Illustrative outputs of the age-structured model of African penguin populations for linking to the pelagic OMP testing process

William Robinson, Éva Plagányi and Doug Butterworth
Department of Mathematics and Applied Mathematics, UCT

INTRODUCTION

Given the move towards adopting an ecosystem approach to fisheries in the pelagic sector, the new joint OMP needs to be tested in the light of not only the risk parameters as considered previously, along with catch statistics, but also parameters denoting risk to the African penguin population(s) *Spheniscus demersus.* Penguins have been chosen as a key predator species to consider because of their conservation status, and because of their potential sensitivity to changes in pelagic fish abundance and distribution as a consequence of their land-based breeding sites. A model of penguin dynamics has been developed for use as a penguin Operating Model to be coupled to the pelagic fish OMP. This paper summarises the base-case penguin model and proposed method for use in evaluating the impact on penguins of predicted future pelagic fish trajectories under alternative harvest strategies (OMPs).

Coupling the pelagic OMP and penguin model

For a given management procedure, 1000 future plausible biomass and recruitment trajectories are produced for each of sardine and anchovy. Assuming functional relationships between these quantities and penguin parameters (see model description), the penguin model can be projected forwards under each of these 1000 scenarios, and the risk to penguins evaluated as described below.

Evaluating risk to which penguin populations?

Previous analyses showed that past trends in penguin abundance in the “western” area (Robben, Dassen, Boulders and Dyer Island) are best explained when taking movement of juvenile birds between these colonies into account. However, numbers at Boulders have now steadied and the numbers at Dyer Island are relatively small, so that these two colonies are ignored in projecting forwards. Given likely different functional relationships between penguins and their fish prey at Dassen and Robben Islands, aspects of these two penguin populations are modelled separately but within a common model framework when doing forward projections, and we assume no future movement between these two colonies.

MODEL

Where $N_{y,a,i}$ is the number of female penguins on 1 April in year *y* of age *a* at island *i*, the equations representing the population dynamics are as follows:

$$N_{y+1,a,i} = N_{y,i}^{breed} H_{max} S_{y,i}^{j} \qquad \text{for } a = 1 \tag{1}$$

$$N_{y+1,a,i} = N_{y,a-1,i} S_{y,i} \qquad \text{for } 2 \le a < m \tag{2}$$

$$N_{y+1,m,i} = \left(N_{y,m-1,i} + N_{y,m,i}\right) S_{y,i} \qquad \text{for } a = m \tag{3}$$

where the number of potential breeders each year is

$$N_{y,i}^{breed} = \sum_{a=4}^{m} N_{y,a,i} \tag{4}$$

and the reproductive success (which incorporates breeding success and survival until the end of the first year), which is density dependent, is

$$S_{y,i}^{j} = \bar{S}_{y,i}^{j} \left(1 - \frac{N_{y,i}^{breed}}{K_i}\right). \tag{5}$$

Other parameters and constants are defined as follows:

H_{max}	is the maximum observed fledging success;
$S_{y,i}$	is the annual adult survival rate at island *i*;
$\bar{S}_{y,i}^{j}$	is the annual reproductive success at island *i* before density dependent effects;
m	is the plus group age, set at 4 years; and
K_i	is a carrying capacity-related factor used for calculating density dependent reproductive success.

Assuming that the populations are in equilibrium in the starting year, the initial age structure is calculated from the estimated initial number of breeders, $N_{0,i}^{breed}$.

The number of juvenile and adult moulters on 1 December (the height of the moult season) each year is given by

$$N_{y,i}^{juveniles} = N_{y,1,i} \left(S_{y,i}^{j}\right)^{8/12} \tag{6}$$

$$N_{y,i}^{adults} = \sum_{a=2}^{m} N_{y,a,i} \left(S_{y,i} \right)^{8/12} \quad (7)$$

The proportion of juveniles in the total moult count is

$$P_{y,i}^{juv} = N_{y,i}^{juveniles} / \left(N_{y,i}^{juveniles} + N_{y,i}^{adults} \right) \quad (8)$$

Annual variation in adult survival and reproductive success

We allow both adult survival and reproductive success to depend on the pelagic fish abundance each year as follows:

$$S_{y,i} = S_{max} \frac{\exp\left(\alpha_i B_y + \beta_i + \eta_{y,i}\right)}{1+\exp\left(\alpha_i B_y + \beta_i + \eta_{y,i}\right)} \qquad \eta_{y,i} \sim N\left(0,\sigma_\eta^2\right) \quad (9)$$

$$\overline{S}_{y,i}^{j} = \frac{\exp\left(a_i B_y + b_i + \mu_{y,i}\right)}{1+\exp\left(a_i B_y + b_i + \mu_{y,i}\right)} \qquad \mu_{y,i} \sim N\left(0,\sigma_\mu^2\right) \quad (10)$$

The constants α_i, β_i, a_i and b_i as well as the random effects $\eta_{y,i}$ and $\mu_{y,i}$ are estimated parameters. B_y is the pelagic abundance index in year *y*. The maximum allowed realistic adult survival S_{max} is set at 0.96.

Fitting procedure

The model is fitted to adult moult counts $\hat{N}_{y,i}^{ad\_moult}$, the proportion of juveniles observed in the moult count $\hat{P}_{y,i}^{juv}$, as well as counts of the numbers of breeders $\hat{N}_{y,i}^{breed}$ (see accompanying document MARAM IWS/DEC08/P/2). We multiply the model values by the proportionality constants q_i^B for breeders and q_i^M for moulters. The breeder proportionality constant is input to the model for both Robben and Dassen Island, as is the moulter proportionality constant for Robben Island. For Dassen Island, q_{DAS}^M is estimated within the model with

$$\ln q_{DAS}^{M} = \frac{1}{n_{M,\mathrm{DAS}}} \sum_{y} \left(\ln N_{y,DAS}^{adults} - \ln \hat{N}_{y,DAS}^{adults} \right), \quad (11)$$

where $n_{M,\mathrm{DAS}}$ is the number of years that there were moult counts at Dassen. Contributions to the negative log-likelihood are as follows:

$$-\ln L_i^{breed} = \sum_y \left[\ln \sigma_B + \left(\ln\left(N_{y,i}^{breed} q_i^B \right) - \ln \hat{N}_{y,i}^{breed} \right)^2 \Big/ 2\sigma_B^2 \right] \quad (12)$$

$$-\ln L_i^{adults} = \sum_y \left[\ln \sigma_M + \left(\ln\left(N_{y,i}^{adults} q_i^M \right) - \ln \hat{N}_{y,i}^{adults} \right)^2 \Big/ 2\sigma_M^2 \right] \quad (13)$$

$$-\ln L_i^{juv\_prop} = \sum_y \left[\ln \sigma_P + \left(\ln P_{y,i}^{juv} - \ln \hat{P}_{y,i}^{juv} \right)^2 \Big/ 2\sigma_P^2 \right] \tag{14}$$

where the sums are over the years in which counts were made.

Penalty terms are added to the negative log-likelihood for the estimated residuals as follows:

$$-\ln L_\eta = \frac{1}{2} \sum_i \sum_y \left(\eta_{y,i} / \sigma_\eta \right)^2 \tag{15}$$

$$-\ln L_\mu = \frac{1}{2} \sum_i \sum_y \left(\mu_{y,i} / \sigma_\mu \right)^2 \tag{16}$$

Additional mortality due to oiling

Two major oil spills affected marine birds on the West Coast in 1994 and 2000. This is incorporated in the model by including an extra mortality term in these two years, resulting in the loss of 2500 birds in 1994 and 1000 birds in 2000. The proportion assumed to be from Robben Island is 40% in each case. Also, an additional 20% of birds in their first year are assumed to die in these two years.

Projections

For future years, the standard deviations of the estimated random effects $\eta_{y,i}$ and $\mu_{y,i}$ are set as the standard deviations of future random effects, $\sigma_{\eta,i}$ and $\sigma_{\mu,i}$.

We are provided with 1000 plausible fish abundance scenarios for the years 2007 to 2027 generated by the sardine and anchovy assessment model, B_S and B_A. For each scenario *s*, we calculate the proportion likely to be found in stratum B,

$$B_{s,y} = \left(B_A p_A + B_S p_S \right) / B_{\max} \tag{17}$$

where p_A and p_B are drawn randomly from a sample of observed proportions, and $B_{\max}$ is the maximum observed combined biomass.

Since our model is stochastic, multiple replications (typically 25) are done for each scenario, and each time the median penguin numbers are calculated and recorded. We thus obtain a distribution of 1000 future penguin population trajectories.

RESULTS

Table 3 gives the estimated parameters and constants for the "base case" model, as well as the likelihood values. The "base-case" model fits to the available data for Robben and Dassen islands are shown in Fig. 5 (moult count data), Fig. 6 (breeder counts) and Fig. 7 (proportion of moulters which are juvenile). Fig. 8 shows the model-estimated reproductive success factor and adult survival estimates.

In Fig. 9-Fig. 12 we present a set of "base case" projections for our model. For this set of results, the sample of observed proportions is from the years 2002-2006 when pelagic abundance was extremely low. In Fig. 9 (Robben Island) and Fig. 10 (Dassen Island) we show fits to the data as well as 20 year projections of penguin abundances. The distributions of results for 1000 simulations show that the median penguin abundances for the pelagic series with catch are slightly lower than those for the pelagic series without catch (Fig. 11), with a larger effect at Robben Island. The stratum B pelagic abundance index is shown in Fig. 12.

