

**Comments on: Insufficient precautionary management of South Africa's
purse-seine fishery for conservation of the African Penguin
(FISHERIES/2013/SWG-PEL/ICTT/4) by Pichegru *et al.***

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This document provides comments on certain parts of FISHERIES/2013/SWG-PEL/ICTT/4 by L Pichegru, K Ludynia, AB Makhado, A McInnes, C Moseley, K Robinson, R Sherley, A Steinfurth, L Waller and RJM Crawford. To aid the reader, these have been inserted in the original text, but are shown in ***bold red italics*** for ease of identification. In the interests of a shorter document, parts of the original document without direct pertinence to the comments made have been excised.

The population of African Penguins *Spheniscus demersus* in South Africa decreased rapidly in the 21st century. This became a focus of substantial research, including by the Island Closure Task Team (ICTT) of the Small Pelagics Scientific Working Group (SWG-PEL) of Department of Agriculture, Forestry and Fisheries (DAFF). We document below some concerns regarding conservation of the African Penguin and make recommendations for a more precautionary management of South Africa's purse-seine fishery that will account for the species' food requirements.

Minimum viable populations

Based on observed rates of extinction of colonies of African Penguins, it was considered that the overall minimum viable population (MVP) for African Penguins was 50 000 pairs (Crawford et al. 2001). The overall population was above this level in 2001 (ca. 62 000 pairs), but it fell below it to ca. 48 000 pairs in 2005, 36 000 pairs in 2007 (Kemper et al. 2007), 26 000 pairs in 2009 (Crawford et al. 2011) and 23 000 pairs in 2012. Based on simulation modelling, MVPs of regional populations of African Penguins should be maintained above 10 000 pairs (Crawford et al. 2001). However, all three regional populations of the species are now below this level: ca. 9 800 pairs in Eastern Cape, ca. 8 900 pairs in Western Cape, ca. 4 600 pairs in Namibia.

As is acknowledged in the paper underlying these estimates (Shannon and Crawford, 1999), its conclusions as regards sustainability of harvests may be altered by the inclusion of density dependence in the model used. This same reservation would apply to estimates of MVPs. If MVP estimates are to play a key role in management decisions related to the penguin population, these analyses would first need to be refined to take density dependence into account and to use updated estimates of demographic parameters values

Food

In South Africa, anchovy and sardine contribute most of the diet of African Penguins in most years (Crawford et al. 2011). For each of the three regional populations of African Penguins, numbers breeding were significantly related to the biomass of sardine and anchovy (Crawford 2007, Crawford et al. 2011). For the Western Cape and Eastern Cape, these relationships are shown in Figure 3.

As time series for both penguins and fish are involved in these relationships, significance cannot be claimed on the basis of simple regression as requirements of independence are not met. Some form of model must first be applied to attempt to remove the autocorrelation effects. (This is not to say that there are no such relationships, only that this is an invalid approach to assess their statistical significance or otherwise.)

Cape Gannets *Morus capensis* also feed mainly on anchovy and sardine (Hockey et al. 2005). Off South Africa's west coast the monthly combined contribution of these two prey species to the diet of Cape Gannets decreased by $31 \pm 8\%$ between 1997–2003 and 2004–2012, suggesting a reduced availability to seabirds of these prey species west of Cape Point, the main foraging region of the gannets (Pichegru et al. 2007, Figure 4).

Certainly the reduction of sardine abundance over this period is well known from acoustic survey results, but the above appears also to claim a reduction in anchovy "availability", which does not similarly correlate with those survey results. Combining both species in Fig. 4 confounds species specific conclusions because of different preferences for these two prey species. It would therefore be desirable to see the prey species split in this Figure.

