1992

THE STATUS OF THE BRITISH GREY SEAL POPULATIONS

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1. BASIC BIOLOGY

The grey seal is Britain's largest land mammal. Males may weigh in excess of 300kg, but most adults are 1.6-2.3m in length and weigh 120-250kg. Pups weigh 13-14kg at birth and grow to around 45kg in the first three weeks of life. Females may live up to 45 years.

The species breeds colonially at a limited number of remote coastal sites between September and December. Most of these sites are on islands off the north and west coast of Scotland, but there are now a number of colonies at mainland sites in Scotland and England (Figure 1). At most colonies females remain ashore with their pups throughout the three-week lactation period. At the end of this period, adult females are mated by males which have maintained a position within the colony. Females return to the sea after mating, but pups may remain ashore for several weeks after they have been weaned. Pups are born with a silky white coat, which shows up clearly in coloured aerial photographs but which is moulted after 2-3 weeks. At each colony pups are born over a 4-6 week period, so that there is no one time when all the pups born at that colony are actually present. The timing of births varies considerably from colony to colony, but year to year variation within a colony is limited to only a few days.

Adults and pups appear to disperse widely after the breeding season and relatively small numbers are observed around the breeding colonies and at other sites which are used for hauling-out. However, during the moult, which occurs from January to March for males and from March to May for females, dense aggregations can be observed at favoured sites.

2. WORLD POPULATION

The grey seal is confined to the North Atlantic, population size is usually assessed by counting the number of pups born each year, either directly or from aerial photographs. There are discrete populations in Canada and the northern USA, the northeast Atlantic, and the Baltic Sea (Figure 2). The population in the northwest Atlantic is increasing, the Baltic population has decreased sharply but now appears to be stable. In the northeast Atlantic there are sizeable populations in Iceland, the Faroe Islands, Norway and the UK. Approximately half of the world's population breeds around the coast of Britain. Very small colonies (producing 1-5 pups per year) exist in France, the Netherlands, Germany and the Kattegat.

3. ESTIMATING PUP PRODUCTION AT BRITISH SITES

This section provides a brief outline of the methods used to estimate pup production of grey seals at each of their major breeding sites, and presents the best estimates currently available.

3.1 Surveys of Pupping Sites

Methods of data collection and analysis are more fully described in Hiby, Thompson and Ward (1987) and Ward, Thompson and Hiby (1987). Very briefly, all major breeding sites in the Inner Hebrides, Outer Hebrides and Orkney island groups are photographed three or four times at an interval of about 10 days, from late September to mid-November each year. Photographs are taken on colour transparency film from the NERC aircraft using a 5 inch format camera on a vibration-damped and motion-compensated mount. The frames are taken in overlapping series and aligned using common features visible on adjacent frames to provide a complete coverage of the areas used for breeding. A census of the white-coated and moulted pups present on a site on each of the days it was photographed is then obtained by inspecting the frames on a micro-fiche viewer. Pups which are obviously dead, judging by their appearance on the photographs, are recorded separately. However, this provides only a lower bound on the number of dead pups and the subsequent analysis is based on the total pup counts. This assumes that pups which die remain visible to the aerial survey for a period which is equal, on average, to the age at which surviving pups leave the site (or, in the case of analyses based on white-coated pups only, to the age at which surviving pups moult).

3.2 Statistical Methods for Estimation of Pup Production

The number of pups born at each site is estimated using a computer model of the growth and decline of the number of pups present on a site during a breeding season. The model has been applied to all data collected since 1983. Prior to 1983, production at each site was estimated by multiplying the maximum aerial survey count by a calibration factor derived from selected ground counts of islands in the Outer Hebrides and Orkneys.

Production can be observed directly from an intensive series of ground counts by dye-marking pups during each count and summing the number of unmarked pups counted over the series. This production estimate can then be compared to the maximum total count of live pups to derive a calibration factor. However, to apply this factor to aerial survey counts it is necessary to assume that only live pups are counted from the photographs, and that the maximum number of live pups present during the season is unaffected by the ground counts themselves. Results of the current analyses indicate that one or both of these assumptions do not hold. The calibration factor method is also unsound as a statistical procedure given that fact that the timing of the breeding season is not known before the flights are conducted. If the flights are widely spaced in time there may be no flights conducted at or near the time that the maximum number of pups are present on a site, leading to a downward bias in the peak count. On the other hand, a number of flights may be conducted during a period when a constant maximum number of pups is present on the site. In that case any random error present in the counts will lead to a positive bias in the maximum count obtained from the photographs as an estimate of the maximum number of pups present.

3.2.1 Variance of Pup Production Estimates

In the model, date of birth is assumed to be normally distributed with a standard deviation of 10 days. The predicted number of pups present on the day of each flight is calculated assuming that the interval between birth and the time at which the pup disappears (when the corpse becomes obliterated or, in the case of surviving pups, the pup goes to sea) is also normally distributed with a mean of 30.5 days and a standard deviation of 5 days - those parameter values are based on observation of known-age pups on the Isle of May in 1985, 1986 and 1987 (Wyile, 1988).

The covariance matrix for the joint distribution of the number of pups present on the flight days is calculated assuming that the birth day and day of disappearance are independent for different pups, and that the number of pups is counted without any error. However, there is almost certainly some dependence between different pups in the actual days of birth and disappearance (for example, we can imagine pups leaving in small groups so that the effective sample size for parameter estimation is less than the number of individual pups present) and there is likely to be a 5% error in the photographic counts (2.5% coefficient of variation (CV)). Therefore the matrix is scaled up to reflect this variation and any further lack of fit in the model. These adjustments have little effect on the production estimate itself but considerable effect on its estimated CV.

3.2.2 Estimating Pup Production at Sites with Small Numbers of Counts

In the current version of the model the likelihood is maximised with respect to the mean date of birth, the covariance matrix scaling factor, and the production. This thus requires a minimum of three counts during the season. In those cases where only two counts are available the scaling factor, and hence the CV, cannot be estimated; when there is only one count (as occurred for some sites in 1985) the production can only be estimated given a mean birth date. In the latter cases the mean date has been interpolated from the estimated mean birth dates for site/years with at least two counts. Figure 3 shows the mean of those estimates by year and island group. There is little change in the values from year to year but a gradual drift over time. For sites in the same island group there is a degree of coherence between changes in the timing of the breeding season. Figure 3 suggests that this may also apply to the island groups. For the moment we have chosen to model mean birth date as a cubic function of year, with quadratic and cubic terms constrained to be the same for islands in the same group. Constant and linear terms are specific to site because there are large mean differences in birth date for sites in the same group and some sites, particularly those experiencing a steady increase or decline in pup production, have shown a trend in birth date over the period of the surveys. Although satisfactory for interpolation over a series of short duration the polynomial fit is not suitable for providing predictions of birth dates for the following year (required for flight planning) and is not appropriate for longer series. Statistical forecasting models will be applied to this data in future years.

3.2.3 Analysis of Surveys Conducted before 1983

The data for years before 1983 were not available in a form suitable for the model, so the results presented for those years are still based on a calibration factor. The value was based on the model results for 1984-90; it was 1.210 for the Outer Hebrides and 1.233 for the Orkneys (regular counts of the Inner Hebrides were not obtained before 1984). With the parameters as set in the model the ratio between production and maximum pups present is 1.19 - any increase in this figure results from displacement of the date at which the maximum count was obtained from the date at which the model calculates the maximum number of pups to have been present.

3.3 Estimates of Pup Production

Tables 1, 2 and 3 give the pup production estimates produced by this procedure for each site in the Inner Hebrides, Outer Hebrides and Orkneys, totals for each group and, in the case of the Outer Hebrides, a sub-total for the Monach Isles which have been colonised during the period covered by the data series and shown a rapid growth of pup production recently. There are some interpolated production values in earlier years included to avoid breaks in the time series for group totals. These are for Haskier in 1966-68 and Shillay in the Monachs for 1972. The 1978 estimate for North Rona is based on ground counts. The 1977 total for the Outer Hebrides, when an adult and pup cull took place, is taken from data records held at SMRU. The basis for the estimate is unclear - aerial survey counts were not obtained for this group in 1977.

3.3.1 Colonies with Incomplete Time Series

A general problem in inferring a trajectory of total pup production for a group of colonies from these data is that not all sites have been surveyed throughout the period because initially they were not used by seals or used by only a few seals. Survey of a site may be initiated when it is first noticed that the site is used by a significant number of seals, resulting in an overestimate of the rate of increase of total production for the group. The effect should be fairly small, however, particularly in recent years. The series for Deasker shows the opposite effect: no pups have been observed there since 1983. It is possible that counts made before 1983 included a number of yearling seals which are present at this site during the breeding season.

Sites on South Ronaldsay in the Orkneys are not suitable for aerial photography, hence the lack of estimates following 1983, since when all Orkneys and Hebrides estimates have been based on aerial survey. However, Scottish Natural Heritage began to make systematic counts of the South Ronaldsay sites during the 1991 pupping season.

3.3.2 Estimation of Coefficient of Variance for Total Pup Production

For any year/site with three or more counts the model can provide an estimate of the error on the production estimate, as a CV. However, with the model set to use a fixed standard deviation of 10 days for the birth curve, the CV generated is unrealistic. This is because it fails to incorporate uncertainty about the true duration of the pupping season for that site in that year.

The following procedure was adopted to overcome this difficulty. In certain years, sufficient flights were conducted over some sites to estimate the birth curve standard deviation and provide a CV for the resulting production estimate (the value of 10 days was based on these results). This applied to 21 of the 35 sites in 1987 and 29 sites in 1988. The average CV over all these site/years, weighted by the production estimates, was 0.09, suggesting a CV of around 10% as a rough guide to the accuracy of a production estimate by this method for a given site in a given year. Summing estimates to provide totals by year, and assuming errors on estimates for different sites are independent, gave CV's of 0.033 in 1987 and 0.017 in 1988 on the total production estimates for those years. This would indicate a CV of 3% as a rough guide to the accuracy of production totals for successive years. However, given that the average number of counts per site were lower in other years, and that variation in weather conditions generates dependence between the errors for sites surveyed on the same flight, it would be safer to increase this figure to, say, 5%.

3.3.3 Sites not Surveyed from the Air

Table 4 gives available estimates for other sites, not included in the aerial survey programme (except that the Isle of May was photographed in 1988, 1989 and 1991). The colonies at the Isle of May, Farne Islands and Donna Nook are readily accessible and the number of pups born at the Farne Islands and Donna Nook are counted each year by the National Trust and the Lincolnshire Trust for Nature Conservation respectively. Sites in Shetland, mainland Scotland, Wales and Cornwall are located on inaccessible beaches or in caves under steep cliffs. These cannot be surveyed effectively from fixed-wing aircraft and can only be visited during calm weather or by helicopter. Most of them are small and they are surveyed at irregular intervals whenever resources are available. The Dyfed Wildlife Trust, with financial support from the Countryside Council for Wales, has begun a survey programme which will run until 1996 and will provide a new estimate for pup production in Wales.

3.4 Pup Production Trends

Figure 4 plots the estimated trajectory of pup production totals for islands in the Orkney group; it suggests a fairly continuous increase in the Orkneys breeding population from the mid 1960s to the present. There is an indication of some discrepancy in the trajectories before and after 1983. This may be partly due to the use of the production:peak-count ratio from the recent analyses to scale up the peak counts for the pre-1983 surveys. The flights in the recent surveys have been more widely spaced in time in order to estimate the spread of the birth curve, so that on average the production:peak count ratio now may be slightly higher than before 1983. In addition, the use of monochrome aerial photographs before 1983 may have led to over-counting under certain conditions. Within the Orkney group there have been dramatic increases in pup production at some islands which are in close proximity to each other, but at others there has been no change or a decline (Figure 6). Thus in the Spurness area (Figure 6c) pup production at Little Linga, Lingaholm and Holm of Huip has increased, but it has declined at the Holm of Spurness and Point of Spurness. Similarly, in the Westray Firth (Figure 6b) pup production has increased at Faray and Faraholm, but it has declined at Ruskholm in recent years.

Figure 5 plots the pup production trajectory for the Outer Hebrides, and the sub-totals for the Monach Isles and the rest of the group. It shows that the increase in the breeding population has occurred primarily at the Monach Isles. The plot also illustrates the effect of the breeding season cull carried out in 1977, which depressed the pup production in 1978 by more than would be expected as a result of the loss of the culled seals from the local population.

The maps in Figures 7 and 8 show the spatial distribution of pup production in the Outer Hebrides and Inner Hebrides as estimated from the surveys carried out in 1984, 1986, 1988, 1990 and 1991.

In Figure 9 the trajectories from the Orkneys and Outer Hebrides have been added to those from the Farnes and Isle of May to illustrate the changes in pup production for the majority of sites in Scotland and Northumberland.

The Inner Hebrides estimates are excluded because the estimates for the group as a whole are not available before 1984; estimates for Loch Eriboll, Helmsdale and the Shetlands are also excluded.

Figure 10 plots the estimated pup production trajectories for the Orkneys, Outer Hebrides, Farnes plus Isle of May, *and* the Inner Hebrides, from 1984 to 1990. The effect of the 1988 seal virus epidemic is clearly visible in the line showing the total for all groups, and also in the Orkney and Farnes plus Isle of May trajectories, but not for the Hebrides. The fact that the total trajectory has remained depressed since 1988 suggests that the effect of the virus was to kill adult seals rather than to cause a temporary drop in fecundity.

4. ESTIMATING THE NUMBER OF SEALS ASSOCIATED WITH BRITISH BREEDING SITES

We believe that the trajectories of pup production estimates provide the most sensitive available indicator of any response by the breeding populations to factors such as disease, disturbance, pollution, food or space limitation, and also provide the most reliable indication of their geographical distributions. There is, however, a requirement to estimate, each year, the surviving number of seals of all ages which were born at any British site, which is motivated by interest in potential interactions with commercial fisheries. Before describing the model used to estimate this number, we consider the parameters which determine the ratio between pup production and the size of the "all-age population", and the possible range of values for this ratio.

4.1 Ratio of Female Population Size to Pup Production

It is sufficient for this purpose to use a simplified population model with "knife-edge" recruitment of female seals to the breeding population at age k years, i.e. females may have their first pup on their k^{th} birthday. Suppose the proportion of pups which survive from birth to age 1 is S_j and annual survival for seals beyond age 1 is S. Let the population have a stable age-structure and an annual rate of increase of λ. Then the ratio of the number of females aged 1 and over at the time of the breeding season to the production of female and male pups during that season equals $(\frac{\lambda}{S})^{(k-1)} \times \frac{1}{F}$, where F represents fecundity (ie the number of pups of either sex produced per year by each adult female). This follows from the balance equation linking production to the population vector. For example, with S and F set to 0.94, k set to 5 years and an annual increase of 1.07 in the size of the population, the female population at the time of the breeding season is about twice as big as the pup production.

The point of this derivation is that it allows the minimum size of the female population associated with an observed production trajectory to be calculated. As S and F cannot exceed one, and assuming a female cannot have a pup before her 5^{th} birthday, the minimum population size equals λ^4 times the pup production, i.e. about 1.3 times for $\lambda = 1.07$.

To calculate the *maximum* female-population:total-pup-production ratio the formula can be recast as $\dfrac{\frac{S_j}{\lambda}}{2(1-\frac{S}{\lambda})}$ which is maximised by letting S tend to 1 and S_j tend to 0.8 (to represent survival to age 1 if no pups die after leaving the breeding sites). With λ set to 1.07 again the maximum ratio equals 5.7.

