

Trends in numbers of Cape gannets (*Morus capensis*), 1956/1957–2005/2006, with a consideration of the influence of food and other factors

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Cape gannets (*Morus capensis*) breed at six colonies in Namibia and South Africa. Population size averaged about 250 000 pairs over the period 1956/1957–1968/1969 and about 150 000 pairs from 1978/1979 to 2005/2006. Over the whole 50-y period, numbers at the three Namibian colonies fell by 85–98%, with greater proportional decreases in the south. There were increases at two South African colonies between 1956/1957 and 2005/2006. The colony at Lambert's Bay increased between 1956/1957 and 2003/2004, but attacks by Cape fur seals (*Arctocephalus pusillus*) on birds at nests caused abandonment of the entire colony in 2005/2006. Long-term changes at colonies are thought to be largely attributable to an altered abundance and distribution of prey, especially sardine (*Sardinops sagax*) and anchovy (*Engraulis encrasicolus*). In both Namibia and South Africa, the numbers of Cape gannets breeding were significantly related to the biomass of epipelagic fish prey. Over the 50-y period, there was also a marked similarity in the proportions of gannets and epipelagic fish in the Benguela system, which were present in Namibia and South Africa. In the 2000s, there was an eastward shift in the distribution of sardine off South Africa and a large increase in the number of gannets breeding at South Africa's easternmost colony. When sardine were scarce off South Africa, gannets fed on anchovy, but off Namibia anchovy only temporarily and partially replaced sardine. Ecosystem management measures that might improve the conservation status of Cape gannets are considered.

Keywords: anchovy, *Arctocephalus pusillus*, Cape fur seal, Cape gannet, distribution, food, long-term change, *Morus capensis*, sardine.

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Introduction

The Cape gannet (*Morus capensis*) is one of three gannet species worldwide, the others being the North Atlantic gannet (*M. bassanus*) and the Australasian gannet (*M. serrator*) (Nelson, 2002). The Cape gannet, regarded as vulnerable (BirdLife International, 2004), has bred at 10 localities off the coasts of Namibia and South Africa, but at only six of these since 1956: Mercury, Ichaboe, and Possession Islands in Namibia; Bird (Lambert's Bay), Malgas (both in the Western Cape), and Bird (Algoa Bay, Eastern Cape) Islands in South Africa (Figure 1) (Crawford *et al.*, 1983b). Information on the numbers of gannets at these six localities is available for the 50-y period 1956/1957–2005/2006 and is reported in this paper.

Cape gannets feed mainly on sardine (*Sardinops sagax*) and anchovy (*Engraulis encrasicolus*) (references in Hockey *et al.*, 2005), species that are also exploited by the purse-seine fisheries of Namibia and South Africa. Industrial fisheries can affect predator populations adversely through competition for shared prey

(Frederiksen *et al.*, 2004). Here we examine the influence of changes in the abundance and distribution of prey, and other factors, on the numbers of Cape gannets and consider ecosystem management measures that might improve the conservation status of the species. Recent declarations by international summits have emphasized the need to account for ecosystem issues in fisheries management, including the requirements of predators that are dependent on species targeted by a fishery. Such policy has been incorporated into law by South Africa (Crawford, 2004).

Material and methods

The numbers of breeding pairs of Cape gannets at colonies were estimated from measurements of the area occupied by breeding birds on aerial photographs that were taken vertically, combined with measures of the densities of nests (Klages *et al.*, 1992).

Photographs were taken in November or December, when most birds are incubating or brooding, using methods described by Shelton *et al.* (1982). The extent of the area occupied by

