Some comments on "Suggestions, comments and questions on penguin-pelagic fish interaction modelling work" (Bergh and Gaylard: MARAM IWS/DEC10/P/BG2)

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For readers' convenience, comments have been entered after the duplication of the paragraphs in MARAM IWS/DEC10/P/BG2. The comments are given in *italics*.

In some instances comments have been given in relation to updated analyses in MARAM IWS/DEC10/PA/P6 rather than to the earlier analyses (MARAM IWS/DEC10/PA/P1) upon which Bergh and Gaylard based their remarks in MARAM IWS/DEC10/P/BG2..

1. There is a clear trend in penguin abundance at Robben and Dassen Islands which is not explained by the model in MCM/2010/SWG-PEL/35. At least some of this is attributable to an eastward shift in pelagic fish stocks, but there is no explicit modelling of this or alternate causes for these trends. Document 35 does not present the estimates of the random effects in equations 12 and 13 (reproduced here as appendix A) , but they are likely to follow the pattern of abundance trends, since there is little or no room for alternative explanation of these trends in the model.

   There are no obvious residual trends in the most recent penguin model fit to the moult count data for Robben Island (see Figs 10 and 11 of MARAM IWS/DEC10/PA/P1, which also shows the random effects in Figs 6 and 7).

2. MCM/2010/SWG-PEL/35 contains 90 estimable parameters fitted to 109 observations. It is very likely over-fitted and thus of doubtful predictive ability, especially considering that a large number of these parameters are "random effects" and thus are of little explanatory value in understanding the underlying causes for trend in the population. We suggest that some model selection process be followed, starting with few estimable parameters, and testing the significance of added complexity in a step-wise manner using the AIC or some other model-selection criterion.

3. Table 12 of MCM/2010/SWG-PEL/35 shows a degradation of the AIC when Biomass dependence is included in the model. This is against a base case model with 86 parameters however. Of interest would be how the AIC responds to inclusion of biomass dependence into a more parsimonious base case model, i.e. given the large degree of flexibility to estimate year by year deviations from expected survival rate (for example), an additional dependence on biomass is not justified by the AIC. However it may well be justified if fewer parameters are used.

   Response 27) of MARAM IWS/DEC10/PA/P2 covers the two points above in detail. Random effects are not free parameters, but ones which ultimately are integrated out to provide final results. Plans are to in due course incorporate this integration within a Bayesian analysis.

4. **If**, as mentioned above, the MCM/2010/SWG-PEL/35 model is relatively insensitive to the inclusion or exclusion of penguin-pelagic biomass interdependence, then it is likely also insensitive to differing a-priori assumptions about the strength of biomass dependence. For example with a strong biomass effect on breeding success and survival assumed a-priori, the log-likelihood function will perhaps be not very different from that under an assumption of no

biomass dependence. We suggest therefore that a range of plausible values for the parameters of the biomass dependence of penguin success (including some which represent strong penguin-pelagic biomass interdependence) (α_i β_i a_i and b_i) see equations (12) and (13) in Appendix A) be assumed as fixed input in order to determine the sensitivity of the likelihood function.

The Bayesian approach referenced above will take due account of the precision of key parameters in drawing final conclusions.

5. At present the model of MCM/2010/SWG-PEL/35 appears to attribute all fluctuation in the annual counts to changes in survival rate – whereas it may be more appropriate to attribute a proportion of this variance to observation error. At present the observation error is limited to a constant under-count rate. A further possibility is variability in the proportion of mature adults that breed.

   The analysis of MARAM IWS/DEC10/PA/P6 is such as allows the data to select to where most fluctuations are appropriately ascribed. Furthermore the random effects for the reproductive success allow for possible variability in the proportion of mature adults that breed. The comments above appear to confuse variance and bias – variance of the type suggested is incorporated through random effects, but the constant under-count rate mentioned is a possible systematic bias.

6. Various papers allude to at least two additional demographic factors being sensitive to food which are not reflected in MCM/2010/SWG-PEL/35. These are (a) the proportion of penguins that breed at 4 years old, and (b) the number of chicks produced per pair. The model described in MCM/2010/SWG-PEL/35 links food abundance to fledgling success and adult survival rates. While fledging success is ultimately a combination of the number of chicks per pair and first year survival, it is proposed that concatenated effects such as this be delinked if delinked demographic data/estimates becomes available and is incorporated into the model. Furthermore, changes in the proportion breeding at 4 years old is not obviously viewed as a combination of other effects, and should perhaps be explicitly addressed in the modelling work.

