

ADVICE ON THE STATUS OF BRITISH GREY SEAL POPULATIONS: 1996

Summary

This document contains advice from the Natural Environment Research Council on the current size and status of British grey seal populations, based on information provided by the Sea Mammal Research Unit (SMRU). The size of the British grey seal population at the start of the 1995 pupping season is estimated to be 105,800, using a new method which takes account of variations from year to year in juvenile survival and age at first pregnancy, and which makes use of more of the available data. This is 6% higher than the equivalent estimate for 1994. The estimated increase in population size each year since 1984 is also 6%. This is very similar to the rate of increase obtained with the previous method. It is estimated that numbers have increased by 30-50% since 1990; if current trends continue the population size in 1997 is estimated to be 119,400. In 1995, 96,800 seals were associated with breeding sites in Scotland and 9,000 with breeding sites in England and Wales.

Appendix 1 describes the method used to estimate pup production from aerial photographs of grey seal breeding sites. Tables 1-4 give production estimates by year and breeding site. Appendix 2 describes how the pup production estimates are used to estimate all-age population size, and Table 5 gives these population estimates. Figure 1 shows the changes in total pup production and female population size for all major breeding colonies since 1984, and Figure 2 shows the trends in pup production in different parts of Britain over the same period. Figure 3 illustrates the location of the major grey seal breeding sites, Figure 4 shows the location of sites where grey seals have been observed during the summer surveys for common seals, and Figure 5 shows the world distribution of grey seals.

Surveys conducted in 1995

Every year SMRU conducts surveys of the major breeding sites for grey seals (*Halichoerus grypus*) in Britain in order to estimate the number of pups born there. In addition, new sites where grey seal pups have been reported or which appear to be suitable for colonization are regularly visited. During 1995 aerial surveys were flown of all the major sites in the Hebrides and Orkney, and of the Isle of May. Ground counts of the numbers of pups born at the Farne Islands were carried out by staff from the National Trust; similar counts were carried out by members of the Lincolnshire Trust for Nature Conservation at Donna Nook on the Humber estuary, and by members of the Dyfed Wildlife Trust in Wales.

Year	Wash	Donna Nook	Blakeney Point	Other Sites
1988	3035	173	701	
1989	1580	126	307	
1990	1532	57	73	
1991	1551			
1992	1724	18	217	
1993	1759	88	267	
1994	2277	60	196	109
1995	2266	115	438	137
1996 ¹	2192	162	372	

¹ Provisional value

Table 1. Maximum counts of common seals made at the Wash each year during August, and counts from other English sites made during the same survey. Blanks for individual sites indicate that no counts were made there during a survey.

Estimation of Pup Production

Pup production in each year is estimated from the aerial survey results using a model of the birth process and the development of pups. The method used to calculate the estimates for this year's advice is the same as that used in 1994 and 1995.

Estimation of Population Size Associated with Regularly Surveyed Sites

The size of the total population associated with the regularly surveyed sites has been estimated by fitting a mathematical model of the seal populations to the series of pup production estimates from these colonies collected since 1984 (when the current methodology was established), to data on population pregnancy rates collected between 1978 and 1981, and to data on population age structure from management culls at the Farne Islands. This method, which is described in Appendix 2, has been substantially modified since 1995, at the suggestion of external referees. It now takes account of variation from year to year in juvenile survival and age at first pregnancy, and makes use of more of the available data on these population parameters. Changes in pup production and the size of the total female population at the regularly surveyed sites are shown in Figure 1. Estimates of the size of the total population provided by the method described in Appendix 2 and by the method used for the 1995 advice are given in Table 5.

Estimates of total population size using the new methodology are 7-10% lower than those from the previous method, but the underlying trend in abundance is the same. The difference in the estimates of total population size is primarily because estimate of age at first pregnancy provided by the method described in Appendix 2 is nearly one year less than that used in the previous method. As a result, the estimated proportion of breeding-age females in the population is higher, and a smaller population is required to account for the number of pups which are born each year.

For illustrative purposes the components of this population which are associated with each of the major breeding areas have been calculated. However, it should be recognized that the distribution of seals outside the breeding seasons may not be the same as the distribution of the breeding sites. Trends in the numbers of pups born in each of these breeding areas since 1984 are shown in Figure 2. The numbers of pups born each year in Orkney has continued to increase over the last 20 years, but there has been very little overall increase in the Inner or Outer Hebrides since 1992. Estimates of pup production and population size for the main colonies surveyed in 1995, which account for more than 85% of all pups born each year, are:

Location	Pup production	Change from 1994	Total population (to nearest 100)
Inner Hebrides	3,073	+10%	9,300
Outer Hebrides	12,564	+3%	38,100
Orkney	12,545	+8%	38,100
Isle of May	1,346	-4%	4,100
Farne Islands	1,070	+4%	3,200
Donna Nook	334	+11%	1,000

None of the changes in pup production between 1994 and 1995 at each location is inconsistent with the observed trend up to 1994 (ie all the estimates lie within the 95% confidence interval of the prediction for pup production in 1995). However, for the second year in succession, estimated pup production for the Isle of May, and the Inner and Outer Hebrides was very close to the lower 95% confidence limit of the predicted pup production. This suggests that the increase in pup production at these sites may be slowing down.

Confidence Limits

Ninety-five percent confidence limits on the pup production estimates at each location are within 14% of the point estimate. The exact limits depend on a number of factors, including the number of surveys which are flown in a particular year. It is also possible to calculate 95% confidence limits for the estimate of the female component of the population; these are approximately 19% on either side of the mean (ie 44,000 - 64,000 for the estimate of 53,800 for the female population in 1995 - see Table 5). The size of the male component has been estimated on the assumption that the number of sexually mature males is 60% of the number of mature females, and that males become sexually mature at four years of age. The procedure used to generate confidence limits on the estimate of female population size could, in principle, be repeated for the combined female and male and male population. However, there are no data currently available on the relative numbers of males and females in the population which could be used in this way.

Sites Surveyed Less Frequently

The other British breeding areas are surveyed less frequently and intensively. Estimates of pup production have been calculated for these, but confidence limits cannot be

estimated. The total population associated with these remaining areas has been calculated using the ratio of total population to pup production for the main areas. The resulting figures are:

Location	Date of last survey	Pup production	Total population (to nearest 100)
Mainland Scotland and South Ronaldsay	Helmsdale 1992 Loch Eriboll & South Ronaldsay 1994	1,200	3,900
Shetland	1977	1,000	3,300
Southwest Britain	Southwest England 1973 Wales 1994	1,500	4,800

Recent and Predicted Changes in the British Grey Seal Population

Taken together, these figures provide an estimate of 105,800 for the size of the British grey seal population at the start of the 1995 pupping season: 96,800 seals are associated with breeding sites in Scotland and 9,000 with breeding sites in England and Wales. The equivalent estimates for 1994 are 91,000 for Scottish sites and 8,800 for those in England and Wales. Britain now holds approximately one third of the world population of grey seals (see Figure 5).

The increase from 1994 to 1995 in the estimate of total population size associated with breeding sites which are monitored annually was 6.8%, with 95% confidence limits of 4.3-9.3%. Total population size at these sites is estimated to have increased by 40% (95% confidence limits 30-50%) from 1990 to 1995. If there is no change in survival or fecundity rates over the next two years, the population size associated with these sites in 1997 is predicted to be 107,400: 14.25% higher than the equivalent estimate for 1995 (95% confidence limits 9.25-19.25%). If there is no change in the number of seals associated with the sites which are surveyed less frequently, the predicted population size in 1997 is 119,400.

Trends in Other Features of the British Grey Seal Population

The Scottish Office has requested advice on the implications of the continuing trend in grey seal numbers for pup mortality, damage to flora and fauna on breeding sites, and the condition of breeding seals and their pups.

Data from the Farne Islands indicate that the mortality rate suffered by grey seal pups rises as the density of breeding adults increases, particularly at sites where access to the sea is restricted. This is probably because the risks of accidental injury to pups and of mothers being separated from their pups increase as the total number of movements of

adult seals between pupping sites and the sea increases. Thus a doubling in the number of pups born at the Farne Islands between 1960 and 1971 lead to an approximately three-fold increase in the number of pups which died each year.

Although the number of seals breeding at some sites (particularly in Orkney and the Outer Hebrides) has risen dramatically over the last two decades, this has not always lead to an increase in density because the seals have spread out to cover a wider area. SMRU plans to analyse the way in which the spatial distribution of seals on these colonies has changed with time to determine whether there is an equilibrium density at each site. If there is, it will set an upper limit to the number of pups born in each colony and to the level of pup mortality.

High densities of breeding seals can lead to a temporary loss of vegetation cover and subsequent erosion of soil during severe winter storms. This situation is exacerbated if the ground has already been undermined by burrowing birds, such as puffins. Seals and puffins share breeding sites at certain locations on the Farne Islands and the Isle of May. One of the justifications for the culls of grey seals at the Farne Islands between 1972 and 1977 was a concern about loss of soil resulting, in part, from seal activity. There is also concern that seals may damage the sensitive machair community on the National Nature Reserve at the Monach Isles, either directly or by affecting the dune structure and allowing sand to inundate the machair. SMRU's aerial photographs can be used to map the relationship between seal distribution and that of sensitive vegetation types, and the Unit is in regular contact with Scottish Natural Heritage about this.

Long-term studies by SMRU at North Rona and the Isle of May have indicated that the weight of adult female grey seals immediately after they have given birth to their pups is likely to be a sensitive measure of their condition. The Unit has been monitoring this parameter for a group of individually-identifiable animals at these colonies for more than a decade. Although female condition has fluctuated from year to year, there is, as yet, no evidence of a trend in condition with time.

Minimum Population Size to Ensure a Satisfactory Conservation Status

EC Directive 92/43/EEC on the conservation of natural habitats and of wild fauna and flora aims, amongst other things, to ensure the favourable conservation status of 632 species of animal and plant, including the grey seal which is listed on Annex IV (species of Community interest). A species' conservation status is considered to be "favourable" when: the population dynamics data indicate that it is maintaining itself on a long-term basis as a viable component of its natural habitat; the natural range of the species is neither being reduced nor is likely to be reduced in the foreseeable future; and there is, and probably will be, a sufficient large habitat to maintain its population on a long term basis. The primary means of achieving this is through the establishment of a network of Special Areas for Conservation (SACs) for each species. Such requirements have clearly been framed for species which are at low levels, and for populations which are declining

or increasing very slowly. However, the fact that grey seal numbers have increased steadily over the last three decades suggests that any population size within the range observed during that period will be sufficient to ensure favourable conservation status, provided there is no reduction in the extent of suitable habitat or change in the factors which are likely to affect abundance. This can be achieved by establishing a network of SACs which covers the documented range of the species and which are imbedded within a larger healthy population. The target population size of 35,000 for the abortive grey seal culling programme of 1977 and 1978 was set by the Scottish Office on the basis that few complaints about seals were received from fishermen in the mid-1960s, when the population was at this level.. NERC provided advice on how this target could be achieved without prejudicing the species' conservation status.

