Scientific Advice on Matters Related to the Management of Seal Populations: 2009

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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 2009. 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

Two species of seal live and breed in UK waters: grey seals (*Halichoerus grypus*) and harbour (also called common) seals (*Phoca vitulina*). Grey seals only occur in the North Atlantic, Barents and Baltic Sea with their main concentrations on the east coast of Canada and United States of America and in north-west Europe. Harbour seals have a circumpolar distribution in the Northern Hemisphere and are sub-divided into five sub-species. The population in European waters represents one subspecies (*Phoca vitulina vitulina*). Other species occasionally occur in UK coastal waters, including the ringed seals (*Phoca hispida*), harp seals (*Phoca groenlandica*), and the hooded seals (*Cystophora crystata*) all of which are Arctic species.

Grey seals

Grey seals (*Halichoerus grypus*)
Grey seals are the larger of the two resident UK seal species. Adult males can weigh over 300kg while the females weigh around 150-200kg. 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.

They are generalists, feeding mainly on the sea bed at depths up to 100m although they are probably capable of feeding at all the depths found across the UK continental shelf. Their diet varies both seasonally and geographically but comprises mainly small demersal fish species, i.e. 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). 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 forage in the open sea and return regularly to haul out on land where they rest, moult and breed. They may range widely to forage and frequently travel over 100km between haulout sites. Foraging trips can last anywhere between 1 and 30 days. Compared with other times of the year, grey seals in the UK spend longer hauled out during their annual moult (between December and April) and during their breeding season (between August and December). Tracking of individual seals has shown that they can feed up to several hundred kilometres offshore although most foraging probably occurs within 100km of a haulout site. 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 site and begin foraging in a new region. Movements of grey seals between haulout sites in the North Sea and the Outer Hebrides have been recorded.

There are two centres of population in the North Atlantic; one in Canada and the north-east USA, centred on Nova Scotia and the Gulf of St Lawrence and the other around the coast of the UK especially in Scottish coastal waters. Populations in Canada, USA, UK and the Baltic are increasing, although numbers are still relatively low in the Baltic where the population was drastically reduced by human exploitation and reproductive failure probably due to pollution. There are clear indications of a slowing down in population growth in UK and Canadian populations in recent years.

Approximately 45% of the world's grey seals breed in the UK and 90% of these breed at colonies in Scotland with the main concentrations in the Outer Hebrides and in Orkney. There are also breeding colonies in Shetland, on the north and east coasts of mainland Britain and in SW England 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 has been levelling off in Orkney and possibly at some colonies in the northern North Sea

In the UK, grey seals typically breed on remote uninhabited islands or coasts and in small numbers in caves. Preferred breeding locations allow mothers with young pups to move inland away from busy beaches and storm surges. Seals breeding on exposed, cliff-backed beaches and in caves may have limited opportunity to avoid storm surges and may experience higher levels of pup mortality as a result. Breeding colonies vary considerably in size; at the smallest only a handful of pups are born, while at the biggest, over 5,000 pups are born annually. In general grey seals are highly sensitive to disturbance by humans hence their preference for remote breeding sites. However, at one UK mainland colony at Donna Nook in Lincolnshire, seals have become habituated to human disturbance and over 70,000 people visit this colony during the breeding season with no apparent impact on the breeding seals.

UK grey seals breed in the autumn, but there is a clockwise cline in the mean birth date around the UK. The majority of pups in SW Britain are born between August and September, in north and west Scotland pupping occurs mainly between September and late November and eastern England pupping occurs mainly between early November to mid December.

Female grey seals give birth to a single white coated pup which they suckle for 17 to 23 days. Pups moult their white natal coat (also called "lanugo") around the time of weaning and then remain on the breeding colony for up to two weeks before going to sea. Adult females mate at the end of lactation and then depart to sea and provide no further parental care. In general, female grey seals return to the same colony to breed in successive years and often breed at the colony in which they were born. Grey seals have a polygynous breeding system, with dominant males monopolising access to females as they come into oestrus. The degree of polygyny varies regionally and in relation to the breeding habitat. Males breeding on dense, open colonies are able to restrict access to a larger number of females (especially where they congregate around pools) than males breeding in sparse colonies or those with restricted breeding space, such as in caves or on cliff-backed beaches.

Harbour seals (also known as common seals)

Harbour seals (*Phoca vitulina*) are found around the coasts of the North Atlantic and North Pacific from the subtropics to the Arctic. Five subspecies of harbour seal are recognized. The European subspecies, *Phoca vitulina vitulina*, ranges from northern France in the south, to Iceland in the west, to Svalbard in the north and to the Baltic Sea in the east. The largest population of harbour seals in Europe is in the Wadden Sea.

Approximately 30% of European harbour seals are found in the UK although this proportion has declined from approximately 40% in 2002. Harbour 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 major estuaries of the Thames, The Wash, Firth of Tay and the Moray Firth. Scotland holds approximately 85% of the UK harbour 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, but had limited impact elsewhere in Britain. Counts in the Wash and eastern England have failed to demonstrate any recovery since the epidemic, in contrast to the adjacent European colonies which have experienced rapid growth since 2002.

Major declines have now been documented in harbour seal populations around Scotland with declines of up to 50% since 2000 in Orkney, Shetland, the Moray Firth and the Firth of Tay.

Harbour 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, harbour seals haul out on land regularly in a pattern that is often related to the tidal cycle. Harbour seal pups are born having shed their white coat and can swim almost immediately.

Adult harbour seals typically weigh 80-100 kg. Males are slightly larger than females. Like grey seals, harbour seals are long-lived with individuals living up to 20-30 years. Harbour 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, harbour seals eat less food than grey seals; 3-5 kg per seal per day depending on the prey species.

Historical status

We have little information on the historical status of seals in UK waters. Remains have been found in some of the earliest human settlements in Scotland and they were routinely harvested for meat, skins and oil until the early 1900s. There are no reliable records of historical population size but the Grey Seal (Protection) Act 1914 was introduced into UK legislation, providing the first legal protection for any mammal in the UK because of a perception that there was a need to protect seals. Harbour seals were heavily exploited mainly for pup skins until the early 1970s in Shetland and The Wash. Grey seal pups were taken in Orkney until the early 1980s, partly for commercial exploitation and partly as a population control measure. Large scale culls of grey seals in the North Sea, Orkney and Hebrides were carried out in the 1960s and 1970s as population control measures.

Grey seal pup production monitoring started in the late 1950s and early 1960s and numbers have increased consistently since. In recent years, there has been a significant reduction in the rate of increase.

Boat surveys of harbour seals in Scotland in the 1970s showed numbers to be considerably lower than in recent aerial surveys which started in the late 1980s, but it is not possible to distinguish the apparent change in numbers from the effects of more efficient counting methods. After harvesting ended in the early 1970s, regular surveys of English harbour seal populations indicated a gradual recovery ,punctuated by two major reductions due to PDV epidemics in 1988 and 2002 respectively.

Legislation protecting seals

In the UK seals are protected under the Conservation of Seals Act 1970 (England, Scotland and Wales) and The Wildlife (Northern Ireland) Order 1985. In Scotland, the legislation will be superceded by the forthcoming Marine Bill (Scotland). The Wildlife (Northern Ireland) Order is also currently under review.

The Conservation of Seals Act prohibits taking seals during a close season (01/09 to 31/12 for grey seals and 01/06 to 31/08 for harbour seals) except under licence. The act allows for specific Conservation Orders to extend the close season to protect vulnerable populations. At present, three such orders are in place providing year round protection to grey and harbour seals on the east coast of England and in the Moray Firth and to harbour seals in Shetland, Orkney and the east coast of Scotland between Stonehaven and Dunbar (effectively protecting all the main concentrations of harbour seals along the east coasts of Scotland and England).

Both grey and harbour seals are listed in Annex II of the EU Habitats Directive, requiring specific areas to be designated for their protection. To date, 16 Special Areas of Conservation (SACs) have been designated specifically for seals. Seals are features of qualifying interest in seven additional SACs.

What are the latest estimates of the number of seals in Scottish waters?

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 frequently. 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 09/1 and SCOS-BP 09/2.

Pup production

The total number of pups born in 2008 at all annually surveyed colonies was estimated to be 41,500. Regional estimates were 3,400 in the Inner Hebrides, 12,700 in the Outer Hebrides, 18,800 in Orkney, and 6,600 at North Sea colonies (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 colonies.

1.1 Trends in pup production

Overall, there has been a continual increase in pup production since regular surveys began in the 1960s. In both the Inner and Outer Hebrides, the rate of increase declined in the early 1990s and production has been relatively constant since the mid 1990s. The rate of increase in Orkney has declined since 2000 and pup production has been relatively constant since 2004. Overall pup production at colonies in the North Sea continues to increase exponentially, although it appears to have levelled off at the Isle of May and Farne Islands and the increase is due to expansion of newer colonies on the mainland coasts in Berwickshire and East Anglia. The differences in pup production between 2007 and 2008 are shown in Table 1. Total pup production at annually monitored colonies increased by 6.9%, in contrast to the 2.4% decrease between 2006 and 2007.

This relatively large annual increase was a widespread feature of the 2008 results. Pup production in the Outer Hebrides and at all colonies in the North Sea increased by between 9 and 21% between 2007 and 2008. The magnitude of the increase was similar at the major sites that are not surveyed using the SMRU aerial photography method., All English colonies are ground counted and showed similar large increases from 2007 to 2008 (Table 1). Such large scale inter-annual fluctuations in pup production are not unusual. For example, similar increases occurred in the Outer Hebrides between 1999-2000 and 2002-2003 and decreases of similar magnitude occurred in Orkney between 2004 and 2005 and at North Sea colonies between 1998 and1999.

On a longer timescale, during the most recent 5-year period (2003-2008) the total pup production for all annually monitored colonies in the Inner and Outer Hebrides and Orkney has not changed. However, as previously reported, pup production at colonies in the North Sea continued to increase at around 7.0% p.a. over the same 5 year period.

Table 1: Grey seal pup production estimates for the main colonies surveyed in 2008,

Location	2008 pup production	Change in pup production from 2007-2008	Average annual change in pup production from 2003-2008
Inner Hebrides	3,356	9.3%	-0.2%%
Outer Hebrides	12,712	13.6%	0.0%
Orkney	18,765	-1.0%	+0.12%
Isle of May + Fast Castle	3,346	21.4%	+5.1%
All other colonies incl Shetland & mainland	3,441 **		
Total (Scotland)	41,600	5.4%*	+1.0%*
Donna Nook +East Anglia	1,950	+19.1%	+17.4%
Farne Islands	1,320	+13.2%	+0.8%
SW England (last surveyed 1994)	200		
Wales ***	1,650		
Total (England & Wales)	5,120	+16.7%*	+8.8%*
Northern Ireland	100		
Total (UK)	46,820	+6.9%*	+1.0%*

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

** estimate from several surveys in Shetland to provide most up-to-date estimate

*** estimate from indicator sites in 2004-05, multiplier derived from 1994 synoptic surveys

1.2 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 must be a result of some combination of reductions in the reproductive rate or survival of pups, juveniles or adults (SCOS-BP 08/2). There is currently a lack of independent data with which to quantify the relative contributions of these factors (SCOS-BP 06/7, 08/2). The same modelling framework employed in 2008 was used to fit and compare six Bayesian state-space models of British grey seal population dynamics, based on regional estimates of pup production from 1984 to 2008. 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 2008, 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%.

Model selection criterion were based on Bayesian posterior model probabilities both with and without penalty weighting for the number of parameters (details of methods are presented in SCOS-BP 09/2 and 09/2a) . As with last year's analysis, models that allow for flexible forms of density dependence, but no movement of recruiting seals among regions, were strongly favoured over those with simpler density dependence or with movement between regions.

This year the model selection criteria appeared to strongly favour one model (EDDSNM) over the other (EDDFNM). In response to the apparent change in model weighting, a further extensive analysis was performed (SCOS-BP 09/2a) to investigate the model selection process. This analysis confirmed that the model selection criteria are unable to discriminate between the extended model with density dependent pup survival and no movement (EDDSNM) and the extended model with density dependent female fecundity and no movement (EDDFNM). Monte Carlo error[1] in the posterior model probabilities was greater than the apparent differences between them.

As in previous years the two models produce mean estimates with non overlapping confidence intervals. Until 2007 SCOS presented the lower (EDDSNM) estimate as the conservative estimate of the total grey seal population, but used the combined confidence limits of both models to reflect the degree of confidence in the population estimate. In 2008 SCOS presented a model weighted average estimate of the population. Because the models had approximately equal weighting the resulting population estimate was close to the average of the mean estimates from the two models. In recognition of the new analysis, SCOS acknowledge that the available model selection criteria do not allow discrimination between the models or to apply any specific weightings. In consequence the estimate of grey seal population size will be taken to be the simple average of the two models and conservative confidence/credibility intervals estimated as the full range from the lower 95% credibility limit of the EDDSNM model up to the upper 95% credibility limit of the EDDFNM model.

The estimated population size associated with all annually monitored colonies in 2008 using these two models was 120,200 (95% CI 85,600-170,700) and 245,800 (95% CI 191,000-359,300) respectively. The overall estimate for the grey seal population associated with the annually monitored sites is therefore 183,000 (conservative CI 85,600-359,300).

The population estimate for the annually monitored sites in 2007 published in the 2008 SCOS report was 160,100. (95% C.I. 84,500 304,500). Using the simple averaging

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[1] Monte Carlo error is uncertainty in the results of stochastic models due to the random processes involved in their fitting,

method applied this year produces a population estimate for the annually monitored sites in 2007 of 178,100 (conservative C.I. 85,700-345,400), about 10% higher.

A comprehensive survey of data available from the less frequently monitored colonies is presented in SCOS-BP 09/1. Total pup production at these sites was estimated to be approximately 5,300 in 2008. Using the average ratio of pup production to population size for the annually monitored sites based on the averaged model estimate, and assuming proportionally similar confidence intervals, produces a population estimate of 23,400 (approx C.I. 11,000 to 45,900) for these sites. Combining these with the annually monitored sites gives an estimated UK grey seal population of 206,000 (conservative C.I. 96,500 to 405,000).

The differences in the published estimates for the total grey seal population in 2007 and 2008 should not be taken as an indication of population change. It is mainly a consequence of changes in the treatment of the model outputs. In fact the trajectory of the average of the two models suggests that the grey seal population increased by around 2.8% between 2007 and 2008.

The fluctuations in published population numbers over recent years reflects limitations in the predictive capacity of the current models based on pup production estimates alone.. This problem points to a need for review of modelling procedures and consideration of the collection of additional biological information to enable an understanding of how numbers of pups relate to the overall population size. 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 of population size. 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).

In 2008 SCOS recommended that additional studies to obtain independent estimates of population size, fecundity and both pup and adult survival should be given high priority. SCOS discussed and approved a series of studies to provide additional insight into the dynamics of the grey seal population :

- A preliminary version of a complementary modelling approach is presented in SCOS BP 09/4. A simple Bayesian method, using generalised additive models to smooth a series of pup production estimates followed by matrix models to scale their results up, was used to estimate the trajectories of four British grey seal populations. A uniform prior on the relative importance of density dependence in fecundity and first year survival is applied to produce an overall estimate and credibility (Bayesian confidence) interval for each population. This approach requires fewer assumptions than the current State Space Models while producing similar population estimates and credibility intervals. SCOS recommends that this and other modelling approaches should be investigated further.
- SMRU have continued the analysis of data from the long-term studies on the Isle of May and North Rona to extract information on fecundity, age at first reproduction and adult survival and the effects of co-variates on population parameters (details of progress are presented in SCOS-BP 09/5).
- A detailed analysis of the haulout behaviour of a large sample of grey seals determined by satellite telemetry was reviewed. Preliminary results indicate that approximately 30% of the grey seal population is hauled out at the time of

the annual harbour seal surveys and that there are no significant regional, sex or age differences in haulout probability. These results will be combined with regional haulout counts of grey seals obtained during the harbour seal moulting and breeding surveys and will be presented to SCOS in 2010.

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.

1.3 Population Trends

Despite the large increase in pup production in the Outer Hebrides in 2008, longer term averages suggest that the growth of pup production in the Inner and Outer Hebrides has effectively stopped while in Orkney it has levelled off (SCOS-BP 09/1 & 09/2; 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 Outer Hebrides. (Detailed annual population estimates are given by region in the Appendices of SCOS-BP 09/2).

1.4 UK grey seal population in a World context

The UK grey seal population represents approximately 45% of the world population on the basis of pup production. The other major populations in the Baltic and Canada are also increasing, but at a faster rate than in the UK (Table 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**[2]
UK	46,900		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 + Eastern Shore	14,400	2007	Declining[5]
USA	1,100	2002	Increasing
WORLD TOTAL	**125,600**		**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

[5] Thomas,L.,Hammill,M.O. & Bowen,W.D. 2007Estimated size of the Northwest Atlantic grey seal population 1977-2007 Canadian Science Advisory Secretariat: Research Document 2007/082 pp31.

Current status of British harbour seals

Each year SMRU carries out surveys of harbour seals during the moult in August. Recent survey counts and overall estimates are summarised in SCOS-BP 09/3. 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 the survey effort has been increased and 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.

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.

Combining the most recent counts (2006-2008) at all sites, approximately 24,250 harbour seals were counted in the U.K: 82% in Scotland; 13% in England; 5% in Northern Ireland (Table 3). Including 2,900 seals counted in the Republic of Ireland produces a total of 27,400 harbour 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. The survey counts are normally presented as minimum estimates of population size. 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. There is some debate about the validity of this multiplier and SMRU are currently undertaking a telemetry study of haulout behaviour to estimate the proportion of the population hauled out during the moult surveys .

Apart from the population in The Wash, harbour 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 do not indicate a recovery following the epidemic. Counts by region for the 2008 season are given in Table 3. These are minimum estimates of the British harbour seal population. Results of surveys conducted in 2008 are described in more detail in SCOS-BP 09/3.

Table 3 Counts of harbour seals by region

Region	**2006-2008**
Shetland	3,057
Orkney	2,867
Outer Hebrides	1,815
Highland (Nairn to Cape Wrath)	884
Highland (Cape Wrath to Appin & Loch Linnhe)	5,043
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)	55
Borders (Berwick upon Tweed to Torness Power Station)	0
Central	1
TOTAL SCOTLAND	**19,771**
Blakeney Point	581
The Wash	2,010
Donna Nook	191
Scroby Sands	81
Other east coast sites	347
South and west England (estimated)	20
TOTAL ENGLAND	**3,230**
TOTAL BRITAIN	**23,001**
TOTAL NORTHERN IRELAND	**1,248**
TOTAL BRITAIN & NORTHERN IRELAND	**24,249**
TOTAL REPUBLIC OF IRELAND	**2,905**
TOTAL FOR GREAT BRITAIN AND IRELAND	**27,154**

Population trends

Counts in Orkney and Shetland in 2006 were 42% lower (95% confidence intervals 10%-62%) than in 2001. Results from 2007 confirmed the magnitude of the decline in Orkney. Counts in 2008 were 15% lower than in 2007 and 33% lower than in 2006. . These latest results suggest that the Orkney harbour seal population declined by 67% since the late 1990s and has been falling at an average rate >13% p.a. since 2001.

Counts in the Outer Hebrides in 2008 were 35% lower than the peak count in 1996. Regular surveys over the intervening period suggest that there has been a sustained but gradual decline of around 3% pa since 1996.

Counts of the Strathclyde region in 2007 were 25% lower than in 2000, but were similar to counts in the mid 1990s.

Surveys in 2007 confirmed that the west coast of Highland Region has not show any decline and surveys in 2008 confirmed that the North coast of Highland Region also showed no decline from the previous 2005 survey but a slight decline from earlier years (1997).

Surveys of the east coast populations in 2008 also showed continuing declines in the Firth of Tay population (SCOS-BP 09/3) and a continued lack of recovery in the Moray Firth or the English East coast populations. Overall, the combined count for the English East coast population (Donna Nook to Scroby Sands) in 2008 was 4.5% lower than the 2007 count and 3.1% higher than the 2006 count but within the range of counts over the previous 3 years (SCOS-BP 09/3, Figure 8, Table 4). This lack of recovery contrasts with the apparent rapid growth in populations in the nearest European population in the Wadden Sea which increased by 15% between 2007 and 2008 and has grown by approximately 13% pa since the 2002 PDV epidemic.

Response to harbour seal declines

These widespread declines give clear cause for concern and have resulted in the implementation of area-specific Conservation Orders by the Scottish Government, providing harbour seals with year-round protection. 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.

In 2008 SCOS recommended that a survey of the harbour seal population of Shetland be given a high priority, that 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. In response, SMRU, with funding support from NERC, Scottish Government Marine Directorate, Scottish Natural Heritage and Natural England, has established a research programme which includes:

1. planned thermal image surveys of harbour seal moulting populations in Shetland and repeat surveys in Orkney,
2. continuation of the annual fixed wing survey of the English and Scottish east coast moulting populations,
3. continuation of the pup production surveys in the Moray Firth and East Anglian populations,
4. a satellite-telemetry based study of proportion of time seals spend hauled out during the moult in two populations with contrasting dynamics, i.e. Orkney and the west coast,
5. completion of analysis of pup survival rates in two populations with contrasting dynamics, i.e. Orkney and the west coast, and
6. continued investigations into disease and environmental factors affecting survival in harbour seals (SCOS-BP 09/6).

Results from 1 to 5 will be presented to SCOS in 2010.

SCOS recommends that a programme of research be developed to address specific hypotheses about the causes of the decline and that SMRU should seek additional funds to support such a research programme. A summary of the issues to be addressed was discussed by SCOS in 2008. Briefly, the following list of questions were identified as the priorities for research.

1. Is it likely that an artefact of the survey methodology or any of the following changes in the seals' behaviour could account for the observed changes in counts without a population change?
    - Changes in timing of peak counts during the moult
    - Changes in patterns of haulout behaviour
    - Movement, e.g. migration to neighbouring regions

2. Is reduced food availability causing any of the following effects? If so are they sufficient to account for the observed declines through:
    - Reduction in pup survival
    - Reduction in adult survival
    - Reduction in fecundity

3. Is the decline due to competition between harbour and grey seals?
    - Do grey and harbour seals compete for food
    - Do grey seals exclude harbour seals from certain habitats
    - Do grey seals prey on young harbour seals

4. Are any of the following direct mortality effects having a significant impact on the harbour seal population?
    - Disease
    - Pollution
    - predation
    - By catch
    - Deliberate killing

Table 4 Sizes and status of European populations of harbour seals.

Region	Number of seals counted[1]	Years when latest information was obtained	Possible population trend[2]
Outer Hebrides	1,800	2008	declining
Scottish W coast	10,700	2007-2008	None detected
Scottish E & N coast	1,400	2008	Declining
Shetland	3,100	2006	Declining
Orkney	2,900	2008	Declining
Scotland	**19,800**		
England	**3,200**	2008	Recent decline[4]
Northern Ireland	**1,250**	2002	Decrease since ‘70s
UK	**24,250**		
Ireland	2,900	2003	Unknown
Wadden Sea-Germany	9,400	2008	Increasing after 2002 epidemic
Wadden Sea-NL	4,100	2008	Increasing after 2002 epidemic
Wadden Sea-Denmark	2,000	2008	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 62ºN	1,200	1996-98	Unknown
Norway N of 62ºN	2,600	1994	Unknown
Iceland	19,000	?	Unknown
Barents Sea	700	?	Unknown
Europe excluding UK	**55,600**		
Total	**83,200**		

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

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

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

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

2. *What is known about the population structure, including survival and age structure, of grey and harbour 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 are two apparently reproductively isolated populations, one that breeds in the Baltic, usually pupping on sea ice in the spring, and one that breeds outside the Baltic, usually pupping on land in Autumn and early winter. These populations appear to have been reproductively isolated at least since the Last Glacial

Maximum[2,3]. The vast majority (85%) of European grey seals breeding outside the Baltic breed around Britain. On the basis of genetic differences there appears to be a degree of reproductive isolation between grey seals that breed in the south-west (Devon, Cornwall and Wales) and those breeding around Scotland[4] and within Scotland, there are significant differences between grey seals breeding on the Isle of May and on North Rona[5]. 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.

Since 2003, a spatially-explicit model has been used to estimate the British grey seal population from geographically structured pup production estimates. 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 suggestion is further supported by recent results from grey seal population models that indicate an absence of large scale redistribution of breeding females between regions (SCOS-BP 09/02), again implying a high degree of philopatry. However, these results apply to large geographical regions, Outer Hebrides, Inner Hebrides, Orkney and North Sea. The lack of large scale redistribution is supported by the results of detailed studies at breeding colonies and re-sightings of photo-identified individuals that indicate breeding females tend to return to their natal breeding colony and remain faithful to that colony for most of their lives[6]. A NERC funded project to continue and extend the photo identification work will begin in 2009 and preliminary results will be presented to SCOS 2010.

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 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 re-sightings of permanently marked animals and have previously been presented to SCOS. Details of the data and recent analyses

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[2] Boskovic, Kovacs,K.M., Hammill,M.O. & White,B.N. 1996 Geographic distribution of mitochondrial DNA haplotypes in grey seals (*Halichoerus grypus*) Canadian Journal of Zoology 74 pp 1787-1796

[3] Graves, J.A., Helyar, A., Biuw, M., Jüssi, M., Jüssi, I. & Karlsson, O. (2008) Analysis of microsatellite and mitochondrial DNA in grey seals from 3 breeding areas in the Baltic Sea. *Conservation Genetics*

[4] Walton M. & Stanley, H.F. 1997. Population structure of some grey seal breeding colonies around the UK and Norway. European Research on Cetaceans. Proc 11th annual conference of European cetacean society. 293-296

[4] Allen, P. J., W. Amos, 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.

[5] 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

are presented in SCOS-BP 09/5, including analyses of the effects of co-variates on survival and fecundity. Briefly, adult female survival rates do not appear to be related to body mass but vary over time at North Rona and are lower than at the Isle of May. Fecundity including a correction for missing years was apparently higher at the Isle of May than at North Rona. Both results are consistent with the differing dynamics at these two colonies and suggest that differences in vital rates among colonies may be widespread.

Harbour 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 significant genetic differentiation between harbour seal populations in European waters[7]. The Irish-Scottish, the English east coast and the Wadden Sea harbour seals were identified as distinct population units. There is probably little movement of breeding animals between these populations although satellite telemetry reveals some interchange between the Wadden Sea and the English east coast populations outside the breeding season. Within the Ireland-Scotland population there is probably occasional movement of animals between regions, but there is no evidence from satellite telemetry of any long-range movements (for example, between the east and west coasts of Scotland) comparable to those observed in grey seals. Similarly, studies of the movements of branded seals in the Kattegat/Skagerrak[8] indicate that there is only limited movement within the western Scandinavia population. However, in both 1988 and 2002 phocine distemper spread rapidly among European harbour seal populations, suggesting that substantial movement of individuals can occur, although the genetic 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 harbour 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 long 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 harbour seal population. With a sufficiently long time series of both pup production estimates and overall population indices (moult counts) the harbour seal population modelling approach under development at SMRU will be capable of generating age structures for the female component of the harbour seal population.

Survival rates

SMRU have recently conducted a comparative study of survival rates of harbour seal pups in the declining Orkney and apparently stable West Coast populations. Results suggest that both populations have similar but high mortality rates and that differential pup mortality is unlikely to be responsible for the observed demographic patterns.

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[7] 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.

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

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 2008 recommended additional effort to improve the estimates of harbour 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. A telemetry study to address the question of haulout proportion has started in summer 2009. Survey methods have been improved and SMRU have continued development of a harbour seal population model.

Harbour Seal Population

3. Is the existing harbour seal decline recorded in several local areas around Scotland continuing or not and what is the position in other areas?

Counts in Orkney and Shetland in 2006 were 42% lower (95% confidence intervals 10%-62%) than in 2001. Results from 2007 confirmed the magnitude of the decline in Orkney. Counts in 2008 were 15% lower than in 2007 and 33% lower than in 2006. . These latest results suggest that the Orkney harbour seal population declined by 67% since the late 1990s and has been falling at an average rate >13% p.a. since 2001.

Counts in the Outer Hebrides in 2008 were 35% lower than the peak count in 1996. Regular surveys over the intervening period suggest that there has been a sustained but gradual decline of around 3% pa since 1996.

Counts of the Strathclyde region in 2007 were 25% lower than in 2000 but were similar to counts in the mid 1990s.

Surveys in 2007 confirmed that the west coast of Highland Region has not shown any decline and surveys in 2008 confirmed that the North coast of Highland Region also showed no decline from the previous 2005 survey but a slight decline from earlier years (1997).

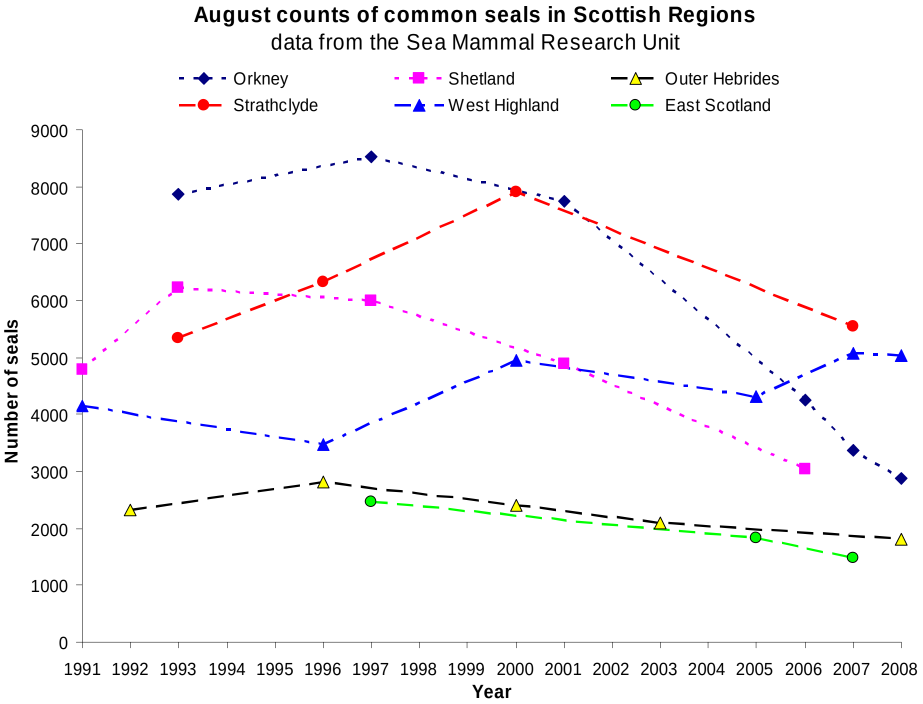
Surveys of the east coast populations in 2008 also showed continuing declines in the Firth of Tay population (SCOS-BP 09/3) and a continued lack of recovery in the Moray Firth or the English East coast populations. Overall, the combined count for the English East coast population (Donna Nook to Scroby Sands) in 2008 was 4.5% lower than the

2007 count and 3.1% higher than the 2006 count but within the range of counts over the previous 3 years (SCOS-BP 09/3, Figure 8, Table 4). This lack of recovery contrasts with the apparent rapid growth in populations in the nearest European population in the Wadden Sea which increased by 15% between 2007 and 2008 and has grown by approximately 13% pa since the 2002 PDV epidemic .

Surveys in 2008 confirmed that the east and north coast of Highland region also showed no decline compared with the previous survey (2005) but a slight decline when compared with an earlier survey (1997).

Surveys of the east coast populations in 2008 also showed continuing declines in the Firth of Tay population (SCOS-BP 09/3). Counts in the Moray Firth have remained constant since 2003 (see Answer to Q10 below for details). The English East coast population remains at approximately 60-70% of its level before the 2002 PDV epidemic. This is in contrast to the apparent rapid growth in populations in the nearest European population in the Wadden Sea which increased by 15% between 2007 and 2008 and has grown by approximately 13% pa since the 2002 PDV epidemic .

Fig. 1. Trends in counts of harbour seals around Scotland.



4. *In light of recent reports of a decline in numbers of harbour seals in the Strathclyde region, should the Scottish Government consider additional conservation measures to protect this vulnerable local population?*

The reported declines are cause for concern, but should be viewed in the context of previous survey results and adjacent areas. The Strathclyde counts decreased by 30% from a peak of 7,900 in 2000, a 5% p.a. decline. The 2007 count was similar to the counts in 1988, 1993 and 1996 and it could be argued that this represents redistribution rather than rapid population increase and decline. However, the drop in numbers between 2000 and 2007 was not matched by any increase in numbers in adjacent populations. Strathclyde region now holds the largest component of the Scottish harbour seal population. SCOS firmly recommends that repeat counts of Shetland, Strathclyde and Orkney should be a priority for future surveys.

It is worth noting that although the Outer Hebridean population has not undergone the same rapid declines seen in the Northern Isles and possibly in Strathclyde, the counts for the Outer Hebrides have shown a consistent gradual decline of approximately 3.5% p.a. that has been maintained since the mid 1990s. Following the same precautionary approach, SCOS recommends that consideration should also be given to extending conservation measures to the Outer Hebrides.

5. *What are the latest results from research investigating the causes of the recent decline in harbour seals and how has this contributed to understanding 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. A list of questions to be addressed is presented above (Question 1, page 15).

A preliminary step in the process was to develop a modelling tool to gauge the relative importance of real or perceived trends in demographic rates. A preliminary demographic model for harbour 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 and modified to incorporate the effects of an extensive seal shooting program. 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 five data collection projects:

1. An extensive air survey programme, supported by intensive ground observation studies, was carried out in summer 2007 and continued in summer 2008 to identify the geographical extent and confirm the magnitude of the declines around the UK. Results were presented in SCOS-BP 08/3 and 09/3 and are discussed above.

2. A comparative study of pup mortality patterns in a declining population (Orkney) and a stable population (Lismore) was carried out in 2007. Pre-weaning mortality was negligible in both regions. A model incorporating a normal time to tag failure and independent survival estimates in each region was fitted. Survival did not follow a simple exponential decay and was best fitted by a gamma distribution that allows for a gradually increasing probability of death, consistent with results in Danish seals that show higher winter mortality. 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 harbour seals.
3. Archived blood samples from grey and harbour seals were screened to assess prevalence of anti-leptospira, toxoplasma and phocine distempter virus antibodies over the period 1991-2005. The results suggested it is unlikely that these infections played a major role in the decline of Scottish harbour seals (SCOS-BP 08/6). . A follow-up comparative study of declining and stable populations was carried out between August and October, 2008. There was no evidence, in our sample of captured animals, of differences in levels of acute disease, no signs of infection, no abnormal parasite infestations, no evidence of a recurrence of PDV infections and no signs of nutritional stress. Thus ruling these out as possible causes for the decline. Detailed results are presented in SCOS-BP 09/6. Samples of faeces, urine and blood serum from harbour seals in Orkney and on the east and west coasts of Scotland were screened for the biotoxin, domoic acid. Levels consistent with chronic exposure levels in other pinnipeds were detected in all areas, but were most prevalent in Orkney and the Firth of Tay.
4. Population surveys have been carried out to further examine the extent and scale of the declines including surveys of Orkney, the Scottish east coast and Outer Hebrides. Detailed results are presented in SCOS-BP 09/3. Further surveys of harbour seal moulting populations in Shetland, Strathclyde and repeat surveys in Orkney and the east coast are planned for 2009.
5. A satellite telemetry based study of proportion of time seals spend hauled out during the moult in two populations with contrasting dynamics, i.e. Orkney and the west coast was started in summer 2009. Results will be presented to SCOS 2010.

New Seal Legislation – Scottish Marine Bill

6. Does the Committee consider that the proposed changes to seal legislation set out in Scottish Marine Bill will improve seal management in Scotland?

SCOS welcomes several innovative aspects of the new Marine Bill relevant to seal management in Scotland. In particular:

SCOS has in the past pointed out that effective population management requires accurate information on numbers of seals killed throughout the year for whatever reason. Under the Conservation of Seals Act, there is no requirement to report seals killed outside the closed season. Placing all shooting under licence will facilitate tighter control and regulation and allow detailed recording of all management actions.

Broadening the scope of the licensing process to include other users of the marine environment, particularly aquaculture facilities removes a clear inconsistency. This should allow regulation of control measures around fish farms and provide records of numbers of seals killed.

Removal of the ambiguities associated with the netsman's defence will clarify the situation and reduce the likelihood of unsuccessful prosecutions.

7. What options exist for the calculation of Permitted/Potential Biological Removals (PBR) or equivalent at national, regional and more local level for possible use in development of a well-managed seal licence system around Scotland?

PBR has a specific definition and is a simple metric for a well defined population. It is designed to assess how many individuals can be removed from a population that experiences either direct or (more often) indirect take without substantial disadvantage to the population and that will allow the population to approach the optimal sustainable population (OSP) level.