An alternative sample of pelagic proportions observed in stratum B which has been considered is for the years 1988-2001. These results are shown in Fig. 13 (penguin abundance projections) and Fig. 14 (2028 abundance distributions) for pelagic series both with and without catch. The alternative pelagic abundance index with probability intervals is shown in Fig. 15. It is clear that the effect of the change in the distribution of pelagic fish is much greater than possible effects due to fishing compared to no fishing. Further detailed model results are presented in the Appendix.

DISCUSSION

Risk can be quantified as the probability of penguin abundance (either in terms of the numbers of breeding pairs or total population size (approximated most closely by the number of moulters)) dropping below some threshold abundance under different OMP variants. However, relative depletion cannot simply be based on historic estimates of carrying capacity because of the possibility that penguin numbers at the turn of the 19^{th} century may have been artificially high due to a competitive release effect as a result of the heavily reduced seal numbers at the time following intensive harvesting. Moreover, Crawford *et al*. (2007) propose a change in carrying capacity from a very high level in the 1920s to a much lower value over the period 1978-2006.

Thus, consistent with the approach adopted during the development of the pelagic OMP, we recommend assessing risk by comparing distributions of penguin abundance under different fish harvesting strategies to those under comparable no-fishing trials (Butterworth 2008).

An accompanying document to be presented outlines and presents results for a wide range of sensitivity analyses. In particular, the model has been shown to be highly sensitive to the assumption made regarding the 2007 pelagic biomass (given the model only has pelagic fish biomass estimates up until 2006 compared to penguin count data being available up until 2008), and further results will be shown for a model case which fixes the 2007 pelagic biomass estimate at the median of the values projected using the pelagic OMP.

LITERATURE CITED

Butterworth, D.S. 2008. Some lessons from implementing Management procedures. In: Fisheries for Global Welfare and Environment, 5th World Fisheries Congress, Eds Tsukamoto, K., Kawamura, T., Takeuchi, T., Beard, T.D., and M.J. Kaiser. pp. 381-397.

Crawford, R.J.M., Underhill, L.G., Upfold, L. and B.M. Dyer. 2007. An altered carrying capacity of the Benguela upwelling ecosystem for African penguins (*Spheniscus demersus*).

ACKNOWLEDGEMENTS

We are grateful for data from Rob Crawford and Les Underhill, as well as inputs from both them and the rest of the penguin task group, as well as the invited externals at the July 2007 NRF/SA Pelagic and Rock Lobster Industries International Stock Assessment Workshop. Mark Maunder's model was useful in moving the process forward. Thanks to Janet Coetzee and Carryn de Moor for providing pelagic fish abundance survey and assessment model results. Funding provided by EP's National Research Foundation grant.

APPENDIX

Additional information on model parameters and fitted relationships is provided in Tables A.1 and A.2, and Figs. A.1 – A.4. The Tables show the Hessian-based standard deviations associated with selected model parameters, for the base case model which uses the (2002-2006) proportions, and the alternative which uses the (1988-2001) proportions. Fig. A.1. shows time series of deterministic reproductive success and adult survival, together with the 95% probability interval, for Robben and Dassen Islands when using the model with values drawn from the 2002-2006 sample of biomass proportions used in 2007 replications. Fig. A.2 shows the deterministic reproductive success and adult survival, together with confidence intervals, for Robben Island and Dassen Island when using the "base case" model. Figs A.3 and A.4 show equivalent plots with values drawn from the 1988-2001 sample of biomass proportions used in 2007 replications.

	value	std dev
a (Robben reproduction)	-0.822	0.421
a (Dassen reproduction)	-0.764	0.532
α (Robben adult survival)	0.830	0.791
α (Dassen adult survival)	1.217	0.510
b (Robben reproduction)	1.298	0.927
b (Dassen reproduction)	1.554	1.573
β (Robben adult survival)	33.997	28.594
β (Dassen adult survival)	1.391	2.206
σ_{out} (Robben reproduction)	0.318	0.142
σ_{out} (Dassen reproduction)	0.609	0.155
σ_{out} (Robben adult survival)	0.523	0.161
σ_{out} (Dassen adult survival)	0.747	0.164

Table A.1: Model parameters shown with Hessian-based standard deviations for the base case model which uses the (2002-2006) proportions.

	value	std dev
a (Robben reproduction)	-0.769	0.430
a (Dassen reproduction)	-0.747	0.531
α (Robben adult survival)	1.977	0.634
α (Dassen adult survival)	1.353	0.522
b (Robben reproduction)	1.493	0.970
b (Dassen reproduction)	1.493	1.579
β (Robben adult survival)	3.618	3.659
β (Dassen adult survival)	0.464	1.954
σ_{out} (Robben reproduction)	0.390	0.156
σ_{out} (Dassen reproduction)	0.619	0.152
σ_{out} (Robben adult survival)	0.920	0.137
σ_{out} (Dassen adult survival)	0.802	0.143

Table A.2: Model parameters with Hessian-based standard deviations for the alternative model which uses the (1988-2001) proportions.

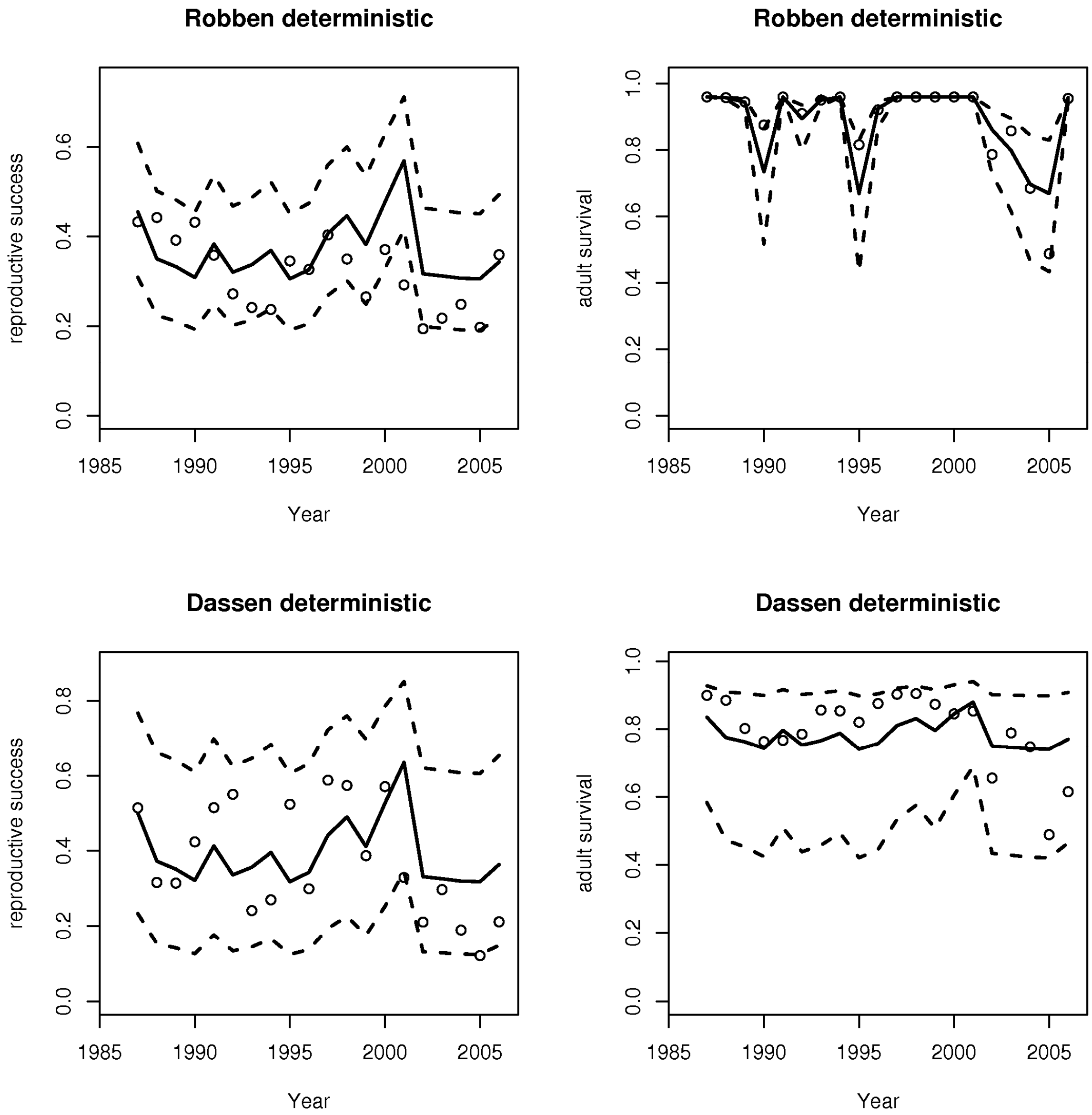


Fig. A.1: Time series of deterministic reproductive success (left) and adult survival (right) for Robben Island (top) and Dassen Island (bottom) for the model with values drawn from the 2002-2006 sample of biomass proportions used in 2007 replications. Dashed lines indicate the 95% probability interval. Circles indicate model-estimated values.