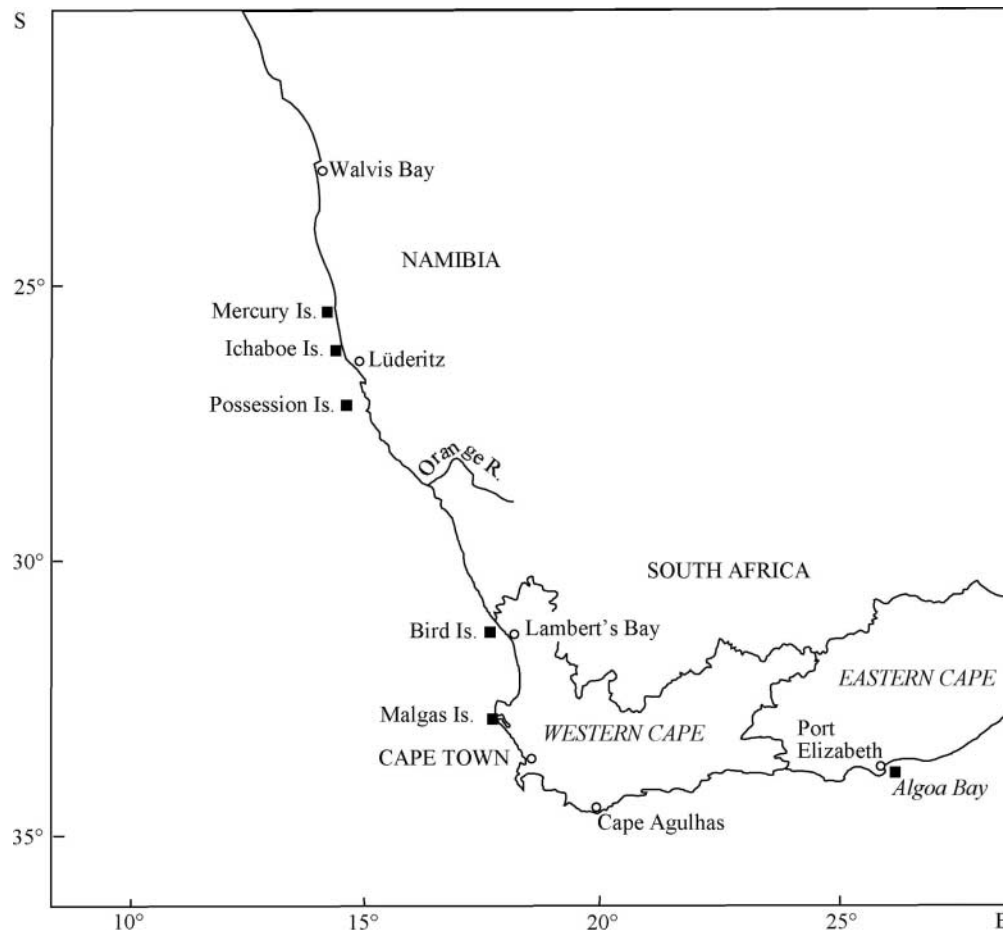


Figure 1. Southern Africa, showing the six extant colonies of Cape gannets and other localities mentioned in the text.

breeding birds was measured using an Ibas interactive image-analysis system. The photographs were scaled from ground measurements of straight edges along walkways, walls, or buildings near the colonies. In 2004/2005, the outer limit of the gannet colony at Lambert's Bay was delimited using a Global Positioning System that had a circular error probability of 4 m for the horizontal position. Estimates of the area occupied by breeding Cape gannets were obtained for 152 of the 300 possible locality/season combinations, with coverage sporadic before the 1980s, but better subsequently.

Measurements of the densities of nests 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 nests within the square were counted. The overall number of nests in the square was taken to be the number of whole nests plus half the number of part nests. The number of measurements made in any season ranged from two at Possession Island in 2002/2003 and 2005/2006, when it was desired to minimize disturbance, to 30 at Algoa Bay in 2005/2006 (mean 17 per locality per season; $n = 33$). Estimates of the density of nests were obtained for 11 seasons at Malgas Island, 10 at Lambert's Bay, 4 at Possession Island, 3 each at Mercury and Ichaboe Islands, and 2 at Algoa Bay. Additionally, three published estimates were available for Algoa Bay (Randall and Ross, 1979; Batchelor 1982). However, information on density was available for just 23% of the locality/season combinations for which the

area occupied by breeding birds was measured. Therefore, for each locality, a mean density was obtained, by giving equal weight to each season for which information existed, and applied throughout the study period.

Trends in the numbers of Cape gannets nesting in Namibia and South Africa were compared with trends in the biomass of sardine and anchovy in these regions using correlation analysis. The Namibian and South African stocks of sardine and anchovy are thought to be relatively discrete (Crawford *et al.*, 1987).

Estimates of biomass for Namibia were obtained from virtual population analysis (VPA) for the period 1956/1957–1988/1989. From 1990/1991, they were obtained by hydroacoustic surveys. For 1956/1957–1982/1983, estimates for South Africa were obtained by VPA. From 1984/1985, estimates were obtained from hydroacoustic surveys (sources in Schwartzlose *et al.*, 1999). No estimates of the abundance of anchovy are available prior to the mid-1960s, when fisheries for this species commenced. However, anecdotal information suggests that anchovy were not abundant off southern Africa in the 1950s and early 1960s (Crawford *et al.*, 1987), so biomass of the species was assumed to be negligible, as it was also off Namibia from 1990 on.

Because the estimates of biomass derived from VPA and hydroacoustic surveys are not strictly comparable, and because of data gaps in the time-series of information, especially of gannet numbers and also of fish biomass, it was not possible to prewhiten the time-series prior to their being cross-correlated.

However, the long gaps between observations up until 1980 preclude the likelihood of serial correlation in the time-series then. In addition to the original data values, decadal averages of values were also correlated. Further, to gauge the influence of the relative abundance of prey on the distribution of gannets, the proportions of gannets nesting in Namibia and in South Africa were compared with the proportional contribution of these two countries to the overall biomass of sardine and anchovy off southern Africa.

