Population increase in the sub-Antarctic fur seal *Arctocephalus tropicalis* at Amsterdam Island

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The breeding population of Arctocephalus tropicalis *at Amsterdam Island during the 1981/82 summer consisted of approximately 6 070 adult males and 19 657 adult females, with 16 512 pups born. These estimates were derived by applying correction factors for undercounting, pup mortality, pregnancy rate and seasonal cycle. Extension of breeding colony sites has occurred since previous censuses in 1955/56 and 1969/70, concomitant with an initial annual intrinsic rate of population increase of 7,8 per cent to 1969/70, followed by an exponential phase of 16,5 per cent to 1981/82. Localised population increases were used to describe the process of recolonisation.*

Die teelbevolking van Arctocephalus tropicalis *te Amsterdameiland word beraam op 6 070 volwasse mannetjies en 19 657 volwasse wyfies, met 16 512 welpies gebore gedurende die 1981/82 somer, wanneer korreksiefaktore vir onderskattings in tellings, die mortaliteit van welpies, tempo van dragtigheid en seisoenale siklusse toegepas word. 'n Uitbreiding van teelkolonieliggings het sedert die vorige tellings van 1955/56 en 1969/70 plaasgevind, in ooreenstemming met 'n aanvanklike jaarlikse inherente tempo van toename van 7,8 persent tot 1969/70, gevolg deur 'n eksponensiële fase van 16,5 persent tot 1981/82. Lokale bevolkingstoenames is gebruik om die proses van herbevolking te beskryf.*

Introduction

The sub-Antarctic fur seal *Arctocephalus tropicalis* hauls out on islands in the South Atlantic and South Indian Oceans where it breeds at Amsterdam (Paulian 1964), Saint Paul (Segonzac 1972), Crozet (Jouventin, Stahl & Weimerskirch 1982), Gough and Tristan da Cunha (Bester 1980) and Marion and Prince Edward (Condy 1978) islands. All these populations were severely reduced through uncontrolled sealing operations in the past. The Amsterdam Island population was, for example, considered extinct as a result of sealing that commenced at the end of the 18th century (Aubert de la Rüe 1932, Jeannel 1940). Following the decline of sealing, increases in these populations were recorded (Paulian 1964, Segonzac 1972, Tollu 1974, Condy 1978, Bester 1980). Various population growth rates have been reported for populations of both *A. tropicalis* and the Antarctic fur seal *A. gazella* (Bonner 1968, Payne 1977). The present paper up-dates the population figure for *A. tropicalis* at Amsterdam Island during the 1981/82 summer, maps the present local distribution of breeding and nonbreeding colonies, and uses this and published information to reflect on the process of recolonisation.

Amsterdam Island (37°50'S, 77°35'E) lies approximately equidistant from Africa and Australia, north of the Subtropical Convergence in the South Indian Ocean. The island is 55 km^2 in area, and except for three localities the rocky beaches of the rugged 28,5 km coastline are backed by steep cliffs preventing access to inland areas. Detailed descriptions of the island appear in Mougin (1973) and Tollu (1974).

Methods

To facilitate mapping the distribution of fur seals, the coastline was divided into segments of 500 m (Fig. 1). Each segment was characterised by the only, or predominant, colony type occupying the beach area. Breeding and nonbreeding colony types were distinguished (Roux & Hes *in press*) by the relative contribution of breeding seals and their pups to a colony as was done for Gough Island by Bester (1982). Counted seals were assigned to the following age/sex classes: adult males (AM), adult females (AF), immatures of both sexes (SAU) and black pups. Underyearlings, i.e. moulted pups less than one year old, were absent during the census period. Live black pups were counted from 30 December 1981 (when more than 99,0% had been born — *vide* Roux & Hes *in press*) to March 1982, and the other age/sex classes from 12 December 1981 to 16 January 1982, except for the southeast coast (segments 16–28) which was censused at the end of February 1982. Systematic searches for pups were made simultaneously by two observers as they walked along a beach, line abreast, adding their individual counts after the whole beach was covered. At inaccessible beaches, counts were done from the cliffs overlooking the beaches, using binoculars. A breeding colony and a nonbreeding colony were censused at least twice weekly at regular intervals from October 1981 to March 1982 to determine the seasonal haul-out cycle, whilst another small breeding colony (Big Rock/Flat Rock beach in segment 2/3) was investigated to construct a cumulative percentage curve of pup mortality and to determine an approximate birthrate (see corrections 1 & 2).

