Penguin model update: an improved penguin mortality relationship with sardine biomass and results of sensitivities to the base case

William Robinson[1] and Doug Butterworth

MARAM (Marine Resource Assessment and Management Group)
Department of Mathematics and Applied Mathematics,
University of Cape Town

September 2011

Introduction

Work on the penguin–fish interaction model has progressed to the point where a candidate base case for Robben Island was presented in document FISHERIES/2011/SWG–PEL/40. However, one concern there was that the likelihood could always be increased by increasing the value of the power parameter n in the biomass–mortality relationship. This indicated that the functional form of that relationship was perhaps not the most appropriate. Here, a new piecewise-linear form has been implemented and proposed as a new base case as it seems generally satisfactory.

Besides the results of updating the base case with the new biomass–mortality functional form, the results of various sensitivity tests to this new base case are presented.

Adult survival

This section is an update to the corresponding section in the Appendix of document FISHERIES/2011/SWG–PEL/40.

The rates of annual adult survival S_y and annual natural mortality M_y are related as

$$S_y = e^{-M_y} \tag{1}$$

where M_y is modelled as follows:

$$M_y = M_{\min} + f_S\left(B_{S,y}\right)e^{X_y} \tag{2}$$

where X_y is distributed $N\left(0,\sigma_y^2\right)$ with

$$\sigma_y = \sqrt{e^{\tilde{\sigma}^2 / f_S\left(B_{S,y}\right)^2} - 1} \tag{3}$$

Thus we have a log-normal random effect, but since the σ_y depend on the biomass $B_{S,y}$, the M_y distributions will all have exactly the same standard deviation. This is appropriate since data related to each year receives roughly equal weighting, and, when projecting, high biomass does not force low mortality.

[1]william.robinson@uct.ac.za

The base case model uses the following constant values: $\tilde{\sigma} = 0.1$ and $M_{\min} = 0.04$.

The parametric biomass-mortality relationship previously used has now been dropped in favour of a series of connected straight lines for the reason given above. The relationship is assumed to be constant above $B_S = 0.4$, below which mortality increases as biomass decreases. (It was found that allowing more complex behaviour for $B_S > 0.4$ did not improve the model fit significantly.) The function is set up to ensure that the gradient increases as biomass decreases, as follows:

$$\begin{aligned} f_S(1.0) &= M_1 \\ f_S(0.4) &= M_1 \\ f_S(0.3) &= f_S(0.4) + M_2 \\ f_S(0.2) &= 2f_S(0.3) - f_S(0.4) + M_3 \\ f_S(0.1) &= 2f_S(0.2) - f_S(0.3) \\ f_S(0.0) &= 2f_S(0.1) - f_S(0.2) \end{aligned} \tag{4}$$

The estimable parameters are M_1, M_2 and M_3, each of which must be positive. In theory, additional M parameters could be added to the final two lines above, but it was found that these did not significantly improve the fit. Linear interpolation is used to calculate the mortality at other biomass values. The old and new functions for $f_S(B_S)$ as estimated in fitting the model are shown in Figure 5.

The prior added to the negative log likelihood for each year to reflect assumptions made above for the X_y parameters is:

$$P_S = \sum_y \left[\ln \sigma_y + \frac{1}{2}\left(\frac{X_y}{\sigma_y}\right)^2 \right] \tag{5}$$

An additional penalty term ("prior") ensures that the annual mortality rates are evenly distributed about the curve relating mortality and biomass, specifically the sum of the residuals is forced to zero (this was found to aid estimation stability):

$$P_{\text{B-M}} = 10^5 \left\{ \sum_y \left[M_y - \left(M_{\min} + \bar{M}_y \right) \right] \right\}^2 \tag{6}$$

Sensitivities

Most of the base case model sensitivities which were tested consider variation in values for parameters which were fixed on input to the model. In these cases the base case value is given in parenthesis below. The following variations were tested:

1. Old mortality–sardine biomass relationship.
2. Expected values for numbers of tag re-sightings each year forced to match observations.
3. Relative detectability of juveniles $p_J = 0.9$ $(p_J = 1.0)$.

4. Age of first breeding attempt $a^* = 3$ $\left(a^* = 4\right)$.
5. Age of first breeding attempt $a^* = 5$ $\left(a^* = 4\right)$.
6. Standard error of the logarithms of the juvenile proportions $\sigma_{\mathrm{J}} = 0.2$ $\left(\sigma_{\mathrm{J}} = 0.1\right)$.
7. Variability about the biomass–mortality relationship $\tilde{\sigma} = 0.05$ $\left(\tilde{\sigma} = 0.1\right)$.
8. Variability about the biomass–mortality relationship $\tilde{\sigma} = 0.2$ $\left(\tilde{\sigma} = 0.1\right)$.
9. Maximum breeding success rate $H_{\max} = 1.5$ $\left(H_{\max} = 1.8\right)$.
10. Proportion of moulters susceptible to observation $q = 0.8$ $\left(q = 0.9\right)$.
11. Proportion of moulters susceptible to observation $q = 1.0$ $\left(q = 0.9\right)$.

The reason for the inclusion of Sensitivity 2 above is that, as evident from Figure 2, the new base case has not changed earlier results of greater numbers of re-sightings than predicted by the model over most years post-2000.

Base case model input values are listed in Table 1.

Results

Table 2 provides a composite list of model parameters which are estimated and the priors assumed for them. Parameter estimates at the joint posterior mode and the medians and 90% probability intervals of the Bayesian posterior distributions are given for the new base case.

Table 3 lists the results of the sensitivity tests. As the primary purpose of this modelling exercise is to predict future trends in penguin abundance in relation to future sardine biomass levels, these results have been expressed in terms of the penguin trends for the next 10 years and how they relate to those for the new base case for levels of future sardine abundance close to those required to sustain penguin numbers.

The tables are followed by various illustrative plots.

Discussion

When expected numbers of banded penguin re-sightings are forced to equal the observed values, the overall fit deteriorates (see Figure 12 (b)). Figure 13 compares estimated annual adult survival for the new base case and the variation forcing the tag data fit. Note that in the variation, the estimates of survival are higher over the period 2004–2008 which is in conflict with the information provided by the moult counts.

Figure 14 shows that the fits for the two mortality–biomass functional forms tested are almost identical, while the projections are quantitatively different. The new functional form predicts more of a decline in penguin numbers at $B_{\mathrm{S}} = 0.2$, but a more substantial increase in numbers at $B_{\mathrm{S}} = 0.3$.

The input parameter which has the greatest sensitivity at low sardine biomass levels is $\tilde{\sigma}$ which is a measure of the variability about the biomass–penguin mortality relationship. This is not an unexpected result, and the value adopted for $\tilde{\sigma}$ warrants further consideration. Sensitivity to the other input parameter value changes is slight, except perhaps for the age at which breeding commences.

Future work

Now that a satisfactory base case model would seem to have been achieved, the following steps will be pursued:

1) exploring alternative assumptions (see document FISHERIES/2011/SWG–PEL/03) for the components of sardine and anchovy abundance upon which mortality and reproductive success might depend;
2) splitting reproductive success into its various components (MARAM IWS/DEC10/REP/1), for some of which further data are available;
3) linking the model with the updated OMP operating models to explore the consequences for future penguin abundance of alternative pelagic fish harvesting levels; and
4) extending the model first to some other Western Cape colonies in isolation, and then in combination.

