

1 **Food for Thought**

2  
3 **South Africa's experimental fisheries closures and recovery of the**  
4 **endangered African penguin**

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22

23 Abstract. In a scientifically-transformative project, South Africa implemented a decade-long  
24 field experiment to understand how fisheries may be affecting its most iconic seabird, the  
25 African penguin *Spheniscus demersus*. This unique effort prohibits the take of anchovy and  
26 sardine within relatively small areas around four African penguin breeding colonies, two in the  
27 Benguela upwelling ecosystem and two in the adjacent Agulhas region. For the Benguela,  
28 fisheries closures within the birds' primary foraging range increased their breeding productivity  
29 and perhaps reduced parental foraging efforts, indicating that the fisheries are competing with the  
30 birds for food. Results were less clear for foraging behaviour in the Agulhas, but no data on  
31 breeding success was collected there. The African penguin is endangered and its population  
32 continues to decline, and fisheries closures have been demonstrated improved demographic traits  
33 that clearly contribute to population growth. Therefore, given the critical conservation status of  
34 the species, fisheries closures should be maintained, at least at Dassen Island where the  
35 population has great capacity to expand and support other nearby colonies. Continuing or  
36 implementing corresponding fisheries closures in the Agulhas region, as well as creating and  
37 testing the value of pelagic closed areas during the non-breeding season when the penguins  
38 disperse widely across these ecosystems, also is warranted. These management actions would  
39 increase penguin food supplies and help to meet societal goals of halting the decline of the  
40 penguin population, as well as maintaining the economic and cultural services provided by  
41 fisheries and ecotourism.

42

43 Keywords: forage fish, anchovy, sardine, seabirds, conservation, societal conflicts, field  
44 experiment

45

46 Main Text

47 A long-term and growing issue in marine ecosystem conservation and management concerns the  
48 simultaneous use in time and space of small pelagic fish and euphausiid crustaceans by industrial  
49 fisheries and marine wildlife, which may cause local- to regional-scale competition, and reduce  
50 prey availability to predators (Croll and Tershy, 1998; Smith *et al.*, 2011; Pikitch *et al.*, 2012,  
51 2014; Sydeman *et al.*, 2017, Gremillet *et al.*, 2018). Fisheries' reductions in available prey can  
52 affect foraging behaviour and effort, rates of energy acquisition, and eventually population  
53 parameters such as breeding success or recruitment. This problem is particularly severe for  
54 seabirds during reproduction when they are constrained to forage relatively close to colonies by  
55 offspring provisioning duties (Furness, 1982; Duffy and Schneider, 1994; Tasker *et al.*, 2000;  
56 Sydeman *et al.*, 2017; Free *et al.*, 2021). The daily metabolic requirements of seabirds during  
57 breeding when parents are feeding themselves and developing offspring are amongst the largest  
58 (proportional to body mass) estimated for marine vertebrates.

59

60 **African penguins and food supplies**

61 The most significant ongoing example of this issue concerns the critically-imperiled African  
62 penguin *Spheniscus demersus*, which has suffered population fragmentation and a >95% decline  
63 over the past century (Sherley *et al.*, 2020). It is now classified as endangered by the  
64 International Union for Conservation of Nature (Birdlife International, 2020) and is one of three  
65 most vulnerable penguin species (Boersma *et al.*, 2020). A combination of climate change and  
66 fisheries removals has reduced the availability of the penguins' primary food resources,  
67 including sardines *Sardinops sagax* and anchovies *Engraulis encrasicolus* in Namibia and South  
68 Africa (Coetzee *et al.*, 2008; Roux *et al.*, 2013; Crawford *et al.*, 2015; Sherley *et al.*, 2017;

69 Crawford *et al.*, 2019). This decline in prey abundance has reduced the survival rates of adult  
70 and juvenile penguins, most acutely since 2000 (Sherley *et al.*, 2014, 2017; Robinson *et al.*,  
71 2015). Recent adult survival estimates for African penguin (Sherley *et al.*, 2014; Robinson *et al.*,  
72 2015) are extremely low in comparison other seabirds in general (Hamer *et al.*, 2001; Appendix  
73 2 in Schreiber and Burger, 2001; Table S1 of Bird *et al.*, 2020), and food stress-related changes  
74 in survival and recruitment is believed to be the primary mechanism underpinning the population  
75 collapse.

76

### 77 **The fisheries experiment**

78 In response to the steep decline of its most iconic seabird, government agencies, conservationists,  
79 and academics with expertise in seabird ecology and fisheries science collaborated to implement  
80 a carefully-planned and unprecedented ocean field experiment along the Western and Eastern  
81 capes of South Africa. This experiment was designed to i) determine whether the fisheries were  
82 affecting the penguins through food resource limitation, and ii) investigate if chick survival and  
83 other proxies for penguin breeding productivity could be enhanced using fisheries time-area  
84 closures, a standard fisheries management technique (e.g., Dunn *et al.*, 2011). Time-area  
85 closures remove specific locations from fishing pressure during selected times. They may  
86 thereby minimize potential fisheries competition with marine wildlife during periods of  
87 biological significance, such as the chick-rearing period for seabirds when parents are  
88 provisioning themselves as well as developing offspring, and are spatially-constrained to central-  
89 place foraging where natural competition for prey is generally high (Burke and Montevicchi,  
90 2009; Weber *et al.*, 2021).

91           The experiment focused on four penguin colonies, two along South Africa's Western  
92 Cape at Dassen and Robben islands, and two along the Eastern Cape at Bird and St. Croix  
93 islands (Figure 1). Fisheries targeting anchovies and/or sardines were alternately closed within  
94 the typical penguin foraging radius (20 km) at each island. For the Western Cape, fisheries at  
95 Dassen Island were closed from 2008–2009 (inclusive) and again from 2014–2016; closures at  
96 Robben Island were implemented from 2011–2013 and again from 2017–2019. This unusual  
97 Before and After Control Impact (BACI) design, with replication and reference colonies, has  
98 provided informative and compelling results.

99

#### 100 **Chick survival**

101 Survival of penguin offspring was studied within the central portion of the highly productive, yet  
102 extremely variable Benguela upwelling system (Fig. 1). On Dassen and Robben islands, the  
103 African penguin once numbered over 300,000 breeding pairs, but today fewer than 3,500 remain,  
104 which currently represents ~20% of the world's population (Sherley *et al.*, 2020). While forage  
105 fish abundance off the Western Cape varied substantially among the years of experimental time-  
106 area closures, survival of penguin chicks to the age of fledging, the key population parameter  
107 under scrutiny, increased during years when fishing was excluded from the foraging areas of  
108 breeding penguins (Sherley *et al.*, 2018; Sherley, 2020, Supplementary Materials). While the  
109 exact effect sizes ranged from ~2% to ~11% depending on model structure (Supplemental  
110 Materials), population models suggest that this increase in chick survival is sufficient to improve  
111 the penguin population growth rate by ~0.5–1.2% per annum (Sherley *et al.*, 2018; OLS  
112 Marine, 2021; Ross-Gillespie and Butterworth, 2021). While other interventions also are  
113 required to increase the penguin's population growth rate, these analyses clearly demonstrate that

114 1) the forage fish fisheries operating in proximity to breeding colonies are competing with the  
115 penguins for food and 2) permanent fisheries closures could offset ~20% of the penguin  
116 population decline which has averaged ~5% per annum (Sherley *et al.*, 2020). Given the high  
117 temporal and spatial variability in forage fish abundance (DFFE, 2021), and recent poor  
118 accessibility of some prey, notably anchovies (e.g., Crawford *et al.*, 2019), the finding of robust  
119 local-scale changes in offspring survival related to fisheries closures is remarkable. This result  
120 suggests that even quite small (<1100 km<sup>2</sup>) fisheries time-area closures near breeding colonies  
121 are likely to positively affect breeding success in seabirds (Free *et al.*, 2021), and suggests that  
122 larger permanent fisheries exclusion zones may confer even greater conservation benefits for  
123 ecosystems and marine wildlife.

124 This critical result, however, has been the subject of heated debate, with no less than ten  
125 recent non-peer reviewed reports prepared for the South African fisheries agencies arguing  
126 technicalities of data analysis and modelling approaches (Supplementary Materials). Topics of  
127 debate, for example, have included whether to use individual-level observations or aggregate  
128 data to annual means (see Supplementary Materials for details). Nonetheless, despite detailed re-  
129 analyses by international panels reviewing experimental results and other interested scientists,  
130 there have been no major changes in the original key findings of Sherley *et al.*, (2018) showing  
131 that chick survival and offspring condition are higher without fisheries in the vicinity of colonies.  
132 These exchanges serve to highlight the critical importance of the penguin demographic data,  
133 especially chick survival, which was not measured across all four colonies, and suggest these  
134 parameters should be weighted most heavily when considering the effects of forage fish  
135 removals in penguin foraging habitat. The implication is clearly that industrial fisheries  
136 removing anchovy and sardine near breeding colonies compete with African penguins for food.

137 Arguably, this is the first time fisheries competition with seabirds for food has been adequately  
138 demonstrated through the use of a well-designed long-term field experiment (see preliminary  
139 comments in Sydeman *et al.*, 2017). The South African experiment thereby shows what is  
140 needed to assess the effects of forage fish fisheries at the local scale to seabirds breeding and  
141 foraging from colonies.

