Annex 1

An examination of the island closure related models produced by the MARAM group

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1. Introduction

Various analyses have been done by the MARAM group relating to the island closures study. The focus here is on Robinson (2013), examining issues of methods and interpretation of results.

2. Methods

a) GLMs

General comments

There are two main concerns with the structure of the GLMs performed by Robinson (2013). Firstly, group means are modelled for each year, hence biologically important variation is averaged out. The appropriate analysis would be to use individual data or weight the means with the inverse of their standard errors. Secondly, the models contain too many predictors for the number of outcomes available, and therefore would have little power to detect significant results.

The relationship between the response and the predictor is summarised as the estimated change in mean response, corresponding to a specified change in the predictor. The estimated change involves a point estimate together with an indication of the uncertainty contained in that estimate. If individual observations are not available, this relationship can be approximated by modelling the means, provided that the analysis is weighted by the inverse of the standard errors of the group means (square root of group size over group variance) or some other weighting that accounts for the different amount of information contained in individual means. In the case of the penguin data sets, the individual observations were available but not requested for use in Robinson (2013). A mean that is based on 100 observations should contribute more in an analysis than one based on a single observation. For example at Dassen Island during the closed years, 2008 and 2009, there are only 13 foraging track observations, while during open years there are 158. In the Robinson (2013) GLMs, the 13 observations have the same weight as the 158, because unweighted means were modelled.

An important aspect of estimation is the precision of the estimate. When the estimated effect of some action is, say, 120 more penguins spared, it makes a difference whether the 95% confidence interval is between 2 and 600; or between 115 and 130. Clearly the narrower the interval, the more precise and useful the result is. This precision is a function of group size: within group variation and between group variation. When modelling means, the only variation available is between means, leading to a confidence interval of the overall (unweighted) mean, which is likely to be spuriously precise, biased and thus uninformative.

The second concern with the models is over-parameterization. If a model contains fewer responses than the number of parameters it attempts to estimate, then there are an infinite number of possible solutions to the estimating equations and the model is said to be unidentifiable. A general rule of thumb is to have at least 10 observations for each parameter being estimated, because it is then possible to also assess the uncertainty in the estimates. The more observations per parameter, the more precise the estimates and associated uncertainty will be. In contrast, when a model is fit that estimates e.g. 9 parameters from 11 data points (see Table 1 in Robinson and Butterworth 2014a), there can be no confidence in any of the parameter estimates, nor in any of the conclusions drawn from such a model. As an example, modelling annual means, and defining year as a categorical (factor) variable, will result in the mean being the estimate for each year. Including any other parameter in the model, will lead to infinitely many possible solutions (estimates) and no idea of how close any of them are to being correct or not.

To avoid the concerns explained above, the raw data should be used in analyses, so that the variation within and between groups, including repeated measures on the same penguin or nest, can be used for valid inference. Use of the raw data also makes it possible to account for potential observation-level confounding factors. For example, environmental conditions or prey biomass levels can be included at the spatial and temporal scale of the observations.

Inclusion of pelagic catches in the set of predictors for GLMs

Linear regression is used to estimate the linear impact of a set of predictors on a response variable. Although causality is implied by the final estimates from linear regressions, causality cannot be revealed or confirmed by such analyses. This comment is relevant to the use of pelagic catches as predictors in linear regressions of various penguin responses. There is thus a need for a conceptual re-evaluation of the merit and meaning of the inclusion of pelagic catches in the set of predictors for GLMs which use metrics for penguin breeding success, survival and foraging as response variables.

It is considered that 6 different situations may exist, as illustrated below:

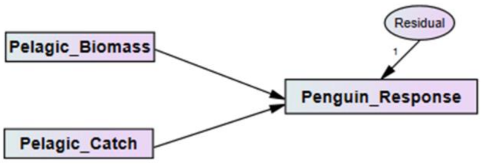

Figure 1. Standard linear model - catch and biomass directly influence penguins

Figure 1 is the standard linear regression situation in which catch and biomass are independent predictors of penguin response.

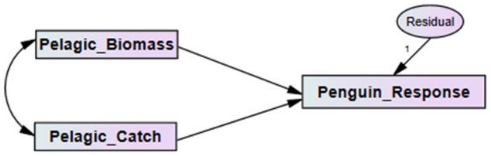

Figure 2. Standard linear model - catch and biomass; covariance between predictors explicit

Figure 2 is a modification of the standard linear regression situation in which covariances between the predictors are explicitly modelled.

