

A Spatial Model of African Penguin *Spheniscus demersus* Populations in the western Cape

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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 only, the model is of a form that can readily be linked to the pelagic OMP (Operational Management Procedure) to take account of the relationship between the breeding success 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 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, the model should 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;
- 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 of the 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 modeled. 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. The second population is Dyer Island because it has the next largest numbers of penguins, recent declines in the population 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 it is relatively small, it was considered important to include because of its position, it has been a focus of several other studies and 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.

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 sub-areas:

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

And hence that there will be two sets of penguin colonies modelled, corresponding to i) and iii) as there are virtually no penguins in area ii). The sardine and anchovy models would consist of all THREE areas, with model-predicted biomass in i) and iii) only being used to try to find a functional relationship with the penguin results. The model described here is for Area i), with 3 sub-areas 1) Robben & Dassen Islands; 2) Boulders and 3) Dyer island.

A summary of all the breeding colonies of penguins in this area is provided in Fig. 1 which also shows the relative abundance of breeding pairs in the different regions, computed from data in Underhill *et al.* (2006). Fig. 2 shows the (estimated) number of breeding pairs of penguins per colony in the “western” area, plotted from data presented in Underhill *et al.* (2006) but excluding interpolated points. Noting that the regional penguin population is dominated (in terms of numbers) by two large colonies, namely Robben Island and Dassen Island, the model here has focused on these two colonies, with the next most important colony being Dyer Island.

The model time step is one year and hence average trends are modelled. Penguins in each sub-area are modelled starting from 1989, except for Boulders which starts in 1991 because this is a recently formed colony. 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. Given time constraints, detailed confidence limits and investigations into the uncertainty associated with the various parameter estimates are not presented here, but this will be included in subsequent updates. Moreover, considerable initial sensitivity analyses have been done but are not reported in detail here, both because of limited time and to aid focusing on the main conclusions of this study.

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 (Table 1). The data are from Underhill *et al.* (2006), and various published studies as well as recent updates from Rob Crawford. Carryn Cunningham kindly provided data on the abundance of anchovy and sardine spawners and recruits.

The moult count data are considered substantially 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 (birds about one year or older) whereas the nest count measures the number of breeding pairs (birds about four years and older) (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 is the one considered the more accurate of the two because it accounts for missing information (see Underhill and Crawford 1999). Rob Crawford confirmed that nest counts have limited accuracy, not all birds may be present, are easier at some islands, and are most difficult at Robben Island. Nest counts usually include active nests (=adult or chick present) and potential nests (=nesting material or lots of fresh dung present) (R. Crawford, pers. commn).

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. 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. 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 1). To obtain an aggregated index for Dassen and Robben islands, the numbers of moulters at each locality were added together. However, data for Dassen Island are only available from 1995 onwards, whereas data for Robben Island are available from 1989. Given that it is preferable to use a longer time series and that data re the numbers of breeding pairs at Dassen Island prior to 1995 show a fairly steady trend, missing moult count data were filled in by assuming that the numbers moulting at Dassen remained constant over the period 1989-1995 (Table 1).

Data for 2006 on the numbers of breeding pairs at Dassen and Robben islands were unavailable at the time of this analysis and was assumed to be half the 2005 value, as was reported at the previous meeting (Table 1). Data on the number of chicks fledged per pair per year were available for Robben Island only (Table 1). Over the period 1989-2005 at Robben Island, African 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) suggests that the increased mortality caused by the oil spill was ameliorated to a large extent by the high abundance of pelagic fish prey. In the first instance an interpolated breeding success value for 2000 is simply assumed. Later model versions could test a range of plausible values for 2000, as well as add an additional mortality term for 2000. Similarly, future analyses could be modified to take into account the large mortality incurred in 1994 as a result of the Apollo Sea oil spill (see e.g. Underhill *et al.* 1999).

One anomaly in the data which the task group will be asked to clarify relates to the data for Dyer Island. The number of female moulters per year is approximately the same, rather than substantially more, than the number of breeding females (Fig. 3). The reason for this is unclear.

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. Data on the estimated abundance of anchovy and sardine recruits and spawners were provided by Carryn Cunningham (Table 3). Some preliminary simulations were run using different combinations of these data to test to what extent they resulted in an improved model fit to the trend data. For each pelagic fish abundance series, a breeding success index was derived as follows: the pelagic fish abundance in each year was converted to a proportion of the maximum value over the period 1985-2006. The breeding success for each year was then assumed equal to the product of this proportion times the maximum observed breeding success (1.04 chicks fledged per year per pair – Table 1) over the same period (Table 3). In essence, this simply assumes that breeding success and fish abundance (either or both species) are linearly correlated. More complex relationships will also be investigated in future analyses. Note that in table 3, the 2006 estimates are very rough being based on the May

recruitment survey only and not the November survey –the value is perhaps higher than anticipated, hence a lower value could also be substituted to test the effect on projections. Data for anchovy were only available up until 2003 and hence to get a series for preliminary investigations, anchovy abundance was assumed to decrease linearly from 2003 to 2006 as shown in Table 3.

A Simple Dynamic Model

The basic dynamic model used to represent the population dynamics of the adult female penguins is as follows:

$$N_{y+1}^a = N_y^a S + \left(N_{y-T+1}^a \right) q_f H_{y-T+1}^a S_j S^{T-1} \quad (1)$$

where N_y^a is the number of mature (past the age at first breeding) adult females on the “counting” day (e.g. 1 November) in area a and year y ,
 S is the post-first-year survival rate,
 T is the average age at first breeding,
 H_y^a is the average breeding success (chicks fledged per pair) per year in area a ,
 q_f is the fraction of chicks that are female,
 S_j is the annual post-fledging survival rate of juvenile penguins in their first year.

Following Crawford *et al.* (2006), base-case values for parameters were fixed as follows: $T = 4$ yr and $q_f = 0.5$. African Penguins are known to breed for the first time when 4-5 years old (Randall 1983, Crawford *et al.* 1999). Crawford *et al.* (2006) concludes that there does not appear to have been a decrease in the age at first breeding of African Penguins over the last decade or so and hence this aspect is not considered in greater detail for preset purposes. To initialize the model, a steady initial population is assumed over the period 1986-1989, although other alternatives could easily be incorporated.

The values of S and S_j were either estimated within the model or fixed based on values reported in the literature. Table 2 summarises literature-derived estimates of adult and first-year survival for African penguins. These confirm the notion that $S_j < S$. As these two parameters are highly correlated, it was not possible to simultaneously estimate both in the model and hence one value was fixed and the other estimated. As previously discussed, it is conventional practice in marine population modelling to estimate S by fitting to an index/indices of abundance for the species because of the sensitivity of population trends to the choice of an adult survival parameter S .

Given that the moult count data is considered more reliable, survival rate was estimated by fitting to the moult count (and not also breeding pairs) data for Robben and Dassen Islands combined (base-case model version). The modelled population trends are plotted together with the data in all instances for purposes of comparison, but the model was only fitted to other data sources when specified, because the trends for Dyer island and Boulders are confounded to some extent by movements of penguins (see sections re adding complexity to the model).

Breeders and Moulters

The equations above provide a model index of the numbers of breeding females in each of the sub-areas. An index is also required of the numbers of female moulters, as this component

includes all birds aged approximately one year and older. Although the model developed here is not fully age-structured, the numbers of 1, 2 and 3 yr olds can be computed as:

$$N_{y+1}^{ages1-3} = q_f S_j (H_y N_y + H_{y-1} N_{y-1} S + H_{y-2} N_{y-2} S^2) \quad (2)$$

The number of moulters is thus simply the sum of Equations (1) and (2). The above equations are modified accordingly to account for additional complexity added to the model.

