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Status of southern elephant seals at South Georgia

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Abstract: Approximately 54% of the world population of southern elephant seals (*Mirounga leonina*) breeds at South Georgia. A partial survey in 1951 and a complete survey in 1985, together with counts at specific sites between these times, suggested that the population (around 100 000 breeding females) had not changed significantly in 34 years. This was in contrast to marked declines in most other populations. To examine this further, we conducted a third survey in 1995. This produced an estimate of 113 444 (s e = 4902) breeding females. Taking into account improved information about the behaviour of female elephant seals since the survey in 1985, there was no significant change in the number of breeding female elephant seals between 1985 and 1995. When combined with information from the 1951 survey, this supports the view that the total population size has not changed significantly during the past 45 years. Evidence for regulation of the population by environmental factors is equivocal. We hypothesize that the lack of any net change in population size may be linked to a limited availability of high quality breeding habitat.

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Introduction

Southern elephant seals (*Mirounga leonina*) have a circumpolar distribution in the Southern Hemisphere and breed mainly on subantarctic islands, such as South Georgia. A recent assessment (SCAR 1991, Laws 1994) suggested that the breeding population at South Georgia produced ~54% of the annual world pup production. Southern elephant seal populations were also identified as being in decline at seven of the fourteen major breeding sites (SCAR 1991). At only one site was the population increasing or stable (Peninsula Valdez) and at the remainder, including South Georgia, the status of the populations was considered to be uncertain. To date, only two assessments of the size of the breeding population at South Georgia have been made (Laws 1960, McCann & Rothery 1988). Together, these suggested that there had been no significant change in the size of the South Georgia breeding population (estimated at *c.* 100 000 breeding females) between the 1950s and the 1980s.

Recent genetical studies using mitochondrial DNA (Hoelzel *et al.* 1993) and serum enzymes (Gales *et al.* 1989) have suggested that the breeding populations of southern elephant seals on subantarctic islands, as well as at Peninsula Valdez in Argentina, are reproductively isolated. From the point of view of the assessment of trends in abundance, each population should, therefore, be treated as being independent. However, declines have occurred mainly at sites in the southern Indian and Pacific Oceans and, in general, populations at sites in the South Atlantic, which includes that on South Georgia, are apparently stable or increasing.

Elephant seals were exploited for their oil at South Georgia between 1904 and 1964 (Laws 1960, McCann 1985) and throughout the 1960s there was a major fishery over the South Georgia shelf from which some fish populations have not yet recovered (Kock 1994). Sealing probably had large effects on the population structure. The potential effect of the fishery is uncertain because recent investigations have shown that elephant seals usually feed far from the South Georgia continental shelf (McConnell, Fedak & Chambers 1992, unpublished data, Sea Mammal Research Unit). Distant resources of squid may be more important for elephant seals than the nearshore fish populations (Rodhouse *et al.* 1992, Rodhouse *et al.* 1993, Boyd *et al.* 1994). These factors, and the need to understand any progessive changes occurring in this population, requires regular assessments of the size of the population. The objectives of this study were to determine the status of the South Georgia population and to provide information about habitat use by elephant seals during the breeding season. The large size of this population and its distribution along isolated coastlines during the breeding season, make it exceedingly difficult to survey. Consequently, this is only the third survey to be carried out since 1950.

Methods

Counting procedures

The principles underlying the methods used in this survey were developed by Rothery & McCann (1987) and had been used during the previous survey of elephant seals at South Georgia (McCann & Rothery 1988). These involved obtaining counts of the adult females at all breeding sites around the island at some time during the breeding season. From knowledge of the statistical distribution of the number of females ashore throughout the breeding season, these counts were used to estimate the total adult female population size at each site. Adult females were chosen as the unit for counting, rather than pups, because it is possible to obtain an accurate census of the adult females and because their haul-out (defined as time spent ashore) behaviour is reasonably well understood and quantified. Pups cannot be censused with the same accuracy because of their smaller size resulting in individuals being hidden from view more frequently than the considerably larger adult females. In addition, at South Georgia, pups move out of harems after weaning and often wander inland where they are lost from view in the vegetation.

