

**Response to: “An evaluation of evidence that purse-seine fishing around African Penguin colonies benefits penguins”**

DS Butterworth and WML Robinson

MARAM (Marine Resource Assessment and Management Group)  
Department of Mathematics and Applied Mathematics,  
University of Cape Town

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

**An evaluation of evidence that purse-seine fishing around African Penguin colonies benefits penguins**

Crawford RJM<sup>1</sup>, Hagen C<sup>2</sup>, Jarre A<sup>3</sup>, Ludynia K<sup>3</sup>, Makhado AB<sup>1</sup>, McInnes A<sup>4</sup>, Robinson K<sup>5</sup>,  
Pichegru L<sup>4</sup>, Shannon LJ<sup>3</sup>, Sherley RB<sup>5</sup>, Steinfurth A<sup>5</sup>, Waller L<sup>6</sup>, Weller F<sup>3</sup>

<sup>1</sup>Department of Environmental Affairs, South Africa

<sup>2</sup>BirdLife, South Africa

<sup>3</sup>Marine Research Institute, University of Cape Town

<sup>4</sup>Percy FitzPatrick Institute of African Ornithology, University of Cape Town

<sup>5</sup>Animal Demography Unit, University of Cape Town

<sup>6</sup>CapeNature

Recent papers tabled at the Island Closure Task Team arrived at different conclusions on whether or not purse-seine fishing around African Penguin colonies benefits the penguins at such colonies. The following text considers the foundations for the different opinions and draws conclusions regarding the benefit of fishing for African Penguins.

*Fishing around colonies is beneficial to African penguins*

Robinson and Butterworth (2014a, 2014b) were of the opinion that fishing around penguin colonies was of benefit to penguins. Their conclusion was based on outputs from GLM analyses of the form:

$$\text{Ln}(F_{y,i}) = \alpha_y + \beta_i + \lambda_i(c_{y,i,p})/(\text{average}_{c_{i,p}}) + \varepsilon_{y,i} \quad (1)$$

where  $F$  is a penguin response variable (e.g. breeding success),  $y$  = year,  $i$  = island,  $\alpha_y$  is a year effect reflecting prevailing environmental conditions,  $\beta_i$  is an island effect,  $\lambda_i$  is a fishing effect,  $c_{y,i,p}$  is the catch taken in year  $y$  in the neighbourhood of island  $i$  of pelagic species  $p$ ,  $\text{average}_{c_{i,p}}$  is the average catch at island  $i$  of species  $p$  taken over the years considered and  $\varepsilon_{y,i}$  is an error term. In a majority of instances they found that  $\lambda_i$  was positive, thence inferring a beneficial influence of fishing for penguins (Robinson and Butterworth 2014a). This inference though is based on the assumption that  $c_{y,i,p}$  is not an indicator of fish availability near island  $i$  (local

availability), although a ready availability of fish in the vicinity of an island might result both in improved catches in the island's proximity and benefit for penguins.

*The assumption promoted by the authors of ICTT/20 that  $c_{y,i,p}$  is an indicator of fish availability (abundance) near island  $i$  is confounded by other effects. The fundamental flaw in making this assumption, which is widely rejected in fisheries, is explained in detail in FISHERIES/2014/APR/SWG-PEL/ICTT/16 (pgs 4-5, items ii, iv and v) and FISHERIES/2014/APR/SWG-PEL/ICTT/17.*

Robinson and Butterworth (2013) used a variant of the above GLM, in which  $\alpha_y$  is replaced by  $\mu B_{y,p}$ , where  $B$  is the annual (recruit or spawner) biomass in year  $y$  of species  $p$ . However,  $c_{y,i,p}$  may be strongly correlated with  $B_{y,p}$ , as was demonstrated for anchovy (spawner) at Dassen Island (Durant et al. 2010) (and occurs at Robben Island) and sardine (recruit and spawner) at both Robben Island and Dassen Island (Table 5 in Sherley 2014a), despite Robinson (2013) and Butterworth (2014b) reporting that the average correlation is relatively small ( $r \sim 0.3$ ).

*Indeed there may be instances where the correlation is higher than 0.3. But that does not negate the implications of the statement by Robinson (2013) that “A review of the correlation coefficients  $r$  between the biomass and catch time-series used in each model considered revealed that the average correlation is  $r \approx 0.3$ , which is reasonably small. (Compare the plots of survey biomass versus catches for the full time-series in Figures 2.4–2.6.) Severe distortion of parameter estimation tends to occur only when  $|r| > 0.7$  (Dormann et al. 2013), and this threshold is breached in only a very few cases. In these cases, the variance-inflation factor 5 (VIF) was calculated. Results never exceeded 10, which is often used as a threshold for indicating severe collinearity, although even higher VIFs are often acceptable (O’Brien 2007).” Clearly if the average is about 0.3, there are many instances where the correlation is similar to or lower than that. One possible exception as cited here certainly does not negate a broadly evident feature of the data as a whole, and the implications that follow from that.*

Robinson and Butterworth (2013) also assume that fish are similarly abundant around neighbouring islands and that these islands thus can be used as controls.

