup>1</sup> 0 67 in 2	$004 \cdot 0.25$ in 200	5·1 in all	other years		

2004; 0.25 in 2005; 1 in all other years

For GIB0 the fit to the data is adequate by age at breeding (Figure 6A), but not so good by year of banding (Figure 6B). We found a model, GIB0c, which improved this last diagnostic by allowing juvsury to vary from year to year. This model is also better than GIB0 according to AIC, but the resulting variation in juvsurv was too extreme to be plausible (see Table 5).

Any emigration (fledglings banded in the study area that grow up to breed outside that area) will negatively bias the estimate of juvsurv in GIB0.



Figure 6: Two diagnostic plots for GIB0 and GIB0c: A, observed ('o', with 95% confidence intervals as vertical lines) and expected (lines) numbers of birds seen breeding, by age; B, observed and expected proportion of birds seen breeding, by year of banding.

#### 4.1.1 Allowing emigration in GIB0

Model GIB0d is a modification of GIB0 to allow the possibility of emigration. This model used exactly the same observations as GIB0, has an additional state in the partition – for adults breeding outside the study area – and an additional parameter, Pbrstd, which is the probability that a bird that was born in the study area and which survives to breed, will do so in the study area. As in GIB0, a bird that survives to age a ( $8 \le a \le 17$ ) without breeding, will breed at that age with probability P1stbr*a*, but in GIB0d this breeding takes place in the study area, or elsewhere, with probabilities Pbrstd and 1–Pbrstd, respectively.

GIB0d estimated a low probability of breeding in the study area (Table 6), but the fit to the data is only very slightly better than for GIB0. Further, plots analogous to Figures 5 and 6 (not shown) show virtually no difference between GIB0 and GIB0d. A profile on the parameter Pbrstd shows that GIB0 and GIB0d are at opposite ends of a continuum of possible model fits with almost identical objective function values (Figure 7).

We conclude that the mark-recapture data set used in these models cannot be used to detect emigration, and so can be used to estimate only a lower bound for juvsurv (an estimate which will be correct only if there is no emigration). We acknowledge that this result is rather obvious, and could have been predicted without any modelling. However, we include it here for comparison with more complicated models.

Table 6:	<b>Comparison of parameter</b>	r estimates and objective	function values for	models GIB0 and GI	B0d.
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Model			<u>estimates</u>	Objective	
	juvsurv	P1stbr10	M1stbr	Pbrstd	function
GIB0	0.88	0.075	1.64	$1^{1}$	590.44
GIB0d	1.00	0.114	1.52	0.22	590.41
<sup>1</sup> Implicit value					





Figure 7: Outputs from a GIB0d profile on the parameter Pbrstd, showing the objective function (zero adjusted), and estimates of juvsurv and the mean age at first breeding. In each panel the point estimates for GIB0d and GIB0 are shown as '×' and 'o', respectively.

#### 4.2 Model GIB1 – including the pre-breeding observations

This model was similar to GIB0 except that it included the observations of pre-breeders, and so required the estimation of resighting probabilities for pre-breeders. These probabilities were assumed to depend on age (but not year) with

$$logit(Pra) = logit(Pr7) + (a-7)*log(MPr)$$

where Pr*a* is the resignating probability for pre-breeders of age *a*. GIB1 used the same transition matrix as GIB0, and estimated the same parameters plus the two parameters determining the resignation probabilities (Pr7 and Mpr).

Resighting probabilities were estimated to increase from 0.08 to 0.97 between ages 4 and 17 (Figure 8A) and although the estimate of juvsurv was similar to that for GIB0, the distribution of ages at first breeding was very different (Figure 8B). Further, the expected numbers of birds seen by age and breeding status were markedly less than the observed numbers (Figure 9 and first line of Table 7).



Figure 8: Estimates from model GIB1: A, resighting probabilities; and B, distribution of ages at first breeding.





Figure 9: Diagnostic plot for GIB1 showing observed ('o', with 95% confidence intervals as vertical lines) and expected (lines) numbers of birds seen breeding, by age: A, as pre-breeders, and B: as adults.

 Table 7: Selected outputs of GIB1 and two variant models: estimates of juvsurv and the expected number of birds seen – as pre-breeders and as adults – expressed as percentages of the observed numbers.

				Expecte	ed number seen
			juvsurv	(as % of obs	served number)
Model	ages 1–4	ages 5–7	ages 8–17	as pre-breeders	as adults
GIB1	0.88	0.88	0.88	88	75
GIB1g	0.86	0.87	0.91	87	75
GIB1g'	0.86	0.87	0.997	99	101

Considerable effort was spent in trying to fix GIB1 by adding parameters, but with no success. For example, model GIB1g had 17 more parameters than GIB1 (3 for juvsurv, 15 for resighting, and 4 for age at first breeding) and fitted marginally better in terms of AIC, but performed just as badly as GIB1 in terms of expected numbers of birds seen (Table 7, Figure 10).

What is puzzling, and so far unexplained, is the model fit labelled GIB1g' (discovered by extensive trial and error). This had the same model structure as GIB1g, and used all the same parameter values, except that juvsurv was increased from 0.91 to 0.997 for the oldest birds. Although GIB1g' fixes the problem of low expected numbers (Table 7, Figure 10) its overall fit, as measured by the objective function, is markedly worse (the objective function is 178 higher).



Figure 10: As Figure 9, but for two variants of GIB1: GIB1g and GIB1g'.

#### 4.3 Model GIB3 – modelling adults only

In this model we excluded all birds that had not been seen breeding, and treated those birds banded as fledglings and subsequently seen breeding as having been banded in the year that they were first seen breeding. The distinction between breeding inside and outside the study area was ignored (so codes S and T were treated as equivalent, as were codes F and G).

Model GIB3 had 4 states and 80 parameters (Table 8). Observations in 2011 of birds that were known to have bred but the success of breeding was unknown (n = 188) were assigned a composition state, interpreted by SeaBird as sbr or fbr.

The nine parameters of the transition matrix were calculated from the four transition base parameters (Psuccess, Tnbrbr, TFbrbr, and Tlbrbr) using the following equations

Tnbrnbr = (1-Tnbrbr) Tnbrfbr = Tnbrbr(1-Psuccess) Tnbrsbr = TnbrbrPsuccess Tfbrnbr = (1-Tfbrbr) Tfbrfbr = Tfbrbr(1-Psuccess)  $Tfbrsbr = Tfbrbr \times Psuccess$  Tlbrnbr = (1-Tlbrbr) Tlbrfbr = Tlbrbr(1-Psuccess)  $Tlbrsbr = Tlbrbr \times Psuccess$ 

GIB3 was the starting point in a series of models of increasing complexity. Because the resighting probabilities estimated in GIB3 differed substantially from those inferred from nest-based data, model GIB3a (and all subsequent variants of GIB3) included normal prior distributions for each year, derived from the nest-based data, for Prsbr and Prfbr. The calculation of the priors is most simply explained by an example. In 1991, there were 31 nests for which breeding failed, and 57 of the 62 parents associated with these nests were observed. Therefore the prior for the resighting probability Psfbr in 1991 had mean 0.92 (=57/62) and standard deviation  $0.035 (=[0.92*(1-0.92)/62]^{0.5})$ . When all parents were seen this resulting degenerate prior (with mean 1 and s.d. 0) was replaced by one with mean 0.99 and s.d. 0.005. For 2011, when breeding success was unknown, a similar procedure was used to calculate a prior for resighting probabilities for all breeders (mean 0.97, s.d. 0.0106), and this was used for both Prfbr and Prsbr.

#### Table 8: Details of model GIB3: A, model states; B, transition matrix; and C, parameters.

A. States nbr, fbr, sbr, lbr (non-breeder, failed and successful breeder, and last year's successful breeder)

B. Trans	ition matri	х			
	Nnbr	Nfbr	Nsbr	Nlbr	
Nnbr	Tnbrnbr	Tnbrfbr	Tnbrsbr	0	
Nfbr	Tfbrnbr	Tfbrfbr	Tfbrsbr	0	
Nsbr	0	0	0	1	
Nlbr	Tlbrnbr	Tlbrfbr	Tlbrsbr	0	
C. Param	neters				
Label		Length	Description		
Psuccess		1	probability b	breeding w	vill be successful
surv		18	annual proba	ability of s	survival
Tnbrbr		1	probability of	of breeding	g a year after being a non-breeder
Tfbrbr		1	probability of	of breeding	g a year after being a failed breeder
Tlbrbr		1	probability of	of breeding	g a year after being a last-year's breeder
Prnbr		19	probability of	of resightin	ng a bird when it is a non-breeder
Prfbr		19	probability of	of resightin	ng a bird when it is a failed breeder
Prsbr		19	probability of	of resighting	ng a bird when it is a successful breeder
Prlbr		1	probability of	of resightii	ng a bird when it is a last-year's breeder
		80			

The addition of these priors made a substantial difference to the estimated resighting probabilities (Figure 11).



