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1 **Food limitation of seabirds in the Benguela ecosystem and management of their prey base**

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19
20 **Abstract**

21 Four of seven seabirds that are endemic to the Benguela ecosystem (African Penguin *Spheniscus*
22 *demersus*, Cape Gannet *Morus capensis*, Cape Cormorant *Phalacrocorax capensis*, Bank Cormorant *P.*
23 *neglectus*) compete with fisheries for prey and have an IUCN classification of Endangered. Prey
24 depletion and food resource limitations have been major drivers of recent large population decreases of
25 each of these species. As populations decrease, colony sizes also dwindle rendering them susceptible to
26 Allee effects and higher probabilities of extinction. Therefore, it is necessary to maintain colonies at sizes
27 that minimise their probability of extinction. Means to ensure an adequate availability of food to
28 achieve this goal include closing important seabird foraging areas (often adjacent to key colonies) to
29 relevant fishing, implementing ecosystem thresholds below which such fishing is disallowed (which are
30 also expected to benefit forage resources) and, should there be an altered distribution of prey,
31 attempting to establish seabird colonies close to the new location of forage resources.

32
33 **1. Introduction**

34 This paper provides a brief review of food limitation of four Endangered (EN) seabirds that breed in
35 the Benguela ecosystem, of the viability of seabird colonies and Allee effects, of forage and consumption
36 thresholds and of potential management interventions that may enhance food availability. The locations
37 of some of the system's important seabird colonies are shown in Figure 1.

38

39 **2. Status of the Benguela's seabirds**

40 Fifteen seabird species breed in the cool Benguela ecosystem, which extends from about Benguela in
41 Angola to Woody Cape in South Africa, being bounded in the north and southeast by the warm Angola
42 and Agulhas Currents, respectively (Figure 1). Seven of these are endemic to the ecosystem (Hockey et
43 al. 2005). Of the endemic species, in terms of criteria of the International Union for Conservation of
44 Nature (IUCN) four are EN (African Penguin *Spheniscus demersus*, Cape Gannet *Morus capensis*, Cape
45 Cormorant *Phalacrocorax capensis*, Bank Cormorant *P. neglectus*), one is Vulnerable (VU, Damara Tern
46 *Sternula balaenarum*), one is Near-Threatened (NT, Crowned Cormorant *Microcarbo coronatus*) and
47 Hartlaub's Gull *Larus hartlaubii* is Least Concern (LC, IUCN 2020). The non-endemic Leach's Storm Petrel
48 *Hydrobates leucorhous* (or *Oceanodroma leucorhoa*) is VU, whereas the other seven non-endemics are LC
49 (IUCN 2020). Although substantial numbers of Leach's Storm Petrel migrate from the Northern
50 Hemisphere into the Benguela system (Pollet et al. 2019), the breeding population of this species in
51 South Africa is Critically Endangered (CR, Taylor et al. 2015). In South Africa small, isolated populations
52 of Great White Pelican *Pelecanus onocrotalus*, Caspian Tern *Hydroprogne caspia* and Roseate Tern
53 *Sterna dougallii* are regarded as regionally VU (Taylor et al. 2015). Leach's Storm Petrel and Roseate
54 Tern do not breed in Namibia, where the Cape Gannet is considered CR (Kemper 2015), the Great White
55 Pelican and Caspian Tern VU (Simmons 2015a, b) and the Damara Tern NT (Simmons et al. 2015).

56

57 **3. Importance and evidence of food limitation**

58 For a seabird population to be self-sustaining, mortality from its mature component must be
59 balanced by recruitment or immigration. Recruitment is influenced by age at first breeding, breeding
60 participation (proportion of mature birds electing to breed), breeding frequency (number of clutches
61 produced annually), breeding success (chicks fledged per clutch) and survival from fledging to breeding.
62 Insufficient food resources may negatively affect these demographic parameters leading to population
63 decreases, as is described below for the Benguela's four EN seabird species, which all feed mainly on
64 three forage resources that are heavily exploited by fisheries when these are readily available. African
65 Penguin, Cape Gannet and Cape Cormorant feed preferentially on sardine *Sardinops sagax* and anchovy
66 *Engraulis encrasicolus* (Hockey et al. 2005). In South Africa, the intensively fished West Coast rock
67 lobster *Jasus lalandii* is an important prey of Bank Cormorant (Dyer et al. 2019), whereas in Namibia the
68 lightly-exploited but nutritionally-deficient bearded goby *Sufflogobius birarbatus* is one of its staple
69 foods (Ludynia et al. 2010a). After the collapse of sardine in Namibia in the 1970s, bearded goby also
70 replaced it as the dominant prey item for African Penguins breeding in Namibia (Ludynia et al. 2010b).

71

72 ***African Penguin***

73 Large decreases of African Penguins at colonies between Lüderitz in Namibia and Dassen Island off
74 west South Africa from the 1960s to the 1980s were recorded following the collapse of sardine stocks
75 off Namibia and South Africa. North of Lüderitz, increases at Mercury and Ichaboe islands after the
76 1960s probably resulted from an increased local abundance of bearded goby (Crawford and Shelton
77 1978, Shelton et al. 1984, Crawford et al. 1985, 2001a). However, this did not prevent an overall
78 decrease of 90% in penguins breeding in Namibia between 1956 and the early 2000s (Figure 2, Crawford
79 2007).

80 By contrast, an increase between the 1950s and 1970s and a later decrease in numbers of penguins
81 at Dyer Island, southwest South Africa, coincided with an increase and subsequent fluctuations in

82 anchovy abundance (Crawford 1998). From 1989–2009 numbers of penguins breeding along west South
83 Africa were significantly correlated with the overall biomass of sardine and anchovy in South Africa, as
84 also was the case from 1999–2009 in Algoa Bay (Figure 2, Crawford et al. 2011). The formation of new
85 penguin colonies at Stony Point and Boulders on South Africa’s mainland and at Robben Island, and
86 increases at these colonies and at Dassen Island, took place during a period of recovery of South Africa’s
87 sardine in the 1980s and 1990s and an increase in the biomass of anchovy at the start of the 21st
88 century. This led to an overall increase in the numbers of penguins breeding in west South Africa
89 (Underhill et al. 2006).

90 After 2004, large decreases in numbers of penguins breeding in west South Africa were associated
91 with a shift to the south and east of adult anchovy and sardine and a collapse of sardine (Crawford et al.
92 2011). Concomitant with the altered distribution of prey there were decreases in penguins at all South
93 African colonies north of Cape Town (the northernmost colony at Lambert’s Bay became extinct in 2006;
94 Crawford et al. 2013). By contrast, in the south numbers increased or stabilized at Boulders and Stony
95 Point and penguins attempted to form a new colony at De Hoop Nature Reserve (Underhill et al. 2006,
96 Crawford et al. 2011). Although trends in numbers of African Penguins at colonies are often regionally
97 coherent (Underhill et al. 2006), at Dyer Island, also in the south, penguins decreased in the 2000s. This
98 may have resulted from heavy exploitation of sardine in its vicinity: 70,000 tonnes of sardine were
99 caught within 30 km of Dyer Island in 2004 (Ludynia et al. 2014) and the exploitation rate of sardine
100 west of Cape Agulhas rose to 30–44% in 2002 and from 2005–2007 (Coetzee et al. 2008). When the
101 colony size at Dyer Island was > 3,500 pairs, numbers of penguins breeding there were negatively
102 related to sardine catches made within 20 nautical miles of the island (Ludynia et al. 2014), suggesting
103 an impact of catches on local food availability.

104 Local or regional abundances or availability of sardine and anchovy have been related to numbers of
105 African Penguins breeding (Crawford 2007, Crawford et al. 2011, Sherley et al. 2013), to adult and

106 immature survival (Crawford et al. 2011, 2019, Sherley et al. 2014, Robinson et al. 2015), to age at first
107 breeding (Whittington et al. 2005), to breeding participation (Crawford et al. 1999b, Durant et al. 2010),
108 to breeding success (Adams et al. 1992, Crawford and Dyer 1995, Crawford et al. 1999b, 2006a, Cury et
109 al. 2011, Sherley et al. 2013) and to foraging performance (Pichegru et al. 2010, Campbell et al. 2019,
110 McInnes et al. 2019). Additionally, onset of breeding was probably delayed during a period of food
111 scarcity (Crawford and Dyer 1995) and the chick fledging period was negatively correlated with prey
112 abundance (Sherley et al. 2013). Delayed breeding and longer fledging periods may reduce the breeding
113 frequency and cause abandonment of unfledged chicks when parents are constrained to leave colonies
114 for pre-moult fattening (Crawford et al. 2018).

115

116 ***Cape Gannet***

117 In Namibia, the Cape Gannet population decreased by 95% after the collapse of that country's
118 sardine stock in the 1970s (Figure 2, Crawford 2007). However, at the same time the numbers of
119 gannets in South Africa increased. Trends in the proportions of forage fish (sardine and anchovy) and
120 gannets found in Namibia and in South Africa were similar (Figure 3) suggesting an impact of food.
121 However, increases of gannets in South Africa did not offset losses in Namibia so that the overall
122 abundance of Cape Gannets decreased (Crawford et al. 2007a).

