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REVIEW

Food, fishing and seabirds in the Benguela upwelling system

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Abstract The Benguela upwelling system off south-western Africa supports sardine *Sardinops sagax* and anchovy *Engraulis encrasicolus* that are harvested by purse-seine fisheries and are the main prey of three endemic seabirds: African Penguin *Spheniscus demersus*, Cape Gannet *Morus capensis* and Cape Cormorant *Phalacrocorax capensis*. There have been large, long-term changes in the abundance and distribution of the fish resources that have influenced seabird populations. After 1956/1957, the numbers of penguins and gannets breeding in Namibia decreased by 90% and 95%, respectively. After 1978/1979, the number of Cape Cormorants breeding in Namibia decreased by 76%. These decreases were significantly related to the biomass of sardine and anchovy in Namibia and are thought to result mainly from a greatly reduced availability of prey. In South Africa, when the sardine collapsed, it was replaced by anchovy. In the Western Cape, the numbers of Cape Gannets and Cape Cormorants were stable after the collapse of the sardine but African Penguins decreased. The sardine resource recovered in the 1980s and 1990s but, at the turn of the century, was displaced to the east, leading to increases and then decreases in the numbers of penguins and gannets in the Western Cape. In the Eastern Cape, there were long-term increases in the numbers of penguins and gannets, until a recent decrease in penguins. In South Africa, the models used to advise allowable catches for sardine and anchovy are being modified to incorporate a model of African Penguins and functional relationships linking penguins and fish stocks. Consideration is also being given to precluding fishing in areas around seabird breeding colonies.

Keywords Benguela · Food · *Morus capensis* · *Phalacrocorax capensis* · *Spheniscus demersus*

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Introduction

The Benguela upwelling system off south-western Africa supports a high abundance of epipelagic fish, notably, sardine *Sardinops sagax* and anchovy *Engraulis encrasicolus* (Schwartzlose et al. 1999). These fish species are the most important prey of three seabirds that are endemic to the region: African Penguin *Spheniscus demersus*, Cape Gannet *Morus capensis* and Cape Cormorant *Phalacrocorax capensis* (Hockey et al. 2005 and references therein). The main seabird breeding localities are grouped in three areas: the Namibian coastline from Cape Cross southwards, South Africa's Western Cape and islands near Port Elizabeth in the Eastern Cape (Fig. 1). The breeding localities in the Western Cape are separated from those in Namibia and in the Eastern Cape by distances of about 400 km and 550 km, respectively.

Commercial purse-seine fisheries for small pelagic fish commenced off Namibia and South Africa after World War II. They initially targeted sardine and, later, also anchovy. Other species were caught, when available. There were collapses of the sardine stocks off South Africa in the early 1960s and off Namibia in the late 1960s (Crawford et al. 1987). The South African sardine began a recovery in the 1980s and was again abundant at the start of the 21st century (Fairweather et al. 2006) but prey remained scarce off Namibia, with severe repercussions for seabirds

