Fluctuations in the population of southern elephant seals *Mirounga leonina* at Kerguelen Island

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An analysis of census information published for the years 1952, 1958, 1960 and 1970 and that obtained during this study in 1977, indicates that both the breeding bull and cow components of this population fluctuated in numbers during the past 25 years. In spite of these fluctuations, the general trend for the cow component was to increase at a rate of 1,4% per year, while the bull component decreased at a rate of 1,9% per year. An analysis based on subdivisions of the study area into distinct regions indicated that the range of fluctuation increased as mean density increased. The population is regarded as a stable fluctuating population and the influence of environmental and social factors on the observed population trends is discussed.

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'n Ontleding van inligting aangaande volkstellings uitgevoer gedurende 1952, 1958, 1960 en 1970 en dié verkry gedurende die huidige studie in 1977 toon aan dat beide die telende bul- en koeikomponente van hierdie bevolking gefluktueer het in getalle gedurende die afgelope 25 jaar. Ten spyte van hierdie fluktuasies was die algemene neiging van die koeikomponent 'n toename in getalle teen 'n tempo van 1,4% per jaar. Daarenteen het die bulbevolking geneig tot 'n vermindering van 1,9% per jaar. 'n Ontleding, gebaseer op 'n onderverdeling van die studiegebied in definitiewe areas, het aangetoon dat die mate van fluktuasie en digtheid dienooreenkomstig toeneem. Die bevolking word beskou as 'n stabiele fluktuerende bevolking en die invloed van omgewings- en sosiale faktore op bevolkingsneigings word bespreek.

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The population of southern elephant seals, *Mirounga leonina,* at the archipelago of Kerguelen represents a major part of one of the three distinct breeding stocks of this species (Laws 1960). Laws (1960) estimated the world stock of southern elephant seals at 600 000 (± 100 000) and Bonner and Laws (1964) indicated that the Kerguelen and Heard Island populations together represent nearly 30% of this total. Although not based on actual counts Laws (1960) estimated the Kerguelen population at 100 000. On the other hand Bajard (1962) based his estimate of 150 000 seals on an extrapolation of actual counts, and Pascal (1979) suggested that this population had grown to 210 000 by 1970.

A description of the study area has been given by Angot (1954). Situated on the Antarctic Convergence the island is well within the breeding zone of elephant seals (Laws (1960)). Survival and breeding of this species is optimal in the circumpolar zone of the Antarctic Convergence, owing to the large, seasonally constant biomass of zooplankton (Carrick & Ingham 1962). Previous accounts of the ecology of this population have been published by Ring (1923), Angot (1954), Bajard (1962) and Pascal (1979). Since intensive exploitation during the 19th and early 20th centuries the population has been affected little by direct human interference, apart from limited sealing activities between 1958 and 1964 (Pascal 1979). This paper discusses fluctuations within this population and factors influencing them over the past 25 years.

Methods

Elephant seals are easily approached on land, and direct ground counts of adult bulls (sexually mature), adult cows and pups at breeding rookeries from Point Molloy to Cap Noir from 13 October to 24 October 1977, form the basis of this study. In addition a fraction of the population breeding along the 2,8 km stretch of coastline from Cabane l'Estacade to Cap Ratmanoff were censused at weekly intervals during the period 19 September to 16 November 1977, thereby providing information on the breeding season haulout pattern.

Adjustment of census information

Practical limitations (the majority of the breeding rookeries of the population are distributed along a 79 km stretch of coastline) did not allow a survey of the total known breeding population within the one day period when the maxi-

mum number of cows were ashore. At the peak haulout period (mid-October) a number of cows had departed after weaning their pups, those remaining representing nursing and prepartum cows. Furthermore, weaned pups only became pelagic at 60 days of age, remaining in close proximity to their birthsite for at least a few weeks thereby representing departed cows. A method to extrapolate the maximum number of cows that would have been ashore at the peak of the breeding haulout period, based on census information of cows and weaned pups obtained within a limited period, either before or after the day when the maximum number was present, therefore had to be developed. Making use of the above mentioned census information obtained at regular intervals, a basis for such a population assessment can be outlined as follows:
By plotting the combined number of adult cows and weaned pups (y) censused during each of the nine surveys conducted in the smaller study area over the defined period (19 September – 16 November) against the number of days that elapsed since the first census (x) a curve representing the maximum number of adult cows that would have been present at each survey, was obtained (Fig. 1). This suggested the existence of a parabolic relationship between the changes in the number of adult cows plus weaned pups present as the breeding haulout period progressed. This curve fitted the quadratic equation $y = 261{,}39 + 307{,}6x - 4{,}57x^2$ ($r^2 = 0{,}977$). This equation could therefore be used with confidence to assess the number of breeding cows that would have been ashore at any specific day between the first and the last survey; to estimate the maximum number of breeding cows that would have been ashore within the area surveyed; and to estimate what percentage of the breeding cow component of the population were present at a specific time when a survey was conducted.

