

Spatial Age-Structured Model of African Penguin colonies at Robben, Dassen and Dyer Islands, and at Boulders

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SUMMARY

A revised form of an earlier model is presented in which Dassen and Robben Islands are split and modelled separately for reasons as outlined in the accompanying document MCM/2007/MAY/SWG-PEL/06a. The latter document summarises all data inputs as used in the model. Some of the equations are given below and a single illustrative example presented to give the Working Group a general idea of the revised model version.

Given the time spent on finalizing data issues and recoding the new version of the model, there has been insufficient time to prepare a comprehensive document. Rather this document should be seen as preliminary only and for the purpose of discussing the model, with a more comprehensive document to be tabled at the next meeting. It must also be appreciated that the single illustrative example presented is by no means considered satisfactory at this stage as there are several aspects in need of further work.

INTRODUCTION

A number of questions have recently been raised regarding the status and management of the African penguin *Spheniscus demersus*. The PWG penguin task team agreed that it would be useful to develop a dynamic model to assist in understanding the population dynamics as well as in an attempt to reconcile the various data sources. This document describes the development of such a model. Although still preliminary, the model is of a form that can readily be linked to the pelagic OMP (Operational Management Procedure) testing process to take account of the relationship between the breeding success (and perhaps also natural mortality) of African penguins and the abundance of both anchovy *Engraulis encrasicolus* and/or sardine *Sardinops sagax* (e.g. Crawford *et al.* 2006).

The aims of the current model under development are as follows:

- 1) to provide a dynamic, rather than static, representation of penguin dynamics;
- 2) to fit to available data to provide estimates of important demographic parameters such as survival rates, which can then be compared to other available estimates;
- 3) to attempt to reconcile some apparent contradictory trends in the different data series;
- 4) by gradually increasing the complexity of the model to represent different plausible hypotheses, to assist in identifying the most parsimonious hypothesis to explain the observed trends in the population;
- 5) to quantify and provide additional substantiation for the relationship between penguin breeding success (in terms of the three variables: mean chicks fledged per year; proportion of mature birds that breed each year and proportion of birds maturing at each age) and pelagic fish abundance; and
- 6) to dynamically project the penguin population assuming various future scenarios to assist in providing advice regarding the management of the penguin population (and possibly pelagic fish populations as well).

It is important to note that the model as presented here is still in the early stage of development and hence results presented are preliminary only. The model is based on the best available data and knowledge of the population, and the task group will contribute to this process by further scrutinizing the actual data, the interpretation made of these data and other model assumptions.

The model is spatial in that several different populations of penguins are represented, and different levels of movement between these populations can be modelled. The main focus of the model is on Dassen and Robben Islands, which are here modelled separately (but with some parameter estimates assumed common to both). The third population is Dyer Island because it has the next largest numbers of penguins, recent declines in the population there are of concern and it is considered an important breeding site for penguins given the eastward shift of sardines. The fourth population is Boulders. Although relatively small, this colony was considered important to include because of its position, its role as the focus of several other studies and because penguins are known to have moved from Dyer island to Boulders, Robben and Dassen, and hence it is useful to quantify to what extent movement of birds away from Dyer island could account for observed declines at Dyer and increases at these other colonies.

The model also includes an Algoa Bay colony but the example presented here assumes no movement from Algoa Bay to the other colonies and hence this component is not linked in the example shown and hence will not be discussed further here.

Model Dimensions

The PWG agreed that for the purposes of coupling penguin and pelagic fish models, the south-western area should be disaggregated into the following areas:

- i) Cape Columbine to Cape Agulhas
- ii) Cape Agulhas to Algoa Bay
- iii) Algoa Bay to Port Alfred

Hence there will be two sets of penguin colonies modelled, corresponding to i) and iii) as there are virtually no penguins in area ii) and so no need for an associated model. The sardine and anchovy models would consist of all THREE areas, with model-predicted biomass in i) and iii) being used only when trying to find a functional relationship with the penguin results. The model described here is primarily for area i), with four sub-areas 1) Robben Island; 2) Dassen Island; 3) Boulders and 4) Dyer island.

A summary of all the data inputs are provided in the accompanying document SWG/EAF/SEABIRDS/26APR07/01. The model time step is one year and hence average trends are modelled. Penguins in each sub-area are modelled starting from 1987. Penguin populations are projected 5 years to 2012 under various scenarios.

The model is coded in AD Model Builder which permits rapid and efficient minimization.

POPULATION MODEL

An Age-Structured Dynamic Model

The basic dynamic model used to represent the population dynamics of the female penguins when assuming no movement between sub-areas is as follows:

$$N_{y+1,a+1}^s = N_y^{breed,s} q_f \cdot \omega_1 \cdot (S_y^{j,s})^{3/4} \quad a=0 \quad (1)$$

$$N_{y+1,a+1}^s = N_{y,a}^s \cdot (S_y^{j,s})^{1/4} S_y^{3/4} \quad a=1 \quad (2)$$

$$N_{y+1,a+1}^s = N_{y,a}^s \cdot S_y \quad 2 \leq a < 4 \quad (3)$$

$$N_{y+1,m}^s = (N_{y,m}^s + N_{y,m-1}^s) \cdot S_y \quad m=5 \quad (4)$$

with

$$N_y^s = \sum_{a=0}^m N_{y,a}^s \quad (5)$$

$$N_y^{breed,s} = \omega_2 \cdot \sum_{a=2}^m v_{y,a} \cdot N_{y,a}^s \quad (6)$$

$$S_y^{j,s} = S_j^* \left(1 - \frac{\sum_{a=2}^m N_{y,a}^s}{K_s^*} \right) \quad (7)$$

$$\omega_1 = f_1(B_y) \cdot H_{\max} \quad (8)$$

$$\omega_2 = f_2(B_{y-1}) \cdot 1 \quad (9)$$

where:

$N_{y,a}^s$	is the number of female penguins of age a on the 1 April in sub-area s and year y ;
$N_y^{breed,s}$	is the number of breeding penguins in area s and year y ;
q_f	is the fraction of chicks that are female;
S_y	is the post-first-year survival rate in year y ;
$S_y^{j,s}$	is the annual post-fledging survival rate of juvenile penguins in year y and sub-area s ;
m	is the largest age considered (the “plus group”, set at 5 years);
$v_{y,a}$	is the proportion of female penguins of age a that mature and commence breeding in year y , determined as a function of a component of pelagic fish abundance B in year $y-1$;
$f_1(B_y)$	is a breeding success factor (multiplier for H_{max}) to compute the average fledging success, and which is a function of a component of pelagic fish abundance B in year y ;
H_{max}	is the maximum observed breeding success (chicks fledged per female per yr);
$f_2(B_{y-1})$	is a factor determining the proportion that breed in year y (with the maximum possible breeding proportion set at 1) which is a function of a component of pelagic fish abundance B in year $y-1$; and
K_s^*	is a carrying capacity-related term for adult penguins in sub-area s , used to introduce density dependence into the penguin dynamics through the dependence of $S_y^{j,s}$ on the total abundance of all penguins aged 2 and older.

Breeders and Moulters

Equation (6) above provides a model value for the numbers of breeding females in each of the sub-areas. The numbers of female juvenile and adult moulters present on the 1 December each year y are given respectively by:

$$N_{y,Juv_moult}^s = N_{y,1}^s \cdot (S_y^{j,s})^{1/4} S_y^{5/12} \quad (10)$$

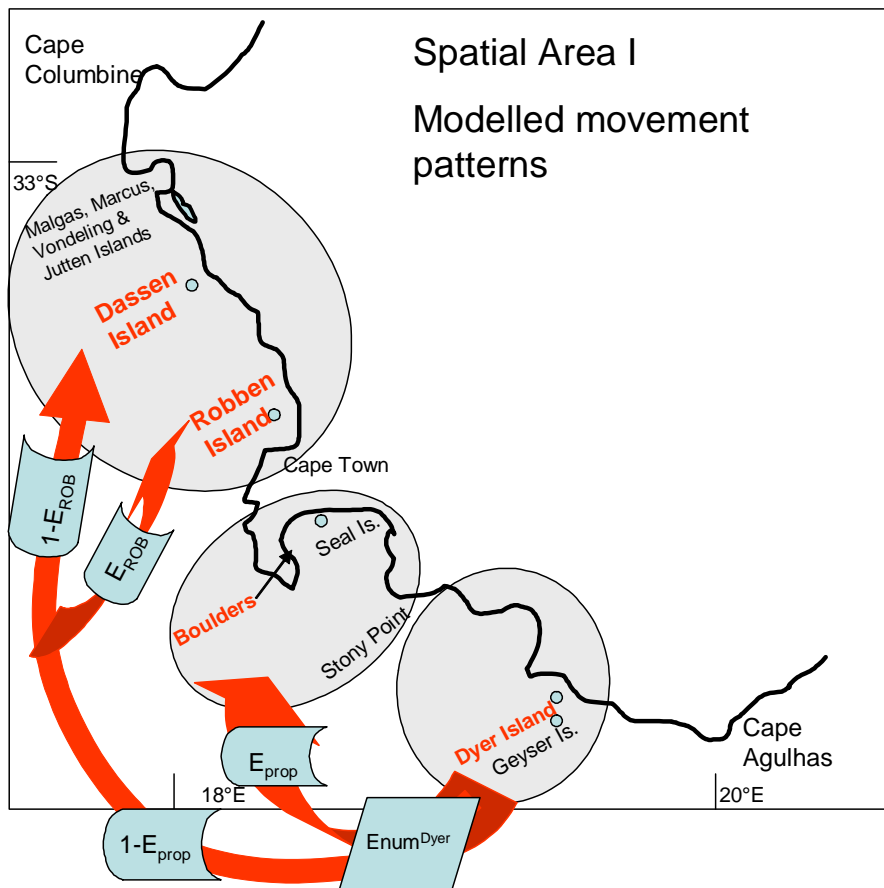
$$N_{y,Ad_moult}^s = \sum_{a=2}^m N_{y,a}^s \cdot S_y^{2/3} \quad (11)$$

and hence the juvenile moulters as a proportion of total moulters is computed as:

$$p_{y,Juv:Tot} = N_{y,Juv_moult}^s / (N_{y,Juv_moult}^s + N_{y,Ad_moult}^s) \quad (12)$$

Adding Immigration and emigration effects

The model allows emigration from Dyer Island to Boulders and to Robben and Dassen Islands. The initial movement model is a simple one and could be improved in future. Basically it assumes that a proportion (estimated within the model) of first-time breeders from Dyer move west. Of these birds moving west, a second proportion (again estimated within the model) are assumed to immigrate to Boulders. The trend in numbers at Boulders can be explained only by immigration and the model estimates the proportion of the westward emigrants that are needed to match the observed trends at Boulders. The remainder of the westward emigrants move to Robben and Dassen Islands, with the relative proportion moving to each island again estimated within the model.