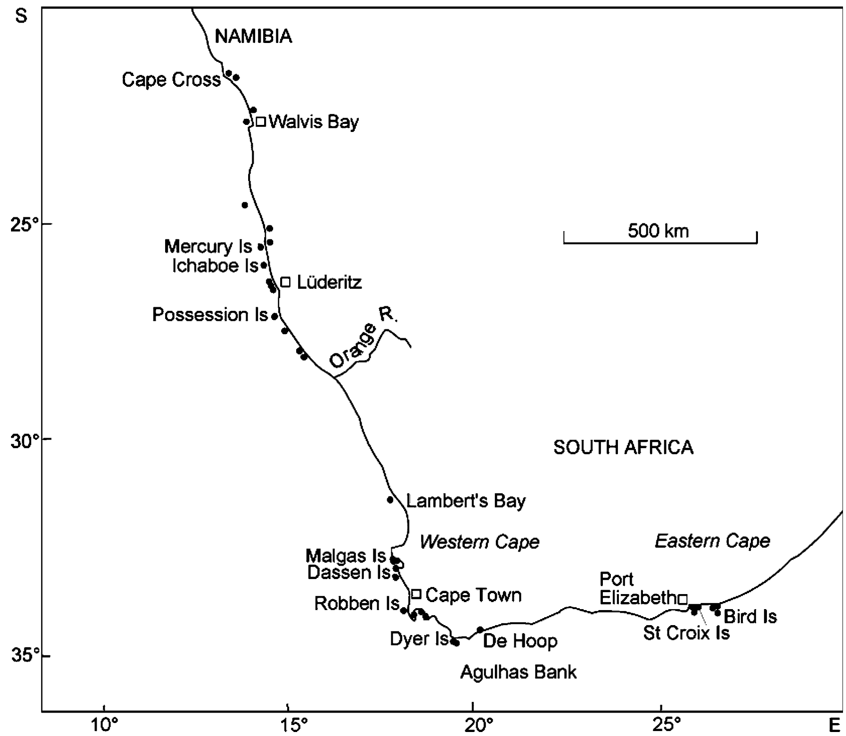

Fig. 1 Southern Africa, showing the locations of the main seabird breeding colonies around the coastline

(Crawford 1998, 1999). In the late 1990s, the distribution of the sardine off South Africa changed (Fairweather et al. 2006), influencing its availability to seabirds.

This paper reviews trends in the catches and biomass of sardine and anchovy and in the abundance of African Penguins, Cape Gannets and Cape Cormorants in the Benguela system and considers means of accounting for the food requirements of seabirds in the management of the purse-seine fisheries.

Trends in fish stocks

Catches

Trends in the catches of sardine and anchovy off Namibia, South Africa and in the Benguela system as a whole are shown in Fig. 2. In Namibia, catches of sardine peaked at 1.4 million t in 1968 but after 1977, were less than 0.2 million t in all years (Fig. 2a). Anchovy was first caught by purse-seine boats in 1964. Catches were small until 1968, when 0.16 million t was landed. In 1978, anchovy became the most important contributor to the purse-seine fishery. This situation continued until 1984, when <0.02 million t was caught. Low catches continued in 1985 and 1986. In 1987, the anchovy catch (0.38 million t) was the highest yet recorded. Thereafter, catches plummeted and by 1996, just 0.001 million t was caught (Schwartzlose et al. 1999).

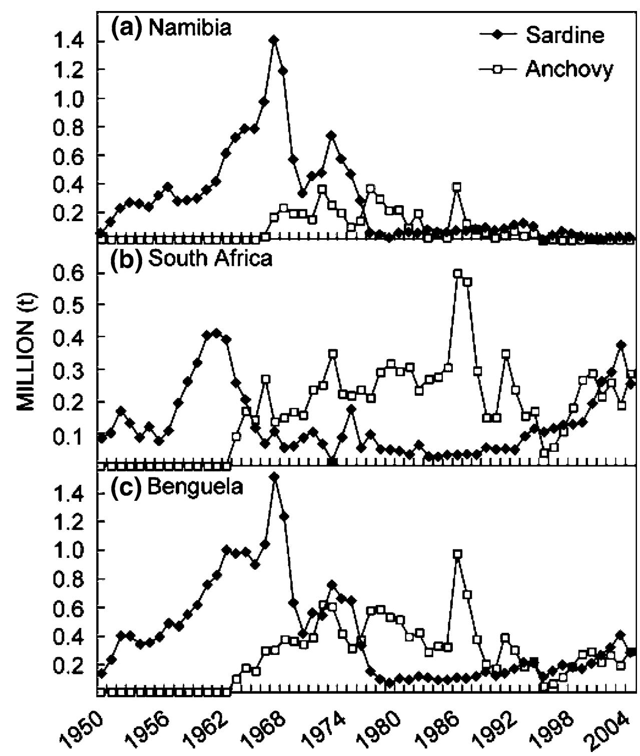

Fig. 2a–c Catches of sardine and anchovy made **a** off Namibia, **b** off South Africa and **c** in the Benguela system, 1950–2005

Off South Africa, catches of sardine fluctuated around 0.1 million t during the early and mid 1950s and then increased to a maximum of around 0.4 million t during

1961–1963 (Fig. 2b). Catches fell to less than 0.1 million t in 1967. Except in 1968, 1972 and 1976, they remained below this level until 1995. Catches above 0.2 million t were recorded from 2002 to 2005. Anchovy catches increased steadily from 1964 onwards, reaching a peak of approximately 0.6 million t in 1987 and 1988. Subsequently, anchovy catches decreased, with some variability, to a minimum of 0.04 million t in 1996 and then increased sharply again (Fig. 2b).

