SCOS 00/5
ANNEX I

Scientific Advice on Matters Related to the Management of Seal Populations: 1999

Scope of this document

Under the Conservation of Seals Act 1970, NERC is required to provide the appropriate Secretary of State with scientific advice on matters related to the management of seal populations.

This document provides advice on:

- General information about British seals (p1)
- Current status of British grey seal populations (pp2/3)
- Current status of British common seal populations (p3)
- Specific questions relating to:
    - Methods for assessing the impact of seals on salmonids (p3)
    - Impact of culls on seal populations and fish predation (pp4/5)
    - Renewal of the Conservation of Seals (England) Order 1996 (p5)
    - Effects of seal scarers (p5)

Further details relating to this advice are provided in two technical annexes:

- Annex I - The Status of British Grey Seal Populations: 1998
- Annex II - The Status of British Common Seal Populations: 1998

General information

Grey seals

The majority of British grey seals breed in the Hebrides and in Orkney. There are also breeding colonies in Shetland, on the north and east coasts of Britain and in south-western Britain. Pup production at breeding sites that are regularly monitored by SMRU (containing about 85% of all pups born) rose steadily through the 1990s. Total population size has also been growing steadily at an average rate of 6.5% per year. There is currently no evidence that the overall rate of increase is slowing down. In 1998, there were an estimated 120,100 grey seals in Britain; about 40% of the world population of grey seals.

Common seals

British common seals occur throughout the north and west of Scotland and around estuaries along the east coast of Britain. A minimum number of 32,800 common seals were counted in the whole of Britain in 1996/97, of which 29,600 (90%) were in Scotland and 3,200 (10%) were in England. The total British population cannot be estimated accurately but is thought to be approximately 47,000 – 55,000 animals. The English population was severely affected by the Phocine Distemper epidemic in 1988. Numbers have increased since then, but they are still below the pre-epidemic level. Britain holds about 45% of the European population, and about 5% of the world population of common seals.

Current status of British grey seal populations

Pup production

Total pup production in 1998 at all regularly surveyed sites was estimated to be 35,680. Regional estimates were 3,087 in the Inner Hebrides, 12,373 in the Outer Hebrides, 16,231 in Orkney, and 3,989 at North Sea sites.

Trends in pup production

In 1997, total pup production fell for the first time since 1984. From 1997 to 1998, there was little change in pup production in the Inner and Outer Hebrides but pup production at breeding sites in Orkney and the North Sea increased by 14%. Total pup production in 1998 was in line with the underlying trend observed since 1984. This suggests that the lower-than-expected pup production in 1997 was the result of natural variation rather than the first sign that the British population is stabilising.

Population size

The size of the British grey seal population at the start of the 1998 pupping season is estimated to be 120,100. This is 5.5% higher than for 1997. The total number of seals in 1998 associated with breeding sites in Scotland is 110,200 (92%); for England and Wales it is 9,900 (8%).

Trends in population size

Since 1984, pup production at regularly surveyed breeding sites has increased at an average rate of 6.5% per year, and there is no evidence that this rate is slowing down. The table below shows the predicted changes in the size of the British grey seal population over the next five years. The 95% confidence limits provide an indication of the uncertainty associated with these predictions.

Predicted changes in grey seal population size if there is no change in survival and fecundity rates (and no change in the number of seals associated with sites that are not surveyed regularly).

Year	Total female population	95% confidence limits on female population		% increase from 1998	Total population (female + male + other sites not surveyed regularly)
1999	65,100	55,000	77,000	6.2%	126,700
2000	69,300	58,500	82,000	13.1%	134,000
2001	73,800	62,000	87,500	20.4%	141,700
2002	78,600	65,000	93,500	28.2%	150,000
2003	83,700	68,000	100,000	36.5%	158,500

Limits to grey seal abundance

The current increase in the size of the British grey seal population cannot continue indefinitely. At some point the population will be limited, probably by a shortage of space at breeding colonies and/or food. Pup production at most colonies in the Hebrides and a number of colonies in Orkney has changed very little suggesting that space is already limited at these sites. It is not possible at present to predict when the colonies that are still increasing will stabilise, but when they do we anticipate that seal density at all sites will increase. This is likely to result in an increase in pup mortality through infection and physical injury, which has already been observed in crowded areas of certain colonies.

However, even if pup production stabilises at all colonies and no new colonies are formed, total population size will continue to increase for a number of years. To illustrate this, the table below shows the predicted changes in the size of the British grey seal population over the next five years if pup production remains constant at the level observed in 1998.

Predicted changes in grey seal population size if pup production remains constant at 1998 levels.

Year	Total female population	95% confidence limits on female population		% increase from 1998	Total female + male + other sites not surveyed regularly
1999	65,100	54,500	77,000	6.2%	126,700
2000	68,600	58,000	81,000	11.9%	132,700
2001	72,100	61,000	85,000	17.6%	138,300
2002	75,300	64,000	88,500	22.8%	143,600
2003	78,500	66,500	92,000	28.1%	148,500

Current status of British common seal populations

Scotland

A new analysis has been conducted of the data from surveys of common seals along the north and west coasts of Scotland as far south as the southern tip of the Mull of Kintyre, and in Orkney, Shetland and the Hebrides. The results indicate that there has been an overall increase of 2.6% per year in the number of animals counted at haul-out sites since 1988, with 95% confidence limits of 1.5% to 4.4%. However, significantly better results were obtained when the coast was divided into ten areas; these were therefore analysed separately. Seven showed a significant increase, one a significant decrease, in two there was no significant change. Further details are given in Annex II. It is not known how these trends in numbers counted at haul-out sites relate to trends in population size.

The Wash and eastern England

Two surveys of common seals in eastern England were carried out during August 1998. The Wash counts were 2,367 and 2,381; these are within the range of the two counts made in 1997. The average annual rate of increase in the number of seals counted in The Wash since 1989 is 6.5%, almost twice that estimated between 1968 and 1988. However, the 1998 count in The Wash is still 20% lower than the last count made before the 1988 Phocine Distemper Virus epidemic. Common seal populations in Denmark, Germany and the Netherlands have recovered more rapidly from the effects of this epidemic and had returned to, or surpassed, their pre-epidemic levels by 1996.

Methods for assessing the impact of seals on salmonids

Information on seal numbers, distribution, dynamics, diet, and foraging behaviour and on the magnitude and causes of other sources of mortality for salmon and sea trout is required if the impact of seals on salmonids is to be assessed. SMRU routinely collects data on the numbers and distribution of both grey and common seals and uses these data to investigate population dynamics. Information on diet and foraging behaviour is only available from certain locations.

NERC believes that the most appropriate use of its resources is to focus on assessing seal numbers and distribution, and on understanding the general characteristics of population dynamics and foraging behaviour. This information is essential to underpin advice on scientific aspects of the management of seal populations.

This information needs to be collected on a finer spatial and temporal scale in in-depth local studies if the problems caused by the interactions between seals and specific prey species are to be addressed. The most appropriate way forward in these cases is through inter-disciplinary collaborative projects with other institutes.

Impact of culls on seal populations and fish predation

The size and composition of a cull that would reduce a seal population to a given proportion of its current size depends, amongst other things, on the time scale over which the reduction is to occur, the desired age structure and sex ratio in the population, and when the cull is carried out.

However, an illustration of the scale of operation which would be necessary can be gained from a calculation of the numbers of pups or older animals which would need to be killed to stabilise the British grey seal population at its 1998 level.

This could be achieved by killing approximately half of all pups born each year. Disturbance (which will have unpredictable effects on the outcome of the cull) could be minimised by killing weaned pups at the end of the pupping season, as was the practice when seal pups were hunted commercially. At current levels of pup production this would involve killing around 18,000 pups each year, but the size of the annual cull would rise to around 25,000 as the age structure of the population stabilised. A reduction in population size would involve killing a greater number of pups each year.

The population could also be stabilised by killing around 6,000 animals one-year and older each year. If a greater number were to be killed, the population would decline. The simplest way to carry out a cull of this kind would be to kill adult seals at the breeding colonies. However, attempts to reduce the population in this way in the 1970s resulted in massive disturbance. Large numbers of seals deserted the colonies that were culled, some of these animals did not return for a number of years and others probably established new colonies. Such responses make it very difficult to predict and monitor the long-term effects of any cull.

Impact of changes in seal numbers on predation of seafish and salmonids

The impact of changes in seal numbers on the numbers of fish consumed each year will depend on a number of factors including the behaviour and average size of the surviving seals and their diet. Grey seal diet composition was last assessed on a Britain-wide scale in 1985. There have been substantial changes in the size of many fish stocks since then and it is likely that grey seal diet has also changed.

However, new information on diet alone will not allow the effects of changes in seal numbers on fish stocks to be predicted reliably, because of the wide range of prey species taken by seals and because of the interactions between these species, their other predators and commercial fisheries. Research on the responses of seals and other fish predators to changes in the availability of their preferred prey is required before the effects of these interactions can be assessed.

Any projected changes in fish consumption resulting from a cull will simply reflect percentage changes in the number of seals unless a number of important interactions are taken into account. These include changes in seal age/sex structure as a result of a reduction in numbers and, most importantly, predation on fish by other fish, seabirds and other marine mammals. For example, a reduction by 25% in the number of grey seals in the North Sea in 1998, approximately 15,000 seals, would lead to a reduction in fish consumed of approximately 28,000 tonnes per year. For common seals, a reduction by 25% in the total number of seals throughout Britain would result in a reduction in annual consumption of about 18,000 tonnes of prey.

Using a simple model without taking these key interactions into account, an illustration of the trade off between reduction in seal population and reduction in fish consumed can be calculated.

To stabilise the North Sea grey seal population at the 1998 level would required the annual removal of 13,000 pups by 2003, which would result in a reduction in the amount of fish consumed in 2003 of 41,500 tonnes, approximately half of which would be sandeels.

In interpreting the results of these simple calculations the following points need to be noted:

- The amount of fish not eaten is based on diet information from 1985; this may have changed significantly in recent years
- The amount of fish not eaten is small compared to catches taken by fisheries
- The amount of fish available to fisheries would be even smaller if predation on fish by other fish, seabirds and other marine mammals were taken into account

- The considerable uncertainty in any estimate of fish 'freed up' for fisheries would likely be within the range of uncertainty of fish stock assessments, forecasts, or reported catches.

The potential impact of changes in seal numbers on predation of salmonids cannot be predicted because of the lack of data on predation rates, and because the effects are more likely to depend on where and which animals are culled.

Renewal of the Conservation of Seals (England) Order 1996

In 1996, NERC advised that if the Home Office wished to promote the complete recovery of the common seal population on the east coast of England, the Conservation of Seals (England) Order should be renewed until the number of seals in The Wash was similar to that observed in 1988.

The Conservation of Seals (England) Order was renewed in 1996 and expires in December 1999. The Home Office has requested advice on whether or not the Order should be renewed.

Since 1989, the number of common seals counted in the August moult surveys of The Wash has increased, on average, by 6.5% per year. Counts at the other major English east coast sites (Blakeney Point and Donna Nook) have also increased. Overall, the estimated rate of increase of the common seal population on the east coast of England is 7.1% per year. This is approximately twice the estimated rate of increase in the 20 years preceding the epidemic. However, other North Sea populations have increased at much higher rates (e.g. approximately 15.5% per year in the Wadden Sea).

If the Home Office wishes to promote the complete recovery of the common seal population on the east coast of England, then NERC advises that the Conservation of Seals (England) Order should be renewed until the number of seals in The Wash is similar to that observed in 1988. If the current rate of recovery in The Wash continues, NERC's best estimate is that this will occur in 2001.

However, NERC notes that, to the best of its knowledge, no applications for licences to take either grey or common seals on the east coast of England have been made while the Order has been in place, apart from annual requests from the National Trust and the Sea Mammal Research Unit. Therefore, a decision not to renew the Order will probably have only a small effect on the recovery of the east coast population, because it is unlikely that many common seals will be killed each year as a result.

Effects of seal scarers

The Scottish Executive has requested advice on the effects of seal scarers on cetaceans and on the impact that local topography may have on the transmission of sounds from seal scarers.

NERC considers that the provision of advice on cetaceans and on technical aspects of the transmission of sound underwater are outside its responsibilities under the Conservation of Seals Act 1970.

ANNEX I

The Status of British Grey Seal Populations: 1998

Surveys conducted in 1998

Each year SMRU conducts aerial surveys of the major grey seal breeding colonies in Britain to determine the number of pups born there. In addition, new sites where grey seal pups have been reported or which appear to be suitable for colonisation are visited regularly. During 1998, five or six surveys were flown over all the major sites in the Hebrides and Orkney, and in the Firth of Forth. Ground counts of the numbers of pups born at the Farne Islands were made by National Trust staff. Similar counts at Donna Nook on the Humber Estuary were made by members of the Lincolnshire Trust for Nature Conservation and on South Ronaldsay by SNH staff. Locations of the main British breeding sites are shown in Figure 1.

Estimated pup production

Pup production at regularly surveyed sites is estimated each year from the aerial survey results using a model of the birth process and the development of pups. The method used to obtain the estimates for this year's advice was similar to that used last year.

Total pup production in 1998 at all regularly surveyed sites was estimated to be 35,680 using this method. Estimates of pup production at each site in the Inner Hebrides, the Outer Hebrides and Orkney are given in Tables 1-3, respectively. The Isle of May and Loch Eriboll are also surveyed by air and estimates of pup production at these sites using this method are given in Table 4.

For sites not surveyed by air, pup numbers are counted directly on the ground either annually (Farne Islands, Donna Nook, South Ronaldsay) or less frequently (SW England, Wales, Helmsdale, Shetland). These counts are included in Table 4.

Estimates of pup production at all major breeding sites in England and Scotland (except Loch Eriboll, Helmsdale and Shetland) for the period 1984 to 1998 are shown in Figure 2.

Pup production estimates for the main island groups are shown in Figure 3a and for the North Sea sites in Figure 3b. In 1998, pup production in the Inner Hebrides was the same as in 1997. In the Outer Hebrides, pup production increased slightly in 1998 while in Orkney it increased significantly. At the North Sea sites, total pup production also increased. Ground counts of new-born pups at the Farne Islands in 1998 were almost the same as in 1997. At Donna Nook, the new-born total continued to increase. Estimated production from aerial surveys at the Isle of May increased significantly. However, the increase since 1996 is in part due to the inclusion of pups born at the recently established site of Fast Castle, near St Abbs Head, in 1997 and 1998.

Trends in pup production

Total pup production at the grey seal breeding sites which are regularly monitored by SMRU has risen steadily through the 1990s. In Scotland, pup production at sites in the Hebrides has been relatively constant since 1993 and almost all of the recent increase has occurred in Orkney (Fig 3a). More than 70% of the increase in Orkney since 1993 has occurred at just five sites (Table 3).

At North Sea sites, the greatest increase in pup production has been at the Isle of May (Fig 3b). At the Farne Islands the increase has been steady but at a much slower rate.

Implications of low pup production in 1997

In 1997, total pup production fell for the first time since 1984 (when the current survey methodology was adopted). However, it increased again in 1998 in line with the underlying trend since 1984 (Fig 2). It appears, therefore, that the low pup production in 1997 was not the beginning of a declining trend. In fact, inspection of Fig 2 shows that the relatively high pup production in 1996 could be considered an equally anomalous point.

However, it is important to recognise that total pup production is the sum of many individual sites and that pup production at these sites varies from year to year. We should therefore expect total pup production also to go up and down from year to year because of this underlying variation. It is important not to over-interpret relatively small changes from one year to the next.

Pup production model assumptions

The model used to estimate production from aerial survey counts of whitecoat and moulted pups assumes that the parameters defining the distribution of birth date are variable from site to site and year to year but that those defining the time to moult and time to leave are constant. The pup production estimate is sensitive to the value used for the latter parameter and hence there is a risk of confounding a trend in mean time to leave with a trend in pup production. Last year's advice on grey seals (SCOS 99/5 Annex I) included a section on factors affecting 1997 estimates of pup production, which considered the possibility that weather conditions on the breeding site might effect mean time to leave. This failed to detect any relationship between rainfall and pup production estimate residuals about the production trend at Ceann Iar in the Monach Isles, Outer Hebrides. However, there are other possible reasons for variation in the time to leave parameter.