Seals were counted between 10 October and 8 November 1995. Operational requirements, including weather conditions, dictated the order in which sites were counted. A yacht (*Damien II*, Sally & Jerome Poncet, Beaver Island, Falkland Islands), which had a steel hull and retractable keel to allow it to cruise close to the shore and to have access to shallow anchorages, was used as the base for the survey. Four different methods were used to census sites. These were:

Method 1. Two or more individual counters traversed beaches on foot. Wherever possible counters walked along the front and the back of harems simultaneously and tallied the number of adult females in each harem or group. After each group was counted tallies were compared and if there was a deviation between the numbers of >10% then the group was recounted.

Method 2. Groups or harems on beaches backed by high ground were occasionally counted from the high ground using binoculars. Using this method, three counts were made by one or more individuals. The mean of these counts was then used to estimate the total number of female elephant seals present.

Method 3. Groups or harems were counted using binoculars either from the deck (2 m above sea level) or from the mast (15m above sea level) of the yacht while it cruised at ~1ms^{-1} close to the shore. The distance of the vessel from the shore varied from <20 m to 300 m. However, in most cases the distance was at the low end of this range.

For all methods, counts were recorded at the level of the group or harem. At a small number of selected sites counts were made simultaneously using two or more of the methods. Counts were then subtotalled for each location, such as a bay, fjord or well-defined stretch of coastline, and each of these locations was counted within a single day. In addition to the number of adult females, the type of beach habitat occupied by each group and the counting method were recorded. The types of habitats were:

Type A. Open beach. Beaches >200 m in length which have an open aspect to landward where all elephant seals were visible for up to several hundred metres inland.

Type B. Long beaches backed by tussac grass. Beaches >200 m in length which were <50 m wide and that were backed by tussac grass knolls in which elephant seals may not have been visible.

Type C. Short beaches backed by tussac grass. Beaches < 200 m in length which were <50 m wide and that were backed by tussac grass knolls in which elephant seals may not have been visible.

Type D. Long, narrow beach. Beaches >200 m in length which were <50 m wide and backed by rock or scree that did not permit access for elephant seals.

Type E. Short, narrow beach. Beaches <200 m in length which were < 50 m wide and backed by rock or scree that did not permit access for elephant seals.

Type F. Rocky shore. Shoreline which did not fit into the previous categories but which would have mainly been formed of rocky and partially tidal platforms.

This classification scheme was developed to assist in the interpretation of potential sources of variability in counts and to provide an indication of habitat use by elephant seals during the breeding season. The distinction between beaches

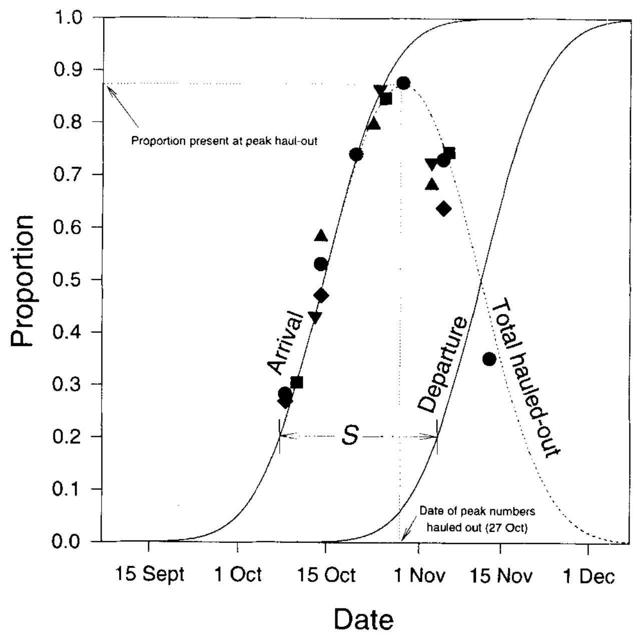

Fig. 1. Diagramatic representation of the model used to examine the changes in the number of female elephant seals present ashore at any stage of the breeding season. Two cumulative normal distribution functions are shown, one for the arrival of females and the other for departures, and the total number hauled-out, and that would be observed ashore, at each stage of the breeding season (dashed line). *S* is the total time spent ashore by a female (27 days). Each of the points shown are those from the five sites where at least three counts were made at different stages of the breeding season. These sites were: ● - King Edward Cove; ■ - Elsehul/ Undine; ▲ - Dartmouth Point; ▼ - Husvik; ◆ - Hestesletten.

of greater than or less than 200 m reflects the capacity of the beach to hold more than one harem respectively but it also reflects a perceived distinction in habitat types at South Georgia to allow beaches within small isolated coves to be classified separately from long narrow beaches in bays or fjords.

