



Fisheries Risks to the Population Viability of
White-capped Albatross *Thalassarche steadi*

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TABLE OF CONTENTS

EXECUTIVE SUMMARY	1
1. INTRODUCTION	2
1.1 The study population	2
2. THE DATA	3
2.1 Fisheries mortality data	3
2.2 Abundance estimates	7
2.3 Mark-recapture data	10
2.4 Nest-based data	10
3. MODELLING OF THE DATA	12
3.1 Initial model runs	12
3.2 Additional models	15
4. TRENDS IN ABUNDANCE	16
5. CONCLUSIONS	17
6. ACKNOWLEDGEMENTS	17
7. REFERENCES	17
APPENDIX 1: SeaBird Input Files for the main models	20
APPENDIX 2: Traces for additional model runs of Section 3.2	23

EXECUTIVE SUMMARY

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This report attempts to assess fisheries risks to the viability of the main population of white-capped albatross (*Thalassarche steadi*), which breeds on the Auckland Islands. Three types of data were available: bycatch, photographic surveys, and mark-recapture (both bird-based and nest-based).

The status of this population is uncertain. The photographic surveys suggest that the adult population declined at 9.8% per year between 2006 and 2009, but this estimate is imprecise, and seems too high to be consistent with other data. It may be possible to decrease uncertainty by analysing data from earlier photographic surveys.

The global bycatch of this species (including cryptic mortality) is estimated to be over 17 000 birds per year, which could present a risk to population viability. About 30% of this bycatch came from New Zealand fisheries, and this percentage appears to be declining. Lack of data concerning cryptic mortality make these estimates very uncertain.

The mark-recapture data provided estimates of adult survival (0.96 with a 95% confidence interval of 0.91–1.00), annual probability of breeding (0.68, confidence interval 0.58–0.81), and breeding success (0.63, confidence interval 0.51–0.75). No information is available about either juvenile survival or the age at first breeding.

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 following two years the last three objectives were addressed (where appropriate) for Southern Buller's albatross (Francis et al. 2008, Francis & Sagar in press) and black petrel (Francis & Bell 2010). In this report I describe work in the fourth year of this project, in which data for white-capped albatross were analysed.

1.1 The study population

The white-capped albatross (*Thalassarche steadi*) is New Zealand's most numerous breeding albatross. It is endemic to New Zealand, breeding primarily on the Auckland Islands, with relatively small numbers breeding at Bollons Island (in the Antipodes Islands group) and at the Forty-Fours (in the Chatham Islands group) (Robertson et al. 1997, Tennyson et al. 1998, Taylor 2000). The population studied here is that breeding at the Auckland Islands, of which the great majority breed on Disappointment Island, with lesser numbers on Auckland and Adam Islands (Figure 1). Eggs are usually laid in mid-November and hatch in February.

White-capped albatross are listed as Near Threatened by IUCN (IUCN 2010) and At Risk (Declining) by New Zealand (as *T. cauta steadi*) (Miskelly et al. 2008). In their assessment of risks to New Zealand seabirds from commercial fishing Baird & Gilbert (2008) found white-capped albatross to be at low-moderate risk, but the paucity of biological information for this species has resulted in its being classified as high priority for research in the draft National Plan of Action – Seabirds Research Plan.

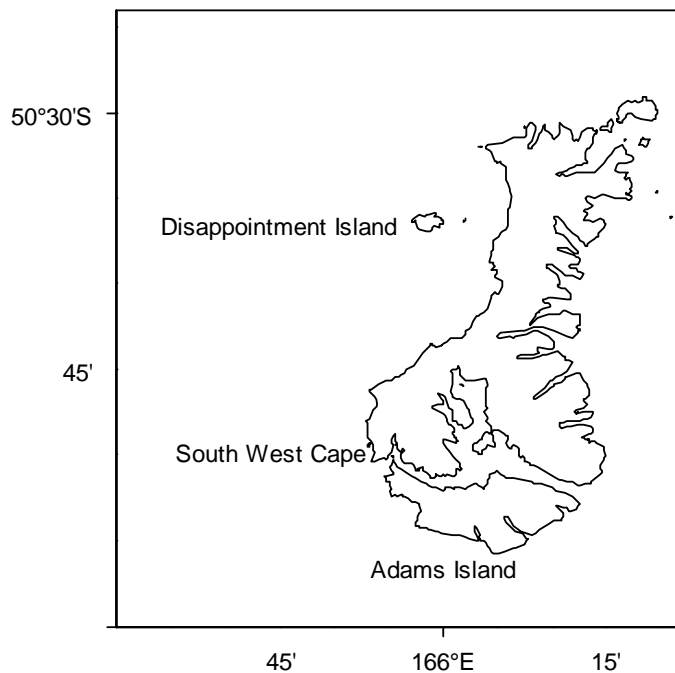


Figure 1: Locations of the three white-capped albatross breeding sites within the Auckland Islands.

2. THE DATA

Three types of data were available for the present study: fisheries mortality, abundance estimates, and mark-recapture data, with the last type being in two categories – bird-based and nest-based.

2.1 Fisheries mortality data

I first describe various estimates of WCAP bycatch, in New Zealand and elsewhere, and then adjust the best estimates for cryptic mortality (defined below).

Waugh et al. (2008) analysed seabird bycatch in New Zealand trawl (TR), surface longline (SLL), and bottom longline (BLL) fisheries during the seven fishing years, 1997/98–2003/04, and presented annual bycatch estimates for all seabirds, and for trawl-caught albatrosses. Four tables from this paper are of interest in the present study. The first two (their tables 2 and 3) tabulate – by species, fishing method, and Fisheries Management Area (FMA) – the 3633 seabirds observed by scientific observers caught, killed, and formally identified to species level. These data are summarised, for white-capped albatross (WCAP), in columns 3–4 of Table 1.

The third table (table 13 of Waugh et al. 2008) provided model-based estimates, by strata (defined by combinations of vessel size, fishing method, FMA – or group of FMAs – and season), of the annual bycatch of all seabirds, both for 2003/04 and an average across all seven years. I summed these estimates across vessel size and season to produce values for all combinations of method and FMA in which WCAP were observed caught (see columns 5–6 in Table 1), and then scaled these sums by the percentage of WCAP in the bycatch to produce estimates of WCAP bycatch (columns 7–8, Table 1). Total estimates were 1136 for 2003/04, and 848 per year over 1997/98–2003/04. Of this latter value, 98% was trawl-caught, and 86% came from FMAs 5 or 6 (the corresponding percentages for 2003/04 are 98% and 90%, respectively). The total WCAP bycatch estimates in Table 1 are slight under-

estimates (perhaps by 1–2%) because table 13 of Waugh et al. (2008) excluded some strata (see footnote 3, Table 1).

Table 1: Estimates, by fishing method (TR = trawl, SLL = surface longline, BLL = bottom longline) and Fisheries Management Area (FMA), of the annual bycatch of white-capped albatross (WCAP) for fishing years 1997/98–2003/04 (columns 7–8), derived from data of Waugh et al. (2008) (columns 3–4 and 5–6 derive from their tables 2–3 and 13, respectively). Combinations of fishing method and FMA with no observed WCAP bycatch were excluded from this table.

Fishing method	FMA	Observed WCAP		Seabird bycatch		WCAP bycatch	
		Number	Percentage ¹	2003/04	average ²	2003/04	average ²
TR	2	4	20	– ³	– ³	–	–
TR	3	25	7.2	479	632	35	46
TR	4	4	3.1	204	198	6	6
TR	5	423	50	693	626	346	313
TR	6	274	70	951	573	663	399
TR	7	27	45	150	144	68	65
SLL	2,4	1	0.41	1113	1283	5	5
SLL	5	33	29	46	43	13	12
SLL	3,7	7	13	– ³	– ³	–	–
BLL	6	1	0.16	338	988	1	2
		<u>799</u>				<u>1136</u>	<u>848</u>

¹Percentage of all observed seabirds formally identified to species level; ²Average annual bycatch for fishing years 1997/98–2003/04; ³No estimate available because table 13 of Waugh et al. (2008) excluded strata with less than 0.5% of the seabird bycatch for 2003/04.

Alternative estimates of trawl-caught WCAP bycatch were made, using a similar approach, but based on table 15 of Waugh et al (2008), which concerns bycatch of albatross from trawl fisheries (rather than all seabirds from all fisheries). Overall, these estimates (Table 2) were about 10% lower than the comparable values in Table 1 (the estimates in Table 1 corresponding to the totals 1034 and 729 in Table 2 are 1118 and 829, respectively).

Table 2: Estimates, by Fisheries Management Area (FMA), of the annual trawl-caught bycatch of white-capped albatross (WCAP) for fishing years 1997/98–2003/04 (columns 6–7), derived from data from Waugh et al. (2008) (columns 2–3 and 4–5 derive from their tables 2–3 and 15, respectively). FMAs with no observed WCAP bycatch were excluded from this table.