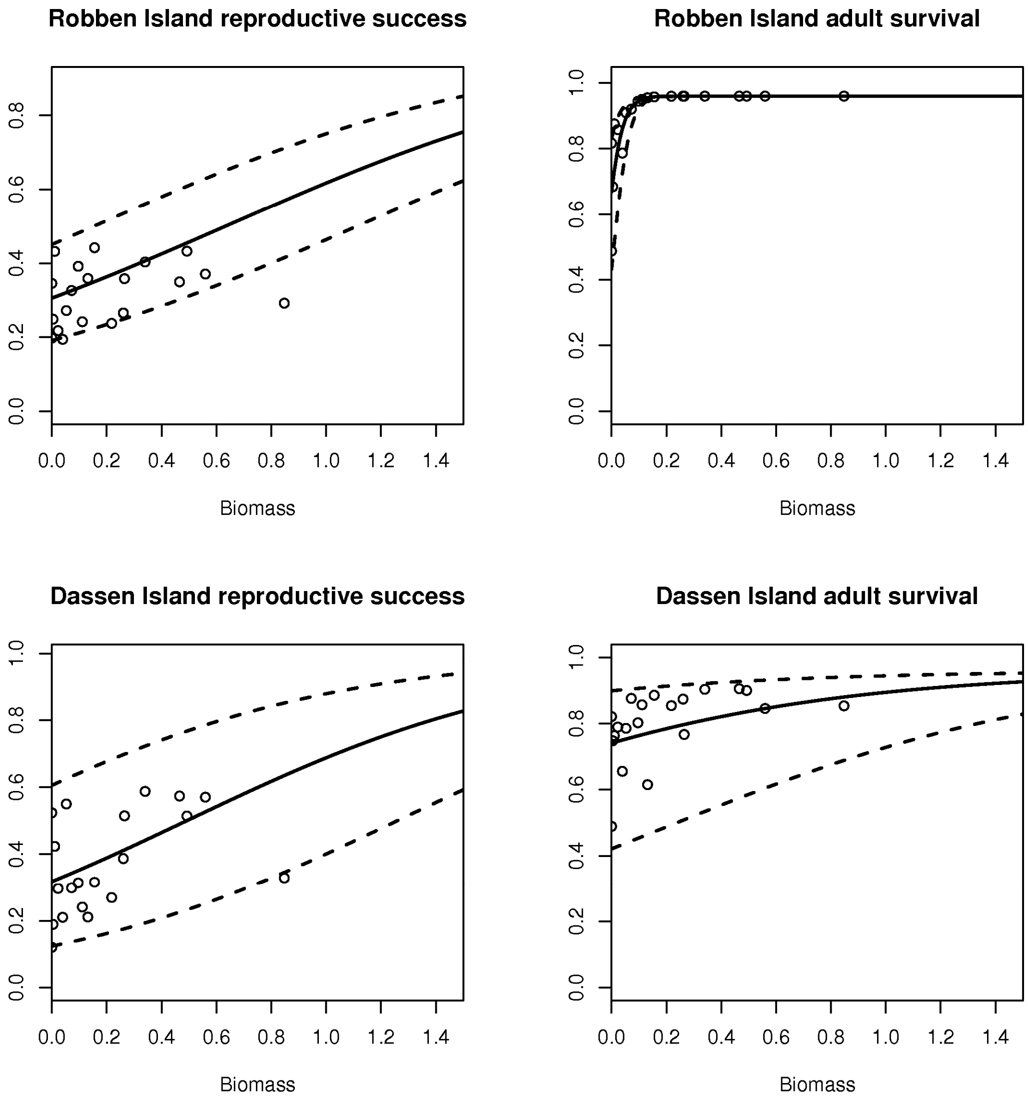


Fig. A.2: Deterministic reproductive success (left) and adult survival (right) with confidence intervals for Robben Island (top) and Dassen Island (bottom) for the “base case” model. Circles indicate model-estimated survival values.

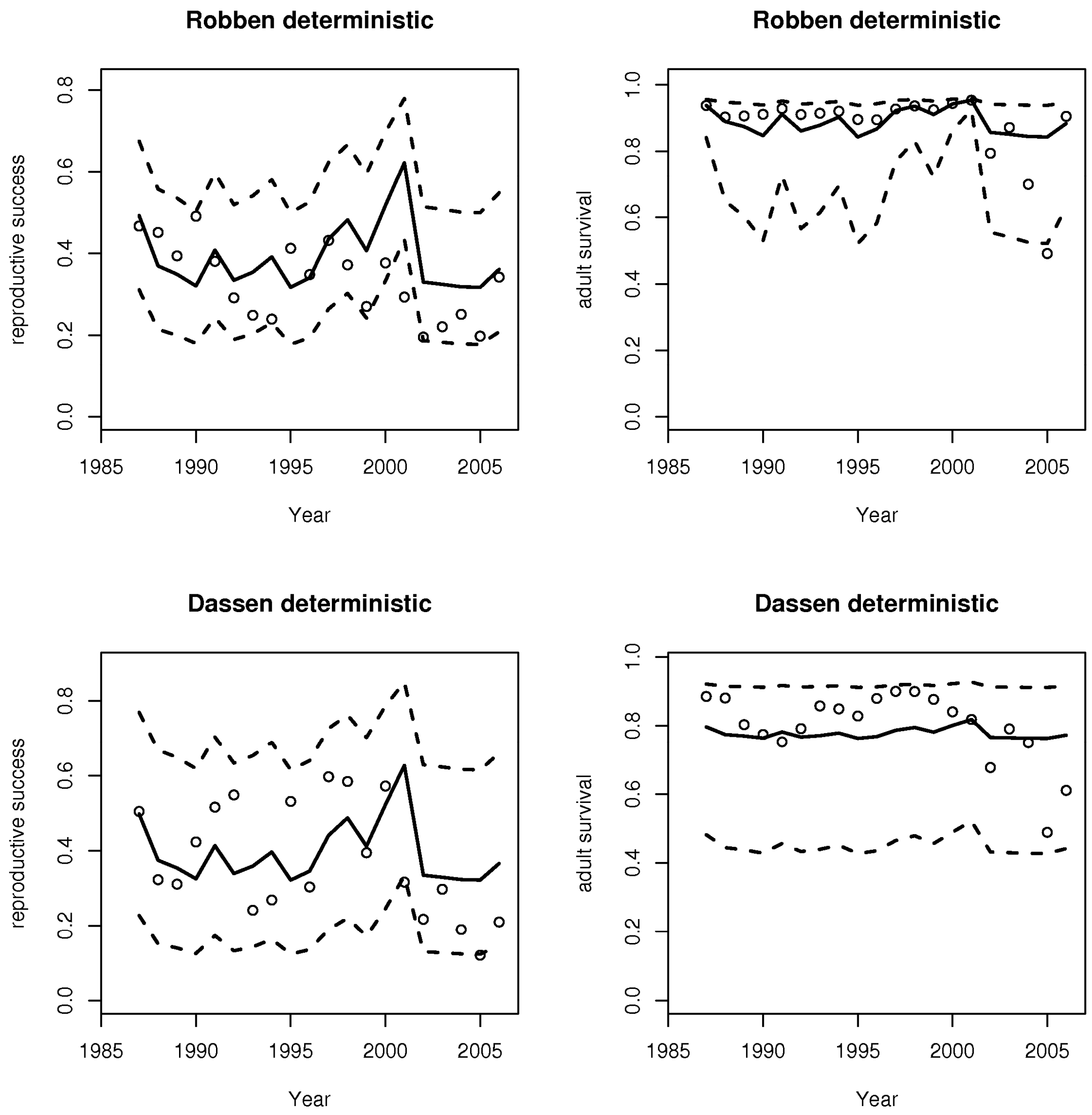


Fig. A.3: Time series of deterministic reproductive success (left) and adult survival (right) for Robben Island (top) and Dassen Island (bottom) for the model with values drawn from the 1988-2001 sample of biomass proportions used in 2007 replications. Dashed lines indicate the 95% probability interval. Circles indicate model-estimated values.