*This reflects a serious misunderstanding of the implicit assumption (see also the more detailed explanation provided in the Note starting on pg 4 of FISHERIES/2014/APR/SWG-PEL/ICTT/25). First note the island factor  $\beta_i$  in equation 1 allows for the possibility of widely different catchabilities (or “available abundances”) (see Note) at the different islands ( $i$ ) – there is NO requirement for “similar abundance”. The implicit assumption, which is far weaker than the authors of ICTT/20 suggest, amounts, essentially only to positive correlation. It is difficult to envisage a plausible situation where that would not apply. Deviations from proportionality will be absorbed into the composite residual  $\varepsilon_{y,i}$ . It would require some extreme correlation structure, related also to the catches made, to result in large biases in estimates of  $\lambda$ , and no examples of that have been provided by the authors of ICTT/20 to allow the associated necessary review of their plausibility.*

This assumption is still to be tested using the small-scale fish surveys discussed below and requires further interpretation in the light of shifts in the centre of gravity of catches (Fairweather et al. 2006) and deterioration of seabird habitats off northwest South Africa (Waller et al. 2014).

*These shifts and argued deterioration are irrelevant in this context. The separations between the island pairs in question are at a much smaller spatial scale.*

The alternative assumption, i.e. that catches made in the vicinity of an island represent the availability of fish near that island, was adopted by Sherley et al. (2013). Those authors showed that, for African Penguins at Robben Island, breeding success and chick-fledging rates were positively related to local food availability, indexed through the annual industrial catch of anchovy made within 56 km (30 nautical miles) of the colony. They further found chick-fledging rates were depressed in 2-chick broods during years when anchovy contributed < 75% by mass to the diet of breeding birds and concluded that these results highlighted the importance of ensuring adequate local food availability for penguins during their reproductive cycle. Similarly, Durant et al. (2010) suggested fishing in the vicinity of Dassen Island might cause reduced participation by penguins in breeding and recommended that management of the purse-seine fishery be adjusted spatially in order to ensure adequate local food supplies for breeding African Penguins.

*As is stated above, the fundamental flaw in making this alternative assumption, which is widely rejected in fisheries, is explained in detail in FISHERIES/2014/APR/SWG-PEL/ICTT/16 (pgs 4-5, items ii, iv and v) and FISHERIES/2014/APR/SWG-PEL/ICTT/17.*

That locations of catches reflect the distributions of epipelagic fish is not a novel concept. It was used by Fairweather et al. (2006) to describe an eastward shift of sardine off South Africa between 1997 and 2005. Later, Sabarros et al. (2012) used catch per effort information, validated against fishery-independent hydroacoustic survey data matching in time and space, to identify locations of peaks of abundance (PoA) in epipelagic fish around the South African coast and magnitudes of the peaks. They demonstrated that at the 17 colonies of African Penguins in South Africa, numbers breeding were positively related to the magnitude of the nearest PoA of anchovy and sardine (combined) and negatively to the distance of the PoA from the colony. Similarly, numbers of Cape Gannets (which also feed mainly on anchovy and sardine) breeding at their three South African colonies were positively related to the magnitude of the nearest PoA and negatively related to its distance from the colony.

*To assert that some broad indications of fish distribution are provided by catches is quite different to making assumptions that catch is proportional to biomass, which is one that is seriously questioned in fisheries (see FISHERIES/2014/APR/SWG-PEL/ICTT/16, pg 5). It is in any case quite incorrect for the South African anchovy, where much of the abundance is on the Agulhas Bank and unfished because of lower densities – indeed before surveys commenced in the mid-1980s, the extended distribution of this species into this area was not known.*

*The claim in Sabarros et al. (2012) that the pelagic CPUE which they define is use-able as an index of abundance, and that this has been validated against hydroacoustic survey data, is scarcely credible. Fig. S2.2 of that paper is reproduced in the Addendum at the end of this document. Coetzee (pers. commn) comments that: “This plot is incorrectly labelled. It is not backscattering but density ( $g.m^{-2}$ ), so is in fact proportional to biomass. Sabarros and co-authors*

*appear to have matched the data in time and space by using only May and November catch data that occurred within 10 nm of the central position of each density position. Obviously these densities are not accurate indications of biomass; they would need to be weighted by interval length, line length, stratum, area etc. to calculate the biomass.” One notes further that the catches considered occur over periods of a month, during which the fish could move substantially, and the data plotted are not species-specific. The  $r^2$  value for the regression line shown is only some 4% and hardly indicative of some meaningful relationship, particularly when one notes that the data points about that line typically range from about four orders of magnitude above to four orders below the line. In any case, CPUE is scarcely used anywhere worldwide in the assessment of pelagic species because of its known unreliability as an index of abundance, inter alia because of likely non-linearity in the relationship (a factor Sabarros et al. ignore in their analyses) (see also FISHERIES/2014/APR/SWG-PEL/ICTT/16, pg 4)*

Given the sophistication of South Africa’s purse-seine fishery and its ability to find fish over wide areas, as demonstrated by Fairweather et al. (2006), it might be expected that the distribution of catches, at least within the area of operation of the fishery, partially reflects the local availability of fish species targeted by the fishery. In view of this, it seems premature to conclude that positive  $\lambda$ s emanating from GLMs demonstrate a beneficial influence of fishing on penguins (Robinson and Butterworth 2014a). Rather they may be interpreted as confirming the importance of good local availability of prey for penguins.