Adding Density Dependence

The density-dependent formulation used in the current model is based on the form suggested in Thomson *et al.* (2000) adapted as follows:

$$S_j \rightarrow S_j^* \left(1 - \frac{N_y^a}{K_a^*} \right) \quad (3)$$

where K_a^* is a carrying capacity-related term for penguins in sub-area a , used to introduce density dependence into the penguin dynamics through the dependence of S_{juv} on penguin abundance N .

Note that the value of the density dependent term lies between zero and 1, so that, for example, when the population size is very small relative to the carrying capacity term K^* , then this term tends to 1. The value of S_j^* is thus set at some maximum value so that the post-fledging juvenile survival rate varies annually in response to density dependent factors. The level of density dependence included in the model can be altered through the choice of values for K^* , with larger K^* values translating into minimal density dependence. By running simulations with gradually decreasing values of K^* (up to a minimum value corresponding to the largest population size observed over the model time period), it is possible to investigate the extent to which density dependence may be responsible for the observed trends in penguin numbers. After some experimentation, a base-case value of K^* was chosen on the grounds that it resulted in a reasonable range of variation in juvenile survival rates. It was not attempted to base K^* on historic estimates of carrying capacity because of the possibility that penguin numbers at the turn of the century may have been artificially high due to a competitive release effect as a result of reduced seal numbers present at the time. Moreover, Crawford *et al.* (2007) propose a change in carrying capacity from a very high level in the 1920s to a much lower value over the period 1978-2006. There was insufficient time during the current analysis to check whether the information in Crawford *et al.* (2007) could be used to refine estimates of K_a^* in the model.

Equation (1) is thus modified as follows:

$$N_{y+1}^a = N_y^a S + (N_{y-T+1}^a) q_f f(B_{y-T+1}^a) \cdot H_{max} S_j^* \left(1 - \frac{N_y^a}{K_a^*} \right) S^{T-1} \quad (4)$$

where:

H_{max} is the maximum observed breeding success (chicks fledged per female per yr); and
 $f(B_y^a)$ is a breeding success factor (multiplier for H_{max}) which is a function of a component of pelagic fish abundance in area a in year y .

The “breeding success” factor described above provides an alternative to using the breeding success data detailed in Table 1. Note that in the base-case model the breeding success factor used is that corresponding to the year in which chicks are born, but other lag times in the response to changes in food availability can also be investigated.

Adding Immigration and emigration effects

Breeding adult African penguins very rarely breed at any other than the colony at which they first established breeding. However, first-time breeders are known to emigrate from and immigrate to other colonies, likely in response to changing food availability (Whittington *et al.* 2005). Based on re-sightings of flipper-banded chicks, 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 was thus modified to allow emigration from Dyer Island to Boulders and Robben and Dassen islands. The simplest case for initial investigation is that of Boulders because the trend in numbers at this colony can only be explained 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 Boulders. The methodology is first explained for the simpler case assuming movement from Dyer Island to Boulders only. For Dyer Island, Equation (4) is modified as follows:

$$N_{y+1}^a = N_y^a S + (N_{y-T+1}^a) q_f f(B_{y-T+1}^a) \cdot H_{\max} S_j^* \left(1 - \frac{N_y^a}{K_a^*}\right) S^{T-1} \cdot (1 - E_y) \quad (5)$$

where E_y is the proportion of first-time breeders that emigrate from Dyer Island. The emigration proportion is estimated 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 $Enum_y^{Dyer}$ is thus:

$$Enum_y^{Dyer} = E_y * q_f f(B_{y-2}^a) \cdot H_{\max} S_j^* \left(1 - \frac{N_y^a}{K_a^*}\right) S^2 (N_{y-2}^a) \quad (6)$$

Equation (2) for Dyer island is modified accordingly to account for the movement of pre-breeders (assumed to be 3 years old). The proportion of the first time breeders given by equation (6) which immigrate to Boulders (BLD) rather than Robben or Dassen islands is determined by parameter I_{prop} , estimated by fitting to trend data for Robben and Dassen islands (RobDas). It follows that Equation (4) must be modified as follows for RobDas and BLD colonies respectively:

$$N_{y+1}^{RobDas} = N_y^{RobDas} S + (N_{y-T+1}^{RobDas}) q_f f(B_{y-T+1}^{RobDas}) \cdot H_{\max} S_j^* \left(1 - \frac{N_y^{RobDas}}{K_{RobDas}^*}\right) S^{T-1} + (1 - I_{prop}) \cdot Enum_y^{Dyer} \cdot S \quad (7)$$

$$N_{y+1}^{BLD} = N_y^{BLD} S + (N_{y-T+1}^{BLD}) q_f f(B_{y-T+1}^{BLD}) \cdot H_{\max} S_j^* \left(1 - \frac{N_y^{BLD}}{K_{BLD}^*}\right) S^{T-1} + I_{prop} \cdot Enum_y^{Dyer} \cdot S \quad (8)$$

RESULTS

There is insufficient time to present results for all scenarios here but this could be presented in greater detail at the Task Group meeting. A selected few results are shown in Figs. 5-11.

Previous analyses have demonstrated the sensitivity of modelled penguin abundance trends to the choice of the adult survival parameters S . In Fig. 5, rather than estimating survival within the model, the average and maximum of published values (Table 1) are substituted. The plots highlight that previous survival estimates are too low to sustain populations, even when it is

assumed as here that all first-time breeders from Dyer island move to Robben and Dassen island. The illustrative example shown uses the anchovy breeding success factor. Preliminary sensitivity analyses suggest that if survival estimates are fixed at the maximum values in Table 1 (i.e. at lower values than estimated by the model), observed population trends can only be reproduced if breeding success is doubled.

Figs. 6 -11 show model-predicted trajectories of the historic and projected numbers of female moulting and breeding penguins at Robben and Dassen island combined, Dyer island and Boulders. Also shown is annual variation in estimated juvenile survival rate, the numbers of chicks fledged per year and the number moving to Boulders. Results are shown firstly for breeding success computed using the observed data from Crawford (Fig. 6), then a sardine breeding success factor (Fig. 7) and finally an anchovy breeding success factor (Fig. 8). These models all assume first-time breeders move from Dyer to Boulders (to match the Boulders population data) but do not move to Dassen and Robben. These examples include a moderate level of density dependence. The effect of reducing density dependence is shown in Fig. 9. Fig. 10 again assumes moderate density dependence and uses the anchovy breeding success factor, but now movement from Dyer island to all other colonies is estimated. Fig. 11 is the same except that the survival estimates are fixed at the values as estimated in Fig. 8 (i.e. the model cannot estimate a lower survival rate to assist in fitting the Dyer island data in this case).

A brief summary of these results follows:

- All estimates of survival rates as tabled in Table 1 are much too low. If adult survival is assumed less than 0.9 yr (i.e. 90% of adults one yr and older survive from one year to the next), the corresponding model estimates of juvenile survival hit the upper bound of 1.0 (i.e. the unrealistic assumption that no post-fledging juveniles die in the first year). Adding the additional constraint that $S > S_j$, meant in most model runs that adult survival was closer to 0.92 – 0.95 yr (see Discussion re survival rates). When density dependence was introduced into the model, juvenile survival rates are seen to drop over the recent period, with the extent of the drop determined by whether the level of density dependence is assumed weak or strong (see S_j trajectories in the Figs for examples). Even under the assumption of strong density dependence, this factor was not sufficient to reproduce the recent downturns in penguin abundance.
- The worst fit to the data was obtained when breeding success was assumed constant (set at the average value) for all years. An improved fit resulted when the breeding success data (from R. Crawford, Table 1) was used. The fit improved substantially when breeding success was computed instead as a function of pelagic fish biomass. The timing of the increase and decrease in penguin abundance in response to pelagic fish abundance is not correct for the simple preliminary scenarios investigated, but shows much promise.. Further explorations need to be done. One interesting result was that the timing of the downturn can be represented exactly if the proportion of first-time breeders that commence breeding (at their natal colony) is a function of sardine recruitment biomass at age 3 (Fig. 12) – this aspect needs further investigation as may suggest that the age at first breeding is more sensitive to changes in prey availability than actual breeding success.
- If the same survival rates are assumed to apply at Dassen/Robben and Boulders, the model is able to predict the numbers of birds that must have immigrated to Boulders each year. Model results suggest approximately 17% of first-time breeders from Dyer moved annually to Boulders.
- The observed decline at Dyer island could not easily be reproduced under any of the preliminary scenarios investigated. If the same adult and survival rates are assumed as for Robben and Dassen Island, then the population at Dyer is predicted to remain approximately steady under all breeding success scenarios. By fitting to the Dyer

penguin moulters and breeders data, the model can estimate the numbers of first-time breeders that must have left Dyer so as to result in the observed declines. However, for most scenarios these estimates hit the upper bound of 1.0 i.e. all first-time breeders move to Robben and Dassen islands. More work is required to try and understand the Dyer colony –the immediate priority is to resolve the data issue as shown in Fig. 4.

