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Food for Thought

South Africa's experimental fisheries closures and recovery of the endangered African penguin

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

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

Main text

A long-term and growing issue in marine ecosystem conservation and management concerns the simultaneous use in time and space of small pelagic fish and euphausiid crustaceans by industrial fisheries and marine wildlife, which may cause local- to regional-scale competition, and reduce prey availability to predators (Croll and Tershy, 1998; Smith *et al.*, 2011; Pikitch *et al.*, 2012, 2014; Sydeman *et al.*, 2017; Gremillet *et al.*, 2018). Fisheries' reductions in available prey can affect foraging behaviour and effort, rates of energy acquisition, and eventually population parameters such as breeding success or recruitment. This problem is particularly severe for seabirds

during reproduction when they are constrained to forage relatively close to colonies by offspring provisioning duties (Furness, 1982; Duffy and Schneider, 1994; Tasker *et al.*, 2000; Sydeman *et al.*, 2017; Free *et al.*, 2021). The daily metabolic requirements of seabirds during breeding when parents are feeding themselves and developing offspring are amongst the largest (proportional to body mass) estimated for marine vertebrates (Nagy *et al.*, 1999).

African penguins and food supplies

The most significant ongoing example of this issue concerns the critically imperiled African penguin *Spheniscus demersus*, which has suffered population fragmentation and a > 95% decline over the past century (Sherley *et al.*, 2020). It is now classified as endangered by the International Union for Conservation of Nature (Birdlife International, 2020) and is one of three most vulnerable penguin species globally (Boersma *et al.*, 2020). A combination of climate change and fisheries removals has reduced the availability of the penguins' primary food resources, including sardines *Sardinops sagax* and anchovies *Engraulis encrasicolus* in Namibia and South Africa (Coetzee *et al.*, 2008; Roux *et al.*, 2013; Crawford *et al.*, 2015, 2019; Sherley *et al.*, 2017). This decline in prey abundance has reduced the survival rates of adult and juvenile penguins, most acutely since 2000 (Sherley *et al.*, 2014, 2017; Robinson *et al.*, 2015). Recent adult survival estimates for African penguin (Sherley *et al.*, 2014; Robinson *et al.*, 2015) are extremely low in comparison to other seabirds in general (Hamer *et al.*, 2001; Appendix 2 in Schreiber and Burger, 2001; Supplementary Table S1 of Bird *et al.*, 2020), and food stress-related changes in survival and recruitment are believed to be the primary mechanism underpinning the population collapse.

The fisheries experiment

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

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

Chick survival

Survival of penguin offspring was studied within the central portion of the highly productive, yet extremely variable Benguela upwelling system (Figure 1). On Dassen and Robben islands, the African penguin once numbered over 300000 breeding pairs, but fewer than 3000 pairs remain today, representing ∼20% of the world's population (Sherley *et al.*, 2020). While forage fish abundance off the Western Cape varied substantially among the years of experimental time–area closures, survival of penguin chicks to the age of fledging, the key population parameter under scrutiny, increased during years when fishing was excluded from the foraging areas of breeding penguins (Sherley *et al.*, 2018, 2019; Sherley, 2020; Supplementary materials). While the exact effect sizes ranged from ∼2 to ∼11% depending on model structure (Supplemental materials), population models suggest that this increase in chick survival is sufficient to improve the penguin population growth rate by ∼0.5–1.2% per annum (Sherley *et al.*, 2018; OLSPS Marine, 2021; Ross-Gillespie and Butterworth, 2021). While other interventions also are required to increase the penguin's population growth rate, these analyses clearly demonstrate that (i) the forage fish fisheries operating in proximity to breeding colonies are competing with the penguins for food and (ii) permanent fisheries closures could offset ∼20% of the penguin population decline which has averaged ∼5% per annum (Sherley *et al.*, 2020). Given the high temporal and spatial variability in forage fish abundance (DFFE, 2021) and recent poor accessibility of some prey, notably anchovies (e.g. Crawford *et al.*, 2019), the finding of robust local-scale changes in offspring survival related to fisheries closures is remarkable. This result suggests that even quite small (<1100 km^2) fisheries time–area closures near breeding colonies are likely to positively affect breeding success in seabirds (Free *et al.*, 2021), and that larger permanent fisheries exclusion zones may confer even greater conservation benefits for ecosystems and marine wildlife.