For most populations the OSP is unknown, but the PBR can be calculated using an assumed intrinsic rate of increase and the lower confidence intervals of the population estimate. However there are problems associated with this method when estimating an acceptable take from declining or stable populations that are below their carrying capacity. The method of PBR calculation implicitly assumes that in the absence of human induced mortality, population control is density dependent and that rates of increase will respond to the population being moved further from the density dependent asymptote. This may not be true in many practical situations, e.g. the current harbour seal declines in Scotland.

These problems are, to some extent, addressed through the application of a correction factor which scales the PBR based on the status of the population and/or our confidence in population parameter estimates. However, a method based on determining the target population and developing specific targeted removal programs would be more robust and hopefully less prone to inconsistencies.

Alternative management procedures and improvements to the basic PBR method are under investigation at SMRU and a wide ranging consultation process has been initiated. Ideally such methods would be based on an underlying population model similar to the models developed for the Moray Firth. However, SCOS note that the long, detailed time series of historical population data and the current annual moult and breeding season survey effort in the Moray Firth make this a particularly well studied management unit. It is unlikely that managers of other harbour seal populations in Scotland will have such detailed information available.

In the interim, a set of criteria have been proposed that will allow a consistent approach to be taken to estimating the appropriate recovery factor for any particular population of seals. A supplementary briefing paper describing this process has been circulated to the members of SCOS and will be presented as a full briefing paper to SCOS 2010.

8. How should these reflect the differences in population of each native seal species and the local differences in harbour seal populations around Scotland?

Clearly the calculated PBR or whatever other population management measures are proposed, must be based on a thorough understanding of the biology of the target species, both in terms of identifying functional management units within populations and quantifying the likely impacts of the actions on their population dynamics.

9. What might be appropriate boundaries for any potential regional or local seal management areas around Scotland for both species of seal?

The answer to this question depends to a large extent on what aspect of the seal population is being managed, e.g. protection of breeding sites and populations, management of important foraging areas or zones of important interactions with fisheries or other marine exploitation activities.

Depending upon the aim, appropriate boundaries can be determined on the basis of seal stock identity, foraging area separation and human political or management areas.

A research project has been established to investigate the use of at sea movement and distribution data in establishing appropriate management units. SCOS defer this answer until the results of the analysis are available.

Moray Firth

10. 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 2008. Results for each sub-region (for 2005 to 2008) are presented in Table 4 and Figure 2 below and in more detail in SCOS-BP 09/3. For the Inner Moray Firth, numbers of harbour seals hauled out in August 2008 varied between 582 and 478. If the adjacent haulout sites in Loch Fleet and at the mouth of the Findhorn were included, the numbers increased to between 670 and 738. If we assume that 60% to 70% of the population was hauled out, the maximum count in 2008 would produce a total population of 1050 to 1230 harbour seals.

Table 4. Counts of harbour 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**	**13-Aug-08**	**20-Aug-08**
Ardersier	260	143	224	210	184	150	173	167	123
Beauly Firth	119	169	94	174	178	115	170	165	135
Cromarty Firth	98	101	118	119	93	67	118	90	90
Dornoch Firth	199	118	256	249	264	153	209	160	130
Inner Moray Firth	**676**	**531**	**692**	**752**	**719**	**485**	**670**	**582**	**478**
Inner MF +Loch Fleet & Findhorn	**834**	**659**	**842**	**894**	**840**	**652**	**851**	**738**	**670**
Inner MF + Dunbeath to Findhorn			**955**	**1057**	**977**		**941**	**840**	**713**

The 2008 counts were slightly lower than the counts for 2007 and 2006, but it is not clear if the decline is continuing or if the population has stabilised at a level approximately 60% to 70% of the counts obtained in the 1990s.

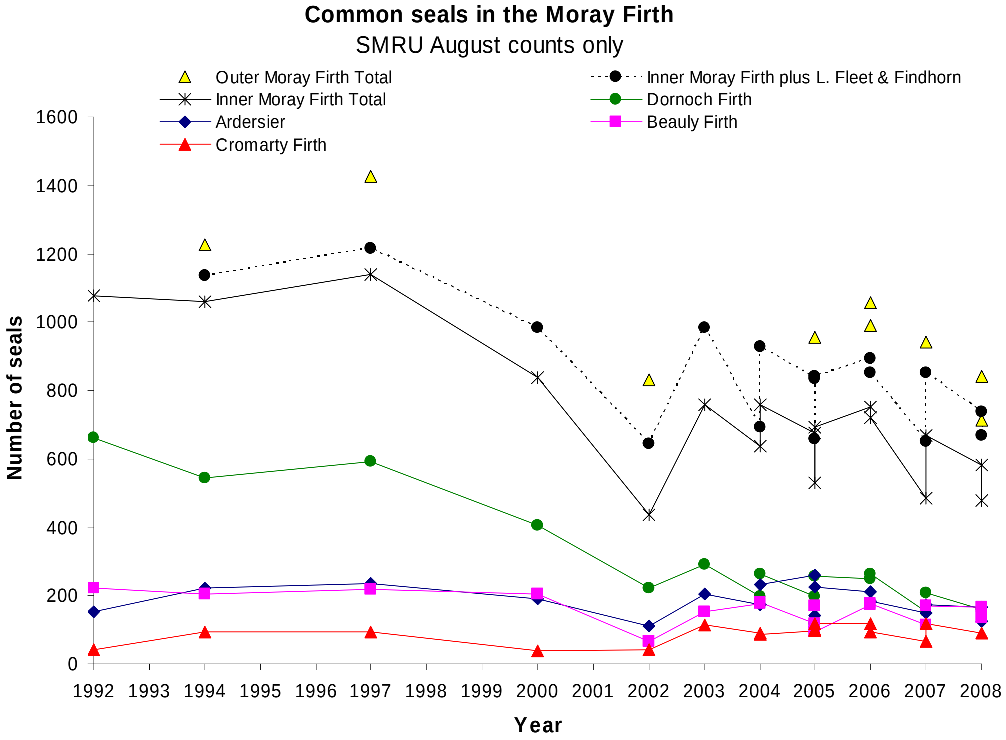


Fig 2. The number of harbour seals counted in areas within the Moray Firth, between 1992 and 2008

11. What should be the basis for the Permitted/Potential Biological Removal (PBR) in respect of the Moray Firth?

See answer to Q 7 & 8

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Marine Areas of Significance for Seals

12. What are the Committees views on the identification of marine areas of significance for seals? Is it preferable in doing this to consider seals alone or to seek to address the wider marine eco-system supporting them?

Marine areas of significance for seals should include suitable foraging habitats, aquatic breeding/mating sites for harbour seals, important transit areas to ensure free movement between haulout and foraging areas and waters adjacent to important haulout sites for rest and reproduction.

SCOS recommends that an ecosystem approach to designating such areas should be applied where possible.

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 harbour 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 S,Wanless	N.E.R.C. C.E.H, Edinburgh;
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, 2009

09/01 Grey seal pup production in Britain in 2008
C.D. Duck

09/02 Estimating the size of the UK grey seal population between 1984 and 2006, and related research.
L. Thomas and J. Harwood

09/02a Further investigations into results presented in Briefing Paper 09_2
L. Thomas

09/03 The Status of British Common Seal Populations in 2008
C.D. Duck & D. Thompson

09/04 Scaling up from pup counts to population trajectories for British grey seals.
M. Lonergan, D.Thompson, L.Thomas & C.D. Duck

09/05 Mass, fecundity and survival in female grey seals (*Halichoerus grypus*) at 2 UK breeding colonies: the breeding status of absent females, and an estimate of overall fecundity**.**
S. Smout, P. King, & P. Pomeroy

09/06 Health assessment in harbour seals around Scotland
A.Hall

C.D. Duck

Grey seal pup production in Great Britain and Ireland in 2008

NERC Sea Mammal Research Unit, Scottish Oceans Institute, University of St Andrews, St Andrews KY16 8LB

Summary

Between September and December 2008, repeat aerial surveys of 59 grey seal breeding colonies in Scotland were completed successfully by SMRU. New breeding colonies on Hoy (Orkney) and on Trodday (north-east Skye) were surveyed for the first time. South Ronaldsay was surveyed aerially as SNH staff were unable to carry out ground counts. Staff from Scottish Natural Heritage (SNH), National Trust, Lincolnshire Wildlife Trust and Natural England counted pups born at colonies in Shetland, the Farne Islands, Donna Nook, Blakeney Point and Horsey (E. Norfolk).

The total number of pups born at annually monitored colonies was estimated to be 41,450. This number was 6.91% higher than the 2007 total of 38,772.

The annually monitored colonies account for approximately 85% of grey seal pups born in the UK. A number of colonies are monitored less frequently for a number of reasons including difficulty of access (Wales, SW England) and the relatively small numbers of pups born (numerous colonies around Scotland).

1. Surveys conducted in 2008

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. The main colonies located in the Inner and Outer Hebrides, Orkney and in the Firth of Forth, were surveyed between four and six times during the 2008 breeding season. Colonies on the north Scottish coast, Loch Eriboll, Eilean nan Ron (Tongue) and the Helmsdale coast south of Duncansby Head, were surveyed either three or four times. Smaller colonies surveyed once included: the Sound of Harris Islands, Fladda Chuain, the Ascrib Islands, Glas Beag (Summer Isles) and Eilean Trodday, off north-east Skye. Inchkeith, in the Firth of Forth was surveyed three times.

Mean birth date at colonies in the Inner Hebrides has been getting progressively earlier. Normally our first survey is between 20 and 25 September. In 2008, an extra survey was carried out on 12 September. Productions at Inner Hebrides colonies were estimated including and excluding this early survey.

A small number of colonies are monitored annually by different organisations: National Trust staff count pups born at the Farne Islands (Northumberland) and at Blakeney Point (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) staff coordinated a fifth survey of grey seal pups born in Shetland. However, poor weather reduced the number of surveys carried out in Shetland.

The Linhof camera functioned properly throughout the survey session. The older film cassette repeatedly developed a fault in the film wind-on mechanism, despite servicing prior to the survey and repair during the survey.

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 the development of pups. The method used to obtain pup production estimates in 2008 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 (Mainland and Shetland colonies and Hoy and

South Ronaldsay in Orkney).

The 2008 total pup production estimate for 59 annually monitored colonies was **41,450**, an increase of **6.91%** from 2007 (**38,772**; Table 1). The trajectory of pup production with 95% confidence limits at all the major breeding colonies in England and Scotland (excluding Loch Eriboll, Helmsdale and Shetland) between 1984 and 2008 is shown in Figure 2a. Figure 2b shows the long-term pup production trajectories at the main island groups from 1960 to 2008. Pup production from the main island groups since 1987 is shown in more detail in Figures 3a (Inner and Outer Hebrides and Orkney) and 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 (Figure 3b). SNH staff count pups in Shetland in a manner compatible with counts from aerially surveyed colonies and, for colonies with sufficient counts, production was estimated using the same modelling procedure.

In 2008, surveys were carried out from an altitude of 335m rather than the usual 365m (1,100 rather than 1,200 feet). The increased resolution of the images improved the quality of counts, although the area covered on each photograph was reduced. Because of the improved counts, the model was run using the standard fixed 50% misclassification parameter (allowing for the misclassification of moulted pups as whitecoats), and re-run with the model allowed to estimate the misclassification proportion for each colony individually. In previous years, allowing the misclassification parameter to run free did not significantly affect either the model fits (cvs) or the production estimates. In 2008, the run estimating the misclassified, produced better fits with consistently lower confidence intervals. The productions reported here differ from previous years in that the misclassification proportion has been allowed to run free.

3. Trends in pup production

The differences in pup production at the main island groups are shown in Table 1. Between 2007 and 2008, total pup production at annually monitored colonies increased by 6.91% overall with the change varying from –0.99% in Orkney to +21.41% at the Isle of May and Fast Castle. Pup production at colonies in the Outer Hebrides increased by 9.28% after four consecutive years of decline (Figure 3a).

2008 appeared to be a good year for grey seals with increases in pup production at most colonies, including those that were not aerially surveyed by SMRU, in particular the Farne Islands. Once again, the North Sea colonies were the only group where an increasing trend has continued (Figures 2b and 3b, Table 1).

Figure 2a and 2b and Table 1 show that 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 2003 and 2008) is shown in Table 1. The overall annual change, for all colonies combined, was +0.47%. Locally, the change varied from –1.07% in the Inner Hebrides to +14.61% at the relatively small colonies of Donna Nook, Blakeney Point and Horsey. Changes for the two preceding five-year intervals, 1993 to 1998 and 1998 to 2003, are also shown in Table 1. These changes in five-yearly intervals are probably the best indication of the current trends in grey seal 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 observer 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 within 2.2% to 2.5% of the point estimate for colonies in the Inner and Outer Hebrides and in Orkney to 16.0% for Fast Castle (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 2008 with pup production estimated using a normal distribution (Table 2). The 95% confidence intervals for the production estimates for these three colonies were 24.0%, 12.0% and 10.3% of the point estimates, respectively. Under Other colonies, Table 2 includes the total count for the colonies listed individually in Table 4. 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

In Shetland, SNH staff coordinated a team of volunteers who carried out boat and ground counts of a number of breeding colonies.

Poor weather severely restricted ground or boat surveys and only one colony (Whalsay Islands) had sufficient counts for SMRU’s modelling process (standard model using normal distribution). As a result, the pup production estimate for Shetland is a combination of estimates from 2008 (Whalsay Is.) and 2007 (most other colonies) and from 2004 (Uyea, S Havra, Fitfull Head and Muckle Roe).

As with 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 2008 was **819** pups. This figure is a combination of modelled estimates, of maximum counts and of the most recent counts from previous surveys. 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.

During their final boat survey, SNH staff observed two individuals killing pups with a fence post on one of the Whalsay Islands and reported the incident to Northern Constabulary. One of the individuals was successfully prosecuted.

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 2009

In the 2009 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 helped collect or provided the data presented in this report. These include: John Walton and colleagues (National Trust, Farne Islands), Rob Lidstone-Scott (Lincolnshire Wildlife Trust, Donna Nook), David Wood (National Trust, Blakeney Point), Ron Morris and Bill Bruce (Forth Seabird Group, Forth inner islands). SNH Shetland for their 2008 grey seal survey. Thanks to Donald Malone for help during the 2008 surveys and to Jess Fedak who carefully and cheerfully entered lots of numbers. We are grateful to Bill Giles who, once again, enthusiastically and expertly piloted the grey seal survey aircraft.

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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.

Table 1. Pup production estimates for colonies in the main island groups surveyed in 2008. 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**	**2008 pup production**	**Overall annual change in pup production**			
			From previous year	**For previous 15 years, in 5 year intervals**		
			2007-2008	**1993-1998**	**1998-2003**	**2003-2008**
Inner Hebrides	3,071	**3,356**	+9.28%	+1.92%	+2.07%	-1.07%
Outer Hebrides	11,189	**12,712**	+13.61%	+0.64%	-0.25%	-1.03%
Orkney	18,952	**18,765**	-0.99%	+8.33%	+3.48%	+0.27%
Isle of May + Fast Castle	2,756	**3,346**	+21.41%	+10.81%	+3.67%	+3.12%
Farne Islands	1,164	**1,318**	+13.23%	+5.17%	+2.77%	+1.09%
Donna Nook + Blakeney Pt + Horsey	1,640	**1,953**	+19.09%	+13.52%	+16.23%	+14.61%
North Sea (i.e. previous 3 areas)	5,560	**6,617**	+19.01%	+8.93%	+5.16%	+5.41%
Total	38,772	**41,450**	**+6.91%**	**+4.75%**	**+2.29%**	**+0.47%**

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, 2008	1,098
	[1]Loch Eriboll, Eilean nan Ron (Tongue) 2008	557
Other colonies	Various, see Table 4	967
[2]Shetland	2008	819
South-west Britain	South-west England, Wales 1994-2005	1,750
Northern Ireland	2005	100 (approx.)
Total		**5,291**

[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] See Table 5 for details of grey seal pup production in Shetland..

Table 3. Estimates of pup production for colonies in the Inner and Outer Hebrides, Orkney and the North Sea, 1960-2008.

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
2008	3356	12712	18765	6617	41450

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

Table 4. Scottish grey seal breeding sites that are not surveyed annually and/or have recently been included in the survey programme. Most recent data 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, 2008	40, 9, 47[1], **40**[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, 2008	60, 64, 42, **64**
	Fladda Chuain, North Skye	SMRU photo	2005, 2007, 2008	73, 43, **129**
	Trodday, NE Skye	SMRU photo	2008 New	**55**
	Heisgeir, Dubh Artach, Skerryvore	SMRU visual	1995, 1989, infrequent	None None
Outer Hebrides	Sound of Harris islands	SMRU photo	2002, 2005, 2007, 2008	358, 396, (194)[2], **296**
	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, 2008	50, 58, 67, 69, 25, **73**
	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, 2008	10, 27, 34, 21, 8, **17**
	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, 2008	<10, 4 86, 72, 110, 171, 206, **247**
Total				**967**

[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 2008. 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 Uyea in 2005 and 2006 are clearly underestimates as only those breeding on beaches that were visible from the mainland could be counted. These data were provided by SNH staff (assisted by SMRU in 2004) and by a team of hardy volunteers.

Location in Shetland	**2004**	**2005**	**2006**	**2007**	**2008**
	Estimated production (90% moulter classification)	**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	107 (max count)
Dale of Walls	66	43	18 (max count)	36 (max count)	10 (max count)
Muckle Roe	23	no count	no count	no count	no count
Rona’s Voe	106	83	50	57	45 (max count)
Mousa	140	117	156	128	122 (max count)
Fetlar	50	32	21 (max count)	23 (max count)	no count
Whalsey Islands	102 (max count)	72	77	103	119
South Havra	4 (max count)	no count	no count	no count	no count
Fitful Head	18 (max count)	no count	no count	no count	no count
Uyea (N. Mainland)	238 (max count)	122 (part only)	114 (part only)	101 (part only)	69 (max count, part only)
NE Unst				3 (max count)	no count
Noss				2 (max count)	no count
Total max counts	**362**	**0**	**39**	**64**	**353**
Modelled total	**581**	**604**	**550**	**557**	**119**
Estimated production (combination using most recent previous estimates)	**943**	**765**	**758**	**803**	**819**

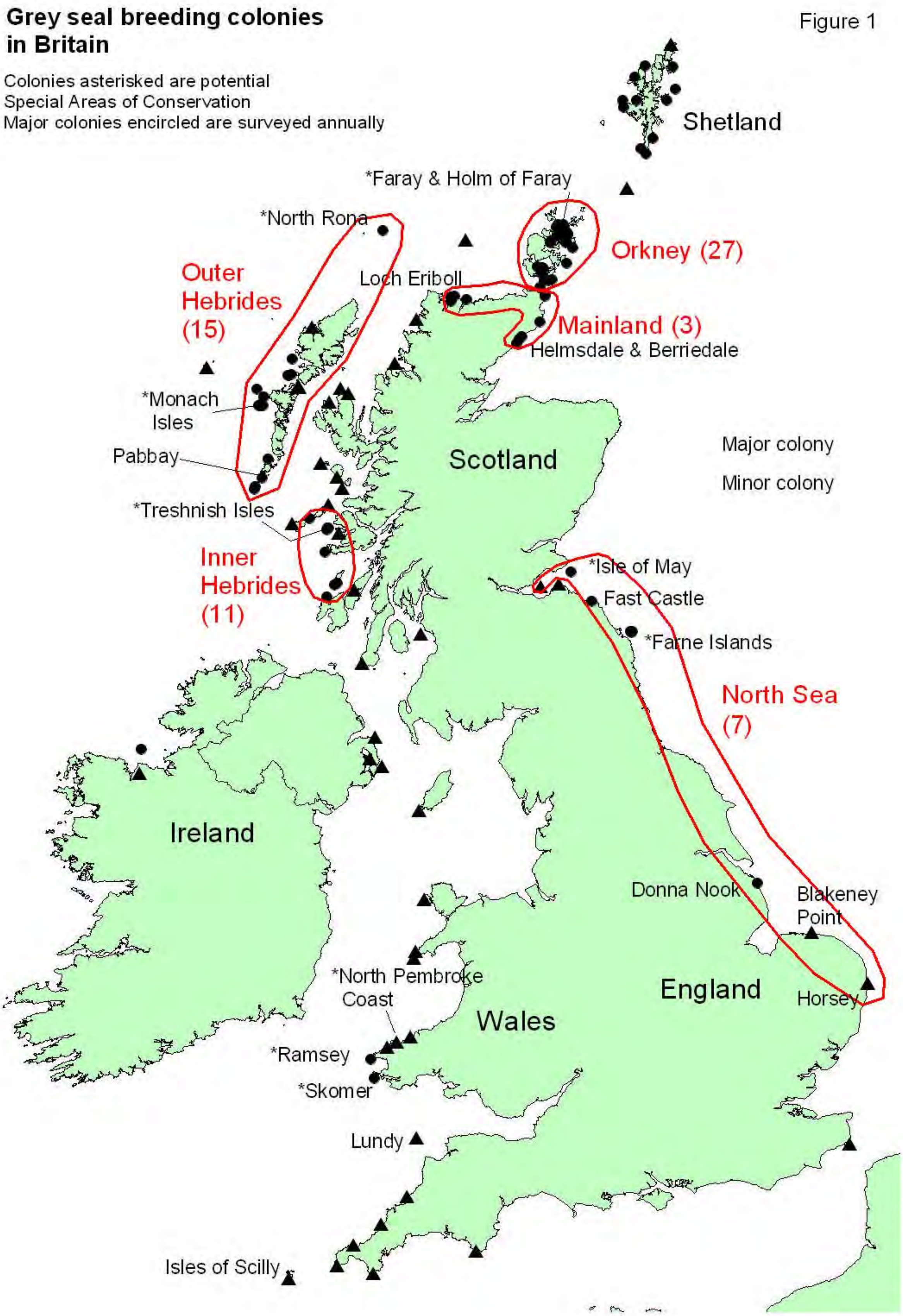

Grey seal breeding colonies
in Britain
Colonies asterisked are potential
Special Areas of Conservation
Major colonies encircled are surveyed annually
Figure 1
Shetland
*Faray & Holm of Faray
*North Rona
Orkney (27)
Outer
Hebrides
(15)
Loch Eriboll
Mainland (3)
Helmsdale & Berriedale
*Monach
Isles
Pabbay
Scotland
Major colony
Minor colony
*Treshnish Isles
Inner
Hebrides
(11)
*Isle of May
Fast Castle
*Farne Islands
North Sea
(7)
Ireland
Donna Nook
Blakeney
Point
*North Pembroke
Coast
England
Horsey
Wales
*Ramsey
*Skomer
Lundy
Isles of Scilly

Figure 2a. Total estimated grey seal pup production, with 95% confidence limits, at all the major, annually monitored colonies in Scotland and England from 1984 to 2008.

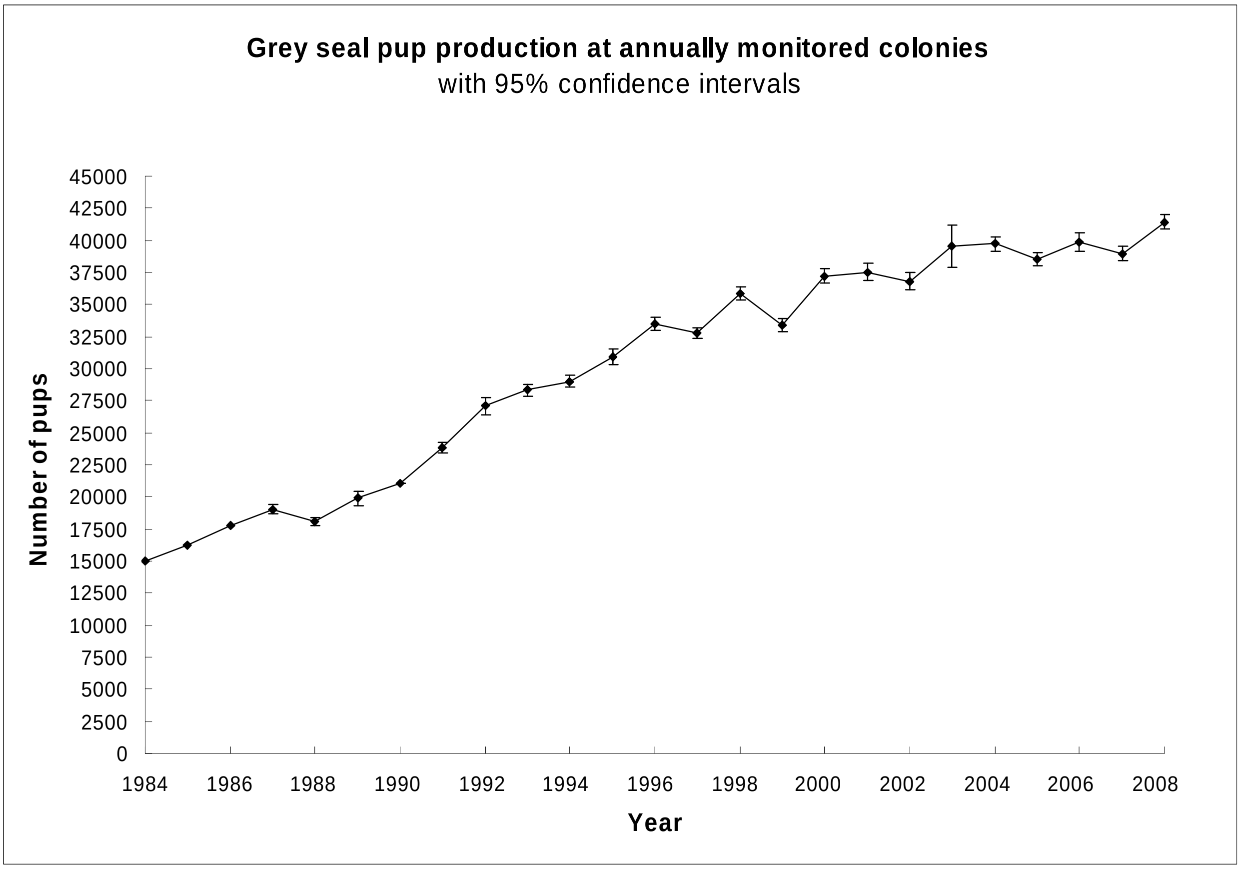


Figure 2b. Grey seal pup production trajectories from 1960 to 2008.

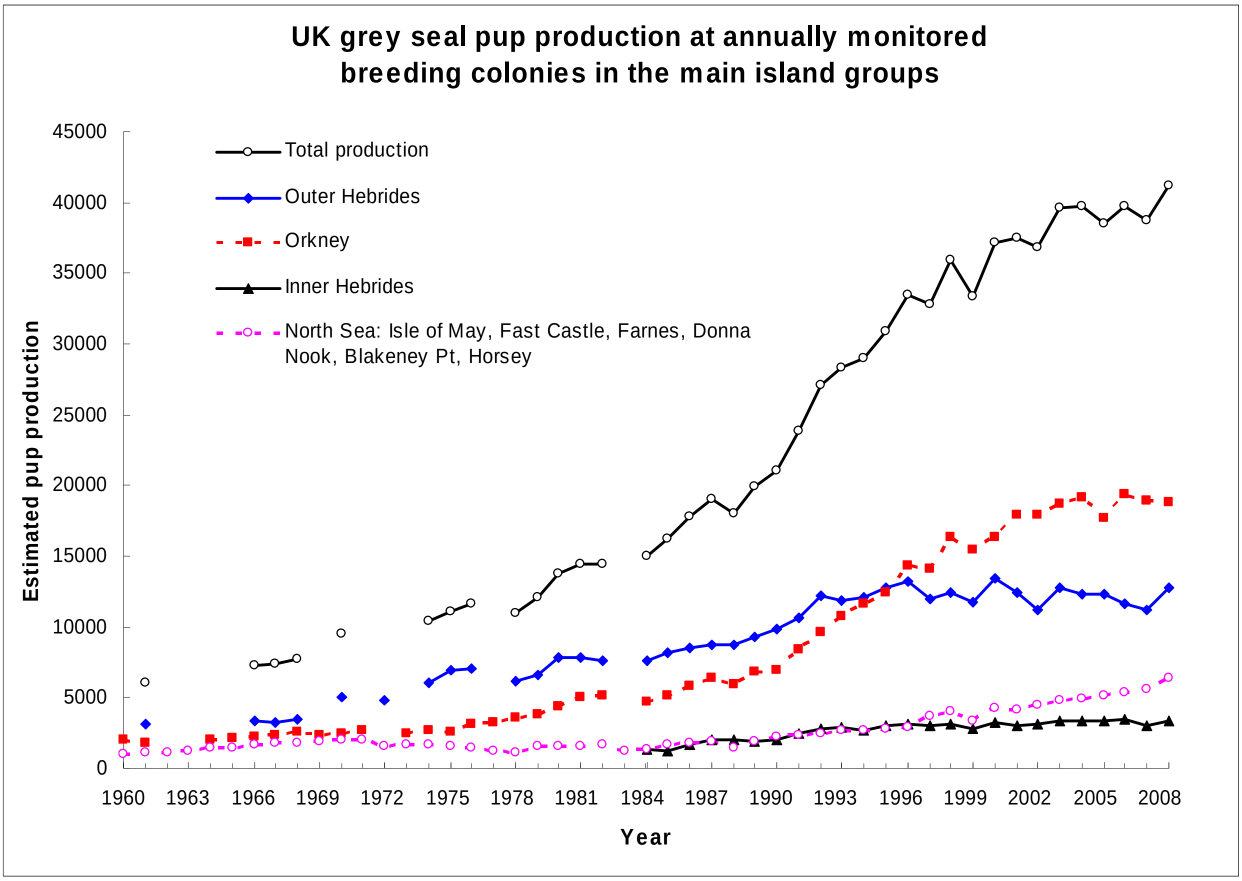
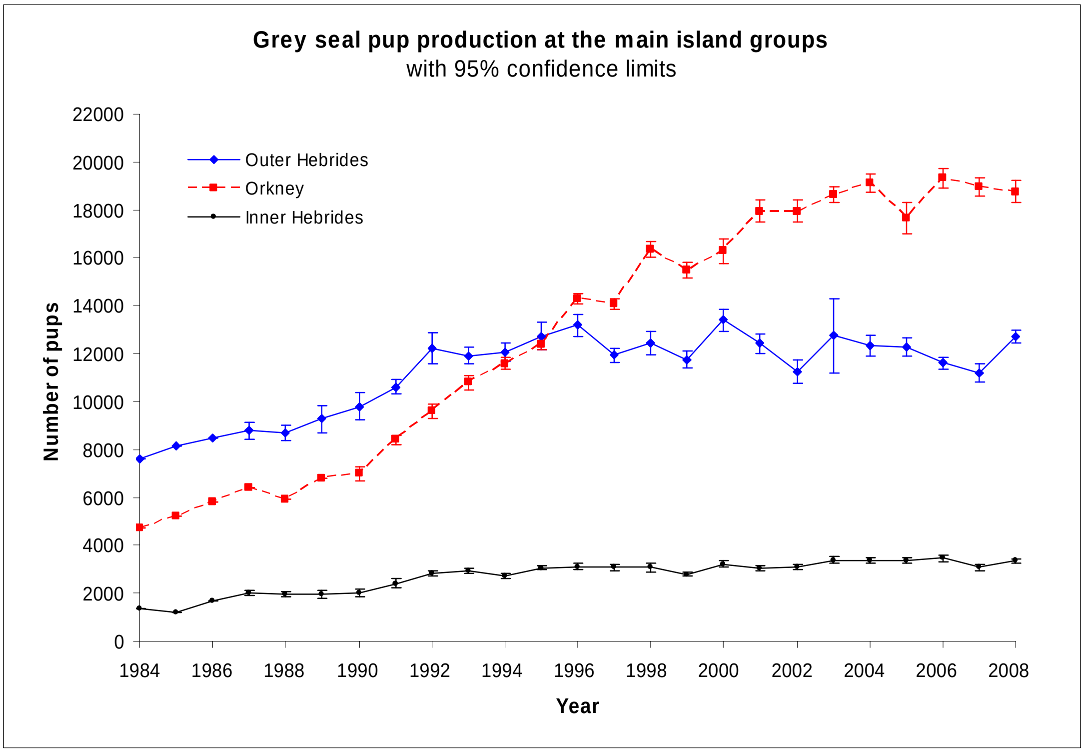
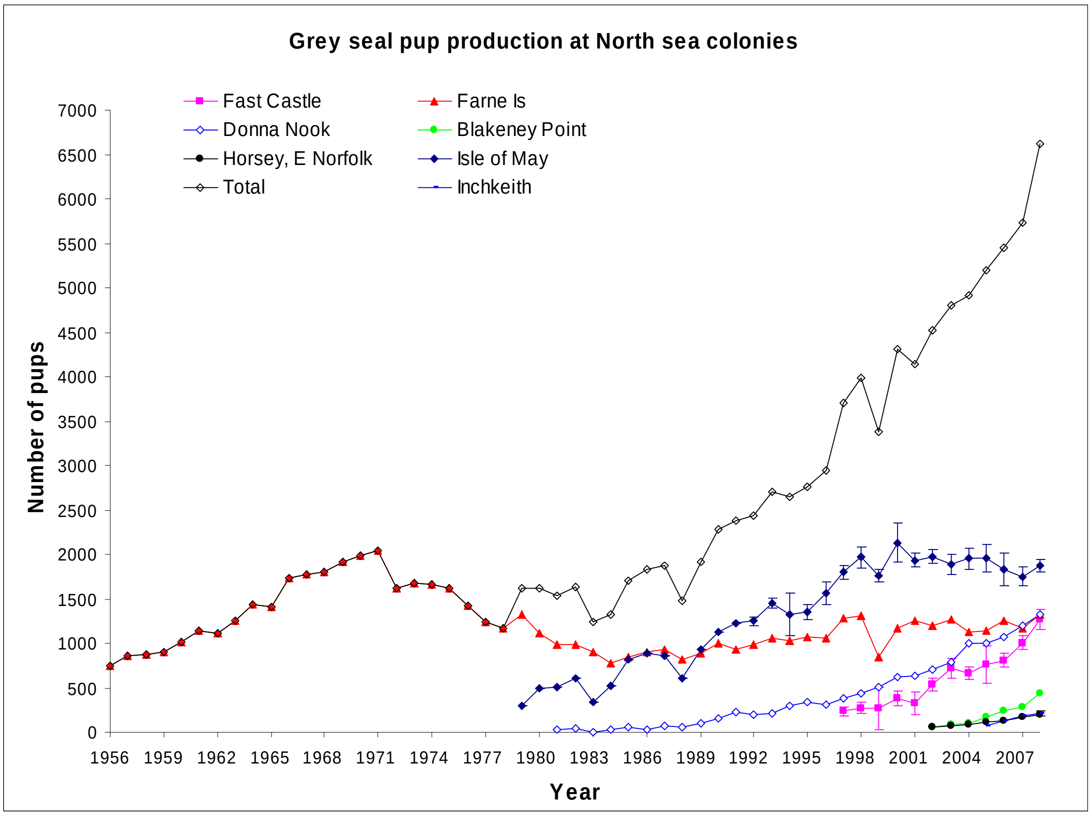


Figure 3. Trends in pup production at the major grey seal breeding colonies since 1984. Production values are shown with their 95% confidence limits where these are available. These limits assume that the various pup development parameters involved in the estimation procedure remain constant from year 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 2008.

NERC Sea Mammal Research Unit and Centre for Research into Ecological and Environmental Modelling, University of St Andrews, St Andrews KY16 8LB

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

Summary

We fitted six Bayesian state-space models of British grey seal population dynamics to regional estimates of pup production from 1984 to 2008. The models and fitting methods were the same as those used by Thomas and Harwood (2008), updated to include the 2008 data. We compared models by calculating Bayesian posterior model probabilities, firstly giving equal prior weight to each model and secondly assigning prior weights that penalized models with more parameters. Results for both sets of priors were similar. As with last year's briefing paper, models that allow for flexible forms of density dependence, but no movement of recruiting seals among regions, were strongly favoured over those with simpler density dependence or with movement between regions. However, unlike last year, the model with density dependent pup survival (EDDSNM) had significantly more support than that with density dependent female fecundity (EDDFNM; posterior model probabilities 0.95 and 0.05 respectively with the weighted prior). The estimated adult population size in 2008 using these two models was 118,700 (95% CI 85,900-168,100) and 255,900 (95% CI 196,500-439,600) respectively. A combined model, containing populations in proportion to their posterior model probability, yielded an estimate of 126,200 (95% CI 89,200-244,800). The estimated model probabilities should be treated with caution because, in theory, it should be hard to distinguish the two models from pup count data alone.

