

Aspects of Modelling Robben Island African Penguin *Spheniscus demersus* Populations

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INTRODUCTION

Crawford *et al.* (2006) present relationships between the breeding success of Robben Island African penguins *Spheniscus demersus* and the abundances of both anchovy *Engraulis encrasicolus* and sardine *Sardinops sagax*. Based on their analysis, they suggest that the management of the purse-seine fishery should ensure adequate escapement of fish to maintain the combined biomass of anchovy and sardine above two million tons. Given that this potentially has important repercussions for the management of the pelagic fishery, their analyses have highlighted the importance of further and more detailed investigations into this issue. This paper provides a brief summary of some further considerations in this regard.

A DYNAMIC MODEL

Ideally a dynamic model needs to be constructed to describe the penguin population dynamics. One of the simplest forms to capture the essence of the population dynamics of the adult female penguins is as follows:

$$N_{y+1} = N_y S + (N_{y-T+1}) q_f H S_J S^{T-1} + I_y \quad (1)$$

where

| | |
|-------|--|
| N_y | is the number of adult females at the start of year y , |
| S | is the post-first-year annual survival rate, |
| T | is the average age at first breeding (taken here to be 4), |
| H | is the average breeding success (fledged chicks per pair per year), |
| q_f | is the fraction of chicks that are female, |
| S_J | is the first year post-fledging survival rate, and |
| I_y | is the number of immigrants in year y , which could be modelled in various ways. |

Note for simplicity in these initial investigations I_y is set = 0, and H is taken to be a constant rather than using year-specific estimates. Following Crawford *et al.* (2006), values for parameters were fixed as follows: $T = 4$ yr and $q_f = 0.5$. Moreover, the averages of the H estimates for Robben Island (0.91) and of the S_J estimates for other colonies (0.51) were used. Assuming further a steady initial population over the period 1986-1989, Fig. 1 shows the sensitivity of population trends for adult penguins to the choice of an adult survival parameter S (and also to S_J).

Given this sensitivity, and also the fact that mark-recapture based estimates of survival rate are often subject to biases that are difficult to quantify, it is conventional practice in marine population modelling to estimate one of the S and S_J parameters parameter by fitting to time series of an index/indices of abundance for the population (or estimate both should priors be provided for a Bayesian analysis). In this case the issue is complicated further because of a suspected large immigration effect. Given the extent of immigration between different penguin

colonies, it may be preferable to seek to estimate such parameter(s) through combined fitting to the abundance data available for all colonies. Such data are available (Underhill *et al.* in prep) but there was insufficient time to prepare further analyses for the current meeting.

INCLUDING DENSITY DEPENDENCE

Butterworth and Plagányi (2005) stressed that it is very important to appreciate that assuming S_j (or H in the example presented here) depends only on pelagic resource abundance B does not provide a viable model structure from which to draw inferences of the effect of pelagic fishing on penguins. Consider an example as follows:

$$H_y = f(B_y) \text{ i.e. penguin breeding success is a function of pelagic abundance in year } y.$$

For a general model, we need to link the penguin model to a model of the (pelagic) resource. Equation (1) is modified as follows:

$$N_{y+1} = N_y S + (N_{y-T+1}) q_f f(B_y) S_j S^{T-1} \quad (2)$$

The problem is that any harvest strategy gives a fixed distribution for B_y and hence for $f(B_y)$. The net effect is thus that the model predicts an overall exponential increasing or decreasing trend in penguin abundance N_y . There has to thus be some density dependence introduced into the equation.

Crawford *et al.* (2006) suggest an *explicit* maintenance of a combined sardine-anchovy biomass of 2 million tonnes to support penguin populations (see Appendix 1). Cunningham and Butterworth (2006) argue that proposals of this nature have to be cast in a probabilistic framework, with the associated analysis necessarily linked to OMP testing so that the variability of B under harvesting is appropriately taken into account. Indeed, a dynamic model is needed to evaluate an appropriate distribution of pelagic abundance B to ensure stability of the penguin population.

An appropriate way to proceed would seem to be to introduce density dependence into the penguin dynamics through the dependence of S_j (say) on N . If S_j is a decreasing function of N , as well as an increasing function of B , the model behaviour will yield broadly stable levels of penguin abundance for a range of pelagic harvest intensities, where such a level decreases as harvesting intensity is increased.