In the Benguela system as a whole, sardine dominated the purse-seine catch in the 1950s and 1960s, and anchovy from 1977 to 1993. At other times, the two species contributed approximately the same catches (Fig. 2c).

Biomass

In Namibia, estimates of the biomass of sardine and anchovy were obtained from virtual population analysis (VPA) for the periods 1952–1988 and 1972–1985, respectively (Le Clus 1986; Thomas 1986; Kreiner et al. 2001). From 1990, they were obtained by acoustic surveys (Boyer and Hampton 2001). In South Africa, VPA was used for the period 1950–1982 (Armstrong et al. 1983) and acoustic surveys from 1984 onwards (Hampton 1987; Fairweather et al. 2006). Estimates obtained by the two methods are not comparable but they provide an indication of the relative stock sizes of the two fish species for the periods when they were applied.

In Namibia, the biomass of sardine was estimated to be above 10 million t from 1963 to 1965 (Fig. 3a). It decreased rapidly to less than 2 million t by 1970. There was a partial recovery from 1972 to 1974, after which, the biomass fell to a very low level in 1979. Thereafter, the biomass remained low. Anchovy was thought to be scarce in 1963 (Newman 1970; Thomas 1985). VPA estimates of biomass decreased with fluctuations between 1972 and 1985 (Le Clus 1986; Fig. 3a). The catch rates of anchovy also decreased during this period (Le Clus 1985).

In South Africa, the biomass of sardine peaked at 1.7 million t in 1959, after which, it decreased sharply until 1966. From 1985 onwards, the stock size increased rapidly. It exceeded 4 million t in 2002 but fell to less than 1 million t in 2005 (Fig. 3b). From 1997 to 2005, the centre of gravity of purse-seine catches of sardine was displaced some 400 km to the east (Fairweather et al. 2006) and the species became considerably less available to seabirds breeding in the Western Cape. Anchovy may have increased in abundance in 1973, although the VPA estimates of biomass possibly reflect catches. After 1985, the anchovy stock showed large fluctuations. In the late 1990s, it grew rapidly. The biomass peaked at almost 8 million t in 2001 and then decreased (Fig. 3b).

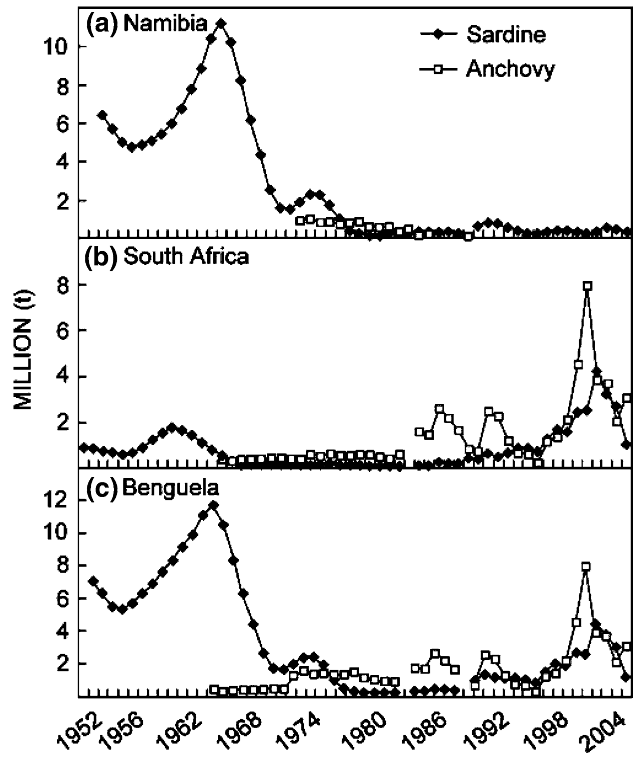

Fig. 3a–c Estimates of the biomass of sardine and anchovy **a** off Namibia, **b** off South Africa and **c** in the Benguela system, 1950–2005