- The model is useful in providing projections of penguin populations over the next few years under a range of scenarios. Under most scenarios populations are predicted to decrease slightly or remain approximately steady. Scenarios in which future prey availability is assumed very low could also be tested.

DISCUSSION

Survival rates

Previous survival rates summarised in Table 2 were generally found to be too low to reproduce the observed population growth rate trends. Ricklefs (2000), using data from 34 studies comprising 32 bird species, demonstrated a strong correlation between annual fecundity (number of fledglings per year) and annual adult mortality. From Table 1, the average fecundity value is 0.64 and the maximum 1.04. Using Ricklefs (2000) relationship and computing adult survival as $S = e^{-M}$, yields corresponding theoretical survival estimates of 0.88 and 0.92 yr. Moreover, Ricklefs (2000) found that from fledging to maturity is a function of annual adult mortality, roughly suggesting from his relationship prereproductive survival rates in this case of the order 0.74 to 0.82/yr. First-year survival rates can naturally be expected to be less than this. Model results similarly suggested adult survival rates of about 0.9/yr and juvenile survival rates ranging from about 0.4 to 0.8 under different scenarios (with inter-annual variation dependent on the degree of density dependence assumed).

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 some parameter estimates are likely biased and should be revised. Preliminary results suggest that the observed trends in penguin abundance can only be explained if penguin breeding success (or pre-reproductive survival) is assumed to depend on prey availability, corroborating the numerous studies stating this by Rob Crawford and colleagues. For some colonies (Boulders, Dyer island), 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. Nonetheless, the model is now sufficiently well developed that it can be used to explore a range of different scenarios and management options. Following further model explorations, the model is of a form that can readily be linked to the pelagic OMP.

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Table 1. 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, to make them comparable with the numbers of breeding pairs, which is simultaneously 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.

Year	Number of female moulters		Number of breeding pairs			Breeding success (chicks/pr)
	Robben and Dassen	Dyer	Robben and Dassen	Dyer	Boulders	Robben
1989	<i>7910</i>		829		38	0.42
1990	<i>7876</i>		1278	8349	54	0.32
1991	<i>8545</i>		1879	6115	131	0.59
1992	<i>8638</i>		2027	7579	158	0.59
1993	<i>9449</i>		2176	2374	241	0.54
1994	<i>10181</i>		2799	4649	359	0.45
1995	10154		2279	4260	366	0.38
1996	9393		3097	3279	416	0.65
1997	9281		3336	2745	726	0.97
1998	12496		3467	1963	555	0.75
1999	15418		4399	2363	906	0.60
2000	18420		5705	2220	949	0.72
2001	19729	2057	6723	2088	1054	0.84
2002	21029	2542	7252	2145	1083	0.90
2003	18624	1902	6433	1929	1033	0.57
2004	17508		8524	2216	1196	0.72
2005	15585	2768	7152	2053	1227	1.04
2006	9557	1422	3697	2057		0.518

Table 2. 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
<i>0.808</i>	<i>Average value</i>		
<i>0.91</i>	<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	1993-1994	Crawford <i>et al.</i> 1999
0.38	Dassen Island	1987-1999	Whittington 2002
<i>0.425</i>	<i>Average value</i>		
<i>0.69</i>	<i>Maximum value</i>		

Table 3. Summary of data on anchovy and sardine abundance (from C. Cunningham) and derived breeding success H indices tested in the model. Values in italics are rough estimates only.

	Sardine				Anchovy	
	November Biomass in 000t	May Recruitment numbers (in billions)	H_y as a function of sardine biomass	H_y as a function of sardine recruitment	May Recruitment numbers (in billions)	H_y as a function of anchovy recruitment
1985	136.8	3.2	0.032	0.057	106.3	0.171
1986	186.8	3.5	0.044	0.064	221.2	0.356
1987	234.5	3.3	0.056	0.059	107.8	0.174
1988	294.8	4.6	0.070	0.082	105.4	0.170
1989	429.3	6.2	0.102	0.111	27.9	0.045
1990	506.2	5.5	0.120	0.098	77.3	0.124
1991	608.7	12.8	0.144	0.231	252.5	0.407
1992	673.0	13.8	0.160	0.249	143.3	0.231
1993	1032.0	14.6	0.245	0.263	68.3	0.110
1994	1255.2	11.2	0.298	0.202	37.0	0.060
1995	1184.6	22.3	0.281	0.402	71.6	0.115
1996	1204.4	10.9	0.286	0.196	29.5	0.047
1997	1169.5	16.2	0.277	0.292	83.6	0.135
1998	1548.0	29.2	0.367	0.526	103.3	0.166
1999	2855.6	36.7	0.678	0.663	187.2	0.301
2000	3533.8	47.7	0.839	0.861	513.6	0.827
2001	3447.6	57.4	0.818	1.036	645.9	1.040
2002	4366.1	50.8	1.036	0.917	222.8	0.359
2003	4067.4	38.7	0.965	0.699	265.9	0.428
2004	3533.3	10.1	0.838	0.183		0.312
2005	2197.3	5.2	0.521	0.095		0.208
2006	1594.4	22.0	0.378	0.396		0.104

Table 4. List of model parameters and descriptions, in the order in which they appear in the text.

Parameter	Description
N_y^a	Number of mature (past the age at first transition) female penguins in sub-area a in year y
S	Post-first-year annual survival rate of penguins
S_j	Average annual post-fledging survival rate of juvenile penguins
$S_{juv}^{*,j}$	Maximum first year post-fledging (juvenile) survival rate of penguins
T	Average age at first breeding
q_f	Fraction of chicks that are female
P	Maximum number of fledged chicks per pair per year
$f(B_y^a)$	Breeding success factor (multiplier for P) which is a function of the biomass of pelagic fish in area a in year y
$K^{*,a}$	Carrying capacity-related term for penguins in area a
E_y	Proportion of first-time breeders emigrating from Dyer Island in year y
$Enum_y^{Dyer}$	Number of first-time breeders emigrating from Dyer Island in year y
I_{prop}	Proportion of Dyer Island emigrants that move to Boulders
R^a	Steady annual growth rate of penguins in sub-area a pre-1989.

