

Revised Spatial Age-Structured Model of African Penguin *Spheniscus demersus* Populations

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SUMMARY

A revised form of an earlier model is summarised in this document, with preliminary results to be presented in a separate document. The three main changes to the model are as follows:

- 1) the delay difference equations have been converted to fully age-structured equations instead so as to be able to model changes in the age at first maturity as requested by the task group;
- 2) rather than using aggregated factors to model various processes, these factors have been split into individual components so as to be more easily distinguished between and understandable; and
- 3) a preliminary Algoa Bay model has been added so that movement from Algoa Bay to the west can be modelled.

Some suggested alternatives for modelling various processes within the model are given as a starting point for discussions by the task group.

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 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 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 three 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 combined for reasons of simplicity and because of their close proximity to each other which suggests that the effects of external factors such as food availability would be highly correlated between the two. The second 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 third 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.

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 three sub-areas 1) Robben and Dassen Islands; 2) Boulders and 3) Dyer island.

A summary of all the breeding colonies of penguins in area i) is provided in Fig. 1 which also shows the relative abundance of breeding pairs in the different sub-areas, computed from data in Underhill *et al.* (2006). The regional penguin population is dominated (in terms of numbers) by two large colonies, namely Robben Island and Dassen Island; thus the model here has focused on these two colonies, with the next most important colony being Dyer Island.

A preliminary model has been constructed for area iii) and is linked to the area i) model so that different movement hypotheses can be tested.

Fig. 2 maps the extent of strata corresponding to pelagic fish biomass estimates used to link to penguin breeding success in the area i) model (which includes Dassen, Robben, Dyer island and Boulders) and preliminary model for area iii) (St Croix).

The model time step is one year and hence average trends are modelled. Penguins in each sub-area are modelled starting from 1987 (1990 for Dyer Island). 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.

DATA

Available Data - Penguins

A number of time series, both published and unpublished, are available and have been used both to compare with model trends and for use in estimating parameters by fitting to these data. The two main forms of data are counts of the numbers of moulting birds at the various colonies and counts of breeding pairs (Tables 1a,b). The data are from Underhill *et al.* (2006), and various published studies as well as recent updates provided by Les Underhill and Rob Crawford.

A summary of the timeline assumed for an “average” penguin is given in Fig. 3.

The moult count data are generally considered more precise as a population measure (based on c. 24 counts per year) than the breeding pairs count (one count per year aimed to hit the peak of the breeding season) (L. Underhill, pers. commn). The moult count measures the size of the adult-plumaged population whereas the nest count measures the number of breeding pairs (L. Underhill, pers. commn). There are two slightly different series available describing the number of birds moulting at Robben Island, and the series used here are the set considered the more accurate of the two because they account for missing information (see Underhill and Crawford 1999).

It has been highlighted (Rob Crawford, pers. commn) that the counts are of birds moulting around the coastline but that at Dassen Island, where many birds construct burrows, birds also moult in burrows and are not counted. Furthermore the counts at Dassen Island do not cover the interior where penguins may be found in appreciable numbers. Therefore, the count at Dassen Island is not of all birds moulting, just an index. Anton Wolfaardt and Les Underhill (pers. commn) have similarly confirmed that the Dassen island moult counts should be treated as an index of abundance, and not as an estimate of the absolute number of penguins. Given that the moulting process takes two weeks, the sum of counts made at two week intervals provides an estimate of the total population moulting at the locality, following adjustments for the fact that the counts are not made at exactly this frequency.

As the model represents numbers of female penguins, an even sex ratio was assumed and the numbers of moulters halved to derive an index of the number of female moulters (Table 1a). To obtain an aggregated index for Dassen and Robben islands, the numbers of moulters at each locality were added together (Table 1b). As no moult count data were available for Dassen Island for the period 1989-1994, these values were assumed equal to the 1990 value (i.e. it is assumed the population stayed approximately constant over this period as is suggested by the breeding pairs count data) so that a combined index could be obtained.

Data on the number of chicks fledged per pair per year were available for Robben Island only (Table 1b). Over the period 1989-2005 at Robben Island, penguin pairs fledged an average of 0.64 chicks annually, with a maximum of 1.04 in 2005 (Crawford *et al.* 1999, 2006). There are no data for the year 2000, which corresponds to the year in which about 1900 birds died and breeding was disrupted following oiling in the *Treasure* spill (Crawford *et al.* 2000). Crawford *et al.* (2006) suggest that the increased mortality caused by the oil spill was ameliorated to a large extent by the high abundance of pelagic fish prey at the time. In the first instance an interpolated breeding success value for 2000 is simply assumed – see later section regarding addition of an extra mortality term for 2000.

Table 1b also summarises preliminary estimates of the numbers of breeding females at Algoa Bay for years as shown.

New data that have been included in the model and provide valuable insights into the age structure, are those provided by Les Underhill regarding adult and juvenile (birds undergoing first moult) penguin moult counts at Dassen, Robben and Dyer Islands. These data as well as a combined Dassen/Robben series are given in Table 2. A combined index of the juvenile proportion for Robben and Dassen was derived by summing adult and juvenile numbers for all years for which data are available for both islands, and using just the Robben island data for the remaining years.

Table 3 summarises estimates of adult and first-year survival for African penguins available in the literature. These confirm the notion that juvenile survival is typically less than adult survival. As previously discussed, it is often practice in marine population modelling to estimate S by fitting to an index/indices of abundance for the species because of problems in quantifying biases in direct estimates of survival rates and of the sensitivity of population trends to the choice of an adult survival parameter S . Model simulations are conducted both with S fixed at values in the literature as well as by estimating S (as well as juvenile survival and recent decreases in S).

An important anomaly in the data discussed by the task group relates to the concern that when considering Robben, Dassen and Dyer Islands, the number of female moulters per year is approximately the same or less, rather than substantially more, than the number of breeding females (Fig. 4). This indicates that only a proportion of the population is counted during the moult counts because for example counts do not cover the interior where penguins may be found in appreciable numbers. It is assumed that the proportion of counted to uncounted birds remains approximately constant from year to year and that the moult counts provide a reliable index of population trends even though only a proportion of the population is counted.

Proportion that breed at various ages

Based on data specifying the age at which known-age African penguins were first observed breeding at Robben Island, Crawford *et al.* (1999) assumed that the following proportions of birds of different ages were breeders:

Age 1 : 0.0; Age 2: 0.10; Age 3: 0.33; Age 4: 0.80 and Age 5+: 1.0.

The base-case model assumes these values, but variants are also run in which these proportions are assumed to vary depending on prey availability (see later section).

Available Data – Pelagic fish

The diet of African penguins is dominated by anchovy and sardine (Hockey *et al.* 2005), and the breeding success of penguins is thought to be correlated with the abundance of these two pelagic fish species. Initial model versions have focused on using estimates of anchovy recruit biomass. Janet Coetzee and Carryn Cunningham kindly provided data on the abundance of anchovy and sardine spawners and recruits. Data from Coetzee were in the form of May recruit survey biomass for the various strata. Inshore and offshore estimates were summed for each stratum and combined biomass series computed by summing over different combinations of strata corresponding to the areas modelled. In each case the biomass estimates for a series were divided by the maximum observed value for that series, yielding relative abundance series. Some examples are given in Table 4, with no final decision as yet as to which series are the most appropriate to use.

POPULATION MODEL

An Age-Structured Dynamic Model

The basic dynamic model used to represent the population dynamics of the adult 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

$$N_y^{breed,s} = \omega_2 \cdot \sum_{a=2}^m v_{y,a} \cdot N_{y,a}^s \quad (5)$$

$$S_y^{j,s} = S_j^* \left(1 - \frac{\sum_{a=2}^m N_{y,a}^s}{K_s^*} \right) \quad (6)$$

$$\omega_1 = f_1(B_y) \cdot H_{max} \quad (7)$$

$$\omega_2 = f_2(B_{y-1}) \cdot 1 \quad (8)$$

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”);
- $v_{y,a}$ is the proportion of female penguins of age a that first attempt breeding in year y ;
- $f_1(B_y)$ is a breeding success factor (multiplier for H_{max}) 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 (5) 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 (assumed counted on the 1 December each year y) are given respectively by:

$$N_{y,Juv_moult}^s = N_{y,1}^s \cdot (S_y^{j,s})^{1/4} S_y^{5/12} \quad (9)$$

$$N_{y,Ad_moult}^s = \sum_{a=2}^m N_{y,a}^s \cdot S_y^{2/3} \quad (10)$$

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

$$P_{y,Juv_Tot} = N_{y,Juv_moult}^s / (N_{y,Juv_moult}^s + N_{y,Ad_moult}^s) \quad (11)$$