FMA	Observed WCAP		Albatross bycatch		WCAP bycatch	
	Number	Percentage ¹	2003/04	average ²	2003/04	average ²
2	4	27	– ³	– ³	–	–
3	25	33	203	238	67	78
4	4	5.6	104	100	6	6
5	423	90	362	316	325	284
6	274	96	583	318	560	306
7	<u>27</u>	56	134	117	<u>75</u>	<u>66</u>
	<u>757</u>				<u>1034</u>	<u>739</u>

¹Percentage of all observed albatrosses formally identified to species level; ²Average annual bycatch for fishing years 1997/98–2003/04; ³No estimate available because table 15 of Waugh et al. (2008) excluded strata with less than 0.5% of the albatross bycatch for 2003/04.

More recent estimates of WCAP bycatch in New Zealand trawl fisheries are somewhat lower than those from Tables 1 and 2 (Figure 2). This could be due, at least in part, to the comparatively low percentages of the total trawl effort that were included in the recent estimates (median 42%, range 33–51% - see table 29 in Abraham & Thompson 2011b) because most inshore trawls were excluded. Observer coverage of inshore trawlers has exceeded 1% in the last two years and simple ratio estimates for these years suggest that several hundred WCAP could be caught each year in this fishery (Table 3) (these estimates should be considered very approximate, because they ignore the probably substantial spatial variation in both observer coverage and WCAP catch rates). Recent GPS tracking of breeding birds showed that their foraging area overlaps the inshore fishery around the south coast of the South Island (see figure 3 of Thompson et al. 2009).

Table 3: Percent observer coverage, and the number of white-capped albatross (WCAP) reported captured (alive and dead) in the inshore trawl fishery from 2006/07 to 2009/10 (pers. comm. K. Ramm, Department of Conservation, Wellington). Also given are simple ratio estimates of total WCAP captures from this fishery based on these data.

Year	Observer coverage (%)	Observed captures		Total captures (ratio estimates)
		Alive	Dead	
2006/07	0.3	0	6	2000
2007/08	0.33	0	2	606
2008/09	3.45	2	11	377
2009/10	1.76	2	7	511

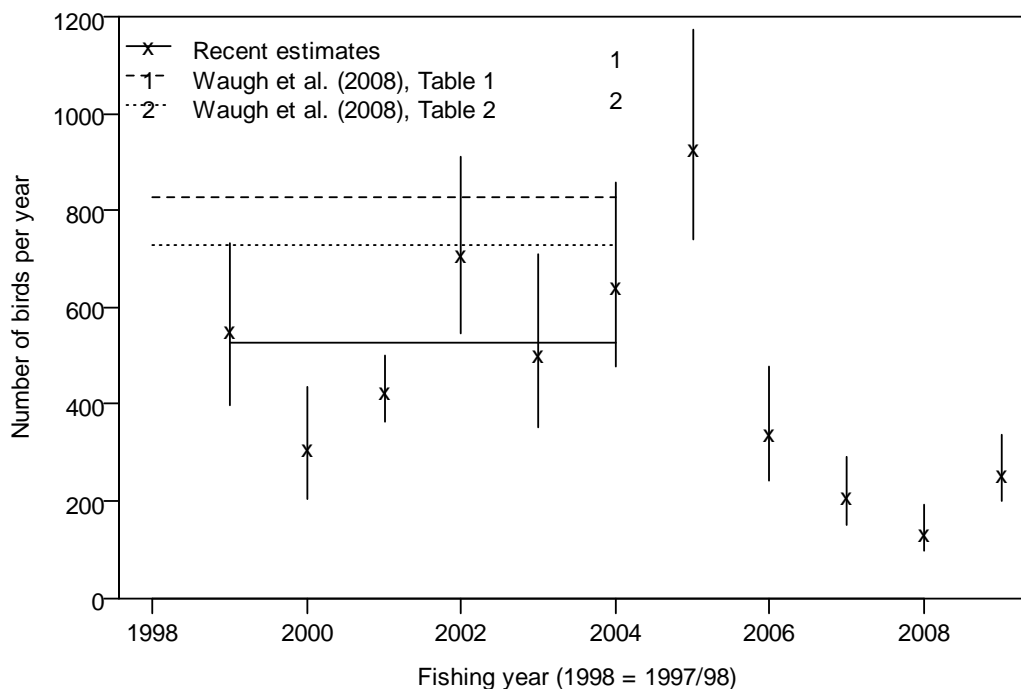


Figure 2: Comparison of recent estimates of annual trawl-caught bycatch of white-capped albatross with those in Tables 1 and 2, derived from Waugh et al. (2008). The recent estimates are taken from table 29 of Abraham & Thompson (2011b) (ratio estimates for 1999–2002) and table A-1 of Abraham & Thompson (2011a) (model estimates for 2003–2009). Horizontal lines show estimated means over the years shown; vertical lines show 95% confidence intervals (for annual recent estimates only).

Baker et al. (2007b) estimated a global annual bycatch for WCAP of more than 8000 birds, although more than 80% of that estimate was considered of low reliability (Table 4, column 1). Figure 2 suggest that their estimates for the New Zealand region were probably too low for the period on which they were based (2001–03), but are likely to over-estimate recent mortality.

Two studies allow us to update four of the estimates of Baker et al. (2007b). Analyses by Watkins et al. (2008) suggested that WCAP mortality from the South African demersal trawl fisheries is 40% higher than estimated by Baker et al. (2007b). The original estimates were based on observations of 121 South African trawls in 2004. Watkins et al. (2008) analysed what appears to be a superset of these data, comprising 190 h of observations on 331 trawls in the South African hake trawl fishery in 2004 and 2005 (0.5% of the total effort in the fishery). They estimated an annual mortality of 7000 shy albatrosses (95% confidence interval 3000–12 500) in the hake fishery, all caused by warp interactions. If 95% of this mortality concerns white-capped albatrosses (as assumed by Baker et al. 2007b) then this translates to 6650 white-capped albatrosses per year, which is 40% higher than the value of 4750 in Table 4. Petersen et al. (2009) estimated an annual bycatch of 570 WCAP from the South African pelagic longline fishery. We can also update the two Namibian bycatch estimates, since both were calculated simply by multiplying the corresponding South African catch rate by Namibian effort.

The ages of the WCAP bycatch vary strongly by area. Necropsy reports show that 92% of the 1135 WCAP killed and returned from New Zealand fisheries over the 13-year period 1996/97 to 2008/09 were adults (Anonymous 2008, Thompson 2009, 2010b, 2010c, 2010a). However, in the South African pelagic longline fishery only 11% of the WCAP bycatch was adults (Petersen et al. 2009).

Table 4: Estimates of the number of white-capped albatrosses killed annually, by fishery. The first column of estimates is from table 1 of Baker et al. (2007b) (giving a mid-point where a range of estimates was presented) and this is followed by their assessment of the estimates' reliability (L = low, M-H = medium-high, H = high). The updated estimates in the next column derive from subsequent work by Watkins et al. (2008) and Petersen et al. (2009). In the final column, those estimates not already including cryptic mortality are either doubled to allow for this or replaced by new estimates that include this mortality (see text for details).

Fishery	White-capped albatrosses killed annually		
	Baker et al. (2007b)	Updated	Adjusted for cryptic mortality
South African demersal trawl	4 750 (L)	6 650 ¹	6 650
Asian distant-water longline	1 255 (L)		2 510 ³
Namibian demersal trawl	910 (L)	1 270 ¹	1 270
Namibian pelagic longline	180 (L)	195 ²	390 ³
New Zealand hoki and squid trawl	513 (MH)		4 920 ⁴
New Zealand longline	60 (MH)		199 ⁴
Australian (line fisheries)	15 (MH)		30 ³
South African pelagic longline	<u>527</u> (H)	570 ²	<u>1 140</u> ³
	8 210		17 110

¹ Watkins et al. (2008); ² Petersen et al. (2009); ³ doubled to allow for cryptic mortality; ⁴ Richard et al. (2011) (the upper figure is for all trawl fisheries, and the lower for both surface and bottom longline fisheries)

2.1.2 Adjustments for cryptic mortality

All but two of the Table 4 bycatch estimates discussed so far (the exceptions are those for the South African and Namibian trawl fisheries) are likely to be substantial under-estimates because they make no allowance for cryptic mortality ('birds that are fatally injured in an encounter with fishing effort but are not [counted] because they are not recovered onboard the fishing vessel', pers. comm. B. Sharp, MFish). At the time of writing, MFish was developing standard procedures for inferring cryptic mortality estimates for seabirds (pers. comm. B. Sharp, MFish). These procedures were used in two ways to produce the total bycatch estimates in the last column of Table 4. First, Richard et al. (2011) used them to estimate what they called annual 'potential fatalities' of WCAP, including cryptic mortality, of 4920 and 199, for New Zealand trawl and longline fisheries, respectively. Second, all other longline estimates were doubled, following the assumptions used by Richard et al. (2011).

Thus the best current estimate of global annual bycatch of WCAP, including cryptic mortality, is just over 17 000 (Table 4, last column). For two components of this total there is some evidence that there has been a downward trend in recent years. Richard et al. (2011) estimated a drop of 68% in annual potential fatalities between the fishing years 2003–04 to 2005–06 to 2006–07 to 2008–09 (see their table A-16). Also, Petersen et al. (2009) reported that total seabird bycatch in the South African pelagic longline fishery declined by almost 70% between 1998 and 2005, although they noted that this bycatch may increase again because of a proposed increase of effort in this fishery.