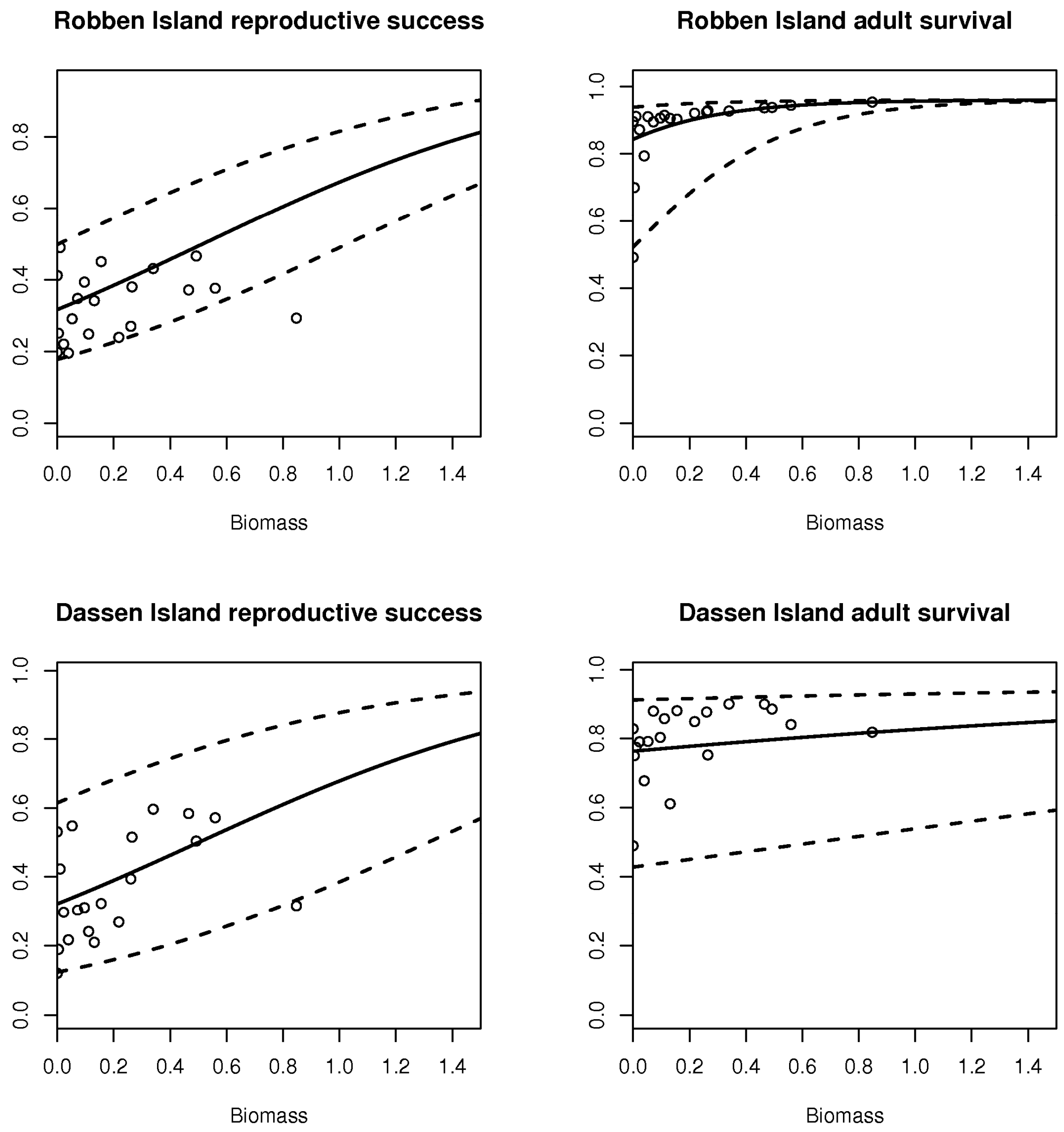
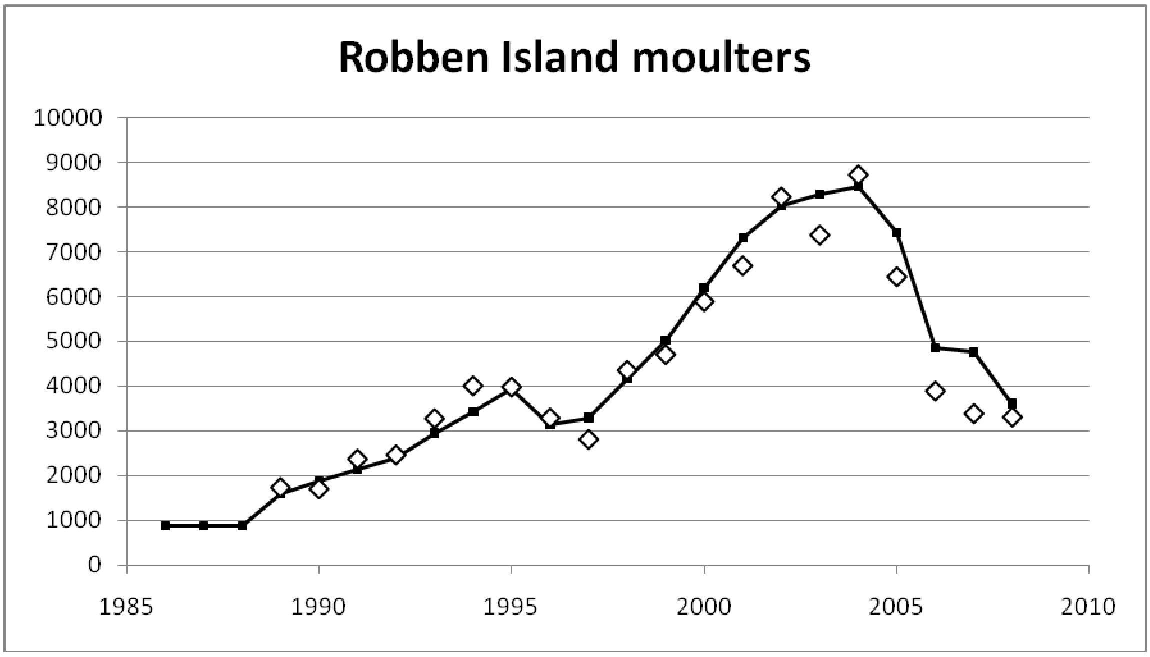


Fig. A.4: Deterministic reproductive success (left) and adult survival (right) with confidence intervals for Robben Island (top) and Dassen Island (bottom) for the model with the 1988-2001 sample of biomass proportions. Circles indicate model-estimated survival values.

Table 3: Model parameters, constants and likelihoods shown for the base-case model.

Model		
Biomass series		Sardine + Anchovy stratum B
Proportions sample		2002-2006
Parameter estimates		
Initial number of breeders	$N_{0,4+}$ (ROB)	42.0
Initial number of breeders	$N_{0,4+}$ (DAS)	7513.1
Reproductive index intercept	a (ROB)	-0.6437
Reproductive index slope	b (ROB)	1.0214
Survival intercept	α (ROB)	0.8706
Survival slope	β (ROB)	29.1677
Reproductive index intercept	a (DAS)	-0.7755
Reproductive index slope	b (DAS)	1.4562
Survival intercept	α (DAS)	1.3970
Survival slope	β (DAS)	0.5837
No. of parameters estimated		98
Proportionality constant	q_M (DAS)	0.351
s.d. of random effects	σ_{out} (Robben reproduction)	0.3047
s.d. of random effects	σ_{out} (Dassen reproduction)	0.5754
s.d. of random effects	σ_{out} (Robben adult survival)	0.5043
s.d. of random effects	σ_{out} (Dassen adult survival)	0.7804
Fixed		
Plus-group age	M	4
Proportionality constant	q_B	0.95
Proportionality constant	q_M (ROB)	0.9
Carrying capacity factor	K (ROB)	19360
Carrying capacity factor	K (DAS)	186400
Maximum reproductive success	H_{max}	1.3717
	σ (data)	0.2
	σ_{in} (random effects)	1.5
Likelihood contributions		
	-*ln*L ROB moulters	-28.214
	-*ln*L DAS moulters	-12.649
	-*ln*L ROB breeders	-28.439
	-*ln*L DAS breeders	-25.402
	-*ln*L ROB juvenile proportion	-31.683
	-*ln*L DAS juvenile proportion	-21.568
	μ (ROB) penalty	0.454
	μ (DAS) penalty	1.618
	η (ROB) penalty	1.244
	η (DAS) penalty	2.977
	***-ln*L TOTAL**	-141.662



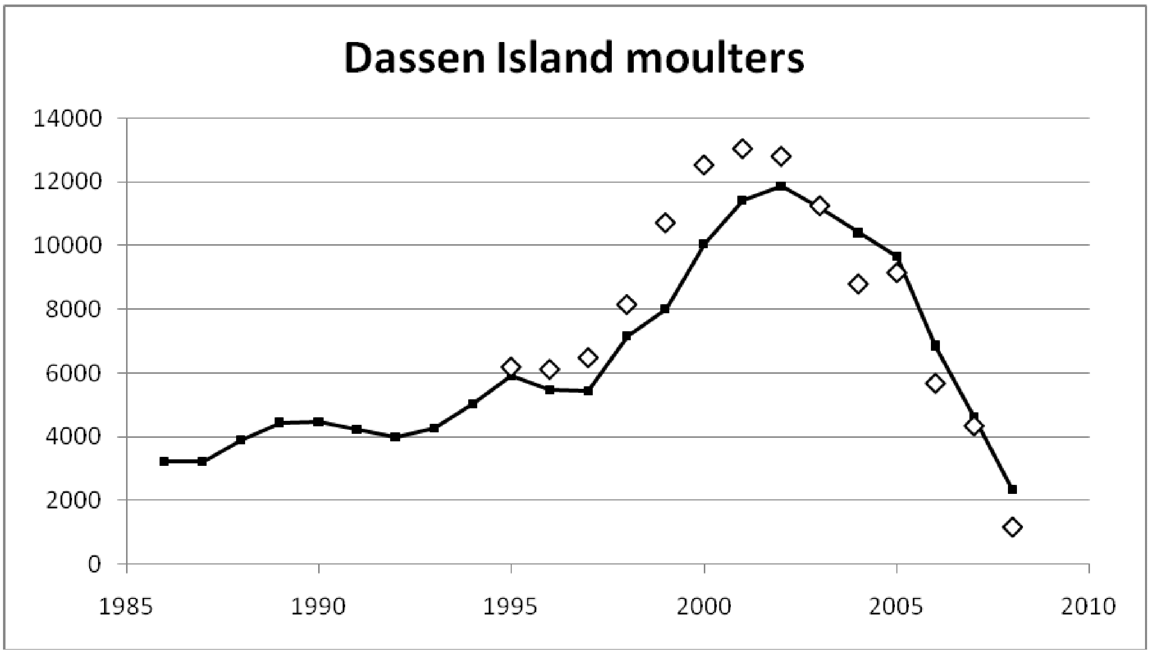
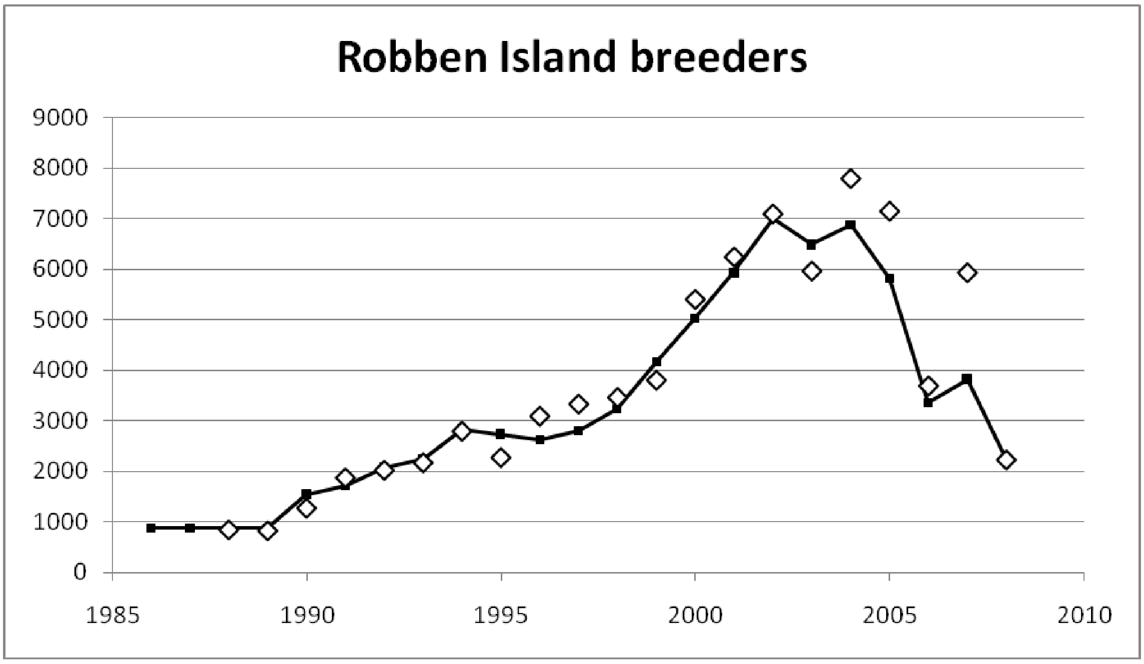


