

POPULATIONS OF SURFACE-NESTING SEABIRDS AT MARION ISLAND, 1994/95–2002/03

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During the 1990s and early 2000s, populations of surface-nesting seabirds at Marion Island showed different trends, but for the majority of species numbers decreased. Reduced numbers of gentoo penguins *Pygoscelis papua*, eastern rockhopper penguins *Eudyptes chrysocome filholi*, Crozet shags *Phalacrocorax atriceps melanogenys* and probably macaroni penguins *E. chrysolophus* are most plausibly attributed to an altered availability of food. Decreases in numbers of dark-mantled sooty albatrosses *Phoebetria fusca*, light-mantled sooty albatrosses *P. palpebrata*, southern giant petrels *Macronectes giganteus* and possibly northern giant petrels *M. halli* may have resulted from mortality of birds in longline fisheries. However, populations of wandering *Diomedea exulans* and grey-headed *Thalassarche chrysostoma* albatrosses fluctuated around a stable level. Numbers of Subantarctic skuas *Catharacta antarctica* and kelp gulls *Larus dominicanus* breeding at Marion Island also decreased. Kerguelen *Sterna virgata* and Antarctic *S. vittata* terns remain scarce at the island. Trends for king penguins *Aptenodytes patagonicus* were not reliably gauged, but numbers probably remained stable or increased. There were large fluctuations in numbers of king penguin chicks surviving to the end of winter.

Key words: albatrosses, Crozet shag, giant petrels, kelp gull, Marion Island, penguins, population size, Subantarctic skua, terns

There are 29 species of birds that breed at the sub-antarctic Prince Edward Islands (Marion Island and Prince Edward Island), which are a South African territory in the south-western Indian Ocean (Cooper and Brown 1990). Of these, 16 species are seabirds that nest above the surface of the ground. They include four species of penguins (Spheniscidae), five of albatrosses (Diomedeidae), two of giant petrels (Procellariidae), a shag or cormorant (Phalacrocoracidae), a skua, a gull and two species of terns (Laridae). All breed at Prince Edward Island, and all except the Indian yellow-nosed albatross *Thalassarche carteri* breed at Marion Island.

Of the remaining species, the lesser or black-faced sheathbill *Chionis minor* breeds at both islands, but is not strictly a seabird. It is one of two sheathbills that together constitute the family Chionidae. Sheathbills forage within seabird, especially penguin, colonies and

along the shoreline (Burger 1996) but do not feed at sea. There are thought to be some 4 000–5 500 lesser sheathbills at the Prince Edward Islands, mostly at Marion Island, where the population may have decreased since the 1970s (Huyser *et al.* 2000). There are eight species of prions and petrels (Procellariidae), two of storm-petrels (Hydrobatidae) and two of diving petrels (Pelecanoididae) that have been reported breeding in burrows in the island group. All these birds, except one of the diving petrels, are thought to breed at Marion Island (Cooper and Brown 1990). The occupation of burrows by these species makes it difficult to estimate their population sizes.

A survey of Prince Edward Island was undertaken in December 2001 to estimate populations of surface-nesting seabirds that breed there (Ryan *et al.* 2003). During 1994/95–2002/03, attempts were made to estimate sizes of populations of surface-nesting seabirds

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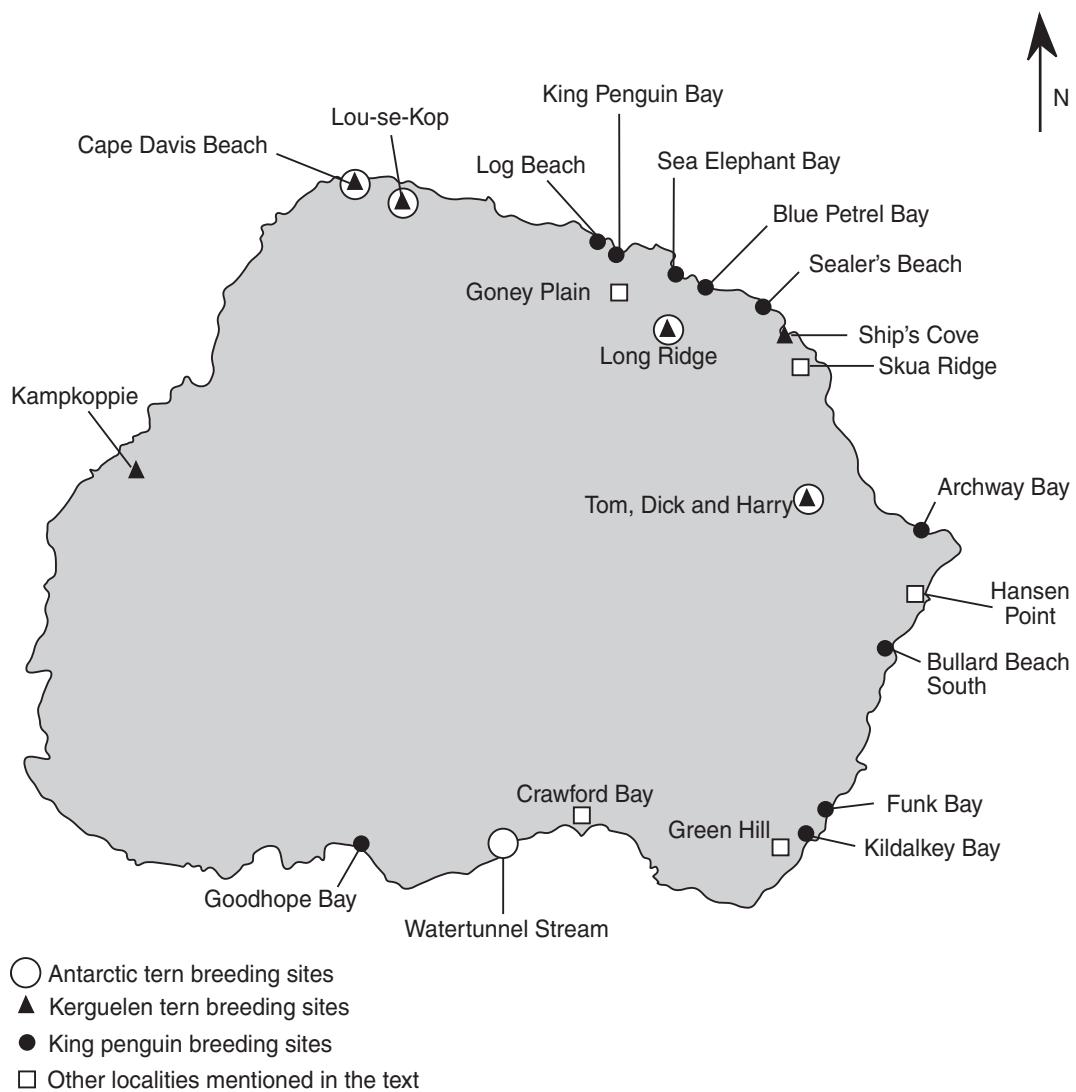


Fig. 1. Localities where king penguins, Antarctic terns and Kerguelen terns bred successfully at Marion Island, 1992/93–2002/03

at Marion Island. This paper collates, and in some instances updates, information reported separately for gentoo penguin *Pygoscelis papua* (Crawford *et al.* 2003c), macaroni penguin *Eudyptes chrysolophus* (Crawford *et al.* 2003a), eastern rockhopper penguin *E. chrysocome filholi* (Crawford *et al.* 2003b), wandering albatross *Diomedea exulans*, grey-headed albatross *Thalassarche chrysostoma* (Nel *et al.* 2002a), northern giant petrel *Macronectes halli*, southern giant

petrel *M. giganteus* (Cooper *et al.* 2001) and Crozet shag *Phalacrocorax [atriceps] melanogenys* (Crawford *et al.* 2003d). Additionally, it provides estimates of population size for king penguin *Aptenodytes patagonicus*, dark-mantled sooty albatross *Phoebetria fusca*, light-mantled sooty albatross *P. palpebrata*, Subantarctic skua *Catharacta antarctica*, kelp gull *Larus dominicanus*, and Antarctic *Sterna vittata* and Kerguelan *S. virgata* tern. Estimates of population size are com-

pared with estimates provided for the 1980s (Cooper and Brown 1990) and some earlier periods.

MATERIAL AND METHODS

King penguin

At Marion Island (290 km^2 , $46^\circ 52' \text{S}$, $37^\circ 51' \text{E}$), an extended egg-laying period, variations in timing of breeding in consecutive years and an irregular breeding schedule make counting of king penguins difficult (van Heezik *et al.* 1995). The egg-laying period lasts from late November to late February (du Plessis *et al.* 1994), with timing of breeding of individual birds largely dependent on whether the previous season was spent breeding and, if so, whether the outcome was a success or a failure (Weimerskirch *et al.* 1992, van Heezik *et al.* 1994). The fledging period of chicks is prolonged by a winter period of fasting (June–September), when chicks are fed infrequently or not at all. Therefore, it is not possible for adults to fledge chicks in time to breed early in the following season, and late breeding usually follows a successful breeding season. However, birds that were unsuccessful or failed to breed in the previous season are able to breed early (Weimerskirch *et al.* 1992, van Heezik *et al.* 1994, 1995). It is considered that repeated monthly counts of adults are necessary to yield a reliable estimate of population size. Peaks in numbers of adults at four colonies have been obtained between December and March (van Heezik *et al.* 1995). In the present study, it was not possible to undertake repeated counts of adults in this early period of breeding. Instead, counts of chicks that survived the winter fast were made in September or October.

Between 1981 and 1990, king penguins were recorded breeding at 15 localities at Marion Island, and they moulted at another two localities (van Heezik *et al.* 1995). In September or October, large numbers of chicks (c. 8 500–15 000) were present at Kildalkey Bay and King Penguin Bay (Fig. 1). There were fewer than 4 000 chicks at each of the other colonies (van Heezik *et al.* 1995).

From 1992 to 2002, there was successful breeding at 10 localities. At Kildalkey and King Penguin bays, the numbers of chicks present in September or October were estimated by counting the numbers in subsections, estimating the proportion of the overall area of the colonies covered by the subsections and dividing the counts by the proportion. Sometimes photographs were taken from surrounding vantage points to assist in this procedure. At the eight smaller colonies, numbers of chicks were counted using a tally counter. Natural

features or prominent birds were used to divide the colonies into smaller groups of birds, which were counted separately and the results summed. In 1999, the numbers of chicks at the colony at Archway Bay were counted three times on 11 occasions between 1 July and 21 November. On each occasion, the coefficient of variation (CV) was computed to provide an indication of the accuracy of the counts.

Sooty albatross species

Coastal counts were undertaken of occupied nest sites of dark-mantled and light-mantled sooty albatrosses each year from 1996/97 to 2002/03. At Marion Island, dark-mantled sooty albatrosses breed only at coastal sites and along Grey-headed Albatross Ridge (Fig. 2a), but light-mantled sooty albatrosses also breed inland (Berruti 1979, Fig. 2b). Therefore, in 1997/98, 2001/02 and 2002/03 the search for nests of light-mantled sooty albatrosses was extended inland. The areas covered included all breeding sites reported by Berruti (1979) and subsequent field personnel. In all years except 2001/02, counts were undertaken in late November and December, when most birds of both species are incubating (Berruti 1979). In 2001/02, the counts were conducted from 18 to 31 December.

Dark-mantled sooty albatrosses breed once every two years, but about 89% of failed breeders breed again the following year (Marchant and Higgins 1990). If it is assumed that about 42% of breeders fail (Weimerskirch and Jouventin 1998; about 65% failed at Marion Island in 1974/75 – Berruti 1979), it is possible to estimate the overall number of pairs breeding at Marion Island in years t and $t+1$ ($B_{t,t+1}$) as

$$B_{t,t+1} = N_t + N_{t+1} - 0.89 * 0.42 * N_t ,$$

where N_t = number of pairs breeding in year t (taken to be the number of occupied nests counted in year t). Such estimates were made for the six pairs of breeding seasons from 1996–1997 to 2001–2002.

Light-mantled sooty albatrosses also are able to lay again in the following season if their breeding attempt fails, but they breed only every second year if successful (Marchant and Higgins 1990). Assuming that a similar proportion of failed breeders will re-lay in the following season and breeding failure to be 65% (Weimerskirch and Jouventin 1998; breeding failure was 69% at Marion Island in 1974/75 – Berruti 1979),

$$B_{t,t+1} = N_t + N_{t+1} - 0.89 * 0.65 * N_t .$$

This relationship was used to estimate the overall number of breeding pairs at Marion Island in 2001–2002 and 2002–2003, the only successive years for

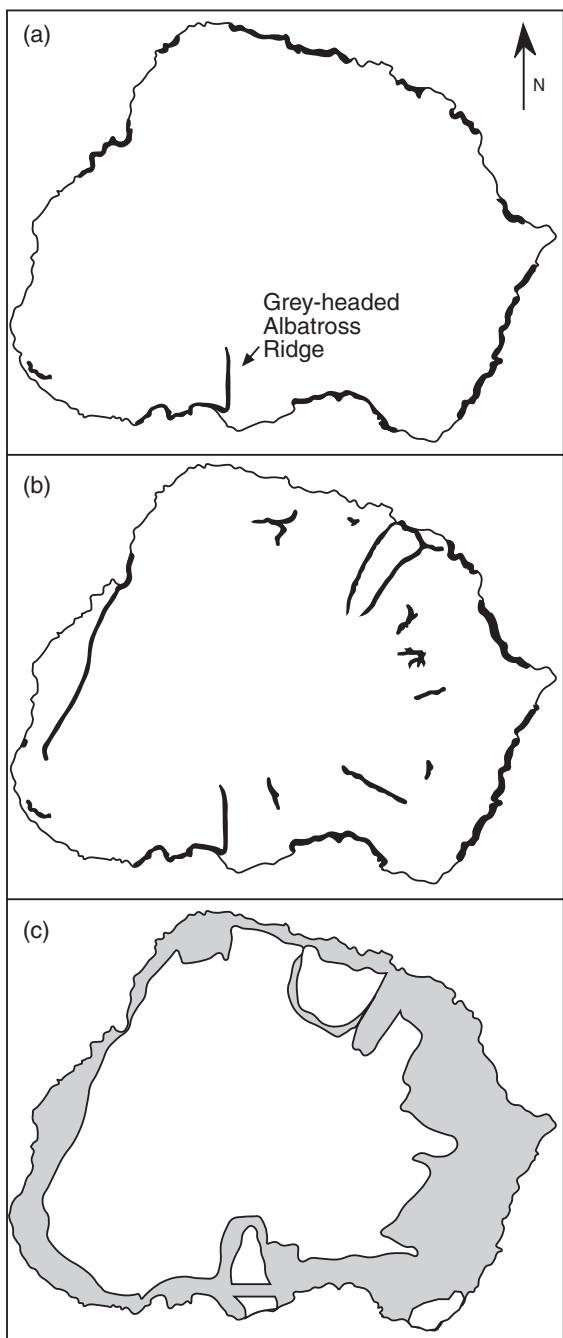


Fig. 2. The distributions at Marion Island in 1997/98 of active nests of (a) dark-mantled and (b) light-mantled sooty albatrosses. Those portions of Marion Island that were searched for active nests of Subantarctic skuas are shaded in (c)

which complete counts of numbers of occupied nests are available.

Subantarctic skua

Numbers of breeding pairs of Subantarctic skuas were estimated at Marion Island from counts of active nests or mobbing behaviour used to identify breeders when nests were not found. Surveys were undertaken from 19 November to 13 December 1997 and from 18 to 31 December 2001. At Marion Island, eggs are laid between 23 October and 19 December, with 70% laid from 2 to 14 November (Williams 1980). The area searched on each of the surveys is shown in Figure 2c and, based on the observations of Hunter (1990), was thought to include the entire breeding population.

Kelp gull

Numbers of active nests of kelp gulls were counted at Marion Island in January of each year between 1998 and 2001, from 18 to 23 December 2001 and in January 2003. At Marion Island, egg laying by kelp gulls is confined to December (Williams *et al.* 1984). A nest was considered active if occupied by an adult or an egg.

Terns

Numbers of breeding pairs of terns were counted or estimated on surveys conducted around Marion Island in November–December and January–February of 1996/97–2000/01 and 2002/03. In 2001/02, searches were made for nests from 18 to 23 December. Eggs of Antarctic terns have been found at Marion Island in February (Berruti and Harris 1976). At Kerguelen and Crozet islands laying is from late December to mid January (Higgins and Davies 1996). Eggs of Kerguelen terns have been found at Marion Island in October (Rand 1954) and recently fledged young have been seen in February (Berruti and Harris 1976). Most adults seen at the Prince Edward Islands from 28 August to 16 September 1984 were paired, and courtship feeding and display flights were observed (Ryan 1987). At Kerguelen Islands, laying is from late August to mid December, depending on weather conditions; at Crozet Islands, it is from early October to early January (Higgins and Davies 1996).

Areas where terns were seen, or where they had been recorded breeding in earlier years, were searched for nests; the numbers of nests were recorded. A nest was deemed to be active if it contained eggs or if fresh faeces were found nearby. Numbers of chicks and fledglings were counted and each taken to repre-

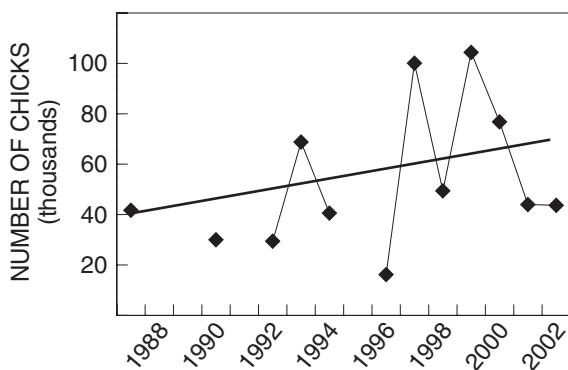


Fig. 3. Overall numbers of post-winter chicks of king penguins counted at Marion Island, 1987–2002, showing the linear trend

sent one nest. For Antarctic terns at South Shetland Islands, 0.93 chicks hatched per nest (Higgins and Davies 1996). For Kerguelen terns at Crozet Islands, 0.78 and 0.24 chicks hatched and fledged per nest respectively (Higgins and Davies 1996). Where adults at nests or chicks could be positively identified, the nests were allocated to the species concerned. In other instances, the number of pairs allocated to each species was determined from the ratio of the species in birds seen overhead. Sometimes nests were not found but breeding was almost certain because adults continually mobbed the observer. In such instances the number of adults was counted and halved to estimate the number of breeding pairs (Ryan 1987).

Identification of Antarctic and Kerguelen terns is difficult when encountering the species for the first time (Berruti and Harris 1976). Different observers were stationed in the field at Marion Island each year and took varying amounts of time to become familiar with identification of the two species. Therefore, identifications were most certain for birds at nests. Observers sometimes found it difficult to be sure of the identification of birds seen overhead, especially in rainy weather. On occasion, observers considered that the number of Antarctic terns may have been underestimated and the number of Kerguelen terns overestimated.

For each species and locality, the number of pairs breeding was assumed to be the maximum number estimated for the locality in the particular season.

Other species

Information was collected on breeding populations of wandering albatross, grey-headed albatross, southern giant petrel and northern giant petrel in 2001/02 and

2002/03 to update that presented by Nel *et al.* (2002a) and Cooper *et al.* (2001). As before, counts of the first three species were made shortly after egg laying was complete. For northern giant petrel, the count in 2001/02 between Skua Ridge and Hansen Point (Fig. 1) and the entire count in 2002/03 were undertaken shortly after egg laying was complete. However, in 2001/02 the count for the remainder of the island was undertaken from 18 to 23 December, 2–3 months later than the other counts. These December counts were adjusted to account for earlier breeding failure by assuming a breeding success of c. 60% to the large chick stage (Cooper *et al.* 2001). For all four species, all known breeding localities were covered including those for giant petrels reported by Hunter (1990). Additionally, extensive searches were made for northern giant petrel farther inland.

RESULTS

King penguin

Numbers of king penguin chicks in September or October estimated for different localities at Marion Island between 1981 and 2002 are listed in Table I. Estimates were made at all breeding localities in 12 years between 1987 and 2002 and showed considerable fluctuation, ranging from 16 000 in 1996 to more than 100 000 chicks in both 1997 and 1999 (mean 54 000, SD 28 000). The linear trend indicated an increase in the number of chicks with time, but this was not significant (Fig. 3, $n = 12$, $r = 0.353$).

On average, the two largest colonies at Kildalkey Bay and King Penguin Bay together held 80% of the chicks. The numbers estimated for those two colonies were significantly positively correlated over time ($n = 12$, $r = 0.758$, $p < 0.005$). There was a significant increase in numbers of chicks estimated for Bullard Beach South ($n = 18$, $r = 0.614$, $p < 0.01$) and a significant decrease in numbers at Goodhope Bay ($n = 15$, $r = -0.680$, $p < 0.01$).

In 1999, the CV on counts at Archway Bay was between 0.4 and 6.8% ($n = 11$, mean 2.5%) for average numbers of chicks ranging from 916–1 230. The estimate of the overall number of post-winter chicks was dominated by the large numbers at Kildalkey Bay and King Penguin Bay, for which a higher CV would be applicable. It is likely that the CV on the overall estimates is of the order of 10%.

Sooty albatross species

Numbers of dark-mantled sooty albatrosses counted at

Table I: Estimates of the number of chicks of king penguins surviving to the end of winter at different breeding localities at Marion Island and overall, 1981–2002. Information for 1981–1990 from van Heezen et al. (1995)

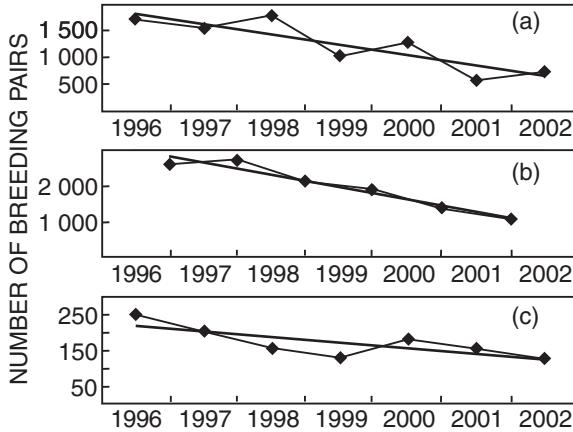


Fig. 4. Trends at Marion Island of (a) number of pairs breeding in any year and (b) estimated overall breeding population for dark-mantled sooty albatrosses, and (c) number of pairs of light-mantled sooty albatrosses breeding around the coast, 1996/97–2002/03. The linear trends are shown

Marion Island decreased from 1 541–1 775 pairs in 1996/97–1998/99 to 564–721 pairs in 2001/02 and 2002/03 (Table II). The distribution of nests in 1997 is shown in Figure 2a. The decrease over time was significant ($n = 7$, $r = -0.873$, $p < 0.02$, Fig. 4a). The estimated overall population at Marion Island decreased from about 2 600–2 700 pairs between 1996/97 and 1998/99 to about 1 100 pairs in 2001/02–2002/03 (Fig. 4b).

Counts of light-mantled sooty albatrosses at Marion Island were 334 pairs in 1997/98 but fewer than 200 pairs in both 2001/02 and 2002/03 (Table II). The distribution of nests in 1997/98 is shown in Figure 2b. The estimated overall population at the island in 2001/02 and 2002/03 was 192 pairs. Numbers breeding around the coastline decreased from 1996/97 to 1999/00, increased in 2000/01 and then decreased again in 2001/02 and 2002/03 (Fig. 4c). The decrease over time was significant ($n = 7$, $r = -0.778$, $p < 0.05$).

Subantarctic skua

For Subantarctic skuas, 749 breeding pairs were counted in 1997/98 and 546 pairs in 2001/02.

Kelp gull

Numbers of kelp gulls at Marion Island, estimated

Table II: Number of breeding pairs of different seabirds counted at or estimated for Marion Island, 1980s and 1994/95–2002/03. Estimates for the 1980s are from Cooper and Brown (1990). For other seasons, sources of information not derived in this paper are: gentoo penguin – Crawford et al. (2003c); macaroni penguin – Crawford et al. (2003a); rockhopper penguin – Crawford et al. (2003b); wandering albatross, grey-headed albatross – Nel et al. (2002a); northern and southern giant petrels (Cooper et al. 2001, Nel et al. 2002a), Crozet shag – Crawford et al. (2003d). Gaps indicate an absence of information

Species	Number of breeding pairs									
	1980s	1994/95	1995/96	1996/97	1997/98	1998/99	1999/00	2000/01	2001/02	2002/03
King penguin	215 230									
Gentoo penguin	888	1 352	1 355	1 119	956	990	846	801	844	806
Macaroni penguin	405 084	434 000	395 000	395 000	405 000	361 000	388 000	407 000	363 000	356 000
Rockhopper penguin	137 652	173 000		150 000					67 000	
Wandering albatross	1 533	1 794	1 765	1 741	1 910	1 760	1 611	1 860	1 869	1 593
Grey-headed albatross	5 037	6 217	5 219	6 600	7 641	7 728	5 573	6 757	6 229	5 005
Dark-mantled sooty albatross	2 055			1 701	1 541	1 775	1 012	1 269	564	721
Light-mantled sooty albatross	201				334				179	127
Northern giant petrel	314	411		387	453	364	275	341	295	196
Southern giant petrel	2 891	2 947		1 198	2 173	1 381	1 468	1 473	1 430	1 759
Crozet shag	589	841		537	388	505	490	443	344	272
Subantarctic skua	900				749				546	
Kelp gull	200				65	88	81	109	24	25
Antarctic tern	<25			0	9	2	8	8	2	10
Kerguelen tern	10			13–18	56	20	27	26	16	12

from counts of active nests, fluctuated between 65 and 109 pairs from 1997/98 to 2000/01. About 25 pairs were estimated as present in both 2001/02 and 2002/03 (Table II).

Terns

Between 1997/98 and 2001/02, Antarctic terns were recorded breeding at five localities at Marion Island and Kerguelen terns at six (Fig. 1). The number of Antarctic terns reported breeding in any season fluctuated between none in 1996/97 and 10 pairs in 2002/03 ($n = 7$, mean = 6 pairs, $SD = 4$ pairs).

The number of Kerguelen tern pairs reported breeding was 13–18 in 1996/97, 16 in 2001/02 and 56 in 1997/98 (Table III). If 1997/98 is excluded, the mean number reported was 19 pairs ($n = 6$, $SD = 6$ pairs).

Other species

Estimates of the breeding populations of wandering albatross, grey-headed albatross, northern giant petrel and southern giant petrel for 2001/02 and 2002/03 are given in Table II. The count of incubating wandering albatrosses in 2001/02 was similar to that for 2000/01, but the numbers of incubating birds decreased in 2002/03. The numbers of incubating grey-headed albatrosses decreased from 6 757 in 2000/01 to 5 005 in 2002/03, when none was found at Crawford Bay

(where there were 37 incubating adults in November 2001).

For the northern giant petrel, there were 67 active nests between Skua Ridge and Hansen Point in September and October 2001. For the remainder of the island, 137 active nests were counted from 18 to 23 December 2001, which after accounting for an assumed breeding failure of 40% (Cooper et al. 2001) represented 228 pairs. This gave an overall estimate of 295 pairs for 2001/02 (Table II). In September 2002, only 196 active nests of northern giant petrels were counted. There were about 1 450 breeding pairs of southern giant petrels in each year from 1999/00 to 2001/02 (Table III). This increased to 1 759 for 2002/03.

DISCUSSION

Comparison of numbers of seabirds presented in this paper with earlier estimates of abundance is made difficult by sometimes poor documentation of the methods used in previous surveys. Information on the timing of former surveys and their extent is often lacking, and it is sometimes unclear whether any adjustments were made to account for failed breeding prior to the surveys (Ryan et al. 2003). More recently, these aspects of surveys have been standardized to a large extent, providing for greater confidence in trends observed since the early 1990s.

Table III: Estimates of the number of Kerguelen and Antarctic terns (pairs) breeding at different localities at Marion Island, 1996/97–2002/03

Colony	Number of breeding pairs													
	1996/97		1997/98		1998/99		1999/00		2000/01		2001/02		2002/03	
	K	A	K	A	K	A	K	A	K	A	K	A	K	A
Tom, Dick and Harry	10–15	0	29	6	11	2	7	2	6	2	6	0	9	4
Watertunnel Stream	0	0	0	0	0	1	0	0	0	1	0	1	0	0
Kampkoppie	0	0	0	0	0	0	9	0	9	0	0	0	0	0
Cape Davis Beach	3	0	5	1	2	0	2	3	2	3	2	1	0	3
Lou-se-Kop	0	0	4	0	4	0	5	0	5	0	1	1	0	0
Long Ridge	0	0	18	2	3	0	2	3	2	3	4	0	3	3
Ship's Cove	0	0	0	0	0	0	2	0	2	0	3	0	0	0
Total	13–18	0	56	9	20	3	27	8	26	9	16	3	12	10

K = Kerguelen

A = Antarctic

King penguin

In 1951/52, Rand (1955) estimated an adult population of 52 410 birds at 16 mapped localities, of which only seven were named as breeding sites (Rand 1954). Van Zinderen Bakker (1971) gives a figure of two million birds for both Marion and Prince Edward Islands for 1965/66. This figure may be regarded as little more than a guess.

Siegfried *et al.* (1978) estimated the Marion Island annual population in the period 1974–1977 as 215 234 breeding pairs in eight colonies, based on aerial photographs taken in March. By the mid 1980s, 10 colonies existed, with new ones reported as being established south of Bullard Beach ("Bullard River") and at Goodhope Bay (Watkins 1987). In 1951/52 the latter locality was used for roosting only (Rand 1955). However, Siegfried *et al.* (1978) report the presence of 21 045 breeding pairs at Goodhope Bay during the period 1974–1977, so uncertainty exists as to when breeding commenced. They did not report a breeding colony at Bullard River in the 1970s, which was first reported to contain 50 chicks in 1981 (van Heezik *et al.* 1995).

Because about 20% of king penguins at Marion Island do not breed in each season (van Heezik *et al.* 1994), the overall population in 1974–1977 would have been about 270 000 pairs. The estimate of 215 230 pairs breeding annually was retained by Cooper and Brown (1990) as being applicable to the 1980s.

Based on numbers of adults counted at colonies between February and March and assumptions concerning absenteeism of mates at sea, failed breeding at the time of the counts and the proportion of birds not breeding in a season, van Heezik *et al.* (1995) estimated the overall population of king penguins at Marion Island in 1990/91 to be of the order of 760 000

adults, equivalent to 380 000 breeding pairs.

At the Crozet Islands, the proportion of chicks of king penguins surviving to the end of the winter fasting period in October during 1986/87–1988/89 was variable, but over three seasons averaged 0.41 (Weimerskirch *et al.* 1992). Applying this rate to the mean post-winter count of chicks obtained at Marion Island during the period 1987–2002 (54 000), the average number of pairs breeding in any season would be 132 000. Assuming 20% of pairs did not breed each season (van Heezik *et al.* 1995), the breeding population at the island would be about 165 000 pairs. This estimate is lower than those of both Williams *et al.* (1979) and van Heezik *et al.* (1995) and highlights the influence of the different assumptions used to estimate the overall population. The assumptions that no failed breeders, absentee breeders or mates were at colonies makes the estimate of van Heezik *et al.* (1995) an upper limit. However, the long period between initiation of breeding and September or October means that the use of post-winter counts of chicks to estimate the number of breeders has a potentially large error. There must have been c. 100 000 breeding pairs in 1997 and 1999 because equivalent numbers of chicks survived the winter fast. The estimate of 165 000 pairs is probably a lower limit. Although the extrapolation from incubation to post-winter chicks precludes accuracy, on average the numbers of chicks surviving to the end of winter have not decreased since the 1980s and may have increased (Fig. 3). Therefore, the population may be regarded as stable to increasing.