Figure 4 compares the total pup production estimate for the Hebrides and Orkney generated using the constant value for mean time to leave with that generated when time to leave is estimated along with the parameters of the birth curve. To emphasise any difference in the two trends the second series is also scaled to start at the same value as the first. The main difference is a discrepancy from 1992 onwards which may be due to a change in survey protocol. From that year coverage was extended inland on some islands and, as moulted pups tend to move inland, may have resulted in an increase in the moulted pup count, equivalent to a slight increase in the time to leave parameter. There are also some minor differences year to year, for example the dip in production estimated for 1997 is less pronounced.

The time to leave parameter is not re-estimated on a regular basis because the data series for many breeding sites are too short to allow reliable estimation of both the time to leave and the birth date parameters, especially given the difficulty of classifying pups to stage from the photographs. It may be possible to improve the survey technique in the future to allow more reliable classification of moulted pups and hence to re-estimate mean time to leave on a regular basis. One possible consequence of not doing so is that changes in production may be overestimated, for example, an increased number of seals on a breeding site may delay the departure of pups born early in the season and hence bias the pup production estimate upwards.

Figure 5 shows the mean birth date estimated for sites in the Outer Hebrides and confirms the coherence in birth dates noted previously for different sites in the group. It is noteworthy that the 1998 mean birth date estimated for Ceann Iar is very close to that predicted last year using a first-order auto-regressive model fitted to estimates for 1987-1997. This suggests that such predictions may be useful in planning the timing of future surveys.

Estimation of population size associated with regularly surveyed sites

The total number of seals associated with the sites surveyed regularly since 1984 (when the current survey methodology was established) is estimated by fitting a population model to the series of pup production estimates from these sites, 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 was substantially modified prior to the SCOS meeting in 1996 according to comments made by external referees. It now takes account of year to year variation in juvenile survival and age at first pregnancy, and makes use of more of the available data on these population parameters.

The estimated size of the female population at all major breeding sites in England and Scotland was 61,289. Figure 6 shows female population estimates (together with pup production estimates generated by the population model) for the years 1984-1998. The estimated total (age 1+) population associated with regularly surveyed sites in 1998 was 106,332. Table 5 gives estimates of the size of the total population over the period 1984-1998.

Population size is not directly estimated by location. Estimates of pup production and total population size (in proportion to pup production) for the main colonies surveyed in 1998, which account for more than 85% of all pups born each year, are given below:

Pup production and total population size estimates for the main colonies surveyed in 1998

Location	1998 pup production	Change from 1997	Total 1998 population (to nearest 100)
Inner Hebrides	3,087	0%	9,200
Outer Hebrides	12,373	+3.5%	36,900
Orkney	16,231	+15.5%	48,400
Isle of May + Fast Castle	2,241 (1,968 IoM only)	+10.5% (+9.5% IoM only)	6,700
Farne Islands	1,309	+2%	3,900
Donna Nook	439	+15%	1,300

Confidence limits

Ninety-five percent confidence limits on the pup production estimates at each site are within 14% of the point estimate. The exact limits depend on a number of factors including the number of surveys flown in a particular year. It is also possible to calculate 95% confidence limits for the estimate of the female component of the population; for 1998, these are ±17% of the estimate (i.e. 51,000 - 72,000 for the estimate of the female population in 1998 - see Table 5). The size of the male component has been estimated by assuming 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 population. However, there are no current data on the relative numbers of males and females in the population that could be used for this purpose.

Population size at sites surveyed less frequently

The total population associated with breeding sites that are not surveyed regularly has been calculated using the ratio of total population to pup production for the main areas. Less than 15% of all pups are born at these sites each year. Confidence limits cannot be calculated for these estimates because they are obtained by simple extrapolation of single counts. The resulting figures are:

Pup production and total population size estimates for breeding sites not surveyed regularly			
Location	Date of last survey	Pup production (to nearest 100)	Total population (to nearest 100)
Mainland Scotland & South Ronaldsay	Helmsdale (including Berriedale) 1997 Loch Eriboll 1998 South Ronaldsay 1998	1,700	5,600
Shetland	1977	1,000	3,300
Southwest Britain	Southwest England 1973 Wales 1994	1,500	4,700

Table 6 shows Scottish breeding sites which are either not surveyed annually or have recently been included in the survey programme. These and other potential breeding sites are checked visually when flying time, flying conditions and other circumstances permit.

Total size of the British grey seal population

Taken together, these figures provide an estimate of 120,100 for the size of the British grey seal population (age 1+) at the start of the 1998 pupping season: 110,200 (92%) seals are associated with breeding sites in Scotland and 9,900 (8%) with breeding sites in England and Wales. The equivalent estimates for 1997 are 104,100 for Scottish sites and 9,800 for sites in England and Wales. Britain holds approximately forty percent of the world population of about 300,000 grey seals.

Trends in population size

The increase, from 1997 to 1998, in the estimate of total population size associated with annually monitored breeding sites was 6.2 %, with 95% confidence limits of 3.75-8.75%. The total population at these sites is estimated to have increased by 35.5% (95% confidence limits 28-45%) between 1993 and 1998.

Predicting population size into the future requires assumptions to be made about survival and reproduction. The method used to estimate total population size assumes that there are no trends over time in the demographic parameters that determine population growth rate. To investigate whether there is evidence that the population growth rate is slowing down, the estimation model was modified to allow trends over time in fecundity and age at first parturition and applied to data from 1984 to 1997.

No significant increase in the log likelihood was found for any of a number of ways in which this was modelled. In interpreting this result, it is important to note that the estimation model is stochastic and allows for variation in pup production via variation in age at first parturition and in pup survival. Thus, there can be deviations in estimated pup production from those observed without having to abandon the assumptions of the model that those fluctuations are occurring about fixed mean values.

In summary, there is no statistically significant evidence for a change in fecundity over time (assumed fixed in the unmodified model) or in the values about which time to parturition or pup survival fluctuates.

Failure to reject the hypothesis that the population parameters have remained constant over time is not the same as saying that the population is growing exponentially. Variation in parameters describing fecundity and survival about their constant mean values can result in a population trajectory that deviates from exponential growth. As time goes on, the observed deviations from the model predictions will increase simply because of the accumulation of stochastic fluctuations.

If there are no changes in survival and fecundity rates (and no change in the number of seals associated with the sites that are not surveyed regularly), the population is predicted to increase further at much the same rate, as shown in the following table. Note that, as expected, predictions become more uncertain (confidence intervals become wider) the farther into the future the prediction is made.

Predicted population size if there are no changes in survival and fecundity rates (and no change in the number of seals associated with sites that are not surveyed regularly)

Year	Total female population	95% confidence limits on female population		% increase from 1998	Total female + male + other sites not surveyed regularly
1999	65,100	55,000	77,000	6.2%	126,700
2000	69,300	58,500	82,000	13.1%	134,000
2001	73,800	62,000	87,500	20.4%	141,700
2002	78,600	65,000	93,500	28.2%	150,000
2003	83,700	68,000	100,000	36.5%	158,500

Limits to grey seal abundance

Although, as noted above, there is no evidence that the rate of increase of the British grey seal population is slowing down, the population will ultimately be limited, probably by a shortage of space on breeding colonies and/or food. There is already evidence of spatial limitation at both regional and local scales. Total pup production in the Inner and Outer Hebrides has remained virtually unchanged since 1993; most of the increase in the British grey seal population in the last five years has been in Orkney and along the North Sea coast. In Orkney, pup production at six colonies is decreasing or stable, at seven colonies it is increasing at about the national average, and at the remaining six colonies it is increasing at greater than 10% per year. Research is currently underway within SMRU to identify the factors that may determine the equilibrium pup production at these sites.

Once all suitable breeding sites have been colonised, we might expect seal density at some sites to rise further. Data from the Farne Islands collected between 1960 and 1971, when this colony was increasing rapidly, have shown that pup mortality rate increases 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 increases as the total number of movements of adult seals between pupping sites and water increases. At the Farne Islands, a doubling in the number of pups born led to a three-fold increase in the number that died each year.

It should be recognised that total population size will continue to rise for some time, even if pup production does stabilise at some equilibrium level. To show this, population size has been calculated under the assumption that pup production remains constant at the 1998 level for the next five years. The predicted increase in population size of approximately 22,000 over this period is approximately two-thirds of the increase predicted in the previous section using a steadily increasing pup production.

Predicted population size if pup production remains constant at the 1998 level					
Year	Total female population	95% confidence limits on female population		% increase from 1998	Total population (female + male + other sites not surveyed regularly)
1999	65,100	54,500	77,000	6.2%	126,700
2000	68,600	58,000	81,000	11.9%	132,700
2001	72,100	61,000	85,000	17.6%	138,300
2002	75,300	64,000	88,500	22.8%	143,600
2003	78,500	66,500	92,000	28.1%	148,500

Size and composition of culls to reduce numbers by a given amount

The size and composition of cull required to reduce the grey seal population to a given proportion of its current size depends, amongst other things, on:

- the time scale over which the reduction is to occur;
- the desired age structure and sex ratio in the target population;
- whether culling is carried out during or outside the pupping season;
- what levels of risk of not attaining, or overshooting, the target level are considered acceptable.

However, an illustration of the scale of operation that would be necessary can be gained from a calculation of the numbers of pups or 1+ animals that would need to be killed to stabilise the population at its 1998 level.

This could be achieved by killing approximately 50% of all pups born each year. Disturbance could be minimised by killing weaned pups at the end of the pupping season, as was the practice when there was commercial hunting of seal pups. At current levels of pup production this would involve killing around 18,000 pups each year. Pup production (and the required pup cull) would continue to rise for the first 5-6 years before eventually stabilising at around 50,000, requiring a continuing annual cull of more than 25,000 pups. To reduce the size of the population would involve killing a greater number of pups each year.

The population could also be stabilised by killing around 6,000 animals one-year and older each year. If larger numbers are killed, the population will decline. The simplest way to carry out a cull of this kind would be to kill adult seals at the breeding colonies. However, attempts to control the population in this way in the 1970s resulted in massive disturbance. Large numbers of seals deserted the colonies that were culled, some of these animals did not return for a number of years and others probably established new colonies. Such responses make it very difficult to predict and monitor the long-term effects of any cull.

Impact of culls on predation of seafish and salmonids

The potential impact of changes in seal numbers on predation of salmonids cannot be predicted because of the lack of data on predation rates, and because the effects are more likely to depend on where and which animals are culled.

The impact of changes in seal numbers on the numbers of fish consumed each year will depend on the average size of the surviving seals and their diet. Grey seal diet composition was last assessed on a Britain-wide scale in 1985. There have been substantial changes in the size of many fish stocks since then and it is likely that grey seal diet has also changed. However, new information on diet alone will not allow the effects of changes in seal numbers on fish stocks to be predicted reliably, because of the wide range of prey species taken by seals and because of the interactions between these species, their other predators and commercial fisheries. Before this can be done, more research must be carried out on the responses of seals and other fish predators to changes in the availability of their preferred prey.

Any projected changes in fish consumption resulting from a cull will simply reflect percentage changes in the number of seals unless a number of important interactions are taken into account. These include changes in seal age/sex structure as a result of a reduction in numbers and, most importantly, predation on fish by other fish, seabirds and other marine mammals. For example, a reduction by 25% in the number of grey seals in the North Sea in 1998, about 15,000 seals, would lead to a reduction in annual fish consumed of approximately 28,000 tonnes (see table below).

Estimates of annual grey seal fish consumption (in tonnes) in the North Sea from diet composition data in 1985. The number of seals in 2003 assumes that there is no change in survival and fecundity rates (and no change in the number of seals associated with sites that are not surveyed regularly).

	1998	1998 with 25% reduction	2003	Difference between 2003 and 1998
Grey seal numbers	60,300	45,225	82,300	22,000
Cod	15.600	11,700	21,300	5,700
Whiting	8,200	6,200	11,200	3,000
Haddock	3,600	2,700	4,900	1,300
Saithe	3,900	2,900	5,300	1,400
Ling	10,300	7,700	14,000	3,700
Plaice	5,700	4,300	7,700	2,000
Sandeels	53,700	40,300	73,400	19,700
Others	12,600	9,500	17,300	4,700
Total	113,600	85,200	155,100	41,500

Using a simple model without taking these key interactions into account, an illustration of the trade off between reduction in grey seal population and reduction in fish consumed can be calculated. If the population continues to grow at the current rate, population size in 2003 is predicted to be 158,500 in total (see above) and 82,300 in the North Sea. The estimated fish consumption in the North Sea in 2003 is given in the table above.

To stabilise the North Sea population at the 1998 level would required the annual removal of 13,000 pups by 2003. The estimated amount of fish not eaten by grey seals in the North Sea in 2003 if the population were stabilised at its 1998 level is shown in the final column of the table above; a total of 41,500 tonnes, approximately half of which would be sandeels.

In interpreting the results of these simple calculations the following points need to be noted:

- The amount of fish not eaten is based on diet information from 1985; this may have changed significantly in recent years;
- The amount of fish not eaten is small compared to catches taken by fisheries;
- The amount of fish available to fisheries would be even smaller if predation on fish by other fish, seabirds and other marine mammals were taken into account;
- The considerable uncertainty in any estimate of fish 'freed up' for fisheries would likely be within the range of uncertainty of fish stock assessments, forecasts, or reported catches.

Table 1. Pup production estimates for islands in the Inner Hebrides group

YEAR	Gunna	Northern Treshnish	Fladda	Sgeir a' Chaisteil & Eirionnach	Lunga	Soa	Eilean nan Ron	Eilean nan Eoin	Nave Island	TOTAL
1984	206	87	169	136	226	63	180	190	75	1332
1985	192	84	109	113	136	63	158	269	66	1190
1986	263	114	149	119	204	111	302	305	144	1711
1987	361	115	194	147	234	102	420	297	132	2002
1988	332	130	231	170	246	102	389	225	135	1960
1989	347	131	234	187	277	101	308	167	204	1956
1990	342	146	183	162	221	107	392	265	214	2032
1991	475	125	288	174	271	97	409	377	195	2411
1992	527	203	347	153	341	98	453	438	256	2816
1993	514	211	324	186	385	91	464	458	290	2923
1994	580	145	280	148	356	96	349	456	309	2719
1995	541	181	368	182	429	116	454	440	339	3050
1996	583	181	351	186	414	92	558	431	321	3117
1997	589	158	365	177	448	81	562	414	282	3076
1998	638	168	315	166	427	63	490	430	390	3087

Table 2. Pup production estimates for islands in the Outer Hebrides group

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	847	62	120	81	67	13						0	0	1949	3142
1962															
1963															
1964															
1965															
1966	1084	230	120	96	242	0	0					38	0	1499	3311
1967	1084	153	80	96	161	0	0					114	0	1574	3265
1968	1084	115	161	96	161	0	0					152	0	1650	3421
1969															
1970	1129	324	714	130	103	41	0	0	84	60	460	605	0	2023	5070
1971															
1972	1141	316	605	167	271	67	0	0	274	49	730	1054	0	1309	4933
1973															
1974	1756	286	692	176	224	83	0	49	459	44	754	1307	0	1647	6173
1975	1538	367	631	212	202	51	0	141	690	217	932	1982	0	1961	6946
1976	1813	394	553	278	217	57	0	111	628	152	1053	1946	0	1886	7147
1977															
1978	1101	321	508	320	172	51	0	560	371	205	626	1764	0	2002	6243
1979	992	377	546	269	159	80	0	672	810	164	826	2474	0	1770	6670
1980	1345	462	794	351	163	31	0	1077	880	242	647	2848	162	1867	8026

Table 2 (continued). Pup production estimates for islands in the Outer Hebrides group