2.2 Abundance estimates

The primary abundance data are aerial-photographic counts of breeding pairs over four years at the main breeding site on Disappointment Island (where about 94% of birds breed) and two other sites (Table 5). These counts show an average rate of decline of 12% y^{-1} (estimated from the slope of a regression of $\log(\text{count})$ on year). This decline appears to be strongly statistically significant because nominal c.v.s for the total counts are very small (about 0.3%), being based on a Poisson distribution (Baker et al. 2007a), for which the standard error is the square root of the count. The 23% drop in abundance between 2008 and 2009 is supported by a similar drop in nest occupancy estimated from close-up photos (Table 6), and the fact that this drop occurred across many areas (Figure 3).

Table 5: Aerial-photographic counts of breeding pairs of white-capped albatrosses on three islands in the Auckland Islands group in December 2006–2009 (Baker et al. 2007a, 2008, Baker et al. 2009, 2010).

	2006	2007	2008	2009
Disappointment Island	110649	86080	91694	70569
SW Cape, Auckland Island	6548	4786	5264	4161
Adams Island		79	131	132
Total	117197	90945	97089	74862

Table 6: Estimates of the percentage of nests that were occupied during each photographic survey in 2007–2009 (with 95% confidence intervals in parentheses) and significance tests for between-year changes in nest occupancy. Results based on data from 15 randomly selected close-up photographs in each year (Baker et al. 2008, Baker et al. 2009, 2010); confidence intervals were calculated from bootstrap resampling; significance tests were based on randomization.

Year	Nest occupancy (%)	Years compared	Significance of change (P value)
2007	71.2 (65.8–76.1)	2007 and 2008	0.096
2008	78.4 (72.7–83.3)	2007 and 2009	0.033
2009	59.7 (51.1–67.7)	2008 and 2009	0.002

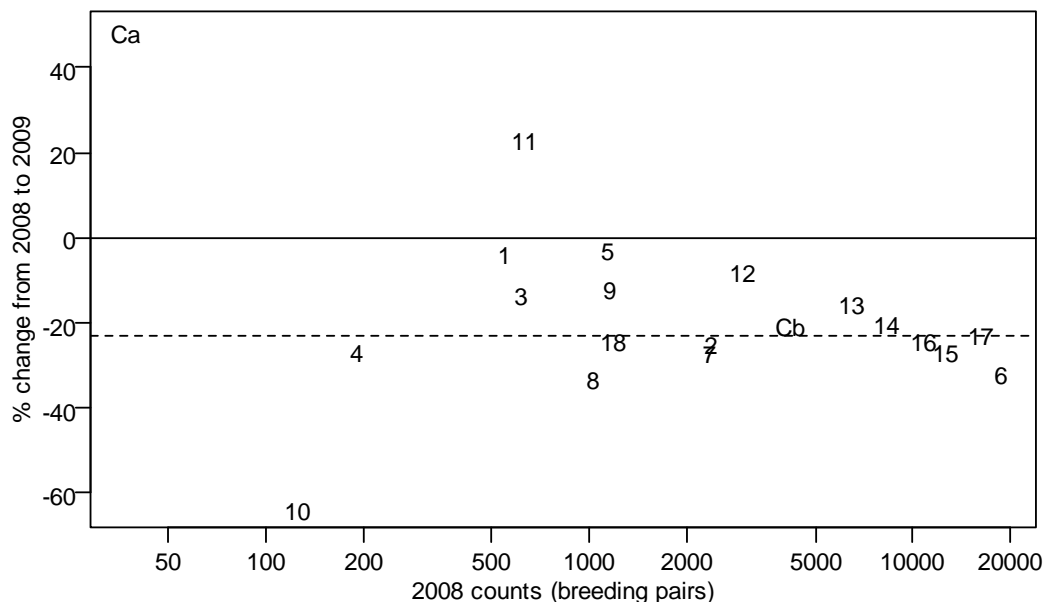


Figure 3: Percentage change in counts, by area, between the 2008 and 2009 photographic surveys. The horizontal dashed line shows the overall change (-23%); plotting symbols identify the 20 areas into which Disappointment Island was divided for these two surveys: areas 1–18 and Castaway a and b (Ca, Cb) (see table 1, Baker et al. 2010).

Baker et al. (2007a) noted that that a source of bias in these counts is that they include some non-breeding birds that were present during the survey. For the purposes of this report I will divide these non-breeders into two types: ‘tryers’ are those that sit on nests; and ‘loafers’ are those that hang around the colony, sometimes standing, but not sitting, on nests. Robertson et al. (2008) estimated that aerial counts of the breeding population of black-browed albatrosses at Ildenso Archipelago, Chile, could be biased high by 12% because of tryers (7%) and loafers (5%).

We have two sources of information about loafers amongst white-capped albatrosses. The first is the close-up photos analysed in Table 6, in which all counted birds were labelled as ‘on nest’, ‘not on nest’, ‘not sure’ (i.e., may or may not have been on the nest), and ‘pair’ (i.e., the presumed partner of a bird on a nest). Amongst these photos was one extreme outlier (in 2008) in which 50% of birds were loafers (there were 65 birds ‘on nest’, 65 ‘not on nest’, and 1 ‘not sure’), compared with a range 0–11% in all other photos. Without this outlier, the 2008 data are consistent with those from other years, and the combined data suggest that the percentage of loafers is probably between 1% and 4%, and unlikely to exceed 5.4% (Table 7). However, the existence of the outlier photo indicates that these estimates are quite uncertain. Note that in calculating these percentages I ignored birds labelled ‘pair’, so that my estimates may be treated as percentages of the counts shown in Table 5. When the ‘pair’ observations are included (as they were by Baker et al. 2008, Baker et al. 2009, 2010) the resulting estimates are percentages of all birds counted. The difference is very small.

Table 7: Minimum and maximum estimates (with 95% confidence intervals in parentheses) of the percentage of birds that were ‘loafers’ (non-breeding birds that hang around the colony, sometimes standing on nests) during the photographic surveys in 2007–2009. Birds categorised as ‘not sure’ were excluded from minimum estimates, but included in maximum estimates; confidence intervals were calculated using bootstrap resampling.

Year	Percentage of birds that are loafers	
	Minimum	Maximum
2007	0.5 (0.0–1.1)	3.0 (2.0–4.1)
2008	5.4 (1.0–13.7)	6.6 (1.8–15.0)
2008 ¹	1.7 (0.9–2.8)	2.9 (1.7–4.6)
2009	1.3 (0.5–2.4)	3.7 (2.2–5.4)

¹Estimates ignoring one extreme photo (photo 14, table 6, Baker et al. 2009)

The second source of information about loafers is some ground-truth counts at SW Cape in 2007 (Baker et al. 2009). Three observers independently counted the number of birds, in each of four areas, at hourly intervals from 1030 to 1630, classifying each counted bird as ‘sitting’ (on a nest), ‘standing’ (on a nest), ‘pair’ (presumed partner of a bird sitting on a nest), or ‘not on a nest’ (and not a partner). These data suggest that the incidence of loafers was lowest (about 1.3%) in the middle of the day – from about 1130 to 1430 – but higher before and after that, exceeding 6% at 1630 (Figure 4). The figure of 1.3% is made up of 0.6% ‘standing’ and 0.7% ‘not on nest’.

The incidence of tryers was estimated by examining occupied nests to see whether they contained an egg (those without an egg were presumed to be occupied by tryers). Two estimates are available. The first, 19% (95% confidence interval, 12–27%), from SW Cape on 1 December 2007 from a sample of 109 nests (Baker et al. 2008), was made late in the day (1630–1730, D. Thompson, pers. comm.). The other estimate was made at Disappointment Island in the middle of the day (1200–1230) on 9 December 2008, when all occupied nests encountered 1 m either side of a randomly placed transect ($n = 478$) were inspected and 6.5% (95% confidence interval, 4.2–8.7%) of occupied nests were found to contain tryers (Baker et al. 2009).