Results

Numbers of breeding birds

Between 1956/1957 and 2005/2006, there were large decreases in the numbers of breeding Cape gannets at all three Namibian colonies (Table 1). The largest proportional decrease (98%) was at the southernmost colony of Possession Island. The decrease at Ichaboe Island was 95%, and that at Mercury Island, the northernmost extant colony of the species, was 85%. All three colonies showed steep decreases between 1956/1957 and the early 1980s. They then stabilized, before decreasing again in the 1990s and early 2000s.

In South Africa, there were increases in the numbers of birds breeding at all three colonies between 1956/1957 and 2003/2004 (Table 1). The number at Lambert's Bay decreased from 1956/1957 to 1969/1970, before increasing to attain a peak of about 14 000 pairs in 1987/1988. From 1988/1989 to 2003/2004, the colony fluctuated between 9 000 and 12 000 pairs. It decreased to half this level in 2004/2005, and there were no birds at the colony on 16 December 2005. The colony at Malgas Island more than doubled in size between 1956/1957 and 1996/1997, with substantial fluctuations during the 1980s and 1990s, but it then decreased again. However, in 2005/2006, there were 40% more birds at the colony than in 1956/1957. At Bird Island in Algoa Bay, the easternmost colony, numbers breeding increased fivefold between 1956/1957 and 2005/2006.

In Namibia, the overall number of gannets breeding fell by 95% from 204 000 pairs in 1956/1957 to 10 000 pairs in 2005/2006 (Table 1). The number breeding in South Africa increased from 50 000 pairs in 1956/1957 to a peak of 145 000 pairs in 2001/2002, and was 135 000 pairs in 2005/2006. The overall number was about 250 000 pairs in 1956/1957 and in the late 1960s. It averaged 151 000 pairs from 1978/1979 to 2005/2006 (s.d. = 15 000 pairs; $n = 13$).

In 1956/1957, Namibia was home to 80% of the breeding Cape gannets. This fell to 50% in 1978/1979 and to 7% in 2005/2006. The proportion breeding in the Western Cape rose from 12% in 1956/1957 to 21% in 1978/1979, then to 25% in 2005/2006. Algoa Bay had 7% of breeding birds in 1956/1957, 28% in 1978/1979, and 68% in 2005/2006. Hence, there has been a shift to the south and east in the centre of the distribution of Cape gannets. The largest number breeding at an individual locality was 175 000 pairs at Ichaboe Island in 1956/1957; the smallest was 351 pairs at Possession Island in 2005/2006 (Table 1).

Density of nests

Average numbers of nests counted per square metre (weighting seasons equally) were: Mercury Island 3.73 (s.d. 0.58; $n = 3$), Ichaboe Island 3.56 (s.d. 0.67; $n = 3$), Possession Island 4.08 (s.d. 1.11; $n = 4$), Lambert's Bay 3.22 (s.d. 0.43; $n = 10$), Malgas Island 2.84 (s.d. 0.19; $n = 11$), and Algoa Bay 2.71 (s.d. 0.22; $n = 2$). The highest average density recorded for any colony in a

season was 5.60 nests m^{-2} at Possession Island in 1978/1979 and the lowest 2.54 nests m^{-2} at Malgas Island in 1999/2000 (Figure 2).

There was a suggestion of a decrease in densities of nests at the three Namibian colonies between 1978/1979 and 2002/2003, although there was a large coefficient of variation (42%) for Mercury Island in 1978/1979, and measurements were conducted in few seasons (Figure 2). If there was a long-term decrease, the decrease in the number of birds breeding in Namibia will have been underestimated. Average densities measured at the three South African colonies fluctuated, but showed no trend.

Relationship between numbers breeding and biomass of fish

Numbers of gannets breeding in Namibia were significantly correlated with the biomass there of sardine ($r = 0.900$; $n = 18$; $p < 0.001$) and of sardine and anchovy combined ($r = 0.928$; $n = 18$; $p < 0.001$). Similarly, in South Africa, the numbers of gannets breeding were significantly correlated with the biomass of sardine ($r = 0.535$; $n = 22$; $p < 0.02$) and of sardine and anchovy combined ($r = 0.661$; $n = 22$; $p < 0.001$). In Namibia, the decadal averages of numbers of gannets breeding and fish biomass both decreased steeply after the 1960s (Figure 3a). The two series were significantly correlated ($r = 0.945$; $n = 6$; $p < 0.005$). In South Africa, the decadal average of numbers of gannets breeding increased almost linearly over the study period, whereas the average biomass of fish increased only after the 1970s (Figure 3b). The two series were significantly correlated ($r = 0.823$; $n = 6$; $p < 0.05$). There were large changes in the biomass of epipelagic fish off Namibia in the 1960s and off South Africa since 2000, as indicated by the large standard deviations (Figure 3).