Adding Immigration and emigration effects

Adult African penguins very rarely breed at any other than the colony at which they first established breeding (Randall *et al.* 1987). However, first-time breeders are known to emigrate from natal colonies, likely in response to changing food availability (Whittington *et al.* 2005). Based on re-sightings of flipper-banded chicks over the period 1989 to 1999, Whittington *et al.* (2005) deduced that the predominant direction of movement of some young penguins was away from the south coast of the Western Cape (in the vicinity of Dyer Island), towards the western side of the Western Cape, centred on Robben and Dassen Islands. The model above was thus modified to allow emigration from Dyer Island to Boulders and to Robben and Dassen islands. The simplest case for initial investigation is that of immigration to Boulders because the trend in numbers at this colony can be explained only by immigration. However, the Boulders colony is relatively small and hence movement from Dyer Island to Boulders alone cannot explain the declining population trend at Dyer Island (unless an *ad hoc* assumption of increasing natural mortality over time is made for that colony). The methodology is first explained for the simpler case assuming movement from Dyer Island to Boulders only. For Dyer Island, Equation (3) for the case $a=2$ is modified as follows:

$$N_{y+1,a+1}^s = N_{y,a}^s \cdot S_y \cdot (1 - E_y) \quad (12)$$

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 (Table 1). Alternatively, this proportion can be set to zero. The actual number of birds emigrating each year $Enum_y^{Dyer}$ is thus:

$$Enum_y^{Dyer} = E_y \cdot S_y \cdot N_{y,2}^s \quad (13)$$

The proportion of the first time breeders that immigrate to Boulders (Bld) rather than to Robben or Dassen islands is determined by parameter E_{prop} , estimated by fitting to trend data for Robben and Dassen islands (RobDas). It follows that Equation (3) (for the case $a=2$) must be modified as follows for the RobDas and Bld colonies respectively:

$$N_{y+1,3}^{RobDas} = N_{y,2}^{RobDas} S_y + (1 - E_{prop}) \cdot Enum_y^{Dyer} \quad (14)$$

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

Starting values and equilibrium assumptions

The starting numbers of adult moulters (ages 2+) in each area are set using model estimates of the number of female moulters at the start of each series N_{0,Ad_moult}^s . As these estimates are assumed to correspond to 1 December, the estimates are adjusted to reflect the total numbers of penguins aged 2 and older on 1 April ($T_{0,2+}$) as follows:

$$T_{0,2+}^s = \frac{N_{0,Ad_moult}^s}{S_y^{2/3}} \quad (16)$$

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 $\omega_1 = H_{ave}$ (i.e. average fledging success computed by averaging the values in Table 1b for Robben island and assuming this may be taken to apply generally) and $\omega_2 = 1$ (i.e. all mature birds breed), simplifies the problem of solving for the starting (equilibrium) number of breeding females $N_0^{breed,s}$ through solving the balance equation:

$$N_0^{breed,s} = T_{0,2+}^s \cdot \left(q_f H_{ave} (S_0^{j,s})^{3/4} \right)^{-1} \cdot \left((S_0^{j,s})^{1/4} \cdot S_0^{3/4} \cdot \left(1 + \sum_{a=3}^{m-1} S_0^{a-2} + \frac{S_0^{m-2}}{(1-S_0)} \right) \right)^{-1} \quad (17)$$

with

$$S_0^{j,s} = S_j^* \left(1 - \frac{T_{0,2+}^s}{K_s^*} \right) \quad (18)$$

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

$$N_{0,a}^s = \begin{cases} N_0^{breed,s} q_f \cdot H_{ave} \cdot (S_0^{j,s})^{3/4} & a = 1 \\ N_0^{breed,s} q_f \cdot H_{ave} \cdot (S_0^{j,s}) S_0^{3/4} & a = 2 \\ N_0^{breed,s} q_f \cdot H_{ave} \cdot (S_0^{j,s}) S_0^{3/4} S_0^{a-2} & 3 \leq a < m \\ N_0^{breed,s} q_f \cdot H_{ave} \cdot (S_0^{j,s}) S_0^{3/4} S_0^{m-2} / (1 - S_0) & a = m \end{cases} \quad (19)$$

In the case of Boulders which was started as a new colony, the 1987 observed number of breeding pairs (7) is used as the starting value and is assumed to be without error.

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/Robben died in these yrs, with the number assumed dead from each age class computed on the assumption of proportionality to the abundance of that age class.

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

$$N_{y+1,a+1}^s = N_{y,a}^s \cdot S_y - p_a M_y^{oil} \quad (20)$$

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. comm) and hence it is assumed that only a small proportion (10%) of age 1 birds survived in those years.

Extra Mortality Events

Given the very large drop in the observed numbers of moulting penguins in 2006, it has been proposed that this may have been caused by a decrease in adult survival rate (over recent years from year ys) as a result of reduced prey availability. Along the same lines as Johnston and Butterworth (2003), the model includes an option that takes this into account by setting:

$$S_y = Z^{ad} \cdot S_y^{cons} \quad \forall \quad y \geq ys \quad (21)$$

where:

S_y^{cons} = the adult annual survival rate, assumed the same for all years prior to year ys ;

and

Z^{ad} = a multiplier (<1) parameter that is estimated within the model and reflects the reduction in adult annual survival from year ys (with S_y assumed the same lower value over this second period).

Fitting procedure

The moult counts are first halved to represent the number of females. These counts are assumed to be unbiased, log-normally distributed indices of the total numbers of adult female penguins such that:

$$I_y^{moult,s} = \hat{I}_y^s e^{\varepsilon_y^s} \quad \text{or} \quad \varepsilon_y^s = \ln(I_y^{moult,s}) - \ln(\hat{I}_y^s) \quad (22)$$

where $I_y^{moult,s}$ is the (observed) moult count 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 (10);

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

ε_y^s from $N(0, (\sigma_y^s)^2)$.

The estimable parameters are thus estimated by minimising the following negative log likelihood function (after removal of constants) with contributions added over sub-areas s :

$$-\ln L = \sum_s [n_s \ln(\hat{\sigma}_s)] + \frac{n_s}{2} \quad (23)$$

with

$$\hat{\sigma}_s = \sqrt{\left[\sum_{y=1}^{n_s} (\ln I_y^{moult,s} - \ln \hat{I}_y^s)^2 \right] / n_s} \quad (24)$$

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:

$$\ln \hat{q}^s = \frac{1}{n_s} \sum_y (\ln I_y^s - \ln \hat{N}_{y,Ad_moult}^s) \quad (25)$$

In model versions that fit to the counts of the numbers of breeding females, the contribution to the log likelihood is computed similarly except that q is assumed equal to 1. As the number of breeding females is a subset of the number of moulters, the former must be less than or equal to the latter. However, given observation error, some of the observed moult counts (expressed in terms of females only) are less than the corresponding number of breeding females. It was thus assumed that the counts of breeding females represent the actual number of breeding females,

but that the (female portion of the) moult counts represent a proportion (given by parameter q) of the total number of female moulters.

Proportion of juveniles:

The log likelihood contribution from the juvenile proportional abundance data is calculated as in Equation (22) with σ given by:

$$\hat{\sigma} = \sqrt{\left[\sum_{y=1}^{n'_s} \left(I_y^{Prop,s} - \hat{p}_{y,Juv:Tot}^s \right)^2 \right] / n'_s} \quad (26)$$

where

- $I_y^{Prop,s}$ is the (observed) juvenile proportional abundance data for sub-area s and year y ;
- n'_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 (11).

Algoa Bay Model

A preliminary model for this region (area iii)) has been constructed and can be linked to the sub-area i) model or treated separately. The same equations are used as for the other sub-areas. Available data on the numbers of breeding pairs (from SWG/EAF/SEABIRDS/7) are used for fitting purposes (for years for which such data are available) (Table 1b). It is assumed in the preliminary model version that a proportion E_2 (estimated within the model) of penguins may move from Algoa Bay to Robben/Dassen over the period y_{e1} to y_{e2} . Preliminary values assumed for these last two parameters are 1999 and 2002 under the assumption that the birds would have moved only when prey availability increased in the west. This process modelled in the same way as given in Equations (12)-(14), except that the penguins are not assumed to move to Boulders (so that the corresponding $E_{prop} = 0$).

Variables in the model that depend on local prey abundance are all modelled separately for Algoa Bay, e.g. there are different area i) and area iii) time series values for the breeding proportion, average number of chicks fledged, proportion maturing at different ages and density dependent factors.

Annual variation in adult survival rate

The simplest version of the model assumes adult survival S is either constant over time or two different values are modelled as described by Equation (21). 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):

$$M_y = -\ln S_y \quad (27)$$

where $M_y = M e^{\eta_y}$ $\eta_y \sim N(0, (\sigma_\eta)^2)$ (28)

and the M and η_y 's become estimable parameters. The following further term is then added to the negative log likelihood:

$$\sum_y (\eta_y)^2 / (2\sigma_\eta^2) \tag{29}$$

where an appropriate value of σ_η is input (with the sensitivity of results to alternatives for this choice desirably checked).

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 (28)).

Parameter constraints

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

- $0 < S \leq 1.0$
- $0 < S_j^* \leq 1.0$
- $0 \leq E \leq 1.0$
- $0 \leq E_{prop} \leq 1.0$
- $0 \leq Z \leq 1.0$
- $0 \leq E_2 \leq 1.0$
- $0 < H_{crit} \leq 1.0$
- $0 < N_{0,Ad_moult}^{RobDas}$
- $0 < N_{0,Ad_moult}^{Dy}$
- $0 < N_{0,Ad_moult}^{Bld}$

Not all these parameters are estimated in every simulation. For example, in versions assuming no movement, E and E_2 are set equal to zero.

Breeding proportions, chicks fledged and proportion mature

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 (8). 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. 6). 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. 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_{crit}^r value, but that the proportion breeding decreases linearly for lower values of B^r . The base-case model estimates B_{crit}^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 (see data section) do not change over time. An example of another option would be the assumption that the proportion maturing at ages 3 and 4 remains fixed at the base-case value if relative prey biomass is below the median B_{crit}^r value, but then increases linearly with higher values of B^r up to some maximum value. The maximum value has preliminarily been set at 0.9 (i.e. 90%), as illustrated in Fig. 7.

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_I functional dependence in Equation (7). The model can currently be run either by using the values for Robben island as shown in Table 1b, 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 B value (1.04 chicks fledged per year per pair – Table 1b).