AMSTERDAM ISLAND

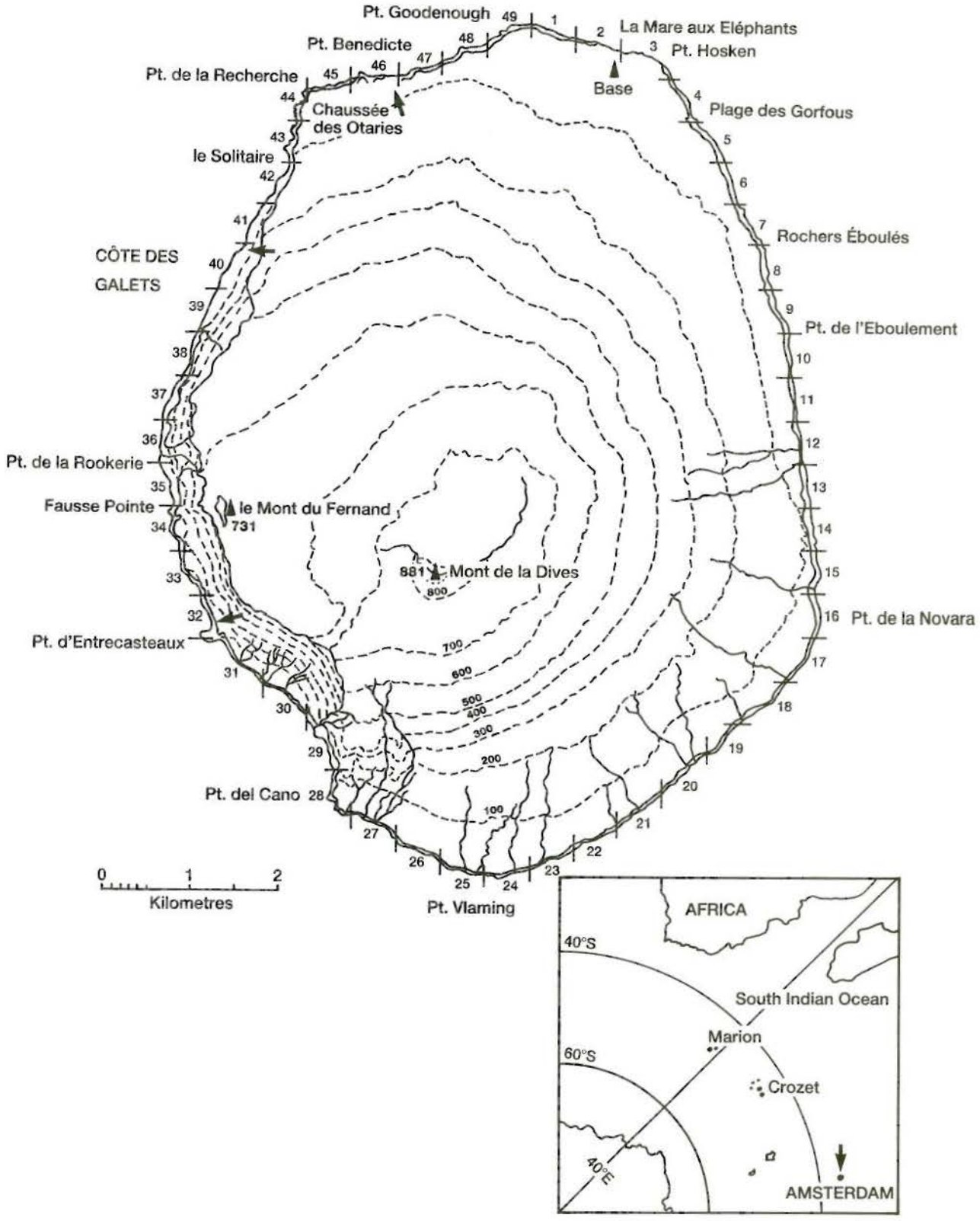

Fig. 1. Amsterdam Island showing its position and the main topographic features, numbers indicating the coastal census segments and arrows (➔) the breeding colony sites of 1955/56.