123 In the 21st century, the movement of Cape Gannets to the south and east continued with a decrease
124 in numbers breeding off west South Africa and an increase in Algoa Bay, matching a shift in the
125 distribution of their prey (Crawford et al. 2015, Sherley et al. 2019). In the west, foraging effort of Cape
126 Gannets increased and nest attendance decreased with reduced consumption of sardine and anchovy,
127 and adult body condition was negatively impacted by increases in the dietary proportion of hake
128 *Merluccius* sp. discarded by fisheries (Cohen et al. 2014). At Malgas Island, Cape Gannets had
129 substantially reduced breeding success when they fed their chicks mainly low-quality fish discards

130 (Grémillet et al. 2008). Between 2011 and 2014 there was a net deficit in energy expenditure during
131 foraging for most Cape Gannets tracked from Malgas Island (Grémillet et al. 2016).

132

133 ***Cape Cormorant***

134 In Namibia, numbers of Cape Cormorants decreased by 62% after the collapse of sardine in the 1970s
135 (Figure 2). It was a lesser decrease and occurred later than those of African Penguins and Cape Gannets,
136 possibly owing to Cape Cormorants benefitting from increased breeding space at Ichaboe Island and
137 making use of alternative prey in the form of bearded goby (Crawford 2007, Crawford et al. 2007b,
138 Erasmus et al. 2021). Additionally artificial nesting platforms constructed in central Namibia provided
139 breeding habitat for Cape Cormorants closer to the reduced range of the sardine (Crawford 2007). By
140 contrast, gannets and most penguins in Namibia bred in the south and suffered food shortages as the
141 sardine's range contracted northwards (Crawford 2007). Cape Cormorants colonised Ilha dos Tigres in
142 southern Angola in the 2000s and > 16,000 pairs bred there in 2017 (Mendelsohn and Haraes 2018).

143 Unlike in Namibia, numbers of Cape Cormorants breeding in west South Africa decreased in the mid-
144 1990s *prior to* recent decreases in that region of African Penguins and Cape Gannets (Crawford et al.
145 2007b). There were substantial mortalities of adult Cape Cormorants at several colonies in west South
146 Africa between 1991 and 2006 caused by avian cholera *Pasteurella multocida*, outbreaks of which may
147 be triggered by stressful events such as food limitation (Crawford et al. 1992a, Ward and Williams 2004,
148 Waller and Underhill 2007). Its initial occurrence at Dassen Island may have been precipitated by a
149 scarcity of forage fish during 1989 and 1990 (Crawford et al. 1992a). Conforming to the recent shift in
150 the distribution of sardine and anchovy, Cape Cormorants decreased off northwest South Africa but
151 remained stable in the south, where new colonies formed (including at Robben Island and Stony Point)
152 and some others increased (Crawford et al. 2016).

153 When food is scarce, as well as experiencing increases in adult mortality, Cape Cormorants, like some
154 other cormorant species, often skip or abandon breeding or delay their first breeding attempt (Berry
155 1976, Crawford et al. 2001b, 2016, Crawford and Dyer 1995). They may also suffer extensive breeding
156 failure (Duffy et al. 1984, Crawford et al. 1992b). In November 2008, Cape Cormorants brooding small
157 chicks expended significantly greater foraging effort at Malgas and Dassen islands than at Dyer Island
158 farther south (Hamann et al. 2012). During May and June 2014 Cape Cormorants north of Cape Town
159 attempted to take bait from hand-lines used to fish for snoek *Thyrsites atun*, a behaviour not previously
160 observed and that suggested poor food availability at that time (Crawford et al. 2016).

161

162 ***Bank Cormorant***

163 In Namibia, Bank Cormorants decreased from 7,166 pairs in 1978–1980 to 3,735 pairs in 1995–1997;
164 a severe reduction of bearded goby in central Namibia in 1994 was a probable cause of the decrease
165 (Crawford et al. 1999a). In South Africa, Bank Cormorants decreased from 1,506 pairs in 1978–1980 to
166 846 pairs in 2010–2013 (Crawford et al. 2015). Total numbers breeding at 11 readily accessible localities
167 between Lambert’s Bay and Dyer Island fell from above 500 pairs during 1978–1987 to 350 pairs from
168 1995 to 2006. The most northern colony (Lambert’s Bay) was extinct by 1999 and there were substantial
169 decreases at the two largest colonies, Malgas and Dassen islands, which are north of Cape Town. There
170 was fluctuating growth at Robben Island, near Cape Town, where birds were oiled by spills in 1994
171 (*Apollo Sea*) and 2001 (*Treasure*). Farther east numbers at two colonies increased. These trends are
172 consistent with a reduced abundance of rock lobsters in the north and an expansion of this resource to
173 the east (Crawford et al. 2008). As with other endangered species, fishing in the immediate vicinity of
174 Malgas and Dassen islands may have reduced densities of lobsters below levels needed to sustain the
175 larger colonies of Bank Cormorants. Where rock lobsters had not been severely depleted, Bank
176 Cormorants showed a positive response to their local availability and modelling suggested that areas

177 with no-take of lobsters at 20–30 km around Bank Cormorant colonies would benefit the conservation
178 of this seabird (Sherley et al. 2017).

179

180 **4. Colony viability and Allee effects**

181 Traditionally, the Benguela’s four Endangered seabirds bred in large colonies and those three that
182 feed mostly on sardine and anchovy have often foraged in large multi-species flocks (Hockey et al.
183 2005). However, as populations have fallen, breeding colonies have decreased in size and on occasion
184 fragmented into smaller units (e.g. Cordes et al. 1999, Crawford et al. 2016, Sherley et al. 2019).

185 The probabilities of extinctions of different-sized colonies of African Penguins over 40 years were
186 obtained from empirical observations on the performance of 41 discrete colonies in southern Africa
187 from 1956–1996 (Crawford et al. 2001a). Only one (< 4 %) of 28 colonies that in 1956 had ≤ 50 pairs was
188 extant in 1996, compared to 26% of those having 251–1,000 pairs, 67% of those having 1,001–5,000
189 pairs and 100% of those with > 5,000 pairs (Figure 4). Whereas three of the 30 breeding colonies extant
190 in 2004 held > 5,000 pairs and, in terms of these probabilities, had no likelihood of extinction within 40
191 years, by 2019 none of the 25 remaining colonies had > 5,000 pairs so that all had some chance of
192 extinction during such a period. In 2019, fifteen colonies had < 250 pairs and hence a 96% chance of
193 extinction by 2059 (Figure 4). In 2019, only seven colonies held > 1,000 pairs and had a 67% probability
194 of surviving to 2059: Mercury Island in Namibia; Dassen, Robben, Dyer, St Croix and Bird (Algoa Bay)
195 islands and Stony Point in South Africa.

196 Fragmented seabird populations may suffer from Allee effects, i.e. reduced fitness at low population
197 size increasing their likelihood of extinction (Ryan et al. 2012). African Penguins that feed in groups have
198 a higher catch of prey per unit effort than solitary birds (McInnes et al. 2017), but colonies may become
199 too small for sufficient foraging groups to form (Ryan et al. 2012). For example, in 2012 more penguins
200 were documented foraging in a single flock of at least 158 birds (Ryan et al. 2012) than were breeding in

201 2019 at 10 of the 25 presumed extant African Penguin colonies. For plunge-diving Cape Gannets, highly-
202 synchronised prey pursuits, which are likely contingent on their ability to locate an adequate number of
203 conspecifics at sea, benefitted from improved foraging efficiency when feeding on sardine schools
204 (Thiebault et al. 2016). A lower number of individuals could also decrease the role of colonies as
205 information centres, or the possibility to use conspecifics as cues to locate prey (e.g. Thiebault et al.
206 2016). Again smaller colonies have a larger proportion of birds nesting at colony edges, where eggs and
207 chicks are at a greater risk to predation (e.g. Cordes et al. 1999), and sex-biased mortality (e.g. Pichegru
208 and Parsons 2014) may decrease productivity of monogamous breeders at small colonies. The higher
209 risks of extinction for small colonies make it imperative to maintain colony sizes above thresholds at
210 which Allee effects are manifest. Furthermore, small numbers of seabirds that have a late age at
211 maturity may take substantial periods to recover, even with fishery closures (e.g. Robinson et al. 2015).

212 In 2010, Mercury Island held 72% of the global population of Bank Cormorants (Roux and Kemper
213 2015) and 73% of Namibia's African Penguins (Crawford et al. 2013). In 2018, c. 70% of the overall Cape
214 Gannet population was at Bird Island, Algoa Bay at the eastern boundary of the Benguela ecosystem
215 (Sherley et al. 2019). In the 2010s, 54% of South Africa's Cape Cormorants bred at Dyer Island (Crawford
216 et al. 2016). Such congregations of large proportions of a species at a single locality may offset Allee
217 effects but render the species highly susceptible to local catastrophic events such as oil spills (e.g.
218 Crawford et al. 2000), disease outbreaks (e.g. Waller and Underhill 2007), severe weather events (e.g.
219 Randall et al. 1986) and reduced availability of resources.