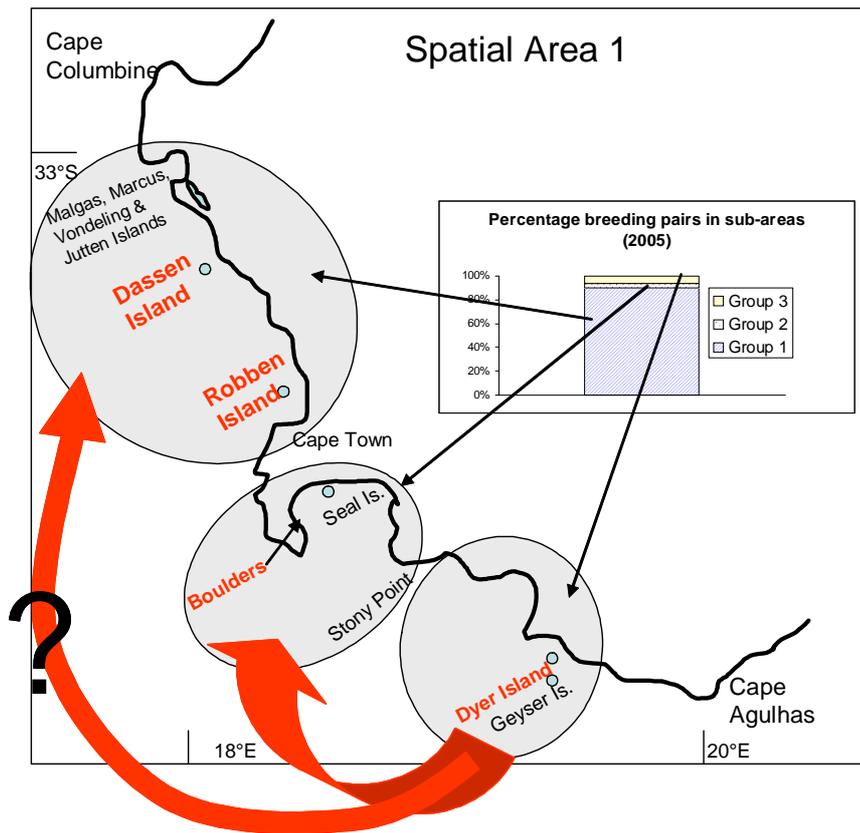


Fig. 1. Map showing location and possible grouping of penguin colonies in the “western” area. The colonies currently included in the model are shown in bold red text. The arrows represent movement of penguins from Dyer Island to Boulders, as well as movement to Robben Island as is explored in the model.

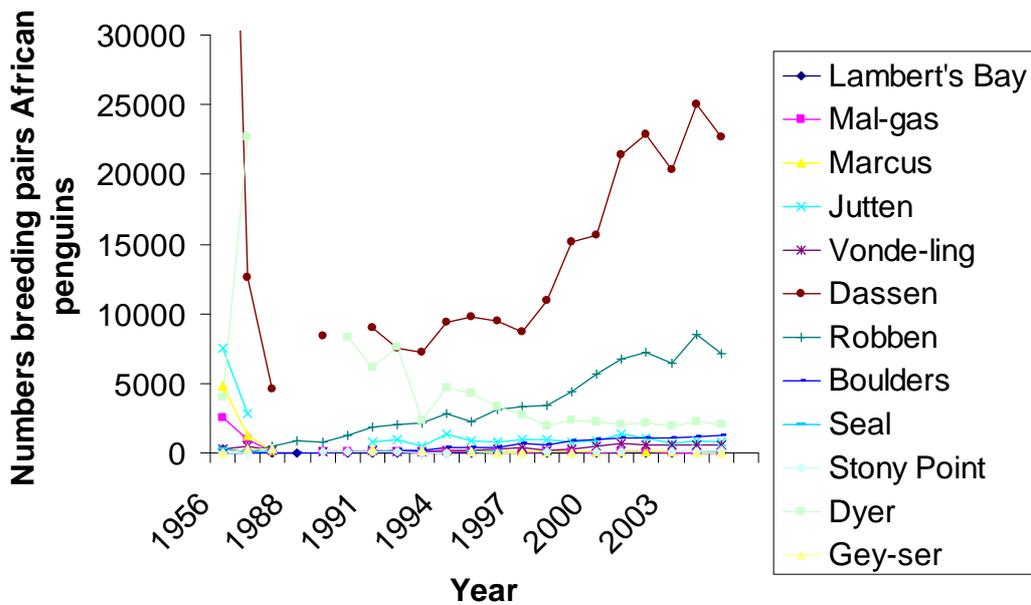


Fig. 3. Summary of data (from Underhill *et al.* 2006) on the numbers of breeding pairs of penguins in the “western” area.

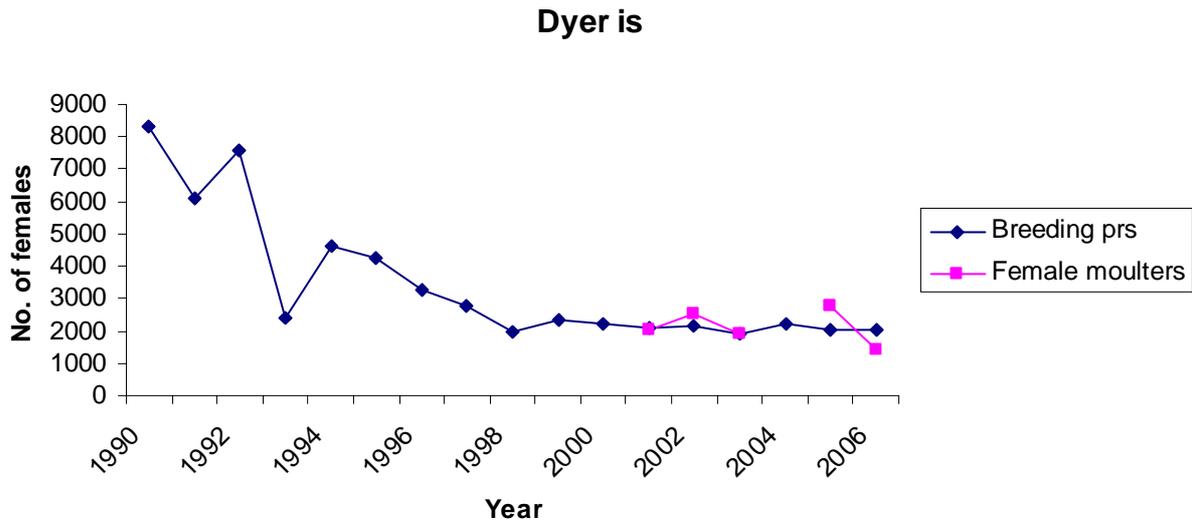


Fig. 4. Plot of numbers of female moulters (assuming a 50:50 sex ratio) and numbers of breeding pairs of penguins at Dyer Island. The number of moulters includes all animals aged (approximately) one year and older whereas breeding females are aged approximately four years and older. The latter index should thus be a smaller subset of the former.