The minimum and maximum ratios correspond to S_j and F, respectively, tending to zero. These calculations are useful in identifying the degree of uncertainty associated with estimates of total population size in the absence of reliable information on either survival rates or fecundity and age at first breeding. They set feasible bounds for the size of the population but they should not be taken as estimates of the maximum of minimum number of British seals. The limits can also be useful for comparison with confidence limits generated by the computer model used to estimate total population size from observed production trajectories. It should be noted that a further degree of uncertainty is involved in extrapolating from female to female-plus-male population size, because males may suffer different rates of mortality, and very little information is available on this.

4.2 Technique used to Estimate Total Population Size

The statistical model used to estimate all-age population sizes is described in Appendix 1. The details of the method are complex but in outline the method is as follows:

Mean fecundity rate (pups born per year per female following the age of first breeding) is determined in the model using data from a cull of females at the Farnes in 1981. The values used in the model for the proportion of females having their first pup at each age are from Harwood and Prime(1978) - recruitment occurs over a 3-year age interval. Using these parameter estimates the number of "mature" females in an isolated population associated with a given group of breeding sites can be estimated, for a given year, from the pup production at those sites in that year. This leaves immature females and males to be estimated. The number of females in each pre-breeding age class in the given year is available from an age-structured population model, given a series of pup production estimates leading up to that year and estimates of age-specific survival rates. Survival was assumed to be the same for all age classes following the first year, with a lower survival for the first year of life, as in the model described at the beginning of this section. These two survival rates are estimated by comparing model-predicted and observed pup productions. Estimates of both parameters are available if the number of pups known to be recruited to the population each year varies as a result of variations in pup production and pup culls. The method is formulated as a maximum likelihood estimation model with the observed pup productions and the number of pregnant females in the Farnes cull as the random variables. The error structure assumes fecundity rate varies independently from year to year and ignores any error in estimation of pup production or fluctuation in survival rate. Subject to these assumptions, confidence limits on the population size estimate for a given year are available, using the likelihood ratio method.

4.3 Construction of Time Series for Use in Population Estimation

4.3.1 Farne Islands Population

By far the longest and most reliable series of pup production estimates available is that for the Farne Islands. The computer model was applied from 1956 to 1971 to give maximum likelihood estimates of 0.94 for F and 0.95 and 0.51 for S and S_j respectively. Ninety-five percent confidence limits on the population estimates are 35% below and 45% above the maximum likelihood estimates, i.e. well within the upper limit calculated at the beginning of this section and roughly equal to the lower limit.

4.3.2 Dealing with the Effects of Culls

Comparison of predicted and observed pup productions is appropriate only if the mature females estimated to be in the population can be assumed to breed only at the included sites, and those sites are not used by other females. Furthermore no change in fecundity rate, other than independent random fluctuations from year to year, are allowed for in the model. Because of possible changes in fecundity and migrations of the breeding populations following adult culls in 1972 and 1975 in the Farnes, the production estimates following 1971 cannot be used for parameter estimation.

One way to proceed is to assume that mortality rates remain the same as those estimated for the pre-cull years and allow the model simply to accumulate the observed productions into the estimated total population, subtracting any animals killed in culls and those eliminated by natural mortality. The population estimates shown in Figure 11 for 1972-92 were calculated on this basis. They include the production estimates obtained for the Isle of May since 1979; thus they refer to the animals **born** at the Farnes or the Isle of May: some of these animals may now be breeding elsewhere. Such estimates are of little value, because even if the assumption of constant mortality holds, the estimates refer to a population for which not even the breeding component is uniquely associated with a defined area. The same problem applies to the Outer Hebrides where a cull in the 1977 breeding season may have led to migrations affecting both the number and age structure of seals in that area. An obvious solution is to add the estimated production trajectories from different areas and derive a population estimate for the entire area which is unaffected by migrations within it. The only difficulty is that gaps in the production trajectories for each area lead to a very fragmented trajectory of totals. However, the surveys conducted each year since 1983 have been very comprehensive and the production totals, illustrated in Figure 12, refer to all sites in Scotland and Northumberland excluding Eriboll, Helmsdale and the Shetlands. These pup production values are listed in Table 5.

4.4 Final Estimates of Total Population Size

Running the computer model on the series of production totals from all sites in Scotland and Northumberland, excluding Eriboll, Helmsdale and Shetland, gave the female population estimates listed in the Table 5 and plotted in Figure 12. It was not possible to estimate both first year survival, S_j and subsequent survival, S. S was fixed at 0.95, the value estimated from the Farnes data from 1956 to 1971. The resulting estimate for S_j was 0.50.

The confidence limits calculated for these estimates of female population size are only slightly wider than those for the pre-1972 Farnes population estimates, which were based on a much longer data series. This is because S was given a fixed value. One way to make the confidence limits incorporate uncertainty concerning the value of this parameter is to recalculate them with *S* set against its biologically determined constraints. Reducing *S* increases the population estimate and the estimate of S_j. It is reasonable to suppose that survival from birth to age 1 should not exceed annual survival beyond age 1. Reducing S to 0.93 increases the estimate of S_j to the same value (given an 80% survival of pups on the breeding sites) and increases the upper limit to 72% above the estimate. The lower limit of 35% below the estimate is given by the argument at the beginning of this section.

In summary, the second column of Table 5 lists, for each year from 1984 to 1992, point estimates for the number of female seals of age 1 or over at the time of the breeding season, which are associated with all the major breeding sites in Scotland and Northumberland, with the exception of Eriboll, Helmsdale and the Shetlands. The estimation model assumes that all these seals were born at one or other of the sites, and use only these sites for breeding; furthermore that these sites are not used for breeding by seals born in other areas. The possible range of error on these estimates, derived as a hybrid of 95% confidence limits and the result of allowing annual survival to vary across its feasible range, is from 35% below to 72% above the point estimates listed.

The third column in Table 5 lists point estimates for the number of female *and* male seals. The estimates assume equal numbers of males and females up to the age of 5 and a female to male ratio of 1.6 for older seals. These figures are based on the assumption that the two sexes have similar survival rates up to the age of sexual maturity and that adult males have an annual survival of 0.8 thereafter. The latter figure is derived from the age structures of males more than 10 years old killed in management culls at the Farne Islands in 1972 and 1975 (Harwood and Prime, 1978). It is not possible to calculate formal confidence limits for the estimate of total population size; if it were, they would certainly be larger than those for the female component of the population. The sensitivity of the estimate to the assumption about adult male survival can be gauged from the fact that the estimates in the third column of Table 3 would be increased by about 10% if adult males and females had identical survival rates.

5. DISTRIBUTION

The distribution of animals outside the breeding season is poorly understood. The location of groups of grey seals that were observed during aerial surveys for common seals (see Duck *et al.*, in prep.) conducted on the west coast of Scotland in August 1988-90, in Orkney in 1989 and in Shetland in 1991 are shown in Figures 13, 14 and 15. As more of the Scottish coast is surveyed in this way it will be possible to build up a more complete picture of the distribution of grey seal haul-out sites at this time of year. However, the use of haul-out sites is known to vary seasonally, and telemetry studies conducted by SMRU over the last five years have indicated that the grey seals which use a particular haul-out site may forage over hundreds of km of coastline, although usually within 20km of the coast.

6. EXPLOITATION AND DELIBERATE KILLING

Licences to take grey seals within the close season (September-December) may be granted by the Secretaries of State for Scotland and the Home Department for five purposes: scientific or education purposes, prevention of damage to fisheries, reduction of population surplus for management, use of a population surplus as a resource, and protection of flora and fauna. Historically most licences were issued to take pups to reduce a population surplus. However, the dramatic decline in demand for seal products in recent years has meant that licences are now only requested for prevention of damage to fisheries and protection of flora and fauna. Table 6 documents the number of grey seals taken under licence since 1962.

No licences to kill grey seals in Scotland were issued under the Conservation of Seals Act, 1970 in 1991. **In England, 12 pups were killed by the National Trust at the Farne Islands under a licence issued by the Home Office.** A number of seals are shot legitimately each year by fishermen and owners of marine fish farms. No reliable figures are available for the number of grey seals killed in this way, but figures provided to SOAFD by the Salmon Net Association and the Scottish Salmon Growers Association indicate that at least 234 grey seals were shot in 1989 and 1990.

7. REFERENCES

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8. FIGURE CAPTIONS

TABLE 1 Pup production estimates for islands in the Inner Hebrides group. See Figure 8 for location of islands.

	Gunna	Northern Treshnish	Fladda	Sgeir a Chaisteil + Eirionnach	Lunga	Soa	Eilean nan ron	Eilean nan Eoin	Nave Island	TOTAL
1984	233	82	186	130	169	0	174	254	130	1358
1985	291	87	126	119	165	68	178	288	61	1383
1986	287	110	147	128	195	114	307	325	137	1750
1987	378	111	208	149	235	118	432	328	126	2085
1988	344	144	227	171	249	101	394	219	124	1973
1989	400	132	243	187	287	107	318	183	194	2051
1990	405	133	203	211	272	120	407	310	200	2261
1991	501	161	317	176	265	106	404	375	195	2500

TABLE 2 Pup production estimates for islands in the Outer Hebrides group. See Figure 7 for location of islands.

Year	Gasker	Coppay	Shillay (Sound of Harris)	Haskier	Causamul	Deasker	Shivinish (Monachs)	Ceann iar (Monachs)	Ceann ear (Monachs)	Shillay (Monachs)	Stockay (Monachs)	Monachs total **	Others	North Rona	TOTAL
1960	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1961	831	61	114	86	64	13	0	-	-	-	-	38	0	1754	2960
1962	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1963	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1964	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1965	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1966	1063	228	114	101	228	0	0	-	-	-	-	38	0	1350	3122
1967	1063	152	76	101	152	0	0	-	-	-	-	114	0	1417	3075
1968	1063	114	152	101	152	0	0	-	-	-	-	152	0	1485	3219
1969	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1970	1107	320	674	137	97	41	0	0	74	61	496	631	0	1821	4829
1971	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1972	1119	313	571	176	256	67	0	0	239	51	787	1097	0	1178	4778
1973	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1974	1721	283	653	185	211	83	0	50	401	45	813	1308	0	1482	5926
1975	1508	363	595	223	190	51	0	144	602	222	1004	1973	0	1765	6667
1976	1777	390	522	293	205	57	0	114	548	156	1134	1951	0	1697	6892
1977	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6030
1978	1080	318	480	337	163	51	0	571	324	210	675	1780	0	1803	6012
1979	972	373	515	284	150	80	0	685	707	168	890	2450	0	1593	6417
1980	1318	457	749	370	154	31	0	1097	768	247	697	2809	162	1680	7733
1981	1230	418	959	293	168	68	0	1302	424	339	913	2978	136	1606	7857
1982	1415	627	207	338	246	110	0	1353	486	204	767	2809	85	1700	7536
1983	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1984	1066	375	357	329	136	0	85	2238	848	227	649	4047	0	1467	7777
1985	1319	424	309	265	155	0	268	2395	857	191	688	4399	0	1295	8166
1986	1199	353	387	218	101	0	289	2973	706	223	587	4778	0	1189	8225
1987	1350	402	369	247	114	0	345	3195	590	215	712	5057	0	1160	8699
1988	1271	398	357	210	119	0	407	3729	391	198	562	5287	0	1123	8765
1989	1347	422	420	188	90	0	552	4112	434	220	546	5864	0	1194	9525
1990	1397	391	355	161	113	0	553	4614	486	169	458	6280	0	1146	9843
1991	1447	451	436	195	98	0	575	5060	523	187	491	6836	0	1319	10782

** Monachs total: Pre-1970 no breakdown available

TABLE 3 Pup production estimates for islands in the Orkney group. See Figure 6 for location of islands.

Year	Muckle Green-holm	Little Green-holm	Little Linga	Holm of Spurnes s	Point of Spurnes s	Lingah olm	Holm of Huip	Fara-holm	Faray	Rusk-holm	Wart-holm	Sweyn-holm & Gairsay	Grass-holm	South Ronald-say	Swona	Pentland Skerry	Aus-kerry	Switha	Stroma	TOTAL
1960	724	197	247	99	0	0	0	465	0	214	41	0	0	123	4	99	0	0	0	2213
1961	530	300	259	136	0	0	0	317	0	263	33	0	0	152	4	49	0	0	0	2043
1962	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1963	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1964	921	485	160	29	0	0	0	25	132	214	16	62	4	115	16	25	0	0	0	2204
1965	662	378	288	152	0	0	0	119	169	255	29	25	74	74	21	86	0	0	0	2332
1966	678	469	354	152	0	0	0	284	173	90	8	66	21	107	16	49	0	0	0	2467
1967	592	460	407	107	0	0	0	284	185	259	8	123	0	132	8	37	0	0	0	2602
1968	641	321	411	304	0	16	0	271	288	201	8	90	41	152	29	53	0	0	0	2826
1969	559	308	592	206	8	33	0	226	33	214	4	86	66	127	37	21	0	0	0	2520
1970	736	329	534	148	45	49	25	181	107	230	4	16	74	103	45	86	0	0	0	2712
1971	580	362	728	173	49	156	33	337	99	107	16	78	45	148	70	37	0	0	0	3018
1972	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1973	497	214	534	255	66	201	95	370	41	16	12	95	103	123	53	53	107	0	0	2835
1974	518	197	493	160	21	70	148	526	82	136	0	148	78	136	74	74	103	0	0	2964
1975	477	238	497	296	49	45	127	502	74	66	4	123	25	197	62	49	185	0	0	3016
1976	596	181	666	358	53	78	74	419	95	62	4	218	25	160	95	66	456	0	0	3606
1977	670	218	703	333	78	58	140	502	66	115	4	214	25	156	95	66	243	0	0	3686
1978	329	218	822	514	136	90	206	736	66	226	4	164	41	169	107	58	164	0	86	4136
1979	539	304	354	469	127	164	395	707	103	288	4	156	78	164	95	66	177	0	144	4334
1980	489	173	695	452	107	358	296	859	185	345	0	185	82	140	111	82	119	0	164	4842
1981	436	206	884	489	45	333	547	748	226	329	4	119	103	82	230	127	304	0	210	5422
1982	448	90	736	724	29	370	559	859	164	304	4	115	115	103	152	148	358	164	214	5656
1983	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1984	490	122	536	514	0	329	350	756	562	336	0	139	86	0	83	67	255	178	164	4967
1985	460	220	698	683	0	384	261	807	600	310	0	136	66	0	257	79	304	171	183	5619
1986	548	226	587	529	0	433	384	781	866	349	0	155	86	0	212	69	332	176	223	5956
1987	613	253	699	589	0	556	614	915	1000	290	0	114	97	0	328	106	249	175	276	6874
1988	409	183	615	436	0	571	550	865	913	248	0	253	89	0	332	64	241	181	234	6184
1989	457	211	636	452	0	718	618	854	1463	242	0	170	44	0	299	72	304	236	277	7053
1990	384	223	691	376	0	819	738	1039	1315	206	0	201	50	0	421	73	269	230	298	7333
1991	512	205	727	382	0	1101	870	948	1677	183	0	205	74	0	471	80	261	264	398	8353

TABLE 4 Pup production estimates for sites other than those covered by aerial surveys. See Figure 1 for location of sites

Year	Farne Islands	Isle of May	SW England	Wales	Donna Nook	Helmsdale	Eriboll	Shetland
1956	751	-	-	-	-	-	-	-
1957	854	-	-	-	-	-	-	-
1958	869	-	-	-	-	-	-	-
1959	898	-	-	-	-	-	-	-
1960	1020	-	-	-	-	-	-	-
1961	1141	-	-	-	-	-	-	-
1962	1118	-	-	-	-	-	-	-
1963	1259	-	-	-	-	-	-	-
1964	1439	-	-	-	-	-	-	-
1965	1404	-	-	-	-	-	-	-
1966	1728	-	-	-	-	-	-	-
1967	1779	-	-	-	-	-	-	-
1968	1800	-	-	-	-	-	-	-
1969	1919	-	-	-	-	-	-	-
1970	1987	-	-	-	15	-	-	-
1971	2041	-	-	-	1	-	-	-
1972	1617	-	-	-	0	-	-	-
1973	1678	-	107	-	0	-	-	578
1974	1668	-	-	-	-	-	-	-
1975	1617	-	-	-	-	-	-	-
1976	1426	-	-	-	-	-	-	-
1977	1243	-	-	645	-	-	-	700
1978	1162	-	-	-	-	-	-	-
1979	1320	300	-	-	-	-	-	-
1980	1118	499	-	-	-	-	-	-
1981	992	505	-	-	34	-	-	-
1982	991	603	-	-	43	-	-	-
1983	902	336	-	-	-	-	-	-
1984	778	517	-	-	30	94	406	-
1985	848	810	-	-	53	-	-	-
1986	908	891	-	-	35	-	-	-
1987	930	865	-	-	72	-	-	-
1988	812	690	-	-	54	-	-	-
1989	892	935	-	-	94	280	666	-
1990	1004	1185	-	-	152	-	-	-
1991	927	1218	-	-	223	321	-	-

TABLE 5 Estimated size of the population associated with all major grey seal breeding sites in Scotland and Northumberland 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	Female + Male Population
1984	15397	30230	53127
1985	16826	32779	57605
1986	17730	35614	62603
1987	19453	38554	67755
1988	18424	36926	64895
1989	20456	40002	70291
1990	21626	43456	76358
1991	23785	47053	82681
1992	-	51069	89749

TABLE 6
Declared number of grey seals killed under licence in Great Britain between 1970 and 1991, including those taken under scientific permit. All figures refer to pups unless otherwise indicated.

