Afr. J. mar. Sci. 25: 537–547
2003

POPULATION, BREEDING, DIET AND CONSERVATION OF THE CROZET SHAG *PHALACROCORAX [ATRICEPS] MELANOGENIS* AT MARION ISLAND, 1994/95–2002/03

R. J. M. CRAWFORD[1], *J. COOPER*[2], *B. M. DYER*[1], *A. C. WOLFAARDT*[3], *D. TSHINGANA*[1], *K. SPENCER*[1], *S. L. PETERSEN*[2], *J. L. NEL*[4], *D. G. KEITH*[1], *C. L. HOLNESS*[1], *B. HANISE*[1], *M. D. GREYLING*[5] *and M. DU TOIT*[1]

The number of Crozet shags or cormorants *Phalacrocorax [atriceps] melanogenis* breeding at subantarctic Marion Island decreased by 68% from 841 pairs in 1994/95 to 272 pairs in 2002/03. The mean number of pairs at colonies also decreased and was significantly related to the overall number of birds breeding in any given season. The decreases coincided with a period of warming and reduced precipitation at Marion Island and with a decrease in the number of gentoo penguins *Pygoscelis papua* breeding there. Both these seabird species forage inshore and there is considerable overlap in their diets. Nototheniid fish and the decapod *Nauticaris marionis* continued to be important in the diet of Crozet shags, but a change in dominance among nototheniid prey suggests availability of prey to shags changed after the mid 1980s. Crozet shags breed for the first time when aged three years. It is probable that about 25% of the mature population did not breed in 1997/98, coincident with a strong *El Niño* Southern Oscillation event. In four seasons, breeding pairs on average fledged 0.30 chicks from first clutches, an amount thought inadequate to sustain the population. Crozet shags at the Prince Edward Islands should now be regarded as Endangered. Placing breeding colonies in the most highly protected zone on Marion Island, considering the establishment of an *ex situ* population and undertaking a genetic study of the specific status of the Crozet shag are recommended conservation measures.

Key words: age at breeding, breeding success, conservation, Crozet shag, diet, Marion Island, *Phalacrocorax [atriceps] melanogenis*, population decrease, Subantarctic

The Crozet shag or cormorant *Phalacrocorax [atriceps] melanogenis* is found only at the subantarctic Crozet Islands and Prince Edward Islands (Prince Edward Island and Marion Island) in the southern Indian Ocean. Together with several other taxa of shags in the Southern Ocean, including the Antarctic shag *P. [a.] bransfieldensis*, South Georgian shag *P. [a.] georgianus*, Heard shag *P. [a.] nivalis* and Macquarie shag *P. [a.] purpurascens*, the Crozet shag is considered to be a member of the imperial cormorant *P. atriceps* complex (Rand 1954, Marchant and Higgins 1990). However, the classification of the shags of the Prince Edward Islands is provisional (Marchant and Higgins 1990) and is not based on a genetic study. An investigation into the specific status of shags at the Prince Edward Islands is therefore urgently required (Barnes 2000). The population at the Crozet Islands was 815–835 pairs in 1981/82 (Jouventin *et al.* 1984), whereas in 1984/85 that at Prince Edward Island was about 120 pairs (Ryan and Hunter 1985) and in 1987/88 that at Marion Island was 589 pairs (Cooper and Brown 1990). Therefore, in the 1980s, the total population of the taxon was of the order of 1 500 pairs. The Crozet shag is listed as Vulnerable in *The Eskom Red Data Book of Birds of South Africa, Lesotho and Swaziland* (Barnes 2000).

The number of Crozet shags breeding at Marion Island has been monitored annually since 1994/95. Additionally, information has been gathered on the ages at which birds breed, on their breeding success and on their diet. This paper reports the results of these studies. It draws attention to a decrease in the number breeding at Marion Island during the 1990s, discusses factors that may have influenced this trend and reconsiders the conservation status of the species at the Prince Edward Islands.

[1] Marine & Coastal Management, Department of Environmental Affairs and Tourism, Private Bag X2, Rogge Bay 8012, South Africa. E-mail: crawford@mcm.wcape.gov.za
[2] Avian Demography Unit, University of Cape Town, Rondebosch 7701, South Africa
[3] Western Cape Nature Conservation Board, Private Bag X9086, Cape Town 8000, South Africa
[4] Council for Scientific and Industrial Research, P. O. Box 320, Stellenbosch 7599, South Africa
[5] School of Biological Sciences, University of Pretoria, Pretoria 0002, South Africa

Manuscript received April 2003; accepted May 2003

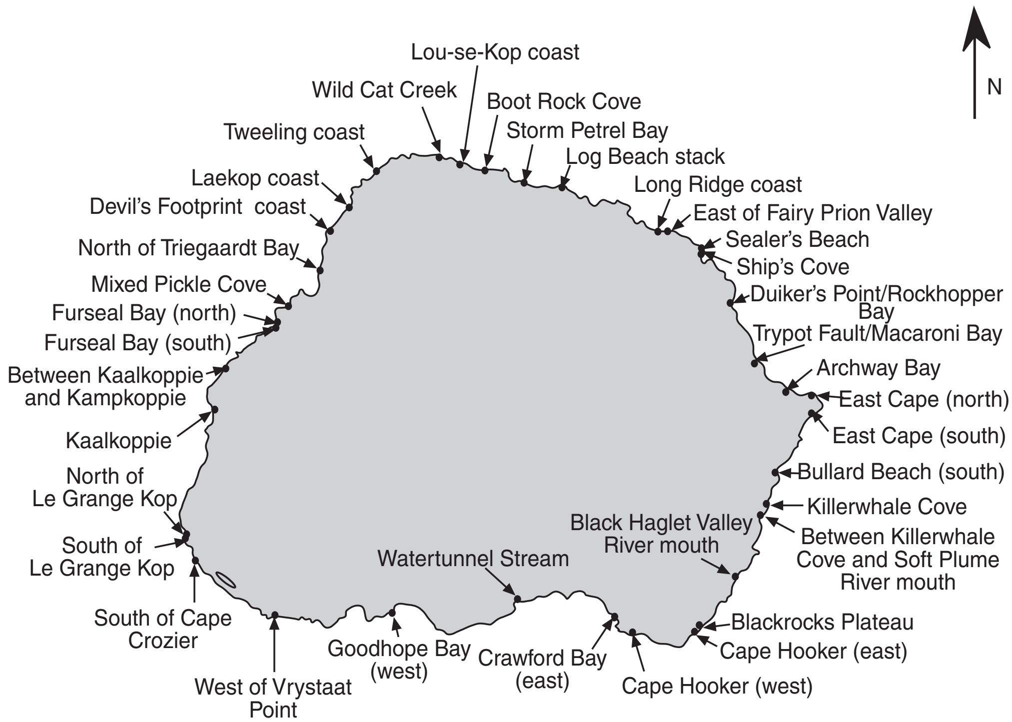

Fig. 1: Localities of breeding colonies of Crozet shags at Marion Island, 1987/88–2001/02

