WHY PLOTS OF RESULTS FOR THE SIMPLE PENGUIN MODEL OF SWG/EAF/SEABIRDS/13APR/01 ARE MISLEADING, AND SOME BROADER CONSEQUENTIAL IMPLICATIONS

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SUMMARY

SWG/EAF/SEABIRDS/13APR/01 investigates the extent to which observed trends in the numbers of African Penguins breeding at Robben Island and in the Western Cape can be matched by a simple population model, and concludes that there is a reasonable match from 1992–2006 in numbers observed to be breeding and the corresponding model estimates when assuming parameter values for juvenile and annual adult survival rates of $S_j = 0.51,\ S = 0.85$ respectively, and an age at first breeding of 3. This result (based on a process error estimation model) conflicts with that of the modeling results presented by Plagányi and Butterworth (SWG/EAF/SEABIRDS/13APR/03) (which currently uses an observation error estimation model), and hence merits further investigation to determine whether this conclusion is justified. Here we first show briefly (by repeating and extending the analyses) that the results presented in SWG/EAF/SEABIRDS/13APR/01 fail to satisfy standard statistical criteria for acceptable fits of a population model to data. We thus reiterate our earlier concerns expressed that the abundance index data are not compatible with the parameter values as given in SWG/EAF/SEABIRDS/13APR/01, and hence that serious attention needs to be given to identify the source of the incompatibility between present demographic parameter estimates and abundance index series. The remainder of this document expands upon this and related issues, and makes suggestions for further areas of investigation.

BASIC MODEL:

If N_t = the number of adult female (age 3+) penguins in year t, all of which first breed at age 3 then:

$$N_{t+1} = N_t S + N_{t-2} P_{t-2} \tfrac{1}{2} \cdot C_{t-2} S_j S^2 \qquad (1)$$

where:
P_t = proportion of females that breed in year t
C_t = fledging success per pair in year t.

[Note that in the interests of simplicity, as in SWG/EAF/SEABIRDS/26APR/01 we treat the product $C_t S_j$ as covering a total time span of 1 year.]

Now B_t = no. breeders (pairs) in year t = $P_t N_t$.

Hence from (1): $$B_{t+1}\big/P_{t+1} = \left(B_t\big/P_t\right)S + B_{t-2}\cdot\tfrac{1}{2}\cdot C_{t-2}S_jS^2 \qquad (2)$$

Expressed as a process error model:

$$B_{t+1} = \left(P_{t+1}\big/P_t\right)S\cdot B_t + \left(\tfrac{1}{2}\cdot P_{t+1}\cdot C_{t-2}S_jS^2\right)B_{t-2} + \eta_{t+1} \qquad (3)$$

or $$\hat{B}_{t+1} = \left(P_{t+1}\big/P_t\right)S\cdot B_t + \left(\tfrac{1}{2}\cdot P_{t+1}\cdot C_{t-2}S_jS^2\right)B_{t-2} \qquad (4)$$

where $B_{t+1} = \hat{B}_{t+1} + \eta_{t+1}$ (5)

Note that the process error model assumes observation errors to be zero, i.e. the observed number of breeding pairs counted each year are exact measures of the actual numbers. The process error term η_{t+1} allows for possible annual variation in demographic parameter values such as S_j and S.

Model put forward in SWG/EAF/SEABIRDS/13APR/01[1]:

This model may be written:

$$\hat{B}_{t+1} = \left(1\big/P_t\right)S\cdot B_t + \left(\tfrac{1}{2}\cdot C_{t-2}S_jS^2\right)B_{t-2} \qquad (6)$$

Note that it is in error through failing to adjust by P_{t+1} when expressing the N_{t+1} in Equation (1) in terms of B_{t+1}.