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
1981	1255	423	1016	278	178	68	0	1279	486	331	847	2944	136	1785	8086
1982	1443	634	219	322	260	110	0	1329	557	199	712	2798	85	1888	7763
1983															
1984	1120	389	386	277	143	0	83	2175	616	209	555	3638	0	1641	7594
1985	1303	408	335	254	168	0	261	2365	748	193	641	4208	0	1489	8165
1986	1258	378	356	225	108	0	283	2931	822	222	572	4830	0	1300	8455
1987	1337	393	365	224	131	0	353	3227	666	223	670	5139	0	1188	8777
1988	1205	354	372	195	122	0	429	3733	418	189	579	5348	0	1093	8689
1989	1294	383	348	176	73	0	512	4041	518	212	535	5818	0	1183	9275
1990	1398	396	321	146	115	0	574	4554	510	174	457	6269	0	1156	9801
1991	1406	440	334	159	94	0	582	5098	543	181	494	6898	0	1286	10617
1992	1527	427	514	179	91	0	576	5852	716	204	599	7947	0	1530	12215
1993	1525	366	431	150	107	0	640	5498	1037	192	524	7891	0	1445	11915
1994	1432	394	491	123	86	0	640	5956	921	196	522	8235	0	1293	12054
1995	1389	392	570	120	55	0	856	6332	977	200	480	8845	0	1342	12713
1996	1508	391	574	133	64	0	721	6648	1254	157	445	9225	0	1281	13176
1997	1301	303	470	79	67	0	795	5660	1656	76	458	8645	0	1081	11946
1998	1444	307	552	90	64	0	865	5711	1649	70	422	8717	0	1199	12373

Table 3. Pup production estimates for islands in the Orkney group

YEAR	Muckle Green-holm	Little Green-holm	Little Linga	Holm of Spur-ness	Point of Spur-ness	Linga-holm	Holm of Huip	Fara-holm	Faray	Rusk-holm	Wart-holm	Sweyn-holm & Gairsay	Grass-holm	Swona	Pent-land Skerry	Aus-kerry	Switha	Stroma	Calf of Eday	Copin-say	Stron-say	TOTAL
1960	734	190	239	90	0	0	0	441	0	208	41	0	0	2	98	0	0	0	0	0	0	2048
1961	537	290	251	124	0	0	0	300	0	256	33	0	0	2	48	0	0	0	0	0	0	1846
1962	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
1963	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
1964	934	469	154	25	0	0	0	22	117	208	16	55	3	14	24	0	0	0	0	0	0	2048
1965	671	366	279	138	0	0	0	113	151	247	29	21	66	19	85	0	0	0	0	0	0	2191
1966	688	454	344	138	0	0	0	270	154	87	8	59	18	14	48	0	0	0	0	0	0	2287
1967	600	445	395	98	0	0	0	270	165	252	8	111	0	6	36	0	0	0	0	0	0	2390
1968	650	310	399	278	0	13	0	257	258	195	8	81	36	27	52	0	0	0	0	0	0	2570
1969	567	298	576	189	8	28	0	214	28	208	4	77	59	35	20	0	0	0	0	0	0	2316
1970	747	318	519	135	45	42	22	171	95	223	4	13	66	43	85	0	0	0	0	0	0	2535
1971	588	351	708	158	49	137	30	320	88	103	16	70	40	67	36	0	0	0	0	0	0	2766
1972	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
1973	503	207	519	233	66	177	88	351	35	15	12	86	92	51	52	87	0	0	0	0	0	2581
1974	525	190	479	146	21	61	137	500	72	132	0	134	69	71	73	84	0	0	0	0	0	2700
1975	483	230	483	271	49	39	117	477	65	63	4	111	21	59	48	152	0	0	0	0	0	2679
1976	605	175	648	328	53	68	68	398	85	60	4	198	21	92	65	375	0	0	0	0	0	3247
1977	679	210	684	305	78	50	130	477	58	111	4	194	21	92	65	199	0	0	0	0	0	3364
1978	333	210	800	471	136	79	192	700	58	219	4	149	36	104	57	134	0	90	0	0	0	3778
1979	546	294	344	430	127	144	368	672	92	280	4	142	69	92	65	145	0	152	0	0	0	3971
1980	496	166	676	415	107	315	275	817	165	336	0	167	74	108	81	97	0	174	0	0	0	4476

Table 3 (continued). Pup production estimates for islands in the Orkney group

YEAR	Muckle Green-holm	Little Green-holm	Little Linga	Holm of Spur-ness	Point of Spur-ness	Linga-holm	Holm of Huip	Fara-holm	Faray	Rusk-holm	Wart-holm	Sweyn-holm & Gairsay	Grass-holm	Swona	Pent-land Skerry	Aus-kerry	Switha	Stroma	Calf of Eday	Copin-say	Stron-say	TOTAL
1981	442	199	860	449	45	293	510	712	202	319	4	108	92	225	125	249	0	223	0	0	0	5064
1982	454	87	716	665	29	326	521	817	146	295	4	104	103	148	147	294	153	227	0	0	0	5241
1983	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
1984	517	127	601	518	0	303	368	834	376	335	0	111	79	85	70	219	119	79	0	0	0	4741
1985	483	191	568	643	0	342	245	796	526	315	0	115	60	260	82	261	151	161	0	0	0	5199
1986	637	227	602	533	0	390	358	752	811	345	0	145	81	191	70	278	157	219	0	0	0	5796
1987	592	231	678	570	0	502	548	837	910	261	0	109	83	327	90	216	153	282	0	0	0	6389
1988	393	181	590	424	0	569	557	833	921	247	0	135	66	336	62	222	167	245	0	0	0	5948
1989	426	191	574	426	0	696	638	760	1452	232	0	164	48	314	62	279	207	304	0	0	0	6773
1990	334	201	625	341	0	807	731	970	1313	179	0	195	49	351	79	252	206	349	0	0	0	6982
1991	459	186	728	388	0	1144	880	976	1602	192	0	214	70	514	96	277	272	414	0	0	0	8412
1992	507	222	845	462	0	1186	1052	1304	1845	204	0	223	56	585	51	206	304	556	0	0	0	9608
1993	601	241	830	385	0	1249	1221	1325	1781	218	0	292	88	604	86	166	324	595	270	514	0	10790
1994	642	262	786	348	0	1527	1294	1238	1909	220	0	272	69	674	65	161	331	508	346	795	146	11593
1995	728	300	795	420	0	2128	887	1387	2136	251	0	461	32	578	71	125	442	339	274	940	118	12412
1996	770	289	834	416	0	2255	1349	1464	1935	243	0	518	64	829	79	123	370	583	399	1480	195	14195
1997	786	332	771	387	0	2294	1071	1464	2024	215	0	336	46	870	66	131	347	638	587	1455	231	14051
1998	883	442	842	429	0	2583	1323	1675	2166	272	0	405	61	1032	69	123	430	784	499	1914	299	16231

Table 4. Pup production estimates for other sites routinely monitored.

YEAR	Farne Islands	Isle of May	Fast Castle	SW England	Wales	Donna Nook	Helms-dale	Loch Eriboll	E. nan Ron, Tongue	Shet-land	South Ronald. (Orkney)
1956	751	.	.	.	.	.	.	.	.	.	.
1957	854	.	.	.	.	.	.	.	.	.	.
1958	869	.	.	.	.	.	.	.	.	.	.
1959	898	.	.	.	.	.	.	.	.	.	.
1960	1020	.	.	.	.	.	.	.	.	.	123
1961	1141	.	.	.	.	.	.	.	.	.	152
1962	1118	.	.	.	.	.	.	.	.	.	.
1963	1259	.	.	.			.	.	.	.	.
1964	1439	.	.	.	.	.	.	.	.	.	115
1965	1404	.	.	.	.	.	.	.	.	.	74
1966	1728	.	.	.	.	.	.	.	.	.	107
1967	1779	.	.	.	.	.	.	.	.	.	132
1968	1800	.	.	.	.	.	.	.	.	.	152
1969	1919	.	.	.	.	.	.	.	.	.	127
1970	1987	.	.	.	.	15	.	.	.	.	103
1971	2041	.	.	.	.	1	.	.	.	.	148
1972	1617	.	.	.	.	0	.	.	.	.	.
1973	1678	.	.	107	.	0	.	.	.	578	123
1974	1668	.	.	.	.	.	.	.	.	.	136
1975	1617	.	.	.	.	.	.	.	.	.	197
1976	1426	.	.	.	.	.	.	.	.	.	160
1977	1243	.	.	.	645	.	.	.	.	700	156
1978	1162	.	.	.	.	.	.	.	.	.	169
1979	1320	300	.	.	.	.	.	.	.	.	164
1980	1118	499	.	.	.	.	.	.	.	.	140
1981	992	505	.	.	.	34	.	.	.	.	82
1982	991	603	.	.	.	43	.	.	.	.	103
1983	902	336	.	.	.	.	.	.	.		.
1984	778	517	.	.	.	30	94	406	.	.	.
1985	848	810	.	.	.	53	.	.	.	.	.
1986	908	891	.	.	.	35	.	.	.	.	.
1987	930	865	.	.	.	72	.	.	.	.	.
1988	812	608	.	.	.	54	.	.	.	.	.
1989	892	936	.	.	.	94	280	666	.	.	.
1990	1004	1122	.	.	.	152	.	.	.	.	.
1991	927	1225	.	.	.	223	321	.	.	.	241
1992	985	1251		.	1308	200	225	612	.	.	246
1993	1051	1454		.	1372	205	.	700	.	.	244
1994	1025	1325		.	1350	302	.	700	.	.	258
1995	1070	1353		.	.	334	300	516	.	.	250
1996	1061	1567		.	.	310	300	726	.	.	250
1997	1284	1796	236	.	.	382	523*	719	.	.	250
1998	1309	1968	273	.	.	439	.	649	.	.	250

* Includes pups on Berridale beaches

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 Shetland. Estimates refer to the number of seals aged 1 and over at the start of the breeding season.

YEAR	Pup Production	Female Population	Female + Male Population
1984	14,992	25,413	44,127
1985	16,265	27,012	46,881
1986	17,796	28,863	50,110
1987	19,035	30,803	53,488
1988	18,071	32,948	57,249
1989	19,926	35,006	60,807
1990	21,093	37,150	64,582
1991	23,815	39,516	68,582
1992	27,075	41,882	72,620
1993	28,338	44,659	77,440
1994	29,018	47,628	82,602
1995	30,932	50,759	88,043
1996	33,426	54,128	93,919
1997	32,771	57,669	100,077
1998	35,680	61,289	106,332

Table 6. Scottish grey seal breeding sites that are either not surveyed annually or have recently been included in the survey programme. Other potential breeding sites are checked visually when flying time, conditions and other circumstances permit.

	Location	Survey method	Last surveyed, frequency	Number of pups
Inner Hebrides	Colonsay/Oronsay mainland	SMRU visual	1994, every 2-3 years	None seen
	Loch Tarbert, Jura	SMRU visual	1998, every 3-4 years	None seen
	West coast Islay	SMRU visual	1998, every 3-4 years	None seen
	Ross of Mull, south coast	SMRU visual	1998, infrequent	None seen
	Treshnish small islands, incl. Dutchman's Cap	SMRU photo & visual	1998, annual	~20 in total
	Staffa	SMRU visual	1998, every other year	~5
	Little Colonsay, by Ulva	SMRU visual	1998, every 3-4 years	6
	Meisgeir, Mull	SMRU visual	1998, every 3-4 years	1
	Craig Inish, Tiree	SMRU photo	1998, every 2-3 years	2
	Cairns of Coll	SMRU photo	1998, every 2-3 years	13
	Muck	SMRU photo	1998, every other year	12
	Rum	SNH ground	1997, annual	10-15
	Canna	SMRU photo	1998, every other year	34
	Rona	SMRU visual	1989, infrequent	None seen
	Ascrib Islands, Skye	SMRU photo	1998, every other year	32
	Heisgeir, Dubh Artach, Skerryvore	SMRU visual	1995, every other year 1989, infrequent	None None
Outer Hebrides	Barra Islands Fiaray & Berneray	SMRU visual	1998, infrequent	61
	Sound of Harris islands	SMRU photo	1997, every 2-3 years	188
	St Kilda	Warden's reports	Infrequent	Pups are born
	Shiants	SMRU visual	1998, every other year	None
	Flannans	SMRU visual	1994, every 2-3 years	None
	Bernera, Lewis	SMRU visual	1991, infrequent	None seen
	Summer Isles	SMRU visual	1989, infrequent	None seen
	Faraid Head	SMRU visual	1989, infrequent	None seen
	Eilean Hoan, Loch Eriboll	SMRU visual	1998, annual	None
	Rabbit Island, Tongue	SMRU visual	1998, every other year	None seen
Orkney	Sule Skerry	SMRU photo	1998	15
	Sanday, Point of Spurness	SMRU photo	1996, 2-3 yearly	8
	Sanday, east and north	SMRU visual	1994, every 2-3 years	None seen
	Papa Stronsay	SMRU visual	1993, every 3-4 years	None seen
	Holm of Papa, Westray	SMRU visual	1993, every 3-4 years	None seen
	North Ronaldsay	SMRU visual	1994, every 2-3 years	None seen
	Calf of Flotta	SMRU photo	1998, annual	121
Others	Firth of Forth islands & Inchcolm	Anecdotal SMRU photo	Infrequent 1997	<10 4

Legends to Figures

Figure 1 Grey seal breeding sites in Great Britain.

Figure 2 Total estimated pup production for all major breeding colonies in Scotland and England (excluding Loch Eriboll, Helmsdale and Shetland) from 1984 to 1998.

Figure 3 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. Although they therefore underestimate the total variability in the estimate, they are useful for comparison of the precision of the estimates in different years.

(a) Outer Hebrides, Orkney and Inner Hebrides

(b) Isle of May, Farne Islands and Donna Nook

Note that the scale of these two figures differs by an order of magnitude.

Figure 4 Comparison of pup production trajectory estimated using a constant time to leave parameter (as in Figure 1) with that generated when that parameter is re-estimated for each breeding site in each year. The latter trajectory is also scaled to have the same value as the former in 1987 for the comparison of trends.

Figure 5 Mean dates of birth for the eleven breeding sites in the Outer Hebrides from 1987 to1998. Dates were produced from the program used to estimate pup production.

Figure 6 Estimated size of the total population at all major breeding sites in Scotland and England from 1984 to 1998, shown with estimated pup production and pup production predicted from the population model.

