POPULATION DYNAMICS OF THE AFRICAN PENGUIN *SPHENISCUS DEMERSUS* AT ROBBEN ISLAND, SOUTH AFRICA

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SUMMARY

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African Penguins *Spheniscus demersus* recolonized Robben Island in 1983 when about nine pairs bred at the island. By 1996, the colony had grown to about 3100 pairs. Adult survival was probably between 0.82 and 0.90 in 1993/94, but fell to 0.75 in 1994/95 when many birds at the island were oiled following the sinking of the *Apollo Sea* in June 1994. Some penguins initiated breeding when two years old, and all were assumed to be breeding at age five. The proportion of mature birds that bred in a year varied between about 0.70 and 1.00. During a breeding season, pairs laid their first clutches between January and August, mostly in February and March. The average clutch was 1.86 eggs. Of lost clutches 32% were replaced, whereas 23% of pairs losing broods relayed and 21% of pairs that successfully fledged chicks relayed. On only one occasion was the laying of a third clutch during a breeding season recorded, and this was unsuccessful. The mean number of chicks fledged per breeding pair varied between 0.32 and 0.59 per annum. Both fledging success and immigration of immature birds to the colony were significantly related to the spawner biomass of Cape Anchovy *Engraulis capensis*, the most important prey item of penguins at the island. Growth of the colony has been driven by immigration. Depending on the values assumed for survival of adults and first-year birds, 59–87% of new adults in the colony resulted from immigration. Several birds banded as chicks at Dassen and Dyer islands were recorded breeding at Robben Island.

INTRODUCTION

Robben Island was recolonized by about nine pairs of African or Jackass Penguins *Spheniscus demersus* in 1983 (Shelton *et al.* 1984). Subsequently, there has been rapid growth of the colony (Crawford *et al.* 1995a, Crawford *et al.* 1995b). In May 1996, there were *c.* 3100 pairs breeding at the island.

Several population parameters of African Penguins have been measured at Robben Island since 1988/89. Estimates for these are reported in this paper. Where population parameters were measured for individual years, we investigated their relationships with annual estimates of the abundance of Cape Anchovy *Engraulis capensis* and South African Sardine *Sardinops sagax*, the two most important prey items of African Penguins at Robben Island (Crawford *et al.* 1995a, Crawford & Dyer 1995).

Measured parameters were used in a model of the population at Robben Island to assess the relative importance for colony growth of intrinsic production and immigration to the island. We discuss the likely origin of immigrating birds, based on observations of banded birds seen breeding.

METHODS

Field observations

Field observations were conducted to estimate the numbers of birds in adult and immature plumage, the numbers breeding in each year and population parameters. Fuller details of methods are given in Crawford *et al.* (1995a).

Counts of penguins in adult and immature plumage, in the feather-shedding phase of moult, were conducted at two-week intervals (Randall *et al.* 1986). As most penguins at Robben Island moult between November and January, counts were summed from July of year t to June of year t+1. Totals were taken as the numbers present at the island in year t.

The number of pairs breeding at the island in any year was assumed to be the maximum count of active nests obtained in that year. At least four counts of active nests were made for each year between 1986 and 1995 (Crawford & Boonstra 1994, Crawford *et al.* 1995b), mostly during the main breeding season of February to September (Crawford *et al.* 1995a).

A study plot containing marked nests was established in 1989. Breeding pairs at these nests were banded. Their performance was monitored at two-weekly intervals from 1989 to 1995, to establish the month when the first clutch was produced, laying frequency, clutch size, and the number of chicks fledged per breeding pair. A chick was considered to have fledged if it reached the stage where more than half its body was covered with final fledgling plumage. Numbers of nests successfully monitored (followed throughout the breeding season) were 65 in 1989, 47 in 1990, 71 in 1991, 61 in 1992, 71 in 1993, 74 in 1994 and 47 in 1995. Breeding was not always successful at these nests.

From 1984 to 1994, 2729 chicks about to fledge were banded at Robben Island. In the same period, 5507 chicks were banded at Dassen Island and 2638 chicks at Dyer Island (records of the South African Bird Ringing Unit, SAFRING). Regular searches throughout the colony at Robben Island were made for banded penguins, and their breeding activity was noted. The searches were especially intensive in 1994 and 1995, when extra staff were employed to monitor the return to islands of birds that had been rescued and rehabilitated after being oiled, following the sinking of the *Apollo Sea* between Robben and Dassen Islands on 20 June 1994 (Underhill *et al.* 1999).

Adult survival

Survival of adult African Penguins was calculated from the decrease in numbers of banded adults seen at the island between 1993 and 1994, and between 1994 and 1995. These years were chosen because of the higher search effort for banded birds in 1994 and 1995. Survival in year t, $s_{ad,t}$ was computed as:

$$s_{ad,t} = \frac{N_{ad,t+1} + ((N_{ad,t} - N_{ad,t+1}) * Pns_{ad})}{N_{ad,t}} \quad ,$$

where $N_{ad,t}$ = number of banded adults seen in year t;
$N_{ad,t+1}$ = number of banded adults seen in year t that were also seen in year t+1;
Pns_{ad} = probability of an adult being alive without being seen during a year.

Pns_{ad} was taken as the proportion of those banded adults, known to be alive in both 1993 and 1995, that were not seen in 1994. To obviate biases introduced by visiting birds, only birds seen at Robben Island in at least two years were considered in determining $N_{ad,\,t}$.

In the population model, an annual survival value of 0.91 derived for adult penguins at St Croix Island was also used (Randall 1983).

Juvenile survival

Survival of first-year birds, $s_{juv,t}$, was not estimated for the penguin colony at Robben Island. Between 1976 and 1981, first-year survival at St Croix Island varied between 0.04 and 0.35, but 0.32 was considered typical (Randall 1983). Other estimates of first-year survival include a minimum of 0.13 at Marcus Island (La Cock *et al.* 1987) and 0.69 at Dyer Island (La Cock & Hänel 1987). For the colony at Robben Island, values of 0.3, 0.5 and 0.7 were used in the model.

