RESPONSES TO PREVIOUS PANEL RECOMMENDATIONS ON PENGUIN RESEARCH

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Responses have been inserted in *red italicised underlined text* after each recommendation

INTERNATIONAL REVIEW PANEL REPORT FOR THE 2010 INTERNATIONAL FISHERIES STOCK ASSESSMENT WORKSHOP
29 November - 3 December 2010, UCT

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Key Issues to be discussed at Workshop

Penguins
Models of the impact of fishing on penguins through reducing overall prey abundance (A sessions)

- Consideration of basic model structure and Bayesian estimation procedure proposed
- Simulation testing of estimation process
- Treatment of estimates close to demographic constraint boundaries
- Specification of robustness tests, particularly as regards the functional form of the penguin parameter-fish abundance relationships
- Extension of model to incorporate further penguin-related data (e.g. tag-recapture)
- Specification of priors
- Incorporation of immigration effects
- Extension to multiple Western Cape colonies

Consideration of analyses related to the impact of pelagic fishing close to breeding colonies (B session)

- What alternative GLM (or other) model formulations, including ones with multiple dependent variables, might be considered to analyse results from the experiment of opening and closing to fishing around pairs of penguin colonies?
- What open/close alternation (if any) scheme within each colony pair might be most appropriate, and what interval for alternation should be considered (single or multiple year periods)?

B. Penguins

B.1 (*). The Panel highlights the considerable value of collaboration among scientists with a diverse range of skills. In the specific case of penguins, the best outcomes will occur when modellers, population ecologists, penguin specialists, and pelagic species specialists all collaborate to ensure that models are realistic biologically, and the appropriate data are available and cleaned.

Such collaborative interchanges have taken place under the auspices of DAFF's Pelagic Working Group.

B.2 (*). The recommendations outlined below require the availability of several data sources which are not currently included in the models. The Panel highlights the importance of providing these data to the modellers as quickly as possible, if key deadlines for OMP development are to be met. In addition, it is important that any data included in the model be fully documented to ensure that the data are analysed appropriately.

This was facilitated through the DAFF interchanges mentioned above, though did not always prove to be a smooth process

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 process errors associated with fitting to these data proved to be so large that this sophistication was not considered warranted in what was a necessarily coarse estimation process– see section S1.2 of MARAM/IWS/DEC14/Peng/3b.

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).*]

This has been done – see MARAM/IWS/DEC14/Peng/3a sections 2.3 and 3.2.5 and MARAM/IWS/DEC14/Peng/3b section S2.5..

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 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

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

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. tag-recapture).*]

Discussions were held to identify a number of potential mechanisms a priori, and hence to suggest which components from acoustic survey results provided the best candidates for relationships. Final choices were informed by what proved to best inform the models (e.g. Robben island penguin adult survival was found to be best linked to the biomass of sardine west of Cape Agulhas as estimated in November surveys).

BA.5 (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 was not pursued given the already substantial technical challenges encountered in what turned out to be a rather complex estimation process – see section 2.1 of MARAM/IWS/DEC14/Peng/3b.

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. μ_S and μ_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.*]

Given the substantial technical challenges encountered with the estimation process (see preceding comment), and given that such further work seemed likely to prove both difficult and time consuming, the time needed to pursue this aspect further was not considered warranted in the light of resource limitations.

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. tag-recapture); Incorporation of immigration effects.*]

This was pursued only in part, in that tag-recapture data for adult penguins were used as fully as possible to assist in the estimation of both survival rates and immigration. However given that the model fits indicated these to be the primary driving features for the model, and with little variation in the overall reproduction process (which includes first year survival) (see MARAM/IWS/DEC14/Peng/3a Figure 8), attempts to fit further data to modelled components of that reproduction process was not considered warranted.

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

Only tagging data for adult penguins were used (see MARAM/IWS/DEC14/Peng/3b section S1.3) in the interests of simplicity, and also given the weak signal at the reproductive level compared to the strong signal in adult survival in other data.

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.*]

In practice (and given resource constraints) this was addressed by sensitivity tests – see MARAM/IWS/DEC14/Peng/3b section S6.

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

This was implemented for the reproductive parameters; a more complex formulation proved necessary for survival – see MARAM/IWS/DEC14/Peng/3b sections S2.1 and 2.3.

BA.11 (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.

This advice was followed for the Robben Island model. Unfortunately resource constraints precluded taking the Dassen Island model further.

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 statistics have been given consideration for the lengthy MCMC chain generated.

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.*]

This was addressed in part – see Table S12 of MARAM/IWS/DEC14/Peng/3b – but not taken further given the low sensitivity of quantities of primary interest (projected penguin population trends) to variations in the age-at-maturity.

