# Response to: "Response to comments on the Robben Island penguin pressure model" 

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For readers' ease, responses have been entered below into the original document in red italics.

## Response to comments on the Robben Island penguin pressure model

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Management recommendations for African penguin colonies based on results of the Robben Island penguin pressure model presented in Weller et al. (2014) were tabled at the Island Closure Task Team on March $12^{\text {th }}, 2014$. As these results contrast with some conclusions of Robinson (2013), the model has been subject to comments (Robinson and Butterworth, 2014; de Moor, 2014) that question the validity of several of the model's conclusions. The following addresses these comments.
Penguin age classes in the model (eggs, chicks, immatures, and adults) have survival rates that are subject to modification when food availability changes. Class-specific parameters (referred to as "food parameters" in the following) are used to connect an index of available prey biomass to the survival rates; in effect, these parameters determine the strength of influence that changes in food availability have on penguin population development, as Robinson and Butterworth (2014) correctly summarize.

Robinson and Butterworth (2014) take issue with two points: a) there is a direct correlation of deviation from mean age class survival with deviation from median food availability; b) the magnitudes of parameters have not been directly estimated in the field, but are based on the expert opinion of the scientists involved in the model's development.
There may be a semantic confusion here, arising from the loose use of the word "availability" without clear definition. Hopefully the Note below clarifies the situation, as whether or not we are taking issue under a) depends on what the authors of ICTT/25 intend to mean by this term (i.e. whether or not they intend it to include catchability as well as biomass per se - see following comment). Our primary concern though remains $b$ ).
a) The correlation of various penguin survival parameters (here, breeding probability and survival rates) to available prey biomass is borne out by a large body of research (Annex 1 ; see also Crawford et al., 2014 ). Breeding success and timing, colony formation, and survival of various age classes have repeatedly been shown to be both positively and negatively driven by
food availability. In this regard it is the conflicting finding of Robinson (2013), where fishing (regardless of the corresponding reduction in local food biomass) is interpreted as having a beneficial effect on penguin recruitment, that requires further confirmation due to its unexpected nature. Crawford et al. (2014) address this in detail.

The issue here is the conversion of biomass present to "available biomass" - "catchability" in standard fisheries terminology. If catchability is constant, the correlations mentioned above are not at issue. But as the Note explains, catchability is not necessarily constant in the situation under consideration here. Unfortunately the reference to Crawford et al. (2014) is unhelpful because, as pointed out in FISHERIES/2014/APR/SWG-PEL/ICTT/24, the arguments made there are, with one exception, all flawed. A particular concern in the context of the matter under consideration here is the complete failure to understand the predation-shoaling model of Clark (1976) evidenced by the authors of Crawford et al., who include the authors of ICTT/23.
b) The provenance of the food parameters is stated as "expert opinion" in Weller et al. (2014). This denotes values that, in the absence of direct estimates, were chosen based on the best judgement of the involved scientists while taking into account all available related data. As the food parameters could not be estimated from available field data, they were chosen such that they mapped the range of observed survival rates for each age class to the range of observed variation in food biomass. Egg and chick survival data used to determine the range were taken from Sherley (2010) and have more recently also been presented on a per nest basis as derived from parametric survival models (i.e. survival during incubation and during chick-rearing) in Sherley et al. (2013) and as per egg and chick survival in e.g. Sherley (2012)). Juvenile survival data were taken from Whittington (2002), and adult survival data from Whittington (2002), later updated by Crawford et al. (2011) and now also confirmed independently by Robinson (2013) and Sherley et al. (in review).

Previous concerns about the reliance of the results of Weller et al. (2014) on selection of parameter values through "expert opinion" have been enhanced by the explanation since offered for the manner in which the the survival rate parameters were chosen. The particular problem is the manner in which the "observed variation in food biomass" has been inferred: through linkage to catches made in the year concerned. That this is a totally flawed approach has been explained in detail in FISHERIES/2014/APR/SWG-PEL/ICTT/24 and the cross-references therein to other of our ICTT papers provided, so that those points need not be repeated here. This problem emphasizes the need for a much fuller justification of the other parameters selected by "expert opinion" in the Weller et al. document before it might be properly assessed. Thus for example Weller et al state that they use a mean adult survival rate for penguins of 0.88 (their Table B.1), and the authors of ICTT/23 claim immediately above that this is consistent with the results of Robinson (2013). Yet Fig. 4.9(e) of Robinson (2013), based directly on fits to penguin tag-recapture data which contain information on survival rates, shows a quite different picture, with the dynamics of the penguin population dominated by the need for a marked reduction in this survival rate in the early 2000's for compatibility with these tag recapture data. This example is indicative of some wider and more fundamental problems with the Weller et al. modelling approach, particularly:

- Lifting parameter estimates provided by one model to substitute in a second when there are data available to estimate those parameters when fitting to that second model The latter approach avoids transplanting the different biases associated with different
methods, thus ensuring self-consistency, and in particular maintains variance-covariance structure thus facilitating defensible statistical inference, which is why it is now almost universally the standard in fisheries with the former being avoided given that the computing power now available is readily able to effect such fits in most cases. .
- Failure to show in a statistically defensible manner that the model developed IS consistent with the available data. This is a sine qua non for use of models for tactical fisheries management advice, which is the issue in question here - models which do not exhibit satisfactory residual diagnostics in their fits to the data are simply not acceptable for use (unless some compelling explanation for the mis-fit can be offered). (This would also seem to be the root of the concerns expressed by de Moor in FISHERIES/2014/APR/SWG-PEL/ICTT/15).

Robinson and Butterworth (2014) furthermore assert that choice of food parameters also influences model-based conclusions regarding the benefit of different fishing restriction regimes around Robben Island to the penguin population, and that these conclusions may thus be suspect. Weller et al. (2014) found that restrictions were on average weakly beneficial to colony growth, but that the outcome was easily masked by variability in prey biomass. Benefits were found to increase and masking to decrease with longer restriction duration.
It is crucial to note that these conclusions, and resulting management recommendations, remain practically unaffected by the choice of food parameters, regardless of uncertainty about exact parameterization. Given the scientific consensus that penguin populations respond positively to improved food availability (Annex 1), the finding that reducing competition for small pelagic prey promotes penguin colony growth is uncontroversial. However, the main conclusion concerns differences in relative benefit of different closure scenarios rather than the absolute gain derived from each. It is readily shown that this is not subject to change depending on food parameter choice.
The three restriction scenarios discussed in Weller et al. (2014) were rerun using a range of food parameter permutations employed in that study to carry out sensitivity tests on model processes (Table 1). The four parameters concerned (affecting egg, chick, immature, and adult survival rates, respectively) were modified to $50 \%$ ('very high' effect strength), $90 \%$ ('high'), $110 \%$ ('low') and $150 \%$ ('very low'; capped at 0.99 ), in addition to standard values ('base', no change).

| Parameter | Very low | Low | Base | High | Very high |
| :--- | :--- | :--- | :--- | :--- | :--- |
| Adult survival | 0.990 | 0.880 | 0.800 | 0.720 | 0.400 |
| Immature survival | 0.990 | 0.770 | 0.700 | 0.630 | 0.350 |
| Chick survival | 0.750 | 0.550 | 0.500 | 0.450 | 0.250 |
| Egg survival | 0.750 | 0.550 | 0.500 | 0.450 | 0.250 |

Table 1. Food parameter values used in the modified fishing restriction scenarios. Categories denote the strength of the effective changes in survival parameters based on underlying pressure drivers. For details see Weller et al. (2014), section 3.2.1.

Figures $1-3$ show the result of running the three scenarios using the modified parameter sets. Fig. 1 (corresponding to Fig. 16a in Weller et al. (2014)) shows a scenario where fishing around Robben Island is restricted for a full 20 years. Fig. 2 (corresponding to Fig. 16b in Weller et al.
(2014)) shows a scenario where fishing is restricted for a single period of three years within 20 years, with closures starting at a progressively later date. Fig. 3 (not pictured in Weller et al. (2014)) shows a scenario were fishing is restricted and unrestricted for alternating three year periods over 20 years (for further scenario details see Weller et al. (2014)).
It is evident that changes in food parameters primarily affect the variance of the outcome (i.e., symmetrical distribution spread) while only minimally influencing mean population gain. The relative benefit of the three scenarios in comparison remains equally clear at each level of modification, even though parameters at the two extreme levels are well beyond those that could be expected to hold stable over a 20 year period. It can therefore be concluded that the discussed findings initially reported in Weller et al. (2014) hold, regardless of the exact parameterization of prey availability influence in the model, and that the associated criticism expressed by Robinson and Butterworth (2014) is unfounded.

