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Reply

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African Penguins and Localized Fisheries Management: Response to Butterworth and Ross-Gillespie

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We present a response to Butterworth and Ross-Gillespie's (2022) comment on our perspectives on how forage fish fisheries are impacting the endangered African penguin (*Sphenicus demersus*), and corresponding management options. Butterworth and Ross-Gillespie overstate model uncertainties and downplay the clear ecological and conservation significance of the fisheries closure experiment. We demonstrate that their criticism of "pseudo-replication" is weak, and not in line with their own analyses nor with the interpretations of many international scientific review panels commissioned by the government of South Africa to evaluate experimental results. Their comment does not alter our fundamental conclusions that forage fisheries operating near penguin breeding colonies compete with the birds for food resources, are detrimental to the penguin's population health, and are impeding recovery. Given that sardines are depleted (DFFE, 2021) and the African penguin is approaching a conservation crisis, we reiterate our position that continuing the precautionary approach of closures at the local scale of central-place foraging penguins is warranted to facilitate their population growth under fisheries management goals to conserve and maintain ecosystem functions.

Keywords: experiment, extinction, fisheries, rebuttal, specialist seabirds, spatial management

Introduction

We thank Butterworth and Ross-Gillespie (2022) for commenting on our article, and welcome the opportunity to further discuss the effects of fisheries targeting anchovy and sardine on African penguins (*Sphenicus demersus*) in South Africa. Previously (Sydeman *et al*., 2021), we argued that South Africa's fisheries closure experiment is the new "gold-standard" for research on fisheries competition with marine wildlife for food resources (Sydeman *et al*., 2017; Tasker and Sydeman, 2022), particularly because it used a Before and After Control Impact (BACI) design to demonstrate impacts on African penguin reproductive success and some related variables. This ongoing experiment is also remarkable from a societal perspective, given the difficult logistics of conducting a decade-long, multi-disciplinary ocean field experiment, and the cooperation shown by the diverse scientists and stakeholders, including industry, in implementing the project. Each of these groups represents societal concerns, from seabird conservation to maintaining fisheries and ecotourism, as well as other ecosystem services for South Africa. The experiment is unique and is recognized globally as a key example of how to study the effects of forage fish fisheries on local prey availability and seabirds (e.g., Sydeman *et al*., 2017; Watters *et al*., 2020; Trathan *et al*., 2021). As fisheries have effectively reduced the size of the African penguin population in Namibia by ~90% of its historic value (Roux *et al*., 2013), and similarly, a ~90% population decline has been registered for South Africa (Crawford *et al*., 2011; Sherley *et al*., 2020, 2021b), the world is paying close attention to the conservation status of this iconic seabird. Recovery may be possible, but only with a concerted effort to minimize all impediments to the penguin's population growth, including mitigating the effects of fisheries operating within the restricted foraging range of the African penguin when breeding (Supplemental Materials, SM1).

Re-evaluating results of the experiment

General Comments. In our original article, and here again in response to Butterworth and Ross-Gillespie (2022, hereafter B&R-G), we acknowledge that the experiment, while in our view scientifically transformative, had various design imperfections, which manifest as analytical complexities and challenge the clarity of experimental results. B&R-G put forward some valid concerns about analytical approaches, but in our view they overstate the importance of various statistical details, and in doing so lose sight of the ecological and conservation significance of the experiment. It is not unusual for ecological field experiments to take decades to produce consistent results (i.e., where all significant effects agree in their direction; Cusser *et al*., 2021), and in this regard we note that four of the five significant (different from zero at the 5% level) results in B&R-G's Figure 1 are consistent with a benefit to the penguins of the closures. Moreover, given the complex adaptive ecosystem in which the experiment was embedded (e.g., Duffy, 1983;

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Bakun et al., 2010; Levin *et al.*, 2013; Trathan *et al.*, 2021), it is, in our view, wholly remarkable that the experiment showed any consistency in effects, and primarily in the one that really matters—that closures of coastal pelagic fisheries for anchovy and sardine operating near colonies positively affects penguin breeding success, as assessed by variation in chick survival and condition (Sherley *et al.*, 2015, 2018, 2021a). Notably, 18 of 20 point estimates for positive population-level effects from the various modelling approaches show the same direction of these effects (Figure 1). Although one could argue, as B&R-G do, about the effect sizes and their statistical significance, the direction of the relationship between fisheries closures and chick survival and condition is clear. In contrast to assertions in B&R-G, our interpretations are consistent with reports of the international review panels, as well as a recent government of South Africa synthesis of the experimental results and penguin's population dynamics (Department of Forestry, Fisheries and the Environment (DFFE) 2021).