Analytical procedures

Counts of adult female elephant seals at each location provides an index of the total number of adult females hauling out at that location during the breeding season. If the number of females hauled-out follows a statistical distribution then, from knowledge of the parameters of the distribution, it is possible to estimate the total number of females that hauled-out in a location based on a single count. Empirical haul-out distributions for adult female southern elephant seals have been proposed by van Aarde (1980), Pascal (1979, 1981, 1985), Hindell & Burton (1988) and Rothery & McCann (1987) based on several different models. Of these, only that produced by Rothery & McCann (1987) modelled the haul-out process based on empirical observations of maternal time budgets during lactation. This method was used to estimate the total haul-out population mainly because of the realistic way in which it models the haul-out process but also because it was applied by McCann & Rothery (1988) to estimate breeding population size in the 1985 survey.

The modelling procedure, described initially by Eq. 2 in Rothery & McCann, (1987) is illustrated in Fig. 1. This shows two cumulative normal distribution functions, one describing the pattern of arrival at the pupping beach, with mean μ and standard deviation s, and the other describing the pattern of departure. On average, the period between arrival and departure, S, will be the duration of lactation plus the period between arrival and birth. The total number of females hauled-out at any time is given by the difference between the two cumulative distribution functions which forms a bell-shaped curve (Fig. 1). The form taken by the distribution of numbers hauled-out depends on the values of s and S. Following Rothery and McCann (1987), if N_H is the size of the haul-out population in a given area and $n(t)$ adult females are counted ashore at time t, then on average

$$n(t) = N_H p(t, \mu, \sigma, S)$$

where $p(t, \mu, s, S)$ is the expected proportion of females hauled out at time t. This equation also describes a straight line relationship between $n(t)$ and $p(t, \mu, s, S)$ which passes through the origin and has a slope equal to N_H, the total size of the haul-out population. The model described by Fig. 1 and Eq. 2 in Rothery & McCann (1987) was fitted to haul-out data, given by $n(t)$, by iterative least-squares regression for five sites that were censused on at least three occasions during the 1995 breeding season (Table I). For comparison, it was also fitted to detailed daily counts from one site (Husvik) from 1988. The values of μ and s which minimized the residual variation around the regression line were used and this produced an estimate of N_H. The value of S was derived from empirical observations as follows.

Arnbom *et al.* (in press) gave an average duration of lactation of 22.9 days (s d = 2.1 days, n = 113) for mothers of male pups and 22.5 days (s d = 2.1 days, n = 111) for mothers of female pups. This agrees with previous estimates of a lactation duration of ~23 days for southern elephant seals (Laws 1956, Carrick *et al.* 1966, van Aarde 1980, McCann 1980). However Arnbom *et al.* (in press) also showed that about 50% of the variation in lactation duration could be due to maternal mass, maternal mass loss rate and date of birth. Although date of birth only contributes 6% of the variation in lactation duration it is the only one of these factors that can be incorporated into the model. Lactation duration declines at a rate of 0.044 days for each day of the breeding period. Thus lactation duration was made to decline at this rate symmetrically around the mean date of parturition of ~15 October (Arnbom *et al.* in press) and the mean duration of lactation. This only resulted in an increase in the variance explained by the model in the case of haul-out distributions from Husvik, where the data used by Arnbom *et al.* were collected, and they were, therefore, only applied to these

Table I. Parameters of the haul-out distribution curves for each of the calibration sites estimate by iterative least-squares regression.