Mathematically, for Dyer Island, Equation (3) for the case $a=2$ is thus modified as follows:

$$N_{y+1,a+1}^s = N_{y,a}^s \cdot S_y \cdot (1 - E_y) \quad (13)$$

where E_y is the proportion of first-time breeders (assumed to be between the ages of 2 and 3 years) that emigrate from Dyer Island. The emigration proportion is estimated (as a constant year-independent value in initial model simulations) within the model by fitting to breeding pairs data for Boulders. The actual number of birds emigrating each year $Enum_y^{Dyer}$ is thus:

$$Enum_y^{Dyer} = E_y \cdot S_y \cdot N_{y,2}^s \quad (14)$$

The proportion of the first time breeders that immigrate to Boulders (Bld) rather than to Robben and Dassen islands is determined by parameter E_{prop} , estimated within the model. Similarly, the proportion of these (i.e. the balance that move to Robben or Dassen) is determined by the parameter E_{ROB} , also estimated within the model. It follows that Equation (3) (for the case $a=2$) must be modified as follows for the Robben, Dassen and Boulders colonies respectively:

$$N_{y+1,3}^{Rob} = N_{y,2}^{Rob} S_y + (1 - E_{prop}) \cdot (E_{ROB}) \cdot Enum_y^{Dyer} \quad (15)$$

$$N_{y+1,3}^{Das} = N_{y,2}^{Das} S_y + (1 - E_{prop}) \cdot (1 - E_{ROB}) Enum_y^{Dyer} \quad (16)$$

$$N_{y+1,3}^{Bld} = N_{y,2}^{Bld} S_y + E_{prop} \cdot Enum_y^{Dyer} \quad (17)$$

Taking account of major oil spills

The Apollo Sea oil spill in 1994 and Treasure oil spill in 2000 resulted in the death of approximately 5000 and 2000 breeding adults, mostly from Robben and Dassen islands (Underhill *et al.* 1999, 2006, Crawford *et al.* 2000). As this is an important additional source of mortality, in the model it is assumed that an additional 2500 and 1000 breeding females from Dassen and Robben died in these yrs, with the number assumed dead from each of these two colonies determined by a fixed input parameter (oil_prop ; set = 0.5 in illustrative example) and from each age class computed on the assumption of proportionality to the abundance of that age class.

Equations (3) (and Equation (4) similarly) for Robben and Dassen is thus modified as follows:

$$N_{y+1,a+1}^s = N_{y,a}^s \cdot S_y - p_a M_y^{oil} \quad (18)$$

where

$$p_a = \frac{N_{y,a}^s}{\sum_{a'=2}^m N_{y,a'}^s}$$

and M_y^{oil} is an additional mortality term set as the observed number of penguins age 2+ that died in year y as a result of oiling.

In addition, it is likely that most if not all chicks fledged in those years will have died (Crawford, pers. commn) and hence it is assumed that only a small proportion (set at 50% here) of age 1 birds survived in those years.

Annual variation in adult survival rate

The simplest version of the model assumes adult survival S is constant over time. Allowing adult survival rate to vary freely from year-to-year as an annual estimable parameter (i.e. $S \rightarrow S_y$) would lead to an over-parameterised model, but process error of this kind can be incorporated in the model by treating it as a random effect. To maintain the $S_y \leq 1$ constraint, it is easiest to transform to an annual adult natural mortality rate (M_y):

$$M_y = -\ln S_y \quad (19)$$

where $M_y = M e^{\eta_y}$ $\eta_y \sim N(0, (\sigma_\eta)^2)$ (20)

and the M and η_y 's become estimable parameters.

In a strict frequentist paradigm, obtaining maximum likelihood estimates requires integration over these random effects. The simpler approach here may be thought of as providing estimates for the

Bayesian posterior modes, given uniform priors for all the estimable parameters except the η_y 's for which normally distributed priors of mean zero and variance σ_η^2 are assumed (see equation (20)).

Starting values and equilibrium assumptions

Given a value for the starting (1989) number of adult moulters (ages 2+) in an area N_{0,Ad_moult}^s , the total initial population size can be computed as well as the initial number of breeding females. Under the assumption that the population of each colony is at equilibrium in the year the model commences, and assuming further that there is zero initial immigration/emigration, as well as that $\omega_1 = H(1989)$ (i.e. fledging success observed in 1989) and $\omega_2 = \omega_2(1989)$ (i.e. proportion of mature birds expected to breed that year), simplifies the problem of solving for the starting number of breeding females $N_0^{breed,s}$ through solving the balance equation:

$$N_0^{breed,s} = N_{0,Ad_moult}^s \cdot \left(q_f \omega_1 (S_0^{j,s})^{\frac{3}{4}} \right)^{-1} \cdot \left((S_0^{j,s})^{\frac{1}{4}} \cdot S_0^{\frac{3}{4}} \cdot \left(1 + \sum_{a=3}^{m-1} S_0^{a-2} + \frac{S_0^{m-2}}{(1-S_0)} \right) \right)^{-1} \quad (21)$$

with

$$S_0^{j,s} = S_j^* \left(1 - \frac{N_{0,Ad_moult}^s}{K_s^*} \right) \quad (22)$$

Given $N_0^{breed,s}$, the initial numbers at each age a can then be computed as:

$$N_{0,a}^s = \begin{cases} N_0^{breed,s} \cdot q_f \cdot \omega_1 \cdot (S_0^{j,s})^{\frac{3}{4}} & a = 1 \\ N_0^{breed,s} \cdot q_f \cdot \omega_1 \cdot (S_0^{j,s}) S_0^{\frac{3}{4}} & a = 2 \\ N_0^{breed,s} \cdot q_f \cdot \omega_1 \cdot (S_0^{j,s}) S_0^{\frac{3}{4}} S_0^{a-2} & 3 \leq a < m \\ N_0^{breed,s} \cdot q_f \cdot \omega_1 \cdot (S_0^{j,s}) S_0^{\frac{3}{4}} S_0^{m-2} / (1-S_0) & a = m \end{cases} \quad (23)$$

Fitting procedure

The estimable parameters are estimated by minimising the total negative log likelihood.

The model is fitted to moult count data (available for Robben, Dassen and Dyer Islands), breeding numbers data (available for Robben, Dassen, Dyer and Boulders) and to data on the proportion of

juvenile to total moulters (available for Robben, Dassen and Dyer). Contributions by each of these to the negative of the log-likelihood ($-\ln L$) are as follows.

Moult counts

The moult counts are assumed to be log-normally distributed indices of the total numbers of adult female penguins such that:

$$I_y^{moult,s} = \hat{I}_y^s e^{\varepsilon_y^s} \quad \text{or} \quad \varepsilon_y^s = \ln(I_y^{moult,s}) - \ln(\hat{I}_y^s) \quad (24)$$

where $I_y^{moult,s}$ is the (observed) moult count (expressed in terms of females only) for sub-area s and year y ;

$\hat{I}_y^s = q^s N_{y,Ad_moult}^s$ is the corresponding model estimated value, where \hat{N}_{y,Ad_moult}^s is the model-estimate of the number of female moulters, as given by Equation (11);

q^s is the constant of proportionality for moulters corresponding to sector s ; and

ε_y^s from $N(0, (\sigma_y^s)^2)$.

The contribution of the moult count data to the negative of the log likelihood function (after removal of constants) is given as shown below with contributions added over sub-areas s :

$$-\ln L^{moult} = \sum_s \left[n_s \ln(\hat{\sigma}_s^{moult}) \right] + \frac{n_s}{2} \quad (25)$$

with

$$\hat{\sigma}_s^{moult} = \sqrt{\frac{\sum_{y=1}^{n_s} (\ln I_y^{moult,s} - \ln \hat{I}_y^s)^2}{n_s}} \quad (26)$$

where

n_s is the number of years for which there are moult count data in sub-area s .

The proportionality constant q^s for sub-area s 's moult numbers is estimated by its maximum likelihood value:

$$\ln \hat{q}^s = \frac{1}{n_s} \sum_y \left(\ln I_y^s - \ln \hat{N}_{y,Ad_moult}^s \right) \quad (27)$$

Breeding pairs

The breeding pairs data are assumed to be log-normally distributed indices of the total numbers of adult female penguins that breed each year, such that:

$$I_y^{breed,s} = \hat{I}_y^s e^{\varepsilon_y^s} \quad \text{or} \quad \varepsilon_y^s = \ln(I_y^{breed,s}) - \ln(\hat{I}_y^{br,s}) \quad (28)$$

where $I_y^{breed,s}$ is the (observed) breeding pairs count for sub-area s and year y ;

$\hat{I}_y^{br,s} = q_{breed}^s N_y^{breed,s}$ is the corresponding model estimated value, where $\hat{N}_y^{breed,s}$ is the model-estimate of the number of breeders, as given by Equation (6);

q_{breed}^s is the constant of proportionality for breeders corresponding to sector s ; and

ε_y^s from $N\left(0, (\sigma_y^s)^2\right)$.