Figure 11: Estimates of resighting probabilities (Prsbr, Prfbr, Prnbr) for models GIB3 and GIB3a, showing the effect of using nest-based prior distributions for Prsbr and Prfbr in the latter model (the means +/- 2 s.e.s for the priors are plotted in red).

Subsequent model modifications, in models GIB3b-d, all involved making further parameters time-varying, and each modification improved the model fit, according to AIC (Table 9).

When the transition parameters were made time-varying (in model GIB3b) it was assumed, for reasons of parsimony, that they all varied in tandem, under the control of a single time-varying parameter, Mbr (which acted as an odds multiplier), and three time-constant probabilities, Pnbrbr, Pfbrbr, Plbrbr. Then time-varying parameters for the first row of the transition matrix were calculated using

 $Tnbrbr_{y} = Pnbrbr \times Mbr_{y}/(1 - Pnbrbr + Pnbrbr \times Mbr_{y})$   $Tnbrnbr_{y} = (1 - Tnbrbr_{y})$   $Tnbrfbr_{y} = Tnbrbr_{y} \times (1 - Psuccess)$  $Tnbrsbr_{y} = Tnbrbr_{y} \times Psuccess$  with analogous equations for the parameters of the second and fourth rows. To avoid redundancy in the estimated parameters Pfbrbr was arbitrarily fixed to 0.51.

Table 9:	Brief	details	of four	variants	of model	GIB3.
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	Number of		
Model	parameters	AIC	Description
GIB3a	80	1476	GIB3 with priors for Prsbr and Prnbr
GIB3b	98	560	GIB3a with time-varying transition parameters
GIB3c	115	105	GIB3b with time-varying Psuccess
GIB3d	132	0	GIB3c with time-varying Prlbr

For model GIB3d, the best in this series of models, estimates of survival, breeding probability, and breeding success were all markedly lower since about 2005, and estimates of breeding success were similar to those based on nest data (Figure 12). Two diagnostic plots show good fits (Figures 13 and 14).



Figure 12: Parameter estimates for model GIB3d. Also shown in the last panel (in red) are nest-based estimates, with 95% confidence intervals, of breeding success.



Figure 13: Observed (lines) and expected ('o') numbers seen by state and year for GIB3d.



It is of interest that estimates of survival from these models appear to be quite robust. Despite substantial improvement in fit with each modification of the model these estimates varied little, except in the last two years (Figure 15).





#### 4.4 Model GIB4 - modelling all the banding data

GIB4 was effectively a combination of the best models for juvenile only (GIB0) and adult only (GIB3d) banding data. It used all the banding data, except for fledglings banded after 2004 (which could not have been seen breeding yet, and thus would contribute nothing) and adults banded in 2011. GIB4 had 21 states and 135 parameters (Table 10). Its parameter estimates were virtually identical to those from GIB0 and GIB3d. When plotted together there were only slight visible differences, mainly for breeding success (Figure 16).

Table 10:	Details of	f model GI	B4: A, 1	model states;	<b>B</b> , transition	matrix; and	C, parameters.
A. States:	age1, age2	,, age17,	nbr, fbr	, sbr, lbr			-

B. Tran	sition n	natrix							
	age1	age2	age3	 age8	 age17	nbr	fbr	sbr	lbr
agel	0	1	0	 0	 0	0	0	0	0
age2	0	0	1	 0	 0	0	0	0	0
age7	0	0	0	 Pjv8	 0	0	Pfbr8	Psbr8	0
age16	0	0	0	 0	 Pjv17	0	Pfbr17	Psbr17	0
age17	0	0	0	 0	 0	0	Pfbr18	Psbr18	0
nbr	0	0	0	 0	 0	Tnbrnbr	Tnbrfbr	Tnbrsbr	0
fbr	0	0	0	 0	 0	Tfbrnbr	Tfbrfbr	Tfbrsbr	0
sbr	0	0	0	 0	 0	0	0	0	1
lbr	0	0	0	 0	 0	Tlbrnbr	Tlbrfbr	Tlbrsbr	0
C. Para	meters:								

juvsurv	1	annual probability of survival for juveniles
adsurv	18	annual probability of survival for juveniles
Psuccess	18	probability breeding will be successful
P1stbr10, M1stbr	1,1	parameters determining age at first breeding
Pnbrbr, Plbrbr, Mbr	1,1,19	parameters determining transition probabilities
Prnbr, Prfbr, Prsbr, Prlbr	19,19,19,18	resighting probabilities
	135	



Figure 16: Comparison of adult parameter estimates from model GIB4 with those from GIB3d.

The good fit shown for GIB3d was preserved in GIB4 (analogues for GIB4 of Figures 13 and 14 above were almost unchanged). However, the lack of fit for fledglings by year of banding illustrated for GIB0 in Figure 6B, remained in GIB4 (Figure 17).



Figure 17: Comparison, for model GIB4 and two variants, of the observed and expected number of times each bird was seen (including sighting at banding) against banding year for birds banded as fledglings.

We found two modifications of GIB4 which overcome this lack of fit (at least to some extent), but neither was plausible. The first of these modifications was GIB4a, which is analogous to GIB0c. That is, juvsurv was allowed to be time-varying, with separate values in each of four groups of years 1991–2003, 2004, 2005, and 2006–2011. The estimated values were similar to those for GIB0c (i.e., 1, 0.67, 0.25, and 1, for the four groups respectively) and the fit was much improved (see the blue line in Figure 17). A different, and initially more promising, approach was used in model GIB4b. This was to allow juvenile survival to vary by cohort (rather than year), with the cohorts banded in 1995 and 1996 having higher survival than the others. This might be plausible if the difference in survival rates occurred in

only the first year (i.e., between ages 1 and 2). However, this didn't work. Even maximum survival (= 1) in this first year didn't increase the overall survival for the 1995 and 1996 cohorts sufficiently to explain the lack of fit in Figure 17. It was only when the survival for these two cohorts was allowed to be higher for the first five years that there was a substantial improvement in fit, and even then, the improvement was not as good as for GIB4a (compare blue and red lines in Figure 17). The increase in early survival rates for the 1995 and 1996 cohorts (Table 11) seems too great and prolonged to be plausible.

Table 11:	Comparison	of invsurv	estimates in	GIB4 and	GIB4h
Table II.	Comparison	UI JUVSUI V	comates m	OID4 allu	UIDID

		juvsurv values by ag						
Model	Cohort	1–5 y	5–6 y	> 6 y				
GIB4	All	0.88	0.88	0.88				
GIB4b	1995 & 1996 <sup>1</sup>	0.98	0.97	0.85				
GIB4b	all others	0.85	0.85	0.85				
<sup>1</sup> The coh	ort labelled 1995 is	that band	led at age	1 in that year				

Further exploration of outputs from model GIB4 revealed an explanation for the apparently poor diagnostic in Figure 17. For birds banded as fledglings, the observed number first seen breeding in each year was greater than the expected number in 2003, 2004, and 2005 (especially so in 2004), but less than that in the succeeding years (Figure 18). This pattern is analogous to the sudden drop in the annual probability of breeding estimated for all adult birds, except that the latter drop occurs one year earlier (see bottom left panel of Figure 16). It seems that whatever caused adults to suddenly become less likely to breed in the mid-2000s, also caused pre-breeders to delay their first attempt at breeding at around the same time. In 2004, when an unusually high number of birds bred for the first time, the birds banded in 1995 and 1996 would have been 11 y and 10 y, and thus able to take advantage of conditions favourable for breeding, whereas birds banded in 1997 or later would have been too young. In principle, the poor behaviour of GIB4 in Figure 17 could be fixed by estimating two sets of parameters to describe the age at first breeding: one for fledglings banded in 1996 or earlier; and one for those banded after 1996. However, this is would not be straightforward in SeaBird. For the moment, at least, we conclude that GIB4 is satisfactory.