Populations of king penguins have increased at Possession Island (Crozet Islands), Kerguelen Islands and Heard Island since the 1960s or early 1970s, with the larger colonies possibly stabilizing during the 1990s (Jouventin and Weimerskirch 1990, Woehler

et al. 2001). At Macquarie Island, South Georgia and Falkland Islands, less frequent or incomplete data also suggest increases in numbers of king penguins. The increases have in instances been recoveries from earlier exploitation to low levels of abundance and may also have resulted from an enhanced availability of myctophid fish, the main prey of king penguins at all breeding localities, including Marion Island (Adams and Klages 1987, Jouventin and Weimerskirch 1990, Marchant and Higgins 1990, Ridoux 1994, Guinet *et al.* 1995, Woehler and Croxall 1997, Ellis *et al.* 1998, Woehler *et al.* 2001). King penguins were exploited at Marion Island's King Penguin Bay in the 1800s (Cooper and Avery 1986).

The similar trends in numbers of chicks surviving to the end of winter at the two largest colonies at Marion Island, which together hold about 80% of the island's population, suggest that environmental conditions may affect either numbers breeding or breeding success. In both 1997 and 1999, when more than 100 000 chicks survived to the end of winter, there were higher than normal ambient temperatures from July–October (Crawford *et al.* 2003e). Goodhope Bay, where there was a long-term decrease in numbers of chicks, is the only colony not situated on the north and east coasts of the island. Human disturbance may cause reductions in king penguin colonies (Jouventin and Weimerskirch 1990), but the colony at Goodhope Bay is well removed from most human disturbance at Marion Island.

Sooty albatross species

Van Zinderen Bakker (1971) estimated the combined numbers of breeding pairs at Marion Island and Prince Edward Island in 1965/66, based on counts of nests, as 1 000 pairs of dark-mantled and 50 of light-mantled sooty albatrosses. Based on surveys undertaken from January 1974 to April 1975 and from April 1976 to May 1977, the annual breeding population of dark-mantled sooty albatrosses at Marion Island was estimated to be 2 032 pairs (Siegfried *et al.* 1978, Berruti 1979, Williams *et al.* 1979). In October and November 1986, there were 1 974 active nests (1 546 birds were incubating, 428 were standing at nests, JC unpublished data). In 1987/88, 2 055 pairs were counted from 8 to 14 October (Cooper and Brown 1990, JC unpublished data). This value decreased to 1 541–1 775 pairs in the mid 1990s and to fewer than 1 000 pairs in the early 2000s.

From 1974 to 1977, the annual breeding population of light-mantled sooty albatrosses at Marion Island was estimated to be 176 pairs (Siegfried *et al.* 1978, Williams *et al.* 1979), of which 97 bred around the coast (Berruti 1979). In October and November 1986, a

coastal count recorded 71 pairs breeding (JC unpublished data). In 1988/89, a count of all breeding localities from 23 November to 27 December indicated a population of 201 pairs, of which once again 97 bred around the coast (Cooper and Brown 1990, JC unpublished data). The overall number breeding was 334 pairs in 1997/98, but fewer than 200 pairs in the early 2000s. The number breeding around the coast decreased from 249 pairs in 1996/97 to 88 pairs in 2002/03 (Fig. 4b).

Numbers of both dark-mantled and light-mantled sooty albatrosses decreased at Possession Island (Crozet Islands) between 1980 and 1994, the former at a much higher rate than the latter. The decreases were caused by a low survival of adults and immature birds, which was attributed to mortality caused by longline fishing in the south-western Indian Ocean (Weimerskirch and Jouventin 1998). Similar mortality may have been responsible for the decreases in the two species of sooty albatross at Marion Island. Since 1994, the number of dark-mantled sooty albatrosses at Possession Island has remained low, whereas the number of light-mantled sooty albatrosses has increased (Woehler *et al.* 2001).

Subantarctic skua

Van Zinderen Bakker (1971) estimated the 1965/66 population as 4 000 birds for both Marion and Prince Edward islands. This figure is assumed to include non-breeding birds. From 1974–1977, there were an estimated 406 pairs of Subantarctic skuas at Marion Island (Siegfried *et al.* 1978, Williams *et al.* 1979). In 1987/88, 900 pairs bred at the island (Hunter 1990). The population decreased to 546 pairs by 2001/02 (Table II). At Marion Island the skuas are essentially terrestrial feeders during the breeding season, eating burrowing petrels, preying on eggs and chicks of penguins and scavenging from carcasses of seals and penguins. In 1987/88, the density of breeding birds was highest in the vicinity of large colonies of penguins, which were thought to be the skuas' main source of food (Hunter 1990). It is possible that their food supply was reduced by the decreases in some penguin species. Increases in skua populations have been shown in response to station garbage (Hemmings 1990), which is no longer made available at Marion Island (pers. obs.). Subantarctic skuas were killed in small numbers between 1996 and 2000 by the longline fishery that operated around the Prince Edward Islands (Nel *et al.* 2002b). In the period 1990/91 to 1992/93 a total of 92 skuas was killed in gin traps set for feral cats *Felis catus* (Bester *et al.* 2002). The estimated number of Subantarctic skuas breeding at Prince Edward Island has increased since the 1980s, but this is attributed to better coverage and more accurate mapping of nests (Ryan *et al.* 2003).

Populations of Subantarctic skuas at Palmer and Admiralty Bay, King George Island (South Shetland Islands) have been stable for 10–20 years, whereas there have been recent decreases at Potter Peninsula and Fildes Peninsula, King George Island (Woehler *et al.* 2001).

Kelp gull

Van Zinderen Bakker (1971) recorded that “not more than 500 gulls occur around the islands” [Marion Island and Prince Edward Island] in 1965/66. From 1974 to 1977, there were an estimated 200 pairs of kelp gulls at Marion Island (Siegfried *et al.* 1978, Williams *et al.* 1979); the same value was assumed for the 1980s (Cooper and Brown 1990). The population in the 1990s was less than half this amount, whereas estimates for Prince Edward Island remained roughly constant (Ryan *et al.* 2003).

Terns

Van Zinderen Bakker (1971) recorded that “not more than 150 [Kerguelan terns] are thought to occur on the islands” in 1965/66. He did not observe Antarctic terns breeding at the Prince Edward Islands. From 1974 to 1977, the population of Antarctic terns at Marion Island was estimated to be fewer than 50 pairs (Williams *et al.* 1979). It was thought to be fewer than 20 pairs in 1979 (Brooke 1984) and fewer than 25 pairs in the 1980s (Cooper and Brown 1990). Between 1996/97 and 2002/03, the highest estimate was 10 pairs, confirming the small size of the population.

Fewer than 50 pairs of Kerguelan terns were estimated for Marion Island during the period 1974–1977 (Williams *et al.* 1979). Less than 10 pairs bred at the island in 1979 (Brooke 1984). Between 28 August and 16 September 1984, 11 Kerguelan terns were counted at the island. They were seen between Kampkoppie and Goney Plain, and the population for Marion Island was estimated as five pairs (Ryan 1987). It was thought to be 10 pairs in the 1980s (Cooper and Brown 1990) but reached 56 pairs in 1997/98. However, this was more than double the next highest estimate for the period 1996/97–2002/03. Excluding 1997/98, the mean of 19 pairs for that period is similar to earlier estimates. The high number reported breeding in 1997/98 matched the unusually good or poor breeding by several other seabirds at Marion Island and may have been influenced by the ENSO (*El Niño* Southern Oscillation) event of 1997/98 (Crawford *et al.* 2003e).

In 1984, Kerguelan terns were not encountered along

the east coast between Ship’s Cove and Green Hill (Ryan 1987), where they have subsequently occupied suitable breeding habitat (Table III, Fig. 1). It was thought that their earlier absence from that area was related to disturbance from feral cats, which were finally eradicated from Marion Island in 1991 (Bester *et al.* 2000, 2002), or from the research station (Ryan 1987). Numbers of Kerguelan terns at Prince Edward Island, 21 km distant and with minimal human disturbance, have decreased since the mid 1980s (Ryan *et al.* 2003).

Other albatrosses and giant petrels

Nel *et al.* (2002a) reported that populations of five seabirds breeding at Marion Island, (wandering albatross, grey-headed albatross, northern giant petrel, southern giant petrel and white-chinned petrel *Procellaria aequinoctialis*) all showed similar trends in the 1980s and 1990s. All were stable or decreasing during the 1980s, followed by a slight recovery during the early to mid 1990s. In the late 1990s, they all stabilized or again decreased in numbers. The trends for wandering albatross were strongly correlated with the trends for other Indian Ocean populations of the same species and corresponded with changes in longline fishing effort for tunas *Thunnus* spp. in the southern Indian Ocean (Nel *et al.* 2002a). Fishing effort for tunas in the region increased greatly during the early 1980s, peaking during the mid 1980s, before decreasing to a low level in 1990 and then increasing again (Tuck and Polacheck 1997). As all five species of seabird were killed in significant numbers by tuna longline fishing vessels operating at the Subtropical Convergence or at other productive oceanographic features where seabirds concentrate (Ryan and Boix-Hinzen 1998), it was thought that by-catch mortality in the tuna fisheries had influenced the trends (Nel *et al.* 2002a, b).

Numbers of wandering and grey-headed albatrosses breeding at Marion Island increased again in 2000/01 and 2001/02 but then decreased to low levels in 2002/03, indicating fluctuations, but no clear trend, in the most recent 10 seasons (Nel *et al.* 2002a, Table II). Numbers of northern giant petrels breeding at Marion Island increased in 2000/01 but were lower in 2002/03 than at any time since 1984/85 (Cooper *et al.* 2001, Table II), suggesting either a reduced population or substantial non-breeding in that season. Numbers of southern giant petrels breeding at the same island remained low in 2000/01 and 2001/02 but improved in 2002/03 (Table II). However, they remain considerably fewer than the 2 235–2 947 pairs recorded between 1984/85 and 1994/95 (Cooper *et al.* 2001).

Other penguins and Crozet shag

There have been substantial decreases in numbers of gentoo penguins, rockhopper penguins and Crozet shags breeding at Marion Island since the mid 1990s (Table II, Crawford *et al.* 2003b, c, d). At most monitored localities in the Antarctic Peninsula numbers of gentoo penguins increased after 1980. However, the colony at Admiralty Bay, King George Island, decreased in size, as did numbers at the subantarctic island of South Georgia (Woehler *et al.* 2001).

The decrease in numbers of rockhopper penguins at Marion Island matches decreases at several other localities in the south-western Atlantic and Indian oceans and south of New Zealand, where altered environmental conditions are thought to have reduced the availability of its prey (Cunningham and Moors 1994, Bingham 1998, Ellis *et al.* 1998, Guinard *et al.* 1998, Woehler *et al.* 2001).

There appears to have been a decrease in numbers of macaroni penguins breeding at Marion Island between 1994/95 and 2002/03 (Table II, Crawford *et al.* 2003a). Numbers of macaroni penguins also have decreased at Prince Edward Island (Ryan *et al.* 2003) and Bird Island, South Georgia, since the mid 1980s, and they may have decreased at the Kerguelen Islands (Woehler *et al.* 2001).

The decreases in populations of gentoo, rockhopper and macaroni penguins and Crozet shags at Marion Island are likely to have resulted from a reduced availability of food that may have resulted from altered environmental conditions (Crawford *et al.* 2003b, c, d). At Marion Island, annual mean surface air temperature has increased and annual precipitation has decreased since the 1960s (Smith 2002) and sea surface temperatures increased by about 1.5°C between 1949 and 1988 (Mélice *et al.* in press). Gentoo penguins and Crozet shags feed near the island, where there is considerable overlap in their diet (Cooper 1985, Adams and Wilson 1987, Espitalier-Noel *et al.* 1988, Adams and Klages 1989). It is likely that availability of prey to these two seabirds has changed since the mid 1980s (Crawford *et al.* 2003c, d).

Potential interactions with marine mammals

Interactions between fur seals and seabirds at the Prince Edward Islands (e.g. Ryan *et al.* 2003) can be expected to increase as populations of fur seals at the islands increase (e.g. Wilkinson and Bester 1990, Bester *et al.* 2003). Increased numbers of fur seals may have caused the reduced number of rockhopper penguins at Amsterdam Island (Guinard *et al.* 1998). In the Ben-

guela ecosystem off the west coast of southern Africa, increases in Cape fur seals *Arctocephalus pusillus* have adversely affected some populations of seabirds through predation and displacement of birds from breeding sites (Crawford *et al.* 1989, David *et al.* 2003). Fur seals and other marine mammals may compete with seabirds for food (e.g. Jouventin and Weimerskirch 1990).

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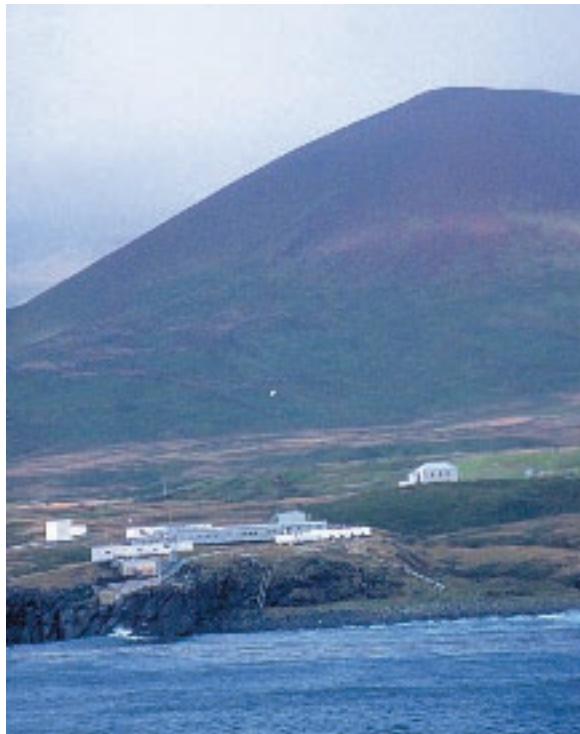
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A view of Marion Island showing the main base in the foreground
(photo B. M. Dyer)



Numbers of dark-mantled (top left, photo L. Upfold) and light-mantled (top right, photo R. J. M. Crawford) sooty albatrosses have decreased at Marion Island, whereas populations of Kerguelen tern (bottom left) and Antarctic tern (bottom right) remain small (photos B. M. Dyer)

COUNTS OF SURFACE-NESTING SEABIRDS BREEDING AT PRINCE EDWARD ISLAND, SUMMER 2001/02

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R. J. M. CRAWFORD³ and M. N. BESTER⁴

The first midsummer survey of surface-nesting seabirds at Prince Edward Island was conducted during December 2001. It was also the first census for most species since the early 1980s. Despite concerns about the impacts of longline fishing mortality on various albatrosses and giant petrels, there was no evidence that populations of these species had decreased. Indeed, the estimate of wandering albatrosses *Diomedea exulans* (Vulnerable) has increased significantly, making Prince Edward Island equal with Marion Island as supporting the largest single-island populations of this species. Species that underwent significant decreases were macaroni penguins *Eudyptes chrysophyphus* (Vulnerable), Crozet shags *Phalacrocorax [atriceps] melanogenys* and Kerguelen terns *Sterna virgata* (Near-Threatened). The reasons for these decreases are unclear, but for macaroni penguins may be partly a consequence of competition for space with the burgeoning population of fur seals *Arctocephalus* spp. The 2001 survey increased the population estimates for Subantarctic skuas *Catharacta antarctica*, light-mantled sooty albatrosses *Phoebetria palpebrata* (Vulnerable) and southern giant petrels *Macronectes giganteus* (Vulnerable), mostly as a result of greater coverage than for previous counts. The 2001 survey confirms that Prince Edward Island remains a globally important breeding site for seabirds.

Key words: albatrosses, giant petrels, gull, penguins, Prince Edward Island, seabirds, shag, skuas, Subantarctic, terns

The subantarctic Prince Edward Islands are globally important breeding sites for seabirds (Williams *et al.* 1979, Cooper and Brown 1990), including eight Threatened and five Near Threatened species (BirdLife International 2000). Accordingly, the islands are recognized as an Important Bird Area (Barnes *et al.* 2001) and are afforded the highest level of conservation protection under South African law, being designated as Special Nature Reserves (Prince Edward Islands Management Plan Working Group 1996). Numbers of surface-nesting seabirds breeding at Marion Island are fairly well known (Cooper and Brown 1990, Crawford *et al.* 2003c), but there have been few counts of seabirds breeding at Prince Edward Island, which is seldom visited by people. All previous visits by ornithologists have been in early spring (August–September) or late summer–autumn (March–May; van Zinderen Bakker 1971a, Berruti *et al.* 1981, Grindley 1981, Imber 1983, Cooper and Brooke 1984, Ryan and Hunter 1985, Ryan 1987, Watkins 1987), which is too early or too late to count several of the summer-nesting seabird species. Also, there have been no dedicated counts of seabirds at the island since the early 1980s.

In order to obtain reliable population estimates for management and conservation purposes, a midsummer survey to Prince Edward Island was conducted during

December 2001. There has been concern for several albatross and petrel populations at this island, given the significant impact longline fishing mortality has had on birds breeding at Marion Island (Nel *et al.* 2002a). Six species breeding at Prince Edward Island are listed as Vulnerable and a further three as Near Threatened as a result of longline fishing mortality (BirdLife International 2000).

Of particular interest was the population of Indian yellow-nosed albatrosses *Thalassarche [chlororhynchos] carteri* (Vulnerable), because this species does not breed on Marion Island, and thus there was no information on its status at the Prince Edward Islands. It is known to be killed in significant numbers by longlines targeting both Patagonian toothfish *Dissostichus eleginoides* around the Prince Edward Islands (Nel *et al.* 2002a) and tunas *Thunnus* spp. more widely in the Southern Ocean (Ryan and Boix-Hinzen 1998, Weimerskirch and Jouventin 1998, Ryan *et al.* 2002). However, there has been no assessment of this species' population at Prince Edward Island since the early 1980s, when it was estimated that 7 000 pairs bred there (Berruti *et al.* 1981), almost 20% of the estimated global population (Tickell 2000).

There was also concern about the populations of penguins at Prince Edward Island, with both crested

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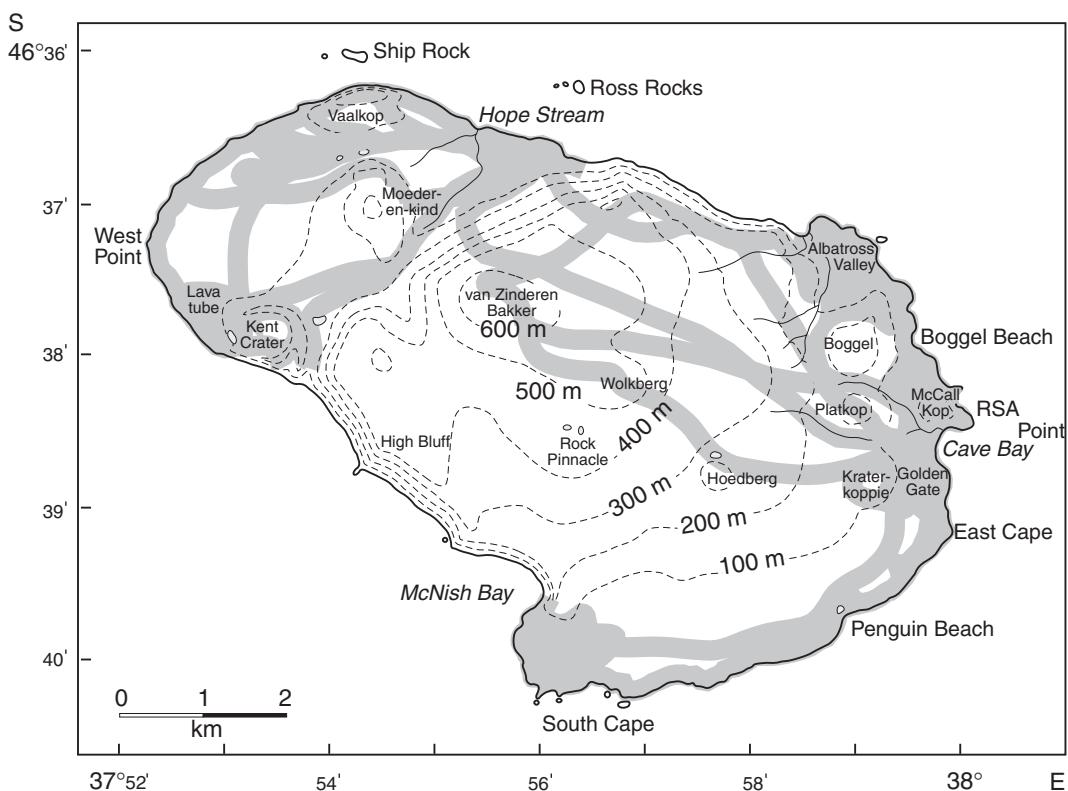


Fig. 1: Prince Edward Island, with areas covered during the seabird survey shaded. Coastal cliffs along the south and north coasts shown as not surveyed directly were scanned from adjacent headlands to estimate minimum numbers of breeding penguins and albatrosses

penguins *Eudyptes* spp. occurring listed as Vulnerable, and gentoo penguins *Pygoscelis papua* listed as Near Threatened (BirdLife International 2000). The population of eastern rockhopper penguins *E. chrysocome filholi* apparently has decreased at Marion Island (Cooper *et al.* 1997, Crawford *et al.* 2003b), and the species has experienced large decreases at several other localities (Cunningham and Moors 1994, Bingham 1998), leading to requests for South Africa to obtain a current estimate for the Prince Edward Island population (Ellis *et al.* 1998). In this paper, the first midsummer counts of surface-nesting seabirds breeding at Prince Edward Island are reported.

MATERIAL AND METHODS

The Prince Edward Islands lie roughly 2 200 km south-east of Cape Town, South Africa in the southern

Indian Ocean. They comprise two main islands: Marion Island (290 km^2 ; $46^{\circ}52' \text{S}$, $37^{\circ}51' \text{E}$) and Prince Edward Island (44 km^2 ; $46^{\circ}38' \text{S}$, $37^{\circ}57' \text{E}$), 21 km apart. Marion Island has a meteorological and research station, but human activities at the near-pristine Prince Edward Island are curtailed to limit human impact (Prince Edward Islands Management Plan Working Group 1996). Prince Edward Island was visited from 17 to 22 December 2001. Teams of 2–3 observers worked systematically around the island, counting all surface-nesting birds either by entering the colonies or by scanning from outside the colonies with binoculars. Coverage included all the readily accessible coastline, as well as parts of the adjacent interior of the island (Fig. 1). Populations of penguins and albatrosses breeding on inaccessible cliff areas were estimated by scan counts from adjacent promontories or from above or below the cliffs.

Coverage of colonially nesting birds probably was adequate, especially for species confined to the coastal

Table I: Estimates of annual-breeding populations (pairs) of seabirds at Prince Edward Island. Previous estimates are from Cooper and Brown (1990) and references therein. Estimates for 2001 are extrapolated from the actual counts, compensating for likely breeding failures prior to the census period, as well as for incomplete coverage in some species (see text for details)

Species	Past estimate	2001	
		Count	Estimate
King penguin	5 000	2 903	3 000
Gentoo penguin	650	128	475 ¹
Macaroni penguin	17 000	4 508	9 000 ¹
Rockhopper penguin	35 000	31 655	45 000
Wandering albatross	1 300	1 687	1 850
Grey-headed albatross	1 500	1 897	3 000
Indian yellow-nosed albatross	7 000	4 870	7 500 ¹
Dark-mantled sooty albatross	700	637	1 000
Light-mantled sooty albatross	50	92	150
Northern giant petrel	180	133	300 ¹
Southern giant petrel	400	567	1 000
Crozet shag	120	39	50
Subantarctic skua	60	210	250 ²
Kelp gull	30	20	30
Antarctic tern	<25	0	<5
Kerguelen tern	20	2	<5

¹ Species that breed primarily in winter or early spring, resulting in considerable extrapolation and thus relatively low confidence in the estimated population

² Because of the highly staggered breeding season and frequent initiation of replacement clutches, this figure excludes any extrapolation for nests that failed prior to the survey

zone. However, coverage was clearly incomplete for solitary or loosely colonial species such as Subantarctic skuas *Catharacta antarctica* and northern giant petrels *Macronectes halli*, both of which also nest well inland. Crude estimates of coverage of suitable habitat for these species were used to extrapolate the likely population. Because many species were already well advanced in their breeding seasons, and some were still just starting, counts were corrected using average breeding success parameters (usually based on studies at adjacent Marion Island) to estimate the likely annual breeding populations. However, for species where it is not possible to check whether nests contain eggs or chicks (e.g. cliff-nesting albatrosses), this may lead to inflated estimates if a considerable number of nests are occupied by pre-breeding or failed pairs.

Limited time did not permit the routine multiple counting necessary to estimate census accuracy, but repeat counts were made of several key sites (e.g. cliff-nesting albatross colonies). Typically, repeat counts of small colonies varied by <5%, whereas counts of larger colonies varied by <10%. Rockhopper penguins were perhaps the hardest to count accurately, given their large numbers, the confounding effects of loafing birds and the rugged nature of much of the

coast, which was often difficult to access because of large numbers of aggressive fur seals *Arctocephalus* spp. (Bester et al. 2003). The count of the main wandering albatross *Diomedea exulans* concentration in Albatross Valley was validated by an independent survey recording the location of each nest (Underhill et al. 2003). To avoid double-counting, GPS fixes were made for most colonies or nest sites. Species distributions were plotted on a revised map of the island.

RESULTS

No new seabird species were found at Prince Edward Island in 2001, but evidence of breeding was obtained for two burrow-nesting species not previously proven to breed at the island (Berruti et al. 1981, Imber 1983, Cooper and Brooke 1984). A burrow with a Kerguelen petrel *Aphrodroma brevirostris* chick was found in the valley between Boggel and Platkop, and an adult grey-backed storm petrel *Garrodia nereis* with a well-vascularized brood patch was caught when it flushed from dense *Acaena magellanica* vegetation near the base of the cliff in Albatross Valley (Fig. 1).

Penguins

Four penguin species breed at Prince Edward Island. King penguins *Aptenodytes patagonicus* breed at three sites, all on the sheltered east coast: Boggel Beach, Cave Bay and Penguin Beach. During the 2001 census, these colonies contained 1 200, 983 and 250 incubating adults, and 78, 261 and 131 large chicks respectively, giving a total count of 2 433 incubating adults and 470 large chicks. The survey took place during the period of peak egg-laying at Marion Island (du Plessis et al. 1994), so the incubator count probably represents most of the 2001/02 cohort. Interpretation of the large chick count (chicks surviving from the 2000/01 cohort) is more problematic (see van Heezik et al. 1994, 1995). Chick counts in December represent only 10–30% of eggs laid (Weimerskirch et al. 1992, van Heezik et al. 1995), suggesting that breeding effort in 2000/01 was 2 500–5 000 pairs. However, the proportion surviving varies as a function of colony size (Hunter 1991) and between years (van Heezik et al. 1995). This suggests an average annual population of some 3 000 pairs (Table I), but confidence in this estimate is low due primarily to natural variability rather than count error. There were small numbers of loafing king penguins at Hope Stream Beach on the west coast, and at the beach east of South Cape.

Gentoo penguins also breed primarily along the east coast (at least eight colonies), with only one colony

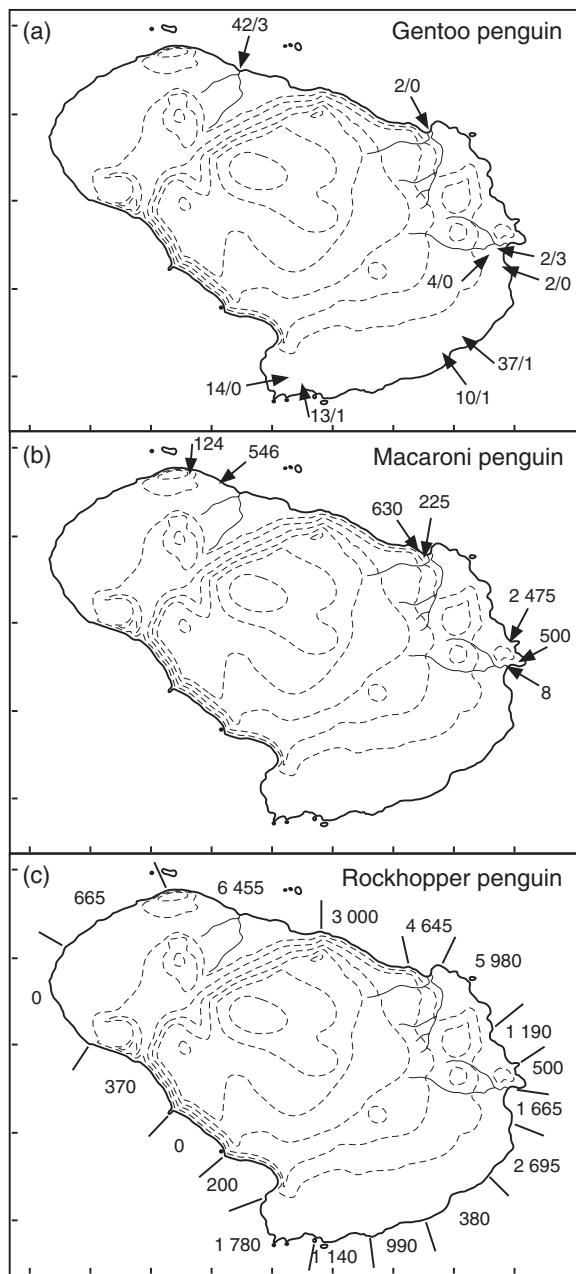


Fig. 2: Distribution of (a) gentoo penguins, (b) macaroni penguins and (c) rockhopper penguins breeding at Prince Edward Island in December 2001. For gentoo penguins, numbers of chicks and of nests with eggs are shown for each colony (depicted as chicks/nests with eggs). For macaroni and rockhopper penguins, numbers of breeding pairs at colonies or along sections of the coast respectively are indicated

on the west coast inland from Hope Stream Beach (Fig. 2a). Gentoo penguins typically breed in winter and spring at the Prince Edward Islands (Adams and Wilson 1987), so relatively few birds were breeding during the December 2001 census, and most had large chicks in crèches ($n = 101$ chicks). However, there were nine pairs incubating eggs, and 18 pairs had 25 fairly small downy chicks still in the nest. Given that gentoo penguins rarely, if ever, rear two chicks at Marion Island (Williams 1980), this represents a minimum of 128 breeding pairs. At Marion Island in 2001, 73% of chicks had fledged by mid December. Assuming an equivalent proportion at Prince Edward Island, the population would have been about 475 pairs (Table I). However, the period of this extrapolation (four months) means that there is considerable uncertainty for this estimate.

Macaroni penguins *Eudyptes chrysophrys* were breeding at seven sites, including two colonies on the west coast between Hope Stream and Vaalkop (Fig. 2b). The largest colonies were on the slopes of McCall Kop. During the census, 4 508 pairs were counted. Most birds had small or medium-sized chicks. Based on breeding success data from Marion Island (Cooper *et al.* 1997), this represents roughly half the total breeding effort, giving an estimated 9 000 pairs at the start of the 2001/02 breeding season (Table I).

