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Chapter

Seabirds of the Benguela Ecosystem: Utilisation, Long-Term Changes and Challenges

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Abstract

The Benguela Current is used by c. 82 seabird species, of which seven are endemic to it. Eggs and guano of formerly abundant seabirds were heavily harvested in the 19th and 20th centuries but decreases in seabird populations led to cessation of these industries at islands. Guano is still scraped from platforms. Seabird ecotourism has grown. There were large recent decreases in numbers of African Penguins *Spheniscus demersus*, Cape Gannets *Morus capensis* and Cape *Phalacrocorax capensis* and Bank *P. neglectus* Cormorants and redistributions of these other species away from the centre of the Benguela ecosystem towards its northern or eastern boundaries. In 2020, seabirds endemic to the Benguela ecosystem and albatrosses and petrels migrating into it had high proportions of globally Near Threatened or Threatened species. The primary threat to four Endangered endemic birds was scarcity of forage resources. A Vulnerable endemic damara tern was susceptible to habitat degradation and disturbance. The principal threat to visiting albatrosses and petrels was by-catch mortality. Identification and effective protection of Important Bird Area breeding and marine foraging and aggregation sites, and a suite of complementary measures, are needed to conserve the seabirds and ensure continuation of their economic and ecosystem benefits into the future.

Keywords: Benguela seabirds, conservation status, distributional changes, forage availability, guano, habitat degradation, long-term change, utilisation

1. Introduction

The Benguela Current Large Marine Ecosystem (BCLME) in the southeast Atlantic Ocean is one of the world's four major eastern boundary currents, which undergo intense upwelling of cool nutrient-rich waters that support high phytoplankton biomasses and abundant forage fish resources [1]. The forage fishes, in turn, are fed upon by numerous predators, including seabirds [2]. The BCLME ranges from approximately Benguela in southern Angola to Woody Cape at the eastern border of Algoa Bay in southern South Africa, being bounded in the north and east by the warm Angola and Agulhas currents, respectively (**Figure 1**).

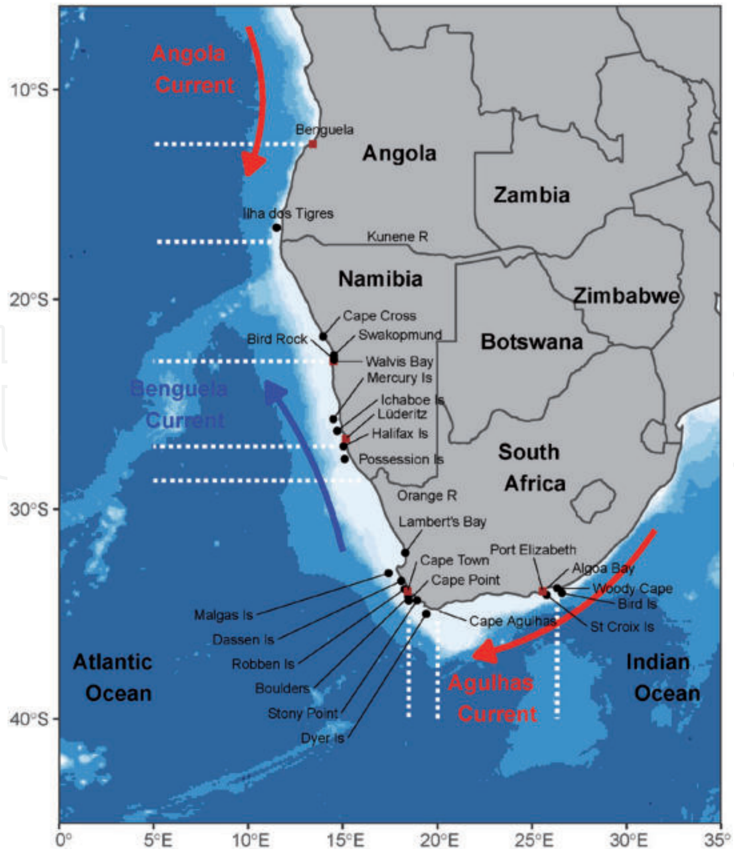

Figure 1.
A map of the Benguela ecosystem showing localities mentioned in the text. The dotted white lines demarcate the seven regions used to investigate distributional changes of seabirds and the guano they produced.

There are 16 species of seabird that breed within the BCLME. Additionally at least 4.4 million birds [3] of c. 66 other species (excluding rare vagrants) migrate to or through the BCLME (**Table 1**). Non-breeding migrants may remain within the BCLME year round.

Species	Common name	IUCN status	Population trend
Aptenodytes patagonicus	King Penguin	Least Concern	Increasing
Ardenna carneipes	Flesh-footed Shearwater	Near Threatened	Decreasing
Ardenna gravis	Great Shearwater	Least Concern	Stable
Ardenna grisea	Sooty Shearwater	Near Threatened	Decreasing
Bulweria bulwerii	Bulwer's Petrel	Least Concern	Stable
Calonectris borealis	Cory's Shearwater	Least Concern	Unknown
Calonectris diomedea	Scopoli's Shearwater	Least Concern	Decreasing
Catharacta antarctica	Brown (Subantarctic) Skua	Least Concern	Decreasing
Catharacta maccormicki	South Polar Skua	Least Concern	Stable
Daption capense	Cape (Pintado) Petrel	Least Concern	Stable
Diomedea amsterdamensis	Amsterdam Albatross	Endangered	Increasing
Diomedea dabbenena	Tristan Albatross	Critically Endangered	Decreasing
Diomedea epomophora	Southern Royal Albatross	Vulnerable	Stable
Diomedea exulans	Wandering Albatross	Vulnerable	Decreasing