Introduction

This paper presents updated estimates of population size and related demographic parameters, based on the models and fitting methods described in Thomas and Harwood (2008). Six models are fit to regional estimates of pup production from 1984-2008, using a Bayesian state space modelling framework, with fitting performed using a computer-intensive algorithm called a Monte Carlo particle filter. Models are compared using methods similar to those of Thomas and Harwood (2008), updated slightly to bring them into line with mainstream practice.

The six models are as follows. Two allow for density dependent pup survival (DDS) and density dependent fecundity (DDF). In both cases, the density dependent relationship follows a Beverton-Holt function. 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. We refer to these as extended density dependent pup survival (EDDS) extended density dependent fecundity (EDDF). The final two models allow extended density dependence but assume no movement between regions (EDDSNM and EDDFNM). All models include an observation model that assumes pup production estimates are normally distributed about the true pup production with no bias and constant coefficient of variation. 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.

Materials and Methods

Models

The models are described fully in Thomas and Harwood (2008) and papers cited therein. In summary, they track seal population numbers in 7 age groups (pups, age 1-5 females and age 6+ females) in each of four regions (North Sea, Inner Hebrides, Outer Hebrides and Orkney). There are four population sub-processes: survival, ageing and pup sexing, movement of recruiting females, and breeding. The six models make different assumptions about these sub-processes. Models have up to 11 parameters. All share 5: adult survival ϕ_a, one carrying capacity parameter-related parameter for each region β_1 - β_4 and the observation precision parameter ψ. Models with density dependent survival (DDS, EDDS, EDDSNM) have a parameter for maximum pup survival $\phi_{p\max}$ and another for constant fecundity α, while models with density dependent fecundity (DDF, EDDF, EDDFNM) have a parameter for maximum fecundity $\alpha_{\max}$ and constant pup survival ϕ_p. Models with extended density dependence (all those starting "E") have an additional parameter, ρ, for the shape of the density-dependent response. DDS, DDF, EDDS and EDDF models have three additional movement parameters, controlling the relative importance of site faithfulness (γ_{sf}) density dependence (γ_{dd}), and distance between regions (γ_{dist}) in affecting movement.

Data and Priors

Our input data were the pup production estimates for 1984-2007 from Duck (2009), aggregated into regions.

Prior distributions for each parameter were the same as those of Thomas and Harwood (2008) and are given in Table 1. We followed previous briefing papers in using a re-parameterization of the model to set priors on the numbers of pups at carrying capacity in each region, denoted χ_r for region *r*, rather than directly on the β s.

Table 1. Prior parameter distributions

Param	Distribution	Mean	Stdev
ϕ_a	Be(22.05,1.15)	0.95	0.04
$\phi_{p\max}$, ϕ_p	Be(14.53,6.23)	0.7	0.1
χ_1	Ga(4,2500)	10000	5000
χ_2	Ga(4,1250)	5000	2500
χ_3	Ga(4,3750)	15000	7500
χ_4	Ga(4,10000)	40000	20000
ρ	Ga(4,2.5)	10	5
γ_{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

Prior distributions for the states were generated using the 1984 data, as described by Thomas and Harwood (2008). The prior distribution on ψ implies a prior mean on observation CV of 0.10 and prior standard deviation of 0.05.

Fitting Method

We used the particle filtering algorithm of Thomas and Harwood (2008). This involves simulating samples from the prior distributions, projecting them forward in time according to the population model, and then resampling and/or reweighting them according to their likelihood given the data. The final output is a weighted sample from the posterior distribution. Many samples are required for accurate estimation of the posterior, and we generated between 121 and 250 runs of 1,000,000 samples, depending on the model (Table 2). Rejection control was used to reduce the number of samples from the posterior that were required to be stored, and the effective sample size of unique initial samples was calculated to assess the level of Monte Carlo error, as detailed in Thomas and Harwood (2008). As an additional check, we ran the simulations for the two best supported models twice, to check the inferences were sufficiently accurate..

Model comparison and model outputs

In previous briefing papers we have compared models using the mean posterior Akaike Information Criterion (AIC). While this has a good justification in likelihood-based inference, it is not a commonly used measure in Bayesian statistics, so we instead calculated the more standard posterior model probability (e.g., Hoeting et al. 1999) – this is the posterior probability that each model is the correct model, given that one of them is.

To calculate posterior model probability, one must specify a prior probability for each model. We did this in two ways. First, we assumed an equal prior probability for each of the six models, as is standard practice. Second, to more closely mimic the previous use of mean posterior AIC, we assumed that each additional parameter in a model halved the prior probability for that model relative to the other models. For example, the prior probabilities for two models, one with 9 parameter and one with 11 would be 0.8 and 0.2 respectively. This effectively places a prior penalty on parameter-rich models relative to simple models.

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 observation precision parameter ψ by fitting the data to the DDS model alone (this being the model with most data support in historical briefing papers). We then took the estimated posterior mean ψ from this run and used this as a fixed value when fitting all six models. We present model selection statistics for all models using the fixed observation error value.

For all models, we also present posterior estimates of the model parameters and estimated pup production from 1984-2008. The models additionally estimate adult female numbers, but do not include adult males. As with previous briefing papers, 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 model probabilities.

Results

Unique ancestral particle numbers

The number of particles retained and effective sample sizes (Table 2) were similar to those of Thomas and Harwood (2008).

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 ($\times 10^7$)	K^* ($\times 10^7$)	U ($\times 10^4$)	ESS_u
ψ estimated				
DDS	121	4.7	14.0	48.6
ψ fixed				
DDS	150	15.9	17.3	235.8
DDF	150	14.3	24.0	267.7
EDDS	150	14.2	8.2	126.6
EDDF	150	9.8	4.2	62.4
EDDSNM	250	34.2	28.8	421.8
EDDFNM	250	24.8	11.0	218.9

Estimate of observation precision parameter

The DDS model run where ψ is estimated produced a posterior mean estimate of 87.9 with 95% posterior credibility interval (CI) of 56.8 to 123.6. This value corresponds to an estimated CV of 0.11 (95%CI 0.09 – 0.13). The value of ψ =87.9 was then used in all model runs reported in subsequent sections.

Comparison of models for density dependence and movement

Smoothed posterior mean estimates of pup production for the six models, run with ψ fixed at 87.9, are shown in Figure 1, while smoothed posterior means and 95% credible intervals are shown in Figure 2. Posterior parameter estimates are shown in Figure 3.

The pup production estimates from the DDS and DDF models show clear, systematic lack of fit in all regions, except perhaps North Sea. For Inner and Outer Hebrides the estimates 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. The DDF model estimates for Outer Hebrides also show some minor discontinuity for the period 1984-1989. This is probably a result of irregularities in the estimated starting age structure. Parameter estimates are quite similar between these models. The posterior distributions of pup survival and fecundity are both very similar to their priors; adult survival has a similar mean to the prior but a smaller variance; the movement parameters are somewhat different from their priors – in particular γ_{dd} is rather smaller, indicating less movement than though a priori; the carrying capacity parameter estimates are somewhat higher than their priors, although more so for the DDS than DDF model.

Estimates of pup production from the EDDS and EDDF models show clear improvements to the fit, better reflecting the levelling off in counts in the Inner and Outer Hebrides. The recent levelling off in the Orkney is, however, again not reflected in the fits. The most recent high estimate from North Sea is well fit, at the expense of a series of negative residuals in previous years. Parameter estimates for pup survival and fecundity are again nearly identical to the prior in both models. Estimated adult survival is low in both models (0.91). The posterior mean estimate of the extended density dependence parameter, ρ, is higher for the EDDS model than the EDDF model (5.5 vs 3.5), although both have high variance. The carrying capacities of pups are estimated to be lower than their prior means and quite similar between the models.

Estimates from the no movement models (EDDSNM and EDDFNM) are similar to the extended density dependence models with movement for North Sea and Orkney, but for Inner and Outer Hebrides the fit does a somewhat better job of capturing the rapid increase in the 1980s, and pup production is estimated to have declined slightly in recent years. Parameter estimates are similar to those from the EDDS and EDDF models, although the estimated ρ is lower for EDDSNM than EDDS.

According to the model selection statistics (Table 3), the models with no movement are strongly favoured over those with movement. Note that the negative log integrated 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. Further, and in contrast to the results reported in Thomas and Harwood (2008), the EDDSNM model is strongly favoured over the EDDFNM model. The choice of priors for the models (equal vs. weighted to penalize parameter-rich models) makes little difference to the posterior model probabilities.

Table 3. Number of parameters, negative log integrated likelihood (-LnIL) and posterior model probabilities (p(M)) for models with fixed observation precision of 88.3 fit to data from 1984-2008. The first posterior model probability assumes equal prior weight to each model while the second penalizes models with more parameters (see text for details).

Model	# params	-LnIL	p(M) equal prior	p(M) wtd prior
DDS	10	774.66	0.00	0.00
DDF	10	771.72	0.00	0.00
EDDS	11	769.83	0.01	0.00
EDDF	11	771.10	0.00	0.00
EDDSNM	8	765.22	0.93	0.95
EDDFNM	8	768.12	0.05	0.05

Estimates of total population size

Estimated sizes of the 2008 adult population under each model are shown in Table 4; estimates for all other years are given in the Appendix.

Table 4. Estimated size, in thousands, of the British grey seal population at the start of the 2008 breeding season, derived from models fit to data from 1984-2008. Numbers are posterior means with 95% credibility intervals in brackets.

	DDS	DDF
North Sea	15.0 (12.0 19.5)	33.4 (25.0 47.6)
Inner Hebrides	9.4 (7.6 11.8)	25.1 (17.4 38.3)
Outer Hebrides	33.7 (26.3 43.1)	96.4 (64.7 155.6)
Orkney	58.2 (46.0 76.8)	123.2 (92.4 172.3)
Total	116.3 (91.9 151.1)	278.3 (199.4 414.0)
	EDDS	EDDF
North Sea	20.2 (12.3 29.4)	27.9 (21.2 37.2)
Inner Hebrides	10.1 (7.6 13.2)	17.0 (12.0 23.7)
Outer Hebrides	38.7 (29.1 50.6)	63.9 (48.0 85.4)
Orkney	74.3 (44.2 103.1)	95.5 (75.9 120.4)
Total	143.3 (93.2 196.3)	204.3 (157.2 266.7)
	EDDSNM	EDDFNM
North Sea	18.8 (12.1 26.9)	29.8 (22.9 46.2)
Inner Hebrides	8.7 (6.9 10.8)	22.6 (17.5 37.6)
Outer Hebrides	32.3 (25.4 39.2)	94.4 (70.4 181.3)
Orkney	58.9 (41.4 91.2)	109.0 (85.6 174.1)
Total	118.7 (85.9 168.1)	255.9 (196.5 439.6)
	Model averaged (wtd prior)	
North Sea	19.4 (12.2 29.6)	
Inner Hebrides	9.5 (6.9 21.8)	
Outer Hebrides	35.7 (25.5 87.7)	
Orkney	61.6 (41.6 107.0)	
Total	126.2 (89.2 244.8)	

Estimates from the DDS model are approximately 2.4 times less than those from the DDF model, and there is no overlap between the 95% posterior credibility intervals. Estimates from the EDDS model are higher than the DDS model, whereas 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, and indeed the total adult population estimate is nearly identical. These estimates are lower than those from 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 intermediate between those of the DDF and EDDF models. Estimates from the EDDSNM model are about 2.2 times smaller than those from the EDDFNM model, and there is no overlap between posterior 95% credibility intervals. These two models have virtually all the posterior model probability (Table 3) but, because much of this is due to the EDDSNM model, the resulting model averaged posterior means are similar to the EDDSNM values (Table 3 and Figure 4). The confidence intervals, however, are much wider, reflecting the estimated small chance that EDDFNM could be the correct model.

Second run of EDDSNM and EDDFNM models

A duplicate run of both these models produced very similar results to the first. The negative log integrated likelihoods were the same to 3 significant figures. Estimates of states and parameter estimates were also identical to 2 or 3 significant figures, apart from the estimate of carrying capacity of pups in Orkney, which differed in both cases by a digit in the second significant figure (i.e., by 1000).

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. By repeating the estimation procedure for the two favoured models, we have shown that Monte Carlo variation is tolerably low.

A second aspect of reliability is bias induced by the fitting algorithm. As discussed in previous reports, we expect this to be negligible given the current implementation of the algorithm, but further investigation is justified.

A third aspect is the stability of results. The model selection results are rather different from those obtained by Thomas and Harwood (2008), who used an almost identical dataset (just 2008 missing), and almost identical methods (slight change in model comparison methods). Previous work has shown that models with density dependent pup survival and fecundity should be nearly indistinguishable based on pup count data, so it is surprising that the current results indicate one model favoured over the other. Until this result is better understood, the conclusion that the EDDSNM model is greatly preferred over EDDFNM based on pup count data should be treated with caution.

Comparison with previous estimates

The estimates of total population size are similar those from last year, comparing the same years and models. The largest difference is the EDDS model, from which Thomas and Harwood (2008) obtained an estimate of adult population size in 2007 of 136, 600 (95%CI 85,400-189,100) and which in this paper is estimated as 140,500 (95%CI 94,100-188,500). Since the algorithm and models are the same, these differences must be caused by the additional year of data adjusting historical estimates.

Estimates of total population size from the EDDSNM model are very similar to those from the DDS model, which is the one traditionally used to report population estimates. Since the DDS model is clearly fitting the data very poorly, there seems ample justification to switch to the EDDSNM model, even if multi-model inference is not used in reporting the “headline” numbers.

Future work

At the 2008 SCOS meeting, the committee asked us to develop and fit a model combining density dependent survival and fecundity. This has proved more difficult than expected, and work on this is ongoing. We have also been working to improve the prior distribution on model parameters, based on new analyses of intensive mark-recapture studies of seals at the Isle of May and North Rhona. These studies provide strong support for fecundity values higher than those obtained in the current density dependent fecundity models.

As detailed by Duck (2009), the aerial survey methods were slightly different in 2008 (the plane flew lower to obtain better quality images). This led to different assumptions about the mis-classification rate for moulted pups being made in the models that produce the pup production estimates, which in turn led to slightly higher estimates of pup production (around 5% higher). Although these estimates are believed to be reliable, it is of interest to know how much the change in assumed mis-classification has affected the resulting estimate of adult population size. We are currently undertaking model runs to determine this, and will report results at the meeting.

Even though the models used in this report fit the data reasonably well, there are still some systematic departures of the estimated pup production from the observed values. We have begun investigating alternative biological models, focussing initially on a model that allows random annual variation in fecundity. We have also been investigating the use of pup production estimates from before 1984, as well as different methods to initialize the population model to avoid artefacts, such as those observed in the early DDF pup production estimates.

As stated earlier, the finding that the EDDSNM model has greater posterior model probability than EDDFNM should be treated with caution because, in theory, the pup production trajectories produced by these two models should be very similar. Further investigation of this finding is a priority.

References

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Hiby, L. and C.D. Duck. Unpublished. Estimates of the size of the British grey seal *Halichoerus grypus* population and levels of uncertainty.

Hoeting, J.A., D. Madigan, A.E. Raftery and C.T. Volinsky. Bayesian Model Averaging: A Tutorial. *Statistical Science* 14: 382-417.

Thomas, L. and J. Harwood. 2007. Estimating the size of the UK grey seal population between 1984 and 2006. *SCOS Briefing Paper 07/3*

Thomas, L. and J. Harwood. 2008. Estimating the size of the UK grey seal population between 1984 and 2007. *SCOS Briefing Paper 08/3*

Figure 1. Posterior mean estimates of true pup production (lines) from six models of grey seal population dynamics, where the observation precision parameter ψ is fixed at 88.3, fit to pup production estimates from 1984-2008 (circles).

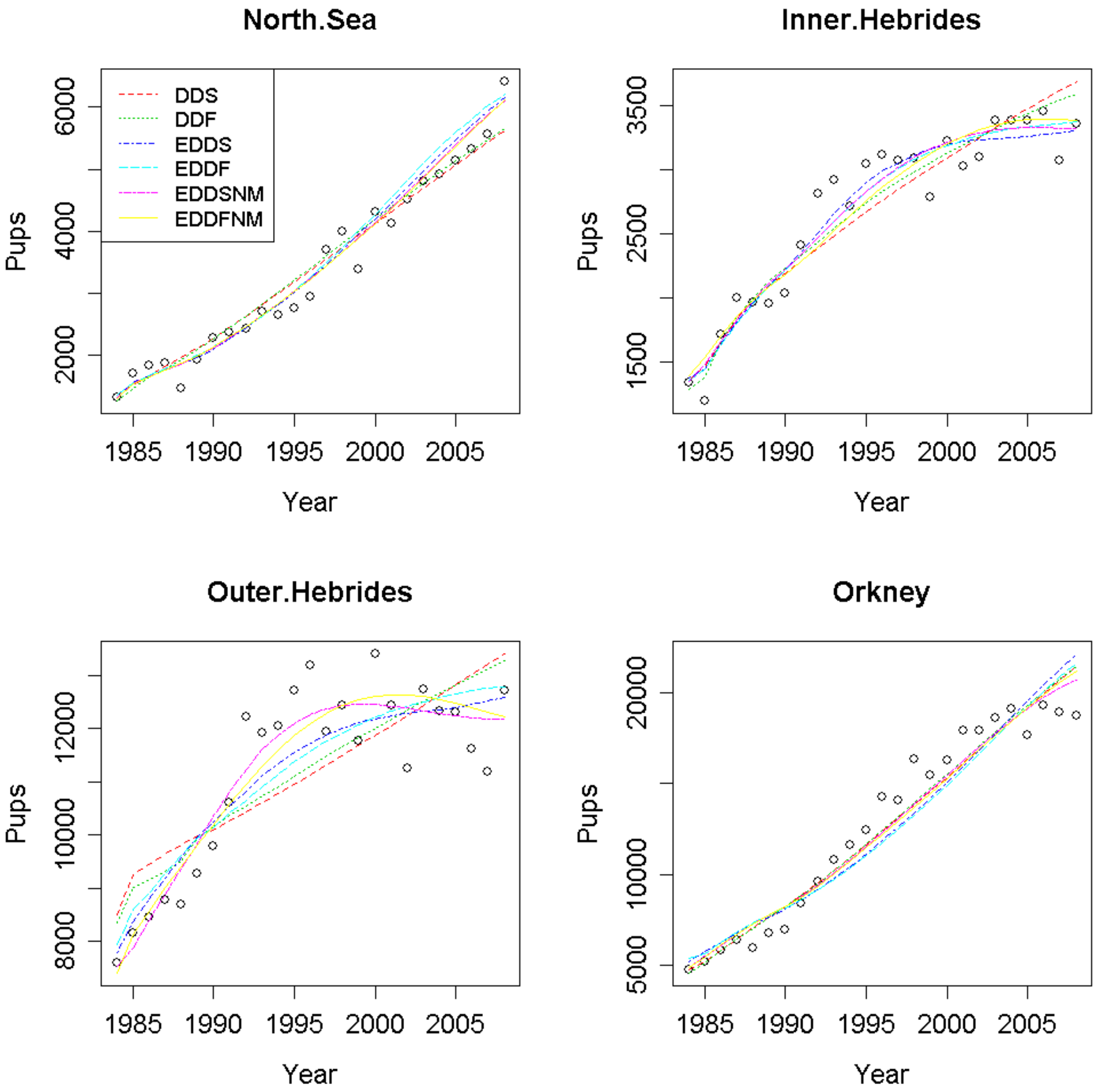
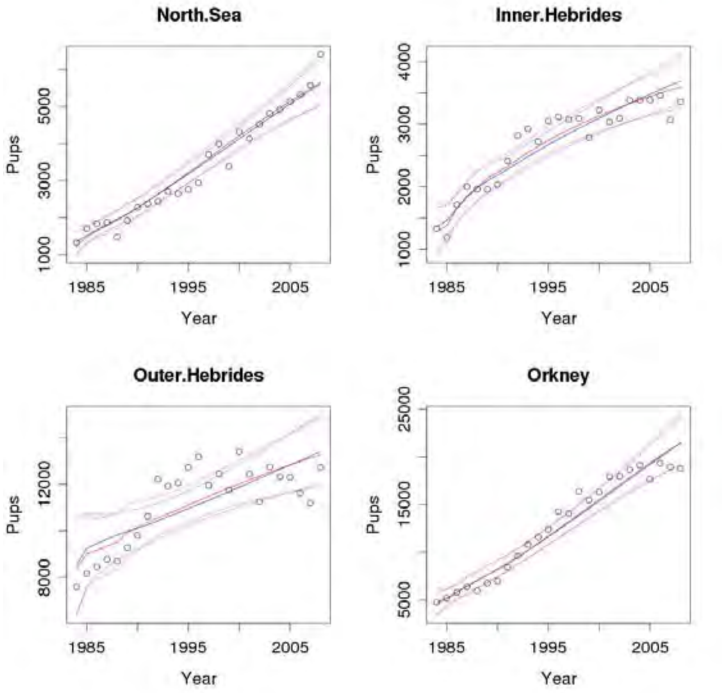
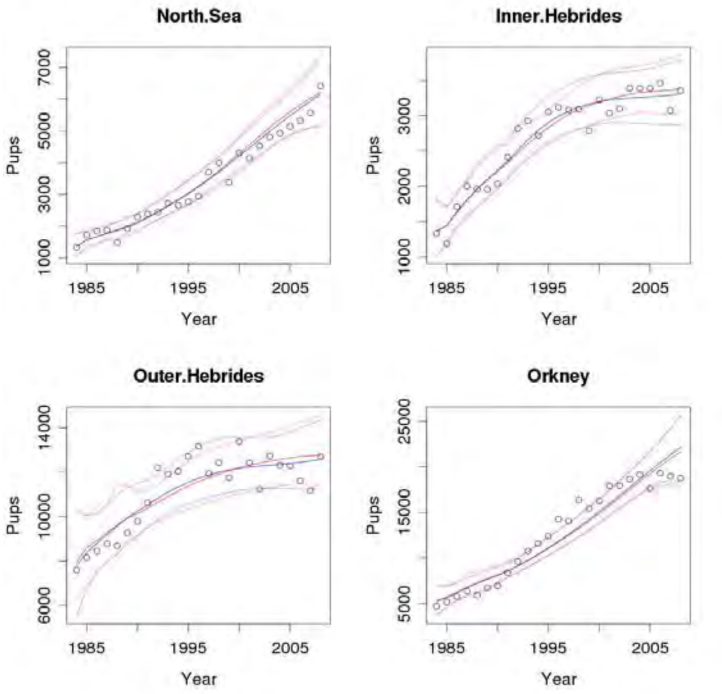


Figure 2. Estimates of true pup production from six models of grey seal population dynamics, where the observation precision parameter ψ is fixed at 87.9, fit to pup production estimates from 1984-2008. Input data are shown as circles, while the lines show the posterior mean bracketed by the 95% credibility intervals. For ease of comparison, estimates from two models are shown on each plot.

(a) Density dependent survival (DDS, blue); density dependent fecundity (DDF, red)



(b) Extended density dependent survival (EDDS, blue); extended density dependent fecundity (EDDF, red)



(c) Extended density dependent survival with no movement (EDDSNM, blue), extended density dependent fecundity with no movement (EDDFNM, red)

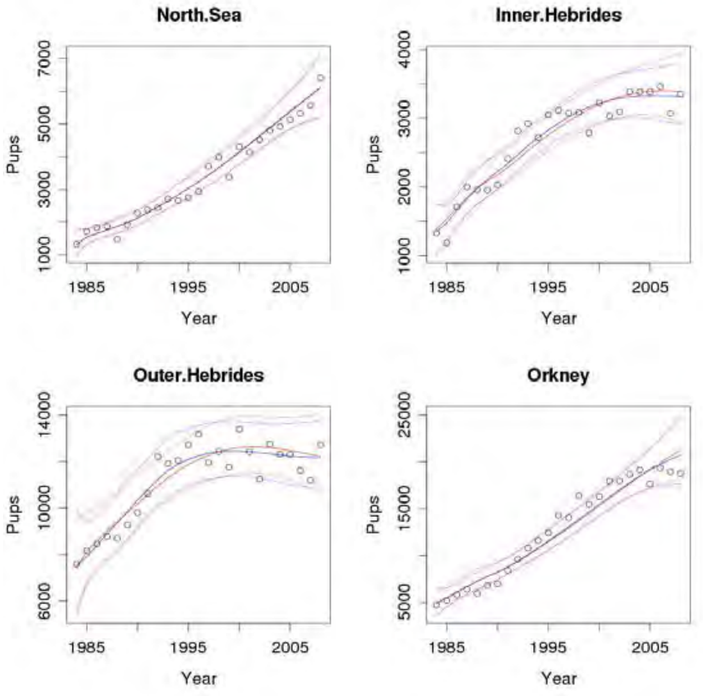
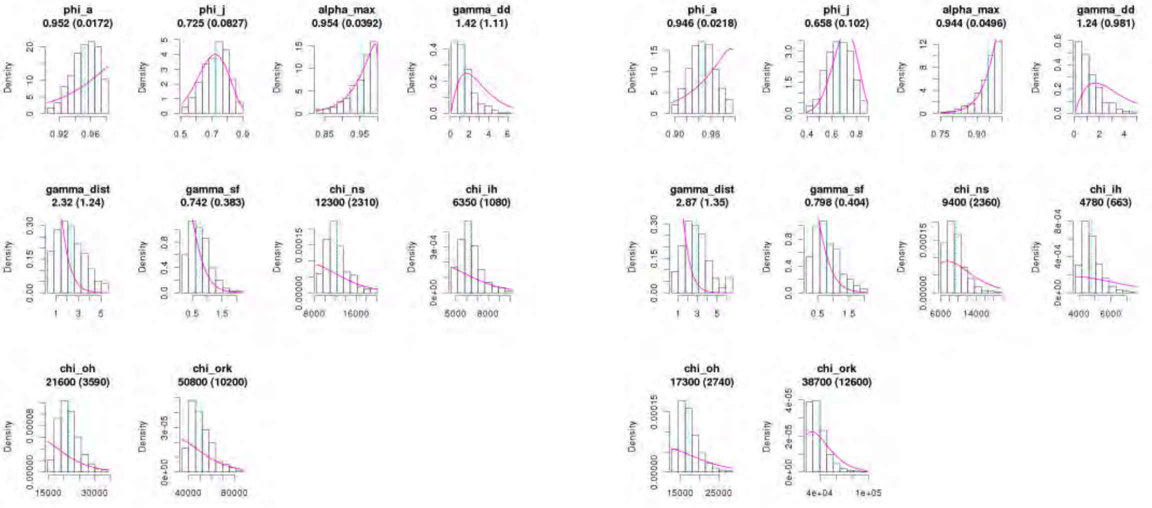
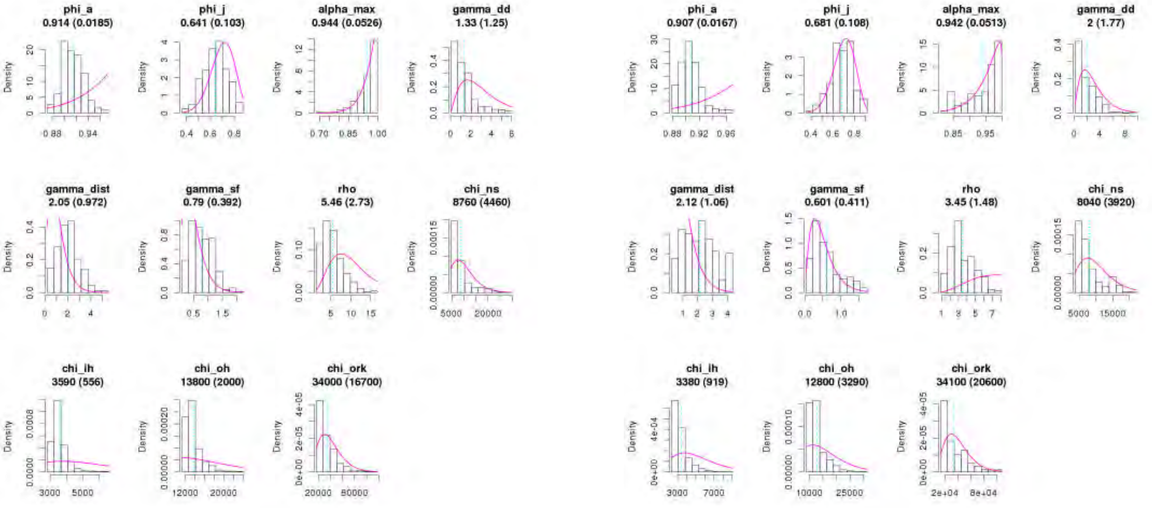


Figure 3. Posterior parameter estimates (histograms) and priors (solid lines) from six models of grey seal population dynamics where the observation precision parameter ψ is fixed at 89.5, fit to pup production estimates from 1984-2007. The vertical line shows the posterior mean, its value is given in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

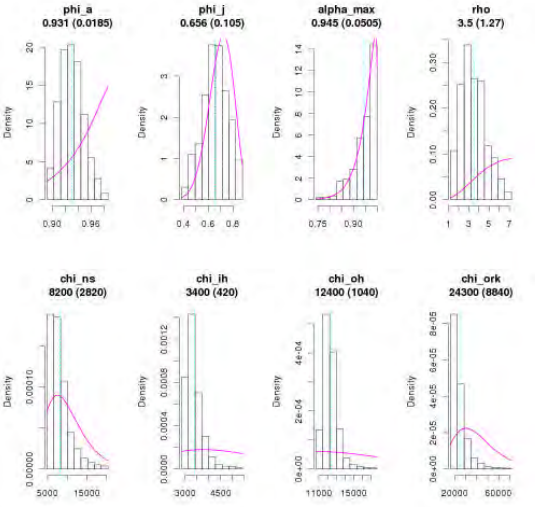

(a) Density dependent survival (DDS)

(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)

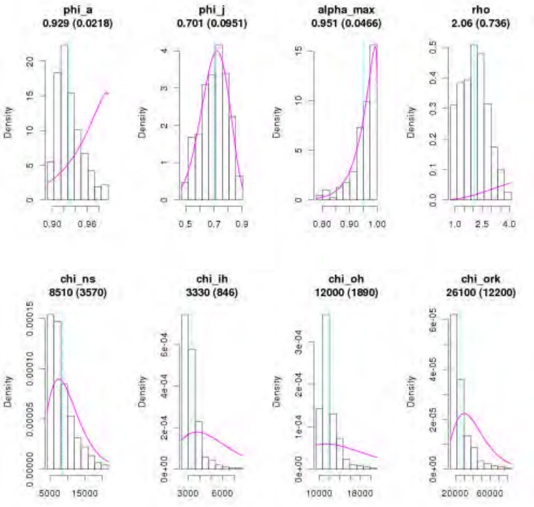
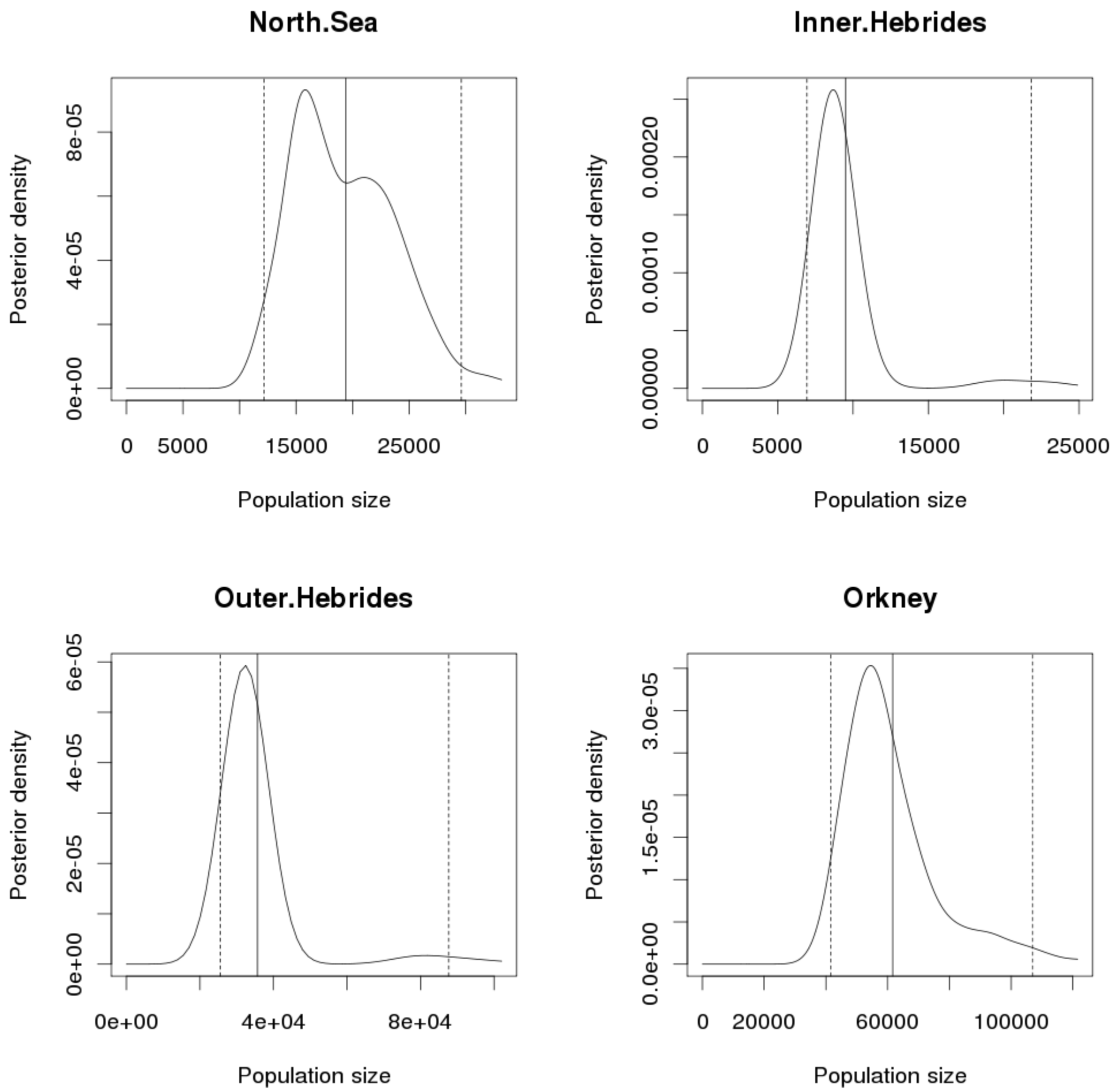


Figure 4. Posterior density of total population size at the beginning of the 2008 breeding season, combining the models and using prior model probabilities that penalize models with more parameters (see text). Only the EDDSNM and EDDFNM models have non-negligible posterior model probabilities, and these are responsible for the (large) left and (small) right peaks in the plots. 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	Orkney	Total
1984	4.5 (3.6 5.6)	4.5 (3.5 5.7)	25.2 (20.2 32.3)	16.7 (13.4 21.2)	50.8 (40.8 64.8)
1985	4.9 (4 6)	4.8 (3.9 6)	25.3 (20.5 31.8)	18.1 (14.8 22.8)	53 (43.2 66.5)
1986	5.3 (4.4 6.4)	5.1 (4.1 6.3)	25.5 (20.9 31.6)	19.6 (16.2 24.3)	55.4 (45.6 68.6)
1987	5.8 (4.8 6.9)	5.4 (4.4 6.7)	25.7 (21.3 31.7)	21.1 (17.6 25.9)	58 (48.1 71.1)
1988	6.2 (5.2 7.4)	5.6 (4.7 7.1)	26.1 (21.6 32.2)	22.8 (19 27.7)	60.7 (50.4 74.3)
1989	6.7 (5.6 7.9)	5.9 (4.9 7.4)	26.4 (21.8 32.6)	24.4 (20.4 29.6)	63.4 (52.7 77.5)
1990	7.1 (6 8.5)	6.1 (5.1 7.7)	26.7 (22 32.9)	26.2 (21.9 31.5)	66.2 (55 80.7)
1991	7.6 (6.4 9)	6.4 (5.3 8)	27.1 (22.2 33.3)	27.9 (23.4 33.6)	68.9 (57.3 83.9)
1992	8 (6.8 9.6)	6.6 (5.5 8.2)	27.4 (22.5 33.7)	29.6 (24.8 35.7)	71.7 (59.6 87.2)
1993	8.5 (7.2 10.2)	6.8 (5.6 8.5)	27.8 (22.8 34.1)	31.4 (26.3 37.9)	74.5 (61.9 90.8)
1994	8.9 (7.5 10.8)	7 (5.8 8.8)	28.2 (23 34.7)	33.2 (27.8 40.2)	77.3 (64.1 94.4)
1995	9.4 (7.9 11.4)	7.2 (6 9)	28.5 (23.3 35.2)	35 (29.2 42.6)	80.2 (66.3 98.2)
1996	9.8 (8.3 12)	7.4 (6.1 9.2)	28.9 (23.5 35.7)	36.9 (30.6 44.9)	83.1 (68.5 101.9)
1997	10.3 (8.6 12.6)	7.6 (6.3 9.5)	29.3 (23.7 36.3)	38.7 (32.1 47.3)	85.9 (70.7 105.6)
1998	10.8 (9 13.2)	7.8 (6.4 9.7)	29.7 (24 36.9)	40.5 (33.5 49.7)	88.8 (72.9 109.5)
1999	11.2 (9.3 13.8)	8 (6.6 9.9)	30.1 (24.2 37.4)	42.3 (34.9 52.3)	91.6 (74.9 113.4)
2000	11.7 (9.6 14.4)	8.1 (6.7 10.1)	30.5 (24.4 38)	44.2 (36.2 54.8)	94.5 (77 117.4)
2001	12.1 (9.9 15)	8.3 (6.8 10.4)	30.9 (24.6 38.6)	46 (37.6 57.4)	97.3 (79 121.4)
2002	12.5 (10.3 15.7)	8.5 (6.9 10.6)	31.3 (24.9 39.2)	47.8 (38.8 60)	100.1 (80.9 125.5)
2003	13 (10.6 16.3)	8.6 (7.1 10.8)	31.7 (25.2 39.9)	49.6 (40.1 62.8)	102.9 (82.9 129.7)
2004	13.4 (10.9 17)	8.8 (7.2 11)	32.1 (25.4 40.5)	51.3 (41.3 65.5)	105.6 (84.7 134)
2005	13.8 (11.1 17.6)	9 (7.3 11.2)	32.5 (25.6 41.1)	53.1 (42.5 68.3)	108.4 (86.6 138.3)
2006	14.2 (11.4 18.2)	9.1 (7.4 11.4)	32.9 (25.9 41.8)	54.8 (43.7 71.1)	111.1 (88.4 142.5)
2007	14.6 (11.7 18.9)	9.3 (7.5 11.6)	33.4 (26.1 42.4)	56.5 (44.8 73.9)	113.7 (90.1 146.8)
2008	15 (12 19.5)	9.4 (7.6 11.8)	33.7 (26.3 43.1)	58.2 (46 76.8)	116.3 (91.9 151.1)