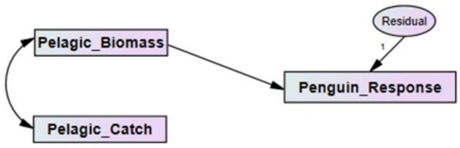

Figure 2b. Standard linear model - catch and biomass; covariance between predictors explicit; no direct impact by catch on penguin response

Figure 2b is a modification of the standard linear regression situation in which covariances between the predictors are explicitly modelled, but in which there is no direct relationship between catch and penguin response.

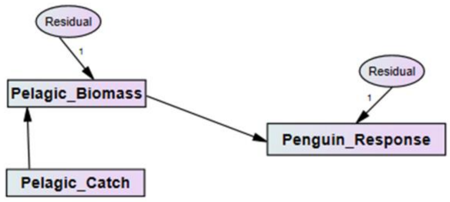

Figure 3. Catch influence via impact on biomass.

Figure 3 is the situation where the impact of pelagic catches are limited to the impact that these catches make on the prey biomass and in which the influence on penguin response is via biomass only.

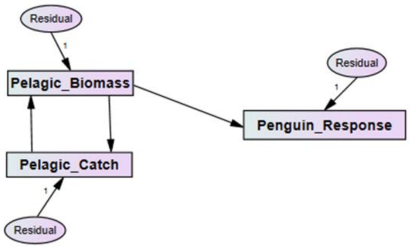

Figure 4. Catch influences biomass; biomass influences catch; influence on penguins is via biomass

Figure 4 is a situation where catches influence biomass, and biomass influences catches, but ultimately there is no direct influence of catches on penguin response.

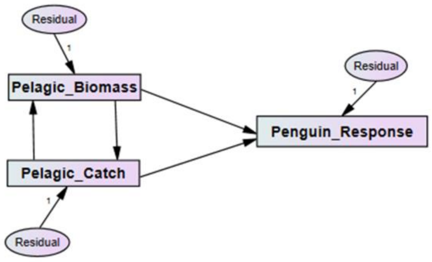

Figure 5. Catch influences biomass; biomass influences catch; catch also has direct influence on penguin response

Figure 5 is the situation in which catches influence biomass, and biomass influences catches, and both catch and biomass have a direct impact on penguin responses.

We note the following:

- The correlations between catch and biomass at the macro level are positive, but not always large enough to require that model Figure 2 should replace Figure 1. Given the relatively optimistic correlation threshold of 0.7 used in Robinson (2013), the smaller scale of these correlations (< 0.7) rules out the need to address problems of collinearity in the regression for a type Figure 1 regression: this is the sole significance of the VIF statistic discussion in Robinson (2013).
- The positive correlation between catch and biomass does not in itself indicate the direction of causality between catch and biomass. Logically, however, since an increase in catch cannot cause an increase in biomass, the direction of causality **MUST BE** in the direction of biomass to catch. Positive correlations between catch and biomass at the macro level have not been confirmed at the local island level, but it is likely that the correlation between catch and biomass at the local level is positive, although possibly weak (i.e. below the VIF threshold where collinearity would complicate interpretation of linear regression results, and invalidate model diagnostics).
- In the absence of a direct link between catch and penguin response, the mechanism given in Figure 4 is the most likely to be in operation, but in which the effect from biomass to catch dominates any negative impact of catch on biomass (because of the positive catch to biomass correlation at the macro level which is assumed to exist at the local level, emphasis: positive but not necessarily strong, could be a weak correlation). In this situation, and under an open island condition, a reduction in catch can only be achieved by reducing the pelagic biomass, catch cannot, under fishing as usual conditions, be reduced independently of pelagic biomass when the island status is open. **Application of a Figure 1 regression under circumstance where Figure 4 is in operation would produce the impression that catch is positively related to penguin response. It would also create an impression that it is possible to vary catch independently of pelagic biomass leading to the conclusion that fishing is good for penguin responses.**
- If catch has a direct effect on penguin response, then Figure 5 is the most likely representation of the interaction, but in which the effect from biomass to catch dominates any negative impact of catch on biomass (because of the positive catch to biomass correlation at the macro level which is assumed to exist at the local level). However, application of a Figure 1 regression when Figure 5 is the operative mechanism will produce a similar outcome as when Figure 4 is operative. Thus the Figure 1 regression cannot give insight into which of Figure 4 or Figure 5 is operative.