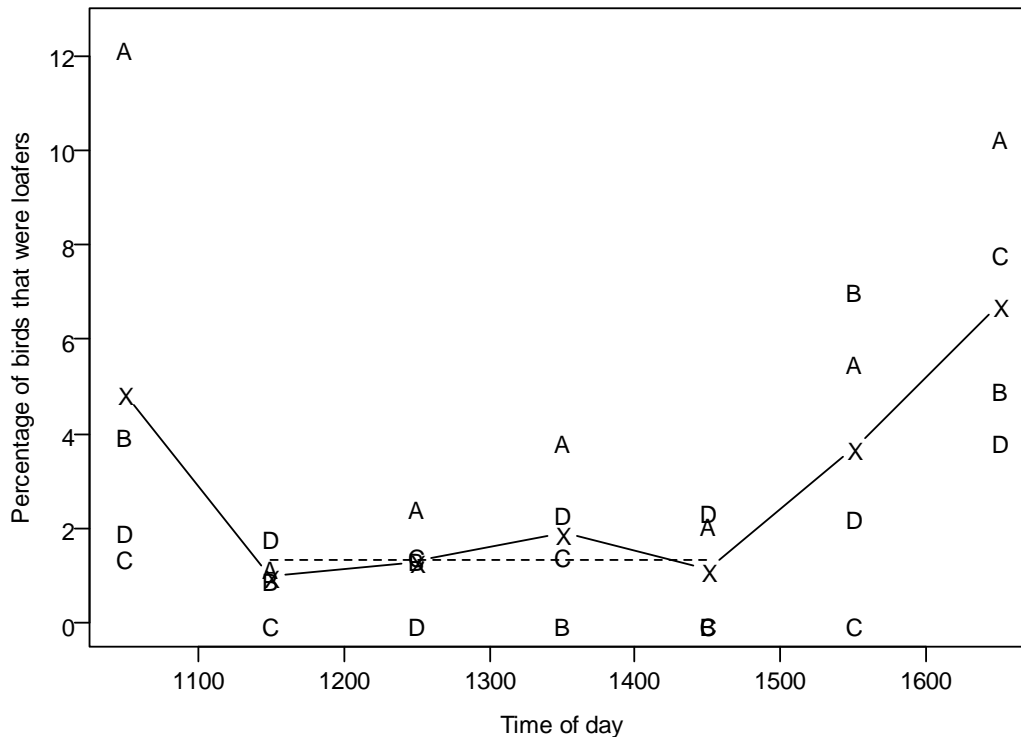


Figure 4: Estimates, from 2007 ground-truth counts at SW Cape, of the percentage of birds that were loafers, showing mean values at each observation time ('X'), and for each area at each observation time ('A'-'D'), and also the average value for the period 1130-1430 (dashed line, 1.3%).

The presence of non-breeders is likely to have had two main effects on the aerial survey estimates. First, bias from this source was probably higher in 2006 than in other years because this survey was later in the day than the other surveys (Table 8). A rough correction for this bias reduced the estimated average annual rate of decline in breeding population numbers from 12% to 9.8% (Table 9; the correction method is described in footnotes to this table). The second effect of the non-breeders is that the precision of the survey estimates will be markedly less than that implied by the Poisson-based c.v.s (see above) because of uncertainty concerning both the proportion of non-breeders at the colony, and the extent to which this may vary from year to year.

Table 8: Start and finish times of aerial-photographic counts of breeding pairs of white-capped albatrosses on three islands in the Auckland Islands group in December 2006–2009 (Baker et al. 2007a, 2008, Baker et al. 2009, 2010).

	2006	2007	2008	2009
Disappointment Island	1447–1610	1318–1437	1055–1155	1200–1310
SW Cape, Auckland Island	after 1610	1525–1545	1210–1240	1330–1348
Adams Island	–	1635–1700	1425–1435	1351–1355

Table 9: Rough attempt to correct for bias in the abundance estimates for 2006–09 (Table 5) caused by variation in the incidence of the two categories of non-breeders (loafers and tryers) with time of day: A, bias by time of day; and B, effect of correcting for bias.

A, Bias by time of day

	Percentage bias due to loafers and tryers by time of day			
	1130-1430	1530	1630	1700
Loafers	1.3 ¹	3.7 ¹	6.7 ¹	
Tryers	6.5 ²	11.5 ³	16.5 ³	19.0 ²
Total	7.8	15.2	23.2	

B, Effect of correcting for bias

	Estimated number of breeding pairs				Average annual rate of decline ⁴
	2006	2007	2008	2009	
Original	117 197	90 945	97 089	74 862	12%
Corrected ⁵	99 383	83 851	89 516	69 023	9.8%

¹Estimates from Figure 4; ²Estimates from nest inspections; ³Estimated by linear interpolation; ⁴Estimated from the slope of a regression of log(count) on year; ⁵Reduced by 15.2% in 2006, and 7.8% in other years

2.3 Mark-recapture data

Mark-recapture data were available for 122 birds that were banded in the four breeding seasons 2005–06 to 2008–09 (33, 19, 46, and 24, respectively). The status of each bird, both at banding and each subsequent resighting in seasons 2006–07 to 2009–10, was recorded as one of the following six categories: not seen (NS, only for birds already banded), not breeding (NB), breeding unsuccessfully (B_U), and breeding successfully up to the egg stage (B_SE), the guard stage (B_SG), or the chick stage (B_SC). The various sub-categories of breeder were of limited use because which sub-categories were recorded in any year was determined to a great extent by the timing of visits to the colony in that year (Table 10).

Table 10: The breeding stages at which the colony was visited in each season and the number of birds recorded in each sub-category of breeder. – denotes a sub-category that could not be recorded for that season because of the timing of visits to the colony.

Season	Stages at which colony visited	Breeding successful to the			Breeding unsuccessful (B_U)
		egg stage (B_SE)	guard stage (B_SG)	chick stage (B_SC)	
2005–06	Guard	–	33	–	0
2006–07	Chick	–	–	22	0
2007–08	Egg and Chick	0	–	42	25
2008–09	Egg and Guard	30	43	–	8
2009–10	Egg and Guard	2	32	–	8

Breeding success could be estimated only in 2007–08, when the study colony was visited at both the egg and chick stages. In this season, 42 of 67 of breeding pairs were successful up to the chick stage. Thus, the probability of breeding success was 0.63 (95% c.i., 0.51–0.75, assuming binomial probabilities), though this will be an under-estimate if there is any further mortality before fledging.

2.4 Nest-based data

Another useful data set, collected at SW Cape at the same time as the mark-recapture data, was nest-based. A number of marked nests in the study area were checked each season to see whether they were being used for breeding and, if so, how many breeders (0, 1, or 2) were observed at the nest during the season. Any unbanded breeder observed at a study nest was banded. Each season more nests were marked, with the number of study nests growing from 26 in 2005–06 to 70 in 2009–10. Once a nest was marked it remained a study nest for all succeeding seasons.

These data provided two useful results, the first of which was an estimate of the probability that a bird breeding within the study colony would be seen during the visit(s) to the colony each season. The estimated probabilities varied widely, from 0.42 in 2006–07 to 0.92 in 2008–09 (Table 11). To see how these values were calculated, consider the first row of Table 11, which shows that 26 of the study nests were used for breeding in 2005–06, but only 33 (= 19 x 1 + 7 x 2) of the 52 breeders associated with these nests were seen. Therefore the probability of seeing a breeder in the study colony in 2005–06 was 0.63 (= 33/52), with s.e. 0.067 (= (0.63 x (1–0.63)/52)^{0.5}). Note that the binomial assumption used in calculating the standard errors is not strictly correct, because the resighting probabilities for the two birds in a breeding pair are not independent, but there seems no obvious way of calculating a more appropriate standard error.

Table 11: The number of study nests used for breeding each season, categorised according to whether 0, 1, or 2 of the breeders at the nest were observed; also the calculated probability of seeing a bird that was breeding in the study colony, with its standard error (s.e.).

Season	Number of breeding nests with			Probability of seeing a breeder	
	0 birds	1 bird	2 birds	estimate	s.e.
2005–06	0	19	7	0.63	0.067
2006–07	11	8	7	0.42	0.069
2007–08	0	23	22	0.74	0.046
2008–09	0	7	36	0.92	0.029
2009–10	2	10	15	0.74	0.060

The second useful result from the nest-based data is that the percentage of study nests used for breeding was markedly lower in 2009–10 than in all other seasons (Table 12), which is consistent with the low abundance estimate in December 2009 (see Table 5). The percentage breeding estimates in Table 12 are difficult to interpret because they show a substantial decline across all years, whether we use estimates from all study nests (the figures on the diagonal in Table 12), or those restricted to the same nests (the sequence of values down each column of Table 12). The problem seems to be that the choice of which additional nests to mark each season was clearly not random, because 97% (68/70) of nests were used for breeding in their first year as study nests. However, if we ignore data for nests in their first year as study nests we find a fairly consistent percentage being used for breeding in 2006–07 to 2008–09 (65%, 59%, and 60%, respectively) followed by a substantial drop, to 36%, in 2009–10 (see figures on the subdiagonal in Table 12).

Table 12: Estimates of the percentage of study nests that were used for breeding in each year. Each column of estimates is based on the same set of nests.

Season of observation	Percentage of study nests used for breeding				
	Nests seen in 2006 (n = 26)	Nests seen in 2007 (n = 37)	Nests seen in 2008 (n = 60)	Nests seen in 2009 (n = 67)	Nests seen in 2010 (n = 70)
2005–06	100	–	–	–	–
2006–07	65	70	–	–	–
2007–08	65	59	75	–	–
2008–09	62	59	60	64	–
2009–10	38	27	35	36	39

3. MODELLING OF THE DATA

I describe results from several models, all implemented in Seabird (Francis et al. 2008). For early models only point estimates were obtained (such estimates are sometimes known as MPD estimates, because they represent the mode of the posterior distribution of the parameter vector). Full Bayesian estimates were also obtained for later models, whose SeaBird input files are given in Appendix 1.