Taking into consideration the high degree of synchronization in the breeding haulout pattern for cows along various stretches of coastline (Pascal 1979) the equation could also be used to assess what percentage of the total cow population, (hauled out but not surveyed at regular intervals), were present at the time when a specific survey was conducted, and to estimate the maximum number of breeding cows which would have been present at the peak of the haul-out period along any part of the coastline.

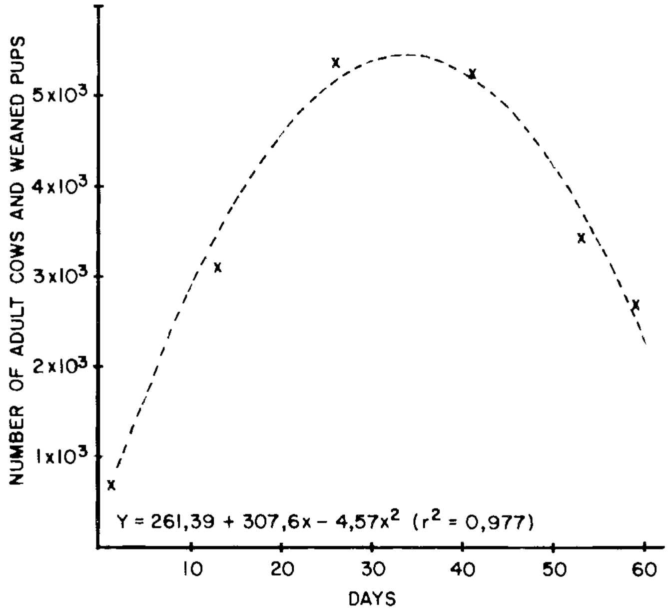

Fig. 1 A theoretical curve describing the changes in the number of adult cows plus weaned pups (x) counted as the breeding haulout period progressed.

Furthermore, considering the little variation that does occur in the haulout pattern from year to year (Pascal 1979), it could be used to estimate maximum cow population size for any other year even with that specific survey conducted outside the peak haulout period. Census information published for the years 1952 (Angot 1954), 1970 (Pascal 1979) and that obtained during the present study, have been treated by this method, thereby allowing direct comparisons of the published information with that collected during this survey.

Population trend

In assuming that population increase or decrease between any two given points in time (i.e. years) for this population

Table 1 Number of southern elephant seals counted during the breeding season at Kerguelen Island along the coastline of the Courbet Peninsular from Point Molloy to Cap Noir, on various days from 13 — 24 October 1977

		No. of animals counted					
Part of coastline	Date	Adult bulls	Adult cows	Unweaned pups	Weaned pups	Dead pups	Total
Point Molloy — Port-aux-Francais	19 October	53	1 161	1 042	85	5	2 346
Port-aux-Francais — Point Guite	21 October	116	1 590	1 474	125	9	3 314
Point de l'Etoile — Point Millot	22 October	174	2 041	1 853	239	28	4 335
Point Millot — Rivere du Chateau	24 October	60	663	590	49	1	1 363
Rivere du Chateau — Point Matley	24 October	178	2 701	2 497	735	33	6 144
Point Matley — Point Morne	24 October	162	1 591	1 554	419	12	3 738
Point Morne — Point de l'Etang	18 October	91	1 235	1 105	47	2	2 480
Point de l'Etang — Point Charlotte	13 October	232	1 245	970	1	8	456
Point Charlotte — Cabane l'Estacade	13 October	321	6 428	5 431	229	44	12 453
Cabane l'Estacade — Cap Ratmanoff	14 October	218	5 229	4 502	152	49	10 150
Cap Ratmanoff — Cap Sandwich	15 October	370	7 148	6 379	174	57	14 128
Cap Sandwich — Morne Vert	16 October	290	3 937	3 533	87	53	7 900
Morne Vert — Cap Digby	16 October	232	3 498	2 831	86	32	6 679
Cap Digby — Cap Noir	16 October	44	188	157	1	1	391
Total		2 541	38 655	33 918	2 429	334	77 877

would be exponential, the intrinsic rate of natural increase or decrease (r) between these given points in time has been estimated using the equation $N_t = N_0e^{rt}$ where N_0 = number of individuals in the population at a point in time when the first observation was made, N_t = number of individuals at a point in time when the second observation was made, t = number of years that have elapsed between the two observations, and e = the base of the natural logarithm (Caughley 1977).

Population fluctuations

In regarding the standard error of the estimate (σ_y') of the linear regression equation y = ax + b as indicative of the degree or range of fluctuation for a specific part of the population over a period of time, the degree of fluctuation (σ_y') where $\sigma_y' = \sigma_y \sqrt{1-r^2}$ (σ_y = standard deviation of mean population size; r^2 = coefficient of determination of the linear regression equation) has been calculated for five segments of the studied population.

