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The Cape Gannet *Morus capensis* is one of several seabird species endemic to the Benguela upwelling ecosystem (BUS) but whose population has recently decreased, leading to an unfavourable IUCN Red List assessment. Application of 'JARA' ('Just Another Red-List Assessment,' a Bayesian state-space tool used for IUCN Red List assessments) to updated information on the areas occupied by Cape Gannets and the nest densities of breeding birds at their six colonies, suggested that the species should be classified as Vulnerable. However, the rate of decrease of Cape Gannets in their most-recent generation exceeded that of the previous generation, primarily as a result of large decreases at Bird Island, Lambert's Bay, and Malgas Island, off South Africa's west coast (the western part of their range). Since the 1960s, there has been an ongoing redistribution of the species from northwest to southeast around southern Africa, and ~70% of the population now occurs on the south coast of South Africa, at Bird Island in Algoa Bay, on the eastern border of the BUS. Recruitment rather than adult survival may be limiting the present population; however, information on the seabird's demographic parameters and mortality in fisheries is lacking for colonies in the northern part of the BUS. Presently, major threats to Cape Gannet include: substantially decreased availability of their preferred prey in the west; heavy mortalities of eggs, chicks and fledglings at and around colonies, inflicted by Cape Fur Seals *Arctocephalus pusillus* and other seabirds; substantial disturbance at colonies caused by Cape Fur Seals attacking adult gannets ashore; oiling; and disease.

Statut et conservation le fou du Cap *Morus capensis*

Le fou du Cap *Morus capensis* fait partie d'un groupe d'espèces d'oiseaux marins endémiques à la région du Benguela dont les populations sont en déclin sévère. En utilisant JARA (un outil Bayesien d'espace-état communnément utilisé dans l'évaluation du statut des espèces dans les Listes Rouges de l'UICN) sur des données récentes de surfaces occupées et de densité de nidification sur les six colonies de fous du Cap, nous estimons que cette espèce devrait être classée Vulnérable. Cependant, le déclin des fous du Cap au cours de leur dernière génération s'est accéléré par rapport à la précédente, principalement à cause du déclin rapide des colonies de Bird Island, Lambert's Bay et de Malgas Island, toutes deux au large de la côte ouest de l'Afrique du Sud. Depuis les années 1960, la distribution de l'espèce s'est progressivement déplacée du nord-ouest vers le sud-est, concentrant maintenant 70% de l'espèce sur une seule colonie, Bird Island/Algoa Bay, à la limite est de la region du Benguela. Plus que la survie adulte, c'est le recrutement des juvéniles qui semble à ce jour limiter la population, bien que les informations manquent encore sur la mortalité associée aux pêcheries, ainsi que sur les paramètres démographiques des colonies du nord de la région du Benguela. Les menaces majeures actuelles pesant sur l'espèce comprennent une pénurie des proies favorites le long de la côte ouest, une mortalité élevée des oeufs et poussins à l'envol par les otaries du Cap *Arctocephalus pusillus* et d'autres oiseaux marins, un dérangement important de certaines colonies par les otaries attaquant poussins et adultes à terre, ainsi que les marées noires et épizooties.

Introduction

The Cape Gannet *Morus capensis* is one of seven seabird species endemic to the Benguela upwelling system off southwest Africa. It has historically bred at ten islands off the coasts of Namibia and South Africa but at only six islands by 1956: Mercury, Ichaboe and Possession in Namibia; Bird at Lambert's Bay (hereafter referred to as Lambert's Bay), Malgas and Bird at Algoa Bay (hereafter referred to as Bird Island, Algoa Bay) in South Africa (Figure 1; Crawford et al. 1983). Although many birds regularly disperse north along the west and east coasts of Africa after breeding (e.g. Broekhuysen et al. 1961; Cyrus and Robson 1980; Klages 1994), the species is not migratory and adults are often present at breeding localities throughout the non-breeding season (Nelson 2005; Pistorius et al. 2015). A number of historical and contemporary pressures from human activities have caused the number of Cape Gannets to decline since the first efforts to estimate their abundance in 1956 (Crawford et al. 2007). For example, Cape Gannets construct their nests from guano, of which they produce substantial quantities at breeding localities (Jarvis 1970). Their guano and that of other seabirds was previously harvested at southern

African islands and platforms, with much of it being shipped to Europe as a fertilizer (Crawford and Shelton 1978; van Sittert and Crawford 2003). Again, Cape Gannets prefer to feed on two energy-rich forage fish species, namely sardine *Sardinops sagax* and anchovy *Engraulis encrasicolus*, though they may also utilise less nutritious fish species, such as saury *Scomberesox saurus*, and scavenge hake *Merluccius* spp. and other benthic species discarded by demersal trawlers (e.g. Berruti et al. 1993; Dundee 2006; Grémillet et al. 2008, 2019; Green et al. 2015). Sardine and anchovy are the mainstay of the region's industrial purse-seine fisheries (Hutchings et al. 2009) and play a major role in the transfer of energy from lower to higher trophic levels (e.g. Cury et al. 2000). However, access to forage fish for the regions' seabirds has changed markedly since the 1950s, with the collapse of Namibia's sardine stock in the early 1970s (Crawford et al. 1983; Watermeyer et al. 2008; Roux et al. 2013) and a more recent decrease in the availability to seabirds of sardine and anchovy off South Africa's west coast after 2003 (Crawford et al. 2019).