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).*]

Resource limitations precluded this being pursued, though it did indeed seem a low priority for the reasons stated in responses given the responses to BA7 and BA13 above.

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

Resource limitations have precluded extending work to this thus far.

B. Consideration of analyses related to the impact of pelagic fishing close to breeding colonies

BB.1 (*). The Panel considered how open/closure alternatives should be implemented in the near future with the objective to maximize the probability of determining whether pelagic fishing near colonies has an impact on penguins. In regard to this question, the Panel drew the following conclusions:

1) Within the current set of models, the ability to estimate the extent of additional (residual) variance will not be impacted by which islands are open or closed to fishing.
2) There is no reason not to start opening closed islands and closing open islands in the short term because doing so will allow data collected from the feasibility study to be part of the experiment (in the event an experiment is conducted) and hence reduce the time needed to draw conclusions.
3) Keeping islands closed (or open) for three-year periods is appropriate to balance two conflicting goals: (a) maximizing contrast and hence minimizing the confounding between treatment effects and the impact of long-term trends in environmental conditions by changing the closure status annually, and (b) allowing use of indices of penguin dynamics which might be impacted by fishing effects in previous years by not changing closure status over a long period of time.
4) A power analysis to decide on whether a full experiment should take place can be conducted at any time, but its reliability will be greater (particularly for new indices) in the future (see Table 1).
5) Monitoring of penguin populations and pelagic fish abundance (the latter ideally through an enhanced programme of surveys in the neighbourhood of key penguin colonies at regular intervals during the penguins' breeding period) is vital to an effective experiment.

Table 2 lists the implications of these recommendations in terms of which islands would be open and closed to fishing from 2011 onwards. [*What open/close alternation (if any) scheme within each colony pair might be most appropriate, and what interval for alternation should be considered (single or multiple year periods)?*]

The recommendations here (see Table 1 below) were implemented, and consequent results, including for new indices, are to be found in MARAM/IWS/DEC14/Peng/4. Though further small scale acoustic surveys to monitor local abundance around islands have been conducted, unfortunately it seems that largish process errors confound the utility that 5) above saw from the results of such surveys – see MARAM/IWS/DEC14/Peng/6.

BB.2 (H). The presented analyses related to power are based on two indices only: fledging success and breeders per moult count. The ability to improve the estimates of the additional variation in the indices will be greatest for those indices which have not been monitored in the past (see Table 1 for an estimate of the extent to which three additional years of data will impact the standard deviation of unexplained variation in fledging success and breeders per moulter). To the extent possible, the types of analyses on which MARAM IWS/DEC10/PB/P2 are based should be extended to other indices. [*Can methods put forward to estimate experiment power be improved?*]

Results have been presented for six indices for Robben and Dassen Island in MARAM/IWS/DEC14/Peng/4.

BB.3 (H). Models relating indices of penguin dynamics to measures of sardine and anchovy abundance should consider the biomass at the local level as a potential covariate (perhaps expressed as density to compare or estimate jointly effects for Robben and Dassen Islands). In addition, the GLM model used to estimate additional variation should include biomass as a covariate and a random year factor, evaluated in a stepwise manner. [*What alternative GLM (or other) model formulations, including ones with multiple dependent variables, might be considered to analyse results from the experiment of opening and closing to fishing around pairs of penguin colonies?*]

Abundance estimates from appropriate strata of the biannual acoustic surveys for pelagic fish over the west and south coasts have been used in these models. However, for the reason given in the response to BB.1 above, use in this manner of the results from the small scale surveys around islands has not proved viable. Results for all the GLM variations mentioned above are reported in MARAM/IWS/DEC14/Peng/4, Table 2.

BB.4 (H). Examine the relationship between sardine and anchovy local abundance estimates from surveys around island colonies and the recruitment and spawning biomass surveys (this relationship may need to be used if only an incomplete set of local estimates of abundance are available).

This examination is reported in MARAM/IWS/DEC14/Peng/6. Unfortunately it seems that the high process error component of the small scale survey data precludes their providing much useful information towards this end.

Table 1: For the index time series already available for monitoring the impact of pelagic fishing near to colonies on the reproductive success of penguins, 95% confidence intervals for the parameter estimate of the standard deviation of the error together with the available data, as well as CIs that would be obtained with three extra years of data given that the point estimate remains the same.