Results

Observed size of breeding population

The census results over a period of 11 days for various parts of the 79 km stretch of coastline from Point Molloy to Cap Noir, are given in Table 1. At the time of the census 38 625 adult cows, 33 918 pups, 2 429 weaned pups, 334 dead pups and 2 541 bulls were counted. These data were collected over a period of nine days prior and two days after the date (15 October) of the peak haulout of breeding cows.

Predicted size of breeding population

With reference to the annual cycle, social organization and breeding behaviour of the southern elephant seal, described in detail elsewhere (Angot 1954; Laws 1960; Carrick, Csordas & Ingham 1962; Condy 1977), it is clear that an estimation of the size of the breeding population (in particular the cow component), would be dependent on the number of days elapsing since the onset of the breeding haulout period. Carrick and Ingham (1962) suggested that maximum counts of each age and sex category ashore at the appropriate time of the year are the most meaningful in attempts to estimate total population size.

Cows

Spontaneous gregariousness of cows during the onset of the breeding season results in the formation of breeding rookeries which, when under control of an adult bull may be defined as a harem. From mid-September the number of cows on land increased rapidly to reach a peak during mid-October. After mid-October the departing cows increasingly outnumbered the arrivals and towards mid-November only a very few cows were observed ashore. Cows gave birth to a single pup four to eight days after hauling out, resulting in pup numbers lagging behind cow numbers by a few days. Pups were suckled daily and weaned at an age of approximately 22 days (22,4 ± 2,0 days; n = 12). Weaned pups congregated in large pods behind breeding rookeries. Cows came into oestrus 17 − 22 days after parturition and returned to sea immediately after weaning their pups, therefore being ashore for 28 − 30 days.

Plotted on a percentage scale against date (Fig. 2) it is important to note that a count of adult cows and weaned

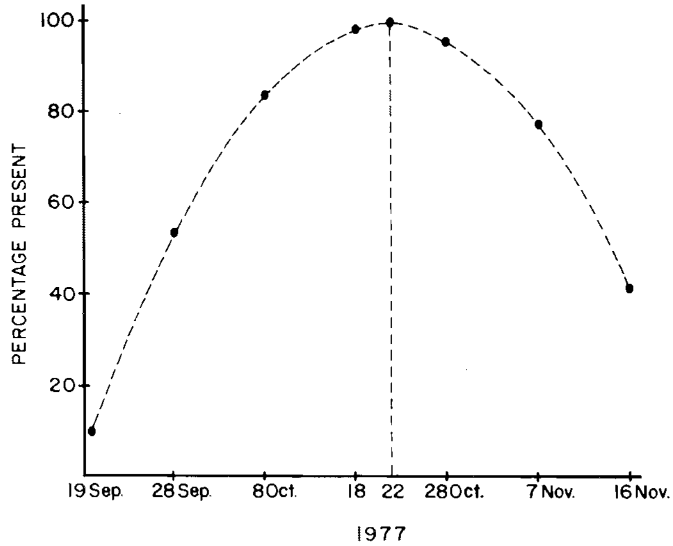

Fig. 2 Percentage of total population (adult cows and weaned pups) predicted to be present on breeding beaches during consecutive days of the breeding season.

pups on 15 October (peak haulout) does not reflect the total adult cow population, such a figure being revealed only by such a count on 22 October. From Fig. 2 it can furthermore be seen that the fraction of the actual breeding cow population that would have been represented by a count of the adult cow plus weaned pup component of the population, at any day between 13 − 24 October would vary between 93,7 and 100%. Therefore, the maximum number of cows that would have been ashore during the breeding haulout period could be predicted by using the available information on the number of adult cows plus weaned pups (Table 1). This predicted assessment for various parts of the coastline is given in Table 2. According to this adjustment 42 414 cows hauled out, a figure 9,8% higher than the actual number of cows that had been counted.

Bulls

Adult bulls are ashore from mid-August to late November and start competing with each other one to two weeks after the onset of the breeding haulout. Bulls occur in their largest numbers towards the peak of the mating period, at which time a hierachy around each harem has already been established. Throughout the breeding period most bulls, except those in undisputable possession of a harem, are constantly on the move, resulting in a daily variation in the number of bulls in or around a specific harem, but only a slight variation in the total number of bulls along a stretch of coastline. It can therefore be assumed that the number of adult bulls present during any specific day of the mating period is a reflection of the actual size of the adult bull component of the breeding population (2 541 adult bulls during 1977; Table 3).