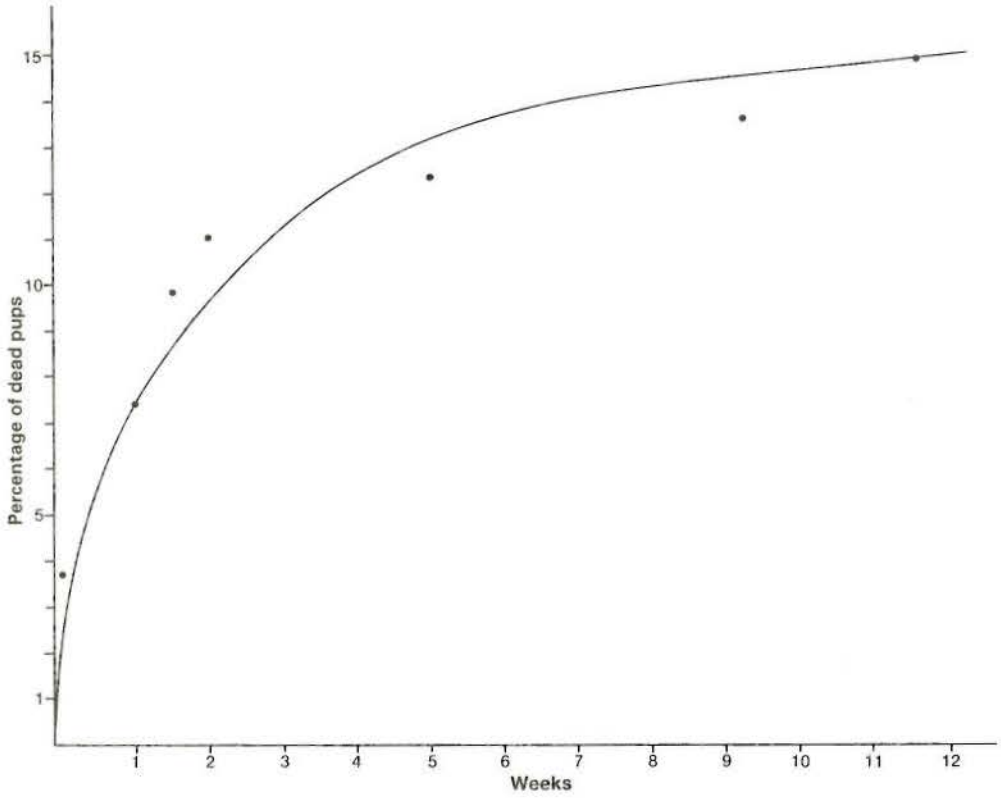

Fig. 2. Cumulative percentage mortality curve for pups at a breeding colony site on Amsterdam Island plotted from the median date of birth (13/12/81).

The seasonal haul-out cycle, where peak numbers are reached during mid-December, followed by a post-breeding season low at the end of January (Roux & Hes *in press*), necessitated adjustments to the censuses, all of which could not be done during the time of maximum haul-out. Pup counts are an underestimate as a result of the irregular terrain (Tollu 1974), and pup carcasses can be washed away (Paulian 1964), or lodged out of sight amongst the rocks. Also, pups may temporarily emigrate from beaches where they were born by February (Bester 1981a, Roux & Hes *in press*).

