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### Food limitation and minimum viable populations of seabirds in the Benguela Current Large Marine Ecosystem

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Evidence for food limitation of seabirds that breed in the Benguela Current Large Marine Ecosystem (BCLME) is summarized below. Ecosystem considerations and EAF (ecosystem approach to fisheries) interventions that relate to food limitation are briefly discussed. Additionally, Minimum Viable Populations (MVPs) of the Benguela's seabirds, especially African Penguins *Spheniscus demersus*, are considered. Finally, some lessons that may be learnt from the Benguela ecosystem regarding competition between fisheries and seabirds for prey are drawn.

#### Evidence for food limitation

Five seabirds that are endemic to the BCLME (four as species, one as a race) feed mostly on three forage resources that are heavily exploited by fisheries: sardine *Sardinops sagax*, anchovy *Engraulis encrasicolus* (both taken by purse-seine nets) and West Coast rock lobster *Jasus lalandii* (caught by a variety of gears). Four of the seabirds feed mainly on sardine and anchovy: African Penguin, Cape Gannet *Morus capensis*, Cape Cormorant *Phalacrocorax capensis* and the nominate race of Greater Crested (Swift) Tern *Thalasseus bergii bergii* (Hockey et al. 2005). In South Africa rock lobster is important in the diet of Bank Cormorant *P. neglectus*, whereas in Namibia bearded goby *Sufflogobius birarbatatus* is the main food of these birds and only lightly exploited by fisheries (Hockey et al. 2005).

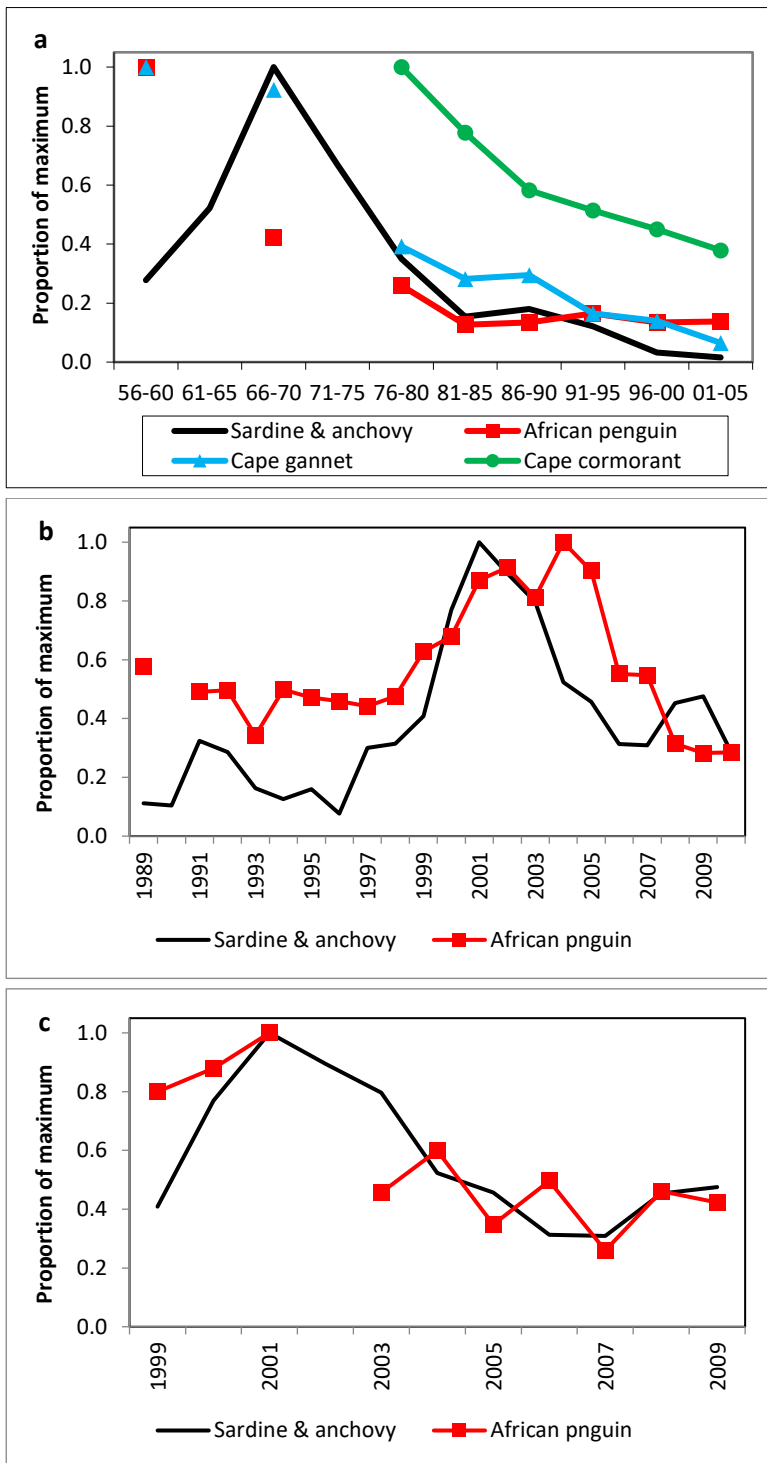
For these five seabirds there is potential for competition with fisheries for food, which has been emphasized by frequent congruence in trends in seabird numbers (or the guano they produce) and prey abundance, as well as by similar changes in the distributions of seabirds and their forage resources. Additionally, in instances strong relationships have been demonstrated between demographic or foraging parameters of seabirds and the availability of their prey. These similarities are briefly reviewed below.