Age at breeding

The proportion of breeders in each age-class i (b_i) was calculated from observations of the youngest ages at which birds banded as chicks bred at Robben Island. Up until the end of 1995, 66 birds of known age had been observed breeding at the island.

Proportion breeding

The proportion of mature birds that bred in any year t (A_t) was estimated from the number of birds in adult plumage counted moulting at the island ($Moult_{ad,t}$) and the maximum count of occupied nest sites ($Nest_{max,t}$). Because mean duration of the feather-shedding stage of moult is 12.7 days (Randall *et al.* 1986), but moult counts were conducted on average every fourteenth day (second week), the moult counts were augmented by a factor of 1.1 (equivalent to 14/12.7). Birds moult to adult plumage when aged between 12 and 22 months (Randall 1989). The median age for this moult is 17 months which, when added to an egg incubation stage of some 40 days and a brood duration of about three months (Randall 1989), amounts to an age of nearly two years. It was assumed that:

$$Moult_{ad,t} * 1.1 = \sum_{i=3}^{6} N_{i,t} \quad ,$$

where $N_{i,t}$ = number of birds alive in age-class i in year t.

However, not all birds in age-classes 3 to 5 are breeders. To account for this, it was assumed that the population was in equilibrium, i.e. for all i:

$$N_{i,t+1} = N_{i,t} \quad .$$

This gives:

$$\sum_{i=3}^{6} N_{i,t} = \sum_{i=3}^{6} N_{3,t} * s_{ad,t}^{\,i-3} + N_{6,t} * s_{ad,t} \quad .$$

Since, at equilibrium:

$$N_{6,t} = N_{6,t} * s_{ad,t} + N_{3,t} * s_{ad,t}^{\,3} \quad ,$$

the count of birds in adult plumage that moulted can be expressed as:

$$Moult_{ad,t} * 1.1 = \sum_{i=3}^{6} N_{3,t} * s_{ad,t}^{\,i-3} + \frac{N_{3,t} * s_{ad,t}^{\,4}}{1 - s_{ad,t}} \quad .$$

Given $s_{ad,t}$, which was taken as $s_{ad,1993}$, it is possible to calculate the number of birds in age-class 3, and hence the numbers in age-classes 4 to 6.

In each age-class, the number of birds in adult plumage that moulted was decreased to account for non-breeders, giving the proportion of breeders that nested in year t:

$$A_t = \frac{Nest_{\max,t} * 2}{Moult_{ad,t} * 1.1 - \sum_{i=3}^{6} (N_{i,t} * (1 - b_i))} \quad .$$

$Nest_{max,t}$ will be a minimum estimate of the number of pairs breeding in year t, as some pairs may not have been nesting at the time of the count. Therefore, A_t may be underestimated.

Population model

The population model was run with a time increment of one year over the period 1988 to 1995. It considered numbers of penguins in six age-classes, $N_{i,t}$ for i = 1 to 6 where t signifies the year. Penguins in age-class one were those that had just fledged; in age-class two those in their second year of life (i.e. aged between one and two); in age-class three those in their third year; in age class four those in their fourth year; in age class five those in their fifth year; and in age-class six all birds aged five years or older.

The number of pairs of penguins at Robben Island that bred in year t (P_t) was computed as:

$$P_t = A_t * \sum_{i=1}^{6} \frac{(N_{i,t} * b_i)}{2} \quad .$$

The number of chicks fledged in any year t was:

$$N_{1,t} = P_t * F_t \quad ,$$

where F_t = the mean number of chicks fledged per breeding pair in year t.

For i = 2, numbers of birds alive at the start of year t were computed as:

$$N_{2,t} = N_{1,t-1} * s_{juv,t-1} \quad .$$

Numbers of birds in this age-class alive at the end of year t were calculated as:

$$N_{2,t} = N_{1,t-1} * s_{juv,t-1} * s_{ad,t} + I_{imm,t} \quad ,$$

where $I_{imm,t}$ = number of birds in immature plumage immigrating to the colony at the end of year t.

Survival of birds was assumed the same for age classes two to six (s_{ad}), but a different value (s_{juv}) was used for first-year birds. $I_{imm,t}$ was taken to be the difference between the count of birds in immature plumage moulting at the island and the number of these estimated to have originated from the island in the preceding year:

$$I_{imm,t} = Moult_{imm,t} * 1.1 - N_{1,t-1} * s_{juv,t-1} * s_{ad,t} \quad ,$$

where $Moult_{imm,t}$ = number of penguins in immature plumage moulting at the island in year t.

For i = 3 to 5, numbers of birds alive at the start of year t were computed as:

$$N_{i,t} = N_{i-1,t-1} * s_{ad,t} + I_{i,t} \quad ,$$

where $I_{i,t}$ = number of birds in age-class i immigrating to the island in year t.

For i = 6, the number of birds alive at the start of year t was computed as:

$$N_{6,t} = N_{6,t-1} * s_{ad,t} + N_{5,t-1} * s_{ad,t} + I_{6,t} \quad .$$

The number of birds in age-classes 3 to 6 immigrating to the island was taken to be the difference between the number of birds in adult plumage moulting at the island in year t and the number of birds in these age-classes estimated to have survived from birds present at the island in the previous year. Thus:

$$\sum_{i=3}^{6} I_{i,t} = Moult_{adt} * 1.1 - \sum_{i=2}^{6} N_{i-1,t-1} * s_{adt-1} - I_{immt-1} \quad .$$

Immigrants in adult plumage were allocated to age-classes 3 to 6 *pro rata* to the numbers of birds that would be in these age-classes in an equilibrium situation.

To investigate how the colony at Robben Island would have performed in the absence of immigration, $I_{imm,t}$ and $I_{i,t}$ were set equal to zero, for all age classes i and years t.