The contribution of the breeding count data to the negative of the log likelihood function (after removal of constants) for all sub-areas s is thus as follows:

$$-\ln L^{breed} = \sum_s \left[n_{b,s} \ln(\hat{\sigma}_s^{breed}) \right] + \frac{n_{b,s}}{2} \quad (29)$$

with

$$\hat{\sigma}_s^{breed} = \sqrt{\frac{\sum_{y=1}^{n_s} \left(\ln I_y^{breed,s} - \ln \hat{I}_y^{br,s} \right)^2}{n_{b,s}}} \quad (30)$$

where

$n_{b,s}$ is the number of years for which there are breeding count data in sub-area s .

The proportionality constant q_{breed}^s for Robben Island is assumed equal to 0.9 (to reflect minor undercounting) and the q_{breed}^s values for the other colonies are set equal to the Robben Island value.

Proportion of juveniles:

The log-likelihood contribution from the juvenile proportional abundance data is given by:

$$-\ln L^{prop} = \sum_s \left[n_{p,s} \ln(\hat{\sigma}_s^{prop}) \right] + \frac{n_{p,s}}{2} \quad (31)$$

with:

$$\hat{\sigma}_s^{prop} = \sqrt{\frac{\sum_{y=1}^{n_{p,s}} (I_y^{Prop,s} - \hat{p}_{y,Juv:Tot}^s)^2}{n_{p,s}}} \quad (32)$$

where

- $I_y^{Prop,s}$ is the (observed) juvenile proportional abundance data for sub-area s and year y ;
- $n_{p,s}$ is the number of years for which there are proportional abundance data in sub-area s ; and
- $\hat{p}_{y,Juv:Tot}^s$ is the model-estimate of the proportion of juvenile moulters to the total number of moulters, as given by Equation (12).

Adult mortality residuals:

The following penalty term is then added to the negative log likelihood:

$$-\ln L^{resid} = \sum_y (\eta_y)^2 / (2\sigma_\eta^2) \quad (33)$$

where

- η_y is the adult survival residual for year y , which is estimated for years $y1$ to $y2$ (set here as 1988 to 2006); and

σ_η is the standard deviation of the log-residuals, which is input (with the sensitivity of results to alternatives for this choice desirably checked).

Parameter estimates and constraints

Parameters estimated in the model were constrained in the following ranges for reasons of biological realism:

$$0 < M \leq 1.0$$

$$0 < S_j^* \leq 1.0$$

$$0 \leq E \leq 1.0$$

$$0 \leq E_{prop} \leq 1.0$$

$$0 \leq E_{ROB} \leq 1.0$$

$$0 < N_{0,Ad_moult}^{Rob}$$

$$0 < N_{0,Ad_moult}^{Das}$$

$$0 < N_{0,Ad_moult}^{Dy}$$

$$0 < N_{0,Ad_moult}^{Bld}$$

Apart from the nine parameters above, an additional 19 η_y parameters are estimated. Not all these 28 parameters are estimated in every simulation. For example, in versions assuming no movement, E and E_{prop} are set equal to zero.

ASSUMED RELATIONSHIPS WITH FOOD AVAILABILITY: BREEDING PROPORTIONS, PROPORTION MATURE AND CHICKS FLEDGED

Breeding proportion

It has been suggested (R. Crawford, pers. commn) that the proportion of birds that choose to breed in a particular year may vary depending on food availability, as reflected by the f_2 functional dependency of Equation (9). A number of different formulations are possible regarding the change in the proportion of mature birds that choose to breed (in April) each year y as a function of relative prey biomass B^r the previous year $y-1$, where prey biomass B^r is computed as relative to the maximum value observed over a series (Fig. 1). The simplest assumption is that 100% of mature birds breed each year. At the other extreme, the proportion breeding may be assumed a simple linear function of prey biomass, but this was not considered realistic by the task group. The illustrative example here assumes 100% of birds breed if relative prey

biomass is above the median B^r value, but that the proportion breeding decreases linearly for lower values of B^r .

Proportion mature

Crawford (pers. commn.) has also suggested that the proportion of birds of different ages that mature each year y may be a function of relative prey biomass B_{y-1}^r the previous year $y-1$, where prey biomass is computed as relative to the maximum value observed over a series. The simplest model assumption is that the base-case input values do not change over time. An option being tried in the model involves assuming that the proportion maturing at ages 3 and 4 remains fixed at 0.9 and 1.0 respectively if relative prey biomass is above the median B^r value, but then decreases linearly with lower values of B^r as illustrated in Fig. 2.

Chick fledging success

One of the most important functional relationships that needs to be determined before the pelagic OMP testing process can take account of the relationship between the breeding success of African penguins and the abundance of pelagic fish concerns the way in which the average numbers of chicks fledged each year relates to pelagic fish biomass, i.e. the f_1 functional dependence in Equation (8). The model can currently be run either by using the observed values for Robben and Dassen Island, or by fitting a functional relationship within the likelihood maximisation. The latter should result in approximately the same level of variability as evident from the Robben island data and the maximum average number of chicks fledged is assumed equal to the maximum observed values.

There are a number of ways in which this relationship could be modelled. Following Plagányi and Butterworth (2006), a breeding success factor $f_1(B_y^a)$ is thus formulated as a function of the available biomass of prey and acts as a multiplier to the maximum observed chick fledging rate (Fig. 3). To reduce the number of parameters in the model, the breeding success factor is scaled such that it is 1 when the pelagic biomass is at the maximum observed value. A useful functional form to use is that classically referred to as a Beverton-Holt stock-recruitment relationship, modified here to represent fledging success as a function of pelagic biomass in area a , B_y^a :

$$f(B_y^a) = \frac{\alpha \cdot B_y^a}{\beta + B_y^a} \quad (33)$$

where α and β are parameters with $\beta = (\alpha - 1)$ so that $f_1(1) = 1$.

When adding a term to allow for fluctuations about this relationship, Equation (33) becomes:

$$f(B_y^a) = \frac{\alpha \cdot B_y^a}{(\alpha - 1) + B_y^a} e^{(\zeta_{ay} - \sigma_{BR}^2/2)} \quad (34)$$

where

ζ_{ay} reflects fluctuation about the expected curve for sub-area s in year y , which is assumed to be normally distributed with standard deviation σ_{BR} (whose value is input in the applications considered here).

In order to work with estimable parameters that are more meaningful biologically, Equation (33) is re-parameterised in terms of the maximum pelagic biomass, B_{MAX}^r , and the “steepness” h of the relationship, where “steepness” is the fraction of maximum fledging success that results when B_y^r drops to 20% of its maximum level, from which it follows that:

$$h = \frac{\alpha}{5\alpha - 4} \quad (35)$$

By ignoring the random variation term and choosing a single parameter value h , the fledging success relationship can thus be set. The parameter h may be thought of as controlling the level of prey biomass below which breeding success is negatively impacted (Fig. 3). Given that this is not known or easily determined, Plagányi and Butterworth (2006) suggest that a prudent approach may be to select two values that roughly bound the likely range in this relationship. Moreover, rather than assuming a deterministic relationship, variability has been added such that the extent of variability about the curve can be changed by adjusting the parameter σ_{BR} .

When fitting the chick fledgling success functional relationship, the contribution to the negative of the log likelihood function (after removal of constants) is computed by summing over the Robben and Dassen Island contributions as follows:

$$-\ln L^{fledge} = \sum_s [n_{f,s} \ln(\hat{\sigma}_s^{fledge})] + \frac{n_{f,s}}{2} \quad (36)$$

with

$$\hat{\sigma}_s^{fledge} = \sqrt{\frac{\sum_{y=1}^{n_{f,s}} \left(\ln I_y^{fledge,s} - \ln \hat{I}_y^{fled,s} \right)^2}{n_{f,s}}} \quad (37)$$

where $I_y^{fledge,s}$ is the (observed) mean fledging success for sub-area s and year y ;

$\hat{I}_y^{fled,s}$ is the corresponding model-estimated value, as given by Equation (33) (or (34)); and

$n_{f,s}$ is the number of years for which there are fledging success data in sub-area s .

For illustrative purposes, in the results presented here chick fledgling success is assumed equal to the observed Robben Island values for Robben, Dyer and Boulders, and the derived Dassen series values for Dassen Island. A single result is shown using the derived Dassen series scaled upwards (multiplied by 1.27) to convert values from mean chicks fledged per breeding attempt to units of per year.

RESULTS AND DISCUSSION

There is insufficient time to present results for all scenarios here hence only a selected illustrative example is shown in detail in Figs. 4-10.

These results were generated using the observed fledging success estimates. The simulation shown assumes that first-time breeders move from Dyer to Boulders (to match the Boulders population data) and to Dassen and Robben. The pelagic abundance series used is the combined sardine and anchovy strata A_E series (see data document).

A few points of interest in the results:

- The results of the revised model version are consistent with previous results presented suggesting that the average and maximum of published survival estimates are too low to sustain populations, even when considering movement from Dyer to Robben/Dassen and Boulders (Table 1).