Fledging success		**Breeders per moulters ratio**	
$\hat{\sigma}_e = 0.182$	95% CI	$\hat{\sigma}_e = 0.209$	95% CI
df = 4	(0.109; 0.523)	df = 11	(0.148; 0.355)
df = 7	(0.120; 0.370)	df = 14	(0.153; 0.330)

Table 2: Specifications for which islands with penguin colonies should be closed (X) and open ( ) to fishing under the approach recommended.

	2008	**2009**	**2010**	**2011**	**2012**	**2013**	**2014**
Dassen	X	X					X
Robben				X	X	X	
St Croix		X	X	X			
Bird					X	x	X

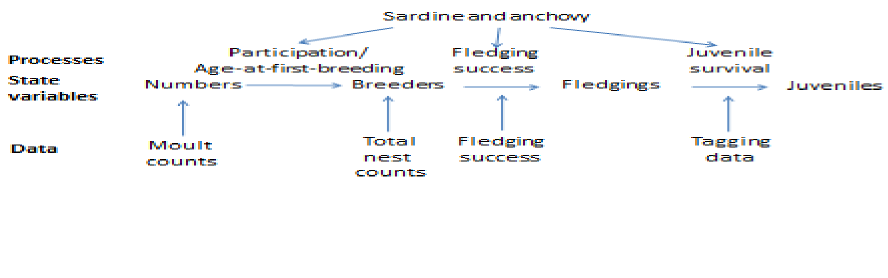

Figure 1. Outline of the dynamics of breeding and juvenile survival.

INTERNATIONAL REVIEW PANEL REPORT FOR THE 2011 INTERNATIONAL FISHERIES STOCK ASSESSMENT WORKSHOP
28 November - 2 December 2011, UCT

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Key Issues to be discussed at Workshop

Penguins

- Review of updated penguin model
  - i) Is the estimation satisfactory, including of the variability in the penguin survival rate-sardine biomass relationship?
  - ii) Are further robustness tests required, including consideration of different hypotheses linking demographic parameters to food availability?

- Review of Penguin Pressure model
  - i) What further work would be needed to make this model operational?

- Linking the penguin model to the pelagic OMP
  - i) What are appropriate performance statistics?
  - ii) How best to balance "future benefit to penguins" vs "future decreased catches"?

B.2. Penguins (MARAM)

Note: A number of the recommendations below effectively repeat those above made a year earlier, so that back reference has been made on those occasions to avoid repetition.

BE.1 (H). Consider additional robustness tests in which:

(a) there is immigration after 1999,
(b) the log-normal distribution for the variation about the penguin survival rate – sardine abundance relationship is replaced by an alternative (e.g. gamma),
(c) the relationships between sardine and anchovy abundance/density (temporal and spatially aspects) and population processes for penguins are based on alternatives selected by the penguin biologists (summarized in FISHERIES/2001/SWG-PEL/3).

[*Are further robustness tests required, including consideration of different hypotheses linking demographic parameters to food availability*]

All these suggestions were pursued, with results reported in MARAM/IWS/DEC14/Peng/3a and 3b.

BE.2 (H). Future projections showed a strong dependency on the value of $\tilde{\sigma}^2$, the parameter which determines variance of the random effects on natural mortality, *M*, decreasing for $\tilde{\sigma}$ =0.10 and increasing for $\tilde{\sigma}$ =0.05. This was attributed to the assumption of a lognormal distribution for the random effects on *M* resulting in lower average survival with increasing $\tilde{\sigma}$. Incorporate a log-normal bias-correction factor for *M* so that the expected value of *M* does not depend on the choice of $\tilde{\sigma}$ [2]. [*Is the estimation satisfactory, including the variability in the penguin survival rate-sardine biomass relationship?*]

Ultimately it proved necessary to introduce a rather different and more complex formulation for the M error distribution – see MARAM/IWS/DEC14/Peng/3a, section 3.2.1.

BE.3 (H). Resolve the problem of systematic deviations in the residuals from the fits to the recaptures from marking in 1990 and 1992. First, check that the basic data are correct and investigate whether information exists about tagging success and other factors in those years. If this investigation does not highlight a problem, one technical solution which could be implemented within the model is to drop the data for these years and another solution is to estimate year-specific initial tag-loss / emigration rates. [*Is the estimation satisfactory, including the variability in the penguin survival rate-sardine biomass relationship?*]

Transients were introduced (see section S2.5 of MARAM/IWS/DEC14/Peng/3b), though these did not fully resolve the fitting problem. Ultimately, however, as shown in Table S12 and Figure S12 of MARAM/IWS/DEC14/Peng/3b, the key outputs which are the projected penguin population trajectories are not that sensitive to this aspect of the model fit.