In the 1950s and 1960s, most Cape Gannets bred in Namibia, but by 1978 numbers were shared evenly between Namibia and South Africa (Crawford et al. 1983). Since 1997, more than 80% of Cape Gannets bred in
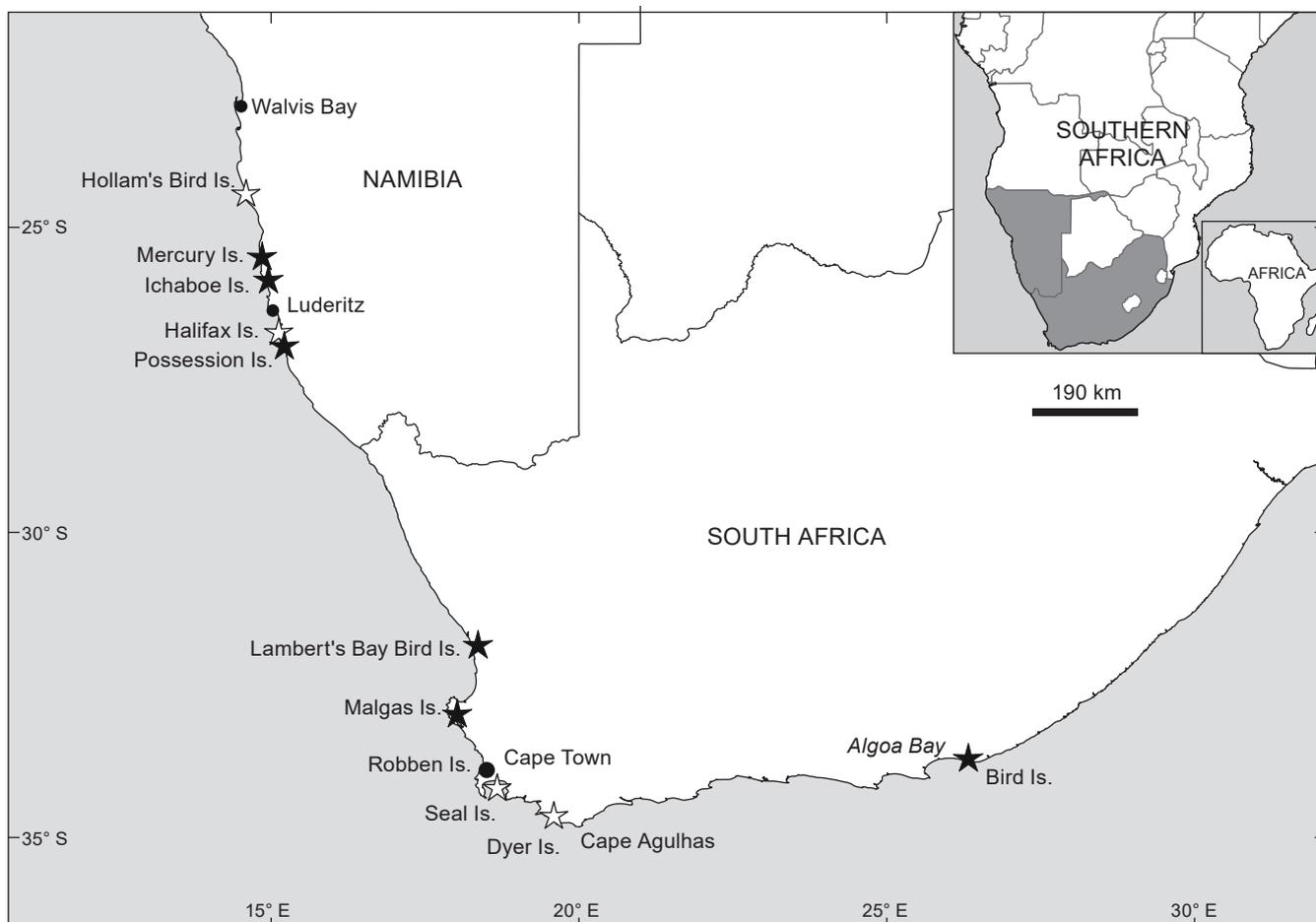
Figure 1: Locations of extant colonies (black stars) and extinct colonies (white stars) of Cape Gannets, and other southern African localities mentioned in the text

South Africa (Crawford et al. 2007). Under the criteria of the International Union for Conservation of Nature (IUCN), in South Africa the Cape Gannet was assessed as Least Concern in 1976 (Siegfried et al. 1976) and 1984 (Brooke 1984), but as Vulnerable in 2000 (Barnes 2000) and 2015 (Hagen 2015). On account of its severe decrease in Namibia, it was regarded as Critically Endangered there in 2015 (Kemper 2015). The global status of the Cape Gannet was Least Concern in 1988, Near Threatened in 1994, Vulnerable in 2000, and Endangered in 2017 (BirdLife International 2019). Its 2017 assessment was based on Bayesian state-space modelling of the numbers breeding at the species' six extant colonies between 1956 and 2016, which indicated a decline of ~52% over three generations of 20.2 years (Birdlife International 2019).

This article presents updated information on the densities of nests, the areas occupied by, and the generation length of Cape Gannets. We revisit the calculation of generation length, reapply the model used in the 2017 assessment directly to estimates of the area occupied by breeding gannets, and propagate the uncertainty around nesting density in revised estimates of the species' abundance, so as to ascertain whether the classification of Endangered remains applicable. We also review the threats faced by the species, and identify interventions needed to secure the species' conservation.

Methods

The numbers of nests of Cape Gannet at the colonies in the breeding season were estimated from measurements of the area occupied by breeding birds (in hectares [ha]) from near-vertical aerial photographs, combined with ground-based measures of nest density (Randall and Ross 1979; Klages et al. 1992). Aerial photographs were taken in November or December, when most birds are incubating or brooding (Shelton et al. 1982). Cape Gannets may commence breeding in mid-August; first clutches are usually complete by early November; and most fledging is complete by the end of March (Staverees et al. 2008). The extent of the area occupied by breeding birds was measured using an interactive image-analysis system, IBAS. The photographs were scaled from ground measurements of straight edges (such as walls or buildings) near the colonies (Crawford et al. 2007). In certain years (see Supplementary Table S1) when it was not possible to take photographs, the area of a gannet colony was estimated by an observer walking around the colony with a GPS system that had a horizontal error of ±4 m (Crawford et al. 2007). Disturbance to birds was reduced by suspending the GPS from a pole that ensured a 2-m gap between the observer and the gannets. In total, between 1956/57 and 2018/19, estimates of the area occupied by breeding birds were available for 27 seasons at Mercury Island, 25 at Ichaboe Island, 23 at Possession Island, 41 at Lambert's Bay, 38 at Malgas Island, and 42 at Bird Island/ Algoa Bay (Figure 3).