Density dependent fecundity (DDF) model

Year	North Sea	Inner Hebrides	Outer Hebrides	Orkney	Total
1984	5.5 (4.2 7)	6.2 (4.5 8.4)	49.4 (35.1 71.8)	20 (15.2 25.3)	81 (59 112.5)
1985	6 (4.7 7.6)	7 (5.3 9.1)	50.5 (36.6 73.7)	21.9 (16.9 27.1)	85.4 (63.6 117.5)
1986	6.7 (5.3 8.3)	7.8 (6.1 9.9)	51.9 (38.4 74.9)	24 (18.8 29.4)	90.4 (68.6 122.6)
1987	7.4 (5.9 9.3)	8.6 (6.9 10.7)	53.4 (39.8 76.6)	26.5 (20.9 32.4)	95.9 (73.6 128.9)
1988	8.2 (6.6 10.3)	9.4 (7.6 11.9)	55 (40.9 78.1)	29.2 (23.1 35.7)	101.8 (78.2 135.9)
1989	9 (7.2 11.3)	10.3 (8.3 12.9)	56.7 (42.1 79.5)	32 (25.4 39.3)	108 (83 143.1)
1990	9.9 (7.8 12.6)	11.1 (8.9 14.1)	58.5 (43.4 81.7)	35.1 (27.9 43.3)	114.6 (88 151.7)
1991	10.8 (8.5 13.9)	12 (9.5 15.3)	60.4 (44.6 84.1)	38.4 (30.3 47.6)	121.5 (92.9 160.9)
1992	11.8 (9.2 15.3)	12.8 (10.1 16.5)	62.3 (45.8 86.1)	41.8 (32.8 52.3)	128.7 (98 170.2)
1993	12.8 (10 16.8)	13.6 (10.7 17.7)	64.3 (47.1 89.7)	45.5 (35.7 57.5)	136.2 (103.5 181.6)
1994	13.9 (10.8 18.4)	14.4 (11.2 18.9)	66.2 (48.3 93.2)	49.4 (38.8 63)	144 (109.1 193.5)
1995	15 (11.6 20.1)	15.2 (11.8 20.2)	68.2 (49.5 96.5)	53.5 (41.7 68.9)	152 (114.7 205.6)
1996	16.2 (12.5 21.8)	16 (12.3 21.5)	70.3 (50.8 100.1)	57.9 (44.8 75.1)	160.4 (120.4 218.6)
1997	17.5 (13.4 23.7)	16.8 (12.8 22.8)	72.3 (52 103.7)	62.4 (48.1 81.9)	169.1 (126.3 232.2)
1998	18.8 (14.4 25.6)	17.6 (13.3 24.2)	74.4 (53.1 108)	67.2 (51.5 89.3)	178 (132.3 247.1)
1999	20.1 (15.3 27.5)	18.4 (13.7 25.5)	76.6 (54.3 111.6)	72.1 (55.1 96.8)	187.2 (138.5 261.5)
2000	21.5 (16.4 29.6)	19.2 (14.2 27)	78.7 (55.5 116.5)	77.2 (58.9 104.7)	196.6 (144.9 277.7)
2001	22.9 (17.4 31.7)	19.9 (14.6 28.4)	80.9 (56.7 121.7)	82.5 (62.8 112.7)	206.2 (151.5 294.5)
2002	24.3 (18.4 33.9)	20.7 (15 29.8)	83.1 (57.8 127.1)	87.9 (66.8 120.8)	216 (158.1 311.6)
2003	25.8 (19.5 36.1)	21.4 (15.4 31.2)	85.3 (58.9 132.3)	93.5 (70.9 129.2)	226 (164.8 328.8)
2004	27.3 (20.6 38.3)	22.2 (15.8 32.6)	87.5 (60.1 137.5)	99.3 (75 137.7)	236.2 (171.5 346)
2005	28.8 (21.7 40.6)	22.9 (16.2 34)	89.7 (61.3 141.9)	105.1 (79.2 146.3)	246.6 (178.3 362.8)
2006	30.3 (22.8 42.9)	23.7 (16.6 35.4)	91.9 (62.4 145.8)	111.1 (83.5 155.1)	257 (185.2 379.3)
2007	31.9 (23.9 45.3)	24.4 (17 36.9)	94.2 (63.5 150.8)	117.2 (87.8 163.8)	267.6 (192.2 396.8)
2008	33.4 (25 47.6)	25.1 (17.4 38.3)	96.4 (64.7 155.6)	123.3 (92.4 172.3)	278.3 (199.4 414)

Extended density dependent survival (EDDS) model

Year	North Sea	Inner Hebrides	Outer Hebrides	Orkney	Total
1984	5.4 (4.2 6.8)	5.6 (4.2 7.4)	30.1 (22.3 38.3)	21.7 (15.3 27.5)	62.8 (46 80)
1985	5.7 (4.5 7.2)	5.9 (4.6 7.6)	31.1 (23.4 39.4)	22.8 (16.9 28.7)	65.5 (49.5 82.9)
1986	6.1 (4.9 7.4)	6.3 (4.9 7.8)	32.2 (24.6 40.7)	24 (18.5 30.4)	68.6 (53 86.3)
1987	6.6 (5.4 7.9)	6.7 (5.3 8.2)	33.3 (24.9 41.5)	25.5 (20.2 31.9)	72 (55.7 89.4)
1988	7 (5.8 8.4)	7.1 (5.6 8.5)	34.4 (26.1 42.9)	27.1 (21.7 33.7)	75.6 (59.1 93.5)
1989	7.5 (6.1 8.9)	7.6 (5.9 9.2)	35.2 (27.1 44.1)	28.8 (23.2 35.8)	79.1 (62.3 98)
1990	8 (6.5 9.5)	8.1 (6.3 9.9)	35.9 (28.1 44.8)	30.7 (25 37.8)	82.6 (65.9 102)
1991	8.5 (7 10.1)	8.5 (6.6 10.5)	36.5 (28.4 45.4)	32.6 (26.8 40.2)	86.1 (68.8 106.1)
1992	9.1 (7.5 10.7)	8.9 (7 11)	36.9 (28.5 46)	34.6 (28.5 42.3)	89.6 (71.4 110)
1993	9.8 (8 11.5)	9.3 (7.2 11.5)	37.3 (28.6 46.7)	36.8 (30.3 44.6)	93.1 (74.1 114.3)
1994	10.5 (8.5 12.3)	9.5 (7.3 11.9)	37.6 (28.7 47.3)	39.1 (32 47.3)	96.7 (76.6 118.8)
1995	11.2 (9 13.1)	9.7 (7.4 12.4)	37.8 (28.8 47.7)	41.5 (34.1 50.3)	100.2 (79.3 123.4)
1996	11.9 (9.5 14)	9.9 (7.5 12.5)	37.9 (28.7 47.9)	44 (36.1 53.4)	103.7 (81.8 127.8)
1997	12.7 (10.1 15)	9.9 (7.6 12.6)	37.9 (28.6 48)	46.6 (38.1 56.6)	107.2 (84.5 132.2)
1998	13.5 (10.8 16)	9.9 (7.6 12.6)	38 (28.6 48.1)	49.3 (40.1 60)	110.7 (87.1 136.7)
1999	14.3 (11.5 17.1)	9.9 (7.6 12.6)	37.9 (28.6 48.2)	52 (42.1 63.4)	114.2 (89.8 141.4)
2000	15.1 (12.1 18.2)	9.9 (7.5 12.6)	37.9 (28.7 48.3)	54.7 (44.1 66.9)	117.7 (92.4 146.1)
2001	15.9 (12.6 19.4)	9.9 (7.5 12.7)	37.9 (28.7 48.5)	57.4 (45.5 70.5)	121.2 (94.2 151)
2002	16.7 (12.8 20.6)	9.9 (7.5 12.7)	38 (28.7 48.8)	60.1 (46.4 74.3)	124.6 (95.4 156.4)
2003	17.4 (12.8 21.9)	9.9 (7.5 12.8)	38 (28.8 49.2)	62.6 (46.8 78.4)	128 (95.8 162.2)
2004	18 (12.6 23.2)	9.9 (7.4 12.9)	38.1 (28.8 49.4)	65.1 (46.8 82.6)	131.3 (95.7 168.1)
2005	18.7 (12.5 24.6)	10 (7.5 12.9)	38.3 (28.9 49.6)	67.5 (46.7 87.1)	134.4 (95.6 174.2)
2006	19.2 (12.4 26.1)	10 (7.5 13)	38.4 (29 49.9)	69.9 (46.1 92.1)	137.5 (95 181.1)
2007	19.7 (12.4 27.7)	10 (7.5 13.1)	38.6 (29 50.3)	72.1 (45.1 97.4)	140.5 (94.1 188.5)
2008	20.2 (12.3 29.4)	10.1 (7.6 13.2)	38.7 (29.1 50.6)	74.3 (44.2 103.1)	143.3 (93.2 196.3)

Extended density dependent fecundity (EDDF) model

Year	North Sea	Inner Hebrides	Outer Hebrides	Orkney	Total
1984	5.7 (4.5 6.7)	5.8 (4.6 7.4)	35.2 (26.3 49.2)	22.8 (17.8 27.8)	69.5 (53.3 91.1)
1985	6 (4.8 7)	6.2 (5 7.8)	36.2 (27.4 50.9)	24 (19 28.9)	72.4 (56.2 94.5)
1986	6.4 (5.2 7.5)	6.6 (5.5 8.1)	37.5 (29 52.2)	25.2 (20.5 30.1)	75.8 (60.2 97.9)
1987	6.9 (5.6 8.1)	7.1 (5.9 8.7)	38.8 (30.7 52.4)	26.7 (22 31.5)	79.5 (64.3 100.7)
1988	7.4 (6.1 8.6)	7.7 (6.3 9.3)	40.2 (32.2 53.1)	28.4 (23.5 33.2)	83.7 (68.1 104.3)
1989	7.9 (6.6 9.3)	8.3 (6.9 10.1)	41.7 (33.2 53)	30.2 (24.7 35.8)	88.1 (71.3 108.1)
1990	8.5 (7.1 10.1)	8.9 (7.3 11.1)	43.1 (34.3 54.4)	32.3 (26.4 38.9)	92.8 (75 114.4)
1991	9.1 (7.5 10.9)	9.6 (7.8 11.9)	44.5 (35.5 56.1)	34.4 (28.1 42.4)	97.5 (78.9 121.3)
1992	9.8 (7.9 11.8)	10.2 (8.3 12.7)	45.8 (36.8 57.6)	36.6 (29.7 45.6)	102.4 (82.7 127.7)
1993	10.5 (8.3 12.8)	10.8 (8.8 13.4)	47.2 (37.8 59.2)	39 (31.4 49.1)	107.4 (86.4 134.5)
1994	11.3 (8.9 13.9)	11.4 (9.3 14.3)	48.6 (39 61.3)	41.5 (33.4 52.6)	112.7 (90.5 142.1)
1995	12.1 (9.5 15)	12 (9.6 15)	49.9 (39.8 63.6)	44.2 (35.5 56.3)	118.2 (94.5 149.9)
1996	13 (10.1 16.2)	12.5 (10 15.8)	51.2 (40.8 65.6)	47.2 (37.8 60.4)	123.9 (98.6 158)
1997	14 (10.8 17.4)	13.1 (10.3 16.5)	52.5 (41.5 67.2)	50.3 (40.3 64.8)	129.9 (103 165.9)
1998	15.1 (11.6 18.7)	13.6 (10.5 17.2)	53.8 (42.5 69)	53.6 (43 69.3)	136 (107.6 174.2)
1999	16.2 (12.4 20.1)	14 (10.8 17.9)	55 (43.1 70.9)	57.1 (46 74)	142.3 (112.3 182.9)
2000	17.4 (13.2 21.6)	14.4 (11 18.6)	56.1 (43.7 72.7)	60.8 (49.1 78.7)	148.7 (117 191.7)
2001	18.7 (14.1 23.1)	14.8 (11.2 19.3)	57.2 (44.3 74.6)	64.6 (52 83.6)	155.3 (121.6 200.6)
2002	20 (15 24.9)	15.2 (11.3 20)	58.2 (44.9 76.3)	68.7 (55 88.4)	162.1 (126.3 209.7)
2003	21.3 (16 26.8)	15.5 (11.5 20.7)	59.3 (45.4 78.1)	72.9 (58.2 93.3)	169 (131.1 218.9)
2004	22.6 (17 28.7)	15.8 (11.6 21.3)	60.2 (46 79.8)	77.3 (61.4 98.5)	176 (135.9 228.2)
2005	24 (18 30.8)	16.1 (11.7 21.8)	61.2 (46.5 81.4)	81.8 (64.7 103.6)	183.1 (140.9 237.7)
2006	25.3 (19.1 32.9)	16.4 (11.8 22.4)	62.2 (47 83)	86.3 (68.1 109)	190.2 (146.1 247.3)
2007	26.6 (20.2 35.1)	16.7 (11.9 23)	63.1 (47.6 84.3)	90.9 (71.9 115.3)	197.3 (151.5 257.7)
2008	27.9 (21.2 37.2)	17 (12 23.7)	63.9 (48 85.4)	95.5 (75.9 120.4)	204.3 (157.2 266.7)

Extended density dependent survival with no movement (EDDSNM) model

Year	North Sea	Inner Hebrides	Outer Hebrides	Orkney	Total
1984	5.3 (4 6.5)	5.6 (4.3 6.9)	26 (20.2 32.7)	20.6 (15.3 26.3)	57.4 (43.8 72.3)
1985	5.6 (4.3 6.9)	5.9 (4.7 7.2)	27.3 (21.2 33.9)	21.8 (16.7 27.1)	60.6 (46.9 75.1)
1986	6 (4.7 7.4)	6.2 (4.9 7.4)	28.6 (22 35.4)	23.2 (18.2 28.5)	64 (49.8 78.7)
1987	6.5 (5.2 7.9)	6.5 (5.2 7.8)	29.7 (22.7 36.4)	24.8 (19.6 30.4)	67.6 (52.6 82.5)
1988	7 (5.6 8.4)	6.9 (5.4 8.3)	30.7 (23.4 37.8)	26.7 (21.2 32.3)	71.3 (55.6 86.8)
1989	7.5 (6.1 9)	7.2 (5.6 8.7)	31.5 (23.9 38.8)	28.5 (22.8 34.7)	74.7 (58.4 91.1)
1990	8 (6.5 9.6)	7.5 (5.8 9.1)	32 (24.3 39.5)	30.5 (24.5 37.1)	78 (61.1 95.3)
1991	8.5 (6.9 10.2)	7.7 (6 9.4)	32.4 (24.7 40.2)	32.5 (26.2 39.6)	81.2 (63.8 99.4)
1992	9.1 (7.4 10.8)	8 (6.2 9.8)	32.7 (24.8 40.6)	34.5 (27.8 42)	84.3 (66.2 103.2)
1993	9.7 (7.8 11.5)	8.2 (6.3 10.1)	32.9 (25 40.7)	36.6 (29.4 44.4)	87.4 (68.6 106.7)
1994	10.3 (8.3 12.2)	8.4 (6.4 10.3)	33 (25.2 40.7)	38.7 (31.1 46.9)	90.4 (71 110.1)
1995	10.9 (8.7 13)	8.5 (6.5 10.6)	33 (25.2 40.5)	40.8 (32.7 49.3)	93.3 (73.1 113.4)
1996	11.6 (9.2 13.8)	8.6 (6.6 10.7)	32.9 (25.2 40.3)	43 (34.3 51.8)	96.1 (75.3 116.6)
1997	12.3 (9.6 14.6)	8.7 (6.7 10.8)	32.8 (25.3 40.1)	45 (35.7 54.3)	98.8 (77.4 119.8)
1998	12.9 (10.1 15.5)	8.8 (6.8 10.9)	32.6 (25.3 39.9)	47 (36.9 57)	101.3 (79 123.2)
1999	13.6 (10.4 16.4)	8.8 (6.8 10.9)	32.5 (25.3 39.6)	48.9 (38 59.6)	103.8 (80.5 126.5)
2000	14.3 (10.7 17.3)	8.8 (6.9 10.9)	32.4 (25.4 39.4)	50.6 (38.9 62.4)	106.1 (81.8 129.9)
2001	14.9 (11 18.2)	8.8 (6.9 10.9)	32.3 (25.4 39.2)	52.2 (39.8 65.5)	108.2 (83 133.8)
2002	15.6 (11.2 19.3)	8.8 (6.9 10.8)	32.2 (25.4 39.1)	53.6 (40.4 68.6)	110.2 (83.9 137.8)
2003	16.2 (11.4 20.4)	8.8 (6.9 10.8)	32.1 (25.4 39.1)	54.9 (40.9 71.9)	112 (84.6 142.1)
2004	16.8 (11.6 21.5)	8.8 (6.9 10.8)	32.1 (25.4 39)	56 (41.3 75.4)	113.6 (85.2 146.8)
2005	17.3 (11.8 22.8)	8.8 (6.9 10.8)	32.1 (25.4 39)	56.9 (41.5 79.1)	115.1 (85.6 151.7)
2006	17.9 (11.9 24.1)	8.7 (6.9 10.8)	32.2 (25.4 39)	57.7 (41.6 83)	116.4 (85.8 156.9)
2007	18.4 (12 25.5)	8.7 (6.9 10.8)	32.2 (25.4 39.1)	58.3 (41.6 87)	117.6 (85.9 162.4)
2008	18.8 (12.1 26.9)	8.7 (6.9 10.8)	32.3 (25.4 39.2)	58.9 (41.4 91.2)	118.7 (85.9 168.1)

Extended density dependent fecundity with no movement (EDDFNM) model

Year	North Sea	Inner Hebrides	Outer Hebrides	Orkney	Total
1984	5.5 (4.4 6.8)	6.5 (5.1 9.5)	38.5 (24.9 88.7)	21.8 (17 26.8)	72.4 (51.4 131.8)
1985	5.9 (4.9 7.3)	6.9 (5.3 9.9)	40.5 (26.7 92.7)	23.2 (18.4 27.9)	76.5 (55.3 137.8)
1986	6.4 (5.3 7.9)	7.4 (5.7 10.5)	42.8 (28.7 97)	24.8 (20.2 30)	81.4 (59.9 145.4)
1987	7 (5.7 8.5)	7.9 (6.1 11.1)	45.2 (30.9 100.4)	26.8 (21.9 32.8)	86.8 (64.6 152.9)
1988	7.6 (6.2 9.3)	8.5 (6.6 11.7)	47.7 (33.2 102.2)	28.9 (23.7 35.6)	92.6 (69.7 158.9)
1989	8.2 (6.7 10.1)	9.1 (7.1 12.4)	50.2 (35.3 103.3)	31.3 (25.6 39.5)	98.7 (74.6 165.4)
1990	8.8 (7.2 11.1)	9.7 (7.6 13.4)	52.8 (37.5 107.4)	33.8 (27.6 43.2)	105.1 (79.8 175)
1991	9.5 (7.7 12.3)	10.4 (8.1 14.4)	55.5 (39.7 111.4)	36.4 (29.7 46.5)	111.7 (85.2 184.5)
1992	10.2 (8.3 13.5)	11 (8.7 15.4)	58.3 (42 115.6)	39.1 (31.9 50)	118.6 (90.8 194.4)
1993	11 (8.9 14.7)	11.7 (9.2 16.4)	61 (44.4 119.6)	42.1 (34.3 54.1)	125.8 (96.7 204.8)
1994	11.8 (9.5 16.2)	12.5 (9.8 17.6)	63.9 (46.7 123.7)	45.2 (36.7 59.8)	133.4 (102.7 217.2)
1995	12.7 (10.2 17.5)	13.2 (10.4 18.6)	66.6 (49.2 128.3)	48.6 (39.2 66)	141.2 (108.9 230.4)
1996	13.7 (10.9 19.2)	14 (11 19.8)	69.4 (51.6 132.2)	52.2 (41.9 72.5)	149.3 (115.3 243.6)
1997	14.7 (11.6 21)	14.8 (11.6 21.1)	72.1 (54 137.5)	56 (44.7 79.3)	157.5 (121.9 258.8)
1998	15.8 (12.4 22.9)	15.5 (12.2 22.4)	74.8 (56.2 141.8)	59.9 (47.8 86.6)	166 (128.6 273.6)
1999	16.9 (13.2 24.9)	16.3 (12.8 23.8)	77.3 (58.4 141.1)	64.1 (50.9 94.2)	174.7 (135.4 283.9)
2000	18.1 (14.1 27)	17.1 (13.5 25.3)	79.8 (60.5 143.6)	68.5 (54.2 102)	183.5 (142.3 297.9)
2001	19.4 (15.1 29.1)	17.9 (14.1 26.7)	82.1 (62.3 147.4)	73.1 (57.6 110.2)	192.4 (149.1 313.5)
2002	20.7 (16 31.4)	18.6 (14.6 28.2)	84.3 (64.1 152.5)	77.8 (61.2 118.7)	201.4 (156 330.7)
2003	22.1 (17.1 33.7)	19.4 (15.2 29.7)	86.4 (65.6 155.5)	82.7 (65 127.4)	210.5 (162.9 346.3)
2004	23.5 (18.1 36.1)	20.1 (15.8 31.2)	88.3 (67 159.7)	87.8 (68.9 136.3)	219.7 (169.8 363.2)
2005	25 (19.3 38.5)	20.8 (16.3 32.8)	90.1 (68.1 164.4)	92.9 (72.9 145.4)	228.8 (176.6 381.1)
2006	26.6 (20.4 41)	21.4 (16.7 34.4)	91.7 (69.1 169.5)	98.2 (77 154.8)	237.9 (183.3 399.7)
2007	28.2 (21.7 43.5)	22 (17.1 36)	93.1 (69.9 175.5)	103.6 (81.3 164.4)	246.9 (190 419.4)
2008	29.8 (22.9 46.2)	22.6 (17.5 37.6)	94.4 (70.4 181.6)	109 (85.6 174.1)	255.9 (196.5 439.6)

Len Thomas

Further investigations into results presented in Briefing Paper 09/2.

NERC Sea Mammal Research Unit and Centre for Research into Ecological and Environmental Modelling, University of St Andrews, St Andrews KY16 8LB

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Summary

In SCOS Briefing paper 09/2 we presented results from fitting a population dynamics model to UK Grey Seal pup production data for 1984-2008. Unlike in previous years, and in particular the 2008 briefing paper, we found substantial support for a density dependent survival model (EDDSNM) over a density dependent fecundity model (EDDFNM). At the SCOS meeting on 23 July 2009, the committee asked us to make further investigations of the matter, and we present our findings here. We conclude that Monte-Carlo error on the model weights is higher than previously thought, and hence the model selection statistics in the 2009 and earlier briefing papers are not accurate. By combining four repeat runs, we obtain a more accurate estimate of model weights, but because of the large variation in model weights from the four repeat runs, we do not consider the combined estimate to be definitive. We outline some options for how these findings might be used in reporting population size estimates.

Introduction

Population size for UK Grey Seals is estimated by fitting models of seal population dynamics to pup production data. In recent years, 6 models have been fit, differing in whether they model density dependence in pup survival (DDS) or fecundity (DDF), whether they allow for simple or extended forms of density dependence, and whether they allow for movement of recruiting females between breeding regions or not. The biggest determinant of the population size estimate is whether the models contain DDS or DDF.

In the 2008 briefing paper (Thomas and Harwood 2008), we used Akaike weights to compare models to data for 1984-2007, based on the mean posterior AICc. This yielded weights of 0.65 for the model with extended DDS and no movement (EDDSNM), 0.35 for the model with extended DDF and no movement (EDDFNM) and essentially zero for the other four models. The corresponding AICc difference between the two best models was 1.23. These results lead us to the conclusion of inconclusive evidence to support one model over the other. This corresponds with previous simulation studies that show there is very little difference in pup production trajectories for models containing DDS and DDF, and hence for a given dataset both models should fit approximately equally well.

However, in the 2009 briefing paper, based on one additional year of data, came to a different conclusion. A different (and more standard) model selection criterion was used: posterior model probability. The posterior model probability was found to be 0.93 or 0.95 (depending on the prior model probabilities used) for the EDDSNM model, 0.05 (for both priors) for the EDDFNM and essentially zero for the other four models. This substantially heavier weighting for the DDS model could lead to a very different estimate of population size if model-averaged estimates were used.

SCOS asked us to make further investigations of the matter, and we present results here.

Methods

Comparison of model selection statistics

One explanation for the difference is that Akaike weights produce different results from posterior model probabilities, and hence we computed both for the 2009 results.

Investigation of analysis differences

Another possible explanation of differences is slight changes in computing algorithm. The analyses are performed using custom-written C code, with post-processing taking place using further C code and R scripts. The code and scripts used in 2008 were compared with those used in 2009 and any differences noted.

Re-run of 2008 results

Unfortunately, raw results from 2008 were no longer available: the simulation-based methods produce very large output files and these were deleted to make room for the 2009 results. Hence, to confirm findings from the above investigation of the computer code, the 2008 analysis was reproduced by running the data for 2004-2007 using the latest code and post-processing scripts.

One additional check we planned to make was to take the above results for 1984-2007, project them forward to 2008 using the simulation model and re-weight using the 2008 data. The idea was that results from this would then be comparable with those published in the 2009 briefing paper. However, the observation error parameter, psi, is fixed in runs used for model selection (see briefing papers for explanation), and a different value for psi was used in the results reported in 2008 (89.50) and 2009 (88.28). This is would cause differences in estimated values, rendering the results incomparable. Therefore this analysis was not undertaken.

Re-run of 2009 results

To assess the level of Monte-Carlo variation in the results presented in the 2009 briefing paper, further runs of the EDDSNM and EDDFNM models were made. We reported in the briefing paper that a duplicate run of the two models had produced negative log integrated likelihood (-LnIL) values were the same to 3 significant figures and estimates of state and parameter values were identical to 2 or 3 significant figures (with one exception – estimated carrying capacity in Orkney). However, the files for those simulations were not retained, so as a double check we performed three additional replicated runs of both models.

Synthesis of results across runs

To produce an estimate with the best accuracy possible using the above runs, we combined results from the four replicate runs of the EDDSNM and EDDFNM models, to give model selection statistics based on 1,000 million particles. To achieve this, similar methods were used as those employed to combine results from each of the 250 runs of 1 million particles that make up the four replicate runs (see previous briefing papers for details). The only difference was that the rejection control criterion was not the 99.99th percentile of the weights, but a fixed value set at approximately 4 times the largest weight (the value used was 250). This was purely to reduce the number of particles down to a manageable number for processing, at some (hopefully small) cost to accuracy.

Evaluation of reliability of model selection statistics

An idea of the reliability of the model selection results from the above synthesis can be obtained by considering the variation in negative log integrated likelihood (-LnIL) obtained from the four replicate runs that went into it. The standard deviation of the four -LnIL values for each model was calculated, and the standard deviation of the -LnIL from the pooled estimate for each model was approximated as this value divided by sqrt(4). Note that this gives only an approximation to the required standard deviation since it assumes all four runs have equal weighting in the pooled estimate, when in reality runs with lower -LnIL will be expected to have higher weight.

These values were used in a parametric bootstrap, where 1000 replicate values of -LnIL were simulated from each of the EDDSNM and EDDFNM models, assuming a normal distribution or -LnIL centred on the value obtained from pooling the four runs and with standard deviation obtained as above. For each of these 1000 runs, posterior model probabilities were calculated.

Results

Comparison of model selection statistics

Mean posterior AICc weights (Table 1) were nearly identical to the posterior model probabilities; hence we conclude that the change in model selection statistic did not cause the change in model weights.

Investigation of analysis differences

The C code used in 2009 was nearly identical to that used in 2008. The only change was made to a part that allows simulating forward under different possible future harvest regimes – this is used in analysis of Canadian data, but not UK data. Post-processing code in both C and R were functionally identical. The C compliers used were identical (Microsoft C++ 6.0 on Windows, gcc on linux). The version of R used for post-processing was not the same (2.7.1 in 2008; 2.9.1 in 2009), but this is unlikely to have made a difference as only well-established R functions are used (except for the weighted average and variance functions from the `Hmisc` package – these were checked and have not changed).

Many simulations are required to obtain results with low Monte-Carlo variation. This is achieved by running simulations in batches of 1,000,000, and parcelling these batches out to various computers. The resulting files are then collated onto one machine and post-processed, to produce a set of relatively compact files from which summary statistics such as posterior means, variances and credibility intervals can be obtained. As many as 250 batches have been run to produce one result (see Table 1 of briefing paper 09/2).

The computers the code was run on were not the same between years, but the code was specifically written to be portable so this should not cause problems. In 2008 the code was run on about 5 machines running Windows XP, plus a 32-bit linux machine (Red Hat release 9) and a 64-bit linux machine (SUSE 10.1). In 2009 the same machines were used, plus a 32-bit Windows Vista machine and a 64-bit linux machine (CentOS 5.3). Results have been extensively checked between machines over the years of code development and have been shown to be identical.

However, in developing additional code for this note, an important bug was found in the Windows operating system or C++ compiler. It appears that when results files are generated that exceed 4GB, the end of the files get corrupted. This occurs in the seal simulations for files containing estimates of population states when more than 75 batches are run on the same machine, and the results are stored in non-compact format[1]. The operating system gives no warning of the error, and the post-processing code was not written to double-check file sizes (this has now been changed). However, batch sizes this large have not been used in previous years (25 or 50 being typical), so this is very unlikely to be an explanation for the observed difference.

Re-run of 2008 results

Results of the re-run of data from 1984-2007 are shown in tables 2-5, and figures 1-2, where they are also compared with the results from Thomas and Harwood (2008). The number of particles simulated was identical to the previous analysis, and the resulting effective sample size was very similar (Table 2). The fitted pup production trajectories appeared visually identical (Figure 1). Unfortunately, the estimated values are not available (only total population size estimates are given in the appendix to the briefing papers) so a numerical comparison is not possible. There are certainly differences, even if they are small, because the model selection statistics differ between runs (see below).

The parameter estimates were also visually nearly identical (Figure 2), although posterior means and standard deviations were not absolutely identical. In most cases, they were identical to 2 significant figures or different by 1 point in the second significant figure, but in some cases particularly the carrying capacity estimates (which are derived parameters and hence multiply small differences among other parameters) were more dissimilar. The biggest differences were in the EDDFNM model, where the posterior mean carrying capacities were 6930, 3000, 11100 and 29500 for the four regions from the 2008 briefing paper and 7430, 2990, 11100 and 27300 from the re-runs. North sea and Orkney (first and last numbers) were particularly different. These are slightly higher levels of Monte-Carlo variation than have been reported previously, where we found repeated runs produced results identical to at least 2 significant figures.

Total population size estimates (Table 3) were also often identical to 2 or 3 significant figures, although in a few cases they differed by 1 point in the second significant figure.

Model selection statistics are given in Tables 4 and 5. Table 4 uses the same statistics (mean posterior AICc and AICc weight) as was used in the 2008 briefing paper. Mean posterior negative log likelihood values were the same between runs to 2 or 3 significant figures, translating into 3 or 4 significant figure accuracy for AICc – but for model selection single digit differences in AICc make important differences to model interpretation, and AICc values differed by up to 5 points between the two sets of runs with the largest difference being in the

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[1] There are two storage formats: in the full format seals of each age, region and year class and parameters are stored in double-precision integer format; in the compact format seals age 2-6 in each colony are summed together and state and parameter results are stored as single precision.

EDDSNM model. These differences make a large difference to the AICc weights, which in the briefing paper run were 0.65 on EDDSNM, 0.35 on EDDFNM and 0 on other models; in the re-run they were 0.90 on EDDSNM, 0.10 on EDDFNM and 0 on the other models.

Table 5 presents the re-run results in terms of posterior model probabilities (this cannot be done for the 2008 briefing paper results as access to the raw data is required to compute integrated likelihood values). The results are very similar to those presented in the 2009 briefing paper: 0.93 for the EDDSNM model and 0.07 on the EDDFNM model, with 0 elsewhere.

Re-run of 2009 results

Results of the re-run of data from 1984-2008 with the EDDSNM and EDDFNM models are shown in tables 6-8, and figures 3-5, where they are also compared with the results from briefing paper 09/2. Findings are similar to those from the re-runs of 2008 results:

- the effective sample sizes from each re-run were quite similar to the original (Table 3)
- the fitted pup production trajectories were visually identical (Figure 3). (Quantitative comparisons could also be made in this case, unlike the 2008 re-runs)
- parameter estimates were the same to 2 or 3 significant figures (Figure 4), except for ϕ_j (pup survival) and χ_{ns} (North Sea carrying capacity) for both models and ρ (extended density dependence parameter) for EDDSNM.
- Total population size estimates were in most cases the same to 2 or 3 significant figures (Table 7)
- Negative log integrated likelihood values were the same to 2 significant figures (Table 8): the values differed among runs by up to 2.22 for EDDSNM and by 3.10 for EDDFNM. This lead to large differences in posterior model probabilities, ranging from 0.97 to 0.54 for EDDSNM and, in parallel, from 0.03 to 0.46 for EDDFNM.
- The large differences in posterior model probabilities led to large differences in model averaged estimates of total population size (Table 7 and Figure 5), which were consistent to only 1 significant figure. Posterior model-averaged confidence intervals were wide in all cases, but were variable among models. Estimates were especially different for the first re-run, where posterior model probabilities were estimated to be 0.54 for EDDSNM, in contrast to the other runs where estimates were >0.8.

Synthesis of results across runs

Effective sample sizes of unique particles (ESS_u) for the pooled EDDSNM and EDDFNM were 1359 and 724 respectively, very close to the sum of the ESS_u of the composite runs (Table 6). Estimated population sizes were very similar to the runs making up the composite estimate (Table 7), as were pup production fits and estimated parameter values (compare Figs. 4 and 6). We expect them to be close to a weighted average of the numbers from each of the 4 replicate runs, weighted such that runs with lower negative log integrated likelihood (-LnIL) values receive more weight as particles from these runs would be most heavily weighted when the particles were combined. We also expect the overall –LnIL value (Table 8) to be a similar weighted average, and so closest to the lowest values obtained from the four replicate runs. Posterior model probabilities were 0.84 for EDDSNM, 0.16 for EDDFNM and 0.00 for all other models regardless of whether the models were given equal prior weight or higher prior weighting to lower parameter models (these calculations used the negative log integrated values for other models obtained from Thomas and Harwood 2009). Model averaged estimates of total population size are given in Table 7, and the model-averaged posterior density plot is shown in Figure 7.

Given these values for posterior model probabilities, the model-averaged estimates of total population size are shown in Figure 6 and Table 7.