- These comments have a bearing on the interpretation of the positive impact of fishing on penguin response variables reported in Robinson (2013). It seems likely that these are the result of a positive correlation between biomass and catch at a local level – it is not the strength of the correlations which is relevant here (i.t.o. VIF statistics etc.), but their average sign which is most likely predominantly positive. In view of this, estimating the impact of a reduction in fishing is only meaningful and causally possible if there is a concomitant reduction in prey biomass, and surely this will be negative for penguins. Since the causality is from biomass to catch, the proposition to reduce catches is in fact a proposition to reduce prey biomass.
- It seems possible that the plethora of positive but non-significant catch to penguin response relationships from the GLMs are due to weak but positive local level catch to biomass correlations under Figure 4 conditions.

The situation changes when islands are experimentally closed to fishing, since the correlation between catch and biomass is eliminated. Experimental closures are therefore necessary to predict the penguin response to setting catches to zero around breeding islands

In summary

The positive correlation between catch and biomass at the macro level confirms that causality is from biomass to catch at this resolution. This is likely also the situation at the local level. The strength of the catch to biomass correlation is less important than its sign. The strength relates only to whether a linear regression would encounter collinearity problems. The sign provides insight into the dominant direction of causality even if the correlation is weak**.** When catch is positively correlated to biomass then under normal fishing conditions, catch cannot be reduced independently of biomass, so any calculations involving a reduction in catch must calculate the associated reduction in prey biomass. A simple linear regression throws no light on whether catch (a) influences penguin responses directly or (b) both directly and via its interaction with pelagic biomass.

When an island is closed, then the normal positive relationship between prey biomass and catch breaks down, since in this situation catch can and is reduced without an associated reduction in prey biomass. **The behaviour of the closed system cannot therefore be predicted by studying the relationship between prey biomass, catch and penguin response under normal fishing conditions, and setting catches to zero in prediction equations to estimate the closed island situation for penguins.**

It may be controversial that the local catch to biomass correlation is positive but weak. If so then the conclusion that catch has a direct positive impact on penguins is at least equally controversial.

Under circumstances of unresolved controversy of this nature there would be confusion about whether the operative mechanism is Figure 1, 4 or 5. Under these circumstances it is safest to exclude catch from the GLMs and use closure status and prey biomass as the relevant predictors.

Vessel effects

We suggest closure status, not catch, should be used in closure analyses as there may be effects on penguins from fishing vessels, other than removal of biomass. It has been suggested that penguins avoid areas where fishing is taking place (Harding 2012) due to the prolonged presence of fishing vessels in the area. The potential mechanism for this could be due to the presence of fishing vessels disrupting the cues (auditory and/or olfactory) used by penguins to find food. Wever et al. (1969) found that African Penguins *Spheniscus demersus* showed sensitivity over 100- 15000 Hz with peak sensitivity over 600 - 4000 Hz, which overlaps completely with boat engine frequency peaks at 600 Hz, 1300 Hz, and 2000 Hz (Sholik and Yan 2002). Thus depending on the volume of the sound, vessels have the potential to disrupt auditory cue used by penguins to locate other foraging seabirds. Penguins are able to detect dimethyl sulphide (Wright et al. 2011), which may be an olfactory cue to the location of a prey source. This scent may be masked by the exhaust fumes from vessels spending prolonged periods of time in one area (e.g. purse-seine fishing). These are two plausible but untested mechanisms that could cause penguins to disassociate from vessels. There may be other mechanisms, but our collective experience of observing penguins and other seabirds at sea strongly supports the hypothesis that penguins, unlike many seabirds such as albatrosses, gulls and gannets, are not attracted to vessels.

b) Power analysis

The power analysis (Robinson and Butterworth 2014a) is based entirely on the linear modelling approach criticised above. In particular, the concerns around over-parameterisation call into question the validity of the estimates of the residual standard error in each model (a crucial determinant of variability in the simulations) and the lack of consideration of the precisions of the means used to estimate the effect of fishing calls into question the precision of the fishing effect in each model. Furthermore, because in future simulations catches are set to 0 in the 20 and 30 nautical mile (nm) blocks around each island, they represent an unrealistic scenario which has the effect of overestimating the actual power. In reality, the closure is ca. 15 nm, with fishing continuing within the 20 and 30 nm blocks while the closure is in place (Pichegru et al. 2012).