Measurements of the nest density at colonies were undertaken during breeding seasons by placing four poles, each 2-m long, on the surface of the ground so as to form a square of 4 m². The numbers of whole nests and part of nests that fell within the square were counted. The overall number of nests in a square was taken to be the number of

whole nests plus half the number of partial nests counted (Randall and Ross 1979; Crawford et al. 2007). The number of nest density measurements made in any season ranged from two at Possession Island in 2002/03 and 2005/06, when the colony was small and we desired to minimise disturbance, to 30 at Algoa Bay in 2005/06 (Crawford et al 2007). Usually 10–25 density measurements were made at a colony in a given breeding season. Density measurements were made at Mercury, Ichaboe and Possession islands in three seasons, at Lambert's Bay in 19 seasons, at Malgas Island in 23 seasons, and at Bird Island/Algoa Bay in 11 seasons (Figure 2). Additionally, three published estimates were available for Bird Island/Algoa Bay (Randall and Ross 1979; Batchelor 1982). As information on the nest densities was not available for many seasons, for each locality a mean density (±SD) was obtained by giving equal weight to each season for which information existed.

In addition, in the 2010/11 and 2018/19 seasons, direct counts of the numbers of Cape Gannet nests at the three
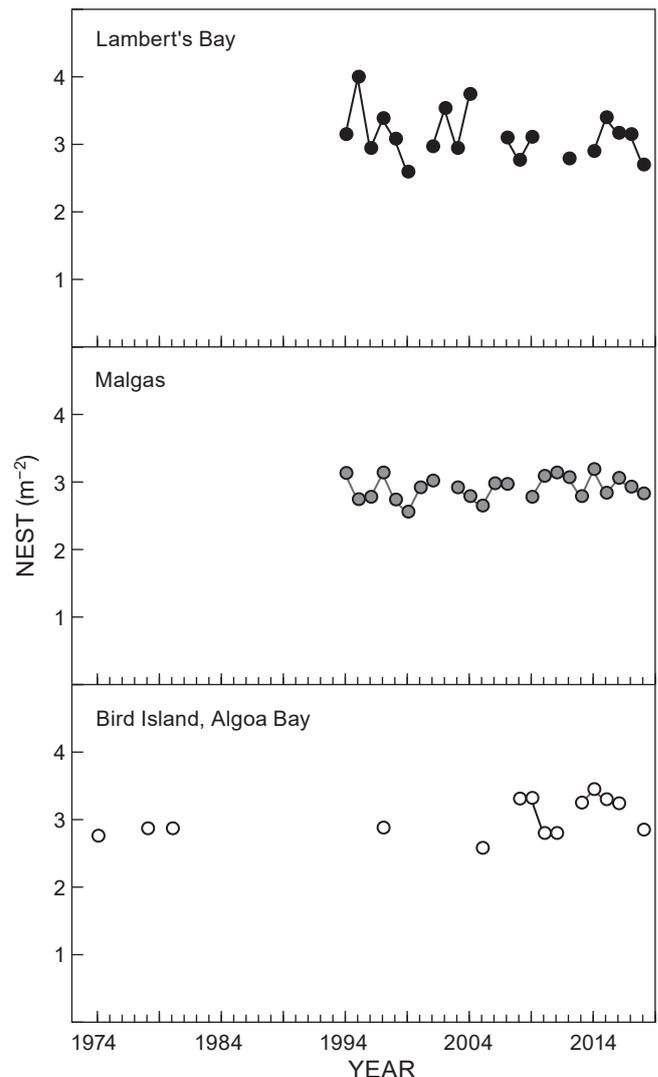
Figure 2: Densities of nests of Cape Gannet *Morus capensis* at the three extant South African colonies, 1974–2018

Namibian colonies were made from aerial photographs (Kemper 2015; MFMR and African Penguin Conservation Project unpubl. data). This method was also applied to the relatively small colony at Possession Island in 2011/12 and 2014/15. We used these eight direct counts of nests to check our model estimates against these cases.

Generation length (G) for Cape Gannet was calculated as:

$$G = \frac{A + 1}{(1 - \phi_\alpha)} \tag{1}$$

where A is age at first breeding, and ϕ_α is adult survival (Birdlife International 2000). In keeping with the IUCN Red List guidelines, which stipulate 'where generation length varies under threat….the more natural, i.e. pre-disturbance, generation length should be used' (IUCN Standards and Petitions Subcommittee 2017, p 26), we used $A = 4$ years, and $\phi_\alpha = 0.93$, based on Crawford (1999) and the 1990 survival estimates from Distiller et al. (2012).

To determine the change occurring in the Cape Gannet population over the last $3G$ years, we used a Bayesian state-space tool for IUCN Red List assessments ('Just Another Red List Assessment' [JARA], https://github.com/henning-winker/JARA; Winker and Sherley 2019). JARA assumes that the underlying trend in the area occupied (I_t) (Supplementary Figure S1) followed a conventional exponential growth model (e.g. Kéry and Schaub 2012):

$$I_{t+1} = I_t \lambda_t \tag{2}$$

where λ_t is the growth rate in year t. On the log scale, the state-process model was:

$$\mu_{t+1,i} = \mu_{t,i} + r_{t,i} \tag{3}$$

where $\mu_{t,i} = \log(I_{t,i})$ and $r_{t,i} = \log(\lambda_{t,i})$, the year-to-year rate of change at breeding colony i is assumed to vary around $\bar{r}_i$ (the underlying mean rate of change for the colony), but with an estimable process variance σ_η^2 that is common to all colonies $r_{t,i} \sim \text{Normal}(\bar{r}_i, \sigma_\eta^2)$. The corresponding observation equation is:

$$\log(y_{t,i}) = \mu_{t,i} + \varepsilon_{t,i} \tag{4}$$

where $y_{t,i}$ is the area occupied for year t, and $\varepsilon_{t,i}$ is the observation residual for year t at breeding colony i. The residual error is assumed to be normally distributed on the log-scale $\varepsilon_{t,i} \sim \text{Normal}(0, \sigma_\varepsilon^2)$ as a function of a common observation variance σ_ε^2.