Four of the endemic seabirds (African Penguin, Cape Gannet, Cape and Bank Cormorants) are classified as Endangered in terms of criteria of the International Union for Conservation of Nature (IUCN) on account of recent large decreases in their populations (BirdLife International 2020).

#### African Penguin

Large decreases of African Penguins at colonies between Lüderitz in Namibia and Dassen Island in the Western Cape from the 1960s to the 1980s followed collapses of sardine stocks off Namibia and South Africa. Increases at Mercury and Ichaboe islands north of Lüderitz after the 1960s probably resulted from an increased local abundance of bearded goby (Crawford and Shelton 1978, Shelton et al. 1984, Crawford et al. 1985, 2001a). However, this did not prevent a decrease of 90% in penguins breeding in Namibia between 1956 and the early 2000s (Figure 1, Crawford 2007).

An increase between the 1950s and 1970s and a later decrease in numbers of penguins at Dyer Island, south Western Cape coincided with an increase and then a fluctuating decrease of anchovy off South Africa (Crawford 1998). Large numbers of African Penguins abandoned a breeding attempt at Dyer Island in 1991, when anchovy in its vicinity was scarce (Crawford and Dyer 1995).



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

The formation of new penguin colonies at Stony Point and Boulders on South Africa’s mainland and at Robben Island and increases at these colonies and at Dassen and Vondeling islands took place during a period of recovery of South Africa’s sardine in the 1980s and 1990s and an increase in the biomass of anchovy at the start of the 21<sup>st</sup> century. This led to an overall increase in the numbers of penguins breeding in the Western Cape (Underhill et al. 2006). After 2004, large decreases in numbers of penguins breeding off western South Africa were associated with a shift to the south and east of adult anchovy and sardine and a collapse of sardine (Crawford et al. 2011). Concomitant with the altered distribution of prey there were decreases in penguins at all colonies located off northwest South Africa (the northernmost colony at Lambert’s Bay became extinct in

2006; Crawford et al. 2013). By contrast, in the south numbers increased or stabilized at Boulders and Stony Point and penguins attempted to form a new colony at De Hoop Nature Reserve (Underhill et al. 2006, Crawford et al. 2011). Trends in numbers of African Penguins at colonies are often regionally coherent (Underhill et al. 2006). However, at Dyer Island, also in the south, penguins decreased in the 2000s. This may have resulted from heavy exploitation of sardine in its vicinity (Crawford et al. 2011). More than 220,000 tonnes of sardine were caught within about 30 km of Dyer Island during 2002–2004 (JJ van der Westhuizen, Department of Agriculture, Forestry and Fisheries, in litt.) and the exploitation rate of sardine west of Cape Agulhas rose to 30–45% in 2002 and from 2005–2007 (Coetzee et al. 2008). When colony size at Dyer Island was > 3,500 pairs, numbers breeding there were negatively related to sardine catches made within 20 nautical miles of the island (Ludynia et al. 2014).