The eastern rockhopper penguin was the most abundant penguin on Prince Edward Island, occurring around most of the coastline, with the highest densities along the northern coast between Vaalkop and Boggel (Fig. 2c). Most colonies were within 100 m of the coast, but birds extended farther inland along the northern cliffs, where colonies extended up to 300 m up the cliffs. The low numbers along the west coast south of Vaalkop probably result from the largely sheer cliffs in this area. One colony among a jumbled pile of lava on top of the cliffs near West Point was more than 300 m away from the landing site, suggesting that colony sites are determined both by the need for an adequate landing site and appropriate cover for nests. A total population of 31 655 pairs was counted during December 2001. Most birds were still on eggs, with a few small chicks. Assuming a hatching success (per nest) of 70% (Cooper *et al.* 1997), the total breeding population is likely to be 45 000 pairs (Table I), but confidence in this estimate is not great because of the count difficulties for this species (see Material and Methods).

Albatrosses

Wandering albatrosses breed on relatively open coastal plains, mostly below 150 m, on both the east and west coasts of Prince Edward Island (Fig. 3a).

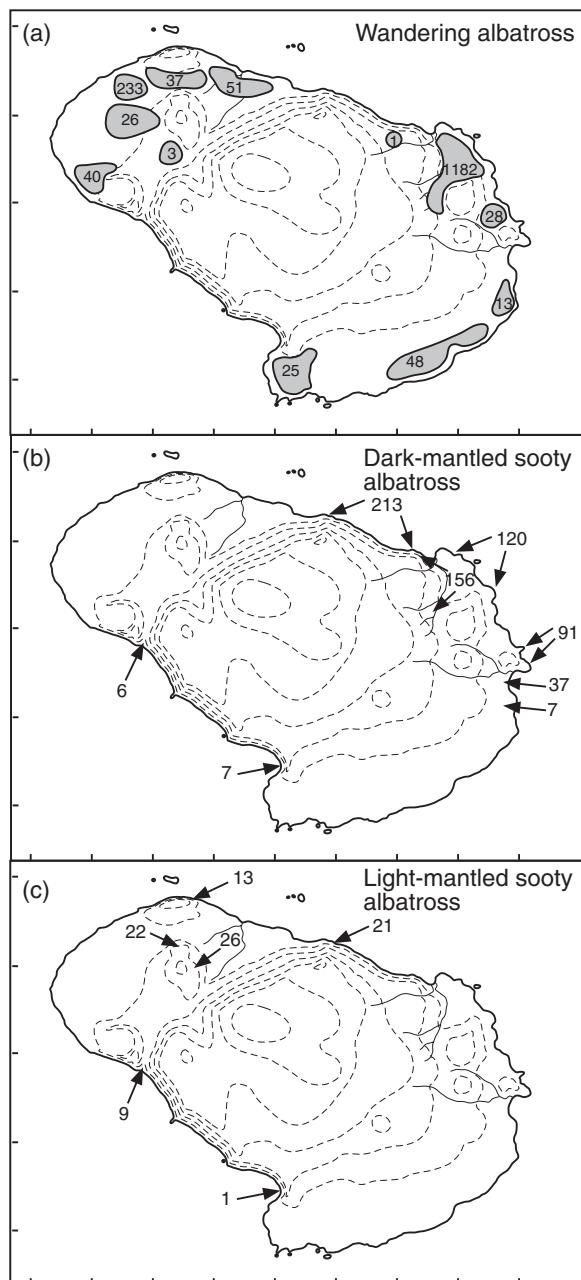


Fig. 3: Distribution of (a) wandering albatrosses, (b) dark-mantled sooty albatrosses and (c) light-mantled sooty albatrosses breeding at Prince Edward Island in December 2001. Numbers of birds at fresh nests are shown for wandering albatrosses, numbers of active nests for the other two species

However, one pair was breeding above the northern sea cliffs at more than 200 m above sea level. During the December census, most pairs were still preparing to breed, although some had already laid eggs, and a few chicks from the previous season were still present. The largest concentration was in Albatross Valley, where there were almost 1 200 pairs. The total count of birds on fresh nests was 1 687, but this is probably an underestimate of the actual breeding population. The count of three study areas on Marion Island on 23 December 2001 (immediately after the Prince Edward survey) yielded 222 fresh occupied nests, but subsequent careful checking of marked nests revealed that 251 eggs were laid, suggesting that the Prince Edward survey underestimated the actual breeding effort during 2001/02 by approximately 10%. Given that the species breeds biennially, it is estimated that the island's annual demi-population is approximately 1 850 pairs.

Grey-headed albatrosses *Thalassarche chrysostoma* only breed on the north-east- and north-facing cliffs of Albatross Valley, with a small isolated group (52 pairs) at the far western end of the cliffs opposite Ross Rocks. Within Albatross Valley, the eastern colonies consist entirely of grey-headed albatrosses, but towards the western end of the valley that species occurs in mixed colonies with Indian yellow-nosed albatrosses. There were no grey-headed albatrosses among the large yellow-nosed albatross colonies on the sea cliffs west of Albatross Valley, other than the small group at the far western end of the cliffs. During December 2001, 1 897 pairs were counted. Most were on eggs or small chicks. Assuming an average hatching success of 60% ($n = 5$ years, unpublished data from Marion Island), this suggests that the annual demi-population is approximately 3 000 pairs (Table I).

Indian yellow-nosed albatrosses also breed on the north-east-facing cliffs of Albatross Valley, but only towards the western end of the Valley (1 300 pairs). The colonies extend from there along the sea cliffs almost to the start of the western coastal plain (opposite Ross Rocks). Accurate counts of these sea cliffs are not easy. The count using binoculars from the point north of Albatross Valley beach was 3 000 pairs; actual counts on different days by different observers were 3 007 and 2 930. From this distance it was not always possible to differentiate birds occupying nests from loafing birds. The species identity of these birds was confirmed by scanning from the top of the sea cliffs. During this exercise, some birds breeding on west-facing slopes were found that would have been invisible during the initial count (570 pairs), and were added to the total estimate. Overall, the count of 4 870 pairs is less accurate and precise than the count of grey-headed albatrosses, but it is likely to be within 10% of the actual population. The yellow-nosed albatrosses were brooding or guarding small to medium-sized

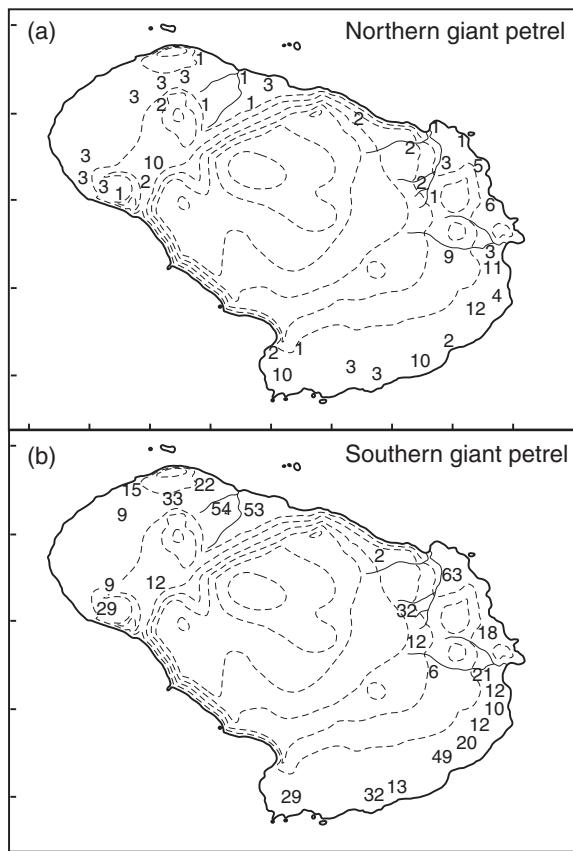


Fig. 4: Distribution of chicks of (a) northern and (b) southern giant petrels at Prince Edward Island in December 2001

chicks. Assuming a breeding success to this stage of approximately 65% (Jouventin *et al.* 1983), this suggests that the annual breeding population is approximately 7 500 pairs (Table I). In addition to the main breeding cliffs, a group of 17 loafing adults was seen on two days on the cliffs below McCall Kop.

Sooty albatrosses *Phoebetria* spp. breed on cliffs. They are difficult to count, because their dark plumage blends with the cliffs much more so than do the mollymawks *Thalassarche* spp. Counts on the inaccessible sea cliffs almost certainly underestimate the true population, especially along the south coast, where the cliffs were not scanned from above. Dark-mantled sooty albatrosses *P. fusca* occurred primarily in the northern and eastern part of the island (Fig. 3b). Unlike at Marion Island they are not confined to coastal cliffs (van Zinderen Bakker 1971b), inhabiting inland cliffs

in Albatross Valley and south of Cave Bay. There were some dense concentrations, with groups of up to 40 pairs in single-species colonies on the coastal cliffs of McCall Kop. In all, 637 pairs were counted on nests. Most were on small chicks. Assuming a mean hatching success of approximately 60% (Berruti 1979, Jouventin and Weimerskirch 1984), this suggests that the annual demi-population is at least 1 000 pairs (Table I).

Light-mantled sooty albatrosses *Phoebetria palpebrata* occurred more at the western end of the island, with the largest numbers on the inland cliffs of Moederen-kind (Fig. 3c). None was recorded on the cliffs in Albatross Valley, but there was a small group at the western end of the adjacent sea cliffs. In all, 92 pairs were counted on nests. Most were on eggs or newly hatched chicks. Assuming a hatching success of 60% (Mougin 1970, Berruti 1979), this suggests a minimum annual demi-population of 150 pairs.

Giant petrels

Breeding northern giant petrels are difficult to count because their nests occur singly or in loose groups up to at least 1 km inland, and are usually sheltered by rock outcrops, making detection and adequate coverage difficult. During the December 2001 survey, 133 nests with chicks were counted, 40 on the western coastal plain and 93 on the eastern coastal plain (Fig. 4a). There were quite a few nests at the periphery of colonies of southern giant petrels *Macronectes giganteus*. Assuming a breeding success of c. 55% to the large chick stage (Cooper *et al.* 2001), this suggests a minimum population of 250 pairs. However, this is almost certainly an underestimate of the island's population, because even within the areas covered during the survey, at least some nests probably were overlooked. Other nests were probably in areas not covered during the survey. It is considered that incomplete coverage of suitable habitat resulted in approximately 20% of pairs being missed. Therefore, it is estimated that the total island population is approximately 300 pairs (Table I).

Southern giant petrels typically nest in larger groups and in more open habitats than northern giant petrels. Also, their chicks have more striking white down, making colonies easier to locate. They occur widely on the island (Fig. 4b). They breed even farther inland than northern giant petrels, with colonies up to 2 km inland and more than 200 m above sea level on the eastern slopes north of Hoedberg. Assuming breeding success to the small-medium chick stage of 40% (Cooper *et al.* 2001), the count of 567 chicks in December 2001 suggests a minimum breeding population of 1 400 pairs. However, the relatively low breeding suc-

cess recorded by Cooper *et al.* (2001) at Marion Island may have been influenced by human disturbance. Southern giant petrels are renowned for being susceptible to disturbance while breeding (e.g. Chupin 1997, BirdLife International 2000). Consequently, breeding success may be higher on Prince Edward Island. Using the same success as northern giant petrels (55%), gives a total population estimate of approximately 1 000 pairs (Table I).

Other birds

Crozet shags *Phalacrocorax atriceps melanogenys* were breeding at six sites, with a possible further site on Ross Rocks (Fig. 5a). All sites were on offshore stacks or inaccessible cliffs. In total, some 39 pairs were nesting during the survey, including birds on Ross Rocks that were too far away to confirm breeding. It is possible that some nests were overlooked on some of the island's sheer cliffs, but the total population is probably less than half that counted in September 1984 (Ryan and Hunter 1985), despite the fact that no colonies were found on the West Coast in 1984 (where they were almost certainly overlooked).

Subantarctic skuas were the most widespread surface-nesting seabird on the island, with a pair found breeding close to the island's peak, i.e. more than 500 m above sea level (Fig. 5a). Within surveyed areas, the dispersion of skuas was decidedly irregular, with dense concentrations in some areas (e.g. the saddle between the western scarp and Moeder-en-kind, Albatross Valley and McCall Kop). In general, nests were concentrated in areas with large numbers of burrowing petrels and were sparse on mire areas (where burrowing petrels are scarce). A total of 210 pairs was counted, but this certainly underestimates the island's population, because their solitary breeding and broad habitat tolerance means that pairs are easy to overlook, and there was incomplete survey coverage. Probably about 20% of pairs were missed, so the total island population is estimated to be 250 pairs (Table I). Breeding was staggered, with some pairs still incubating eggs, while others had almost fully feathered chicks. There were also "clubs" of non-breeding and loafing skuas scattered around the island, usually near ponds or lakes (Fig. 5b). The seven main clubs supported some 400 skuas during the December 2001 survey.

Kelp gull *Larus dominicanus* nests were scattered sparsely around the island, either singly or in small groups. Of the total of 20 nests found, 19 were along the coast, on cliff ledges, offshore stacks, in sheltered caves or in open areas on the cliff tops (Fig. 5c). One pair nested well inland at the small pond adjacent to Hoedberg. All occupied nests contained eggs, and

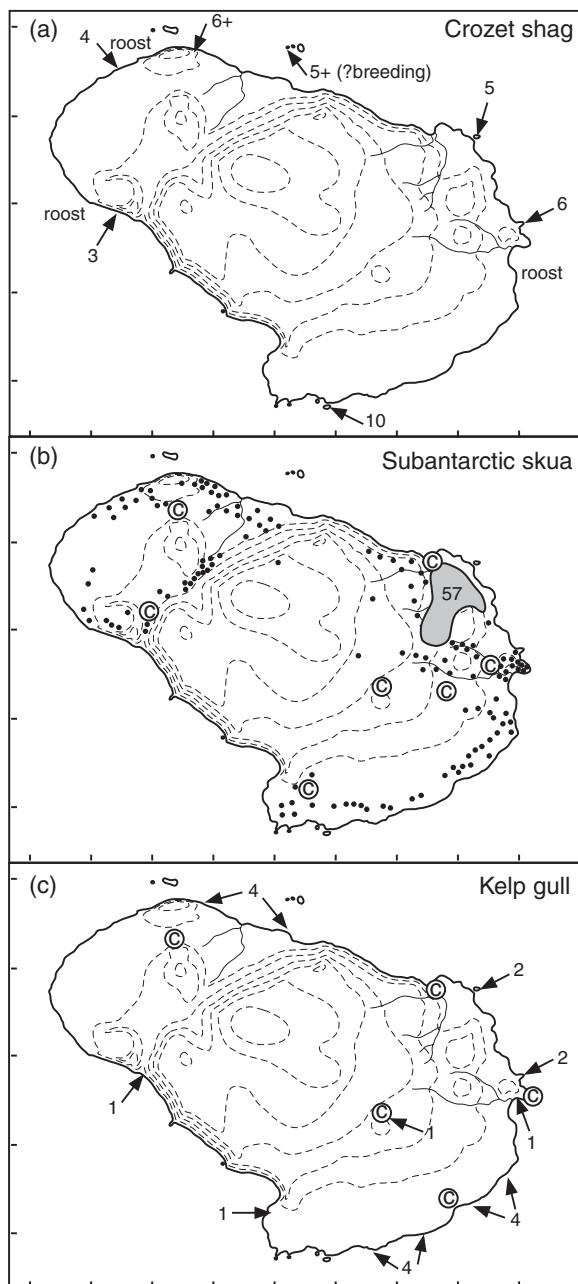


Fig. 5: Distribution of breeding pairs of (a) Crozet shags, (b) Subantarctic skuas and (c) kelp gulls at Prince Edward Island in December 2001. Location of roosts and clubs (C) of non-breeding birds are also shown

several empty nests were defended, suggesting that not all eggs had been laid yet, and others probably were overlooked. The overall breeding population was probably about 30 pairs (Table I). There were also five gull roosting "clubs" (Fig. 5c), containing some 150 birds. The largest club was at the pond north-west of Moeder-en-kind, with approximately 70 birds.

Only two pairs of Antarctic terns *Sterna vittata* were seen, in display flights over the sea west of Vaalkop. No evidence of breeding was found. Kerguelen terns *Sterna virgata* were observed along the east coast between Cave Bay and South Cape, where they were surprisingly scarce (cf. Ryan 1987). Only two pairs were found breeding: one pair had a medium-sized chick some 250 m inland in well-vegetated black lava north-east of South Cape, and another pair defended an empty scrape close to the coast between South Cape and Penguin Beach. By comparison, Kerguelen terns were highly visible along the north-east coast of Marion Island in December 2001, with several pairs feeding fledged young, and others still on eggs (pers. obs.).

DISCUSSION

In general, the present estimates of surface-nesting seabird populations are either similar to previous estimates, or there have been increases attributable in most cases to better coverage and extrapolation for breeding failures prior to the survey (Table I). The accuracy of the estimates is compromised both by count accuracy and by the necessity to correct for breeding failure prior to the survey. The error caused by extrapolation is potentially large and is related to the time between the start of breeding and the survey. It is most problematic for winter-breeding species such as gentoo penguins, but it is also significant for early-summer breeders that already had large chicks at the time of the survey, such as macaroni penguins, yellow-nosed albatrosses and northern giant petrels. Also inter-year variation in the proportion of adults breeding cannot be addressed, which may be considerable (especially for biennially breeding species). One difficulty with assessing trends in the distributions and abundance of seabirds at Prince Edward Island based on this survey is that most previous counts were poorly documented. It is often unclear whether any attempt was made to compensate for incomplete coverage or for failed breeding attempts (e.g. Williams *et al.* 1979, Berruti *et al.* 1981). However, some clear patterns emerged from the December 2001 survey.

King penguins still breed at the same three sites where they bred in the 1970s and 1980s (Grindley 1981, Watkins 1987). Although the estimate in 2001 is smaller than previous estimates, this difference is trivial given the considerable natural variation in breeding effort shown by this species (van Heezik *et al.* 1995). Gentoo penguins also still breed at the same general sites where they were recorded in 1984 (Adams and Wilson 1987), with the exception of Boggel, where no birds were seen in 2001. The estimated population is less than that for 1984, but given the uncertainty about the extrapolation for this winter-breeding species, it is not possible to draw any firm conclusions about trends at Prince Edward Island.

Numbers of macaroni penguins appear to have decreased considerably, with the estimate in 2001 roughly half the previous estimate (Table I). This is despite the discovery of several previously undocumented colonies, including the first colonies on the west coast. Until this survey, only three colonies were known from Prince Edward Island (Watkins 1987). Most of the decrease has taken place at the large colonies on the slopes of McCall Kop. Part of this decrease might be a consequence of the burgeoning fur seal population at the island (Bester *et al.* 2003). Macaroni penguins from the southern colony at McCall Kop used to land at the northern end of Cave Bay (pers. obs.), but this area has become overrun with fur seals, forcing the penguins to land on the more exposed ledges at RSA Point. Some colonies at Marion Island also have decreased (Cooper *et al.* 1997, Crawford *et al.* 2003a), so there may be system-wide factors causing the decrease.

The distribution of rockhopper penguin colonies is little changed, at least for the eastern part of the island (Grindley 1981). The population estimate in 2001 is slightly higher than the previous best estimate (Table I), although this may represent greater coverage in this survey, as well as bias introduced by counting loafing birds as breeders in colonies observed from a distance. The stable population at Prince Edward Island contrasts with a decreasing population at Marion Island (Cooper *et al.* 1997, Crawford *et al.* 2003b), suggesting that the decrease at Marion Island may be attributable to local effects there (e.g. human disturbance) rather than system-wide changes (e.g. in foraging conditions around the islands). This inference is consistent with the limited concordance in performance of rockhopper penguin colonies at Marion Island, and contrasts with the pattern for macaroni penguins (Cooper *et al.* 1997, Crawford *et al.* 2003a).

Among albatrosses, there is little evidence that long-line fishing mortality has caused appreciable population decreases. Indeed, population estimates for all species have increased (Table I). Whether this merely re-

flects a more complete survey is uncertain, but there is little evidence of recent decreases in the populations of wandering and grey-headed albatrosses such as observed at Marion Island (Nel *et al.* 2002b). The demipopulation of wandering albatrosses estimated during this survey brings Prince Edward Island on par with Marion Island as supporting the largest single-island populations of wandering albatrosses (*sensu stricto*; Tickell 2000). The estimate of light-mantled sooty albatrosses also has increased, but this almost certainly reflects better coverage during the present survey. Perhaps the most encouraging finding of the survey was that numbers of Indian yellow-nosed albatrosses are unchanged, despite their known mortality on both toothfish and tuna longlines. This species is listed as Vulnerable (BirdLife International 2000) and has decreased by roughly one-third over the past two decades at the species' main breeding site, Amsterdam Island, apparently as a result of longline mortality (Weimerskirch and Jouventin 1998). The present survey confirms the global importance of Prince Edward Island for this species.

Estimates of both giant petrel populations have increased. Although confidence in these figures is low because of the advanced stage of breeding at the time of the survey, it is still evident that the populations are larger than previously estimated. In the case of northern giant petrels, this may be as a result of better coverage, but for southern giant petrels it is likely that the population has actually increased, contrary to the global pattern (BirdLife International 2000). Interestingly, the increase at Prince Edward Island coincides with a dramatic decrease in numbers of southern giant petrels at neighbouring Marion Island. Since the mid-1990s, the Marion breeding population has fallen from around 3 000 to only 1 500 pairs (Cooper *et al.* 2001, Nel *et al.* 2002b). This decrease is unlikely to be due entirely to mortality. Emigration to Prince Edward Island, possibly as a result of increased disturbance on Marion Island associated with the cat-eradication programme (Nel *et al.* 2002b) may be a factor. During the survey, three birds banded as chicks on Marion Island and breeding at Prince Edward Island were found, indicating that at least some Marion birds recruit to Prince Edward Island. The birds were banded in 1985, 1989 and 1990, during the period of the cat-eradication programme, which ended successfully in 1991 (Bester *et al.* 2002).

Among other species, the estimate of the kelp gull population is roughly constant, whereas that of Subantarctic skuas is considerably higher than previous estimates (Table I), perhaps because of the better coverage and accurate mapping of nests. Skuas breed farther inland and at higher elevations at Prince

Edward Island than at Marion Island (Hunter 1990), presumably on account of the much greater abundance of burrowing petrels at Prince Edward Island. The other coastal species apparently have decreased in numbers. Populations of Crozet shags and Kerguelen terns, both localized endemics to the Kerguelen Province, have decreased to less than half the numbers counted in 1984 (Ryan and Hunter 1985, Ryan 1987). In the case of the tern, this corresponds with an increase in the population on Marion Island (Ryan 1987, Crawford *et al.* 2003c), and thus there may not be cause for concern. The apparent switch to Marion Island is surprising given the importance of terrestrial invertebrates in the diet of this species (Stahl and Weimerskirch 1981) and the adverse impact that introduced house mice *Mus musculus* have had on invertebrate populations on Marion Island (Huyser *et al.* 2000). The eradication of cats from Marion Island may have been a factor.

There is greater concern about the decrease in Crozet shag numbers at Prince Edward Island, because this mirrors a marked decrease in this species at Marion Island (Crawford *et al.* 2003d). The decrease at Prince Edward Island has included the loss of at least two breeding colonies. There was no sign of breeding at the site of the largest colony on the north-east coast in 1984 (Ryan and Hunter 1985), nor on the coast between South Cape and McNish Bay. There was also no evidence of breeding at two current roost sites: birds have bred on the cliffs west of Kent Crater (JC pers. obs.) and the colony on the coast south of Cave Bay was the second largest colony in 1984 (Ryan and Hunter 1985). The reason for the decrease in Crozet shag numbers are not known, but the fact that they have occurred at Prince Edward Island as well as Marion Island suggests that the changes are probably not the result of human disturbance, but more likely due to a change in the availability of their prey (Crawford *et al.* 2003d).

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An Indian yellow-nosed albatross with chick at Prince Edward Island (photo B. M. Dyer)

UNUSUAL BREEDING BY SEABIRDS AT MARION ISLAND DURING 1997/98

R. J. M. CRAWFORD*, C. M. DUNCOMBE RAE*, D. C. NEL† and J. COOPER‡

In 1997/98, breeding at subantarctic Marion Island was exceptionally good for five species of seabirds capable of foraging over wide areas and for a tern. The number of king penguin *Aptenodytes patagonicus* chicks surviving to the start of spring in 1997 was considerably more than previously recorded. Greater numbers of wandering *Diomedea exulans* and grey-headed *Thalassarche chrysostoma* albatrosses, northern giant petrels *Macronectes halli* and Kerguelen terns *Sterna virgata* bred than previously recorded, and more southern giant petrels *M. giganteus* did so than in any other year since 1994. For southern giant petrels, reproductive success was higher than in any other year, as was survival of chicks of northern giant petrels. Conversely, for two seabirds that feed close to the island, gentoo penguin *Pygoscelis papua* and Crozet shag *Phalacrocorax (atriceps) melanogenys*, 1997/98 was a particularly poor breeding season. Gentoo penguins initiated breeding later than usual and fledged few chicks. The number of Crozet shags that bred decreased; probably about 25% of the adult population did not breed. For two species with an intermediate foraging range that eat mainly crustaceans, macaroni *Eudyptes chrysolophus* and eastern rockhopper *E. chrysocome filholi* penguins, breeding was not noticeably different from normal except that chicks of rockhopper penguins fledged with a slightly heavier mass than in other years. However, for both these penguins, the mass of adults on arrival at colonies decreased substantially in the following (1998/99) breeding season. The unusual breeding by most of the seabirds coincided with the *El Niño* Southern Oscillation (ENSO) event of 1997/98. This synchrony contrasts with lagged responses to ENSO events of seabirds that breed farther south in the Southern Ocean. Continued monitoring of seabirds over well-separated sites in the Southern Ocean may elucidate how climatic perturbations operating at a global scale impact seabirds in the region.

Key words: albatrosses, breeding, Crozet shag, *El Niño*, giant petrels, Kerguelen tern, Marion Island, penguins, Subantarctic

Synchrony in the life-history parameters of different seabirds breeding at a particular locality has sometimes been observed. For example, at Adélie Land, Antarctica, in the 1976/77 breeding season, there was low breeding success followed by high mortality of adults for emperor *Aptenodytes forsteri* and Adélie *Pygoscelis adeliae* penguins, snow petrels *Pagodroma nivea* and southern or Antarctic fulmars *Fulmarus glacialisoides* (Chastel *et al.* 1993, Croxall 1992). At Prydz Bay, Antarctica, there were similar trends in breeding success for Adélie penguins, Antarctic petrels *Thalassoica antarctica* and southern fulmars during the seasons 1983/84–1987/88 (Whitehead *et al.* 1990). Concordant fluctuations in the abundance of seabirds has also been noted, e.g. off central and southern California between 1986 and 1994 (Ainley *et al.* 1995).

Aspects of the biology of several species of seabirds have been monitored at subantarctic Marion Island in the southern Indian Ocean for varying periods of time (Cooper *et al.* 1997, 2001, Nel *et al.* 2002). For most monitored species, there was an unusual aspect to breeding during 1997/98 in that parameters measured were either abnormally high or low, suggesting that

the environment influenced breeding. This paper collates information on breeding in that season to demonstrate its unusual nature and notes its association with the *El Niño* Southern Oscillation (ENSO) event of the same period.

MATERIAL AND METHODS

Information on breeding by 10 seabirds at Marion Island (290 km²; 46°52'S, 37°51'E) was collated from the literature as follows: king penguin *A. patagonicus* 1987–2002 (van Heezik *et al.* 1995, Crawford *et al.* 2003c); gentoo penguin *Pygoscelis papua* 1994/95–2002/03 (Crawford *et al.* 2003d); macaroni penguin *Eudyptes chrysolophus* 1979/80–2002/03 (Cooper *et al.* 1997, Crawford *et al.* 2003a), eastern rockhopper penguin *E. chrysocome filholi* 1983/84–2002/03 (Cooper *et al.* 1997, Crawford *et al.* 2003b); wandering albatross *Diomedea exulans* 1981/82–2002/03, grey-headed albatross *Thalassarche chrysostoma* 1984/85–2002/03 (Nel *et al.* 2002, Crawford *et al.* 2003c),

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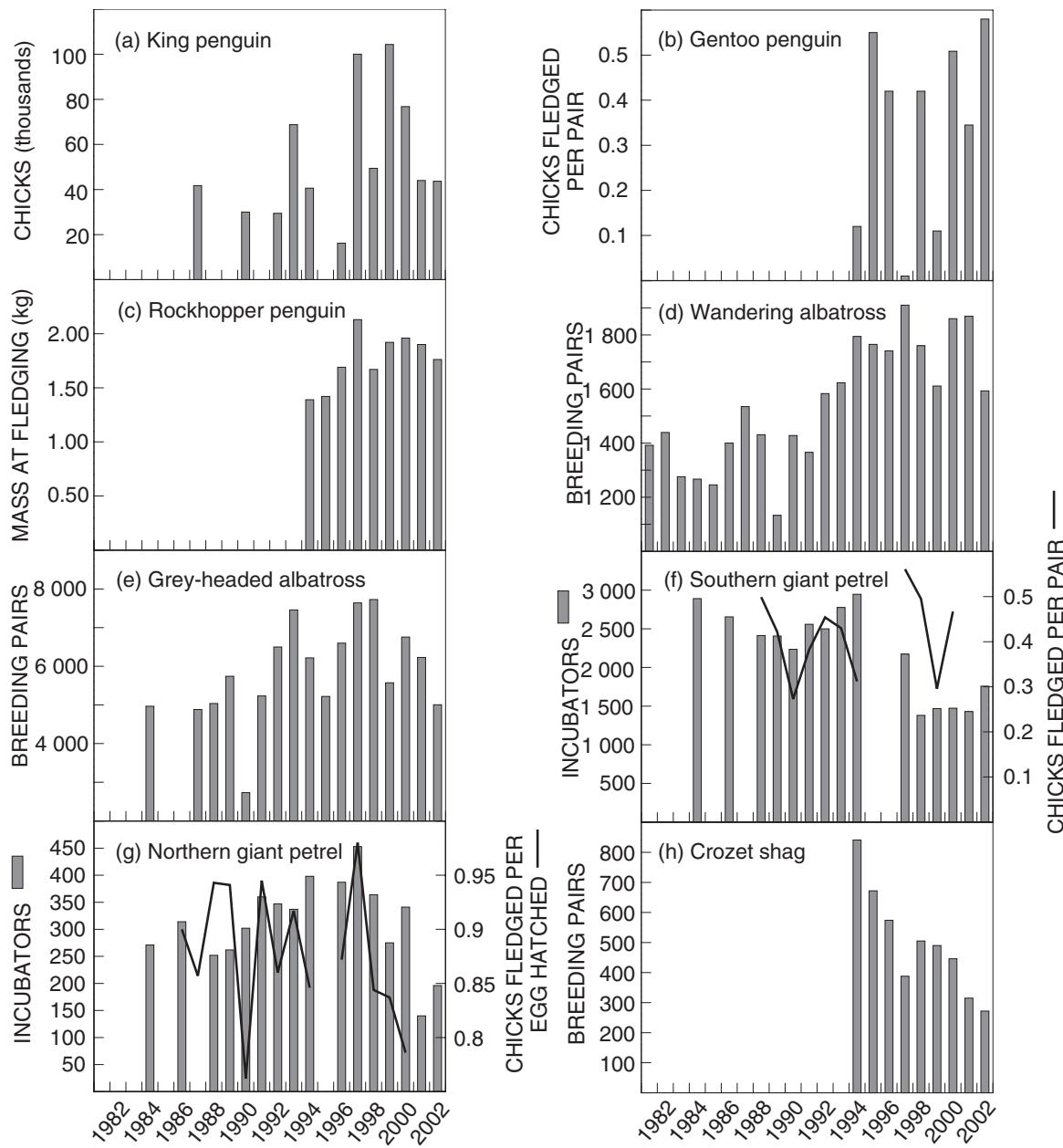


Fig. 1: Trends in selected reproductive parameters measured for some seabirds at Marion Island, 1981–2002. For summer-breeding species, the year indicated refers to the year in which the austral summer began: (a) estimated number of king penguin chicks at the commencement of spring; (b) reproductive success of gentoo penguin; (c) mass at fledging of rockhopper penguin chicks; (d) number of pairs of wandering albatross breeding; (e) number of pairs of grey-headed albatross breeding; (f) number of pairs breeding and number of chicks fledged per pair for southern giant petrel; (g) number of pairs breeding and number of chicks fledged per egg that hatched for northern giant petrel; (h) number of pairs of Crozet shags breeding. Gaps indicate an absence of data. Information for (a) from van Heezik *et al.* (1995) and Crawford *et al.* (2003c); (b) from Crawford *et al.* (2003d); (c) Crawford *et al.* (2003b); (d) and (e) Nel *et al.* (2002) and Crawford *et al.* (2003c); (f) and (g) Cooper *et al.* (2001) and Crawford *et al.* (2003c); (h) Crawford *et al.* (2003e)

southern giant petrel *Macronectes giganteus* 1984/85–2002/03, northern giant petrel *M. halli* 1984/85–2002/03 (Cooper *et al.* 2001, Crawford *et al.* 2003c), Crozet shag *Phalacrocorax [atriceps] melanogenis* 1994/95–2002/03 (Crawford *et al.* 2003e) and Kerguelen tern *Sterna virgata* 1996/97–2002/03 (Crawford *et al.* 2003c).