The estimated posterior of the population size (number of breeding pairs) at each colony became:

$$\hat{I}_{t,i} = \exp(\mu_{t,i}) \times \delta_i \times 10\,000$$
$$\delta_i = \text{gamma}(\alpha_i, \beta_i)$$
$$\alpha_i = \bar{D}_i^2 / \sigma_{D,i}^2$$
$$\beta_i = \bar{D}_i / \sigma_{D,i}^2 \tag{5}$$

where δ_i is a colony-specific informative gamma prior for nest density, parameterised via shape (α_i) and rate (β_i) parameters, using the observed mean ($\bar{D}_i$) and SD ($\sigma_{D,i}$) for nest density (m^2) at each colony. The global population $I_{p,t}$ for year t was computed from the sum of all individual colony trajectory posteriors:

$$I_{p,t} = \sum_i \hat{I}_{t,i} \tag{6}$$

The percentage change ($C\%$) in numbers at each colony was calculated from the posteriors of the estimated population ($\hat{I}_{t,i}$) as the difference between a three-year average around the final observed data point T, and a three-year average around year $T - (3G)$ (e.g. Supplementary Figure S2). The year $T + 1$ is always projected to obtain a three-year average around T (to reduce the influence of short-term fluctuations: Froese et al. 2017).

We implemented JARA in JAGS v4.3.0 (Plummer 2003) via the library jagsUI v1.5.1 (Kellner 2019) for R. The initial for the first modelled count $I_{t=1,i}$ was drawn in log-space from a 'flat' normal distribution, with the mean equal to the log of the first observation $y_{t=1,i}$ and a standard deviation of 1 000. We used vague normal priors of Normal(0,1000) for $\bar{r}_i$, and inverse gamma priors for both the state and observation process variance of $\sigma^2 \sim 1/\text{gamma}(0.001, 0.001)$, which is approximately uniform on the log scale (Winker et al. 2018). The model was fitted by running three Monte Carlo Markov chains (MCMC) for 50 000 iterations, with a burn-in of 25 000, and a thinning rate of 5. Convergence was diagnosed using the 'coda' package (Plummer et al. 2006), adopting minimal thresholds of $p = 0.05$ for Geweke's (1992) diagnostics. Unless otherwise specified, we report medians and 95% Bayesian credible intervals (BCI).

Results

Generation length (G)
Using values of $A = 4$ years, and $\phi_\alpha = 0.93$ per annum, we obtained an estimate of $G = 18.3$ years, and $3G = \sim55$ years.

Nesting densities
Mean (±SD) densities of nests·m^{-2} at the six breeding localities of Cape Gannet were: Mercury Island 3.73 ± 0.57; Ichaboe Island 3.56 ± 0.67; Possession Island 4.39 ± 1.12; Lambert's Bay 3.11 ± 0.36; Malgas Island 2.90 ± 0.17; and Bird Island/Algoa Bay 3.00 ± 0.276. There was no evidence of a trend in the nest density at any of the three colonies at which densities were obtained in 10 or more seasons (Figure 2).

Population-count estimates
The state-space model (SSM) estimate for the total number of breeding pairs of Cape Gannet at the six colonies declined from 264 558 (95% BCI: 193 839–365 146) in 1956/57 to 134 775 (110 013–166 901) in 2018/19 (Supplementary Figure S2). In Namibia, estimated numbers declined from ~210 000 pairs (~80% of the global population) in 1956/57 to ~7 000 pairs (~5% of the global population) in 2018/19. Estimated numbers at Mercury Island decreased from ~9 000 pairs in 1956/57 to ~3 500 pairs in 1969/70, recovered to ~4 500 pairs in 1978/79, and after 1980 fluctuated at around ~2 000 pairs (Figure 3). Cape Gannets occupied much of Ichaboe Island in 1956/57 and 1967/68 (Rand 1963; Crawford 1991), and ~180 000

pairs bred at the island in 1956/57; estimated numbers declined to ~50 000 pairs in 1981/82, and fluctuated around this level until the end of the 1980s, then decreased again to a present population of ~5 000 pairs (Figure 3). The numbers at Possession Island decreased from ~20 000 pairs in 1956/57 to ~2 900 pairs from 1980–1992, and then to the present population of only ~130 pairs (Figure 3).

Seven of the eight direct counts of nests fell within the 95% credible intervals of the SSM estimate for the corresponding year and colony (Supplementary Figure S3).