There are a number of ways in which this relationship could be modelled. Following Plagányi and Butterworth (2006), a breeding success factor $f_1(B_y^s)$ 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. 8). 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 :

$$f(B_y^a) = \frac{\alpha \cdot B_y^a}{\beta + B_y^a} \tag{30}$$

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

When adding a term to allow for fluctuations about this relationship, Equation (30) becomes:

$$f(B_y^a) = \frac{\alpha \cdot B_y^a}{(\alpha - 1) + B_y^a} e^{(\zeta_{ay} - \sigma_{BR}^2/2)} \tag{31}$$

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 (31) is re-parameterised in terms of the maximum pelagic biomass, B'_{MAX} , and the “steepness” h of the relationship, where “steepness” is the fraction of maximum fledging success that results when B'_y drops to 20% of its maximum level, from which it follows that:

$$h = \frac{\alpha}{5\alpha - 4} \quad (32)$$

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. 8). 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} .

For illustrative purposes, h is set equal to 0.66 (see Fig. 8) and a deterministic relationship is assumed in the simulations presented. Alternatively, a best fit value of h is obtained in the model by adding a term to the negative log likelihood that compares the time series of observed and model chick fledging success rates.

RESULTS AND DISCUSSION

There is insufficient time to present results for all scenarios here hence only a few results are mentioned to assist in discussing the further development/refinement of the model.

Previous analyses have demonstrated the sensitivity of modelled penguin abundance trends to the choice of the adult survival parameter S . In previous analyses, rather than estimating survival within the model, the average and maximum of published values (Table 3) were substituted. The results suggested that these survival estimates are too low to sustain populations, even when considering movement from Dyer to Robben/Dassen and Boulders.

Simulations using the revised model do not change this conclusion. As an illustration, results are presented for the Robben/Dassen model on its own, i.e. when assuming no movement. Even with most reproductive parameter settings at their maximum values, the maximum observed juvenile and adult survival values result in approximately constant trends (Fig. 9a). In other words, if the maximum of the survival values from Table 3 are used, if no movement is assumed the model is unable to replicate the observed increase rates. As an alternative investigation, the two survival parameters were estimated within the model when assuming no movement, with the results suggesting that to replicate the observed trends, unrealistically high survival rates are required (0.94 and 0.98) (Fig. 9b). In addition to simulate the recent downturn in the numbers of moulters and breeders (Fig. 9), the model estimates an additional mortality factor equivalent to assuming that adult survival w.e.f. 2004 has decreased to 0.62.

These results were generated using the observed fledging success estimates. As an alternative, it was assumed that for all years the average number of chicks fledged per pair was equal to the maximum observed value of 1.04. In this case an increase in the number of moulters ensued when assuming the maximum observed survival values, but it was still not enough to explain the large observed increase in the moult counts.

Next model simulations were conducted which assume that first-time breeders move from Dyer to Boulders (to match the Boulders population data) and to Dassen and Robben. In the first instance survival parameters were estimated but this again resulted in unrealistically high values (0.91, 0.93) in an attempt to match the observed trends. If the survival parameters were fixed at the maximum observed values, the movement was still not sufficient to explain the observed increase in the number of breeders at Robben/Dassen (as the Dyer numbers are not high enough) (Fig. 10b).

A substantial improvement results when movement from Algoa is assumed, although this component of the model is still preliminary only and the associated results should similarly be regarded as preliminary only. An example of results when applying the full model is shown in Figs 11a-c with model estimates summarised in Table 5.

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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We are grateful for data from Rob Crawford and Les Underhill, as well as inputs from both them and the rest of penguin task group. Thanks to Janet Coetzee and Carryn Cunningham for providing pelagic fish abundance estimates. Penn Lloyd provided valuable additional insights.

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Table 1a. Summary of raw data provided by R. Crawford and L. Underhill. Counts of the numbers of moulting birds have been halved to represent the number of female moulters per year, so as to make them comparable with the numbers of breeding pairs, which also comprises a count of the numbers of breeding females per year.

Dyer	No. breeding prs = no. breeding females	
	Female moulters	Female breeders
1990		8349
1991		6115
1992		7579
1993		2374
1994		4649
1995		4260
1996		3279
1997		2745
1998		1963
1999		2363
2000	2289	2220
2001	2383	2088
2002	2108	2145
2003	2526	1929
2004	3088	2216
2005	1707	2053
2006	1674	2057
2007	1472	
Robben		
	Female moulters	Female breeders
1988		849
1989	1729	829
1990	1696	1278
1991	2365	1879
1992	2458	2027
1993	3269	2176
1994	4001	2799
1995	3974	2279
1996	3282	3097
1997	2804	3336
1998	4348	3467
1999	4699	4399
2000	5882	5705
2001	6681	6723
2002	8219	7252
2003	7368	6433
2004	8712	8524
2005	6435	7152
2006	3884	3697
2007	3314	
Dassen		
	Female moulters	Female breeders
1988		6508
1989		8428
1990		8720
1991		9012
1992		7563
1993		7199
1994		9389
1995	6180	9792
1996	6111	9502
1997	6477	8651
1998	8148	10918
1999	10719	15155
2000	12537	15598
2001	13048	21409
2002	12809	22883
2003	11255	20319
2004	8796	24901
2005	9149	22687
2006	5672	13283

Table 1b. Summary of data input to model. Data kindly provided by R. Crawford and L. Underhill. Counts of the numbers of moulting birds have been halved to represent the number of female moulters per year, so as to make them comparable with the numbers of breeding pairs, which also comprises a count of the numbers of breeding females per year. The breeding success data from R. Crawford represent the average numbers of chicks fledged per pair (i.e. per female) per year. Data shown in italics are interpolated or computed as described in the text.

	Number of female moulters		Number of breeding pairs				Breeding success (chicks/pr)
	Robben and Dassen	Dyer_update	Robben and Dassen	Dyer	Boulders	Algoa	Robben
1987					7		
1988			<i>7357</i>		34		
1989	<i>7909</i>		<i>9257</i>		38		0.42
1990	<i>7876</i>		<i>9998</i>	8349	54		0.32
1991	<i>8545</i>		<i>10891</i>	6115	131		0.59
1992	<i>8638</i>		<i>9590</i>	7579	158		0.59
1993	<i>9449</i>		<i>9375</i>	2374	241	22747	0.54
1994	<i>10181</i>		<i>12188</i>	4649	359		0.45
1995	<i>10154</i>		<i>12071</i>	4260	366		0.38
1996	<i>9392</i>		<i>12599</i>	3279	416		0.65
1997	<i>9280</i>		<i>11987</i>	2745	726		0.97
1998	<i>12496</i>		<i>14385</i>	1963	555		0.75
1999	<i>15418</i>		<i>19554</i>	2363	906	18490	0.60
2000	<i>18419</i>	2289	<i>21303</i>	2220	949	20331	0.36
2001	<i>19729</i>	2383	<i>28132</i>	2088	1054	22695	0.84
2002	<i>21029</i>	2108	<i>30135</i>	2145	1083		0.90
2003	<i>18624</i>	2526	<i>26752</i>	1929	1033	10193	0.57
2004	<i>17508</i>	3088	<i>33425</i>	2216	1196	13865	0.72
2005	<i>15584</i>	1707	<i>29839</i>	2053	1227	8050	1.04
2006	<i>9557</i>	1674	<i>16980</i>	2057	1075	11467	0.518
2007		1472				5418	

Table 2. Summary of adult and juvenile (birds undergoing first moult) penguin moult counts (from L. Underhill). The numbers represent males and females combined. The proportion of juveniles is computed as the number of juveniles divided by the sum of the adult and juvenile numbers. A combined index for this proportion for Robben and Dassen Islands combined has been derived by summing adult and juvenile numbers for all years for which data are available for both islands, and using just the Robben island data for the remaining years.

	Robben		Dassen		Combined	Dyer		Prop. Juvs/total
	Ad	Juv	Ad	Juv	Prop. Juvs/total	Ad	Juv	
1989	3459	842			0.196			
1990	3392	866			0.203			
1991	4730	911			0.161			
1992	4915	1598			0.245			
1993	6538	1597			0.196			
1994	8002	1585			0.165			
1995	7948	1373	12360	1578	0.127			
1996	6563	1403	12222	1767	0.144			
1997	5608	2138	12953	4823	0.273			
1998	8696	2351	16296	3418	0.188			
1999	9397	2834	21438	8380	0.267			
2000	11765	2803	25074	8462	0.234	4579	269	0.055
2001	13362	2565	26095	6683	0.190	4765	501	0.095
2002	16439	3921	25619	8380	0.226	4216	405	0.088
2003	14737	3330	22511	5409	0.190	5052	432	0.079
2004	17424	3440	17592	3864	0.173	6177	239	0.037
2005	12871	2617	18298	5134	0.199	3414	385	0.101
2006	7768	2653	11345	2184	0.202	3348	161	0.046
2007	6629	2023			0.234	2944	180	0.057

Table 3. Summary of adult and juvenile survival rates estimated for African penguins.

<i>Adult survival rate</i>			
Value	Locality	Period	Source
0.91	St Croix Island	1976-1982	Randall 1983
0.69	Dyer Island	1979-1985	La Cock and Hänel 1987
0.82	Robben Island	1993-1994	Crawford <i>et al.</i> 1999
0.80	Dassen Island	1990-1999	Whittington 2002
0.82	Robben Island	1990-1999	Whittington 2002
0.8-0.9	Western Cape	1994-2002	Altwegg 2006
0.69	Robben Island	2006?	L. Underhill pers comm
0.808	<i>Average value (excl. last entry which is for one yr)</i>		
0.91	<i>Maximum value</i>		
<i>Juvenile survival rate</i>			
Value	Locality	Period	Source
0.32	St Croix Island	1976-1982	Randall 1983
0.69	Dyer Island	1979-1985	La Cock and Hänel 1987
0.31	Robben Island	1987-1999	Whittington 2002
0.38	Dassen Island	1987-1999	Whittington 2002
0.425	<i>Average value</i>		
0.69	<i>Maximum value</i>		

Table 4. Summary of anchovy and sardine biomass abundance estimates from surveys (from J. Coetzee, MCM) summed over strata as shown (see Fig. 2 for summary of strata) and after dividing values by the maximum for each series so that the indices shown represent biomass as a proportion of the maximum observed value over the time series. The values have been plotted in Fig. 5.