Species	Common name	IUCN status	Population trend
Diomedea sanfordi	Northern Royal Albatross	Endangered	Decreasing
Eudyptes chrysocome	Southern Rockhopper Penguin	Vulnerable	Decreasing
Eudyptes chrysolophus	Macaroni Penguin	Vulnerable	Decreasing
Eudyptes moseleyi	Northern Rockhopper Penguin	Endangered	Decreasing
Fregetta grallaria	White-bellied Storm-Petrel	Least Concern	Decreasing
Fregetta tropica	Black-bellied Storm-Petrel	Least Concern	Decreasing
Gelochelidon nilotica	Common Gull-billed Tern	Least Concern	Decreasing
Hydobates leucorous (Oceanodroma leucorhoa)	Leach's Storm-Petrel	Vulnerable	Decreasing
Hydrobates pelagicus	European Storm-Petrel	Least Concern	Unknown
Hydroprogne caspia	Caspian Tern	Least Concern	Increasing
Larus cirrocephalus	Grey-headed Gull	Least Concern	Stable
Larus dominicanus vetula	Kelp Gull	Least Concern	Increasing
Larus hartlaubii	Hartlaub's Gull	Least Concern	Increasing
Larus pipixcan	Franklin's Gull	Least Concern	Increasing
Larus ridibundus	Common Black-headed Gull	Least Concern	Unknown
Lugensa brevirostris	Kerguelen Petrel	Least Concern	Decreasing
Macronectes giganteus	Southern Giant-Petrel	Least Concern	Increasing
Macronectes halli	Northern Giant-Petrel	Least Concern	Increasing
Microcarbo coronatus	Crowned Cormorant	Near Threatened	Stable
Morus capensis	Cape Gannet	Endangered	Decreasing
Morus serrator	Australian Gannet	Least Concern	Increasing
Oceanites oceanicus	Wilson's Storm-Petrel	Least Concern	Stable
Onychoprion (Sterna) fuscatus	Sooty Tern	Least Concern	Unknown
Pachyptila belcheri	Slender-billed Prion	Least Concern	Stable
Pachyptila desolata	Antarctic Prion	Least Concern	Decreasing
Pachyptila salvini	Salvin's Prion	Least Concern	Stable
Pelagodroma marina	White-faced Storm-Petrel	Least Concern	Decreasing
Pelecanus onocrotalus	Great White Pelican	Least Concern	Unknown
Phaethon aethereus	Red-billed Tropicbird	Least Concern	Decreasing
Phaethon lepturus	White-tailed Tropicbird	Least Concern	Decreasing
Phaethon rubricauda	Red-tailed Tropicbird	Least Concern	Stable
Phalacrocorax capensis	Cape Cormorant	Endangered	Decreasing
Phalacrocorax lucidus	White-breasted Cormorant	Least Concern	Unknown

Species	Common name	IUCN status	Population trend
Phalacrocorax neglectus	Bank Cormorant	Endangered	Decreasing
Phalaropus fulicarius	Red (Grey) Phalarope	Least Concern	Unknown
Phalaropus lobatus	Red-necked Phalarope	Least Concern	Decreasing
Phoebetria fusca	Sooty Albatross	Endangered	Decreasing
Phoebetria palpebrata	Light-mantled Albatross	Near Threatened	Decreasing
Procellaria aequinoctialis	White-chinned Petrel	Vulnerable	Decreasing
Procellaria cinerea	Grey Petrel	Near Threatened	Decreasing
Procellaria conspicillata	Spectacled Petrel	Vulnerable	Increasing
Pterodroma incerta	Atlantic Petrel	Endangered	Decreasing
Pterodroma macroptera	Great-winged Petrel	Least Concern	Decreasing
Pterodroma mollis	Soft-plumaged Petrel	Least Concern	Stable
Puffinus assimilis	Little Shearwater	Least Concern	Decreasing
Puffinus puffinus	Manx Shearwater	Least Concern	Unknown
Spheniscus demersus	African Penguin	Endangered	Decreasing
Stercorarius longicaudus	Long-tailed Jaeger	Least Concern	Stable
Stercorarius parasiticus	Arctic (Parasitic) Jaeger	Least Concern	Stable
Stercorarius pomarinus	Pomarine Jaeger	Least Concern	Stable
Sterna albifrons	Little Tern	Least Concern	Decreasing
Sterna dougallii	Roseate Tern	Least Concern	Unknown
Sterna hirundo	Common Tern	Least Concern	Unknown
Sterna paradisaea	Arctic Tern	Least Concern	Decreasing
Sterna vittata	Antarctic Tern	Least Concern	Unknown
Sternula balaenarum	Damara Tern	Vulnerable	Decreasing
Sula leucogaster	Brown Booby	Least Concern	Decreasing
Sula sula	Red-footed Booby	Least Concern	Decreasing
Thalassarche carteri	Indian Yellow-nosed Albatross	Endangered	Decreasing
Thalassarche cauta	Shy Albatross	Near Threatened	Unknown
Thalassarche chlororhynchos	Atlantic Yellow-nosed Albatross	Endangered	Decreasing
Thalassarche chrysostoma	Grey-headed Albatross	Endangered	Decreasing
Thalassarche melanophrys	Black-browed Albatross	Least Concern	Increasing
Thalassarche salvini	Salvin's Albatross	Vulnerable	Unknown
Thalasseus b. bergii	Greater Crested (Swift) Tern	Least Concern	Stable
Thalasseus maximus	Royal Tern	Least Concern	Stable
Thalasseus sandvicensis	Sandwich Tern	Least Concern	Stable
Xema (Larus) sabini	Sabine's Gull	Least Concern	Stable

Table 1.
The conservation status of seabirds that occur in the BCLME (rare vagrants have been excluded). Where known, the recent global population trend is indicated [4]. Information is sorted on genus and then species. Grey shading indicates species or races that breed only in the BCLME. The Royal Tern occurring in the BCLME has recently been reclassified as the West African Crested Tern Thalasseus albididorsalis.