In order to investigate the state of the environment at Marion Island, monthly average maximum and minimum air temperatures for each year from 1994 to 2001 taken from the meteorological station at Transvaal Cove were obtained from the South African Weather Service. The values for the months June–October were compared with long-term climatic means for the period 1961–1990 to provide a deviation from the means. Sea surface temperature (SST) anomalies for the south-west Indian Ocean were reviewed for the period April–October 1997. These images were obtained from the NOAA/NESDIS website (http://www.osdpd.noaa.gov/PSB/EPS/SST/al_climo.html) and represent anomalies from satellite-derived information at 36-km resolution. There have been long-term increases in both the annual mean surface air and sea temperatures at Marion Island (Smith 2002, Mélice *et al.* in press b).

RESULTS

Breeding of seabirds

In 1997, an estimated 100 000 king penguin chicks survived the winter at Marion Island, more than in any other year for which there is information for all colonies, except 1999 (104 000, Fig. 1a). The mean for 12 years with complete information for all colonies (1987, 1990, 1992–1994, 1996–2002) was 50 000 (SD 31 000, Crawford *et al.* 2003c).

In 1997, the first egg of gentoo penguins was laid on 20 July, 95% of nests had eggs by 3 August and the last egg was laid on 13 August. For other years from 1994 to 2001, these dates ranged from 1 June–11 July, 14 June–25 July and 18 June–1 August respectively. Therefore, laying was at least nine days later in 1997/98 than in any other season for which information exists for Marion Island. Breeding pairs fledged an average of just 0.01 chicks from first clutches laid in 1997/98, compared with 0.11–0.58 during other seasons (Fig. 1b). In 1997/98, Subantarctic skuas *Catharacta antarctica* returned to Marion Island at the end of August and inflicted substantial mortality on the eggs and small chicks of gentoo penguins (Crawford *et al.* 2003d).

For macaroni penguins, no parameter investigated was noticeably different from normal. For rockhopper penguins there were no obvious differences in the

number of birds breeding or in breeding success at monitored colonies during 1997/98 (Crawford *et al.* 2003b). However, the mass of chicks at fledging was slightly higher in that season than in any other during the period when measurements were made (Fig. 1c).

Numbers of wandering albatrosses breeding at Marion Island peaked in 1997/98 (Fig. 1d). Numbers of grey-headed albatrosses breeding attained their highest values in 1997/98 and 1998/99 (Fig. 1e, Nel *et al.* 2002).

The count of incubating southern giant petrels in 1997 (2 173) was 48% higher than in any other year between 1996 and 2002. There was no count in 1995, but counts for all years between 1984 and 1994 were higher than in 1997. Overall breeding success was higher in 1997/98 than in any other split year in which it was measured (Fig. 1f, Cooper *et al.* 2001). The count of incubating northern giant petrels was higher in 1997 than in any other year. The overall breeding success was not measured in 1997/98, but survival of chicks in a long-term study was higher in 1997/98 than in any other split year (Fig. 1g, Cooper *et al.* 2001).

In 1997, 388 pairs of Crozet shags bred at Marion Island. This was the lowest number recorded until 2001 (Fig. 1h). It was 100–150 pairs fewer than the number breeding in 1996 and 1998, suggesting that about 25% of the adult population may not have bred in 1997 (Crawford *et al.* 2003e).

In 1997/98, 56 pairs of Kerguelen terns were reported breeding at Marion Island, more than double the maximum for other seasons between 1996/97 and 2002/03 and more than any previous estimate of numbers breeding at the island (Crawford *et al.* 2003c).

Environmental conditions

The mean maximum air temperature at Marion Island during the months June–October 1997 was 1.2°C above the average for the years 1961–1990. In the same period the minimum temperature was about 1°C above average. Temperatures during the months June–October were similarly high in 1996 and 1999, whereas 1998 was only 0.5°C above the 30-year average (Fig. 2).

The satellite-derived SST showed positive anomalies around Marion Island from April to September 1997. SST anomalies for June are shown in Figure 3a. Warm water west of tropical America showed well-developed *El Niño* conditions. By October 1997, anomalously warm water in the south-western Indian Ocean was restricted to the region north of Marion Island (Fig. 3b). At the island the SST was close to the long-term average. South of the island, it was considerably colder than the climatology. *El Niño* conditions in the western Pacific had intensified.

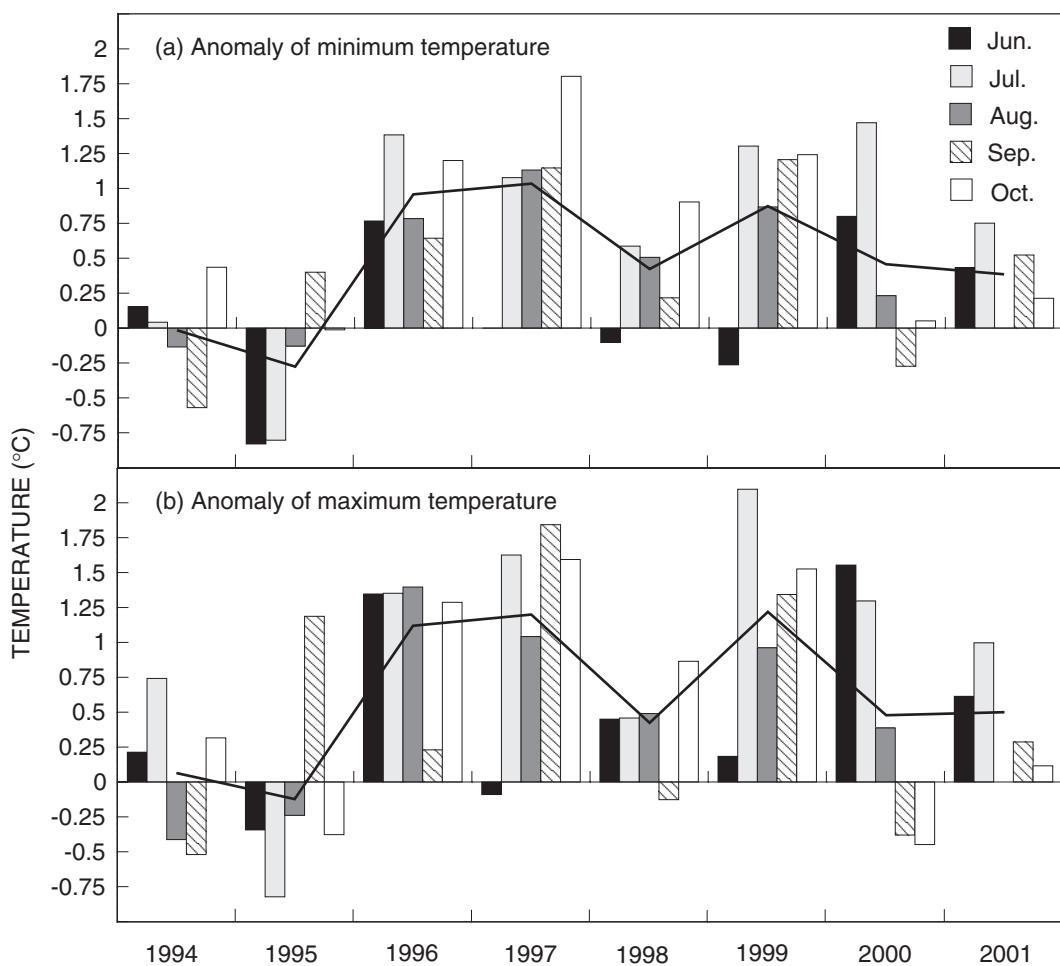


Fig. 2: The anomaly for (a) minimum and (b) maximum surface air temperatures at Marion Island for June–October for each year during the period 1994–2001. The climatic monthly mean temperature used is for the period 1961–1990. The line shows the average anomaly for the months June–October. Information was provided by the Weather Office at Marion Island

DISCUSSION

Information presented in this paper is only that which suggests that some aspect of breeding at Marion Island by the seabirds concerned was unusual in 1997/98. Not all parameters measured for the 10 species considered were necessarily unusual and none was for the macaroni penguin.

For some species, breeding in 1997/98 appears to have been exceptionally good. The number of king penguin chicks surviving to the start of spring in 1997 was considerably more than previously recorded.

Greater numbers of wandering and grey-headed albatrosses, northern giant petrels and Kerguelen terns bred in 1997/98 than previously, and more southern giant petrels did so than in any other year since 1994. For southern giant petrels, reproductive success was higher in 1997/98 than in any other year, as was survival of chicks of northern giant petrels. Chicks of rock-hopper penguins fledged with a slightly heavier mass than in other years. Conversely, for gentoo penguins and Crozet shags, 1997/98 was a particularly poor breeding season. Gentoo penguins initiated breeding later than usual (Williams 1980b) and fledged few chicks. The number of Crozet shags that bred decreased; probably

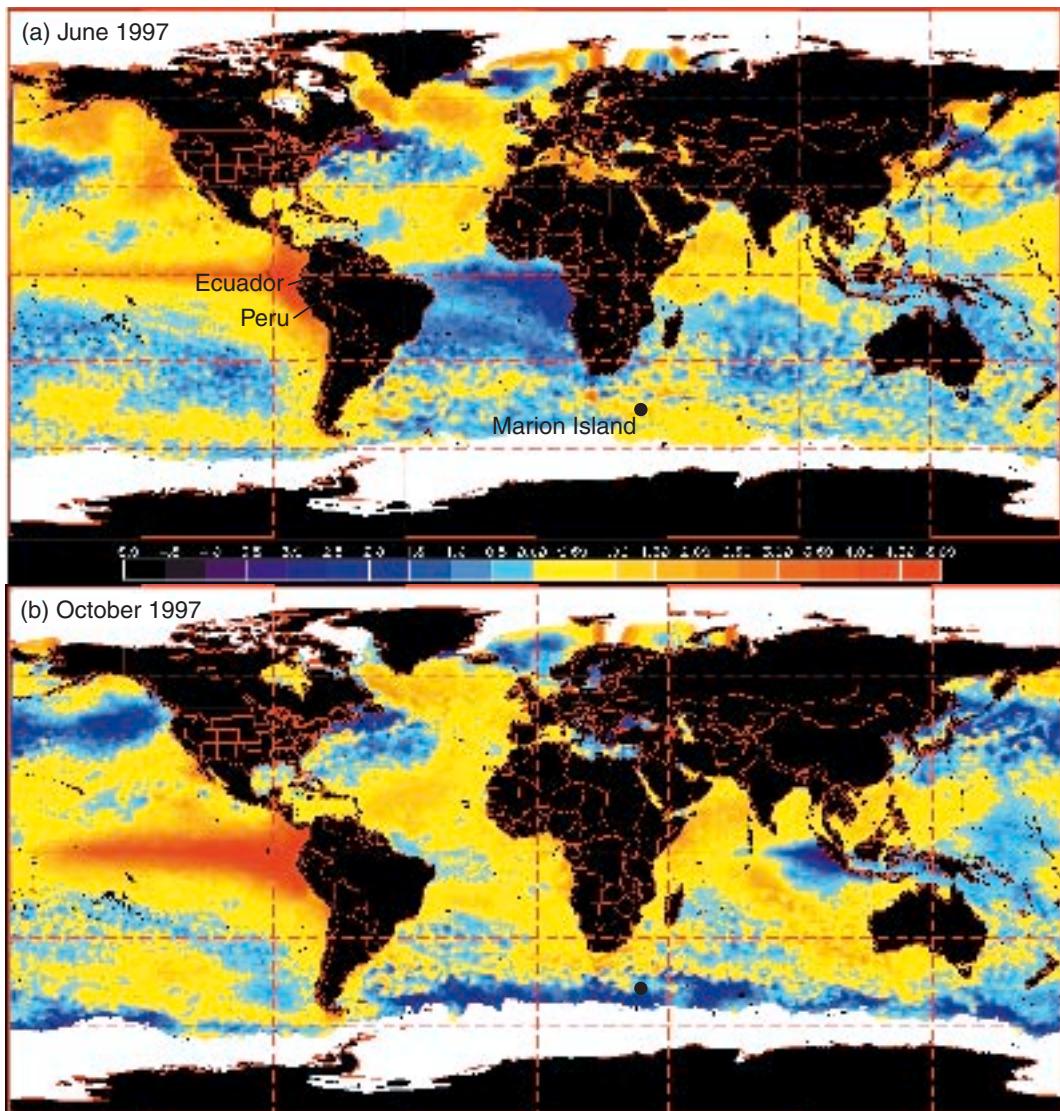


Fig. 3: SST anomalies in the world's oceans in (a) June and (b) October 1997 indicating the location of Marion Island. In June 1997, anomalously warm SST was clearly apparent off the coasts of Peru and Ecuador (*El Niño* conditions). Less marked warm anomalies were also apparent in the south-west Indian Ocean in the vicinity of Marion Island. In October 1997, the *El Niño* conditions had intensified, but the warm anomaly around Marion Island had moderated. The area south of the islands showed anomalously cold conditions. Source: http://www.osdpd.noaa.gov/PSB/EPS/SST/al_climo.html

about 25% of the adult population did not breed.

In 1997, the period July–October was characterized by warmer ambient temperatures than in most other recent years (Fig. 2), perhaps as a result of the anomalously warm SST around the island (Fig. 3a). Similarly

in 1999, the period July–October had higher maximum ambient temperatures than other recent years (Fig. 2). The milder climates in 1997 and 1999 may have increased survival of king penguin chicks in the later part of winter. It is estimated that more than 100 000

chicks survived to the start of spring in both these years (Fig. 1a). However, the number of chicks surviving until spring reflects not only survival through winter but survival of eggs and chicks during the early portion of the breeding season as well as the number of pairs breeding in a particular season. At Marion Island, king penguins commence laying from mid November (Cooper and Brown 1990) and there is marked interannual variation in the number of breeding birds (van Heezen *et al.* 1995).

Similar to 1997/98, gentoo penguins also bred relatively late (95% of nests had eggs by 24 July) and had a low breeding success in 1999/00 (Fig. 1b, Crawford *et al.* 2003d). It is uncertain how the warmer climate in these years may have influenced the later than usual start to breeding, if it did. It is possible that the availability of prey organisms around Marion Island was affected. Gentoo penguins feed near the island when breeding. In 1984, the mean foraging range from colonies was 14 km and the maximum 103 km (Adams and Wilson 1987). Inshore fish, especially nototheniids, form a large proportion of their diet during the breeding season (La Cock *et al.* 1984, Adams and Klages 1989). A late start to breeding by gentoo penguins renders their eggs and small chicks susceptible to heavy predation by Subantarctic skuas, most of which return to the island in late August and September (Williams 1980a).

The other seabird with a low breeding effort at Marion Island in 1997/98, the Crozet shag, is also a diving seabird that forages inshore (Cooper 1985). At Marion Island, where it feeds largely on nototheniid fish, there is considerable overlap between its diet and that of the gentoo penguin (Espitalier-Noel *et al.* 1988).

SST anomalies at Marion Island at the close of 1997 and the start of 1998 were higher than any previously recorded (Mélice *et al.* in press a), and may have influenced the unusual nature of breeding by most of the seabirds in the 1997/98 season.

Rockhopper penguins forage 4–157 km (mean 33 km) from Marion Island when breeding, macaroni penguins 59–303 km (mean 178 km, Brown 1987). Both species prey extensively on crustaceans, there being incomplete dietary segregation (Brown and Klages 1987). Breeding by these penguins was normal in 1997/98, except that fledgling rockhopper penguins were slightly heavier than usual (Fig. 1c). However, masses of both macaroni and rockhopper penguins on arrival at colonies showed a marked decrease in 1998/99, suggesting a reduced availability of food for these species in winter and early spring 1998. Also, breeding success of rockhopper penguins decreased substantially in 1998/99 (Crawford *et al.* 2003a, b). Macaroni and rockhopper penguins return to Marion

Island to breed in late spring between 3 October and 20 November (Crawford *et al.* 2003a, b).

Five of the seabirds that experienced good breeding at Marion Island in 1997/98 (king penguin, both albatrosses, both giant petrels) all have wide foraging ranges (Marchant and Higgins 1990, Weimerskirsch *et al.* 1997). The giant petrels are also predators and scavengers at Marion Island (Hunter and Brooke 1992). When breeding, king penguins at Marion Island have a mean foraging range of 300 km (maximum 900 km, Adams 1987). Grey-headed albatrosses have a mean range of 2 182 km (maximum 4 060 km) when incubating and 722 km (maximum 1 812 km) during early chick-rearing (Nel *et al.* 2000). Their foraging is associated with oceanographic features, including eddies, north of Marion Island when incubating and southwest of the island when feeding chicks. The distance of these features from Marion Island may change with time (Nel *et al.* 2001).

The sixth seabird to experience good breeding at Marion Island in 1997/98, the Kerguelan tern, feeds mainly within 200 m of the island in surface waters and to a limited extent near lakes on the island (Ryan 1987).

All seabirds are not necessarily affected by environmental conditions in the same way but, if food availability influences breeding, species with similar feeding regimes are most likely to be influenced similarly. For example, at South Georgia in years of low availability of Antarctic krill *Euphausia superba*, the reproductive performance of birds that feed on krill (gentoo penguin, macaroni penguin, black-browed albatross *Thalassarche melanophrys*) was reduced, whereas that of birds feeding on fish and squid (wandering albatross, grey-headed albatross) was unaffected (Croxall *et al.* 1988). By contrast, for two penguin species at King George Island, South Shetland Islands, with different winter foraging grounds, the trends in the number of birds breeding were inversely related (Trivelpiece *et al.* 1990).

Of 15 correlations between breeding success and indices of weather for five seabirds at Marion Island, only one was significant at the 5% level (similar to the one in 20 at this level, for which significance might be expected by chance), leading to the conclusion that breeding success was probably more influenced by food availability than meteorological conditions (Cooper and Lutjeharms 1992). In 1997/98, inshore feeders experienced poor breeding, whereas species that were able to forage far from the island bred in large numbers and, when measured, breeding was successful.

There was a strong and unusual ENSO event during 1997/98 that began in April 1997 and attained its first peak in July/August of that year (Wolter and Timlin 1998). Although there were positive SST anomalies in

the eastern central Pacific and around Marion Island from April to September 1997 (http://www.osdpd.noaa.gov/PSB/EPS/SST/al_climo.html), this does not necessarily indicate that the warm sea and air temperatures at Marion Island in winter and spring 1997 resulted from the ENSO event. However, anomalous oceanographic events in well-separated parts of the world's oceans are often synchronous (e.g. Crawford *et al.* 1995), as are regimes of fish populations (e.g. Schwartzlose *et al.* 1999). Similarly, ENSO events have a wide-scale influence on seabirds. Their impact on seabirds off western South America has been well documented. Numbers of one or more of Humboldt penguin *Spheniscus humboldti*, guanay cormorant *Phalacrocorax bougainvillii*, Peruvian booby *Sula variegata* and Peruvian pelican *Pelecanus thagus* decreased as a result of mortality and reduced breeding following ENSO events in 1953, 1957/58, 1965, 1972 and 1982/83 (Jordán 1964, Jordán and Fuentes 1966, Tovar 1983, Hays 1986, Tovar *et al.* 1987, Ainley *et al.* 1988, Crawford and Jahncke 1999). The foraging behaviour of penguins (Culik *et al.* 2000) and boobies *Sula* spp. (Jahncke and Goya 2000) was altered.

ENSO events have influenced seabirds in more tropical parts of the Pacific Ocean, for example the Galapagos penguin *Spheniscus mendiculus* (Boersma 1978, 1998), flightless cormorant *Nannopterum harrisi* (Harris 1979), dark-rumped petrel *Pterodroma phaeopygia* (Cruz and Cruz 1990), red-tailed tropic bird *Phaethon rubricauda* (Schreiber 1994) and black-footed albatross *Phoebastria nigripes* (Ludwig *et al.* 2000). The 1982/83 event influenced seabirds throughout the western Pacific Basin as far north as Alaska (Graybill and Hodder 1985, Ainley *et al.* 1988, Massey *et al.* 1992).

Several studies of seabirds and seals in the Southern Ocean have suggested the possibility that ENSO events may affect their breeding success or survival. Poor breeding success of snow petrels in Adélie Land in 1966/67, 1976/77 and 1983/84 followed the ENSO events of 1965, 1976 and 1982/83 (Chastel *et al.* 1993). Two years of low availability of Antarctic krill to predators at South Georgia (1977/78, 1983/84) each occurred one year after a major ENSO event (Croxall *et al.* 1988). Large-scale oceanographic processes such as ENSO and the Antarctic Circumpolar Wave (ACW) may be responsible for periodic decreases in the availability of food to Weddell seals *Leptonychotes weddelli* and other top predators in the Southern Ocean (Hastings *et al.* 1999). Annual variability in numbers of wandering albatrosses and northern giant petrels breeding at Marion Island was positively correlated with the annual maximum ENSO index (Nel *et al.* 2002).

During the 1982/83 ENSO event, seabirds off Cali-

fornia responded to an apparently altered foodweb well before the physical environment there had changed enough to be noted by oceanographers. Conversely, altered breeding success of the black-legged kittiwake *Rissa tridactyla* in Alaska lagged changes for seabirds farther south (that were influenced by the Pacific gyres) by about one year (Ainley *et al.* 1988). Synchronous biological responses to environmental change over well-separated geographical areas are likely to be mediated via the Earth's atmosphere, whereas lagged responses may be mediated through the oceans (Crawford *et al.* 1991).

The anomalous breeding by seabirds at Marion Island (47°S) in 1997/98 coincided with the ENSO event of that period. Warm SST south of the Kerguelen Islands (49°S) occur within a year of ENSO events (Guinet *et al.* 1998). Farther south, at South Georgia (54°S) and Adélie Land (66°S), responses by seabirds have lagged ENSO events by about one year (Croxall 1992, Chastel *et al.* 1993), although at King George Island breeding success of both Adélie and chinstrap penguins *Pygoscelis antarctica* was significantly reduced during the ENSO event of 1982/83 (Trivelpiece *et al.* 1990). To the north, indices of seabird abundance in the Benguela (25–35°S) and Humboldt systems (the latter directly impacted by ENSO events) two years later were significantly negatively related before the initiation of purse-seine fisheries that influenced the food supply for birds in both systems (Crawford and Jahncke 1999). There was an irruption of Southern Ocean seabirds along the South African coast in 1984, one year after the 1982/83 ENSO event (Ryan *et al.* 1989).

Monitoring of seabirds over widespread areas in the Southern Ocean under the auspices of the Ecosystem Monitoring Program of the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) has the potential to elucidate further how climatic perturbations operating at a global scale may impact seabirds and seals in the region (Guinet *et al.* 1994). This should facilitate differentiation between changes in predator populations that are caused by the commercial exploitation of prey species, such as Antarctic krill, and those that result from environmental variability.

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In 1997/98 there was unusually good breeding at Marion Island by (clockwise from top) king penguins (photo B. M. Dyer), grey-headed albatrosses, northern giant petrels and southern giant petrels (photos R. J. M. Crawford)

POPULATION AND BREEDING OF THE GENTOO PENGUIN *PYGOSCELIS PAPUA* AT MARION ISLAND, 1994/95–2002/03

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The numbers of gentoo penguins *Pygoscelis papua* breeding at subantarctic Marion Island fell by 40% from 1994/95 to 2002/03, from 1 352 pairs to 806 pairs. Apart from a slight increase in 1998/99, there was a steady decrease in numbers breeding between 1995/96 and 2000/01, when the population stabilized. There is indication that in some years not all breeders nested and that some birds relocated to another colony after disturbance. From first clutches, pairs on average fledged between 0.01 chicks in 1997/98 and 0.58 chicks in 2002/03 (mean 0.38 ± 0.21). In 1994/95, replacement clutches increased the overall production of fledged chicks by 11%. Based on demographic parameters measured at other localities, the production of chicks at Marion Island was inadequate to maintain the population during the period 1995/96–2000/01. Consistency in trends in breeding success at five colonies suggests that factors operating at a mesoscale, rather than those specific to particular colonies, often influenced breeding success. Laying was later than normal in 1997/98, when there was almost total breeding failure with large losses of eggs and small chicks to returning Subantarctic skuas *Catharacta antarctica*. Future research on this Near Threatened species at Marion Island must take full account of its susceptibility to human disturbance.

Key words: breeding success, gentoo penguin, Marion Island, population trend, *Pygoscelis papua*, Subantarctic

The gentoo penguin *Pygoscelis papua* is one of four species of penguin that breeds at the Prince Edward Islands, including Marion Island, in the southern Indian Ocean. It has a circum polar distribution, breeding between 46 and 66°S at subantarctic islands and on the Antarctic Peninsula (Marchant and Higgins 1990). The world population is of the order of 317 000 pairs (Ellis *et al.* 1998). The Crozet and Prince Edward islands are the northernmost breeding localities for the species (Woehler 1993). Gentoo penguins breed in several distinct colonies at Marion Island, most colonies being located in the eastern portion of the island (Adams and Wilson 1987, Fig. 1).

From 1994/95–2002/03, counts were undertaken of the numbers of gentoo penguins breeding at Marion Island to assess trends in the population there, as part of South Africa's contribution to the CCAMLR Ecosystem Monitoring Program (CEMP) of the Commission for the Conservation of Antarctic Marine Living Resources (SC-CAMLR 1995). The species is regarded as Near Threatened in South Africa (Barnes 2000) and internationally (BirdLife International 2000). Also from 1994/95 to 2002/03, breeding success was measured at five colonies and information was obtained on the timing of breeding and on the mass of chicks at

fledging, following CEMP protocols. This paper reports results and considers factors that may have influenced trends in the population.

MATERIAL AND METHODS

Population

Counts of active nests and of unoccupied, recently constructed nests of gentoo penguins were undertaken at least once during July and August in every year between 1994/95 and 2002/03 for each colony at Marion Island (290 km²; 46°52'S, 37°51'E). Egg laying at Marion Island commences in June, with most first clutches initiated in July (Williams 1980a). Active nests were defined as those with either an adult or a chick present. In years when more than one count was undertaken in July and August, the highest count obtained at a colony was used as an estimate of the breeding population at that colony. This makes the assumption that birds did not nest at more than one colony in July and August of the same year.

During the period 1995/96–2000/01 at each of five

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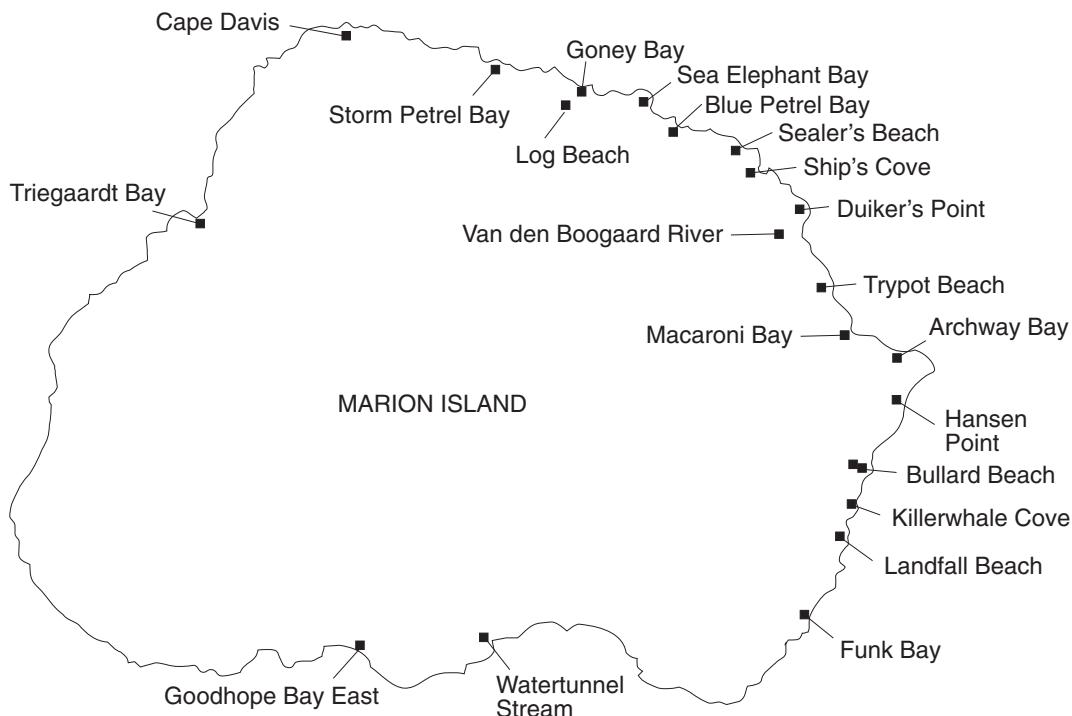


Fig. 1: The locations of breeding colonies of gentoo penguins at Marion Island, 1994/95–2002/03

colonies, the numbers of occupied nests were counted three times on the same day in order to estimate the error of counts. The relationship between the standard deviation (SD) of counts and size of the colonies counted was established, and used to calculate the coefficient of variation (CV) on counts of the overall breeding population of gentoo penguins at Marion Island.

Counts of nests during surveys were undertaken at any time of the day. The influence of this on the count of active nests was investigated by conducting counts at 08:00, 10:00, 12:00, 14:00 and 16:00 at the Van den Boogaard River colony on 15 July 1994 and at the Trypot Beach colony on 15 July 1995, 30 July 1996, 3 July 1998, 25 July 1998 and 16 July 1999.