The investigation of sensitivity presented here is valuable and useful, and indeed demonstrates some robustness of model results. But that touches only one of the problematic issues associated with the model structure used. As long as the E parameter of the model (see Fig. 1 of FISHERIES/2014/APR/SWG-PEL/ICTT/7) remains below 1, the structure of the model does not admit any result other than greater catches having an increased negative impact on penguins. Yet inferences from the empirical data (Robinson 2013) are in many cases not compatible with that relationship. If this model was formally fit to those data, it would manage that by estimating values for the E parameter which are greater than 1, but that hardly makes for realistic interpretation within the model structure assumed.
Thus in the context of the issue at hand - the impact of fishing in the vicinity of islands on penguin reproductive success - the restricted structure of the model renders it a "self-fulfilling prophecy". It can produce results in one direction only. Yet there are plausible mechanisms that can lead to results in the other direction, as expanded in the Note below. The Weller et al. model fails the key test of being unable to reproduce what inferences from the empirical data indicate, because of a structure which lacks adequate flexibility.

## Note

At the simplest level, an index $\boldsymbol{R}$ related to breeding success will be a monotonically increasing function of initial resource biomass in the region of interest $B$, e.g. under linear proportionality:

$$
\begin{equation*}
R=\gamma B \tag{1}
\end{equation*}
$$

where $\gamma$ reflects what is often termed "catchability". More generally though, $\boldsymbol{B}$ will be reduced during the season (or period under consideration) by the catch made ( $\mathcal{C}$ ), while $\gamma$ will be impacted by the effect of fishing on the schools, e.g. the mechanism put forward by Clark (1976) which suggests that $\gamma$ will be an increasing function of $\mathbf{C}^{l}$. Thus:

[^0]\[

$$
\begin{equation*}
B \rightarrow f(C, B) \tag{2}
\end{equation*}
$$

\]

where $\frac{\partial_{f}}{\partial c}<0$. For example, under Pope's approximation the average biomass during the season would be:

$$
\begin{equation*}
f(C, B)=0.5\left(1-e^{-M}\right) B-0.5 e^{-M / 2} C \tag{3}
\end{equation*}
$$

and under the Clark mechanism:

$$
Y \rightarrow g\left(C_{z} B\right)
$$

where for example

$$
\begin{equation*}
g(C, B)=\tilde{g}\left(C / B^{\omega}\right) \tag{5}
\end{equation*}
$$

where $\omega$ measures the extent to which the effect of the catches is absolute $(\omega=0)$ or relative $(\omega=1)$. In either event $\frac{\partial g}{\partial c}>0$.
Writing $\boldsymbol{R}=g(C, B) f(C, B)$, taking logarithms gives:

$$
\begin{equation*}
\ln R=\ln g(C, B)+\ln f(C, B)=g^{*}(C, B)+f^{*}(C, B) \tag{6}
\end{equation*}
$$

where $\frac{\partial g^{*}}{\partial c}>0$ and $\frac{\partial f^{*}}{\partial c}<0$.
Linearising (first order Taylor series expansion) about some typical biomass $\tilde{B}$ and $\boldsymbol{C}=0$ gives:

$$
\begin{align*}
\ln R=g_{0}^{*}+\left.\frac{\partial g^{*}}{\partial C}\right|_{\tilde{B}, 0} C & +\left.\frac{\partial g^{*}}{\partial B}\right|_{\tilde{B}, 0}(B-\tilde{B})+f_{0}^{*}+\left.\frac{\partial f^{*}}{\partial C}\right|_{\tilde{B}, 0} C+\left.\frac{\partial f^{*}}{\partial B}\right|_{\tilde{E}, 0}(B-\tilde{B}) \\
& =g_{0}^{*}+c_{1} C+d_{1}(B-\tilde{B})+c_{2} C+d_{2}(B-\tilde{B}) \tag{7}
\end{align*}
$$

where $c_{1}, d_{1}, c_{2}$ and $d_{2}$ are constants with $c_{1}>0$ and $c_{2}<0$. Re-arranging.