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

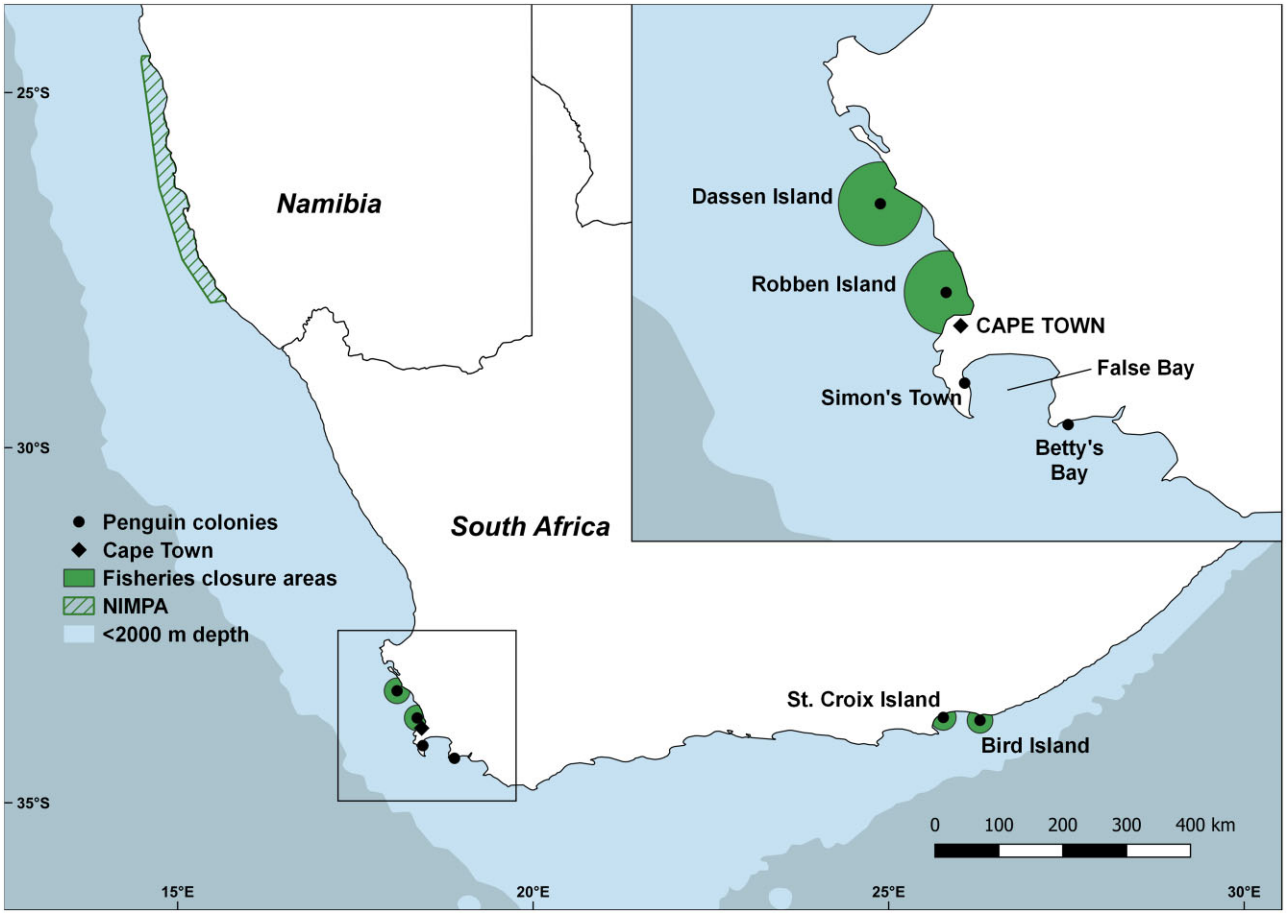

Figure 1. Map of southern Africa, showing South Africa and Namibia, locations of the African penguin colonies and fisheries closures adjacent to breeding islands, Cape Town, False Bay, and the Namibian Islands' Marine Protected Area (NIMPA).

through the use of a well-designed long-term field experiment (see preliminary comments in Sydeman *et al.*, 2017). The South African experiment thereby shows what is needed to assess the effects of forage fish fisheries at the local scale to seabirds breeding and foraging from colonies.