BE.4 (H). Summarize the results of the projections of the penguin model in terms of (a) the probability of declining below current abundance, and (b) the difference in the change in penguin numbers with fishing to that without fishing, with particular focus on the next 5-10 years. [*What are appropriate performance statistics*]

Figure 10 of MARAM/IWS/DEC14/Peng/3a and Table S12 of MARAM/IWS/DEC14/Peng/3b implement aspects of this suggestion.

BE.5 (H). Impose a uniform prior on $\tilde{\sigma}$, and alternatively an inverse gamma prior on $\tilde{\sigma}^2$. [*Is the estimation satisfactory, including the variability in the penguin survival rate-sardine biomass relationship?*]

The technical difficulties which arose in this regard, and how they were resolved, is detailed in section 3.2.6 of MARAM/IWS/DEC14/Peng/3a.

BE.6 (H). Estimate a linear (constrained not to decrease) relationship between reproductive success and anchovy abundance rather than assuming there is no dependence of reproductive success on anchovy abundance, and hence develop a posterior distribution for this parameter based on MCMC sampling which could admit relatively low reproductive success at low anchovy biomasses. [*Is the estimation satisfactory, including the variability in the penguin survival rate-sardine biomass relationship?*]

Ultimately little dependence was evident; see Figures 8 and S9 of MARAM/IWS/DEC14/Peng/3a and 3b respectively.

[2] Initial implementation of this recommendation during the review indicated that it removed most of the dependency on $\tilde{\sigma}$.

BE.7 (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 posterior distributions 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.

[*Is the estimation satisfactory, including the variability in the penguin survival rate-sardine biomass relationship?*]

See response above to BA.5.

BE.8 (H). The credibility of the work will be considerably enhanced by further simulation testing which should:

(a) consider 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 there is no impact on some of these demographic parameters,
(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.

See response above to BA.6.

BE.9 (H). As currently formulated, fledging success and juvenile survival are lumped in a single time-varying parameter. Develop a conceptual model of the penguin population and show how each parameter/process in the current model pertains to actual biological processes. Ideally, fledging success and juvenile survival should be modelled as separate processes, and 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 should be included in the likelihood function. [*Is the estimation satisfactory, including the variability in the penguin survival rate-sardine biomass relationship?*]

See response above to BA.7.

BE.10 (H). Standard diagnostics for MCMC analyses (e.g. Gelman-Rubin R, Geweke statistic, trace plots for multiple chains, etc.) should be provided for the final reference case model(s). MCMC diagnostics should be provided for parameters and derived variables. [*Is* *the estimation satisfactory, including the variability in the penguin survival rate-sardine biomass relationship?*]

See response above to BA.12.

BE.11 (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. Although many of these sensitivities have already been evaluated (MARAM IWS/DEC11/P/PENG/P1), this should be repeated for the final version of the model. [*Is the estimation satisfactory, including the variability in the penguin survival rate-sardine biomass relationship?*]

See response above to BA.13 Final sensitivity results are reported in Table S12 of MARAM/IWS/DEC14/Peng/3b.

BE.12 (M). Compute the historical time-trajectory of moult numbers had there been no harvests of anchovy or sardine.

This has not (yet) been done – the perhaps more important and interesting result seemed to be that had there been no immigration of penguins to Robben Island during the 1990s, as reported in Figure 7 of MARAM/IWS/DEC14/Peng/3a.

BE.13 (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. [*Is the estimation satisfactory, including the variability in the penguin survival rate-sardine biomass relationship?*]

See response above to BA.14.

BE.14 (L). A model which includes multiple Western Cape colonies should be developed. [*Is the estimation satisfactory, including the variability in the penguin survival rate-sardine biomass relationship?*]

See response above to BA.15

B.3 Penguins (Other)

BF.1 (*). The Panel noted that the Penguin Pressure Model (MARAM IWS/DEC11/P/PENG/P2) was a work in progress. The absence of a detailed technical specification precluded formal review, but the Panel acknowledged some innovative features of the approach. While the exploratory nature of the modelling approach currently precludes its use in providing direct management advice, it appears to be a useful tool for synthesis of current information and understanding, and should assist in identifying and prioritising further research. In relation to identifying and prioritizing future research, the Panel supported the inclusion of factors in the model even when data are not currently available to parameterize the relationship between the factors and penguin population dynamics, provided that account is taken of the uncertainty associated with any such relationships.

This model has now been published: Weller, F., Cecchini, L.-A., Shannon, L. J., Sherley, R. B., Crawford, R. J. M., Altwegg, R., Scott, L., Stewart, T., and Jarre, A. 2014. A system dynamics approach to modelling multiple drivers of the African penguin population on Robben Island, South Africa. Ecological Modelling, 277: 38–56.