Full description of the Robben Island Penguin–Fish interaction model and base case Bayesian results

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Introduction

Work on the penguin–fish interaction model has progressed to the point where a reasonable base case for Robben Island has been achieved.

Methodology

The Appendix describes the full model dynamics. A fundamental component of the model is the assumed relationship between pelagic fish abundance and penguin adult mortality. The statistical distribution assumed for the variability of mortality about the value suggested by the relationship was first described in document FISHERIES/2011/SWG–PEL/01.

Tag data for the full model period (1989–2010) have now been included using a multinomial likelihood following the procedure described in document MCM/2010/SWG-PEL/53. Over-dispersion has been estimated using the program MARK applied to these data in isolation.

Immigration of three year old birds has also been allowed over the period 1989–1999. This can now be estimated given tag-recapture data over this period which remove the confounding between immigration and survival rates that otherwise applies.

Table 1 lists the moult count data to which the model is fitted. Estimates of the direct impact of the two major oil spills are given in Table 2. Table 3 provides a composite list of model parameter values assumed on input.

Bayesian integration was executed using the MCMC algorithm implemented in AD Model Builder. A chain of length 5,500,000 was run, discarding the first 500,000 and saving every 1000th iteration. Thus a sample of 10,000 was used to estimate posterior distributions. Initial checks revealed nothing to suggest any problems with convergence.

Results

Table 4 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. Table 5 lists the time series of the 90% probability intervals of the Bayesian posterior distributions for the key parameters, namely penguin numbers, survival rates and random effects on mortality. Table 6 gives results for the parameters relating to the tag data analysis. The tables are followed by various illustrative plots.

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Discussion

Generally the fits to the data and the residual patterns shown in Figures 2–4 appear acceptable. There are however two features that warrant further attention:

a) a tendency for observed re-sightings to exceed expected numbers after the year 2000, and

b) a PMLE of the power parameter n in the mortality rate verses sardine biomass relationship that is on the boundary of the prior specified (see Table 4 and Figure 8).

These aspects will be investigated further, initially by checking whether they remain given alternative assumptions for some of the parameters fixed on input (see Table 3).

Note estimates of annual immigration over the 1989–1994 period with 90% probability intervals ranging from about 100 to 1200 (see Table 4). This range seems reasonably compatible with numbers of penguins counted at Dyer and Dassen Islands (the likely origins of these immigrants) over the period in question, though perhaps an upper bound should be introduced.

Future work

Now that a satisfactory base case model has been attained, the following steps will be pursued:

1) checking sensitivity to alternative choices for the values of parameters fixed as input (see Table 3);

2) exploring alternative functional forms for the relationships between mortality and reproductive success with resource abundance;

3) 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;

4) splitting reproductive success into its various components (MARAM IWS/DEC10/REP/1), for some of which further data are available;

5) linking the model with the updated OMP operating models to explore the consequences for future penguin abundance of alternative pelagic fish harvesting levels; and

6) 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. 2010. A proposed new method for obtaining penguin moult count estimates. MCM/2010/SWG–PEL/Island Closure Task Team/05.

Robinson W, Butterworth DS. 2010. Penguin survival estimates from tag data using a multinomial likelihood. MCM/2010/SWG–PEL/53.

Appendix

Description of the Robben Island Penguin–Fish interaction Model

Basic dynamics

The model considers the number of female penguins $N_{y,a}$ at the start (1 January) of year y of age a at Robben Island. The initial population size (at the start of year 1988) N_0 and its age structure are:

$$N_{y_0,a} = \begin{cases} N_0 e^{-a\lambda} & \text{for } 1 \le a < A \\ \dfrac{N_0 e^{-a\lambda}}{1-e^{-\lambda}} & \text{for } a = A \end{cases} \tag{A1}$$

where A is the plus-group age. Both N_0 and λ are parameters whose values are estimated.

The following equations describe the population trajectory:

$$N_{y+1,a} = \begin{cases} \dfrac{1}{2}H_y\left(\displaystyle\sum_{a=a^*}^{A} N_{y,a}\right)S_y^{4/12}\left(1-p_y^{\text{oil}}\right) & \text{if } a=1 \\ N_{y,a-1}^* S_y & \text{if } a=2 \\ N_{y,a-1}^* S_y + I_y & \text{if } a=3 \\ N_{y,a-1}^* S_y & \text{if } a=4 \\ \left(N_{y,a-1}^* + N_{y,a}^*\right)S_y & \text{if } a=A \end{cases} \tag{A2}$$

with

$$N_{y,a}^* = N_{y,a}\left(1 - \frac{N_y^{\text{oil}}}{\left(\displaystyle\sum_{a=1}^{A} N_{y,a}\right)S_y^{m_y/12}}\right) \tag{A3}$$

where

S_y is the adult (post 1 January of first year of life) annual survival rate in year y (taken to the power 4/12 in the equation for $a=1$ since the peak of the breeding season is assumed to be on 1 May),

H_y is the annual reproductive success (number of chicks per mature female reaching 1 January of the year following birth, where 50% of these chicks are assumed to be female),

a^* is the age at which the penguins first attempt to breed (taken here to be $a^* = 4$),

p_y^{oil} is the proportion of chicks estimated to have died as a result of an oil spill in year y,

I_y is the number of penguins (all assumed to be of age 3) immigrating to Robben Island in year

y (preliminary investigations suggest it appropriate to estimate this as three constant levels for the periods 1989–1991, 1992–1994 and 1995–1999),

N_y^{oil} is the number of juvenile and adult penguins estimated to have died as a result of oiling in year y, and

m_y is the month in which the oil spill occurred in year y.

See Table 2 for the values used for p_y^{oil}, N_y^{oil} and m_y.

Population model

Both the annual adult survival rate S_y and the annual reproductive success H_y are assumed to depend on some function of prey biomass (the deterministic effect), but to be influenced also by some noise (random effects). For reproductive success, the estimates are drawn from a beta distribution which ensures that biologically plausible bounds are respected. However, this approach does not work for the adult penguin survival rate at Robben Island, because a unimodal beta distribution can only have a very small variance when the mean is close to the boundary. This gives a high weight to years in which survival values want to go close to the maximum, which itself drives estimates towards the upper boundary. This is undesirable since it implies that when prey biomass is high, survival can only be very close to the maximum. Thus the alternative approach below was developed and has been found to work satisfactorily.

Adult survival depends on the normalized annual biomass levels $B_{S,y}$, where the time series I_S is some function of the sardine and anchovy November spawner biomass and May recruit biomass survey results for particular spatial regions:

$$B_{S,y} = I_{S,y} \big/ \max\{I_S\} \tag{A4}$$

Similarly, reproductive success depends on a similar index of biomass level:

$$B_{H,y} = I_{H,y} \big/ \text{mean}\{I_H\} \tag{A5}$$

In the base case implemented here, B_S is taken to be the sardine November survey biomass west of Cape Agulhas (strata A–C), and B_H is anchovy recruit survey biomass west of Cape Infanta.