This chapter summarises the former and present utilisation of the BCLME's seabirds and their products, changes in their distribution and abundance, their conservation status and factors influencing it, and future challenges if healthy seabird populations and their benefits are to be maintained. In order to investigate distributional changes, the BCLME was divided into seven regions: southern Angola, northern, central and southern Namibia, and western, southwestern and southern South Africa, as indicated on **Figure 1**.

2. Utilisation

2.1 Penguin eggs

From the late 1400s, African Penguins *Spheniscus demersus* and other seabirds in the BCLME were caught as food by early explorers, as fuel to supply ship boilers and to be rendered down for their fat [5, 6]. However, the primary attraction of African Penguins was their eggs. Collection of these on a large scale may have begun as early as 1652 [7]. Details of numbers of eggs collected at different breeding localities are available for each year from 1871–1967 (after which collections ceased) with gaps from 1879–1890, 1894–1896 and in 1904 and 1914 [7].

Annual collections averaged c. 192,000 eggs from 1871–1878, c. 537,000 eggs from 1891–1931 and c. 76,000 eggs from 1935–1967 (**Figure 2**). The overall harvest for the 80 years between 1871 and 1967 for which records were kept was c. 23.4 million eggs, with a maximum of 801,500 eggs in 1899. About 99% of the eggs were taken off western South Africa (84% from Dassen Island), with small proportions coming from southern Namibia (< 1%) and southwestern South Africa (c. 1%). Although ease of access to colonies and of gathering eggs would have influenced localities selected for collections, their geographical distribution approximated that of African Penguins at the time. In the early 1900s, Dassen Island off western South Africa was the largest colony holding an estimated 0.57–0.93 million breeding pairs between 1910 and 1930 [8, 9]. In 1956, no African Penguins bred in Angola or northern Namibia. The proportions then breeding in central and southern Namibia and in western, southwestern and southern South Africa were 5%, 25%, 62%, 3% and 5%, respectively [10].

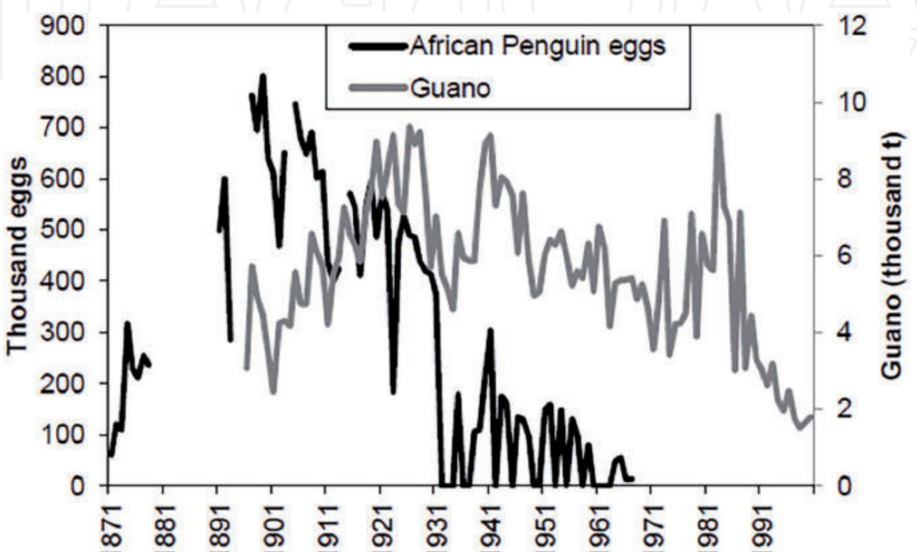

Figure 2.
Trends in total collections of African Penguin eggs and seabird guano in the BCLME, 1871–1999.

At Dassen Island, c. 48% of penguin eggs produced in the early 20th century were collected; this was unsustainable and led to an estimated decrease in the number of penguins there aged two years or older, from c. 1.45 million in 2010 to c. 0.22 million in 1956 and 0.14 million in 1967 [8].

2.2 Guano

In the 1840s, after the value of guano as an agricultural fertilizer became known, accumulated deposits of seabird guano were stripped from many southern African islands [11]. Then, from the late 1800s until the mid-1980s or early 1990s, fresh deposits of seabird guano were regularly collected at a number of islands off Namibia and South Africa. At Ichaboe Island in central Namibia sporadic guano extraction persisted until 2016. From 1896, annual records of quantities removed from different islands were maintained [12]. Most of the guano extracted from the islands was produced by Cape Gannets *Morus capensis* and Cape Cormorants *Phalacrocorax capensis*. Phosphatic sand was at times removed from African Penguin breeding areas at Dassen Island to mix with guano or to spread over breeding areas of Cape Gannets, which build their nests from guano [13]. In southern Africa, the African Penguin, Cape Gannet and Cape Cormorant became known as the 'guano-producing' seabirds, although other cormorants and Great White Pelicans *Pelecanus onocrotalus* would have contributed small amounts to guano depositions at some localities. Between 1930 and 1971 platforms were constructed by private entrepreneurs to collect guano at Bird Rock, Swakopmund and Cape Cross on the northern Namibian coast, which was mainly produced by Cape Cormorants [14]. Annual records of quantities taken from each platform were maintained [15]. Between 1900 and 1999, an average of c. 5,700 t of seabird guano (after subtraction of additions of phosphatic sand) was extracted annually in the BCLME, with a maximum of c. 9,600 t and a minimum of c. 1,500 t (**Figure 2**).