	<u>Anchovy</u>			<u>Sardine</u>			<u>Anchovy</u>	
	A_E	C_E	D	A_E	C_E	D	G series	I series
1985	0.13	0.15	0.48	0.11	0.07	0.14	0.13	0.13
1986	0.27	0.21	0.17	0.07	0.11	0.01	0.27	0.27
1987	0.36	0.28	0.20	0.14	0.17	0.00	0.36	0.36
1988	0.25	0.18	0.22	0.03	0.03	0.01	0.25	0.25
1989	0.08	0.08	0.15	0.19	0.29	0.28	0.08	0.08
1990	0.08	0.04	0.02	0.09	0.11	0.03	0.08	0.08
1991	0.23	0.04	0.03	0.09	0.04	0.06	0.23	0.23
1992	0.20	0.19	0.40	0.24	0.12	0.22	0.20	0.20
1993	0.21	0.21	0.56	0.29	0.09	0.11	0.21	0.21
1994	0.06	0.08	0.06	0.21	0.30	0.01	0.06	0.06
1995	0.17	0.17	0.17	0.51	0.62	0.04	0.17	0.30
1996	0.03	0.03	0.02	0.18	0.27	0.05	0.03	0.15
1997	0.17	0.15	0.09	0.45	0.45	0.38	0.17	0.15
1998	0.18	0.17	0.12	0.22	0.31	0.00	0.06	0.15
1999	0.32	0.34	0.19	0.28	0.39	0.00	0.24	0.15
2000	1.00	1.00	1.00	0.47	0.31	0.16	0.10	0.01
2001	0.79	0.52	0.87	1.00	1.00	1.00	0.02	0.51
2002	0.56	0.45	0.15	0.85	0.76	0.17	1.00	1.00
2003	0.57	0.45	0.13	0.73	0.99	0.12	0.01	0.96
2004	0.42	0.55	0.16	0.07	0.09	0.02	0.02	0.91
2005	0.12	0.11	0.01	0.02	0.02	0.00	0.01	0.56
2006	0.11	0.11	0.01	0.08	0.09	0.00	0.07	0.20

Table 5. Summary of example results for full model including all areas and assuming movement.

Model	Full model with movement				
<u>Parameter estimates</u>					
No. of parameters estimated					
<i>S</i>	0.91				
<i>Z [S*Z]</i>	0.66	0.60			
<i>S_{j*}</i>	0.72				
<i>E</i>	0.90				
<i>E_{prop}</i>	0.15				
<i>E₂</i>	0.59				
<i>H_{crit}</i>	0.01				
<i>a</i>	1.15	fix			
<i>N_{0,2+} (RD)</i>	9242				
<i>N_{0,2+} (Dy)</i>	9558				
<i>N_{0,2+} (Alg)</i>	20249				
<u>Likelihood contributions</u>					
-ln L RD moult	-25.143				
-ln L RD breed	-33.178				
-ln L Dy moult	-10.182				
-ln L Dy breed	-15.615				
-ln L Bd breed	12.552				
-ln L Alg breed	-3.598				
-ln L RD prop	-36.350				
-ln L Dy prop	-13.577				
-ln L TOTAL	-125.090				
<i>q</i> RD	0.64				
<i>q</i> Dy	0.86				
<u>Model version</u>	<u>Age 1</u>	<u>2</u>	<u>3</u>	<u>4</u>	<u>5</u>
<i>Proportion mature at age</i>	0	0.1	0.33	0.8	1
<i>Pelagic series</i>	0				
<i>Z start year</i>	2004				
<i>Algoa emmig. start / end yrs</i>	1993	2006			
<i>K factor</i>	10				
<i>Hmax</i>	1.04				
	<u>1994</u>	<u>2000</u>			
<i>No's die (oiling)</i>	2500	1000			

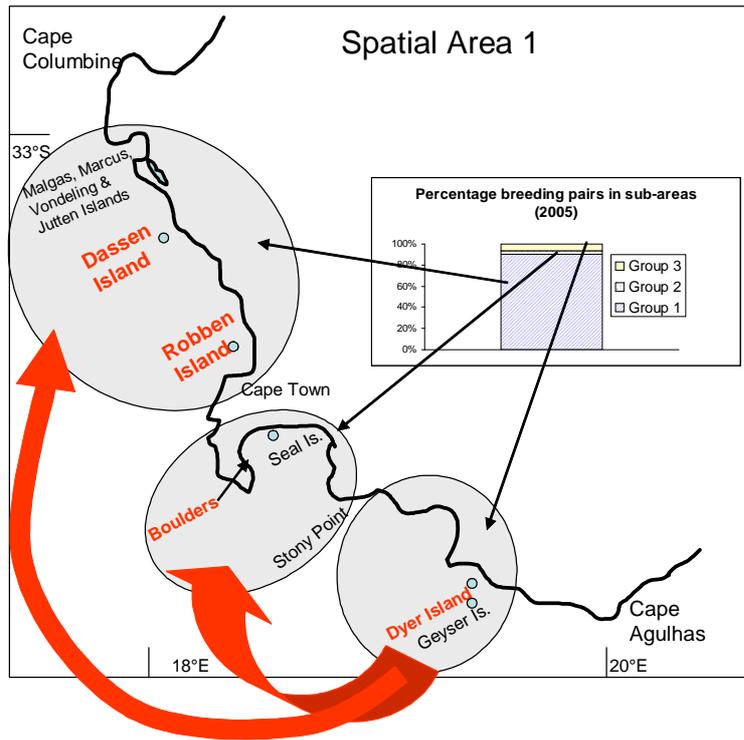


Fig. 1. Map showing location and possible grouping of penguin colonies in the “western” area (area i)). The colonies currently included in the model are shown in bold red text. The arrows represent movement of penguins from Dyer Island to Boulders, as well as movement to Robben and Dassen Islands as is explored in the model.

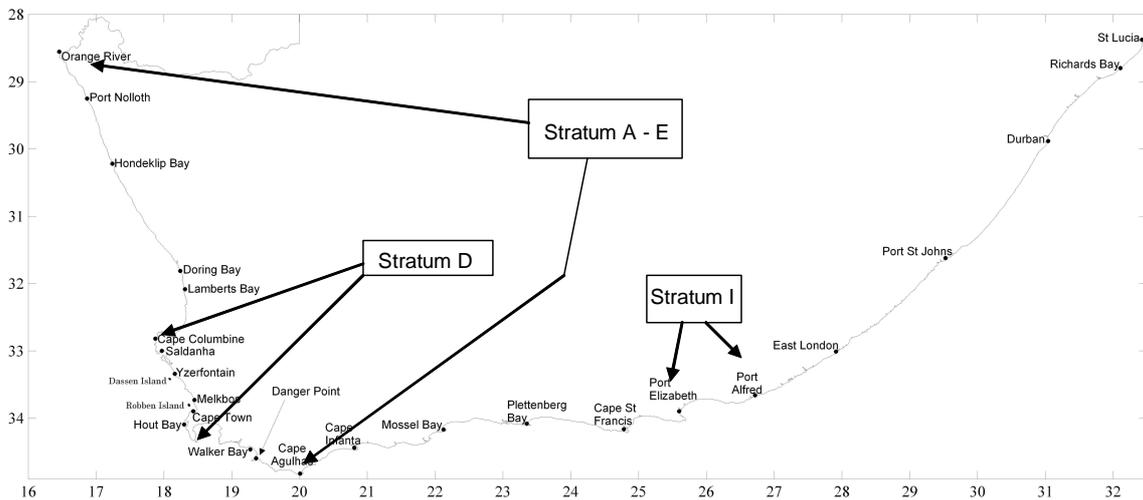


Fig. 2. Map showing extent of strata corresponding to pelagic fish biomass estimates used to link to penguin breeding success in the area i) model (which includes Dassen, Robben, Dyer island and Boulders) and preliminary model for St Croix in area iii). Basic map provided by Janet Coetzee (MCM).