142

### 143 **Foraging behaviour**

144 While experimental fisheries closures have provided noteworthy results on breeding success at  
145 Robben and Dassen islands, the effects of fishing closures on penguin foraging behaviours,  
146 designed to provide mechanistic explanations for changes in chick survival, were not definitive.  
147 Foraging parameters measured include foraging trip duration and maximum foraging distance,  
148 behaviours thought to respond to the local availability of food resources (Campbell *et al.*, 2019;  
149 McInness *et al.*, 2019). The estimates of the impacts on foraging behaviour are generally much  
150 more variable than those on chick survival or condition (Pichegru *et al.*, 2012; Ross-Gillespie  
151 and Butterworth, 2021), particularly for colonies on the Eastern Cape where chick survival data  
152 are unavailable for context (Bird and St. Croix islands; Fig. 1). The lack of robust results  
153 regarding penguin foraging behaviour undoubtedly relates to the high variability in foraging  
154 measurements among individuals that may be due to day-to-day changes in prey availability (*cf.*  
155 Bertrand *et al.*, 2012). More robust studies of individual movements and foraging behaviour  
156 would likely require great effort and expense (Soanes *et al.*, 2013). The rapid pace of the decline  
157 of the African penguin (~5% per annum; Sherley *et al.*, 2020) exacerbates these concerns.  
158 Indeed, while the cost of devices to track seabirds has declined since the fisheries closures began  
159 in 2008, the difficulty of finding enough birds to study of the right age and stage of the breeding

160 season has greatly increased. Most importantly to us, though, is the fact that measurements of  
161 foraging behaviour remain difficult to link to changes in survival of chicks, immature  
162 individuals, or adults, which are key elements in the population ecology of seabirds in general  
163 and specifically to the recovery of the African penguin. Unfortunately, the logistical difficulties  
164 of working on St. Croix and Bird islands mean that chick survival was measured only for the  
165 colonies on the Western Cape, making full multivariate comparisons with those on the Eastern  
166 Cape impossible.

167

### 168 **Horizon scan**

169 There are remarkably few BACI ocean experiments from which to draw comparisons about the  
170 efficacy of fisheries exclusions on fish availability to predators and wildlife population dynamics  
171 (Sydeman *et al.*, 2017). Following the widespread decline of Steller sea lions *Eumetopias*  
172 *jubatus* in the Alaskan North Pacific, 20–40-km trawling exclusion zones were established along  
173 the Aleutian Archipelago during the late 1990s. Regrettably, proposed replication of these time-  
174 area closures and control sites were not instituted as was done in South Africa, resulting in  
175 ambiguous findings (McDermott *et al.*, 2016). Additionally, in the early 2000s a quasi-  
176 experimental closure off the North Sea coast of the UK strongly suggested a negative impact of  
177 the sandeel *Ammodytes marinus* fishery on black-legged kittiwake *Rissa tridactyla* breeding  
178 productivity on the Isle of May, but not that of four diving species also breeding on the island  
179 (Frederiksen *et al.*, 2008). Elsewhere, data from Magellanic penguins *Spheniscus magellanicus*,  
180 a species found in Argentina that is closely related to the African penguin, shows that penguins  
181 that forage closer to their breeding colony have higher reproductive success, further supporting  
182 the importance of protected areas around penguin breeding colonies (Boersma and Rebstock,



183 2009; Boersma *et al.*, 2015). Looking forward, the Convention for the Conservation of Antarctic  
184 Marine Living Resources (CCAMLR), of which South Africa is part, is considering the  
185 implementation of time-area closures of krill fisheries in Antarctic Peninsula ecosystems to  
186 protect penguin and seal breeding productivity (Trathan and Godø, 2018). Norway, South  
187 Korea, Japan, Ukraine, and other nations have economic or conservation interests in Antarctic  
188 krill fisheries, and the South African experiment is demonstrating the value of area-based  
189 fisheries closures for marine predators. Finally, relative to this discussion, fisheries policies  
190 designed to eliminate the potential for localized prey depletion and effects on marine predators  
191 appear to work very well. In the Alaskan North Pacific, the U.S. North Pacific Fishery  
192 Management Council prohibited fishing for most forage fish (e.g., Pacific sand lance *Ammodytes*  
193 *hexapterus* and capelin *Mallotus villosus*) and euphausiid crustaceans in 1997 (Witherell *et al.*,  
194 2000). Hence, in this region, forage fish fisheries competition with marine wildlife has never  
195 developed into a management issue, and its most important groundfish fisheries are considered  
196 healthy as a result of this basic policy to protect mid trophic level food resources for the benefit  
197 of all upper trophic level species.

198

### 199 **Implications for penguin conservation**

200 The African Penguin Biodiversity Management Plan guides conservation actions to facilitate  
201 penguin recovery in southern Africa. The original plan, which discussed a variety of ongoing  
202 threats to the penguin, called for provision of adequate prey resources in both the breeding and  
203 non-breeding seasons, with fisheries considered a key factor in determining year-round food  
204 resource availability. To date, the fisheries closure experiment has only addressed the potential  
205 effects on penguin breeding productivity. Given the key role of juvenile and adult survival to the

206 decline in the penguin population (Sherley *et al.*, 2014, 2017; Robinson *et al.*, 2015), data  
207 collection could be broadened to investigate the importance of fishing during the non-breeding  
208 season by implementing pelagic time-area closures. Moreover, South Africa could link its  
209 approach with efforts to restore the marine ecosystem and fisheries of its Benguela Current  
210 Commission partner, Namibia (Utne-Palm *et al.*, 2010). In Namibia, the sardine fishery was  
211 closed in 2018 after the stock dropped below the crash reference point of 50,000 t of spawning  
212 biomass (Kainge *et al.*, 2020; Erasmus *et al.*, 2021) following over-fishing decades ago (Roux *et*  
213 *al.*, 2013). The Namibian Islands Marine Protected Area (NIMPA; Fig. 1) was implemented in  
214 2009 (Ludynia *et al.*, 2012) and is designed to promote both seabird and fisheries recovery.  
215 However, because the forage fish community was so severely depleted, Namibian African  
216 penguin populations collapsed and have yet to recover to any appreciable degree (Crawford,  
217 2007; Sherley *et al.*, 2020). That this ecological breakdown persists after four years of a  
218 complete moratorium on sardine fishing in Namibia could be viewed as a worst-case scenario for  
219 the situation in South Africa if the fisheries and penguin competition is not carefully managed.  
220 The evidence suggests the importance of reducing competition with fisheries immediately to  
221 stem the decline of the African penguin.

222

223 To that end, we welcome the recent news that the Minister of Forestry, Fisheries and the  
224 Environment has established a Governance Forum which is, in turn, seeking to find a balance  
225 between minimizing the costs to the small-pelagics fishing industry while maximizing the  
226 protection of foraging areas for breeding African penguins. Through a series of meetings, this  
227 group has developed a proposal to close areas around three penguin colonies to purse-seine  
228 fishing: Dassen Island, Dyer Island, and St. Croix Island (Coetzee *et al.*, 2021). These three

229 colonies have all hosted populations of ~20,000 pairs at some point since 1979. Dyer Island  
230 occupies an important strategic location between the formerly large colonies on the Western  
231 Cape (Dassen and Robben islands) and the Eastern Cape colonies. St. Croix Island was, until  
232 recently, the only colony still home to >3,000 breeding pairs, but numbers there have declined  
233 sharply from ~3,600 pairs 2019 to ~1,500 pairs in 2021 (Sherley *et al.*, 2020, 2021). Dassen  
234 Island was once the location of the largest African penguin colony in the meta-population and is  
235 the nearest colony of >150 pairs to Namibia (Sherley *et al.*, 2020). Continued increasing  
236 breeding productivity on Dassen Island, as has happened in the past decade with closures, could  
237 lead to spill-over effects. For example, there may be increased dispersal and recruitment of  
238 young penguins into Namibia as well as to Robben Island near Cape Town (Sherley *et al.*, 2017).  
239 The public-relations opportunity of increasing the Robben Island population is enormous. At  
240 one colony in South Africa where the penguin population is relatively small but stable, Simon's  
241 Town (also known as "Boulders"; Sherley *et al.*, 2020; Fig. 1), penguin ecotourism is valued at  
242 >10 million USD/year (van Zyl, 2014; van Zyl and Kinghorn, 2018). The Robben Island  
243 population, once numbering about 8,500 pairs (Sherley *et al.*, 2020), is visited by approximately  
244 325,000 people/year (2017–2019; [https://nationalgovernment.co.za/entity\\_annual/1936/2019-  
245 robben-island-museum-annual-report.pdf](https://nationalgovernment.co.za/entity_annual/1936/2019-robben-island-museum-annual-report.pdf)). Thus, Robben Island penguins allow South Africa to  
246 engage and educate hundreds of thousands of people as they visit a recovering penguin colony.  
247 This opportunity to herald the fisheries closures could enhance appreciation for marine wildlife  
248 and demonstrate the commitment of South Africa to manage fisheries using a multi-species,  
249 ecosystem-wide perspective.

250

251 **Conclusion**

252 The scientific, conservation, and economic value of South Africa's long-term fisheries closures  
253 with forage fish and penguins is considerable. The Benguela Current ecosystem is highly  
254 dynamic and both fish and penguins are mobile. On one hand, we know that many seabird  
255 species, including the African penguin, exhibit a non-linear threshold response in breeding  
256 success to fluctuations in local forage stock abundance (Cury *et al.*, 2011) and to the distance  
257 they must travel to feed chicks (Boersma and Rebstock, 2015; Weber *et al.*, 2021). On the other  
258 hand, Free *et al.* (2021) suggest that mobile marine top predators and forage fish may not  
259 respond to fisheries protected areas as well as more immobile organisms, though this depends  
260 upon the persistence of forage patches within the birds foraging range (e.g., Davoren *et al.*,  
261 2003). There is recognition, however, that restricting fishing near predator breeding locations  
262 would likely produce greater benefits (Free *et al.*, 2021). This is also supported by key results  
263 from the Western Cape, which show the importance of fisheries time-area closures to African  
264 penguins as centrally-foraging seabirds. Indeed, the closure experiment has demonstrated that  
265 protecting primary foraging areas to safeguard predators' access to marine food resources  
266 reduces competition with forage fish fisheries.