Guano extraction sometimes displaced or caused disturbance to seabirds, reducing breeding success [16]. It also created hollows on some islands, allowing rain to accumulate, which on occasion flooded nests of some seabird species and also reduced breeding success [17].

2.3 Tourism

Seabird tourism is a rapidly expanding industry in the BCLME. In South Africa, Boulders at Simon's Town, Stony Point at Betty's Bay and Robben Island provide opportunities for the public to observe African Penguins and other seabirds in their natural habitat and have become popular tourist destinations that generate socio-economic gains through gate fees, provision of jobs and benefits to surrounding areas [18]. For example, Boulders provided 885 jobs directly associated with its penguin colony and expenditure related to the colony was approximately ZAR 311 million [19]. It contributed to the overall branding of Cape Town as a popular destination for international visitors [18]. The Stony Point penguin colony received an average of 77,500 visitors p. a. from 2010–2019 [20]. The Cape Gannet colony at Lambert's Bay is an important source of revenue for that community [20]. Land tours to view breeding and roosting seabirds operate in Namibia, e.g. [21]. Boat-based seabird viewing operates out of several southern African ports, including around the largest African Penguin colony at St Croix Island [20].

It was estimated that seabird tourism contributed c. ZAR 500 million to the South African economy in 2020 [20].

3. Long-term changes in distribution and abundance

3.1 Guano

Production of guano at the platforms in northern Namibia commenced in the 1930s when the average yield was c. 450 t p.a.; it then increased to a peak of c. 3,350 t in the 1980s before a decrease in the 1990s. By contrast, yields in central and southern Namibia and western South Africa peaked in the 1920s at c. 3,500 t, 1,900 t and 2,300 t p.a., respectively, and then decreased. In southwestern South Africa, production peaked at c. 400 t p.a. in the 1910s and then decreased. In southern South Africa it increased from c. 120 t p.a. in the 1890s to an average of c. 340 t p.a. between the 1920s and 1980s (**Figure 3**). Hence, there were long-term increases in guano yields in northern Namibia and southern South Africa but

