

Scientific Advice on Matters Related to the Management of Seal Populations: 2007

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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, information and advice in response to parliamentary questions and correspondence, and responds on behalf of NERC to questions raised by government departments about the management of marine mammals in general.

This report provides scientific advice on matters related to the management of seal populations for the year 2006. 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 (Table 2). 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 human exploitation. There are clear indications of a slowing down in population growth in UK and Canadian populations in recent years.

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. Each mature female grey seal gives birth to a single white-coated pup, which is nursed for about three weeks before being weaned and moulting into its adult coat.

About 45% of the world population of grey seals is found in Britain and over 90% of British grey seals breed in Scotland (Tables 1 & 2), 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.

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 may 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.

Grey seals feed mostly on fish that live on or close to the seabed. In the UK their 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 haulout 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, Swedish, Danish, German and Dutch waters. Britain is home to approximately 33% of the population of the European sub-species (Table 4). 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. Scotland holds approximately 85% of the UK common seal population, with 11% in England and 4% in Northern Ireland.

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 Wash¹, but had limited impact elsewhere in Britain. Counts in the Wash and eastern England have continued to decline for the 4 years since the epidemic.

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, gadoids, 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.

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.

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 is now 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 Q 1)

Current status of British grey seals

Variation in the number of pups born in a seal population can be used as an indicator of change in the size of the population and with sufficient understanding of population dynamics may allow estimation of total numbers of seals. 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 07/1 and SCOS-BP 07/2.

Pup production

The total number of pups born in 2006 at all annually surveyed colonies was estimated to be 39,700. Regional estimates were 3,500 in the Inner Hebrides, 11,600 in the Outer Hebrides, 19,300 in Orkney, and 5,300 at North Sea sites (including Isle of May, Fast Castle, Donna Nook and Farne Islands). A further 5,500 pups were estimated to have been born at other scattered sites.

Trends in pup production

The differences in pup production between 2005 and 2006 are shown in Table 1. Total pup production at annually monitored colonies increased by 3.7%, in contrast to the 3.0% decrease in the preceding year.

Despite this inter-annual increase, the 2006 results suggest 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 (2001-2006) the total pup production for all annually monitored colonies has increased at 1.1% p.a. (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 at around 4% p.a.. In most other areas the pup production is either stable or decreasing slowly.

In Orkney, pup production increased by 9.6% between 2005 and 2006 in contrast to the observed decrease of 7.7% between 2004 and 2005. This is consistent with the recent history of high inter-annual variability in pup production in this region. This is probably a

consequence of the population being close to a food resource limitation. Inter-annual variations in prey availability will mean that in some years the population's food requirement will exceed the supply. Fecundity of breeding females and/or survival of weaned pups are likely to be sensitive to such effects and may be more susceptible to subtle changes in environmental factors that alter food availability. A retrospective description of the regional trends in pup production of the UK grey seal population was 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, a clear but more recent slow down in the Northern Isles and continued exponential growth in the North Sea population. The 2006 pup production estimates are consistent with these patterns.

Table 1: Grey seal pup production estimates for the main colonies surveyed in 2006

Location	2006 pup production	Change in pup production from 2005-2006	Average annual change in pup production from 2002-2006
Inner Hebrides	3,461	+2.2%	+2.3%
Outer Hebrides	11,612	-5.6%	+0.3%
Orkney	19,332	+9.7%	+0.3%
Isle of May + Fast Castle	2,631	-3.2%	+0.9%
All other colonies (2004 Shetland data)	3,605 (3871)**		
Total (Scotland)	40,641	+3.2%*	+1.2%*
Donna Nook	1,437	+12.6%	+15.6%
Farne Islands	1,254	+10.2%	-0.2%
SW England & Wales (last surveyed 1994)	1,750		
Total (England & Wales)	4,441	+11.5%*	+9.0%*
Total (UK)	45,082	+3.3%*	+1.2%*

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

** estimate incorporating the more complete 2004 Shetland survey data

Population size

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

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 07/2). There is a lack of independent data with which to quantify the relative contributions of these factors (SCOS-BP 06/7). A modified version of the modelling framework employed last year was used to fit and compare models of British grey seal population dynamics, based on regional estimates of pup production from 1984 to 2006. 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. This year the model was modified to allow direct estimation of observation (i.e. counting) error which had previously been set to an unrealistically high fixed value of 25%. Again, the two simplest models produced the best fits to the time series of pup productions. The density dependent survival and density dependent fecundity models fitted more or less equally well to the data but the estimated confidence intervals of these models did not overlap. The estimated adult population size in 2006 for these two models was 116,000 (95% CI 90-154,000) for density dependent survival and 248,000 (190-377,000) for density dependent fecundity, with the other two models having intermediate values. A more detailed description of the methodology is given in SCOS-BP 07/2. It was recognised that inability to select among models may indicate that none included the range of density dependent factors influencing the grey seal population and hints at the error likely if using a simple model as a predictive tool. It is now a research priority to improve our understanding of the processes underlying density-dependent population change in the grey seal population. In addition to revisiting the original model assumptions, attempting to refine the prior distributions of demographic parameters and investigating the effects of environmental variability, it is essential that we obtain an independent estimate of total population size that does not rely on modelling the relationship between population size and pup production (details of progress are given below).

Future estimates of population size may be derived from an approach based on a range 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 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 90,000 – 154,000, with a point estimate of 116,000. Seals from sites that are monitored less often add approximately 17,000 to this total, giving an estimated population of 107,000 – 171,000. Based on this model, the total grey seal population is continuing to grow at around 2.5% p.a. with most of the increase occurring in the Orkney and North Sea populations. 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 pup production estimates

The largest uncertainty in the population estimates is that associated with the relationship between numbers of pups and adults. However, there are also uncertainties associated with the estimates of pup production, which are believed to lie within a range of –10% to +13% of the values provided and had been previously assigned a fixed CV of 25% in the population models. The modified model used to generate total population estimates provided an independent estimate of the measurement errors in pup production estimates. The fitted estimate of the CV of the pup production estimates was 8.3% (95% credibility interval 6.8-10.1%). There are additional unknown uncertainties associated with the estimates of pup production at colonies that are not surveyed annually and uncertainties about the value used for adult male survival, about which little is known.

Trends in pup production

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 07/1 & 07/2; 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. If we assume that the slow down in the rate of increase of the pup production is due only to density dependence in pup survival, the total grey seal population has continued to grow at around 2.5% p.a. for the past 5 years with most of the increase occurring in the Orkney and North Sea populations (3.7% and 2.8% p.a. respectively) and slower growth in the Western Isles (1% p.a.). If however, density dependence is acting only on fecundity of adult females the population would have been growing at around 4.3% p.a. over the last five years. (Detailed annual population estimates are given by region in the Appendices of SCOS-BP 07/2).

Table 2. Relative sizes of grey seal populations. Pup production estimates are used because of the uncertainty in overall population estimates

Region	Pup Production	Years when latest information was obtained	Possible population trend²
Scotland	40,600	2006	Stable or slowly increasing
NE England	2,700	2006	Increasing
SW Britain	1,800	2006	Increasing
UK	45,100		Increasing
Ireland	300	1998	Unknown*
Wadden Sea	200	2004	Increasing**
Norway	1200	2003	Unknown**
Russia	800	1994	Unknown**
Iceland	1200	2002	Declining**
Baltic	4,000****	2003	Increasing**
Europe excluding UK	7,700		Increasing
Canada - Sable Island	41,500	2004	Increasing***
Canada - Gulf St Lawrence	6,100	2000	Declining**
WORLD TOTAL	100,400		Increasing

* Kiely, O. & Myers, A.A. 1998. Grey Seal Pup Production At The Inishkea Island Group, Co. Mayo and Blasket Islands, Co. Kerry Biology Proceedings Of The Royal Irish Academy, **98b**: 113–122

** Data summarised in:- Grey Seals of the North Atlantic and the Baltic. 2007 Eds: T. Haug, M. Hammill & D. Olafsdottir. NAMMCO Scientific publications Vol. 6

*** Bowen, W.D., McMillan, J.I. & Blanchard, W. 2007. Reduced Population Growth Of Gray Seals At Sable Island: Evidence From Pup Production And Age Of Primiparity. Marine Mammal Science, 23(1): 48–64

**** Baltic pup production estimate based on mark recapture estimate of total population size and an assumed multiplier of 4.7

The UK grey seal population represents approximately 45% of the world population on the basis of pup production. The other major populations in the Baltic and Canada are also increasing, but at a faster rate than in the UK.

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 07/3. 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.

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.

Table 3 Counts of common seals by region

Region	1996-2006
Shetland	3,021
Orkney	4,256
Outer Hebrides	1,981
Highland (Nairn to Cape Wrath)	1,056
Highland (Cape Wrath to Appin & Loch Linnhe)	4,966
Strathclyde (Appin to Mull of Kintyre)	6,702
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	23,368
Blakeney Point	719
The Wash	1,695
Donna Nook	299
Scroby Sands	71
Other east coast sites	225
South and west England (estimated)	20
TOTAL ENGLAND	3,029
TOTAL BRITAIN	26,397
TOTAL NORTHERN IRELAND	1,248
TOTAL BRITAIN & NORTHERN IRELAND	27,645
TOTAL REPUBLIC OF IRELAND	2,905
TOTAL FOR GREAT BRITAIN AND IRELAND	30,550

Between 1996 and 2006, about 27,650 common seals were counted in the whole of the U.K., of which 23,400 (85%) were in Scotland, 3,000 (10%) were in England and 1,250 (5%) were in Northern Ireland (Table 3 above). Approximately 2,900 common seals were counted in the

Republic of Ireland in 2003, making a total of 30,550 common seals for the British Isles. Not all individuals in the population are counted during surveys because at any one time a proportion will be at sea. Telemetry based mark recapture estimates suggest that approximately 60-70% of the population are counted during the moult surveys, leading to an estimate for the total British population of 50,000-60,000 animals.

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 the most affected region and counts since 2002 indicate a continued decline following the epidemic. Counts by region for the 2006 season are given in the Table 3 above. These are minimum estimates of the British common seal population. Results of surveys conducted in 2006 are described in detail in SCOS-BP 07/3.

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 in moult counts since the late 1990s. The data suggest that these areas may be undergoing a major population decline. Surveys of the east coast populations in 2006 also showed continuing declines in both the Tay and the Wash populations (SCOS-BP 07/3) 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.

Table 4 Sizes and status of European populations of common seals. In most cases, numbers given predate the PDV epidemic of 2002.

Region	Number of seals counted¹	Years when latest information was obtained	Possible population trend²
Outer Hebrides	2,000	2003	None detected
Scottish W coast	12,300	1996-2005	None detected
Scottish E coast	1,800	2006	Declining
Shetland	3,000	2006	Declining
Orkney	4,300	2006	Declining
Scotland	23,400		
England	3,050	2004-2006	Recent decline ⁴
Northern Ireland	1,250	2002	Decrease since '70s
UK	27,600		
Ireland	2,900	2003	Unknown
Wadden Sea-Germany	9,400	2006	Increasing after 2002 epidemic
Wadden Sea-NL	4,100	2006	Increasing after 2002 epidemic
Wadden Sea-Denmark	2,000	2006	Increasing after 2002 epidemic
Lijmfjorden-Denmark	1,400	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 62°N	1,200	1996-98	Unknown
Norway N of 62°N	2,600	1994	Unknown
Iceland	19,000	?	Unknown
Barents Sea	700	?	Unknown
Europe excluding UK	55,600		
Total	83,200		

¹ –counts 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.

data sources: www.smru.st-and.ac.uk; ICES Report of the Working Group on Marine Mammal Ecology 2004; Harding *et al.* submitted to Ecology Letters

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 has been established including increased monitoring to confirm the magnitude and geographical extent of the declines and comparative studies of pup survival in areas of contrasting population dynamics.

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

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 elsewhere². 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 Sea³. 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 females tend to return to their natal breeding colony and remain faithful to that colony for most of their lives⁴.

Age structure.

While the population was growing at a constant rate, i.e. a constant exponential change in pup production, the stable age structure for the female population could be calculated. However, since the mid 1990s this has not been possible as changes in pup production growth rates imply changes in age structure. In the absence of a population wide sample or a robust means of identifying age specific changes in survival or fecundity we are unable to estimate the age structure of the female population. There is no useful information on age structure for the male component of the population.

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

³ SMRU unpublished data

⁴ Pomeroy, P.P., Twiss, S. & Redman, P. 2000. Philopatry, site fidelity and local kin associations within grey seal breeding colonies. *Ethology* 106 (10): 899-919

Survival rates

Survival rates and fecundity estimates for adult females breeding at North Rona and the Isle of May have been estimated from resights of permanently marked animals. Details of the data and analyses are presented in SCOS-BP 07/6. Briefly survival rates were different at the two sites, being lower and more variable at the older, decreasing colony at North Rona. Recapture probabilities for tags were higher at the Isle of May as was tag loss rate.

A novel and cost-effective method to estimate grey seal pup survival is currently under development. The method is based upon wireless sensor network technology is a cooperative venture with University College London and Edinburgh University.

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 waters⁵. There is probably little movement of breeding animals between these populations although satellite telemetry reveals some interchange between the Wadden Sea and the English east coast populations outside the breeding season. 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/Skagerrak⁶ 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.

Age structure.

The absence of any historical cull data or a detailed time series of pup production estimates means that there are no reliable data on age structure of the UK common seal populations. Some age structure data were available from seals found dead during the PDV epidemics in 1988 and 2002. However, these were clearly biased samples and could not be used to generate population age structures.

In the absence of consistent time series of pup productions or any systematic sampling of the population for age data, we are unable to define the age structure of the UK common seal population.

Survival rates

SMRU are currently undertaking a comparative study of survival rates of common seal pups in the declining Orkney and apparently stable West Coast populations. Results will be presented to SCOS in 2008.

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

⁵ 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.

⁶ Härkönen, T. & Harding, K.C. (2001) Spatial structure of harbour seal populations and the implications thereof. *Canadian Journal of Zoology*, 79, 2115-2127.

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 and English waters? (SEERAD/DEFRA Q 3)

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 were 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).

No new diet data have been collected since then, so estimates of consumption have been based on the 2002 species compositions and the latest output from the grey seal population model (DDS). Diet data were pooled into a generic North Sea diet and a Western Scotland diet.

Consistent with previous SCOS advice, estimated total fish consumption based on the 2006 DDS model population estimates west of Scotland is 86,500 tonnes (95% CI = 74,000 – 101,000 tonnes) and in the North Sea (including Shetland based on 2004 counts) 147,300 tonnes (95% CI = 123,000 – 176,000 tonnes). Approximately 92% of the total of 233,833 tonnes is estimated to be consumed in Scottish waters. Consumption by grey seals in English waters of the North Sea is estimated to have been 18,000 tonnes (95% CI = 15,000 – 21,500 tonnes). We have no reliable information on which to base an estimate of consumption in SW Britain, but pup production there accounts for only 4% of the UK pup production so consumption would be around 10,000 tonnes p.a..

At present we can not determine the grey seal population size with reasonably narrow limits of confidence. If the DDF model population estimates were applied, the estimated fish consumption would be approximately 2.5 times greater. Until the issues of model construction have been resolved, extreme caution should be employed when using these estimates of fish consumption.

Common seals

There is insufficient diet information to allow us to accurately estimate the total prey consumption of the Scottish common seal population.. However, based upon current knowledge of the likely daily ration of about 3 kg of fatty fish per day or up to 5 kg of gadoids per day, the consumption by common seals in Scotland would be around 42,000 to 71,000 tonnes depending on the proportion of each prey type. We do not have sufficient information to put any sort of realistic confidence intervals around these estimates. The equivalent consumption figures for the English common seal population would be around 5,000 to 9,500 tonnes.

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 Q 4)

Controlling seal populations could potentially be achieved by non-lethal reduction of the birth rate or by excluding seals from sensitive habitats and regions. These sorts of interventions have been attempted on a trial basis, on small scales in the past. Neither SMRU nor the Department of Fisheries and Oceans, Canada, have carried out any recent research on this issue. Different forms of chemical sterilization are available and some are known to be effective in seals. In the past, the technology for delivering chemicals has been deficient and, while this remains the case, we are aware that progress is being made. Nevertheless, the main uncertainties surround the potential secondary effects of this type of intervention on colony structure, which could have the unintended consequences of stimulating population growth, and also the cost-benefit trade-off associated with this type of population control.

SCOS BP 06/9 provided information about current research, funded by SEERAD, being undertaken to use acoustic deterrent devices (ADDs) to exclude seals from sensitive regions. During the last year a programme of laboratory and field based tests of aversive sounds specifically designed to act as seal deterrents with minimal impacts on non target species have been conducted. Initial results are promising and may lead to more effective local control. A detailed description of the work will be presented to SCOS in 2008.

General

Seal Populations

5 *What progress has been made with integrating grey seal population models of seal abundance to provide a combined distribution of uncertainty or to select between the models? (SEERAD/DEFRA – 5)*

In 2005 and 2006, 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 the population. 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. Applications under NERC's December 05 and December 06 responsive mode funding rounds were unsuccessful despite the proposal being classified as of an appropriate standard. In response to the pressing need for this study, SMRU have modified their harbour seal work package to incorporate a comprehensive survey of grey seal non-breeding haulout locations during late summer 2007. This will provide much of the raw data required to produce an independent estimate of the grey seal population.

A Bayesian state-space modelling framework similar to that 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 2006 (SCOS-BP 07/2). 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 2006, 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 were described in SCOS-BP 06/2.

Improved fitting methods have allowed estimation of the measurement error of the pup production estimates. The reduced CV on these estimates has slightly improved the confidence intervals of the different models and reduced the differences between the basic

and extended models. However, there is still insufficient information in the pup production data to distinguish between different population models based on pup count data alone. There is therefore a strong need for additional comprehensive data on either a population vital rate or adult population size. A data collection effort to provide the basic information for such a study is currently underway.

An in-depth analysis of the results of SMRU's long-term reproductive biology studies on the Isle of May and North Rona is currently underway. Initial results describing differences in survival and recruitment between the declining North Rona population and the increasing Isle of May population are presented in two briefing papers (SCOS-BP 07/6 & 07/7). The apparent similarity in fecundity and differences in survival, with lower survival and recruitment at North Rona lend support to the density dependent survival model.

6. *What progress has been made in improving estimates of the common seal population?(SEERAD/DEFRA-6)*

In response to the observed declines in common seal populations in the Northern Isles and along the East coast, an intensive series of surveys is currently underway. At the time of the writing of this report, SMRU and FRS staff are conducting a series of co-ordinated helicopter and fixed wing air surveys of the entire Scottish and English common seal population. The aims are to identify the geographical extent and confirm the estimated magnitude of the declines identified over the past few years. These surveys are being co-ordinated with a photographic survey of the hauled out component of the grey seal population to obtain raw data to develop an independent estimate of total population size.

In 2006 with funding support from SNH, a series of repeated aerial and ground surveys of the Moray Firth between Helmsdale and Findhorn were carried out during the breeding season, 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 are presented in SCOS-BP 07/3. In addition SMRU carried out a survey of the breeding population in eastern England to continue the time series of pup production estimates. Results are presented in SCOS-BP 07/4.

Annual moult surveys of eastern England continued (SCOS BP 07/3), 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.

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? DEFRA (7)*

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 was presented 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 colonies⁷. 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.

An application of a method for classifying offshore sub-division of the foraging habitats for both grey and harbour seals in UK waters is under development.

8 *What possible research options might be considered to investigate the causes of the recent reduction in common seal numbers in specific local areas and which of these should be pursued as a priority?(SEERAD Q-7)*

In response to the reported declines, SMRU convened an internal workshop to identify the salient features of the declines and develop a research programme to address the most likely candidate causal factors. The report of the workshop was considered by the Scottish Seals Working Group and a proposed work package has been developed.

The appropriate first step in such an investigation is to gauge the relative importance of real or perceived trends in demographic rates. This will be achieved by building a demographic model for common seal population dynamics, building a model for the aerial observation process. Implementing both of these within a Bayesian estimation framework as a single state-space model. Using all supplementary data to generate informed priors for as many parameters as possible to infer the temporal trends in survival, fecundity and the timing of moult necessary to generate the observed dynamics. This will help focus on the more likely proximate causes and provide a framework for testing the potential ultimate causes as information on their effects becomes available. An initial version of the model has been developed and is presented in SCOS-BP 07/5.

In addition, because of the urgency of the problem SMRU have implemented two data collection projects. The first priorities were determined to be an extensive air survey supported by intensive ground observation studies to identify the geographical extent and confirm the magnitude of the declines around the UK; a comparative study of pup survival in areas with contrasting population dynamics and a retrospective analysis of stored blood and tissue samples for blood chemistry and toxicological indicators of differences between declining and stable area.

9. *What are the latest results from satellite tagging in respect of usage of specific marine areas around Scotland by grey and common seals? (SEERAD Q-8/ DEFRA Q-14)*

The possible introduction of Marine Special Areas of Conservation (MSAC) for particular species has stimulated discussion on the appropriate delineation criteria. Usage, the expected proportion of time spent by a population of animals in a unit of space, is one potential indicator of the importance of different spatial regions for the species. It is therefore reasonable to define MSACs so as to include as much of the species usage as possible.

However, this needs to be weighted against several practical concerns (e.g. mapping, navigation and policing) and MSAC boundaries may need to be simple or enclose only up to a certain total area.

Substantial data sets on movements and foraging behaviour have been collected from both grey and common seals over the past 10 years. When combined with aerial survey information on distribution of haulout sites and relative abundance of each species at these sites, the tracking data allows us to develop population scale habitat usage maps for the entire UK. These maps provide a basis for developing objective criteria for defining MSACs.

SCOS-BP 07/8 describes a process for delineating MSACs taking into account a range of considerations. Usage maps for both common and grey seals were imported from previous work. A range of scenarios were run for each species to define regions that include different percentages of the total usage or to represent SACs with total areas fixed to a required value. The example scenarios required simple rectilinear boundaries drawn at a scale no smaller than 35km (so, no boundary segment could be smaller than 35km). This can be reduced in future versions of the design to enable the MSAC boundaries more closely to enclose regions of high usage at the cost of making them more complicated.

To examine the possibility of combined SACs, the same algorithm was applied to a combined map. This was produced as a point-by-point weighted average of the grey and common seal maps. Preliminary results are presented in SCOS-BP 07/8.

It is recognised that usage as defined above may not be the only indicator of the importance of an area. There are also potential issues with applying a static approach to what may be a dynamic system in terms of inter annual and longer term variations in usage.

10. *What are the key questions about seal populations that remain to be addressed to better inform practical seal management issues? (SEERAD Q-9)*

SCOS defer this answer until 2008.

As part of its strategic review process, SMRU will convene a workshop in January or February 2008. Current and past members of SCOS and SMRU research staff will address this specific question. The results will inform the strategic review and a report of the discussions and conclusions will be provided to SEERAD and will form part of the SCOS 2008 advice.

Seal Diet

11. *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? (SEERAD Q-10 / DEFRA Q-8)*

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, in the Western Isles by around 1% p.a. and in the Northern Isles and North Sea by around 2-3.5% p.a.. 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.

Improvement in diet information will only be useful in the context of improved precision in grey seal population estimates. This can be achieved by obtaining an independent estimate of population size (see question 1).

12. *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? (DEFRA Q-9)*

The recent detailed estimates of grey seal diet suggest that predation by grey seals may affect the dynamics of some fish populations. However, simple comparisons between very uncertain 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 incorporating the revised consumption data had only a minor effect on the cod assessment. Estimated cod consumption in the North Sea in 2002 was the equivalent of 3.7% of total stock biomass, mostly relatively small fish.

Further research

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 11 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 used to infer diet 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 among 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 at SMRU.

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 estimate the population size of grey seals is a major source of the uncertainty in prey consumption estimates and our ability to describe the effects of predation on fish stocks.

13 *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?(DEFRA Q-10)*

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. Hence this work is of particularly high priority.

14 *Does the Committee endorse the draft proposal from SMRU which seeks to establish a more detailed picture of common seal diet to complement that for grey seals?(SEERAD Q-11)*

Yes (provided that meaningful information on prey availability and dynamics are available)

15. *How can the consumption of salmon and sea trout smolts by seals best be evaluated and how useful would such work be? (SEERAD Q-12)*

Seals enter some rivers throughout the year, and there is concern that they may prey heavily on salmonid smolts. This could potentially jeopardise the continued existence salmonid populations in certain rivers. However, to date we have no quantitative information on which to base an assessment of the scale of the problem. Seals may eat smolts, but would do so under-water and therefore would be undetected. Assessing potential predation by estimating seal usage of rivers during smolt runs and using estimated feeding rates based on metabolic requirements could provide a maximum estimate of impact, but would not estimate actual losses.

As direct observation is not possible some telemetry system is required. Feeding rates can be assessed with stomach temperature sensors but again, in the absence of identification of prey they can not provide any useable estimates of predation on smolts. A plausible method of which we are aware is a system being developed by FRS, AST and SNH, in collaboration with SMRU, that uses tags placed within sea trout smolts together with instruments placed on seals to detect the presence of these tags in the seals stomachs. 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 sea trout smolts, and will work best as part of large scale mark recapture efforts where high proportions of the smolts in particular river systems are fitted with implanted tags.

DNA from faecal samples can be used to identify prey species and ongoing development of analytical methods based on micro-satellite DNA may provide quantitative estimates of consumption of salmonids. Such methods are costly and are unlikely to be part of a routine monitoring programme, but could provide useful estimates of rates of predation in experimental study populations.

16. *What work might be done to improve our knowledge of seal diet by directly observing mortality of prey fish? (DEFRA Q-11)*

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 (SCOS 06/5).

Camera systems placed directly on the seals are currently being researched by SMRU and have been used successfully to study predation. This method 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 by SMRU.

Direct tracking of potential prey fish may reveal locations where mortality occurs and these may be related to abundance of potential predators. Advanced acoustic transmitters may also telemeter temperature and thus show when fish have been consumed by warm blooded animals. Subsequent movements patterns may enable differentiation between predation by seals and cetaceans.

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

17 What work might be done to improve our knowledge and understanding of the main causes of seal mortality?(DEFRA Q-12)

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.

18. *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 English waters? (DEFRA Q-13)*

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 better 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.

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; studies that show the extent to which surrounding habitat is important to the dynamics of seal populations within the SAC are also needed. 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.

19 *What are the likely implications of the recent outbreak of PDV in Denmark for Scottish seal populations. (SEERAD Q-14)*

PDV epidemics occurred in both 1988 and 2002. In both cases the mortality was highest in the English common seal population in the Wash and adjacent sites. Mortality was approximately 50% in 1988 and 22% in 2002. Mortality rates were low in most of Scotland in 1988 (with the exception of Strathclyde) and effectively zero in 2002. The current outbreak started in the same area of the Baltic and is apparently spreading west. However, the spread is apparently slower than in previous epidemics. At the time of writing there has been no evidence of the disease in the Wadden Sea. It is unlikely therefore to spread into the UK population until much later than in the previous epidemics. The post moult behaviour of common seals involves less time spent at haulout sites and much longer foraging trips. Contact rates would be lower and we would expect the spread of the virus to be less efficient.

We do not know what will happen if the virus arrives after the moult, but it may be that any disease event would be less dramatic than in previous epidemics. It seems unlikely that the Scottish common seal population will suffer higher mortality than in previous outbreaks.

Grey seals can become infected and may act as carriers for the virus but do not appear to suffer any increased mortality as a result of PDV infection.

20 *What is the latest estimate of seal populations in the Moray Firth management area? (SEERAD Q-14)*

Two aerial surveys of the Inner Moray Firth including Loch Fleet and Findhorn were completed in August 2006. Results for each sub-region (for 2005 and 2006) are presented in Table 4 below and in more detail in SCOS-BP 07/3. For the Inner Moray Firth, numbers hauled out in August 2006 varied between 719 and 752. If the adjacent haulout sites in Loch Fleet and at the mouth of the Findhorn were included, the numbers increased to between 840 and 894.

Both 2006 counts were slightly higher than counts from 2005. The maximum count in 2006 was 9% higher than the equivalent counts for 2005 and within 1% of the maximum counts in 2003 and 2004. The maximum was 34% lower than the peak count obtained in 1997 (SCOS-BP 06/3). Numbers in this area appear to have stabilised following a period of decline between 1997 and 2002

Table 4. Counts of common seals in the Moray Firth

Location	8-Aug-05	9-Aug-05	18-Aug-05	4-Aug-06	20-Aug-06
Ardersier	260	143	224	210	184
Beaully Firth	119	169	94	174	178
Cromarty Firth	98	101	118	119	93
Dornoch Firth	199	118	256	249	264
Inner Moray Firth Total	676	531	692	752	719
Inner Moray Firth + Loch Fleet & Findhorn	834	659	842	894	840
Inner Moray Firth + Dunbeath to Findhorn			955	1057	

21 *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? (SEERAD Q-15)*

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.

22 *What is the latest estimate of seal populations in the Firth of Tay and surrounding area and how might this information be used to inform a potential local management plan along similar lines to that being piloted in the Moray Firth?(SEERAD Q-16)*

A single survey of the seals in the Firth of Tay was carried out in August 2006. A total of 342 common seals were counted, 2% greater than the mean count for 2005. Numbers of common seals declined rapidly after 2002, declining by approximately 50% by 2005 (Table 5). This rapid decline has occurred in a Special Area of Conservation designated for common seals. The cause of this decline is unknown but is not thought to be due to deliberate culling of seals. A total of 1379 grey seals were counted on the same survey in 2006. There has been no general trend in the number of grey seals counted over the period of the common seal decline.

Regular census data is essential for assessing the status of the seal population within the SAC and for setting and monitoring management goals.

Table 5. 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	14 Aug 2005 ¹	14 Aug 2006
Eden Estuary	31	0	0	80	223	267	341	93	78	139	90
Abertay & Tentsmuir	409	428	456	289	262	153	167	53	126	82	34
Upper Tay	27	73	148	89	113	115	51	83	134	104	91
Broughty Ferry & Buddon Ness	0	169	169	117	35	165	109	232	121	36.	127
Firth of Tay Total	-	670	773	575	633	700	668	461	459	361	342

¹Thermal imaging survey

²In 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.