Figure 18: Observed and expected numbers of birds first seen breeding, by year.

#### 4.4.1 Population trajectories with GIB4

With model GIB4 we can estimate trajectories of population numbers on a relative (but not absolute) scale. The initial (1991) breeding population size, N0, was arbitrarily fixed to 1000 birds and the

recruitment (number of 1-year old fledglings) in year y was set equal to half the number of successful breeders in year y-1.

The estimated trajectory for the adult population fell into two periods, with a slight decrease (0.3%) per year) between 1991 and 2004, followed by a more rapid decrease (5.8%) per year) thereafter (Figure 19B). The trajectory for breeders shows, as expected, much more year-to-year variation, but its dominant feature is that it has fluctuated around 47% of its 1991 level for the last 6 years (Figure 19C).



Figure 19: Estimated population trajectories from model GIB4 and two variants for A, all birds; B, adults; and C, breeders.

A comparison between estimated trajectories for models GIB4 and GIB4a provides a useful reminder about the importance of model plausibility. The trajectories from these two models are very different (compare black and blue lines in Figure 19). In purely statistical terms, GIB4a is clearly superior (its AIC is lower by 46, and it has better diagnostics in Figure 17). However, since GIB4a is biologically implausible, we should treat GIB4 as providing a better indication of the status of this population.

One way of estimating *absolute* population trajectories using only mark-recapture data is simply to divide the number of birds seen in each year by the corresponding estimated resighting probability. This works well only for the breeders because resighting probabilities are too poorly known, or variable, for other birds. And for breeders it doesn't work in the early years of a banding programme when there are still many adults yet to be banded. Two versions of this trajectory were estimated using the resighting probabilities from GIB4: the first was restricted to 1995–2010, and the second to 2001–2010. Both versions agreed quite well with that already presented for GIB4, but the first version was lower in the early years and higher in the later years (Figure 20A), and the agreement was better with the second version (Figure 20B).



Figure 20: Comparison of two methods of estimating a population trajectory for breeders in the study area from model GIB4: by dividing the numbers observed by the estimated resighting probabilities (red line), and as shown in Figure 19 (blue line). The former trajectory, which is absolute, was restricted to years 1995–2010 (in panel A) or 2000–2010 (in panel B); the latter trajectory is relative, and so has been scaled to have the same average as the former (over the same years).

#### 4.4.2 Model GIB4c – testing the assumption of philopatry

GIB4 assumes philopatry. That is, all birds born within the study area will also breed there if they survive (no emigration), and all birds that breed in the study area were born there (no immigration). GIB4c is a modification of GIB4 which allows us to examine how much support the banding data provide for the assumption of philopatry. The modification to allow for emigration of pre-breeders was analogous to that for GIB0d: an extra state was added to the partition for birds breeding outside the study area, and an extra parameter, Pbrstd, was added to allow birds that were bred in the study area to choose to breed outside that area (i.e., to emigrate). To allow for immigration of pre-breeders, the number of recruits (at age 1) was calculated as 0.5\*Nsbr\*(1+Pimm) (instead of 0.5\*Nsbr). Thus, immigration was treated as occurring at age 1 and being proportional to the number of fledglings produced by breeders inside the study area, an extra 5 would immigrate.

Note that the decision to model immigration as occurring at age 1 was simply a matter of modelling convenience. It would make no difference to the modelling results if we chose to have immigration occur at a later age, as long as it occurred before the age of first breeding. Note also that birds that immigrate at age 1 might decide to emigrate when they first breed.

Model GIB4c was unable to detect either emigration or immigration. As with GIB0d, parameters Pbrstd and juvsurv were confounded in GIB4c. Parameters indicating no emigration (Pbrstd = 1.0, juvsurv = 0.88) fit the observations just as well as those implying subtantial emigration (Pbrstd = 0.22, juvsurv = 1.0). Also, changing the value of Pimm had no effect on the fit to the observations.

#### 4.5 Model GIB5 – adding breeder counts

Model GIB5 had the same structure as GIB4 (see Table 10), but it used an additional set of observations – the combined counts of breeders (twice the number of breeding pairs) in the three annual-count areas (Rhys's Ridge, Amherst to Astrolabe, and Fly Square – see Figure 2) for 1998–2011 – and estimated one more parameter: N0, the number of breeders in 1991. The counts from these three areas were

combined because they were so strongly correlated (see Figure 4B). Lacking any quantitative information about the precision of these counts, we arbitrarily assigned them a normal error distribution with CV 0.05. Adding these counts had virtually no effect on the estimated trajectories from GIB4 except to scale them (Figure 21). Note that these trajectories represent the combined population in the three annual-count areas.



Figure 21: Estimated population trajectories from model GIB5 compared to those from GIB4 (the latter were scaled to have the same mean as those from GIB5). Trajectories are shown for A, all birds; B, adults; and C, breeders. Also shown, in green, are the breeder count observations (vertical lines are +/- 2 s.e.s).

The SeaBird input files for GIB5, which was considered to be the best model in this study, are given in Appendix 1. The remaining results in Section 4 concern this model or its variants.

#### 4.5.1 Model GIB5a – testing the assumption of philopatry (again)

We showed above (with model GIB4c) that the banding data alone do not allow us to detect either immigration or emigration of pre-breeders. Model GIB5a was designed to see whether the addition of the breeder count data makes any difference in this respect. Its relationship to GIB5 is exactly the same as that between GIB4 and GIB4c.

Although parameter estimates for GIB5 and GIB5a differ – for both N0 and the juvenile parameters – the objective function values for the two models are the same to 1 decimal place (Table 12). Thus, the observations do not allow us to distinguish between low juvenile survival (juvsurv=0.88) with no immigration or emigration (Pimm=0, Pbrstd=1) and full juvenile survival (juvsurv=1) with considerable emigration (Pbrstd=0.22) and a small degree of immigration (Pimm=0.028). [Note that the mean age at first breeding depends on juvsurv, as well as P1stbr10 and M1stbr. Between models GIB5 and GIB5a the changes in these parameters are compensatory, in the sense that the mean age at first breeding changes very little – see last column in Table 12.]

 Table 12: Comparison of objective function values and parameter estimates (for those parameters which differ significantly) for models GIB5 and GIB5a.

	Objective						Age a	t first breeding		
Model	function	N0	juvsurv	Pimm	Pbrstd	P1stbr10	M1stbr	Mean age (y)		
GIB5	14586.5	1552	0.88	(0)+	(1)+	0.075	1.63	12.42		
GIB5a	14586.5	1540	1.0	0.028	0.22	0.114	1.52	12.43		
+ Implici	+ Implicit values of these parameters									

. .

Posterior profiles for Pimm and Pbrstd from model GIB5a were useful to further explore the effect of uncertainty associated with immigration and emigration.

The profile on Pimm showed that this parameter can change substantially (from 0 to 0.5) with only a small effect on the fit to the mark-recapture data and hardly any effect on the priors or fit to the counts

(Figure 22A). As Pimm increases there are compensatory changes in N0, Pbrstd, and the mean age of first breeding (Figure 22B-D) (but essentially no change to juvsurv). From this profile we can infer that an approximate 95% confidence interval for Pimm is (0,0.43) [because at Pimm = 0.43 the objective function is greater by 2 than at the best fit]. Variation within this range of values for Pimm causes a substantial change in the estimated trajectory for the whole population, a much smaller change in the adult trajectory, and even smaller change in the trajectory for breeders (Figure 23).



Proportion immigrating (Pimm)

Figure 22: Output from the profile of Pimm on model GIB5a, showing various quantities of interest plotted against Pimm: A, the total objective function (heavy lines) and its three components (MRdat [mark-recapture data], breeder counts, and prior distributions); B, the initial number of breeders (N0); C, the proportion breeding in the study area (Pbrstd); and D, mean age at first breeding.



Figure 23: Comparison of selected population trajectories from the GIB5a profile on parameter Pimm (those for Pimm = 0, 0.4, and 0.5) with those for models GIB5 and GIB5a. Trajectories are plotted for A, all birds; B, adults; and C, breeders.

The profile on Pbrstd is similar to that for model GIB0d, showing that, in terms of fit to the observations, all values between about 0.22 and 1 are equally possible. Values lower than 0.19 (the lower bound of the 95% confidence interval for Pbrstd) are inconsistent with the banding data, though not with the counts or priors (Figure 24). Variation within this range of values for Pbrstd causes a substantial change

in the estimated trajectory for the whole population, but virtually no change in the adult and breeder trajectories (Figure 25).