MATERIAL AND METHODS

Population

Numbers of active nests of Crozet shags around the whole coastline of Marion Island (290 km^2; 46°52´S, 37°51´E; Fig. 1) were counted in each season from 1994/95 to 2002/03. Additionally, detailed information was available for a count made in October 1987 (Cooper and Brown 1990, JC unpublished data). A nest was defined as being active if it consisted of nest material and an adult or a chick was occupying it. The locations of breeding colonies were recorded and, except in 2002/03, counts were assigned to localities. Counts were undertaken from 21 November to 6 December 1994, from 20 November to 2 December 1995, from 19 November to 6 December 1996, from 20 November to 12 December 1997, from 25 November to 9 December 1998, from 25 November to 13 December 1999, from 23 November to 7 December 2000, from 18 to 23 December 2001 and from 28 November to 8 December 2002. At Marion Island, breeding is seasonal, eggs are normally laid between October and January, and 50% of eggs of first clutches are laid by 11 November. Eggs laid after November are mostly replacements (Williams and Burger 1979).

The census in 2001 was undertaken later in the breeding season than were counts in other years. This may have resulted in additional nest failure before active nests were counted. In 2001, the numbers of pairs at three colonies were counted each week during November and December. The proportional decrease in nests between 29 November, close to the midpoint of surveys for the years 1994–2000 and 2002, and 20 December, the mid point of the 2001 census, was calculated and used to adjust the 2001 count to make it comparable with those for the other surveys. In 2000, repeat counts were undertaken at several colonies in order to determine the coefficient of variation (*CV*) for counts.

Table I: Minimum numbers of Crozet shags from different cohorts present (P) and breeding (B) at Marion Island, at approximate ages. Numbers of chicks banded for each cohort are shown

Cohort	Number banded	Numbers per approximate age (years)													
		1		2		3		4		5		6		7	
		P	B	P	B	P	B	P	B	P	B	P	B	P	B
1994/95	200	22	0	1	0	3	3	8	4	1	1	0	0	1	1
1995/96	49	0	0	0	0	0	0	0	0	0	0	0	0		
1996/97	39	0	0	0	0	1	1	0	0	1	1				
1997/98	11	0	0	0	0	0	0	0	0						
1998/99	28	1	0	0	0	1	0								
1999/00	56	0	0	0	0										
Overall	383	23	0	1	0	5	4	8	4	2	2	0	0	1	1

Age at breeding

From 1994/95 to 1999/00, cohorts of Crozet shag chicks were banded in such a way that each cohort could be distinguished. Until January 1998, the chicks were banded with individually numbered 16-mm stainless steel bands and with 16.5-mm (internal diameter) coiled, coloured plastic bands of depth 16 mm. Subsequently, the stainless steel bands were coloured (powder coated) and only this band was applied. Numbers of chicks banded in each season are shown in Table I.

From December 1994 to May 2002, research assistants stationed at Marion Island conducted observations on the presence of known-age Crozet shags at breeding colonies. If a bird was observed at a nest containing nest material, it was assumed to be breeding. Chicks fledge during summer, so information on resightings of birds was summarized for the 12-month periods July–June. In these periods, the maximum number of banded birds from a cohort observed at any colony was assumed to represent the minimum number of birds of known age at that colony. Generally it was not possible to distinguish birds of the same cohort, but on a few occasions the unique numbers on the metal bands were read.

Breeding success

The breeding success of Crozet shags was estimated in 1998/99, 1999/00, 2001/02 and 2002/03. In 1998/99, 33 nests were monitored at Duiker's Point/Rockhopper Bay and 22 at Trypot Fault/Macaroni Bay (Fig. 1). In 1999/00, 74 nests were monitored at Trypot Fault/Macaroni Bay. In 2001/02, 35 nests were monitored at Duiker's Point/Rockhopper Bay and 45 at Trypot Fault/Macaroni Bay. In 2002/03, 20 nests were monitored at Duiker's Point/Rockhopper Bay, 55 at Trypot Fault/Macaroni Bay and 14 at Archway Bay. Positions of nests in these colonies were mapped so that progress at each nest could be followed.

The colonies were visited at intervals of 2–17 days: in 1998/99 from 9 November to 31 January (19 visits); in 1999/00 from 11 October to 26 January (10 visits); in 2001/02 from 1 November to 19 February (16 visits); in 2002/03 from 1 November to 27 December (eight visits). Nests were examined with binoculars, and the content of each was noted, except if a nest had an adult in a prone position, when eggs or small chicks were not visible.

All large post-brooded chicks at nests were assumed to have fledged and, for each season, the mean number of chicks fledged per nest was calculated. Nests for which breeding was still in progress at the conclusion of observations were excluded from the analysis: three in 1998/99; five in 1999/00; none in 2001/02; eight in 2002/03.

Diet

Freshly regurgitated pellets were collected at breeding colonies in 1997/98 (n = 1, 28 January), 1998/99 (n = 51, 1 December–1 March), 2000/01 (n = 44, 4 December–27 January) and 2001/02 (n = 3, 24 December). Prey remains were removed from pellets using forceps and sorted into polychaete, crustacean, cephalopod and fish components. Crustaceans were identified by reference to Baker *et al*. (1990) and Branch *et al*. (1991), cephalopod beaks by reference to Clarke (1986) and fish otoliths by reference to Hecht (1987), Williams and McEldowney (1990) and Reid (1996). For each pellet, the number of polychaetes represented was taken