220

221 **5. Forage thresholds**

222 ***Forage abundance thresholds***

223 In a meta-analysis of long-term studies in seven marine ecosystems from around the globe, Cury et
224 al. (2011) demonstrated key thresholds in prey (fish and krill) abundance, below which seabirds

225 dependent on that food type suffered reduced and more variable breeding success. The threshold was
226 equal to the long-term average biomass of prey and equivalent to one-third of the maximum observed
227 prey biomass. Similar relationships were established at the species level, namely for 13 of the 14
228 seabirds studied, including African Penguin and Cape Gannet from the Benguela ecosystem. The so-
229 called “1/3 for the birds” rule provides a benchmark for management of forage fish fisheries at a level
230 that would sustain seabird productivity over the long-term (Cury et al. 2011).

231 In a related study, Robinson et al. (2015) showed that annual mortality of adult African Penguins at
232 Robben Island increased markedly when the biomass of sardine aged 1 y or older off west South Africa
233 fell below 25% of its maximum value. The lower forage threshold observed for adult mortality (25%)
234 than for breeding success (33%) confirmed the theoretical prediction of Cairns (1987) that decreases in
235 forage abundance would influence seabird breeding success ahead of survival. When data for African
236 Penguins at Dassen and Robben islands were grouped, a generalised additive model (GAM) showed that
237 adult survival decreased when standardised (i.e. centred and scaled) sardine abundance off west South
238 Africa fell below a threshold of zero (Figure 5).

239 It is noteworthy that off west South Africa, Cape Gannets were better able to buffer effects of
240 reduced prey abundance than African Penguins (Distiller et al. 2012, Sherley et al. 2014, Robinson et al.
241 2015). After an eastward displacement of the main forage resources and the collapse of sardine
242 (Coetzee et al. 2008), adult gannets, due to their movement capabilities, were able to feed on
243 alternative food, such as saury *Scomberesox saury* and hake offal (Grémillet et al. 2008, 2019, Crawford
244 et al. 2014, 2019). Consequently, their survival was unrelated to standardised estimates of the overall
245 abundance of sardine and anchovy (Figure 5).

246

247 ***Forage consumption thresholds***

248 Saraux et al. (2021) investigated thresholds for the consumption of forage fish stocks by seabirds in
249 five marine ecosystems: off Norway, South Africa, Peru, in the Baltic Sea (Sweden) and at Shetland
250 (Scotland). In each of these systems, the predation pressure, estimated as the proportion of a forage fish
251 stock consumed by seabirds, was generally small (median = 1% of biomass) but increased sharply when
252 prey biomass decreased below a threshold of 15 to 18% of its maximum recorded value. A threshold of
253 18% was considered a limit not to be reached in order to avoid a sharp rise in the natural mortality rate
254 of forage fish resources, and below which extra cautious management of fisheries would be required
255 (Saroux et al. 2021). Similarly, Essington et al. (2015) advised that a risk-based management scheme that
256 reduces fishing when populations become scarce would protect both forage fish and their predators
257 from collapse, with little effect on long-term average catches.

258

259 **6. Other Forage Considerations**

260 ***Forage quality***

261 Condition of prey may influence its ability to sustain predator populations in addition to its
262 abundance (e.g. Grémillet et al. 2008). For example, poor food quality likely caused unprecedented
263 breeding failures at many seabird colonies on the east coast of Great Britain in 2004 (Wanless et al.
264 2005), decreased mass at fledging of Common Guillemots (Murre) *Uria aalge* in the Baltic Sea and
265 brought about breeding failures and mass mortality of this species in the Northeast Pacific in 2015–2016
266 (Osterblom et al. 2006, Piatt et al. 2020). In South Africa, the condition of sardine deteriorated in the
267 2000s (Ndjaula et al. 2013), possibly contributing to some of the seabird population decreases. As also
268 mentioned above, reliance on fish offal as a food source reduced Cape Gannet chick survival (Grémillet
269 et al. 2008).

270

271 ***Fisheries mortality***

272 In addition to contributing to collapses of forage resources (e.g. Essington et al. 2015), fishing may
273 cause localised depletion of prey; as such, the fisheries mortality rate (F) can be employed as another
274 management threshold. For example, the performance of three species of *Pygoscelis* penguins breeding
275 near the Antarctic Peninsula was reduced when local harvest rates of Antarctic krill *Euphausia superba*
276 were $\geq 10\%$ of the estimated biomass (Watters et al. 2020). By comparison, the exploitation rate of
277 South Africa's sardine west of Cape Agulhas increased substantially after 1999 and reached 44% in 2006
278 (Coetzee et al. 2008). Spatially explicit thresholds in fishing mortality need to be carefully defined to
279 assist in management of fish stocks so as to support viable seabird populations in the Benguela system.

280

281 ***Forage availability***

282 It is not only the absolute abundance of prey but also its availability that impacts energy acquisition,
283 demography and population trends of seabirds. For example, Crawford et al. (2019) used long-term
284 information on the diet of Cape Gannets off west South Africa to derive an index of the availability of
285 anchovy and sardine per unit biomass to seabirds in that region, terming it a Forage Availability Index
286 (*FAI*). The study demonstrated a substantial decrease in the availability of anchovy and sardine to
287 seabirds in the 2000s compared to the 1990s. Breeding numbers of Cape Gannets and Cape Cormorants
288 and survival of adult African Penguins at both Dassen and Robben islands were significantly related to
289 the *FAI*. For gannets, the numbers breeding increased when the *FAI*, which increases as anchovy and
290 sardine contribute more to the diet, was $> c. -1$ and for cormorants when it was $> c. 1$. The higher
291 threshold for Cape Cormorants than Cape Gannets at which numbers breeding were predicted to
292 increase probably resulted from the fact that, unlike Cape Gannets but similarly to African Penguins,
293 Cape Cormorants are mostly unable to access alternative food such as saury and hake offal (Crawford et
294 al. 2019). Notably, frequent aggregations of anchovy close to the seabed were thought to have reduced

295 their availability to purse-seiners, and were suggested as a reason for a large under-catch of the total
296 allowable catch (TAC) of anchovy in recent years (DAFF 2016).

297 The importance of prey depth was highlighted in a modelling study from the Humboldt upwelling
298 system off western South America, where it primarily determined foraging success of Peruvian Boobies
299 *Sula variegata* and Guanay Cormorants *P. bougainvilliorum*, which feed mainly on Peruvian anchoveta
300 *Engraulis ringens* (Boyd et al. 2017). Peruvian Boobies and Guanay Cormorants are the ecological
301 equivalents in that system of Cape Gannets and Cape Cormorants in the Benguela system (Crawford et
302 al. 2006b).

303 African Penguins and other diving piscivores may herd prey shoals upwards, thereby facilitating their
304 availability to surface-feeding predators (e.g. McInnes and Pistorius 2019). Hence their loss will influence
305 ecosystem functioning.

306

307 **7. Possible interventions to enhance food availability**

308 Various international agreements require participating parties to implement an ecosystem-based
309 approach to fisheries management (or ecosystem approach to fisheries, EAF). For example, the Code of
310 Conduct for Responsible Fisheries of the United Nations' Food and Agriculture Organisation, adopted in
311 1995, stated that *Management measures should not only ensure the conservation of target species but*
312 *also of species belonging to the same ecosystem or associated with or dependent upon the target species*
313 (<http://www.fao.org/3/v9878e/v9878e00.htm>). The sixth Aichi Target of the Convention on Biological
314 Diversity's Strategic Plan for Biodiversity 2011–2020 reads: *By 2020 all fish and invertebrate stocks*
315 *and aquatic plants are managed and harvested sustainably, legally and applying ecosystem based*
316 *approaches, so that overfishing is avoided, recovery plans and measures are in place for all*
317 *depleted species, fisheries have no significant adverse impacts on threatened species and*
318 *vulnerable ecosystems and the impacts of fisheries on stocks, species and ecosystems are within*

319 *safe ecological limits* (<https://www.cbd.int/convention/text/default.shtml>). In South Africa, the Marine
320 Living Resources Act of 1988 attempts to provide legislative support for the EAF but is in urgent need of
321 updating and further amendment better to achieve this (Cochrane et al. 2015).

322 One tool available to manage fisheries so as to avoid harmful impacts on associated or dependent
323 species (ADS) is marine spatial planning, for example the implementation of fishing closures around
324 important seabird colonies (e.g. Ludynia et al. 2012, Sherley et al. 2015, 2018). In northeast Scotland,
325 Black-legged Kittiwakes *Rissa tridactyla* benefitted from closure of fishing for sandeels *Ammodytes*
326 *marinus*, an important prey for kittiwakes, around breeding colonies (Daunt et al. 2008, Furness 2020).
327 In the Californian upwelling ecosystem off west North America, a precautionary ecosystem approach
328 that avoids localised depletion of forage resources (including anchovy and sardine) near predator
329 concentrations is deemed necessary. In 1983, nearshore (within 3 to 6 km of the coast) fishing for
330 anchovy was prohibited, the main objectives being to protect pre-recruit anchovy, live bait and
331 recreational fisheries, and predator forage (Pacific Fisheries Management Council 1983, Thayer and
332 Sydeman 2020). At the time, the anchovy-dependent Brown Pelican *Pelecanus occidentalis* was listed
333 as Federally Endangered in USA (Anderson et al. 1982). In the Humboldt upwelling ecosystem off west
334 South America, fishing for Peruvian anchoveta close to a Peruvian Booby colony increased the birds'
335 foraging effort. The more the fishery reduced the quantity of anchoveta in the area, the farther the
336 breeding boobies needed to forage from the colony to find food (Bertrand et al. 2012). In the Benguela
337 system, in which similarly to the California and Humboldt systems sardine and anchovy are key forage
338 resources, short-term fishery closures around African Penguin colonies, even though not matched to the
339 late age at recruitment and high mate and site fidelity of the penguins (Crawford et al. 2013), have
340 increased breeding productivity and decreased parental foraging costs (Pichegru et al. 2010, Sherley et al.
341 2015, 2018, Sydeman et al. 2021).