Adult survival

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

$$S_y = e^{-M_y} \tag{A6}$$

where M_y is modelled as follows:

$$M_y = M_{\min} + \bar{M}_y e^{X_y} \qquad (A7)$$

where

$$\bar{M}_y = M_{\min}^* + f_S\left(B_{S,y}\right) \qquad (A8)$$

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

$$\sigma_y = \sqrt{e^{\tilde{\sigma}^2 \left/ \left(M_{\min}^* + f_S\left(B_{S,y}\right)\right)^2\right.} - 1} \qquad (A9)$$

Thus we have a log-normal random effect, but since the σ_y depend on the biomass B_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.

The reason that the $M_{\min}^*$ term is introduced is that when calculating M_y the possibility that the term additional to $M_{\min}$ could go to zero when biomass is high is excluded. This would be a problem as then σ_y would go infinite in equation (A9), rendering the associated data point redundant because of its infinite variance. The lower bound on achieved M_y remains $M_{\min}$, but the lower bound on the median of its distribution is $M_{\min} + M_{\min}^*$. The base case model uses the following constant values: $\tilde{\sigma} = 0.1$, $M_{\min} = 0.04$ and $M_{\min}^* = 0.02$.

The biomass–mortality relationship is defined as

$$f_S\left(B_{S,y}\right) = \left(a + \frac{B_{S,y}}{b}\right)^{-n} \qquad (A10)$$

Instead of a and b, the expression can be re-parameterised in terms of the values of $\bar{M}_y$ at $B_S = 0.1$ and $B_S = 1$ in order to introduce estimable parameters which are more orthogonal (i.e. have low correlation, which assists with statistically stable estimation). If $U = \bar{M}\left(B_S = 1\right)$ and $V = \bar{M}\left(B_S = 0.1\right) - \bar{M}\left(B_S = 1\right)$, then

$$b = \frac{0.9}{\left[U - M_{\min}^*\right]^{-1/n} - \left[U + V - M_{\min}^*\right]^{-1/n}} \qquad (A11)$$

$$a = \left[U - M_{\min}^*\right]^{-1/n} - \frac{1}{b} \qquad (A12)$$

The estimable parameters are U, V and n, where sensibly $V \geq 0$.

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

$$P_S = \frac{1}{2}\sum_y \left(\frac{X_y}{\sigma_y}\right)^2 \tag{A13}$$

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

$$P_{\text{B-M}} = 10^5 \left\{\sum_y \left[M_y - \left(M_{\min} + \bar{M}_y\right)\right]\right\}^2 \tag{A14}$$

Reproductive success

The parameters $\bar{H}_y^* = f_H\left(B_{H,y}\right)$ are estimated on the interval $[0,1]$. These are the transformed predicted annual reproductive success rates $\bar{H}_y$ which fall in the interval $[0, H_{\max}]$:

$$\bar{H}_y = H_{\max}\bar{H}_y^* \tag{A15}$$

The assumed relationship between $\bar{H}_y^*$ and the fish abundance index $B_{H,y}$ is currently assumed to be a constant given that earlier analyses have not provided any indication of dependence:

$$f_H\left(B_{H,y}\right) = h \tag{A16}$$

but alternative functional forms may be considered in future.

The parameters H_y^* are estimated for each year on the interval $[0,1]$ and then transformed to the range $[0, H_{\max}]$ to obtain the annual reproductive success rates H_y as follows:

$$H_y = H_{\max}H_y^* \tag{A17}$$

We assume that the H_y^* parameters are beta-distributed about the predicted values $\bar{H}_y^*$. Setting $\kappa_{H,y} = \bar{H}_y^*\left(1-\bar{H}_y^*\right)/\sigma_H^2 - 1$, the parameters of this beta distribution $\alpha_{H,y}$ and $\beta_{H,y}$ are:

$$\alpha_{H,y} = \bar{H}_y^*\kappa_{H,y} \qquad \beta_{H,y} = \kappa_{H,y}\left(1-\bar{H}_y^*\right) \tag{A18}$$

The prior added to the negative log likelihood for each year, which reflects the assumption that H_y^* is beta-distributed, is:

$$P_{H,y} = -\ln\left(\frac{\Gamma\left(\alpha_{H,y}+\beta_{H,y}\right)}{\Gamma\left(\alpha_{H,y}\right)\Gamma\left(\beta_{H,y}\right)}\right) - \left(\alpha_{H,y}-1\right)\ln H_y^* - \left(\beta_{H,y}-1\right)\ln\left(1-H_y^*\right) \tag{A19}$$

An additional penalty term ensures that the annual reproduction success rates are evenly distributed about the assumed relationship curve, i.e. the sum of the residuals is forced to zero (this was found to aid estimation stability):

$$P_{\text{B-R}} = 10^5 \left\{ \sum_y \left[H_y - \bar{H}_y \right] \right\}^2 \tag{A20}$$

Moult counts

The population model is fitted to annual moult count data for both adult and juvenile birds by taking them into account through the following negative log-likelihood functions:

$$-\ln L_{\text{M}} = \sum_y \left[\ln \sigma_{\text{M},y} + \frac{1}{2\sigma_{\text{M},y}^2} \left(\ln N_y^{\text{obs}} - \ln N_y^{\text{model}} \right)^2 \right]$$

$$-\ln L_{\text{J}} = \sum_y \left[\ln \sigma_{\text{J}} + \frac{1}{2\sigma_{\text{J}}^2} \left(\ln J_y^{\text{obs}} - \ln J_y^{\text{model}} \right)^2 \right] \tag{A21}$$

$\sigma_{\text{M},y}$ and σ_{J} are respectively the standard errors of the logarithms of the adult moult counts and juvenile proportions of these counts about their true values (i.e. these reflect observation errors). The terms in the likelihood for the adult moult counts are weighted according to the CVs of the observations (see Table 1) with

$$\sigma_{\text{M},y} = \sqrt{\text{CV}\left(N_y^{\text{obs}}\right)^2 + 0.05^2 + \sigma_{\text{add}}^2} \tag{A22}$$

where the additional variance σ_{add}^2 is an estimable parameter, with the true additional variance forced to be at least 0.05^2. The value of σ_{J} is fixed at $\sigma_{\text{J}} = 0.1$.

$N_y^{\text{model}} = q_{\text{M}} \sum_{a=2}^{A} N_{y,a} S_y^{11/12}$ is the number of female birds in adult plumage (aged 2 and over) counted in year y, where the peak of the counting season is the end of November, and q_{M} is the proportion of these birds susceptible to observation (assumed here to be $q_{\text{M}} = 0.9$).

$J_y = \dfrac{p_{\text{J}} N_{y,1}}{\sum_{a=1}^{A} N_{y,a}}$ is the proportion of juvenile birds in the model at the time of the moult count (note that $S_y^{11/12}$ factors in numerator and denominator cancel), with p_{J} being the detectability of juvenile moulters relative to adults in the counting process, which is assumed here to be $p_{\text{J}} = 1$.

