Scientific Advice on Matters Related to the Management of Seal Populations: 2004

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Scientific advice

Background

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

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

This report provides scientific advice on matters related to the management of seal populations for the year 2004. It begins with some general information on British seals, gives information on their current status, and addresses specific questions raised by the Scottish Executive Environment Rural Affairs Department (SEERAD) and the Department of the Environment, Fisheries and Rural Affairs (DEFRA). Appended to the main report are briefing papers used by SCOS, which provide additional scientific background for the advice.

General information on British seals

Grey seals

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

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

About 39% of the world population of grey seals is found in Britain and over 90% of British grey seals breed in Scotland, the majority in the Hebrides and in Orkney (Table 1). There are also breeding colonies in Shetland, on the north and east coasts of mainland Britain and in Devon, Cornwall and Wales. Although the number of pups born at colonies in the Hebrides has remained approximately constant since 1992, the total number of pups born throughout Britain has grown steadily since the 1960s when records began. In 2003, there was an estimated 45,000 grey seal pups born in Britain. This is believed to equate to a total population of between 77,100 and 120,800 grey seals.

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

Table 1. The size and status of grey seal populations in the North Atlantic region

Region	Population[1] size	Year when latest information was obtained	Type of data (see key[2])	Pup production status	Population status
Mainland Scotland & Shetland	12,000	1998-2003	1	Increasing on Mainland; Shetland unknown	Possibly increasing
Outer Hebrides	31,400	2003	2	No significant changes since 1992	Possibly still increasing
Inner Hebrides	8,300	2003	2	No significant change since 1992	Possibly still increasing
Orkney	44,900	2003	2	Increasing but rate may be slowing	Increasing
Scottish North Sea coast	6,500	2003	2	Increasing	Increasing
Scotland	**103,100**				
English North Sea coast	5,200	2000	2	Increasing	Increasing
Southwest (England/Wales)	5,000	1999	1	Stable	Stable
England & Wales	**10,200**				
Total (UK)	**113,300**				
USA	4,000	2002	1		Probably increasing
Ireland	2,000	1997-99	1		Unknown
Norway	3,000-3,500	1986	1		Unknown
Germany	71	1991	1		Increasing
The Netherlands	500	2000	1		Increasing
Baltic	12,053	2000	1		Increasing
Iceland	5,000	2002	1		Declining
Faroes	3,000	1966	1		Unknown
Barents Sea	3,400	1990	1		Unknown
Europe (excluding UK)	**36,600**				
Canada	**173,500**	1998	2		Increasing
Total	**319,600**				

[1] Counts are rounded to the nearest 100 seals.
[2] 1 – Estimates based upon occasional pup counts or counts of seals hauled out
2 - Estimates based upon systematic annual pup counts using aerial survey

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

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

Common seals (also known as harbour seals)

Common seals are found around the coasts of the North Atlantic and North Pacific from the subtropics to the Arctic. Common seals in Europe belong to a distinct sub-species which, in addition to the UK, is found mainly in Icelandic, Norwegian, Danish, German and Dutch waters. Britain holds approximately 40% of the world population of the European sub-species (Table 2). Common seals are widespread around the west coast of Scotland and throughout the Hebrides and Northern Isles. On the east coast, their distribution is more restricted with concentrations in The Wash, Firth of Tay and the Moray Firth

Between 1996 and 2003, about 33,800 common seals were counted in the whole of Britain, of which 29,800 (88%) were in Scotland and 3,500 (12%) were in England (Table 2). A total of 1,200 seals were counted in Northern Ireland (Table 2). Not all individuals in the population are counted during surveys because at any one time a proportion will be at sea. Accounting for those animals that are not seen using a conversion factor leads to an estimate for the total British population of approximately 50-60 thousand animals. The population along the east coast of England (mainly in The Wash) was reduced by 52% following the 1988 phocine distemper virus (PDV) epidemic. A second epidemic in 2002 resulted in a decline of 22% in The Wash [1], but had limited impact elsewhere in Britain.

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

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

Common seals normally feed within 40-50 km around their haul out sites. They take a wide variety of prey including sandeels, whitefish, herring and sprat, flatfish, octopus and squid. Diet

[1] Thompson, D., Lonergan, M. and Duck, C. (submitted) Population dynamics of harbour seals (*Phoca vitulina*) in England: monitoring population growth and catastrophic declines.

varies seasonally and from region to region. Because of their smaller size, common seals eat less food than grey seals; 3-5 kg per seal per day depending on the prey species.

Table 2 Sizes and status of European populations of common seals. In most cases, numbers given predate the PDV epidemic of 2002.

Region	**Number of seals counted**[1]	**Years when latest information was obtained**	**Possible population trend**[2]
Outer Hebrides	2,000	2003	None detected
Scottish W coast	12,800	1996-2000	None detected
Scottish E coast	2,000	1996-2003	Declining in Moray Firth
Shetland	4,900	1996-2001	None detected
Orkney	7,800	1996-2001	None detected
Scotland	**29,500**		
England (E & S coast)	**3,500**	2001	Recent decline[3]
Northern Ireland	**1,200**	2002	Decrease since 1970s
UK	**34,200**		
Ireland	2,900	2003	Increasing
Wadden Sea (Germany)	11,500	2000	Recent decline[3]
Wadden Sea (Netherlands)	3,300	2000	Recent decline[3]
Wadden Sea (Denmark)	2,100	2000	Recent decline[3]
Lijmfjorden (Denmark)	1,000, 495	1998-2000	Recent decline[3]
Kattegat/Skagerrak	9,752	2000	Recent decline[3]
West Baltic	315	1998	Small increase
Kalmarsund (East Baltic)	270	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	660	?	Unknown
Europe excluding UK	**53,600**		
Total	**88,300**		

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

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

[3] – Thought to have declined as a result of the 2002 PDV epidemic.

Responses to questions raised by the Scottish Executive

In the past, the Advice from SCOS has contained annexes explaining the data used to assess the status of UK grey and common seal populations. Following the pattern first used in 2003, the structure of the Advice has changed and information about population status will now be given in response to questions. Accompanying documentation in the form of SCOS Briefing Papers (SCOS-BP) is intended to provide the additional detail necessary to understand the background for the Advice provided.

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

Current status of British grey seals

The number of pups born in a seal population can be used as an indicator of the size of the population. Each year, SMRU conducts aerial surveys of the major grey seal breeding colonies in Britain to determine the number of pups born (pup production). These sites account for about 85% of the number of pups born throughout Britain. The total number of seals associated with these regularly surveyed sites is estimated by applying a population model to the estimates of pup production. Estimates of the total number of seals at other breeding colonies that are surveyed less frequently are then added in to give an estimate of the total British grey seal population. Further details are given in SCOS-BP 04/2.

Pup production

The total number of pups born in 2003 at all annually surveyed colonies was estimated to be 39,436. Regional estimates were 3,386 in the Inner Hebrides, 12,741 in the Outer Hebrides, 18,652 in Orkney, and 4,657 at North Sea sites. A further 5,500 pups were likely to have been born at other scattered sites.

Table 3: Grey seal pup production estimates for the main colonies surveyed in 2003

Location	2003 pup production	Change in pup production from 2002-2003	Change in pup production from 1999-2003
Inner Hebrides	3,386	+9.4%	+3.6%
Outer Hebrides	12,741	+13.3%	-0.1%
Orkney	18,652	+4.0%	+4.8%
Isle of May + Fast Castle	2,599	+3.6%	+5.0%
All other colonies	3,672		
Total (Scotland)	41,050		
Donna Nook	792	+11.7%	+11.0%
Farne Islands	1,266	+5.5%	+8.7%

SW England & Wales (last surveyed 1994)	1,750		
Total (England & Wales)	3,808		
Total (UK)	44,858	+7.4%*	+3.3%

*Annual change in pup production calculated from annually monitored sites only

Trends in pup production

The differences in pup production between 2002 and 2003 are shown in the table above. Total pup production at annually monitored colonies increased by 7.4%, in contrast to a decline of 3.2% in the previous year.

This continues a recent general trend of increasing variability in the pup production at all annually monitored colonies (SCOS-BP 04/2). The reasons for this variability are not known. It is possible that, as the population grows, breeding females become more susceptible to subtle changes in environmental factors such as food availability and that this is reflected in the increased variation in pup production.

Overall, there appears to have been a gradual decline in the rate at which pup production has been increasing over the past 10 years. In the late 1980s, pup production increased at well over 6% per annum. During the most recent 5 year period it has increased at about 3.3% per annum. However, there have been marked regional differences; pup production at colonies in the North Sea and Orkney has continued to increase at rates only slightly lower than those observed in the 1980s, whereas there has been little change in pup production at colonies in the Western Isles since 1992.

Population size

Pup production is used in a model of the grey seal population that provides an estimate of the total population size. While pup production was increasing steadily year-on-year, it was reasonable to use a simple model that assumed that the population growth rate was not affected by density. However, there are now strong indications that the rate of increase in pup production is slowing and a new population model that includes the likely effects of density on growth rate was developed in 2003 (SCOS-BP 04/6). Based on pup production figures from 2003 and the assumption that the slow-down in pup production is caused by reduced juvenile survival, the total UK grey seal population associated with regularly-monitored colonies is estimated to be between 77,100 and 120,800 with a point estimate of 96,200 (Table 4). Adding in seals from sites that are monitored less often gives a point estimate of 113,300 grey seals. These data suggest an increase of 3.5% for the estimated population size of 109,500 in 2002 (SCOS-BP 03/4). The majority of these seals, approximately 91%, are associated with colonies in Scotland and the remaining 9%, with colonies in England and Wales.

Uncertainty in the estimates

The estimate of total population size depends critically on the factors responsible for the recent deceleration in pup production. Direct observations have indicated that pup survival tends to decrease as colony size increases, and this process was used as the basis for the estimates of total population size provided above and those in 2003. However, an analysis of changes in pup production at individual colonies suggests that reductions in the reproductive rate and/or adult survival may also be involved in the recent declines in the rates of increase (SCOS-BP 04/4). Incorporating each of these processes individually into the model provides equally good explanations of observed changes in pup production (SCOS-BP 04/6, SCOS-BP 04/7) but higher population estimates. The reproductive rates or survival rates predicted by these formulations are, however, much lower than those that have been observed at individual colonies (SCOS-BP 03/6) and it is because of this that the population estimate based on density-dependent pup survival is presented. Further work is required to determine which processes are operating, either solely or in combination, together with further development of the population model.

Table 4: Estimated total population in 2003 of grey seals associated with regularly monitored sites. See SCOS-BP 04/6.

Region	**Population Size**	**95% Confidence Interval**
North Sea	11,700	9,600-14,700
Inner Hebrides	8,300	6,800-10,200
Outer Hebrides	31,400	25,200-39,300
Orkney	44,900	25,500-56,600
Total	**96,300**	**77,100-120,800**

Besides the uncertainty associated with which model to use in the calculation of the total population size, there are uncertainties associated with the estimates of pup production, which are believed to lie within a range of –10% to +13% of the values provided. However, the population modelling described in SCOS-BP 04/6 indicates that the true level of uncertainty may be even greater than this. A new approach to estimating total pup production is therefore being investigated (SCOS-BP 04/3). Even when this approach is implemented, unknown uncertainties associated with the estimates of pup production at colonies that are not surveyed annually will remain. These also have to be combined with the uncertainties about the value used for adult male survival, about which little is actually known.

Trends in population size

There is now convincing evidence that pup production in the Inner and Outer Hebrides has stabilised (SCOS-BP 04/2). However, even if this trend continues, the British grey seal population as a whole is likely to continue increasing for some years (SCOS-BP 03/3).

Current status of British common seals

Each year SMRU carries out surveys of common seals during the moult in August. Recent survey counts and overall estimates are summarised in SCOS-BP 04/5. It is impractical to survey the whole coastline every year but current plans by SMRU are to survey the whole coastline across 5 consecutive years. Seals spend the largest proportion of their time on land during moult and they are therefore visible during this period to be counted in the surveys. Most regions are surveyed by a method using thermographic, aerial photography to identify seals along the coastline. Conventional photography is used in The Wash. Additional surveys using visual counts are conducted annually in the Inner Moray Firth by the University of Aberdeen.

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

Apart from the population in The Wash (SCOS-BP 04/1), common seal populations in the UK were relatively unaffected by PDV in 1988. The overall effect of PDV in 2002 on the common seal population in the UK may have been to reduce the total population by less than 2%.

Counts by region are given in the Table 5 below**.** These are minimum estimates of the British common seal population.

Table 5 Counts of common seals by region

Region	**1996-2003**
Shetland	4,883
Orkney	7,752
Outer Hebrides	2,098
Highland (Nairn to Cape Wrath)	1,225
Highland (Cape Wrath to Appin & Loch Linnhe)	4,947
Strathclyde (Appin to Mull of Kintyre)	6,918
Strathclyde, Firth of Clyde (Mull of Kintyre to Loch Ryan)	991
Dumfries & Galloway (Loch Ryan to English Border at Carlisle)	6
Grampian (Montrose to Nairn)	182
Tayside (Newburgh to Montrose)	232
Fife (Kincardine Bridge to Newburgh)	305
Lothian (Torness Power Station to Kincardine Bridge)	40
Borders (Berwick upon Tweed to Torness Power Station)	0
TOTAL SCOTLAND	**29,579**
Blakney Point	399
The Wash	2,513
Donna Nook	231
Scroby Sands	75
Other east coast sites	225
South and west England (estimated)	20
TOTAL ENGLAND	**3,463**
TOTAL BRITAIN	**33,042**

TOTAL NORTHERN IRELAND	**1,248**
TOTAL BRITAIN & NORTHERN IRELAND	**34,290**
TOTAL REPUBLIC OF IRELAND	**2,905**
TOTAL FOR GREAT BRITAIN AND IRELAND	**37,195**

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

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

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

Common seals
Samples from seals in Northern Ireland, the west and east coasts of Scotland, the east coast of England, the Dutch and German Waddensea, the Kattegat/Skagerrak, Norway, the Baltic Sea and Iceland have been subjected to genetic analysis. This analysis suggested that there are six genetically distinct common seal populations in European waters (Ireland-Scotland, English east coast, Waddensea, western Scandinavia, Baltic and Iceland)[4]. There is probably very little movement of breeding animals between these populations. Within the Ireland-Scotland population there is probably occasional movement of animals between regions, but there is no evidence from satellite telemetry of any long-range movements (for example, between the east and west coasts of Scotland) comparable to those observed in grey seals. Similarly, studies of the movements of branded seals in the Kattegat/Skagerrak[5] indicate that there is only limited movement within the western Scandinavia population. However, in both 1988 and 2002 phocine distemper spread rapidly among European common seal populations, suggesting that substantial movement of individuals can occur, although the genetics studies suggest these movements are

[2] Graves, J.A., Helyar, A., Biuw, M., Jüssi, M., Jüssi, I. & Karlsson, O. (in prep) Analysis of microsatellite and mitochondrial DNA in grey seals from 3 breeding areas in the Baltic Sea.
[3] SMRU unpublished data
[4] Goodman, S.J. (1998) Patterns of extensive genetic differentiation and variation among European harbour seals (Phoca vitulina vitulina) revealed using microsatellite DNA polymorphisms. Molecular Biology and Evolution, 15, 104-118.
[5] Härkönen, T. & Harding, K.C. (2001) Spatial structure of harbour seal populations and the implications thereof. Canadian Journal of Zoology, 79, 2115-2127.

unusual or that they do not usually result in seals moving between regions to reproduce.

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

Projects funded by DEFRA, SEERAD and SNH will produce estimates of diet composition and consumption of fish by grey seals in the Inner and Outer Hebrides, Orkney, Shetland and along the east coast of Britain for the year 2002. Preliminary results are provided in SCOS-BP 04/15 and SCOS-BP 04/16. On-going analysis of information from telemetry studies (see section 7) will provide a basis for estimating fish consumption by seals in different regions of Scotland. However, until final results are available, calculations of the consumption of fish by grey seals in Scottish waters have been based on previous estimates of diet composition and the most recent estimates of population size.

Total fish consumption depends on the proportion of the diet that is composed of fish and type of fish consumed. For the purposes of this calculation, it is assumed that sources of food for UK seals, other than fish, such as crustaceans and molluscs (including squid), make an insignificant contribution to the diet.

Grey seals
Based upon the total energy requirements calculated in SCOS-BP 03/9, the annual food consumption of grey seals in Scotland would be between 69,000 and 118,000 tonnes of fatty fish, such as sandeels, herring or mackerel. Alternatively, if these seals ate only whitefish then the annual consumption would be between 129,000 to 220,000 tonnes.

Common seals
Information about the total prey consumption of the Scottish common seal populations is less advanced. However, based upon current knowledge of the likely daily ration of about 3 kg of fatty fish per day or up to 5 kg of whitefish per day, the consumption by common seals in Scotland would be between 49,000 and 60,000 tonnes if the diet was entirely composed of fatty fish and 82,000 and 100,000 tonnes if the diet was entirely composed of whitefish.

Total for Scotland
Overall, the consumption of fish by seals in Scottish waters is likely to lie in the range 118,000 to 320,000 tonnes. The greatest uncertainties in this calculation are caused by lack of knowledge of diet and uncertainties in the population estimates. If we use the estimate of diet composition from the mid 1980s as an indication of diet composition today, the total annual fish consumption is likely to lie between 180,000 and 255,000 tonnes.

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

The only non-lethal method of population control involves reducing the birth rate. There have been no new developments in birth control for seals in the last year, but we provide a brief review of the current state of knowledge.

Immunological non-lethal control of birth rate

Investigations into the potential use of vaccines to reduce birth rates in some wildlife populations have been under way for at least a decade[6]. In most cases, vaccines have been developed to target the proteins that encase the eggs of mammals, known as the *zona pellucida*. Vaccination against these proteins results in an immune response which prevents sperm entering and fertilizing eggs after ovulation.

Trial vaccination of wild animals, including grey seals[7], have resulted in significant, long-term reductions in birth rates. Typical results are reductions to about 10% of normal birth rates and these can be sustained for periods of several years. In the case of seals, significantly reduced birth rates were present up to 5 years after immunization. The general conclusions are that this method is effective at reducing birth rate, it can be delivered by remote means, it is safe to pregnant animals, it results in no long-term debilitating health problems for the animals concerned, and it has no implications for passage through the food chain. Some of the early problems associated with having to give multiple doses of the vaccine appear to have been solved.

Non-lethal chemical control

Recent developments in the chemical control of reproduction using methods of dosing wild animals with contraceptives have also been shown to be effective when used with slow-release delivery systems. However, these are normally effective for much shorter periods than the immunological methods.

Application to Scottish seal populations

A desk study[8] to investigate non-lethal method of population control was carried out in 1994. At that time, the following issues were identified:

1. Availability of appropriate drugs or techniques;
2. Delivery mechanisms;
3. Assessment of the effectiveness of the treatment;
4. Assessment of the side effects of the treatment;
5. Human safety and, in particular, the effects within the food chain;
6. Cost-effectiveness

With respect to seals, the development of immunocontraception since this report was written has probably addressed all of these concerns except that of cost and the effectiveness of the treatment. The treatment has been shown to be effective at the level of individual seals but additional work is required to assess the scale, practicality and consequences of implementing the treatment at the level of the population.

Attempts to control the growth of a seal population by birth control may have unexpected consequences. In most wildlife populations, social and nutritional factors act to reduce the birth rate at high population densities. Recent studies of the structure of grey seals colonies, reported in the Advice given in 2003 (SCOS-BP 03/12), suggest that social structure may constrain the birth rate of this species. Grey seal colonies are generally on isolated stretches of coastline or islands

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[6] Bagavant, H., Thillai-Koothan, P., Sharma, M.G., Talmar, G.P. & Gupta, S.K. (1994) Antifertility effects of porcine zona pellucida-3 immunization using permissible adjuvants in female bonnet monkeys (*Macaca radiate*) reversibility, effect on follicular development and hormonal profiles. *Journal of Reproduction and Fertility* 102, 17-25.

[7] Brown, R.G., Bowen, W.D., Eddington, J.D., Kimmins, W.C., Mezei, M., Parsons, J.L. & Pohajdak, B. (1997). Evidence for a long-lasting single administration contraceptive vaccine in wild grey seals. *Journal of ReproductiveIimmunology* 35, 43-51.

[8] Gardiner, K.J., Racey, P.A. & Hiby, L. (1994) Population management of seals: an evaluation of non-lethal methods of population control. Report to Ministry of Agriculture Fisheries and Food, 8 pp.

(SCOS-BP 04/2). Female seals tend to return to specific locations to breed, perhaps throughout their lives, and females that are breeding for the first time tend to colonise close to the location in which they were born themselves[9]. These behavioural and social factors are capable of reducing the birth rate, at least temporarily, and this may be one factor that is currently responsible for slowing the rate of increase in pup production in UK grey seals. An important implication of this for management is that attempts to use non-lethal birth control methods at breeding colonies that result in high levels of disturbance could disrupt their natural social cohesion and hence lead to unintended increases in pup production.

5. Is there sufficient evidence of 'regional' fidelity to enable the identification of independent seal populations/sub-populations around the Scottish coast? If so, what is known about the geographic distribution and population dynamics of such 'regional' units?

Currently, there is insufficient information on the regional fidelity of Scottish seals to allow us to identify independent sub-populations. However, work currently underway in SMRU is likely to generate the required information over the course of the next 2-5 years. This is described below and in the answer to question 7.

Grey seals

Detailed studies of the behaviour of individual grey seals at North Rona and the Isle of May have indicated that females tend to return to the colony where they were born, and that females who return to their natal colony show a strong tendency to return to the same site within the colony each year to give birth. These findings are supported by genetic analysis, which indicates that there are significant differences in the genetic structure of these two colonies. This implies that colonies may constitute regional units. However, analysis of resightings of adult females using photo-identification has shown that approximately 5% of females within any colony are likely to move to another location each year, suggesting that further work is required to develop biologically realistic models of the factors that determine when animals move between colonies, and where they move.

In addition, the distribution of grey seal breeding colonies is not a particularly good guide to the distribution of seals outside the breeding season. This is more closely related to the distribution of sites used for resting (hauling out). Haul out sites in Scotland are not randomly distributed around the coast. Sites are either relatively close together or separated by large areas of coastline where there are few, if any, suitable haul out sites. If, as seems likely, the probability of a seal moving from one site to another depends on the distance between those sites, the distribution of haul out sites will create local sub-populations between which there is little movement.

Common seals

Common seals have always been regarded as having a more coastal and local movement pattern than grey seals, although there is limited information about their reproductive and foraging movements. Studies in the Kattegat / Skagerrak, Alaska and the UK suggest that common seals do show some fidelity to specific regions and tend to return to breed in their own birth region. The haul-out sites used by Scottish common seals have a similar distribution to those used by grey seals, suggesting that it may also be possible to identify discrete sub-populations for this species.

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[9] Pomeroy, P.P., Twiss, S.D. & Redman, P. 2000. Philopatry, site fidelity and local kin associations within grey seal breeding colonies. *Ethology.* 106: 899-919

6. Could a consideration of population dynamics and modelling techniques be used to determine the number of seals required within a 'regional' population to keep it viable over the next 50, 100 and 200 years?

Population Viability Analysis (PVA), which is regularly conducted for endangered or threatened species, seeks to identify how many individuals are required to reduce the probability of extinction within a specified period to an acceptable level. PVAs have proved useful for comparing the effectiveness of different conservation strategies aimed at reducing the risk of species extinction, but they are not particularly useful for assessing long term viability. Determining whether a regional population has "favourable conservation status", as defined in the European Directive on Species and Habitats (Council Directive 92/43/EEC), may be a better way of ensuring its long term viability. Amongst other things, favourable conservation status depends on the existence of sufficient habitat for the species and freedom from disturbance, as well as simple population size. Efforts to identify the important characteristics of seal habitat are underway within SMRU (SCOS-BP 04/10), supported by funding from the Scottish Executive, SNH, MoD and DTI.

7. At the current level of knowledge, is it possible to define potential management units for grey and common seals in Scottish waters? If not, are there any areas of research that would improve our ability to define such management units?

The impacts of management on a regional seal population will depend on whether it is increasing or decreasing, the threats it faces (for example, from habitat loss or disturbance) and the amount of movement to and from neighbouring populations. Ideally, the seal population within a management unit should be relatively discrete, so that the impacts of management are largely confined to that unit. As noted above, the distribution of grey seal and common seal haul out sites around Scotland is such that it may create local populations between which there is very little movement. At present we have no objective criteria for identifying the boundaries of these units. The extensive database on the movements of animals equipped with satellite-relayed dataloggers, built up by SMRU over the last decade, is currently being analysed to determine the probability that an individual will move between any two haul out sites, and how this is affected by environmental and demographic factors. These probabilities, in combination with information on the distribution of haul out sites obtained from SMRU's annual aerial surveys and genetic analysis, will provide the information needed to define potential management units.