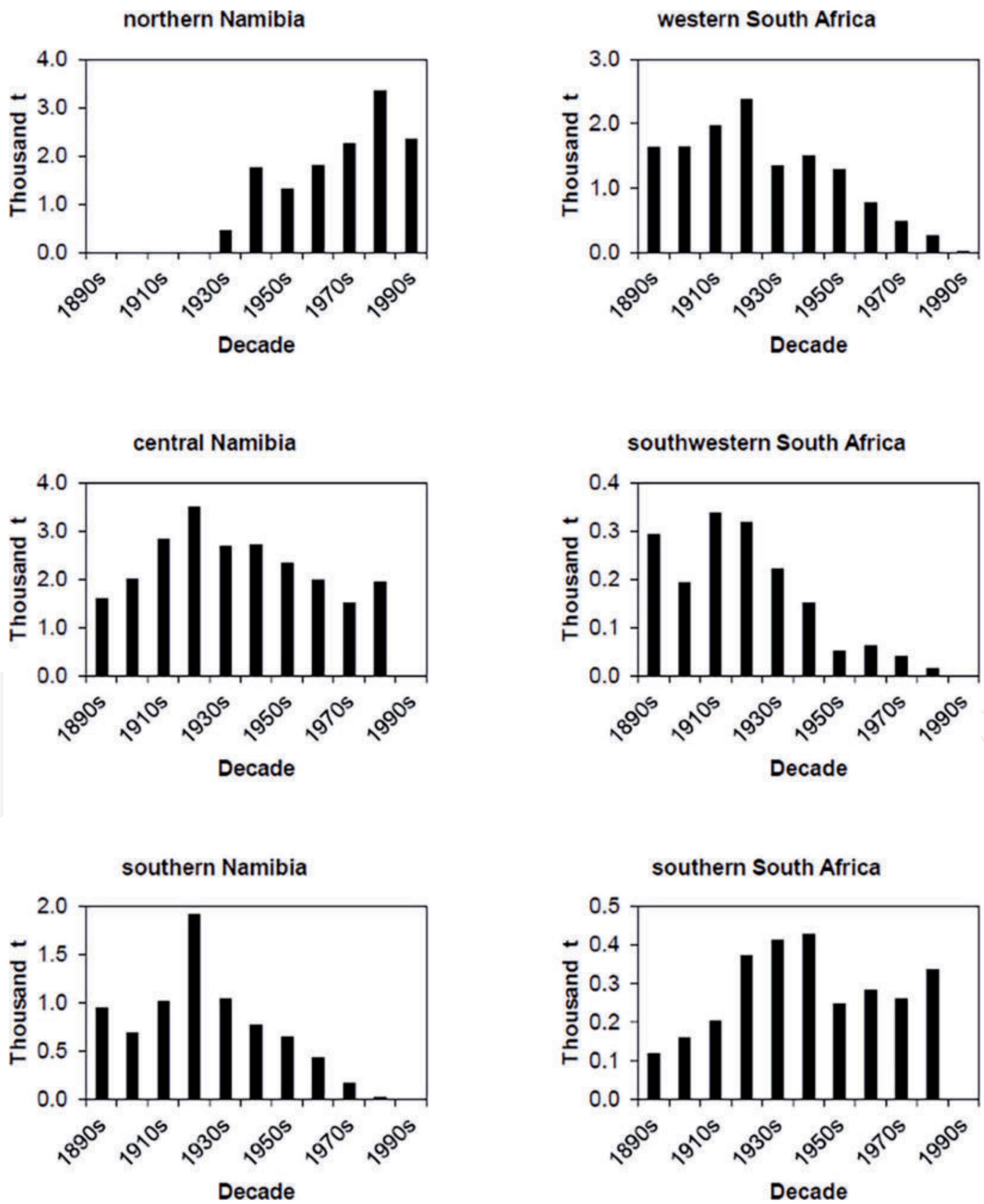

Figure 3.
Average collections of seabird guano in six regions of the BCLME over 11 decades, 1890s–1990s.

decreases in the four intervening regions. The trends after the 1920s accord with the provision of nesting habitat for cormorants in the north, and with decreases of Cape Cormorants in central and southern Namibia after the 1970s and in western South Africa after the 1980s [15, 22]. They also match decreases of Cape Gannets at colonies in Namibia after the 1950s and in western South Africa after the 1990s, but an increase in the Cape Gannet colony at Bird Island, Algoa Bay in southern South Africa [23]. Guano extraction at islands was gradually halted to minimize its adverse impacts on dwindling seabird colonies [24].

3.2 'Guano-producing' seabirds

Average numbers of the BCLME's three 'guano-producing' seabirds that bred in each of the selected regions were determined for seven decades from the 1950s to the 2010s. Information was collated from [25, 26] for African Penguins, [23] for Cape Gannets and [15, 22, 27, 28] for Cape Cormorants. Unpublished data held by the Benguela Current Convention (BCC) were also utilized. Methods used to estimate numbers of breeding birds are described in the afore-mentioned sources. Aerial photography was frequently applied for large surface-nesting colonies of the three seabird species, whereas ground surveys were employed for smaller colonies or when nests were on cliffs, under boulders or vegetation, or in burrows.

For all decades, averages were obtained for each breeding locality and summed for all localities in a region. In the 1960s, there was no reliable information on numbers of African Penguins that bred in South Africa or on numbers of Cape Cormorants that bred in Namibia and southern South Africa, so these values were interpolated from information for the 1950s and 1970s. Various small colonies of African Penguins and Cape Cormorants were not counted in all decades. However, except as detailed above, reliable estimates were available for all major colonies and the absence of information for some minor colonies is not expected meaningfully to influence the trends that are shown in **Figure 4**.

In the period under consideration, no African Penguins bred in southern Angola or northern Namibia. Cape Gannets only bred at Mercury and Ichaboe islands in central Namibia, Possession Island in southern Namibia, Lambert's Bay and Malgas islands in western South Africa and Bird Island, Algoa Bay in southern South Africa. Cape Cormorants bred in all seven regions.

Estimates of the number of Cape Cormorants breeding in northern Namibia increased between the 1950s and the 1970s, when there were c. 75,000 pairs, and then decreased. Cape Cormorants were first recorded breeding in southern Angola in the 2000s and c. 16,000 pairs bred there in 2017 [28]. About 40,000 pairs bred in southern Angola and northern Namibia between the 1980s and 2010s (**Figure 4**). In the 1950s, central and southern Namibia held c. 200,000 and c. 50,000 pairs of 'guano-producing' seabirds, respectively. By the 2010s, the average numbers breeding had decreased in central Namibia by c. 85% and in southern Namibia by c. 95%. There were large decreases of African Penguins and Cape Gannets in both these regions (**Figure 4**).

In western South Africa, average numbers of the 'guano-producing' seabirds fell by c. 75% from c. 200,000 pairs in the 1950s to c. 50,000 pairs in the 2010s. As in central and southern Namibia, there were large losses of African Penguins. There also was a severe decrease of Cape Cormorants (**Figure 4**). In southwestern South Africa, average numbers of the 'guano-producing' seabirds increased from c. 7,500 pairs in the 1950s to c. 60,000 pairs in the 1970s, as a result of increases of both African Penguins and Cape Cormorants. Numbers then decreased to an average of c. 30,000 pairs in the 2010s, following a large decrease in African Penguins after the 1970s (**Figure 4**). In southern South Africa, average numbers of the