3.1 Initial model runs

The mark-recapture data were modelled using Seabird (Francis et al. 2008). Two birds (bands O37586 and O37552) required special treatment. The former was found dead the year after it was banded (2009), and so was treated as ‘not seen’ in that and subsequent years. The latter was the only one of eight birds banded as non-breeders that has not been sighted again. It was ignored in the modelling on the grounds that it may well have survived and bred outside the study area.

Several alternative models were evaluated, but all models considered only the adult population, dividing this into two categories – breeders (br) and non-breeders (nbr) – and all parameter prior distributions were uniform on (0,1). Initial model runs produced only point estimates (i.e., the mode of the posterior distribution) and the base model was chosen as the one with the lowest AIC (Akaike Information Criterion) value (Akaike 1974). This model showed good agreement between the observed and expected numbers of resightings by year and status (Figure 5).

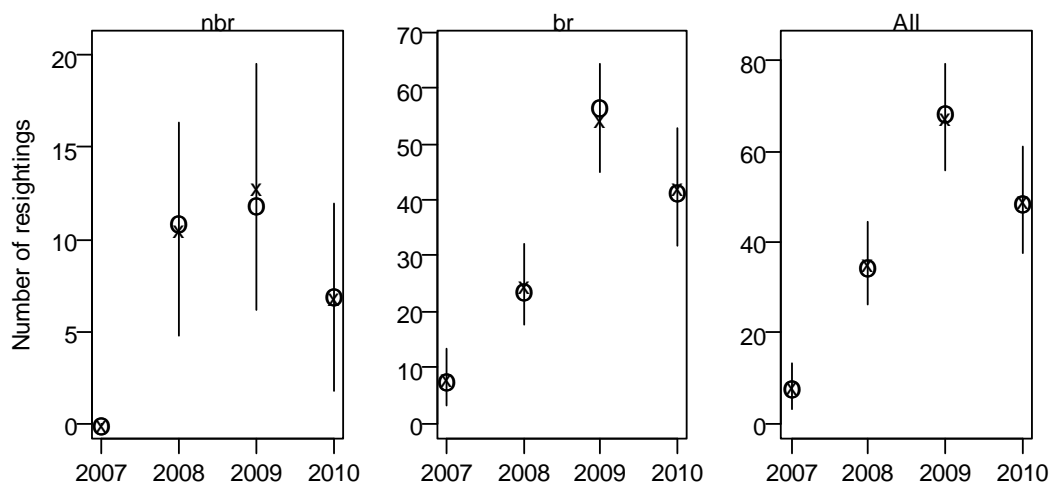


Figure 5: Observed ('O') and expected ('x', with 95% c.i.s. as vertical lines) numbers of resightings of banded birds each year by class (nbr and br) and overall ('All'). Expected numbers, and their confidence intervals, are from the point estimates of the base model.

Ten parameters were estimated in the base model (Table 13). AIC values for four alternative models showed that: the data were insufficient to allow the estimation of survival by year (model 1a); there was clear evidence of between-year variation in resighting probabilities (models 1b, 1c); and the probability that a bird would breed in any year clearly differed according to its breeding status in the previous year (model 1d) (Table 14).

Table 13: Names, descriptions, and estimates (medians of the posterior distribution) of the ten parameters estimated in the base model (where only one estimate is given it was assumed that this applied to all years; the four values given for the resighting parameters apply to years 2007–2010).

Name	Description	Estimate(s)
surv	annual probability of survival	0.96
Prbr	probability of resighting a breeder	0.43, 0.75, 0.92, 0.57
Pnbr	probability of resighting a non-breeder	¹ , 0.67, 0.43, 0.21
Tbrbr	probability a bird that bred in one year would breed in the next	0.63
Tnbrbr	probability a bird that didn't breed in one year would breed in the next	0.78

¹Not estimable because no banded birds were observed as non-breeders in 2007

Table 14: Details of four variants of the base model which were found (on the basis of AIC) to be inferior to it.

Model	Difference from base model	Number of parameters	ΔAIC
Base	–	10	0
1a	surv differs by year (but same in 2009 and 2010)	13	3.6
1b	Pnbr same for 2008–2010	8	4.8
1c	Prbr same for 2008–2010	7	7.1
1d	Tbrbr = Tnbrbr	9	1.6

Bayesian estimates were made for the base model with an MCMC chain of length 1 million, thinned to length 1000. Traces appeared adequate for some parameters (e.g., surv) but were less good for others (e.g., Tbrbr and Prbr 2009) (Figure 6). Perhaps a more useful diagnostic is obtained by comparing, for each parameter, the three cumulative distributions derived from dividing the chain into three equal parts. This showed that the posterior distributions were reasonably well determined for surv and Tnbrbr, but not for Tbrbr (Figure 7) (similar plots were not done for the resighting parameters, which are nuisance parameters).

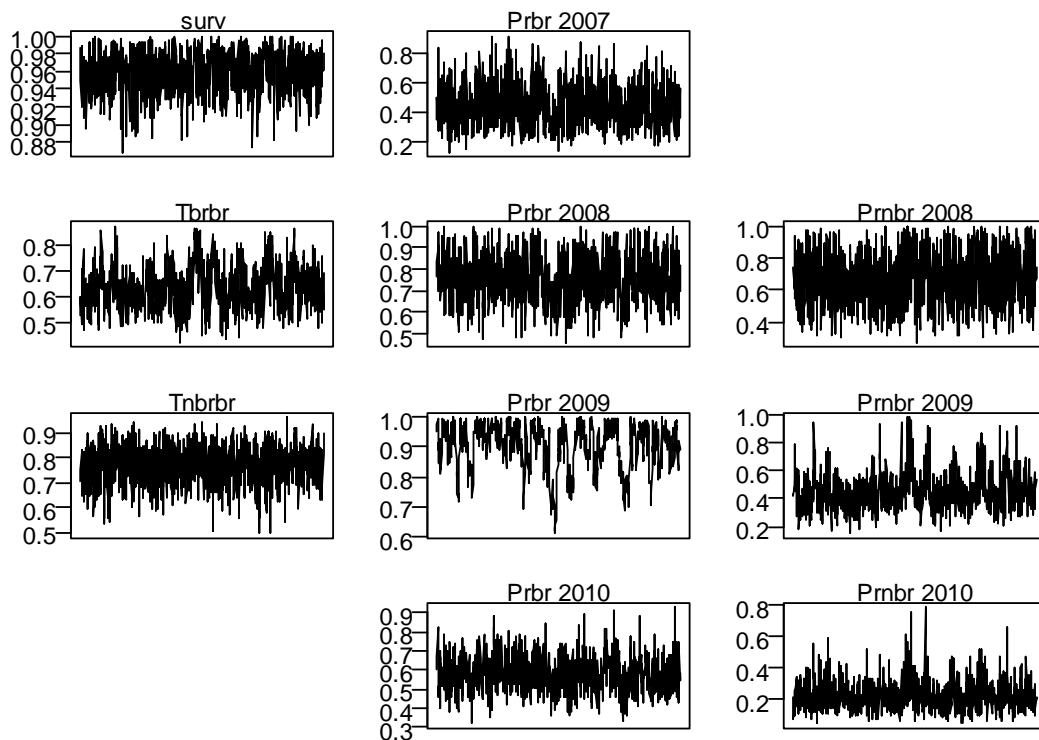


Figure 6: Traces for all parameters from a preliminary MCMC run of the base model.

From this MCMC chain, annual survival was estimated to be 0.96 (median of the posterior); the probability of breeding in any year was lower for those that bred in the previous year (0.63) than for those that didn't (0.75); and the probability of resighting a banded bird varied strongly from year to year and was markedly higher for breeders than for non-breeders (Table 13).

The proportion of years in which adults breed (estimated from the first eigenvector of the transition matrix) was 0.68 (95% c.i. 0.58–0.81). Thus white-capped albatrosses are intermediate between annual and biannual breeders.

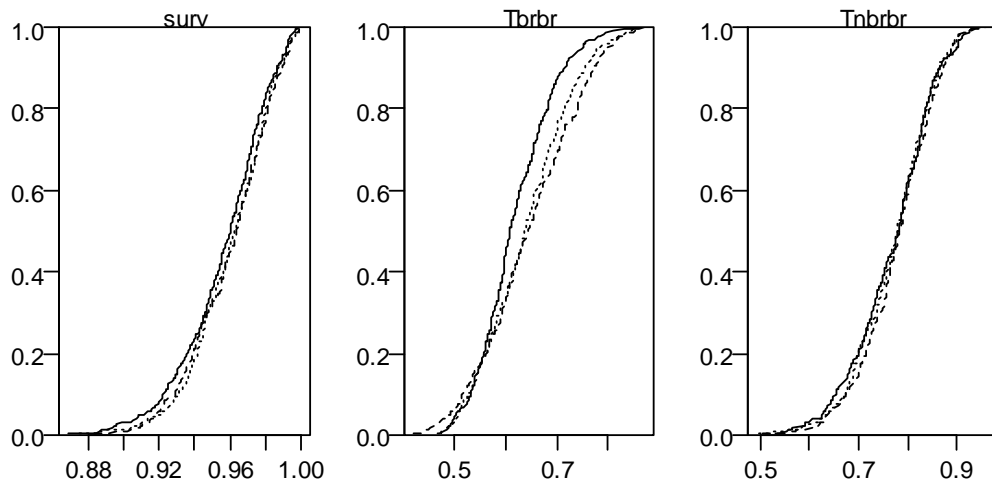


Figure 7: Comparison, for selected parameters (surv, Tbrbr, Tnbrbr), between the three cumulative distributions estimated from the first, middle, and last third of the MCMC chain.