8. What are the historical trends in the abundance of common seals in the Moray Firth area?

Systematic counts of the number of common seals in the Moray Firth began in 1988 when Dr Paul Thompson, University of Aberdeen, began a series of annual counts of the Inner Moray Firth which has been maintained until the present day. Prior to this, there were occasional counts over parts of the Moray Firth area both by SMRU and other organisations during the 1980s. However, there are no historical data on earlier trends in abundance. The University of Aberdeen annual surveys cover both the breeding and moulting period of the seals and are described in SCOS-BP 04/15. In addition, SMRU has carried out aerial surveys of the whole Moray Firth on 6 occasions since 1992 (SCOS-BP 04/5, Table 2). Historical data are shown in the following figure:

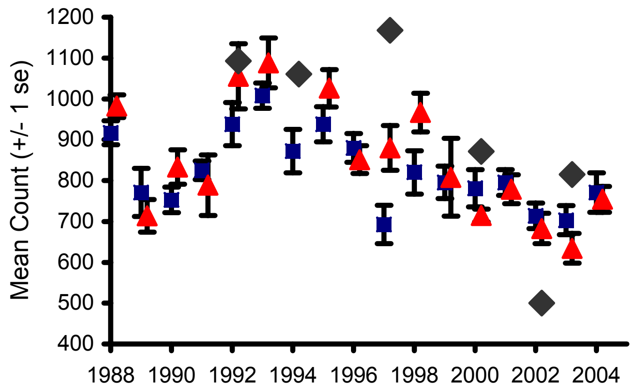


Figure caption: Trends in the number of harbour seals hauled out in inner Moray Firth. Data are from AU pupping season surveys (Blue Squares), AU moult surveys (Red triangles) and SMRU Moult surveys (Black Diamonds).

The number of seals counted by the University of Aberdeen declined from a mean count of about 950 in 1988 to a mean of about 750 in 1989, apparently as a result of deaths caused by Phocine Distemper Virus (PDV). Annual mean counts then increased rapidly from 1989 to a peak of about 1000 seals in 1993, representing an estimated population size of 1650. Thereafter, haul-out counts have declined steadily so that current mean counts are around 700 seals. Counts done by SMRU have followed the same general trend as those from the University of Aberdeen, and suggest that the trends seen for the Inner Moray Firth are indicative of those for the region as a whole.

9. What would be the projected consequences of different levels of removal of seals (and different proportions of male and female animals) on the common and grey seal populations:

- ***at the Scottish level?***
- ***in the Moray Firth area?***
- ***in the Dornoch Firth cSAC?***

The Dornoch Firth cSAC

Counts made by the University of Aberdeen have indicated that common seal numbers in the Dornoch Firth cSAC have declined by two thirds since 1993, a much more rapid decline that observed anywhere else within the Moray Firth. Any additional removals from this area are likely to delay the recovery of seal numbers within the cSAC and could lead to a continuation of the decline. As noted below, it is very unlikely that there is a local grey seal population restricted to the Moray Firth area, let alone the Dornoch Firth. So, removals of grey seals from the cSAC are unlikely to have any detectable impact on grey seal populations. However, there is a risk that common seals might be shot in mistake for grey seals but this would have the same consequences for the local common seal population as deliberate killing of common seals. Given this, we feel that the removal of any seals from the Dornoch Firth cSAC would have a negative effect on the status of the cSAC.

The Moray Firth area

Grey seals often move over long distances to forage (SCOS-BP 03/8) so those seen in the Moray Firth could come from any sector of the Scottish population. However, removals in the Moray Firth are most likely to affect the grey seal population in the North Sea. Historical levels of removals, and those proposed in the Moray Firth Management Plan, are unlikely to have a significant effect on this population (SCOS-BP 04/7).

As noted in SCOS-BP 04/9 and 04/14, common seal numbers in the Inner Moray Firth have declined by around 36% since 1994. Much of this decline is probably the result of deliberate removal of seals.

We know much less about the dynamics of common seal populations than we do about grey seals. However, scientists in the USA[10] have developed a simple precautionary approach for regulating the number of removals that may be licenced from a declining or endangered marine mammal population under the US Marine Mammal Protection Act. The "Permitted Biological Removal" (PBR) is the number of animals that can be taken from a population while not significantly increasing the risk of population extinction. The PBR is calculated based on a minimum estimate of population size (taking uncertainty into account). This means that the PBR is low when there is potential for mis-identification (such as for seals in the Moray Firth). The PBR should be recalculated whenever new information about population size is available; in this case annually. If the population estimate becomes lower or more uncertain the PBR is reduced correspondingly. Assuming that we can reasonably take the Moray Firth as a management unit for common seals, a simple PBR calculation suggests that, with the current population estimate, a removal of 49 seals could be permitted (SCOS-BP 04/9).

Approximately one third of all the seals shot in the Moray Firth over the last decade were not identified to species. The PBR of 49 seals assume that all seals that are shot but not identified are common seals. Training of those involved in the management of seal populations is likely to reduce the number of unidentified seals that are killed. The recording of scientific information about the animals killed would be of benefit to reduce the uncertainty and conservatism built in to the PBR estimate and should be strongly encouraged. Moreover, the shooting of seals during the breeding season is difficult to justify under any circumstances because of the danger that mothers of nursing pups might be shot. Every effort should be made to develop methods of management that eliminate the need to shoot seals.

The Scottish level

The impact of removals on a wildlife population depend to a large extent on the way in which survival and reproductive rates change with population size, and on the geographical structure of the population. As noted in the response to Question 1., there is considerable uncertainty about the mechanisms that are responsibility for the recent slowing in the growth of the British grey seal population, and nothing is known about the nature of these mechanisms in common seal populations. As a result, it is not possible to make any generalisations about the impact of removals on the entire Scottish populations. Any proposals to remove animals will have to be evaluated at an appropriate geographical scale.

10. Is it possible to establish/identify the likely causes of the recent decline in common seal numbers in the Sound of Barra area and the Western Isles more generally?

The latest estimate from the Sound of Barra shows that the number of common seals using the Sound of Barra has declined by about 75% since records began in 1992. Possible causes of the declining counts include increased death rate of seals or reduced birth rate, movement of seals out of the areas being surveyed or inaccurate counting methods. During the past 10 years, two events

[10] Wade, P.R. (1998) Calculating limits to the allowable human-caused mortality of cetaceans and pinnipeds. *Marine Mammal Science* 14, 1:38.

in the region could have influenced the presence of seals. These include the construction of a causeway across the Sound of Eriskay and the proposal to create a Special Area of Conservation (SAC) for common seals in the region of the Sound of Barra. There was strong local opposition to the creation of the SAC and this could have led to increased level of shooting in the region. The number of common seals has declined by almost 90% within the SAC since 1992.

While it is not currently possible to provide a formal assessment of the accuracy of counting, this is not thought to be the likely cause of the apparent decline in the Sound of Barra. The method counts the number of seals seen out of the water and greatest inaccuracies are likely to be introduced by changes in the proportion of seals that are ashore at the time of counting. However, this is very unlikely to have produced the systematic decline observed to date (SCOS-BP 04/5, Table 4).

There has been no evidence of increased mortality of seals in the region based upon reports of carcasses recovered, although it is possible that the level of increase required could go unnoticed in this region and there has been no systematic collection of data about seal carcasses. The decline in the number of seals pre-dates the outbreak of PDV in 2002 so PDV is not likely to have been a cause of the decline. As with grey seals (SCOS-BP 04/7), in theory, the presence of salmon farms in the Outer Hebrides could have resulted in additional mortality of common seals. Since salmon farms are mainly located along the eastern shores of the Outer Hebrides, which is habitat more suitable for common seals than for grey seals, any effect of shooting seals around salmon farms is likely to be greater on common seals than grey seals. However, we have no reason to believe that the level of shooting associated with salmon farms should have increased in the last few years.

It is possible that the construction of the causeway across some recognized seal habitat could have resulted in a re-distribution of seals from the main areas where they are usually counted. However, the total count of common seals for the Outer Hebrides in 2003 was the lowest on record and does not support the view that all the seals lost from the Sound of Barra are being counted elsewhere. Interestingly, numbers in the Sound of Harris have not declined in parallel with those in the Sound of Barra so the decline seems to be specific to the region of the Sound of Barra itself. Overall there is a possibility that the decline in the Sound of Barra has resulted from changes in the suitability of habitat caused by the causeway but some local opposition to a seal SAC in the region could have stimulated an increase in shooting.

Responses to issues raised by the DEFRA

DEFRA asked for advice in relation to two issues:

1. Non-lethal methods of resolving the problem of seal-fisheries interactions

A partial response to this is given in the response to Question 4 from the Scottish Executive (see above). There are currently no completely effective methods of eliminating the negative impacts of seals on fisheries and the methods that are used depend on the characteristics of the fishery. However, most concern appears to surround rod and line salmon fisheries in fresh water and river estuaries, coastal set-net salmon fisheries and static gear crustacean fisheries.

Modification of gear to reduce the impact of seal predation is likely to be the most effective method of reducing the problem but it is recognised that this may be expensive both in terms of the research required to determine the best design of gear and the cost of replacing fishing gear. The locations in which gear is placed may also affect the frequency of interactions so that fishing activities carried out adjacent to areas where seals are know to haul out are likely to be subject to more problems from seals. Avoidance of fishing in those regions would reduce interactions.

Deterrence of seals using emetics (chemicals that make the animals vomit) hidden in bait and acoustic “seal scarers” have been used within fisheries. However, there is little current evidence to suggest that either method is effective. Acoustic scarers are most often used by fish farms and there are ongoing studies to assess the impact that these devices have on local cetacean populations. Secondary effects of acoustic scarers on cetaceans could affect the extent to which they can be used in specific circumstances.

A study partly funded by SEERAD will be commencing in 2005 to examine the effectiveness of acoustic scarers on managing the presence of seals in salmon rivers. This will also investigate alternative designs of scarers that could have less impact on cetaceans.

2. Review the Conservation of Seals (ENGLAND) Order 1999

The Conservation of Seals (ENGLAND) Order 1999 extends the close season all year round for both grey and common seals in the region from the Scottish Border to Newhaven.

Before the PDV epidemic of 2002, the number of common seals in England had returned to a number similar to the estimates that preceded the previous epidemic in 1988. Since most of the common seals in England and Wales occur in the region of The Wash (SCOS-BP 04/5), trends in abundance from counts in The Wash are probably representative of the whole region. Based on counts made before and after the PDV epidemic of 2002, the common seal population in England was reduced by about 13% as a result of the epidemic (SCOS-BP 04/1). Although this is within the margin of error of the counting method, estimates from carcasses recovered suggest that the decline could have been as high as 35%.

Until further surveys are carried out in 2004, the presumption should be that PDV has led to a decline in the size of the common seal population in England and, consequently, there would be no justification for lifting the current Conservation Order.

ANNEX I

NERC Special Committee on Seals

Terms of Reference

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

Current membership
Professor IL Boyd, University of St Andrews;
Dr T Coulson, University of Cambridge;
Dr K. Kovacs, Norwegian Polar Institute, Tromso, Norway;
Professor JH Lawton, Chief Executive, NERC, Swindon;
Dr A McLay, FRS Marine Laboratory, Aberdeen;
Professor Marc Mangel, University of California, Santa Cruz;
Dr EJ Millner-Gulland (Chair), Imperial College, London;
Dr J. Pinnegar, CEFAS, Lowestoft;
Professor W Sutherland, University of East Anglia;
Dr PM Thompson, University of Aberdeen;
Katherine Branch (Secretary), NERC, Swindon.

ANNEX II

Briefing papers for SCOS

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

The structure piloted in 2003 is being used again on 2004. The Annexes and the information papers have been combined into one format known as a *briefing paper*. The intention is to ensure that the science underpinning the Advice is made more transparent and is provided in more detail but also in a format that encourages rapid assimilation of the essential information. This is necessary because, with the current structures for considering the Advice as described in SCOS (SCOS-BP 03/1), there is likely to be increased scrutiny of the outputs from SCOS. *Briefing papers* will provide up-to-date information from the scientists involved in the research and will be attributed to those scientists. It is hoped that scientists who have not traditionally been involved in SCOS might also be willing to contribute by providing briefing papers. .

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

ANNEX II

List of briefing papers submitted to SCOS 2004. Those shown bold have been released with the Advice.

1. Counts of common seals before and after the PDV epidemic (SMRU)

2. Grey seal pup production in Britain in 2003 (C.D. Duck)

3. Estimating Annual Pup Production in Grey Seal Breeding Colonies: A state-space approach (Matthiopoulos & Harwood)

4. The nature of density dependence in British grey seal populations (Thomas, van Lamsweerde & Harwood)

6. A comparison of grey seal population models incorporating density dependent pup survival and fecundity (Thomas & Harwood)

7. Possible impacts on the British grey seal population of deliberate killing related to salmon farming (Thomas & Harwood)

8. The Moray Firth Management Plan (Boyd)

9. Some comments on the Moray Firth Seal Management Plan (Harwood)

10. Distribution and movements of harbour seals around Orkney, Shetland and the Wash (Sharples & Hammond)

11. Harbour seal diet in the UK (Cunningham, Sharples & Hammond)

12. The occurrence of salmonids in harbour seal scat samples collected in the Moray Firth (Middlemas & Mackay, FRS)

13. Results of Feeding Experiments to Determine the Effect of Digestion on the Recovery and Reduction of Salmon Otoliths (Middlemas, Grellier, Mackay, Moss, Armstrong & Hammond)

14. Recent trends in the abundance of harbour seals in the Moray Firth (Thompson & Barton, University of Aberdeen)

15 Digestion experiments with captive grey seals" by K. Grellier and P.S. Hammond

16 Progress on assessing grey seal diet in 2002 - II: west coast of Scotland
R Harris & PS Hammond

Counts of common seals before and after the PDV epidemic

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

Summary

Counts of common seals on the east coast of the UK before and after the arrival of the PDV epidemic in late 2002 showed no substantial change in the number of seals in most regions. This result was consistent with the relatively small number of seals found dead in most of these regions during the PDV epidemic. However, it was not consistent with the relatively large number (estimated to be 35% of the population) found dead in the region of The Wash. Counts showed a 13% decline in numbers in this region but this is well within the likely inaccuracy of the counting method. Serology results show that many of the seals throughout the east coast of the UK were infected with PDV. Unless the counts of seals are biased, these results suggest that PDV had less impact on common seals in the UK in 2002 than during the previous outbreak in 1988.

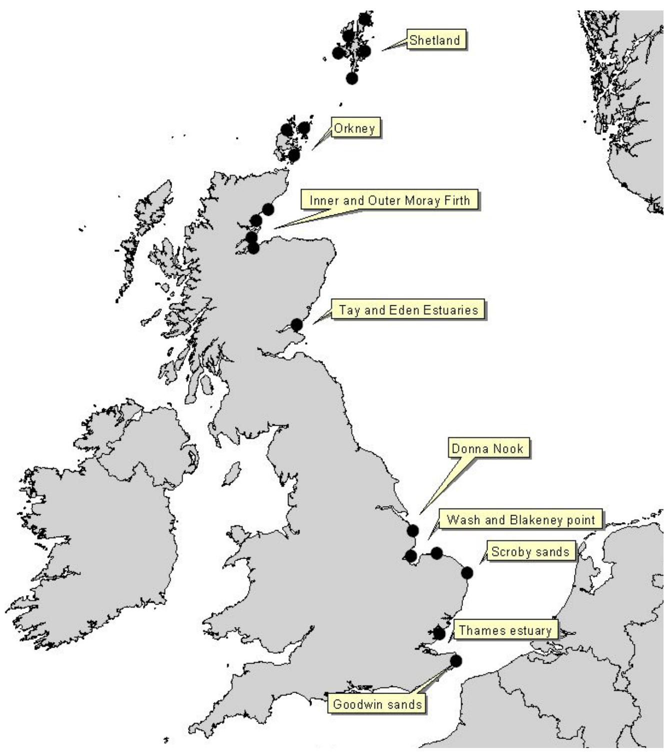


Fig. 1. Locations of major common seal moulting and haulout sites on the east coast of the UK.

Introduction

The effects of the epidemic of phocine distempter virus (PDV) among common seals in the North Sea during 2002, was assessed in the regions of the UK that were likely to have been most affected. Aerial surveys to estimate the minimum number of common seals in the UK have been carried out regularly by SMRU. The same methods were used to estimate the numbers of common seals *before* and *after* the epidemic.

The largest concentrations of common seals in the regions bordering the North Sea are in Orkney and Shetland. The two sites at which common seals occur in greatest numbers on the east coast of the Scottish mainland are the Firth of Tay and the Moray Firth. In England most of the common seals occur is the southeast of England with the greatest concentration in The Wash (Fig. 1.)

Methods

Counts of seals were carried out using the methods described in SCOS (2003). Regions where common seals are known to haul out on sand banks in the Moray Firth, Tay Estuary, The Wash and SE England were photographed from the air during August. All surveys took place within 2 hours of low tide. This is the time of year when the maximum number of seals is expected to be out of the water. Counts were carried out in 2002 in advance of the spread of PDV into the UK and these were repeated again in 2003 after the last case of PDV had been reported.

Counts

The results of the common seal aerial surveys carried out in early August 2002 and 2003 are given in Table 1. For some areas counts were repeated on consecutive days to estimate variability. We were unable to survey Orkney due to bad weather and this survey will be conducted in 2004.

Table 1. Numbers of common seals counted ashore at major east coast haulout sites during their August moult in 2002 and 2003 (pre and post the PDV epidemic)

Location	**Area**	**Counts 2002 (pre-epidemic)**		**Counts 2003 (post-epidemic)**	
		First count	Second count	First count	Second count
Moray Firth	Dornoch, Beauly, Cromarty Firths and Ardersier (Inner Moray Firth)	438		759	
	Findhorn	144		167	
	Dornoch to Loch Fleet	62		56	52
	Total	**644**		**982**	
Tay estuary	Abertay, Tentsmuir, Broughty Ferry and Buddoness and the Upper Tay	327		368	
	Eden Estuary	341		93	
	Total	**668**		**461**	

Wash	Wash	2916	3037	2529	2496
	Blakeney point	631	346	400	
	Donna Nook	231		341	
	Total	**3778**		**3270**	
SE England	Thames, Essex, Kent, Suffolk	75		101	

Moray Firth
The number of seals counted in the Inner Moray Firth in 2002 was lower than counts in previous years (1141 in 1997 and 838 in 2000). In contrast there had been a slight increase in the number of seals at haulout sites adjacent to the Inner Moray Firth (particularly at Findhorn and on the coast from Dornoch to Dunbeath). The count in 2003 recorded a substantial increase in the number of seals in the Inner Moray Firth (approximately 1.5 times the 2002 count), with little change in the number of animals outside this region. These results may be within the margins of variability of the survey method but they could also suggest changes in the behaviour or distribution of seals between surveys. For example, it is possible that a larger proportion of the population was hauled out and, therefore, available to be counted in 2003 than in 2002. The number in 2003 was also slightly greater than the counts from recent surveys from shore-based surveys (Thompson & Barton 2003).

There was, therefore, no evidence of a decline in the number of common seals in the Moray Firth between the two surveys. This is consistent with the very small number of common seal carcasses found in this area during the course of the epidemic. (Table 2; Hall *et al*. 2003).

Tay Estuary
The number of seals in the Tay Estuary itself was similar in 2002 and 2003. However, the number found in the Eden Estuary (adjacent to the Tay Estuary and contiguous in terms of its common seal population) in 2003 was approximately one-third of the count in 2002 but it is likely that this was an artefact of human disturbance of seals on the day of the survey. Seals in this region were also counted regularly by SMRU using boat surveys and these results do not suggest there has been any significant change in the number of animals in the Tay Estuary. Only 46 dead seals (~3.7% of the population) were reported in this region and the surrounding coastline during the PDV epidemic.

The Wash and the English East Coast
The number of seals counted in The Wash and surrounding regions in 2003 was 13% less than in 2002. This suggests that the impact of the epidemic on this population was less than expected based upon the relatively high number of animals found during the epidemic. A total of 2132 common seals was found dead in this region (Table 2). By comparison the counts in The Wash declined by about 50% following the 1988 outbreak.

There are several possible reasons for the discrepancy between the observed mortality estimates from carcasses and the estimate derived from the aerial surveys. (1) The total population size (Table 2) used to calculate the percentage mortality was corrected for the estimated population growth rate in the Wash between 2002 and 2003 (approximately 6%) and for the number of seals at sea when the counts were made (35%). Errors in these estimates would bias the mortality estimate. (2) It is also possible that carcasses were washed onto UK coasts from Europe thus inflating the estimates of the number of UK seals that died. The potential effects of wind, tide and currents on the location of carcasses during the outbreak will be investigated, including the use of ‘man overboard’ models which may indicate the probability of dead animals from the European populations being stranded on UK shores. (3) There may also have been some multiple recording of carcasses. (4) Seals from European waters are also known to haul out at sites on the East coast of England so any changes in their movements could have affected the counts in southeast England. (5) In addition, an underestimate of the mortality rate based on counts before and after the epidemic would occur if the disease affected many more juveniles than adults and our counts are biased towards adults.

Further analysis of these counts will be carried out as part of the long-term abundance and distribution of the common seal data set for The Wash. Comparisons will also be made with the results of air surveys being conducted in Europe, particularly the Waddensea is continuing.

Serology

Based upon a sample of 20 common seals from The Wash, Tay Estuary, Moray Firth and Orkney there is evidence that between 30-50% of seals carry antibodies to PDV that are in a range suggesting that they have been exposed to the disease. However, an equivalent sample from the Scottish west coast showed that there had been no exposure to the disease in that region.

Conclusions

The current data suggest that the PDV epidemic of 2002 had less impact on common seals in the UK than the outbreak that occurred in 1988. Moreover, in the southeast of England, the apparent declines in the population based on *before* and *after* counts do not support the levels of mortality estimated from the number of seal carcasses recovered. There are many reasons why both the estimated number of carcasses or the counts of seals could be inaccurate. Nevertheless, while the indicators of the impact of PDV in south east England are inconsistent, those in Scotland all point to a low level of impact. Moreover, based on the serology results, a large proportion of seals on the Scottish east coast and in Orkney are likely to be immune to PDV. This is not the case on the west coast of Scotland where seals show no evidence of exposure. However, given the apparently low mortality caused by PDV on the east coast and in Orkney, it appears unlikely that even if the PDV infection was to occur on the west coast it would result in an appreciable increase in mortality.

References

Hall, A.J., Pomeroy, P.P. & Lonergan, M. (2003) The phocine distemper virus outbreak. SCOS Briefing Paper 03/10.

Thompson, P.M. & Barton, T.R. (2003) Recent trends in the abundance of common seals in the Moray Firth. SCOS Briefing Paper 03/16.

Table 2. PDV mortality estimates for common seals on the east coast of the UK in 2002, based on carcasses washed ashore.

2002 July-Dec

Region	**Locality**	**Minimum population size 2002 counts (mean)**	**The Mean growth rate over the last 5 years**	**Estimated 'true' population size [1]**	**Total No dead (all species)**	**Total No dead (common seals) [2]**	**Mortality rate based on observed numbers dead as a proportion of 'true' population size (%) [3]**	**Julian Date when 50% of total number of dead seals counted**	**Julian Date of first confirmed case of PDV**
Scotland	Moray Firth (Wick to Peterhead)[4]	714	0.97	1098	178	49	4.5	293	253
	Tay (Montrose to Kincardine Bridge)	816	Not known	1255	114	46	3.7	283	289
England	England E. Coast (Wash, Blakeney Point, Donna Nook, Thames Estuary)	3966	1.059	6102	2343	2132	34.9	268	224

[1] Corrected for proportion of population hauled out when counts were made

[2] Where species unidentified, number of common seals estimated from the proportion identified to species on a monthly pro-rata basis

[3] No. identified as common seals plus pro-rata unknown for the Moray firth (87%)

[4] Breeding season counts from the ground

Table produced in collaboration with the Institute of Zoology, University of Aberdeen and the Scottish Agricultural College, Veterinary Investigation Centre

C.D. Duck

Grey seal pup production in Britain in 2003

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

1. Surveys conducted in 2003

Each year SMRU conducts aerial surveys of the major grey seal breeding colonies in Britain (Scotland) to determine the number of pups born. In addition, new locations where grey seal pups have been seen or reported, or which appear to be suitable for colonization, are visited regularly. During the 2003 breeding season, five surveys were flown over the main colonies in the Inner and Outer Hebrides, Orkney and the Firth of Forth. Other new or important colonies in the Outer Hebrides, Orkney and the north Scottish coast were surveyed between three and four times. Regrettably, four films covering the first two surveys of the Inner and Outer Hebrides were lost during the autumn postal strike. Films are always posted by Special Delivery and this is the first time in 13 years that any films have gone astray.

SMRU purchased a second Linhof camera (JIF grant to J Harwood) and the second film cassette proved invaluable when the original cassette failed shortly after return from servicing.

Ground counts of pups born at the Farne Islands were made by the National Trust staff. Similar counts at Donna Nook were made by staff of the Lincolnshire Wildlife Trust and at South Ronaldsay by staff of Scottish Natural Heritage. The locations of the main grey seal breeding colonies in the UK are shown in Figure 1.