Grey Seal Abundance and Salmon Mortality

The fact that at-sea mortality of salmon in the River North Esk has not declined although the high seas fishery has been virtually eliminated is clearly a cause for concern to Scottish salmon fishermen. As the Salmon Advisory Committee has recognized, the fact that total seal numbers have increased over this period does not necessarily mean that seals are responsible for all, or even part, of the increase in mortality. SMRU's studies of the movements of grey seals have shown that seals from the Farne Islands, the Isle of May and the Moray Firth visit the coast around the North Esk and may be responsible for some of the at-sea predation on salmon from this river. The number of seals (as indicated by pup production) associated with these colonies was relatively constant between 1972 and 1985, but numbers have increased by 50% over the last decade (see Table 4). If the component of at-sea mortality which is not explained by known catches in coastal and high seas fisheries shows the same pattern, this would add weight to the argument that seals are responsible.

As we indicated in 1995, more research on the response of seals to changes in the availability of their preferred prey is required before it will be possible to provide robust advice on the likely effect of changes in seal numbers on fish stocks. SMRU has now received funding from the European Commission for a major collaborative study (which involves the Marine Laboratory in Aberdeen and the Danish Institute for Fisheries Research, amongst others) of the effect of the industrial fishery for sandeels on the Wee Bankie in the Firth of Forth on sandeel predators. This should provide information on the effect of changes in the abundance of preferred prey on the diet of grey seals, because catches on the Wee Bankie vary greatly from year to year. However, the situation in the North Esk also provides a good opportunity to investigate the response of seals to changes in the availability of salmon in a confined area. The Salmon Advisory Committee has also recommended further research along these lines and there may be an opportunity for a joint approach by NERC and the SO to this problem.

TABLE 5: Estimated size of the population associated with all major grey seal breeding sites in Scotland and eastern England, except Loch Eriboll, Helmsdale and the Shetlands. Estimates refer to the number of seals of age 1 and over at the time of the breeding season.

YEAR	Pup Production	Female Population - New Method	Female + Male Population - New Method	Female + Male Population - Old Method
1984	14970	25696	44835	48011
1985	16246	27477	47943	51526
1986	17770	29459	51422	55362
1987	19005	31561	55111	59597
1988	18260	33858	59156	64115
1989	20043	36046	62945	68198
1990	21351	38457	67133	72749
1991	24230	41034	71608	77583
1992	27334	43923	76650	83247
1993	28541	47032	82094	89814
1994	29355	50305	87816	96577
1995	30932	53766	93862	103609

Legends to Figures

- Figure 1. Estimates of the size of the total female grey seal population associated with all major breeding colonies in Scotland and England (except Loch Eriboll, Helmsdale and the Shetlands) from 1984 to 1995, with the predicted and observed pup productions over the same period.
- Figure 2. Trends in pup production at the major grey seal breeding areas since 1984. Production values are shown with their upper and lower 95% confidence limits, where these are available. These limits assume that the various pup development parameters which are involved in the estimation procedure remain constant from year to year. They therefore underestimate the total variability in the estimate, but they are useful for comparison of the precision of the estimates in different years.
2a. Orkney, Inner Hebrides and Outer Hebrides. 2b. Farne Islands and Isle of May.
- Figure 3. The location of the main grey seal breeding sites in Britain
- Figure 4. Distribution of the number of grey seals hauled out in Scotland as revealed by surveys for common seals conducted in the summers of 1988-1993.
- Figure 5. Distribution and size of grey seal populations in the North Atlantic.

**SCOS 96/2
ANNEX I
APPENDIX 1**

**THE USE OF AERIAL PHOTOGRAPHY TO MONITOR PUP
PRODUCTION OF GREY SEALS (*Halichoerus grypus*) IN
SCOTLAND**

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Summary

1. Grey seal pup production can be effectively monitored using aerial photography combined with stochastic modelling of the birth process and the development of pups. The resulting time series can provide evidence of temporary or longer term changes in demographic rates.
2. We use this approach to generate a time series of pup production estimates for the major grey seal colonies in Scotland over the last 34 years. Pup production has increased at an average rate of 4% per year over this period, but the time series also shows the effects of a number of different historical events. The rate of increase appears to have been reduced over the last two years.

Introduction

Approximately 40% of the world population of the grey seal (*Halichoerus grypus*) breeds on 37 widely dispersed sites (Fig. 1) around the British Isles (Reijnders et al. 1993). The total number of births at these sites (known as the pup production) has been monitored since the 1960's using aerial photographic survey. Each year, and at each site, a series of flights is carried out during the breeding season. The entire site is photographed on each flight so that all the pups present can be counted from the photographs. This paper describes how the counts are used to estimate pup production, including the number of pups born after the last flight of the series. We use this approach to generate a time series of pup production estimates for the British grey seal population over the last 34 years.

Although the main reason for monitoring pup production has been the estimation of total population size, the production estimates themselves provide a more sensitive indicator of demographic fluctuations than population size itself. This is because pup production can be estimated more accurately than total population size and, for long-lived animals like grey seals, individual fecundity should be more variable than survival (Stearns 1992). Thus the effects of changes in food availability, disease or anthropogenic factors (such as disturbance at breeding sites) should be evident as deviations from the long-term trend in pup production. These figures should also respond to changes in population age structure or distribution resulting from management culls. We use the time series of pup productions at British colonies to illustrate these effects.

Even when a species pups colonially at a limited number of sites, there is rarely - if ever - a time when the total number of pups born can be counted on a single visit (Erikson et al. 1993). The number of pups present at any time is determined by the birth rate up to that time and the rate of disappearance. It is not possible to determine which of the pups visible on a photograph were already counted on earlier flights so, to estimate production, the birth rate has to be inferred from the counts and integrated over the duration of the season. Birth rate can be estimated by fitting the count series to an underlying statistical model of the way in which the number of pups varies through the pupping season (Rothery and McCann 1987, Hiby et al. 1988). Pup production can only be estimated from a single count if the timing of the season and other parameters of the model are known and can be assumed to remain constant (Summers 1978, Rothery and McCann 1987).

Survey Methodology

Details of the survey and photo-analysis techniques used are described in Hiby et al. (1988). The essential features are: a minimum of four flights over each site are conducted each year to trace the rise and fall of pup numbers during the breeding season; the photographs provide complete coverage of the breeding site; the image quality is sufficient to allow pups to be distinguished from adult seals, gulls, sheep and rocks, and to allow them to be classified into one of two developmental stages. Since 1985 colour transparency film has been used on all flights, facilitated by the development of an image-motion-compensated camera mount (Hiby et al. 1987). This, and the use of pre-focusing to the mean survey height, has provided spatial resolution to about 5cm on the ground. The use of colour film has allowed a proportion of pups which have moulted their natal coat to be distinguished from pre-moulted "whitecoat" pups (see below). Since 1993 pups feeding from their mothers have also been counted on all photographs.

Each site has been photographed at least four times each year since 1991, usually at intervals of about 10 days. However, the number and timing of flights has been extremely variable over earlier years. To maintain the integrity of the series, the estimation technique must be able to cope with the limited series of counts.

Estimation Procedure

In the estimation procedure, variations in birth *rate* over the pupping season are modelled by a probability density function (pdf) for birth *date* times the estimate of total pup production at the site. Because the distribution of births may be skewed, three parameters are required to define the birth date pdf. Thus at least four counts are required to estimate pup production. At least one more is required to estimate confidence limits. There are not enough counts for most sites in most years to allow the required parameter estimation, so counts need to be divided into stages. The use of staged counts to estimate seal pup production is well established (Radford et al. 1978, Myers & Bowen 1989). However, in this case, the need to identify stages from photographs created special problems. Although five developmental stages have been defined for grey seal pups (Boyd et al. 1962) it is only practical to distinguish two from aerial photographs: whitecoat (including partially moulted) and fully moulted.

A pdf for birth date

Birth rate can be directly observed using a series of ground counts in which pups are dye-marked to distinguish them from pups born subsequently. When the numbers of pups born during each inter-count interval are plotted over time (Fig. 2) they provide an illustration of the underlying pdf of birth date. The curves are usually unimodal, so relatively few parameters are required to define the pdf. Minor fluctuations, as in the plots for the Farnes sites, may be due to weather conditions influencing the choice of adjacent sites by pregnant females. However, data from North Rona in 1972 (Fig. 3a) are bimodal, even when subareas of the site are plotted separately (Fig. 3b). The nearest alternative sites are over 100km away, so the interruption in birth rate is less likely to be due to changing site preferences. Another possible explanation is that North Rona contains more than one group of seals showing some inter-dependence in birth timing. Recent DNA studies (Amos et al. 1995) have shown that matings in successive years between the same seals are more common than expected by random association, so perhaps non-random associations between females also occur.

Interpretation of the observed birth rate patterns is complicated by the marked fidelity of female grey seals to breeding site (Pomeroy et al, 1994). The effect of an event on the distribution of births, whether in time or space, may carry over for a number of years. Over that time it may be confounded with other events. For the purpose of estimating total production the birth date pdf does not need to incorporate such complexities as long as it is able to accommodate whatever changes in distribution may occur from time to time. As a minimum, it must allow for changes in spread and location of the birth curve. Some observed distributions are skewed to the right so the model also needs to accommodate a varying degree of skew. The lognormal was chosen for the birth date pdf

$$f(x) = \frac{1}{x\sqrt{2\pi}\sigma} \cdot \exp\left(-\frac{1}{2\sigma^2}(\ln x - \mu)^2\right)$$

μ and σ give the mean and variance of x as $\exp(\mu + \frac{1}{2}\sigma^2)$ and $\exp(2\mu + \sigma^2)\{\exp(\sigma^2) - 1\}$, whereas the median is simply $\exp(\mu)$. A third parameter ψ marks the start of the season, providing the link between x and the birth date, so that the pdf with respect to birth date, t , is given by the lognormal

density with x replaced by $(t - \psi)$. Births start from day ψ in that the probability density is zero before then. If ψ is much less than the mean of x the density is almost symmetrical, whereas if ψ is only a few days less the density is heavily skewed to the right.

Developmental stages.

The four parameters of the birth curve are estimated by matching expected counts of whitecoat and moulted pups to the observed counts on each flight. For a given set of parameter values, the expected number of whitecoat pups is the integral, from ψ to the time of the flight, of the birth rate at time t times the probability that a pup born at time t will still be visible as a whitecoat. That age-dependant probability has been calculated from data on known-age pups collected from 1985 to 1987 at the Isle of May (Wylie, 1988). The age at which surviving pups completed their moult was found to be normally distributed with a standard deviation of 5 days about a mean of 23 days. Mean age at moult was not found to differ significantly between years.

The age at which surviving pups left the breeding site was also normally distributed with a standard deviation of 7 days about a mean of 31.5 days. The ages of moulting and leaving were found to be uncorrelated, so that the probability a pup contributes to the moulted count for a given flight is simply the probability it has not left times the probability it has moulted by the time of that flight. The probability it is present as a whitecoat is the probability it has not left times the probability it has *not* moulted by that time. This contrasts with the model used by Myers and Bowen (1989) in which the durations of successive stages are uncorrelated - for our data age at moult and age at leaving are uncorrelated so the duration of white and moulted stages are negatively correlated.

Misclassification of pups

The classification of pups in photographs as whitecoat or moulted is subjective. However, it is unlikely that a whitecoat will be classified as moulted whereas some moulted animals may appear so pale that they are classified as whitecoats. In order to determine the extent of this misclassification bias, staged counts were made at visits to seven pupping sites in Orkney in 1994. Only 55% of moulted pups recorded during these counts were classified as moulted in the aerial photographs.

The expected whitecoat count for a given flight is thus increased in the model by including a proportion of misclassified moulted pups. The expected count of moulted pups is reduced accordingly. Misclassification may result from the colour of the moulted pelage, the position in which the pup is lying, and the light conditions when the photograph was taken. It may therefore vary between flights. The replicate estimates of misclassification proportion obtained from the seven Orkney sites had a standard deviation of 0.07. This number has been used to introduce an extra variance component for the counts of whitecoats and moulted pups, as described below.