The following corrections were therefore made to counts:

1. A cumulative percentage curve of pup mortality after the median date of birth (13 December 1981), was drawn for a breeding colony at which dead pups were counted and removed at least twice weekly throughout the summer, including the period before the median pupping date. The data are expressed as percentages of the number of pups born at each particular census (Fig. 2). Live pup counts on other beaches were then increased by the percentage mortality estimated at the time of census to determine the number of births. The median birth date was calculated using a simplified probit analysis (Caughley 1977).
2. Since adult female counts at breeding colonies were usually less than the final number of births, numbers of adult females and pups were taken as being equal to account for postpartum females, a female normally bearing only one pup (Paulian 1964). The cumulative number of paint-marked adult females (n = 96) hauling out at the prescribed breeding colony site, where all unmarked females were marked at each of twelve censuses, showed that only 84,0 per cent of the females were matched with pups (n = 81). This was assumed to be the birth rate, and adult female counts were therefore further adjusted to include non-pregnant females (a 16 % increase).
3. The 34,0 per cent correction factor, approximately the same for both the Marion and Gough islands *A. tropicalis* populations (Condy 1978, Bester 1980), was used to compensate for the underestimation of the number of pups when counting. This correction, which would result in an increase in the estimated adult female population size (see 2 above) is not allowed for in Table 1, so as to make possible comparisons with previous surveys (Paulian 1964, Segonzac 1972).
4. Counts of adult males made after the peak haul-out during the breeding season were adjusted according to decreases

Table 1
Corrected numbers of fur seals occurring on the coastline of Amsterdam Island from 12-12-81 to 08/03/82.

Sector	Segment numbers	Date	AM*	AF**	SAU	Pups***
NE	1–14	14/12/81 – 02/01/82	1547	2380	2628	1999
SE-SW	15–29	27/02/82 – 28/02/82	892	686	244	576
SW-W	30–34	12/12/81 – 24/12/81	752	2885	162	2423
W-NW	35–42	13/01/82	1306	4211	970	3537
NW	43–47	16/12/81	1103	2137	978	1795
N	48–49	20/12/81	470	676	103	568
Total			6070	12975	5085	10898

* includes correction 4 ** includes correction 2
*** includes correction 1

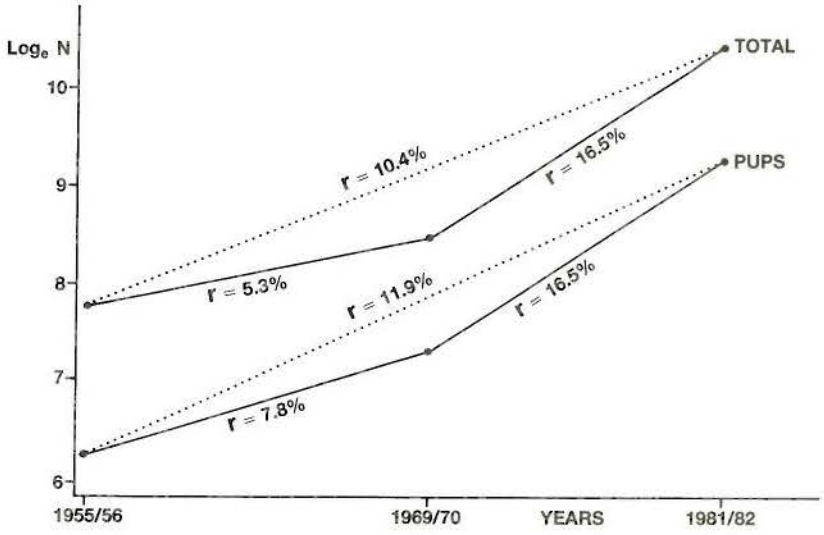

Fig. 3. Intrinsic rate of increase (r) in fur seal numbers at Amsterdam Island for the periods 1955/56-1969/70, 1969/70-1981/82 and 1955/56-1981/82.

