Additional perspectives for the Stock Assessment Review Panel on penguin population modelling for decision making

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The Penguin Pressure Model Working Group (PPMWG) has on short notice been presented with a list of questions and criticisms regarding the penguin pressure model (PPM), continuing a debate previously carried out in Butterworth et al. (2015) and Weller et al. (2016a). That document (Butterworth 2016) demonstrates a number of persistent disagreements and misunderstandings. We believe that rather than again entering into arguments about individual points, it will be more productive if we attempt once more to clarify the purpose of the PPM and its position relative to other current models investigating African penguin dynamics, in particular the model of Robinson et al. (2015) (ROB). This should also address the majority of the comments in that document.

The PPM was developed to aid decision-making in the conservation management of African penguins, and to help fulfil the provisions set out by the African Penguin Biodiversity Management Plan (Government Gazette No. 36966, 31 Oct. 2013).

The ecology of the African penguin is complex, and available data are of uneven depth and quality. It cannot be expected that any single model would be able to satisfactorily capture penguin population dynamics, especially in the context of a highly variable prey base both in time and space. There is thus a necessity for multiple models to enable robust decision-making. The PPM aims to explicitly account for all pressures known to act on a penguin population, using rigorously estimated parameters where available, and best available information otherwise. The PPM uses expert knowledge to accommodate biological processes and pressure mechanisms where information is sparse. The model's purpose is the investigation of the interaction and relative impact of the various modelled pressures, and the exploration of management strategies that will help in reversing the downward population trend. This positions the PPM somewhat differently from other models of these penguin populations.

All models have assumptions that must be accounted for, which guide their structure and parameterisation and shape the nature and interpretation of their outputs. Models of very different structure can be fitted to any data set and might fit similarly well, i.e. a good fit does not guarantee that the model describes a biological process well. The choice of model structure is therefore probably the biggest element of expert judgment when models are involved for decision making and should be based on the best knowledge of the biology of the species in question. The PPM takes a system dynamics approach whereas the ROB model follows a stock assessment approach. Recent criticism of the PPM has fundamentally centred on the allegation that several of its assumptions would not be acceptable for *a stock assessment model*, together with an implication that any other type of model would be inferior to address questions in marine conservation. One major point is the use of expert knowledge to inform demonstrated but sparsely parameterized processes. We agree that if a parameter can be rigorously estimated, it should be. If it cannot, it may be excluded from the model (i.e., treated as a null effect) – this is the approach of ROB, e.g. with regard to the impacts of climate effects and predation on penguins. Alternatively, a best estimate from ecological principles and system knowledge can be used – this is the approach of the PPM. The former trades in some accuracy in the representation of the system for increased precision of estimates, the latter does the opposite. Both methods are valid, and their results should be regarded as complementary, not antithetical.

The weak fit of PPM results to past population size estimates at Robben Island has also been repeatedly emphasized by Butterworth and colleagues as an indication of flaws in the model (Butterworth et al., 2015; Butterworth 2016). We suggest that this is based on a misconception about the role of such a fitting process. Population records constitute one realized trajectory through the parameter space spanned by all possible configurations of the factors influencing population dynamics. Where the focus is on short-term forecasts based on current dynamics, basing a model on a close fit to this realised trajectory is useful. However, the PPM specifically aims to include each facet of the sum of ecological knowledge about the population's situation, parameterized as well as possible, and to investigate the entire possible outcome space. It focuses on extrapolation from biological understanding of processes, rather than from one instantiation of these processes. Replication of records is a desirable verification of our interpretation of how all involved mechanisms played out in the past, but exact fit is not required.

Neither does a good fit to recorded data necessarily mean that a model is good at predicting the future dynamics of the system, or that it constitutes a realistic representation of the modelled system. In the poorly understood African penguin system, a good fit to the records appears in fact to be more indicative of well-tailored assumptions about past circumstances. Neither the PPM nor ROB does a good job of reproducing recorded dynamics without such assumptions; compare the bottommost curves in Figs. 7 and 10 of Butterworth (2016). ROB achieves a good fit by estimating immigration as the difference between the contribution of local recruitment and the actual observed population trajectory, which results in introducing huge numbers of immigrants to Robben Island in specific years. In particular, the model estimates that ~700 females per year, apparently corresponding to an equal number of males, were recruiting to the population in 1989 and 1990 (Robinson et al. 2015), at a time when the entire breeding population at the island was in the order of 1000 pairs (Sherley et al. 2014a). The good model fit therefore requires debatable assumptions about the availability of migrants from other colonies. Perhaps this explains why the ROB model predicts that the Robben Island population would continue to decline at nearly 1% per annum after 2012, even if sardine revert to their 1984-1998 distribution, a period of time in reality when penguin populations increased at colonies around Cape Town (Robben Island, Dassen Island and Boulders Beach; Underhill et al. 2006).