Breeding Success as a Key Variable. We do not agree with B&R-G that our emphasis on breeding success (nor criticisms about pseudo-replication and "best" modelling approaches, see below), invalidates our interpretation that continuing closures is a reasonable and necessary management action. We focused our review on the survival of penguin chicks in the Western Cape because this variable directly addressed the principal question of the experiment—do fisheries in the vicinity of colonies affect penguin reproductive success (paraphrasing B&R-G 2022; SM2)? Moreover, chick survival (i.e., fecundity), unlike many of the other variables measured (e.g., adult foraging behaviour; SM3), can be directly integrated into age-structured population viability models to access population-level effects (e.g., Nur and Sydeman, 1999; Jenouvrier *et al.*, 2009; Sherley *et al.*, 2018). While the effect size of fisheries closures near colonies on breeding success alone may appear relatively small (a ∼1% increase in population growth; Figure 1), this could offset ∼20% of the current population decline (∼5% per annum; Sherley *et al.*, 2020, 2021b; B&R-G, 2022). Most importantly, this population response meets a threshold agreed upon by all parties, including fisheries scientists, during the early stages of the experiment (Figure 1, SM4). Moreover, as we describe in more detail below, fishing near colonies has the capacity to affect sequential population processes in the life history of the penguins (Dunn *et al.*, 2016), leading to much larger impacts at the population level than it has been possible to document so far (SM5). As an example, chick condition is predominately measured during the second half of the chick-rearing period, and refers mostly to the condition of chicks that will survive to fledging age; condition is therefore most appropriately applied as a sequential effect to influence juvenile survival and subsequent population growth (e.g., Sherley et al. 2018, Sydeman et al. 2021; SM5).

"Pseudo-Replication" is Not an Issue. While we understand B&R-G's preference for an aggregated analytical approach, the strengths and weaknesses inherent in the variety of analytical approaches used to date have been under scrutiny by quantitative ecologists, statisticians, and international review panels for over a decade, and simply stated, there is no universally agreed-upon method to analyze these experimental data (SM6). In fact, both modelling approaches (those that use aggregated or disaggregated data; Figure 1, A = aggregated, D = disaggregated) provide evidence for positive effects of closures on penguin reproductive output (chick survival and/or condition). The results of various approaches, including those using individual data that B&R-G have repeatedly criticized, appear valid and are generally considered to provide useful insights (DFFE, 2021). We agree that there is uncertainty in all approaches, but quoting Box (1976) "…since all models are wrong, the scientist must be alert to what is importantly wrong. It is inappropriate to be concerned about mice when there are tigers abroad." One of the strengths in this exchange with B&R-G and others regarding experimental results is that re-examining model structures demonstrates fisheries effects on penguin reproductive performance despite the uncertainty inherent in each model (Figure 1; SM7; Sherley and Winker, 2019; de Moor, 2020).

Food supply and population biology of African Penguins

We agree with B&R-G that fisheries, food supply, and localized prey depletion are part of a complex web of pressures on the penguin population (e.g., Weller *et al.*, 2014, 2016). However, we view fisheries harvest within the primary foraging grounds near colonies as an impact that can be mitigated with spatial (localized fisheries) management. As the long-term population viability of the species is at stake, we cannot "fiddle while Rome burns" to untangle all of the effects, find perfect analytical solutions to complicated data (if they even exist), nor simply continue to research the problem and watch a dire situation become a conservation crisis (see Godø and Trathan, in press, for a similar management debate and potential solution in the Southern Ocean). This call for management action is not new. Seabird scientists with the South African DFFE as well as many university-based marine ecologists in South Africa have long requested spatial management of anchovy and sardine (the primary prey of African penguins) catches near penguin colonies (e.g., Crawford, 2006). When these calls for spatial management first came in 2006, the African penguin was classified as Vulnerable by the International Union for the Conservation of Nature (IUCN) and there were ∼39,000 breeding pairs (Crawford, 2006; Sherley *et al.*, 2020). Sixteen years later, the population has declined by >60%. There are less than 15,000 breeding pairs left, and the species is now listed as Endangered (Sherley *et al.*, 2021a; BirdLife International, 2020).