Estimating adult survival S by fitting to data:

Rather than fixing S at the suggested value of 0.85, S may also be estimated by minimising the following negative log likelihood function (after removal of constants):

$$-\ln L = n\ln(\sigma) + \frac{n}{2} \qquad (7)$$

where σ is the standard deviation of the process errors η_t assumed to be normally distributed, so that:

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[1] We apologise for an error in reflecting this equation in SWG/EAF/SEABIRDS/13APR/04 with the LHS shown effectively as $\hat{B}_t$ instead of $\hat{B}_{t+1}$

$$\hat{\sigma} = \sqrt{\left[\sum_{t=1991}^{2004}\left(B_t^{obs} - \hat{B}_t\right)^2\right] \Big/ n} \qquad (8)$$

where *n* is the number of years (14), since for simplicity of illustration we ignore here possible model modifications needed for the years following 2004.

Alternative comparisons of models and data

For the reason given above, comparisons have focused on fits to the data over the period 1991 to 2004. From SWG/EAF/SEABIRDS/13APR/01, values are assumed as for case a) in that document: $P_t = 0.68$ (1987 – 1995); 0.97 (1996 – 2006), $S_j = 0.51$, $S = 0.85$ (though note some problems with these assumed values for P_t as elaborated in Appendix 1).

The inputs are the C_t series (Crawford *et al.* 2006) and B_t series for Robben Island and for the Western Cape as a whole (from Underhill *et al.* 2006).

RESULTS

The results of these comparisons are shown in Figs 1-2. The negative log likelihoods for the fits shown are listed in the Table below.

With corrected equation (Equation 2)			With equation used in SWG/EAF/SEABIRDS/13APR/01 (Equation 6)		
Robben	-ln L	Diff	*Robben*	-ln L	Diff
S = 0.85	102.9	7.9	S = 0.85	102.1	2.2
S estimated (0.99)	95.1		S estimated (0.93)	99.9	
W. Cape	-ln L		*W. Cape*	-ln L	
S = 0.85	125.1	2.2	S = 0.85	128.9	0.2
S estimated (0.93)	122.8		S estimated (0.82)	128.7	

DISCUSSION OF SIMPLE MODEL FITS

For Robben Island (Fig. 1) for both models estimation of *S* is justified in terms of AIC (log likelihood difference > 1), and *S* = 0.85 falls outside the 95% likelihood profile estimate for the confidence interval for *S*. For *S* = 0.85, there is a systematic upward trend in residuals for both models, and for the corrected Equation (2) only two of the residuals are (weakly) negative.

Similar conclusions follow for the applications to data for the Western Cape as a whole (Fig. 2). In log likelihood terms the differences between estimating *S* and fixing it at 0.85 are not as severe. However for the model of SWG/EAF/SEABIRDS/13APR/01, there are distinct systematic upward trends in residuals whether *S* is fixed at 0.85 or estimated.

For both Robben Island and the Western Cape as a whole then, only the fits with Equation (2) and estimating *S* evidence reasonably random residual patterns.

This serves to show how misleading the plots of SWG/EAF/SEABIRDS/13APR/01 are in terms of suggesting at a quick glance that the model advocated there is able to reasonably mimic the observed data. There are indications in the residual plots of model misspecification, and results differ significantly at the 5% level from those achievable with alternative parameter values. The reason this occurs is in part that process error estimators seek to reflect annual changes in data, rather than average trends over time as do observation error estimators; plots of abundance *vs* time as in SWG/EAF/SEABIRDS/13APR/01 are thus appropriate to gauge the quality of fit for the latter but not the former.

It is important to realize that these considerations are not simply academic niceties. In testing the pelagic OMP in a manner that takes penguins into account, the penguin population has to be projected into the future using a model that incorporates reliable representation of not only broad trends, but also of variations about these trends (“residuals”). The parameters of these statistical projection models are based on the fits of the models to past data; if those fits fail to satisfy standard statistical criteria, the associated projections will not enjoy confidence.