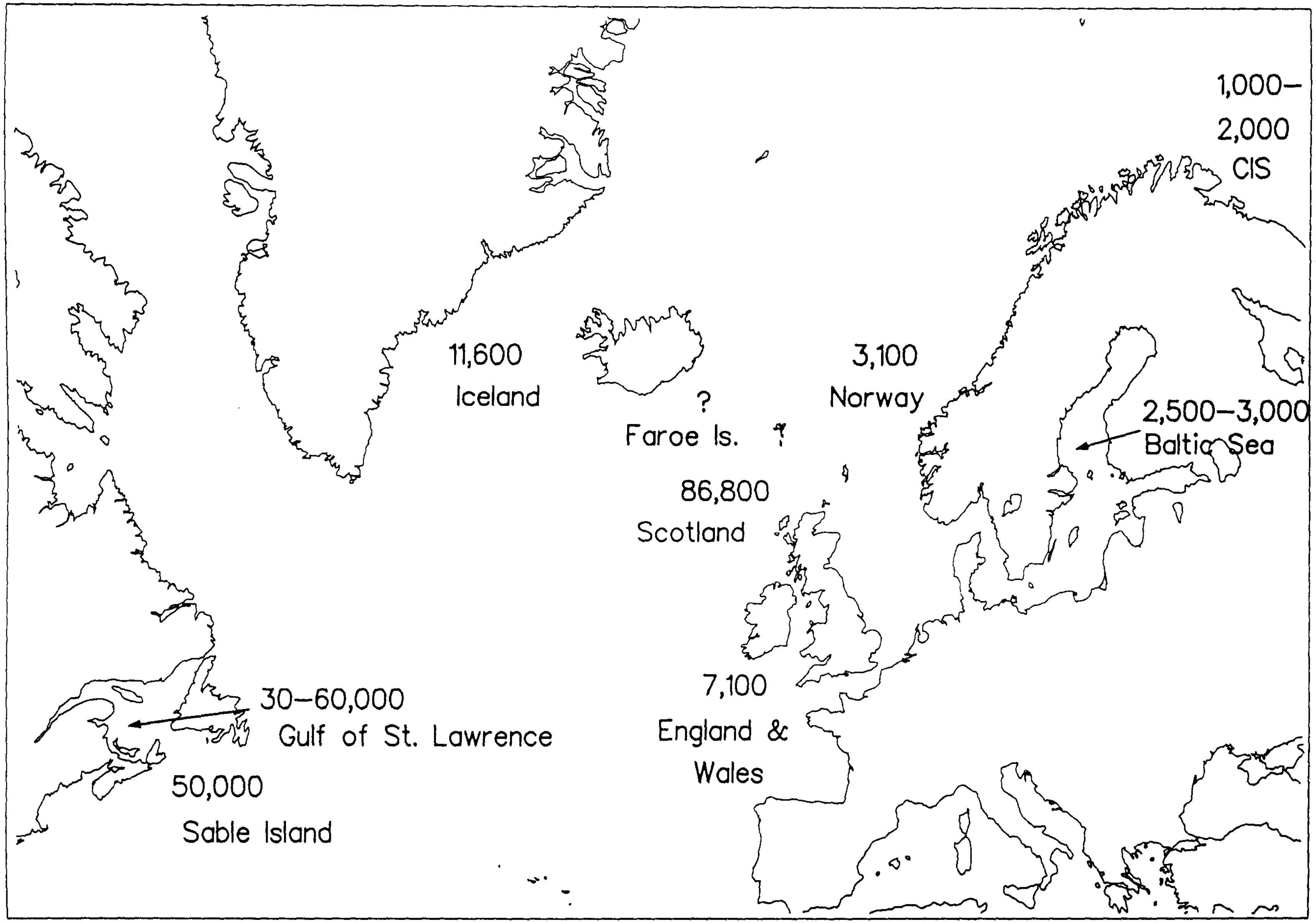
Year	Orkney and east coast	Outer Hebrides	Shetland	Farne Islands
1970	726 + 5 ad		60	6
1971	975	5 + 6 ad	31 + 8 ad	5 + 12 ad
1972	699	7	30	581 + 748 ad
1973	837 + 4 ad	386	49	3 + 17 ad
1974	975	868	73	4 + 5 ad
1975	1050	754	68	804 + 663 ad
1976	1010 + 10 ad	600	72	4 + 4 ad
1977	841	394 + 324 ad	10	209 + 134 ad
1978	1067	85	59	117 + 58 ad
1979	1015	200 + 1 ad	37	137 + 80 ad
1980	1195	7 ad	40	35 + 58 ad
1981	1200 + 19 ad*	2 ad	40	64 + 162 ad
1982	1166 + 18 ad*	-	49	134 + 54 ad
1983	8 ad*	-	1 ad*	24 + 4 ad
1984	2 ad*	-	1 ad*	37
1985	1 ad*	4 ad* + 1 ad		37
1986	2 ad*	-		31
1987	21 ad*	15 ad*		13
1988	-	-		-
1989	-	-		-
1990	-	-		18
1991	-	-		12 + 1 ad

* taken by fishermen or fish farmers

MAIN GREY SEAL BREEDING SITES

FIGURE 1

Figure 2



Distribution and Abundance of Grey Seals in the North Atlantic

Figure 3 Mean Birth Dates in Main Island Groups

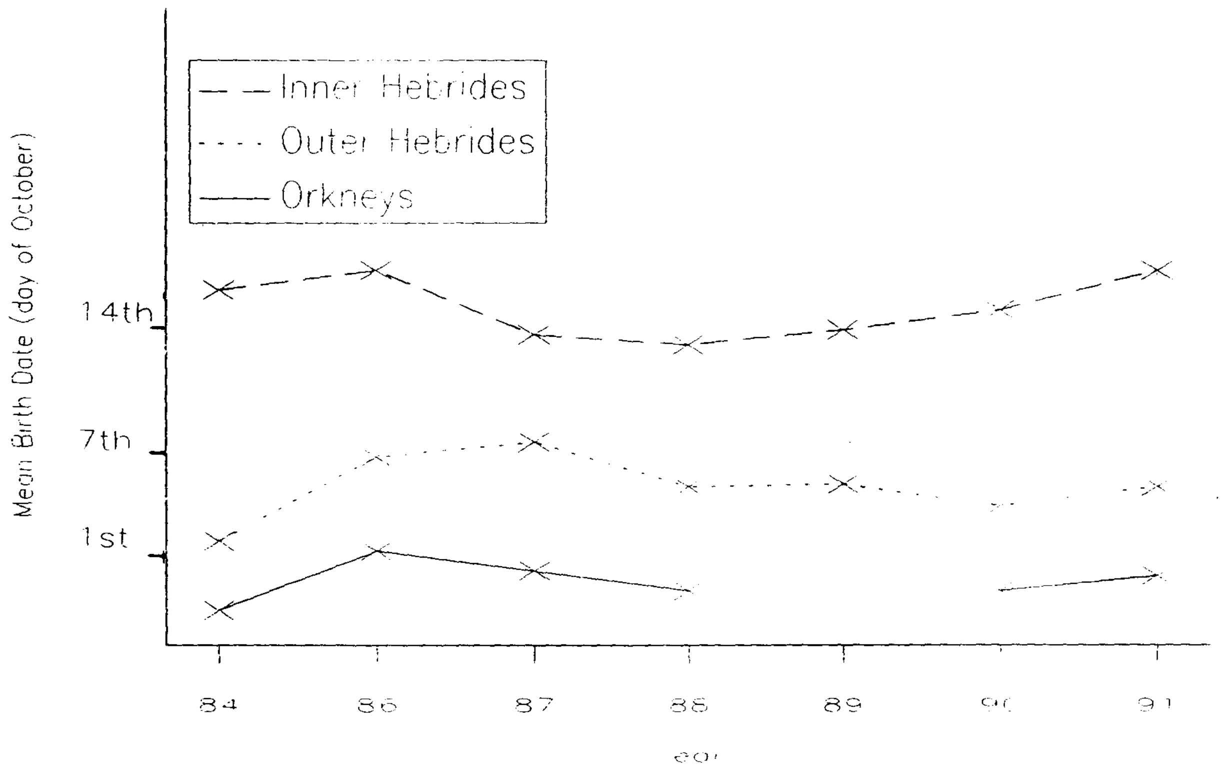


FIGURE 4

pup production in orkney

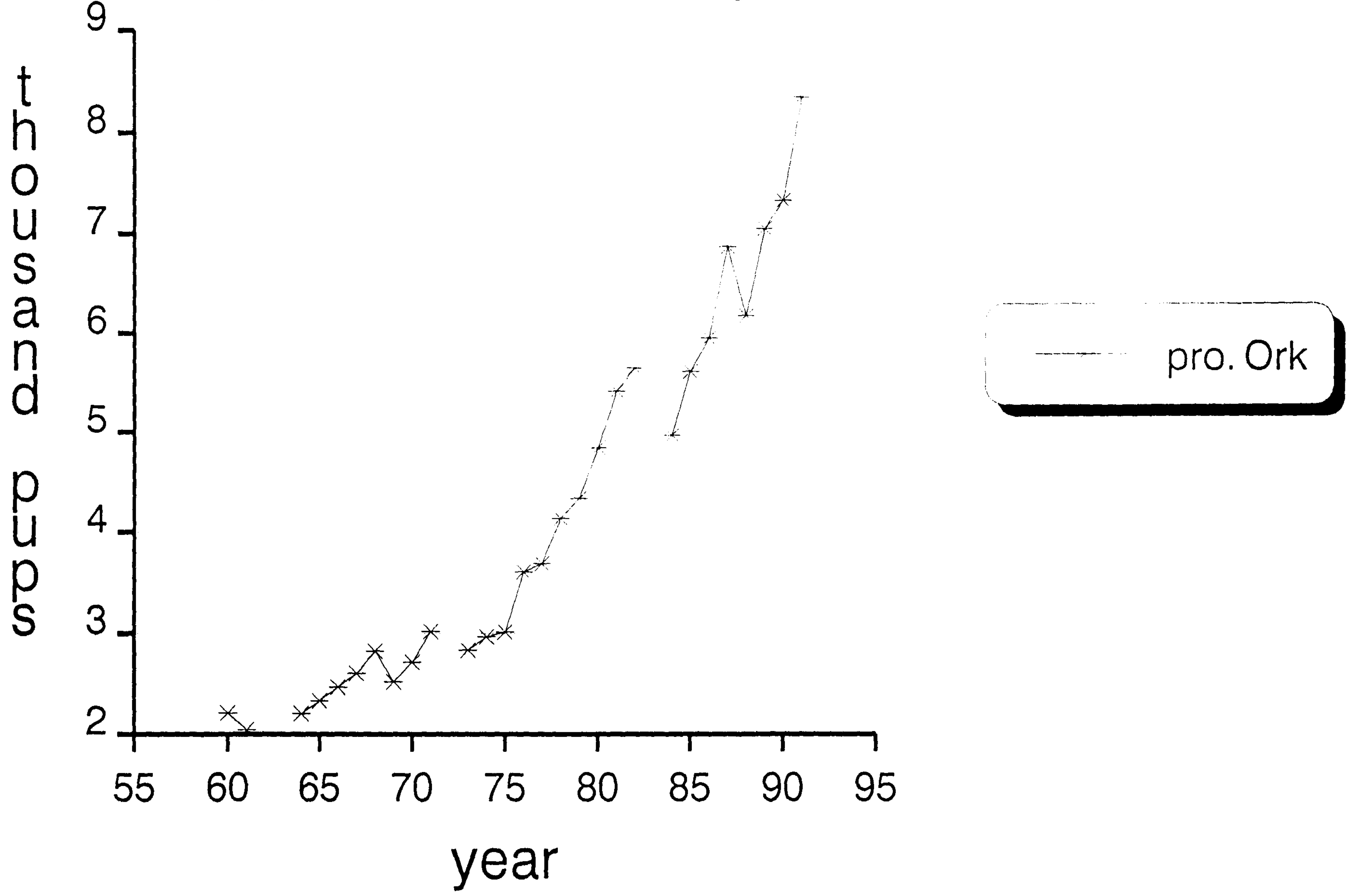
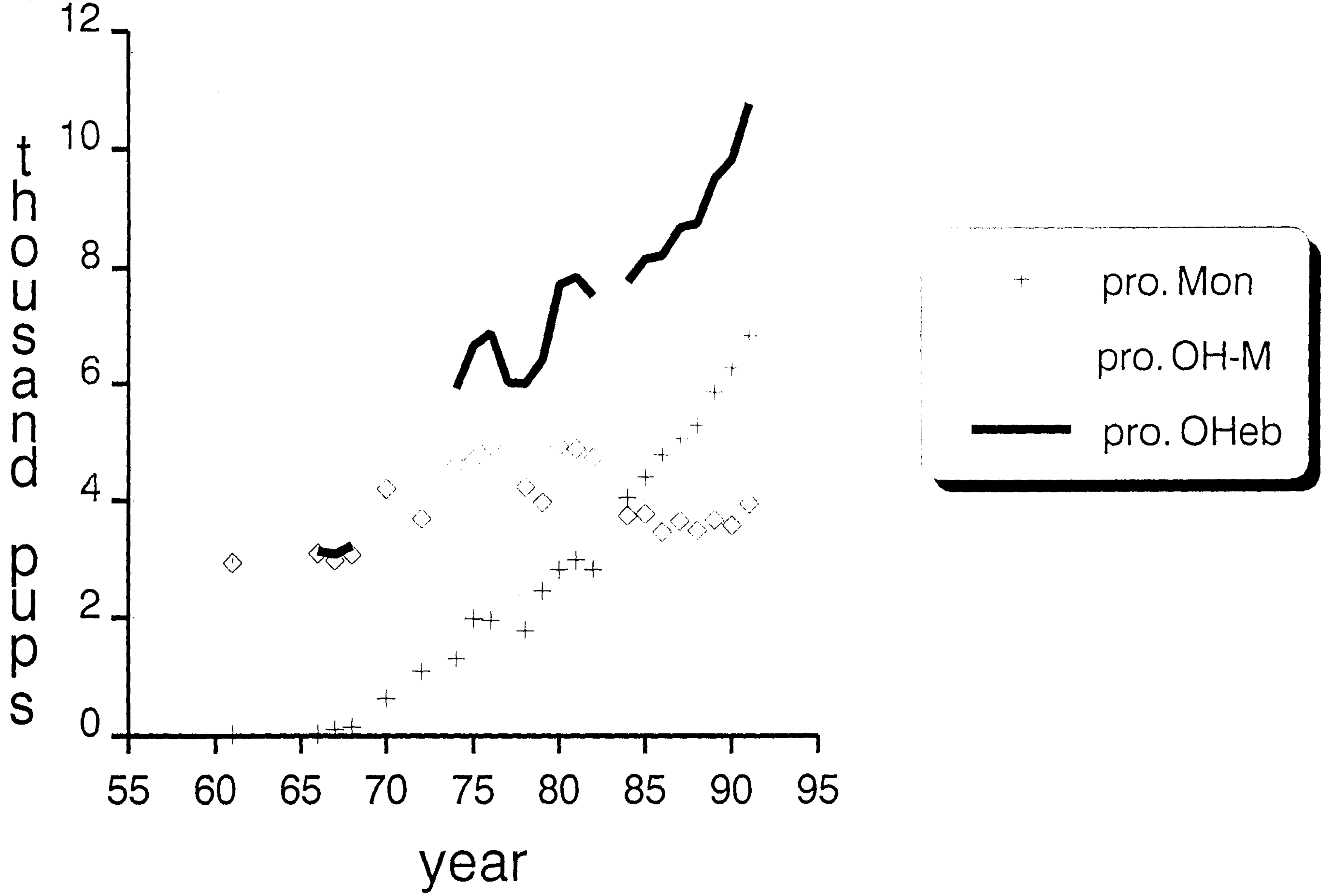