Fig. 5: Base-case model-predicted trajectories of the numbers of female moulting penguins at Robben Island (top panel) and Dassen Island (lower panel). Observed data are shown as diamond points not joined by a line.



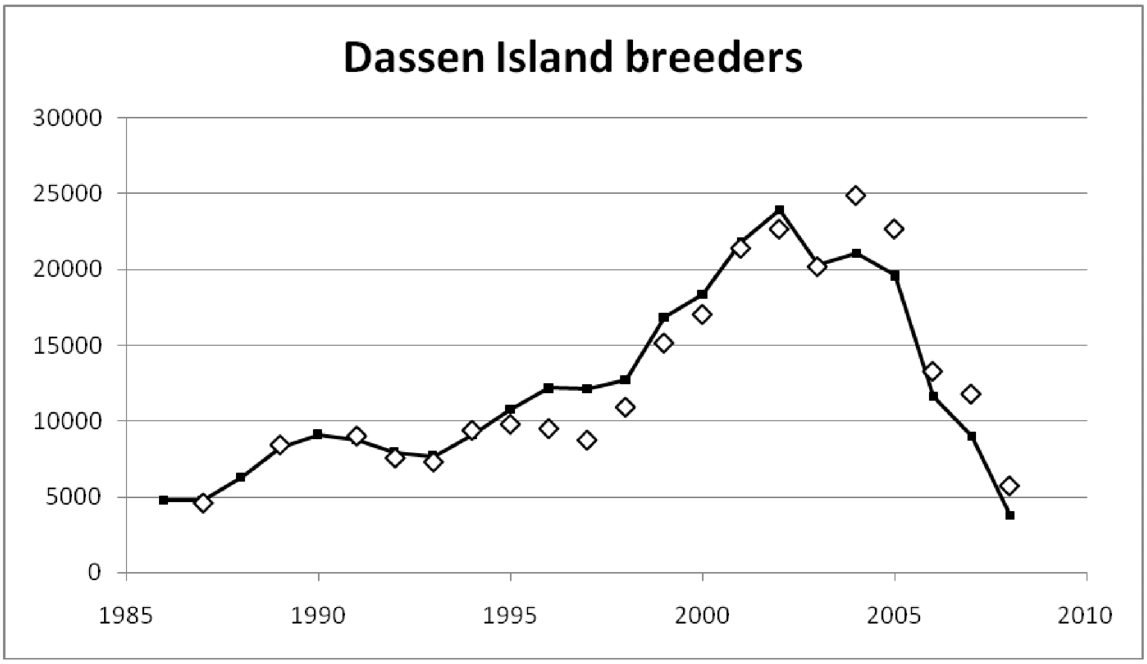
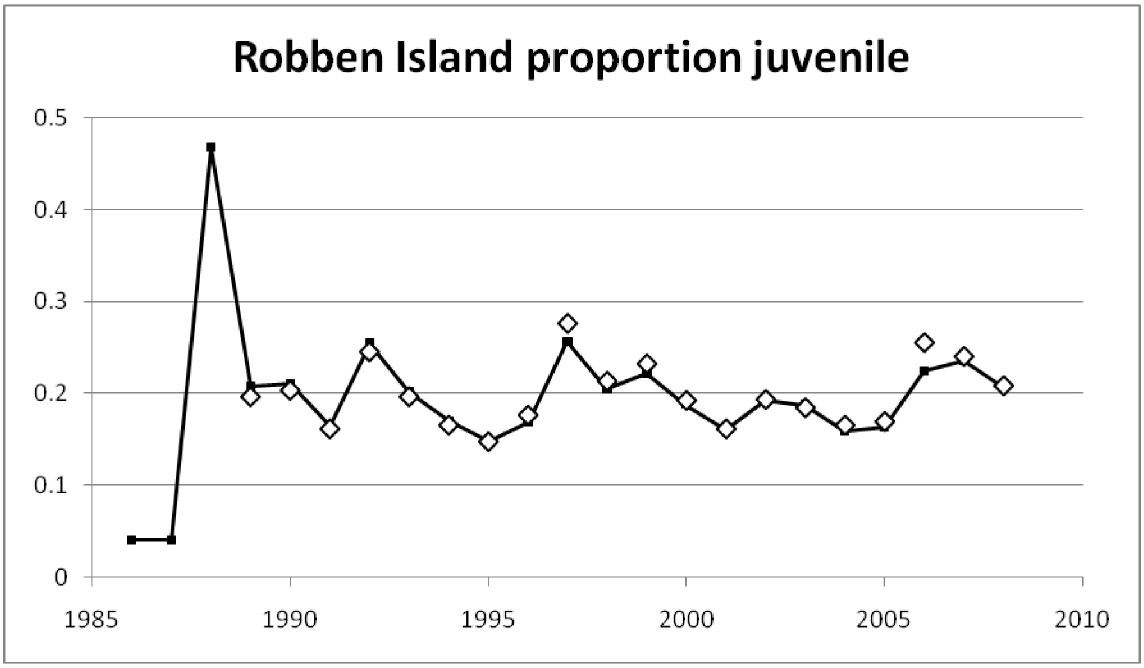


Fig. 6: Base-case model-predicted trajectories of the numbers of breeding pairs at Robben and Dassen Islands. Observed data are shown as diamond points not joined by a line.