The model was initiated in 1988, setting:

$$\sum_{i=3}^{6} N_{i,1988} = Moult_{ad,1988} * 1.1 \quad ,$$

again assuming that the relative numbers of birds in age-classes 3 to 6 would be the same as in an equilibrium situation, and

$$N_{2,1988} = Moult_{juv,1988} * 1.1 \quad .$$

The mean number of chicks fledged per breeding pair in 1988, F_{1988}, was taken as the mean of F_t for 1989 to 1995.

Sensitivity of model results to s_{ad}, s_{juv}, A_t and F_t was examined by changing these parameters.

Relationship between population parameters and prey abundance

Using correlation analysis, we investigated the relationships of the mean number of chicks fledged per breeding pair (F_t), the proportion of mature adults breeding (A_t) and the number of immature birds recruiting to the colony at Robben Island ($I_{imm,t}$) to the abundance of the main prey items of African Penguins at the island – anchovy and sardine (Crawford *et al.* 1995a). The spawner biomass of anchovy and sardine was estimated acoustically (Hampton 1992, updated).

RESULTS

Numbers of birds

Numbers of penguins in adult plumage moulting at Robben Island increased from 3125 in 1988 (July 1988 to June 1989) to 7213 in 1993, but fell to 6346 in 1995 (Fig. 1). This number was strongly correlated with the maximum count of active nests in the same year (r = 0.945, P < 0.001, n = 8; Fig. 2).

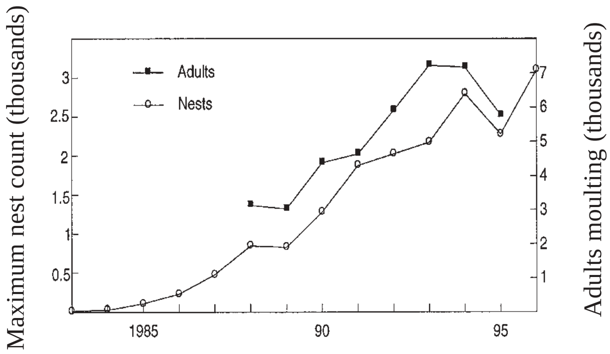


Fig. 1. *Trends in the numbers of African Penguins breeding pairs and moulting adults at Robben Island, 1983–1996.*

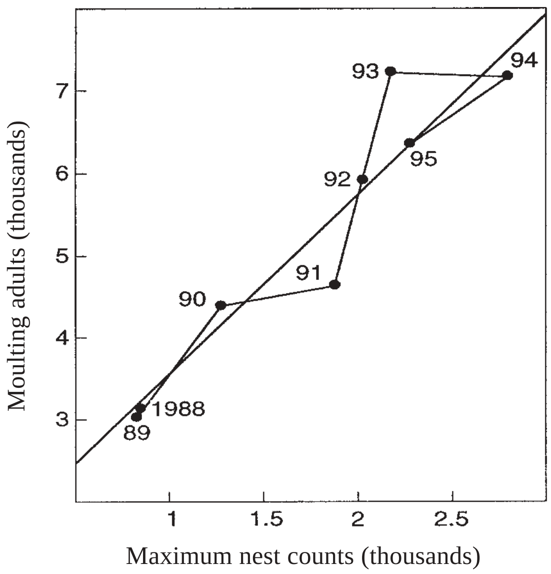


Fig. 2. *The relationship between the maximum count of nests at Robben Island and the number of adult African Penguins moulting. The main breeding season is from February to September, and the main moult of adults from November to January. The count of nests was related to the following moult, i.e. that commencing the same year as breeding.*

Adult survival

Eighty-six uniquely banded adults were known to be alive at Robben Island in both 1993 and 1995. Of these, 18 were not seen in 1994, giving the probability of a banded adult not being seen (Pns_{ad}) as 18/86 = 0.21.

Of the 139 banded adults alive in 1993, 107 were seen in 1994 so that survival of adults in 1993 ($s_{ad,1993}$) was 0.82. Survival of adults in 1994 ($s_{ad,1994}$) was 0.75 (102 of 148 banded adults seen in 1994 were also seen in 1995).

Age at first breeding

Ages at which known-aged birds were first observed breeding at Robben Island are shown in Fig. 3. One bird (S11911) banded at Robben Island on 28 May 1993 was seen with two eggs at monitored nest 100 on 8 February 1995, when aged one year and eight months. The clutch was abandoned before 22 February 1995, and there was no further attempt at breeding at this nest in 1995. Four birds aged between two and three years were seen holding nest sites, one with eggs and two with chicks. None of these nests was monitored, so the outcomes of the breeding attempts are not known. An additional 12 birds (18% of the known-aged breeders) were breeding when aged between three and four years. The most commonly recorded age at first breeding was four years (36%), with 18% first seen breeding when aged between five and six years. By age six, 80% of all known-age birds were breeding. Although the first recorded observation of breeding for 13 birds was when they were older than six years, it is likely that earlier breeding attempts were not observed. In the model it was assumed that 0% of birds aged one year, 10% of those aged two, 33% of those aged three, 80% of those aged four and 100% of all older birds were breeders.

Proportion breeding

The proportion of mature birds estimated to breed varied between 0.69 in 1988 and 1.03 in 1991. The maximum proportion that can breed is 1.00, indicating that in 1991 the count of birds in adult plumage may have been too low or that proportions of birds breeding at each age were higher than those estimated. In the model, a maximum value of 1.0 was allowed for A_t.

From 1988 to 1993, the proportion of mature birds breeding was positively related to the spawner biomass of anchovy (r = 0.808, $P \sim 0.05$, n = 6), but in 1994 and 1995 relatively high breeding proportions were associated with a low anchovy biomass. Over the entire period (1988–1995), there was a significant positive relationship between breeding proportion and spawner biomass of sardine (r = 0.709, $P < 0.05$, n = 8; Fig. 4). Sardine abundance thus explained 50% (r^2 = 0.50) of the observed variation in breeding proportion.