N_y^{obs} is the number of female adult moulters observed in year y (taken to be one half of the total adult moulters counted).

J_y^{obs} is the observed proportion of moulters in immature plumage counted in year y.

Tag data

In addition to the moult counts, tag data for the period 1989–2010 has been incorporated into the analysis. This provides an independent estimate of annual survival rates and allows for the estimation of immigration. The multinomial likelihood of the encounter histories is calculated through the estimation of re-sighting probabilities and survival rates for each year. This is the method used in program MARK. A variation on the standard MARK procedure which has been included in the analysis is the estimation of a "transient" factor relating to birds tagged which are never seen again, modelled as additional mortality in the year following tagging to reflect emigration. This factor is assumed to be equal for all years, except for the years of the major oil spills (*Apollo Sea* in 1994 and *Treasure* in 2000) for which separate values are estimated, as these birds are more likely to be linked to Robben Island than would be the case for normal "transients".

The log-likelihood function for the multinomial distribution, ignoring the constant multinomial coefficient, is:

$$\ln L_{\text{T-R}} = \frac{1}{\hat{c}} \sum_{j=1}^{m} n_j \ln \hat{p}_j \tag{A23}$$

where $\hat{p}_j$ is the estimated probability of the j th encounter history occurring and n_j is the number of times which that history has been observed. The number of unique encounter histories is m. In order to account for over-dispersion, the likelihood is scaled by a factor of $1/\hat{c}$, which was obtained from analysing the data using MARK.

Objective function

The overall log posterior is thus:

$$-\ln P_{\text{post}} = -\ln L_{\text{M}} - \ln L_{\text{J}} - \ln L_{\text{T-R}} + P_S + P_{\text{B-M}} + P_H + P_{\text{B-R}} \tag{A24}$$

Tables

Table 1: Counts of birds moulting at Robben Island with CVs (MCM/2010/SWG-PEL/Island Closure Task Team/05) and the proportion of juveniles.

Year	Number of adult female moulters	CV	Proportion of juveniles
1988	1734	0.197	0.188
1989	1698	0.184	0.202
1990	2362	0.176	0.160
1991	2470	0.101	0.240
1992	3272	0.097	0.200
1993	3958	0.100	0.166
1994	3967	0.115	0.147
1995	3337	0.112	0.174
1996	3650	0.069	0.238
1997	4278	0.066	0.218
1998	4750	0.058	0.224
1999	5847	0.056	0.194
2000	6441	0.065	0.158
2001	6181	0.058	0.180
2002	7234	0.044	0.198
2003	8488	0.047	0.164
2004	6221	0.063	0.168
2005	3830	0.059	0.259
2006	3227	0.083	0.229
2007	2579	0.114	0.212
2008	1872	0.087	0.326
2009	2215	0.090	0.284

Table 2: Model inputs relating to oiling

Constant	Description	Value
N_{1994}^{oil}	Number of adult females which died as a result of the 1994 oil spill	600
N_{2000}^{oil}	Number of adult females which died as a result of the 2000 oil spill	750
p_{1994}^{oil}	Proportion of chicks which died due to the 1994 oil spill	0.29
p_{2000}^{oil}	Proportion of chicks which died due to the 2000 oil spill	0.38
m_{1994}	Month of the 1994 oil spill	5.7
m_{2000}	Month of the 2000 oil spill	5.9

Table 3: Parameter values fixed on input

Parameter	Description	Value
A	Plus group age	5
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 (A9)	0.1
σ_H	Standard deviation of reproductive success	0.1
q_M	Proportion of moulters susceptible to observation	0.9
M_{min}	Minimum allowed mortality rate (A7)	0.04
M_{min}^*	Additional term in biomass–mortality relationship (A7)	0.02
H_{max}	Maximum allowed reproductive success (A15)	1.8
p_J	Detectability of juveniles relative to adults in the moult count	1.0

Table 4: 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]	0.379	0.311	0.402	0.497
$M_{trans,1994}$		U[0, 1]	0.000	0.001	0.006	0.010
$M_{trans,2000}$		U[0, 1]	0.000	0.000	0.000	0.000
$\ln N_0$	Log of initial population size	U[1, 10]	6.794	6.422	6.783	7.161
λ	Initial population profile parameter	U[0, 3]	0.211	0.179	0.214	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]	427.7	127.4	404.5	688.8
$I_{1992-1994}$		U[0, 3000]	973.6	530.8	858.7	1202.1
$I_{1995-1999}$		U[0, 3000]	0.0	0.1	3.1	4.9
U	$M\left(B_S = 1\right)$	U[0.02, 0.2]	0.025	0.022	0.024	0.030
V	$M\left(B_S = 0.1\right) - M\left(B_S = 1\right)$	U[0, 0.75]	0.437	0.376	0.429	0.476
n	Biomass–mortality relationship	U[1, 8]	8.000	6.718	7.331	7.938
X_y	Adult mortality random effects	U[-4.5, 4.5]				
h	Reproductive success relationship	U[0, 1]	0.509	0.486	0.517	0.547
H_y	Reproductive success	U[0.0001, 0.9999]				
$-\ln L_M$	Moult count likelihood		−42.9			
$-\ln L_J$	Juvenile proportion likelihood		−48.1			
$-\ln L_{T\text{-}R}$	Tag re-sighting likelihood		6112.7			
P_S	Prior on X_y parameters		5.5			
P_H	Prior on H_y^* parameters		−24.3			
$-\ln P_{post}$	Total negative log posterior		6002.8			

Table 5: Time series of the medians and 90% probability intervals of the Bayesian posterior distributions for the number of adult female moulting penguins N (see Figure 6), the annual survival rate S (see Figure 7) and the random effects on mortality X .

	N			S			X		
	5%	50%	95%	5%	50%	95%	5%	50%	95%
1988	1421	1800	2270	0.56	0.65	0.73	-0.48	-0.17	0.12
1989	1693	1977	2326	0.69	0.77	0.83	-0.80	-0.39	-0.03
1990	1962	2228	2540	0.69	0.78	0.85	-0.76	-0.24	0.19
1991	2391	2745	3148	0.85	0.93	0.96	-2.90	-0.95	0.25
1992	2449	2743	3078	0.53	0.62	0.70	0.20	0.53	0.81
1993	3143	3407	3699	0.74	0.84	0.93	-0.99	0.21	0.99
1994	3483	3812	4173	0.82	0.87	0.92	-1.20	-0.44	0.15
1995	3593	3906	4234	0.82	0.87	0.92	-1.29	-0.60	-0.05
1996	3529	3798	4097	0.75	0.80	0.85	-0.73	-0.33	0.03
1997	3935	4208	4504	0.79	0.85	0.91	0.46	1.26	1.82
1998	4635	4964	5306	0.87	0.93	0.96	-3.41	0.03	1.22
1999	5194	5488	5797	0.80	0.86	0.92	-0.20	0.71	1.33
2000	5553	5890	6251	0.96	0.96	0.96	-4.48	-4.37	-3.91
2001	6220	6641	7065	0.90	0.95	0.96	-4.00	-1.64	0.06
2002	6562	7052	7612	0.80	0.88	0.96	-3.22	1.19	1.91
2003	7295	7925	8588	0.80	0.91	0.96	-3.07	0.84	2.00
2004	5784	6361	7001	0.57	0.65	0.74	0.21	0.60	0.92
2005	3790	4117	4482	0.47	0.53	0.59	-0.23	-0.03	0.18
2006	3205	3520	3866	0.58	0.65	0.72	-0.26	0.06	0.33
2007	2222	2478	2758	0.47	0.53	0.60	-0.33	-0.15	0.04
2008	1796	1996	2221	0.57	0.65	0.73	-0.13	0.24	0.52
2009	1941	2192	2477	0.72	0.80	0.87	-0.88	-0.32	0.15
2010	2028	2420	2843	0.73	0.83	0.90	-1.08	-0.33	0.29

Table 6: Results of fitting to penguin tagging data.