In South Africa, fewer than 6 000 pairs bred at Lambert's Bay between 1956/57 and 1978/79. The colony grew to ~11 000 pairs in 1987/88, and then fluctuated around ~10 000 pairs from 1988/89 to 2003/04; in subsequent
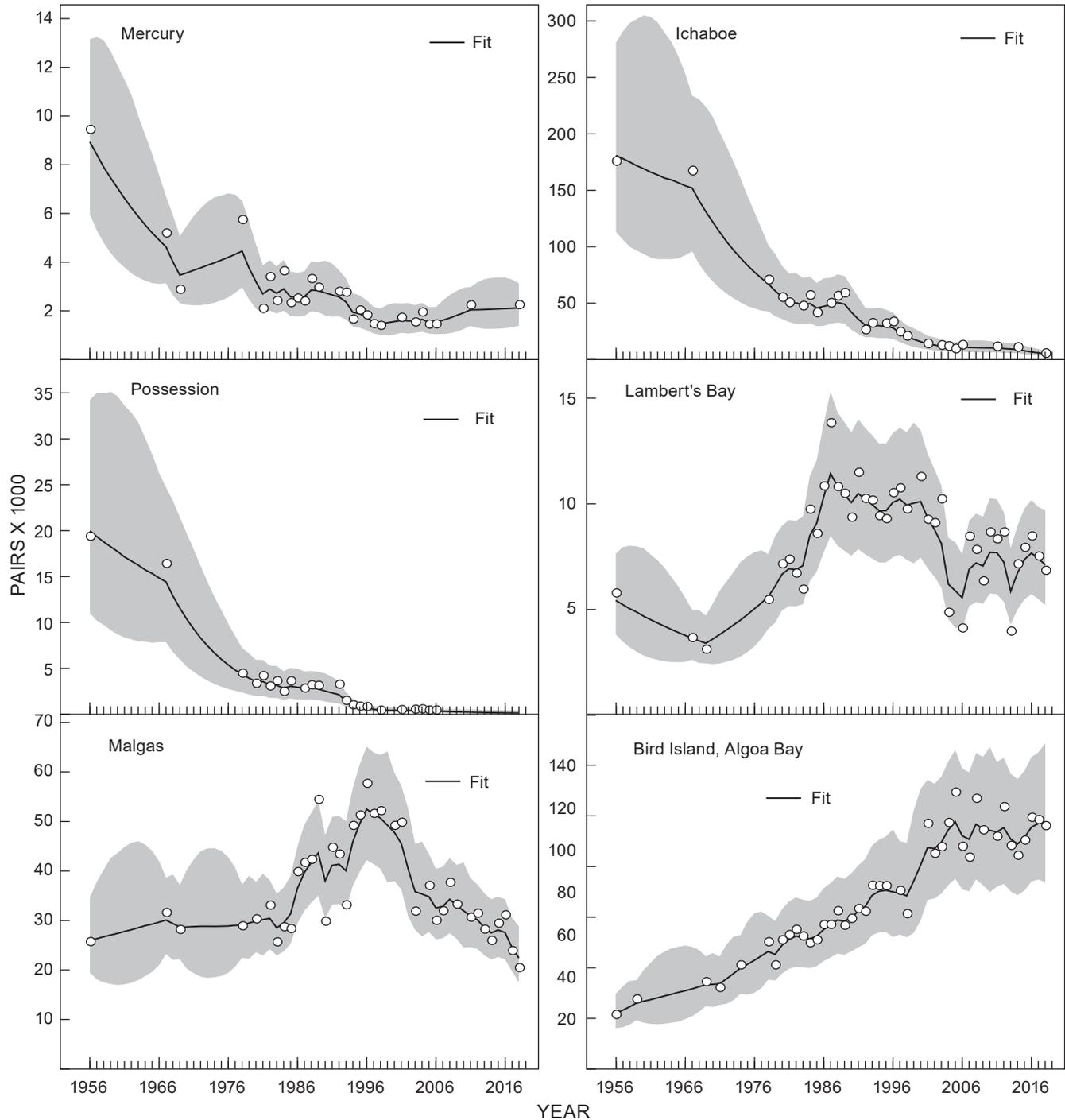
Figure 3: Bayesian state-space model estimates (black lines) and 95% credible intervals (grey polygons) of the number of Cape Gannet *Morus capensis* breeding pairs at the six extant colonies, 1956/57–2018/19. White points show the raw estimated number transformed from the area occupied by breeding gannets in each year and the mean nest density (see Methods for details)

years, between ~5 500 and 7 700 pairs were estimated to have bred there (Figure 3). At Malgas Island, there were ~26 000 pairs between 1956/57 and 1983/84. The colony increased to a peak of ~52 000 pairs in 1996/97; since then it decreased in a fluctuating fashion to ~22 000 pairs in 2018/19 (Figure 3). The colony at Bird Island/Algoa Bay grew from ~22 000 pairs in 1956/57 to ~95 000 pairs in 2004/05, and subsequently varied around that number (Figure 3).

Percentage change (C%) and conservation status

The median $C\%$ in the global population over the last 3 generations was estimated as −44.7% (−63.8% to −18.9%) (Figure 4), or −1.0% per annum (Figure 5). The median rate of decrease was slower when only the last 2 generations were considered (−0.18% per annum), indicating a period of population stability (Figure 5; Supplementary Figure S2). The annual rate of decline appears to have accelerated again during the most recent generation (−0.97% per annum), though the confidence in this latest estimate was lowest (greatest variance, shown in Figure 5). Overall, the majority (>87%) of the plausible estimates (the posterior probability distribution) for $C\%$ exceed the decline thresholds for the IUCN Red List threat categories, with a 56.9% probability that the population meets the A2 criteria for a global classification of Vulnerable, and 31.0% probability of meeting the same criteria for Endangered (Figure 4). Only 0.12% of the plausible rates of change were positive.

Discussion

Methodology

Previous estimates gave ~254 000 and ~249 000 pairs of Cape Gannets breeding in 1956/57 and 1968/69, respectively (Crawford et al. 2007). Applying the method of Crawford et al. (2007) to the most recent nesting-area data suggests ~135 000 pairs bred in 2018/19, a change of approximately −46% in the 50 years since 1968/69. This accords well with our SSM estimates, which produced a median decline of −44.7% over the 3 generations (54.9 years) prior to 2018/2019, from ~247 000 pairs in about 1963/64 to ~135 000 pairs in about 2018/19 (Supplementary Figure S2). In contrast, nest densities varied between colonies, from 2.9 to 4.4 m$^{−2}$, without clear trends at any of the three regularly monitored colonies (Figure 2). This suggests that the area used for nesting expands or contracts in response to increases or decreases in the numbers breeding (though nest density remains relatively constant). Nest sites may be chosen to minimise both aggressive interactions between neighbours (Jarvis 1971) and the loss of eggs and small chicks to predators (de Ponte Machado 2010), as breeding success is higher in the interior of a colony than at the periphery (Staverees et al. 2008; Mullers et al. 2009; Green and Pistorius 2013).