Foraging behaviour

While experimental fisheries closures have provided noteworthy results on breeding success at Robben and Dassen islands, the effects of fishing closures on penguin foraging behaviours, which may provide mechanistic explanations for changes in chick survival, were not definitive. Foraging parameters measured include foraging trip duration and maximum foraging distance, behaviours thought to respond to the local availability of food resources (Campbell *et al.*, 2019; McInness *et al.*, 2019). The estimates of the impacts on foraging behaviour are generally much more variable than those on chick survival or condition (Pichegru *et al.*, 2012; Ross-Gillespie and Butterworth, 2021), particularly for colonies on the Eastern Cape where chick survival data have not been collected and are therefore unavailable for context (Bird and St. Croix islands; Figure 1). The lack of robust results regarding penguin foraging behaviour undoubtedly relates to the high variability in foraging measurements among individuals that may be due to day-to-day changes in prey availability (cf. Bertrand *et al.*, 2012). Additionally, the foraging data collected to date are 2-dimensional; information on diving behaviour and use of the water column may reveal key changes in foraging effort relative to fisheries closures. More robust studies of individual movements and diving, however, would require effort and expense (Soanes *et al.*, 2013), and the rapid pace of decline of the penguin (Sherley *et al.*, 2020) limits what should be done next in terms of additional studies of foraging dynamics. Indeed, while the cost of devices to track seabirds has declined since the fisheries closures began in 2008, it has become increasingly difficult to find enough birds of the right age and stage of the breeding season for tracking studies. Most importantly, though, is the fact that measurements of foraging behaviour remain difficult to link to changes in survival of chicks, immature individuals, or adults, which are key elements in the recovery potential for African penguin and population ecology of seabirds in general.

Horizon scan

There are remarkably few BACI ocean experiments from which to draw comparisons about the efficacy of fisheries exclusions on fish availability to predators and wildlife population dynamics (Sydeman *et al.*, 2017). Following the widespread decline of Steller sea lions *Eumetopias jubatus* in the Alaskan North Pacific, 20–40-km trawling exclusion zones were established along the Aleutian Archipelago during the late 1990s. Regrettably, proposed replica-

tion of these time-area closures and control sites was not instituted as was done in South Africa, resulting in ambiguous findings (McDermott *et al.*, 2016). Additionally, in the early 2000s a quasi-experimental closure off the North Sea coast of the UK strongly suggested a negative impact of the sandeel *Ammodytes marinus* fishery on black-legged kittiwake *Rissa tridactyla* breeding productivity on the Isle of May, but not that of four diving species also breeding on the island (Frederiksen *et al.*, 2008). Elsewhere, data from Magellanic penguins *Spheniscus magellanicus*, a species found in Argentina that is closely related to the African penguin, shows that penguins that forage closer to their breeding colony have higher reproductive success, further supporting the importance of protected areas around penguin breeding colonies (Boersma and Rebstock, 2009; Boersma *et al.*, 2015). Looking forward, the Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR), of which South Africa is part, is considering implementing time–area closures of krill fisheries in Antarctic Peninsula ecosystems to protect penguin and seal breeding productivity (Trathan and Godø, 2018). Norway, South Korea, Japan, Ukraine, and other nations have economic or conservation interests in Antarctic krill fisheries, and the South African experiment demonstrates the value of area-based fisheries closures for marine predators. Finally, relative to this discussion, fisheries policies designed to eliminate the potential for localized prey depletion and effects on marine predators appear to work very well. In the Alaskan North Pacific, the U.S. North Pacific Fishery Management Council prohibited fishing for most forage fish (e.g. Pacific sand lance *Ammodytes hexapterus* and capelin *Mallotus villosus*) and euphausiid crustaceans in 1997 (Witherell *et al.*, 2000). Hence, in this region, forage fish fisheries competition with marine wildlife has never developed into a management issue, and its most important groundfish fisheries are considered healthy as a result of this basic policy to protect mid trophic level food resources for the benefit of all upper trophic level species.

Implications for penguin conservation

The African Penguin Biodiversity Management Plan guides conservation actions to facilitate penguin recovery in southern Africa. The original plan, which discussed a variety of ongoing threats to the penguin, called for provision of adequate prey resources in both the breeding and non-breeding seasons, with fisheries considered a key factor in determining year-round food resource availability. To date, the fisheries closure experiment has only addressed the potential effects on penguin breeding productivity. Given the key role of juvenile and adult survival to the decline in the penguin population (Sherley *et al.*, 2014, 2017; Robinson *et al.*, 2015), data collection could be broadened to investigate the importance of fishing during the non-breeding season by implementing pelagic time–area closures. Moreover, South Africa could link its approach with efforts to restore the marine ecosystem and fisheries of its Benguela Current Commission partner, Namibia (Utne-Palm *et al.*, 2010). The sardine fishery in Namibia was closed in 2018 after the stock dropped below the crash reference point of 50000 t of spawning biomass (Kainge *et al.*, 2020; Erasmus *et al.*, 2021) following over-fishing decades ago (Roux *et al.*, 2013). The Namibian Islands Marine Protected Area (NIMPA; Figure 1) was implemented in 2009 (Ludynia *et al.*, 2012) and is designed to promote both seabird and fisheries recovery. However, because the forage fish community was so severely depleted, Namibian African penguin populations collapsed and have yet to recover to any appreciable degree (Crawford, 2007; Sherley *et al.*, 2020). That this ecological breakdown persists after four years of a complete moratorium on sardine fishing in Namibia could be viewed as a worst-case scenario for the situation in South Africa if the fisheries and penguin competition is not carefully managed. The evidence suggests the importance of reducing competition with fisheries immediately to stem the decline of the African penguin.