References

Moseley C, Wanless R, Altwegg R, Crawford R, Badenhorst A, Coetzee J. 2011. Hypotheses for relating anchovy and sardine abundance with African Penguin population processes. FISHERIES/2011/SWG–PEL/03.

Parma A, Punt AE, Stefansson G. 2010. International review panel report for the 2010 International Fisheries Stock Assessment workshop. MARAM IWS/DEC10/REP/1.

Robinson W, Butterworth DS. 2011. Full description of the Robben Island Penguin–Fish interaction model and base case Bayesian results. FISHERIES/2011/SWG–PEL/40.

Tables

Table 1: Parameter values fixed on input

Parameter	Description	Value
A	Plus group age	5
p_J	Detectability of juveniles relative to adults in the moult count	1.0
a^*	Age of first breeding attempt	4
σ_J	Standard errors of the logarithms of the juvenile proportions	0.1
$\tilde{\sigma}$	Parameter related to variability about adult mortality vs fish abundance	0.1
σ_H	Standard deviation of reproductive success	0.1
$H_{\max}$	Maximum allowed reproductive success	1.8
q_M	Proportion of moulters susceptible to observation	0.9
$M_{\min}$	Minimum allowed mortality rate	0.04

Table 2: List of estimated parameters, prior distributions and Bayesian posterior probability intervals

Parameter	Description	Prior	Mode	5%	Median	95%
$p_{TR,y}$	Re-sighting probabilities	U[0, 1]				
M_{trans}	"transient" mortality of tagged birds	U[0, 1]	0.349	0.268	0.354	0.446
$M_{trans,1994}$		U[0, 1]	0.000	0.000	0.000	0.001
$M_{trans,2000}$		U[0, 1]	0.000	0.000	0.000	0.000
$\ln N_0$	Log of initial population size	U[1, 10]	6.853	6.469	6.853	7.238
λ	Initial population profile parameter	U[0, 3]	0.211	0.176	0.213	0.256
σ_{add}	Additional variance in moult counts	U[0, 1]	0.000	0.000	0.000	0.000
$I_{1989-1991}$	Immigration of three year old birds	U[0, 3000]	561.1	285.7	567.6	852.5
$I_{1992-1994}$		U[0, 3000]	1121.6	690.9	1024.5	1373.1
$I_{1995-1999}$		U[0, 3000]	42.1	9.2	95.9	271.6
M_1	Biomass–mortality relationship	U[0, 0.5]	0.096	0.004	0.010	0.021
M_2	Biomass–mortality relationship	U[0, 0.5]	0.039	0.010	0.069	0.141
M_3	Biomass–mortality relationship	U[0, 0.5]	0.119	0.023	0.148	0.251
X_y	Adult mortality random effects	U[-4.5, 4.5]				
h	Reproductive success relationship	U[0, 1]	0.520			
H_y	Reproductive success	U[0.0001, 0.9999]				
$-\ln L_M$	Moult count likelihood		–42.5			
$-\ln L_J$	Juvenile proportion likelihood		–48.0			
$-\ln L_{T\text{-}R}$	Tag re-sighting likelihood		6113.3			
P_S	Prior on X_y parameters		–6.0			
P_H	Prior on H^*_y parameters		–23.9			
$-\ln P_{post}$	Total negative log posterior		5993.0			

Table 3: Results of the sensitivity analyses in terms of the numbers of observable female adult moulters in 2009 and projected in 2020 for alternative future sardine biomass B_S.

Future $B_S = 0.2$	**2009**	**2020**	**2020/2009**	**ratio to base case**
New base case	2097	936	0.45	
1. Old B–M relationship	2151	1368	0.64	1.58
2. Force tag data fit	2436	1244	0.51	1.14
3. $p_J = 0.9$	2118	974	0.46	1.03
4. $a^* = 3$	2111	884	0.42	0.94
5. $a^* = 5$	2097	1035	0.49	1.11
6. $\sigma_J = 0.2$	2080	876	0.42	0.94
7. $\tilde{\sigma} = 0.05$	2052	785	0.38	0.86
8. $\tilde{\sigma} = 0.2$	2132	1342	0.63	1.41
9. $H_{max} = 1.5$	2081	933	0.45	1.00
10. $q = 0.8$	2096	929	0.44	0.99
11. $q = 1.0$	2097	944	0.45	1.01
Future $B_S = 0.3$				
New base case	2097	5985	2.85	
1. Old B–M relationship	2151	3552	1.65	0.58
2. Force tag data fit	2436	5483	2.25	0.79
3. $p_J = 0.9$	2118	6477	3.06	1.07
4. $a^* = 3$	2111	5671	2.69	0.94
5. $a^* = 5$	2097	6423	3.06	1.07
6. $\sigma_J = 0.2$	2080	5635	2.71	0.95
7. $\tilde{\sigma} = 0.05$	2052	5682	2.77	0.97
8. $\tilde{\sigma} = 0.2$	2132	6388	3.00	1.05
9. $H_{max} = 1.5$	2081	5914	2.84	1.00
10. $q = 0.8$	2096	5909	2.82	0.99
11. $q = 1.0$	2097	6059	2.89	1.01

Figures

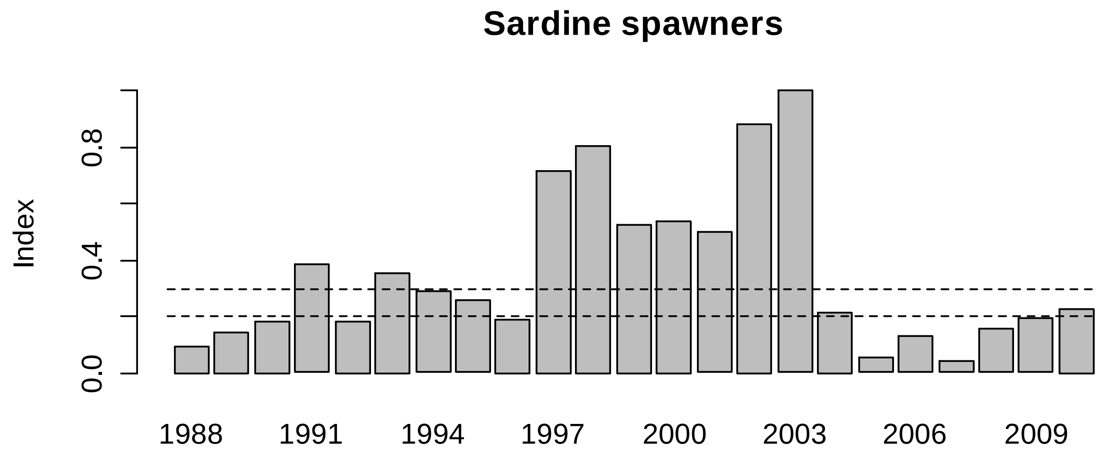


Figure 1: Index of sardine November survey biomass west of Cape Agulhas. Dashed horizontal lines at 0.2 and 0.3 indicate the range of biomass levels used for the projections illustrated in Figure 11.

