Scientific Advice on Matters Related to the Management of Seal Populations: 2008

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Scientific advice

Background

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

Formal advice is given annually based on the latest scientific information provided to SCOS by the Sea Mammal Research Unit (SMRU – a NERC Collaborative Centre at the University of St Andrews). SMRU also provides government with scientific reviews of applications for licences to shoot seals, 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 2007. It begins with some general information on British seals, gives information on their current status, and addresses specific questions raised by the Scottish Government Marine Directorate (SGMD) 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 throughout Britain has grown steadily since the 1960s when records began, there is clear evidence that the growth is levelling off. The numbers born in the Hebrides have remained approximately constant since 1992 and growth is levelling off in Orkney and possibly in the northern North Sea

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 Wash [1], but had limited impact elsewhere in Britain. Counts in the Wash and eastern England have failed to recover since the epidemic, in contrast to the adjacent European colonies which have experienced rapid growth since 2002. Major declines have now been documented in most populations around Scotland with declines of up to 50% since 2000.

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 SGMD and DEFRA. Accompanying documentation in the form of SCOS Briefing Papers (SCOS-BP ??/??) Numbers need to be provided 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?*** (SGMD/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). The annually surveyed sites account for about 85% of all grey seal pups born throughout Britain. The remaining sites producing around 15% of the pups are surveyed less often. The total number of seals associated with the 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 08/1 and SCOS-BP 08/2.

Pup production

The total number of pups born in 2007 at all annually surveyed colonies was estimated to be 38,900. Regional estimates were 3,100 in the Inner Hebrides, 11,200 in the Outer Hebrides, 19,000 in Orkney, and 5,600 at North Sea sites (including Isle of May, Fast Castle, Donna Nook and Farne Islands). A further 5,300 pups were estimated to have been born at other scattered sites.

Trends in pup production

The differences in pup production between 2006 and 2007 are shown in Table 1. Total pup production at annually monitored colonies decreased by 2.4%, in contrast to the 3.3% increase in the preceding year.

This small inter-annual decrease, is a further indication 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 (2002-2007) the total pup production for all annually monitored colonies has increased slowly, at a rate of 0.7% p.a. 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 4.0% p.a. over the same period. In most other areas the pup production is either stable or decreasing slowly and even in the North Sea the growth is concentrated in the central and southern colonies.

In Orkney, pup production decreased by 2% between 2006 and 2007 in contrast to the 9.6% increase between 2005 and 2006 and a decrease of 7.7% between 2004 and 2005. 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 2007 pup production estimates are consistent with these patterns but may also indicate that growth is slowing in the northern sector of the North Sea.

Table 1: Grey seal pup production estimates for the main colonies surveyed in 2007

Location	2007 pup production	Change in pup production from 2006-2007	Average annual change in pup production from 2002-2007
Inner Hebrides	3,071	-11.3%	+0.1%
Outer Hebrides	11,189	-3.6%	-0.9%
Orkney	18,952	-2.0%	+0.9%
Isle of May + Fast Castle	2,756	+4.8%	+1.6%
All other colonies incl Shetland & mainland	3,519		
Total (Scotland)	39,487	-2.8%*	+0.3%*
Donna Nook +East Anglia	1,640	+14.1%	+15.0%
Farne Islands	1,164	-7.2%	-0.5%
SW England & Wales (last surveyed 1994)	1,750		
Total (England & Wales)	4,554	+2.5%*	+7.6%*
Total (UK)	44,041	-2.3%*	+0.5%*

*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 08/2). 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 again used to fit and compare six state space models of British grey seal population dynamics, based on regional estimates of pup production from 1984 to 2007. One model (DDS) assumed that pup survival was density dependent and that females recruiting to the breeding population show fitness dependent movement between regions. A companion model (DDF) assumed that fecundity was density dependent. Two extended models (EDDS and EDDF) allowed more flexible forms of density dependence in pup survival or fecundity. The last two models (EDDSNM and EDDFNM) also allowed the more flexible forms of density dependence, but assumed that there was no movement of females, i.e. that females recruited to the breeding population in the region of their birth. As in 2007 the models directly estimated observation (i.e. counting) error which had previously been set to an arbitrarily high fixed value with a C.V. of 25%.

Using a model selection criterion based on parsimony, we found that the models with no movement (EDDSNM and EDDFNM) were preferred over the other models.

As in previous years, the survival and fecundity models produced similar quality fits with relatively small differences in the model selection criterion values between the model with density dependent survival and that with density dependent fecundity, although the model incorporating density-dependent pup surival was slightly preferred. The estimated adult population size in 2007 for from the density dependent survival model was 117,600 (95% CI 89,100 to 168,900) and from density dependent fecundity model was 239,700 (95% CI 188,800 to 356,200). The estimated 95% credibility intervals of these models did not overlap.,

When biologically reasonable models give different results it is often considered useful to incorporate model uncertainty and present model averaged posterior mean estimates. The model averaged estimate of the total British grey seal population is 160,100 (95% C.I. 84,500 304,500). While the multi-model confidence intervals are wider and more realistically reflect our uncertainty in the density dependence mechanism, the model averaged mean is less useful. A more detailed description of the methodology is given in SCOS-BP 08/2. It is 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.

A comprehensive survey of data available from the less frequently monitored colonies is presented in SCOS-BP 08/1. Total pup production at these sites was estimated to be approximately 5,400 in 2007. Using the average ratio of pup production to population size for the annually monitored sites, and assuming similar confidence intervals, produces an all age population estimate of 22,200 (approx C.I. 11,700 to 42,000) for these sites. Combining these with the annually monitored sites gives an estimated UK grey seal population of 182,000 (C.I 96,200 to 346,000).

For consistency, in previous reports we have presented population estimates based on the slightly preferred density dependent survival model. However, SCOS now considers that it is more appropriate to present a model-averaged estimate with the commensurately larger confidence intervals to unequivocally demonstrate the level of uncertainty around the mean estimate. Consequently, the published population estimate is significantly higher than that of 2006. This does not however indicate a major increase in population size since 2006.

It is now a research priority to improve our understanding of the processes underlying density-dependent population change in the grey seal population. We need to reduce the confidence interval about our estimate. 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).

SCOS recommends that continued efforts to extract information on fecundity, age at first reproduction and adult survival from the long term studies on the Isle of May and North Rona should remain a high priority. Additional studies to obtain independent estimates of population size, fecundity and both pup and adult survival should receive high priority.

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. Since 2006 the model used to generate total population estimates provides 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.

Population Trends

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 08/1 & 08/2; 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. The actual growth rate will depend on the mechanism through which density dependence acts. For example, if the slow down was due entirely to density dependent pup survival or density dependent fecundity, the estimated annual growth rate for the overall population over the past 5 years would have been 2% and 4.3% p.a. respectively. Most of this increase occurred in the Orkney and North Sea populations with slower growth in the Western Isles. (Detailed annual population estimates are given by region in the Appendices of SCOS-BP 08/2).

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 trend
Scotland	39,500	2007	Stable or slowly increasing
E England	2,800	2007	Increasing
SW Britain	1,800	2007	Increasing
Northern Ireland	100	2005	Stable?
UK	**44,200**		**Increasing**
Ireland	1,600	2005	Unknown[1]
Wadden Sea	200	2004	Increasing [2]
Norway	1,200	2003	Unknown[2]
Russia	800	1994	Unknown[2]
Iceland	1,200	2002	Declining[2]
Baltic	4,000	2003	Increasing[2,4]
Europe excluding UK	**9,000**		**Increasing**
Canada - Sable Island	54,200	2007	Increasing[3]
Canada - Gulf St Lawrence	15,000	2000	Declining[2]
USA	1,100	2002	Increasing
WORLD TOTAL	**123,500**		**Increasing**

[1] Ó Cadhla, O., Strong, D., O'Keeffe, C., Coleman, M., Cronin, M., Duck, C., Murray, T., Dower, P., Nairn, R., Murphy, P., Smiddy, P., Saich, C., Lyons, D. & Hiby, A.R. 2007. An assessment of the breeding population of grey seals in the Republic of Ireland, 2005. Irish Wildlife Manuals No. 34. National Parks & Wildlife Service, Department of the Environment, Heritage and Local Government, Dublin, Ireland.
[2] 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
[3] 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
[4] 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 36% 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 08/3. It was considered to be impractical to survey the whole coastline every year and SMRU aimed to survey the whole coastline across 5 consecutive years. However, in response to the observed declines around the UK an attempt was made to survey the entire Scottish and the English east coast populations during 2007. 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 to survey populations in the estuaries of the English and Scottish east coasts.

Table 3 Counts of common seals by region

Region	**1996-2007**
Shetland	3,021
Orkney	3,379
Outer Hebrides	1,981
Highland (Nairn to Cape Wrath)	800
Highland (Cape Wrath to Appin & Loch Linnhe)	5,109
Strathclyde (Appin to Mull of Kintyre)	4,732
Strathclyde, Firth of Clyde (Mull of Kintyre to Loch Ryan)	811
Dumfries & Galloway (Loch Ryan to English Border at Carlisle)	23
Grampian (Montrose to Nairn)	102
Tayside (Newburgh to Montrose)	166
Fife (Kincardine Bridge to Newburgh)	215
Lothian (Torness Power Station to Kincardine Bridge)	56
Borders (Berwick upon Tweed to Torness Power Station)	0
TOTAL SCOTLAND	**20,035**
Blakeney Point	550
The Wash	2,162
Donna Nook	214
Scroby Sands	71
Other east coast sites	225
South and west England (estimated)	20
TOTAL ENGLAND	**3,242**
TOTAL BRITAIN	**23,277**
TOTAL NORTHERN IRELAND	**1,248**
TOTAL BRITAIN & NORTHERN IRELAND	**24,525**
TOTAL REPUBLIC OF IRELAND	**2,905**
TOTAL FOR GREAT BRITAIN AND IRELAND	**27,430**

The estimated number of seals in a population based on 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.

Combining the most recent counts (1997-2007) at all sites, approximately 24,500 common seals were counted in the whole of the U.K, of which 20,000 (82%) were in Scotland, 3,200 (13%) 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 27,400 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 40,000-46,000 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 2007 season are given in the Table 3 above. These are minimum estimates of the British common seal population. Results of surveys conducted in 2007 are described in detail in SCOS-BP 08/3.

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. Results from 2007 confirmed the magnitude of the decline in Orkney and showed that a similar decline (25%) has occurred in Strathclyde. Results from the West coast of Highland Region did not show any decline (see answer to Question 9 below for a fuller description of the declines). . Surveys of the east coast populations in 2007 also showed continuing declines in the Tay populations (SCOS-BP 08/3) and no recovery in the Moray Firth or the English East coast populations. 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 some cases, numbers given predate the PDV epidemic of 2002.

Region	Number of seals counted[1]	Years when latest information was obtained	Possible population trend[2]
Outer Hebrides	2,000	2003, 2006	None detected
Scottish W coast	10,675	2005, 2007	None detected
Scottish E coast	1,339	2007	Declining
Shetland	3,000	2006	Declining
Orkney	3,400	2007	Declining
Scotland	**20,000**	2005-2007	Declining
England	**3,050**	2004-2007	Recent decline[4]
Northern Ireland	**1,250**	2002	Decrease since '70s
UK	**24,500**	2003-2007	
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	**80,100**		

[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.

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. 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.
SCOS recommends that a survey of the common seal population of Shetland be given a high priority. Repeat surveys of Orkney and other regions would be desirable. Additional studies to obtain independent estimates of the proportions of the population ashore during surveys and any improvement in our knowledge of demographic parameters should be encouraged.

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?(SGMD/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 elsewhere[2]. The vast majority (85%) of European grey seals breeding outside the Baltic breed around Britain. Within Britain there is again a clear genetic distinction between those seals that breed in the southwest (Devon, Cornwall and Wales) and those breeding around Scotland. Within Scotland there is clear separation between grey seals breeding on the Isle of May and on North Rona[3]. Until 2002, SMRU treated this last group as a single population for the purpose of estimating total population size. Estimates of the numbers of seals associated with different regions were obtained by dividing up the total population in proportion to the number of pups born in each region.

In 2003, work began to develop a spatially-explicit model of the British grey seal population. A preliminary application of this model (SCOS-BP 03/4) indicated that there was little movement of breeding animals between Inner Hebrides, Outer Hebrides, Orkney and North Sea. This conclusion is supported by the results of detailed studies at breeding colonies and re-sightings of individual seals that have been photo-identified. These studies have indicated that breeding females tend to return to their natal breeding colony and remain faithful to that colony for most of their lives[4]. This suggestion is supported by the grey seal population models that indicate an absence of large scale redistribution of breeding females between regions (SCOS-BP 08/2)

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.

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 recent analyses are presented in SCOS-BP 08/4. 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. Both survival and probability of returning to be re-sighted in subsequent years were related to post partum mass.

Common seals
Samples from seals in Northern Ireland, the west and east coasts of Scotland, the east coast of England, Dutch and German Wadden Sea, Kattegat/Skagerrak, Norway, Baltic Sea and Iceland have been subjected to genetic analysis. This analysis suggested that there are genetically distinct common seal populations in European waters[5]. There is probably little movement of breeding animals between these populations although satellite telemetry reveals

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[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] Allen, P. J., Amos, W. et al. (1995). Microsatellite variation in grey seals (*Halichoerus grypus*) shows evidence of genetic differentiation between two British breeding colonies. *Molecular Ecology* **4**(6): 653-662.

[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

[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.

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/Skagerrak[6] 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. 24 young pups at each site were fitted with small satellite transmitters. A power analysis assuming exponential decrease indicated that we should be able to identify a difference of 20% or more in survival rates with these sample sizes. A simple model incorporating a common tag loss function for both sites suggests that mortality in Orkney was higher than at Lismore.

Current work
Work is currently underway to develop recommendations for spatial management units and to connect these to population structure. This is partly built from studies of movements and habitat use (SCOS-BP 05/3 and 05/5). Defining optimal management areas for UK seals requires an arrangement of relatively isolated groups of colonies. The motivation behind this requirement is that management actions taken in one unit should have minimal impact on the others. Clustering algorithms have been developed to subdivide grey seal breeding colonies into maximally isolated groups according to at-sea distance (SCOS-BP 06/5) and a method for optimal design of marine SACs based on at sea location data was presented in 2007 (SCOS-BP 07/8)

SCOS recommends additional effort to improve the estimates of common seal population size including improved estimates of the proportion hauled out during the moult, inclusion of high resolution digital imagery of all seals during thermal image surveys and the acquisition and use of new, reliable thermal imaging equipment. In addition, complementary modelling activities to support the collection of data should be given high priority.

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

***3. What is the latest estimate of consumption of fish by seals in Scottish and English waters?* (SGMD/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, SGMD 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.

Results of the 2002 studies on grey seal diet around the UK were summarised in SCOS-BP 06/6 and details are given in the reports to SGMD-SNH and DEFRA, which are available under project MF0319 at //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 model averaged estimate of the grey seal population models (EDDSNM & EDDFNM). Diet data were pooled into a generic North Sea diet and a Western Scotland diet.

In previous SCOS advice, estimated total fish consumption was based on regional grey seal population estimates calculated separately for the North Sea and Scottish west coast. The total pup production at all UK colonies in the North Sea and in North and West Scotland scaled by the average conversion factor between pup production and estimated population size for that area from the DDS model.

This year the published population estimate is based on a model averaged result from a new population model which produces a significantly higher population estimate compared to 2006 and wider confidence intervals. The estimated consumption of fish by grey seals in 2007, based on these new estimates was 108,000 tonnes (approximate 95% CI = 50,000 – 219,000 tonnes) in the west of Scotland and 223,000 tonnes (approximate 95% CI = 120,000 – 380,000 tonnes) in the North Sea (including seals from Shetland). Approximately 92%.of the total of 331,000 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 27,000 tonnes (approximate 95% CI = 14,000 – 46,000 tonnes). We have no reliable information on which to base an estimate of consumption in SW Britain where pup production there accounts for only 4% of the UK pup production. Consequently, if all else were equal consumption would be around 12,000 tonnes p.a..

Two issues are immediately apparent from these estimates. First, the 2007 estimate is much higher than the 2006 estimate. This is a consequence of the new method of presenting grey seal population estimates and does not represent an actual increase of this magnitude in consumption. Based on the population trajectory we estimate that prey consumption in the North Sea would have increased by approximately 3.5% and in West Scotland by approximately 1% since 2006. Second, the confidence intervals are much wider than previous published estimates. Again this reflects the wider confidence intervals on the model averaged population estimate and more accurately illustrates the uncertainties associated with estimating seal 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 37,000 to 61,000 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 6,000 to 10,000 tonnes.

A six year series of diet samples from St Andrews Bay indicated that common seal diet was heavily dominated by sandeels, especially in winter and spring, with gadoids (whiting, cod), and flatfish (dab, plaice, flounder) being the other main prey. Despite the closure of the local, large scale industrial fishery for sandeels during the study the importance of sandeels was remarkably consistent over years (71-77% of the diet).

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? (SGMD/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 by the Department of Fisheries and Oceans, Canada. 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.

SCOS BP 06/9 provided information about current research, funded by SGMD, being undertaken to use acoustic deterrent devices (ADDs) to exclude seals from sensitive regions. During 2007 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.

Trials of the effectiveness of commercially available ADDs for deterring seals from specific areas and as barriers to upstream movement of seals were carried out between November 2007 and February 2008 on the River Conon. Additional trials aimed at testing individual rather than population level responses were also carried out in the River Ness in 2007. To date, a total of 12 treatment (ADD switched on) and seven control trials have been carried out. Further experiments are planned to increase the sample size before analysing the results.

5. What are the latest results from satellite tagging in respect of usage of specific coastal and marine areas around Scotland by grey and common seals and whether or not these suggest potential foraging sites?

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. In

2007 groups of common seal pups were tagged in Orkney and the Firth of Lorne to provide pup survival information (funded by Scottish Government). In addition, these have provided the first detailed information on post weaning dispersal of common seal pups in Scotland. Adult common and grey seals were tagged in St Andrews Bay and at the Farne Islands in co-ordinated projects funded by D.B.E.R.R. and S.N.H. In conjunction with these satellite telemetry studies SMRU have conducted a series of monthly aerial surveys (April to October) to monitor numbers of both species hauling out along the coast from Caithness to Northumberland and in eastern England during June-August. Data from these studies will be combined with previous studies of habitat preference to generate seasonal maps of habitat usage for the Scottish east coast. A detailed description of habitat preference modelling based on grey seals in the North Sea has recently been published (Aarts et al 2008- appended as SCOS-BP 08/8).

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(SCOS-BP 07/8).

In the absence of direct measures of food ingestion we can not unequivocally identify foraging sites, but on the basis of dive and movement patterns we believe that foraging occurs throughout the movement range . Individuals of both species show behaviour indicating a mixture of periods of wide ranging foraging movements with little or no concentration on particular areas and regular repeated foraging in discrete patches. Overall, the intensity of habitat useage is assumed to indicate level of foraging activity and allows identification of foraging hotspots.

6. Are there any disease outbreaks which are likely to have a significant impact on Scottish seal populations within the next 12 months and, if so, what practical mitigation measures might be possible and appropriate?

No disease outbreaks likely to impact on Scottish seal populations have been identified in 2008. The discovery of 9 dead adult common seals in St Andrews Bay in June/early July of 2008 was an unusual event, but the pathology was unclear and no further mortality has been observed. The unidentified disease outbreak in Swedish and Danish waters in 2007 has apparently ended and did not extend to the North Sea populations. Preliminary results of blood tests from harbour and grey seals caught at the Farne Islands and in St Andrews Bay suggest that PDV is not currently circulating in the UK.

Seal Populations

7. What progress has been made in integrating grey seal population abundance models or selecting between these models using the grey seal survey work undertaken in 2007?

A Bayesian state-space modelling framework similar to that employed in 2007 was used to fit and compare models of British grey seal population dynamics, based on regional estimates of pup production from 1984 to 2007 (SCOS-BP 08/2). The models allowed for different forms of density dependence in either pup survival or fecundity, as well as fitness-dependent movement of recruiting females between regions. In answers to Q1 (above) we described the improvement in quality of fit obtained with models excluding fitness-dependent movement. However, as in 2007, there were insufficient differences between models incorporating density dependent pup survival or density dependent fecundity 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; some of these other modelling approaches were described in SCOS-BP 06/2.

Improved fitting methods have also 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. In response to the different results from these two competing models which appear to be more or less equally biologically reasonable, a model averaging exercise was carried out. This has produced confidence intervals that more realistically demonstrate the inability to differentiate between the models, but does not provide a more realistic posterior mean population size. There is therefore insufficient information in the pup production data to distinguish between different population models based on pup count data alone and 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.

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.

The requirement for a synoptic grey seal survey coincided with a need for a synoptic census of the common seal population in response to the observed population declines. Both were identified as pressing issues. In response a co-ordinated series of aerial surveys of the numbers of grey seals hauled out in August was carried out in conjunction with surveys of moulting common seals in August 2007. Poor weather throughout summer 2007 meant that a synoptic census could not be completed. However the East coast from the Wash to the Pentland Firth, the west coast from the Clyde to Torridon including the Inner Hebrides, Orkney and the off-lying Scottish Islands were all surveyed.

Sex and age structured haulout behaviour patterns are being extracted from satellite telemetry data from grey seals. SMRU aimed to complete the grey seal haulout survey in conjunction with the common seal thermal image survey in August 2008. In addition, SMRU have extended the time series of summer counts of grey seals along the east coast and instigated a series of repeat counts to obtain estimates of variability. Photographs will be analysed in 2008-2009 to provide sex and age structured haulout counts in appropriate categories defined by the ongoing study of haulout behaviour from telemetry data.

Further analysis of the data from SMRU's long-term reproductive biology studies on the Isle of May and North Rona is currently underway. A refined analysis of mark resightings for adult females on the Isle of May has included the effect of covariates such as post partum mass. Preliminary results suggest that the Bayesian methods may allow us to impute un-observed breeding states and indicate some dependence of both survival and resighting probabilities on body mass. Detailed description of these analyses is presented in

SCOS-BP 08/4. Differences in survival and recruitment between the declining North Rona population and the increasing Isle of May population were 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.

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

Scotland

In response to the observed declines in common seal populations in the Northern Isles and along the East coast, an intensive series of moult surveys was carried out in August 2007, in addition to the regular, annual moult surveys in the Moray Firth and Firth of Tay. In conjunction with the attempted synoptic survey of grey seals surveys took place in Orkney, the Scottish East coast, the west coast from the Clyde to Torridon and the Inner Hebrides. Poor weather and logistical/technical problems prevented a synoptic survey of the entire Scottish population.

In 2007 a series of repeated aerial surveys of the Moray Firth between Helmsdale and Findhorn were carried out during the breeding season, continuing the long time-series of counts carried out by University of Aberdeen researchers. Results are presented in SCOS-BP 08/3.

This represents a considerable increase in survey effort since the discovery of the decline in common seals. The effort is designed both monitor the rate of decline, to establish the extent of the decline and to provide information that would be useful when attempting to determine the cause(s) of the decline.

England

Annual moult surveys of eastern England continued (SCOS BP 08/3), extending the time-series and allowing comparison between UK and European populations during recovery from 2002 PDV epidemic. Survey counts increased in 2007 for the first time since the 2002 PDV epidemic but the number of seals has not recoverd to pre-epidemic levels. This contrasts with the Wadden Sea population that continued to show strong recovery, growing at around 12% per annum

A survey of the breeding population in eastern England was also carried out. This continues the time series of pup production estimates for the region. Results are presented in SCOS-BP 08/3.

Issues concerning the methods used to estimate common seal numbers

Over the past 3 years the number of grey seals counted during the English east coast common seal surveys has increased dramatically. These increases suggest that changes in the behaviour of grey seals may have occurred. The common seal surveys rely entirely on a combination of vertical and oblique photographic counts that facilitate unequivocal identification of most individuals to species level. Until recently, grey seals have usually occurred in large densely packed groups and common seals separately in more dispersed groups. Common seals did not occur within the large grey seal groups and only a small number of grey seals were found in the dispersed common seal groups. Coincident with the increase there has been a marked increase in the numbers of grey seals dispersed throughout the major common seal haulout groups at Blakeney, Donna Nook and on the outer banks of the Wash.

In response to this change, and in conjunction with the attempted synoptic grey seal survey in 2007, all large groups of grey and or common seals and any dispersed groups thought to contain grey seals were photographed during the thermal imaging surveys. A preliminary analysis of these photographs indicated that in 2007 a significant proportion (>10%) of the putative common seals in Orkney may have been grey seals. Clearly the photographic effort in 2007 could have been biased towards groups containing grey seals so that the estimated proportion mis-allocated may be overestimated. In order to clarify the situation all seals seen during the thermal image surveys from August 2008 onwards will be photographed to check species identification.

We do not have sufficient photographic records to be able to reprocess previous thermal image survey results. However, observations along the east coast suggest that the problem results from an increase in grey seal numbers at common seal haulouts. As the common seal population has declined and the grey seal population has increased over the past decade it is likely that the level of mixing has become more pronounced and that the level of miss allocation of grey seals as common seals would have been lower in previous surveys. In that case the observed declines in common seal numbers in the Northern Isles may have been more pronounced than reported previously.

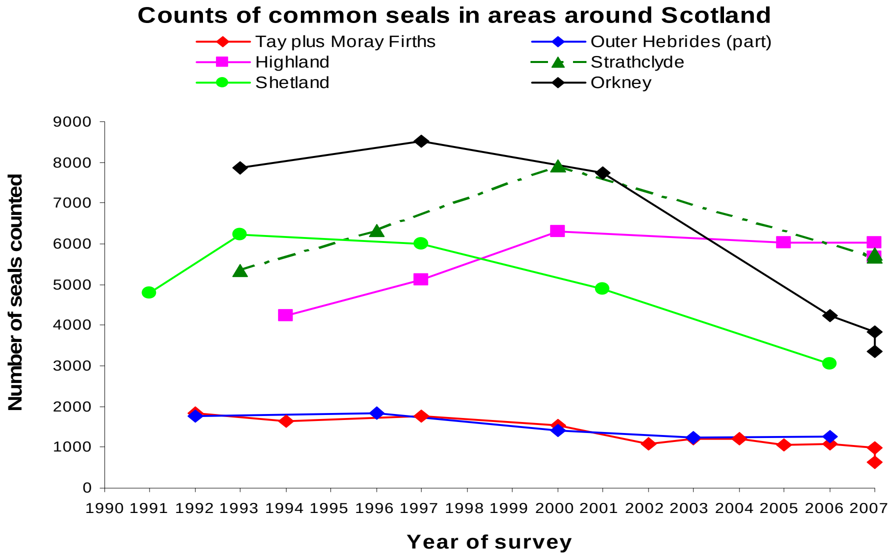
9. ***Is the decline in common seal numbers in specific local areas continuing or not and what is the position in other areas?***

Results of surveys carried out in 2007 are presented in detail in SCOS-BP 08/3. Strathclyde Region was surveyed for the first time since 2000. The number counted in Strathclyde, including the southern Inner Hebrides, declined by ~25% from 7300 in 2000 to 5500 in 2007. Counts within the Firth of Clyde were actually higher in 2007 meaning that the decline in the rest of the region was in excess of 30%.

The 2007 counts for both Orkney and the Firth of Tay were lower than in 2006. The magnitude of the decline was consistent continuation of the decline observed since 2000. The 2007 counts in the Moray Firth were similar to 2006 and close to the average for the previous 5 years. Along the west coast between Torridon and Loch Linnhe the 2007 count was similar to the count from 2005 and, again apparently consistent with previous data suggesting no recent decline. Variability in count data means that we can not unequivocally state whether declines have continued or stabilised on the basis of consecutive annual counts.

The combined results of the 2006 and 2007 surveys (Fig.1 & SCOS-BP 08/3) indicate that there have been significant population declines in Orkney (approx 40%-50%), Shetland (approx 40%), Strathclyde (approx 25%) and the Firth of Tay (>50%) since 2000. The decline observed in the inner Moray Firth (approx 20-30%) probably began before 2000 and here the population may have stabilised at a lower level. Only the west coast of Highland region and the Outer Hebrides (based on partial survey in 2006) appear to be stable at levels equivalent to those seen in the 1990s. The English east coast population remains at approximately 60-70% of its pre-2002-epidemic level.

Fig. 1. Trends in counts of common seals around Scotland. Data from the Sea Mammal Research Unit. Counts for the Outer Hebrides exclude North Uist and Benbecula as part of each island were not counted in 2006.



In 2006 SCOS reported that common seal populations in the Northern Isles and along the North Sea coast were declining. The 2007 survey results suggest that these declines are continuing and may be more widespread. Only the populations on the west coast of Highland region show no sign of a population decline at this time.

10. *What are the latest results from research investigating the causes of the recent decline in common seals and how has this improved understanding of potential causes?*

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 was developed and is appended as SCOS-BP 08/5.

The appropriate first step in such an investigation is to gauge the relative importance of real or perceived trends in demographic rates. To this end a demographic model for common seal population dynamics combined with a model for the aerial observation process has been implemented within a Bayesian estimation framework as a single state-space model. A preliminary model was presented in SCOS-BP 07/5. This approach has been further developed using a multi year series of repeated counts within the breeding and moulting periods in the Moray Firth. The advantages of detailed repeat counts for a specific region were found to outweigh the costs in loss of spatial generality. The resulting model indicates that the approach will provide useful insights into the causes of the decline by allowing us 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.

In addition, because of the urgency of the problem SMRU implemented three data collection projects:

1. An extensive air survey programme, supported by intensive ground observation studies was carried out in summer 2007 to identify the geographical extent and confirm the magnitude of the declines around the UK. Results presented in SCOS-BP 08/3 confirmed

the magnitude of the declines in Orkney and the east coast site, and demonstrated that similar declines occurred in Strathclyde (see answer to Q8 above).

2. A comparative study of pup mortality patterns in samples of pups from Orkney and Lismore. Small satellite transmitters were applied to 24 pups in each location. Pre-weaning mortality was negligible in both regions, but early post weaning mortality in Orkney during the first 3 months was approximately double that in the Lismore sample. However by late winter survival rates had converged. Preliminary analysis of environmental covariates suggest that mortality may be linked to local water temperatures which might indicate that pups were in poor condition at the onset of winter. This could be an indication of food limitation of some form. In response to these initial results SMRU have begun a study of mass and water temperature dependent field metabolic rates and food ingestion capacity in captive juvenile common seals.
3. Archived blood samples from live caught and autopsied grey and harbour seals were screened to assess prevalence of anti-leptospira, toxoplasma and phocine distempter virus antibodies in harbour and grey seals, over the period 1991-2005. Details of methods and results are presented in SCOS-BP 08/6. The seroprevalence results suggest it is unlikely that these infections have played a major role in the decline of UK and particularly Scottish harbour seals since around 1999. Although PDV did cause some mortality in the Tay and Moray Firth populations, very few carcasses washed ashore in the Northern or Western Isles. Since 2003 no cases of infection have been reported and antibody titres continue to decline as would be predicted from the epidemiology of the disease.