Figure 1

Grey seal breeding sites
in Great Britain

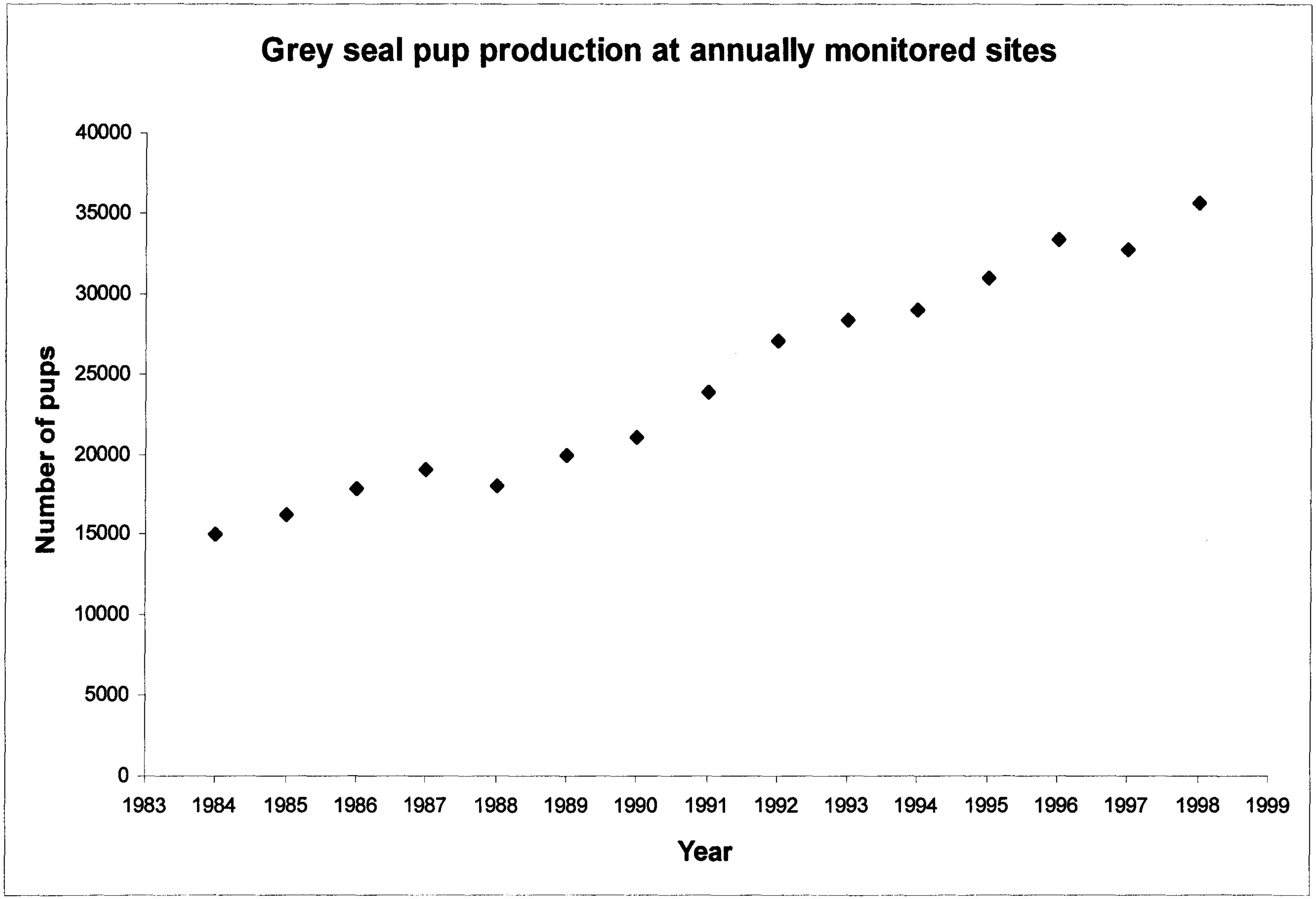

Grey seal pup production at annually monitored sites
Number of pups
40000
35000
30000
25000
20000
15000
10000
5000
0
1983
1984
1985
1986
1987
1988
1989
1990
1991
1992
1993
1994
1995
1996
1997
1998
1999
Year

Figure 2

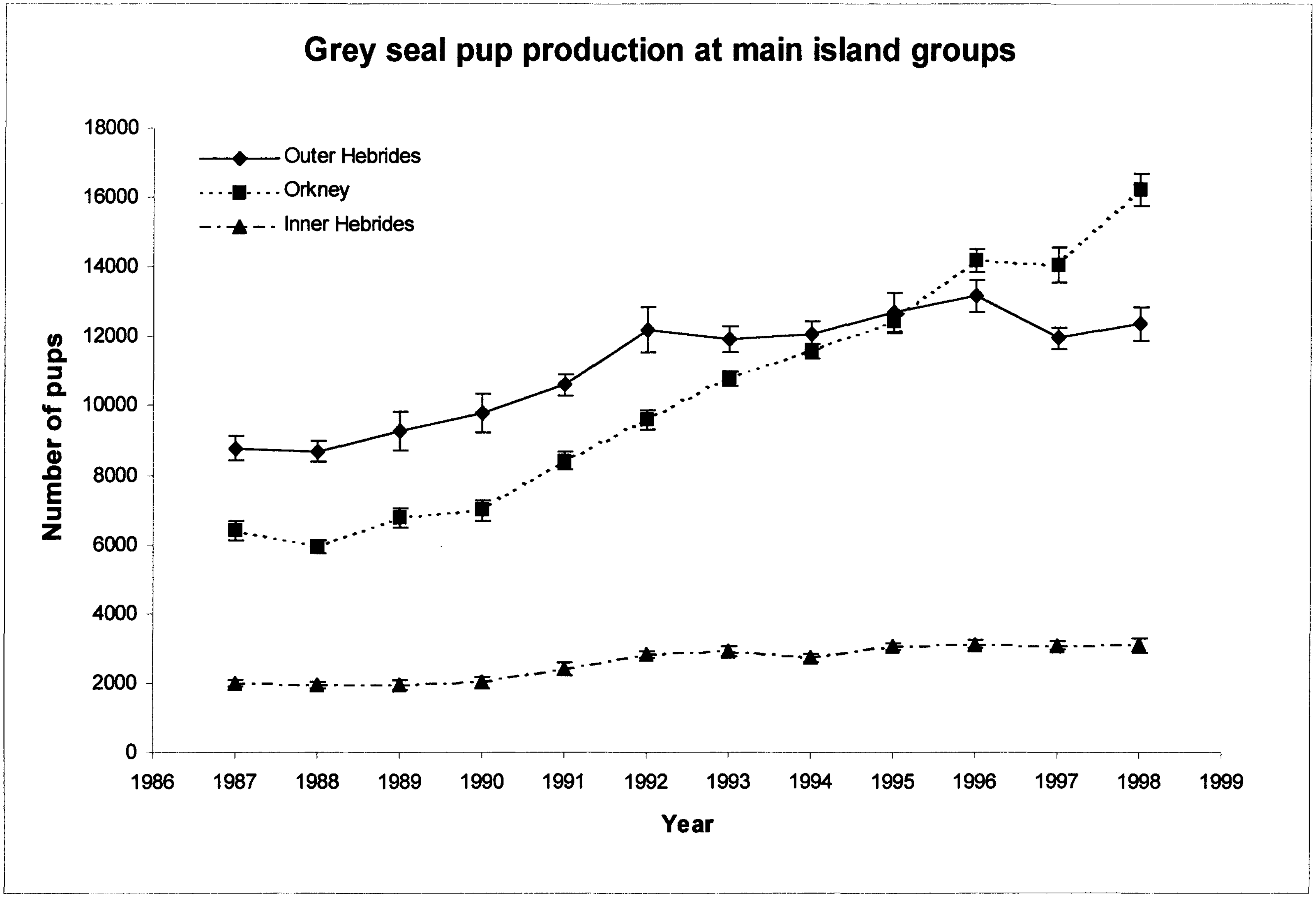
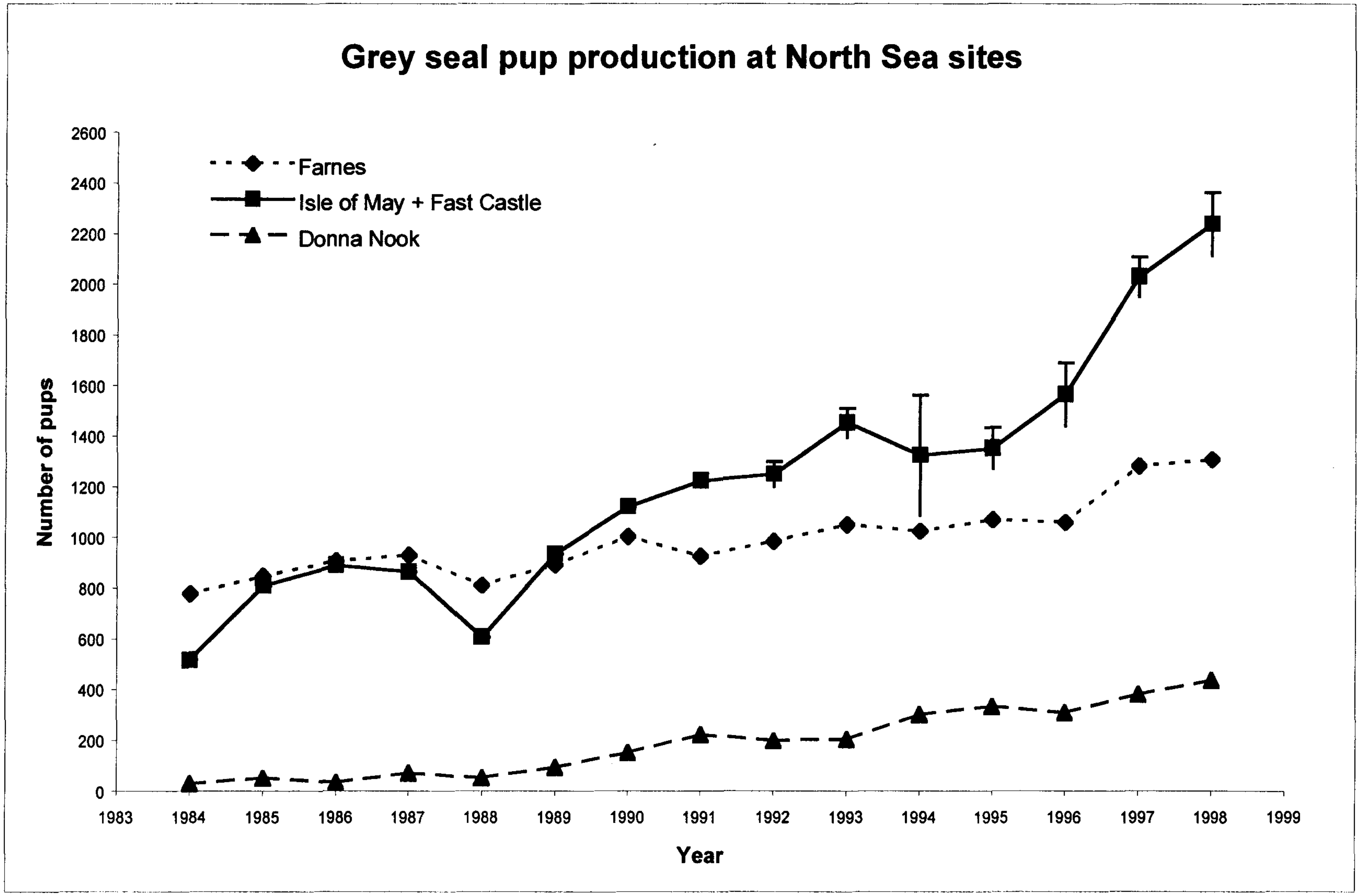

Grey seal pup production at main island groups
Outer Hebrides
Orkney
Inner Hebrides
Number of pups
18000
16000
14000
12000
10000
8000
6000
4000
2000
0
1986
1987
1988
1989
1990
1991
1992
1993
1994
1995
1996
1997
1998
1999
Year

Figure 3a



Grey seal pup production at North Sea sites
Farnes
Isle of May + Fast Castle
Donna Nook
Number of pups
2600
2400
2200
2000
1800
1600
1400
1200
1000
800
600
400
200
0
1983
1984
1985
1986
1987
1988
1989
1990
1991
1992
1993
1994
1995
1996
1997
1998
1999
Year

Figure 3b

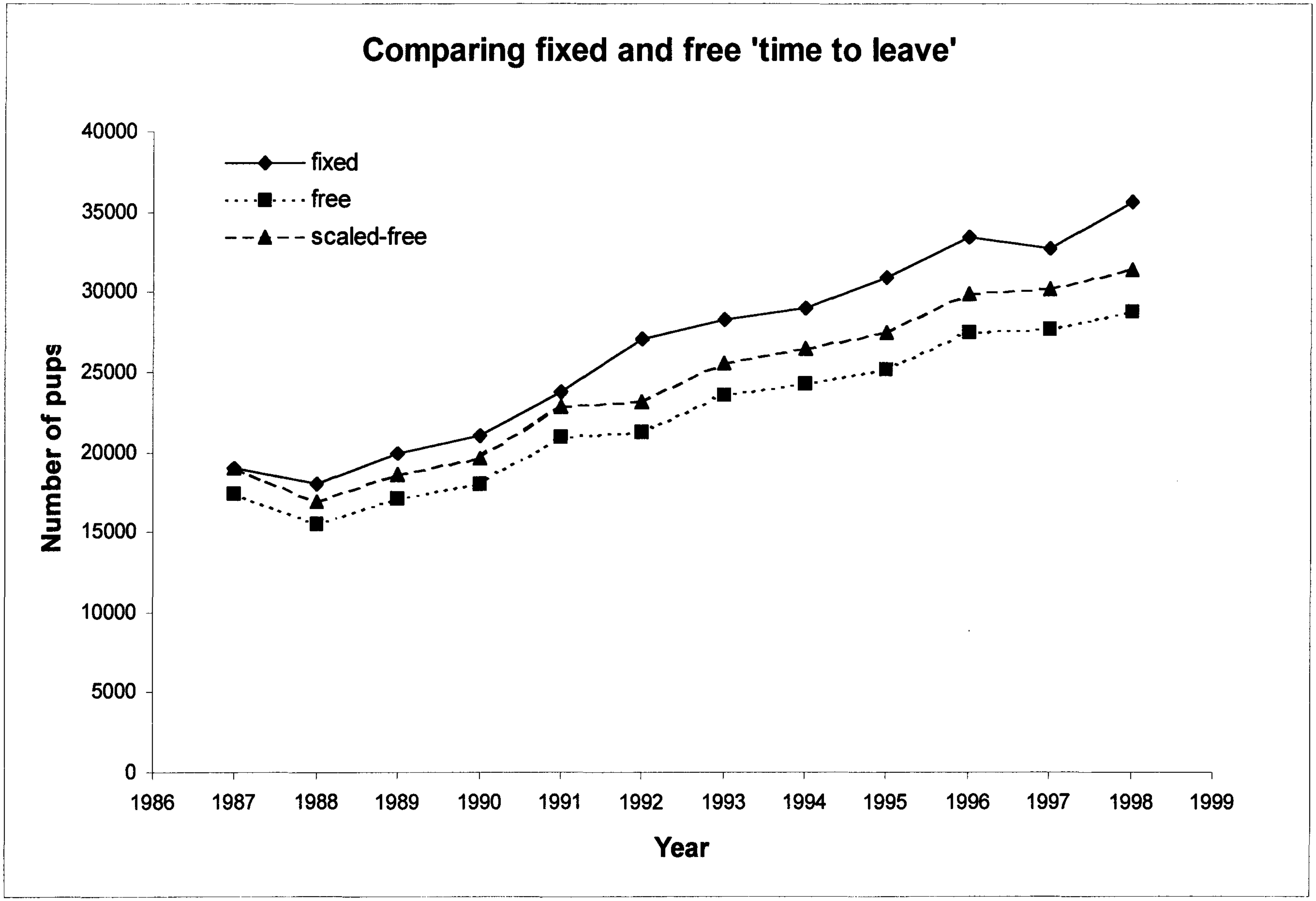

Comparing fixed and free 'time to leave'
fixed
free
scaled-free
Number of pups
40000
35000
30000
25000
20000
15000
10000
5000
0
1986
1987
1988
1989
1990
1991
1992
1993
1994
1995
1996
1997
1998
1999
Year