Site	Mean date of arrival	s d date of arrival	Regression slope (N)	r^2	Maximum number hauled-out	Date of maximum numbers	n	Estimated total population size[1]
King Edward Cove	14 Oct	8.8	677.1	0.994	92.8	27 Oct	6	106 073
Elsehul/Undine	15 Oct	8.9	164.3	0.996	143.1	27 Oct	3	110 779
Dartmouth Point	12 Oct	10.4	495.3	1.000	399.3	28 Oct	3	108 437
Husvik 1995	15 Oct	8.9	370.4	0.910	315.3	25 Oct	3	110 779
Hestesletten	16 Oct	13.5	417.2	0.982	284.8	29 Oct	3	130 520
Mean								113 444
s e								4902
Husvik 1988	15 Oct	9.6	476.8	0.990	400.9	28 Oct	60	
King Edward Point	19 Oct	6.6	107.7	0.978	103.4	2 Nov	43	

[1]The haul-out probability distribution from each site was used to provide independent estimates of the estimated total population size.

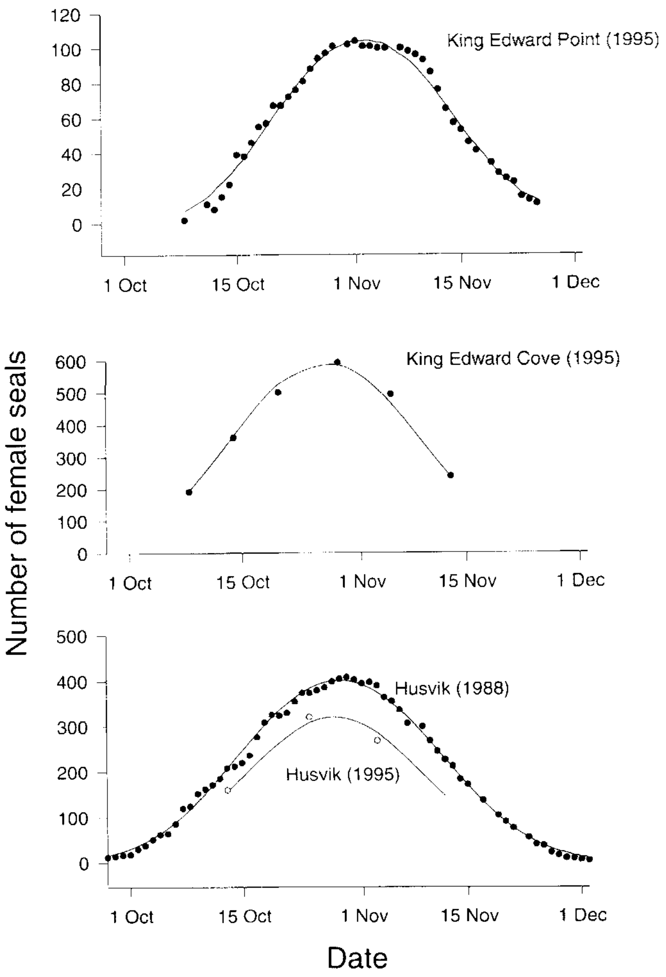

Fig. 2. The distribution of numbers of female elephant seals counted (dots) at three different sites together with the results of the model fitting procedure (lines).

distributions.

The mean duration of time hauled-out between arrival and parturition was estimated from individual females marked on the day of arrival at Husvik, in 1988. This showed that the pre-partum haulout period lasted on average for 4.48 days (s d =2 .25 days, n = 107). Given this and since the median duration was four days, the duration of this phase of the pre-partum haul-out period was set at four days. Thus females were assumed to haul out, on average, for a total of 27 days.

The error associated with estimating the total haul-out population size at each of the five locations shown in Table I was estimated by dividing the detailed haul-out distributions from Husvik in 1988 and King Edward Point in 1995 into three exclusive portions of 10 days; one before the peak of numbers, another straddling the peak and the other following the peak. These groups were then resampled at random and without replacement to simulate the results of three censuses at each site, one during each of the three periods, with 10 replicates. Each replicate was then used to produce an estimate of the total haul-out population size. The distribution about this mean was then used to calculate the coefficient of variation for each site.