FIGURE 5

pup production in the outer hebrides



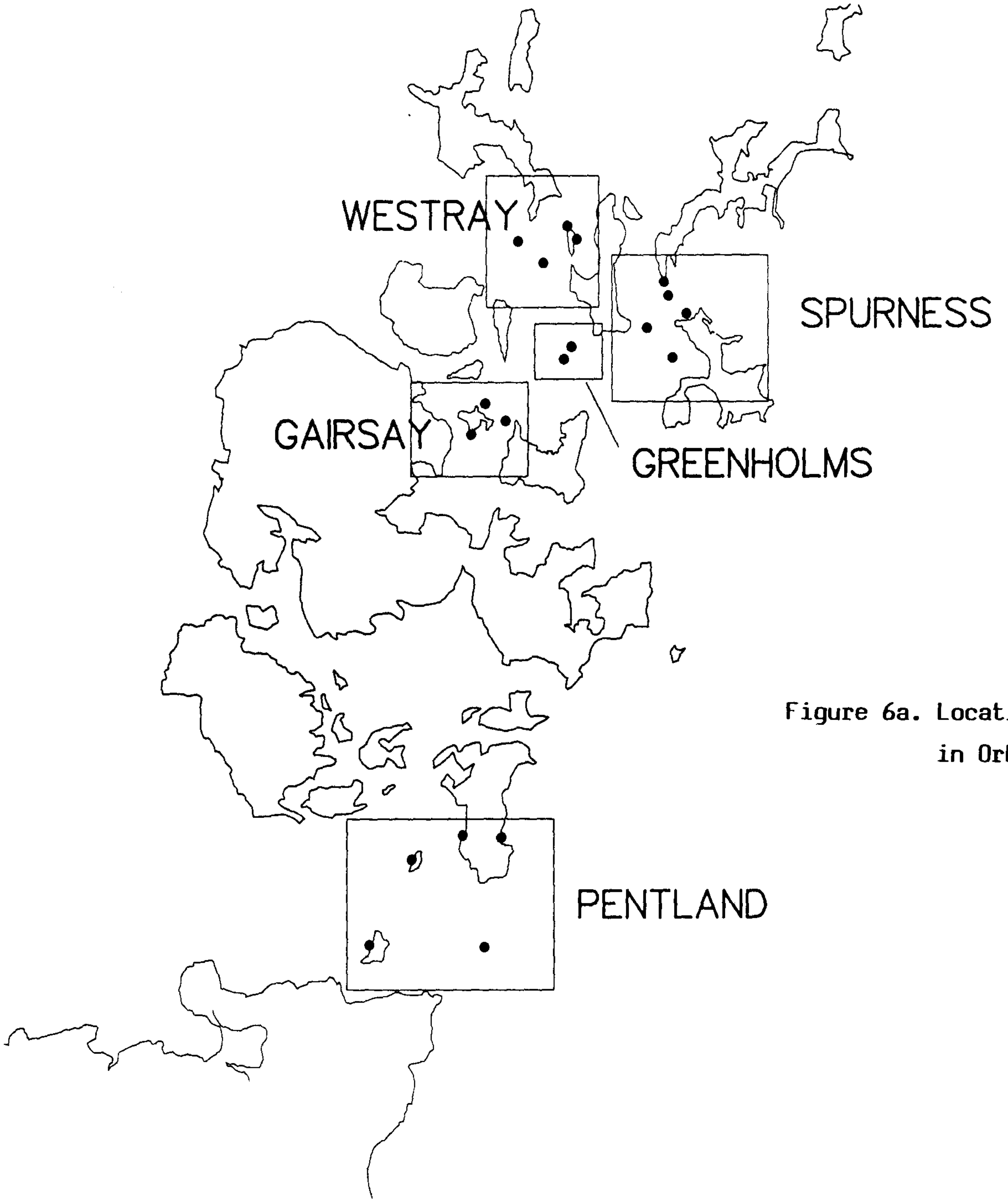


Figure 6a. Location of grey seal colonies in Orkney

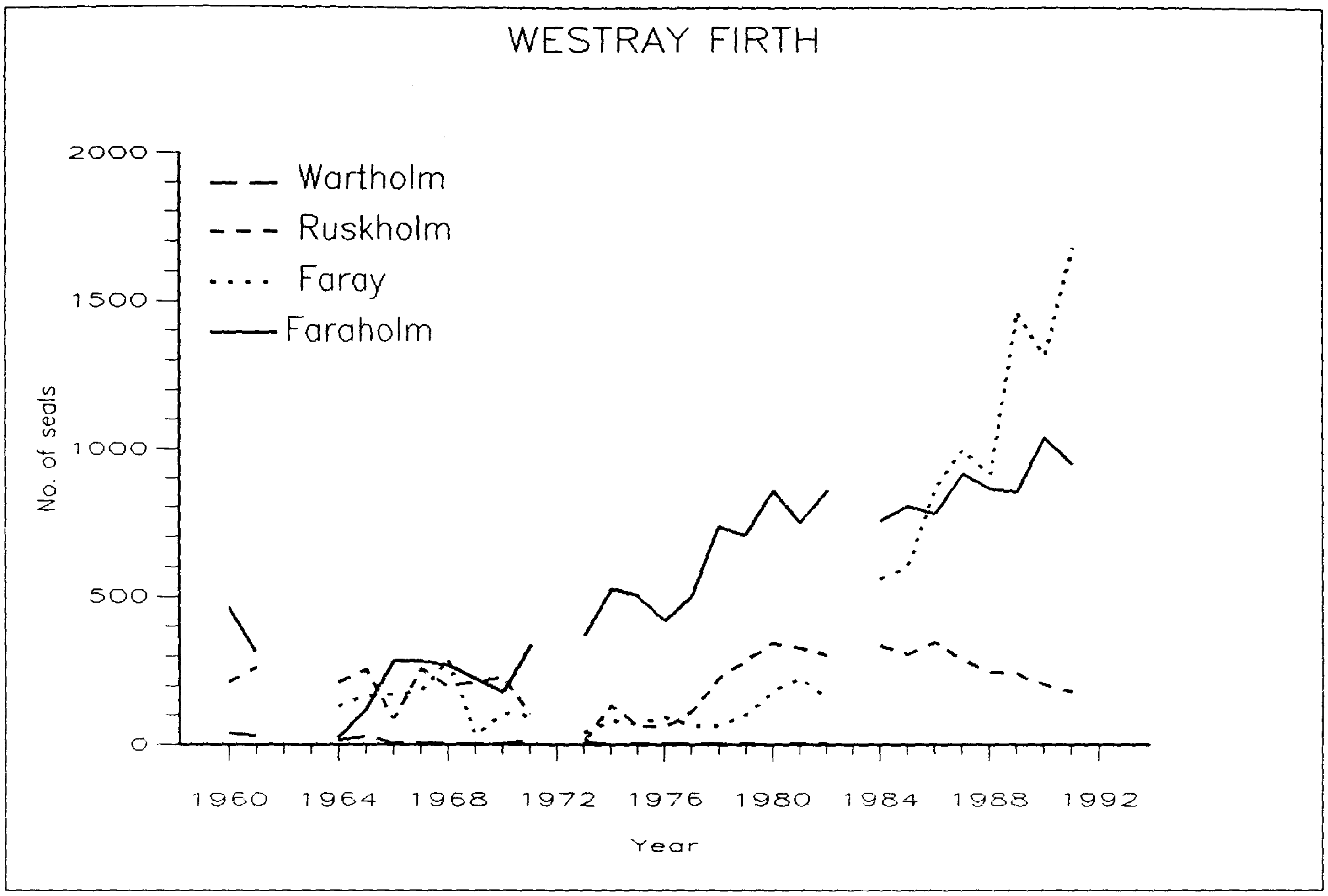


Figure 6b. Changes in pup production at grey seal colonies in the Westray Firth area of Orkney

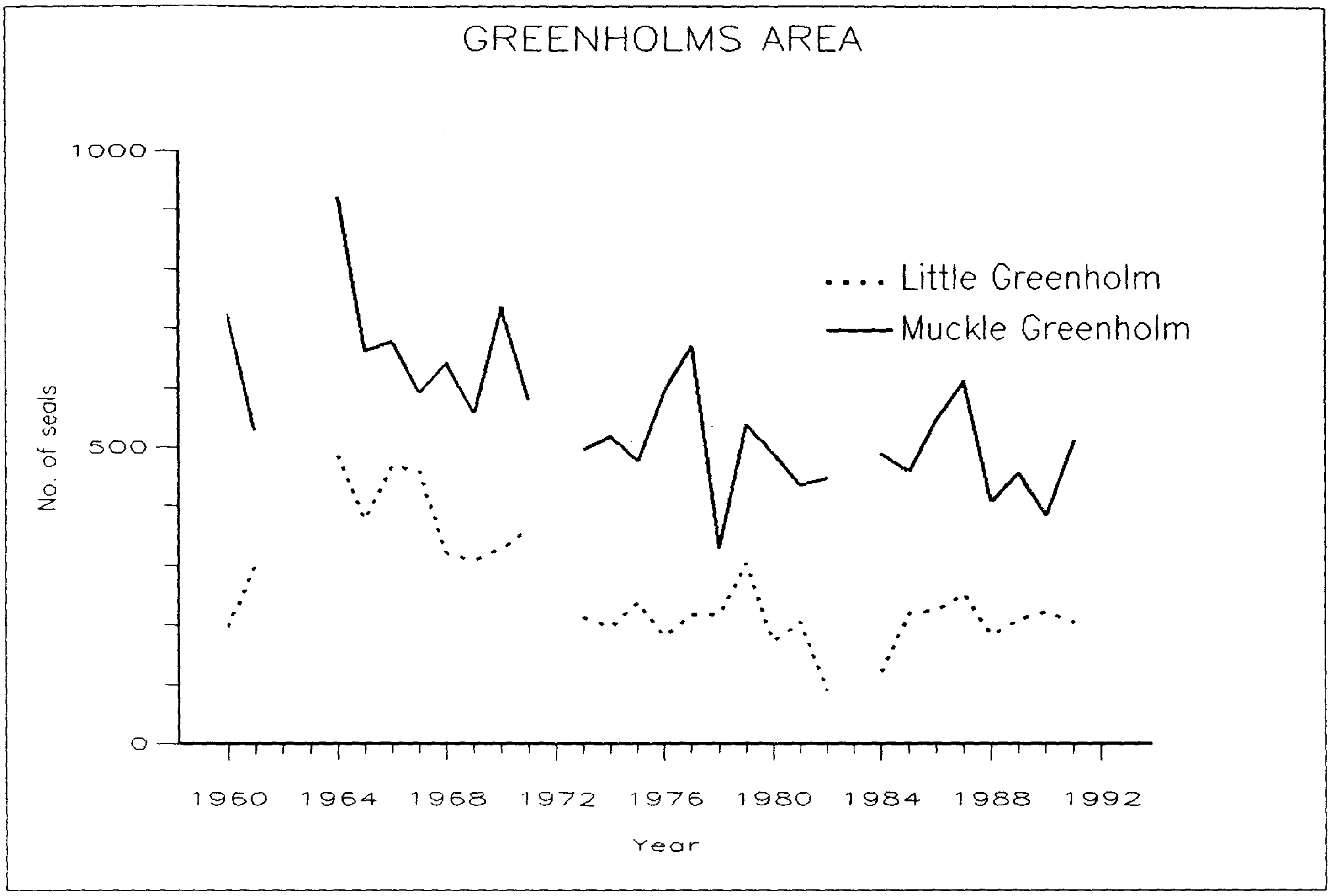


Figure 6d. Changes in pup production at grey seal colonies in the Greenholms area of Orkney.

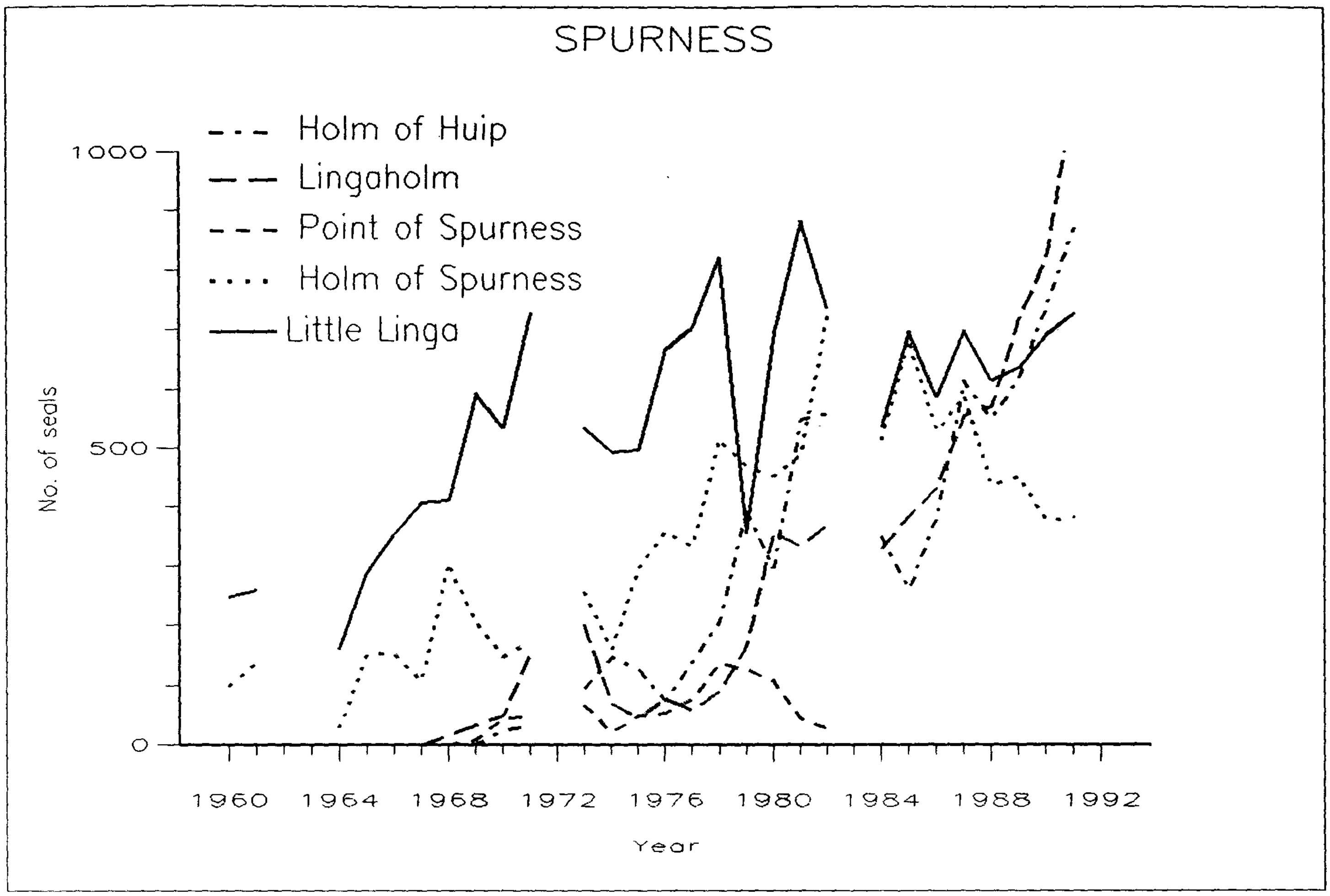


Figure 6c. Changes in pup production at grey seal colonies in the Spurness area of Orkney.