Figure 4

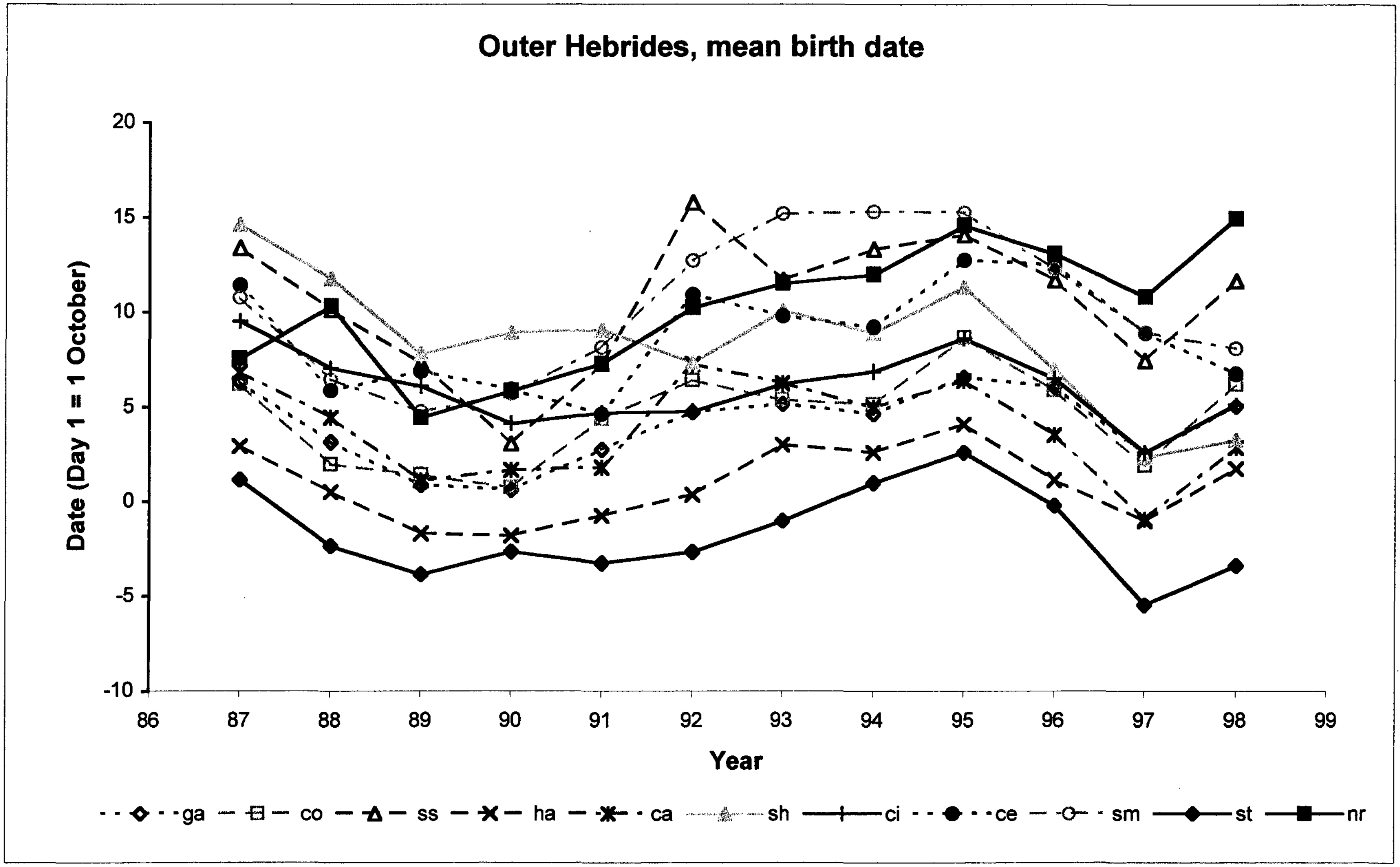

Outer Hebrides, mean birth date
Date (Day 1 = 1 October)
20
15
10
5
0
-5
-10
86
87
88
89
90
91
92
93
94
95
96
97
98
99
Year
ga
co
ss
ha
ca
sh
ci
ce
sm
st
nr

Figure 5

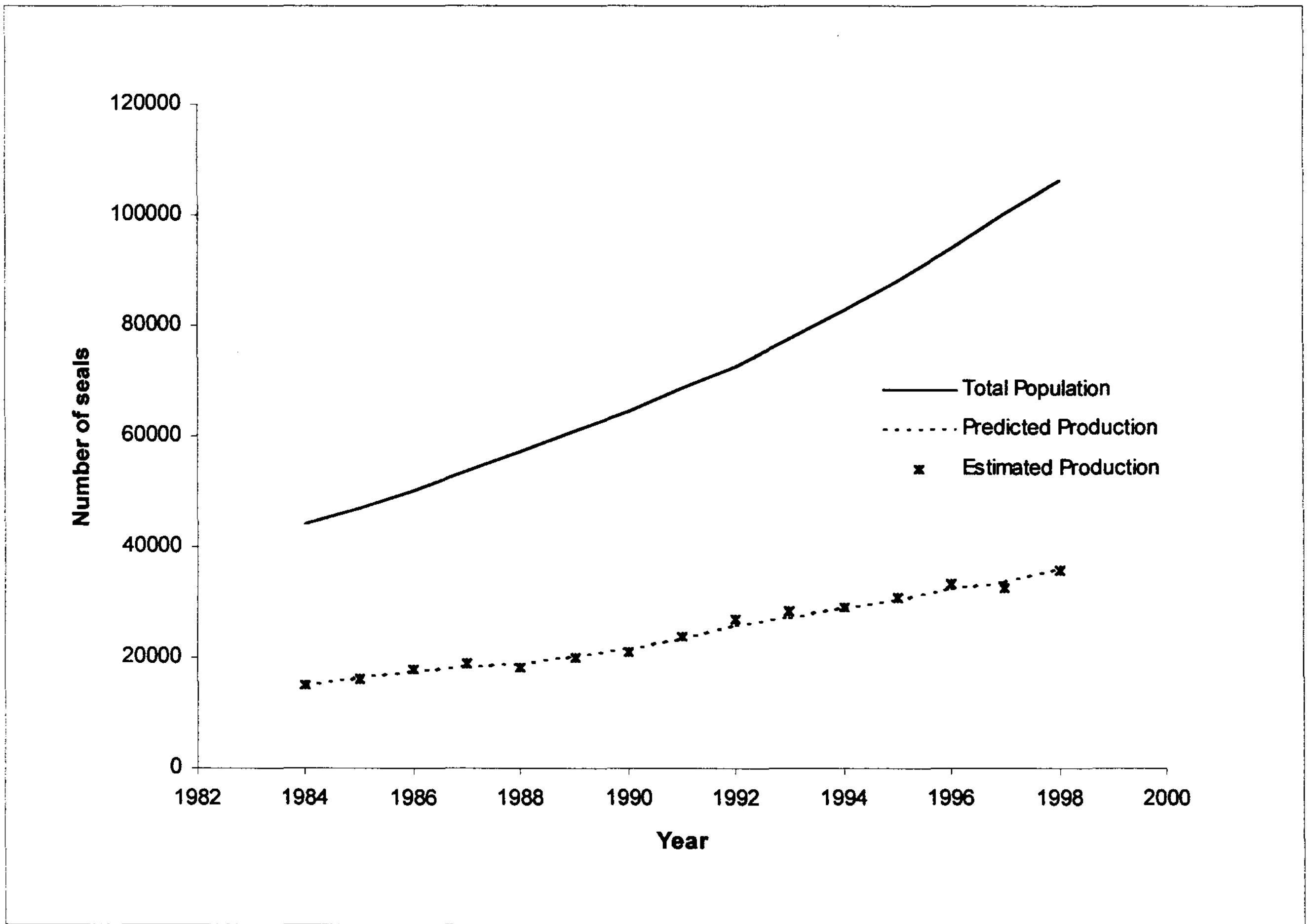

120000
100000
80000
60000
40000
20000
0
Number of seals
1982
1984
1986
1988
1990
1992
1994
1996
1998
2000
Year
Total Population
Predicted Production
Estimated Production

Figure 6

ANNEX II

The Status of British Common Seal Populations: 1998

1. Rates of change in the abundance of Scottish common seals: an analysis of SMRU thermal imager counts from 1988 to 1997

Introduction

The objective of this analysis was to estimate rates of change in common seal abundance along a number of sections (subregions) of the Scottish coastline. The basic data were counts of moulting common seals summed over each completed subregion. A subregion is a section of mainland or island coastline running between geographical features that can be easily identified during survey flight, usually headlands. For example, one subregion extends from Dornoch to Duncansby Head, another from Duncansby Head to Strathy Point and a third from Strathy Point to Cape Wrath. Sometimes a subregion may be an entire island, such as Skye, Mull or Islay. These subregions form subsets of the local government Region (now replaced by Councils) containing that section of coastline.

As it was not possible to survey all Regions within the same year, the surveys were designed to complete just one or two of the local government Regions in each year. However, Highland and Strathclyde Regions are very extensive and were usually not completed in their entirety. So for this analysis subregions have been amalgamated into ten new groups as shown in Figure 1 and Table 1. Each new group consists of a set of contiguous subregions, all of which have been surveyed at least twice.

A stochastic model for the counts

We denote the number of seals in a given area *i* in year *t* by $N_{i,t}$ and assume that the expected proportion hauled out during the moult in that area is constant at P_i and that the annual rate of population change in that area is also constant at r_i. Hence the expected count in area *i* and year *t*, $C_{i,t}$ is

$$E(C_{i,t}) = P_i N_{i,0} e^{r_i t}$$

where year 0 is 1987 so that *t* takes the values 1 to 10. The proportion P_i is unknown so that only r_i and the composite parameter $P_i N_{i,0}$ (denoted below by β_i) are estimable. However we assume that P_i is sufficiently close to 0.5 and $N_{i,0}$ is sufficiently large for the distribution of $C_{i,t}$ about its expectation to be approximately Normal. We consider two possibilities concerning the variance of $C_{i,t}$. One is that the variance increases in proportion to the expected count. That would be the case if random variation in P_i is negligible and variation in the counts results from binomial variation in the number of seals hauled out at the time of the survey. Because seals tend to haul out in groups the variance could greatly exceed the mean and the constant of proportionality would reflect the typical group size. The other is that the standard deviation increases in proportion to the expected count, which would be the case if random variation in P_i was the dominant factor. The latter model might be appropriate if the areas under consideration were very small so that year-to-year shifts in distribution between adjacent areas dominated counts. However the results below show that for areas of the scale of the groupings in table 1 the former model is more appropriate.

Thus, assuming that the variance of $C_{i,t}$ equals k times its expectation, the likelihood for the counts is given by

$$\prod_{i=1}^{10} \prod_{t \in \{t_{i1}, t_{i2}, ..\}} \frac{1}{\sqrt{2\pi k \beta_i e^{r_i t}}} \exp\left(\frac{-1}{2k\beta_i e^{r_i t}} \left(C_{i,t} - \beta_i e^{r_i t} \right)^2 \right),$$

where $\{t_{i1}, t_{i2}, ..\}$ is the set of survey years for group i.

The likelihood can be maximised iteratively with respect to k and r_i, with β_i given at each step by

$$\frac{\sqrt{b^2 + 4ac} - b}{2a} \text{ where } a = \sum_t \frac{e^{r_i t}}{2k},\ b = \sum_t \frac{1}{2} \text{ and } c = \sum_t \frac{{C_{i,t}}^2}{2ke^{r_i t}}.$$

The same likelihood can be calculated for the counts over each individual subregion j in each group, replacing $C_{i,t}$ by $C_{i,j,t}$ and β_i by $\beta_{i,j}$ but retaining a common growth rate r_i for each subregion in the same group. Figure 3 plots the resulting mean square residual error, $C_{i,j,t} - \beta_{i,j} e^{r_i t}$, against the mean count for each subregion. With many subregions counted over only two years there is bound to be a wide scatter but the plot does suggest an increase in variance proportional to mean count even at the subregion scale. This confirms that for counts summed across each group the assumption of variance proportional to the expected total holds. Furthermore the maximum obtained using a likelihood with standard deviation rather than variance proportional to the expected count is significantly lower.

Results

Table 2 gives the maximum likelihood (ML) estimate and 95% confidence limits for the mean rate of increase over each group, r_i. Figure 2 shows the trajectories corresponding to the ML estimates for β_i and r_i: $E(C_{i,t}) = \beta_i e^{r_i t}$. The confidence limits were calculated for each group in turn by using the likelihood ratio method, that is, finding values for the chosen rate, below and above the ML estimate, at which twice the log likelihood was 3.84 (the 5% level for the χ^2 distribution) less than twice the maximum. The ML estimate for the variance:mean ratio for the group total counts over the surveys was 8.

Constraining the growth rates to be equal over all groups gave an estimate of 0.026 for the overall mean rate of increase, r, with 95% confidence limits from 0.015 to 0.043. However, the improvement in fit in estimating group-specific rates was highly significant.

Of the ten groups considered, seven show a significant increase in numbers counted up to the 1997 survey. One shows a significant decrease in numbers and two no significant change. The areas showing a decrease in abundance were the mainland coastline from Plockton south to Arisaig, and the mainland coastline from Oban to the southern tip of the Mull of Kintyre plus the islands of Jura, Islay and Colonsay. The changes are thus consistent with some movement of population westwards and northwards away from the Southwest coastline. There was a significant but moderate increase in total numbers counted over the ten years from 1988 to 1997 for the whole area considered, that is, the far north and west coasts of Scotland from Dornoch to the southern tip of the Mull of Kintyre plus Orkney, Shetland and the Hebrides.

Discussion

The use of a thermal imager from an aerial platform allows near-synoptic survey over long sections of coastline. It is possible, with this method, to survey the entire coastline of Scotland within two or three moulting haul-out seasons and thus to minimise the effect of any shift in distribution on apparent trend in abundance.

However, maximising the coverage in this way precludes conducting many repeat surveys over most regions and a number of regions have been surveyed only twice. Even if such regions were considered in isolation, it would still be possible to estimate confidence limits on the change in abundance by considering the counts over the component subregions. Constraining the rate of change to be the same in each subregion, but allowing the initial abundance to differ, would provide a set or replicates and sufficient degrees of freedom to estimate the error on the estimated rate of change. The risk is that the power to detect significant change in the mean rate is reduced if rates vary considerably between subregions if, for example, many seals move between subregions from year to year. Any difference between subregions inflates the error term in the model in the same way as neglecting interaction in a two-way ANOVA does.

In the current analysis it has been possible to avoid this risk by adding counts over groups of adjacent subregions. The required degrees of freedom were still available because some of the groups had been surveyed over more than two seasons. The key assumption is that the variance of a total count can be related to its expectation so that even for a group completed only twice a measure of error on each total count is available.

The two approaches can be combined by considering all groups simultaneously but retaining the subregion counts instead of summing over each group. The results are broadly similar to those for the summed counts but, as expected, the confidence limits are wider, as differences between subregions within the same group contribute to the error term. Using this approach, the ML estimate for the variance:mean ratio is increased from 8 to 260. These data are shown in Figure 3, which shows that variance increases in proportion to the expected count, not to the square of the expected count, so that the proportional error reduces with the expected size. These results suggest that, if the objective is to monitor change in numbers, infrequent surveys over a large area are more useful than frequent surveys over a restricted area.

However, Figure 3 also highlights a risk inherent with the use of very infrequent surveys. The outlier evident in the plot is the Rousay subregion in Orkney which includes Eynhallow and other islands close to Rousay (see SCOS 99/7 Annex I Appendix 2). In the 1997 thermal image survey, and in previous visual surveys by boat and helicopter, several hundred seals were counted at haulout sites on Eynhallow but almost none were counted in the 1993 thermal image survey. Up to the 1993 survey, counts at haulout sites on the Holm of Scockness followed a similar pattern but, in contrast to Eynhallow, have remained very low since the 1993 survey. This level of variation has not occurred in any other subregion and one possible explanation is that disturbance at an unusually large scale had occurred just prior to the 1993 survey in that subregion. It is not possible say whether the seals "missing" from the Rousay subregion on that day were counted on other Orkney haulout sites. However, one way to address this problem in future surveys would be to use the estimated variance:mean ratio for a subregion count to identify such outliers automatically before the end of the survey. For example, given an expected count around 800 and a variance:mean ratio of 26, the standard deviation for the count would be around 150 so we would not expect a count of less than around 500 on any one survey. A second visit to the same subregion during the same survey might then identify the reason for the outlying count. Such a protocol carries an obvious risk of upward bias and care would be needed in its application.

2. Common seals surveys in eastern England 1998

In 1988, the numbers of common seals in The Wash declined by approximately 50% as a result of the phocine distemper virus (PDV) epidemic; prior to this, numbers had been increasing. Following the epidemic, from 1989, the area has been surveyed annually with one or two counts in the first half of August each year (Table 3).

One complete and one partial survey of common seals were carried out in Lincolnshire and Norfolk during August 1998 (Table 3). The Wash counts were within the range of the two 1997 counts. The average annual rate of increase in the number of seals counted in The Wash since 1989 is 6.5% (SE = 0.94%). This is significantly greater than the average annual rate of increase between 1968 and 1988 of 3.5% (SE = 0.29%).

The 1998 count in The Wash remains lower (by 20%) than the pre-epidemic count in 1988. This is in contrast to populations on the east and south sides of the North Sea which recovered rapidly from the effects of PDV and, by 1996, were similar to or exceeded their pre-epidemic levels.

The 1998 counts at Blakeney Point (Table 3) were much higher than previous years. Normally, grey and common seals are distinguishable at mixed haul-out sites by the overall pattern of group distribution and the spacing between individual animals. In the second survey at Blakeney Point, however, grey seals appeared to be distributed evenly through the haul-out site making them difficult to distinguish. Thus, the second count may be too high. However, the National Trust warden at Blakeney Point has confirmed that total seal numbers have increased and that the proportion of grey seals is close to that determined from the aerial photographs.