Breeding

In all years between 1994/95 and 2002/03, the mean number of chicks fledged per breeding pair was estimated for the colonies at Trypot Beach, Macaroni Bay, Archway Bay, Hansen Point and Duiker's Point (Fig. 1), except at Duiker's Point in 1995/96. The number of

active nests at these colonies varied between 9 and 197. Colonies were visited every two weeks between 1 July and 15 September, and then weekly until 15 October. The numbers of active nests and of chicks in crèches were counted three times on most visits, and the means obtained. The maximum average number of active nests recorded on a single visit to a colony in a particular year was assumed to represent the number of breeding pairs at that colony, and the maximum average number of crèched chicks to represent the number of chicks that fledged from the colony, after subtraction of the number of crèched chicks known to have died.

Gentoos may replace lost clutches 66 days later (Williams 1980a, Marchant and Higgins 1990). Replacement clutches were not taken into account in determining chick production per breeding pair, but were monitored at Trypot Beach in 1994/95.

From 1994/95 to 2001/02, the breeding chronology of gentoo penguins was studied by monitoring the progress of up to 50 nests at Trypot Beach, using CEMP protocols (SC-CAMLR 1995). The positions of nests within colonies were mapped, so that the progress of individual nests could be followed. In

2002/03, only the dates at which chicks entered crèches were recorded.

Trypot Beach was visited daily from 1 June until 50 nests had eggs or, if fewer than 50 pairs bred, all breeders had eggs. In this period, the arrival of adults at the colony was monitored in all years except 1994/95, 2000/01 and 2002/03. As adults were not banded, the number arriving on a given day was taken to be the difference between the numbers seen at the colony on that day and on the previous day. Because some birds may depart for sea, this may have underestimated numbers returning in the early stages of site establishment. At Marion Island, gentoo penguins moult in January and early February and by March and April have returned to breeding areas (Rand 1954). In some years, they are later absent again from breeding areas for only a few days, so that the dates of their return to colonies to breed are not well defined.

Once all breeders, or those at 50 nests, had eggs, nests were examined at two-day intervals until 48 days after the first egg was judged to have been laid, and then again on a daily basis until chicks had entered a crèche. Birds at Marion Island have a maximum clutch of two eggs (Williams 1980a). Eggs are laid at intervals of 3–5 days – a mean of 3.4 days was reported for Marion Island (Van Zinderen Bakker 1971) – and incubated for a period of 35–36 days (Marchant and Higgins 1990). The day when each of the chicks was first seen was recorded, as well as dates when chicks entered crèches (except in 2001).

In 1994/95, all nests were checked on each visit and the numbers of adults, eggs and chicks present at each nest were recorded, as well as the numbers of chicks in crèches. However, the checking of individual nests caused considerable disturbance (see also Williams 1980a). Therefore, from 1995/96, nests were examined from a distance using binoculars. Prone adults were assumed to be incubating, although some may have been brooding small chicks, so that from 1995/96 to 2001/02 hatching may have taken place earlier than indicated.

Dates when chicks fledged were gauged from decreases in the numbers of chicks in crèches, after accounting for any observed mortality of crèched chicks. Mortality of chicks from the start of the crèche stage to fledging at Marion Island ranges from 5% (van Zinderen Bakker 1971) to 28% (Williams 1980a). Chicks were not banded, and once they reached the crèche stage it was not always possible to distinguish those that originated from study nests from those hatched at other nests at Trypot Beach. The date when the first chick fledged was determined for three years, but the date when the last chick fledged only in 1994/95. The chronology of clutches that were assumed to be replacements (parents were not banded) was monitored

at Trypot Beach in 1994/95.

For each of the 1994/95–2002/03 breeding seasons, the mass at fledging of between 7 and 88 chicks (366 in total) was obtained. Weighing was undertaken from mid November onwards, after chicks had moved away from their nest sites towards the beach (SC-CAMLR 1995). In 1994/95, chicks weighed included those produced by replacement clutches.

RESULTS

Population

The time of day had little influence on the count of the number of active nests of gentoo penguins. At the Van den Boogaard River colony on 15 July 1994, five counts undertaken two-hourly between 08:00 and 16:00 varied between 33 and 35 active nests. At the Trypot colony, five counts conducted at these times on 15 July 1995 all gave 96 active nests. On 30 July 1996, counts varied between 68 and 72 active nests; on 3 July 1998 between 34 and 36 active nests; on 25 July 1998 between 69 and 71 active nests; and on 16 July 1999 between 37 and 39 active nests. When there was variation in the counts, maxima were obtained at any time between 08:00 and 16:00. Therefore, counts undertaken on surveys were not modified to account for the time of day when they were conducted.

During the period 1995/96–2000/01, CVs for counts at five colonies, where the mean number of occupied nests varied between 9 and 162, ranged from 0.0 to 3.2%. The SD of counts was significantly related to the size of colonies ($SD = 0.010 \times \text{colony size}$, $n = 23$, $r = 0.607$, $p < 0.005$). This resulted in a CV of about 1% for the counts of the overall breeding population in all years.

The number of gentoo penguin pairs breeding at Marion Island was about 1 350 in 1994/95, and 1995/96, then decreased by 40% to about 800 in 2000/01 and 2002/03 (Fig. 2). Between 1994/95 and 2002/03, numbers decreased at all colonies, except at Goodhope Bay (east) and Triegaardt Bay, on the western part of the island, and Goney Bay on the north coast (Fig. 1). The colony at Van den Boogaard River numbered 35 pairs in 1994/95, but was not subsequently used by gentoo penguins (Table I). In 2001/02, a new colony of 24 pairs formed at Log Beach, near Goney Bay. This colony increased to 49 pairs in 2002/03. At Goney Bay, there were 42–64 pairs from 1994/95 to 2002/03, just two pairs in 2001/02, but 75 pairs in 2002/03. At Triegaardt Bay, two pairs bred in 1994/95, none in 1995/96 and 7–11 pairs from 1996/97 to 2002/03. Numbers counted at Goodhope Bay East fluctuated be-

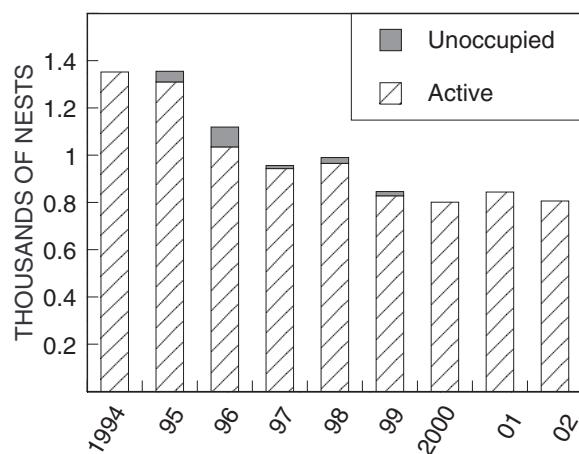


Fig. 2: Trends in the overall numbers of breeding pairs and of active nests counted at Marion Island between 1994/95 and 2002/03

tween seven and 17 pairs between 1994/95 and 2002/03.

There were sometimes large fluctuations in the number of pairs recorded breeding at other colonies.

For example, at Bullard Beach there were 161 pairs in 1996/97, 114 in 1997/98 and 176 in 1998/99.

Breeding

For all colonies combined, the mean numbers of chicks fledged per pair from first clutches laid in a breeding season varied from 0.01 in 1997/98 to 0.58 in 2002/03 (Table II). When equal weight was given to each year's value, the overall mean number of chicks per pair fledged from first clutches was 0.38 ($SD = 0.21$, $n = 9$). From 1995/96 to 2001/02, pairs fledged on average 0.30 chicks per pair.

In 1994/95 at Trypot Beach, 16 replacement clutches produced a total of three fledged chicks. The 115 pairs at this colony raised 26 chicks to fledging from their initial clutches. Replacement laying resulted in the number of chicks fledged per breeding pair increasing by 11%, to 0.25 chicks per pair.

Trends in breeding success were often similar at the five intensively studied colonies (Fig. 3), with relatively poor breeding (<0.25 chicks per pair) at all colonies in 1994/95 (except Macaroni Bay), 1997/98 and 1999/00, and better breeding (>0.25 chicks per pair) at all colonies in 1995/96, 1996/97, 1998/99, 2000/01 (except

Table I: Maximum counts of active nests obtained during July and August at separate colonies of gentoo penguins at Marion Island, 1994/95–2002/03. Also shown are the numbers of unoccupied nests recorded in these months, numbers breeding at colonies in 1984/85 (from Adams and Wilson 1987) and the estimate of the overall breeding population

Colony	Maximum count									
	1984/85	1994/95	1995/96	1996/97	1997/98	1998/99	1999/00	2000/01	2001/02	2002/03
Trypot Beach	114	115	96	59	83	76	41	58	69	77
Macaroni Bay	15	21	28	15	17	13	10	10	10	9
Archway Bay	66	194	186	114	12	121	113	76	100	116
Hansen Point	55	58	63	56	41	42	23	29	34	38
Bullard Beach	66	201	171	161	114	176	142	166	174	77
Killerwhale Cove	18	9	4	5	7	11	7	5	4	1
Landfall Beach	42	45	51	32	32	37	28	20	28	16
Funk Bay	86	79	76	71	66	58	65	71	58	59
Watertunnel Stream	28	37	38	23	15	20	22	21	16	13
Goodhope Bay (east)	6	11	13	12	17	7	9	15	13	12
Triegaardt Bay	0	2	0	7	8	8	7	9	11	11
Cape Davis	55	47	44	36	39	33	31	25	26	19
Storm Petrel Bay	31	43	38	43	37	45	29	23	20	38
Log Beach	0	0	0	0	0	0	0	0	24	49
Goney Bay	46	62	61	61	64	42	42	64	2	75
Sea Elephant Bay	90	137	151	127	110	87	97	63	78	29
Blue Petrel Bay ¹⁵	48	48	48	39	40	28	27	28	29	
Sealer's Beach	42	49	47	35	22	34	30	17	24	26
Ship's Cove	71	101	141	89	79	96	71	67	86	73
Duiker's Point	29	58	54	41	31	19	33	35	39	39
Van den Boogaard River	13	35	0	0	0	0	0	0	0	0
Total active nests			1 352	1 310	1 035	943	965	828	801	844
Additional unoccupied nests			0	45	84	13	25	18	0	0
Overall population (pairs)	888	1 352	1 355	1 119	956	990	846	801	844	806

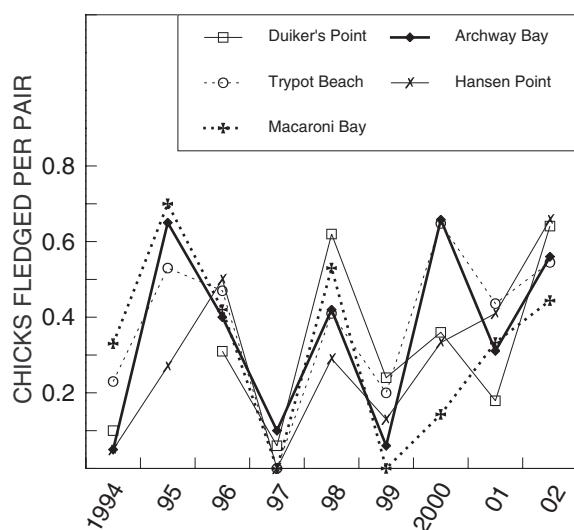


Fig. 3: Trends in the breeding success of five colonies of gentoo penguins at Marion Island, 1994/95–2002/03

Macaroni Bay), 2001/02 (except Duiker's Point) and 2002/03. In 1997/98, which was a particularly poor year, no chicks fledged at the colonies at Trypot Beach (83 pairs), Macaroni Bay (17 pairs) and Hansen Point (45 pairs). The highest mean number of chicks fledged per breeding pair at any colony was 0.70 at Macaroni Bay in 1995/96.

Adults began arriving at the colony at Trypot Beach between 1 and 26 June, depending on the year (Table III). In all years, the last adult had arrived by 23 July. Except in 1997/98 (20 July) and 2001/02 (1 June), the date when the first egg was presumed to have been laid was between 18 June and 11 July, a period of 23

days. In 1997/98, 95% of nests had eggs by 3 August, in 2001/02 by 14 June. In other years, this date varied between 12 and 25 July, a difference of 13 days. The earliest that an egg hatched was 16 July 2001. The date at which one-third of the eggs had hatched varied between 28 July and 30 August. Chicks began entering crèches between 28 August and 17 September and two-thirds of chicks were in crèches by between 2 and 24 September. Chicks began to fledge between 18 September and 6 October. In 1994/95, the last chick fledged on 29 December.

In 1994/95, replacement clutches were laid between 25 September and 5 October. From these, the first egg hatched on 30 October and the last on 9 November. The only three chicks to enter the post-guard stage had done so by 5 December.

The mean mass of chicks at fledging varied between 3.66 kg in the 1998/99 season and 5.66 kg in the 2000/01 season (Table II). However, in 1998/99 only seven fledglings were weighed. The minimum mass recorded for a fledged chick was 3.1 kg and the maximum 7.0 kg. The mean mass of the 366 fledged chicks weighed during the seasons 1994/95–2002/03 was 4.90 kg.

DISCUSSION

Population size and trend

Rand (1954) first estimated the number of gentoo penguins at Marion Island. He observed colonies of 50–100 birds each at 15 named (but only 10 mapped) localities on circumnavigating the island in summer 1951/52, which could be taken to represent of the order of 375–750 breeding pairs. However, Rand (1955), re-

Table II: Overall breeding success (i.e. chicks fledged per pair) and mean, maximum and minimum mass at fledging of chicks for gentoo penguins at Marion Island, 1994/95–2002/03. The sample sizes (*n*) and standard deviations (*SD*) of the means are indicated. For breeding success, *n* is the number of nests monitored and *SD* is the standard deviation of the means at five colonies (four colonies in 1995/96)

Season	Chicks fledged per pair			Mass at fledging (kg)				
	<i>n</i>	Mean	<i>SD</i>	<i>n</i>	Mean	<i>SD</i>	Maximum	Minimum
1994/95	466	0.12	0.12	88	4.45	0.45	5.40	3.40
1995/96	403	0.55	0.19	37	4.00	1.18	5.10	3.70
1996/97	357	0.42	0.07	57	4.79	0.70	6.25	3.25
1997/98	310	0.01	0.05	24	4.87	0.56	6.30	3.60
1998/99	319	0.42	0.13	7	3.66	0.51	4.50	3.10
1999/00	251	0.11	0.10	38	5.29	0.75	6.60	3.50
2000/01	232	0.51	0.22	50	5.66	0.57	6.70	4.50
2001/02	255	0.35	0.10	15	5.29	0.56	6.10	4.20
2002/03	279	0.58	0.09	50	5.52	0.60	7.00	4.50

Table III: Dates at various stages in the breeding cycle of gentoo penguins at Marion Island, 1994/95–2002/03 (1994/95 at Archway Bay, 1995/96–2002/03 at Trypot Beach)

Stage of breeding	Date								
	1994/95	1995/96	1996/97	1997/98	1998/99	1999/00	2000/01	2001/02	2002/03
First adult at colony		26 Jun.	15 Jun.	14 Jun.	15 Jun.	4 Jun.		1 Jun.	
Median date of arrival		4 Jul.	28 Jun.	2 Jul.	24 Jun.	29 Jun.		10 Jun.	
Modal date of arrival		12 Jul.	11 Jul.	20 Jul.	24 Jun.	25 Jun.		1 Jun.	
Arrival of adults completed		12 Jul.	11 Jul.	20 Jul.	2 Jul.	23 Jul.		18 Jun.	
First egg laid	27 Jun.	2 Jul.	11 Jul.	20 Jul.	26 Jun.	18 Jun.	20 Jun.	1 Jun.	
Median laying date	11 Jul.	7 Jul.	22 Jul.	1 Aug.	13 Jul.	7 Jul.	6 Jul.	10 Jun.	
Modal laying date	1 Jul.	11 Jul.	11 Jul.	20 Jul.	30 Jun.	30 Jun.	7 Jul.	2 Jun.	
95% of nests with eggs	23 Jul.	12 Jul.	17 Jul.	3 Aug.	25 Jul.	24 Jul.	19 Jul.	14 Jun.	
Last egg laid	25 Jul.	12 Jul.	1 Aug.	13 Aug.	30 Jul.	27 Jul.	22 Jul.	18 Jun.	
First egg hatched	1 Aug.	21 Aug.	15 Aug.	18 Aug.	16 Aug.	4 Aug.	31 Jul.	16 Jul.	
One-third of eggs hatched*	7 Aug.	30 Aug.	21 Aug.	29 Aug.	21 Aug.	10 Aug.	18 Aug.	28 Jul.	
Median date of hatching	15 Aug.	1 Sep.	23 Aug.	28 Aug.	25 Aug.	16 Aug.	12 Aug.	28 Jul.	
Modal date of hatching	10 Aug.	30 Aug.	21 Aug.	31 Aug.	30 Aug.	25 Aug.	17 Aug.	1 Aug.	
Last egg hatched	28 Aug.	12 Sep.	30 Aug.	6 Sep.	5 Sep.	28 Aug.	25 Aug.	9 Aug.	
First chick crèching	30 Aug.	6 Sep.	15 Sep.	14 Sep.	13 Sep.	4 Sep.	17 Sep.	28 Aug.	
Two-thirds of chicks crèching*	15 Sep.	21 Sep.	24 Sep.	14 Sep.	23 Sep.	18 Sep.	20 Sep.	2 Sep.	
Median date of crèching	9 Sep.	17 Sep.	21 Sep.	16 Sep.	1 Oct.	11 Sep.	20 Sep.	31 Aug.	
Modal date of crèching	8 Sep.	20 Sep.	18 Sep.	14 Sep.	23 Sep.	18 Sep.	20 Sep.	2 Sep.	
Last chicks crèching	18 Sep.	27 Sep.	27 Sep.	18 Sep.	18 Oct.	18 Sep.	23 Sep.	2 Sep.	
First date of fledging	18 Sep.	3 Oct.	6 Oct.						
Last date of fledging	29 Dec.								

*Dates when one-third of eggs had hatched and two-thirds of chicks were in crèches refer to eggs that hatched and chicks that entered crèches respectively

porting on what is assumed to be the same survey, refers to a total of 561 birds counted at only 13 named localities. Because the author was only present on Marion Island from October 1951 to April 1952 (Rand 1954), he would have missed the main peak of egg-laying in June and July (this study), so his count may reasonably be regarded as an underestimate of the then breeding population.

Van Zinderen Bakker (1971) considered the population of gentoo penguins at Marion Island in 1965/66 to be between 2 000 and 3 000 birds, mapping them at 18 colonies. He did not describe the method used to assess the population, but noted that it was "... difficult to estimate the number of non-breeding birds" (p. 252). Williams *et al.* (1975) gave the population at Marion Island in 1974 as 1 603. They did not indicate a unit but, as their estimate appeared in a table that also cites Van Zinderen Bakker's 1965/66 estimate of 2 000–3 000, it may be assumed to be of individual birds. Williams *et al.* (1975) also did not provide details of census methods, except to indicate that their count was undertaken between January and March and excluded Crawford and Triegaardt bays. Gentoo penguins were not reported at these two bays by Rand (1954, 1955), van Zinderen Bakker (1971) or Siegfried *et al.* (1978), or at Triegaardt Bay by Adams and Wilson (1987). In 1984/85, 28 pairs bred at Watertunnel Stream, at the extreme west of Crawford Bay (Adams

and Wilson 1987). From 1994/95 to 2002/03, Triegaardt Bay supported a maximum of 11 pairs and Watertunnel Stream a maximum of 38 pairs (Table I). Therefore, the exclusion of these bays by Williams *et al.* (1975) is unlikely to have substantially influenced their estimate. However, the main breeding season is completed by the end of December (Table III). Throughout the year, birds come ashore in the late afternoon, departing again to sea in the early morning (Van Zinderen Bakker 1971), so if birds had completed breeding by January–March, they may have been missed. The estimate of Williams *et al.* (1975) can be considered a lower limit, but cannot reasonably be compared with that of Van Zinderen Bakker (1971) for 1965/66. More information is provided by Siegfried *et al.* (1978) for the period 1974–1977. They report a total of 1 345 breeding pairs in at least 18 one-kilometre grid squares concentrated on the islands' eastern coast. Therefore, 18 may be considered the minimum number of colonies then present. Williams *et al.* (1979) cite a presumably rounded-off figure of 1 300 pairs for what is considered to represent the same survey.

Evidence exists for changes in the numbers and distribution of breeding colonies commencing within a few years of the occupation of Marion Island in January 1948. A breeding colony was present adjacent to the eponymously named Gentoo Lake, close to the meteorological station, in 1948 (photographed and de-

scribed by Bennetts 1948, Crawford 1952, 1982, 1999). However, by 1952 this colony had been permanently abandoned, almost certainly owing to disturbance caused by taking eggs for human consumption (Bennetts 1948, King 1952, 1954, Rand 1954). The first author noted that the gentoo penguins "soon leave their nest" on human approach and that the eggs "are very good eating"! Rand (1954) reported that "egging [was] indulged in to a great extent by some reliefs".

Rand (1955) counted 15 birds ashore at Kaalkoppie on the west coast in summer 1951/52, a locality mapped as a breeding site in 1965/66 by van Zinderen Bakker (1971) and for the period 1974–1977 by Siegfried *et al.* (1978), who reported a colony of 35 pairs. By August 1984 this colony no longer existed, according to the mapped breeding distribution given by Adams and Wilson (1987). No records exist of birds ashore at Kaalkoppie subsequently. It is highly likely that a volcanic eruption and lava flow in 1980, which blocked access (with a cliff 6–12 m high) to a boulder beach previously used by southern elephant seals *Mirounga leonina* and gentoo and macaroni penguins *Eudyptes chrysophthalmus* at this locality (Verwoerd *et al.* 1981, Berruti 1982), made it no longer suitable for gentoo penguins to come ashore and to breed. Berruti (1982) reported no gentoo penguins present when visiting the locality in November 1980, an estimated 2–3 months after the eruption (Verwoerd *et al.* 1981).

Based variously on the small scales of published breeding distribution maps, the use of one-kilometre grids instead of named colonies, and the difficulty of identifying all the named breeding localities in the 1951/52 survey (Rand 1954, 1955, van Zinderen Bakker 1971, Siegfried *et al.* 1978, Adams and Wilson 1987), it is not considered sensible to be more precise about changes in the presence and distribution of breeding colonies of gentoo penguins at Marion Island prior to 1984/85.

In August 1984, there were 888 pairs of gentoo penguins at 24 colonies (some of which were at the same locality and therefore have been combined in Table I) at Marion Island (Adams and Wilson 1987), a decrease of some 450 pairs in about eight years since the period 1975–1977 (Siegfried *et al.* 1978). An observation was made during January 1981 of apparent predation of a gentoo penguin chick by a feral cat *Felis catus* (Berruti 1981). Penguin remains, unidentified to species, were found in 5–11% of cat stomachs during the periods 1974–1976, 1981–1983 and 1986–1989 (van Aarde 1980, van Rensburg 1985, Bloomer and Bester 1990). Van Rensburg (1985) reports a single gentoo penguin as the prey remains of a cat in the period 1981–1983. It is therefore possible, although it will remain unproven, that feral cats were responsible,

at least in part, for the population decline of gentoo penguins at Marion Island between the mid 1970s and mid 1980s. Cats were eradicated from the island in 1991 (Bester *et al.* 2002). Because gentoo penguins are primarily winter breeders at Marion Island, when burrowing petrels, the main avian prey of cats at the island, are largely absent (Cooper and Brown 1990), they may have been at some risk if cats had switched diets in winter. Gentoo penguin chicks have been recorded being killed by feral cats on subantarctic Macquarie Island (Garnett and Crowley 2000), but at a level not considered to have been a significant threat (Ellis *et al.* 1998). Jones (1984) reported that cats at Macquarie Island fed more on penguins during winter; 3% of scats contained penguin remains overall. Feral cats have been recorded preying on several other species of penguins, to a level to cause conservation concern in some cases (e.g. Berruti 1986, Darby and Seddon 1990, Stahel and Gales 1987, Ellis *et al.* 1998).

By 1994/95, the population had increased to the level observed in 1974–1977. Then, in five years between 1995/96 and 2000/01, it decreased by 554 pairs, from 1 355 pairs to 801 pairs (Table I). This is equivalent to a decrease of 8% per year. The low CV (about 1%) on the annual estimates of the overall population at Marion Island suggests a 95% probability of the population size falling within 2% of the estimate. At Bird Island, South Georgia, estimates also were considered accurate to 2% (Croxall and Rothery 1995).

The population estimated for Prince Edward Island, which is 21 km north-east of Marion Island, increased from about 200 pairs in 1976/77 (Williams *et al.* 1979) to 655 pairs in August 1984 (Adams and Wilson 1987), but then decreased to an estimated 475 pairs in 2001/02 (Ryan *et al.* 2003), again indicating substantial fluctuation.

It is of interest that the decrease in the number of gentoo penguins breeding at Marion Island between 1974–1977 and 1984/85 (about 450 pairs) and the increase at Prince Edward Island in the same period (also about 450 pairs) are so similar. At Bird Island, South Georgia immigration of gentoo penguins, especially first breeders, from the main island of South Georgia was considered likely. At Crozet Islands about 33% of first breeders breed at a locality other than their natal one (Croxall and Rothery 1995). At Bird Island, South Georgia, no birds banded as breeders were recorded breeding at another colony (Williams and Rodwell 1992). At South Shetland Islands, 90% of gentoo penguins reunited with their partner in the following year (Trivelpiece and Trivelpiece 1990). For the African penguin *Spheniscus demersus*, long-term emigration of first-time breeders to localities where feeding conditions are favourable at the time has

been reported but, because breeders show high fidelity to their mates, birds once breeding thereafter return to the same locality to breed (Crawford 1998, Crawford *et al.* 2001).

At Marion Island, it is probable that some gentoo penguins have moved between colonies. This appears to have taken place between Van den Boogaard River and Ship's Cove in 1995/96 and between Goney Bay and Log Beach in 2001/02 (Table I). The colony at Ship's Cove increased by 40 pairs between 1994/95 and 1995/96, approximately equivalent to the loss of the 35 pairs at Van den Boogaard River in the same period. Gentoo penguins at Van den Boogaard River were caught in 1994/95 to obtain diet samples. Disturbance brought about by such sampling may have caused birds to leave this locality in 1995/96 to join the colony at Ship's Cove, which is 1 km to the northwest (Fig. 1). Reasons for the formation of a colony at Log Beach in 2001/02 are not at this stage understood, although it should be noted that Rand (1954) reported a colony as present at this locality in 1951/52. These movements are inferred and were not shown by banding.

Several early observers and researchers reported that gentoo penguins at Marion Island are afraid of humans (e.g. Bennetts 1948, Crawford 1952, Van Zinderen Bakker 1971). They are also highly susceptible to human disturbance at subantarctic Heard Island (E. J. Woehler, Australian Antarctic Division, pers. comm.). Disturbance has caused Cape gannets *Morus capensis*, which normally show strong fidelity to breeding localities (Crawford *et al.* 1994, Klages 1994), to colonize new islands (Crawford *et al.* 1983). Apart from diet sampling and examination of nests of gentoo penguins in 1994/95, monitoring of gentoo penguins at Marion Island was not intrusive and disturbance is not considered to have caused the large decrease in numbers breeding there between 1995/96 and 2000/01.

Some other populations of gentoo penguins also have shown large fluctuations in numbers (Woehler and Croxall 1997, Woehler *et al.* 2001). For example, at Bird Island, South Georgia, the breeding population decreased by 75% between 1977 and 1979. It increased to half of its 1977 level in 1980 but decreased again from 1983 to 1984, from 1987 to 1988 and from 1990 to 1991, in between and in 1992 recovering to levels approximating that of 1980 (Croxall and Prince 1979, Williams 1990, Croxall and Rothery 1995). Superimposed on these short-term fluctuations was a longer-term decrease from the mid 1970s to the mid 1990s, as was also observed at King George Island (Woehler *et al.* 2001), more similar to the persistent downward trend at Marion Island from 1995/96 to

2000/01 (Fig. 2). At several localities on the Antarctic Peninsula there have been significant long-term increases in populations of gentoo penguins (Quintana and Cirelli 2000, Woehler *et al.* 2001). However, there have been large decreases at some island localities, including the Falkland Islands (Bingham 1998) and Bird Island, South Georgia (Woehler *et al.* 2001), which support about 75% of the total species' population (BirdLife International 2000).

Breeding

Fluctuations in the numbers of gentoo penguins breeding at specific colonies at Marion Island, for example at Bullard Beach between 1996/97 and 1998/99, suggest that, in some years, not all gentoo penguins breed. At Crozet Islands, only 84% of early breeders and 73% of late breeders bred in the following year (Bost and Jouventin 1990). Extensive non-breeding by adult birds has been shown for gentoo penguins and macaroni penguins at Bird Island, South Georgia, in some years (Williams and Rodwell 1992, Croxall and Rothery 1995).

In 1974/75 and 1976/77 at Marion Island, 17–60% of nests at different colonies (mean 43%) raised one chick to independence at an age of 60–90 days (Williams 1980a). This mean of 0.43 chicks fledged per pair falls within the range (0.01–0.58) recorded from first clutches between 1994/95 and 2002/03. There was an almost complete breeding failure at Marion Island in 1997/98, which was also observed for gentoo penguins at South Georgia in the 1977/78 and 1990/91 breeding seasons, when there was reduced availability of Antarctic krill *Euphausia superba* inshore for birds to feed on (Croxall and Prince 1979, Croxall and Rothery 1995).

In 1994/95, replacement clutches at Trypot Beach improved overall breeding success by 11%. At Crozet Islands, replacement clutches accounted for 15–20% of all clutches laid (Bost and Jouventin 1990). At Bird Island, South Georgia, six out of 203 pairs replaced clutches in 1988, but none did so in 1987 (Williams 1990).

Some gentoo penguins may breed at an age of two years (Croxall and Rothery 1995). However, the mean age at first breeding for male gentoo penguins is thought to be 3.5 years, the mean age at first breeding for all birds 3 years, adult survival 85% and survival of birds in their first and second years 80% in good years (Marchant and Higgins 1990, Trivelpiece and Trivelpiece 1990, Croxall and Davis 1999). If it is assumed that age at first breeding is three years and that all adults breed each year, it would be necessary for

pairs to fledge 0.55 chicks per year to maintain the population in equilibrium. This is greater than the overall mean of 0.38 chicks per pair per year from first clutches for the period 1994/95–2002/03 and more than the values recorded in 1994/95 and from 1996/97 to 2001/02 (Table II). If production is increased by 20% (to 0.46 chicks per pair) to allow for replacement clutches, it is still too low to achieve equilibrium with an age at first breeding of three years. For equilibrium with an age at first breeding of two years, it would be necessary for pairs to fledge on average 0.47 chicks per year. Given the likelihood that not all adults breed in each season (Croxall and Rothery 1995), production appears to have been inadequate to sustain the population at Marion Island, especially in 1994/95 and from 1995/96 to 2001/02.

Williams (1980a) and La Cock *et al.* (1984) note that breeding success of gentoo penguins is low at the Crozet and Prince Edward islands, at the northern extent of the species' breeding range. At Bird Island, South Georgia, gentoo penguins fledged 1.13 chicks per pair in the 1976/77 breeding season, about half of this in 1978/79 but none in 1977/78 (Croxall and Prince 1979), i.e. an average of about 0.56 chicks per pair per year. In five of 15 years at this locality, productivity was more than one chick per pair, there were two seasons of almost complete breeding failure and in the remaining eight seasons breeding success was from 0.59 to 0.94 chicks per pair (Croxall and Rothery 1995). At Cierva Point, Antarctic Peninsula, during 1992/93, 83% of pairs raised at least one chick to fledging (Quintana and Cirelli 2000). At the Falkland Islands, gentoo penguins fledged an average of 0.84 chicks per pair per year over a 12-year period (1990–2001, Bingham 2002). The lower production of chicks at northern than at southern breeding localities will require that, for populations to remain viable, other demographic parameters are more favourable at northern than at southern localities, e.g. that adult survival is higher or that birds breed at a younger age. Such parameters have not been measured at Marion Island.