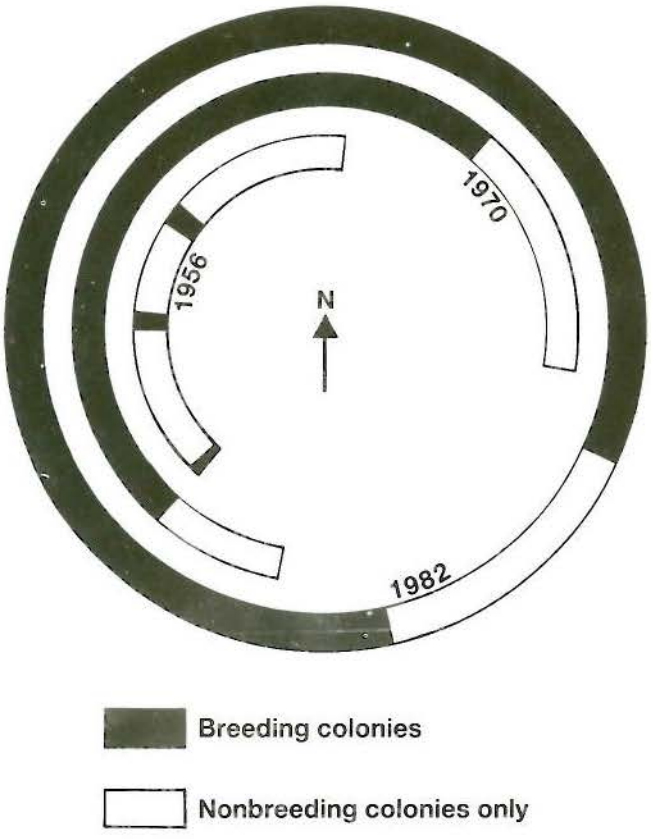

Fig. 4. Schematic representation of the changes in the distribution of fur seals at Amsterdam Island (1955/56-1981/82), with the island represented as a circle.

Table 2
Comparative counts of *A. tropicalis* for various seasons between 1955/56 and 1981/82 at Amsterdam Island.

Year	Class					Source
	AM	AF	SAU	Pups	Total	
1955/56	317	808	693	500	2318	Paulian (1964)
1969/70	?	3370	?	1498	4868	Segonzac (1972)
1981/82	6070	12975	5085	10898	35028	This study

observed on study colonies, which were counted at least twice weekly during summer (Roux & Hes *in press*).

Estimates of intrinsic population growth rates using counts of 1955/56 (Paulian 1964), 1969/70 (Segonzac 1972) and 1981/82 (present study) were based on the exponential function,

$$N_t = N_o e^{rt}$$

(e.g. Caughley 1977), as applied to estimates of seal population growth rates elsewhere (Condy 1978, Bester 1980, Van Aarde 1980).

Results

Population estimate

The total population size, excluding the absent underyearlings and correction 3, are shown in Table 1. Using all corrections (1 – 4 in Methods), the estimated adult breeding population in the 1981/82 season was 6 070 adult males and 19 657 adult females, with 16 512 births. During the first six weeks following the median birth date, pup mortality was 13,6 per cent.

Population increase

By using pup figures from Table 2, the annual intrinsic rate of natural increase (r) was 7,8 per cent and 16,5 per cent from 1955/56 to 1969/70 and from 1969/70 to 1981/82 respectively. The overall annual rate of increase was 11,9 per cent (1955/56 — 1981/82, Fig. 3). These rates are very close to the rates calculated from estimated total numbers (Fig. 3).

Local distribution and population increases

The schematic representation of the local distribution of breeding and nonbreeding colonies (Fig. 4) shows that during 1955/56 less than half of the coastline was used by nonbreeders, with the population concentrated on the west coast where only three small breeding colonies were found. By 1969/1970, further extensions of breeding colonies had occurred primarily in the northwestern sector, with nonbreeders hauling out on all beaches except in the southeastern sector. In the present study all accessible beaches were occupied by fur seals. Breeding colonies were, however, confined to the beaches which were occupied by fur seals during 1969/70 (81,0 % of the coastline in 1969/70, Fig. 4).

The initial annual rate of population increase in the northern sector was very high (Fig. 5), resulting in the formation of numerous breeding colonies by 1969/70 (Fig. 4). On the other hand, the rate of increase was halved during the next 12 years in this area (segments 47 – 49, Fig. 1), during which time the south and east coasts (segments 4 – 29) were colonised (Figs. 4 and 5). A high rate of increase has been sustained in the newly colonised southeastern sector until 1981/82, similar to the rate of increase during the earlier period on the northern sector (Fig. 5).