23. What are the trends in the abundance of common seals at Strangford Lough and how should these be interpreted?

A preliminary analysis of data from a long term monitoring program involving frequent ground counts of seals in the Strangford Lough area including the Narrows shows a very pronounced annual cycle with numbers reaching a peak in summer, during the breeding season. Briefly, the results suggest that harbour seal counts have declined by 3% per annum (95% CI: 1-5%) producing a 35% decline over the period 1994 to 2006. Total grey seal counts have grown at 8% pa (95% CI: 6-10%) equivalent to an overall 200% increase over the same period. The summer peak in harbour seal pups has become less high but wider.

Recent tracking studies of seals tagged within Strangford Lough have suggested that the population feeds mainly in the Irish Sea and that seals that occur within the Lough also haul out regularly in areas outside. Therefore, changes in the number of seals at Strangford Lough are likely to be closely linked to the dynamics in the population using the wider Irish Sea coast.

ANNEX II

Briefing papers for SCOS

The following briefing papers are included to ensure that the science underpinning the SCOS Advice is available in sufficient detail. *Briefing papers* provide up-to-date information from the scientists involved in the research and are attributed to those scientists.

Briefing papers do not replace fully published papers. Instead, they are an opportunity for SCOS to consider both completed work and work in progress. It is also intended that current *briefing papers* should represent a record of work that can be carried forward to future meetings of SCOS.

List of briefing papers appended to the SCOS Advice, 2007

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Grey seal pup production in Britain in 2006

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1. Surveys conducted in 2006

Each year SMRU conducts aerial surveys of the major grey seal breeding colonies in Scotland, where most grey seals breed, to determine the number of pups born. Other smaller colonies, where grey seal pups have been seen or reported, or locations which appear to be suitable for colonisation, are visited less frequently. During the 2006 breeding season, between three 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 third survey of grey seal pups in Shetland, following on from their excellent surveys in 2004 and 2005. The counts were either from boats or from the ground. National Trust staff counted pups born at the Farne Islands and at the 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. SNH staff counted South Ronaldsay in Orkney three times this year (instead of four) due to inclement weather conditions.

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

All the major colonies in Scotland were surveyed at least five times. A small number of the most recent or most difficult colonies were surveyed three times (Loch Eriboll, Eilean nan Ron at Tongue, Sule Skerry and Helmsdale). The new colony on Pabbay, south of Barra in the Outer Hebrides (Figure 1), was photographed again and is now included with the rest of the Outer Hebrides colonies. The colony on Rothiesholm on Stronsay, in Orkney, was also surveyed and has been fully incorporated into the Orkney group.

The Linhof cameras functioned more or less properly throughout the survey session. One developed a fault with the film wind-on mechanism (this has happened a number of time before), resulting in a large rebate between frames. This does not result in any loss of data, just an amount of wasted film. The cameras will be serviced prior to next breeding season.

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 2006 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 2006 at all annually monitored colonies was estimated to be 39,727, an increase of +3.3% from the 2005 production of 38,460 (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 2006 is shown in Figure 2a. Figure 2b shows the long-term pup production trajectories at the main island groups from 1960 to 2006. Pup production from the main island groups since 1987, 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.

For colonies not surveyed by air, pups were counted directly from the ground. Ground 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 are counting pups

annually at the new Blakeney Point colony and Naturally English staff count the new colony at Horsey in east Norfolk. SNH staff counted pups on South Ronaldsay and in Shetland in a manner compatible with counts from aerially surveyed colonies and production was estimated using the same modelling procedure. The South Ronaldsay data are now included with the main Orkney production estimates.

The recently established colonies in the Outer Hebrides and Orkney and along the Helmsdale coast 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 and there are occasions when it 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 2005 and 2006, total pup production at annually monitored colonies increased by +3.3% overall, with the change varying from -5.6% in the Outer Hebrides to +12.6% in the Lincolnshire and Norfolk colonies. Orkney, which produces most pups, increased by 9.6%

In spite of the observed increases, the 2006 results continue to support the trend of an overall slowing in the rate of increase in the number of pups being born and that production remains variable from year to year. The most notable changes in 2006 were: the increase in pup production in Orkney (where it returned to the 2004 level); and the overall decline in the Outer Hebrides (Tables 1 and 3, Figures 2b and 3a).

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). More recently, there were declines in pup production in 1997 (mainly due to a reduction in the number of pups born in the Outer Hebrides), in 1999 (in all island groups), in 2002 (mainly in the Outer Hebrides) and in 2005 (primarily in the Orkney colonies). In the years following each of these declines, there was a marked increase in production the following year (of 9.5%, 11.5%, 7.4% and 3.9% in 1998, 2000, 2003 and 2006 respectively). The recovery in 2006 was

considerably smaller than in previous years.

The overall annual percentage change in pup production at each of the main island groups over the past five years (between 2002 and 2006) is shown in Table 1. These varied from -0.2% at the Farne Islands to +15.6% at the relatively small colonies of Donna Nook, Blakeney Point and Horsey. The overall annual change, for all colonies combined, was +1.2%. 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), particularly at colonies in the Outer Hebrides and in Orkney. 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 1992 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 and incorporate a fixed mean time-to-leave (and a variable standard deviation) derived from studies on the Isle of May.

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.

When counts of pups from the ground were used to populate the model, using a higher percentage of correctly classified pups produced a better fit with lower confidence intervals. This is because individual pups can be observed for longer and the classification is very likely to be more accurate.

5. Confidence limits

Ninety-five percent confidence limits on the pup production estimates varied from being within 2.2% of the point estimate for the Outer Hebrides to 7.2% for 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 colonies not surveyed annually (Tables 2 and 4). Confidence limits cannot be calculated for the provided estimates because they represent single counts. Loch Eriboll, Eilean nan Ron (Tongue) and the coast between Duncansby Head and Helmsdale are exceptions and these colonies were surveyed three times in 2006 and pup production estimated using a normal distribution. 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 5,500 pups were born at colonies not surveyed annually.

Note that the surveys described here do not account for seals breeding in caves. Small groups of grey seals breed in caves in the Outer

Hebrides, along the coast of Sutherland, in Orkney and in Shetland.

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.

Five colonies were counted three times or more and for these, pup production was estimated using the standard SMRU model using a normally distributed birth curve (Table 5). A number of colonies that were surveyed in previous years were omitted due to the time required for survey and/or the small numbers of pups found. Two colonies were counted fewer than three times and the maximum count used (Table 5). As with the previous surveys, the model was run using both a 50% moult classification and a 90% classification. The model produced better fits to the counts, with lower confidence intervals, using the 90% classification and we recommend that the 90% moult 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 2006 was 677 pups. This figure is a combination of modelled estimates, of maximum counts and of the most recent counts from previous years. This is an underestimate of grey seal pup production in Shetland, since a number of colonies were either not surveyed, or were not surveyed in their entirety (e.g. Uyea). 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 colony, the island of Uyea, can only be accessed by boat and operating and weather restrictions prevented 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 (all of it) 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. The report summarising this survey is in the final stages of preparation.

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 Ards breeding colonies, not those inside Strangford Lough. The main breeding colonies were 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. In 2005, 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 approximately 100 grey seal pups were born in Northern Ireland in 2005 and Table 2 shows this estimated number.

9. Proposed surveys for 2007

In the 2007 breeding season, we propose to continue the current survey protocol to obtain at least five counts for each main grey seal colony in Scotland.

10. Acknowledgements

We are grateful to all those who provided or helped collect the data presented in this report. These include: John Walton (National Trust, Farne Islands), Rob Lidstone-Scott (Lincolnshire Wildlife Trust, Donna Nook), Ruth Priestley (SNH, South Ronaldsay), David Wood (National Trust, Blakeney Point) and Ron Morris and Dave Jones (Forth Seabird Group, Forth inner islands). Karen Hall (SNH) coordinated the 2006 Shetland grey seal survey, ably assisted by a hardy team of volunteers. Thanks to Alicia Pomeroy who cheerfully helped during our 2006 aerial survey and to Bill Giles enthusiastically and expertly piloted the survey aircraft

Table 1. Pup production estimates for colonies in the main island groups surveyed in 2006. 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	2006 pup production	Overall annual change in pup production			
		2005-2006	1992-1996	1997-2001	2002-2006
Inner Hebrides	3,461	+2.18%	+2.49%	+0.14%	+2.26%
Outer Hebrides	11,612	-5.57%	+2.19%	+1.55%	+0.28%
Orkney	19,332	+9.57%	+9.76%	+4.95%	+0.30%
Isle of May + Fast Castle	2,631	-3.20%	+3.86%	+3.27%	+0.93%
Farne Islands	1,254	+10.19%	+1.68%	-1.71%	-0.19%
Donna Nook + Blakeney Pt + Horsey (new)	1,437	+12.62%	+14.62%	+14.51%	+15.60%
North Sea (i.e. previous 3 locations)	5,322	+3.70%	+4.00%	+3.03%	+4.0%
Total	39,727	+3.29%	+5.27%	+3.13%	+1.24%

Table 2. Pup production estimates for breeding colonies surveyed less regularly. The 2006 production estimate for Shetland is lower than for 2004 (943) because fewer colonies were surveyed.

Location	Date and location of last survey	Pup production
Mainland Scotland*	Helmsdale (Duncansby Head to Helmsdale, 2005	1,284 (modelled from 3 counts)
	**Loch Eriboll, Eilean nan Ron (Tongue) 2005	701 (modelled from 3 counts)
Other colonies	Various, from Table 4	943
Shetland	2006	677
South-west Britain	South-west England	1,750
	Wales 1994	
Northern Ireland	2005	100 (approx.)
Total		5,455

*South Ronaldsay is now included with the main Orkney breeding colonies.

**Loch Eriboll, Eilean nan Ron and Helmsdale 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, 1960-2006.

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 ¹
1997	3076	11946	14051	3698	32771
1998	3087	12434 ²	16367	3989	35877 ²
1999	2787	11759	15462	3380	33388
2000	3223	13396	16281	4303	37210
2001	3032 ³	12427	17938	4134	37531 ³
2002	3096	11248	17942 ⁴	4520 ⁴	36816 ⁴
2003	3386	12741 ⁵	18652 ⁵	4805 ⁵	39584 ⁵
2004	3385	12319	19123 ³	4921	39748
2005	3387	12297 ⁶	17644 ⁶	5132	38460 ⁶
2006	3461	11612	19332	5322	39727

¹Calf of Flotta included with Orkney total (1996).²Berneray and Fiaray (off Barra) included in the Outer Hebrides total (1998).³Oronsay included with Inner Hebrides (2001).⁴South Ronaldsay included in the Orkney total; Blakeney Point and Horsey (both Norfolk) included with North Sea (2002).⁵North Flotta, South Westray, Sule Skerry included with Orkney; Mingulay included with Outer Hebrides (2003)⁶Pabbay included with Outer Hebrides; Rothiesholm (Stronsay) included with Orkney (2005).

Table 4. **Scottish grey seal breeding sites that are not surveyed annually and/or have recently been included in the survey programme. Data from 2006 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, 2006	40, 9
	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	2005, 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, 1989, infrequent	None None	
Outer Hebrides	Sound of Harris islands	SMRU photo	2002, 2005	358, 396
	St Kilda	Warden's reports	Infrequent	Few pups are born
	Shiant	SMRU visual	1998, every other year	None
	Flannans	SMRU visual	1994, every 2-3 years	None
	Berneria, Lewis	SMRU visual	1991, infrequent	None seen
	Summer Isles	SMRU photo	2002, 2003, 2005, 2006	50, 58, 67, 69
	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	Sanday, Point of Spurness	SMRU photo	2002, 2004, 2005, 2006	10, 27, 34, 21
	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, 2006	<10, 4 86, 72, 110, 171
	Total			943

Table 5. Pup production estimates and maximum pup counts for grey seal colonies in Shetland from 2004 to 2006. 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 productions for 2005 and 2006 are clearly underestimates as only those breeding beaches on Uyea that were visible from the mainland could be counted. These counts were provided by SNH staff (assisted by SMRU in 2004) and by a team of hardy volunteers.

Location in Shetland	2004	2005	2006
	<i>Estimated production (90% moult classification)</i>	<i>Estimated production (90% moult classification)</i>	Estimated production (90% moult classification)
Papa Stour	196	135	196
Dale of Walls	66	43	18 (max count)
Muckle Roe	23	no count	no count
Rona's Voe	106	83	50
Mousa	140	117	156
Fetlar	50	37	21 (max count)
Whalsey Islands	102 (max count)	72	77
South Havra	4 (max count)	no count	no count
Fitful Head	18 (max count)	no count	no count
Uyea (N. Mainland)	238 (max count)	122 (part only)	114 (part only)
Total max counts	362		39 +
Modelled total	582	609	593/632
Minimum pup production	943	654	677

Grey seal breeding colonies in Britain

Figure 1

Colonies asterisked are potential Special Areas of Conservation
 Major colonies encircled are surveyed annually



Figure 2a. Total estimated pup production, with 95% confidence limits, for all the major, annually monitored colonies in Scotland and England from 1984 to 2006.

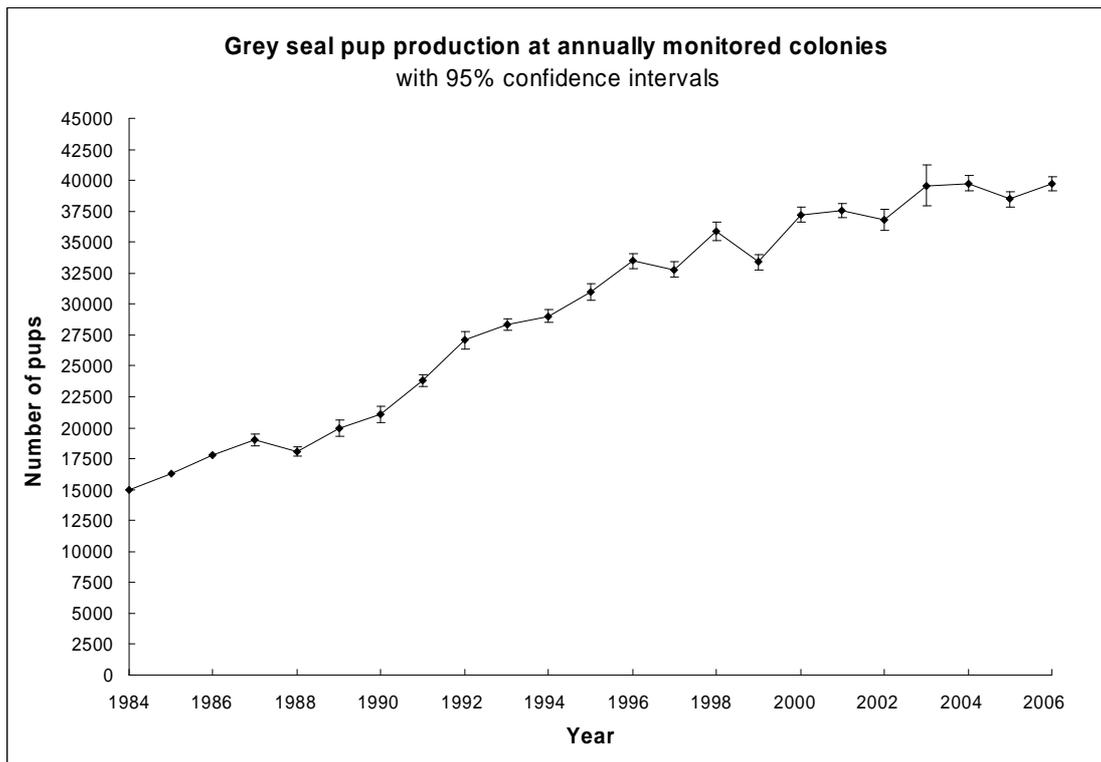


Figure 2b. Grey seal pup production trajectories from 1960 to 2006.

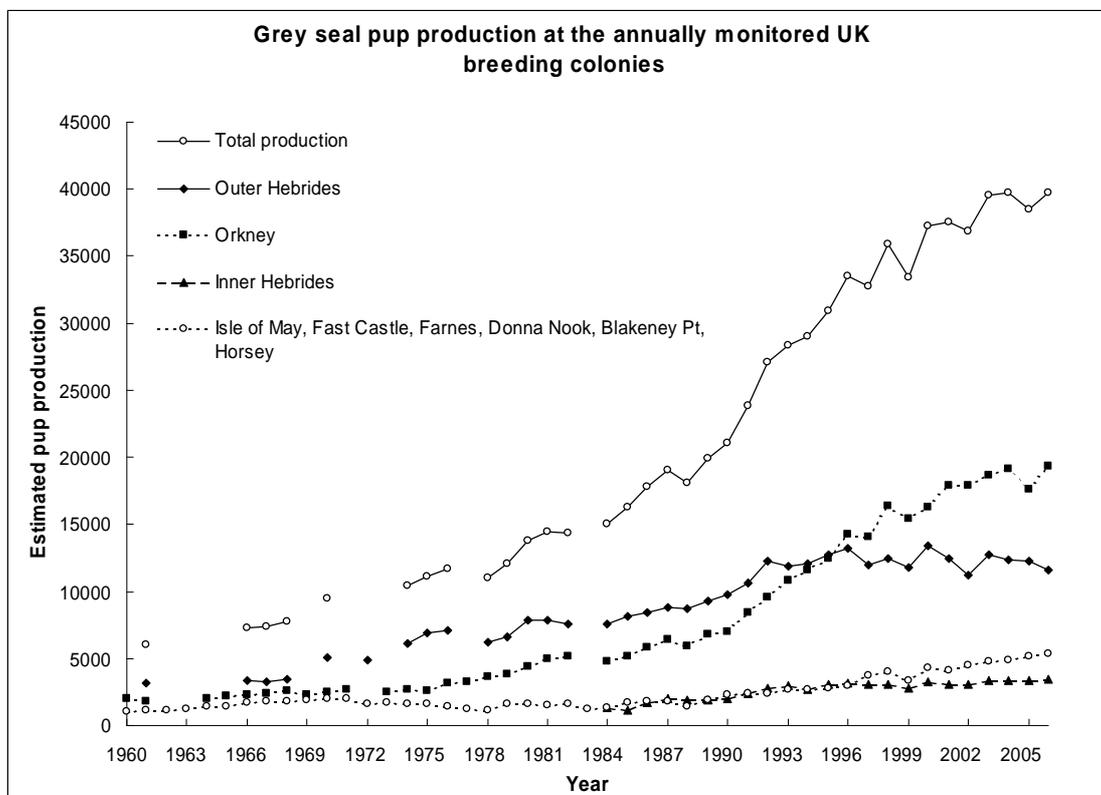
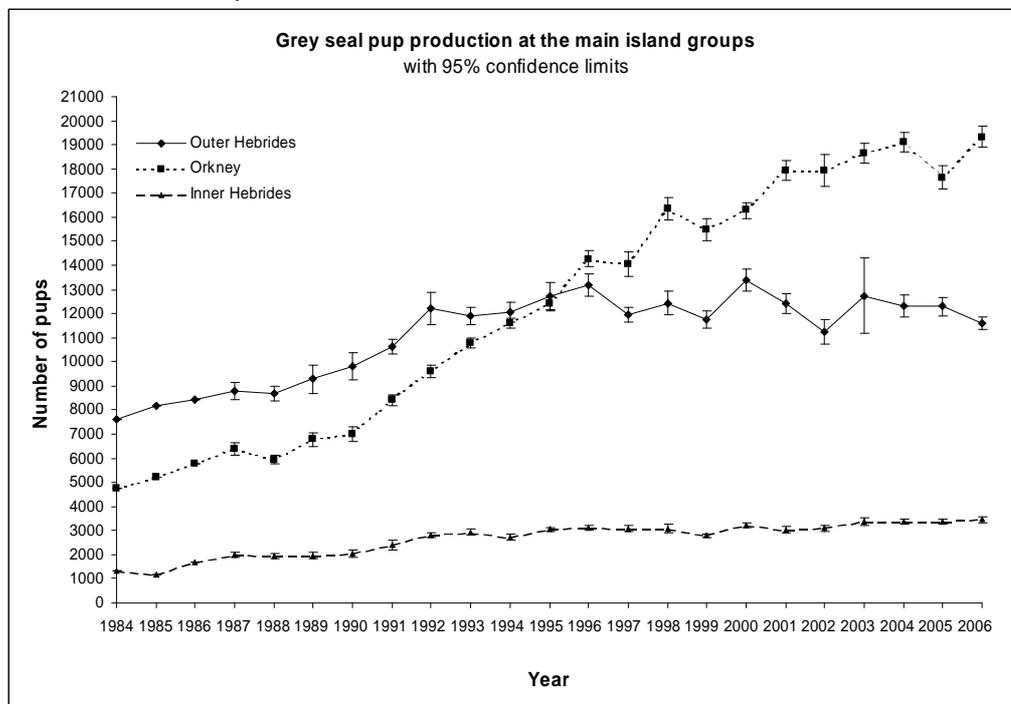
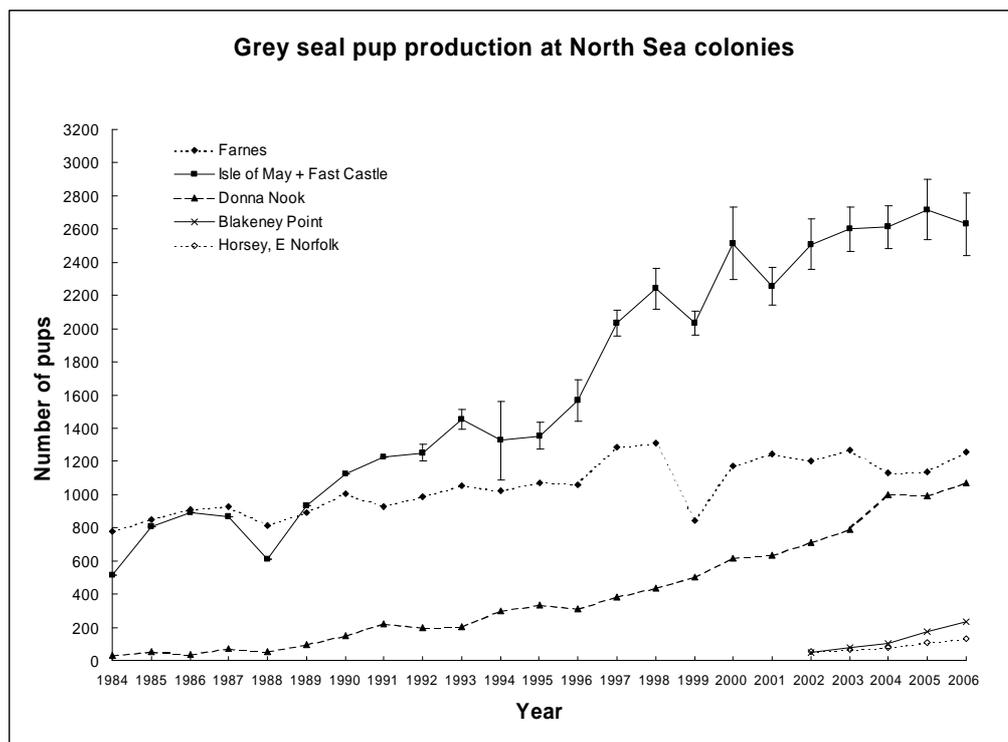


Figure 3. Trends in pup production at the major grey seal breeding colonies since 1984. Production values are shown with their 95% confidence limits where these are available. These limits assume that the various pup development parameters involved in the estimation procedure remain constant from year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

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 2006.

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Summary

We fit and compared four Bayesian state-space models of British grey seal dynamics, based on regional estimates of pup production from 1984 to 2006. The models were the same as those used in our 2005 and 2006 briefing papers: they 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. The fitting algorithms we employed were more sophisticated, allowing us to use a more appropriate observation error value than in previous years. However, Monte Carlo variation in results was also higher. We found relatively small differences in model selection criterion values between the model with simple density dependent survival and that with simple density dependent fecundity, although the former was slightly preferred. The estimated adult population size in 2006 for these two models was 116,000 (95% CI 90-154,000) and 248,000 (190-377,000) respectively, with the other two models taking intermediate values.

Introduction

In this paper, we present estimates of population size and related demographic parameters using the modelling framework of Thomas and Harwood (2005), fit to pup production data from 1984-2006. 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 fit and compare the same four models used by Thomas and Harwood (2005, 2006). Two models 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). The models are formulated within the Bayesian statistical framework, and informative priors were specified on the model parameters and initial states (the 1984 population numbers).

As in previous reports, the models were fit using a computer-intensive algorithm called a Monte Carlo particle filter (Liu 2001). However, in previous years we had employed a relatively simple particle filter and this forced us to assume that the observation error was fixed at an implausibly large value (25% coefficient of variation). For this report, we developed a more sophisticated fitting algorithm that allowed us to estimate the observation error and use this estimated value when fitting and comparing the models.

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:

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

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:

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

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

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

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

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

For the observation process, we assume that pup production estimates follow a normal distribution with a constant coefficient of variation (CV), the value of which is governed by a model parameter, ψ , where $CV = 1/\sqrt{\psi}$ (i.e., ψ is a precision parameter). We estimated the value of ψ in an initial model run, and applied this estimate to other runs – see *Model outputs and comparison*, below.

In summary, the DDS and DDF models have 11 parameters. They share 9: adult survival ϕ_a , one carrying capacity parameter-related parameter for each region $\beta_1 - \beta_4$, three movement parameters γ_{sf} , γ_{dd} , and γ_{dist} , and the observation precision parameter ψ . 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 α_{\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 1984-2006 from Duck and Mackey (2007), aggregated into regions.

Prior distributions for each parameter are given in Table 1, and are shown on Figure 3. 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
$\phi_{p_{\max}}, \phi_p$	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, α_{\max}	Be(22.05,1.15)	0.95	0.04
ψ	Ga(2.1, 66.67)	140	96.61

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). The prior distribution on ψ implies a prior mean on observation CV of 0.10 and prior standard deviation of 0.05.

Fitting Method

We used an extension of the particle filtering algorithm of Thomas and Harwood (2004, 2005, 2006), implemented in the C programming language. A particle filter is an algorithm that produces 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. An introduction to particle filtering algorithms in the context of wildlife studies is given by Newman *et al.* (2006), and a more detailed description of the

algorithm used here, applied to a similar model of seals, is given by Newman *et al.* (submitted). An outline of the main features of the algorithm is given below, for completeness – it is not necessary to read the rest of this subsection to understand the results that follow.

Integrating out the observation error parameter. We have found that it is not practical to estimate both the observation precision parameter ψ simultaneously with the states and other model parameters (because of the strong influence of ψ on the likelihood and hence particle weights for a given set of state values). Instead, we integrate ψ out of the model, and estimate the marginal posterior of this parameter conditional on estimates of the states and other model parameters (Newman *et al.* submitted). Given a gamma prior on ψ and a normal observation model, ψ has a gamma posterior distribution. The resulting likelihood weights in the integrated model are then based on the t -distribution.

Initial rejection control. The aim of this procedure is to weed out at an early stage sets of parameter and state combinations that are simulated from the prior but clearly have very low density in the posterior, so that computer time can be focussed on areas of parameter and state space that have higher posterior density. We simulated sets of 1,000,000 particles from the prior distributions, projected them forwards from 1984 to 1985 and calculated likelihood weights based on the 1985 data. We then applied rejection control, an algorithm that probabilistically removes particles with low weight (Liu 2001), using the mean of the particles weights as the rejection control criterion. This typically resulted in about a quarter of the particles being retained. We repeated this process until we had at least 1,000,000 particles surviving the initial rejection control stage.

Auxiliary particle filter (Liu and West 2001). With this procedure, we projected forward one time step at a time, starting in 1985, initially deterministically. We then resampled the particles using the deterministic weights – i.e., according to the expected pup production in the next time period – thereby producing a set of “promising” particles. Resampled copies of the same ancestor particle will have the same parameter values, so to maintain parameter diversity we used kernel smoothing to jitter the parameter values (see Liu and West 2001 for details). This can cause bias (Newman submitted), so we kept the amount of kernel

smoothing to a minimum, using a discount value of 0.997 (a value of 1.0 results in no jittering at all). After kernel smoothing, particles were then projected forward stochastically to the next time period, and weights were adjusted to take account of the initial resampling.

Final rejection control. At the last time period, rejection control was used to reduce the number of particles that must be stored. The rejection control criterion was the mean of the particle weights. This reduced the number of particles stored per run from 1,000,000 to between 200,000 and 600,000, depending on the model used.

Multiple runs. The above procedures generated samples based on 1,000,000 particles (although fewer were stored after the final rejection control). However, even this many samples gave a very imprecise estimate of the posterior distributions of interest for all models. Hence, many multiple runs (between 100 and 300) were required to reduce Monte Carlo error to acceptable levels. To reduce the resulting outputs down to a manageable level for post-processing (i.e., calculating posterior distributions on quantities of interest), it was necessary to apply further rejection control, this time using a rejection control criterion of the 99.99th percentile of the particle weights from all of the multiple runs for a particular model.

Model outputs and comparison

In previous reports, we have used the effective sample size of particles as a metric of reliability of the particle filter. This is not tenable with the new algorithm because the resampling ensures a high effective sample size of particles, but many of these particles are derived from the same initial (or “ancestral”) particle generated from the prior distributions. Hence, here we report the number of unique ancestral particles in our final sample, and we would ideally like this to be 1000 or more for each model.

To compare the models, we calculated the mean posterior Akaike Information Criterion (AIC) using the same method as Thomas and Harwood (2004, 2005, 2006). 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.

It is not useful to compare models where the observation error parameter has been estimated independently for each model. To understand why, consider two competing models, one of which fits the data well and the other poorly. Because the “good” model closely fits the data, the estimated error CV will be small, so the likelihood surface will be quite peaked, and small deviations in predicted pup counts from the observations will give rise to low negative log likelihood values, and so high AIC. On the other hand, because the “poor” model does not fit the data, the estimated error CV will be large, so the likelihood surface will be quite flat, and even large deviations in predicted pup counts from the observations may be assigned relatively large negative low likelihood values and so low AIC. Hence, a poor model can end up with a lower (i.e., “better”) AIC than a good one.

To resolve this paradox, we first estimated the measurement error parameter by fitting the data to the DDS model alone. We then took the estimated posterior mean and fit all four models using this fixed value. We present model selection statistics for these four models using the fixed observation error value.

For all four models, we also present posterior estimates of the model parameters and estimated pup production from 1984-2006. 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).

Results

Unique ancestral particle numbers

Including the estimated observation error in our algorithms meant that much more computer time was required for comparable accuracy, and we did not achieve our goal of generating at least 1000 unique ancestral particles for all models, despite simulating almost one billion particles in total. We therefore consider our results below to be somewhat provisional, pending further runs.

