Scientific Advice on Matters Related to the Management of Seal Populations: 2006

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Scientific advice

Background

Under the Conservation of Seals Act 1970, the Natural Environment Research Council (NERC) has a duty to provide scientific advice to government on matters related to the management of seal populations. NERC has appointed a Special Committee on Seals (SCOS) to formulate this advice so that it may discharge this statutory duty. Terms of Reference for SCOS and its current membership are given in ANNEX I.

Formal advice is given annually based on the latest scientific information provided to SCOS by the Sea Mammal Research Unit (SMRU – a NERC Collaborative Centre at the University of St Andrews). SMRU also provides government with scientific reviews of applications for licences to shoot seals, and information and advice in response to parliamentary questions and correspondence.

This report provides scientific advice on matters related to the management of seal populations for the year 2005. It begins with some general information on British seals, gives information on their current status, and addresses specific questions raised by the Scottish Executive Environment Rural Affairs Department (SEERAD) and the Department of the Environment, Food and Rural Affairs (DEFRA). Appended to the main report are briefing papers used by SCOS, which provide additional scientific background for the advice.

General information on British seals

Grey seals

The grey seal (*Halichoerus grypus*) is the larger of the two species of seal that breed around the British Isles. It is found across the North Atlantic Ocean and in the Baltic Sea. There are two centres of population in the North Atlantic; one in Canada centred on Nova Scotia and the Gulf of St Lawrence and the other around the coast of the UK, especially in Scottish coastal waters. The largest population is in Canada (Figure 1). Populations in Canada, UK and the Baltic are increasing, although numbers are still relatively low in the Baltic where the population was drastically reduced by over-exploitation that took place over many decades.

In Europe, grey seals come ashore on remote islands and coastlines to give birth to their pups in the autumn, to moult in spring, and at other times of the year to haul out and rest between foraging trips to sea for food. Female grey seals give birth to a single white-coated pup, which is nursed for about three weeks before being weaned and moulting into its adult coat.

About 39% of the world population of grey seals is found in Britain and over 90% of British grey seals breed in Scotland (Figure 1), the majority in the Hebrides and in Orkney. There are also breeding colonies in Shetland, on the north and east coasts of mainland Britain and in Devon, Cornwall and Wales. Although the number of pups born at colonies in the Hebrides has remained approximately constant since 1992, the total number of pups born throughout Britain has grown steadily since the 1960s when records began. In 2005, there were an estimated 44,000 grey seal pups born in Britain. This is believed to equate to a total population of between 97,000 and 159,000 grey seals.

Adult male grey seals may weigh up to 350 kg and grow to over 2.3 m in length. Females are smaller, reaching a maximum of 250 kg in weight and 2 m in length. Grey seals are long-lived animals. Males will live for over 20 years and begin to breed from about age 10. Females often live for over 30 years and begin to breed at about age 5.

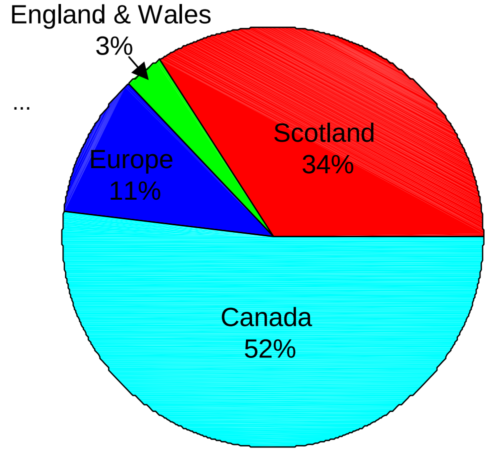

Figure 1. The relative size of grey seal populations in the North Atlantic region, including the Baltic

Grey seals feed mostly on fish that live on or close to the seabed. The diet is composed primarily of sandeels, whitefish (cod, haddock, whiting, ling), and flatfish (plaice, sole, flounder, dab) but varies seasonally and from region to region. Food requirements depend on the size of the seal and fat content (oiliness) of the prey but an average consumption estimate is 7 kg of cod or 4 kg of sandeels per seal per day.

Grey seals often haul out on land, especially on outlying islands and remote coastlines exposed to the open sea. Tracking of individual seals has shown that they can feed up to several hundred kilometres offshore during foraging trips lasting several days. Individual grey seals based at a specific haul out site often make repeated trips to the same region offshore but will occasionally move to a new haulout and begin foraging in a new region. Movements of grey seals between haulouts in the North Sea and the Outer Hebrides have been recorded.

Common seals (also known as harbour seals)

Common seals (*Phoca vitulina*) are found around the coasts of the North Atlantic and North Pacific from the subtropics to the Arctic. Common seals in Europe belong to a distinct sub-species which, in addition to the UK, is found mainly in Icelandic, Norwegian, Danish, German and Dutch waters. Britain is home to approximately 40% of the world population of the European sub-species (Table 1). Common seals are widespread around the west coast of Scotland and throughout the Hebrides and Northern Isles. On the east coast, their distribution is more restricted with concentrations in The Wash, Firth of Tay and the Moray Firth.

Between 1996 and 2005, about 34,400 common seals were counted in the whole of Britain, of which 29,500 (86%) were in Scotland and 3,650 (10%) were in England (Table 1). A total of 1,200 seals were counted in Northern Ireland (Table 1). Not all individuals in the population are counted during surveys because at any one time a proportion will be at sea. Using a conversion factor to account for those animals that are not seen, leads to an estimate for the total British population of 50-60 thousand animals. The population along the east coast of England (mainly in The Wash) was reduced by 52% following the 1988 phocine distemper virus (PDV) epidemic. A second epidemic in 2002 resulted in a decline of 22% in The Wash [1], but had limited impact

[1] Thompson, D., Lonergan, M. and Duck, C. (2005) Population dynamics of harbour seals (*Phoca vitulina*) in England: monitoring population growth and catastrophic declines. *Journal of Applied Ecology* 42, 638-648.

elsewhere in Britain. Counts in the Wash have continued to decline for the 4 years since the epidemic.

Table 1 Sizes and status of European populations of common seals. In most cases, numbers given predate the PDV epidemic of 2002. (data sources: www.smru.at-and.ac.uk; ICES Report of the Working Group on Marine Mammal Ecology 2004;, Harding *et al*. submitted to Animal Ecology)

Region	**Number of seals counted[1]**	**Years when latest information was obtained**	**Possible population trend[2]**
Outer Hebrides	2,000	2003	None detected
Scottish W coast	12,800	1996-2005	None detected
Scottish E coast	2,000	1996-2006	Declining
Shetland	3,000	2006	Declining
Orkney	4,250	2006	Declining
Scotland	**24,050**		
England	**3,650**	2001-2005	Recent decline[4]
Northern Ireland	**1,250**	2002	Decrease since ‘70s
UK	**28,950**		
Ireland	2,900	2003	Unknown
Wadden Sea-Germany	9,100	2005	Increasing after 2002 epidemic
Wadden Sea-NL	3,450	2005	Increasing after 2002 epidemic
Wadden Sea-Denmark	1,720	2005	Increasing after 2002 epidemic
Lijmfjorden-Denmark	1,407	2003	Recent decline [3]
Kattegat/Skagerrak	11,700	2003	Recent decline[3]
West Baltic	300	1998	Recent decline[3]
East Baltic	300	1998	Increasing
Norway S of 62ºN	1,200	1996-98	Unknown
Norway N of 62ºN	2,600	1994	Unknown
Iceland	19,000	?	Unknown
Barents Sea	700	?	Unknown
Europe excluding UK	**53,600**		
Total	**82,550**		

[1] – many of these estimates represent counts of seals rounded to the nearest 100. They should be considered to be minimum estimates of total population size.

[2] – There is a high level of uncertainty attached to estimates of trends in most cases.

[3] – Declined as a result of the 2002 PDV epidemic, no recovery.

[4] – Wash population declined due to 2002 PDV but has continued to decline to 2006.

Common seals come ashore in sheltered waters, typically on sandbanks and in estuaries, but also in rocky areas. They give birth to their pups in June and July and moult in August. At these, as well as other times of the year, common seals haul out on land regularly in a pattern that is often related to the tidal cycle. Common seal pups are born having shed their white coat and can swim almost immediately.

Adult common seals typically weigh 80-100 kg. Males are slightly larger than females. Like grey seals, common seals are long-lived with individuals living up to 20-30 years.

Common seals normally feed within 40-50 km around their haul out sites. They take a wide variety of prey including sandeels, whitefish, herring and sprat, flatfish, octopus and squid. Diet varies seasonally and from region to region. Because of their smaller size, common seals eat less food than grey seals; 3-5 kg per seal per day depending on the prey species.

Responses to questions raised by the Scottish Executive and DEFRA

In the past, the Advice from SCOS has contained annexes explaining the data used to assess the status of UK grey and common seal populations. Following the pattern first used in 2004, the structure of the Advice has changed and information about population status will now be given in response to questions from SEERAD and DEFRA. Accompanying documentation in the form of SCOS Briefing Papers (SCOS-BP ??/??) is intended to provide the additional detail necessary to understand the background for the Advice provided.

1. ***What are the latest estimates of the number of seals in Scottish and English waters?*** (SEERAD/DEFRA)

Current status of British grey seals

The number of pups born in a seal population can be used as an indicator of the size of the population. Each year, SMRU conducts aerial surveys of the major grey seal breeding colonies in Britain to determine the number of pups born (pup production). These surveyed sites account for about 85% of the number of pups born throughout Britain. The total number of seals associated with these regularly surveyed sites is estimated by applying a population model to the estimates of pup production. Estimates of the total number of seals at other breeding colonies that are surveyed less frequently are then added in to give an estimate of the total British grey seal population. Further details are given in SCOS-BP 06/1 and SCOS-BP 06/2.

Pup production

The total number of pups born in 2005 at all annually surveyed colonies was estimated to be 38,500. Regional estimates were 3,400 in the Inner Hebrides, 12,300 in the Outer Hebrides, 17,600 in Orkney, and 5,100 at North Sea sites (including Isle of May, Fast Castle, Donna Nook and Farne Islands). A further 5,400 pups were estimated to have been born at other scattered sites.

Trends in pup production

The differences in pup production between 2004 and 2005 are shown in Table 2. Total pup production at annually monitored colonies decreased by 3.0%, in contrast to the 0.5% increase in the preceding year.

The 2005 results therefore continue the general trend of a decreasing growth rate and provide further support for the suggestion that, overall, pup production in grey seals in the UK is stabilising. Although some new colonies are being formed and populations in the central North Sea are still growing rapidly, these are not sufficient to maintain the high rates of increase observed through the late 1980s and early 1990s when pup production increased at over 6% per annum. During the most recent 5-year period (2001-2005) the total pup production for all annually monitored colonies has increased at 1.26% per annum (see Table 2) and the trend suggests a gradual approach towards a stable level of pup production. However, there have been regional differences (SCOS-BP 06/1 and 06/4). At colonies in the North Sea pup production has continued to increase but in most other areas the pup production is either stable or decreasing slowly.

In Orkney, pup production fell by 7.7% between 2004 and 2005. This is consistent with the recent history of high inter-annual variability in pup production in this region. It is likely to be a further indication that the Orkney population is experiencing some limiting factors. For example, if the population is close to a food resource limitation, then fecundity of breeding females and/or survival of weaned pups may be more susceptible to subtle changes in environmental factors that alter food availability. Recent surveys indicate that the harbour seal population in the Northern Isles has also declined since the late 1990s (see below). However, there is no information to suggest a direct link between these two population indices.

A retrospective description of the regional trends in pup production of the UK grey seal population is presented in SCOS BP 06/4. It describes the clear slow down of the growth of the breeding colonies in the Western isles, which apparently reached some asymptote in the mid 1990s and a clear but more recent slow down in the Northern Isles. Meanwhile, the pup production trajectory of the North Sea colonies is not significantly different to exponential growth.

Table 2: Grey seal pup production estimates for the main colonies surveyed in 2005

Location	2005 pup production	Change in pup production from 2004-2005	Average annual change in pup production from 2001-2005
Inner Hebrides	3,387	<0.1%	+3.2%
Outer Hebrides	12,297	-0.18%	+0.7%
Orkney	17,644	-7.7%	+0.3%
Isle of May + Fast Castle	2,718	+4.1%	+4.2%
All other colonies	3,586		
Total (Scotland)	39,632		
Donna Nook	1,276	+18.4%	+19.4%
Farne Islands	1,138	+0.4%	-2.4%
SW England & Wales (last surveyed 1994)	1,750		
Total (England & Wales)	4,164		
Total (UK)	43,796	-3.0%	+1.3%

*Average annual change in pup production calculated from annually monitored sites only

Population size

Because pup production is used to estimate the total size of the grey seal population, the estimate of total population size depends critically on the factors responsible for the recent deceleration in pup production.

ANNEX I

The recent levelling off in pup production could be a result of reductions in the reproductive rate or survival of pups or adults (SCOS-BP 06/2). There is a lack of independent data with which to quantify the relative contributions of these factors (SCOS-BP 06/7). We used the same Bayesian state-space modelling framework employed last year to fit and compare models of British grey seal population dynamics, based on regional estimates of pup production from 1984 to 2005. The models allowed for a number of different forms of density dependence in either pup survival or fecundity, as well as movement of recruiting females between regions. Again, the four models fitted more or less equally well to the data although the model with simple density dependent fecundity fit slightly better and also produced more believable parameter estimates than the next best model (simple density dependent pup survival). The estimated adult population size in 2005 for these two models was 240,000 (95% CI 171-361,000) and 105,000 (80-142,000) respectively, with the other two models having intermediate values. A more detailed description of the methodology is given in SCOS-BP 06/2.

In the past 3 years it has been argued that the population estimate based on simple density-dependent pup survival provided the most appropriate estimate of total population size for use in the Advice. This was based on the fact that if a decline in reproductive rate is assumed to be responsible for the reductions in pup production, the estimates of current reproductive rate are lower than those that have been observed at individual colonies (SCOS-BP 03/6). If instead a decline in pup survival is assumed to be the mechanism behind changes in population growth, the estimates of current pup survival are within the observed range. It is now a research priority to improve our understanding of the processes underlying density-dependent population change in the grey seal population, and to obtain an independent estimate of total population size that does not rely on modelling the relationship between population size and pup production.

Future estimates of population size will be derived from an approach based on weighted averages of different models. However, for consistency this year we have continued to base the Advice on the density dependent pup-survival model, using the approach that has been used for the last 3-4 years – i.e. assuming that population growth has slowed because of increased juvenile mortality. Consequently, our best estimate of current size of the grey seal population associated with the regularly surveyed colonies is 80,000 – 142,000, with a point estimate of 105,000. Seals from sites that are monitored less often add approximately 17,000 to this total, giving an estimated population of 97,000 – 159,000. These data show no evidence for a major change in seal numbers over the last two years. The majority of these seals, approximately 90 %, are associated with colonies in Scotland and the remaining 10 %, with colonies in England and Wales.

Uncertainty in the estimates

Besides the uncertainty associated with which model to use in the calculation of the total population size, there are uncertainties associated with the estimates of pup production, which are believed to lie within a range of –10% to +13% of the values provided. However, the population modelling described in SCOS-BP 06/2 indicates that the true level of uncertainty may be even greater than this. A new approach to estimating total pup production is being investigated (see SCOS-BP 04/3). Even when this approach is implemented, unknown uncertainties associated with the estimates of pup production at colonies that are not surveyed annually will remain. These have to be combined with the uncertainties about the value used for adult male survival, about which little is known.

Trends in population size

There is now convincing evidence that the growth of pup production in the Inner and Outer Hebrides has effectively stopped while in Orkney it has slowed substantially (SCOS-BP 06/1; SCOS-BP 06/4). However, even if this trend continues, the British grey seal population as a whole is likely to continue increasing for some years (see SCOS-BP 03/3) because there is a time lag in changes in pup production being translated into changes in population size.

Current status of British common seals

Each year SMRU carries out surveys of common seals during the moult in August. Recent survey counts and overall estimates are summarised in SCOS-BP 06/3. It is impractical to survey the whole coastline every year but current plans by SMRU are to survey the whole coastline across 5 consecutive years. Seals spend the largest proportion of their time on land during the moult and they are therefore visible during this period to be counted in the surveys. Most regions are surveyed by a method using thermographic, aerial photography to identify seals along the coastline. Conventional photography is used in The Wash. Additional surveys using visual counts are conducted annually in the Inner Moray Firth by the University of Aberdeen.

Table 3 Counts of common seals by region up to 2005

Region	1996-2005
Shetland	4,883
Orkney	7,752
Outer Hebrides	2,098
Highland (Nairn to Cape Wrath)	1,056
Highland (Cape Wrath to Appin & Loch Linnhe)	4,966
Strathclyde (Appin to Mull of Kintyre)	6,918
Strathclyde, Firth of Clyde (Mull of Kintyre to Loch Ryan)	581
Dumfries & Galloway (Loch Ryan to English Border at Carlisle)	42
Grampian (Montrose to Nairn)	113
Tayside (Newburgh to Montrose)	101
Fife (Kincardine Bridge to Newburgh)	445
Lothian (Torness Power Station to Kincardine Bridge)	104
Borders (Berwick upon Tweed to Torness Power Station)	0
TOTAL SCOTLAND	**29,059**
Blakney Point	741
The Wash	2,124
Donna Nook	470
Scroby Sands	57
Other east coast sites	225
South and west England (estimated)	20
TOTAL ENGLAND	**3,637**
TOTAL BRITAIN	**32,696**
TOTAL NORTHERN IRELAND	**1,248**
TOTAL BRITAIN & NORTHERN IRELAND	**33,944**
TOTAL REPUBLIC OF IRELAND	**2,905**
TOTAL FOR GREAT BRITAIN AND IRELAND	**36,849**

The estimated number of seals in a population based on most of these methods contains considerable levels of uncertainty. A large contribution to uncertainty is the proportion of seals not counted during the survey because they are in the water. We cannot be certain what this proportion is, but it is known to vary in relation to factors such as time of year, state of the tide and weather. Efforts are made to reduce the effect of these factors by standardising the time of year and weather conditions and always conducting surveys within 2 hours of low tide. About 40% of common seals are likely not to be counted during surveys but because of the uncertainties involved in the surveys, the counts are normally presented as minimum estimates of population size. It is on this basis that the most recent count totalling about 34,000 common seals in the UK is likely to indicate a total population of 50,000-60,000 seals.

Apart from the population in The Wash, common seal populations in the UK were relatively unaffected by PDV in 1988. The overall effect of the 2002 PDV epidemic on the UK population was even less pronounced. However, again The Wash was most the most affected region and counts in 2004 suggested a continued decline following the epidemic. Counts by region for the 2005 season are given in the Table 3 above. These are minimum estimates of the British common seal population. Results of surveys conducted in 2005 are described in detail in SCOS-BP 06/3.

Preliminary results from surveys carried out in 2006 found a decline in apparent abundance in Orkney and Shetland of 42% (95% confidence intervals 10%-62%) compared with 2001. A partial survey of the Outer Hebrides did not show a similar decline. However, results from all three areas are consistent with a gradual decline since the late 1990s. The data suggest that these areas may be undergoing a major population decline that is not related to changes in environmental quality. Surveys of the east coast populations in 2006 also showed continuing declines in both the Tay and the Wash populations (SCOS BP 06/3) and no recovery in the Moray Firth. This is in contrast to the apparent rapid growth in populations in the nearest European population in the Wadden Sea.

These apparently widespread declines give clear cause for concern. It is recommended that appropriate monitoring and management action should be instigated as a precautionary measure. A targeted research programme should be established as soon as possible, to identify the likely causes and long-term management implications of these declines.

2. *What is known about the population structure of grey and common seals in European and Scottish waters? Is there any evidence of populations or sub-populations specific to local areas?* (SEERAD/DEFRA)

Grey seals

Within Europe there is a clear genetic and behavioural distinction between the grey seal population that breeds within the Baltic Sea and those populations breeding elsewhere[2]. The vast majority (85%) of European grey seals breeding outside the Baltic breed around Britain. Within Britain there is again a clear genetic distinction between those seals that breed in the southwest (Devon, Cornwall and Wales) and those breeding around Scotland and in the North Sea[3]. Until 2002, SMRU treated this last group as a single population for the purpose of estimating total population size. Estimates of the numbers of seals associated with different regions were obtained by dividing up the total population in proportion to the number of pups born in each region.
In 2003, work began to develop a spatially-explicit model of the British grey seal population. A preliminary application of this model (SCOS-BP 03/4) indicated that there was little movement of breeding animals between Inner Hebrides, Outer Hebrides, Orkney and North Sea. This conclusion is supported by the results of detailed studies at breeding colonies and re-sightings of individual seals that have been photo-identified. These studies have indicated that breeding

[2] Graves, J.A., Helyar, A., Biuw, M., Jüssi, M., Jüssi, I. & Karlsson, O. (submitted) Analysis of microsatellite and mitochondrial DNA in grey seals from 3 breeding areas in the Baltic Sea. *Conservation Biology*

[3] SMRU unpublished data

females tend to return to their natal breeding colony and remain faithful to that colony for most of their lives.

Common seals

Samples from seals in Northern Ireland, the west and east coasts of Scotland, the east coast of England, Dutch and German Wadden Sea, Kattegat/Skagerrak, Norway, Baltic Sea and Iceland have been subjected to genetic analysis. This analysis suggested that there are genetically distinct common seal populations in European waters[4]. There is probably little movement of breeding animals between these populations. Within the Ireland-Scotland population there is probably occasional movement of animals between regions, but there is no evidence from satellite telemetry of any long-range movements (for example, between the east and west coasts of Scotland) comparable to those observed in grey seals. Similarly, studies of the movements of branded seals in the Kattegat/Skagerrak[5] indicate that there is only limited movement within the western Scandinavia population. However, in both 1988 and 2002 phocine distemper spread rapidly among European common seal populations, suggesting that substantial movement of individuals can occur, although the genetics studies suggest these movements do not usually result in seals reproducing in locations they visit temporarily.

Current work

Work is currently underway to develop recommendations for spatial management units and to connect these to population structure. This is partly built from studies of movements and habitat use (SCOS-BP 05/3 and 05/5). Defining optimal management areas for UK seals requires an arrangement of relatively isolated groups of colonies. The motivation behind this requirement is that management actions taken in one unit should have minimal impact on the others. Clustering algorithms have been developed to subdivide grey seal breeding colonies into maximally isolated groups according to at-sea distance (SCOS-BP 06/5)

3. What is the latest estimate of consumption of fish by seals in Scottish waters? (SEERAD)

Estimates of diet composition and consumption of fish by grey seals for the year 2002 have been calculated during a study funded by DEFRA, SEERAD and SNH. The study covered grey seal populations in the Inner and Outer Hebrides, Orkney, Shetland and the east coast of Britain. On-going analysis of information from telemetry studies will provide a basis for estimating fish consumption by seals in different regions of Scotland. The greatest uncertainties in these calculations are caused by lack of knowledge of common seal diet and uncertainties in the population estimates of both species.

The recently completed studies on grey seal diet around the UK have provided new information on fish consumption for the year 2002. Results are summarised in SCOS-BP 06/6 and details are given in the reports to SEERAD-SNH and to DEFRA, which are available under project code MF0319 at (http://www2.defra.gov.uk/research/project_data/Default.asp).

Common seals

Based upon current knowledge of the likely daily ration of about 3 kg of fatty fish per day or up to 5 kg of whitefish per day, the consumption by common seals in Scotland would be between

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[4] Goodman, S.J. (1998) Patterns of extensive genetic differentiation and variation among European harbour seals (Phoca vitulina vitulina) revealed using microsatellite DNA polymorphisms. Molecular Biology and Evolution, 15, 104-118.

[5] Härkönen, T. & Harding, K.C. (2001) Spatial structure of harbour seal populations and the implications thereof. Canadian Journal of Zoology, 79, 2115-2127.

48,000 and 59,000 tonnes if the diet was entirely composed of fatty fish and 80,000 and 98,000 tonnes if the diet was entirely composed of whitefish.

4. Have there been any recent developments, in relation to non-lethal methods of seal population control, which mean that they could now effectively be applied to Scottish seal populations where appropriate? (SEERAD/DEFRA)

Controlling seal populations could potentially be achieved by non-lethal reduction of the birth rate or by excluding seals from sensitive habitats and regions. Although these sorts of interventions have been attempted on a trial basis, on small scales in the past, there is no new information to suggest that a breakthrough has been made in the technology or methodology associated with either approach. Neither SMRU nor the Department of Fisheries and Oceans, Canada, have carried out any recent research on this issue.

SCOS BP 06/9 provides information about current research, funded by SEERAD, being undertaken to use acoustic deterrent devices (ADDs) to exclude seals from sensitive regions.

General

Seal Populations

5 What progress has been made with resolving the question of which population model is likely to offer the most reliable estimate of the grey seal population?

In 2005, we reported that the most practicable and feasible means of resolving this question was to derive one or more independent estimates of the total population size or some well defined component of it. A detailed proposal was developed to conduct high-resolution photographic surveys of grey seal haulout sites around the entire Scottish coast during the summer, i.e. outside the breeding and moulting seasons. After suitable calibration the results would produce regional age- and sex-structured estimates of the number of hauled-out grey seals. Age and sex structured models of haulout behaviour based on the historical archive of behavioural data from grey seal satellite telemetry studies would be developed concurrently. Unfortunately, an application under NERC's December 05 responsive mode funding round was unsuccessful. We are currently seeking alternative funding and reappraising the priorities of the proposed work package.

The same Bayesian state-space modelling framework employed in 2005 was used to fit and compare models of British grey seal population dynamics, based on regional estimates of pup production from 1984 to 2005 (SCOS-BP 06/2). The models allowed for a number of different forms of density dependence in either pup survival or fecundity, as well as fitness-dependent movement of recruiting females between regions. As in 2005, there were insufficient differences between models to allow model selection, and the population estimates produced by the different models are very different, which could have major management implications. Improvements and alternatives to the model-fitting methods are being investigated in collaboration with various researchers; these other modelling approaches are described in SCOS-BP 06/2. One consistent conclusion from this and previous work is that it is very difficult to distinguish between different population models based on pup count data alone, and there is therefore a strong need for additional comprehensive data on either a population vital rate or adult population size.

6. What progress has been made in improving estimates of the common seal population?

With funding support from SNH, a series of repeated aerial surveys were carried out in the Moray Firth and Tay during the August moult to improve estimates of variability (SCOS BP 06/3). At the time of the writing of this report, SMRU and FRS staff are conducting a series of co-ordinated air and ground surveys of the Moray Firth between Helmsdale and Findhorn with the twin aims of calibrating the survey methodologies and continuing the long time-series of counts carried out by University of Aberdeen researchers. Results will be presented to SCOS 2007.

Annual moult surveys of eastern England continued (SCOS BP 06/3), extending the time-series and allowing comparison between UK and European populations during recovery from 2002 PDV epidemic. English populations show no sign of recovery whereas the Wadden Sea population is showing strong recovery, apparently growing at 12% p.a. The disparity in recovery patterns is reminiscent of the situation during the 3-4 years after the 1988 epidemic.

Counts of hauled out seals obtained during a breeding season survey of Strangford Lough have been corrected using concurrent satellite telemetry data to estimate total population size. Preliminary results suggest that around 40% of the population was observed in the aerial survey, but more work needs to be done to evaluate the precision of the resulting population estimates.

By using survey data from other times of year, along with the proportion of time that tagged animals haulout, it is becoming possible to correct haulout counts for the proportion not seen, i.e. produce population estimates. However, this is not possible in the moult and may be problematic during the breeding season if individual animals behave very differently dependent on sex, age and reproductive status. In this case, a concurrent telemetry study would be required whenever the population structure might have changed. Even with such corrections, a breeding season estimate would suffer from many of the same problems inherent in the grey seal pup production estimates.

In response to the recorded declines in the common seal populations in the Northern Isles and on the East coast, there is an increased need to develop census methods that can identify short-term population changes. SMRU will undertake a review of the current methodology and develop new methods in time to modify surveys flown during 2007.

7. What progress has been made in the process of defining the nature of any sub-divisions in the grey and common seal populations and what validity do these have?

There have been no further developments to report on either species in terms of genetic separation of stocks or populations in the UK.

A method for objectively grouping grey seal breeding colonies on the basis of the inter-colony swimming distances, using standard clustering algorithms has been developed and is described in SCOS BP 06/5.

The validity of any system of sub-divisions depends on the level of exchange across the boundaries. We have limited information on this phenomenon. Common seal tracking studies (SCOS-BP 05/5) indicate a lack of broad scale movements between populations of breeding age seals. There are insufficient data from juveniles to determine extent of movements although preliminary results of a tracking study on rehabilitated juvenile common seals suggests some limited movement between what would usually be considered separate populations (RSPCA unpublished data).

Some progress has been made in determining the effects of movement between grey seal breeding colonies[7]. Information on movement of adult female grey seals between the four main breeding sites in the North Sea was derived from photo i.d. capture–recapture analyses. These results were incorporated into a spatially explicit model of grey seal population dynamics. The incorporation of movement, and the way in which it was modelled, affected both local and regional dynamics.

ANNEX I

Seal Diet

8. What work might be done to follow up and maintain the detailed picture of grey seal diet obtained from the recent grey seal diet survey and how useful would such work be?

Although grey seal pup production around north and west Scotland appears to be stabilising, lags in the system mean that the overall population will continue to grow for some time. Pup production in the North Sea is still increasing. The amount of fish that grey seals consume will thus also continue to increase in the near future. It is prudent to assume that their diet is likely to change as the abundance of fish prey changes, as it did between 1985 and 2002. It will therefore be important to reassess grey seal diet in the relatively near future.

In addition to obtaining range-wide descriptions of grey seal diet, it would be beneficial to obtain seasonally-structured samples from a number of indicator sites, timed to coincide with fish population surveys. Such data are essential for developing predictive consumption models incorporating robust functional response models. Such models are required to assess impacts of potentially rapid environmental and fishery induced changes in prey availability.

Estimates of grey seal diet composition and fish consumption are sensitive to the otolith measurement used in calculations. Because of the importance of cod, a commercially exploited species, in the diet of grey seals it would be desirable to obtain more data on the effects of digestion on cod otoliths. Consumption estimates could be improved by including size-specific digestion coefficients for cod in particular; further feeding trials would be required.
However, the main source of uncertainty in fish consumption estimates is due to uncertainty in the seal population estimates. The greatest improvement in precision would be achieved by obtaining an independent estimate of the size of the grey seal population.

9**.** *How has the detailed picture of grey seal diet informed estimates of their impact on fish populations and what further fisheries and/or seal research might be appropriate to refine such estimates?*

The recent detailed estimates of grey seal diet suggest that predation by grey seal may affect the dynamics of some fish populations. However, simple comparisons between estimates of prey consumption by grey seals and very uncertain estimates of fish stock size do not allow an assessment of the impact of seals on fish stocks and fisheries because of the complexity and dynamics of the ecosystem in which these species coexist. In particular, we cannot use these results to infer grey seal impacts on a fish stock without information on rate of production of the stock and estimates of other sources of mortality including the predation rates of other predators and fisheries. Incorporation of the new data into multi-species fish stock assessment models is the next step to help understand the impact of grey seals on fish stocks.

The new diet data are being provided to the ICES Study Group on Multispecies Assessments in the North Sea and will be incorporated into the assessment models. This also forms an integral part of the BECAUSE project, an investigation into the quantitative role of species interactions as a first step towards the implementation of the ecosystem approach into fisheries management (http://www1.uni-hamburg.de/BECAUSE/). Preliminary analyses incorporating grey seal diet data into North Sea cod assessments (Chris Darby, CEFAS) indicated that the new consumption data had only a minor effect on the cod assessment. Estimated cod consumption in 2002 was the equivalent of 3.7% of total stock biomass, mostly relatively small fish.

Further research

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Current research into the preferences shown by grey seals for different types of prey (known technically as the multi-species functional response), as well as improved multi-species models, are a high priority. This research priority is aligned with the research detailed for Question 8 concerning the measurement of grey seal diet using research focussed on particular locations in conjunction with local studies of the fish populations. A key assumption of scat analysis is that each scat is a representative sample of the seals' diet. If the spatial distributions of prey species differ and some prey are more likely to be taken at a greater distance from the haul-out, or if the transit time of food through the gut varies substantially between prey species, then estimates of diet based on scat samples might be biased. To evaluate the extent of this potential 'spatial bias' for UK grey seals, we have used experimental data on otolith passage rates and telemetry data to run simulations in which fish remains are returned to shore in seal scats. Although prey that are consumed far from shore or pass through the gut in a short time may be under-represented in scats, preliminary results indicate that for UK grey seals, which generally forage close to shore, any bias is small. Further analyses are underway.

It is recognised that estimating fish consumption relies on accurate diet composition data but it is equally dependent upon accurate population size estimates. At present, the inability to differentiate between the candidate population models for grey seals is the major source of the uncertainty in prey consumption estimates and our ability to describe the effects of predation on fish stocks.

10. What work might be done to establish a more detailed picture of common seal diet to complement that for grey seals and how useful would such work be?

Information on the diet of common seals around Scotland is patchy and mostly out of date (SCOS 04/11). The relative abundance of fish stocks has changed markedly since most of the existing information was collected and current estimates are needed to place our knowledge of common seal diet on a similar level to that of the grey seal. Reliable information on diet is required both for fisheries management and seal conservation.

A synoptic and up-to-date assessment of common seal diet composition and prey consumption throughout Scotland has been proposed. If funding is available, faecal samples will be collected seasonally from all major common seal haulout areas around Scotland and the east coast of England. Logistical difficulties mean that the helicopter based collection methods used during the recent grey seal work are unlikely to yield sufficient sample sizes in many areas and alternative methods based on local personnel or multiple field trips from St Andrews will be required. There is some experimental information on rates of digestion of prey remains (primarily fish otoliths) for common seals, but additional experiments will be needed for some major prey species. There is also a need to develop behavioural models for common seals to aid in prediction of movement patterns and prey selection.

The results will allow assessment of regional and seasonal variation in diet and, in conjunction with foraging distribution data, will allow us to provide seasonally and geographically structured estimates of prey consumption. Common seal predation will be included in ICES multi-species assessment models and the new results will refine the inputs to those models.

Nutritional stress related to food availability may be one of the ultimate causes of the recently observed declines in UK common seal populations. Identifying the causes and possible remedial measures will require detailed, range-wide knowledge of harbour seal diet as well as information on food requirements.