Discussion

The estimated total population size of *A. tropicalis* at Amsterdam Island reflects the large increases that have occurred since the turn of the century. This would be considered a minimum estimate as the decrease in immature seal numbers during the peak haul-out of adults, and the absent underyearlings, were not included. The undercount correction factor as applied to pup counts here is similar to two other *A. tropicalis* populations (Condy 1978, Bester 1980), yet conservative in comparison to the figure of 54,1 per cent calculated for *A. gazella* (Payne 1977). This assumed undercount correction factor does not compensate for the likely density-dependent variation in counting efficiency between the different segments of Amsterdam Island, and on the different habitats, and therefore lowers the accuracy of the estimate.

Although the birth rate (84,0 %) assumed in the present study is probably an underestimate, since some adult females that hauled out at the study colony may have pupped elsewhere (Paulian 1964, Bester 1981a), it approximates pregnancy rates of increasing populations of *A. australis* (82,5 %; Vaz-Ferreira 1976) and *A. gazella* (86,0 %; Payne 1977). Pup mortality up to six weeks of age is also comparable to other expanding *Arctocephalus* populations (13,8 % — Payne 1977, 10,0 % — Bester 1980). Moreover, the synchrony in the summer haul-out of adult fur seals (Paulian 1964, Payne 1977, Bester 1981a, Roux & Hes *in press*) validates the adjustment to adult male figures according to the progression of the breeding season (Bester 1980).

The estimated mean annual increase in pup numbers (11,9 %) over 26 years is similar to that for *A. tropicalis* at Marion Island over the 23 years from 1951 (10,0 %; Condy 1978), but considerably lower than that for the same species at Gough Island (15,9 % over 22 years, Bester 1980) and *A. gazella* at South Georgia (16,8% over 14 years, Payne 1977). At Amsterdam Island the rates of population increase for the periods 1955/56 — 1969/70, and 1969/70 — 1981/82 show a phase of slow increase (5,3 % per annum), followed by a phase of rapid increase (16,5 % per annum) very similar to the 8,9 per cent before 1955/56 and the 15,9 per cent since then up to 1977/78 at Gough Island (Bester 1980). This observation, and examination of the trends in the extension of breeding and nonbreeding colonies, as well as the localised increases in fur seal numbers at Amsterdam Island, demonstrates the process of recolonisation of Amsterdam Island by fur seals. Four successive phases can be recognised:

Phase 1 — Characterised by low numbers of primarily non-breeding seals with few births occurring. Represents the period between cessation of sealing (1813 – 1875) and the establishment of the first breeding colony, probably after 1930