Population trend

Cows

Census information published for the years 1952 (Angot 1954), 1958 (Bajard 1962), 1960 (Bajard 1962) and 1970 (Pascal 1979), for various stretches of the coastline from Point Molloy to Cap Digby is summarized and compared to the results obtained during this survey in Table 2. The

Table 2 Observed and adjusted size of the breeding cow population during various years (1952, 1958, 1960, 1970 & 1977) along specified stretches of coastline. The relationship between the number of adult cows plus weaned pups and number of days that have elapsed since the first census for a specified year has been conducted $y = 261{,}39 + 307{,}6x - 4{,}57x^2$.

	No. of adult cows plus weaned pups observed							
	1952				1970		1977	
Part of coastline	*Observed	Adjusted	**1958	**1960	***Observed	Adjusted	Observed	Adjusted
Point Molloy — Port-aux-Francais	953	990	2 040	1 550	1 025	1 250	1 246	1 253
Port-aux-Francais — Point Guite	785	790			1 082	1 320	1 715	1 716
Point Guite — Point Morne	3 060	3 060	5 350	4 600	7 037	8 274	8 408	8 636
Point Morne — Point Charlotte	1 585	1 586	2 700	2 000	3 306	4 034	2 528	2 626
Point Charlotte — Cap Ratmanoff	12 750	12 754	20 240	15 500	16 861	21 233	12 038	12 767
Cap Ratmanoff — Cap Sandwich	—	—			5 329	6 711	7 322	7 604
Cap Sandwich — Morne Vert	—	—	11 640	16 400	5 665	7 386	4 024	4 135
Morne Vert — Cap Digby	—	—			3 869	5 044	3 584	3 683
Cap Digby — Cap Noir	—	—			928	1 257	189	194
Total					45 102	56 509	41 054	42 614
Subtotal[1]			41 970	40 050	44 174	55 252	40 865	42 420
Subtotal[2]	19 133	19 180	30 300	23 650	29 311	36 111	25 935	26 998

*Data from Angot (1954) **Data from Bajard (1962) ***Data from Pascal (1979)
Subtotal[1] = Total for years for which information is available for the coastline from Point Molloy — Cap Digby.
Subtotal[2] = Total for years for which information is available for the coastline from Point Molloy — Cap Ratmanoff.

observed and adjusted values given for 1952 are based on the number of adult cows plus weaned pups counted by Angot (1952) and the quadratic equation for the extrapolation as described previously.

The figures for 1958 and 1960 are those that have been published by Bajard (1962) without adjustments. Adjustments could not be made due to the fact that Bajard's data referred only to the adult component of the studied population. According to him these figures represent the maximum number of individuals that had been ashore during October, and would therefore be directly comparable with the census information collected during the other years. The observed values for 1970 are based on those given by Pascal (1979), while the adjusted values were obtained through extrapolation similar to that done for 1952 and 1977. It is of interest to note that the predicted total for 1970 is only 1,5% higher than the prediction made by Pascal (1979). However, the method developed here to predict maximum cow population size is somewhat more concise than that developed by Pascal (1979). It could therefore be argued that similar treatment of the data procured over 25 years from the same locality would improve comparisons based on the adjusted figures.

Using the equation $N_t = N_o e^{rt}$ and data given in Table 2 (subtotal[2]) the intrinsic rates of increase or decrease (r) for the periods 1952 – 1958, 1959 – 1960, 1961 – 1970, 1971 – 1977, and 1952 – 1977 have been calculated (Fig. 3B). This information illustrates an increase of 7,6% per year between 1952 and 1958; a decline of 12,4% per year between 1958 and 1960; an increase of 4,4% per year between 1961 and 1970, another decline of 4,5% per year between 1971 and 1977; and finally a mean increase of 1,4% per year between 1952 and 1977.

In plotting the information summarized under Subtotal[1],

Table 3 Number of adult bulls counted during October of various years, along specified stretches of coastline from Point Molloy to Cap Noir

	No. of adult bulls				
Part of coastline	*1952	**1958	**1960	***1970	1977
Point Molloy — Port-aux-Francais		140	120	850	53
Port-aux-Francais — Point Guite					116
Point Guite — Point Morne	180	460	430	629	116
Point Morne — Point Charlotte	435	800	630	395	323
Point Charlotte — Cap Ratmanoff	780	1 370	1 090	701	539
Cap Ratmanoff — Cap Sandwich	—			1 009	370
Cap Sandwich — Morne Vert	—	1 530	1 310	474	290
Morne Vert — Cap Digby	—			377	232
Cap Digby — Cap Noir	—	—	—	185	44
Total				4 620	2 541
Subtotal[1]		4 300	3 580	4 435	2 497
Subtotal[2]	1 395	2 630	2 150	1 725	1 436

*From Angot (1954) **From Bajard (1962) ***From Pascal (1979)
Subtotal[1] = Point Molloy — Cap Digby
Subtotal[2] = Point Guite — Cap Ratmanoff