$$
\begin{array}{r}
\ln R=\left(g_{0}^{*}-d_{1} \tilde{B}-d_{2} \tilde{B}\right)+\left(d_{1}+d_{2}\right) B+\left(c_{1}+c_{2}\right) c \\
=\beta+\mu B+\lambda C \tag{8}
\end{array}
$$

with $\lambda=c_{1}+c_{2}$. Thus for year $y$ and colony $i$, and where $C^{*}$ is now normalised by the average catch at the island:
or

$$
\begin{gather*}
\ln R_{y, i}=\beta_{i}+\mu B_{y}+\lambda_{i} C_{y, i}^{*}  \tag{9a}\\
\ln R_{y, i}=\beta_{i}+\alpha_{y}+\lambda_{i} C_{y, i}^{*} \tag{9b}
\end{gather*}
$$

i.e. exactly of the forsm assumed by Robinson (2013).

Importantly $\lambda_{i}=c_{1, i}+c_{2, i}$ where $c_{1, i}>0$ and $c_{2, i} \leqslant 0$ so that the sign of $\lambda_{i}$ can be positive or negative, depending on which of the effects of the catch is dominant in a particular case: availability of the fish to the predators $\left(c_{1}\right)$ or the average abundance present given catching $\left(c_{2}\right)$. The net impact of these and other effects can be reliably determined only by empirical analysis, which was the original rationale behind the island closure experiment (and its feasibility study), and the reason for the approach selected for the evaluation of its results (see also discussion on pg 7 of . FISHERIES/2014/APR/SWG-PEL/ICTT/24).

## Other issues

de Moor may wish to separately address these points. The comments offered below are not exhaustive, particularly because other concerns with the Weller et al. analyses, unlike those above, are not central to the immediate key issue which is inferences about the impact of fishing close to colonies on penguin reproductive success. Given though that the de Moor/WellerSherley exchange is raised below, the opportunity is taken to add a few core comments.

A further comment (de Moor, 2014) concerns a scenario in Weller et al. (2014) that attempts to recreate observed population developments on Robben Island between 1988 and 2008 using the model environment. This scenario was intended to test the capability of the model to simulate recorded data, given specifically chosen but plausible assumptions about parameter values. These included a reduction in climate pressures during this period, changes in marine predation pressure in 2003, and immigration by immatures (the latter is not explicitly included in current model versions due to lack of data).

De Moor (2014) presents the following criticisms:
a) The scenario fails to correctly reproduce recorded numbers. - Peak numbers of simulated adults are indeed lower than recorded peak numbers, as more weight was put on replicating the shape than the magnitude of the trace. This should arguably have been remedied, and in fact can be addressed without leaving plausible parameter space by slightly lowering maximum marine predation rates after 2003.

This is problematic - as mentioned above the penguin tag-recapture data indicate a drop in the adult penguin survival rate at that time, which implies an increase in some component contributing to natural mortality.
b) Model fit was achieved by targeted modification of parameter values, creating an unreasonable combination of parameter states, including lack of known oil spills. - This criticism misses the point of the scenario. The observed population trace can be thought of as a single replicate, based on a specific combination of parameter values. The scenario demonstrates the capability of the model to encompass this unique output in its output space, using specific parameter values from the implemented (plausible) parameter space. Naturally this requires picking these values; the important restriction is that they must be part of the plausible range. The plausibility of the chosen values is discussed in Weller et al. (2014). Note that the assumption that the catastrophic oil spills known to have occurred during the modeled period were excluded is mistaken; as stated, these spills were included, and the less quantifiable chronic oiling was disabled.
c) Immigration should have been included as a model process as an 'expert guess'. - As discussed above, parameters based on expert opinion are not 'guesses', but inferences from the best available data and the experts' understanding of processes. In the case of immigration, the data were judged to still be too scarce and/or the analysis of available data to be in too early a stage to allow reasonable parameterization. Migration between colonies is instead assumed to constitute part of the adaptations made to survival values to achieve a base equilibrium population; this is the factor that was adjusted to temporarily simulate increased immigration in
this scenario. Migration is clearly a very important process in colony development, and will be included in the model as soon as sufficient results are available.

Two immediate questions that arise from the above are:
i) exactly how is that "expert opinion" able to achieve supposedly more reliable values than the now standard practice of estimating those values when fitting the model to the available data; and
ii) why were the available data "judged to still be too scarce" when Robinson (2013) has already demonstrated how the tag-recapture data can be used to estimate the parameters in question with reasonable precision? This position taken by the authors of Weller et al. is rendered stranger still when one considers that in earlier PWG meetings, with some of the those authors present and supporting, Robinson was advised that it was essential that these tag-recapture data be incorporated in any model of penguin dynamics.