11. What are the key questions about seal populations that remain to be addressed to better inform practical seal management issues?

There are two clearly identifiable priority questions for UK seal management.
The most urgent issues are those surrounding the rapid, widespread decline of common seal populations around the UK. The pertinent questions and suggested work programs to address them are described above (Q10) and in SCOS-BP 08/5.
The second priority is to reduce the size of the confidence intervals around the grey seal population estimate. The pertinent questions and suggested actions to address them are given above in answers to Q1,2,3,7,8,9.

Seal Diet

12. ***What work might be done to follow up and maintain the detailed picture of grey seal diet obtained from the major survey in 2002, given the infrequent opportunities for such surveys, and how useful would this be in informing seal management?***

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 a simple range-wide description of grey seal diet, it would beneficial to obtain seasonally-structured samples from a number of indicator sites, timed to coincide with fish population surveys. To be most effective we should aim to develop an integrated study of seal diet and behaviour in conjunction with detailed fisheries and fish population information. Such data are essential for developing predictive consumption models incorporating robust functional response models. These models are required to assess impacts of potentially rapid environmental and fishery induced changes in prey availability. Evidence for these effects has come from recent analyses of time series of blubber biopsies from known female grey seals at North Rona and the Isle of May. These have demonstrated temporal, spatial and inter-individual differences in foraging patterns and have shown inter-annual consistencies in individual diets (SCOS-BP 08/7).

SCOS recommends that SMRU integrate their diet and foraging studies with the wider marine research community. For example SMRU should become involved in a current application under FP7 to study the dynamics of forage fish and their predators (FACTS).

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).

13. How is the research into quantifying the consumption of salmon and sea trout smolts and salmon kelts by seals progressing?

SMRU recently completed an analysis of the diet composition and prey consumption of harbour seals in St Andrews Bay using analysis of hard prey remains from scats. The diet was heavily dominated by sandeels, especially in winter and spring with Gadoids (whiting, cod), and flatfish (dab, plaice, flounder). However, the diet of harbour seals within the Tay estuary of Tay was markedly different from that in the surrounding area. Sandeels were still prevalent as prey but, outside winter, salmonids formed a significant proportion of the diet. Based on a limited sample these estimates are likely to be imprecise and should not be over-interpreted. Nevertheless, it is clear that salmonids form more than a minor part of harbour seal diet in this area.

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.

Smolts are the life stage when salmon and trout first leave fresh water and enter the marine environment. FRS in collaboration with Wyremicro Ltd and SMRU in association with SNH and the Atlantic Salmon Trust have developed a seal-mounted detector that can record each time a seal consumes a sea trout post smolt fitted with a passive integrated transponder (PIT tag). The aim is to quantify the consumption of smolts by seals, which has not proved to be possible using other means. The Mk III version currently in development uses a mobile phone transmitter to relay information to shore and will be tested in the SMRU pool during next winter.

Seal Legislation

14. Does the Committee consider that the options for proposed changes to the Conservation of Seals Act 1970 set out in the paper Sustainable Seas for All- a consultation on Scotland's first marine bill will improve seal management in Scotland?

For reference, the relevant text from the consultation on the new legislations:
Grey and Harbour Seals is attached as an appendix

In the past, SCOS has expressed a wish for an improvement in the collection of data about seals killed outside the close season and in circumstances not covered by the current Act. This includes the issue of seals killed under the "netsmen's defence". The Advice provided by SCOS will be improved if information can be collected about all seals killed throughout the year.

To the extent that the measures set out in the paper *Sustainable Seas for All- a consultation on Scotland's first marine bill* - will help to reduce the incidence of management actions on seals that go unrecorded, SCOS welcomes the proposed changes to the Conservation of Seals Act. The broadening of powers to issue licences to all users of the marine environment, and thereby to properly manage the killing of seals, is also welcomed. However, SCOS re-emphasises the need to retain a year-round system for gathering accurate information about seal management.

15. Does the Committee consider that there is a significant scientific requirement to change the current close seasons for each native seal species?

The current close season for grey seals is 1st September to 31st December and for common seals it is 1st June to 31st August. The close season was designed to cover the breeding season for each species. There have been changes in the timing of breeding in grey seals but they have not moved outside the close season (with the exception of some colonies in SW Britain that have an extended breeding season). SCOS does not see a need to change the definition of the close season for grey seals. However, in some locations common seal pups will be born before 1 June and females in the late stages of pregnancy could be more vulnerable. If the proposed legislation includes provision for a close season rather than changing to a system of year-round licencing then SCOS recommends that the close season for common seals should be extended from 1 May until 31 August each year.

Moray Firth

16. What is the latest estimate of seal population numbers in the Moray Firth management area?

Two aerial surveys of the Inner Moray Firth including Loch Fleet and Findhorn were completed in August 2007. Results for each sub-region (for 2005 to 2007) are presented in Table 4 and fig.2 below and in more detail in SCOS-BP 08/3. For the Inner Moray Firth, numbers of common seals hauled out in August 2007 varied between 485 and 670. If the adjacent haulout sites in Loch Fleet and at the mouth of the Findhorn were included, the numbers increased to between 652 and 851.

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	15-Aug-07	24-Aug-07
Ardersier	260	143	224	210	184	150	173
Beauly Firth	119	169	94	174	178	115	170
Cromarty Firth	98	101	118	119	93	67	118
Dornoch Firth	199	118	256	249	264	153	209
Inner Moray Firth	**676**	**531**	**692**	**752**	**719**	**485**	**670**
Inner MF +Loch Fleet & Findhorn	**834**	**659**	**842**	**894**	**840**	**652**	**851**
Inner MF + Dunbeath to Findhorn			**955**	**1057**	**977**		**941**

Both 2007 counts were slightly lower than counts from 2006. The maximum counts in 2007 for the inner Moray Firth and for the entire area from Dunbeath to Findhorn were 11% lower than the equivalent counts in 2006 but similar to the average counts since 2002. The maximum was 35 to 40% lower than the peak count obtained in 1997 (SCOS-BP 08/3). Again the counts are consistent with the population having stabilised following a period of decline between 1997 and 2002

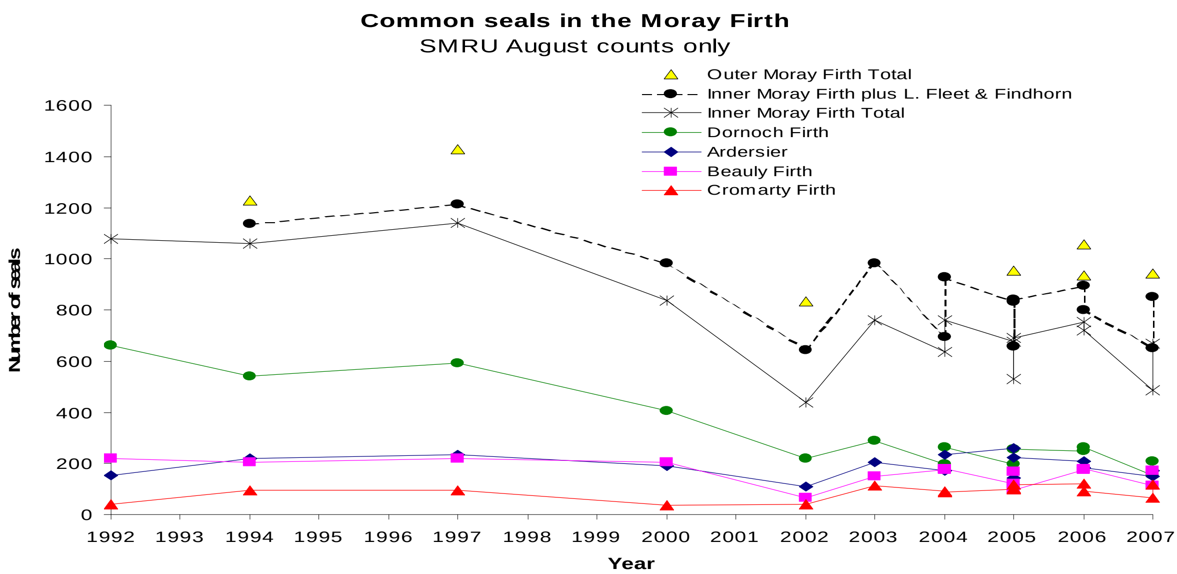


Fig. 2. The number of common seals counted in the Firth of Tay during the moult, 1990-2007.

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

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

Seals and Salmon Netting Stations

18. What research is currently available on interactions between seals and salmon netting stations and what new research might usefully be done in this area?

SCOS is not aware of any recent studies of interactions of seals and salmon netting stations in UK waters. Swedish studies of increased bag-net strength, increased mesh sizes in leaders (to allow salmon to escape pursuing seals) and ADD all led to increased catches. Models of the predation process indicate significant under reporting of fish removal and significant negative after-effects on catches after seal visits. Such methods could be tested at Scottish salmon netting stations.

More generally, there are additional questions similar to those concerning seals in salmon rivers: how many seals are involved, what is the extent and intensity of the problem and are specific "rogue" seals involved. Telemetry studies of seals caught in rivers and seals tagged in the outer banks of the Firth of Tay are providing information on seal activity in salmon rivers and show that targeted telemetry studies can provide information at spatial scales relevant to the seal/fishery interaction.

Seals and Fish Farms

19. What research is currently available on interactions between seals and fin fish farms and what new research might usefully be done in this area?

Very little research has been directed specifically at the interactions between seals and fin fish farms. This has been recognised as a problem for some time in terms of the damage caused to cages and fish, but also in terms of secondary effects because of salmon escaping from cages and mixing with local wild populations. More recently, however, the potential effects of methods used to control seals around fin fish farms, involving acoustic deterrent devices (ADDs) and/or shooting seals in the vicinity of farm cages, have been increasingly viewed as a concern. This is partly because of potential effects of ADDs on other marine mammals and partly because the decline of common seals has focussed attention on ways in which it may be possible to reduce unnecessary killing of seals by man.

Telemetry studies of seals caught in rivers and seals tagged in the outer banks of the Firth of Tay are providing information on seal activity in salmon rivers and show that targeted telemetry studies can provide information at spatial scales relevant to the seal/fishery interaction.

The potential effects of ADDs on cetaceans is the subject of current research sponsored by the Scottish Aquaculture Research Forum. We are also aware that the industry itself has taken major steps in recent years to introduce highly tensioned nets that are less susceptible to damage by seals. However, there is little understanding of which seals, in terms of species, sex or age, are most associated with fin fish farms, whether predation behaviour at fin fish farms is characteristic of most seals or is confined mainly to particular individuals. We also know very little about the number of seals shot by fin fish farmers and this information is important for the purpose of seal population management and also to help develop mitigation that is appropriate to the conservation status of seals.

Although there is a lot of experience within the fin fish farming industry of operating different methods to deter and control seals there has been no systematic assessment of (1) the relative scale of the problem in different fin fish farms in relation to geographical location or fish farm characteristics (cage design, rearing regime); or (2) mitigation methods used to control seals. There is little evidence that consistent metrics of “the seal problem” are used across Scottish fin fish farms that could allow comparison between sites and that might quickly show up management approaches that work. We know that some fin fish farms have very few problems with seals. If this is a function of location then perhaps there is potential to provide better advice about where it is best to locate farms. On the other hand it is possible that some farms have serendipitously found effective mitigation methods. By using current industry knowledge it may be possible to design solutions to the problem of seal-fin fish farm interactions by applying techniques that are currently available.

Marine Renewables

20. What research is currently underway in relation to possible impacts of marine renewable energy development (offshore wind, wave or tidal) on seals?

Research is currently being conducted at the European Marine Energy Centre (EMEC) in Orkney and in connection with the installation and testing of the Strangford Lough commercial demonstrator tidal turbine. Research in connection with construction activity and noise is also being conducted to examine whether radiated sound from wind turbines or from construction noise may affect marine mammals. Archived and new tracking data from seals is being used in Strategic Environmental Assessments for all offshore renewable energy developments and this has added greatly to our knowledge of the habitat preferences of seals, especially commons seals. The results of these studies have been reported regularly in recent SCOS reports.

Both the tidal and wave test sites at EMEC are subject to long-term monitoring of marine mammals using visual observations. Data are being collected by EMEC subcontractors under the advice of SMRU and data analysis routines have been developed to examine the statistical power to detect changes in habitat use by seals that have resulted from activities at each site. The monitoring at the tidal power test site has been under way for about 2 years and the monitoring at the wave power test site is beginning during summer 2008.

Similar visual observations have been made at Strangford Lough in Northern Ireland, an SAC with seals designated as a feature, and these data are now being used to detect changes resulting from the installation of a tidal generator during May 2008. In addition, at this site a sonar monitoring system has been installed that, together with visual observation made of the surface from the tubine pile during periods of operation, allows monitoring personnel to detect and track incoming submerged objects and to shut the turbine down if necessary. This type of monitoring will also be undertaken at EMEC where the experimental capacity of the facility will permit the development of improved and automated systems for detecting incoming objects, classifying these and, if necessary, automatically shutting down the turbine to reduced the possibility of injuring marine life.

The potential for marine renewable energy devices having effects upon marine mammals may be high depending upon the characteristics of the system. There are many uncertainties associated with the effects that some types of energy generating systems could have. Research and experience are narrowing these uncertainties. At present, the approach being adopted involves adaptive management of renewable energy developments involving pre-installation base-line monitoring to provide sufficient statistical power to detect changes, operational monitoring together with precautionary mitigation and the development of smart mitigation methods to ensure that appropriate operational monitoring can be carried out economically and continuously on fully commercial systems.

The biggest single source of uncertainty in predicting the impact of tidal turbines is our lack of knowledge of the responses of seals to the devices. SMRU are currently involved in a study of the movements of common seals in and around the Strangford narrows, in conjunction with the observation programmes described above. Using high resolution GPS FastLoc cell phone transmitters the study is documenting the movements of seals in the vicinity of the tidal turbine site.

21. What value might there be in developing guidance on possible mitigation measures to avoid disturbance to seals (and other marine mammals) during marine renewable construction or installation along the lines of the JNCC "Guidelines for Minimising Acoustic Disturbance to Marine Mammals from Seismic Surveys"? (see link - http://www.jncc.gov.uk/pdf/Seismic_survey_guidelines_200404.pdf)

SCOS considers that a consistent approach to the management of the effects that marine energy projects could have on marine mammals is to be encouraged. The JNCC guidelines are an example of an UK initiative that has been adopted broadly at an international level. Any guidelines will need to be constructed in a manner that allows them to evolve as our knowledge develops.

22. In relation to the EMEC tidal power test centre off Eday (Orkney), what would be an appropriate PBR for common seals and grey seals in this area?

The Potential Biological Removal (PBR) is the formula implemented under the US Marine Mammal Protection Act for licencing the numbers of animals that can be taken from a depleted population. The PBR is computed from the formula (Wade 1998)

$$PBR = N_{MIN} \bullet R_{MAX} \bullet F_R / 2$$

where N_{MIN} is a minimum population estimate (usually the lower 20th percentile of the distribution of the population estimate), R_{MAX} is the maximum rate of increase of the population (often set at a default value of 0.1 2 for seals), and F_R is a correction factor which is normally set at 1.0, but can be decreased for populations that are considered to be particularly at risk. The PBR is designed to ensure that there is a very low probability that the managed population will decline.

Setting a PBR for the Eday tidal test site depends on the management aims, assumptions about the population segments likely to be affected and on the choice of recovery factor which is determined by the current status of the population and our degree of confidence in the data. . In this case, we have made an assessment for each species based on the estimated populations associated with the northern Orkney islands (to incorporates nearby SAC, SSSI and SWT reserves).

For the increasing grey seal population, with a recovery factor of 1 this produces a PBR of 1770 for the all age population associated with the Northern Orkney breeding colonies. Given the uncertainty in adult population estimates and the fact that the pup production in Orkney appears to be stabilising a more conservative recovery factor of 0.5 may be more appropriate. This would reduce the PBR to 885 respectively.

In light of the recent large declines in common seals, a precautionary recovery factor of 0.1 would be appropriate. This produces a PBR of 23 for the population associated with the Northern Orkney haulout sites.

However, it is not clear how such a management regime would affect the rapidly declining harbour seal population in Orkney. It is also important to realise that the PBR is meant to represent the total, non natural mortality applied to the population and other potential removals should be considered when setting appropriate limits for the EMEC site.

Climate Change

23. Is there any evidence of significant impacts on seal populations from climate change and are there practical adaptation measures that might be considered to alleviate these?

At present there is no direct evidence of significant effects of climate change on seal populations. However, indirect effects including new biotoxins, disease agents and parasites and possible changes in prey availability, which are difficult to detect and document, are a potential factor in the recent declines in common seals in Shetland, Orkney and along the northern North Sea coasts.

The precautionary position would be to assume that climate change is more likely to add stresses to populations than to be either neutral or beneficial. In these circumstances, practical measures to actively manage human factors that may either intentionally or inadvertently add additional stress to seal populations need to be encouraged.

In practice, we need to maintain or improve our power to detect effects through maintenance and improvement of data collection and ensuring that, whenever practical, we have the capacity quickly to introduce new management approaches. Some of changes suggested to the Conservation of Seals Act will help to enhance data flow and the power to detect changes. Depending upon how they are implemented, they could also result in a more rapid response to evidence of effects.

SCOS recommends that a study of the effects of environmental factors on aspects of the breeding biology and reproductive success of grey and common seals should be made a priority.

ANNEX I

NERC Special Committee on Seals

Terms of Reference

1. To undertake, on behalf of Council, the provision of scientific advice to the Scottish Government and the Home Office on questions relating to the status of grey and common seals in British waters and to their management, as required under the Conservation of Seals Act 1970.

2. To comment on SMRU's core strategic research programme and other commissioned research, and to provide a wider perspective on scientific issues of importance, with respect to the provision of advice under Term of Reference 1.

3. To report to Council through the NERC Chief Executive.

Current membership

Professor Marc Mangel (Chair),	University of California, Santa Cruz;
Dr J Armstrong,	Fisheries Research Services;
Professor IL Boyd,	University of St Andrews;
Dr K. Kovacs,	Norwegian Polar Institute, Tromso, Norway;
Dr J. Greenwood,	CREEM, University of St Andrews;
Professor J. Pemberton,	University of Edinburgh;
Professor D. Bowen,	Bedford Institute of Oceanography, Canada;
Dr A. Bjørge,	Institute of Marine Research, Bergen, Norway;
Dr G. Englehardt,	CEFAS, Lowestoft;
Dr S. Reid (Secretary),	NERC, Swindon

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, 2008

08/01 Grey seal pup production in Britain in 2007
C.D. Duck and B.L. Mackey

08/02 Estimating the size of the UK grey seal population between 1984 and 2006, and related research.
L. Thomas and J. Harwood

08/03 The Status of British Common Seal Populations
C.D. Duck, D. Thompson & B. Mackey

08/04 Life history parameters at contrasting grey seal breeding colonies east and west of mainland UK, based on mark-recapture analysis.
S. Smout *et al*.

08/05 Report of SMRU workshop: research priorities for investigating the harbour seal population decline.
D. Thompson

08/06 The prevalence of anti-leptospira, toxoplasma and phocine distempter virus antibodies in harbour and grey seals, 1991-2005
A.J. Hall et al.

08/07 Regional, annual and individual differences in blubber fatty acid composition at two grey seal breeding colonies in the UK.
A. Arriola *et al* .

C.D. Duck and B.L. Mackey

Grey seal pup production in Britain in 2007

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

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

1. Surveys conducted in 2007

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

Each year SMRU conducts aerial surveys of the major grey seal breeding colonies in Scotland to determine the number of pups born. These main colonies are located in the Inner and Outer Hebrides, Orkney, the north coast and in the Firth of Forth. During the 2007 breeding season, between three and six surveys were flown over these main colonies. 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.

A small number of colonies are monitored annually by different organisations: National Trust staff count pups born at the Farne Islands and at Blakeney Point in Norfolk. Staff from the Lincolnshire Wildlife Trust count pups born at Donna Nook and staff from English Nature count pups born at Horsey, on the east Norfolk coast. Scottish Natural Heritage (SNH) coordinated a fourth survey of grey seal pups born in Shetland, either from boats or from the ground. SNH staff also counted pups born on South Ronaldsay in Orkney four times. Part of the east coast of South Ronaldsay could not be completed on any survey.

All 51 of the major colonies in Scotland were surveyed aerially by SMRU on four or more occasions. Three colonies on the north coast were surveyed three times (Loch Eriboll, Eilean nan Ron at Tongue and Helmsdale).

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 have been serviced.

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 pup production estimates in 2007 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 three times and for all Shetland colonies and for South Ronaldsay.

The 2007 total pup production estimate for all annually monitored colonies was **38,772**, a decrease of **–2.46%** from 2006 (39,727; 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 2007 is shown in Figure 2a. Figure 2b shows the long-term pup production trajectories at the main island groups from 1960 to 2007. 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, Blakeney Point, Horsey and South Ronaldsay in Orkney but less frequently in SW England and Wales due to the inaccessibility of breeding colonies. SNH staff count 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.

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 from the quarter between south and west and there are occasions when is not possible to survey these colonies. Pabbay, slightly further to the north, is not similarly affected.

3. Trends in pup production

The differences in pup production at the main island groups are shown in Table 1. Between 2006 and 2007, total pup production at annually monitored colonies decreased by –2.5% overall with the change varying from –11.3% in the Inner Hebrides to +14.1% in the Lincolnshire and Norfolk colonies. Orkney, which produces most pups, decreased by –2.0%. For the first time, Donna Nook overtook the Farne Islands as the largest breeding colony in England.

Figure 2a and 2b and Table 1 show quite clearly that overall grey seal pup production is indeed beginning to level off at annually monitored colonies.

The trajectories in Figures 2a and 2b are beginning to show that total pup production at the annually monitored colonies is stabilising. Over the past five years, the only colonies that showed any significant increase were at the southern end of the North Sea, at Donna Nook, Blakeney Point and at Horsey (Table1). Since 2001, the increase at the Isle of May and Fast Castle was entirely due to the Fast Castle contribution.

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 on previous occasions.

The overall annual percentage change in pup production at each of the main island groups over the past five years (between 2002 and 2007) is shown in Table 1. The overall annual change, for all colonies combined, was +0.7%. Locally, the change varied from –0.9% in the Outer Hebrides to +15.0% at the relatively small colonies of Donna Nook, Blakeney Point and Horsey. Changes for the two preceding five-year intervals are also shown in Table 1.

Pup production fluctuates between years but since 1996, the fluctuations have been more pronounced 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 2.0% of the point estimate for Orkney colonies to 5.3% 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 intervals cannot be calculated for most of the estimates provided 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 2007 with pup production estimated using a normal distribution (Table 2). The 95% confidence intervals for the production estimates for these three colonies were 10.0%, 18.0% and 10.6% respectively. Table 2 also includes the total count for the colonies listed individually in Table 4 (under Other colonies). These and other potential breeding locations are surveyed when flying time, weather conditions and other circumstances permit. Table 2 indicates that at least 5,400 pups were born at colonies not surveyed annually.

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 Sutherland coast, in Orkney and in Shetland.

7. Pup production in Shetland

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 (only part of one colony, Uyea, is countable from land) 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 counted previously were omitted due to the time required for survey and/or the small numbers of pups found. Four 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% and a 90% moulter classification. The model produced better fits to the counts, with lower confidence intervals, using the 90% classification these estimates are in Table 5. Moulted pups are more likely to be correctly classified during ground counts because the counters are relatively close to the pups and can assess more accurately whether a pup has fully moulted or not.

The minimum pup production for Shetland in 2007 was 803 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. The frequently severe weather conditions during the autumn months may limit any 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 operational and weather restrictions prevented boat surveys.

The last four breeding seasons have seen an excellent effort in improving the information on grey seal pup production in Shetland. Pups born at exposed colonies, such as Rona's Voe and Dale of Walls, can be highly susceptible to

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. Pup production was estimated to be 1,574 (O'Cadhla et al., 2007). Including an estimate of 100 pups born in Northern Ireland, this gives a total of just under 1,700 pups born in Ireland.

To complete the production estimate for the whole of the island of Ireland, in 2005 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. SMRU previously surveyed breeding grey seals in Northern Ireland in 2002.

In addition, the National Trust and the Northern Ireland Environment Agency (formerly the Environment and Heritage Service, Northern Ireland) conduct monthly boat surveys of seals in Strangford Lough. 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.

Outside 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 (14 and 26 pups respectively). These surveys suggest that approximately 100 grey seal pups were born in Northern Ireland in 2005 and Table 2 shows this estimated number.

9. Proposed surveys for 2008

In the 2008 breeding season, we propose to continue the current survey protocol and obtain four or five counts for each of the main grey seal colonies 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 and colleagues (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 Bill Bruce (Forth Seabird Group, Forth inner islands). SNH Shetland for their 2007 grey seal survey. Thanks to Ryan Saunders who cheerfully helped during our 2007 survey and to Bill Giles who, once again, enthusiastically and expertly piloted the survey aircraft.

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Table 1. Pup production estimates for colonies in the main island groups surveyed in 2007. 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 production estimates for the Isle of May, Fast Castle, the Farne Islands, Donna Nook, Blakeney Point and Horsey in east Norfolk.

Location	**2007 pup production**	**Overall annual change in pup production**			
		previous year	**5 year intervals**		
		2006-2007	**1992-1997**	**1997-2002**	**2002-2007**
Inner Hebrides	**3,071**	-11.27%	+2.16%	+0.35%	+0.07%
Outer Hebrides	**11,189**	-3.64%	+0.70%	-0.49%	-0.88%
Orkney	**18,952**	-1.97%	+8.35%	+4. 53%	+0.85%
Isle of May + Fast Castle	**2,756**	+4.75%	+7.93%	+3.73%	+1.57%
Farne Islands	**1,164**	-7.18%	+4.07%	-0.45%	-0.51%
Donna Nook + Blakeney Pt + Horsey	**1,640**	+14.13%	+14.00%	+15.60%	+14.95%
North Sea (i.e. previous 3 areas)	**5,560**	+4.47%	+7.00%	+3.94%	+4.03%
Total	**38,772**	**-2.46%**	**+4.44%**	**+2.39%**	**+0.68%**

Table 2. Pup production estimates for breeding colonies surveyed less regularly.

Location	**Location and year of most recent survey**	**Pup production**
[1]Mainland Scotland	[1]Helmsdale (Duncansby Head to Helmsdale, 2007	1,201
	[1]Loch Eriboll, Eilean nan Ron (Tongue) 2007	630
Other colonies	Various, see Table 4	885
[2]Shetland	2007	803
South-west Britain	South-west England, Wales 1994-2005	1,750
Northern Ireland	2005	100 (approx.)
Total		**5,369**

[1]Loch Eriboll, Eilean nan Ron and Helmsdale are surveyed annually with production estimates derived using the same modelling process as for the main breeding colonies.

[2]A number of colonies in Shetland have been surveyed annually since 2004.

Table 3. Estimates of pup production for colonies in the Inner and Outer Hebrides, Orkney and the North Sea, 1960-2007.

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
2007	3071	11189	18952	5560	38772

[1]Calf of Flotta included with Orkney total (1996).
[2]Berneray and Fiaray (off Barra) included in the Outer Hebrides total (1998).
[3]Oronsay included with Inner Hebrides (2001).
[4]South Ronaldsay included in the Orkney total; Blakeney Point and Horsey (both Norfolk) included with North Sea (2002).
[5] North Flotta, South Westray, Sule Skerry included with Orkney; Mingulay included with Outer Hebrides (2003)
[6] Pabbay 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 2007 are in bold type.**

	Location	**Survey method**	**Last surveyed**	**Number of pups counted**
Inner Hebrides	Loch Tarbert, Jura	SMRU visual	2003, 2007	10, **4**
	West coast Islay	SMRU visual	1998, every 3-4 years	None seen
	Oronsay Strand	SMRU photo	2005, 2006, 2007	40, 9, **47**[1]
	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, 2007	22, **10**
	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, 2007	60, 64, **42**
	Fladda Chuain, North Skye	SMRU photo	2005, 2007	73, **43**
	Heisgeir, Dubh Artach, Skerryvore	SMRU visual	1995, 1989, infrequent	None None
Outer Hebrides	Sound of Harris islands	SMRU photo	2002, 2005, 2007	358, 396, (**194**) [2]
	St Kilda	Warden's reports	Infrequent	Few pups are born
	Shiants	SMRU visual	1998, every other year	None
	Flannans	SMRU visual	1994, every 2-3 years	None
	Bernera, Lewis	SMRU visual	1991, infrequent	None seen
	Summer Isles	SMRU photo	2002, 2003, 2005, 2006, 2007	50, 58, 67, 69, **25**
	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, 2007	10, 27, 34, 21, **8**
	Sanday, east and north	SMRU visual	1994, every 2-3 years	None seen
	Papa Stronsay	SMRU visual	1993, every 3-4 years	None seen
	Holm of Papa, Westray	SMRU visual	1993, every 3-4 years	None seen
	North Ronaldsay	SMRU visual	1994, every 2-3 years	None seen
	Eday mainland	SMRU photo	2000, 2002	8, 2
Others	Firth of Forth islands esp. Inchkeith & Craigleith (by North Berwick)	SMRU photo, Forth Seabird Group	Infrequent, 1997 2003, 2004, 2005, 2006, 2007	<10, 4 86, 72, 110, 171, **206**
Total				**885**

[1] Pup production calculated from four counts

[2] 2005 count used in total as pups were missed in 2007

Table 5. Pup production estimates and maximum pup counts for grey seal colonies in Shetland from 2004 to 2007. 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**	**2007**
	Estimated production ***(90% moulter classification)***	*Estimated production* ***(90% moulter classification)***	**Estimated production** (90% moulter classification)	**Estimated production** (90% moulter classification)
Papa Stour	196	135	153	168
Dale of Walls	66	43	18 (max count)	36 (max count)
Muckle Roe	23	no count	no count	no count
Rona's Voe	106	83	50	57
Mousa	140	117	156	128
Fetlar	50	32	21 (max count)	23 (max count)
Whalsey Islands	102 (max count)	72	77	103
South Havra	4 (max count)	no count	no count	no count
Fitful Head	18 (max count)	no count	no count	no count
Uyea (N. Mainland)	238 (max count)	122 (part only)	114 (part only)	101 (part only)
NE Unst				3 (max count)
Noss				2 (max count)
Total max counts	**362**	**0**	**39**	**64**
Modelled total	**581**	**604**	**550**	**557**
Estimated production	**943**	**765**	**758**	**803**


Grey seal breeding colonies
in Britain
Figure 1
Colonies asterisked are potential
Special Areas of Conservation
Major colonies encircled are surveyed annually
Shetland
*Faray & Holm of Faray
*North Rona
Orkney (26)
Outer
Hebrides
(15)
Loch Eriboll
Helmsdale & Berriedale
*Monach
Isles
Pabbay
Scotland
Major colony
Minor colony
*Treshnish Isles
Inner
Hebrides
(11)
*Isle of May
Fast Castle
*Farne Islands
North Sea
(6)
Ireland
Donna Nook
Blakeney
Point
*North Pembroke
Coast
England
Horsey
Wales
*Ramsey
*Skomer
Lundy
Isles of Scilly

Figure 2a. Total estimated pup production, with 95% confidence limits, for all the major, annually monitored colonies in Scotland and England from 1984 to 2007.