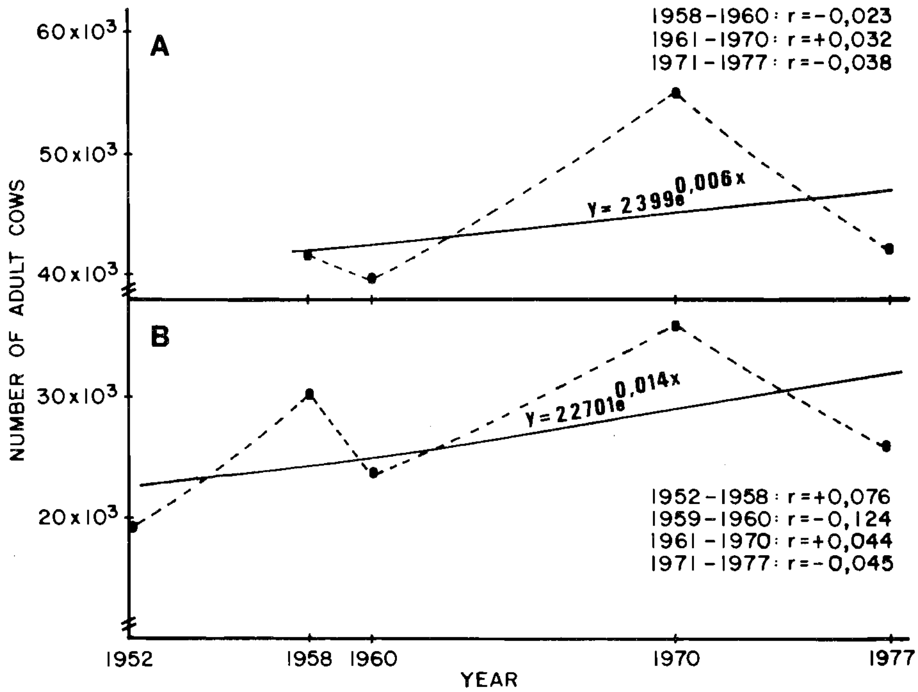

Fig. 3 Population trend in the adult cow southern elephant seal population at Kerguelen Island from 1952 — 1977. Figures A and B are based on adjusted counts for the coastline from Point Molloy to Cap Digby (subtotal 1; Table 2) from Point Molloy to Cap Ratmanoff (subtotal 2; Table 2) respectively. r values represent the intrinsic rate of natural increase given by

$$r = \frac{\log_e N_t - \log_e N_o}{t}$$

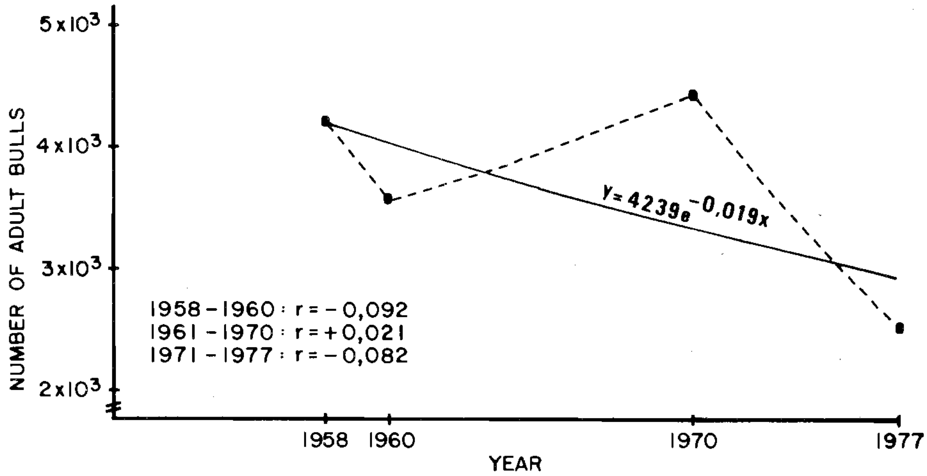

Fig. 4 Population trend in the adult bull southern elephant seal population from 1958 — 1977, based on information available for the coastline from Point Molloy to Cap Digby. r values represent the intrinsic rate of natural increase given by

$$r = \frac{\log_e N_t - \log_e N_o}{t}$$

Table 2, a trend comparable to that described above pertained (Fig. 3A); a decrease of 2,3% per year from 1958 — 1960, an increase of 3,2% per year from 1961 — 1970, and a decrease of 3,8% per year from 1971 — 1977. The mean intrinsic rate of natural increase was 0,6% per year.

Bulls

No adjustments were made for the adult bull population counted during various years. Published data for this component of the population are summarized and compared to the census results obtained during the present study in Table 3. Values for the intrinsic rate of natural decrease or increase based on the subtotal[1] data in Table 3 were calculated in a similar way to that calculated for cows (Fig. 4). This illustrates a decrease of 9,2% per year from 1958 — 1960, an increase of 2,1% per year from 1961 — 1970 and a decrease of 8,2% per year from 1971 — 1977 for the bull population breeding along the coastline from Point Molloy to Cap Digby. The mean rate of decrease from 1958 — 1977, a period of 19 years, was 1,9%.