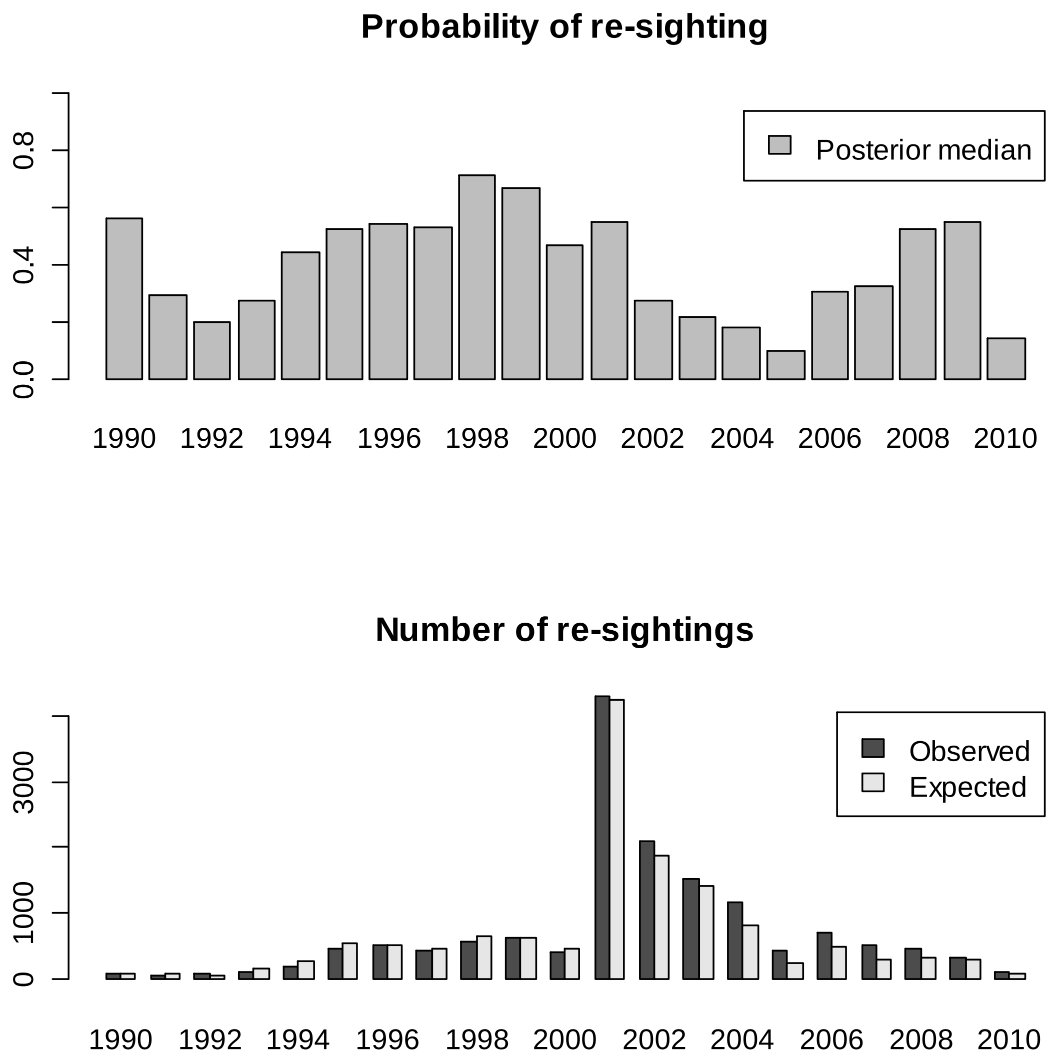


Figure 2: Results of fitting to tag-recapture data for the new base case. Top: annual probability of re-sighting banded birds. Bottom: comparison of observed and expected numbers of banded penguins re-sighted each year for the joint posterior mode.

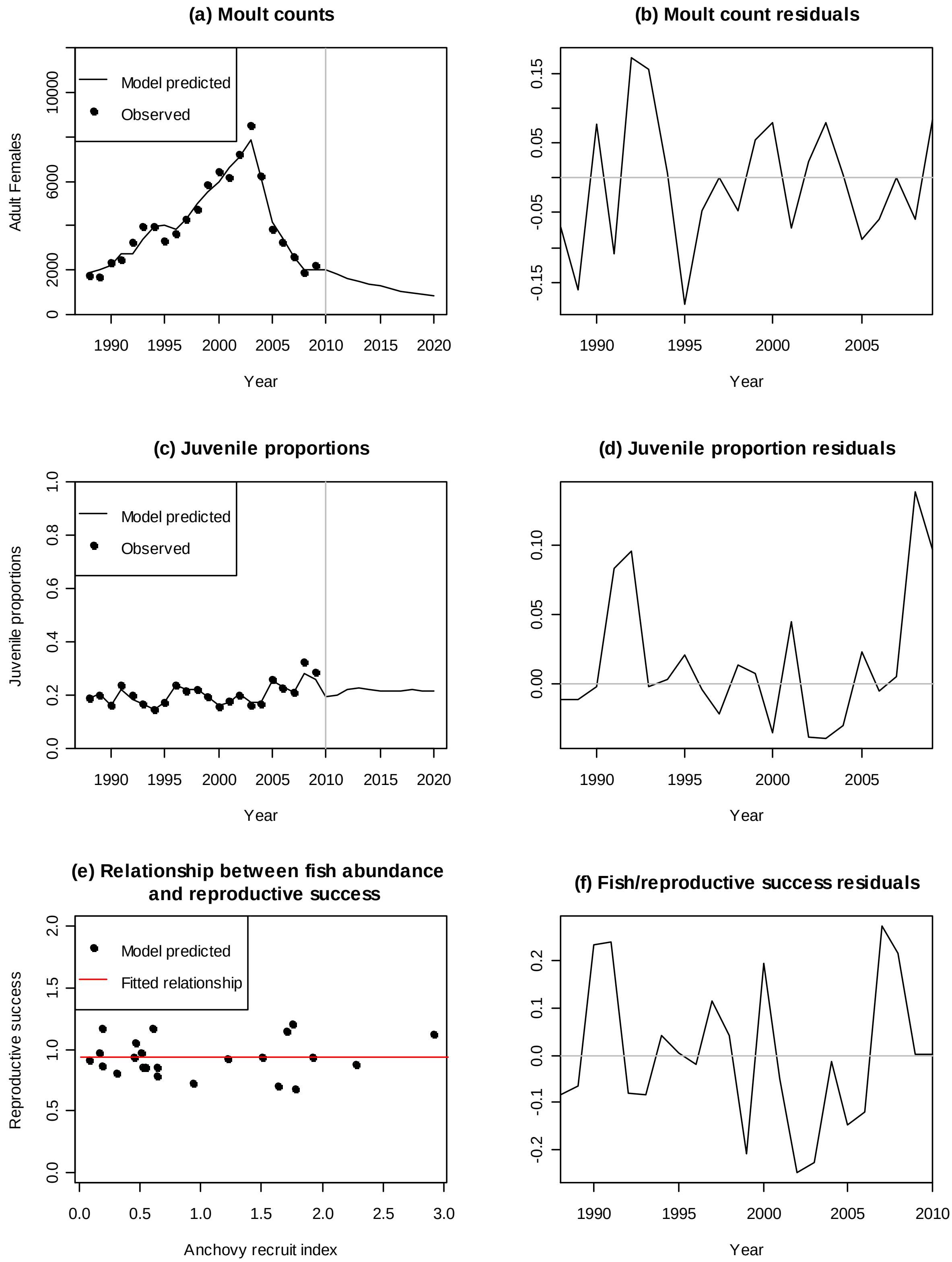


Figure 3: Fits to data/relationships and associated residuals at the joint posterior mode for the new base case. Projections beyond 2010 assume $B_S = 0.2$. The residuals in (b) and (d) are the differences between the logarithms of the observations and the model predicted values. The residuals in (f) are the differences between the estimated reproductive success rates and the assumed relationship.