Pup mortality

Mortality of pups is, to some extent, irrelevant to the estimation procedure so long as dead pups remain visible in photographs and are counted. Pups classified as dead on the photographs (as judged by posture, blood-stained pelage and gulls feeding on pups) are included in the whitecoat counts, which are then increased by a further 5% to allow for rapid disappearance of some dead pups. Pup mortality should not, therefore, lead to an underestimate of production. Mortality could lead to overestimation by causing an accumulation of whitecoats on the site which would have moulted, had they survived. However, this effect should not be significant given the apparently low mortality rates on the sites. Measured mortality rates for grey seal pups vary substantially between sites (Baker, 1984) but this may be partially due to the presence of the observers. A single ground count carried out towards the end of the season in 1994 at seven sites in the Orkneys found only 2.7% dead pups among the 5247 counted. Aerial photographs over all undisturbed sites show an average of 3.4% dead pups.

Additional checks

In order to check whether values used for mean time to leave, time to moult and misclassification proportion were consistent, the number of flights was increased to a minimum of six per site in 1993. Furthermore, an independent age-related classification was introduced. Suckling mother/pup pairs can be readily identified on the photographs and, starting in 1993, these were counted as an indication of the number of pups in the pre-weaning stage.

The proportion of time pups spend feeding was estimated from data collected at North Rona in the Outer Hebrides from 1987 to 1989 (SMRU, unpublished data). A study site containing about fifteen pups was monitored by scan sampling. The activity of every known-age pup visible was noted on each scan. Figure 4 shows the decline with age in the number of observations made for

each pup. It provides an estimate of 18.5 days as the mean age at weaning. Figure 5 shows the proportion of scans on which feeding was noted, again plotted as a function of age. Here feeding is defined as the pup being on the nipple, whether or not it was actively sucking. It is thus equivalent to the activity recorded from the aerial photographs. Figure 5 provides an estimate of the probability a pre-weaned pup is feeding at any time during daylight hours; it appears to increase linearly with age: $P(\text{feeding}) = 0.014 + 0.0034 \times (\text{age in days})$. Multiplying this value by the probability a pup of a given age is unweaned thus gives the unconditional probability that a pup of that age will be feeding at the time of a survey flight. Integrating birth rate times this probability from ψ to the time of the flight then gives the expected count of feeding pups.

The expected counts corresponding to the Rona data are consistently higher than those observed on the aerial photographs, possibly because of the high proportion of experienced mothers on the Rona study site. The estimation model thus includes an adjustment factor to reduce the expected number of feeding pups, which represents the sixth and final parameter defining the expected counts.

Maximum likelihood (ML) estimation of model parameters.

Maximum likelihood is used as the fitting criterion for the estimation model, for efficiency and to derive confidence limits for total production (PR) using the likelihood ratio method. The vector of counts is assumed to have a multivariate normal density, defined by a vector of expectations and matrix of variances and covariances. So if, for example, four flights were completed over a given island and whitecoat, moulted and feeding pups were counted on each flight then the vector of expectations has twelve elements.

The calculation of the expected counts has already been described. The variances and covariances (for example, the covariance between the number of whitecoats on the first flight and moulted on the third flight) are calculated by assuming, in the first instance, that birth, weaning, moulting and leaving are independent processes for the different pups sharing the site. Probabilities such as $P\{W_1M_3\}$ are then calculated. $P\{W_1M_3\}$ is the probability that a pup is present as a whitecoat on the first flight and as a moulted pup on the third flight. It is obtained by integrating, from ψ to the time of the earlier flight, the pdf for birth at time t , times the probability a pup born at t is in the specified stages at the times of the earlier and later flights. That probability depends on the ages the pup would attain by the times of those flights and on the parameters governing moulting and leaving. In this particular example it

requires that the pup has not left by the time of the third flight and moults sometime between the first and third flights. Alternatively, it may moult before the first flight and then be misclassified. Following this notation $P\{W_1W_1\}$ is simply the probability a pup is present as a whitecoat on the first flight (so the expected count of whitecoats on the first flight is $P\{W_1W_1\} \cdot PR$). The required covariance is then

$$(P\{W_1M_3\} - P\{W_1W_1\} \cdot P\{M_3M_3\}) \cdot PR$$

The rest of the covariance matrix is calculated similarly.

Having defined the expectations and covariances in this way it is straightforward to calculate the probability density of the vector of observed counts and maximise with respect to the various parameters. It is necessary to maximise iteratively except that the ML value for PR is available as a function of the other parameters at each iteration. Confidence limits on the production estimates are also straightforward to calculate. They are the values for PR above and below the ML estimate for which the log of the maximum likelihood with respect to the rest of the parameters is $\chi^2_{1,05}/2.0$ less than its overall maximum.

The assumption that the birth and development processes are independent for different pups is not justified. As mentioned previously, observed birth curves are more noisy than expected by binomial variance, given the number of pups produced. There are also indications of dependence in leaving time from the studies of known-age pups on the Isle of May. As a result the theoretical variances calculated for pup counts as described above are smaller than the scatter of observed counts about the fitted curves would indicate. To remedy this, and obtain realistic confidence limits for PR, the covariance matrix is scaled by an extra free parameter added to the set used to iteratively maximise the likelihood. The calculations described above thus determine only the *relative* magnitude of the covariances. The average absolute magnitude is determined by the fit of the expected to observed counts. The size of the scaling parameter can be interpreted as a sort of mean interdependent group size. For example, if all births were twins which completed all developmental stages in parallel the expected size of the scaling factor would be 2. In addition to this scaling, the variances and covariances relating to the whitecoat and moulted counts are increased to allow for variation in the misclassification proportion. First derivatives of the expected counts with respect to that proportion are calculated numerically. This vector of derivatives is then post-multiplied by its transpose and the resulting matrix multiplied by the variance of the misclassification proportion to give the additional variance and

covariance components required. The effect of this modification is to reduce the weight assigned by the model to the whitecoat and moulted counts as compared to the counts of total pups.

Estimates of Pup Production

The results for the most extensive set of flights, in 1993 and 1994, are considered first. The model was applied to large sites only, to avoid using very small counts of feeding pups. Figure 6 shows the results for the largest, Ceann Iar in the Outer Hebrides, with maximum counts of approximately 5,000 pups. The likelihood for counts of whitecoats, moulted and feeding pups was maximised in each case with respect to all the parameters of the birth curve, the misclassification proportion, the mean time to leave, the feeding rate adjustment and the variance scaling.

The model appears to provide reasonable fits to the data, suggesting that the parameter values are consistent. The mean age of leaving over the sites was 32.5 days, which is close to the estimate of 31.5 days from the Isle of May data. The mean estimate for the proportion of moulted pups correctly classified was 0.56, in close agreement with the value of 0.55 from the Orkney ground counts

A reduced model, not involving counts of feeding pups, was then used to generate the trajectory of production estimates for each site from 1987 to 1994.

Survey flights before 1987 were designed to locate a peak total pup count which was multiplied by a scaling factor to give the production estimate (Summers 1978). They are not directly comparable to the ML estimates. The scaling factors, which were derived from series of ground counts on selected islands, were 1.5 and 1.6 for the Orkneys and Outer Hebrides respectively, and 1.8 for North Rona. These values are higher than the peak count to production ratios suggested by the current estimation model. One reason for this is that pup mortality on the selected sites was high and the peak counts used to define the ratio were for live pups. It was assumed that dead pups would disappear rapidly and not be counted on the aerial photographs. Recent results suggest mortality is low on undisturbed sites and that dead pups do not disappear rapidly.

In order to affect a comparison, the peak count to production ratios for years before 1987 have been estimated from the 1987 to 1994 results. There are two possibilities with respect to deriving ratios from the current estimation model. One is to use the ratio of estimated production to the actual highest count of

total pups. The other is to use the maximum expected count from the model on the grounds that flights before 1987 were more efficient at locating the peak than recent flights, which were more widely spaced in time. The former option has been used, recognising that this might give a small upward bias to the ratio. The average ratio for each site from 1987 to 1991 was used. Post-1991 ratios were not used because these have increased recently as a result of an increase in the spread and skew of the birth curve (Figure 7). Pre-1987 peak counts, multiplied by these revised ratios, gave the production estimate trajectories illustrated in Figure 8.

Confidence limits

Confidence limits on production estimated for a group of sites depend on how many sites are in the group and how many other model parameters are to be estimated from the counts. Total production for large groups of sites, such as the Outer Hebrides or Orkneys, is normally of interest and the total production for all sites is needed to estimate population size. Combining confidence limits calculated for individual sites is not straightforward because errors for different sites may not be independent. However, the coefficient of variation (CV) for a group will certainly be less than that for any one of its components. The CV estimated for production at Ceann Iar was 7% (see Figure 6). The CV on the total production estimated for all sites is thus less than 7%, and is only a minor component of the CV on estimated all-age population size (Hiby, unpublished data).

The CV's on trajectories of relative production in Figure 8 should also be less than 7%. Although fewer flights were carried out each year before 1993, we assumed that mean age at leaving was constant over this period. This was on the grounds that, unlike birth rates, parameters relevant to pup development should not change from year to year and hence comparison of production from year to year should not be affected by uncertainty about those parameters. The figures suggest that a 19% change in production between any 2 years would be detectable with type I error less than 5%.

Interpretation of time series

Figure 8 shows a discontinuity in the Orkney time series from 1982 to 1984, probably due to the move from monochrome to colour film. On certain sites, boulders look like whitecoat pups on monochrome photographs. There is also some indication of the same effect in the Outer Hebrides series, but there the cull in 1977 (Harwood and Greenwood, 1985) may have led to a drop in production in the early 1980's. The immediate effect of the cull on production in 1977 and subsequent years is obvious and is larger than would be expected purely as a result of the number of breeding females killed.

In Figure 9, the Orkney and Outer Hebrides production estimates are shown again for the period 1984 to 1994, along with those for the Isle of May and Inner Hebrides sites, which were not surveyed before 1984. The figure shows a drop in total production in 1988 with recovery by 1992. The phocine distemper epidemic, which affected a large proportion of common seals (*Phoca vitulina*) breeding in Europe occurred in 1988. No increase in grey seal mortality was evident at that time but these figures suggest that there was an effect on fecundity or age at first breeding.

Figure 9 indicates a slowing down over the last two years in the rise of total production, following a particularly rapid increase up to 1992. Figure 7 shows the effect of an increase in the spread of the birth curve since 1992. Such apparent changes in estimated production depend on the assumption that mean time to leave has not changed over the same period. To check this the model was rerun from 1987 to 1994, fitting to whitecoat counts only. Counts of moulted pups were used only to provide model predictions of the component of the whitecoat count resulting from misclassification of moulted pups. The model was thus conditional on moulted pup counts and independent of the value of the time to leave parameter. The trajectories were more noisy than those obtained with the full set of counts, but show the same patterns.

Figure 9 does not show how the increase in production in each island group is distributed between the sites. Production has not changed in parallel on different sites. For example, in the Outer Hebrides, sites on the Monach Isles accounted for less than half of total production in 1984 and about two thirds in 1993. In the Orkneys sites which accounted for a third of total production in 1987 have not increased at all in recent years, so that by 1993 they contributed only a sixth of the total production in that region..