Population fluctuations

This analysis is based on a subdivision of the study area from Point Molloy to Cap Digby into five distinct regions for which comparable data on population size during various years are available (Fig. 5). With regard to the population breeding between Point Molloy and Point Guite (Fig. 5A) and between Point Guite and Point Morne (Fig.

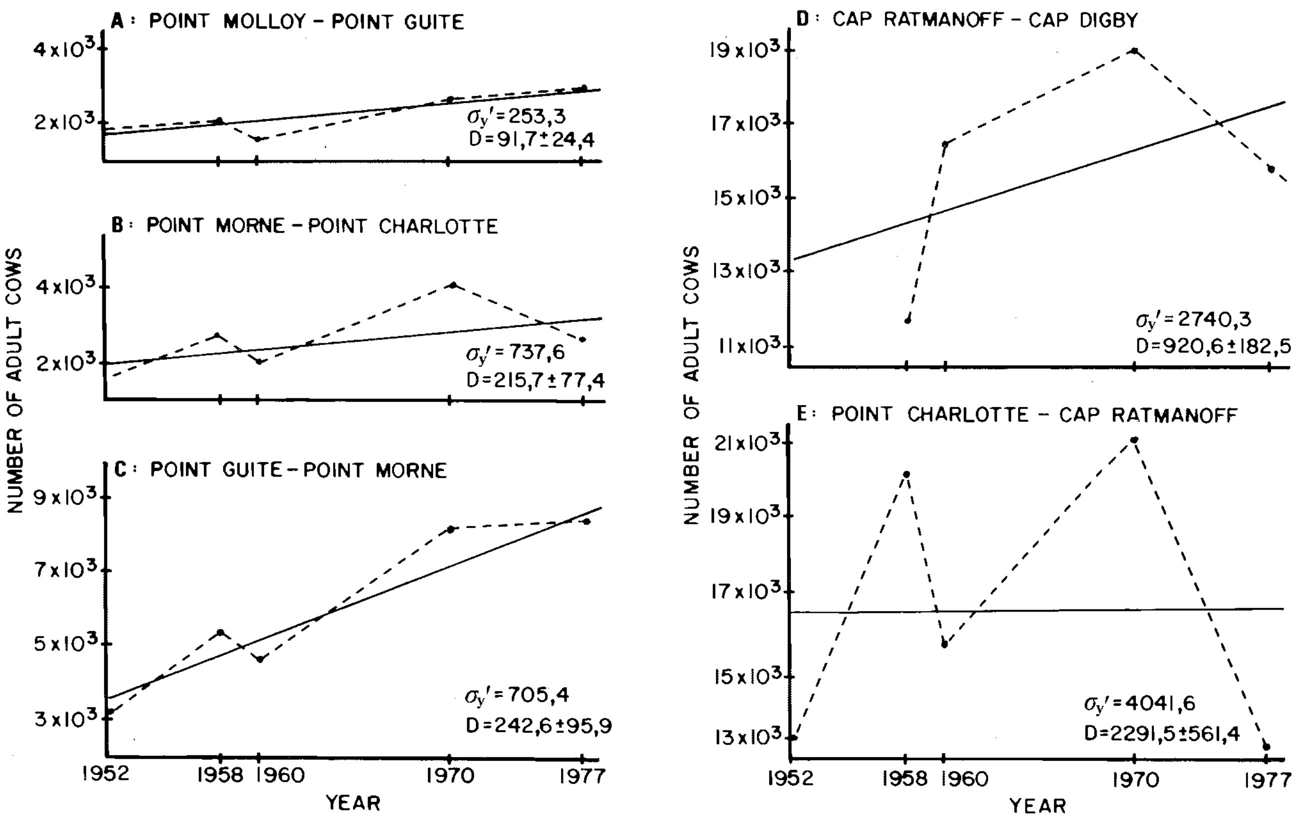

Fig. 5 Population fluctuations in the adult cow southern elephant seal population along various stretches of coastline from Point Molloy to Cap Digby. D = mean density calculated for the specific stretch of coastline based on observed densities during various years from 1952 – 1977. σ = standard error of the estimate of the linear regression where $\sigma_{y'} = \sigma_y \sqrt{1-r^2}$.

5C) the general trend seems to be that of an increase in population size.

Contrary to this the trend for the population breeding between Point Morne and Point Charlotte was to increase from 1952 – 1958, to decrease from 1959 – 1960, to increase from 1961 – 1970 and finally, to decrease from 1971 – 1977 (Fig. 5B); a pattern of fluctuation very similar to that observed for the population breeding between Point Charlotte and Cap Ratmanoff (Fig. 5E), as well as for the total population. Insufficient data for the population breeding between Cap Ratmanoff and Cap Digby did not enable a similar evaluation. However, this part of the population increased from 1958 – 1970, and decreased from 1971 – 1977.