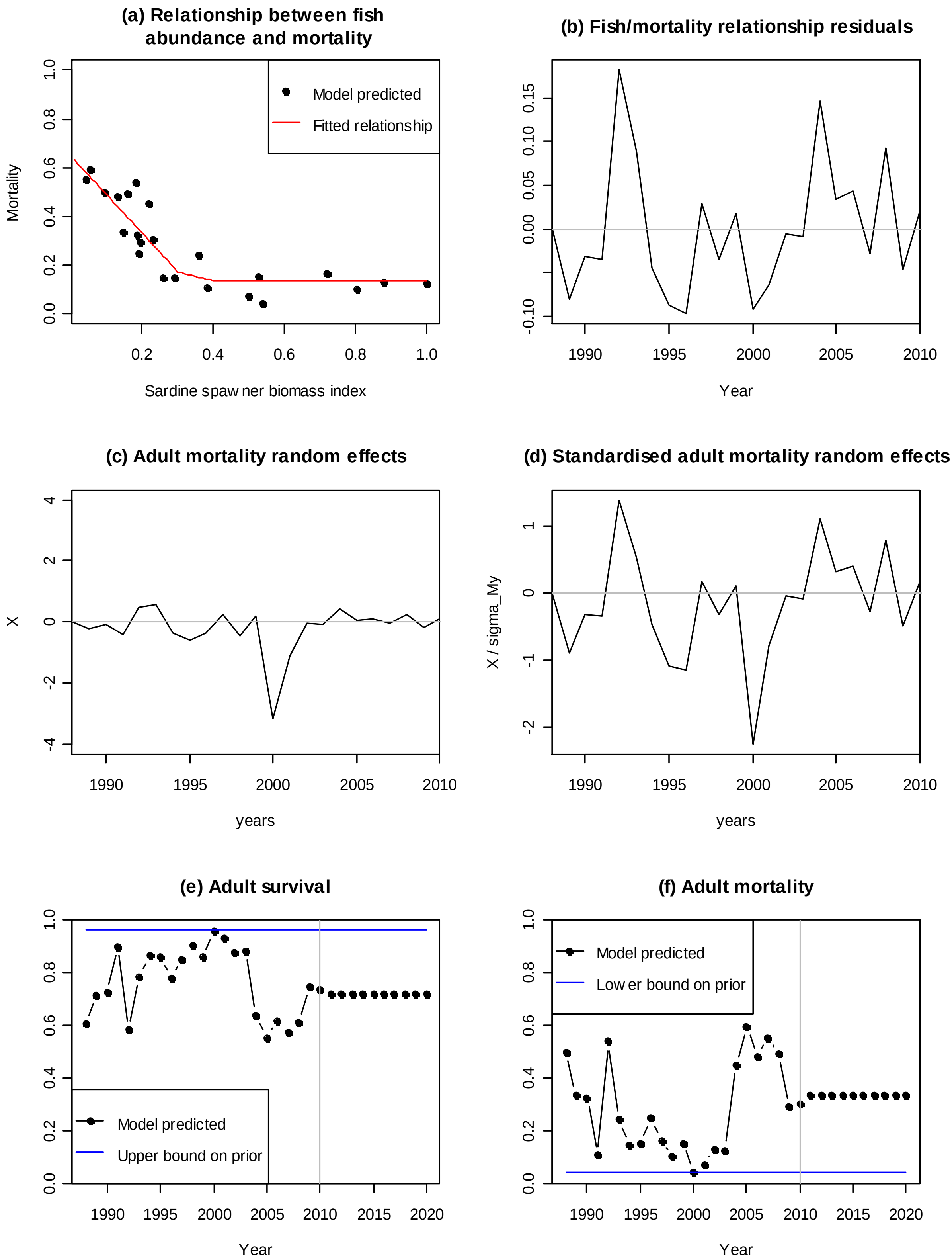


Figure 4: Further fits to data/relationships and associated residuals for the joint posterior mode for the new base case. Projections beyond 2010 assume $B_S = 0.2$. Residuals in (b) are the differences between the estimated annual mortality rates and those predicted by the relationship with fish abundance. The random effects X_y are in (c), and are standardised in (d) by dividing by σ_y. Plot (e) shows the time series of the estimates for the adult survival rates, and (f) shows the corresponding mortality rates.