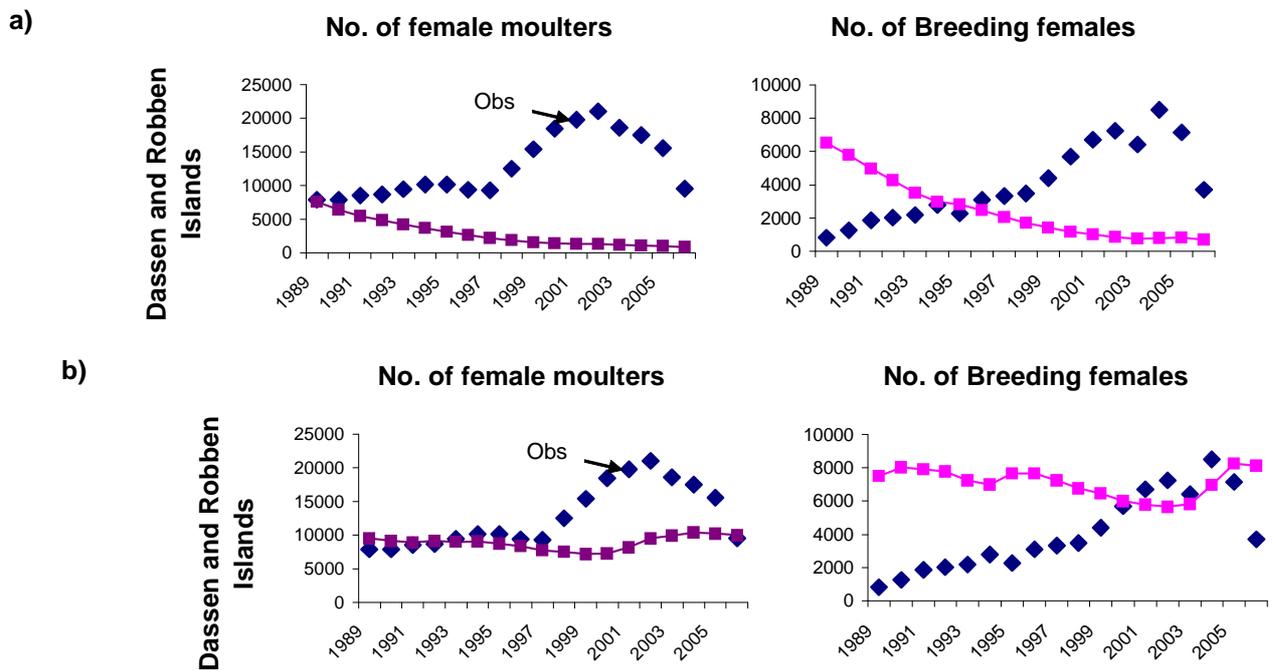


Fig. 5. Demonstration using the dynamic model of penguin dynamics of the sensitivity of modelled penguin abundance trends to the choice of the adult and juvenile survival parameters S_i and S_j . Rather than estimating survival within the model, in a) the average of the values in Table 1 are used and in b) the maximum values in table 1 are used. Plots highlight that previous survival estimates are too low to sustain populations, even when it is assumed as here that all first-time breeders from Dyer island move to Robben and Dassen islands.

Model version: BR(data); S= 0.95

Movement from Dyer to Boulders only

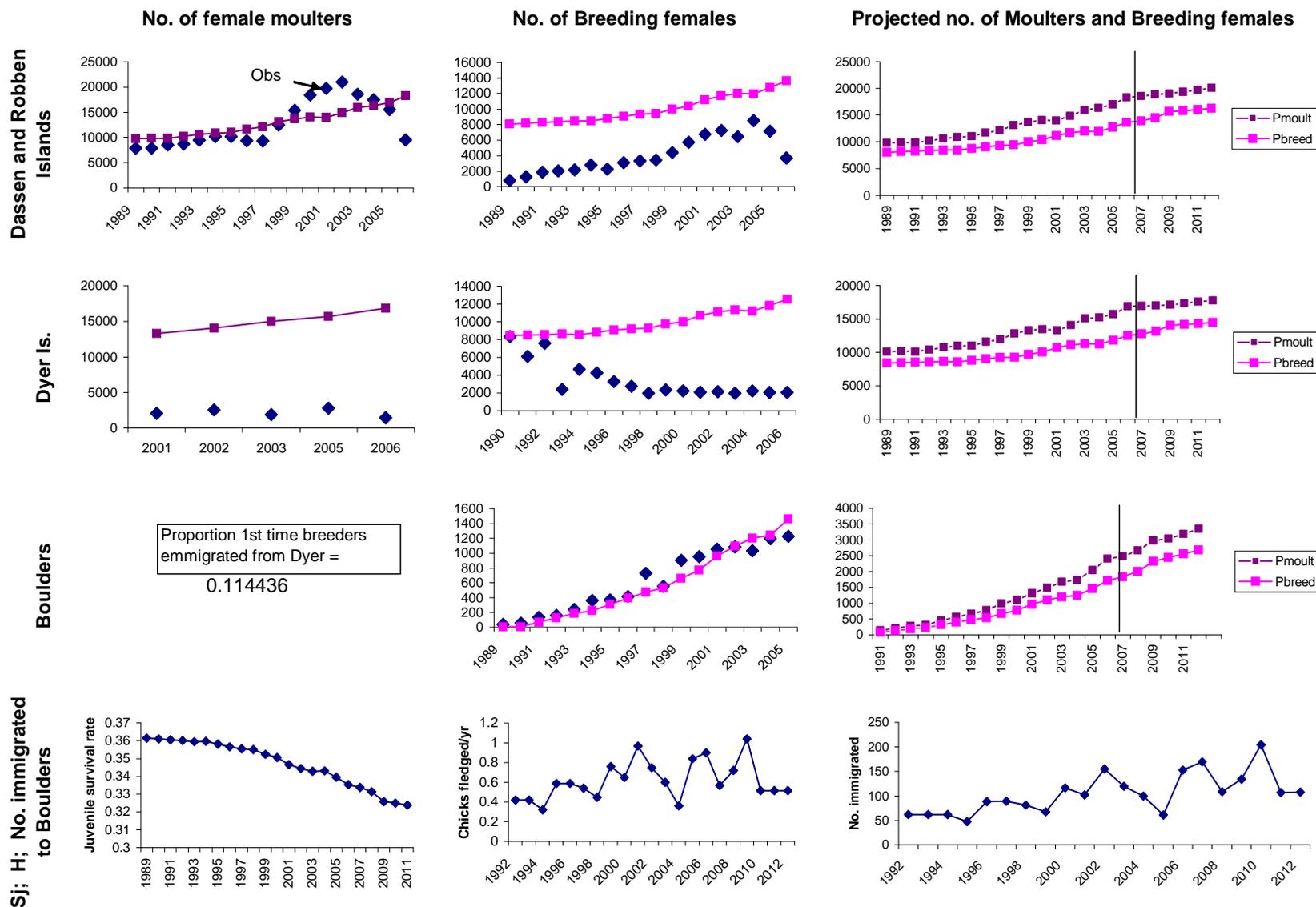


Fig. 6. Model-predicted trajectories of the numbers of female moulting penguins (left panel), number of breeding pairs (centre) and projected numbers of both population components (right) at Robben and Dassen island combined (top panel); Dyer island (2nd from top) and Boulders (3rd from top). The bottom panel shows annual variation in estimated juvenile survival rate (left), the numbers of chicks fledged per year (middle) and the number moving to Boulders (right). Observed data are shown as diamond points not joined by a line.