11. What work might be done to improve our knowledge of seal diet by directly observing mortality of prey fish?

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Direct observation of seal predation is possible only in specific situations, e.g. for the small number of seals that enter rivers, or using sophisticated technology that can help to sample predation in an unbiased way.

Studies are under way in rivers surrounding the Moray Firth and these are helping to build a picture of prey taken by seals within these rivers. Moreover, studies conducted by FRS that are focussed on salmonids have used tags placed within smolts together with instruments placed on seals to detect the presence of these tags within the seals following predation. Early feasibility tests of the detection system using captive seals have been successful. This may provide a method of assessing the impact that seals could be having upon the survival of smolts, although the method would be difficult to apply to species other than salmonids and would not be feasible in many situations.

Camera systems placed directly on the seals are currently being researched and have been used successfully to study predation. This has the advantage that it can sample across the range of activities of individual seals but is currently limited by practicalities associated with data recovery and cost.

Side-scan sonar systems may also allow detailed investigation of the behaviour of seals around fish. Although expensive, and not without technical challenges, these systems are currently being investigated for this type of use and practical tests are currently being conducted.

It is likely that all these methods will be used in future for directly observing predation by free-ranging seals. However, each method has strengths and weaknesses that are specific to the circumstances and the questions being addressed. For the time being, all of these methods are in need of further development.. Up to a point, all are prey-focussed methods. Only the camera system has the likelihood of showing predation across the full range of prey taken by an individual but even this system can be made to be prey focussed depending on the individual seals selected to carry the camera.

Records of predation events during targeted observation surveys suggest that predation by seals on downstream-migrating, post-spawning kelts may have significant effects on repeat spawning probabilities in some river systems. An observation programme designed to quantify kelt mortality due to seal predation in the river Ness and other suitable river systems, in conjunction with estimates of spawning escapement, will allow us to estimate the proportion of kelt mortality attributable to this short-term and potentially controllable predation event.

Although it may be feasible to infer predation rates from observed prey mortality schedules in simple, easily observable systems it is highly unlikely that mortality rates of marine fish, even those targeted by fisheries, would ever be known at sufficient resolution to identify the likely source of the predation pressure.

However, prey population data are an essential component in improving prey consumption estimates and developing functional response models to provide predictive capabilities. Bayesian statistical methods have been used to fit a model of prey consumption to data on the diet and prey availability of grey seals. Availability of fish to the seals was estimated using Generalised Additive Models applied to International Bottom Trawl Survey data, together with models of seal movement based on telemetry data. These results were used to predict the way in which prey consumption and seal-induced prey mortality might vary with prey abundance.

The biomass of fish removed by grey seals foraging in the North Sea was estimated for 1985, a year in which the two most important prey species - cod and sandeels - were relatively abundant, and for 2002 when stocks of both species were at low levels. The total North Sea consumption of the fish stocks estimated by the 2002 diet study (SCOS 06/6) was reasonably well predicted by the model– though local variation between sites within the North Sea was not so well predicted.

Seal Conservation

12. What work might be done to improve our knowledge and understanding of the main causes of seal mortality?

Partitioning the total deaths within a seal population to particular causes is difficult, especially for those components that are "natural". Anthropogenic causes of mortality may be measurable and it may be possible to assess whether they are likely to affect population dynamics.

SEERAD currently records the numbers of seals shot under license, but this is likely to represent only a small part of the total anthropogenic mortality. FRS and SMRU maintain databases that might allow estimation of bycatch within fisheries. However, accounting for seals shot during periods, or in regions, where licenses are not required has not been possible. Nevertheless, the success of a close liaison between biologists and managers during the current pilot study in the Moray Firth region has suggested that there could be significant improvement in the gathering of such data. A combination of confidential reporting schemes combined with systematic surveys to determine the likelihood of reporting and appropriately targeted public information campaigns are likely to provide useful information.

Knowledge about the main sources of seal mortality in the UK could be obtained using a number of different approaches. Indirect methods, e.g. mark-recapture studies can be used to determine the importance of various factors on survival probabilities, but are limited to investigating those covariates of survival that are monitored at the time of marking. Direct methods can either estimate deaths due to specific sources of mortality (such as deliberate killing and by-catch) or, in the case of strandings schemes, such efforts might establish the different causes of death following post mortem examination of carcasses that wash ashore. There are disadvantages and biases associated with all these methods and therefore an integrated approach would be recommended, utilizing data from all possible sources. Future mortality studies should be systematic, standardized and implemented over a sufficiently long time period given the small sample sizes that are likely to be obtained on an annual basis. A fuller description of the potential methodologies is presented in SCOS 06/7.

13. How might local studies (data collection or research) of designated Special Areas of Conservation most effectively contribute to maintaining the favourable conservation status of seal populations in Scottish waters?

SAC sites must be monitored with the aim of determining conservation status. Considerations are similar for both species, but the data currently available and the ease of data collection are much simpler for grey seals than for common seals.

The knowledge required to show the favourable conservation status of seals within an SAC can be broken down into two components: (1) those associated with measuring the population size and how this changes through time and (2) those associated with understanding why the population may be changing. The second of these is essential if it becomes necessary to identify causes of decline and to introduce mitigation actions. Only by knowing the causes or the underlying biology of the species in that region can a rational set of mitigation actions be developed.

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Current monitoring at a national level, of both common and grey seals, is focussed upon providing information about trends in abundance. Both monitoring procedures place trends in SACs in the context of the population as a whole. However, the estimates for common seals are generally not sufficiently frequent, mainly due to costs, to allow detection of trends on the time scales required to satisfy appropriate monitoring of SAC status (exceptions are the sites on the east coast which are surveyed annually). Consequently, recent studies by SMRU (SCOS BP 05/7) have attempted to develop new methods involving mark-recapture using photographic identification of seals and more regular counting using inexpensive methods. The final conclusions of these studies have not yet been reported but it is possible that local mark-recapture could be used in some circumstances to monitor population status.

Studies of the underlying biology needed to interpret trends in abundance include methods that allow the current indices of population size to be represented appropriately as an absolute population size together with confidence limits and those that show the extent to which surrounding habitat is important to the dynamics of seal populations within the SAC (see response to Question 16). Both of these issues need to be tackled with studies that are specific to each SAC as well as studies that have broad relevance to understanding the dynamics of seal populations across all SACs.

SCOS recommends that an assessment should be made of the information available about each SAC and that this should guide development of a set of research actions required to allow appropriate assessment of the conservation status of each.

13. What is the latest estimate of seal populations in the Moray Firth management area?

Three aerial surveys of the Inner Moray Firth including Loch Fleet and Findhorn were completed in August 2005. Results for each sub-region are presented in Table 4 below and in more detail in SCOS-BP 06/3. For the Inner Moray Firth, numbers hauled out in August 2005 varied between 531 and 692. If the adjacent haulout sites in Loch Fleet and at the mouth of the Findhorn are included, the numbers increase to between 659 and 842. Additionally, a total of 508 grey seals were counted on 9 August 2005.

Both the maximum and the mean of the three counts in 2005 were 9% lower than the equivalent counts for 2004. The maximum was 40% lower than the peak count obtained in 1997 (SCOS-BP 06/3).

Because of the apparent changes in populations in the Northern Isles, a summary of the preliminary results of the 2006 moult surveys is appended to Table 4. The count for the inner Moray Firth including Findhorn and Loch Fleet was 6% higher than the maximum count in 2005 and close to the maximum count in 2004.

Table 4. Counts of common seals in the Moray Firth

Location	8-Aug-05	9-Aug-05	18-Aug-05	4-Aug-06
Ardersier	260	143	224	210
Beauly Firth	119	169	94	174
Cromarty Firth	98	101	118	119
Dornoch Firth	199	118	256	249
Inner Moray Firth Total	**676**	**531**	**692**	**752**
Inner Moray Firth + Loch Fleet & Findhorn	**834**	**659**	**842**	**894**

14. What recent developments have there been in relation to the calculation of Permitted/Potential Biological Removals (PBR) and related approaches that SEERAD should be aware of either in relation to the Moray Firth or more generally?

There have been no recent developments in the context of PBR calculations. Previous calculations and results of the preliminary model (SCOS 04/07) represent the best current advice.

Seals and the Wider Marine Ecosystem

15. How might seal distribution data be employed to inform the process of identifying multi-purpose Marine Protected Areas (as defined in Section 8.3.3 of Net Benefits: A Sustainable and Profitable Future for UK Fisheries http://www.strategy.gov.uk/downloads/su/fish/pdf/NetBenefits.pdf).

The distribution data for grey and common seals could be used in the selection process of Marine Protected areas of direct conservation importance to seals At present, the chosen SACs relate only to the terrestrial requirements of seals, i.e. haulout and breeding sites. If it is deemed necessary to protect seal foraging habitat, the distribution data and the resultant predictions of at-sea distributions of foraging effort are essential and probably sufficient to define potential Marine Protected Areas for seals. An analytical framework for including habitat preferences in models of grey seal distribution has been developed at SMRU.

In addition, the identification of foraging hotspots for both species of seal in UK waters, if they exist, may help define areas of high prey density or prey availability and will allow identification of areas of potential conflict between marine predators and fisheries. Such information is again vital for determining the extent and potential effectiveness of Marine Protected Areas. In the absence of such foraging information for other marine predators, and in light of observations of associations between suites of marine predators, the seal distribution data may be a useful proxy for preliminary identification of general marine predation hotspots.

ANNEX I

NERC Special Committee on Seals

Terms of Reference

1. To undertake, on behalf of Council, the provision of scientific advice to the Scottish Executive and the Home Office on questions relating to the status of grey and common seals in British waters and to their management, as required under the Conservation of Seals Act 1970.
2. To comment on SMRU's core strategic research programme and other commissioned research, and to provide a wider perspective on scientific issues of importance, with respect to the provision of advice under Term of Reference 1.
3. To report to Council through the NERC Chief Executive.

Current membership
Dr J Armstrong, FRS Laboratory
Prof IL Boyd, SMRU, University of St Andrews
Dr T Coulson, Imperial College
Dr K Kovacs, Norwegian Polar Institute
Prof M Mangel, University of California
Dr EJ Millner-Gulland (Chair), Imperial College, London
Prof J Pemberton, University of Edinburgh
Dr J Pinnegar, CEFAS
Prof PM Thompson, University of Aberdeen
Sophie Hodgson (Secretary), NERC, Swindon

ANNEX II

Briefing papers for SCOS

Until 2003, additional information has been appended to the draft Advice in two forms. One of these concerned the status and trends of grey and common seal populations and this had been presented as annexes to the Advice. The other had been a set of ad-hoc information papers. The Annexes had normally been unattributed and had formed a part of the Advice. In addition, SCOS had usually been provided with several verbal presentations of work in progress.

The Annexes and the information papers have been combined into one format known as a *briefing paper*. The intention is to ensure that the science underpinning the Advice is made more transparent and is provided in more detail but also in a format that encourages rapid assimilation of the essential information. The *briefing papers* will provide up-to-date information from the scientists involved in the research and will be attributed to those scientists. It is hoped that scientists who have not traditionally been involved in SCOS might also be willing to contribute by providing briefing papers. .

Briefing papers do not replace fully published papers. Instead, they are an opportunity for SCOS to consider both completed work and work in progress. Some of the *briefing papers* will be provided along with the Advice and the Advice will refer to detail within briefing papers where appropriate. It is also intended that current *briefing papers* should represent a record of work that can be carried forward to future meetings of SCOS.

ANNEX II

List of briefing papers appended to the SCOS Advice, 2006.

06/01 Grey seal pup production in Britain in 2005.
C.D. Duck and B.L. Mackey

06/02 Estimating the size of the UK grey seal population between 1984 and 2005, and related research.
L. Thomas and J. Harwood

06/03 The Status of British Common Seal Populations
C.D. Duck, D. Thompson and B. Mackey

06/04 A retrospective description of regional patterns in grey seal pup production trends in the UK
D. Thompson, C.D. Duck and M. Lonergan

06/05 Defining management areas for UK grey seals
J. Matthiopoulos, G. Aarts and C.D. Duck

06/06 Grey seal diet composition and prey consumption in the North Sea and west of Scotland
P.S. Hammond, K. Grellier and R.N. Harris

06/07 Improving knowledge and understanding of the main sources of seal mortality in the UK
A.J. Hall

06/08 Summary of grey seal satellite telemetry haulout data available to parameterise population size models.
B.J. McConnell

06/09 Acoustic Deterrent Device Trials
I.M. Graham, D. Fowden and R.N. Harris

06/10 Detecting relationships between ocean climate variation and grey seal survival; insights from the seabird literature.
P. M. Thompson

06/11 Grey seal pup production in Wales
A. J. McMath and T. B. Stringell

C.D. Duck and B.L. Mackey

Grey seal pup production in Britain in 2005

NERC Sea Mammal Research Unit, Gatty Marine Laboratory, University of St Andrews, St Andrews KY16 8LB

NOTE: THIS PAPER AND ITS CONTENTS SHOULD NOT BE REFERENCED WITHOUT PRIOR PERMISSION FROM THE AUTHORS

1. Surveys conducted in 2005

Each year SMRU conducts aerial surveys of the major grey seal breeding colonies in Britain (mostly in Scotland) to determine the number of pups born. In addition, new locations where grey seal pups have been seen or reported, or which appear to be suitable for colonisation, are visited regularly. During the 2005 breeding season, between five and six surveys were flown over the main colonies in the Inner and Outer Hebrides, Orkney and the Firth of Forth.

Scottish Natural Heritage (SNH) coordinated a second survey of grey seal pups in Shetland, following on from the excellent survey in 2004. Again, counts were either from boats or from the ground. National Trust staff counted pups born at the Farne Islands and at a relatively new colony at Blakeney Point in Norfolk. Staff of the Lincolnshire Wildlife Trust counted pups born at Donna Nook and staff from English Nature counted pups at another recent colony at Horsey, on the east Norfolk coast. South Ronaldsay in Orkney was not counted this year due to staff being on maternity leave. The intention is that South Ronaldsay will be counted in 2006.

The locations of the main grey seal breeding colonies in the UK are shown in Figure 1.

A new colony on Pabbay, south of Barra in the Outer Hebrides (Figure 1), was photographed for the first time and has been included with the rest of the Outer Hebrides colonies. The colony on Rothiesholm on Stronsay, in Orkney, was surveyed for a second time and has been fully incorporated into the Orkney group.

All the major colonies had five or more counts. Nine colonies had six counts, including three of the four biggest (Ceann Iar, Ceann Ear and Linga Holm). A small number of the most recent or most difficult colonies had three (Loch Eriboll, Eilean nan Ron at Tongue, Sule Skerry. Helmsdale and Pabbay) or four counts (Calf of Flotta, South Fara and North Flotta).

Both Linhof cameras were serviced after the 2004 season. The shutter on the second camera failed during a survey of the Monach Isles but this was noticed during the survey. The colonies on the most recently exposed film were resurveyed immediately and no data was lost. An intermittent electrical problem was traced to a faulty connector and should be resolved. This had the effect of non-exposure of occasional frames during a run, a problem only detectable after the films have been processed.

2. Estimated pup production

Numbers of pups born (pup production) at the regularly surveyed colonies is estimated each year from counts derived from the aerial photographs using a model of the birth process and development of pups. The method used to obtain the estimates for the 2005 pup production was similar to that used in previous years. A lognormal distribution was fitted to colonies surveyed four or more times and a normal distribution to colonies surveyed only three times and for all colonies in Shetland.

Total pup production in 2005 at all annually monitored colonies was estimated to be 38,460, a decrease of -3.0% from the 2004 production of 39,650 (Table 1). The trajectory of pup production, with 95% confidence limits, at the major breeding colonies in England and Scotland (excluding Loch Eriboll, Helmsdale and Shetland) between 1984 and 2005 is shown in Figure 2a. Figure 2b shows the long-term pup production trajectories at the main island groups from 1960 to 2005. Production from the main island groups is shown in more detail in Figure 3a (Inner and Outer Hebrides and Orkney) and in Figure 3b (North Sea colonies). The time series of production estimates for the four regional island groups is given in Table 3.

In 2003, the confidence limits for the Outer Hebrides production were unusually large (Figure 3a). Four films were lost during a postal strike that contained the data for the first one or two counts of the Outer Hebridean colonies. The confidence limits for 2004 and for 2005 are considerably smaller than in 2003 and are more consistent with those from previous years.

For colonies not surveyed by air, pups were counted directly from the ground. These counts are conducted annually at the Farne Islands, Donna Nook and South Ronaldsay in Orkney but less frequently at SW England and Wales. National Trust staff have started to count pups annually at the new Blakeney Point colony and Naturally English staff count the new colony at Horsey in east Norfolk. SNH staff (normally) count South Ronaldsay pups in a manner compatible with counts from aerially surveyed colonies, and production is estimated using the same modelling procedure as for the aerially surveyed colonies. The South Ronaldsay data are now included with the main Orkney production estimates.

The recent colonies in the Outer Hebrides and Orkney continue to be surveyed annually. Berneray and Mingulay at the southern end of the Outer Hebrides are highly susceptible to moderate to severe turbulence if there is any significant wind in the quarter between south and west. There are occasions when is not possible to survey these colonies. Pabbay, slightly further to the north, is not affected by wind to the same extent.

3. Trends in pup production

The differences in pup production at the main island groups are shown in Table 1. Between 2004 and 2005, total pup production at annually monitored colonies decreased by -3.0% overall, the change varying from -7.7% in Orkney to +18.4% at Donna Nook. There has been virtually no change in estimated total production at the 11 colonies in the Inner Hebrides for the last 3 years (Table 3).

The 2005 results continue to support the trend observed in recent years, that there is an overall slowing in the rate of increase in the number of pups being born. The most notable change in 2005 was the reduction in the number of pups born in Orkney (Tables 1 and 3, Figures 2b and 3a). This is partially explained by the lack of a production estimate (of around 500 pups) for South Ronaldsay, but also by reduced production at 16 of 23 colonies in Orkney, in particular at four large colonies: Linga Holm (-14.1%), Faray (-11.8%), Holm of Huip (-13.4%) and Calf of Eday (-17.9%).

Between 1984 and 1996, pup production estimates from annually monitored colonies showed a fairly consistent annual increase, with the notable exception of 1988 (Figures 2 and 3). There were further declines in pup production in 1997 (mainly due to a reduction in the number of pups born in the Outer Hebrides), 1999 (in all island groups), 2002 (mainly in the Outer Hebrides) and again in 2005 (primarily in the Orkney colonies). In the years following each of these declines, there was a marked increase in total pup production (of 9.5%, 11.5% and 7.4% in 1998, 2000 and 2003 respectively). Will this increase occur in 2006?

The overall annual percentage change in pup production at each of the main island groups over the past five years (between 2001 and 2005) is shown in Table 1. These varied from -2.4% at the Farne Islands to +19.4% at the small colonies of Donna Nook, Blakeney Point and Horsey. The overall change, for all colonies combined, was +1.3%. Changes for the two preceding five-year intervals are shown for comparison.

Pup production fluctuates between years but since 1996, the fluctuations have been more variable than previously (Figures 2a and 2b). This is also reflected in the annual rate of change in production between years. It is difficult to determine what causes these changes but they could indicate that the grey seal population is approaching the limits of size. To even out these fluctuations, the average percentage rate of annual change in pup production for five yearly intervals since 1990 are shown in Table 1. These figures are probably the best indication of the current trends in pup production.

4. Pup production model assumptions

The model used to estimate pup production from aerial survey counts of whitecoated and moulted pups assumes that the parameters defining the distribution of birth dates are variable from colony to colony and from year to year, but that those defining the time to moult and the time to leave the colony remain constant. The pup production estimates are sensitive to the value used for the latter parameter and there is, therefore, an argument for allowing this parameter to vary between colonies.

Previously (in 2001), we considered the effect of allowing the time-to-leave parameter to vary. However, although the resulting pup production trajectory is slightly lower, the variations in production are consistent between the two methods. The results presented here are consistent with the Advice provided in previous years.

Similarly, the proportion of white pups misclassified as moulted (or vice versa) can vary. Variation may be counter dependent or may be simply a function of the quality of the aerial photograph, the prevailing light conditions under which the photograph was taken and the orientation in which any pup might be lying. The estimation model was re-run for Orkney and Outer Hebrides colonies, allowing the misclassification proportion to run free and to be estimated by the modelling process. The resulting fits were generally an improvement on those from the 'standard' run. The resulting production values were slightly, but not significantly, higher than those from the standard run. The values presented here are from the standard model and are consistent with data from previous years.

5. Confidence limits

Ninety-five percent confidence limits on the pup production estimates varied from being within 2.7% of the point estimate in Orkney to 6.7% in the Isle of May and Fast Castle combined (Figures 3a and 3b).

6. Pup production at colonies less frequently surveyed

Approximately 15% of all pups are born at these colonies each year (Tables 2 and 4). Confidence limits cannot be calculated for these estimates because they represent single counts. In 2005, Loch Eriboll and Eilean nan Ron (Tongue) were surveyed three times and production estimated using a normal distribution. For the first time, most of the coast between Duncansby Head and Helmsdale was also surveyed three times. Snow showers and an aircraft technical problem prevented the third survey of the middle section of this coast from being completed. The results are in Table 2. This table also includes the total count from the colonies listed individually in Table 4 (under Other colonies). These and other potential breeding locations are surveyed when flying time, weather conditions and other circumstances permit. Table 2 indicates that at least 5,400 pups were born at colonies not surveyed annually.

7. Pup production in Shetland

Karen Hall (SNH, Shetland) coordinated a team of volunteers who carried out boat and ground counts of a number of breeding colonies in Shetland.

Seven colonies were counted three times or more and for these, pup production was estimated using the standard SMRU model (Table 5) with a normally distributed birth curve. A number of colonies that were surveyed in 2004 were omitted due to the time required for survey and/or the small numbers of pups found in 2004. As with data from the 2004 survey, the model was run using both a 50% moulter classification and a 90% classification. The latter produced considerably better fits with lower confidence intervals. Both production estimates are included in Table 5. We recommend that the 90% moulter classification productions should be used. This is because moulted pups are more likely to be correctly classified during ground counts because the counters are relatively close to the pups and can assess accurately whether a pup has fully moulted or not.

The minimum pup production for Shetland in 2004 was 609 pups. This figure is clearly an underestimate of grey seal pup production in Shetland, given that a number of colonies were either not surveyed at all, or were not surveyed in their entirety (e.g. Uyea). A series of severe gales affected Shetland during October and November 2005. These gales prevented surveys being carried out at the optimal intervals and possibly removed pups from the more exposed beaches. The frequently severe weather conditions during the autumn months may play a very important role in limiting the potential increase in grey seal pup numbers on the restricted and exposed breeding beaches and caves in Shetland.

The biggest colony in Shetland, at Uyea, was only partially counted. This was because part of the island of Uyea can only be accessed by boat and operating restrictions prevented any surveying by boat. The last two breeding seasons have seen an excellent effort in updating the information on grey seal pup production in Shetland. In future, given logistic difficulties and the extreme nature of the weather, effort should be concentrated on the five main colonies of Papa Stour, Rona's Voe, Mousa and the considerably more difficult pair of Uyea and the Whalsay Islands.

8. Grey seal pup production in Ireland.

In the 2005 season, there was a major effort to determine the number of grey seal pups born in the Irish Republic, coordinated by Oliver O'Cadhla from the Coastal Monitoring Research Centre in Cork. To complete the production estimate for the whole of the island of Ireland, SMRU surveyed the breeding colonies on the east and south coast of Northern Ireland, as an extension of the existing grey seal survey of Scotland. Four surveys were carried out; the first has to be abandoned due to poor visibility.

Approximately 40 grey seal pups are born inside Strangford Lough and here, grey seals appear to breed some 3-4 weeks earlier than those breeding on the small islands to the east of the Ards Peninsula. From a previous SMRU survey in 2002, the surveys were timed to cover the latter breeding colonies, not those inside Strangford Lough. The main breeding colonies are on the Copeland Islands at the mouth of Belfast Lough and on the North Rocks off the east coast of the southern end of the Ards Peninsula. On the Copeland Islands, the maximum pup count was 16 and on North Rocks the maximum count was 9 pups. These numbers were considerably lower than counts made in 2002. The National Trust and the Environment and Heritage Service of Northern Ireland make monthly counts of seals within Strangford Lough. Their counts show that approximately 40 grey seal pups are born within the Lough. This suggests that no more than 100 grey seal pups were born in Northern Ireland in 2005 (Table 2 shows this estimated number).

9. Proposed surveys for 2006

In the 2006 breeding season, we propose to continue the current survey protocol to obtain at least five counts for each colony.

10. Acknowledgements

Thanks to all those who provided or helped collect the data presented in this report. These include: John Walton (Farne Islands), Rob Lidstone-Scott (Donna Nook), David Wood (Blakeney Point), Miriam Duck (Horsey and Blakeney Point), Ron Morris and Dave Jones of the Forth Seabird Group (Forth inner islands), Danielle Harris (SMRU aerial survey), Bill Giles and Peter Holt (pilots for SMRU surveys). The 2005 Shetland grey seal survey was only completed due to the exceptional efforts of a number of people including: Karen Hall, Howard Towll, A Prior, K Passfield, G Hughes, N Davies, A Taylor, P Ellis, H Moncrieff, P Harvey, T Ash, Malkie, P French, R Riddington, S Smith and J Wills.

Table 1. Pup production estimates for colonies in the main island groups surveyed in 2005. The overall annual changes, over successive 5-year intervals are also shown. These annual changes represent the exponential rate of change in pup production. The total for the North Sea represents the combined estimates for the Isle of May, Fast Castle, the Farne Islands, Donna Nook Blakeney Point and Horsey in east Norfolk.

Location	**2005 pup production**	**Overall annual change in pup production**			
		2004-2005	**1991-1995**	**1996-2000**	**2001-2005**
Inner Hebrides	3,387	+0.06%	+4.45%	-5.14%%	+3.16%
Outer Hebrides	12,297	-0.18%	+3.53%	+0.58%	+0.70%
Orkney	17,644	-7.73%	+4.24%	+3.66%	+0.30%
Isle of May + Fast Castle	2,718	+4.06%	+2.60%	+9.93%	+4.24%
Farne Islands	1,138	+0.44%	+3.32%	-2.21%	-2.37%
Donna Nook + Blakeney Pt + Horsey (new)	1,276	+18.37%	+12.98%	+18.00%	+19.39%
North Sea (i.e. previous 3 locations)	5,132	+4.29%	+3.91%	+6.96%	+5.31%
Total	**38,460**	**-3.00%**	**+6.10%**	**+2.31%**	**+1.26%**

Table 2. Pup production estimates for breeding colonies surveyed less regularly. The production estimate for Shetland is lower than for 2004 (943) because fewer colonies were surveyed and severe gales may have reduced production on those colonies that were surveyed (see text).

Location	**Date and location of last survey**	**Pup production**
Mainland Scotland*	Helmsdale (Duncansby Head to Helmsdale, 2005	1,174 (mostly modelled, 3 counts)
	**Loch Eriboll, Eilean nan Ron (Tongue) 2005	877 (modelled, 3 counts)
Other colonies	Various, from Table 5	924
Shetland	2005	611
South-west Britain	South-west England Wales 1994	1,750
Northern Ireland	2005	100 (estimate)
Total		**5,436**

*South Ronaldsay has been included with the main Orkney breeding colonies.

**Loch Eriboll and Eilean nan Ron are surveyed annually and production estimates obtained using the same modelling process as the main breeding colonies.

Table 3. Estimates of pup production for colonies in the Inner and Outer Hebrides, Orkney and the North Sea, 1960-2005.

YEAR	Inner Hebrides	Outer Hebrides	Orkney	North Sea	Total
1960			2048	1020	
1961		3142	1846	1141	
1962				1118	
1963				1259	
1964			2048	1439	
1965			2191	1404	
1966		3311	2287	1728	7326
1967		3265	2390	1779	7434
1968		3421	2570	1800	7791
1969			2316	1919	
1970		5070	2535	2002	9607
1971			2766	2042	
1972		4933		1617	
1973			2581	1678	
1974		6173	2700	1668	10541
1975		6946	2679	1617	11242
1976		7147	3247	1426	11820
1977			3364	1243	
1978		6243	3778	1162	11183
1979		6670	3971	1620	12261
1980		8026	4476	1617	14119
1981		8086	5064	1531	14681
1982		7763	5241	1637	
1983				1238	

Table 3 continued.

YEAR	Inner Hebrides	Outer Hebrides	Orkney	North Sea	Total
1984	1332	7594	4741	1325	14992
1985	1190	8165	5199	1711	16265
1986	1711	8455	5796	1834	17796
1987	2002	8777	6389	1867	19035
1988	1960	8689	5948	1474	18071
1989	1956	9275	6773	1922	19926
1990	2032	9801	6982	2278	21093
1991	2411	10617	8412	2375	23815
1992	2816	12215	9608	2437	27075
1993	2923	11915	10790	2710	28338
1994	2719	12054	11593	2652	29018
1995	3050	12713	12412	2757	30932
1996	3117	13176	14273[1]	2938	33504
1997	3076	11946	14051	3698	32771
1998	3087	12434[2]	16367[1]	3989	35877
1999	2787	11759[2]	15462[1]	3380	33388
2000	3223	13396	16281[1]	4303	37210
2001	3032	12427[2]	17938[1]	4134	37531
2002	3096	11248[2]	17942[1]	4520	36816
2003	3386	12741[2]	18652[1]	4805	39584
2004	3385	12319	19123[3]	4921	39748
2005	3387	12297[4]	17644[4]	5132[4]	38460

[1] Production estimates for North Flotta, South Westray, Sule Skerry and South Ronaldsay included in the Orkney total for the first time.
[2] Production estimates for Mingulay, Berneray and Fiaray (latter two off Barra) included in the Outer Hebrides total for the first time.
[3] Blakeney Point included with Donna Nook for the first time.
[4] Pabbay included with Outer Hebrides; Rothiesholm on Stronsay included with Orkney; Horsey, Norfolk included with North Sea.

Table 4. Scottish grey seal breeding colonies that are not surveyed annually and/or have recently been included in the survey programme. Data from 2005 are in bold type.

	Location	**Survey method**	**Last surveyed, frequency**	**Number of pups**
Inner Hebrides	Loch Tarbert, Jura	SMRU visual	2003, every 3-4 years	10
	West coast Islay	SMRU visual	1998, every 3-4 years	None seen
	Oronsay Strand	SMRU photo	2005	**40**
	Ross of Mull, south coast	SMRU visual	1998, infrequent	None seen
	Treshnish small islands, incl. Dutchman's Cap	SMRU photo & visual	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	2003, every 2-3 years	22
	Muck	SMRU photo	1998, 2005	36, **18**
	Rum	SNH ground	2003, annual	10-15
	Canna	SMRU photo	2002, 2005	54, **25**
	Rona	SMRU visual	1989, infrequent	None seen
	Ascrib Islands, Skye	SMRU photo	2002, 2005	60, **64**
	Fladda Chuain, North Skye	SMRU photo	2005	**73**
	Heisgeir, Dubh Artach, Skerryvore	SMRU visual	1995, every other year 1989, infrequent	None None
Outer Hebrides	Barra Islands Fiaray & Berneray	SMRU photo	annual	Included with Outer Hebrides
	Sound of Harris islands	SMRU photo	2002, 2005	358, **396**
	St Kilda	Warden's reports	Infrequent	Few 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 photo	2002, 2003, 2005	50, 58, **67**
	Islands close to Handa	SMRU visual	2002	10
	Faraid Head	SMRU visual	1989, infrequent	None seen
	Eilean Hoan, Loch Eriboll	SMRU visual	1998, annual	None
	Rabbit Island, Tongue	SMRU visual	2002, every other year	None seen
Orkney	Sule Skerry	SMRU photo	1998 - 2002	Included with Orkney
	Sanday, Point of Spurness	SMRU photo	1999, 2002, 2004, 2005	62, 10, 27, **34**
	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
	Eday mainland	SMRU photo	2000, 2002	8, 2
Others	Firth of Forth islands, Inchcolm; Craigleith (by North Berwick)	SMRU photo, Forth Seabird Group	Infrequent, 1997 2003, 2004, 2005	<10, 4 86, 72, **110**
Total				**924**

Table 5. Pup production estimates and maximum pup counts for grey seal colonies in Shetland in 2004 and 2005. Frequent severe gales in 2005 restricted the opportunity to count and probably removed significant numbers of pups from some of the breeding beaches. The estimated pup production figure for 2005 is clearly an underestimate as not all colonies and only the part of Uyea that was visible from land were surveyed.