The proportions of Cape gannets breeding in Namibia and in South Africa showed marked similarity to the proportional contribution of these two countries to the overall biomass of sardine and anchovy in the southern African region (Figure 4). Until 1968/1969, Namibia held most of the gannets (80%) and most of the epipelagic fish (85%). In 1978/1979, the numbers of gannets and the biomass of epipelagic fish in the two countries were almost equivalent. This was approximately the case until 1982/1983, after which the proportions of gannets and fish in Namibia and South Africa decreased and increased, respectively. In 2005/2006, 93% of the gannets and 97% of the combined biomass of sardine and anchovy were in South Africa.

Discussion

Population size

Whereas numbers of Cape gannets decreased in the 20th century, numbers of North Atlantic and Australasian gannets both increased (Montevicchi and Myers, 1997; Nelson, 2002; Wanless *et al.*, 2005). North Atlantic gannets increased at a rate of about 3% through the 20th century, and now number some 343 000 pairs, making it the world's most abundant gannet (Nelson, 2002). The population of Australasian gannets in New Zealand increased from 21 000 pairs in 1946/1947 to 46 000 pairs in 1980/1981 (Wodzicki *et al.*, 1984), and numbers have continued to grow (Bunce *et al.*, 2002). There were 6 600 pairs breeding in Australia in 1980/81, which increased to about 20 000 pairs at the end of the 20th century, a rate of increase of 6% per annum (Bunce *et al.*, 2002). The total population of Australasian gannets was about 53 000 pairs in 1990 and about 66 000 pairs now, making it the least numerous of the world's three gannets (Nelson, 2002).

Table 1. Pairs of Cape gannets estimated to be breeding at the six extant colonies, 1956/57–2005/06.

Season	Mercury	Ichaboe	Possession	Total for Namibia	Lambert's Bay	Malgas	Algoa Bay	Total for South Africa	Total for Namibia and South Africa
1956/57	9 396	175 116	19 258	203 770	5 915	25 040	19 092	50 047	253 817
1957/58	–	–	–	–	–	–	–	–	–
1958/59	–	–	–	–	–	–	–	–	–
1959/60	–	–	–	–	–	–	24 683	–	–
1960/61	–	–	–	–	–	–	–	–	–
1961/62	–	–	–	–	–	–	–	–	–
1962/63	–	–	–	–	–	–	–	–	–
1963/64	–	–	–	–	–	–	–	–	–
1964/65	–	–	–	–	–	–	–	–	–
1965/66	–	–	–	–	–	–	–	–	–
1966/67	–	–	–	–	–	–	–	–	–
1967/68	5 147	166 601	16 296	188 044	3 711	30 801	–	–	–
1968/69	–	–	–	–	–	–	–	–	249 426*
1969/70	2 835	–	–	–	3 149	27 442	30 791	61 382	–
1970/71	–	–	–	–	–	–	–	–	–
1971/72	–	–	–	–	–	–	28 726	–	–
1972/73	–	–	–	–	–	–	–	–	–
1973/74	–	–	–	–	–	–	–	–	–
1974/75	–	–	–	–	–	–	36 791	–	–
1975/76	–	–	–	–	–	–	–	–	–
1976/77	–	–	–	–	–	–	–	–	–
1977/78	–	–	–	–	–	–	40 593	–	–
1978/79	5 696	69 908	4 357	79 961	5 595	28 168	45 032	78 796	158 757
1979/80	–	–	–	–	–	–	36 796	–	–
1980/81	–	54 328	3 260	–	7 345	29 546	45 720	82 612	–
1981/82	2 063	49 683	4 100	55 846	7 570	–	–	–	–
1982/83	3 364	–	2 942	–	6 888	32 261	49 458	88 606	–
1983/84	2 380	46 758	3 537	52 675	6 102	19 826	–	–	–
1984/85	3 603	56 208	2 383	62 194	10 024	27 980	44 688	82 691	144 885
1985/86	2 286	40 704	3 533	46 524	8 832	27 619	45 745	82 196	128 720
1986/87	2 480	–	–	–	11 161	38 895	51 195	101 251	–
1987/88	2 361	49 261	2 742	54 363	14 265	40 720	51 219	106 204	160 567
1988/89	3 279	55 614	3 097	61 990	11 125	41 324	56 111	108 560	170 550
1989/90	2 932	58 239	3 040	64 210	10 793	53 194	50 921	114 908	179 118
1990/91	–	–	–	–	9 630	29 075	53 376	92 081	–
1991/92	–	–	–	–	11 834	43 715	56 869	112 418	–
1992/93	2 760	25 525	3 158	31 443	10 550	42 380	55 945	108 875	140 318
1993/94	2 723	31 484	1 399	35 607	10 462	32 320	65 173	107 955	143 562
1994/95	1 619	–	922	–	9 705	48 043	65 040	122 788	–
1995/96	1 992	31 183	767	33 942	9 560	50 109	65 040	124 709	158 651
1996/97	1 794	32 657	726	35 177	10 826	56 376	–	–	–
1997/98	1 434	23 702	–	–	11 065	50 425	63 353	124 844	–
1998/99	1 358	19 972	339	21 668	10 027	50 960	55 075	116 063	137 731
1999/00	–	–	–	–	–	–	–	–	–
2000/01	–	–	–	–	11 631	48 058	–	–	–
2001/02	1 694	13 268	400	15 362	9 525	48 680	87 257	145 462	160 823
2002/03	–	–	–	–	9 364	–	76 571	–	–
2003/04	1 503	11 837	437	13 777	10 529	31 070	78 929	120 528	134 305
2004/05	1 910	10 947	477	13 334	4 962	–	87 569	–	–
2005/06	1 414	8 669	351	10 433	0	36 156	98 419	134 575	145 008