Proportion breeding in study area (Pbrstd)

Figure 24: Output from the profile of Pbrstd on model GIB5a, showing various quantities of interest plotted against Pbrstd: A, the total objective function (heavy lines) and its three components (MRdat [mark-recapture data], breeder counts, and prior distributions); B, the initial number of breeders (N0); C, juvenile survival (juvsurv); D, the proportion immigrating (Pimm); and E, mean age at first breeding.



Figure 25: Comparison of selected population trajectories from the GIB5a profile on parameter Pbrstd (those for Pbrstd = 0.2, 0.4, and 1.0) with those for models GIB5 and GIB5a. Trajectories are plotted for A, all birds; B, adults; and C, breeders.

We conclude that the inclusion of the count data in model GIB5a does not add much support for our assumption of philopatry. However, the loss of this assumption does not much change the conclusions about the status of the adult population given above (Table 13).

Table 13: Conclusions about the status of the adult population from models GIB4 (which used only mark-recapture data and assumed philopatry) and GIB5a (which used both mark-recapture and count data and did not assume philopatry). The numbers given for GIB4 are those presented above in the text associated with Figure 19; those for GIB5a are derived from the trajectories plotted in Figures 23 and 25.

	Mean annual change 1	<u>n number of adults</u>
Model	1991–2004	2005-2011
GIB4	-0.3%	-5.8%
GIB5a	-0.2% to 0.4%	-5.6% to -5.1%

Mean number of breeders, 2006–2011, as percentage of number in 1991 47% 47% to 52%

#### 4.5.2 Quantifying uncertainty in model GIB5

In order to quantify uncertainty in GIB5 this model was re-run in Bayesian mode. A single Monte Carlo Markov Chain (MCMC) of length 1 million was generated, starting at a point randomly offset from the point estimate, and every thousandth sample was retained. Thus, instead of obtaining a single best estimate for each parameter we generated a set of 1000 estimates, which may be thought of as a sample from the marginal posterior of that parameter. Plots of traces for each parameter suggest that the chain converged reasonably well for many, but not all parameters (see Appendix 1). Because the Bayesian run was very slow (it took 15 days) no attempt was made to experiment with alternative parameterizations that might improve convergence.

In examining uncertainty, perhaps the most important quantities to focus on are adult survival and the population trajectory. The precision of estimates of adult survival decreased with the estimates (the width of 95% confidence intervals for was typically 0.04 before 2005, and 0.06 after that date) (Table 14). This level of precision is quite adequate to demonstrate the statistical significance of the drop in survival rate from 2005 because the estimated difference between the mean survival rates for the periods 1991–2004 and 2005–2010 is 0.066 (median) with 95% confidence interval (0.054, 0.078). The Bayesian estimates also demonstrate the clear significance of the decline in population numbers (Figure 26). For example the mean number of breeders in 2006–2011 was estimated to be 50% (95% confidence interval 47–53) of that in 1991–2004. The increase in breeders between 2006 and 2011 is also significant (from a regression against year the estimated rate of increase is 4.2% per year, with 95% confidence interval 2.3–6.1). Another quantity of interest is the mean age of first breeding which was estimated to be 12.4 y, with 95% confidence interval 11.9–13.3.

An alternative way to estimate uncertainty in parameter estimates is from the inverse Hessian at the MPD estimate. For this model this approach substantially underestimates uncertainty (Figure 27). Note however, that for key quantities the MPD point estimates did not differ substantially from the MCMC medians (Table 14, Figure 26).

Table 14: Point (MPD) and Bayesian (median of MCMC sample) estimates of adult survival (parameter
adsurv) with 95% confidence intervals (lo.bnd, hi.bnd) derived from the MCMC sample. The value
labelled 2000 denotes the estimated survival between the 1999–2000 and 2000–2001 breeding seasons. See
Appendix 3 for analogous tables for all other parameters.

rappend	IIA 5 IUI an	anogous	tabits it	an oun	ci paran	itter 5.					
	1991–92	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002
MPD	0.965	0.953	0.977	0.971	0.960	0.977	0.948	0.925	0.962	0.958	0.947
MCMC	0.963	0.953	0.975	0.969	0.960	0.976	0.948	0.924	0.962	0.958	0.945
lo.bnd	0.937	0.918	0.951	0.949	0.937	0.956	0.925	0.898	0.941	0.939	0.927
hi.bnd	0.982	0.987	0.992	0.986	0.980	0.990	0.967	0.946	0.978	0.974	0.963
	2003	2004	2005	2006	2007	2008	2009-	10			
MPD	0.960	0.922	0.841	0.909	0.870	0.921	0.9	06			
MCMC	0.959	0.920	0.842	0.910	0.867	0.921	0.9	03			
lo.bnd	0.939	0.892	0.810	0.878	0.838	0.892	0.8	65			
hi.bnd	0.975	0.945	0.873	0.938	0.896	0.950	0.9	39			



Figure 26: Comparison between Bayesian (or MCMC, blue lines) and point (or MPD, red lines) estimates of population trajectories from model GIB5. For the Bayesian estimates, the solid line is the median and the broken lines indicate a 95% confidence interval.



Figure 27: Demonstration that Bayesian (MCMC) confidence intervals for GIB5 parameters were always wider than those from the MPD (taken as 4 times the s.e. estimated from the inverse Hessian). Parameters 23-40 are for adult survival. Omitted from this plot is Prlbr(1998), for which the MPD estimate was at a bound and the ratio of confidence interval widths exceeded 1500.

#### 4.5.3 Scaling up to the whole population

Model GIB5 applies to only that part of the Gibson's wandering albatross that breeds inside the three annual count areas shown in Figure 2. For the whole Auckland Islands population, Walker & Elliott (1999) averaged values for years 1991, 1993–95 and 1997 to obtain an estimated population size of 5831 breeding pairs. For the same years, model GIB5 estimated an average of 1505 breeders (from the Bayesian medians). Scaling up the GIB5 estimates by the ratio of these values produces an estimate of current (2011) population size of 6318 breeders, or 3159 breeding pairs (Figure 28).



Figure 28: Estimated population trajectories for the whole Auckland Islands population of Gibson's wandering albatross. These were calculated by scaling up the Bayesian GIB5 trajectories to match the Walker & Elliott (1999) estimate for the whole population (see text for details).

#### 4.5.4 The effect of reduced survival on productivity

It is possible that the reduction since 2004 in productivity (breeding success and proportion breeding) is a direct consequence of reduced adult survival. When an adult dies its partner cannot nest until it finds another mate (this may take several years) and any current nest fails since albatrosses cannot incubate and raise chicks on their own. Thus the death of a breeding bird reduces both breeding success and the proportion of birds breeding.

Detailed data on breeding pairs show that the reduction in productivity was not primarily caused by the reduction in adult survival. The drop in 2005 in the probability of breeding was also seen in birds whose mate from the previous season was still alive (Figure 29A). Also, if we restrict attention to nests in which both birds were known to be alive at the end of the breeding season, we still find that breeding success was lower from 2005 (Figure 29B).



Figure 29: Investigation of relationship between adult survival and productivity: A, the observed proportion breeding each year for birds whose mate from the previous season was known to be alive (Matealive, dashed line), those whose mate was dead (Mate-dead, dotted line), and all birds (solid line); and B, observed breeding success by nest for those nests where both birds were alive at the end of the breeding season (Both-alive, solid line), for other nests (Other, dashed line), and for all nests (solid line).

#### 4.6 Model GIB6 - the effect of 'strayers'

So far we have ignored the problem of 'strayers' – adult banded birds that sometimes bred outside the study area. This occurred relatively rarely, affecting 2.6% (165/6337) of breeding observations and 4.9% (70/1434) of banded birds (excluding those never seen breeding). Model GIB6 was constructed to examine the effect of these strayers. It differed from GIB5 only in excluding the 70 strayers from the mark-recapture data set. Neither model estimates (Figure 30) nor population trajectories (Figure 31) were much affected by this exclusion.



Figure 30: Comparison of adult parameter estimates from models GIB5 and GIB6, showing that the removal of strayers had little effect.



Figure 31: Comparison of population trajectories estimated from models GIB5 and GIB6, showing that the removal of strayers had little effect.