Clutch size

The mean clutch observed during 1989–1995 was 1.86±0.04 eggs (n = 581). The lowest mean clutch in any year was 1.81 (1993 and 1995), and the highest was 1.92 (1994, Table 1).

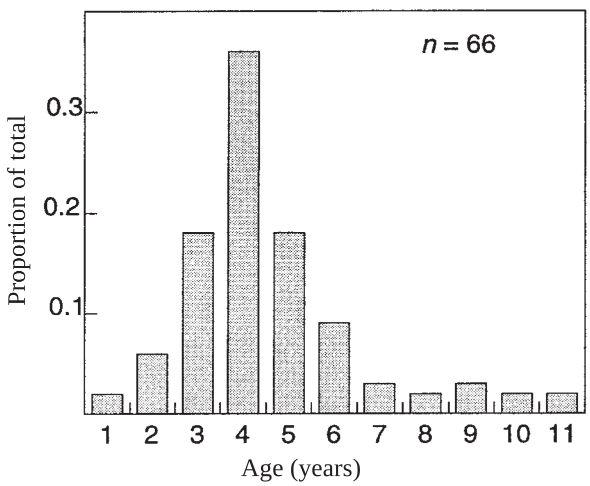


Fig. 3. *The age at which known-age African Penguins were first observed breeding at Robben Island (n = 66).*

TABLE 1

Clutch sizes of African Penguins at Robben Island, 1989–1995

Year	Nests with			Mean clutch size
	1 egg	2 eggs	3 eggs	
1989	11	86	0	1.89
1990	11	51	0	1.82
1991	15	79	2	1.87
1992	8	62	0	1.89
1993	17	73	0	1.81
1994	8	91	0	1.92
1995	13	54	0	1.81
1989–95	**83**	**496**	**2**	**1.86**

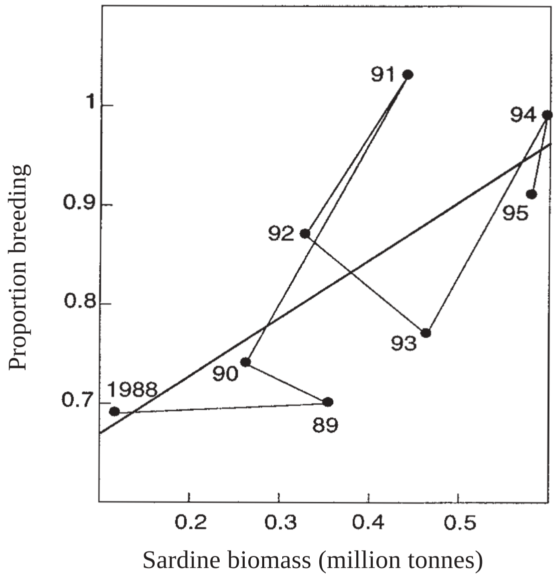


Fig. 4. *The relationship between the proportion of mature African Penguins estimated to have bred at Robben Island and the biomass of South African Sardine, 1988–1995.*

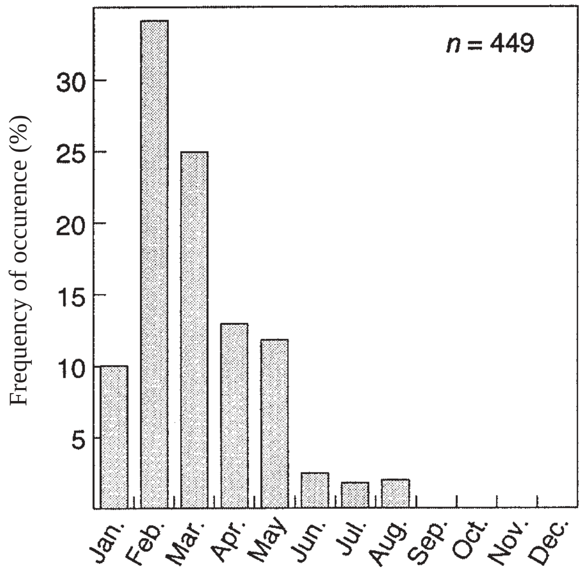


Fig. 5. *The month in which African Penguins laid their first clutch at Robben Island, 1989–1995 (n = 449).*

Month of production of first clutch

Most pairs (34%) laid their first clutches in February (Fig. 5). A few pairs laid for the first time in the breeding season in January, and some as late as August (Table 2). Overall 94% of all clutches were laid before the end of May.

Breeding success and replacement laying

Between 1989 and 1995, the mean number of chicks fledged per breeding pair per year ranged between 0.32 in 1990 and 0.59 in 1991 and 1992 (Fig. 6). It was significantly related to anchovy spawner biomass ($r = 0.859$, $P < 0.02$, n = 7). The overall mean number of chicks fledged per breeding pair, giving equal weighting to years, was 0.47 ± 0.11.

Over the same period, for first clutches that were monitored (n = 429), breeding by 48% of pairs failed at the incubation stage and by a further 28% at the brood stage. From the first clutches of a breeding season, 24% of pairs successfully fledged a chick. Of pairs whose first clutch failed at the incubation stage, 32% relayed. When the first clutch failed at the brood stage, 23% relayed, and when a chick was successfully fledged, 21% of pairs relayed. Overall, 27% of breeding pairs laid a second clutch.

Of second clutches monitored (n = 112), 30% failed at the incubation stage and 40% at the brood stage, whereas 30% produced at least one fledged chick. There was no significant difference between the number of first and second clutches that were successful ($\chi^2 = 1.316$ using Cochran's continuity correction for the 2×2 contingency table, $P = 0.254$).

The laying of a third clutch was recorded once, in 1995. The pair concerned laid two eggs in early February, which were lost before the end of the month. A second clutch of one egg was laid in early May and again lost before the end of the month. Finally, two eggs were laid in late June, and hatched in early August but the brood was lost by the end of this month.