	Probability of re-sighting				Number of re-sightings	
	Mode	5%	50%	95%	Observed	Expected
1990	0.56	0.40	0.56	0.73	80	71.2
1991	0.28	0.18	0.29	0.45	57	68.6
1992	0.19	0.13	0.20	0.29	80	57.5
1993	0.26	0.19	0.27	0.37	107	156.3
1994	0.45	0.35	0.45	0.55	182	264.6
1995	0.53	0.46	0.53	0.59	469	550.0
1996	0.55	0.48	0.55	0.61	514	516.7
1997	0.53	0.46	0.53	0.60	443	460.5
1998	0.72	0.65	0.71	0.78	580	648.6
1999	0.67	0.60	0.67	0.73	616	618.3
2000	0.47	0.40	0.47	0.54	409	458.4
2001	0.55	0.53	0.55	0.57	4302	4250.2
2002	0.27	0.25	0.27	0.30	2081	1884.2
2003	0.22	0.20	0.22	0.25	1512	1420.1
2004	0.18	0.16	0.18	0.21	1181	818.9
2005	0.10	0.08	0.10	0.13	440	247.3
2006	0.31	0.26	0.31	0.36	712	484.9
2007	0.33	0.27	0.33	0.38	505	288.7
2008	0.52	0.44	0.53	0.61	469	320.2
2009	0.54	0.44	0.55	0.67	330	285.6
2010	0.14	0.10	0.15	0.21	100	71.6

Figures

Sardine spawners
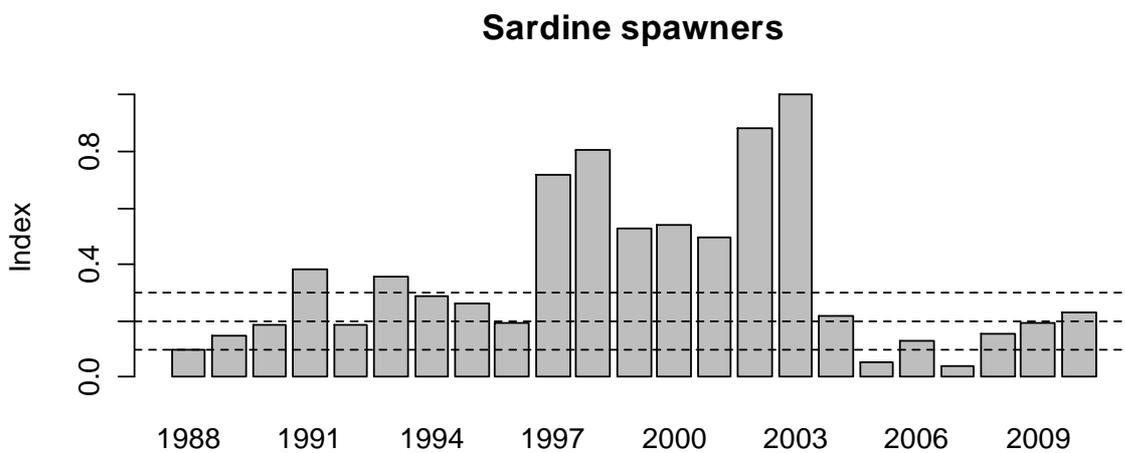
Figure 1: Index of sardine November survey biomass west of Cape Agulhas. Dashed horizontal lines indicate the three biomass levels used for the projections illustrated in Figure 11.

