Population Changes and Demography of the Northern Rockhopper Penguin on Amsterdam and Saint Paul Islands

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Abstract.—We investigated changes in population size and demography of the Northern Rockhopper Penguin (*Eudyptes chrysocome moseleyi*) between 1971 and 1995 on Amsterdam and Saint Paul islands. During an intensive survey between 1993 and 1995, breeding success was similar to that reported from other sites, although the first egg (A-egg) loss rate was lower on Amsterdam Island than at other localities. The mean age of first return to the breeding site and of first reproduction were respectively $\bar{X}$ = 4.2 ± SD of 2.1 years and $\bar{X}$ = 4.7 ± SD of 1.7 years. The adult survival rate, calculated between 1988 and 1993, was significantly lower one year after banding [$\bar{X}$ = 72.2 ± SD of 1.6%] than in subsequent years [$\bar{X}$ = 84.0 ± SD of 1.1%] due to the effect of banding. Immature survival rate was estimated at 39% during the first year after banding. Two birds banded as chicks have been found in Australia, suggesting that immatures winter off Southern Australia.

The population on Amsterdam Island decreased at a rate of 2.7% per year between 1971 and 1993. Using the demographic parameters measured, we calculated a modelled rate of increase of 0.940 between 1988 and 1993, a value close to the observed rate of 0.943. Between 1982 to 1993, mean sea surface temperature near Amsterdam and Saint Paul islands decreased significantly, and this change was significantly related to the decline of Amsterdam Island population during the same period. Mean sea surface temperature decline could affect the Rockhopper Penguin population through changes of distribution and abundance of prey. Other factors such as the large increase of the Sub-Antarctic Fur Seal population at Amsterdam Island between 1971 and 1993 could have reduced the penguin population. Between 1971 and 1993, the Saint Paul population of penguins increased by 5.5% per year, but this is not significantly related to the mean sea surface temperature decrease. This small Rockhopper Penguin population may still be recovering to its level before exploitation in the 1930s. *Received 20 October 1997; accepted 3 March 1998.*

Key words.—Amsterdam and Saint Paul islands, demography, *Eudyptes chrysocome moseleyi*, Northern Rockhopper Penguin, population trends, survival.

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Populations of penguins have changed dramatically during the past decades. Species such as King (*Aptenodytes patagonica*) and Chinstrap (*Pygoscelis antarctica*) penguins have increased dramatically (Weimerskirch *et al.* 1989; Jouventin and Weimerskirch 1990, 1991; Croxall 1992; Frazer *et al.* 1992). Other species such as Emperor (*Aptenodytes forsteri*), Rockhopper (*Eudyptes chrysocome*), Magellanic (*Spheniscus magellanicus*) and Yellow-eyed penguins (*Megadyptes antipodes*) have decreased severely (Boersma *et al.* 1990; Jouventin and Weimerskirch 1990, 1991; Marchant and Higgins 1990; Moore 1992; Cunningham and Moors 1994; Cooper *et al.* 1997). The reasons for these changes are not always well understood (Jouventin and Weimerskirch 1991; Croxall 1992). Mean sea surface temperature in the southern hemisphere has increased markedly, resulting probably from global climate change (Duffy 1990). Variations in sea surface temperature may affect seabird breeding success (Boersma *et al.* 1990; Jouventin and Weimerskirch 1991; Guinet *et al.* 1994, 1998) and therefore population size. For example, the population decrease of Southern Rockhopper penguins (*Eudyptes chrysocome filholi*) at Campbell Island has been related to increased sea temperature (Cunningham and Moors 1994), with variations in sea temperature likely affecting the distribution and the abundance of prey (Croxall 1992; Cunningham and Moors 1994).

The Rockhopper Penguin is the most widespread species in the genus *Eudyptes*. It breeds from islands near the Antarctic Polar Front to Subtropical waters (Marchant and Higgins 1990). The subspecies *E. c. chrysocome* is confined to the Falkland Islands. The

Southern Rockhopper Penguin (*E. c. filholi*), the most numerous subspecies, breeds in the sub-Antarctic zone. The Northern Rockhopper Penguin (*E. c. moseleyi*) breeds in the Subtropical area on Tristan da Cuñha and Gough islands, in the southern Atlantic Ocean, and on Amsterdam and Saint Paul islands, in the southern Indian Ocean (Marchant and Higgins 1990). The population status and breeding biology of the northern subspecies are not well known compared with that of the Southern Rockhopper Penguin. This paper examines the demography and population trends of the Northern Rockhopper Penguins breeding at Amsterdam and Saint Paul islands.