- The fits of the model to the data are still unsatisfactory (Fig. 1 and 9) and further work is needed in this regard (see also comments in accompanying document by Butterworth and Plagányi).
- Figure 6 summarises the three model relationships (mean chicks fledged, the proportion of mature birds that breed each year and the proportion of birds of ages 3 and 4 that first mature each year) that are determined are functions of the pelagic fish abundance input series. In the illustrative example here, the observed chick fledging success values are used but these will ultimately be used to estimate a functional response within the model.
- Note from Fig. 7 that the juvenile survival rate is modelled as density dependent, and hence for example it is seen to decrease over the last few years following the observed population increases. A low level of density dependence was set in the example shown.
- The effect of modelling adult survival as a random effect is shown in Fig. 7. The average adult survival rate over the modelled period ranges between about $0.93 - 0.65 \text{ yr}^{-1}$, with an average of 0.88 yr^{-1} . In the example shown, the σ_n value was set relatively high (0.6 – Table 1). A random effects term will similarly be added to the juvenile survival rate in further investigations – the main use of the approach is to study the trends in the residuals. Note that the model result suggests a decrease in adult survival rate in 2005 down to about 0.72 , which is consistent with the hypothesis proposed by some task group members of a large decrease in adult survival over this period. Note that if adult survival decreased this dramatically in 2005, it suggests, as shown in Fig. 7, that an additional 20 000 adult penguins (males and females from Robben and Dassen Islands) must have died in these years. It would be very useful to obtain independent evidence of such large numbers of dead birds. From preliminary discussions with R. Crawford, it appears that unusual numbers of dead birds were not observed on the islands during the moult counts, although this may have been simply because the focus was on live birds. Dr Graham Avery (Iziko Museum) records all birds on the beach each month and removes them (behind the dunes) to prevent duplication. In correspondence with Dr Avery, his observations are suggesting some recent increase in penguin mortality due to both seal predation and moult “stress”, but these observations are based on tens rather than hundreds or thousands of observations.
- Fig. 8 shows modelled numbers of birds that moved to Boulders and to Dassen and Robben in the illustrative simulation. Given the poor fit to the Dyer Island proportion of juveniles data (which show a very low proportion of juveniles), it may be necessary to modify the movement model to allow movement of younger birds too. Earlier model results (not repeated here) showed that if movement from Algoa Bay westwards was assumed for years when pelagic recruit abundance was high, this could both explain the observed decrease in

penguin breeding counts at Algoa Bay, and assist in explaining the observed increases at Dassen and Robben island without having to invoke unrealistically high survival or fecundity estimates. However, task group members noted that there were few observations of penguins emigrating westwards, given the predominant conclusion from movement studies of a counter clockwise movement of birds. It is worth bearing in mind though that the cited studies were conducted prior to the very large increases in pelagic abundance on the west coast and hence further discussion is needed as to the feasibility of the hypothesis that birds moved westwards to exploit the high food availability.

- Three modifications to the movement model that are currently being developed/investigated are: a) to allow emmigration of younger birds from Dyer island; b) to allow the proportions moving to vary with time; and c) to account for some immigration of birds from Namibia.
- Fig. 10 shows a comparison of the total observed numbers and trends of breeding pairs in the western Cape as a whole, compared to the total number in the model (summed over Dassen, Robben, Dyer and Boulders, and hence accounting for approximately 90-95% of all birds in the western Cape). The lower figure shows the model estimate of the total number (males and females aged 1 and older) and total breeders in the western Cape, and the predicted trends.
- Fig. 11 shows an example of a model fit when multiplying the Dassen Island chick fledgling success values by 1.27.
- Fig. 12 shows an example of the model fit to the Robben Island fledgling success data when using the combined anchovy and sardine strata A_E abundance index.

Conclusions

The model developed here has proved a useful tool for exploring various hypotheses and providing a dynamic picture of penguin dynamics. The model has been built up from a very simple form to a more complex form that permits simulating movement of birds between colonies. The simplest form of the model integrates current understanding of penguin population dynamics to test whether the various parameter estimates are compatible with the data. These investigations suggest that there may be problems with both the data used in and assumptions of the model.

For most colonies, the trends in penguin numbers can only be explained if immigration to and emigration from colonies is assumed. The model as described here is still in the process of development and hence results should be viewed as preliminary only.

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Table 1. Summary of example results for full model including all areas and assuming movement from Dyer to other colonies.

Model	Illustrative example				
<u>Parameter estimates</u>					
No. of parameters estimated					
M	0.11	$S_y(\text{ave})$	0.88		
S_{j^*}	0.80	$S_{j(\text{ave ROB})}$	0.76	$S_{j(\text{ave DAS})}$	0.75
E	0.77				
E_{prop}	0.12				
E_{ROB}	0.59				
E_2	0.00				
H_{crit}	n/a				
a	n/a				
$N_{0,2+} (ROB)$	2779				
$N_{0,2+} (DAS)$	10490				
$N_{0,2+} (Dy)$	9766				
$N_{0,2+} (BLD)$	7				
<u>Likelihood contributions</u>					
$-\ln L$ ROB moult	-15.280				
$-\ln L$ ROB breed	-11.343				
$-\ln L$ DAS moult	-33.562				
$-\ln L$ DAS breed	-39.896				
$-\ln L$ Dy moult	-8.685				
$-\ln L$ Dy breed	-7.922				
$-\ln L$ Bd breed	-6.005				
$-\ln L$ Alg breed	n/a				
$-\ln L$ ROB prop	-27.005				
$-\ln L$ DAS prop	-6.706				
$-\ln L$ Dy prop	-6.005				
$-\ln L$ S resid	9.799				
$-\ln L$ TOTAL	-146.604				
q moult ROB	0.718	q moult ROB	0.900		
q moult DAS	0.403	q moult DAS	0.900		
q moult Dy	0.724	q moult Dy	0.900		
<u>Model version</u>	<u>Age 1</u>	<u>2</u>	<u>3</u>	<u>4</u>	<u>5</u>
Proportion mature at age	0	0	Varies	Varies	1
Pelagic series	44				
$\Sigma(S_{res})$	0.6				
Z start year	2005	n/a			
Algoa emmig. start / end yrs	0	0	n/a		
K factor (Rob, Das, Dy, BLD)	10	10	10	5	
H_{max}	0.97				
	<u>1994</u>	<u>2000</u>	<u>Prop. Fledglings</u>		
No's die (oiling)	2500	1000	0.5		

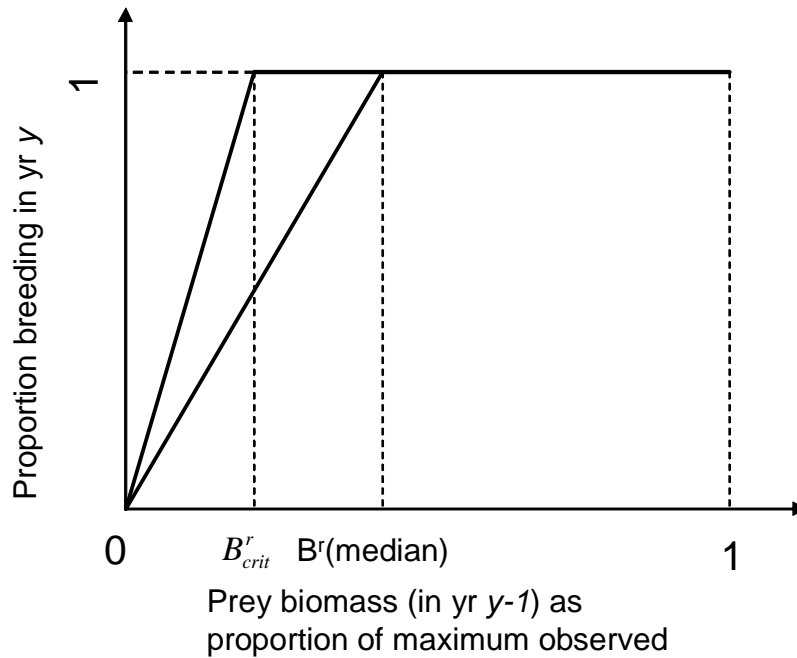


Fig. 1. Schematic showing different possible assumptions regarding the change in the proportion of mature birds that choose to breed (in April) each year y as a function of relative prey biomass B^r the previous year $y-1$, where prey biomass is computed as relative to the maximum value observed over a series. The simplest assumption is that 100% of mature birds breed each year. Other options would be to assume 100% of birds breed if relative prey biomass is above the median B^r value or an estimated B^r_{crit} value, but that the proportion breeding decreases linearly for lower values of B^r .

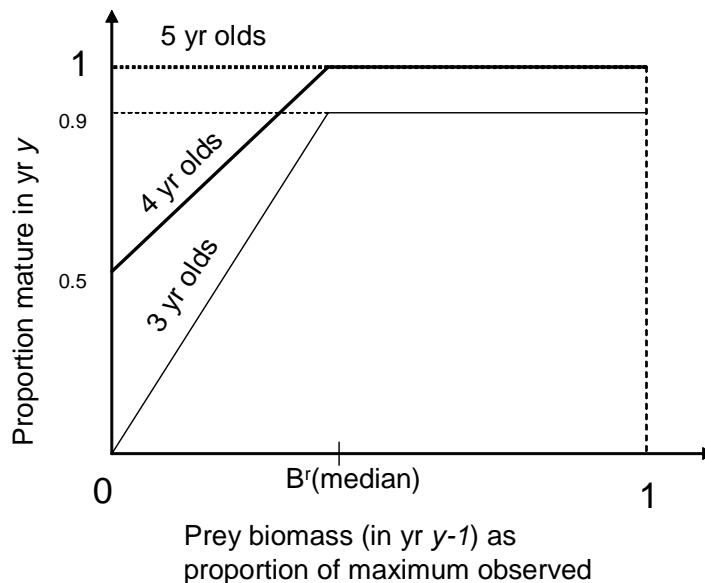


Fig. 2. Schematic showing initial input assumption regarding the change in the proportion of birds of different ages that mature each year y as a function of relative prey biomass B^r the previous year $y-1$, where prey biomass is computed as relative to the maximum value observed over a series. The simplest assumption is that these proportions do not change over time. An option being tried in the model involves assuming that the proportion maturing at ages 3 and 4 remains fixed at 0.9 and 1.0 respectively if relative prey biomass is above the median B^r value, but then decreases linearly with lower values of B^r as shown.

