Progress on the implementation of recommendations from the December 2010 MARAM International Workshop

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The recommendations pertinent to the penguin modelling in MARAM IWS/DEC10/REP/1 are listed below in bold. These are followed by comments on the model development in these areas, with references to the model summary paper MARAM IWS/DEC11/P/PENG/P1.
A. Models of the impact of fishing on penguins through reducing overall prey abundance

BA. $1(H)$. Some of the annual moult counts (and hence the proportion of juvenile birds at the time of moult counts) have estimates of associated precision (e.g. MARAM IWS/DEC10/PA/P4). These measures should be used to weight the data in the likelihood function. There will likely be sources of uncertainty not captured by these measures of precision which should be accounted for (if necessary) using an "additional variance" term. [Consideration of basic model structure and Bayesian estimation procedure proposed.]

The uncertainties and "additional variance" have been included in the adult moult count likelihood (equation 22).

BA. 3 (H). The tagging data should be included explicitly in the likelihood function along the lines of MARAM IWS/DEC10/PA/P3. These data have the potential to reduce the uncertainty associated with estimates of survival and should tighten the relationship between survival and measures of sardine and anchovy abundance. Moreover, use of the tagging data will provide a link with previous work, e.g. by Altwegg ${ }^{1}$. Implementation of this recommendation will require access by the MARAM analysts to all of the available tagging data. Altwegg and the MARAM analysts should collaborate to identify an appropriate set of specifications for how the tagging data are to be included in the likelihood function (i.e. whether a separate survival term is to be estimated for the first year after tagging, whether some parameters are to be shared between Dassen and Robben Islands, etc.) Inclusion of the tagging data should reduce the number of point estimates of survival rate which end up at the upper bounds for their priors. [Extension of model to incorporate further penguin-related data (e.g. tag-recapture).]

Tagging data for the full period have been extracted and these have been included in the likelihood function (equation 23). An additional "transient" survival rate has been estimated for the first year after tagging. The number of point estimates of adult survival rate which are at the upper bound of their priors has been reduced to one.

BA. 4 (H). Penguin biologists should identify a set of hypotheses to relate specific measures of sardine and anchovy abundance/density (temporal and spatially aspects) with population processes for penguins (ideally fledging success, juvenile survival, age-at-first breeding, and

[^0]adult survival). An attempt should then be made to identify whether there are data that could be used to quantify these measures of abundance/density. In cases in which data do not currently exist to quantify the measures, collection of such data should be identified as a research priority. [Extension of model to incorporate further penguin-related data (e.g. tagrecapture).]

The paper FISHERIES/2011/SWG-PEL/3 was drafted listing various hypotheses.

BA. $5(\mathrm{H})$. The uncertainty in the biomass trajectories for sardine and anchovy should be accounted for when evaluating the relationships between penguin demographic parameters and sardine/anchovy abundances. This can be achieved by (a) selecting a small number (e.g. 10) of sardine and anchovy biomass trajectories from the posteriors estimated using the sardine and anchovy assessment models and using these trajectories as input data to the penguin model, with application of the Markov Chain Monte Carlo (MCMC) algorithm conditioned on each of the trajectories, (b) selecting a representative number of parameter vectors for the penguin model from each of the MCMC chains to construct the parameter vectors for the penguin model, and (c) basing the inferences regarding the impact of alternative OMPs for anchovy and sardine on these parameter vectors.

This has not been attempted. This may be included once the new pelagic OMP has been completed.

BA. $6(H)$. The credibility of the work will be considerably enhanced by further simulation testing. The initial simulations conducted (MARAM IWS/DEC10/PA/P7) suggest that there is little bias if there is no model-misspecification. However, the only source of variability included in these simulations was that associated with the moult count data. The Panel have the following recommendations in regard to simulation testing: (a) consider further simulations in which there is an impact of sardine and anchovy on the dynamics of the penguin population via, for example, impacts on fledging success, participation in, and age-at-first, breeding, juvenile survival and adult survival even if the current model suggests that this is not the case, (b) allow for error when measuring the covariates related to sardine and anchovy abundance, and (c) generate values for the random effects for survival and reproductive success. The distributions of estimates for key parameters (e.g. $\mu_{S}$ and $\mu_{H}$ ) from the simulations should be compared with those from the posteriors based on the actual data. The distributions for estimates of the impact of reduced pelagic fish catches on future penguin population trends should be similarly compared. [Simulation testing of estimation process.]

Further simulation testing will be conducted in due course.