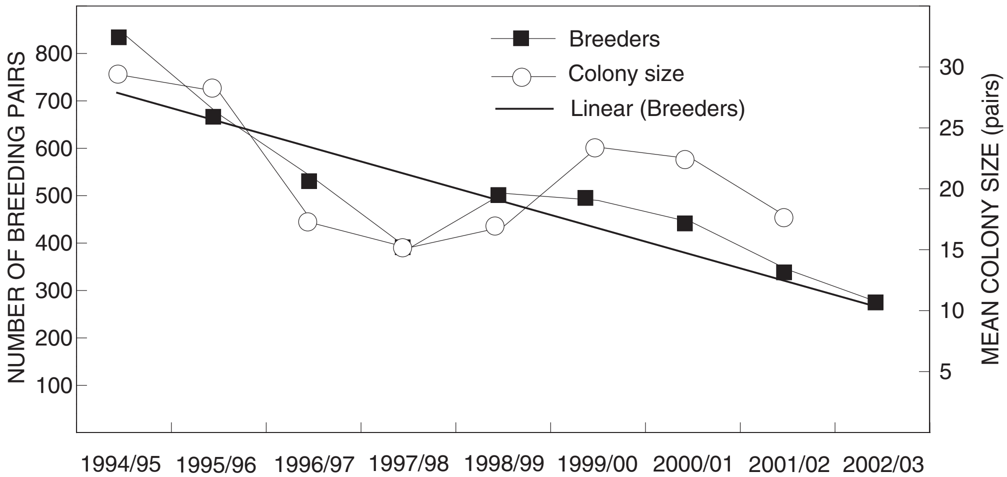

Fig. 2: Numbers of breeding pairs and mean size of colonies of Crozet shags at Marion Island, 1994/95–2002/03. The linear regression for the number of breeding pairs is shown

to be the number of mandibles present. The number of cephalopods present was taken to be the higher number of either upper or lower rostra found. The number of each fish species present was estimated by dividing the number of otoliths for that species by two and regarding any remainder as representing one fish. The contribution to the diet was estimated by percentage frequency of occurrence and, except for crustacean components for which numbers could not be determined, by percentage of the overall number of prey items found. Both these methods may overestimate the contribution to the diet of fish and cephalopods, whose harder otoliths and beaks take longer to digest, but the method nevertheless provides useful information for largely piscivorous birds (Espitalier-Noel *et al*. 1988).

RESULTS

Population

From 1994/95 to 2001/02, Crozet shags at Marion Island bred at 37 localities, all in close proximity to the coast (Fig. 1). In any one season they bred at between 19 and 25 localities. The mean size of colonies varied between 15 pairs in 1997/98 and 29 in 1994/95 (Fig. 2). In the eight seasons, the overall mean size of colonies was 24 pairs (n = 179, SD = 22 pairs). Solitary pairs were seen on seven occasions. The largest breeding colony encountered was 94 pairs at Trypot Fault/ Macaroni Bay in 1994/95. The small size of colonies facilitated accurate counts and, in 2000, the CV on the overall count was 1%.

In 2001, the count of active nests at three colonies decreased from 67 on 29 November to 58 on 20 December. Therefore, counts made during the period 18–23 December were multiplied by a factor of 1.156 to account for nest failure prior to the survey.

The breeding population at Marion Island decreased by 68% from 841 pairs in 1994/95 to 272 pairs in 2002/03 (Table II). There was a steep decrease to 388 pairs in 1997/98, an increase to about 500 pairs in both 1998/99 and 1999/00 and then a decrease from 2000/01 to 2002/03 (Fig. 2). The decrease from 1994/95 to 2002/03 was approximately linear and significantly related to time ($n = 9$, $r = -0.883$, $p < 0.002$). There was also a significant correlation between numbers breeding and the mean size of breeding colonies ($n = 8$, $r = 0.806$, $p < 0.02$).

There was considerable fluctuation in numbers breeding at some localities, e.g. Trypot Fault/Macaroni Bay, but a steady decrease at others, e.g. between Killerwhale Cove and Soft Plume River mouth between 1995/96 and 1999/00. Breeding stopped altogether at Goodhope Bay (west) after 1995/96 and at Bullard Beach (south), Watertunnel Stream and Storm Petrel Bay after 2000/01. At some localities, e.g. Killerwhale Cove and south of La Grange Kop, Crozet shags bred sporadi-

Table II: Counts of active nests of Crozet shags at different localities or sections of Marion Island, 1987/88 and 1994/95–2001/02. The counts in 2001/02 were adjusted to account for failed breeding prior to the survey using information from three monitored colonies (see text). In 2002/03, counts were not assigned to equivalent localities and sections, but totalled 272 active nests

Locality or section	Counts									
	1987/88	1994/95	1995/96	1996/97	1997/98	1998/99	1999/00	2000/01	2001/02	2001/02 adjusted
Trypot Fault	16	94	90	38	25	18	87	30	45	52
Archway Bay to East Cape	43	50	52	23	38	30	21	13	11	13
Bullard Beach (south)	42	60	42	40	44	47	54	48	0	0
Killerwhale Cove	0	0	0	0	2	0	0	0	3	3
Between Killerwhale Cove and Soft Plume River mouth	45	53	56	39	28	25	12	6	11	13
Black Haglet Valley River mouth	0	8	3	8	0	17	13	5	0	0
Blackrocks Plateau	0	0	0	25	0	38	52	57	53	61
Cape Hooker	0	78	72	50	45	11	0	0	0	0
Crawford Bay (east) 15	0	0	11	20	0	2	0	0	0	
Watertunnel Stream	0	31	31	15	6	29	16	35	0	0
Goodhope Bay (west)	23	53	54	0	0	0	0	0	0	0
West of Vrystaat Point	0	5	0	9	0	0	1	1	0	0
South of La Grange Kop	0	0	6	0	5	3	0	13	3	3
North of La Grange Kop	0	15	5	0	0	7	7	0	13	15
Kaalkoppie	0	14	12	0	0	13	0	0	0	0
Between Kaalkoppie and Kampkoppie	18	10	0	10	5	0	0	8	5	6
Furseal Bay (south)	0	35	9	10	6	5	46	26	6	7
Furseal Bay (north)	51	0	10	8	0	0	0	0	5	6
Mixed Pickle Cove	0	23	9	0	4	46	0	1	7	8
North of Triegaardt Bay	24	5	1	0	0	4	4	0	10	12
Devil's Footprint coast	0	0	6	2	6	4	1	0	0	0
Laekop coast	0	16	5	4	0	4	3	0	17	20
Tweeling coast	38	0	0	7	0	12	0	0	0	0
Wild Cat Creek	0	0	0	5	6	7	7	1	9	10
Lou-se-Kop coast	5	63	30	22	7	16	21	8	12	14
Boot Rock Cove	12	0	5	15	9	6	9	0	6	7
Storm Petrel Bay	26	73	82	46	31	29	31	64	0	0
Log Beach stack	55	7	9	13	32	38	24	16	4	5
Long Ridge coast	25	1	0	3	3	0	0	0	0	0
East of Fairy Prion Valley	0	52	59	0	0	66	18	30	16	18
Sealer's Beach	25	85	0	43	37	0	60	72	49	57
Ship's Cove	35	0	13	62	0	3	1	0	0	0
Duiker's Point/Rockhopper Bay	91	10	11	29	29	27	0	9	13	15
Total	589	841	672	537	388	505	490	443	298	344

cally in small numbers. Fluctuations at the adjacent colonies east of Fairy Prion Valley and at Sealer's Beach were often out of phase, suggesting some movement between these localities (Table II).