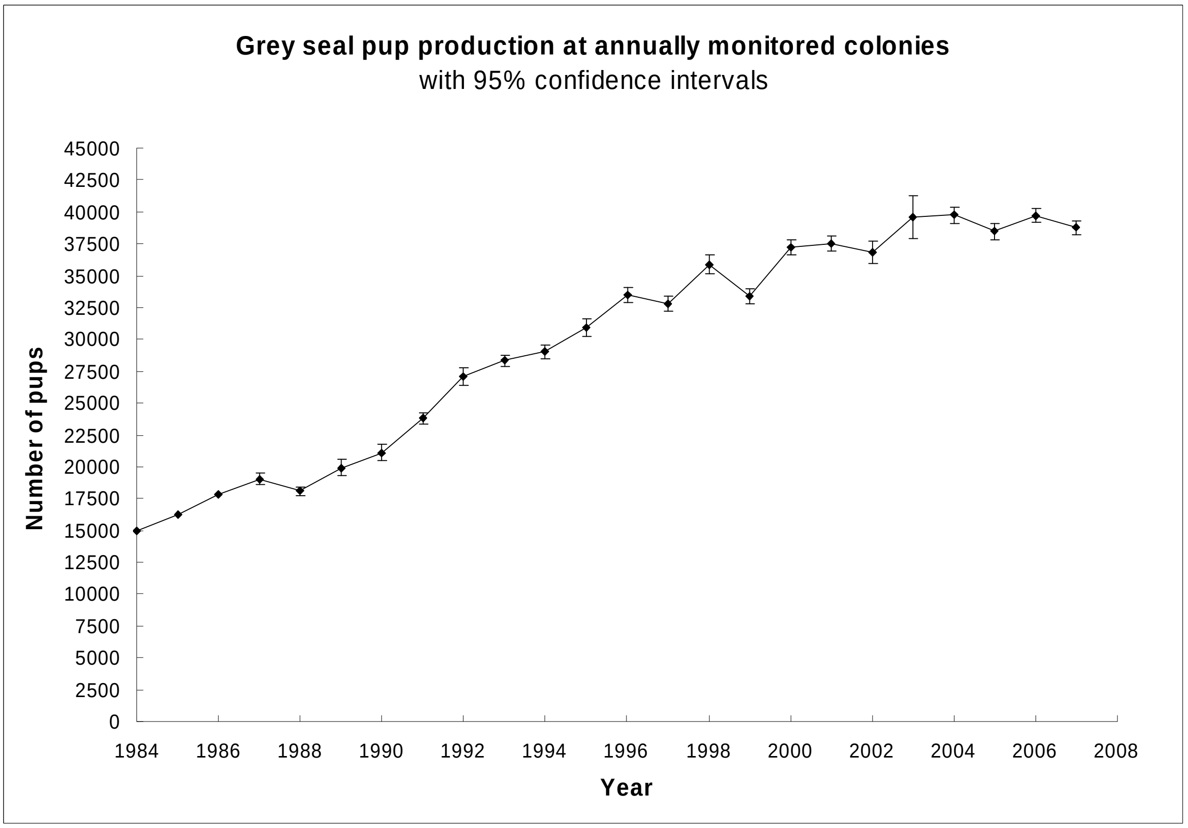


Figure 2b. Grey seal pup production trajectories from 1960 to 2007.

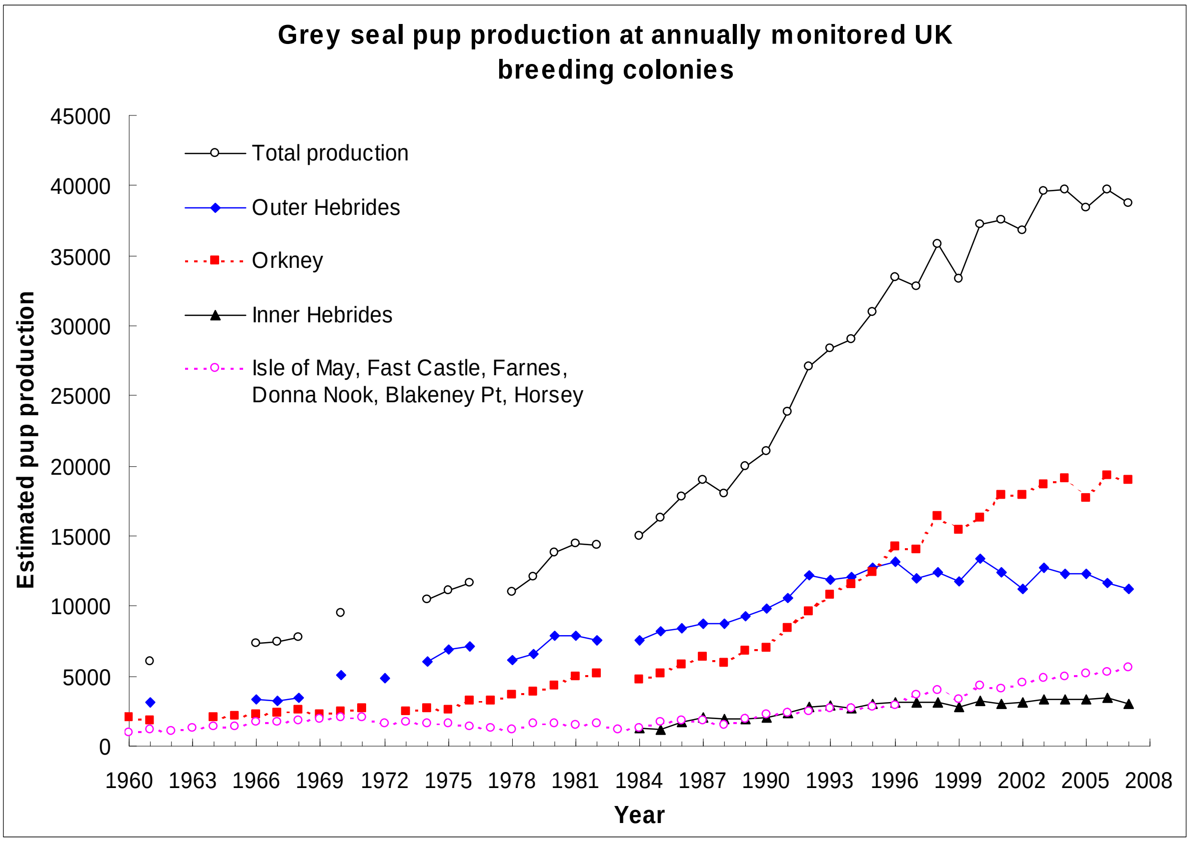
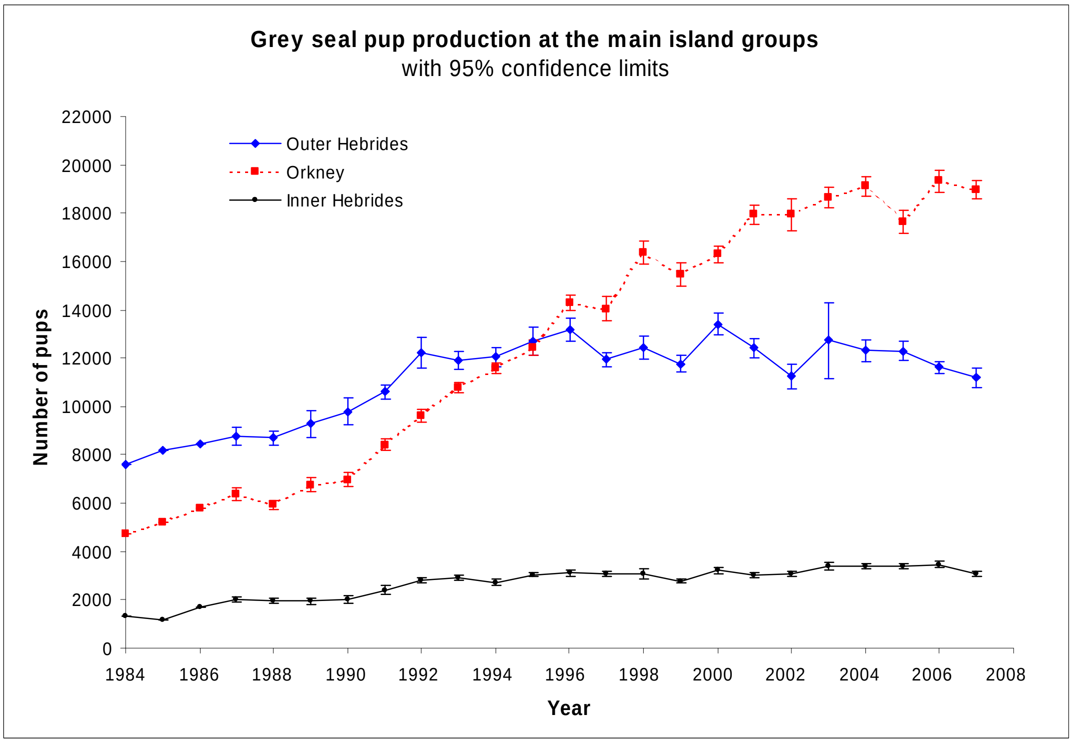
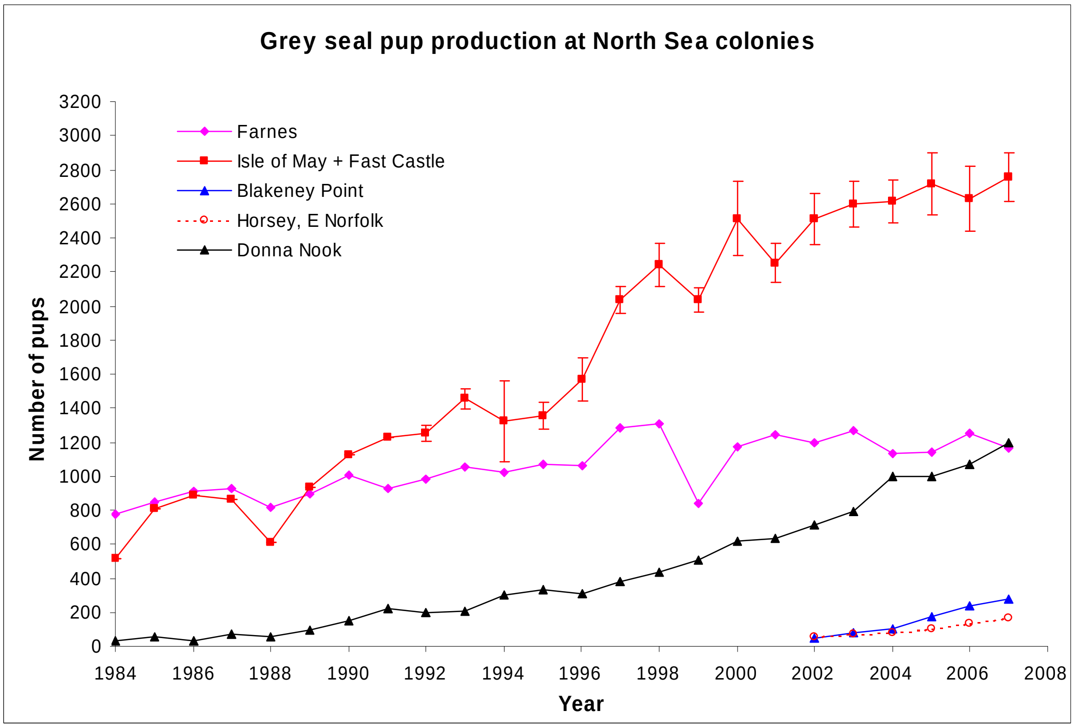


Figure 3. Trends in pup production at the major grey seal breeding colonies since 1984. Production values are shown with their 95% confidence limits where these are available. These limits assume that the various pup development parameters involved in the estimation procedure remain constant from year 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 2007.

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Summary

We fitted and compared six Bayesian state-space models of British grey seal dynamics, based on regional estimates of pup production from 1984 to 2007. One model (DDS) assumed that pup survival follows a Beverton-Holt density dependent function, and that females recruiting to the breeding population show fitness dependent movement between regions. A companion model (DDF) assumed that density dependence occurs instead in fecundity. Two models (EDDS and EDDF) allowed more flexible forms of density dependence in pup survival or fecundity. The last two models (EDDSNM and EDDFNM) also allowed the more flexible forms of density dependence, but assumed no movement of females. The models were fit using a particle filtering algorithm similar to that used in previous briefing papers, but with improvements designed to give less bias in estimates of model parameters and population numbers. The DDS and DDF models did not fit the pup production data well; all of the other models provided an adequate fit, although there was still some evidence of systematic differences between model predictions and data. Using a model selection criterion based on parsimony, we found that the EDDSNM and EDDFNM models were preferred over the other models, with the former having slightly more support. The estimated adult population size in 2007 for these two models was 117,600 and 239,700 respectively. We calculated a combined 95% posterior credibility interval that accounts for the uncertainty about which model is correct – this gave the interval 84,500-304,500 adult seals.

Introduction

In this paper, we present estimates of population size and related demographic parameters, derived from state-space models of the grey seal population fit to regional estimates of pup production from 1984-2007. The state-space modelling framework is described in detail in a series of recent papers (Buckland *et al.* 2004, Thomas *et al.* 2005, Newman *et al,* 2006, Buckland *et al.* 2007) and the models used here are variations of those first introduced by Thomas and Harwood (2003). Similar models have also been applied to the Northwest Atlantic grey seal population (Thomas *et al*. 2007)

We fit and compare six population models, the first four of which are the same as those used by Thomas and Harwood (2005, 2006, 2007). 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. Also, female seals are assumed to show fitness-dependent dispersal among regions in the year before they recruit into the breeding population. Two further models extend the density dependent 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). Based on results of initial runs, we also fit two more models that allow extended density dependence but assume no movement between regions (EDDSNM and EDDFNM). The models are formulated within the Bayesian statistical framework, and informative priors are specified on the model parameters and initial states (the 1984 population numbers). In addition to comparing the models, we also make joint inference from them.

As in previous reports, the models are fit using a computer-intensive algorithm called a Monte Carlo particle filter (Liu 2001). Improvements to the algorithm have been made, designed to increase the reliability of the results.

Materials and Methods

Models

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.

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 and EDDSNM models includes an extra parameter, ρ, that can alter the shape of the relationship between pup survival and pup numbers:

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

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

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

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

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

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

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

while for the DDF and EDDF models,

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

where $\alpha_{r,t}$ is the fecundity rate in region r at time t, as defined below. We assume no movement between regions in the EDDSNM and EDDFNM models.

We model breeding by assuming that the number of pups produced is a binomial random variable, with rate $\alpha_{r,t}$. For the DDS, EDDS and

EDDSNM 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 and EDDFNM models are similar, with

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

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 $\mathrm{CV} = 1/\sqrt{\psi}$ (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 β_1 - β_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 $\alpha_{\max}$. The EDDS and EDDF models have one additional parameter, ρ, for the shape of the density-dependent response. The EDDSNM and EDDFNM models have no movement parameters, and hence have 9 parameters each.

Data and Priors

Our input data were the pup production estimates for 1984-2007 from Duck and Mackey (2008), aggregated into regions.

Prior distributions for each parameter are given in Table 1, and are shown on Figure 1(b). 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.

Prior distributions for the states in the DDS, EDDS and EDDSNM model 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, EDDF and DDFNM 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.

Table 1. Prior parameter distributions

Param	Distribution	Mean	Stdev
ϕ_a	Be(22.05,1.15)	0.95	0.04
$\phi_{p\max}$, ϕ_p	Be(14.53,6.23)	0.7	0.1
χ_1	Ga(4,2500)	10000	5000
χ_2	Ga(4,1250)	5000	2500
χ_3	Ga(4,3750)	15000	7500
χ_4	Ga(4,10000)	40000	20000
ρ	Ga(4,2.5)	10	5
γ_{dd}	Ga(2.25,1.33)	3	2
γ_{dist}	Ga(2.25,0.49)	1.10	0.70
γ_{sf}	Ga(2.25,0.22)	0.5	0.33
α, $\alpha_{\max}$	Be(22.05,1.15)	0.95	0.04
ψ	Ga(2.1, 66.67)	140	96.61

Fitting Method

We used the particle filtering algorithm of Thomas and Harwood (2007), with two small, but significant, improvements. The first (tempering the resampling probabilities) was designed to decrease the Monte-Carlo variation between samples. This allowed implementation of the second improvement (increasing the kernel smoothing discount), which reduced the bias in estimates of parameters and states at a cost of increased Monte-Carlo variation. Overall, the estimates should be a better representation of the fit of the model to the data, compared with previous reports. An outline of the main features of the algorithm is given below, for completeness – it is not necessary to read the rest of this sub-section to understand the results that follow. The algorithm was coded in ANSI standard C and is freely available on request.

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.* (in press).

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.* in press). 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 resulted in about a quarter to a tenth of the particles being retained (depending on the model and assumptions about observation error). 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. The improvement to the algorithm of Thomas and Harwood (2007) came at this stage: instead of resampling with probability proportional to the weights, we instead used probability proportional to the weights to the power of 0.25. This “tempered resampling” means that the particles become less focussed on the current and past data, and retain more diversity to better cope with future data points that may not match the current parameter values. This helps in the current dataset because later data points are much more strongly indicative of low carrying capacity values (relative to the prior) than the early data points.

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 *et al.* in press), so we kept the amount of kernel smoothing to a minimum, using a discount value of 0.99997 (a value of 1.0 results in no jittering at all). Note that this is considerably less than the value used in previous reports (and in Newman *et al.* in press) of 0.997. 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 around 700,000.

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 (up to 225) were used 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 99.9999th percentile of the particle weights from all of the multiple runs for a particular model.

Model outputs and comparison
One metric of the degree of Monte Carlo error in the results is the number of unique ancestral particles in our final sample. Thomas and Harwood (2007) set a target of 1,000 or more unique particles for reliable estimation of parameter and state means. However, this does not account for some of these particles having low weight and some high weight. We therefore also calculated the effective sample size (Liu 2001) of unique particles, computed as:

$$\mathrm{ESS}_{\mathrm{u}} = \frac{U}{1+\left[\mathrm{CV}\left(w_u\right)\right]^2}$$

where U is the number of unique particles and $\mathrm{CV}(w_u)$ is the coefficient of variation of the sum for each unique particle of the weights of particles with that ancestor.

To compare the models, we calculated the mean posterior Akaike Information Criterion, including the small sample correction, ($\mathrm{AIC_c}$) using the same method as Thomas and Harwood (2006, 2007).

As explained by Thomas and Harwood (2007) It is not useful to compare models where the observation error parameter has been estimated independently for each model. Hence, we first estimated the measurement error parameter by fitting the data to the DDS model alone (this being the model with most data support in previous briefing papers). We then took the estimated posterior mean and fit both models using this fixed value. We present model selection statistics for these two models using the fixed observation error value.

For all models, we also present posterior estimates of the model parameters and estimated pup production from 1984-2007. The models additionally 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).

We also present model averaged estimates of population size, combining the models according to their posterior $\mathrm{AIC_c}$ weights (Burnham and Anderson 2001). We comment on the utility of this procedure in the Discussion. Note that this implicitly assumes that *a priori* all models have equal weight.

Results

Unique ancestral particle numbers

Using the revised algorithm we achieved a considerably higher retention of ancestral particles than that of Thomas and Harwood (2007), well over their target of 1,000 (Table 2). Effective sample sizes of unique particles was between 60 and 600; further runs are required to determine what level of Monte-Carlo variation this represents but we anticipate it will be low. One indicator of this is that the histograms of posterior parameter estimates that follow show little evidence of the multi-modality ("roughness") associated with low sample size in past reports.

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

Model	K (x10^7)	K^* (x10^7)	U (x10^4)	ESS_u
ψ estimated				
DDS	170	9.6	55.2	410.7
ψ fixed				
DDS	150	7.6	18.5	339.6
DDF	150	10.6	29.6	574.8
EDDS	150	11.4	9.0	114.7
EDDF	150	6.9	4.5	59.0
EDDSNM	225	24.4	33.5	445.0
EDDFNM	225	19.1	12.0	203.9

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. The estimates of pup production (Figure 1a) show clear, systematic lack of fit in all regions, particularly the Inner and Outer Hebrides where they fail to reflect the observed rapid growth and then levelling-off in pup production since the mid 1990s. The recent slowing in growth in Orkney is also not reflected in the estimates, while the rapid growth in North Sea pup production is under-estimated.

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. The estimated posterior mean of ψ is 89.5, and we used this value in the two 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:

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

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 0.11 (corresponding 95% credibility interval 0.08 - 0.13).

Comparison of models for density dependence and movement

Smoothed posterior estimates of pup production (Thomas *et al.* 2005) for the six models, run with ψ fixed at 89.5, are shown in Figure 2.

Unsurprisingly, the DDS model estimates (Figure 2a) are almost identical to those from the analysis where ψ was estimated (Figure 1a). The DDF model estimates (Figure 2b) are also similar, although the estimates for Outer Hebrides show some discontinuity for the period for 1984-1989 – likely a result of an estimated non-stable starting age structure.

Estimates of pup production from the EDDS and EDDF models (Figures 2c and 2d) show clear improvements to the fit, better reflecting the strong recent increases in the North Sea and the levelling off in counts in the Inner and Outer Hebrides. The recent levelling off in the Orkney is, however, not reflected in the fits. Qualitatively, the EDDS model appears to be a slightly closer fit to the data, especially in the initial time periods in the Outer Hebrides. Parameter estimates for fecundity are again nearly identical to the prior in both models (Figures 3c and 3d), as is pup survival for the EDDF model. Estimated adult survival is low in both models (0.92 and 0.91). The posterior mean estimate of the extended density dependence parameter, ρ, is higher for the EDDS model than the EDDF model (6.4 vs 3.7), although both have high variance; carrying capacities are estimated to be slightly higher under the EDDS model.

Estimates from the no movement models (EDDSNM and EDDFNM; Figures 2e and 2f) are similar to the extended density dependence models with movement for North Sea and Orkney, but for Inner and Outer Hebrides (particularly the latter), pup production is estimated to have declined slightly in recent years. Parameter estimates (Figures 3e and 3f) are similar to those from the EDDS and EDDF models.

According to the AIC_c statistics (Table 3), the models with no movement are strongly favoured over those with movement. Note that the mean posterior negative log-likelihood is actually smaller for these models than those with movement, indicating that they are a better fit to the data even without taking into account the 3 parameters saved by excluding the movement model.

Table 3. Mean posterior negative log-likelihood, AICc and Akaike weights for models with fixed observation precision of 89.5 fit to data from 1984-2007.

Model	-LnL	AIC_c	ΔAIC_c	Akaike (AIC_c) weight
DDS	750.37	1525.88	20.98	0.00
DDF	747.57	1520.29	15.39	0.00
EDDS	746.71	1521.18	16.29	0.00
EDDF	749.39	1526.54	21.65	0.00
EDDSNM	742.40	1504.90	0.00	0.65
EDDFNM	743.02	1506.13	1.23	0.35

Estimates of total population size
Estimated size of the 2007 adult population under each model are shown in Table 4; estimates for all other years are given in the Appendix.

Estimates from the DDS model are approximately 2.5 times less than those from the DDF model, and there is no overlap between the 94% posterior credibility intervals. Estimates from the EDDS model are higher than the DDS; those from the EDDF model are lower than the DDF model, making the results from the two extended density dependent models rather closer. The EDDSNM model estimates are closer to those of the DDS model – they are lower than the EDDS model because adult numbers are estimated to have declined in the Inner and Outer Hebrides since the 1990s (Appendix). The EDDFNM model estimates are between those of the DDF and EDDF models. Estimates from the EDDSNM model are about half those from the EDDFNM model, and there is no overlap between posterior 95% credibility intervals. These two models have nearly all the posterior AICc weight (Table 3), and since the support for them is not too different, the posterior distribution of population size averaging across models is distinctly bimodal (Figure 4).

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. In previous reports, we used the *ad hoc* target of 1000 unique ancestral particles; with our adjusted fitting algorithm we far exceeded this target and on that basis expect the Monte Carlo variation to be low. Nevertheless, the effective sample size of unique particles (ESS_u) is low for some models, particularly the EDDF model, so we cannot be sure that statistics such as posterior AIC_c, which we have found to be particularly sensitive to small sample sizes of particles, are accurate. Further investigation of this is needed (e.g., by repeat runs as performed by Newman *et al.* (in press)).

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.* (in press) found that using a discount parameter of 0.997, led to negligible bias in the marginal posterior parameter and state estimates. However, a preliminary study using the 1984-2007 data and comparing state estimates for the DDS model with and without kernel smoothing (Thomas, unpublished) showed some bias in state estimates, particularly in the early part of the time series, resulting in non-negligible bias in model selection criterion estimates. In this report we used a considerably more conservative discount parameter of 0.99997. We anticipate that any remaining bias is very small, but this again requires further investigation.

Table 4. Estimated size, in thousands, of the British grey seal population at the start of the 2007 breeding season, derived from models fit to data from 1984-2007. Numbers are posterior means with 95% credibility intervals in brackets.

	DDS	DDF
North Sea	14.1 (11.2 19.0)	32.4 (23.1 46.2)
Inner Hebrides	9.2 (7.6 11.6)	25.5 (16.7 39.1)
Outer Hebrides	32.9 (25.9 42.3)	100.2 (62.4 160.2)
Orkney	57.4 (45.3 76.2)	123.4 (88.9 172.8)
Total	113.6 (90.0 149.1)	281.6 (191.2 418.3)
	EDDS	EDDF
North Sea	17.7 (10.7 26.5)	25.1 (19.8 32.5)
Inner Hebrides	9.5 (6.6 13.5)	16.6 (12.5 21.6)
Outer Hebrides	36.3 (24.7 50.5)	61.8 (45.8 80.0)
Orkney	73.1 (43.4 98.6)	92.5 (73.5 117.5)
Total	136.6 (85.4 189.1)	196.0 (151.6 251.6)
	EDDSNM	EDDFNM
North Sea	17.1 (10.6 25.9)	27.2 (20.7 38.2)
Inner Hebrides	8.3 (6.5 10.5)	21.4 (16.5 32.1)
Outer Hebrides	31.3 (24.0 39.1)	88.1 (67.0 143.0)
Orkney	60.9 (40.9 93.5)	103.0 (79.5 142.9)
Total	117.6 (89.1 168.9)	239.7 (188.8 356.2)
	Model averaged	
North Sea	20.5 (11.1 33.6)	
Inner Hebrides	12.9 (6.5 27.2)	
Outer Hebrides	51.2 (23.8 11.5)	
Orkney	75.4 (40.4 130.0)	
Total	160.1 (84.5 304.5)	

Comparison with previous estimates
The estimates of total population size are somewhat different from those from last year, comparing the same years and models. For example, the 2006 estimate from Thomas and Harwood (2007) under the DDS model was 115,700 (95%CI 90,400-154,400), compared with the estimate for 2006 in the current report (Appendix) of 111,000 (88,300-144,700). The previous 2006 estimate for the DDF model was 248,000 (190,100-377,700), compared with new estimate of 270,400 (191,200-418,300). The change may be partially caused by the small increase in estimated observation error, or by the additional year of pup production estimates, but is almost certainly largely caused by the decreased bias due to less kernel smoothing being used in the fitting algorithm this year.

The DDS and DDF models were those best supported in last year's analysis; a no-movement model had been previously tried (Thomas and Harwood 2003) and found to be poorly supported by the data. Our new algorithm should lead to more accurate model selection, and it shows considerable support for models that do not include movement of recruiting females between regions. Estimates of total population size from the EDDSNM model are very similar to those from the DDS model reported last year (e.g., the 2006 estimates from EDDSNM are 116,300 with 95% CI 82,100-168,900); those from the EDDFNM model are a small amount lower than from the DDF estimates (2006 estimates from EDDFNM are 231,100 with 95%CI 177,700-342,100). Hence changing from reporting total population size estimates based on DDS and DDF to those based on EDDSNM and EDDFNM will not have a great effect on the reported "headline" values.

Multi-model inference
Incorporating model uncertainty is often recommended when there are multiple competing models that are biologically reasonable but give different results (e.g., Burnham and Anderson 2001). In this case, the multi-model confidence intervals usefully reflects our uncertainty about whether the EDDSNM or EDDFNM models are more accurate descriptions of the species' biology. However, the model averaged posterior mean estimates seem less useful: being between the EDDSNM and EDDFNM estimates, they are all in regions of low posterior density (Figure 4) and so have less support than any of the single model estimates. One potential course of action for summarizing the estimates in advice to non-specialists would be to report the posterior mean EDDSNM and EDDFNM estimates, together

with their AICc weights (which could be referred to as “model weights”), and the joint confidence interval.

Future work
Work aimed at further testing and improving the fitting algorithm is ongoing, as is work, 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. Even though the models used in this report fit the data much better than those employed in previous years, there are still some systematic departures of the estimated pup production, and alternative biological models will be investigated in an attempt to obtain better fits. One avenue of research will the to allow random variation in demographic parameters between years. In addition, we will investigate the use of pup production estimates from the period before 1984 to generate prior distributions for the initial population states. Although the EDDSNM and EDDFNM models provide much better fits to recent pup production estimates for most regions, they do not capture the recent changes in pup production in Orkney. This may be because of the large number of individual colonies in Orkney, many of which have very different growth trajectories. We will therefore investigate the development of a separate, spatially-structured model for this region.

Nevertheless, by far the biggest source of uncertainty comes from which is the appropriate demographic parameter to model density dependence in. We have previously demonstrated that a single additional estimate of total population size could resolve much of this uncertainty (Thomas and Harwood 2005, Matthiopoulos *et al.* 2006), and we hope to obtain such an estimate in the foreseeable future.