Evaluation of reliability of model selection statistics

The estimated standard deviation of -LnIL for the pooled run, based on the four replicate runs, was 0.49 for the EDDSNM model and 0.78 for the EDDFNM model. Based on these figures, the 1000 bootstrap replicates produced highly variable posterior model probabilities (Figure 8) – upper and lower 2.5th quantiles were 0.45 and 0.97.

Discussion

We have found that the unexpected posterior model probability results reported this year's briefing paper is most likely due to Monte Carlo variation in results between runs. It was previously known that Monte-Carlo variation existed, but it was thought to be too small to affect findings significantly. However, while Monte-Carlo variation in the 3rd significant figure for estimates of population size and demographic parameters is not problematic, variation at this level in negative log integrated likelihood (-LnIL) values for models is a problem. This is because this level of variation translates into considerable uncertainty about posterior model probabilities when models have very similar -LnIL values. We already know there is very little signal in pup production data to distinguish between DDS and DDF models, so we expect -LnIL values to be very similar between these types of models. Therefore, it is particularly important to have accurate -LnIL values here if we are to have confidence in our calculated posterior model probability values.

Even with 1,000 million particles per model, it appears there is still considerable uncertainty attached to our current estimate of posterior model probability of 0.84 for EDDSNM and 0.16 for EDDFNM. Our estimates of model-averaged population sizes be treated with scepticism until a way is found to obtain better precision on model selection statistics.

One simple solution that could be implemented for next year's SCOS meeting is to base inference on more runs with the same algorithm. For example, repeating the parametric bootstrap but assuming 10,000 million particles per model, the 2.5th and 97.5th quantiles on posterior model probability for EDDSNM were 0.74 and 0.90. This is feasible, and also practical, but is an inelegant solution. A better solution is to develop better algorithms, and this will be pursued. Thirdly, there is hope that an independent estimate of population size will be obtained by next year, and this will provide much more reliable model discrimation.

SCOS should consider whether and how to report model-averaged estimates of population size, given the above uncertainty. Options include:

- Report the model-averaged estimates of population size and credibility interval, based on the new pooled runs.
- Report the model-averaged credibility interval, but the population size based on one or both competitive models.
- Assume equal weight for both models, and calculate model-averaged estimates and credibility intervals on this basis.
- Ignore model averaging and report population sizes and credibility intervals based on one or more model separately.

References

Thomas, L. and J. Harwood. 2008. Estimating the size of the UK grey seal population between 1984 and 2007. *SCOS Briefing Paper 08/3*

Tables and Figures

Table 1. Model selection statistics for 6 models fit in 2009 briefing paper. The first 5 columns are identical to those from Table 3 of the briefing paper. –LnIL is the negative integrated likelihood; p(M) equal prior is posterior model probabilities given equal priors; p(M) wtd prior is posterior model probabilities given weighted priors. The last 2 columns were not presented in the briefing paper – they show the mean posterior negative log likelihood and mean posterior AICc weight. MPAICc was used as a model selection statistic in previous briefing papers.

Model	# params	-LnIL	p(M) equal prior	p(M) wtd prior	-MPLnL	MPAICc weight
DDS	10	774.66	0.00	0.00	784.20	0.00
DDF	10	771.72	0.00	0.00	780.81	0.00
EDDS	11	769.83	0.01	0.00	782.30	0.00
EDDF	11	771.10	0.00	0.00	787.00	0.00
EDDSNM	8	765.22	0.93	0.95	774.56	0.96
EDDFNM	8	768.12	0.05	0.05	777.65	0.04

Table 2. Number of particles simulated (K), number of unique ancestral particles (U) and effective sample size of unique particles (ESS_u) for data from 1984-2007. Columns 3-4 are from the 2008 briefing paper; columns 5-6 are from the re-runs.

Model	*K* ($x10^6$)	*U 2007* ($x10^3$)	ESS_u	*U 2007* ($x10^3$)	ESS_u
		2008 briefing paper		re-run	
DDS	150	18.5	339.6	18.7	421.5
DDF	150	29.6	574.8	28.6	531.1
EDDS	150	9.0	114.7	9.1	144.9
EDDF	150	4.5	59.0	4.6	65.5
EDDSNM	225	33.5	445.0	33.6	554.5
EDDFNM	225	12.0	203.9	12.1	229.8

Table 3. 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. Results are from the 2008 briefing paper and the re-run of the same data.

	DDS		DDF	
	2008 briefing paper	re-run	2008 briefing paper	re-run
North Sea	14.1 (11.2 19.0)	13.8 (11.2 18.3)	32.4 (23.1 46.2)	32.8 (23.0 47.4)
Inner Hebrides	9.2 (7.6 11.6)	9.1 (7.4 11.5)	25.5 (16.7 39.1)	25.8 (16.7 39.7)
Outer Hebrides	32.9 (25.9 42.3)	32.5 (26 41.9)	100.2 (62.4 160.2)	100.7 (62.0 164.4)
Orkney	57.4 (45.3 76.2)	56.6 (45.2 75.3)	123.4 (88.9 172.8)	124.9 (89.0 180.5)
Total	113.6 (90.0 149.1)	112 (89.9 147)	281.6 (191.2 418.3)	284.1 (190.8 431.9)
	EDDS		EDDF	
North Sea	17.7 (10.7 26.5)	17.8 (10.1 26.7)	25.1 (19.8 32.5)	25.4 (19.8 32.1)
Inner Hebrides	9.5 (6.6 13.5)	9.5 (6.7 12.6)	16.6 (12.5 21.6)	16.6 (12.6 24.8)
Outer Hebrides	36.3 (24.7 50.5)	36.7 (27 49.3)	61.8 (45.8 80.0)	62.1 (47.4 86)
Orkney	73.1 (43.4 98.6)	72.5 (38.6 101.3)	92.5 (73.5 117.5)	94.4 (74.5 123.7)
Total	136.6 (85.4 189.1)	136.5 (82.3 189.9)	196.0 (151.6 251.6)	198.5 (154.3 266.6)
	EDDSNM		EDDFNM	
North Sea	17.1 (10.6 25.9)	16.7 (10.9 25.5)	27.2 (20.7 38.2)	26.4 (20.8 39.5)
Inner Hebrides	8.3 (6.5 10.5)	8.3 (6.6 10.4)	21.4 (16.5 32.1)	20.8 (16.6 32.9)
Outer Hebrides	31.3 (24.0 39.1)	31 (24.2 38)	88.1 (67.0 143.0)	86.8 (66.7 150.9)
Orkney	60.9 (40.9 93.5)	59.7 (40 94.8)	103.0 (79.5 142.9)	99.9 (78.8 146.5)
Total	117.6 (89.1 168.9)	115.7 (81.6 168.7)	239.7 (188.8 356.2)	234 (182.8 369.8)

Table 4. Mean posterior negative log-likelihood, AICc and Akaike weights for models with fixed observation precision of 89.5 fit to data from 1984-2007. Columns 2-5 are from the 2008 briefing paper, columns 6-9 are from the re-run and column 10 compares the AICc between the two sets of runs.

Model	-LnL	AIC$_c$	ΔAIC$_c$	Akaike (AIC$_c$) weight	-LnL	AIC$_c$	ΔAIC$_c$	Akaike (AIC$_c$) weight	Diff. in AIC$_c$ between runs
	2008 briefing paper				re-run				2008-rerun
DDS	750.37	1525.88	20.98	0.00	751.01	1524.50	24.77	0.00	1.38
DDF	747.57	1520.29	15.39	0.00	747.29	1517.06	17.32	0.00	3.23
EDDS	746.71	1521.18	16.29	0.00	747.76	1520.52	20.78	0.00	0.67
EDDF	749.39	1526.54	21.65	0.00	751.31	1527.62	27.89	0.00	-1.07
EDDSNM	742.40	1504.90	0.00	0.65	741.07	1499.73	0.00	0.90	5.16
EDDFNM	743.02	1506.13	1.23	0.35	743.27	1504.11	4.38	0.10	2.01

Table 5. Number of parameters, negative log integrated likelihood (-LnIL) and posterior model probabilities (p(M)) for the re-run 2008 analysis reported above. This method of calculating model selection statistics was the one used in the 2009 briefing paper.

Model	# params	-LnIL	p(M) equal prior	p(M) wtd prior
DDS	10	742.61	0.00	0.00
DDF	10	737.60	0.00	0.00
EDDS	11	737.73	0.00	0.00
EDDF	11	742.84	0.00	0.00
EDDSNM	8	731.02	0.93	0.93
EDDFNM	8	733.66	0.07	0.07

Table 6. Number of particles simulated (K), number of unique ancestral particles (U) and effective sample size of unique particles (ESS$_u$) for four replicate analyses of data from 1984-2008, and particles pooled across runs.

Run	K (x10^6)	U *2008* (x10^3)	ESS_u	K (x10^6)	U *2008* (x10^3)	ESS_u
	EDDSM			EDDFNM		
	2009 briefing paper			re-run 1		
2009 briefing paper	250	28.8	421.8	250	11.0	218.9
re-run 1	250	28.0	346.6	250	10.8	165.0
re-run 2	250	28.2	310.7	250	10.9	201.1
re-run 3	250	28.2	305.2	250	10.8	159.3
pooled	1000	81.6	1359.2	1000	32.3	724.0

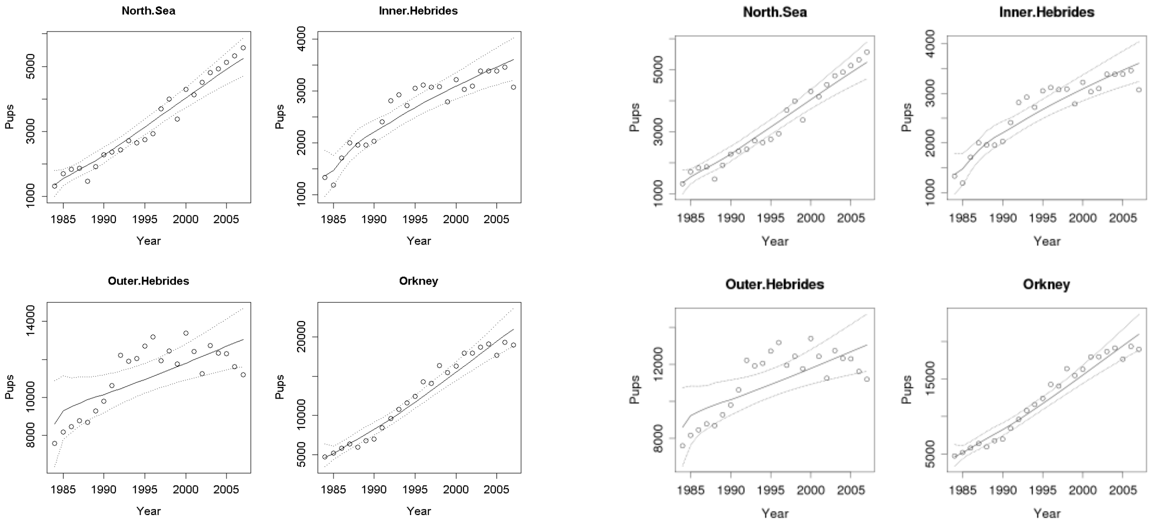
Table 7. Estimated size, in thousands, of the British grey seal population at the start of the 2008 breeding season, derived from models fit to data from 1984-2008. Numbers are posterior means with 95% credibility intervals in brackets. Results are from four replicate runs on the same data, and pooled across runs.

	EDDSNM				
	2009 briefing paper	re-run 1	re-run 2	re-run 3	pooled
North Sea	18.8 (12.1 26.9)	18.9 (12.2 26.9)	18.6 (12.1 26.9)	18.4 (12 27.1)	18.7 (12.1 26.9)
Inner Hebrides	8.7 (6.9 10.8)	8.6 (6.8 10.8)	8.6 (7 10.8)	8.6 (6.7 10.9)	8.6 (6.8 10.8)
Outer Hebrides	32.3 (25.4 39.2)	31.8 (24.7 39.2)	32 (24.7 39)	31.7 (25 39.5)	32 (24.9 39.2)
Orkney	58.9 (41.4 91.2)	57.2 (40.9 90)	58 (41.6 91.5)	57.4 (38.8 90.9)	57.9 (40.7 90.9)
Total	118.7 (85.9 168.1)	116.5 (84.6 166.9)	117.3 (85.4 168.3)	116.2 (82.6 168.4)	117.1 (84.6 167.9)
	EDDFNM				
	2009 briefing paper	re-run 1	re-run 2	re-run 3	pooled
North Sea	29.8 (22.9 46.2)	29.3 (22.1 43.7)	29.2 (22.6 41.8)	30 (22.7 47)	29.6 (22.5 45)
Inner Hebrides	22.6 (17.5 37.6)	22.2 (17.1 35.5)	22.3 (17.2 34.7)	22.8 (17.4 36.7)	22.5 (17.2 36.4)
Outer Hebrides	94.4 (70.4 181.3)	92 (68 174.8)	92 (69.9 157.2)	96.4 (70.1 214.4)	93.7 (69.7 177.2)
Orkney	109.0 (85.6 174.1)	107.2 (82.6 158.7)	107.3 (83.3 154.5)	109.6 (84.3 170.6)	108.2 (83.8 165.9)
Total	255.9 (196.5 439.6)	250.6 (189.7 412.6)	250.7 (193 388.2)	258.7 (194.5 468.6)	254 (193.2 424.6)
	model averaged				
Total	126.2 (89.2 244.8)	178.3 (91.0 352.6)	121.3 (87.7 215.2)	130.3 (87.4 273.7)	138.9 (88.8 285.9)

Table 8. Negative log integrated likelihood (-LnIL) and posterior model probabilities (p(M)) for models with fixed observation precision of 88.28 fit to data from 1984-2008. Results are for four replicate runs on the same data, and pooled across runs. The –LnIL values used for the "All other models" (i.e., DDF, DDS, EDDF, EDDS) were the same in all four runs (because replicate runs of these models were not performed), and are given in Thomas and Harwood (2009).

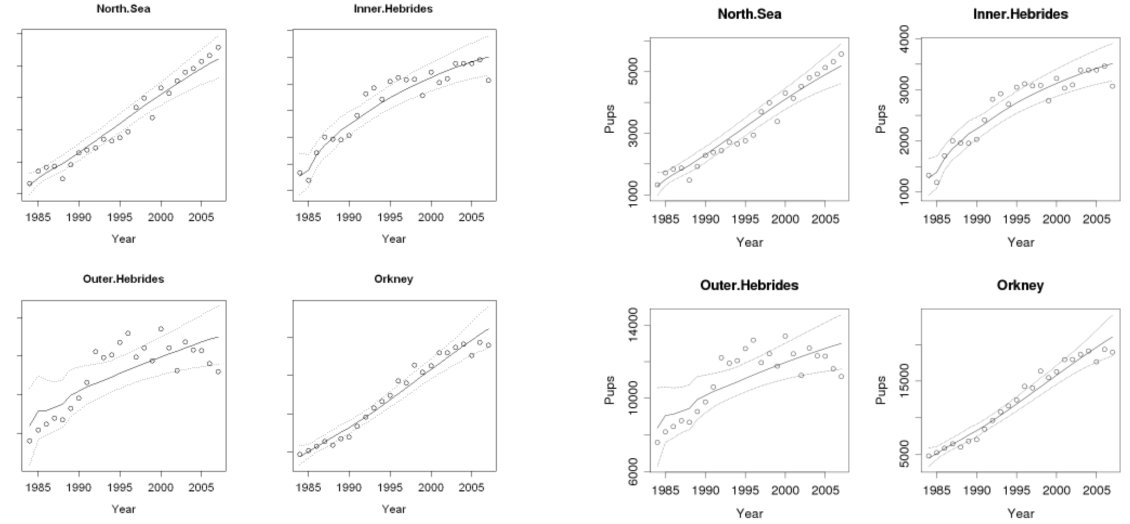
Run	-LnIL	p(M) equal prior	p(M) wtd prior	-LnIL	p(M) equal prior	p(M) wtd prior	Sum p(M) equal prior	Sum p(M) wtd prior
	EDDSNM			EDDFNM			All other models	
2009 briefing paper	765.22	0.93	0.95	768.12	0.05	0.05	0.02	0.00
re-run 1	765.20	0.55	0.54	765.37	0.45	0.46	0.00	0.00
re-run 2	764.00	0.97	0.97	767.64	0.03	0.03	0.00	0.00
re-run 3	766.22	0.88	0.90	768.47	0.09	0.10	0.03	0.00
pooled	764.86	0.84	0.84	766.53	0.16	0.16	0.00	0.00

Figure 1. Comparison of pup production estimates from 2008 briefing paper (left side) and re-runs (right side).



(a) Density dependent survival (DDS)

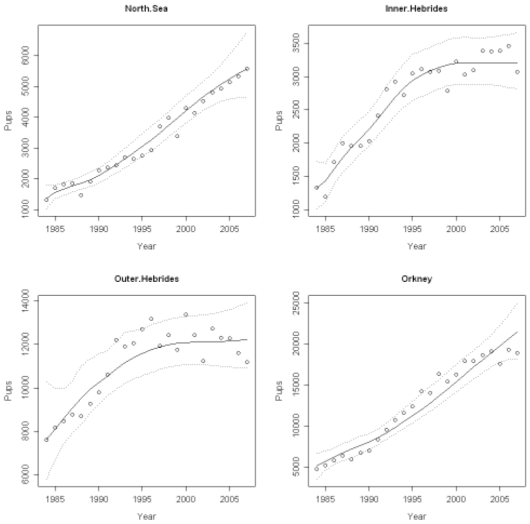
(a.ii) rerun DDS



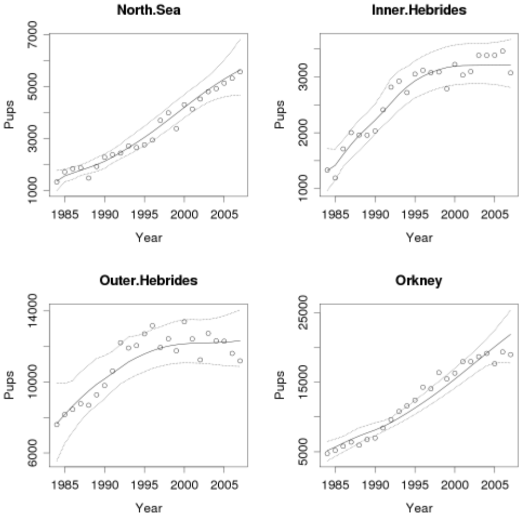
(b) Density dependent fecundity (DDF)

(b.ii) rerun DDF

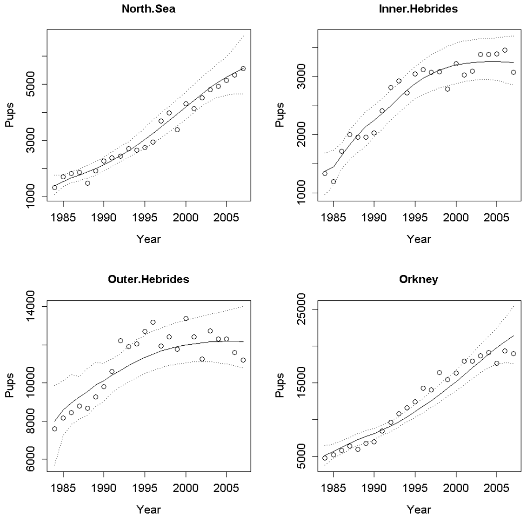
(c) Extended density dependent survival (EDDS)



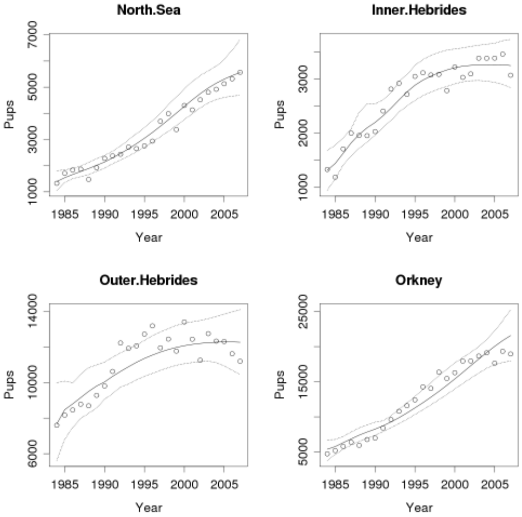
(c.ii) rerun EDDS



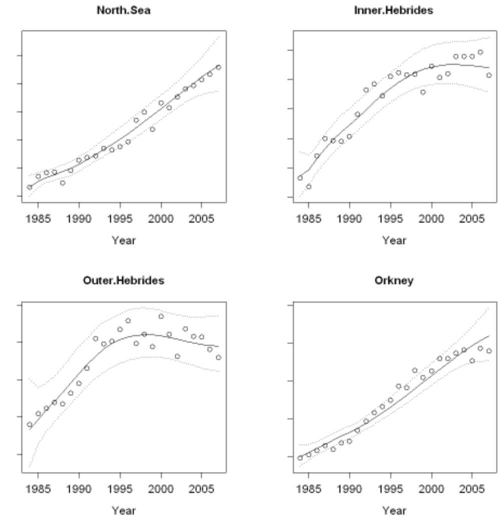
(d) Extended density dependent fecundity (EDDF)



(d.ii) rerun EDDF



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



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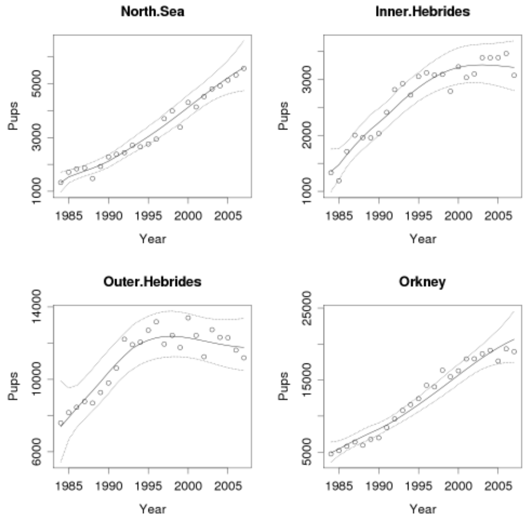
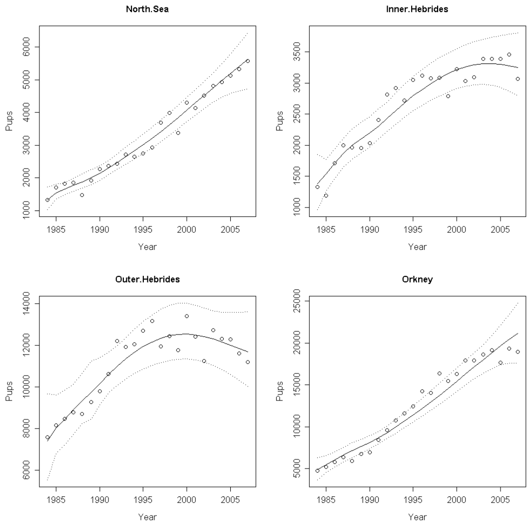


(f) Extended density dependent fecundity with no movement (EDDFNM)



(f.ii) rerun EDDFNM

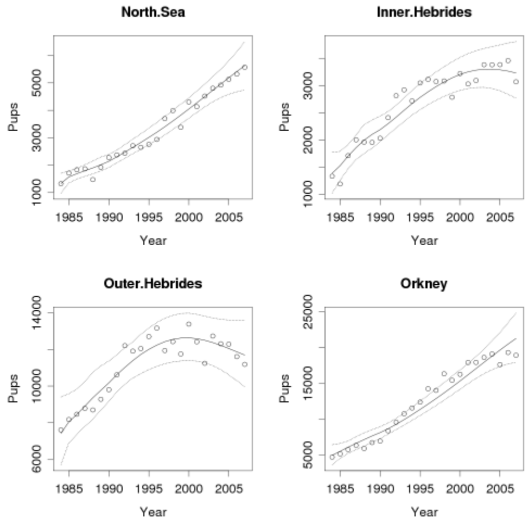
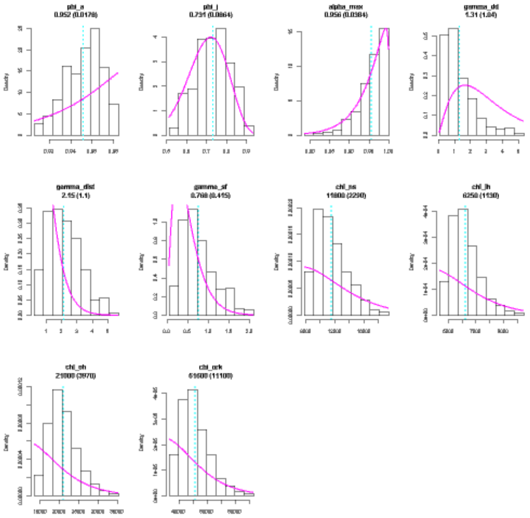
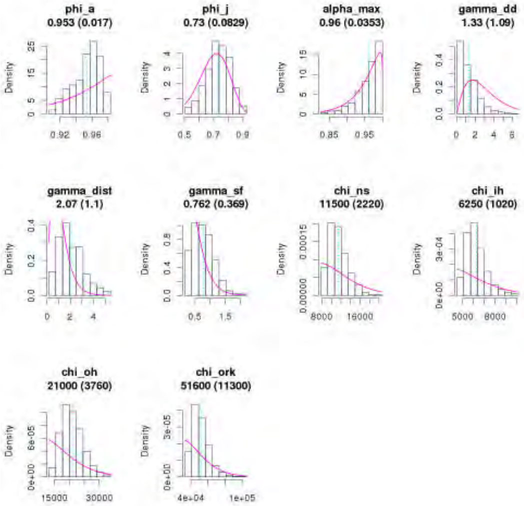


Figure 2. Comparison of posterior parameter estimates from 2008 briefing paper (left side) and re-runs (right side). The plot and text sizes in the two columns are slightly different due to minor changes in post-processing code between 2008 and present.

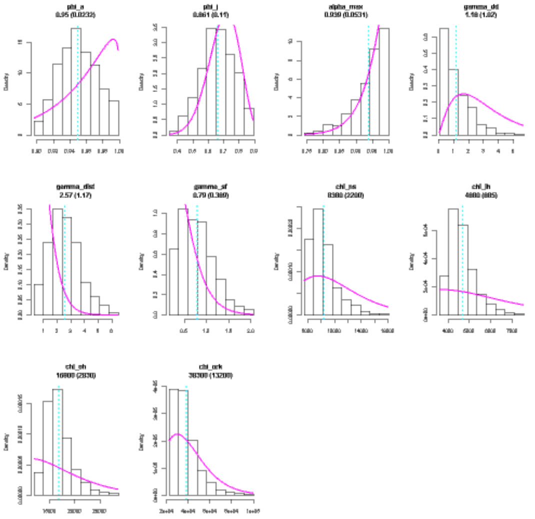
(a) Density dependent survival (DDS)



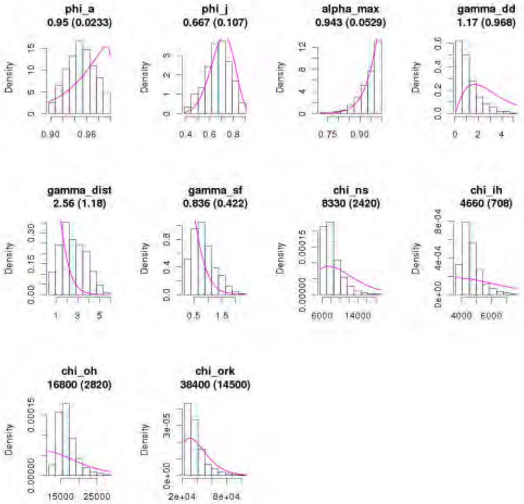
(a.ii) Density dependent survival (DDS)



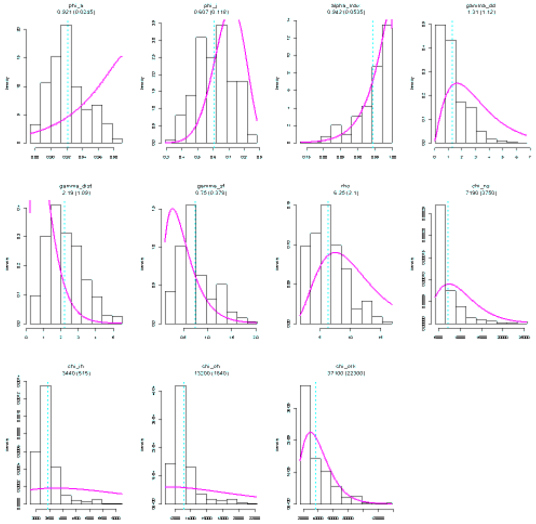
(b) Density dependent fecundity (DDF)



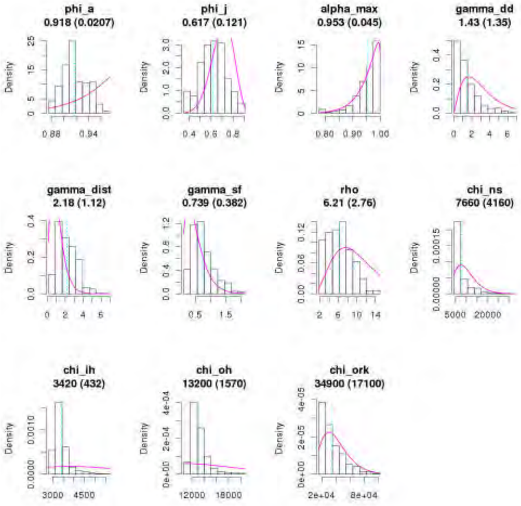
(b.ii) rerun DDF



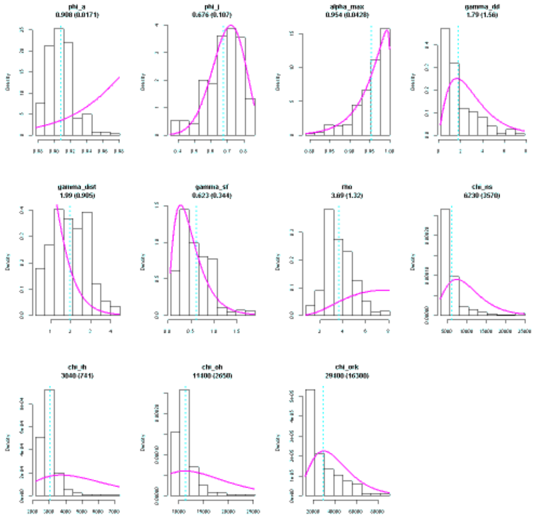
(c) Extended density dependent survival (EDDS)



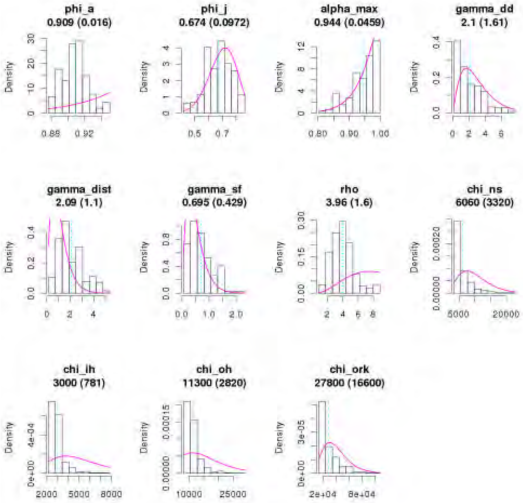
(c) rerun EDDS



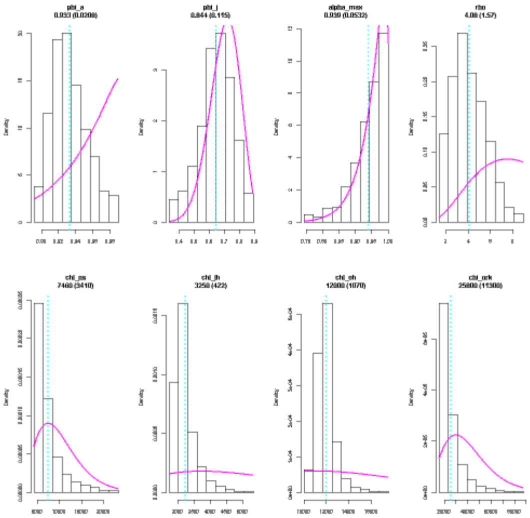
(d) Extended density dependent fecundity (EDDF)



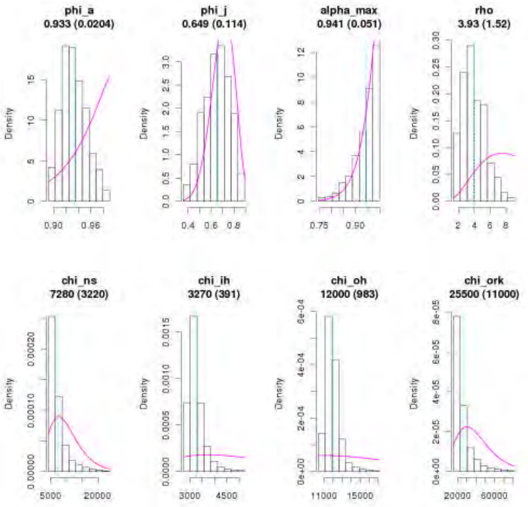
(d) rerun EDDF



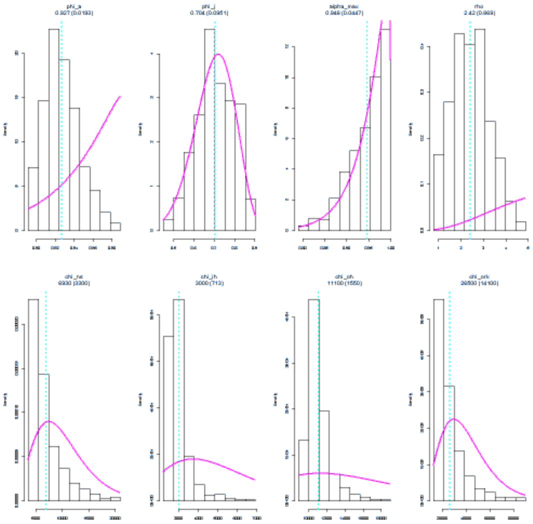
(e) Extended density dependent survival with no movement (EDDSNM)



(e.ii) rerun EDDSNM



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



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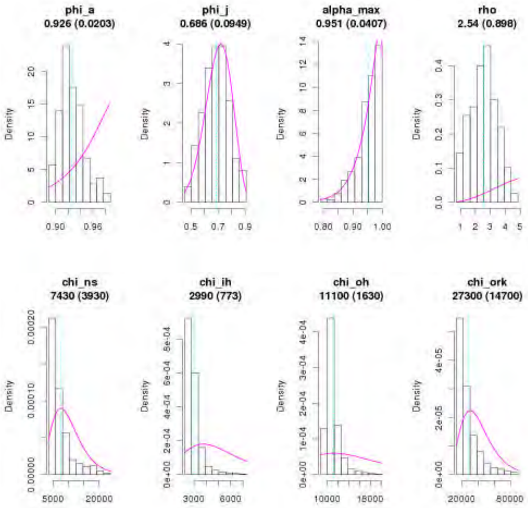
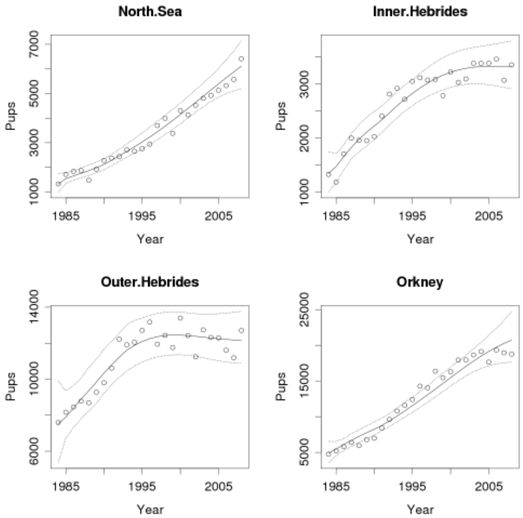
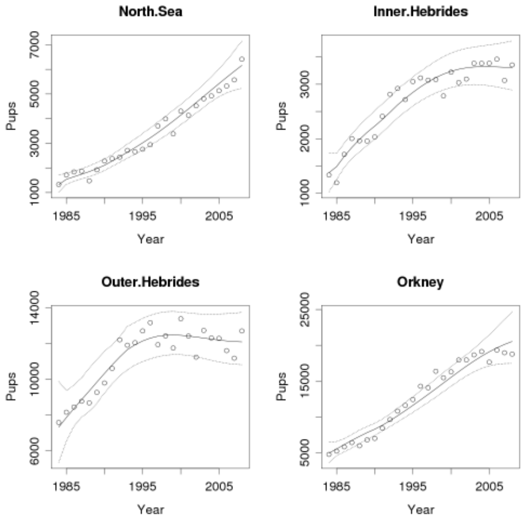


Figure 3. Comparison of pup production estimates from 2009 briefing paper (top left side) and re-runs (rest of page).