2. Estimated pup production

Numbers of pups born (pup production) at the regularly surveyed colonies is estimated each year from counts derived from the aerial photographs using a model of the birth process and development of pups. The method used to obtain the estimates for the 2003 pup production was similar to that used in previous years. A lognormal distribution was fitted to colonies surveyed four or more times (main Outer Hebrides, Orkney, Firth of Forth) and a normal distribution to colonies surveyed only three times (Inner Hebrides, new Outer Hebrides and new Orkney). This division was necessary because one Outer and two Inner Hebridean counts were on the films that were lost in transit to the processors.

Total pup production in 2003 at all annually monitored colonies was estimated to be 39,436, an increase of 7.4% from the 2002 production of 36,704 (Table 1). The trajectory of pup production, with 95% confidence limits, at the major breeding colonies in England and Scotland (excluding Loch Eriboll, Helmsdale and Shetland) between 1984 and 2003 is shown in Figure 2a. Figure 2b shows the pup production trajectories at the main island groups from 1960 to 2003. Production from the main island groups is shown in more detail in Figure 3a (Inner and Outer Hebrides and Orkney) and in Figure 3b (North Sea colonies). The time series of production estimates for these four island groups is given in Table 3.

The confidence limits for the Outer Hebrides for 2003 are unusually large. This is probably due to missing the first counts for most of the islands. On Ceann Iar, for instance, the existing first count, from mid October, was the highest. In previous years, the first Outer Hebrides survey was carried out on the same date as the first survey for the Inner Hebrides. For all islands other than Stockay, the first counts have always been very low. To reduce costs (flying, film, processing and counting time) the early flight was omitted in 2003.

For colonies not surveyed by air, pups were counted directly from the ground. These counts are conducted annually at the Farne Islands, Donna Nook and South Ronaldsay in Orkney and less frequently at SW England, Wales and in Shetland. Scottish Natural Heritage staff count South Ronaldsay in a manner compatible with counts from aerially surveyed colonies. For the past two years counts from South Ronaldsay have been modeled in the same manner as counts from aerially surveyed colonies to estimate pup production. From 2003, the South Ronaldsay data have been included with the main Orkney production estimates.

Note that the total pup production for 2002 (36,704) differs slightly from the figure presented to SCOS in 2003 (36,246; Duck 2003). This is due to the inclusion of three new colonies in the Outer Hebrides (Berneray, Fiaray and Mingulay which are all close to Barra) and four colonies in Orkney (North Flotta, South Westray, Sule Skerry and South Ronaldsay). Mingulay, North Flotta and South Westray were surveyed for the first time in 2003. The remaining colonies were surveyed previously, with the results included in Table 2. Table 3 has been adjusted to accommodate previous counts from these new colonies.

3. Trends in pup production

The differences in pup production at the main island groups are shown in Table 1. Total pup production at annually monitored colonies increased by 7.4%; the increase varying from 3.6% at the Isle of May and Fast Castle to 13.3% in the Outer Hebrides. This is one of the biggest increases in production at the Outer Hebrides in recent years. This was in part due to the inclusion of two recently established colonies Berneray and Fiaray and one new colony Mingulay).

Despite these increases, the results from 2003 continue to support the trends observed in recent years. Firstly, the rate of increase in grey seal pup production does not appear to be as high as it was during the late 1980s and early 1990s (Table 2). Secondly, production continues to appear to be more variable from year to year than previously (Figure 2b). Thirdly, although production in the Outer Hebrides increased in 2003, there is still no apparent overall change since 1992 (Figures 2b and 3a). Fourthly, the increased number of pups born in Orkney was relatively small despite the inclusion of four new colonies (Figures 2b and 3a). Once again, it appears that the rate of increase in Orkney is slowing down. There was a significant increase in the number of pups counted along the coast between Duncansby Head and Helmsdale. On a single photographic survey in 2003, 947 pups were recorded compared with 676 in 2001.

Table 1. The percentage change in grey seal pup production at annually surveyed colonies in the main island groups between 2002 and 2003 with the overall annual change over the previous five years (1999 and 2003). Note that production in 1999 was unusually low at all the main island groups.

Location	Change 2002-2003	Overall annual change 1999-2003
Inner Hebrides	+9.4%	+3.6%
Outer Hebrides	+13.3%	-0.1%
Orkney	+4.0%	+4.8%
Isle of May & Fast Castle	+3.6%	+5.0%
Farne Islands	+5.5%	+8.7%
Donna Nook	+11.7%	+11.0%
Total	**+7.4%**	**+3.2%**

Between 1984 and 1996, pup production estimates from annually monitored colonies showed a fairly consistent annual increase, with the notable exception of 1988 (Figures 2 and 3). There were further declines in pup production in 1997 (mainly due to a reduction in the number of pups born in the Outer Hebrides), 1999 (in all island groups) and in 2002 (again, mainly in the

Outer Hebrides). In the years following each of these declines, there was a marked increase in total pup production (by 9.5%, 11.5% and 7.4% in 1998, 2000 and 2003 respectively).

The overall annual percentage change in pup production at each of the main island groups between 1999 and 2003 is shown in Table 1. These changes varied from –0.1% at the Outer Hebrides to +11% at the small colony at Donna Nook. The overall change, for all colonies combined, was +3.2%. In Table 2, the changes for the two preceding five year intervals are shown for comparison.

Pup production fluctuates between years but in recent years, since 1996, the fluctuations have been more variable than previously (Figures 2a and 2b). This is also reflected in the annual rate of change in production between years. It is difficult to determine what causes these changes but they could indicate that the grey seal population is approaching the limits of size. To even out these fluctuations, the average percentage rate of annual change in pup production for five yearly intervals since 1989 is shown in Table 2. These figures probably provide the best indication of the current trend in pup production.

4. Pup production model assumptions

The model used to estimate pup production from aerial survey counts of whitecoat 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 estimate is sensitive to the value used for the latter parameter and there is, therefore, an argument for allowing this parameter to vary between colonies.

In previous versions of this Advice, we have 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.

5. Confidence limits

Ninety-five percent confidence limits on the pup production estimates varied from being within 4.3% of the point estimate in Orkney to 24.5% in the Outer Hebrides (Figures 3a and 3b). The value for the Outer Hebrides is considerably greater than any in any previous years and is likely to be due to the lack of an early count for the bigger colonies. It would be interesting to repeat the estimation process using a normal distribution to determine the effect on the confidence limits.

6. Pup production at colonies less frequently surveyed

Approximately 15% of all pups are born at these colonies each year (Tables 3 and 5). Confidence limits cannot be calculated for these estimates because they represent single counts. Loch Eriboll and Eilean nan Ron (Tongue) were surveyed four times and production estimated using a lognormal distribution. The results are in Table 3. Table 3 also includes the total counts from the colonies listed in Table 5 (under Other colonies). These and other potential breeding locations are checked when flying time and conditions and additional circumstances permit. Table 3 indicates that approximately 5,500 pups are born at colonies not surveyed annually. A survey of grey seals breeding in Shetland is planned for this coming season in collaboration with Scottish Natural Heritage.

Table 2. Pup production estimates for colonies in the main island groups surveyed in 2003. The overall annual changes, over successive 5-year intervals are also shown. These annual changes represent the exponential rate of change in pup production. The total for the North Sea represents the combined estimates for the Isle of May, Fast Castle, the Farne Islands and Donna Nook.

Location	**2003 pup production**	**Overall annual change in pup production**		
		1989-1993	1994-1998	1999-2003
Inner Hebrides	3,386	+12.0	+2.7	+3.6
Outer Hebrides	12,741	+7.5	+0.3	-0.1
Orkney	18,652	+7.3	+8.5	+4.8
Isle of May + Fast Castle	2,599	+10.4	+15.7	+5.0
Farne Islands	1,266	+3.1	+6.9	+8.7
Donna Nook	792	+20.1	+9.2	+11.0
North Sea (i.e. previous 3 locations)	4,657	+7.8	+11.7	+6.9
Total	**39,436**	**+10.0**	**+4.9**	**+3.2**

Table 3. Pup production estimates for breeding colonies surveyed less regularly

Location	**Date and location of last survey**	**Pup production**
Mainland Scotland*	Helmsdale (Duncansby Head to Helmsdale, 2003	947 (one count)
	**Loch Eriboll, Eilean nan Ron (Tongue) 2003	966 (modeled, 4 counts)
Other colonies	Various, from Table 5	759
Shetland	1977	1,000
South-west Britain	South-west England Wales 1994	1,750
Total		**5,422**

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

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

Table 4. Estimates of pup production for colonies in the Inner and Outer Hebrides, Orkney and the North Sea, 1960-2003.

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 4 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*	2938	33504
1997	3076	11946	14051	3698	32771
1998	3087	12434**	16367*	3989	35877
1999	2787	11759**	15462*	3380	33388
2000	3223	13396	16281*	4303	37210
2001	3032	12427**	17938*	4134	37531
2002	3096	11248**	17942*	4418	36714
2003	3386	12741**	18652*	4657	39436

**** Production estimates for North Flotta, South Westray, Sule Skerry and South Ronaldsay included in the Orkney total for the first time.***
** Production estimates for Mingulay, Berneray and Fiaray (latter two off Barra) included in the Outer Hebrides total for the first time.

Sule Skerry, Berneray and Fiaray colonies have been removed from Table 5 and included in the main production Tables for the appropriate island group in the Appendix. North Flotta and South Westray were new Orkney colonies surveyed for the first time in 2003.

Table 5. Scottish grey seal breeding sites that are not surveyed annually and/or have recently been included in the survey programme. Data from 2003 are in bold type.

	Location	Survey method	Last surveyed, frequency	Number of pups
Inner Hebrides	Loch Tarbert, Jura	SMRU visual	2003, every 3-4 years	**10**
	West coast Islay	SMRU visual	1998, every 3-4 years	None seen
	Ross of Mull, south coast	SMRU visual	1998, infrequent	None seen
	Treshnish small islands, incl. Dutchman's Cap	SMRU photo & visual	annual	~20 in total
	Staffa	SMRU visual	1998, every other year	~5
	Little Colonsay, by Ulva	SMRU visual	1998, every 3-4 years	6
	Meisgeir, Mull	SMRU visual	1998, every 3-4 years	1
	Craig Inish, Tiree	SMRU photo	1998, every 2-3 years	2
	Cairns of Coll	SMRU photo	2003, every 2-3 years	**22**
	Muck	SMRU photo	1998, every other year	**36**
	Rum	SNH ground	2003, annual	10-15
	Canna	SMRU photo	2002, every other year	54
	Rona	SMRU visual	1989, infrequent	None seen
	Ascrib Islands, Skye	SMRU photo	2002, every other year	60
	Heisgeir, Dubh Artach, Skerryvore	SMRU visual	1995, every other year 1989, infrequent	None None
Outer Hebrides	Barra Islands Fiaray & Berneray	SMRU photo	annual	Included with Outer Hebrides
	Sound of Harris islands	SMRU photo	2002, every 2-3 years	358
	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	**50, 58**
	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	1998, every other year	None seen
Orkney	Sule Skerry	SMRU photo	1998 - 2002	Included with Orkney
	Sanday, Point of Spurness	SMRU photo	1999, 2002	62, 10
	Sanday, east and north	SMRU visual	1994, every 2-3 years	None seen
	Papa Stronsay	SMRU visual	1993, every 3-4 years	None seen
	Holm of Papa, Westray	SMRU visual	1993, every 3-4 years	None seen
	North Ronaldsay	SMRU visual	1994, every 2-3 years	None seen
	Eday mainland	SMRU photo	2000, 2002	8, 2
Others	Firth of Forth islands, Inchcolm; Craigleith (by North Berwick)	SMRU photo, Forth Seabird Group	Infrequent, 1997 2003	<10, 4 **86**
Total				**759**


Figure 1
Grey seal breeding colonies
in Britain
Colonies asterisked have been
put forward as potential Special Areas of Conservation
Shetland
*Faray & Holm of Faray
*North Rona
Orkney
Loch Eriboll
Outer
Hebrides
Helmsdale & Berriedale
*Monach
Isles
Major colony
Minor colony
*Treshnish Isles
Inner
Hebrides
*Isle of May
St Abbs Head
Farne Islands
Donna Nook
*North Pembroke
Coast
*Ramsey
*Skomer
Lundy
Isles of Scilly

Figure 2a. Total estimated pup production, with 95% confidence limits, for all the major, annually monitored colonies in Scotland and England from 1984 to 2003.

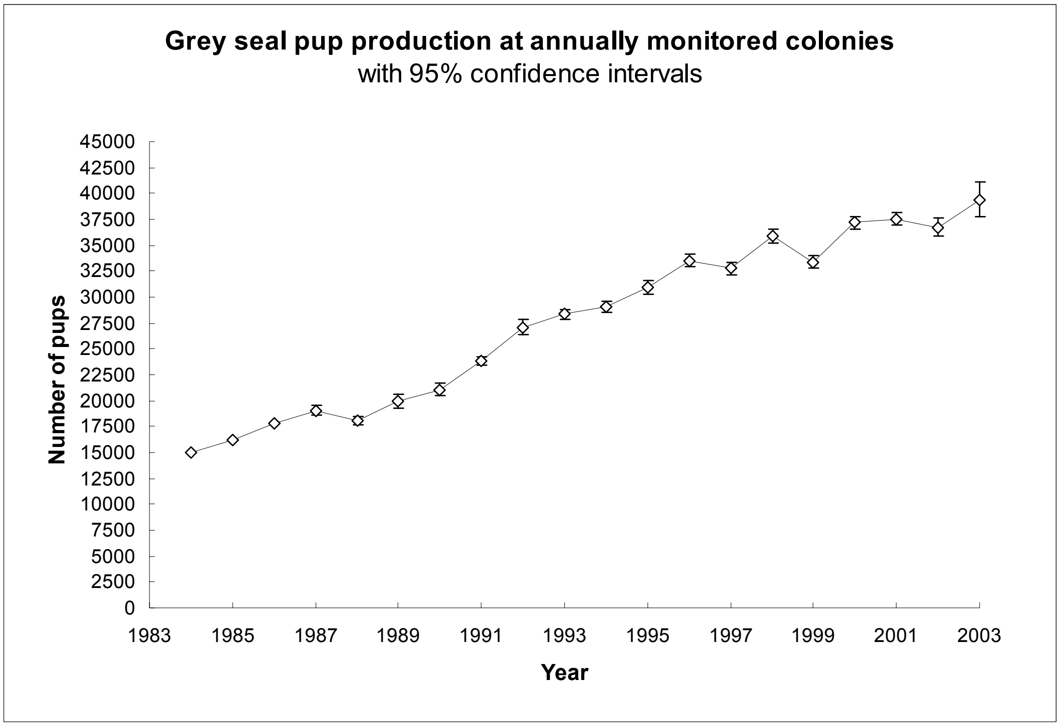


Figure 2b. Grey seal pup production trajectories from 1960 to 2003.

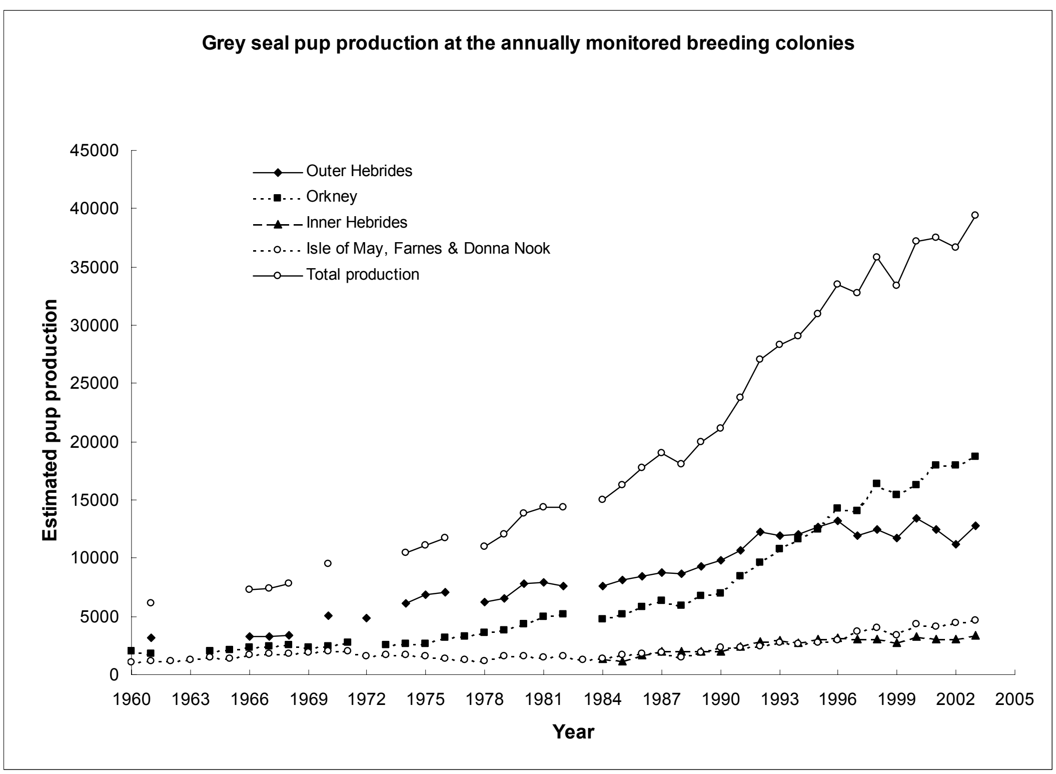
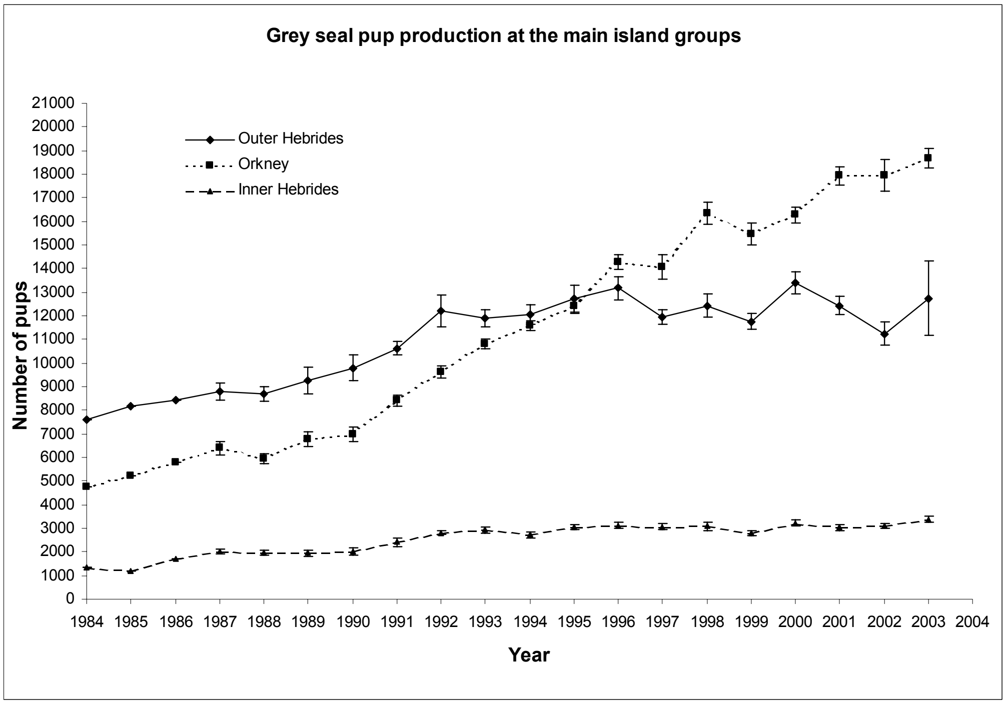
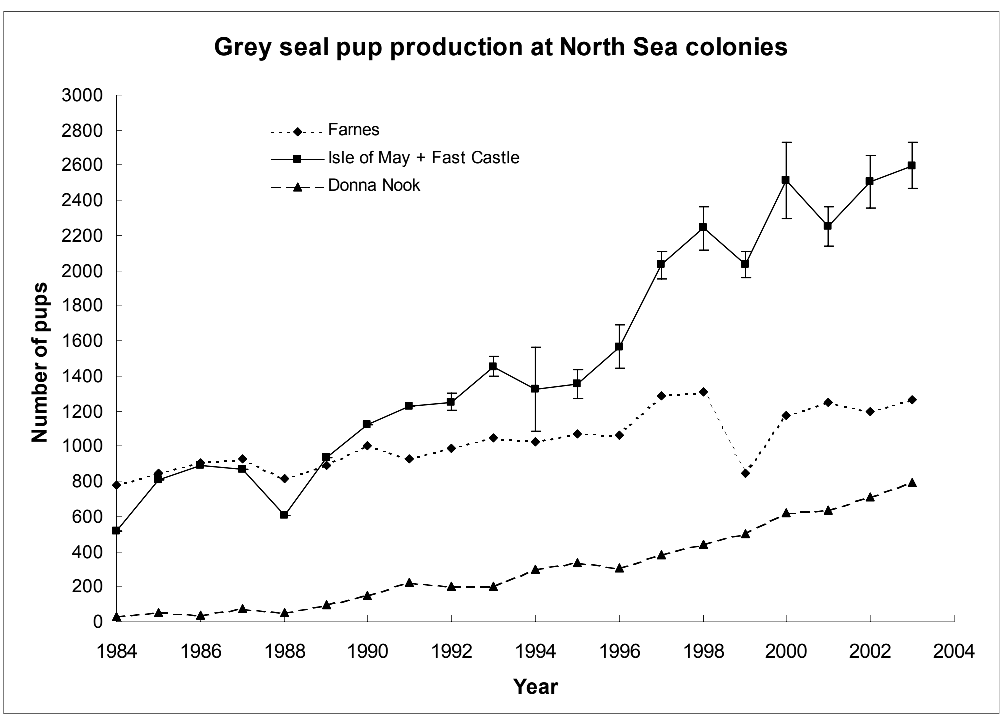


Figure 3. Trends in pup production at the major grey seal breeding colonies since 1984. Production values are shown with their 95% confidence limits where these are available. These limits assume that the various pup development parameters involved in the estimation procedure remain constant from year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

3a) Outer Hebrides, Orkney and Inner Hebrides



3b) Farne Islands, Isle of May and Donna Nook



Jason Matthiopoulos & John Harwood

Estimating Annual Pup Production in Grey Seal Breeding Colonies: A state-space approach

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

Abstract

Estimates of pup production from aerial survey data are fundamental to the estimation of grey seal population size. The methodology currently used to estimate pup production assumes that births are log-normally distributed within a season and requires exact knowledge of a large number of parameters. Here, we describe a state-space approach to estimating pup production from survey data that explicitly models the way in which births, pup mortality, pup loss and departure vary during the breeding season, and accounts for misclassification error in the aerial observations. We adopt a Bayesian approach that allows us to use independent information on parameter values, and deals explicitly with uncertainty in parameters and predictions. Preliminary results using simulated data demonstrate that, despite containing 30 parameters, the model can be fitted successfully to relatively sparse data. The results not only quantify pup production but can, potentially, also provide insights about the demographic processes taking place during the breeding season

1. Introduction

In the past, technological and logistical limitations have meant that the marine environment was almost impenetrable to human observation. As a result, the abundance of most marine organisms has been difficult to estimate. More recently, systematic transect surveys, and mark-recapture techniques have been used for this purpose with considerable success. However, certain marine mammals, like grey seals, have strong associations with the coastal habitat for activities such as breeding, resting and moulting. This aspect of their life history makes transect surveys difficult to design but offers us the opportunity of large scale, aerial observation while they are visible, on shore. Recognising this, NERC-funded aerial surveys of all the major grey seal breeding colonies have been carried out by SMRU since the early sixties. The main objective of these surveys has been to estimate pup production at these colonies and thus arrive at an estimate of total population size.

There is no time during the breeding season for which we can be sure that all the pups born at a particular colony are present there. Therefore, statistical techniques must be used to infer pup production from a series of counts spaced over the breeding season. Until now, SMRU's solution to this problem has employed maximum likelihood methods to fit a parametric (lognormally-shaped) model of the distribution of births within a season to the time series of pup counts. This was the only possible approach given the computational limitations of the time at which it was developed and it has served well as a way of quantifying long-term population trends. However, it suffers from three distinct disadvantages. First, it does not recognise that the processes occurring during the breeding season are, dynamic, developing over time, and autocorrelated. As a result, it is an awkward framework for modelling demographic stochasticity and does not permit modelling of the density dependent processes that have been hypothesised to occur on the colonies. Second, it relies on extensive and accurate parameterisation. This means that the final estimates of pup production are potentially sensitive to the parameter values used and the user obtains no feedback from the fitting process on how plausible these parameters are. Third, it can only approximately deal with prediction uncertainty and does not deal with parameter uncertainty.

In this paper, we adopt a state-space approach to modelling the breeding season which combines a dynamical model (either difference or differential equations) for the biological process, with a model of the process by which observation of the system are made (the observation process). In this way, the two fundamental processes that give rise to the end product, the data, are handled in a single framework. This has two virtues: it avoids the usual misuses of distributional assumptions for observation error and it allows the estimation of parameters relevant to observation error.