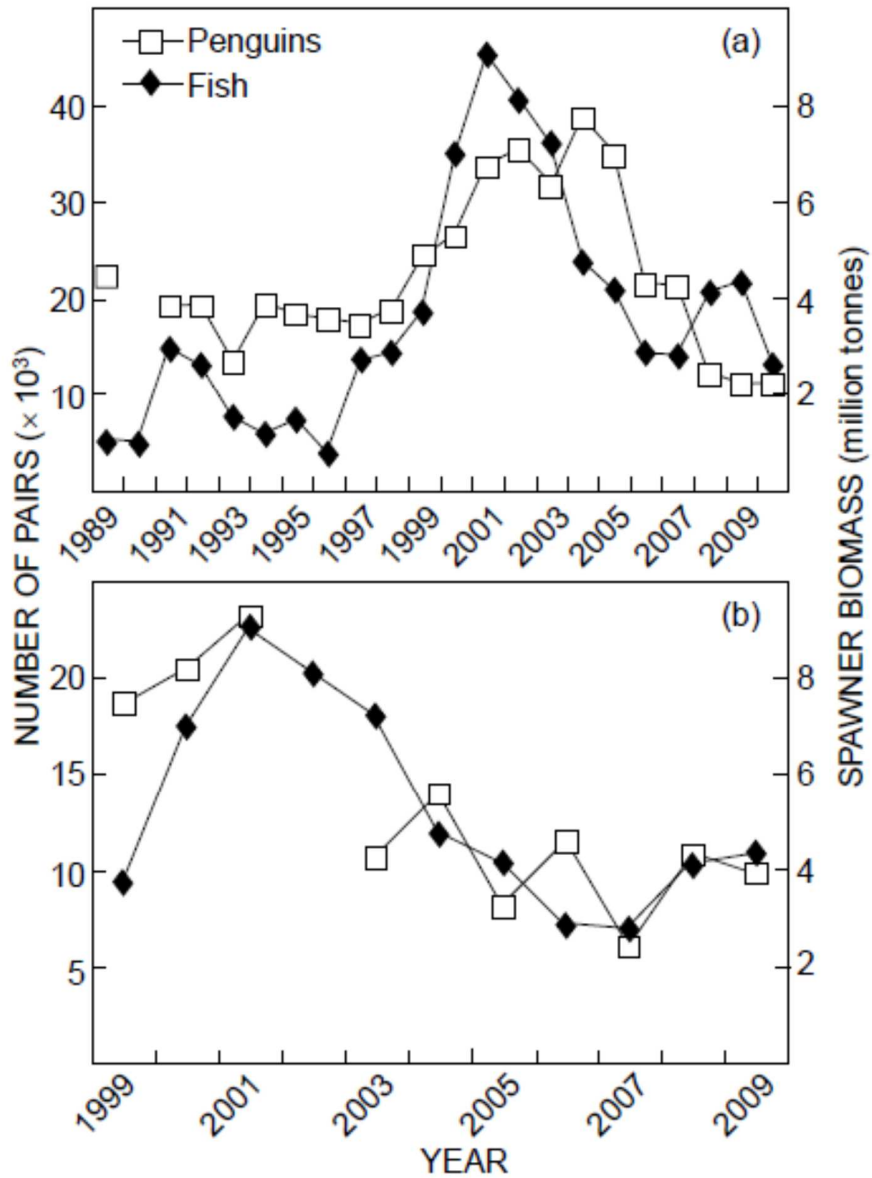


Figure 3: Comparison of trends in estimates of the combined spawner biomass of anchovy and sardine and numbers of nests occupied by African Penguins in (a) the Western Cape, 1989–2010 and (b) the Eastern Cape, 1999–2009 (from Crawford et al. 2011).

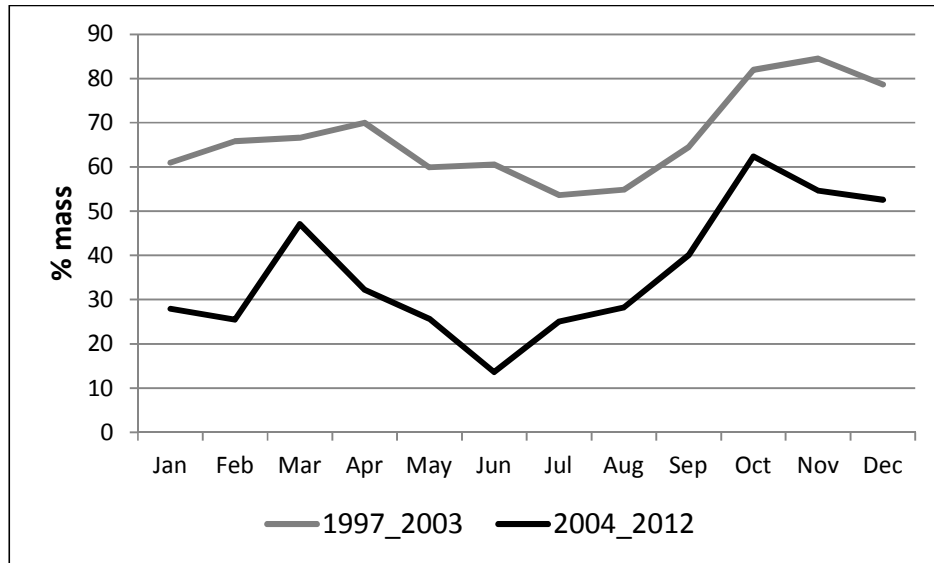


Figure 4: Average percent contribution by mass of anchovy and sardine (combined) to the diet of Cape Gannets breeding on South Africa's west coast by month for 1997–2003 and 2004–2012, showing the large decrease in these preferred prey items after 2003.

Energy needs, foraging behaviour and fishing catches

Energetic requirements

During the breeding season, in order to survive and raise one or two chicks, a pair of African Penguins needs to eat approximately 1.1 kg of small pelagic fish per day during the 38 days of the incubation period and 1.4 kg of fish per day over the four months of the chick-rearing period (calculation from Cook et al. in prep).

These needs roughly correspond to totals of 273 to 2 026 tons of fish within 20–40 km of each of the five colonies involved in the feasibility study (see Table 1) over the five months of the breeding season, and 3 210 tons of fish overall for five of the largest African Penguin colonies in South Africa.

Though naturally of general interest, given that these estimates are so small compared to the biomass and annual production of the major small pelagic species, their relevance to the questions at issue is unclear.

Table 1. Energy needs in tons of small pelagic fish for African Penguins breeding at the five colonies involved in the feasibility study, to survive and breed successfully during the breeding season.

	Dassen & Robben islands	Dyer Island	St Croix & Bird islands	Total
Penguin breeding pairs in 2012*	4 347	1 300	9 656	15 303
Fish needed per pair during the 38 d of incubation (kg)	1.1 x 38 = 41.8	41.8	41.8	
Fish needed per pair during the four months of the chick rearing period (kg)	1.4 x 30 x 4 = 168	168	168	
Fish needed per pair during the whole breeding season	168 + 41.8 = 209.8	209.8	209.8	
Fish needed per area during the breeding season (tons) (2 to 4 months season)	912	272.7	2 025.8	3 210.5

* from Crawford et al. (2012)

Such needs compete over small ranges (< 40 km) with the purse-seine fishery, which operates out of nearby harbours such as Saldanha, Hout Bay, Gansbaai and Port Elizabeth and removes 10 to 100 times that amount of fish in these areas (van der Lingen and van der Westhuizen 2012). The present competition is largely detrimental to the birds – there is clear evidence that in some places the energy spent by adults in searching for food significantly increases with increased fishing catches within 20 nm of the breeding locality, and decreases when a no-take zone is implemented (see below, Pichegru et al. 2010, 2012, Figure 5, Annex 2).

The Pichegru et al. referencing is unclear, as there are multiple documents for these years listed under References. To the extent that this intends to imply justification of the statements made by Pichegru et al. (2010a), it should be noted that that analysis has been comprehensively rebutted in Butterworth et al. 2011).