Results

Counting errors

Most of the counts were carried out by one person. However, for a sample of 59 counts, his counts were compared with those made simultaneously by another person who was counting independently. There was no tendency for the primary counter to have a positive or a negative bias and the mean percentage difference on each count was ± 0.9%.

Cross-method calibration of counts was carried out on 17 occasions and this showed an average difference of ± 0.2% between Methods 1 and 2 and ± 4.4% between Methods 1 and 3. In only two of the nine cases where Methods 1 and 3 were compared was there any difference in the number counted but in both of these Method 3 gave a lower estimate than did Method 1. Eighty-five percent of all animals were counted with Method 3. Methods 1 and 2 were used to count 13% and 2% of animals respectively.

Model fitting

The model provided a generally good fit to the observations (Fig. 2). Resampling of the detailed observations of the haul-

Table II. Population size estimates for each of the four Sealing Divisions defined by Laws (1960). Standard errors are shown in brackets for each estimate as well as the equivalent estimates for the two previous surveys of the elephant seal population at South Georgia.

Division	Number of female elephant seals		
	1995	1985	1951
I (Cape Nuñez - Cape Buller)	16 673 (447)[2]	17 745	20 000
II (Cape Buller - Larsen Point)	17 320 (656)[2]	16 920	15 000
III (Larsen Point - Cape Disappointment)	52 775 (2803)[3]	42 892	32 500[1]
IV (Cape Disappointment - Cape Nuñez)	26 675 (1421)[2]	24 676	32 500[1]
Total	113 444	102 233	100 000

[1]Estimate based on anecdotal data.
[2]Not significantly different from estimated number in 1985 (P>0.05).
[3]Significantly greater than estimated number in 1985 (P<0.05).

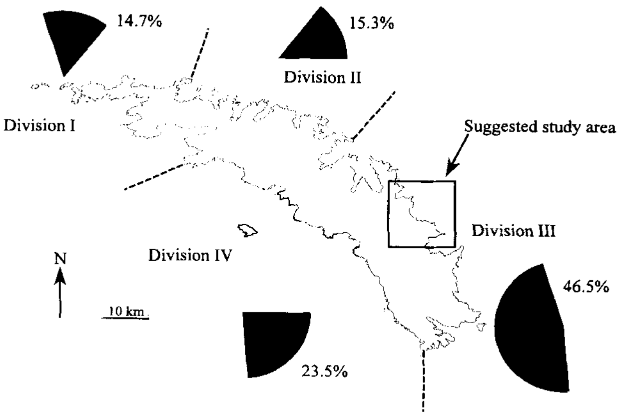

Fig. 3. Map of South Georgia showing former Sealing Divisions and the proportion of the breeding female population in each Division. The box shows the area which contained 19.3% of the breeding females and which could be assessed more frequently than the whole of the population.

out pattern for Husvik in 1988 and King Edward Point in 1995 (Fig. 2) suggested that the model fitting procedure estimated the total haul-out population size with a coefficient of variation of 0.037 and 0.055 respectively. A coefficient of variation of 0.045 was therefore used to assess the variance in the counts due to the estimation procedure.

Estimates of total number

After exclusion of repeated counts for some sites and using only the counts made closest to the date of the maximum number ashore, a total of 73 341 adult female elephant seals was counted during the survey. When this was corrected for the dates that counts were made at each location, the total haul-out population size of adult females was 113 444 (s e = 4902). The standard error of this estimate combines the error due to variation in haul-out behaviour between locations (estimated by calculating the total haul-out population size separately using the model parameters derived for each of the five locations given in Table I) with the error associated with the estimation procedure derived by randomly resampling the detailed haul-out distributions for Husvik in 1988 and King Edward Point in 1995. If the parameters for the model of hauling out behaviour were changed to those used by McCann & Rothery (1988), the estimated haul-out population of adult females was 101 797.