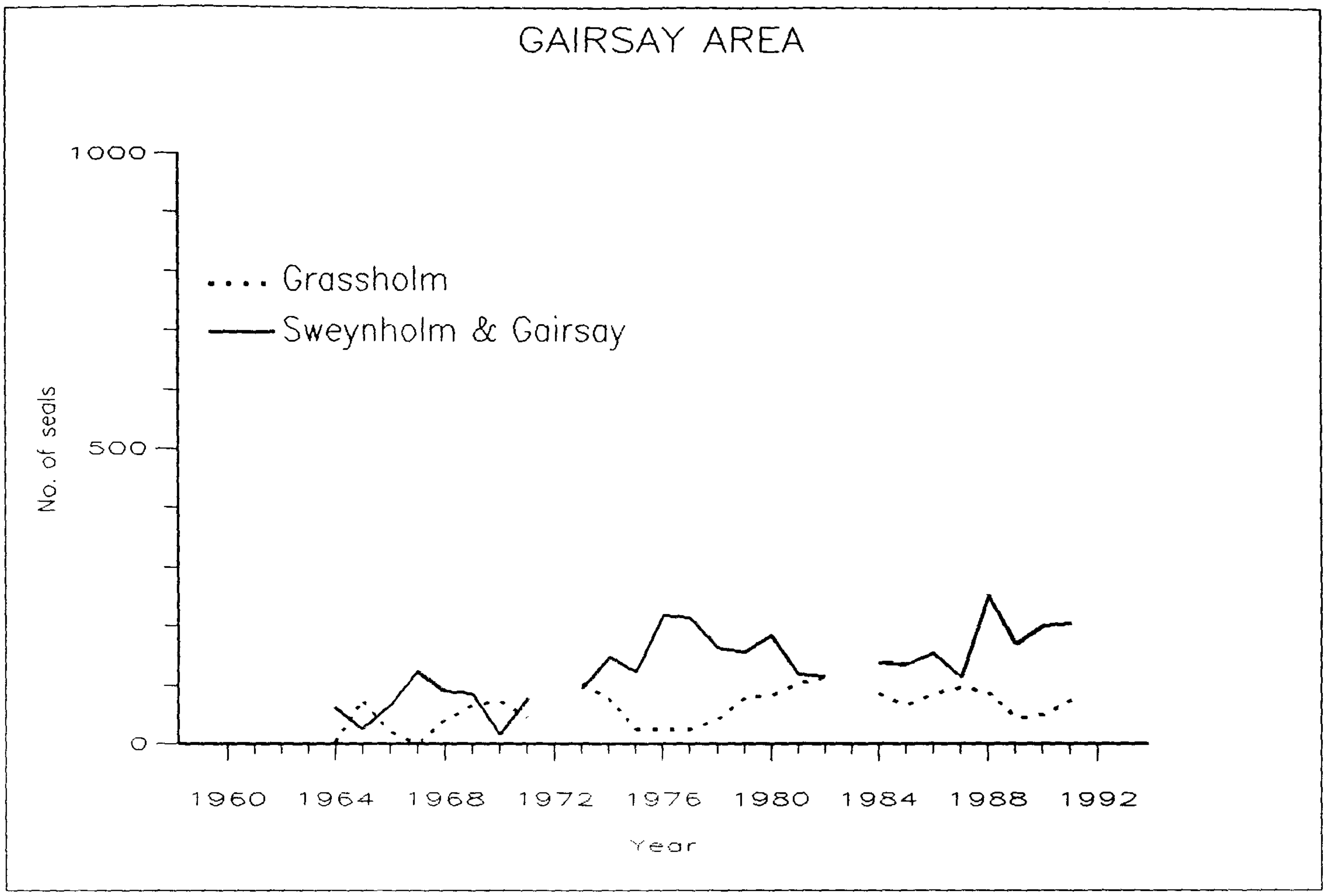


Figure 6e. Changes in pup production at grey seal colonies in the Gairsay area of Orkney.

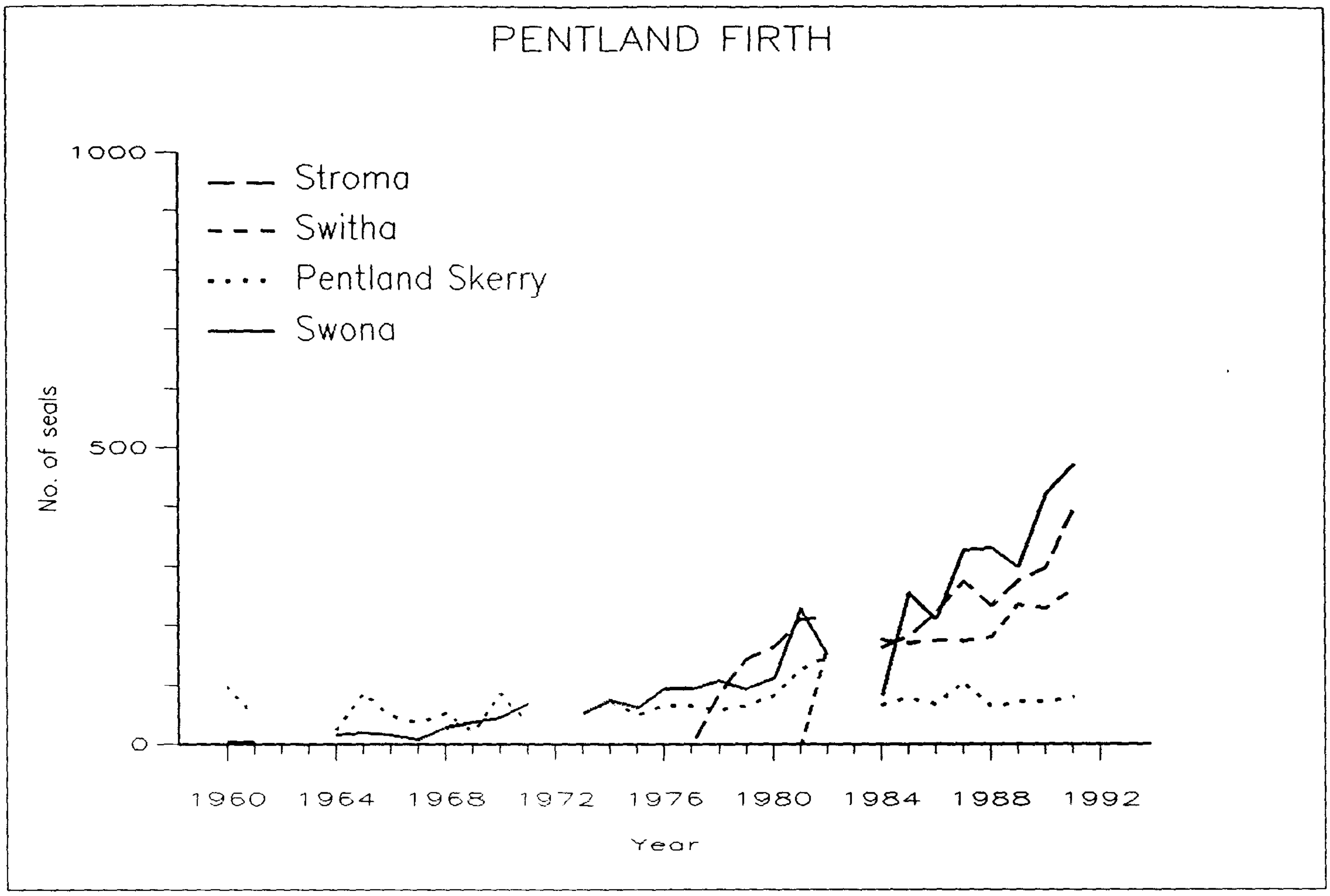


Figure 6f. Changes in pup production at grey seal colonies in the Pentland Firth, Orkney.

FIGURE 7

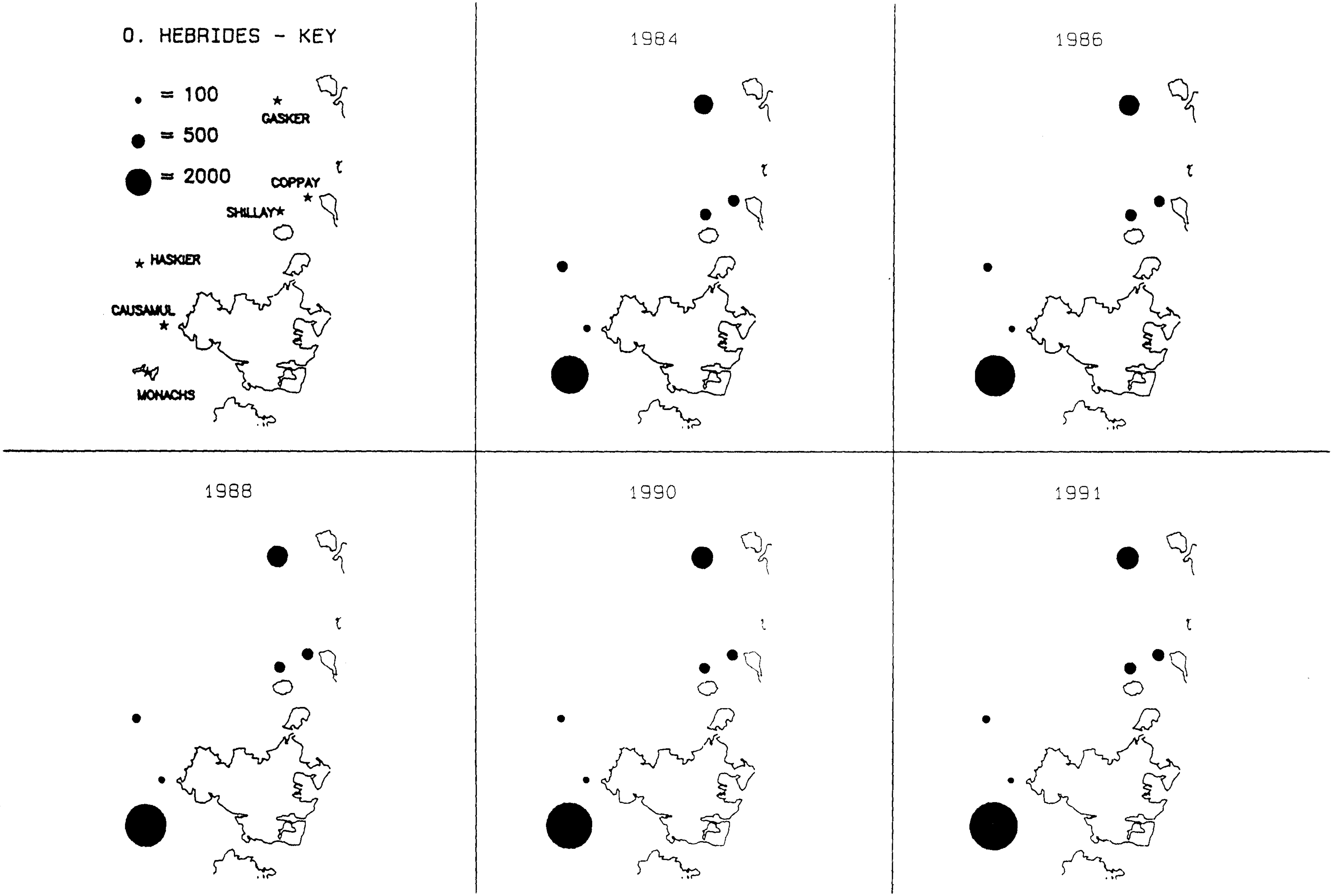

O. HEBRIDES - KEY
= 100
= 500
= 2000
GASKER
COPPAY
SHILLAY
HASKIER
CAUSAMUL
MONACHS
1984
1986
1988
1990
1991

FIGURE 8

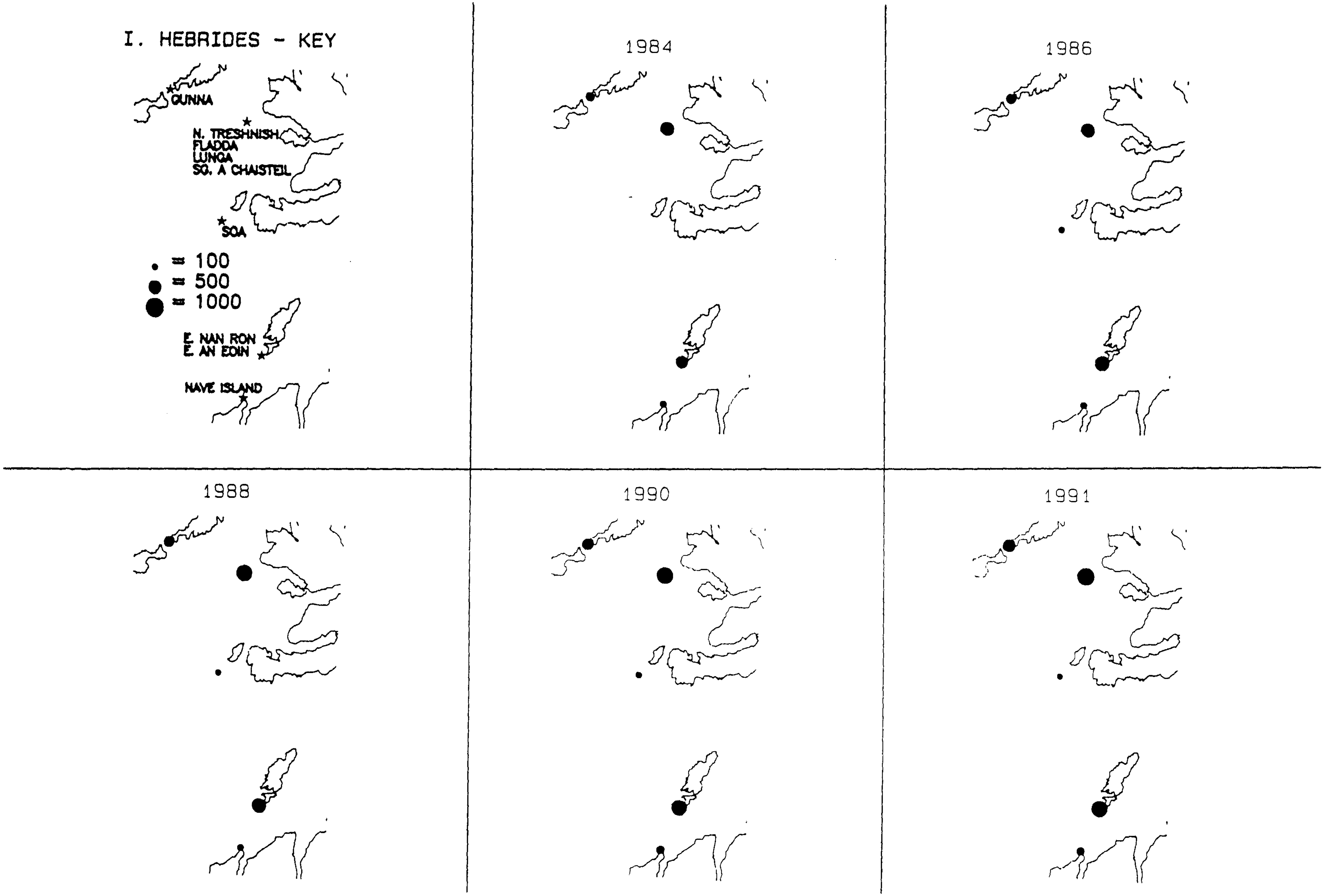

I. HEBRIDES - KEY
GUNNA
N. TRESHNISH
FLADDA
LUNGA
SG. A CHAISTEIL
SOA
= 100
= 500
= 1000
E. NAN RON
E. AN EOIN
NAVE ISLAND
1984
1986
1988
1990
1991

FIGURE 9

pup prodn. main areas excl. inner hebs.