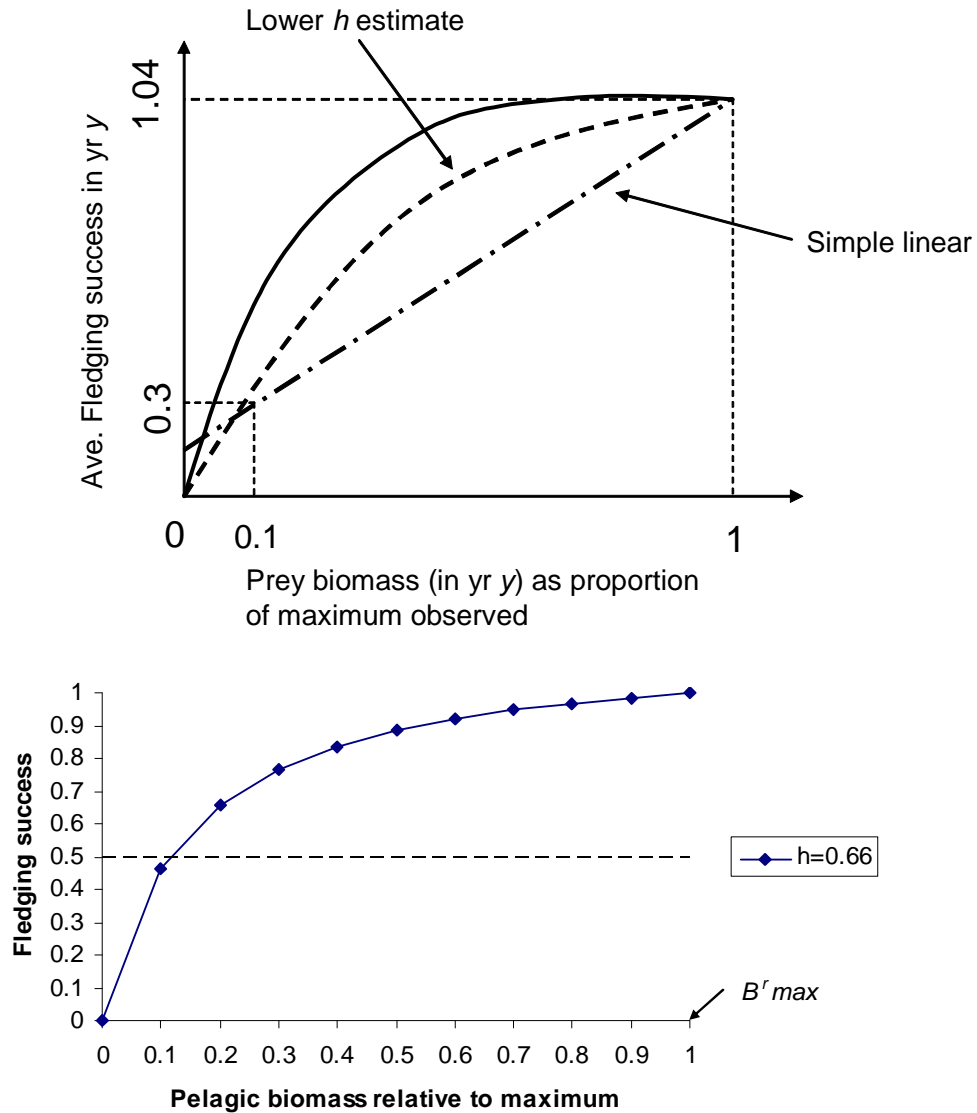


Fig. 3. Schematic showing different possible assumptions regarding the change in the average fledging success each year y as a function of relative prey biomass B^r in the same year y , i.e. the f_l functional dependence in Equation (8). Prey biomass is computed as relative to the maximum value observed over a series. The shape of the curve is determined by a single “steepness” parameter h with different values leading to either a near-linear decrease in fledging success as prey abundance decreases versus a scenario in which fledging success drops below the maximum observed level only at relatively low levels of prey abundance. The lower curve shows the formulation assumed in the preliminary base-case model.

S = 0.90

S_j (ave) Robben; Dassen = 0.76

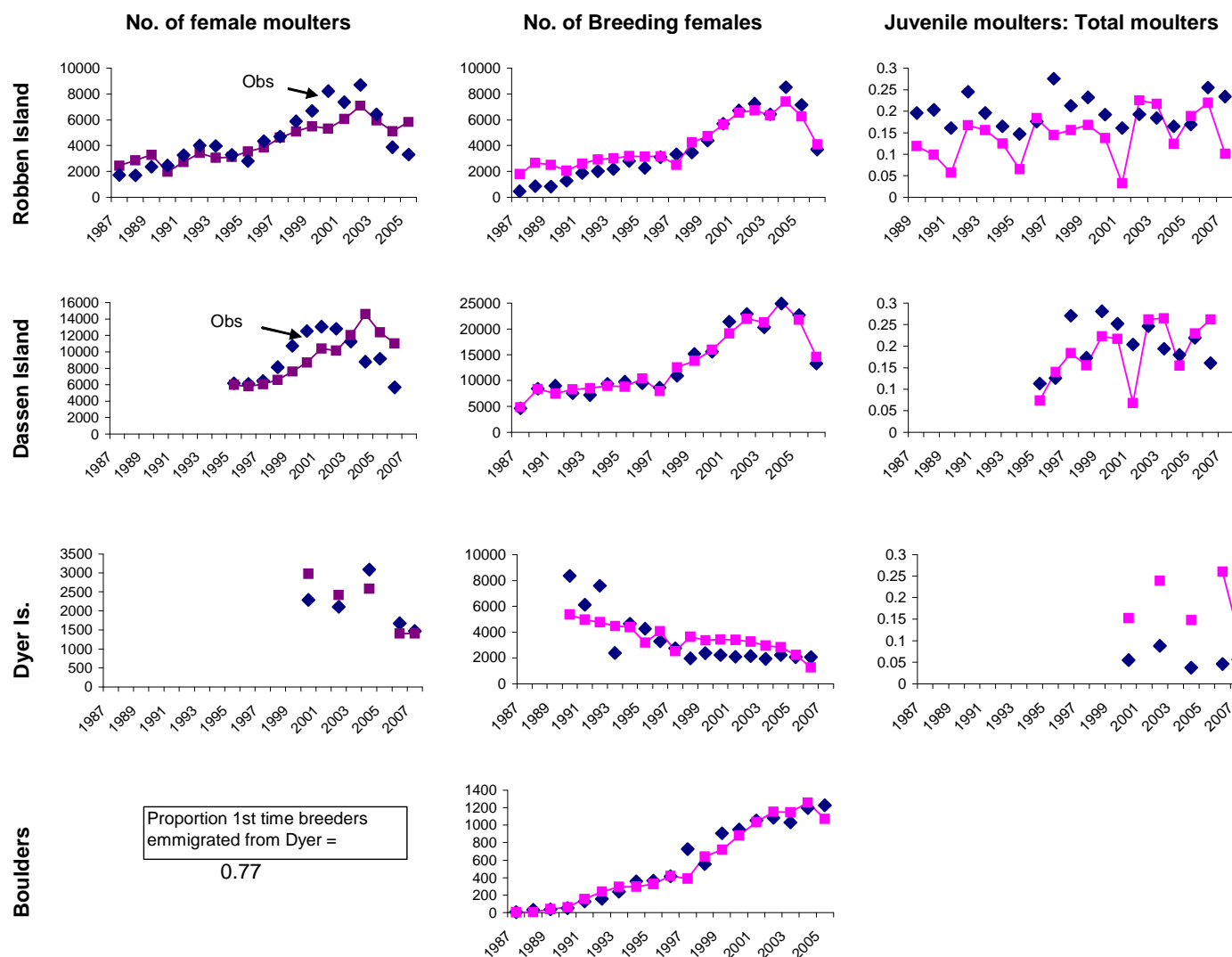


Fig. 4. Illustrative preliminary results from full model. Model-predicted trajectories of the numbers of female moulting penguins (left panel), number of breeding pairs (2nd from left), and proportion juveniles (right) at Robben (top panel), Dassen (2nd from top); Dyer island (3rd from top), and Boulders. Observed data are shown as diamond points not joined by a line.