METHODS

The study was conducted on Amsterdam Island (37°50'S, 77°31'E) in the Southern Indian Ocean. A colony (*c.* from 100 to 300 pairs) was monitored at Pointe d'Entrecasteaux, on the south-western part of Amsterdam Island, seven hours walk from the base, from 1988 to 1993. Nest sites were mapped. Visits to the colony were timed to coincide with male and female arrivals, laying and hatching, 15 days before chick departure to sea, and molting period, all based on dates for breeding phenology described by Paulian (1953), Duroselle and Tollu (1977) and Tollu (1978).

The number of incubating adults present at the colony in the first half of September was taken as the number of breeding pairs. To monitor breeding success, each nest of the study colony was monitored on average 9 to 10 days per month during the breeding season, from the end of August through the end of December in 1993. We counted the number of hatchlings in the first part of October, and the number of surviving chicks around mid-December. The latter figure was considered as the number of "fledged" chicks (mortality after 15 December was considered negligible: only 1% in 1993: unpubl. data). Additional data were obtained in 1994 and 1995 from two other colonies at Entrecasteaux.

All incubating birds in the study colony were flipper-banded and web-punched to evaluate the rate of band loss (Richdale 1949). Adults and immatures were recaptured throughout the study period, in the study area and in surrounding colonies. Birds were sexed from measurements (body weight, culmen and flipper: Warham 1975), and their behaviour during laying, incubating and chick guarding periods. Survivorships of adults and immatures from 1988 to 1993 were estimated using SURGE (Clobert *et al.* 1985). Different models were tested on recapture-resighting histories; the most appropriate model for the data set was selected for the model with the lowest Akaike's Information Criterion (Pradel 1989).

Population censuses were carried out at Fausse Pointe, La Rambarde and Entrecasteaux, the three breeding sites of Rockhopper Penguins on Amsterdam Island, in 1988 and annually from 1990 to 1993. On Saint Paul Island (38°43'S, 77°30'E, 80 km south of Amsterdam Island), censuses were carried out at Grand Morne and Terrasse des Pingouins, from 1988 to 1991, and in 1993. Censuses were made in September by estimating the number of occupied nests in 25 m^2 quadrats and the total surface area of each colony. Counts from photographs were used only for inaccessible colonies (for those of La Rambarde and the Terrasse des Pingouins).

International Global Ocean Service System (IGOSS) monthly sea surface temperatures (accuracy: 0.25°C) were used for comparison with the numbers of Rockhopper Penguins (Reynolds and Smith 1994). Statistical tests were carried out using the Systat (Wilkinson 1996) package. All mean values, $\bar{X}$, are given ± standard deviation (SD) unless otherwise indicated in the text.

RESULTS

Egg loss and breeding success

Most of the eggs lost were A-eggs (Table 1: $\chi^2_1 = 23.7$, P <0.001). Overall breeding success was significantly higher for B-eggs than for A-eggs [42.4% vs. 15.3%], ($\chi^2_1 = 9.4$, P = 0.002) (Table 1). During the rearing period, mortality rates of A- and B-chicks were not significantly different (Table 1: $\chi^2_1 = 3.27$, n.s.). Breeding success varied significantly among years from 1993 to 1995 ($\chi^2_2 = 34.8$, P < 0.001): 28% in 1993 (n = 202 nests), 35% in 1994 (n = 176 nests) and 52% in 1995 (n = 185 nests).

Ages of first return to the colony and first breeding

The mean age of first return to the breeding colony of birds banded as fledglings was

Table 1. Number of eggs laid and percentage of eggs lost, chicks dead and fledged for A-eggs and B-eggs during the breeding cycle in 1993.

	Eggs laid (n)	Egg loss	Chick mortality (for 100 chicks hatched)	Chicks fledged
A	111	57.7%	63.8%	15.3%
B	92	22.8%	45.1%	42.4%
A+B	203	41.9%	52.5%	27.6%

$\bar{X}$ = 4.2 ± SD of 2.1 years (range 1-8, n = 20). Two birds bred at two years of age and the mean age of first breeding was $\bar{X}$ = 4.7 ± SD of 1.7 years (n = 13).