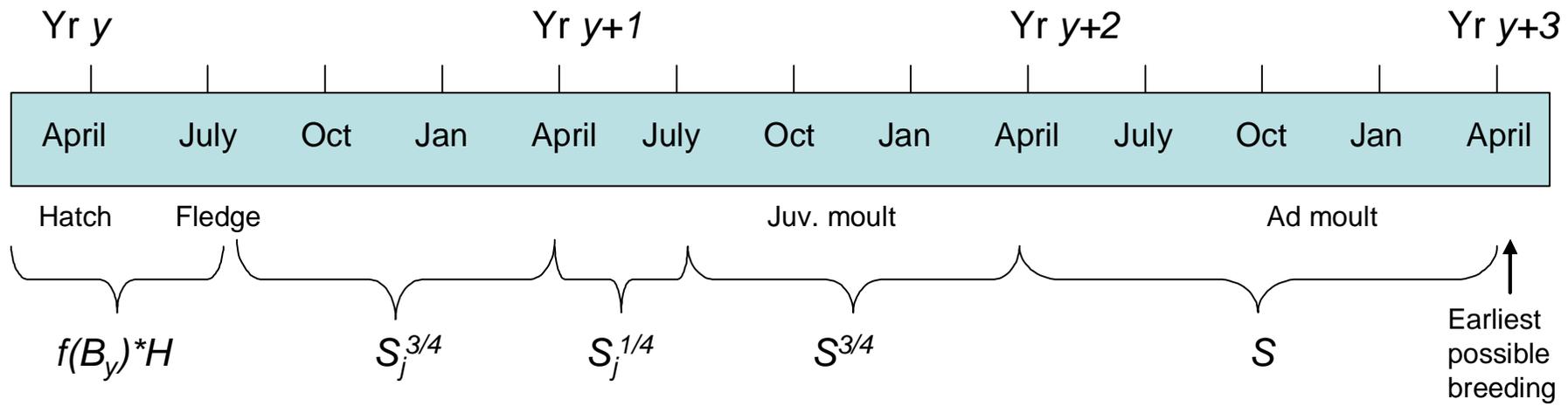


Fig. 3. Schematic summary of timeline detailing life history of an average penguin, to illustrate different survival factors applied in the modelling analyses.

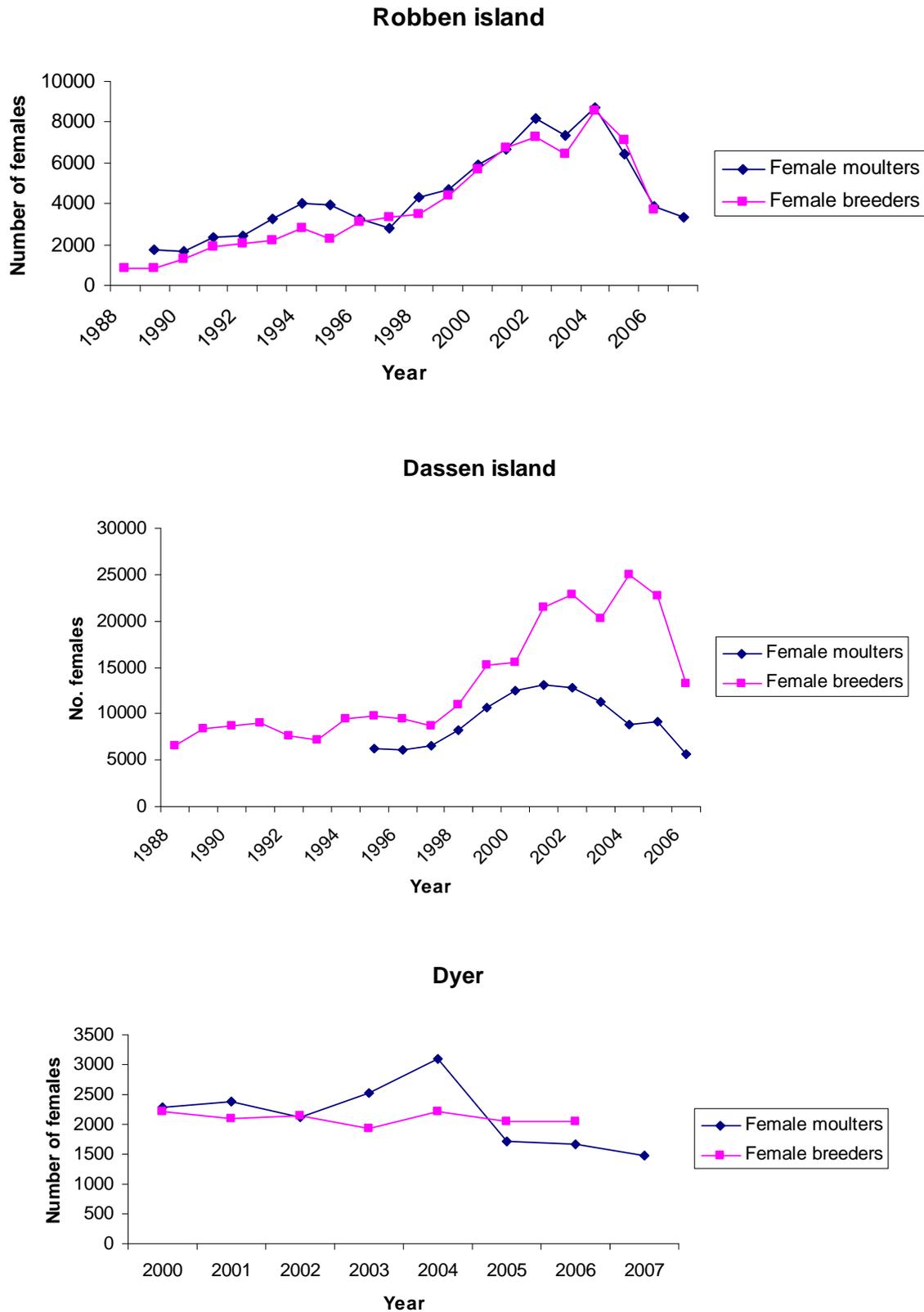


Fig. 4. Plot of numbers of female moulters (assuming a 50:50 sex ratio) and numbers of breeding pairs of penguins at Robben, Dassen and Dyer Island. The number of adult moulters includes all animals aged (approximately) two year and older whereas breeding females are aged approximately four years and older. The latter index would thus be smaller than the former if both reflected complete censuses.

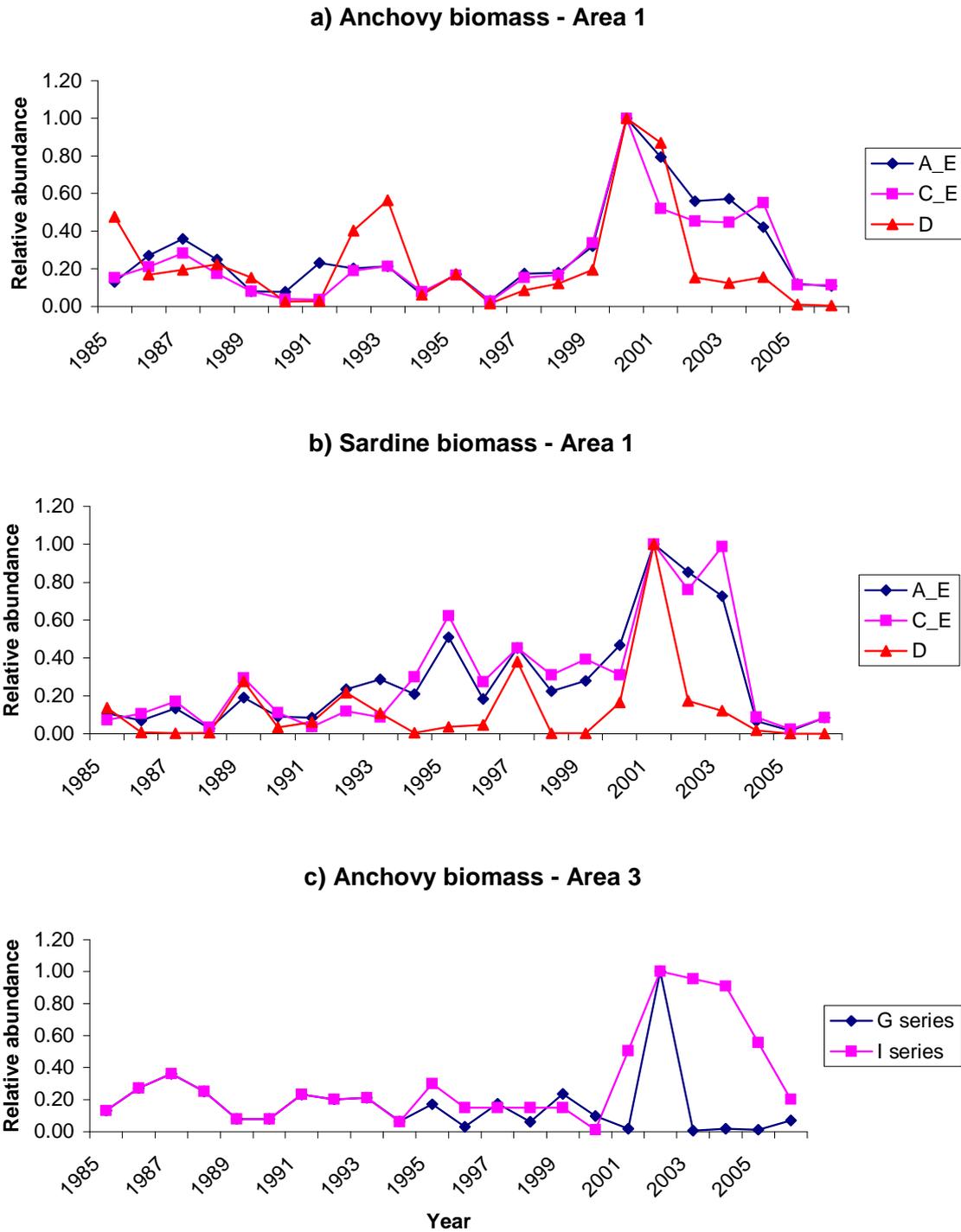


Fig. 5. Estimates from surveys (from J. Coetzee) of May anchovy and sardine recruit biomass in different strata. The data have been variously aggregated across different strata and are shown as a proportion of the maximum observed value for each series.