To demonstrate the capability of the model to reproduce observed dynamics using a plausible parameter space, without having to work around this unimplemented mechanism, the development of the Robben population from 2004 through 2012 was replicated (Figure 4). No immigration is thought to have occurred during this period (Robinson 2013), which features a steady decline in population size. Fig. 4a shows recorded numbers of breeding pairs, Fig. 4b shows simulated numbers of breeding pairs. This scenario uses recorded biomass and fisheries catch data, and all pressures except catastrophic oil spills (known to not have occurred during this period) are enabled. Mean survival rates for all age classes were set to $90 \%$ of base survival rates, simulating a period of years with slightly higher than average pressures. The result is a fair approximation of observed dynamics using reasonable assumptions about parameter values.

From the additional investigations and analyses detailed above, it appears that the model is fit for the purpose for which it was intended, and that the conclusions previously drawn from the model are well founded.

This "purpose" needs to be elaborated further. If a model does not exhibit a statistically acceptable fit to available data, how can any conclusions pertinent to tactical management recommendations be drawn from it?
Related to this concern is an underlying fundamental flaw in rationale offered for the approach adopted by Weller et al.: that assessing ecosystem effects, as in this instance, requires an approach differing from traditional fish stock assessment models as these are "restricted by the necessity for the factors and relationships involved to be well parameterized", and that "difficulties associated with parameter estimation due to scarcity of data have meant that explicit consideration of multiple pressures driving penguin population dynamics necessitates a move to a different paradigm". This is completely incorrect. Analyses of the type and level of complexity in Weller et al. are now routinely conducted under such "traditional" approaches, with "data scarcity" aspects handled, for example through specification of priors within a Bayesian estimation approach. This flawed rationale offered by the authors of Weller et al. is no acceptable reason for the model in question not to have been fit to the available data in a "conventional" manner. The model has potential to inform tactical management recommendations, but such proper fitting of the model to the data is an essential pre-requisite.

## Acknowledgements

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## References added

Clark, C. W. (1976). Mathematical bioeconomics. New York: John Wiley \& Sons. 352 pp. Robinson WML. 2013. Modelling the impact of the South African small pelagic fishery on African penguin dynamics. PhD thesis, University of Cape Town. xiv +207 pp.


High


Low


Very high


Base


Figure 1
Fishing restriction in place for entire run of 20 years. Final population difference between fishing and nonfishing runs is plotted against frequency of occurrence in 200 runs. For details see Weller et al. (2014) (section 3.3.2.2). The scenario was run using the five parameter levels detailed in Table 1. Results are shown below.

| Parameter level | Mean growth in \% of starting <br> population (3500 adults) after <br> 20 years (range found in 5 <br> scenario replicates) |
| :---: | :--- |
| Very low | $\mathbf{7 . 2 - 7 . 7 ~ \% ~}$ |
| Low | $\mathbf{8 . 2 - \mathbf { 8 . 6 } \%}$ |
| Base | $\mathbf{8 . 2 - \mathbf { 8 . 5 } \%}$ |
| High | $\mathbf{8 . 2 - \mathbf { 8 . 6 } \%}$ |
| Very high | $\mathbf{7 . 1 - 7 . 7 \%}$ |

## Very low



## High



Low


Very high


Base


Figure 2
Fishing restriction in place for 3 years within 20 years. Each box and whiskers represent median, quartiles and standard deviation of final population differences between 200 fishing and non-fishing runs, with closures starting in a specific year. For details see Weller et al. (2014) (section 3.3.2.2). The scenario was run using the five parameter levels detailed in Table 1. Results are shown below.

| Parameter level | Mean growth in \% of starting <br> population (3500 adults) after <br> 20 years |
| :---: | :---: |
| Very low | $\mathbf{0 . 4} \%$ |
| Low | $\mathbf{0 . 4} \%$ |
| Base | $\mathbf{0 . 4} \%$ |
| High | $\mathbf{0 . 4} \%$ |
| Very high | $\mathbf{0 . 4} \%$ |