One possible formulation is that based on Thomson *et al.* (2000) adapted as follows:

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

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 related term K^* (note K^* differs from, being greater than the penguin carrying capacity K), then this term tends to 1. Estimating or specifying the value of S_j is not straightforward: one approach is to set this value based on the maximum realistic population growth rate in the absence of fishing. The choice of an appropriate value for K^* would also need to give consideration of the possibility that penguin

numbers at the turn of the 19th Century may have been abnormally high due to a competitive release effect as a result of seal numbers having been reduced close to extinction in what was the only major human-harvest-induced perturbation to the ecosystem at that time.

ACKNOWLEDGEMENTS

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APPENDIX 1

Crawford *et al.* (2006) fitted a regression relating breeding success H to the combined biomass of anchovy and sardine B as follows:

$$H = 0.159 * \ln B + 0.461 \quad (\text{A.1})$$

Based on their analysis, they suggest that there is a threshold fish biomass (approx 2 million tons) below which breeding success decreases. However, the form of the relationship fitted (linearity in $\ln B$) automatically imposes a convex shape on an H vs. B plot, which therefore may inevitably show behaviour suggestive of a threshold effect. In order to determine whether the existence of such a threshold is supported statistically, it becomes necessary to undertake further analyses.

A curve of the form:

$$H = \alpha \cdot B^\gamma + \beta \quad (\text{A.2})$$

was thus fit to the same data (see Fig. A.1) using AD Model Builder which allows for fairly straightforward implementation of the Markov Chain Monte Carlo (MCMC) method to perform Bayesian integrations to provide posterior credibility intervals. Note that equation (A.2) has an intercept parameter and hence the curve is not forced to go through the origin. The aim of the analysis was to check for statistical evidence that the “curvature” parameter $\gamma < 1$ (i.e. a convex relationship). The maximum likelihood estimates obtained were $\alpha = 0.24$, $\beta = 0.24$ and

$\gamma = 0.38$ (Fig. A.1). To examine the uncertainty around this relationship, an MCMC analysis was conducted, based upon uniform priors for α , β and γ , to compute the distribution (based on 1000 retained values) for H as a function of the following B values: $B = 1, 2, 3, 4$ and 5 million tons. Fig. A.1 shows the median and upper and lower 5%-ile's for each of these distributions. The median posterior γ value obtained was 1.79 (note > 1) with upper and lower 5%-ile's of 2.137 and 0.277 respectively.

The results of the MCMC analysis thus demonstrate that these data are not sufficient (from a statistical perspective) to support the hypothesis of a threshold-type relationship compared, for example, to a linear relationship between breeding success and pelagic biomass over the range of resource biomass spanned by the data. This follows from a 90% credibility interval for γ that extends well to either side of 1, thus admitting both convex (threshold-like) and concave relationships, with the latter actually having the greater support in the data.

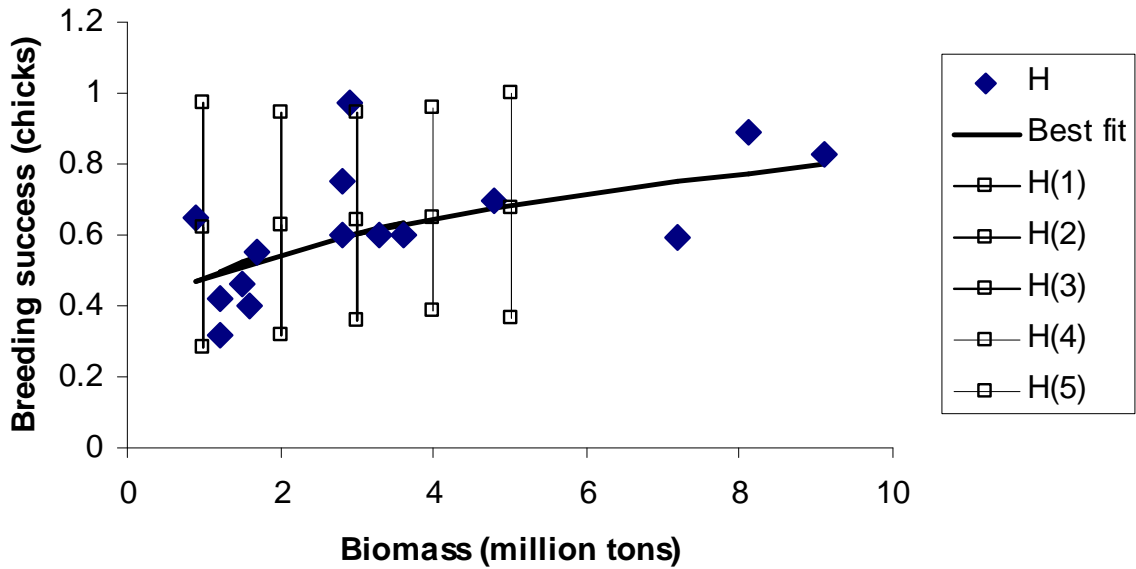


Fig. A.1. The maximum likelihood estimate ($H = 0.24B^{0.38} + 0.24$) of a relationship between breeding success and resource biomass obtained by using the data from Crawford *et al.* (2006). The vertical lines represent the posterior medians and upper and lower 5%-ile's (computed using an MCMC approach) for the predicted values as a function of a range of biomass values.