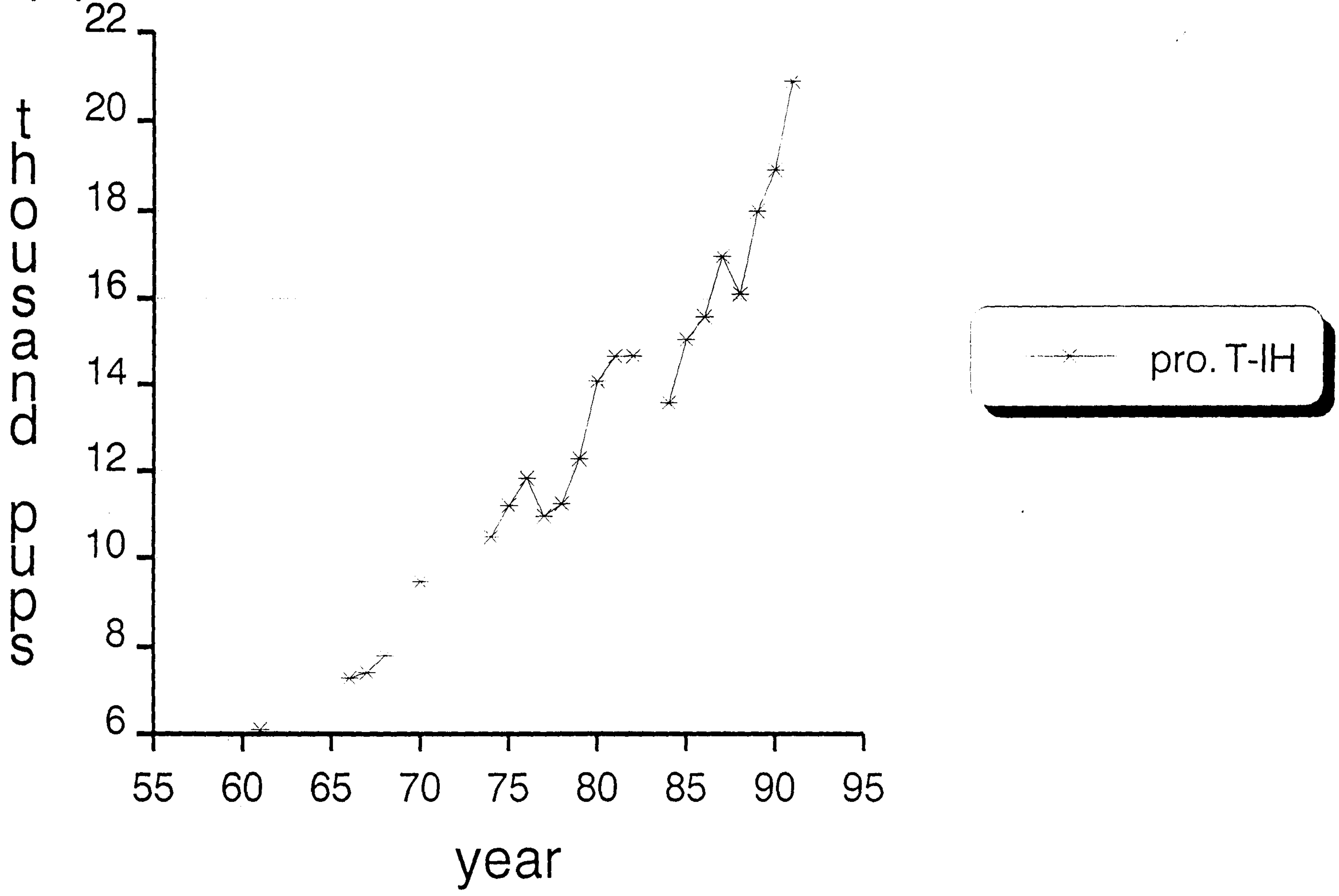


FIGURE 10

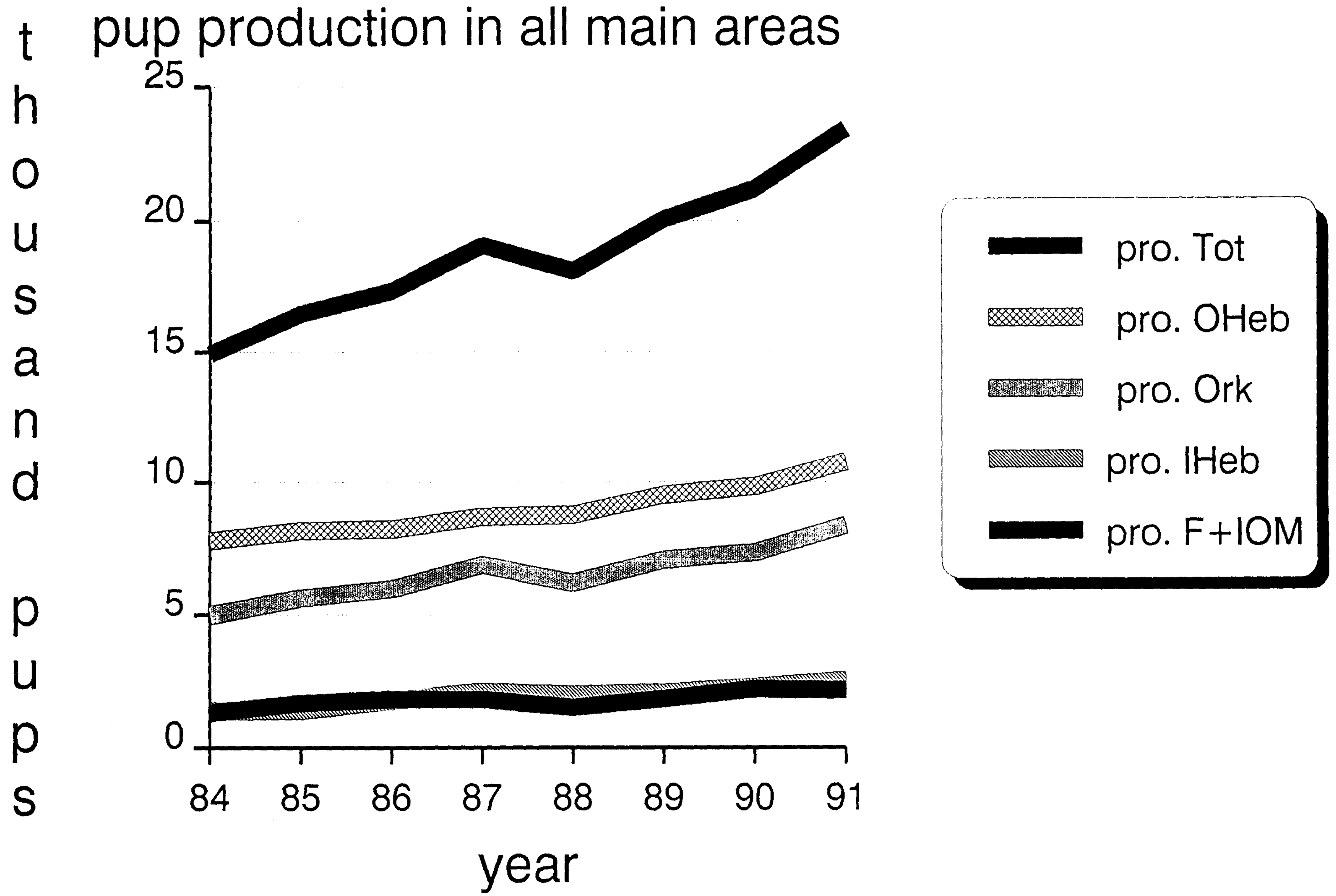

pup production in all main areas
thousand pups
25
20
15
10
5
0
84
85
86
87
88
89
90
91
year
pro. Tot
pro. OHeb
pro. Ork
pro. IHeb
pro. F+IOM

FIGURE 11

population estimates for the farnes+IOM

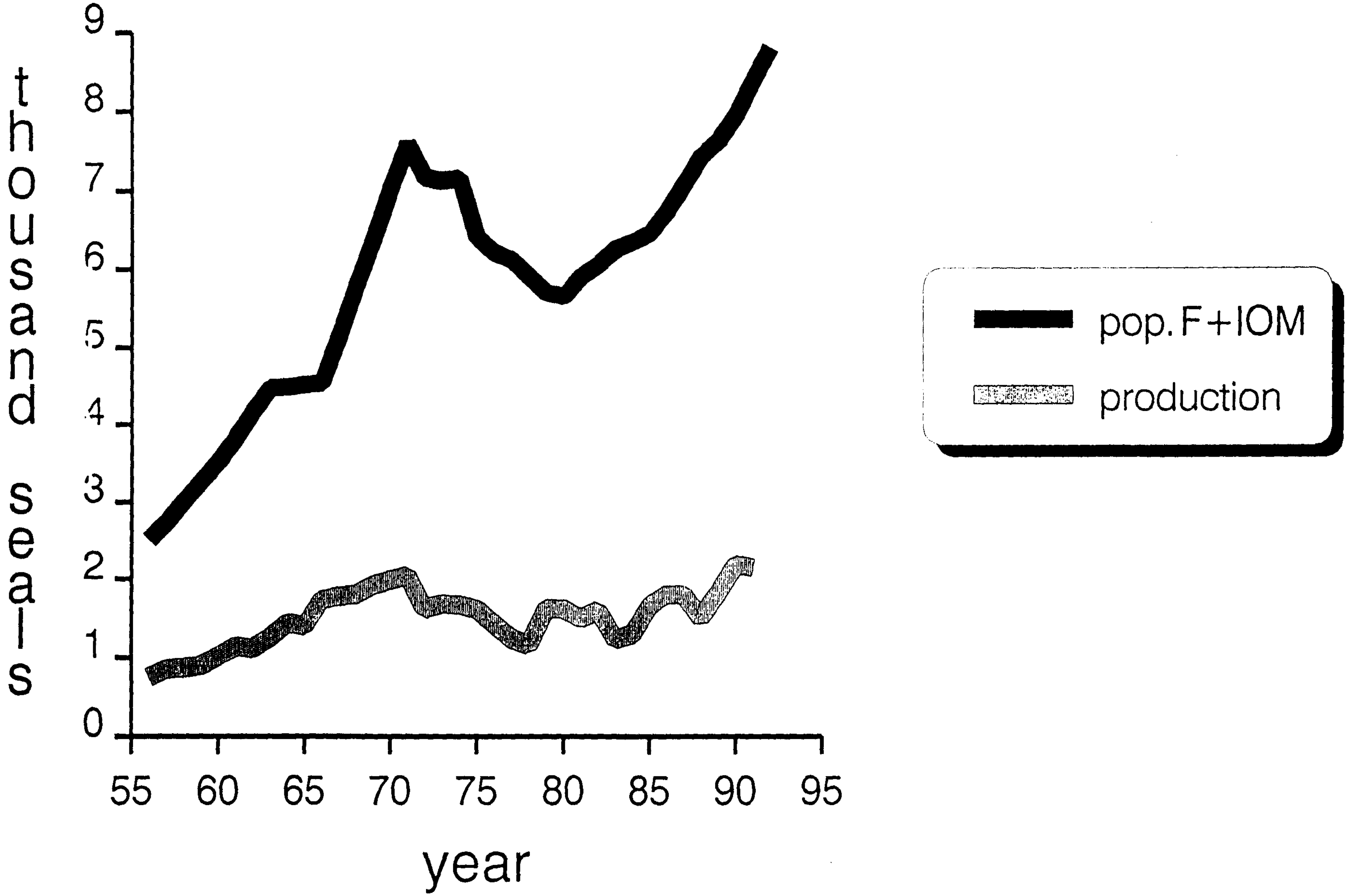
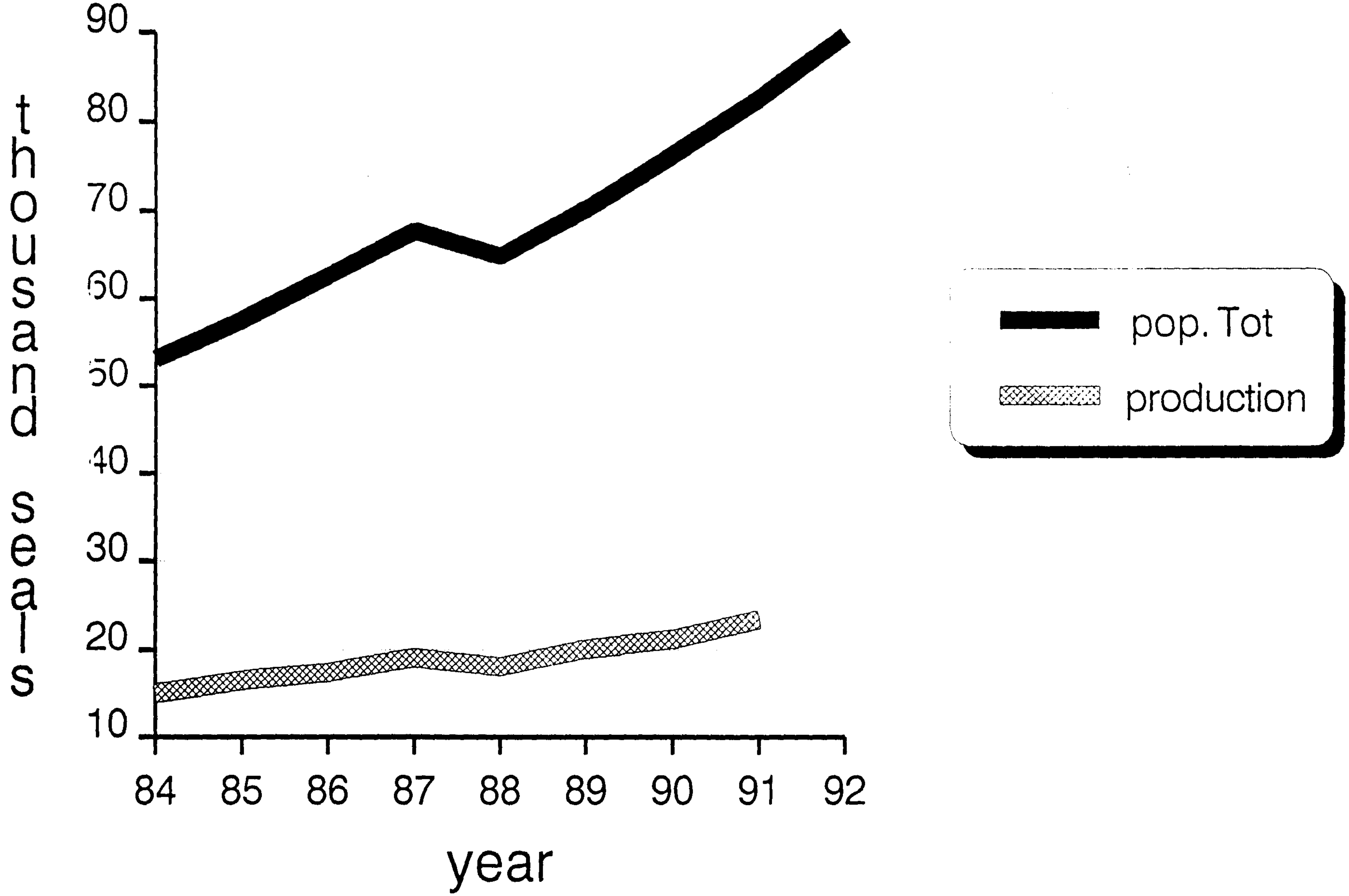