We use Monte-Carlo Markov-Chain (MCMC) techniques to fit the state-space model to data. These are computer-intensive Bayesian techniques that are currently enjoying widespread use. The computer-intensive nature of MCMC has released us from traditional restrictions on statistical models and allows us to fit a complex and realistic state-space model. The Bayesian nature of MCMC enables us to use independent information about model parameters in the form of prior distributions and specify the model only to the extent dictated by such independent information. It also deals naturally with uncertainty in the estimates of parameters and predictions. Finally, the wide-spread use of MCMC has led to the development of tools for its implementation. We used such a toolbox, WinBUGS.

The development of our model has been motivated by the kind and quantity of available data. Hence, in the following section, we review the relevant data. In sections 3 and 4 we present the process and observation models. In section 5 we present the validation of our framework using simulated data.

2. Available data

Grey seal pups are born with a white coat which they moult after about 20 days to reveal a coat pattern similar to that of adult seals. Some time after moulting they leave the breeding colony. Pups may die at any time during their stay on the colony. Dead pups may be washed off the colony by storms. They also become less visible with time as they decay, become covered in mud, or are consumed by scavengers.

2.1 Aerial surveys

Pups that are visible in aerial photographs are classified as either whitecoated or moulted. Whenever possible, pups are classified as dead (as judged by posture, blood-stained pelage and the presence of scavengers). Since 1993 the numbers of pups feeding from their mothers have also been recorded. At least four surveys are carried out each year. In 1988, 1993 and 1996, additional surveys were made.

2.2 Ground surveys

Pups numbers have been censused directly at the Farne Islands since the 1950s, and from time to time at the Isle of May and the Monach Isles by observers based on the colonies. Pups that have been counted are dye-marked with a unique colour for each census to avoid double counting and to allow loss rates to be estimated.

2.3 Age to moulting

Wyile (1988) found that age at moulting was symmetrically distributed with a mean of 23 days and standard deviation of 5 days. Mean time to moult does not appear to differ significantly between years so it may be mostly determined by physiology. If this is true then it may also be assumed to be the same across colonies.

2.4 Age to departing

Age at departure is symmetrically distributed with a mean of 31.5 days and a standard deviation of 7 days. They. also state that time to moult and time to departure are uncorrelated. This implies that the durations of the two stages are negatively correlated. Therefore, the simplest way of modelling these is as functions of age.

2.5 Misclassification of pups

While it is unlikely that a whitecoat will be classified as moulted, some moulted animals may appear so pale that they are classified as whitecoats. Only 55% of moulted pups recorded on the ground are classified as moulted in aerial photographs. Misclassification is time- and colony-dependent. the standard deviation on the proportion of misclassification was found to be 0.07.

2.6 Pup mortality

Mortality over the entire breeding season is estimated at 3.4%. This is most likely age-dependent.

2.7 Loss of dead pups

Rushton (unpublished) found that the rate of loss of dead pups at the Farne Islands and the Isle of May was approximately 0.023 per day. These rates are likely to vary between colonies.

3. Process model

This is an age/stage structured model. Time and age are discrete and measured in days. There are as many age classes as there are days in the breeding season. The pup population's state vector for a given day is

$$\mathbf{m}_t = \left[w_{t,1},\ldots,w_{t,k},w'_{t,1},\ldots,w'_{t,k},m_{t,1},\ldots,m_{t,k}m,'_{t,1},\ldots,m'_{t,k},\right]^T \quad 1.$$

where w represents whitecoats, m represents moulters, and dead animals are represented by a prime (w' and m'). Our full notation is summarised in Table 1. In the model, tracking of pups after death is needed because dead pups remain on the beach, appear on the aerial photographs and have the potential to influence our estimates. The biological process comprises six sub-processes examined individually below (also see overview of the model in Fig. 1).

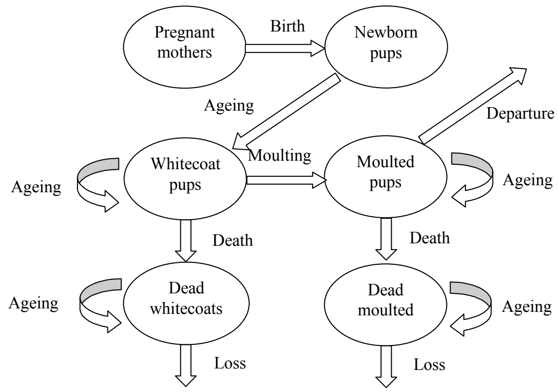


Figure 1: Overview of the processes and states described by the model.

3.1 Pupping

A finite pool (N_t) of pregnant females that have yet to breed on day t becomes depleted as individual females pup. The number of births (n_t) on a given day is modelled as a binomial process with probability p_t and number of trials determined by the remaining, pregnant females in the previous day

$$n_t \sim B(N_{t-1}, p_t) \qquad 2.$$

The quantity p_t is the probability that an individual female will give birth on a particular day. This is a function of time. In the simplest case, before the start of the breeding season, at a given time t_0 during the year, the per-capita pupping probability is zero and after the start of the breeding season it is constant and equal to a value $p_{\max}$. This can be implemented as a step function

$$p_t = \begin{cases} 0 & \text{if} \quad t < t_0 \\ p_{\max}/2 & \text{if} \quad t = t_0 \\ p_{\max} & \text{if} \quad t > t_0 \end{cases} \qquad 3.$$

. Because pupping is a depletion process of a finite number of pregnant mothers, the formulation in eq. 3 tend to give a monotonically decreasing number of pups born as a function of time. This is because of the abrupt transition from 0 to $p_{\max}$. Direct observations by members of SMRU at several colonies suggest that pup production has an initial increase phase followed by a longer decline phase. This can be modelled by making the transition from 0 to $p_{\max}$ more gradual,

$$p_t = p_{\max} \frac{\exp(a_0 + a_1 t)}{1 + \exp(a_0 + a_1 t)} \qquad 4.$$

Similar functions are used to describe other processes in the model, so it is useful at this stage to review some of the properties of eq. 4.

i. Non-positive values of a_1 make p_t either a strictly decreasing function of time or time-invariant. This is not biologically realistic because it means either that the breeding season has no defined beginning or that seals breed during the entire year. We therefore require $a_1 > 0$.
ii. The half saturation point for eq. 4, i.e. the time at which the probability equals $p_{\max}/2$ is given by $t_0 = -a_0/a_1$. This ratio determines (but is not the same as) the start of the breeding season along the time axis.
iii. The derivative of the function at the half-saturation point is $\left.\frac{dp_t}{dt}\right|_{t_0} = a_1$. So, the parameter a_1 controls how sharply, the per-capita, daily, breeding probability increases with time around the half-saturation point. Note that the formulation in eq. 3 is a limiting case of eq. 4 for $a_1 \to \infty$.

In summary, eqs 2 and 4 model the daily number of births as the dynamic interaction between the per-capita probability of pupping (deterministically increasing with time from zero to the value $p_{\max}$) and the number of available pregnant females (stochastically decreasing with time from N_0 to zero).

This is the simplest possible formulation of the process that gives the right-skewed pupping curve observed in several colonies. Further extentions are possible. For example, there is anecdotal evidence (M. Fedak, pers com) that pregnant grey seals have some control over the timing of their delivery. They seem to exercise this control in response to the density of other mothers on the breeding colony. Modelling pupping as a state-space process means that eq. 4 can be extended to include such density-dependent effects. Further extensions of this model involving higher order terms of time and density are also possible. Such terms could represent declines in the probability of pupping towards the end of the breeding season, multiple waves of births (P. Pomeroy, pers com), or switches from conspecific attraction to conspecific avoidance. Covariates other than time and density could be derived from the age structure of mature females to model age-related effects on fecundity (P. Pomeroy, pers com). Clearly, given the limited availability of data on density-dependent and age-related effects such improvements must be left for the future.

3.2 Ageing of pups

The model operates on a daily time scale. So, if a pup does not die or depart the breeding colony, it moves to the next age state at the end of each day. We have also included ageing for dead pups as this enables us better to model their decay and eventual disappearance.

3.3 Pup mortality

The number of whitecoat deaths ($s_{t,i}$) and the number of deaths of moulted pups ($r_{t,i}$) are modelled as binomial processes with daily, age-dependent mortality c_i

$$s_{t,i} \sim B(w_{t,i}, c_i) \qquad 5.$$

and

$$r_{t,i} \sim B(m_{t,i}, c_i) \qquad 6.$$

The daily mortality probability is assumed to decrease with age from a maximum value ($c_{\max} \leq 1$) to a minimum value ($c_{\min} \geq 0$)

$$c_i = c_{\min} + c_{\max} \exp(-\gamma i) \qquad 7.$$

3.4 Moulting of pups

This process is represented by the transition from the *w* state to the *m* state. The number of whitecoat pups of age *i* that moult on day *t* is modelled as a binomial process

$$l_{t,i} \sim B(w_{t,i} - s_{t,i}, b_i) \qquad 8.$$

where b_i is the age-dependent probability of moulting. Moulting does not happen at the same age for all pups. We therefore use a sigmoidal formulation with a maximum daily probability .

$$b_i = b_{\max} \frac{\exp(\beta_0 + \beta_1 i)}{1 + \exp(\beta_0 + \beta_1 i)} \qquad 9.$$

Setting $b_{\max} = 1$ and using very large values for β_1 implies that all pups moult on exactly the same age, given by $-\beta_0/\beta_1$.

3.5 Loss of dead pups

As noted above, dead pups tend to disappear as they age. We distinguish between the number of dead whitecoats ($v_{t,i}$) and the number of moulted pups ($u_{t,i}$) that are lost

$$v_{t,i} \sim B(w'_{t,i}, h) \qquad 10.$$

$$u_{t,i} \sim B(m'_{t,i}, h) \qquad 11.$$

We assume that the daily probability of loss is constant. However, the cummulative probability of loss increases with time.

3.6 Departure of moulted pups

Finally, moulted pups that are still alive eventually leave the colony. Their number from each age class is given by

$$q_i \sim B(m_{t,i} - r_{t,i}, d_i) \qquad 12.$$

With age-related probability

$$d_i = d_{\max} \frac{\exp(\delta_0 + \delta_1 i)}{1 + \exp(\delta_0 + \delta_1 i)} \qquad 13.$$

Setting $d_{\max} = 1$ and using very large values for δ_1 implies that all pups leave on exactly the same age, given by $-\delta_0/\delta_1$.

Table 1: Overview of notation used

Symbol	***Description***
	Variables
$\mathbf{m}_t$	State vector in day *t*
$w_{t,i}$	Whitecoat pups of age *i* on day *t*

$w'_{t,i}$	Whitecoat pups that died *i* days ago and are still visible by day *t*
$m_{t,i}$	Moulted pups of age *i* on day *t*
$m'_{t,i}$	Moulted pups that died *i* days ago and are still visible by day *t*
N_t	Remaining pregnant mothers on day *t*
n_t	Births on day *t*
$s_{t,i}$	Whitecoat pups, aged *i,* dying on day *t*
$l_{t,i}$	Surviving whitecoats, aged *i*, moulting on day *t*
$v_{t,i}$	Dead whitecoats that are lost on day *t*
$r_{t,i}$	Moulted pus dying on day *t*
$q_{t,i}$	Moulted pups, aged *i*, that leave the colony on day *t*
$u_{t,i}$	Dead, moulted pups that are lost on day *t*
ψ_τ	Live whitecoats counted during the survey at day τ
μ_τ	Live moulters counted during the survey at day τ
ψ'_τ	Dead whitecoats counted during the survey at day τ
μ'_τ	Dead moulters counted during the survey at day τ
	Functions
p_t	Daily probability of pupping on day *t*
c_i	Daily probability of dying at age *i*
b_i	Daily probability of moulting at age *i*
h_i	Daily probability that a carcass will disappear on the ith day after death
d_i	Daily probability of departing the colony at age *i*
	Constants
k	Days in the breeding season and number of age classes
	Parameters
$p_{\max}, a_0, a_1$	Parameters for pupping probability
$c_{\min}, c_{\max}, \gamma$	Mortality parameters
$b_{\max}, \beta_0, \beta_1$	Moulting parameters
h	Carcass loss parameters
$d_{\max}, \delta_1, \delta_2$	Departure parameters
$\phi_{\_,\_}$	Probabilities for observation matrix

Overall, the balance equations in the model take the following form

$$N_{t+1} = N_t - n_t \qquad 14.$$

$$w_{t+1,0} = n_t \qquad 15.$$

$$w_{t+1,i+1} = w_{t,i} - s_{t,i} - l_{t,i} \qquad 16.$$

$$w'_{t+1,0} = \sum_{i=0}^{k} s_{t,i} \qquad 17.$$

$$w'_{t+1,i+1} = w'_{t,i} - v_{t,i} \qquad 18.$$

$$m_{t+1,0} = 0 \qquad 19.$$

$$m_{t+1,i+1} = m_{t,i} + l_{t,i} - r_{t,i} - q_{t,i} \qquad 20.$$

$$m'_{t+1,0} = \sum_{i=0}^{k} r_{t,i} \qquad 21$$

$$m'_{t+1,i+1} = m'_{t,i} - u_{t,i} \qquad 22$$

4. Observation model

We introduce four states for whitecoats/moulters and alive/dead. We also introduce a fifth state, specific to the observation model: pups that are present on the colony but not counted in the aerial photographs. If the survey takes place on day τ then live whitecoats and moulters are denoted by ψ_τ, μ_τ respectively. The equivalent primed symbols are, as previously, used to denote counts of dead pups. The observation model formalises the processes of double-counting, non-observation, and misclassification. The processing of the aerial photographs ensures that there is no double-counting. The number of unobserved pups is denoted by χ_τ. We model misclassification by the following augmented matrix of observation probabilities

$$\phi = \left(\begin{array}{cccc:c} \phi_{w,\psi} & \phi_{w,\mu} & \phi_{w,\psi'} & \phi_{w,\mu'} & \phi_{w,\chi} \\ \phi_{m,\psi} & \phi_{m,\mu} & \phi_{m,\psi'} & \phi_{m,\mu'} & \phi_{m,\chi} \\ \phi_{w',\psi} & \phi_{w',\mu} & \phi_{w',\psi'} & \phi_{w',\mu'} & \phi_{w',\chi} \\ \phi_{m',\psi} & \phi_{m',\mu} & \phi_{m',\psi'} & \phi_{m',\mu'} & \phi_{m',\chi} \end{array} \right) \qquad 23.$$

where, for example, $\phi_{m,\psi}$ is the probability that a moulter will be classified as a whitecoat. The fifth column lists the probabilities that a pup of a particular class is not observed at all. Note that the possibilities described by each row are exhaustive, so the elements of each row in eq. 23 add up to 1.

The total number of whitecoats is given by

$$w_\tau = \sum_{i=0}^{\tau} w_{\tau,i} \qquad 24.$$

We also use m_τ, w'_τ, m'_τ to denote total numbers of pups in the other three classes. We denote by ϕ_ψ the probability that a pup from any class will be classified as a whitecoat

$$\phi_\psi = \frac{\phi_{w,\psi} w_\tau + \phi_{m,\psi} m_\tau + \phi_{w,\psi} w'_\tau + \phi_{m,\psi} m'_\tau}{w_\tau + m_\tau + w'_\tau + m'} \qquad 25.$$

The classification probabilities $\phi_\psi, \phi_\mu, \phi_{\psi'}, \phi_{\mu'}$ and the probability ϕ_χ that a pup will not be observed can be defined collectively using matrix notation

$$(\phi_\psi, \phi_\mu, \phi_{\psi'}, \phi_{\mu'}, \phi_\chi) = (w_\tau, m_\tau, w_\tau, m_\tau).\phi \frac{1}{w_\tau + m_\tau + w'_\tau + m'} \qquad 26.$$

Note that these contain no age-specific information and, for the present model, we ignore this process as we believe that it introduces more parameters than the additional data can support. However, we have not yet verified this in practice.

The vector of probabilities in eq. 26 is used to model the observed counts for each survey as follows

$$(\psi_\tau, \mu_\tau, \psi'_\tau, \mu'_\tau, \chi_\tau) \sim \text{Multinomial}\left(w_\tau + m_\tau + w'_\tau + m', (\phi_\psi, \phi_\mu, \phi_{\psi'}, \phi_{\mu'}, \phi_\chi)\right) \qquad 27.$$

Table 2: The true value of each parameter (*Val.*) is accompanied by the median estimate from MCMC and the 95% confidence interval.

Par.	*Val.*	*2.5%*	*Med.*	*97.5%*	*Par.*	*Val.*	*2.5%*	*Med.*	*97.5%*
N_0	500	473	492	511	β_0	-30	-35.6	-34.5	-33.6
$p_{\max}$	0.4	0.39	0.46	0.52	β_1	6	4.15	4.42	4.69
a_0	-16	-17.8	-16.3	-15.0	h	0.1	0.099	0.101	0.103
a_1	4	3.69	4.05	4.42	$d_{\max}$	1	0.96	0.99	1.00
$c_{\max}$	0.05	0.050o	0.052	0.054	δ_0	-30	-32.5	-29.2	-25.7
γ	0.01	0.007	0.009	0.011	δ_1	4	3.70	4.13	4.57
$b_{\max}$	1	0.987	0.989	0.991					

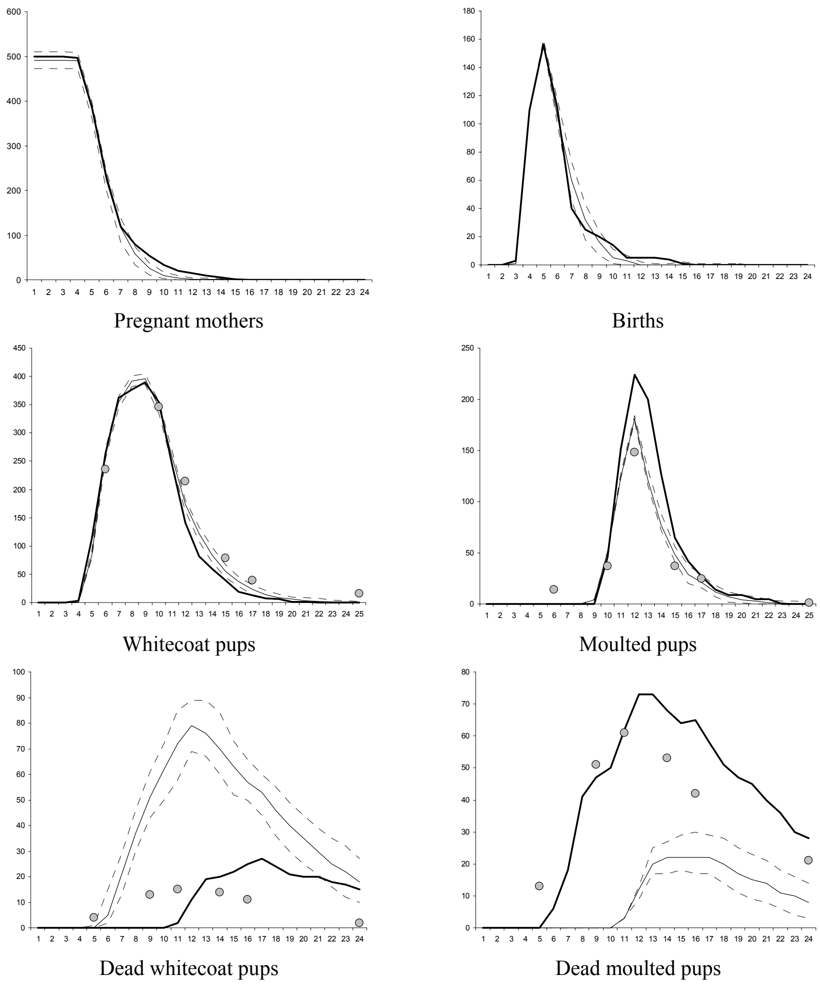


Figure 2: The state variables of the process model as functions of time. Thick black lines represent the true process. Thin white lines are model estimates. The dashed lines are the 95%-tiles around the model's estimates. The dots in the lower four graphs represent the data on which the entire model-fitting exercise was based. Note that the heavy biases in the data have been built into this particular example by the high misclassification probabilities in eq. 28.

5. Validation

The model-fitting code was written in WinBugs v1.4 and is available in the Appendix. We validated the code using data from a simulation. The objective of this exercise was twofold. First, we wanted to check that model-fitting was able to retrieve the correct parameters and to bracket the true pup production. This was a lenient test of the methodology because the mechanism that generated the simulated data was exactly the same as the model fitted. However, a minimum requirement is that the method performs well under conditions of no model uncertainty.

A critical feature of this model is that it contains a large number of parameters compared to the number of data that are typically available from the aerial surveys. In contrast to classical model fitting, such models can be fitted using Bayesian techniques provided that the priors set on the parameters are sufficiently informative. Under a state-space approach, the entire set of states are also quantities to be estimated. Hence, in addition to the parameters of the model (30 in total), the procedure has to estimate the number of pups born on each day, the number of live pups of each age and class, dying, moulting and departing, and the number of dead pups that disappear. For a breeding season of 25 days, such as the example examined here, this gives an additional 3,775 quantities to be estimated. We found that it was numerically impossible to fit the model unless the misclassification matrix in eq. 23 was known almost exactly. In reality, this is probably the easiest information to obtain, by ground-truthing the aerial surveys. We therefore provided the algorithm with very tight priors that were centred at the true misclassification probabilities. The specific values used were,

$$\left(\begin{array}{cccc:c} 0.9 & 0.03 & 0.03 & 0.02 & 0.02 \\ 0.3 & 0.6 & 0.04 & 0.04 & 0.02 \\ 0.2 & 0.05 & 0.7 & 0.03 & 0.02 \\ 0.2 & 0.2 & 0.25 & 0.25 & 0.1 \end{array}\right) \qquad 28.$$

We also used relatively informative priors for the remaining parameters, except for the total number of pregnant mothers.

We run the MCMC algorithm for 100,000 iterations, discarding the first 500 for burn-in. This took approx 50 hours on a 3.2GHz Pentium IV. We first checked that the algorithm was able to estimate the true parameters correctly (Table 2). The estimates were close to the truth for most of the parameters in the process model and all posterior distributions were tighter than the priors provided for them initially. Most importantly, total pup production (represented by the number of pregnant mothers N_0 at the beginning of the breeding season) was estimated almost exactly. Of the other parameters, only $b_{\max}$, β_0 and β_1 were not bracketed by the confidence intervals. All three of these parameters relate to the timing and rate of moulting as a function of age so we expected this process to be misrepresented in the predictions of the model. As expected, the posterior estimates for the element of the misclassification matrix did not differ significantly from the values given in eq. 28.

We then compared the time series of estimated pup numbers with the truth (Fig. 2). The process of depletion of pregnant mothers and its complement, the daily number of births, were estimated accurately, albeit with over-tight confidence intervals between the 9th and 15th day of the breeding season. As expected by the parameter estimates in Table 2, the number of moulted pups was underestimated. Instead, the algorithm overestimated mortality.

8. Discussion

We have outlined a state-space model of the breeding season in grey seals. We have demonstrated how, using MCMC, this model can be fit to data such as those collected by the annual SMRU aerial surveys. Our primary objective was to develop and validate a methodology for estimating pup-production in grey seals. In principle, the same methodology can be used to estimate other parameters of interest for grey seals (such as the rates of pup mortality and moulting) and to estimate production for other species with a similar biology.

The present approach explicitly models mortality and the loss of dead pups. Our preliminary examination using simulated data indicated that the parameter *h,* determining the rate of loss of dead pups from the colony, was the most significant factor affecting the estimate of pup production. Of course, this may be a particular property of the parameterisation used to generate the simulated data but it nevertheless hints at the importance of correctly modeling mortality and loss. However, the MCMC method used for fitting the model to data automatically provides measures of uncertainty for parameters and population predictions.

Despite these advantages, the new framework currently suffers from two major drawbacks. First, the implementation of MCMC in WinBUGS, although relatively user-friendly, is very slow and numerically unstable. This means that the fitting process requires dedicated user supervision. A possible cure for this may be to increase the time interval at which the model operates from one day to the shortest time interval between surveys. For example, for a sixty-day breeding season, using a four-day time step would make no difference to the estimate of pup production but would get to it 16 times faster. It would also reduce the quantities to be estimated from 21,690 to 1,395 and therefore reduce the chances of WinBUGS crashing. Second, the estimation demands made by the state-space model on the survey data are too large. In the example of this report, we assumed that seven surveys were available and that informative priors could be provided for all parameters. In reality, seven surveys over a single colony in a single year is extremely rare and our independent information for some of the parameters is sketchy at best. Even under the favourable conditions provided in the simulated example, MCMC failed to estimate the moulting parameters correctly. This problem can only be addressed by supplying the model with more data. This can be done either by dedicated data-collection for the lesser known model parameters or by pooling survey data from different colonies. The Bayesian approach adopted here makes this particularly easy. Validation trials, such as the one carried out here, must be used to guide further data collection by indicating those parameters to which estimation is most sensitive.