   Much of this is already covered by the response to a similar comment (number 4) in MARAM IWS/DEC10/PA/P10's comments on remarks by Altwegg and Crawford in MARAM IWS/DEC10/PA/P8. Regarding changes over time in the proportion first breeding at age 4, this is likely to be subsumed by the random effects for reproductive success, but is nevertheless noted as a factor for a possible explicit sensitivity test in MARAM IWS/DEC10/PA/P2 (see pg 14).

7. Direct estimates of adult survival rates using mark-recapture data should be used to inform the model, probably as the centres of prior distributions in the Bayesian context.

   Indeed – this is planned further work: MARAM IWS/DEC10/PA/P6 mentions (see pg 7 thereof) the intent in due course to extend that model to colonies other than Robben Island alone and to take account of tag-return data in the likelihood (which would use the multinomial methods described in MARAM IWS/DEC10/PA/P3).

8. There is poor correlation between penguin abundance with sardine and anchovy abundance in stratum B as a whole (see Figs 1 and 2). However there is a strong correlation with pelagic catches close to Dassen Island (Fig 3), less so at Robben Island (Fig. 4). See also Table 1. It is reasonable to assume that the catches are indicative of local abundance in the vicinity of the islands in which case it appears that the penguin population sizes are indeed responsive to local food availability.

Correlations with penguin number counts are confounded by the influence of penguin dynamics. This is why all correlations attempted in MARAM IWS/DEC10/PB/P3 use relative measures (e.g. breeders per adult moulter) rather than total counts for explanatory variables. If correlations with measures of absolute numbers are to be considered, this has to be done within the framework of a population mode, inter alia to remove auto-correlation effects.

9. It remains somewhat unclear how the local density of fish is likely to respond in future to (a) the large scale condition of pelagic fish stocks and (b) the intensity of fishing close to islands. It seems that the MCM/2010/SWG-PEL/35 does not address these questions at present.

   Essentially models such as those of MARAM IWS/DEC10/PA/P6 are intended to address (a), and those of MARAM IWS/DEC10/PB/P3 to address (b).

10. The “River Model” (Document MCM/2010/SWG-PEL/ Island Closure Task Team/10) does on the other hand address (b) above. The reduction in food availability due to fishing as estimated by this model is small. This is however under the assumption that the entire “river” of recruits is available to foraging penguins as it passes the islands. If less than 100% is available to penguins, then the effect of fishing on local food density is greater.

    Evidence on spatial distribution from recruit surveys presented in MARAM IWS/DEC10/P/BG3 shows that effectively the entire river IS available.

11. Document MCM/2010/SWG-PEL/ Island Closure Task Team/19 fits a model relating penguin abundance to local pelagic catch. It determines a positive correlation between these quantities and concludes that fishing is good for penguin success. The underlying premise of this model is that the fishing activity is the cause of the penguin abundance. We believe that this premise is false, and that it is much more likely that both penguin abundance AND fishing activity are consequents of local fish density, i.e. penguins do well because food is available, not because the fleet is fishing.

    As pointed out in the response above to point 8, the models in question fit to RELATIVE measures, and deliberately NOT to penguin abundance as stated in comment 11 immediately above.

12. It is unclear how much of the uncertainty from the penguin model and from the pelagic fish models are being carried forward into the Bayesian projections of penguin abundance. For example, are stochastic realisations of future projections all coupled to a common (median) view of the past, or to a variety of possible historic scenarios?

    The approach in MARAM IWS/DEC10/PA/P1 was a first cut at the problem which did not take estimation uncertainty into account fully. This will be achieved through the fully Bayesian approach that is now being pursued.

13. Can iterate by iterate pelagic/penguin forecasts for ‘OMP-08’ and ‘no-catch’ be paired, allowing for the distribution of the **difference** between pelagic biomasses at the end of the planning horizon to be shown? (As a supplement to Fig.9 of MCM/2010/SWG-PEL/35 which shows the separate distributions).

    Bayesian posterior estimates for differences of this nature can indeed be produced in due course.

14. Document 35 suggests that we are unable to reject the null hypothesis that there is only a small benefit that can be achieved for the penguin population size by limiting the pelagic catch. An important quantity relevant to the validity of such a conclusion is the power of the test, i.e. if the true effect is large (i.e. penguins quite sensitive to pelagic catches) what is the

chance that one would have rejected the null hypothesis? The random effects structure of the model, which absorbs the trends observed into year specific survivorships, would most likely make it very difficult to reject this null hypothesis. We suspect therefore that the power of the test is very low. Some insight about the power of the test is provided by reporting model diagnostics (e.g. log-likelihood of the effect) where a large effect is incorporated, as is requested in an earlier point.

The credibility intervals forthcoming from a fully Bayesian approach will allow this issue to be addressed.