FIGURE 12

poulation estimates for all main areas



GREY SEAL DISTRIBUTION - BY 10KM SQUARES

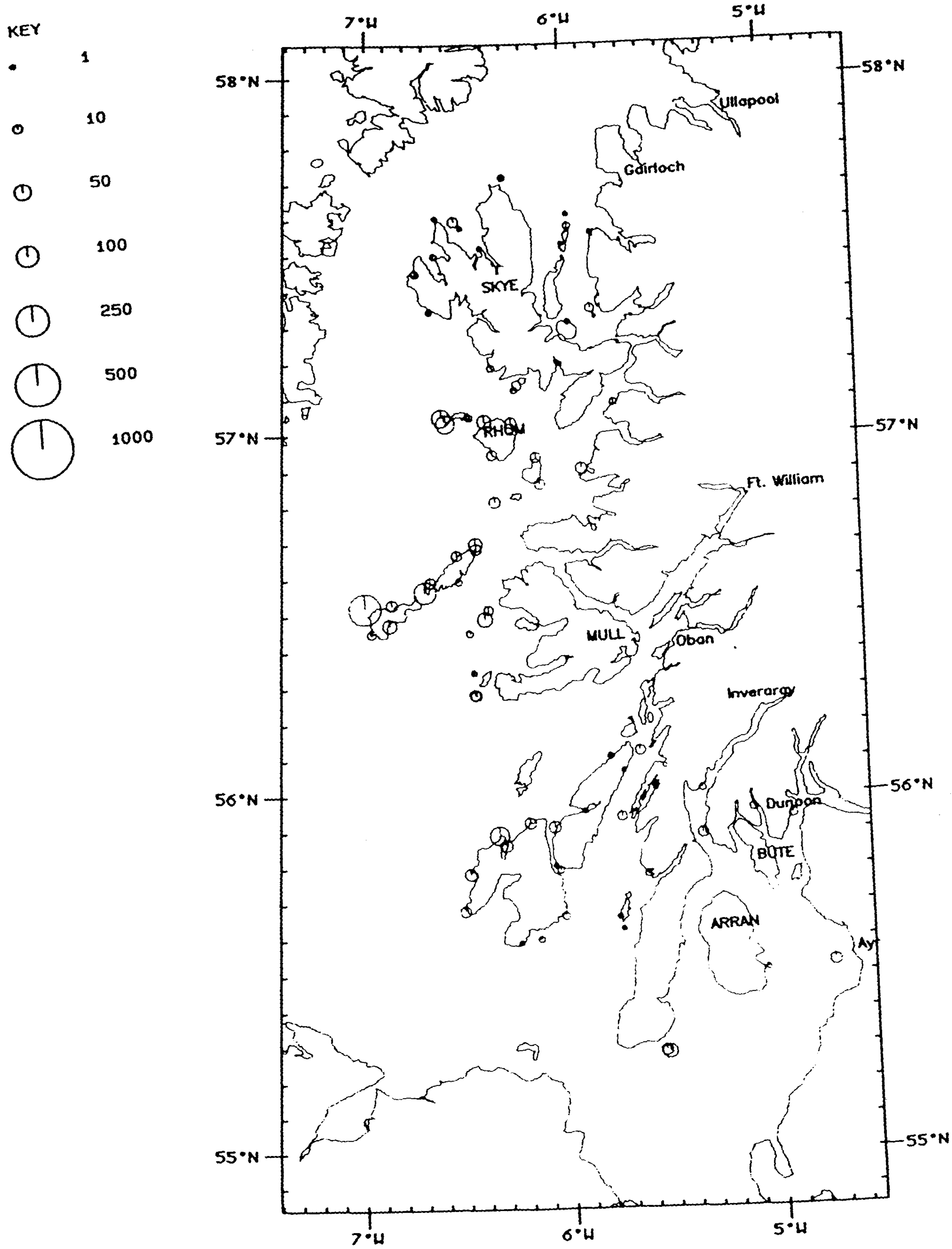


Fig. 13. August grey seal distribution from common seal surveys

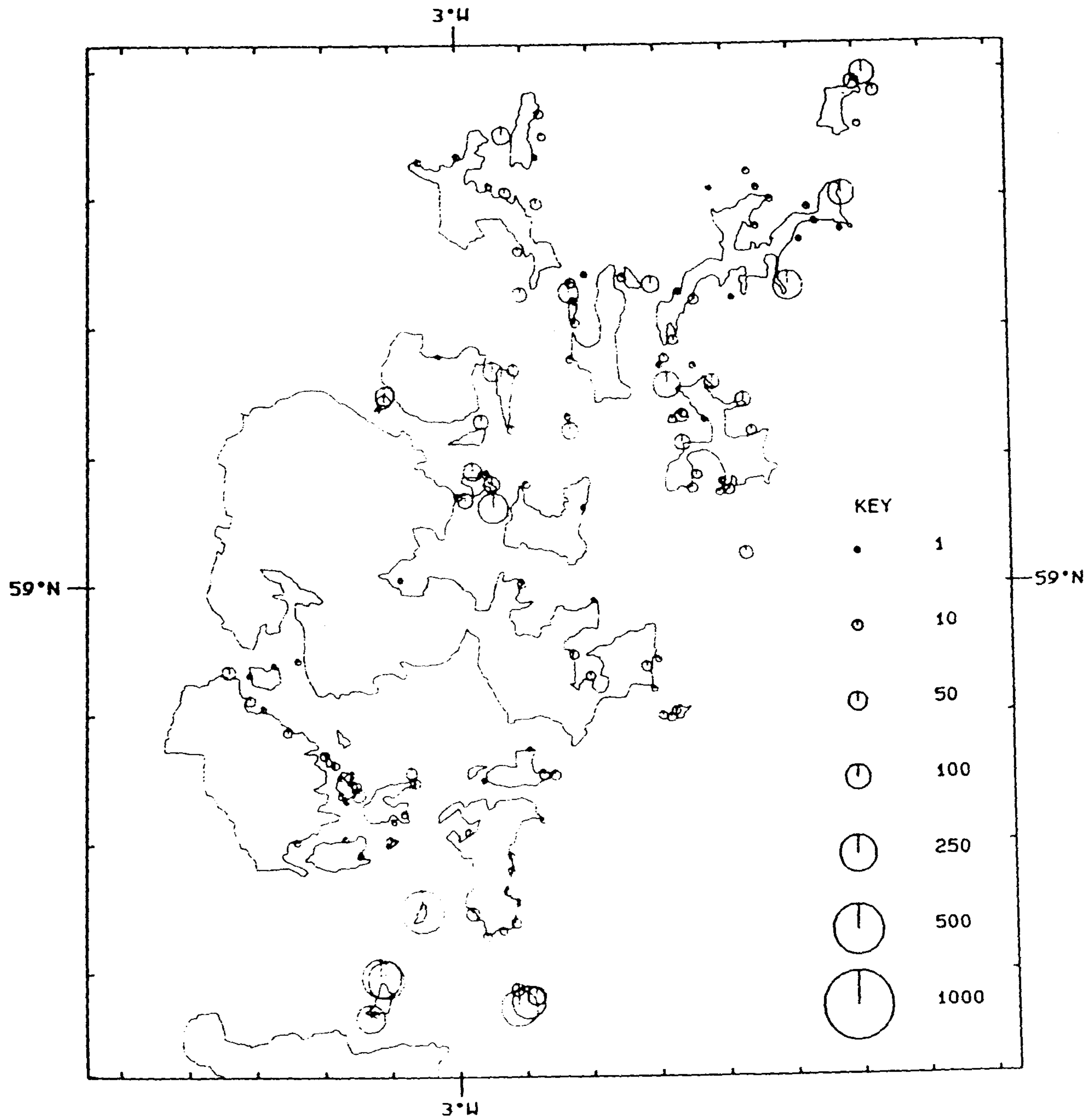


Fig. 14. Numbers of grey seals counted in Orkney during August 1990 during common seal surveys

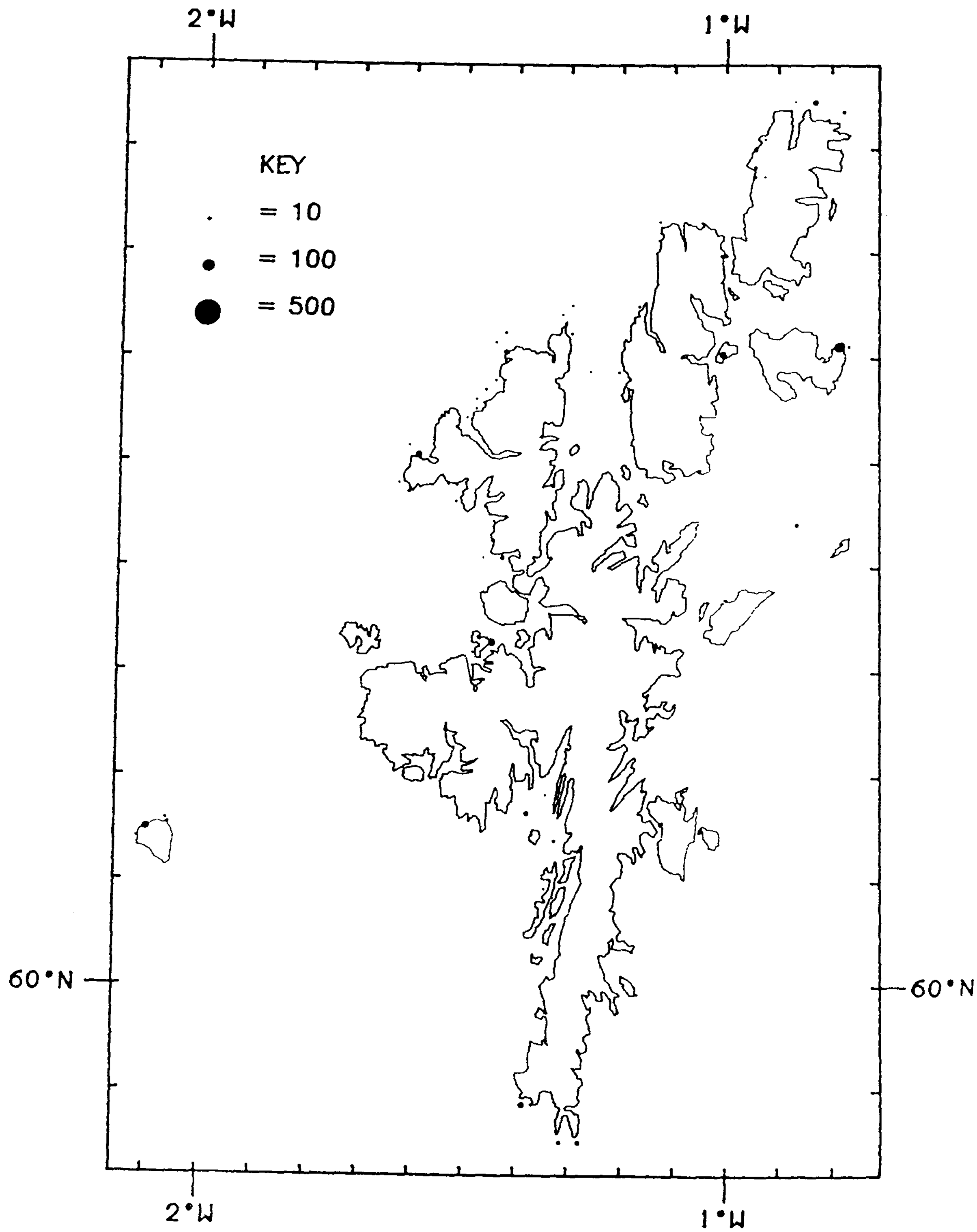


Figure 15. Distribution and numbers of grey seals counted in Shetland during surveys of common seals carried out in August 1991.

Appendix 1:

Estimates of population size and related parameters for the Farne Islands' grey seal population.

A.R. Hiby

SUMMARY

This report describes an attempt to estimate the trajectory of population size of female grey seals at the Farnes since 1956 and to place confidence intervals on the estimate for 1972. In order to avoid introducing previously estimated population sizes, and thereby introducing an unknown degree of uncertainty into the population size estimates, the method attempts to estimate simultaneously all parameters and population sizes from all the available data using a maximum likelihood approach. Confidence limits are then placed on the 1972 population estimate using the likelihood ratio method. The validity of the application of this method in this case is investigated using simulation studies. These are also used to investigate the effect on the estimation procedure of violating some of the many assumptions required to construct a model of population growth involving a manageable number of parameters.

INTRODUCTION

This report describes a procedure which has been used to estimate the size of the grey seal population associated with the Farne Islands (defined as the number of females of age one and over that were born at the Farne Islands, or the Isle of May, and which are alive at the time of the breeding season in each year) from 1956 to 1982, and the confidence regions for these estimates.

This procedure uses the following data:-

(1) The number of pups born each year from 1956 to 1982 (p_t, where t = 56, ..., 82).

(2) The number of female pups killed each year in management culls.

(3) The number of adult females killed each year in these culls.

(4) The ages of all the animals killed. The large culls of 1972 and 1975 did not take representative samples of the population. This is because the number of seals taken on each island were not in proportion to the size of the population on that island. The age structures of these culls have been processed to give random samples of the population age structure in those years, for animals above the age (i_o) at which they appear to be fully represented in the culls. (C_t is the total number of females above this age in the cull in year t, and $c_{i,t}$ is the number in each age class - $i = i_o, ..., 29$).

(5) Observations from a sample of 52 sexually mature females take in 1981, 49 of which were pregnant.

A mathematical model of the growth of the female section of the Farnes' population is used to give a joint probability density for these data, conditional on a number of unknown parameters. This probability density function is then maximised with respect to these parameters to give maximum likelihood estimates. The parameters are then used to estimate population size in each year.

The following notation is used in the model:-

$n_{i,t}$	-	number of females aged i alive in the population at the time of the breeding season in year t - before any culls have take place.
$n_{29,t}$	-	number of females age 29 and over in year t.
P_t	-	total female population in year t (i.e. $P_t = \sum_{i=1}^{29} n_{i,t}$).
S_j	-	survival of natural mortality from birth to age 1.
S	-	annual survival for all other age classes (note that $n_{29,t+1} = S(n_{28,t} + n_{29,t})$).
F	-	average number of offspring produced each year by a female aged 7 or above. Age-specific fecundities for age classes under 7 are taken from Harwood and Prime (1978, J. appl. Ecol. 15: 401-11), except that the small number of females which reproduce at age 4 is ignored.