Probability of re-sighting

Number of re-sightings
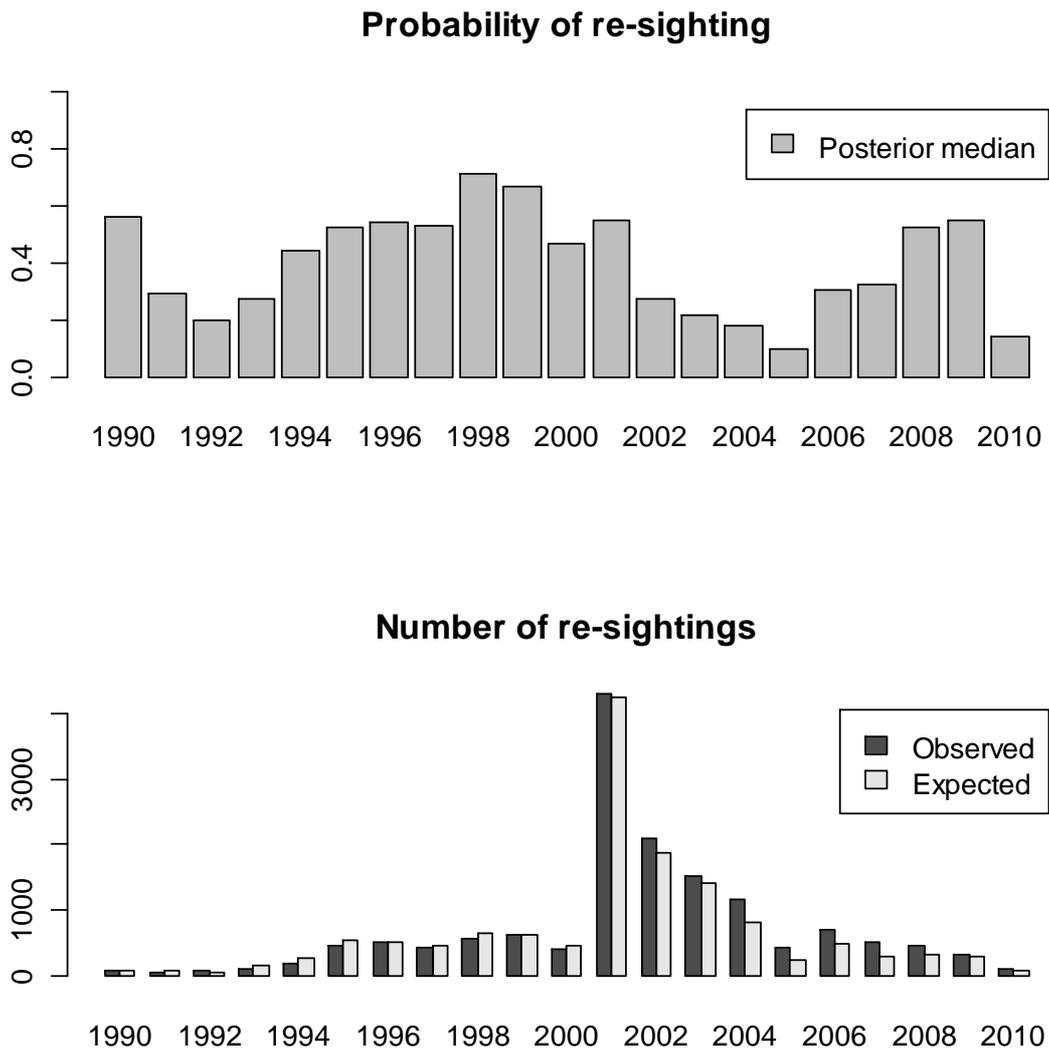
Figure 2: Results of fitting to tag-recapture data. Top: annual probability of re-sighting banded birds. Bottom: comparison of observed and expected numbers of banded penguins re-sighted each year for the joint posterior mode.
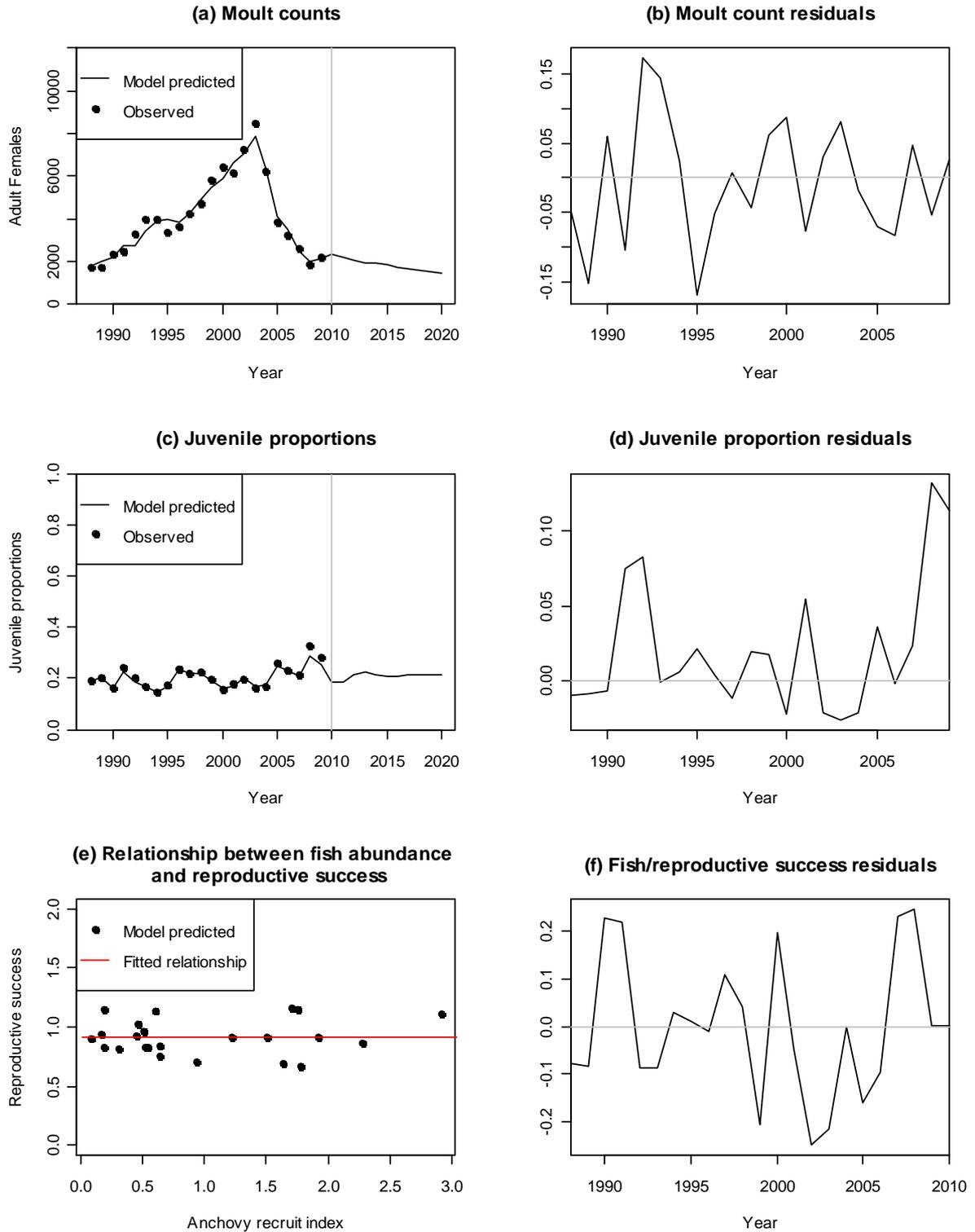
Figure 3: Fits to data/relationships and associated residuals at the joint posterior mode. Projections beyond 2010 assume $B_S = 0.2$. The residuals in (b) and (d) are the differences between the logarithms of the observations and the model predicted values which appear in equation (A21). The residuals in (f) are the differences between the estimated reproductive success rates and the assumed relationship (A16).
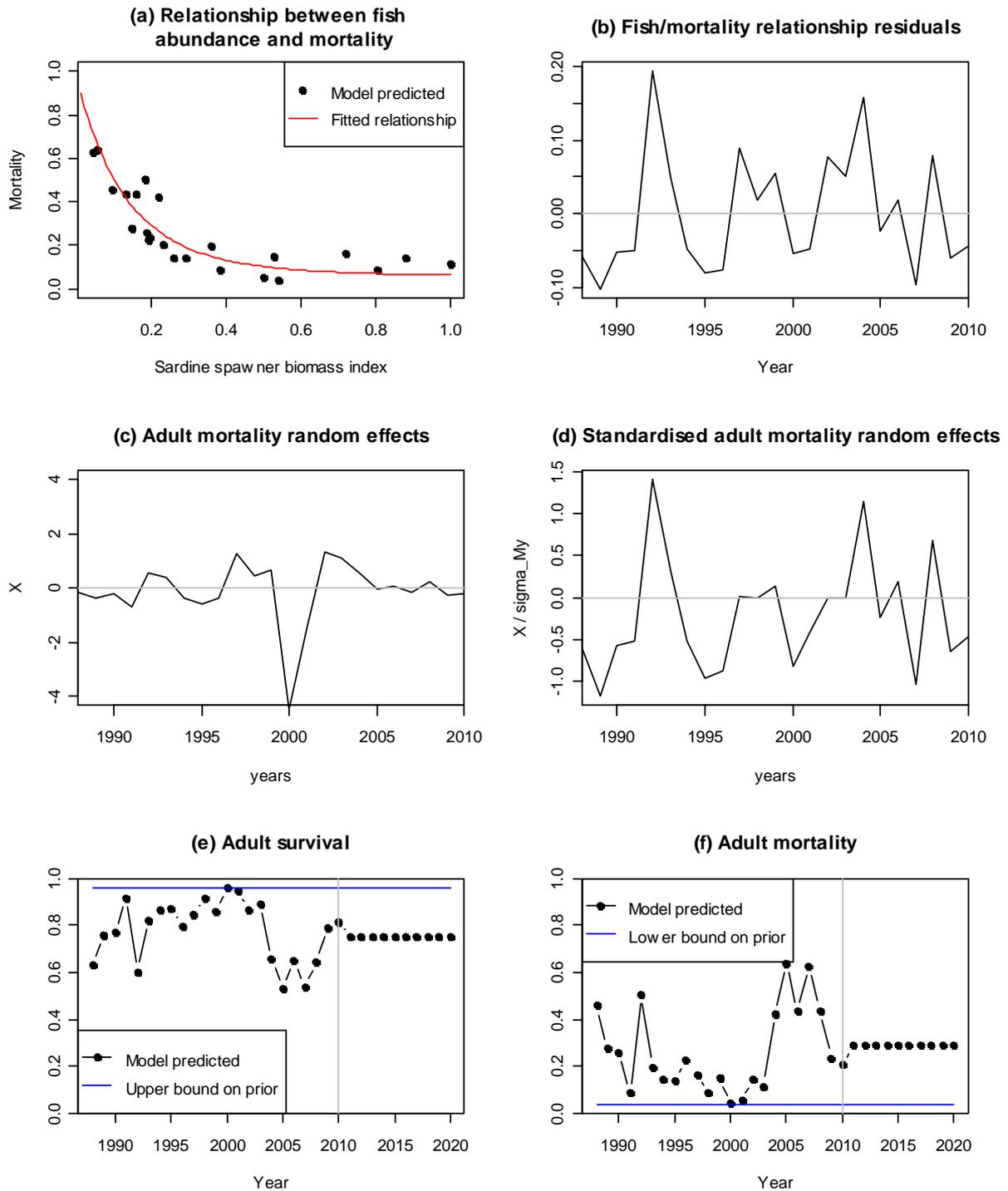
Figure 4: Further fits to data/relationships and associated residuals for the joint posterior mode. Projections beyond 2010 assume $B_S = 0.2$. The residuals in (b) are the differences between the estimated annual mortality rates and those predicted by the relationship with fish abundance (A8). The random effects in (c) are the X_y in (A7), 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.

