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AN INTERPRETATION OF THE GROWTH OF THE ADELlE PENGUIN ROOKERY AT CAPE ROYDS, 1955-1990

Summary: The population dynamics of the Cape Royds rookery were modelled by computer, in order to determine the probable causes of the dramatic increase since 1980 in the numbers of Adelie penguins, *Pygoscelis adeliae,* breeding in the Ross Sea region, Antarctica.

Variations in the extent of sea-ice around the rookery during incubation and chick rearing cannot feasibly explain the population increase and another factor or event must be introduced, which increases chick production per breeding pair and decreases adult mortality. The timing of the event is critical and rules out the cessation of human impacts or the depletion of competing baleen whales as causal factors. The event is seen as most probably the result of a recent warming of the Ross Sea climate.

Keywords: Adelie penguin; *Pygoscelis adeliae;* Cape Royds; Ross Sea; population trends; population dynamics; computer simulation; human impacts; Antarctic whaling; climatic change.

Introduction

At Cape Royds (77°33'S) and other rookeries in the Ross Sea region, a large increase in the Adelie penguin *(Pygoscelis adeliae* Hombron and Jacquinot) population occurred in the 1980s, the number of breeding birds at Cape Royds doubling in just 6 years (Taylor, Wilson and Thomas, 1990). One explanation for this increase may be a trend to the earlier break-out of sea-ice each summer that occurred during the 1970s and beginning of the 1980s (Taylor and Wilson, 1991). Late break-out of sea-ice has been shown to have a negative effect on the breeding success of Adelie penguins (Spurr, 1975; Ainley, Le Resche and Sladen, 1983). It has also been suggested that a changing Ross Sea climate may have improved the chances of fledglings, pre-breeders and birds of breeding age surviving between breeding seasons, and led to adults breeding at an earlier age (Taylor *et al.,* 1990; Taylor and Wilson, 1991). We constructed computer models simulating the population dynamics of the Cape Royds rookery to help test the soundness of these hypotheses.

Methods

The size and dynamics of the population at Cape Royds from 1955 to 1990 were modelled on a Macintosh computer using Stella, a program which enables designing, editing and simulating by way of a graphical interface. Data from interpretations of the age structure and dynamics of two different Adelie rookeries in the

Ross Sea during the 1960s - Cape Hallett (Reid, 1968) and Cape Crozier (Ainley *et al.,* 1983) - were used for two independent simulations. The underlying model was the same for both.

The model assumes that the sex ratio is equal and that birds return to their natal rookery to breed. Both these assumptions seem reasonable (Ainley *et al.,* 1983). Effects of possible fluctuations in food sources, disease and predation are not explicitly taken into account.

Both Reid (1968) and Ainley *et al.* (1983) gave the age composition of their populations at the end of the summer. Since the number of breeding pairs of Adelie penguins at Cape Royds is counted each Antarctic spring, Reid's and Ainley's data were converted to a spring representation using their respective mortality rates for different age classes (Table 1). Age structures were then calculated for total populations containing 2000 breeding pairs (Table 1), corresponding to the first estimate of the size of the breeding population at Cape Royds in 1955 (Austin, 1957). Reid (1968) calculated that some Adelie penguins live to 20 years, and Ainley *et al.* (1983) found that only a few reached 16 to 19 years of age.

The basic model was manipulated by making breeding success dependent on sea-ice conditions during the egg-laying stage. The percentage of birds attempting to breed was linearly decreased from the usual level when there was no sea-ice to be traversed (and hence no time/energy costs in traversing) on their way to the rookery in the spring, to the lowest value when the expanse of ice was greatest. Maximum ice

Table 1: *Values for chick productivity. age-specific mortality. age composition of breeding populations. and modelled composition of a total population containing 2000 breeding pairs. based on data from Reid (1968. Table* 1). *and Ainley* et al. (1983. *Tables 8.16.9.6 and* 9.12).