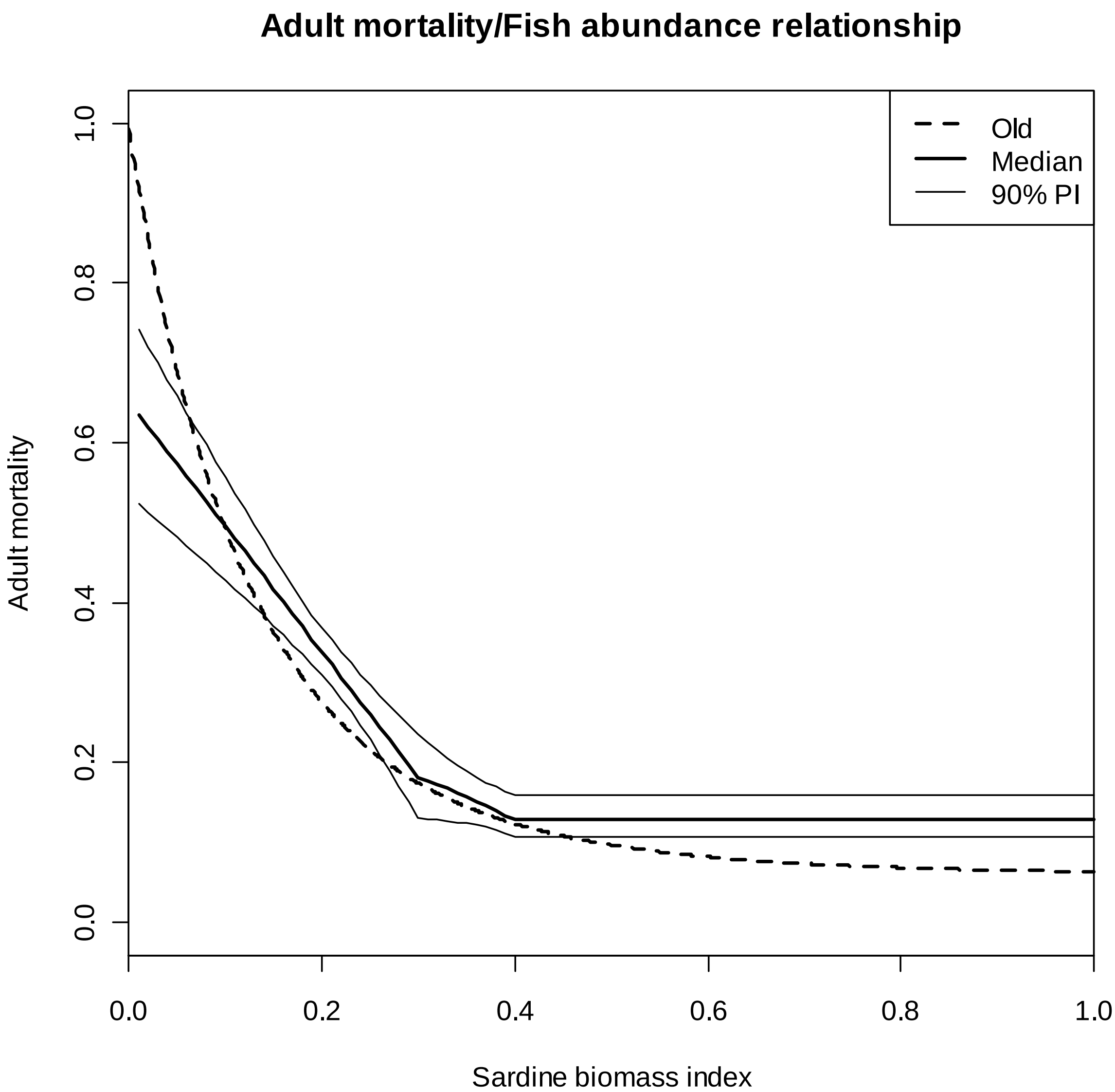


Figure 5: Solid curves show the posterior median and 90% probability interval of the relationship between penguin adult mortality and the sardine spawner biomass west of Cape Agulhas for the new base case. The dashed curve shows the posterior median of the parametric relationship estimated previously.

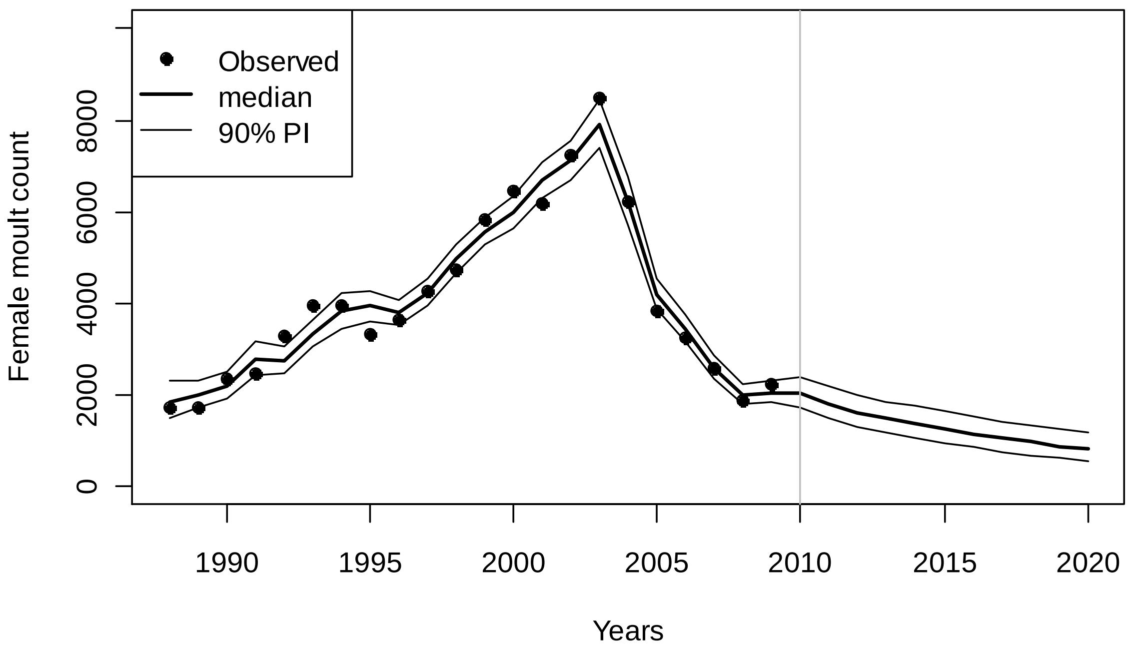


Figure 6: Time series of observed counts of female moulting penguins and the median and 90% probability interval of the Bayesian posterior distribution of the model predicted moult counts for the new base case.

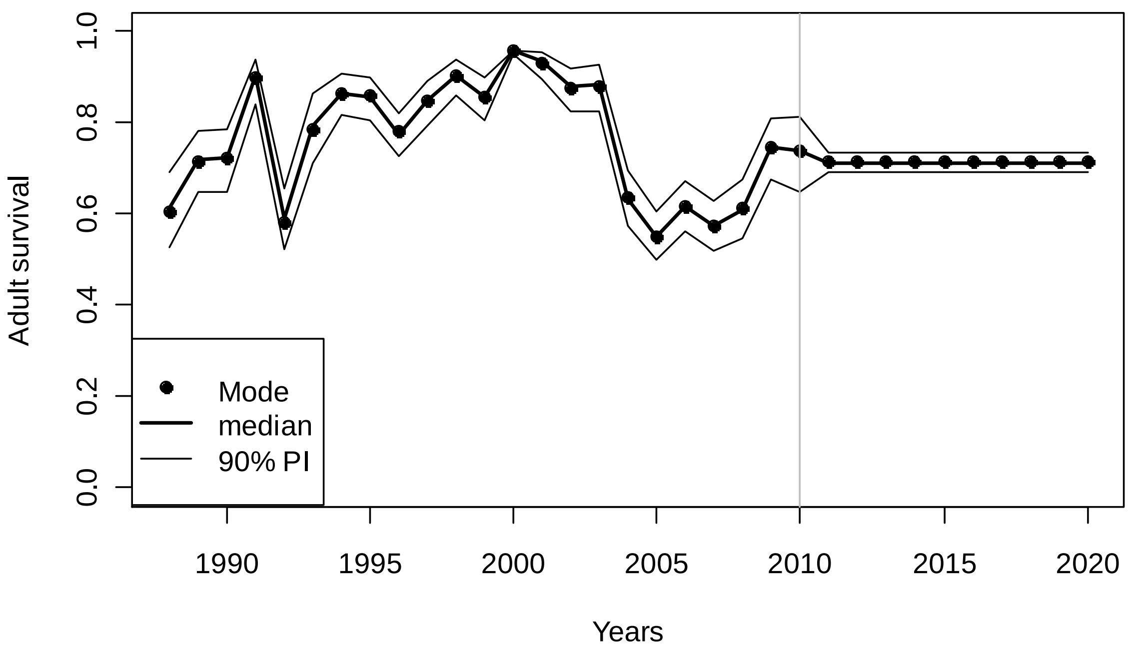


Figure 7: Time series of the adult annual survival rates at the joint posterior mode and the median and 90% probability interval of the Bayesian posterior distribution for the new base case.