Table 2. Number of particles simulated (K), number saved after final rejection control step (K^*) and number of unique ancestral particles (U).

Model	K ($\times 10^7$)	K^* ($\times 10^7$)	U
ψ estimated			
DDS	300	4.90	1011
ψ fixed			
DDS	100	2.64	311
EDDS	100	1.08	176
DDF	100	0.16	187
EDDF	300	0.76	194

Estimate of observation precision parameter

Posterior estimates of both states and parameters from the DDS model run where ψ is estimated are shown in Figure 1. In this case, we achieved our target of >1000 unique ancestral particles, and the histograms showing parameter estimates are quite smooth, with little evidence of multi-modality that would indicate substantial Monte Carlo variability.

Estimated pup production generally tracks the observations well (Figure 1a), although there are several periods where the model consistently over- or under-predicts – for example in the North Sea colony, estimated pup production is higher than the observed value for 1992-1996 and then lower than the observed value for 8 out of the subsequent 10 years. Nevertheless, the estimates are much closer to the data than for previous analyses (e.g., Thomas and Harwood 2006), something we return to in the discussion.

Histograms of marginal parameter estimates (Figure 1b) indicate that the posterior estimates are almost identical to the priors for $\phi_{p\max}$ and α , indicating that essentially nothing has been learnt from the data about these parameters. In contrast, posteriors for the other parameters are somewhat modified relative to the priors. This is similar to the findings of Thomas and Harwood (2005), who used a more formal sensitivity analysis.

The estimated posterior mean of ψ is 151, and we used this value in the 4 model runs reported in the next sub-section. As an aside, posterior mean observation CV can easily be estimated, as the weighted average of the CV for each particle:

$$CV\hat{V} = \frac{\sum_{k=1}^{K^*} w^{[k]} \left(1/\sqrt{\psi^{[k]}}\right)}{\sum_{k=1}^{K^*} w^{[k]}}$$

where $w^{[k]}$ is the weight associated with particle k , $\psi^{[k]}$ is the observation precision parameter for that particle, and K^* is the total number of particles. Using this method, the computed estimate of CV is 0.083 (corresponding 95% credibility interval 0.068, 0.101).

Comparison of models for density dependence

Smoothed posterior estimates of pup production (Thomas *et al.* 2005) for the four models, run with ψ fixed at 151, are shown in Figure 2. For all of these models we did not achieve a sufficient sample of unique particles (Table 1).

The DDS model estimates (Figure 2a) are almost identical to those from the analysis where ψ was estimated (Figure 1a), which is re-assuring despite the low number of unique particles. The state estimates are quite similar among the other 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. All of the models show runs of positive and negative residuals, as noted for the DDS model earlier. Also, they are all rather better fits than previous analyses (e.g., Thomas and Harwood 2006, Figure 1) – something we discuss later.

There is some evidence of a lack of smoothness in the estimates – e.g., for the DDF model, Outer Hebrides 1986, and EDDF model, Outer Hebrides around 1995. These may be artefacts caused by Monte Carlo error, due to the low sample size of ancestral particles used in producing these results.

According to the AIC and AICc statistics (Table 3), the DDS and DDF models were strongly favoured over the EDDS and EDDF models. The DDS model was also slightly favoured over DDF (1.92 AIC and AICc points lower). However, we caution that these results are likely subject to high Monte Carlo error, and are potentially biased by the fitting method used (see Discussion).

Posterior parameter estimates are shown in Figure 3. There is clear evidence of multimodality in many of the histograms, particularly for the DDS and EDDS models, indicating high Monte Carlo variation. Hence we do not attempt to make any inferences about the estimated values.

Table 4. Estimated size, in thousands, of the British grey seal population at the start of the 2006 breeding season, derived from models fit to data from 1984-2006. Numbers are posterior means with 95% credibility intervals in brackets.

	DDS	EDDS
North sea	13.8 (11 17.9)	14.6 (10.1 20.3)
Inner Hebrides	9.5 (7.1 12.7)	9.6 (7.6 13)
Outer Hebrides	33.8 (26.5 44.6)	36.1 (28.6 52.6)
Orkney	58.5 (45.8 79.1)	64.3 (40.3 100.6)
Total	115.7 (90.4 154.4)	124.6 (86.6 186.4)
	DDF	EDDF
North sea	28.3 (21.6 41.1)	26.9 (22.3 30.5)
Inner Hebrides	23.1 (16.8 34.9)	17.7 (15.9 21.9)
Outer Hebrides	86.8 (63.7 151.2)	67.4 (60.1 83.5)
Orkney	109.8 (88 150.4)	98.7 (87.3 108.8)
Total	248 (190.1 377.7)	210.6 (185.6 244.8)

Table 3. Mean posterior log-likelihood, AIC, AICc and Akaike weights for models with fixed observation precision of 151 fit to data from 1984-2006.

Model	LnL	AIC	Δ AIC	Akaike (AIC) weight	AICc	Δ AICc	Akaike (AICc) weight
DDS	-681.18	1386.36	0.00	0.72	1390.32	0.00	0.72
EDDS	-687.10	1400.12	13.82	0.00	1404.86	13.83	0.00
DDF	-682.15	1388.29	1.92	0.28	1392.24	1.92	0.28
EDDF	-686.65	1399.30	12.93	0.00	1402.97	12.93	0.00

Discussion

Reliability of results

One aspect of reliability is Monte Carlo variation – i.e., variability in results that would be obtained by repeatedly running the fitting algorithm on the same data. We set an *ad hoc* target of 1000 unique ancestral particles, and this seems justified from our results: the initial DDS run that had >1000 unique particles appeared to show low Monte Carlo variation (as evidenced by smooth estimated pup production trajectories and posterior parameter distributions), while the runs with fixed ψ value, which had <1000 unique particles showed evidence of high Monte Carlo variation. A more formal approach was taken by Newman *et al.* (submitted), who used replicate runs of the algorithm on replicate simulated datasets to quantify both bias and Monte Carlo variation – although they only looked at parameter estimates and not states. For their model (similar to the DDS model here, with estimated ψ), 300 million particles appeared to be enough to reduce Monte Carlo variation to negligible levels. In our runs, the same number of particles appeared adequate for the DDS model, but clearly more will be required for the other models, particularly DDF and EDDF. For example, for EDDF, 300 million particles produced 194 unique ancestral particles (Table 1), implying that 1546 million particles will be required to produce 1000 unique ancestral particles.

A second aspect of reliability is bias induced by the fitting algorithm. The kernel smoothing of parameters that is employed within the auxiliary particle filter preserves the first two moments of the parameter distributions, but does not preserve the relationship between parameters and states. Using simulated data and comparisons with Markov chain Monte Carlo estimates, Newman *et al.* (submitted) found that using the discount

parameter of 0.997, as employed here, led to negligible bias in the marginal posterior parameter estimates. However, they did not investigate bias in the state estimates. A preliminary study comparing state estimates for the DDS model with and without kernel smoothing (Thomas, unpublished) shows that the better fit reported in this report relative to last years' report may be largely due to kernel smoothing bias rather than the better observation error model. This matter needs further investigation.

Comparison with previous estimates

Despite differences in algorithm and observation error models, the estimates of total population size are rather similar to those from last year. For example, the 2005 estimate from Thomas and Harwood (2006) under the DDS model was 105.2 (95%CI 79.3-141.7), compared with estimates for 2005 in the current report (Appendix 1) of 113.0 (88.9-149.7). Compared with Thomas and Harwood (2006), the DDS estimates are slightly higher, the DDF estimates slightly lower, and the EDDDS and EDDF estimates are closer to the DDS and DDF estimates, respectively. There is still a nearly 2-fold difference in population size estimates between the DDS and DDF model, and although the model selection statistics in Table 3 cannot be considered reliable due to Monte Carlo variation, there appears still to be little to choose among these competing biological models.

One might expect that, since the estimated observation error is much lower than that assumed by Thomas and Harwood, confidence intervals on the population size estimates might be narrower. While there is some tendency for this, the effect is not great.

Future work

We are currently engaged in work aimed at further testing and improving the fitting algorithm. We are also working, in collaboration

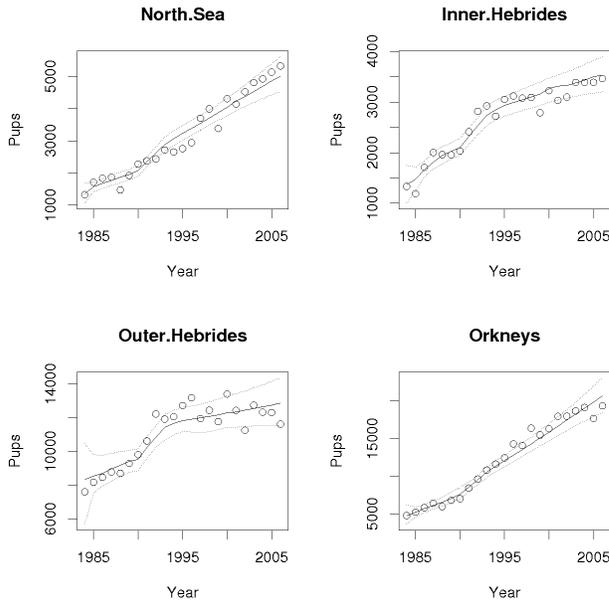
with others at SMRU, to improve the prior distributions on model parameters, based on intensive mark-recapture studies of seals at the Isle of May and North Rhona. However, by far the biggest source of uncertainty comes from which is the appropriate demographic parameter to model density dependence in. We have previously demonstrated the utility of obtaining a single additional estimate of total population size (Thomas and Harwood 2005, Matthiopoulos *et al.* 2006), and we now hope to obtain such an estimate in the foreseeable future.

References

- Buckland, S.T., K.B. Newman, L. Thomas and N.B. Koesters. 2004. State-space models for the dynamics of wild animal populations. *Ecological Modelling* 171: 157-175.
- Duck, C.D. and B.L. Mackey 2007. Grey seal pup production in Britain in 2006. *SCOS Briefing Paper 07/2*.
- Hiby, L. and C.D. Duck. Unpublished. Estimates of the size of the British grey seal *Halichoerus grypus* population and levels of uncertainty.
- Jamieson, L.E. and S.P. Brooks. 2004. Density dependence in North American ducks. *Animal Biodiversity and Conservation* 27:113-128.
- Liu, J.S. 2001. *Monte Carlo Strategies in Scientific Computing*. Springer-Verlag, New York.
- Liu, J., and West, M. 2001. Combined parameter and state estimation in simulation-based filtering. In *Sequential Monte Carlo Methods in Practice.*, eds. Doucet, A., de Freitas, N., and Gordon, N. 197–223. Springer-Verlag, Berlin.
- Matthiopoulos, J., L. Thomas, B. McConnell, C.D. Duck, D. Thompson, P. Pomeroy, J. Harwood, E.J. Milner-Gulland, N. Wolf and M. Mangel. 2006. Putting long-term, population monitoring data to good use: the causes of density dependence in UK grey seals. *SCOS Briefing Paper 06/8*
- Newman, K.B., C. Fernández, L. Thomas., and S.T. Buckland. Submitted. Inference for state-space models for wild animal populations.
- Newman, K.B., S.T. Buckland, S.T. Lindley, L. Thomas and C. Fernández. 2006. Hidden process models for animal population dynamics. *Ecological Applications* 16:74-86.
- Ruxton, G.D. and P. Rohani. 1998. Fitness-dependent dispersal in metapopulations and its consequences for persistence and synchrony. *Journal of Animal Ecology* 67: 530-539.
- Spiegelhalter D. J., Best N. G., Carlin B. P. and van der Linde A. 2002. Bayesian measures of model complexity and fit (with discussion). *Journal of the Royal Statistical Society B.* 64, 583-640.
- Spiegelhalter D. J., A. Thomas, N.G. Best and D. Lunn. 2005. WinBUGS 2.10.
- Thomas, L. and J. Harwood 2004. A comparison of grey seal population models incorporating density dependent fecundity and pup survival. *SCOS Briefing Paper 04/6*
- Thomas, L. and J. Harwood. 2005. Estimating the size of the UK grey seal population between 1984 and 2004: model selection, survey effort and sensitivity to priors. *SCOS Briefing Paper 05/3*
- Thomas, L. and J. Harwood. 2006. Estimating the size of the UK grey seal population between 1984 and 2005, and related research. *SCOS Briefing Paper 06/3*
- Thomas, L., S.T. Buckland, K.B. Newman, and J. Harwood. 2005. A unified framework for modelling wildlife population dynamics. *Australian and New Zealand Journal of Statistics* 47: 19-34.
- Thomas, L., T. van Lamsweerde and J. Harwood. 2004. The nature of density dependence in British grey seal populations. NERC Special Committee on Seals Briefing Paper 04/4.

Figure 1. Posterior estimates from a DDS model of grey seal population dynamics where the observation precision parameter ψ is estimated, fit to pup production estimates from 1984-2006.

(a) Estimates of true pup production (solid lines), together with 95% credibility interval (dotted lines) and observed pup production (circles).



(b) Parameter estimates (histograms) and priors (solid lines). The vertical line shows the posterior mean; its value is given in the title of each plot after the parameter name, with the associated standard error in parentheses.

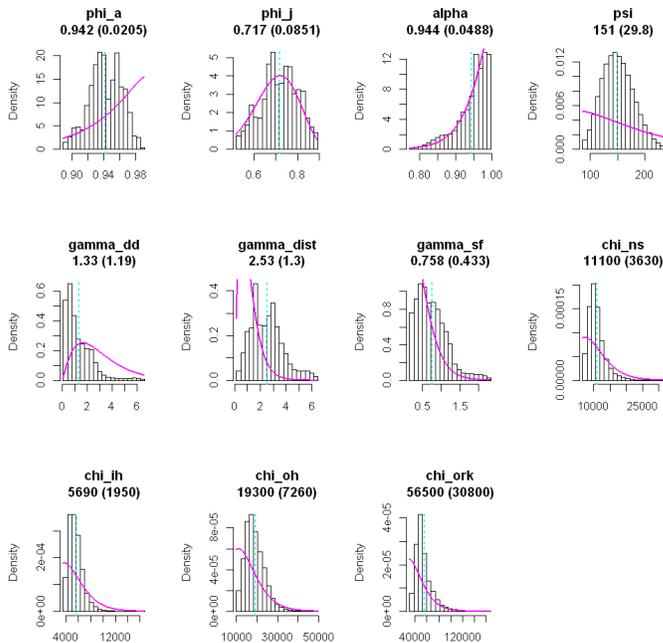
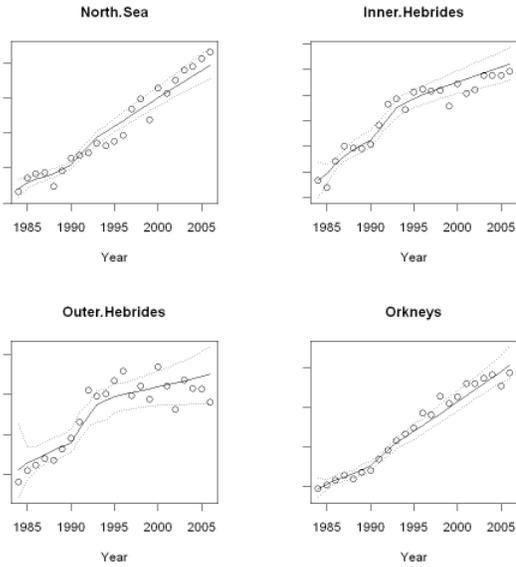
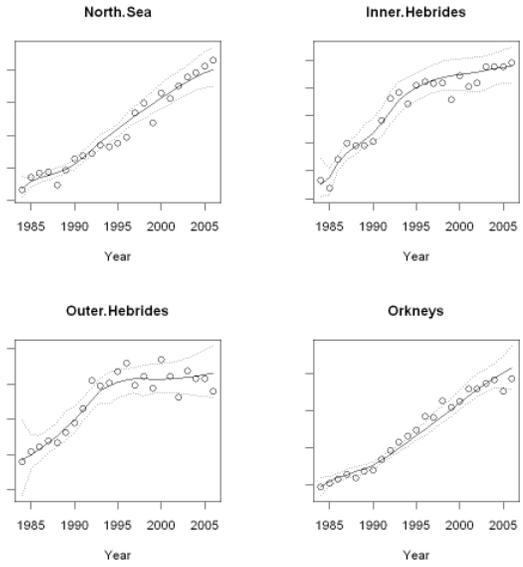


Figure 2. Estimates of true pup production from four models of grey seal population dynamics, where the observation precision parameter ψ is fixed at 151, fit to pup production estimates from 1984-2006. Input data are shown as circles, while the lines show the posterior mean bracketed by the 95% credibility interval.

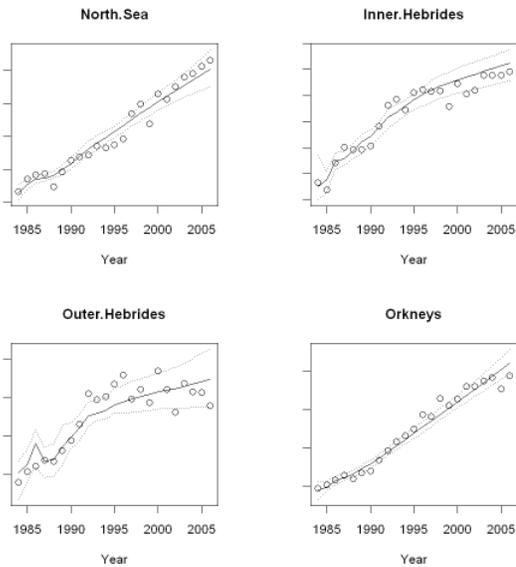
(a) Density dependent survival (DDS)



(b) Extended density dependent survival (EDDS)



(c) Density dependent fecundity (DDF)



(d) Extended density dependent fecundity (EDDF)

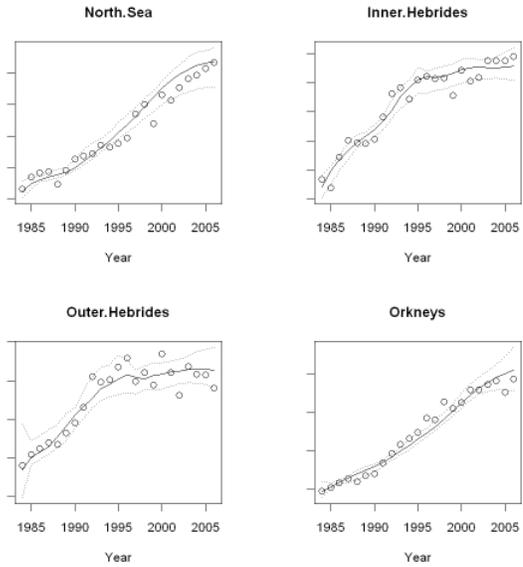
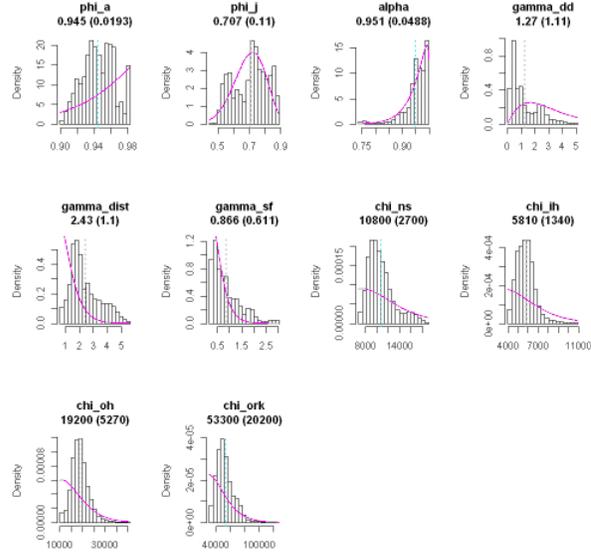
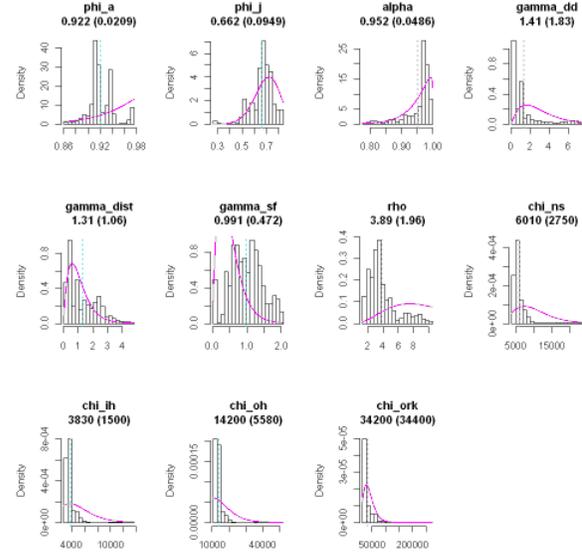


Figure 3. Posterior parameter estimates (histograms) and priors (solid lines) from four models of grey seal population dynamics where the observation precision parameter ψ is fixed at 151, fit to pup production estimates from 1984-2006. The vertical line shows the posterior mean, its value is given in the title of each plot after the parameter name, with the associated standard error in parentheses.

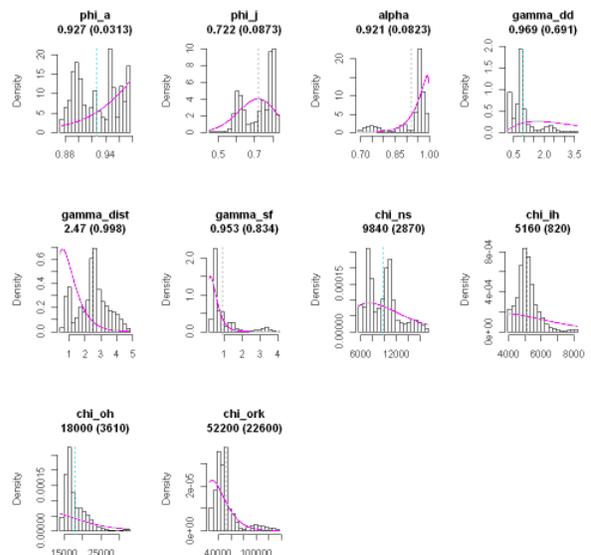
(a) Density dependent survival (DDS)



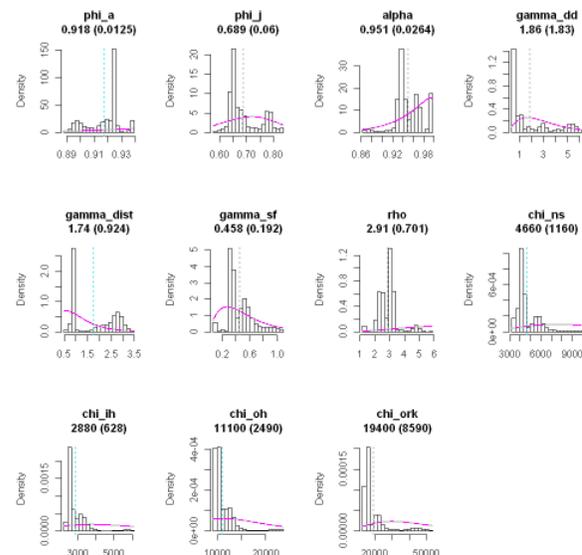
(b) Extended density dependent survival (EDDS)



(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	4.6 (3.8 5.6)	4.7 (3.6 5.7)	24.4 (19.2 31.6)	16.7 (13.7 22.2)	50.3 (40.3 65.2)
1985	5 (4 6.1)	4.9 (3.9 6.1)	24.5 (19.4 31.8)	18 (14.9 23.6)	52.4 (42.3 67.6)
1986	5.5 (4.7 6.7)	5.4 (4.5 6.7)	26.4 (20.9 33.9)	19.9 (17 26.3)	57.3 (47.1 73.6)
1987	6.1 (5.3 7.3)	5.9 (5 7.5)	28.1 (22.8 36.5)	22 (18.9 29.2)	62.1 (52 80.4)
1988	6.6 (5.8 8.1)	6.4 (5.4 8.2)	29.8 (24.6 38.7)	24.1 (20.9 31.9)	66.9 (56.6 86.9)
1989	7 (6.1 8.6)	6.7 (5.5 8.6)	30.2 (24.6 39.6)	25.8 (22.4 34.2)	69.7 (58.7 91)
1990	7.4 (6.4 9.2)	7 (5.6 9.1)	30.3 (24.6 40.2)	27.6 (24 36.6)	72.2 (60.6 95.1)
1991	7.9 (6.8 9.7)	7.2 (5.7 9.5)	30.2 (24.6 39.7)	29.4 (25.5 38.9)	74.7 (62.7 97.8)
1992	8.3 (7.2 10.3)	7.4 (5.8 9.8)	30.3 (24.7 39.4)	31.3 (27.2 41.2)	77.2 (64.9 100.6)
1993	8.7 (7.5 10.8)	7.6 (5.9 10.1)	30.5 (25 39.2)	33.2 (28.8 43.5)	79.9 (67.2 103.5)
1994	9.1 (7.8 11.3)	7.8 (6 10.4)	30.7 (25.2 39.1)	35.1 (30.1 45.9)	82.7 (69.1 106.6)
1995	9.5 (8.1 11.8)	8 (6.1 10.6)	30.9 (25.3 39.3)	37 (31.6 48.3)	85.5 (71.2 110)
1996	9.9 (8.4 12.4)	8.1 (6.2 10.9)	31.2 (25.5 39.5)	39 (33 50.7)	88.3 (73.1 113.4)
1997	10.4 (8.7 12.8)	8.3 (6.3 11)	31.4 (25.6 39.7)	41 (34.5 53.1)	91 (75.1 116.6)
1998	10.8 (9 13.3)	8.4 (6.4 11.1)	31.7 (25.7 40.1)	42.9 (35.8 55.6)	93.8 (76.9 120.1)
1999	11.2 (9.3 13.8)	8.6 (6.5 11.2)	31.9 (25.8 40.5)	44.9 (37.2 58.3)	96.6 (78.8 123.9)
2000	11.6 (9.6 14.4)	8.7 (6.6 11.4)	32.2 (25.9 41.1)	46.9 (38.5 61)	99.3 (80.5 127.8)
2001	12 (9.8 14.9)	8.9 (6.7 11.6)	32.5 (26 41.6)	48.8 (39.7 63.7)	102.1 (82.3 131.9)
2002	12.3 (10.1 15.6)	9 (6.8 11.9)	32.7 (26.1 42.2)	50.8 (41 66.5)	104.9 (84 136.1)
2003	12.7 (10.3 16.2)	9.1 (6.8 12.1)	33 (26.2 42.8)	52.7 (42.3 69.6)	107.6 (85.6 140.6)
2004	13.1 (10.6 16.8)	9.3 (6.9 12.3)	33.3 (26.3 43.3)	54.7 (43.5 72.7)	110.3 (87.3 145.1)
2005	13.5 (10.8 17.3)	9.4 (7 12.5)	33.6 (26.4 44)	56.6 (44.7 75.9)	113 (88.9 149.7)
2006	13.8 (11 17.9)	9.5 (7.1 12.7)	33.8 (26.5 44.6)	58.5 (45.8 79.1)	115.7 (90.4 154.4)

Extended density dependent survival model

Year	North Sea	Inner Hebrides	Outer Hebrides	Orkneys	Total
1984	5.2 (4.3 6.7)	5.5 (4.4 6.8)	26.7 (22 33.6)	19.5 (14.7 22.9)	56.9 (45.5 70)
1985	5.6 (4.6 6.9)	5.8 (4.8 7.1)	27.9 (22.3 34.4)	20.7 (16.1 24.5)	60.1 (47.8 72.9)
1986	6 (5.1 7.3)	6.1 (5.2 7.4)	29.8 (25 36.3)	22.1 (18.4 26.1)	64.2 (53.7 77.1)
1987	6.5 (5.6 7.8)	6.6 (5.6 7.8)	32 (27.3 38.6)	23.8 (19.5 27.6)	68.9 (58 81.8)
1988	7 (6.2 8.4)	7.1 (6 8.3)	34.1 (28.9 41.3)	25.5 (20.8 29.2)	73.7 (61.9 87.2)
1989	7.5 (6.6 9)	7.6 (6.3 8.8)	35.1 (29.6 41.8)	27.5 (22.2 31.2)	77.6 (64.8 90.9)
1990	8.1 (7.1 9.6)	8.1 (6.8 9.4)	35.7 (29.9 42.6)	29.5 (24.1 33.6)	81.4 (67.8 95.1)
1991	8.6 (7.4 10.3)	8.5 (7.1 10.1)	36.1 (29.7 43.7)	31.7 (26 36.1)	84.9 (70.2 100.2)
1992	9.2 (7.8 10.9)	8.9 (7.2 10.8)	36.1 (29.5 43.9)	34.1 (28.1 39)	88.3 (72.6 104.6)
1993	9.8 (8.2 11.7)	9.1 (7.3 11.1)	36.1 (29.4 44.6)	36.6 (30.7 42.2)	91.6 (75.6 109.6)
1994	10.4 (8.4 12.4)	9.2 (7.5 11.1)	35.9 (29.2 45.3)	39.3 (33.3 45.6)	94.8 (78.4 114.5)
1995	11 (8.8 13.1)	9.3 (7.7 11.2)	35.7 (29.2 44.9)	42.1 (35.1 49.3)	98 (80.8 118.5)
1996	11.6 (9.1 14.2)	9.3 (7.6 11.3)	35.5 (29.4 45.9)	44.8 (36.7 53)	101.2 (82.7 124.4)
1997	12.1 (9.3 15)	9.4 (7.7 11.3)	35.3 (29.1 47.2)	47.5 (38.4 56.5)	104.4 (84.5 129.9)
1998	12.6 (9.8 15.7)	9.4 (7.7 11.4)	35.3 (28.5 48.3)	50.1 (39.9 60)	107.4 (86 135.5)
1999	13.1 (10.1 16.5)	9.4 (7.7 11.7)	35.3 (28.3 49.3)	52.6 (41.8 63.4)	110.3 (87.8 141)
2000	13.4 (10.4 17.2)	9.4 (7.6 12.1)	35.3 (28.3 50)	54.7 (44.1 67.6)	112.9 (90.4 146.8)
2001	13.8 (10.7 17.8)	9.4 (7.5 12.3)	35.5 (28.3 50.6)	56.7 (45.9 72.2)	115.4 (92.4 152.8)
2002	14.1 (10.8 18.3)	9.5 (7.5 12.5)	35.6 (28.5 51.1)	58.4 (45.5 77.2)	117.6 (92.3 159.1)
2003	14.3 (10.8 18.9)	9.5 (7.5 12.6)	35.7 (28.6 51.6)	60 (45.4 82.5)	119.6 (92.4 165.6)
2004	14.4 (10.7 19.5)	9.6 (7.6 12.8)	35.9 (28.7 51.9)	61.5 (44 88.2)	121.4 (90.9 172.4)
2005	14.5 (10.5 20)	9.6 (7.6 12.9)	36 (28.6 52.3)	62.9 (42.1 94.2)	123 (88.8 179.3)
2006	14.6 (10.1 20.3)	9.6 (7.6 13)	36.1 (28.6 52.6)	64.3 (40.3 100.6)	124.6 (86.6 186.4)