Location in Shetland	**2004**			**2005**	
	Estimated production		**Maximum count**	**Estimated production**	
	50% moulter classification	90% moulter classification		50% moulter classification	90% moulter classification
Papa Stour	174	196		113	135
Dale of Walls	60	66		39	43
Muckle Roe	20	23			
Rona's Voe	99	106		74	83
Mousa	110	140		107	117
Fetlar	51	50		28	37
Modelled total	**513**	**582**		**See below**	**See below**
Whalsey Islands			102	45	72
South Havra			4		
Fitful Head			18		
Uyea (North Mainland)			238	114 (part only)	122 (part only)
Total max counts			**362**		
Minimum pup production	**876**	**943**		**520**	**609**

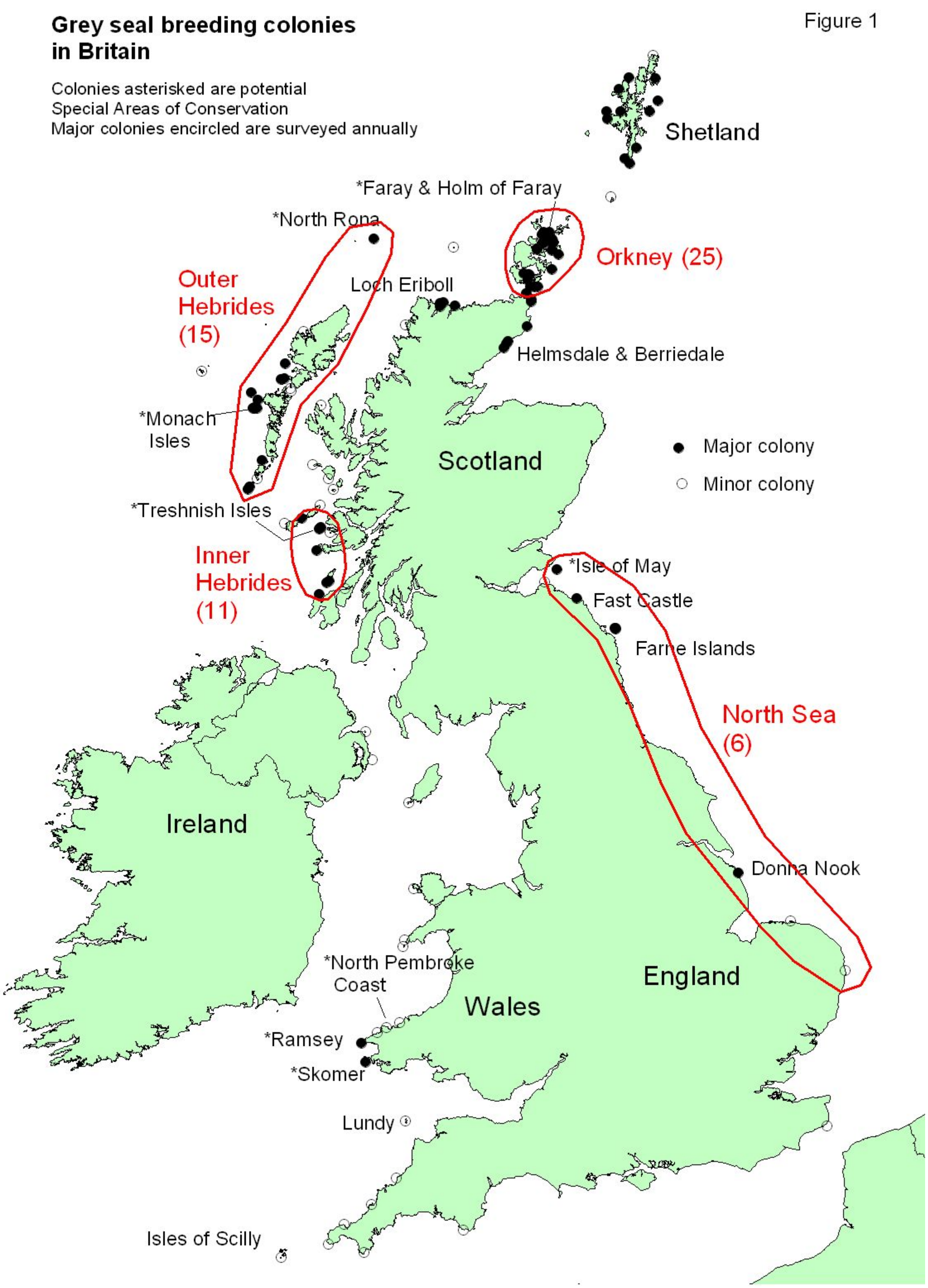

Grey seal breeding colonies
in Britain
Figure 1
Colonies asterisked are potential
Special Areas of Conservation
Major colonies encircled are surveyed annually
Shetland
*Faray & Holm of Faray
*North Rona
Orkney (25)
Outer
Hebrides
(15)
Loch Eriboll
Helmsdale & Berriedale
*Monach
Isles
Scotland
Major colony
Minor colony
*Treshnish Isles
Inner
Hebrides
(11)
*Isle of May
Fast Castle
Farne Islands
North Sea
(6)
Ireland
Donna Nook
*North Pembroke
Coast
England
Wales
*Ramsey
*Skomer
Lundy
Isles of Scilly

Figure 2a. Total estimated pup production, with 95% confidence limits, for all the major, annually monitored colonies in Scotland and England from 1984 to 2005.

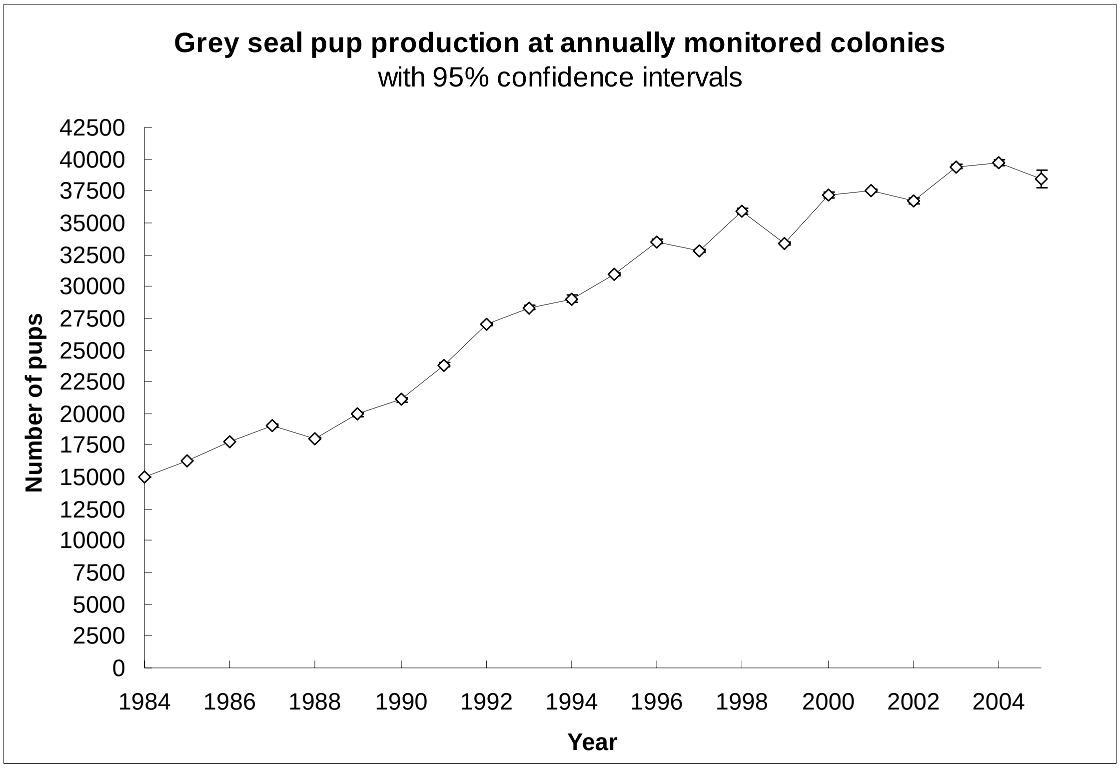


Figure 2b. Grey seal pup production trajectories from 1960 to 2005.

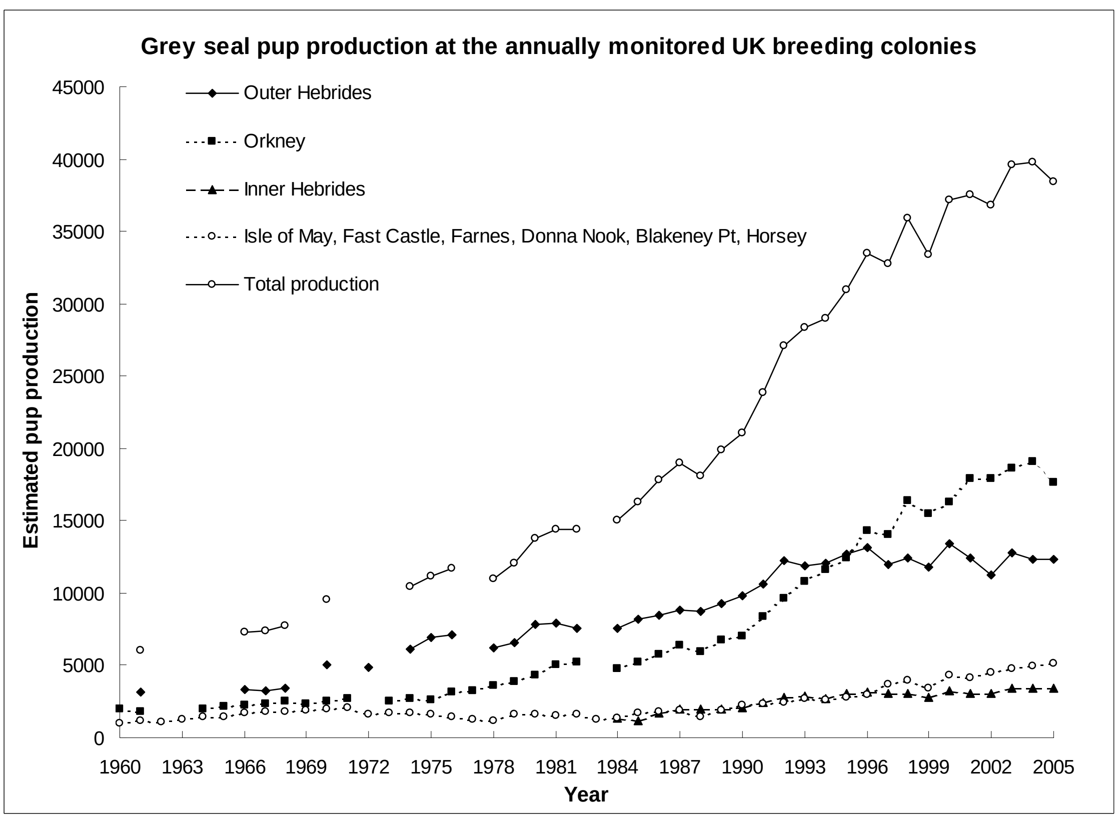
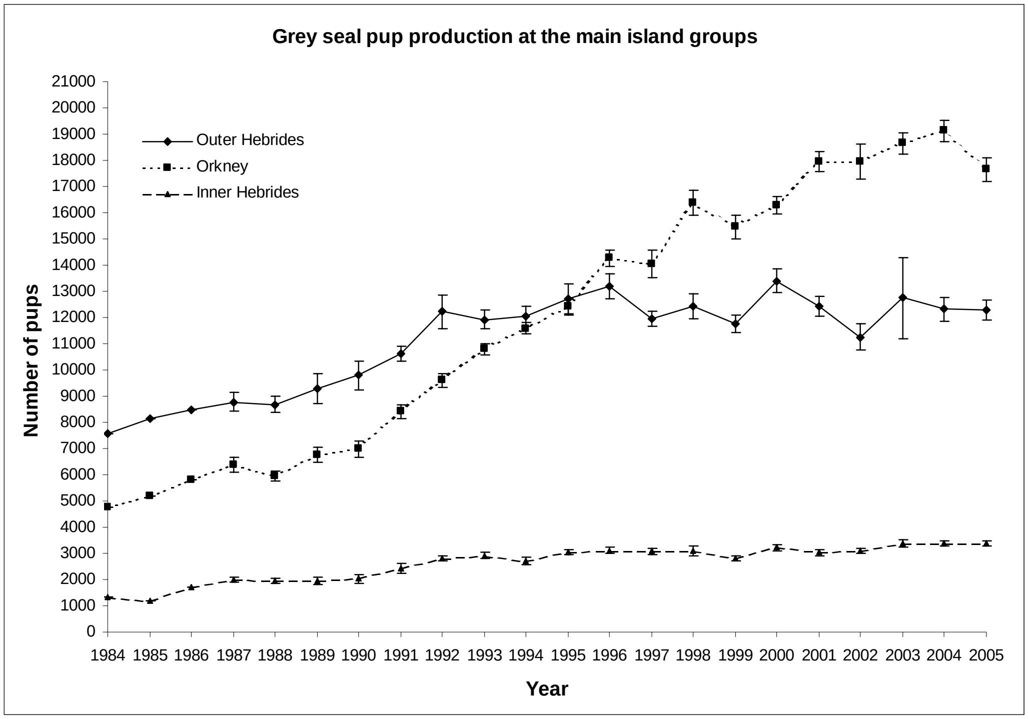
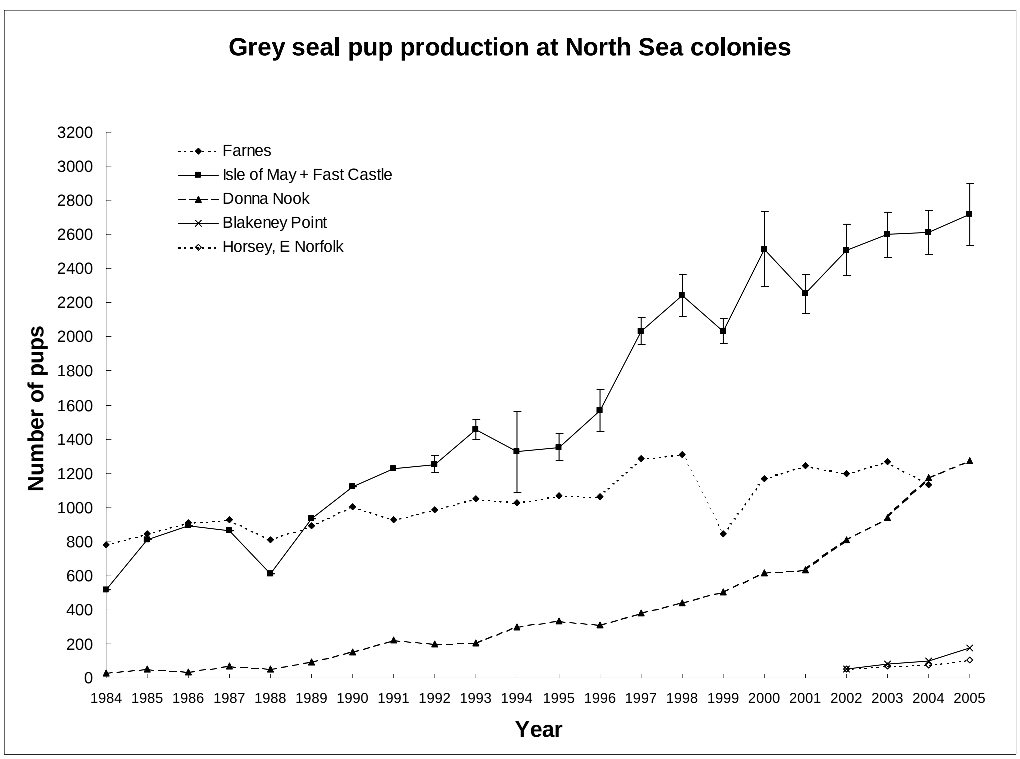


Figure 3. Trends in pup production at the major grey seal breeding colonies since 1984. Production values are shown with their 95% confidence limits where these are available. These limits assume that the various pup development parameters involved in the estimation procedure remain constant from year to year. Although they therefore underestimate total variability in the estimates, they are useful for comparison of the precision of the estimates in different years. Note that Figures 3a and 3b differ in scale by an order of magnitude.

3a) Outer Hebrides, Orkney and Inner Hebrides



3b) North Sea colonies



Len Thomas and John Harwood

Estimating the size of the UK grey seal population between 1984 and 2005, and related research.

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NOTE: THIS PAPER AND ITS CONTENTS SHOULD NOT BE REFERENCED WITHOUT PRIOR PERMISSION FROM THE AUTHORS

Summary

We used the same Bayesian state-space modelling framework employed in our 2005 briefing paper to fit and compare models of British grey seal population dynamics, based on regional estimates of pup production from 1984 to 2005. The models allowed for a number of different forms of density dependence in either pup survival or fecundity, as well as fitness-dependent movement of recruiting females between regions. As in our 2005 report, there were only small differences between models in model selection criterion values (adjusted posterior log-likelihoods), although the model with simple density dependent fecundity fit slightly better and also produced more believable parameter estimates than the next best model (simple density dependent pup survival). The estimated adult population size in 2005 for these two models was 240,000 (95% CI 171-361,000) and 105,000 (80-142,000) respectively, with the other two models taking intermediate values.

In joint work with various researchers, we are investigating various improvements and alternatives to the model-fitting methods. These include: (i) improving the particle filtering algorithm we currently use; (ii) comparing the performance of the particle filter with a custom-written Markov chain Monte-Carlo (MCMC) sampler; (iii) testing the limits of generic, but accessible MCMC samplers available in the WinBUGS software; and (iv) investigating the utility of the Kalman Filter on various simplified models. One conclusion from this and previous work is that it is very difficult to distinguish between different population models based on pup count data alone, and there is therefore a strong need for additional comprehensive data on either a population vital rate or adult population size.

Introduction

In this paper, we present updated estimates of population size and related demographic parameters using the modelling framework of Thomas and Harwood (2005) fitted to pup production data from 1984-2005. The biological system is represented using a state-space model – a stochastic time-series model that includes a "state process" for the evolution of the true but unknown state of the population through time, and an "observation process" that describes the measurements taken on the population (Buckland *et al.* 2004, Thomas *et al.* 2005, Newman *et al,* 2006).

We fitted and compared the same four models used by Thomas and Harwood (2005). Two allow for density dependent pup survival (DDS) and density dependent fecundity (DDF). In both cases, the density dependent relationship follows a Beverton-Holt function. Two further models extend this function by adding an extra parameter that allows the effect of density dependence to be lessened until the population is close to carrying capacity (see Thomas and Harwood 2005). We refer to these as extended density dependent pup survival (EDDS) extended density dependent fecundity (EDDF).

To fit the models, we use the same computer-intensive algorithm as Thomas and Harwood (2005), a type of Monte-Carlo particle filter (Liu 2001). We also discuss current research on alternative approaches.

Materials and Methods

Models

In constructing the state processes, we divide the seal population in each region into 7 age classes: pups (age 0), age 1 – age 5 adult females (pre-breeding), and age 6 and older females. Note that our models do not include adult males.

The time step for the process models is 1 year, beginning just after the breeding season. The models are made up of four sub-processes: survival, age incrementation, movement of recruiting females and breeding.

Survival is modelled as a binomial random process. For the DDS model, we assume that pup survival follows a Beverton-Holt function of the form:

$$\phi_{p,r,t} = \frac{\phi_{p\max}}{1+\beta_r n_{0,r,t-1}}$$

where $n_{0,r,t-1}$ is the number of pups born in region *r* in year *t*-1, $\phi_{p,r,t}$ is survival rate of these pups, $\phi_{p\max}$ is maximum pup survival rate, and $1/\beta_r$ is proportional to the carrying capacity of the region. The EDDS model includes an extra parameter, ρ, that can alter the shape of the relationship between pup survival and pup numbers:

$$\phi_{p,r,t} = \frac{\phi_{p\max}}{1+\left(\beta_r n_{0,r,t-1}\right)^{\rho}} \qquad (1)$$

For the DDF and EDDF models, we assume pup survival is constant across regions and times, i.e., $\phi_{p,r,t} = \phi_p$.

Since half of the pups born will be male, the expected number of female pups surviving in both models will be $0.5\,\phi_{p,r,t} n_{0,r,t-1}$. For all models, we assume that adult female survival rate, ϕ_a is constant across regions and time.

Age incrementation is deterministic – all seals age by one year (although those in the age 6+ category remain there).

To model movement, we assume that only females breeding for the first time may move from their natal region. Once a female has started breeding she remains faithful to that region. We assume that movement is fitness dependent (Ruxton and Rohani 1998), such that females will only move if the value of the density dependent parameter (pup survival or fecundity) is higher elsewhere, and the probability of movement is proportional to the difference in the density dependent parameter between regions. In addition, we assume that females are more likely to move among regions that are close together, and that females show some degree of site fidelity – that is, they may not move even if conditions for their offspring will be better elsewhere. We model movement from each region as a multinomial random variable where probability of movement from region *r* to region *i* at time *t* is:

$$\rho_{r\to i,t} = \begin{cases} \dfrac{\theta_{r\to i,t}}{\sum_{j=1}^{4}\theta_{j\to i,t}} & : \sum_{j=1}^{4}\theta_{j\to i,t} > 0 \\ I_{i=r} & : \sum_{j=1}^{4}\theta_{j\to i,t} = 0 \end{cases}$$

where $I_{i=r}$ is an indicator that is 1 when *i*=*r* and 0 otherwise, and

$$\theta_{r\to i,t} = \begin{cases} \gamma_{sf} & : i = r \\ \dfrac{\gamma_{dd}\,\max\left(\Delta_{i,r,t},0\right)}{\exp\left(\gamma_{dist} d_{r,i}\right)} & : i \neq r \end{cases}$$

where γ_{sf}, γ_{dd}, and γ_{dist} are three movement parameters that index the strength of the site fidelity, density dependence and distance effects respectively, $\Delta_{i,r,t}$ is the difference in the density dependent parameter between regions *i* and *r* (see below), and $d_{r,i}$ is the 20% trimmed mean of the distances between colonies in regions *r* and those in region *i* (standardized so that the largest distance is 1.0). For the DDS and EDDS models,

$$\Delta_{i,r,t} = \phi_{p,i,t} - \phi_{p,r,t}$$

while for the DDF and EDDF models,

$$\Delta_{i,r,t} = \alpha_{i,t} - \alpha_{r,t}$$

where $\alpha_{r,t}$ is the fecundity rate in region *r* at time *t*, as defined below.

We model breeding by assuming that the number of pups produced is a binomial random variable, with rate $\alpha_{r,t}$. For the DDS and EDDS models, we assume this value is constant across regions and times, i.e., $\alpha_{r,t} = \alpha$. For the DDF model, we assume this value follows a Beverton-Holt function of the form:

$$\alpha_{r,t} = \frac{\alpha_{\max}}{1+\beta_r n_{6+,r,t}}$$

The EDDF model is similar, with

$$\alpha_{r,t} = \frac{\alpha_{\max}}{1 + \left(\beta_r n_{6+,r,t}\right)^{\rho}} \qquad (2)$$

For the observation process, we assume that pup production estimates follow a normal distribution with a constant coefficient of variation (CV) which we assume to be a known value. In the runs reported here, we fixed this CV at 25% (see Discussion).

In summary, the DDS and DDF models have 10 parameters. They share 8: adult survival ϕ_a, one carrying capacity parameter-related parameter for each region β_1 - β_4, and three movement parameters γ_{sf}, γ_{dd}, and γ_{dist}. They differ in two parameters: the DDS model has maximum pup survival $\phi_{p\max}$ and constant fecundity α, while the DDF model has constant pup survival ϕ_p and maximum fecundity $\alpha_{\max}$. The EDDS and EDDF models have one additional parameter, ρ, for the shape of the density-dependent response.

Data and Priors

Our input data were the pup production estimates for 1984-2005 from Duck and Mackey (2006), aggregated into regions. Estimates for recent years in North Sea region are slightly higher than those used previously as a new colony at Blakeney Point has been included.

Prior distributions for each parameter are given in Table 1, and are shown on Figure 2. We followed Thomas and Harwood (2005) in using a re-parameterization of the model to set priors on the numbers of pups at carrying capacity in each region, denoted χ_r for region *r*, rather than directly on the β s.

Table 1. Prior parameter distributions

Param	Distribution	Mean	Stdev
ϕ_a	Be(22.05,1.15)	0.95	0.04
$\phi_{p\max}$, ϕ_p	Be(14.53,6.23)	0.7	0.1
χ_1	Ga(4,2500)	10000	5000
χ_2	Ga(4,1250)	5000	2500
χ_3	Ga(4,3750)	15000	7500
χ_4	Ga(4,10000)	40000	20000
ρ	Ga(4,2.5)	10	5
γ_{sf}	Ga(2.25,1.33)	0.5	0.33
γ_{dd}	Ga(2.25,0.49)	3	2
γ_{dist}	Ga(2.25,0.22)	ln(3)	ln(2)
α, $\alpha_{\max}$	Be(22.05,1.15)	0.95	0.04

Prior distributions for the states in the DDS and EDDS models were generated using the priors for the parameters in conjunction with the 1984 data, as described by Thomas *et al.* (2005). Prior states for the DDF and EDDF model were generated in a similar manner, as described by Thomas and Harwood (2005).

Fitting Method

We used the same particle filtering algorithm as Thomas and Harwood (2004, 2005), implemented in the C programming language. An introduction to particle filtering algorithms in the context of wildlife studies is given by Newman *et al.* (2006), and a detailed description of a similar algorithm to the one used here, applied to a similar model of seals, is given by Thomas *et al.* (2005). The differences between the algorithm of Thomas *et al.* (2005) and the one used here are outlined by Thomas and Harwood (2004).

Model outputs and comparison

The output from a particle filter is a set of weighted samples (particles) taken from the prior distributions on the parameters and states and projected forward stochastically through the time series. The weights relate to the manner in which the particles were sampled, how they were projected forward and the likelihood of the observed pup production given the simulated pup numbers. We can use these particles to estimate quantities of interest such as posterior means or credibility (confidence) intervals on parameters and states. One issue that arises is the accuracy of the estimates, in terms of Monte-Carlo error. We can calculate the effective sample size of the particles as

$$\text{ESS} = \frac{K}{1 + [\text{CV}(w)]^2}$$

where K is the number of particles and CV(w) is the coefficient of variation of the weights of these particles. Our aim was to simulate enough particles to achieve an ESS of at least 1000, although that was not possible in the time available. We report ESS achieved in the Results section.

For all four models, we present posterior estimates of the model parameters and estimated pup production from 1984-2005. The models also estimate adult female numbers, but do not include adult males. We therefore calculated total pre-breeding population sizes by assuming that the number of adult males is 73% of the number of adult females (Hiby and Duck, unpublished).

To compare the models, we calculated the mean posterior Akaike Information Criterion (AIC) using the same method as Thomas and Harwood (2004, 2005). This criterion is a form of penalized likelihood, which recognizes the fact that models with more parameters are expected to fit better *a priori* by adding a penalty proportional to the number of model parameters. It is similar in spirit to the Bayesian Deviance Information Criterion (Spiegelhalter et al. 2002). Models were compared using Akaike weights (Burnham and Anderson 1998, p124), which can be thought of in the Bayesian context as the posterior probability of each model being the best approximating model.

Since the observations are assumed to be normally distributed random variables, there is an argument for using the bias-adjusted version of AIC, denoted AICc (Burnham and Anderson, 1998, p51). This criterion contains an extra term that imposes a stronger penalty on models with more parameters, with the effect of this extra term decreasing as the number of observations increases.

Results

Effective sample size (ESS)
Using our relatively simple particle filtering algorithm, an extremely large number of particles were required to achieve a unit increase in ESS (Table 2). Because of time constraints, we did not achieve our target of ESS ≥ 1000 for any model. Nevertheless, the Monte-Carlo error in our results is likely to be reasonably small – for example, dividing the particles from the EDDS model into two, estimated mean adult population size in 1984 is 60.1×10^4 from the first half (ESS=114) and 60.8×10^4 from the second (ESS=148).

Table 2. Number of particles (K) and effective sample size (ESS) for the results presented here. Note that number of particles is before rejection control, ESS is afterwards (see Thomas and Harwood 2004 for details).

Model	K ($\times 10^7$)	ESS	ESS/K ($\times 10^7$)
DDS	6.75	747	110.7
EDDS	13.50	254	18.8
DDF	6.75	575	85.2
EDDF	59.40	191	3.2

Comparison of models for density dependence
Smoothed posterior estimates of pup production (Thomas *et al.* 2005) for the four models are shown in Figure 1. The estimates are quite similar between models, although subjectively, the extended density dependence models appear to do a better job of capturing the recent levelling-off of pup production in the Inner and Outer Hebrides and continuing growth in the North Sea. However, none of the models' estimates can reproduce the rapid increase in pup production in the Hebrides and Orkney in the early 1990s.

There was little difference in posterior likelihood, AIC or AICc between the models (Table 3). The model with the minimum AIC and AICc is the DDF model, but the next best model (DDS) has a mean posterior AIC only 1.70 higher (1.79 higher for AICc). All four models are within 4 AIC and AICc points of one another, meaning there is not strong support for one model over another (Burnham and Anderson 1998, p63).

Although the models produce similar estimates of pup production, they give substantially different estimates of total predicted population size (Table 4 and Appendix 1). The DDF model estimates that there are 2.3 times as many seals as the DDS model, with the other two falling in between.

Posterior parameter estimates for the models are shown in Figure 2. For the DDS and DDF models, the posterior mean adult survival (ϕ_a) is similar to the prior of 0.95 (although the variance is much reduced), but it is substantially lower (0.91) in the extended density dependence models. The juvenile survival and fecundity parameters (ϕ_j and α) are almost unchanged relative to the prior in all four models. Similarly, the movement parameters (γ s) are also little changed, except for the density dependence parameter γ_{dd} , which has a posterior mean that is half the prior mean in the DDS and DDF models. Posterior distributions of the carrying capacity parameters (χ s) are somewhat tighter than the priors, with posterior mean estimates that vary between models. Posterior mean carrying capacities for the Outer Hebrides were rather greater than the prior means for the DDS and DDF models (Figure 2), and this is reflected in the fit of the pup production estimates (Figure 1), which fail to reflect the levelling off of pup production since the mid-1990s. In the extended density dependence models, the posterior for ρ has lower mean and variance than the prior – in particular for the EDDF model, where the prior mean of 10 is just outside the 95% credibility interval of the posterior.

Table 3. Mean posterior log-likelihood, AIC , AICc and Akaike weights for models fit to data from 1984-2005.

Model	LnL	AIC	ΔAIC	Akaike (AIC) weight	AICc	ΔAICc	Akaike (AICc) weight
DDS	-719.55	1459.01	1.70	0.21	1461.96	1.79	0.22
EDDS	-718.67	1459.35	2.04	0.18	1462.82	2.66	0.14
DDF	-718.65	1457.31	0.00	0.50	1460.17	0.00	0.55
EDDF	-719.21	1460.41	3.10	0.10	1463.89	3.72	0.09

Table 4. Estimated size, in thousands, of the British grey seal population at the start of the 2005 breeding season, derived from models fit to data from 1984-2005. Numbers are posterior means with 95% credibility intervals in brackets.

	DDS	EDDS
North sea	12.0 (9.3 16.3)	18.2 (9.9 26.2)
Inner Hebrides	8.9 (6.9 11.7)	10.5 (7 14.3)
Outer Hebrides	32.2 (23.8 43.3)	41.3 (27.4 55.2)
Orkney	52.2 (39.2 70.4)	74.1 (44.3 98.4)
Total	105.2 (79.3 141.7)	144.1 (88.6 194.1)
	DDF	EDDF
North sea	26.6 (19.3 38.6)	21.9 (16.4 29.7)
Inner Hebrides	21.9 (15.3 33.4)	15.2 (11.5 25.6)
Outer Hebrides	85.8 (58.1 135.8)	59.5 (44.5 95.6)
Orkney	106.6 (77.9 153.1)	83.8 (64.4 119.4)
Total	240.9 (170.5 361)	180.3 (136.9 270.3)

Posterior estimates of the derived parameters (pup survival for the DDS and EDDS models and fecundity for the DDF and EDDF models) are given for each year and region in Appendix 2. Estimated pup survival is very low under the DDS model (as low as 0.19 for Outer Hebrides in 2005), but is higher in the EDDS model (the corresponding estimate is 0.42), likely due to the lower estimate of adult survival in the EDDS model. Estimated fecundity is as low as 0.45 in the DDF model (for Outer Hebrides 2005), and again is higher in the EDDF model (corresponding estimate 0.80), for the same reason.

Discussion

Implications and reliability of results

Our results are very similar to those given last year (Thomas and Harwood 2005), as would be expected when 21 of the 22 years of data are in common and the same analysis methods were used. We again found little to choose among the candidate models, but large differences in estimated total population size. Although our analysis methods can be improved (see below), we believe that an additional source of information about one or more of the population parameters, population age structure, or numbers of one or more adult age class is required before it will be possible to unambiguously distinguish between the models.

The particle filtering algorithm that we used is simple and reliable (without bias), but inefficient in the sense that a large amount of computer time is required to produce an acceptable level of Monte-Carlo error. To obtain results in a reasonable timescale, we fixed observation CV at 25%, a value considerably higher than the 7% estimated for individual colonies by Hiby and Duck (unpublished). It is therefore possible that both the precision of our estimates and our ability to distinguish between models could be improved. We are in the process of amending our fitting algorithms to increase efficiency using tools such as auxiliary particle filtering, limited kernel smoothing and integrating out the observation error parameter (Doucet *et al.* 2001, Lui 2001, Thomas *et al.* 2005, Newman *et al.* submitted).

Other related work

We have completed a study comparing the performance of particle filtering with a custom-written MCMC sampler, using a complex, but tractable model of US Pacific west coast salmon and then a seal model very similar to the DDS model presented above (Newman *et al.*

submitted). The particle filtering algorithm included the tools mentioned above, while the MCMC sampler was highly tuned to the exact state-space model used. We found that while the particle filter produced similar posterior mean estimates to MCMC, it was much less efficient (more computer time required for the same accuracy). However, the particle filtering algorithm used can easily be adapted to work with many population dynamics models, while the MCMC algorithm would need to be re-derived if changes were made to the model, and deriving the sampler used was very challenging. Even for the highly optimized MCMC sampler, converge was very slow for the seal example, underlining the difficulties associated with fitting models based on pup count data alone.

We have also been investigating the potential for using the off-the-shelf MCMC software WinBUGS (Spiegelhalter *et al.* 2005) to fit state-space models, giving the potential advantage that developing code to fit several plausible models is simplified. This is joint work with Richard Parker (St Andrews) and Lara Jamieson (Cambridge). We have been able to fit Bayesian versions of the autoregressive models used by Thomas *et al.* (2004), and have used a recently-released reversible-jump (RJ) MCMC add-in for WinBUGS to perform model selection via estimating posterior model probabilities. We have validated our results using data from the North American Breeding Waterfowl Survey against results obtained by Jamieson and Brooks (2004) using custom-written RJMCMC code. We are currently investigating the feasibility of fitting more complex models to seal data that track both numbers of pups and breeding females, and include density dependence but not movement. Preliminary results indicate that both update times and convergence in WinBUGS are very slow.

We are also continuing work that investigates how the Kalman filter might be applied to these models. This is joint work with Panagotis Besbeas and Byron Morgan (Kent). We have fit various state-space models to pup production data from the colonies at Isle of May (exponential growth) and Faray (sigmoid growth), together with survival estimates from mark-recapture data, and are comparing results obtained from the Kalman filter with those from a particle filter. One difficulty for the Kalman filter is that the single colony state-space models based on pup-count data are technically non-observable, meaning that pup counts alone cannot be used to infer the adult states. For particle filters, we use a Bayesian paradigm, and the models are rendered observable by the use of prior information. The non-observability of the models based on pup production data alone in the likelihood context further underlines the need to obtain additional data.