Robinson and Butterworth (2014a) present results from a number of GLMs in which the degrees of freedom is small. This casts some doubt on the reliability of the residual error variance which is the basis of subsequent power analyses. In order to address this, two options were explored. The first is to use the upper 95% confidence interval of the residual variance in the power analyses. The other is to treat the year effects as random effects (Robinson and Butterworth 2014b). Although this approach is an improvement because it introduces additional variance into the power analyses, viz. the year factor variance, it nevertheless suffers from the limitations which arise because the penguin response value which is used in the input data is a simple year average. Thus, since the random effects model assigns the same variance to each year effect, the nuances of the number of observations per year and their within year seasonal distributions are not dealt with, which would result in different effective weights for annual averages from different years. Lastly, it is not clear whether the problems with small degrees of freedom are addressed by the use of year as a random effect. Sample size recommendations for multi-level mixed effects models is an unsettled issue in statistics (Bell et al. 2010).

As such, it would be concerning if the analyses of Robinson and Butterworth (2014a, 2014b) were used for management-decision making.

3. Issues of interpretation

Based on observed positive correlations between catch and some penguin fitness components, Robinson (2013) and Butterworth and Robinson (2014a) conclude that fishing around Dassen and Robben islands does not affect penguins and in some cases may even have a positive effect. The mechanism that is used to explain this is that fishing may break up the shoals of fish, resulting in more smaller shoals, making it more likely that a predator (such as penguins) will encounter a shoal. Centuries of ecological research show that prey densities positively affect predator densities (e.g. Power 1992). The Butterworth – Robinson mechanism must therefore be strong enough to override basic ecological principles. Such a strong assertion requires solid empirical evidence before it can be regarded as a plausible explanation. Observations that would be needed to support this mechanism are a) whether fishing does indeed break up shoals of fish, b) if a) is true a measure of how big these remaining shoals are and how long it takes before the fish aggregate again and c) whether there is a threshold shoal size which penguins are able to detect. Furthermore, it should be noted that there are no observations that splitting fish schools assists foraging by penguins, whereas some research has indicated that penguins sometimes feed cooperatively and may benefit from exploiting large schools of fish (see Additional information).

It is also pertinent to document prior observations regarding the impact of food availability on African Penguins. If catches of sardine or anchovy, the main prey of African Penguins, have a positive impact on penguins, it might be expected that numbers of penguins in each of three regions where they breed (southern Namibia, Western Cape, Eastern Cape) would increase following the commencement or expansion of commercial fishing of these species. Instead, in each region large decreases of penguins were observed (Shelton et al. 1984, Crawford et al. 2001, 2009).

Alternatively, if African Penguins are benefitted by a ready availability of prey, numbers breeding and demographic parameters of penguins might be expected to be positively related to prey availability and vice versa. This has almost invariably been the case. In each of the three regions noted above, numbers breeding were positively correlated with abundance of sardine and anchovy (Crawford 2007, Crawford et al. 2008, 2011). Similar positive relationships between numbers breeding and prey abundance have been observed at the colony scale (Crawford et al. 2008, Sherley et al. 2013). By contrast, severe fragmentation of penguin colonies occurred under conditions of food scarcity (Cordes et al. 1999).

Decreases of penguins at colonies between Lüderitz in Namibia and Dassen Island in the Western Cape, South Africa from the 1960s to the 1980s followed collapses of sardine stocks off Namibia and South Africa. Increases at Mercury and Ichaboe islands north of Lüderitz after the 1960s probably resulted from an increased local abundance of pelagic goby (Crawford and Shelton 1978, 1981, Shelton et al. 1984, Crawford et al. 1985, 2001). An increase and later decrease in numbers of penguins at Dyer Island, South Africa coincided with an increase and then a fluctuating decrease of anchovy off South Africa (Crawford 1998). Large numbers of African Penguins abandoned breeding at Dyer Island in 1991 when anchovy in its vicinity was scarce (Crawford and Dyer 1995).

The formation of new colonies at Stony Point, Boulders on South Africa's mainland and Robben Island and increases at these colonies and at Dassen and Vondeling islands took place during a period of recovery of South Africa's sardine in the 1980s and 1990s (Crawford et al. 2001, Underhill et al. 2006). After 2004, large decreases in numbers of penguins breeding off western South Africa were associated with an eastward shift of adult anchovy and sardine and a collapse of South Africa's sardine (Crawford et al. 2011). As the prey of penguins shifted south and east, there were decreases in penguin numbers at colonies located off northwest South Africa (the northernmost colony at Lambert's Bay became extinct). Numbers also decreased at the more southerly Dyer Island, while numbers at nearby colonies such as Boulders Beach and Stony Point, stabilised or increased (Crawford et al. 2011). More than 220 000 tonnes of sardines were caught within about 30 km of Dyer Island during 2002- 2004 (JJ van der Westhuizen, unpublished information) and the exploitation rate of sardines west of Cape Agulhas rose to 30 - 45% in 2002 and 2005 - 2007 (Coetzee et al. 2008). This high catch of sardines had no apparent benefit for penguins at Dyer Island, but rather appears to have had an adverse influence. When colony size at Dyer Island was > 3 500 pairs, numbers breeding there were negatively related to sardine catches made within 20 nautical miles of the island (Ludynia et al. 2014).