#### 4.7 Looking forward with model GIB5

The medium-term prospect for this population will be affected by declines in three separate demographic variables: the number of adults (Figure 32A) (affected by the decline in adult survival); the proportion of adults breeding (Figure 32B); and the proportion of breeding attempts that are successful (Figure 32C). The combined effect of these three declines has caused the estimated mean annual fledgling production since 2006 to be only 19% of the corresponding value in the 1990s (Figure 32D). This dramatic drop in production is consistent with the drop in numbers of fledglings banded (compare solid and dashed lines in Figure 32D).

20-year forward projections of the population were used to investigate the medium-term prospect for this population under five different scenarios. With the first scenario (labelled 'status quo') in which all demographic parameters remained at their current (2011) values, the number of adults declined at an average rate of 6.6% per year (see solid line, Figure 33). In the next three scenarios, one demographic parameter was fixed at its 1991 level but all others remained at their status quo levels. This showed that improvements in breeding proportion or success alone would have little effect (see blue lines), but with an improvement in adult survival the average rate of decline decreased to 1.6% per year (see dotted red line). Finally, when all parameters were restored to their 1991 values the rate of decline was only 0.6% per year (see dashed red line).

The key result to be taken from these projections is that the demographic parameter most important to the future status of this population is the rate of adult survival. Until this increases to somewhere near its level in the early 1990s the adult population will continue to decline. Of course, the population rates of change quoted in the previous paragraph are only approximate. This is because of uncertainties associated with both the philopatry assumption (see Section 4.5.1) and individual parameter estimates (see Section 4.5.2). In particular, we cannot say whether a return of all parameters to 1991 levels would cause the adult population to decline slowly or increase slowly.



Figure 32: Four demographic trends estimated from model GIB5 (solid lines). The dashed line in panel D shows the number of fledglings banded (as 1-year olds) in the study area in the following year, scaled to have the same mean value as the solid line for years 1995–2010.



Figure 33: Estimated population trajectory for adults from model GIB5 with 20-year projections under five alternative scenarios about three demographic parameters: adult survival (adsurv); breeding success (Psuccess); and proportion of adults breeding. These scenarios differ according to whether each parameter remains at its status quo (=2011) level or recovers immediately to its 1991 level.

#### 5. COMPARISONS WITH ESTIMATES FOR D. exulans

It is of interest to compare parameter estimates for Gibson's wandering albatross from this study (Table 15) with published estimates for several populations of its congener *D. exulans*: in South Georgia in the southern Atlantic Ocean (Croxall et al. 1998); the Crozet Islands in the Indian Ocean (Weimerskirch & Jouventin 1987, Weimerskirch et al. 1997); and Macquarie Island (de la Mare & Kerry 1994).

# Table 15: Estimates of demographic parameters for Gibson's wandering albatross from model GIB5 (with 95% confidence intervals in parentheses): A, parameters that changed in about 2005; and B, other parameters.

A, Parameters that changed in about 2005

			Averag	ge annual values	
Parameter		Before 2005	Since 2005		
Adult survival (y <sup>-1</sup> )	0.954	(0.950-0.959)	0.889	(0.877 - 0.898)	
Proportion of adults breeding	0.530	(0.518-0.541)	0.369	(0.356-0.384)	
Breeding success	0.597	(0.578–0.613)	0.253	(0.228–0.276)	
B, Other parameters					
Parameter		Estimate			
Mean age at first breeding (y)	12.4	(11.9–13.3)			
Juvenile survival (y <sup>-1</sup> )	0.880	(0.866–0.899)			

For adult survival, the pre- and post-2005 estimates for Gibson's (0.954 and 0.889 y<sup>-1</sup>) lie within the range of estimates (0.87–0.97 y<sup>-1</sup>) tabulated by Moloney et al. (1994) for the Crozet Islands and South Georgia (see their table 3). The pre-2005 estimate of 0.954 y<sup>-1</sup> is slightly below the value of 0.96 y<sup>-1</sup>, which was estimated for both South Georgia and Crozet Islands populations for the period before there was large-scale longline fishing in the southern hemisphere and these populations were believed to be

stable or slowly increasing (Weimerskirch et al. 1997, Croxall et al. 1998). The post-2005 estimate of  $0.889 \text{ y}^{-1}$  is lower than estimates for *D. exulans* populations for periods at which they were declining.

Compared with that for Gibson's, the estimated proportion of adults breeding each year for *D. exulans* was higher in the Crozet Islands (0.588, Moloney et al. 1994) and lower in Maquarie Island (where it dropped from about 0.43 in 1957 to 0.28 in 1981, de la Mare & Kerry 1994).

Estimates of breeding success for *D. exulans* vary widely, but are mostly similar to, or greater than, the pre-2005 value of 0.597 estimated for Gibson's. In the Crozet Islands the rate increased as the population recovered (from 0.62 in 1966–79 to 0.73 in 1980–93 (median values), Weimerskirch et al. 1997); in South Georgia it increased from 0.60 (pre-1970) to 0.70 (post-1987) (Croxall et al. 1998); and at Macquarie Island it decreased from 0.86 (1954–64) to 0.56 (1968–86) (de la Mare & Kerry 1994).

The estimated mean age of first breeding for Gibson's (12.4 y) is slightly higher than estimates for *D. exulans* (11.7 y in the Crozet Islands, 11.9 y in Macquarie Island, and 10.6 y in South Georgia: Weimerskirch & Jouventin 1987, de la Mare & Kerry 1994, Croxall et al. 1998).

To make estimates of juvenile survival from different sources comparable, they were converted to estimates of the proportion of birds that survive from fledging (at age 1 y) to age 11 y. The estimate of  $0.28 (= 0.88^{10})$  for Gibson's (95% confidence interval, 0.24–0.34) was within the ranges estimated for the Crozet Islands (ranging from 0.11 for 1970–76 to 0.38 for 1986–94, Weimerskirch et al. 1997) and South Georgia (from 0.36 pre-1970 to 0.27 since 1987, Croxall et al. 1998).

#### 6. CONCLUSIONS

We first state our conclusions in relation to reworded objectives 2–4 (see Section 1) and then summarise other results.

*Objective 2*. There is cause for concern about status of the population of Gibson's wandering albatross on the Auckland Islands. Since 2005, the adult population has been declining at a rate of 5.7%/yr (95% c.i. 4.5–6.9) because of sudden and substantial reductions in three demographic rates: adult survival, proportion breeding, and the proportion of breeding attempts that are successful (Table 15A). In 2011 it was 64% (95% c.i. 58–73) of its estimated size in 1991. The breeding population dropped sharply in 2005, to 59% of its 1991 level, but has been increasing since 2005 at 4.2% per year (95% c.i. 2.3–6.1) because of slow increases in adult survival and proportion breeding. The current (2011) breeding population is estimated to be only 54% of the average of 5831 pairs estimated by Walker & Elliott (1999) for 1991–97.

*Objective 3.* It is difficult to assess the effect of fisheries mortality on the viability of this population. There is some information about bycatch of Gibson's in New Zealand waters, and of wandering albatrosses (species unknown) in Australian waters, but little is known about the effect of fisheries in international waters. Three conclusions are possible from the available data: most fisheries mortality of Gibson's is caused by surface longlines; mortality from fishing is now probably lower than it was; and there is no indication in the data that the sudden and substantial drops in demographic rates described in Table 15A were caused primarily by fishing.

*Objective 4.* No attempt was made to assess the effect of alternative management strategies because none has been suggested. However, forward projections showed that, of the three demographic parameters in Table 15A, the most important to the future status of this population is adult survival.

The extent to which this species exhibits philopatry (i.e., breeds where it was born) is not known, and this compromised our ability to estimate juvenile survival. Assuming full philopatry, the annual rate of juvenile survival was estimated to be 0.880 (95% c.i. 0.866-0.899); this will be an under-estimate if philopatry is partial. The mean age of first breeding was estimated to be 12.4 y (95% c.i. 11.9-13.3).