Acknowledgements

We thank Mike Lonergan for suggesting the use of AICc.

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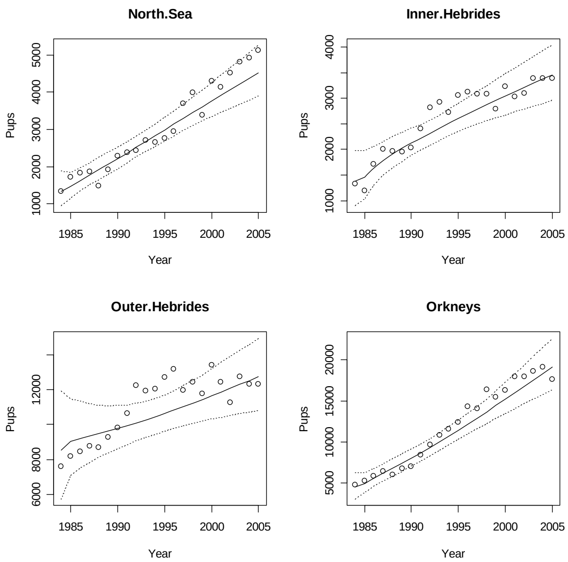
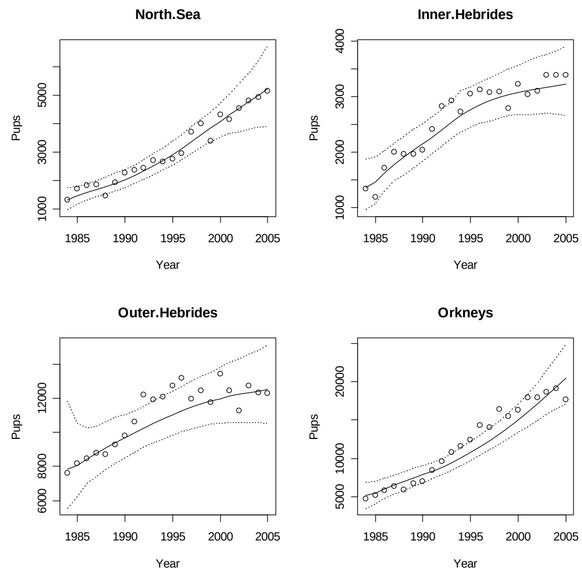
Figure 1. Estimates of true pup production from four models of grey seal population dynamics fit to pup production estimates from 1984-2005. Input data are shown as circles, while the lines show the posterior mean bracketed by the 95% credibility interval.

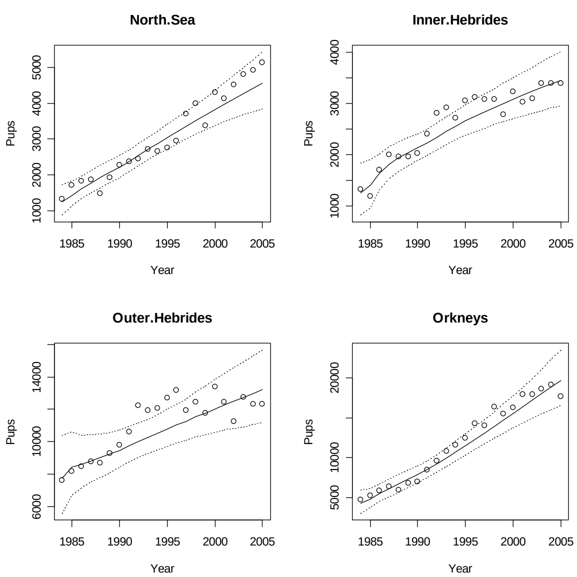
(a) Density dependent survival (DDS)



(b) Extended density dependent survival (EDDS)



(c) Density dependent fecundity (DDF)



(d) Extended density dependent fecundity (EDDF)

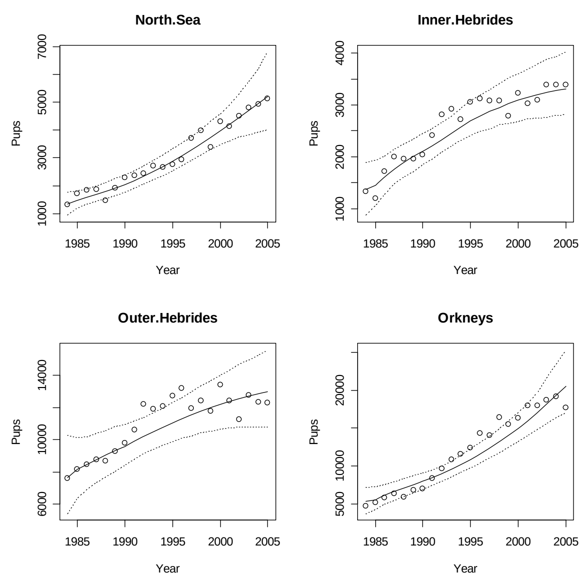
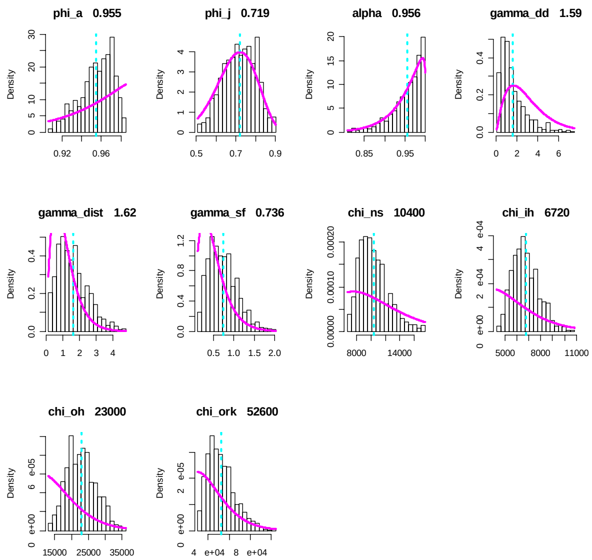
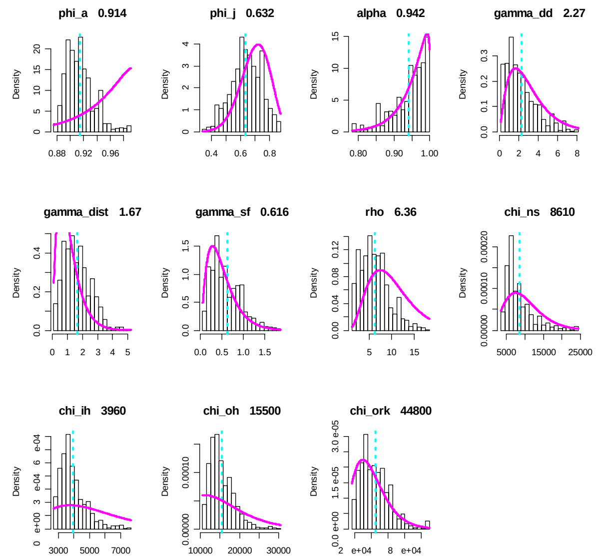


Figure 2. Posterior parameter estimates (histograms) and priors (solid lines) from four models of grey seal population dynamics fit to pup production estimates from 1984-2005. The vertical line shows the posterior mean, its value is given in the title of each plot after the parameter name.

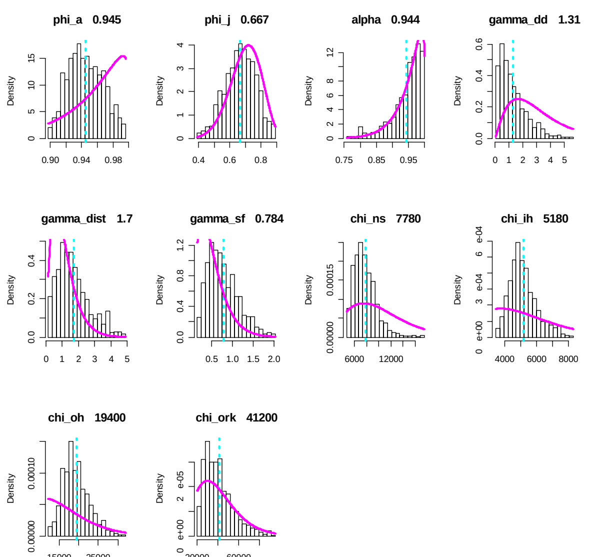
(a) Density dependent survival (DDS)



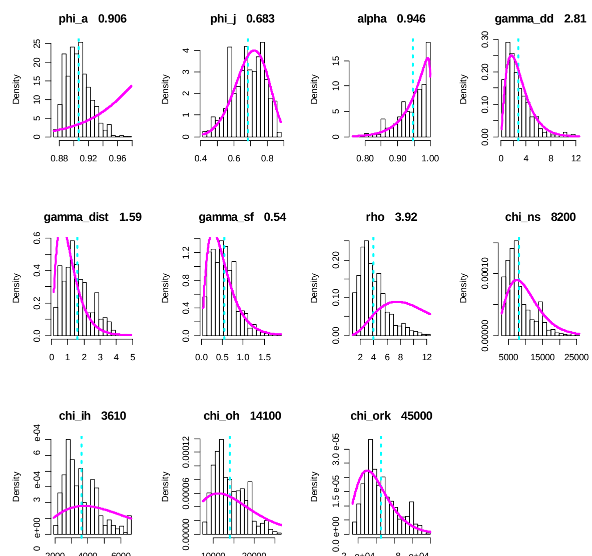
(b) Extended density dependent survival (EDDS)



(c) Density dependent fecundity (DDF)



(d) Extended density dependent fecundity (EDDF)



Appendix 1

Estimates of total population size, in thousands, at the beginning of each breeding season from 1984-2005, made using four models of British grey seal population dynamics. Numbers are posterior means followed by 95% credibility intervals in brackets.

Density dependent survival model

Year	North Sea	Inner Hebrides	Outer Hebrides	Orkneys	Total
1984	4.3 (3.4 5.7)	4.3 (3.1 5.9)	24.2 (18.9 32.2)	15.6 (11.6 20.7)	48.5 (37 64.5)
1985	4.7 (3.8 6.1)	4.6 (3.6 6.1)	24.4 (19.3 31.9)	17 (13.2 22.2)	50.7 (39.8 66.2)
1986	5.1 (4.2 6.5)	4.9 (3.9 6.4)	24.6 (19.7 31.9)	18.5 (14.8 23.7)	53 (42.6 68.4)
1987	5.5 (4.5 6.9)	5.2 (4.2 6.6)	24.8 (20.1 32)	20.1 (16.3 25.3)	55.5 (45.2 70.9)
1988	5.9 (4.9 7.3)	5.4 (4.5 6.9)	25.1 (20.4 32.2)	21.7 (17.8 27.1)	58.1 (47.6 73.6)
1989	6.2 (5.2 7.8)	5.7 (4.7 7.2)	25.4 (20.7 32.6)	23.4 (19.5 29)	60.7 (50.1 76.6)
1990	6.6 (5.5 8.3)	5.9 (4.9 7.5)	25.8 (21 33.1)	25.1 (20.9 31)	63.4 (52.3 79.9)
1991	7 (5.8 8.8)	6.2 (5.1 7.8)	26.1 (21.3 33.6)	26.8 (22.4 33)	66.1 (54.5 83.2)
1992	7.4 (6.1 9.3)	6.4 (5.2 8.1)	26.5 (21.5 34)	28.6 (23.8 35.2)	68.8 (56.6 86.6)
1993	7.8 (6.4 9.8)	6.6 (5.4 8.4)	26.9 (21.7 34.6)	30.4 (25.1 37.5)	71.6 (58.6 90.2)
1994	8.1 (6.7 10.3)	6.8 (5.5 8.7)	27.3 (21.9 35.2)	32.2 (26.4 39.8)	74.4 (60.5 94)
1995	8.5 (6.9 10.8)	7 (5.7 9)	27.7 (22.1 35.8)	34 (27.7 42.1)	77.2 (62.4 97.7)
1996	8.9 (7.2 11.3)	7.2 (5.8 9.3)	28.1 (22.3 36.3)	35.9 (29 44.6)	80.1 (64.3 101.6)
1997	9.2 (7.4 11.9)	7.4 (5.9 9.6)	28.5 (22.4 37.1)	37.7 (30.2 47.3)	82.9 (66 105.8)
1998	9.6 (7.7 12.4)	7.6 (6.1 9.9)	29 (22.6 37.7)	39.5 (31.4 49.8)	85.7 (67.8 109.8)
1999	9.9 (7.9 12.9)	7.8 (6.2 10.1)	29.4 (22.8 38.5)	41.4 (32.6 52.3)	88.6 (69.5 113.8)
2000	10.3 (8.2 13.5)	8 (6.3 10.4)	29.9 (23 39.3)	43.2 (33.8 55.2)	91.4 (71.3 118.3)
2001	10.6 (8.4 14.1)	8.2 (6.5 10.8)	30.4 (23.1 40.1)	45 (34.9 57.9)	94.2 (72.9 122.9)
2002	11 (8.6 14.6)	8.3 (6.6 11.1)	30.8 (23.3 40.9)	46.8 (36 60.9)	97 (74.5 127.5)
2003	11.3 (8.8 15.3)	8.5 (6.7 11.3)	31.3 (23.4 41.8)	48.6 (37.1 64.4)	99.7 (76.1 132.8)
2004	11.6 (9.1 15.8)	8.7 (6.8 11.5)	31.8 (23.6 42.5)	50.4 (38.2 67.4)	102.5 (77.7 137.2)
2005	12 (9.3 16.3)	8.9 (6.9 11.7)	32.2 (23.8 43.3)	52.2 (39.2 70.4)	105.2 (79.3 141.7)

Extended density dependent survival model

Year	North Sea	Inner Hebrides	Outer Hebrides	Orkneys	Total
1984	5.1 (3.8 6.7)	5.4 (3.8 7.4)	28.9 (20.4 38)	21 (13.9 27.8)	60.4 (42 79.8)
1985	5.4 (4.2 7)	5.7 (4.1 7.6)	29.9 (21.3 38.4)	22 (15.4 28.6)	63.1 (45 81.6)
1986	5.8 (4.6 7.3)	6.1 (4.5 7.9)	30.9 (21.8 39.1)	23.2 (16.9 29.5)	66 (47.8 83.8)
1987	6.2 (4.9 7.7)	6.5 (4.9 8.3)	32 (22.2 40)	24.5 (18.6 30.9)	69.2 (50.6 86.9)
1988	6.6 (5.3 8.2)	6.9 (5.1 8.8)	33 (22.8 41.1)	26 (20.2 32.6)	72.6 (53.4 90.7)
1989	7.1 (5.6 8.7)	7.4 (5.5 9.3)	34 (23.1 42.1)	27.7 (21.7 34.4)	76.2 (55.8 94.5)
1990	7.6 (5.9 9.3)	7.8 (5.7 9.9)	35 (23.7 43.1)	29.4 (23.1 36.4)	79.8 (58.4 98.7)
1991	8.1 (6.2 9.9)	8.3 (5.9 10.5)	35.9 (24.1 44.3)	31.3 (24.7 38.3)	83.5 (60.9 103)
1992	8.7 (6.7 10.7)	8.7 (6.1 10.8)	36.7 (24.5 45.6)	33.3 (26.5 40.5)	87.3 (63.8 107.6)
1993	9.3 (7.1 11.4)	9.1 (6.3 11.2)	37.4 (24.9 46.4)	35.4 (28.2 42.9)	91.2 (66.5 111.9)
1994	10 (7.6 12.3)	9.4 (6.3 11.7)	38 (25.4 47.2)	37.7 (30.1 45.4)	95.1 (69.5 116.7)
1995	10.7 (7.8 13.2)	9.7 (6.5 12.1)	38.6 (25.8 48.2)	40.1 (31.9 48.4)	99.1 (72 121.9)
1996	11.5	9.9 (6.6	39 (26	42.8	103.2

	(8.1 14.2)	12.4)	49)	(33.4 51.7)	(74.1 127.3)
1997	12.3 (8.3 15.2)	10 (6.7 12.6)	39.4 (26.3 49.8)	45.7 (35.3 55.5)	107.3 (76.7 133.1)
1998	13 (8.5 16.2)	10.1 (6.9 12.8)	39.7 (26.3 50.5)	48.7 (36.9 59.7)	111.6 (78.7 139.3)
1999	13.8 (8.8 17.3)	10.2 (6.9 13.1)	40 (26.5 51.5)	51.9 (38.6 64.2)	115.9 (80.8 146.1)
2000	14.6 (9 18.5)	10.2 (6.9 13.3)	40.2 (26.3 52.2)	55.3 (40.1 68.9)	120.3 (82.4 153)
2001	15.4 (9.2 19.7)	10.3 (6.9 13.5)	40.4 (26.3 53)	58.8 (41.3 74)	124.8 (83.7 160.2)
2002	16.1 (9.3 21)	10.3 (7 13.7)	40.6 (26.4 53.6)	62.5 (42.2 80)	129.5 (85 168.3)
2003	16.8 (9.5 22.6)	10.4 (7 13.8)	40.8 (26.7 54.1)	66.3 (43.2 86.1)	134.3 (86.3 176.5)
2004	17.5 (9.7 24.3)	10.5 (6.9 14)	41 (26.8 54.7)	70.2 (43.7 92)	139.2 (87.2 185.1)
2005	18.2 (9.9 26.2)	10.5 (7 14.3)	41.3 (27.4 55.2)	74.1 (44.3 98.4)	144.1 (88.6 194.1)

Density dependent fecundity model

Year	North Sea	Inner Hebrides	Outer Hebrides	Orkneys	Total
1984	5.6 (4 7.7)	6.1 (3.9 9.3)	40.5 (28.1 59.5)	18.5 (13.3 24.8)	70.7 (49.4 101.3)
1985	6.2 (4.6 8.3)	6.7 (4.8 9.8)	41.8 (30 61)	20.4 (15.1 26.6)	75.1 (54.5 105.8)
1986	6.8 (5.2 9.1)	7.5 (5.6 10.4)	43.5 (32 62.6)	22.5 (16.9 28.8)	80.2 (59.7 110.9)
1987	7.5 (5.8 9.9)	8.2 (6.2 11.1)	45.1 (33.6 64.7)	24.9 (19.1 31.5)	85.8 (64.8 117.2)
1988	8.3 (6.4 10.9)	9 (6.9 12)	46.9 (35.3 66.4)	27.6 (21.3 34.7)	91.7 (69.9 124)
1989	9.1 (7 11.9)	9.7 (7.5 12.8)	48.7 (37 69.5)	30.5 (23.6 38.5)	98 (75.2 132.6)
1990	10 (7.7 13.1)	10.5 (8.1 13.8)	50.6 (38.4 71)	33.6 (26 42.5)	104.7 (80.2 140.4)
1991	10.9 (8.4 14.3)	11.2 (8.7 14.8)	52.5 (39.9 72.8)	36.9 (28.5 47.3)	111.5 (85.5 149.1)
1992	11.8 (9.1 15.6)	12 (9.3 15.8)	54.5 (41.2 75.6)	40.4 (31.2 52.4)	118.7 (90.8 159.4)
1993	12.8 (9.8 17)	12.7 (9.8 16.6)	56.5 (42.2 78.8)	44.2 (33.8 57.9)	126.2 (95.7 170.3)
1994	13.8 (10.6 18.4)	13.5 (10.4 17.9)	58.6 (43.6 83.1)	48.2 (37.1 63.7)	134.1 (101.6 183.1)
1995	14.9 (11.3 19.9)	14.2 (10.9 19)	60.8 (44.9 87.1)	52.5 (40.3 70)	142.4 (107.4 196.1)
1996	15.9 (12.1 21.5)	15 (11.4 20.3)	63.1 (46.2 90.7)	57 (43.7 76.9)	151 (113.4 209.4)
1997	17 (12.9 23.1)	15.7 (11.8 21.6)	65.4 (47.5 94.8)	61.7 (47.2 84.4)	159.9 (119.4 223.9)
1998	18.2 (13.7 24.8)	16.5 (12.3 22.9)	67.8 (48.6 99.5)	66.6 (51.1 92)	169.1 (125.7 239.3)
1999	19.3 (14.5 26.6)	17.2 (12.8 24.3)	70.3 (49.9 104.9)	71.8 (54.4 100)	178.6 (131.6 255.8)
2000	20.5 (15.3 28.4)	18 (13.2 25.8)	72.7 (51.5 110.9)	77.1 (58.2 107.9)	188.4 (138.1 273.1)
2001	21.7 (16.2 30.4)	18.8 (13.6 27.3)	75.3 (52.8 115.7)	82.7 (62.3 116)	198.4 (144.9 289.4)
2002	22.9 (17.1 32.4)	19.5 (14 28.8)	77.8 (54.1 120.2)	88.4 (65.7 125.4)	208.7 (151 306.8)
2003	24.1 (17.9 34.6)	20.3 (14.4 30.3)	80.5 (55.4 124.8)	94.3 (69.7 134.5)	219.2 (157.4 324.1)
2004	25.4 (18.5 36.6)	21.1 (14.8 31.8)	83.1 (56.7 130.3)	100.4 (73.8 143.3)	230 (163.7 342.1)
2005	26.6 (19.3 38.6)	21.9 (15.3 33.4)	85.8 (58.1 135.8)	106.6 (77.9 153.1)	240.9 (170.5 361)

Extended density dependent fecundity model

Year	North Sea	Inner Hebrides	Outer Hebrides	Orkneys	Total
1984	5.5 (4.2 7.4)	5.8 (4.2 7.8)	32.2 (23.7 45.9)	22.3 (16 28.2)	65.7 (48 89.3)
1985	5.8 (4.5 7.7)	6.1 (4.7 8)	33.4 (25.1 47.9)	23.4 (17.3 29.3)	68.8 (51.5 92.9)
1986	6.2 (5 8)	6.5 (5.1 8.5)	34.7 (26.4 49.8)	24.7 (18.6 30.6)	72.1 (55.1 97)
1987	6.6 (5.4 8.5)	7 (5.5 9.6)	36 (27.8 52.2)	26.2 (20 32.1)	75.8 (58.7 102.4)
1988	7.1 (5.8 9.5)	7.5 (6 10.7)	37.4 (29.1 53.9)	27.8 (21.6 33.8)	79.8 (62.5 107.9)
1989	7.6 (6.2 10.5)	8 (6.4 11.7)	38.8 (30.4 55.5)	29.6 (23.2 36.8)	84.1 (66.2 114.5)
1990	8.2 (6.6 11.3)	8.5 (6.8 12.5)	40.2 (31.8 56.4)	31.6 (24.9 40.6)	88.5 (70.2 120.8)
1991	8.7 (7.1 12.5)	9.1 (7.3 13.1)	41.6 (33.1 58.9)	33.6 (26.8 43)	93 (74.3 127.5)
1992	9.4 (7.6 13.5)	9.6 (7.7 14)	43 (34.1 60.7)	35.8 (28.7 45.4)	97.7 (78.2 133.5)
1993	10.1 (8.1 14.4)	10.1 (8.2 14.4)	44.4 (35.4 63.2)	38.1 (30.6 49.4)	102.7 (82.3 141.4)
1994	10.8 (8.7 15.3)	10.7 (8.6 15.1)	45.7 (36.5 66)	40.6 (32.7 54.2)	107.8 (86.6 150.6)
1995	11.5 (9.3 16.4)	11.2 (9 15.8)	47.1 (37.7 68.1)	43.3 (34.9 59.3)	113.2 (90.9 159.6)
1996	12.4 (9.9 17.3)	11.7 (9.4 16.7)	48.5 (38.8 70.8)	46.2 (37.1 63.8)	118.8 (95.2 168.6)
1997	13.3 (10.7 18.5)	12.2 (9.7 17.8)	49.9 (39.5 73.6)	49.4 (39.9 68.9)	124.7 (99.9 178.8)
1998	14.2 (11.5 19.9)	12.7 (10 18.9)	51.2 (40.2 76)	52.7 (42.3 75.3)	130.8 (104 190.1)
1999	15.2 (12.3	13.1 (10.3	52.5 (41.2	56.3 (44.7	137.2 (108.5

	21.4)	20.1)	78.5)	81)	201)
2000	16.2 (13 23)	13.5 (10.6 21.1)	53.8 (42 81)	60.2 (47.5 85.9)	143.8 (113.1 211)
2001	17.3 (13.8 24.5)	13.9 (10.8 22)	55 (42.6 83.7)	64.4 (50.5 91.4)	150.6 (117.7 221.6)
2002	18.4 (14.6 25.8)	14.3 (11 23)	56.2 (43.1 86.4)	68.8 (53.9 99)	157.7 (122.6 234.2)
2003	19.5 (15.4 27.1)	14.6 (11.1 23.9)	57.3 (43.6 88.6)	73.5 (57.5 104.8)	164.9 (127.6 244.4)
2004	20.7 (16 28.4)	14.9 (11.3 24.8)	58.4 (44.1 92.1)	78.5 (60.9 112.6)	172.5 (132.4 258)
2005	21.9 (16.4 29.7)	15.2 (11.5 25.6)	59.5 (44.5 95.6)	83.8 (64.4 119.4)	180.3 (136.9 270.3)

Appendix 2

Estimates of derived, time and region-varying population parameters in 1985-2005 for the four models of British grey seal population dynamics. Numbers are posterior means followed by 95% credibility intervals in brackets.

Density dependent survival model – estimated annual pup survival $\phi_{p,r,t}$

Year	North Sea	Inner Hebrides	Outer Hebrides	Orkneys
1985	0.417 (0.251 0.65)	0.342 (0.172 0.575)	0.249 (0.098 0.479)	0.48 (0.304 0.693)
1986	0.401 (0.238 0.632)	0.331 (0.169 0.554)	0.239 (0.092 0.46)	0.464 (0.301 0.677)
1987	0.383 (0.226 0.619)	0.312 (0.162 0.531)	0.236 (0.091 0.457)	0.444 (0.283 0.664)
1988	0.368 (0.215 0.605)	0.297 (0.153 0.518)	0.233 (0.091 0.456)	0.427 (0.267 0.653)
1989	0.355 (0.203 0.589)	0.286 (0.147 0.507)	0.23 (0.09 0.451)	0.412 (0.252 0.645)
1990	0.342 (0.193 0.58)	0.276 (0.142 0.497)	0.228 (0.09 0.446)	0.398 (0.239 0.637)
1991	0.331 (0.185 0.567)	0.269 (0.138 0.489)	0.226 (0.089 0.442)	0.385 (0.227 0.627)
1992	0.32 (0.178 0.56)	0.262 (0.133 0.481)	0.223 (0.089 0.439)	0.373 (0.216 0.618)
1993	0.31 (0.17 0.551)	0.255 (0.129 0.472)	0.221 (0.087 0.434)	0.36 (0.205 0.609)
1994	0.3 (0.163 0.538)	0.249 (0.126 0.462)	0.218 (0.087 0.43)	0.348 (0.195 0.599)
1995	0.291 (0.157 0.529)	0.243 (0.122 0.454)	0.216 (0.087 0.426)	0.337 (0.187 0.59)
1996	0.282 (0.151 0.521)	0.237 (0.119 0.449)	0.213 (0.086 0.422)	0.326 (0.179 0.581)
1997	0.274 (0.146 0.51)	0.232 (0.116 0.441)	0.211 (0.085 0.418)	0.316 (0.172 0.572)
1998	0.267 (0.141 0.501)	0.227 (0.113 0.431)	0.208 (0.085 0.414)	0.306 (0.165 0.564)
1999	0.26 (0.137 0.494)	0.223 (0.111 0.425)	0.205 (0.084 0.408)	0.297 (0.158 0.557)
2000	0.253 (0.132 0.484)	0.219 (0.108 0.419)	0.203 (0.083 0.403)	0.288 (0.152 0.549)
2001	0.247 (0.129 0.476)	0.215 (0.107 0.415)	0.2 (0.082 0.401)	0.28 (0.146 0.538)
2002	0.241 (0.124 0.465)	0.211 (0.104 0.409)	0.198 (0.082 0.397)	0.272 (0.141 0.525)
2003	0.235 (0.121 0.457)	0.207 (0.102 0.402)	0.195 (0.081 0.394)	0.265 (0.136 0.516)
2004	0.23 (0.118 0.45)	0.204 (0.1 0.399)	0.193 (0.08 0.389)	0.258 (0.132 0.509)
2005	0.225 (0.115 0.443)	0.2 (0.099 0.393)	0.191 (0.079 0.386)	0.251 (0.128 0.5)

Extended density dependent survival model – estimated annual pup survival $\phi_{p,r,t}$

Year	North Sea	Inner Hebrides	Outer Hebrides	Orkneys
1985	0.616 (0.338 0.83)	0.604 (0.325 0.826)	0.567 (0.184 0.82)	0.622 (0.338 0.832)
1986	0.614 (0.338 0.83)	0.6 (0.293 0.826)	0.57 (0.187 0.818)	0.62 (0.338 0.832)
1987	0.612 (0.338 0.829)	0.595 (0.278 0.824)	0.565 (0.179 0.81)	0.618 (0.338 0.831)
1988	0.61 (0.316 0.829)	0.588 (0.241 0.822)	0.559 (0.175 0.806)	0.616 (0.338 0.831)
1989	0.607 (0.286 0.828)	0.58 (0.215 0.818)	0.551 (0.169 0.797)	0.615 (0.338 0.831)
1990	0.605 (0.264 0.826)	0.573 (0.199 0.809)	0.543 (0.159 0.793)	0.613 (0.338 0.831)
1991	0.603 (0.24 0.826)	0.565 (0.194 0.802)	0.535 (0.157 0.789)	0.611 (0.338 0.83)
1992	0.6 (0.227 0.826)	0.555 (0.179 0.798)	0.526 (0.154 0.777)	0.609 (0.315 0.829)
1993	0.597 (0.214 0.824)	0.54 (0.172 0.788)	0.514 (0.151 0.767)	0.608 (0.296 0.829)
1994	0.593 (0.206 0.823)	0.521 (0.163 0.769)	0.503 (0.147 0.754)	0.605 (0.274 0.828)
1995	0.589 (0.194 0.821)	0.5 (0.143 0.752)	0.491 (0.14 0.745)	0.603 (0.251 0.827)
1996	0.583 (0.183 0.817)	0.482 (0.121 0.739)	0.479 (0.137 0.739)	0.601 (0.23 0.827)
1997	0.576	0.466	0.468	0.598

	(0.174 0.815)	(0.104 0.726)	(0.123 0.73)	(0.209 0.826)
1998	0.568 (0.163 0.812)	0.453 (0.092 0.727)	0.459 (0.108 0.724)	0.595 (0.192 0.824)
1999	0.558 (0.152 0.809)	0.441 (0.087 0.727)	0.45 (0.115 0.721)	0.592 (0.18 0.823)
2000	0.548 (0.145 0.8)	0.431 (0.08 0.719)	0.444 (0.113 0.717)	0.588 (0.165 0.823)
2001	0.538 (0.135 0.796)	0.426 (0.083 0.709)	0.438 (0.108 0.716)	0.583 (0.155 0.823)
2002	0.527 (0.131 0.796)	0.423 (0.1 0.705)	0.434 (0.104 0.713)	0.578 (0.146 0.823)
2003	0.517 (0.125 0.794)	0.421 (0.101 0.701)	0.431 (0.106 0.708)	0.571 (0.137 0.819)
2004	0.506 (0.12 0.789)	0.419 (0.098 0.702)	0.43 (0.113 0.703)	0.564 (0.129 0.814)
2005	0.494 (0.114 0.784)	0.415 (0.096 0.7)	0.428 (0.111 0.701)	0.555 (0.124 0.811)

Density dependent fecundity model – estimated annual fecundity $\alpha_{r,t}$

Year	North Sea	Inner Hebrides	Outer Hebrides	Orkneys
1985	0.805 (0.658 0.909)	0.747 (0.553 0.871)	0.63 (0.416 0.793)	0.851 (0.704 0.94)
1986	0.787 (0.633 0.899)	0.718 (0.534 0.851)	0.62 (0.407 0.782)	0.838 (0.695 0.933)
1987	0.771 (0.607 0.89)	0.692 (0.519 0.835)	0.611 (0.399 0.775)	0.825 (0.676 0.926)
1988	0.756 (0.586 0.881)	0.673 (0.496 0.824)	0.603 (0.39 0.769)	0.813 (0.656 0.921)
1989	0.741 (0.563 0.875)	0.657 (0.476 0.814)	0.594 (0.38 0.765)	0.801 (0.636 0.919)
1990	0.727 (0.546 0.866)	0.643 (0.458 0.805)	0.586 (0.371 0.757)	0.79 (0.617 0.914)
1991	0.712 (0.522 0.858)	0.63 (0.44 0.796)	0.576 (0.359 0.752)	0.777 (0.596 0.908)
1992	0.696 (0.502 0.853)	0.615 (0.42 0.788)	0.566 (0.347 0.747)	0.764 (0.573 0.903)
1993	0.68 (0.477 0.846)	0.6 (0.402 0.779)	0.557 (0.337 0.743)	0.749 (0.547 0.897)
1994	0.665 (0.455 0.836)	0.585 (0.386 0.771)	0.547 (0.329 0.74)	0.735 (0.523 0.889)
1995	0.649 (0.433 0.826)	0.571 (0.37 0.76)	0.538 (0.317 0.735)	0.72 (0.503 0.881)
1996	0.634 (0.41 0.815)	0.559 (0.356 0.751)	0.529 (0.305 0.731)	0.705 (0.48 0.874)
1997	0.619 (0.391 0.805)	0.547 (0.337 0.743)	0.52 (0.295 0.726)	0.69 (0.456 0.867)
1998	0.605 (0.371 0.797)	0.535 (0.321 0.736)	0.51 (0.288 0.716)	0.675 (0.435 0.859)
1999	0.59 (0.353 0.789)	0.523 (0.307 0.727)	0.501 (0.278 0.709)	0.66 (0.418 0.85)
2000	0.576 (0.337 0.779)	0.512 (0.294 0.718)	0.492 (0.269 0.703)	0.645 (0.396 0.842)
2001	0.562 (0.322 0.769)	0.501 (0.281 0.711)	0.484 (0.259 0.695)	0.63 (0.373 0.835)
2002	0.549 (0.307 0.76)	0.491 (0.269 0.703)	0.475 (0.246 0.688)	0.615 (0.354 0.827)
2003	0.536 (0.293 0.752)	0.481 (0.259 0.697)	0.467 (0.237 0.682)	0.601 (0.336 0.819)
2004	0.523 (0.279 0.744)	0.471 (0.248 0.689)	0.458 (0.23 0.674)	0.586 (0.318 0.81)
2005	0.511 (0.267 0.735)	0.461 (0.238 0.682)	0.45 (0.224 0.668)	0.572 (0.303 0.803)

Extended density dependent fecundity model – estimated annual fecundity $\alpha_{r,t}$

Year	North Sea	Inner Hebrides	Outer Hebrides	Orkneys
1985	0.934 (0.732 0.998)	0.921 (0.668 0.997)	0.898 (0.52 0.993)	0.939 (0.75 0.998)
1986	0.932 (0.732 0.998)	0.917 (0.629 0.997)	0.895 (0.512 0.993)	0.937 (0.736 0.998)
1987	0.93 (0.72 0.997)	0.912 (0.597 0.996)	0.892 (0.535 0.992)	0.936 (0.732 0.998)
1988	0.929 (0.702 0.997)	0.908 (0.57 0.994)	0.889 (0.529 0.991)	0.935 (0.732 0.998)
1989	0.927 (0.687 0.997)	0.904 (0.553 0.994)	0.885 (0.521 0.989)	0.934 (0.725 0.998)
1990	0.926 (0.668 0.997)	0.9 (0.538 0.994)	0.882 (0.514 0.987)	0.933 (0.712 0.998)
1991	0.923 (0.652 0.997)	0.895 (0.552 0.992)	0.877 (0.504 0.986)	0.932 (0.7 0.998)
1992	0.921 (0.634 0.997)	0.89 (0.55 0.99)	0.872 (0.487 0.985)	0.93 (0.692 0.998)
1993	0.918 (0.618 0.996)	0.883 (0.53 0.987)	0.867 (0.472 0.983)	0.929 (0.682 0.998)
1994	0.915 (0.602 0.996)	0.876 (0.506 0.984)	0.861 (0.457 0.981)	0.927 (0.666 0.998)
1995	0.912 (0.586 0.995)	0.868 (0.485 0.982)	0.855 (0.445 0.979)	0.925 (0.65 0.998)
1996	0.909 (0.569 0.995)	0.859 (0.466 0.98)	0.848 (0.436 0.978)	0.924 (0.635 0.998)
1997	0.905 (0.554 0.995)	0.851 (0.447 0.977)	0.841 (0.429 0.976)	0.921 (0.612 0.998)
1998	0.9 (0.539 0.995)	0.843 (0.436 0.974)	0.834 (0.422 0.974)	0.919 (0.597 0.998)
1999	0.895 (0.525 0.994)	0.833 (0.425 0.972)	0.826 (0.415 0.971)	0.917 (0.577 0.998)
2000	0.89	0.824	0.818	0.914

	(0.512 0.993)	(0.415 0.968)	(0.409 0.969)	(0.558 0.998)
2001	0.883 (0.497 0.992)	0.814 (0.406 0.966)	0.81 (0.403 0.968)	0.911 (0.54 0.998)
2002	0.877 (0.485 0.992)	0.805 (0.396 0.963)	0.802 (0.397 0.966)	0.908 (0.523 0.998)
2003	0.87 (0.473 0.992)	0.796 (0.386 0.965)	0.794 (0.39 0.964)	0.904 (0.507 0.997)
2004	0.863 (0.46 0.99)	0.786 (0.379 0.961)	0.787 (0.384 0.962)	0.9 (0.492 0.997)
2005	0.854 (0.446 0.989)	0.776 (0.374 0.959)	0.779 (0.373 0.96)	0.895 (0.476 0.997)

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The status of British common seal populations

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Summary

In August 2005, the Sea Mammal Research Unit (SMRU) conducted helicopter-based thermal imaging survey for common seals around most of the coast of mainland Scotland. The survey covered the entire east coast from the Farne Islands in Northumberland to Duncansby Head, the north coast to Cape Wrath and the Scottish west coast as far south as Loch Linnhe, including Skye, the Small Isles and Lismore. The survey also covered the Firth of Clyde and Dumfries and Galloway from Machrihanish on South Kintyre to Silloth, in Cumbria.