The PPM, in contrast, attempts an explanation by postulating shifts in demographic parameters and predation pressure, together with a much smaller amount of immigration. The merits of either solution may be argued, and in fact demonstrate the value of considering different modelling approaches as the dual approach highlights uncertainty in our understanding of this system and therefore of future dynamics. The ability of the ROB model to "reproduce the abundance data almost exactly" is the result of this model being directly fitted to these data and designed to fit them closely. This cannot be used to argue that the ROB model is necessarily better than other models.

Further, as we have argued in the past, we strongly suggest that the over-aggregation of processes that reflect interesting and relevant biological variation should be avoided when modelling the demographics of this species (Weller et al. 2016a). Demographic processes that might be compounded to simplify modelling may, in reality, respond to different ecological drivers operating over vastly different spatial scales (Appendix 1). Moreover, these processes may not necessarily be positively correlated (see Appendix 1). Where they are not, this could result in difficulty detecting underlying functional relationships as suggested by the panel at the 2014 International Stock Assessment

Workshop. Again, we would propose that the decision of Robinson et al. (2015) to model reproductive success as one aggregated parameter covering the period from hatching to eight months of age resulted in the lack of any correlation with the presumed single food biomass driver (anchovy), leading them to dismiss the viability of island closures as a conservation tool. However, the disaggregation of the life of young African penguins into sub-stages with different survival drivers is indicated by empirical data (Appendix 1). The PPM implements this as part of its approach of explicitly modelling biological processes where possible, and thus is able to show stage-specific responses to drivers, and test these relationships in the context of island closure scenarios.

At this time, we have access to the results of several good models that use different techniques and assumptions to answer questions about strategies to reverse the population trend of African penguins (see also Sherley 2016). Rather than trying to collapse them to the standards of a single commonly used method, their separate strengths should be combined. We urge that the many remaining uncertainties be addressed by further developing these separate approaches and using them to offset one another's weaknesses.

The models of Robinson et al. (2015), Weller et al. (2014, 2016b), Sherley et al. (2015) and Sherley (2016) all agree that current low sardine biomass in the wider Benguela system plays a fundamental role in impeding a recovery of African penguin populations (see also Weller et al. (2016b) TRACE document, 3.3.8.2.1, Fig. 7). Furthermore, the approaches by Weller et al. (2014, 2016b), Sherley et al. (2015) and Sherley (2016), show that fishing restrictions in the vicinity of individual colonies can be expected to help slow the ongoing decline – a type of scenario that was not modelled in ROB, apparently due to conclusions based on the demographic structure choices noted above.

We therefore suggest that the combined, best scientific knowledge indicates the need for management actions on both of these dimensions, combining management measures for rapidly rebuilding the sardine stock in the southern Benguela upwelling (sub-)system with continued closures to purse seining of the agreed areas around the penguin breeding colonies.

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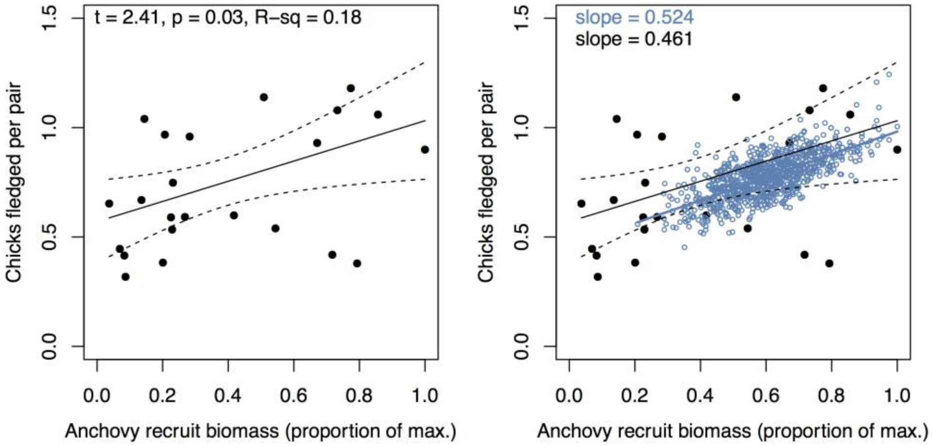
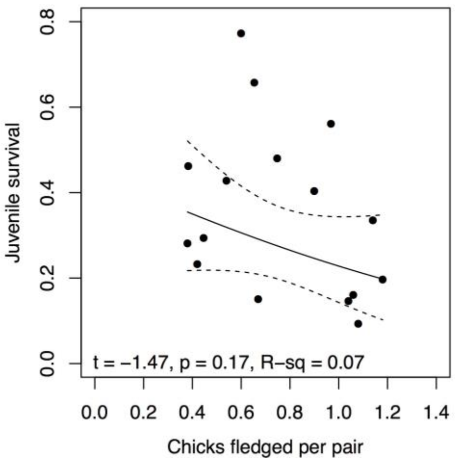
Appendix 1: Some observations from data pertinent to debates around empirical and modelling results relating to the island closures feasibility study.