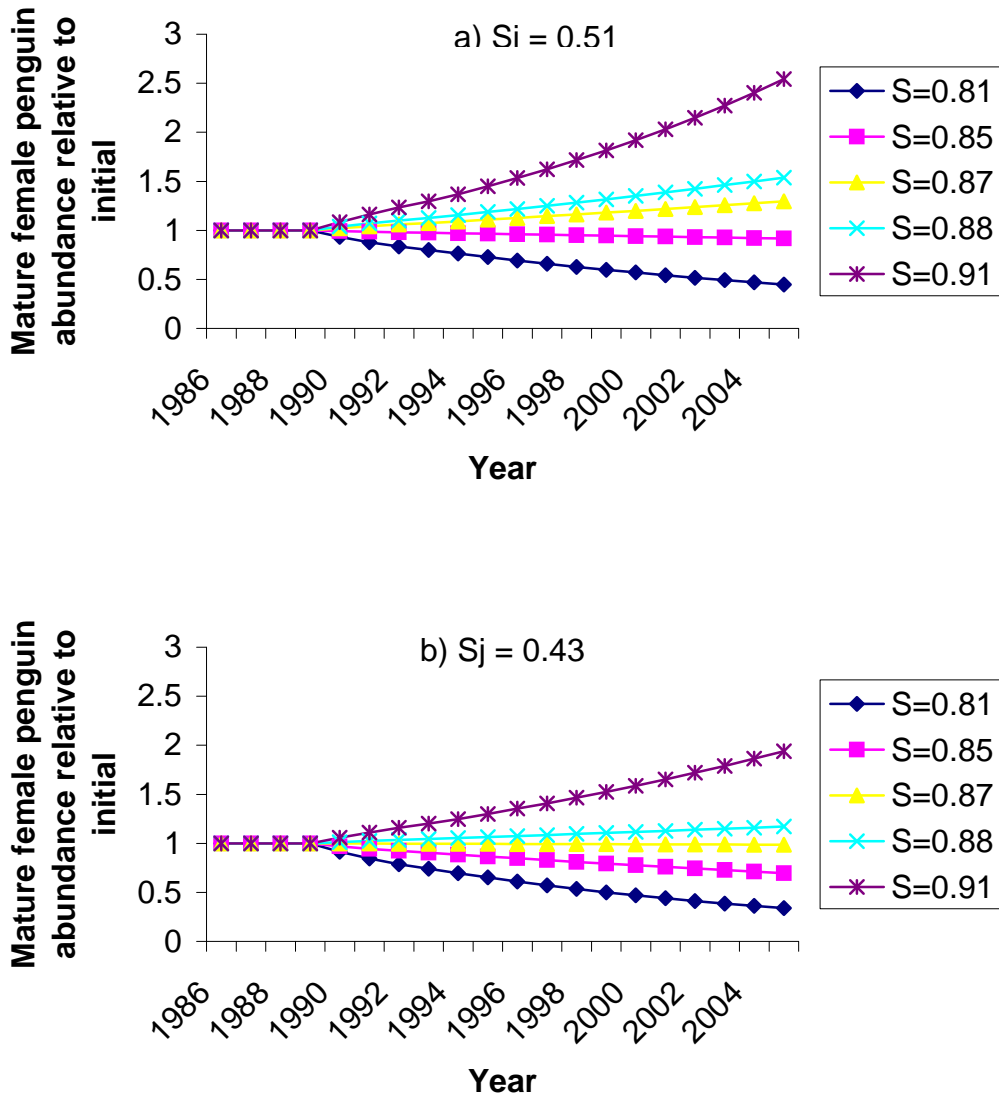


Fig. 1. Demonstration using a simple dynamic model of penguin dynamics of the sensitivity of modelled penguin abundance trends (shown relative to the 1989 level) to the choice of the adult survival parameter S and first year post-fledging survival rate parameter S_j (see text for details).