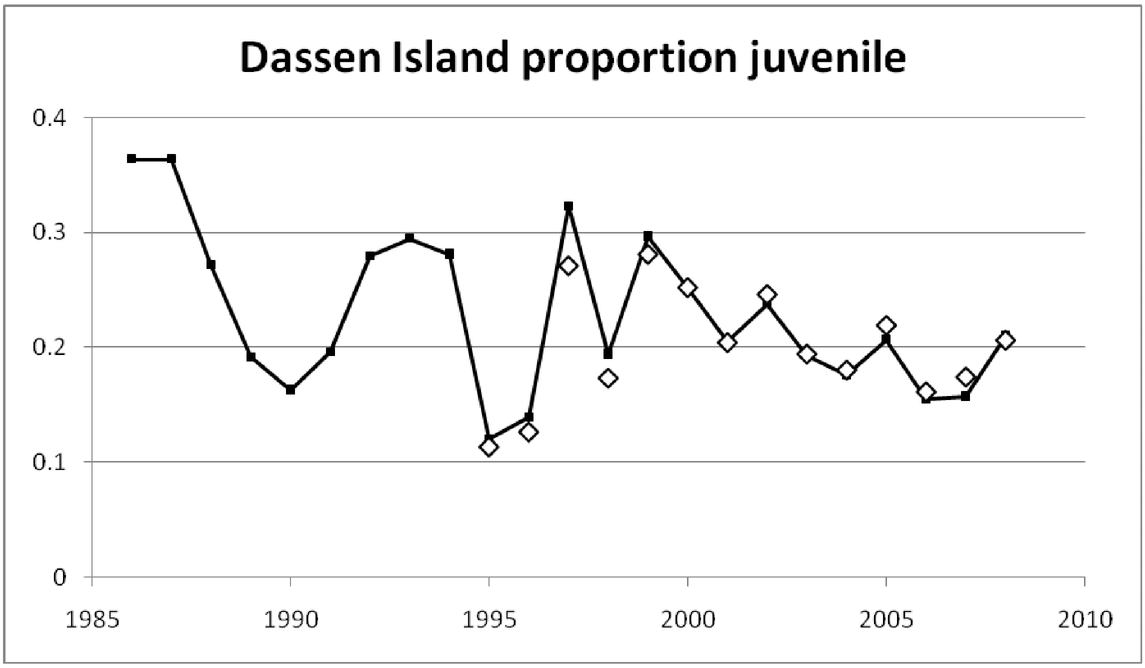
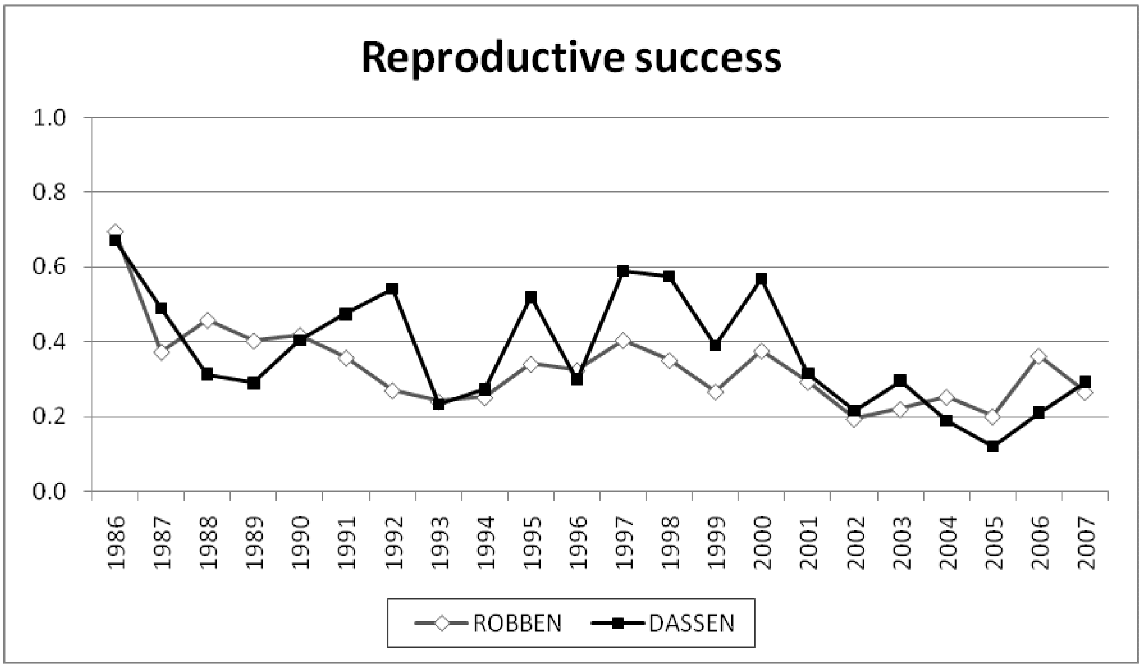


Fig. 7: Base-case model-predicted trajectories of the proportion of juvenile birds at Robben and Dassen Islands. Observed data are shown as diamond points not joined by a line.



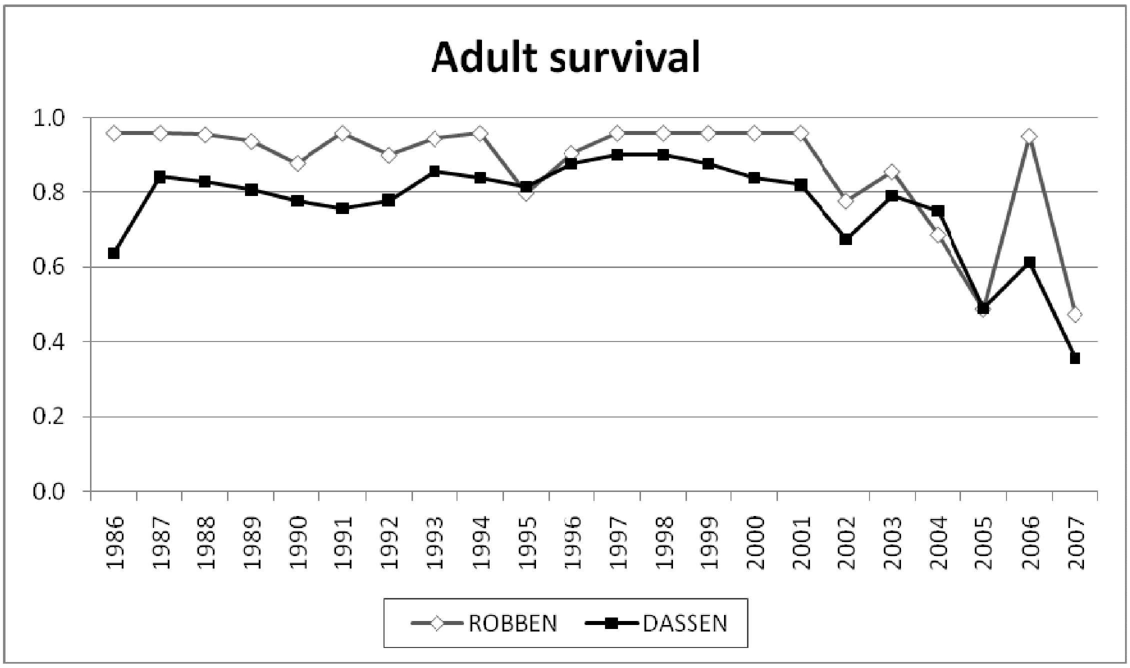


Fig. 8: Base-case model-predicted estimates of a) relative reproductive success (which encompasses breeding effort, fledging success and survival to the end of the first year) and b) the adult survival rate for Robben (diamond symbols) and Dassen (square symbols) Islands.

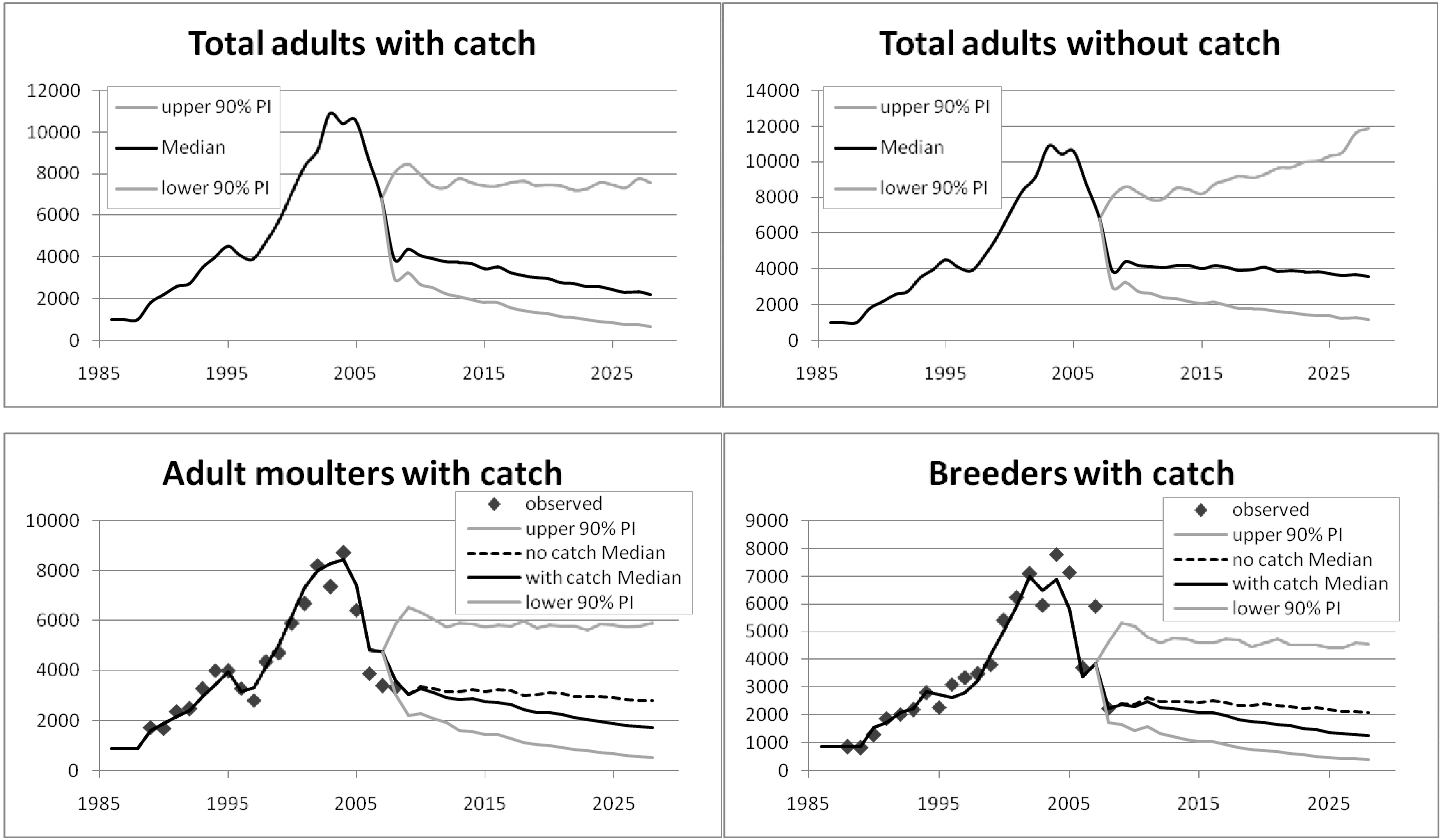


Fig. 9: Robben Island total numbers of adult penguins for pelagic biomass series with and without catch, and fits to moulter and breeder data, with 20 year projections.