TABLE 2

Month of laying of first clutch by African Penguins at Robben Island, 1989–1995

Year	Number of first clutches observed in							
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug
1989	0	37	25	3	1	3	2	0
1990	0	25	12	4	1	2	3	0
1991	0	39	16	9	7	1	2	7
1992	0	10	12	11	21	3	0	0
1993	10	25	6	18	8	1	1	0
1994	31	6	24	9	9	0	0	0
1995	4	11	17	4	6	1	0	2

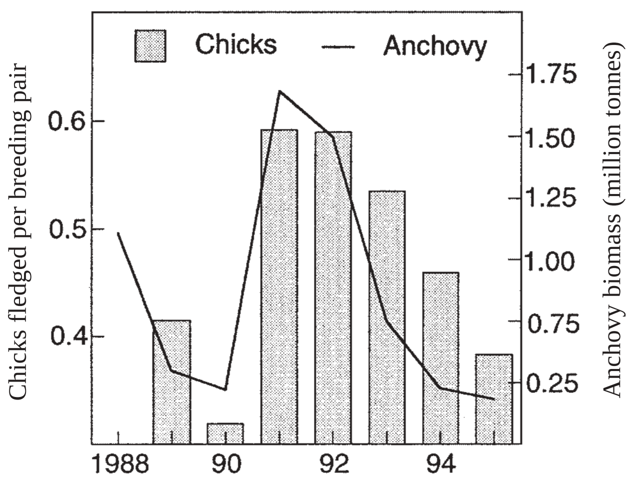
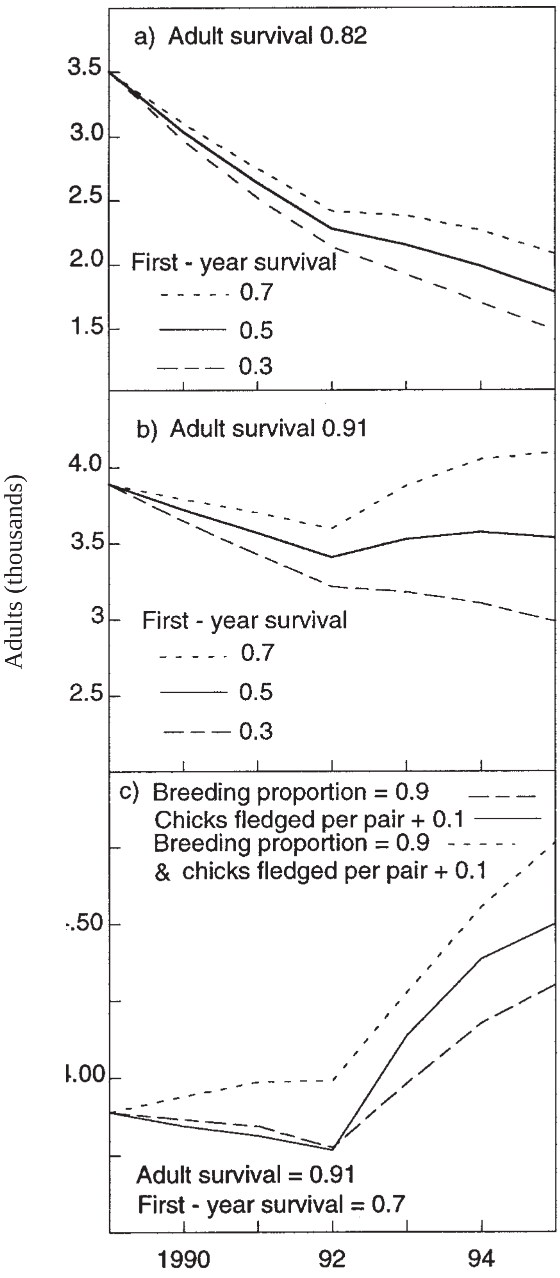


Fig. 6. *The mean number of chicks fledged per breeding pair of African Penguins at Robben Island compared with the biomass of Cape Anchovy, 1989–1995.*

Immigration

In the absence of immigration, model estimates of numbers of adults at the colony decreased for all values of s_{juv} used when s_{ad} was set at 0.82 (Fig. 7a). For s_{ad} = 0.91, numbers of adults decreased for s_{juv} = 0.3, decreased marginally for s_{juv} = 0.5, and increased marginally for s_{juv} = 0.7 (Fig. 7b). Colony growth was obtained with s_{ad} = 0.91 and s_{juv} = 0.7 when the proportion of mature birds breeding (A_t) was kept constant at a relatively high value of 0.9, or the number of chicks fledged per breeding pair (F_t) was increased by 0.1 in each year (Fig. 7c). However, even with both these changes, the model was not able to simulate the observed growth of the colony if immigration was disallowed.

When immigration was permitted in the model, for s_{ad} = 0.82 and s_{juv} = 0.5, the number of birds in immature plumage estimated to immigrate to Robben Island ($I_{imm,t}$) increased from 664 in 1989 to 1463 in 1990, and then fell to 840 in 1994 (Fig. 8). This number was significantly related to the spawner biomass of anchovy (r = 0.897, P < 0.01, n = 7).



For the same values of survival, the number of penguins in adult plumage estimated to immigrate to the colony was negative in 1989, 1994 and 1995, i.e. the model indicated emigration, but positive from 1990 to 1993 (Fig. 9). There was no significant relationship between this number and the spawner biomass of either anchovy or sardine.

For s_{ad} = 0.82, it was estimated that of birds recruiting to the adult population at Robben Island during 1990 to 1995, depending on the value used for s_{juv}, 13–29% resulted from chicks hatched at the island. The lower value was obtained for a first-year survival of 0.3, and the higher for a survival of 0.7. For a first-year survival of 0.5, 21% of recruits to the adult population were raised at the island. Thus 71–87% of incoming adults were estimated to be immigrants. Of incoming adults, 50–66% were of birds that immigrated to the island in their second-year (I_{imm} in the model), i.e. of birds in immature plumage. Some of the new adults at Robben Island were from chicks hatched at the island by immigrants. If they are discounted, just 6–14% of recruits to the adult population resulted from birds already at Robben Island in 1990, or their progeny.