3. Status of common seals in The Wash

Introduction

In the summer of 1988 an epidemic of phocine distemper virus (PDV) spread through the European common seal (*Phoca vitulina*) population. More than 18,000 carcasses washed ashore over a 5 month period. In 1989, the size of the worst affected populations was around 60% of the predicted size if no mass mortality had occurred. The PDV epidemic was intensively studied and widely reported. However, predicting its long-term consequences has been difficult because of our lack of basic population data, and lack of understanding of the status of the pre-epidemic populations.

This analysis investigates data from the series of aerial survey counts of the numbers of seals hauled out in The Wash during the annual moult. The population was apparently recovering from a period of heavy exploitation in the 1960s and 70s when it was severely impacted by the 1988 PDV outbreak. Available information on pup culls and hunting statistics are used to generate a series of possible population trajectories for the pre-epidemic population.

Methods

Aerial Surveys

The entire tidal region of The Wash, including the salt marsh, and the coastline for 50km either side of the estuary was surveyed annually from 1988 to 1998. All groups with more than 10 animals were photographed using SMRU's Image Motion Compensation aerial survey camera. Prior to 1988, irregular surveys were conducted using a combination of visual counts and oblique photography. Only complete censuses, i.e. those in which all haul-out sites in The Wash were surveyed during a single low tide period, were included in the analysis.

Optimum timing for these annual surveys was determined by examining seasonal and daily distributions of the numbers of seals hauled out on particular banks. Haul-out sites in The Wash are remote, so patterns were monitored at similar but accessible sites in the Moray Firth. The numbers of seals on selected sandbanks were recorded at ten minute intervals throughout the tidal cycle to determine the best time window for surveying. To determine the best date for surveys, a series of land-based counts was carried out in the Beauly, Cromarty and Dornoch Firths. Counts were conducted during 5-9 day periods at 3-4 week intervals between February and December 1985. In addition, historical patterns of seasonal haul-out abundance in The Wash were examined, derived from aerial surveys carried out in the 1960s and 1970s.

<u>Population model</u>

A simple matrix model was constructed to generate trajectories for the female component of the population. In the absence of data from The Wash, we used estimates of age at first parturition, age specific fecundity and survival estimates from published studies of a large sample of seals which died along the European coast during the PDV epidemic.

A transition matrix was constructed of the form:

$$
T = \begin{array}{ccccccccc}
0 & 0 & 0 & f_1 & f_2 & f_3 & f_{adult} & \dots\dots\dots & f_{adult} \\
S_{pup} & 0 & 0 & 0 & 0 & 0 & 0 & \dots\dots\dots & 0 \\
0 & S_{imm} & 0 & 0 & 0 & 0 & 0 & \dots\dots\dots & 0 \\
0 & 0 & S_{imm} & 0 & 0 & 0 & 0 & \dots\dots\dots & 0 \\
0 & 0 & 0 & S_{imm} & 0 & 0 & 0 & \dots\dots\dots & 0 \\
0 & 0 & 0 & 0 & S_{adult} & 0 & 0 & \dots\dots\dots & 0 \\
0 & 0 & 0 & 0 & 0 & S_{adult} & 0 & \dots\dots\dots & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & S_{adult} & \dots\dots\dots & 0 \\
. & . & . & . & . & . & . & . & . \\
. & . & . & . & . & . & . & . & . \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & \dots\dots\dots & 0
\end{array}
$$

where f_{adult} = probability an adult female will give birth to a female pup that year;

and $f_1 = 0.11*f_{adult}$; $f_2 = 0.5*f_{adult}$; $f_3 = 0.75*f_{adult}$.

S_{pup}, S_{imm} and S_{adult} are the probabilities of surviving to the next breeding season for a pup, an immature and an adult female, respectively. Maximum age was set arbitrarily at 31 years. In the absence of empirical data it was assumed that the 1905 starting population had a stable age distribution.

Annual records of the numbers of seals killed during bounty schemes were used to define removals from the following year's age structure. In the absence of information on either the age structure or the timing of the culls, it was assumed that the probability of being killed was independent of age and sex. In addition, between 1962 and 1972, between 250 and 870 pups were killed annually. A sex ratio of 1:1 for the pups killed was assumed. The bounty hunts and especially the pup hunts provided a lower bound for the population model. A trajectory was classed as unfeasible if the number of pups killed exceeded the predicted pup production.

Two versions of the model were run. Firstly for a population with unconstrained growth i.e. where rate of increase was independent of population size, and secondly for a population constrained by a carrying capacity. Growth rate was varied by scaling both fecundity and survival.

Results

Timing of surveys

The numbers ashore increased rapidly and monotonically as the banks were exposed, reached a plateau and then declined rapidly and monotonically as the bank was submerged (Figure 4). Simulated surveys, assuming that the individual count series represented components of one population, indicated that >90% of the maximum possible count was obtained anywhere between 1.5h before and 2h after low water.

Numbers hauled out in the three estuaries in the Moray Firth increased from March to August (Figure 5a, b). The highest mean counts in all three areas were recorded in early August. In the Beauly and Cromarty Firths these maximum counts coincided with the minimum estimates of coefficient of variation. Seasonal patterns in The Wash were examined by regressing log(count) on year and examining the residuals. A second-degree polynomial regression of residuals on time of year (day number) was highly significant. The fitted curve had a maximum at day 227, i.e. 15 August.

Aerial survey flights were therefore carried out during the first half of August, as close to low water as possible, and always within plus or minus two hours.

Population trend

One or two complete surveys of The Wash were carried out in each year from 1988 to 1998. The counts increased between the late 1960s and 1988 at an average rate of 3.4% per year (Figure 6). The count then fell by approximately 50% between 1988 and 1989, coincident with the PDV epidemic. After 1989, counts increased at an average of 6.5% per year but increased at an average rate of 8.4% per year between 1991 and 1998. The post-epidemic rate of increase was significantly higher than the pre-epidemic rate.

Figure 7 shows The Wash counts together with counts from the Wadden Sea population. It is apparent that although the initial effect of the epidemic was similar, i.e. approximately 50% reduction, the growth rate in The Wash was much lower than that in the Wadden Sea both before and after the epidemic.

Population models

With the original fecundity and survival estimates, an undisturbed population grew at 12% per year. Even with the minimum starting population of 100 females in 1905, the model population grew rapidly so that the bounty hunts and pup culls had little effect on the trajectory. To produce a trajectory with a reasonable fit to the observed pre-epidemic counts the intrinsic rate of increase had to be reduced to approximately 4% per year.

By constraining the model population to follow a logistic growth curve it was possible to produce a range of apparently plausible trajectories. The constrained model was run with a range of starting populations (N_0), a range of carrying capacities (K) and a range of intrinsic rates of increase (r). For each combination of N_0, K and r, the scaling factor C was calculated which minimised the sum of squares (SS) $\Sigma(n_t - C*N_t)^2$, where n_t was the model prediction for time t and N_t was the count at time t.

For the range of r and N_0 values used, only models with $K \geq 2200$ produced feasible trajectories. For all models with $r \geq 8\%$, the minimum SS was obtained with the lowest feasible K, i.e. 2,200. As r was reduced further, the minimum SS was obtained at higher K values (e.g. r = 6%, K = 3,800; r = 4%, K = 4,200). The overall minimum SS fit was for a population with r = 12%, K = 2,200, N_0 = 100, as shown in Figure 8.

Discussion

The population of common seals in The Wash was increasing during the period 1970 to 1988. In 1988, counts then fell by approximately 50% as a result of the epidemic. Similar declines were noted in the adjacent European populations in the Wadden Sea and the Kattegat/Skaggerak. After the epidemic, The Wash population shows evidence of a gradual recovery, with a post-epidemic growth rate approximately twice the pre-epidemic rate.

However, the growth rates in The Wash are much lower than those observed in other populations in the southern North Sea. In fact the post-epidemic rate in The Wash is similar to the pre-epidemic rate in the Wadden Sea. It is not clear why there should be such a discrepancy.

The observed growth rates in several, apparently closed, common seal populations have approached 15% per year. If this represents the intrinsic rate of increase of an undisturbed common seal population it seems clear that some factor was restricting the rate of increase in The Wash before the PDV epidemic and is, to a lesser extent, still restricting growth.

The heavy pup hunting 1968-1973 and earlier bounty schemes must have had some effect on the population trajectory. However, simple population modelling suggests that these alone could have had little effect on an unconstrained population with r = 12%, unless the starting population was below 70 females. Thus, either the intrinsic rate of increase for The Wash is lower than for adjacent populations, or some density dependent factor is constraining the growth rate.

With the population constrained to follow a logistic growth curve, the best fit trajectory was for a population with r = 12%, a relatively low carrying capacity of around 2,200 females and a low starting population of only 100 females in 1905. This model fit suggests that the moult count represents approximately 68% of the total age 1+ population, similar to estimates derived from telemetry studies.

Because of uncertainty in the accuracy of hunting statistics and the complete absence of counts before 1968, the fitted trajectory is unlikely to be an accurate reflection of the real population trend. However, the exercise does indicate that some form of constraint must be acting on The Wash common seals. This has important implications for management. If our model population is realistic it would imply that that the population may have been close to its maximum level in 1988 and that pup hunting between 1962 and 1972 had a significant effect on the population, removing almost the entire pup production in at least two years.

4. Common seals in the Moray Firth

The University of Aberdeen has been studying the behavioural and population ecology of common seals in the Moray Firth since 1987. Throughout this period, 2-10 shore-based counts have been made at all major haul-out sites in the inner Moray Firth during both pupping (15 June – 15 July) and moult (1 – 31 August) periods. These data therefore provide an index of abundance of seals in this study area in each year of the study which, based on telemetry data, accounted for approximately 60 % of the population.

The resulting data on changes in this index of the abundance of Moray Firth seals are presented in Figure 9. Mean counts from the time-series of counts during the pupping and moult periods were highly correlated ($r = 0.8$, $n=11$, $p<0.01$). Following a slight reduction in numbers resulting from the 1988 PDV outbreak, there was an increase in annual mean counts between 1989 and 1993 (Pupping: $F_{1,3}=17.11$, $r^2=0.85$, $p<0.05$; Moult: $F_{1,3}=24.12$, $r^2=0.89$, $p<0.05$). However, unlike the fluctuating but sustained increase seen in other parts of the North Sea, there has been a 3-4% decline in annual mean counts in the period 1992 – 1999 (Pupping: $F_{1,6}=7.7$, r2=0.56, $p<0.05$; Moult: $F_{1,5}=26.15$, $r^2=0.84$, $p<0.001$).

Table 1. Counts of common seals in groups of subregions of Scotland from thermal image surveys carried out in comparable years between 1988 and 1997. The groups of subregions are shown in Figure 1.

Group	Region	Amalgamated Subregions	Year of thermal survey							
			1988	1989	1990	1991	1992	1993	1996	1997
1a	Highland	Applecross, Rona, Raasay	72						184	
1b	Highland	Ardnamurchan, Sound of Mull, L Linnhe	251						323	
2	Orkney & Highland	All, Helmsdale						7983		8764
3	Shetland	All				4797		6227		5991
4	Outer Hebrides	All			2329				2820	
5	Highland	Pentland Firth, Tongue. Kinlochbervie, Eddrachillis, Enard, Summer Isles				537				719
6	Strathclyde	Mull, Lismore	1142	1338	1499	1288	1165	1547	1670	
7	Highland	Skye	1233	1269			1296		1728	
8	Highland	Plockton, Kyle, Sleat, L Nevis, Arisaig	854	793					650	
9	Highland & Strathclyde	Coll, Tiree, Muck, Eigg, Rum, Canna			596				1400	
10	Strathclyde	L Etive, Lorn, West Kintyre, Islay, Jura, Colonsay, Oronsay			2881				2280	

Table 2. Maximum likelihood (ML) estimate of mean rate of increase and 95% confidence limits (CL) for each group.

Group	ML estimate for r_i	Lower 95% CL	Upper 95% CL
1	0.057	0.010	0.110
2	0.023	0.001	0.045
3	0.028	0.010	0.045
4	0.048	0.001	0.090
5	0.049	-0.005	0.100
6	0.036	0.015	0.060
7	0.042	0.020	0.065
8	-0.032	-0.067	0.002
9	0.143	0.095	0.190
10	-0.039	-0.065	-0.012

Table 3. Numbers of commons seals counted on the east coast of England since 1988. Data are from fixed-wing aerial surveys carried out during the August moult.

Date of survey	**13.8.88**	**8.8.89 12.8.89**	**11.8.90**	**2.8.91 11.8.91**	**1.8.92 16.8.92**	**8.8.93**	**6.8.94 12.8.94**	**5.8.95 15.8.95**	**2.8.96**	**2.8.97 8.8.97**	**7.8.98 14.8.98**
Blakeney Point	701	- 307	73	- -	- 217	267	- 196	438 392	372	250 371	535 738
The Wash	3087	1531 1580	1532	1226 1551	1724 1618	1759	2277 1745	2266 1902	2151	2561 2360	*2367 2381
Donna Nook	173	- 126	57	- -	18 -	88	60 146	115 36	162	240 262	294 201
Scroby Sands	-	- -	-	- -	- -	-	61 -	- 49	51	58 72	52 -
The Tees	-	- -	-	- -	- -	-	- 35	- -	-	- -	- -
Holy Is (Nrthlnd)	-	- -	-	- -	- -	-	- 13	- -	-	- 12	- -
Essex & Kent	-	- -	-	- -	- -	-	- -	90 -	-	- -	- -

* One area used by common seals was missed on this flight (100 – 150 seals); this data point has been excluded from all analyses.

Figure 1

Harbour seal thermal image surveys carried out between 1988 and 1997. Groups of subregions surveyed in comparable years.

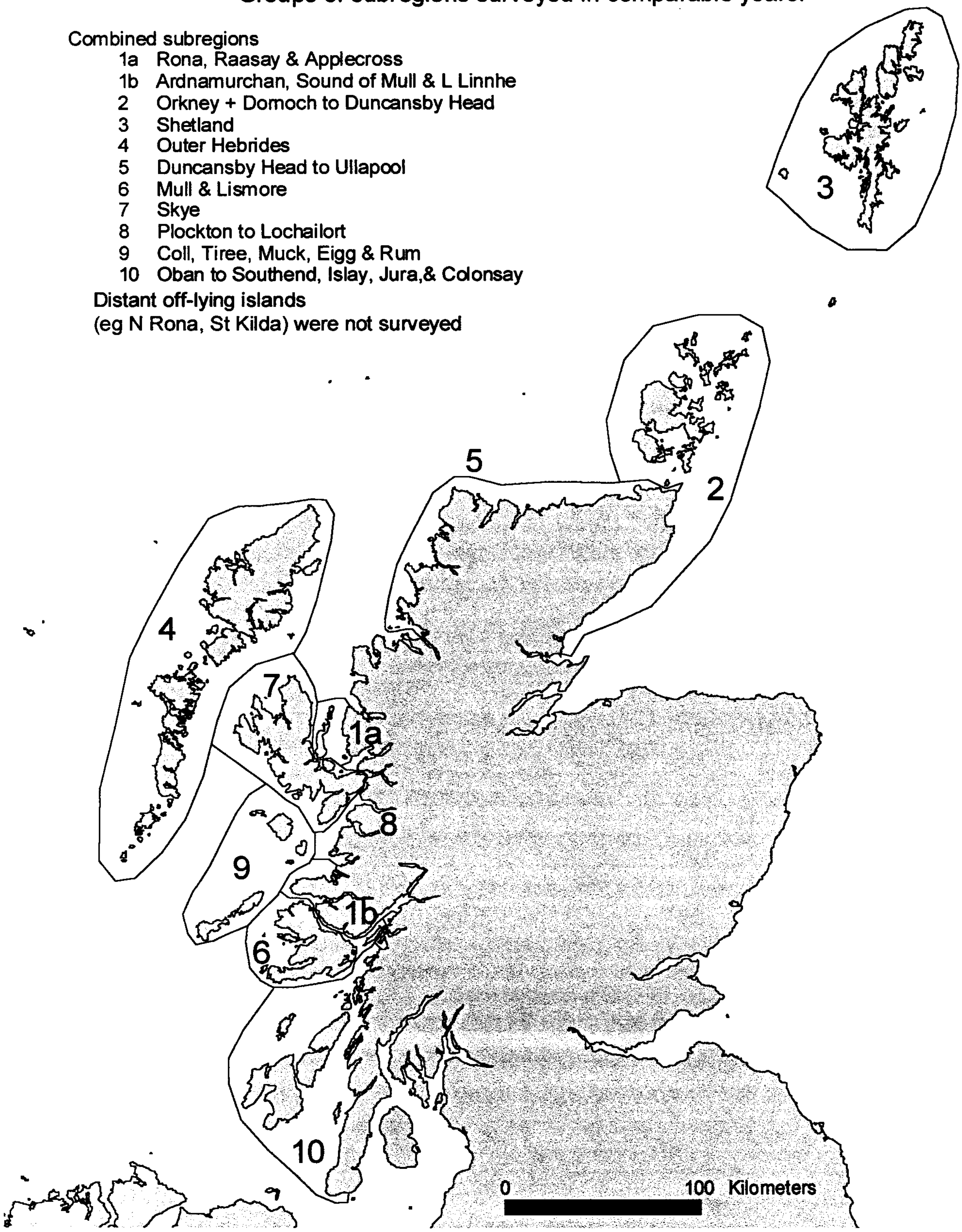


Figure 2. Total count and fitted growth curve in each of the ten groups of subregions.