*The many problems and associated inconsistencies with this last assertion have been explained above (see particularly FISHERIES/2014/APR/SWG-PEL/ICTT/16 and 17). No cogent rebuttal of the GLM analyses by Robinson and the reliability of their resultant  $\lambda$  estimates has been offered by the authors of ICTT/20 (see also FISHERIES/2014/APR/SWG-PEL/ICTT/25). How else then are these positive values to be interpreted?*

Indeed, Sherley (2014a) carried out an analysis replicating that of Robinson and Butterworth (2014a) for one penguin time-series, but in addition used AICc-based model selection<sup>1</sup> to compare objectively a series of candidate models containing catches in the vicinity of islands and annual biomass estimates. He concluded: “much of the variance in the Active nest proportion that can be explained by catches in the vicinity of the islands can also be explained by the annual biomass estimates and vice-versa. This would seem to support the explanation mentioned on pg. 92 of Robinson (2013), but later discarded, that ‘fishery catches are naturally higher when a high abundance of fish is present in dense shoals—precisely the feeding environment which favours penguins’. In other words, both the fishing industry and the penguins are able to find sardine and anchovy close to Robben and Dassen islands in years when fish are abundant close to these islands” (Sherley 2014a).

*Counters to these arguments are provided above, and the comment by Robinson quoted is in the context of “other things being equal” – in practice they are not, which is one of the fundamental reasons why catch does not provide a reliable index of abundance (see*

---

<sup>1</sup> Note that the objection raised by Butterworth (2014a) that the “model selection approach is partly flawed” because AICc is not comparable between models fit using MLE and REML is not applicable as model selection was carried out using ML estimated results, with final values from the mixed model presented based on REML (see methods section in Sherley 2014a).

*FISHERIES/2014/APR/SWG-PEL/ICTT/16, pgs 4-5). But furthermore and importantly, Sherley (2014a) has completely misunderstood the nature of the power analysis computations being carried out, as explained in FISHERIES/2014/APR/SWG-PEL/ICTT/14. The issue here is Type II, not Type I error. To suggest that model selection be used in circumstances of time series of insufficient length to detect alternative further effects is hardly scientifically appropriate.*

Should this be the case, it need not be “surprising” (Robinson 2013) that penguins and fishers both benefit from a ready availability of fish near islands – provided catches do not always reduce the local availability of prey below the threshold required by penguins to meet their food requirements. That threshold will depend *inter alia* on the size of the colony, reducing as numbers of birds at the colony decreases (e.g. Gaston et al. 2007). For example, a greater density of prey in the neighbourhood of Dassen Island would have been required to sustain the penguin colony there in 2004 (when 25,000 pairs were breeding) than in 2013 (when 2,600 pairs bred). However, this effect is not considered in equation (1). A density dependent response in the recruitment of immature penguins to Robben Island (Crawford et al. 2007) confirms the likelihood that densities of prey in the vicinities of colonies will influence the population dynamics of African Penguins. The need to understand how local food availability may be modified by fishing, and at what levels of local prey availability penguins may be adversely influenced by catches near islands, was a strong motivation to initiate small-scale surveys of fish abundance around colonies of African Penguins.

*The density dependent response estimation in Crawford et al. (2007) uses a method well known amongst fisheries scientists to be flawed, as was originally pointed out by John Pope. The regression indicated in the equation on the right hand column of pg 573 of that paper includes the independent variable P on the right as well as the left hand side of the equation in a form that makes a negative correlation inevitable, but does not in fact provide any confirmation of the relationship claimed. Fig. Add.1 of the Addendum uses results from the Robben island penguin dynamics model of Robinson (2013), which uses a statistically justifiable estimation approach, to assess this relationship. Though some density-dependence is indicated, the effect is much weaker than indicated by, and with an  $r^2 \sim 0.2$  much less than the  $r^2 \sim 0.8$  claimed by Crawford et al. (2007). In any case, Fig. 4.8(e) of Robinson (2013) shows a trendless relationship between penguin recruitment success and anchovy recruit biomass, hence providing no indication that reducing the extent of fishing would have an impact – a conclusion supported by the “river model” results of Butterworth and de Moor (2010) which indicate that over the first decade of the current century, the fishery reduced the anchovy abundance off the west coast by typically only some 10% of the amount that would otherwise have been present. To put the claim above that a greater prey density was needed to feed penguins at Robben and Dassen in 2004 than in 2013, given the earlier higher numbers, in an appropriate context, one should note that the annual food requirements of penguins of a little more than some 20 000 tons (Robinson 2013, pg 161) constitute a mere 0.5% of the average annual production of sardine and anchovy resources over the first decade of the current century of about 4 million tons (de Moor and Butterworth, 2010). Thus consumption by penguins is negligible compared to the other sources of natural mortality on these fish, so changes in penguin numbers by even, say, three-fold above their current levels would have a minimal impact on the abundances of their prey.*