Figure 10 shows the production estimates for North Rona which, as a large and isolated breeding site, was treated separately from the rest of the Outer

Hebrides. The declines in production coincide with periods of research work carried out at North Rona (1985 to 1989, and 1993 to 1994) and suggest the monitoring technique is sufficiently sensitive to reveal the effect of disturbance on production.

These differences mean that it is not possible to monitor total production by counting only a few, currently important, sites. To reduce cost the frequency of surveys rather than their spatial coverage should be reduced. In fact the surveys need to include potential sites as well as those currently used for breeding because newly colonised sites can increase rapidly in size. If a new colony is not included in the estimate of total production until it is of significant size the rate of increase in total production will be overestimated. Calf of Eday and Copinsay are two sites in the Orkneys which were not used for breeding before 1990 and had grown to 7.5% of total production by 1993.

Another possible way to reduce the cost of monitoring is to estimate the number of pups present on each site by sampling rather than complete coverage of the areas used for breeding. However, that option was rejected because of the highly contagious distribution of pups. In these circumstances, sampling leads to a large increase in the variance of the production estimate unless the sampling units can be kept very small, which is impractical for aerial survey.

Acknowledgements

We would like to thank Mike Fedak, John Harwood and Paddy Pomeroy of the Sea Mammal Research Unit for their invaluable help in preparation of the manuscript.

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Figure legends

Figure 1. Location of grey seal breeding sites in Britain.

Figure 2. Variation in birth rate for grey seal pups at four different breeding sites, based on through-count data.

Figure 3. Variation in birth rate of grey seal pups at North Rona: (a) total births (b) births occurring in non-adjacent subareas.

Figure 4. The number of behavioural data scans of known-age pups obtained at the North Rona study site from 1987 to 1989.

Figure 5. The proportion of scans of unweaned pups at the North Rona study site on which feeding was recorded.

Figure 6. Observed and expected pup counts for the Ceann Iar breeding site in 1993. w , m and s are the counts of whitecoat, moulted and feeding pups on each of six flights (s is scaled by ten). Continuous curves give the expected numbers corresponding to ML estimates of the birth and development parameters.

Figure 7. Total production estimated for all breeding sites in the Outer Hebrides (upper curve) and the sum of the maximum counts obtained at the same sites (lower curve). Pre-1987 productions were obtained as a multiple of the maximum counts.

Figure 8. Total production estimated for all sites in the Outer Hebrides and the Orkneys since the 1960's, when regular monitoring began.

Figure 9. Total production estimated for all sites in the Inner and Outer Hebrides, the Orkneys and the Isle of May from 1984 to 1994.

Figure 10. Total production estimated for North Rona from 1984 to 1994.

**SCOS 96/2
ANNEX I
APPENDIX 2**

**POINT AND INTERVAL ESTIMATES FOR COMPONENTS OF THE
GREY SEAL POPULATION IN SCOTLAND AND EASTERN
ENGLAND.**

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Introduction

The number of pups born at most of the grey seal breeding sites in Britain has been monitored annually since the 1960's, mainly by aerial photographic survey (Hiby, Duck & Thompson, 1995). This paper describes how the estimates of pup production are currently used to estimate all-age population size. The size of the British grey seal population in a particular year is defined here as the number of seals which were born at any British breeding site and which are still alive just before the breeding season. The breeding population is assumed to be closed to immigration and emigration. The term "population" is not meant to imply any degree of genetic or behavioural similarity between individuals. The genetic differences observed between colonies (Allen et al., 1996), the consistent differences in mean pupping date between breeding sites, and the fidelity of individual seals to breeding and resting sites (Pomeroy et al., 1994; Hiby, 1995) all suggest that mixing between sites is limited in most years.

A variety of data sources can be used to monitor the number of grey seals living around the British Isles. Although the main source is the sequence of pup production estimates, a number of other types of information are also available. Some, like the size of pup culls carried out in the 1960's, are required to accommodate subsequent fluctuations in the production sequence. Others, such as the age structure and pregnancy rate of seals sampled at the Hebrides and the Farne Islands (Boyd, 1985), provide information on parameters such as fecundity and survival. There are also observations which, though not incorporated in the present study, could be used to relax some of the assumptions inherent in the current estimation procedure or to increase the precision of the estimate. Examples are the counts of the numbers of grey seals hauled out in summer obtained during aerial surveys for common seals (Duck et al., submitted) or variations in return rates to particular sites obtained from capture-recapture analysis of sightings of individually-recognizable animals (Hiby, 1995).

Raftery et al. (1995) developed a Bayesian approach to the estimation of the abundance of bowhead whales off Point Barrow, Alaska based mainly on acoustic detections but also using a variety of other types of relevant information. This information is summarised as a vector of inputs (θ) to a population dynamics model which generates a vector of outputs ϕ . Normally, one or more functions of the θ and ϕ (such as total abundance in a given year) are of particular interest. Prior belief about the model inputs and outputs is summarised as a *premodel distribution*, which is restricted to the *postmodel distribution* by the deterministic population dynamics model, p which links θ and ϕ (ie $\phi = p(\theta)$).

The problem of monitoring grey seal abundance can be addressed within this framework. Estimates of age-specific fecundity and survival, and an initial population vector of numbers-at-age, are inputs. A Leslie matrix model then gives pup

productions and later population vectors as deterministic functions of the inputs. However, I have chosen a different approach because I was not confident of assigning appropriate prior distributions to all inputs. For those which can be estimated by sampling, such as fecundity (estimated from the proportion of pregnant females), an appropriate prior distribution is obvious. But for juvenile survival, in particular, no information exists other than that implied by combining the population dynamics model with the remaining information. It is therefore unclear how a prior distribution for juvenile survival (and its variation from year to year) can be defined.

My approach involved constructing a stochastic model linking the observed pup production estimates to all other sources of information. Three components of the model were recognised: a vector of parameters defining the probability distributions used; a vector of observable random variable outputs (such as the pup productions and number of pregnant females in a sample); and one or more unobservable outputs of particular interest (such as the final total female population size or its growth over a given interval). The objective was to obtain point and interval estimates for the unobservable outputs given the observable outputs. This involved first obtaining maximum likelihood estimates for the parameters. The probability density function (pdf) for the observable outputs forms the likelihood function for the parameters. Then the conditional pdf for the unobservable outputs, given the observable outputs and parameter estimates, was derived. Finally this was multiplied by the asymptotic pdf for the parameter estimates and integrated over the feasible parameter space to generate the density of the unobservable outputs conditioned only on the observable outputs.

Defining the pdf for all the outputs involves running repeated simulations and using the results to approximate the densities. Obviously the results should not depend on the random number sequences used to drive the simulation, which means using many repeats and relatively long computer runs. However, an advantage of this approach is that it allows extra observations such as the haul-out counts mentioned above to be readily incorporated, because extending the simulations to cover extra variables is usually straightforward.

The motivation for this work was not so much to derive a "best" estimate of grey seal abundance as to provide reliable estimates of confidence limits. In common with most other monitoring exercises, the upper or lower confidence limit on the variable of interest may be more relevant to management decisions than a point estimate. For example, in considering grey seals in relation to commercial fisheries, it is probably more useful to be able to state that grey seals consume no more than x tons of a given fish species than to provide a point estimate. This study illustrates one way of assigning such limits. It shows that they may depend critically on sources of information not normally sought in deriving the point estimate - in this case year-to-year variation in juvenile survival.

Methods

The basis of the stochastic model is a Leslie matrix using age-specific survival and fecundity values to generate a vector of abundance-at-age values for female grey seals and a prediction of the total pup production in each year. Nine age-class frequencies are recognised in the model in addition to the pups: the number of females at each age from one to eight, and the number aged nine or over. Two such models are used, one for the grey seal population at the Farne Islands before 1972 and the other for the total British population from 1984 to 1995.

Data sources

The Farnes Islands are a group of rocky islands lying off the north-east coast of England where pup production has been monitored annually since 1956 (Bonner & Hickling, 1971). Prior to culls of breeding females carried out in 1972 and 1975, there was no evidence of mixing between this site and other groups. After the culls, pup production at the Farnes declined by more than expected from the number of adult females killed, suggesting that significant emigration had occurred. Some Farnes seals moved to the Isle of May (in the Forth estuary) where the breeding population grew substantially in size from the late 1970's onwards. Only a few pups had been born each year at the Isle of May before 1972, so until then the Farnes was several hundred km from the next nearest breeding site. I have assumed that all seals born at the Farnes before 1972 returned to breed there, and that all seals breeding at the Farnes before 1972 were born there. Under this assumption, it is possible to fit to the pup production estimates at the Farnes, which are based on frequent and virtually error-free counts, using a Leslie matrix model for an isolated population. Furthermore, the culls themselves provide data on survival and age at recruitment for that same population.

Series of production estimates also exist for other breeding sites in the British Isles, but it is not normally safe to assume those groups are totally isolated. There may have been, and may still be, significant movements of seals between the various groups. For example, inspection of the production series for the Outer Hebrides shows that some emigration occurred after the management cull there in 1977 (Harwood & Greenwood, 1985), probably to the Orkneys. It would be possible to incorporate parameters for interchange between different groups in the model but that would be difficult, given that movements may be sporadic and age-specific. A simpler alternative is to apply the model to the total estimated production for all British sites, or at least those for which reliable annual estimates are available, so that inter-site movements have no effect on predicted productions. Thus the second Leslie matrix model is applied to the sum of production estimates for all sites in the Inner and Outer Hebrides, the Orkneys, the Isle of May, Donna Nook (near the Humber estuary) and

the Farne Islands. These sites account for almost 90% of pup production in Britain and have all been monitored consistently since 1984. Data relevant to age at recruitment for the total population, and to the pregnancy rate for recruited females, is available from a sample of females shot outside the breeding season in the Hebrides and the Farnes between 1979 and 1981 (Boyd, 1985).

The various sources of data relevant to the estimation of current population size can thus be summarised as follows:

- (1) A series of pup production estimates for the Farne Islands from 1956 to 1971, and the size of pup culls in 1963 to 1965.
- (2) A series of pup production estimates for all annually-monitored breeding sites in the British Isles from 1984 to 1995.
- (3) The age distribution of female grey seals culled at the Farnes at the end of the breeding season in 1972 and 1975.
- (4) The distribution of age at first pregnancy for females in the Farnes culls.
- (5) The proportion of females pregnant at each age in samples taken outside the breeding season from the Hebrides and Farne Islands between 1979 and 1981.

Both Leslie matrix models are defined by parameters determining adult and juvenile survival, age at recruitment and pregnancy rate, and the variation in those quantities from year to year. In addition, pup production estimates for the total population from 1984 to 1995, which are based mainly on aerial photographic counts, are subject to estimation error. This is incorporated in the second model as a CV of 7% on estimated total production.

In defining the stochastic aspects of the model it was necessary to consider which processes in the growth of a seal colony would be most effected by year to year variation. I concluded that first-year survival and age at recruitment to the breeding population would be the most variable, and variation in adult survival and pregnancy rate among older females could be neglected. It is clear that the first few weeks of a pup's life, following its departure from the breeding site, will be particularly hazardous and affected by environmental conditions and its own condition on weaning. Secondly, the observation of marked fidelity by older breeding females to exact locations on breeding sites (Pomeroy et al, 1994) suggests that variation in birth rate may result from variation in the proportion of younger females included in the breeding population. The age structure of females on recently established and rapidly growing colonies is biased to younger females (Hiby et al, submitted), suggesting that growth spurts in total production may be the result of recruitment of young females to a colony.