Common seals were surveyed by fixed-wing aircraft in Lincolnshire, Norfolk, Suffolk and the Thames Estuary in England and the Firth of Tay and the Moray Firth in Scotland were surveyed twice during the August moult. Scottish sites were surveyed twice to help determine the variation in numbers of seals ashore during the survey period. The fixed-wing surveys were extended to include seals (mainly grey seals) on the more distant off-lying islands (Isle of Man, the Flannan Isles, Sula Sgeir, North Rona and Sule Skerry) which had never previously been surveyed in August.

In Scotland, the number of common seals counted did not differ significantly in most of the areas surveyed. The exception was in the Firth of Clyde, where the count was 60.0% of the previous survey from August 1996. In The Wash, August counts of common seals were 9.3% lower than in 2004 and 34.6% lower than the pre-epidemic counts in 2002. Counts at other Lincolnshire and Norfolk sites were similar to pre-epidemic counts. In the Moray Firth, numbers counted in 2005 were lower than in 2004. In the Firth of Tay, numbers were lower than in any previous year.

From surveys carried out in 2005 and earlier, the minimum number of common seals counted in Scotland was 29,059 and 3,637 in England, making a total of 32,696.

During the 2006 breeding season, SMRU and the Fisheries Research Services (FRS) conducted repeat ground and air surveys common seals in the Moray Firth.

Preliminary results from surveys carried out in 2006 found a significant decline in apparent abundance by 42% (95% confidence intervals 10%-62%) compared with 2001 in Orkney and Shetland. A partial survey of the Outer Hebrides did not show a recent decline. Results from all three areas are consistent with a gradual decline since the late 1990s. The analysis suggested that this is a highly significant change that exceeds those specified by current environmental quality metrics. Surveys of the east coast populations in 2006 also show continuing declines in both the Tay and the Wash populations (SCOS BP 06/04) and no recovery in the Moray Firth. This is in contrast to the apparent rapid growth in populations in the nearest European population in the Wadden Sea.

Introduction

Most surveys are carried out during the common seal annual moult, in August. At this time during their annual cycle, common seals tend to spend longer at haulout sites and the greatest and most consistent numbers of seals are found ashore. However, during a survey, there will be a number of seals at sea and not counted. Thus the numbers presented here represent the minimum number of common seals in each area and should be considered as an index of population size.

Surveys of the Scottish coast are undertaken on an approximately five-yearly cycle, although the Moray Firth and Firth of Tay are surveyed more frequently. The 2005 survey formed the first part of the second complete survey of common seals around Scotland. The remainder of the Scottish coast, including the Northern and Western Isles, should be surveyed in August 2006.

The Lincolnshire and Norfolk coast, which holds over 95% of the English common seal population, is usually surveyed twice annually. In 2005, this survey was extended to include more of the Suffolk, Essex and Kent coast. In addition, English Nature funded a second breeding season survey (in early July) of common seals in Lincolnshire and Norfolk, including The Wash.

Methods

Surveys of the estuarine haulout sites on the east coast of Britain were made using large format vertical aerial photography from a twin-engined fixed-wing aircraft. On sandbanks, seals are relatively easily located and this method of survey is highly cost-effective. Seals hauling out on rocky or seaweed covered shores are well camouflaged and difficult to detect. Surveys of these coastlines are by helicopter using a thermal imaging camera. The thermal imager can detect groups of seals at distances of over 3km. This technique enables rapid, thorough and synoptic surveying of complex coastlines.

Results

1. Common seals in Scotland

In August 2005, the area surveyed for common seals by thermal imager included the whole east and north coast of Scotland and the west coast south from Cape Wrath to Loch Linnhe (including Skye, the small Isles and Lismore) and south from Machrihanish on south Kintyre to Silloth, in Cumbria, in the Solway Firth (Figure 2). In addition, fixed wing surveys were made of the Firth of Tay, the Moray Firth and the more distant offshore islands of the Isle of Man, the Flannan Isles, Sula Sgeir, North Rona and Sule Skerry, which are outside normal helicopter operational range. No common seals were seen at any of the off-lying islands surveyed.

The numbers of common seals counted in areas surveyed in August 2005 are in Table 1 and their distribution shown in Figure 1. The overall distribution of common seals around the British Isles is shown in Figure 2. This figure uses data from Scotland and England from 1996 and 1997, the first time the whole of Scotland was surveyed, for Northern Ireland from 2002 and for the Irish Republic from 2003. For ease of viewing at this scale, counts were aggregated into 10km squares.

Table 2 provides a comparison of counts of common seals in different Regions of Scotland between 1988 and 2005. These data are all from surveys carried out in August. Highland and Strathclyde Regions were not fully surveyed in any single year. The counts presented here are composites from surveys carried out in different years. The 'third' survey, in 2000, was never completed due to financial constraints. The total for that year includes data from the most recent previous survey (in 1996 or 1997).

Moray Firth

SMRU's aerial surveys of the Moray Firth began in August 1992. The counts are in Table 4, and the trends shown in Figure 4. In 2005, all the Inner Moray Firth counts were lower than the 2004 maximum count. The highest count in 2005 was on the 18th August using the thermal imaging camera. In this count numbers in the Dornoch Firth and Ardersier were comparable to 2004, Beauly Firth numbers had decreased, while Cromarty Firth numbers increased. Compared to 2002 (the last complete survey of the Moray Firth) the proportion of animals found outside the Inner Moray Firth (i.e. at Findhorn, Loch Fleet and along the coast to Dunbeath) decreased from 44.5% to 27.5%.

Paul Thompson, from Aberdeen University's Lighthouse Field Station, in Cromarty, has more detailed annual counts of common seals in the Inner Moray Firth in the summer months since 1988.

Firth of Tay

The maximum count of common seals in the Firth of Tay in 2005 was 21% lower than the 2004 count (Table 5). The 2005 counts were the lowest recorded to date (Figure 5). The distribution of seals has changed within the Firth. Compared to 2004, the proportion of animals at Abertay and Tenstmuir has increased while the proportion at Broughty Ferry and Buddon Ness has decreased.

2. Common seals surveys in England

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 once or twice annually in the first half of August each year (Figure 1, Table 1).

Two aerial surveys of common seals were carried out in Lincolnshire and Norfolk during August 2005 (Table 1). One count showed evidence of disturbance at several sites in the south east of The Wash. The higher 'undisturbed' count mean 2005 count for The Wash (1,946) was 9.3% lower than the mean 2004 count (2,146) and 34.6% lower than the mean pre-epidemic 2002 count (2,976).

We developed two population growth models that explicitly modelled variability in both observation and population growth processes (Thompson, Duck & Lonergan (submitted). We were able to show that uncertainty in proportion of animals observed dominates in this system, allowing growth rates within each period to be treated as constant. The two population trajectory models produced encouragingly similar results. The population was increasing at a little over 3% pa until 1988 (95% CI: 2.1-4.1(state space model (SSM)), 2.5-4.5 (GLM)) (Figure 2). The 1988 count was obtained approximately one week before the first reports of sick and dead seals being washed up on the UK coast. The number hauling out fell by approximately 50% between 1988 and 1989 (95% CI: 44-59(SSM), 48-62(GLM)), coincident with the PDV epidemic. After 1989 the number increased again, at almost 6% pa (95% CI: 4.8-6.7(SSM), 5.1-6.8(GLM)). The post epidemic rate of increase was significantly higher than the pre epidemic rate ($p<0.001$, pair-wise comparison of parameter estimates). The population was affected by a recurrence of the PDV epidemic in August 2002. The first indications of morbidity due to the epidemic were reported in early August, shortly after the 2002 survey. The dates of the surveys and the disease outbreak in 2002 were almost exactly the same as in 1988. However mortality was lower than in 1988, at around 22% (95% CI: 9-33(SSM), 11-33(GLM)).

As the time series of counts at both Blakeney and Donna Nook are sparse in comparison to the Wash they have not been subjected to the same analysis. The mean 2005 count at Donna Nook was 43% higher than the mean 2004 count and 23% higher than the pre-epidemic 2002 count. The mean 2005 count at Blakeney was 10% higher than the mean 2004 count and 45% higher than the mean pre-epidemic 2002 count (Table 1).

Overall, the combined count for the English East coast population in 2005 (using only the undisturbed count for the Wash) was 1% higher than the maximum count in 2004. This apparent lack of recovery contrasts with the rapid recovery of the Wadden Sea population that is apparently increasing at around 15% p.a. A similar pattern was observed after the 1988 epidemic with the English population showing a delayed and/or slower recovery compared with the rest of Europe.

Breeding season Wash surveys 2004 and 2005

A total of 651 pups and 1699older harbour seals (1+ age classes) were counted in the Wash during the 2005 breeding season survey. These were distributed over 29 separate haulout groups. Pups were widely distributed, being present at all but two of the occupied sites. The 2005 pup count was 6% higher than the 2004 pup count (613 pups) and 19% higher than the 2001 pre-epidemic count. The 2005 adult count was 3.8% lower than the equivalent 2004 count and 5.7% lower than the pre-epidemic adult count in 2001. Differences in timing of surveys mean that direct comparisons are problematic, but there is no indication of a major decline in pup production after the 2002 PDV epidemic and there may already be signs that the pup production is increasing. This is in contrast to the further decline in the moult counts between 2003 and 2005.

3. Minimum estimate of the size of the British common seal population

The most recent minimum estimate of the number of common seals in Scotland is 29,059 from surveys carried out in 2001, 2002, 2003, 2004 & 2005. The most recent minimum estimate for England is 3,637. This comprises 3,392 seals in Lincolnshire and Norfolk in 2004 plus 225 seals in Northumberland, Cleveland, Essex and Kent between 1994 and 2003 and an estimated 20 seals from the south and west coasts.

Table 1 contains counts by region for the period 1996-2005. These are presented as the most recent counts available for each region. Where multiple counts were obtained in any August (in The Wash, for example), the maximum values have been used Table 1 includes numbers from both Northern and the Republic of Ireland. The Irish surveys were funded by the Environment and Heritage Service and the National Parks and Wildlife Service for the north and south respectively.

4. Common seal surveys 2006

Moray Firth – Pupping season

During the pupping season (15th June – 15th July) repeat ground and air surveys were completed of the whole Moray Firth area. A total of five concurrent ground and fixed-wing surveys were completed and a single (concurrent) thermal imaging survey. The preliminary count data (ground counts only) are shown in Figure 6 and are compared with counts from the previous two years (data from the University of Aberdeen). A comparison between the fixed-wing and ground counts from all sites from the first three surveys is shown in Figure.7. The remaining data are still to be analysed.

Northern Ireland

Two thermal imaging surveys of part of Northern Ireland were carried out in 2006. The first survey, on 23 May, was incomplete due to weather constraints. The second survey, on 11 July, was a successful breeding season survey.

Preliminary results 2006

In August 2006 we surveyed Shetland, Orkney, part of the Outer Hebrides as part of our second full survey of Scotland using a helicopter equipped with thermal imager. This survey was part funded by Scottish Natural Heritage.

Fixed wing and/or helicopter surveys of the Firth of Tay and the Moray Firth and the English east coast populations were completed.

Preliminary results from surveys carried out in 2006 found a significant decline in apparent abundance by 42% (95% confidence intervals 10%-62%) compared with 2001 in Orkney and Shetland (Table 6). A partial survey of the Outer Hebrides did not show a recent decline. Results from all three areas are consistent with a gradual decline since the late 1990s. The analysis suggested that this is a highly significant change that exceeds those specified by current environmental quality metrics. Surveys of the east coast populations in 2006 also show continuing declines in both the Tay and the Wash populations (SCOS BP 06/04) and no recovery in the Moray Firth. This is in contrast to the apparent rapid growth in populations in the nearest European population in the Wadden Sea.

Figure 1. The number and distribution of common seals around the coast of Scotland surveyed in August 2005. All areas were surveyed by helicopter using a thermal imaging camera. The remaining areas: Shetland, Orkney, Western Isles and the remainder of Strathclyde are due to be surveyed in August 2006.

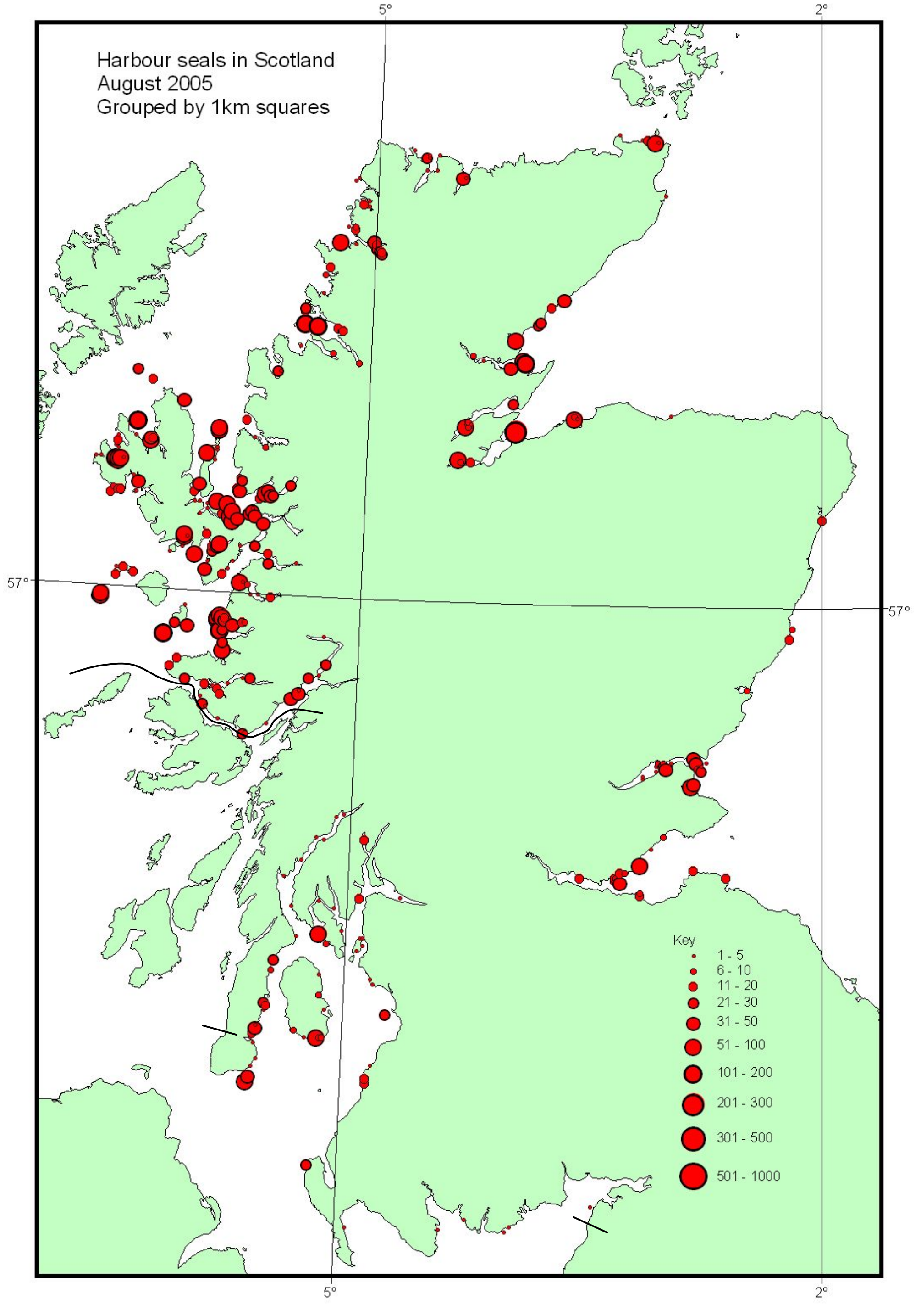
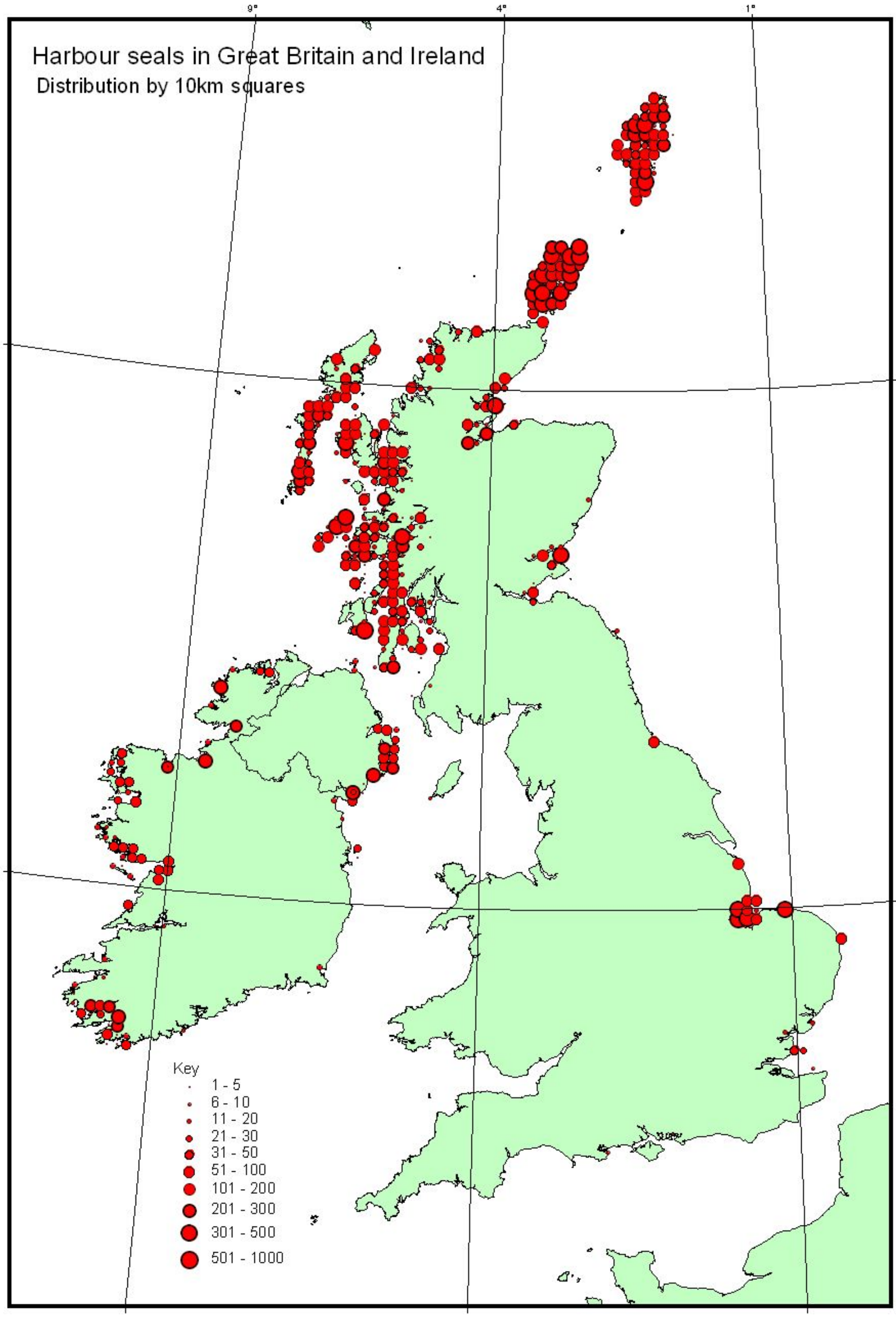


Figure 2. The August distribution of harbour seals in Great Britain and Ireland, by 10km squares. These data are from surveys carried out between 1996 and 1997 for Scotland and England in 2002 and 2003 for Ireland. An updated version of this Figure will be produced once the 2006 surveys have been completed.



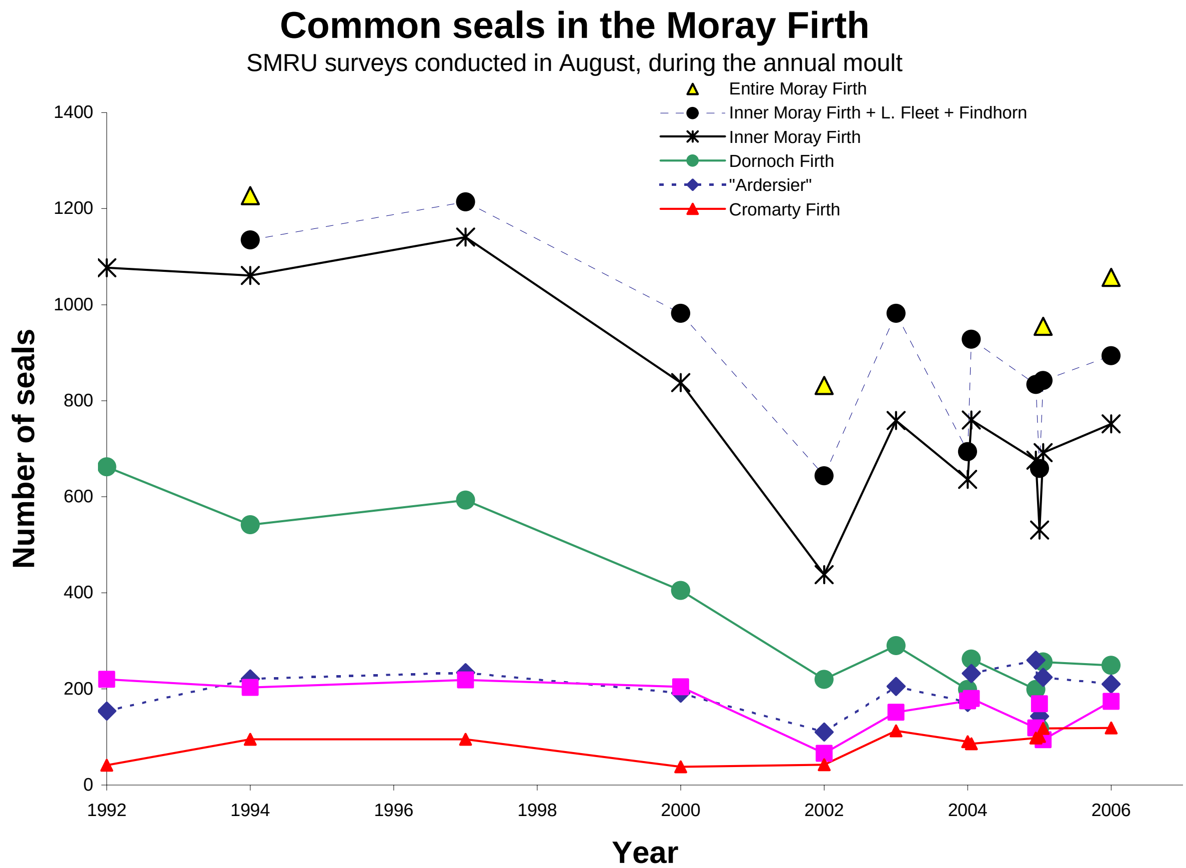


Figure 3. The number of common seals counted in the Moray Firth by the Sea Mammal Research Unit

Figure 4. The number of common seals counted in the Firth of Tay by the Sea Mammal Research Unit.

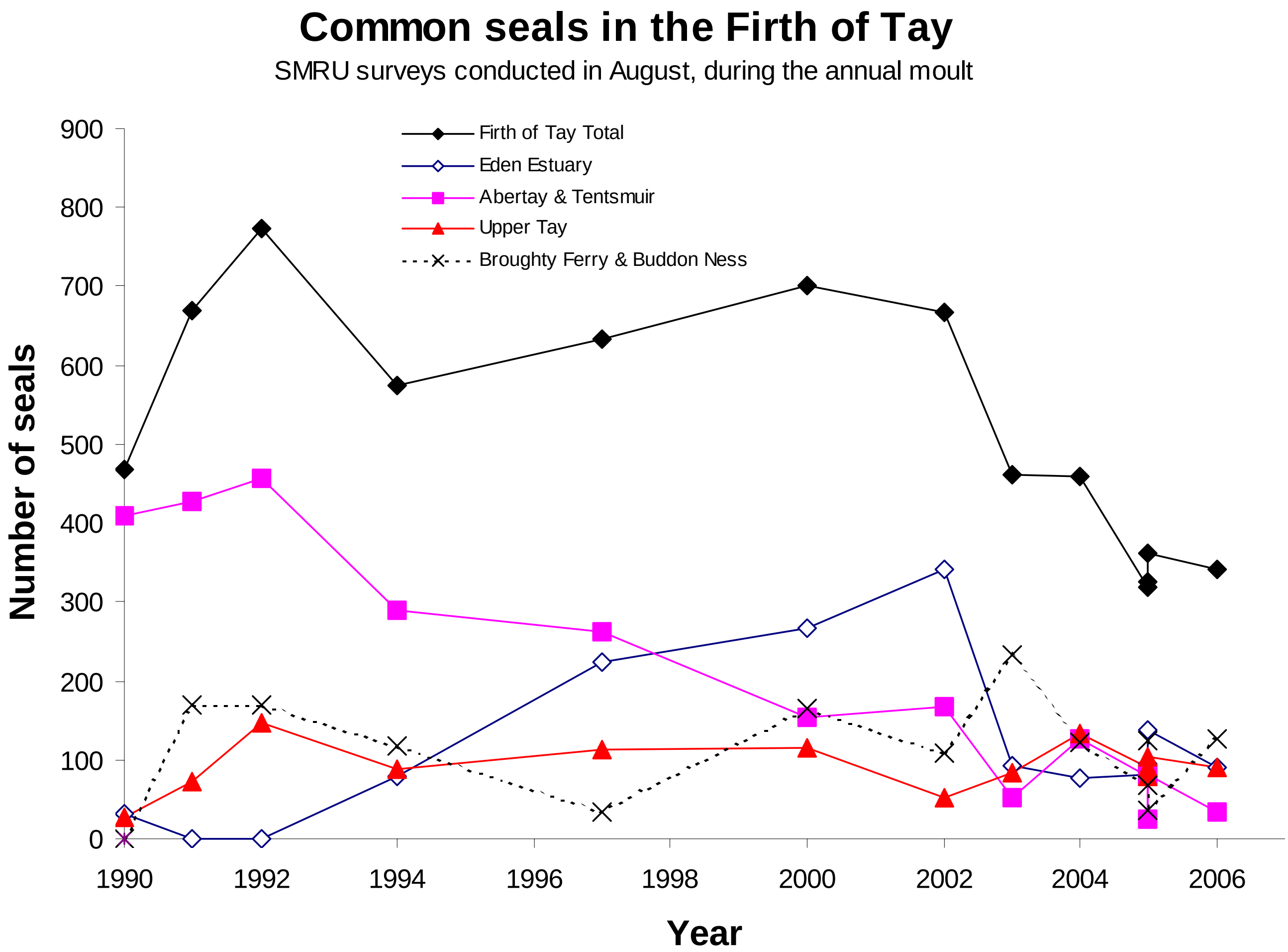


Figure 5. Counts of common seals in The Wash in August 1967 -2006. These data are an index of the population size through time. Fitted lines are exponential growth curves (growth rates given in text).

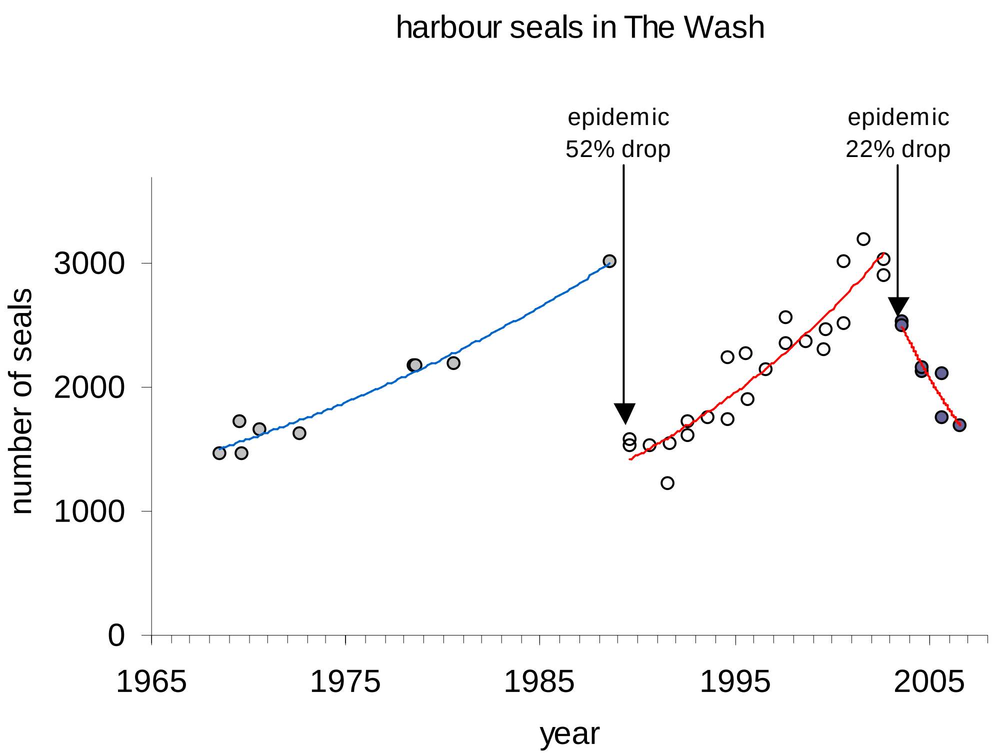


Figure 6. Mean adult harbour seal breeding season counts from the Moray Firth 2004 to 2006. N.B Data for 2004 and 2005 were from the University of Aberdeen

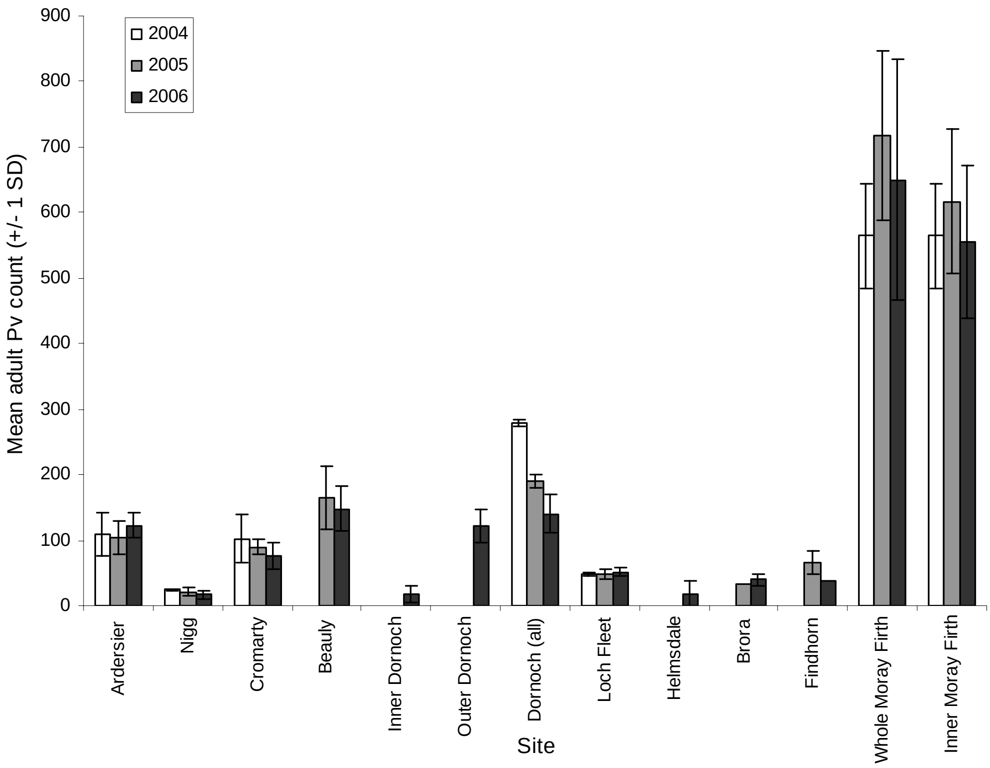


Figure 7. SMRU mean adult harbour seal breeding season counts from the Moray Firth (fixed wing and ground counts) from first three pupping season surveys in June and July 2006.