For seasons for which there were sufficient data, the number of pairs breeding in Namibia, South Africa, and in total are also shown.

*Assumed to be the sum of those in Namibia in 1967/1968 and those in South Africa in 1969/1970.

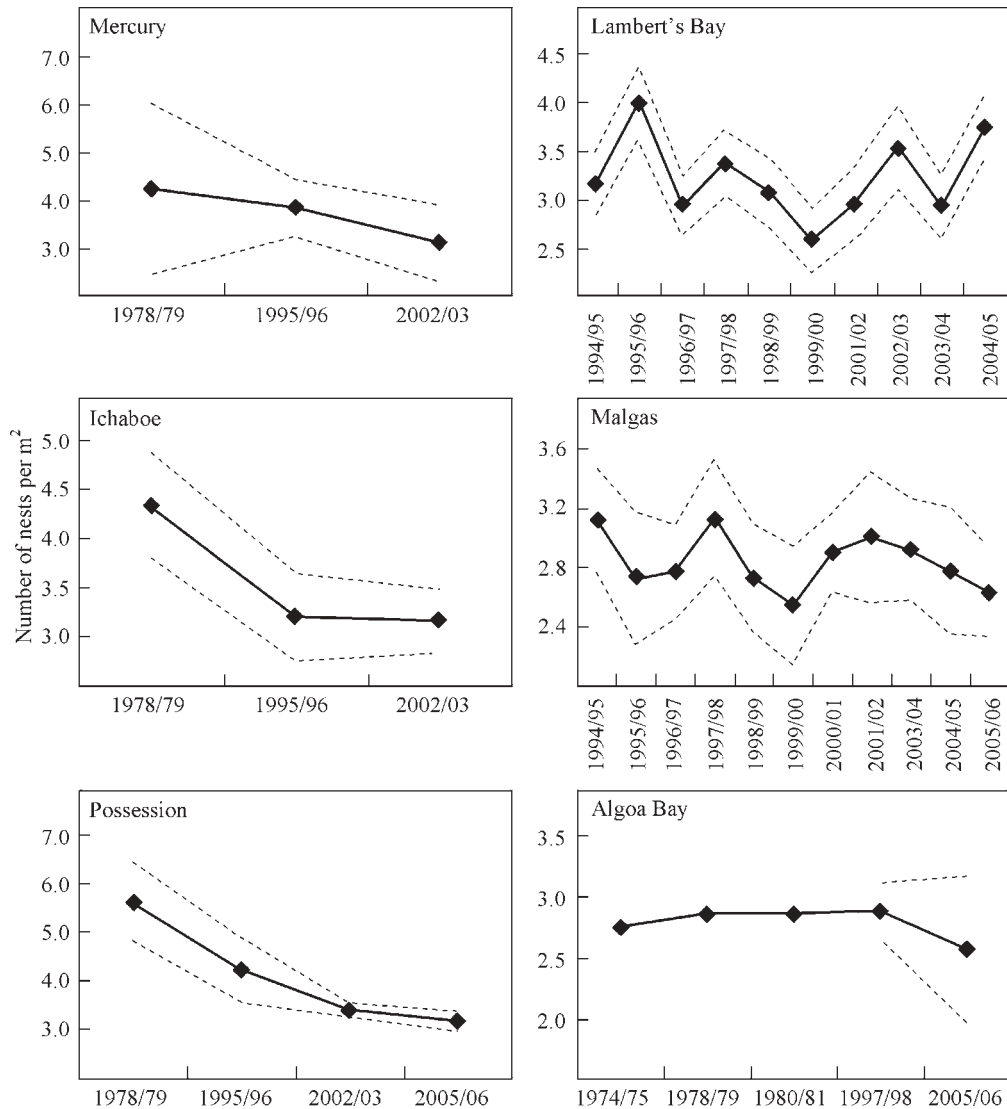


Figure 2. Densities of nests of Cape gannets at the six extant colonies, for seasons in which these were measured. Where available, the standard deviations of measurements are shown as dotted lines. Information for Mercury, Ichaboe and Possession Islands in 1978/1979 is from Crawford *et al.* (1983b) and data on which that paper was based. Information for Algoa Bay from 1974/1975 to 1980/1981 is from Randall and Ross (1979) and Batchelor (1982).