Adult mortality/Fish abundance relationship
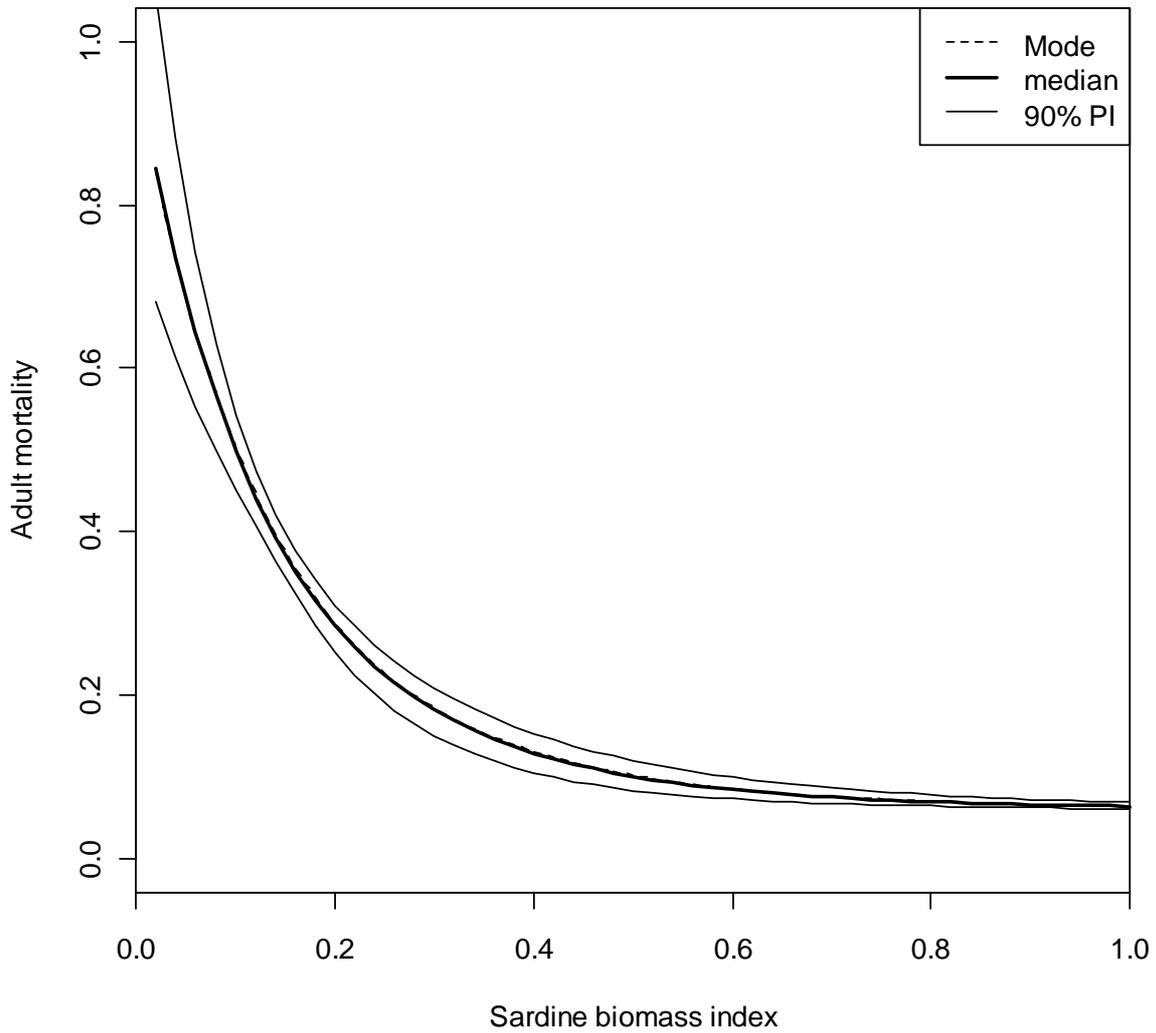
Figure 5: Estimated relationship between penguin adult mortality and the sardine spawner biomass west of Cape Agulhas showing the value at the joint posterior mode and the posterior median and 90% probability interval.
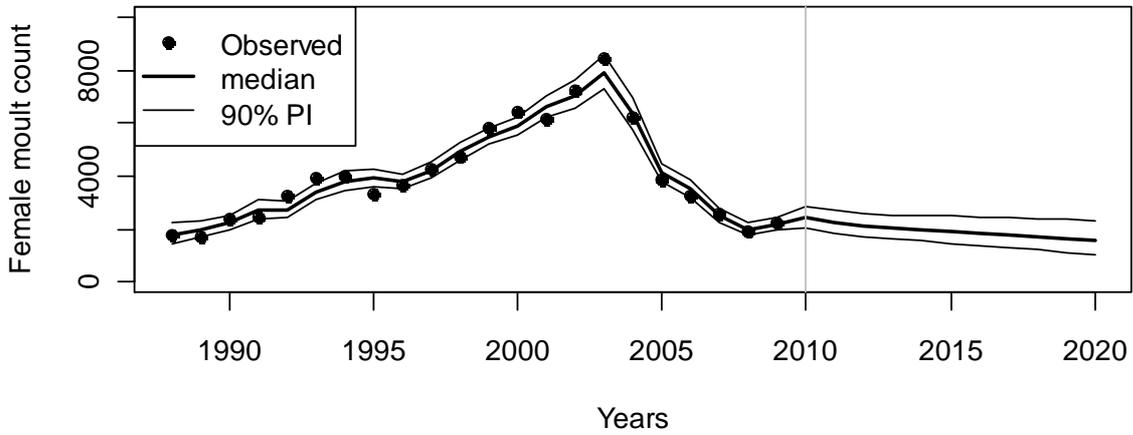
Figure 6: Time series of observed counts of female moulting penguins and the median and 90% probability interval of the Bayesian posterior distribution of the model predicted moult counts.
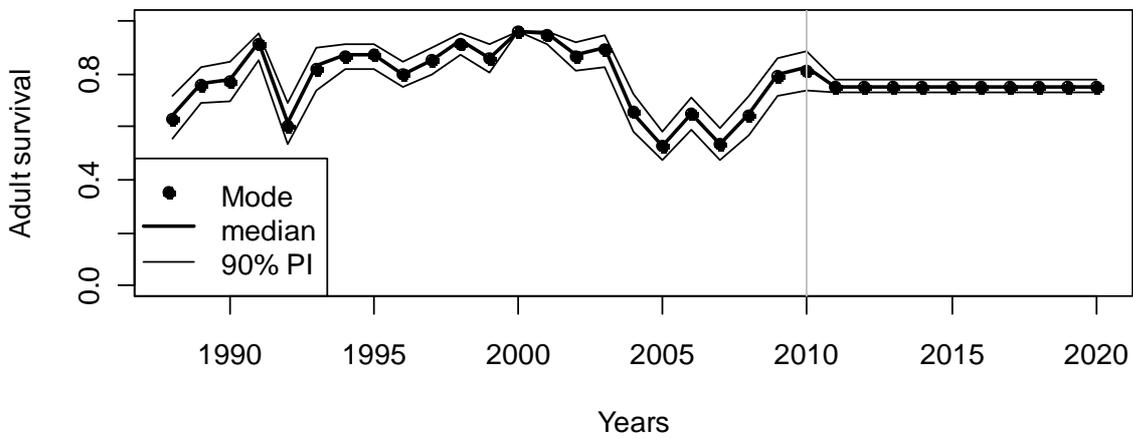
Figure 7: Time series of the adult annual survival rates at the joint posterior mode and the median and 90% probability interval of the Bayesian posterior distribution.