Parameter	Reid	Ainley
Chick productivity per pair	1.1	1.2
Mortality (%)		
fledglings	48	49
1 year olds	14	49
2 years and older	14	11
Composition of breeding population (%)		
3 years old	2.5	9
4 years old	21	30
5 years old	85	52
6 + years	95	85
Modelled composition of total population (No. of birds)		0
0 years	0	1030
I year	1149	550
2 years	988	538
3 years	849	496
4 years	731	461
5 years	628	4178
6 + years	3504	

extent was set at 40 km, due to estimates of sea-ice cover truncating at this distance. The lowest values for breeding success were estimated from the effects of the extensive sea-ice year of 1968 on Adelie penguins breeding at Cape Crozier (Ainley *et al.,* 1983), and corresponded to 2%, 15%, 35%, and 60% of the total population of birds 3, 4, 5 and older than 5 years, respectively. The approximate extent of sea-ice cover in the spring and summer (Fig. 1) was estimated from published and unpublished records (Taylor, 1962;
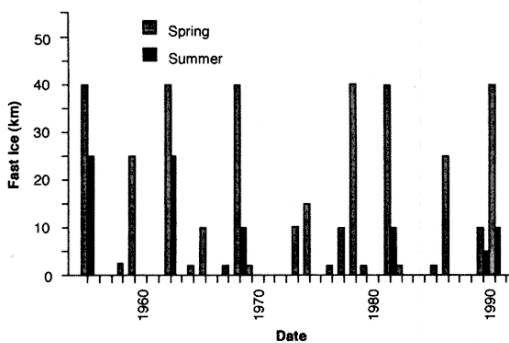

Figure 1: *Estimated extent of the fast sea ice at Cape Royds on* 1 *December during incubation (spring) and on* 5 *January during chick rearing (summer) since 1955. Zero values indicate no ice. Estimates of 40 km are minimum distances.*

Stonehouse, 1967; Prebble, 1968; Spurr, 1975; Yeates, 1975; Wilson, 1990; unpublished reports on files of Antarctic Division, DSIR; K-J. Wilson, *pers. comm.;* P. Sagar, *pers. comm.; pers. obs.)* and entered into the model in the form of a table.

The number of chicks produced was made dependent on the sea-ice conditions during the chick-feeding stage, in much the same way as during egg laying, by linearly decreasing the number of pairs producing chicks by 50%, 50%, 50%, and 30% for birds aged 3, 4, 5 and those older respectively when the sea-ice was 40 km or more in extent. These values were also estimated from the effects of the extensive sea-ice year of 1968 at Cape Crozier (Ainley *et al.,* 1983).

The model was set up by representing the age groups from 0 to 5 year olds and birds older than 5 years as variables. At the beginning of a breeding cycle the number of pairs attempting to breed and the number able to produce chicks were calculated based on the ice data and the current population sizes in each age group. The number of chicks produced was then added to the 0 year old variable. The variables were then decreased corresponding to the yearly mortality. Finally, the rookery was made to age by one year.

Greater and lower values for mortality, chick productivity, effects of sea-ice on chick productivity and effects of sea-ice on mortality were tried in attempts to closely simulate fluctuations in the actual population.

Results

When based solely on age structure and population dynamics (Table I), the two independent simulations of the estimated nesting population at Cape Royds over the period of 1955 to 1990 are quite different (Fig. 2). The trend simulated from Cape Hallett data represents a slowly increasing population, and this corresponds well with the observed trend starting in the early 1960s continuing on to the early 1980s (Fig. 2a). The trend simulated from Cape Crozier data represents a population in steady decline (Fig. 2b). Neither model is able to explain the marked decline in the late 1950s and early 1960s and the sharp increase in the 1980s at Cape Royds.

Adding the effects of sea-ice to the simulation of the breeding population using Reid's data (1968) changes a slightly increasing population to an almost stable one, and the simulated yearly fluctuations display little synchronism with what actually occurred (Fig. 3). The major population trends in the late 1950s and 1980s could not be simulated by varying the effects of sea-ice years. Changing the values for mortality and chick productivity in relation to each other, or varying the effects of sea-ice on chick productivity or mortality had little influence on changing the overall shape of the graph.
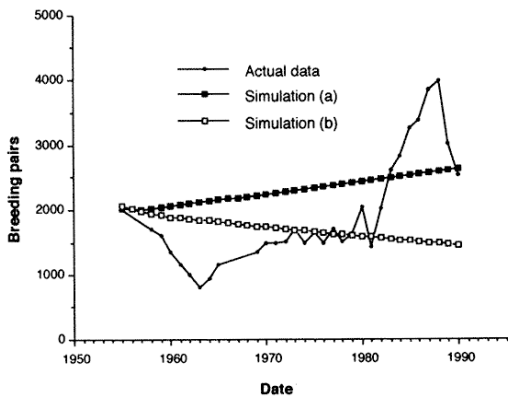
Figure 2: *The simulated number of breeding pairs of Adelie penguins at Cape Royds (1955-1990) based on the data of (a) Reid* (1968) *and (b) Ainley* et al. (1983), *compared with the actual numbers counted (Taylor* et al., *1990, and unpublished).*
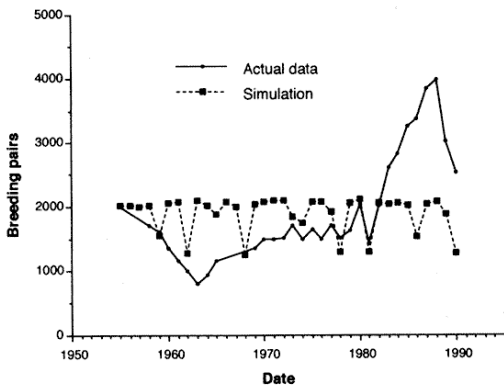