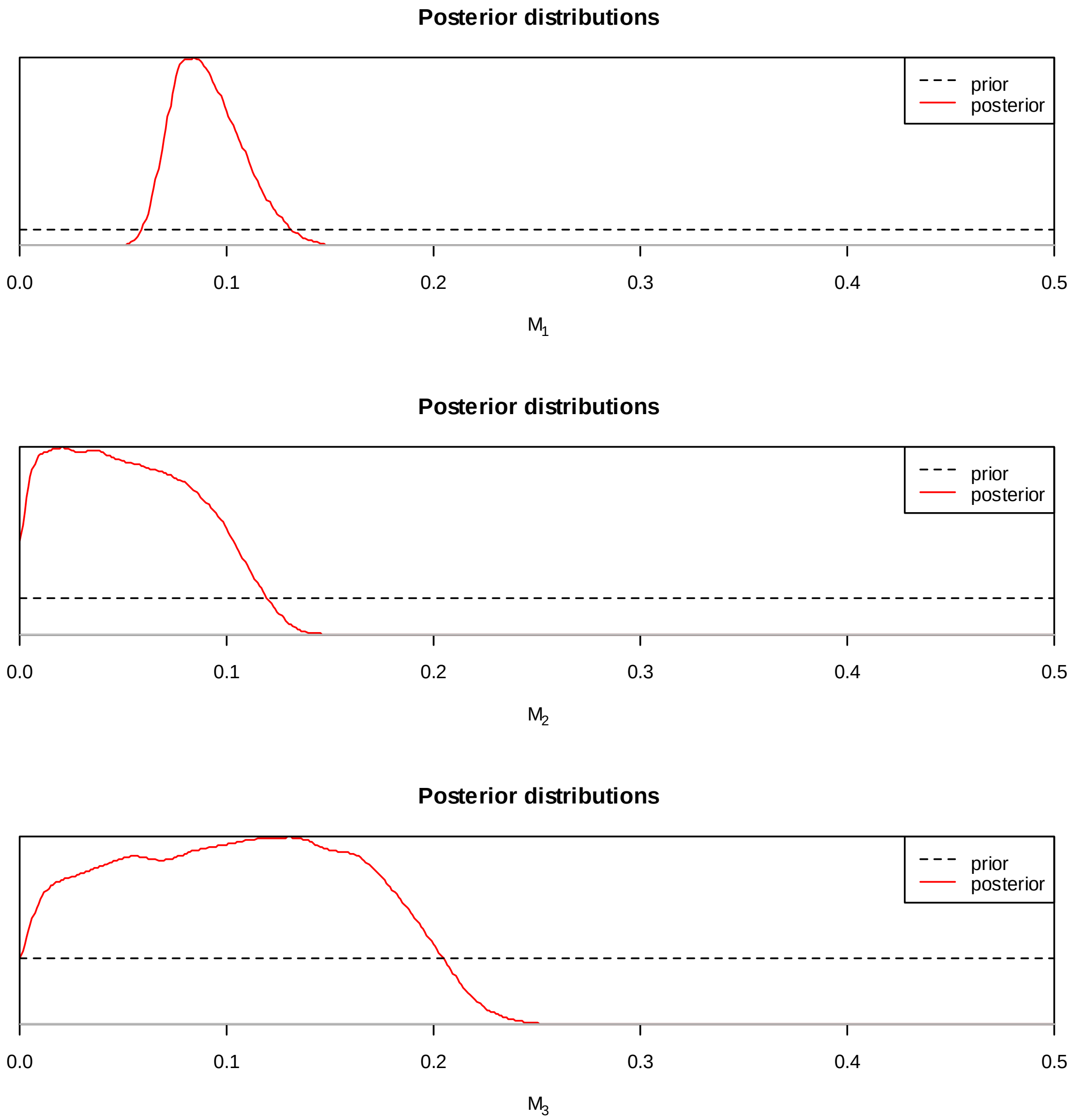


Figure 8: Prior and posterior distributions of the parameters in the mortality–biomass relationship for the new base case.

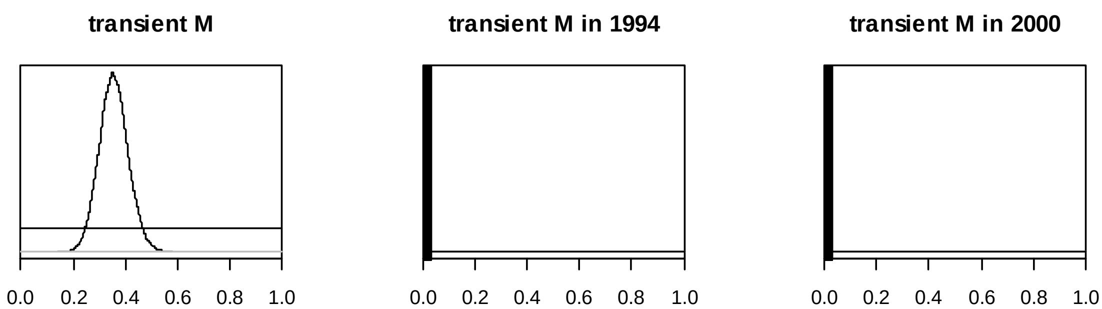


Figure 9: “Transient” mortality comparison of priors and posteriors for the new base case. The “transient M” applies for all years except those with major oil spills (1994 and 2000) from which many penguins were tagged for which separate estimates are made. The solid black bars indicate the posterior to be entirely at transient M=0.

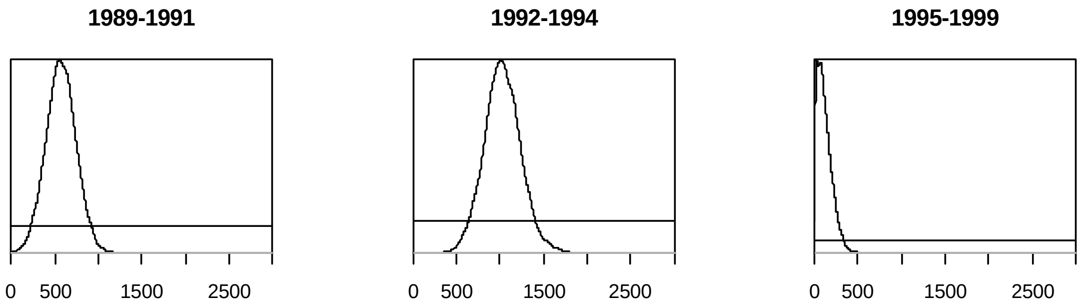


Figure 10: Immigration, taken to be constant over the periods shown: comparison of priors and posteriors for the new base case.