Model version: BR(sardine); S= 0.95

Movement from Dyer to Boulders only

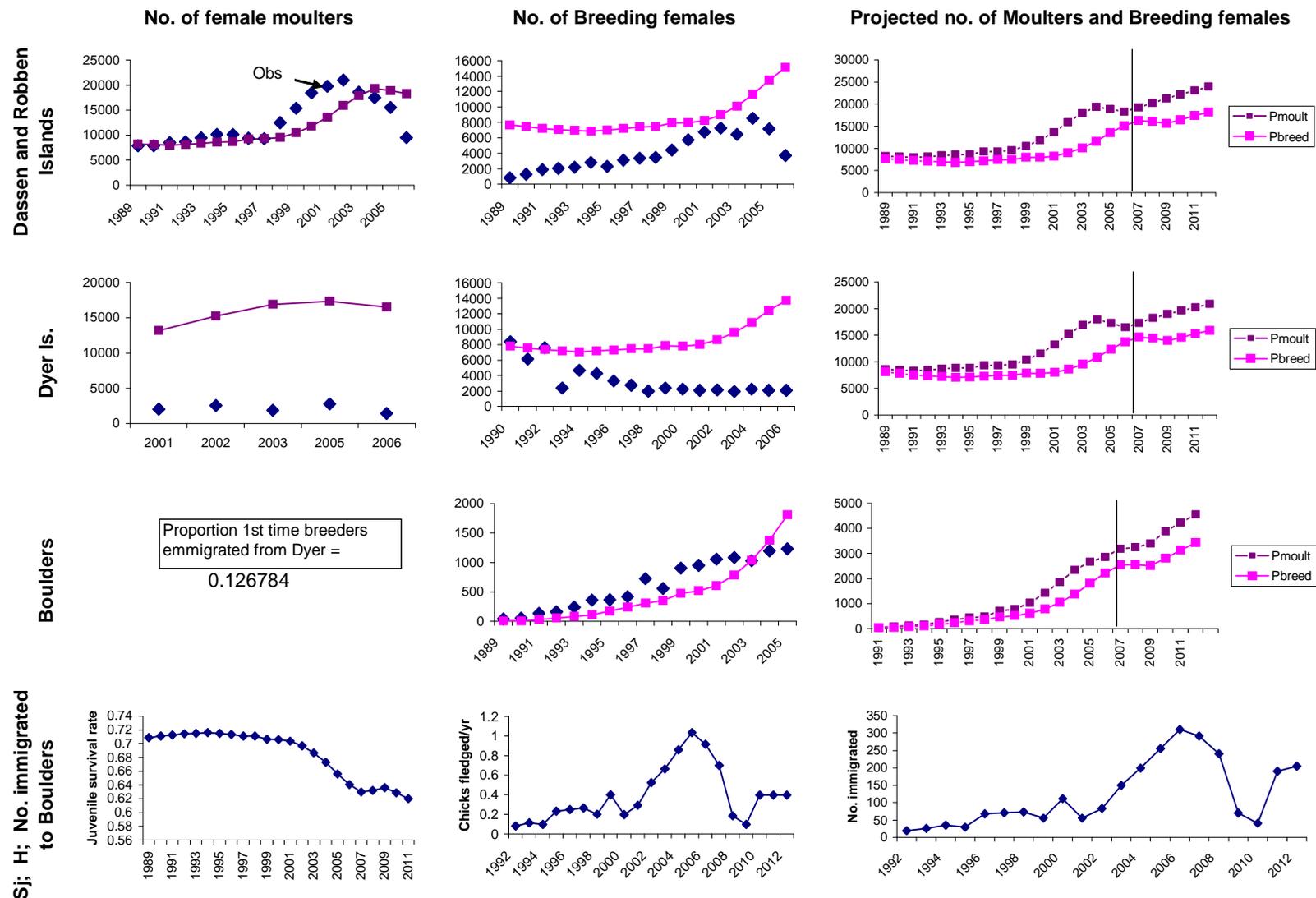


Fig. 7. Model-predicted trajectories of the numbers of female moulting penguins (left panel), number of breeding pairs (centre) and projected numbers of both population components (right) at Robben and Dassen island combined (top panel); Dyer island (2nd from top) and Boulders (3rd from top). The bottom panel shows annual variation in estimated juvenile survival rate (left), the numbers of chicks fledged per year (middle) and the number moving to Boulders (right). Observed data are shown as diamond points not joined by a line.

Model version: BR(anchovy); S= 0.95

Movement from Dyer to Boulders only

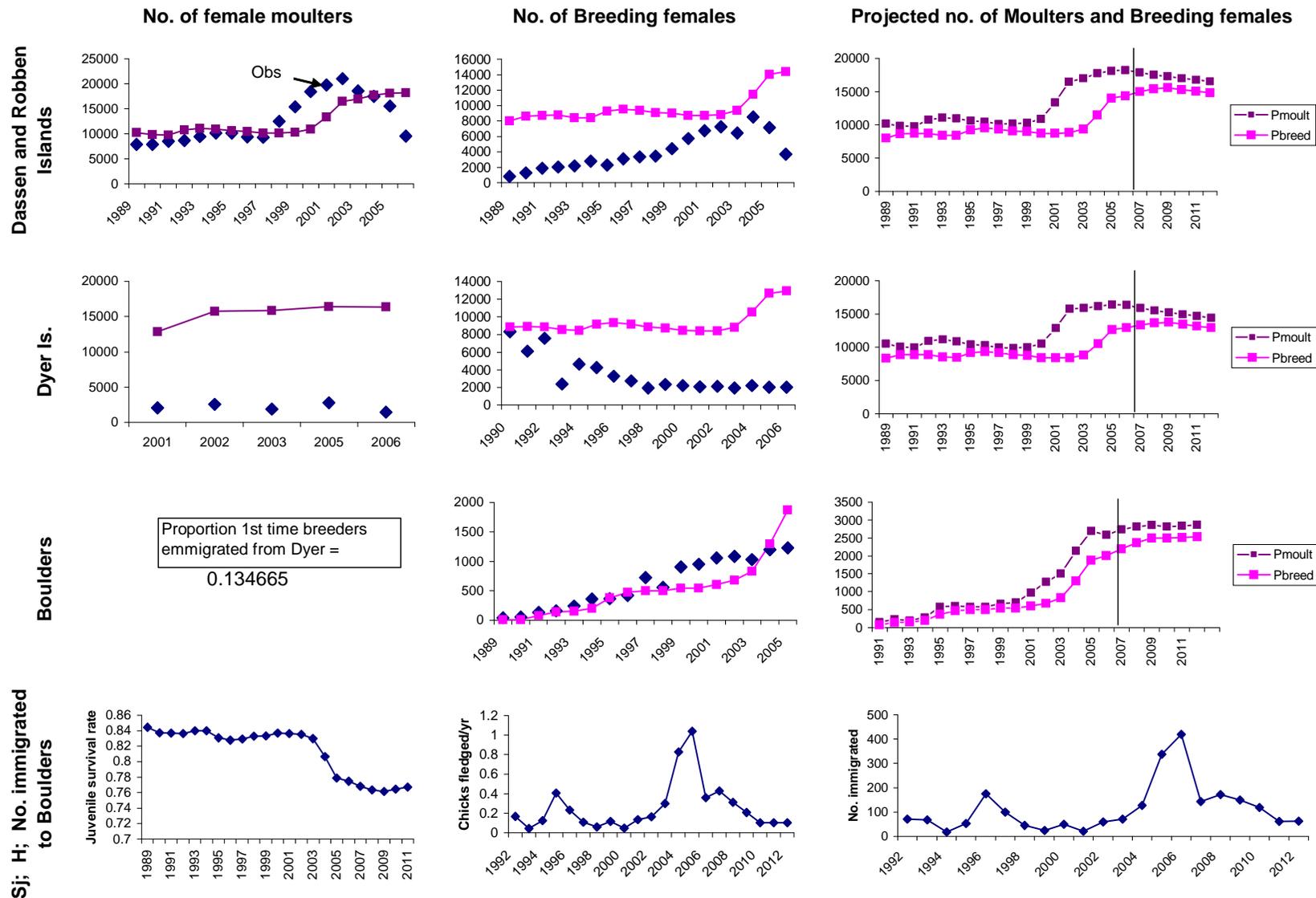


Fig. 8. Model-predicted trajectories of the numbers of female moulting penguins (left panel), number of breeding pairs (centre) and projected numbers of both population components (right) at Robben and Dassen island combined (top panel); Dyer island (2nd from top) and Boulders (3rd from top). The bottom panel shows annual variation in estimated juvenile survival rate (left), the numbers of chicks fledged per year (middle) and the number moving to Boulders (right). Observed data are shown as diamond points not joined by a line.