Seven of the eight direct counts of nests fell within the 95% credible intervals of the corresponding SSM estimate (Supplementary Figure S3). While this gives some credence to our approach for estimating abundance, the direct counts all come from the now relatively small Namibian colonies. Moreover, it is important to emphasise
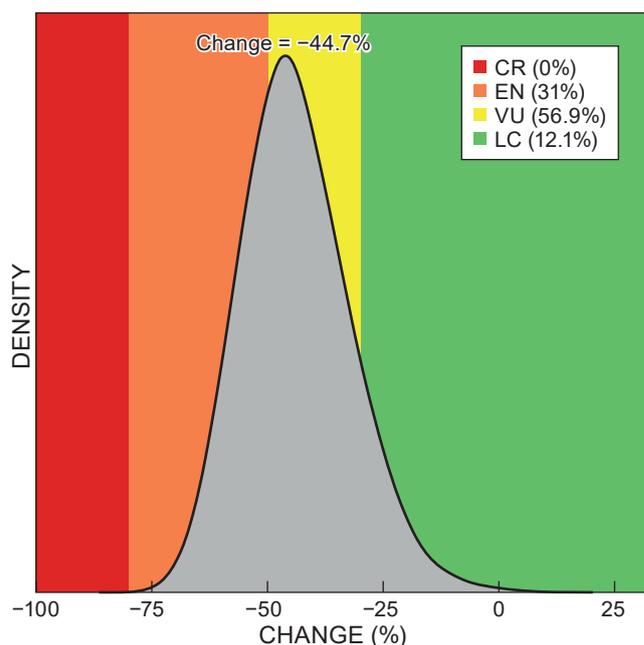
Figure 4: Posterior probability density of the percentage change ($C\%$) of the overall population of Cape Gannet *Morus capensis* over three generation lengths (3G). Note that all probabilities are negative; the median rate of change was −44.7%. IUCN Red List categories: CR = Critically Endangered; EN = Endangered; VU = Vulnerable; LC = Least Concern
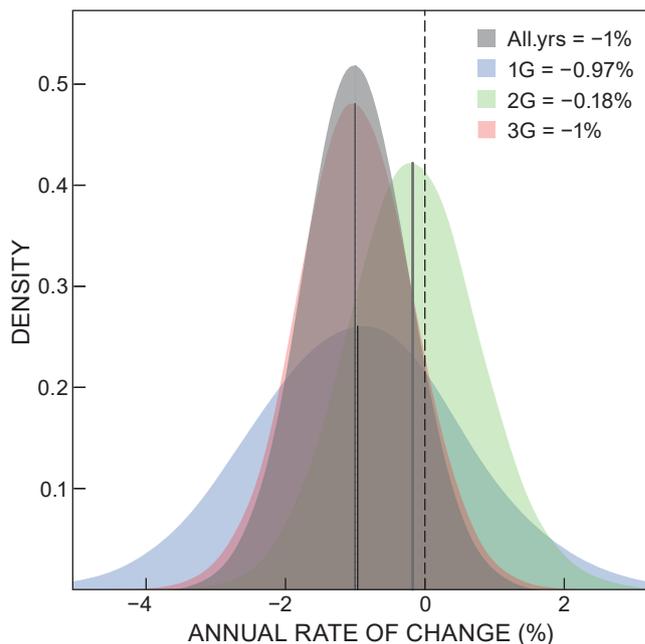
Figure 5: Posterior probability densities for the annual rate of change of the overall population of Cape Gannet *Morus capensis* over the last three generations (3G), the two most-recent generations (2G), the years corresponding to the most-recent generation (1G), and for all available years (All.yrs). Generation length (G) = 18.3 years

that our results represent modelled population estimates, not direct counts of the number of occupied nests as presented elsewhere (e.g. Kemper 2015).

It is possible to obtain direct nest counts from aerial photographs, even for the very large gannet colonies (Shelton et al. 1982). Whereas these are likely to be more precise than our estimates, they are more time-consuming to undertake, and to date no work has been done to assess the uncertainty associated with that approach. Unmanned aerial vehicles (UAVs or drones) can now be used to census seabird colonies cheaply, accurately and precisely (Hodgson et al. 2018), with minimal disturbance if best-practise guidelines are followed carefully (Brisson-Curadeau et al. 2017). Future estimates to census Cape Gannet populations could benefit from using UAV technology to assess the intra-annual variability in colony attendance, to quantify the relative error in using direct counts versus estimates of the area occupied (as applied here), and to calibrate UAV images with aerial photographs from manned aircraft to reduce the cost and increase the frequency of population estimates in the future.

Conservation status

The most recent IUCN Red List assessment for the Cape Gannet reported a −51.5% change in the numbers breeding over 61 years (1956–2017), resulting in a global status of Endangered (Birdlife International 2019). Our revised abundance estimates yielded a lesser decline (−44.7%), with the balance of evidence suggesting a global classification of Vulnerable as the most appropriate status. Although the analysis we undertook for the Birdlife International (2019) assessment was also based on a Bayesian SSM model fit, it differed from the analysis reported on here in two keys ways. First, the SSM for the Birdlife International (2019) assessment was applied to numbers of breeding pairs that had been calculated without accounting for uncertainty in the estimates of nest density. In contrast, in the present study we have considered both the uncertainty in the nest-density estimates and the estimates of the area occupied by breeding birds in modelling our revised abundance estimates. Greater uncertainty will increase the spread of the posterior probabilities for %C across the thresholds for the IUCN threat categories. Second, we suggest revising the generation length from 20.2 years (Birdlife International 2019) to 18.3 years based on the results of Crawford (1999) and Distiller et al. (2012). This is the main reason for our more-conservative estimate in the median decline of −44.7% versus −51.5%, since the greatest rate of decrease in the Cape Gannet population occurred as a result of large losses of gannets in Namibia in the 1960s and early 1970s (Figure 3; Supplementary Figure S2) following the loss of sardine stocks in the northern Benguela (Roux et al. 2013). With a shorter generation time, these early declines contribute less to the 3G decline estimates in our results than in those used by Birdlife International (2019). Moreover, these losses were ameliorated to some extent by increases at South African colonies in the 1980s and 1990s (Figure 3), initially in the Western Cape, as sardine and anchovy recovered in the southern Benguela, then at Bird Island/Algoa Bay, as those fish shifted eastwards