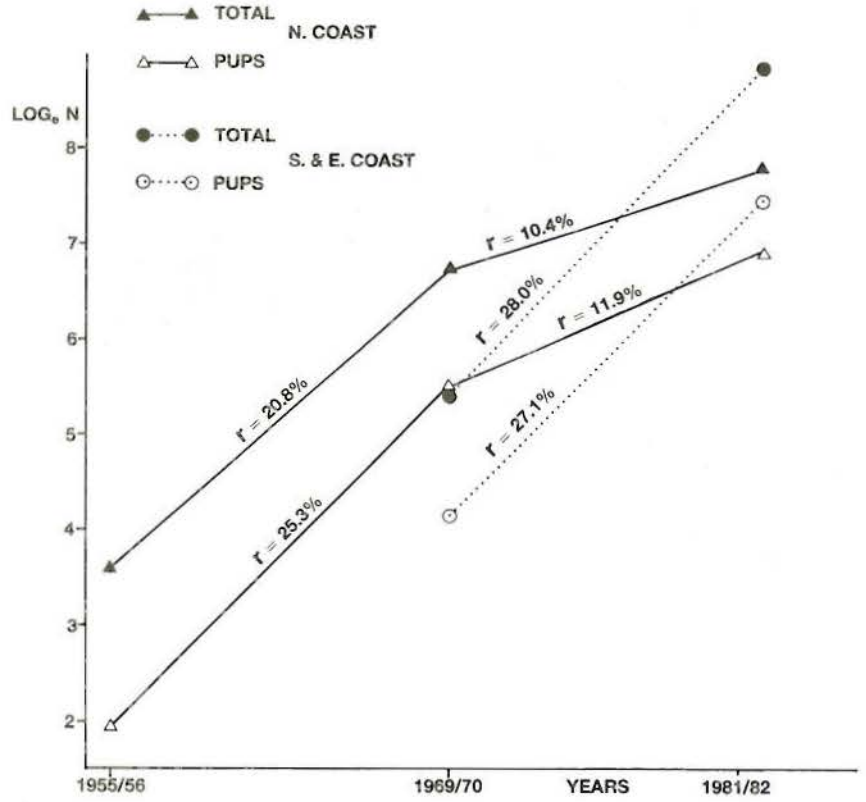

Fig. 5. Localised increases (r) in fur seal numbers in the Northern sector (blocks 47-49) and the South and Eastern sector (blocks 4-29) for the periods 1955-1969, 1970-1981 and 1955-1981.

(Paulian 1964). This phase is of long duration (60 – 100 years), and the rate of increase is low.

Phase 2 — Reproductive success increases owing to the establishment of a few breeding colonies. This phase lasted from before 1952, when the first breeding colony was found (Paulian 1964), until approximately 1970. The annual rate of increase is lower than 10,0 per cent. The distribution of seals remains centred in the vicinity of the first established breeding colonies (by analogy with Bester 1982). This type of phase was recognised for the Gough Island *A. tropicalis* population by Bester (1980), and identified as a slowly increasing establishment phase. At the Crozet Islands this species is apparently also in Phase 2, because a single breeding colony has been found there (Jouventin, Stahl & Weimerskirch 1982).

Phase 3 — The increase in fur seal numbers leads to the formation of new breeding colonies, resulting in rapid recolonisation of all available beaches. During this phase the rate of population increase is high (16,5 %), with recently created colonies showing a particularly high rate of increase (28,0 %) mainly as a result of emigration from crowded, established colonies (Bester 1981a), which in turn experience a drop in the rate of increase. This phase was also noted in the Gough (Bester 1980) and Marion island (Condy 1978) *A. tropicalis* populations. The lower overall rate (10,0 %) for Marion Island probably results from the absence of any mid-range census data which could demonstrate a clear separation into phases 2 and 3. At Amsterdam Island the rapid recolonisation will probably last for 14 to 20 years after its onset in about 1969/70.

Phase 4 — This phase can be predicted by extrapolation from the changes in numbers at high-density, established breeding colonies, where the rate of increase decreases as numbers increase and there is an extension of breeding colonies to other parts of the coastline. At Gough Island the *A. tropicalis* population approached an asymptote in numbers after a phase of exponential growth and extension of breeding colony sites (Bester 1980).

The observed population growth forms of the Amsterdam Island and other *A. tropicalis* populations is consistent with intrinsic growth from a small nucleus of survivors of the sealing era, and cannot be explained by influxes of seals from elsewhere as has apparently been the case in *A. gazella* at Heard Island (Budd 1970), Marion Island (Condy 1978), and possibly Iles Kerguelen (Bester 1981b). Saint Paul Island (38°43′S, 77°30′E), close to Amsterdam Island, supported only 6,8 per cent of the total population for both islands during 1969/70 and probably benefited from an influx of seals from Amsterdam Island (Segonzac 1972). This pattern can also be inferred from data presented for *A. gazella* at South Georgia, where the first established breeding colonies were found at Bird Island in 1956 (Phase 2), followed by a rapid increase (Phase 3) which culminated in a sharp decline in the annual increases (Phase 4) by 1961/62 (Bonner 1968). Payne (1977) however, showed that this apparent decline was not real after applying corrections to account for the difficulty of counting larger numbers of seals, but considered it unlikely that the rapid increase would continue for more than 10 years. The recolonisation of the mainland of South Georgia from the Bird Island nucleus had already commenced before 1964, and subsequently (1958 to 1972) sustained a high (Phase 3) rate of increase (Payne 1977). The results presented here therefore support Bester's (1980) suggestion that the differences in published population growth rates for *A. tropicalis* and *A. gazella* reflect different phases in population growth following cessation of exploitation.

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