Age at first breeding

Minimum numbers of banded Crozet shags from the 1994/95–1999/00 cohorts that were present and breeding at colonies at Marion Island are shown in Table I. No birds aged two years or younger were observed at nest sites, whereas 80% of three-year-old birds and substantial proportions of older age-classes were breeding. Therefore, the age at which Crozet shags commence breeding can be assumed to be three years.

First-time breeders did not necessarily recruit to natal colonies. A chick banded at Trypot Fault/Macaroni Bay on 28 December 1994 was at the colony at Archway Bay on 21 January and 25 November 1999, on the last occasion with an incubating mate. One chick banded at Cape Hooker on 13 January 1995 was breeding at Bullard Beach South in December 1998, another at Killerwhale Cove in January 1999.

Breeding success

In 1998/99, 11 of 52 monitored nests were successful: 10 pairs fledged one chick and one pair fledged

Table III: Contribution of different prey items to the diet of Crozet shags at Marion Island by frequency of occurrence and by number, 1998/99–2001/02

Prey species	Frequency of occurrence (%)	Contribution by number (%)
Polychaeta	2	0.69
Crustacea		
Euphausiacea		
Euphausia lucens	1	
Thysanoëssa vicina	1	
Isopoda	1	
Amphipoda	1	
Decapoda		
Nauticaris marionis	42	
Cephalopoda		
Octopus magnificus	33	1.04
Unidentified octopus	2	0.03
Fish		
Muraenolepidae		
Muraenolepis marmoratus	1	0.02
M. microps	50	0.09
Moridae		
Antimora rostrata	2	0.03
Congiopodidae		
Zanclorhynchus spinifer	2	0.07
Nototheniidae		
Dissostichus eleginoides	7	0.17
Gobionotothen marionensis	57	10.23
G. gibberifrons	1	0.02
Lepidonotothen squamifrons	4	0.12
L. larseni	55	7.04
Notothenia acuta	5	0.71
N. coriiceps	24	0.92
N. neglecta	1	0.02
N. rossii	1	0.02
Paranotothenia magellanica	39	1.79
Pagothenia bernacchii	3	0.07
Trematomus sp.	1	0.02
Unidentified nototheniid	65	75.16
Harpagiferidae		
Harpagifer georgianus	23	1.42
Unidentified fish	4	0.33
Total		100.00

two chicks. On average, pairs fledged 0.23 chicks. Of the 41 failed nests, 15 failed at an early stage (prior to the first egg being laid) and 26 during incubation. In 1999/00, 32 of 69 nests were successful: 29 pairs fledged one chick and three pairs fledged two chicks. On average, pairs fledged 0.51 chicks. Of the 37 failed nests, four failed at an early stage, 24 during incubation and nine during chick rearing. Laying after nest failure was observed at three nests. Laying was also observed at three nests that had successfully fledged chicks. However, because parents were not marked in any of these instances, it is not certain that these were second clutches. In 2001/02, seven of 80 nests were successful: six pairs fledged one chick and one pair two chicks. On average, pairs fledged 0.09 chicks. Of the 73 failed nests, six failed at an early stage, 56 during incubation and 11 during chick rearing. In 2002/03, 17 of 81 nests were successful: five pairs fledged one chick and 12 pairs fledged two chicks. On average, pairs fledged 0.36 chicks. Of the 64 failed nests, 56 failed during incubation and eight during chick rearing.

If each of the four seasons is given equal weighting, pairs fledged an average of 0.30 chicks per season ($SD = 0.21$ chicks, $n = 4$).

Diet

From 1998/99 to 2001/02, nototheniid fish dominated the diet of Crozet shags breeding at Marion Island (Table III). *Gobionotothen marionensis* was in 57% of the 99 regurgitated pellets investigated and *Lepidonotothen larseni* in 55%. By number, these two fish species were also the dominant contributors to prey that could be identified. Other nototheniids frequently found were *Paranotothenia magellanica* and *Notothenia coriiceps*. Eight other nototheniids were encountered, as well as four species of fish from three other families. Of these *Harpagifer georgianus* was found in 23% of the pellets. The decapod benthic shrimp *Nauticaris marionis* was in 42% of the pellets and the cephalopod *Octopus magnificus* in 33%. Other prey items found occasionally were euphausiids, polychaetes, isopods and amphipods (Table III).

DISCUSSION

Population

In 1951/52, the population of Crozet shags at Marion Island was estimated to be 250–400 adults. However, there were at least 172 active nests at eight colonies, reading Rand (1954) and Rand (1956) together, making the upper estimate the more likely one. No breeding birds were found between Goodhope Bay and Furseal Bay on the west coast (Rand 1954, 1956). The upper estimate of 400 adults for 1952 was repeated by Williams *et al.* (1975), who gave their own count of 647 birds for the period January–March 1974 over 75% of the island's coastline. Based on counts made between January 1974 and April 1975 and from April 1976–May 1977, Siegfried *et al.* (1978) and Williams *et al.* (1979) estimated the population to be 285 breeding pairs distributed in 16 kilometre squares (and thus representing a minimum of 16 colonies), mostly on the island's eastern coast. This estimate is lower than any of the nine made between 1987/88 and 2001/02 but similar to that for 2002/03 (Table II). However, uncertainty regarding the methods used by Siegfried *et al.* (1978) and Williams *et al.* (1979) precludes strict comparison. The breeding population may have increased from 587 pairs in 1987/88 (Cooper and Brown 1990) to 841 pairs in 1994/95. However, the count in 1987/88 was undertaken about one month earlier than those from 1994/95 to 2002/03 and before most eggs would have been laid (Williams and Burger 1979).