Posterior distributions
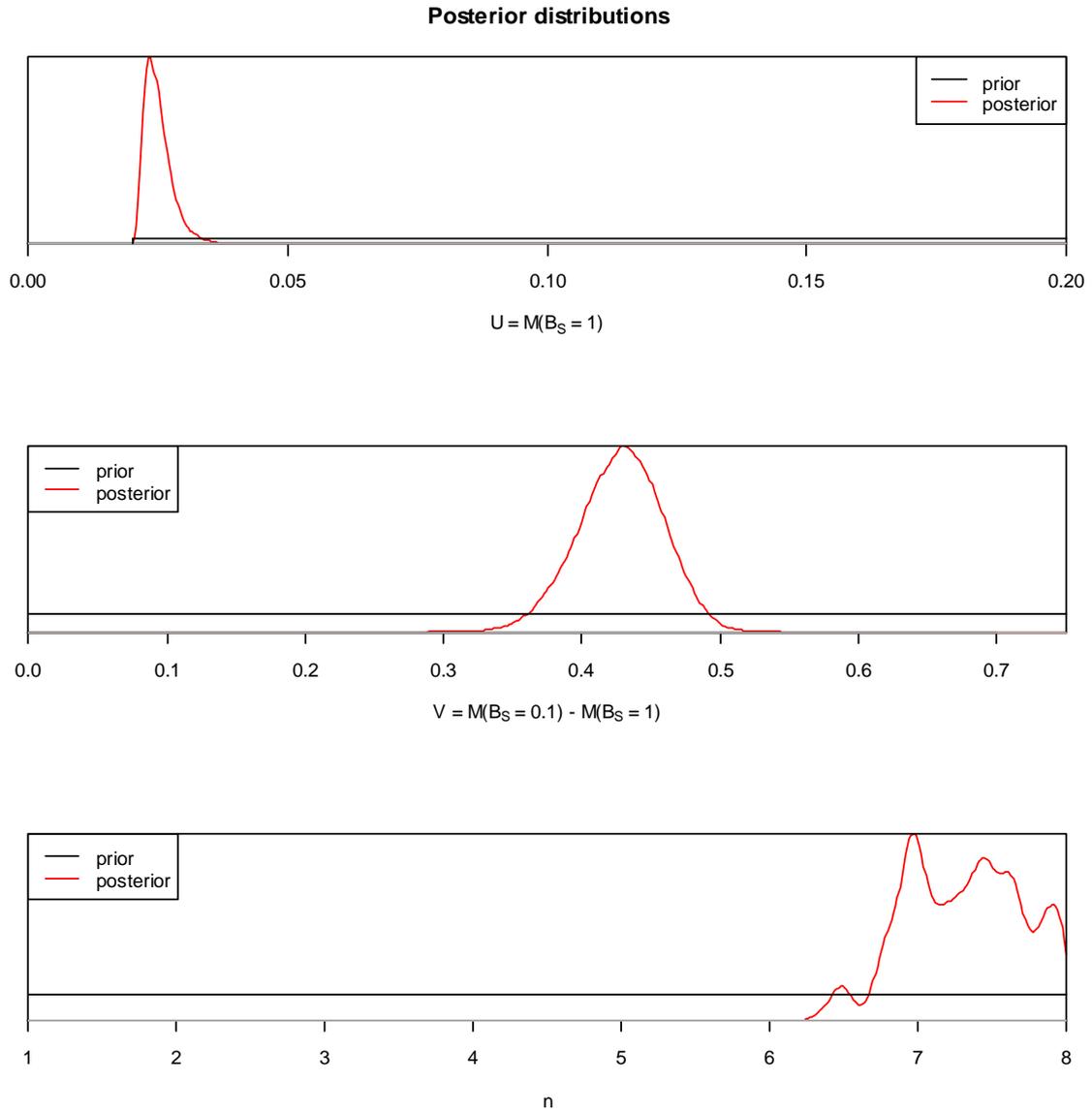
Figure 8: Prior and posterior distributions of the parameters in the mortality–biomass relationship.
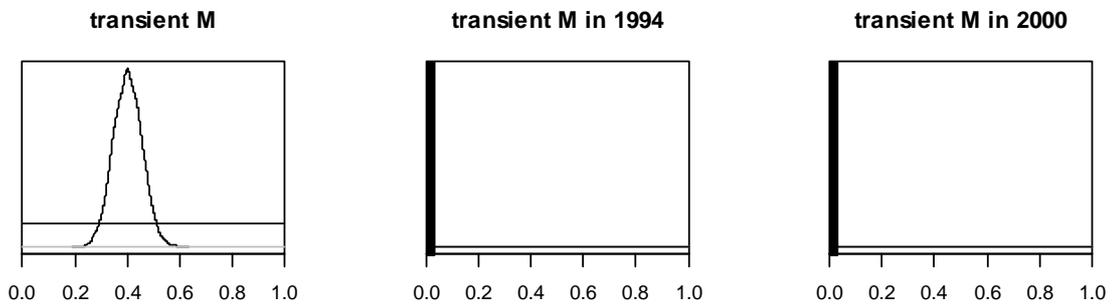
Figure 9: "Transient" mortality comparison of priors and posteriors. The "transient M" applies for all years except those with major oil spills (1994 and 2000) from which many penguins were tagged for which separate estimates are made. The solid black bars indicate the posterior to be entirely at M=0.