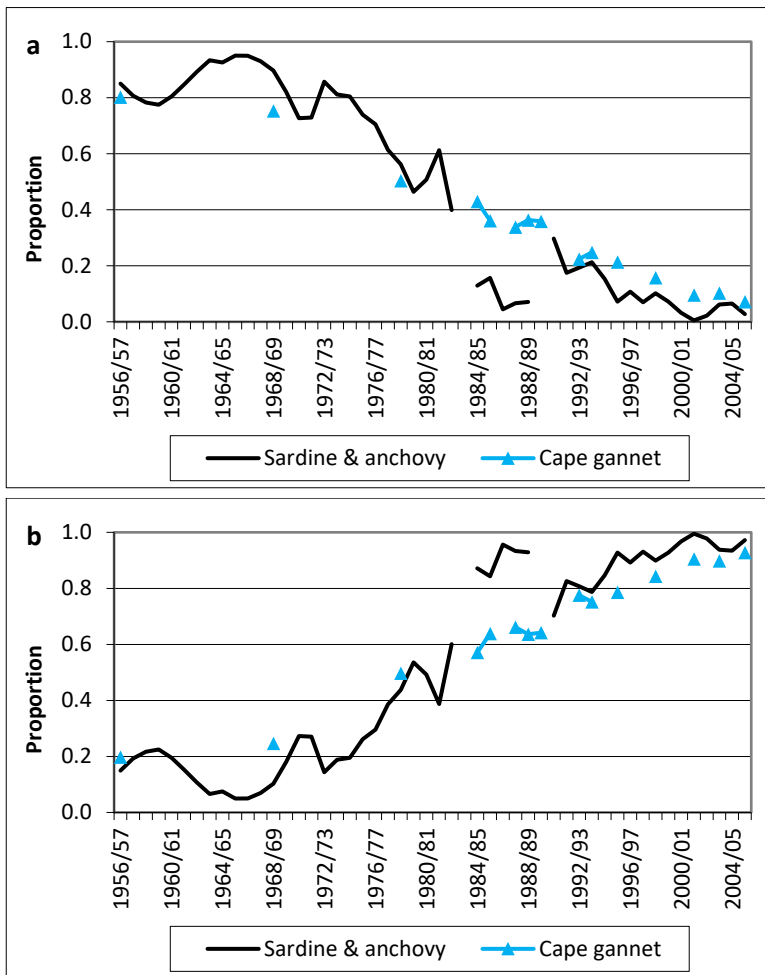
From 1989–2009 numbers of penguins breeding in the Western Cape were significantly correlated with the overall biomass of sardine and anchovy in South Africa, as also was the case from 1999–2009 in the Eastern Cape (Figure 1, Crawford et al. 2011).

Several demographic parameters of African Penguins have been positively related to estimates or proxies of the abundance of sardine and/or anchovy at various spatial scales, including adult survival (Sherley et al. 2014, Robinson et al. 2015), breeding participation (Crawford et al. 1999, Durant et al. 2010) and breeding success (La Cock 1986, Adams et al. 1992, Crawford and Dyer 1995, Crawford et al. 1999b, 2006, Cury et al. 2011, Sherley et al. 2013). Onset of breeding by African Penguins was probably delayed during a period of food scarcity (Crawford and Dyer 1995). The fledging period for chicks has been negatively correlated with prey abundance (Sherley et al. 2013).

### **Cape Gannet**

In Namibia, Cape Gannets decreased by 95% after the collapse of that country's sardine stock (Figure 1, Crawford 2007). However, in South Africa numbers of gannets increased. Trends in the proportions of the Benguela ecosystem's sardine and anchovy and Cape Gannets found in Namibia and in South Africa were similar (Figure 2, Crawford et al. 2007a). In the 21<sup>st</sup> century, the move of Cape Gannets to the south and east continued with a decrease in numbers breeding in the Western Cape and an increase in the Eastern Cape, again matching a shift in the distribution of their prey (Crawford et al. 2015).