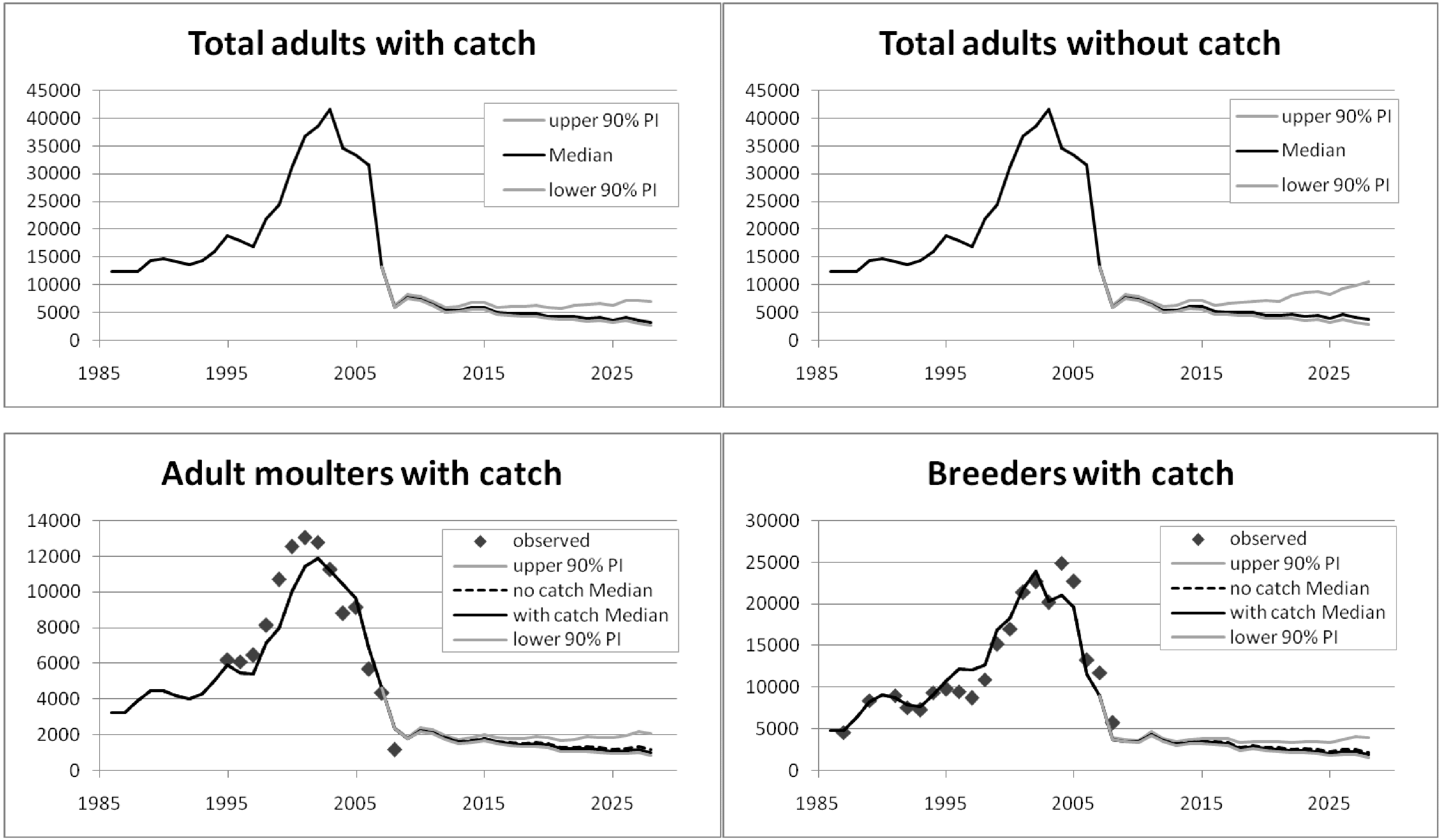


Fig. 10: Dassen Island total numbers of adult penguins for pelagic biomass series with and without catch, and fits to moulter and breeder data, with 20 year projections.

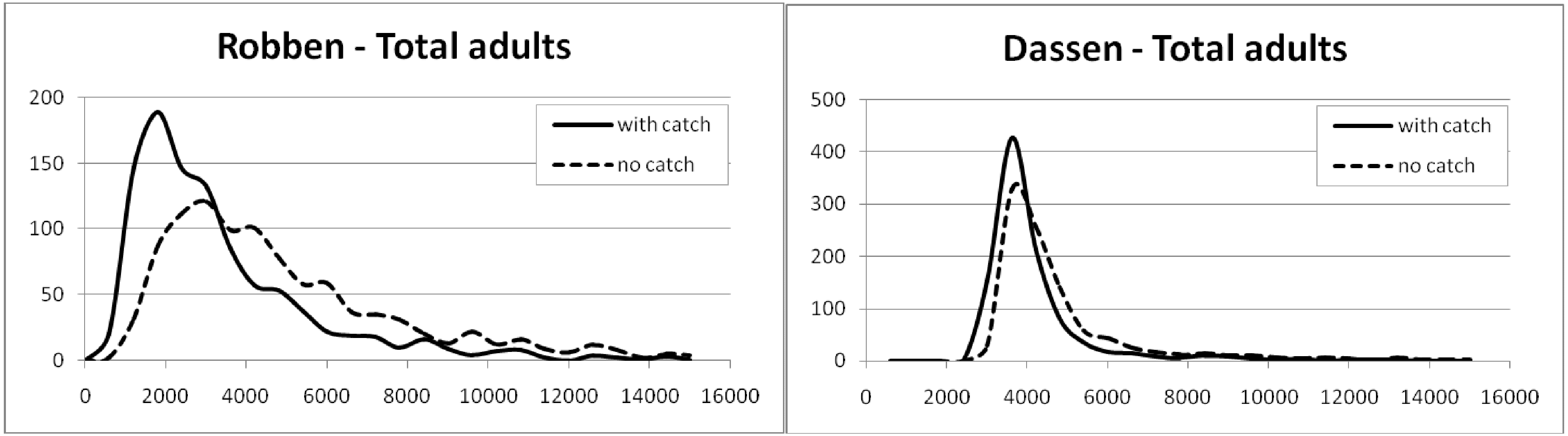


Fig. 11: Distributions of results for penguin abundance in 2028 for 1000 fish abundance scenarios with and without catch.

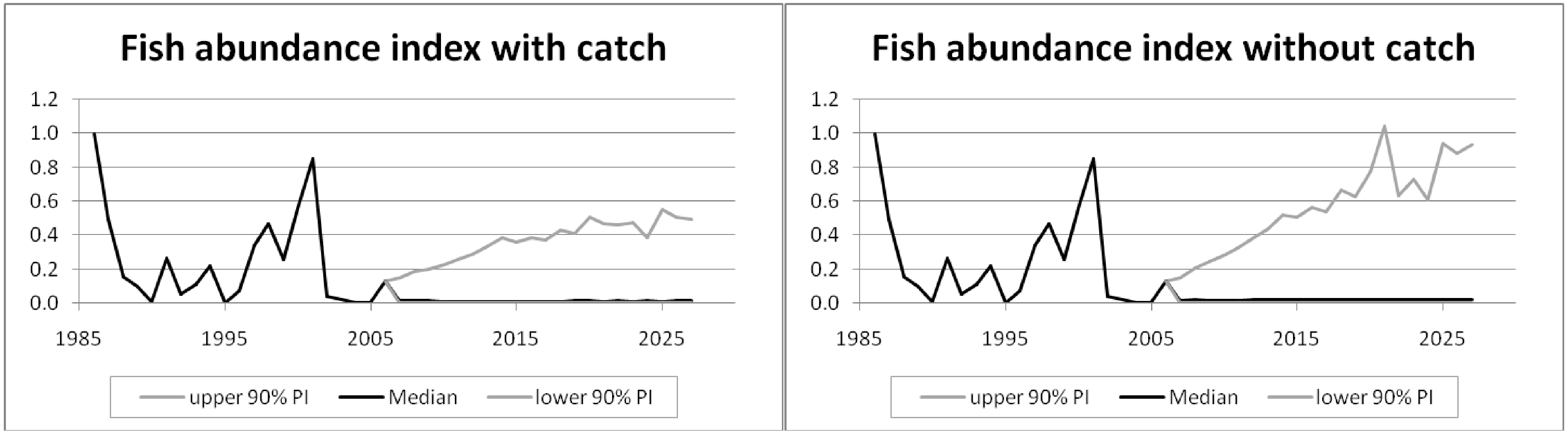


Fig. 12: Median fish abundances with probability intervals. Future stratum B proportions are drawn randomly from the set of 2002-2006 observations.