267

268 The African penguin shares life history traits with other seabird species, and its fisheries case  
269 history resembles other ongoing and developing fisheries-wildlife conflicts both in South Africa  
270 and elsewhere in the world (e.g., Bertrand *et al.*, 2012; Frederiksen *et al.*, 2008; Watters *et al.*,  
271 2020). Because most seabirds breed on land in conspicuous groups, their lifestyle provides  
272 opportunities to measure and evaluate important traits such as offspring production and survival  
273 of juveniles and adults, thereby providing clear results of experimental forage fish fisheries  
274 manipulations. South Africa fisheries management may be considered a model system for

275 resolving complex natural resources management issues in marine ecosystems globally. If  
276 fisheries exclusions can be continued and perhaps increased in number and area, the recovery  
277 and health of the African penguin throughout its range and the scientific basis for solutions to  
278 minimize the impacts of forage fish fisheries on marine wildlife could be significantly enhanced.

279

## 280 **References**

- 281 Bertrand, S., Joo, R., Smet, C. A., Tremblay, Y., Barbraud, C., and Weimerskirch, H. 2012.  
282 Local depletion by a fishery can affect seabird foraging. *Journal of Applied Ecology*, 49:  
283 1168–1177.
- 284 Bird, J. P., Martin, R., Akcakaya, H. R., Gilroy, J., Burfield, I. J., Garnett, S. T., Symes, A. *et al.*  
285 2020. Generation lengths of the world’s birds and their implications for extinction risk.  
286 *Conservation Biology*, 34: 1252–1261.
- 287 BirdLife International. 2020. *Spheniscus demersus*. The IUCN Red List of Threatened Species  
288 2020: eT22697810A157423361. [https://dx.doi.org/10.2305/IUCN.UK.2020-](https://dx.doi.org/10.2305/IUCN.UK.2020-3.RLTS.T22697810A157423361.en)  
289 [3.RLTS.T22697810A157423361.en](https://dx.doi.org/10.2305/IUCN.UK.2020-3.RLTS.T22697810A157423361.en).
- 290 Boersma, P. D., and Rebstock, G. A. 2009. Foraging distance affects reproductive success in  
291 Magellanic penguins. *Marine Ecology Progress Series*, 375: 263–275.
- 292 Boersma, P. D., Rebstock, G. A., and Garcia-Borboroglu, P. 2015. Marine protection is needed  
293 for Magellanic penguins in Argentina based on long-term data. *Biological Conservation*,  
294 182: 197–204.
- 295 Boersma, P. D., Garcia-Borboroglu, P., Gownaris, N. J., Bost, C. A., Chiaradia, A., Ellis, S.,  
296 Schneider, T. *et al.* 2020. Applying science to pressing conservation needs for penguins.  
297 *Conservation Biology*, 34: 103–112.

- 298 Burke, C. M., and Montevecchi, W. A. 2009. The foraging decisions of a central place seabird in  
299 response to fluctuations in local prey conditions. *Journal of Zoology*, 278: 354–361.
- 300 Campbell, K. J., Steinfurth, A., Underhill, L. G., Coetzee, J. C., Dyer, B. M., Ludynia, K.,  
301 Makhado, A. B. *et al.* 2019. Local forage fish abundance influences foraging effort and  
302 offspring condition in an endangered marine predator. *Journal of Applied Ecology*, 56:  
303 1751–1760.
- 304 Coetzee, J. C., van der Lingen, C. D., Hutchings, L., and Fairweather, T. P. 2008. Has the fishery  
305 contributed to a major shift in the distribution of South African sardine? *ICES Journal of*  
306 *Marine Science*, 65: 1676–1688.
- 307 Coetzee, J. C., Makhado, A. B., van der Lingen, C. D., Ebrahim, Z., Kock, A., Lawrence, C., and  
308 Shabangu, F. W. 2021. African penguin colony closures: Finding a balance between  
309 minimizing costs to the small pelagic fishing industry while maximising coverage of  
310 foraging area for breeding African penguins. Department of Forestry, Fisheries and the  
311 Environment Report O&C/2021/SEP/Extended Penguin TT/01. 12 pp.
- 312 Crawford, R. J. M. 2007. Food, fishing and seabirds in the Benguela upwelling system. *Journal*  
313 *of Ornithology*, 148: S253–S260.
- 314 Crawford, R. J. M., Makhado, A. B., Whittington, P. A., Randall, R. M., Oosthuizen, W. H., and  
315 Waller, L. J. 2015. A changing distribution of seabirds in South Africa -- the possible  
316 impact of climate and its consequences. *Frontiers in Ecology and Evolution*, 3: 1–11.
- 317 Crawford, R. J. M., Sydeman, W. J., Thompson, S. A., Sherley, R. B., and Makhado, A. B. 2019.  
318 Food habits of an endangered seabird indicate recent poor forage fish availability off  
319 western South Africa. *ICES Journal of Marine Science*, 76: 1344–1352.

- 320 Croll, D. A., and Tershy, B. R. 1998. Penguins, fur seals, and fishing: prey requirements and  
321 potential competition in the South Shetland Islands, Antarctica. *Polar Biology*, 19: 365–  
322 374.
- 323 Cury, P. M., Boyd, I. L., Bonhommeau, S., Anker-Nilssen, T., Crawford, R. J. M., Furness, R.  
324 W., Mills, J. A. *et al.* 2011. Global seabird response to forage fish depletion--one-third  
325 for the birds. *Science*, 334: 1703–1706.
- 326 Davoren, G. K., Montevecchi, W. A., and Anderson, J. T. 2003. Search strategies of a pursuit-  
327 diving marine bird and the persistence of prey patches. *Ecological Monographs*, 73: 463–  
328 481.
- 329 DFFE. 2021. A synthesis of current scientific information relating to the decline in the African  
330 penguin population, the small pelagic fishery and island closures. Draft Report to the  
331 Minister, Department of Forestry, Fisheries and the Environment. 71 pp.
- 332 Duffy, D. C., and Schneider, D. C. 1994. Seabird-fishery interactions: a manager's guide.  
333 *Birdlife Conservation Series*, 1: 26–38.
- 334 Dunn, D. C., Boustany, A. M., and Halpin, P. N. 2011. Spatio-temporal management of fisheries  
335 to reduce by-catch and increase fishing selectivity. *Fish and Fisheries*, 12: 110–119.
- 336 Erasmus, V. N., Currie, B., Roux, J.-P., Elwen, S. H., Kalola, M. S., Tjizoo, B., Kathena, J. N. *et*  
337 *al.* 2021. Predatory species left stranded following the collapse of the sardine *Sardinops*  
338 *sagax* (Pappe, 1854) stock off the northern Benguela upwelling system: A review.  
339 *Journal of Marine Systems*, 224: 103623.
- 340 Frederiksen, M., Jensen, H., Daunt, F., Mavor, R. A., and Wanless, S. 2008. Differential effects  
341 of a local industrial sand lance fishery on seabird breeding performance. *Ecological*  
342 *Applications*, 18: 701-710.

- 343 Free, C. M., Jensen, O. P., and Hilborn, R. 2021. Evaluating impacts of forage fish abundance on  
344 marine predators. *Conservation Biology*, early view. doi:10.1111/cobi.13709.
- 345 Furness, R. W. 1982. Competition between fisheries and seabird communities. *Advances in*  
346 *Marine Biology*, 20: 225–307.
- 347 Gremillet, D., Ponchon, A., Paleczny, M., Palomares, M.-L. D., Karpouzi, V., and Pauly, D.  
348 2018. Persisting worldwide seabird-fishery competition despite seabird community  
349 decline. *Current Biology*, 28: 4009–4013.
- 350 Hamer, K. C., Schreiber, E. A., and Burger, J. 2001. Breeding biology, life histories and life-  
351 history-environment interactions in seabirds. In *Biology of Marine Birds*, pp. 217–262.  
352 Ed. by E. A. Schreiber, and J. Burger. CRC Press, Boca Raton.
- 353 Kainge, P., Kirkman, S. P., Estevao, V., van der Lingen, C. D., Uanivi, U., Kathena, J. N., van  
354 der Plas, A. *et al.* 2020. Fisheries yields, climate change, and ecosystem-based  
355 management of the Benguela Current Large Marine Ecosystem. *Environmental*  
356 *Development*, 36: 100567.
- 357 Ludynia, K., Kemper, J., and Roux, J.-P. 2012. The Namibian Islands' Marine Protected Area:  
358 Using seabird tracking data to define boundaries and assess their adequacy. *Biological*  
359 *Conservation*, 156: 136–145.
- 360 OLSPS Marine. 2021. Changes in penguin population growth rate based on individual chick  
361 survival data from the island closure experiment. Department of Forestry, Fisheries and  
362 the Environment Report FISHERIES/2021/JUN/SWG-PEL/40. 12 pp.
- 363 McDermott, S. F., Haist, V., and Rand, K. M. 2016. Evaluating the efficacy of trawl exclusion  
364 zones by estimating local Atka mackerel abundance and movement patterns in the