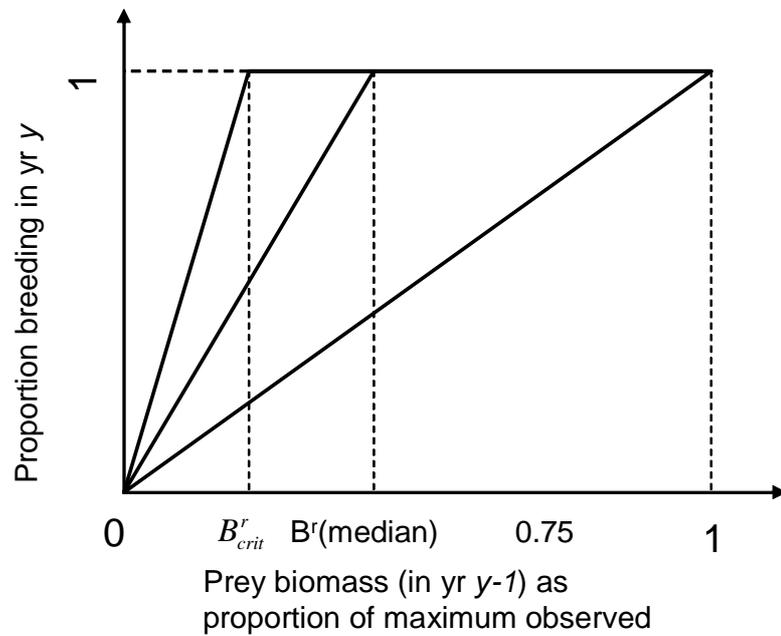


Fig. 6. Schematic showing different possible assumptions regarding the change in the proportion of mature birds that choose to breed (in April) each year y as a function of relative prey biomass B^r the previous year $y-1$, where prey biomass is computed as relative to the maximum value observed over a series. This is the f_2 functional dependency of Equation (8) described in the text. 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. 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 .

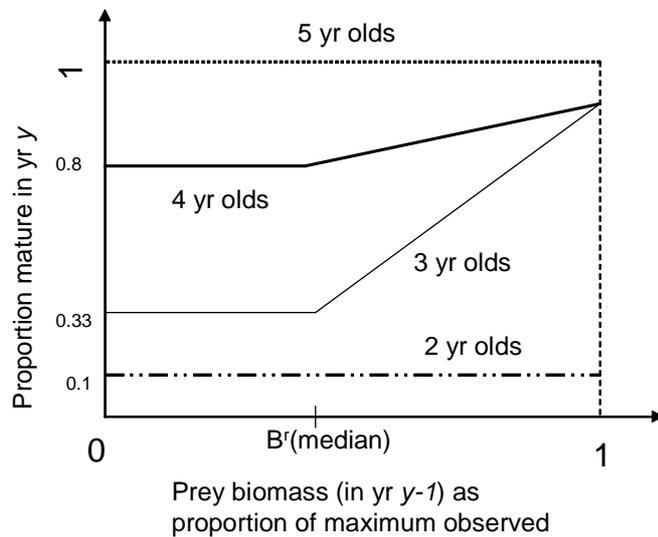


Fig. 7. Schematic showing different possible assumptions regarding the change in the proportion of birds of different ages that mature each year y as a function of relative prey biomass B^r the previous year $y-1$, where prey biomass is computed as relative to the maximum value observed over a series. The simplest assumption is that these proportions do not change over time. An example of another option being tried in the model involves assuming that the proportion maturing at ages 3 and 4 remains fixed at the base-case value if relative prey biomass is below the median B^r value, but then increases linearly with higher values of B^r up to some maximum value.

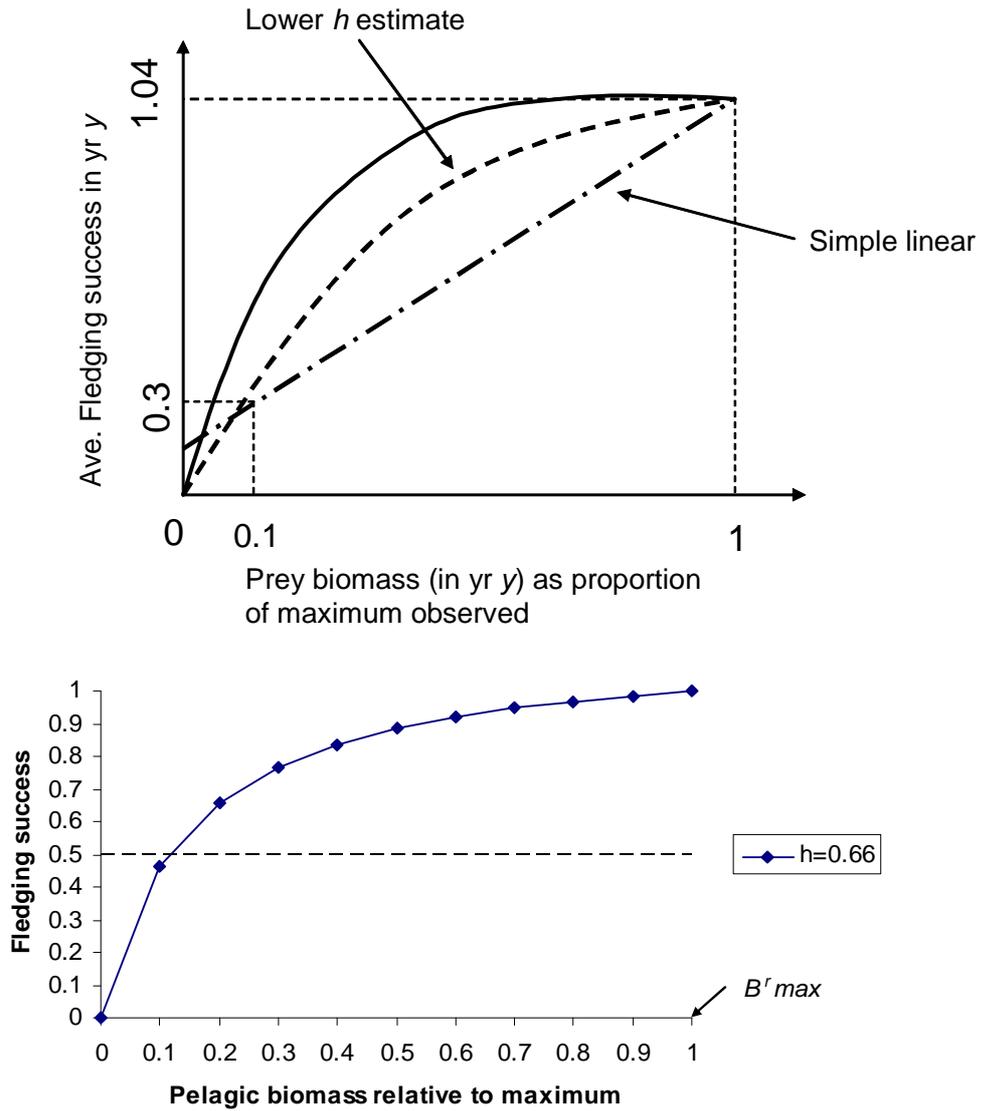


Fig. 8. Schematic showing different possible assumptions regarding the change in the average fledging success each year y as a function of relative prey biomass B^r in the same year y , i.e. the f_l functional dependence in Equation (7). Prey biomass is computed as relative to the maximum value observed 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.

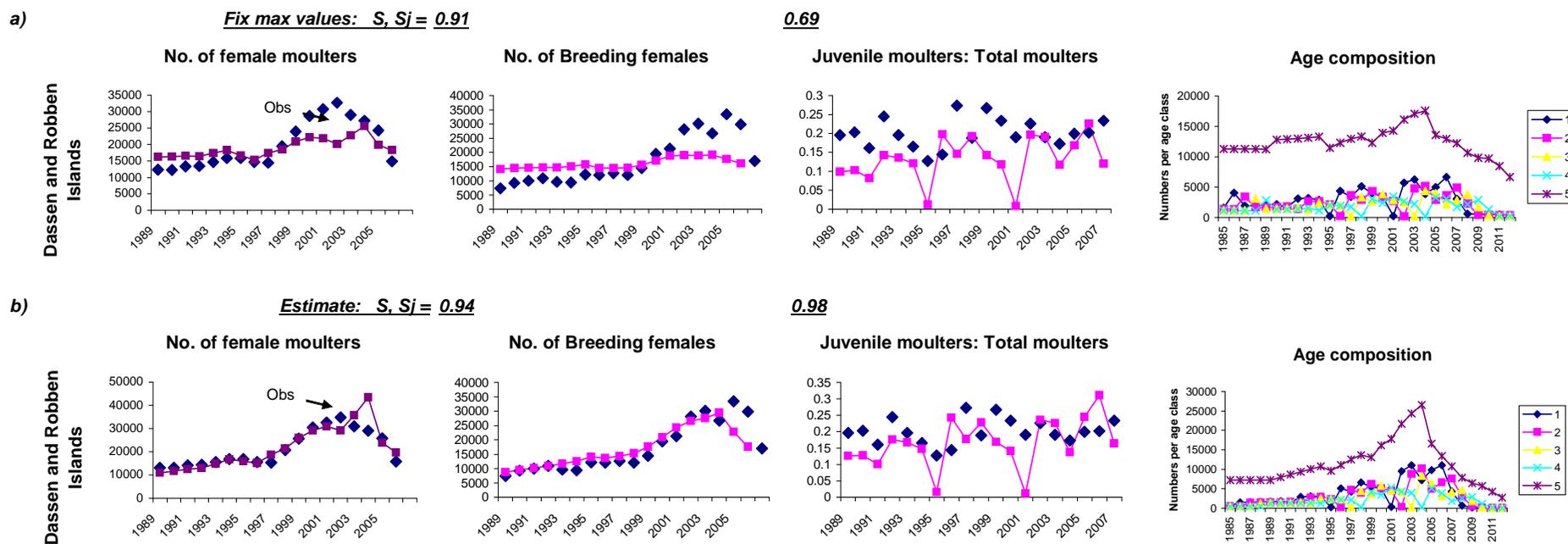


Fig. 9. Summary of results from Robben/Dassen model on its own (i.e. when assuming no movement) and for scenarios with: a) survival values fixed at the maximum of the observed values (Table 3), and then b) estimated within the model. In both cases the proportion of mature birds which are assumed to breed each year is fixed at 1, and the chick fledgling success rates are assumed equal to the observed values listed in Table 1b.