Importance of Observational Studies. While we agree with B&R-G that the experiment needs to be viewed in the wider context of the decline of penguin abundance over recent decades, the voluminous body of literature from observational studies can help put the experimental results in an ecosystem context (see Sydeman *et al.*, 2017). The literature, largely based on correlational analyses, overwhelmingly indicates that access to forage fish resources is the key driver of variation in penguin breeding numbers, reproductive success, and survival (e.g., Crawford, 2007; Crawford *et al.*, 2006, 2008, 2011, 2019; Ludynia *et al.*, 2010; Sherley *et al.*, 2013, 2015, 2018; Roux *et al.*, 2013; Robinson *et al.*, 2015). The observational data on African penguins in southern Africa also are corroborated by other lines of evidence. First, there have been concurrent population declines and changes in survival and behaviour of Cape gannets (*Morus capensis*) and Cape cormorants (*Phalacrocorax capensis*), other species that also feed primarily on sardine and anchovy (e.g., Distiller *et al.*, 2012; Cohen *et al.*, 2014; Crawford *et al.*, 2014, 2016; Sherley *et al.*, 2019). Second, global meta-analyses have identified clear effects of prey availability on seabird breeding success

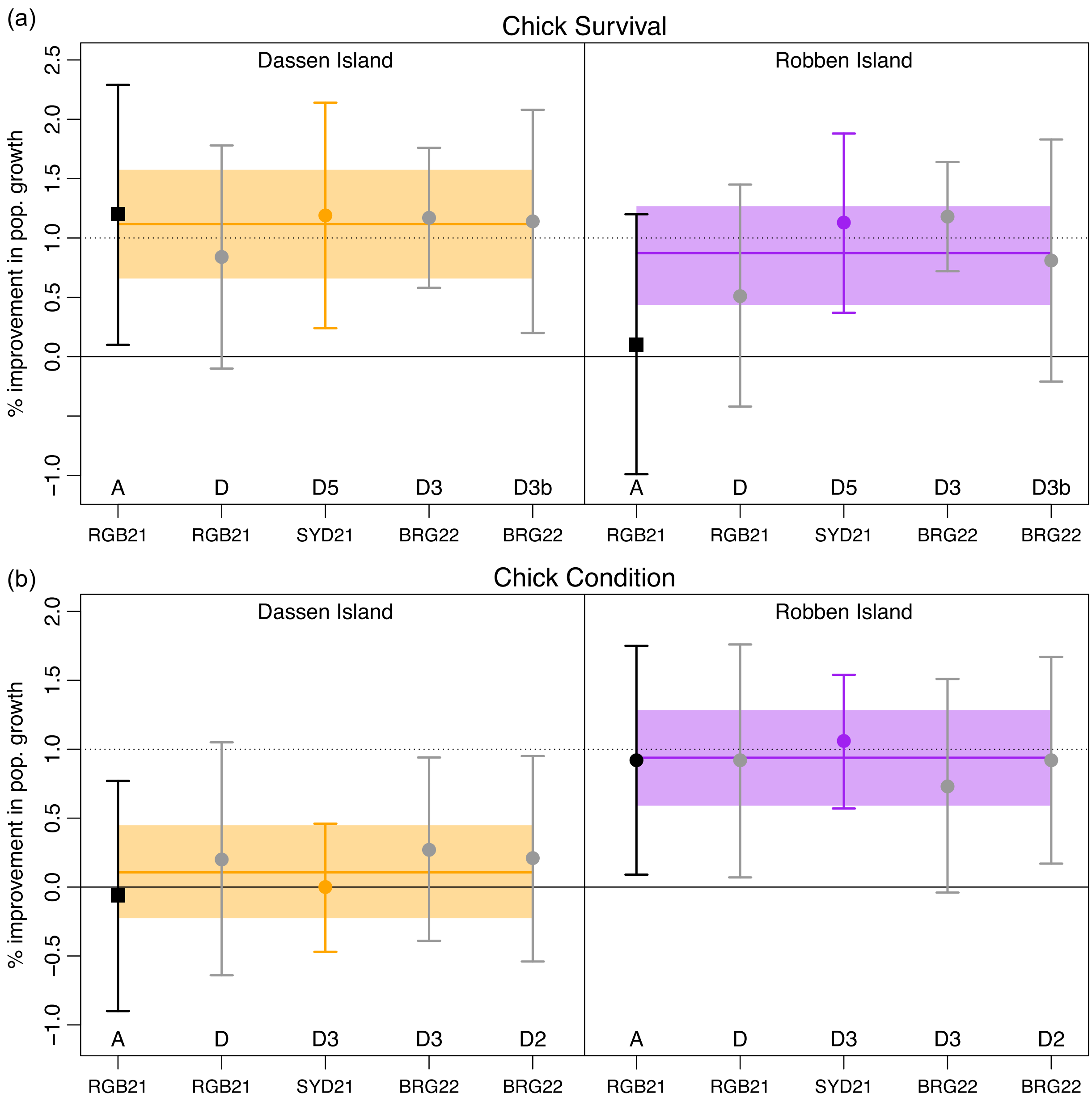

Figure 1. Comparison of various estimated island closure effects sizes and their uncertainty (95% confidence limits) expressed as % changes in the African penguin population growth rate that accrue from changes in (a) chick survival rates and (b) chick body condition (via the relationship described in Sherley et al. 2018 and based on Horswill et al. 2014). The horizontal black line shows a zero effect size and the horizontal dotted grey line shows a 1% improvement in the penguin population growth rate (a threshold agreed as indicative of a biologically meaningful impact of fishing in the context of the island closures; SM4 and SM6). The horizontal orange (Dassen Island) and purple (Robben Island) lines and polygons show the overall mean effect size and 95% credible intervals from all five models presented in each island-metric case estimated using hierarchical Bayesian meta-analyses (McCarthy and Masters 2005; SM12). All of these results come from models that have the same covariate structure in the fixed-effects component of the model (Island + Closure + Island × Closure), but differ in either the type of data used (labels above the *x*-axis: A = annually aggregated data are used, D = disaggregated (individual-observation-level) data are used) and the structure in the random-effects component of the model. The results labelled RGB21 show means ± 2 × standard error (SE) taken directly from Table 1 in Ross-Gillespie and Butterworth (2021). For each metric and each island, the result shown by the black square and error bars represents B&R-G's preferred approach using the aggregated data. The result labelled SYD21, in orange for Dassen Island and purple for Robben Island, shows the mean ± 1.96 × SE from the best fitting models that retained the Island × Closure interaction from Sydeman et al. (2021) – these models have Year/NestID (chick survival) or Year/Month (chick condition) as their random effect structure, which is also the structure used by Sherley et al. (2021a). Those labelled BRG22 show results using disaggregated data from Table SM-3 of B&R-G: D3 = the best fitting models (lowest AIC) from Table SM-3 of B&R-G (random effect = Year/NestID/Island for chick survival and Year/Month/Island for chick condition); D3b = the second-best fitting chick survival model from Table SM-3b (where the Year SD is fixed); D2 = the chick condition model with the random effect structure suggested by the 2020 panel (random effect = Year/Island; Haddon et al. 2020). The code and data to reproduce this figure are available on GitHub: https://github.com/rbsherley/IJMS_AP_IC.