If first-year survival and age at recruitment are subject to year-to-year variation, those parameters are also likely to differ between the two population models. Thus, there

are four survival parameters: first year survival for the Farne Islands before 1972; first year survival for the total population from 1984 to 1995; the level of variation in first-year survival, expressed as a coefficient of variation (CV); and adult survival, considered as constant from year to year and the same for the two models. Similarly, for age at recruitment, we have mean values for both population models, a CV for year-to-year variation, and a pregnancy rate for recruited females which is constant and the same for both models. This submodel for pregnancy rate allows a young female recruited to the breeding population in a "good" year to be excluded in a following "bad" year, leading to a reduced pregnancy rate for females which have their first pup at a relatively young age. This is in agreement with the findings of Boyd (1985), but contradicts the assumption of Harwood & Prime (1978) that pregnancy rate is constant with respect to age following the age of first pregnancy. The difference in age of recruitment suggested by the Farnes cull data and the samples taken later at the Farnes and Hebrides supports the idea that age at recruitment may show both temporal and spatial variations.

Two more parameters are required to define the stochastic population models: the initial population sizes for the two models. Strictly speaking, initial numbers for each of the nine age classes are required. In practice, a single initial population size, ten years prior to the start of the estimated production series, was specified for each model. The numbers in each of the nine age classes were then set by assuming a stable age structure for a population growing at 7% per year. The effect of this assumption on the predicted productions ten years later is minimal because, by then, all the females included in the initial age vector will be fully recruited to the breeding population.

All 10 parameters were used to maximise the joint pdf for the data sources listed above - that pdf was calculated as described below. However, there is very little information in the data on the level of year-to-year variation in first-year survival. So, whereas the joint pdf was maximised with respect to the other nine parameters using an iterative scheme, the process was repeated for three different choices for the first-year survival CV, in order to illustrate the effect on the interval estimate for population size.

Joint pdf for all data sources

The joint pdf forms the likelihood function for the nine free parameters. The pdf consisted of three terms, corresponding to three independent sets of data:

1. For the Farnes productions and cull data: the numbers in successive five-year age groups, and numbers having had their first pup at age five, six or seven and over. These quantities were simulated by "growing" the model population from the initial age vector, choosing values each year for first-year survival and age at recruitment

from normal densities with the specified CVs. The simulation was repeated 500 times, and the expectations and covariance matrix calculated from the sample of values obtained. The logged production values, numbers in the 1972 cull in successive five-year age groups, and numbers having had their first pup at the three specified ages were assumed to form a multivariate normal density, defined by the vector of expectations and the covariance matrix. It is important to note that, for example, the number of culled females having had their first pup at different ages does not simply follow a multinomial distribution. All females aged, say, 20 yr in the 1972 cull belong to the same cohort, and pass through the ages at which they would be likely to be recruited to the breeding population at the same time. They do not, therefore, represent independent observations of the age at recruitment. The simulation provides realistic distributions for these values and the correlations between them, and thus realistic errors on the parameter estimates. The first term in the likelihood provides information on the initial size of the Farnes population, the mean age at recruitment for the Farnes before 1972, first-year survival at the Farnes before 1972, the variation in age at recruitment from year to year, and adult survival. Of these parameters the last two are of relevance to the total population size in that they also appear in the second term of the likelihood.

2. The pdf for the total production estimates from 1984 to 1995. This was estimated using the same code as for the Farnes production estimates, but with ages at recruitment and first-year survival drawn from densities having mean values appropriate to the total population rather than the Farnes alone. Furthermore the production values output by the model simulated the effect of estimation error by selecting values from a normal density with mean equal to the actual production calculated for that year from the model and a CV of 7%.

3. The pdf for the numbers pregnant at each age in the samples studied by Boyd (1985). This provides information on the pregnancy rate for recruited females and the age at recruitment for the total population. I assumed that the expected age at recruitment and pregnancy rate for these samples would apply to the total population, because the samples were taken at the Inner and Outer Hebrides as well as the Farnes and only a few years before the start of the pup production series. A separate simulation based on the numbers of females shot at each age in each of the years 1979 to 1981 was repeated 500 times, to generate the means and covariances for the number pregnant at each age, drawing the age at recruitment from a normal density in each year. The "age at recruitment" has been introduced as a single value for each year, implying that none of the females under that age would be pregnant. In fact recruitment in the model was not that "knife-edged", because the probability that a female of a given age was recruited in a given year was calculated using a normal ogive centred on the age at recruitment, instead of a step function. The standard deviation was 0.5 years so that if, for example, the age at recruitment in a given year was 5 yr, 3% of 4 yr old, 50% of 5 yr old and 97% of 6 yr old females were recruited

in that year. This avoids discontinuities in the change in log likelihood with respect to age at recruitment, but the exact value assumed for the steepness of the ogive has negligible effect on the estimates obtained

The likelihood for all the data sources combined was then calculated by evaluating the three terms of the likelihood at the data values and parameter values at that stage of the iterative scheme. A total recalculation of the pdf at each iteration step would have taken too long, so a two-stage scheme was used. For the starting parameter values the expectations and covariances of the data were calculated as described above. At successive iterations only the expectations were recalculated, using a single run of each simulation and neglecting the stochastic variations, and the covariance matrix simply adjusted using approximate first derivatives with respect to each parameter. The likelihood was maximised with respect to the parameters in this way, then the covariance matrix was recalculated at the maximum likelihood (ML) values of the parameters and the iterative scheme restarted with this revised covariance matrix. The whole process was repeated until it converged, usually after two or three recalculations of the covariance matrix.

Point and interval estimates of unobservable variables

The method described above yields ML estimates for the nine free parameters in the model, the tenth parameter - the CV of first-year survival - being held at different values. Those values have little effect on the point estimates for the other nine parameters, but they do affect their variances. The variances were estimated by inverting the matrix of second derivatives of the log likelihood with respect to the parameters. By asymptotic properties of ML estimates, the inverse provides an estimate of the parameter covariance matrix.

Although some of the parameter estimates may be of interest in themselves, the main objective was to estimate the values of unobservable model outputs such as the total female population size in the last year of the production series. Point estimates of such quantities were obtained by exploiting the computer code used to estimate the joint pdf for all the data sources to include one or more such unobservable outputs in the pdf. The vector of expectations and the covariance matrix were extended to hold the sample mean, variance and covariances for the additional outputs. The pdf for the unobservable outputs, conditional on the values of the observable outputs (i.e. the productions, cull and pregnancy sample data), is the extended pdf divided by the original pdf. Point estimates for the unobservable outputs are the values which maximise this conditional pdf.

Maximising the conditional pdf reduces to minimising one term in the joint pdf for observable and unobservable outputs, ie. $v'\Sigma^{-1}v$ where Σ^{-1} is the estimated covariance matrix and v is the vector of residuals. This is to be minimised with respect to the

residual elements corresponding to the unobservable outputs. Denote these elements by the subvector x , so that the vector of residuals v is composed of p (the subvector of residuals for the observable outputs), followed by x . Similarly, Σ can be partitioned into submatrices Σ_1 and Σ_2 , corresponding to covariance matrices for observable and unobservable outputs, and Σ_{12} , a matrix of covariances between the two types of output. Then $v'\Sigma^{-1}v$ becomes $p'\Sigma_1^{-1}p + x'\Sigma_2^{-1}x + 2p'\Sigma_{12}^{-1}x$ which, differentiating with respect to x and equating to zero, yields $x'\Sigma_2^{-1} = p'\Sigma_{12}^{-1}$, a set of linear equations in x . Solving for x then provides residuals for the unobservable outputs which can be added to their expectations to give the point estimates.

This procedure gives vectors of point estimates, examples of which are provided in the Results section. Any set of unobservable outputs can be treated in this way, for example we can obtain a vector of production values for the total population for comparison with the production estimates used as inputs to the model. Those production estimates were subject to a known level of observation error and the model generates "best" estimates of the actual production values in the light of all other sources of data.

To obtain confidence limits on any particular estimate, we can again use the pdf for that unobservable output conditional on the observable outputs. Instead of maximising the conditional pdf, we now wish to derive confidence intervals from it, but to do that we must recognise that the conditional pdf itself depends on the values of the model parameters. That is, we have $f(x_1|x_2,\theta)$ where x_1 and x_2 represent the unobservable and observable outputs and θ represents the vector of parameters, currently at their ML values. To obtain $f(x_1|x_2)$, the pdf for the unobservable outputs conditioned only on the data, we have to multiply by $f(\theta)$ and integrate over the feasible parameter space. Asymptotic properties of ML estimates were used again to approximate $f(\theta)$ by a multivariate normal density with the covariance matrix derived earlier. Numerical integration with respect to θ then gave $f(x_1|x_2)$.

Confidence limits for x_1 can be read from $f(x_1|x_2)$ as the values of x_1 including 95% of the distribution - these correspond to values of $f(x_1|x_2)$ equal to approximately 15% of its maximum. They are 95% confidence limits in the sense that this procedure has probability 0.95 of generating an interval estimate for x_1 which includes the true value of x_1 .

Results

The following results were derived assuming a CV of 0.1 on first-year survival. The effect of increasing or decreasing this level of variation are considered later. The ML estimates for the nine free model parameters are:

Adult survival = **0.969**
 Pregnancy rate = **0.954**
 CV on age at recruitment = **0.082**

Mean age at recruitment, Farnes pre-1972 = **5.80**
 Mean age at recruitment, total population 1984-1995 = **4.91**

First-year survival, Farnes pre-1972 = **0.507**
 First-year survival, total population 1984-1995 = **0.392**

Initial number of 1-year old females, Farnes 1946 = **73**
 Initial number of 1-year old females, total population 1974 = **1441**

The diagonal elements of the following matrix give the estimated CVs of the ML estimates in the order presented above, the off-diagonal elements their pairwise correlations.

param:	1 adult surv.	2 preg. rate	3 CV of recruit.	4 recruit. Farnes	5 recruit. total	6 1-year surv. F	7 1-year surv. t	8 init. no. Farnes	9 init. no. total
1	.0183	-.0075	.0554	.1557	.0511	-.1710	-.0920	-.1143	-.0964
2		.0077	-.1082	-.0483	.0417	-.8323	-.6331	-.9357	-.6482
3			.1229	.2022	-.0513	.0436	.0392	.1207	.0365
4				.0166	-.0035	-.0251	.0110	.0926	.0102
5					.1313	-.0420	.4451	-.0466	.4806
6						.0921	.5449	.6606	.5585
7							.1478	.6034	.3660
8								.1369	.6180
9									.1455

Figures 1 and 2 show the series of pup production estimates for the Farnes from 1956 to 1968 and total population from 1984 to 1995. The model fits are shown by the continuous curves.

Production estimates for the Farnes for 1969 to 1971 have been excluded because of the effects of pup culls carried out at the Farnes in the 1963 to 1965 breeding seasons.

The effects of those culls on the age structure of the adult culls carried out in 1972 and 1975 are clearly visible in Figure 3, reproduced from Hardwood & Prime (1978). That figure suggests that most of the 1963 to 1965 cohort was missing by 1972, whereas using records of the number of pups killed and assuming 20% natural mortality of pups on the breeding beach prior to the culls (Bonner & Hickling, 1971), less than half of that cohort should have been missing. This suggests that the level of natural mortality of pups on the breeding beach was far greater than 20%, at least in the years of the pup culls, and means that it is difficult to produce a model prediction for pup production at the Farnes following recruitment of the survivors of the pup culls. If the level of natural mortality on the beach is increased to generate the effect apparent in Figure 3, then the predicted drop in production from 1969 onwards is much greater than that observed. This suggests some form of compensation, perhaps via a drop in the mean age of recruitment, which may have been very high on the densely packed breeding beaches prior to the 1972 cull. However, introducing sufficient extra parameters to model such possible mechanisms would nullify any gain in precision resulting from inclusion of the 1969 to 1971 production estimates.