Density dependent fecundity model

Year	North Sea	Inner Hebrides	Outer Hebrides	Orkneys	Total
1984	5.8 (5 7.1)	6.4 (4.8 9.9)	44.6 (33.9 55.1)	19.6 (17.5 22.1)	76.4 (61.2 94.3)
1985	6.3 (5.6 7.8)	7 (6 10.9)	45.9 (35.2 58.8)	21.4 (18.7 23.9)	80.7 (65.4 101.3)
1986	6.9 (6.2 8.6)	7.7 (6.6 11.6)	47.7 (37.8 62.1)	23.3 (20.3 26.5)	85.7 (70.8 108.8)
1987	7.7 (6.8 9.6)	8.6 (7.1 12.5)	49.9 (40.6 66.4)	25.8 (22.2 29.4)	92 (76.7 117.9)
1988	8.4 (7.2 10.5)	9.4 (7.9 13.4)	51.4 (41.7 70.4)	28.5 (24.3 32.7)	97.6 (81.1 127.1)
1989	9.1 (7.7 11.5)	10.2 (8.5 14.3)	52.9 (42.7 73.6)	31.1 (26.6 36.1)	103.3 (85.6 135.5)
1990	9.9 (8.2 12.7)	11.1 (9.2 15.4)	54.8 (44 77.7)	34.1 (29.1 39.8)	109.8 (90.6 145.6)
1991	10.7 (8.9 13.8)	11.9 (9.9 16.5)	56.8 (45.5 81.6)	37.3 (32 43.8)	116.7 (96.4 155.7)
1992	11.7 (9.6 15.1)	12.8 (10.4 17.6)	59.1 (46.8 85.9)	40.8 (35.1 48.5)	124.4 (101.9 167)
1993	12.7 (10.3 16.5)	13.7 (11 18.7)	61.6 (48.2 90.8)	44.7 (38 53.8)	132.7 (107.4 179.7)
1994	13.8 (11 17.9)	14.6 (11.6 19.7)	64 (49.5 95.3)	48.8 (41.1 59.4)	141.1 (113.2 192.3)
1995	14.9 (11.8 19.5)	15.5 (12.2 20.9)	66.1 (50.9 99.9)	52.9 (44.5 65.6)	149.4 (119.4 206)
1996	16 (12.6 21.1)	16.3 (12.8 22.2)	68.2 (52.2 104.8)	57.3 (47.9 71.9)	157.8 (125.5 220)
1997	17.1 (13.4 22.9)	17.1 (13.4 23.5)	70.2 (53.6 109.7)	61.9 (51.5 78.5)	166.3 (131.9 234.6)
1998	18.3 (14.3 24.8)	17.8 (13.9 24.8)	72.2 (55 114.4)	66.7 (55.1 85.3)	175 (138.2 249.3)
1999	19.5 (15.1 26.7)	18.5 (14.4 26.1)	74.1 (56.3 119.2)	71.6 (58.9 92.3)	183.6 (144.7 264.3)
2000	20.7 (16 28.6)	19.2 (14.9 27.4)	75.9 (57.6 123.9)	76.6 (62.8 99.7)	192.4 (151.3 279.6)
2001	21.9 (16.9 30.6)	19.9 (15.3 28.7)	77.7 (58.9 128.6)	81.7 (66.9 107.3)	201.3 (158 295.2)
2002	23.2 (17.9 32.7)	20.6 (15.7 29.9)	79.6 (60.2 133.2)	87.1 (71.1 115.3)	210.4 (164.8 311)
2003	24.4 (18.8 34.7)	21.2 (16.1 31.2)	81.4 (61.5 137.7)	92.5 (75.3 123.5)	219.6 (171.7 327.1)
2004	25.7 (19.7 36.8)	21.9 (16.3 32.4)	83.2 (62.7 142.2)	98.1 (79.5 132.1)	228.9 (178.3 343.5)
2005	27 (20.7 38.9)	22.5 (16.6 33.7)	85 (63.4 146.7)	103.9 (83.7 141.1)	238.4 (184.4 360.4)
2006	28.3 (21.6 41.1)	23.1 (16.8 34.9)	86.8 (63.7 151.2)	109.8 (88 150.4)	248 (190.1 377.7)

Extended density dependent fecundity model

Year	North Sea	Inner Hebrides	Outer Hebrides	Orkneys	Total
1984	5.2 (4.8 5.9)	5.7 (5 6.5)	27.9 (23.9 34.2)	20.7 (18.1 22.4)	59.4 (51.8 69)
1985	5.5 (5.1 6.4)	6 (5.3 6.8)	29.9 (25.8 34.8)	21.9 (19.1 23.3)	63.3 (55.3 71.3)
1986	6 (5.6 6.8)	6.4 (5.8 7.1)	32.1 (28.7 36.6)	23.4 (21 24.9)	67.9 (61 75.4)
1987	6.5 (6.1 7.3)	6.9 (6.3 7.6)	34.2 (31.7 38.5)	24.9 (23.1 26.6)	72.6 (67.2 80.1)
1988	7 (6.6 8)	7.5 (6.9 8.3)	36.4 (34.3 41.2)	26.7 (24.9 28.6)	77.6 (72.7 86.1)
1989	7.5 (7.1 8.6)	8.1 (7.4 8.8)	38.5 (36.4 42.9)	28.7 (26.7 31.1)	82.9 (77.6 91.4)
1990	8 (7.6 9.2)	8.8 (7.9 9.4)	40.7 (38.3 44.8)	30.9 (28.5 33.6)	88.5 (82.2 97.1)
1991	8.6 (8.1 10.1)	9.4 (8.6 10.1)	42.9 (40.1 46.9)	33.2 (30.4 36.1)	94.2 (87.2 103.2)
1992	9.3 (8.7 11)	10.2 (9.4 10.8)	45.2 (41.7 49.3)	35.7 (32.8 39.1)	100.4 (92.7 110.2)
1993	10.2 (9.5 12)	10.9 (10.3 11.7)	47.4 (43 52.4)	38.6 (35.6 42.5)	107.1 (98.5 118.4)
1994	11.1 (10.3 13.1)	11.7 (10.8 12.6)	49.5 (44.9 55.6)	41.7 (38.5 45.9)	114 (104.6 127.3)
1995	12.1 (11 14.4)	12.5 (11.2 13.3)	51.6 (46 59.1)	45 (41.4 50)	121.2 (109.7 136.8)
1996	13.3 (11.8 15.6)	13.2 (11.7 14.5)	53.5 (47.2 62.3)	48.8 (44.4 54.7)	128.8 (115.2 147.1)
1997	14.6 (12.7 16.8)	13.8 (12 15.6)	55.1 (48.4 65.2)	53.1 (47.4 59.3)	136.6 (120.5 156.9)
1998	16 (13.6 18.1)	14.4 (12.4 16.5)	56.5 (49.1 67.5)	57.4 (50.8 64.4)	144.3 (125.9 166.5)
1999	17.5 (14.6 19.3)	14.8 (12.5 17.4)	57.8 (49.8 69.8)	62.2 (54.5 69.7)	152.3 (131.4 176.3)
2000	18.9 (15.6 20.9)	15.3 (12.7 18.3)	59.1 (50.8 72.1)	67.1 (58.4 75.1)	160.4 (137.5 186.4)
2001	20.4 (16.6 22.6)	15.7 (13 19.1)	60.4 (52.2 74.2)	72.4 (62.5 80.7)	168.8 (144.3 196.7)
2002	21.8 (17.8 24.3)	16.1 (13.3 19.9)	61.8 (53.9 76.4)	77.8 (66.9 86.3)	177.4 (151.9 206.9)
2003	23.2 (18.9 26)	16.5 (13.7 20.5)	63.2 (56 78.4)	83.2 (71.6 92)	186 (160.2 216.9)
2004	24.5 (20.1 27.6)	16.8 (14.6 21)	64.6 (57.6 80.1)	88.5 (76.5 97.7)	194.4 (168.8 226.5)
2005	25.8 (21.2 29.1)	17.3 (15.5 21.5)	66 (58.8 81.9)	93.6 (81.8 103.4)	202.7 (177.3 235.9)
2006	26.9 (22.3 30.5)	17.7 (15.9 21.9)	67.4 (60.1 83.5)	98.7 (87.3 108.8)	210.6 (185.6 244.8)

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The status of British common seal populations

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

Summary

In Scotland in August 2006, the Sea Mammal Research Unit (SMRU) planned to survey common seals in Shetland, Orkney, the Outer Hebrides and Strathclyde. Ultimately, due to thermal imager failure and time constraints, helicopter-based thermal imaging surveys for common seals were limited to Orkney, Shetland, the Moray Firth (between Findhorn Bay and Helmsdale) and most of the Outer Hebrides. A second survey of the Moray Firth and a survey of the Firth of Tay were carried out in August from a fixed wing aircraft.

In England, common seals were surveyed from fixed-wing aircraft in Lincolnshire, Norfolk and Suffolk.

In 2006, the number of common seals counted during the moult in Orkney and Shetland had significantly decreased since the previous surveys in 2001. Further analysis showed there was an estimated population decline over this time of 42% in Orkney (95% CI 32-51), and 41% in Shetland (95% CI 29-51; Lonergan *et al.*, 2007). Numbers in the Moray Firth were slightly higher than in 2005 and numbers in the Western Isles comparable to 2003 for the same area. Numbers in the Firth of Tay remained reasonably constant, showing no sign of any recovery. Numbers in The Wash continued to decline following the 2002 phocine distemper outbreak. In contrast, numbers at Donna Nook and Blakeney Point remained relatively constant.

The analysis suggested that the highly significant changes in moult counts exceed those specified by current environmental quality metrics. This is in contrast to the apparent rapid growth in populations in the nearest European population in the Wadden Sea following the 2002 phocine distemper outbreak.

From surveys carried out between 2000 and 2006, the minimum number of common seals counted in Scotland was **23,368** and in England 3,029 making a UK total of 30,550 (Table 1). In 2002, **1,248** common seals were counted in Northern Ireland

During the 2006 breeding season, SMRU and the Fisheries Research Services (FRS) conducted repeat ground and air surveys of common seals in the Moray Firth, replacing surveys carried out by the University of Aberdeen.

Introduction

Most surveys of common seals are carried out during their 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 common seals around the Scottish coast are carried out on an approximately five-yearly cycle, although the Moray Firth and Firth of Tay are surveyed more frequently. The 2006 survey aimed to complete the second survey of common seals around the whole of Scotland, which SMRU started in 2005. However, due to equipment failure part of the east coast of the Outer Hebrides (part of Benbecula and most of North Uist) and the Strathclyde west coast (from Mull to Machrihanish) could not be completed.

The Lincolnshire and Norfolk coast, which holds over 95% of the English common seal population, is usually surveyed twice annually. In 2004, this survey was extended to include more of the Suffolk, Essex and Kent coast. In addition, English Nature funded a breeding season survey (in early July) of common seals in Lincolnshire and Norfolk, including The Wash.

Funding from Scottish Natural heritage

Scottish Natural Heritage (SNH) has provided funding for common seals surveys in every survey year since 1996. Without this additional funding, we would not have known about the serious decline in numbers in Shetland and Orkney, as we would not have been able to carry out surveys of these island groups in either 2001 or 2006.

Methods

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.

Surveys of the estuarine haulout sites on the east coast of Britain were made using large format vertical aerial photography or hand-held oblique photography from a twin-engined fixed-wing aircraft. On sandbanks, where seals are relatively easily located, this method of survey is highly cost-effective.

Results

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

Minimum population estimates based on the most recent and complete surveys of common seals in the UK are shown in Table 1. Most of the Outer Hebrides count was from 2006; the counts for the two uncompleted areas (Benbecula and North Uist) were from 2003. The Table also includes numbers from both Northern Ireland and the Republic of Ireland. Where multiple counts were obtained in any August (in The Wash, for example), the highest counts from any one survey have been used.

The overall distribution of common seals around the British Isles, based on the most recent complete regional surveys, is shown in Figure 1. This figure uses data from Scotland and England from between 2000 and 2006, for Northern Ireland from 2002 and for the Irish Republic from 2003. For ease of viewing at this scale, counts have been aggregated into 10km squares.

The most recent minimum estimate of the number of common seals in Scotland is **23,368** from surveys carried out between 2000 and 2006 (Table 1). The most recent minimum estimate for England is **3,029**. This comprises 2,784 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. Including the **1,248** common seals counted in Northern Ireland in 2002, gives a UK total of **30,550**.

2. Common seals in Scotland: moult

In August 2006, the area surveyed for common seals by thermal imager included the whole of Shetland and Orkney, the Moray Firth (between Findhorn Bay and Helmsdale) and most of the Outer Hebrides. Part of the east coasts of Benbecula and North Uist (between Wiay and Leac na Thobha, just north of Loch Madadh or Maddy) were not surveyed due to equipment failure.

The number and distribution of common seals counted during the thermal imaging surveys in August 2006 are shown in Figure 2.

The counts of common seals in different parts of Scotland, from surveys carried out between 1988 and 2006 are shown in Figure 3. In 2006, the number of common seals counted in Orkney and Shetland had significantly decreased since the previous surveys in 2001 (Table 1; Figure 3). Further analysis showed there was an estimated population decline over this time of 42% in Orkney (95% CI 32-51), and 41% in Shetland (95% CI 29-51) (Loneragan *et al.*, 2007). Numbers in the Outer Hebrides were comparable to the 2003 survey for the same areas (Figure 3).

Moray Firth

SMRU's aerial surveys of the Moray Firth began in August 1992. The counts are in Table 2 and the trends shown in Figure 4. This figure represents a combination of both thermal imaging and fixed wing surveys of the area. Both 2006 counts were slightly higher than counts from 2005. Numbers in this area appear to have stabilised following a period of decline between 1997 and 2002. These declines may have been due to a bounty system for seals which previously operated in the area (Thompson *et al.*, 2007).

Paul Thompson, from Aberdeen University's Lighthouse Field Station, in Cromarty, has detailed annual counts of common seals in the Inner Moray Firth from June, July and August between 1988 and 2005. We have been able to update Figure 4 to produce a current time-series combining the University of Aberdeen's data with SMRU data. This Figure will be presented at the SCOS meeting and will be included when this document is updated.

Firth of Tay

In 2006 in the Firth of Tay, 342 common seals were counted; a number intermediary between counts obtained in 2005 (Table 3, Figure 5). Numbers in this Special Area of Conservation (SAC) remain low compared with counts from between 1990 and 2002.

3. Common seals in Scotland: breeding season

Moray Firth

During the 2006 breeding season, SMRU and the Fisheries Research Services (FRS) conducted repeat ground and air surveys common seals in the Moray Firth. A total of five concurrent ground and fixed wing aerial surveys were completed. On 7th July 2006, a thermal imaging survey was carried out for a comparison of different survey techniques. The number of adults and pups counted during these surveys are shown in Figures 5 and 6 respectively.

With the exception of one survey, counts of adults and pups were consistently higher from aircraft survey

counts than from ground counts. This was because two groups of seals were missed during the aircraft survey. The single count using a thermal-imaging camera produced the highest count of the three methods. Surveys by ground and by fixed-wing aircraft tend to focus on areas where seals are known to haul ashore. In certain areas seals can be extremely difficult to detect. In contrast, the thermal-imaging survey covers the entire coastline within the Moray Firth.

4. Common seal surveys in England: moult

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 (Table 4, Figure 8).

One aerial survey of common seals were carried out in Lincolnshire and Norfolk during August 2006 (Tables 1 and 4). The total count for the Wash (1,695) was 13% lower than the mean 2005 count and 43% lower than the mean pre-epidemic 2002 count (2,976).

Overall, the combined count for the English East coast population in 2006 was 12% lower than the mean count in 2005. This apparent lack of recovery or continued decline contrasts with the rapid recovery of the Wadden Sea population that has been increasing at around 15% p.a. since 2002 and increased by 8.8% between 2005 and 2006. This failure to recover from the 2002 epidemic is a cause for concern and should be investigated.

5. Common seals in England: breeding season

A detailed description of the breeding season surveys in the Wash is presented in SCOS BP 07/XX. A total of 1013 pups and 2267 older seals were counted in July 2006. These were distributed over 39 separate haulout groups, although the number of sites is to some extent a function of the arbitrary divisions of sites. Pups were widely distributed, being present at all occupied sites in 2006. The 2006 pup count was much higher than in any previous survey, being 55% greater than the 2005 count. Again, the 2006 adult count was much higher than in previous breeding season surveys, 28% higher than the 2004 count.

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 2006.

A simple model of the birth and haulout patterns

(SCOS BP 07/4) suggests that the dramatic increase is unlikely to be due to changes in the timing of the survey.

6. Common seal surveys 2007

Breeding season: Moray Firth

During the pupping season (15th June – 15th July 2007) five fixed-wing surveys were carried out in the Moray Firth. Four surveys covered the coast from Findhorn to Helmsdale and one was restricted to the coast south of (and not including) the Dornoch Firth, due to low cloud. Preliminary investigation shows the maximum counts of pups to be higher than in 2006 but maximum counts of adult to be lower.

The Wash, Donna Nook and Blakeney Point

A series of four surveys was planned during June/July 2007. In the event, the program was curtailed by weather and RAF bombing range activity and only two surveys were completed, one of which is directly comparable to the results from preceding years' surveys. A comprehensive series of pup surveys are therefore planned for 2008.

Moult - Planned surveys

A survey covering the whole of the Scottish coast is planned for August 2007. This should be completed in one season using two helicopters, and a fixed wing to cover the outlying islands. Priority areas include: Shetland, Orkney, Outer Hebrides, Strathclyde, Moray Firth, Firth of Tay and Firth of Forth.

In England, two fixed-wing surveys of the Lincolnshire and Norfolk coast will be carried out.

Acknowledgements

We are extremely grateful to all the Countryside Agencies for providing funding for carrying out surveys in their areas. SNH has provided very significant funding for Scottish surveys since 1996; Natural England (and English Nature) have funded recent surveys of The Wash and surrounding coasts. The Irish surveys were funded by the Environment and Heritage Service and the National Parks and Wildlife Service for the north and south respectively.

We are also gratefully acknowledge the technical expertise enthusiastically provided by the companies supplying the survey aircraft and pilots: PDG Helicopters and Air Partner (formerly Gold Air International).

References

Lonergan, M., C.D.Duck, D. Thompsom, B. L. Mackey, L. Cunningham and I.L. Boyd (2007). Using sparse survey data to investigate the declining abundance of British harbour seals. *J. Zoology*, **271**: 261-269.

Thompson P.M., Mackey B., Barton, T.R., Duck, C. & Butler, J.R.A. (2007). Assessing the potential impact of salmon fisheries management on the conservation status of harbour seals (*Phoca vitulina*) in north-east Scotland. *Animal Conservation* **10**:48-56.

Figure 1. The August distribution of harbour seals in Great Britain and Ireland, by 10km squares. These data are from surveys carried out between 2000 and 2006.

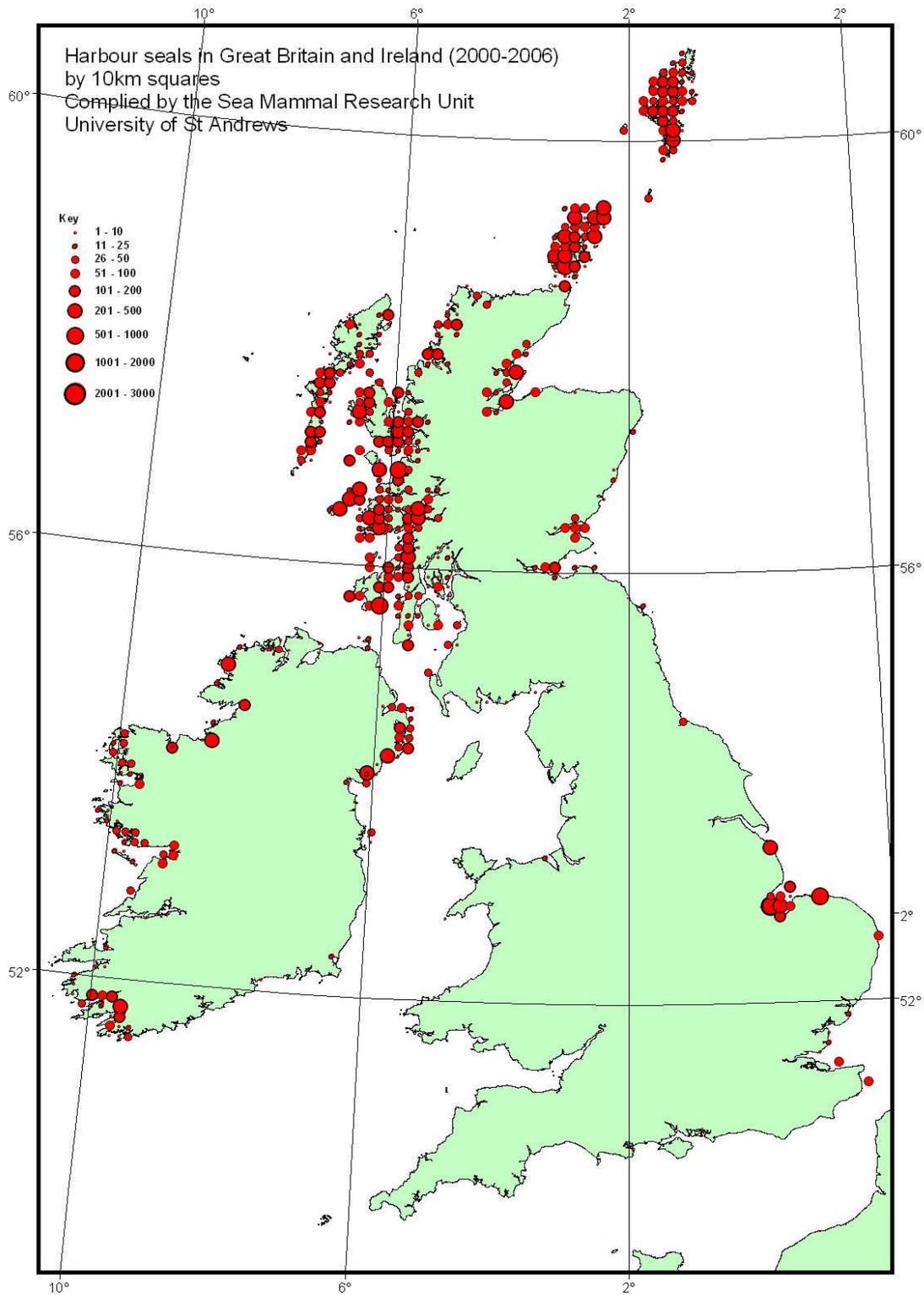


Figure 2. The number and distribution of common seals around the coast of Scotland surveyed in August 2006. All areas were surveyed by helicopter using a thermal imaging camera. Lines delineate the areas surveyed.

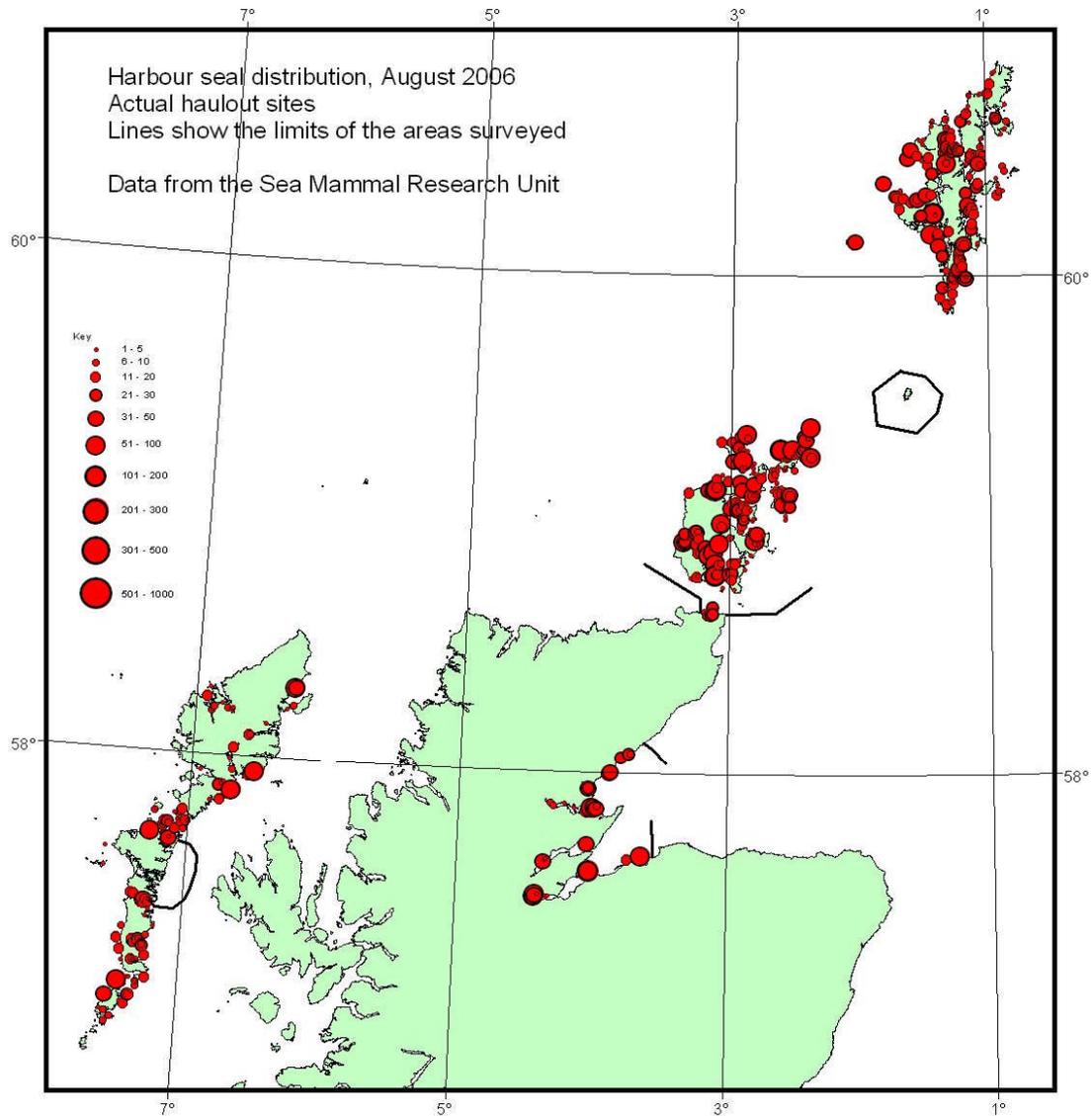


Figure 3. Trends in counts of common seals around Scotland. Data from the Sea Mammal Research Unit.

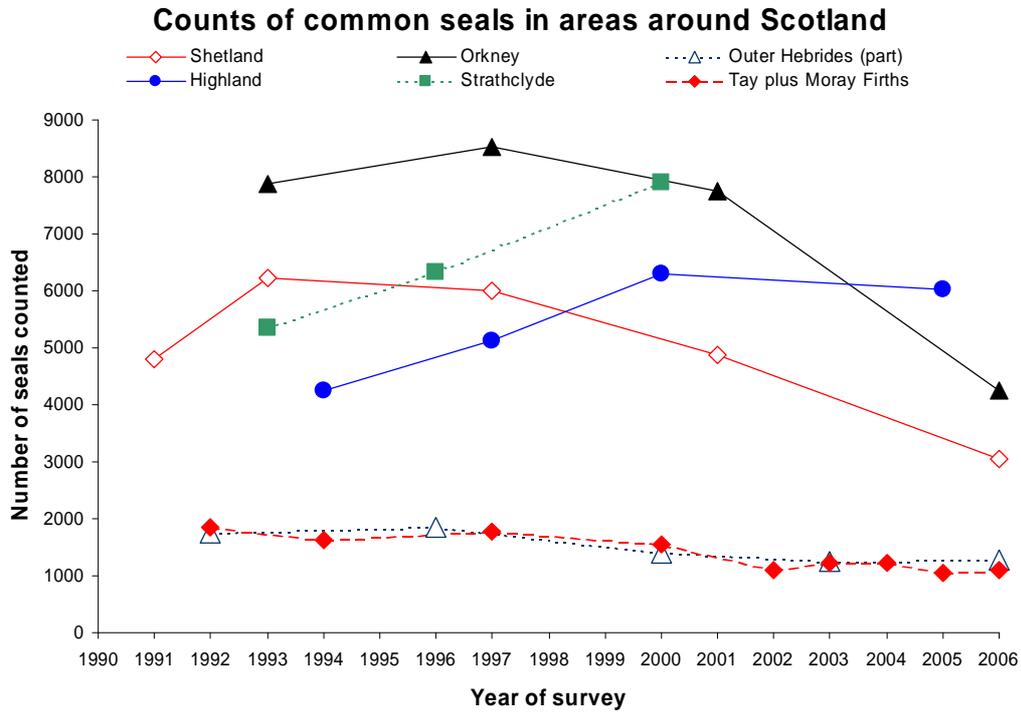


Figure 4. The number of common seals counted in the Moray Firth by the Sea Mammal Research Unit, 1992-2006

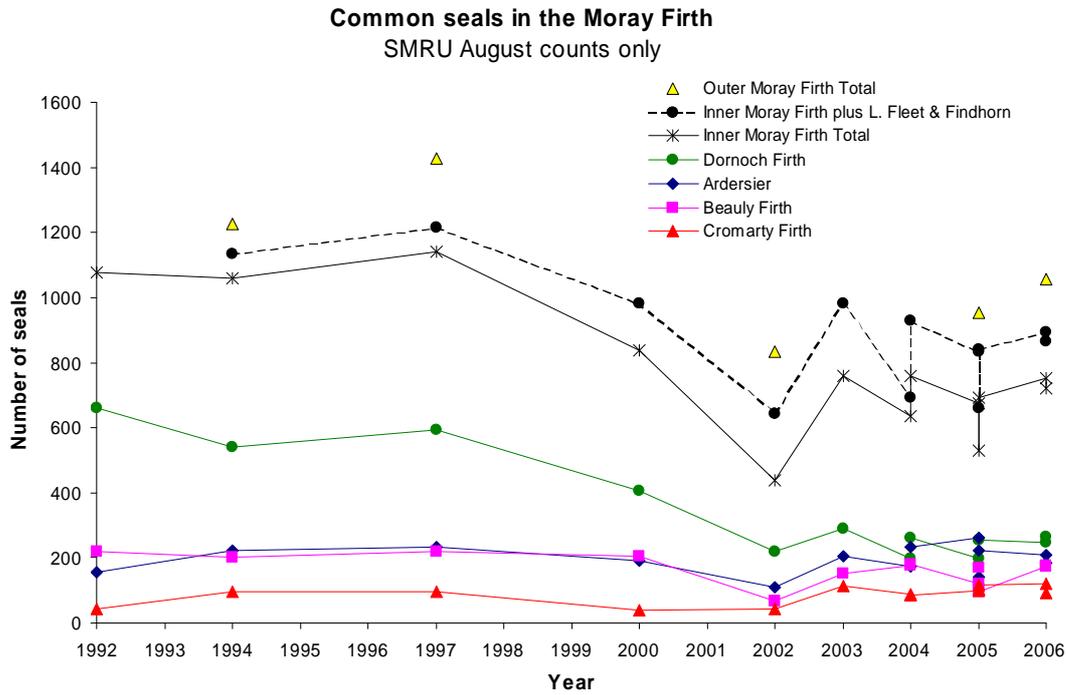


Figure 5. The number of common seals counted in the Firth of Tay by the Sea Mammal Research Unit, 1990-2006.