Several demographic parameters of African Penguins have been positively related to estimates or proxies of the abundance of sardine and/or anchovy at various spatial scales, including adult survival (Robinson 2013, Sherley et al. 2014), breeding participation (Crawford et al. 1999, Durant et al. 2010) and breeding success (La Cock 1986, Adams et al. 1992, Crawford and Dyer 1995, Crawford et al. 1999, Crawford et al. 2006, Cury et al. 2011, Sherley et al. 2013, Pichegru et al. 2014). There was likely delayed onset of breeding by African Penguins during a period of food scarcity (Crawford and Dyer 1995). The fledging period for chicks has been negatively correlated with prey abundance (Sherley et al. 2013).

Given (a) ambiguity about how catch in the vicinity of African Penguin colonies may influence penguins, (b) the absence of any empirical proof for a benefit of fishing on penguins, and (c) the above substantial body of evidence that a ready availability of food benefits African Penguins, it is not defensible at present to expect fishing to benefit penguins. Furthermore, studies conducted elsewhere have demonstrated both the importance of sufficient availability of prey to sustain seabird processes at colonies (e.g. Hunt et al. 1986, Gaston et al. 2007, Cury et al. 2011) and a negative impact of local depletion of prey by fishing on foraging parameters of seabirds that compete with fisheries for anchovy (Bertrand et al. 2012).

4. Additional Information: Foraging behaviour and strategy of African Penguins

Adult African Penguins tend to forage in groups (Frost et al. 1976, Wilson and Wilson 1990). Based on observations of co-operative foraging by this species, head-dipping movements by birds that may signal readiness to dive, some synchronous diving, groups of penguins circling shoals of pelagic fish and the position of bite marks on fish (Wilson and Duffy 1986, Hockey et al. 2005, Ryan et al. 2012), it has been inferred that at least some African Penguins herd prey into dense schools (rather than splitting such schools) and then strike them from below (Wilson and Wilson 1990, Ryan et al. 2012). The conspicuous plumage of adult African Penguins appears to promote dense, defensive schooling of small pelagic fish, creating so-called ‘bait balls’ that are easier to exploit (Wilson et al. 1987).

In addition to facilitating group foraging, an advantage postulated for colonial breeding in seabirds and water-birds is acquisition of information that facilitates food finding (Erwin 1978, van Vessem and Draulans 1986). It is noteworthy that, after Namibia’s sardine collapsed, at Possession Island colonies of penguins fragmented as birds fed predominately on squid, which may have been present in densities too low to favour co-operative hunting (Cordes et al. 1999). For other seabirds, individual foraging success also may increase with increasing group size (Götmark et al. 1986).

Prey supply has an important impact on bird biology, affecting activity, distribution, energetics, competitive abilities, breeding success and survival (e.g. Furness and Monaghan 1987, Montevecchi et al. 1988, Garthe et al. 1999). Foraging strategies of seabirds are determined by the dispersion and availability of different prey resources, the energetic costs of foraging and the rate at which food must be delivered to the nest during breeding (Lack 1968, Weimerskirch et al. 1994). Any alterations in the marine environment caused by either natural phenomena or human-induced activities require flexible behavioural responses by seabirds (Crawford 1998, Pichegru et al. 2010, Baylis et al. 2012). Whereas volant seabirds (for example, albatrosses and petrels) may exploit food sources distant from their breeding sites (Weimerskirch et al. 1993, Péron et al. 2010), African Penguins are constrained by both their fidelity to sites once breeding and their mode of locomotion (Wilson 1985, Hockey et al. 2005). Since swimming is slower and more energetically expensive than flying (Pinshaw et al. 1977, Schmidt-Nielsen 1999), penguins require predictable food resources close to their colonies during breeding (Sherley et al. 2013). The sine qua non for African Penguins to breed successfully at colonies and after that to survive to moult will be a sufficient density of prey in the neighbourhood of colonies.

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