(Cury *et al.*, 2011). Third, the extensive body of literature on "wasp-waist" food web dynamics (e.g., Cury *et al.*, 2000) clearly shows that forage fish control the trophic efficiencies from primary production to upper trophic level predators including seabirds, marine mammals, and large predatory fish. Moreover, the lack of observations on other effects are important to consider. For example, there is little evidence for the African penguin that widespread disease or consistent predation accounts for the high adult mortality rates observed (Sherley *et al.*, 2014; Robinson *et al.*, 2015), even though the estimated adult survival rate of African penguins (~0.711) is amongst the lowest measured for any seabird to date (Bird et al., 2020; SM8; see below for more discussion of this topic). In summary, there is wide agreement among seabird and marine ecosystem ecologists that food availability is a primary driver of the population dynamics of African penguins, as well as seabirds and other higher trophic level predators in general, though effects are often non-linear and can be challenging to model (e.g., see rebuttal of Pikitch *et al.*, 2018 to Hilborn *et al.*, 2017; Koehn *et al.*, 2021).

What Next? Recently, five sub-populations of penguins in South Africa have been extirpated, while seven other extant sub-populations are approaching "quasi-extinction" (<1000 individuals), population levels at which stochastic and Allee effects (e.g., Ryan *et al.*, 2012) may become more likely. We suggest that given the penguin's worsening conservation status, described by B&R-G and DFFE (2021) as dire, long-term closures for anchovy and sardine fisheries within the penguin's primary feeding habitats near breeding islands is a responsible incremental step in conservation and precautionary fisheries management. There is no disagreement that chronic suppression of African penguin breeding success (by fisheries or any other factor) will be detrimental to the penguin's recovery over time as effects are cumulative, and the long-term effects must be considered. We note that the long-term effect of fisheries closures at African penguin colonies has not been investigated, and cannot be assessed by the experiment conducted to date given the alternating schedule of closures (de Moor, 2020; SM9). Breeding success has delayed effects on seabird population dynamics that cannot easily be assessed by a decade-long field study (African penguins usually do not breed for the first time until they are 3–6 years old; Whittington *et al.*, 2005). Importantly, lessening the costs of reproduction during breeding could have positive effects on adult survival (e.g., Stearns, 1992; Dobson and Jouventin, 2010), and there is some evidence from the experiment that fisheries closures may reduce the cost of reproduction. As fisheries on forage fish extract fish and alter the prey fields available to seabirds, seabirds may move further away to forage more successfully (e.g., Bertrand et al., 2012; SM3). Having to travel further from their colonies to search for and handle prey carries an energetic cost, which may lessen and/or delay their ability to feed developing offspring, and affect the long-term body condition and survival of provisioning parents (Boersma and Rebstock, 2009).