Fishing catches and exclusions around the penguin colonies

We tested the influence of the size of catches within 10, 20 and 30 nm the islands (data from van der Lingen and van der Westhuizen 2012 and updated for 2008 and for Dyer Island by CvdL) for each foraging parameters separately, using the entire dataset of GPS deployments, and not the averages per island. That way, our sample size is > 50 for each island. When all islands were tested together, the effect of fishing on foraging effort was either not significant or negative (i.e. decreased foraging effort with increased catches), usually becoming significant only with catches within 30 nm (see Annex 3).

Because the variability between islands in both foraging effort and fishing catches was high, it made biological sense to test each island separately. In order to estimate the strength of the

relationship between penguins' foraging effort and catches, results of regressions are shown in Table 2.

Foraging effort significantly increased with the size of catches only for birds from St Croix Island (Table 2), which emphasizes the importance of isolating St Croix Island from the feasibility study. Up to 25% of the variability in foraging path length and maximum distance and 12% of trip duration were explained by the size of catches. The strongest effect of the catches on the foraging behaviour of the St Croix birds was observed with catches within 20 nm of the colony.

The statistically significantly positive results claimed here for St Croix contrast with the lack of significance for similar results in Robinson and Butterworth (2013, Fig. A5). The reason appears to be that the analyses here have, in combining data over years, incorrectly treated these as independent. This conflicts with the view expressed by the lead author of this paper in Ryan et al. (2010) of the necessity that year effects (arising from interannual variations in fish abundance) be taken into account in such analyses, and hence that analyses of the type carried out (more recently also in Robinson and Butterworth (2013)) were incorrect. As pointed out in Butterworth et al. (2011) however, such analyses actually do take those effects into account, exactly as Ryan et al. (2010) insist to be necessary. Yet this paper, with a common author, proceeds to carry out such analyses without doing this. The correct procedure is as Ryan et al. (2010) originally suggested, which requires that the process error (additional variance) associated with year, or an associated related covariate such as one related to fish abundance, also be taken into account in such analyses, at the very least as a random effect. This will impact (likely substantially) the results of the tests of significance presented in Table 2 of the paper, which are invalidated by the non-independence of the data input because of this year-dependence.

For all the other islands, size of catches within 10–30 nm of the colonies had limited influence on the birds' foraging effort during the breeding season.

The significant interactions between foraging effort of birds from Bird Island, and to a lesser extent from birds from Dassen Island, were negatively correlated with catches within 10–30 nm of the colony, but the interactions remained weak ($r^2 \leq 10.3\%$). Foraging effort for birds from Robben and Dyer islands was not influenced by catches (all $P \geq 0.049$), except for a weak but positive relation between the maximum distance for Dyer birds, and between trip duration of birds from Robben, both increasing with catches within 10 nm of the island.

In Algoa Bay

Algoa Bay hosts > 50% of the South African penguin population, with St Croix Island being the world's largest African Penguin colony at present. Penguins breeding on St Croix Island show a direct negative effect of fishing on their behaviour, as well as a rapid decrease in effort spent at sea when fishing within their foraging area ceases. Trip duration, foraging path length and maximum distance all increase with the size of catches within 20 nm of the colony (Table 2). Their foraging dives also switch from outside the fishing exclusion zone when fishing is allowed

(2008, 2012) to largely inside the area when the exclusion is in place (2009–2011, Pichegru et al. 2012).

Table 2. Results of the regressions between foraging parameters and catches within 10, 20 and 30 nm of the colony. P gives the significance of the relation, t the direction (positive or negative) and r^2 the strength of the relation. Green colours highlight significant relationships, and orange colours highlight the strongest relationships.

		Trip duration (h)			Path length (km)			Max distance (km)		
		r-sq (adjusted)	t	P	r-sq (adjusted)	t	P	r-sq (adjusted)	t	P
Dassen	catches10	8.4	-3.17	0.002	0.1	-1.04	0.301	0	-0.89	0.373
	catches20	4.1	-2.29	0.024	3.8	-2.23	0.028	4.8	-2.44	0.016
	catches30	0	-0.96	0.337	5.8	-2.67	0.009	8.2	-3.13	0.002
Robben	catches10	5	2.38	0.02	3.6	2.06	0.042	1.4	1.49	0.141
	catches20	0	0.86	0.39	0	0.36	0.722	0	-0.05	0.957
	catches30	0.7	-1.28	0.203	2.4	-1.79	0.078	2.5	-1.8	0.076
Dyer	catches10	0	0.49	0.628	0	0.6	0.552	7.5	2.33	0.023
	catches20	0	0.41	0.687	0	0.62	0.538	4.2	1.84	0.071
	catches30	0	0.28	0.78	0	0.49	0.624	5.2	2.01	0.049
St Croix	catches10	5.9	2.73	0.007	25.6	6.01	0.0001*	12.3	3.92	0.0001*
	catches20	12.3	3.92	0.00001*	25.6	6.00	0.0001*	24.4	5.83	0.0001*
	catches30	9.8	3.49	0.001	6.3	2.79	0.006	16.4	4.59	0.0001*
Bird Island	catches10	4.7	-3.27	0.001	6.9	-3.94	0.0001*	0.7	-1.53	0.127
	catches20	6.9	-3.97	0.0001*	10.2	-4.81	0.0001*	1	-1.74	0.084
	catches30	6.7	-3.92	0.0001*	10.3	-4.83	0.0001*	1.1	-1.76	0.079

*, still significant after Bonferroni corrections, with $P < 0.001$.

At St Croix, the 20 km-radius fishing closure around the island is insufficient to offset the negative impacts of increases in fishery catches at the boundary of the reserve, i.e. “fishing the line”, as observed in 2010. The increase in catches in the vicinity of St Croix Island of 1 200 tonnes from 2009 to 2010 should be considered in the context of the penguins’ energetic needs: the 7 000 pairs of African Penguins breeding on St Croix Island in 2010 required roughly 1 000 tonnes of fish to maintain themselves through the breeding season and each raise a brood of two chicks (Nagy et al. 1984). The change in catches from 2009 to 2010 represents more than the total amount of food required by penguins breeding on St Croix Island.