There was a 68% decrease in numbers of Crozet shags breeding at Marion Island between 1994/95 and 2002/03 (see also Woehler *et al*. 2001). There was a large (40%) decrease in numbers of gentoo penguins *Pygoscelis papua* breeding at Marion Island over the same period (Crawford *et al*. 2003a) and the two trends are significantly correlated (n = 9, r = 0.889, $p < 0.002$). At Marion Island there is considerable overlap in the diets of these two species, which forage close to the island (Cooper 1985, Adams and Wilson 1987, Espitalier-Noel *et al*. 1988, Adams and Klages 1989).

Mean annual surface air temperature at Marion Island increased by 1.2ºC between 1969 and 1999 and was higher in the years 1996–1999 than in any year between 1950 and 1995. Precipitation at the island decreased after the mid 1960s and the 1990s were the driest of five decades for which this parameter has been measured at the island (1950s–1990s, Smith 2002). Over a 43-year period (1956–1998), sea surface temperature increased at Marion Island by 1.55ºC (Mélice *et al*. in press). Such long-term changes in climate may have influenced oceanic processes near Marion Island. A large decrease in the number of rockhopper penguins *Eudyptes chrysocome* at Campbell Island south of New Zealand between the early 1940s and 1985 was 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). A decrease of rockhopper penguins at Amsterdam Island in the south-western Indian Ocean between 1971 and 1993 may have been caused by a drop in sea surface temperature affecting the distribution and abundance of prey (Guinard *et al*. 1998).

Off South Africa, the size of breeding colonies of swift terns *Sterna bergii* decreases when food is scarce, presumably because the density of prey within the foraging range of colonies is reduced (Crawford 2003). The trend to smaller colony sizes of Crozet shags recorded in this study may indicate a reduced density of prey around Marion Island.

The few Crozet shags breeding in 1997/98 coincided with a strong *El Niño* Southern Oscillation (ENSO) event. In the same season, breeding at Marion Island by five seabird species able to forage far from the island was exceptionally good, whereas for gentoo penguins it was noticeably poor (Crawford *et al*. 2003b).

Age at breeding and proportion breeding

Similarly to Crozet shags, South Georgian shags are able to breed when three years old but their average age at first breeding is about five years (Shaw 1986).

The trough in the numbers of Crozet shags breeding in 1997/98, when counts of active nests decreased to 72–77% of those in the immediately preceding and following seasons, may have resulted from strong recruitment of first-time breeders to the breeding population in 1998/99. However, it more probably arose from about 25% of mature birds choosing not to breed in 1997/98. In periods of food scarcity off southern Africa, Cape cormorants *Phalacrocorax capensis* and swift terns may defer the age at which they first breed by 1–3 years (Crawford *et al*. 2001, 2002). It is quite possible that the Crozet shag also does so, which would contribute to decreased numbers of mature birds breeding in certain years.

Breeding success

Williams and Burger (1979) reported that the average clutch of Crozet shags at Marion Island was 2.6 eggs and that, in 1976/77, 54.8% of eggs failed to hatch and 78% of chicks died. This means that pairs on average fledged 0.26 chicks from first clutches in that season. The value is similar to the mean of 0.30 chicks per pair obtained for the four seasons reported here. At the Crozet Islands, clutch size was 2.9 eggs, of which 31–39% produced fledged young, equivalent to 0.90–1.13 chicks per pair (Derenne *et al.* 1976). At Heard Island in 1986/87, Heard shags fledged a maximum of seven chicks from 27 nests, i.e. 0.26 chicks per pair (Pemberton and Gales 1987). For Antarctic shags, food availability is considered an important determinant of breeding success. Many pairs fledged three chicks in 1978/79 when food was plentiful, but in 1979/80 when food was limited, many pairs failed to fledge chicks or fledged just one chick (Marchant and Higgins 1990). At Signy Island, South Orkney Islands, South Georgian shags fledged 1.9–2.0 chicks per pair on average during 1980/81 and 1981/82 (Shaw 1986).

At Marion Island in 1974–1977, Williams and Burger (1979) noted that 39% of egg mortality resulted from high seas washing away nests, 37% from failure to hatch and the remainder from disappearance of single eggs. Most mortality (78%) of chicks was attributed to starvation. Storms often prevented adults foraging at sea and chicks starved as a result. In the present study, 187 (87%) of unsuccessful breeding attempts failed before hatching and 28 (13%) during chick rearing. Some cormorants may stop breeding at an early stage when food is scarce (e.g. Cape cormorant *P. capensis*, Crawford *et al*. 1992).

There are no published estimates of post-fledging survival of Crozet shags. Information for other cormorants suggests that survival may be 80–90% per year, except in the first year when it is likely to be lower (Cramp and Simmons 1977, Crawford *et al*. 1991, 1992, Orta 1992). If no new breeders recruited to colonies at Marion Island during the period 1995/96–2002/03, so that the decrease in the number of breeders from 1994/95–2002/03 was solely attributable to mortality, the annual mortality rate of adults would have been 14%. This is an underestimate because observations of known-age birds showed that some young birds did recruit to the breeding population. Therefore, the maximum survival rate is probably 85% per year.

If all birds breed for the first time when aged three years, all mature birds breed each year and survival of birds of all ages is 85% per year, it would be necessary for pairs on average to fledge 0.49 chicks per year to maintain the population in equilibrium. If 50% of fledged chicks survive their first year, pairs would need to fledge 0.83 chicks per year to achieve the equilibrium situation. If annual survival of adults is <85%, a higher production of fledged chicks would be required. The average breeding success at Marion Island is much lower than the value required to maintain the population, even assuming high levels of survival for both adults and first-year birds and that all mature birds breed every year. Inadequate reproduction is probably a major cause of the decrease in numbers of Crozet shags at the Prince Edward Islands. By contrast, breeding success at the Crozet Islands was likely to have been sufficient to maintain the population there.

Cape cormorants may lengthen their breeding season when food is plentiful (Crawford *et al*. 1999). The breeding season of Crozet shags also may be lengthened in periods of abundant food. Winter breeding of Crozet shags at Prince Edward Island was recorded in 1984, suggesting the possibility of double brooding (Ryan and Hunter 1985). Replacement laying following failed clutches is probable (Williams and Burger 1979). Double brooding and replacement laying will serve to increase the output of fledged chicks in conditions that are favourable for breeding.