(Roy et al. 2007; Coetzee et al. 2008). However, while the current analysis suggests a global Red List status of Vulnerable would be appropriate, it is worth noting that substantial decreases at South Africa's two western colonies in the most recent 1G (since 2000) have again accelerated the rate of decrease (Figure 5).

Regional population change

The redistribution of Cape Gannets after 1967/68 in an anti-clockwise direction, from northwest to southeast around the southern African coast, is thought to have resulted from a similar relocation of its main prey species—sardine and anchovy (Crawford et al. 2007, 2015). Sardine off Namibia was depleted through overfishing in the 1960s and 1970s and has not recovered (e.g. Roux et al. 2013). In South Africa, there was a movement of mature sardine and anchovy from the west to south coasts at the end of the 1990s, and in the present century sardine has been heavily exploited west of Cape Agulhas (Roy et al. 2007; Coetzee et al. 2008). Additionally, there was a substantial decrease in the epipelagic availability of sardine and anchovy off South Africa's west coast after 2003 (Crawford et al. 2019).

Cape Gannets likely colonised Halifax and Possession islands in the mid-19th century, possibly due to the displacement of birds from Ichaboe Island during intensive harvesting of guano there from 1843–1845 (Crawford et al. 1983). However, they did not establish a new colony off South Africa during their recent redistribution. Seal Island in False Bay, where they had previously bred (Crawford et al. 1983), was fully occupied by Cape Fur Seals *Arctocephalus pusillus* at this time (Shaughnessy 1984), and attempts to settle at Robben Island in ~1968 and at Dyer Island in 1984/85 (Berruti 1985; Crawford et al. 1986) may have been cut short by disturbance. Consequently, >70% of all Cape Gannets now nest at Bird Island/Algoa Bay, at the eastern extremity of their breeding distribution, where the population seems to have reached an asymptote (Figure 3). However, gannets at this colony are in poorer condition than those at the smaller South African colonies and have to work harder to find food, probably as a result of intraspecific competition (e.g. Moseley et al. 2012; Rijklief 2016). Outside their breeding season, adults may disperse >1 000 km from the colonies and juveniles may move >2 000 km (Broekhuysen et al. 1961; Klages 1994), but there are no suitable breeding localities for the species in southern Africa east of Bird Island/Algoa Bay.

Threats

Present threats to the Cape Gannet include scarcity of nutritious prey, mortality in fisheries, predation at or around colonies, disturbance at (see above) or displacement from colonies, oiling, disease and extreme weather events. Each of these pressures is discussed briefly below.

Although Cape Gannets are able to switch their prey (e.g. Crawford et al. 2014; Grémillet et al. 2019), scarcity of good-quality prey is thought to be the main cause of the ongoing population decrease (e.g. Lewis et al. 2006; Pichegru et al. 2007; Cohen et al. 2014; Crawford et al. 2015). The numbers of Cape Gannet breeding in both Namibia and South Africa were significantly related to the biomass of sardine and anchovy (Crawford et al. 2007). In

western South Africa, they were also related to the epipelagic availability of these prey species (Crawford et al. 2019). Scarcity of energy-rich prey may decrease the proportion of adult Cape Gannets that breed (Crawford and Dyer 1995) and may have influenced recent variability in the numbers of nests at colonies (see Figure 3). The lack of energy-rich prey may also reduce breeding success (e.g. Crawford 1999; Grémillet et al. 2008; Cury et al. 2011), inhibit chick growth (Mullers et al. 2009) and nest attendance (Rishworth et al. 2014), increase foraging effort (Grémillet et al. 2016), and negatively impact adult body condition (Cohen et al. 2014). Parents in better body condition spent longer periods at their nests (Rishworth et al. 2014). Faced with scarcity of their natural prey, Cape Gannets exploited fishery waste from trawlers (Tew Kai et al. 2013), but this low-quality resource still results in low adult body condition and reproductive performance (Moseley et al. 2012).

Considerable numbers of Cape Gannet were killed off southern Africa in demersal-trawl and demersal- and pelagic-longline fisheries at the turn of the recent century (Watkins et al. 2008; Petersen et al. 2009a, 2009b), but the numbers killed off South Africa have subsequently been much reduced via mitigation measures (Maree et al. 2014; Rollinson et al. 2017). Many juveniles were exhausted on arrival off Angola and easily killed by fishermen (Broekhuysen et al. 1961); the extent of such deliberate killing for food is unknown.

Cape Fur Seals killed an estimated 27 000 fledglings around Malgas Island over the course of three breeding seasons (Makhado et al. 2006) and >900 gannets around Ichaboe Island in May 2000 (du Toit et al. 2004). Fur seals caused cessation of breeding at Hollam's Bird Island between 1938 and 1956, by entirely displacing gannets from that locality (Crawford et al. 1983), and, by attacking adults ashore, the fur seals also caused the abandonment of the gannet colony at Lambert's Bay in 2005/06 (Wolfaardt and Williams 2006) and of ~10% of the colony at Malgas Island in 2017/18 (Dyer et al. 2018). The removal of some damage-causing animals has prevented further losses. At Ichaboe Island and Bird Island/Algoa Bay, periods of non-attendance by parents caused by poor foraging conditions resulted in many eggs or small chicks being eaten by Kelp Gulls *Larus dominicanus* (Mullers and Tinbergen 2009; Rishworth and Pistorius 2015). At Lambert's Bay, between 2009 and 2013, Kelp Gulls ate an average of 13% of the eggs laid by Cape Gannet (Saul and Fortuin 2015). At Malgas Island, Kelp Gulls took 10–70% of the colony's egg production between 2012 and 2018 (Pichegru 2017; SANParks unpublished data). In addition, Great White Pelicans *Pelecanus onocrotalus* have eaten gannet chicks at Malgas Island, especially smaller individuals (Pichegru et al. 2007; de Ponte Machado 2010), although active management put in place by South African National Parks since 2008 has drastically reduced this impact.