Future research

We agree with B&R-G (2022) that continued monitoring and additional research on South Africa's coastal pelagic fish and fisheries and African penguin is warranted. We strongly disagree that "determining the causes of decline" is the priority question. It is very well known that the African penguin in South Africa suffers chronically poor adult (and possibly juvenile) survival and, with little doubt, prey availability and food limitation is the driving force behind these changes in survival and related drastic population collapse of ~5% pa since 2001 (and alarmingly ~10% pa on the Western Cape; Robinson *et al.*, 2015; Sherley *et al.*, 2020, 2021b). Removal and/or disruption of prey shoals by fisheries (i.e., exploitative and/or interference competition), could have effects on adult survival, as well as breeding success, but the effects of fisheries closures on adults have not been thoroughly examined. Indeed, the survival rate of breeding-age African penguins is well below the standard for a healthy seabird population (SM8), and is far below what is needed to maintain the population in equilibrium (~0.85–0.88, Crawford *et al.*, 2006). Adult survival is related to sardine abundance (Figure 5 in Crawford *et al.*, 2022; see also Robinson *et al.*, 2015 for a similar relationship on the inverse, i.e., mortality rates). According to DFFE (2021), sardines have been in a "depleted state" in South Africa since the mid-2000s. Seabirds have evolved life-history strategies to cope with fluctuating prey levels, but if low prey abundances are magnified by fishing, increased in frequency (Essington *et al.*, 2015), or are prolonged, the risk of significant population declines and extinction is heightened, especially for dietary specialist, foraging-range-restricted seabirds (Koehn *et al.*, 2021). Therefore, in our opinion, the next clear research step is to develop a better understanding of spatial and temporal variation (flux) in the sardine stock, fisheries effects on stock dynamics, and the effects of variation in sardine on adult survival and juvenile recruitment of the African penguin (see Trathan *et al.*, 2022). Both fisheries and climate-ecosystem dynamics have been implicated as responsible for changes in the distribution and relative abundance of sardine in South Africa (Coetzee *et al.*, 2008; Mhlongo *et al.*, 2015). Certainly more research along these lines would be illuminating for understanding the conservation status of the penguin, and for implementing well-designed ecosystem-based fisheries management.

Summary and conclusion

We are concerned that B&R-G's ongoing lack of concession on the minutia of modelling does not help to resolve the urgent socio-ecological issue at hand (Norberg *et al.*, 2022), — i.e., the plight of African penguins in southern Africa. Spatial protection around all major seabird colonies was implemented in Namibia in 2009 (Ludynia *et al.*, 2012), but similar long-term management is not in place in South Africa. The key findings of the experiment serve as a strong basis for implementing the spatial management tools that will slow the penguin's decline (SM10). Our exchange with B&R-G also serves as an example to the public that experts may not agree (Norberg *et al.*, 2022). We note that fisheries aggregations appear to concentrate near islands across the globe, with both the fisheries and seabirds extracting prey on the local scale, which is a pattern of concern (see Pichegru *et al.*, 2010, 2012; Watters *et al.*, 2020; Trathan *et al.*, 2021). Seabirds have long been used as indicators of fish availability by fishers (Sydeman *et al.*, 2017), so the overlap of birds and fisheries in time and space is not coincidental. In the case of African penguins and other central-place foraging seabirds, localized fisheries management in the form of spatial closures makes sense ecologically (Free *et al.*, 2021; SM11) and possibly economically as fisheries operating near colonies may be able to move a short distance and maintain landings. Critically, localized fisheries management can be adaptive and need not be permanent; the need for the closures could easily be re-evaluated in the future once harvest control rules that lead to mutually acceptable outcomes for fisheries and seabirds have been implemented (e.g., Koehn *et al.*, 2021), and/or the penguin population has recovered to an agreed-upon level. Thus, we support implementing a series of localized fisheries closures over the long-term to protect, as best as possible, the food resources of the six remaining large penguin colonies in South Africa.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

Conflict of interest statement

RBS contributed to the Small Pelagic Scientific Working Group of the Department of Environment, Forestry and Fisheries (South Africa) between 2010 and 2021.

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