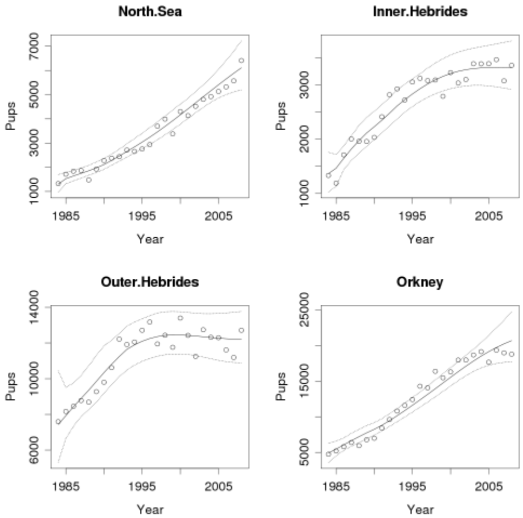
(a) Extended density dependent survival with no movement (EDDDSNM) – from briefing paper



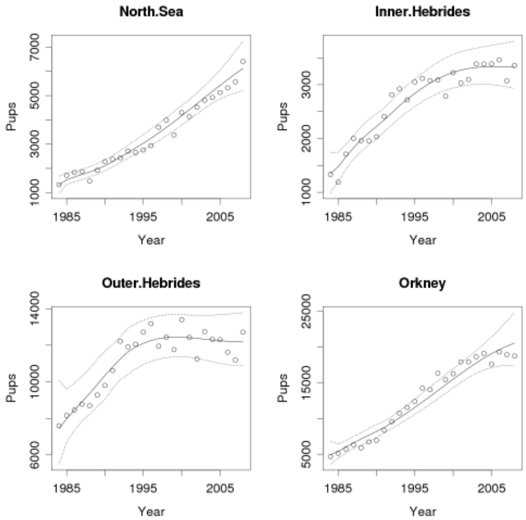
re-run 1



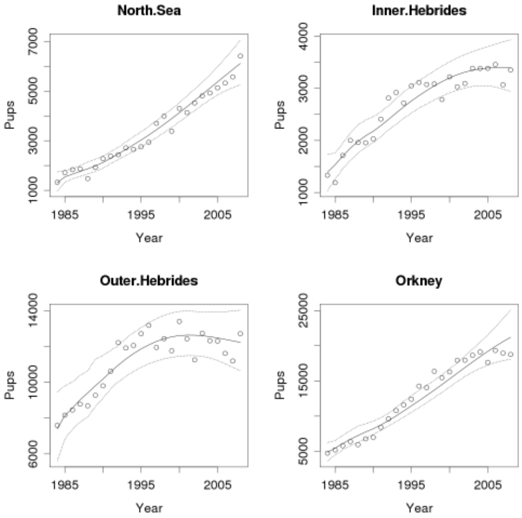
re-run 2



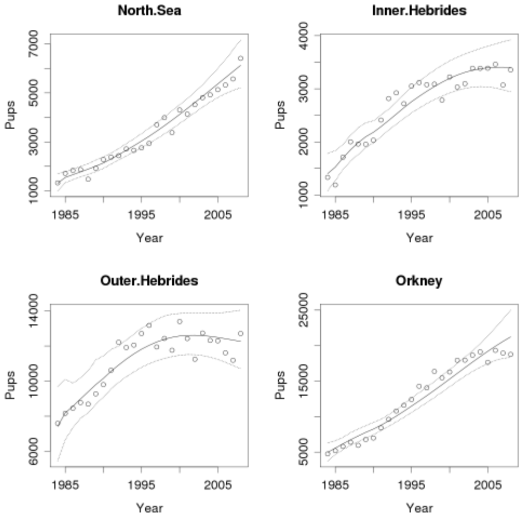
re-run 3



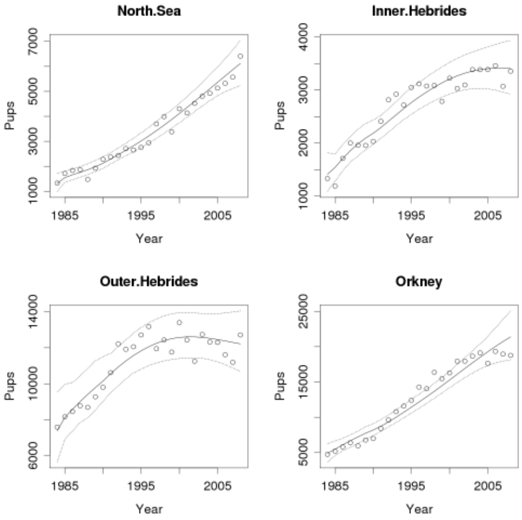
(b) Extended density dependent fecundity with no movement (EDDFNM) – briefing paper



re-run 1



re-run 2



re-run 3

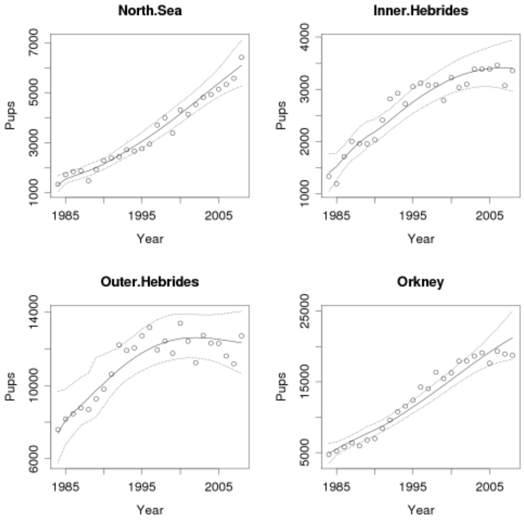
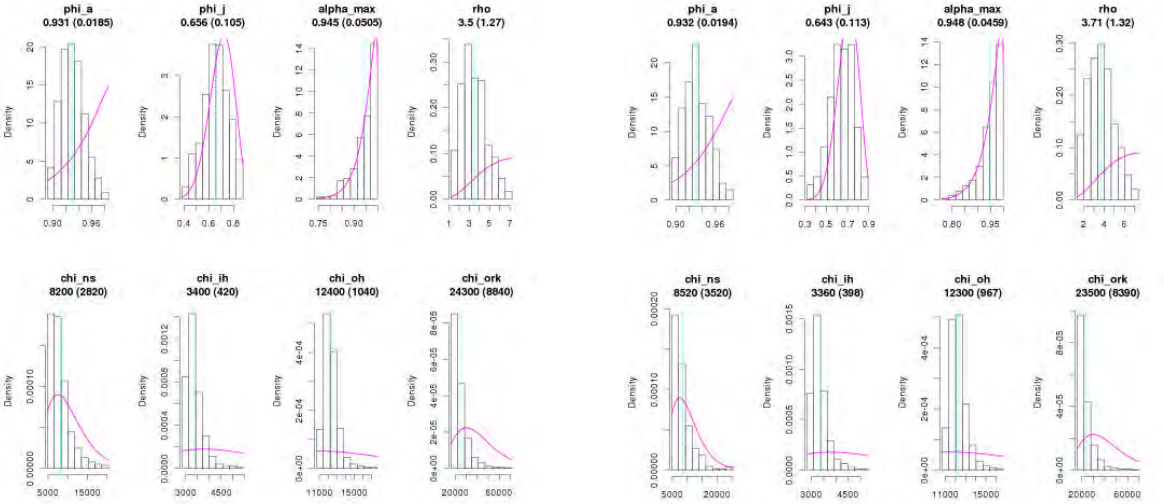


Figure 4. Comparison of posterior parameter estimates from 2009 briefing paper (top left side) and re-runs (rest of page).

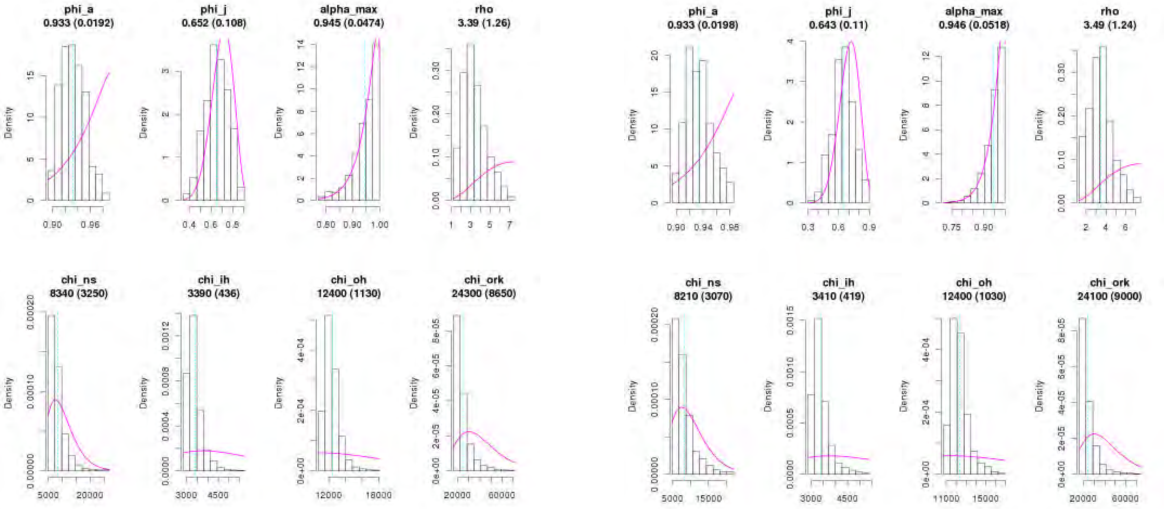


(a) Extended density dependent survival with no movement (EDDDSNM) – briefing paper

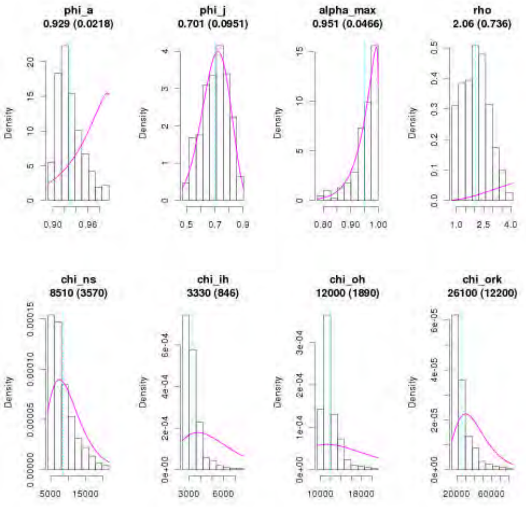
re-run 1

re-run 2

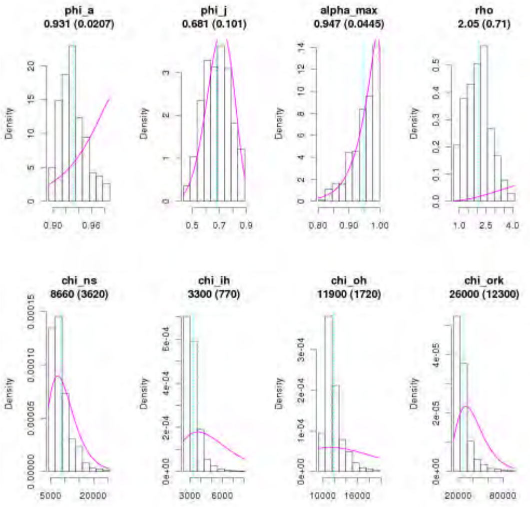
re-run 3



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



re-run 1



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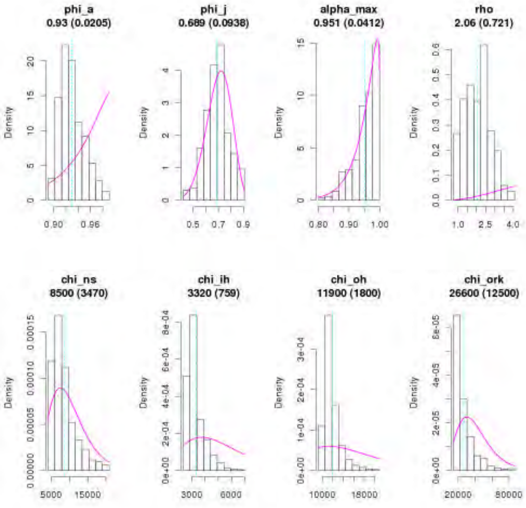


re-run 3

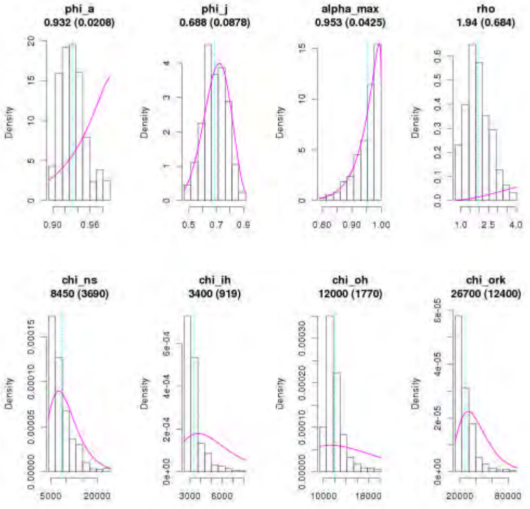
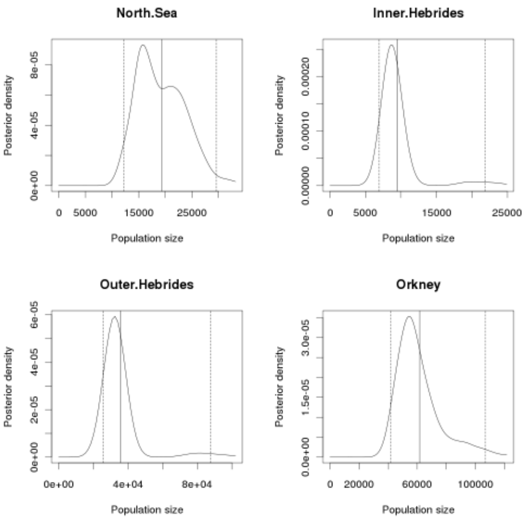
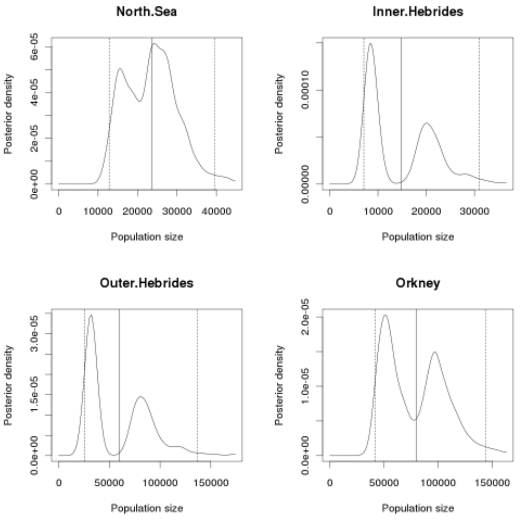


Figure 5. Posterior density of total population size at the beginning of the 2008 breeding season, from four replicate runs of algorithms that combine the models and using prior model probabilities that penalize models with more parameters. Solid vertical lines are the mean posterior estimates; dashed lines indicate posterior 95% credibility intervals.

2009 Briefing paper

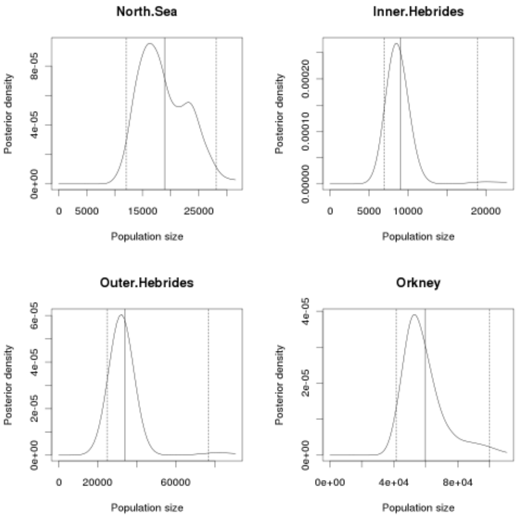


Re-run 1



Re-run 2

Re-run 4



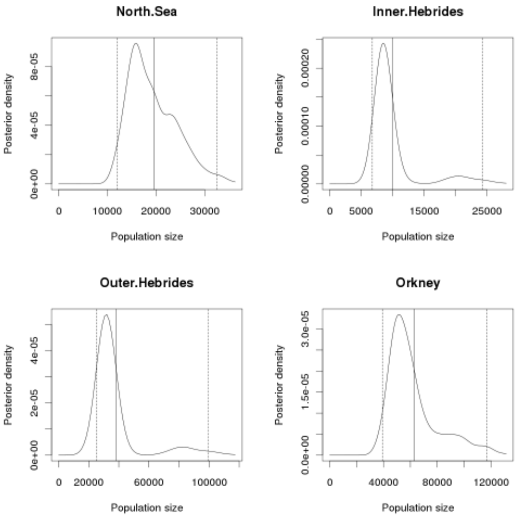
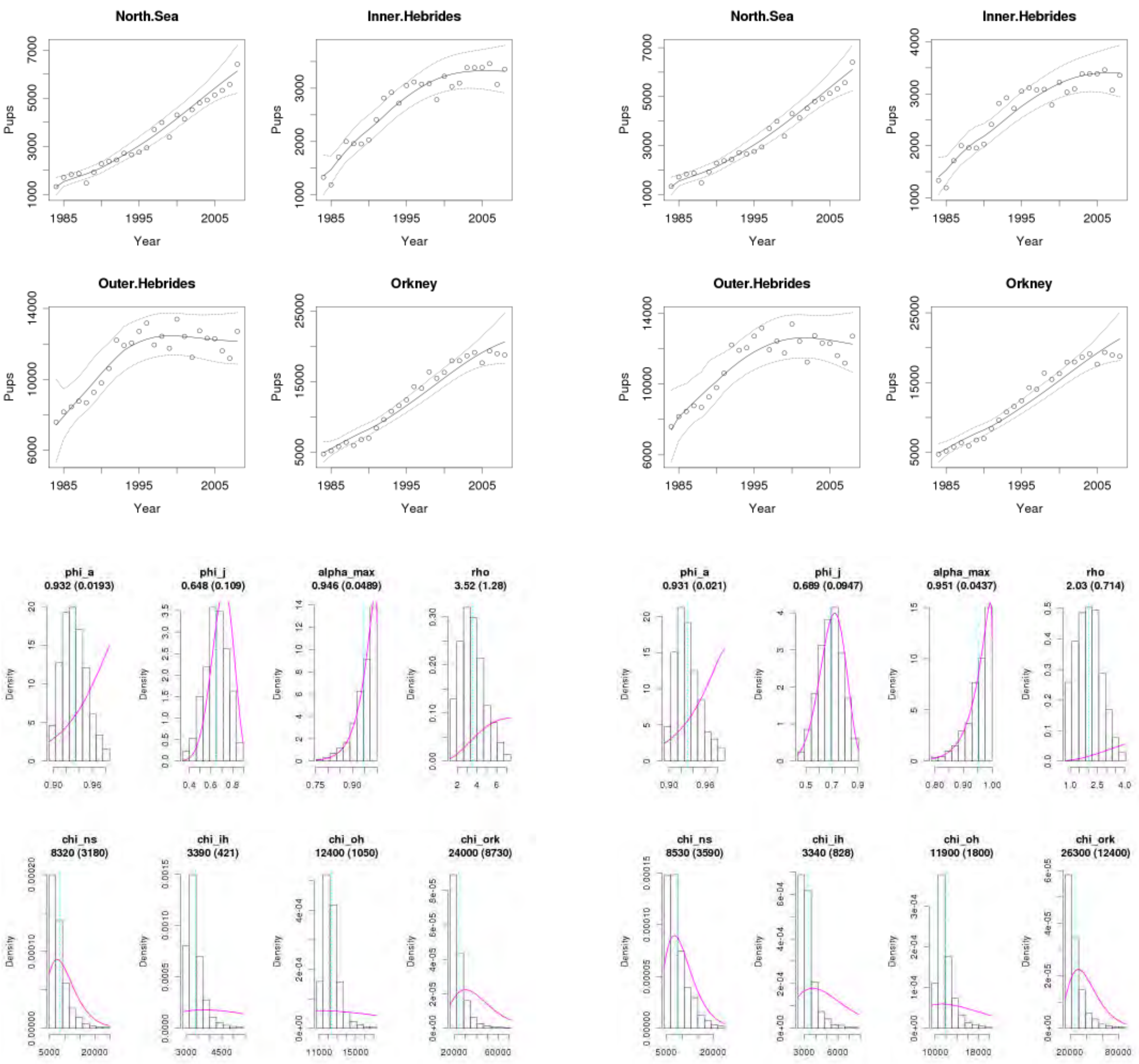


Figure 6. Posterior estimates of pup production and parameters pooling across all four runs made on data from 1984-2009.



(a) EDDSNM

(b) EDDFNM

Figure 7. Posterior density of total population size at the beginning of the 2008 breeding season, pooling across four runs that each combine the models and using prior model probabilities that penalize models with more parameters.

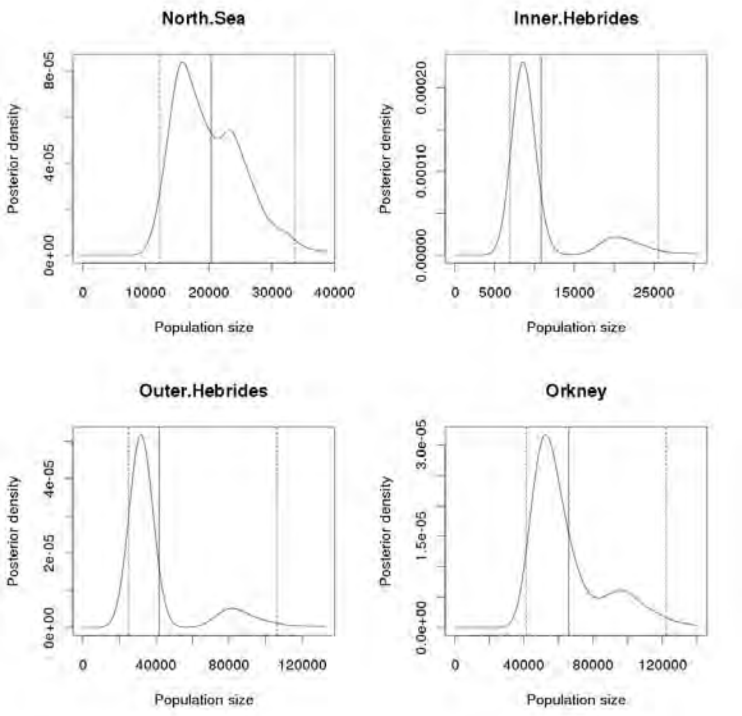
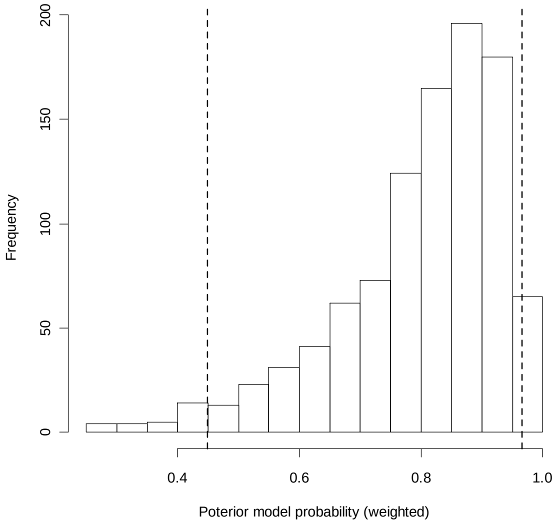


Figure 8. Histogram showing the range of posterior model probabilities for the EDDSNM model generated from 1000 replicates of a parametric bootstrap generating values of negative log integrated likelihood for EDDSNM and EDDFNM models. Vertical dashed lines show upper and lower 2.5th quantiles.



C.D. Duck & D. Thompson

The status of British common seal populations in 2008

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

Summary

In August 2008, the Sea Mammal Research Unit (SMRU) planned to complete the survey of common seals around the whole of the coast of Scotland which started in 2007 and to survey common seals between the Humber Estuary and east Norfolk in England. On account of their continued decline, common seals in Orkney were resurveyed.

In Scotland, helicopter thermal image surveys were restricted to the north-east, north and north-west Scottish coast from Findhorn to Rubha Reidh, west of Loch Ewe; Orkney; the Western Isles and the Small Isles. A second survey of the Moray Firth was carried out in August from a fixed wing aircraft. For logistical reasons we were, once again, unable to survey Shetland.

In England, common seals were surveyed from fixed-wing aircraft in Lincolnshire, Norfolk, Suffolk, Essex and Kent. The Tees Seal Research Programme kindly provided information on seals in the Tees Estuary.

In 2008, most groups of common and grey seals were again photographed using a digital camera to confirm numbers and species identity. 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 2008, the minimum number of common seals counted in Scotland was **19,988** and in England **3,230** making a UK total of **23,218** (Table 1). In 2002, **1,248** common seals were counted in Northern Ireland

The number of common seals counted in Orkney (2,867) was 15.2% lower than in 2007 (3,379). Numbers in north and east Highland, from Nairn to Cape Wrath (884), were 12.9% higher than in 2005 and 2007 (783). The count for the Outer Hebrides (1,815) was 8.4% lower than the aggregated count from 2003 and 2006 and 13.5% lower that the full 2003 count (2,098). In west Highland, from Cape Wrath to Appin in Loch Linnhe, common seal numbers in 2007 and 2008 (5,043), were 1.6% greater than the previous count in 2005 (4,966). In the Moray Firth, both breeding and moult season counts were similar to 2007 counts. In the Firth of Tay, moult counts were the lowest recorded to date, although the survey was later than in previous years.

During the 2008 breeding season, SMRU conducted repeat air surveys of common seals breeding in the Moray Firth, continuing the time series started 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 (Figure 1) are carried out on an approximately five-yearly cycle, with the exception of the Moray Firth and Firth of Tay which are surveyed annually. In 2006, 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 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 to be not well suited to the survey requirements. In 2008, areas missed in 2007 (the Western Isles, the far north and west coast and the Small Isles) were surveyed, with the exception of Shetland. Additional funding from Scottish Natural Heritage (SNH) allowed us to complete a third consecutive survey of Orkney. In 2007 and 2008, the entire Scottish coast was surveyed with the exception of Shetland (Figure 2).

In August 2009, a survey of Shetland will be the main priority and, with additional funding from SNH, will be combined with a fourth consecutive survey of Orkney.

In 2008, as in 2007, we photographed most groups of seals with a high-resolution digital camera to confirm species identity and numbers in groups. 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 have also funded the 2008 and 2009 surveys 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 and two previous surveys of common seals in the UK, are shown in Table 1. The Table includes numbers from both Northern Ireland and the Republic of Ireland. For eastern England, where repeat counts were obtained (for The Wash, Donna Nook, Blakeney Point and Scroby Sands) the mean value has been used.

The most recent minimum estimate of the number of common seals in Scotland is **19,988** from surveys carried out between 2006 and 2008 (Table 1). This is 17.9% lower than the previous total for Scotland (24,080) from surveys carried out between 2001 and 2007 (Table 1). The most recent minimum estimate for England is **3,230**, which is almost identical to the 2007 count of **3,242**. The 2008 count comprises 2,863 seals in Lincolnshire and Norfolk plus 367 seals in Northumberland, Cleveland, Essex and Kent between 2007 and 2008 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 **24,466.**

2. Common seals in Scotland: moult

In August 2008, the area surveyed for common seals using a thermal imager included the whole of Orkney, the far north and west coast between Nairn in the Moray Firth and Rubha Reidh in Wester Ross, the Outer Hebrides and the Small Isles.

The number and distribution of common seals counted during the thermal imaging surveys in August 2008 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 2008 are shown in Figure 4 and Table 1. The number of common seals counted in Orkney (2,867) was **15.2%** lower than in 2007 (3,379). Numbers in north and east Highland, from Nairn to Cape Wrath (884), were **19.5%** lower than in the complete 2005 survey (1,056). The count for the Outer Hebrides (1,815) was **8.4%** lower than the aggregated count from 2003 and 2006 and **13.5%** lower than the last complete 2003 count (2,098). In west Highland, from Cape Wrath to Appin in Loch Linnhe, common seal numbers in 2007 and 2008 (5,043), were **1.6%** higher than in the previous 2005 count (4,966).

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 up to Helmsdale (SMRU moult, all MF).

SMRU's aerial surveys of the Moray Firth began in August 1992. The counts are shown 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. In 2008, both counts were lower than counts from both 2006 and 2007 (Table 2). It is not very clear whether common seal numbers in this area have stabilised following a period of decline between 1997 and 2002 or whether the decline is continuing at a reduced rate. 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 2008, the Firth of Tay count was the lowest recorded at 222, even lower than the 2007 counts which were below 300 for the first time. Numbers in this Special Area of Conservation (SAC) are approaching 33% of the number counted between 1990 and 2002. There were 147 common seals in the Firth of Forth in 2007. Previously we suggested that these seals were from the same population. Even if this is the case, numbers have declined considerably in recent years.

3. Common seals in Scotland: breeding season

Moray Firth

During the 2008 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. The mean count in 2008 of 528 was virtually identical to the 2007 mean count of count of 526.

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).

Two aerial surveys of common seals were carried out in Lincolnshire and Norfolk during August 2008 (Tables 1 and 4). The mean count for The Wash (2,010) was similar to the series of moult counts obtained since the 2002 PDV epidemic and 32.5% lower than the mean pre-epidemic 2002 count (2,976).

Overall, the combined count for the English East coast population (Donna Nook to Scroby Sands) in 2008 was 4.5% lower than the 2007 count and 3.1% higher than the 2006 count but within the range of counts over the previous 3 years (Figure 8, Table 4). 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 15% between 2007 and 2008. This failure of The Wash common seals to recover from the 2002 epidemic is a cause for concern and should be investigated.

Common seals in the Tees Estuary are monitored by the Industry Nature Conservation Association (INCA). There appears to be a very slow recovery with august numbers now around 40 (Woods 2008). Low but increasing numbers of pups are born (most died in 2008).

5. Common seals in England: breeding season

A total of 994 pups and 2009 older seals (1+ age classes) were counted in The Wash during the 2008 breeding season survey compared with 984 pups and 2353 older seals in July 2006. Pups were widely distributed, being present at all occupied sites in 2008. The 2008 adult and pup counts were therefore similar to the previous two years which were much higher than in previous surveys since 2002, pup counts being being 55% greater than the 2005 count and adult count 28% higher. The change in pup counts between 2004-2005 and 2006-2008 is unexplained. The similarity of pup counts in 2006-2008 suggests that, like the moult counts, the production is not increasing rapidly as seen in the Wadden Sea.

6. Proposed common seal surveys 2009

Breeding season: Moray Firth

During the pupping season (15th June – 15th July 2008) five fixed-wing surveys will be 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 Shetland and Orkney is planned for August 2009, weather and equipment permitting. The same methods will be used as in previous years, 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) 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 northern and southern Ireland respectively.

We thank Becci Jewell for her assistance during the helicopter surveys and are grateful for the technical expertise enthusiastically provided by the companies supplying the survey aircraft and pilots: PDG Helicopters and Giles Aviation (formerly Air Partner and Gold Air International).

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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.**

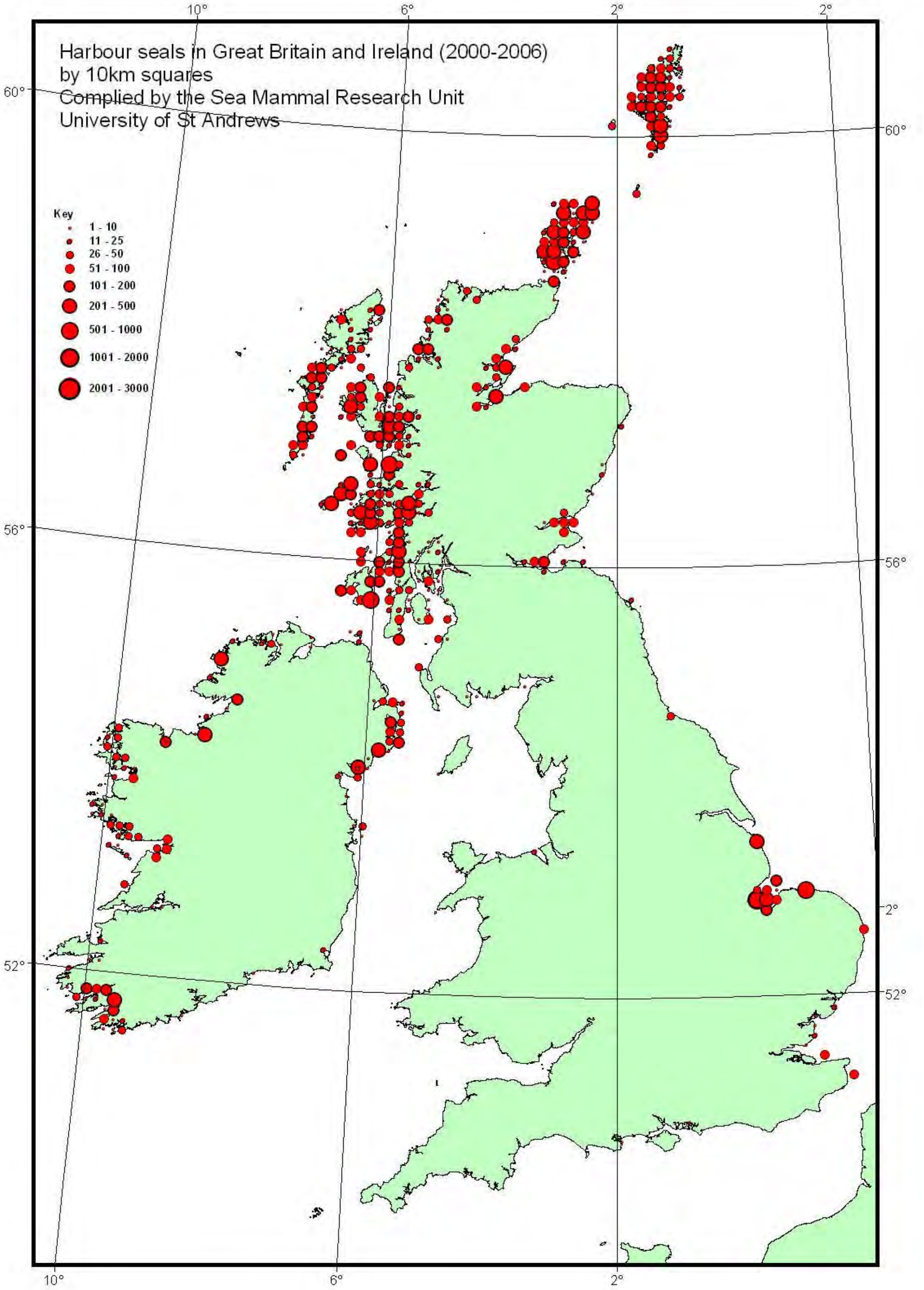

Figure 2. The number and distribution of common seals around the coast of Scotland surveyed in August 2007 and 2008. All areas were surveyed by helicopter using a thermal imaging camera.