342 A second means to account for the foraging requirements of marine predators is the identification
343 and implementation of ecosystem thresholds, below which fishing would be prohibited. Ecosystem
344 thresholds have already been widely applied to minimise by-catch mortality of ADS in fisheries (e.g.
345 Rollinson et al. 2017, Da Rocha et al. 2021) and are increasingly proposed as means to ensure sufficient
346 quantities of prey for predators, such as seabirds (e.g. Cury et al. 2011, Smith et al. 2011, Sydeman et al.
347 2017, Hill et al. 2020). In the Californian upwelling ecosystem a harvest rule disallows fishing of sardine
348 when its biomass is below 150,000 metric tonnes (Pacific Fisheries Management Council 2003, Thayer
349 and Sydeman 2020).

350 A third mechanism to achieve adequate food for seabirds is to offset mismatches in the distributions
351 of the breeding localities and the prey of seabirds through establishment of colonies nearer to the food
352 supply. Guano platforms in Namibia served this purpose for Cape Cormorants (Crawford 2007) and an
353 attempt to establish a new African Penguin colony in South Africa closer to the present distributions of
354 sardine and anchovy has been initiated (BirdLife South Africa 2016).

355

356 ***Recommendations from the 2020 AEWA Benguela Current Forage Fish Workshop***

357 In November 2020, a *Benguela Current Forage Fish (BCFF) Workshop*, organized by the African-
358 Eurasian Migratory Waterbird Agreement (AEWA), in collaboration with the Benguela Current
359 Convention (BCC) and BirdLife South Africa, recommended actions to be undertaken as a matter of
360 urgency under the auspices of BCC, AEWA and the AEWA Benguela Coastal Seabird International
361 Working Group, as well as by the national governments of Angola, Namibia and South Africa. These
362 included:

- 363 • developing tools to increase the availability of sufficient forage [fish] for threatened endemic
364 Benguela seabird species, such as setting ecosystem thresholds (i.e. sizes of forage resource
365 populations below which a range of precautionary measures relating to fishing would be

366 implemented at various spatial scales) and closing key foraging areas to fishing, adjacent to major
367 seabird colonies;

368 • ensuring the existence or creation of suitable seabird breeding habitat within the contracted or
369 altered distributions of forage fish species to partially alleviate the impact of an altered
370 distribution of prey on affected seabird species;

371 • and facilitating and prioritising the recovery of seabird colonies to sufficient sizes to minimise
372 known and potential Allee effects, thus reducing the probability of colony extinctions (AEWA
373 2020).

374

375 **8. Conclusion**

376 In conclusion, it is apparent that food limitation has been a major driver of adverse trends in the
377 population sizes and conservation status of four Benguela seabirds that compete with fisheries for food.
378 Hence it will be important to manage the impact of fisheries on the availability of prey to these seabirds,
379 including through the use of measures that were successfully applied elsewhere or that have empirical
380 support for use in the Benguela ecosystem.

381

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387

388 **10. References**

389 Adams NJ, Seddon PJ, van Heezik YM. 1992. Monitoring of seabirds in the Benguela upwelling system:
390 can seabirds be used as indicators and predictors of change in the marine environment? *South*
391 *African Journal of Marine Science* 12: 959–974.

392 AEW. 2020. Benguela Current Forage Fish Workshop recommendations: 4 pp.

393 Anderson DW, Gress F, Mais KF. 1982. Brown Pelicans: influence of food supply on reproduction. *Oikos*
394 39: 23–31.

395 Berry HH. 1976. Physiological and behavioural ecology of the Cape cormorant *Phalacrocorax capensis*.
396 *Madoqua* 9: 5–55.

397 Bertrand S, Joo R, Arbulu C, Tremblay Y, Barbraud C, Weimerskirch H. 2012. Local depletion by a fishery
398 can affect seabird foraging. *Journal of Applied Ecology* 49: 1168–1177.

399 BirdLife South Africa. 2016. Proposal to re-establish an African Penguin colony at De Hoop Nature
400 Reserve. BirdLife South Africa, Cape Town: 18 pp.

401 Boyd C, Grünbaum D, Hunt GL, Punt AE, Weimerskirch H, Bertrand S. 2017. Effects of variation in the
402 abundance and distribution of prey on the foraging success of central place foragers. *Journal of*
403 *Applied Ecology* 54: 1362–1372.

404 Cairns DK. 1987. Seabirds as indicators of marine food supplies. *Biological Oceanography* 5: 261–271.

405 Campbell KJ, Steinfurth A, Underhill LG, Coetzee JC, Dyer BM, Ludynia K, Makhado AB, Merkle D,
406 Rademan J, Upfold L, Sherley RB. 2019. Local forage fish abundance influences foraging effort and
407 offspring condition in an endangered marine predator. *Journal of Applied Ecology* 13409: 1365–2664.

408 Cochrane KL, Joyner J, Sauer WHH, Swan J. 2015. An evaluation of the Marine Living Resources Act and
409 supporting legal instruments as a framework for implementation of an ecosystem approach to
410 fisheries in South Africa. *African Journal of Marine Science* 37: 437–456.

411 Coetzee JC, van der Lingen CD, Hutchings L, Fairweather TP. 2008. Has the fishery contributed to a major
412 shift in the distribution of South African sardine? *ICES Journal of Marine Science* 65: 1676–1688.

413 Cohen LA, Pichegru L, Grémillet D, Coetzee J, Upfold L, Ryan PG. 2014. Changes in prey availability
414 impact foraging behaviour and fitness of Cape gannets over a decade. *Marine Ecology Progress Series*
415 505: 281–293.

416 Cordes I, Crawford RJM, Williams AJ, Dyer BM. 1999. Decrease of African Penguins at the Possession
417 Island group, 1956–1995 – contrasting trends for colonial and solitary breeders. *Marine Ornithology*
418 27: 117–126.

419 Crawford RJM. 1998. Responses of African penguins to regime changes of sardine and anchovy in the
420 Benguela system. *South African Journal of Marine Science* 19: 355–364.

421 Crawford RJM. 2007. Food, fishing and seabirds in the Benguela upwelling system. *Journal of*
422 *Ornithology* 148 (Suppl 2): S253–S260.

423 Crawford RJM, Dyer BM. 1995. Responses by four seabirds to a fluctuating availability of Cape anchovy
424 *Engraulis capensis* off South Africa. *Ibis* 137: 329–339.

425 Crawford RJM, Shelton PA. 1978. Pelagic fish and seabird interrelationships off the coasts of South West
426 and South Africa. *Biological Conservation* 14: 85–109.

427 Crawford RJM, Cruickshank RA, Shelton PA, Kruger I. 1985. Partitioning of a goby resource amongst four
428 avian predators and evidence for altered trophic flow in the pelagic community of an intense,
429 perennial upwelling system. *South African Journal of Marine Science* 3: 215–228.

430 Crawford RJM, Allwright DM, Heyl CW. 1992a. High mortality of Cape Cormorants (*Phalacrocorax*
431 *capensis*) off western South Africa in 1991 caused by *Pasteurella multocida*. *Colonial Waterbirds* 15:
432 236–238.

433 Crawford RJM, Underhill LG, Raubenheimer CM, Dyer BM, Martin J. 1992b. Top predators in the
434 Benguela ecosystem – implications of their trophic position. *South African Journal of Marine Science*
435 12: 675–687.

436 Crawford RJM, Dyer BM, Cordes I, Williams AJ. 1999a. Seasonal pattern of breeding, population trend
437 and conservation status of bank cormorants *Phalacrocorax neglectus* off southwestern Africa.
438 *Biological Conservation* 87: 49–58.

439 Crawford RJM, Shannon LJ, Whittington PA. 1999b. Population dynamics of the African Penguin at
440 Robben Island. *Marine Ornithology* 27: 135–143.

441 Crawford RJM, Davis SA, Harding R, Jackson LF, Leshoro TM, Meÿer MA, Randall RM, Underhill LG,
442 Upfold L, Van Dalsen AP, Van der Merwe E, Whittington PA, Williams AJ, Wolfaardt AC. 2000. Initial
443 impact of the *Treasure* oil spill on seabirds off western South Africa. *South African Journal of Marine*
444 *Science* 22: 157–176.

445 Crawford RJM, David JHM, Shannon LJ, Kemper J, Klages NTW, Roux J-P, Underhill LG, Ward VL, Williams
446 AJ, Wolfaardt AC. 2001a. African Penguins as predators and prey – coping (or not) with change. *South*
447 *African Journal of Marine Science* 23: 435–447.