Robinson (2013) cites Clark (1976) to suggest a possible mechanism for fishing benefiting penguins – “that fishing vessels tend to break up large shoals of pelagic fish, and predators are more likely to encounter prey if there are many small shoals rather than a few large shoals” (pg. 176). However, the argument above is applied inconsistently by Robinson (2013) and seemingly at odds with the original sentiment of Clark (1976). Robinson (2013 pg. 92) also states that “One possible mechanism underlying the apparent benefit of fishing to penguins is that the shoaling behaviour of small pelagic fish is a predator defence mechanism: although larger shoals are more readily located, surface to volume effects mean that in a larger shoal an individual fish is less likely to be eaten” (pg. 92). Clark (1976) states “Since predators are assumed to have fixed appetites, we can assume that the rate of predation is proportional to the rate of detection of schools. The rate of detection is in turn proportional to the visual volume of the school, provided the latter is small in relation to the total volume of seawater over which predators search”. In other words, large schools are easier to detect and to extract food from.

*Of course this is part of Clark’s argument, but not all of it, and the authors of ICTT/20 evidence a complete failure to understand his analyses. Consider the same biomass, divided either into a few large shoals, or many smaller shoals (e.g. as a result of disturbance caused by fishing). A single large shoal is indeed easier to find than a single small shoal. But in each case the probability of finding a single shoal has to be multiplied by the number of shoals. What Clark effectively shows is that as a result of the surface to volume effect, the combined surface area is larger in the case of the smaller shoals, hence rendering it easier for predators to find a shoal in that case, and consequently forage more successfully.*

Furthermore, tight schooling behaviour makes feeding less efficient for planktivores so that pelagic fish will in any event need to spread out to feed (Eggers 1976). By working together, seabirds targeting fish schools benefit by disrupting the cohesiveness of predator avoidance tactics (Shealer 2002) and individual foraging success may increase with increasing group size (Götmark et al. 1986). Adult African Penguins tend to forage in groups (Frost et al. 1976, Wilson and Wilson 1990) and, based on observations of head-dipping movements 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), it has been inferred that at least some African Penguins forage co-operatively, herding prey into dense schools (rather than splitting such schools) and then striking them from below (Wilson and Wilson 1990, Ryan et al. 2012). The conspicuously striped 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). Co-operative foraging by groups of African Penguins that numbered between 25 and 165 individuals was recently observed in Algoa Bay (Ryan et al. 2012).

Foraging strategies of seabirds are constrained 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). Thus, 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). 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). While volant seabirds (for example, albatrosses and petrels) may exploit food sources distant from their breeding sites (Weimerskirch et al. 1993, Péron et al. 2010), penguins are more limited in their foraging capabilities (Wilson 1985). For this reason penguins are especially sensitive as marine sentinels: they reflect the rate and nature of changes occurring in their marine environment (Boersma 2008). Effectively, any alterations in the marine environment caused by either natural phenomena and/or human-induced activities require flexible behavioural responses (Crawford 1998, Pichegru et al. 2010, Baylis et al. 2012) but African Penguins are constrained by their mode of locomotion and fidelity to sites once breeding (Hockey et al. 2005).

*This is very interesting in a natural history context, but as realized some three decades ago in fisheries assessment (see comments in Butterworth, 1989, pg 635) of little help in a modelling context. Many and complex mechanisms are at work, and not all in the same direction in response to changes in fishing intensity. Though some can be measured, others cannot, and may well be in the opposite directions to those which can. Thus associated issues cannot be resolved by micro-studies and related modelling, but rather only by empirical measurements of combined effects (see also FISHERIES/2014/APR/SWG-PEL/ICTT/25). It is for this reason the island closure program and the method to analyse the results were proposed and agreed in their present form.*

Advantages postulated for colonial breeding in seabirds and water-birds include the acquisition of information that facilitates food finding (Erwin 1978, van Vessem and Draulans 1986) and 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). The *sine qua non* for African Penguins hoping to breed successfully at colonies and after that to survive to moult will be a sufficient density of prey in the neighbourhood of colonies. If that is prevented by excessive catches near colonies, it will be detrimental to penguins.

*Certainly, but the comparison with Namibia is quite misleading. There fishing in the 1960-80 period reduced sardine biomass by certainly one order of magnitude if not two. In contrast the impact of current fishing mortalities on the SA anchovy population, which dominates the small pelagic biomass off the Robben and Dassen island penguin colonies during their peak breeding and fledging period, and is in any case generally undercaught compared to the TAC awarded, is only slight (Butterworth and de Moor, 2010).*

*Fishing around colonies is detrimental to African penguins*

The opinion that purse-seine fishing around colonies of African Penguins is detrimental to African Penguins was expressed in several papers.

Pichegru et al. (2014) presented preliminary results on the responses of African Penguins to island closures in Algoa Bay. They showed that the foraging effort of penguins breeding at St Croix Island was significantly related to the size of fish catches made near the island. Furthermore, when fishing was excluded from the immediate vicinity of the island, penguins switched from foraging mostly outside the fishing exclusion zone to feeding mainly within it

(Pichegru et al. 2012). In this instance, fishery extractions near the island seem likely to have reduced prey density below a sustainable threshold for foraging by penguins. A re-opening of the exclusion zone to fishing caused decreases in breeding success and chick growth (Pichegru et al. 2014).