The results inferences drawn here need further embellishment given that the fish catches made near the island are almost entirely of sardine (an average of 95% over the last five years), whereas the penguin diet reportedly consists almost entirely of anchovy (97% - Pichegru et al., 2012a).

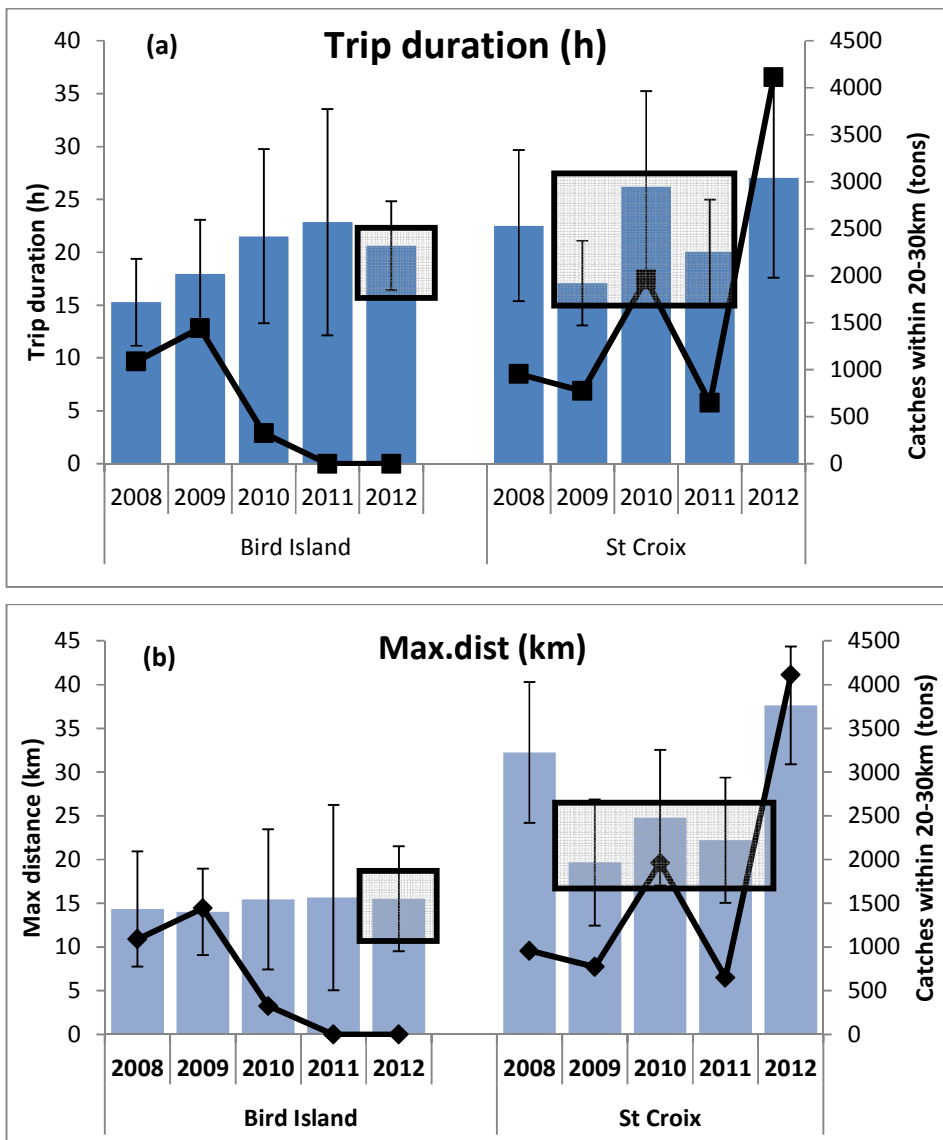


Figure 6: Average (\pm SD) trip duration (a) and maximum distance (b) from the colony of foraging chick-rearing penguins from Bird and St Croix islands in 2008–2012. The shaded squares show the durations of fishing exclusions around the two islands.

Opening the waters around St Croix Island to fishing in 2012 had disastrous consequences for this colony, with a major increase in foraging effort (Figure 6), as well as a decrease in breeding pairs, breeding success and chick growth (Pichegru et al. 2012b). In the light of these results, it is evident that a larger, more permanent purse-seine fishing exclusion zone is necessary for the recovery of the penguin colony on St Croix Island. Such a no-take zone should increase penguin numbers, as suggested by the steady increase in breeding success on St Croix Island during the time of the closure, with concomitant stable breeding numbers and chick growth rates, and reduced energy expenditure by the parents while foraging. Further analyses are needed to determine to which extent this closure could also increase adult and juvenile survival.

Given both the observation and process errors associated with the measurements made here, claims of strong definitive conclusions based on a single year comparison seem inadvisable – statistical analyses need to be offered.

No such difference was observed in the birds' behaviour when the exclusion was around Bird Island, likely because fishing pressure in that area is generally low, possibly due to its long distance from Port Elizabeth harbour. However, the foraging effort of penguins at Bird Island has increased continuously since 2008, independent of catches, suggesting on-going deterioration of the environment, and vulnerability of this colony to increases in fishery catches in its vicinity.

Recent deployment of PTTs on non-breeding penguins revealed that during the few weeks before moulting, penguins from Bird Island remained within Algoa Bay fairly close to their colony (C. Harding, Masters thesis). This finding suggests potential additional benefits of fishing exclusions around penguin colonies in Algoa Bay, as foraging areas of penguins outside their breeding season would be protected, likely increasing adult survival.

Conclusions

There is increasing evidence that the west and south coast populations should be seen separately. There are differences in the foraging patterns both during breeding and outside the breeding season and St Croix is the only island for which foraging effort of penguins increases as fish catches increase. Foraging effort is negatively correlated with catches within 30 nm of the colonies of Dassen and Bird islands, and is not correlated (or weakly but positively) on Dyer and Robben islands. The large movements of fish along the west coast probably preclude small fishing exclusions from significantly increasing food availability for penguins within their foraging range. Competition for food between seabirds and fisheries should therefore be controlled over a larger scale. Spatial management of fisheries is an urgent requirement to increase food availability for penguins.