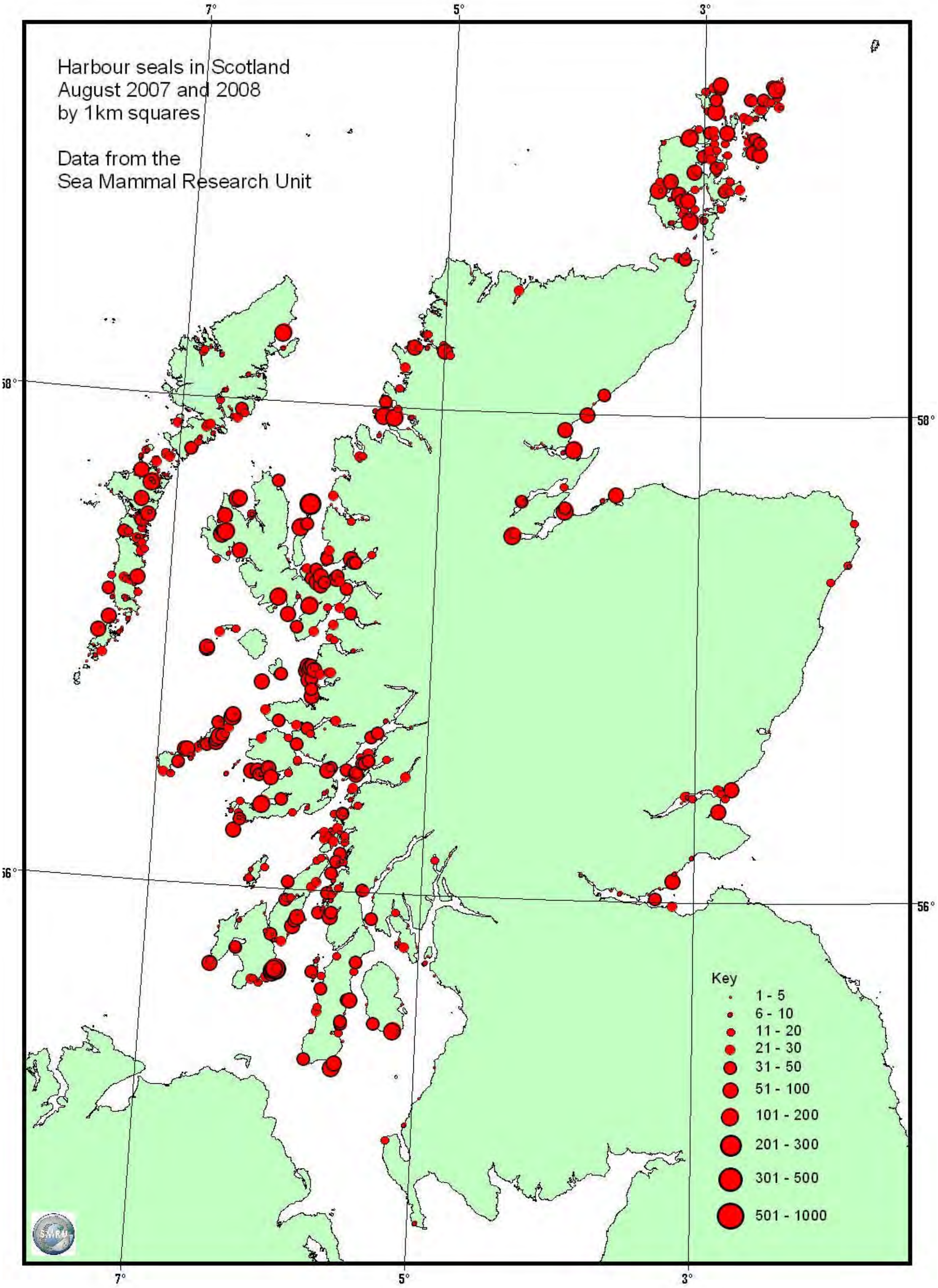

Figure 3. The number and distribution of grey seals around the coast of Scotland surveyed in August 2007 and 2008. All areas were surveyed by helicopter using a thermal imaging camera.

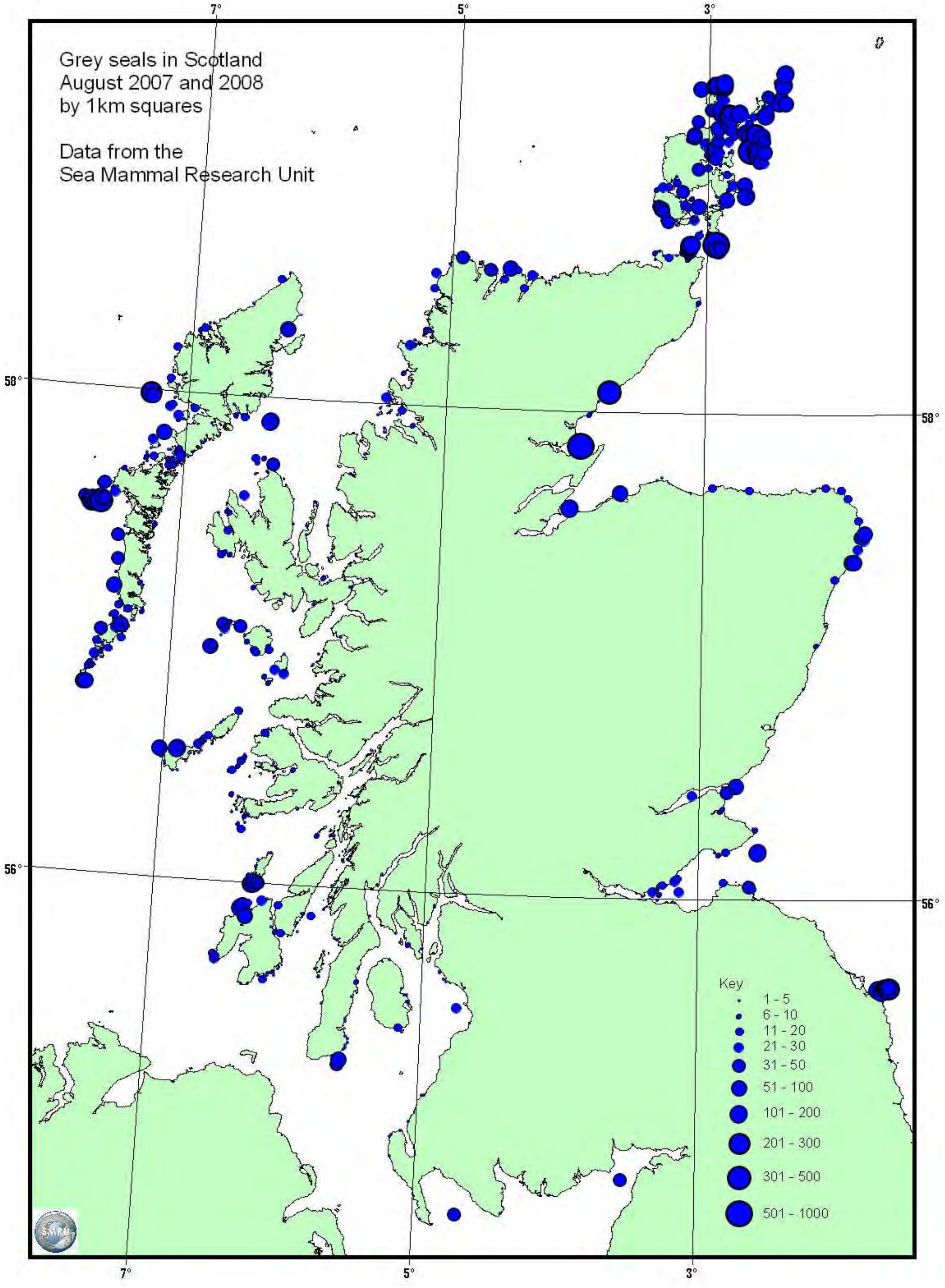

Figure 4. Trends in counts of common seals around Scotland. Data from the Sea Mammal Research Unit. The 2006 survey of the Outer Hebrides was omitted as part of the east coast of Benbecula and North Uist was not completed.

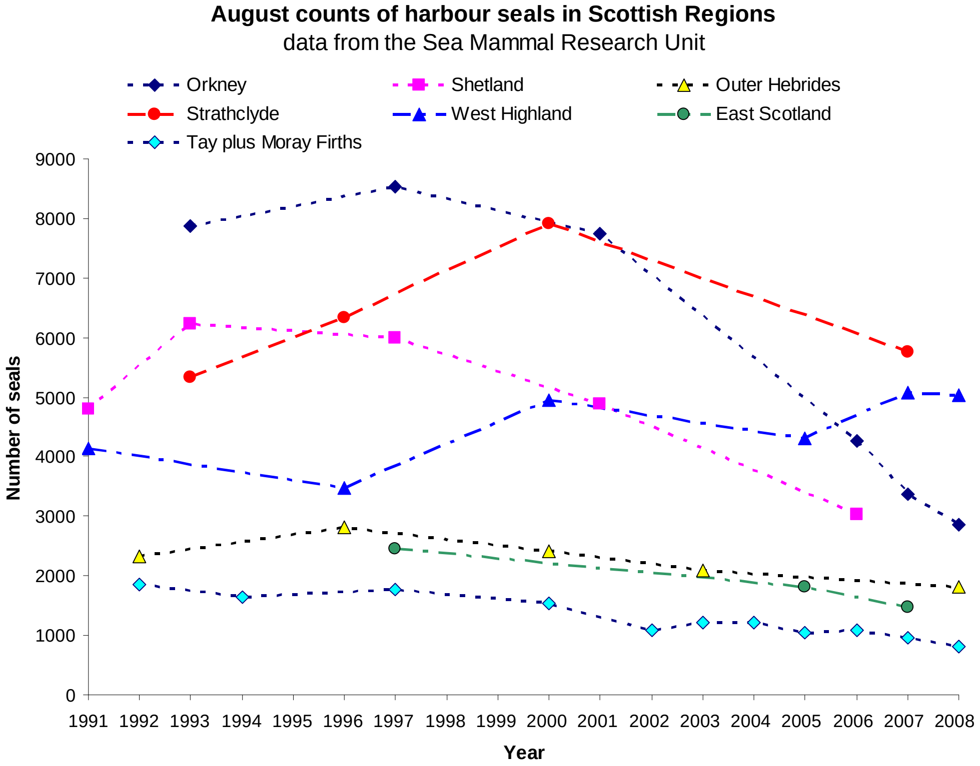

Figure 5. Trends in common seal numbers in the Moray since 1988. Seals were counted during their breeding season and during their moult by the University of Aberdeen's Lighthouse Field Station (LFS, Inner Firth) and more recently by SMRU (breeding season counts are for the Inner Firths plus Loch Fleet).

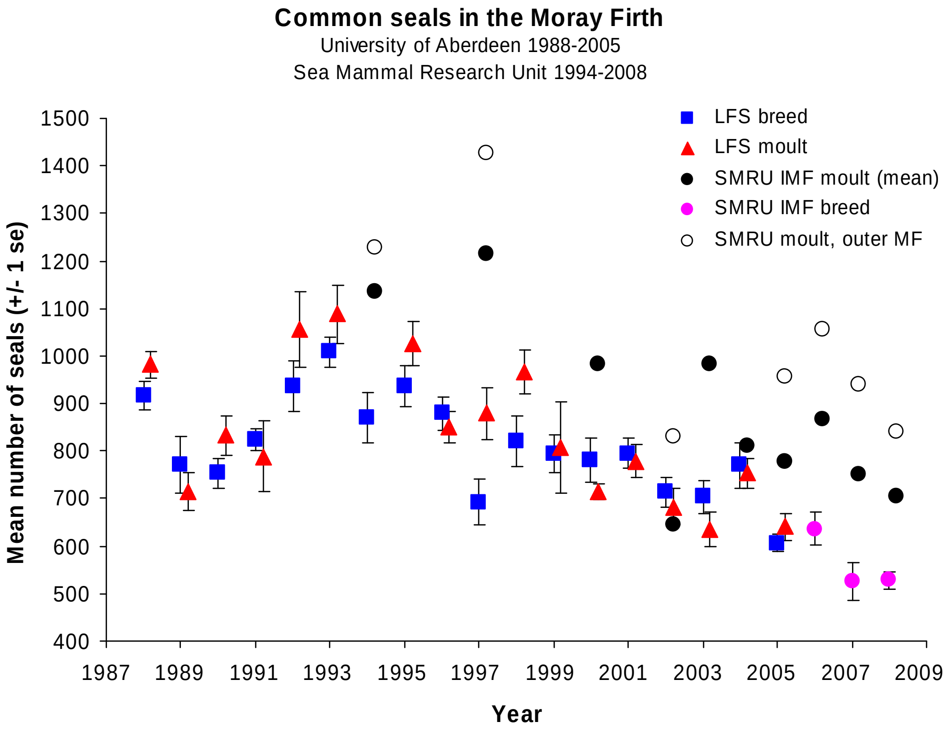

Figure 6. The number of common seals counted in areas within the Moray Firth, between 1992 and 2008, by the Sea Mammal Research Unit.

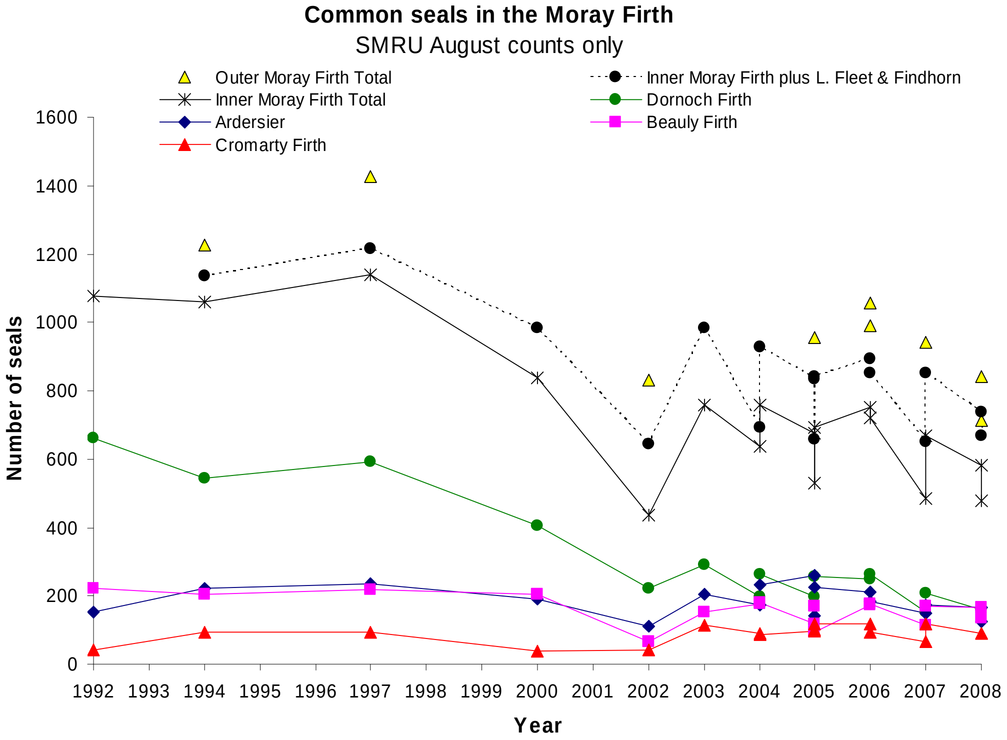

Figure 7. The number of common seals counted in the Firth of Tay, between 1990 and 2008, by the Sea Mammal Research Unit.

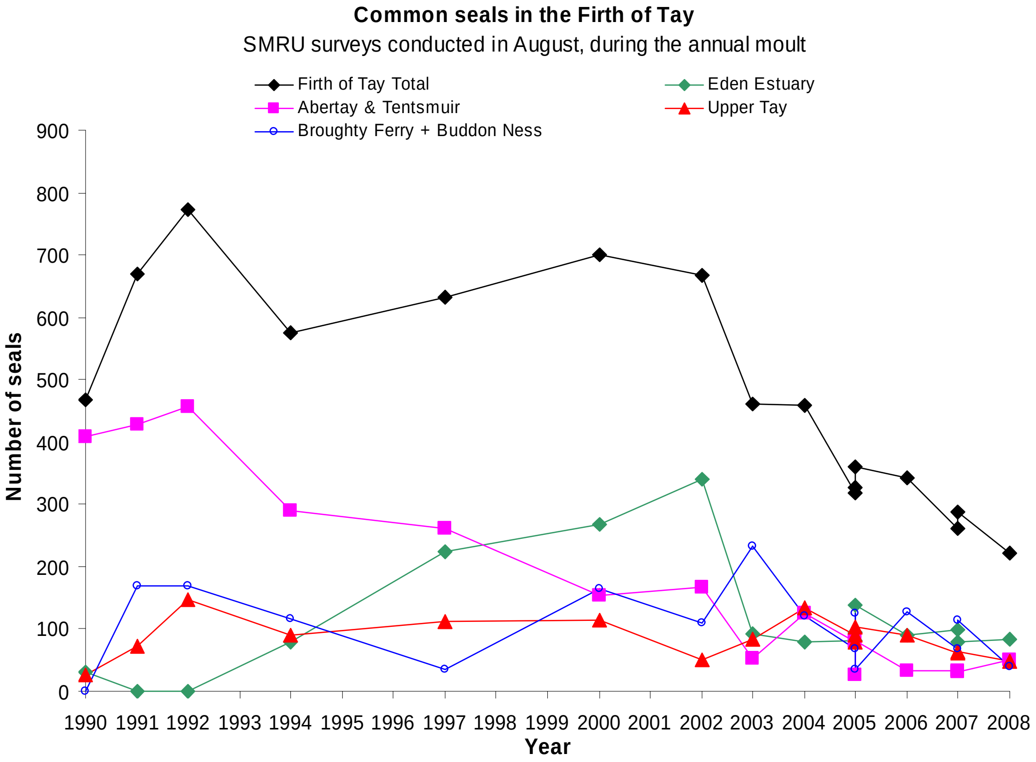

Figure 8. Counts of common seals in The Wash in August, 1967 - 2008. These data are an index of the population size through time. Fitted lines are exponential growth curves (growth rates given in text).

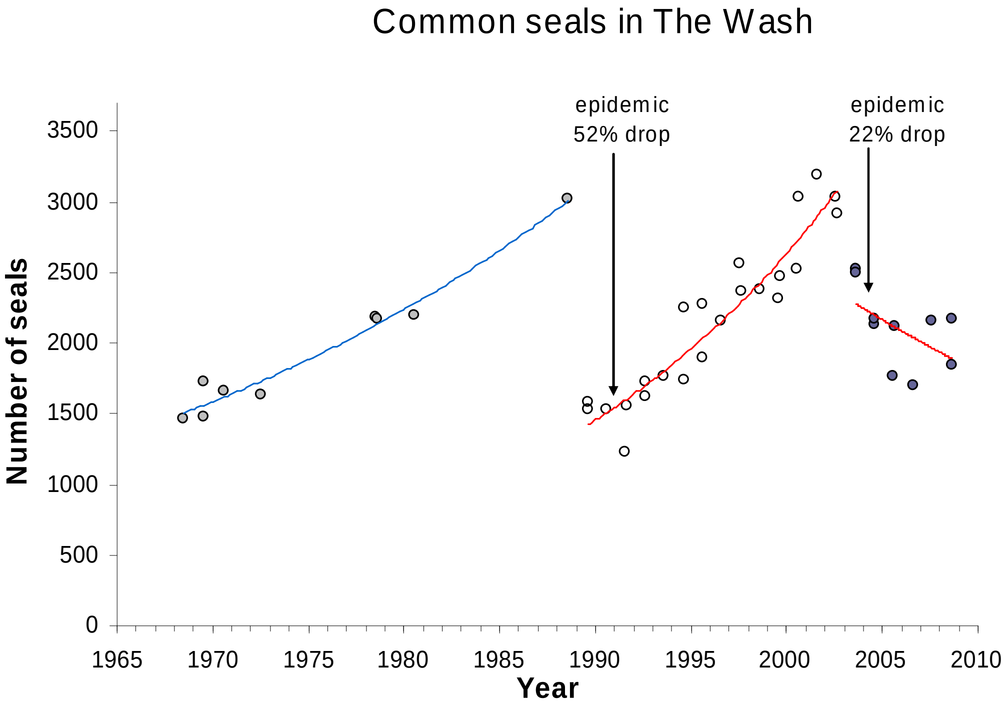

Table 1. Minimum estimate of the UK common seal population from the most recent regional surveys and from two previous surveys.

Region	**Current estimate** year	**Previous estimate** year	**Earlier estimate** year
Shetland	**3,057** 2006	**4,883** 2001	**5,991** 1997
Orkney	**2,867** 2008	**3,379** 2007	**4,256** 2006
Outer Hebrides	**1,815** 2008	**1,981** 2003, 2006	**2,098** 2003
Highland East & North (Nairn to Cape Wrath)	**884** 2008	**783** 2005, 2007	**1,266** 1997, 2004
Highland West (Cape Wrath to Appin, Loch Linnhe)	**5,043** 2007, 2008	**4,966** 2005	**4,947** 1996-7, 2000
Strathclyde West (Appin to Mull of Kintyre)	**4,949** 2007	**6,702** 2000, 2005	**5,342** 1996
Strathclyde, Firth of Clyde (Mull of Kintyre to Loch Ryan)	**811** 2007	**581** 2005	**991** 1996
Dumfries & Galloway (Loch Ryan to English Border at Carlisle)	**23** 2007	**42** 2005	**6** 1996
Grampian (Nairn to Montrose)	**102** 2007	**113** 2005	**62** 1997
Tayside (Montrose to Newburgh)	**166** 2007	**101** 2005	**92** 1997
Fife (Newburgh to Kincardine Bridge)	**215** 2007	**445** 2005	**617** 1997
Lothian (Kincardine Bridge to Torness Power Station)	**55** 2007	**104** 2005	**40** 1997
Borders (Torness to Berwick upon Tweed)	**0** 2007	**0** 2005	**0** 1997
Central (Upper Forth)	**1** 2007	**0** 2005	**0** 1997
TOTAL SCOTLAND	**19,988**	**24,080**	**25,708**
	(all 2008)	(2007)	(2006)
Blakeney Point	**581**	**550**	**719**
The Wash	**2,010**	**2,162**	**1,695**
Donna Nook	**191**	**214**	**299**
Scroby Sands	**81**	**71** 2006	**64** 2004
Other east coast sites	**347**	**153** 1994, 2000, 2005	**235** 1994, 2000, 2003
South and west England (estimated)	**20**	**20**	
TOTAL ENGLAND	**3,230**	**3,242**	**2,777**
TOTAL BRITAIN	**23,218**	**27,322**	**28,485**
TOTAL NORTHERN IRELAND	**1,248**		
TOTAL BRITAIN & N. IRELAND	**24,466**	**28,570**	**29,733**
TOTAL REPUBLIC OF IRELAND	**2,905**		
TOTAL GREAT BRITIAN & IRELAND	**27,371**	**31,475**	**32,638**

Table 2. Numbers of common seals in the Moray Firth during August (SMRU surveys). See Figure 6.

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	13 Aug 2008[1]	20 Aug 2008
Ardersier	154	-	221	234	191	110	205	172	232	260	143	195	224	210	184	150	173	167	123
Beauly Firth	220	-	203	219	204	66	151	175	180	119	169	-	94	174	178	115	170	165	135
Cromarty Firth	41	-	95	95	38	42	113	90	86	98	101	-	118	119	93	67	118	90	90
Dornoch Firth (SAC)	662	-	542	593	405	220	290	199	262	199	118	-	256	249	264	153	209	160	130
Inner Moray Firth Total	**1077**	**-**	**1061**	**1141**	**838**	**438**	**759**	**636**	**760**	**676**	**531**	**-**	**692**	**752**	**719**	**485**	**670**	**582**	**478**
Findhorn	-	-	*58*	*46*	*111*	*144*	*167*	*0*	*98*	*90*	*58*	*148*	*74*	*63*	*68*	*82*	*94*	*69*	*115*
Loch Fleet	-	*16*		*27*	*33*	*62*	*56*	*58*	*70*	*68*	*70*	-	*76*	*79*	*53*	*85*	*87*	*87*	*77*
Loch Fleet to Dunbeath	-	*92*		*214*		*188*	-	-	-	-	-	-	*113*	*163*	*137*		*90*	*102*	*43*
Outer Moray Firth Total				**1428**		**832**							**955**	**1057**	**989**		**941**	**840**	**713**

[1] Thermal imaging survey

Table 3. Numbers of common seals in the Firth of Tay during August. See Figure 7.

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]	29 Aug 2008
Eden Estuary	31	0	0	80	223	267	341	93	78	81	95	139	90	99	79	83
Abertay & Tentsmuir	409	428	456	289	262	153	167	53	126	80	26	82	34	32	30	50
Upper Tay	27	73	148	89	113	115	51	83	134	90	80	104	91	62	64	49
Broughty Ferry & Buddon Ness	0	169	169	117	35	165	(109)	232	121	68	125	36.	127	68	114	40
Firth of Tay Total (SAC)	**-**	**670**	**773**	**575**	**633**	**700**	**(668)**	**461***	**459**	**319**	**326**	**361**	**342**	**261**	**287**	**222**

[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**	**11/8**	**2/8**	**1/8**	**8/8**	**6/8**	**5/8**	**2/8**	**2/8**	**7/8**	**3/8**	**4/8**	**4/8**	**11/8**	**9/8**	**6/8**			**3/8**	**8/8**
		12/8		**11/8**	**16/8**		**12/8**	**15/8**		**8/8**	**14/8**	**13/8**	**12/8**		**12/8**	**10/8**	**14/8**	**09/8**	**15/8**		**16/8**
Year	**1988**	**1989**	**1990**	**1991**	**1992**	**1993**	**1994**	**1995**	**1996**	**1997**	**1998**	**1999**	**2000**	**2001**	**2002**	**2003**	**2004**	**2005**	**2006**	**2007**	**2008**
Blakeney Point	701	-	73	-	-	267	-	438	372	250	535	715	895	772	346		577	741		550	620
		307		-	217		196	392		371	738	602	disturb		631	399	715	677	719		541
The Wash	3087	1531	1532	1226	1724	1759	2277	2266	2151	2561	2367[1]	2320	2528	3194	3037	2529	2126	1768		2162	1846
(SAC)		1580		1551	1618		1745	1902		2360	2381	2474	3029		2916	2497	2167	2124	1695		2174
Donna Nook	173	-	57	-	18	88	60	115	162	240	294	321	435	233	341	231	242	372		214	132
		126		-	-		146	36		262	201	286	345		-		346	470	299		250
Scroby Sands	-	-	-	-	-	-	61	-	51	58	52	69	84	75			49				60
		-		-	-		-	49		72	-	74	9				64		71		101
The Tees	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-		41[3]
		-		-	-		35	-		-	-	-	-				-				
Holy Island, Northumber-land	-	-	-	-	-	-	13	-	-	12[2]	-	-	10	-	-		-	17[2]	-	7	
		-		-	-			-			-	-					-				
Essex, Suffolk & Kent	-	-	-	-	-	-	-	90	-	-	-	-	-	-	-		-		-		299
		-		-	-		-	-		-	-	-	-		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.

[3] Tees data kindly provided by Robert Woods, INCA (Woods, 2008).

Mike Lonergan, Dave Thompson, Len Thomas & Callan Duck

Scaling up from pup counts to population trajectories for British grey seals.

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

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

Summary

We present a simple Bayesian method, using generalised additive models to smooth a series of pup production estimates followed by matrix models to scale their results up, and use it to estimate the trajectories of four British grey seal populations (*Halichoerus grypus*). A uniform prior on the relative importance of density dependence in fecundity and first year survival is applied to produce an overall estimate and credibility (Bayesian confidence) interval for each population. This approach requires fewer assumptions than the State Space Models currently used in the assessment of these populations, and produces similar credibility intervals. The forms of the density dependent effects are outputs rather than assumptions of the technique. We briefly discuss the potential and limitations of the method and suggest that, even where more complex models and strategies are to be adopted, this approach provides at least a useful tool for investigating such datasets and planning and structuring their analysis.

Introduction

Grey seals are colonial breeders. Their pups are born on land and remain ashore for several weeks, initially with their mothers then alone. This behaviour, along with their white coats, makes the pups relatively easy to observe. Counting the other components of these populations is much less straightforward, since, while they do haul out on land, the animals spend most of their time at sea and submerged. Grey seal population estimation therefore effectively comes down to scaling up from numbers of pups. This situation is an extreme example of a widespread problem in ecology, since there are many species where some parts of the population are much harder to observe than others.

Grey seals are abundant around Britain and on the eastern seaboard of the US and Canada. They are also present, in smaller numbers, in the Baltic Sea and around the northern European coastline. Females mature at around six years of age and give birth to a single pup in the autumn. Since 1984, pup production at the main British grey seal colonies has been monitored by series of aerial surveys carried out throughout the breeding season. Each year, between 3 and 6 flights are made over each colony using a fixed-wing aircraft with a vertically fitted large format camera. The numbers of animals in each photograph are counted and used to estimate the total numbers of pups that were born at each colony. A consistent methodology has been used to estimate total numbers throughout this study and, where sufficient surveys have been completed, calculate the estimates' precision (Thomas *et al.* 2005; SCOS 2007). Previous analyses have summed the data within each of four areas: the North Sea, Orkney, the Inner Hebrides and the Outer Hebrides. We follow this and use the total pup production estimates from each area (figure 1) as inputs to our models.

Until around 1995, when the previously steady growth started to slow (figure 1), British grey seal population sizes were relatively straightforward to estimate. More recent estimates of the total population size depend critically on the assumptions made about where in the species' lifecycle density dependent effects occur. A set of State Space Models has been used to model the population and advise government agencies involved in its management (SCOS 2007). State Space Modelling is a Bayesian technique to represent the complexities of datasets with uncertainty in both the development of the system and the observations made of it (Thomas *et al.*, 2005). The models of these populations started from priors on fecundity, the survival of pups and adults, the parameters of the density dependent effects (of an assumed functional form), and the amount of movement between areas. They assumed these parameters were equal in all areas, and contained age-structured matrix models, incorporating stochastic effects in the birth, death and movement processes as well as in the pup production estimation, of the numbers of females in the populations (Newman et al., in press;

Buckland *et al.,* 2007). These models are very computationally intensive, requiring statistical expertise, customised software and a full day on a fast PC to fit each one to these 96 datapoints (L. Thomas, unpublished data). This has led us to attempt a simplification that might be accessible to a wider range of biologists and conservation managers.

Material and Methods

We fitted generalised additive models, with log link functions and gamma set to 1.4 (to reduce overfitting), separately to each of the four regional pup production time series. The mgcv library (Wood, 2006) within the R statistical environment (R Development Core Team, 2006) was used for this. A quasi-Poisson error structure was adopted for all the models as the data is based on counts. The calculated precisions for the individual colonies' pup production estimates (supplementary figure 1) also appear consistent with this.

Pup production in each region showed a period of exponential growth, though with different annual growth rates (figure 1 and supplementary figure 2). Separate deterministic age structured matrix models were therefore fitted for the female population in each region. 10,000 replicate pup production trajectories were calculated for each one, using the Bayesian covariance matrices for the gam models to allow for the dependencies between their smooths' parameters (Wood 2006). Each trajectory's maximum annual growth rate was then calculated. Scaling the replicate pup production trajectories up into population trajectories requires them to be combined with suitable sets of demographic parameter values. These need to be drawn from the joint conditional probability distribution for the demographic parameters given the maximum growth rates. Explicitly calculating these distributions is not straightforward, but they can be approximated numerically by drawing from an unconditional joint probability distribution for the demographic parameters and discarding those results whose maximum growth rate falls outside a small neighbourhood of the required value. Newman *et al.* (in press) provide, independent, prior distributions for maximum (low population density) fecundity and adult and pup survival (table 1). 10,000 sets of parameter values were drawn from these priors and the rates of stable exponential growth that each would produce calculated. The set of demographic parameter values with the most similar exponential growth rate was then associated with each of the replicate pup trajectories.

Two sets of deterministic matrix models were then populated, with one assuming that all the density dependence was in fecundity and the other putting it all into pup survival. For the variable fecundity model, each replicate's one-year olds were calculated by dividing half the previous year's pups by the relevant pup survival parameter, then a similar process filling in the subsequent 2,3,4 and 5-year-old classes. The numbers of individuals in the older age groups during the early years of the study were estimated from the stable age structure for an exponentially growing population. The numbers of adult, six-plus, females were then projected forwards. Each year's effective fecundity was then calculated. If any of the fecundity estimates were higher than the maximum fecundity for that replicate, the process was repeated with the replicate set of demographic parameters that produced the next most similar growth rate. Equivalent calculations were made for the model with density dependent pup survival, though these used the fecundities to calculate numbers of adults, then worked back down in age. For each replicate, the recent younger age classes were filled in using the pup survival estimates from the years with most similar estimated adult numbers. Further details and code for these calculations are contained in the electronic supplementary material.

Two different methods were used to combine the results of the two models of each region. In one the two posterior distributions of population estimates were simply summed, while the other defined an informal uniform prior on where the result lay between the two extremes and repeatedly drew two uniform random variables, using one to identify a replicate and the other to determine the weighting of the results of the two population models for that replicate, creating a distribution that effectively smeared across the two directly modelled extremes. Total, rather than female only, population estimate distributions were then calculated by multiplying each replicate by a draw from a normal distribution with mean 1.73 and standard deviation of 0.1, to allow for the uncertainty in the sex-ratio within these populations.

Results

Figure 1 shows the smoothed pup production trajectories for each of the regions. It can be seen that the growth rates have at least slowed substantially everywhere except in the North Sea. The 2007 estimate for the Outer Hebrides is higher than any of the others in 64 out of the 10,000 replicates pup production trajectories, implying a significant decline in that region. For 95% of these replicates, the highest values occurred within the period 1995-2002.

Everywhere except the North Sea, the density dependent effects cause the pairs of matrix models to diverge (figure 2). Estimates of the 2007 population are given for each region in table 2, and have a slightly higher precision than those produced by the State Space Models for 2006 (SCOS 2007) and 2007 (L. Thomas, unpublished data). Adult survival is the only demographic parameter substantially altered by the model fitting (table 1 and supplementary figure 3), and some impression of the patterns of density dependence implied by the two models are visible (supplementary figures 4 & 5).

Discussion

This approach effectively pushes all the uncertainty in the system into the error terms of the gams. These models therefore have lower precision than the colony based pup production estimates and estimate each year's expected, rather than actual, pup production. The uncertainty then passes through into the population estimates and could be expected to inflate their credibility intervals. The similarity of the credibility interval widths to those from the more detailed State Space Models suggests that the additional effects, such as demographic stochasticity and movement between areas, which are explicitly represented in those models, may have limited impact on the precision of their results in this case. Alternatively, the extra parameters and assumptions about the functional forms for density dependence and movement within the State Space Models, may absorb a sufficiently large proportion of this small dataset to negate the benefits of their more accurate representation of the system. Another possibility is that the use of different demographic parameter values in each region, made possible by the other simplifications in model structure, is the key to the performance of these scaled gam models. Additionally, the process of matching each replicate's maximum growth rate to that of a set of demographic parameter values, rather than simply drawing directly from the priors, may actually extract most of the information available to the more complete Bayesian analysis.

The uniform prior on the relative impact of density dependence on fecundity and pup survival is clear and unambiguous. It is much easier to calculate than a set of intermediate models, but reflects the current state of ignorance as to the true balance between these factors. While it is straightforward to apply here, it might be harder to justify its combination with formal likelihood based model selection techniques, such as Akaike's Information Criterion (Burnham and Anderson 2001), which penalise models for including additional parameters.

This approach could be seen as a retrograde step, since it does not attempt as complete a description of the system or utilisation of the data, as the State Space Models. It could also be criticised for its limited predictive and explanatory power. However, any projection of models requires extrapolation, and needs to be done cautiously. For these populations, the most obvious danger would be in the projection of density dependent effects beyond the range of existing data, which requires a belief that their functional forms have been adequately described. It is also possible that, if the State Space Models were modified in the light of these results, for example by modifying them to allow adult survival to vary between areas, the precision of their estimates would improve. However, as the most appropriate analysis of datasets will always depend on their size and the availability of resources, this sort of less demanding methodology may also be appropriate for other small datasets.

Acknowledgements

Collection of this data is funded by NERC and SNH, and involves many people at the Sea Mammal Research Unit and elsewhere. Its analysis and interpretation has been discussed with many colleagues at St Andrews and the members of the NERC Special Committee on Seals. We are grateful to them all.

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Table 1: Distributions of parameter values. The priors are taken from Newman et al. (in press), the posterior values are those used by the replicate model runs in each region under the alternative assumptions of all density dependence being in fecundity or pup survival.

	prior			posterior							
				North Sea		Orkney		Inner Hebrides		Outer Hebrides	
	distribution	mean	sd	mean	sd	mean	sd	mean	sd	mean	sd
max pup survival	Beta(14.53,6.23)	0.7	0.1	0.7	0.1	0.7	0.1	0.7	0.1	0.7	0.1
adult survival	Beta(22.05,1.15)	0.95	0.04	0.92	0.01	0.96	0.01	0.95	0.02	0.91	0.01
max fecundity	Beta(22.05,1.15)	0.95	0.04	0.95	0.05	0.95	0.05	0.95	0.05	0.95	0.05

Table 2: Estimates (mean and 95% credibility intervals) of the total size of the grey seal populations in each region before breeding in 2007. The results for the two models are given along with those from simple (equally weighted) model averaging and applying the uniform prior across the two models.

[1] all the CIs include uncertainty in the population sex-ratio.

[2] the CIs are estimated conservatively by summing those of the individual models.