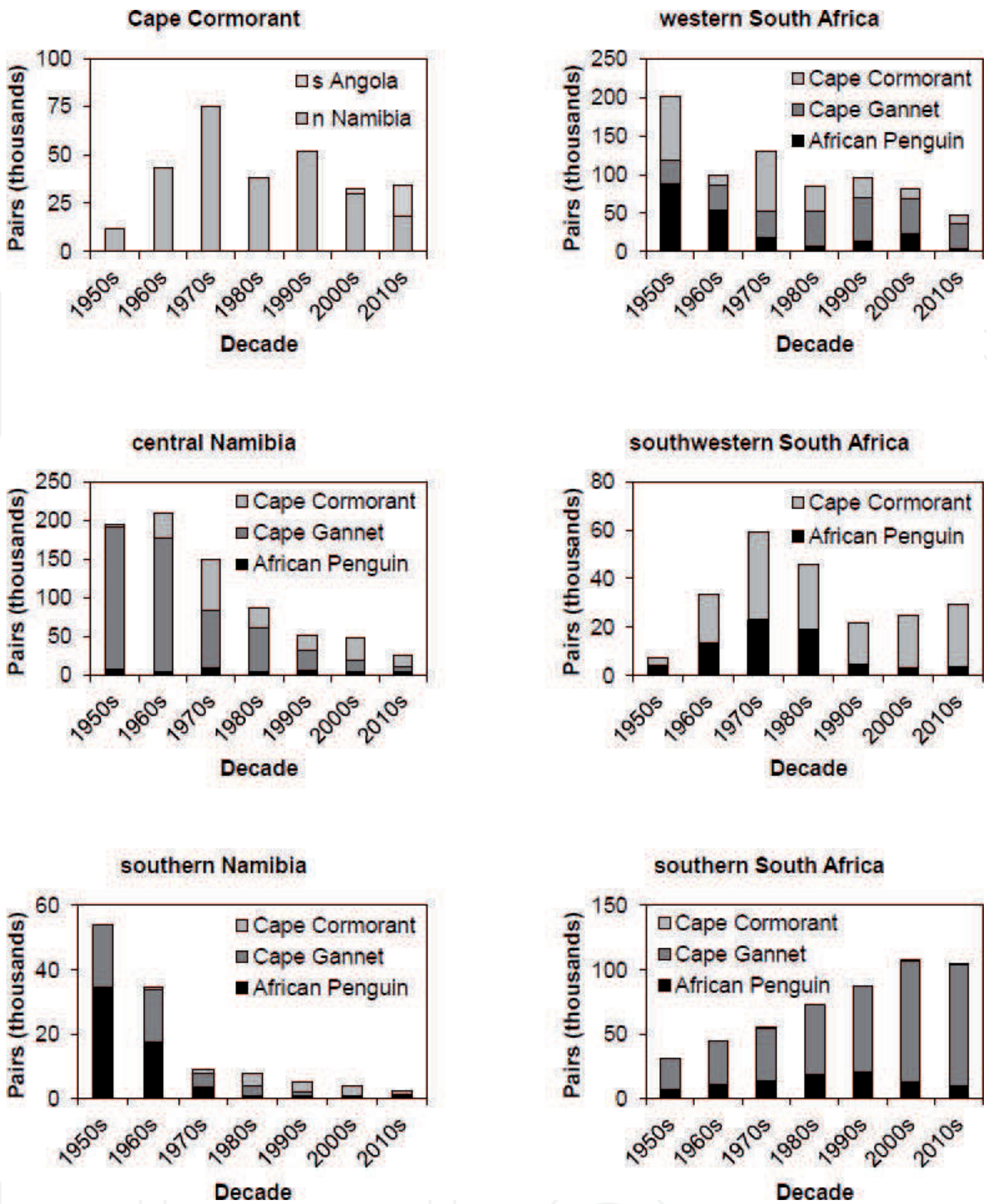

Figure 4.
Average estimates of breeding pairs of African Penguins, Cape Gannets and Cape Cormorants in seven regions of the BCLME over seven decades, 1950s–2010s. Of these species, only Cape Cormorants bred in the northernmost two regions where average numbers breeding are shown in the top left box.

'guano-producing' seabirds trebled from c. 30,000 pairs in the 1950s to >100,000 pairs in the 2000s and 2010s, primarily as a result of a large increase in the number of Cape Gannets (**Figure 4**).

In summary, in the BCLME between the 1950s and 2010s there were substantial increases in numbers of Cape Cormorants in northern regions and of Cape Cormorants and Cape Gannets in southern regions, but large decreases of these two species and of African Penguins in central regions. Construction of platforms in northern Namibia facilitated a northern expansion of Cape Cormorants and the species also colonized Ilha dos Tigres in southern Angola [28]. Cape Cormorants likewise established several new colonies in the south, both at islands and mainland localities [22]. Cape Gannets were unsuccessful in attempts to form new colonies, but greatly enlarged their southernmost colony at Bird Island in Algoa Bay [23]. African Penguins formed three new colonies in the south and attempted to initiate another southern colony, but were unable to offset huge decreases at central colonies [25]. The average numbers of the three 'guano-producing' seabirds taken together fell by 50% from c. 500,000 pairs in the 1950s to c. 250,000 pairs in the 2010s. Over the same period, average numbers for African Penguins decreased by c. 84% from c. 141,000 pairs to c. 23,000 pairs and for Cape Gannets by c. 49% from c. 259,000 pairs to c. 133,000 pairs. Average numbers for Cape Cormorants increased from c. 100,000 pairs in the 1950s to c. 250,000 pairs in the 1970s [15] and then decreased to c. 91,000 pairs in the 2010s.

3.3 Other seabirds

In South Africa, in addition to shifts to the south and east of the three 'guano-producing' seabirds reported in the previous section, there were decreased proportions of birds breeding in the north and increases in the south for Bank Cormorant *P. neglectus*, White-breasted Cormorant *P. lucidus*, Crowned Cormorant *Microcarbo coronatus*, Kelp Gull *Larus dominicanus*, Greater Crested (Swift) Tern *Thalasseus bergii* and Damara Tern *Sternula balaenarum* [29–35]. There is little or no competition by White-breasted and Crowned Cormorants, Kelp Gulls and Damara Terns with fisheries for forage resources [36], so environmental change may have influenced the redistributions of the seabirds [33].

In Namibia, in addition to the northward expansion of Cape Cormorants mentioned above, the proportion of Bank Cormorants that bred north of Ichaboe Island increased from 28% in 1995–1997 [37] to 84% in 2010 [38].