- 365 Central and Eastern Aleutian Islands. *Marine and Coastal Fisheries: Dynamics,*  
366 *Management, and Ecosystem Science*, 8: 334–349.
- 367 McInnes, A. M., Ryan, P. G., Lacerda, M., and Pichegru, L. 2019. Targeted prey fields  
368 determine foraging effort thresholds of a marine diver: Important cues for the sustainable  
369 management of fisheries. *Journal of Applied Ecology*, 56: 2206–2215.
- 370 Pichegru, L., Ryan, P. G., van Eeden, R., Reid, T., Gremillet, D., and Wanless, R. 2012.  
371 Industrial fishing, no-take zones and endangered penguins. *Biological Conservation*, 156:  
372 117–125.
- 373 Pikitch, E., Boersma, P. D., Boyd, I. L., Conover, D. O., Cury, P., Essington, T., Heppell, S. S. *et*  
374 *al.* 2012. Little fish, big impact: Managing a crucial link in ocean food webs. Lenfest  
375 Ocean Program, Washington, D.C. 108 pp.
- 376 Pikitch, E. K., Rountos, K. J., Essington, T. E., Santora, C., Pauly, D., Watson, R., Sumaila, U.  
377 R. *et al.* 2014. The global contribution of forage fish to marine fisheries and ecosystems.  
378 *Fish and Fisheries*, 15: 43–64.
- 379 Robinson, W. M. L., Butterworth, D. S., and Plaganyi, E. E. 2015. Quantifying the projected  
380 impact of the South African sardine fishery on the Robben Island penguin colony. *ICES*  
381 *Journal of Marine Science*, 72: 1822–1833.
- 382 Ross-Gillespie, A., and Butterworth, D. S. 2021. Updated analysis of results from data arising  
383 from the Island Closure Experiment. Department of Forestry, Fisheries and the  
384 Environment Report FISHERIES/2021/JUN/SWG-PEL/39rev. 15 pp.
- 385 Roux, J.-P., van der Lingen, C. D., Gibbons, M. J., Moroff, N. E., Shannon, L. J., Smith, A. D.  
386 M., and Cury, P. M. 2013. Jellyfication of marine ecosystems as a likely consequence of

- 387           overfishing small pelagic fishes: lessons from the Benguela. *Bulletin of Marine Science*,  
388           89: 249–284.
- 389   Schreiber, E. A., and Burger, J. 2001. *Biology of Marine Birds*. p. 740. CRC Press, Boca Raton.
- 390   Sherley, R. B. 2020. Revisiting the key results in MARAM/IWS/2019/PENG/P4 in light of the  
391           2019 Panel recommendations. Department of Forestry, Fisheries and the Environment  
392           Report FISHERIES/2020/JUL/SWG-PEL/53rev. 27 pp.
- 393   Sherley, R. B., Abadi, F., Ludynia, K., Barham, B. J., Clark, A. E., and Altwegg, R. 2014. Age-  
394           specific survival and movement among major African penguin *Spheniscus demersus*  
395           colonies. *Ibis*, 156: 716–728.
- 396   Sherley, R. B., Ludynia, K., Dyer, B. M., Lamont, T., Makhado, A. B., Roux, J.-P., Scales, K. L.  
397           *et al.* 2017. Metapopulation tracking juvenile penguins reveals an ecosystem-wide  
398           ecological trap. *Current Biology*, 27: 1–6.
- 399   Sherley, R. B., Barham, B. J., Barham, P. J., Campbell, K. J., Crawford, R. J. M., Grigg, J.,  
400           Horswill, C. *et al.* 2018. Bayesian inference reveals positive but subtle effects of  
401           experimental fishery closures on marine predator demographics. *Proceedings of the*  
402           *Royal Society B-Biological Sciences*, 285: 20172443.
- 403   Sherley, R. B., Barham, B. J., Barham, P. J., Campbell, K. J., Crawford, R. J. M., de Blocq, A.,  
404           Grigg, J. *et al.* 2019. A Bayesian approach to understand the overall effect of purse-seine  
405           fishing closures around African penguin colonies. Department of Forestry, Fisheries and  
406           the Environment Report FISHERIES/2019/NOV/SWG-PEL/32. 1–25 pp.
- 407   Sherley, R. B., Crawford, R. J. M., de Blocq, A., Dyer, B. M., Geldenhuys, D., Hagen, C.,  
408           Kemper, J. *et al.* 2020. The conservation status and population decline of the African  
409           penguin deconstructed in space and time. *bioRxiv*, 2020.01.15.907485.

- 410 Sherley, R. B., Crawford, R. J. M., Dyer, B. M., Hagen, C., Upfold, L., McInnes, A., and  
411 Masotla, M. J. 2021. Updated population trajectories and conservation status of the  
412 African penguin in South Africa following the 2021 census. Department of Forestry,  
413 Fisheries and the Environment Report FISHERIES/2021/JUL/SWG-PEL/46. 6 pp.
- 414 Smith, A. D. M., Brown, C. J., Bulman, C. M., Fulton, E. A., Johnson, P., Kaplan, I. C., Lozano-  
415 Montes, H. *et al.* 2011. Impacts of fishing low-trophic level species on marine  
416 ecosystems. *Science*, 333: 1147–1150.
- 417 Soanes, L. M., Arnould, J. P. Y., Dodd, S. G., Sumner, M. D., and Green, J. A. 2013. How many  
418 seabirds do we need to track to define home-range area? *Journal of Applied Ecology*, 50:  
419 671–679.
- 420 Sydeman, W. J., Thompson, S. A., Anker-Nilssen, T., Arimitsu, M., Bennison, A., Bertrand, S.,  
421 Boersch-Supan, P. *et al.* 2017. Best practices for assessing forage fish fisheries-seabird  
422 resource competition. *Fisheries Research*, 194: 209–221.
- 423 Tasker, M. L., Camphuysen, C. J., Cooper, J., Garthe, S., Montevecchi, W. A., and Blaber, S. J.  
424 M. 2000. The impacts of fishing on marine birds. *ICES Journal of Marine Science*, 57:  
425 531–547.
- 426 Trathan, P. N., and Godø, O. R. 2018. An experimental approach for the Antarctic krill fishery:  
427 advancing management and conservation through the use of Krill Reference Areas and  
428 Krill Fishing Areas. CCAMLR Report WS-SM-18/05. 1–24 pp.
- 429 Utne-Palm, A. C., Salvanes, A. G. V., Currie, B., Kaartvedt, S., Nilsson, G. E., Braithwaite, V.  
430 A., Stecyk, J. A. W. *et al.* 2010. Trophic structure and community stability in an  
431 overfished ecosystem. *Science*, 329: 333–336.

- 432 van Zyl, H. 2014. The economic value and contribution of the Simon's Town penguin colony.  
433 Report to the City of Cape Town. Independent Economic Researchers, Cape Town, South  
434 Africa. 20 pp.
- 435 van Zyl, H., and Kinghorn, J. 2018. The economic value and contribution of the Simon's Town  
436 penguin colony. Report to the City of Cape Town. Independent Economic Researchers,  
437 Cape Town, South Africa. 19 pp.
- 438 Watters, G. M., Hinke, J. T., and Reiss, C. S. 2020. Long-term observations from Antarctica  
439 demonstrate that mismatched scales of fisheries management and predator-prey  
440 interaction lead to erroneous conclusions about precaution. *Scientific Reports*, 10: 2314.
- 441 Weber, S. B., Richardson, A. J., Brown, J., Bolton, M., Clark, B. L., Godley, B. J., Leat, E. *et al.*  
442 2021. Direct evidence of a prey depletion “halo” surrounding a pelagic predator colony.  
443 *Proceedings of the National Academy of Sciences of the United States of America*, 118:  
444 e2101325118.
- 445 Witherell, D., Pautzke, C., and Fluharty, D. 2000. An ecosystem-based approach for Alaska  
446 groundfish fisheries. *ICES Journal of Marine Science*, 57: 771–777.

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448

**449 Data availability**

450 No data were used in the production of the main text of this article, however, there were data  
451 utilized in the analyses described in the Supplementary Materials. Those data and their  
452 associated code are available on GitHub ([https://github.com/rbsherley/IJMS\\_AP\\_IC](https://github.com/rbsherley/IJMS_AP_IC)). Please see  
453 the Supplementary material for more information.

454

455 **Supplementary material**

456 Supplementary material detailing “Best practices to analyse data relative to forage fish fisheries  
457 closures at penguin colonies” is available at ICESJMS online.

