

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

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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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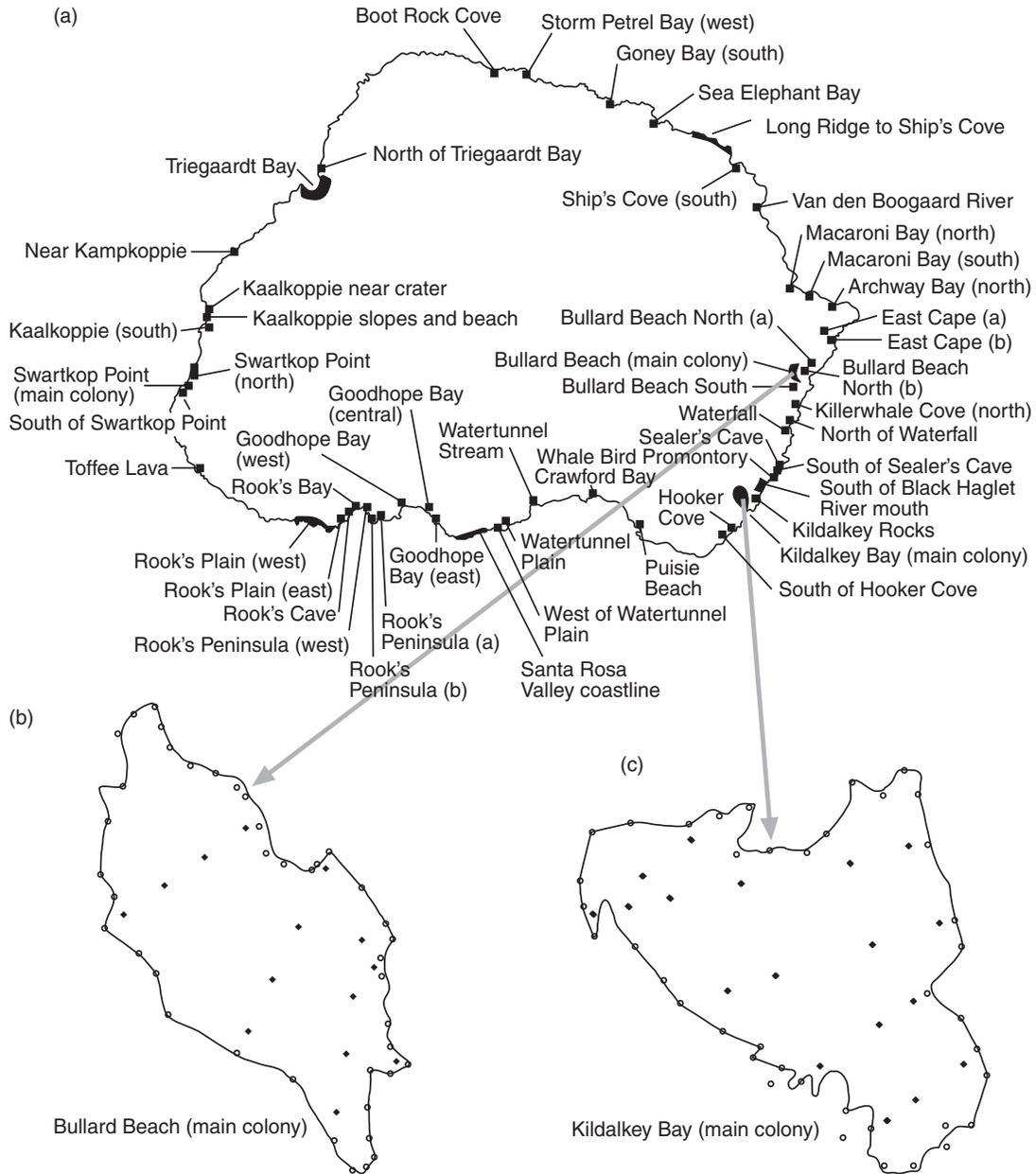


Fig. 1: Marion Island, showing (a) the locations of the breeding colonies of macaroni penguins. The extents of the main colonies at (b) Bullard Beach and (c) Kildalkey Bay are indicated, together with the locations of markers near the colony edges (open circles) and the locations of squares within the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