We must stress that the purpose of these illustrative computations is NOT to advocate the values of *S* (0.99 and 0.93) that follow from maximum likelihood estimation under Equation (2). Other biological knowledge indicates that certainly the first and possibly also the second are unrealistically high. Rather it is to show that there are clear inconsistencies between the parameter values advocated in SWG/EAF/SEABIRDS/13APR/01 and the available abundance index data, and these need to be addressed.

BROADER CONSEQUENTIAL IMPLICATIONS

Leslie matrix results

Log linear regressions of breeder numbers over 1996-2005 for Robben Island and the Western Cape as a whole reflect annual increase rates of 11.4% and 9.6% respectively (we select this period as SWG/EAF/SEABIRDS/13APR/01 suggest an unchanged *P* over these years).

Leslie matrix analysis readily provides values of the maximum steady annual growth rate (*R*) of which a population is capable given values for its demographic parameters. These are obtained by solving the following equation (readily derived from a generalization of equation 1):

$$\exp[RT] = \exp[R(T-1)]S + 0.5\,P\,C\,S_j\;S^{T-1} \qquad (9)$$

where *T* is the age at first breeding.

Substituting the values advanced in SWG/EAF/SEABIRDS/13APR/01 (T=3, P=0.97, C=1, S_j=0.51, S=0.85) yields R=2.0%, far below the observed rates.

Results for some alternative inputs are of interest:

i) Increase S from 0.85 to 0.9 : R= 7.0%
ii) Increase S_j to equal S=0.85 : R= 9.3%
iii) Decrease T=3 to T=2: R=11.8%
iv) Adopt T=3, P=0.97, C=0.8, S_j=0.7, S=0.9 (as suggested per Res Altwegg email 23 April): R=8.3%
v) Case iv) with T=4: R=6.2%

Note that results for the Plagányi-Butterworth model have considered proportions first breeding at age 2 of 10%; 3 of 33%; 4 of 80% and 5+ of 100% as per Crawford *et al.* (1999). From iv) and v) above, it is thus clear that this model can hardly reflect observed increased rates over 1996-2005 without further parameter value changes or immigration.

Reconciliation options

What options are available to reconcile demographic parameter estimates and the high increase rates observed over 1996-2005 of some 10% p.a., without pushing adult survival S unrealistically high? (Note that in any case S will be constrained from going too high in fitting the Plagányi-Butterworth model by the need to fit information on relative numbers of juvenile and adult moulters). It is important to appreciate that one cannot simply ignore existing estimates for some of these parameters; if this is to be done, cogent reasons for bias in the original estimates need to be advanced.

a) Increase S above 0.9, as long as relative numbers in moult counts remain fit?
b) Increase S_j, maximally to S? But i) are Randall (1983), La Cock and Hänel (1987), and Whittington (2002) estimates negatively biased to such an extent? As these (ranging from 0.31 to 0.69) are well below direct estimates of adult survival, are they not indicative that S_j is appreciably below S?
c) Decrease T? How far? Below 3 seems unrealistic. How would this be reconciled with estimates generally >3 reported in Crawford *et al*. (1999)?
d) Increase P? But this is already suggested to be 0.97 and it cannot exceed 1.
e) Increase C, perhaps over 1? Even if there is some evidence for multiple breeding within a year at Dassen Island, are regular proportions of over 1 fledged chick a year per pair consistent with the data?
f) Strong transient effects? The Plagányi-Butterworth model takes due account of these.
g) Temporal variations in parameter values? This possibility will be checked by considering random effects components of survival rates in the Plagányi-Butterworth model, but even if this mechanism can admit high increase rates in the short-term, for biological realism the random components would need to show reasonable correlation with measures of potentially related factors such as food abundance, as will be tested through fitting functional relationships in the Plagányi-Butterworth model.

h) Temporal bias in trends in abundance indices (i.e. was there an undetected increase in count efficiency over 1996-2005)? The counts should be standardized by making allowance, if indicated, for possible co-variates such as different observers having differing efficiencies.
i) Immigration? Immigration of juveniles from Dyer Island may account for some of the increase at Robben Island, but for the Western Cape as a whole one would need appreciable immigration from the Algoa Bay colonies or from Namibia.