The largest present colony of North Atlantic gannets is about 60 000 pairs at St Kilda, Outer Hebrides, Scotland (Wanless *et al.*, 2005). At Bird Rocks, Canada, there were 100 000–125 000 pairs in 1833 (Nelson, 2002). The largest colony of Australasian gannets is 8 000 pairs at Gannet Island, New Zealand (Wodzicki *et al.*, 1984). Therefore, Ichaboe Island (175 000 pairs of Cape gannets in 1956/1957) held the largest known gannetry. The colony of Cape gannets at Bird Island in Algoa Bay (98 000 pairs) is at present the largest gannetry in the world.

Influence of food

The significant correlations between the numbers of Cape gannets and the biomass of epipelagic fish in Namibia and South Africa suggest that numbers of gannets are strongly influenced by the abundance of food. Especially in Namibia, the large decrease in abundance of epipelagic prey appears to have had a major impact on the gannet colonies. Changes in prey abundance accounted for

some 86–89% of the variability in numbers of gannets nesting in Namibia, compared with 44–68% of the variability in South Africa. Gannets increased in South Africa throughout the study period, whereas estimates of fish biomass increased towards the end of the period. Until the mid-1980s, assessments of fish stocks in South Africa were based on information for the region west of Cape Agulhas only.

As the Namibian sardine collapsed, its range contracted to the north, placing the remaining shoals increasingly distant from Cape gannet colonies. Most anchovy also were located well north of the gannet colonies (Crawford *et al.*, 1987). In accord with this altered distribution of prey, Possession Island, the southernmost colony in Namibia, had the greatest decrease after 1956/1957 and Mercury Island, the northernmost, the least decrease.

When sardine were decreasing in Namibia, anchovy, because it had replaced sardine in South Africa's catches, were fished intensively in a deliberate management effort to minimize its possible

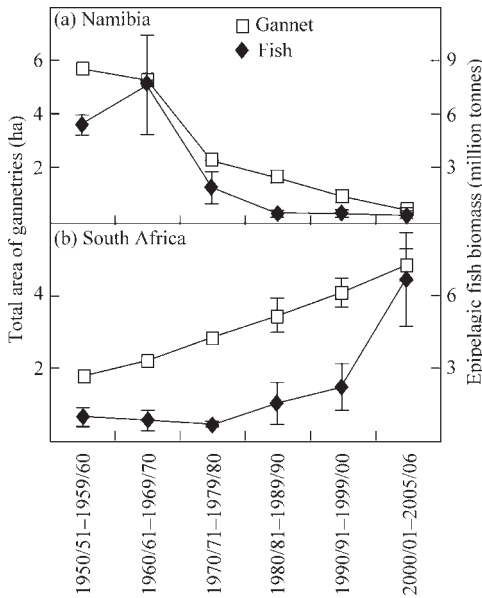


Figure 3. Trends in the average area of Cape gannet breeding colonies and the average biomass of epipelagic fish (sardine and anchovy) in each decade from the 1950s to the 2000s: (a) off Namibia and (b) off South Africa. The standard deviations of the means are shown, where available.

competition with sardine (Crawford *et al.*, 1987). It had a short-lived period of abundance in Namibia, where it never fully replaced sardine. The largest catch of anchovy in Namibia, <0.4 million tonnes in 1987, was just 26% of the peak catch of

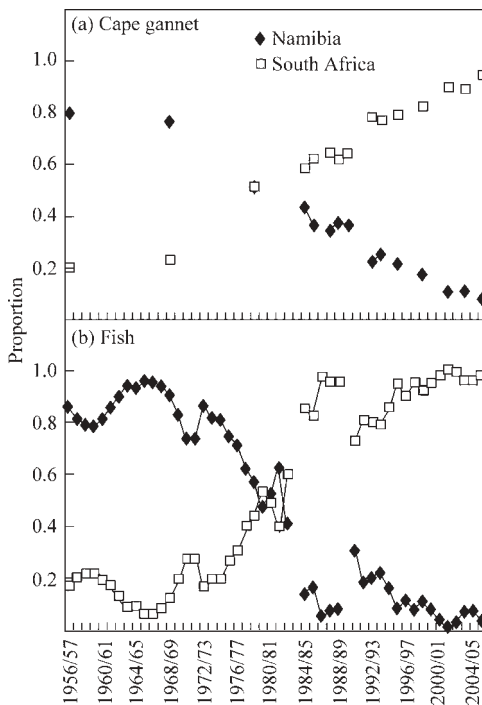


Figure 4. Trends in the proportions of (a) Cape gannets and (b) epipelagic fish (sardine and anchovy) off southern Africa found off Namibia and South Africa, 1956/1957–2005/2006.