Unlike African Penguins off northwest South Africa, which were unable to supplement their diet with an alternative prey and experienced substantially increased adult mortality when sardine and anchovy shifted to the southeast, Cape Gannets buffered their diet and adult survival by feeding increasingly on alternative prey (Crawford et al. 2014). This included portions of hakes *Merluccius* spp. discarded by bottom trawlers. Hakes have lower energy content than sardine and anchovy and during pronounced scarcity of these clupeids proved insufficient for many gannets successfully to rear chicks (Grémillet et al. 2008). In the Western Cape, foraging effort of Cape Gannets increased and nest attendance decreased with reduced consumption of sardine and anchovy, and adult body condition was negatively impacted by increases of hake in the diet (Cohen et al. 2014). There was a net deficit in energy during foraging for most Cape Gannets tracked from Malgas Island between 2011 and 2014 (Grémillet et al. 2016).



**Figure 2.** Trends in the proportions of the Benguela ecosystem's sardine and anchovy and Cape Gannets found in a) Namibia and b) South Africa, 1956/1957–2005/2006 (redrawn from information in Crawford et al 2007a).

### Cape Cormorant

In Namibia, numbers of Cape Cormorants decreased by 62% after the collapse of sardine there in the 1970s (Figure 1). It was a lesser decrease and occurred later than those of African Penguins and Cape Gannets (Crawford 2007). The likely reason for this is that as sardine collapsed, its range contracted northwards away from islands in the south of Namibia, where all that country's gannets and almost all its penguins breed. However, artificial platforms constructed in central Namibia provided alternative breeding localities for Cape Cormorants closer to the reduced range of the sardine (Crawford 2007).

Unlike in Namibia, numbers of Cape Cormorants breeding in South Africa's Western Cape decreased in the mid-1990s ahead of recent decreases in that region of African Penguins and Cape Gannets (Crawford et al. 2007b). There was heavy mortality of Cape Cormorants from avian cholera caused by the bacterium *Pasteurella multocida* at several colonies in the Western Cape between 1991 and 2006 (Crawford et al. 1992a, Ward and Williams 2004, Waller and Underhill 2007), which prevented their taking advantage of the increased abundance of sardine and anchovy at the turn of the century. The initial outbreak of cholera occurred at Dassen Island and may have been precipitated by scarcity of forage fish during 1989 and 1990 (Crawford et al. 1992a). Conforming to the recent shift in the distribution of sardine and anchovy Cape Cormorants decreased off northwest South Africa but remained stable in the south, where new colonies have formed and others have increased (Crawford et al. 2016).

When food is scarce, as well as experiencing increases in mortality, Cape Cormorants may substantially reduce breeding success, skip or abandon breeding and defer their age at first breeding (Berry 1976, Crawford et al. 1992b, 2001b, 2016, Duffy et al. 1984, Crawford and Dyer 1995). In November 2008, Cape Cormorants brooding small chicks expended significantly greater foraging effort at Malgas and Dassen islands in the north

Western Cape than at Dyer Island in the south (Hamann et al. 2012). During May and June 2014 Cape Cormorants attempted to take bait from handlines used to fish for snoek *Thyrsites atun*, a behaviour not previously observed and suggestive of poor food availability at that time (Crawford et al. 2016).

### **Greater Crested Tern**

Estimates of numbers of Greater Crested Terns breeding in southern Africa are not available prior to the 1980s (Cooper et al. 1982). Up until the early 2000s, numbers breeding were significantly related to the biomass of sardine and anchovy (Crawford et al. 2002). In the 2000s, there were large increases in the numbers of Greater Crested Terns breeding in the Western and Eastern Cape Provinces, which are most plausibly attributed to good recruitment and an increase in the proportion of mature birds breeding (Crawford 2009). Numbers increased coincidentally with a greatly increased abundance of sardine and anchovy and have since remained high (Crawford et al. 2015). After 2005, numbers breeding in the north Western Cape decreased, whereas numbers breeding farther south in that province increased, matching the displacements to the south and east of sardine and anchovy. In southern Africa, Greater Crested Terns show low fidelity to breeding localities, which enables a rapid adjustment of the location of breeding to an altered availability of prey (Crawford 2009).