Two one-year old birds, banded as chicks in December 1992 at Amsterdam Island, were found dead on the southern coast of Australia near Melbourne, one (band E444) found on 29 July 1993 at Pelican Point near Carpenter Rocks, SA (37°54'S, 140°22'E) and another (band E329) found on 21 September 1993 near Wreck Beach, Harmers Haven (38°39'S, 145°35'E).

Survival

The annual adult survival rate of Rockhopper Penguins was calculated from 1988 to 1994 for 1,130 banded birds. The most appropriate model was the model P_t, S_{2age}: this model accounts for a recapture rate dependent on time (P_t), as a result of variable recapture effort, and for two age classes of survival, the "first year after banding" and the "subsequent years" (S_{2age}). Adult survival rate was significantly lower [$\bar{X}$ = 72.2 ± SD of 1.6%, 95% confidence interval: 68.9-75.2%] during the first year after banding than in subsequent years [$\bar{X}$ = 84.0 ± SD of 1.1%, 95% confidence interval: 81.6-86.1%], suggesting there was an effect of banding on the survival of birds.

Immature survival rate was calculated between 1988 and 1994 for 514 birds banded as chicks. The most appropriate model was P_{age}, S_{2age}, i.e. the recapture effort varied according to the age of the birds, and survival according to two age classes. The survival rate was significantly lower for the first year [$\bar{X}$ = 27.4 ± SD of 24.7%, 95% confidence interval: 3.2-81.0%] than during subsequent years [$\bar{X}$ = 82.9 ± SD of 20.0%, 95% confidence interval: 23.4-98.7%]. If we assume that the adverse effect of banding was equivalent for chicks and adults, banding would have decreased chick survival about 12%, suggesting a survival of unbanded chicks of at least 39%.

Population trends

Between 1971 and 1993, the number of Northern Rockhopper Penguins on Amsterdam Island decreased significantly (Spearman's rank correlation coefficient, $r_{s,7}$ = -0.82, P = 0.025; Fig. 1) from 58,000 to 24,890 pairs (Fig. 1), at a rate of 2.7% per year. Between 1971 and 1988, the rate of decrease was 1.8% per year (from 58,000 to 39,871), and the decrease was more rapid between 1988 and 1993 (5.7%, from 39,871 to 24,890).

Using the demographic parameters estimated above, we modeled the rate of increase of the population using a Leslie matrix (Leslie 1945, 1949). The demographic parameters used in the model were the age of first reproduction (two years), the age when all birds have been recruited into the breeding population (seven years), the percentage of breeders (10% at two years, 20% at three years, 50% at four years, 80% at five years, 90% at six years and 100% at seven years and later), the fecundity (0.8 chicks for all age classes) and the annual survival (38% at one year, 83% at two to four years and 84% at more than four years). Based on these parameters, the modeled rate of increase is 0.94, a value close to the rate of increase based on the counts of breeding pairs between 1988 and 1993 (0.943), suggesting that we can be confident of our estimates of demographic parameters. Conversely the numbers on Saint Paul Island significantly increased ($r_{s,5}$ = 0.90, P < 0.025) from 1971 to 1993 at a rate of 5.5% per year (from 4,000 to 9,023; Fig. 1).

Between 1982 and 1993, the annual mean sea surface temperature decreased significantly around Amsterdam and Saint Paul islands (Pearson's correlation coefficient, r_{10} = 0.628, n = 12, P = 0.029, Fig.1). The decrease correlated with numbers of Rockhopper Penguins from 1982 to 1993 at Amsterdam Island ($r_{s,6}$ = 0.812, P < 0.05). In addition, mean sea surface temperatures in February were highly correlated ($r_{s,4}$ = 0.959, P = 0.002) with the numbers at Amsterdam Island (census performed the following September). However, there was no significant relationship between spring mean sea surface temperatures and the numbers of Rockhopper Penguins at Amsterdam Island ($r_{s,6}$ = 0.37, n.s.), nor was there a significant relationship between the population size at