*Certainly Pichegru et al. (2014) present defensible analyses pointing to a negative impact on penguin reproduction of fishing in the vicinity of St Croix. However, as pointed out in FISHERIES/2014/APR/SWG-PEL/ICTT/17, acceptance of these results is inconsistent with the arguments offered above by the authors of ICTT/20 and related papers that catch is an index of abundance and that such greater abundance promotes improved reproductive success. Basically these two positions cannot both be correct.*

Weller et al. (2014) presented a system dynamics model of the African Penguin population at Robben Island. The modelled population of penguins was found to be strongly driven by food availability, including that within the penguins' foraging area around the island. The impact of short-term fishing restrictions around the island was found to be generally beneficial to the modelled population, but easily masked by food-driven variability in population growth. The nature of the expert opinion used in the model was queried by Robinson and Butterworth (2014b). However, the importance of food, including the local food supply, for a wide range of processes that influence the population dynamics of African Penguins has been extensively documented – see some examples in Annex 1.

*The problems with the Weller et al. (2014) are further elaborated in FISHERIES/2014/APR/SWG-PEL/ICTT/25. The issue is not whether local food “supply” is important for penguins when breeding, which is not in contention. Rather it is the impact of current levels of fishing on that “supply”? Essentially the Weller et al. approach, by its very structure, assumes what it then claims to prove, and furthermore is at variance with what more empirical analysis of the data themselves indicate (see FISHERIES/2014/APR/SWG-PEL/ICTT/16, pgs 2-3).*

### *Conclusion*

Contra to the conclusions of Robinson (2013) and Robinson and Butterworth (2013, 2014a, 2014b), the preponderance of evidence given above suggests that African Penguins may be adversely influenced by purse-seine fishing in the vicinity of their breeding colonies, especially if the abundance of prey is reduced below the threshold that enables them to meet their energy requirements. At many of South Africa's colonies, numbers of African Penguins have collapsed in the recent century (Crawford et al. 2011). In order for African Penguin colonies to grow thresholds in local prey availability will need to be higher than those that may currently apply. Therefore, spatial management of the purse-seine fishery needs to be applied at small scales, as well as at large scales.

*As is clear from the responses given earlier, the “evidence given above” as regards the impact of pelagic fishing in the vicinity of breeding colonies is, with the exception **ONLY** of the recent Pichegru et al. (2014) GLMM analysis for St Croix, universally flawed (in some instances simply as a result of a failed understanding). It therefore provides **NO** basis to refute the conclusions of*

*the papers listed (which independently concur with the St Croix analysis just mentioned). Given that over the last decade or so, anchovy abundance (a key basis for food for the Robben and Dassen island colonies during their breeding and fledging period) has been almost without exception at levels much higher than those since surveys began in the mid-1980s (Butterworth and de Moor, 2010) – a period when the Robben and Dassen island colonies grew - it is also very clear that no evidence or cogent argument has been presented by the authors of ICTT/20 in support of their assertion that: “In order for African Penguin colonies to grow thresholds in local prey availability will need to be higher than those that may currently apply”.*