458

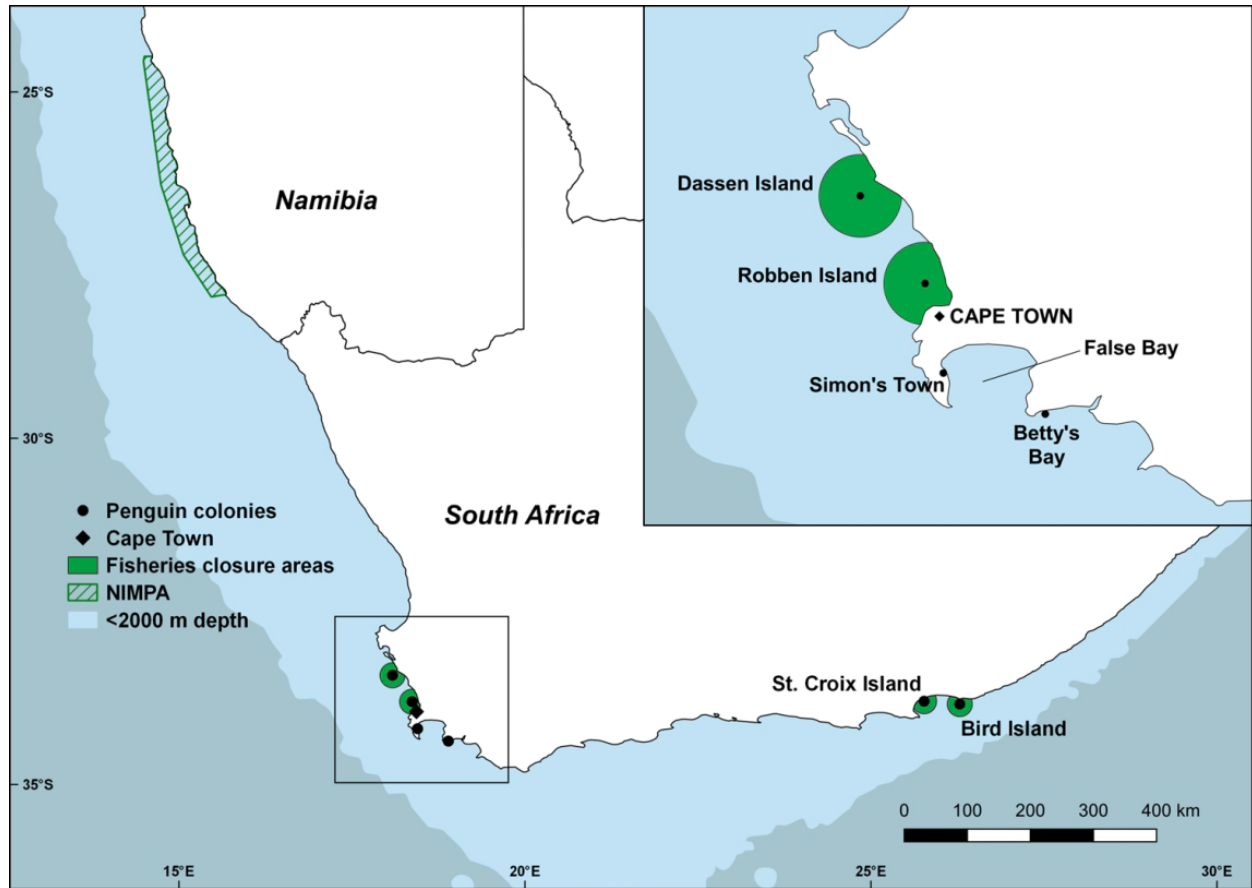
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471 **Figure 1. Map of southern Africa, showing South Africa and Namibia, locations of the**  
 472 **African penguin colonies and fisheries closures adjacent to breeding islands, Cape Town,**  
 473 **False Bay, and the Namibian Islands' Marine Protected Area (NIMPA).**

474

## Supplementary Materials

### Best Practices to Analyse Data Relative to Forage Fish Fisheries Closures at Penguin Colonies

#### *On the use of aggregated versus disaggregated data*

One of the primary concerns whether the penguin data should be analysed at the level of the annual mean (e.g., Table S1), referred to as the “aggregated data” approach (e.g., Ross-Gillespie and Butterworth, 2021a,b), or at the level of the original observations (i.e., each penguin nest, foraging trip or chick), referred to as the disaggregated data approach (e.g., Sherley *et al.*, 2018). In both cases, mixed models and random effects may be applied to account for the non-independence of samples made within each year. For the aggregated approach, 2 annual means or estimates, one from each island, are produced per year with associated error terms. For the disaggregated approach, 10s (adult foraging behaviour) to 100s (chick condition and survival) of observations made within each island in a given year (e.g., 417 chicks monitored for survival at Robben Island in 2008; Table S1) would be used. These approaches may result in differences in apparent fisheries closure effects on the birds.

Critics of the disaggregated approach argue that it produces estimates of closure effects that are too precise (i.e., negatively biased standard errors) relative to the aggregated approach (Butterworth, 2020a), unless “island” is included in both the fixed and random components of the models. Critics of the aggregated data argue that this approach will suffer from a risk of over-parameterisation of coefficient estimates as the sample size would fall well short of the 10–15 data points per predictor variable recommended by simulation studies to obtain stable parameter estimates (Babyak, 2004). Consequently, the concern is that the aggregated approach lacks statistical power to detect all but very large effect sizes (Green, 1991). For example, models using the aggregated approach to examine the effect of fisheries on chick survival (e.g., model R3 in Table B2 of Ross-Gillespie and Butterworth, 2021a) typically use 22 data points (see Table S1) to estimate 6 parameters (the intercept, a fixed island main effect, a fixed closure main effect, a fixed interaction between island and the closure effect, the SE for year as a random effect, and the residual SE). If models using aggregated data lack statistical power, there is a greater risk of making a Type II error, but if models applied to the disaggregated data give overly precise estimates, there is a risk of making a Type I error, i.e., if the random effect structure is not carefully chosen (Arnqvist, 2020; Silk *et al.*, 2020).

Simulation studies have demonstrated that linear mixed-effects models (LMMs) can be used in these circumstances, when random effects are chosen based on the known sampling structure in the data (Silk *et al.*, 2020), and particularly when model selection methods are used to choose the random effect structure (Matuschek *et al.*, 2017).

Matuschek *et al.* (2017) state:

*“Our simulations have shown that determining a parsimonious model with a standard model selection criterion is a defensible choice to find this middle ground between Type I error rate and power”.*

46 This is (presumably) why a 2019 international review panel that assessed the various analyses  
 47 from the fisheries closures said,

48  
 49 *“Given the nature of the experiment, use of individual data is to be preferred. However, this is*  
 50 *only the case if an appropriate random effects structure is chosen. Model selection methods*  
 51 *should be applied to select an appropriate random effects structure”* (Die *et al.*, 2019).

52  
 53 In re-assessing the aggregated and disaggregated approaches again in 2020, an equivalent  
 54 international panel made additional recommendations, noting that:

55  
 56 *“Individual-based models are vulnerable to underestimating the standard errors of important*  
 57 *model outputs if the model is incorrectly specified; aggregated models are vulnerable to*  
 58 *assigning inappropriate weights by stratum. Both types of error can lead to biased estimates of*  
 59 *closure effects and the standard errors of the estimates of these effects”* (Haddon *et al.*, 2020).

60  
 61 For the aggregated approach, they recommended taking into account the variance associated  
 62 with, and number of data points used to calculate, the annual averages. For the disaggregated  
 63 approach they suggested including a model with a hierarchical random effects structure with  
 64 Island nested within Year (i.e., specified as Year + Year:Island, or Year/Island in R) in the  
 65 candidate model set.

66  
 67 Below is a summary of the latest analyses that have been carried out towards implementing the  
 68 2019 and 2020 panel recommendations, focusing on the chick condition and chick survival  
 69 datasets at Robben and Dassen islands. This focus was chosen because these are metrics where  
 70 biologically meaningful effects have been detected at the population level.

71  
 72 ***Chick condition***

73 Ross-Gillespie and Butterworth (2021a,b) implemented recommendations for the aggregated  
 74 approach and compared outputs from these models to models using the disaggregated approach  
 75 with a Year/Island hierarchical random effects structure. These comparisons on like-for-like  
 76 datasets yield similarly precise estimates of the closure effect (see Figure 1 of Ross-Gillespie and  
 77 Butterworth 2021a). For example, Figure S1 shows the estimated effect of fishing (and  
 78 approximate 95% confidence intervals) on chick condition at Dassen and Robben islands from  
 79 four models. Effect sizes have been converted to % change in the population growth rate using  
 80 the conversion factor of 0.108 from Appendix A of Ross-Gillespie and Butterworth (2021a). A  
 81 negative effect indicates a negative effect of fishing on the penguin population growth rate.  
 82 Model 1 (RGB\_A\_Y) and Model 2 (RGB\_D\_Y) of Figure S1 shows the effect sizes from what  
 83 Ross-Gillespie and Butterworth (2021a) call the “best” implementation of the aggregated  
 84 approach, and the disaggregated approach respectively (values are taken from Table 1 in Ross-  
 85 Gillespie and Butterworth, 2021a). Note that the SE (printed above the x-axis) are nearly  
 86 identical.

87  
 88 Ross-Gillespie and Butterworth (2021a,b) did not implement the 2019 or 2020 panel  
 89 recommendations for the disaggregated approach, which would include “...best practices for  
 90 fitting mixed effects models (e.g., Zuur *et al.*, 2009),... and that “model selection methods  
 91 should be applied to select an appropriate random effects structure” (Die *et al.*, 2019). In

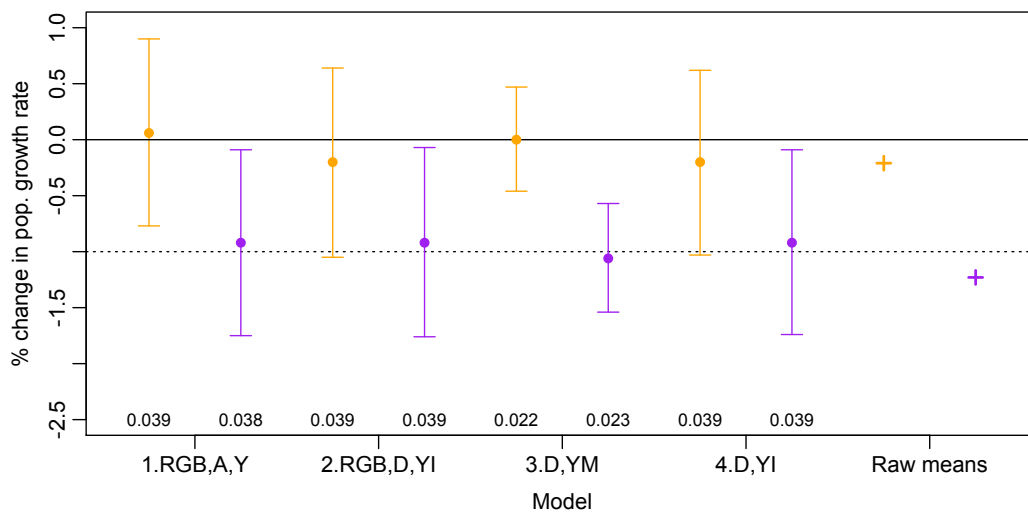


92 particular, the 2020 panel recommended the addition of Year/Island to the candidate set, not that  
 93 Year/Island necessarily reflects the best choice of the random effect. Leaving Month out of the  
 94 random effect ignores a source of hierarchical structure in the data that is known to be important,  
 95 and it is far from clear that Month can reasonably be nested in Island (Haddon *et al.*, 2020).  
 96 Having Island in both the fixed and random components of the model also may lead to parameter  
 97 estimation issues (Sherley, 2020a), and is also not in keeping with best practices for fitting mixed  
 98 effects models; as Zuur *et al.* (2009) state,

99  
 100 “Because we have as many explanatory variables as possible in the fixed component, the random  
 101 component (hopefully) does not contain any information that we would like to have in the fixed  
 102 component”.