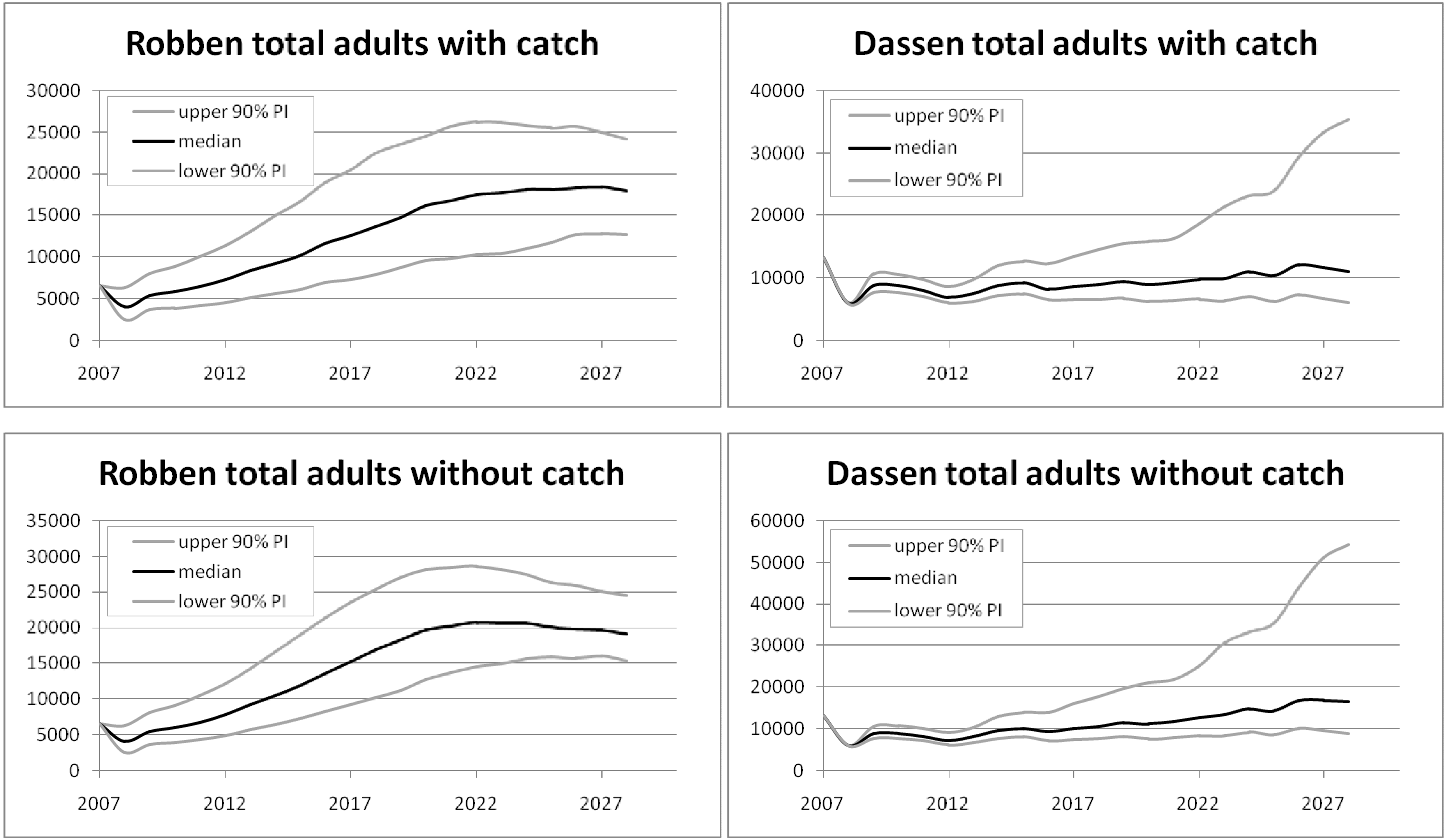
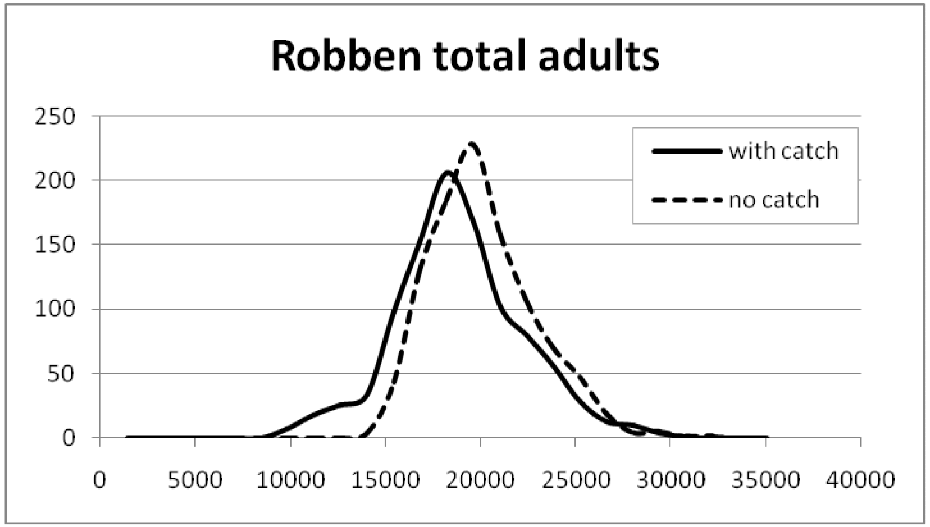


Fig. 13: Penguin abundance projections with the 1988-2001 sample of pelagic stratum B proportions.



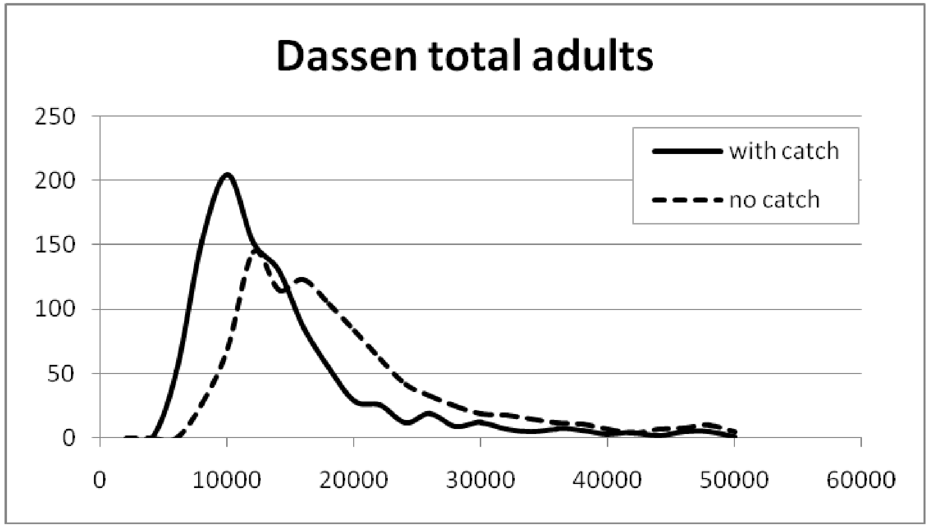
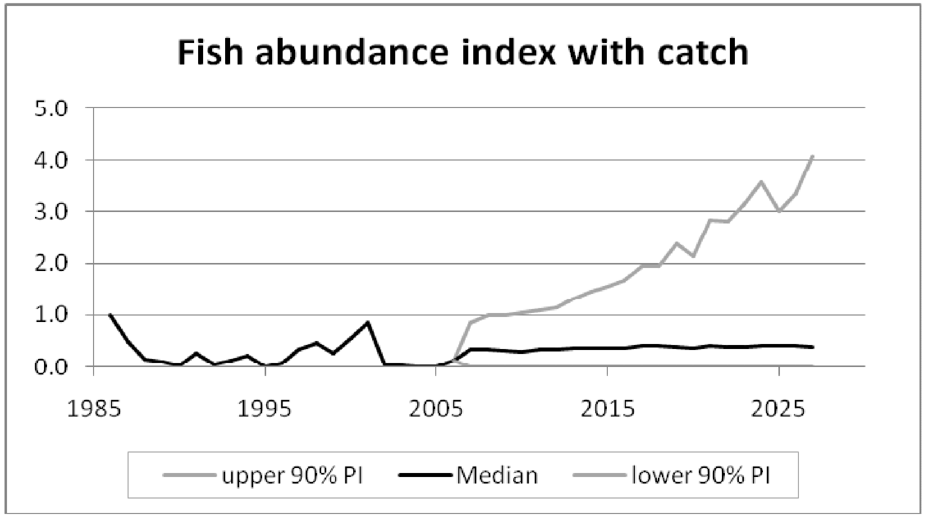


Fig. 14: Distributions of adult penguin abundances in 2028 with and without catch for the 1988-2001 sample of stratum B proportions.



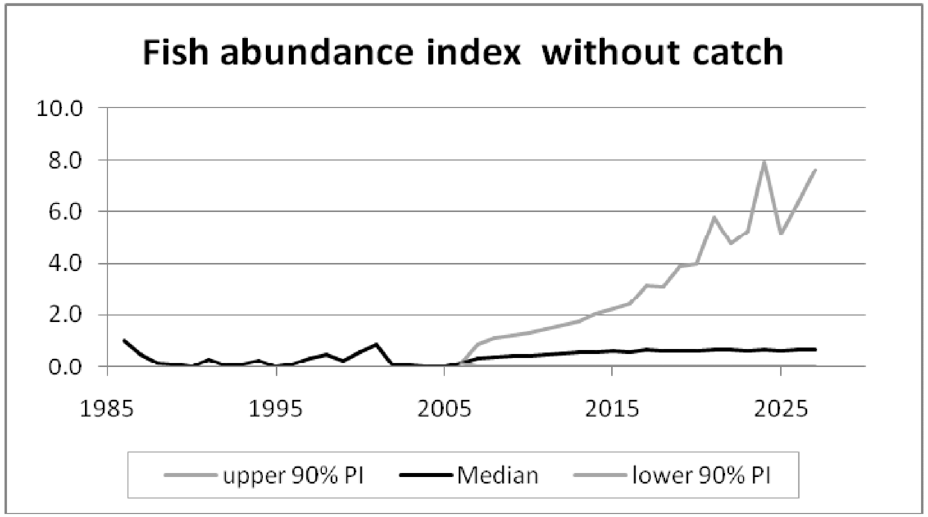


Fig. 15: Median and 90% probability intervals for the pelagic abundance index calculated with the 1988-2001 sample of stratum B proportions.