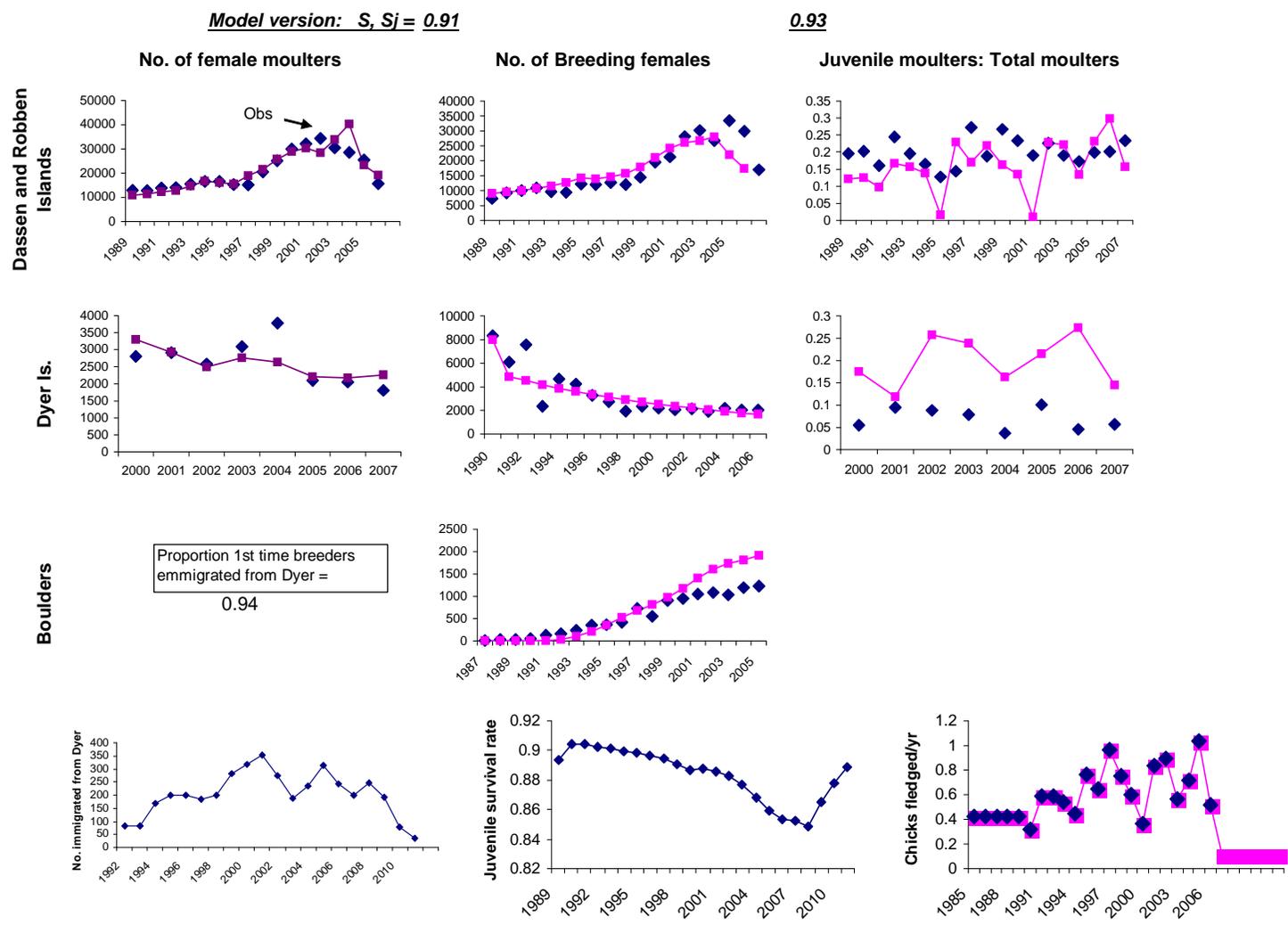


Fig. 10a. Summary of results when assuming movement occurs from Dyer island to Dassen/Robben and Boulders, and when estimating both the movement and survival parameters.

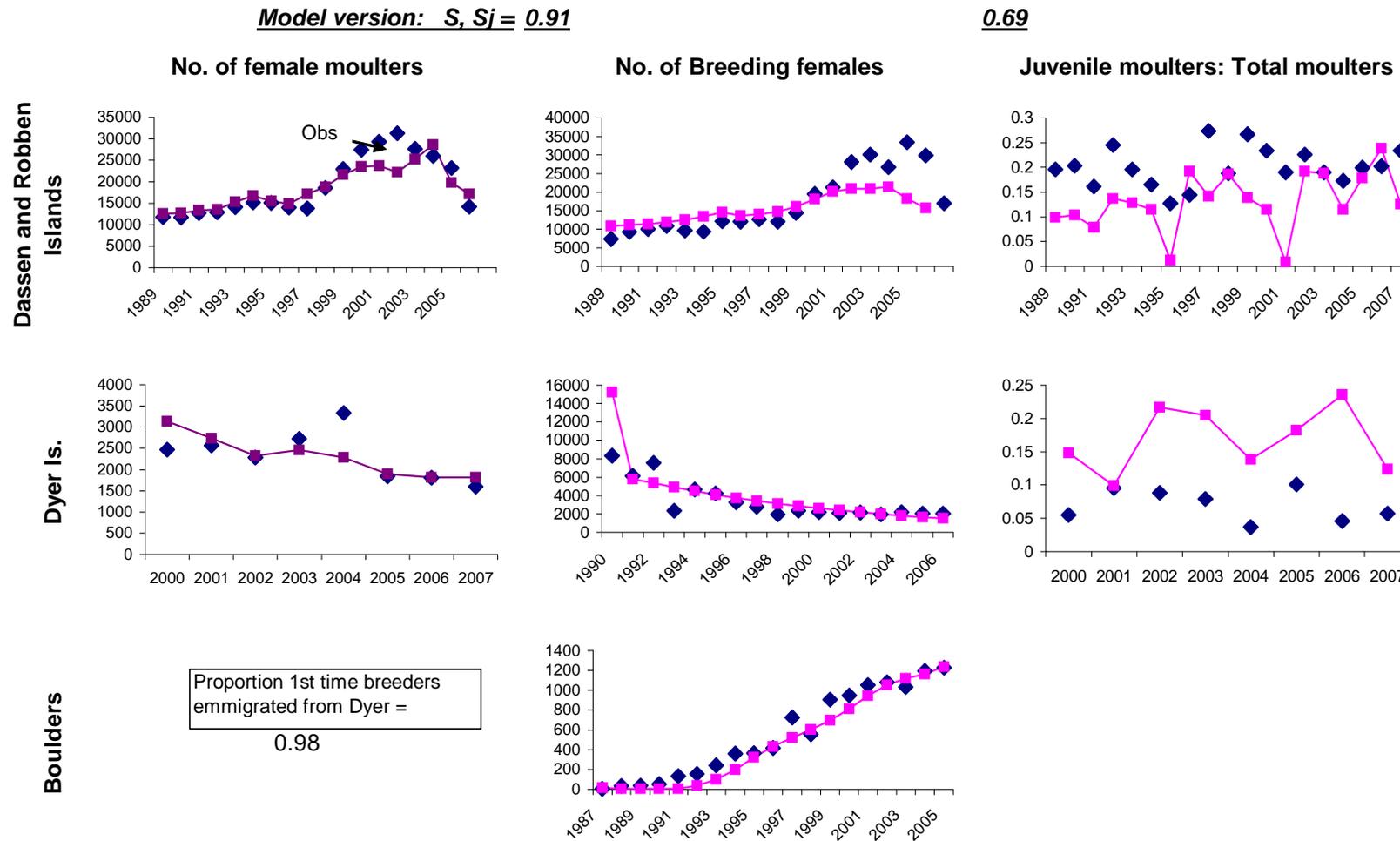


Fig. 10b. Summary of results when assuming movement occurs from Dyer island to Dassen/Robben and Boulders, and when estimating the movement parameters but fixing the survival parameters at the maximum values shown in Table 3.