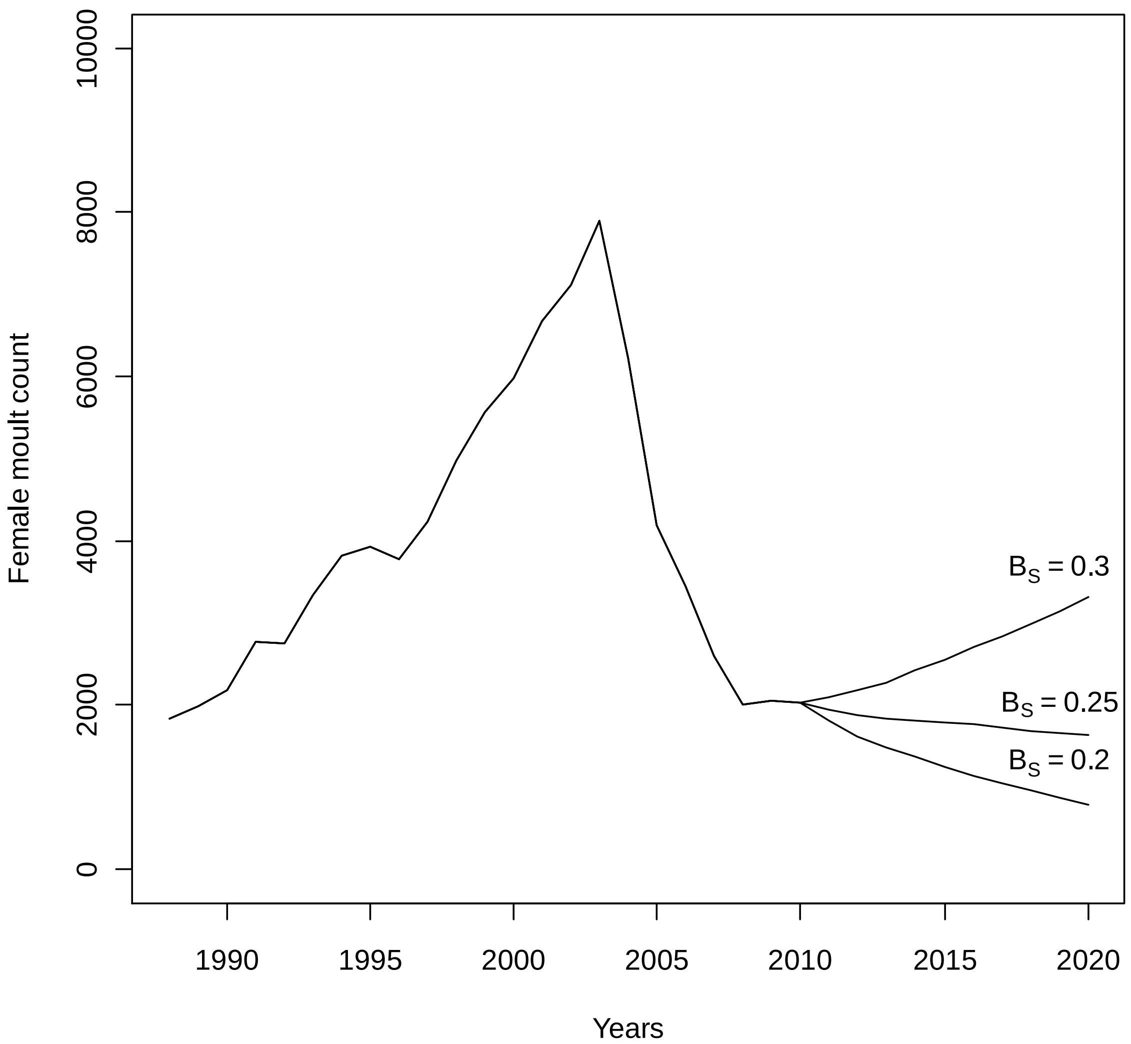
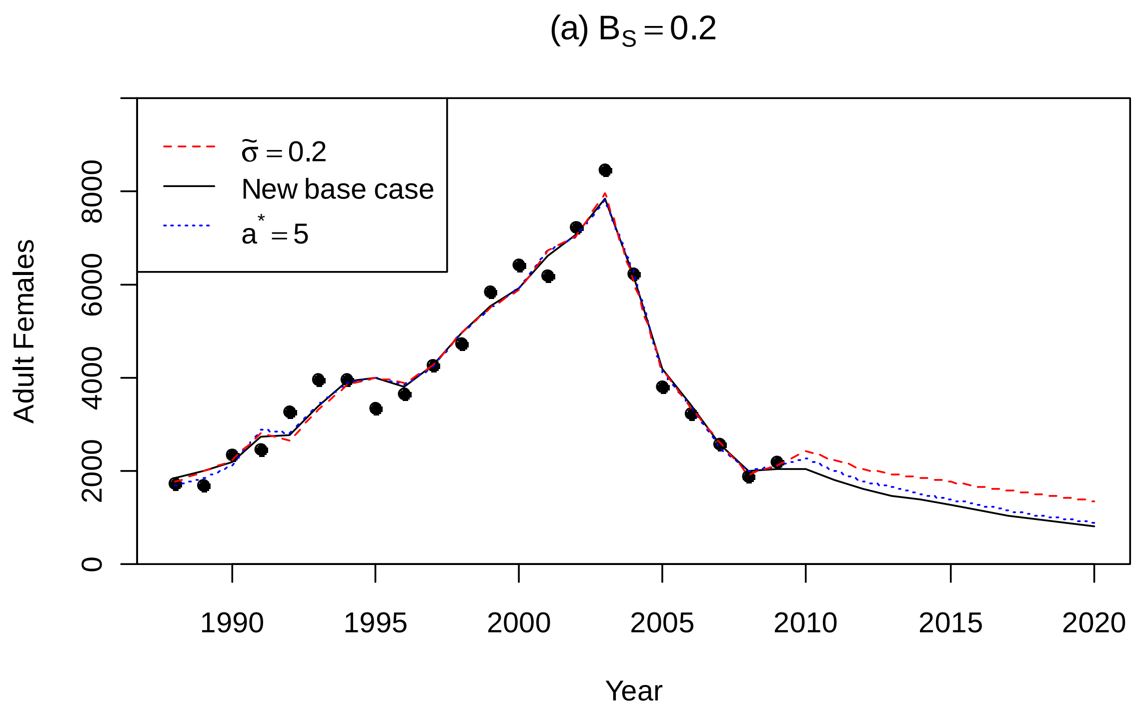


Figure 11: Projections of penguin moult counts from the joint posterior mode for the new base case from 2010 for fixed future sardine spawner biomass levels west of Cape Agulhas for $B_S = 0.2$, $B_S = 0.25$ and $B_S = 0.3$.