Less dens. dep.; BR(anchovy); S= 0.95

Movement from Dyer to Boulders only

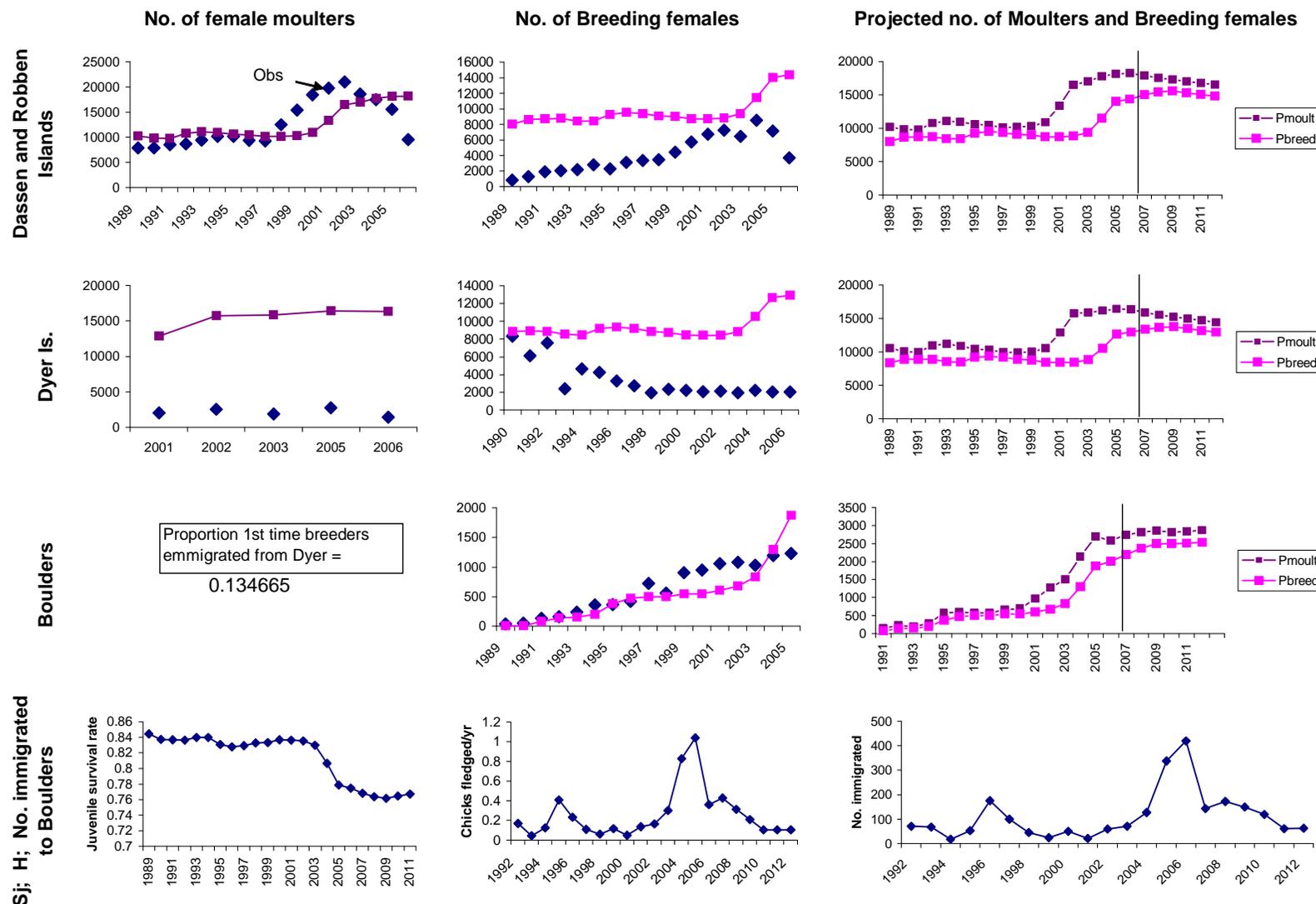


Fig. 9. Model-predicted trajectories of the numbers of female moulting penguins (left panel), number of breeding pairs (centre) and projected numbers of both population components (right) at Robben and Dassen island combined (top panel); Dyer island (2nd from top) and Boulders (3rd from top). The bottom panel shows annual variation in estimated juvenile survival rate (left), the numbers of chicks fledged per year (middle) and the number moving to Boulders (right). Observed data are shown as diamond points not joined by a line.

Model version: BR(anchovy); S= 0.95

Move from Dyer to Boulders and Robben/Dassen

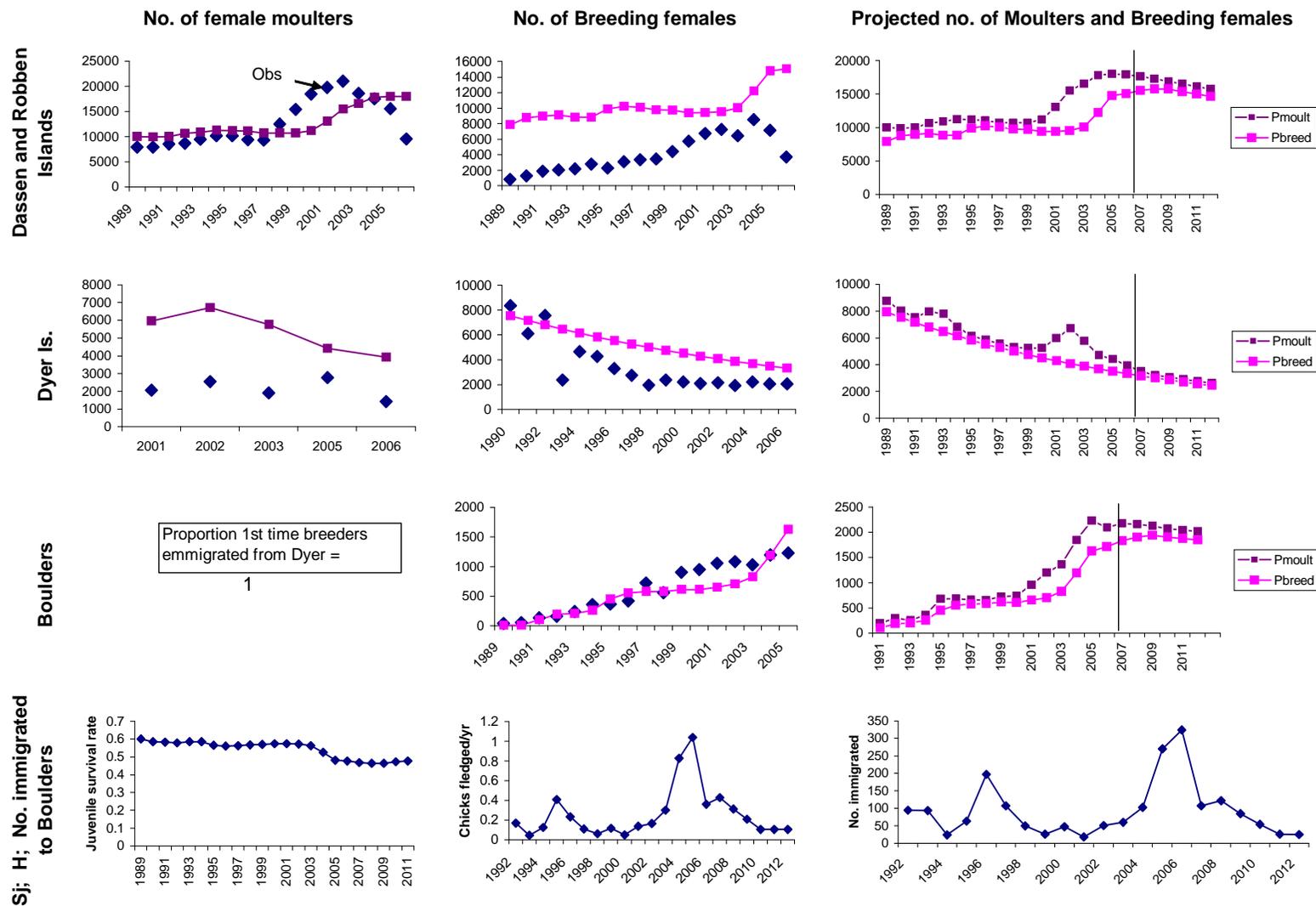


Fig. 10. Model-predicted trajectories of the numbers of female moulting penguins (left panel), number of breeding pairs (centre) and projected numbers of both population components (right) at Robben and Dassen island combined (top panel); Dyer island (2nd from top) and Boulders (3rd from top). The bottom panel shows annual variation in estimated juvenile survival rate (left), the numbers of chicks fledged per year (middle) and the number moving to Boulders (right). Observed data are shown as diamond points not joined by a line.