For s_{ad} = 0.91, the model estimated emigration of slightly fewer than 1000 adults during 1990 to 1995. Of birds recruiting to the adult population, depending on the value of s_{juv}, 18–41% resulted from chicks hatched at the island. The balance was of birds that came to the island in immature plumage (I_{imm}). Birds at the island in 1990, or their progeny, gave rise to 12–29% of incoming adults.

Of the 66 birds of known age that were observed breeding at Robben Island, 53 were banded as chicks at Robben Island, nine as chicks at Dassen Island and four as chicks at Dyer Island. Respectively, these represent 19.4, 1.6 and 1.5 chicks per thousand banded at these localities between 1984 and 1994. Therefore, proportions of banded chicks immigrating from Dassen and Dyer Islands were almost identical, but substantially less than the proportion of chicks banded at Robben Island that returned to the island to breed.

DISCUSSION

The number of adults at Robben Island increased steadily until 1993, but then decreased (Fig. 1). The number of breeding pairs increased until 1994, but fell in 1995. The decreases in numbers of adults and breeding pairs in 1994/95 resulted from the oiling of penguins at Robben Island in June 1994, after sinking of the *Apollo Sea* to the north of Robben Island. Oil washed ashore at the island, where about 2400 birds were rescued for rehabilitation (Crawford 1994). Approximately half of the penguins that were treated following sinking of the *Apollo Sea* died (Williams 1995), so the loss at Robben Island would have amounted to about 1200 birds.

Fig. 7. *Model estimates of the number of African Penguins in adult plumage that would have been present at Robben Island in the absence of immigration for different values of first-year survival, 1989–1995:*
a) adult survival = 0.82
b) adult survival = 0.91.
In c) the estimated number of adults in the absence of immigration is shown for different values of the proportion of mature birds breeding and the number of chicks fledged per breeding pair for adult survival = 0.91 and first-year survival = 0.7.

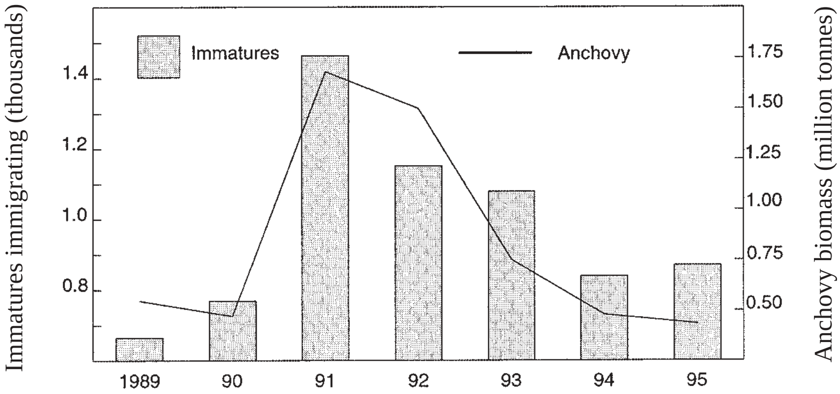


Fig. 8. *The number of African Penguins in immature plumage (assumed equivalent to birds aged two) estimated to have recruited to Robben Island, assuming an adult survival of 0.82 and a first-year survival of 0.50, compared with the biomass of Cape Anchovy, 1989–1995.*

The number of adults counted at Robben Island decreased by almost 900 between 1993 and 1995 which, when a factor of 1.1 is applied (correction for moult counts), represents some 1000 adults. Between 1994 and 1995 the number of active nests fell by 520, again representing some 1000 birds. Both these results are in broad agreement with the estimated loss of 1200 penguins, mostly but not exclusively birds in adult plumage, during rehabilitation.

The estimated survival of adults at Robben Island decreased from 0.82 in 1993/94 to 0.75 in 1994/95. Given that there were some 8000 adults at Robben Island at the start of 1994, after adjustment of counts of moulting birds by a factor of 1.1, the reduced survival represents the loss of about 600 birds. This is somewhat less than the mortality believed to have occurred. As intensive searches for banded birds only began towards the end of 1994, after rehabilitated penguins had been released between 26 July and 11 September (Underhill *et al.* 1999), it is possible that adult survival in 1993/94 was underestimated. A decreased survival of 0.14 between 1993/94 and 1994/95 would have approximated the probable loss of 1000 birds in adult plumage that resulted from oiling. If the value for adult survival in 1994/95 was correct, this suggests adult survival in 1993/94 may have been as high as 0.89.

For s_{ad} = 0.91, the model predicted overall emigration of adults from Robben Island during 1990 to 1995, whereas for s_{ad} = 0.82 there was immigration. Emigration is considered unlikely, so s_{ad} was probably less than 0.91. For the period under consideration, excepting 1994, s_{ad} was probably between 0.82 and 0.90.

At St Croix Island, Randall (1983) estimated adult survival to vary between 88% and 96% during 1976/77 to 1981/82, with an average annual survival of 91%. At Dyer Island, an annual survival of 69% was estimated for adults during 1979 to 1985 (La Cock & Hänel 1987). At Marcus Island between 1979 and 1985, adult survival ranged between 33% and 70%, with an average of 62% (La Cock *et al.* 1987), but these latter values were probably too low as no allowance was made for birds being alive but not being sighted. Recently, Underhill *et al.* (1999) assumed survival of adult African Penguins to average 85% per annum.

Randall (1983) noted the ages at first breeding of nine African Penguins at St Croix Island. Three were in their fourth year, three in their fifth year and three in their sixth year. At Robben Island a bird made an unsuccessful attempt to breed in its second year, and four birds were breeding in their third year. It was assumed that all birds in their sixth year were breeders. Adélie Penguins *Pygoscelis adeliae* breeding at a young age had a higher mortality than those breeding later in life (Ainley & DeMaster 1980). However, Adélie Penguins first breeding at a late age, and therefore inexperienced, were relatively unsuccessful (Ainley & DeMaster 1980). There may be advantage in not breeding too early or too late in life.