Appendix: Implementation in WinBUGS

WinBUGS is an interactive Windows version of the BUGS program for Bayesian analysis of complex statistical models using Markov chain Monte Carlo (MCMC) techniques. The package's speed and user-friendliness implies certain limitations in modelling particularly in relation to multinomial processes. We overcame these by re-interpreting the multinomial observation model eq 27 as a sequence of nested binomial processes.

```
model{

  nN[1]<-round(n0)
  for (i in 1:tmax)
    {
    m[1,i]<-round(minit)
    w[1,i]<-round(winit)
    wd[1,i]<-round(wdinit)
    md[1,i]<-round(mdinit)
    }

  fw[1]<-fwps/(fwps+fwmu+fwpsd+fwmud+fwchi)
  fw[2]<-fwmu/(fwps+fwmu+fwpsd+fwmud+fwchi)
  fw[3]<-fwpsd/(fwps+fwmu+fwpsd+fwmud+fwchi)
  fw[4]<-fwmud/(fwps+fwmu+fwpsd+fwmud+fwchi)
  fw[5]<-fwchi/(fwps+fwmu+fwpsd+fwmud+fwchi)
  fm[1]<-fmps/(fmps+fmmu+fmpsd+fmmud+fmchi)
  fm[2]<-fmmu/(fmps+fmmu+fmpsd+fmmud+fmchi)
  fm[3]<-fmpsd/(fmps+fmmu+fmpsd+fmmud+fmchi)
  fm[4]<-fmmud/(fmps+fmmu+fmpsd+fmmud+fmchi)
  fm[5]<-fmchi/(fmps+fmmu+fmpsd+fmmud+fmchi)
  fwd[1]<-fwdps/(fwdps+fwdmu+fwdpsd+fwdmud+fwdchi)
  fwd[2]<-fwdmu/(fwdps+fwdmu+fwdpsd+fwdmud+fwdchi)
  fwd[3]<-fwdpsd/(fwdps+fwdmu+fwdpsd+fwdmud+fwdchi)
  fwd[4]<-fwdmud/(fwdps+fwdmu+fwdpsd+fwdmud+fwdchi)
  fwd[5]<-fwdchi/(fwdps+fwdmu+fwdpsd+fwdmud+fwdchi)
  fmd[1]<-fmdps/(fmdps+fmdmu+fmdpsd+fmdmud+fmdchi)
  fmd[2]<-fmdmu/(fmdps+fmdmu+fmdpsd+fmdmud+fmdchi)
  fmd[3]<-fmdpsd/(fmdps+fmdmu+fmdpsd+fmdmud+fmdchi)
  fmd[4]<-fmdmud/(fmdps+fmdmu+fmdpsd+fmdmud+fmdchi)
  fmd[5]<-fmdchi/(fmdps+fmdmu+fmdpsd+fmdmud+fmdchi)

  for (t in 1:tmax-1)
    {
    # PROCESS MODEL
    p[t] <-pmax*exp(a0 + a1 * t)/(1+exp(a0 +a1 * t))
    nnN[t]<-step(nN[t])*nN[t]
    onN[t]<-equals(nnN[t],0)*1+nnN[t]-equals(nnN[t],0)*nnN[t]
    pp[t]<-p[t]-equals(nnN[t],0)*p[t]
    n[t] ~ dbin(pp[t], onN[t])
    nN[t+1]<-nN[t]-n[t]
    w[t+1,1] <- n[t]
    m[t+1,1] <- 0

    for (i in 1:tmax-1)
        {
        # Mortality
        ci[t,i] <- cmax*exp(-ga*i) # Daily, age-specific probability of dying

        nw[t,i]<-step(w[t,i])*w[t,i]
        ow[t,i]<-equals(nw[t,i],0)*1+nw[t,i]-equals(nw[t,i],0)*nw[t,i]
        pciw[t,i]<-ci[t,i]-equals(nw[t,i],0)*ci[t,i]
        s[t,i] ~ dbin(pciw[t,i], ow[t,i])  # Number of whitecoats dying

        nm[t,i]<-step(m[t,i])*m[t,i]
        om[t,i]<-equals(nm[t,i],0)*1+nm[t,i]-equals(nm[t,i],0)*nm[t,i]
```

```
        pcim[t,i]<-ci[t,i]-equals(nm[t,i],0)*ci[t,i]
        r[t,i] ~ dbin(pcim[t,i], om[t,i]) # Number of moulters dying


        # Moulting
        b[t,i] <- bmax * exp(b0+b1*i)/(1+exp(b0+b1*i))       #Probability of moulting
        trim[t,i] <-w[t,i]-s[t,i]
        ntrim[t,i]<-step(trim[t,i])*trim[t,i]
        otrim[t,i]<-equals(ntrim[t,i],0)*1+ntrim[t,i]-equals(ntrim[t,i],0)*ntrim[t,i]
        pbw[t,i]<-b[t,i]-equals(ntrim[t,i],0)*b[t,i]
        l[t,i] ~ dbin(pbw[t,i], otrim[t,i])   # No of whitecoats moulting

        # Departure
        d[t,i] <- dmax * exp(d0+d1*i)/(1+exp(d0+d1*i)) # Probability of departing
        trid[t,i] <- m[t,i]-r[t,i]
        ntrid[t,i]<-step(trid[t,i])*trid[t,i]
        otrid[t,i]<-equals(ntrid[t,i],0)*1+ntrid[t,i]-equals(ntrid[t,i],0)*ntrid[t,i]
        pd[t,i]<-d[t,i]-equals(ntrid[t,i],0)*d[t,i]
        q[t,i] ~ dbin(pd[t,i], otrid[t,i])      # No of moulters departing

        # Loss
        nwd[t,i]<-step(wd[t,i])*wd[t,i]
        owd[t,i]<-equals(nwd[t,i],0)*1+nwd[t,i]-equals(nwd[t,i],0)*nwd[t,i]
        phwd[t,i]<-h-equals(nwd[t,i],0)*h
        v[t,i] ~ dbin(phwd[t,i], owd[t,i])

        nmd[t,i]<-step(md[t,i])*md[t,i]
        omd[t,i]<-equals(nmd[t,i],0)*1+nmd[t,i]-equals(nmd[t,i],0)*nmd[t,i]
        phmd[t,i]<-h-equals(nmd[t,i],0)*h
        u[t,i] ~ dbin(phmd[t,i], omd[t,i])



        # Update rules for process model
        w[t+1,i+1] <- w[t,i]-s[t,i]-l[t,i]
        m[t+1,i+1] <- m[t,i]+l[t,i]-r[t,i]-q[t,i]
        wd[t+1,i+1] <- wd[t,i]-v[t,i]
        md[t+1,i+1] <- md[t,i]-u[t,i]

        }

    wd[t+1,1] <- sum(s[t,1:tmax-1])
    md[t+1,1] <- sum(r[t,1:tmax-1])


    # OBSERVATION MODEL
    trw[t] <- sum(w[t,1:tmax])
    trm[t] <- sum(m[t,1:tmax])
    trwd[t] <- sum(wd[t,1:tmax])
    trmd[t] <- sum(md[t,1:tmax])

    total[t] <- trw[t]+trm[t]+trwd[t]+trmd[t]
   ototal[t]<-equals(total[t],0)*1+total[t]-equals(total[t],0)*total[t]

    f[t,1]<-(fw[1]*trw[t]+fm[1]*trm[t]+fwd[1]*trwd[t]+fmd[1]*trmd[t])/ototal[t]
    f[t,2]<-(fw[2]*trw[t]+fm[2]*trm[t]+fwd[2]*trwd[t]+fmd[2]*trmd[t])/ototal[t]
    f[t,3]<-(fw[3]*trw[t]+fm[3]*trm[t]+fwd[3]*trwd[t]+fmd[3]*trmd[t])/ototal[t]
    f[t,4]<-(fw[4]*trw[t]+fm[4]*trm[t]+fwd[4]*trwd[t]+fmd[4]*trmd[t])/ototal[t]
    f[t,5]<-(fw[5]*trw[t]+fm[5]*trm[t]+fwd[5]*trwd[t]+fmd[5]*trmd[t])/ototal[t]

    fobs[t]<- 1-fw[5]
    pfobs[t]<-fobs[t]-equals(total[t],0)*fobs[t]
    z0[t]~dbin(pfobs[t], ototal[t])                       # Number of observed pups

    denom1[t]<-f[t,1]+f[t,2]+f[t,3]+f[t,4]
    odenom1[t]<-equals(denom1[t],0)*1+denom1[t]-equals(denom1[t],0)*denom1[t]
    p1[t]<-(f[t,1]+f[t,2])/odenom1[t]
    oz0[t]<-equals(z0[t],0)*1+z0[t]-equals(z0[t],0)*z0[t]
    pp1[t]<-p1[t]-equals(z0[t],0)*p1[t]
    z1[t]~dbin(pp1[t],oz0[t])                              # Number of pups observed as alive
```

```
    denom2[t]<-f[t,1]+f[t,2]
    odenom2[t]<-equals(denom2[t],0)*1+denom2[t]-equals(denom2[t],0)*denom2[t]
    p2[t]<-f[t,1]/odenom2[t]
    oz1[t]<-equals(z1[t],0)*1+z1[t]-equals(z1[t],0)*z1[t]
    pp2[t]<-p2[t]-equals(z1[t],0)*p2[t]
    psi[t]~dbin(pp2[t],oz1[t])            # Number of pups observed as alive whitecoats

    denom3[t]<-f[t,3]+f[t,4]
    odenom3[t]<-equals(denom3[t],0)*1+denom3[t]-equals(denom3[t],0)*denom3[t]
    z2[t]<-z0[t]-z1[t]
    p3[t]<-f[t,3]/odenom3[t]
    oz2[t]<-equals(z2[t],0)*1+z2[t]-equals(z2[t],0)*z2[t]
    pp3[t]<-p3[t]-equals(z2[t],0)*p3[t]
    psid[t]~dbin(pp3[t],oz2[t])           # Number of pups observed as dead whitecoats

    }

  n0 ~ dgamma(1.44,0.003)

  a0 ~ dnorm(-16, 0.88)
  a1 ~ dnorm(4, 14.06)
  pmax ~ dbeta(39.6, 59.4)

  ga ~ dgamma(100, 10000)
  cmax ~ dbeta(4999.95,94999)

  b0 ~ dnorm(-30, 3.36)
  b1 ~ dnorm(6, 84)
  bmax ~ dbeta(9899.01,99.99)

  h ~ dbeta(9999.9,89999.1)

  d0 ~ dnorm(-30, 0.25)
  d1 ~ dnorm(4,14.1)
  dmax ~ dbeta(98.01,0.99)

  fwps~dbeta(89999.1,9999.9)
  fwmu~dbeta(2999.97,96999.)
  fwpsd~dbeta(2999.97,96999.)
  fwmud~dbeta(1999.98,97999.)
  fwchi~dbeta(1999.98,97999.)
  fmps~dbeta(29999.7,69999.3)
  fmmu~dbeta(59999.4,39999.6)
  fmpsd~dbeta(3999.96,95999.)
  fmmud~dbeta(3999.96,95999.)
  fmchi~dbeta(1999.98,97999.)
  fwdps~dbeta(19999.8,79999.2)
  fwdmu~dbeta(4999.95,94999.)
  fwdpsd~dbeta(69999.3,29999.7)
  fwdmud~dbeta(2999.97,96999.)
  fwdchi~dbeta(1999.98,97999.)
  fmdps~dbeta(19999.8,79999.2)
  fmdmu~dbeta(19999.8,79999.2)
  fmdpsd~dbeta(24999.8,74999.2)
  fmdmud~dbeta(24999.8,74999.2)
  fmdchi~dbeta(9999.9,89999.1)

  winit~dunif(0,.01)
  minit~dunif(0,.01)
  wdinit~dunif(0,.01)
  mdinit~dunif(0,.01)

  }
```

Len Thomas, Thomas van Lamsweerde and John Harwood

The nature of density dependence in British grey seal populations

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

Summary

We analysed time series of pup production estimates from 42 British grey seal colonies for evidence of density dependence. Nearly 90% of colonies showed evidence of density dependence with a 1 year time lag (likely to be caused by changes in adult survival or fecundity), whereas only 2 colonies showed evidence of density dependence with a 6 year time lag (likely to be caused by variations in first-year survival).

Introduction

In recent years, the growth rate of many grey seal colonies in Scotland has slowed considerably, suggesting that some density dependent processes are operating. The only such process that has been documented for grey seals relates to pup mortality at the Farne Islands (Harwood & Prime 1978). However, the levels of pup mortality required to explain the observed declines in growth rate are much higher than those that have recorded at any British grey seal colony (Thomas & Harwood 2003). This has led to speculation that other density dependent processes may be involved.

Fecundity and adult survival rates are notoriously difficult to estimate precisely, and it is not surprising that there is no evidence of density dependence in these demographic parameters for British grey seals. We have therefore adopted a more empirical approach to the problem by analysing the time series of pup production estimates from individual grey seal colonies, using an approach developed by Dennis and Taper (1994). The way that density dependence is formulated in this approach means that any relationships that are detected cannot be incorporated directly into process models of grey seal population dynamics. However, we believe that it is a useful diagnostic tool for identifying those density dependent processes that are likely to be most important. Density dependence in adult survival or fecundity will affect growth rate with a 1 year time lag, whereas density dependence in pup survival will affect growth rate with a time lag of approximately 6 years (the mean age at which females breed for the first time – Harwood & Prime 1978).

Material and Methods

Dennis and Taper (1994) developed a test for detecting density dependence in a time series of observations of population abundances. The null hypothesis is that the population is undergoing stochastic exponential increase, stochastic exponential decline, or a random walk. The basic model is a Ricker equation of the form:

$$N_t / N_{t-1} = \exp(\beta_0 + \beta_1 N_{t-1} + \beta_2 N_{t-6} + \sigma Z_t)$$

where N_t is pup production in year t, and σZ_t represents random variation in the population growth rate (the Z_t are independent Normal(0,1) deviates). Values of β_1 or $\beta_2 \leq 0$ are taken as evidence of density dependence.

Transforming the model to a logarithmic scale and rearranging gives the following linear relationship:

$$X_t = X_{t-1} + \beta_0 + \beta_1 \exp(X_{t-1}) + \beta_2 \exp(X_{t-6}) + \sigma Z_t$$

where $X_t = \ln(N_t)$. We fitted this relationship to data on the estimated pup production at 42 British grey seal colonies between 1984 and 2002. Data from 10 other colonies were excluded, either because of missing data points or because the colonies were first surveyed after 1984.

Simple linear regression provides unbiased estimates of the parameters of this model, but estimates of uncertainty are biased because of the non-independence of the dependent and independent variables in the regression. To overcome this, we estimated confidence limits about the parameter estimates using a parametric bootstrap. After fitting each model, we generated 2000 simulated datasets from the estimated model

$$X_t = X_{t-1} + \hat{\beta}_0 + \hat{\beta}_1 \exp(X_{t-1}) + \hat{\beta}_2 \exp(X_{t-6}) + \hat{\sigma} Z_t^{[i]}$$

where $Z_t^{[i]}$ is a pseudo random Normal(0,1) deviate generated independently for each time point t and simulation i. We then re-fit the model to each of these 2000 simulated datasets to obtain 2000 bootstrap estimates of the model parameters. To calculate 95% two-sided confidence intervals on each model parameter, we ordered the 2000 bootstrap estimates, and selected the 50th and 1951st We declared the estimate of that parameter to be statistically significant if this confidence interval did not include 0.0.

Results

Table 1 summarizes the results of the analysis. Thirty-seven of the 42 colonies showed evidence of density dependence with a 1 year time lag, whereas only two colonies showed evidence of a 6 year lag. However, 15 colonies showed evidence of a *positive* relationship between pup-productions separated by 6 years. This implies that survival of pups may be enhanced in years of high production.

Table 1. Results of time series analysis of density dependence in British grey seal colonies

Parameter β_1 (1-year lag)

	n	negative	positive	not significant
All colonies	**42**	**37**	**0**	**5**
North Sea	3	3	0	0
Inner Hebrides	9	9	0	0
Outer Hebrides	11	8	0	3
Orkney	19	17	0	2

Parameter β_2 (6-year lag)

	n	negative	positive	not significant
All colonies	**42**	**2**	**15**	**25**
North Sea	3	0	3	0
Inner Hebrides	9	1	2	6
Outer Hebrides	11	0	4	7
Orkney	19	1	6	12

Discussion

Our results suggest that the predominant form of density dependence in British grey seal populations operates with a 1 year time lag. This is most likely to be the result of changes in adult survival or fecundity. Harwood & Rohani (1996) concluded that there are few obvious sources of density-dependent adult survival. We have therefore modified the model we use to estimate grey seal population size to include density dependent fecundity as well as density dependent first-year survival.

Dennis and Taper's (1994) method assumes that there is no observation error. However, it is well known that the presence of observation error produces an inflated Type I error rate, so we expect the frequency of false positive results in Table 1 to be higher than the nominal 5% level. Shenk *et al.* (1998) performed extensive simulations to assess the effect of observation error on the performance of this and other methods. Their Figure 6 indicates that a coefficient of variation (CV) of 10% results in only a small increase in the Type I error rate, although this increases sharply at a CV of 40% and greater. Since the CV of grey seal pup production estimates is around 7% we conclude that ignoring observation error did not have a major effect on our results.

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C.D. Duck & D. Thompson

The Status of British Common Seal Populations

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

Summary

In August 2003, SMRU conducted surveys of common seals in Lincolnshire and Norfolk in England; in the Outer Hebrides, the Firth of Tay and the Moray Firth in Scotland; and for the first time, in the Republic of Ireland. All surveys were during the common seal annual moult, in August.

Counts of common seals in Lincolnshire and Norfolk were broadly similar to counts from previous recent and within 1% of the pre-epidemic counts in 1988. Counts from the Essex and Kent coast were similar to the single previous count made in 1995.

In the Moray Firth, numbers counted in 2003 were greater than in 2002, similar to 2001 but lower than in any preceding years. In the Firth of Tay, numbers were lower than in any previous counts.

The Outer Hebrides were surveyed for Scottish Natural Heritage for additional data relating to the selection of a Special Area of Conservation for common seals in the archipelago. The 2003 count of common seals was the lowest to date (of four since 1992) using a helicopter mounted thermal imager.

In the summer of 2002, a Phocine Distemper Virus (PDV)epizootic occurred, beginning, as in 1988, in Denmark and spreading across the southern North Sea to southeast England. The first British seal casualties were reported on almost exactly the same date as in 1988. Large numbers of seal carcasses were recorded around the coast of south-east England, approximately 50% more than in the 1988 epidemic. Conversely, analysis of the Wash population count data indicates that the mortality in 2002 was significantly lower than in 1988. Relatively few dead seals were reported from Scottish coasts.

Introduction

SMRU's surveys of common seals are carried out during their annual moult, in August. The Lincolnshire and Norfolk coast, which holds >95% of the English common seal population, is surveyed annually, usually twice. Surveys of the Scottish coast are undertaken on an approximately five-yearly cycle, although some areas are surveyed more frequently than this (e.g. Moray Firth and Firth of Tay).

Surveys are carried out during the 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 therefore not counted. Thus the numbers presented here represent the minimum number of common seals in each area and are used as an index of population size.

In the summer of 2002, a Phocine Distemper Virus epizootic occurred, beginning, as in 1988, in Denmark and spreading across the southern North Sea to southeast England. The first British seal casualties were reported on almost exactly the same date as in 1988. Large numbers of seal carcasses were recorded around the coast of south-east England, approximately 50% more than in the 1988 epidemic. Relatively few dead seals were reported from Scottish coasts.

Methods

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

We intended to survey the Moray Firth and the Firth of Tay on successive days for a 5 to 7 day period to determine the variation in numbers of seals hauled ashore. Unfortunately, we could not carry out any repeat surveys due to persistent sea fog settling in the Firths. These repeat surveys will be attempted next August. For logistic expediency, the Moray Forth was surveyed by helicopter using the thermal imaging camera while the Firth of Tay was surveyed by fixed-wing aircraft. On account of the very low cloud base, oblique photographs were obtained using a hand-held camera.

Results

Common seals in eastern England

In 1988, the numbers of common seals in The Wash declined by approximately 50% as a result of the phocine distemper virus (PDV) epidemic. Prior to this, numbers had been increasing. Following the epidemic, from 1989, the area has been surveyed once or twice annually in the first half of August each year (Figure 1, Table 1).

Two aerial surveys of common seals were carried out in Lincolnshire and Norfolk during August 2003 (Table 1). Bad weather prevented surveying at Donna Nook on the first flight and human disturbance prevented counting at Blakeney Point on the second flight.

The mean count for The Wash (2,513) was 16% lower than the 2001 count (2,976). We developed two population growth models that explicitly modelled variability in both observation and population growth processes (Thompson, Duck & Lonergan (submitted). We were able to show that uncertainty in proportion of animals observed dominates in this system, allowing growth rates within each period to be treated as constant. The two population trajectory models produced encouragingly similar results. The population was increasing at a little over 3% pa until 1988 (95% CI: 2.1-4.1(state space model (SSM)), 2.5-4.5 (GLM)) (Figure 1). The 1988 count was obtained approximately one week before the first reports of sick and dead seals being washed up on the UK coast. The number hauling out fell by approximately 50% between 1988 and 1989 (95% CI: 44-59(SSM), 48-62(GLM)), coincident with the PDV epidemic. After 1989 the number increased again, at almost 6% pa (95% CI: 4.8-6.7(SSM), 5.1-6.8(GLM)). The post epidemic rate of increase was significantly higher than the pre epidemic rate ($p<0.001$, pair-wise comparison of parameter estimates). The population was affected by a recurrence of the PDV epidemic in August 2002. The first indications of morbidity due to the epidemic were reported in early August, shortly after the 2002 survey. The dates of the surveys and the disease outbreak in 2002 were almost exactly the same as in 1988. However mortality was lower than in 1988, at around 22% (95% CI: 9-33(SSM), 11-33(GLM)).

As the time series of counts at both Blakeney and Donna Nook are sparse in comparison to the Wash they have not been subjected to the same analysis. However, counts at both sites decreased between 2002 and 2003. The single count at Blakeney in 2003 was 37% lower than the higher count in 2002. The single count at Donna Nook in 2003 was 32% lower than in 2002 (Table 1). These declines are in contrast to the average annual rates of increase at these sites since 1989 of 12.5% (SE=2.7%) and 19.4% (SE=3.9% respectively. In both cases the counts may have been reduced by human disturbance prior to the survey flights.

Overall, the English East coast population appears to have increased at an average annual rate of 7.2% (SE=0.49%) between 1989 and 2002 and decreased by approximately 22% between 2002 and 2003.

Common seals in Scotland

In August 2003, areas surveyed for common seals included the Inner Moray Firth, the Firth of Tay and the Outer Hebrides. The Outer Hebrides were surveyed for Scottish Natural Heritage (SNH) to provide additional information on areas potentially selected for designation as Special Areas of Conservation for harbour seals under the European Union's Habitat's Directive. The Firth of Tay and the Moray Firth were surveyed for DEFRA to provide a comparison with the 2002 surveys, to determine the extent of the effect of the 2002 PDV epizootic which primarily affected colonies in the southern North Sea.

Moray Firth

SMRU's aerial surveys of this area began in August 1992 and counts are in Table 2. The 2003 count for the Inner Moray Firth was greater than in 2002 but lower than in previous years. Following a period when a bounty system for seals was in operation in the Moray Firth, the 2002 count was the lowest in our time series. In contrast, numbers of seals at haulout sites adjacent to the Inner Moray Firth (at Findhorn and on the coast from Dornoch to Dunbeath) appear to have increased. Paul Thompson, from Aberdeen University's Lighthouse Field Station, in Cromarty, has more detailed annual counts of common seals in the Inner Moray Firth in the summer months since 1988.

Tay Estuary

The 2003 harbour seal count for the Firth of Tay was the lowest in the time series (Table 3). The biggest changes were in the Eden Estuary and at Abertay and Tentsmuir. Although both of these locations are susceptible to disturbance by trippers walking on the beach, there was no obvious evidence of any recent disturbance (i.e. there were no obvious traces of seals having been hauled ashore at frequently used haulout sites, or of human footprints going to and from these locations). The count at Buddon Ness, a haulout site within a military firing range and therefore less accessible to general public, was greater than in previous years, adding to the suspicion that seals had been disturbed sometime prior to the survey.

SMRU's aerial surveys of common seals in the Firth of Tay began in August 1990. Prior to 2003, numbers overall have remained relatively constant although the location of seals within the Firth has changed with increased use of the Eden Estuary at the expense of the Tentsmuir Sands (Table 3). The 2003 count was lower than in previous years.

Outer Hebrides

The total harbour seal count for the Outer Hebrides was the lowest of the four surveys completed since 1992 (Table 4). The count for the proposed Special Area of Conservation in the Sound of Barra declined below 100 for the first time and was less than 12% of the first count in 1992. The number of harbour seals in the Sound of Harris, on the other hand, was slightly greater than in 2002. The 2003 survey of the Outer Hebrides was funded by Scottish Natural Heritage.

Table 1. Numbers of commons seals counted on the east coast of England since 1988. Data are from fixed-wing aerial surveys carried out during the August moult.