To allow comparison of the population size between different parts of the coastline of South Georgia, the population size was estimated separately for each of the former Sealing Divisions. Although these probably have no biological significance, this follows the geographical boundaries defined by Laws (1960) and again used by McCann & Rothery (1988). This shows that almost half of the population was located in Division III which represents the south-east portion of South Georgia from Larsen Point to Cape Disappointment

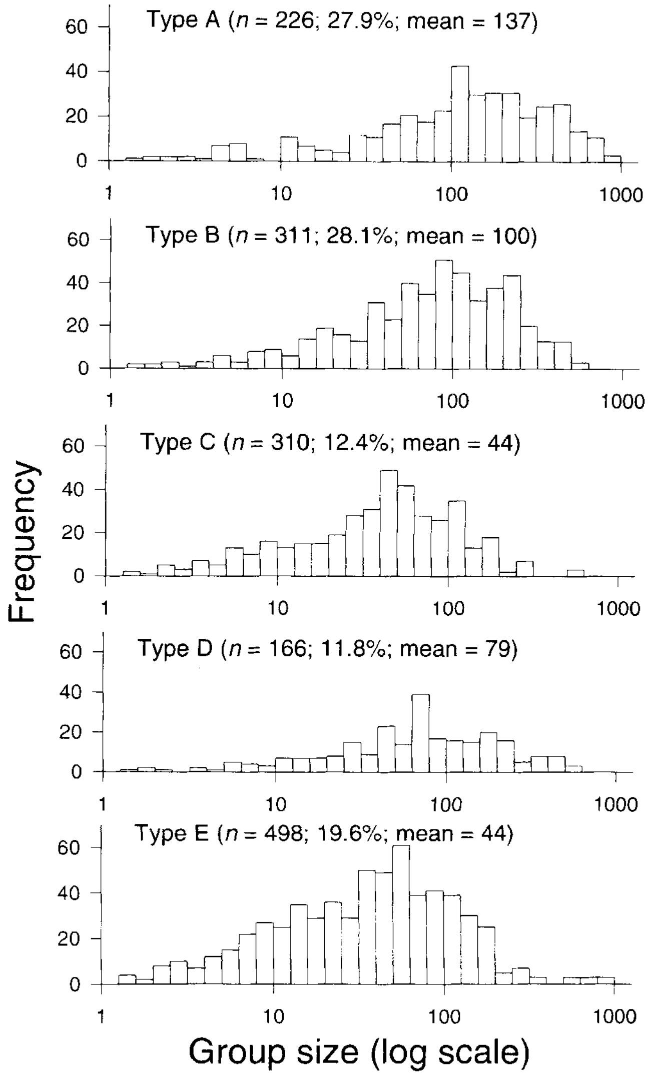

Fig. 4. The frequency distribution of group size, expressed in terms of the total number of female elephant seals in the groups during the breeding season, plotted on a log-scale of group size in relation to the type of beach occupied by the group. See text for a description of beach types. Also given is the number of groups from each beach type (n), the percentage of the total number of females in the population using each beach type and the mean group size.

(Table II, Fig. 3).

Habitat and group size

The greatest proportion of females was counted on beaches defined as Type B (long, tussac-backed beach) but this was only slightly greater than the proportion present on beaches defined as Type A (long, open beach); together these types of beaches were used by 56% of females (Fig. 4). Over 30% used Type C and E beaches which are representative of the many small coves and inlets along the coast. Only about 10% used Type D beaches and almost none (0.2%) used Type F