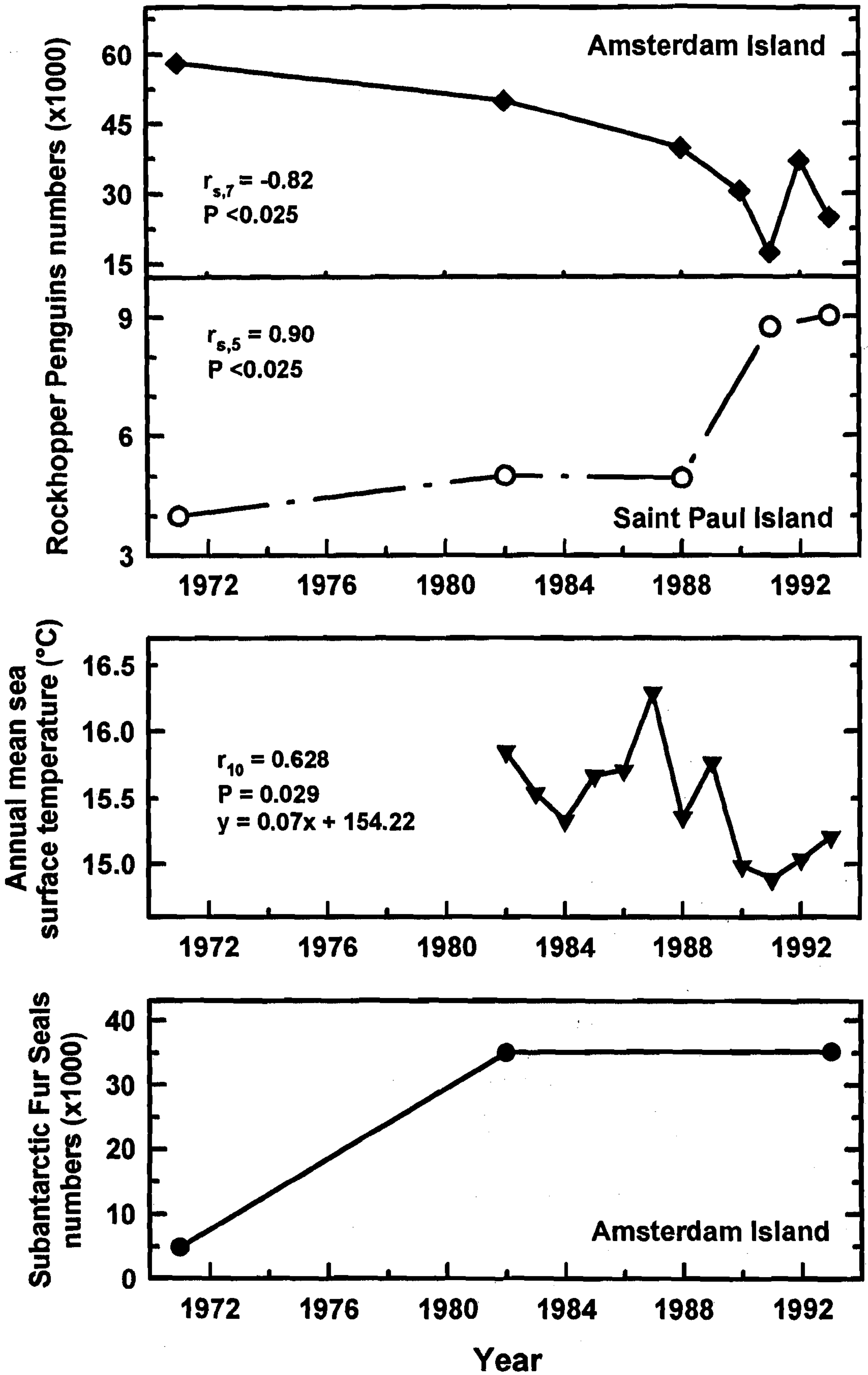

Figure 1. Population numbers of Northern Rockhopper Penguins and Subantarctic Fur Seals, and annual mean sea surface temperatures at Amsterdam and Saint Paul islands between 1971 and 1993.

Saint Paul Island and spring or annual sea surface temperatures from 1982 to 1993 ($r_{s,6}$ = 0.4, and $r_{s,4}$ = 0.6, both n.s.).

DISCUSSION

Comparisons with other sites and species

A comparison between the Rockhopper Penguin of Amsterdam Island and those at other localities indicates that breeding success can vary widely from site to site (Warham 1963; Williams 1980; Stahl *et al.* 1985; Marchant and Higgins 1990; Cooper *et al.* 1997; this study). The proportion of B-egg loss did not differ from that observed elsewhere, while A-egg loss rate was about 10% lower on Amsterdam Island than on other sites (Gwynn 1953; Warham 1963; Williams 1980; St.Clair and St.Clair 1996). Moreover, mortality at Amsterdam Island was equivalent for A and B-chicks, being very close to mortalities reported for Marion Island (46%: Williams 1980). Northern Rockhopper Penguins at Amsterdam Island may pay more attention to A-eggs than they do at other breeding localities.