Figure 4 provides point estimates for total female population size from 1984 to 1995, and point estimates for pup production in those same years, conditional on all the available data. These are, in effect, a weighted average of the input production estimates and the expectations generated by the model, part of the residual having been attributed to observation error.

Figure 5 provides point estimates for the number of females at each age-class in 1995, again conditional on all the available data, so that they do not form exactly a stable age structure. The estimates provide a basis for projection of the population into the future under various possible management regimes or assumptions concerning density-dependent mechanisms.

Figure 6 illustrates the density for the 1995 female population size estimate, following integration over the feasible parameter space. Lower and upper confidence limits of 44,000 and 64, were obtained by centring the distribution on the point estimate of 54,000. Figures 7a-c illustrate the effects of the size of the CV on first-year survival on the distribution for the 1994 female population estimate. There is a marked effect on the width of the confidence interval for population size. This is not surprising, because the estimate of total population size includes an element of extrapolation from observed productions to the pre-recruitment section of the female population in the final year. If first-year survival is highly variable, the uncertainty concerning this section of the population is bound to increase. Figure 7d illustrates the reduction in interval width that would result if the CV of the input production estimates is reduced from 7% to 3.5%.

The point estimates for female population size are listed in Table 1, along with point

estimates for female plus male population size. The procedure used to generate confidence limits on the estimate of female population size could be repeated for the female plus male population. However, the results would not be meaningful because the estimate of the male component of the population is based entirely on an assumption that the number of sexually mature males is 60% of the number of sexually mature females, and that males become sexually mature at age four. Currently, there are no data on the relative numbers of males and females in the population which could be used in the model to provide an additional term in the likelihood.

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TABLE 1: Estimated size of the population of grey seals associated with all major breeding sites in Scotland and eastern England, except Loch Eriboll, Helmsdale and the Shetlands. Estimates refer to the number of seals of age 1 and over at the start of the breeding season.

YEAR	Pup Production	Female Population	Female + Male Population
1984	14970	25696	44835
1985	16246	27477	47943
1986	17770	29459	51422
1987	19005	31561	55111
1988	18260	33858	59156
1989	20043	36046	62945
1990	21351	38457	67133
1991	24230	41034	71608
1992	27334	43923	76650
1993	28541	47032	82094
1994	29355	50305	87816
1995	30932	53766	93862

Legends to figures

Figure 1

Pup production estimates for the Farne Islands from 1956 to 1968, and expectations generated by the simulation model for the Farnes population

Figure 2

Pup production estimates for the total grey seal population of Scotland and eastern England (except Loch Eriboll, Helmsdale and the Shetlands) from 1984 to 1995, and expectations generated by the simulation model for the total population

Figure 3

The age-frequency distribution for female grey seals shot at the Farne Islands in (a) 1972 and (b) 1975. Reproduced from Harwood & Prime (1978).

Figure 4

Trajectories of point estimates for the size of the total female population from 1984 to 1995 (upper curve), pup production over the same period (lower curve) and pup production estimates input to the model (*). The trajectories were obtained at the ML estimates for all free parameters and are conditional on the realised values of all data sources.

Figure 5

Point estimates for the number of female seals at ages one to eight and age nine and over in 1995. The estimates were obtained at the ML estimates for all free parameters and are conditional on the realised values of all data sources.

Figure 6

The pdf for the estimate of female population size in 1995 centred on the point estimate of 53,766. 95% confidence limits can be read from the curve by locating points at which the relative density is approximately 15% of its maximum value, i.e. about 1.2 on the scale used in the figure.

Figure 7

Comparison of the pdf for the estimate of female population size in 1994 at different levels of for the coefficient of variation in first-year survival. (a) $CV = 0.1$, (b) $CV = 0.05$, (c) $CV = 0.2$, (d) $CV = 0.1$, but the level of error in the estimates of total production used as inputs to the model reduced from 7% to 3.5%.

**SCOS 96/2
ANNEX II
APPENDIX 1**

**USING THERMAL IMAGING TO DETERMINE THE ABUNDANCE
AND DISTRIBUTION OF COMMON SEALS (*Phoca vitulina* L.) IN
SCOTLAND DURING THEIR AUGUST MOULT.**

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SUMMARY

1. Aerial surveys were used between 1988 and 1994 to carry out the first complete survey of all the main areas used by harbour seals in Scotland during the annual moult from 27 July to 13 August. Surveying was restricted to within two hours of low tides occurring between 0930 and 2100hrs BST.
2. Rocky haul-out sites along the entire north, west and island coasts were surveyed using an area-scanning thermal imager mounted in a helicopter. Haul-out sites on sandbanks in the Firth of Tay and Moray Firth, on the east coast, were surveyed using conventional aerial photography from a fixed-wing aircraft.
3. The minimum number of harbour seals in Scotland is estimated to be 26,397. 24,700 harbour and 13,100 grey seals were counted during 80 hr of helicopter survey time along approximately 7,400km of rocky coastline. 1,700 harbour and 2,450 grey seals were counted on east coast sandbanks during 2 hr of fixed-wing survey time.
4. A helicopter-mounted thermal imager allows seals along complicated coastlines to be surveyed rapidly and accurately. The imager will readily detect every seal hauled-out so all survey effort can be concentrated on counting the groups which have been located. Areas devoid of seals can be surveyed rapidly, yet thoroughly.

INTRODUCTION

Prior to 1988, British harbour seal (*Phoca vitulina* L.) populations were surveyed during their breeding season, in June and early July (Bonner, Vaughan & Johnston, 1973; Anderson, 1981; Vaughan, 1983). Surveys were conducted from small inflatable boats and seals hauled-out were counted with the aid of binoculars. Not only were these surveys time consuming, but subsequent studies of harbour seal haul-out behaviour have shown that the largest and most consistent numbers of seals haul-out during the annual moult (Thompson & Rothery, 1987; Thompson *et al.*, 1989), which takes place shortly after the breeding season. In addition, boat surveys are highly dependent on favourable weather conditions.

In Scotland, harbour seals are found along sheltered parts of the coast where they haul-out onto sandbanks and on bare or seaweed-covered rocks. On sandbanks they are conspicuous and can be easily counted using conventional aerial photography (Summers & Mountford, 1975). However, on rocky sites seals can be very difficult to detect, as a result visual surveys are time consuming. In addition, groups of seals are widely dispersed along the extensive Scottish west coast, makes conventional photography an impractical survey technique (Vaughan, 1983).

In this paper we describe the use of a thermal imager to carry out the first complete survey of harbour seals in Scotland during the annual moult. Although thermal imaging is widely used in industry and medicine, it has not been widely used for surveying wild animals. A number of trials using infrared line-scanners mounted in aircraft to census white-tailed deer (*Odocoileus virginianus*) (Croon *et al.*, 1968; Graves, Bellis & Knuth, 1972; Wyatt, Triverdi & Anderson, 1980) and sandhill cranes (*Grus canadensis*) (Sidle *et al.* 1993) have been reported. Boonstra *et al.* (1994) used an area-scanning thermal imager to survey individual red squirrels (*Tamiasciurus hudsonicus*), Arctic ground squirrels (*Spermophilus parryii*), snowshoe hares (*Lepus americanus*) and meadow jumping mice (*Zapus hudsonius*) and their nests or burrows. Seals hauled-out in the intertidal zone which is exposed at low tide are easily detected using thermal imagery because their body surface is warm relative to the substrate on which they are lying. This is especially the case while they are moulting.

METHODS

Surveying techniques

Two methods of aerial surveying were used during this study. The rocky coast of north and west Scotland and the Scottish islands were surveyed from a helicopter (Aerospatiale AS 350B Squirrel) using a Barr and Stroud IR 18 Thermal Imaging Sensor. East coast sandbank haul-out sites in the Firth of Tay and the Moray Firth were surveyed from a Piper Chieftain Navajo aircraft using a Linhoff Aerotechnica

aerial camera mounted in an Image Motion Compensating cradle (Hiby, Thompson & Ward, 1988) with 126 mm Agfa® Aviphot Chrome 200 PE1 (ISO 200) colour reversal aerial film.

The IR18 Imager is sensitive to infrared radiation with a wavelength between 8 and 14 μm , the wavelength emitted by mammals. The Imager operates using a high-pressure pure-air cooled cadmium mercury telluride detector. It was fitted with a combined x 2.5 and x 9 telescope, operated on a liquid-damped pan-and-tilt head (Vinton Cameras, Bury St. Edmunds, Suffolk) and positioned in the left doorway of the helicopter. With the helicopter operating to the right of the coast at a distance of 0.5 km and height of 120 m, this arrangement provided an unobstructed oblique view of the coast along the left side, in front and partially behind the aircraft. Surveys were carried out at speeds varying between 50 and 160 $\text{km}\cdot\text{hr}^{-1}$.

Groups of seals hauled-out could be detected at distances of up to 3 km on low magnification, although seals were identified and usually counted on high magnification. With practice, the thermal images of harbour and grey seals (*Halichoerus grypus*) - the only two seal species which occurred in the area - could be readily differentiated. Whenever confusion arose, species identity was confirmed visually using binoculars. The rapid detection of seals hauled-out allowed sections of coast devoid of seals to be surveyed extremely efficiently.

The thermal image was displayed on a small monitor and simultaneously recorded onto videotape. Seals hauled-out were counted from the monitor as they were encountered and the time of sighting, species identity and number in the group recorded directly onto 1:50,000 maps. The locations of haul-out sites were recorded to an accuracy of ± 50 m. Whenever necessary, numbers in large groups were confirmed from oblique photographs taken using a 300 mm telephoto lens and by recounting the videotape. Data were entered into a computer database at the end of each flight. Geographical subregions were defined prior to surveying. Start and end times of survey effort were recorded for each subregion as it was completed and incorporated into the database.

Harbour seals did not appear to be disturbed by the helicopter at the operating distance which was used, and remained hauled-out. However, grey seals occasionally took to the water. The numbers of seals in groups which did take to the water were usually determined before the group moved and could be confirmed by counting the thermal "footprints" remaining on the rocks or seaweed.

Fixed-wing surveys were conducted from a height of 365 m. After the film had been processed, seals were identified and counted either using a microfiche reader or a binocular microscope.

Timing of surveys

All surveys were timed to coincide with the harbour seal annual moult (Thompson & Rothery, 1987) between late July and mid-August. Thermal image surveys were carried out between 27 July and 10 August from 1988 to 1993 and fixed-wing surveys between 7 and 13 August from 1990 to 1994. In order to maximise the numbers of seals observed, surveying was restricted to within 2 hr of low tides occurring between 0930 and 2100hrs BST. There is evidence that numbers of seals hauled-out are greatest within this period, particularly when low tides occur in the afternoon (Smith, 1990; Thompson & Harwood, 1990). Low tide times were determined using Admiralty Tide Tables.