BA. $7(H)$. As currently formulated, fledging success and juvenile survival are lumped in a single time-varying parameter. This is appropriate given that the data used in MARAM IWS/DEC10/PA/P6 would not allow these processes to be distinguished. However, there are data to inform some of the processes involved in reproduction. Figure 1 outlines the penguin dynamics, which biological processes impact the various life stages, and the data available for each process / life-stage. The Panel recommends: (a) modelling fledging success and juvenile
survival as separate processes, (b) including the data on fledging success [initially as relative indices but as absolute measures in sensitivity tests], on total nest counts, and on juvenile survival rates from tag-recapture data in the likelihood function, (c) including relationships between fledging success and juvenile survival and measures of sardine and/or anchovy abundance in the model, (d) calculating the rates of immigration based on the differences between the estimated annual number of age- 1 animals and the numbers expected given the number of breeders, the fledging success rate, and the juvenile survival rate (c.f. MARAM IWS/DEC10/PA/P5). In the longer term, models could consider participation in, and age-at, first breeding (see below). [Consideration of basic model structure and Bayesian estimation procedure proposed; Extension of model to incorporate further penguin-related data (e.g. tagrecapture); Incorporation of immigration effects.]

Modelling fledging success and juvenile survival separately has yet to be attempted. Thus the associated data and possible relationships with pelagic abundance have not yet been included.

BA. 8 (L) Consideration should be given to the use of juvenile tagging data to estimate migration rates independently.

This would require a very careful analysis of the data. This has not yet been attempted.

BA. 9 (H). The Panel expects that many model runs (e.g. based on different density-dependence assumptions, relationships between population processes and measures of sardine and anchovy abundance, etc.) will be conducted. It highlights the need to assign weights to the different models using objective approaches. For example, the model-estimates of immigration can be validated using inferences based on trends at Dyer Island. In addition, models in which parameter estimates hit biologically-based bounds should be downweighted. [Specification of robustness tests, particularly as regards the functional form of the penguin parameter-fish abundance relationships.]

BA. 10 (H). The survival and reproductive success parameters should be assumed to be betadistributed. [Consideration of basic model structure and Bayesian estimation procedure proposed.]

This was implemented. It was found that the beta distribution is not appropriate for the adult survival parameters, as a unimodal distribution with a high mean can only have a very small variance, which is undesired. A log-normal approach has been implemented instead.

BA. $11(\mathrm{H})$. With regard to moult counts, the current estimation method is treating the moult counts for Robben Island as absolute (with a known bias). The Panel supports this assumption. In regard to Dassen Island where an appreciable proportion of the population is not covered in the moult counts, the Panel recommends that these counts be treated as relative counts, and that sensitivity be evaluated with respect to different assumed values for the constant of proportionality. In very recent years, there is evidence of substantial numbers of penguins from these two colonies moulting at locations further south before returning to these colonies to breed; the Panel recommends that moult counts for this period be omitted when fitting the model.

All Robben Island moult counts are included in the current model. Numbers of birds from Robben Island potentially moulting at other locations (e.g. Stony Point) are relatively small, and those birds could come from various locations.

BA. 12 (H). Standard diagnostics for MCMC analyses (e.g. Gelman-Rubin R, Geweke statistic, trace places for multiple chains, etc.) should be provided for the final reference case model(s). MCMC diagnostics should be provided for parameters and derived variables. [Consideration of basic model structure and Bayesian estimation procedure proposed.]

These diagnostics will be included when final results are presented.

BA. 13 (H). The sensitivity of the model results to different assumptions regarding the age-at-first-breeding, including ogives relating the probability of first breeding with age, should be examined in tests of sensitivity. Such assumptions should, at least initially, assume time independence, given the technical complexities of incorporating such possible dependence. [Consideration of basic model structure and Bayesian estimation procedure proposed.]

Some simple sensitivities to values of different age-at-first-breeding have been conducted.

BA. 14 (L). Data on time-trends in age-at-first breeding should be collated and analysed for incorporation in the model. Care needs to be taken when analysing these data to account for the probability of missing the first time an animal breeds. [Extension of model to incorporate further penguin-related data (e.g. tag-recapture).]

This has been looked at in the past by Phil Whittington.

BA. 15 (L). A model which includes multiple Western Cape colonies should be developed. [Extension to multiple Western Cape colonies.]

Not yet attempted.


[^0]:    ${ }^{1}$ Altwegg R. 2009. Survival of African penguins at Robben and Dassen islands from 2002 to 2006. MCM/2009/SWG-PEL/16: 11-17.