1.4 million tonnes of sardine in 1968. Before 1967 and after 1988, Namibia’s annual catch of anchovy never exceeded 0.1 million tonnes. From 1968 to 1988, it averaged 0.18 million tonnes, 32% of Namibia’s average catch of sardine of 0.57 million tonnes from 1956 to 1967 (Schwartzlose *et al.*, 1999; updated).

Changes in the numbers of gannets in Namibia accord with this partial and only temporary replacement of sardine by anchovy. From 1981/1982 to 1989/1990, the number of gannets in Namibia fluctuated about a level of 58 000 pairs, 30% of the average of 196 000 pairs up to 1967/1968. In the 1990s, the numbers of gannets breeding in Namibia fell further to an average of 30 000 pairs, and then in the early part of the 21st century to about 13 000 pairs.

In Namibia, from 1957 to 1959, sardine contributed 90% by mass of the diet of Cape gannets, whereas anchovy were not recorded. From 1978 to 1982, anchovy contributed 53% by number of the prey items eaten (sources in Hockey *et al.*, 2005). In the same period, anchovy contributed 34% by mass of the diet, whereas sardine contributed <1% (RJMC, unpublished). From 1989 to 2004, anchovy contributed 7% by mass of the diet and sardine 11% (BLD, unpublished), emphasizing the continuing decrease in availability of these epipelagic fish species to gannets in Namibia.

In South Africa, maintenance of the numbers of Cape gannets, in spite of the collapse of South Africa’s stock of sardine, is attributable to a ready availability then of anchovy. In the period 1953–1956 in the Western Cape, sardine contributed 60% by mass of the diet of Cape gannets and anchovy 13%. From 1978 to 1989, sardine formed 18% of the diet and anchovy 44% (sources in Hockey *et al.*, 2005). In every year from 1978 to 1984, sardine contributed <10% of the diet and anchovy >44% (up to 64%) (Schwartzlose *et al.*, 1999). Anchovy replaced sardine as the dominant species in South Africa’s purse-seine catch from 1966 to 1995, and there is evidence that it increased in the Western Cape in the 1960s following the decrease of the sardine (Schwartzlose *et al.*, 1999).

During the 1980s, sardine biomass recovered in South Africa, and it was high by the end of the 20th century. However, after 2000, there was a marked eastward shift in the distribution of the species (Van der Lingen *et al.*, 2005), which led to a decreased availability of this prey species to gannets at Lambert’s Bay and Malgas Island, but an increased availability to birds in Algoa Bay. Numbers of gannets breeding at Malgas Island and Lambert’s Bay decreased, whereas numbers in Algoa Bay showed a sharp increase. In Algoa Bay from 1979 to 1990, sardine contributed 31% by mass of the diet of Cape gannets and anchovy 24% (Klages *et al.*, 1992). From 1993 to 2000, sardine contributed 45% and anchovy 18%. From 2001 to 2006, the values were 72% and 15%, respectively (RJMC and NTW, unpublished). Therefore, unlike the situation in Namibia, the combined contribution of these epipelagic fish species to the diet of gannets has steadily increased in Algoa Bay.

It seems evident from the similar trends in the proportions of gannets and epipelagic fish in Namibia and South Africa that large changes in the availability of fish have had a major influence on the numbers of gannets breeding in different areas. The changes are likely to have been primarily responsible for the shift from Namibia to the Eastern Cape in the location of the majority of breeding gannets.

The extent to which the shift in the distribution of Cape gannets has been influenced by differences in local rates of

production and survival of gannets or by movements of birds is uncertain. Both the production of young birds and the emigration of first-time breeders away from localities where food was scarce to those where conditions were more favourable are likely to have had an influence. In 1970, following the collapse of the Namibian sardine, there was much starvation of chicks at all three Namibian colonies (Crawford *et al.*, 1983a). Off Australia, when a mass mortality of sardine in 1998 led to a sudden reduction in the availability of prey, there was poorer breeding success by younger than by older Australasian gannets, unlike years when food was not limited (Bunce *et al.*, 2005). In 2003/2004, Cape gannets at Namibian colonies had longer foraging trips of longer duration, spent less time at the colony, and left chicks unattended more frequently than those at colonies in the Western Cape (Lewis *et al.*, 2006). Off South Africa, reproductive success of African penguins (*Spheniscus demersus*) is significantly related to food availability (Crawford *et al.*, 2006a).

Some growth of colonies of Cape gannets is thought too rapid to attribute to local breeding alone (Crawford *et al.*, 1983b). Movements of young gannets between colonies off western southern Africa, including from Namibia to South Africa, have been noted (Crawford, 1999). Similarly, the rapid growth of at least some North Atlantic gannetries is attributed partially to the immigration of young breeders from elsewhere (Nelson, 2002). The formation of new colonies of Australasian and North Atlantic gannets indicates that there must be some emigration of birds (Norman, *et al.* 1998; Nelson, 2002). Emigration of young African penguins to colonies where feeding conditions are favourable at the time has been demonstrated and is thought an important mechanism whereby the species copes with long-term changes in the distribution of prey (Crawford, 1998).