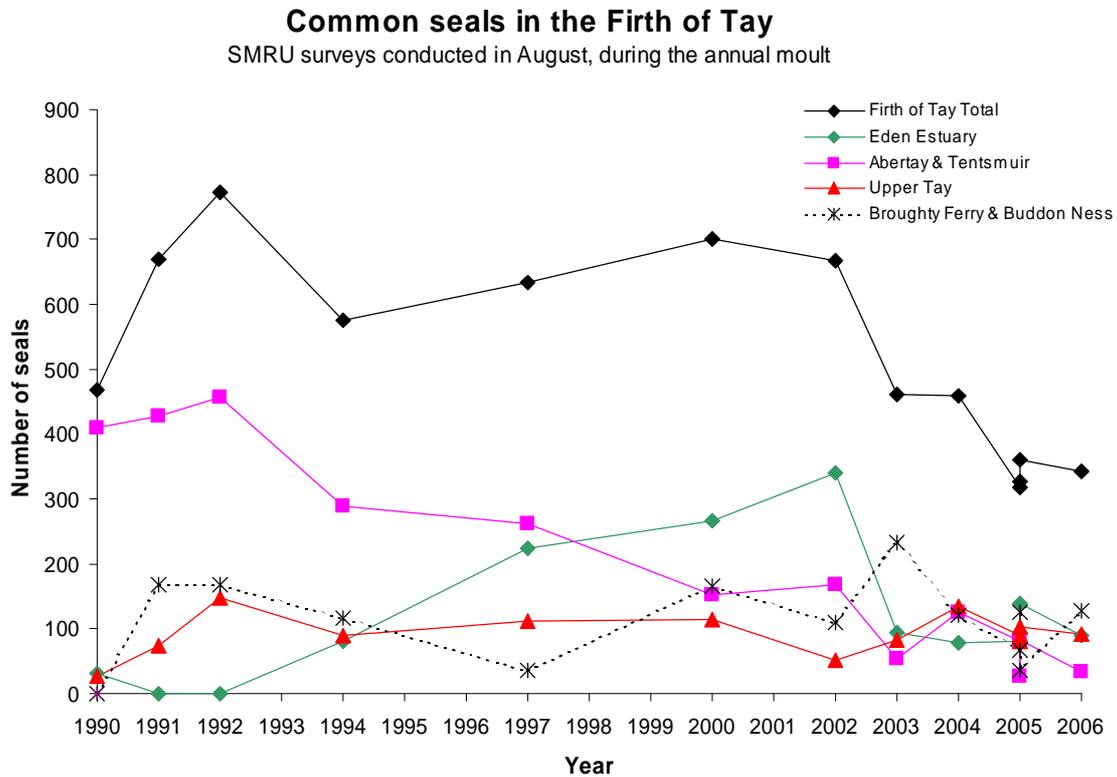


Figure 6. The number of common seal adults in the Moray Firth (Findhorn Bay to Helmsdale) during the 2006 breeding season

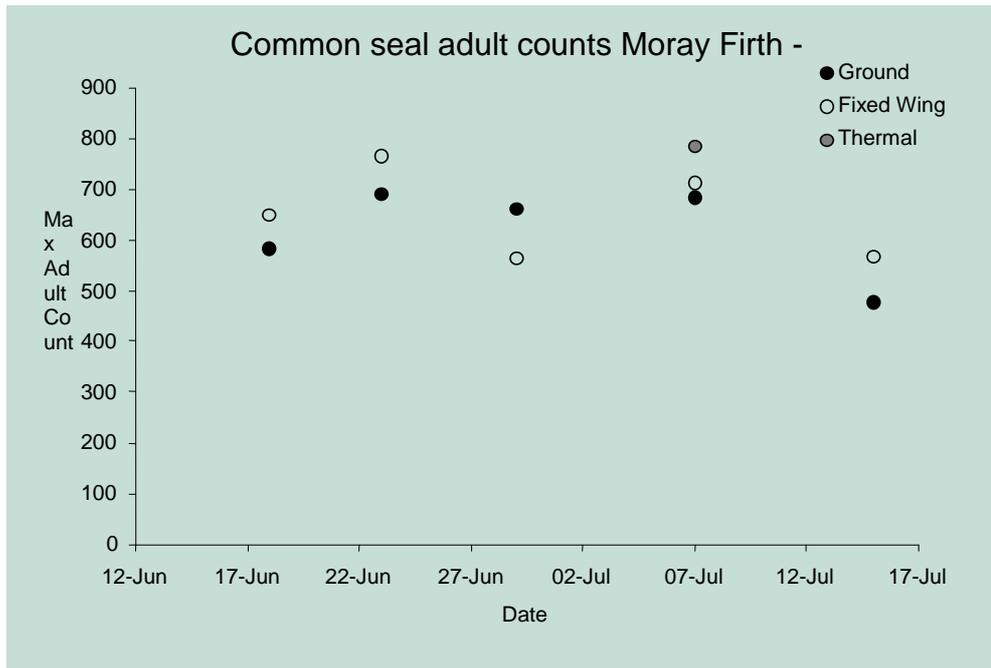


Figure 7. The number of common seal pups in the Moray Firth during the 2006 breeding season

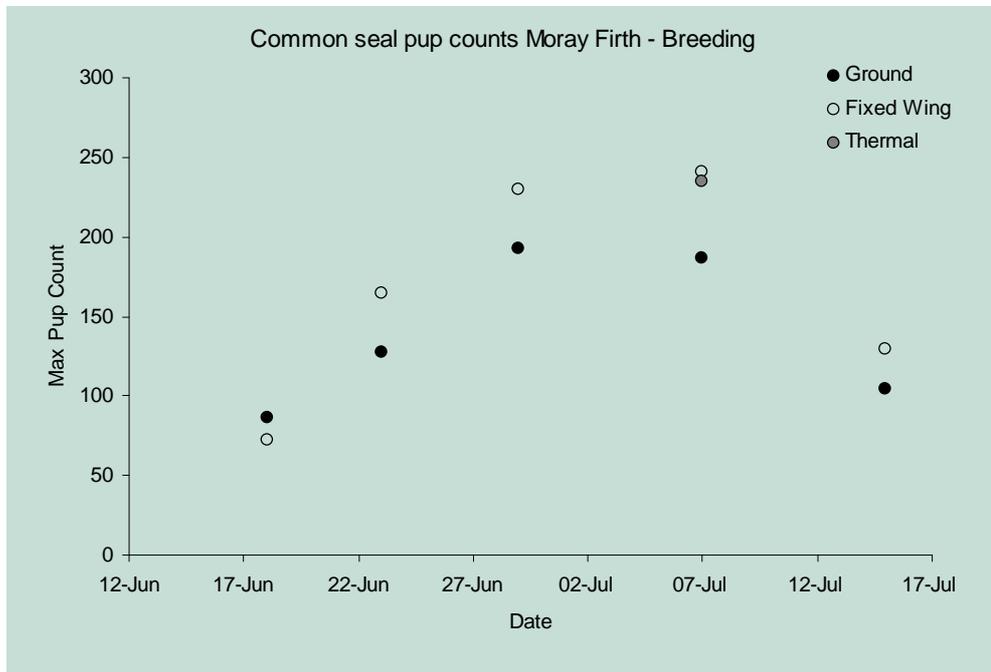


Figure 8. Counts of common seals in The Wash in August 1967 - 2006. These data are an index of the population size through time. Fitted lines are exponential growth curves (growth rates given in text).

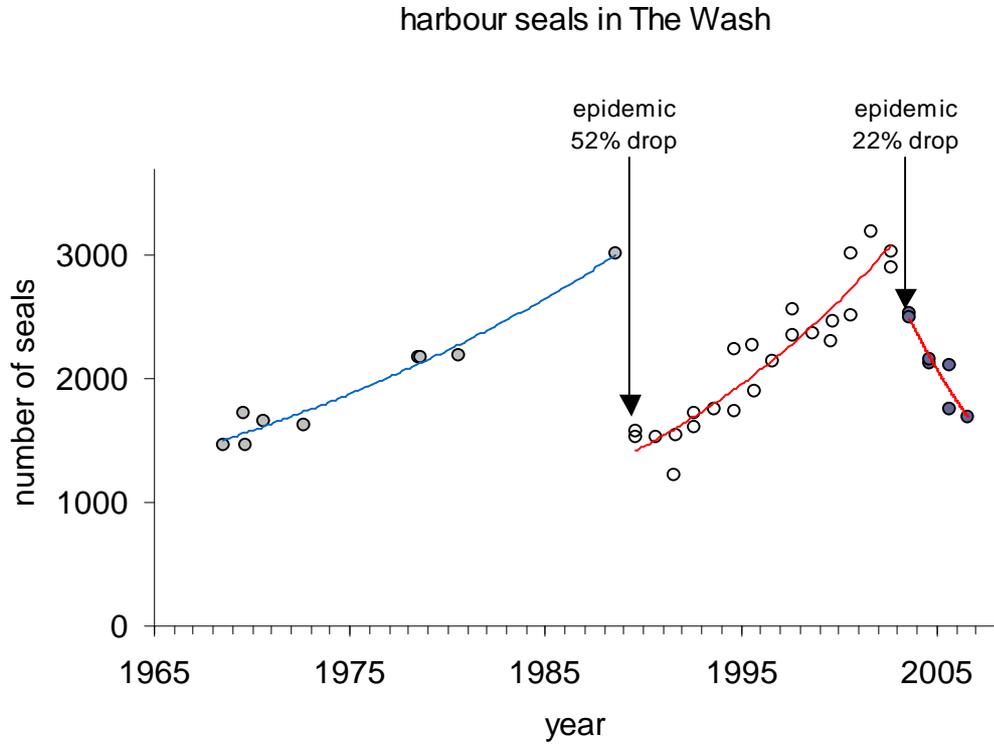


Table 1. Minimum estimate of the UK common seal population using data from completed regional surveys.

Region	Year of survey	Current estimate	Previous estimate (year of survey)
Shetland	2006	3,021	4,883 (2001)
Orkney	2006	4,256	7,752 (2001)
Outer Hebrides N Uist, Benbecula from 2003, other areas 2006	2006, part 2003	1,981	2,098 (2003)
Highland East & North (Nairn to Cape Wrath)	2005	1,056	1,232 (1997)
Highland West (Cape Wrath to Appin, Loch Linnhe)	2005	4,966	4,947 (1996/1997)
Strathclyde West (Appin to Mull of Kintyre)	2000, part 2005	6,702	5,342 (1996)
Strathclyde, Firth of Clyde (Mull of Kintyre to Loch Ryan)	2005	581	991 (1996)
Dumfries & Galloway (Loch Ryan to English Border at Carlisle)	2005	42	6 (2000)
Grampian (Montrose to Nairn)	2005	113	62 (1997)
Tayside (Newburgh to Montrose)	2005	101	121 (1997)
Fife (Kincardine Bridge to Newburgh)	2005	445	414 (1997)
Lothian (Torness Power Station to Kincardine Bridge)	2005	104	40 (1997)
Borders (Berwick upon Tweed to Torness Power Station)	2005	0	0 (1997)
TOTAL SCOTLAND		23,368	27,888
Blakeney Point	2006	719	741 (2005)
The Wash	2006	1,695	2,124 (2005)
Donna Nook	2006	299	470 (2005)
Scroby Sands	2006	71	57 (2004)
Other east coast sites	1994, 2000, 2003	225	
South and west England (estimated)		20	
TOTAL ENGLAND		3,029	
TOTAL BRITIAN		26,397	
TOTAL NORTHERN IRELAND	2002	1,248	
TOTAL BRITAIN & N. IRELAND		27,645	
TOTAL REPUBLIC OF IRELAND	2003	2,905	
TOTAL GREAT BRITIAN AND IRELAND		30,550	

Table 2. Numbers of common seals in the Moray Firth during August (SMRU surveys).

Location	07 Aug 1992	30 July 1993 ¹	13 Aug 1994	15 Aug 1997 ¹	11 Aug 2000	11 Aug 2002 ¹	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 ¹	20 Aug 2006
Ardersier	154	-	221	234	191	110	205	172	232	260	143	195	224	210	184
Beaully Firth	220	-	203	219	204	66	151	175	180	119	169	-	94	174	178
Cromarty Firth	41	-	95	95	38	42	113	90	86	98	101	-	118	119	93
Dornoch Firth (SAC)	662	-	542	593	405	220	290	199	262	199	118	-	256	249	264
Inner Moray Firth Total	1077	-	1061	1141	838	438	759	636	760	676	531	-	692	752	719
<i>Findhorn</i>	-	-	58	46	111	144	167	0	98	90	58	148	74	63	68
<i>Dornoch to Loch Fleet</i>	-	16		27	33	62	56	58	70	68	70	-	76	79	53
<i>Loch Fleet to Dunbeath</i>	-	92		214		145	-	-	-	-	-	-	113	163	137

¹Thermal imaging survey**Table 3. 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

¹Thermal imaging survey²In 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 4. 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		577 715	741 677	
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	
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	
Scroby Sands	-	- -	-	- -	- -	-	61 -	- 49	51	58 72	52 -	69 74	84 9	75			49 64		
The Tees	-	- -	-	- -	- -	-	- 35	- -	-	- -	- -	- -	- -	-	-		- -	- -	-
Holy Island, Northumberland	-	- -	-	- -	- -	-	13	- -	-	12 ²	- -	- -	10	-	-		- -	17 ²	-
Essex, Suffolk & Kent	-	- -	-	- -	- -	-	-	90 -	-	- -	- -	- -	- -	-	- 72		- 190		

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.

David Thompson

Distribution of breeding harbour seals (*Phoca vitulina*) in the Wash.

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

Summary

Single aerial surveys of the population of harbour seals in the Wash and adjacent areas were carried out in the breeding season in 2001, 2004, 2005 & 2006. Initially designed to look at distribution and relative importance of breeding sites. Surveys were conducted near peak of breeding. Simple model of birth and haulout behaviour suggests that the counts should have been close to the peak and should have represented a high proportion of the total production.

548 pups were counted in 2001, 613 in 2004, 651 in 2005 and 1013 in 2006. If we assume these counts to be within a few days of the peak the results indicate no decline in pup production after the epidemic in 2002, post epidemic counts were all higher. They also suggest a major jump in pup production in 2006, despite a apparent continued decline in abundance shown by the moult counts. At present we do not have a plausible explanation for this jump in pup production

Introduction

In general, harbour seal population monitoring programmes have been designed to track and detect medium to long-term changes in population size. As it is difficult to estimate absolute abundance, monitoring programmes have usually been directed towards obtaining indices of population size. If consistent, such time series are sufficient to describe populations' dynamics and have been used to track the long-term status of the English harbour seal population. However, these indices are based on the numbers of individuals observed hauled out, so their utility depends on this being constant over time and unaffected by any changes in population density or structure.

Counts are usually carried out during the annual moult, when the highest and most stable numbers of seals haulout. Unfortunately such counts do not provide a sensitive index of the current state of the population. It is generally accepted that breeding success is a more sensitive index. The breeding season is also the time when disturbance of seal haulout groups is likely to have direct effects. E.g. disturbance of mother/pup pairs will lead to temporary separation which may have direct effects on pup survival, especially if the disturbance is repeated.

Most of the UK harbour seal population breeds on rocky shore habitats, where identifying and counting pups is both difficult and expensive. However, on the English east coast harbour seals breed on open sand banks where pups are relatively easy to observe and count. As a first step towards improving the monitoring program (to increase its sensitivity to short term changes), we identified a need for a baseline survey to map the distribution of breeding harbour seals. In June 2001 Fenland District Council commissioned SMRU to conduct an aerial survey of the entire breeding population in the Wash. In 2004, 2005 and 2006 English Nature commissioned repeat breeding season surveys to check that the observed distribution was consistent and to begin the process of building up a pup count data set.

Breeding season surveys 2004, 2005 & 2006

Breeding season surveys were carried out on 4/7/2004, 27/06/2005 and 30/06/2006, over the period 1.5 hours before and 2 hours after low water. All tidal sand banks and all creeks accessible to seals were examined visually. All groups of more than 10 animals were photographed using either colour reversal film in a vertically mounted 5X4" format, image motion compensated camera or with a hand held digital SLR camera. The equipment and techniques are described in detail in Hiby, Thompson & Ward (1986) and Thompson et al. (2005). Photographs were processed and all seals were identified to species. Harbour seals were then classified as either pups or 1+ age class. No attempt was made to further differentiate the 1+ age class.

Pup Birth and Haulout models

To examine the potential consequences of differences in timing of the single pup surveys we generated two simple models of the expected number of pups visible on shore throughout the breeding season.

For illustration, a preliminary analysis was carried out to examine the likely effects of the assumptions about haulout behaviour on the number of pups ashore. Dates of birth were assumed to be normally distributed with a standard deviation of 7 days, i.e. 95% of births would occur during a 28

day breeding season. Three arbitrarily chosen scenarios are presented in figure 6: 1) all pups were ashore and countable on all low tides for the first seven days after which the probability of being hauled out declined by 10% per day; 2) all pups were ashore and countable on all low tides for the first seven days after which they hauled out on one tide per day for four days then one tide every other day for four days and then left the study area; 3) all pups were ashore and countable on all low tides for the first seven days after which they left the study area.

A more detailed model of the expected numbers of pups on the banks has been developed using data from three separate harbour seal populations for which series of pup counts are available within one breeding season (Moray Firth and Dutch Wadden Sea) or estimates of the spread of the birth curve over several seasons are available (Sable Island, Canada). The model assumed a small initial mortality rate within the first 2 days, a period of continuous haulout, i.e. where the probability a pup was on the beach and counted was equal to one, and a linearly decreasing tendency to haulout over the next 4 weeks. Minimum probability of hauling out was arbitrarily set to 20%, but this did not affect the behaviour of the model.

Results

Figure 1 shows the distribution of haulout sites in the Wash and Table 1 gives the counts of seals at each site obtained during the 2004, 2005 and 2006 breeding seasons, with similar data from a survey carried out in 2001 for Fenland District Council.

A total of 548 pups and 1802 older seals (1+ age classes) were counted in the Wash during the 2001 breeding season survey, 613 pups and 1766 older seals were counted in 2004, 651 pups and 1699 older seals were counted in 2005 and 1013 pups and 2267 older seals were counted in 2006. These were distributed over 39 separate haulout groups (Figure 1), although the number of sites is to some extent a function of the arbitrary divisions of sites. Pups were widely distributed, being present at all but two of the occupied sites in 2004 and 2005 and at all occupied sites in 2006. The 2005 pup count was 6% higher than the 2004 pup count (613 pups) and 19% higher than the 2001 pre-epidemic count. The 2006 pup count was much higher than in any previous survey, being 55% greater than the 2005 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. Again, the 2006 adult count was much higher than in previous breeding season surveys, 28% higher than the 2004

count.

Differences in timing of surveys (see later) 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 2006.

The distribution of pups was relatively constant over the period 2001 to 2006. Although site-to-site comparisons are not particularly close, when pooled into the four sub-regions the overall geographical spread was similar (fig 2). There was a gradual increase in the number of pups present on the outer banks in the west of the Wash. In 2001 only one pup was seen there, in 2004 around 5% of total pup production was on the outer western banks, in 2005 this had further increased to 9%. In 2006 a total of 129 pups were present on these banks, representing 13% of the total count.

Pup Birth and Haulout models

Model A. Three scenarios are presented in figure 6: 1) all pups were ashore and countable on all low tides for the first seven days after which the probability of being hauled out declined by 10% per day (Black curve); 2) all pups were ashore and countable on all low tides for the first seven days after which they hauled out on one tide per day for four days then one tide every other day for four days and then left the study area (Pink curve); 3) all pups were ashore and countable on all low tides for the first seven days after which they left the study area (Green curve). It is clear that even this wide range of assumed haulout behaviours has little effect on the pattern of counts. Model 3 is the worst-case scenario where the observed decrease could be achieved by missing the peak by 7 days on either side. Models 1 and 2 would require that surveys missed the peak by 8 to 9 days either side (Indicated by the arrows for models 1 and 3). The counts in 2004 and 2005 were 3 days either side of the 2006 survey date. Assuming the 2006 survey coincided with the peak number ashore, we would expect the counts in 2004 and 2005 to be within 5 to 8% of the peak number.

Model B. The more realistic model of the expected numbers of pups on the banks was fitted to the series of pup counts from the Moray Firth in 2005 (SMRU data) and to an old data set from the Dutch Wadden Sea (Reijnders & Fransz. 1978). The model assumed a small initial mortality rate over first 2 days. The model then fitted an estimated standard deviation of the birth curve and the slope of the tendency to haulout less frequently. Fitted

curves for the two pup count series in the Moray Firth and the Wadden Sea are shown in figure 7. The simple model fitted well to the observed numbers of pups in both cases, but the fitted parameters for the birth curve were different between sites suggesting that site-specific pup counts will be needed to fit the appropriate curves for the Wash population

Discussion

The most significant event in the Wash in recent years was the recurrence of a PDV epidemic in 2002. Our standard annual moult surveys indicated that the effect of this epidemic were less severe than in 1988. However, there was still a significant reduction of 22% in our population index, so we might expect a commensurate decrease in pup production. However, if there were differential sex and/or age linked mortality, the effects of the epidemic on the dynamics of the population could be more or less severe than expected. For example, the sample of seal carcasses examined during the 1988 epidemic showed a preponderance of adult males. Unfortunately the moult counts cannot differentiate the population into sex or age classes, and there was little information on the sex and age structure of the seals found dead in 2002.

There was no apparent decrease in pup production between the pre and post epidemic counts. There are several potential explanations for the lack of a decline. If there was differential mortality, the number of adult females lost to the epidemic may have been small. Alternatively any decrease in adult female population could have been masked by variations in fecundity. Alternative scenarios involving temporary immigration are thought to be less likely.

The most dramatic result of the three year survey program is the 50% increase in pup count between 2005 and 2006. The large increase in pup count in 2006 was unexpected and hard to explain. The moult counts in the Wash have continued to decline since the 2002 epidemic and even when combined with the adjacent sites at Blakeney and Donna Nook the moult counts have been stable since the epidemic.

As we are conducting only single counts there is a potential danger of confusing timing effects with actual changes. Therefore, before attempting to draw conclusions about the causes or implications of changes in pup production it is important that we are able to discount the possibility that the difference in counts were artefact of the changes in timing of the surveys. We did this in two stages.

First we minimised the potential effects by altering the timing in response to the previous year and then we investigated the potential effects of the remaining changes in timing through a simple modelling exercise.

The timing of the 2004 surveys was constrained by aircraft and staff availability, and the count in 2004 was approximately 12 days later than in 2001. Although we have no hard information, local observers suggested that the number of pups might decline in early July as pups wean and/or begin to spend time foraging with their mothers. We would therefore expect the 2004 count to represent the same or a lower proportion of the pup production compared to the 2001 count. The 2004 pup count was in fact 12% higher than the pre-epidemic count. As a result, we carried out the 2005 count midway between the 2001 and 2004 count dates. The pup count increased slightly between the 2004 and 2005 counts. Assuming that this indicated that the surveys were occurring around the peak, we carried out the 2006 count midway between the dates of the 2004 and 2005 flights.

We presented the output of a simple illustrative model designed to investigate how a wide range of assumptions about the timing of changes in haulout behaviour would affect the expected number of pups visible on shore throughout the breeding season. The standard deviation of the birth curve was fixed at seven days as this represented the mid point between the fitted values from the WaddenSea and Moray Firth data (see below). It is clear that a wide range of assumed haulout behaviours had little effect on the pattern of counts. Even in the worst-case scenario the observed difference between 2004/05 and 2006 require us to have missed the peak by 7 days on either side. We would conclude that the observed increase in 2006 was unlikely to be entirely the result of differences in timing and therefore represents a real change in the number of pups ashore around the peak time.

The more realistic model of the expected numbers of pups on the banks was developed as a preliminary attempt to allow us to estimate total pup production and confidence intervals from single counts. Using data from three separate harbour seal populations for which series of pup counts are available indicates that the method is feasible but the geographical differences between the parameters of the fitted birth curves means that we need to incorporate pup counts from the Wash population to develop appropriate estimates. It is likely that a series of pup counts from one season would allow estimation of the shape and therefore

the cumulative total of the birth curve. If successful this would facilitate a pup-production monitoring program based on single annual counts with occasional more intensive surveys, e.g. every 5 years a series of 4 or 5 surveys to re-estimate birth curve parameters. This would provide data to be compared with the annual total population index surveys in August to allow more responsive and sensitive management of the harbour seal population.

Clearly the observed differences over the three years cannot be accounted for the differences in survey dates.

The observed large increase could be generated in various ways:

1. It could result from a major change in the shape of the birth curve. The timing of births may have been more synchronised in 2006, i.e. the variance in birth dates decreased significantly. To account for the observed change by increased synchronisation of the birth dates, the standard deviation would have to decrease to 2 days for model 3 and to less than 2 days for the other models.
2. There may have been a significant change in the haulout behaviour of pups. Pups may have remained ashore for significantly longer than in previous years. Observations of pups travelling to foraging sites with their mothers have been recorded in Canada (Bowen et al. 1999) and the proportion of time spent at sea was highly variable between years. However, such effects were apparent mainly in older pups and it is unlikely that such changes could account for the observed differences in pup counts here.
3. Immigration of a large number of adult females. The absence of any substantial populations on the east coast means that the source of seals would have to be either the Wadden Sea or the Scottish East coast. In fact the Scottish populations have been declining rapidly over the past 5-10 years (Figure 8) making them an unlikely source of pregnant females.
4. A stepwise increase in fecundity. At present we have no information to allow us to differentiate between these options and it is likely that a combination of some or all could be operating. However, in each case the explanation would represent a major change in harbour seal demographics.

The results of the 2001 pup survey suggested that there had been a significant shift in spatial distribution of breeding seals over the preceding 30 years. The 2004 and 2005 distribution was similar

to the 2001 distribution, suggesting that there has been a real shift in distribution with a much higher proportion of pups being found along the banks of the creeks along the southern edge of the Wash, mostly inside the RAF Danger area. The proportional increase in the inner Wash coincided with a dramatic reduction in the relative importance of the banks along the western edge of the Wash, although this difference may be decreasing. The main increase in 2006 was on banks in the east of the Wash, although the apparent increasing trend on the outer Western banks has also continued.

In conclusion, although these single surveys do not give us an accurate estimate of total pup production, the data do indicate that:

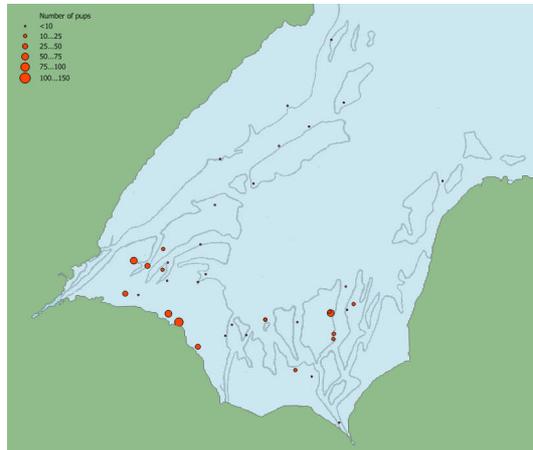
- 1) The breeding population, or at least the pup production was not dramatically reduced by the 2002 PDV epidemic;
- 2) Mortality on breeding females and recruiting females was probably not higher than the population average;
- 3) The pup production has not followed the decrease in moult counts;
- 4) Some major change in distribution, fecundity or haulout behaviour must have occurred between 2005 and 2006.
- 5) A single series of multiple pup counts within one season will allow us to estimate the pup production in years with only a single count around the peak pupping dates, and provide confidence intervals on the pup production estimates.