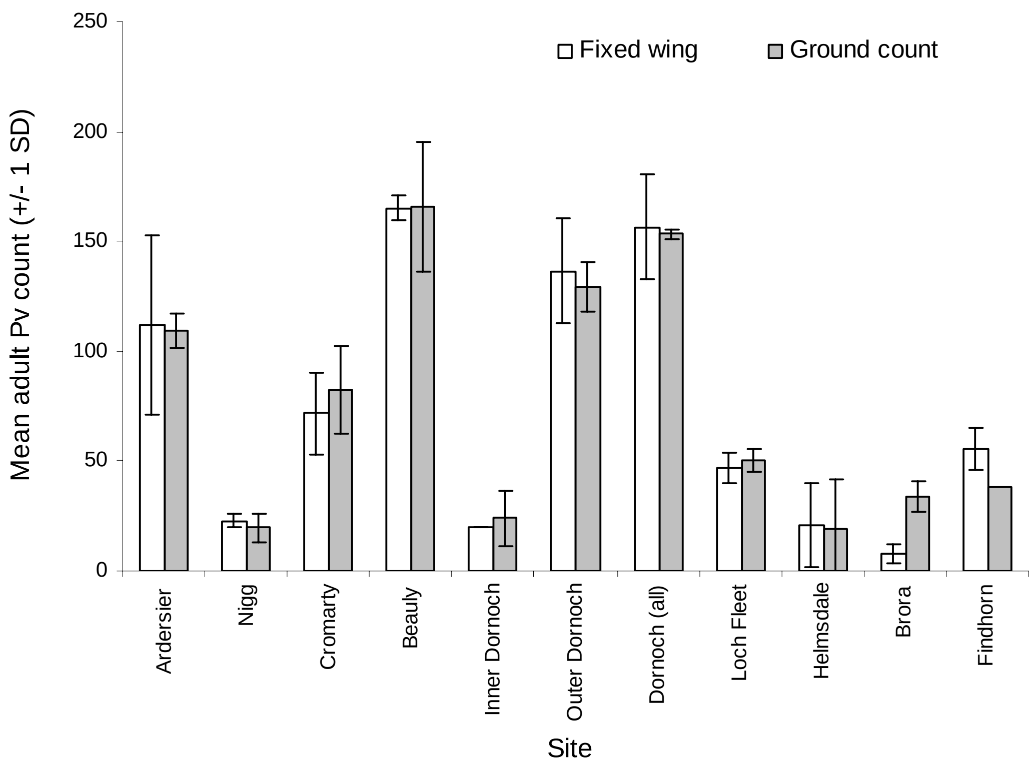


Table 1. Minimum estimates of the UK common seal population. Figures in bold type are from surveys carried out in 2005 (preliminary results of 2006 surveys are presented later in tables)

Region	Year of survey	2000-2005	Previous estimate
Shetland	2005	4,883	4,883
Orkney	2005	7,752	7,752
Outer Hebrides	2003	2,098	2,098
Highland East & North (Nairn to Cape Wrath)	2005	**1,056**	1,232
Highland West (Cape Wrath to Appin, Loch Linnhe)	2005	**4,966**	4,947
Strathclyde West (Appin to Mull of Kintyre)	2000	6,918	6,918
Strathclyde, Firth of Clyde (Mull of Kintyre to Loch Ryan)	2005	**581**	991
Dumfries & Galloway (Loch Ryan to English Border at Carlisle)	2005	**42**	6
Grampian (Montrose to Nairn)	2005	**113**	113
Tayside (Newburgh to Montrose)	2005	**101**	121
Fife (Kincardine Bridge to Newburgh)	2005	**445**	414
Lothian (Torness Power Station to Kincardine Bridge)	2005	**104**	40
Borders (Berwick upon Tweed to Torness Power Station)	2005	**0**	0
TOTAL SCOTLAND		**29,059**	
Blakeney Point	2005	**741**	
The Wash	2005	**2124**	
Donna Nook	2005	**470**	
Scroby Sands	2004	57	
Other east coast sites	1994, 2000, 2003	225	
South and west England (estimated)		20	
TOTAL ENGLAND		**3637**	
TOTAL BRITIAN		**32696**	
TOTAL NORTHERN IRELAND	2002	**1,248**	
TOTAL BRITAIN & N. IRELAND		**33,944**	
TOTAL REPUBLIC OF IRELAND	2003	**2,905**	
TOTAL GREAT BRITIAN AND IRELAND		**36,849**	

Table 2. A comparison of the number of common seals in the Scottish Regions counted by the Sea Mammal Research Unit. All surveys were in August, during the common seal annual moult. The year (or years) of survey is in brackets. In Highland and Strathclyde Regions, different subregions were frequently surveyed in different years. Thus the total for the incomplete 'Third' survey of Highland Region comprises new data from some subregions plus old data from subregions surveyed in 1996 or 1997. Dumfries & Galloway, Tayside, Fife, Lothian and Borders were surveyed in their entirety only twice, in 1997 and 2005.

Region	'Early' 1988-1991	'First' 1988-1993	'Second' 1996/1997	'Third' 2000/2001	'Fourth' 2005/2006
Shetland	**4797** (1991)	**6227** (1993)	**5991** (1997)	**4883** (2001)	3021 preliminary(2006)
Orkney	**7137**[1] (1989)	**7873** (1993)	**8523** (1997)	**7752** (2001)	4256 preliminary(2006)
Outer Hebrides		**2329** (1992)	**2820** (1996)	**2413** (2000)	**2098** (2003)
Highland		**4241**[2] (1988-1991)	**5177** (1996, 1997)	**6291**[2] (1996, 1997, 2000)	**6022** (2005)
Strathclyde		**5341**[2] (1988-1993)	**6333** (1996)	**7909**[2] (1996, 2000)	
Dumfries & Galloway		**8** (1992)	**6** (1996)		**42** (2005)
Grampian			**62** (1997)		**113** (2005)
Tayside			**92** (1997)		**101** (2005)
Fife			**617** (1997)		**445** (2005)
Lothian			**40** (1997)		**104** (2005)
Borders			**0** (1997)		**0** (2005)

[1] Visual helicopter survey by University of Aberdeen and Sea Mammal Research Unit
[2] Sum from subregions counted in different years

Table 3. Numbers of common seals in the Moray Firth during August (SMRU surveys).

Location	**07 Aug 1992**	**30 July 1993**	**13 Aug 1994**	**15 Aug 1997**[1]	**11 Aug 2000**	**11 Aug 2002**	**7 Aug 2003**	**10 Aug 2004**	**13 Aug 2004**	**8 Aug 2005**	**9 Aug 2005**	**16 Aug 2005**[1]	**18 Aug 2005**[1]	**4 Aug 2006**
Ardersier	154	-	221	234	191	110	205	172	232	260	143	195	224	210
Beauly Firth	220	-	203	219	204	66	151	175	180	119	169	-	94	174
Cromarty Firth	41	-	95	95	38	42	113	90	86	98	101	-	118	119
Dornoch Firth (pSAC)	662	-	542	593	405	220	290	199	262	199	118	-	256	249
Inner Moray Firth Total	**1077***	**-**	**1061***	**1141**	**838**	**438**	**759**	**636**	**760**	**676**	**531**	**-**	**692**	**752**
Findhorn	-	-	*58*	*46*	*111*	*144*	*167*	*0*	*98*	*90*	*58*	*148*	*74*	*63*
Dornoch to Loch Fleet	-	*16*		*27*	*33*	*62*	*56*	*58*	*70*	*68*	*70*	-	*76*	*79*
Loch Fleet to Dunbeath	-	*92*		*214*		*145*	-	-	-	-	-	-	*113*	*163*

*Note that the 1992 and 1994 Moray Firth Totals both include the data from 1993.

[1]Thermal imaging survey

Table 4. Numbers of common seals in the Firth of Tay during August.

Location	13 Aug 1990	11 Aug 1991	07 Aug 1992	13 Aug 1994	13 Aug 1997[1]	12 Aug 2000	11 Aug 2002	7 Aug 2003[2]	10 Aug 2004	8 Aug 2005	9 Aug 2005	14 Aug 2005[1]	14 Aug 2006
Eden Estuary	31	0	0	80	223	267	341	93	78	81	95	139	90
Abertay & Tentsmuir	409	428	456	289	262	153	167	53	126	80	26	82	34
Upper Tay	27	73	148	89	113	115	51	83	134	90	80	104	91
Broughty Ferry & Buddon Ness	0	169	169	117	35	165	109	232	121	68	125	36.	127
Firth of Tay Total	**-**	**670**	**773**	**575**	**633**	**700**	**-**	**461***	**459**	**319**	**326**	**361**	**342**

- [1]Thermal imaging survey
- [2]In August 2003 low cloud prevented the use of vertical photography;

  counts were from photographs taken obliquely and from direct counts of small groups of seals.

Table 5. Number of common 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. 1990	2.8.91 11.8.91	1.8.92 16.8.92	8.8. 1993	6.8.94 12.8.94	5.8.95 15.8.95	2.8. 1996	2.8.97 8.8.97	7.8.98 14.8.98	3.8.99 13.8.99	4.8. 00 12.8.00	4.8. 2001	11.8.02 12.8.02	9.8.03 10.8.03	6.8.04 14.8.04	09.8.05	15.8.06
Blakeney Point	701	- 307	73	- -	- 217	267	- 196	438 392	372	250 371	535 738	715 602	895 disturb	772	346 631	399	577 715	741 677	719
The Wash	3087	1531 1580	1532	1226 1551	1724 1618	1759	2277 1745	2266 1902	2151	2561 2360	2367[1] 2381	2320 2474	2528 3029	3194	3037 2916	2529 2497	2126 2167	1768 2124	1695
Donna Nook	173	- 126	57	- -	18 -	88	60 146	115 36	162	240 262	294 201	321 286	435 345	233	341 -	231	242 346	372 470	299
Scroby Sands	-	- -	-	- -	- -	-	61 -	- 49	51	58 72	52 -	69 74	84 9	75			49 64		71
The Tees	-	- -	-	- -	- -	-	- 35	- -	-	- -	- -	- -	- -	-	-		- -	-	
Holy Island, Northumber-land	-	- -	-	- -	- -	-	13	- -	-	12[2]	- -	- -	10	-	-		- -	17[2]	
Essex, Suffolk & Kent	-	- -	-	- -	- -	-	- -	90 -	-	- -	- -	- -	- -	-	- 72	190	- -	101	

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

[2]Holy Island surveyed by helicopter using a thermal imaging camera

Survey year	1991	1993	1997	2001	2006
Orkney		7873	8523	7752	4256
Shetland	4797	6224	5991	4883	3021
Total (Orkney & Shetland)	4797	14097	14514	12635	7277

Survey year	1992	1996	2000	2003	2006
Outer Hebrides*	1760	1847	1401	1247	1263
Outer Hebrides**	2329	2820	2413	2098	

*Excludes Benbecula and North Uist

**Includes Benbecula and North Uist

Table 6. Number of harbour seals counted in Orkney and Shetland in surveys carried out between 1991 and 2006.

Dave Thompson, Callan Duck and Mike Lonergan

A retrospective description of regional patterns in grey seal pup production trends in the UK

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Summary

This paper presents a summary of the population trend analysis from Duck *et al.* (in press), which also describes the pup production estimation model. Pup production trajectories differ between areas. Older Hebridean colonies have declined since 1984, at 1.2% p.a. Fitted logistic models suggest that the Inner Hebrides and the Monachs populations levelled off in the mid 1990s, the Orkney population is also approaching an asymptote, but the effect is less pronounced and more recent. The North Sea population shows no evidence of density dependent effects. The UK grey seal population is approaching some form of asymptote after decades of continuous growth, while the West Atlantic population continues to grow exponentially.

Pup production trajectories are highly variable within sub-regions; e.g. in Orkney 80% of the increase between 1984-2002 occurred at only six colonies.

Methods

Simple exponential and logistic growth models were fitted to the pup production estimates (Jeffries *et al.* 2003; Brown *et al.* 2005). The exponential model assumed density independent growth at constant annual rate. The logistic model assumed density dependent growth described by

$$N_t = N_{t-1} * R\left[1-\left(\frac{N_{t-1}}{K}\right)^Z\right]$$

where N_t is the pup production in year *t*, *R* is the intrinsic rate of increase, *K* is the carrying capacity and *Z* determines when the density dependent effects operate.

We assumed that the true pup production N_t in any year was equal to the model estimate C_t plus an error term that was approximately independently, normally distributed with an expectation of zero and a constant coefficient of variation. This allows us to approximate the log likelihood of the data under the model as

$$\ln L = -\frac{1}{2}\ln\left[\sum_{t=1}^{T}\left(\frac{(C_t - N_t)}{N_t}\right)^2\right]$$

The breeding colonies fall naturally into four geographical sub-populations: Outer Hebrides, Inner Hebrides, Orkney and the North Sea. Because of observed differences in the pup production trajectories in the different sub-populations, we fitted growth models to each subpopulation independently. Relative goodness of fit of exponential and logistic models was assessed using likelihood ratio (LR) tests.

Results

The full time series of pup production estimates is shown in (reference to the Duck paper SCOS 01/06). For the purposes of examining time series the colonies have been aggregated into the usual four regional sub-populations; Inner Hebrides, Outer Hebrides (including North Rona), Orkney and North Sea (Isle of May, Fast Castle, Farne Islands, Donna Nook).

The pup production estimates for the UK population of grey seals have increased throughout the monitoring period. Between 1961 and 2003 the average annual rate of increase in pup production was 5.0% (95% c.i. ± 0.30%). Due to changes in both survey methodology and estimation procedures, it is difficult to compare pup production estimates pre and post 1983. Since 1984 the methods have remained constant and pup production estimates are directly comparable.

Between 1984 and 1996 estimates of the total number of pups born at regularly surveyed colonies increased year on year, with the exception of 1988. The 1988 pupping season coincided with the phocine distemper outbreak in European harbour and grey seals (Dietz *et al.* 1989). In recent years, the total pup production appears to have been more variable. Since 1996 the estimated total pup production has oscillated; pup production fell in 1997, 1999 and 2002. Over the period 1984 to 1996 the total pup production closely followed an exponential growth curve with an annual rate of increase of 6.9% (95% c.i. ± 0.70%). Fig. 1 shows the temporal pattern of residuals from this fitted relationship. After 1996 the residuals become increasingly negative, indicating that the growth rate has decreased since the mid 1990s.

The patterns of increase of pup production differ between areas with several regions apparently exhibiting a decreased growth rate in recent years and others apparently continuing to grow exponentially. Data for each of the sub-regions were used to fit both simple exponential and logistic growth curves (Fig. 2). The Outer Hebrides were further subdivided into the Monach Isles, a group of islands that were inhabited by people until the 1940s and only then became available for seal breeding, and the rest of the Outer Hebrides that were all established grey seal breeding colonies before monitoring began.

Pup production on the older Outer Hebrides sites has gradually declined since 1984, at a rate of 1.2% p.a. (Fig. 2a). The growth of the colonies in the Inner Hebrides and at the Monach Isles in the Outer Hebrides show clear signs of levelling off. Logistic growth models provided significantly better descriptions of the growth patterns than exponential models in both the Inner Hebrides and the Monachs (Inner Hebrides LR= 23.7, d.f.=2, $p<0.00001$; Monach Isles LR = 36.8, d.f.=2, $p<0.00001$). The timing of the density dependent effects was similar in the two areas; fitted logistic curves reached 95% of the fitted 2003 level in 1994 in the Inner Hebrides and 1995 in the Monach Isles (Fig. 2b & 2c). The Orkney trajectory was also significantly better described by a logistic growth model (LR= 15.8, d.f.=2, $p<0.0004$), but the density dependent effect is less pronounced and the population has approached its carrying capacity more recently; fitted logistic curve reached 95% of the fitted 2003 level in 2001 (Fig. 2d). The North Sea population does not currently display any evidence of density dependent effects (LR= 0.73, d.f.=2, p=0.70), and is best described by a simple exponential growth curve with a rate of increase of 6.5% p.a. (Fig. 2e).

Within sub-regions, pup production has not changed in parallel at all colonies. For example, 80% of the increase in pup production in Orkney between 1984 and 2002 was a consequence of changes at only six colonies (Lingaholm, Faray, Swona, Stroma, Holm of Huip and Copinsay) and three new colonies, founded since 1990 (Copinsay, Stronsay and Calf of Eday), now contribute >26% of the entire Orkney pup production.

Fig. 3 shows the pup production estimates for North Rona, a large and isolated breeding colony approximately equidistant between the Outer Hebrides and Orkney colonies. There are marked declines in production between 1984 and 1989, and again between 1993 and 2002. These declines coincide with periods of research work carried out at North Rona. However, similar trends are apparent in the pup production estimates from the other older colonies in the Outer Hebrides that are topographically similar to North Rona (Fig. 3) but are remote and have experienced no disturbance over the study period.

Discussion

Bowen, McMillan & Mohn (2003) describe sustained exponential population growth on the Sable Island colony, which represents the majority of the West Atlantic population of grey seals. Conversely, the UK breeding population shows clear signs of approaching some form of asymptotic limit. At present we do not know what mechanism is controlling the growth rates, but the close fit to logistic growth models indicates some form of density dependent control of population growth. It is also clear that the timing of these effects varies between regions and it has been suggested that density dependent effects may be operating at the individual colony level (Gaggiotti *et al.* 2002).

A standard method of monitoring dispersed populations, such as the grey seal breeding population, is to select and intensively monitor indicator sites. The observed, uncorrelated, inter-annual variations in pup production at neighbouring colonies mean that it is not possible to monitor total production by counting only a few, important, colonies.

In fact, monitoring selected 'indicator' sites could have led to incorrect management decisions in at least two ways. Firstly, selection of any site would be unlikely to provide a consistent index of population trajectory. Secondly, the sensitivity of survey method, as shown by the apparent population response to the PDV epidemic in 1988, raises the possibility of using the survey methods to monitor transient effects on pup production. Examination of the North Rona trajectory in isolation appeared to indicate a possible correlation between research activity and declines in pup production. However, examination of the synoptic survey data for undisturbed but topographically similar colonies in the Hebrides showed similar patterns of decline that could not be linked to research effort on North Rona.

Within the Hebrides there is an apparent relationship between growth rates and topography. Pup production at the older 'traditional' grey seal colonies of Gasker, Coppay, Shillay, Haskier and North Rona has either stabilised or declined since 1980 and all of the increase in pup production since then has occurred on the relatively new colonies on the Monach Islands. These older colonies are topographically similar in that the breeding sites are on the grassy/muddy tops of steep sided islands with limited access to the sea. The fast growing colonies are typically found on low-lying islands with extensive beach areas and wide unrestricted access to the sea. It may be that this represents the preferred breeding habitat for grey seals and that the observed distribution of breeding colonies pre 1960 was constrained by the pattern of human habitation. For example, the Monach Isles were inhabited until the 1940s and some have until recently been occupied during the breeding season. The observed trajectories could be explained by a large bias in recruitment towards the Monach Isles once they became available. It is not immediately obvious why there should be such differences in recruitment between sites. One interesting possibility is that the older traditional sites may have provided sub-optimal breeding conditions and were used primarily because more suitable habitat was not available. This may also account for the apparently high pup mortality on North Rona. If true, this could have important implications for conservation of other seal species. Concentrating on protecting current breeding sites for severely depleted populations such as Mediterranean and Hawaiian monk seals (Monachus monachus & M. schauinslandi) seals may be a sub-optimal conservation strategy.

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Jeffries, S., Huber, H., Calambokidis, J., & Laake, J. (2003) Trends and status of harbor seals in Washington state: 1978- 1999. *Journal of Wildlife Management*, 67, 207-218.

Fig. 1. Combined pup production at all grey seal colonies that have been monitored annually using a consistent methodology since 1984, with an exponential growth derived from data for 1984 to 1996 and showing residuals for the period 1984 to 2003.

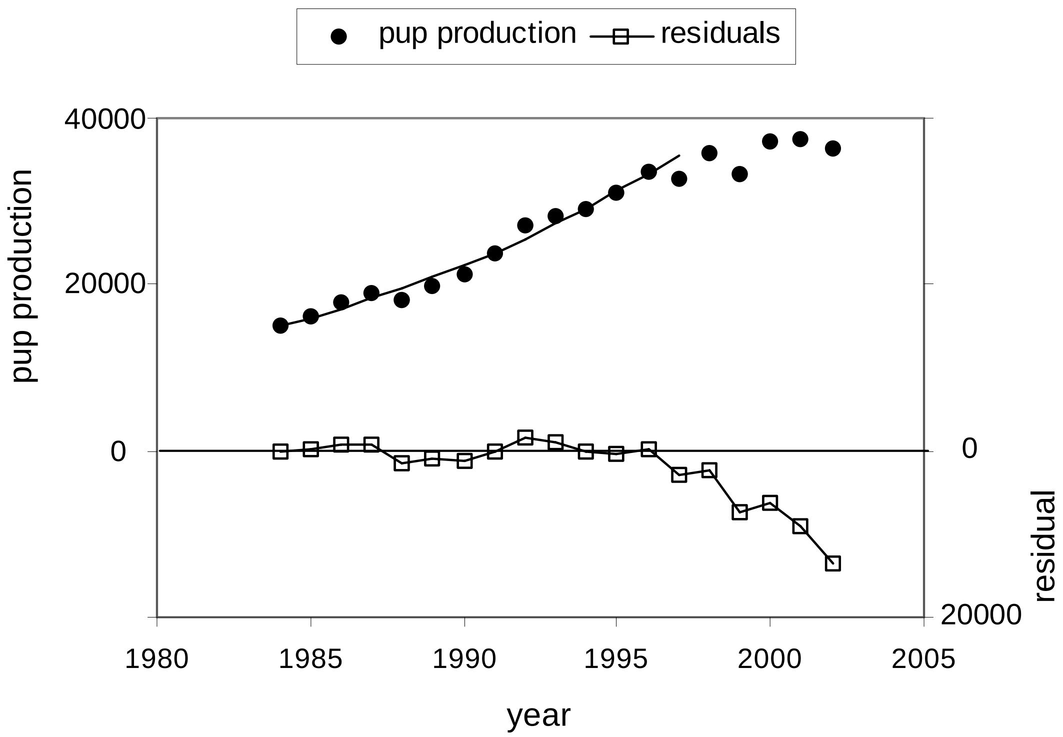


Fig. 2. Estimated pup production in five geographical sub-regions with best fit growth models: a) old Outer Hebrides (exponential decline); b) Monach Isles (logistic growth); c) Inner Hebrides (logistic growth); d) Orkney (logistic growth); e) North Sea (exponential increase)

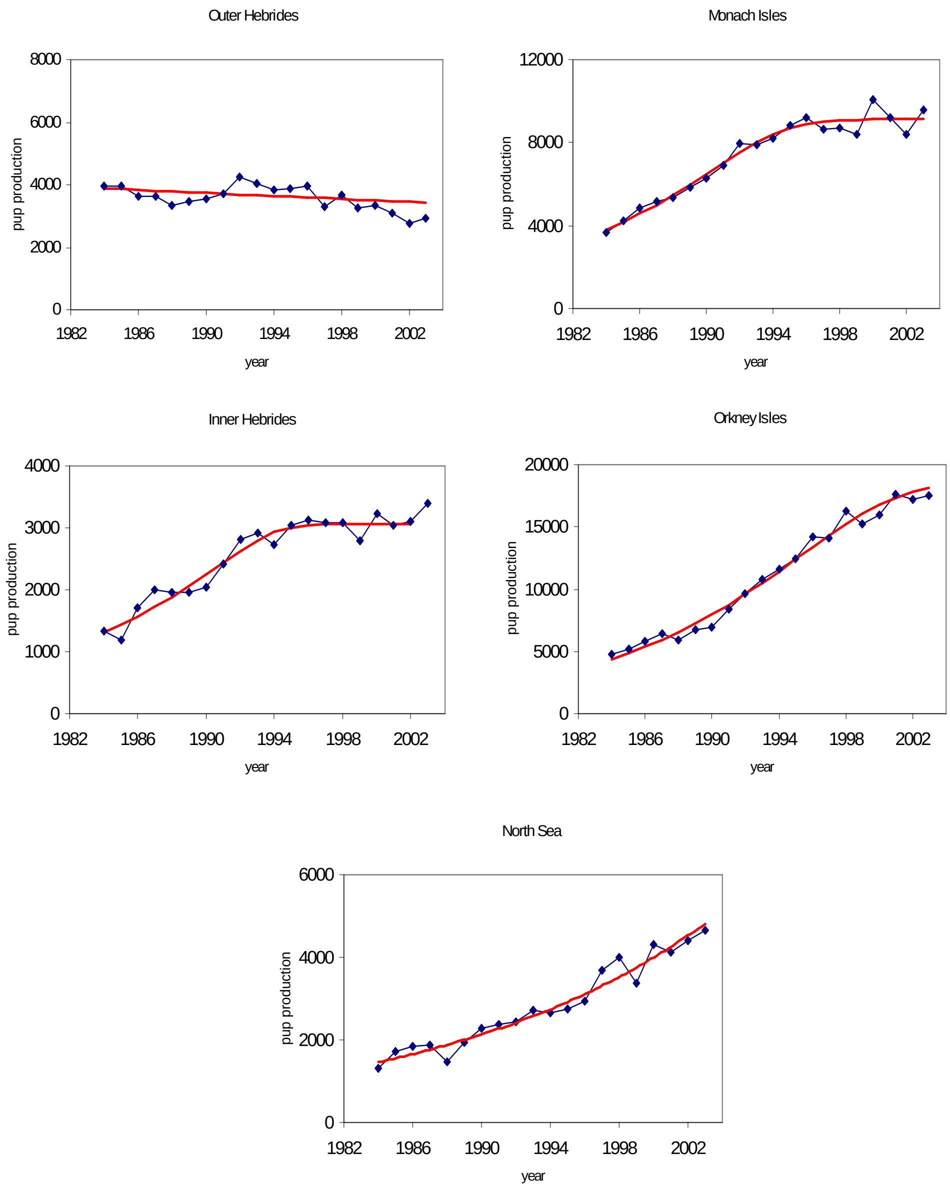
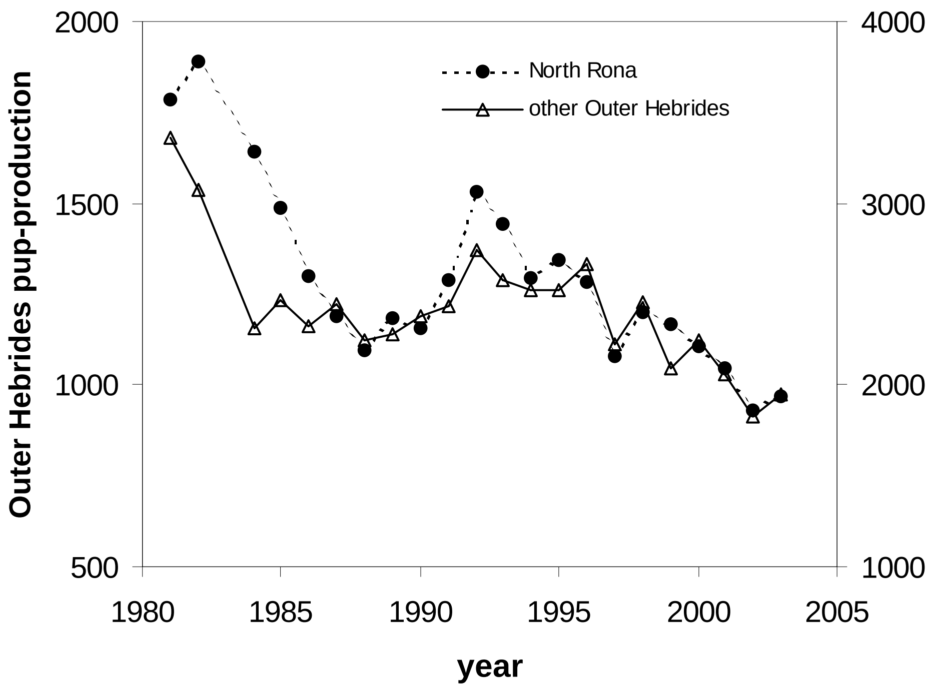


Fig.3. Variations in estimated pup production at the North Rona colony and at the other old (i.e. excluding the Monach Isles) established Hebridean colonies.



J. Matthiopoulos, G.M. Aarts & C.D. Duck

Defining management areas for UK grey seals

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Summary

We use standard clustering algorithms to objectively group grey seal breeding colonies according to the at-sea distances between them. We discuss the appropriateness of defining management areas on the basis of these results.

1. Introduction

Defining optimal management areas for UK seals requires us to come up with an arrangement of relatively isolated groups of colonies (both haulout and breeding). The motivation behind this requirement is that management actions taken in one region, have minimal impact on the others. Quantifying isolation requires some concept of distance, the most naïve of which is Euclidean distance in geographical space. An improvement on this metric, for marine mammals, is provided by at-sea distance. In this paper, we use clustering algorithms to subdivide grey seal breeding colonies into groups according to at-sea distance.

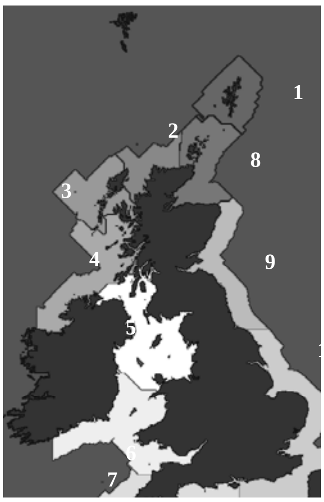

Figure 1: The 10 regions resulting from a clustering of breeding colonies by at-sea distance.

2. Methods

The locations of 115 breeding colonies around the coasts of the UK were extracted from the database maintained by SMRU for the purposes of the annual aerial survey. The matrix of pair-wise, at-sea distances between them was calculated using an algorithm developed in-house (Matthiopoulos, unpubl.). The matrix was used as input to the “cluster” package in R (R Development Core Team 2004) to define 10 clusters of colonies.

3 Results

To visualize the results, we first generated a buffer zone around the entire UK coastline, allocated each point in that zone to the nearest breeding colony and then to the cluster to which the colony belonged (Fig. 1). There were considerable similarities between the resulting map and the more empirical version suggested by Duck et al. (2005).

4 Discussion

There are three points to consider in interpreting the map in Fig. 1. First, it was based on breeding colonies only. Although the distribution of breeders is an important consideration in defining management units, it should carry no more *a priori* importance than the distribution of foragers. There are limited data and almost no analytical work on the connectedness between grey seal breeding colonies and haulouts. It is therefore not possible to produce a combined (breeding/haulout) metric suitable for clustering.

Second, geographical distance is not necessarily the only determinant of isolation. It is unlikely that distance imposes a physical impediment to transitions between colonies since grey seals are capable of traveling between any two breeding colonies, many times over, between two breeding seasons. A more suitable and direct measure of isolation is the probability of transition between any two colonies as a function of local environmental characteristics, density dependence, geographical distance and site fidelity. We are currently conducting work in this direction.

Finally, the number of clusters was selected arbitrarily. It is easy to change this number, or use automatic selection criteria to come up with a number of clusters that optimizes some generic criterion. However, ideally, the number of clusters should be directly linked to the degree of isolation that is required by management. This, in turn, should be determined by population models that predict the impact of local decisions on global or neighbourhood dynamics.

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P.S. Hammond, K. Grellier & R.N. Harris.

Grey seal diet composition and prey consumption in the North Sea and west of Scotland

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THE TEXT OF THIS PAPER IS DRAWN FROM DETAILED REPORTS TO SEERAD-SNH AND TO DEFRA. THESE REPORTS WILL BE PUBLICLY AVAILABLE AT THE END OF AUGUST

Introduction

The grey seal is a major marine predator in British waters. Its large size and increasing numbers since the 1960s have resulted in concerns amongst some fishermen, who have called for culls or other means to control the population. The focus of this debate has been the North Sea, although the same issues occur off western Scotland.

Essential information for assessing the impact of grey seals on fisheries includes which species of fish are taken and how much is consumed. Reliable information has previously come from the analysis of hard prey remains recovered from scats collected at seals' haul-out sites. However, for most areas, the most recent information available dates back to 1985. Since then, there have been declines in stocks of most commercially exploited fish species that are major grey seal prey items around Britain, and the grey seal population has increased markedly. Updated estimates of grey seal diet are needed to inform seal management policy in relation to the impact of an increasing grey seal population on declining fish stocks.