Is it to be inferred from these statements that the authors of this paper now consider the current closed areas alternating around Robben and Dassen Islands to have no beneficial effect for penguins, and so merit discontinuation?

Breeding success

The relationship between breeding success of African Penguins in the Western Cape, and abundance of their main prey, anchovy and sardine, has recently been discussed by Sherley et al. (2013). The following is an excerpt from that paper. “During the late 1990s and early 2000s, both fish species increased markedly in abundance, but after 2004, sardine biomass decreased to below average levels. In addition, adults of both stocks were principally located to the east of Cape Agulhas from 2001 to 2009 and were thus distant from seabird colonies on South Africa’s West Coast. The number of African Penguin pairs counted at Robben Island from 2001 to 2009 and the fledging period of chicks from successful nests increased and decreased in apparent response to the biomass of sardine prior to each breeding season, possibly linked through adult condition at the onset of breeding. [The latter relationship has been tested up to 2012 and holds with the additional years added to the dataset (Sherley 2012)]. Breeding success and chick-fledging rates increased during the study period and showed positive relationships with local food availability, indexed through the annual industrial catch of anchovy made within 56 km (30 nautical miles) of the colony. In addition, chick-fledging rates were depressed in 2-chick broods during years when anchovy contributed < 75% by mass to the diet of breeding birds. Previously reported relationships between the overall abundance of forage fish in South Africa and penguin breeding success were not supported.” [These earlier relationships applied to information collected before or during the early stages of the eastward shift in pelagic prey species.] “Taken together, these results highlight the combined importance of ensuring adequate local food availability for seabirds during the reproductive cycle and safeguarding regional prey abundance during the non-breeding season.”

A similar interaction between local and regional prey availability was reported for Dassen Island by Durant et al. (2010): “At Dassen Island, the proportion of burrows occupied for breeding by African penguins from 1995 to 2008 was affected positively by the interaction between the overall biomass of sardine and anchovy. However, sardine had a positive effect while anchovy had a negative one. This unexpected negative relationship may result from a reduced local availability of anchovy linked to the fishing effort that continued to be focussed in the vicinity of Dassen Island, while the growing anchovy stock experienced an eastward shift away from Dassen Island in recent years, creating a spatial mismatch between penguin and available anchovy.”

Based on studies on other seabird species (references given in Sherley et al. 2013), the relationships noted by Durant et al. (2010) and Sherley et al. (2013) are thought to be mediated through the body condition that adult penguins are able to acquire prior to breeding and maintain during the energetically expensive chick-rearing period (Sherley et al. 2013). Having good body condition prior to breeding may be insufficient to ensure the survival of an adult and its brood if conditions around the colony are poor or mediocre once breeding has commenced. However, if local prey resources are abundant, birds initiating breeding in good condition need to invest less in self-maintenance and could invest more energy in increasing the body condition of their brood

prior to fledging. Similarly, adults in poorer condition at the onset of breeding may be able to successfully rear their chicks and recover some of their own body condition simultaneously.

Pre-fledging mass (one measure of a chick's body condition) can influence first year survival in penguins (Olsson 1997), which will in turn influence recruitment rates. As juvenile African Penguins appear to disperse quickly away from breeding colonies (Sherley et al. in review), and thus are not reliant on prey close to breeding colonies once fledged, their first year survival could also reasonably be considered to rely on a combination of local and regional prey availability.

Given the above, the demographic response to increasing prey availability around breeding colonies might be expected to be slow (e.g. require many years for a measureable effect on adult and juvenile survival) if the abundance of adult fish available to African Penguins during the non-breeding season remains low with the stocks displaced to the east of Cape Agulhas.

It is not exactly clear what is meant here by “juvenile survival” – if from hatching to first birthday, then this conclusion about juvenile survival is at variance with what is said in the preceding paragraph.

Island closure feasibility study

In 2007, SWG–PEL approved an island closure feasibility study with aim to evaluate the power of a long-term experiment to detect the effects of fishery closures around penguin colonies on penguin life-history parameters and foraging behaviour. Broad trends from this study to date have been summarized by Robinson and Butterworth (2013), who noted that:

“When biomass is used rather than estimating a year factor separately for each year, relationships of reproduction and survival rates to pelagic biomass are nearly all positive. Estimates of the impact of additional fishing on penguin parameters related to reproduction are preponderantly positive rather than negative. Estimates of this impact on penguin survival rates are near equally split between positives and negatives.”

These results are not substantially different from those reported above, i.e. that survival and reproductive success are related to regional and local food availability and that local food availability can be indexed by fish catches on the west coast. What is important to penguins is the density of food they encounter and the distance they have to travel to find it. It has been recognised that measures of the local density of fish around islands will be of importance (e.g. Merkle et al. 2012), but unfortunately these small-scale surveys are still of relatively short duration and have not been considered in the feasibility study. Adult survival will be influenced by the condition of birds at the conclusion of breeding and the probability that they will be able to gain sufficient energy reserves in order to complete a successful moult, which in turn will depend upon the distance of suitable food from the breeding colony. A recent study showed that penguins from the west coast of South Africa covered >400 km in search for food during the pre-moult period (C. Harding, MSc thesis), stressing the importance of adequate food supplies for penguins over large areas. African Penguins do not feed for about three weeks when moulting, in which period they replace all their feathers (Hockey et al. 2005). At the end of moult, few energy reserves remain, which if not rapidly replenished may cause mortality.

The final design of the feasibility study was agreed by consensus and was not based on the ornithologists' best understanding of the biology of African Penguins. In particular, it was noted that the longevity of penguins, their delayed age at breeding and the long periods over which processes such as recruitment to colonies were expected to operate required long-term closures around colonies (see e.g. Crawford 2010, Pichegru et al. 2010b, Wanless and Moseley 2010) rather than rapid alternations of closures between "paired colonies", which were favoured in order to provide estimates of process error (Butterworth 2010). Therefore, the inconclusive results of the feasibility study to date are not entirely unexpected.