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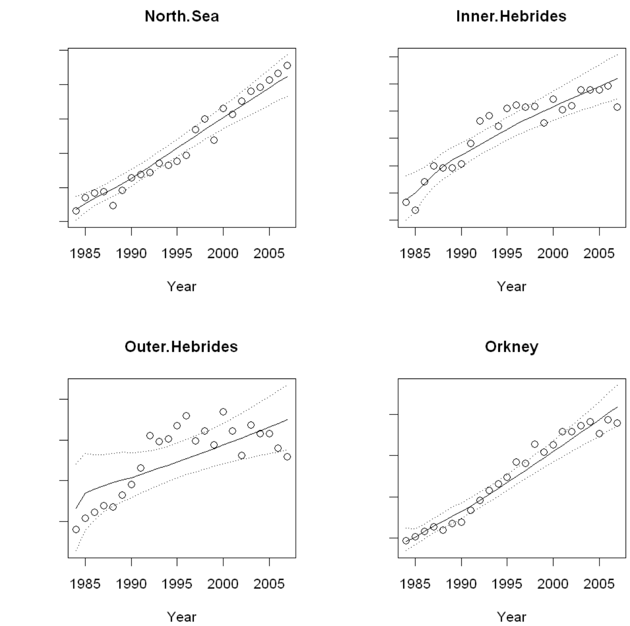
Figure 1. Posterior estimates from a DDS model of grey seal population dynamics where the observation precision parameter ψ is estimated, fit to pup production estimates from 1984-2007.

(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.

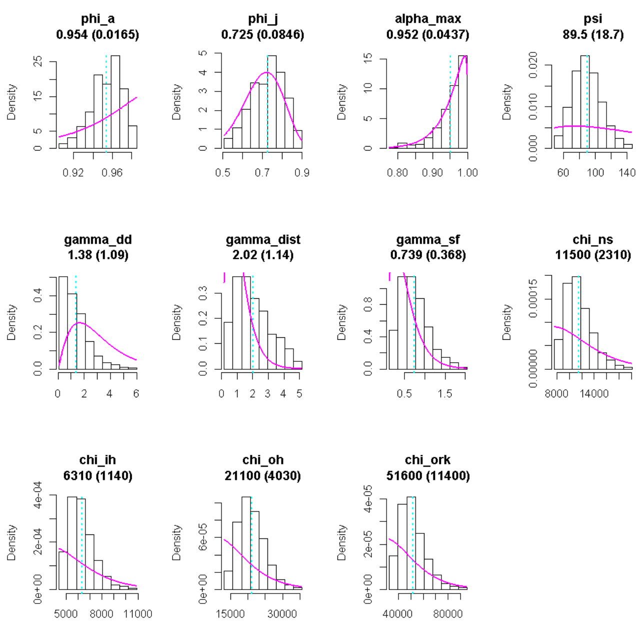
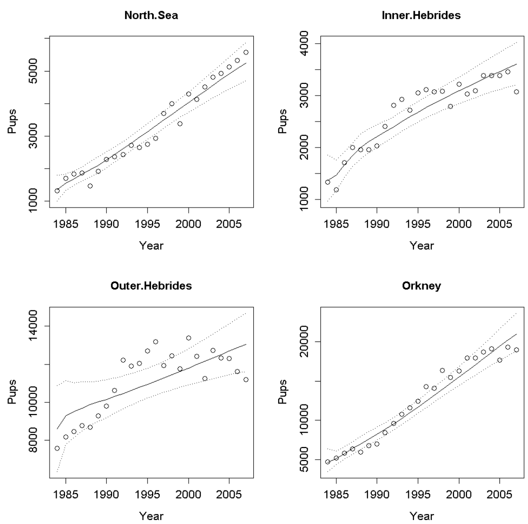
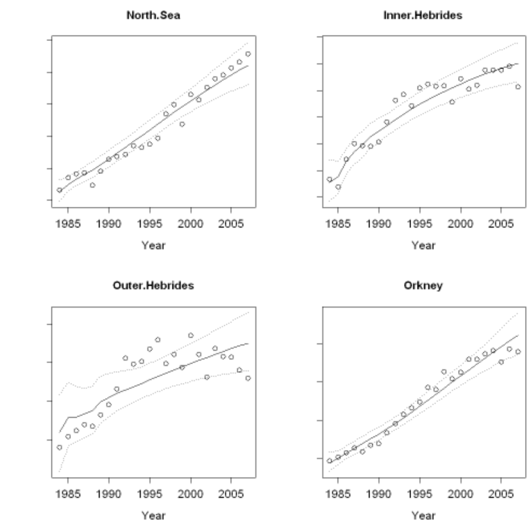


Figure 2. Estimates of true pup production from six models of grey seal population dynamics, where the observation precision parameter ψ is fixed at 89.5, fit to pup production estimates from 1984-2007. Input data are shown as circles, while the lines show the posterior mean bracketed by the 95% credibility interval.

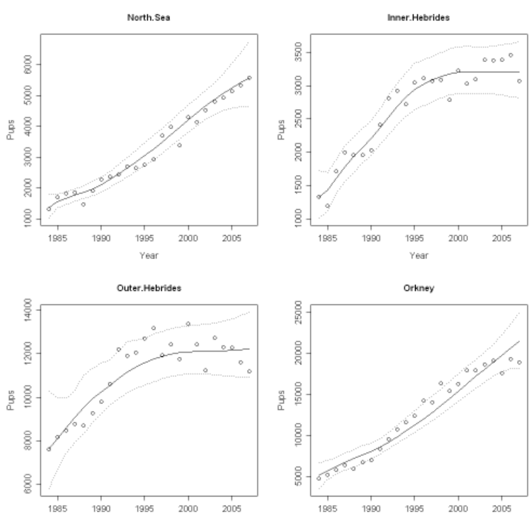
(a) Density dependent survival (DDS)



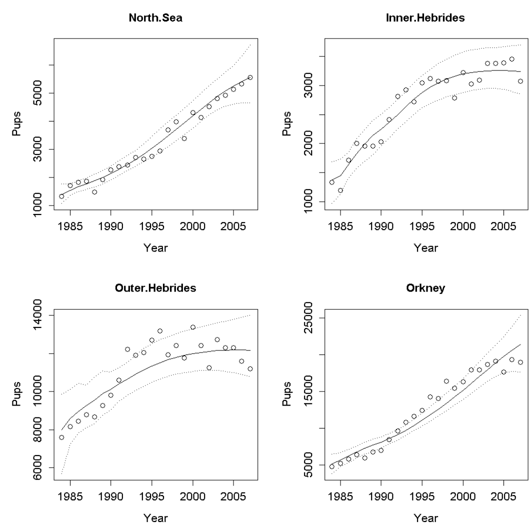
(b) Density dependent fecundity (DDF)



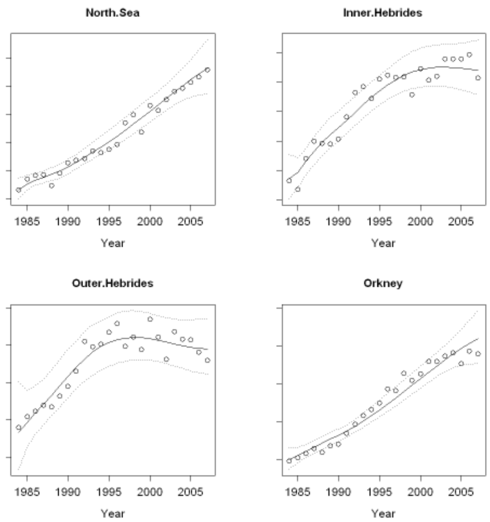
(c) Extended density dependent survival (EDDS)



(d) Extended density dependent fecundity (EDDF)



(e) Extended density dependent survival with no movement (EDDSNM)



(f) Extended density dependent fecundity with no movement (EDDFNM)

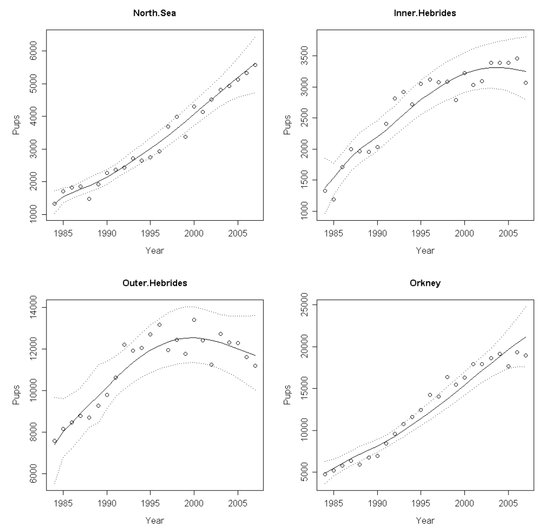
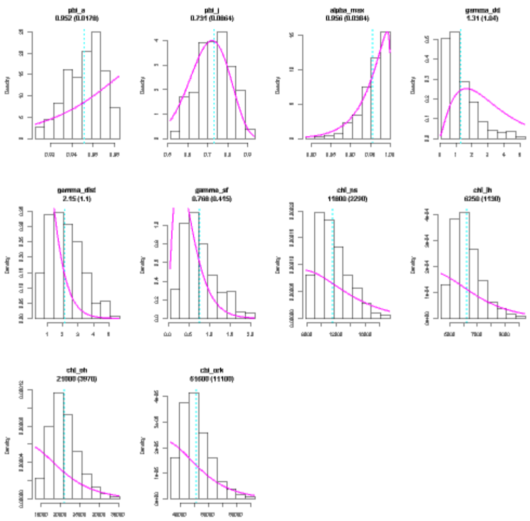
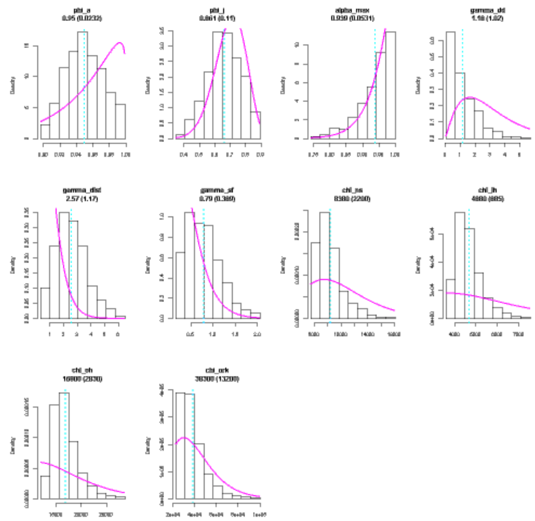


Figure 3. Posterior parameter estimates (histograms) and priors (solid lines) from six models of grey seal population dynamics where the observation precision parameter ψ is fixed at 89.5, fit to pup production estimates from 1984-2007. The vertical line shows the posterior mean, its value is given in the title of each plot after the parameter name, with the associated standard error in parentheses.

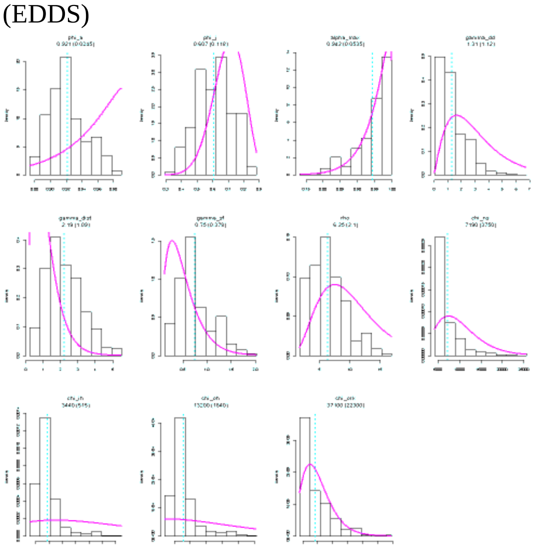
(a) Density dependent survival (DDS)



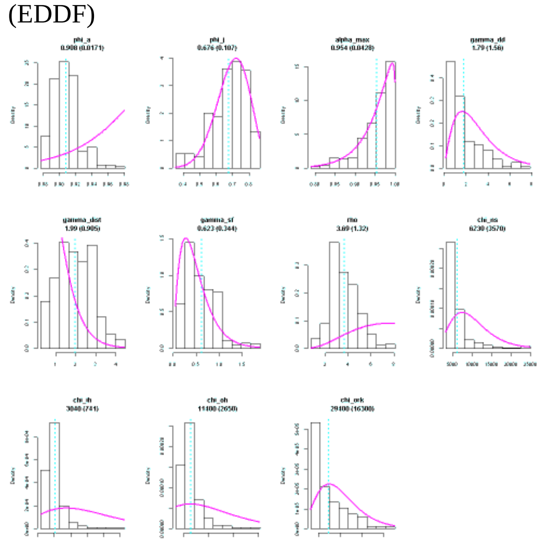
(b) Density dependent fecundity (DDF)



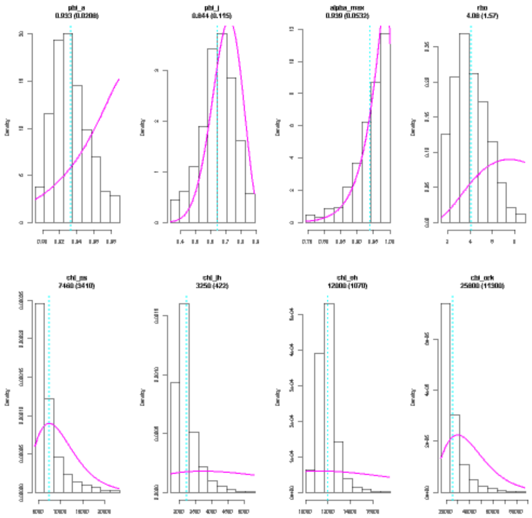
(c) Extended density dependent survival (EDDS)



(d) Extended density dependent fecundity (EDDF)



(e) Extended density dependent survival with no movement (EDDSNM)



(f) Extended density dependent fecundity with no movement (EDDFNM)

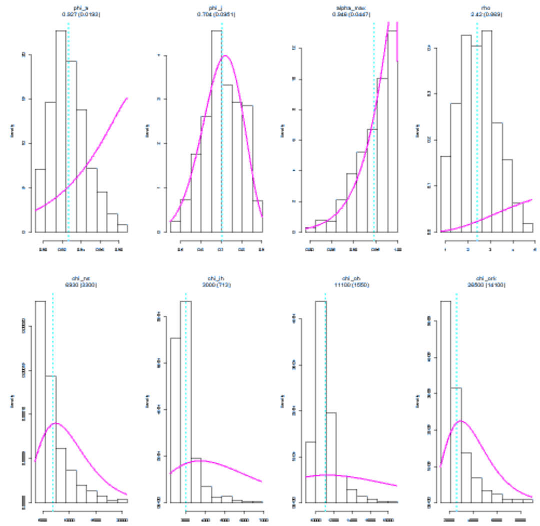
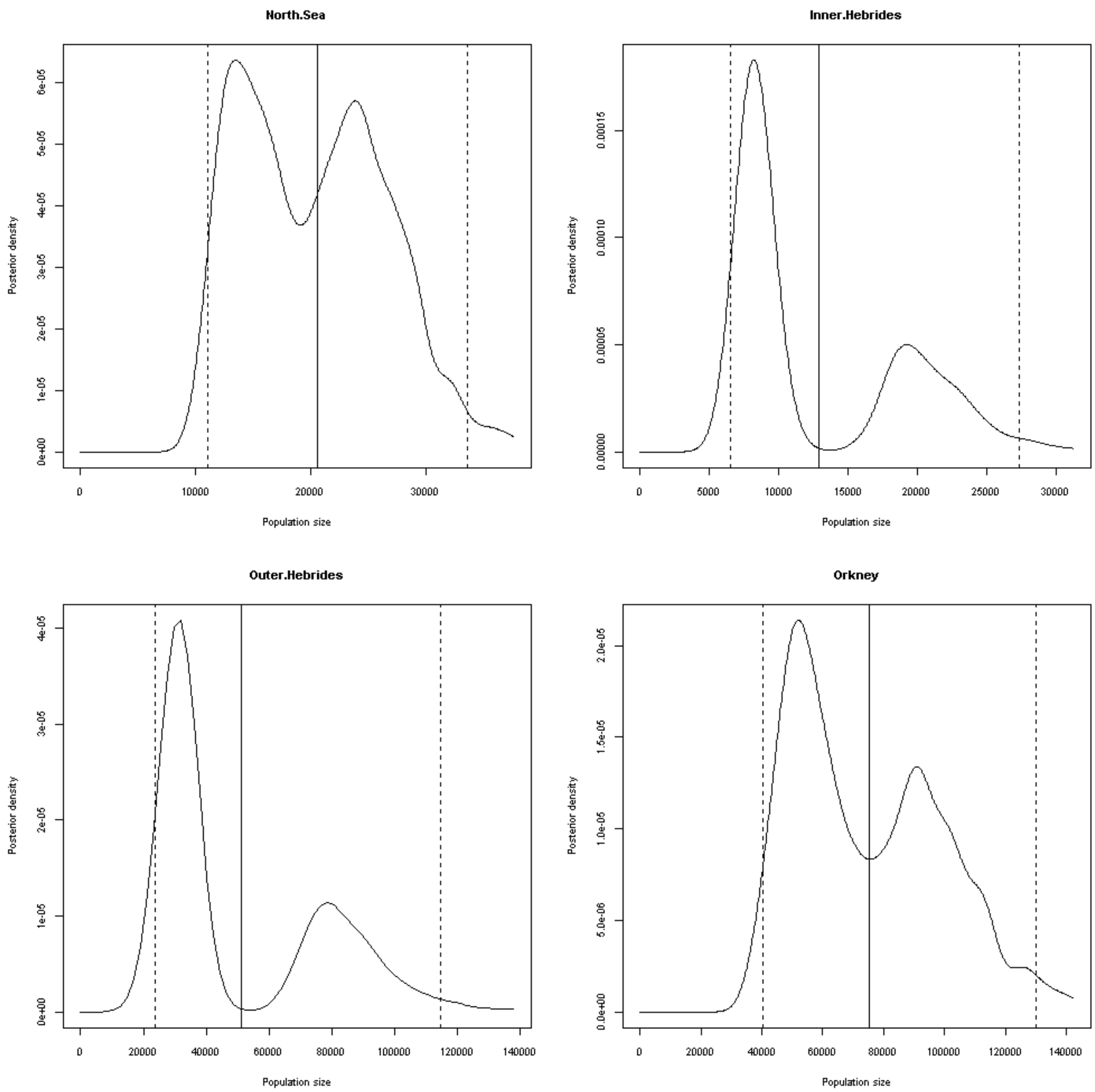


Figure 4. Posterior density of total population size at the beginning of the 2007 breeding season, combining the models. The two peaks in each plot represent the posterior modes of the EDDSNM and EDDFNM models (right and left peaks, respectively); the other models had almost zero support. Solid vertical lines are the mean posterior estimates; dashed lines indicate posterior 95% credibility intervals.



Appendix

Estimates of total population size, in thousands, at the beginning of each breeding season from 1984-2007, made using six models of British grey seal population dynamics. Numbers are posterior means followed by 95% credibility intervals in brackets.

Density dependent survival (DDS) model

Year	North Sea	Inner Hebrides	Outer Hebrides	Orkneys	Total
1984	4.5 (3.6 5.6)	4.5 (3.5 5.9)	25.4 (19.9 34)	16.6 (13.4 20.8)	51.1 (40.4 66.3)
1985	4.9 (4 6)	4.8 (3.8 6.2)	25.5 (20.1 33.4)	18 (14.8 22.2)	53.3 (42.8 67.9)
1986	5.3 (4.4 6.6)	5.1 (4.1 6.5)	25.7 (20.4 33.3)	19.6 (16.2 23.8)	55.8 (45.2 70.3)
1987	5.8 (4.8 7.1)	5.4 (4.4 6.8)	25.9 (20.8 33.3)	21.2 (17.8 26.1)	58.4 (47.8 73.3)
1988	6.2 (5.2 7.6)	5.7 (4.6 7.1)	26.2 (21.1 33.4)	22.9 (19.2 28.1)	61 (50.2 76.3)
1989	6.6 (5.6 8.1)	6 (4.8 7.5)	26.5 (21.4 33.8)	24.6 (20.7 30.1)	63.7 (52.5 79.4)
1990	7.1 (5.9 8.6)	6.2 (5 7.8)	26.8 (21.8 34.1)	26.3 (22.2 32.3)	66.4 (54.9 82.8)
1991	7.5 (6.3 9.2)	6.4 (5.2 8.1)	27.1 (22.1 34.4)	28.1 (23.7 34.5)	69.1 (57.3 86.2)
1992	7.9 (6.6 9.7)	6.6 (5.4 8.4)	27.4 (22.4 34.8)	29.9 (25.2 36.8)	71.9 (59.6 89.7)
1993	8.4 (7 10.3)	6.8 (5.6 8.6)	27.8 (22.7 35.2)	31.7 (26.7 39.1)	74.7 (61.9 93.2)
1994	8.8 (7.3 10.8)	7 (5.8 8.9)	28.1 (22.9 35.7)	33.5 (28.2 41.5)	77.5 (64.2 96.9)
1995	9.2 (7.7 11.4)	7.2 (5.9 9.1)	28.5 (23.2 36)	35.4 (29.6 43.9)	80.3 (66.4 100.4)
1996	9.7 (8 12)	7.4 (6.1 9.3)	28.8 (23.4 36.3)	37.3 (31 46.4)	83.2 (68.6 104.1)
1997	10.1 (8.3 12.6)	7.6 (6.2 9.6)	29.2 (23.7 36.7)	39.1 (32.5 48.9)	86 (70.7 107.9)
1998	10.5 (8.6 13.3)	7.8 (6.4 9.8)	29.6 (23.9 37.3)	41 (33.9 51.4)	88.9 (72.8 111.8)
1999	10.9 (9 13.9)	8 (6.5 10)	29.9 (24.2 37.9)	42.9 (35.2 54)	91.7 (74.9 115.8)
2000	11.3 (9.3 14.6)	8.1 (6.7 10.2)	30.3 (24.4 38.5)	44.7 (36.6 56.6)	94.5 (76.9 119.8)
2001	11.8 (9.6 15.2)	8.3 (6.8 10.4)	30.7 (24.7 39.1)	46.6 (37.9 59.2)	97.3 (78.9 123.9)
2002	12.2 (9.8 15.9)	8.5 (7 10.6)	31.1 (24.9 39.7)	48.4 (39.2 61.8)	100.1 (80.9 128)
2003	12.6 (10.1 16.5)	8.6 (7.1 10.8)	31.4 (25.1 40.2)	50.3 (40.5 64.5)	102.9 (82.8 132)
2004	12.9 (10.4 17.2)	8.8 (7.2 11)	31.8 (25.3 40.7)	52.1 (41.8 67.3)	105.6 (84.7 136.2)
2005	13.3 (10.7 17.8)	8.9 (7.3 11.2)	32.2 (25.5 41.2)	53.9 (43 70.2)	108.3 (86.5 140.4)
2006	13.7 (10.9 18.4)	9.1 (7.5 11.4)	32.6 (25.7 41.8)	55.7 (44.2 73.2)	111 (88.3 144.7)
2007	14.1 (11.2 19)	9.2 (7.6 11.6)	32.9 (25.9 42.3)	57.4 (45.3 76.2)	113.6 (90 149.1)

Density dependent fecundity (DDF) model

Year	North Sea	Inner Hebrides	Outer Hebrides	Orkneys	Total
1984	5.6 (4.4 7.2)	6.3 (4.3 8.5)	53.4 (35.8 104)	19.5 (15 24.9)	84.8 (59.5 144.6)
1985	6.2 (5 7.8)	7.1 (5.3 9.1)	54.5 (37.3 105.5)	21.5 (17 26.9)	89.4 (64.7 149.3)
1986	6.9 (5.6 8.6)	7.9 (6.1 9.9)	56.1 (38.9 106.9)	23.8 (19.2 29.4)	94.7 (69.9 154.9)
1987	7.7 (6.3 9.5)	8.8 (6.9 11)	57.6 (40.3 108.8)	26.3 (21.3 32.4)	100.4 (74.8 161.7)
1988	8.5 (6.9 10.5)	9.7 (7.6 12.2)	59.2 (41.6 110.5)	29.1 (23.6 35.5)	106.6 (79.8 168.8)
1989	9.4 (7.6 11.7)	10.5 (8.3 13.3)	61 (42.8 111.8)	32.1 (25.9 39.4)	113 (84.7 176.2)
1990	10.3 (8.2 12.9)	11.4 (9 14.7)	62.8 (44.1 112.3)	35.4 (28.4 43.8)	120 (89.7 183.6)
1991	11.3 (8.9 14.2)	12.3 (9.6 15.9)	64.8 (45.2 112.2)	38.9 (31.1 48.6)	127.2 (94.8 190.9)
1992	12.3 (9.7 15.7)	13.2 (10.1 17.2)	66.8 (46.4 114.6)	42.6 (33.8 53.7)	134.8 (99.9 201.1)
1993	13.4 (10.4 17.3)	14.1 (10.7 18.3)	68.8 (47.4 115)	46.5 (36.6 58.9)	142.7 (105.1 209.6)
1994	14.5 (11.1 19)	14.9 (11.3 19.5)	70.8 (48.5 115.7)	50.7 (39.6 64.8)	150.9 (110.5 219)
1995	15.7 (12 20.7)	15.8 (11.8 20.8)	72.9 (49.6 118.6)	55.1 (42.7 71.1)	159.4 (116 231.2)
1996	16.9 (12.8 22.6)	16.6 (12.3 22.2)	75 (50.7 122.1)	59.7 (45.8 77.9)	168.3 (121.6 244.6)
1997	18.1 (13.6 24.5)	17.5 (12.7 23.6)	77.2 (51.7 125.8)	64.6 (49.2 85.1)	177.4 (127.3 259)
1998	19.4 (14.5 26.4)	18.3 (13.2 25)	79.4 (52.8 129.8)	69.7 (52.6 92.4)	186.9 (133.1 273.6)
1999	20.8 (15.4 28.5)	19.1 (13.6 26.5)	81.6 (53.8 132.5)	75 (56.2 100.5)	196.6 (139.1 287.9)
2000	22.2 (16.4 30.5)	20 (14 28)	83.9 (54.8 135)	80.5 (59.9 109)	206.5 (145.1 302.5)
2001	23.6 (17.3 32.6)	20.8 (14.4 29.5)	86.2 (55.8 138)	86.2 (63.6 117.5)	216.7 (151.2 317.8)
2002	25 (18.2 34.9)	21.6 (14.8 31.1)	88.5 (56.9 140.1)	92.1 (67.6 126.3)	227.1 (157.5 332.3)
2003	26.4 (19.2 37.1)	22.4 (15.2 32.6)	90.8 (57.9 142.1)	98.1 (71.6 135.1)	237.7 (164 347)
2004	27.9 (20.2 39.4)	23.2 (15.6 34.2)	93.1 (59 145.2)	104.2 (75.7 144)	248.5 (170.6 362.9)
2005	29.4 (21.2 41.6)	24 (16 35.8)	95.5 (60.2 149.7)	110.5 (80 153.2)	259.4 (177.4 380.4)
2006	30.9 (22.1 43.9)	24.8 (16.4 37.5)	97.9 (61.3 155.1)	116.9 (84.4 162.8)	270.4 (184.2 399.3)
2007	32.4 (23.1 46.2)	25.5 (16.7 39.1)	100.2 (62.4 160.2)	123.4 (88.9 172.8)	281.6 (191.2 418.3)

Extended density dependent survival (EDDS) model

Year	North Sea	Inner Hebrides	Outer Hebrides	Orkneys	Total
1984	5.3 (3.7 6.8)	5.3 (4.2 7)	29.2 (20.6 38.9)	21 (13.4 29.3)	60.9 (42 82.1)
1985	5.6 (4.1 6.9)	5.7 (4.5 7.4)	30.2 (21.7 40)	22.1 (14.3 30)	63.6 (44.6 84.3)
1986	6 (4.5 7.3)	6 (4.8 7.7)	31.3 (22.5 40.8)	23.4 (15.6 30.9)	66.7 (47.3 86.7)
1987	6.5 (4.9 7.8)	6.4 (5.1 8.2)	32.4 (22.9 41.4)	24.8 (17 32)	70 (49.8 89.4)
1988	6.9 (5.4 8.2)	6.8 (5.3 8.6)	33.4 (23.3 42.2)	26.4 (18.5 33.7)	73.6 (52.5 92.8)
1989	7.4 (5.9 8.7)	7.3 (5.5 9)	34.2 (23.4 42.7)	28.1 (20.1 35.5)	77 (55 95.9)
1990	7.9 (6.3 9.2)	7.8 (5.7 9.6)	34.8 (23.4 43.2)	29.9 (21.8 37.8)	80.3 (57.2 99.8)
1991	8.4 (6.7 9.8)	8.2 (5.8 10.2)	35.2 (23.4 43.7)	31.8 (23.6 39.7)	83.7 (59.4 103.4)
1992	8.9 (7.2 10.5)	8.6 (5.9 10.7)	35.6 (23.5 44.3)	33.8 (25.3 41.4)	87 (61.8 107)
1993	9.6 (7.6 11.3)	9 (5.9 11.3)	35.8 (23.5 44.9)	35.9 (27.1 43.3)	90.3 (64.1 110.7)
1994	10.2 (7.9 12.2)	9.3 (6 11.8)	36 (23.6 45.3)	38.2 (28.8 45.4)	93.6 (66.4 114.7)
1995	10.9 (8.3 13)	9.4 (6.1 12.1)	36 (23.6 45.8)	40.6 (30.6 47.8)	96.9 (68.6 118.7)
1996	11.6 (8.6 13.9)	9.5 (6.2 12.1)	36.1 (23.7 46.2)	43.1 (32.4 50.5)	100.2 (70.9 122.6)
1997	12.3 (8.9 14.8)	9.5 (6.3 12.1)	36 (23.9 46.5)	45.6 (34 53.7)	103.4 (73 127.1)
1998	13 (9.2 15.8)	9.5 (6.3 12.3)	35.9 (24 46.8)	48.3 (35.6 57.2)	106.7 (75.1 132.1)
1999	13.7 (9.5 16.8)	9.5 (6.4 12.5)	35.8 (24 47.2)	51 (37.1 60.8)	110 (77 137.3)
2000	14.4 (9.7 17.9)	9.4 (6.4 12.6)	35.7 (24.1 47.7)	53.8 (38.5 64.6)	113.3 (78.7 142.8)
2001	15 (9.9 19)	9.4 (6.5 12.8)	35.7 (24.2 48.1)	56.5 (39.8 68.7)	116.6 (80.4 148.5)
2002	15.6 (10.1 20)	9.3 (6.5 12.9)	35.7 (24.3 48.4)	59.3 (41 73)	120 (81.8 154.4)
2003	16.2 (10.2 21.1)	9.3 (6.5 13)	35.8 (24.4 48.9)	62.1 (42 77.7)	123.3 (83.1 160.7)
2004	16.6 (10.4 22.4)	9.4 (6.6 13.2)	35.9 (24.4 49.3)	64.8 (42.9 82.6)	126.7 (84.2 167.5)
2005	17 (10.5 23.7)	9.4 (6.6 13.3)	36 (24.5 49.7)	67.6 (43.4 87.5)	130 (85 174.2)
2006	17.4 (10.6 25.1)	9.4 (6.6 13.4)	36.2 (24.6 50.1)	70.3 (43.7 93)	133.3 (85.5 181.6)
2007	17.7 (10.7 26.5)	9.5 (6.6 13.5)	36.3 (24.7 50.5)	73.1 (43.4 98.6)	136.6 (85.4 189.1)