Figure 3: *The simulated number of breeding pairs of Adelie penguins at Cape Royds (1955-1990) based on the data of Reid* (1968), *taking into account the effects of sea ice on chick production, compared with the actual numbers counted.*

suggested that human disturbance lowered recruitment of young breeding birds by dissuading pre-breeders from returning to settle at a rookery, rather than by scaring off established breeders. This effect was introduced into the model for the period 1956-1962 as an extra mortality factor multiplied Ortto the existing mortalities for the age groups 1,2,3 and 4 years. The factor needed to fit the actual population decline was 3 for Reid's (1968) data and 1.8 for the data of Ainley *et al*. (1983). Part of this factor will represent the natural decline which occurred in many Ross Sea rookeries
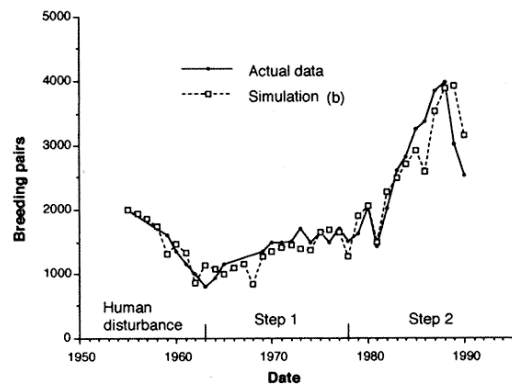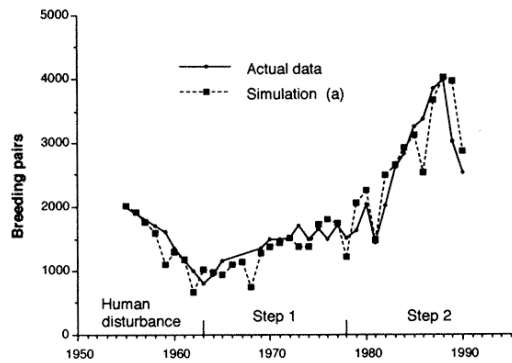

Figure 4: *The simulated number of breeding pairs of Adelie penguins at Cape Royds (1955-1990) based on the data of (a) Reid* (1968) *and (b) Ainley* et al. (1983), *taking into account the effects of: sea ice on chick production, a natural decline and human disturbance during the late 1950s and early 1960s, and events leading to increased chick productivity and decreased mortality in the late 1960s through the 1980s, compared with the actual numbers counted (see text).*

In order to simulate the population decline in the late 1950s - early 1960s, it was necessary to increase mortality of immature and adult birds. Stonehouse (1967) reported that human disturbance occurred at Cape Royds in the years 1956 through to 1962. Ainley *et al*. (1983) and Wilson, Taylor and Barton (1990)

during that period (Taylor *et al.*, 1990). The results of these changes closely parallel the observed data (Fig. 4).

In order to simulate the steep population rise in the 1980s, it was necessary to increase production of fledged chicks per breeding pair and decrease the mortality of immatures and adults. Both factors were introduced into the model in two steps, the first starting in 1963 about the time when increases in mean annual surface temperatures became apparent in the region (Jacka, Christou and Cook, 1984), and the second from 1978 when summer temperature increases became more marked and the levels of lakes fed by glacial melt-water rose in the vicinity of McMurdo Sound (Chinn and McSaveney, 1987; Taylor *et al.*, 1990; Taylor and Wilson, 1991). The factors were multiplied onto the values calculated in the original model so the effects of ice were retained.