None of the arguments made here to support long-term closures are in any way clear. The mechanisms suggested need to be elaborated in mathematical form so that it is evident exactly what they are suggested to be and how they are proposed to operate, so that their plausibility can be properly assessed. This is a pre-requisite to any attempted justification of the final statement made.

Although a case can still be made for continued experimental closures to provide the contrast for more precise estimation of the effects of interest (Robinson and Butterworth 2013), only poor catches have been effected around Bird Island since that locality has been open to fishing. We point out again that reproductive success of African Penguins does not depend only on fish availability but also climate (e.g. heat, flooding) and these factors also should be considered.

Extra factors can certainly be considered, but that first requires that time series of the associated data be available (none were offered in the data provision discussions that initiated recent updated analyses). Even if these data are available, it does not necessarily follow that inferences will be improved by taking them into account in the analyses – model selection criteria would need to be applied in assessing the associated bias-variance trade-off in estimating additional parameter values.

Recommendations

Given the continued worsening conservation status of the African Penguin, we recommend a more precautionary approach to addressing the food requirements of African Penguins, which would aim:

1. Further to explore the effectiveness of long-term closures around breeding localities in improving the conservation status of the African Penguin by reverting to a long-term closure around St Croix Island and extending that closure to have a radius of 20 nm. In this regard it is of interest to note that the present best-performing colonies in the Western Cape (Boulders, Stony Point) are within or near to an area of permanent closure (False Bay). As St Croix Island now has South Africa's largest colony of African Penguins it is important to give it full protection;

In circumstances where the great majority (some 80%) of the relationships investigated in Robinson and Butterworth (2013) are suggestive (though not always significantly

so) of positive rather than negative impacts of fishing on penguin reproductive success, how can this conclusion be rationalised?

2. Maintaining sardine biomass west of Cape Agulhas above the threshold at which mortality rapidly increases (survival rapidly decreases) by adjusting quotas according to biomass measured during annual acoustic surveys and implementing spatial management of the fisheries. This presently falls inside the mandate of the ICTT and the Task Team should further explore it;

This is already being explored by the PSWG as a part of the small pelagics OMP revision process. However, the above seems to suggest that some variant of a constant escapement harvesting strategy must necessarily be used. Given the stochastic aspects of the situation, and the objective (amongst others) of more rather than less variable TACs from year to year, there seems no reason for such a restriction; rather alternative harvesting strategies should continue to be evaluated on the basis of their comparative behaviour in terms of pre-agreed performance statistics, rather than based on a priori design considerations which do not guarantee optimal results.

3. Move from a feasibility study to an experimental study in the Western Cape, where time series of information are accumulating, including of fish density during the breeding season. In this study, both fish availability and other factors that influence reproductive success should be accounted for. However, closures should be implemented for a longer time period (i.e. > 5 years) in order to detect impacts on penguin populations and demography.

There is an existing procedure to determine whether and when to move from the current feasibility study to a full experiment in the Western Cape, but as indicated above comments made in this paper seem to suggest that the authors consider that impacts of fishing near Robben and Dassen islands on reproductive success are unlikely. It is unclear here whether continuation of some variant of the existing exercise is being suggested, or something entirely different. Furthermore the issues associated with taking other factors into account have been explained above. Before considering this further, it is necessary that what is proposed is set out in much more detail, and subjected to prior statistical analysis as to the likelihood of yielding meaningful results within a realistic time period.

References

- Berruti A, Underhill LG, Shelton PA, Moloney C, Crawford RJM. 1993. Seasonal and interannual variation in the diet of two colonies of the Cape Gannet *Morus capensis* between 1977/1978 and 1989. Colonial Waterbirds 16: 158–175.
- Butterworth DS. 2010. On whether to alternate between pairs of islands in the penguin feasibility study. MCM/2010/SWG_PEL/Island Closure Task Team/20: 2 pp.
- Coetzee JC, van der Lingen CD, Hutchings L, Fairweather TP. 2008. Has the fishery contributed to a major shift in the distribution of sardine? ICES Journal of Marine Science 65: 1676–1688.

- Cook T, Reid T, Ryan PG, Grémillet D, Ropert-Coudert Y, Crawford RJM, Pichegru L. in prep. Seabirds' temporal and spatial requirements in the Benguela upwelling ecosystem: insights for an ecosystem approach to fisheries.
- Crawford RJM. 2007. Food, fishing and seabirds in the Benguela upwelling system. *Journal of Ornithology* 148 (Suppl 2): S253–S260.
- Crawford RJM. 2010. Trialling fishing closures as a means to ensure food security for African Penguins – considerations regarding their alternation. MCM/2010/SWG_PEL/Island Closure Task Team/23: 5 pp.
- 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 21st century: a consideration of food availability. *African Journal of Marine Science* 33: 139–156.
- Crawford RJM, David JHM, Shannon LJ, Kemper J, Klages NTW, Roux J-P, Underhill LG, Ward VL, Williams AJ, Wolvaardt AC. 2001. African Penguins as predators and prey – coping (or not) with change. *South African Journal of Marine Science* 23: 435–447.
- Crawford RJM, Dyer BM, Fox R, Geldenhuys D, Leshoro TM, Makhado AB, McGeorge C, Pichegru L, Sherley R, Upfold L, Visagie J, Waller LJ. 2012. Numbers of African Penguins breeding in South Africa, 2000–2012. FISHERIES/2012/SWG-PEL/ICTT/4: 6 pp.
- Crawford RJM, Shannon LJ, Whittington PA. 1999. Population dynamics of the African Penguin at Robben Island. *Marine Ornithology* 27: 135–143.
- Crawford RJM, Tree AJ, Whittington PA, Visagie J, Upfold L, Roxburg[h] KJ, Martin AP, Dyer BM. 2008. Recent distributional changes of seabirds in South Africa: is climate having an impact? *African Journal of Marine Science* 30: 189–193.
- 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.
- De Moor CL, Butterworth DS, Coetzee JC. 2008. Revised estimates of abundance of South African sardine and anchovy from acoustic surveys adjusting for echosounder saturation in earlier surveys and attenuation effects for sardine. *African Journal of Marine Science* 30: 219–232.
- Distiller G, Altwegg R, Crawford RJM, Klages NTW, Braham B. 2012. Factors affecting adult survival and inter-colony movement at the three South African colonies of Cape Gannet. *Marine Ecology Progress Series* 461: 245–255.
- Durant JM, Crawford RJM, Wolvaardt AC, Agenbag K, 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.
- Grémillet D, Pichegru L, Kuntz G, Woakes AG, Wilkinson S, Crawford RJM, Ryan PG. 2008. A junk-food hypothesis for gannets feeding on fishery waste. *Proceedings of the Royal Society, London Biological Series* 18: 1–8.
- Harding C. Msc Thesis. Distribution of African penguins during their pre-moult period.
- Hockey PAR, Dean WRJ, Ryan PG. 2005. *Roberts birds of southern Africa*, 7th edn. Cape Town: John Voelcker Bird Book Fund.
- IUCN 2011. IUCN Red List of Threatened Species. Version 2011.1. <www.iucnredlist.org>. Downloaded on 24 October 2011.
- Kemper J, Underhill LG, Crawford RJM, Kirkman SP. 2007. Revision of the conservation status of seabirds and seals breeding in the Benguela ecosystem. In: Kirkman SP (Ed.) Final Report