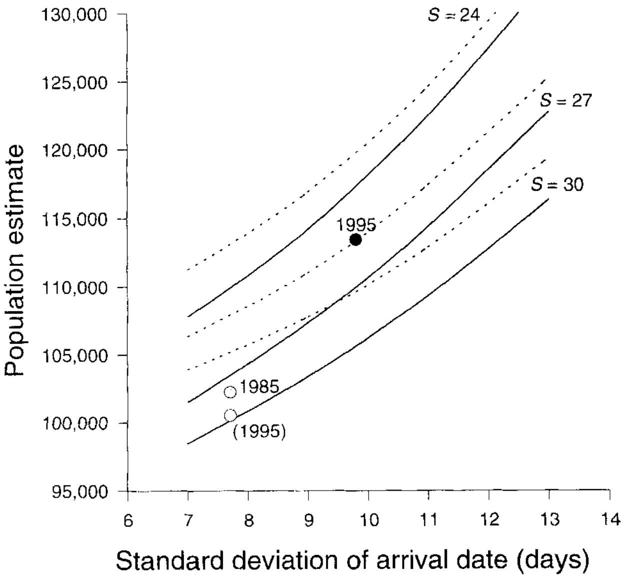

Fig. 5. Analysis of the sensitivity of the estimated population size to variation in the parameter values used in the model. Variation in the standard deviation is shown on the x-axis, three values of *S* are shown and, for each of these values of *S*, two values for the mean arrival date are used. These are μ = 14 Oct. (solid line) and μ = 15 Oct. (dashed line). The solid dot is the population estimate for 1995; the shaded dot is the population estimate for 1985 and the circle is the population estimate for 1995 if the model parameters used to fit the data from 1985 are used.

beaches.

Although the overall mean group size counted was 44 seals, the mean group size adjusted for the date of censusing to include all individuals using a particular location was 73 seals. The distribution of group sizes showed that the largest groups were on Type A beaches and the smallest were on Type C and D beaches (Fig. 4). Mean group size appears to correlate, in general, with the length of the beach.

Discussion

Population size

The estimate of 113 444 for the total size of the population of adult female elephant seals hauled-out at South Georgia in the breeding season of 1995 is significantly greater than the estimate of 102 233 produced in 1985 (Table II, $P<0.05$). Both surveys were carried out using almost identical methods with most counts being carried out from a sailing vessel travelling close to the shoreline. Although McCann & Rothery (1988) provided no assessment of the precision of the counting methods used in 1985, the assessments of these methods in 1995 suggested that most potential sources of error were negligible.

The current study suggests that the population of breeding elephant seals at South Georgia may have increased between 1985 and 1995 but this apparent change should be interpreted with caution. The population estimate is highly sensitive to the values of μ, s and *S* (the mean and standard deviation of the arrival date and the duration of haul-out respectively) as shown in Fig. 5. During the 1985 survey a greater number of repeat counts were made of specific beaches than during the 1995 survey and these were used to derive the estimates of the haul-out parameters for the version of the model used to estimate abundance, as was the case in this study. These suggested a mean peak date of haul-out of 23 October and a standard deviation of the haul-out distribution(s) of 7.7 days (Rothery & McCann 1987), both of which are sufficiently different from the equivalent values used in this study (Table I) to account for a difference of 5000–10 000 in the total population estimate (Fig. 5). This may be a true difference, rather than one due to sampling error, because interannual variation in the haul-out distribution for breeding has been observed for female Antarctic fur seals (*Arctocephalus gazella*) at South Georgia (Duck 1990, Boyd 1993, Lunn & Boyd 1993) and for northern elephant seals (*Mirounga angustirostris*) in California (Stewart & Yochem 1991). Comparison between the haul-out distribution for Husvik in 1988 with that of 1995 (Table I) suggests that similar small, but potentially significant, variation may exist for southern elephant seals at South Georgia. This could account for the difference in the standard deviation in the haul-out distribution between 1985 and 1995 and would suggest that the difference in population estimates between these years are real.

However, since 1985, detailed information has become available which suggests that the value of *S* used in the analysis of the 1985 data (S = 30) was too high and a value of S = 27 is more appropriate. As can be seen from Fig. 5, which uses the survey data from 1995, this change alone would have led to an increase in the 1985 estimate to at least 105 000. To assess the implications of this, the 1995 data were re-analysed with S = 30 and this produced a population estimate of 108 983 (s e = 4628) which is not significantly different from the population estimate of 102 233 for 1985 ($P>0.05$).

Therefore, overall, it would appear that the population in 1985 was underestimated by 3–5% and, consequently, there was no significant change in the number of female elephant seals breeding at South Georgia between 1985 and 1995. While it is possible that the apparent long-term stability of the population is an artefact of the few surveys undertaken, censuses of specific sites between the synoptic surveys of 1951 and 1985 did not support the view that the population had been changing through that time (McCann & Rothery 1988). Moreover, the similarity of the estimates from this study and the one from 1985, combined with the short interval between these surveys, relative to the generation time of 5–10 years (McCann 1985), also suggest that no significant change had occurred during this time period. This is because there would probably have been insufficient time for the population to have recovered from a significant decline, or to have generated a significant increase in size followed by a decline, during the ten year interval between surveys. Taken together, this supports the conclusion that the elephant seal population at South Georgia, in addition to showing no net change over the past 45 years, has not fluctuated substantially between the synoptic surveys.