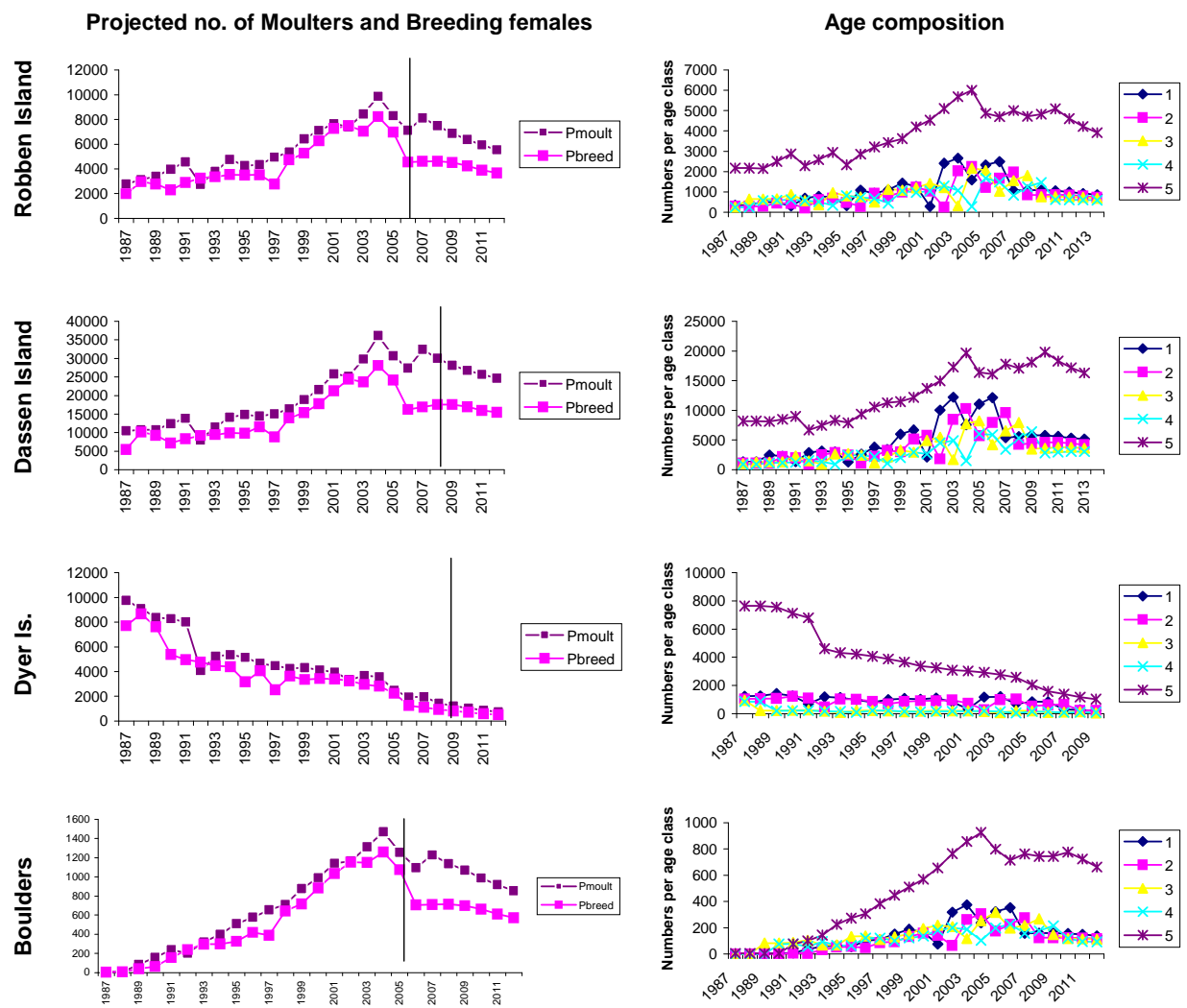


Fig. 5. Illustrative preliminary results from full model. Age structure.

F

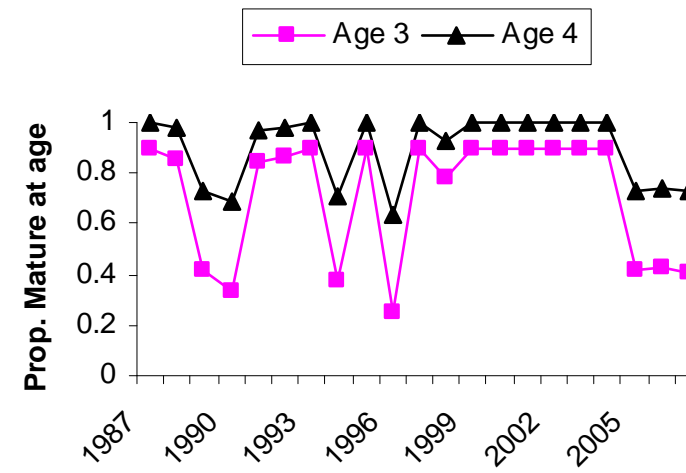
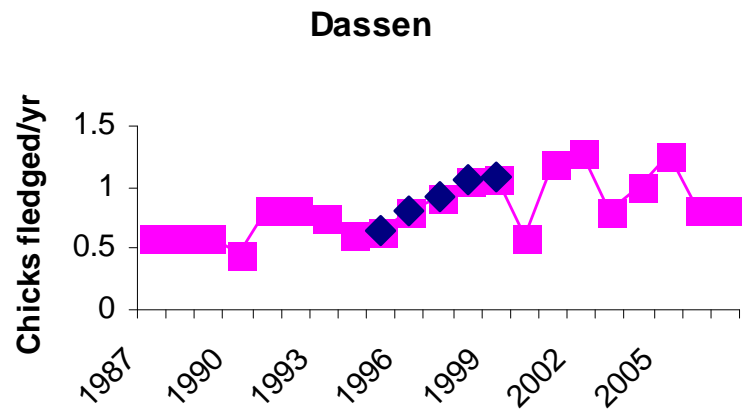
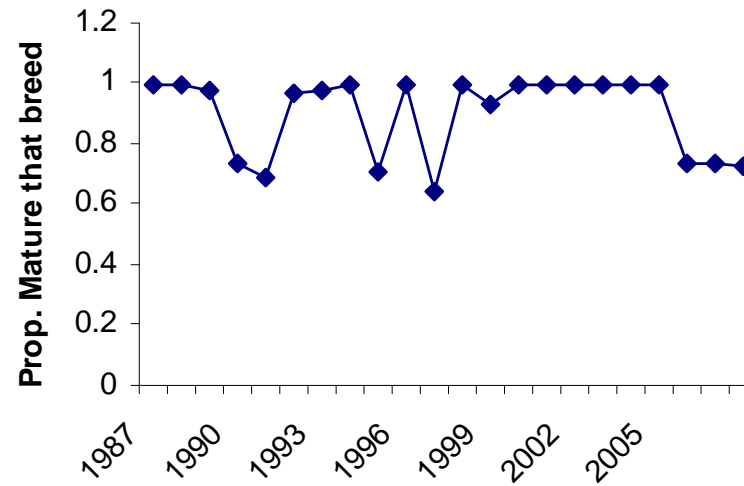
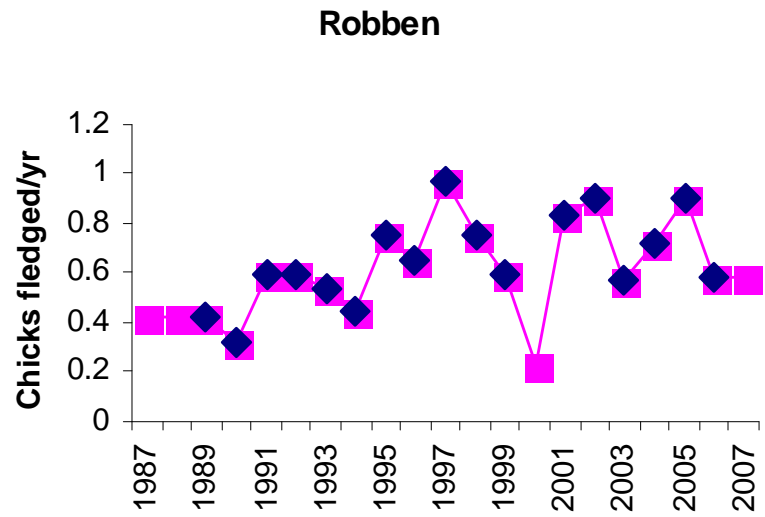


Fig. 6. Illustrative preliminary results from full model. Functional relationships with pelagic abundance.