Oil-spills are a serious threat to Cape Gannets. In 1979, fish-oil killed at least 709 gannets at Lambert's Bay but improvements in fish-offloading techniques lowered this risk (Crawford et al. 1983). However, fish oil from fish-processing vessels or onshore factories poses a chronic threat to gannets in Namibia (du Toit and Bartlett 2001; Kemper 2015). In 1983, the MT *Castillo de Bellver*

oil spill affected >5 000 Cape Gannets in the vicinity of Saldanha Bay; ~1 500 gannets were caught, of which 65% were de-oiled and successfully released (Wolfaardt et al. 2009). De-oiled birds had only slightly lower survival rates than un-oiled gannets (Altwegg et al. 2008). Recent harbour developments in Algoa Bay are likely to increase the risk of seabirds subjected to oil-fouling in that region (Adeniji et al. 2017). This is of concern for Cape Gannets, given that 70% of the global population now occurs at Bird Island/Algoa Bay.

Avian cholera *Pasteurella multocida* killed 172 Cape Gannets at Malgas Island in 1991 and almost 400 at Lambert's Bay in 2002 (Crawford et al. 1992; Ward and Williams 2004). In 2018, avian influenza (H5N8) was confirmed in Cape Gannets in South Africa and may have killed >1 600 birds (Khomenko et al. 2018; Roberts 2018). At Lambert's Bay, four heat waves (35–40 °C) killed at least 80 adult gannets attempting to shelter their nests in 1998 and 2000 (Ward and Williams 2004). Furthermore, storms (heavy rain and strong winds) can cause shorter nest-attendance times and mortality of Cape Gannet chicks (Crawford et al. 1986; Rishworth and Pistorius 2015; Pistorius et al. 2015).

Conservation interventions

Assuming an age at first breeding of 4 years, and annual survival of birds aged ≥2 years and <2 years of 0.91 and 0.71, respectively (Crawford 1999), an annual production of 0.32 fledglings per pair is required to maintain a (closed) Cape Gannet population in equilibrium (Makhado et al. 2006). Long-term averages in breeding success have generally exceeded 0.32 fledglings per pair (e.g. Adams et al. 1992; Staverees et al. 2008; Crawford et al. 2019). In contrast, from 1990–2009, the annual survival of adult Cape Gannets averaged 0.83 at Lambert's Bay, 0.88 at Malgas Island, and 0.90 at Bird Island/Algoa Bay (Distiller et al. 2012), and mortality immediately after fledging was deemed too high to sustain the population at Malgas Island (Makhado et al. 2006). Although better information on juvenile and immature survival and on demographic parameters at Namibian colonies is required, recruitment rather than adult survival may be limiting the Cape Gannet population (Distiller et al. 2012). In South Africa, adult Cape Gannets buffer their survival in periods of scarcity of sardine and anchovy by switching their diet to include saury or less-nutritious hake offal discarded by bottom trawlers (Crawford et al. 2014; Grémillet et al. 2019), but this can have demographic implications through reduced breeding success and lower chick quality (e.g. Grémillet et al. 2008; cf. Grémillet et al. 2019).

To improve the conservation status of the Cape Gannet it will be necessary to maintain the present high rates of adult survival while at the same time increasing recruitment. The major threats to adult survival are mortality caused by fisheries, oiling and outbreaks of disease, which can be countered by requiring fisheries in the Benguela ecosystem to implement best-practice bycatch mitigation, by marine spatial planning that minimises the risk of oil spills near colonies (where gannets have their highest densities), and by implementing standard protocols to reduce the possibility of pathogens spreading (e.g. rapid disposal of carcasses: Khomenko et al. 2018). Recruitment seems to be mainly limited by insufficient high-quality prey off the west coast of southern Africa, and by disturbance and high

post-fledging mortality inflicted by Cape Fur Seals around some colonies. Predation mortality at or near colonies can be reduced by removing damage-causing animals (e.g. Makhado et al. 2009).

Although it would not reverse the changes in the distribution and availability of their main prey species, ecosystem-based management should implement forage thresholds (e.g. Cury et al. 2011; Crawford et al. 2019) and marine spatial planning (e.g. Distiller et al. 2012) to ensure sufficient food for Cape Gannets and other seabirds (e.g. Sherley et al. 2017, 2018). In South Africa, there is substantial overlap of areas where gannets feed when breeding and where purse-seiners catch sardine and anchovy (Okes et al. 2009; Pichegru et al. 2009), whereas in Namibia, although some core gannet feeding areas fall within the Namibian Islands' Marine Protected Area (MPA) (Ludynia et al. 2012), an improvement in forage resources for gannets depends on the recovery of the Namibian sardine stock. The new Greater Addo MPA in Algoa Bay, and in particular the eastward extension of the MPA from Bird Island, may benefit the Cape Gannet in the future as breeding adults generally forage to the east of the island, albeit often far outside the bay (Botha and Pistorius 2018). Given a lack of alternative breeding localities in the eastern part of their range, it is particularly important to stabilise the deceasing smaller colonies in the western part, where the impact of top-down processes is expected to increase as the Cape Gannet colony sizes decrease (Crawford et al. 2018).

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