Overall there were large decreases in Bank Cormorants after the 1970s [30, 38]. In South Africa there were also decreases of Damara Terns after the 1990s [34] but populations of the other four seabirds showed stability or increased [33].

3.4 Other biota

Off South Africa, in the 1990s and 2000s there were shifts to the south and east in the distributions of three important forage resources heavily exploited by commercial fisheries: Cape rock lobster *Jasus lalandii* [39], anchovy *Engraulis encrasicolus* [40] and sardine *Sardinops sagax* [41]. The shifts may have been influenced by localised overfishing [39, 41] and environmental change [40, 42]. At the same time, an increased contribution of bearded goby *Sufflogobius bibarbatus* to the diet of Bank Cormorants off western South Africa suggested a southward expansion of the Namibian stock of this fish species [43]. When Namibia's sardine stock collapsed in the 1960s, its range contracted to the north [44] and it was largely replaced by bearded goby, jellyfish and possibly Cape horse mackerel *Trachurus capensis* [45, 46].

4. Conservation and management

4.1 Conservation status

The conservation status of the 82 seabirds that breed in or visit the BCLME was assessed in 2018 or 2019 by the International Union for Conservation of Nature (IUCN) and is shown in **Table 1**, along with the species' population trends [4]. Sixteen seabird species breed in the BCLME, of which seven are endemic to it and for two others the local races are endemic (**Table 1**). All nine endemic taxa and three wider-ranging species (Leach's Storm Petrel *Hydobates leucorous*, Australian Gannet *M. serrator* and Roseate Tern *Sterna dougallii*) breed only along the coastline, whereas the other four non-endemic species (Great White Pelican, White-breasted Cormorant, Grey-headed Gull *L. cirrocephalus* and Caspian Tern *Hydroprogne caspia*) also breed at suitable inland localities. Four of the endemic seabirds feed to a large extent on forage resources that are targeted by commercial fisheries: African Penguin, Cape Gannet and Cape Cormorant on sardine and anchovy; Bank Cormorant on rock lobster [36]. Food scarcity was a major driver of recent large decreases of these species [24], which led to all being listed by the IUCN as Endangered (EN) [47]. The other three endemic seabirds do not compete with fisheries for prey. The Crowned Cormorant population was stable but relatively small and is currently listed as Near Threatened (NT) [47], whereas Damara Tern decreased on account of disturbance at, or loss of, breeding habitat and is currently listed as Vulnerable (VU) [47–49]. The loss of breeding habitat also influenced other Benguela seabirds [24]. In 2020, Hartlaub's Gull (endemic to the BCLME) and the wider-ranging Great White Pelican, Australian Gannet, which in the BCLME hybridises with Cape Gannet [6], White-breasted Cormorant, Kelp and Grey-headed gulls, Greater Crested, Roseate and Caspian terns were globally Least Concern (LC); Leach's Storm Petrel, which mainly breeds in the northern hemisphere and has decreased, was VU [47]. However, in South Africa the small and isolated populations of Leach's Storm Petrel (c. 5 pairs) and Roseate Tern (c. 125 pairs) were regarded as Critically Endangered (CR) and EN, respectively, and the small populations of Great White Pelican (c. 2,500 pairs) and Caspian Tern (c. 310 pairs) as VU [50]. Leach's Storm Petrel and Roseate Tern have not been recorded breeding in Angola or Namibia. In 2020, six of the seven seabirds endemic to the BCLME were EN, VU or NT. Of the other nine species that breed in the BCLME, globally one was VU but regionally four were CR, EN or VU.

The 66 seabird species that migrate to the BCLME are made up of four penguins, 13 albatrosses, three prions, 18 petrels and shearwaters, five storm petrels, three tropicbirds, two boobies, two phalaropes, five skuas or jaegers, three gulls and eight terns. One pair of one of the terns (Sandwich *T. sandvicensis*) bred at Halifax Island in 2014 [51]. Three *Eudyptes* penguins were classified as EN or VU (**Table 1**). However, threats to these penguins occur mainly outside the BCLME [47]. In 2020, the Tristan Albatross *Diomedea dabbenena* was CR and the Amsterdam *D. amsterdamensis*, Northern Royal *D. sanfordi*, Sooty *Phoebetria fusca*, Atlantic Yellow-nosed *Thalassarche chlororhynchos*, Indian Yellow-nosed *T. carteri* and Grey-headed *T. chrysostoma* albatrosses were all EN. Three of the other albatrosses were VU and two were NT. The Atlantic Petrel *Pterodroma incerta* was EN, all three *Procellaria* petrels were VU or NT and two *Ardenna* shearwaters were NT. All the other migrant seabirds were LC (**Table 1**). Incidental by-catch in fisheries was a major cause of mortality and a driver of population decreases for several albatrosses and large petrels [52, 53] and is the main at-sea threat faced by such species in the BCLME [54–57]. The introduction of invasive mammal predators, such as mice, on sub-Antarctic islands, e.g. Marion and Gough islands, has had a significant impact on populations of some albatrosses and petrels that visit the BCLME, e.g. [58].

4.2 Conservation challenges

Amongst challenges facing seabirds that breed in the BCLME are geographical shifts of forage resources that led to mismatches in the distributions of the birds' breeding localities and their prey and, as a consequence, to reduced sizes of many colonies and, in instances, to one or a few localities holding large proportions of certain species' populations.