### **Bank Cormorant**

In Namibia, Bank Cormorants decreased from 7,166 pairs in 1978–1980 to 3,735 pairs in 1995–1997; a severe decrease in bearded goby in central Namibia was one of the probable causes of the decrease (Crawford et al. 1999a). In South Africa, Bank Cormorants decreased from 1,506 pairs in 1978–1980 to 846 pairs in 2010–2013 (Crawford et al. 2015). In the Western Cape, numbers at 11 readily accessible localities decreased from above 500 pairs during 1978–1987 to 350 pairs from 1995 to 2006. The most northern colony (Lambert's Bay) was extinct by 1999 and there were substantial decreases at the two largest colonies (Malgas and Dassen islands), also north of Cape Town. There was fluctuating growth at Robben Island, where the colony was twice affected by oil spills. Farther east numbers at two colonies increased. These trends are consistent with a reduced abundance of rock lobsters in the north and an expansion of this resource to the east (Cockcroft et al. 2008, Crawford et al. 2008a). As with sardine and anchovy in relation to African Penguins and Cape Cormorants, fishing of lobsters around colonies between Lambert's Bay and Dassen Island may have reduced densities of forage below levels needed to sustain the larger colonies of Bank Cormorants. Where rock lobsters had not been severely depleted, Bank Cormorants showed a positive response to their local availability and modelling suggested that areas with no-take of lobsters at 20–30 km around Bank Cormorant colonies would benefit the conservation of this bird (Sherley et al. 2017).

### **Ecosystem considerations and EAF interventions**

Large fisheries for sardine developed off western South Africa and in Namibia after World War 2, especially in the 1950s. South Africa's sardine stock collapsed in the 1960s, when it was replaced by anchovy in purse-seine catches (Crawford et al. 1987). Namibia's sardine stock collapsed in the 1970s. Because of earlier replacement of sardine by anchovy in South Africa, it was thought desirable to subject Namibian anchovy to heavy fishing to prevent a similar substitution occurring, a move that was largely successful (Butterworth 1984). However, rather than this fishing strategy facilitating a recovery of sardine in the northern Benguela ecosystem, most of the energy flow was diverted away from epipelagic fish resources towards jellyfish, detritus, benthic recycling and the bearded goby (Roux et al. 2013), exacerbating the impact of the sardine's demise on seabirds that feed in the epipelagic zone. African Penguins, Cape Gannets and Cape Cormorants remained at low levels of abundance in Namibia after the collapse of the sardine there. Their numbers, as well as the quantity of guano they produced, were significantly correlated with the biomass of the epipelagic fish resources (mainly sardine, Crawford and Shelton 1978, Crawford 2007).

In South Africa, both sardine and anchovy have undergone substantial fluctuations in abundance but one of these species has generally been reasonably plentiful (Schrawtzlose et al. 1999, Coetzee et al. 2008). However, recent shifts in their distributions, possibly due to altered environmental conditions or intense localised fishing (Fairweather et al. 2006, Roy et al. 2007, Coetzee et al. 2008), brought about a mismatch in the whereabouts of these forage resources and the localities of both seabird colonies and fish processing plants (Coetzee et al. 2008, Blamey et al. 2015, Crawford et al. 2015). Continued fishing near to processing plants may have further depleted prey densities around western seabird colonies (Crawford et al. 2008b). Furthermore, off west South Africa there was a decrease in the availability of prey species in the early 21<sup>st</sup> century (Crawford et al. 2019).