## 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.
- Baylis AMM, Zuur AF, Brickle P, Pistorius PA. 2012. Climate as a driver of population variability in breeding Gentoo Penguins *Pygoscelis Papua* at the Falkland Islands. *Ibis* 154: 30–41.
- Boersma PD. 2008. Penguins as Marine Sentinels. *BioScience* 58: 597–607.
- Butterworth DS. (2014a). Some responses to comments by Sherley in FISHERIES/2014/MAR/SWG-PEL/ICTT/13. FISHERIES/2014/MAR/SWG-PEL/ICTT/14 2 pp.
- Butterworth DS. (2014b). A composite proposal related to the penguin colony closure programme. FISHERIES/2014/MAR/SWG-PEL/ICTT/16 8 pp.
- Clark CW. 1976. *Mathematical Bioeconomics*. New York: John Wiley & Sons.
- 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. 1998. Responses of African Penguins to regime changes of sardine and anchovy in the Benguela system. *South African Journal of Marine Science* 19: 355–364.
- Crawford RJM. 2007. Food, fishing and seabirds in the Benguela upwelling system. *Journal of Ornithology* 148 (Suppl 2): S253–S260.
- 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, 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 21<sup>st</sup> century: a consideration of food availability. *African Journal of Marine Science* 33: 139–156.
- 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, Shannon LJ, Whittington PA. 1999. Population dynamics of the African Penguin at Robben Island. *Marine Ornithology* 27: 135–143.
- 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, Underhill LG, Upfold L, Dyer BM. 2007. An altered carrying capacity of the Benguela upwelling ecosystem for African Penguins (*Spheniscus demersus*). *ICES Journal of Marine Science* 64: 570–576.
- 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.
- 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.
- Eggers DM. 1976. Theoretical effects of schooling by planktivorous fish predators on rate of prey consumption. *Journal of the Fisheries Research Board of Canada* 33: 196–197.
- Erwin RM. 1978. Coloniality in terns: the role of social feeding. *Condor* 80: 211–215.
- Fairweather TP, van der Lingen CD, Booth AJ, Drapeau L, van der Westhuizen JJ. 2006. Indicators of sustainable fishing for South African sardine (*Sardinops sagax*) and anchovy (*Engraulis encrasicolus*). *African Journal of Marine Science* 28: 661–680.
- Frost PGH, Siegfried WR, Burger AE. 1976. Behavioural adaptations of the Jackass Penguin, *Spheniscus demersus* to a hot, arid environment. *Journal of Zoology* 179: 165–187.
- Furness RW, Monaghan P. 1987. Seabird ecology. Chapman & Hall, New York.
- Garthe S, Grémillet D, Furness RW. 1999. At-sea activity and foraging efficiency in chick-rearing Northern Gannets (*Sula bassana*): a case study in Shetland. *Marine Ecology Progress Series* 185: 93–99.
- Gaston AJ, Ydenberg RC, Smith GEJ. 2007. Ashmole’s halo and population regulation in seabirds. *Marine Ornithology* 35: 119–126.
- Götmark F, Winkler DW, Andersson M. 1986. Flock-feeding on fish schools increases individual success in gulls. *Nature* 319: 589–591.
- Hockey PAR, Dean WRJ, Ryan PG (eds). 2005. Roberts Birds of Southern Africa, 7<sup>th</sup> edn. John Voelcker Bird Book Fund, Cape Town.
- La Cock GD. 1986. The Southern Oscillation, environmental anomalies and mortality of two southern African seabirds. *Climatic Change* 8: 173–184.
- Lack D. 1968. Ecological adaptations for breeding birds. Methuen, London.
- Montevecchi WA, Birt VL, Cairns DK. 1988. Dietary changes of seabirds associated with local fisheries failures. *Biological Oceanography* 5: 153–161.
- Péron C, Delord K, Phillips RA, Charbonnier Y, Marteau C, Louzao M, Weimerskirch H. 2010. Seasonal variation in oceanographic habitat and behaviour of White-Chinned Petrels *Procellaria aequinoctialis* from Kerguelen Island. *Marine Ecology Progress Series* 416: 267–284.
- Pichegru L, Grémillet D, Crawford RJM, Ryan PG. 2010. Marine no-take zone rapidly benefits Endangered penguin. *Biology Letters* 6: 498–501.
- 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.
- Pichegru L, Ryan PG, van Eeden R, Reid T, Grémillet D, Wanless R. 2012. Industrial fishing, no-take zones and endangered penguins. *Biological Conservation* 156: 117–125.

- Pinshaw B, Fedak MA, Schmidt-Nielsen K. 1977. Terrestrial locomotion in penguins: it costs more to waddle. *Science* 195: 592–594.
- Robinson WML. 2013. Modelling the impact of the South African small pelagic fishery on African penguin dynamics. PhD Thesis, University of Cape Town.
- Robinson W[ML], Butterworth DS. 2013. GLMs relating penguin demographics and foraging behaviour to forage fish abundances. FISHERIES/2013/SWG–PEL/ICTT/13: 47 pp.
- Robinson WML, Butterworth DS. 2014a. Island closure feasibility study power analysis results for Dassen and Robben islands. FISHERIES/2014/MAR/SWG–PEL/ICTT/5: 11 pp.
- Robinson WML, Butterworth DS. 2014b. 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.
- Ryan PG, Edwards L, Pichegru L. 2012. African Penguins *Spheniscus demersus*, bait balls and the Allee effect. *Ardea* 100: 89–94.
- 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: 291–301.
- Schmidt-Nielsen K. 1999. Animal physiology – adaptation and environment. Cambridge University Press, Cambridge.
- Shealer DA. 2002. Foraging behaviour and food of seabirds. In Schreiber EA, Burger J (eds) *Biology of Marine Birds*. CRC Press, Boca Raton, pp 217–262.
- Sherley RB. 2014a. Comments on ‘Island closure feasibility study power analysis results for Dassen and Robben islands’ (FISHERIES/2014/MAR/SWG–PEL/ICTT/5). FISHERIES/2014/MAR/SWG–PEL/18: 12 pp.
- 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*. *Marine Ecology Progress Series*. 473: 291–301.
- Sherley RB, Barham PJ, Barham BJ, Crawford RJM, Dyer BM, Leshoro TM, Makhado AB, Upfold L, Underhill LG. 2014. Growth and decline of a penguin colony and the influence on nesting density and reproductive success. *Population Ecology* 56: 119–128.
- Van Vessem J, Draulans D. 1986. The adaptive significance of colonial breeding in the Grey Heron *Ardea cinera*: inter- and intra-colony variability in breeding success. *Ornis Scandinavica* 17: 356–362.
- Waller LJ, Chesselet Y, Crawford RJM, Dyer BM, Makhado AB, Meyer MA, Nel P, Oosthuizen WH, Seakamela SM, Upfold L, Visagie J, Wheeler MJ. 2014. A worsening environment off South Africa’s north-west coast for marine top predators. FISHERIES/2014/MAR/SWG–PEL/ICTT/3: 10 pp.
- Weimerskirch H, Doncaster C, Cuenot-Chaillet F. 1994. Pelagic seabirds and the marine environment: foraging patterns of Wandering Albatrosses in relation to prey availability and distribution. *Proceedings of the Royal Society of London B* 255: 91–97.
- Weimerskirch H, Salamolard M, Sarrazin F, Jouventin P 1993. Foraging Strategy of Wandering Albatrosses through the Breeding Season : A Study Using Satellite Telemetry. *Auk* 110: 325–342.
- Weller F, Lee-Anne Cecchini L-A, Shannon LJ, Sherley RB, Crawford RJM, Res 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.
- Wilson RP 1985. The Jackass Penguin (*Spheniscus demersus*) as a pelagic predator. *Marine Ecology Progress Series* 25: 219–227.
- Wilson RP, Duffy DC. 1986. Prey seizing in African Penguins *Spheniscus demersus*. *Ardea* 74: 211–214.
- Wilson RP, Wilson MPT. 1990. Foraging ecology of breeding *Spheniscus* penguins. In: LS Davis, JT Darby (eds). *Penguin Biology*. Academic Press, San Diego, CA, pp. 181–206.
- Wilson RP, Ryan PG, James A, Wilson M-P. 1987. Conspicuous coloration may enhance prey capture in some piscivores. *Animal Behaviour* 35: 1558–1560.