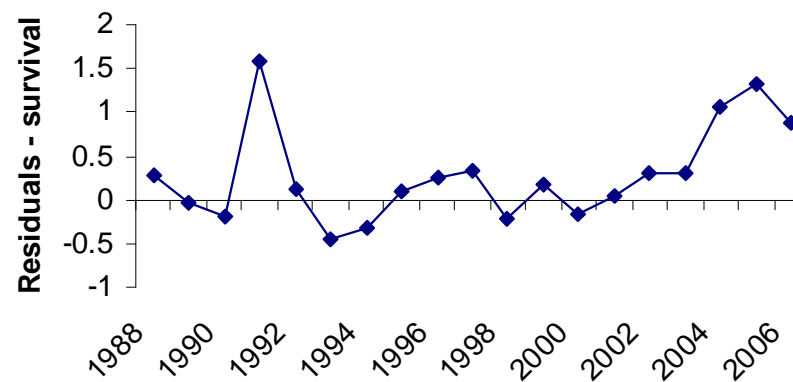
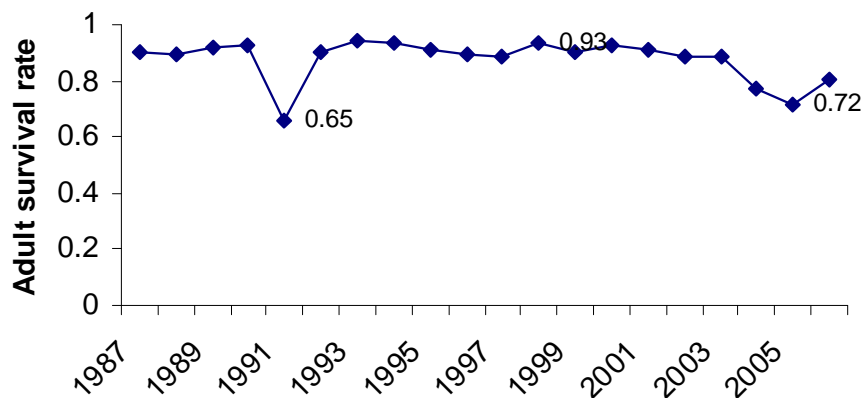
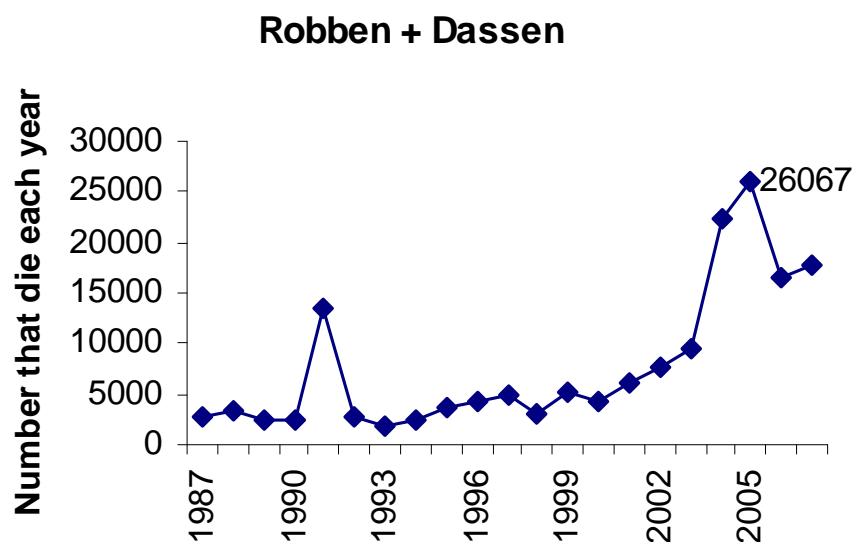
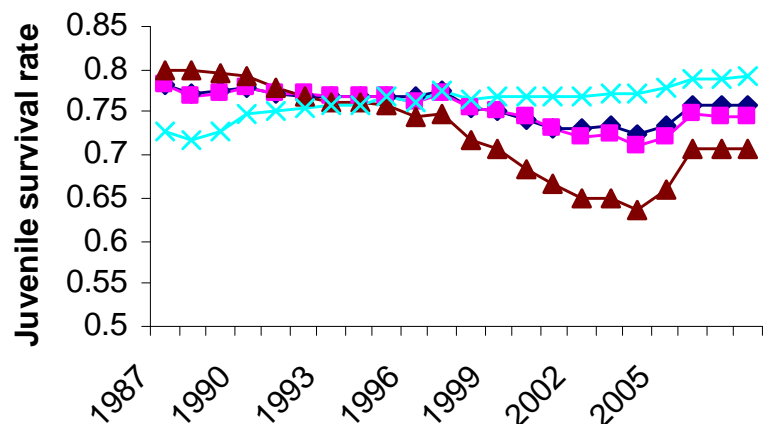
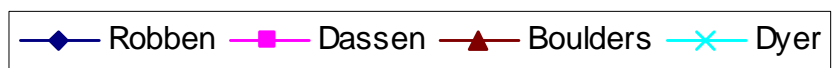


Fig. 7. Illustrative preliminary results from full model. Juvenile and adult survival.

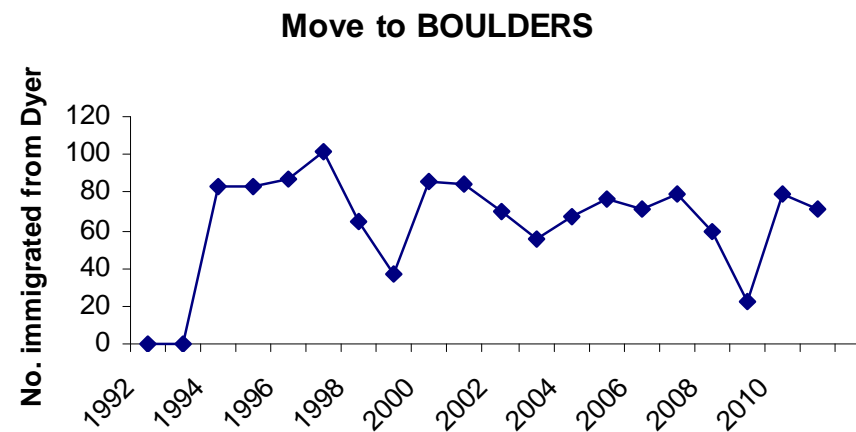
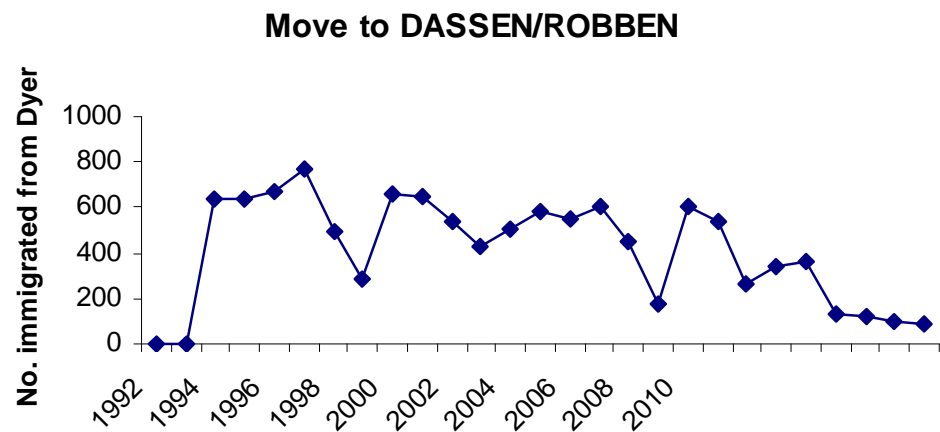


Fig. 8. Illustrative preliminary results from full model. Numbers moving.

$S = 0.90$

Residuals

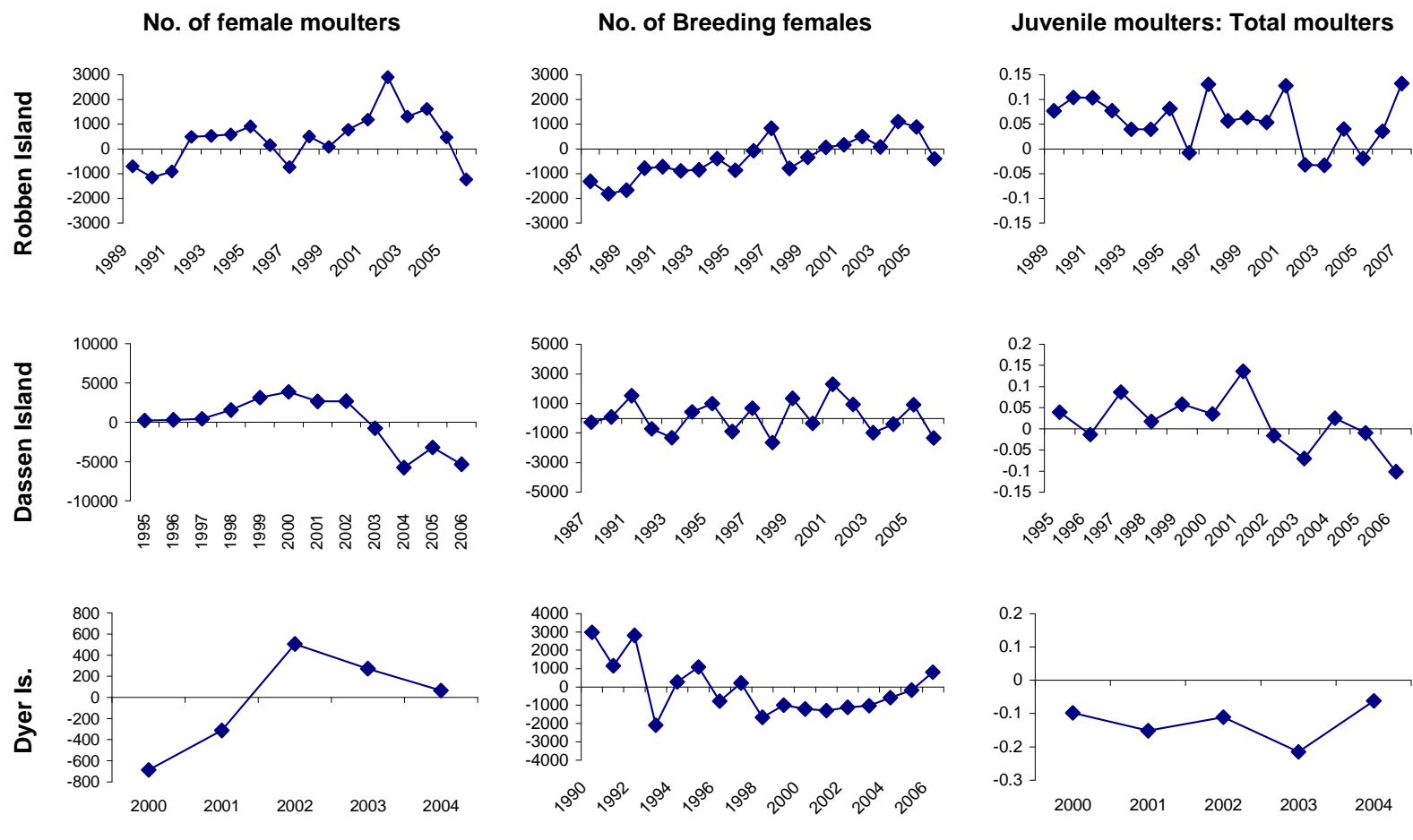


Fig. 9. Illustrative preliminary results from full model. Model residuals.