The objectives of these projects were:

- To estimate grey seal diet composition in the North Sea (including Orkney and Shetland) and off western Scotland.
- To estimate consumption of commercial fish species by grey seals in these areas in 2002.
- To investigate seasonal and regional variation in grey seal diet.
- To relate changes in grey seal diet composition and consumption between 1985 and 2002 to changes in relative and absolute abundance of fish prey.

Methods

At the Gatty Marine Laboratory captive seal facility, initial trials to determine experimental protocols were conducted. Then, 86 feeding trials with seven grey seals and 18 prey species were conducted to derive estimates of species- and grade-specific digestion coefficients (to account for partial digestion) and recovery rates (to account for complete digestion).

Diet composition and prey consumption were estimated using scat sampling methods. Scats were collected on a monthly or quarterly basis throughout 2002 along Britain's North Sea coast, in Orkney and Shetland, and off the west coast of Scotland. Fish otoliths and cephalopod beaks recovered from scats were identified and measured. Each otolith was graded for the amount of digestion.

The methods used to estimate diet composition and prey consumption by grey seals broadly followed those used in previous analyses of grey seal diet by the Sea Mammal Research Unit. For diet composition, measurements of fish otoliths and cephalopod beaks recovered from scats were used to estimate the weight of prey associated with each structure, which were summed over species and expressed as percentages in the diet by weight. For consumptions, the amount of prey in the scat samples was converted to energy, equated to estimated energy requirements for the population in the region, converted back to weight, and expressed as tonnes consumed per annum. These methods were used to reanalyse the data from 1985. Estimates of quantities of fish consumed were then compared with estimates of fish stock biomass for 1985 and 2002 from ICES assessments.

Results

The experiments resulted in revised estimates of digestion coefficients to account for partial digestion of otoliths as they pass through the gut of a seal and the first estimates of recovery rates to account for complete digestion of otoliths by grey seals. These new data significantly improved the analyses and allowed a direct comparison with the reanalysed data from 1985.

The comprehensive coverage of scat sampling, both seasonally and regionally, forms the basis of a set of reliable estimates of diet composition and prey consumption that will form an important benchmark for the future.

Diet composition: Western Scotland

Sandeel, gadoids and herring were the main prey of grey seals in the Hebrides area in 2002. Benthic species (especially in the Inner Hebrides) and flatfish (especially in summer) were also important.

In the northern Inner Hebrides, dragonet, sandeel, cod and haddock were the main species in the diet. In the Minch, the diet was dominated by sandeel in quarter 1, and by cod, haddock, ling and sprat in the rest of the year. In the southern Inner Hebrides, sandeel and cod were the main prey. Sandeel dominated the diet in all seasons in the northern Outer Hebrides, with herring (quarters 2-4), cod (quarter 1) and ling also important. In the Monach Isles, the dominant species in the diet were sandeel (particularly in quarters 1 and 4) and herring (particularly in quarters 2 and 3). Gadoids made up most of the rest of the diet throughout the year, especially ling and rockling in quarter 1, and cod and haddock in the rest of the year. In the southern Outer Hebrides, sandeel (mainly in quarter 1) and gadoids (especially haddock) were dominant and plaice was a significant contributor to the diet in quarters 2 and 3.

We found limited evidence of changes in grey seal diet composition in the Hebrides in 2002 compared to 1985. The main differences overall were a decreased proportion of sandeel and an increased proportion of herring in 2002 compared to 1985. Among the gadoid species, the contribution of cod to the diet remained about the same, haddock increased and ling decreased in 2002 compared to 1985. Species that featured strongly in the diet in 2002 but not in 1985 included lemon sole, rockling, bullrout and dragonet. Megrim contributed about 7% to the diet in 1985 but was virtually absent in 2002.

Diet composition: North Sea

We found marked changes in grey seal diet composition between 1985 and 2002 in the North Sea. The core species (sandeels, cod and other gadoids) were similar in both time periods, but the proportions they contributed were different both regionally and seasonally. At Donna Nook, benthic prey (dragonet and seascorpions) were more important and sandeel less important in 2002 than in 1985. Much less cod and much more whiting were consumed in 2002 compared with 1985. In the central North Sea region, the general changes were less pronounced; the percentage of gadoids in the diet was lower and the percentage of sandeel was higher in 2002 compared with 1983-88. Within the gadoids, however, the percentage of cod in the diet overall declined almost 5-fold, and the percentage of haddock increased by an order of magnitude. In Orkney, the overall change in diet between 1985 and 2002 was dominated by an increase in the percentage of gadoids and a decrease in the percentage of sandeel. There was a particularly large increase in the percentages of cod and haddock taken in the first quarter of the year. In Shetland, the diet was greatly dominated by sandeel, with some gadoids.

Consumption estimates: Western Scotland

Estimated annual consumption of prey by grey seals in the Hebrides area increased between 1985 and 2002 from 53,000 tonnes to 77,000 tonnes, in line with the increase in the grey seal population in this area.

The amount of sandeel, cod and whiting taken per seal declined between 1985 and 2002, whereas the amount of herring and haddock consumed per seal increased three-fold.

Consumption estimates: North Sea

Estimates of annual consumption of commercially important fish prey by grey seals in the North Sea increased markedly from 39,000 tonnes in 1985 to 116,000 tonnes in 2002, in line with the increase in population size. The estimated amount of sandeel consumed increased from 29,000 t in 1985 to 69,000 t in 2002, and estimated consumption of cod increased from 4,100 t to 8,300 t.

The amount of cod taken per seal declined slightly between 1985 and 2002. The amounts of haddock and plaice taken per seal increased markedly between 1985 and 2002.

Comparison of estimated consumption with estimates of fish stock size

In the North Sea, grey seal predation was not significant in the North Sea in 1985; estimated prey consumption was less than 1% of estimated total stock biomass (TSB) for all species. In 2002, consumptions relative to stock size of most prey species were several times higher but only for cod (3.7%) sandeel (2.7 %) and plaice (1.5 %) were the percentages greater than 1%.

West of Scotland consumption of most assessed species in 1985 was small relative to stock size (less than 5% of estimated TSB) except for cod and megrim. In 2002, estimated consumption of all species (except megrim) was higher than in 1985, both in absolute terms and relative to stock size. These comparisons suggest that, for some species, consumption relative to stock size was approximately five times higher in 2002 than in 1985.

These relative changes between 1985 and 2002 are caused by a combination of three factors: an overall increased consumption of prey by grey seals (driven by the increase in seal numbers); changes in diet composition; and declines in most assessed fish stocks.

Discussion

The question of the impact that grey seals may have on fish stocks and, therefore, fish catches is an important one in light of the results presented here. Might grey seals limit the ability of cod, especially, and other gadoid stocks to recover in the North Sea and/or west of Scotland? Alternatively, might declines in fish stocks impact grey seal population growth in these areas? We are unable to answer these questions but to help address them a model of grey seal interactions with their prey would be a useful tool. Defra has previously supported the development of such models; they should be further developed and parameterised with results from this project to address this and other management-related questions.

Grey seal diet should be reassessed in the relatively near future. In addition, the diet of harbour seal populations should be systematically assessed as a priority.

Ailsa.J. Hall

Improving knowledge and understanding of the main sources of seal mortality in the UK

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NOTE: THIS PAPER AND ITS CONTENTS SHOULD NOT BE REFERENCED WITHOUT PRIOIR PERMISSION OF THE AUTHOR

Summary

Information and knowledge about the main sources of seal mortality in the UK could be obtained using a number of different approaches. The indirect methods that employ, for example mark-recapture studies, to determine the importance of various factors on survival probabilities are limited in their utility as inferences can only be made using group and individual covariates of survival that are monitored at the time of marking. Direct methods can either estimate deaths due to specific sources of mortality (such as deliberate killing and by catch in fishing gear) or in the case of strandings schemes, might establish the different causes of death following post mortem examination of carcasses the wash ashore. There are disadvantages and biases associated with all these methods therefore an integrated approach would be recommended, utilizing data from all possible sources. Future mortality studies should be systematic, standardized and implemented over a sufficiently long time period given the small sample sizes that are likely to be obtained on an annual basis.

Introduction

This paper deals with the question to SCOS – "What sort of work might be done to improve our knowledge and understanding of the main sources of seal mortality?" It outlines the approaches that could, and to a limited extent that have, been taken in the UK in the past to answer this question. It also summarizes the advantages and disadvantages associated with each method.

Methods

Indirect

The probability that animals will survive a given time period can be estimated indirectly, using mark-recapture studies. In addition to estimating annual survival probabilities, these studies can be used to investigate the importance of various factors in determining mortality. Long-term monitoring of permanently marked adult populations, such as those being conducted on North Rona and the Isle of May (Pomeroy, Twiss & Duck, 2000; Pomeroy, Twiss & Redman, 2000), can be used to investigate adult female survivorship and temporary marks can be applied to younger age classes for shorter-term survival studies. Indeed this method has been applied to grey seals during their first year of life using both passive 'hat' tags and mobile phone tags. Factors investigated as important predictors of mortality during this life stage included pupping site, mass and condition at weaning and immunity (Hall, McConnell & Barker, 2001; Hall, McConnell & Barker, 2002). Interestingly, maternally transferred persistent organic pollutants were not significant predictors of first year survival (Hall & Thomas, 2005). However, these studies are very limited in their applicability and can only be used to investigate the role of potential sources of mortality where any covariates of interest can be recorded for each individual or group at the time of marking.

From an epidemiological perspective, certain correlational study designs might be applicable to questions regarding sources of seal mortality, although they have much less power and can only at best be used to generate hypotheses. For example, juvenile survival rates, monitored using mark-recapture methods in populations with different exposure profiles (e.g. with contrasting contaminant levels or disease exposure rates), might suggest potential sources when different mortality estimates among populations are observed.

Direct

There are several methods by which seal carcasses might be obtained for mortality studies.

Deliberate killing
A number of animals are shot each year and those taken under license should be reported to the Scottish Executive and DEFRA. These numbers might give estimates of mortality due to such fisheries interactions and if carcasses could be recovered for post mortem examination some limited information on the potential causes of mortality or morbidity from various diseases (e.g. skin lesions and the occurrence of pox virus), as has been carried out in the past (Baker, 1987; See also Thomas and Harwood, 2004, SCOS Briefing paper 04/7). However, these animals do represent a biased sample of the population.

Live captures
SMRU has a Home Office License to capture and release seals and associated morbidity data could be collected on all animals sampled. This may also allow potential sources of mortality to be investigated where captured animals were diagnosed with conditions likely to be terminal (e.g. malnourishment, net entanglement or severe skin disease). However, this is limited in its range and power since most animals captured are overtly healthy. Disease surveillance through, for example, serology surveys could be (and to a very limited extent are being) obtained.

By catch
Since the 1950s a flipper tagging database has been maintained and collated by SMRU. This includes seals tagged both by SMRU and by other organizations such as the seal rescue centers and the University of Aberdeen. The location of tags and tagged seals found largely by members of the public (reported via London Zoo) are recorded, together with any related data on potential cause of death. Occasionally fishermen report the by-catch of tagged seals but a low return rate means the dataset is very limited in its utility. Of the 24,205 tagging records in the database between 1951 and 2006, 332 (1.4%) were returned as fisheries by caught.

An observer scheme (deploying observers on board fishing vessels) for estimating the by catch of cetaceans in various specific fisheries has been funded by DEFRA since 2005 (see http://www.defra.gov.uk/wildlife-countryside/ewd/rrrpac/cetacean-bycatch/cetacean.pdf). In addition to the information on the cetacean species involved, observers often record data on by-caught seals. These data may then be related to the type of fishery, the vessel and possibly gear-type used in addition to the fishing effort. At present seals are *not* systematically recorded as they are not the primary object of the program. However, this scheme is due to continue in the short term and further useful data on seal by-catch rates might be obtained using the same or a similar observer scheme.

Strandings
Following the 1988 phocine distemper virus outbreak among European seals, a marine mammal strandings scheme was funded by DEFRA and SEERAD employing veterinary pathologists and technicians to carry out post mortem examinations on carcasses recovered ashore or on euthanazed live stranded animals. Although this long-term scheme has been running since the early 1990s, it has been limited to cetaceans, largely because of lack of funds. Specific funding for the investigation of the second outbreak of PDV in seals did allow for the collection of seal carcasses but this was limited to the duration of the outbreak. Over the last 14 years the cetacean scheme has produced some very valuable information, on sources of mortality and the influence of extrinsic factors such as persistent contaminant exposure (Hall *et al.*, 2006; Jepson *et al.*, 2003; Jepson *et al.*, 2005), see also http://www.defra.gov.uk/wildlife-countryside/resprog/findings/cetacean/index.htm for the final report for the period 1995-2000 and http://www.defra.gov.uk/wildlife-countryside/resprog/findings/cetacean05/cetstrand0005-full.pdf for the 2000 - 2004 report) and on some life history parameters for small cetaceans.

Despite the focus on cetaceans, seals have been recorded in the strandings database and post mortem investigations have been carried out on a small number of grey seals from England and Wales (n=33 between 1995-2000). The strandings scheme in Scotland is administered by the Scottish Agricultural College (SAC) Veterinary Investigation Centre and details of seals stranded north of the border since 1992 are included here (Reid, R.J. personal communication). A summary of the total number, species and estimated age of seals reported to SAC is shown in Table 1 and the number of grey and harbour seals recorded by year is shown in Fig.1. The decline in reports is largely due to the variable effort involved and the fact that when reporters realize that carcasses are not being collected for post mortem they tend not to report findings in future. However, these data illustrate the potential resource that could be available for studying the main sources of mortality, if a strandings scheme for seals as well as cetaceans was instigated. Although a large proportion of animals reported are pups and juveniles (Table 1) this does reflect the mortality rates for the different age classes, because juvenile mortality rates are high and adult mortality rates are very low.

Rescue and Rehabilitation Centres
A number of seal rescue and rehabilitation centers exist around the UK coast (SMRU issues tags to around 12 centres across the country) and this is also a potential source of information on mortality and morbidity in seals. According to our database a total of 2,338 seals have been tagged and released by these centres since 1985, 964 by the RSPCA Norfolk Wildlife Hospital. The vast majority of these are also pups and juveniles with only 16 adults recorded in the last 16 years.

Discussion

There are various advantages and disadvantages from each method of data collection and some of these are highlighted below.

***Indirect methods*:**

- ⇒ Integrated with other population monitoring studies
- ⇒ Provide probability estimates that are interpretable by stakeholders
- ⇒ But do not provide definitive causes of death
- ⇒ Limited to investigating factors hypothesized *a priori*
- ⇒ Need large sample sizes for short term studies or long term monitoring for older age classes

***Direct methods*:**

Deliberate killing

- ⇒ Positive identification of cause of death
- ⇒ Samples likely to be relatively fresh
- ⇒ Can provide associated morbidity information
- ⇒ But limited regionally
- ⇒ Biased sample of the population

Live captures

- ⇒ Provide information on morbidity that might lead to mortality
- ⇒ Provide disease surveillance data
- ⇒ Limited in range and power

By catch

- ⇒ Positive identification of cause of death
- ⇒ Can be related to different aspects of the fishery
- ⇒ Fresh carcasses
- ⇒ Morbidity data could also be collected
- ⇒ Restricted by cooperation of fishermen

Strandings

- ⇒ All causes of death investigated
- ⇒ Potentially many regions covered
- ⇒ But limited to proportion that wash ashore
- ⇒ Regions with inaccessible coastlines excluded
- ⇒ Carcasses often too decomposed for cause of death

Rescue and Rehabilitation

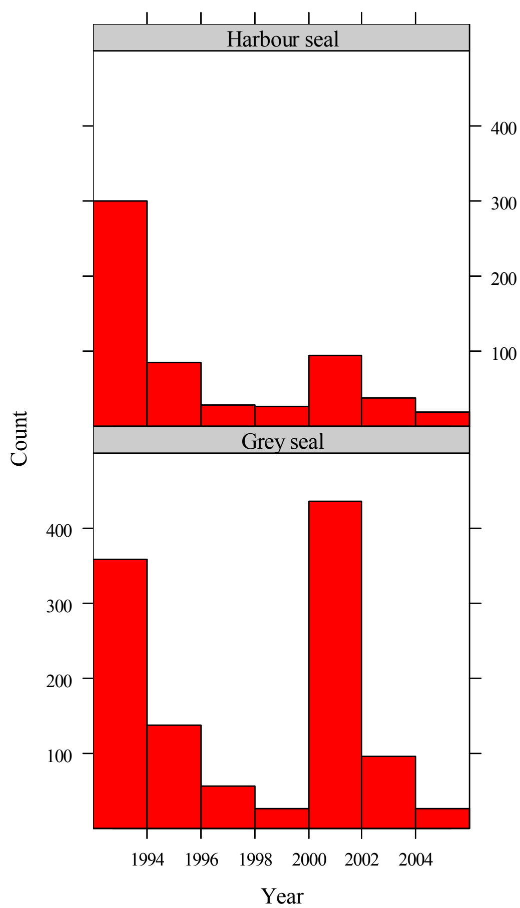
- ⇒ Freshly dead with associated health history prior to natural death or euthanasia
- ⇒ Limited by location

A preliminary study which brings together all the current information on sources of mortality – from the strandings and by catch schemes to the rescue centre data - would be a profitable first step and allow the strengths and weaknesses associated with each approach to be evaluated, with recommendations for modifications in the future.

Table 1. The number of seals reported to SAC, 1992-2006

Species	Pups	Adults and Juveniles	Unknown	Total
Grey	226	853	55	1134
Harbour	78	477	33	588
Hooded		7		7
Harp		1		1
Ringed		1		1
Unknown	117	787	67	971
Total	421	2126	105	2702

Fig. 1. No. harbour and grey seals reported to SAC by year



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Bernie McConnell

Summary of grey seal satellite telemetry haulout data available to parameterise population size models.

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Summary

Although we have gathered an extensive grey seal telemetry data set, it is spread over the factors of year, month, individual, age, sex, capture region and haulout site. Modelling the probability of hauling out will determine the importance of these factors. In turn this will determine whether the current data set is sufficient or whether there are important gaps, which need to be filled.

Introduction

In 2006 a proposal entitled "Putting long-term, population monitoring data to good use: The Causes of Density Dependence in UK grey seals" was submitted to NERC. The aim of this proposal was to provide a grey seal population estimate which is independent of (and thus would aid in the model selection within) the current candidate population models that are based on pup counts at the breeding season.

The proposal entailed aerial photographic surveys of the major grey seal haulouts outside the breeding season. These counts would be converted to population estimates by modelling the probability of haulout (and thus being available for counting) based on historical satellite telemetry data. The purpose of this paper is to summarise this telemetry data set.

Most of the data are from SMRU studies, but we also include data from collaborative studies and the permission of the relevant co-investigators is required (Dornoch Firth, Paul Thompson; Brittany, Cecile Vincent).

Methods

Haulout events, and how they are relayed ashore

In 1985 SMRU designed and deployed the first ever Argos satellite tag that successfully tracked a seal at sea. In 1991 we incorporated dive and haulout data in the uplink stream. Our philosophy was, and is, to process and compact data on-board in order to overcome the bandwidth constraints in relaying marine mammal data via the Argos system.

The 'status' of a tagged seal is assigned by the tag itself from one of three mutually exclusive choices: haulout, dive, and at-surface. A haulout starts when the tag is continuously dry for 10 minutes and ends when it is continuously wet for four minutes.

Haulout records are stored in an internal buffer as StartDatetime and EndDateTime. However, not all data collected can be transmitted through the limited bandwidth of the Argos satellite system. To avoid sampling bias, haulout data (and other data types) are selected for transmission from the buffer in a pseudo-random manner. For the purpose of this exercise, we need to know not only when a seal is definitely hauled out, but also when it is definitely *not* hauled out. The latter cannot be implied from just the absence of haulout records, since haulout records may be missing. Thus, from 1995 onwards, we also incorporated HauloutSequenceNumber into haulout records. Thus, from data received ashore, we can be certain that a seal was *not* hauled out if, and only if, the adjoining haulout records are consecutively numbered.

The tag also computes and transmits 6-h (in the more recent tags, 2-h) summary data which include the proportion of time spent hauled out in each period. This transmission format acts as a bias check on the haulout records received. But while the temporal resolution of 6-h is too coarse for the modelling the effect of, say, tide, the data are adequate for examining seasonal effects.

Post-processing haulout records.

There are number of attributes of a haulout site that may influence the probability of a seal hauling out. These include substrate, tidal availability and proximity to foraging sites. Thus it is important to assign a specific haulout site to a haulout record. In this section we outline how haulout records are mapped to specific haulout sites, how the data may be descretized through time, and how tidal status is appended.

Argos satellite location fixes are deficient in two respects when studying grey seal haulout behaviour: frequent low accuracy, and irregular and sparse in time.

1. Track accuracy can be increased by filtering out the most inaccurate location and then smoothing (e.g. independently GAM smoothing of latitude and longitude; pers. comm. Lonergan).
2. The smoothed track is then used to estimate the location of each haulout record.

From historical aerial surveys we know the major haulout sites in the UK. These are in the process of being catalogued in such a way that is useful to a number of studies within SMRU. The sites are tagged with hierarchical sites names are a variety of spatial scales to aid clumping of neighbouring sites.

3. The estimated haulout locations are snapped to the nearest catalogued haulout site. The snapping distance can be inspected to determine the aptness of each snap. Some haulout records are undoubtedly far from land and may occur in localised areas. Such records are infrequent (< 5% of total records) and are probably due to the seal resting at sea with the tag dry and. For the purpose of this exercise they are discarded.
4. The nearest Secondary Tidal Prediction Port is then assigned to each haulout record.
5. The aim of the modelling exercise will be to estimate the probability of a grey seal being hauled out. Thus haulout records are descretized into hourly point observations and the haulout status is assigned appropriately. NA values are assigned to the haulout status in the intervals between non-consecutive HauloutSequenceNumbers.
6. The tide phase and height at the local Secondary Tidal Prediction Port is then assigned to each hourly record.

For illustration, an example of haulout data processed to stage 6 is shown in Fig 1. for one grey seal. At this preliminary stage in the analysis it is important to note the high level of inter individual variability in haulout patterns

Extent of data.

In the last twenty years tag software has evolved and thus the quantity and quality of haulout information has changed through time. This complicates summarising the available data. A total of 225 grey seals (45% female) have been tracked of which 190 (85%) are post 1990 and thus have HauloutSequenceNumber in the haulout records. In the description of the data below we consider the complete set of 225 individuals.

a. Seal by capture region and date
Fig 2 shows the progression of deployments at different capture sites. Choice of site and year were determined mainly by the availability of funding.

b. Seals by capture region
Fig 3 shows that the numbers of seals are unequally spread between capture regions. However, since grey seals may range far, the distribution of haulout sites used will probably be of greater interest than where they happened to be caught. Most haulout records have yet to be assigned haulout sites in the process described above.

c. Coverage by year
Fig 4 shows that coverage is unequally spread across years. It would be highly interesting if year *per se* was a significant factor influencing the probability of hauling out. It could be that the proportion of time spent hauled out is inversely proportional to food availability.

d. Sex
45% of tagged animals were female.

e. Coverage by month and age.
Tags are glued to the fur of the seal and thus detach at the annual moult. In post weaned pups this moult is delayed for a year. Fig 5 shows the separate seasonal coverage for seals tagged as post-weaned “pups of the year” and of “not pups of the year”. The former shows greatest coverage from December (breeding) onwards. The latter illustrates the large number of deployments in early summer (post

moult) - the coverage being peaking in summer and tailing off into the breeding season in the latter part of the year. The rather ugly term “not pups of the year” includes both juvenile and adults. Seals may be aged from an extracted incisor, but this is not routinely done. However the morphometric measurements taken at capture give an approximate guide to age.

f. Tag longevity

Mean tag longevity was 132 days. However, the quantity of haulout (and other) data generally tailed off in the last few weeks of tag life - probably due to battery depletion. Longevity frequency distribution is shown in Fig 6. This variability illustrates the unequal contribution of each seal to the haulout records.

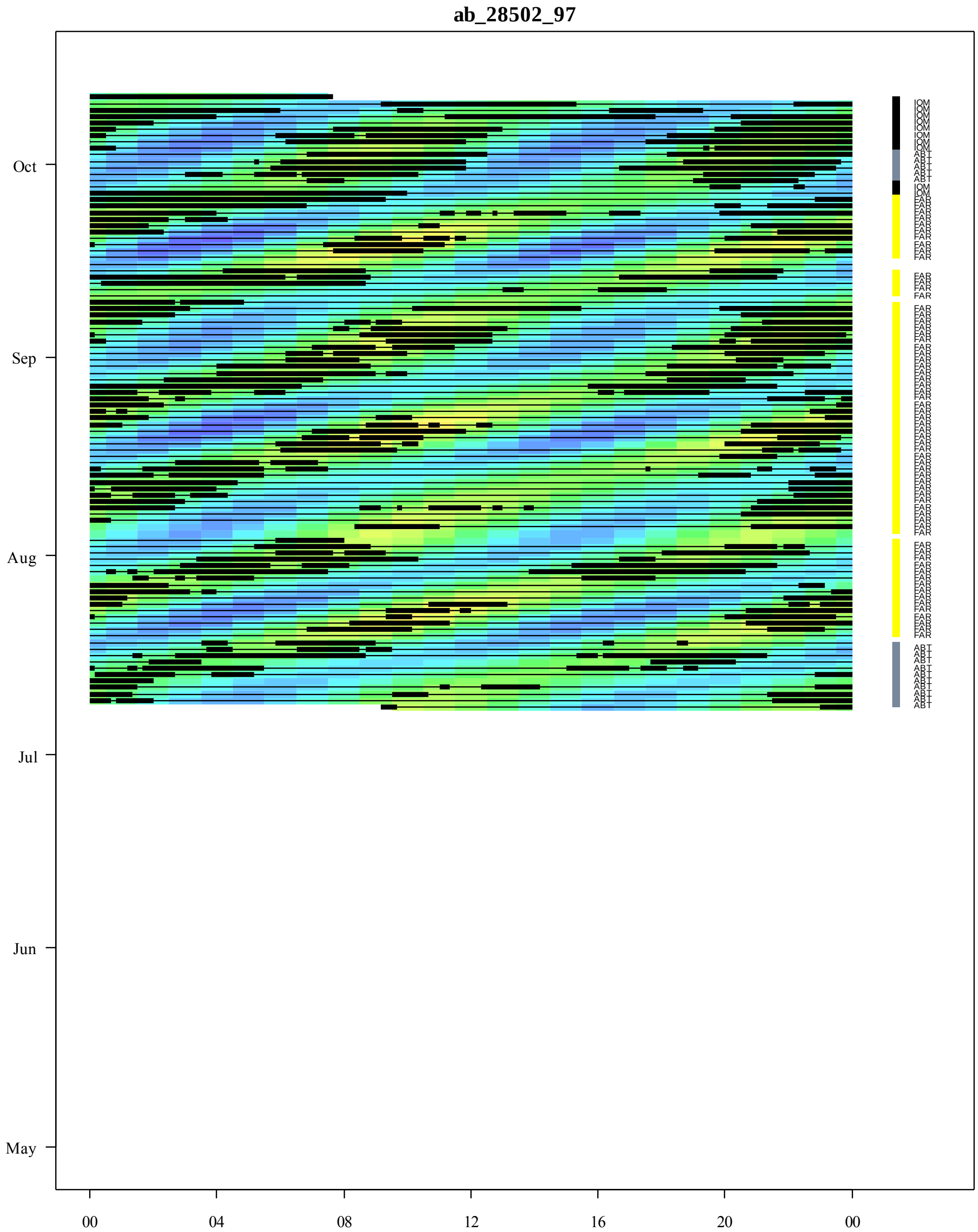


Fig 1. An example of post-processed haulout records. Thick lines show hauled out records. Thin lines show when the seal was definitely not hauled out (i.e. when the neighbouring haulout records had consecutive `HauloutSequenceNumbers.`

Tidal height is shown in background where green is low water and blue is high water

This grey seal hauled out primarily at the Farnes (yellow legend) and Abertay sites. There appears to be a regular pattern of hauling out at low water, but less during the afternoon.

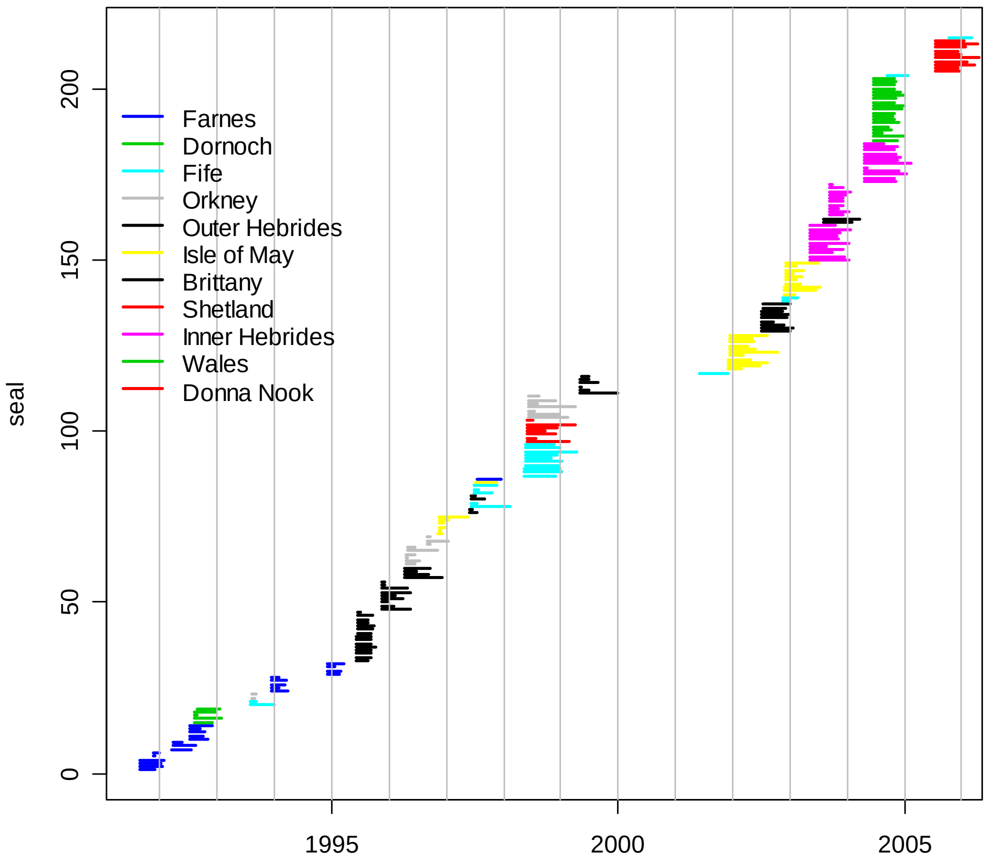


Fig 2. Deployments of tags on grey seals by date and capture region. Note that `HauloutSequenceNumbers` were only incorporated from 1995 onwards.

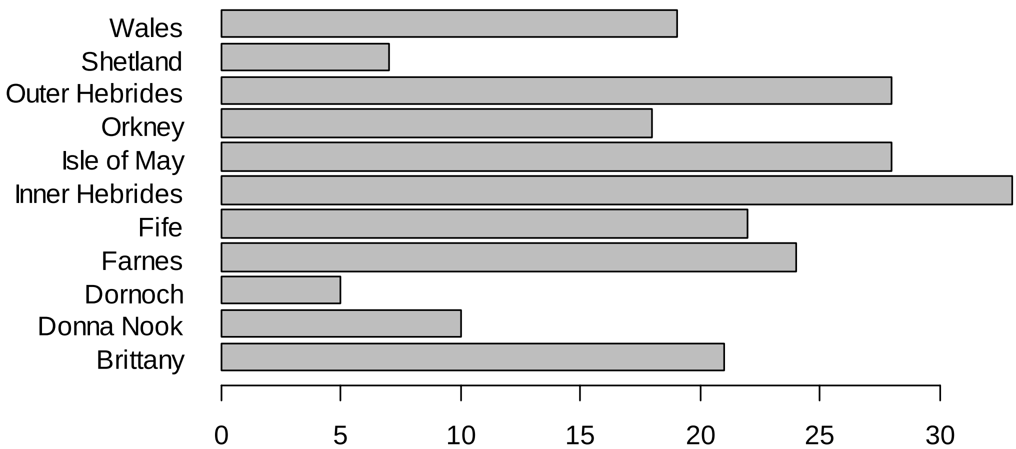


Fig 3. The number of grey seals tagged at different capture regions

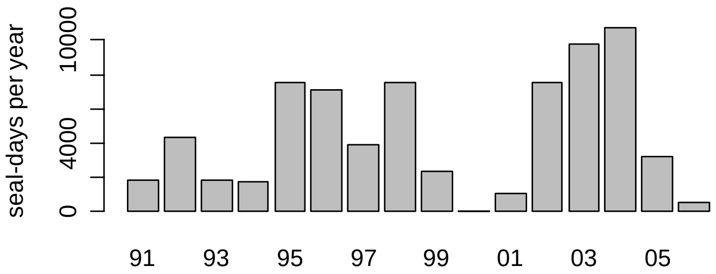


Fig 4. Coverage grouped by year

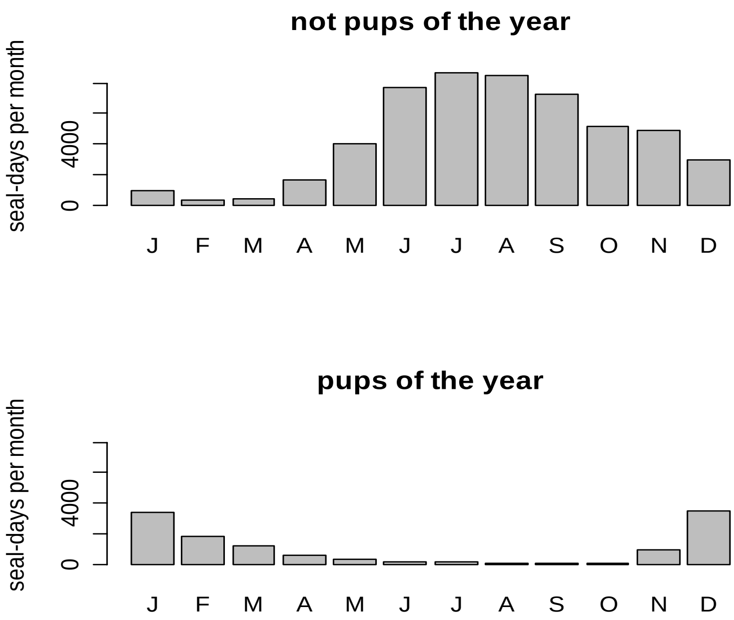
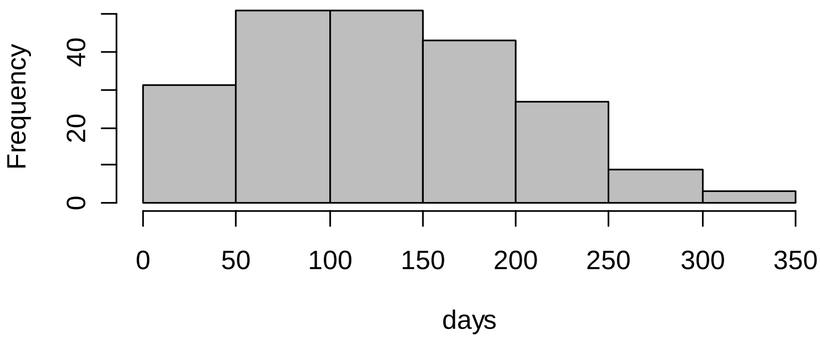


Fig 5. Seasonal coverage group by age class.