## Very low



High


## Low



Very high


## Base



Figure 3
Fishing restriction in place for alternating periods of 3 years over 20 years. Final population difference between fishing and non-fishing runs is plotted against frequency of occurrence in 200 runs. For details see Weller et al. (2014) (section 3.3.2.2). The scenario was run using the five parameter levels detailed in Table 1. Results are shown below.

| Parameter level | Mean growth in \% of starting <br> population (3500 adults) after <br> 20 years (range found in 5 <br> scenario replicates) |
| :---: | :---: |
| Very low | $\mathbf{1 . 0 - \mathbf { 1 . 3 } \%}$ |
| Low | $\mathbf{1 . 1 - \mathbf { 1 . 5 } \%}$ |
| Base | $\mathbf{1 . 1 - \mathbf { 1 . 7 } \%}$ |
| High | $\mathbf{1 . 1 - \mathbf { 1 . 6 } \%}$ |
| Very high | $\mathbf{0 . 8 - \mathbf { 1 . 5 } \%}$ |



Figure 4. a) Estimates of breeding pairs on Robben Island from nest counts, 2004 - 2012. b) Model population development in breeding pairs, 2004 - 2013, starting from the 2004 breeding pair estimate (7798). The trace shows distribution of pair numbers in 200 runs, using recorded biomass and fisheries catch data, with all pressures except catastrophic oil spills enabled, and mean survival rates for all age classes set to $90 \%$ of base survival rates (simulating a period of years with higher than average pressures).

## References

Adams NJ, Seddon PJ, van Heezik YM. 1992. Monitoring of seabirds in the Benguela upwelling system: can seabirds be used as indicators and predictors of change in the marine environment? South African Journal of Marine Science 12: 959-974.
Cordes I, Crawford RJM, Williams AJ, Dyer BM. 1999. Decrease of African Penguins at the Possession Island group, 1956-1995 contrasting trends for colonial and solitary breeders. Marine Ornithology 27: 117-126.
Crawford RJM. 2007. Food, fishing and seabirds in the Benguela upwelling system. Journal of Ornithology 148 (Suppl 2): S253S260.
Crawford RJM, Dyer BM. 1995. Responses by four seabirds to a fluctuating availability of Cape anchovy Engraulis capensis off South Africa. Ibis 137: 329-339.
Crawford RJM, Shannon LJ, Whittington PA. 1999. Population dynamics of the African Penguin at Robben Island. Marine Ornithology 27: 135-143.
Crawford RJM, Barham PJ, Underhill LG, Shannon LJ, Coetzee JC, Dyer BM, Leshoro TM, Upfold L. 2006. The influence of food availability on breeding success of African Penguins Spheniscus demersus at Robben Island, South Africa. Biological Conservation 132: 119-125.
Crawford RJM, Underhill LG, Coetzee JC, Fairweather T, Shannon LJ, Wolfaardt AC. 2008. Influences of the abundance and distribution of prey on African Penguins Spheniscus demersus off western South Africa. African Journal of Marine Science 30: 167-175.
Crawford RJM, Altwegg R, Barham BJ, Barham PJ, Durant JM, Dyer BM, Geldenhuys D, Makhado AB, Pichegru L, Ryan PG, Underhill LG, Upfold L, Visagie J, Waller LJ, Whittington PA. 2011. Collapse of South Africa's penguins in the early 21st century. Afr. J. Mar. Sci. 33: 139-156.