Diet

Cooper (1985) noted that, in their non-breeding season, Crozet shags at Marion Island usually foraged within 400 m of the island and that they appeared to feed mainly on the seabed. The benthic nature of feeding was also noted by Blankley (1981) and Espitalier-Noel *et al*. (1988). Blankley and Grindley (1985) thought that Crozet shags foraged within 50 m of the island at depths of 1–15 m. The taxon is similarly regarded as an inshore, benthic feeder at the Crozet Islands (Stahl *et al*. 1985, Ridoux 1994).

At Marion Island in 1951/52, stomachs of both adult and immature Crozet shags contained partly digested fish (Rand 1956). In 1979/80, fish formed the largest part of three diet samples collected (Blankley 1981). In 1984/85, fish, the shrimp *Nauticaris marionis* and octopods contributed 71, 19 and 7% respectively of the overall mass of 47 diet samples collected using a stomach-flushing technique. Fish and octopods contributed 93 and 6% respectively of numbers of prey items found in 38 regurgitated pellets. *Lepidonotothen* (*Notothenia*) *squamifrons* was the most abundant fish in the diet. *Paranotothenia magellanica* contributed <1% by number (Espitalier-Noel *et al*. 1988), although regarded as the most abundant inshore nototheniid at the Prince Edward Islands by Gon and Klages (1988).

Octopods were less important by number in the years 1998/99–2001/02, constituting just 1% of prey items, whereas fish contributed 98% of those that could be recognized. *N. marionis* remained an important component of the diet. However, *L. squamifrons* was only the seventh most numerous of the 12 nototheniids encountered and occurred in just 4% of pellets. *P. magellanica* was present in almost 40% of pellets and both *Gobionotothen marionensis* and *L. larseni* in more than 50% (Table III). The last two species were not recorded in Crozet shag diet by Espitalier-Noel *et al*. (1988). *G. marionensis* larvae dominated the catch made by neuston nets around the Prince Edward Islands in May and June 1980 (Miller 1982). However, Gon and Klages (1988, p. 41) noted that "… several marine biological studies around PEI [Prince Edward Islands] during the last 7–8 years failed to collect substantial numbers of *G. marionensis*." *Harpagifer bispinis* identified in the diet of Crozet shag by Blankley (1981) may have been *H. georgianus* (Fischer and Hureau 1985).

It is apparent that the relative importance of nototheniid species in the diet of Crozet shags at Marion Island changed between 1984/85 and 1998/99–2001/02. By contrast, there was little difference in the species of fish eaten by Heard shags at Heard Island in three seasons between 1979/80 and 1987/88, although there was a significant reduction in numbers of polychaetes found in pellets collected at a roosting site between 1985/86 and 1987/88 (Green *et al.* 1990b).

At the Crozet Islands during 1982–1983, fish accounted for 62% of the number of prey items and 82% of the reconstituted mass of the diet of Crozet shags. Two fish species, *L. larseni* and *P. magellanica*, together contributed 45% of the reconstituted mass. *N. marionis* was found in 33% of diet samples (Ridoux 1994). Fish, including nototheniids and often *Harpagifer* spp., dominates the diet of Macquarie shags (Brothers 1985, Green *et al*. 1990a), breeding Heard shags (Green *et al*. 1990b), South Georgian shags (Wanless *et al*. 1992) and Antarctic shags (Casaux *et al*. 1998), all members of the *P. atriceps* complex.

It is not certain that the poor breeding success of Crozet shags at Marion Island can be attributed to a reduced availability of food. However, the similar downward trend between 1994/95 and 2002/03 in numbers of gentoo penguins, whose diet overlaps considerably with that of Crozet shags (Espitalier-Noel *et al*. 1988, Adams and Klages 1989), suggests this may be the case. The changed composition of the diet of Crozet shags between 1984/85 and 1998/99–2001/02 is indicative of an altered availability of prey species between these two periods.

Conservation

The number of Crozet shags breeding at Prince Edward Island decreased from 120 pairs in September 1984 to an estimated 50 pairs in December 2001, i.e. by about 58% (Ryan *et al*. 2003). This is similar to the decrease at Marion Island of 68% between 1994/95 and 2002/03. The combined population of Crozet shags at the Prince Edward Islands for 2001/02 was about 400 pairs. Assuming that the population at Crozet Islands has remained stable since the early 1980s, the overall population of this species in 2001/02 would have been about 1 200 pairs.

Although some movement of shags between breeding colonies at Marion Island has been observed, the species is mainly sedentary (Marchant and Higgins 1990). Movements between the Prince Edward Islands and the Crozet Islands (950 km to the east) are not expected and there have been no such movements shown by banding. The populations at the two island groups should be managed separately.

Using an age at first breeding of three years and an adult survival rate of 85% per year, the average life expectancy of Crozet shags that attain breeding age is about seven years. Therefore, the decrease of 68% at Marion Island between 1994/95 and 2002/03 occurred in just more than a single generation. In terms of the criteria of the World Conservation Union (IUCN 2001), the population at Prince Edward Islands should now be regarded as Endangered, rather than Vulnerable (Barnes 2000).

Crozet shags at the Prince Edward Islands are susceptible to human disturbance when breeding, with Subantarctic skuas *Catharacta antarctica* being quick to take exposed eggs (Rand 1956, Barnes 2000, pers. obs.). In the mid 1980s, a gillnet set from the shore to catch fish for scientific purposes at Transvaal Bay resulted in the death of at least one shag because of entanglement and subsequent drowning (Barnes 2000, JC pers. obs.). Use of such nets at the Prince Edward Islands has not been allowed since this event.

In view of the current poor conservation status of the Crozet shag at the Prince Edward Islands, three conservation measures are proposed for consideration by the Prince Edward Islands Management Committee in terms of the island's management plan (Prince Edward Islands Management Plan Working Group 1996):

1. Placing all breeding colonies at Marion Island within the most-protected Zone 4 category (along with gentoo penguins *Pygoscelis papua* and southern giant petrels *Macronectes giganteus*, which are currently so treated with a 100-m perimeter around their colonies) so that access will be strictly limited under special entry permit for approved conservation and research purposes only.
2. Investigating the desirability and feasibility of establishing an *ex situ* captive population.
3. Undertaking a genetic study of the specific status of the Crozet shag.