The proportion of breeders laying at Robben Island was estimated to vary between about 0.7 and 1.0. Off Peru, Humboldt Penguins *S. humboldti* did not breed during the severe El Niño conditions of 1983 (Hays 1986). Galápagos Penguins *S. mendiculus* also may defer breeding during severe El Niños (Boersma 1978). For the African Penguin such extreme absenteeism of breeders has not yet been noted, but nevertheless indications are that in some years a substantial proportion of the breeding population may opt not to breed.

On average, Randall (1983) estimated that breeding pairs fledged 0.38 chicks per year at St Croix Island. At Dassen Island, Frost *et al.* (1976) recorded 0.37–0.67 chicks fledged

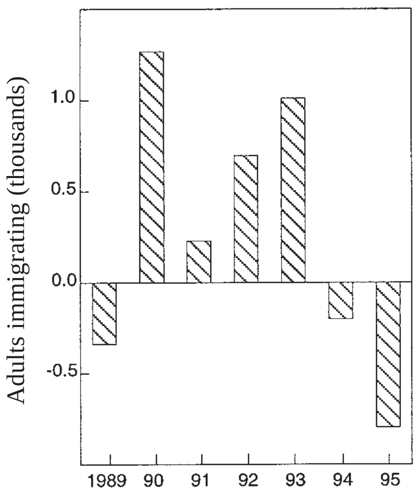


Fig. 9. *The number of African Penguins in adult plumage (assumed equivalent to birds older than two years) estimated to have recruited to Robben Island, assuming an adult survival of 0.82 and a first-year survival of 0.50, 1989–1995.*

per pair. At Marcus Island, La Cock & Cooper (1988) recorded 0.63 chicks fledged per pair. At Robben Island, the number of chicks fledged per pair ranged between 0.32 and 0.59, values similar to those recorded elsewhere.

At Marcus Island 22% of pairs laid second clutches (La Cock & Cooper 1988). This value is similar to the 27% observed at Robben Island. However, at St Croix Island, 93% of pairs that lost clutches early in the year replaced them, the modal number of clutches laid was two, it was common for pairs to lay three clutches and some pairs laid as many as four clutches in a year (Randall 1983). Therefore at St Croix Island, replacement laying seems more common.

In 1994, breeding at several of the monitored sites was disrupted by removal of oiled parents for rehabilitation. Had there not been an oil spill, production may have been higher than the measured value of 0.46 chicks fledged per breeding pair. In the same year, both the proportion of birds breeding and I_{ad} would have been overestimated because the count of moulting adults that followed the breeding season would have been depressed by the loss of birds from oiling.

At Robben Island, breeding performance and immigration of immature birds appear to have been closely related to the biomass of anchovy during 1989–1995. Immature birds modelled as immigrants (I_{imm}) could have resulted from genuine immigrants, or from enhanced survival in their first and second years of birds fledged at Robben Island. The proportion of mature birds breeding was also related to the abundance of anchovy during 1989–1993. In 1994 and 1995, this relationship did not hold, probably because an increased population of sardine provided an alternative food source. The proportion of mature birds breeding has increased over the study period, as the biomass of sardine has increased. Clearly, the reproductive performance of penguins at Robben Island is strongly influenced by the availability of food.

Even with s_{ad} as high as 0.91, while using other parameters measured at Robben Island, it was necessary for s_{juv} to be greater than 0.5 for the colony at the island to sustain itself (Fig. 7). At lower values of s_{juv}, numbers of adults at the island would have decreased in the absence of immigration. In this event, Robben Island would have acted as a sink of production elsewhere.

Limited growth of the colony in the absence of immigration was modelled by assuming $s_{ad} = 0.91$, $s_{juv} = 0.7$ and maintaining a consistently high breeding proportion of 0.9 or increasing the average number of chicks fledged per breeding pair in each year by 0.1 (Fig. 7c). However, even then the modelled growth did not match that observed. With the combination of parameters most conducive to population growth, the model estimated an increase of *c.* 750 adults between 1989 and 1995 in the absence of immigration (Fig. 7c). The actual growth of the colony during this period was in excess of 4000 adults (Fig. 1). Therefore, growth of the colony at Robben Island in the early 1990s must have been driven primarily by immigration.

Estimates of the breeding populations of African Penguins at Dassen and Dyer Islands, as well as at Robben Island, are available for the period 1984 to 1994 (Crawford *et al.* 1995b). Assuming that, on average, equivalent numbers of chicks were fledged per breeding pair at each of these localities, it is possible to combine estimates of their mean breeding populations and of proportions of chicks settling at Robben Island, obtained from banded birds, to gauge the relative contribution of these three islands to growth of the colony at Robben Island. When this is done, 40% of the growth is estimated to have arisen from production at Robben Island, 37.5% from production at Dyer Island and 22.5% from production at Dassen Island.

For the period 1989 to 1995, the model estimated 59–87% of the new adults at the colony to have arisen from immigration, depending on the values of parameters used. The proportion of breeders calculated to have immigrated from Dassen and Dyer Islands (60%) is at the lower end of this range. Birds also may have immigrated to Robben Island from other colonies, where far fewer chicks were banded between 1984 and 1994 (records of SAFRING and Marine and Coastal Management). Using estimates of breeding populations provided in Crawford *et al.* (1995b), production of fledglings in the Western Cape Province at colonies other than Dassen, Dyer and Robben Islands would have amounted to about 10% of the production at Dassen and Dyer Islands. This would have marginally increased the proportion estimated to have immigrated to 62%.

Since 1991, the proportions of mature birds breeding have generally been high. This will have resulted in a higher production of chicks, which will have influenced the number of adults from 1993 onwards. The impact is evident in the slowed rates of decrease or improved rates of increase of numbers of adults predicted after 1992 under all scenarios that assumed no immigration (Fig. 7).