448 Crawford RJM, Dyer BM, Upfold L, Ward VL. 2001b. Age at first breeding of Bank, *Phalacrocorax*
449 *neglectus*, and Cape Cormorants, *P. capensis*. *Ostrich* 72: 145–148.

450 Crawford RJM, Barham PJ, Underhill LG, Shannon LJ, Coetzee JC, Dyer BM, Leshoro TM, Upfold L. 2006a.
451 The influence of food availability on breeding success of African penguins *Spheniscus demersus* at
452 Robben Island, South Africa. *Biological Conservation* 132: 119–125.

453 Crawford RJM, Goya E, Roux J-P, Zavalaga CB. 2006b. Comparison of assemblages and some life-history
454 traits of seabirds in the Humboldt and Benguela systems. *African Journal of Marine Science* 28: 553–
455 560.

456 Crawford RJM, Dundee BL, Dyer BM, Klages NTW, Meÿer MA, Upfold L. 2007a. Trends in numbers of
457 Cape gannets (*Morus capensis*), 1956/57–2005/06, with a consideration of the influence of food and
458 other factors. *ICES Journal of Marine Science* 64: 169–177.

459 Crawford RJM, Dyer BM, Kemper J, Simmons RE, Upfold L. 2007b. Trends in numbers of Cape
460 Cormorants (*Phalacrocorax capensis*) over a 50-year period, 1956–57 to 2006–07. *Emu* 107: 253–261.

461 Crawford RJM, Cockroft AC, Dyer BM, Upfold L. 2008. Divergent trends in bank cormorants
462 *Phalacrocorax neglectus* breeding in South Africa’s Western Cape consistent with a distributional
463 shift of rock lobsters *Jasus lalandii*. *African Journal of Marine Science* 30: 161–166.

464 Crawford RJM, Altwegg R, Barham BJ, Barham PJ, Durant JM, Dyer BM, Geldenhuys D, Makhado AB,
465 Pichegru L, Ryan PG, Underhill LG, Upfold L, Visagie J, Waller LJ, Whittington PA. 2011. Collapse of
466 South Africa’s penguins in the early 21st century: a consideration of food availability. *African Journal*
467 *of Marine Science* 33: 139–156.

468 Crawford RJM, Kemper J, Underhill LG. 2013. African Penguin (*Spheniscus demersus*). In: Garcia
469 Borboroglu P, Boersma PD (eds), Penguins Natural History and Conservation. University of
470 Washington Press, Seattle and London: 211–231.

471 Crawford RJM, Makhado AB, Waller LJ, Whittington PA. 2014. Winners and losers – responses to recent
472 environmental change by South African seabirds that compete with purse-seine fisheries for food.
473 *Ostrich* 85: 111–117.

474 Crawford RJM, Makhado AB, Whittington PA, Randall RM, Oosthuizen WH, Waller LJ. 2015. A changing
475 distribution of seabirds in South Africa – the possible impact of climate and its consequences.
476 *Frontiers in Ecology and Evolution* 3: 10, 1–10.

477 Crawford RJM, Randall RM, Cook TR, Ryan PG, Dyer BM, Fox R, Geldenhuys D, Huisamen J, McGeorge C,
478 Upfold L, Visagie J, Waller LJ, Whittington PA, Wilke CG, Makhado AB. 2016. Cape cormorants
479 decrease, move east and adapt foraging strategies following eastward displacement of their main
480 prey. *African Journal of Marine Science* 38: 373–383.

481 Crawford RJM, Makhado AB, Oosthuizen WH. 2018. Bottom-up and top-down control of the Benguela
482 ecosystem’s seabirds. *Journal of Marine Systems* 188: 133–141.

483 Crawford RJM, Sydeman WJ, Thompson SA, Sherley RB, Makhado AB. 2019. Food habits of an
484 endangered seabird indicate recent poor availability of abundant forage resources. *ICES Journal of*
485 *Marine Science* 76: 1344–1352.

486 Cury PM, Boyd IL, Bonhommeau S, Anker-Nilssen T, Crawford RJM, Furness RW, Mills JA, Murphy EJ,
487 Österblom H, Paleczny M, Piatt JF, Roux J-P, Shannon L[J], Sydeman WJ. 2011. Global seabird
488 response to forage fish depletion – one-third for the birds. *Science* 334: 1703–1706.

489 Da Rocha N, Oppel S, Prince S, Matjila S, Shaanika TM, Naomab C, Yates O, Paterson JRB, Shimooshili K,
490 Frans E, Kashava S, Crawford R. 2021. Reduction in seabird mortality in Namibian fisheries following
491 the introduction of bycatch regulation. *Biological Conservation* 253: 108915.

492 DAFF (Department of Agriculture, Forestry and Fisheries). 2016. Status of the South African Marine
493 Fishery Resources 2016. Cape Town, DAFF.

494 Daunt F, Wanless S, Greenstreet SPR, Jensen H, Hamer KC, Harris MP. 2008. The impact of the sandeel
495 fishery closure on seabird food consumption, distribution, and productivity in the northwestern
496 North Sea. *Canadian Journal of Fisheries and Aquatic Sciences* 65: 362–381.

497 Distiller G, Altwegg R, Crawford RJM, Klages NTW, Barham B. 2012. Factors affecting adult survival and
498 inter-colony movement at the three South African colonies of Cape Gannet. *Marine Ecology Progress*
499 *Series* 461: 245–255.

500 Duffy DC, Berruti A, Randall RM, Cooper J. 1984. Effects of the 1982–3 warm water event on the
501 breeding of South African seabirds. *South African Journal of Science* 80: 65–69.

502 Durant JM, Crawford RJM, Wolvaardt AC, Agenbag CJ, Visagie J, Upfold L, Stenseth NC. 2010. Influence of
503 feeding conditions on breeding of African penguins – importance of adequate local food supplies.
504 *Marine Ecology Progress Series* 420: 263–271.

505 Dyer BM, Cooper J, Crawford RJM, Sherley RB, Somhlaba S, Cockcroft A, Upfold L, Makhado AB. 2019.
506 Geographical and temporal variation in the diet of Bank Cormorants *Phalacrocorax neglectus* in
507 South Africa. *Ostrich* 90: 373–390.

508 Erasmus VE, Currie B, Roux J-P, Elwen SH, Kalola MS, Tjizoo B, Kathena JN, Iitembu JA. 2021. Predatory
509 species left stranded following the collapse of the sardine *Sardinops sagax* (Pappe, 1854) stock off
510 the northern Benguela upwelling system: a review. *Journal of Marine Systems* 224: 103623.

511 Essington TE, Moriarty PE, Froehlich HE, Hodgson EE, Koehn LE, Oken KL, Siple MC, Stawitz CC. 2015.
512 Fishing amplifies forage fish population collapses. *PNAS* 112: 6648–6652.

513 Furness RW. 2020. Sandeel stocks and seabirds in the North Sea. *AEWA Doc. BCFF Inf.* 6: 12 pp.

514 Grémillet D, Pichegru L, Kuntz G, Woakes AG, Wilkinson S, Crawford RJM, Ryan PG. 2008. A junk-food
515 hypothesis for gannets feeding on fishery waste. *Proceedings of the Royal Society of London B:*
516 *Biological Sciences* 275: 1149–1156.

517 Grémillet D, Péron C, Kato A, Amélineau F, Ropert-Coudert Y, Ryan PG, Pichegru L. 2016. Starving
518 seabirds: unprofitable foraging and its fitness consequences in Cape gannets competing with
519 fisheries in the Benguela upwelling ecosystem. *Marine Biology* 163: 35.

520 Grémillet D, Collet J, Weimerskirch H, Courbin N, Ryan PG, Pichegru L. 2019. Radar detectors carried by
521 Cape gannets reveal surprisingly few fishing vessel encounters. *PLoS ONE* 14: e0210328.

522 Hamann MH, Grémillet D, Ryan PG, Bonadonna F, van der Lingen CD, Pichegru L. 2012. A hard-knock life:
523 the foraging ecology of Cape cormorants amidst shifting prey resources and industrial fishing
524 pressure. *African Journal of Marine Science* 34: 233–240.

525 Hill SL, Hinke J, Bertrand S, Fritz L, Furness RW, Ianelli JN, Murphy M, Oliveros-Ramos R, Pichegru L,
526 Sharp R, Stillman RA, Wright PJ, Ratcliffe N. 2020. Reference points for predators will progress
527 ecosystem-based management of fisheries. *Fish and Fisheries* 21: 368–378.

528 Hockey PAR, Dean WRJ, Ryan PG (eds). 2005. *Roberts Birds of Southern Africa, 7th edn.* John Voelcker
529 Bird Book Fund, Cape Town.

530 IUCN. 2020. IUCN Red List version 2020-1. <https://www.iucnredlist.org>. Downloaded on 07 May 2020.

531 Kemper J. 2015. Cape Gannet *Morus capensis*. In: Simmons RE, Brown CJ, Kemper J (eds), *Birds to watch*
532 *in Namibia. Red, rare and endemic species.* Windhoek, Namibia: Ministry of Environment and
533 Tourism and Namibia Nature Foundation. pp 149–151.