In the Benguela system as a whole, sardine was abundant and anchovy scarce in the 1950s and early 1960s. From the mid 1970s to the mid 1990s, the combined biomass of these two prey species was low but it improved at the turn of the century as both species increased off South Africa (Fig. 3c).

Trends in the numbers of seabirds

Estimates of the numbers of African Penguins breeding in Namibia, the Western Cape and the Eastern Cape were obtained from Rand (1963a, 1963b), Shelton et al. (1984), Crawford et al. (1995, 2001, updated), Kemper (2006) and Underhill et al. (2006). Estimates of the numbers of Cape Gannets breeding in these regions were obtained from Crawford et al. (2007). Estimates of the numbers of Cape Cormorants breeding in Namibia and the Western Cape were obtained from Rand (1963a, 1963b), Cooper et al. (1982), Crawford and Dyer (1995) and Hockey et al. (2005) and were updated from unpublished information. Cape Cormorants breed only in low numbers (several hundred pairs) in the Eastern Cape (Cooper et al. 1982).

In Namibia, the number of African Penguins that bred decreased by about 50% between 1956/1957 and 1967/1968, and by 90% between 1956/1957 and 2004/2005

(Fig. 4a). The numbers of Cape Gannets decreased by 8% between 1956/1957 and 1967/1968, by a further 31% by 1978/1979 and by 95% between 1956/1957 and 2005/2006 (Fig. 4a). The numbers of Cape Cormorants fell by 76% between 1978/1979 and 2005/2006 (Fig. 4a). The number estimated to be breeding in 1956/1957 is likely to be too low because birds may have initiated breeding after aerial photographs, on which they were counted, were taken in November. However, it is likely that there was a real increase in the number breeding between 1956/1957 and the 1970s because extra space for nesting was provided by the building of a platform north of Walvis Bay and by the extension of platforms near Cape Cross (Cooper et al. 1982). Additionally, breeding space became available at Ichaboe Island, as the number of gannets there decreased (Crawford 1991).

In the Western Cape, the number of African Penguins breeding decreased by 42% between 1956/1957 and 1979/1980, and by 64% between 1956/1957 and 1993/1994 (Fig. 4b). The number breeding increased in the late 1990s and early 2000s as the South African stocks of sardine and anchovy attained high levels, but in 2006/2007, the number breedings was just 33% of that in 1956/1957. Between 1956/1957 and the mid 1980s, the number of Cape Gannets breeding in the Western Cape was relatively stable (Fig. 4b). The number approximately doubled by 1996/1997 but then decreased. The number of Cape Cormorants in the Western Cape was stable from 1956/1957 to 1991/1992 (Fig. 4b), although the proportion breeding decreased in periods of food scarcity, such as 1990/1991 (Crawford and Dyer 1995). However, the number fell by 60% by 1993/1994 and remained at a low level thereafter.