The similarity in trends in breeding success at Marion Island at all five study colonies where this parameter was measured suggests that it is often influenced by factors operating at a mesoscale, e.g. over the foraging range of birds, rather than factors that are specific to individual colonies, as for example human disturbance that is restricted in nature. In 1984, 82% of all foraging trips of gentoo penguins at Marion Island were <40 km (Adams and Wilson 1987), indicating that birds feed near the island. There is also similarity in inter-season trends in breeding success of macaroni penguins at different colonies at Marion

Island (Cooper *et al.* 1997). Unlike the situation at Marion Island, there was no correlation between breeding success of gentoo penguins at different colonies at Bird Island, South Georgia (Williams 1990), although in years of substantially reduced availability of food there was pervasive poor breeding there (Croxall and Rothery 1995).

At Marion Island, the mass of chicks at fledging was not related to breeding success in the same year. For example, the heaviest chicks were weighed in the 1999/00 season, when breeding success was poor. This may result from the difficulty experienced by some field workers in catching chicks to weigh, without causing too much disturbance – e.g. in the 1998/99 season when breeding was reasonably successful but only seven chicks were weighed. Further, when food is scarce, chicks of low mass are more likely to die than when food is abundant, which may lead to a disproportionate number of heavy chicks surviving (Williams and Croxall 1990). Between 1994/95 and 2002/03, the mean mass at fledging varied from 3.66 to 5.66 kg (Table II), with an overall average of 4.9 kg, compared with 4.43 kg obtained by Williams (1980a) for three chicks in 1974/75 and 1976/77.

At the Crozet and Prince Edward islands, north of the Antarctic Polar Front, the laying period of gentoo penguins extends over five months, although more than 80% of pairs initiate laying within a period of three weeks. South of the Polar Front egg laying is more synchronous (Bost and Jouventin 1990). At Bird Island, South Georgia, 95% of clutches are initiated within a period of 14.5 days or less (Williams 1990). Laying is earliest at the northernmost breeding localities, and progressively later as one moves southwards (Williams 1980a).

At Marion Island, the reoccupation of nesting areas is gradual (Van Zinderen Bakker 1971). Egg laying has been reported in the first week of June (Crawford 1952). An egg was seen at Archway Bay on 7 June 1994 (ACW pers. obs.). However, egg laying normally commences between 16 and 25 June (Van Zinderen Bakker 1971, Williams 1980a) and peaks in late June or July. Relaying by failed breeders continues until early November (Adams and Wilson 1987). In 2001/02, egg laying at Marion Island was considerably earlier than usual, taking place from about 1 to 18 June. By contrast, laying was deferred in 1997/98 until about 20 July–30 August (Table III).

At the Crozet Islands, the date when the first egg was produced fell between 24 June and 15 July in four years. Peak laying varied by about a month between 21 and 25 July and 20 and 24 August (Bost and Jouventin 1990). In the present study, the date when the first egg was laid in the colony at Trypot Beach

was between 18 June and 11 July over six years. Except for 2001/02, the date at which 95% of nests had eggs was between 12 July and 3 August. Therefore, the variability in the onset of laying at the Crozet and Prince Edward islands is similar, but laying is usually initiated earlier at the Prince Edward Islands. At the Crozet Islands, the laying of replacement clutches commenced in early August and overlapped that of delayed first breeders (Bost and Jouventin 1990).

The timing of the more synchronous laying on South Georgia Island may vary by up to five weeks between years. Delayed breeding may result from a shortage of food in inshore waters or a severe preceding winter (Croxall and Prince 1979, Williams 1990, Croxall and Rothery 1995). It has been suggested that delayed laying at the Crozet Islands may result from food scarcity early in the breeding season (Bost and Jouventin 1990).

At Marion Island, the deferred laying in 1997/98 was associated with almost total breeding failure. Subantarctic skuas *Catharacta antarctica* returned to the island at the end of August (see also Williams 1980b) and inflicted substantial mortality on the eggs and small chicks of gentoo penguins (MDG pers. obs). Van Zinderen Bakker (1971) also noted that skuas preyed mainly upon nests of late-laying birds at Marion Island. Skuas *Catharacta* spp. are the main cause of mortality of both eggs and chicks of gentoo penguins at Cierva Point, Antarctic Peninsula (Quintana and Cirelli 2000).

The late breeding in 1997/98 coincided with a strong *El Niño* event that split year, which commenced in April and peaked in July/August (Wolter and Timlin 1998), when laying took place. For several seabirds at Marion Island, breeding was either exceptionally poor or unusually good in 1997/98. Poor breeding was experienced by species that forage close to the island, suggesting that availability of food was decreased for these birds (Crawford *et al.* 2003). *El Niño* events have also affected breeding by seabirds at other localities in the Southern Ocean (e.g. Croxall 1992, Chastel *et al.* 1993), including gentoo penguins (Croxall *et al.* 1988). Analysis of historical data on the abundance of seabirds off Peru and southern Africa indicated that, although their population dynamics are to a large extent influenced by local phenomena, linkages between these two regions are possible during extreme environmental conditions such as large *El Niño* events (Crawford and Jahncke 1999).

At Marion Island the gentoo penguin is protected from casual human disturbance by being placed in the highest protected management zone, with a 100-m perimeter around each breeding colony. Entrance is by way of a special permit issued for scientific and

conservation purposes only (Prince Edward Islands Management Plan Working Group 1996). This level of protection should continue in the intended revision of the management plan (Crawford and Cooper 2003). Any planned research activities on this Near Threatened species at Marion Island must be designed so as to reduce the effects of human disturbance on breeding success to the absolute minimum.

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A gentoo penguin at Marion Island (photo B. M. Dyer)

POPULATION OF THE MACARONI PENGUIN *EUDYPTES CHRYSOLOPHUS* AT MARION ISLAND, 1994/95–2002/03, WITH INFORMATION ON BREEDING AND DIET

R. J. M. CRAWFORD*, J. COOPER† and B. M. DYER*

There is indication that numbers of macaroni penguins *Eudyptes chrysolophus* at subantarctic Marion Island have decreased since the early 1980s. Estimates of the population at the island fell from about 405 000 pairs in 1983/84 and 434 000 pairs in 1994/95 to about 356 000 pairs in 2002/03. Two large colonies, at Bullard Beach and Kildalkey Bay, account for about 85% of the overall population. At both these colonies, the area occupied by breeders showed no trend between 1983/84 and 2002/03, but the mean density of nests decreased. However, error on estimates of abundance at these colonies precludes demonstration of a significant decrease in the overall population. Numbers of occupied nests at other colonies decreased from 79 000 in 1994/95 to 31 000 in 2002/03. At three small colonies there was a significant decrease of 88% between 1982/83 and 2002/03. At Marion Island, macaroni penguins usually breed for the first time when aged about three years. From 1994/95 to 2002/03, pairs fledged an average of 0.46 chicks per year, a number considered insufficient to maintain the population. However, during that period there was a significant increase in reproductive success with time. In the same period, the masses of males and females on arrival at breeding colonies were significantly correlated. Both showed a marked decrease in 1998/99, after the *El Niño* of 1997/98. In most seasons from 1994/95 to 2001/02 crustaceans dominated the food, but the mass of chicks at fledging was significantly related to the contribution of fish to the diet.

Key words: breeding, diet, *Eudyptes chrysolophus*, macaroni penguin, Marion Island, population, Subantarctic

The macaroni penguin *Eudyptes chrysolophus* has a subantarctic distribution in the south-eastern Pacific, south Atlantic and south-western Indian oceans, breeding at several localities between southern Chile and Heard and McDonald Islands, including South Africa's Prince Edward Islands (Marchant and Higgins 1990). The species is regarded as Vulnerable because a majority of the world population appears to have decreased by at least 20% in the past three generations (36 years; Ellis *et al.* 1998, BirdLife International 2000). In South Africa, it is regarded as Near Threatened (Barnes 2000).

Photographs of some colonies at the Kerguelen Islands indicated an increase of 20% between 1963 and 1985 (Weimerskirch *et al.* 1989). In 1984, the population in southern Chile also was thought to be increasing (Schlatter 1984). However, numbers at Bird Island, South Georgia, which supports about 30% of the world's population, have halved since 1976/77 (Croxall *et al.* 1988, Ellis *et al.* 1998, Woehler *et al.* 2001). There have also been decreases at Willis Islands and other localities in South Georgia and at Bouvet Island (Woehler and Croxall 1997, Isaksen *et al.* 1997, Ellis *et al.* 1998, Trathan *et al.* 1998). Numbers at three small colonies at Marion Island (290 km²; 46°52'S, 37°51'E), one of the Prince Edward Islands,

decreased between 1979 and 1999 (Cooper *et al.* 1997, Woehler *et al.* 2001).

At Marion Island, most of the macaroni penguins breed in two large colonies, at Bullard Beach and Kildalkey Bay, although smaller colonies are distributed around the island (Rand 1955, van Zinderen Bakker 1971, Williams 1978, Watkins 1987, Fig. 1). This paper considers information on trends in the two large colonies, as well as the smaller colonies, especially for the period 1994/95–2002/03. It also presents information on breeding and diet that was collected at some of the smaller colonies at Marion Island in the same period.

MATERIAL AND METHODS

Population

In 1983, 45 and 40 concrete markers with numbered riser poles were placed c. 2 m from the edges of the two large macaroni penguin colonies at Bullard Beach and Kildalkey Bay respectively. Additionally, 14 squares were sited within the colony at Bullard Beach and 18 within that at Kildalkey Bay (Fig. 1).

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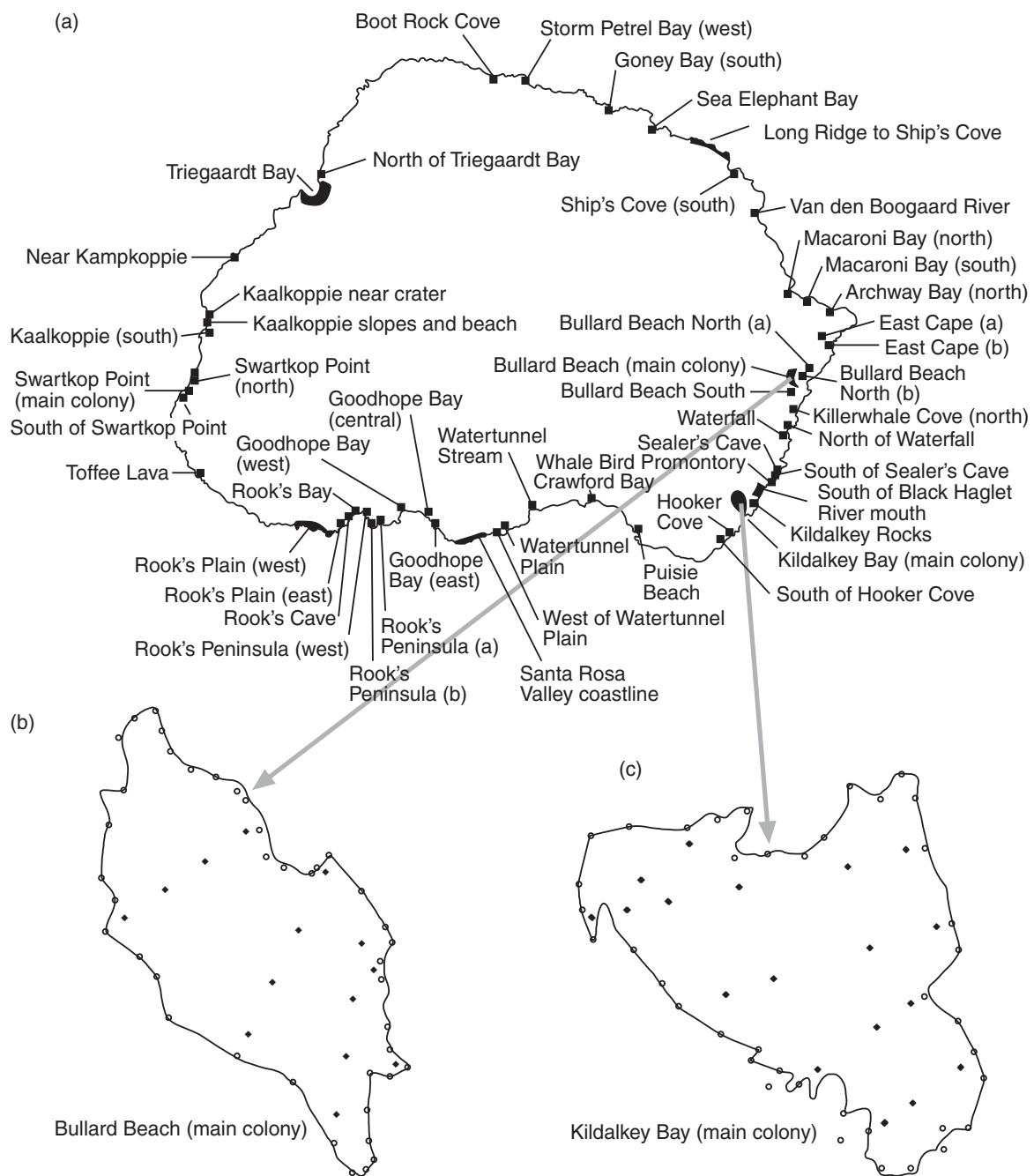


Fig. 1: Marion Island, showing (a) the locations of the breeding colonies of macaroni penguins. The extents of the main colonies at (b) Bullard Beach and (c) Kildalkey Bay are indicated, together with the locations of markers near the colony edges (open circles) and the locations of squares within the colonies (closed squares) used to measure the densities of nests

The corners of each square were marked with concrete blocks and riser poles. Each square measured 5 m × 5 m. In 1983, the colonies were tacheometrically surveyed and mapped (1:1 000) by the University of Cape Town's Department of Surveying. The maps indicated the locations of the blocks near the colony boundaries, the squares within the colonies, other prominent features (such as streams, banks, the high-water mark), contours in intervals of 2 m, magnetic north and true north. In all breeding seasons from 1983/84 to 2002/03, the extents of the distributions of breeding birds at these two colonies were mapped in late November or early December during incubation (Cooper and Brown 1990). Birds loafing on the edges of colonies were excluded from the maps. However, records of the extent of the colony at Bullard Beach could not be traced for 1987, 1990 and 1992.

Also during incubation, the numbers of active nests in each square were counted. If more than half a nest was within the boundaries of a square, it was assumed to fall within that square. If not, it was excluded. The squares were approached slowly to minimize disturbance (see Williams 1980). At Marion Island, macaroni penguins are tolerant of human disturbance (Watkins 1987). For both Bullard Beach (main colony) and Kildalkey Bay (main colony), the mean density of nests was calculated and, together with the overall area occupied, used to estimate the number of breeding pairs. Nests tended to be more dense on horizontal ground than on inclined ground (Watkins 1987). The areas occupied by breeders were obtained by means of a planimeter scaled against an area of known size. In August of each year, the concrete blocks near the colony edges and marking the squares were checked to ensure that they were in their correct positions and that all sides of squares measured 5 m.

From 1994/95 to 2000/01 and in 2002/03, the number of active nests at all breeding localities (Williams 1978), except Bullard Beach (main colony) and Kildalkey Bay (main colony) in all years, the main colony at Swartkop Point in 1994/95 and Bullard Beach North (b) and Crawford Bay in 1998/99, were counted in late November or early December. In 2001/02, the counts were made from 18 to 23 December. Counts were conducted at all colonies with the aid of tally counters, sometimes using binoculars. The main colony at Swartkop Point, which extends over several terraces, was counted by making use of natural features, including the terraces, to break the colony into smaller sections. The number of pairs breeding at the main colony at Swartkop Point in 1994/95 was assumed to be the same as in 1995/96; numbers at Bullard Beach North (b) and Crawford Bay in 1998/99 were assumed intermediate between counts made in 1997/98 and 1999/00.

The count in 2001/02 was conducted about three weeks later than in the other years, so breeding attempts by a greater proportion of pairs may have failed. Therefore, the counts in 2001/02 (but not the estimates for the main colonies at Bullard Beach and Kildalkey Bay) were multiplied by a factor of 1.3. This was on the basis of information collected at Macaroni Bay (north), where numbers breeding decreased from 207 pairs in late November to 161 pairs on 18 December. Macaroni Bay (north) was the only colony of more than 100 breeding pairs for which such information was available.

Counts of the numbers of pairs breeding at Macaroni Bay (north), Archway Bay and Van den Boogaard River in the north-east of Marion Island were made in each season from 1979/80 to 2002/03 as close as possible to the period 20–24 November, when most birds are incubating (Cooper and Brown 1990, Cooper et al. 1997). From 1994/95 to 2002/03, each count was made three times and the mean and standard deviation were calculated.

Breeding

A study of the breeding of macaroni penguins was carried out at Macaroni Bay (north), Archway Bay and Van den Boogaard River from 1979/80 to 2002/03 and at Bullard Beach South from 1994/95 to 2002/03. These colonies are all reasonably close to the island's main base.

Breeding phenology was investigated at Macaroni Bay (north) from 1994/95 to 1999/00. The arrival of adults and, except in 1997/98, the progress of nests and the fledging of chicks were monitored (chicks were not monitored after the crèche stage in 1999/00), using protocols outlined by the Commission for the Conservation of Antarctic Marine Living Resources (SC-CAMLR 1995).

Because adults were not banded, the number arriving on a given day was taken to be the difference between the numbers seen at the colony on that day and on the previous day. The numbers of adults were counted daily from about 3 October until 10 November.

The distributions of nests were mapped so that the progress of individual nests could be followed. Nests were checked daily from 7 October until 100 of them had eggs. Thereafter, nests were checked at two-day intervals until 48 days after the first egg was laid. The normal clutch of macaroni penguins is two eggs (Williams 1980). Averages at Marion Island for laying interval, incubation period of second-laid eggs and incubation period of first-laid eggs were 4.5, 35.9 and 38.0 days respectively (Williams 1981). Subsequently, each nest was again checked daily until its chick en-

Table I: Estimates of the numbers of breeding pairs of macaroni penguins at different localities at Marion Island, 1994/95–2002/03. The count in 2001/02 was adjusted to account for its later date using information on nest failure at Macaroni Bay. In 2002/03 penguins were counted in zones, not at localities

Locality	1994/95	1995/96	1996/97	1997/98	1998/99	1999/00	2000/01	2001/02	2001/02 adjusted	2002/03
Macaroni Bay (north)	411	398	341	315	360	225	219	161	517	
Macaroni Bay (south)	461	431	230	306	295	213	208	133	560	
Archway Bay (north)	210	214	143	142	165	144	131	18	278	
East Cape (a)	255	166	120	115	103	143	142	61	216	
East Cape (b)	36	30	10	9	20	17	23	0	39	
Bullard Beach North (a)	52	45	18	33	13	34	261	0	59	
Bullard Beach North (b)	340	253	232	329	292	255	32	0	329	
Bullard Beach South	3 680	3 139	2 979	3 227	3 354	3 111	3 246	1 339	4 081	
Killerwhale Cove (north)	88	114	83	122	108	115	121	0	148	
North of Waterfall	4	0	5	0	0	0	0	23	0	
Waterfall	925	379	668	833	1 022	845	868	507	493	
Sealer's Cave	46	30	0	0	0	0	0	0	39	
South of Sealer's Cave	9	0	8	0	5	5	9	0	0	
Whale Bird Promontory	465	462	480	515	429	465	480	192	601	
South of Black Haglet River mouth	3 069	2 903	1 880	2 422	2 484	2 482	2 062	714	3 774	
Kildalkey Rocks	27	23	20	24	0	0	0	0	30	
Hooker Cove	244	243	227	215	149	177	190	0	316	
South of Hooker Cove	14	13	11	14	57	4	3	8	17	
Puisie Beach	1 207	1 136	781	640	618	600	720	0	1 477	
Crawford Bay	4 939	5 000	1 909	1 086	1 293	1 500	1 800	290	6 500	
Watertunnel Stream	9	8	12	6	16	14	12	0	10	
Watertunnel Plain	0	14	164	0	10	6	3	0	18	
West of Watertunnel Plain	16	0	9	9	0	0	0	0	0	
Santa Rosa Valley coastline	2 491	2 715	1 799	2 051	2 385	2 063	2 145	500	3 530	
Goodhope Bay (east)	9	0	2	8	0	8	7	1 474	0	
Goodhope Bay (central)	7 490	7 594	4 660	4 484	5 121	4 181	4 070	7 971	9 872	
Goodhope Bay (west)	12 561	13 015	7 459	4 768	10 509	10 716	10 569	12 337	16 920	
Rook's Peninsula (a)	52	62	56	0	69	37	40	304	81	
Rook's Peninsula (b)	273	291	263	234	0	0	0	0	378	
Rook's Peninsula (west)	2 000	2 139	2 374	1 472	2 169	2 219	2 176	1 643	2 781	
Rook's Bay	3 212	3 089	3 446	2 301	2 274	2 261	2 510	2 373	4 016	
Rook's Cave	3 991	4 003	4 180	3 211	4 695	3 590	3 731	2 850	5 204	
Rook's Plain (east)	534	433	652	380	803	543	609	817	563	
Rook's Plain (west)	934	1 832	731	1 049	753	846	812	613	2 382	
Toffee Lava	4	4	0	0	0	0	0	0	5	
South of Swartkop Point	1 832	1 027	1 200	1 854	2 294	1 614	1 872	1 344	1 335	
Swartkop Point (main colony)	16 465	16 465	10 330	10 352	14 646	15 472	17 255	13 656	21 405	8 481
Swartkop Point (north)	80	78	45	102	190	85	85	9	101	
Kaalkoppie (south)	78	101	57	94	27	98	94	107	131	
Kaalkoppie slopes and beach	3 613	3 350	2 935	1 549	3 341	3 557	3 360	3 580	4 355	
Kaalkoppie near crater	1 370	1 194	1 110	773	889	1 003	898	1 089	1 552	
Near Kampkoppie	158	145	160	172	176	173	171	173	189	
Triegaardt Bay	4 739	4 184	3 598	4 113	5 420	5 469	5 705	4 876	5 439	
North of Triegaardt Bay	11	10	6	10	19	0	0	0	13	
Boot Rock Cove	110	83	43	89	55	48	45	46	108	
Storm Petrel Bay (west)	6	2	1	2	3	0	0	0	3	
Goney Bay (south)	2	2	1	0	0	0	0	0	3	
Sea Elephant Bay	76	57	61	80	64	51	52	63	74	
Long Ridge to Ship's Cove	34	24	18	20	11	9	11	23	31	
Ship's Cove (south)	457	464	291	279	470	286	295	92	603	
Van Den Boogaard River	33	39	27	23	25	24	22	0	51	22
Subtotals	79 122	77 403	55 835	49 832	67 201	64 708	67 075	59 386	76 353	31 355
Bullard Beach (main colony)	170 550	146 480	156 816	163 117	125 736	139 746	153 416	141 491	141 491	143 969
Kildalkey Bay (main colony)	184 051	171 094	182 333	191 573	169 988	183 614	186 792	161 678	161 678	180 812
Total	433 723	394 977	394 984	404 522	362 925	388 068	407 283	362 555	379 522	356 136

tered a crèche. Numbers of chicks in crèches were counted daily until fledging was complete (latest date was 29 February 1999), and a record was kept of all chicks that died.

Breeding success was measured at Macaroni Bay (north), Archway Bay and Van den Boogaard River from 1979/80 to 2002/03 and at Bullard Beach South from 1994/95 to 2002/03. Counts of the numbers of newly hatched chicks (from 1983/84) and chicks in crèches (from 1979/80) were made as close as possible to 4 January and 10 February respectively (Cooper *et al.* 1997). At Marion Island, hatching commences towards the end of December (Cooper and Brown 1990). For each season, the number of chicks fledged per pair was calculated. From 1994/95 to 2002/03, the number of nests used to estimate breeding success varied between 928 and 2 164.

The mass of adults at arrival at breeding colonies was measured at the main colony at Bullard Beach for each season from 1994/95 to 2002/03. Sexes of adults were discriminated using bill measurements. Males are larger than females, have longer bills and arrive at colonies earlier than do females (Marchant and Higgins 1990). Males were weighed about 14 October and females about 18 October. Sample size was 100–128 for males and 100 for females (except 17 in 1995/96 and 44 in 1998/99). For the same period, but at different colonies, the mass at fledging of 129–250 chicks (10–20 February) was obtained. This was a sample of chicks that fledged.

At Macaroni Bay (north), the age at first breeding of macaroni penguins was investigated by banding 159 fledglings in 1996/97 and 156 in 1997/98. In subsequent seasons, observations on banded birds were conducted at this locality. A bird was considered to be breeding if it was seen at a nest site with a mate, egg or chick.

Diet

The diet of macaroni penguins was investigated in each season from 1994/95 to 2001/02, mostly at the main colony at Bullard Beach. From 30 to 45 stomach samples were collected each season between 12 December and 29 February, which is during the chick-rearing period (Cooper and Brown 1990). Birds were caught when they came ashore, and their stomachs were flushed using a water-offloading technique modified from that described by Wilson (1984). Water was poured down a tube into the stomach, rather than pumped into it. Samples were preserved in alcohol or frozen. In the laboratory, all liquid was drained from

samples through a sieve. Each sample was sorted into crustacean, cephalopod, fish and other components. These components were then weighed.

The original biomass of cephalopods and fish ingested was not calculated, nor were prey species individually identified. At Marion Island in 1983/84 and 1984/85, use of regressions relating lower rostral length of cephalopod beaks to length of the dorsal mantle and hence to mass increased the contribution by mass of cephalopods from 2 to 8–13%. Use of regressions relating otolith diameter to fish length and hence to mass increased the estimated contribution by mass of fish from 0–10 to 5–25%. As a result, the estimated contribution of crustaceans in the diet decreased from 88–98 to 62–87% (Brown and Klages 1987).

RESULTS

Population

Estimates of the breeding population of macaroni penguins at Marion Island decreased from 434 000 pairs in 1994/95 to 356 000 pairs in 2002/03 (Table I). The main colonies at Bullard Beach and Kildalkey Bay contributed 80–91% of the overall number of pairs (c. 90% in 1983/84, Watkins 1987). Estimated numbers at these two colonies decreased from an average of 386 000 pairs in the period 1983/84–1993/94 ($n = 8$, $SD = 13\,000$) to an average of 328 000 pairs in 1994/95–2002/03 ($n = 9$, $SD = 21\,000$). From 1994/95 to 2002/03, trends in numbers at the two colonies were positively related ($n = 9$, $r = 0.637$, $p < 0.10$).

At Bullard Beach (main colony), the estimated number breeding fell from 174 000–213 000 pairs during the period 1983/84–1993/94 to 126 000–163 000 pairs during 1995/96–2002/03 (Fig. 2a). In the entire period, the area occupied by breeders fluctuated from 8 to 9 ha, except in 1991/92 and 1993/94 when it was 9.8 to 10 ha (Fig. 2b). However, there was a trend to a decrease in density of nests (Fig. 2c), which was accompanied by an increase in the coefficient of variation (CV) on the mean density of nests – from about 20% up until 1990/91 to 30–41% from 1995/96 to 2002/03 (Fig. 2d).

At Kildalkey Bay (main colony), the estimated number breeding varied from 180 000 to 210 000 pairs throughout the period of observations, except in 1995/96, 1998/99 and 2001/02, when the estimates were between 161 000 and 172 000 pairs (Fig. 2a). There was no trend in the area occupied by breeders, which fluctuated between 9.0 and 9.6 ha (Fig. 2b). Again there was a trend for the density of nests to de-

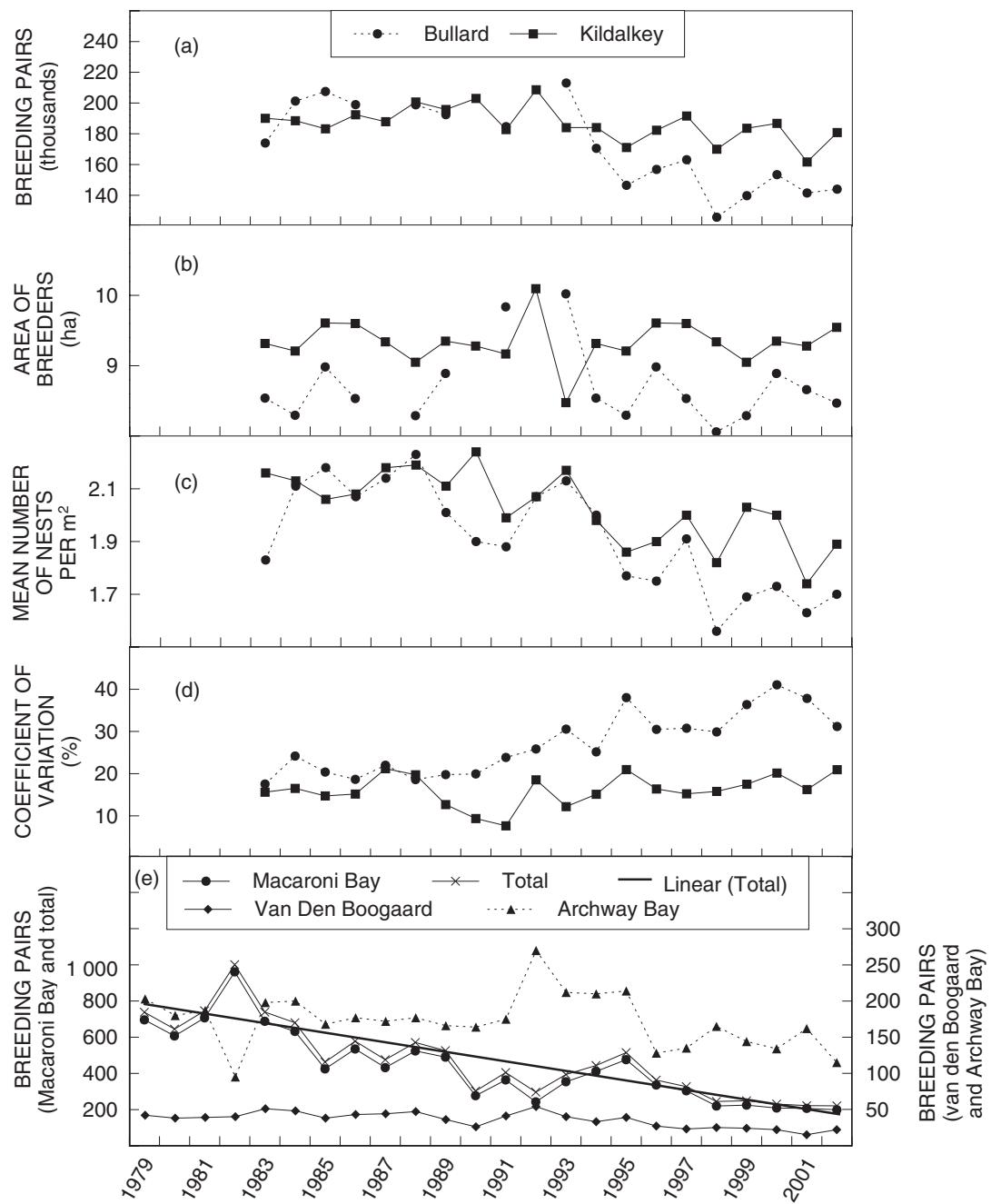


Fig. 2: Estimates of (a) numbers of breeding pairs, (b) area occupied by breeders, (c) mean density of nests and (d) coefficient of variation on the densities of nests for the main colonies of macaroni penguins at Bullard Beach and Kildalkey Bay, 1983/84–2002/03. In (e) numbers of pairs breeding at Macaroni Bay (north), Archway Bay, Van den Boogaard River and overall at these three colonies are shown for 1979/80–2002/03 (updated from Cooper *et al.* 1997). The linear trend for overall numbers at the three colonies is also shown. The year refers to the year in which the breeding season was initiated

crease ($n = 20$, $r = -0.737$, $p < 0.001$, Fig. 2c). However, the CV on the density of nests did not increase to the same extent as at Bullard Beach, remaining below 21% (Fig. 2d). This suggests that there was a more uniform decrease in the density of nests throughout the main colony at Kildalkey Bay than was the case for Bullard Beach.