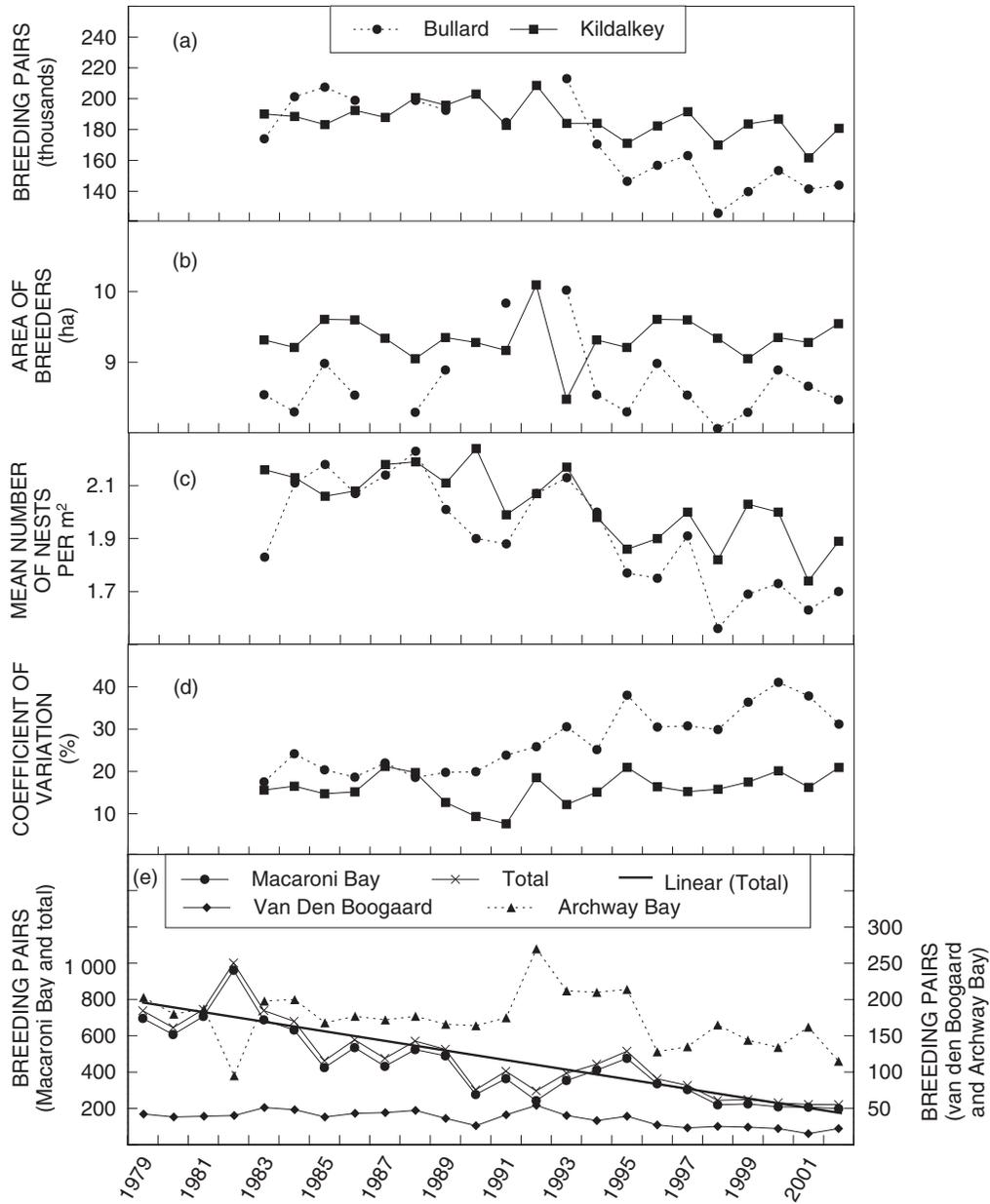


Fig. 2: Estimates of (a) numbers of breeding pairs, (b) area occupied by breeders, (c) mean density of nests and (d) coefficient of variation on the densities of nests for the main colonies of macaroni penguins at Bullard Beach and Kildalkey Bay, 1983/84–2002/03. In (e) numbers of pairs breeding at Macaroni 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 79 000 pairs (1994/95) 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 ($< 4 000$ 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

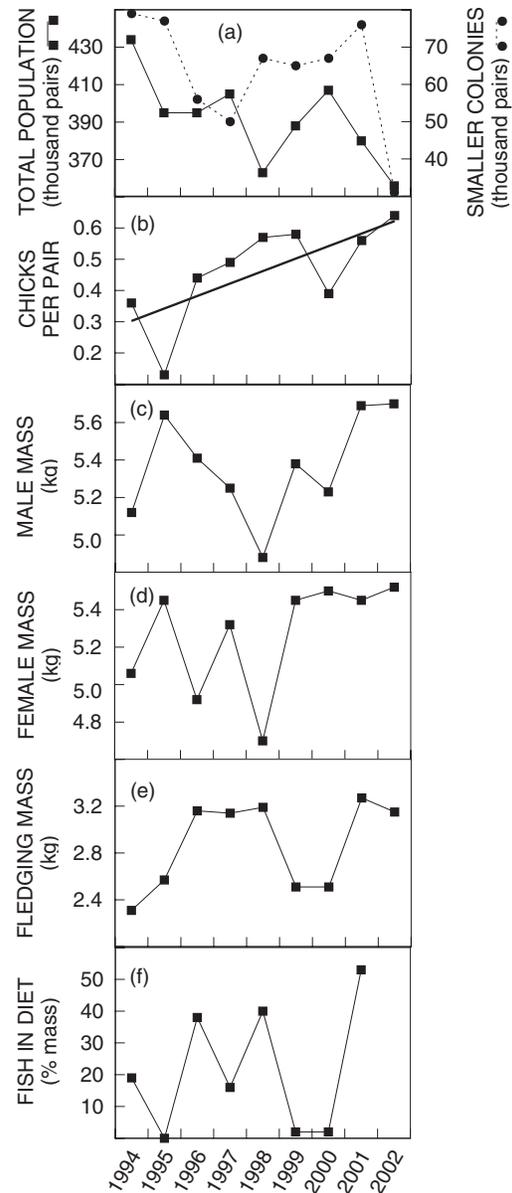


Fig. 3: Trends in (a) numbers of macaroni penguins breeding at Marion Island and at all colonies except the main colonies at Bullard Beach and Kildalkey Bay, (b) average number of chicks fledged per pair (the linear trend is also shown), (c) mean mass of males on arrival at breeding colonies, (d) mean 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 (Mélise *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*, *Thyssanoessa 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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