1989-1991 **1992-1994** **1995-1999**
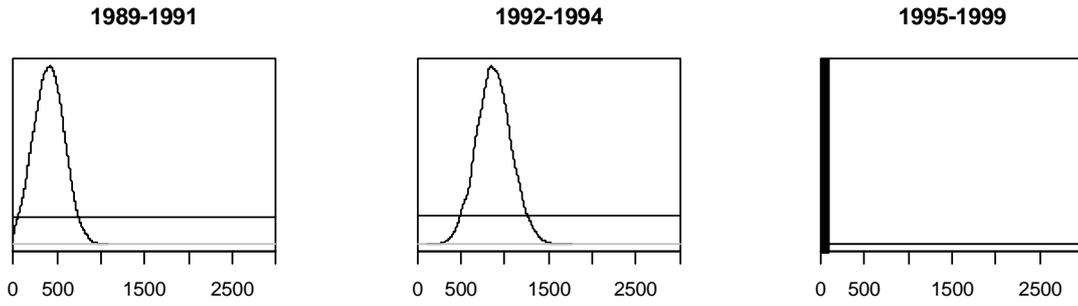
Figure 10: Immigration, taken to be constant over the periods shown: comparison of priors and posteriors.
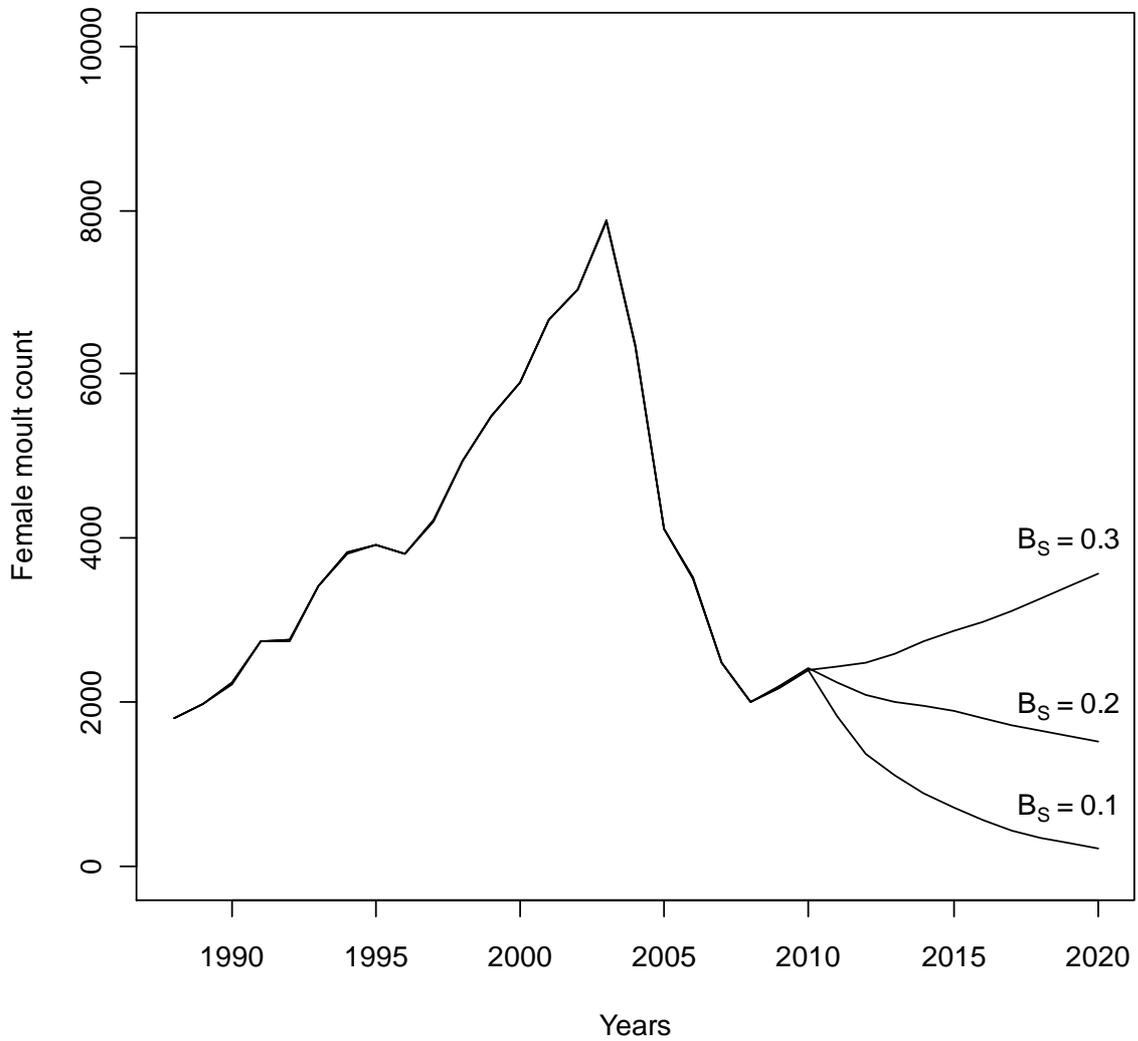
Figure 11: Projections of penguin moult counts from the joint posterior mode from 2009 for fixed future sardine spawner biomass levels west of Cape Agulhas for $B_S = 0.1$, $B_S = 0.2$ and $B_S = 0.3$.