Extended density dependent fecundity (EDDF) model

Year	North Sea	Inner Hebrides	Outer Hebrides	Orkneys	Total
1984	5.6 (4.4 6.8)	5.9 (4.1 7.7)	34.1 (26.3 51.9)	22.2 (16.8 27.6)	67.9 (51.7 94)
1985	5.9 (4.6 7)	6.3 (4.8 7.9)	35.4 (27.8 48.9)	23.3 (18.3 28.5)	70.9 (55.5 92.4)
1986	6.4 (5 7.6)	6.7 (5.3 8.1)	36.8 (29.3 48.2)	24.6 (19.8 29.4)	74.4 (59.5 93.4)
1987	6.8 (5.4 8.2)	7.2 (5.8 8.7)	38.3 (31.2 49.2)	26.1 (21 31.1)	78.3 (63.4 97.2)
1988	7.3 (5.7 8.9)	7.7 (6.3 9.2)	39.7 (32.5 49.5)	27.8 (22.7 32.7)	82.5 (67.2 100.3)
1989	7.8 (6.2 9.5)	8.3 (6.8 9.9)	41.2 (33.3 50.5)	29.6 (24.3 34.4)	87 (70.6 104.4)
1990	8.4 (6.6 10.3)	8.9 (7.2 10.7)	42.7 (34.2 51.2)	31.6 (26 36.8)	91.6 (74.1 109)
1991	9 (7 11.1)	9.6 (7.7 11.3)	44.1 (34.8 52.1)	33.7 (27.7 39.5)	96.4 (77.2 114)
1992	9.7 (7.5 11.9)	10.2 (8.2 11.9)	45.5 (35.8 54.2)	35.9 (29.3 42.1)	101.3 (80.8 120.2)
1993	10.4 (8.1 12.8)	10.8 (8.7 12.7)	46.9 (36.7 57.2)	38.3 (31.1 44.9)	106.4 (84.5 127.6)
1994	11.1 (8.6 13.8)	11.4 (9.1 13.4)	48.3 (37.5 59.3)	40.9 (33.3 47.9)	111.8 (88.6 134.5)
1995	12 (9.2 14.9)	12 (9.5 14.2)	49.7 (38.3 61.3)	43.6 (35.7 51.6)	117.3 (92.8 142.1)
1996	12.9 (9.9 16.1)	12.6 (9.8 15)	51 (39.1 63)	46.6 (38 55.4)	123.1 (96.9 149.5)
1997	13.8 (10.6 17.4)	13.2 (10.2 15.8)	52.2 (39.8 64.7)	49.8 (40.5 59.3)	129 (101.2 157.3)
1998	14.9 (11.4 18.7)	13.7 (10.5 16.7)	53.4 (40.5 66.7)	53.2 (43.1 63.9)	135.2 (105.5 166)
1999	15.9 (12.2 20)	14.1 (10.8 17.4)	54.6 (41.1 68.5)	56.9 (45.8 68.6)	141.5 (109.8 174.5)
2000	17 (13 21.3)	14.5 (11 18.1)	55.6 (41.8 70.5)	60.7 (48.7 74.1)	147.9 (114.6 183.9)
2001	18.2 (13.9 22.8)	14.9 (11.3 18.7)	56.6 (42.6 72.3)	64.8 (51.7 80.5)	154.6 (119.5 194.2)
2002	19.4 (14.9 24.4)	15.2 (11.5 19.3)	57.6 (43.3 73.8)	69.1 (54.9 87.2)	161.3 (124.6 204.7)
2003	20.5 (15.8 26.1)	15.6 (11.7 19.8)	58.5 (44 75.3)	73.6 (58.2 93.9)	168.2 (129.8 215)
2004	21.7 (16.8 27.9)	15.8 (11.9 20.2)	59.4 (44.5 76.6)	78.2 (61.8 100.2)	175.1 (135 224.9)
2005	22.9 (17.8 29.6)	16.1 (12.1 20.7)	60.2 (45 77.7)	82.9 (65.5 106.2)	182.1 (140.4 234.2)
2006	24 (18.8 31)	16.3 (12.3 21.1)	61 (45.4 78.9)	87.7 (69.5 111.9)	189 (146 243)
2007	25.1 (19.8 32.5)	16.6 (12.5 21.6)	61.8 (45.8 80)	92.5 (73.5 117.5)	196 (151.6 251.6)

Extended density dependent survival with no movement (EDDSNM) model

Year	North Sea	Inner Hebrides	Outer Hebrides	Orkneys	Total
1984	5.3 (4.1 6.7)	5.6 (4.3 7.1)	26 (20 32.5)	20.3 (14.9 26.8)	57.2 (43.3 73.1)
1985	5.6 (4.5 7.1)	5.9 (4.6 7.4)	27.4 (21.3 34)	21.6 (16.2 27.6)	60.5 (46.6 76.1)
1986	6.1 (4.9 7.6)	6.2 (4.9 7.7)	28.7 (22.1 35.3)	23.1 (17.7 28.9)	64 (49.5 79.5)
1987	6.5 (5.2 8.1)	6.5 (5.1 8.1)	29.9 (22.8 36.9)	24.7 (19.3 30.5)	67.7 (52.5 83.6)
1988	7 (5.7 8.6)	6.9 (5.4 8.5)	30.9 (23.3 38.6)	26.5 (20.9 32.4)	71.4 (55.3 88.2)
1989	7.5 (6.1 9.2)	7.2 (5.6 9)	31.7 (23.6 39.5)	28.4 (22.5 34.6)	74.8 (57.8 92.3)
1990	8 (6.5 9.8)	7.5 (5.7 9.3)	32.2 (23.9 40.5)	30.4 (24.1 36.8)	78.2 (60.2 96.5)
1991	8.5 (6.9 10.5)	7.8 (5.9 9.7)	32.6 (24.1 41.2)	32.5 (25.8 39.2)	81.4 (62.7 100.7)
1992	9.1 (7.3 11.2)	8 (6.1 10)	32.8 (24.2 41.7)	34.6 (27.4 41.6)	84.5 (65 104.6)
1993	9.6 (7.8 11.9)	8.2 (6.2 10.3)	32.9 (24.3 41.9)	36.7 (29.2 44.2)	87.5 (67.4 108.3)
1994	10.2 (8.2 12.6)	8.4 (6.3 10.5)	32.8 (24.4 41.8)	39 (30.8 47)	90.4 (69.7 111.9)
1995	10.8 (8.6 13.3)	8.5 (6.3 10.6)	32.7 (24.4 41.5)	41.2 (32.4 49.9)	93.2 (71.8 115.3)
1996	11.4 (9 14.1)	8.6 (6.4 10.8)	32.4 (24.4 41.1)	43.5 (33.9 53)	95.9 (73.6 118.9)
1997	12.1 (9.3 14.9)	8.6 (6.5 10.8)	32.2 (24.3 40.6)	45.7 (35.3 56)	98.5 (75.4 122.3)
1998	12.7 (9.5 15.7)	8.6 (6.5 10.8)	31.9 (24.3 40.1)	47.9 (36.7 59.1)	101 (77 125.7)
1999	13.3 (9.8 16.6)	8.6 (6.5 10.7)	31.6 (24.2 39.7)	49.9 (37.8 62.5)	103.4 (78.3 129.4)
2000	13.8 (10 17.5)	8.5 (6.5 10.6)	31.4 (24.1 39.3)	51.9 (38.9 65.8)	105.7 (79.6 133.2)
2001	14.4 (10.2 18.4)	8.5 (6.6 10.6)	31.2 (24.1 39.1)	53.7 (39.7 69)	107.8 (80.5 137)
2002	14.9 (10.4 19.4)	8.4 (6.6 10.5)	31.1 (24 38.9)	55.3 (40.3 72.2)	109.7 (81.3 141)
2003	15.4 (10.5 20.5)	8.4 (6.5 10.5)	31.1 (24 38.8)	56.7 (40.7 75.3)	111.6 (81.8 145.1)
2004	15.9 (10.6 21.7)	8.3 (6.5 10.5)	31.1 (24 38.7)	58 (40.9 79.4)	113.3 (82 150.4)
2005	16.3 (10.6 23.1)	8.3 (6.5 10.5)	31.1 (24 38.8)	59.1 (41 83.9)	114.8 (82.1 156.2)
2006	16.7 (10.6 24.5)	8.3 (6.5 10.5)	31.2 (24 38.9)	60 (41 88.6)	116.3 (82.1 162.4)
2007	17.1 (10.6 25.9)	8.3 (6.5 10.5)	31.3 (24 39.1)	60.9 (40.9 93.5)	117.6 (81.9 168.9)

Extended density dependent fecundity with no movement (EDDFNM) model

Year	North Sea	Inner Hebrides	Outer Hebrides	Orkneys	Total
1984	5.6 (4.6 6.9)	6.4 (5.1 8.6)	35.6 (23.7 93.8)	21.5 (17.1 26.3)	69.1 (50.5 135.6)
1985	6 (5 7.4)	6.8 (5.4 9.1)	37.5 (26.1 95.1)	22.9 (18.5 27.1)	73.2 (54.9 138.7)
1986	6.5 (5.4 8)	7.2 (5.8 9.7)	39.8 (27.9 94.2)	24.5 (19.9 29.2)	78 (59 141.1)
1987	7 (5.9 8.7)	7.7 (6.3 10.4)	42.1 (29.7 92.2)	26.4 (21.7 31.7)	83.3 (63.5 143)
1988	7.6 (6.3 9.4)	8.3 (6.7 11)	44.5 (31.6 90.5)	28.5 (23.4 34.1)	88.9 (68 145)
1989	8.2 (6.8 10.3)	8.9 (7.2 11.8)	47 (33.5 89)	30.8 (25.3 37)	95 (72.9 148.1)
1990	8.8 (7.3 11.2)	9.5 (7.7 12.6)	49.6 (35.7 89)	33.3 (27.2 40.5)	101.2 (77.9 153.4)
1991	9.5 (7.8 12.3)	10.2 (8.2 13.5)	52.3 (38 91.7)	35.8 (29.1 44.3)	107.7 (83.1 161.8)
1992	10.2 (8.3 13.4)	10.9 (8.7 14.3)	55 (40.4 94.7)	38.5 (31.2 47.3)	114.5 (88.6 169.7)
1993	10.9 (8.9 14.6)	11.5 (9.2 15.2)	57.8 (42.6 97.2)	41.4 (33.5 51.6)	121.7 (94.3 178.7)
1994	11.8 (9.5 15.9)	12.3 (9.7 16.3)	60.6 (45 100.1)	44.5 (35.9 56.6)	129.1 (100.1 188.8)
1995	12.6 (10.1 17.3)	13 (10.3 17.4)	63.4 (47.4 103)	47.8 (38.4 61.7)	136.8 (106.2 199.4)
1996	13.6 (10.7 18.8)	13.8 (10.9 18.5)	66.2 (49.8 106.5)	51.3 (41.1 67.1)	144.8 (112.5 210.9)
1997	14.5 (11.4 20.2)	14.5 (11.4 19.6)	68.9 (52.2 110)	55.1 (44 73.1)	153 (119 222.8)
1998	15.6 (12.1 21.8)	15.3 (12 20.7)	71.5 (54.5 113.1)	59 (46.9 79.2)	161.4 (125.6 234.8)
1999	16.7 (12.9 23.5)	16.1 (12.6 21.9)	74 (56.8 115.9)	63.2 (50.1 85.7)	169.9 (132.4 246.9)
2000	17.8 (13.7 25.3)	16.8 (13.2 23.1)	76.4 (58.9 118.8)	67.5 (53.3 92.5)	178.6 (139 259.7)
2001	19 (14.6 27.1)	17.6 (13.8 24.3)	78.6 (60.7 122.5)	72.1 (56.6 99.4)	187.3 (145.6 273.3)
2002	20.3 (15.5 28.9)	18.3 (14.3 25.6)	80.7 (62.4 126.1)	76.9 (60.1 106.2)	196.1 (152.3 286.8)
2003	21.6 (16.4 30.7)	19 (14.9 26.9)	82.5 (63.7 129.9)	81.8 (63.8 113.2)	204.9 (158.7 300.7)
2004	22.9 (17.4 32.6)	19.7 (15.3 28.2)	84.2 (64.8 132.9)	86.9 (67.5 120.3)	213.7 (165.1 313.9)
2005	24.3 (18.5 34.4)	20.3 (15.8 29.5)	85.7 (65.7 136.6)	92.2 (71.4 127.5)	222.5 (171.4 328)
2006	25.7 (19.6 36.3)	20.8 (16.2 30.8)	87 (66.4 139.9)	97.6 (75.5 135)	231.1 (177.7 342.1)
2007	27.2 (20.7 38.2)	21.4 (16.5 32.1)	88.1 (67 143)	103 (79.5 142.9)	239.7 (183.8 356.2)

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The status of British common seal populations in 2007

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Summary

In August 2007, the Sea Mammal Research Unit (SMRU) planned to survey common seals around the whole of the coast of Scotland and between the Humber Estuary and east Norfolk in England. The Scottish surveys were to be carried out in two helicopters each equipped with a new generation thermal imager. Unfortunately we were unable to purchase new imagers and, at very short notice, had to use an untested imager that was not ideally suited to our survey methods.

In Scotland, surveys were restricted to: the east coast from the Farne Islands to Helmsdale; Orkney; and the west coast from Gairloch to the Solway Firth. Areas not surveyed included Shetland, the far north coast from Helmsdale to Gairloch, the Outer Hebrides and the Small Isles. A second survey of the Moray Firth was 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 2007, most groups of seals common and grey, were also photographed using a digital camera. For some areas, there were significant differences between the original counts (from the thermal image in real time) and the recounted digital images. The numbers used in this Briefing Paper are all from recounts, with the assumption that these are the more accurate.

From surveys carried out between 2003 and 2007, the minimum number of common seals counted in Scotland was **20,035** and in England **3,242** making a UK total of **27,430** (Table 1). In 2002, **1,248** common seals were counted in Northern Ireland

The number of common seals counted in Orkney (3,379) was 26.0% lower than in 2006 (4,256). Numbers in Strathclyde in 2007 (5,543) were 14.7% lower than in the previous count (2000 and 2005). In the Moray Firth, both breeding and moult season counts were lower than in 2006. In the Firth of Tay, moult counts were the lowest recorded to date. In west Highland, numbers from surveys in 2005 and 2007 were slightly greater than from surveys in 1996, 1997 and 2000.

During the 2007 breeding season, SMRU and the conducted repeat air surveys of common seals breeding in the Moray Firth, continuing the surveys previously carried out by the University of Aberdeen. Breeding season surveys were also carried out in England, between the Humber Estuary and Scroby Sands.

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 (Figure 1), although the Moray Firth and Firth of Tay are surveyed more frequently. In 2005, significant declines in common seal numbers were found in Shetland and in Orkney and elsewhere on the North Sea coast on the UK (Lonergan *et al.* 2007). In 2006, we were unable to complete a Scottish-wide survey due to equipment failure. In 2007, we attempted to survey the entire Scottish coast using two survey helicopters each equipped with a thermal imaging camera. At very short notice, we were informed that were would not be allowed to use a new generation imager and had to use an untested imager that proved not to be well suited to the survey requirements. We surveyed a significant part of the Scottish coast (Figure 2) but omitted Shetland, the Western Isles, the far north coast and the Small Isles. These areas will be surveyed in August 2008 along with a third consecutive survey of Orkney.

In 2007, we photographed most groups if seals with a high-resolution digital camera. These images were used to determine the classification of seals within haulout groups and will be used to determine the age and sex structure of grey seals. The grey seal data will be used to inform the models used to estimate the total grey seal population size.

The Lincolnshire and Norfolk coast, which holds over 95% of the English common seal population, is usually surveyed twice annually during the August moult and since 2004, Natural England have funded breeding season surveys (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 and would not have detected the recent declines. SNH are also funding the 2008 survey of Orkney.

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. In addition, digital images were obtained using a digital camera equipped with an image-stabilised zoom lens. Both common and grey seals were digitally photographed and the images used to classify group composition.

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 fixed-wing aircraft. On sandbanks, where seals are relatively easily located, this survey method is highly cost-effective.

Results

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

The overall distribution of common seals around the British Isles, from surveys carried out between 2000 and 2006, is shown in Figure 1. For ease of viewing at this scale, counts have been aggregated into 10km squares.

Minimum population estimates, based on the most recent surveys of common seals in the UK, are shown in Table 1. Most of the Outer Hebrides count was from 2006 (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 single survey have been used.

The most recent minimum estimate of the number of common seals in Scotland is **23,035** from surveys carried out between 2003 and 2007 (Table 1). The most recent minimum estimate for England is **3,242**. This comprises 2,926 seals in Lincolnshire and Norfolk in 2007 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 **27,430.**

2. Common seals in Scotland: moult

In August 2007, the area surveyed for common seals using a thermal imager included the whole of Orkney, the east coast between Seahouses in Northumberland and Helmsdale in Sutherland, the west coast from just north of Gairloch to the Solway Firth, including all islands bar the Small Isles and the Outer Hebrides.

The number and distribution of common seals counted during the thermal imaging surveys in August 2006 are shown in Figure 2 with the distribution of grey seals in Figure 3.

The trends in counts of common seals in different regions of Scotland, from surveys carried out between 1988 and 2007 are shown in Figure 4. There were further declines in Orkney, Stathclyde and the Moray Firth and firth of Tay. There was little change in Highland. The lower of the two points in 2007 for Orkney, Highland and Strathclyde represent the recounts from digital images.

Moray Firth

Aberdeen University's Lighthouse Field Station, in Cromarty, obtained detailed annual counts of common seals in the Inner Moray Firth from June, July and August between 1988 and 2005. These counts of the inner Moray Firth are in Figure 5. SMRU's counts of a slightly larger area, including Loch Fleet and Findhorn, are also shown (SMRU moult) along with counts of the outer Moray Firth, including the Brora coast (SMRU moult, all MF).

SMRU's aerial surveys of the Moray Firth began in August 1992. The counts are in Table 2 with the trends in different parts of the Moray Firth in Figure 6. This figure represents a combination of both thermal imaging and fixed wing surveys of the area. Both 2007 counts were lower than counts from 2005 (Table 2). 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).

Firth of Tay

In the Firth of Tay in 2007, both counts were under 300 for the first time. Numbers in this Special Area of

Conservation (SAC) are now less than half the number counted between 1990 and 2002. There were 147 common seals in the Firth of Forth in 2007. Previously were suggested that these were from the same population. Even if so, numbers have declined considerably in recent years.

3. Common seals in Scotland: breeding season

Moray Firth

During the 2007 breeding season, SMRU conducted five air surveys common seals in the Moray Firth between mid June and mid July. The mean number of adults counted during these surveys, with the standard error, is shown in Figure 5 and was the lowest recorded to date.

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 was carried out in Lincolnshire and Norfolk during August 2007 (Tables 1 and 4). The total count for the Wash (2,162) was 21.6% higher than the single 2006 count and 27.4% lower than the mean pre-epidemic 2002 count (2,976).

Overall, the combined count for the English East coast population in 2007 was 7.9% higher than the count in 2006 but within the range of counts over the previous 3 years. This apparent lack of recovery or continued decline contrasts with the rapid recovery of the Wadden Sea population that has been increasing rapidly. 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 total of 984 pups and 2353 older seals (1+ age classes) were counted in the Wash during the 2007 breeding season survey compared with 1013 pups and 2267 older seals in July 2006. Pups were widely distributed, being present at all occupied sites in 2007. The 2007 adult and pup counts were similar to those from 2006 count which were much higher than in any previous survey, pup counts being being 55% greater than the 2005 count and adult count 28% higher.

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 07/04) suggested that the dramatic increase is unlikely to be due to changes in the timing of the survey.

6. Common seal surveys 2008

Breeding season: Moray Firth

During the pupping season (15th June – 15th July 2008) five fixed-wing surveys were carried out in the Moray Firth.

The Wash, Donna Nook and Blakeney Point

A series of five fixed wing surveys was carried out between 14th June and 13 July 2008 to provide data to estimate pup production in the Wash and adjacent sites.

Moult - Planned surveys

A survey covering the remaining parts of Scotland is planned for August 2008, weather and equipment permitting. The same methods will be used as in 2007, incorporating digital still images.

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).

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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.**

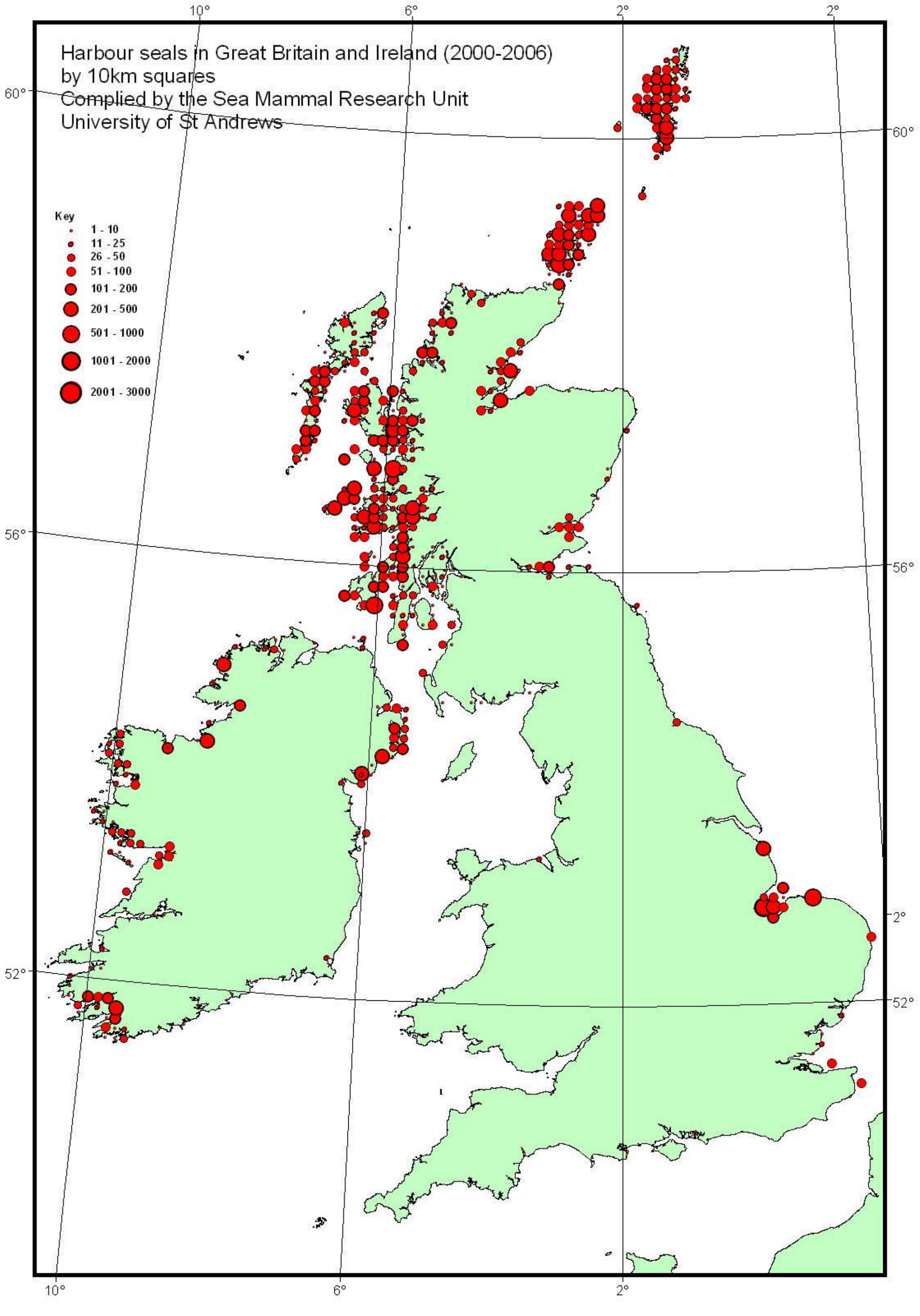

Figure 2. The number and distribution of common seals around the coast of Scotland surveyed in August 2007. All areas were surveyed by helicopter using a thermal imaging camera. Lines delineate the areas surveyed.

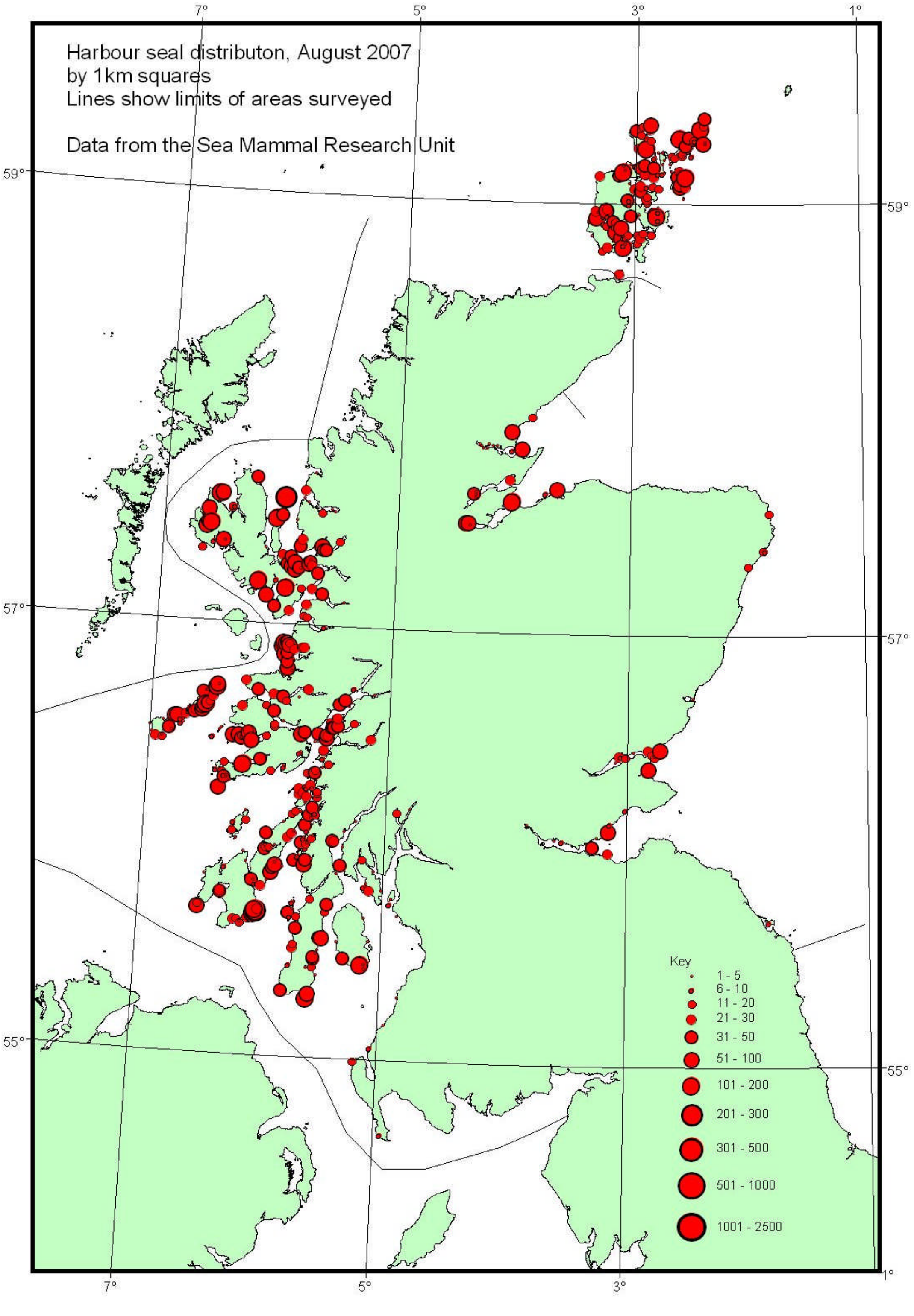

Figure 3. The number and distribution of grey seals around the coast of Scotland surveyed in August 2007. All areas were surveyed by helicopter using a thermal imaging camera. Lines delineate the areas surveyed.