Model	2007 Regional Population (in thousands, mean & 95%CIs[1])				
	North Sea	Orkney	Inner Hebrides	Outer Hebrides	Total[2]
Density dependent pup survival	20.8 (16.3-25.6)	45.7 (35.5-58.1)	8.0 (5.9-10.7)	34.4 (27.4-41.7)	109.8 (88.1-134.2)
Density dependent fecundity	24.4 (19.7-29.3)	123.9 (102.6-150.1)	24.1 (18.6-33.8)	69.7 (56.8-85.4)	229.9 (191.0-276.7)
model averaged	22.6 (17.0-28.6)	80.3 (37.0-145.3)	14.1 (6.2-31.9)	47.0 (28.4-82.6)	164.0 (88.6-288.4)
uniform prior	**22.6 (18.0-27.5)**	**84.0 (45.3-131.6)**	**16.0 (8.1-27.6)**	**52.0 (33.4-74.8)**	**174.3 (104.8-261.0)**

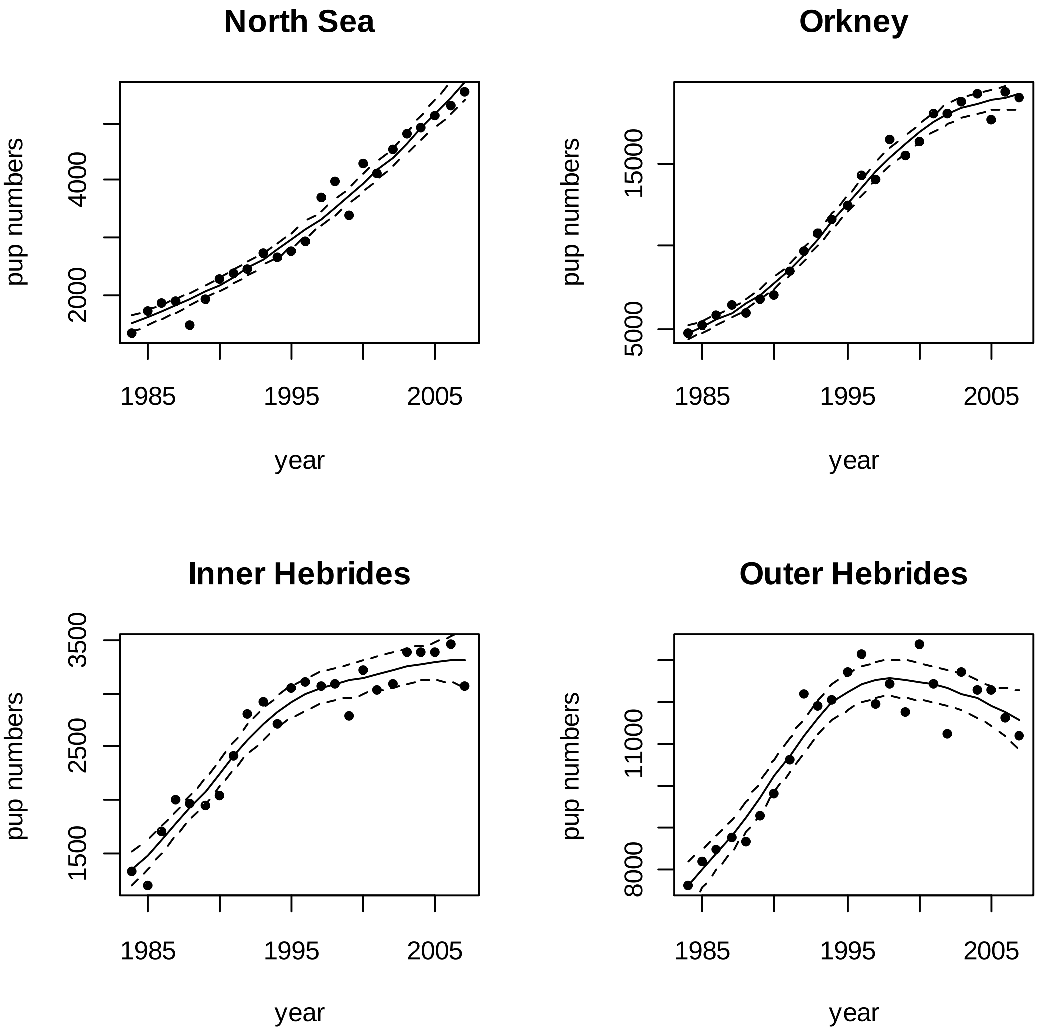

Figure 1: Grey seal pup production estimates (points) and smoothed estimates (with 95% credibility intervals) for each of the four regions.

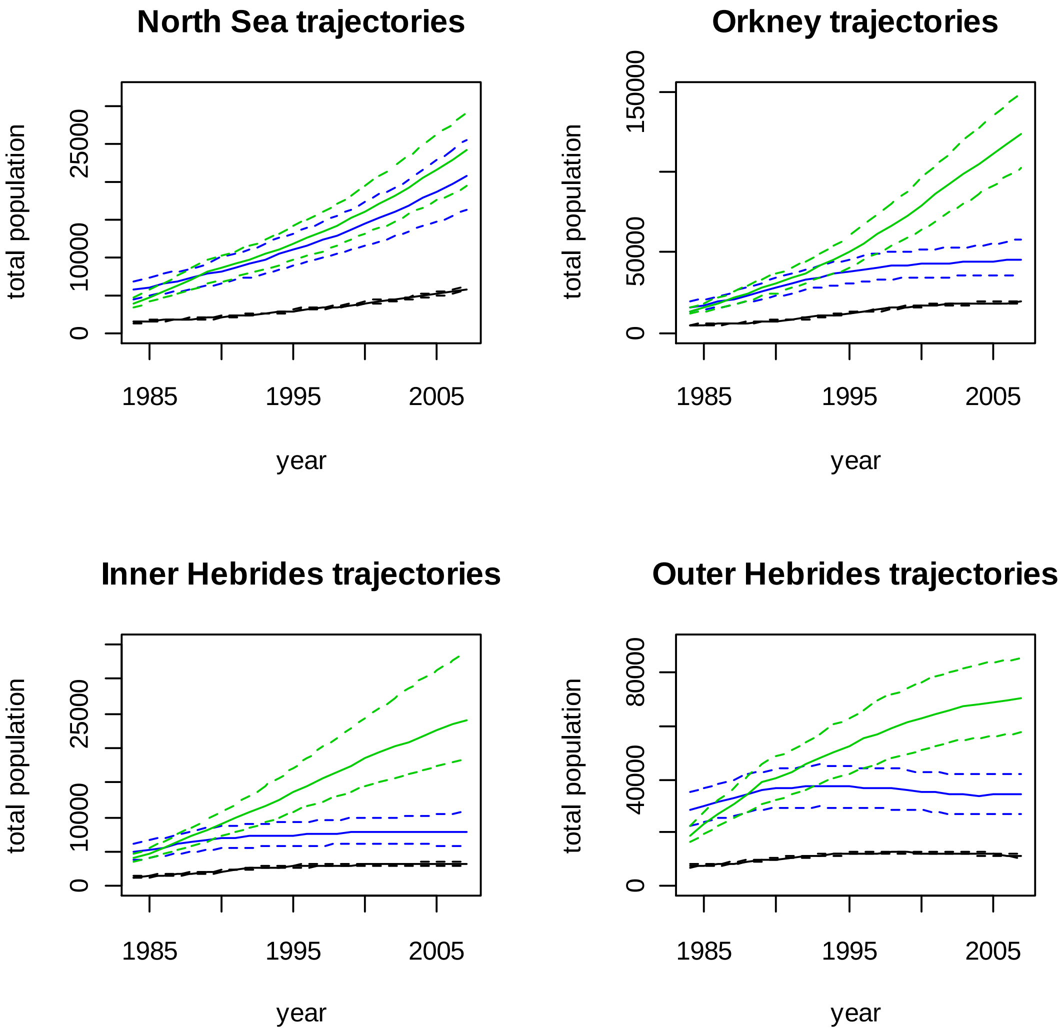

Figure 2: Population trajectories (mean values and 95% credibility intervals) for each region. In each case the black lines are the smoothed pup production estimates; the blue lines are the total population estimates from the density dependent pup survival models and the green lines those from the models with density dependent fecundity.

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

Mass, fecundity and survival in female grey seals (*Halichoerus grypus*) at 2 UK breeding colonies: the breeding status of absent females, and an estimate of overall fecundity.

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

Summary

Adult female grey seals were observed from 1979-2005 at the Isle of May (IoM) breeding colony, and from 1985-2005 at the North Rona (NR) breeding colony. Associated measurements of individual covariates (mass, and breeding status) were also recorded. We present the results of an integrated Bayesian analysis of these mark resighting data using a state-space framework, and investigate the dependence of individual survival and fecundity on mass. Unknown values of mass and breeding status covariates are estimated, and overall estimates of fecundity are thus obtained for each colony.

Introduction

At present, there is considerable uncertainty in estimates of UK grey seal population size, particularly because of uncertainty in vital rates and how these are affected by intrinsic and extrinsic factors. A key parameter needed to improve our understanding of grey seal population dynamics at colony and larger spatial scales is fecundity. Current grey seal fecundity may be estimated inadequately by historical estimates based on sampling shot seals (eg Boyd 1985, Farnes 0.94, Hebrides 0.83): such estimates do not indicate whether early established pregnancies are actually brought to term and the pattern of age-specific fecundity may have shifted. Estimates of apparent individual fecundity based on observations at NR and IoM breeding colonies are high, but are based only on those animals that attend the colony in a given year, potentially giving an inflated fecundity rate. Nulliparous animals may be less likely to attend (or be resighted at) a breeding colony than breeding animals. Therefore, it is of considerable importance to find a method to impute the breeding status of seals that are not observed, and which may be absent from the colony.

There is potential to address these questions by exploring the underlying annual breeding biology of the seals. Here we combine data on individual covariates – maternal mass and breeding status of individual seals during the breeding season, along with their mark re-sighting histories. We then investigate the way mass changes from year to year, dependent on the breeding status of animals. In turn, we can also model the relationship between mass and probability of breeding.

When these processes are considered together, and using serial observations of mass of individuals before and after unobserved years, we develop a method for obtaining an overall estimate of fecundity.

We also examine the relationship between mass and survival rates.

We performed an integrated analysis of the capture-mark-resighting data and mass data, based on a simple CJS model. We adapted this model and fitted it within a state-space framework to allow us to model the way in which mass changes from year to year dependent on breeding status. We allowed for the possibility of (a) a logistic relationship between maternal mass and survival (b) a logistic relationship between maternal mass and fecundity.

CJS models require the estimation of re-capture (or re-sighting) probabilities, often regarded as nuisance parameters in such studies. However in this case we expect that re-sighting probabilities may vary according to the breeding status of an animal because it is possible that non-breeders do not attend the breeding colony during the breeding season, and this in itself is of interest.

We also allow for the presence of transient animals, which we define as mothers that attend the colony in only one year.

The analysis was carried out using a Bayesian state-space framework (Newman et al 2006) an approach which enabled us to estimate both the values of parameters such as re-sighting rates, and also the values of missing covariate data e.g. mass, and also the pupping status of seals where this was not observed directly (King *et al* 2008). Missing data and parameters were estimated simultaneously using MCMC. Given the values of individual pupping states, it was then possible to estimate overall fecundity.

Methods

1. Field Work

On Rona, seals were observed from 1985 onwards, and identified by means of pelage markings, brands and flipper tags. On the Isle of May, adult females were observed from 1987 onwards and identified by means of flipper tags and brands. Regular daily surveys of all visible 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. Effort, (estimated as the number of person-days spent looking for animals) was assumed to have been constant over the period of the observational study.

Grey seals are capital breeders. Mothers sustain all demands of the breeding and lactation period for themselves and offspring from stored reserves. Mass change data were collected for some but not all individuals present in a given year. Individual mothers were immobilised and weighed to the nearest kg on up to three occasions during the 18d lactation period. Captures were timed to coincide as nearly as possible with the start and end of lactation, to allow extrapolation, using rate of mass loss, to the key reference points of maternal postpartum mass (MPPM: mother's mass after giving birth) and maternal weaning mass (MWM: mother's mass on the date the pup was weaned). Thus maternal expenditure in kgs can be approximated by the difference (MPPM-MWM).

Mass data were available for 133 individual animals included in the mark re-sighting study at the Isle of May, and 191 animals at North Rona.

2. Analysis

Mass change from year to year

We expect that the mass of an individual female animal in year *j+1* will be related to her mass in year *j*, and that this relationship will depend on the pupping status of the female in both years. We aim to construct and parameterise a model for the way in which mass changes over time, and to use this within the integrated analysis in order to estimate missing values of mass and pupping-status covariate data. It is of particular interest to impute missing values of pupping status, because we wish to determine the overall fecundity of the grey seals.

For those seals that pup in year *j*, we expect that mothers will lose weight during lactation and that this expenditure can be represented by a general parameter β. For an individual we write the expected value of MWM as λ and we assume observations are Normally distributed

$$\lambda_{i,j} = MPPM_{i,j} - \beta$$
$$MWM_{i,j} \sim Normal(\lambda_{i,j}, \sigma_w)$$

For non-breeding seals, no lactation takes place, and for convenience we write $MMNULL_{i,j}$ to represent the mass of non-breeders in year *j*.

After parturition and lactation, we expect that, on average, seals will gain mass before the beginning of the next breeding season in year *j+1*. For seals that breed in year *j+1*, we estimate a general 'mass gain' term for the whole study population in year *j*, ε_j.

$$\mu_{i,j+1} = MWM_{i,j} + \varepsilon_j$$
$$MPPM_{i,j+1} \sim Normal(\mu_{i,j+1}, \sigma_p)$$

We allow that the rate of mass gain may be different for animals that do not go on to breed in year *j+1*, and represent this difference by a general parameter δ. For non-breeders in year *j+1*, we can then calculate their expected mass in year *j+1*

$$\mu_{i,j+1} = MWM_{i,j} + \varepsilon_j - \delta$$
$$MPPM_{i,j+1} \sim Normal(\mu_{i,j+1}, \sigma_p)$$

This model for the change in mass of individual animals from year to year is illustrated in Figure 1. The diagram is constructed with δ is assumed positive (i.e. non-breeders gain less mass than breeders). However, a Normal (mean=0, sd=100) prior was used for δ and this allows for the parameter to take positive or negative values.

Survival rates

We assume that survival from year *j* to *j+1* is a Bernouilli process, and allow for the possibility that it is related to individual mass $MWM_{i,j}$ in year *j*, and also annual mass gain ε_j during the interval between *j* and *j+1*. For the Isle of May, we write the probability of survival ϕ_j from year *j* to *j+1* as a logistic expression:

$$\text{logit}(\phi_{i,j}) = a + c(MWM_{i,j} + \varepsilon_j)$$
$$s_{i,j+1} = Bernouilli(\phi_{i,j})$$

The symbol *s* indicates the 'state' of the individual, and takes values 1 if it is alive and 0 if it is dead. Parameters c and a are to be estimated.

For North Rona, previous analyses of the data suggest that there is a general variation in annual survival for this colony. Therefore, for the North Rona data, we also include a term b_j to be estimated for each year. This allows for further variation in survival between years, beyond any variation which would be explained by the change in ε_j alone.

$$\text{logit}(\phi_{i,j}) = a + c(MWM_{i,j} + \varepsilon_j) + b_j$$

For North Rona, where previous work on this data set indicates that the presence of transients may be significant, we include a term to allow for this in order to avoid a potential bias in estimates of Φ (Pradel et al 1997). If the animal is first observed in year j_1, then for this year we write:

$$s_{i,j_1} = Bernouilli((1 - p_{transient})\phi_{i,j_1})$$

Fecundity

We model pupping as a Bernouilli process, and assume that *f* the probability of pupping for individual *i* in year *j* can be written as a logistic function, dependent on the mother's mass at the end of lactation in year *j* and on the mass gain ε_j:

$$\text{logit}(f_{i,j+1}) = g + h(MWM_{i,j} + \varepsilon_j)$$
$$b_{i,j+1} = Bernouilli(f_{i,j+1})$$

The variable $b_{i,j}$ indicates the pupping status of a seal and takes the value 1 if a female pups, 0 if she does not pup in year *j*. *g* and *h* are parameters to be estimated.

In order to estimate the overall fecundity of the female grey seal population at each colony, we divide the total number of pups born by the total number of years for which individuals in the study were alive.

$$\frac{\sum_{j=1}^{n_{years}} \sum_{i=1}^{n_{seals}} b_{i,j}}{\sum_{j=1}^{n_{years}} \sum_{i=1}^{n_{seals}} s_{i,j}}$$

Re-sighting probability

Fecundity rates of seals observed at the breeding colony are consistently high. It is possible that non-breeding seals are less likely to attend the colony than breeding seals, and because seals that are absent in a given breeding season cannot be observed, we anticipate that the re-sighting probabilities for breeding and non-breeding seals may differ. We therefore estimate separate parameters p_{pup} for the re-sighting probability of breeding females, and $p_{no\ pup}$ for the re-sighting probability of non-breeding females.

3. Results

Mass gain

For the Isle of May β, the estimated mass expenditure during lactation is 58.9kg (57.2,60.7), (the interval in brackets represents the 95% symmetric credible interval, and this notation will be used consistently throughout this paper). The estimated value of δ, the difference in mass gain between breeders and non-breeders, is 41.2 (31.4,50.4). The positive value of δ implies that breeders gain more mass than non-breeders during the year.

For North Rona, the estimate for β is 67.0kg (65.6,68.2), larger than the value at North Rona. The estimated value of δ is 46.01 (36.1,52.7). Again, the positive value of δ implies that breeders gain more mass than non-breeders. Also, as for the Isle of May, $\delta < \beta$ i.e. those animals that do not breed in general do not gain as much weight as breeders, but they may make a 'net gain' by not breeding, once the costs of breeding are taking into account.

The variation in mass gain between years, ε_j, for is shown in Figure 2 for both breeding colonies. An examination of the overlap between the 95% credible intervals suggests there are significant differences between some years, both at North Rona and the Isle of May.

Survival

There does not appear to be any significant relationship between maternal mass and survival at the Isle of May, and the same is true for the North Rona data (Figure 3). There is evidence for time-dependence in survival at North Rona (Figure 4). The imputed arithmetic mean survival rate at the Isle of May is 0.936 (0.910, 0.958) consistent with the results of previous analysis of data from these sites (Smout, King and Pomeroy SCOS 2007).

Re-sighting probability

Estimates of re-sighting probability for animals that are breeding and for non-breeding animals are shown in the table. Both at the Isle of May and at North Rona, $p_{pup} > p_{no\ pup}$.

	North Rona	Isle of May
p_{pup}	0.834(0.773,0.901)	0.779(0.732,0.837)
$P_{no\ pup}$	0.200(0.119,0.314)	0.179(0.0708,0.376)

Transients

$p_{transient}$ was estimated at 0.185 (0.109,0.262) at North Rona, somewhat higher than a previous estimate of 0.0515 (0.00683,0.107) based on data from the North Rona colony (Smout Pomeroy and King SCOS 2009).

Fecundity

The relationship between fecundity and mass at each colony is shown in Figure 5.

Overall fecundity estimates, based on recorded and imputed covariates b_{ij}, are 0.872 (0.819, 0.905) for the Isle of May, and 0.785 (0.767,0.802) at North Rona.

4. Discussion

This paper reports the first attempts to derive general estimates of grey seal fecundity using a state-space model incorporating maternal mass covariates, and allowing for the presence of transients.

Initial results show significant variation in mass gain between years for pupping seals, both at the Isle of May and at North Rona.

At both sites, $\delta < \beta$, and a possible interpretation is that there is a net mass cost of breeding: breeders gain more mass during the year than non-breeders. However, nulliparous females do not suffer the large mass loss attributable to lactation, and thus end up with a net gain.

There is little indication for a clear relationship between mass and survival rate. This appears counter-intuitive: it might be expected that animals in poor condition, with low mass, would be more likely to die than those in good condition. This result may reflect that, in adult UK grey seals, the effects of any food shortage and poor body condition may be evident mainly through a failure by individuals to breed. Those in very poor condition are probably rarely seen at the breeding colony. However, it is likely that a comparison of relative expenditure in year j and resighting probability could pick this out. If the adult female population comprises such a component, these animals will remain undetected. We will explore this further.

Senescence occurs in grey seals (Bowen et al, 2005) and older heavier seals are more likely to die. The effects of mass and age will be investigated further using this dataset, and there is the potential either to use the Bayesian framework to impute ages where these are not known, or to carry out the analysis for a subset of the data for which the ages of animals are known.

There appears to be a positive relationship between mass and fecundity, and this enables the imputation of pupping status in years where it cannot be observed directly. As a result, we are able to impute overall fecundity for the two colonies.

Fecundity at Rona appears to be somewhat lower than that at the Isle of May, and this is consistent with a negative trend in pup production at NR and other Outer Hebrides colonies. In contrast, the increasing pup production at the Isle of May continues. The early 1980's estimates of fecundity had a similar difference between OH and N. Sea sites even though they were obtained in very different ways (Boyd 1985). Even if we assume that our estimates are correct, it is difficult to know whether the 5-7% lower figures now at both sites represent a density-dependent reduction in fecundity or a simple reflection of the typical mammalian decline in fecundity as pregnancy progresses.

With the methodology presented here, because we estimate unknown binary states, it is difficult to calculate the 'mean values' of these estimates and therefore to estimate a quantity such as DIC in order to carry out model selection We therefore cannot easily discriminate between plausible competing models and decide on an appropriate level of model complexity e.g. to decide whether or not to include an term for annual variation in survival at the Isle of May. Future work will concentrate on developing this aspect, by implementing RJMCMC.

Complementary analysis of the mark re-sighting data has concentrated on the addressing issues of possible bias in survival estimates which may arise from the heterogenous marking methods used during the long-term observational studies (Smout King and Pomeroy, *submitted*). We aim to take account of the outcomes of that work, and to integrate tag loss and heterogenous recapture rates into the covariate models.

We intend to explore possible correlations between environmental variables such as climate and SST, and the time-dependent terms in our models (the variation in annual mass gain at North Rona and the Isle of May, and variation in survival at North Rona) with a view to including environmental drivers such as climatic variables or prey availability into the models.

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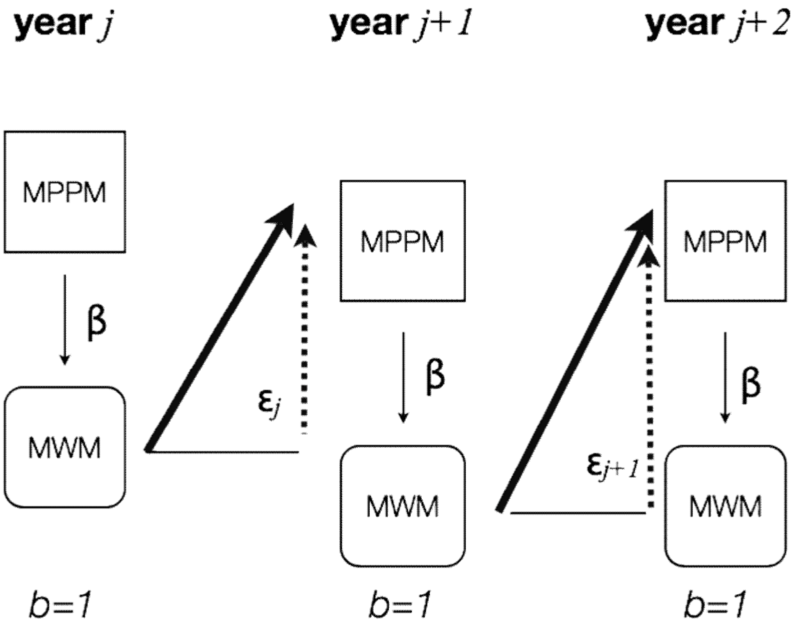
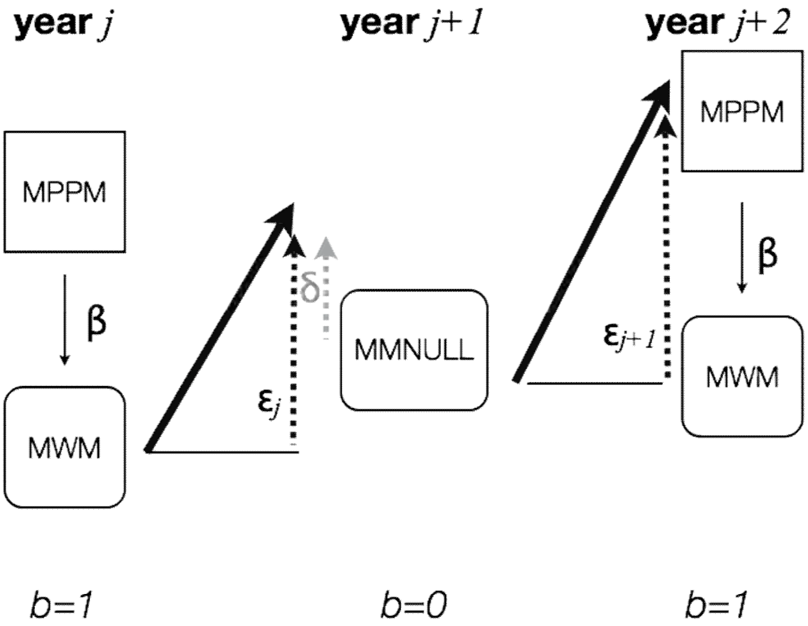
Newman, K.B., S.T. Buckland, S.T. Lindley, L. Thomas & C Fernández. (2006). Hidden process models for animal population dynamics. Ecological Applications 16: 74-86.

Smout S., R. King, P. Pomeroy Estimating Demographic Parameters for Capture-Recapture Data in the Presence of Multiple Mark Types *submitted*

Figure 1: Model for the way in which maternal mass changes from year to year according to breeding status.



Female A pups in year *j, j+1 and j+2. b* indicates pupping status, 1 if a pup is born, 0 if there is no pup. During the breeding season, seal A loses mass between parturition and weaning due to expenditure during lactation. This expenditure is represented by *β*. On average, seal A subsequently gains mass and the amount of mass gain (between the end of the first breeding season and the time of measurement of MPPM, just after parturition in the year j) is εj



Female A pups in year *j* and does not pup in year *j+1*. In year *j+1*, mass is written MMNULL because there is no lactation. The seal gains mass between years *j* and *j+1*, but the mass gain is different to ε_j by amount *δ*. It should be noted that there are no data for mass in years where females do not give birth: values of MMNULL for these years are estimated based on subsequent/previous mass measurements for a given animal.

Figure 2: Annual mass gain ε for females at North Rona and the Isle of May. The mass gained represents the mass increment in kg for an adult female, from the end of lactation in the year shown, to the maternal post-partum mass in the next year.

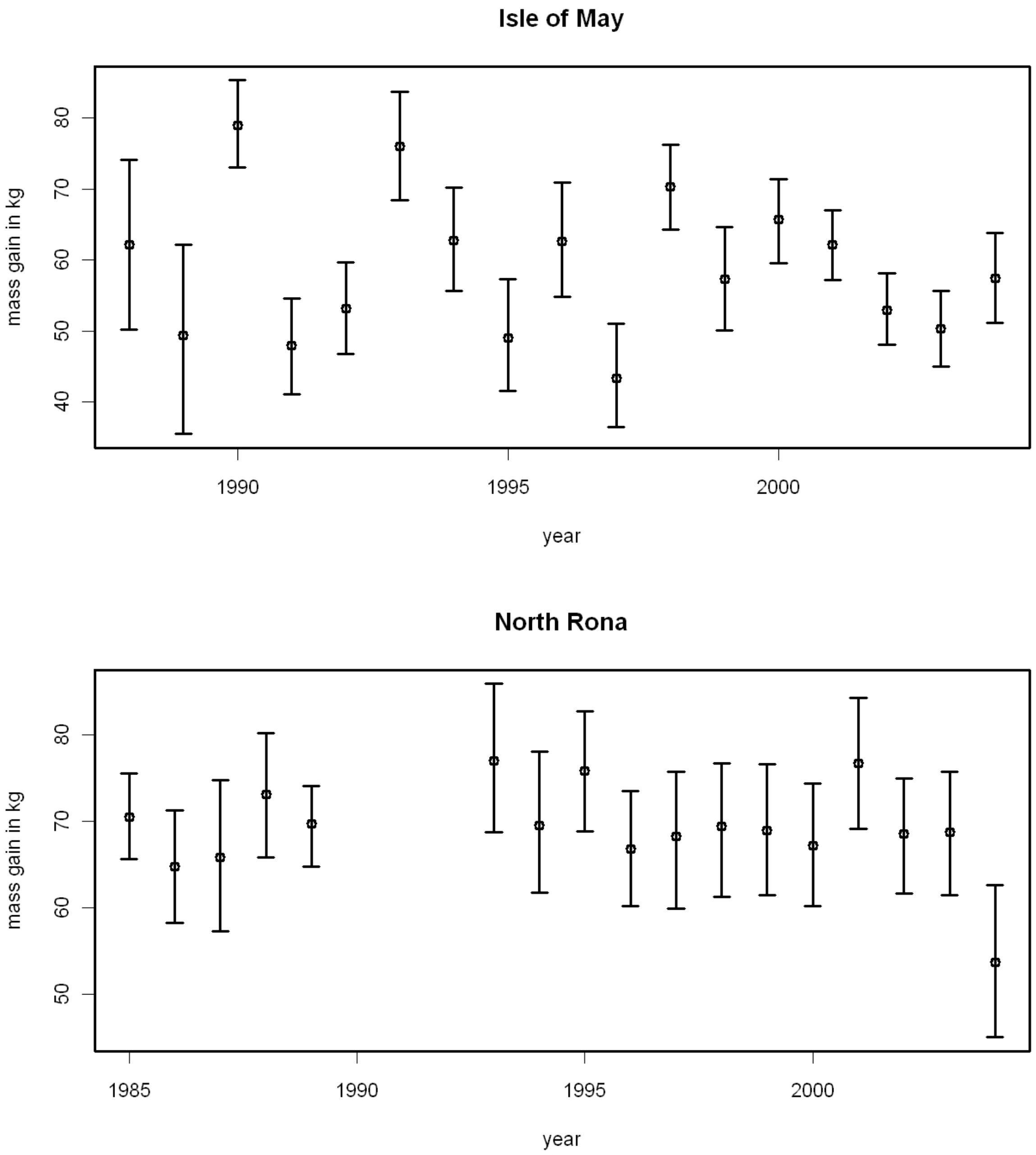


Figure 3: The relationship between survival rate and mass for North Rona and the Isle of May. ‘Mass’ here represents the sum of MWM and the mass-gain ε, and the range shown represents the range inferred from known values of MWM and model estimates of ε.

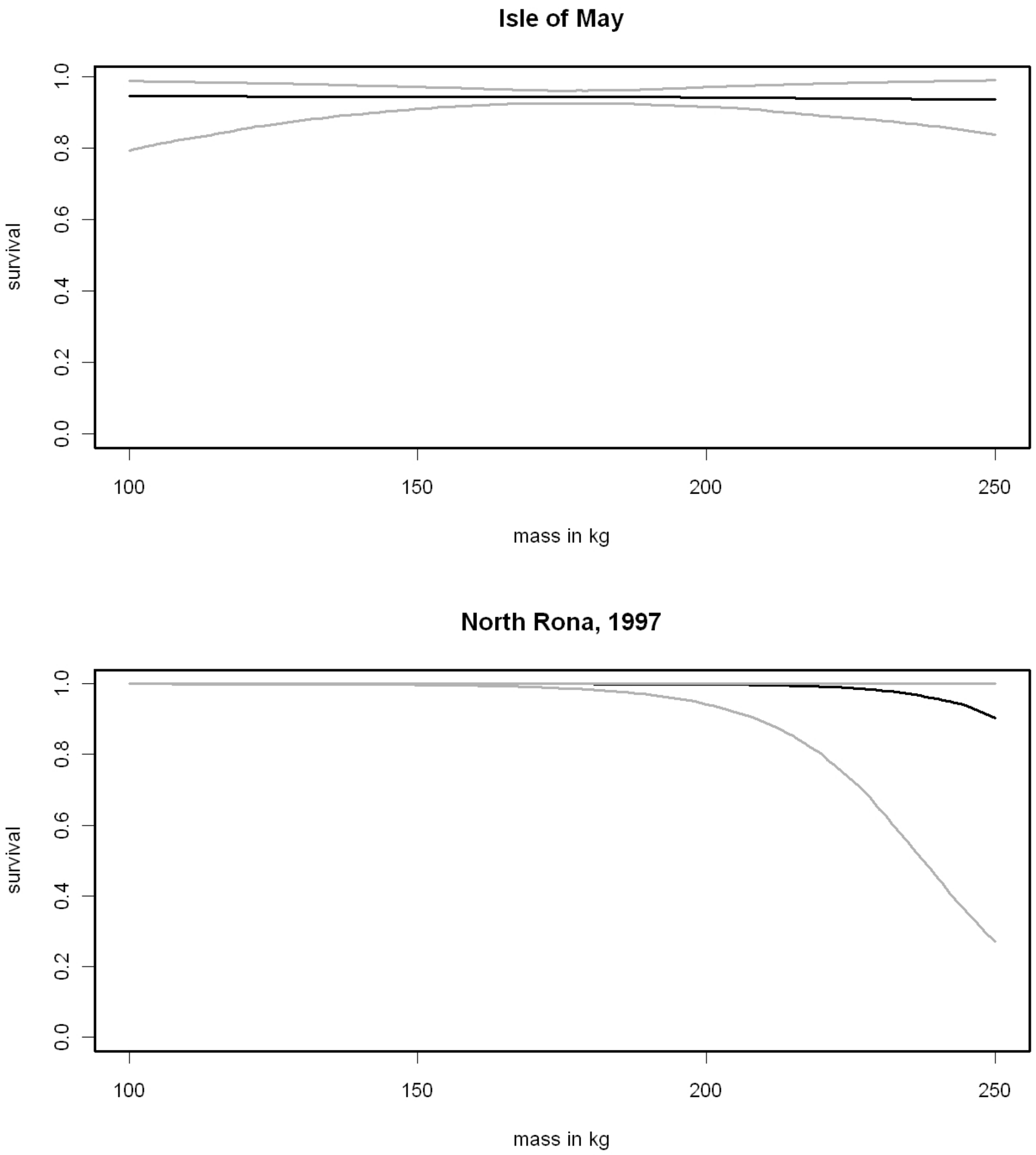


Figure 4: Annual variation of the survival rate for North Rona for an animal with MWM 130kg. 95% Bayesian CIs are shown. Values of ϕ are calculated for each year j from the expression $\mathrm{logit}(\phi_{i,j}) = a + c(MWM_{i,j} + \varepsilon_j) + b_j$, with parameters re-sampled from the Markov Chain.

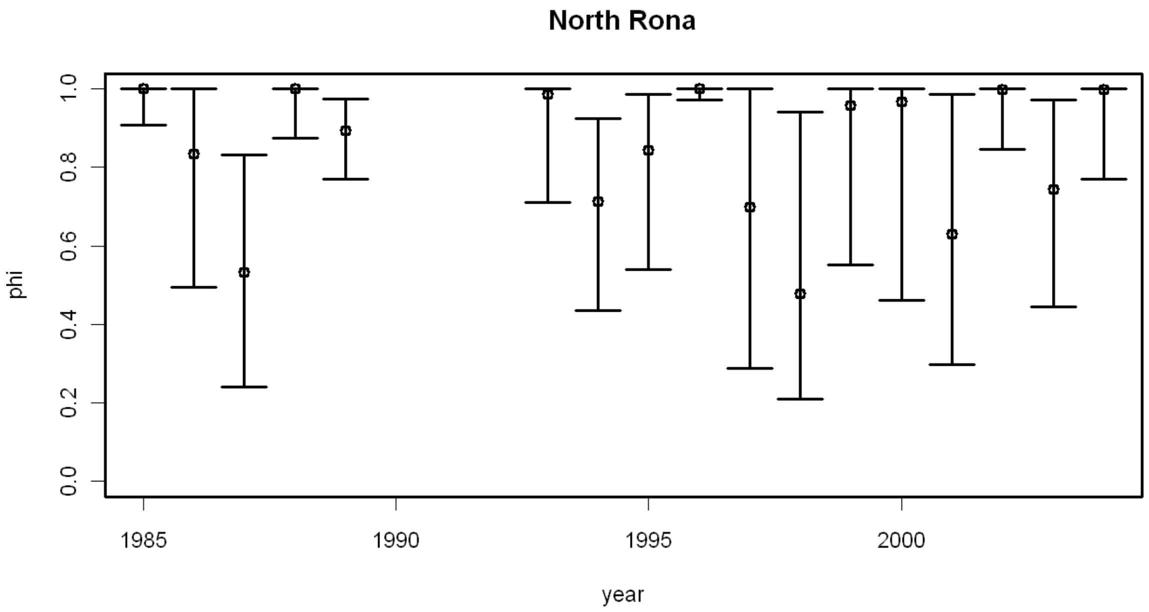


Figure 5: Fecundity as a function of mass (the sum of MWM and the mass-gain ε) at North Rona and the Isle of May.