To obtain $n_{1,t+1}$ the observed number of pups born in year t (pt) is divided by two (to give the number of female pups) and multiplied by 0.8 (to allow for deaths from natural mortality before the pups culls); the number of female pups killed in year t is then subtracted from this and the resulting figure is multiplied by $S_j/0.8$.

Given starting values for S_j & S, the set of observed pup productions and an initial age vector the model will generate a series of age vectors for all subsequent years. The age vector in 1956 was calculated by assuming that the population had attained a stable age distribution. Thus the procedure estimates the parameters S_j, S, λ (the annual rate of increase of population) and P_t by fitting the model to the available data.

Up to this point the model is entirely deterministic. The effect of ignoring stochasticity in, for example, the proportion of seals of each age surviving natural mortality, and in the sex ratio of newborn pups, was investigated by using simulation models of population growth, described in a later section.

We now describe how the model is used to determine the joint probability density function for the available data, conditional on the unknown parameters. The model defines the expectation of each data point, the density then follows from assumptions concerning the variability in pup production and sampling variability in the structure of adult culls.

Expected pup production in each year, conditional on the parameters and earlier observed pup productions, is obtained by applying age specific fecundities to the age structure generated by the model for that year. To obtain age specific fecundities we assume that once a female has had a pup the probability she has a pup in each subsequent year is independent of age and independent from year to year. The proportion of females having their first pup at each age has been determined by studies of tooth growth rings in adult seals (Harwood & Prime, 1978).

Using those results we have the expected pup production in t:

$$E(p_t) = 0.16\ n_{5,t} + (0.45 + 0.16F)\ n_{6,t} + \sum_{i_o}^{29} \frac{Fn_{i,t}}{2}$$

where F, the mean fecundity for sexually mature females, is a further parameter to be estimated. In fact F replaces S_j as an independent parameter for, once S, λ and F are specified, S_j is easily determined using a balance equation for growth of a population with a stable age structure.

The probability density of p_t, conditional on earlier pup productions, is obtained by assuming p_t is normally distributed about $E(p_t)$ with standard deviation σ_t, i.e:

$$f\ (p_t \mid p_{56} \cdots p_{t-1}, \underline{\theta}) = N\ (E(p_t \mid p_{56} \cdots p_{t-1}, \underline{\theta})\ ,\ \sigma_t)$$

where $\underline{\theta}$ is the vector of parameters S, λ, P_{56} and F.

The joint probability density for p_{56}, p_{57} ... p_t is then obtained by multiplying the conditional density by the joint density for p_{56}, p_{57}, ... p_{t-1}. Only pup productions before 1972 are used. This is because adult culls starting in 1972 have caused a drop in observed pup productions which is larger than would be expected purely as a result of the number of mature females killed, and which is probably due to emigration to other breeding sites. There is no provision in the model for reproducing this effect.

σ^2_t gives the expected squared difference between predicted and observed pup productions in year t. In the results given in this report we have taken σ^2_t to be constant at σ^2. We have also repeated the estimation procedure with σ_t proportional to $E(p_t)$. This gave very similar results.

We cannot write down the joint density for pup productions from 1956 to 1971, which will form the first term in the likelihood function:

To extend the likelihood function to include data from the 1972 and 1975 culls of adult females, we need the

$$L_1 \; (\underline{\theta}, \sigma \mid p_{56} \cdots p_{71}) = \prod_{t=56}^{71} \frac{1}{\sqrt{2\pi\sigma^2}} \exp\left\{-\frac{1}{2\sigma^2} \left(E (p_t \mid p_{56} \cdots p_{71}, \underline{\theta}) - p_t\right)^2\right\}$$

expected age class frequencies conditional on the model parameters and earlier pup productions. Let i_o represent the minimum age at which females are fully represented in the breeding beach culls, C_t the total number of females of age i_o or over killed in year t, and $c_{j,t}$, the number of females of age j killed in year t. The expectation of $c_{j,t}$ conditional on model parameters and earlier pup productions and culls is:

$$E\,(c_{j,t}) = C_t \frac{n_{jt}}{\sum_{i=i_o}^{29} n_{i,t}}$$

This is only valid for t = 75 if we assume that the 1972 cull did not effect the age structure of the population, except by the removal of the animals killed in 1972 from each age class. Assuming the culls represent random samples, the probability distribution for $C_{i_o,t}$ to $C_{29,t}$ is multinomial. This gives the joint probability distribution for the age structured culls is 1972 and 1975, which forms the second term in the likelihood function:

$$L_2\left(\underline{\theta} \mid c_{i_o,72} \cdots c_{29,72} \; ; \; c_{i_o,75} \cdots c_{29,75}\right)$$

$$= \frac{C_{72}\,!}{c_{i_o,72} \cdots c_{29,72}} \prod_{j=i_o}^{29} \left(\frac{n_{j,72}}{\sum_{i=i_o}^{29} n_{i,72}}\right)^{c_{j,72}} \cdot \frac{C_{75}\,!}{c_{i_o,75} \cdots c_{29,75}} \prod_{k=i_o}^{29} \left(\frac{n_{k,75}}{\sum_{i=i_o}^{29} n_{i,75}}\right)^{c_{k,75}}$$

Lastly we extend the likelihood function to include the results of a sample of 52 sexually mature females taken before the breeding season in 1981. Let n_p represent the number of females found to be pregnant, and let a further parameter M represent the number of sexually mature females in the population breeding at the Farnes in 1981. Note that M is not simply that part of the total female population in 1981 which is sexually mature because, following the 1972 and 1975 culls, a proportion of the sexually mature females which have been born at the Farne Islands no longer breed there. Then the pregnancy rate in the population at the Farnes in 1981 was p_{81}/M and, assuming the cull was a random sample, the distribution of n_p is binomial, $B(52, p_{81}/M)$. Furthermore, assuming the breeding season culls have not effected the fecundity of sexually mature females in the population remaining at the Farnes, the expected pup production in 1981 is:

$$E(p_{81}) = FM$$

and the density of p_{81} is normal, $N(FM,\sigma)$. So for the last term in the likelihood function we have:

$$L_3\;(F, M, \sigma \mid p_{81}, n_p)$$

$$= \frac{1}{\sqrt{2\pi\sigma^2}} \exp\; -1/2\sigma^2\,(FM - p_{81})^2 \cdot \frac{52\,!}{n_p!\,(52-n_p)\,!} \left(\frac{p_{81}}{M}\right)^{n_p} \left(1 - \frac{p_{81}}{M}\right)^{52-n_p}$$

The introduction of this term is necessary to restrict the possible range of values for the parameter F. It is not equivalent to simply using the proportion of pregnant females in the sample, to estimate F because of the year to year variation in pregnancy rate.

The likelihood function incorporating all the data is

$$L(\underline{\theta}, \sigma, M \mid p_{56} \cdots p_{71}, p_{81}, c_{i_o,72} \cdots c_{29,72}, c_{i_o,75} \cdots c_{29,75}, n_p) = L_1 \cdot L_2 \cdot L_3$$

MAXIMISING THE LIKELIHOOD FUNCTION

By differentiating log L with respect to σ and equating to 0 we obtain:

$$\hat{\sigma}^2 = \frac{1}{17}\left[\sum_{t=56}^{71}\left(E\left(p_t \mid \underline{\theta}\right) - p_t\right)^2 + \left(\hat{F}\hat{M} - p_{81}\right)^2\right] = \frac{SS}{17}$$

where SS is the sum of squares of differences between observed and expected pup productions in years 1956 to 1971 and 1981.

Substituting $\hat{\sigma}^2$ back into log L and eliminating all terms not including any of the parameters we obtain:

$$\log L \;\alpha\; -\frac{17}{2}\log SS + \sum_{j=i_o}^{29} c_{j,72}\log\left(\frac{n_{j,72}}{\sum_{i=i_o}^{29} n_{i,72}}\right) + \sum_{k=i_o}^{29} c_{k,75}\log\left(\frac{n_{k,75}}{\sum_{i=i_o}^{29} n_{k,75}}\right) + n_p\log\left(\frac{p_{81}}{M}\right) + (52 - n_p)\log\left(1 - \frac{p_{81}}{M}\right)$$

This expression was maximised with respect to $\underline{\theta}$ (λ, S, P_{56} and F) and M using initial estimates and a simplex routine. At each iteration the population growth model is run, using the parameter value attained by that stage, to generate the expectations of p_t, $c_{i,t}$ and n_p conditional on those parameter values. This procedure also generates the age-structured trajectory of the female population corresponding to each set of parameter values used and, in particular, the trajectory corresponding to the maximum likelihood estimates of the parameters. Because the female pup productions are assumed to known without error, and the population growth model, given the pup production, is deterministic, any element of the age-structured trajectory is a functions of the parameters, and is thus a maximum likelihood estimate of the corresponding element in the real population. In particular, the procedure gives maximum likelihood estimates for the total female population in each year.

RESULTS

The maximum likelihood estimates for the initial rate of population growth λ, the annual survival rate for females aged 1 year and over ", the mean fecundity for sexually mature females F, and the number of sexually mature females in the population breeding at the Farnes in 1981 are as follows:-

$\hat{\lambda}$ = 1.0787
$\hat{S}$ = 0.98
$\hat{F}$ = 0.94
$\hat{M}$ = 1597

In addition, we have, from the balance equation, the survival of pups from birth to age 1, excluding the effect of pup culls:

$\hat{S}_j \quad = \quad 0.34$

The estimated trajectory of total female population size from 1956 to 1981, P_{56} .. .P_{81}, is shown in Fig 1a.

Up to 1972 the estimates refer to the female population local to the Farnes, i.e. females actually or potentially breeding at the Farnes. This is implicit in the way expected pup production is linked by age-specific fecundity to 'the population' in the model. This means that if any females emigrated from the Farnes to breed elsewhere before 1972, then the parameter S refers to the proportion surviving natural mortality and emigration, rather than natural mortality only. From 1972 onwards it is clear that a significant number of females have left the Farnes population. The trajectory beyond 1972 thus refers to a population which would still be breeding at the Farnes if the culls had not taken place, but which is now partly located elsewhere. The situation is simplified if we assume that no significant migration occurred before 1972, so that S refers solely to survival of natural mortality, and that the rate of natural mortality did not change as a result of the culls. In that case all the population estimates P refer to the number of females alive in year t which have been born at the Farnes, and which before 1972 were all at the Farnes but which are now more widely dispersed. It is unlikely, given the high value of the S estimate, that significant emigration occurred before 1972.

Confidence Limits for P_{72}

We have attempted to assess the reliability of this procedure for estimation of population size by deriving confidence limits on the estimate for 1972, the last year for which the estimates apply to the local population.

It is possible to obtain an indication of the reliability of the P_{72} estimate by noting to what degree the fit of the model to the data is impaired when the population trajectory is constrained to pass through a different value in 1972.

Let $P_{72,0}$ be any value for the size of the model female population in 1972 and $\underline{\hat{\theta}},\hat{\underline{M}}$ the maximum likelihood estimates obtained when the model is constrained to pass through $P_{72,0}$.
Denote by L.R. the ratio

$$L\,(\underline{\hat{\theta}},\hat{M})\;/\;L\,(\underline{\hat{\theta}},\hat{M})$$

where L is the likelihood and $\underline{\hat{\theta}}$ and $\hat{M}$ are the m.l. estimates in the non-constrained case. Under

$$H_o\;:\;P_{72}\;=\;P_{72,0},$$

-2 log (L.R.) is distributed asymptotically as χ^2_ν where ν is the number of constraints imposed, i.e. 1 in this case.

This was used to construct a 95% confidence interval for P_{72}. Values $\hat{P}_{72,u}$ and $\hat{P}_{72,l}$ were found for which -2 log (L.R.) was equal to the 95% critical level of the χ^2_1 distribution. This is a 95% interval because the interval $(\hat{P}_{72,l}, \hat{P}_{72,u})$ can only fail to include the true 1972 population size, say $P_{72,o}$ if -2 log (L.R.) exceeds $\chi^2_{1,95}$ which has probability .05.

The confidence interval resulting from this procedure was (3100, 5600).
We were not certain whether the conditions required for use of the distribution were fulfilled by our data, in particular, whether the data set is sufficiently large to invoke asymptotic properties of m.l. estimators. In the next section we describe the simulation studies carried out to investigate the effects of violating some of the model assumptions on the estimation procedure. These also provide a test of the validity of the method used to construct confidence limits. The results suggest that the procedure used to set confidence limits does produce a 95% confidence interval, at least when the assumptions of the model are not violated.

Violation of Model Assumptions

A large number of assumptions have been made in order to formulate a model of population growth and hence estimate population size in each year. One assumption, namely that concerning emigration from the Farnes population, has been discussed in the preceding section. We now consider two other assumptions and investigate what effect their violation may have on the estimation procedure.

1. Stable age structure.

A starting age vector is required to initiate modelling of population growth and it was assumed that in 1956 the population had attained a stable age structure. The need for this assumption can be simply overcome by eliminating the observed pup production in years 1956 to 1962 from the likelihood function. From this time on the population age structure, as far as it effects expected pup production, is entirely determined by earlier observed pup production. At the same time, the cull data from 1972 and 1975 is eliminated from the likelihood function because the expected age class frequencies deprive largely from the structure of the starting age vector. The resulting parameter estimates are:

$$\hat{S} = 0.95$$
$$\hat{F} = 0.94$$
$$\hat{M} = 1590$$
and
$$\hat{S}_j = 0.51$$

The estimated population trajectory is shown in Fig. 1b, and the 95% confidence interval for P_{72} is (3000, 6800). The estimates are generally similar to those obtained above except that the 'adult' and 'juvenile' survival parameters are lower and higher respectively and more similar to the value 0.935 for adult survival suggested by Harwood & Prime (J. appl. Ecol., 15 : 401-411). The population estimate for 1972 is higher, at 4637 as compared to 3971 when using the stable starting age structure assumption. As expected the confidence interval is wider but encompasses the previous interval.

2. *Survival rates and sex ratio*

In the model used in the estimation procedure the proportion of pups and 'adults' surviving natural mortality is exactly S_j and S each year, constant with time and independent of age, and exactly half the pups born each year are females. These assumptions permit a very simple model structure but are clearly unrealistic. There must be at least binomial variation in the proportions surviving per year and in the sex ratio of newborn pups. The effect of ignoring this variation has been investigated using data generated by simulation model of population growth identical to that envisaged in the estimation procedure.

Date is generated by the simulation model by adding random error from appropriate distributions to expected pup productions in 1956 to 1981 and a sample of 52 'animals' is taken from the simulated population to estimate pregnancy rate in 1981, as for the real population. These data are subjected to the same estimation procedure as applied to the data from the real population, and the estimates of parameters compared to the parameter values used to drive to simulation. The procedure was repeated many times to identify and biases in the estimates and to see in what proportion of runs the confidence interval for the 1972 population size failed to include the value attained in the simulation.

No significant biases were observed in the average results of several hundred runs. As the proportion of confidence intervals for P_{72} failing to include the true value, the results were as follows:

a. When the simulation model was exactly as envisaged in the estimation procedure, with no stochasticity in survival rates or sex ratio, about 5% of P_{72} confidence intervals failed to include the value attained in the simulation.

b. The failure rate increased to 10-15% when binomial variation was included in survival rate for each age class and sex ratio of newborn pups.

c. The rate increased to around 40% when, in addition to binomial variation, a year to year variation in survival rate was imposed by using, for year t, a value for S_t normally distributed about S with standard deviation 0.02. Such a level of variation in survival rate may well apply in the real population.

Variation in survival rate induces positive serial correlation in the error term for p_t about $E(p_t)$ - about 0.2 in case (b) and 0.5 in case (c) - which in turns leads to an underestimate in the width of the confidence interval. Judging by the residuals of the seal pup productions about the fitted model such serial correlation is not apparent in the real population, but estimated serial correlations based on such a short series of available data are subject to high variance and the situation is still uncertain.