The CV provides an estimate of uncertainty regarding the density of nests. A CV of $x\%$ indicates a 95% probability of observations falling within $2x\%$ of the mean. There will also be error on the demarcation of the areas occupied by breeding birds that will increase the CV of estimates of numbers breeding. Therefore, it is not yet shown that there has been a statistically significant reduction in numbers breeding in the main colonies at Bullard Beach and Kildalkey Bay, although there are indications that these colonies are decreasing in size.

Estimates of the overall numbers of macaroni penguins breeding at all colonies except the large colonies at Bullard Beach and Kildalkey Bay fluctuated between 50 000 pairs (1997/98) and 31 000 pairs (2002/03) from 1994/95 to 2001/02, but fell to 31 000 pairs in 2002/03 (Table I, Fig. 3a). Because of the adjustment to account for breeding failure, the estimate for 2001/02 is less certain than those for other years.

The CV on counts of smaller colonies (< 4000 pairs) was $\leq 4\%$ in all except one instance. This suggests that numbers breeding at the smaller colonies decreased in 1996/97, 1997/98 and 2002/03 (Fig. 3a).

The combined number of macaroni penguins breeding at Macaroni Bay (north), Archway Bay and Van den Boogaard River was 738 pairs in 1979/80, increased to 1 001 pairs in 1982/83 and then decreased, with fluctuation, by 88% to 221 pairs in 2002/03 (Fig. 2e). From 1979/80 to 2002/03, the modelled linear rate of decrease of the combined number of pairs at the three colonies was 26 pairs per year, i.e. 3.5% of the 1979/80 population (c. 3.7% for 1980/81–1999/00, Woehler *et al.* 2001). This trend was significant ($n = 24$, $r = -0.892$, $p < 0.001$). The decreases were similarly significant for the colonies at Macaroni Bay North ($n = 24$, $r = -0.863$, $p < 0.001$) and Van den Boogaard River ($n = 24$, $r = -0.723$, $p < 0.001$), but not for that at Archway Bay ($n = 24$, $r = -0.268$, $p < 0.5$). However, the colony at Archway Bay decreased from a stable (except in 1982) level during the period 1979/80–1991/92 (average 174 pairs) to another stable level during 1996/97–2002/03 (average 40 pairs), after increasing to an average of 227 pairs from 1992/93 to 1997/98 (Fig. 2e).

Breeding

Dates at various stages in the breeding of macaroni penguins during the period 1994/95–1999/00 are shown in

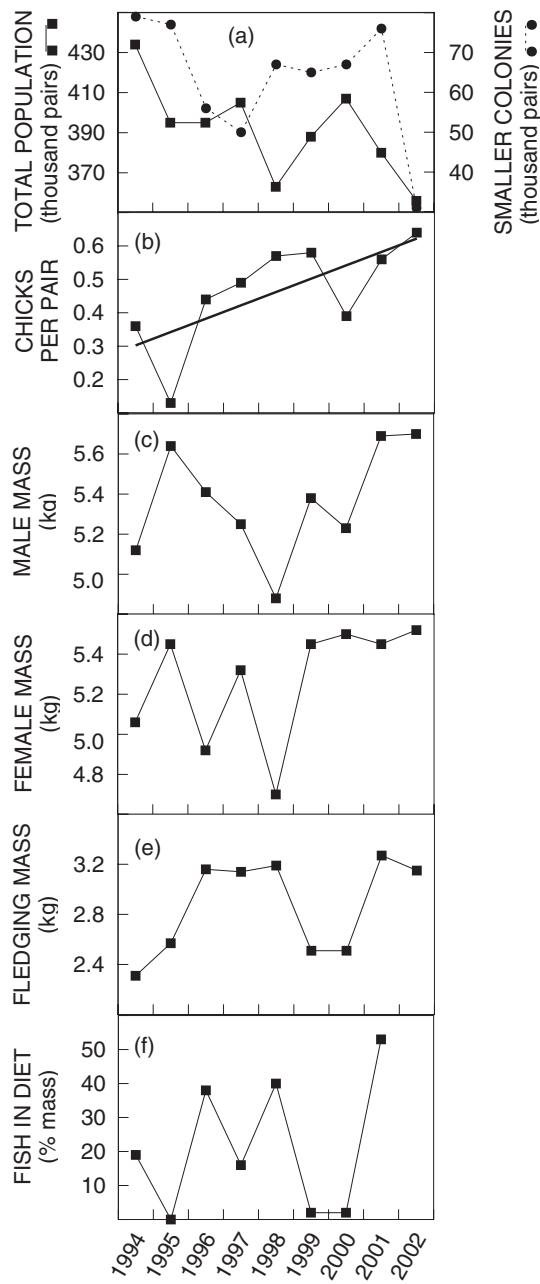


Fig. 3: Trends in (a) numbers of macaroni penguins breeding at Marion Island and at all colonies except the main colonies at Bullard Beach and Kildalkey Bay, (b) average number of chicks fledged per pair (the linear trend is also shown), (c) mean mass of males on arrival at breeding colonies, (d) mean mass of females on arrival at breeding colonies, (e) mean mass of chicks at fledging and (f) the contribution of fish to the diet during the chick-rearing period, 1994/95–2002/03. The year refers to the year in which the breeding season was initiated

Table II: Dates at various stages in the breeding of macaroni penguins at Macaroni Bay (north), Marion Island, 1994/95–1999/00

Stage of breeding	Date					
	1994/95	1995/96	1996/97	1997/98	1998/99	1999/00
First adult at colony	10 Oct.	03 Oct.	06 Oct.	15 Oct.	07 Oct.	07 Oct.
Median date of arrival of adults	20 Oct.	19 Oct.	16 Oct.	19 Oct.	20 Oct.	21 Oct.
Modal date of arrival of adults	24 Oct.	30 Oct.	18 Oct.	18 Oct.	06 Nov.	14 Oct.
Arrival of adults completed	30 Oct.	04 Nov.	27 Oct.	01 Nov.	06 Nov.	04 Nov.
First egg laid	28 Oct.	27 Oct.	23 Oct.		31 Oct.	02 Nov.
Median laying date	03 Nov.	04 Nov.	01 Nov.		05 Nov.	03 Nov.
Modal laying date	03 Nov.	05 Nov.	02 Nov.		02 Nov.	04 Nov.
95% of nests with eggs	08 Nov.	10 Nov.	05 Nov.		11 Nov.	04 Nov.
Last egg laid	10 Nov.	13 Nov.	09 Nov.		09 Nov.	04 Nov.
First egg hatched	07 Dec.	07 Dec.	05 Dec.		15 Dec.	10 Dec.
One-third of eggs hatched	11 Dec.	13 Dec.	05 Dec.		15 Dec.	10 Dec.
Median date of hatching	15 Dec.	11 Dec.	07 Dec.		20 Dec.	13 Dec.
Modal date of hatching	13 Dec.	11 Dec.	09 Dec.		18 Dec.	14 Dec.
Last egg hatched	23 Dec.	16 Dec.	09 Dec.		25 Dec.	16 Dec.
First chick in crèche	03 Jan.	03 Jan.	31 Dec.		04 Jan.	01 Jan.
Two-thirds of chicks in crèche	05 Jan.	10 Jan.	31 Dec.		09 Jan.	04 Jan.
Median date of entering crèche	08 Jan.	10 Jan.	01 Jan.		18 Jan.	03 Jan.
Modal date of entering crèche	04 Jan.	09 Jan.	31 Dec.		13 Jan.	04 Jan.
Last chick in crèche	13 Jan.	18 Jan.	02 Jan.		01 Feb.	05 Jan.
First date of fledging	12 Jan.	20 Jan.	07 Jan.		30 Jan.	
Median date of fledging	04 Feb.	07 Feb.	29 Jan.		14 Feb.	
Modal date of fledging	21 Feb.	20 Feb.	15 Feb.		28 Feb.	
Last date of fledging	27 Feb.	26 Feb.	21 Feb.		29 Feb.	

Table II. The first adults were noticed at colonies between 3 and 10 October. Arrival of adults was complete by 27 October–6 November. Egg laying took place between 23 October and 13 November. In five seasons, dates at which 95% of nests had eggs varied by just eight days (4–11 November). Eggs hatched between 5 and 25 December. Dates by which one-third of eggs had hatched varied between 5 and 15 December. In 1996/97, all eggs hatched within a period of five days. In 1999/00 the period of hatching lasted six days, in 1995/96 10 days, in 1998/99 11 days and in 1994/95 17 days. Chicks entered crèches between 31 December and 1 February. Two-thirds of chicks were in crèches by between 31 December and 10 January. Fledging began about 12 January and was completed by 29 February.

From 1994/95 to 2002/03, the mean number of chicks fledged by macaroni penguin pairs (based on counts of incubating birds and of chicks in crèches at set times) varied between 0.13 and 0.64, with an overall mean (weighting years equally) of 0.46 ($n = 9$, $SD = 0.15$). Apart from decreases in 1995/96 and 2000/01, the mean number of chicks fledged per pair increased with time (Fig. 3b). The increase was significant ($n = 9$, $r = 0.669$, $p < 0.05$).

Mass on arrival at colonies of males was significantly correlated with that of females ($n = 9$, $r = 0.708$, $p < 0.05$). Birds of both sexes were relatively heavy on ar-

rival in 1995/96, 2001/02 and 2002/03, but were light in 1998/99 (Fig. 3c, d).

Mean mass of chicks at fledging ranged from 2.31 to 3.27 kg. It was below 2.6 kg in 1994/95, 1995/96, 1999/00 and 2000/01, but above 3.1 kg in the other five seasons (Fig. 3e). It was significantly related to the contribution of fish to the diet during chick rearing ($n = 8$, $r = 0.788$, $p < 0.05$) and positively, but not significantly, related to the number of chicks fledged per pair ($n = 9$, $r = 0.555$, $p < 0.2$).

Of 19 macaroni penguins whose age at first breeding was ascertained, five were two years old and 14 were three years old.

Diet

In most seasons, crustaceans dominated the diet of macaroni penguins at Marion Island during the chick rearing stage (Table III). However, fish constituted 37–52% of the mass of regurgitations in 1996/97, 1998/99 and 2001/02 (Fig. 3f).

DISCUSSION

Rand (1955) mapped 10 breeding colonies as present at Marion Island in 1951/52. He roughly estimated a total population of 205 800 breeding birds, based on

Table III: The contribution by mass (%) of cephalopods, fish, crustaceans and other organisms to the diet of macaroni penguins at Marion Island during the chick-rearing periods of the 1983/84–1984/85 (Brown and Klages 1987) and 1994/95–2001/02 breeding seasons. Mass was not corrected to account for the original biomass of cephalopods and fish ingested. The number of diet samples collected (*n*) is indicated

Season	<i>n</i>	Contribution by mass (%)			
		Cephalopods	Fish	Crustaceans	Other
1983/84	30	2	0	98	0
1984/85	45	2	10	88	0
1994/95	30	6	19	75	0
1995/96	45	1	0	96	3
1996/97	45	2	37	61	0
1997/98	45	1	17	82	0
1998/99	40	4	40	56	0
1999/00	45	3	2	95	0
2000/01	45	9	2	89	0
2001/02	37	1	53	46	0

estimates of breeding areas for eight named colonies and utilizing an average nest density. His combined estimate for the two largest colonies, Bullard Beach and Kildalkey Bay, of 180 000 birds represents 88% of his island total. Van Zinderen Bakker (1971) estimated the sizes of the two largest breeding colonies, Bullard Beach and Kildalkey Bay, respectively as 500 000 and one million birds, based on assessments of colony areas and nest densities. Together, this represents 75% of his total island estimate of two million birds. It is considered that these two early estimates for the 1950s and 1960s must be treated with great caution.

Williams (1978) mapped 30 breeding colonies around Marion Island during the period 1974–1977, then stated as containing an estimated 450 000 breeding pairs. He showed that most occurred on grey lava, where landing is relatively easy on shallow boulder beaches, with only seven colonies on black lava, which tends to form steep and broken shores. This estimate, more precisely given as 449 892 pairs, was made from both ground counts in the smaller colonies and from aerial photographs of moulting birds in the large colonies in March (Siegfried *et al.* 1978). It can be deduced from data in Siegfried *et al.* (1978) that the Bullard Beach colony was estimated as containing 209 280 breeding pairs and that of Kildalkey Bay 202 430 pairs (together representing 92% of the estimated island population). Photographs of the main colony at Kildalkey Bay indicate an increase in the area occupied by breeders between 1949 and 1977 (Watkins 1987).

In November 1983, techniques similar to those used in this study provided an estimate of 405 084 pairs (Watkins 1987).

In 1980, a volcanic eruption at Kaalkoppie on the island's western coast displaced a breeding colony of macaroni penguins estimated in 1974–1977 to contain

7 571 breeding pairs (Siegfried *et al.* 1978, Verwoerd *et al.* 1981, Berruti 1982). Fewer than 400 pairs were found breeding, all unsuccessfully, in the summer following the eruption, and many birds were seen swimming ashore, apparently not being able to land because of a newly formed lava cliff at the site of the landing beach (Berruti 1982). Probably as a consequence of the eruption, a new colony of some 200 pairs was established about 2 km north of Kaalkoppie in 1980/81 (Berruti 1981). A second hitherto unreported colony of 200–300 pairs was then also found at Kaalkoppie at a site not accessible or visible prior to the eruption (Berruti 1981). By 1983/84, the Kaalkoppie colony had grown to 3 552 pairs (Watkins 1987).

Although a reduced number of macaroni penguins at Marion Island after 1983 is not yet statistically shown, there are several indications that the population has decreased since that date. There was a significant decrease in numbers breeding at three small colonies between 1979/80 and 2002/03, mainly after 1982/83 (Fig. 2e). The population for all colonies, except the main colonies at Bullard Beach and Kildalkey Bay, decreased between 1994/95 and 2002/03 (Fig. 3a – the estimate for 2001 is less certain than those for other years because of the need to account for nest failure prior to the time of this survey). From 1983/84 to 2002/03 at the main colonies at Bullard Beach and Kildalkey Bay, there was no long-term trend in the area occupied by breeders, but the density of nests decreased. Therefore, a decrease between 1983/84 and 2002/03 in the overall number of macaroni penguins breeding at Marion Island is likely. At nearby Prince Edward Island, numbers of macaroni penguins approximately halved from 17 000 pairs in 1976/77 (Watkins 1987) to 9 000 pairs in 2001/02 (Ryan *et al.* 2003).

At Marion Island there have been long-term trends

in climatic parameters. Annual mean surface air temperature at the island increased by 1.2°C between 1969 and 1999. Annual precipitation decreased between the mid 1960s and the mid 1990s (Smith 2002). Sea surface temperature increased by 1.4°C between 1949 and 1998 (Mélice *et al.* in press). It is possible that climate change has influenced the availability of food to macaroni penguins at Marion Island, as has been postulated for rockhopper penguins *Eudyptes chrysocome* at Campbell Island to the south of New Zealand (Moors 1986, Cunningham and Moors 1994), at Amsterdam Island in the southern Indian Ocean (Guinard *et al.* 1998) and at Marion Island (Crawford *et al.* 2003a).

At Bird Island, South Georgia, mean masses of macaroni penguins on arrival at colonies in 1977 (4.69 kg males, 4.80 kg females, Croxall *et al.* 1988) were lighter than those observed at Marion Island, except for females in 1998/99. At Heard Island, mass on arrival of females (5.21 kg, Downes *et al.* 1959 cited in Marchant and Higgins 1990) was within the range observed at Marion Island (Fig. 3d).

In 1998/99, the masses of both male and female macaroni penguins returning to colonies at Marion Island were less than in other years (Fig. 3c, d) and there was a decrease in the overall number of birds breeding (Fig. 3a). Food may have been less available to birds before the breeding season of 1998/99. The species leaves the island after moulting by 25 April or earlier (Rand 1954, JC pers. obs.) before returning at the start of the next breeding season. Even when breeding, macaroni penguins may forage up to 300 km from the island (Brown 1987). In 1997/98, breeding by many seabirds at Marion Island was considerably better or worse than usual and may have been influenced by the *El Niño* of 1997/98 (Crawford *et al.* 2003b). Breeding by macaroni penguins does not appear to have been affected in 1997/98, although at colonies other than the main colonies at Bullard Beach and Kildalkey Bay, reduced numbers were recorded (Fig. 3a). At Bird Island, South Georgia and Adélie Land, responses of seabirds, including macaroni penguins at Bird Island, to *El Niño* events have lagged such events by one year (Croxall *et al.* 1988, Croxall 1992, Chastel *et al.* 1993).

The phenology of breeding at Marion Island (Table II) is in agreement with that indicated by Cooper and Brown (1990). At Kerguelen Island, adults return to colonies slightly earlier (from 29 September), but egg laying commences in the first days of November, similar to the situation at Marion Island (Weimerskirch *et al.* 1989). At Heard Island, birds return to colonies after October 20, later than at Marion Island (Downes *et al.* 1959, cited in Marchant and Higgins 1990). At South Georgia, average arrival date is 3 November

(Croxall and Prince 1987).

Assuming an age at first breeding of three years, an annual survival rate for all age-classes of 76.5% (thought applicable to adults – Croxall and Davis 1999) and a period at sea of nine months for birds in their first year (Table II), it would be necessary for pairs on average to fledge 0.90 chicks per year to maintain a population in equilibrium. Immature birds may have a lower survival rate than adults. Not all adult birds breed in each year and there may not be an equal sex ratio. At Heard Island in 1953, there was probably an excess of males (Downes *et al.* 1959, cited in Marchant and Higgins 1990). Each of these factors will require a higher production of chicks to maintain the population in equilibrium. The averages of 0.43 chicks fledged per pair recorded for the period 1974–1977 (Williams 1980), 0.35 for 1979/80–1995/96 (Cooper *et al.* 1997) and 0.46 for 1994/95–2002/03 are all much less than the level required to maintain a population in equilibrium. The latter two values may be underestimates because some chicks may have left crèches before the counts, which were made about 10 February (Table II). However, as with rockhopper penguins (Crawford *et al.* 2003a), it appears that inadequate reproduction may be a major cause of the likely population decrease. At Marion Island, coherence of trends in breeding success at different colonies suggests that macaroni penguins are influenced by events operating at a wide rather than a local scale (Cooper *et al.* 1997).

Paradoxically, although the overall population has probably been decreasing (Fig. 3a), there was a significant increase in breeding success between 1994/95 and 2002/03, when the average of 0.64 chicks fledged per pair was the highest at that date recorded at Marion Island (Fig. 3b), but still probably insufficient to maintain the population. At Heard Island, pairs fledged about 0.34 chicks on average. At Bird Island, South Georgia, from 1977 to 1987 macaroni penguins fledged chicks from 44% of eggs laid (Croxall *et al.* 1988).

At Marion Island during 1973–1974, macaroni penguins fed mostly on euphausiids (Williams and Laycock 1981). In 1983/84 and 1984/85, crustaceans, mainly a decapod shrimp *Nauticaris marionis*, euphausiids *Euphausia vallentini*, *Thysanoessa vicina* and amphipods *Themisto gaudichaudii*, again contributed most of the food eaten during the chick-rearing period. When chicks were small, the diet was mainly crustaceans, whereas fish and cephalopods dominated the food when chicks were larger (Brown and Klages 1987). In the early stage of chick rearing, macaroni penguins are thought to forage up to 50 km from Marion Island (Brown and Klages 1987), and during late chick rearing 59–303 km from the island (Brown 1987). At Elephant and King George islands (South Shetland Islands) and Bird Island, South Georgia,

crustaceans dominate the diet of macaroni penguins (Brown and Klages 1987, and references therein).

At Marion Island, the significant correlation between the contribution of fish to the diet and mass of fledglings suggests that availability of fish influences the condition of chicks at fledging. At South Georgia, when Antarctic krill *Euphausia superba* are scarce, macaroni penguins take increased proportions of the smaller amphipod *Themisto* sp. In such years, they can usually catch sufficient prey to achieve comparable breeding success with years of normal krill availability. However, meal mass and chick mass at fledging are significantly reduced (Croxall and Davis 1999). Sometimes, when food is scarce, chicks of low mass are more likely to die than when food is abundant, which may lead to a disproportionate number of heavy chicks surviving (Williams and Croxall 1990).

There is indication that condition of chicks at fledging may influence first-year survival. Decreases in numbers breeding at Marion Island in 1997/98, 1998/99 and 2002/03 (Fig. 3a) came three years after low masses at fledging in 1994/95, 1995/96 and 1999/00 (Fig. 3e). The lag is equivalent to the usual age at first breeding of macaroni penguins at Marion Island. The decreased numbers breeding may therefore result from poor recruitment of first-time breeders to the parent population.

The observed age at first breeding of macaroni penguins at Marion Island of about 3 years is considerably less than the 7.5 years reported by Croxall and Davis (1999). Based on an adult survival of 76.5% (Croxall and Davis 1999), average longevity of breeders then reduces from about 10.5 years to about six years. In terms of criteria of The World Conservation Union (IUCN), a population decrease of >50% in three generations merits a classification of Vulnerable (IUCN 2001). The decrease of 88% in numbers breeding at the three small colonies monitored between 1979/80 and 2002/03, a period of 23 years or 3.83 generations, is equivalent to a decrease of 69% in three generations. At all colonies other than the main colonies at Bullard Beach and Kildalkey Bay, there was a decrease of 60% between 1994/95 and 2002/03 (1.33 generations, Table I). The overall decrease of 18% between 1994/95 and 2002/03 is equivalent to 40% in the last three generations. Therefore, listing of the macaroni penguin as Near Threatened (Barnes 2000) or Vulnerable (BirdLife International 2000) appears appropriate in the context of Marion Island.

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DECREASE IN NUMBERS OF THE EASTERN ROCKHOPPER PENGUIN *EUDYPTES CHRYSOCOME FILHOLI* AT MARION ISLAND, 1994/95–2002/03

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The number of eastern rockhopper penguins *Eudyptes chrysocome filholi* breeding at subantarctic Marion Island decreased from about 173 000 pairs in 1994/95 to about 67 000 pairs in 2001/02. During 1994/95–2002/03 pairs fledged on average 0.40 chicks per year, an amount thought insufficient to balance mortality of breeding adults, and there was a decrease in the mass at arrival at breeding colonies of both males and females. Except in 1997/98, the mass of chicks at fledging was less than that recorded at two other localities. These factors suggest an inadequate supply of food for rockhopper penguins at Marion Island. Decreases of rockhopper penguins at several other localities also have been attributed to inadequate food. Rockhopper penguins at Marion Island continued to feed mainly on crustaceans during chick rearing. There was a marked increase in the contribution of fish to the diet in 1999/00 that coincided with an increase in mass at arrival at colonies of both males and females. Trends in numbers of pairs breeding in different sections of Marion Island were not always consistent, indicating the need for island-wide monitoring to establish the overall trend.

Key words: breeding success, diet, *Eudyptes chrysocome*, Marion Island, mass, population decrease, rockhopper penguin, Subantarctic

The rockhopper penguin *Eudyptes chrysocome* has a circumpolar distribution in the southern hemisphere, where it breeds at subantarctic and south temperate islands (Marchant and Higgins 1990). Three subspecies have been recognized, the southern *chrysocome*, northern *moseleyi* and eastern *filholi* forms. It is *filholi* that occurs at South Africa's Prince Edward Islands in the southern Indian Ocean, along with three other species of penguins. Eastern rockhopper penguins also breed at Crozet, Kerguelen, Heard, MacDonald, Macquarie, Campbell, Auckland and Antipodes islands, so their distribution extends from the south-western Indian Ocean to islands south of New Zealand (Ellis *et al.* 1998).

Woehler (1993) estimated the overall population of eastern rockhopper penguins to be at least 832 000 pairs. A decrease of 94% was reported for Campbell Island between the early 1940s and 1985 and attributed to rising sea surface temperatures causing euphausiids to move offshore, thereby affecting availability of prey to the penguins and the growth and survival of chicks (Moors 1986, Cunningham and Moors 1994). The

population at Antipodes Islands is thought to have decreased between 1972/73 and 1989/90 and that at Auckland Island from 5 000–10 000 pairs in 1972/73 to 2 700–3 600 pairs in 1990 (Cooper 1992, Woehler and Croxall 1997, Ellis *et al.* 1998).

There have also been decreases in populations of other subspecies of rockhopper penguin. At Amsterdam Island in the south-western Indian Ocean, the population of northern rockhopper penguins decreased at a rate of 2.7% per year between 1971 and 1993. This decrease may have been caused by a drop in sea surface temperature affecting the distribution and abundance of prey organisms, or by a large increase in numbers of Subantarctic fur seals *Arctocephalus tropicalis* at the island (Guinard *et al.* 1998). At the Falkland Islands, the population of southern rockhopper penguins decreased by about 90% between 1932/33 and 1995/96 (Bingham 1998a).

At Marion Island in the Prince Edward Islands group, numbers of eastern rockhopper penguins breeding at three small study colonies decreased between 1983/84 and 1999/00 (Cooper *et al.* 1997, Woehler *et al.* 2001).

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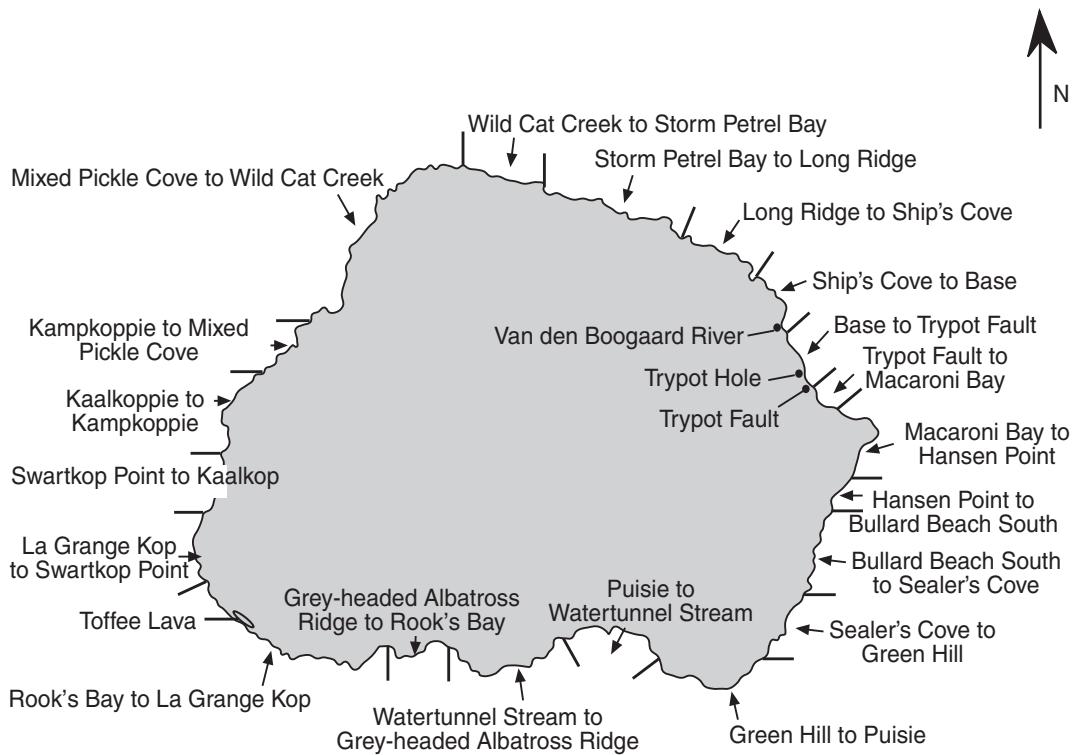


Fig. 1: Marion Island, showing the sections of the coast where breeding pairs of rockhopper penguins were counted and the location (dots) of colonies monitored to estimate breeding success

This paper presents further evidence for reduced numbers of rockhopper penguins at Marion Island and considers reasons for the decrease.

MATERIAL AND METHODS

Population trend and breeding success

Counts of the number of rockhopper penguins breeding at Trypot Hole, Trypot Fault and the Van den Boogaard River in north-eastern Marion Island (290 km^2 ; $46^{\circ}52'S$, $37^{\circ}51'E$; Fig. 1) were made annually from 1983/84–2002/03 as close to 4 December as possible. At the same colonies, counts of the numbers of newly-hatched chicks and chicks in crèches were made as close as possible to 4 January and 28 February respectively (Cooper *et al.* 1997). These counts were undertaken from outside the colonies and are unlikely to have disturbed the breeding birds. From 1994/95

to 2002/03, each count was made three times and the mean and standard deviation calculated. For each season, the average number of chicks fledged per pair was calculated. Chicks in crèches were assumed to have fledged.

From 21 November to 6 December 1994, from 13 November to 6 December 1996 and from 18 to 23 December 2001, all localities where rockhopper penguins breed at Marion Island were visited and the number of breeding pairs was counted or estimated. Counts at accessible colonies were made with the aid of binoculars and tally counters. Estimates were made for less accessible colonies by counting nesting birds in a visible section of the colony and multiplying by a factor to account for birds that probably could not be seen, for example in areas with cliff overhangs or in inaccessible lava tunnels that obscured birds. In 1996, the approximate error on counts and estimates was gauged from repeat counts and on-the-spot consideration of uncertainty of the area occupied by breeding birds. Because the count in 2001 was conducted 2–3 weeks

later than in the other two years and hence breeding attempts by a greater proportion of pairs may have failed, the counts in 2001 were adjusted to account for failures between 7 December and the date of the survey using information collected at the three colonies where long-term monitoring is undertaken.

Counts were made of all active rockhopper penguin nests along two sections of the Marion Island coastline from 20 November to 17 December 1997, from 29 November to 15 December 1998, from 23 November to 8 December 1999, from 20 November to 7 December 2000 and from 28 November to 8 December 2002. The sections surveyed were Storm Petrel Bay to Hansen Point in the north-east of the island and Rook's Bay to Swartkop Point, but excluding Toffee Lava, in the south-west (Fig. 1). The sections were chosen because they were relatively easy to survey, so counts were thought more accurate than for other sections, and because they covered different parts of the island. In 1994, 1996 and 2001 these sections accounted for 25, 24 and 34% respectively of the overall count.

Timing of breeding

In 1994/95, the breeding phenology of rockhopper penguins was studied by monitoring the arrival of adults at Van den Boogaard River and Trypot Fault and the progress of 55 nests and the fledging of chicks at Trypot Hole. Methods used were those outlined by the Commission for the Conservation of Antarctic Marine Living Resources (SC-CAMLR 1995). Because adults were not banded, the number arriving on a given day was taken to be the difference between the numbers seen at the colony on that day and on the previous day. The distributions of nests were mapped, so the progress of individual nests could be followed.