- of the BCLME (Benguela Current Large Marine Ecosystem) Project on Top Predators as Biological Indicators of Ecosystem Change in the BCLME. Avian Demography Unit, Cape Town, pp 697–704.
- Merkle D, Coetzee J, Mushanganyisi K, Rademan J. 2012. Small scale hydro-acoustic surveys 2012. Fisheries/2012/SWG-PEL/ICTT/9: 9 pp.
- Nagy KA, Siegfried WR, Wilson RP. 1984. Energy utilization by free-ranging Jackass Penguins, *Spheniscus demersus*. Ecology 65: 1648–1655.
- Olsson O. 1997. Effects of food availability on fledging condition and post-fledging survival in king penguin chicks. Polar Biology 18: 161–165.
- Petersen SL, Ryan PG, Grémillet D. 2006. Is food availability limiting African Penguin *Spheniscus demersus* at Boulders? A comparison of foraging effort at mainland and island colonies. Ibis 148: 14–26.
- Pichegru L, Cook T, Handley J, Voogt N, Nupen L, Watermeyer J, McQuaid CD. 2013. Sex-specific foraging behaviour and a field sexing technique for Endangered African Penguin. Endangered Species Research DOI: 10.3354/esr00477.
- Pichegru L, Grémillet D, Crawford RJM, Ryan PG 2010a. Marine no-take zone rapidly benefits endangered penguin. Biology Letters 6: 498–501.
- Pichegru, McInnes A, Ryan PG (2012b) Monitoring the effect of closing to fishing areas around African penguin breeding colonies in Algoa Bay - Report from field season 2012. Fisheries/2012/SWG-PEL/ICTT/1b.
- Pichegru L, Ryan PG, Steinfurth A. 2010b. Experimental closures around African Penguin colonies – justification for retaining the same closures in 2011. MCM/2010/SWG_PEL/Island Closure Task Team/22: 4 pp.
- Pichegru L, Ryan PG, van der Lingen CD, Coetzee J, Ropert-Coudert Y, Grémillet D. 2007. Foraging behaviour and energetics of Cape Gannets *Morus capensis* feeding on live prey and fishery discards in the Benguela upwelling system. Marine Ecology Progress Series. 350: 127–136.
- Pichegru L, Ryan PG, van Eeden R, Reid T, Grémillet D & Wanless R (2012a) Industrial fishing, no-take zones and endangered penguins. *Biological Conservation*. 156 : 117-125
- Robinson W, Butterworth DS. 2012. Projections of the Robben Island African Penguin population. Fisheries/2012/Nov/SWG-PEL/62: 1–6.
- Robinson W, Butterworth DS. 2013. GLMs relating penguin demographics and foraging behaviour to forage fish abundances. Fisheries/2013/SWG-PEL/ICTT/03: 1–47.
- Shaw KA, Waller LJ, Crawford RJM, Oosthuizen WH (eds) 2011. Proceedings of the African Penguin BMP-s Stakeholder Workshop 26-28 October 2010, Die Herberg, Arniston, South Africa. CapeNature, Stellenbosch. pp 1–57.
- Shannon LJ, Crawford RJM. 1999. Management of the African Penguin *Spheniscus demersus* – insights from modelling. Marine Ornithology 27: 119–128.
- 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. 2010. Update on the breeding productivity of African Penguins (*Spheniscus demersus*) on Robben Island. FISHERIES/2012/SWG-PEL/ICTT/06.

- Sherley RB, Ludynia K, Lamont T, Roux J-P, Crawford RJM, Underhill LG. In review. The initial journey of an endangered penguin: implications for seabird conservation. *Endangered Species Research*.
- Steinfurth A, Robinson K. 2012. Foraging strategies and energetic requirements of African Penguins in the Western Cape: An approach to fisheries and ecosystem management. FISHERIES/2012/SWG-PEL/ICTT/1a: 9 pp.
- Van der Lingen CD, van der Westhuizen 2012. Catches of sardine and anchovy around four penguin-breeding colonies, 2009–2012. FISHERIES/2012/NOV/SWG-PEL/ICTT/10: 10 pp.
- Waller L, Geldenhuys D, Ludynia K. 2012. Preliminary Summary of Foraging Areas of Breeding African Penguins at Dyer Island FISHERIES/2012/SWG-PEL/ICTT/1c: 1 p.
- Wanless R, Moseley C. 2010. Arguments in favour of maintaining the closures around Dassen and St Croix islands. MCM/2010/SWG_PEL/Island Closure Task Team/24: 2 pp.
- Wolfaardt AC, Underhill LG, Altwegg R, Visagie J. 2008. Restoration of oiled African Penguins a decade after the Apollo Sea spill. *African Journal of Marine Science* 30: 421–426.