Area surveyed

The entire Scottish mainland coast from Dornoch in the Moray Firth to Sillioth on the south Solway Firth, including all but the most distant offshore islands (St. Kilda, the Flannan Isles, Sula Sgeir, Sule Skerry, Sule Stack and Fair Isle), were surveyed between 1988 and 1993 using the thermal imager. The offshore islands were omitted due to Civil Aviation Authority restrictions on the use of helicopters operating over open water. Three areas (Mull, Lismore and part of north-west Skye) were surveyed in every year. A section of the west coast, from Kyle of Lochalsh to Smirisary on Ardnamurchan and the whole of Skye, was surveyed in 1988 and in 1989 to assess the effects of the 1988 phocine distemper virus on the Scottish west coast seal population. Skye was surveyed again in 1992. Fixed-wing surveys of the Firth of Tay were carried out in 1990, 1991, 1992 and 1994 and of the Moray Firth in 1992 and 1994. The Scottish east coast from the English border to St. Andrews and from Carnoustie to Lossiemouth were not included in the survey on account of the small numbers of harbour seals inhabiting these areas.

RESULTS

The area surveyed in each year is given in Table 1. Data from surveys of areas in bold type were used to estimate the minimum size of the Scottish harbour seal population.

Harbour seals

The distribution of harbour seals in Scotland during August is shown in Fig. 1. During the surveys 26,397 harbour seals were counted. The numbers of seals along major sections of the coast are presented in Table 2 with a more detailed breakdown of numbers in Appendix 1. The most recent data for those areas which were surveyed more than once have been used. However, it could be argued that the mean value is more appropriate. In practice, the difference between the total based on the most recent counts and that based on the average (25,549) is only 3%. Most of this difference is explained by the large difference between the counts made in Shetland in 1991 (4,797) and 1993 (6,227).

Grey seals

The distribution of the 15,567 grey seals seen during the surveys is shown in Fig. 2. The haul-out behaviour of grey seals during the summer is unpredictable and numbers at haul-out sites can vary widely from day to day. Thus this information on grey seal numbers and distribution must be interpreted with caution.

Results of repeat surveys

The islands of Mull, Lismore and part of north-west Skye (Loch Dunvegan and the Ascrib Islands) were surveyed in each year between 1988 and 1993. The results from these surveys are given in Table 3. There was little variation in the numbers of harbour seals in the same area in different years, although distribution was more variable. For instance, the whole of Skye was resurveyed in 1992 to determine whether the observed decline in numbers in Loch Dunvegan and the Ascrib Islands (Table 3) was representative of the island as a whole. The 1992 total was within 5% of that recorded in 1988 and 1989, even though numbers in the north-west had continued to decline

The variation in the counts from Mull may be related to the timing of surveys during the day. In 1988, the survey was carried over two days and may not have been representative. In 1989, 1990 and 1993, low tides occurred in the afternoon and surveys were carried out between 1215 and 1840hrs. In 1991 and 1992 low tides occurred in mid-morning and surveys were carried out between 0735 and 1226hrs. In Shetland, most of the 1991 surveys were conducted between 0905 and 1409hrs, in 1993 they were carried out between 1430 and 1917hrs. However, the time of surveying (i.e. of low tide) had no statistically significant effect on the size of counts in either area.

Time required for surveys

A complete survey of harbour seals in Scotland required 80 hr of helicopter time and 2 hr of fixed-wing aircraft time. If time spent in transit is included, the survey required 120 hr of helicopter and 8 hr of fixed-wing time. Approximately 7,400km of coast was surveyed using the thermal imager, at an average speed of 92.5km.hr⁻¹.

DISCUSSION

The use of a thermal imager mounted in a helicopter allowed extensive stretches of complicated coasts to be surveyed rapidly and thoroughly. With the imager it was possible to detect groups of seals at distances of up to 3 km. Thus, observer effort could be concentrated on scanning the coast, and identifying and counting seals in groups detected. As a result, it was possible to carry out a synoptic survey of large areas, such as the whole of Scotland, relatively quickly and thus avoid problems caused by redistribution of seals between geographical regions. The results presented here were collected over six years, but with a more efficient survey design the same area could have been surveyed in two or three years.

Thermal image surveying is most efficient when the contrast between the seals and their haul-out sites is at a maximum on cool, slightly overcast days. The imager cannot operate through medium to heavy rain but will 'see' through light mist or drizzle. On hot sunny days, thermal contrast is reduced. More care is required to detect and count seals, and aircraft survey speed must be reduced.

Alternative methods for surveying harbour seals on rocky coasts are considerably less effective than the use of thermal imaging. Boat surveys are time consuming and as a result, synoptic surveys of extended areas are impossible. If the time of surveying is standardized with respect to tide state or period of moult, as is desirable, this will reduce the interval available for surveying even further. Visual aerial surveys from aircraft are considerably faster than boat surveys, and can be appropriate in areas where haul-out sites can be easily located or where their location is known in advance (Summers & Mountford, 1975; Thompson & Harwood, 1990). However, there is always a risk that some groups of seals will be missed.

We modified the traditional timing of surveys for Scottish harbour seals for two reasons. During the breeding season, harbour seal females tend to move away from main aggregations to relatively undisturbed locations. Pups are usually born below the high water mark and have to swim with their mothers at the next incoming tide (Thompson *et al.* 1994). As a result, the numbers of seals which are visible at any one time is highly variable during the breeding season. Secondly, during their moult, harbour seals spend more time hauled-out of the water than at other times of the year, and the highest and most consistent counts are made at this time (Thompson 1989; Thompson & Harwood, 1990).

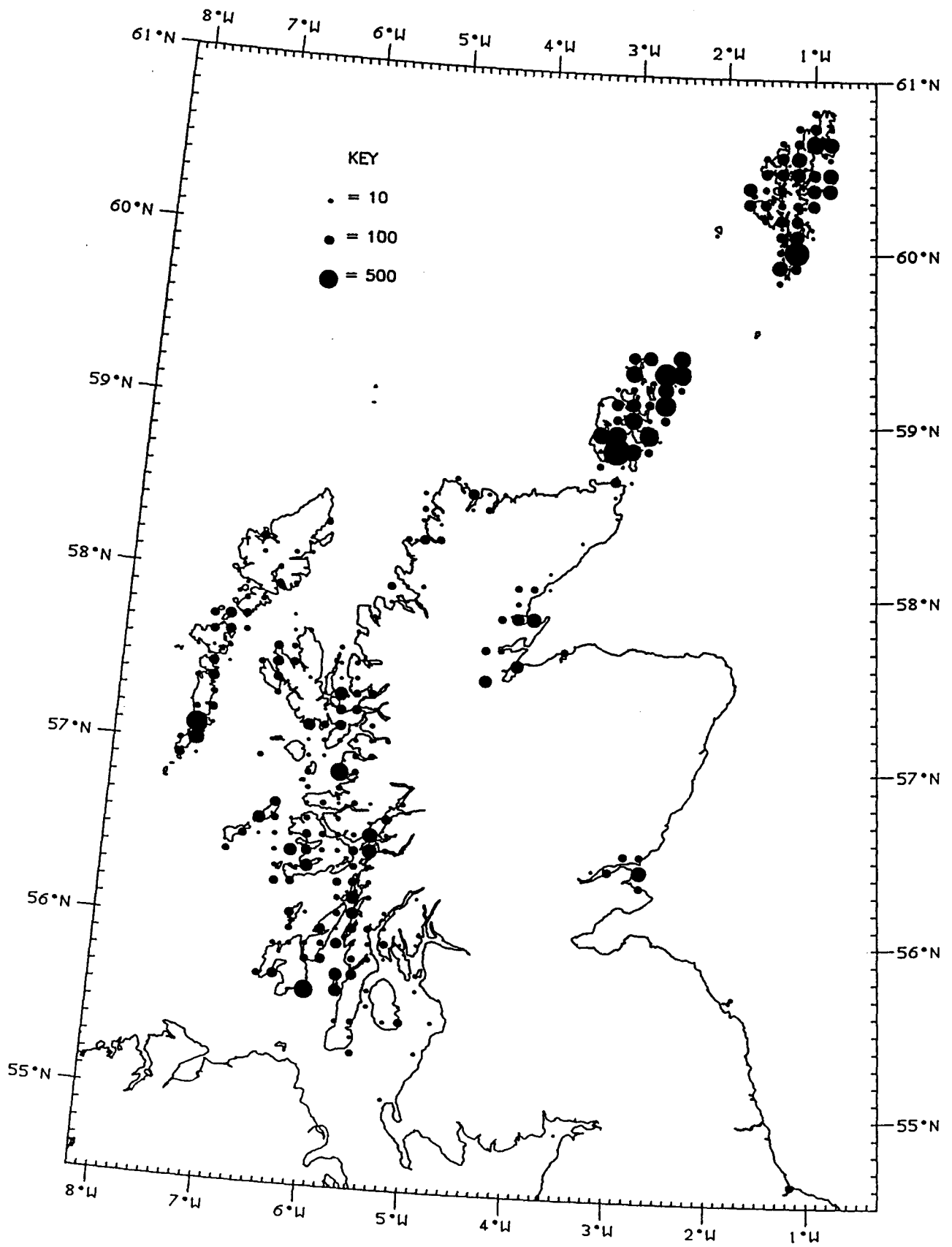
The data presented here represent the numbers of seals hauled-out at the time of surveying. An unknown number of seals will be at sea during the survey period, and therefore the total population is greater than the count obtained. The relationship between numbers hauled-out during the moult and total population size has not been precisely established. A study of harbour seals in Orkney using radio telemetry (Thompson & Harwood, 1990) showed that almost all adult males and approximately 60% of adult females hauled-out in early August. However, these results were based on a small sample of animals from only one location.

For sufficiently large geographical areas, such as Mull and Skye, repeat counts varied relatively little between years, suggesting that populations in these areas are reasonably stable. However, at smaller, more local sites (northwest Skye or Lismore) variation was greater (Table 3). As a result, fluctuations in numbers of seals at particular locations can be readily mis-interpreted. In northwest Skye, numbers of harbour seals declined by almost 50% between 1989 and 1992 while numbers on the entire island increased by 2%. By 1993, numbers in the northwest returned to their 1988/1989 level. These data imply there was considerable redistribution of harbour seals around Skye between 1989 and 1993.