References

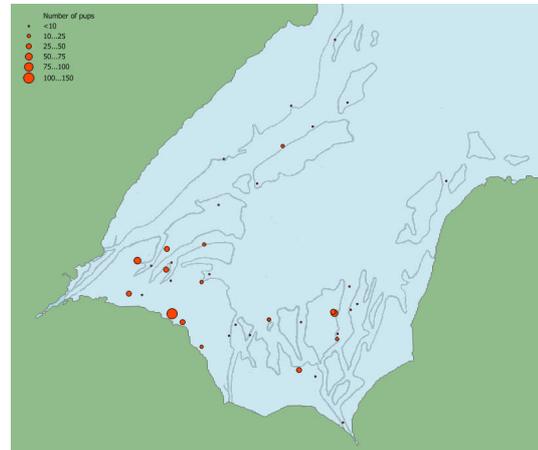
- Bowen, W.D., Boness, D.J., & Iverson, S.J. (1999) Diving behaviour of lactating harbour seals and their pups during maternal foraging trips. *Canadian Journal of Zoology - Revue Canadienne de Zoologie*, **77**, 978-988.
- Hiby, A. R., Thompson, D. & Ward, A. J. (1987). Improved census by aerial photography - an inexpensive system based on non-specialist equipment. *Wildl. Soc. Bull.* **15**, 438-43.
- Reijnders, P.J.H. & Fransz, H.G. 1978. Estimation of birth rate and juvenile mortality from numbers of juveniles in a seal population with normally dispersed reproduction. I.C.E.S. C.M. 1978/N:7
- Reijnders, P.J.H. (1978) Recruitment in the harbour seal (*Phoca vitulina*) population in the Dutch Wadden Sea. *Neth. J. Sea. Res.* **12(2)**: 164-179
- Thompson, D, Lonergan, M & Duck, C.D. (2005) Population dynamics of harbour seals (*Phoca vitulina*) in England: growth and catastrophic declines. *J. Appl. Ecol.* **42** (4): 638-648
- Vaughan, R. W. (1978). A study of common seals in the Wash. *Mammal Rev.* **8**, 25-34.

Figure 1. Distribution of pups in the Wash, a) 2001; b)2004; c)2005; d)2006. Names of haulout sites together with latitudes and longitudes and numbers of seals at each site are given in table 1

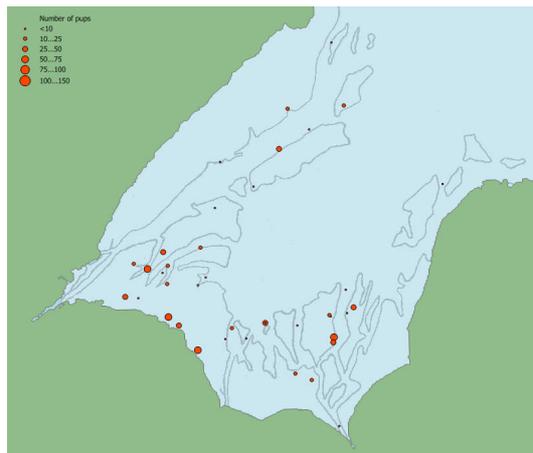
a. 2001



b. 2004



c. 2005



d. 2006

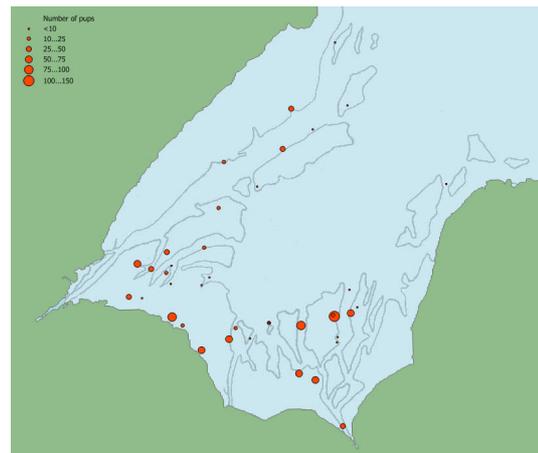


Figure 2. Distribution of harbour seal pups in the Wash during the 2001, 2004, 2005 & 2006 breeding seasons pooled into geographical sub regions (Vaughan, 1978). The most dramatic changes are the gradual increase in the Outer western banks and the sudden increase on the Eastern Banks in 2006

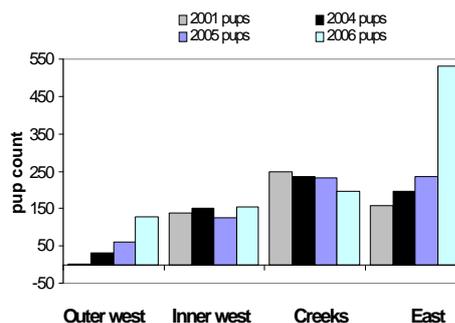


Figure 3 Illustration of potential effects of different assumptions about haulout patterns on the predicted number of pups visible on shore throughout the breeding season. Mean birth date set arbitrarily at day 30, standard deviation of 7 days (similar to that of data from the Wadden Sea). Three scenarios are presented: 1) all pups ashore and countable for the first 7 days after which the probability of being hauled out declined by 10% per day (Black curve); 2) all pups were ashore and countable for the first 7 days, then hauled out on one tide per day for four days then one tide every other day for four days and then left the study area (Pink curve); 3) all pups were ashore and countable on all low tides for the first seven days after which they left the study area (Green curve).

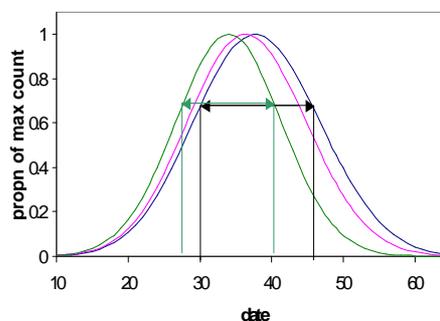
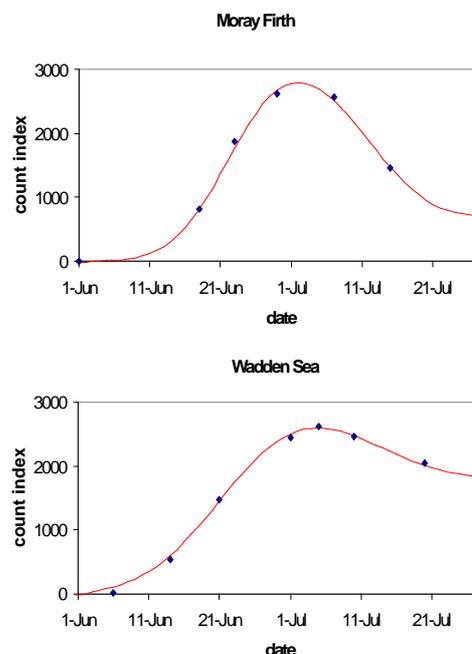


Figure 4. Fitted models incorporating birth curve, initial mortality and declining haulout tendencies in harbour seal pups. Model fits (red curves) are shown for both the Moray Firth and Wadden Sea data (blue dots) described in text. The model fits well to each data set, but the fitted standard deviations are different in the two model runs, and higher than those for the small colony on Sable



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A preliminary model of the demographic causes of the UK common seal decline

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

Summary

Decreasing numbers of moulting common seals in Scotland have prompted concerns about the state of the population. Proximately, the observed declines could be due to changes in 1) fecundity, 2) mortality or 3) the timing of moult in relation to the window of aerial survey. It is essential that the relative contribution of these factors is evaluated on the basis of all available data. To this end, we begin the development and parameterization of a Bayesian demographic model for UK common seals.

1. Introduction

Recent analysis of aerial counts of UK common seals (Lonergan et al. 2007) has detected a drop in the numbers of seals moulting in several Scottish regions and hinted at the possibility of a population decline rate as high as 10% pa.

There are several possible biological mechanisms that may have brought this about (disease, pollution, food quality, food quantity, food accessibility, human disturbance, predation etc). As has been demonstrated by past experience with other seal species (e.g. Steller sea lions), it is difficult to conduct empirical studies and develop models for every such mechanistic hypothesis. This is practically impossible if the causes lie with more than one mechanism. However, any effect on the observations will be mediated by one or more of the following three factors:

- Fecundity
- Survival
- Timing of moult in relation to the time of the aerial surveys

These can be modeled simultaneously in an attempt to map all the possible scenarios that can account for the observed decline in counts. The motivating objectives of this work are to:

1. Construct a modeling framework for the dynamics of UK common seals
2. Fit this simultaneously to count data from different Scottish regions
3. Detect temporal trends in demographic and observation processes
4. Suggest likely proximate causes of observed decline

5. Postulate about the likely ultimate causes of observed decline and thus recommend the type of data that would best inform future modeling.

Having only been started after last year’s SCOS, this work is still at the early stages. However, we are in a position to report on progress with objectives 1 and 2 and provide some illustrative output.

2. Methods

AVAILABLE INFORMATION

The model was fitted to aerial count data collected during the period of moult. Telemetry data, collected outside the breeding and moulting seasons, provide information about the baseline proportion of time spent hauled-out. Variability in haulout numbers throughout the year obtained from historical data (aerial & ground counts) informs about the approximate timing of moult at the start of the count time series. Haulout data collected in different countries informs about the differences in haul-out behaviour between different sexes and ages. Mark-recapture data analysed in the literature, provide ballpark information on baseline sex- and age-specific rates of survival.

MODEL DESCRIPTION

We use a state-structured model comprising 3 sub-adult stages and 1 adult stage for each sex. The deterministic version of the model is

$$N_{t+1} = R_t N_t \tag{1}$$

where,

$$R_t = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 0 & \frac{1}{2}b_t \\ s_{j,t} & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & s_{j,t} & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & s_{m,t} & s_{m,t} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & \frac{1}{2}b_t \\ 0 & 0 & 0 & 0 & s_{j,t} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & s_{j,t} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & s_{f,t} & s_{f,t} \end{pmatrix}$$

$$\text{and } N_t = \begin{pmatrix} m_{1,t} \\ m_{2,t} \\ m_{3,t} \\ m_{4,t} \\ f_{1,t} \\ f_{2,t} \\ f_{3,t} \\ f_{4,t} \end{pmatrix} \quad (2)$$

The stochastic version of the process model is

$$\begin{aligned} m_{1,t+1} &\sim \text{Binomial}(f_{4,t}, \frac{1}{2}b_t) \\ m_{2,t+1} &\sim \text{Binomial}(m_{1,t}, s_{j,t}) \\ m_{3,t+1} &\sim \text{Binomial}(m_{2,t}, s_{j,2,t}) \\ m_{4,t+1} &= X_{t+1} + Y_{t+1} \\ X_{t+1} &\sim \text{Binomial}(m_{3,t}, s_{m,3,t}) \\ Y_{t+1} &\sim \text{Binomial}(m_{4,t}, s_{m,4,t}) \\ f_{1,t+1} &\sim \text{Binomial}(f_{4,t}, \frac{1}{2}b_t) \\ f_{2,t+1} &\sim \text{Binomial}(f_{1,t}, s_{j,t}) \\ f_{3,t+1} &\sim \text{Binomial}(f_{2,t}, s_{j,2,t}) \\ f_{4,t+1} &= V_{t+1} + W_{t+1} \\ V_{t+1} &\sim \text{Binomial}(f_{3,t}, s_{f,3,t}) \\ W_{t+1} &\sim \text{Binomial}(f_{4,t}, s_{f,4,t}) \end{aligned} \quad (3)$$

Fecundity is modeled as a Binomial rather than a Poisson process because twins practically never occur. If $p(d)$ is used to denote the probability that a seal of a particular class is hauled out at time d , the number of animals observed in an aerial survey conducted at time d in the year will be, on average,

$$P_t = \sum_{i=1}^4 (m_{i,t} p_{m,i,t}(d) + f_{i,t} p_{f,i,t}(d)) \quad (4)$$

The stochastic version of this observation model is

$$P_t = \sum_{i=1}^4 (Z_{m,i,t} + Z_{f,i,t}) \quad (5)$$

$$\text{where } \begin{aligned} Z_{m,i,t} &\sim \text{Binomial}(m_{i,t}, p_{m,i,t}(d)) \\ Z_{f,i,t} &\sim \text{Binomial}(f_{i,t}, p_{f,i,t}(d)) \end{aligned}$$

This model can be simplified by closer examination of the three processes involved

Fecundity By assuming no senescence we can treat all stage 4 females as reproductively equal. We

would like to incorporate a possible Year effect into fecundity. This may be done using a logistically-transformed polynomial function

$$b_t = \frac{\exp(\beta_0 + \beta_1 t + \beta_2 t^2 + \dots)}{1 + \exp(\beta_0 + \beta_1 t + \beta_2 t^2 + \dots)} \quad (6)$$

The number of terms to be added to the polynomial is an issue of model selection. This fecundity parameter is a combination of the rate of births and pup survival during the first 12 months of their life.

Survival Age-dependence in survival is incorporated by assuming that subadults all have a certain baseline survival σ_j and that adults of the same sex have baseline survival σ_m and σ_f . Assuming that temporal trends affect all classes identically, year effects can then be introduced as follows,

$$s_{*,t} = \frac{\exp(\sigma_{*,0} + \sigma_{*,1}t + \sigma_{*,2}t^2 + \dots)}{1 + \exp(\sigma_{*,0} + \sigma_{*,1}t + \sigma_{*,2}t^2 + \dots)} \quad (7)$$

Where * stands for $j, m, \text{ or } f$ depending on whether it refers to sub-adults, adult males or adult females.

Moult The probability of observing an animal on the haulout, at any given time d in the year, can be modeled as the mixture of a constant, background probability of being hauled-out and two pulses during the periods of pupping and moulting. In this work, we focus on the period of moult and therefore implement a model with a single pulse,

$$p_{sex,i,t}(d) = \pi_{sex,i} + \rho_{sex,i} \exp\left(-\frac{(d - \delta_{sex,i,t})^2}{\gamma_{sex,i}^2}\right) \quad (8)$$

for $0 \leq \pi_{sex,i} \leq 1$ and $0 \leq \rho_{sex,i} \leq (1 - \pi_{sex,i})$. Note that, the values for the mixture constants $\pi_{sex,i}, \rho_{sex,i}$ and the pulse dispersion parameter $\gamma_{sex,i}$ are time-invariant implying that the relative shape of the curves is assumed not to change between years. The absolute timing of the moult is allowed to drift from one year to the next according to the expression

$$\delta_{sex,i,t} = c_{sex,i} + c_1 t + c_2 t^2 + \dots \quad (9)$$

Where $c_{sex,i}$ is the date of the peak of the moult (for a particular class of animals) in the first year of the survey.

INFERENCE

Given the restricted information content (length and frequency) of the population time series, we restricted our attention to 1st order trends (linear at the scale of the predictors). Since our main objective

was to detect and quantify trends in demography and the timing of moult, we used non-informative priors for the trend parameters, centred around zero (corresponding to a null hypothesis of no trend).

Priors for demographic parameters

We used informative priors for the baseline demographic parameters $\beta_0, \sigma_j, \sigma_m, \sigma_f$. These were derived mainly from Härkönen et al (2002 – Table 5) who report on the estimated vital rates of several populations of harbour seals. For each baseline parameter, we used the highest and lowest quoted values as the 2.5- and 97.5-percentiles of a Beta distribution. Fecundity was calculated as the product of the reported fertility rate and pup survival.

The values in Härkönen et al (2002) take no account of sex. We therefore specified male survival as a proportion of female survival (Boyd 2000) and gave this a Beta prior distribution whose bulk was between 0.8 and 1.

To set variances for the uninformative priors of the trend parameters we used the following rationale: Class-specific vital rates can vary between 0 and 1 and could, theoretically, perform such a transition in less than one year. However, the annual survey data could not be used to detect such rapid changes. A value of 10 for the trend parameters in the logistic curves of eqs. (6) and (7) results in a transition from 0 to 1 in half a year. Hence, using the value 5 as the standard deviation for the prior distribution of the trend parameters, gives an uninformative prior which nevertheless only brackets identifiable values within its 2.5- and 97.5-percentiles.

Priors for age-specific haulout probabilities

Harkonen *et al.* (1999 - Figure 2) report on the resighting frequency of freeze-branded seals hauling out in the Kattegat and Sekagerrak seas off Sweden in the summer months. The data, generated over a 13 year study of 163 seals, is age- and sex-specific, but is not accompanied by estimates of uncertainty. The authors stratified their data into seven 15-day periods and estimated haulout probabilities for times during each interval. The 12-class model of Harkonen *et al.* (1999) was converted to an 8-class model by merging the last 3 age classes for each sex. This was done by weighting the haulout proportions of different ages according to a survival curve assuming a survival rate of 0.9 and a maximum life expectancy of 20 years. We obtained the following defining characteristics of the haulout curves:

Background haulout probability (outside moult or pupping seasons) – We used the lowest observed proportion for each age and sex as the background probability.

Relative haulout peak time – The peak position value is estimated by comparing the date of the peak for each stage to the date of the peak for the overall

population. The overall peak is taken as the 6th of August. This value (Fig. 5 in Harkonen et al., 1999) is also supported for UK seals by Thompson *et al.* (2005).

Duration of moult – The approximate width of the haulout pulse was estimated by looking at the time taken for the stage plot to return to a low level. By estimating from the right hand side of the plot we tried to remove any residual effect from the breeding pulse that occurs before the moult. The value used was the estimated standard deviation of a normal pulse fitting the observed curves for each sex and age.

Peak haulout probability – The height of the haulout pulse was obtained as the maximum value for resighting frequency in the data for each stage. The value given corresponds to the estimated proportion of the stage that is hauled out at its peak haul out time. The degree of variation in the peak was assumed to be within 15 days of the observed peak. Thus, the standard deviation of the baseline peak date parameter is taken to be 7 days, giving a rough 95% confidence interval 15 days either side of the recorded peak.

The expected value for the trend in peak date parameter was taken to be zero. To calculate a plausible variance for this parameter we observed that the number of animals counted in the annual aerial surveys was larger than the number expected due to background haulout proportions, thus the surveys probably occur during the moult. If the length of the moult pulse is taken to be two months and the initial survey was conducted at the peak day (Thompson et al, 2005) then the peak could have moved by a maximum of 30 days in 20 years. If this is treated as a rough 95% confidence interval then the standard deviation of the parameter is $15/20 = 0.75$.

Priors for initial population structure

To provide priors for the vector N_1 of the population classes at the beginning of the observation period we first assumed that prior to observation, the population had been growing or declining exponentially according to the baseline vital rates. Based on this assumption we estimated an initial (stable) population structure for every MCMC trial run. These were derived from the candidate, baseline vital rates being considered by the current MCMC trial. The resulting, relative proportions of different ages and sexes in the population were scaled up to absolute numbers as follows: If h_i is relative population structure and p_i is haulout probability at the time of the first year's survey, we are interested in N_i , the absolute numbers in each class. Let N and M be the actual population size and the observed count in the first year so that $N_i = Nh_i$ and $M = \sum_{i=1}^8 N_i p_i$. Combining these two relations

gives the absolute age structure in the first year as a function observed numbers, haulout probabilities and the stable age structure

$$N_i = \frac{Mh_i}{\sum_{i=1}^8 p_i h_i} \quad (10)$$

Estimation

The model was implemented in WinBugs and fitted to data from the region of Skye only. To improve estimation speed, we used the normal approximation for all the stochastic processes listed in eqs 3 and 5. Some years in the data had no counts. For the time being, we dealt with these by using a GAM to interpolate between the observations. Posteriors were obtained by running 5 MCMC chains for 10^6 iterations and sampling from the last 2×10^5 thinned at intervals of 10.

3. Results

The MCMC chains converged quickly but mixed poorly. This was perhaps a problem with the priors or an indication of low information content in the count data. All posteriors appeared to differ from the priors (Fig. 1) but several were multimodal, indicating problems with identifiability. To investigate those more fully, we plotted the alternative multifactor explanations as a contingency table (Fig. 2). We identified four likely scenarios and then plotted the estimated demographic trends under each of them (Fig. 3).

4. Future improvements/extentions

- 1) Use hierarchical modelling to fit simultaneously to all Scottish regions
- 2) Use the precise date of each survey as a covariate in the model (so that d in eq. 8 is specific to each survey count).
- 3) Fit to the count time series with missing observations
- 4) Standardise priors to improve mixing and obtain additional prior information from anecdotal data

5. Main conclusions

- 1) There is a finite number of dominant explanations which are currently confounded (Fig. 2 & Fig. 3).
- 2) Nevertheless, it seems unlikely that the observations are an artifact of drift in the timing of moult, at least in Skye (Fig. 2).

We have drafted a model, estimation methodology and output devices that enable us to begin generating mechanistic hypotheses about the apparent decline in common seal numbers. Despite its narrow geographic scope and preliminary nature, this approach can serve as the basis for a comprehensive and more robust analysis to be presented to SCOS next year.

Acknowledgements. Thanks to L. Thomas, D. Thompson, C. Duck & I. Boyd for their input.

References

- Boyd, I.L. (2000) *Pinniped life history*. Encyclopedia of Marine mammals. Pp929-934.
- Härkönen, T., Harding, K.C. & Heide-Jørgensen, M-P. (2002) *Rates of increase in age-structured populations: a lesson from the European harbour seals*. Canadian Journal of Zoology, 80, 1498-1510.
- Loneragan, M., Duck, C.D., Thompson, D., Mackey, B.L., Cunningham, L. & Boyd, I.L. (2007) *Using sparse survey data to investigate the declining abundance of British harbour seals*. Journal of Zoology.
- Thompson, D., Loneragan, M. & Duck C. (2005) *Population dynamics of harbour seals Phoca vitulina in England: monitoring growth and catastrophic declines*. Journal of Applied Ecology, 43, 638-648.

<i>Parameter</i>	<i>Prior</i>	<i>Informative?</i>	<i>Parameter</i>	<i>Prior</i>	<i>Informative?</i>
$\frac{Exp(\beta_0)}{1 + Exp(\beta_0)}$	Beta(7.48,7.32)	Yes	$\rho_{f,2}$	0.17	Constant
β_1	$N(0,25)$	No	$\rho_{f,3}$	0.16	Constant
$\frac{Exp(\sigma_{j,0})}{1 + Exp(\sigma_{j,0})}$	Beta(149,13)	Yes	$\rho_{f,4}$	0.11	Constant
$\frac{Exp(\sigma_{f,0})}{1 + Exp(\sigma_{f,0})}$	Beta(149,13)	Yes	$\gamma_{m,1}$	30	Constant
s_f / s_m	Beta(75,5)	Yes	$\gamma_{m,2}$	15	Constant
$\sigma_{j,1}$	$N(0,25)$	No	$\gamma_{m,3}$	15	Constant
$\sigma_{f,1}$	$N(0,25)$	No	$\gamma_{m,4}$	15	Constant
$\sigma_{m,1}$	$\sigma_{f,1}$	Constant	$\gamma_{f,1}$	23	Constant
$\pi_{m,1}$	0.11	Constant	$\gamma_{f,2}$	15	Constant
$\pi_{m,2}$	0.10	Constant	$\gamma_{f,3}$	30	Constant
$\pi_{m,3}$	0.10	Constant	$\gamma_{f,4}$	30	Constant
$\pi_{m,4}$	0.03	Constant	$c_{m,1}$	$N(204,4)$	Yes
$\pi_{f,1}$	0.17	Constant	$c_{m,2}$	$N(219,4)$	Yes
$\pi_{f,2}$	0.15	Constant	$c_{m,3}$	$N(219,4)$	Yes
$\pi_{f,3}$	0.06	Constant	$c_{m,4}$	$N(234,4)$	Yes
$\pi_{f,4}$	0.06	Constant	$c_{f,1}$	$N(219,4)$	Yes
$\rho_{m,1}$	0.22	Constant	$c_{f,2}$	$N(189,4)$	Yes
$\rho_{m,2}$	0.16	Constant	$c_{f,3}$	$N(204,4)$	Yes
$\rho_{m,3}$	0.14	Constant	$c_{f,4}$	$N(219,4)$	Yes
$\rho_{m,4}$	0.29	Constant	c_1	$N(0,0.56)$	No
$\rho_{f,1}$	0.23	Constant			

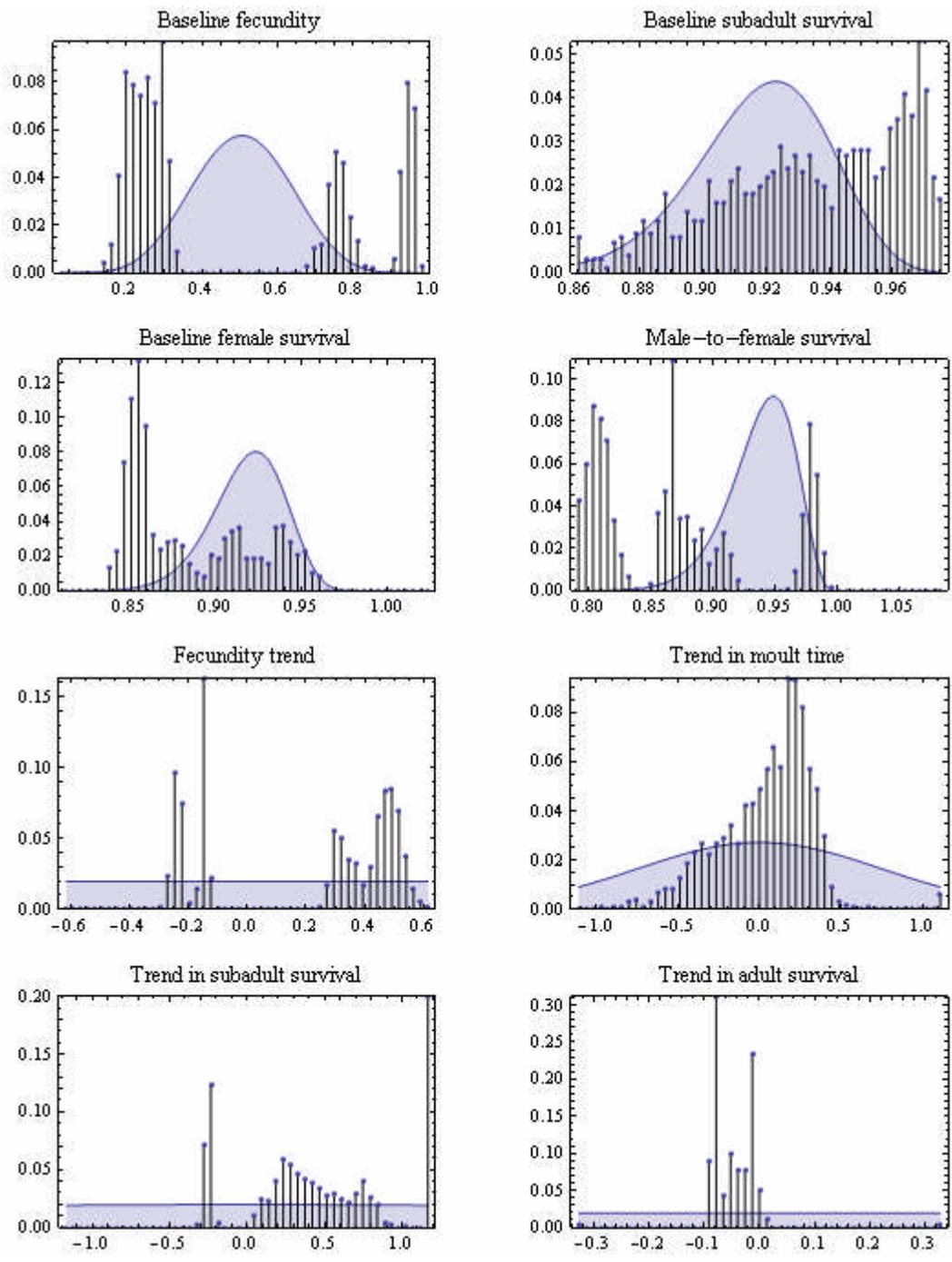


FIGURE 1: Prior (shaded curves) and posterior (histograms) distributions for eight parameters of interest.

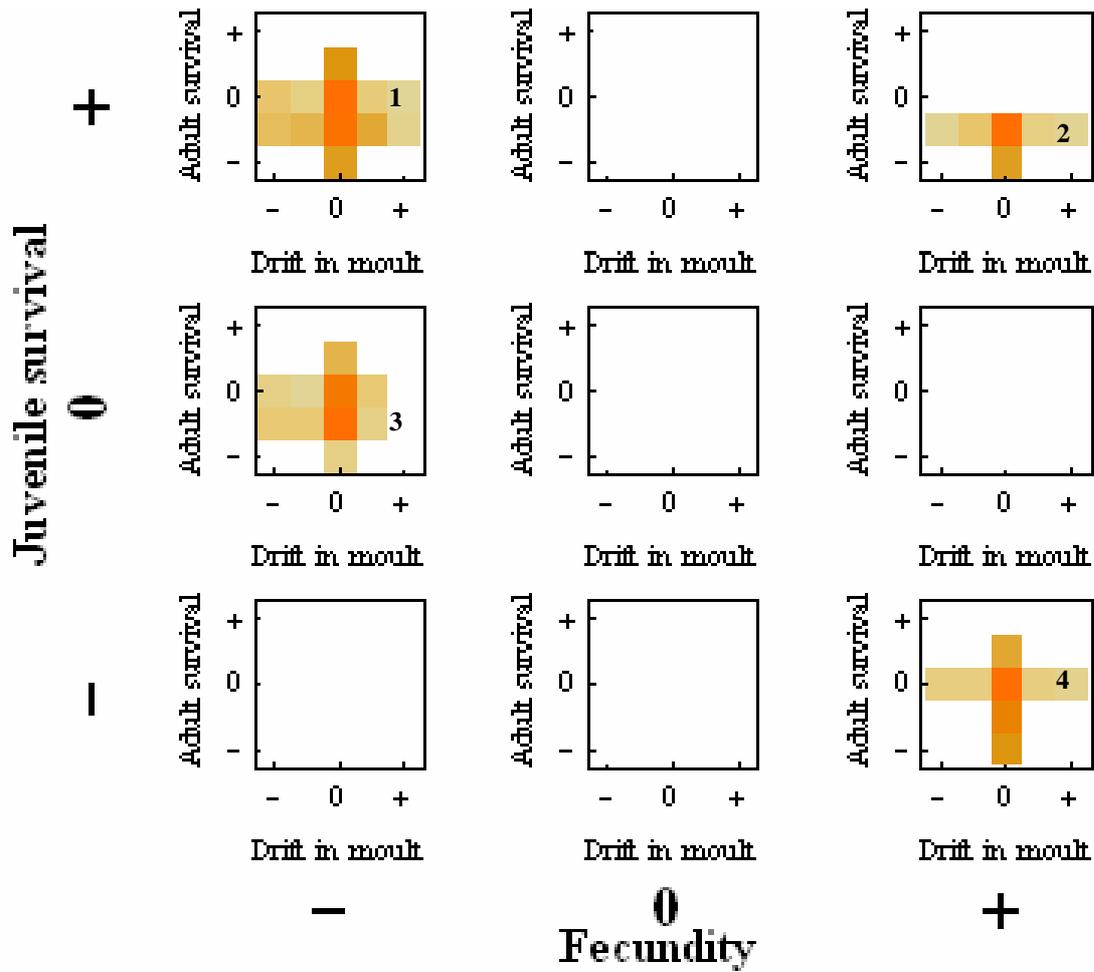


FIGURE 2: Exploration of multifactor explanations for the observed counts. The processes considered in this contingency table are changes (increase: “+”, decrease: “-”, no change: “0”) in fecundity, juvenile survival, adult survival and the timing of moult. The colours indicate the ability of a particular contingency to explain the observed counts. They can be thought of as the likelihood (conditional on model structure) that a particular combination of factors is the explanation for the observations. Colours range from white (unlikely explanation) to orange (most likely explanation). For example, under scenario 2, a reduction in adult survival is capable of causing a reduction in counts despite an increase in fecundity and subadult survival.