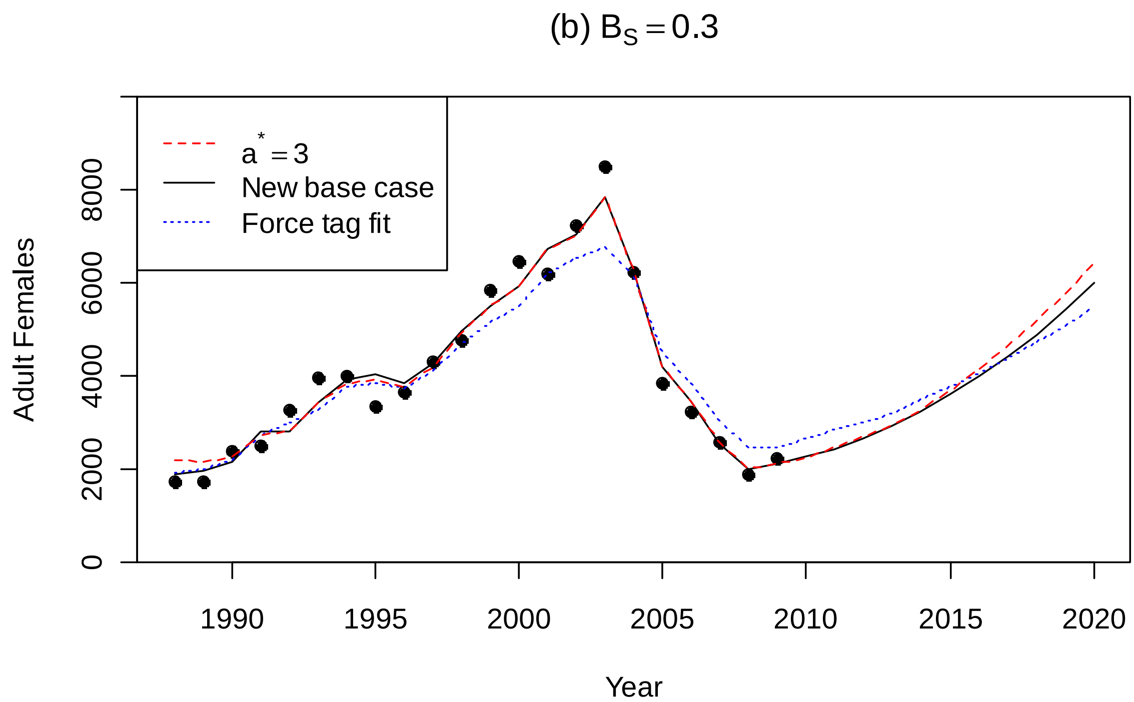


Figure 12: The fits to moult counts and projections of penguin numbers for some sensitivities are shown: (a) at lower future sardine biomass $(B_S = 0.2)$ increasing the value of the variability about the mortality versus biomass relationship $\tilde{\sigma}$ to 0.2 was found to have a positive influence on penguin numbers, while reducing the age at which penguins first attempt breeding to $a^* = 3$ had the largest negative effect; (b) at a higher future sardine biomass level $(B_S = 0.3)$, the largest positive effect is obtained by increasing the age at which breeding is first attempted to $a^* = 5$. A negative effect occurs when the tag counts are forced to fit the expected values exactly.

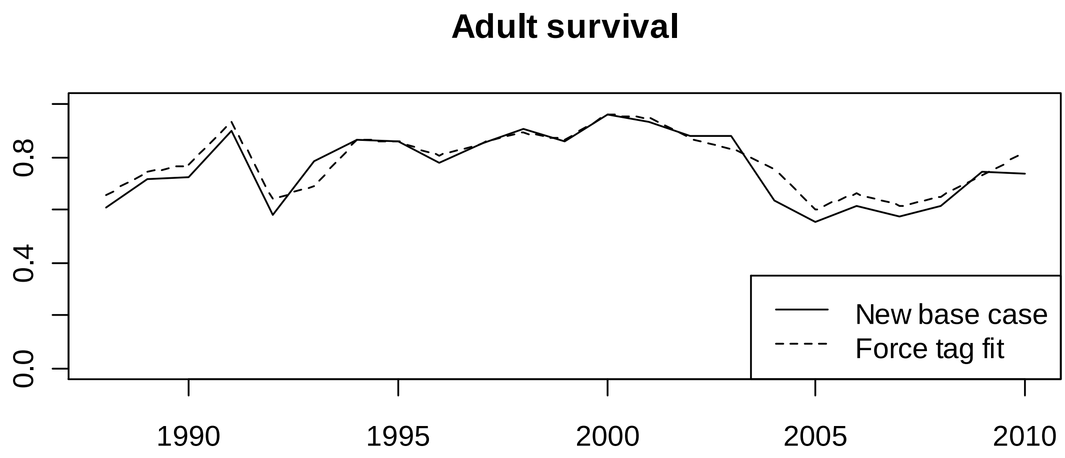
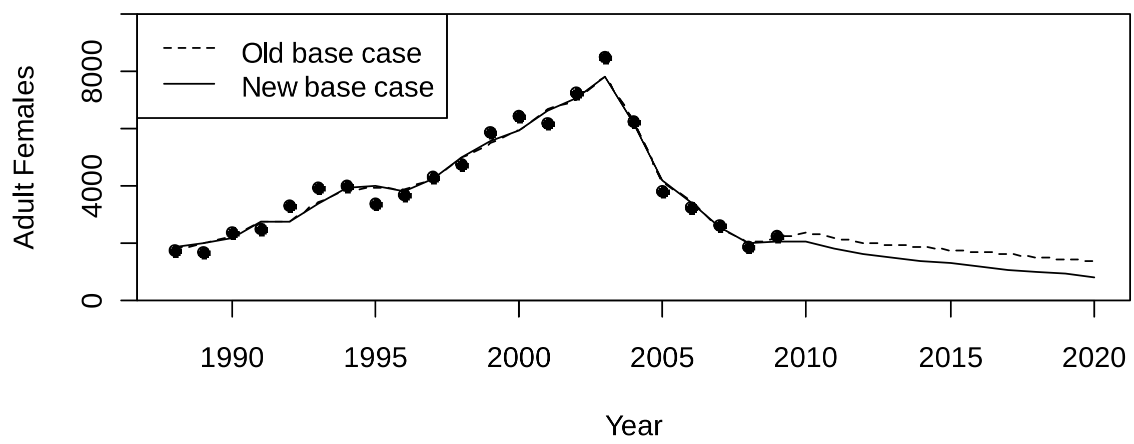


Figure 13: Comparison of adult survival rates for the new base case and the model variation where expected numbers of tag re-sightings are forced to match the observed counts.

(a) $B_S = 0.2$



(a) $B_S = 0.3$

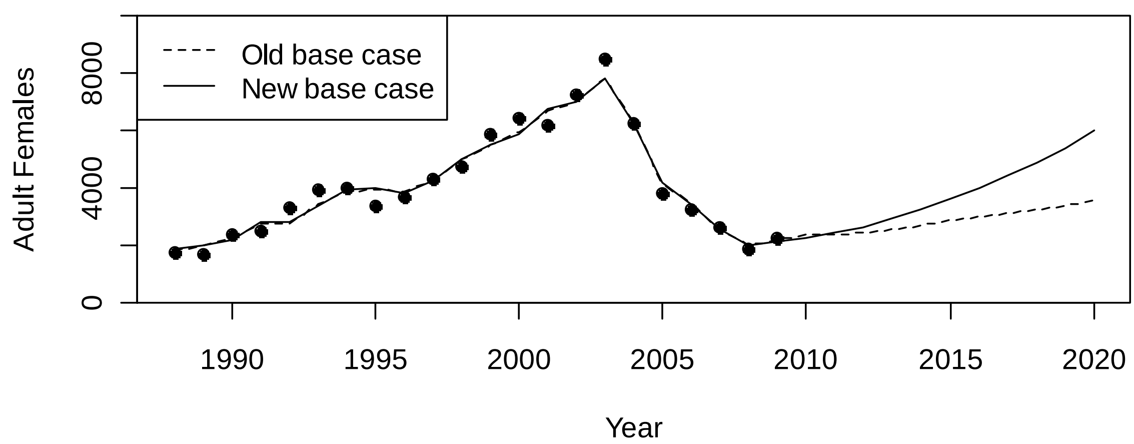


Figure 14: The fits and projections for the different mortality–biomass relationships for future sardine biomass levels $B_S = 0.2$ and $B_S = 0.3$.