To that end, the Minister of Forestry, Fisheries and the Environment has established a Governance Forum which is, in turn, seeking to find a balance between minimizing the costs to the small-pelagics fishing industry while maximizing the protection of foraging areas for breeding African penguins. Through a series of meetings, this group has developed a proposal to close areas around three penguin colonies to purse-seine fishing: Dassen Island, Dyer Island, and St. Croix Island (Coetzee *et al.*, 2021), which have all hosted populations of ∼20000 pairs at some point since 1979. Dyer Island occupies an important strategic location between the formerly large colonies on the Western Cape (Dassen and Robben islands) and the Eastern Cape colonies. St. Croix Island was, until recently, the only colony still home to > 3000 breeding pairs, but numbers there have declined sharply from ∼3600 pairs in 2019 to ∼1500 pairs in 2021 (Sherley *et al.*, 2020, 2021). Dassen Island was once the location of the largest African penguin colony in the meta-population and is the nearest colony of >150 pairs to Namibia (Sherley *et al.*, 2020). Continued increasing breeding productivity on Dassen Island, as has happened in the past decade with closures, could lead to spillover effects. For example, there may be increased dispersal and recruitment of young penguins into Namibia as well as to Robben Island near Cape Town (Sherley *et al.*, 2017). The public-relations opportunity of increasing the Robben Island population is enormous. At another colony in South Africa where the penguin population is relatively small but stable, Simon's Town (also known as "Boulders"; Sherley *et al.*, 2020; Figure 1), penguin ecotourism is valued at >10 million USD/year (van Zyl, 2014; van Zyl and Kinghorn, 2018). The Robben Island population, once numbering about 8500 pairs (Sherley *et al.*, 2020), is visited by approximately 325000 people/year (2017–2019; https://nationalgovernment.co.za/entity_annual/1936/2019-robben-island-museum-annual-report.pdf). Thus, visitor access to Robben Island penguins allows South Africa to engage and educate hundreds of thousands of people as they visit a recovering penguin colony. This opportunity to herald the fisheries closures could enhance appreciation for marine wildlife and demonstrate the commitment of South Africa to manage fisheries using a multi-species, ecosystem-wide perspective.

Conclusion

The scientific, conservation, and economic value of South Africa's long-term fisheries closures for forage fish and penguins is considerable. The Benguela Current ecosystem is highly dynamic and both fish and penguins are mobile. On one hand, we know that many seabird species, including the African penguin, exhibit a non-linear threshold response in breeding success to fluctuations in local forage stock abundance (Cury *et al.*, 2011) and to the distance they must travel to feed chicks (Boersma and Rebstock, 2009; Weber *et al.*, 2021). On the other hand, Free *et al.* (2021) suggest that mobile marine top predators and forage fish may not respond to fisheries protected areas as well as more immobile organisms, though this depends upon the persistence of forage patches within the birds foraging range (e.g. Davoren *et al.*, 2003). There is recognition, however, that restricting fishing near predator breeding locations

would likely produce greater benefits (Free *et al.*, 2021). This is also supported by key results from the Western Cape, which show the importance of fisheries time–area closures to centrally foraging African penguins. Indeed, the closure experiment has demonstrated that protecting primary foraging areas to safeguard predators' access to marine food resources reduces competition with forage fish fisheries.

The African penguin shares life history traits with other seabird species, and its fisheries case history resembles other ongoing and developing fisheries–wildlife conflicts both in South Africa and elsewhere in the world (e.g. Frederiksen *et al.*, 2008; Bertrand *et al.*, 2012; Watters *et al.*, 2020). Because most seabirds breed on land in conspicuous groups, their lifestyle provides opportunities to measure and evaluate important traits such as offspring production and survival of juveniles and adults, thereby providing clear results of experimental forage fish fisheries manipulations. South Africa fisheries management may be considered a model system for resolving complex natural resources management issues in marine ecosystems globally. If fisheries exclusions can be continued and perhaps increased in number and area, the recovery and health of the African penguin throughout its range and the scientific basis for solutions to minimize the impacts of forage fish fisheries on marine wildlife could be significantly enhanced.

Supplementary data

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

Data availability

No data were used in the production of the main text of this article, however, there were data utilized in the analyses described in the Supplementary materials. Those data and their associated code are available on GitHub (https://github.com/rbsherley/IJMS_AP_IC). Please see the Supplementary material for more information.

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