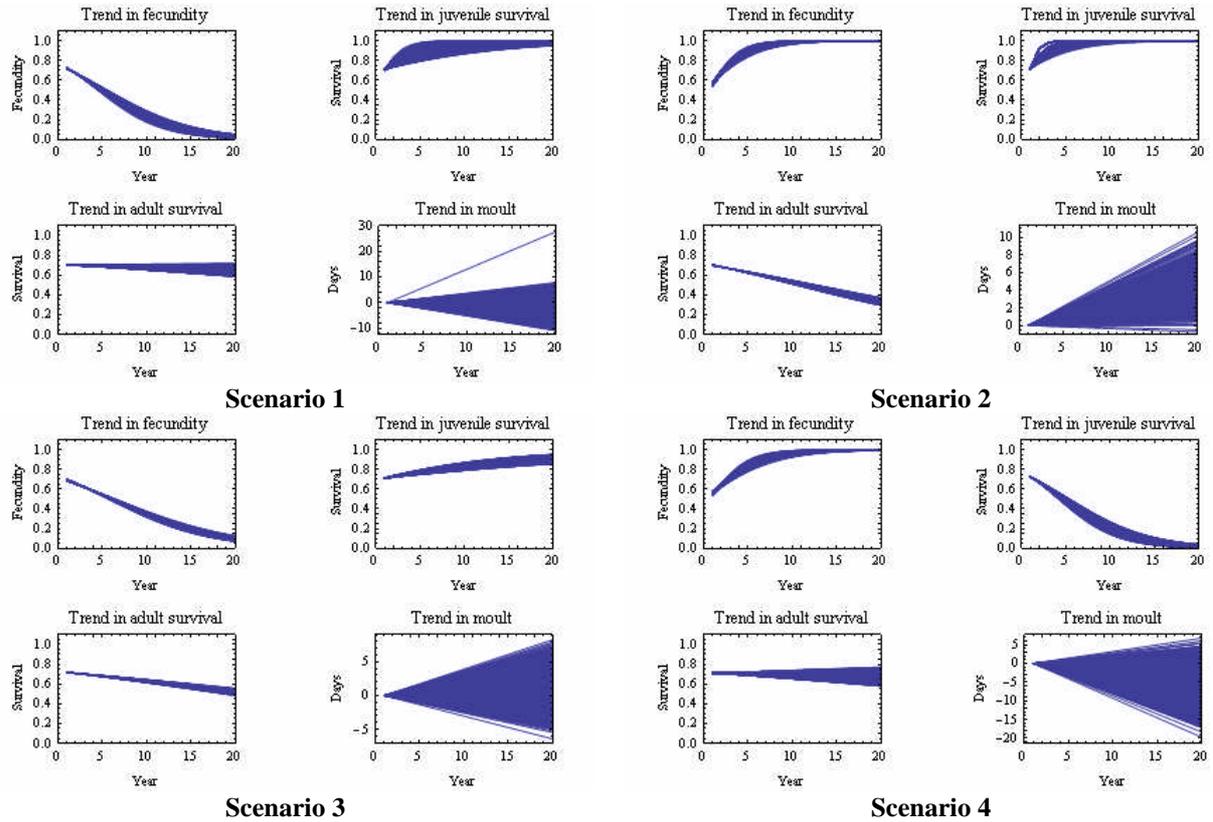


FIGURE 3: Trends in demographic processes under the four likely scenarios in Fig. 2. To represent uncertainty, each of these plots is generated by superimposing 1,000 curves parameterized from MCMC replicates within the region described by the corresponding scenario. The aspect of interest in these plots is the scale of the y-axes. This indicates the necessary magnitude of a particular effect under each of the scenarios.

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Life history parameters at contrasting grey seal breeding colonies east and west of mainland UK, based on mark-recapture analysis

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

Summary

Annual capture-recapture data were obtained for individual grey seals (*Halichoerus grypus*) at the Isle of May and North Rona grey seal colonies by means of pelage (photo-id), brands, or flipper tags during long-term observational studies between 1979-2006. Bayesian methods were used to parameterise a range of mark-recapture models, allowing for site and time-dependence in the demographic parameters. In addition, the following factors were explored:

1. The effect of observer effort on recapture probability
2. Temporary emigration
3. Fecundity
4. Tag loss
5. Environmental effects, based on the NAO

DIC was used to select the 'best' candidates from competing models. The models with strongest support were those in which survival and recapture probability were colony-dependent and time-dependent. Survival rates appeared to be generally lower and more variable at Rona than on the Isle of May. Tagloss rates were also site-dependent. In addition, for branded animals, there was support for a model linking the recapture probability to observer effort. This model also provided an estimate for temporary emigration (about 22% of the study females were likely to be absent from a colony in any given year). Estimates of colony fecundity rate (probability of pupping, given that a female is present) were approximately 98% at both sites. By combining estimates of temporary migration and fecundity, it was then possible to estimate annual pup production per female at these colonies (~76% per female per site, for both sites).

Introduction

In order to understand the processes that drive grey seal population dynamics at local and

regional scales, it is crucial to understand how and why the life histories of these animals have changed over time. Such changes may be responses to external driving factors such as climate, pollution

and prey availability, or they may be caused by shifts in population size or structure. One major function of long term empirical studies, in which individual animals are observed over many years, is to provide estimates of life history parameters such as survival and fecundity, and to explore the factors that influence these parameters. Long term data sets from grey seal (*Halichoerus grypus*) breeding colonies the Isle of May and North Rona offer a unique opportunity to make a comparative study of colonies with contrasting pup production trajectories. At Rona, pup production is in decline, while the Isle of May shows continued growth in pup production. Here we present the results of mark recapture models for seals at these colonies. Survival, fecundity and recapture probability are estimated for the two sites, and the effects of different methods of marking are examined. In addition a method for estimating temporary migration is implemented.

Methods

Breeding grey seals have been studied on North Rona in the Outer Hebrides from the 1960s, and at the Isle of May in the Firth of Forth from the 1980s. There has never been a consistent long term marking program, and therefore the number and type of marks applied has changed according to studies and sites. Branded seals on North Rona were followed from 1986-2006, with flipper tagged adults first observed from 1979 onwards and photo-id (based on pelage markings) used to identify adults from 1998 onwards. On the Isle of May, branded adults were observed from 1987 and flipper tagged adults from 1988 onwards. No photo-id records for the Isle of May seals are considered here.

At each study colony, regular daily surveys of all animals were made during the time that workers are present during the breeding season. Re-sighting effort was therefore estimated from the number of days spent by observers at the colony, which we will refer to as catch-effort.

Open population mark recapture models based on Cormack Jolly Seber (CJS) models were fitted in WinBUGS using Bayesian methods. It should be noted that, in such models, it is generally not possible to distinguish between the effects of death and permanent migration, so that the inferred survival rates of seals are really 'apparent survival rates' indicating the probability of seals persisting at the colony, rather than elsewhere.

One of the underlying assumptions of the CJS model is that there is no temporary migration (Williams and Nichols, 2002). However in the presence of additional covariate information (in terms of catch effort) we relax this assumption, allowing for random temporary migration. Typically (without additional external information) it is not possible to distinguish the effects of temporary migration (in which an animal may be absent during one breeding season, but present for subsequent breeding seasons) from imperfect re-sighting of animals that are present (i.e. re-sighting probability < 1). The simple re-sighting probability P is given by the product:

$$P = \beta \times \psi \quad (1)$$

where

β is the probability that an animal is present

ψ is the re-sighting probability, given that an animal is present

These parameters are typically confounded and only their product can be estimated without additional external information.

A simple formulation for the likelihood of the observed data in such a mark-recapture model, where I individual seals are studied over T years, would be:

$$\sum_{i=1}^I \left(\sum_{j=1}^{J_i-1} \phi_j (p_j f^{q_{i,j}} (1-f)^{1-q_{i,j}})^{x_{i,j}} (1-p_j)^{(1-x_{i,j})} \right) \chi_{J_i} \quad (2)$$

where

i refers to an individual seal, and j to a year.

ϕ_j is the apparent survival.

p_j (lowercase) is the probability that a seal is re-sighted in year j

f is 'colony' fecundity, here taken to mean the probability that a seal has a pup, given that she is present at the breeding colony.

$x_{i,j}$ is observational data. If an individual i is seen in year j , this takes the value 1, otherwise it is 0

$q_{i,j}$ is observational data. If an individual is seen to have pupped in year j , this takes the value 1, otherwise if the seal does not pup it is 0.

χ_j is the probability that a seal is not seen again after year j , and J_i is the final year that individual i is observed.

χ_j can be calculated iteratively as follows :

$$\chi_j = \phi_{j+1}(1 - P_{j+1}) + (1 - \phi_{j+1})\chi_{j+1} \quad (3)$$

$$\chi_T = 1$$

The following modifications were made to this model:

1. Recapture probability ψ varied according to mark type m , with separate parameters $\psi_{m,j}$ for branded, tagged, or photo-id'd animals. Recapture probability was modelled as a function of observer effort, E , where effort was measured in units of observer-weeks spent at the study site. This was investigated according to the following 'catch-effort' model (King and Brooks 2004):

$$\psi_{m,j} = 1 - (1 - \alpha_m)^{E_{m,j}} \quad (4)$$

where m is mark type, j is year, and α_m is the underlying re-sighting probability per unit effort and is assumed to be mark-dependent.

A further modification to this model takes temporary emigration into account. The equation then becomes:

$$p_{m,j} = \beta \left(1 - (1 - \alpha_m)^{E_{m,j}} \right) \quad (5)$$

where β is the probability that an animal is present in any year, and the expression inside the brackets now represents the probability that an animal is seen, given that it is present (equivalent to ϕ in equation 1).

This formulation will now be referred to as the 'modified catch-effort model'.

- Tags can be lost, but brands and pelage markings can reasonably be considered to be permanent. A seal that loses its tag will not be observed subsequently, and so will appear to have died/permanently emigrated, and so the apparent survival of the seals is expected to depend on mark type. If the probability of tag loss in a given year (assumed to be constant over time) is γ then

$$\begin{aligned} \phi_{T,j} &= (1 - \gamma) \phi_{B,j} \\ \phi_{P,j} &= \phi_{B,j} \end{aligned}$$

where T refers to tagged seals, B refers to branded seals, and P (uppercase) refers to pelage - marked seals identified by photo - id.

Models were fitted to a matrix of sufficient statistics, which summarise the mark recapture data (Brooks and Catchpole 2002). The DIC was used as an initial model discrimination tool, and can be regarded as a Bayesian alternative to the AIC. The proposed set of models (see Table 3) is not exhaustive but addresses the following questions:

- What are the values of important life history parameters ϕ , and f at the two sites, North Rona and the Isle of May?
- Are these parameters time-dependent, or constant?
- Does re-sighting probability depend on mark type, and/or on site?
- What is the estimated rate of tag loss in adult females?
- Can we estimate the probability that a female is present on the colony in a given year, based on the modified catch-effort model?

Results

30 models were fitted in total and a selection of these models is listed in Table 1. The models with strongest support were those in which survival and recapture probability were site-dependent: this suggests that there is support in the data for the conclusion that values of P and ϕ at the two colonies were different during the study period. The better models were those in which P and ϕ were time-dependent. The time-dependence of survival rates (based on model s18) for each colony is shown in Figure 1.

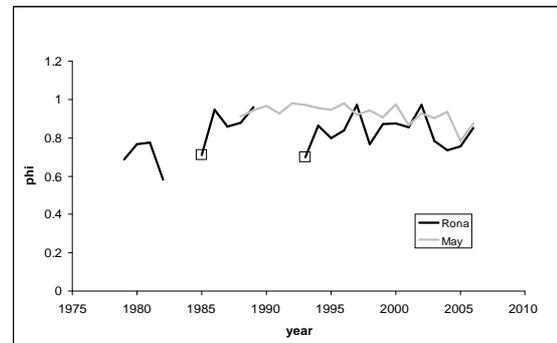


Figure 1: Estimated survival at North Rona and the Isle of May during the years of the observational study. Note that ϕ cannot be estimated during years where no observers are present, and the estimates of ϕ in the first year of observation after such a 'gap' (marked with squares) represent the probability of survival during the whole unobserved period. They appear low compared with other estimates of ϕ , and should not be directly compared with annual estimates.

It appears that survival rates were generally lower and more variable at Rona than on the Isle of May.

Model selection indicated that recapture probability does depend on mark type, with brands being the mark type that was most readily re-sighted. Tags were less easily seen, and the re-sighting rate for tags on the Isle of May was significantly lower than the rate on Rona (Figure 2).

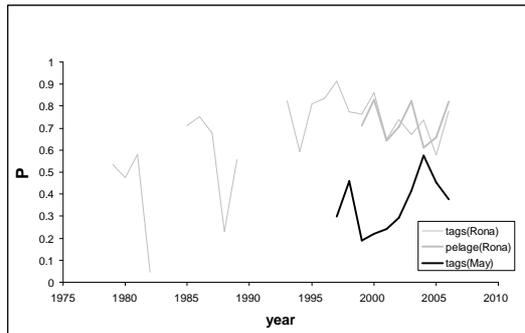


Figure 2: Time-dependent recapture probability is shown for tags and pelage on Rona, and for tags on the Isle of May, for those years where marked seals and observers were present.

Including tag loss in the models appeared to improve the model fit. Tag loss rates appeared to be site-dependent with higher loss rates (11% (3.5-18%)) on the Isle of May compared with Rona (4.2% (0.4-9.2%)), (95% credible intervals, based on the marginal posterior distribution for each parameter, are shown in brackets).

For branded animals, there was support for a model linking recapture probability to observer effort. The estimated value for parameter α was 0.81 (0.56-0.99) for Rona, and 0.54 (0.41-0.88) for the Isle of May. Time-dependent re-sighting rates for pelage and tags at both sites are shown in Figure 2. Re-sighting rates appear similar for brands, tags and pelage on Rona, and when observers are present, the modified mark-effort model suggests that re-sighting probability for brands is always high on Rona while annual estimates of P for tags and pelage are more variable. Re-sighting rates for branded animals are more variable, and for tagged animals are lower, on the Isle of May.

The modified catch-effort model for brands provides an estimate of the probability of presence at the colony in any given year, β . This was 78% (74-81%), and did not differ between sites.

Estimates of colony-based fecundity (probability of pupping, given that a female is present at the colony) were obtained by fitting models to the individual capture histories in order to estimate the parameter f , which was approximately 97.5% (97-98%) for the 'best' model. There was no support for a difference in f between sites.

Discussion

Model fitting and selection was successfully carried out within the Bayesian framework, incorporating

some novel approaches including the estimation of tag loss, effort-dependent recapture rates, and temporary migration. The 'best' models that emerged, and the parameter estimates, suggest the following conclusions and questions.

1. Survival rates for adult females appear to be different at the two sites, and are lower and more variable at North Rona. This is consistent with the overall observed downward trend in pup production at Rona, compared with increasing production at the Isle of May. However, further data on (i) migration patterns and (ii) recruitment would be needed to build a model of colony dynamics.
2. Re-sighting probabilities are highest for branded animals, consistent with the perception by observers that the visibility of brands is generally higher than that of tags. Recapture probabilities for tagged animals are lower on the Isle of May than on Rona, and this may be due to the different conditions for observing animals on the Isle of May due to its more complex topography, leading to lower reading rates for the tags.
3. Recapture rates were related to re-sighting effort for branded animals but not for pelage or tagged animals – a surprising result, which suggests that other sources of variability in recapture probability which have not been taken into account in the current models may be having a strong effect.
4. The 'best models' did not include those with NAO effects on survival, so a straightforward immediate link between climatic variation and the life history parameters of adult seals has not been demonstrated in the present study.
5. Tag loss rates of 10% for the Isle of May are higher than the results of independent estimates of tag loss based on tagging data from tagged pup cohorts. This difference may be due to the effects of tag age or seal age. We will investigate this further.
6. The estimate of colony-based fecundity is higher than existing estimates of grey seal pregnancy rates of 0.943 for the east coast and 0.83 for the west coast of the UK (Boyd et al. 1985). The probable explanation for this is that females that are not pregnant are more likely to be absent from the breeding colony than breeding females.
7. The production of pups at the breeding colony by an individual female, irrespective of breeding behaviour elsewhere during temporary migration, is the product $\beta \times f$. Based on the 'best model', the estimate of this quantity is 0.76 (0.74-0.78) for the Isle of May and Rona. This estimate does not provide any indication as to the breeding behaviour of females that are absent from the colony and makes no assumptions as to whether or not these absent females are breeding.

Ongoing and future work

1. Repeat the analysis and model selection using classical statistical methods, in order to assess any possible problems with the somewhat controversial DIC.
2. Implement model selection within the Bayesian framework using RJMCMC (King et al. 2006). This will allow for a quantitative comparison of models and model averaging, if appropriate.
3. Incorporate the effects of double-tagging and age-related tag loss.
4. Explore the effects of individual covariates such as mass and body composition on the life histories of females.
5. Investigate environmental factors e.g. the implications of prey abundance and distribution, and environmental indices other than the NAO. This may enable us to distinguish competing environmental effects at the different colonies.

References

- Boyd I.L. 1985, "Pregnancy and ovulation rates in Grey seals (*Halichoerus grypus*) on the British coast" *Journal of Zoology* 205, 265-272
- Brooks S.P and Catchpole E.A. 2002, "Bayesian methods for analysing ringing data" *Journal of Applied Statistics* 29, 187-206
- King R. and Brooks S.P. 2004, "A Classical study of Catch-Effort Models for Hector's Dolphins" *Journal of the American Statistical Association* 99, 325-333
- King R. Brooks S.P. Morgan B.J.T. and Coulson T. 2006, "Factors Influencing Soay Sheep Survival: A Bayesian Analysis" *Biometrics* 62, 211-220
- Williams B. K. and Nichols J. D. 2002, "Analysis and Management of Animal Populations" San Diego: Academic Press.

Table 1: Mark-recapture models fitted to data from North Rona and the Isle of May. The ‘best model’ (lowest DIC) is highlighted in bold.

model	parameters	DIC
1	ϕ is constant, P is mark-dependent. ϕ, P_{mark}	1392
2	ϕ varies by site, P is mark-dependent. ϕ_{site}, P_{mark}	1355
3	ϕ varies by site, P varies by site and is mark-dependent. $\phi_{site}, P_{site,mark}$	1294
4	ϕ varies by site and mark type: ϕ for tags is related to ϕ for brands by γ . P is site-dependent and mark-dependent. $\phi_{mark,site}$ $\phi_{brand,site}$ $\phi_{pel,site}=\phi_{brand,site}$ $\phi_{tag,site}=(1-\gamma)\phi_{brand,site}$ $P_{site,mark}$	1280
5	ϕ varies by site and mark type: ϕ for tags is related to ϕ for brands by γ . γ is now site-dependent. P is site-dependent and mark-dependent. $\phi_{mark,site}$ $\phi_{brand,site}$ $\phi_{pel,site}=\phi_{brand,site}$ $\phi_{tag,site}=(1-\gamma_{site})\phi_{brand,site}$ $P_{site,mark}$	1279
6	ϕ varies by site and mark type: ϕ for tags is related to ϕ for brands by γ . P is estimated annually. $\phi_{mark,site}$ $\phi_{brand,site}$ $\phi_{pel,site}=\phi_{brand,site}$ $\phi_{tag,site}=(1-\gamma_{site})\phi_{brand,site}$ $P_{site,mark,year}$	1189
7	ϕ varies by site and mark type: ϕ for tags is related to ϕ for brands by γ . P varies according to modified catch effort model for brands, tags and pelage. β is the same at both sites. $\phi_{site,mark}$ $\phi_{brand,site}$ $\phi_{pel,site}=\phi_{brand,site}$ $\phi_{tag,site}=(1-\gamma_{site})\phi_{brand,site}$ P based on modified catch-effort model: $P_{mark,site,year}=\beta(1-(1-\alpha_{site,mark})^{E_{mark,site,year}})$	1234
8	ϕ varies by site and mark type: ϕ for tags is related to ϕ for brands by γ . P varies according to modified catch effort model for brands, tags and pelage. β is site-dependent. $\phi_{mark,site}$ $\phi_{brand,site}$ $\phi_{pel,site}=\phi_{brand,site}$ $\phi_{tag,site}=(1-\gamma_{site})\phi_{brand,site}$ $P_{mark,site,year}=\beta_{site}(1-(1-\alpha_{site,mark})^{E_{mark,site,year}})$	1236

9	ϕ varies by site and mark type: ϕ for tags is related to ϕ for brands by γ . P varies according to modified catch effort model for brands, for tags and pelage P is estimated annually $\phi_{mark,site}$ $\phi_{brand,site}$ $\phi_{pel,site}=\phi_{brand,site}$ $\phi_{tag,site}=(1-\gamma_{site})\phi_{brand,site}$ $P_{site,mark,year}$ for tags, pelage $P_{brand,site,year}$ based on catch-effort model $P_{brand,site,year}=\beta(1-(1-\alpha_{site})^{E_{brands,site,year}})$	1181
10	ϕ varies with nao, and ϕ for tags is related to ϕ for brands by γ . P varies according to modified catch effort model for all mark types. $\phi_{mark,site,year}$ $\phi_{site,brand,year} = \text{logit}(k1, k2, nao_{year})$ $\phi_{site,pelage,year}$ $\phi_{site,tag,year}=(1-\gamma_{tags})\phi_{site,brand,year}$ P based on catch-effort model for all mark types $P_{site,mark,year}=\beta(1-(1-\alpha_{site,mark})^{E_{site,mark,year}})$	1223
11	ϕ varies with nao, and ϕ for tags is related to ϕ for brands by γ . P varies according to modified catch effort model for brands, for tags and pelage P is estimated annually $\phi_{site,mark,nao}$ $\phi_{site,brand,year}=\text{logistic}(k1_{site},k2_{site},nao_{year})$ $\phi_{site,pel,year}=\phi_{site,brand,year}$ $\phi_{site,mark,year}=(1-\gamma_{site})\phi_{site,brand,year}$ $P_{site,mark,year}$ for tags, pelage P_{brand} modified catch-effort model $P_{brand}=\beta(1-(1-\alpha_{site})^{E_{brands,site}})$	1179
12	ϕ estimated annually, ϕ for tags is related to ϕ for brands by γ . P varies according to modified catch effort model for all mark types $\phi_{site,mark,year}$ $\phi_{pel,year}=\phi_{brand,year}$ $\phi_{tag,year}=(1-\gamma_{site})\phi_{brand,year}$ $P_{mark,site,year}=\beta(1-(1-\alpha_{site,mark})^{E_{mark,site,year}})$	1155
13	ϕ estimated annually, ϕ for tags is related to ϕ for brands by γ . P is estimated annually $\phi_{site,mark,year}$ $\phi_{pel,year}=\phi_{brand,year}$ $\phi_{tag,year}=(1-\gamma_{site})\phi_{brand,year}$ $P_{site,mark,year}$ for all mark types	1143
14	ϕ estimated annually, ϕ for tags is related to ϕ for brands by γ . P varies according to modified catch effort model for brands, for tags and pelage P is estimated annually $\phi_{site,mark,year}$ $\phi_{pel}=\phi_{brand}$ $\phi_{tag}=(1-\gamma_{site})\phi_{brand}$ $P_{site,mark,year}$ for tags, pelage P_{brand} modified catch-effort model $P_{brand}=\beta(1-(1-\alpha_{site})^{E_{brands,site}})$	1127

P. Pomeroy, S. Smout, S. Moss, S. Twiss & R. King

Low and delayed recruitment at grey seal breeding colonies in the UK.

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

Summary

Resights of tagged and cohort-branded pups as breeding adults on North Rona and IoM indicate that cumulative resight rates of marked seals were at best 0.10 on NR and 0.31 on IoM. Double tagged cohorts were resighted at the highest rates, but there was evidence of interannual variation as some cohorts were never seen. Absolute tag loss estimates were higher at NR than at IoM, but would not alone explain the low resight rates there.

Within the last decade, recruitment at IoM appears to be occurring several years later than expected, consistent with the effects of density dependence. There are too few tag returns from NR to allow support similar conclusions, but this lack and the continued decline of pup production in OH suggests that recruitment is a problem. These findings have direct implications for current population models.

Introduction

Much of the basic life history information available until now for grey seals in the UK was collected through synoptic "sample collection" in the 1960s, '70s and '80s when the population was increasing strongly. Data suggested that females recruited into the breeding population aged 3-5 and by age 5, over 90% of females would be breeding. Recently however, the UK grey seal population's annual rate of pup production has declined from more than 6% in the 1990's to 0.5% in 2004 (Duck et al. 2005). It is clear that demographic parameters have changed and examination of long term data offers the clearest perspective of how these changes are occurring. Recently, effort has been directed at deriving models to determine total grey seal population size and identify the demographic parameters most likely to change with density dependence, but in most instances these models are limited by the information supplied at the outset. Long term empirical studies should inform such models with realistic priors, within their limits. Here we consider empirical evidence of recruitment patterns at two UK grey seal breeding colonies with contrasting pup production trajectories.

Methods

Breeding grey seals have been studied on North Rona (NR) Outer Hebrides from the 1960s and Isle of May (IoM) Firth of Forth from the 1980s.

Annual pup production at NR has fallen from around 2500 in the 1960s to around 1000 presently, while the IoM grew from a handful of pups born in the 1970s to over 2500 in recent years.

There has never been a consistent long term marking programme for UK grey seals therefore the number and types of marks applied has changed according to studies and sites (Table 1).

Pups on NR were tail tagged in 1961-2 and cohort branded from 1960-1972, then flipper tagged and only in 1990 were they also cohort branded. In 1991-2, pups were double tagged. In 1995-6, pups at both colonies were tagged using subcutaneous RFID chips which are not considered here as they are not visible.

Adult females have been identified from their pelage since 1998 but this facility has been maintained only at NR.

At each study colony, regular daily surveys of all visible animals were made during the time that workers were present during the breeding season. Any tagged animals present were identified as practicable, either remotely or by direct inspection. The percentage of tagged seals that was identified of those present was estimated typically as c.90% on NR and c.70% on IoM. We use "resight" to mean a definite sighting of a particular animal.

We examined tag loss in double marked animals. Arithmetic annual tag loss rates were calculated as (tags lost/tag years) and compared to tag loss rates generated from survival models (Smout et al. SCOS 07).

Observed resights of pups at IoM were compared to expected schedules using the product of mortality and tag loss rates to decrement cohorts according to a simple deterministic model assuming no emigration.

Results

Resights at NR – flipper tags

Cumulative resights of marked pups as breeding females represent up to 10% of the females marked

in cohorts at NR (Table 1). There were no resights of any pups tail-tagged at NR in the 60s: tail tags were deemed a failure as they were sometimes lost before weaning (Boyd & Campbell 1971). Resights from other NR cohorts have been sparse, even though up to c. 25% of female pups were tagged in some cohorts. There have been no resights to date of any of the 400 female pups flipper-tagged there from 1994 and 1997-2000.

One female breeding on NR in 1995 and not seen since had been tagged as a 1977 pup in Shetland. A female branded on the Monachs in summer 1996 has bred regularly on NR.

It is difficult to draw any conclusions about age at primiparity on NR with such sparse data, however the median age of females tagged as pups when they were first seen breeding on NR was 10, range 7-18 (n=18).

The annual tag loss rate for adult females at NR was estimated as 0.04 (35/832), agreeing with the 0.04 estimate generated by survival model (Smout et al SCOS 07).

Resights at NR – pup cohort brands

Applied in the 1960s, there has been extreme variability in their resighting (Table 2). None of the 380 female pups branded in 1960-61 were ever resighted. The resight rate for all branded cohorts has been low but was similar to the flipper tag resighting rates at NR. Resightings rarely represented more than 10% of the number of branded pups expected to be alive at any stage. None of these cohort branded animals has been seen on NR since 1998.

Resights at IoM

Cumulative resights of individually marked pups as breeding females represent up to 31% of the females marked in cohorts at IoM (Table 1). The highest resight rates have been from the 1990, 1991 and 1992 cohorts, all of which were double marked.

Fewer females from 1993 onwards have been resighted breeding on IoM (<10% of those marked). No females from the 2000 or later cohorts have been resighted on IoM to date.

As at NR, the number of resights obtained is not a simple function of the number of tags applied – some of the largest tagged cohorts have not had any resights.

The youngest seals observed breeding were aged 4 and 5, but there were few of these (Figs 1, 2). The cumulative resight curves in Fig. 1 give some indication that females aged 10 and over were still appearing for the first time on the colony. This can be seen more clearly by displaying the age at which known females appear on the colony, and for the time being we will refer to these as recruits (Fig 2.) There were very few recruits below age 6. The

bimodal distribution peaks at 6 and 10-12 with a few animals appearing even after that. It is clear that this tendency for later recruits is not confined to the earlier 90-92 cohorts (Fig. 2 blue) but is as pronounced in the 93, 94 and 97 cohorts (Fig 2. red), counterintuitively, as they might be expected to be biased towards younger animals.

Annual tag loss rate at IoM was estimated as 0.02 (31/1406). However, survival models produced an estimate of 0.10. This discrepancy is being examined but is likely to be accounted for by the former method being biased heavily to older seals and the assumptions used in the arithmetic calculation.

We set first-year survival at 0.62 (Hall et al. 2001), 0.52 and 0.48 with 0.95 survival thereafter to generate a range of expected schedules of females alive. These were then modified by upper and lower tag loss rates (0.02 and 0.10) to produce a schedule of expected numbers of females alive and tagged.