**References added** (aside from ICTT documents for this meeting which are referenced in the text by their number)

- Butterworth DS 1989. The Benguela Ecology Programme: successful and appropriate? S. Afr. J. Sci.* 85: 633-643.
- Butterworth DS and de Moor CL. 2010. An extension to the simple implementation of the “river model” to estimate the impact of fishing on the amount of anchovy available to west coast penguin colonies which takes account of within season variability in recruitment. Document: MCM/2010/SWG-PEL/Island Closure Task Team/20. (Also MARAM IWS/DEC10/P/BG3) 12 pp.*
- de Moor .CL and Butterworth DS 2010. Catch to natural predation ratios for sardine and anchovy. Marine and Coastal Management document: MCM/2010/SWG-PEL/Island Closure Task Team/15: 1-5.*
- Dormann CF, Elith J, Bacher S, Buchmann C, Carl G, Carre G, Marquez JRG, Gruber B, Lafourcade B, Leitao PJ, Munkemuller T, McClean C, Osborne PE, Reineking B, Schroder B, Skidmore AK, Zurell D, and Lautenbach S. 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography, 36: 027-046.*
- O'Brien RM. 2007. A caution regarding rules of thumb for Variance Ination Factors. Quality & Quantity, 41: 673-690.*

Annex 1. Some examples of studies that have demonstrated a dependency of African Penguins on food

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).