#### 7. ACKNOWLEDGMENTS

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#### 8. REFERENCES

- Abraham, E.R.; Thompson, F.N. (2011). Summary of the capture of seabirds, marine mammals, and turtles in New Zealand commercial fisheries, 1998–99 to 2008–09. *New Zealand Aquatic Environment and Biodiversity Report No. 80.*
- Agreement on the Conservation of Albatrosses and Petrels (2009). ACAP species assessment: Antipodean albatross *Dimomedea antipodensis*. Downloaded from <u>http://www.acap.aq</u> on 24 June 2010.
- Anonymous (2008). Summary of autopsy reports for seabirds killed and returned from observed New Zealand fisheries 1 October 1996 30 September 2005, with specific reference to 2002/03, 2003/04, 2004/05. DOC Research & Development Series 291. 110 p.
- Brothers, N.; Duckworth, A.R.; Safina, C.; Gilman, E.L. (2010). Seabird bycatch in pelagic longline fisheries is grossly underestimated when using only haul data. PLoS ONE 5: e12491. doi:10.1371/journal.pone. 0012491
- Croxall, J.P.; Prince, P.A.; Rothery, P.; Wood, A.G. (1998). Population changes in albatrosses at South Georgia. *In*: Albatross biology and conservation Robertson, G.; Gales, R. (eds.). Surrey Beatty & Sons, Chipping Norton. pp 69–83.
- de la Mare, W.K.; Kerry, K.R. (1994). Population dynamics of the wandering albatross (*Diomedea exulans*) on Macquarie Island and the effects of mortality from longline fishing. *Polar Biology* 14: 231–241.
- Fox, J.W. (2010). Geolocator manual v8 (March 2010). Unpublished report, British Antarctic Survey, Cambridge, UK.
- Francis, R.I.C.C. (2011). Fisheries risks to the population viability of White-capped albatross. Final Report for Year 4 Ministry of Fisheries Research Project PRO200602 Objectives 1–4. 22 p. (Unpublished report held by Ministry for Primary Industries, Wellington.)
- Francis, R.I.C.C.; Bell, E.A. (2010). Fisheries risks to the population viability of black petrel (*Procellaria parkinsoni*). New Zealand Aquatic Environment and Biodiversity Report No. 51.
- Francis, R.I.C.C.; Fu, D.; Sagar, P.M.; Gilbert, D.J. (2007). Final Report for Year 1 of Ministry of Fisheries Seabird Modelling ProjectPRO200602. Final Research Report for Ministry of Fisheries Research Project PRO200602. 65 p. (Unpublished report held by Ministry for Primary Industries, Wellington.)
- Francis, R.I.C.C.; Sagar, P.M. (2012). Modelling the effect of fishing on southern Buller's albatross using a 60-year dataset. *New Zealand Journal of Zoology 39(1):3–17.*
- Francis, R.I.C.C.; Sagar, P.M.; Fu, D. (2008). Final Report for Year 2 of Ministry of Fisheries Seabird Modelling Project PRO200602. Final Research Report for Ministry of Fisheries Research Project PRO200602. 134 p. (Unpublished report held by Ministry for Primary Industries, Wellington.)
- Gales, R.; Brothers, N.; Reid, T. (1998). Seabird mortality in the Japanese tuna longline fishery around Australia, 1988–1995. *Biological Conservation* 86: 37–56.

- IUCN (2010). IUCN Red List of Threatened Species. Version 2010.3. Downloaded from <<u>www.iucnredlist.org</u>> on 26 September 2011.
- Klaer, N.; Polacheck, T. (1997). Bycatch of albatrosses and other seabirds by Japanese longline fishing vessels in the Australian Fishing Zone from April 1992 to March 1995. *Emu* 97: 150–167.
- Moloney, C.L.; Cooper, J.; Ryan, P.G.; Siegfried, W.R. (1994). Use of a population model to assess the impact of longline fishing on wandering albatross *Diomedea exulans* populations. *Biological Conservation* 70(3): 195–203.
- Murray, T.E.; Bartle, J.A.; Kalish, S.R.; Taylor, P.R. (1993). Incidental capture of seabirds by Japanese southern bluefin tuna longline vessels in New Zealand waters, 1988–1992. *Bird Conservation International 3*: 181–210.
- Nicholls, D.G.; Robertson, C.J.R.; Prince, P.A.; Murray, M.D.; Walker, K.J.; Elliott, G.P. (2002). Foraging niches of three Diomedea albatrosses. *Marine Ecology Progress* Series 231: 269–277.
- Robertson, H.A.; Dowding, J.E.; Elliott, G.P.; Hitchmough, R.A.; Miskelly, C.M.; O'Donnell, C.F.J.; Powlesland, R.G.; Sagar, P.M.; Scofield, R.P.; Taylor, G.A. (2013). Conservation status of New Zealand birds, 2012. Department of Conservation, Wellington. 22 p.
- Scofield, P.; Sagar, P. (2006). Albatrosses. *In*: The state of New Zealand's birds. Wilson, K.-J. (ed.). The Ornithological Society of New Zealand. (Available at <u>http://osnz.org.nz/publications/state-new-zealand-birds-2006)</u>.
- Thompson, D.R. (2009). Autopsy report for seabirds killed and returned from observed New Zealand fisheries 1 October 2005 to 30 September 2006. *DOC Marine Conservation Services Series* 2. 35 p.
- Thompson, D.R. (2010a). Autopsy report for seabirds killed and returned from New Zealand fisheries, 1 October 2008 to 30 September 2009. 25 p. Draft report prepared for the Conservation Services Programme, Department of Conservation: Contract INT2007/02
- Thompson, D.R. (2010b). Autopsy report for seabirds killed and returned from observed New Zealand fisheries 1 October 2006 to 30 September 2007. *DOC Marine Conservation Services Series 3*. 37 p.
- Thompson, D.R. (2010c). Autopsy report for seabirds killed and returned from observed New Zealand fisheries 1 October 2007 to 30 September 2008. *DOC Marine Conservation Services Series* 5. 33 p.
- Trebilco, R.; Gales, R.; Lawrence, E.; Alderman, R.; Robertson, G.; Baker, G.B. (2010). Characterizing seabird bycatch in the eastern Australian tuna and billfish pelagic longline fishery in relation to temporal, spatial and biological influences. *Aquatic Conservation: Marine and Freshwater Ecosystems* 20: 531–542.
- Walker, K.; Elliott, G. (1999). Population changes and biology of the wandering albatross *Diomedea exulans gibsoni* at the Auckland Islands. *Emu(99)*: 239–247.
- Walker, K.; Elliott, G. (2006). At-sea distribution of Gibson's and Antipodean wandering albatrosses, and relationships with long-line fisheries. *Notornis* 53(3): 265–290.
- Walker, K.; Elliott, G. (2009). Gibson's wandering albatross research Adams Island 2009. 11 p. Unpublished report produced for the Department of Conservation.
- Weimerskirch, H.; Brothers, N.; Jouventin, P. (1997). Population dynamics of wandering albatross *Diomedea exulans* and Amsterdam albatross *D. amsterdamensis* in the Indian Ocean and their relationships with long-line fisheries: conservation implications. *Biological Conservation* 79: 257–270.
- Weimerskirch, H.; Jouventin, P. (1987). Population dynamics of the wandering albatross, *Diomedea exulans*, of the Crozet Islands: causes and consequences of the population decline. *Oikos 49*: 315–322.