In plotting the calculated degree of fluctuation ($\log_e$ of the standard error of the estimate) for each part of the coastline against calculated mean density ($\log_e$) for each of these parts, a significant positive ($r = 0,97$; $p<0,01$; $n = 5$) linear relationship between these two parameters could be illustrated. This relationship approximated a straight line with the equation $y = 0,94 + 1,20$, where $y = \log_e$ of the degree of fluctuation and $x = \log_e$ of the estimated mean density (mean number of females/km coastline counted during the five surveys).

Change in sex ratio

Overall bull to cow sex ratio of adults hauled out during the breeding season has been calculated at 1:12,5; 9,8; 11,2, 12,2 and 16,7 for 1952, 1958, 1960, 1970 and 1977, indicating an increase in the number of females per male from 1958 to 1977.

Discussion

Over exploitation of seals at Kerguelen from 1911 – 1913 resulted in a cessation of sealing operations (Ring 1923). However, the population recovered well over the next 40 years (Angot 1954). Sealing operations at Kerguelen recommenced during 1958 but only 12 000 bulls were taken over a period of seven years (Pascal pers. comm.), which would probably have had a negligible effect on breeding.

Fluctuations aside, the mean rate of increase for the cow component of the population was 1,4% per year from 1952 – 1977. This is considerably lower than suggested by Pascal (1979). He ascribed the increase from 1952 – 1970, partially to the decrease in whale numbers during the last few decades, resulting in less competition for food. Reasons for the decline (4,6% per annum) between 1971 and 1977 are not known but it is of the same order as that found for populations at Marion Island (4,6%; Condy 1977) and Possession Island (6,1%; Barrat & Mougin 1978).

In contrast to the cows, bulls at Kerguelen have decreased at a mean rate of 1,9% per year from 1958 – 1977. Fluctuations in their numbers occurred but the rate of decrease of 8,2% from 1971 – 1977 was nearly double that observed for cows, resulting in a change in the overall sex ratio of the population. Any influence of the apparent imbalance in sex ratio on reproductive success is still obscure.

Published information on populations comprising less than 10 000 individuals revealed contrasting results; the population at the Valdes Peninsular (Argentina) increased from 1952 – 1970 (Daciuk 1973); and the population at Marion Island (46°25′S 51°45′E) decreased at a rate of 4,6% per year from 1957 – 1975 (Condy 1977). At Possession Island (46°25′S 51°45′E) an increase from 1910 to 1935 – 1940 and a decrease from 1940 – 1976 have been suggested (Barrat & Mougin 1978).

Accepting Carrick and Ingham's (1962) suggestion that the population at Kerguelen had stabilized at its 'natural level' at the time when they published their work (a possibility substantiated by the fact that the size of the cow component of the population has not actually changed much from 1960 to 1977 it might be accepted that the general tendency for the growth rate of the cow population was to level out (possibly at the asymptotic level), after an initial increase since sealing activities were halted.

Solomon's (1960) definition for stability of a population provides for the inclusion of the observed fluctuations in this population; therefore, factors responsible for the regulation of this population's numbers, are also causing the fluctuations. The differences observed in the overall trend between bull and cow numbers suggest that the factors influencing (regulating) the bull population may differ from those influencing the cow population.

Slobodkin (1961) concluded that observed fluctuations in populations are at least in some part intrinsically regulated by thse animals themselves and are not completely dependent on environmental sources. If informal oscillations do not exist in nature it would be expected that observed fluctuations will be correlated with some changing factors in the environment, that is, food supply and predation. It is furthermore expected that any population that is fluctuating in response to non-seasonal environmental variables should show an essentially random fluctuation pattern, a pattern which is not as yet identifiable with the limited information available for this population.

The observed fluctuations in both sexes are probably the net result of factors operating at different levels on this population. Being the subject of historical controversy (Krebs 1978) no attempt is made to separate the influence of these factors on the population. Instead, a short discussion on environmental and intrinsic population factors possibly responsible for the observed fluctuations will be given as follows:

Food

Annual food consumption of the world stock of southern elephant seals has been estimated at 4 500 × 10^3 tons and 1 500 × 10^3 tons for squid and fish respectively (Laws 1977), therefore suggesting that the population at Kerguelen, estimated at 117 397 in 1977 (based on Laws's (1960) calculation that total population size = pup count × 3,2) consumes approximately 880 × 10^3 tons of squid and 193 × 10^3 tons of fish per year.