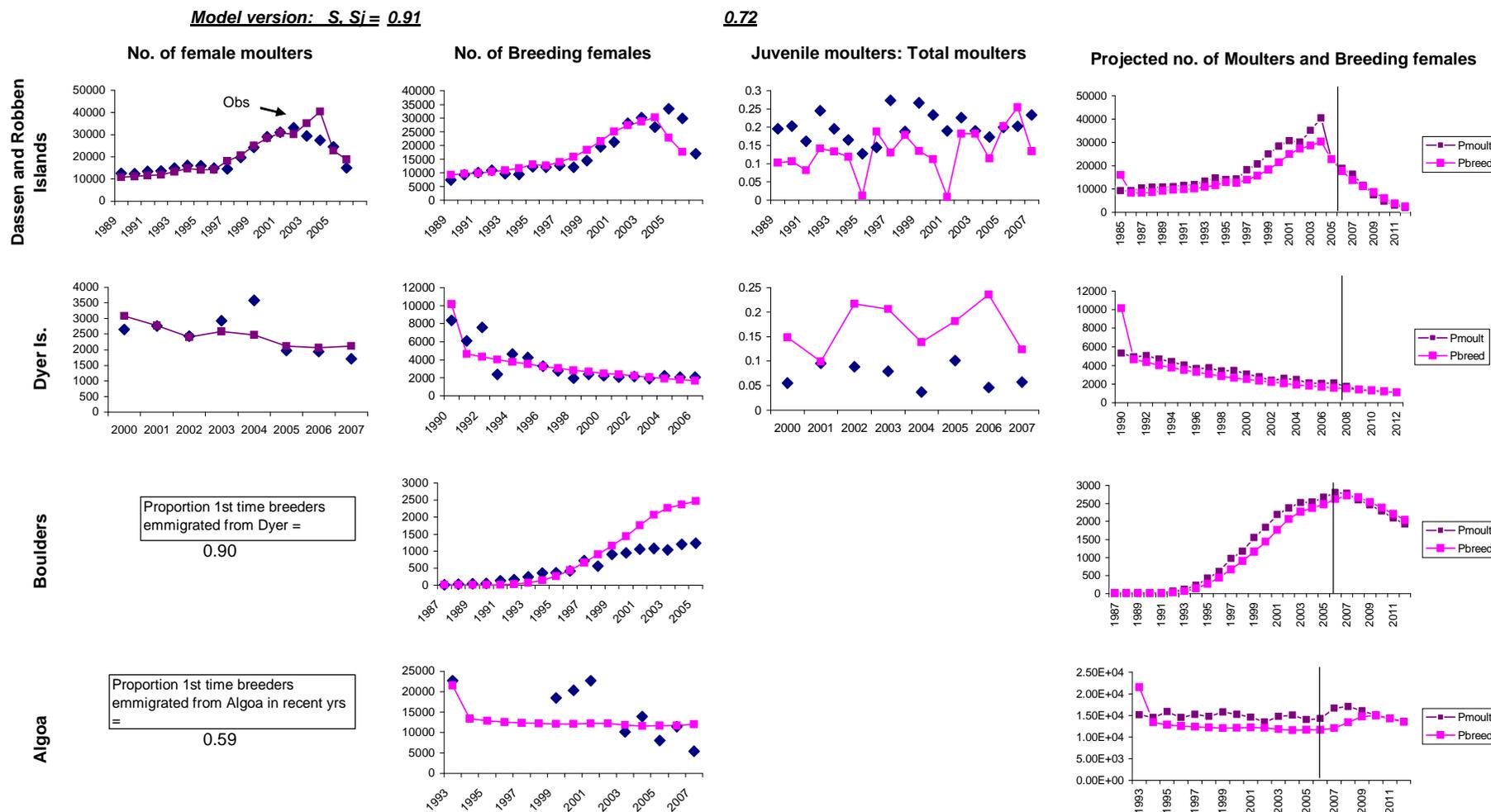


Fig. 11a. Illustrative preliminary results from full model. Model-predicted trajectories of the numbers of female moulting penguins (left panel), number of breeding pairs (2nd from left), proportion juveniles and projected numbers of both population components (right) at Robben and Dassen island combined (top panel); Dyer island (2nd from top), Boulders (3rd from top) and Algoa Bay. Observed data are shown as diamond points not joined by a line. Note the mismatch for Boulders is because emigration form Dyer island is assumed to occur over the full period.

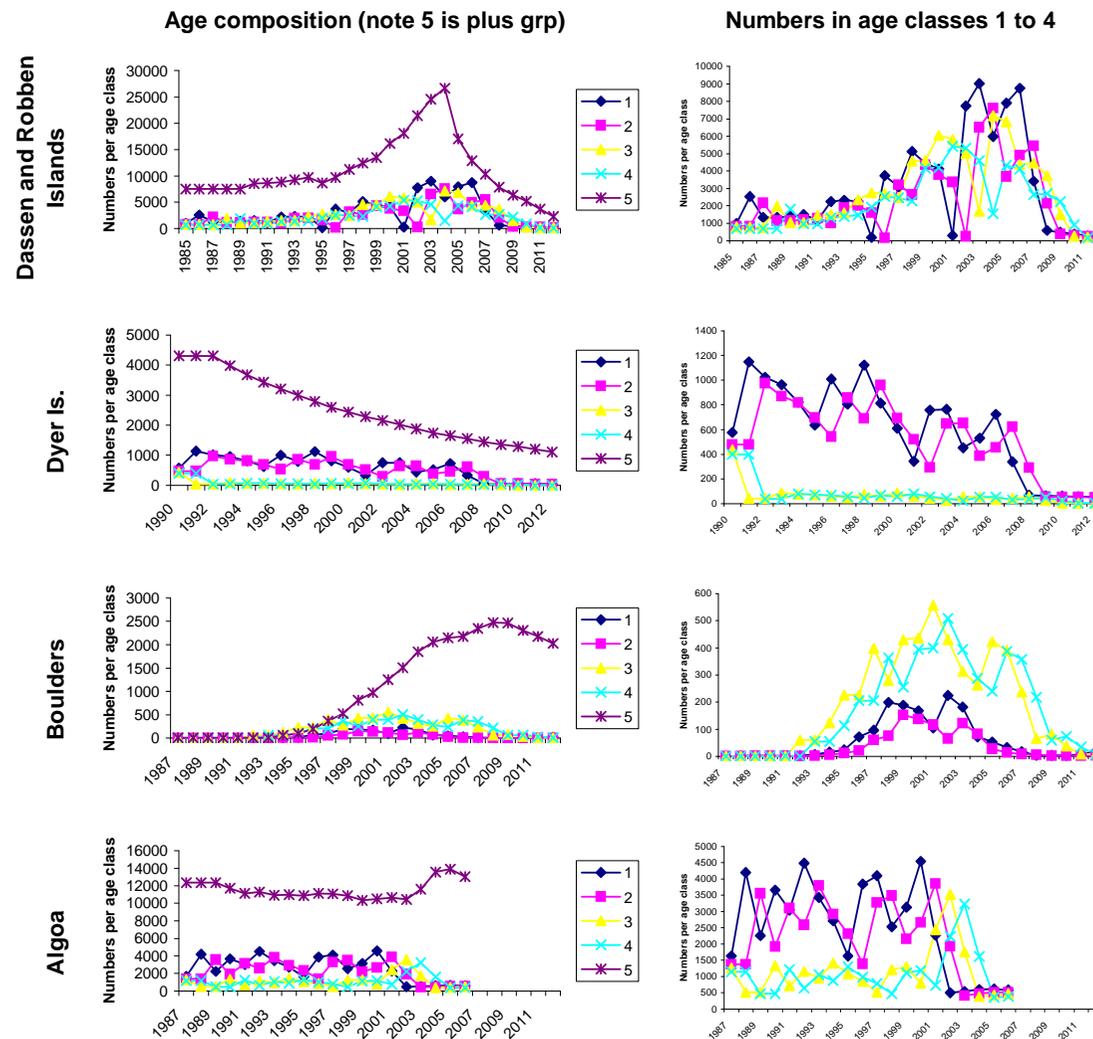


Fig. 11b. Illustrative preliminary results from full model. Age structure.

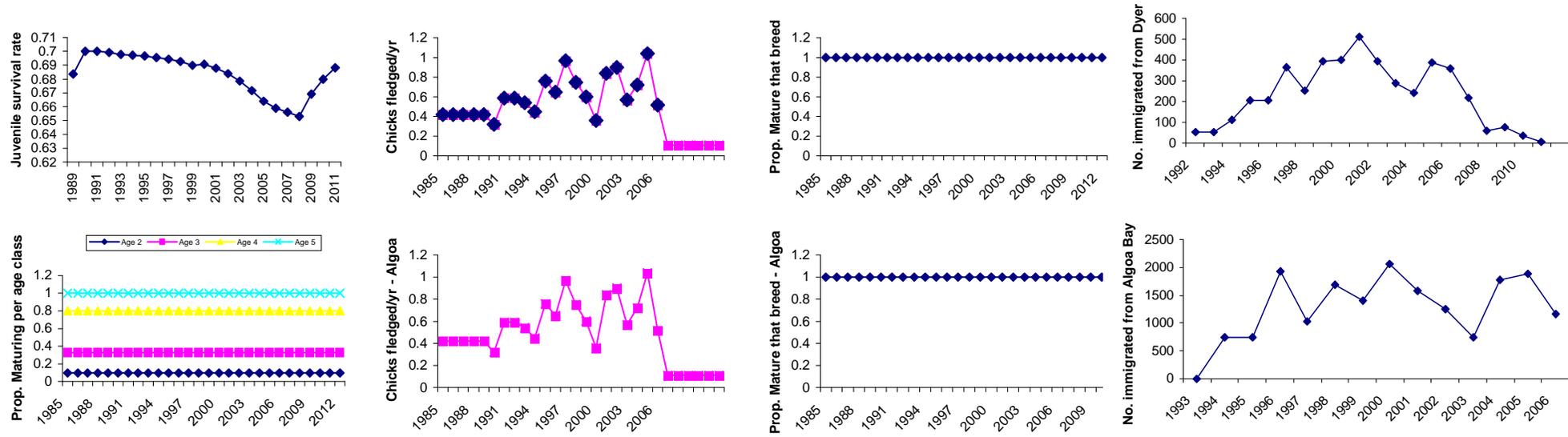


Fig. 11c. Illustrative preliminary results from full model.