Habitat use

The long-term apparent stability of the South Georgia elephant seal population suggests either that elephant seals are highly buffered against long-term changes in the ecosystem or that the factors which are contributing to the maintenance of population size are themselves stable through time. The view that elephant seals are highly buffered against long-term instability in the food supply or other key environmental factors is not supported by evidence from other populations of higher predators at South Georgia. Both Antarctic fur seals and king penguins (*Aptenodytes patagonicus*) have been increasing rapidly (Croxall *et al* 1988, Boyd 1993) whereas albatross populations have been in decline (e.g. Prince *et al.* 1994). Moreover, elephant seals have been in decline at several other breeding sites, possibly as a result of long-term environmental changes (Burton *et al.* in press). While it is possible that the apparent lack of any net change in the population at South Georgia is caused by unkown factors in the marine environment, it is also feasible that factors in the terrestrial environment used by elephant seals could be contributing to this process. Thus an environmental factor which has long-term stability, such as availability of breeding habitat, might be influential in limiting the growth of the population.

The results of this study suggest that the size of the breeding groups may be limited by habitat type in that small beaches (<200 m long) tend to hold smaller groups of elephant seals. Although there is no information about reproductive success in southern elephant seals in relation to group size or habitat type, or about the preference shown by adult females for different types of beach habitat, it is possible that some form of limitation of population growth could be occurring due to habitat limitation. Indeed, for northern elephant seals, Stewart (1992) observed changes in the distribution of breeding groups in relation to changes in habitat characteristics. As a general observation, proportionately more of the beaches within small coves or inlets are occupied by female elephant seals than of the larger beaches and yet these smaller beaches account for only 32% of the total population (Fig. 4). If small beaches provide higher quality breeding habitat for elephant seals then their availability is a potential limiting factor. Arnbom *et al.* (in press) observed that females in small groups on large isolated beaches were liable to a high degree of disturbance from subordinate males and that this may have been a factor in reducing the time spent hauled-out by females as the breeding season progressed. The larger groups of females on the larger beaches may have been, in part, a defensive response by females to harrassment. On small beaches subordinate males will often be restricted in their movement around harems by the terrain, thus reducing the potential for disturbance. Similar effects of disturbance have been observed in northern elephant seals (Stewart 1992). The net effect of this may be that, from the perspective of females, choosing a specific type of beach on which to pup may bring advantages in terms of reproductive success. However, further data on the relationship between breeding habitat, group size and breeding success, including detailed behavioural studies, will be required to test this hypothesis.

Future population assessments

Although the number of elephant seals at specific locations appears to fluctuate between years (McCann & Rothery 1988), when averaged over large stretches of the coastline, such as the former Sealing Divisions, there was consistency in the estimated total numbers (Table II). This means that, in future, trends in abundance could be monitored by surveying specific areas, although this would obviously not preclude the need for periodic synoptic surveys to ensure that trends in the specific study areas remained representative of the population as a whole. Such an approach has been used successfully to monitor changes in the abundance of southern elephant seals at Macquarie Island (Hindell & Burton 1987). There is also merit in carrying out more intensive observations of a smaller area than was covered by this study, which might include several counts of the whole area within a single breeding season, because this would produce a more precise estimate of abundance and it would increase the statistical power to detect future trends in abundance.

The greatest concentration of elephant seals on South Georgia occurred along the coastline in the south-east of the island (Table II). Large sections of this are accessible on foot from shore-based facilities and, mainly for reasons of cost, could be surveyed with greater regularity than is possible when having to use a charter vessel for such an operation. In particular, the coastal region between Ocean Harbour and Moltke Harbour (Fig. 3) could be surveyed in this way and it is suggested that this region of coastline should be monitored at intervals of five years. In 1995, this section of coastline held 21 947 female elephant seals which represents 19.3% of the total South Georgia population. This would also be an area potentially suitable for surveys based on aerial photography.

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