Date of survey	13.8.88	8.8.89 12.8.89	11.8. 1990	2.8.91 11.8.91	1.8.92 16.8.92	8.8. 1993	6.8.94 12.8.94	5.8.95 15.8.95	2.8. 1996	2.8.97 8.8.97	7.8.98 14.8.98	3.8.99 13.8.99	4.8. 00 12.8.00	4.8. 2001	11.8.02 12.8.02	
Blakeney Point	701	- 307	73	- -	- 217	267	- 196	438 392	372	250 371	535 738	715 602	895 dist.	772	346 631	 399
The Wash	3087	1531 1580	1532	1226 1551	1724 1618	1759	2277 1745	2266 1902	2151	2561 2360	*2367 2381	2320 2474	2528 3029	3194	3037 2916	2529 2497
Donna Nook	173	- 126	57	- -	18 -	88	60 146	115 36	162	240 262	294 201	321 286	435 345	233	341 -	231
Scroby Sands	-	- -	-	- -	- -	-	61 -	- 49	51	58 72	52 -	69 74	84 9	75		
The Tees	-	- -	-	- -	- -	-	- 35	- -	-	- -	- -	- -	- -	-	-	
Holy Island, Northumberland	-	- -	-	- -	- -	-	- 13	- -	-	- 12	- -	- -	- 10	-	-	
Essex, Suffolk & Kent	-	- -	-	- -	- -	-	- -	90 -	-	- -	- -	- -	- -	-	- 72	 190

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

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

Location	07/08/92	30/7/93	13/8/94	15/8/97	11/8/00	11/8/02	7/8/03
Ardersier	154		221	234	191	110	205
Beauly Firth	220		203	219	204	66	151
Cromarty Firth	41		95	95	38	42	113
Dornoch Firth (pSAC)	662		542	593	405	220	290
Inner Moray Firth Total	**1077**		**1061**	**1141**	**838**	**438**	**759**
Findhorn			*58*	*46*	*111*	*144*	*167*
Dornoch to Loch Fleet		*16*		*27*	*33*	*62*	*56*
Loch Fleet to Dunbeath		*92*		*214*		*145*	
Moray Firth Total (including Loch Fleet to Dunbeath)	**1185***		**1227***	**1428**	**982**	**789**	**982**
Moray Firth Total (excluding Loch Fleet to Dunbeath)	**1185***		**1227***	**1214**	**982**	**644**	**982**

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

Table 3 . Numbers of common seals in the Firth of Tay.

Location	13/8/90	11/8/91	07/08/92	13/8/94	13/8/97	12/8/00	11/8/02	7/8/2003
Eden Estuary	31	0	0	80	223	267	341	93
Abertay & Tentsmuir	409	428	456	289	262	153	167	53
Upper Tay	27	73	148	89	113	115	51	83
Broughty Ferry		83	97	64	35	52		90
Buddon Ness		86	72	53	0	113	109	142
Firth of Tay Total	**467**	**670**	**773**	**575**	**633**	**700**	**668**	**461***

* 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. Numbers of harbour seals in the Sound of Barra, Sound of Harris and in the Outer Hebrides.

Location	Aug 1992	July 1996* Adults	Aug 1996	July 2000* Adults	Aug 2000	Aug 2002	Aug 2003
Sound of Barra, pSAC	762	287	510	94	140	127	89
Sound of Barra, remainder	123	45	97	43	169	156	127
Sound of Barra, Total	**885**	**332**	**607**	**137**	**309**	**283**	**216**
Sound of Harris	375	107	471	184	323	180	242
Outer Hebrides, Total	**2,329**		**2,820**		**2,413**		**2,098**

*Breeding season surveys, remainder during August moult.

Surveys in July 1996, July and August 2000 and August 2002 and 2003 were funded by Scottish Natural Heritage.

Table 5. Numbers of common and grey seals in counties in the Republic of Ireland in August 2003.

Date (in 2003)	County	Harbour seals	Grey seals
12-13 Aug	Donegal	555	215
13 Aug	Leitrim	0	0
13 Aug	Sligo	376	129
13-14 Aug	Mayo	316	275
14-16 Aug	Galway	484	79
16 Aug	Clare	164	24
16-17 Aug	Limerick	0	0
17-18 Aug	Kerry	430	55
18-19 Aug	Cork	489	81
19 Aug	Waterford	1	0
19 Aug	Kilkenny	0	0
19 Aug	Wexford	17	193
19 Aug	Wicklow	0	8
20 Aug	Dublin	34	211
20 Aug	Meath	0	0
20 Aug	Louth	39	17
Total, Republic of Ireland		**2,905**	**1,287**

Common seals in the Republic of Ireland

The National Parks and Wildlife Service, Department of the Environment, Heritage and Local Government of the Republic of Ireland commissioned a survey of harbour seals in August 2004. The survey was organised and carried out by the Coastal and Marine Resource Centre, University College, Cork and the Sea Mammal Research Unit, University of St Andrews. This was the first complete survey of harbour seals in the Republic. The previous most recent and most complete survey was in 1978 (Summers *et al*., 1980). The survey was completed in 9 days, one day less than anticipated. A total of 2,905 harbour seals were counted (Cronin *et al*., 2004). A breakdown of this total, by county, is in Table 5.

Minimum estimate of the size of the British common seal population

The most recent minimum estimate of the number of common seals in Scotland is 29,579 from surveys carried out in 1996, 1997, 2000, 2001, 2002 and 2003. The most recent minimum estimate for England is 3,463. This comprises 2,987 seals in Lincolnshire and Norfolk in 2003 plus 225 seals in Northumberland, Cleveland, Essex and Kent between 1994 and 2003 and an estimated 20 seals from the south and west coasts.

Table 6 contains counts by region for the period 1996-2003. These are presented as the most recent counts available for each region. Where multiple counts were obtained in any August (in The Wash, for example), the mean values have been used. Table 6 includes numbers from Ireland, both the North and the Republic. The distribution of harbour seals in Great Britain and Ireland is shown in Figure 2. Data have been aggregated into 10km squares.

Common seal surveys proposed for 2004 and 2005

In August 2004 we intend to carry out a series of repeat surveys over the same stretch of coastline on five consecutive days (weather and other circumstances permitting). This trial will incorporate both the fixed-wing vertical photography and the helicopter mounted thermal imagery. Fixed-wing suvey sites will be the Firth of Tay and the Moray Firth (as planned for 2003) whil ehte helicopter sites will be based around the pSAC in north-west Skye.

In August 2005 we propose to start a new Scottish-wide survey of harbour seals. Due to financial limitations, we were unable to complete the survey of the Scottish coast which started in 2000. The areas not surveyed included the far north and west coasts, from Helmsdale to Loch Torridon, the Small Isles and the south-west coast from Macrihanish to Carlisle. Depending on available funds we will endeavour to survey these areas first, with the Northern Isles and possibly including parts of the east coast (e.g. the Firth of Forth and the south coast of the Outer Moray Firth). The areas surveyed in 2000 (Loch Torridon to Macrihanish) and the Outer Hebrides will be surveyed the following year.

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Table 6. Minimum estimates of the UK common seal population by region. Figures in bold type have been updated with data from surveys carried out in 2003.

Region	Year of survey	1996-2003
Shetland	2001	4,883
Orkney	2001	7,752
Outer Hebrides	2003	**2,098**
Highland East & North (Nairn to Cape Wrath)	1997, 2003	**1,225**
Highland West (Cape Wrath to Appin, Loch Linnhe)	1996, 1997, 2000	4,947
Strathclyde West (Appin to Mull of Kintyre)	2000	6,918
Strathclyde, Firth of Clyde (Mull of Kintyre to Loch Ryan)	1996	991
Dumfries & Galloway (Loch Ryan to English Border at Carlisle)	1996	6
Grampian (Montrose to Nairn)	1997, 2003	**182**
Tayside (Newburgh to Montrose)	1997, 2003	**232**
Fife (Kincardine Bridge to Newburgh)	1997, 2003	**305**
Lothian (Torness Power Station to Kincardine Bridge)	1997	40
Borders (Berwick upon Tweed to Torness Power Station)	1997	0
TOTAL SCOTLAND		**29,579**
Blakeney Point	2003	**399**
The Wash	2003	**2,513**
Donna Nook	2003	**231**
Scroby Sands	2001	75
Other east coast sites	1994, 2000, 2003	**225**
South and west England (estimated)		20
TOTAL ENGLAND		**3,463**
TOTAL BRITAIN		**33,042**
TOTAL NORTHERN IRELAND	2002	**1,248**
TOTAL BRITAIN & N. IRELAND		**34,290**
TOTAL REPUBLIC OF IRELAND	2003	**2,905**
TOTAL FOR GREAT BRITAIN AND IRELAND		**37,195**

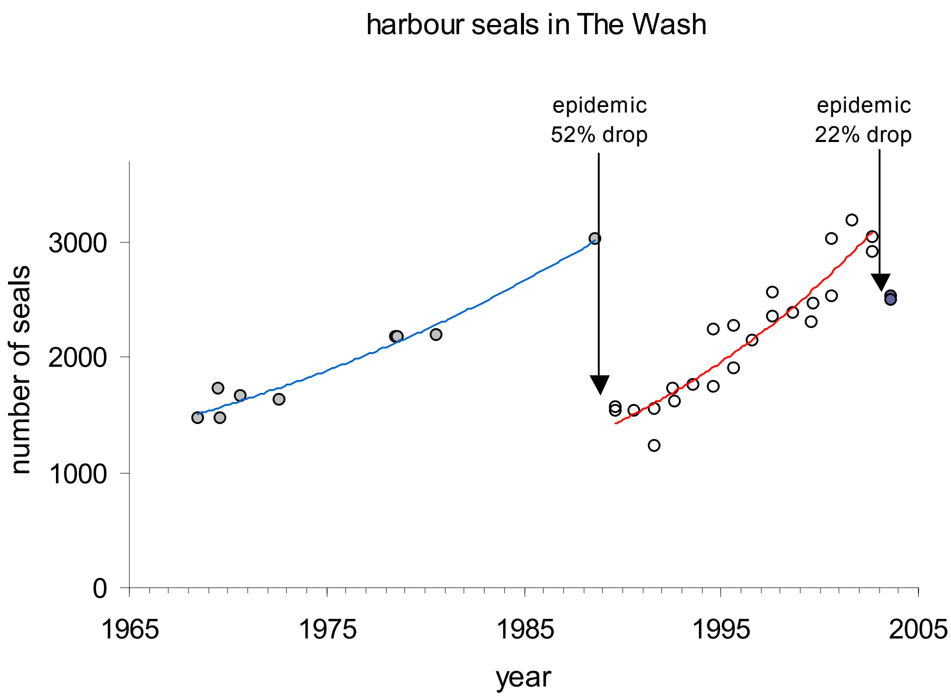
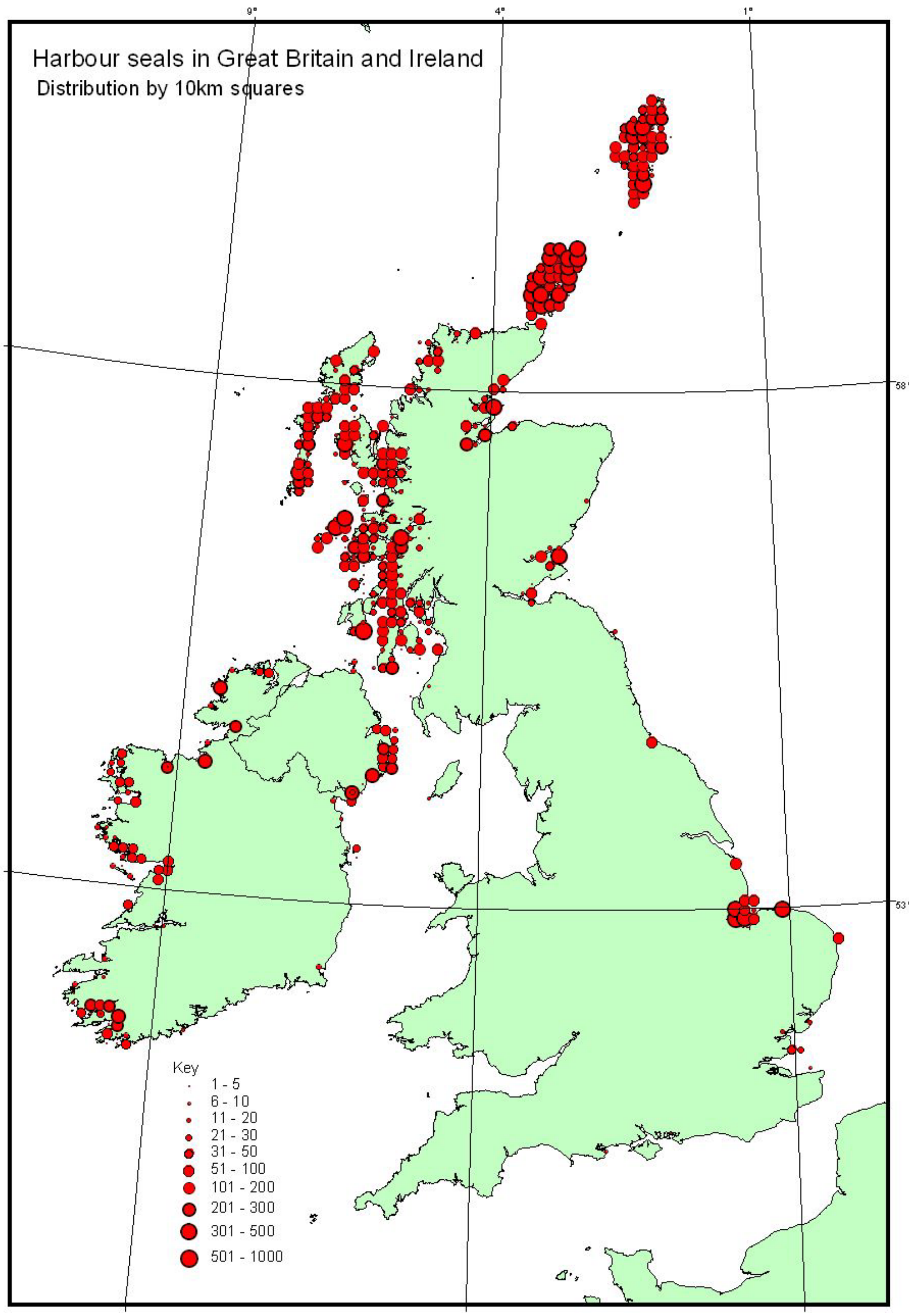


Figure 1. Counts of common seals in The Wash in August. These data are an index of the population size through time. Fitted lines are exponential growth curves (growth rates given in text). Growth rate was significantly higher after the 1988 epidemic and the estimated mortality was significantly lower in 2002 than in 1988.

Figure 2 The August distribution of harbour seals in Great Britain and Ireland, by 10km squares. These data are from surveys carried out between 1996 and 2003.



Len Thomas and John Harwood

A comparison of grey seal population models incorporating density dependent pup survival and fecundity

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

Summary

We fitted state-space models for density dependent pup survival and density dependent fecundity to regional estimates of British grey seal pup production. The results provide inconclusive evidence for one model over the other, but this could be because of limitations in the fitting algorithm used. Nevertheless, the results illustrate the very large difference in estimated total population size in 2003 under the two models: 96,000 under the density dependent pup survival model and 394,000 under the density dependent fecundity model.

Introduction

In this paper, we compare two spatially-explicit, stochastic models for density dependent population regulation in British grey seals. In the first, the density dependent parameter is first-year survival, while in the second it is fecundity. Our models are fit to the 1984-2003 annual pup production data at the level of region (North Sea, Inner Hebrides, Outer Hebrides and Orkney). Both models also include fitness-dependent movement of recruiting females between regions. The fitting algorithm is a modification of the computer-intensive Bayesian procedure presented at the last SCOS meeting (Thomas and Harwood 2003).

Our primary goals are: (1) to determine whether the pup production data alone provide evidence for one model over the other, and (2) to quantify differences in estimated total seal numbers under the two models. An alternative approach to question (1) using auto-regression (Thomas et al. 2004) found that the annual rate of change in pup production was negatively affected by pup production in the previous year, as would be predicted if density dependent fecundity were the dominant mechanism.

Materials and Methods

Models

The density dependent survival (DDS) model is identical to that presented in Thomas and Harwood (2003), and the density dependent fecundity (DDF) model is a small modification of it. Both models are formulated as state-space models (Buckland *et al.* 2004). In essence, this means that they are composed of a state process, which models the true but unknown state of the population (i.e., the number of animals in each age group and region in each time period), and an observation process, which models how the survey data are generated given the true states.

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

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

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

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

where $n_{0,r,t-1}$ is the number of pups born in region *r* in year *t*-1, $\phi_{p,r,t}$ is survival rate of these pups, $\phi_{p\max}$ is maximum pup survival rate, and $1/\beta_r$ reflects the carrying capacity of the region. For the DDF model, we assume pup survival is constant across regions and times, i.e., $\phi_{p,r,t} = \phi_p$.

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

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

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

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

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

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

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

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

while for the DDF model,

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

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

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

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

This implies that the probability of a female breeding in a particular year is influenced by the conditions during the previous breeding season.

For the observation process, we assume that pup production estimates follow a normal distribution with a constant coefficient of variation (CV) which we assume to be a known value.

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

Data and Priors

Our input data were the pup production estimates for 1984-2003 from Duck (2004), aggregated into regions. Some new colonies have been added to the regional totals, as described by Duck (2004). These made only minor differences to the estimates of pup production for the years 1984-2002, compared with the data used in Thomas and Harwood (2003).

We also included the Helmsdale colony in the North Sea region. This colony was previously excluded from the analysis, but the 2003 pup production estimate of 947 was too big to ignore. Helmsdale is not surveyed every year, so we estimated production for missing years by fitting a loess smooth (function `loess` in SPlus, with span set to 0.75) to the years where data were available and predicting the missing values.

Prior distributions for each parameter are given in Table 1, and are shown on Figures 3 and 4. Prior distributions for the states were generated using the priors for the parameters in conjunction with the 1984 data, as described by Thomas *et al.* (in press). We then fit the models to the data for 1985-2003.

Table 1. Prior parameter distributions

Parameter	Prior	Expected value
ϕ_a	Beta(22.05,1.15)	0.95
$\phi_{p\max}$, ϕ_p	Beta(14.53,6.23)	0.7
β_1	Gamma(4,2.07x10^{-4})	8.29x10^{-4}
β_2	Gamma(4, 2.96x10^{-4})	1.18x10^{-3}
β_3	Gamma(4,7.40x10^{-5})	2.96x10^{-4}
β_4	Gamma(4,5.76x10^{-5})	2.30x10^{-4}
γ_{sf}	Gamma(2.25,1.33)	3
γ_{dd}	Gamma(2.25,0.49)	ln(3)
γ_{dist}	Gamma(2.25,0.22)	0.5
α , $\alpha_{\max}$	Beta(22.05,1.15)	0.95

Fitting Method

We used a modified version of the particle filtering algorithm that was outlined in Thomas and Harwood (2003) and described in detail in Thomas et al. (in press). The algorithm (which is also called sequential importance sampling or SIS) is a computer-intensive method for estimating the posterior distribution of the parameters and states of a state-space model. It is well suited to the analysis of time series data, as data point are introduced one at a time into the algorithm, making it potentially more efficient than other computer-intensive techniques such as Markov chain Monte Carlo (MCMC). Particle filtering methods were first developed for engineering applications and have only recently been applied to biological problems. Consequently, much methodological work is still required.

Our alterations to the 2003 algorithm were designed to address two issues: (1) high Monte Carlo variation in results (i.e., differences in estimates of parameters and states between multiple runs using different random number seeds) caused by particle depletion (see Thomas and Harwood 2003); (2) possible biases in estimated state values caused by kernel smoothing at each time period. The new algorithm is simple and reliable but inefficient, because a large amount of computer time is required to produce reliable estimates.

We start by defining prior distributions on the parameters and the states (i.e., the numbers of seals in each region and age class before the first time period). We simulate a a large number parameter and state vectors from these priors. Each pair of parameter and state vectors is called a 'particle'.

We stochastically project each particle forward to the first time period using the state process (i.e., our model of the population dynamics), and calculate the likelihood of the simulated pup production generated for each particle, given the observed pup production in the first year and the observation model. These likelihoods form weights for each particle. Many of these weights are very small, indicating that the starting state and parameter combinations are unfeasible, given the observed pup production in the first year. To avoid wasting computer memory and time on these very unlikely particles, we implement rejection control (Lui 2001), which probabalistically discards particles below a critical value (in our case we used the mean of the particle weights), and reweights the remaining particles so that they estimate the same distribution as before the rejection control step. This reduced set of particles is then projected forwards to the end of the time series, and the weights re-calculated given the likelihood of the pup production estimates for the second and subsequent years of data. Many of these weights will be very small, so we again implement rejection control to reduce the number of particles that need to be stored. The distribution of particles at the end is a weighted estimate of the posterior distribution of the parameters and states.

We can calculate the effective sample size of the remaining particles as

$$\mathrm{ESS} = \frac{N_T}{1+\left[\mathrm{CV}(w)\right]^2}$$

where N_T is the number of particles after rejection control and CV(w) is the coefficient of variation of the weights of these particles. We have found that for these models, reliable inferences require an ESS of around 1000. This is rarely achieved in one run of the above algorithm, but there is no problem in adding to the final particle numbers by making multiple runs, so long as the same critical values are used for rejection control in all runs (i.e., the mean particle weights from the first run). In the results reported here, we used 50 runs each starting with 100,000 particles, giving an ESS of 893 for the DDS model and 914 for the DDF model. The observation CV was fixed to a relatively high value (25%) to avoid a prohibitively large number of runs

Model outputs and comparison

For both models, we present posterior estimates of the model parameters and estimated pup production from 1984-2003. The models also estimate adult female numbers, but do not include adult males. We therefore calculated total pre-breeding population sizes by assuming that the number of adult males is

73% of the number of adult females (Hiby and Duck, unpublished).

To compare the models, we calculated the mean posterior Akaike Information Criterion (MPAIC) using the same method as Thomas and Harwood (2003). Since the two models have the same number of parameters, the ranking according to this criterion will be the same as that using the mean posterior likelihood.

Results

Posterior estimates of true pup production for the two models are shown in Figures 1 and 2 (these estimates are known technically as smoothed estimates; see Thomas *et al.* in press). The estimates are very similar, although the DDS model is a slightly better fit (Table 2). There is some evidence of poor choice of prior for the Outer Hebrides region in the DDF model, causing some initial oscillations in pup production numbers (see Discussion). Neither model does a good job of tracking the rapid increase in pup production in the Inner and Outer Hebrides in the late 1980s and early 1990s, and the subsiquent stabilization in pup numbers in both regions. In this sense, neither model can be said to fit the data well.

Although the models produce almost identical estimates of pup production, they give substantially different estimates of total pre-breeding population size, with the estimates from the DDF model being four times higher than those from the DDS model (Table 3).

Table 2. Mean posterior log-likelihood, AIC and Akaike weights

Model	LnL	AIC	Akaike weight
DDS	-658.8	1337.5	0.68
DDF	-659.4	1339.0	0.32

Table 3. Estimated size, in thousands, of the British grey seal population at the start of the 2003 breeding season, from density dependent survival (DDS) and fecundity (DDF) models. Numbers are posterior means with 95% confidence limits in brackets.

Region	DDS	DDF
North sea	11.7 (9.6-14.7)	46.6 (33.1-61.8)
Inner Hebrides	8.3 (6.8-10.2)	37.5 (25.7-49.3)
Outer Hebrides	31.4 (25.2-39.3)	152.0 (102.4-209.4)
Orkney	44.9 (25.5-56.6)	157.4 (113.1-209.7)
Total	96.2 (77.1-120.8)	393.6 (274.4-530.2)

Posterior parameter estimates for the models are given in Figures 3 and 4. Adult survival (ϕ_a) is estimated to be 0.98 for the DDS model and 0.99 for the DDF model, rather higher than the prior of 0.95 . The juvenile survival and fecundity parameters (ϕ_j and α) are almost unchanged relative to the prior in both models. Similarly, the movement parameters (γ s) are little changed. Posterior distributions of the density dependence parameters (β s) are slightly tighter than the priors, and are similar between models.

Discussion

For the runs reported here, we fixed the CV of the pup production estimates at 25%. This value is much higher than that estimated by Hiby and Duck (unpublished) of 7% at the colony level, and less for regional aggregations. The effect of using a higher CV is to reduce the influence of the data on the posterior states and parameter, relative to the priors. We therefore regard our results as preliminary, pending improvements in the fitting algorithm.

We are actively working on improving the fitting methods. The current algorithm is simple (and therefore reliable) but inefficient. The relatively high CV set on pup production produces a relatively flat likelihood surface and this results in relatively little particle depletion. The current algorithm ran for 17 hours on our machine; if the CV had been set at 10%, it would have required approximately two weeks to achieve the same precision. We expect to be able to improve efficiency, while at the same time maintaining reliability, using tools such as auxiliary particle filtering, simulated annealing and tempering, and limited kernel smoothing (Doucet *et al.* 2001, Lui 2001, Newman *et al.* in press, Thomas *et al.* in press). We are also working with K. Newman and C. Fernandez on an MCMC implementation of the DDS model, which we hope to compare with the particle filtering algorithm.