The production of fish on the Kerguelen shelf area (50 000 km^2) has been estimated at 230 × 10^3 tons per year (Everson 1977), therefore suggesting that the total production is comparable with that utilized by elephant seals if they feed exclusively in this area. Laws (1973) indicated that 15 − 20 Russian trawlers are working around Kerguelen with a probable production of 120 × 10^3 tons per year. This figure is approximately 33% higher than the maximum sustainable yield (80 × 10^3) suggested for the initial standing stock by Everson (1977), which would naturally result in a decrease in standing population size. Confirmation for this is the gradual decline in the reported catch during the past decade (Everson 1977).

A reduction in food availability might have forced a specific sex or age component of the elephant seal population into suboptimal or marginal feeding zones, which might have induced an increase in mortality rate or a decrease in reproduction rate. Carrick, Csordas and Ingham (1962) suggested that competition between cows to achieve sufficient dispersion to enable each to feed adequately must push the subordinates, which will mainly be younger and smaller animals, outside the island feeding zone, and induce psychosomatic conditions that inhibit sexual development.

Although not very accurate these crude estimates for production, consumption by elephant seals and exploitation by fishing trawlers, tentatively suggest that the observed population decrease since 1970 has been the result of competition with the fishing fleet. If confirmed this would be a reversal of the usual interaction between fishing interests and seals (Laws 1973).

Predation

Carrick and Ingham (1962) indicated that the killer whale *Orcinus orca* is an important predator of elephant seals, especially of immature individuals. Moreover, Condy (1977) suggests that the observed decrease in the elephant seal population at Marion Island is due to a lowered recruitment of the third year age class of cows, caused through predation by killer whales. Furthermore Barrat and Mougin (1978) ascribed the observed decrease in the elephant seal population at Possession Island to possible killer whale predation. In addition, killer whales have been implicated as a potentially serious mortality factor for Weddell seals *Leptonychotes weddelli* (Stirling 1971).

During the present study no evidence was obtained for killer whale predation on elephant seals. Only three subadult bulls and two cows had scars which could possibly be ascribed to killer whales, and only one killer whale was observed during the total study period (September 1977 − December 1977); a situation very different from Marion Island (Condy, Van Aarde & Bester 1978).

Although predation by killer whales might be important in the observed decrease of small populations of elephant seals such as those at Marion and Possession Islands, the available information suggests that such predation does not have any influence on the large Kerguelen population.

Emigration and immigration

Thousands of elephant seals have been tagged or branded at various breeding sites, but the records available suggest no inter-island migration of breeding animals. Carrick *et al.* (1962) showed that most long distance movements by seals were made by immature individuals. They believed that any larger scale movements between breeding grounds should have been revealed by a much larger number of sightings.

Nicholls (1970) demonstrated that 60% of bulls and 77% of cows from the Macquarie Island population reproduce within 4 km from their birthsites, and that all individuals breed within 30 km of their birthsites. The possibility that emigration or dispersal to different breeding grounds on the same island, could cause such marked fluctuations seems rather limited.

Social factors

Social factors such as intrasexual and intraspecific competition induced by for example, a shortage of food are probably largely responsible for observed population fluctuations. Depressed growth rate of elephant seal pups caused by excessive disturbance within the breeding colonies disrupting suckling had the effect of lengthening the time taken to reach physical maturity (Bryden 1968), a factor which will influence population trend within space and time.

Tremendous increases in population size along moderately inhabited coastlines of Kerguelen has not resulted in changes in harem size, while a slight increase along densely populated coastlines resulted in tremendous increases in harem size and a decrease in the number of harems (Van Aarde 1980). This increase in harem size with an increase in population size can be ascribed to limited breeding space, where the high density of breeding seals resulted in harems coalescing into continuous masses of cows and pups with bulls dispersed amongst and around them. This in turn has probably lead to an increase in density dependent pup mortality.

Not only would this have induced intrasexual strife for breeding space but would also have influenced reproductive success resulting in the observed fluctuations and especially the decrase from 1971 to 1977. Nikol'skii (1972) argued that changes in reproductive ability can be realized either through a change in growth rate and in the time of maturity, or through a change in the fecundity of individuals of the same size. Le Boeuf (1974) showed that changes in colony number and composition affect the reproductive success of bulls as well as cows. The significant positive linear relationship between density and the range of fluctuation (standard error of the mean) suggest an increase in the range of fluctuation with an increase in population size. It therefore seems to illustrate that an increase in population size results in an increase in fluctuations, probably due to an increase in the influences of regulating factors on that specific part of the population. Although decreases in some parts of the population could have resulted in the increase in other parts of the population, this would not be enough to account for the observed changes in numbers. It is therefore concluded that observed fluctuations in this population, with special reference to the cow component, are the nett result of the operation of various regulatory factors on the population; promoting stabilization of this population, following an initial increase after the reduction induced by sealing.

However, competition with fishing fleets since the onset of this decade possibly resulted in the observed downward trend in the bull population. This would not eventually only influence reproductive success but also the overall trend of the cow population.

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