Fig 6. Frequency distribution of tag longevity.



I.M. Graham, D. Fowden & R.N. Harris

North Esk Acoustic Deterrent Device Trial

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Summary

A preliminary trial into the effectiveness of an Acoustic Deterrent Device (ADD) at deterring seals from a specific area of river and as a barrier to upstream movement of seals was carried out between January-May 2006 on the North Esk river. The ADD was switched on and off alternately for periods of several days from February-May and surveys were carried out to estimate the number of seals present. The results suggest that the ADD may have been effective as a barrier to seal movement upstream: seals were observed upstream of the ADD on only 7% of surveys when the ADD was operating compared to 39% of surveys when it was switched off. The ADD was not fully operative at all times, possibly explaining why the ADD was not 100% effective as a barrier. Once the seasonal trend in the use of the river had been accounted for, the ADD had no significant deterrent effect on the presence or abundance of seals within the survey area. This trial should be repeated in different situations to allow inferences to be made about the effectiveness of the ADD used over longer time periods, in different rivers, locations within a river or at other times of the year.

Introduction

Acoustic Deterrent Devices (ADDs) have been in use as anti-predator controls at marine salmon farms since the 1980s, but views on their effectiveness are equivocal (Quick, Middlemas & Armstrong, 2004). It has been proposed that ADDs could be used to assist in the management of seal-salmon conflicts by keeping seals out of rivers. The objectives of this study were to assess from a management perspective 1) whether or not seals could be effectively deterred from a specific area of the North Esk using an ADD and 2) to test its efficiency as a barrier to upstream movement of seals.

Methods

An ADD (Lofitech Seal Scarer; Lofitech AS, Leknes, Norway) was purchased by Martin Stansfeld and installed by Lofitech at Kinnaber Fishings on the North Esk on 4th February 2006. The ADD was switched on and off alternately for periods of 3-8 consecutive days in February and March 2006. The ADD was then switched on for the entire month of April and switched off for the entire month of May 2006. Surveys were carried out within 2 h of high tide from a fixed location on the north bank of the North Esk at Kinnaber Fishings, between January-May 2006. The number of seals present was estimated at the end of each survey and each time that a seal was observed at the surface during the survey, the species, location and time were recorded.

Work in other rivers has shown that seal abundance in rivers varies seasonally (Butler *et al.*, in press; Carter *et al.*, 2001; Middlemas *et al.*, 2006) therefore where a seasonal trend was detected, the effect of the ADD was tested accounting for this trend. The Generalized Additive Modelling function of the mgcv library (version 1.3-17) in R (version 2.3.1) was used to describe the underlying seasonal patterns in seal presence and abundance (Thompson, Lonergan & Duck, 2005) by fitting smoothing splines to the data (Wood & Augustin, 2002). The effect of the ADD on seal presence within the survey area and as a barrier to seal movement upriver was modelled with a binomial error distribution. The effect of the ADD on the number of seals observed within the survey area was modelled with a Poisson error distribution. As the time taken to carry out surveys was variable, the log of the survey time was used as an offset in the analysis of the number of seals observed. To standardize the surveys for the logistic regression analyses, only one hour per survey was considered: this was taken to be the last hour of the survey, for surveys ending before or less than thirty minutes after high tide, or the hour of the survey centred on high tide. This excluded two surveys with less than an hour of observation within an hour of high tide. All statistical analyses were carried out using R (version 2.3.1) and the significance of variables was assessed from the change in deviance (χ^2) caused by removing that term from the model.

Results

Seals were seen on 20 of the 57 surveys carried out between January-May 2006 (Table 1). On five of these, two or more seals were present during the survey. Both species of seal, common and grey, were observed in the survey area.

***Table 1**. Monthly breakdown of (a) the number of surveys carried out, (b) the number of surveys in which seals were present and (c) the number of surveys in which seals were observed upstream of the ADD with the ADD turned on and off.*

Month	ADD off			ADD on		
	a	b	c	a	b	c
Jan	6	4	-	0	-	-
Feb	9	6	5	11	3	1
Mar	10	4	4	11	1	0
Apr	0	-	-	6	2	1
May	4	0	0	0	-	-
Total	29	14	9	28	6	2

Seals were present on fewer surveys when the ADD was switched on compared with when it was switched off (for all months 21% compared to 48%, Table 1). Seal presence within the survey area declined from January to May (χ^2 = 10.00, df = 1, p = 0.002). When this trend in seal presence was controlled for, the effect of the ADD on seal presence within the survey area was not significant (χ^2 = 2.88, df = 1, p = 0.09).

The number of seals counted during surveys varied from January to May (χ^2 = 19.93, df = 5, p = 0.002). The effect of the ADD on the number of seals counted within the survey area was not significant (χ^2 = 3.30, df = 1, p = 0.10).

Seals were observed upstream of the ADD on fewer surveys when the ADD was switched on compared with when it was switched off (for all months 7% compared to 39%, Table 1). There was a decline from February to May in the number of surveys during which seals were detected upstream of the ADD (χ^2 = 5.22, df = 1, p = 0.022; Figure 1). When this decline was controlled for, seals were detected upstream of the ADD on fewer surveys when the ADD was switched on compared with when it was switched off (χ^2 = 6.32, df = 1, p = 0.012; Figure 1).

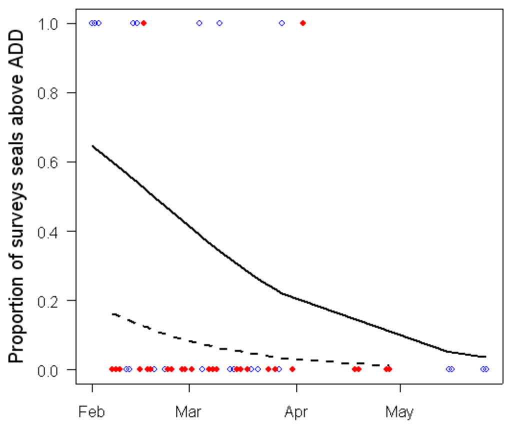

***Figure 1**. The proportion of surveys in which a seal was seen upstream of the ADD with the ADD turned on (broken line) or off (solid line). Fitted lines incorporate the seasonal trend in the presence of seals upstream of the ADD. Points indicate whether or not a seal was detected upstream of the ADD during a survey with the ADD turned on (red, filled points) or off (blue, open circles).*

Discussion

The results of this preliminary trial suggest that the ADD may have been effective as a barrier to seal movements upstream but that the ADD had no significant deterrent effect on seal presence or abundance within the survey area.

Although seals were detected upstream of the ADD on fewer surveys when the ADD was switched on, the ADD was not 100% effective as a barrier: a seal was observed upstream of the ADD on one occasion in February and on one occasion in April. Some initial problems were experienced with maintaining an adequate power supply to the ADD therefore it is probable that the ADD was not fully operative when the seal passed it in February. Difficulties with the maintenance and operation of an ADD are likely to be experienced when using an ADD for routine management purposes, therefore although the reduced effectiveness of the ADD may be simply due to the fact that the ADD was not 100% operative this is still a valid result.

The ADD had no significant deterrent effect on seal presence or abundance within the survey area. There could be two reasons for this: either the ADD was not effective at deterring seals from the area of the North Esk in which it was deployed or there was insufficient statistical power to be able to demonstrate a reduction in seal presence or abundance (the results were significant at the 10% level). Previous studies with ADDs in rivers have similarly produced mixed results on their effectiveness (Olesiuk *et al.*, 1996; Yurk & Trites, 2000).

The presence and abundance of seals was assessed within the area visible to the observer (DF) from the north bank and seals up to 800 m downstream of the ADD were visible to the observer. The effective range of the ADD according to the manufacturer is reported to be approximately 300 m, but may be less in a river where the shallow water depth and bottom profile will affect sound transmission. Therefore seals present when the ADD was operative may have simply remained out-with the effective range of the ADD. However, on all six occasions that seals were present when the ADD was operating, they were observed within 350 m of the ADD and on four of the six occasions seals were observed either upstream or within 100 m of the ADD.

There was no information available on seal foraging behaviour or the normal seasonal variation in seal presence and abundance in the North Esk prior to the trial. Fitting seasonal trends to the data should have corrected for the presence of any existing patterns, although the possibility that the ADD caused the observed trends cannot be excluded. Studies in the Rivers Dee, Don and Spey however have found a similar decline in seal abundance from winter to early summer (Butler *et al.*, in press; Carter *et al.*, 2001).

This was a preliminary trial that was necessarily limited in a number of respects. It examined the effectiveness of one particular type of ADD only, over a relatively short time period, at a certain time of the year, in one river and at only one location within that river. Nevertheless, the results of the trial suggest that ADDs might be useful in the management of seal-salmon conflicts. Further trials in differing situations would allow inferences to be drawn concerning the wider applicability of these results.

Acknowledgements

We would like to thank Martin Stansfeld and the Esk District Salmon Fishery Board for making this study possible. Thanks also to Mike Lonergan for his assistance with the statistics and to Ian Boyd and Stuart Middlemas for their valuable comments. This work was funded by the Scottish Executive, several private charitable donations, Scottish Natural Heritage and the Atlantic Salmon Trust.

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Paul M. Thompson

DETECTING RELATIONSHIPS BETWEEN OCEAN CLIMATE VARIATION AND GREY SEAL SURVIVAL; INSIGHTS FROM THE SEABIRD LITERATURE.

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Summary

Several recent studies of NE Atlantic seabirds indicate that adult survival is influenced by variability in ocean climate. Given similarities in seabird and pinniped ecology and life-histories, these findings suggest that further investigations of density independent variations in grey seal adult survival would be worthwhile. The seabird literature also highlights how variations in recruitment may mask effects of changes in survival at the colony level. The integration of the SMRU grey seal pup production estimates with CMR analyses of individual-based data would appear to offer a unique opportunity to further investigate whether there is similar variation in survival in UK grey seals.

Introduction

Following the 2005 SCOS meeting, there was discussion on the extent to which recent changes in grey seal population trends have been influenced by density-dependent and density independent changes in adult mortality. In particular, SCOS recognized that it has proved difficult to explain the recent leveling of grey seal pup production in the Hebrides unless one assumes that density independent changes in adult mortality have occurred. Potential driving forces include large-scale environmental variation and changes in either natural predation or human persecution. However, earlier exploration of the time-series of grey seal pup production estimates found no evidence that large-scale climate variation influenced observed trends, and the recent focus has been on possible changes in patterns of shooting.

In contrast to these analyses of the grey seal data, several recent studies of North Atlantic seabirds have shown that adult survival is related to climate variation. Furthermore, relationships exist between adult survival and both Sea Surface Temperature (SST) and the winter North Atlantic Oscillation (wNAO). Because there have been significant trends in both these indices in recent decades, this raises the possibility that these factors could influence a trend in survival.

Grey seals and seabirds share many ecological characteristics. In particular, they have similar life-histories, exhibiting delayed reproduction, long lives, and the potential to skip reproduction in poor seasons. The methods used for monitoring population trends are also similar, in that they are based upon censuses of breeding colonies and observed trends in abundance may be influenced by changes in the probability of reproduction. Finally, like grey seals, many UK seabird populations have shown dramatic increases in abundance over the last century, but there is now evidence of decline in some of these.

The aim of this briefing paper is to review recent work on the influence of climate variation on North Atlantic seabird populations, and to explore whether these findings can provide insights into SCOS's efforts to understand recent trends in grey seal pup production.

Methods

Five recent publications have used data from long-term studies of marked seabird populations to explore relationships between climate variation and adult survival. These include analyses of data from six species (Common Guillemot (Sandvik et al., 2005; Votier et al., 2005), Brunnich's Guillemot (Sandvik et al., 2005), Razorbill (Sandvik et al., 2005), Puffin (Harris et al., 2005; Sandvik et al., 2005), Kittiwake (Frederiksen et al., 2004; Sandvik et al., 2005) & Fulmar (Grosbois and Thompson, 2005)), collected from a wide range of colonies from the west coast of the UK (Votier et al., 2005), the North Sea (Frederiksen et al., 2004), the Northern sles (Grosbois and Thompson, 2005; Harris et al., 2005), and Norway (Harris et al., 2005; Sandvik et al., 2005) (Fig 1). For Puffins, Common Guillemots and Kittiwake, analyses were also based on data from at least two colonies in different regions.

In all cases, data were analysed using Capture-Mark-Recapture techniques within program MARK. Survival models incorporating effects of large-scale climate variation (wNAO) and, where available, more local measures of environmental variation (eg. SST and estimates of prey stocks) were compared using AIC. In some cases, effects of other anthropogenic impacts such as industrial fishing and oil spills were also included in models.

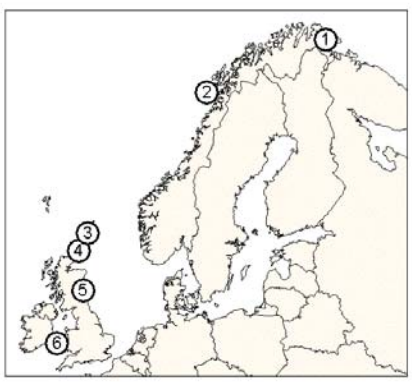

Fig 1. A map showing the study areas mentioned in the text and referred to in Fig 2.
1 = Hornoya, 2 = Rost, 3 = Fair Isle, 4 = Orkney, 5 = Isle of May, 6 = Skomer.

Results

All five studies found significant relationships between adult survival and climate variation, but the relative importance of the wNAO and SST differed between studies.

Where an effect of the wNAO was detected, the pattern was similar in both species (fulmars and common guillemots), with lower survival rates when the wNAO was +ve. However, this pattern is complicated by an underlying trend in the wNAO, meaning that any effects of longer term variation in the wNAO are difficult to discriminate from other unidentified factors that exhibit a trend. Nevertheless, additional analyses of the fulmar data found that the de-trended wNAO remained a significant influence on female, but not male, survival.

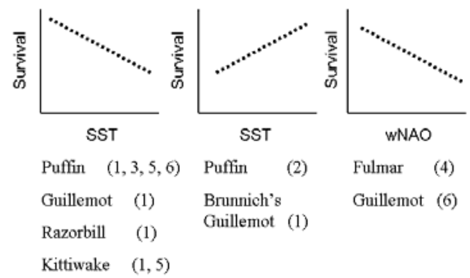

Fig 2. A schematic showing the direction of the most significant relationships detected between adult survival and environmental variables. Figures in brackets refer to the study area, as shown in Fig 1.

The nature of relationships between SST and adult survival varied between species at a single location, and also within a species at different locations (Fig 2). Both of the studies involving multiple species (Sandvik et al., 2005) or multiple sites (Harris et al., 2005) interpreted these differences in relation to species and geographical differences in prey, and the specific response of those prey populations to water temperature. For example, Puffins at sites with a negative relationship between survival and SST tend to prey upon capelin and sandeels, which are less abundant at warmer temperatures. In contrast, Puffins at the site with a positive relationship between survival and SST specialize on herring, which are more abundant during warmer conditions (Harris et al., 2005).

Discussion

All studies found a relationship with either the wNAO or SST. These two environmental variables are correlated, but the strength of the correlation varies geographically (Becker and Pauly, 1996; Ottersen et al., 2001). Differences in the relative importance of each of these variables may therefore depend upon the region in which studies were conducted, or variations in the extent to which the more "local" variables matched the scale at which birds foraged. It seems likely that the influence of both wNAO and SST is indirect, probably through temperature-mediated influences on prey availability, but the wNAO's influence on wind patterns could also affect flight energetics.

These CMR analyses of individually marked birds were able to detect subtle impacts on demography that were not apparent from analyses of trends in colony size. For example, CMR studies of guillemots on Skomer detected effects of both the wNAO and oil spills, but colony size continued to increase at 5% per annum despite a doubling of over-winter mortality in some years (Votier et al., 2005). These analyses highlight that there are generally an excess of non-breeders to buffer these effects. One prediction resulting from this work is that recruitment should also be related to the wNAO, and this has subsequently been confirmed through studies of another guillemot colony on the Isle of May (Crespin et al., 2006).

Implications for studies of grey seal population dynamics

These recent studies suggest that relationships between seabird survival and climate variation are widespread. Due to their smaller body size, seabirds may simply be poorly buffered against environmental variability compared with pinnipeds. Nevertheless, these findings suggest that further investigations on the impact of climate variation on grey seal adult survival would be worthwhile.

Importantly, variations in seabird survival were only detected through CMR studies of individual-based data. This highlights the potential value of integrating long-term studies of marked grey seals from North Rona and the Isle of May with the broader scale time-series of data on pup production.

If, as a seen in guillemots, changes in grey seal adult survival are buffered by increases in recruitment, then young female seals may be over-represented in breeding colonies following years in which adult survival was low. Because young females would also be expected to have lower reproductive success, one possible indicator of a year with poor adult survival is low average reproductive success in the following breeding season. Interestingly, this is what was seen following the 1988 PDV outbreak. Again, the integration of individual based data with the grey seal pup production time-series might permit discrimination between these alternative hypotheses concerning the mechanisms underlying observed changes in reproductive success.

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Grey seal pup production in Wales

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NOTE: THIS PAPER AND ITS CONTENTS SHOULD NOT BE REFERENCED WITHOUT PRIOR PERMISSION OF THE AUTHORS

1. Surveys

West Wales

The grey seal pupping data for Skomer Island is the longest running dataset for the area (beginning 1974, then annually since 1983). The data set for Skomer MNR as a whole runs from 1991 to the present. Within the west Wales breeding population, Skomer Island and MNR data alone cannot be extrapolated directly to the whole west Wales 'population' (Bull, 2004). The reason for this is that Skomer MNR constitutes a relatively small proportion of the breeding population and could also be considered to be on the geographic edge of the breeding population distribution. However, the Skomer MNR data are complementary and an essential reference as it provides a continuous record and provides detailed west Wales population specific data.

The 1992-94 grey seal census (Baines *et al.*, 1995) established a breeding 'population' baseline for the area between Caldey Island in the southeast and Aberystwyth in mid Cardigan Bay.
The majority of pup production occurred on Ramsey Island and the north Pembrokeshire mainland, between St David's Head and the Teify Estuary. The coastal topography of Ramsey Island and the North Pembrokeshire mainland, and the distribution of pupping sites there, are such that comprehensive recording of pupping and survival was not able to be repeated after the west Wales census without major logistical and financial resources. Consequently, since then effort was directed at recording pup production and survival at 'key sites' selected from recommended survey sites reported in Baines *et al*., (1995).

Selection of sites was based on field of view from cliff top and pup production, and data were collected from these key sites during the three seasons 1995-1997 (Strong 1995, 1996, 1998) and more recently in 2005 (Strong *et al*., 2006). Methods developed in these four studies were low cost and their aims were to provide an'index' of pup production for Ramsey Island and the north Pembrokeshire mainland. The cliff top monitoring sites represented 48% of the Ramsey Island production (Table 1) and 22% of the north Pembrokeshire mainland production (Table 2) (between St David's Head and the Teify estuary) as recorded by Baines *et al.*, (1995). Pups were counted from cliff tops and therefore not dye marked, a key methodological difference between Strong (1995; 1996; 1997) and both Baines *et al*., (1995) and Skomer MNR data.

North Wales

Prior to 2000, the status of the grey seals in Wales north of Aberystwyth had not been examined fully. However, Anderson (1977) reported on seal numbers in October, 1974, some daily counts of seals using the West Hoyle Bank in the Dee Estuary have been made each month at the Hilbre Island Bird Observatory since the 1960s, and counts are made on Bardsey Island and recorded in the Observatory log book.

A full census of grey seal pup production was undertaken in north Wales for the 2001 season (Westcott, 2002). The entire coast was surveyed between Aberystwyth in the south and the Dee estuary in the east and included all islands adjacent to these coasts. This provided baseline data on grey seal distribution at haul out sites and on pup production, which was followed in 2002 by more focused surveys of distribution and abundance (Westcott & Stringell, 2004) and pup production (Westcott and Stringell, 2003).

In 2003, pup production for north Wales was estimated using plot sampling methodology based on a random selection of pupping sites stratified over pup density (Stringell *et al*., 2004).

2. Recent Pup production estimates

West Wales

Strong *et al*., (2006) counted pups from cliff tops at nine sites on Ramsey Island and eight sites on the north Pembrokeshire mainland. Data were recorded using Smith's five stage age classification system although the total number of white-coated pups was used as the predictor in the statistical model. In the modelling calculations, the average time to moulting was taken as 21 days. Estimates of pup production were generated using a statistical modelling method based on maximum likelihood (MLE) and 95% confidence intervals were calculated with non-parametric bootstrapping.

Pup production on Ramsey Island in 2005 was estimated between 258 and 350 with a point estimate of 297. On the north Pembrokeshire mainland pup production was estimated at between 145 and 198 with a point estimate of 168 (Table 3).

North Wales

The timing of the north Wales breeding season and the number of pups born was described for the first time in Westcott (2002). In 2001, a full census of all potential pupping sites revealed a direct or 'through' count of 103 pups, of which 20 died before the completion of lactation.

In 2002, a repeat census was conducted and observed pups born between August 18 and November 11 (Westcott & Stringell, 2003). A direct count of 110 pups was made, of which nine died before weaning.

In 2004, pup counts were made using a plot sampling approach to test the efficiency of plot sampling over a full census (Stringell *et al*., 2004). Pup production estimates varied depending on sample coverage probabilities (see Table 4) but a sensible extrapolation of the estimate indicated pup production in north Wales as between 104 and 120 with the point estimate of 112.

3. Trends in pup production

West Wales (taken from Strong *et al*., (2006))

Estimates are reported and compared with data obtained for the same sampling locations for 1992-2000. The data for
1992-94 were extracted from the report of Baines *et al.,* (1995), and estimations were made using a different methodology. The data for 1995-2000 were collected and estimated using the same methods but with some variation in observer.

Data for 1992-1994 are from Baines *et al.,* (1995), for 1995-1997 are from Strong, (1998), for 1998 -2000 are from Ramsey Island Annual Seal Reports (RSPB unpublished), data for 2005 are from Strong *et al*., (2006).

95% Confidence Intervals for pup production MLE estimates are shown in Table 3.

Comparing MLE data with the dye-marking data obtained by Baines *et al.,* (1995) suggests that there was little variation in observed pup production in north Pembrokeshire between 1995 and 2000, with levels somewhat lower in these latter years than in 1992-1994 (Figure 1), however this difference may be an artifact due to the methodological difference in the two data sets. If so, it may well be that the population has followed the apparent oscillation around a level value as that of the Skomer MNR population during this time.

Pup production in 2005 is higher than that observed over the years 1992-2000. This difference cannot be reasonably explained on uncertainty or methodological grounds. An increase has also been observed at the mainland sites within the MNR, but not so on Skomer Island itself.

Given the lack of any upward or downward trend in the MNR data, coupled with this collation of the available north Pembrokeshire mainland and Ramsey Island data, it would be reasonable to suggest that the population of grey seals in Pembrokeshire and the Pembrokeshire Marine SAC was varying around an approximately constant level, except for an apparent increase for 2005. This conclusion assumes that proportional variations were occurring in the unobserved parts of the population.

The evidence does not predict this increase from any trend in the previous data, leaving the possibility that 2005 was a 'one off' bumper year, especially for north Pembrokeshire. The gap in the data does not preclude such a trend, but such data as we have for Ramsey Island via RSPB monitoring, do not support the presence of such a trend.

There is no evidence for any adverse effects on the population of the grey seal within the SAC, which seems to have been close to current levels for all years for which comparable data are available.

North Wales

In 2002, 110 pups were located at 35 different north Wales sites, with 74 born at sea cave sites, and 36 at 'open' beach sites (Westcott, 2002). This compares with 103 located in 2001 at 38 different sites, when 37 were cave-born, 65 were born at 'open' beaches and the origin of one was unknown (Westcott & Stringell, 2003). In both seasons, all except one pup were born between the beginning of August and the end of November, with the great majority born in September and October. However, within those limits, there was considerable local variation in the timing of pup production for the region.

Stringell *et al.,* (2004) found 112 (± 8) pups in 2004 using estimation techniques. The similar pup production figures reported in these three surveys indicated that pup production was reasonably stable over that period.

4. Pup production models

West Wales (taken from Strong *et al.,* 2006).

Pup production estimates in Strong *et al*., (2006) were arrived at by applying maximum likelihood (MLE) methods. The model used is comparable to but simpler than that proposed by Conservation Research Ltd. in Strong (1998). The total number of white-coated pups was used as the predictor in the statistical model.

The births curve is modelled by the normal function:

$$y = ae^{\frac{-(x-b)^2}{2c^2}}$$

Where b and c are the mean and standard deviation of the observed total white- coat data and a is derived from the mean time to moult.

Parameters b and c are estimated from observed data using curve fitting in NCSS (Hintze, 2004). The integral of the birth curve yields the estimate of the total production.

A simulated population of production estimates is generated using these parameters and published standard deviations of time to moult (Conservation Research Ltd. in Strong (1998), Matthews (2004) and Poole & Poole (1998)). The population of production estimates thus generated is used to obtain maximum likelihood estimates of mean production and confidence intervals by pooling of the simulated population. The confidence intervals thus obtained use a non-parametric bootstrapping method.

The statistical modelling to yield pup production estimates is based on a number of assumptions and often parameters derived from data other than that recorded in the observations.
Table 5 indicates the change in MLE pup production estimates based on different average time to moult values, which differ from region to region.

In Strong *et al.*, (2006), an average time to moulting of 21 days was used, rather than the 23 days used in Strong (1998), as it represented the data from over 10 years of survey at the MNR (Matthews (2004) and Poole & Poole (1998)) and was assumed to be more likely to be representative of the 'true' values in north Pembrokeshire.

The statistical modelling has the further advantage that it is not dependent on frequent observations, but rather on assessing the shape of the distribution effectively. The importance here is to gain a reliable estimate of start time, and to be confident that our data points cover the distribution adequately, especially around the peak.

The methods of Strong *et al*., (2006) were compared to the Conservation Research Ltd model and Sea Mammal Research Unit predictions made in previous reports, (Strong, 1997, and Baines *et al.,* 1995), by applying our method to their data, where they was presented in an appropriate form. For these comparisons an average time to moult of 23 days was taken Our production estimates correlated well with those previously published (Fig 2), especially where the sample size was high (for large sites and pooled data), and this correlation is significant at 0.1% level. This demonstrates that Strong *et al.,* (2006) methods return estimates consistent with those previously employed, but consistently underestimated the other models by about nine pups. This variation is small compared to the breadth of the confidence intervals.

North Wales

To determine pup production in North Wales in 2004, design based plot sampling was used (Stringell *et al*., 2004). Here capture probabilities in each sampled plot are known and so the assumptions of this method are met. Grey seal pups were counted at randomly selected pupping sites (plots) as a stratified sample of sites previously identified during seal censuses. Stratified sampling was used to increase the precision of the (overall population) estimate and stratification was based on pup number (density). Sampling effort was apportioned to each stratum with Neymans Optimal Allocation and each plot was visited several times during the pupping season to provide a cumulative count per plot. Pup abundance was calculated using a Horvitz-Thompson intuitive estimator. To determine the 95% confidence interval of the estimate the asymptotic normal method was employed thus assuming an approximately normal distribution.

5. Future work

Future work will be directed towards re-analysis of existing seal census data to assess suitable methods for cross-Wales monitoring of grey seal pup production, pup distribution and habitat availability. Extant photographic pelage records of grey seals in Wales will be analysed with a view to creating a catalogue of images supported by a network of interested parties across the Irish Sea.

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Tables 1 and 2 Proportion of historic North Pembrokeshire pup production covered by 2005 monitoring sites (from Strong *et al.,* 2006).

Table 1. Proportion of pups born on the nine Ramsey sites as a percentage of the whole Ramsey Island production. Data from Baines *et al*, (1995).

	1992	1993	1994	Total
Whole Island Production (A)	499	464	433	1396
Nine monitoring sites production (B)	217	230	225	672
B / A %	44	50	52	48

Table 2. Proportion of pups born on the eight north Pembrokeshire mainland sites as a percentage of the north Pembrokeshire mainland coast (Teify estuary to St David's Head). Data from Baines *et al*, (1995).

	1994	1993	1992	Total
All sites (A)	600	588	525	1713
Eight monitoring sites (B)	134	120	125	379
B / A %	22	20	24	22

Table 3. 95% Confidence Intervals for 2005 pup production MLE estimates for west Wales grey seals (from Strong *et al.,* 2006).

	Ramsey totals				Mainland totals		
		Lower 95%	Upper 95%			Lower 95%	Upper 95%
95	171	148	201		133	115	156
96	183	159	216		120	105	142
97	209	182	247	97	112	97	132
98	173	150	204	2005	168	145	198
99	171	148	201				
2000	164	143	194				
2005	297	258	350				

Table 4. Abundance estimates and 95% confidence limits of grey seal pups in north Wales using plot sampling on randomly selected pupping sites stratified over pup density. Estimate derived from Horvitz-Thompson intuitive estimator (Stringell *et al*., (2004)). Figures in bold indicate chosen pup production estimate as listed in text.

Coverage probabality	Coverage criteria	Estimate Ň	SE Ň	Lower 95% CI	Upper 95% CI
0.86	**Visited sites (39) / all sites (45)**	**112**	**4.15**	**104**	**120**
1.00	Visited sites (39) / visited sites (39)	101	0.00	101	101
0.44	Selected sites (20) / all sites (45)	108	11.60	85	130
0.51	Selected sites (20) / visited sites (39)	96	9.57	78	115

Table 5. Effect of time to moult on pup production estimates at Ramsey derived by maximum likelihood statistical modelling (Strong *et al.,* 2006).

Average time to moult	**23days**	**21days**	**18days**
1995	156	171	199
1996	167	183	213
1997	191	209	244
1998	158	173	202
1999	156	171	199
2000	150	164	192
2005	271	297	346

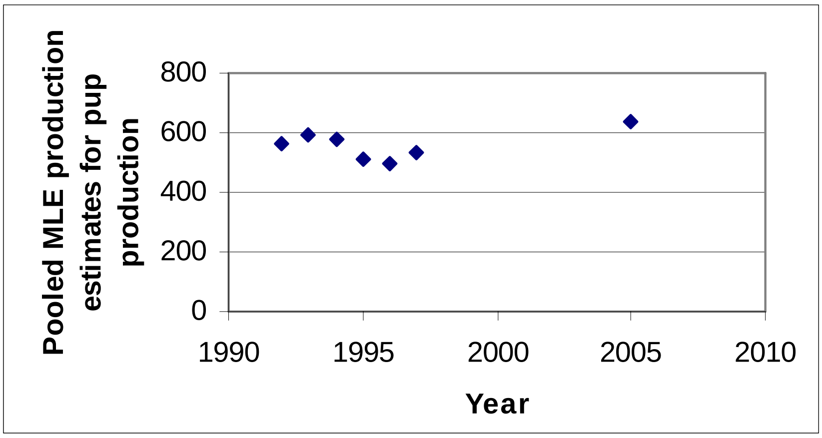

Figure 1. Pooled MLE estimates for pup production within Pembrokeshire Marine SAC and north Pembrokeshire.

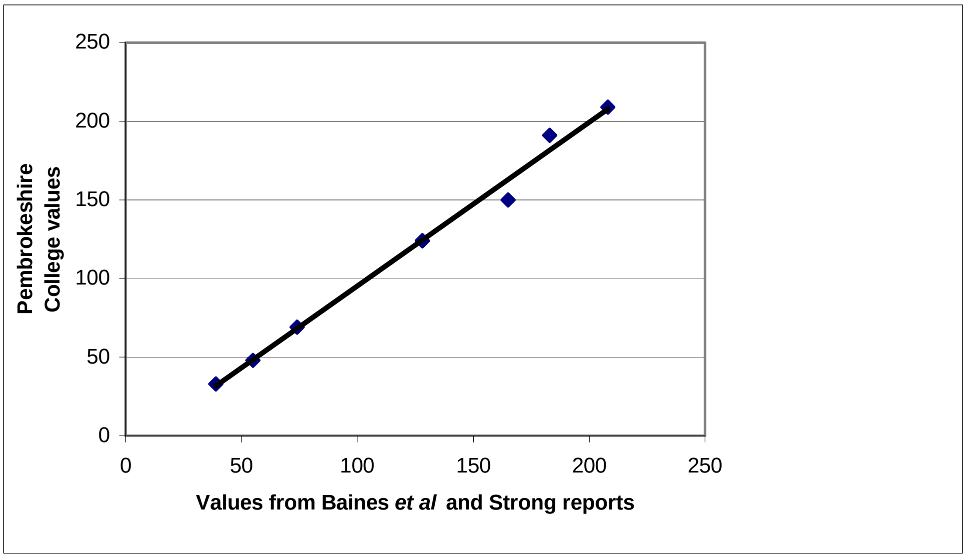

Figure. 2. Correlation between values quoted in Baines *et al.*, (1995) and Strong, (1998) and the same data reworked through Strong *et al*., (2006) methods.