It is of theoretical interest to compare parameter estimates from the simple MPD run of the base model with those from the more time-consuming MCMC run. There was excellent agreement for the most important parameter, adult survival (surv), and reasonable agreement for the other parameters, though there were consistent differences, with the MCMC point estimates being higher for both transition parameters and Prnbr, and lower for Prbr (Figure 8).

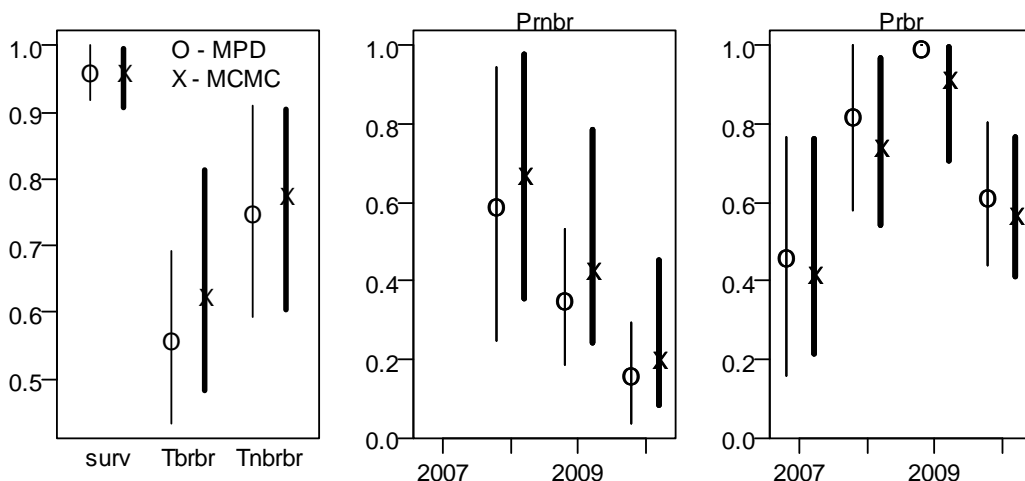


Figure 8: Comparison of parameter estimates and 95% c.i.s from the MPD ('O', light lines) and MCMC ('X', heavy lines) runs of the base model. C.i.s for MPD estimates are plus or minus 2 s.e.s, where s.e.s are from the inverse Hessian; for MCMCs, point estimates are medians and c.i.s are the 2.5% and 97.5% quantiles.

3.2 Additional models

Following Working Group discussion of the initial runs, MCMC runs of three additional models (labelled Add1–3) were considered. All these differed from the base model in assuming normal priors (based on the estimates and s.e.s in Table 11) for Prbr (the resighting probabilities for breeders), and differed from each other in terms of which parameters were time-varying (Table 15).

Table 15: Comparison of the assumptions of the base and three additional models.

Model	Prior for PrbrResighting ¹	Time-varying parameters	
		Survival	Transition ²
Base	Uniform	No	No
Add1	Normal	Yes	No
Add2	Normal	No	Yes
Add3	Normal	Yes	Yes

¹Prbr and Prnbr; ² Tbrbr and Tnbrbr

Model diagnostics were markedly better for Add2 and Add3 than for the base model (compare Figure 6 with Appendix Figures A2.1–2), but were poor for Add3 (Appendix Figure A2.3).

These additional models do not substantially change our view of the population. It does not seem sensible to try to pick a best model from amongst them: none is clearly superior to all others, and all have drawbacks. It is perhaps best to consider the differences between estimates from these models as illustrating our uncertainty.

The differences in parameter estimates are shown in Figure 9. In Add1, where survival was allowed to be time-varying, the estimated survival was markedly lower, and less certain, in 2010 (note that this survival is for the period between the last two abundance estimates in the Decembers of 2008 and 2009). One hypothesis that would explain both the low abundance estimate in December 2009 (see Table 5), and this apparently low survival for 2010, is that 2009–10 was a season in which significantly fewer birds than usual chose to breed. Model Add3 did not support this hypothesis (the estimated survival for 2010 was even lower), but this model may be unreliable because, as already noted, some of its diagnostics were poor.

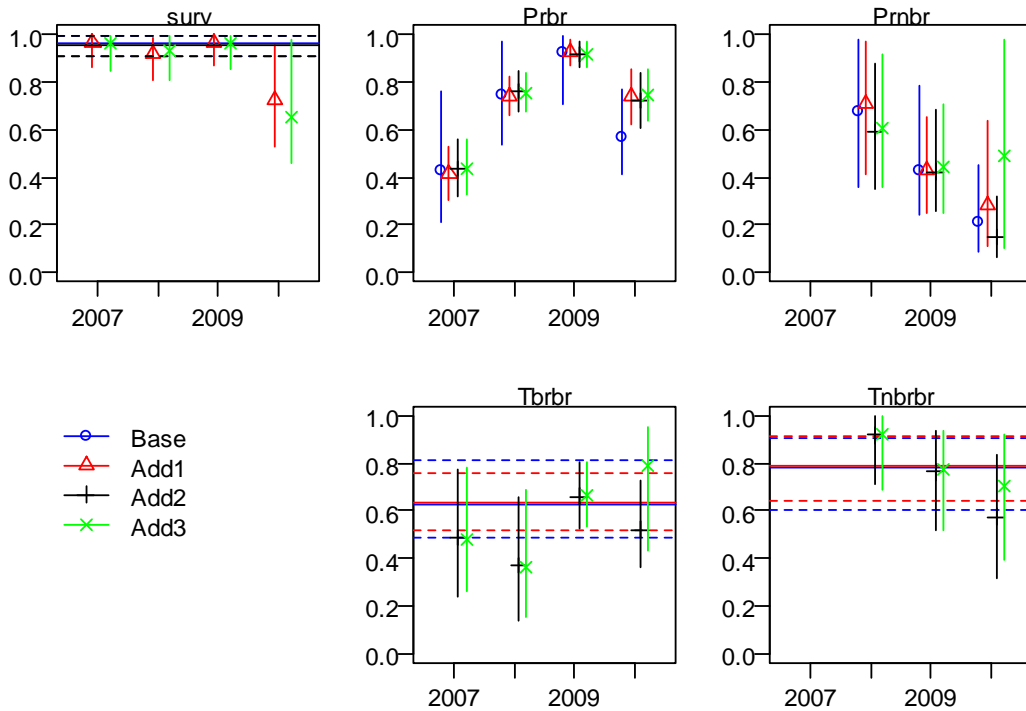


Figure 9: Comparison of parameter estimates and 95% c.i.s from the base and three additional models (Add1–3). For time-varying parameters, the estimate is plotted as a point and the c.i. by a vertical line; for time-invariant parameters, the estimate is plotted as a solid horizontal line, and the c.i. bounds as dashed lines.

4. TRENDS IN ABUNDANCE

The most direct evidence concerning trends in abundance for the study population is provided by the photographic surveys, which suggest that the adult population declined at about $9.8\% \text{ y}^{-1}$ between 2006 and 2009 (Table 9B). This rate is poorly estimated because of uncertainties about year-to-year variation in both the proportion of non-breeders at the breeding colonies, and the proportion of adults that breed each year.

The other available evidence suggests that a value of $9.8\% \text{ y}^{-1}$ may be too high. The base model for the mark-recapture data estimated annual adult survival was 0.96 (95% c.i., $0.907\text{--}0.995$). This is consistent with a decline of $9.8\% \text{ y}^{-1}$ only if we take the lower end of the confidence interval for survival *and* assume no recruitment to the population. For model Add1, the average annual adult survival was 0.88 (95% c.i., $0.81\text{--}0.95$ calculated from the fourth root of the product of the survival estimates for four years), but this model suggests high survival in all but the last year (Figure 9), which is very different from the pattern of decline implied by the photographic data. A decline of $9.8\% \text{ y}^{-1}$ corresponds to a loss of 22 200 adults per year (calculated from an exponential trend line through the corrected estimates in Table 9B), which is higher than the estimated global bycatch (including cryptic mortality) of 17 100 (Table 4), which is for both adults and juveniles. Note, however, that the lack of data about cryptic mortality makes this last estimate very uncertain.

5. CONCLUSIONS

The status of the study population is uncertain. The most direct evidence (the photographic survey) suggests that the adult population declined at about 9.8% per year between 2006 and 2009. However, this estimate is imprecise, and seems too high to be consistent with either bycatch estimates or adult survival rates estimated from mark-recapture data.

It might be possible to decrease uncertainty about population trends by analysing data from earlier aerial photographs (the utility of these photographs is currently being investigated).