The impact of closing areas around African Penguin colonies was investigated from 2008. In both the Western Cape and the Eastern Cape, pairs of colonies around which fishing was allowed or disallowed were selected to investigate the possible impact of purse-seine fishing in the vicinities of colonies on the foraging behaviour and population dynamics of penguins (Robinson 2013). Concerns with the experiment included that the islands being compared were not necessarily subject to the same environmental conditions (Waller et al. 2014) and that, to assist statistical comparisons, closures around colonies were short (one to three years) despite the known longevity of penguins (up to > 27 years, Hockey et al. 2005) and their relative late age at first breeding (usually four years or older, Crawford et al. 2013). A late age at breeding enables first breeders to assess the suitability of localities for breeding over a lengthy period. Once breeding, African Penguins show strong fidelity to mates and hence to their breeding localities (Crawford et al. 2013). In spite of these misgivings, promising results were obtained. The closures to fishing sometimes decreased energy expended by breeding birds during foraging or increased breeding success (Pichegru et al. 2010, Sherley et al. 2015, 2018).

Based on observed positive correlations between catches around and fitness components of African Penguins at some islands, it was concluded that fishing around islands does not adversely affect penguins and in some cases may have a positive effect (Robinson and Butterworth 2014a, 2014b). However, both penguin fitness and local fish catches may benefit by increased biomass of fish around colonies. Furthermore, a benefit for penguins of fishing is considered unlikely given the many positive relationships between numbers or demographic parameters of African Penguins and prey abundance outlined above, that similar relationships have been demonstrated for many other seabird species (e.g. Cury et al. 2011) and that African Penguins have decreased markedly since the commencement of purse-seine fishing in southern Africa or heavy fishing near colonies (e.g. Dyer Island).

At a wider spatial scale, a threshold (about one quarter of the maximum) was demonstrated in the biomass of sardine off western South Africa below which survival of adult African Penguins decreased rapidly (Robinson et al. 2015). Modelling indicated that, although fishing would likely adversely impact projected future trends of African Penguins, the effect was relatively small compared with uncertainties regarding the spatial distribution of sardine (Robinson et al. 2015). This emphasises the desirability of maintaining forage resources above a level at which survival of dependent predators is impacted, especially those such as African Penguins that are long-lived and have delayed maturity.