Model version: BR(anchovy); S= Fixed S and Sj at Robben/Dassen values

Move from Dyer to Boulders and Robben/Dassen

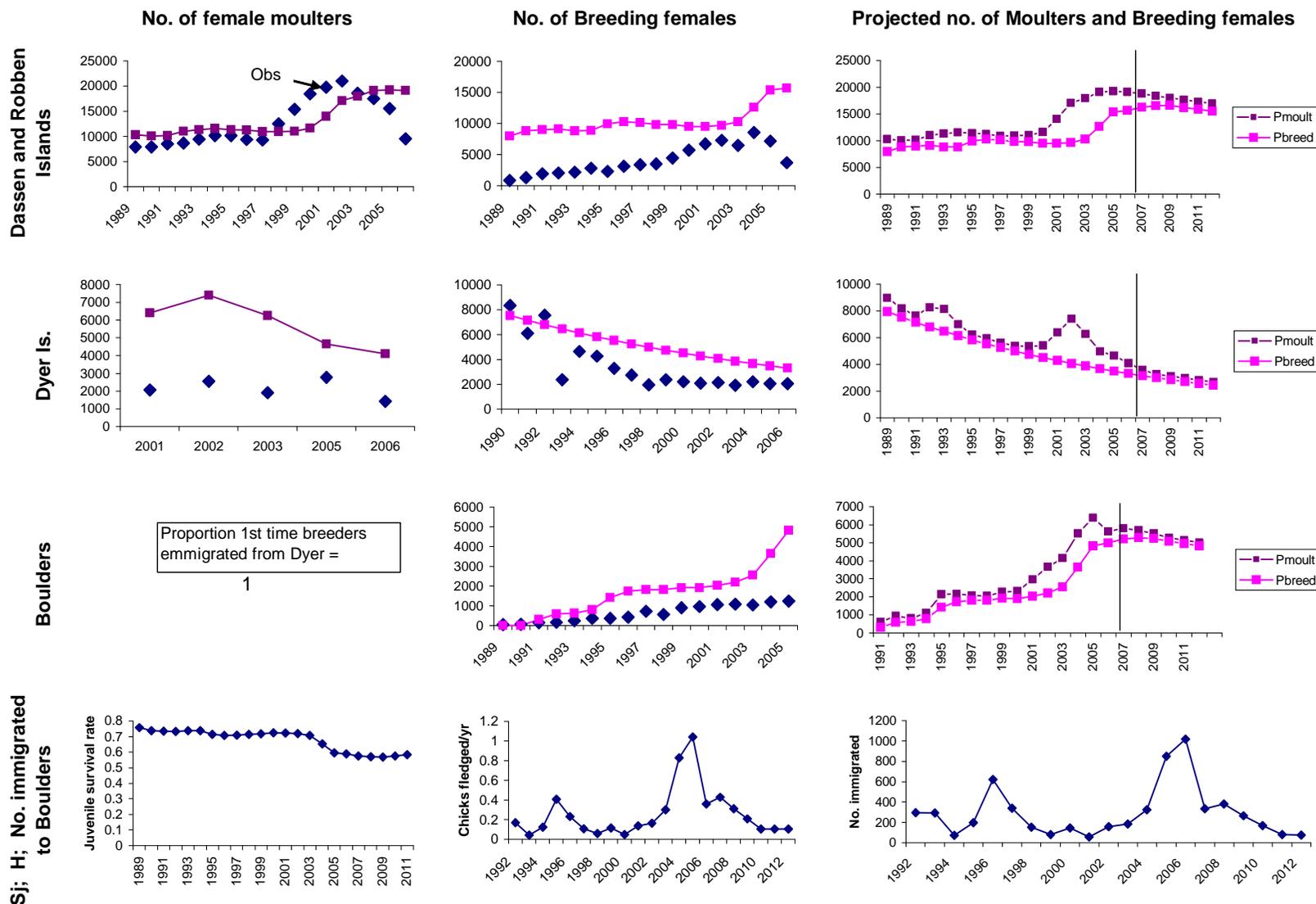


Fig. 11. Model-predicted trajectories of the numbers of female moulting penguins (left panel), number of breeding pairs (centre) and projected numbers of both population components (right) at Robben and Dassen island combined (top panel); Dyer island (2nd from top) and Boulders (3rd from top). The bottom panel shows annual variation in estimated juvenile survival rate (left), the numbers of chicks fledged per year (middle) and the number moving to Boulders (right). Observed data are shown as diamond points not joined by a line.

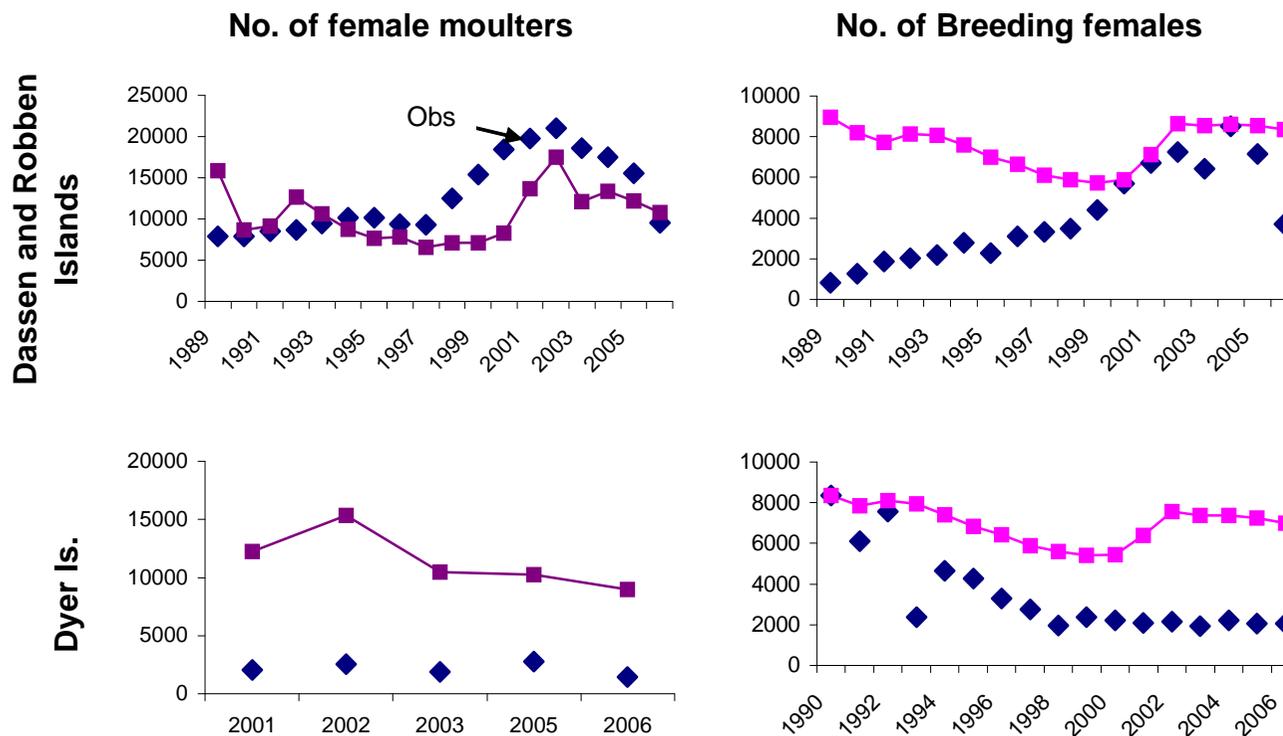


Fig. 12. Example reproduction of the timing of the population downturn when assuming the proportion of first-time breeders that commence breeding (at their natal colony) is a function of sardine recruitment biomass at age 3. Model-predicted trajectories of the numbers of female moulting penguins (left panel) and number of breeding pairs at Robben and Dassen island combined. Observed data are shown as diamond points not joined by a line.