Plots of the known number of females alive (dashed red lines Fig 1a-c) suggest that in 1990-1 the 10% tag loss rate seems high, but in 1992 resights were even lower than any of the early survival and tag loss rate combinations predicted. Note that the effects of different first year survival rates are subtle after the first few years compared to different tag loss rates.

Public tag returns for pups

Information from returned (pup) tags tends to occur within the first year after application and the few data relate mostly to IoM animals. However there are insufficient data available for each cohort to provide useful additional information (Hall & McConnell, pers comm.).

Discussion

This study has found few recruits of marked female seals on NR as breeding adults. More recent resight rates for single tagged pups marked in the 1980s and 90s were similar to the highest resight rates for those branded in the 1960s. It is unfortunate that the early branding programme was never followed up. Most of the data available on NR cohort branded animals from later studies refers to post-recruitment years and is not considered here.

The complete absence of some cohorts from resights has several possible explanations: complete failure of the cohort, through catastrophic mortality caused

either by marking, disease, starvation/environmental effects, or a complete loss of all marks. This was suspected in the case of NR tail tagged pups in 1960 and 1961, but does not explain the disappearance of the branded animals from the same years. Later flipper-tagged cohorts, particularly at NR but also at IoM, have also been poorly represented, thus large fluctuations in early (first year?) survival rates beyond those used in projections here must remain a possibility.

The first resights of individual females on the study colonies do not necessarily correspond to their age at primiparity. However, several observations support a delayed age of recruitment on the IoM. (i) In cohorts for which we have the most data, only a small proportion are seen breeding by age 5. This is not an artifact of marking or resightability as the double marked cohorts bear out. (ii) The almost complete absence of the later marked cohorts, both at NR (94-present) and IoM (97-present), suggest that recruitment for these cohorts has barely begun. Similar phenomena have been observed at Sable Island (Bowen et al. 2007).

On the Isle of May, the numbers of females seen approaches the expected number alive using the best estimates of survival and tag loss rates. This suggests that fidelity to their natal breeding site is particularly high. However as isolated reports of tagged animals from other E coast sites continue, it would be very instructive to carry out a comprehensive survey of Fast Castle and Donna Nook in the next breeding season.

Marking methods for studying recruitment of grey seals are problematic. Although cohort brands are very visible, they are non-specific, making an accurate census of those present on a colony extremely difficult, particularly when animals come and go freely. The Jumbo Rototags flipper tags used here have been found in other studies to be among those with the lowest loss rates. Loss rates of 0.02 (new tags) and 0.06 (old tags) were reported for Weddell seals (Testa and Rothery, 1992). There has always been the suspicion that flipper tagged pups may suffer greater mortality in fishing gear, but if this were true it suggests a gear-specific effect working on NR pups more than those at IoM. A better model of tag loss is being prepared to investigate this, based on the age specific loss of tags, but inevitably, passive tags must be retained for the years between weaning and breeding to be informative and losses in the intervening period are a problem. The newer

SMRU active tags offer superb opportunities for information from the earlier years but are expensive, especially when experiencing high initial losses (40-50%).

Ongoing and future work

- Continue resighting effort at NR and IoM.
- Extend resight effort on E. coast to Fast Castle and Donna Nook.
- Develop more realistic tag loss model based on age-specific probability of loss using observed data (different for NR and IoM).
- Does tag loss account for missing animals?
- Does emigration account for missing animals – can presence be used as a proxy for philopatry?
- Use presence and recruitment estimates in breeding colony location framework aka Matthiopoulos to model breeding site use and give pointers to total population size

References:

- Bowen WD, McMillan, JI & Blanchard W. 2007. Reduced population growth of gray seals at Sable Island: evidence from pup production and age of primiparity. *Mar. Mamm. Sci.* 23(1):48-64.
- Boyd JM & Campbell RN. 1971. The Grey seal (*Halichoerus grypus*) at North Rona, 1959-1968. *J. Zool., Lond.* 164: 469-512.
- C.D. Duck and B.L. Mackey. 2005 Grey seal pup production in Britain in 2004. SCOS 2005
- AJ Hall, BJ McConnell, RJ Barker 2001 Factors affecting first-year survival in grey seals and their implications for life history strategy. *Journal of Animal Ecology*; 70:138-149
- Pomeroy P, Anderson S, Twiss S & McConnell B. 1994. Dispersion and site fidelity of breeding female grey seals on North Rona, Scotland *J Zool Lond* 233: 429-447.
- Pomeroy P, Twiss S & Redman P. 2000. Philopatry, site fidelity and local kin associations within grey seal breeding colonies *Ethology* 106: 899-919.
- Smout, Pomeroy & King. SCOS 2007.
- Testa JW & Rothery P. 1992 Effectiveness of various cattle ear tags as markers for Weddell seals. *Mar. Mamm. Sci.* 344- 353.

Table 1. Summary of tags applied to grey seal pups at North Rona and Isle of May and cumulative resights of these to date. * indicates years in which no visible tags were applied.

North Rona flipper and tail tagging					
	total pups			females	%
	tagged	males	females	resighted	resighted
1960#	223	114	109	0	0.0
1961#	541	294	247	0	0.0
-	-	-	-	-	
1979	20	9	11	1	9.1
1980	500	255	245	0	0.0
1981	20	9	11	1	9.1
-	-	-	-	-	
1985	82	41	41	3	7.3
1986	208	116	92	5	5.4
1987	46	25	21	1	4.8
1988	20	10	10	1	10.0
1989	33	17	16	1	6.3
-	-	-	-	-	
1993	296	152	144	4	2.8
1994	301	161	140	0	0.0
1995	*	*	*	*	*
1996	*	*	*	*	*
1997	322	166	156	0	0.0
1998	108	57	51	0	0.0
1999	71	36	35	0	0.0
2000	40	17	23	0	0.0
post 1978	2067	1071	996	17	1.7
				+1 Shetland tagged pup	
Isle of May flipper tagging					
	total pups			females	%
	tagged	males	females	resighted	resighted
1990	139	70	69	15	21.7
1991	174	87	87	27	31.0
1992	171	92	79	11	13.9
1993	353	177	176	14	8.0
1994	369	175	194	17	8.8
1995	*	*	*	*	*
1996	*	*	*	*	*
1997	521	263	258	4	1.6
1998	96	45	51	1	2.0
1999	140	65	75	5	6.7
2000	29	15	14	0	0.0
2001	147	84	63	0	0.0
2002	195	102	93	0	0.0
2003	93	41	52	0	0.0
2004	59	30	29	0	0.0
2005	32	12	20	0	0.0
<i>totals</i>	<i>2518</i>	<i>1258</i>	<i>1260</i>	<i>94</i>	<i>7.5</i>

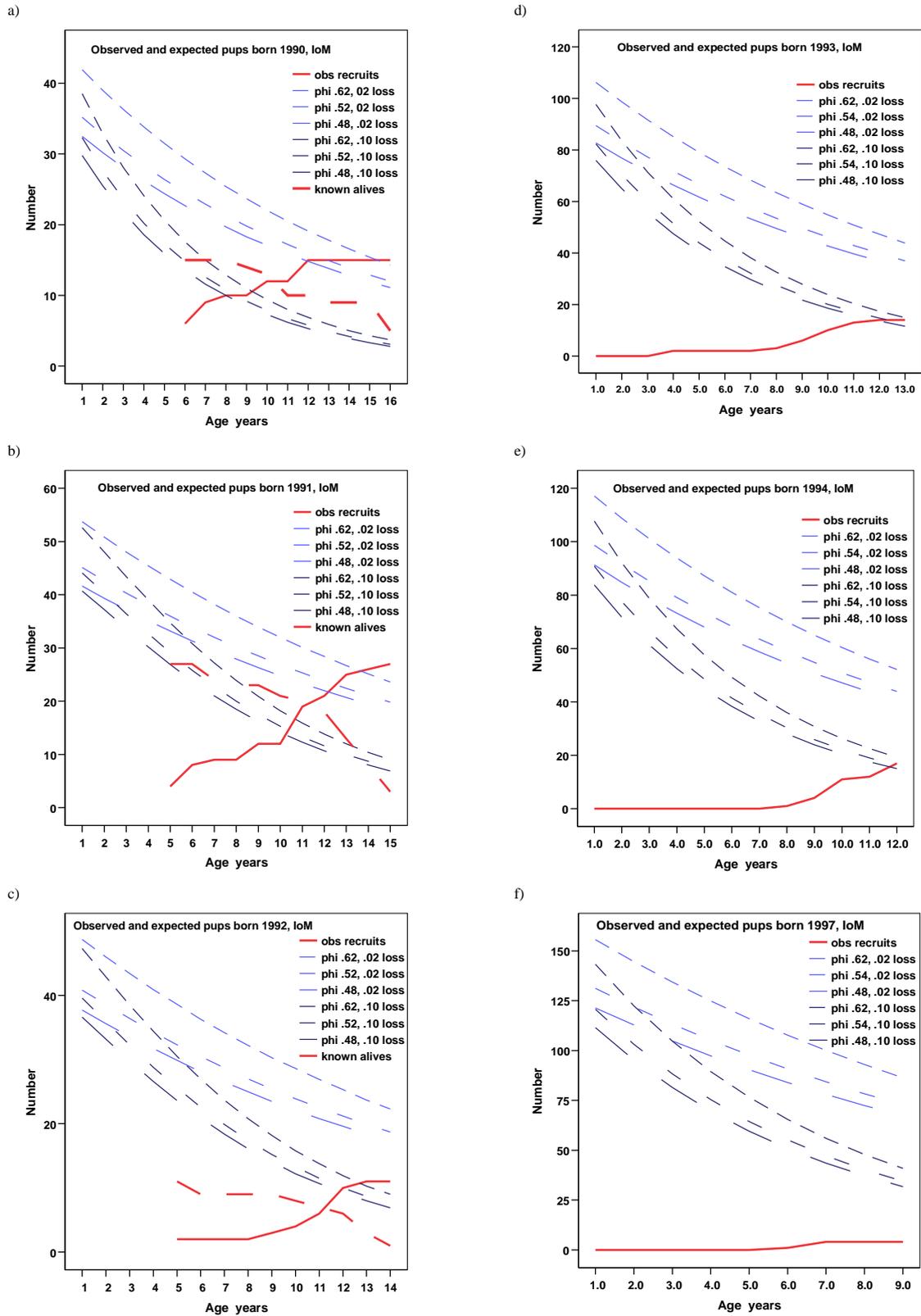


Fig. 1. Observed and expected numbers of female pups born at the Isle of May in (a) 1990; (b) 1991; (c) 1992; (d) 1993; (e) 1994 and (f) 1997. Cumulative number of resights of individually marked females breeding is shown by a continuous red line. Number of individually marked females known to be alive is shown by a dashed red line. Expected numbers of pups alive and tagged are shown by blue dashed lines using different first year survival rates (ϕ) and tag loss ($loss$) rates as indicated.

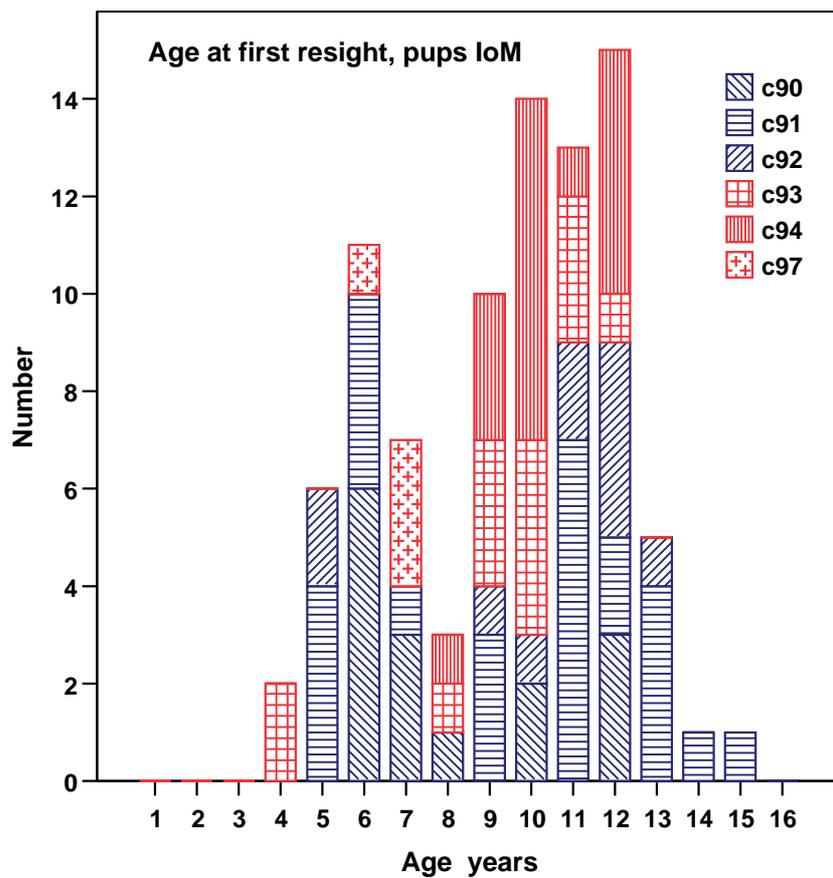


Fig. 2. Age at first breeding resight of pups marked in cohorts from 1990 – 1997 at IoM. Cohorts 1990-2 are shown in blue and cohorts 1993,4 & 7 are shown in red.

J. Matthiopoulos

Preliminary Methods for Designing Marine SACs for UK pinnipeds on the basis of space use

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

Summary

Maps of usage of the marine environment by UK grey and common seals are used to delineate areas of potential conservation interest. To facilitate discussion on this topic between interested parties, several designs are presented, based on different specifications of total area and seal usage enclosed by the SAC boundaries.

1. Introduction

The imminent introduction of Marine Special Areas of Conservation (MSAC) for particular species has stimulated discussion on the appropriate delineation criteria. Usage, the expected proportion of time spent by a population of animals in a unit of space, is an indicator of importance of different spatial regions for the species. It is therefore reasonable to define MSACs so as to include as much of the species usage as possible. However, this needs to be weighted against several practical concerns (e.g. mapping, navigation and policing) and MSAC boundaries may need to be simple or enclose only up to a certain total area. Further, it may be easier to deal with both species of seal in a combined way by designing joint MSACs. To facilitate the discussion between scientists, stake-holders and policy-makers this briefing paper examines several scenarios arising from different sets of constraints.

2. Methods

Two usage maps were imported from previous work on each of the two species. Both maps were based on aerial survey and satellite telemetry data. The aerial survey data provided information about the position of haulout sites and the relative numbers of animals using them. The telemetry data provided information about the range and fine-scale features of usage of the marine environment. The details of the methodology are described in Matthiopoulos et al. 2004. The grey seal map included telemetry data collected in the period 1991-99 (approx. 110 individuals). The common seal map included SMRU's entire telemetry data set to date (approx. 120 animals).

All scenarios required rectilinear boundaries drawn at a scale no smaller than 35km (so, no boundary segment could be smaller than 35km). This

can be reduced in future versions of the design to enable the MSAC boundaries more closely to enfold regions of high usage at the cost of making them more complicated. In each scenario, either seal usage or SAC area was fixed to a required value. To examine the possibility of combined SACs, the same algorithm was applied to a combined map. This was produced as a point-by-point weighted average of the grey and common seal maps. The weights used for this purpose depend on which species is considered to have a higher priority. Two cases are examined, by weighting the two maps equally or by relative total population size.

3. Results

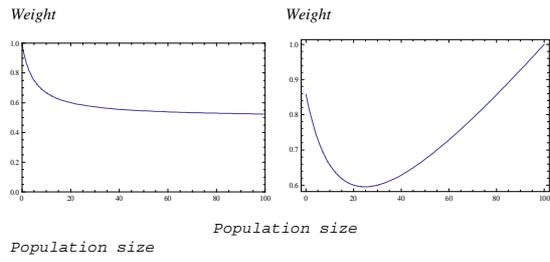
6 scenarios are presented at the end of the paper.

4. Discussion

Two caveats should be considered in interpreting these outputs. The importance of a location does not necessarily scale linearly with usage. A particular behavioural activity may be essential for the survival of an animal but may be completed in a relatively short time.

Further, the algorithms used to propose MSACs have taken no account of the uncertainty in the usage estimates or the potential temporal variability in seal distributions. This is particularly relevant to the grey seal map which is already 7 years old. Both of the above limitations suggest that SAC delineation would become more robust if it was driven by models of habitat preference rather than usage.

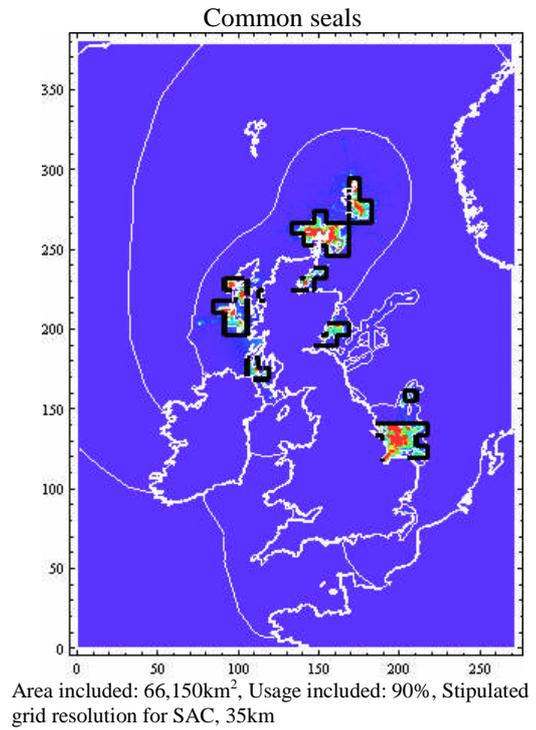
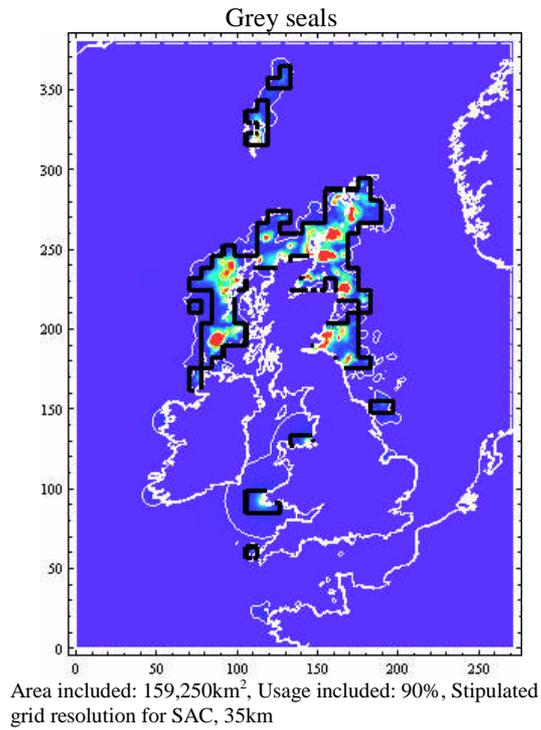
Combined SAC may in some cases reduce the complexity and weighting between species, especially if these overlap spatially. However, the choice of the weighting needs to be carefully considered. For example, instead of giving equal importance to each species (scenario 5) or to each individual animal (scenario 6) it may make sense to weight according to rarity by using a decreasing function of population size. The functions plotted in the following figures approximate scenarios 5 and 6 for large populations but give relatively higher importance to smaller populations.



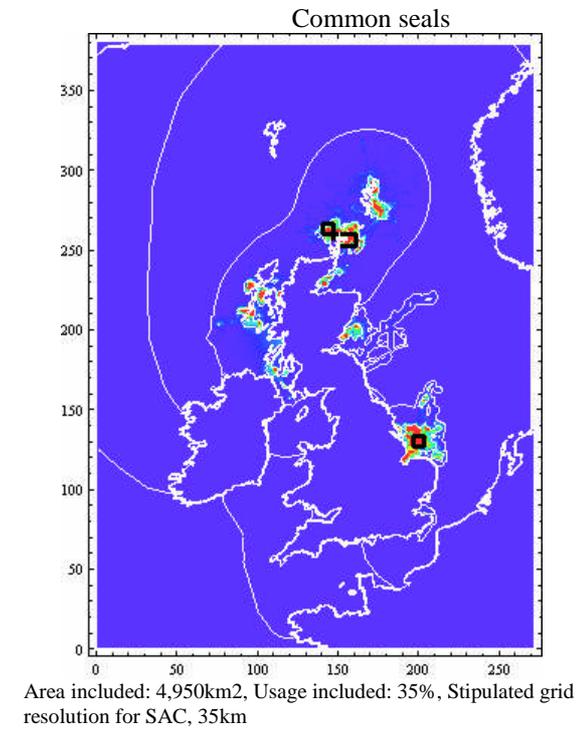
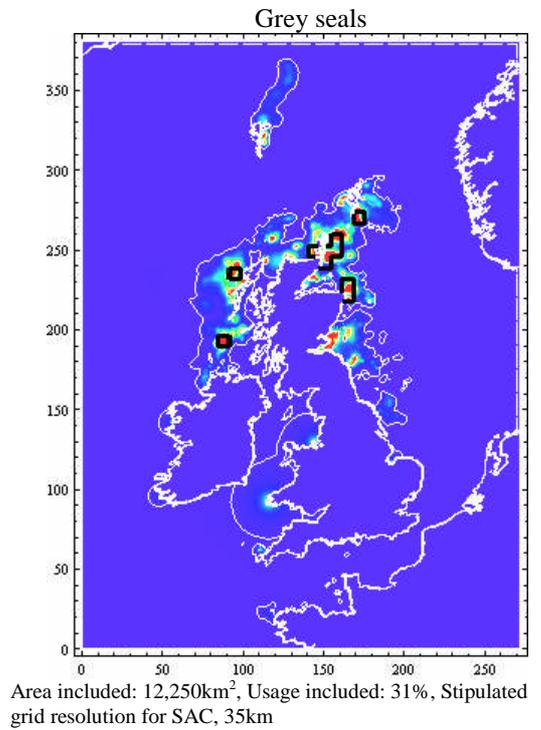
References

Matthiopoulos, J., McConnell, B., Duck, C. & Fedak, M. (2004) Using satellite telemetry and aerial counts to estimate space use by grey seals around the British isles. *Journal of Applied Ecology*. 41, 476-491.

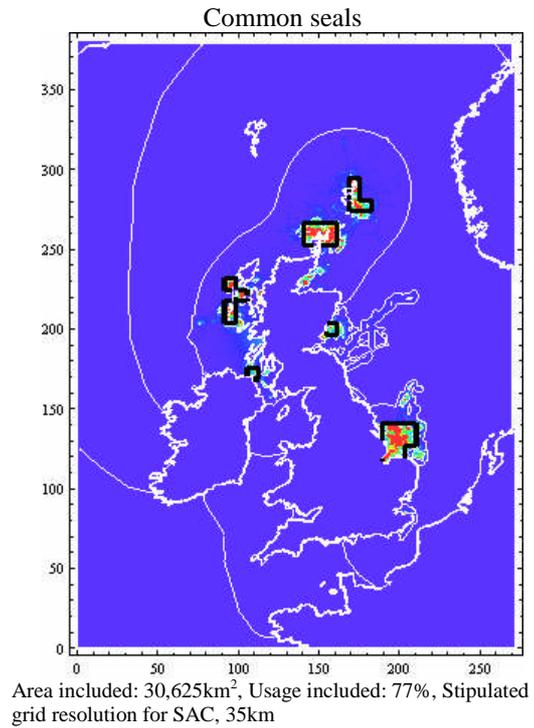
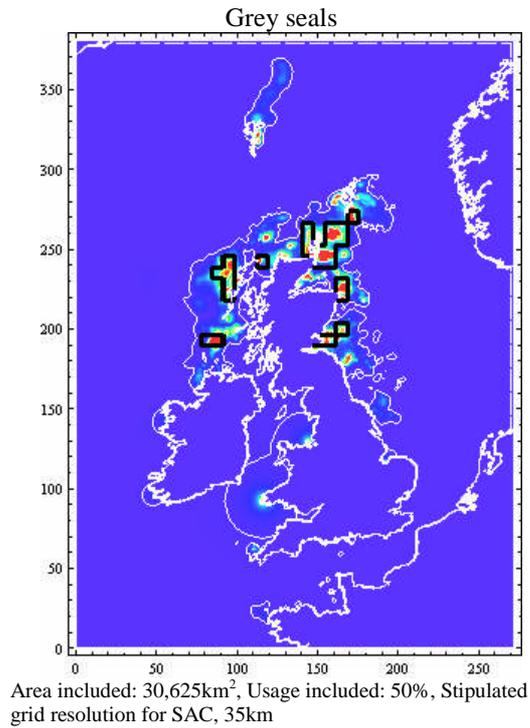
Scenario 1: Species considered separately. ~90% of all usage included in SAC



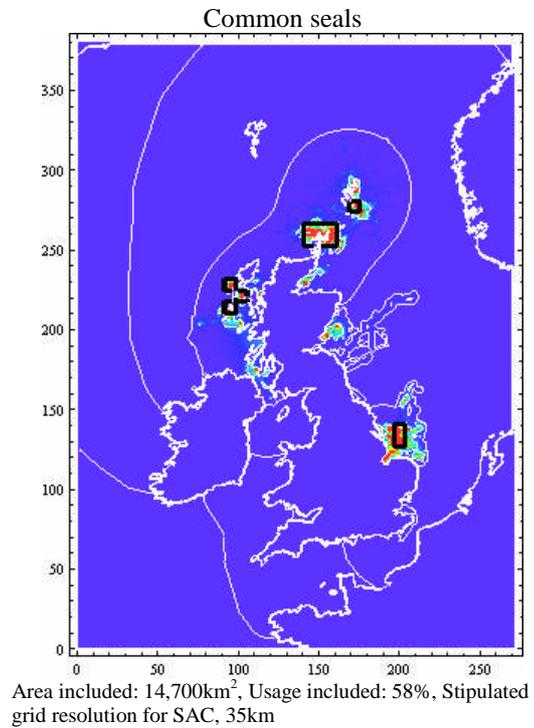
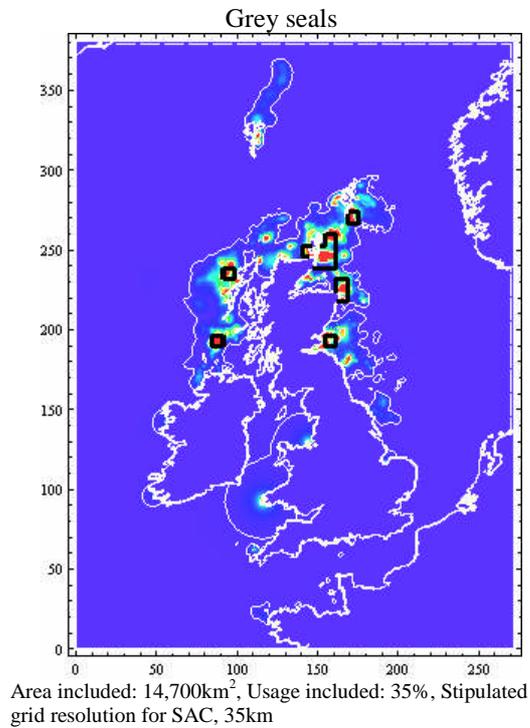
Scenario 2: Species considered separately. ~30% of all usage included in SAC



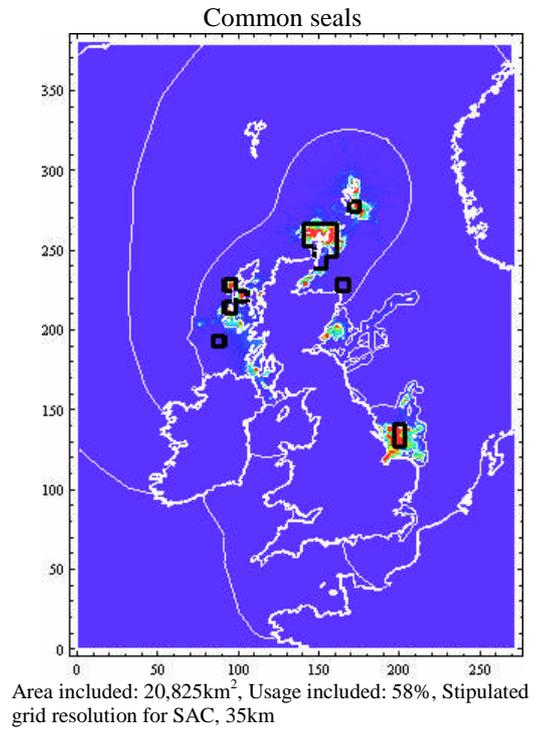
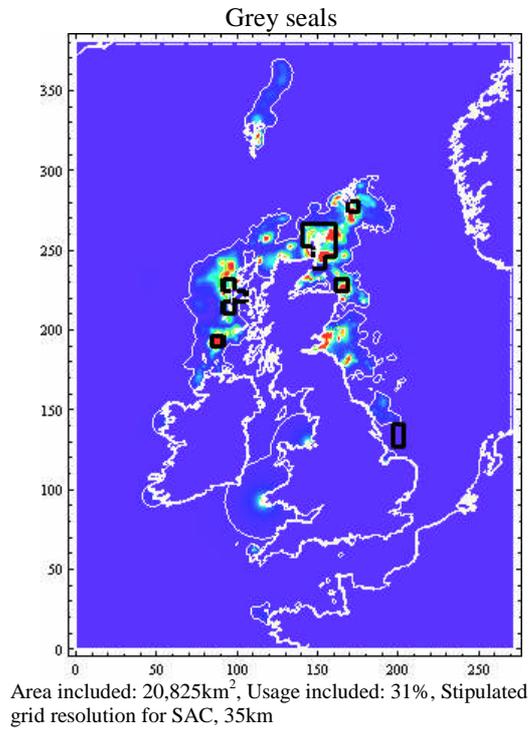
Scenario 3: Species considered separately. Fixed total area of SACs (~30,000km²).



Scenario 4: Species considered separately. Fixed total area of SACs (~15,000km²).



Scenario 5: Species weighted equally. Smallest area containing at least 30% of each species' usage



Scenario 6: Species weighted by pop. size. Smallest area containing at least 30% of each species' usage