If this trend towards a higher proportion of mature birds breeding is maintained, and if an increased production of chicks can be achieved, the colony's dependence on immigration for growth and even stability will be lessened. The relationship between breeding proportion and an increasing biomass of sardine (Fig. 4), suggests that the breeding proportion may continue to be high. Breeding success may increase if sardine provides a stable food supply, as opposed to anchovy which was highly variable during the study period (Hampton 1992). The recent variability in the anchovy resource has affected the reproductive performance not only of penguins, but also of three other seabirds that feed on anchovy (Crawford & Dyer 1995).

The number of breeding pairs of African Penguins at Robben Island recovered in 1996 when, for the first time more than 3000 active nests were counted. Thus, early indications are that the loss to oiling will not halt the increase of the penguin colony at Robben Island, which as yet shows no sign of asymptotic behaviour (Fig. 1). The colony is the sixth largest for the species (Crawford *et al.* 1995b) and it has the potential to expand even further. Its proximity to Cape Town and ready access make it a suitable colony to develop for ecotourism. Implications for management of ecotourism to African Penguin colonies are addressed by Shannon & Crawford (1999).

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REFERENCES

AINLEY, D.G. & DEMASTER, D.P. 1980. Survival and mortality in a population of Adélie Penguins. *Ecology* 61: 522–530.

BOERSMA, P.D. 1978. Breeding patterns of Galápagos Penguins as an indicator of oceanographic conditions. *Science* 200: 1481–1483.

CRAWFORD, R.J.M. 1994. 10,000 African Penguins rescued from oil spill. *African Wildlife Update* 3(4): 1, 8.

CRAWFORD, R.J.M. & BOONSTRA, H.G.v.D. 1994. Counts of moulting and breeding Jackass Penguins *Spheniscus demersus* – a comparison at Robben Island. *Mar. Orn.* 22: 213–219.

CRAWFORD, R.J.M., BOONSTRA, H.G.v.D., DYER, B.M. & UPFOLD, L. 1995a. Recolonization of Robben Island by African Penguins, 1983–1992. In: Dann, P., Norman, I. & Reilly, P. (Eds). The penguins: ecology and management. Chipping Norton: Surrey Beatty & Sons. pp. 333–363.

CRAWFORD, R.J.M. & DYER, B.M. 1995. Responses by four seabirds to a fluctuating availability of Cape Anchovy *Engraulis capensis* off South Africa. *Ibis* 137: 329–339.

CRAWFORD, R.J M., WILLIAMS, A.J., HOFMEYR, J.H., KLAGES, N.T.W., RANDALL, R.M., COOPER, J., DYER, B.M. & CHESSELET, Y. 1995b. Trends of African Penguin *Spheniscus demersus* populations in the 20th Century. *S. Afr. J. mar. Sci.* 16: 101–118.

FROST, P.G.H., SIEGFRIED, W.R. & COOPER, J. 1976. Conservation of the Jackass Penguin (*Spheniscus demersus* (L.)). *Biol. Conserv.* 9: 79–99.

HAMPTON, I. 1992. The role of acoustic surveys in the assessment of pelagic fish resources on the South African continental shelf. *S. Afr. J. mar. Sci.* 12: 1031–1050.

HAYS, C. 1986. Effects of the 1982–83 El Niño on Humboldt Penguin colonies in Peru. *Biol. Conserv.* 36: 169–180.

LA COCK, G.D. & COOPER, J. 1988. The breeding frequency of Jackass Penguins on the west coast of South Africa. *J. Field Orn.* 59: 155–156.

LA COCK, G.D., DUFFY, D.C. & COOPER, J. 1987. Population dynamics of the African Penguin *Spheniscus demersus* at Marcus Island in the Benguela upwelling ecosystem. *Biol. Conserv.* 40: 117–126.

LA COCK, G.D. & HÄNEL, C. 1987. Survival of African Penguins *Spheniscus demersus* at Dyer Island, southern Cape, South Africa. *J. Field. Orn.* 58: 284–287.

RANDALL, R.M. 1983. Biology of the Jackass Penguin *Spheniscus demersus* (L.) at St Croix Island, South Africa. PhD. thesis. University of Port Elizabeth.

RANDALL, R.M. 1989. Jackass Penguins. In: Payne, A.I.L. & Crawford, R.J.M. (Eds). Oceans of life off southern Africa. Cape Town: Vlaeberg. pp. 244–256.

RANDALL, R.M., RANDALL, B.M., COOPER, J. & FROST, P.G.H. 1986. A new census method for penguins tested on Jackass Penguins *Spheniscus demersus*. *Ostrich* 57: 211–215.

SHANNON, L.J. & CRAWFORD, R.J.M. 1999. Management of the African Penguin *Spheniscus demersus* – insights from modelling. *Mar. Orn.* 27: 119–128.

SHELTON, P.A., CRAWFORD, R.J.M., COOPER, J. & BROOKE, R.K. 1984. Distribution, population size and conservation of the Jackass Penguin *Spheniscus demersus*. *S. Afr. J. mar. Sci.* 2: 217–257.

UNDERHILL, L.G., BARTLETT, P.A., BAUMANN, L., CRAWFORD, R.J.M., DYER, B.M., GILDENHUYS, A., NEL, D.C., OATLEY, T.B., THORNTON, M., UPFOLD, L., WILLIAMS, A.J., WHITTINGTON, P.A. & WOLFAARDT, A.C. 1999. Mortality and survival of African Penguins *Spheniscus demersus* involved in the *Apollo Sea* oil spill: an evaluation of rehabilitation efforts. *Ibis* 141: 29–37.

WILLIAMS, A.J. [1995]. Factors to consider in the capture and transport of penguins. In: Barrett, J., Erasmus, Z. & Williams, T.[A.J.] (Eds). Proceedings coastal oil spills: effect on penguin communities and rehabilitation procedures. Tygerberg Nature Reserve November 1994. [Cape Town]: Cape Nature Conservation. pp. 15–18.