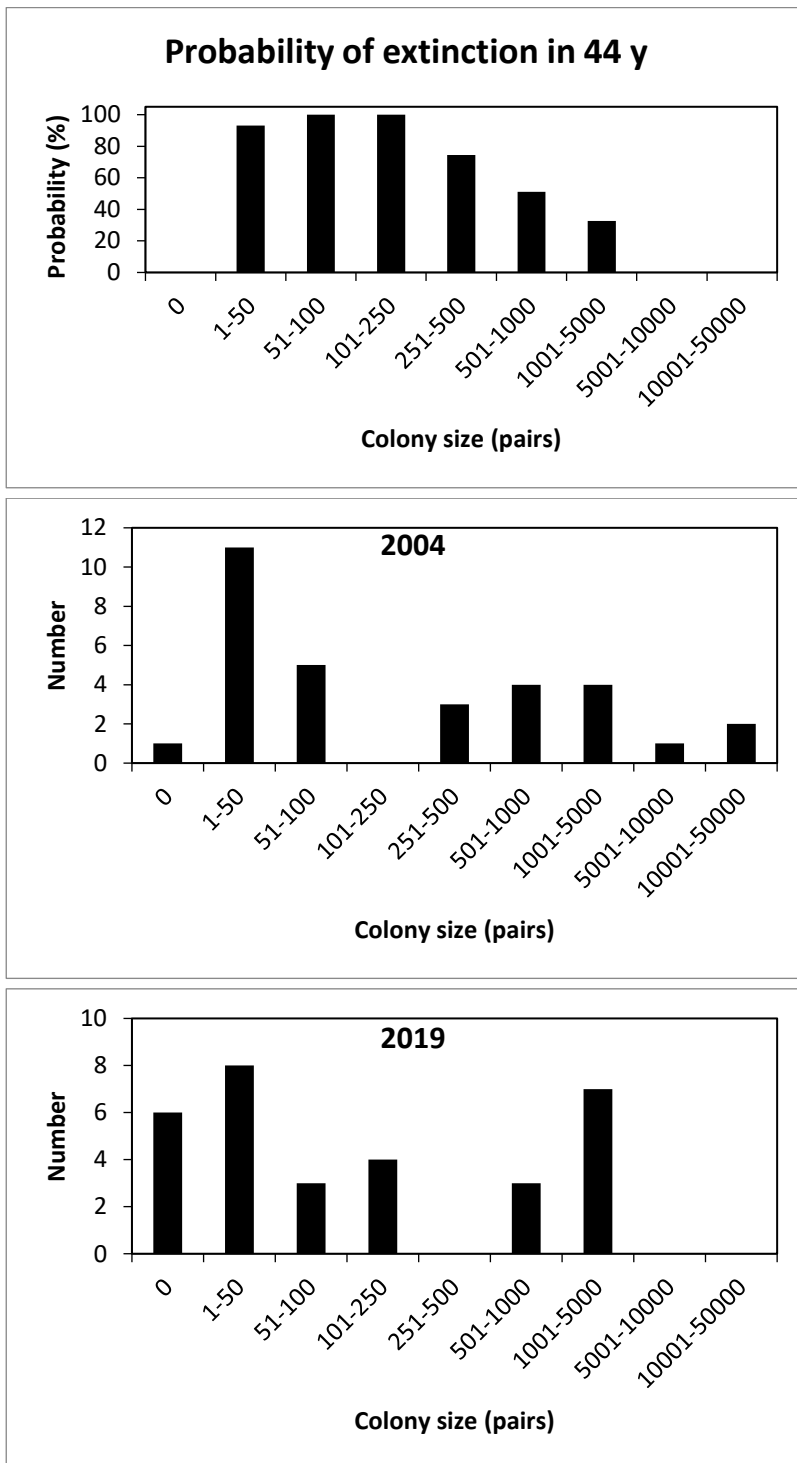
In contrast to the three seabirds that compete with fisheries for prey, have small foraging ranges while breeding and had large recent decreases in South Africa (African Penguin, Cape and Bank Cormorants), three others with presumed similar foraging ranges that do not compete to a substantial extent with fisheries (White-breasted Cormorant *P. lucidus*, Crowned Cormorant *Microcarbo coronatus* and Kelp Gull *Larus dominicanus*) maintained or increased their populations in the long-term (Crawford et al. 2015). This suggests that fisheries caused local depletions of prey for African Penguin, Cape and Bank Cormorants. However, African Penguin, Cape Gannet, Cape, Bank, White-breasted and Crowned Cormorants, Kelp Gulls and Greater Crested Terns have all exhibited some movement to the south and east, indicating the likelihood of some environmental forcing (Crawford et al. 2015).

### **Minimum Viable Populations**

A consequence of the large decreases of the Benguela's flock-foraging seabirds (African Penguin, Cape Gannet, Cape Cormorant) is that the sizes of their colonies have decreased substantially (Crawford et al. 2001a, 2016, Sherley et al. 2019). If group foraging confers an advantage to these birds, as has been shown for African Penguins (McInnes et al. 2017), diminishing colonies may become too small for sufficient foraging groups to form and suffer from an Allee effect (Ryan et al. 2012). Additionally, dwindling colonies mean that more birds nest near colony edges, where eggs and chicks are at greater risk to predators (e.g. Cordes et al. 1999). Amongst penguins taken to a rescue centre, females had higher mortality rates than males (Pichegru and Parsons 2014). If a similar sex-biased mortality exists in the wild, it may skew sex ratios at small colonies and thereby further decrease productivity. Therefore, it is of interest to investigate the long-term performance of colonies of different sizes.