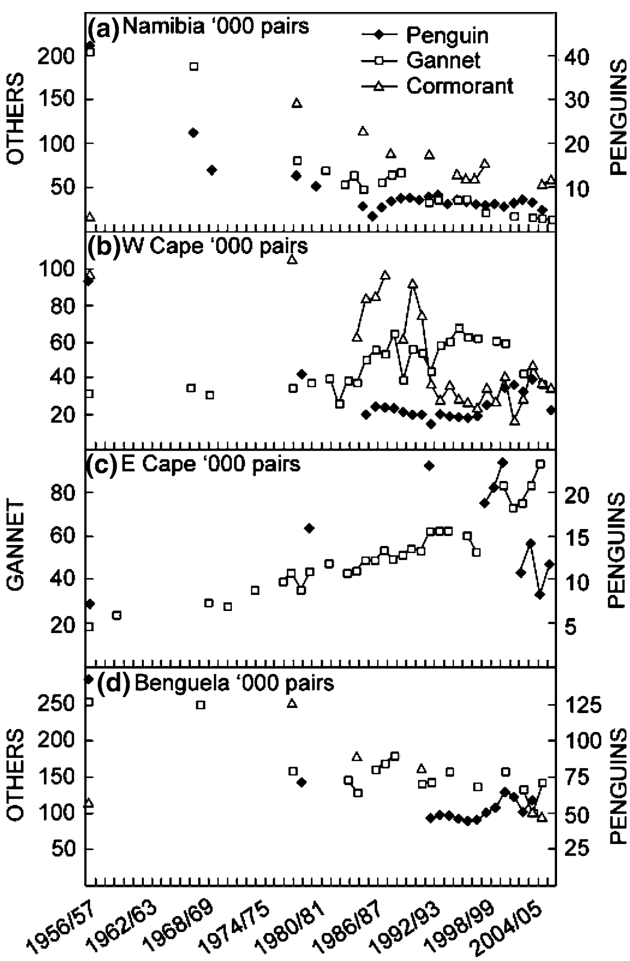

Fig. 4a–d Trends in the breeding populations of African Penguin, Cape Gannet and Cape Cormorant **a** in Namibia, **b** in South Africa's Western Cape, **c** in South Africa's Eastern Cape (Cape Cormorants are omitted as very few breed in this region) and **d** in the Benguela system, 1956/1957–2005/2006

In the Eastern Cape, the number of gannets increased throughout the period of observations (see also Randall and Ross 1979; Klages et al. 1992). There were five times as many gannets breeding in 2005/2006 as in 1956/1957 (Fig. 4c). The number of penguins breeding in this region increased threefold between 1956/1957 and 1993/1994, remained at a high level until 2001/2002 and then decreased by about 50% (Fig. 4c).

Taking the Benguela system as a whole, and, therefore, the species populations, the number of African Penguins fell by 60% from 141,000 pairs in 1956/1957 to 57,000 pairs in 2004/2005. The number of Cape Gannets decreased by 45% from 253,000 pairs in 1956/1957 to 140,000 pairs in 2005/2006. The number of Cape Cormorants fell by 19% from 111,000 pairs in 1956/1957 to 91,000 pairs in 2005/2006. However, the 1956/1957 population was probably underestimated (see above).

Influence of food on seabird trends

The influence of food on trends in seabird populations is the most clear for Namibia. Large decreases in the numbers of African Penguins and Cape Gannets occurred as the fishery for Namibian sardine expanded and as the stock later collapsed. The decrease of penguins, which have a foraging range of up to about 40 km when breeding (Heath and Randall 1989; Petersen et al. 2006), preceded that of gannets, which are able to forage up to 240 km from colonies (Grémillet et al. 2004). As the sardine collapsed, its range contracted to the north, making it increasingly less available to the penguin and gannet colonies, which occur in the vicinity of Lüderitz. The fish processing plant at Lüderitz was closed in 1974 because boats had to travel too far to the north before encountering fish shoals (Crawford et al. 1987). The Cape Cormorant may have benefited from an increase in breeding space at the guano platforms and at Ichaboe Island, and from an increased abundance of pelagic goby *Sufflogobius bibarbatus*, which partially replaced the sardine off central Namibia (Crawford et al. 1985). In addition, the platforms north of Walvis Bay gave Cape Cormorants access to the diminishing resources of sardine. However, cormorant numbers also fell substantially after the 1970s.

For the periods for which reliable information is available, the sizes of seabird populations breeding in Namibia were significantly related to the combined biomass of anchovy and sardine (Fig. 5). Because of the irregular estimates of seabird abundance, the comparisons were made using the means for five-year periods: African Penguin ($r = 0.916$, $n = 8$, $P < 0.002$), Cape Gannet ($r = 0.973$, $n = 8$, $P < 0.001$) and Cape Cormorant ($r = 0.899$, $n = 6$, $P < 0.01$). In each instance, fish biomass accounted for more than 80% of the variation in the numbers of seabirds breeding. The abundance of Cape Gannets ($r = 0.745$, $n = 8$, $P < 0.05$) and Cape Cormorants ($r = 0.932$, $n = 6$, $P < 0.01$) was significantly related to the combined catch of anchovy and sardine, suggesting that the availability of fish to these seabirds and the purse-seine fishery was similar.