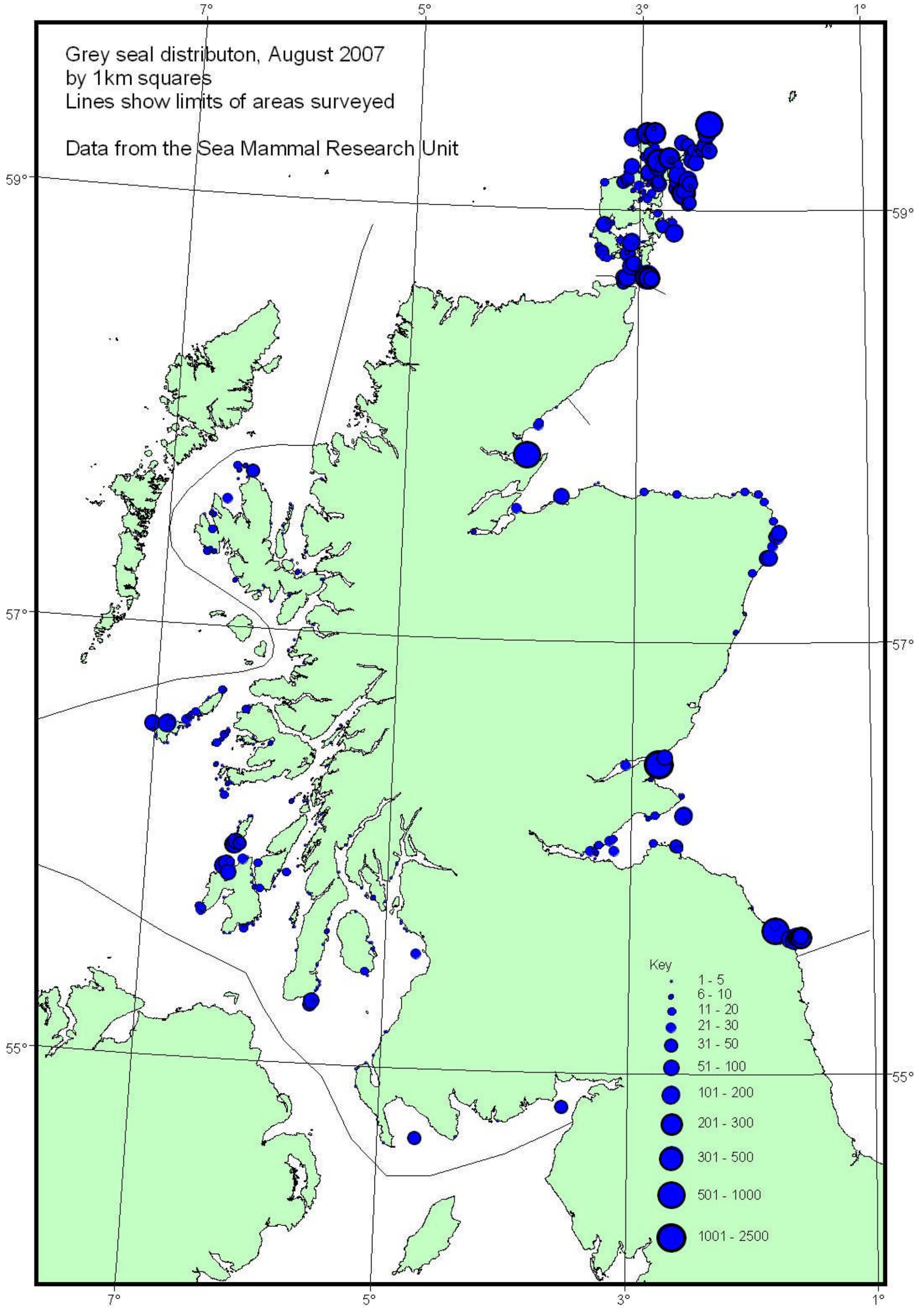

Figure 4. Trends in counts of common seals around Scotland. Data from the Sea Mammal Research Unit. Counts for the Outer Hebrides exclude North Uist and Benbecula as part of each island were not counted in 2006. The lower counts in 2007 are from recounts using digital images.

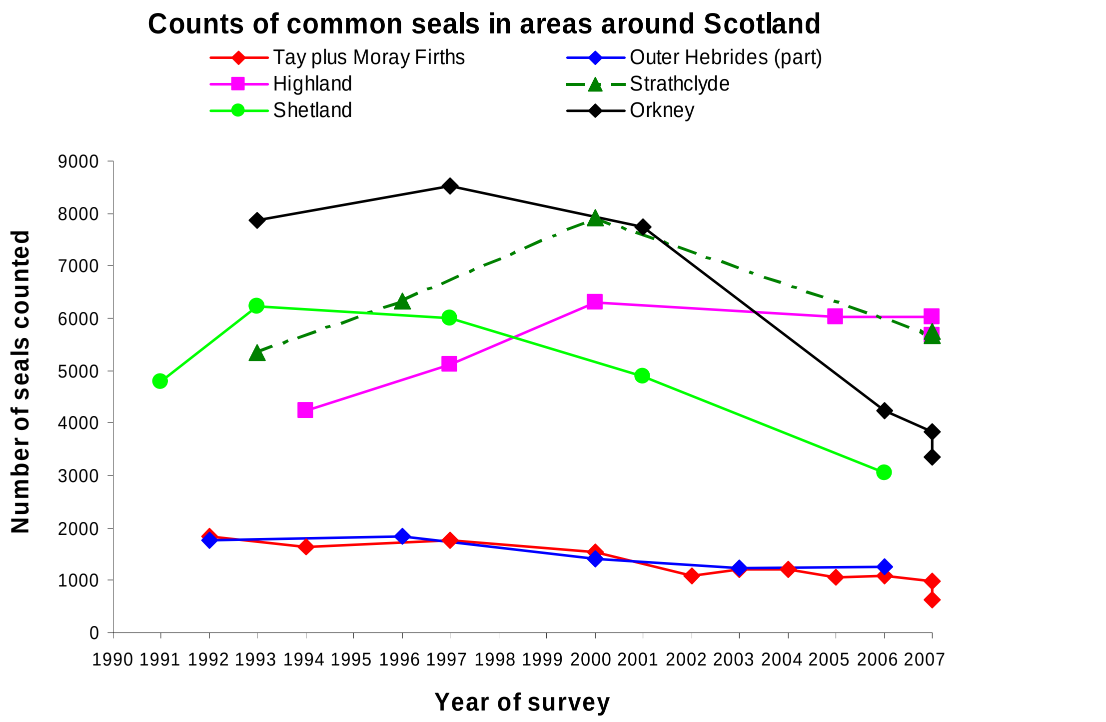

Figure 5. Trends in common seal numbers in the Moray since 1988. Seals were counted during their breeding season and during their moult by the University of Aberdeen's Lighthouse Field Station (LFS, Inner Firth) and more recently by SMRU (Inner Firth + Finhorn and L Fleet; Outer Firth).

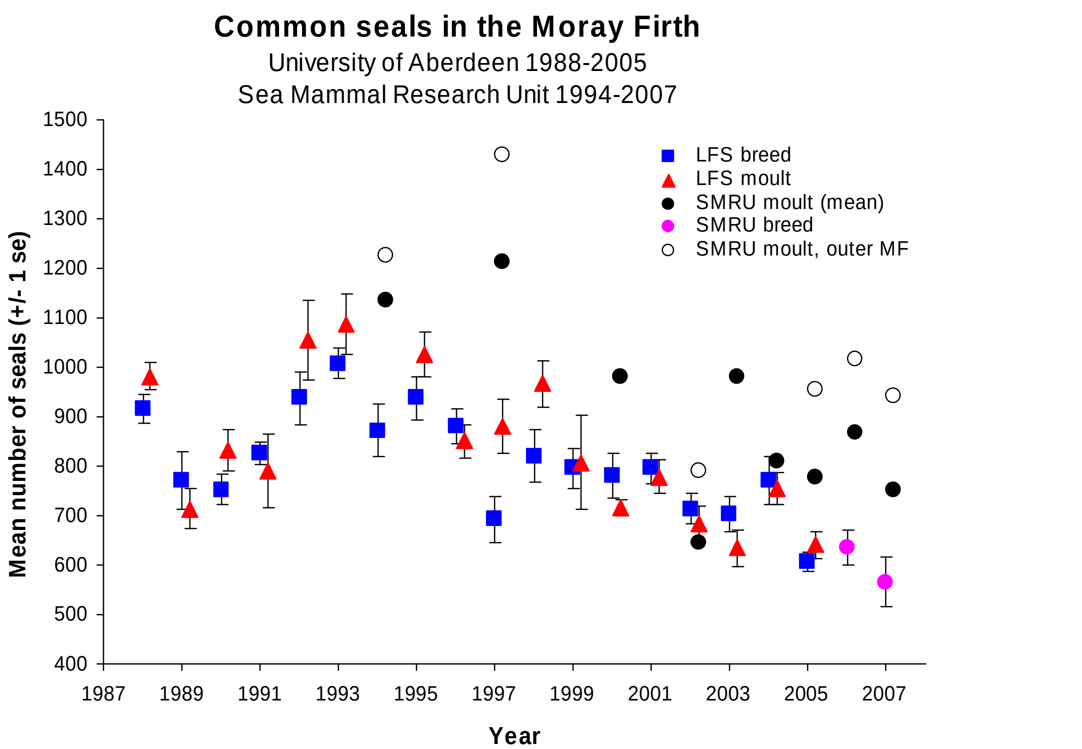

Figure 6. The number of common seals counted in areas within the Moray Firth by the Sea Mammal Research Unit, 1992-2007.

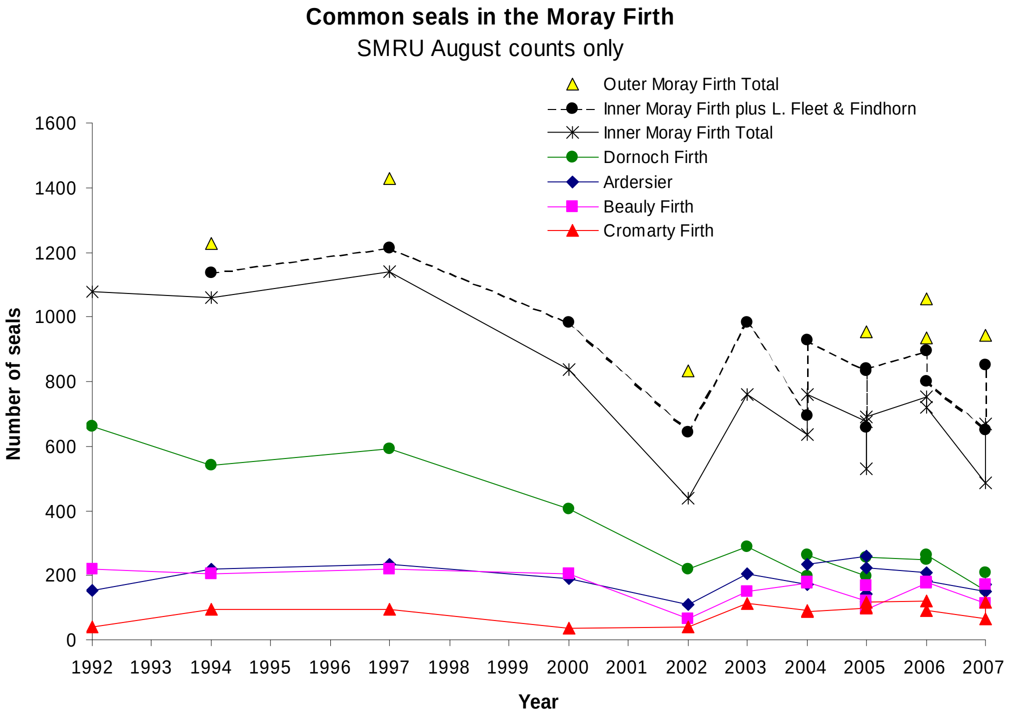

Figure 7. The number of common seals counted in the Firth of Tay by the Sea Mammal Research Unit, 1990-2007.

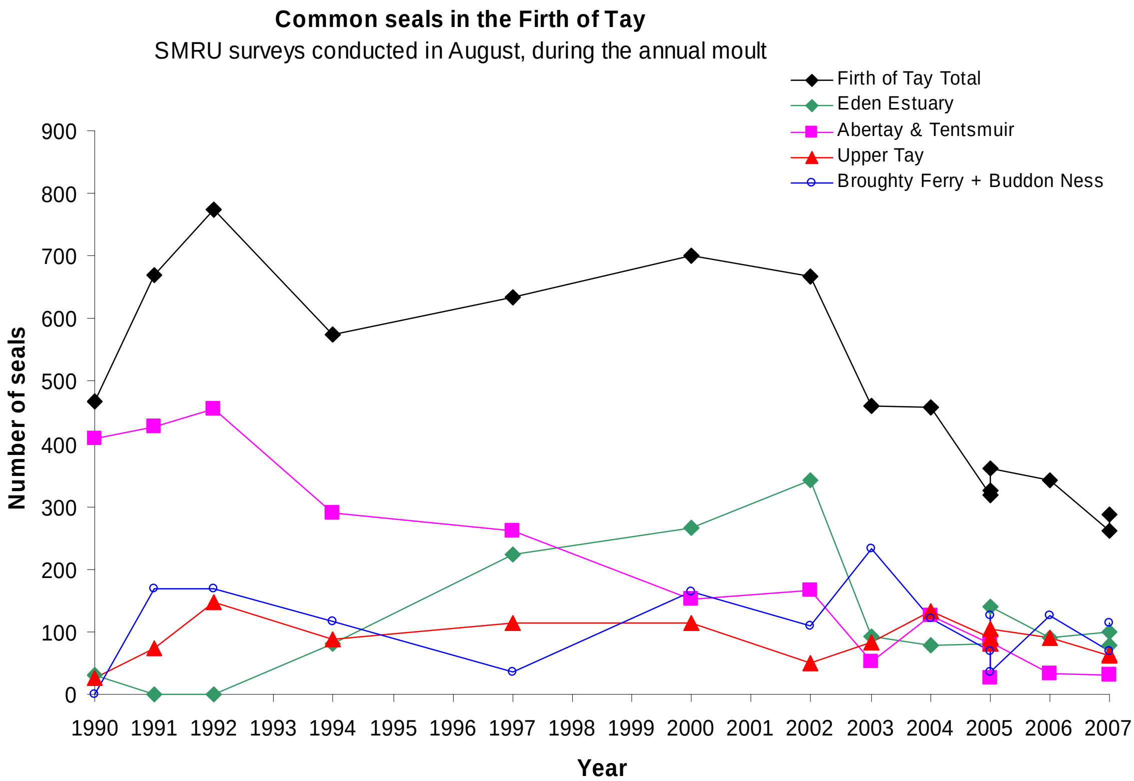

Figure 8. Counts of common seals in The Wash in August, 1967 - 2007. These data are an index of the population size through time. Fitted lines are exponential growth curves (growth rates given in text).

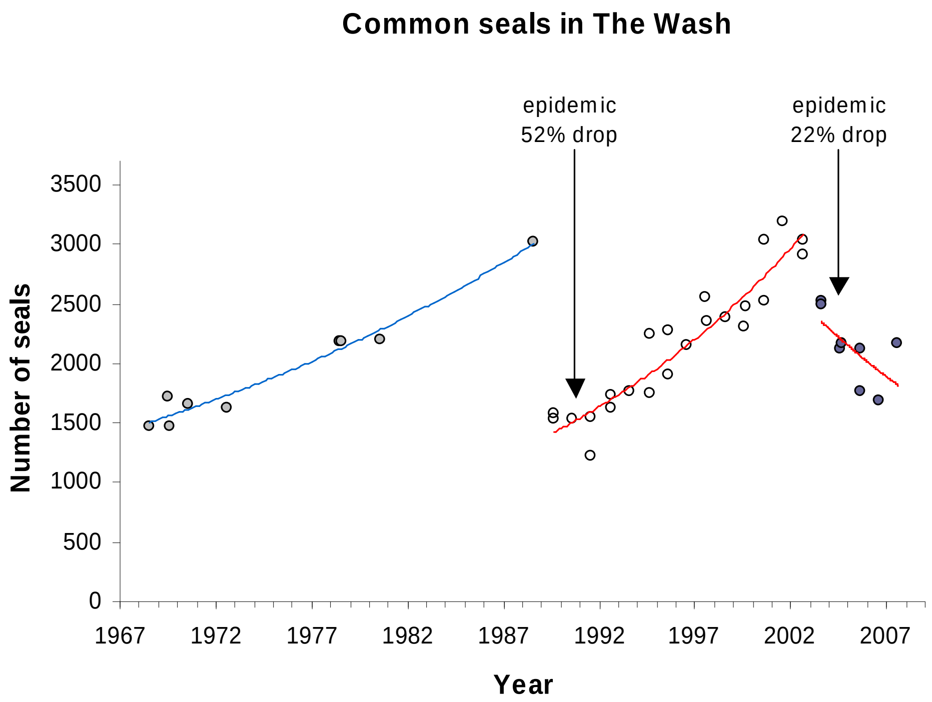

Table 1. Minimum estimate of the UK common seal population from the most recent regional surveys.

Region	Year of survey	Current estimate	Previous estimate (year of survey)
Shetland	2006	**3,021**	**4,883** (2001)
Orkney	2007	**3,379**	**4,256** (2006)
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, 2007	**800**	**1,056** (2005)
Highland West (Cape Wrath to Appin, Loch Linnhe)	2005, 2007	**5,109**	**4,396** (1996, 1997, 2000)
Strathclyde West (Appin to Mull of Kintyre)	2007	**4,732**	**6,702** (2000, 2005)
Strathclyde, Firth of Clyde (Mull of Kintyre to Loch Ryan)	2007	**811**	**581** (2005)
Dumfries & Galloway (Loch Ryan to English Border at Carlisle)	2007	**23**	**42** (2005)
Grampian (Montrose to Nairn)	2007	**102**	**113** (2005)
Tayside (Newburgh to Montrose)	2007	**166**	**101** (2005)
Fife (Kincardine Bridge to Newburgh)	2007	**215**	**445** (2005)
Lothian (Torness Power Station to Kincardine Bridge)	2007	**55**	**104** (2005)
Borders (Berwick upon Tweed to Torness Power Station)	2007	**0**	**0** (2005)
Central (Upper Forth)	2007	**1**	**0** (2005)
TOTAL SCOTLAND	**2005-2007**	**20,035**	**23,996**
Blakeney Point	2007	**550**	**719** (2006)
The Wash	2007	**2,162**	**1,695** (2006)
Donna Nook	2007	**214**	**299** (2006)
Scroby Sands	2006	**71**	**64** (2004)
Other east coast sites	1994, 2000, 2003	**225**	
South and west England (estimated)		**20**	
TOTAL ENGLAND		**3,242**	
TOTAL BRITIAN			
TOTAL NORTHERN IRELAND	2002	**1,248**	
TOTAL BRITAIN & N. IRELAND			
TOTAL REPUBLIC OF IRELAND	2003	**2,905**	
TOTAL GREAT BRITIAN AND IRELAND		**27,430**	

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

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	15 Aug 2007[1]	24 Aug 2007
Ardersier	154	-	221	234	191	110	205	172	232	260	143	195	224	210	184	150	173
Beauly Firth	220	-	203	219	204	66	151	175	180	119	169	-	94	174	178	115	170
Cromarty Firth	41	-	95	95	38	42	113	90	86	98	101	-	118	119	93	67	118
Dornoch Firth (SAC)	662	-	542	593	405	220	290	199	262	199	118	-	256	249	264	153	209
Inner Moray Firth Total	**1077**	**-**	**1061**	**1141**	**838**	**438**	**759**	**636**	**760**	**676**	**531**	**-**	**692**	**752**	**719**	**485**	**670**
Findhorn	-	-	*58*	*46*	*111*	*144*	*167*	*0*	*98*	*90*	*58*	*148*	*74*	*63*	*68*	*82*	*94*
Dornoch to Loch Fleet	-	*16*		*27*	*33*	*62*	*56*	*58*	*70*	*68*	*70*	-	*76*	*79*	*53*	*85*	*87*
Loch Fleet to Dunbeath	-	*92*		*214*		*145*	-	-	-	-	-	-	*113*	*163*	*137*		*90*

[1]Thermal imaging survey

Table 3. Numbers of common seals in the Firth of Tay during August. See Figure

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	4 Aug 2007	7 Aug 2007[1]
Eden Estuary	31	0	0	80	223	267	341	93	78	81	95	139	90	99	79
Abertay & Tentsmuir	409	428	456	289	262	153	167	53	126	80	26	82	34	32	30
Upper Tay	27	73	148	89	113	115	51	83	134	90	80	104	91	62	64
Broughty Ferry & Buddon Ness	0	169	169	117	35	165	109	232	121	68	125	36.	127	68	114
Firth of Tay Total	**-**	**670**	**773**	**575**	**633**	**700**	**-**	**461***	**459**	**319**	**326**	**361**	**342**	**261**	**287**

[1]Thermal imaging survey

[2]In August 2003 low cloud prevented the use of vertical photography; counts were from photographs taken obliquely and from direct counts of small groups of seals.

Table 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	8/8 12/8	11/8	2/8 11/8	1/8 16/8	8/8	6/8 12/8	5/8 15/8	2/8	2/8 8/8	7/8 14/8	3/8 13/8	4/8 12/8	4/8	11/8 12/8	9/8 10/8	6/8 14/8	09/8	15/8	3/8
Year	**1988**	**1989**	**1990**	**1991**	**1992**	**1993**	**1994**	**1995**	**1996**	**1997**	**1998**	**1999**	**2000**	**2001**	**2002**	**2003**	**2004**	**2005**	**2006**	**2007**
Blakeney Point	701	- 307	73	- -	- 217	267	- 196	438 392	372	250 371	535 738	715 602	895 disturb	772	346 631	399	577 715	741 677	719	550
The Wash	3087	1531 1580	1532	1226 1551	1724 1618	1759	2277 1745	2266 1902	2151	2561 2360	2367[1] 2381	2320 2474	2528 3029	3194	3037 2916	2529 2497	2126 2167	1768 2124	1695	2162
Donna Nook	173	- 126	57	- -	18 -	88	60 146	115 36	162	240 262	294 201	321 286	435 345	233	341 -	231	242 346	372 470	299	214
Scroby Sands	-	- -	-	- -	- -	-	61 -	- 49	51	58 72	52 -	69 74	84 9	75			49 64		71	
The Tees	-	- -	-	- -	- -	-	- 35	- -	-	- -	- -	- -	- -	-	-		- -	-	-	
Holy Island, Northumber-land	-	- -	-	- -	- -	-	13	- -	-	12[2]	- -	- -	10	-	-		- -	17[2]	-	
Essex, Suffolk & Kent	-	- -	-	- -	- -	-	- -	90 -	-	- -	- -	- -	- -	-	- 72	190	- -	101	-	

[1] One area used by common seals was missed on this flight (100 – 150 seals); this data point has been excluded from analyses
[2]Holy Island surveyed by helicopter using a thermal imaging camera.

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

Mark-recapture data, individual covariates and the estimation of life-history parameters for grey seals (*Halichoerus grypus*)

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Summary

Annual capture-recapture data were obtained for individual grey seals (*Halichoerus grypus*) at the Isle of May grey seal colony. Animals were identified using brands or flipper tags during long-term observational studies between 1987 & 2006. Bayesian methods were used to parameterise mark-recapture models, allowing for the effect of individual covariates on life history parameters.

Support was found for a model in which recapture probability was given by the product of two probabilities: an underlying mark-dependent recapture rate, and a mass-dependent term. This term can be interpreted as the probability that a seal whose mass in measured in a given year attends the colony in the following year. Further, because the breeding status of 'absent' seals was imputed during the Bayesian analysis, an estimate of overall female fecundity was obtained.

Introduction

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. The long term data sets from the grey seal (*Halichoerus grypus*) breeding colony at the Isle of May offers a unique opportunity to study the effect of characteristics of individual animals on life history. There are 2 important motivations for investigating such effects:

1. The biology of marine mammals is intrinsically interesting[1]
2. It may be possible to make inferences, based on mass-measurements made on seals that are observed at the colony, as to the breeding status of those seals in years when they are not observed (and possibly are not present). This is of considerable interest in informing population dynamics models of the grey seal population in general.

Here we present some initial results of a mark recapture modelling study. The relationships between individual survival and mass, and between recapture probability and mass, are investigated. For the purposes of developing this methodology a simple model for the relationship between the masses of an individual in successive years, and the effect on mass of breeding status, is assumed. An estimate of overall female fecundity is obtained.

Methods

1. Field Work

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. Regular daily surveys of all animals were made during the time that workers were present during the breeding season. New animals were marked, and re-sightings of previously marked animals were noted. The breeding status of animals was also recorded when this was known. Some animals were captured and measured, and the values of individual covariates such as mass were recorded. However, mass measurements could not be made for all those animals present, and no mass measurements could be made for animals that were not sighted in a given year. For some of the observed animals, it was not possible to determine breeding status, and it was never possible to observe breeding status for un-observed animals. Therefore covariate data for some individuals in some years were missing.

134 individual animals were included in the study. Each animal was observed and had its mass recorded on one or more occasions.

2. Analysis

In order to explore the relationship between life history and individual covariates, open population mark recapture models were fitted using Bayesian methods in order to deal with the problem of missing covariate data.

A simple formulation for the likelihood of the observed data based on the Cormack Jolly Seber (CJS) model where I individual seals are studied over T years, would be:

Box 1[2]

$$\prod_{i=1}^{N}\left(\prod_{j=L_i}^{J_i}\phi_{i,j}\,p_{i,j}{}^{x_{i,j}}(1-p_{i,j})^{(1-x_{i,j})}\right)\chi_{i,k_i} \qquad (1)$$

where

N is the number of seals in the study, which covers T years in total.

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

$\phi_{i,j}$ is the apparent survival for seal i in year j.

$p_{i,j}$ is the probability that seal i is re-sighted in year j

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

$\chi_{i,j}$ is the probability that a seal i is not seen again after year j

J_i is the final year that individual i is observed, and L_i is the first year it is observed.

$\chi_{i,j}$ can be calculated iteratively as follows:

$$\chi_{i,j} = \phi_{i,j+1}(1-p_{i,j+1}) + (1-\phi_{i,j+1})\chi_{i,j+1}$$
$$\chi_{T} = 1$$

Tag loss is expected to reduce the apparent survival of animals that are marked with tags. If tags are lost with annual rate γ then we expect the survival rates to be related as follows:

$$\phi_T = (1-\gamma)\phi_B \qquad (2)$$

where T refers to tagged seals, and B refers to branded seals.

In a previous analysis of this data set[2], CJS models were fitted in order to estimate colony-level estimates of survival and fecundity. The DIC statistic was used to select from the candidate models. The results suggested that tag loss and time-dependence in recapture probability were factors that should be included for the Isle of May data.[3] This model structure was then used as a starting point in the development of the covariate-based models.

Possible covariate-dependence in capture probability and survival probability:

1. Recapture probability $p_{i,j}$ for a seal i in year j carrying mark type $\mu_{i,j}$ was modelled as a product of two probabilities:

$$p_{i,j} = w_{\mu_{i,j}} u_{i,j}$$

$$w_{\mu_{i,j}} = Pr(observed \mid present)$$

$$u_{i,j} = Pr(present)$$

$w_{\mu_{i,j}}$ represents the probability that animal i in year j carrying mark type μ is seen, given that it is present, and the term $u_{i,j}$ represents the probability of presence (the 'attendance probability').

$$u_{i,j} = \frac{e^{\alpha_j+\beta m_{i,j-1}}}{1+e^{\alpha_j+\beta m_{i,j-1}}} \qquad (3)$$

Where α_j is a time-dependent parameter and β a time-independent parameter.

2. Survival probability $\phi_{i,j}$ was modelled as a logistic function of female mass in year *j-1*:

$$logit(\phi_{i,j}) = \rho + \kappa m_{i,j-1} \qquad (5)$$

Where ρ and κ are coefficients to b estimated.

The mass of an individual animal in year j was assumed to be related to the mass in year *j-1*. A naïve model for the process of weight gain assumed the that net weight gain during foraging was on average likely to equal the net loss during parturition and lactation and that this weight gain/loss could be represented by a single parameter τ. Therefore when an animal did not reproduce during a given year, a corresponding weight gain of τ was expected in that year. If $q_{i,j}$ is an indicator variable which takes value 1 if a pup was born to seal i in year j and 0 if no pup was born in that year, then the expected value of m could be estimated from the value of m in year *j-1* as follows:

$$\hat{m}_{i,j} = m_{i,j-1} + \tau - q_{i,j}\tau \qquad (6)$$

Observed values and predictions were assumed to be related according to a Normal distribution so that

$$m_{i,j} \sim N(\hat{m}_{i,j}, \sigma^2) \qquad (7)$$

Where the parameter σ was estimated during model-fitting.

The value of $q_{i,j}$ was not always known, e.g. when an animal was not observed in a given year, possibly because it was absent from the colony due to temporary migration. In the data set, these 'unknown breeding states' were recorded as -1. The use of Bayesian methods made it possible to impute the 'missing' values of covariate data (breeding state and mass).

An estimate for the net fecundity of the seals in the study was then obtained, given that all breeding states could then be treated as known, by dividing the total number of pupping events by the total number of years for which animals were in the study. Note that this estimate takes account of years for which seals were in the study but were unobserved, including those years in which animals may have been absent from the colony. It therefore provides an estimate of fecundity for the females in the study whether they were present at the colony or elsewhere.

Results

Initial model-fitting produced estimates for parameter κ in the logistic expression for ϕ with 95% credible intervals that included 0 (95% CI = (-0.8,0.6)): therefore, we concluded that there is no evidence in this data that ϕ depends on mass, and adopted a simplified model in which ϕ was held constant (i.e. survival was independent of both mass *m* and year *j*). The mean value of ϕ was then 0.963 (95% CI (0.947, 0.981)).

Credible intervals for β, the mass-dependent term in the logistic expression for *p*, indicated it was distinct from zero. The estimate (the mean of the posterior distribution) for β was 0.418 (95% CI = (0.154, 0.615)). Plots of the relationship between normalised mass and attendance probability based on estimates of β and α are shown in Figure 1 for years 1 and 11 of the study.

Figure 1: The probability of attendance vs normalised mass for 1987 (upper) and 1997 (lower). Black line represents the relationship based on mean parameter values from the posterior distribution. Grey lines are constructed based on random draws of parameters from the Markov chain.

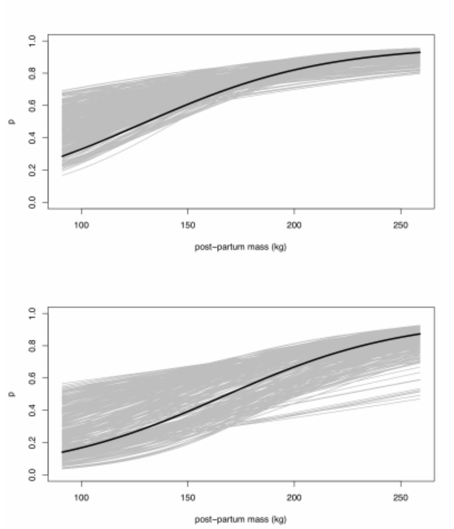
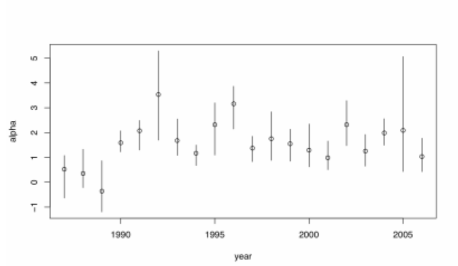


Figure 2 shows the time-dependence in parameter α.

Figure 2: Estimates of α, the time-dependent logistic parameter for attendance probability. 95% confidence intervals are shown.



The posterior mean value of w_{brand} was 0.9622 (95% CI = (0.905,0.977)) and for w_{tag} was 0.634 (95% CI = (0.519,0.770)).

The posterior mean of τ was 0.100 (95% CI = (0.004, 0.234)). The mean value is equivalent to a mass of 0.28kg.

The posterior mean for σ was 0.658 (95% CI = (0.624, 0.694)).

Posterior mean tag loss rate for γ was 1.90% per annum, (95% CI = (0.1%, 5.5%)).

Based on observed and imputed breeding status for the time interval over which individual seals were in the study, the posterior mean fecundity rate was 0.84 (95% CI = (0.82%, 0.85%)) which is somewhat lower than indicated by earlier studies[4].