Small colonies may suffer from Allee effects, or inverse density dependence, which increase their chances of extinction [59]. For example, African Penguins that feed in groups have a greater catch per unit effort than solitary birds [60], but diminishing colonies may become too small for sufficient foraging groups to form [59]. Dwindling colonies also mean that higher proportions of birds nest near colony edges, where eggs and chicks are at a greater risk of predation [61]. Amongst African Penguins taken to a rescue centre, females had higher mortality rates than males [62]. If a similar sex-biased mortality exists in the wild, it may skew sex ratios at small colonies. Empirical information on the performance of 41 discrete colonies of African Penguins showed that only one of 28 colonies that had fewer than 250 pairs survived for 40 years, compared to 50% of colonies with 500–1,000 pairs, 67% of those having 1,000–5,000 pairs and all larger colonies [63]. This makes it imperative to maintain colonies at sizes sufficient to have reasonable longevity.

In 2010, Mercury Island held 72% of the global population of Bank Cormorants [38] and 73% of Namibia's African Penguins [25]. In 2018, c.70% of the Cape Gannet population was at Bird Island, Algoa Bay at the eastern boundary of the BCLME [23]. In the 2010s, 54% of South Africa's Cape Cormorants bred at Dyer Island [22]. Such congregations of large proportions of a species at a single locality may offset Allee effects but render the species highly susceptible to local catastrophic events such as oil spills [64].

As indicated above, major threats to seabirds that breed in the BCLME include food scarcity, which has resulted from altered distributions of prey and overfishing, and disturbance at, or a loss of, breeding habitat. At a global perspective, a priority identified for seabird conservation was effective protection of Important Bird Area (IBA) breeding and marine IBA feeding and aggregation sites, as part of networks of Marine Protected Areas (MPAs) [52]. IBA and MPA initiatives should mitigate both the loss of breeding habitat [65] and food scarcity. Around African Penguin colonies commercial fishing of forage resources decreased numbers breeding [66], whereas closures to fishing reduced energetic costs of foraging [67] and improved chick condition and breeding success [68, 69]. Numbers of Bank Cormorants breeding showed a positive response to local availability of rock lobsters and modelling suggested that prohibition of commercial lobster catches around colonies would benefit this bird [70].

A second measure that could enhance food availability is the identification and implementation of thresholds (below which fishing would be disallowed) of forage fish abundance (or availability) that are necessary to maintain adequate reproduction and survival of dependent predators [71–73]. In addition to abundance and availability of food, quality of prey is an important consideration if energetic requirements of seabirds are to be met [43, 74, 75]. A third means to achieve sufficient food is to offset mismatches in the distributions of breeding localities and prey of seabirds through the establishment of colonies nearer to the food supply. Guano platforms in Namibia served this purpose for Cape Cormorants and an attempt to establish a new African Penguin colony in South Africa has been initiated [76].

Other threats to seabirds that breed in the BCLME include competition for breeding space [77] and high mortality from predation [78], disease [79, 80] and pollution [81]. Marine developments and operations, such as ship-to-ship bunkering, finfish aquaculture and proposed offshore windfarms, are emerging as further threats to the BCLME's breeding seabirds. Given that 63% of these seabirds are globally or regionally CR, EN, VU or NT, it will be necessary to control all factors impacting their populations.

A second priority identified for seabird conservation at a global scale was reduction of by-catch to negligible levels [52, 53]. Substantial strides have been made in mitigating seabird by-catch in South African and Namibian fisheries [54–57]. South Africa has recently committed to eradicate the house mouse *Mus muscullus* from Marion Island in 2023. If successful, this is likely to reduce losses of some albatrosses and petrels that visit the BCLME.

4.3 Ecosystem role

When breeding, seabirds are central-place foragers that bring large quantities of nutrients from the ocean to their colonies. This influences the functioning of island and headland ecosystems through increasing algal growth and changing the structure of intertidal communities, which in turn increases the population sizes of some shorebird species [82]. Inputs by seabirds of nitrogen (N) and phosphorus (P) are substantial, with concentrations per unit of surface area among the highest measured on the Earth's surface. Furthermore, an important fraction of the total excreted N and P is readily soluble, increasing the short-term bioavailability of these nutrients in coastal waters [83]. Not only do seabirds have such beneficial bottom-up impacts but they may exert valuable top-down control by removing substandard individuals, thus aiding long-term survival of prey populations [84]. Seabirds also facilitate feeding by other species; e.g. African Penguins herd prey shoals upwards making them available to birds restricted to feeding near the surface [85].

5. Conclusions

The productive waters of the Benguela upwelling system provide foraging opportunities for large numbers of seabirds, including 16 species that breed in the BCLME and c. 66 species that visit it.

In the 1800s and 1900s collections of penguin eggs took place over almost 100 years but proved unsustainable. Seabird guano was extracted over >100 years but purse-seine fisheries initiated after World War 2 depleted forage resources and led to decreases of guano-producing seabirds. Recently seabird ecotourism in the BCLME has been expanding.

After the 1950s guano production decreased in the central BCLME but increased in the north and was stable in the south until the cessation of extractions at islands. After the 1970s there were decreases of and shifts to the north or south in distributions of the three 'guano-producing' seabirds. There were similar redistributions of several other seabirds. The altered distributions likely resulted from both intensive fishing and environmental change.

The conservation status of seabirds breeding in the BCLME has deteriorated. Main threats to these species include food scarcity and loss of breeding habitat, which need to be controlled if socio-economic and ecosystem benefits of seabirds are to be maintained. Although fishery by-catch and invasive mammalian predators are important threats to several seabirds that visit the BLCME, South Africa and Namibia have taken steps to mitigate these.

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Conflict of interest

The authors have no conflict of interest to declare.

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