The altered distribution of prey available to Cape gannets is emphasized by the fact that, whereas many birds previously undertook extensive movements northwards along the West African coast after breeding (Broekhuysen *et al.*, 1961; Crawford *et al.*, 1983b), the proportion of birds making such movements is now greatly reduced (Oatley, 1988; Klages, 1994).

Influence of other factors

Other factors have also influenced the numbers of Cape gannets breeding. Until the 1980s, guano was collected at each of the six extant gannet colonies, usually annually. Thereafter, as revised policies to conserve seabirds at islands were implemented, the collection of guano was discontinued (Best *et al.*, 1997). The last collections were made at Mercury Island in 1984, Possession and Malgas Islands in 1985, Algoa Bay in 1988, Ichaboe Island in 1989, and Lambert's Bay in 1991. Subsequently, there were no large increases in numbers of gannets nesting at the three Namibian colonies and at Lambert's Bay, northernmost of the South African colonies. There also was no immediate increase in the colony at Algoa Bay. However, there was a substantial increase in numbers nesting at Malgas Island in 1986/1987, the second season after termination of guano scraping, and in several of the following seasons (Table 1). Cape gannets construct their nests almost entirely from guano (Hockey *et al.*, 2005). Hence, the removal of guano leads to a loss of nesting material. In the 1989/1990 season, nests at Malgas Island, 4.5 y after the last guano scrape there, had a mean height of 106 mm, compared with 31 mm at Lambert's Bay, where scraping was still being undertaken (Crawford and Cochrane, 1990).

In 2005/2006, Cape fur seals killed about 200 gannets in the colony at Lambert's Bay and caused abandonment of breeding by the entire colony (Wolfaardt and Williams, 2006). Such disturbance may have caused partial abandonment in the previous season, when the colony decreased in size by about 50%. Seals also killed about 20 gannets in the colony at Malgas Island in 2005/2006 (L. Pichegru, pers. comm.). Prior to these observations, there had only been one record of a seal killing a Cape gannet ashore (Crawford and Cooper, 1996), although seals regularly kill fledglings around islands (David *et al.*, 2003). Clearly, attacks by seals on birds ashore may have a major impact on colonies of Cape gannets, unless controlled. The recent shift of sardine away from western South Africa (Van der Lingen *et al.*, 2005) may have influenced this new behaviour by Cape fur seals, by causing them to seek alternative sources of food.

Ecosystem considerations

An altered abundance or distribution of prey may have a substantial influence on predators, particularly those such as Cape gannets that are constrained to be central-place foragers when rearing young and that generally show a strong fidelity to breeding localities (Hockey *et al.*, 2005). In ecosystems supporting sardine and anchovy, regime changes in abundance have been reported (Schwartzlose *et al.*, 1999). It is important to develop an understanding of ecosystem changes during periods of regime shifts so that appropriate management of resources can be applied at such times. For example, the decision to fish anchovy intensively in Namibia as sardine there was decreasing may have influenced the subsequent prolonged scarcity of epipelagic fish in the northern Benguela, which resulted in large decreases in numbers of African penguins (Crawford, 1998) and Cape gannets in Namibia. Fishing has the potential to shorten and decrease peaks in abundance of fish stocks and to deepen and lengthen troughs. Such changes may present a challenge even to long-lived predators, which are able to cope with natural interannual variability in resources (Crawford *et al.*, 2006a).

Environmental change, as well as fishing, may influence the availability of prey to central-place foragers (e.g. Frederiksen *et al.*, 2004; Crawford *et al.*, 2006b). In such instances, it may be appropriate to incorporate spatial considerations into the management of fish resources. For example, under the present scenario where most sardine in the Benguela system is located east of Cape Agulhas, the continued extraction of most of the allowable catch along the west coast, where most canning and reduction plants as well as most seabird breeding localities are located, will further exacerbate the shortage of food available to seabirds in the area. However, commercial fishing quotas are set frequently on the assumption that prey abundance is the only important factor for multispecies management (Camphuysen, 2005).

It is often the production of seabirds that is first influenced by prey scarcity (Cairns, 1987). However, in averting decreases in populations, it is important also to minimize mortality (Crawford *et al.*, 2006a). It may be necessary to cull animals, such as individual seals, that are inflicting excessive mortality on, or causing extensive disturbance to, threatened species (David *et al.*, 2003). Again, an understanding of processes is likely to assist management interventions. For example, increased predation by predators on seabirds has been noted when alternative food resources for predators have diminished (Votier *et al.*, 2004), and the individual seals damaging seabird colonies in southern Africa are almost all young males (David *et al.*, 2003).

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