The factor for chick productivity was 1.1 for the first step and 1.2 for the second as measured at Cape Royds during the 1984-85 and 1985-86 summers. When using Reid's (1968) data the mortality factors needed to fit the actual population trend were 0.83 for the first step and 0.73 for the second. For the data of Ainley *et al.* (1983) they were 0.8 for the first step and 0.63 for the second.

Discussion

The long life expectancy of the Adelie penguin makes it fairly immune to short term fluctuations in breeding success and this can be seen in the simulation showing effects of extensive sea-ice (Fig. 3). After a summer with late break-out of sea-ice the breeding population returns almost to normal the following year. The effects of decreased productivity due to sea-ice are never dramatic when seen over periods of several years. This is mainly because summers in which the sea-ice is late breaking out are usually separated by at least 2 relatively ice-free summers.

The data of Reid (1968) and Ainley *et al.* (1983) represent populations with different age structures. The high mortality rate given by Ainley *et al.* (1983) for 1 year old birds counter-balances a slightly higher rate of chick production per breeding pair and lower adult mortality. However, neither data set is able to reflect the actual population dynamics of Adelie penguins at Cape Royds in the 1960s through the 1980s, because they represent populations that are slightly increasing and decreasing, respectively. The expansion of the population in the 1980s was much more rapid than in the 1960s or 1970s. We have found that the effects of sea-ice cannot reasonably explain this shift without the introduction of another factor (event), represented by the added fluctuations of productivity and mortality in the model. It is important to note how quickly the

simulated population responds to these changes. The decrease in mortality results in an immediate increase in the number of nesting birds, and an accumulating effect occurs after about 5 years when increased numbers of young birds reach breeding age.

The new mortality rates for birds aged 2 years and older assigned to represent the event when using Reid's (1968) data corresponded to decreases of 12% for the first step (1963-1977) and 10% for the second (1978-1990). For the data of Ainley *et al.* (1983) they corresponded to 9% and 7%. For the event to simulate actual population trends, productivity needed to be increased over the two steps to 1.3 and 1.4 chicks fledged per breeding pair for the data of Reid (1968) and Ainley *et al.* (1983), respectively.

The exact nature of the event is open to speculation. Major changes in numbers of Adelie and other Antarctic penguins have previously been attributed to human disturbance, to increased availability of krill following the reduction of baleen whales, or to climatic changes (Sladen, 1964; Conroy, 1975). Human disturbance during the late 1950s and 1960s is thought to have been a factor in the decline of the Adelie populations at Cape Hallett (Wilson *et al.*, 1990) and Cape Royds (Stonehouse, 1965). However, it is likely that natural environmental factors were also involved as there were synchronous population decreases at four other Ross Island rookeries that had not been disrupted by humans (Taylor *et al.*, 1990). Half of the biomass of baleen whales entering the Antarctic feeding grounds had disappeared by 1940, and over 80% by 1960 (Mackintosh, 1970). By 1950 there was biological evidence that the reduction of fin and sei whales had not only improved these species' own growth and reproductive parameters but also those of other whales and seals (Croxall and Prince, 1979; Gambell, 1985). Any similar benefits for penguin populations (Sladen, 1964) could be expected to have commenced at about the same time and, as suggested by Taylor *et al.* (1990) are unlikely to have seriously influenced the dramatic increase in the population of Adelie penguins in the Ross Sea 30 to 40 years later. These conclusions are supported by our simulation which shows that the timing of the main event is critical (i.e., it began to take effect around 1978).

Mean air temperatures at Antarctic and Southern Ocean stations near the longitude of the Ross Sea show a warming trend since the mid 1960s that became even more pronounced in the early 1980s (Jacka *et al.*, 1984; Taylor and Wilson, 1991). It has been hypothesized that such climatic trends could have caused year-round changes in sea-ice conditions, increased marine productivity and the availability of food, lowered winter mortality and enhanced breeding success of the penguins (Taylor and Wilson, 1991).

Considering the widespread nature and synchronous timing of the recent upsurge in penguin

numbers throughout the Ross Sea, the cessation of human impacts seems a most unlikely cause. Likewise, the timing of the event appears to rule out any connection with reduced baleen whale stocks. We favour the alternative hypothesis that the marked increase of Adelie penguin breeding during the 1.980s at Cape Royds, and elsewhere in the Ross Sea, is linked to an ameliorating climate apparent from the early 1960s to the mid 1980s.

Acknowledgements

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