103  
 104 We followed the 2019 and 2020 panel recommendations and applied information-criterion model  
 105 selection to objectively compare the relative support for a model with a Year/Island random  
 106 effect versus a Year/Month random effect (as proposed by Sherley *et al.*, 2018). This approach  
 107 yields a  $\Delta\text{AICc}$  of 685.7 in favour of the model with the Year/Month random effect structure.  
 108 Model 3 and 4 are fit to the disaggregated data using the ‘lmer’ function in the *lme4* library for R  
 109 (Bates *et al.*, 2015), with an island main effect, a closure main effect, and a closure $\times$ Island  
 110 interaction as the fixed effects. Although Model 3 does yield more precise estimates of the  
 111 closure effect than Model 4 (with the Year/Island random effect structure; compare Model 3.  
 112 D\_YM and Model 4. D\_YI in Figure S1), it unequivocally provides a better fit to the data based  
 113 on the objective use of information criterion-based model selection. The code and data to  
 114 reproduce Figure S1 and to make the AICc-based model comparison are available on GitHub  
 115 ([https://github.com/rbsherley/IJMS\\_AP\\_IC](https://github.com/rbsherley/IJMS_AP_IC)).

116



117  
 118 Figure S1: Fisheries effects point estimates (circles) and approximate 95% confidence intervals (mean  $\pm$   
 119  $\times 2$  standard errors (SE) for 1 and 2, and mean  $\pm \times 1.96$  SE for 3 and 4) for models examining the  
 120 impact of fishing with 20 km of Dassen Island (orange) and Robben Island (purple) on African penguin  
 121 chick condition from 2008 to 2018. The effect sizes have been converted into the % change in the  
 122 population growth rate using the conversion factor of 0.108 from Appendix A of Ross-Gillespie and  
 123 Butterworth (2021a); a negative effect means that fishing being allowed around that island is predicted  
 124 to have a negative effect on population growth rate. The raw means calculated directly from the data are  
 125 shown as plus signs (+) for reference. The SE for each effect is printed above the x-axis below the

126 corresponding effect. RGB = point estimates and approximate 95% confidence intervals taken directly  
 127 from Table 1 of Ross-Gillespie and Butterworth (2021a); A = uses the aggregated data approach; D =  
 128 uses the disaggregated data approach; Y = Year is used in the random effect structure; YM =  
 129 Year/Month (month of sampling nested in the year of sampling) is used in the random effect structure.  
 130 YI = Year/Island (island of sampling, nested in the year of sampling) is used in the random effect  
 131 structure. Model 3 gives a more parsimonious fit to the data than Model 4 ( $\Delta\text{AICc} = 685.7$ ).  
 132

133 Use of the model with the Year/Month random effect structure was labelled as “flawed science”,  
 134 in a letter to the Editor in Chief of Proceedings of the Royal Society B (see Sherley *et al.*, 2018)  
 135 requesting that they retract the paper (see Coetzee, 2021 FISHERIES/2021/AUG/SWG-  
 136 PEL/57)<sup>1</sup>. Yet, all modelling approaches shown in Figure S1 yield a fisheries effect on chick  
 137 condition at Robben Island that is statistically different from zero at the 5% level (Figure S1).  
 138 This is important because an objective way to link chick condition to population demography has  
 139 been developed and agreed upon by all parties (Sherley *et al.*, 2018; Ross-Gillespie and  
 140 Butterworth 2021b). However, some disagreement about the overall value of this effect (relative  
 141 to the current rate of decline) remains (e.g., Sherley *et al.*, 2020, Butterworth, 2021), and only the  
 142 model using disaggregated data and the Year/Month random effect exceeds a previously agreed  
 143 threshold for a biologically meaningful effect at the population level (−1% change in population  
 144 growth rate, shown by the dashed line in Figure S1).  
 145

#### 146 ***Chick survival***

147 Criticisms of the disaggregated approach (e.g., Sherley *et al.*, 2018; Sherley, 2020a) have again  
 148 focused on whether this model produces overly precise estimates (OLSPS Marine, 2021, pg. 4).  
 149 There are also questions about whether or not the closure effects were biased by a small  
 150 percentage of the chicks that were not monitored from hatching (see Sherley, 2020b), and  
 151 whether the interaction between island and the closure status should be retained even if the data  
 152 and model selection show no support for an interaction (Bergh, 2020, pg. 4; Butterworth, 2020b,  
 153 pg. 7).  
 154

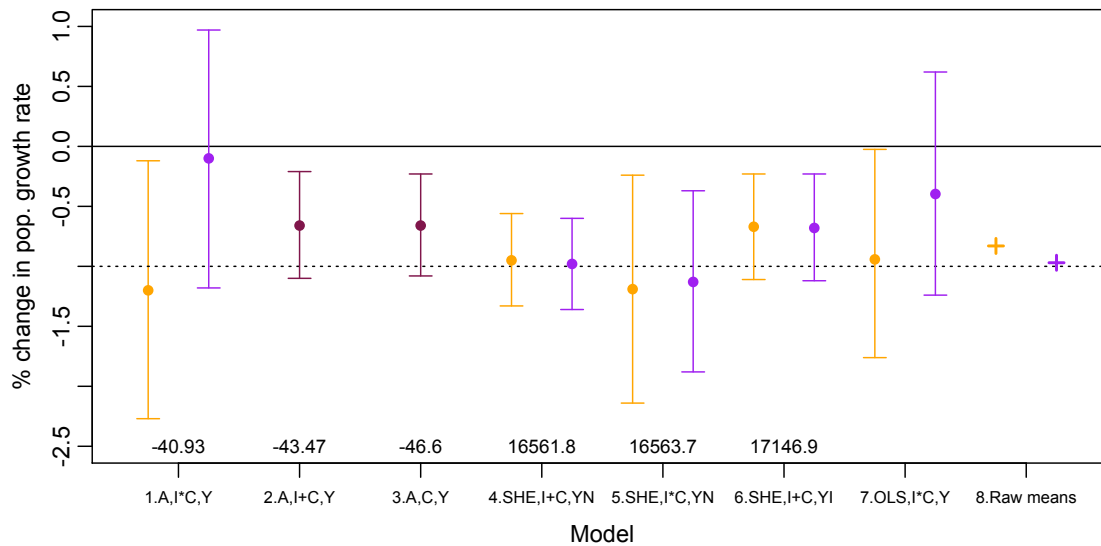
155 Ross-Gillespie and Butterworth (2021a) tried to implement the 2020 panel recommendations for  
 156 the aggregated data approach (Ross-Gillespie and Butterworth, 2021a, Appendix B), but had  
 157 difficulty in estimating an island-dependent variance, so their results for the aggregated approach  
 158 (and those shown in Figure S2) do not explicitly take sample size into account. They indicated  
 159 that this was unlikely to make much difference to inference from their approach as the sample  
 160 sizes were large (see Ross-Gillespie and Butterworth 2021a, pg. 2). Although direct comparisons  
 161 in Table B2 of their Appendix B show that the closure effect at Robben Island is some 3 times  
 162 larger when sample size is taken into account explicitly – and would be much more similar to the  
 163 effect they report from the disaggregated approach – it would remain not significantly different  
 164 from zero at the 5% level. For the disaggregated approach, Ross-Gillespie and Butterworth  
 165 (2021a) did not attempt to implement the panel recommendation of using model selection  
 166 including a model with Year/Island in the random effect structure. Instead, they reproduce results  
 167 from OLSPS Marine (2021) from a fit to the disaggregated data using Laplace approximation<sup>2</sup>

---

<sup>1</sup> The criticism and application to have the paper retracted are independent of a coding error in Sherley *et al.* (2018) and Sherley (2020a), which was noted by the 2020 panel (see Haddon *et al.*, 2020). That error has been corrected and did not affect the conclusions of that paper or the results presented here.