534 Ludynia K, Jones R, Kemper J, Garthe S, Underhill LG. 2010a. Foraging behaviour of bank cormorants in
535 Namibia: implications for conservation. *Endangered Species Research* 12: 31–40.

536 Ludynia K, Roux JP, Jones R, Kemper J, Underhill LG. 2010b. Surviving off junk: low-energy prey
537 dominates the diet of African penguins *Spheniscus demersus* at Mercury Island, Namibia, between
538 1996 and 2009. *African Journal of Marine Science* 32: 563–572.

539 Ludynia K, Kemper J, Roux J-P. 2012. The Namibian Islands' Marine Protected Area: using seabird
540 tracking data to define boundaries and assess their adequacy. *Biological Conservation* 156: 136–145.

541 Ludynia K, Waller LJ, Sherley RB, Abadi F, Galada Y, Geldenhuys D, Crawford RJM, Shannon LJ, Jarre A.
542 2014. Processes influencing the population dynamics and conservation of African penguins on Dyer
543 Island, South Africa. *African Journal of Marine Science* 36: 253–267.

544 McInnes AM, Pistorius PA. 2019. Up for grabs: prey herding by penguins facilitates shallow foraging by
545 volant seabirds. *Royal Society open science* 6: 190333.

546 McInnes AM, McGeorge C, Ginsberg S, Pichegru L, Pistorius PA. 2017. Group foraging increases foraging
547 efficiency in a piscivorous diver, the African penguin. *Royal Society open science* 4: 170918.

548 McInnes AM, Ryan PG, Lacerda M, Pichegru L. 2019. Targeted prey fields determine foraging effort
549 thresholds of a marine diver: important cues for the sustainable management of fisheries. *Journal of*
550 *Applied Ecology* 56: 2206–2215.

551 Mendelsohn JM, Haraes L. 2018. Aerial census of Cape Cormorants and Cape Fur Seals at Baía dos Tigres,
552 Angola. *Namibian Journal of Environment 2* Section A: 1–6.

553 Ndjaula HO, Gerow KG, van der Lingen CD, Moloney CL, Jarre A. 2013. Establishing a baseline for
554 evaluating changes in body condition and population dynamics of sardine (*Sardinops sagax*) in the
555 southern Benguela ecosystem. *Fisheries Research* 147: 253–263.

556 Osterblom H, Casini M, Olsson O, Bignert A. 2006. Fish, seabirds and trophic cascades in the Baltic Sea.
557 *Marine Ecology Progress Series* 323: 233–238.

558 Pacific Fisheries Management Council. 1983. Northern Anchovy Fishery Management Plan Amendment
559 5. Portland, Oregon, 229 pp.

560 Pacific Fisheries Management Council. 2003. Allocation of the Pacific Sardine Harvest Guideline – Coastal
561 Pelagic Species Fishery Management Plan Amendment 11. Portland, Oregon, 48 pp.

562 Piatt JF, Parrish JK, Renner HM, Schoen SK, Jones TT, Arimitsu ML, Kuletz KJ, Bodenstein B, García-Reyes
563 M, Duerr RS, Corcoran RM, Kaler RSA, McChesney GJ, Golightly RT, Coletti HA, Suryan RM, Burgess
564 HK, Lindsey J, Lindquist K, Warzybok PM, Jahncke J, Roletto J, Sydeman WJ. 2020. Extreme mortality
565 and reproductive failure of common murres resulting from the northeast Pacific marine heatwave of
566 2014-2016. *PLoS ONE* 15: e0226087.

567 Pichegru L, Parsons NJ. 2014. Female-biased mortality in African penguins. *African Journal of Marine
568 Science* 36: 279–282.

569 Pichegru L, Grémillet D, Crawford RJM, Ryan PG. 2010. Marine no-take zone rapidly benefits Endangered
570 penguin. *Biology Letters* 6: 498–501.

571 Pollet IL, Ronconi RA, Leonard ML, Shutler D. 2019. Migration routes and stopover areas of Leach’s
572 Storm Petrels *Oceanodroma leucorhoa*. *Marine Ornithology* 47: 55–65.

573 Randall RM, Randall BM, Erasmus T. 1986. Rain-related breeding failures in Jackass Penguins. *Gerfaut
574 76: 281–288.*

575 Robinson WML, Butterworth DS, Plaganyi EE. 2015. Quantifying the projected impact of the South
576 African sardine fishery on the Robben Island penguin colony. *ICES Journal of Marine Science* 72:
577 1822–1833.

578 Rollinson DP, Wanless RM, Ryan PG. 2017. Patterns and trends in seabird bycatch in the pelagic longline
579 fishery off South Africa. *African Journal of Marine Science* 39: 9–25.

580 Roux J-P, Kemper J. 2015. Bank Cormorant *Phalacrocorax neglectus*. In: Simmons RE, Brown CJ, Kemper J
581 (eds). Birds to watch in Namibia: red, rare and endemic species. Ministry of Environment and
582 Tourism and Namibia Nature Foundation, Windhoek: 155–157.

583 Ryan PG, Edwards L, Pichegru L. 2012. African penguins *Spheniscus demersus*, bait balls and the Allee
584 effect. *Ardea* 100: 89–94.

585 Saraux C, Sydeman W, Piatt J, Anker-Nilssen T, Hentati-Sundberg J, Bertrand S, Cury P, Furness RW, Mills
586 JA, Österblom H, Passuni G, Roux J-P, Shannon LJ, Crawford RJM. 2021. Seabird-induced natural
587 mortality of forage fish varies with fish abundance: evidence from 5 ecosystems. *Fish and Fisheries*
588 22: 262–279.

589 Shelton PA, Crawford RJM, Cooper J, Brooke RK. 1984. Distribution, population size and conservation of
590 the Jackass penguin *Spheniscus demersus*. *South African Journal of Marine Science* 2: 217–257.

591 Sherley RB, Underhill LG, Barham BJ, Barham PJ, Coetzee JC, Crawford RJM, Dyer BM, Leshoro TM,
592 Upfold L. 2013. Influence of local and regional prey availability on breeding performance of African
593 penguins *Spheniscus demersus*. *Marine Ecology Progress Series* 473: 291–301.

594 Sherley RB, Abadi F, Ludynia K, Barham BJ, Clark AE, Altwegg R. 2014. Age-specific survival and
595 movement among major African penguin *Spheniscus demersus* colonies. *Ibis* 156: 716–728.

596 Sherley RB, Winker H, Altwegg R, van der Lingen CD, Votier SC, Crawford RJM. 2015. Bottom-up effects
597 of a no-take zone on endangered penguin demographics. *Biology Letters* 11: 20150237: 1–4.

598 Sherley RB, Botha P, Underhill LG, Ryan PG, van Zyl D, Cockcroft AC, Crawford RJM, Dyer BM, Cook TR.
599 2017. Defining ecologically-relevant scales for spatial protection using long-term data on an
600 endangered seabird and local prey availability. *Conservation Biology* 31: 1312–1321.

601 Sherley RB, Barham BJ, Barham PJ, Campbell KJ, Crawford RJM, Grigg J, Horswill C, McInnes A, Morris TL,
602 Pichegru L, Steinfurth A, Weller F, Winker H, Votier SC. 2018. Bayesian inference reveals positive but
603 subtle effects of experimental fishery closures on marine predator demographics. *Proceedings of the*
604 *Royal Society B*: 285: 20172443: 1–9.

605 Sherley RB, Crawford RJM, Dyer BM, Kemper J, Makhado AB, Masotla M, Pichegru L, Pistorius PA, Roux
606 J-P, Ryan PG, Tom D, Upfold L, Winker H. 2019. The status and conservation of Cape Gannets *Morus*
607 *capensis*. *Ostrich* 90: 335–346.

608 Simmons RE. 2015a. Caspian Tern *Hydroprogne caspia*. In: Simmons RE, Brown CJ, Kemper J (eds), *Birds*
609 *to watch in Namibia. Red, rare and endemic species*. Windhoek, Namibia: Ministry of Environment
610 and Tourism and Namibia Nature Foundation. pp 88–90.

611 Simmons RE. 2015b. Great White Pelican. In: Simmons RE, Brown CJ, Kemper J (eds), *Birds to watch in*
612 *Namibia. Red, rare and endemic species*. Windhoek, Namibia: Ministry of Environment and Tourism
613 and Namibia Nature Foundation. pp 173–175.

614 Simmons RE, Braby RJ, Braby SJ. 2015. Damara Tern *Sternula balaenarum*. In: Simmons RE, Brown CJ,
615 Kemper J (eds), *Birds to watch in Namibia. Red, rare and endemic species*. Windhoek, Namibia:
616 Ministry of Environment and Tourism and Namibia Nature Foundation. pp 91–95.

617 Smith ADM, Brown CJ, Bulman CM, Fulton EA, Johnson P, Kaplan IC, Lozano-Montes H, Mackinson S,
618 Marzloff M, Shannon LJ, Shin Y-J, Tam J. 2011. Impacts of fishing low-trophic level species on marine
619 ecosystems. *Science* 333: 1147–1150.