One other caveat regarding our results is the oscillations in estimated pup production in the Outer Hebrides under the DDF model. We suspect this is due to the way we set priors on initial states for this model, and plan to investigate this further.

The populations estimates from the DDS model are comparable to those produced last year (Thomas & Harwood 2003). However, those from the DDF model are very much higher because of the low levels of fecundity that are predicted in the final years of the time series. It seems clear that these models cannot be distinguished using time series of pup production estimates aggregated at a regional level.

Neither model provides a particularly convincing fit to the time series of pup production, and they predict levels of survival or fecundity that are very much lower than those that have been observed at individual grey seal colonies. The poor fit may be a result of the specific functional form used to model density dependence in both models. In the case of the DDS model it is based on empirical observations. However, there are no data that can be used to specify alternate forms for the DDF model. In addition, we show elsewhere (Thomas and Harwood 2004) that the observed changes in pup production could also be a consequence of an increase in the numbers of seals being killed to protect salmon farms. However, the numbers that would be required seem unfeasibly high. Until these inconsistencies have been resolved, there will remain considerable uncertainty about the current size of the British grey seal population.

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Figure 1. Estimates of pup production from the density dependent survival model (DDS). Input data are shown as circles, while the lines show the weighted mean of the particle values, bracketed by 2.5th and 97.5th percentiles.

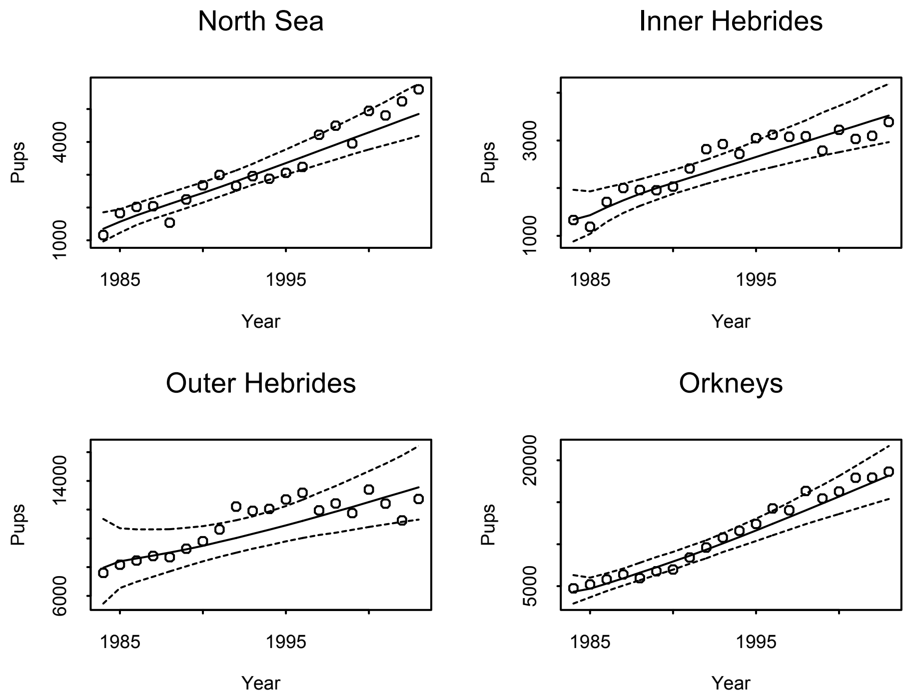


Figure 2. Estimates of pup production from the density dependent fecundity model (DDF).

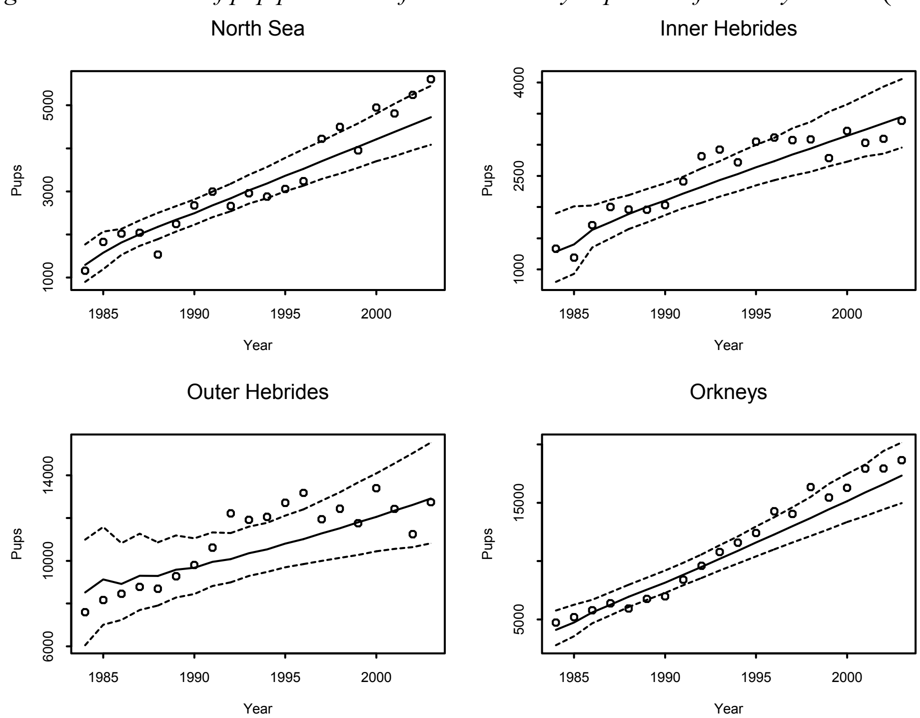


Figure 3. Posterior parameter estimates (histograms) and priors (solid lines) from the density dependent survival model (DDS). The vertical line shows the posterior mean, its value is given in the title of each plot after the parameter name.

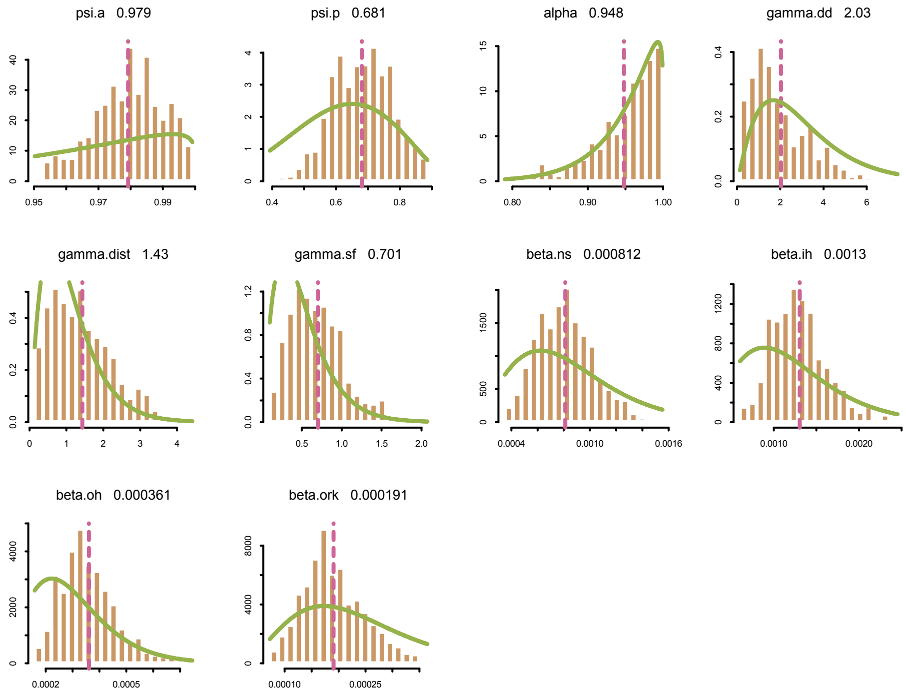
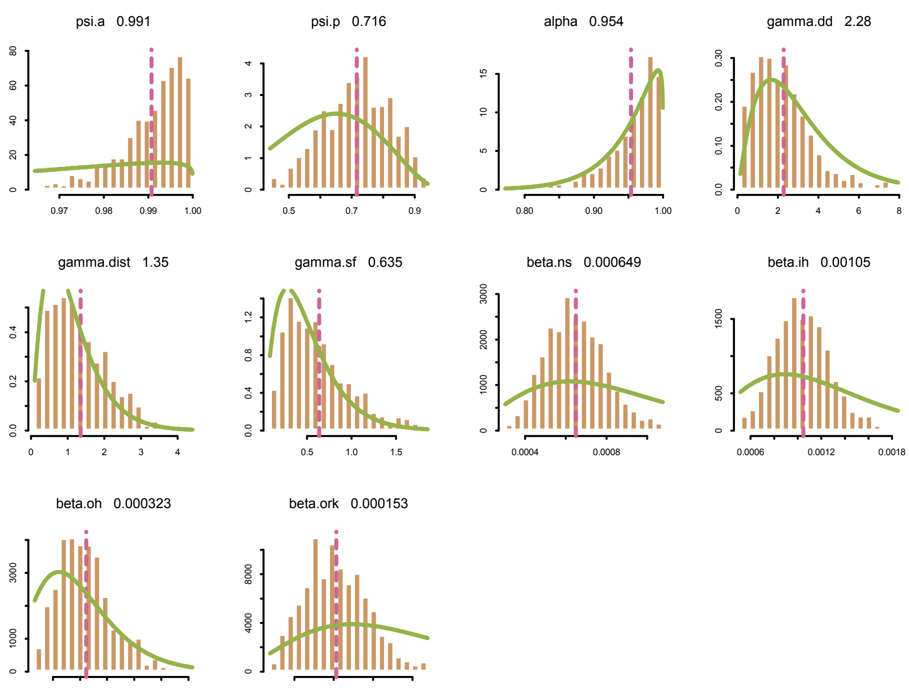


Figure 4. Posterior parameter estimates (histograms) and priors (solid lines) from the density dependent fecundity model (DDF).



Len Thomas and John Harwood

Possible impacts on the British grey seal population of deliberate killing related to salmon farming

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

We develop a stochastic population dynamics model of the British grey seal population in which the population naturally grows at an exponential rate. We used this to test the hypothesis that there is additional mortality associated with the protection of salmon farms. We used two indices of salmon farming intensity to estimate this additional mortality and fitted the resulting models to the observed 1984-2002 pup production data at a regional level.

The best fitting model relates seal mortality to salmon production in tonnes. Estimated anthropogenic mortality rates in recent years are highest in the Outer Hebrides (~6%, 95% CI ~2-11%), lower in the Inner Hebrides (~3%, 95%CI ~1-4%) and very low in the Orkneys (<1%, 95% CI 0-1%). These fits require that up to 4000 seals were shot each year in the Outer Hebrides, up to 570 in the Inner Hebrides, and up to 660 in Orkney. Re-running the model with known mortalitites in the Moray Firth included made little difference to the results.

We conclude that salmon farming activity alone can explain the observed pattern of pup production. However, the levels of unreported mortality required in the Outer Hebrides appear unfeasibly high.

Introduction

The aim of this paper is to determine whether the observed pattern of grey seal pup production at a regional level could be explained by deliberate killing of seals to protect salmon farms, and to estimate how many seals would have been killed if this was the case. We used a modified version of the stochastic population dynamics model used to estimate grey seal population size (Thomas and Harwood 2004) in which we assume that seal survival and fecundity are density independent. Survival rates of both pups and adults are reduced in proportion to two alternative indices of farming activity: annual salmon production in tonnes and total staff numbers. In addition, we consider a model in which the effect of a unit change in farming activity is assumed to be the same in all regions, and one in which the effect is different for each region. Finally, there are two different ways in which data on salmon farming can be related spatially to grey seal populations. In total, therefore, there are eight different combinations of data and model. We fitted these to regional pup production data for 1984-2002 using the particle filtering algorithm described in Thomas and Harwood (2004). Model fits were compared using mean posterior Akaike Information Criterion (MPAIC; see Thomas and Harwood 2003). Using the best model, we translate the mortality estimate into an estimate of the number of seals killed.

Data on salmon farming activity in the North Sea was not available separately from that on the west coast, so it was not possible to incorporate this in the model. However, data on actual estimates of the actual number of seals shot in the Moray Firth were available and we investigated the effects of incorporating this information in the model.

Material and Methods

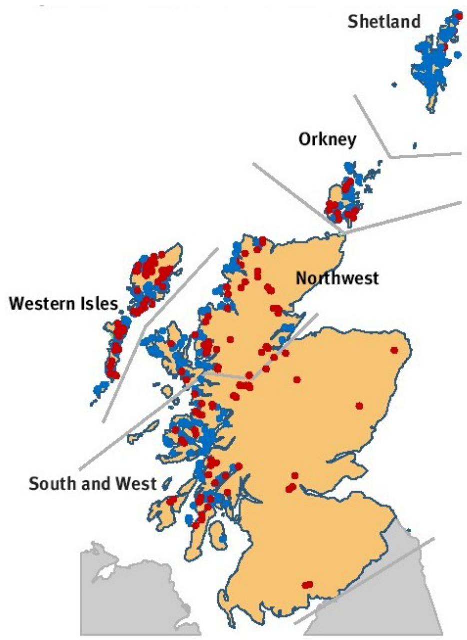
Data

We used pup production estimates for 1984-2002 (Duck 2003), aggregated at a regional level (North Sea, Inner Hebrides, Outer Hebrides and Orkney).

Salmon farming data by region are given in Stagg and Smith (2003) for 1994-2002 and Stagg and Gauld (1998) 1992-1994. Data for 1984-1992 are not available by region, but were provided at the national level by R.M. Smith (Fisheries Reserch Services Marine Lab, Aberdeen, pers. comm.). To estimate regional numbers, we calculated the proportion of the annual national salmon production and staff numbers in each region for 1992-1994, and pro-rated the 1984-1992 totals according to these proportions.

The regions used to summarise salmon production (Figure 1) do not coincide exactly with those used to designate grey seal colonies. The Orkney and Western Isles salmon regions are equivalent to the Orkney and Outer Hebrides seal regions, and the South and West salmon region is essentially equivalent to the Inner Hebrides seal region. However, seals from the Outer Hebrides are known to frequent the north west coast of the mainland, so we fitted one set of models in which Outer Hebrides seals were only affected by activity in the Western Isles salmon region, and another set in which they were affected by the Western Isles and the Northwest salmon regions combined.

Figure 1. Salmon production regions and locations of active smolt sites (in red, not used in analysis) and salmon sites (in blue). Figure courtesy of Fisheries Research Services.



The Northwest salmon region contains a majority of farms on the west coast, but it also contains three in the Moray Firth. The latter area is part of the North Sea seal region. Farming activity data for these three farms are not available separately, and we initially assumed that no North Sea seals were shot by salmon farmers. However, Butler (2004) has estimated the numbers of grey, common and unknown species of seal killed in the Moray Firth area for the period 1994-2002. We assumed that the proportion of the unknown seals that were grey seals was equal to the proportion of known seals that were grey seals. This produced the data in Table 1. These data were not used in the initial model runs, but the best-fitting model was re-run with these numbers as a form of sensitivity analysis.

Table 1. Estimated number of seals killed in Moray Firth 1994-2002.

Year	1994	1995	1996	1997	1998
Grey seals	136	132	132	128	137
Year	1999	2000	2001	2002	
Grey seals	192	181	234	110	

Models
We used a set of state-space models similar to the density independent model described by Thomas and Harwood (2004, model M_2). This assumes constant natural adult survival ϕ_a, pup survival ϕ_p and fecundity α. Without density dependence, there is no movement of recruiting females among regions. Additionally, we assumed that the anthropogenic rate of mortality is additive to natural mortality, that it is linearly related to salmon farming activity, and that it is the same for adults and pups. The number of adult seals surviving in a given year, *t*, is a binomial random variable with probabiltiy $\phi_a - \delta_r s_{r,t}$ where $s_{r,t}$ is the level of salmon farming activity (production or staff) in region *r* at time *t*, and δ_r is a model parameter equivalent to the level of additional seal mortality per unit of farming activity. Similarly, pup survival is a binomial random variable with probability $\phi_p - \delta_r s_{r,t}$.

We ran two different models. In the full model, we allowed the effect of a unit change in farming activity, δ_r, to vary by region. This model has 6 parameters: $\phi_a, \phi_p, \alpha, \delta_2, \delta_3$ and δ_4. Note that δ_1 cannot be estimated because we assume no farming activity in the North Sea region. We also ran a reduced model in which we assumed that effect of a unit change in farming activity was the same for all regions, i.e., $\delta_r = \delta$. This model has 4 parameters: ϕ_a, ϕ_p, α and δ.

Fitting method and priors
We used the algorithm described by Thomas and Harwood (2004), with measurement error CV fixed at 25%. We used 100 runs with 100,000 particles

starting each run. This produced an effective sample size greater than 1000 in all cases.

Priors for the biological model parameters were the same as those used by Thomas and Harwood (2004). Prior distributions on the additional mortality parameters, $\underline{\delta}$, were specified as follows: (1) since the parameters are bounded $(0,+\infty)$ a gamma distribution was used; (2) the priors should be quite uninformative, so the standard deviations were set equal to the mean; (3) the upper 95th percentile of the prior distribution was set so that the decrease in mortality at the maximum value of farming activity (production or staff numbers) was 0.1.

Table 2. Prior parameter distributions

Parameter	Prior	Expected value
ϕ_a	Beta(22.05,1.15)	0.95
ϕ_p	Beta(14.53,6.23)	0.7
α	Beta(22.05,1.15)	0.95
δ [1]	Gamma(1,4x10^{-7}) Gamma(1,3.5x10^{-5})	4x10^{-7} 3.5x10^{-5}

[1] First row is for salmon production, second is for staff numbers

Comparison of models

To compare the models, we calculated the mean posterior Akaike Information Criterion (MPAIC) using the same method as Thomas and Harwood (2003). We also calculated Akaike weights (Burnham and Anderson 1998 p124), which can be thought of in this context as the posterior probability of each model being the best approximating model.

Results

Models where the salmon activity data for the Outer Hebrides seal region was made up of both Western Isles and Northwest salmon regions had consistently lower MPAIC values than those where just the Western Isles data was used (Table 3). The reduced model was preferred over the full model. Salmon production was preferred as a covariate over staff numbers when Western Isles and Northwest regions were combined. The best model, therefore, had one δ parameter, salmon production as the index of farming activity and combined the production data from the Western Isles and the Northwest.

Posterior parameter estimates for this model are shown in Figure 6, and estimated true pup production in Figure 7. The fit of the model to the data looks reasonable, except for Inner Hebrides where it has not fit the rapid increase and subsequent stabilization in pup production. The estimated mean adult survival rate (0.92) is rather lower than the prior (0.95), and the δ parameter is an order of magnitude higher.

Table 3. Mean posterior log-likelihood, AIC and Akaike weights. The model with lowest mean posterior AIC is highlighted.

Model	LnL	AIC	Akaike weight
Outer Hebrides = Western Isles			
Production, 1δ	-625.0	1258.0	0.02
Production, 3δs	-624.1	1260.2	0.01
Staff, 1δ	-624.5	1257.1	0.03
Staff, 3δs	-623.8	1259.5	0.01
Outer Hebrides = Western Isles + Northwest			
Production, 1δ	-621.5	1250.9	0.67
Production, 3δs	-621.9	1255.9	0.06
Staff, 1δ	-622.9	1253.8	0.16
Staff, 3δs	-622.9	1257.9	0.02

The estimated total population sizes, mortality rates (δ x salmon production) and anthropogenic mortality are shown in Figures 8-10. Highest mortality rates occur in the Outer Hebrides (6.7% in 2000, 95%CI 2.3-10.9%), and these also correspond with the highest absolute mortality (4100 seals in 2000, 95% CI 1,100-8,200). Estimated mortality rates are much lower in the Inner Hebrides and Orkney, peaking at 3.4% in 2001 (95% CI 0.5-4.4%) and 0.7% in 2002 (95% CI 0.2-1.2%) respectively. Estimated numbers shot peak at 570 (95% CI 160-1100) in the Inner Hebrides and 660 (95% CI 180-1300) in the Orkney..

Re-fitting this model including the known kills in the Moray Firth produced very similar results. Estimated mean posterior adult survival was slightly higher (0.93) as was δ (1.19 x 10^{-6}). The estimated population sizes in the Hebrides and Orkney regions in 2002 were 3-7% lower, but estimated mortality rates were 16% higher. As a result, the estimated absolute mortality in these regions was 7-13% higher. Estimates of population size were also lower in the North Sea region. The resulting estimates of mortality rates are shown in Table 4. The highest estimated mortality rate was 1.31, in 2001.

Table 4. Estimated additional mortality rate of seals in North Sea region, from the model with lowest mean posterior AIC, refit with known

mortality of seals in the Moray Firth included. Figures in brackets are 95% confidence intervals.

Year	1994	1995	1996	1997	1998
Grey seals	1.06 (0.88-1.33)	0.98 (0.81-1.24)	0.94 (0.77-1.18)	0.86 (0.70-1.10)	0.87 (0.71-1.12)
Year	1999	2000	2001	2002	
Grey seals	1.17 (0.95-1.53)	1.05 (0.84-1.38)	1.31 (1.04-1.73)	0.58 (0.46 0.78)	

Discussion

Increases in salmon production coincided with a stabilization in the pup production estimates, particularly in the Outer Hebrides. However, our analysis shows that, in the absence of any density dependence, a very large number of seals would have to be shot to achieve this. It seems unlikely that the shooting of 4000 seals per year in the Outer Hebrides could have gone undetected.

In order to perform these analyses we had to fix the CV of the pup production estimates at 25%, following Thomas and Harwood (2004). This weakened our ability to discriminate among the models and widened the confidence limits on our estimates of population size, mortality rates and absolute mortality. Use of other model selection criteria such as Bayes Factors (Carlin and Louis 2000) or the Deviance Information Criterion (Spiegelhalter et al. 2002), may result in a different model being selected as preferable. Multi-model inference could also be used (Burnham and Anderson 1998).

We assumed that the seal mortality rate was affected by salmon farming activity, implying that for a given level of activity larger seal populations result in a higher absolute level of mortality. However, an alternative model would have been to assume that salmon farming activity affected the actual number of seals killed..

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Figure 2. Annual production of salmon (tonnes) in the four grey seal regions. "Outer Hebrides" is based only on data from the Western Isles salmon production region.

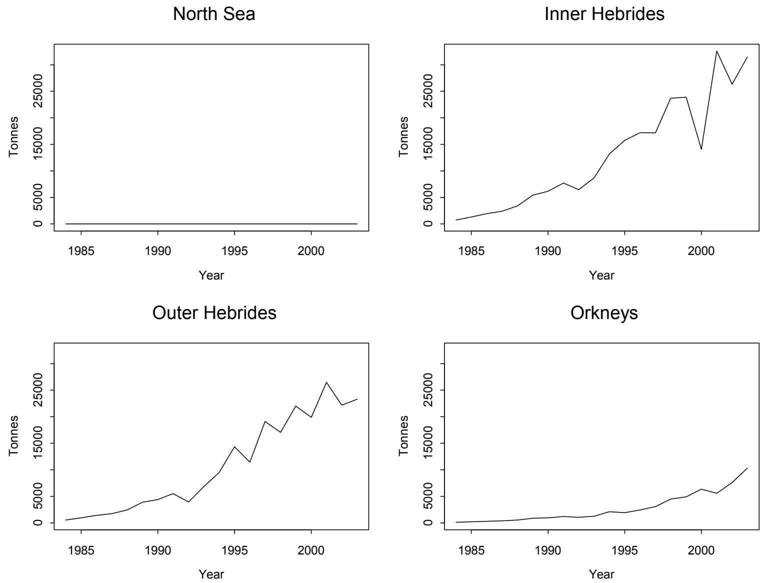


Figure 3. Annual production of salmon (tonnes) in the four grey seal regions. "Outer Hebrides" values are based on data from the Northwest and Western Isles salmon production region.

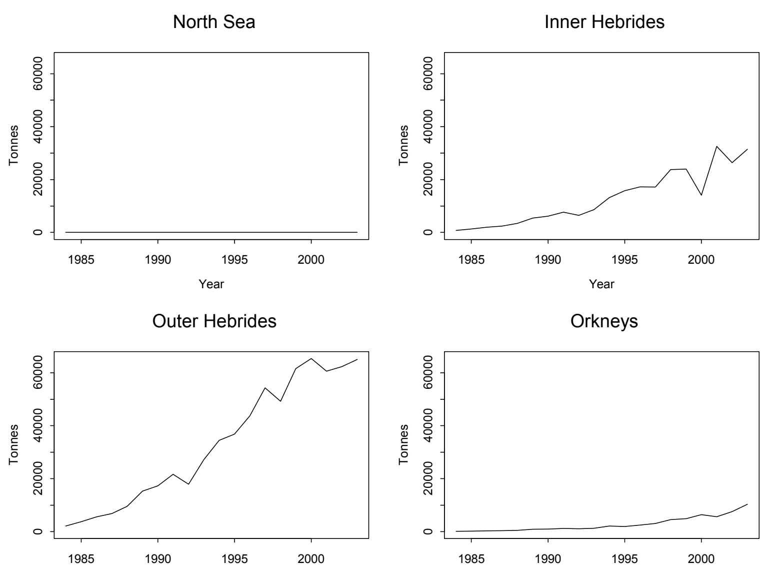


Figure 4. Annual staff numbers (full time + part time) in the four grey seal regions. OuterHebrides figures are based only on data from the Western Isles salmon production region.