<sup>2</sup> Somewhat ironically, OLSPS Marine (2021) report these as likely to return negatively biased standard errors relative to the Bayesian approach with Gibbs sampling also used there and in e.g. Sherley (2020). The extent to

168 and just Year in the random component of the model, and then apply a correction factor of 1.12  
 169 to the confidence intervals in an attempt to convert from a maximum likelihood to a restricted  
 170 maximum likelihood (REML) estimate (see Ross-Gillespie and Butterworth 2021a, pg. 2). Their  
 171 “best implementation” of the aggregated approach yields a closure effect at Dassen Island that  
 172 both exceeds the  $-1\%$  threshold and differs from zero at the 95% level (Model 1 in Figure S2),  
 173 while their “best implementation” of the aggregated approach does not. Additionally, the closure  
 174 effect at Robben Island is not different from zero in either framework (see Figure 1 of Ross-  
 175 Gillespie and Butterworth 2021a). In contrast, the Bayesian approach (using Gibbs sampling) to  
 176 model the disaggregated data in OLSPS Marine (2021), which is reproduced here as Model 7 in  
 177 Figure S2, also indicates a closure effect at Dassen Island that is significantly different from zero  
 178 at the 5% level (and a point estimate of  $-0.94\%$ ).  
 179



180  
 181 Figure S2: Fisheries effects point estimates (circles) and approximate 95% confidence intervals (mean  $\pm$   
 182  $\times 1.96$  SE) for models examining the impact of fishing within 20 km of Dassen Island (orange) and  
 183 Robben Island (purple) on African penguin chick survival from 2008 to 2018. Dark red points and error  
 184 bars are from models without island-specific estimates (models in a frequentist framework with additive  
 185 effects only). The effect sizes have been converted into the % change in the population growth rate  
 186 using the conversion factor of 0.124 from Appendix A of Ross-Gillespie and Butterworth (2021a); a  
 187 negative effect means that fishing being allowed around that island is predicted to have a negative effect  
 188 on population growth rate. The raw means calculated from the data in Table 1 are shown as plus signs  
 189 (+) for reference. A = model uses the aggregated data approach (Models 1 to 3) and are implemented in  
 190 R using REML estimation. Values printed above the x-axis for Models 1 to 3 are AICc-values (smaller  
 191 AICc values = better relative support for a model). Model 1 reproduces the “best implementation of  
 192 the aggregated approach” from Table 1 and Figure 1 of Ross-Gillespie and Butterworth (2021a).  
 193 SHE = model uses the disaggregated data approach and are based on updates to models in Sherley  
 194 (2020a) implemented in a Bayesian framework using MCMC sampling in JAGS. Values printed above  
 195 the x-axis for Models 4 to 6 are PSIS-LOO-values (smaller PSIS-LOO values = better relative support  
 196 for a model). Model 7 directly plots the values from the Bayesian approach using Gibbs sampling in  
 197 OLSPS Marine (2021). For all models, I\*C = model contains an Island  $\times$  Closure interaction in the  
 198 fixed effects component; I+C = model contains additive Island and Closure effects; C = model contains

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which the “REML-like” correction applied by Ross-Gillespie and Butterworth (2021a) is appropriate is entirely unclear, but this approach yields a closure effect at Dassen Island that does not differ from zero at the 95% level.

199 only a main effect of closure in the fixed effects component; Y = Year is used in the random effect  
 200 structure; YN = Year/NestID (ID of the nest in which chicks were sampled nested in the year of  
 201 sampling) is used in the random effect structure; YI = Year/Island (island of sampling, nested in the  
 202 year of sampling) is used in the random effect structure. AICc values and PSIS-LOO values are not  
 203 directly comparable to one another.

204  
 205 Figure S2 also shows results for a model fit that implements the random effect structure  
 206 originally proposed for models using the disaggregated data on chick survival – nest identity  
 207 (Nest ID) nested within the year of sampling (e.g., specified as Year/NestID in R). This random  
 208 effect structure was originally selected because chicks in the same nest are provisioned by the  
 209 same parents, so their probabilities of survival are clearly non-independent of one another  
 210 (Sherley *et al.*, 2013, 2018). As with Month in the chick condition models above, leaving NestID  
 211 out of the random effect ignores a source of hierarchical structing in the data that is known to be  
 212 important (Sherley *et al.*, 2013). This model (Model 4 in Figure S2), fit using a Bayesian  
 213 framework based on Markov Chain Monte Carlo (MCMC) estimation in JAGS (v. 4.3.0;  
 214 Plummer 2003) is an update of M3 in Table 3 of Sherley (2020a) with the coding error therein  
 215 corrected (see footnote 1). It implements the Year/NestID random effect and shows closure  
 216 effects at both Dassen Island and Robben Island that are credibly different from zero at the 5%  
 217 level and both very close to the -1% threshold (-0.95% and -0.98% respectively).

218  
 219 Although it has been claimed that this model structure – with Year/NestID in the random effect –  
 220 should produce estimates that are too precise relative to the aggregated approach and a model  
 221 with Year/Island in the random effect (see above), Figure S2 shows that this is not necessarily  
 222 the case. Model 6 in Figure S2 is identical to Model 4, except that it uses Year/Island in the  
 223 random component of the model rather than Year/NestID. The precisions of the closure effects  
 224 are very similar between the two models (SE are ~0.016 and ~0.018 respectively). Moreover,  
 225 objective model selection indicates that Model 4 (Year/NestID) provides a better fit to the data  
 226 (PSIS-LOO = 16561.8) than Model 6 (Year/Island, PSIS-LOO = 17146.9, Figure S2). In this  
 227 case, model selection was carried out using Pareto smoothed importance sampling, leave-one-out  
 228 cross-validation (PSIS-LOO; Vehtari *et al.*, 2019); as with AICc, the lower the value the more  
 229 relative support there is for a model.

230  
 231 Finally, the results in Figure S2 strongly suggest that the differences in the precision of the  
 232 estimates between the approach favoured by Ross-Gillespie and Butterworth (2021a,b; Model 1  
 233 in Figure S2) and Sherley and colleagues (Sherley *et al.*, 2018; Sherley, 2020a; Model 4 in  
 234 Figure S2) are not due to the choice of the random effects structure but actually whether or not  
 235 the interaction effect is retained in the fixed effect structure. Model 1 (closure main effect SE =  
 236 0.044) and Model 2 (closure main effect SE = 0.018) in Figure S2 are both applied to the  
 237 aggregated data and are identical apart from whether or not the island × closure interaction is  
 238 retained in the model respectively. The  $\Delta$ AICc between the 2 models is 2.5 (in favour of the  
 239 model without the interaction, Figure S2), which suggests no strong evidence to retain it. Model  
 240 3 is simplified further by dropping the Island main effect and has  $\Delta$ AICc = 5.67 lower than  
 241 Model 1. Moreover, Model 5 (closure main effect SE = 0.039) and Model 4 (closure main effect  
 242 SE = 0.016) are both applied to the disaggregated data and are identical apart from whether or  
 243 not the island × closure interaction is retained in the model respectively. As with the aggregated  
 244 approach, the model without the interaction (Model 4) provides the better relative fit to the data  
 245 based on objective PSIS-LOO model selection. Some subjective arguments for necessarily

246 retaining the island  $\times$  closure interaction have been offered. For example, Bergh (2020) says  
 247 “Figure 5 of FISHERIES/2020/JUL/SWG-PEL/53REV provides estimates under the constraint  
 248 that the closure effect is equal across the two islands (at least in its Figure 5). There seems no  
 249 reason for these estimates to be equal. The separate estimates for the closure effect at these  
 250 islands should be presented” (see also Butterworth, 2020b, pg. 7). To our knowledge, however,  
 251 no objective reason why model selection should be used to select the random component of the  
 252 models (as per the 2019 and 2020 panel recommendations) but not the fixed component has yet  
 253 been put forward. Thus, at the time of writing, Model 4, Figure S2, would appear to be the best  
 254 implementation of the 2019 and 2020 panel recommendations for assessing the impact of the 20  
 255 km fishing closures on African penguin chick survival.

256  
 257 Detailed methods on the Bayesian model implementation and model selection are provided on  
 258 page 3 and 15 of Sherley (2020a) and the data and code to run the Bayesian models referenced in  
 259 Figure S2 and to reproduce Figure S2 are available on GitHub  
 260 ([https://github.com/rbsherley/IJMS\\_AP\\_IC](https://github.com/rbsherley/IJMS_AP_IC)).

261  
 262 Table S1: Annual estimates of the mean survival rates for African penguin chicks monitored at Dassen  
 263 Island and Robben Island between 2008 and 2018 used by OLSPS Marine (2021) and Ross-Gillespie and  
 264 Butterworth (2021) in the aggregated data approach.  $\Phi_{74}$  is the proportion of chicks surviving to 74 days  
 265 post hatching and is based on a lognormal survival function. N = the number of chicks monitored in each  
 266 year at each island. The methods used to derive these annual estimates are given in Appendix D of Ross-  
 267 Gillespie and Butterworth (2021).

Year	Island	Closure	$\Phi_{74}$	N	Island	Closure	$\Phi_{74}$	N
2008	Dassen	Closed	0.7718	246	Robben	Open	0.6395	417
2009	Dassen	Closed	0.6062	229	Robben	Open	0.5479	252
2010	Dassen	Open	0.5314	121	Robben	Open	0.6119	227
2011	Dassen	Open	0.5394	193	Robben	Closed	0.6376	289
2012	Dassen	Open	0.7481	124	Robben	Closed	0.7092	237
2013	Dassen	Open	0.7609	160	Robben	Closed	0.7977	234
2014	Dassen	Closed	0.7677	133	Robben	Open	0.7628	188
2015	Dassen	Closed	0.7864	107	Robben	Open	0.7595	298
2016	Dassen	Closed	0.8361	119	Robben	Open	0.7200	246
2017	Dassen	Open	0.7888	156	Robben	Closed	0.8322	212
2018	Dassen	Open	0.7539	54	Robben	Closed	0.7811	262

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271 Supplementary References:

- 272 Arnqvist, G. 2020. Mixed models offer no freedom from degrees of freedom. *Trends in Ecology*  
 273 *and Evolution*, 35: 329–335.
- 274 Babyak, M. A. 2004. What you see may not be what you get: A brief, nontechnical introduction  
 275 to overfitting in regression-type models. *Psychosomatic Medicine*, 66: 411–421.
- 276 Bates, D., Maechler, M., Bolker, B., and Walker, S. 2015. Fitting linear mixed-effects models  
 277 using lme4. *Journal of Statistical Software*, 67: 1–48.
- 278 Bergh, M. 2020. Comments on “Revisiting the key results in MARAM/IWS/2019/PENG/P4 in  
 279 light of the 2019 Panel recommendations (FISHERIES/2020/JUL/SWG-PEL/53REV) by  
 280 Richard B. Sherley”. Department of Forestry, Fisheries and the Environment Report:  
 281 FISHERIES/2020/AUG/SWG-PEL/84. 1–4 pp.
- 282 Butterworth, D.S. 2020a. On estimates of the impact of fishing from analyses of the island  
 283 closure experiment which model individual penguin responses directly. Department of  
 284 Forestry, Fisheries and the Environment Report: FISHERIES/2020/JAN/SWG-PEL/08.  
 285 1–2 pp. (available at  
 286 [https://zivahub.uct.ac.za/articles/report/On\\_estimates\\_of\\_the\\_impact\\_of\\_fishing\\_from\\_a](https://zivahub.uct.ac.za/articles/report/On_estimates_of_the_impact_of_fishing_from_a_nalyses_of_the_island_closure_experiment_which_model_individual_penguin_responses_directly/13669625)  
 287 [nalyses\\_of\\_the\\_island\\_closure\\_experiment\\_which\\_model\\_individual\\_penguin\\_responses](https://zivahub.uct.ac.za/articles/report/On_estimates_of_the_impact_of_fishing_from_a_nalyses_of_the_island_closure_experiment_which_model_individual_penguin_responses_directly/13669625)  
 288 [directly/13669625](https://zivahub.uct.ac.za/articles/report/On_estimates_of_the_impact_of_fishing_from_a_nalyses_of_the_island_closure_experiment_which_model_individual_penguin_responses_directly/13669625))
- 289 Butterworth, D.S. 2020b. A response to Sherley: FISHERIES/2020/JUL/SWG-PEL/53REV.  
 290 Department of Forestry, Fisheries and the Environment Report:  
 291 FISHERIES/2020/AUG/SWG-PEL/82. 1–38 pp. (available at:  
 292 [http://webcms.uct.ac.za/sites/default/files/image\\_tool/images/302/pub/2020/FISHERIES](http://webcms.uct.ac.za/sites/default/files/image_tool/images/302/pub/2020/FISHERIES_2020_AUG_SWG-PEL_82.pdf)  
 293 [2020\\_AUG\\_SWG-PEL\\_82.pdf](http://webcms.uct.ac.za/sites/default/files/image_tool/images/302/pub/2020/FISHERIES_2020_AUG_SWG-PEL_82.pdf))
- 294 Butterworth, D. S. 2021. The Penguin decline –where should most analysis effort *really* be  
 295 focused. Department of Forestry, Fisheries and the Environment Report:  
 296 FISHERIES/2021/MAR/SWG-PEL/10. 1–4 pp. (available at  
 297 [https://zivahub.uct.ac.za/articles/report/The\\_Penguin\\_decline\\_where\\_should\\_most\\_analyses](https://zivahub.uct.ac.za/articles/report/The_Penguin_decline_where_should_most_analyses_effort_really_be_focused_/14472948/1)  
 298 [effort\\_really\\_be\\_focused\\_/14472948/1](https://zivahub.uct.ac.za/articles/report/The_Penguin_decline_where_should_most_analyses_effort_really_be_focused_/14472948/1))
- 299 Coetzee, J.C. 2021. Background for the SWG-PEL’s position that the analyses contained in  
 300 Sherley et al. 2018 and subsequently in documents presented to the SWG-PEL during the  
 301 course of 2019 and 2020 were flawed. Department of Forestry, Fisheries and the  
 302 Environment Report: FISHERIES/2021/AUG/SWG-PEL/57. 1–5 pp.
- 303 Die, D. J., Punt, A. E., Tiedemann, R., Waples, R., and Wilberg, M. J. 2019. International  
 304 Review Panel Report for the 2019 International Fisheries Stock Assessment Workshop,  
 305 2–5 December 2019, UCT. Department of Forestry, Fisheries and the Environment  
 306 Report: MARAM/IWS/2019/General/5. 1–18 pp. (available at  
 307 [https://zivahub.uct.ac.za/articles/report/International\\_Review\\_Panel\\_Report\\_for\\_the\\_201](https://zivahub.uct.ac.za/articles/report/International_Review_Panel_Report_for_the_2019_International_Fisheries_Stock_Assessment_workshop/14473032/1)  
 308 [9\\_International\\_Fisheries\\_Stock\\_Assessment\\_workshop/14473032/1](https://zivahub.uct.ac.za/articles/report/International_Review_Panel_Report_for_the_2019_International_Fisheries_Stock_Assessment_workshop/14473032/1))
- 309 Green, S. B. 1991. How many subjects does it take to do a regression analysis. *Multivariate*  
 310 *Behavioral Research*, 26: 499–510.
- 311 Haddon, M., Parma, A., Punt, A. E., and Wilberg, M. J. 2020. Report of the International Review  
 312 of some aspects if the Island Closure Experiment., 3–9 December 2020. Department of  
 313 Forestry, Fisheries and the Environment Report: FISHERIE/2020/DEC/SWG-  
 314 PEL/REVIEW/07. 1–7 pp. (available at  
 315 [https://zivahub.uct.ac.za/articles/report/Report\\_of\\_the\\_International\\_Review\\_of\\_some\\_a](https://zivahub.uct.ac.za/articles/report/Report_of_the_International_Review_of_some_aspects_of_the_Island_Closure_Experiment/14510178/1)  
 316 [spects\\_of\\_the\\_Island\\_Closure\\_Experiment/14510178/1](https://zivahub.uct.ac.za/articles/report/Report_of_the_International_Review_of_some_aspects_of_the_Island_Closure_Experiment/14510178/1))

- 317 Matuschek, H., Kliegl, R., Vasishth, S., Baayen, H., and Bates, D. 2017. Balancing Type I error  
318 and power in linear mixed models. *Journal of Memory and Language*, 94: 305–315.
- 319 OLSPS Marine. 2021. Changes in penguin population growth rate based on individual chick  
320 survival data from the island closure experiment. Department of Forestry, Fisheries and  
321 the Environment Report: FISHERIES/2021/JUN/SWG-PEL/40. 1–12 pp.
- 322 Plummer, M. 2003. JAGS: A program for analysis of Bayesian graphical models using Gibbs  
323 sampling. In: Hornik, K., Leisch, F., and Zeileis, A. (eds.), *Proceedings of the Third  
324 International Workshop on Distributed Statistical Computing (DSC 2003)*. Vienna,  
325 Austria. ISSN 1609-395X. (available at: [http://www.ci.tuwien.ac.at/Conferences/DSC-  
326 2003/Proceedings/Plummer.pdf](http://www.ci.tuwien.ac.at/Conferences/DSC-2003/Proceedings/Plummer.pdf))
- 327 Ross-Gillespie, A., and Butterworth, D. S. 2021a. Updated analysis of results from data arising  
328 from the Island Closure Experiment. Department of Forestry, Fisheries and the  
329 Environment Report: FISHERIES/2021/JUN/SWG-PEL/39rev. 1–15 pp. (available at  
330 [https://zivahub.uct.ac.za/articles/report/Updated\\_analysis\\_of\\_results\\_from\\_data\\_arising  
331 from\\_the\\_Island\\_Closure\\_Experiment/15073404](https://zivahub.uct.ac.za/articles/report/Updated_analysis_of_results_from_data_arising_from_the_Island_Closure_Experiment/15073404))
- 332 Ross-Gillespie, A. and Butterworth, D.S. 2021b. Re-analysis of the Island Closure Experiment  
333 results to implement the suggestions of the December 2020 International Panel.  
334 Department of Forestry, Fisheries and the Environment Report:  
335 FISHERIES/2021/APR/SWG-PEL/35. 1–40 pp.
- 336 Sherley, R. B. 2020a. Revisiting the key results in MARAM/IWS/2019/PENG/P4 in light of the  
337 2019 Panel recommendations. Department of Forestry, Fisheries and the Environment  
338 Report: FISHERIES/2020/JUL/SWG-PEL/53rev. 1–27 pp. (available at  
339 <https://drive.google.com/file/d/1tt-CHQ5m-Ugw1-eYwM7prjh0K23QTKvm/view>)
- 340 Sherley, R. B., Barham, B. J., Barham, P. J., Campbell, K. J., Crawford, R. J. M., Grigg, J.,  
341 Horswill, C. et al. 2018. Bayesian inference reveals positive but subtle effects of  
342 experimental fishery closures on marine predator demographics. *Proceedings of the  
343 Royal Society B-Biological Sciences*, 285: 20172443.
- 344 Sherley, R. B., Hagen, C., Ludynia, K., McInnes, A. M., Shannon, L., Staasen, M., and Waller,  
345 L. 2020. Some observations on the relative impacts of different drivers on change in the  
346 African penguin population growth rate. Department of Forestry, Fisheries and the  
347 Environment Report: FISHERIES/2020/SEP/SWG-PEL/92. pp. 1–7. (available at  
348 [https://drive.google.com/file/d/12HV1w1moEYbUPNNvRCDkhlr\\_YwgXGpYU/view](https://drive.google.com/file/d/12HV1w1moEYbUPNNvRCDkhlr_YwgXGpYU/view))
- 349 Sherley, R. B., Underhill, L. G., Barham, B. J., Barham, P. J., Coetzee, J. C., Crawford, R. J. M.,  
350 Dyer, B. M., Leshoro, T. M., and Upfold, L. 2013. Influence of local and regional prey  
351 availability on breeding performance of African penguins *Spheniscus demersus*. *Marine  
352 Ecology Progress Series*, 473: 291–301.
- 353 Silk, M. J., Harrison, X. A., and Hodgson, D. J. 2020. Perils and pitfalls of mixed-effects  
354 regression models in biology. *PeerJ*, 8: e9522.
- 355 Vehtari, A., Simpson, D., Gelman, A., Yao, Y., and Gabry, J. 2019. Pareto Smoothed Importance  
356 Sampling. arXiv 1507.02646v6.
- 357 Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., and Smith, G. M. 2009. *Mixed Effects  
358 Models and Extensions in Ecology with R*. Springer, New York.
- 359