620 Sydeman WJ, Thompson SA, Anker-Nilssen T, Arimitsu M, Bennison A, Bertrand S, Boersch-Supan P,
621 Boyd C, Bransome N, Crawford RJM, Daunt F, Furness R, Gianuca D, Gladics A, Koehn L, Lang J,

622 Logerwell E, Morris T, Phillips EM, Provencher J, Punt A, Saraux C, Shannon L, Sherley R, Simeone A,
623 Wanless R, Wanless S, Zador S. 2017. Best practices for assessing forage fish fisheries – seabird
624 resource competition. *Fisheries Research* 194: 209–221.

625 Sydeman WJ, Hunt GL, Pikitch EK, Parrish JK, Piatt JF, Boersma PD, Kaufman L, Anderson DW, Thompson
626 SA, Sherley RB. 2021. South Africa’s experimental fisheries closures and recovery of the endangered
627 African penguin. *ICES Journal of Marine Science*. <https://doi.org/10.1093/icesjms/fsab231>

628 Taylor MR, Wanless RM, Peacock F (eds). 2015. The Eskom red data book of birds of South Africa,
629 Lesotho and Swaziland. BirdLife South Africa, Johannesburg.

630 Thayer J, Sydeman W. 2020. Implementing ecosystem considerations in California Current forage
631 fisheries. Presentation to AEWA Benguela Current Forage Fish Workshop: 20 pp.

632 Thiebault A, Semeria M, Lett C, Tremblay Y. 2016. How to capture fish in a school? Effect of successive
633 predator attacks on seabird feeding success. *Journal of Animal Ecology* 85: 157–167.

634 Underhill LG, Crawford RJM, Wolfaardt AC, Whittington PA, Dyer BM, Leshoro TM, Ruthenberg M,
635 Upfold L, Visagie J. 2006. Regionally coherent trends in colonies of African penguins *Spheniscus*
636 *demersus* in the Western Cape, South Africa, 1987–2005. *African Journal of Marine Science* 28: 697–
637 704.

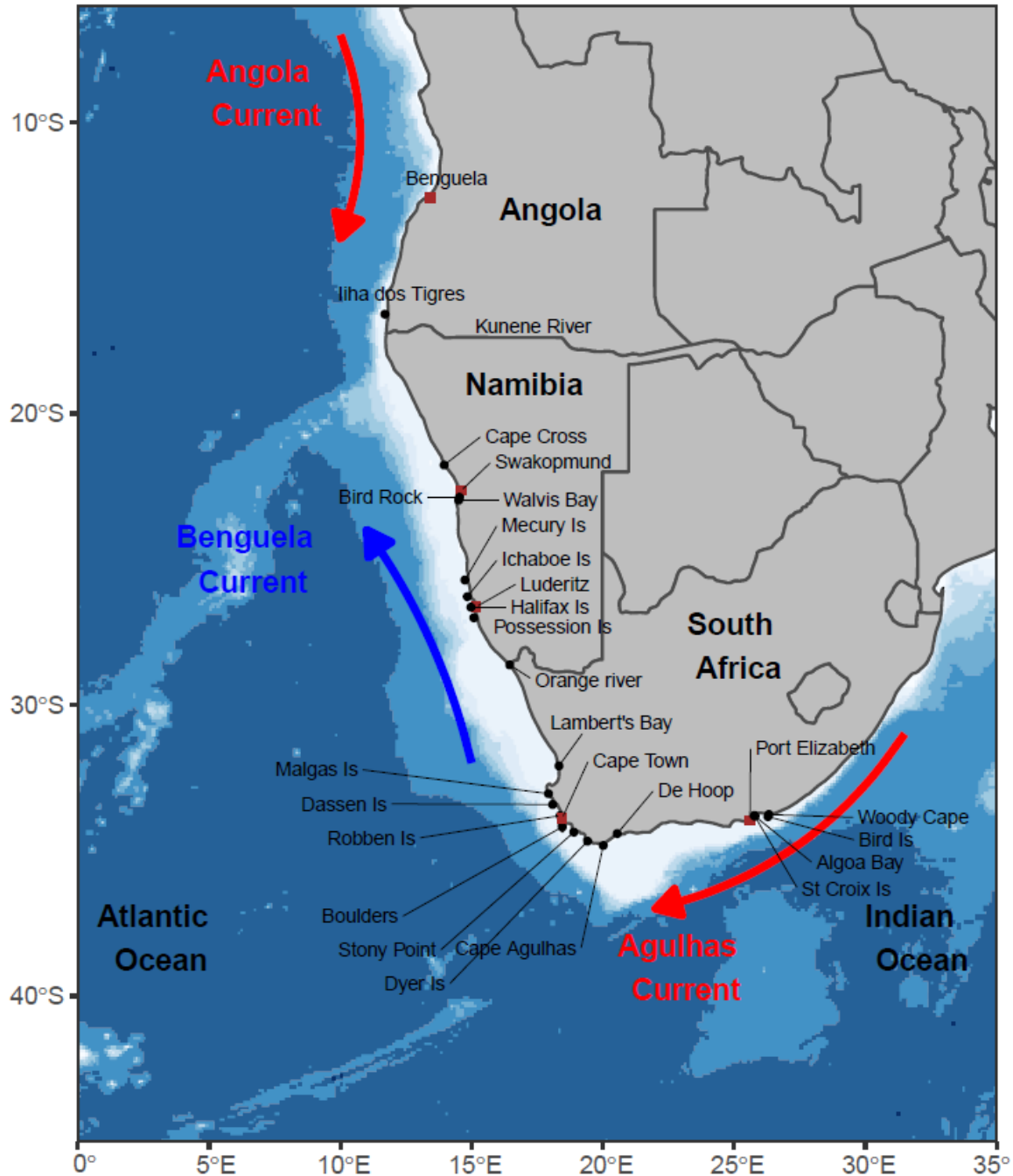
638 Waller LJ, Underhill LG. 2007. Management of avian cholera *Pasturella multocida* outbreaks on Dyer
639 Island, South Africa, 2002–2005. *African Journal of Marine Science* 29: 105–111.

640 Wanless S, Harris MP, Redman P, Speakman JR. 2005. Low energy values of fish as a probable cause of a
641 major seabird breeding failure in the North Sea. *Marine Ecology Progress Series* 294: 1–8.

642 Ward VL, Williams AJ. 2004. Coastal killers: causes of seabird mortality. *Bird Numbers* 13: 14–17.

643 Watters GM, Hinke JT, Reiss CS. 2020. Long-term observations from Antarctica demonstrate that
644 mismatched scales of fisheries management and predator-prey interaction lead to erroneous
645 conclusions about precaution. *Nature Scientific Reports* 10: 2314.

646 Whittington, P[A], Klages N[TW], Crawford R[JM], Wolfaardt A[C], Kemper J. 2005. Age at first breeding
647 of the African Penguin. *Ostrich* 76: 14–20.

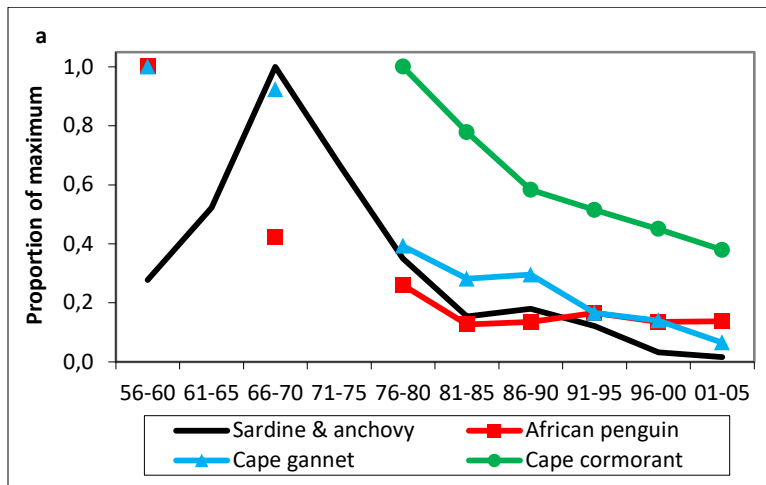


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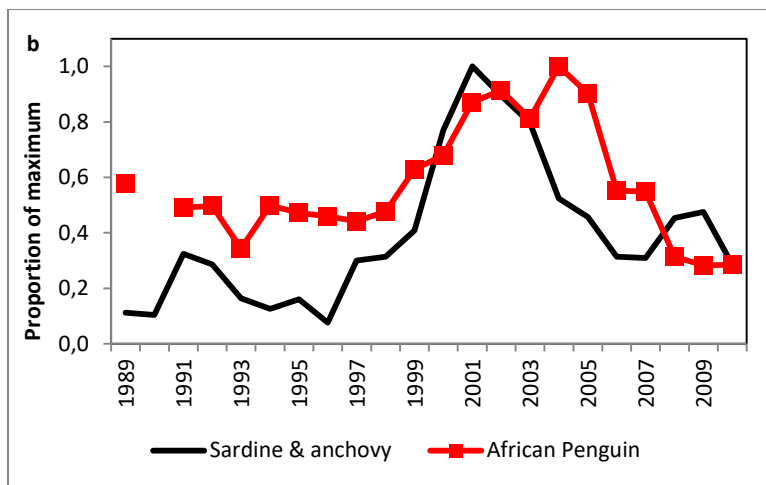
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650 **Figure 1.** A map of the Benguela Current ecosystem showing locations of some of the region's important
 651 seabird breeding colonies and other localities mentioned in the text.