ACKNOWLEDGEMENTS

The 1987 census was undertaken by C. J. Gilbert. We are grateful to P. A. Whittington (Department of Zoology, University of Port Elizabeth) and A. J. Williams (Western Cape National Conservation Board) for commenting on the manuscript. The banding records were administered by the South African Bird Ringing Unit, University of Cape Town. The research was funded by the Department of Environmental Affairs and Tourism through Marine & Coastal Management and the South African National Antarctic Programme.

LITERATURE CITED

ADAMS, N. J. and N. T. [W.] KLAGES 1989 — Temporal variation in the diet of the gentoo penguin *Pygoscelis papua* at sub-Antarctic Marion Island. *Colonial Waterbirds* **12**: 30–36.

ADAMS, N. J. and M-P. WILSON 1987 — Foraging parameters of gentoo penguins *Pygoscelis papua* at Marion Island. *Polar Biol.* **7**: 51–56.

BAKER, A. de C., BODEN, B. P. and E. BRINTON 1990 — *A Practical Guide to the Euphausiids of the World*. London; Natural History Museum Publications: 96 pp.

BARNES, K. N. (Ed.) 2000 — *The Eskom Red Data Book of the Birds of South Africa, Lesotho and Swaziland*. Randburg; BirdLife South Africa: 169 pp.

BLANKLEY, W. O. 1981 — Marine food of kelp gulls, lesser sheathbills and imperial cormorants at Marion Island (sub-antarctic). *Cormorant* **9**: 77–84.

BLANKLEY, W. O. and J. R. GRINDLEY 1985 — The intertidal and shallow subtidal food web at Marion Island. In *Antarctic Nutrient Cycles and Food Webs*. Siegfried, W. R., Condy, P. R. and R. M. Laws (Eds). Berlin; Springer: 630–634.

BRANCH, M. L., GRIFFITHS, C. L., KENSLEY, B. and J. SIEG 1991 — The benthic Crustacea of subantarctic Marion and Prince Edward Islands: illustrated keys to the species and results of the 1982–1989 University of Cape Town surveys. *S. Afr. J. Antarct. Res*. **21**: 3–44.

BROTHERS, N. P. 1985 — Breeding biology, diet and morphometrics of the king shag *Phalacrocorax atriceps purpurascens* at Macquarie Island. *Aust. Wildl. Res*. **12**: 81–94.

CASAUX, R. J., BARRERA-ORO, E. R., FAVERO, M. and P. SILVA 1998 — New correction factors for quantification of fish represented in pellets of the imperial cormorant *Phalacrocorax atriceps*. *Mar. Ornithol*. **26**: 35–39.

CLARKE, M. R. 1986 — *A Handbook for the Identification of Cephalopod Beaks*. Oxford; Clarendon Press: 273 pp.

COOPER, J. 1985 — Foraging behaviour of non-breeding imperial cormorants at the Prince Edward Islands. *Ostrich* **56**: 96–100.

COOPER, J. and C. R. BROWN 1990 — Ornithological research at the sub-Antarctic Prince Edward Islands: a review of achievements. *S. Afr. J. Antarct. Res*. **20**: 40–57.

CRAMP, S. and K. E. L. SIMMONS 1977 — *Handbook of the Birds of Europe, the Middle East and North Africa. The Birds of the Western Palearctic.* **1**. *Ostrich to Ducks*. Oxford; University Press: 722 pp.

CRAWFORD, R. J. M. 2003 — Influence of food on numbers breeding, colony size and fidelity to localities of swift terns in South Africa's Western Cape, 1987–2000. *Waterbirds* **26**: 44–53.

CRAWFORD, R. J. M., COOPER, J., DYER, B. M., UPFOLD, L., VENTER, A. D., WHITTINGTON, P. A. and A. C. WOLFAARDT 2002 — Longevity, inter-colony movements and breeding of crested terns in South Africa. *Emu* **102**: 265–273.

CRAWFORD, R. J. M., COOPER. J., DU TOIT, M., GREYLING, M. D., HANISE, B., HOLNESS, C. L., KEITH, D. G., NEL, J. L., PETERSEN, S. L., SPENCER, K., TSHINGANA, D. and A. C. WOLFAARDT 2003a — Population and breeding of the gentoo penguin *Pygoscelis papua* at Marion Island, 1994/95–2002/03. *Afr. J. mar. Sci*. **25**: 463–474.

CRAWFORD, R. J. M., DUNCOMBE RAE, C. M., NEL, D. C. and J. COOPER 2003b — Unusual breeding by seabirds at Marion Island during 1997/98. *Afr. J. mar. Sci*. **25**: 453–452.

CRAWFORD, R. J. M., DYER, B. M. and L. UPFOLD 1999 — Seasonal pattern of breeding by Cape and crowned cormorants off western South Africa. *Ostrich* **70**: 193–195.

CRAWFORD, R. J. M., DYER, B. M., UPFOLD, L. and V. L. WARD 2001 — Age at first breeding of bank, *Phalacrocorax neglectus*, and Cape Cormorants, *P. capensis*. *Ostrich* **72**: 145–148.

CRAWFORD, R. J. M., RYAN, P. G. and A. J. WILLIAMS 1991 — Seabird consumption and production in the Benguela and western Agulhas ecosystems. *S. Afr. J. mar. Sci.* **11**: 357–375.

CRAWFORD, R. J. M., UNDERHILL, L. G., RAUBENHEIMER, C. M., DYER, B. M. and J. MÄRTIN 1992 — Top predators in the Benguela system – implications of their trophic position. *S. Afr. J. mar. Sci*. **12**: 675–687.

CUNNINGHAM, D. M. and P. J. MOORS 1994 — The decline of rockhopper penguins *Eudyptes chrysocome* at Campbell Island, Southern Ocean and the influence of rising sea temperatures. *Emu* **94**: 27–36.

DERENNE, P., MARY, G. and J-L. MOUGIN 1976 — Le cormoran à ventre blanc *Phalacrocorax albiventer melanogenis* (Blyth) de l'archipel Crozet. *Com. natn. Fr. Rech. Antarct*. **40**: 191–219.

ESPITALIER-NOEL, G., ADAMS, N. J. and N. T. [W.] KLAGES 1988 — Diet of the imperial cormorant *Phalacrocorax atriceps* at sub-Antarctic Marion Island. *Emu* **88**: 43–46.

FISCHER, W. and J. C. HUREAU (Eds) 1985 — *FAO Species Identification Sheets for Fishery Purposes Southern Ocean.* **2**. Rome; FAO: 471 pp.