Additional References in Comments

- Butterworth, D.S., Brandão, A., de Moor, C.L. and Robinson, W. 2011. Claim by Pichegru et al. that marine no-take zone benefits penguins remains premature.
http://rsbl.royalsocietypublishing.org/content/6/4/498.abstract/reply#roybiolett_el_82***
- Ryan, P.G., Pichegru, L. and Gremillet, D. 2010. Parlous conservation status of African Penguins provides the correct wider context.
<http://rsbl.royalsocietypublishing.org/content/early/2010/02/04/rsbl.2009.0913.abstract/reply#content-block>***
- Shannon, L.J. and Crawford, R.J.M. 1999. Management of the African Penguin *Spheniscus demersus* – insights from modelling. *Marine Ornithology* 27: 119-128.***

ANNEX 3. GENERAL LINEAR MODELS TESTING THE EFFECT OF FISHING CATCHES WITHIN 10, 20, 30 NM OF THE COLONY ON THE FORAGING PARAMETERS OF BREEDING PENGUINS.

I- All islands are tested together

1- Trip duration

a- General Linear Model: TripDur versus catches 10

Factor Type Levels Values

Analysis of Variance for TripDur, using Adjusted SS for Tests

Source	DF	Seq SS	Adj SS	Adj MS	F	P
catches1	1	98.5	98.5	98.5	0.77	0.382
Error	548	70470.8	70470.8	128.6		
Total	549	70569.3				

Term	Coef	SE Coef	T	P
Constant	20.1424	0.5576	36.12	0.000
catches1	-0.000105	0.000120	-0.88	0.382

b- General Linear Model: TripDur versus catches 20

Factor Type Levels Values

Analysis of Variance for TripDur, using Adjusted SS for Tests

Source	DF	Seq SS	Adj SS	Adj MS	F	P
catches2	1	1628.8	1628.8	1628.8	12.95	0.000
Error	548	68940.4	68940.4	125.8		
Total	549	70569.3				

Term	Coef	SE Coef	T	P
Constant	21.2340	0.6052	35.08	0.000
catches2	-0.000120	0.000033	-3.60	0.000

c- General Linear Model: TripDur versus catches 30

Factor Type Levels Values

Analysis of Variance for TripDur, using Adjusted SS for Tests

Source	DF	Seq SS	Adj SS	Adj MS	F	P
catches3	1	4297.7	4297.7	4297.7	35.54	0.000
Error	548	66271.6	66271.6	120.9		
Total	549	70569.3				

Term	Coef	SE Coef	T	P
Constant	22.1341	0.6003	36.87	0.000
catches3	-0.000100	0.000017	-5.96	0.000

2- Path length

a- General Linear Model: PathLength versus catches 10

Factor Type Levels Values

Analysis of Variance for PathLeng, using Adjusted SS for Tests

Source	DF	Seq SS	Adj SS	Adj MS	F	P
catches1	1	4704	4704	4704	4.20	0.041
Error	541	606050	606050	1120		
Total	542	610755				

Term	Coef	SE Coef	T	P
Constant	58.068	1.657	35.04	0.000
catches1	0.000738	0.000360	2.05	0.041

b- General Linear Model: PathLength versus catches 20

Factor Type Levels Values

Analysis of Variance for PathLeng, using Adjusted SS for Tests

Source	DF	Seq SS	Adj SS	Adj MS	F	P
catches2	1	456	456	456	0.40	0.525
Error	541	610299	610299	1128		
Total	542	610755				

Term	Coef	SE Coef	T	P
Constant	60.474	1.826	33.12	0.000
catches2	-0.000064	0.000101	-0.64	0.525

c- General Linear Model: PathLength versus catches 30

Factor Type Levels Values

Analysis of Variance for PathLeng, using Adjusted SS for Tests

Source	DF	Seq SS	Adj SS	Adj MS	F	P
catches3	1	14746	14746	14746	13.39	0.000
Error	541	596009	596009	1102		
Total	542	610755				

Term	Coef	SE Coef	T	P
Constant	63.940	1.826	35.02	0.000
catches3	-0.000186	0.000051	-3.66	0.000

3- Maximum distance

a- General Linear Model: MaxDist versus catches 10

Factor Type Levels Values

Analysis of Variance for MaxDist, using Adjusted SS for Tests

Source	DF	Seq SS	Adj SS	Adj MS	F	P
catches1	1	44.4	44.4	44.4	0.39	0.534
Error	543	62375.2	62375.2	114.9		
Total	544	62419.6				

Term	Coef	SE Coef	T	P
Constant	18.4261	0.5300	34.77	0.000
catches1	0.000072	0.000115	0.62	0.534

b- General Linear Model: MaxDist versus catches 20

Factor Type Levels Values

Analysis of Variance for MaxDist, using Adjusted SS for Tests

Source	DF	Seq SS	Adj SS	Adj MS	F	P
catches2	1	767.2	767.2	767.2	6.76	0.010
Error	543	61652.5	61652.5	113.5		
Total	544	62419.6				

Term	Coef	SE Coef	T	P
Constant	19.5149	0.5786	33.73	0.000
catches2	-0.000083	0.000032	-2.60	0.010

c- General Linear Model: MaxDist versus catches 30

Factor Type Levels Values

Analysis of Variance for MaxDist, using Adjusted SS for Tests

Source	DF	Seq SS	Adj SS	Adj MS	F	P
catches3	1	3946.4	3946.4	3946.4	36.65	0.000
Error	543	58473.3	58473.3	107.7		
Total	544	62419.6				

Term	Coef	SE Coef	T	P
Constant	20.7498	0.5699	36.41	0.000
catches3	-0.000096	0.000016	-6.05	0.000