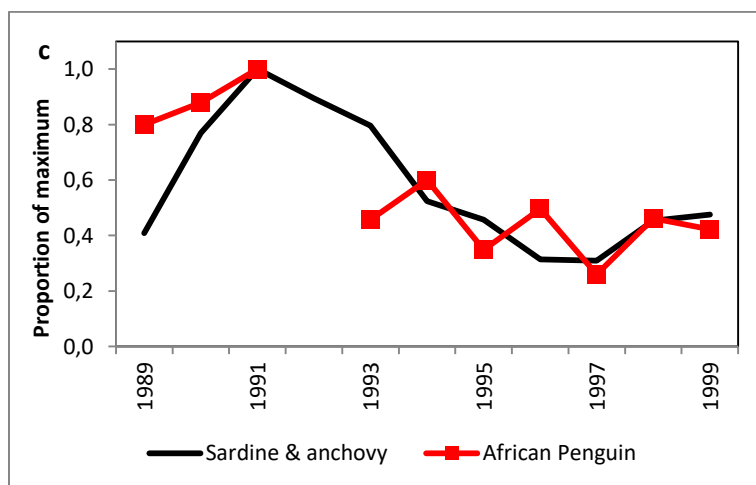
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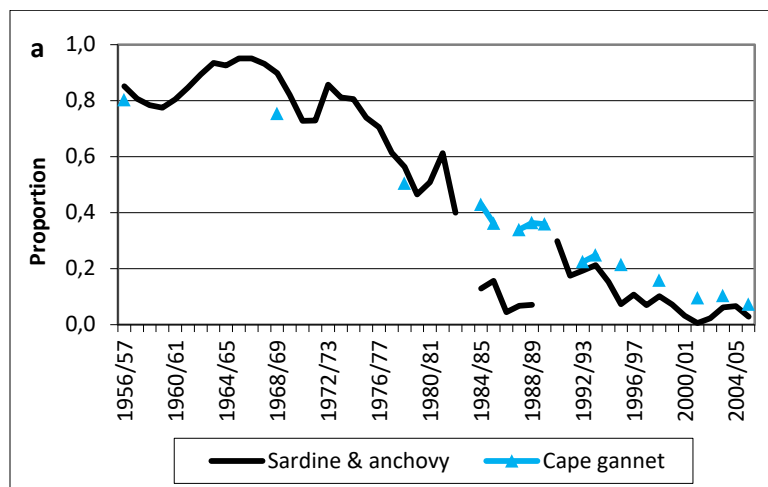
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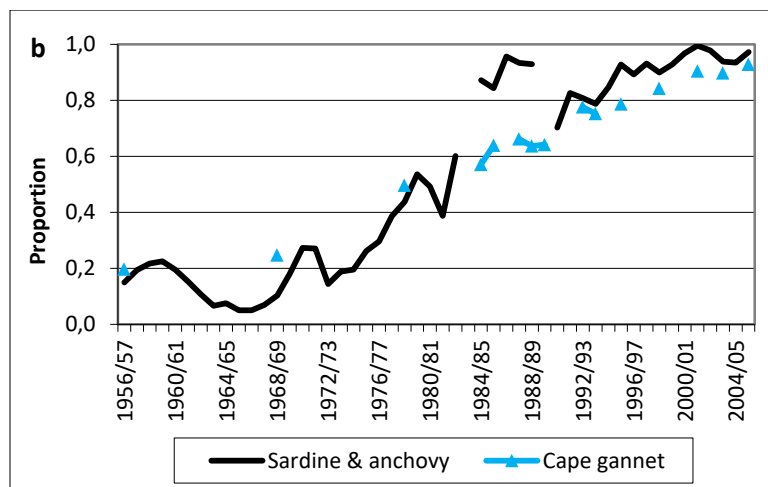
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656 **Figure 2.** Comparison of trends in standardised estimates (maximum = 1) of the combined biomass of
657 sardine and anchovy and breeding populations of seabirds that feed on these forage species for (a)
658 Namibia 1956/60–2001/05 (redrawn from information in Crawford 2007), (b) west South Africa 1989–
659 2010 and (c) Algoa Bay 1999–2009 (redrawn from information in Crawford et al. 2011). For west South
660 Africa and Algoa Bay fish estimates are for the whole of South Africa.

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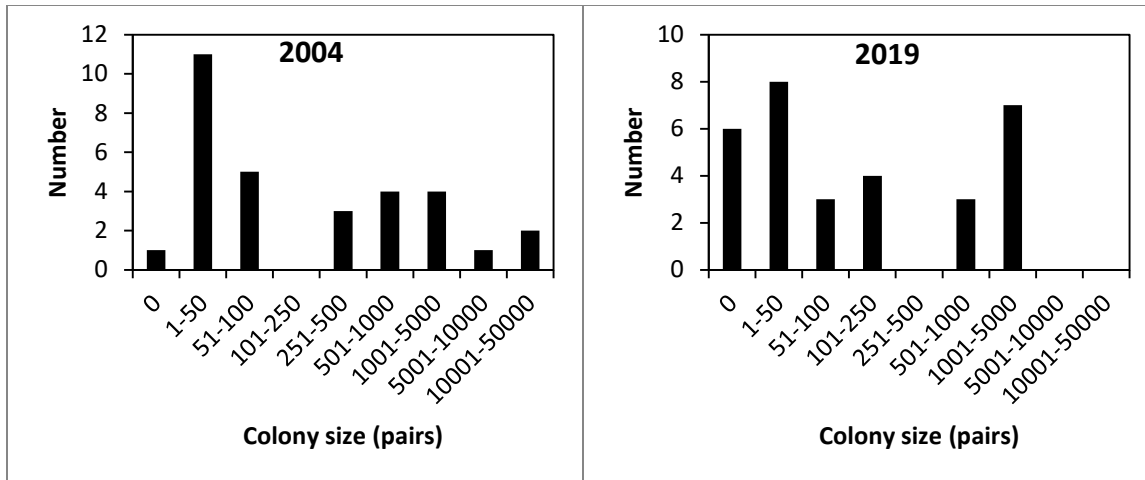
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665 **Figure 3.** Trends in the proportions of the Benguela ecosystem's sardine and anchovy and Cape Gannets
666 found in a) Namibia and b) South Africa, 1956/1957–2005/2006 (redrawn from information in Crawford
667 et al 2007a).



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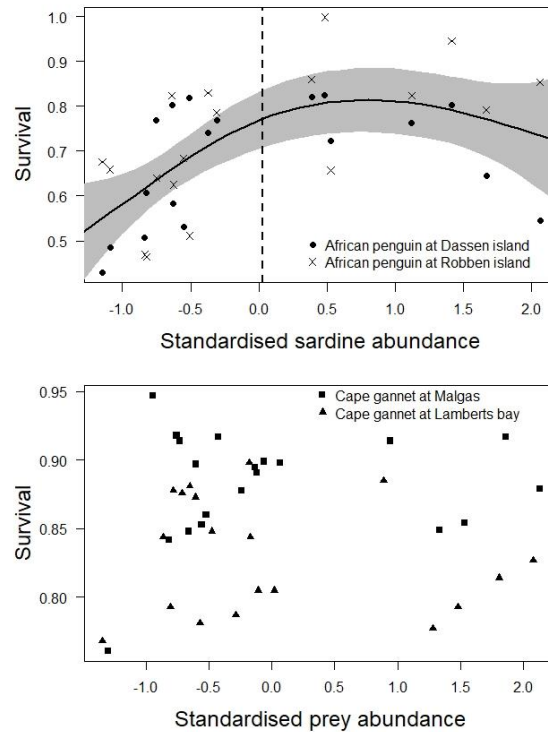
672 **Figure 4.** Top: numbers of African Penguin colonies of different sizes in 2004 (left) and 2019 (right).

673 Numbers of colonies where breeding occurred since 1956 that were extinct in 2004 and 2019 are

674 indicated by colony size = 0. Bottom: probabilities of extinction over a 40-y period of African Penguin

675 colonies of different sizes derived from empirical information in Crawford et al. (2001a).

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679 **Figure 5.** Estimated adult survival off west South Africa of (top) African Penguins at Dassen and Robben
 680 islands and (bottom) Cape Gannets at Lambert’s Bay and Malgas Island compared with the standardised
 681 abundance of prey off west South Africa (i.e. centred and scaled by dividing by the standard deviation).
 682 Estimates of survival were from Sherley et al. (2014) for African Penguins and Distiller et al. (2012) for
 683 Cape Gannets. Estimates of prey abundance were updated from Cury et al. (2011). The prediction (and
 684 95% confidence interval) of the GAM is indicated with the black curve (and grey polygon) for African
 685 Penguins. The vertical dashed line represents the threshold below which adult survival decreased
 686 markedly with decreasing sardine abundance. For Cape Gannets, no significant relationship was found
 687 between adult survival and prey (sum of anchovy and sardine) abundance.