Discussion

This work is still under development, but initial results suggest there may is sufficient information in the data to inform our understanding of seal breeding behaviour.

Intuitively, we expect that mass should be an indicator of future survival in breeding females: in particular it seems obvious that females of very low mass might have poor survival prospects. However we do not find evidence for this, possibly due to a lack of power in our methods/data to detect a true effect.

There is evidence for a positive relationship between *p* and mass. It seems unlikely that the re-sighting process itself is strongly influenced by changes in mass. However the probability of attendance at the breeding colony in a given year might plausibly be related to female mass in the previous year if (a) the probability of breeding is related to mass and (b) attendance is positively correlated with breeding. To model fecundity explicitly in terms of mass therefore seems a logical next step in the development of the model.

Estimates of α_j, the time-dependent logistic coefficient for *p*, show considerable overlap between years but some years that are distinctly different, e.g. 1989. This is consistent with previous findings that, at the whole-colony level, recapture probability for the seals in the study is time-dependent. However it should be noted that the term w_μ (mark-dependent re-sighting probability) takes no account of observer effort, which may be a important factor in the determining the true probability for a marked animal that is present during the breeding season[3].

The tag loss estimate of 1.8% appears reasonable, and consistent with previous double-tagging studies of pup recruitment.

Ongoing and future work

The following are aims for future work:

1. Develop the model for the relationship between individual mass and breeding status, making use of more realistic biological ideas.
2. Incorporate the existing mark-recapture data set for North Rona within the same analytical framework, and perform an integrated analysis allowing for the possibility of site-dependence in parameters.
3. Explore the effect of further individual covariates e.g. body composition on the life histories of females.
4. Multi-state models have been parameterised for this data set, dealing with animals that carry multiple marks. The possibility of non-independent tag-loss for double-tagged animals is taken into account. In order to avoid possible biases it may be helpful to incorporate this multi-state approach into the covariate models in future.
5. 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[5].

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D. Thompson

Report of SMRU workshop: research priorities for investigating the harbour seal population decline.

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Attendees: D Thompson, L Cunningham, C Duck, M Fedak, J Gordon, I Graham, K Grellier, A Hall, P Hammond, J Harwood, M Lonergan, B Mackey, J Matthiopoulos, S Murphy, S Northridge, R Sharples, S Smout, C Sparling, M Walton, A Winship.

Background

Recent aerial surveys of the harbour seal population in the Northern Isles and the UK east coast have produced lower counts than previously. The apparent decline is large and may have serious implications for conservation and management.

With the limited funding that is likely to be available to address these issues it is important that we try to develop a coherent research programme. This workshop was designed to begin this process.

We started with a set of obvious and simple questions:

1. Is the perceived decline real?
2. Is the decline continuing?
3. What are the likely proximate causes? Can we identify the main contender/s?
4. What are the likely ultimate causes? Can we identify the main contender/s?
5. Can we prioritise the work packages required?

Is the perceived decline real?

There are two aspects to this:

Do the numbers indicate a decline, i.e. is the recent drop in the Northern Isles significant and/or are there any indications of trends?

The results of the aerial surveys of Orkney, Shetland, Outer Hebrides and the UK east coast were presented and discussed.

- If we consider the counts up to 2002 as just random samples of stable populations, the 2006 counts in Orkney and Shetland are significantly lower than previous counts. The subset of the Hebridean population was not. However, if a trend is fitted, all three areas indicate a possible gradual decline since the late 1990s. The available data do not allow us to say if there has been a step change or a gradual decrease since 2001.
- Similar pattern seen in the Tay, some debate about the possibility that the number of seals in the Firth of Forth has increased slightly, but not enough to account for the observed decline. The important point here is that the decline in the Tay has been gradual since 2000.
- Similar pattern seen in the Moray Firth but pre-dates the decline in the Tay. Again a gradual decline.
- Continued decline in the Wash. Increasing until the 2002 epidemic, 22% decline then and continued 12-13% pa decrease since 2003. Interestingly, no sign of a slowdown in the Wadden Sea population that has been increasing at around 12% pa since 2003

CONCLUSION is that the population survey data indicate a widespread decline in harbour seal populations from Shetland to the Wash, and possibly in the Outer Hebrides. The decline has been gradual in all three locations where populations have been surveyed annually, but we cannot rule out the possibility of a step change in Orkney and/or Shetland.

Is it likely that an artefact of the survey methodology or the seals' behaviour could account for the observed changes in counts without a population change?

We had a wide-ranging discussion of the relationship between the annual moult counts and the total population.

- Survey method was clearly identical to previous surveys; all were conducted within the normal 2 hour window either side of LW. No systematic difference in terms of the time of day, stage in tidal cycle or direction of the survey track around the islands. Wash, Tay and Moray Firths surveys used same methods and same operators throughout the time series.
- Implications of changes in timing of the surveys relative to LW discussed with reference to Louise Cunningham's work around Skye. Particular tidal patterns and the possibility of movement between haulouts means that the results are likely to be locally important, but less so in context of wide-ranging surveys. Thought unlikely that such local effects could have caused changes of the observed magnitudes.

Changes in timing of peak counts during the moult have been observed in European harbour seal populations. These have been shown to be primarily due to changes in age structure resulting from differential mortality in disease epidemics. Is this a likely cause of the reduced counts?

- Decreased counts of the observed magnitude could result from timing changes. Use '88 PDV data to obtain plausible estimates of the possible biases.
- To produce the required changes in age/sex structure would almost certainly require a major source of differential mortality, to date only seen in the in the PDV epidemics that removed half the population. Use '88 PDV data to estimate the scale of population change required to produce such effects.
- If same factor is invoked for each region it must have happened gradually to account for the gradual declines at the east coast sites. Check other sources of information in UK for indications of changes in breeding or moult timing e.g. John Watkins in Wash.
- Data from the regularly spaced counts throughout the breeding and moult seasons in the Moray Firth are not thought to indicate a systematic change in the timing of the moult. This data should be re-examined in detail.

General feeling was that it was unlikely that timing changes would have caused the decreased counts. If timing was responsible it would indicate a huge shift in age and sex structure that would itself be a major ecological effect.

Changes in patterns of haulout behaviour could cause the observed shifts if, for example, reduced food availability caused seals to spend more time offshore and reduce the proportion of time ashore.

Contra-indications: moult count; so at the time of year when animals have a direct physiological need to haulout. Moult is slowed or prevented by staying in water (observations from grey seals in pool).
All studies to date indicate approx 60-70% population hauled out during early August. To produce observed changes would require seals to spend between 60% and 100% longer foraging. This would indicate a population under extreme food stress.

Movement There have been large scale movements/redistributions of harbour seals between adjacent areas within regions such as Orkney and the Wash, but no suggestions in the literature of re-distributions over larger geographical scales. All populations on the UK east coast have declined, and the nearest large population in the Outer Hebrides has not shown any sign of an increase. There are also no reports of large increases in numbers of seals in the inner Hebrides or along the North or West coasts. A redistribution on this scale (around 7-12000 seals) would have been noticed. There is simply nowhere for the Orkney and Shetland seals to have gone.

We cannot rule out a re-location of seals from the southeast of England to the Wadden Sea, where the large population is increasing as rapidly as the English population is declining.

CONCLUSION it is highly unlikely that the observed declines are the result of either a behavioural change in proportion of time spent at haulout sites or a redistribution of seals around the UK.

Unlikely that the age structure could have been perturbed to such an extent that the timing of moult would shift enough to account for observed decreases, unless there had been a major mortality of some component of the population.

Future survey methods

First priority from a management perspective is to determine whether or not the decline is continuing. There will therefore be strong political pressure to conduct surveys next year for direct comparison with the 2006 results.

Major problem of low statistical power. 10% p.a. change is very difficult to detect with the current low level of survey effort. We have estimates of count variability from detailed observations in Moray Firth, the Wash and Orkney. These and targeted repeat surveys should be used next year to increase the power to identify the short term trend.

Moult V Breeding Season

Discussed the advantages and disadvantages of switching to breeding season surveys of harbour seals for population monitoring (see later for pup's as indicator of fecundity problems).

- Provide a more sensitive indication of current population status,
  - but in the absence of a population index we would be in the same position we are with the grey seal population.
  - comprehensive pup production estimates require 3-5 counts each. Current cost constraints restrict us to a single count every 5 years. Prohibitively expensive for annual monitoring for either Orkney or Shetland.
- It may be possible to define sub-regions within these archipelagos that could be monitored from land to obtain pup production estimates.
  - previously rejected as a strategy for obtaining population indices in the moult because of large scale local re-distributions.
  - Examine historical data from breeding season surveys to check feasibility of indicator site study.
- It would be much cheaper to obtain pup production estimates for the east coast sites for which there are already annual moult surveys.
  Follow up on funding to extend initial Wash breeding season surveys

SUMMARY

We suggest that the observed decrease in counts of harbour seals indicates a widespread and significant population decline.

For political and scientific reasons it is imperative that we conduct repeat surveys of the areas showing declines and of adjacent areas for comparison. We should develop a modified repeat survey (reduced coverage?) to provide estimates of the variability of the counts in rocky shore habitats to increase the power of a single synoptic census next year.

It is essential that any funding body is aware that a single count may not produce a definitive answer and plans should be put in place to increase the intensity of survey effort over the next 10 years. Also we should remember that there are similar requirements for grey seal population monitoring. These may be addressed simultaneously thereby improving the cost benefit calculations.

POSSIBLE CAUSES

Split into two types:

Proximate causes. Reduction in population has to result from reduced fecundity or reduced survival of one or more components of the population.

To predict population trends in the short to medium term we need to identify the proximate causes and obtain information on the intensity of the effect.

Ultimate causes. Although it may be possible to manage the population to alter the proximate causes in some circumstances, it is unlikely to be successful in the long run without detailed knowledge of the factors causing a change in fecundity or survival. From a management (and political) perspective identifying these factors is essential.

N.B. it is clearly possible that different factors may be responsible for the declines in different regions and/or habitats. The marine and terrestrial environments of Northern Shetland are very different to those of Norfolk and the southern North Sea.

It is not clear that investigation of either set of causes should be given priority.

Understanding the proximate cause may help focus the search for ultimate causes, but conversely many of the potential ultimate causes could affect both fecundity and survival.

A major recommendation is that a sensitivity analysis be developed and carried out to investigate the scale of changes required to produce the observed effects. The initial suggestion is that this could be based on the type of framework developed for the Steller sea lion model. This would 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.

PROXIMATE CAUSES: FECUNDITY & SURVIVAL**.**

It was noted that absolute measures of these demographic parameters would be useful, but that comparative measures from populations of different status are the minimum requirement. It may not be necessary to obtain real values as long as biases can be held constant between sampling areas.

SURVIVAL.
Various versions and combinations of mark recapture and telemetry methods were discussed. It was generally felt that the entire range of techniques should be considered and should be used where appropriate to local circumstances. An attempt should be made to quantify direct anthropogenic mortality. Size class structure may be possibly determined from vertical air photos.

It was particularly interesting that adult survival estimates in part of the Moray Firth remained high (around 0.95) throughout the period of the general decline in the area.

At this stage we should simply state that we give high priority to an investigation of the patterns of survivorship in various harbour seal populations without tying down to any one method. A high priority should be given to investigating and assessing the available methods.

Methods considered included:
Pelage recognition from photo id studies: can provide robust estimates of survival and migration rates between area.

Application of marks, e.g. modified seal hats for pups and targeted surveys.

Application of telemetry. Modified (i.e. miniaturised) phone tags on pups or standard tags on adults. Long life flipper transmitters are being tested in Netherlands. Satellite tags etc. obvious synergy with foraging behaviour studies.

Application of implantable transmitters. Methods are being improved and used with some success in harbour seals in California.

All of these techniques are feasible, some with little or no development. All could be used to produce information on survival of various age and sex classes. All would also produce significant information on other aspects of their biology.

FECUNDITY
Various methods of estimating pregnancy rates were discussed; hormones in blood spot and/or faecal samples, targeted catching surveys to obtain blood samples, use of by-caught and deliberately killed seals to examine reproductive states and recent histories. Again, as with survival it was clear that the entire range of techniques should be considered and should be used where appropriate to local circumstances.
At this stage we should simply state that we give high priority to an investigation of the patterns of fecundity in various harbour seal populations without tying down to any one method. A high priority should be given to investigating and assessing the available methods.

Pup production estimates. Not withstanding what we said about it as a stand alone population census method, in conjunction with time series of population indices a series of pup production estimates will provide a sensitive index of current state and provide estimates of fecundity. After some time the data can also be used to produce estimates of survival from a sensible population n model. For some areas this would be relatively easy and cheap.

ULTIMATE CAUSES
It should be remembered that the declines may result from multiple factors and different factors may be acting in different areas.

The apparent absence of any apparent mass mortality events in Orkney or Shetland and the gradual declines elsewhere probably indicate that we are not dealing with a major disease event of the order of the PDV epidemics.

Moderate increases in annual mortality due for example to chronic disease, shooting, toxic algae, nutritional stress, predation etc could easily have gone un-noticed in all areas.

Some factors eg shooting predation can be excluded for some areas (e.g. Wash) but not others.

There is a wide range of possible causes. Investigating each would need a targeted project. For example:.

General health/pollutant burdens. SMRU has a set of samples collected over the last 10 years including a lot during the decline period. It should be possible to conduct a range of screening analyses to test for various diseases, immune system function, pollution burdens and possible stress hormones. This may also supply some information on fecundity. **Because of the availability of the samples and the low cost, these screening studies should be given a high priority. Additional sampling study should be considered.**

Diet. Very little information at all from Scottish harbour seals. Apart from east coast sites nothing of any recent relevance. The coincidence of a general decline at a time when sea bird populations are showing repeated breeding failures due to poor food years means that we should give priority to assessing harbour seal diet. Similar lack of recent information for English populations. Clear priority for some of the funding bodies, identified as a priority before the population decline was noticed and still seen as a priority.

Important for assessing possible competition with grey seals, other marine predators and fisheries. **Should be targeted to allow such comparisons, i.e. should be geographically and temporally co-ordinated with other species and fisheries studies where possible.**

Energetics. Young harbour seals may be close to a thermal limit. Possible parallels with Steller where nutritional stress on juveniles probably the main cause. Even healthy pups are not thermo-neutral below about 8 degrees, so food availability would be critical. Poor food resources could leave them vulnerable after weaning. Can use pool to assess the energetic requirements of size range of harbour seals, concurrently with the diet studies.

Growth & Condition. Comparisons of length at age and body condition in areas of differing status. i.e. Age length from tooth ages and body measurements. May provide comparative information on condition in areas of differing status.

Spatial overlap with grey seals (and other marine predators/fisheries). Interesting observation that harbour seals prey heavily on sand eels during the season when grey seals are mostly absent for breeding. Relatively simple to design a telemetry study to compare habitat useage apparent preferences of the two seal species in selected regions.

Anthropogenic Mortality. Attempts to quantify it. We should capitalise on good relations with fisheries and aquaculture. Serious effort should be put into collecting by-caught and deliberately targeted seals of both species. Samples obtained would be invaluable for many of the above studies. Low cost, long-term moderate effort.

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The prevalence of anti-leptospira, toxoplasma and phocine distempter virus antibodies in harbour and grey seals, 1991-2005

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1. Introduction

The exposure of animals to infectious diseases can be assessed from the prevalence of antibodies in their blood (serology). The geographical distribution and particularly the age-specific prevalence proportions can indicate whether diseases are likely to be endemic or epidemic within a population. However, it is not possible to distinguish past from recent exposure so this approach does have its limitations. Nevertheless in many mammalian species, particularly marine mammals, the absence of cases of disease or carcasses to examine means it is often the only way of determining the range of infectious agents circulating in the population.

Leptospirosis, toxoplasmosis and phocine distemper virus have all been reported among pinnipeds worldwide, being endemic (host adapted) and epidemic diseases in both otariid and phocid seals. In this paper we examine the prevalence proportions of antibodies to these major diseases in harbour (*Phoca vitulina*) compared to grey (*Halichoerus grypus*) seals and assess the potential contribution of these infectious agents to the observed decline in UK harbour seal abundance.

(a) Leptospirosis

Leptospira interrogans serovar pomona is a globally re-emerging disease that is endemic among California sea lions (*Zalophus californianus*) and periodic epidemics occur on an approximately 4-5 yearly basis (Calle et al. 2002, Lloyd-Smith et al. 2007). The disease causes renal failure and abortion in pregnant females. The peak seroprevalence in California sea lions is above 50%. In addition, the disease has been reported in Pacific harbour seals (Stevens et al. 1999) but prevalence data among European seals has, to our knowledge, not been reported.

(b) Toxoplasmosis

This disease is caused by the protozoa *Toxoplasma gondii*. It is frequently implicated in reproductive failure and abortion in sheep and can be transmitted to humans. It has a 2-stage life cycle. The single definitive host is the cat but mammals and birds are intermediate hosts in which *T. gondii* undergoes both sexual and asexual lifecycles. Antibody titres of >1:512 in sheep are considered positive for the disease itself. Exposure in marine species may be from oocytes shed by terrestrial hosts in sewage or agricultural runoff but the disease may also be naturally occurring or endemic in marine mammals.

The presence of anti-*toxoplasma gondii* antibodies have been reported from a wide range of marine mammals (Dubey et al. 2003) and toxoplasmosis has been diagnosed in Pacific harbour seals. A relatively large serological survey was carried out between 1995 and 1997 in Canadian phocid seals (Measures et al. 2004) including grey (n=112) and harbour seals (n=34). Antibody prevalence proportions were low at 9% for both these phocid species and titres were also low.

(c) Phocine Distemper Virus (PDV)

Phocine distemper is a disease of the respiratory and nervous systems caused by a morbillivirus known as phocine distemper virus. It has caused two major epidemics among European harbour seals in 1988 and 2002 (Harkonen et al. 2006) and is thought to be endemic in Arctic phocid seals (Duignan et al. 1997). In susceptible harbour seals it has a very high fatality rate and spreads rapidly, particularly in regions where large haulout sites occur. Grey seals are probably asymptomatic carriers (Hammond et al. 2005).

Serological surveys have been very useful in determining the proportion of the population that is likely to be susceptible between outbreaks (Thompson et al. 2002, Pomeroy et al. 2005) and studies in harbour seals after the 2002 epidemic found high variability in the regional prevalence proportions. Animals sampled from the west coast of Scotland had no titres and proportions ranged from 55% in the Wash, 40% in the Moray Firth and 30% in both Orkney and the Tay (n=100).

In all previous serological surveys, canine distemper virus (CDV) has been used as the antigen against which the antibody titres were measured. This is unlikely to have biased the results too much given the very close relationship between PDV and CDV. Antibodies against one will cross react significantly against the other. In addition, PDV is much more difficult to culture in the standard laboratory Vero cells used in the assay. However, in this paper we report the first results of anti-*PDV* antibodies in harbour seals sampled since 2003. This homologous assay has been developed at the Queen's University Belfast and is possible because of the recent availability of a cell line (SLAM cells) more suitable for the culture of PDV.

2. Methods

(a) Leptospirosis

Leptospira antibodies were analysed using the microagglutination test (MAT) at the Veterinary Laboratories Agency in conjunction with the Institute of Zoology. Serum samples were filtered in saline and transferred to microtitre plates where they were mixed with live antigen. The following 19 interrogans (pathogenic) serovars were tested: Canicola, Icterohaemorrhagia (the causative organism of Weil's disease), Ballum, Copenhageni, Pomona, Tarassovi, Grippotyphosa, Mozium, Australis, Bratislava Autumnalis, Sejroe, Mini, Bim, Bataviae, Zanoni and Javanic, Hardjo-prajito and Hardjo-bovis. Plates were incubated at 37^{0}C for 2 hours. The agglutination reaction was assessed using a phase contrast dark field microscope. Positive samples were then titrated to determine the level of antibody present against any given serovar. Serial dilutions of between 1:25 to 1:12,800 were used.

The serum samples screened were obtained from live harbour seals captured between 1991 and 2005 (n=122) in Orkney (n=17), the Moray Firth (n=83), Islay and Jura (n=5), Skye (n=9) and the Wash (n=8).

In addition, 46 serum samples from dead stranded harbour seals, whose carcasses were fresh and which were subsequently necropsied by the Institute of Zoology or that died during the 2002 phocine distemper virus epidemic, were also tested. Of these, 40 stranded in SE England, 5 in NE England and 1 in NW England.

Samples were also obtained from female grey seals captured during the breeding season on the Isle of May (2000-2001, n=41) and North Rona (2000-2001, n=20). In addition samples from live grey seals outside the breeding season were obtained from Ramsey, Bardsey and Hilbre Islands on the Northwest coast (2004, n=19), the Moray Firth (1992-1995, n=23), the Tay Estuary (2004, n=7), Brittany coast (199-2002, n=11), Coll and Tiree in the Outer Hebrides (2004, n=8) and Donna Nook in Lincolnshire (2005, n=9).

Samples from 23 stranded dead grey seals whose carcasses were sufficiently fresh (1992 and 2003, from England and Wales) were also analysed.

(b) Toxoplasmosis

Antibody titres against toxoplasmosis were measured at the University of Barcelona using a modified direct agglutination test with formalin fixed tachyzoites as the antigen. Sera were diluted from between 1:25 to 1:500.

Serum samples from 56 live captured harbour seals were analysed for toxoplasma antibodies. All sera were collected in 2003 from animals in Islay and Jura (n=5), the Moray Firth (n=15), Orkney (n=18) and the Tay Estuary (n=18).

In addition 47 grey seal sera from live captured animals were tested. Animals were captured between 1998 and 2004 in the Tay Estuary (1998, n=5), the Farne Islands (1999 n=8), Brittany (1999 and 2002, n=15) and Wales and the Dee Estuary (2004, n=19).

(c) Phocine Distemper

PDV antibodies were measured using a virus neutralization test (VNT). Dilutions of sera were incubated with a fixed amount of PDV and inoculated into SLAM cells. Following incubation for up to a week at 37^{0}C the wells were examined for the viral cytopathogenic effect (CPE), which occurs with the absence of neutralising antibody. The maximum titre is the dilution (or its reciprocal) at which the proportion of wells infected is reduced from four to two.

The number of animals sampled in each location is shown in Table 1. All samples were collected between 2004 and 2007 at various times of the year. In the Inner Hebrides and

Orkney 25 and 21 pups respectively were sampled as part of a first year survival study. All the other animals were adults.

3. Results

(a) Leptospirosis

Of the 123 live harbour seal serum samples analysed, 9 (7%) had positive titres against *leptospira interrogans serovar australis*. This was the only serovar that produced a reaction in any of the live sera tested. The geometric mean (GM) titre was 1:58. Positive samples were from the Moray Firth (5/17, 29%) and Orkney (4/17, 24%), and all positive samples were collected in 2003.

In the dead harbour seals, 10/46 (22%) were seropositive against one or more serovar. All of these animals had stranded during the 2002 PDV epidemic, 9 in SE England and 1 in NE England. All 10 had significant titres against serovars Bratislava and australis and 4 against autumnalis. The geometric mean Bratislava titre was 1:746, the australis GM titre was 1:238 and autumnalis GM titre was 1:35. There were 6 animals with very high titres (>1600) against Bratislava and a significant positive correlation between the Bratislava and australis titres (R^2=0.53).

Sera from a total of 157 live grey seals were also tested of which 62 (39%) were seropositive against *leptospira interrogans serovar australis* and 2 additionally against Copenhageni (GM titre 1:200). The Australis titres were significantly higher (GM 1:183) than in the live harbour seals. Thirteen animals were from Hilbre, Ramsey and Bardsey islands (68%), 4 from Donna Nook (44%), 26 from the Isle of May (63%) and 19 from North Rona (95%). The positive samples were collected between 2000 and 2005.

Three of the 23 dead grey seals were seropositive (13%) against serovar Bratislava (GM titre 1:317) and Australis (GM titre 1:800). One animal was also positive against serovar Autumnalis (titre 1:25). These positive sera were collected between 1997 and 2002 and all were stranded on the Welsh coast.

(b) Toxoplasmosis

Of the 56 harbour seal sera analysed, only 3 (5%) had low titres (1:25) against *Toxoplasma gondii*. These animals were from the Moray Firth, Orkney and the Tay Estuary respectively.

A number of animals in all the populations of grey seals sampled also had low titres (at 1:25 or 1:50); 3/5 (60%) from the Tay, 1/8 (13%) from the Farne Islands, 4/15 (27%) in Brittany and 3/19 (16%) from Wales and the Dee Estuary). The overall prevalence in grey seals was 23%.

Only one harbour seal from Orkney had antibodies to both leptospirosis (1:200) and toxoplasmosis (1:25).

(c) Phocine distemper

Although the sample size for the various regions was relatively small, overall 10 (17%) of the 63 adults screened had significant (probably protective) titres against PDV. The proportions varied by region and were highest in the Wash, where they were similar to the prevalences reported in 2003. The small number of animals sampled from the Tay and adults sampled from Orkney means that these proportions should be treated with some caution but overall only 4/43 (9%) adults from Scottish populations had protective antibodies.

Three of the pup samples were also seropositive, probably as a consequence of maternal transfer.

The frequency distributions of titres in those populations with seropositive animals (i.e. the Wash, the Tay and Orkney) are shown in Figure 1.

4. Discussion

(a) Leptospirosis

The prevalence of anti-leptospirosis antibodies in live harbour seals was low (9%) but interestingly all the positive animals were sampled in the same year (2003). The prevalence was higher in the dead harbour seals (22%) and these were all animals that stranded during the 2002 PDV epidemic. However, to our knowledge, no cases of disease have been reported. It is possible that there was some interaction between leptospira and PDV during the outbreak, in the same way that herpes virus is a prevalent secondary infection because of the immunosuppressive effects of PDV.

In grey seals the prevalence was much higher at 39% overall. The prevalence was greater in animals from the West coast of Scotland and was very high (95%) among the females breeding on North Rona. This high prevalence proportion suggests the disease could be endemic in this species in this region. The lack of sporadic epidemics (such as is seen in California sea lions), signs of renal lesions in dead animals or prematurely aborted foetuses in the populations, suggests that the organism may not be the serovars Bratislava or Australis, but some other unidentified type that is entirely host adapted. Further studies of this spirochaete are clearly needed in future.

(b) Toxoplasmosis

From the results presented here, this infection is unlikely to be a significant disease issue for UK seals. The prevalence proportions were low (as were the titre levels) although again the prevalence was higher in grey than harbour seals (5% in harbour seals and 23% in grey seals).

(c) Phocine Distemper

The prevalence of anti-PDV antibodies in UK harbour seals by region has fallen since the previous survey in 2003, testing the survivors of the 2002 outbreak. Overall the percent seropositive in adult Scottish harbour seals (9%) is now similar to that estimated prior to the 2002 epidemic (between 3-9%, Thompson et al. 2002). Although sporadic cases of PDV were reported among Scottish seals, there was no sign of a widespread outbreak. The Wash was the only region that saw a substantial epidemic in 2002 and the seroprevalence proportion in the adults appears to remain at around 50%.

In conclusion, the seroprevalence results presented here suggest it is unlikely that these infections have played a major role in the decline of UK and particularly Scottish harbour seals since around 1999. Although PDV did cause some mortality in the Tay and Moray Firth populations, very few carcasses washed ashore in the Northern or Western Isles. Since 2003 no cases of infection have been reported and antibody titres continue to decline as would be predicted from the epidemiology of the disease.

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6. Acknowledgements

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Table 1: Total number of adults and pups sampled in each region

	Inner Hebrides	Moray Firth	Northern Ireland	Outer Hebrides	Orkney	Skye	The Tay	Thames	The Wash	TOTAL
Adults	2	6	2	19	4	7	5	5	13	63
Pups	25	0	0	0	21	0	0	0	0	46
Total	27	6	2	19	25	7	5	5	13	109

Table 2: Number and percentage of animals that were seronegative and seropositive (titre > 1:20) in each region.

Titre	Inner Hebrides	Moray Firth	Northern Ireland	Outer Hebrides	Orkney	Skye	The Tay	Thames	The Wash	TOTAL
Negative	26	6	2	19	21	7	3	5	6	95
Positive	1**	0	0	0	4*	0	2	0	7	14
%	4%	0%	0%	0%	16%	0%	40%	0%	54%	13%

* 2 of these were pups
** this was a pup

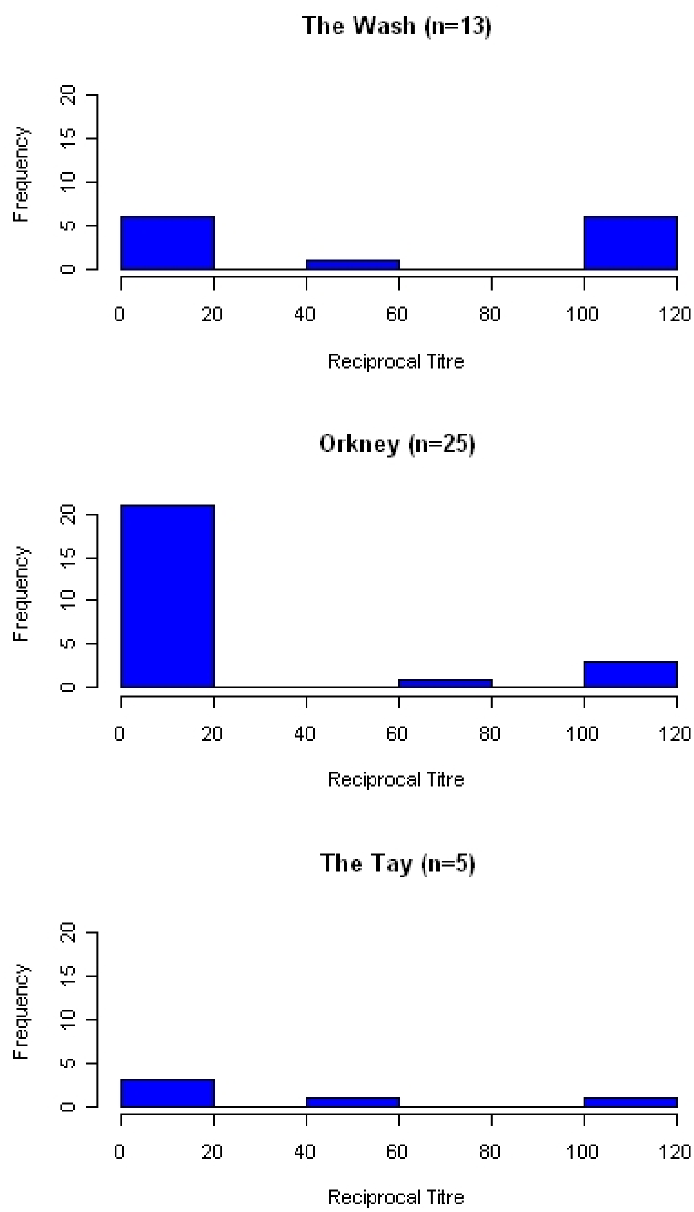

Figure 1 : Frequency distribution of anti-PDV titres in three populations of harbour seals with seropositive animals (reciprocal titre >20)

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Regional, annual and individual differences in blubber fatty acid composition at two grey seal breeding colonies in the UK.