In the Western Cape, there were sometimes contrasting trends for the three seabird species. Following the collapse of the South African sardine, the numbers of African Penguins decreased, whereas the numbers of Cape Gannets and Cape Cormorants were stable. In the 1960s and 1970s, anchovy replaced sardine in the system (Crawford et al. 1987) and was available to Cape Gannets and Cape Cormorants (Berruti et al. 1993; Crawford and Dyer 1995). However, the southern distribution of most of the parent stock of anchovy placed it beyond the limited foraging range of penguins at the western colonies. These colonies decreased but the southern penguin colony of Dyer Island

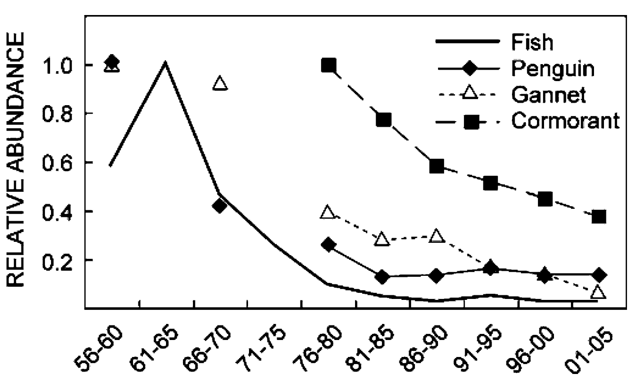

Fig. 5 Comparison of trends in the combined biomass of anchovy and sardine and the numbers of African Penguins, Cape Gannets and Cape Cormorants breeding in Namibia. Because of the irregular estimates of seabird abundance, the comparisons are of the means for five-year periods: 1956–1960 to 2001–2005. All means are expressed as proportions of the maximum observed. The estimate for Cape Cormorants for 1956/1957 has been omitted because it was based on aerial photographs taken before the main breeding season of Cape Cormorants in Namibia

increased (Crawford 1998). When sardine increased in the 1980s, there was concomitant growth of several penguin colonies in the Western Cape (Crawford et al. 2001). The numbers of Cape Gannets increased similarly (Crawford et al. 2007). The overall number of African Penguins breeding in the Western Cape increased at the end of the 20th century as pelagic fish abundance increased off South Africa and then decreased as sardine became less available. At this time, the numbers of gannets also decreased. However, the responses of penguins and gannets were not synchronous. The Cape Cormorant decreased in the early 1990s and did not take advantage of the increased abundance of pelagic fish towards the end of that decade. Although the effect of food on trends in seabird numbers is not as clear cut for the Western Cape as for Namibia, in instances, seabird abundance has been influenced by food. The numbers of Cape Gannets breeding in South Africa were significantly related to the abundance of sardine and anchovy (Crawford et al. 2007). The numbers of African Penguins breeding at certain colonies in the region were strongly related to pelagic fish biomass (e.g. Cury et al. 2000; Crawford et al. 2001).

Other factors have also influenced the trends of seabirds in the Western Cape. Repeated outbreaks of avian cholera *Pasteurella multocida* caused extensive mortality of Cape Cormorants from 1991 to 2006, especially at Lambert's Bay, Dassen and Dyer islands. More than 14,000 Cape Cormorants were killed at Dassen Island in 1991, 7,000 at Lambert's Bay in 2002 and more than 27,000 at Dyer Island between 2002/2003 and 2005/2006 (Crawford et al. 1992; Williams and Ward 2002; Waller and Underhill 2007). Predation by seals *Arctocephalus pusillus* around breeding colonies was thought to be unsustainable for African Penguins at Dyer Island and Lambert's Bay, and for Cape Gannets at Malgas Island (Marks et al. 1997; Crawford et al. 2001; Makhado et al. 2006).