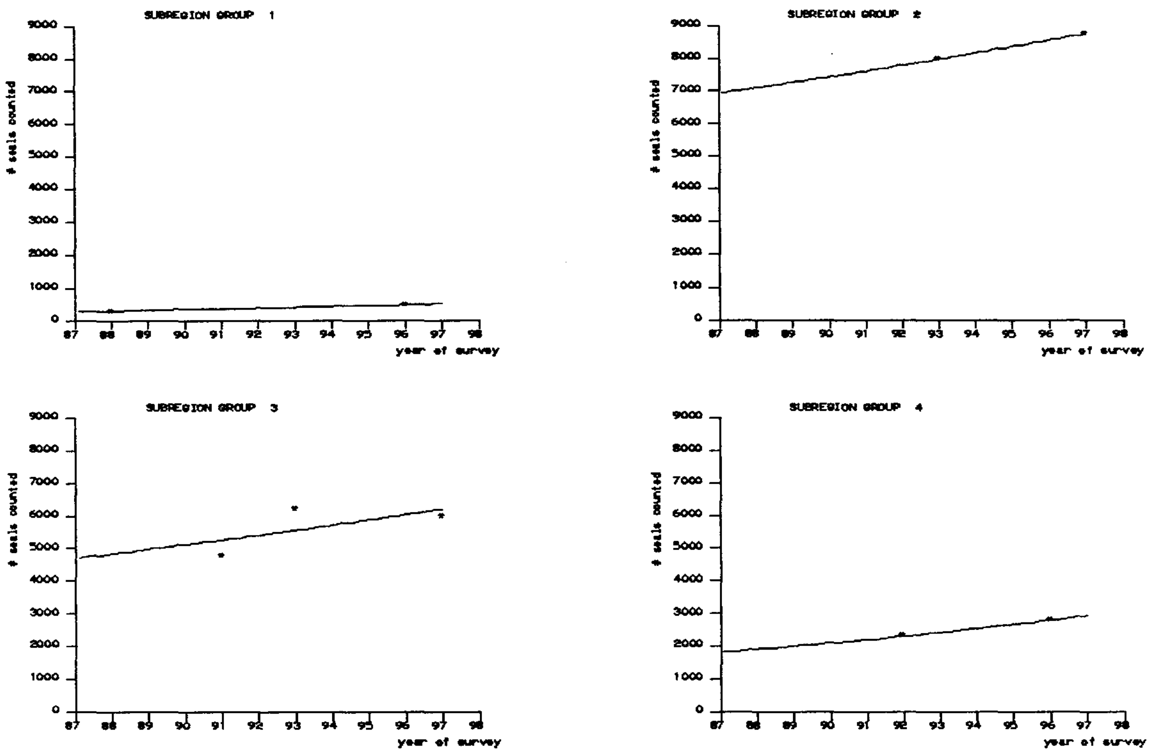


Figure 2 (continued)

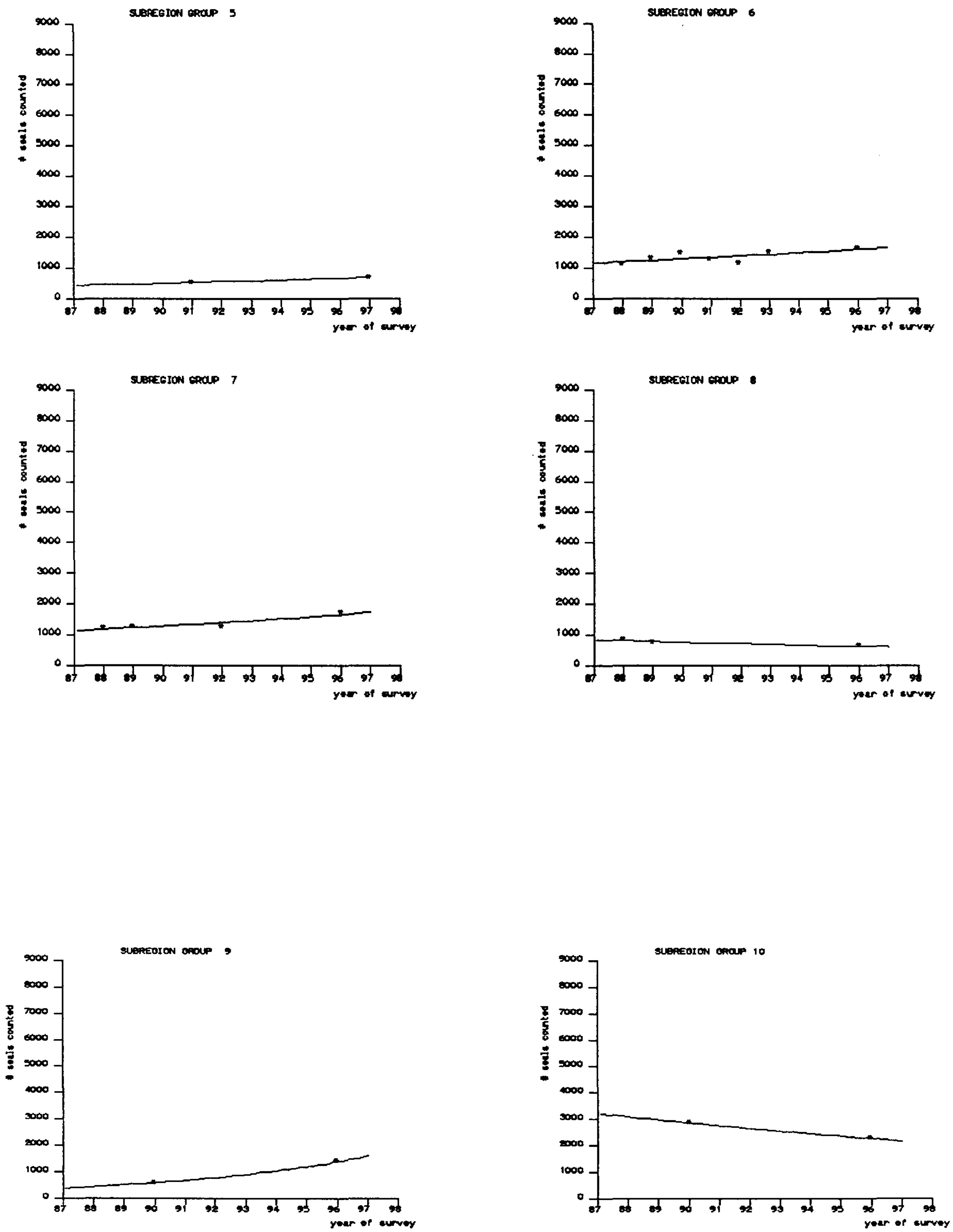
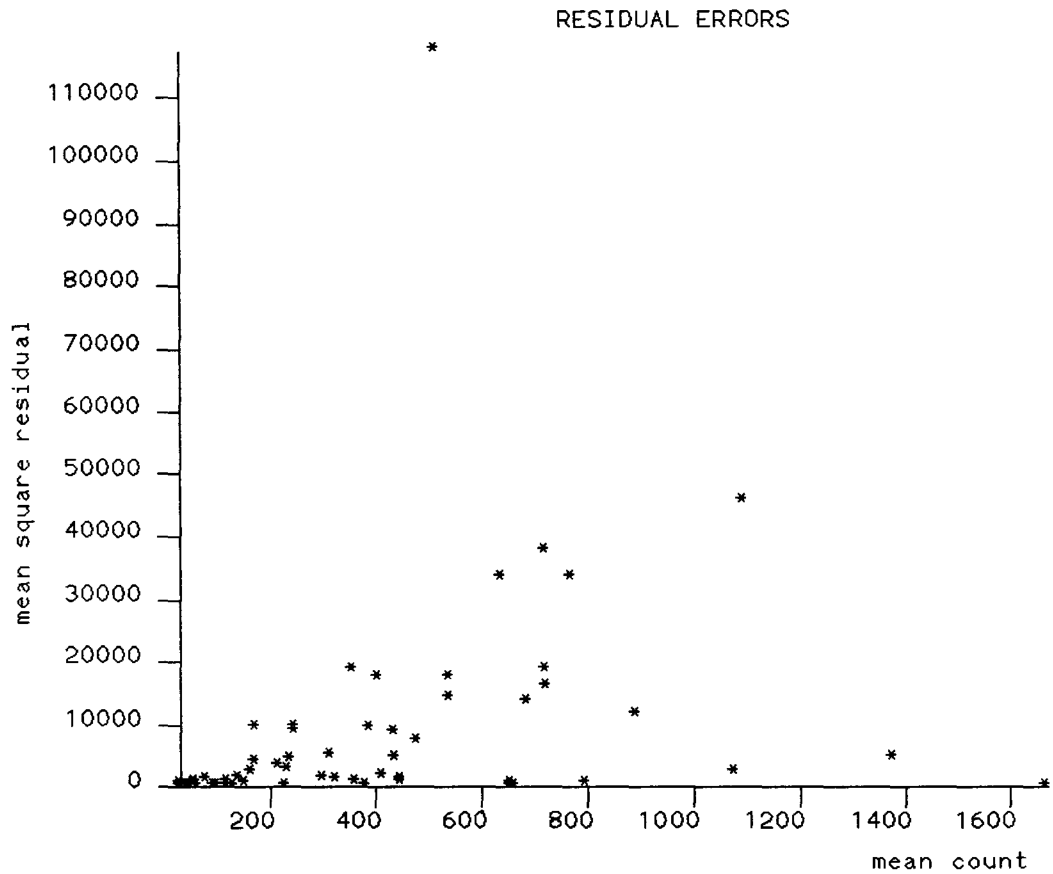


Figure 3. Mean square residual error vs mean count for each subregion.



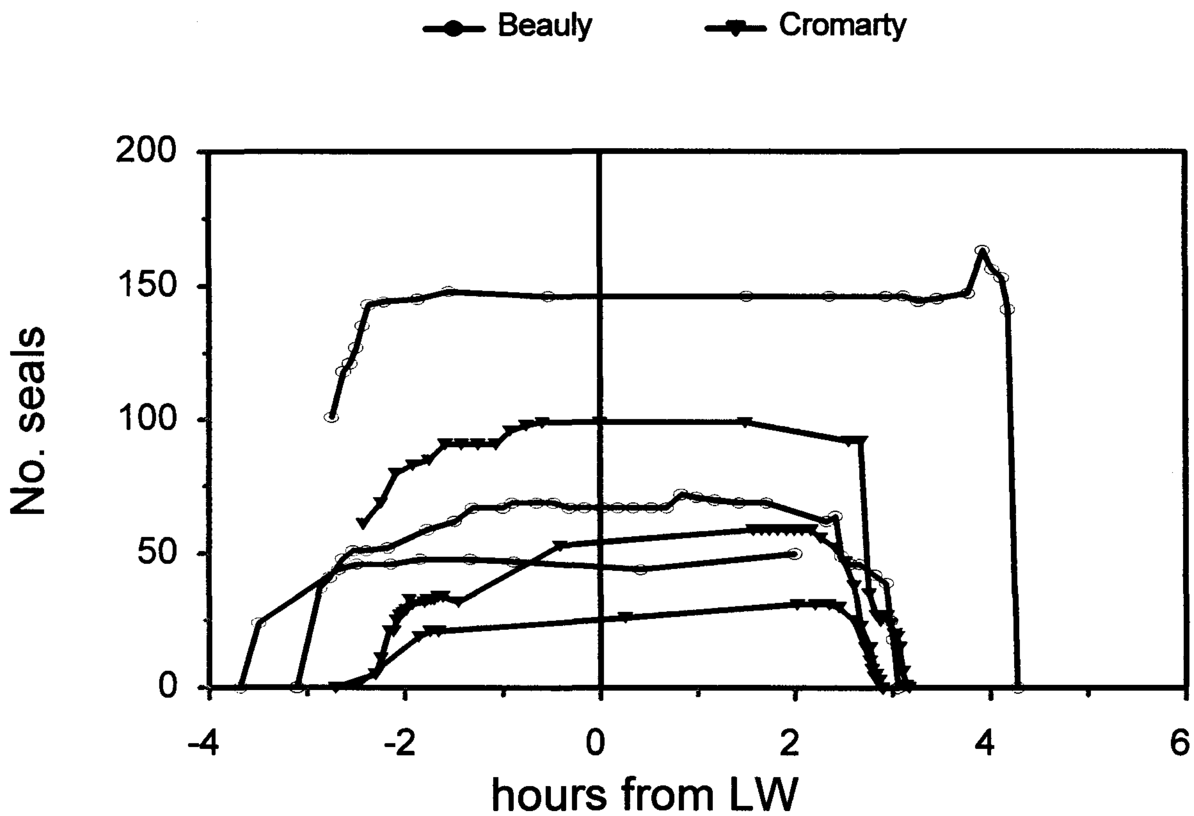


Figure 4 Numbers of seals hauled out on selected banks as a function of time from low water.

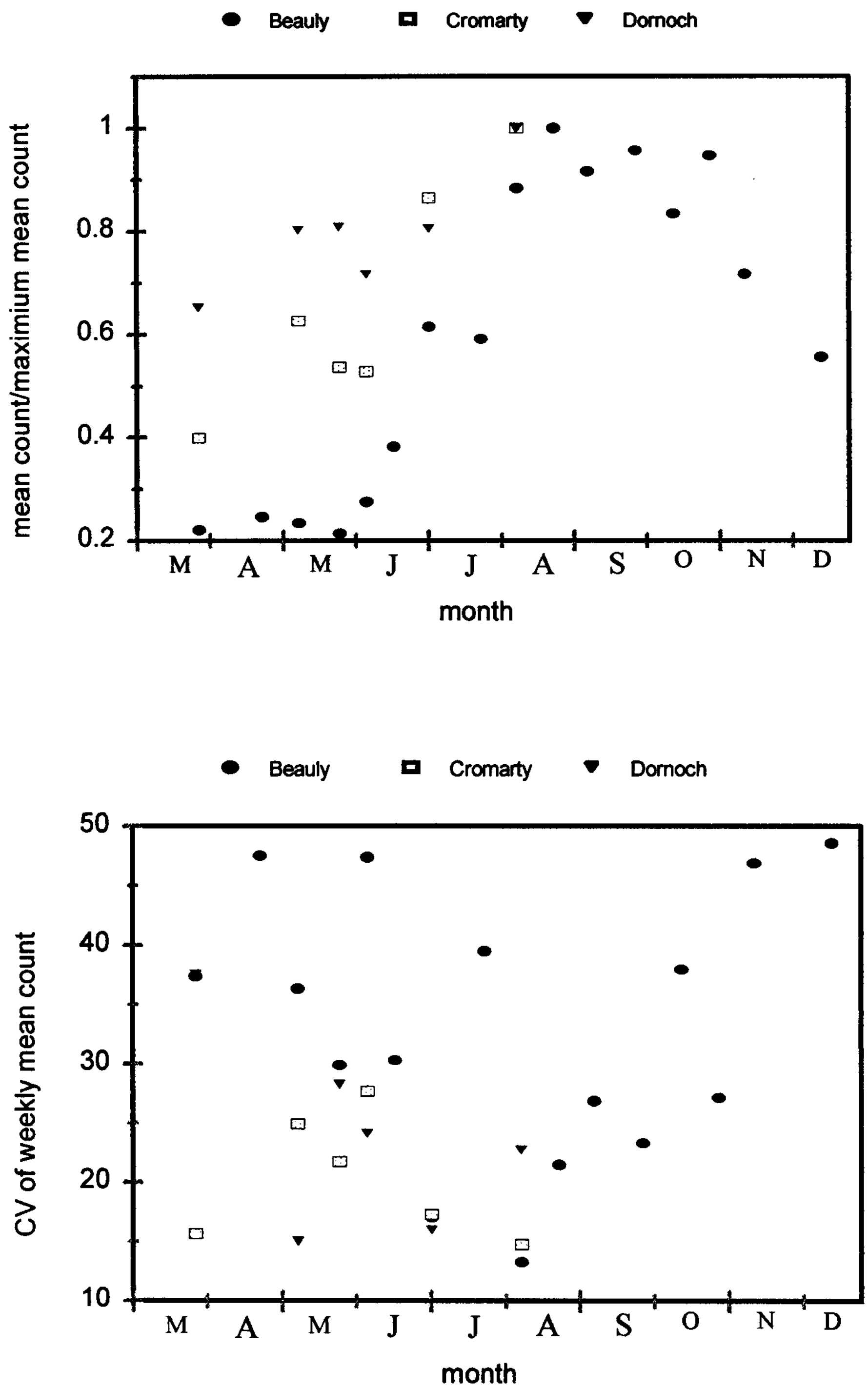


Figure 5. Counts of common seals in the inner Moray Firth in 1985.
a) weekly mean count expressed as proportion of maximum weekly mean.
b) CV of weekly counts.