The global bycatch of this species (including cryptic mortality) is estimated to be over 17 000 birds per year, which could present a risk to population viability. About 30% of this bycatch came from New Zealand fisheries, and this appears to have decreased substantially in recent years, presumably because of the introduction of mitigation measures in 2006. Lack of data concerning cryptic mortality make these estimates very uncertain.

Because of the great uncertainty in the status of this population, no attempt was made to evaluate alternative management strategies.

The mark-recapture data provided estimates of adult survival (0.96, with a 95% confidence interval 0.91–1.00), annual probability of breeding (0.68, confidence interval 0.58–0.81), and breeding success (0.63, confidence interval 0.51–0.75). No information is available about either juvenile survival or the age at first breeding.

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7. REFERENCES

- Abraham, E.R.; Thompson, F.N. (2011). Estimated capture of seabirds in New Zealand trawl and longline fisheries, 2002–03 to 2008–09. *New Zealand Aquatic Environment and Biodiversity Report No. 79*. 74 p.
- 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*. 172 p.
- Akaike, A. (1974). A new look at the statistical model identification. *IEEE Transactions on Automatic Control AC-19*: 716–723.
- 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.
- Baird, S.J.; Gilbert, D.J. (2008). Final report from seabird risk assessment workshop held 10 May 2007 as part of objective 3 of ENV2005/01. Final Research Report for MFish project ENV2005/01. 56 p. (Unpublished report held by Ministry for Primary Industries, Wellington.)
- Baker, B.; Jensz, K.; Cunningham, R. (2009). Data collection of demographic, distributional and trophic information on the white-capped albatross to allow estimation of effects of fishing on population viability - 2008 field season. Final Research Report for Ministry of Fisheries project PRO2006-01H. (Unpublished report held by Ministry for Primary Industries, Wellington). 13 p.

- Baker, B.; Jensz, K.; Cunningham, R. (2010). Data collection of demographic, distributional and trophic information on the white-capped albatross to allow estimation of effects of fishing on population viability - 2009 field season. Final Research Report for Ministry of Fisheries project PRO2006-01I. (Unpublished report held by Ministry for Primary Industries). 13 p.
- Baker, B.; Jensz, K.; Double, M.; Cunningham, R. (2007a). Data collection of demographic, distributional and trophic information on selected seabird species to allow estimation of effects of fishing on population viability. Final Research Report for Ministry of Fisheries project PRO2006-01F. (Unpublished report held by Ministry for Primary Industries). 12 p.
- Baker, B.; Jensz, K.; Double, M.; Cunningham, R. (2008). Data collection of demographic, distributional and trophic information on selected seabird species to allow estimation of effects of fishing on population viability. 11 p. Final Research Report for Ministry of Fisheries project PRO2006-01G. (Unpublished report held by Ministry for Primary Industries). 11 p.
- Baker, G.B.; Double, M.C.; Gales, R.; Tuck, G.N.; Abbott, C.L.; Ryan, P.G.; Petersen, S.L.; Robertson, C.J.R.; Alderman, R. (2007b). A global assessment of the impact of fisheries-related mortality on shy and white-capped albatrosses: conservation implications. *Biological Conservation* 137: 319–333.
- 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*. 57 p.
- 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 Project PRO200602. Final Research Report for Ministry of Fisheries Research Project PRO200602. (Unpublished report held by Ministry for Primary Industries, Wellington.) 65 p.
- Francis, R.I.C.C.; Sagar, P.M. (in press). Modelling the effect of fishing on southern Buller's albatross using a 60-year dataset. *New Zealand Journal of Zoology*.
- 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. (Unpublished report held by Ministry for Primary Industries, Wellington.) 134 p.
- IUCN (2010). IUCN Red List of Threatened Species. Version 2010.1. Downloaded from <www.iucnredlist.org> on 14 December 2010.
- Miskelly, C.M.; Dowding, J.E.; Elliott, G.P.; Hitchmough, R.A.; Powlesland, R.G.; Robertson, H.A.; Sagar, P.M.; Scofield, R.P.; Taylor, G.A. (2008). Conservation status of New Zealand birds. *Notornis* 55(3): 117–135.
- Petersen, S.L.; Honig, M.B.; Ryan, P.G.; Underhill, L.G. (2009). Seabird bycatch in the pelagic longline fishery off southern Africa. *African Journal of Marine Science* 31(2): 191–204.
- Richard, Y.; Abraham, E.R.; Filippi, D. (2011). Assessment of the risk to seabird populations from New Zealand commercial fisheries. 66 p. Final Research Report for Ministry of Fisheries projects IPA2009/19 and IPA2009/20 (Unpublished report held by the Ministry of Primary Industry, Wellington)
- Robertson, C.J.R.; Robertson, G.G.; Bell, D. (1997). White-capped albatross (*Thalassarche steadi*) breeding at Chatham Islands. *Notornis* 44: 156–158.
- Robertson, G.; Moreno, C.A.; Lawton, K.; Kirkwood, R.; Valencia, J. (2008). Comparison of census methods for black-browed albatrosses breeding at the Ildefonso Archipelago, Chile. *Polar Biology* 31: 153–162.
- Taylor, G.A. (2000). Action plan for seabird conservation in New Zealand. Part A: threatened seabirds. Threatened species occasional publication No. 16 Department of Conservation, Wellington. 233 p.
- Tennyson, A.; Imber, M.; Taylor, R. (1998). Numbers of black-browed mollymawks (*Diomedea m. melanophrys*) and white-capped mollymawks (*D. cauta steadi*) at the Antipodes Islands in 1994-95 and their population trends in the New Zealand region. *Notornis* 45: 157–166.
- Thompson, D.; Sagar, P.; Torres, L. (2009). A population and distribution study of white-capped albatross (Auckland Islands) Contract Number: POP2005/02. 17 p. Draft annual report prepared for the Conservation Services Programme, Department of Conservation.

- 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.
- Watkins, B.P.; Petersen, S.L.; Ryan, P.G. (2008). Interactions between seabirds and deep-water hake trawl gear: an assessment of impacts in South African waters. *Animal Conservation* 11: 247–254.
- Waugh, S.M.; MacKenzie, D.I.; Fletcher, D. (2008). Seabird bycatch in New Zealand trawl and longline fisheries 1998-2004. *Papers and Proceedings of the Royal Society of Tasmania* 142(1): 45–66.

APPENDIX 1: SeaBird Input Files for the main models

In this appendix I provide the SeaBird input files for the base model and describe how these input files were modified for the additional models of Section 3.2.

A1.1 The population file for the base model

```
@n_classes 2
@classes Nnbr Nnbr
@initial 2006
@current 2010
@final 2010

@initialisation
  N0 1000
  n_equilibrium 50
  Ipartition 1 1

@annual_cycle
  time_steps 1
  surv_props 1
  recruitment_time 1
  transition_time 1

@transition
  parameter_map 1 2 3 4
  parameter_names Tnbrnbr Tnbrbr Tbrnbr Tbrbr

@recruitment
  classes Nnbr
  parameter_names Nrec

@survival
  parameter_map 1 1
  parameter_names surv

@selectivity_names sel

@selectivity sel
  parameter_map 1 1
  parameters 1

@resight_p Presight
  parameter_map 1 2
  parameter_names Prnbr Prbr

## USER-DEFINED BASE PARAMETERS
@base_parameter
  name surv
  values 0.9

@base_parameter
  name Tbrbr
  values 0.5

@base_parameter
  name Tnbrbr
  values 0.5

@base_parameter
  name Prnbr
  values 0.0 0.9 0.9 0.9
  year_blocks 2006 2008 2009 2010
```



```

@base_parameter
  name Prbr
  values 0.9 0.9 0.9 0.9
  year_blocks 2006 2008 2009 2010

## USER-DEFINED DERIVED PARAMETERS
@derived_parameter
  name Tnbrbr
  formula 1-Tnbrbr

@derived_parameter
  name Tbrnbr
  formula 1-Tbrnbr

@derived_parameter
  name Nrec
  formula 10

```

A1.2 Modifications to the population file

For the additional models the following modifications were made to the above population file.

For models Add1 and Add3, the @base_parameter command block for surv was changed to

```

@base_parameter
  name surv
  values 0.9 0.9 0.9 0.9
  year_blocks 2006 2007 2008 2009

```

and for models Add2 and Add3, the @base_parameter command blocks for Tbrbr and Tnbrbr were changed to

```

@base_parameter
  name Tbrbr
  values 0.5 0.5 0.5 0.5
  year_blocks 2006 2007 2008 2009

@base_parameter
  name Tnbrbr
  values 0.5 0.5 0.5
  year_blocks 2006 2008 2009

```

A1.3 The estimation file for the base model

```

@estimator Bayes
@max_iters 2500
@max_evals 4000
@grad_tol 1e-6

@mark_recapture MRdat
  step 1
  proportion_mortality 0
  resight_p Presight
... [banding data omitted to save space]

@estimate
  parameter surv
  lower_bound 0
  upper_bound 1
  prior uniform

```

```
@estimate
  parameter Prnbr
  lower_bound 0 0 0 0
  upper_bound 0 1 1 1
  prior uniform
```

```
@estimate
  parameter Prbr
  lower_bound 0 0 0 0
  upper_bound 1 1 1 1
  prior uniform
```

```
@estimate
  parameter Tbrbr
  lower_bound 0
  upper_bound 1
  prior uniform
```

```
@estimate
  parameter Tnbrbr
  lower_bound 0
  upper_bound 1
  prior uniform
```

A1.4 Modifications to the estimation file

For the additional models the following modifications were made to the above estimation file.