#### APPENDIX 1: SeaBird Input Files for model GIB5

#### A1.1 The population file

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Nlbr
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@current 2011
@final 2011
@initialisation
 NO 1500
  n_equilibrium 50
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@annual cycle
  time_steps 1
  surv_props 1
  recruitment_time 1
  transition_time 1
@transition
  parameter_map
  0
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                 0
                   0 0 0
                          0
                            0
                               0
                                 0 0
                                      0
                                        0
                                           0
                          0 0 0 0 0 0
  0 0 0 1 0 0 0 0 0
                 0
                   0 0 0
                                        0
                                           0
  0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0
  0 0 0 0 0 0 0 2 0 0 0 0 0 0 0 0 0 0 12 23
                                           0
  0 0 0 0 0 0 0 0 3
                   0 0 0
                          0
                            0
                               0 0 0 13 24
                 0
                                           0
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                                           0
  0 0 0 0 0 0 0 0 0 5 0 0 0 0 0 0 15 26 0
  0 0 0 0 0 0 0 0 0 0 6 0 0 0 0 0 16 27
                                           0
  0 0 0 0 0 0 0 0 0 0 0 0 7 0 0 0 0 17 28
                                           0
  0 0 0 0 0 0 0 0 0
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                                 0 0 18 29
                                           0
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                                           0
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                                           0
  1
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Pbrs8 Pbrs9 Pbrs10 Pbrs11 Pbrs12 Pbrs13 Pbrs14 Pbrs15 Pbrs16 Pbrs17 Pbrs18
Tnbrnbr Tnbrfbr Tnbrsbr
                     Tfbrnbr Tfbrfbr Tfbrsbr
                                           Tlbrnbr Tlbrfbr Tlbrsbr
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 classes N1
 parameter_names Nrec
@survival
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  parameter_names juvsurv adsurv
@selectivity names selbr
@selectivity selbr
 parameter_map 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 2 2 1
  parameters 0 1
@resight_p Presight
  parameter_map 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 2 3 4 5
  parameter_names Const0 Prnbr Prfbr Prsbr Prlbr
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  values 0
@base_parameter
 nameConst1
```

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@base_parameter
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          values
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  2005 2006 2007 2008 2009
@base parameter
  name juvsurv
  values
         0.95
@base_parameter
  name adsurv
          values
  0.95 0.95 0.95 0.95 0.95
  year_blocks 1991 1993 1994 1995 1996 1997 1998 1999 2000 2001 2002 2003 2004
  2005 2006 2007 2008 2009
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  values 0.1
@base_parameter
  name
         Mlstbr
  values 3
@base_parameter
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  values 0.31
@base_parameter
        Pfbrbr
  name
  values 0.51
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  name
        Plbrbr
  values 0.66
@base_parameter
  name Mbr
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  2005 2006 2007 2008 2009 2010
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  values
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  2006 2007 2008 2009 2010 2011
@base_parameter
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  year_blocks 1991 1994 1995 1996 1997 1998 1999 2000 2001 2002 2003 2004 2005
  2006 2007 2008 2009 2010 2011
@base_parameter
  name
       Prlbr
          values
  0.95 0.95 0.95 0.95 0.95
  year_blocks 1991 1995 1996 1997 1998 1999 2000 2001 2002 2003 2004 2005 2006
  2007 2008 2009 2010 2011
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 step1
 formula 0.5*Nsbr
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@derived_parameter
  nameP1stbr8
            1/(1+(1-Plstbr9)*Mlstbr/Plstbr9)
  formula
@derived_parameter
  nameP1stbr11
  formula 1/(1+(1-Plstbr10)/(Mlstbr*Plstbr10))
@derived_parameter
  nameP1stbr12
  formula 1/(1+(1-Plstbr11)/(Mlstbr*Plstbr11))
@derived_parameter
  nameP1stbr13
  formula
            1/(1+(1-P1stbr12)/(M1stbr*P1stbr12))
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  nameP1stbr14
  formula 1/(1+(1-P1stbr13)/(M1stbr*P1stbr13))
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  formula 1/(1+(1-P1stbr14)/(M1stbr*P1stbr14))
@derived_parameter
  nameP1stbr16
  formula 1/(1+(1-P1stbr15)/(M1stbr*P1stbr15))
@derived_parameter
  nameP1stbr17
  formula
           1/(1+(1-P1stbr16)/(M1stbr*P1stbr16))
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@derived_parameter
  namePbrf9
            (1-Psuccess)*Plstbr9
  formula
@derived_parameter
  namePbrf10
  formula
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@derived_parameter
  namePbrf11
  formula (1-Psuccess)*P1stbr11
@derived_parameter
  namePbrf12
  formula (1-Psuccess)*P1stbr12
@derived_parameter
  namePbrf13
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@derived_parameter
  namePbrf14
  formula (1-Psuccess)*P1stbr14
@derived_parameter
  namePbrf15
          (1-Psuccess)*P1stbr15
  formula
@derived_parameter
  namePbrf16
            (1-Psuccess)*P1stbr16
  formula
@derived_parameter
  namePbrf17
            (1-Psuccess)*Plstbr17
  formula
@derived_parameter
  namePbrf18
  formula
           (1-Psuccess)
## Define Pbrsx
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  namePbrs8
  formula
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@derived_parameter
  namePbrs9
           Psuccess*P1stbr9
  formula
```

@derived\_parameter namePbrs10 Psuccess\*P1stbr10 formula @derived\_parameter namePbrs11 formula Psuccess\*P1stbr11 @derived\_parameter namePbrs12 formula Psuccess\*P1stbr12 @derived\_parameter namePbrs13 formula Psuccess\*P1stbr13 @derived\_parameter namePbrs14 formula Psuccess\*P1stbr14 @derived\_parameter namePbrs15 formula Psuccess\*P1stbr15 @derived\_parameter namePbrs16 formula Psuccess\*P1stbr16 @derived\_parameter namePbrs17 formula Psuccess\*P1stbr17 @derived\_parameter namePbrs18 formula Psuccess ## Define Pjvx @derived\_parameter namePjv8 1-Pbrf8-Pbrs8 formula @derived\_parameter namePjv9 formula 1-Pbrf9-Pbrs9 @derived\_parameter namePjv10 formula 1-Pbrf10-Pbrs10 @derived\_parameter namePjv11 formula 1-Pbrf11-Pbrs11 @derived\_parameter namePjv12 formula 1-Pbrf12-Pbrs12 @derived\_parameter namePjv13 formula 1-Pbrf13-Pbrs13 @derived\_parameter namePjv14 formula 1-Pbrf14-Pbrs14 @derived\_parameter namePjv15 1-Pbrf15-Pbrs15 formula @derived\_parameter namePjv16 1-Pbrf16-Pbrs16 formula @derived\_parameter namePjv17 1-Pbrf17-Pbrs17 formula ## Define Tnbrxxx @derived\_parameter nameTnbrbr formula Pnbrbr\*Mbr/(1-Pnbrbr+Pnbrbr\*Mbr) @derived\_parameter nameTnbrnbr formula 1-Tnbrbr @derived\_parameter nameTnbrfbr Tnbrbr\*(1-Psuccess) formula

```
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  formula
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## Define Tfbrxxx
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@derived_parameter
  nameTfbrnbr
  formula
           1-Tfbrbr
@derived_parameter
  nameTfbrfbr
  formula Tfbrbr*(1-Psuccess)
@derived_parameter
  nameTfbrsbr
  formula Tfbrbr*Psuccess
## Define Tlbrxxx
@derived_parameter
  nameTlbrbr
  formula Plbrbr*Mbr/(1-Plbrbr+Plbrbr*Mbr)
@derived_parameter
  nameTlbrnbr
  formula 1-Tlbrbr
@derived_parameter
  nameTlbrfbr
  formula
           Tlbrbr*(1-Psuccess)
@derived_parameter
  nameTlbrsbr
  formula Tlbrbr*Psuccess
```

#### A1.1 The estimation file

```
@estimator Bayes # Use the Bayes estimation method
@max_iters 2500
@max_evals 4000
@grad_tol 1e-6 # Set the tolerance for the convergence test at 0.002
@MCMC
start 1
keep 1000
length 1000000
stepsize 0.02
@profile
  parameter juvsurv
  n 7
  1 0.79
  u 0.97
@mark_recapture MRdat
  step 1
  proportion_mortality 0
  resight_p Presight
  composite_class_indices 22
  composite_class_22 19 20
... [banding data omitted]
@abundance brcounts
  years 1998 1999 2000 2001 2002 2003 2004 2005 2006 2007 2008 2009 2010 2011
  step 1
  proportion_mortality 0
  selectivity selbr
  1998 1582
  1999 1486
  2000 976
  2001 1350
  2002 1428
  2003 1568
  2004 1724
  2005 858
```

2006 558 2007 800 2008 636 2009 772 2010 766 2011 850 dist normal cv 0.05 ## Parameters to be estimated @estimate parameter initialisation.NO lower\_bound 1000 upper\_bound 2000 prior uniform-log @estimate parameter juvsurv lower\_bound 0 upper\_bound 1 prior uniform @estimate parameter Plstbr10 lower\_bound 0.01 upper\_bound 0.99 prior uniform