GON, O. and N. T. W. KLAGES 1988 — The marine fish fauna of the sub-Antarctic Prince Edward Islands. *S. Afr. J. Antarct. Res*. **18**: 2–54.

GREEN, K., WILLIAMS, R. and D. J. SLIP 1990a — Diet of the Macquarie Island cormorant *Phalacrocorax atriceps purpurascens*. *Corella* **14**: 53–55.

GREEN, K., WILLIAMS, R., WOEHLER, E. J., BURTON, H. R., GALES, N. J. and R. T. JONES 1990b — Diet of the Heard Island cormorant *Phalacrocorax atriceps nivalis*. *Antarct. Sci.* **2**: 139–141.

GUINARD, E., WEIMERSKIRCH, H. and P. JOUVENTIN 1998 — Population changes and demography of the northern rockhopper penguin on Amsterdam and Saint Paul Islands. *Colon. Waterbirds* **21**: 222–228.

HECHT, T. 1987 — A guide to the otoliths of Southern Ocean fishes. *S. Afr. J. Antarct. Res*. **17**: 1–87.

IUCN 2001 — *IUCN Red List Categories and Criteria Version 3.1*. Gland, Switzerland; IUCN: 23 pp.

JOUVENTIN, P., STAHL, J. C., WEIMERSKIRCH, H. and J-L. MOUGIN 1984 — The seabirds of the French subantarctic islands and Adélie Land, their status and conservation. *ICBP Tech. Publn* **2**: 609–625.

MARCHANT, S. and P. J. HIGGINS 1990 — *Handbook of Australian, New Zealand and Antarctic Birds.* **1**. *Ratites to Ducks.* Melbourne; Oxford University Press: 1400 pp.

MILLER, D. G. 1982 — Results of a combined hydroacoustic and midwater trawling survey of the Prince Edward Island group. *S. Afr. J. Antarct. Res.* **12**: 3–10.

MOORS, P. J. 1986 — Decline in numbers of rockhopper penguins at Campbell Island. *Polar Rec*. **23**: 69–73.

ORTA, J. 1992 — Family Phalacrocoracidae (cormorants). In *Handbook of the Birds of the World.* **1**. *Ostrich to Ducks*. Del Hoyo, J., Elliott, A. and J. Sargatal (Eds). Barcelona; Lynx Edicions: 326–353.

PEMBERTON, D. and R. P. GALES 1987 — Notes on the status and breeding of the imperial cormorant *Phalacrocorax atriceps* at Heard Island. *Cormorant* **15**: 33–40.

PRINCE EDWARD ISLANDS MANAGEMENT WORKING GROUP 1996 — *Prince Edward Islands Management Plan*. Pretoria; Department of Environmental Affairs and Tourism: 64 pp.

RAND, R. W. 1954 — Notes on the birds of Marion Island. *Ibis* **96**: 173–200.

RAND, R. W. 1956 — Cormorants on Marion Island. *Ostrich* **27**: 127–133.

REID, K. 1996 — *A Guide to the Use of Otoliths in the Study of Predators at South Georgia*. Cambridge; British Antarctic Survey: 40 pp.
RIDOUX, V. 1994 — The diets and dietary segregation of seabirds at the subantarctic Crozet Islands. *Mar. Ornithol*. **22**: 1–192.
RYAN, P. G., COOPER, J., DYER, B. M., UNDERHILL, L. G., CRAWFORD, R. J. M. and M. N. BESTER 2003 — Counts of surface-nesting seabirds breeding at Prince Edward Island, summer 2001/02. *Afr. J. mar. Sci*. **25**: 441–452.
RYAN, P. G. and S. HUNTER 1985 — Early breeding of imperial cormorants *Phalacrocorax atriceps* at Prince Edward Island. *Cormorant* **13**: 31–34.
SHAW, P. 1986 — Factors influencing the breeding performance of Antarctic blue-eyed shags *Phalacrocorax atriceps*. *Ornis Scandinavica* **17**: 141–150.
SIEGFRIED, W. R., WILLIAMS, A. J., BURGER, A. E. and A. BERRUTI 1978 — Mineral and energy contributions of eggs of selected species of seabirds to the Marion Island terrestrial ecosystem. *S. Afr. J. Antarct. Res.* **8**: 75–87.
SMITH, V. R. 2002 — Climate change in the sub-Antarctic: an illustration from Marion Island. *Climate Change* **52**: 345–357.
STAHL, J. C., JOUVENTIN, P., MOUGIN, J. L., ROUX, J. P. and H. WEIMERSKIRCH 1985 — The foraging zones of seabirds in the Crozet Islands sector of the Southern Ocean. In *Antarctic Nutrient Cycles and Food Webs*. Siegfried, W. R., Condy, P. R. and R. M. Laws (Eds). Berlin; Springer: 478–486.
WANLESS, S., HARRIS, M. P. and J. A. MORRIS 1992 — Diving behaviour and diet of the blue-eyed shag at South Georgia. *Polar Biol*. **12**: 713–719.
WILLIAMS, A. J. and A. E. BURGER 1979 — Aspects of the breeding biology of the imperial cormorant, *Phalacrocorax atriceps*, at Marion Island. *Gerfaut* **69**: 407–423.
WILLIAMS, A. J., BURGER, A. E., BERRUTI, A. and W. R. SIEGFRIED 1975 — Ornithological research on Marion Island, 1974–75. *S. Afr. J. Antarct. Res.* **5**: 48–50.
WILLIAMS, A. J., SIEGFRIED, W. R., BURGER, A. E. and A. BERRUTI 1979 — The Prince Edward Islands: a sanctuary for seabirds in the Southern Ocean. *Biol. Conserv*. **15**: 59–71.
WILLIAMS, R. and A. McELDOWNEY 1990 — A guide to the fish otoliths from waters off the Australian Antarctic Territory, Heard and Macquarie Islands. *Aust. natn. Antarct. Res. Exped. Res. Notes* **75**: 173 pp.
WOEHLER, E. J., COOPER, J., CROXALL, J. P., FRASER, W. R., KOOYMAN, G. L., MILLER, G. D., NEL, D. C., PATTERSON, D. L., PETER, H-U., RIBIC, C. A., SALWICKA, K., TRIVELPIECE, W. Z. and H. WEIMERSKIRCH 2001 — A statistical assessment of the status and trends of Antarctic and sub-Antarctic seabirds. [Cambridge, UK]; Scientific Committee on Antarctic Research: 43 pp.

Crozet shag at Marion Island (photos R. J. M. Crawford)