Clearly identification of which of these factors most likely accounts for the current inconsistency between demographic parameters and trends has important implications for the modeling exercise, and also the interpretation of the marked reductions in counts over the last two years.

Why not an aggregated model for the Western Cape as a whole?

This appealing thought underlay the advance of the simple model of SWG/EAF/SEABIRDS/13APR/01. It has the advantages of avoiding the need to model migration of juvenile penguins between the various colonies.

However the primary problem is that use of breeding counts alone (available for all the major colonies) is inadequate because of important potential variation in the proportion breeding from year to year (possibly in response to food availability). This would be solvable if moult counts were similarly generally available, but these series are not complete for certain colonies, and further for the important Dassen Island colony the count is negatively biased to a much greater extent than at Robben Island. The more detailed model is needed to be able to make reliable use of these important data, and also to make allowance for different fledging success estimates for Robben and Dassen Islands.

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Appendix 1 – A note on the computation of an index of the proportion of adults breeding (P_t)

In SWG/EAF/SEABIRDS/JAN/04, this is calculated as :

$$P_t = \frac{2 \cdot NRI_t}{ARI_t}$$

where ARI_t = number of birds at Robben moulting in each split year; and
NRI_t = number of pairs breeding at Robben Island.

It is noted in SWG/EAF/SEABIRDS/JAN/04 that P_t is an index not the actual proportion because counts of moulting birds were only undertaken around the coast and because African penguins moult to adult plumage when about 18 months but many breed for the first time when aged 4 years.

Note in the simple model presented in SWG/EAF/SEABIRDS/13APR/01, the average P_t values are taken as the actual proportion of birds aged three years or older breeding in year t, but there is no real basis for this conclusion given the comments above. Moreover, even ignoring the preceding point, the average values computed are unlikely to be unbiased estimates of the true averages given that several of the P_t values as shown below are greater than 1.

Year	Robben Island NRI Breeding pairs	2 * NRI	ARI Moulters	P_t	P_t Average over period
1987	476	952			
1988	849	1698			
1989	829	1658	3459	0.48	
1990	1278	2556	3392	0.75	
1991	1879	3758	4730	0.79	
1992	2027	4054	4915	0.82	
1993	2176	4352	6538	0.67	
1994	2799	5598	8002	0.70	
1995	2279	4558	7948	0.57	0.68
1996	3097	6194	6563	0.94	
1997	3336	6672	5608	**1.19**	
1998	3467	6934	8696	0.80	
1999	4399	8798	9397	0.94	
2000	5705	11410	11765	0.97	
2001	6723	13446	13362	**1.01**	
2002	7252	14504	16439	0.88	
2003	6433	12866	14737	0.87	
2004	8524	17048	17424	0.98	
2005	7152	14304	12871	**1.11**	
2006	3697	7394	7768	0.95	0.97