1. There is a significant linear relationship between the breeding success (number of chicks fledged per pair) at Robben Island between 1989 and 2012 and the anchovy recruit biomass when the square-root of the sample size (N) is used to weight the breeding success observations ($t = 2.41$, d.f. = 21, $p = 0.03$) to take some account of the precision in those estimates. This empirical relationship is shown in the left-hand panel of the plot below. The Weller et al. (2016) model does not use chicks fledged per pair to drive penguin population dynamics, but decomposes this process into clutch size, egg survival and chick survival because different pressures act upon these different parts of the life-cycle. However, if we simulate values for chicks fledged per pair based on outputs from the separate parts of the process and relate these to anchovy biomass, we obtain a very similar relationship. This contrasts with the apparently flat relationship in Figure 8 of Robinson et al. (2015).

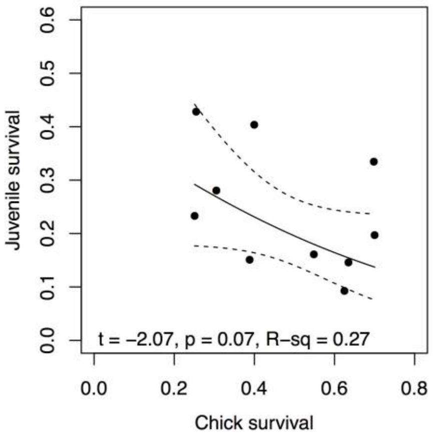
The right-hand panel of the plot below shows the empirical relationship (repeated from the left hand-panel in black) and the model output in blue. Biomass is scaled to be a proportion of the maximum observed in both cases, so the slope estimates are comparable. The model outputs are 10 years means from 1000 model runs resampling food biomass from the period 1989 to 2012.



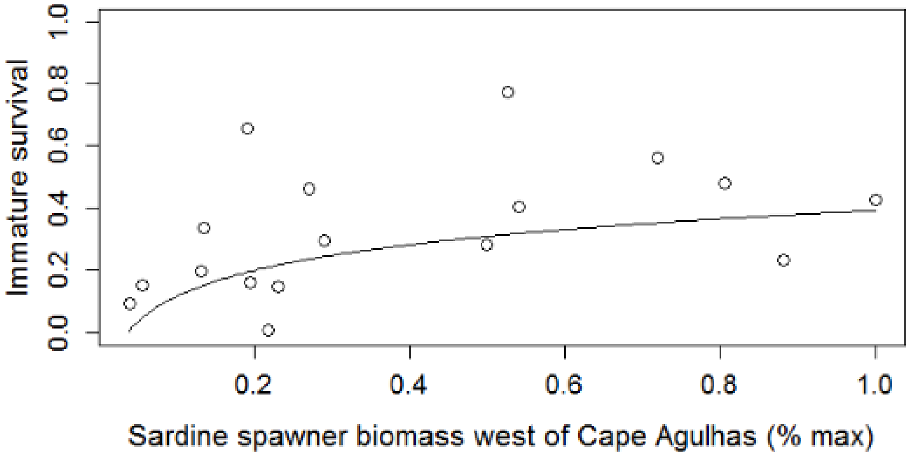
2. In discussions at the 2014 IWS, the panel concluded that treating chick survival from hatching and survival at sea to 8 months old as a single compound process (as in Robinson et al. 2015) was fine as long as the two components parts of the process were not negatively correlated. The plot below shows the relationship between the best available estimates of penguin first-year survival at Robben Island (from Sherley et al. 2014b) and penguin breeding success at Robben Island between 1994 and 2012. There is a negative trend, though the relationship is not significant ($t = -1.47$, d.f. = 14, $p = 0.17$).



Similarly, the relationship between penguin chick survival (from hatching to fledging) and juvenile survival (survival over the first year at sea after fledging) over the period 2001 to 2012 (t = −2.07, d.f. = 8, p = 0.07) is negative, though marginally not significant. See figure overleaf. In both cases the standard errors have been used to weight the juvenile survival observations to take account of the precision in each estimate.



3. Juvenile survival (survival over the first year at sea after fledging) for penguins from Robben Island appears to be positively related to the biomass of sardine spawners west of Cape Agulhas rather than anchovy recruit biomass. See below reproduced from Weller et al. (2016).



These observations underline why it would be prudent to consider survival to fledging separately from first-year survival at sea when modelling African penguin demographics.