At the end of the 20<sup>th</sup> century, the minimum viable population for African Penguins was considered to be > 40,000 pairs, likely of the order of 50,000 pairs, a figure that was equivalent to its level in 2000 (Crawford et

al. 2001a). This was based on empirical information regarding the performance of 41 discrete colonies at Halifax, North Reef and Possession islands over 40 years from 1956–1996, during which period Namibia's sardine stock collapsed and its range contacted northwards (Cordes et al. 1999, Crawford et al. 2001a). Only one of the 28 colonies that in 1956 had fewer than 250 pairs was extant in 1996. Half of the colonies that in 1956 had between 500 and 1,000 pairs survived, as did 67% of those having between 1,000 and 5,000 pairs and all larger colonies (Figure 3). In 2004, three colonies held > 5,000 pairs but none attained this level in 2019, when seven colonies (Mercury, Dassen, Robben, Dyer, St Croix and Bird in Algoa Bay islands and the mainland colony of Stony Point) held 1,000–4,000 pairs, three from 500–1,000 pairs and 15 < 250 pairs (Figure 3). Five colonies became extinct between 2004 and 2019. Assuming equivalent rates of extinction to those recorded in the latter half of the 20<sup>th</sup> century, only seven of the currently extant colonies have a > 50% probability of surviving until 2060, whereas three have an even chance of surviving to that date and the others a high likelihood of prior extinction. This makes it imperative that every effort be made to secure the future of each of the ten colonies that at present holds > 500 pairs.



**Figure 3.** Top: probabilities of extinction over a period of 40 y of African Penguin colonies of different sizes derived from empirical information for southern Namibia (redrawn from information in Crawford et al. 2001a). Centre and bottom: numbers of colonies of African Penguins having different sizes in 2004 and 2019, respectively (updated from information in Crawford et al. 2013 using unpublished data of Ministry of Fisheries and Marine Resources, Namibia and Department of Environment, Forestry and Fisheries, South Africa). Also shown are numbers of colonies where breeding occurred since 1956 that were extinct in 2004 and 2019.

For Cape Gannets, a concern is that there are only six extant colonies and that c. 70% of the overall population now breeds at the easternmost of these, namely Bird Island in Algoa Bay at the eastern extremity of the BCLME (Sherley et al. 2019).



## Lessons learnt regarding food limitation in the BCLME

Lessons learnt from the Benguela ecosystem regarding seabird-fisheries competition for forage resources include:

1. Sustained over-exploitation of epipelagic forage resources may alter the functioning of an ecosystem and hold seabirds that feed primarily in the epipelagic zone at low levels of abundance over a long period of time (e.g. Roux et al. 2013).
2. Collapses of forage resources below certain thresholds, or their displacement beyond the foraging ranges of breeding seabirds, may cause large decreases of seabirds that are difficult to reverse (e.g. Crawford et al. 2008b, Robinson et al. 2015).
3. A decreased availability of forage resources can similarly delay recovery of seabird populations (e.g. Crawford et al. 2019).
4. Depletions in densities of prey species around seabird colonies may be exacerbated by fisheries that are not regulated at appropriate spatial scales (e.g. Crawford et al. 2011, Ludynia et al. 2014).
5. Even for highly migratory forage resources, such as sardine and anchovy, local closures to fishing may enhance prey availability for, decrease energy expenditure by and increase productivity of seabirds (e.g. Pichegru et al. 2010, Sherley et al. 2015, 2020).
6. Seabirds showing high fidelity to breeding sites, having short foraging ranges when breeding and little flexibility to adapt their diet (e.g. African Penguin, Cape and Bank Cormorants) are less able to cope with distributional changes of preferred forage species than those that are able to change their breeding locality (e.g. Greater Crested Tern), or have extended foraging ranges (e.g. Cape Gannet), or are able to switch their diet to different prey items (e.g. Cape Gannet) (e.g. Crawford et al. 2014).
7. The existence or creation of suitable breeding habitat within the contracted or altered distributions of forage species may partially alleviate the impact of an altered distribution of prey on some seabirds, especially those that are readily able to initiate new colonies (e.g. Crawford 2007, Crawford et al. 2007a).
8. Probabilities of extinction of colonies of flock-foraging seabirds may increase substantially as colony sizes decrease; hence for these species it is necessary to maintain colonies of sufficient size (e.g. Crawford et al. 2001a).
9. Monitoring of seabirds that do not compete with fisheries for prey may provide useful insights into the relative impacts of fishing and environmental forcing on seabirds (e.g. Crawford et al. 2015).

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