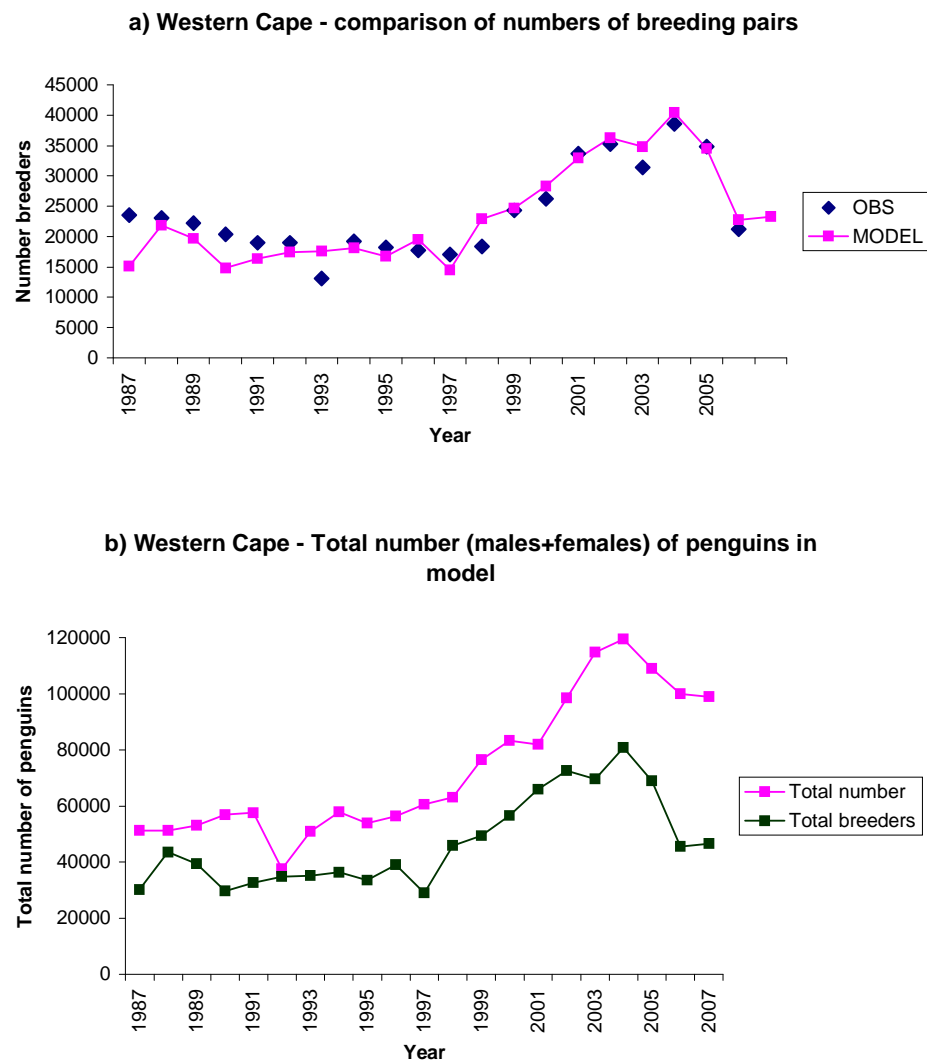


Fig. 10. Illustrative preliminary results from full model. Comparison of total observed numbers and trend of penguins in the Western Cape with the total numbers of birds as estimated by the model.

S = 0.89

S_j (ave) Robben; Dassen = 0.76

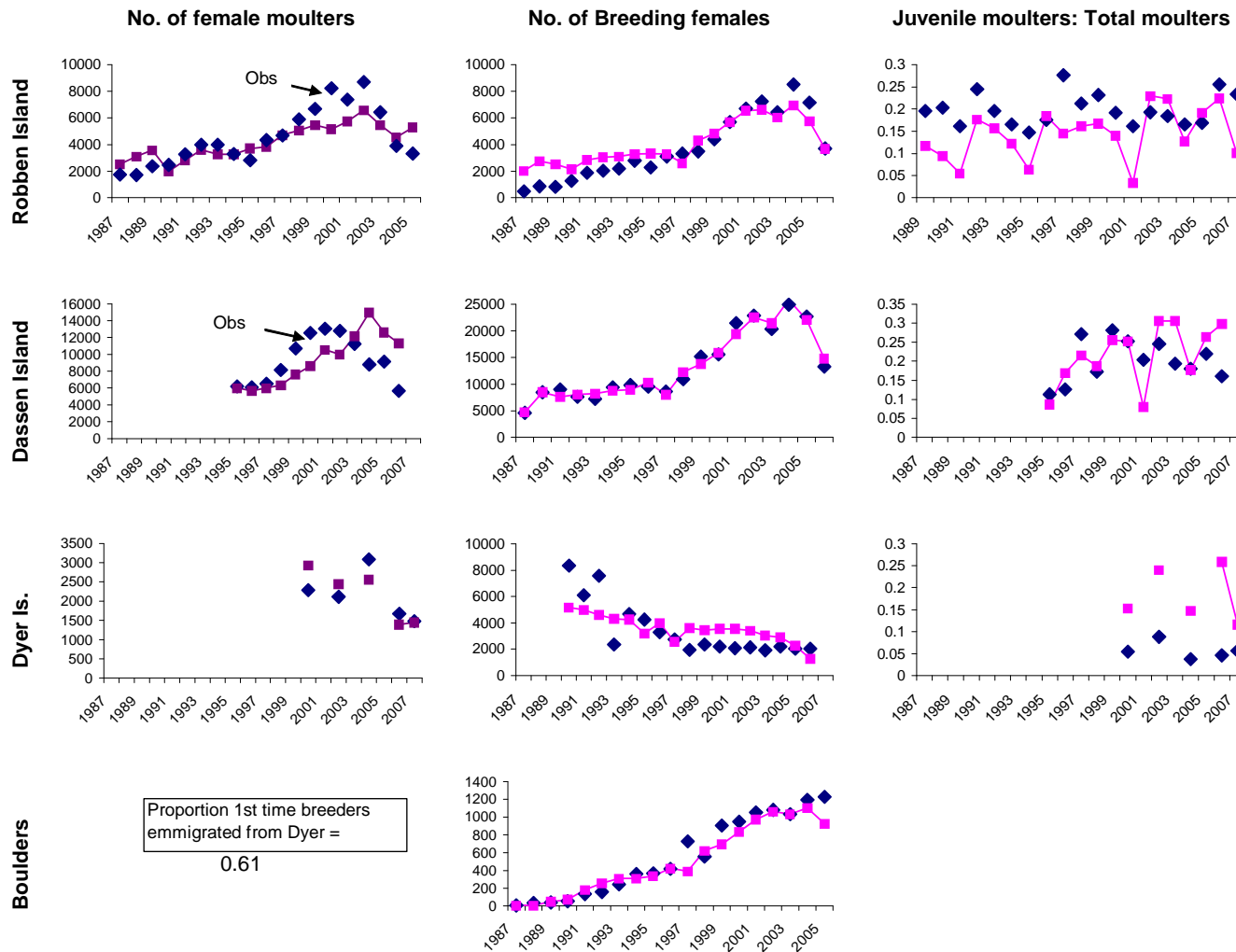


Fig. 11. Illustrative preliminary results from model with scaled up Dassen fledging success series. Model-predicted trajectories of the numbers of female moulting penguins (left panel), number of breeding pairs (2nd from left), and proportion juveniles (right) at Robben (top panel), Dassen (2nd from top); Dyer island (3rd from top), and Boulders. Observed data are shown as diamond points not joined by a line.

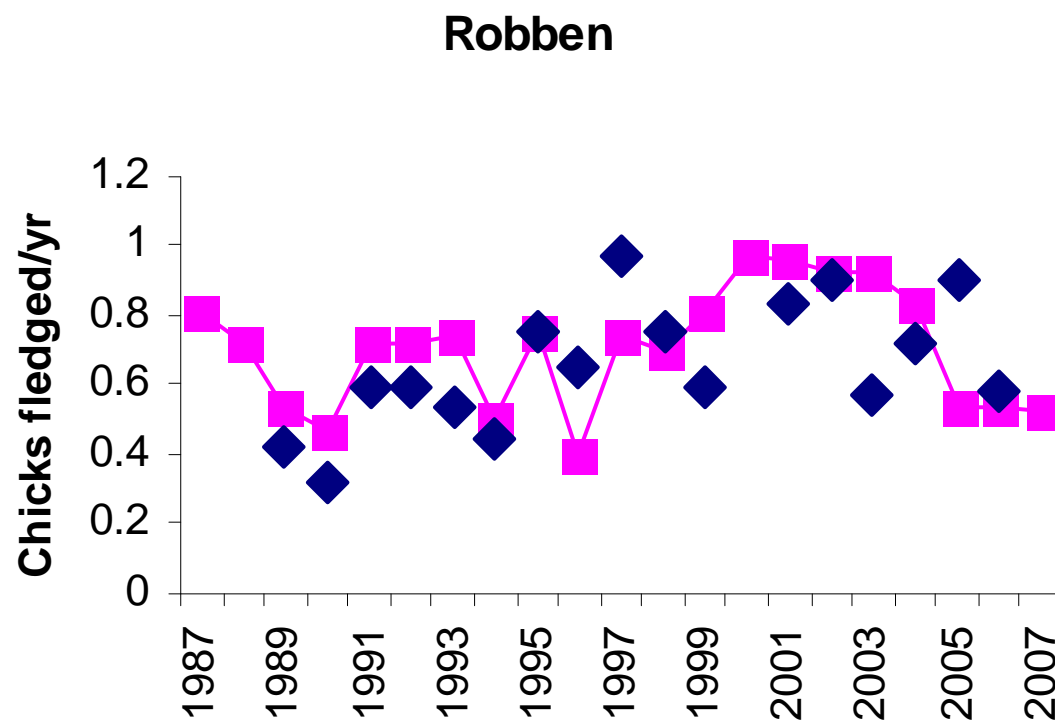


Fig. 12. Example of model fit to Robben island fledgling success data when using the combined anchovy and sardine strata A_E abundance index.