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Summary

Blubber from breeding females in early lactation was used to assess annual, regional and individual variation in FA composition over six years in a decade. FA profiles collected from two widely separated UK colonies, North Rona (NR) and Isle of May (IOM), were clearly distinguished from each other in all years. At both colonies dramatic year-to-year changes were seen, but these occurred during 1996-1998 for IOM and 2004-2006 for NR. The first evidence in support of dietary consistency between years in individual seals is reported.

Introduction

Grey seals are important generalist marine predators, their prey includes gadoids, sandeels (Ammodytes spp.) and herring (Clupea harengus) (Hammond & Grellier 2006, Hammond & Harris 2006), which are also of commercial importance (Harwood & Croxall 1988). Fatty Acid Signature Analysis (FASA) has proved a useful tool for studies of the feeding ecology of marine organisms many FAs in the marine foodweb are transferred between organisms with little or no modification, and that dietary FAs are deposited in the lipid stores of predators relatively unchanged (Iverson 1993). Despite the relative lack of FA modification, the overall FA composition of blubber can differ significantly from that of the diet as a result of the selective metabolism, uptake and release of specific FAs (Walton et al. 2007). Nevertheless, blubber FAs can be used successfully to observe relative variations in the diet of marine mammals, and FA studies of geographical and temporal variations in seal diet, for instance between populations or within populations over time, have been reported widely (Kakela et al. 1993, Smith et al. 1996, Iverson et al. 1997, Walton et al. 2000, Moller et al. 2003, Walton & Pomeroy 2003, Beck et al. 2005, Budge et al. 2006, Walton et al. 2007). However, few studies have yet addressed the variability in fatty acid profiles over an extended period of time. In order for FASA to be useful for monitoring dietary variations within and between populations over time, samples must be obtained from specific colonies over a number of years, and preferably also from known individuals to quantify individual variation and assess the stability of individual feeding patterns. The research presented in this paper is part of a longitudinal study of two UK grey seal breeding colonies where individual adult females have been identified, studied and sampled over a number of years (Pomeroy et al 1999). This unique situation was used to generate a natural experiment to examine the variation in fatty acid profiles at individual, colony and annual levels. The two colonies are situated in markedly different marine regimes: North Rona in the Northeast Atlantic and the Isle of May in the North Sea, separated by approximately 300 miles. These two systems have undergone major, but different, changes in recent decades (Hislop 1996, DeYoung et al. 2004). As a result, we can assume that prey availability has changed over this period and therefore the response of the predators to their prey is of particular interest. Although seal diet cannot be estimated directly, we used FASA to assess dietary differences based in the FA content of blubber in grey seals on these contrasting colonies. Grey seals breed synchronously every year in the autum. During this period they do not feed so they sustain the maternal and offspring demands form blubber reserves build up during the pre-breeding period. Therefore, blubber collected at post partum offers and integrated but standardised picture of recent dietary history.

We studied the variations in FA composition during six years spanning a decade (1996-1998 and 2004-2006), this study will provide a comprehensive long-term data set on grey seals in North Rona and Isle of May. We applied a new multivariate approach to the problem of how to assess differences and variation in FA composition.

Methods

Colonies of grey seals at North Rona (NR) (59°06'N, 05 °50'W) and Isle of May (IOM) (56°10'N, 2 °33'W) were studied during the breeding seasons in 1996-1998 and 2004-2006. In total 67 known individual breeding females were captured on each island, and many of these were sampled in several of the six years. For this study, females were captured at early lactation, within 5 days after giving birth and a full depth blubber biopsy was extracted using a 6mm diameter biopsy punch. Samples were stored in chloroform:methanol (2:1) with 0.05% of BHT as antioxidant until further analysis. The total numbers of blubber samples obtained each year for each colony are shown in Table 1. Lipid was extracted from the blubber biopsies and identified by reference to standards as described in Walton et al. (2000).

All 58 fatty acids detected in the early lactation blubber samples were included in the analysis. Data were in the form of the relative proportion of each of the fatty acids in each sample. Prior to analysis, proportions were arcsine transformed to improve normality. The arcsine transformed FA proportions were used as explanatory variables and Year and Colony were re-coded into a single classifying variable to examine regional and interannual differences.

Random Forest (RF) is available in the randomForest package (Breiman 2001, Liaw & Wiener 2002). RF is a multivariate approach capable of producing unbiased classifications from data sets with a large number of variables. Unlike many other classification techniques RF is insensitive to cases where the number of variables exceeds the number of observations. RF uses bootstrapping techniques to provide classification errors and variable importance and also provides a measure of the similarity between observations. These similarities are measured as proximities and stored in a multidimensional matrix. Because of the difficulty in visualising multidimensional proximities we performed multidimensional scaling on the distance matrix (i.e. the inverse of the proximity matrix) to project the multidimensional distances down in to a low dimensional space. A scatterplots of the first two dimensions often provides a useful graphical representation of the clustering into a lower dimensional space while preserving the distances between the observations. The proximity matrix can also be displayed as a heatmap indicating the proximities between particular observations and classification groups. A heatmap is a representation in a colour gradient of the values obtained by a given variable. Each colour illustrates coded squares that specify a proximity value between samples or groups where a colour image represents similar samples or profiles.

While other classification methods require inclusion of a cross validation to obtain an unbiased estimate of the classification error, RF estimates the overall error and the classification error in each tree and the results are given in the output as a confusion matrix. This is central for the evaluation of the RF classification for the different classes.

Similarity between samples from the same individuals

We also tested if samples from the same individuals in different years were more similar than the overall colony sampled in the same years at the same location. The number of samples collected from the same individuals between years ranged from 0 to 19 (Table 3). The similarity between the same seal in different year was tested by comparing the RF proximity values of samples from the same individuals in different years to the proximity values of unmatched samples in the same years. For each combination of two years within a colony the proximities of matched (animals sampled in both years) and unmatched samples where compared with bootstrapped Wilcoxon tests. Due to the small sample size of matched samples in comparison to the unmatched in any of the pair of years compared, a random subset of the unmatched samples, of the same size as the number of matched samples, was extracted at each of 1000 bootstraps. The Wilcoxon test was then performed between the matched samples and each of the 1000 bootstrapped subsets. The median of the 1000 bootstrap p values was then used as measure of significance.

Results

Blubber fatty acid composition

We obtained 127 blubber samples from IOM and 115 from NR at early lactation during 6 breeding seasons (Table 1). The FAs that were present in relative amounts greater than 2% were 18:1n-9, 22:6n3, 16:1n-7, 16:0, 20:1n-9, 20:5n-3, 18:1n-11, 22:5n-3, 14:0, 22:1n-11, 18:2n-6, 18:1n-7, and 18:4n-3. Altogether these 13 FAs accounted for approximately 85% of the total fatty acids in both colonies in all years. The remaining 45 FAs were found at much lower percentages.

Regional differences

Samples from NR and IOM were well differentiated in each of the 6 years studied (Table 2). Only 3 out of 127 IOM and 5 out of 115 NR samples were allocated to the wrong colony. The misclassified IOM samples belonged to 1997, 2005 and 2006 and all of them were classified as NR 2006. Four out of the five misclassified NR samples were allocated to the IOM group corresponding to the same year from which the sample originated; one sample from NR 1997 was misclassified to the IOM 1996 group.

Annual differences within colonies

The degree of misclassification between years within the same colony was higher than the between-colony misclassification. For IOM samples, misclassification error rates were much greater during 04-06 than during 96-98 (Table 2). The misclassifications observed in 96-98 occurred mainly within the three years of that period, with one IOM 1997 sample classified as NR 2006. Annual differentiation was less obvious during 04-06 at the IOM, with more classification errors. Again, most misclassifications fell within the three years of the same period, with 2 animals from IOM 2005 and 2006 incorrectly classified as NR 2006. We observed a different pattern for the NR samples. Samples from 96-98 were poorly differentiated from each other with high classification errors between the three years (Table 2). In contrast, samples from 04-06 were highly differentiated from each other, with very low classification errors.

Plots of the first two dimensions of the multidimensional scaling emphasise the confusion matrix results (Figure 1). The highest degree of differentiation and of cluster separation from the other samples was observed for samples from IOM 96-98 (Figure 1a). NR samples from 04-06 appear fairly well differentiated from each other and from the rest of the NR and IOM samples, while IOM samples from 04-06 formed a cluster that was distinct from the rest of the samples from both colonies, but showed some overlap between itself (Figure 1b). In contrast samples from NR 96-98 formed a cluster without any obvious differentiation between the 3 years (Figure 1c), but this entire group (NR 96-98) was well differentiated from all other groups. The apparent overlap between NR 04 and IOM 04-06 seen in Figure 1 shows the limitation of 2-dimensional scatterplots for visualising multidimensional data. However, these differences can be observed in the heatmap,. where a complete picture of the overall patterns and similarities of samples within and between years and colonies can be observed (Figure 2). The heatmap shows the high degree of similarity within IOM samples from the last three years and for NR samples from the first three years and the lack of similarities between IOM 04-06 and NR 04. The heatmap also highlights the degree of similarity between samples from a specific colony in a specific year. These similarities are correlated with the degree of similarities between the different groups; therefore it is expected to observe that between samples similarity will be greater for the years that were well identified and clustered. This is the case for IOM samples from 96-98 and NR 04-06, where the degree of similarity between samples of a given group is higher than that observed in the last three years at IOM and first three years at NR.

Individual variation

There was some weak support for the hypothesis that samples from the same individual seals in different years were more similar than unmatched samples from the same colony. At the IOM, out of 15 annual comparisons, there were only two pairs of consecutive years (96-97 and 05-06, Table 3) in which samples from the same seals in two different years were more similar than unmatched samples from the same pair of years. At NR, matched samples were more similar than unmatched samples in 4 out of 15 annual comparisons: 96-97, 96-98, 97-98 and 05-06.

FA importance in classifying between groups

The most important FA for distinguishing a particular colony in a given year relative to other is shown in Figure 3. The plot is based on the variable importance values generated by the random forest. The most important FAs for classifying the groups are not necessarily the FAs found in high proportions in the blubber. In fact the six most important FAs selected by the random forest classification in their relative abundance found in blubber were all less that 10% (Figure 4).

The relative amounts of linoleic (18:2n-6) and α-linolenic acid (18:3n-3) were different between both colonies. Within NR samples both FAs had constant amounts during the six years, while samples from IOM had higher amounts during 96-97 and decreased towards 04-06 reaching the same levels found in NR samples. FA 18:3n-1 was variable in both colonies, but a similar decrease was observed in 2006 when compared to the amounts found in 2005. The FA iso-18 in NR and IOM colonies had similar amounts and showed the same pattern of changes between years, to the exception of IOM 1997. Year 96 and 98 had low relative amounts in both populations and a 04-06 were relatively more abundant. The opposite pattern is observed for 16:3n-1, with high levels for 96-98 to the exception of IOM 97 and a decrease in 04-06 levels in both populations. Among the first six most important FA to classified groups the EFA 22:5n-3 had the highest relative amounts, with the exception of IOM 97 with higher and NR 04 and 06 with lower relative amounts, both colonies in the rest of the years were very similar.

Discussion

Our results show that although the fatty acid composition of seal blubber from North Rona and Isle of May changes over time, the colonies still remain clearly distinguishable throughout the decade. Thus, the biggest variation occurred between colonies. The clear changes occurring over time suggest that the prey species consumed, and/or the FA composition of that prey, underwent substantial changes over time at both colonies, but that these changes occurred at different periods. While the IOM seals experienced a dramatic change in dietary lipids during 96-98, the FA composition of NR seals remained stable during the same period. In contrast, the IOM colony appeared to have a relatively stable composition during 04-06, while the NR colony experienced major changes.

The large number of known individuals within each colony that were sampled repeatedly during several years allowed us to explore how individual pattern in FA composition changed over time. Previous cross sectional studies have demonstrated a high degree of individual variation in diet of seals due to factors such as age, sex and body condition (Grahl-Nielsen & Mjaavatten 1995, Beck et al. 2005, Bowen & Harrison 2007). In addition, if individual preferences or specialisation for specific prey species exist, and these are capable of being maintained irrespective of relative prey availability, one would assume that the lipid composition of individuals would remain more similar in consecutive years compared to the overall colony. Our analyses found some evidence of such individual similarity between certain years. Comparisons showed a slightly higher individual similarity compared to the overall colony with the degree of individual similarities decreasing as the years between sampling increased. Significant similarities between years were observed to some extent. At the IOM colony, only 1-year comparison (96-97) was statistically significant (Table 3). This occurred at a time when large changes were observed between years at the IoM. The lack of similarity between individuals at other times could be a result of the reduced or change in the prey species available. This is in accordance to the results observed in the heatmap (Figure 2). However, during 96-98 in IOM the individuals within each year were very similar, while there are clear differences between the individuals in consecutive years. In contrast, during the same period NR individuals captured in consecutive years were very similar (Table3), and there was no clear distinction between the individuals within each year and between years (Figure 2) with very similar FA profiles. If prey availability during that period in the NR area was more stable, seals would retain their individual preferences. This behaviour would be expected if seals do not need to adjust to dramatic changes in the availability of their main prey species. Although the low number of samples for years 04-06 might be expected to influence the results, significant similarities in FA composition were observed between the same individuals when 2005-2006 were compared (n = 5 in IOM and n = 7 in NR).

Individual dietary preferences and strategies may be a function of age. Younger animals may be more likely to respond to changes in prey availability. The average age in 1996 for the same individuals compared was 22 ± 6 year at NR and 15 ± 5 years at IOM. It is likely that preferences and strategies would be well established, thus the age factor will not have a significant influence in the similarities or dissimilarities between the same individuals in different years. We conclude that animals' diet is driven in response to changes in the prey availability. To our knowledge this is the first time that is possible to infer how individual seals shift their diet in time in response to the availability in the environment, as it is expected in general predators.

Ongoing and future work
This work forms part of AA's PhD thesis.

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Table 1. Total number of blubber samples from grey seal mothers at North Rona and Isle of May.

	IOM	NR
1996	33	23
1997	29	25
1998	30	25
2004	10	10
2005	14	14
2006	11	18
Total	**127**	**115**

Table 2. Confusion matrix showing the samples correctly and incorrectly allocated by random forest classification analysis of fatty acid composition of blubber at early lactation. The overall and group-wise classification had an error rate of 22 %.

Location		Isle of May						North Rona						
		1996	1997	1998	2004	2005	2006	1996	1997	1998	2004	2005	2006	C. error
Isle of May	**1996**	30	-	3	-	-	-	-	-	-	-	-	-	0.09
	1997	2	26	-	-	-	-	-	-	-	-	-	1	0.10
	1998	-	-	30	-	-	-	-	-	-	-	-	-	0.00
	2004	-	-	-	6	3	1	-	-	-	-	-	-	0.40
	2005	-	-	-	2	9	2	-	-	-	-	-	1	0.36
	2006	-	-	-	1	1	8	-	-	-	-	-	1	0.27
North Rona	**1996**	1	-	-	-	-	-	11	7	4	-	-	-	0.52
	1997	1	-	-	-	-	-	6	11	7	-	-	-	0.56
	1998	-	-	2	-	-	-	1	4	18	-	-	-	0.28
	2004	-	-	-	1	-	-	-	-	-	9	-	-	0.10
	2005	-	-	-	-	-	-	-	-	-	-	12	2	0.14
	2006	-	-	-	-	-	-	-	-	-	-	-	18	0.00

Table 3. Degree of fatty acids profile similarity between samples from the same individuals in different years compared to the overall similarity of unmatched samples collected in the same years at the same location. Numbers of animals sampled each year and number of same individuals compared between years are shown in brackets .Year comparisons where similarity of matched samples are significantly higher than for unmatched samples (***); numerically higher than for unmatched samples but not significant (*); equal to unmatched samples (=).

Isle of May	1996 (33)	1997 (29)	1998 (30)	2004 (10)	2005 (14)
1997 (29)	*** (15)				
1998 (30)	* (15)	= (19)			
2004 (10)	= (5)	= (7)	= (7)		
2005 (14)	= (1)	= (2)	* (2)	= (5)	
2006 (11)	= (3)	* (4)	* (4)	= (4)	*** (5)

North Rona	1996 (23)	1997 (25)	1998 (25)	2004 (10)	2005 (14)
1997 (25)	*** (17)				
1998 (25)	*** (12)	*** (9)			
2004 (10)	0	0	= (2)		
2005 (14)	* (1)	= (1)	* (2)	= (2)	
2006 (18)	= (3)	* (3)	* (4)	= (3)	*** (7)

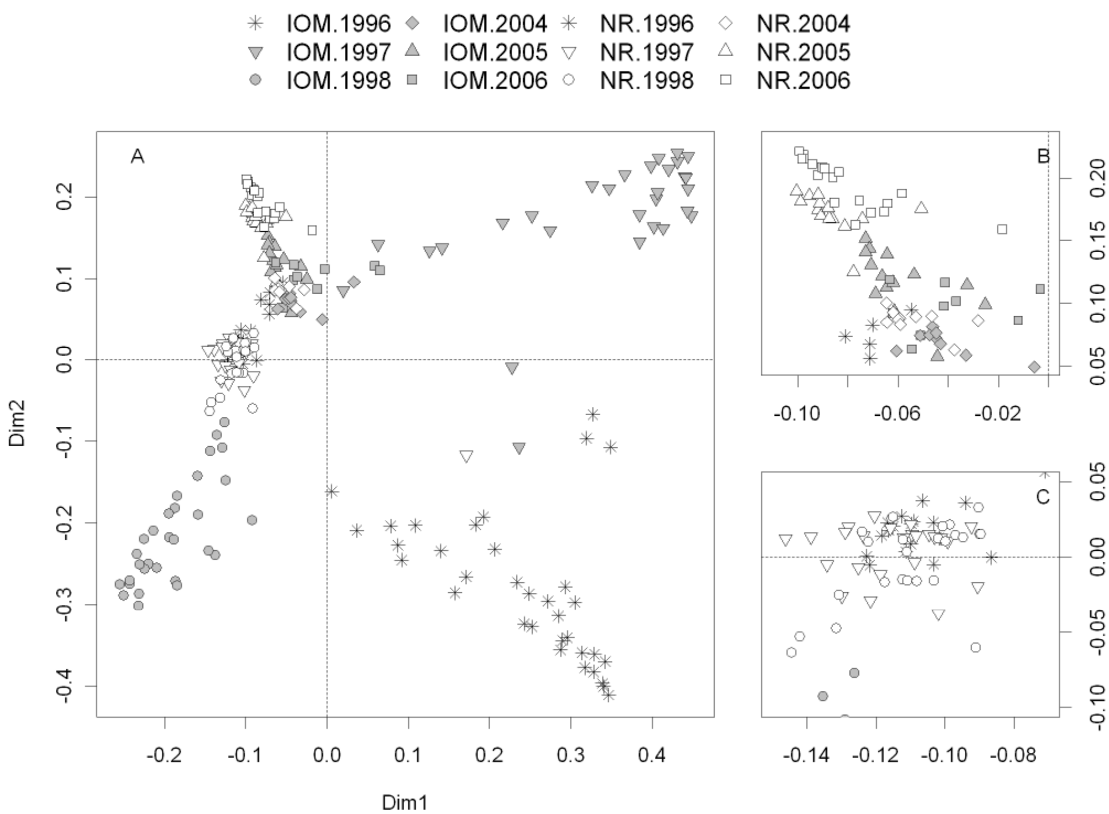

Figure 1. Multidimensional plot of the first two dimensions based in the proximity matrix to visualise clustering and similarities between groups. Plot of early lactation blubber samples from grey seals (*Haliochoerus* grypus) obtained during six years at North Rona and Isle of May. A) Both colonies represented during six years; B) Zoom into the samples from NR and IOM 04-06 and C) Zoom into the samples from NR 96-97.

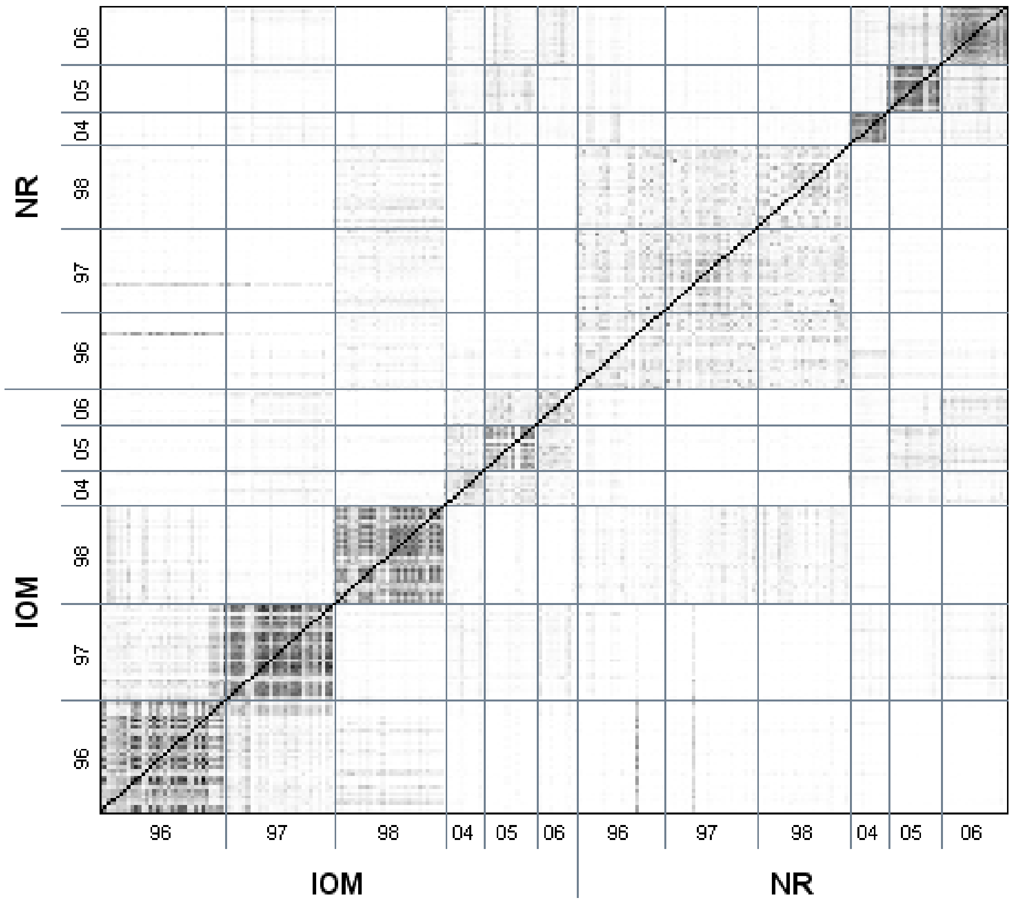

Figure 2. Heat map of the proximity matrix obtained from random forest. The proximity matrix has been restructured in a way that the samples would be placed in their classified group. Each cell represents a sample classified in a given group. The diagonal black line is the distance between a sample and itself, ie zero. It is a symmetrical matrix where each sample in each colony for every year is represented in each axes. The cell darkness represents the similarity between samples in a given group (square) and between samples in different years. The intersection between a colony-year represented in x axis and another in y-axis illustrate the degree of similarity between one year another. Darker cells indicate higher similarity and lighter colour represents lower similarity between samples in a given group or between year-groups.

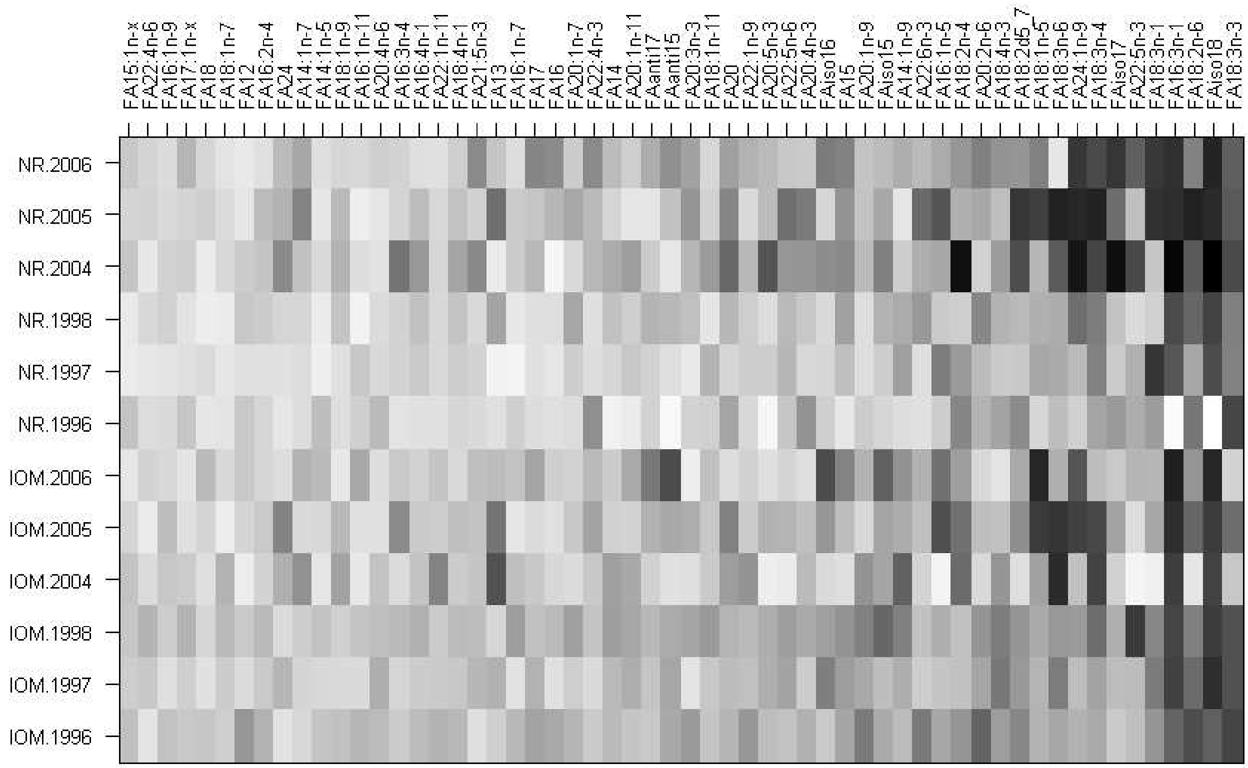

Figure 3. Variable importance plot. The continuous white-black colour scale represents the decrease or increase of FA importance obtained from the random forest, where black corresponds to the most important and white to the less important variable used to distinguish between groups.

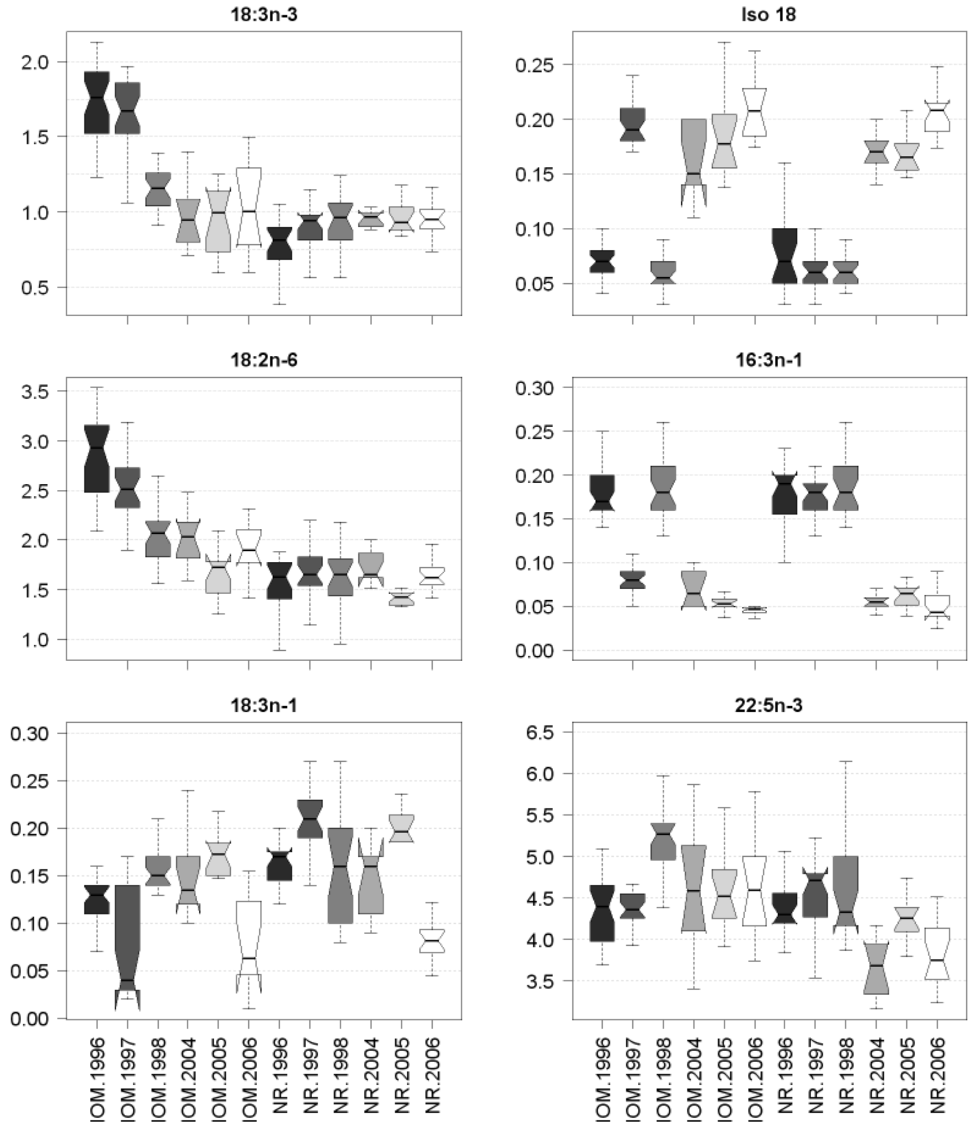

Figure 4. First six most important FA in classifying between groups. Boxes and whiskers represent the range containing 50% and 95% of the data respectively. Notches in the boxes extend to ±1.58 times the interquartile range divided by the square root of the sample size. None overlapping notches in two boxes indicate a ~95% probability that the medians in the two groups are different.