Information on pelagic fish abundance in the Eastern Cape is not readily available before the mid 1980s, so its influence on the long-term trends in seabirds in that province cannot be gauged.

The importance of changes in the distribution of prey species was recently highlighted when the eastward displacement of sardine off South Africa placed the bulk of this forage resource between the breeding localities for seabirds that are in the Western Cape and in the Eastern Cape, and, consequentially, beyond the foraging ranges of many seabirds in both of these regions. By 2005, the centre of distribution of sardine catches was at about 22°E off the South African south coast (Fairweather et al. 2006). In an apparent attempt by penguins to adapt to this shift in the distribution of prey, a penguin-breeding colony was initiated at De Hoop on the mainland in 2003. Decreases in the number of African Penguins breeding were observed at those colonies in the Western Cape that are west of Cape Town (unpublished information). However, the eastward displacement of the sardine placed more of it within the foraging range of Cape Gannets in the Eastern Cape, which led to a sharp increase in its contribution to their diet (Crawford et al. 2007). The wide foraging range of Cape Gannets buffers them to a greater extent than African Penguins against changes in the distribution of fish prey. From 1988 to 2004, the coefficient of variation for the breeding success of Cape Gannets at Malgas Island was 31%, compared to 37% for African Penguins at Robben Island from 1989 to 2005 (unpublished information).

Accounting for the food requirements of seabirds

From the foregoing, it is apparent that both the abundance and the distribution of prey have influenced trends in seabird numbers in the Benguela system. The recent decreases in seabird populations suggest a need to account for their food requirements in the management of the purse-seine fisheries, with which they compete for prey. These fisheries take a substantially greater proportion of the anchovy and sardine stocks than do the birds. In the 1980s, the average annual catch of anchovy and sardine was 580,000 t (Crawford et al. 1987), whereas it was estimated that seabirds in the Benguela ecosystem consumed about 155,000 t of these species each year (Crawford et al. 1991).

At Robben Island, the proportion of adult African Penguins that bred and their breeding success were both significantly related to fish biomass (Crawford et al. 1999, 2006), indicating the possibility of coupling models of seabirds and fish stocks to gauge levels of escapement of fish that are necessary to maintain seabird populations (Crawford 2004). Such reproductive parameters are likely to respond more rapidly to variations in food availability than population sizes (e.g. Cairns 1987). The models that are used to advise the total allowable catches (TACs) for anchovy and sardine in South Africa are, at present, being modified to incorporate a model of African Penguins and functional relationships linking penguins and the fish stocks. For example, the breeding success of penguins, and its variation, can be estimated for a certain level of fish abundance and be used to predict, in the Monte Carlo style, the probability of the African Penguin population falling below specified values over a certain time frame. Hence, the risk for the penguin population of alternative management strategies for fish stocks may be ascertained.

Unlike the earlier situation in Namibia, when the range of sardine contracted to the north as the stock collapsed (Crawford et al. 1987), the eastward displacement of the sardine off South Africa occurred when the sardine was at a high level of abundance. High TACs continued to be allocated but, because most fish factories were in the Western Cape, substantial catches continued to be made in the west (Fairweather et al. 2006), further depleting the abundance of prey around seabird breeding colonies in the Western Cape. The desirability of closing fishing areas around seabird breeding colonies, and the means of measuring the success of such interventions, are, at present, being discussed by scientists charged with advising on the management of the South African purse-seine fishery.

Another issue that is likely to be addressed in the South African context is the establishment of target levels for seabird populations (e.g. Underhill and Crawford 2005). Targets will be chosen so as to reduce the risk of the extinction of species (Crawford et al. 2001; Crawford 2004). A final matter that merits consideration is the definition of exceptional ecosystem circumstances. In the operational management procedure (OMP) used to advise TACs for sardine and anchovy in South Africa, circumstances are defined when a departure from the procedure may be justified, e.g. when a resource falls to a very low level. Similarly, it will be advisable to define ecosystem circumstances that will allow deviation from the OMP.

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