For all additional models the @estimate command block for Prbr was changed to

```
@estimate
  parameter Prbr
  mu 0.42 0.74 0.92 0.74
  cv 0.16 0.062 0.032 0.081
  lower_bound 0.22 0.61 0.83 0.56
  upper_bound 0.63 0.88 1.00 0.92
  prior normal
```

For models Add1 and Add3, the @estimate command block for surv was changed to

```
@estimate
  parameter surv
  lower_bound 0 0 0 0
  upper_bound 1 1 1 1
  prior uniform
```

and for models Add2 and Add3, the @estimate command blocks for Tbrbr and Tnbrbr were changed to

```
@estimate
  parameter Tbrbr
  lower_bound 0 0 0 0
  upper_bound 1 1 1 1
  prior uniform
```

```
@estimate
  parameter Tnbrbr
  lower_bound 0 0 0
  upper_bound 1 1 1
  prior uniform
```

APPENDIX 2: Traces for additional model runs of Section 3.2

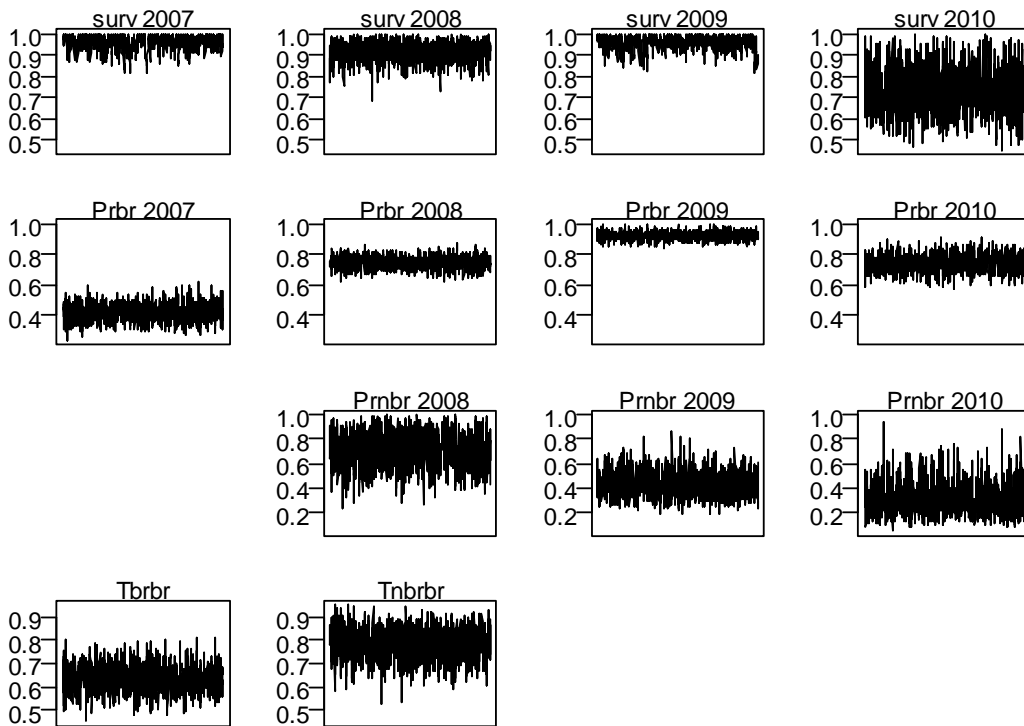


Figure A2.1: Traces for all parameters from an MCMC run of the additional model Add1. To aid comparison between related parameters the same vertical scale is used for all plots in the same row.

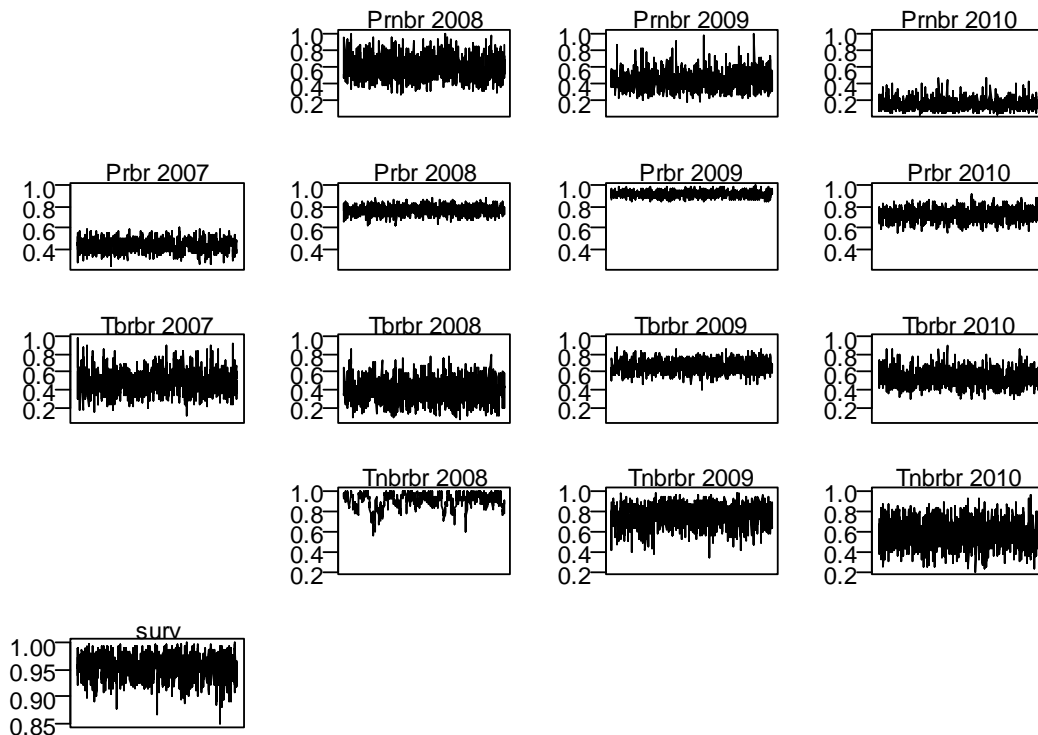


Figure A2.2: As for Figure A2.1, but for the additional model Add2.

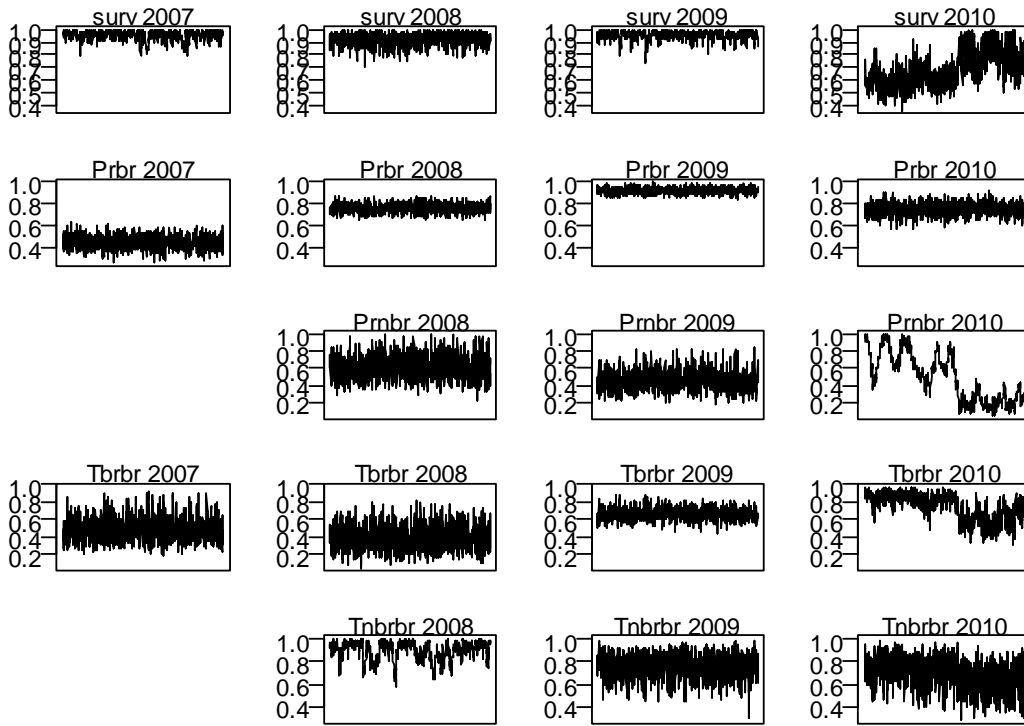


Figure A2.3: As for Figure A2.1, but for the additional model Add3.