Crawford RJM, Hagen C, Jarre A, Ludynia K, Makhado AB, McInnes A, Robinson K, Pichegru L, Shannon LJ, Sherley RB, Steinfurth A, Waller L, Weller F. 2014. An evaluation of evidence that purse-seine fishing around African Penguin colonies benefits penguins. FISHERIES/2014/MAR/SWG-PEL/ICTT/???
Cury PM, Boyd IL, Bonhommeau S, Anker-Nilssen T, Crawford RJM, Furness RW, Mills JA, Murphy EJ, Österblom H, Paleczny M, Piatt JF, Roux J-P, Shannon L[J], Sydeman WJ. 2011. Global seabird response to forage fish depletion - one-third for the birds. Science 334: 1703-1706.
de Moor CL. 2014. A short comment on Weller et al. (2014). FISHERIES/2014/MAR/SWG-PEL/ICTT/22: 1 p.
Durant JM, Crawford RJM, Wolfaardt AC, Agenbag CJ, Visagie J, Upfold L, Stenseth NC 2010. Influence of feeding conditions on breeding of African Penguins - importance of adequate local food supplies. Marine Ecology Progress Series 420: 263-271.
La Cock GD. 1986. The Southern Oscillation, environmental anomalies and mortality of two southern African seabirds. Climatic Change 8: 173-184.
Pichegru L, Ludynia K, Makhado AB, McInnes A, Moseley C, Robinson K, Sherley R, Steinfurth A, Waller L, Crawford RJM. 2014. Insufficiently precautionary management of South Africa's purse-seine fishery for conservation of the African Penguin. FISHERIES/2014/SWG-PEL/ICTT/2a: 30 pp.
Robinson WML. 2013. Modelling the impact of the South African small pelagic fishery on African penguin dynamics. PhD Thesis, University of Cape Town.
Robinson WML, Butterworth DS. 2014. Comments on the benefit to penguins of fishing restrictions around Robben Island predicted by Weller et al. Robben Island penguin model simulations. FISHERIES/2014/MAR/SWG-PEL/ICTT/7: 4 pp.
Sabarros PS, Durant JM, Grémillet D, Crawford RJM, Stenseth NC. 2012. Seabird community ecology - differential responses of three sympatric marine predators to spatio-temporal variability of shared resources. Marine Ecology Progress Series 468: 291301.

Sherley RB. 2010. Factors influencing the demography of endangered seabirds at Robben Island, South Africa. PhD thesis, University of Bristol, Bristol.
Sherley RB. 2012. Update on the breeding productivity of African Penguins (Spheniscus demersus) on Robben Island. FISHERIES/2012/SWG-PEL/ICTT/06. 8 pp.
Sherley RB, Abadi F, Ludynia K, Barham BJ, Clark AE, Altwegg R. In review. Age-specific survival and movement among major African Penguin colonies. Ibis
Sherley RB, Underhill LG, Barham BJ, Barham PJ, Coetzee JC, Crawford RJM, Dyer BM, Leshoro TM, Upfold L. 2013. Influence of local and regional prey availability on breeding performance of African Penguins Spheniscus demersus. Mar. Ecol. Prog. Ser. 473: 291-301.
Weller F, Cecchini L-A, Shannon LJ, Sherley RB, Crawford RJM, Altwegg R, Scott L, Stewart T, 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.
Whittington PA. 2002. Survival and movements of African Penguins, especially after oiling. PhD thesis, University of Cape Town, Cape Town.

## Annex 1.

Some examples of studies that have demonstrated a dependency of African Penguins on food. Reproduced with permission from Crawford et al. (2014).

Positive correlations between numbers breeding and prey abundance: a) at a regional scale - Crawford (2007), Crawford et al. (2008), Crawford et al. (2011); b) at a colony scale - Crawford et al. (2008), Sabarros et al. (2012), Sherley et al. (2013).

Positive correlation between breeding participation and prey abundance: Crawford et al. (1999), Durant et al. (2010).

Positive correlations between breeding success and prey abundance: a) at a regional scale - Adams et al. (1992), Crawford and Dyer (1995), Crawford et al. (1999), Crawford et al. (2006), Cury et al. (2011); b) at a local scale Sherley et al. (2013), Sherley et al. (2014), Pichegru et al. (2014).

Negative correlation between mean fledging period and prey abundance: Sherley et al. (2013).
Positive correlations between survival and prey abundance: Robinson (2013), RB Sherley (unpublished information).

Delayed onset of breeding during prey scarcity: Crawford and Dyer (1995).
Large-scale abandonment of breeding during local food scarcity: Crawford and Dyer (1995).
Breeding failure during local food scarcity: La Cock (1986).
Colony fragmentation during prey scarcity: Cordes et al. (1999).


[^0]:    ${ }^{1}$ While the Clark model, which produces this effect through $\gamma$ being a decreasing function of school size, and mean school size being reduced through fishing disturbing schools, has been used for illustration here, it is not the only mechanism that might be at work to produce a trend in this same direction. For example, the purse-seine catching operations are not $100 \%$ efficient, and will see some injured fish left in the water which are potentially more easily taken by predators. A well-known example of this effect is discarding of fish/fish parts by trawlers leading to increasing populations of some species of scavenging seabirds.