The average age of first return to the colony in this study is similar to the average age of first reproduction, probably as a result of sampling bias, pre-breeders being more likely to be overlooked than breeders. The ages of first return in Adélie (*Pygoscelis adeliae*), Yellow-eyed and Fiordland penguins (*Eudyptes pachyrhynchus*) are about one year less than the ages of first reproduction (Richdale 1949; Warham 1973, 1974; Ainley *et al.* 1983). This suggests that for Rockhopper Penguins breeding at four or five years of age, the average age of first return could be around three years of age.

The 10.6% lower survival during the first year after banding compared to adult's survival was either the result of band loss or of decreased survival or recapturability. In our study, we have tried to measure band loss effect by using the web-punched technique (Richdale 1949). We have never recovered any web-punched bird without a band, but many unbanded birds may have been undercounted, due to the intensity of observation effort (see above), and mud did not facilitate the resighting of punched webs. This suggests however that band loss may play a minor role and that banding is more likely to increase mortality during the first year after banding. Adult annual survival rates have been studied for few species of penguins. Those of King, Adélie and Yellow-eyed penguins were 95.2%, 89.4%, and 86.5% (Richdale 1957; Ainley *et al.* 1983; Weimerskirch *et al.* 1992), respectively. The Amsterdam Island Rockhopper Penguin's annual survival rate was slightly lower (84% vs. 86%) than that of the Royal Penguin (*Eudyptes schlegeli*), its closest, but larger, studied relative (Carrick and Ingham 1970).

The estimated immature survival rate of 39% for Rockhopper Penguins during the first year after fledging is similar to that observed for Fiordland Penguins during their first four years of life (41%: Carrick and Ingham 1970), and for Yellow-eyed Penguins during the years before their first return to their breeding sites (41%: Richdale 1949). Individuals older than one year appear to have annual survival rates similar to those of adults.

Population changes

This study indicates that Northern Rockhopper penguins have decreased on Amsterdam Island over the past 25 years, as the southern subspecies has at other sites (Cunningham and Moors 1994; Cooper *et al.* 1997). However, population numbers fluctuated within a wide range between 1988 and 1993 (from 17,400 to 39,871). Variations of sea surface temperature and El Niño Southern Oscillation (ENSO) events are believed to affect the breeding success of other species of penguins (Boersma *et al.* 1990; Duffy 1990), but their long term effects on population numbers are poorly known (Croxall 1992). Cunningham and Moors (1994) suggested that the decrease in Rockhopper Penguin numbers at Campbell Island (94% since the early 1940s) was related to rising sea surface temperatures and warmer waters affecting Rockhopper Penguins through changes in the distribution, availability or abundance of their prey. At Amsterdam Island, the 57% decrease between 1971 and 1993 was correlated with a decrease in mean sea surface temperature (around 0.8°C) between 1982 and 1993 around Amsterdam and Saint Paul islands. Prey may have shifted towards more northern waters, less accessible for breeding penguins.

Other factors may have been involved in the decrease in the penguin population. The number of Sub-Antarctic Fur Seals (*Arctocephalus tropicalis*) at Amsterdam Island increased dramatically in the 1970s (from 4,868 to 35,028) and stabilized between 1982 and 1993 (from 35,028 to 35,200: Guinet *et al.* 1994). This increase in the fur seal population coincided with the sharp decrease of Rockhopper Penguins during the same period (Figure 1). Fur seals occasionally hunt and prey upon Rockhopper Penguins (Roux 1986). Even if the latter must represent a minor part of fur seal diet (Roux 1986), a regular and recent increase in predation pressure could partly account for the decrease in the Rockhopper Penguin population. Further studies are needed to estimate the impact of fur seals on Rockhopper Penguins.

In contrast to Amsterdam Island, the population of Rockhopper Penguins at Saint Paul Island has increased by 56% over the same period. This increase may not have been caused by the change in sea surface temperature. This population was heavily exploited at the end of the 1930s by crayfishermen on Saint Paul Island who used them as bait, in contrast to the Amsterdam Island population which was not affected in this way (Segonzac 1972). The increase in the small Rockhopper Penguin population at Saint Paul may reflect slow recovery to levels before exploitation. The population here may follow the general trend once recovery is complete. However, it is not clear why that population should only now recover when killing stopped probably 50 years ago.

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