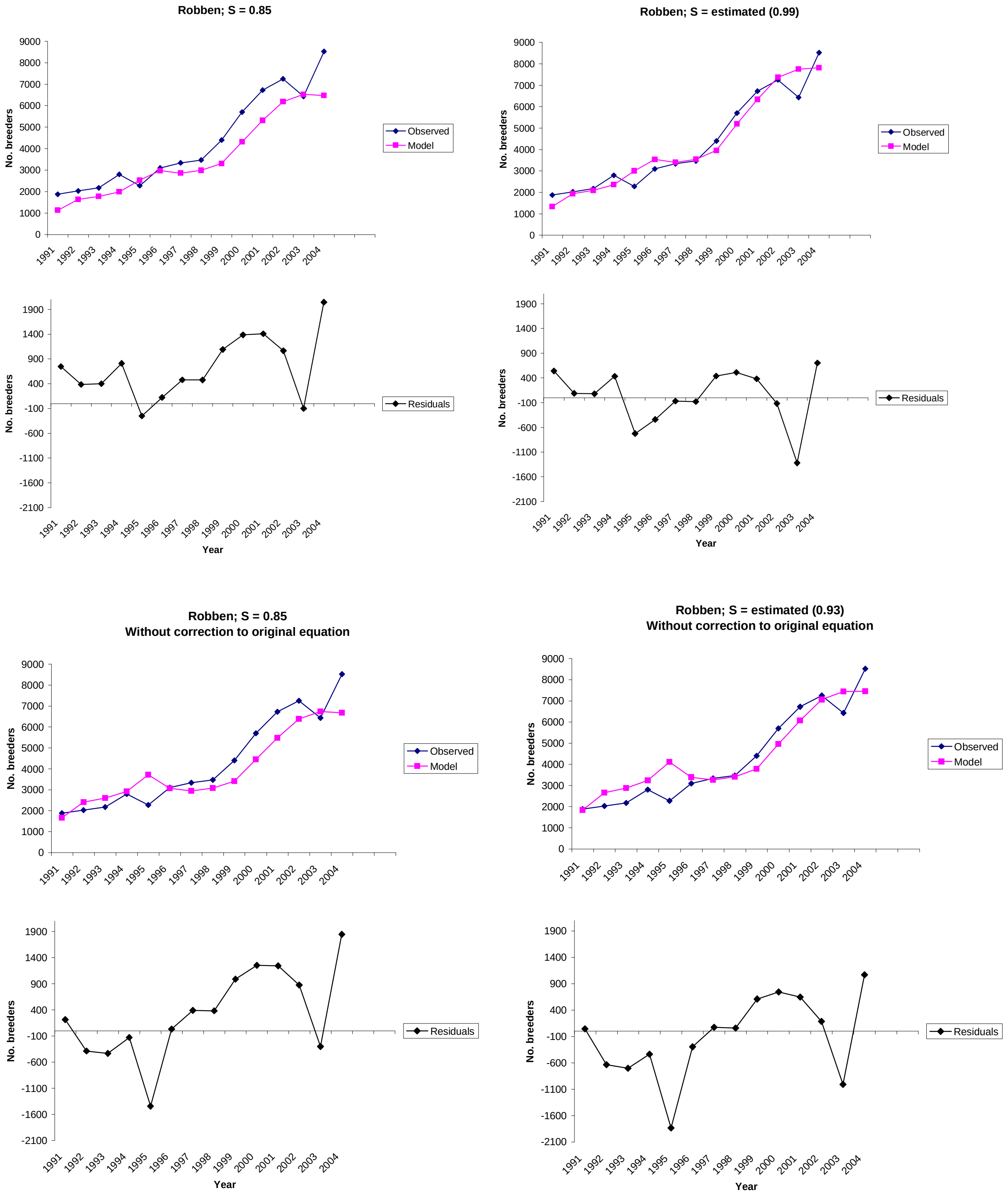
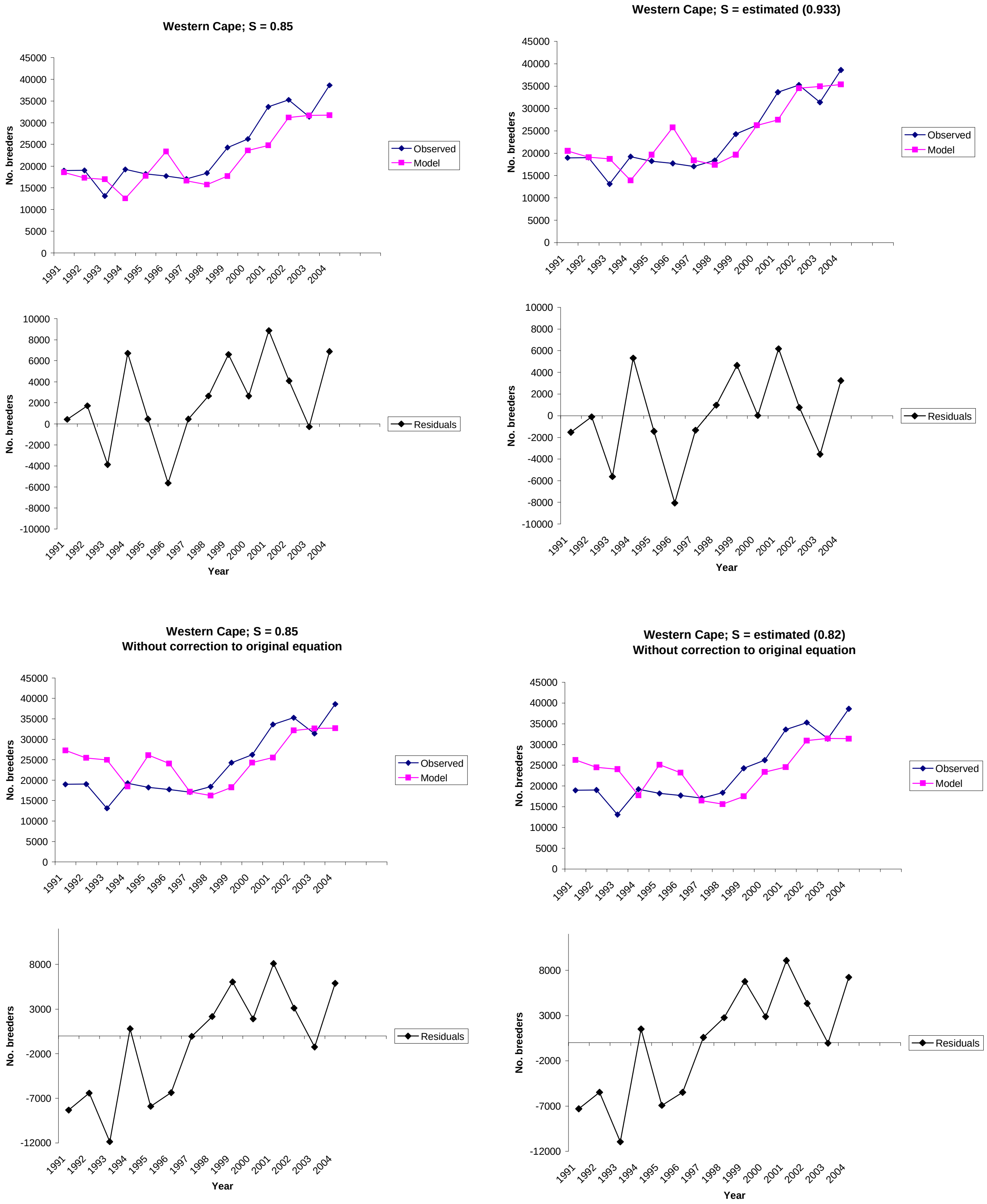


Fig. 1. Comparison in the top four figures of the Equation (2) model and observed trends (with associated residuals in the lower panels) for Robben Island when fixing adult survival *S* = 0.85 compared to estimating *S*. The lower four figures show the results from the model version as put forward in SWG/EAF/SEABIRDS/13APR/01 i.e. without the P_{t+1} adjustment.



Western Cape; S = 0.85

Western Cape; S = estimated (0.933)

Western Cape; S = 0.85
Without correction to original equation

Western Cape; S = estimated (0.82)
Without correction to original equation

Fig. 2. Comparison in the top four figures of the Equation (2) model and observed trends (with associated residuals in the lower panels) for the Western Cape when fixing adult survival S = 0.85 compared to estimating

S. The lower four figures show the results from the model version as put forward in SWG/EAF/SEABIRDS/13APR/01 i.e. without the P_{t+1} adjustment.