At Marion Island, adult rockhopper penguins re-occupy colonies during late October and early November. Laying takes place in late November and early December, and chicks hatch in late December and early January and fledge by mid March (Cooper and Brown 1990). The normal clutch of rockhopper penguins is two eggs (Williams 1980a). Averages at Marion Island for laying interval, incubation period of second-laid eggs and incubation period of first-laid eggs were 4.4, 34.2 and 39.1 days respectively (Williams 1981). Incubation does not commence until the second egg is laid and eggs are not warmed to steady temperatures until the second half of the incubation period (Burger and Williams 1979).

In 1994/95, the numbers of adults at Van den Boogaard River and Trypot Fault were counted daily from 20 October until 21 November. Nests at Trypot Hole

were checked daily from 15 November until all chicks were in crèches. The days when each egg and chick was first seen were recorded, as well as days when chicks entered crèches. When all chicks were in crèches, their numbers were counted daily until fledging was complete. Records were kept of all chicks that died.

Mass of adults on arrival at colonies and of chicks at fledging

For each of the 1994/95–2002/03 breeding seasons, the mass at arrival at breeding colonies of 37–113 males and 40–102 females and the mass at fledging of 106–250 chicks was obtained. Males and females were weighed between 28 October and 14 November. Sexes were discriminated using bill measurements. Males are larger than females and have longer bills (Marchant and Higgins 1990). At Marion Island, mean culmen length for males is 45.7 mm (SD 1.4 mm) and for females 40.6 mm (SD 1.7 mm, Williams 1980b). Chicks that had obtained final fledging plumage were weighed in early March.

Diet

From 1994/95 to 2001/02, 30–45 stomach samples were collected each season between 6 January and 9 March, during the chick-rearing period (Cooper and Brown 1990). Birds were caught when they came ashore and their stomachs emptied using a stomach-flushing technique modified (water was poured down a tube rather than pumped into the stomach) from that described by Wilson (1984). Generally each bird's stomach was flushed only once. Samples were preserved in ethanol or frozen. In the laboratory, all liquid was drained from the sample through a small-meshed sieve. Each drained sample was then sorted into crustacean, cephalopod and fish components and then weighed to obtain their relative contribution to the diet.

The original biomass of cephalopods and fish ingested was not estimated. At Marion Island in 1984, the use of regressions relating lower rostral length of cephalopod beaks to length of dorsal mantle and mass increased the estimated contribution by mass of cephalopods from 2.5% (estimated from regurgitations) to 5%. Use of regressions relating otolith diameter to fish length and fish mass increased the estimated contribution by mass of fish from 6 to 14%. As a result the estimated contribution of crustaceans in the diet decreased from 91 to 81% (Brown and Klages 1987).

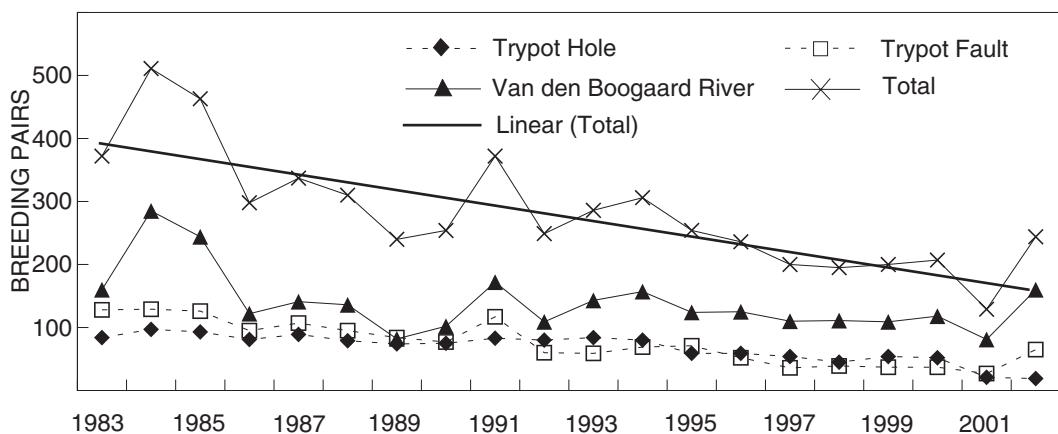


Fig. 2: Trends in numbers of rockhopper penguins breeding at three colonies at Marion Island and of these three colonies combined, 1983/84–2002/03 (updated from Cooper *et al.* 1997). The linear trend for the combined count is shown

RESULTS

Population trend and breeding success

The combined number of rockhopper penguins breeding at Trypot Hole, Trypot Fault and Van den Boogaard River decreased in a fluctuating manner from 372 pairs in 1983/84 to 306 pairs in 1994/95 and to 129 pairs in 2001/02. It then increased to 244 pairs in 2002/03. The overall decrease between 1983/84 and 2002/03 was 34%, that between 1994/95 and 2002/03, 20%. Trends at the three colonies were similar (Fig. 2) and significantly related to each other. The strongest correlation was obtained between the nearby colonies of Trypot Hole and Trypot Fault ($n = 20$, $r = 0.750$, $p < 0.001$). Correlations for the more distant colony at Van den Boogaard River with Trypot Hole ($n = 20$, $r = 0.700$, $p < 0.001$) and Trypot Fault ($n = 20$, $r = 0.505$, $p < 0.05$) were weaker. The modelled rate of linear decrease of the combined number of pairs at the three colonies was 13 nests per year, i.e. 3.5% of the 1983/84 population. This trend was significant ($n = 20$, $r = -0.803$, $p < 0.001$). A least-squares model was used: $N_t = a - bt$, where a and b are constants and N_t the number of breeding pairs at time t , $t = 0$ being 1983.

The number of active nests at Trypot Hole, Trypot Fault and Van den Boogaard River combined decreased from 129 on 7 December 2001 to 70 between 10 and 14 January 2002, i.e. by 59 nests in 36 days. Assuming a linear decrease over this period, about 21 nests or 16% of the total would have been lost by December 20, the midpoint of the 2001/02 total island survey. There-

fore, the late total island count in 2001/02 was increased by 16%. The assumption of linear decrease may not be valid if nest failures occur at specific times in the breeding cycle.

Estimates of the overall population of rockhopper penguins at Marion Island decreased from about 173 000 pairs in 1994/95 to 67 000 pairs in 2001/02, i.e. by 61% (Table I). In 1996/97, the approximate error on counts was thought to be 5–20%, depending on the ease with which counts were undertaken. The highest errors were assumed for areas with dangerous cliff overhangs and inaccessible lava tunnels that obscured birds and for inaccessible beaches that were surveyed through binoculars. There was substantial variability on estimates for these regions, e.g. for Watertunnel Stream to Grey-headed Albatross Ridge. The estimated overall error on the 1996 count was 15%.

Estimates of the number of nests in the two sections of the island that were regularly counted decreased by 46%, from about 43 000 in 1994/95 to 23 000 in both 2001/02 and 2002/03 (Table I). This decrease was approximately linear, with the annual loss being about 5.6% of the total in 1994/95 (Fig. 3). The trend was significant ($n = 8$, $r = -0.948$, $p < 0.001$). From 1994/95 to 1997/98 counts decreased in both sections. From 1997/98 to 2002/03, the trends for the two sections were dissimilar. Numbers breeding between Storm Petrel Bay and Hansen Point decreased from 1997/98 to 1998/89 and again from 2000/01 to 2001/02, but were stable between 1998/99 and 2000/01 and increased in 2002/03. Conversely, numbers between Rook's Bay and Swartkop Point increased from 1997/98 to 1998/99 and from 2000/01 to 2001/02, but

Table 1: Counts of numbers of breeding pairs of rockhopper penguins for sections of the coast of Marion Island, 1987/88 and 1994/95–2002/03. Totals for regularly counted sections are indicated, as are the overall totals for years in which a complete count was conducted. For 2001/02 the count is shown, as well as an adjustment to account for failure of nests after 6 December, the date of completion of the 1994/95 and 1996/97. The adjustment was based on information collected at colonies that were monitored for breeding success (see text)

Region	Number of breeding pairs					
	1987/88	1994/95	1996/97	1997/98	1998/99	1999/00
Base to Trypot Fault	1 137	1 386	1 351	731	502	662
Trypot Fault to Macaroni Bay	350	293	274	195	88	78
Macaroni Bay to Hansen Point	6 650	8 588	6 038	5 273	5 132	5 244
Hansen Point to Bullard Beach South	900	1 130	958			
Bullard Beach South to Sealer's Cove	5 100	11 640	8 072			
Sealer's Cove to Green Hill	2 960	5 392	5 535			
Green Hill to Puisie	18 900	29 803	19 433			
Puisie to Watertunnel Stream	20 000	7 990	6 142			
Watertunnel Stream to Grey-headed Albatross Ridge	17 800	13 960	22 489			
Grey-headed Albatross Ridge to Rook's Bay	1 200	4 565	3 640			
Rook's Bay to La Grange Kop, excluding Toffee Lava	4 450	10 765	8 081	6 719	9 615	7 022
Toffee Lava	2 000	8 774	10 357			
La Grange Kop to Swartkop Point	3 300	6 645	5 694	6 344	8 399	6 531
Swartkop Point to Kaalkoppie	4 800	13 521	10 193			
Kaalkoppie to Kampkoppie	500	2 446	1 827			
Kampkoppie to Mixed Pickle Cove	5 100	7 411	5 677			
Mixed Pickle Cove to Wild Cat Creek	16 000	15 977	13 633			
Wild Cat Creek to Storm Petrel Bay	5 530	7 632	6 008			
Storm Petrel Bay to Long Ridge (including Long Ridge)	9 950	5 329	5 028	6 122	5 751	4 688
Long Ridge to Ship's Cove	5 650	6 309	5 570	5 236	4 055	4 201
Ship's Cove to Base	5 375	3 521	4 118	3 535	2 518	3 007
Total for sections counted regularly	36 862	42 836	36 154	34 155	36 060	31 506
Total	137 652	173 077	150 118			
						55 998
						66 664
						23 184
						22 719
						23 184

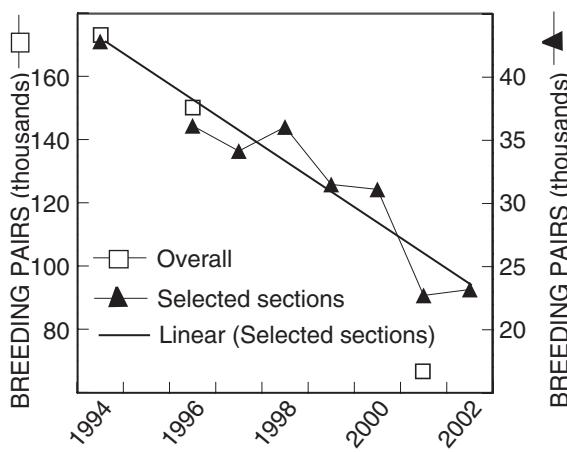


Fig. 3: Trends in numbers of rockhopper penguins breeding at Marion Island for selected sections of the island and overall, 1994/95–2002/03. The linear trend for the two sections of the island that were regularly counted is shown

decreased from 1998/99 to 2000/01 and in 2002/03.

From 1994/95 to 2002/03 the estimated mean number of chicks fledged by rockhopper penguin pairs, based on counts of incubating birds and of chicks in crèches at set times, varied between 0.35 and 0.46, except in 1998/99 (0.25), with an overall mean (weighting years equally) of 0.40 ($n = 9$, $SD = 0.07$, Fig. 4a).

Timing of breeding

In 1994/95, male rockhopper penguins began arriving at Trypot Fault on 29 October and at Van den Boogaard River on 30 October. Females were seen in these colonies for the first time on 2 November and 5 November respectively, i.e. 4–6 days after the first arrival of males.

Dates at various stages in the breeding of rockhopper penguins during the 1994/95 breeding season are shown in Table II. Egg-laying lasted from 17 November to 3 December and hatching from 25 December to 8 January. Chicks entered crèches between 19 and 29 January and fledged between 8 February and 14 March.

Mass of adults on arrival at colonies and of chicks at fledging

Between 1994/95 and 2002/03 there was a tendency for mass of both males and females on arrival at colonies to decrease (Fig. 4b). Mass on arrival of males was sig-

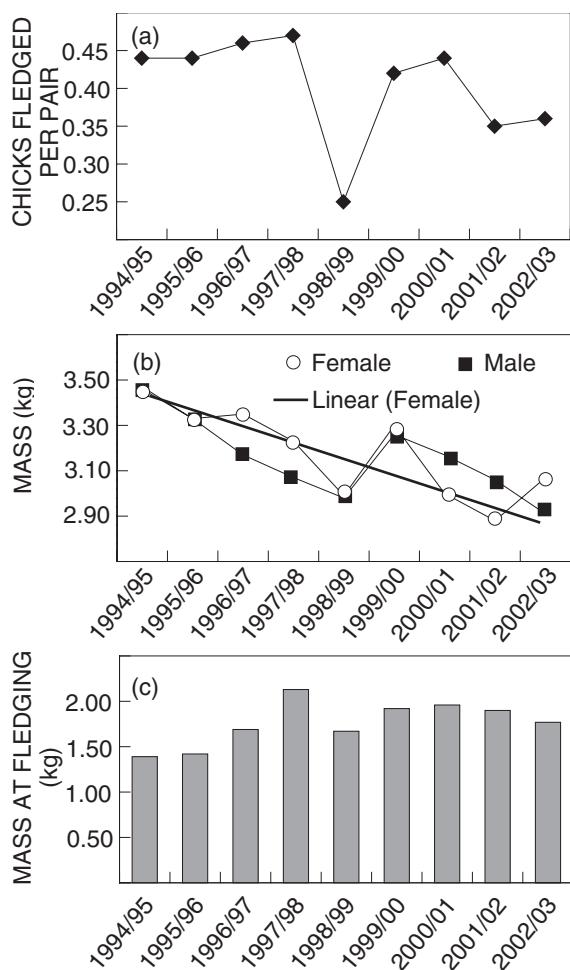


Fig. 4: Trends at Marion Island for rockhopper penguins in (a) chicks fledged per pair, (b) mass on arrival at colonies to breed of males and females and (c) mass of chicks at fledging, 1994/95–2002/03

nificantly correlated with that of females ($n = 9$, $r = 0.752$, $p < 0.02$). The average mass of birds on arrival at colonies (giving equal weight to both sexes) was related to trends in the combined number of rockhopper penguins breeding at Trypot Hole, Trypot Fault and Van den Boogaard River ($n = 9$, $r = 0.725$, $p < 0.05$) and to average breeding success at these colonies ($n = 9$, $r = 0.660$, $p \approx 0.05$).

Mean mass of chicks at fledging was 1.39–1.77 kg from 1994/95 to 1996/97, in 1998/99 and in 2002/03, but from 1.90 to 2.13 kg in 1997/98 and from 1999/00 to 2001/02 (Fig. 4c).

Table II: Dates at various stages in the breeding of rockhopper penguins at Marion Island during the 1994/95 season

Stage of breeding	Date
First adult at colony	29 October
Median date of arrival of adults	9 November
Modal date of arrival of adults	9 November
Arrival of adults completed	20 November
First egg laid	17 November
Median laying date	25 November
Modal laying date	21 November
95% of nests with eggs	25 November
Last egg laid	3 December
First chick hatched	25 December
One-third of chicks hatched	29 December
Median date of hatching	1 January
Modal date of hatching	29 December
Last chick hatched	8 January
First chick in crèche	19 January
Two-thirds of chicks in crèche	24 January
Median date of entering crèche	24 January
Modal date of entering crèche	24 January
Last chick in crèche	29 January
First date of fledging	8 February
Median date of fledging	25 February
Modal date of fledging	2 March
Last date of fledging	14 March

Diet

Crustaceans dominated the diet of rockhopper penguins at Marion Island during the chick-rearing period in all seasons from 1994/95 to 2001/02 (Table III). Except in 1999/00, they contributed 86–99% of the mass of food collected. In 1999/00, fish formed 79% of the diet in February and 39% for the period January–March.

DISCUSSION

Population estimates 1965/66–1996/97

Van Zinderen Bakker (1971) gives the first estimate of a population of one million rockhopper penguins for both Marion and Prince Edward islands for 1965/66, although it is not known what census method he used to obtain this figure. For northern rockhopper penguins at Amsterdam Island, the average age at first reproduction is 4.7 years and adult survival rate is 84% per year (Guinard *et al.* 1998). For a population in equilibrium, this requires that, for every 100 birds aged 4.7 years or older, there are 85 birds aged between 1.7 and 4.7 years. In such a situation, van Zinderen Bakker's estimate for 1965/66 is equivalent to about 270 000 breeding pairs. In the 1970s, there were thought to be

Table III: The contribution by mass (%) of cephalopods, fish and crustaceans to the diet of rockhopper penguins at Marion Island during the chick-rearing periods of the 1983/84–1984/85 (Brown and Klages 1987) and 1994/95–2001/02 breeding seasons. Mass was not corrected to account for the original biomass of cephalopods and fish ingested. The number of diet samples collected (*n*) is indicated

Season	<i>n</i>	Contribution by mass (%)		
		Cephalopods	Fish	Crustaceans
1983/84	35	0	0	100
1984/85	50	3	6	91
1994/95	31	9	5	86
1995/96	30	0	1	99
1996/97	30	5	2	93
1997/98	45	0	5	95
1998/99	33	1	5	94
1999/00	45	1	39	60
2000/01	44	6	6	88
2001/02	41	1	10	89

35 000 pairs of rockhopper penguins at Prince Edward Island (Cooper and Brown 1990). Subtracting this value from van Zinderen Bakker's estimate leaves a population of 235 000 pairs at Marion Island in 1965/66. Because of the inherent uncertainties with this calculation, and the estimate it is based on, the figure obtained should be treated with caution.

In the 1973/74 breeding season, the population of rockhopper penguins at Marion Island was estimated from ground counts to be 424 600 birds (here taken to represent 212 300 pairs; Watkins 1987), but in the period 1974–1977 only 93 286 pairs were counted (Williams *et al.* 1975, 1979, Siegfried *et al.* 1978). The 1973/74 count was conducted along c. 75% of the island's coastline (not including Crawford and Triegaardt bays) during the months of January–March 1974 (Williams *et al.* 1975), so would not have accounted for breeders that failed beforehand. The 1974–1977 count was conducted in January and February (actual year(s) of counts not given) and was thought to have included 75% of the total breeding population (Siegfried *et al.* 1978), so again may be regarded as an underestimate. Data given in Siegfried *et al.* (1978) can be interpreted to show that Crawford and Triegaardt bays were surveyed during the period 1974–1977. The large difference (more than a factor of two) between these two 1970s counts that overlapped in time is puzzling.

For 1987/88, a count of the entire island between 26 November and 9 December gave a total of 137 652 breeding pairs (Cooper and Brown 1990, JC unpublished data). Counts were recorded for similar sections to those used during the period 1994/95–2002/03

(Table I). These early estimates vary widely, reflecting the difficulty in conducting accurate counts and the different times of the surveys. The four estimates between 1965/66 and 1987/88 have a mean of about 169 000 pairs (SD 66 000 pairs), a value not dissimilar to the estimates of 173 000 pairs for 1994/95 and 150 000 pairs for 1996/97 (Table I). The mean for the six estimates up until 1996/97 is 167 000 pairs (SD 52 000 pairs).

Population trend

From 1983/84 to 2002/03, there was a significant decrease in the number of rockhopper penguins breeding at three small colonies (Trypot Hole, Trypot Fault, Van den Boogard River) in north-eastern Marion Island (Cooper *et al.* 1997, Woehler *et al.* 2001, Fig. 2). From 1994/95 to 2002/03, there was a significant decrease in the number of rockhopper penguins in sections in the north-east and south-west of Marion Island that account for one-quarter to one-third of the overall population. From 1994/95 to 2001/02, there was a persistent decrease in the three estimates of the overall population at Marion Island. Assuming an error of 20% on counts, the largest thought to apply for any sector counted in 1996/97, the minimum population in 1994/95 would have been 138 000 pairs and the maximum population in 2001, 80 000 pairs. This indicates a substantial decrease of at least 42% over the period 1994/95–2001/02. Estimates of the decrease in number of breeding rockhopper penguins at Marion Island between 1994/95 and 2002/03, based on counts at the three small monitored colonies, of two sections of the island and of the total population range from 20–61%.

The decrease in the number of rockhopper penguins at Marion Island accords with decreases observed at several other localities in the south-western Atlantic Ocean, south-western Indian Ocean and off New Zealand (Moors 1986, Cunningham and Moors 1994, Ellis *et al.* 1998, Guinard *et al.* 1998, Woehler *et al.* 2001).

In December 2001, 31 655 pairs of rockhopper penguins were counted at Prince Edward Island. Most birds were on eggs and a few small chicks were present. Assuming that 70% of nests hatched chicks (Cooper *et al.* 1997), the total breeding population for 2001/02 was considered to be about 45 000 pairs (Ryan *et al.* 2003). The population in the 1980s was thought to be about 35 000 pairs (Cooper and Brown 1990). The higher estimate for 2001/02 may have resulted from greater coverage in that year and from bias introduced from counting loafing birds as breeders in colonies that were observed at a distance. Therefore,

the population at Prince Edward Island appears to have been stable since the 1980s (Ryan *et al.* 2003). This contrasts with the decrease recorded at Marion Island over the same time period.

Dissimilarity in trends of rockhopper penguins has been observed in other regions. The population of the northern subspecies decreased at Amsterdam Island between 1972 and 1994, whereas at St Paul Island, 80 km distant, it increased over the same period (Guinard *et al.* 1998). There were large decreases of southern rockhopper penguins at the Falkland Islands, but the number breeding in Chile and Argentina apparently remained stable during the 1980s and 1990s (Bingham 1998b).

Trends in the numbers of rockhopper penguins breeding at Trypot Hole, Trypot Fault and Van den Boogard River were significantly related to each other during the seasons 1983/84–1995/96 (Cooper *et al.* 1997). These significant relationships persisted for the period 1983/84–2002/03. All three colonies are located in north-eastern Marion Island, and the correlation was strongest for the colonies at Trypot Hole and Trypot Fault, which are in close proximity to each other. The significant relationships may be influenced by environmental conditions before or at the onset of breeding (Cooper and Lutjeharms 1992, Cooper *et al.* 1997). The sometimes dissimilar trends over wider scales, e.g. between the north-east and south-west of Marion Island and between Marion and Prince Edward islands, suggest that any such influence is relatively local in nature and that monitoring over wider areas is required to ascertain trends in the overall population.

Breeding success

Estimates of mean age at first breeding (4.7 years) and adult survival (84% per year) measured at Amsterdam Island (Guinard *et al.* 1998) require that pairs fledge on average 0.64 chicks for the population to remain in equilibrium. This assumes that fledglings departing to sea have the same survival as adults, that chicks fledge at an age of 0.7 years and that all birds aged 4.7 years or older breed. The incubation period of about 39 days (Williams 1980a) and the fledging period of about 70 days (Marchant and Higgins 1990) together last for about 0.3 years. At Amsterdam Island, survival of first-year birds was estimated to be 39% per year (Guinard *et al.* 1998). In some years all pairs may not breed (Cooper *et al.* 1997) and for the adult population there may not be an equal sex ratio. Therefore, for equilibrium, breeding success would need to be >0.64 chicks per pair. However, two rockhopper penguins at Amsterdam Island bred at two years of age

(Guinard *et al.* 1998), so there is potential for birds to start breeding when younger than 4.7 years.

At Marion Island during the period 1975–1977, rockhopper penguins fledged on average 0.35 chicks per pair (Williams 1980a). From 1985/86–1995/96, they fledged on average 0.48 chicks per pair (Cooper *et al.* 1997). From 1994/95–2002/03, the average was 0.40 chicks per pair. These values all are considerably lower than the rate required for a population to remain in equilibrium. The two last values may be underestimates because some chicks leave colonies before the numbers of chicks in crèches are counted. Counts of chicks in crèches were made about 28 February, but chicks may fledge from 8 February. In 1994/95, the median date of fledging was 25 February, whereas most chicks fledged on 2 March (Table II). However, at Trypot Hole in 1994/95, the number of chicks that fledged was overestimated because 15 chicks died after entering the crèche (Marine & Coastal Management unpublished data).

At Campbell Island, where there has been a large decrease in the population (Cunningham and Moors 1994), pairs fledged on average 0.47–0.51 chicks per year (Marchant and Higgins 1990), below the 0.64 required to maintain equilibrium. At Macquarie Island, 0.73 chicks per pair reached the crèche stage (Warham 1963) and at Falkland Islands 77% of pairs fledged chicks (Strange 1982). As observed for Amsterdam Island (Guinard *et al.* 1998) and Campbell Island (Cunningham and Moors 1994), it appears that the decrease at Marion Island is at least partly attributable to inadequate reproduction. However, age at first breeding and survival have not yet been measured at Marion Island, so the possibility that reduced survival brought about the decrease in the population cannot be excluded.

Breeding success was especially poor in 1998/99 (Fig. 4a), when there also was a large decrease in mass of males and females arriving at breeding colonies (Fig. 4b). It is of interest that this was one year after a large ENSO (*El Niño* Southern Oscillation) event in 1997/98 that affected breeding by several seabirds at Marion Island (Crawford *et al.* 2003).

Timing of breeding

The timing of breeding in 1994/95 (Table II) agreed with the approximate schedule reported by Cooper and Brown (1990). At Macquarie Island, females return to breeding colonies on average 6.5 days after males (Warham 1963). At Marion Island, there also is a tendency for females to return later than males.

Throughout their distribution, rockhopper penguins generally breed between August and March, perhaps

starting later at higher latitudes (Marchant and Higgins 1990). However, adults arrive at Marion Island about 10 days later than would be expected from the sea surface temperature there (Marchant and Higgins 1990). At Macquarie Island laying occurs from 8 to 18 November and at Campbell Island from 6 to 15 November (Warham 1963, Marchant and Higgins 1990). Although both these localities are at higher latitudes, laying is earlier than at Marion Island (17 November–3 December).

Mass of adults on arrival at colonies and of chicks at fledging

The generally persistent decrease in the mass of rockhopper penguins arriving at Marion Island during the seasons 1994/95–2002/03 indicates that the availability of food prior to breeding may have decreased. Mass on arrival of males and females was significantly related, suggesting that both sexes were influenced similarly. For both sexes there was a partial recovery in the mass on arrival in 1999/00 (Fig. 4b), when the contribution of fish to the diet during the chick-rearing period was markedly higher than in other seasons (Table III).

Rockhopper penguins lose mass while breeding (Marchant and Higgins 1990), so that a lower mass on arrival at breeding colonies may increase the likelihood of nest failure. From 1994/95 to 2002/03, reproductive success was positively related to mean mass on arrival of males and females.

At Marion Island, the proportion of rockhopper penguins that breeds varies between seasons (Cooper *et al.* 1997). A reduced proportion of birds breeding may have contributed to the decrease in the breeding population and to the significant relationship observed between mass on arrival and numbers breeding at the three monitored colonies.

Unlike the decrease of mass of adults on arrival at colonies from 1994/95 to 2002/03, the mass of chicks at fledging tended to be higher in the most recent seasons (Fig. 4c). This suggests that adults use different feeding areas before breeding and while feeding chicks. Their distribution during the non-breeding period is not well known. A few sightings at sea indicate possible movement along the Subtropical Convergence (Marchant and Higgins 1990). Rockhopper penguins from Falkland Islands appear to move north after moulting and are at sea for six months (Strange 1982). Greater insight into the distribution of adults from Marion Island when not breeding would be valuable in understanding factors that influence their mass on arrival at breeding colonies.

Although mass of chicks at fledging was often

higher after 1997/98 than in earlier seasons, breeding success was lower from 1998/99 to 2002/03 than from 1994/95 to 1997/98 (Fig. 4a, b). When food is scarce, chicks of low mass are more likely to die than when food is abundant, leading to a disproportionate number of heavy chicks surviving (Williams and Croxall 1990).

In each of the nine seasons for which it was measured, the mass of chicks at fledging was lower than that reported for the Falkland Islands (2.22 kg, Strange 1982). In all seasons except 1997/98, when mean mass at fledging was 2.13 kg, it was lower than that reported for Campbell Island (1.99 kg, Cunningham and Moors 1994). Measurements of birds at Campbell and Falkland islands (Marchant and Higgins 1990) do not suggest that they are noticeably larger than those at Marion Island. As suggested by Cunningham and Moors (1994) for Campbell Island, the low mass at fledging may decrease survival of first-year birds.

Diet

At Marion Island during 1973 and 1974, the diet of rockhopper penguins included euphausiids (Williams and Laycock 1981). During the seasons 1983/84–1985/86, crustaceans (85% by mass), mainly *Nauticaris marionis* and *Euphausia vallentini*, constituted most of the food, with fish (10%) and cephalopods (5%) of lesser importance (Brown and Klages 1987). The proportion of crustaceans in the diet was high during early chick rearing. Then, proportions of fish and cephalopods increased to peak in about late February, before decreasing sharply. The diet of chicks in their last two weeks before fledging was almost exclusively crustaceans. These changes were thought to be related to foraging strategy, with crustaceans being taken inshore during the guard-stage and pelagic fish and cephalopods offshore when adults are freed to travel farther (Brown and Klages 1987, Adams and Brown 1989). Feeding was believed to be inshore again in the final two weeks of chick rearing, after breeding by macaroni penguins *Eudyptes chrysophonus*, which also feed mainly on crustaceans at Marion Island, had ended (Brown and Klages 1987). In every season from 1994/95 to 2001/02, crustaceans again dominated the diet. This proportion would have been lower had it been corrected to account for the original biomass of fish ingested (Brown and Klages 1987).

If inadequate supplies of food are responsible for the poor breeding success of rockhopper penguins at Marion Island, and hence the population decrease, availability of crustaceans is likely to be lower than previously. This could result from an altered distribution of prey, as postulated for Campbell Island (Cunningham and Moors 1994) and Amsterdam Island

(Guinard *et al.* 1998), decreased abundance of prey, or competition with other predators for food. Pomfret *Brama brama*, a teleost of the family Bramidae found in the North Atlantic Ocean, off south-western Africa, Australia, New Zealand and Chile (Smith and Heemstra 1986), has recently been caught near Marion Island by longline boats targeting Patagonian toothfish *Dissostichus eleginoides*, suggesting increased sea temperatures there (B. P. Watkins, Marine & Coastal Management, *in litt.*), which have been demonstrated by Mélice *et al.* (in press).

At Prince Edward Island, where numbers of rockhopper penguins are thought to be stable, the population of macaroni penguins has probably decreased (Ryan *et al.* 2003). At Marion Island during January and February, rockhopper penguins are thought to forage 4–157 km from breeding colonies (early chick rearing) and macaroni penguins 59–303 km (late chick rearing, Brown 1987). Dietary segregation of these two penguin species is considered incomplete (Brown and Klages 1987, Adams and Brown 1989). Further information on the extent of overlap of feeding grounds of these and other predators of euphausiids is required in order to evaluate the extent of possible competition for resources.

Regardless of the reasons for scarcity of food, several factors combine to indicate that an inadequate supply of food has been responsible for the decrease in the number of rockhopper penguins at Marion Island. These include poor breeding success, decreasing masses of males and females on arrival at the start of the breeding season and a low mass of chicks at fledging.

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Eastern rockhopper penguins at Marion Island (photo B. M. Dyer)