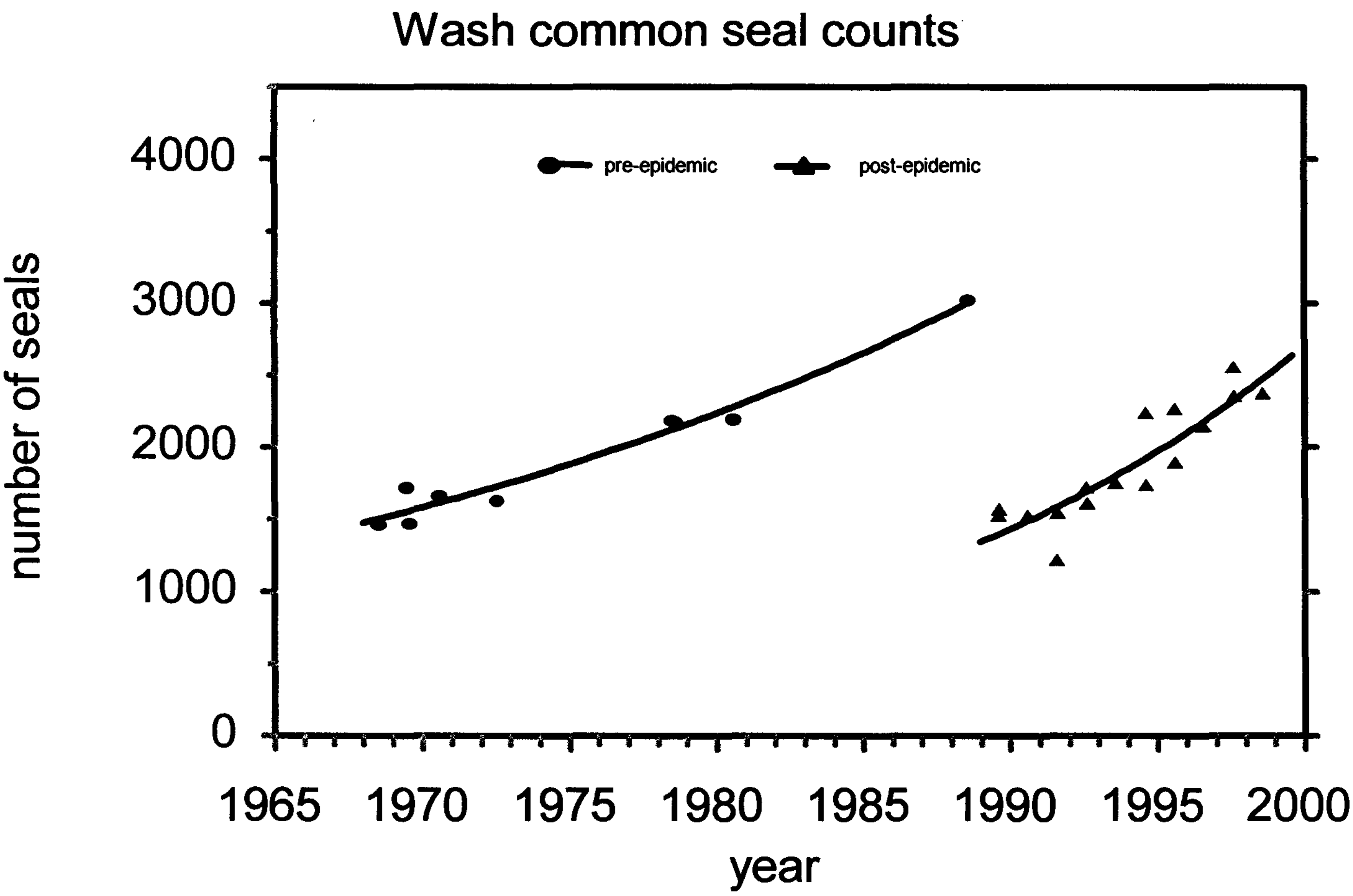


Figure 6 Moult counts of common seals in the Wash, 1968-1998. Exponential growth curves have been fitted separately to the pre and post epidemic counts.

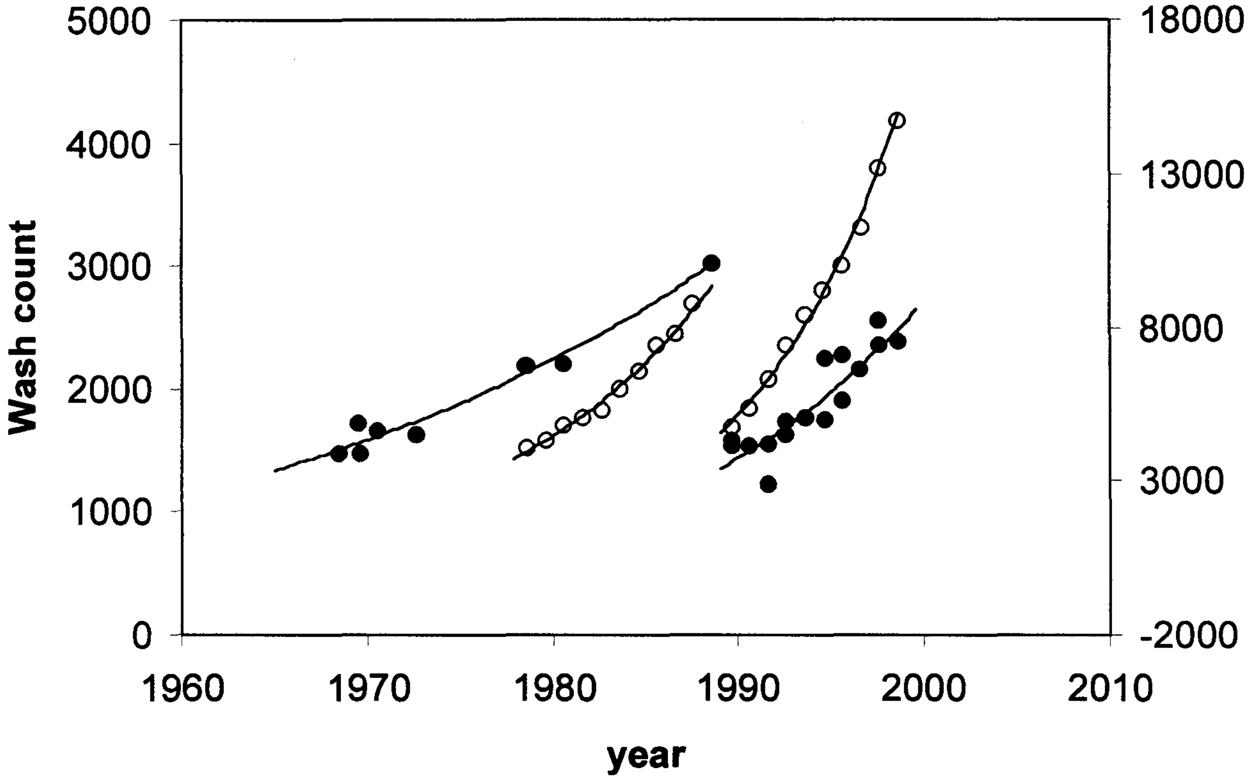


Figure 7 Counts of common seals hauled out during the moult, in the Wash, 1968-1998 (filled circles) and the Wadden Sea 1978-1998 (open circles). Exponential growth curves have been fitted separately to the pre and post epidemic counts.

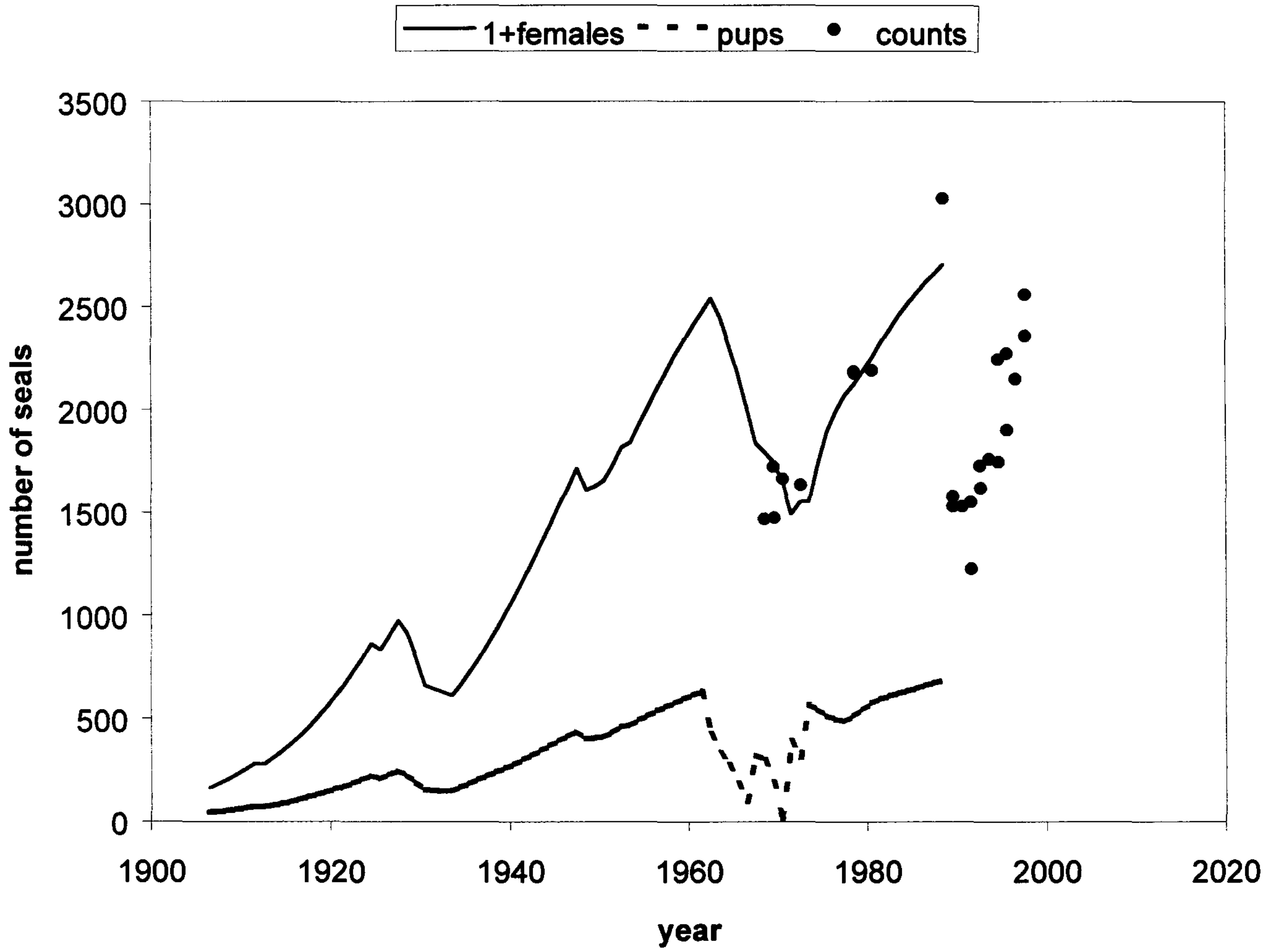


Figure 8	Predicted trajectories for the 1+ female population and pup production in the Wash. Population size constrained by a carrying capacity, and growth rate defined by a logistic growth curve. Closed circles represent moult counts.

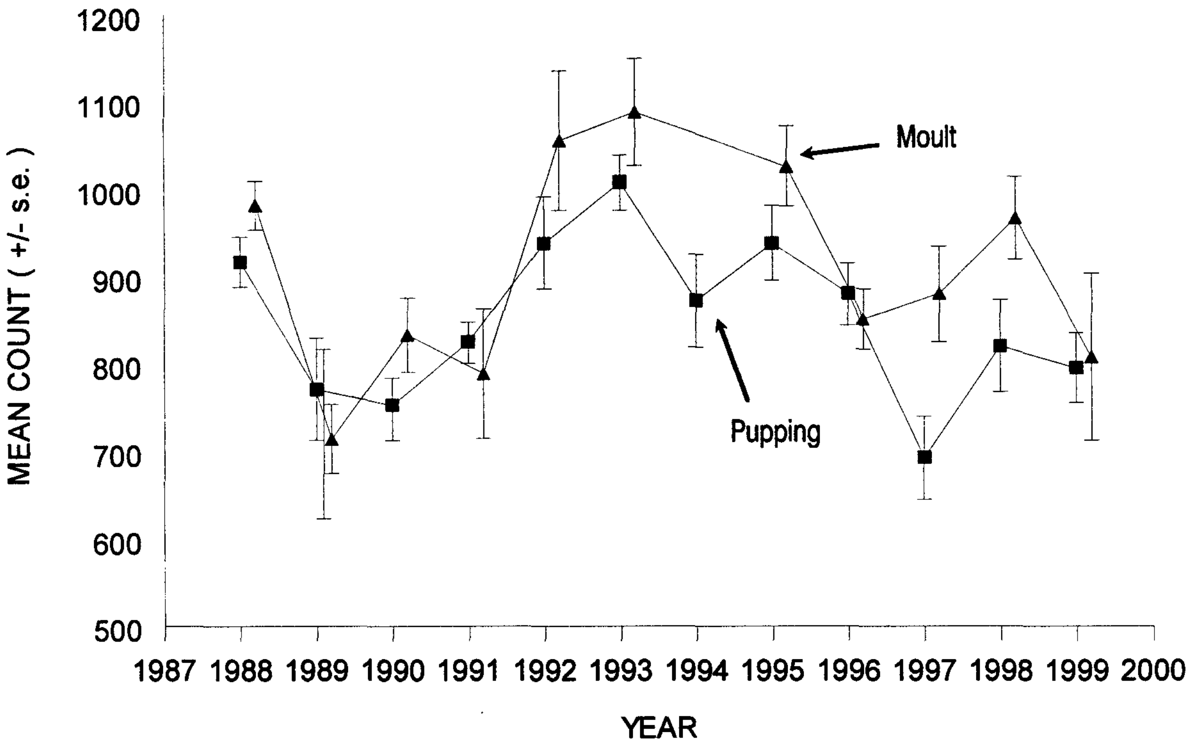


Figure 9. Changes in the mean number of seals counted at inner Moray Firth haul-out sites during the pupping and moult periods.