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Harbour seals in August - by 10km squares



Grey seals in August 1988-1994, by 10k squares

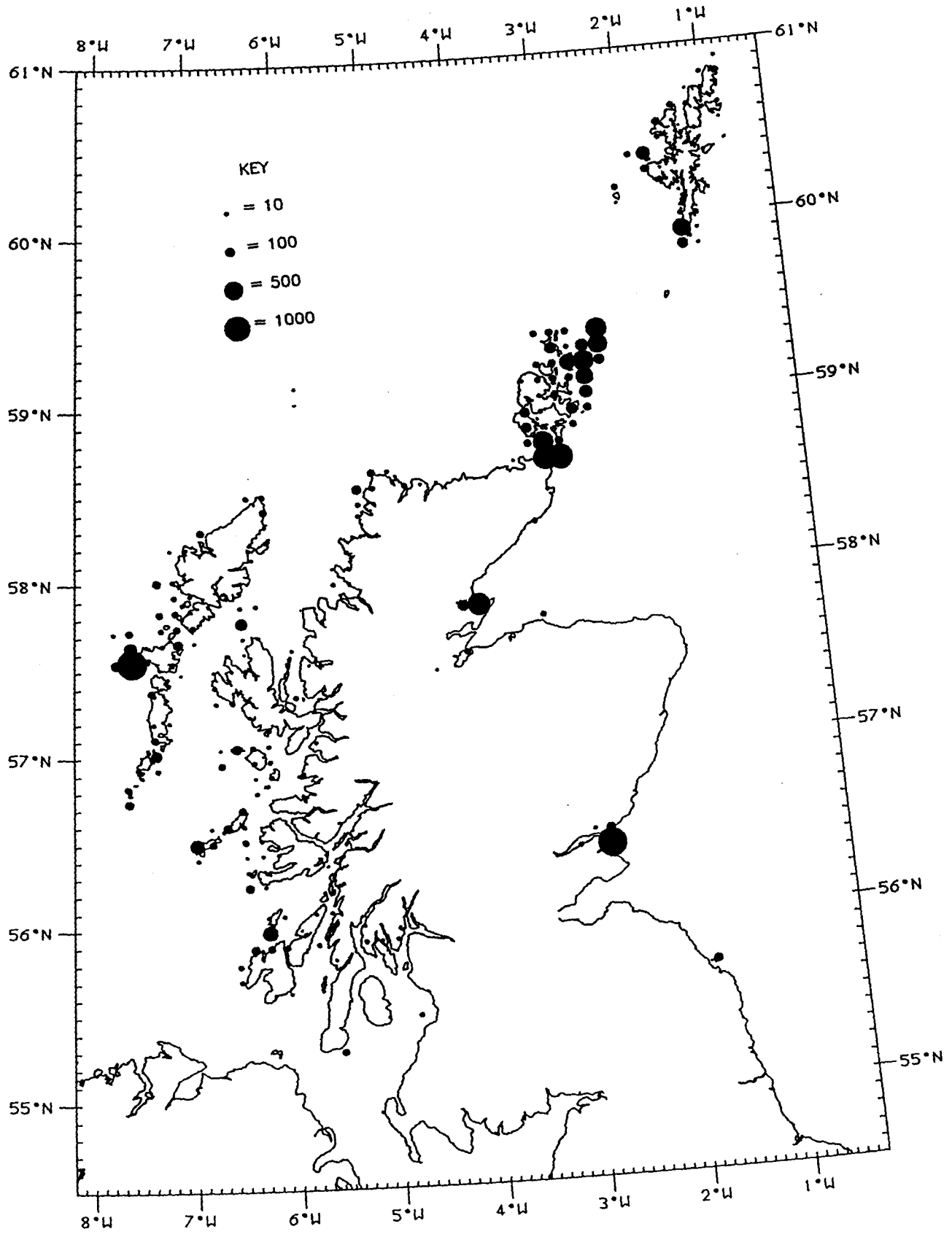


TABLE 1

Date and survey method for sections of the Scottish coast. In six sessions, all the main harbour seal haul-out sites were surveyed. The surveys of areas in bold type provided the data presented in Table 2 and the Appendix.

Year	Survey Method	Area surveyed
1988	Thermal Imager	Mull, Lismore, all Skye, Loch Broom to Applecross, Plockton to Arisaig, Ardnamurchan to Loch Linnhe, Rona, Raasay
1989	Thermal Imager	Mull, Lismore, all Skye, Plockton to Arisaig, Firth of Clyde
1990	Thermal Imager	Mull, Lismore, NW Skye, Firth of Lorn, west Kintyre, Islay, Jura, Colonsay, Coll, Tiree, Muck, Rum, Eigg, Canna
1990	Fixed-wing	Firth of Tay
1991	Thermal Imager	Mull, Lismore, NW Skye, Duncansby Head to Loch Broom, Shetland
1991	Fixed-wing	Firth of Tay
1992	Thermal Imager	Mull, Lismore, all Skye, Outer Hebrides, Appin, Dumfries & Galloway
1992	Fixed-wing	Firth of Tay, Moray Firth
1993	Thermal Imager	Mull, Lismore, NW Skye, Outer Moray Firth, Shetland, Orkney
1994	Fixed-wing	Firth of Tay, Inner Moray Firth

TABLE 2

Numbers of harbour and grey seals hauled-out in Scotland during August. Data from the most recent aerial surveys carried out between 1988 and 1994.

Location	Year of survey	Survey Method	Harbour seals	Grey seals
Shetland	1993	Thermal imaging	6,227	1,290
Orkney (including Stroma)	1993	Thermal imaging	7,873	6,821
Outer Hebrides	1992	Thermal imaging	2,278	2,826
East coast (Firth of Tay and Moray Firth)	1994	Conventional photography	1,694	2,439
Far north coast (Dornoch to Loch Torridon)	1988-1993	Thermal imaging	678	312
West coast (Loch Torridon to Loch Ryan including Skye and the Inner Hebrides)	1988 - 1993	Thermal imaging	7,639	1,875
Dumfries and Galloway	1992	Thermal imaging	8	4
TOTAL	1988-1994		26,397	15,567

TABLE 3

Numbers of harbour seals in areas surveyed more than once between 1988 and 1994.

Location	Type of survey	Year						
		1988	1989	1990	1991	1992	1993	1994
Firth of Tay	Fixed-wing			467	670	773		575
Moray Firth	Fixed-wing					1077		1061
Lismore	Thermal Imager (TI)	535	369 398	425	405	340	597	
Mull	TI	607	940	1008	883	825	946	
Skye, total	TI	1233	1269			1296		
Skye, L.Dunvegan & Ascrib Islands	TI	621	598	395	342	321	619	
Applecross	TI	48	26					
Plockton	TI	282	158					
Kyle of Lochalsh	TI	43	15					
Sound of Sleat	TI	43	53					
Loch Nevis	TI	30	68					
Arisaig	TI	456	499					
Orkney	Helicopter, visual		7137				7873	
Shetland	TI				4797		6227	

APPENDIX

Numbers of harbour and grey seals seen in Scotland from aerial surveys carried out during the harbour seal summer annual moult, between 1988 and 1994. Data represent the minimum number of seals in each area. For areas which were surveyed more than once, the most recent data are presented.

Location	Date of survey	Harbour seals	Grey seals	Unknown
<u>Shetland</u>				
South-east Mainland	2/8/93	807	9	
Yell	3/8/93	353	15	
Unst	3/8/93	288	85	
Fetlar and Hascosay	3/8/93	568	14	
Whalsay	3/8/93	512	0	
Out Skerries	3/8/93	326	0	
Mousa	2/8/93	455	23	
East Mainland	2,3/8/93	335	0	
Bressay	2/8/93	83	0	
Yell Sound	3,4/8/93	929	7	
North-west Mainland	4/8/93	65	99	
St Magnus Bay	4/8/93	660	316	
West Mainland	4/8/93	185	35	
South-west Mainland	2/8/93	385	35	
Foula	4/8/93	3	38	
The Deeps	2/8/93	273	8	
<u>Orkney</u>				
North and East Mainland	5,6/8/93	950	218	
South and West Mainland	6/8/93	131	58	
Burray and South Ronaldsay	5,6/8/93	377	99	
Hoy and South Walls	6/8/93	341	248	

Cava, Flotta, Rysa, Barrel of Butter	6/8/93	801	14	
Shapinsay	5,6/8/93	287	41	
Rousay, Egilsay, Wyre, Eynhallow	6/8/93	185	93	
Graemsay	6/8/93	8	0	
Stronsay	5,6/8/93	659	550	
Eday and Calf of Eday	5/8/93	55	236	
Sanday	5/8/93	1661	1182	
Westray and Papa Westray	5/8/93	122	374	
Auskerry	5/8/93	75	79	
North Ronaldsay	5/8/93	417	637	
Muckle and Little Greenholm	6/8/93	1	27	
Sweynholm, Gairsay, Grassholm	6/8/93	180	13	
Lingaholm, Little Linga, Holm of Huip, Holms of Spurness	5,6/8/93	47	285	
Faray, Faraholm, Ruskholm	5/8/93	6	129	
Copinsay	5/8/93	1	98	
Switha, Swona, Stroma	6/8/93	914	1438	
Pentland Skerries	6/8/93	1	972	
<u>Outer Hebrides</u>				
Lewis	31/7- 2/8/92	230	199	
Harris	31/7- 2/8/92	287	232	1
North Uist	1,2/8/92	333	477	
Benbecula	1,2/8/92	212	0	
South Uist	3/8/92	785	120	
Barra etc	3/8/92	458	278	6
<u>East coast</u>				
Firth of Tay Eden Mouth to Buddon Ness	13/8/94	575	1468	0

Findhorn coast	13/8/94	58	30	
Inner Moray Firth Grampian border to Dornoch	13/8/94	1061	941	17
<u>Far north coast</u>				
North-west Moray Firth Dornoch to Duncansby Head	30/7/93	110	33	
Pentland Firth Duncansby Head to Strathy Point	3/8/91	0	1	
Tongue Strathy Point to Cape Wrath	31/7/91	211	88	
Kinlochbervie Cape Wrath to Rubha Ruadh	31/7/91	33	157	
Eddrachillis Bay Rubha Ruadh to Point of Stoer	1/8/91	207	3	
Enard Bay Point of Stoer to Rubha Coigeach	1/8/91	6	9	
Summer Isles R. Coigeach to head Loch Broom	1/8/91	80	21	
Little Loch Broom Head Loch Broom to Stattic Point	7/8/88	1	0	
Gruinard Bay Stattic Pt to Greenstone Point	7/8/88	3	0	
Loch Ewe Greenstone Point to Rubha Reigh	7/8/88	7	0	
Gairloch Rubha Reigh to Sgeir Glas	7/8/88	2	0	
Torrison Sgeir Glas to Rubha na Fearn	7/8/88	18	0	
<u>West coast</u>				
Applecross (R. na Fearn to R. na h-Uamha incl. Crowlin Islands)	7/8/88	48	11	
Plockton R. na h-Uamha to Kyle of Lochalsh	6/8/89	158	0	

Kyle of Lochalsh Kyle to Garbhan Cosach	6/8/89	15	0	
Sound of Sleat Garbhan Cosach to An Fhaochag	7/8/89	53	6	
Loch Nevis An Fhaochag to Mallaig	7/8/89	68	0	
Arisaig Mallaig to Smirisary	7/8/89	499	20	
Ardnamurchan Smirisary to Auliston Point	31/7- 8/8/88	118	0	
Sound of Mull Auliston Point to Rudha na Ridire	3/8/88	23	0	
Loch Linnhe Rubha na Ridire to Salachan Glen	29/7- 3/8/88	110	0	
Loch Creran Salachan Glen to Rubha nam Faoileann	7/8/92	12	0	
Loch Etive R. nam Faoileann to Dunstaffnage	4/8/90	35	0	
Firth of Lorn Dunstaffnage to Craignish Point	4,5/8/90	461	10	
West Kintyre Craignish Point to Southend	5,6/8/90	1153	17	
Firth of Clyde Southend to Loch Ryan	9,10/8/89	381	117	2
<u>West coast islands</u>				
Skye	3,4/8/92	1296	242	0
Rona	7/8/88	21	5	
Raasay	7/8/88	3	0	
Canna	8/8/90	41	151	
Rum	8/8/90	10	57	
Eigg	8/8/90	29	31	
Muck	8/8/90	25	17	
Coll	7/8/90	367	167	

Tiree	7/8/90	124	337	
Mull	9/8/93	950	103	0
Lismore	10/8/93	597		0
Treshnish Isles	2/8/88	29	56	8
Jura	6/8/90	156	38	
Colonsay	6/8/90	109	17	
Oronsay	6/8/90	24	303	1
Islay	6/8/90	724	170	1
<u>Dumfries & Galloway</u>				
Loch Ryan to English Border	5/8/92	8	4	