@estimate parameter M1stbr lower\_bound 0.1 upper\_bound 5 prior uniform @estimate parameter Psuccess 0.1 0.1 0.1 0.1 upper\_bound 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 prior uniform @estimate parameter adsurv prior uniform @estimate parameter Pnbrbr lower\_bound 0 upper\_bound 1 prior uniform @estimate parameter Plbrbr lower\_bound 0 upper\_bound 1 prior uniform @estimate parameter Mbr 0.2 0.2 0.2 0.2 0.2 upper\_bound 10 10 10 10 10 10 10 10 10 10 10 10 10 10 10 10 10 10 10 prior uniform @estimate parameter Prnbr prior uniform @estimate parameter Prfbr prior normal-by-stdev mu 0.9 0.971 0.979 0.937 0.926 0.936 0.976 0.977 0.893 0.926 0.976 0.986 0.967  $0.908 \ 0.963 \ 0.968 \ 0.932 \ 0.974 \ 0.974$ stdev 0.039 0.02 0.012 0.02 0.022 0.02 0.012 0.013 0.025 0.022 0.01 0.008 0.013 0.024 0.015 0.016 0.019 0.013 0.011 @estimate parameter Prsbr prior normal-by-stdev mu 0.895 0.953 0.975 0.957 0.996 0.99 0.992 0.99 0.975 0.991 0.99 0.99 0.99 0.99  $0.99 \ 0.99 \ 0.99 \ 0.99 \ 0.974$ stdev .021 0.016 0.01 0.013 0.004 0.005 0.006 0.005 0.009 0.006 0.005 0.005 0.005 0.005 0.005 0.005 0.005 0.005 0.011 @estimate parameter Prlbr 0.01 0.01 0.01 0.01 1.00 1.00 1.00 1.00 prior uniform

#### **APPENDIX 2: MCMC Diagnostics for GIB5**

In this appendix we present traces for all parameters from the Bayesian run of model GIB5 described in Section 4.5.2.









Figure A1.6: Traces of Prlbr for each year.



Figure A1.8: Traces of all non-time-varying parameters.

#### **APPENDIX 3:** Other parameter estimates from GIB5

Estimates from model GIB5 of adult survival, the most important parameter, are given in Table 14 above. This appendix contains similar tables of estimates for all other parameter from this model.

Table A3.1:	Point (MPD) and	Bayesian (median	of MCMC s	ample) of all r	on-time-series	parameters
from model	GIB5 with 95% co	onfidence intervals	derived fror	m the MCMC	sample.	

• • •				
	N0	juvsurv	P1stbr10	M1stbr
MPD	1552	0.880	0.0747	1.63
MCMC	1565	0.880	0.0747	1.65
lo.bnd	1406	0.866	0.0546	1.43
hi.bnd	1730	0.899	0.0971	1.90

#### Table A3.2: As for Table A3.1, but for parameter Psuccess.

	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	20
04	2005											
MPD	0.654	0.606	0.658	0.645	0.712	0.637	0.612	0.518	0.648	0.662	0.509	0.5
51	0.403											
MCMC	0.650	0.586	0.65	0.644	0.706	0.635	0.611	0.515	0.648	0.665	0.511	0.5
49	0.397											
lo.bnd	0.577	0.453	0.581	0.594	0.648	0.588	0.560	0.455	0.598	0.610	0.463	0.5
03	0.344											
hi.bnd	0.725	0.688	0.706	0.689	0.755	0.678	0.657	0.578	0.69	0.717	0.553	0.5
94	0.457											
	2006	2007	2008	2009	2010							
MPD	0.232	0.238	0.306	0.233	0.256							
MCMC	0.236	0.231	0.306	0.226	0.258							
lo.bnd	0.184	0.179	0.250	0.174	0.216							
hi.bnd	0.298	0.288	0.370	0.283	0.313							

#### Table A3.3: As for Table A3.1, but for parameter Mbr.

	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	20
03	2004											
MPD	4.726	1.215	3.345	4.779	2.802	5.209	3.183	0.770	1.686	2.570	3.079	2.5
67	0.747											
MCMC	5.500	1.296	3.449	5.523	3.012	5.317	3.473	0.809	1.807	2.814	3.412	2.7
05	0.786											
lo.bnd	3.024	0.925	2.612	3.820	2.335	4.091	2.725	0.678	1.469	2.282	2.655	2.2
32	0.665											
hi.bnd	9.389	2.263	4.500	7.648	3.777	7.557	4.331	0.955	2.237	3.631	4.363	3.2
92	0.934											
	2005	2006	2007	2008	2009	2010						
MPD	0.327	0.579	0.496	0.759	0.724	0.953						
MCMC	0.346	0.612	0.523	0.813	0.764	1.018						
lo.bnd	0.292	0.519	0.440	0.664	0.643	0.826						
hi.bnd	0.409	0.731	0.621	0.988	0.921	1.274						

Table A3.4: As for Table A3.1, but for parameter Prnbr.														
	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	20		
04	2005													
MPD	0.754	0.042	0.536	0.813	0.334	0.443	0.655	0.701	0.643	0.818	0.826	0.7		
87	0.733													
MCMC	0.766	0.054	0.551	0.795	0.346	0.471	0.619	0.707	0.649	0.832	0.838	0.7		
92	0.740													
lo.bnd	0.427	0.015	0.439	0.636	0.262	0.357	0.509	0.644	0.563	0.726	0.763	0.7		
05	0.682													
hi.bnd	0.985	0.107	0.671	0.961	0.456	0.613	0.734	0.773	0.721	0.933	0.911	0.8		
71	0.792													
	2006	2007	2008	2009	2010	2011								
MPD	0.653	0.786	0.709	0.716	0.693	0.757								

MCMC	0.650	0.784	0.710	0.721	0.694	0.769
lo.bnd	0.599	0.732	0.662	0.659	0.631	0.654
hi.bnd	0.698	0.829	0.757	0.777	0.761	0.879

#### Table A3.5: As for Table A3.1, but for parameter Prfbr.

	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	20
04	2005											
MPD	0.896	0.971	0.982	0.945	0.931	0.940	0.981	0.979	0.910	0.930	0.979	0.9
86	0.973											
MCMC	0.906	0.966	0.980	0.941	0.930	0.938	0.980	0.978	0.908	0.930	0.977	0.9
85	0.971											
lo.bnd	0.838	0.930	0.957	0.903	0.887	0.899	0.957	0.953	0.863	0.888	0.958	0.9
71	0.946											
hi.bnd	0.971	0.996	0.997	0.984	0.972	0.974	0.998	0.998	0.957	0.969	0.996	0.9
98	0.994											
	2006	2007	2008	2009	2010	2011						
MPD	0.916	0.959	0.967	0.926	0.967	0.972						
MCMC	0.915	0.957	0.966	0.922	0.966	0.971						
lo.bnd	0.870	0.929	0.933	0.887	0.941	0.950						
hi.bnd	0.960	0.987	0.994	0.957	0.991	0.992						

#### Table A3.6: As for Table A3.1, but for parameter Prsbr.

	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	20
04	2005											
MPD	0.915	0.956	0.979	0.965	0.998	0.990	0.991	0.990	0.965	0.984	0.983	0.9
87	0.990											
MCMC	0.912	0.957	0.978	0.964	0.996	0.990	0.990	0.990	0.964	0.983	0.982	0.9
87	0.990											
lo.bnd	0.876	0.926	0.961	0.942	0.989	0.980	0.980	0.979	0.948	0.972	0.973	0.9
78	0.980											
hi.bnd	0.948	0.986	0.995	0.986	1.000	0.998	0.999	0.998	0.98	0.993	0.991	0.9
96	0.999											
	2006	2007	2008	2009	2010	2011						
MPD	0.990	0.990	0.990	0.990	0.990	0.972						
MCMC	0.990	0.990	0.990	0.990	0.990	0.972						
lo.bnd	0.981	0.980	0.981	0.980	0.980	0.952						
hi.bnd	0.999	0.998	0.999	0.999	0.999	0.993						

#### Table A3.7: As for Table A3.1, but for parameter Prlbr.

	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	20
05	2006											
MPD	0	0.138	0.149	0.055	0.010	0.068	0.111	0.092	0.095	0.144	0.189	0.1
38	0.081											
MCMC	0	0.138	0.151	0.056	0.013	0.069	0.115	0.095	0.096	0.147	0.189	0.1
47	0.089											
lo.bnd	0	0.093	0.110	0.033	0.010	0.044	0.077	0.053	0.066	0.105	0.144	0.1
00	0.043											
hi.bnd	0	0.197	0.190	0.088	0.025	0.106	0.157	0.153	0.133	0.191	0.241	0.1
90	0.157											
	2007	2008	2009	2010	2011							
MPD	0.115	0.108	0.069	0.114	0.032							
MCMC	0.115	0.107	0.075	0.133	0.047							
lo.bnd	0.046	0.045	0.031	0.058	0.015							
hi.bnd	0.200	0.186	0.139	0.219	0.125							