*Addendum: Extract from supplementary material for Sabarros et al. (2012).*

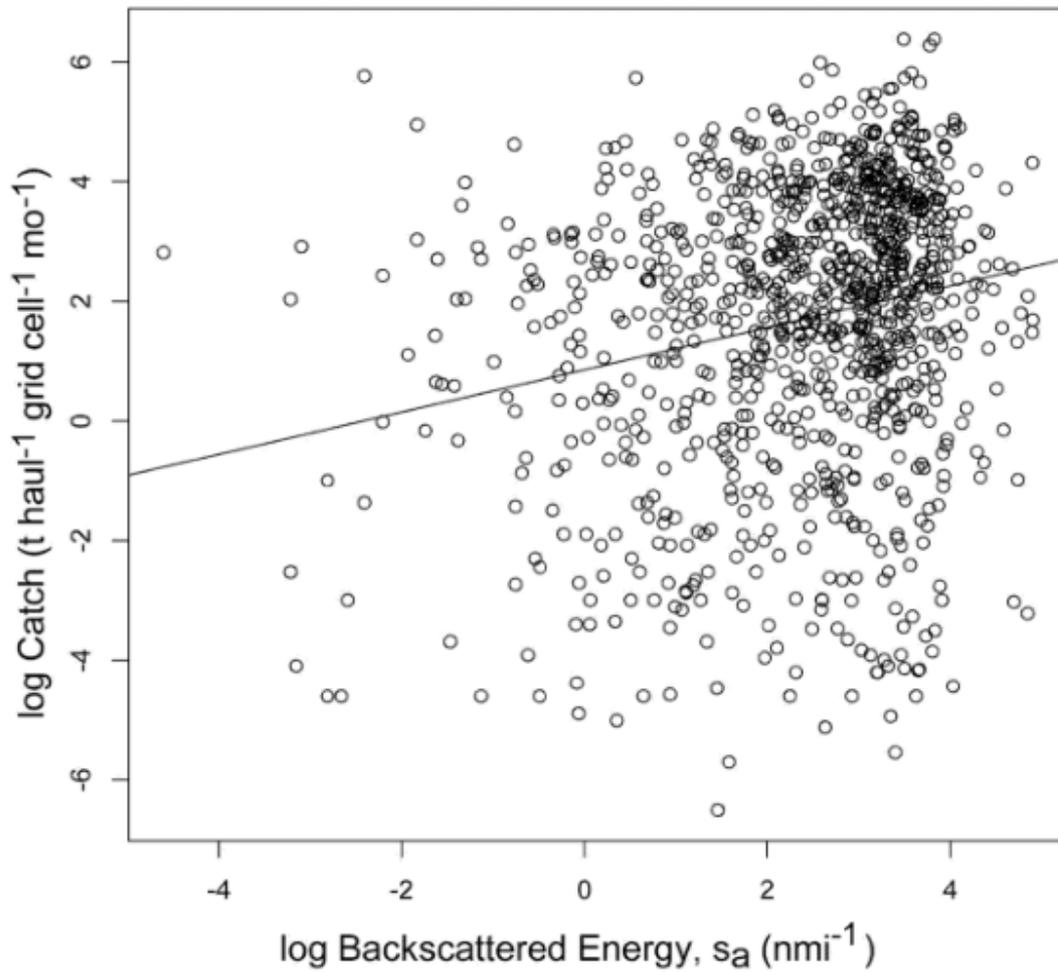


Fig. S2.2. Relationship between raw catch data and hydroacoustic data that concur in time and space

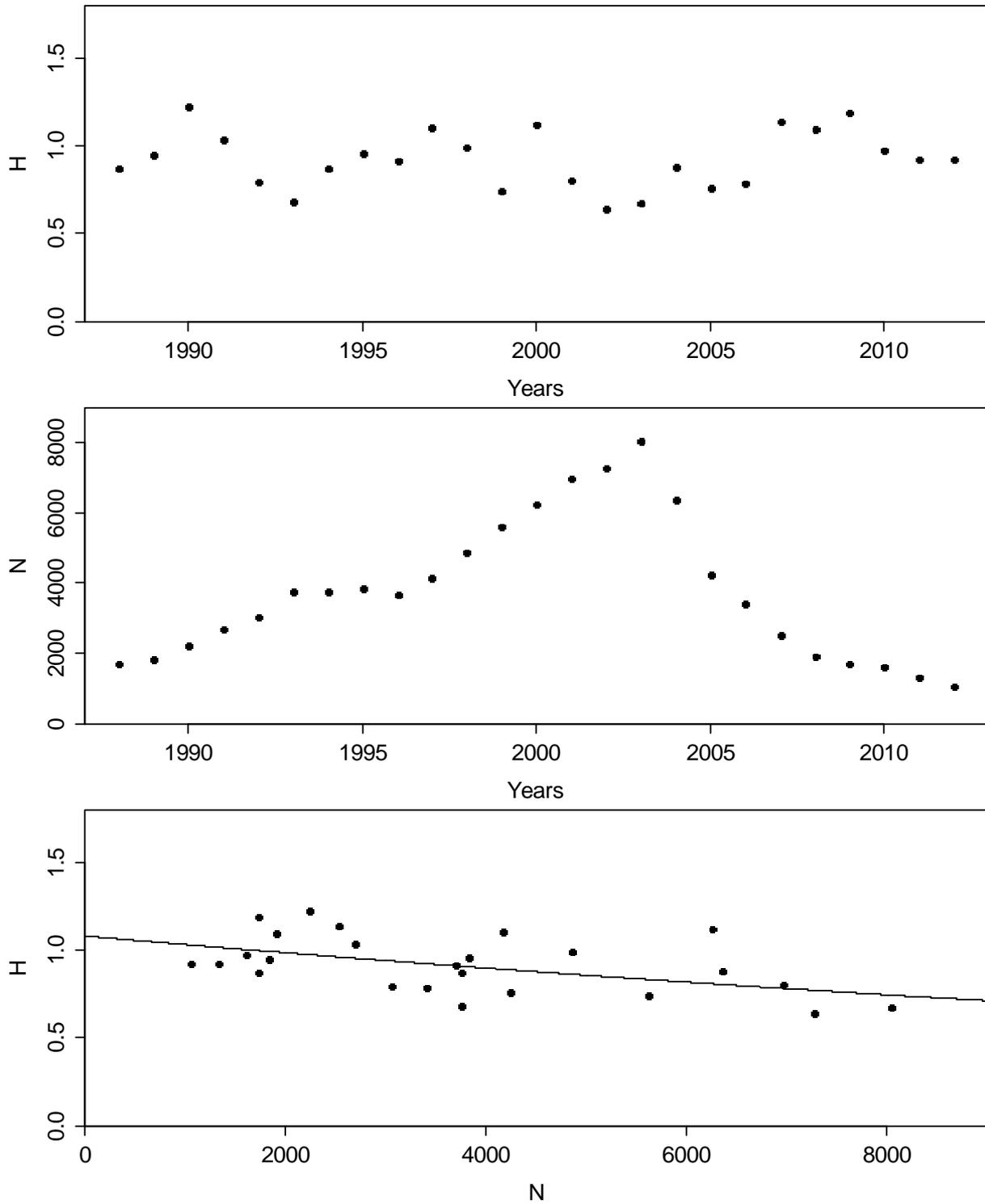


Fig Add.1: Top: Annual reproductive success  $H$ . Middle: Number of adult female penguins  $N$ . Bottom: Regression of  $\ln H$  versus  $N$ .