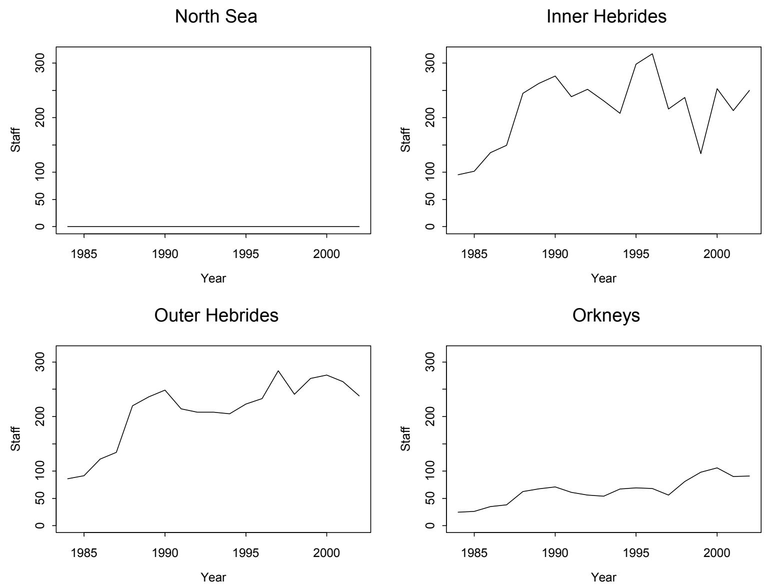


Figure 5. Annual staff numbers (full time + part time) in the four grey seal regions. "Outer Hebrides" figures are based on data from the Northwest and Western Isles salmon production region.

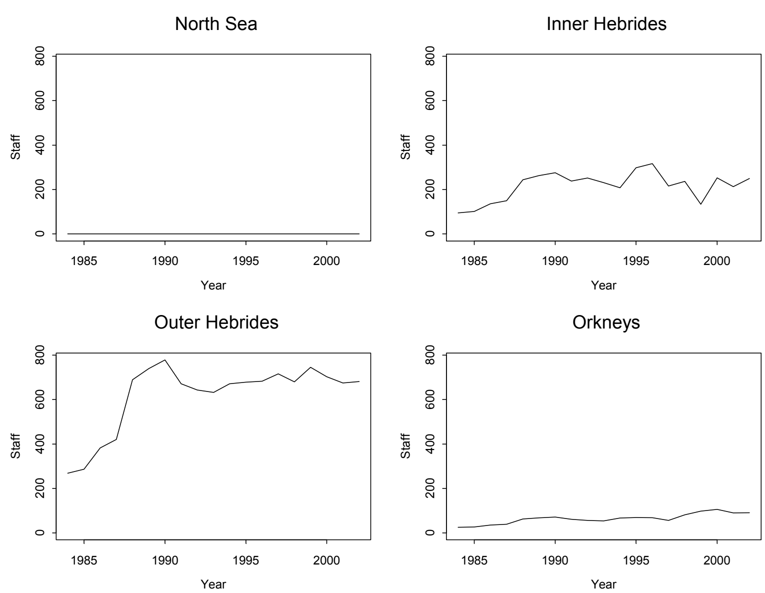


Figure 6. Posterior parameter estimates (histograms) and priors (solid lines) from the model with lowest mean posterior AIC: that with one δ parameter, salmon productivity as the index of farming activity and combined the production data from western isles and northwest.   The vertical line shows the posterior mean, and its value is given in the title of each plot after the parameter name.

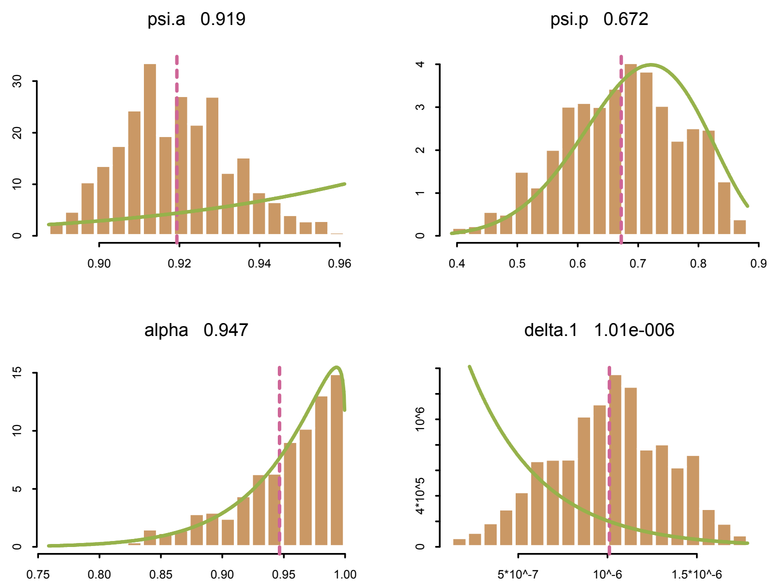


Figure 7. Estimates of pup production from the model with lowest mean posterior AIC. Input data are shown as circles, while the lines show the weighted mean of the particle values, bracketed by 2.5th and 97.5th percentiles.

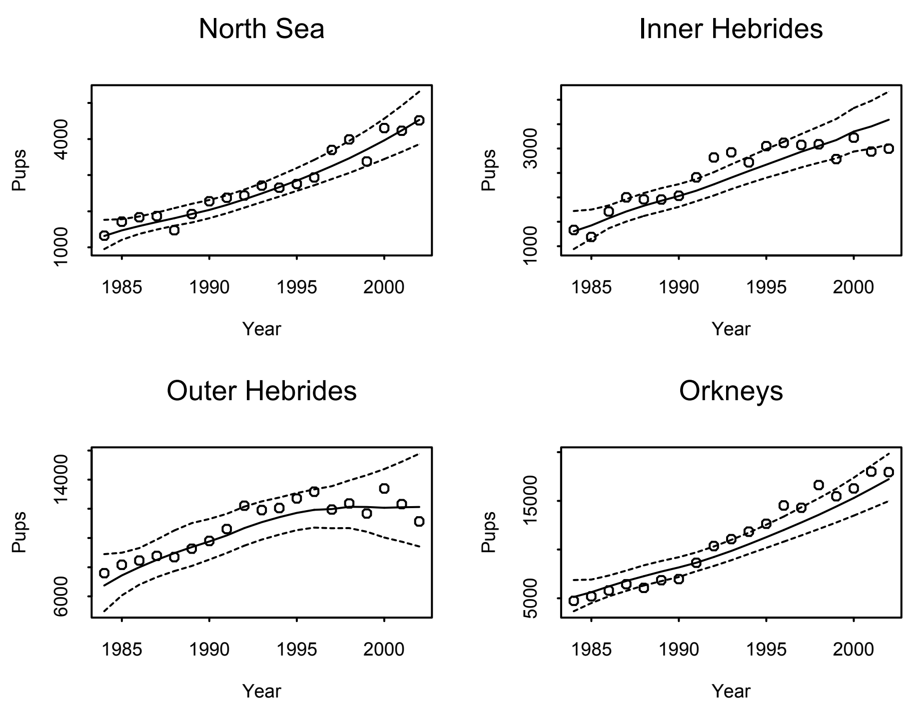


Figure 8. Estimated total population size (adults and pups) after the breeding season from the model with the lowest mean posterior AIC.

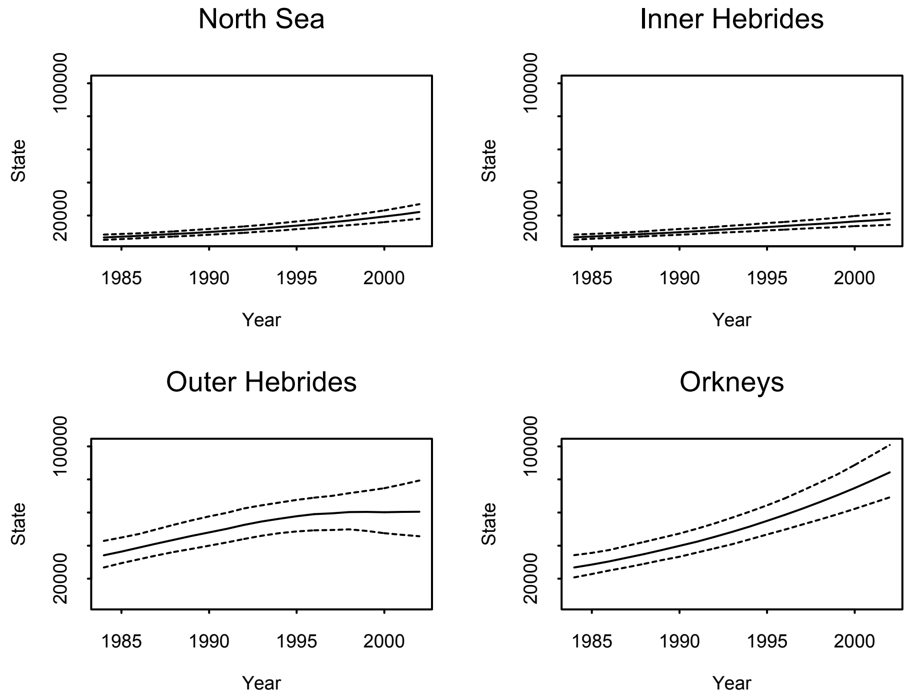


Figure 9. Estimated mortality rate from the model with the lowest mean posterior AIC.

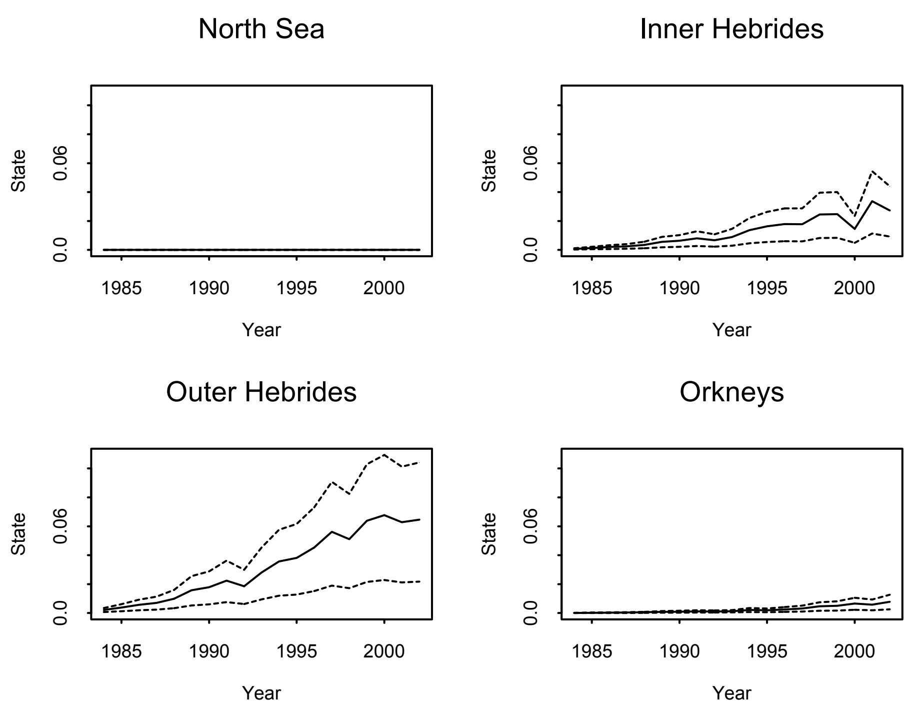


Figure 10. Estimated anthropogenic mortality(adults and pups) from the model with lowest mean posterior AIC.

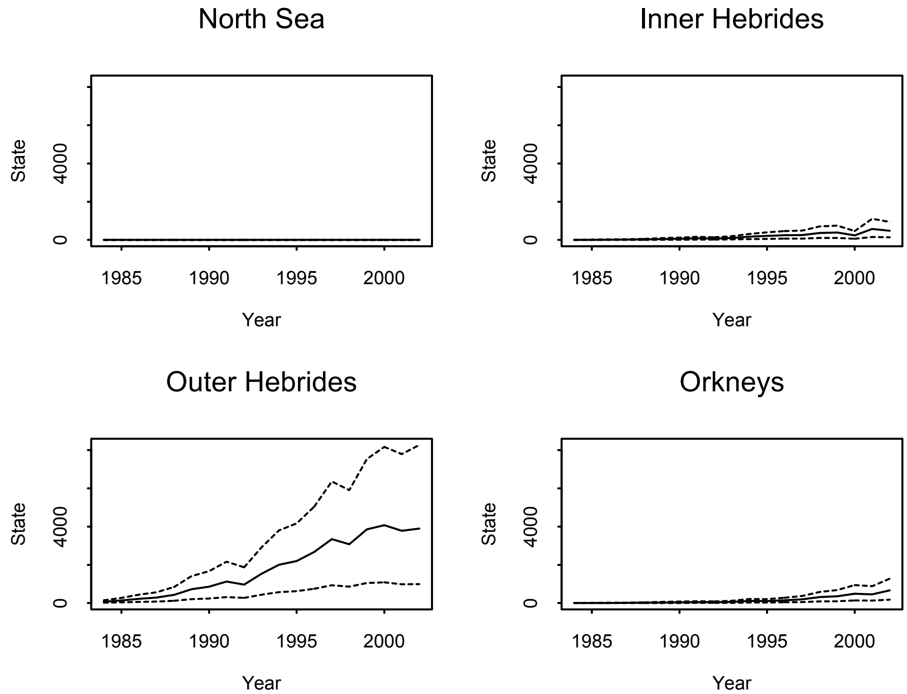
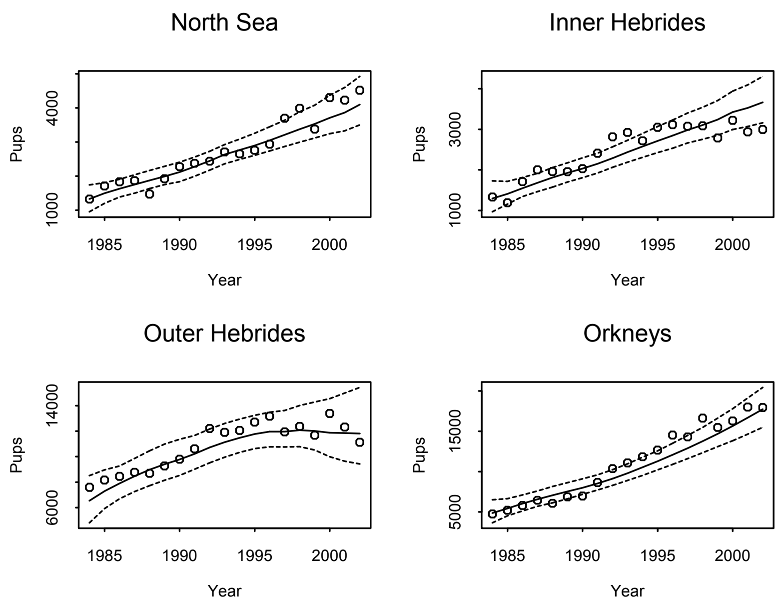


Figure 11. Estimates of pup production from the model with lowest mean posterior AIC, refit with known mortality of seals in the Moray Firth included. Input data are shown as circles, while the lines show the weighted mean of the particle values, bracketed by 2.5th and 97.5th percentiles.



I.L. Boyd

The Moray Firth Management Plan

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

Introduction

Many of the questions placed before SCOS in 2004 relate to seals in the Moray Firth. The number of common seals in the Moray Firth has been declining for about a decade and this could be the result of sustained levels of killing by local salmon fishermen. In order to address the need to conserve seals and to protect salmon fisheries, a management plan has been drafted.

Background

One of the principal reasons for many of the measures within the Conservation of Seals Act 1970 was because of the need to protect coastal salmon fisheries. This Act is now the UK's only primary legislation specifically protecting seals.

Even when the populations of seals in the UK were much smaller than they are now, seals were a pest within salmon fisheries. The concentration of salmon in river estuaries, or in association with fixed coastal nets, may attract seals. Salmon fishermen have long wished for the capability to control seal predation by shooting. The Conservation of Seals Act 1970 provides this capability while protecting seals during their breeding seasons. Common and grey seals can only be shot under license between 1 June and 31 August and 1 September and 31 December respectively. During other times of year no license is needed to shoot seals but the methods of killing are regulated. The Conservation of Seals Act also enables the Minister to place a Conservation Order on particular species at specific times and places in order to increase protection of seals.

Seventeen major salmon rivers enter the sea at the Moray Firth and salmon fishing is a major local industry in the region. Salmon numbers have declined recently and some of these rivers are candidate Special Areas of Conservation (cSACs) for salmon. In addition, there is a cSAC for common seals in the Dornoch Firth which is part of the larger Moray Firth region.

During the open season of 2002, some of the 12 District Salmon Fishery Boards, which are responsible for managing the salmon fishery in each catchment, ran a bounty scheme for controlling seal numbers in the Moray Firth region. This scheme meant that hunters were paid to shoot seals whether or not they were directly involved in salmon predation. The scheme came to an end when phocine distemper virus (PDV) re-emerged in 2002 because, as a result of the threat of PDV, a Conservation Order was put in place to protect seals throughout Scotland. Thereafter, licenses were only issued to shoot seals when they were interfering directly with a fishery. The Conservation Order expired on 3 Sept 2004.

The need for a new approach

A side-effect of the Conservation Order 2002-2004 was to terminate the bounty scheme in the Moray Firth. However, at the time when the bounty scheme was operating there was considerable concern from Scottish Natural Heritage (SNH) that the scheme was likely to undermine the favourable conservation status of common seals in the region as defined under the EC Habitats Directive (Council Directive 92/43/EEC). If continued, this could lead to a legal challenge to the bounty scheme from Europe.

In addition, in the past SCOS has expressed concern about the principles associated with having an open season for shooting seals because this means that there are no data returned about the number of seals being killed, either within the Moray Firth or elsewhere. Such a situation means that the scientific advice cannot take account of the levels of shooting.

The Moray Firth Management Plan
Based on the presumption that some form of control of seals would be needed in the Moray Firth after 3 September 2004, the Moray Firth Partnership, which includes representation from the District Salmon Fishery Boards, asked Dr James Butler of the Spey District Salmon Fishery Board to develop a draft management plan for seals in the region.

This paper describes the proposals in the draft management plan. The Plan has already been accepted in outline by the Scottish Seals Working Group, a consultative group established by the Scottish Executive, but many details still need to be considered. The Scottish Parliament has also approved the Conservation of Seals (Scotland) Order 2004 (Appendix I) that applies to the Moray Firth. This has been put in place partly to provide the legal and administrative (in terms of issuing licences to shoot seals) framework for the Management Plan and to preserve the integrity of the Special Area of Conservation for common seals in the Dornoch Firth.

Management plan

The proposals put forward in the draft Management Plan include:

1. Defining regions in which salmon would be protected from seals (Fig. 1) by attempting to exclude seals from those regions. The Plan is not specific about the procedures used for exclusion but it is assumed this would normally involve shooting individuals that stray into these zones.

2. Permitting higher levels of shooting during the close seasons and particularly during the period 1 June to 31 August when salmon mostly enter the rivers.

3. There would be no change to the protection measures currently used by salmon netsmen. Although fish farms are excluded from this practice and cannot shoot seals during the close season in defence of their nets.

4. Research and monitoring would be undertaken to provide information about the number of seals in the region; species, sex and age of seals killed; movements of seals involved in salmon predation; measurement of damage to salmon attributable to seals and development of methods for the non-lethal removal of seals.

Until methods can be developed to scare seals away from the salmon protection zones, the proposal would be to remove 99 common seals and 64 grey seals annually. The rationale for these numbers is that, for common seals, the removal of 99 seals annually is close to the average annual removals over the past 10 years. For grey seals, the numbers are substantially less than the average annual removal over the past 10 years but the number required to be removed is weighted to the perceived requirements for the salmon protection zones.

The estimated number of seals shot over the past 10 years is shown in Table 1. This suggest that approximately 2847 were shot in the Moray Firth region between 1994 and 2003. Although these are presented by species, it is possible that in addition to the many unidentified seals, significant numbers will have been misidentified. Although the draft management plan contains the best estimate of the number of seals shot, it is possible that the estimate is less than the true number because there has been no formal system of reporting the number of seals shot and there is reticence amongst the salmon fishery managers to provide information.

Table 1. Estimated number of seals shot in the Moray Firth from 1994-2003.

Year	Common seal	Grey seal	Unidentified
1994	101	102	67
1995	100	99	67
1996	97	98	67
1996	89	94	67
1998	106	104	67
1999	192	161	67
2000	128	131	98
2001	66	88	256
2002	92	56	144
2003	21	16	6
Total	**992**	**949**	**900**

Research requirement

SMRU has responded to the research needs associated with the implementation of the Management Plan by:

1. Establishing a new 2-year project funded from charitable sources to collect information about seals shot under the scheme, train those shooting seals in species identification and carry out a study of the movement of seals in and out of the salmon protection zones. This project is being carried out in collaboration with the Association of Salmon Fishery Boards;

2. Establishing a second project funded by the Scottish Executive to examine ways of scaring seals from salmon protection zones using acoustic devices. This project is being carried out in collaboration with FRS;

3. Extending current efforts to develop population and movement models to specifically address the needs of the Moray Firth scheme.

4. Undertaking a programme of more regular surveys of the Moray Firth region to provide updated estimates of the seal population size. This is being carried out in collaboration with Dr Paul Thompson, University of Aberdeen.

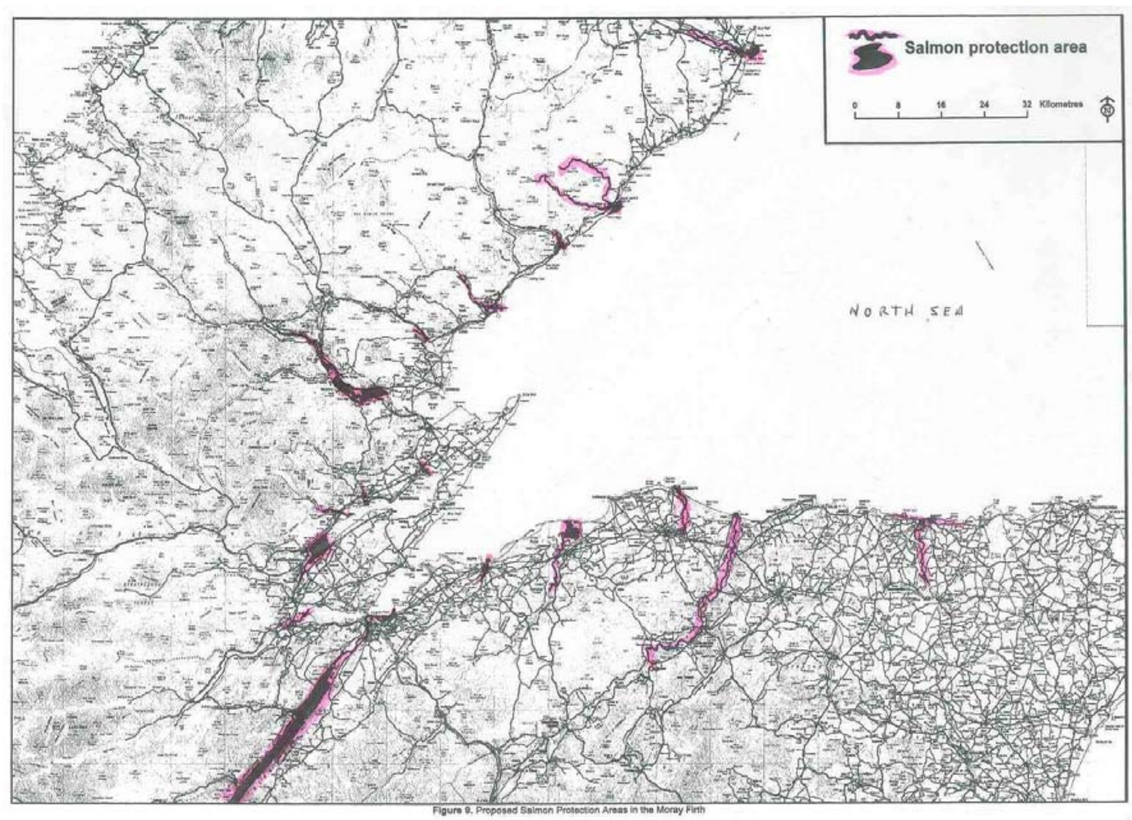


Figure 1. Map of the Moray Firth region showing the proposed salmon protection areas.

SCOTTISH STATUTORY INSTRUMENTS

2004 No. 283

SEA FISHERIES

The Conservation of Seals (Scotland) Order 2004

Made - - - -	*9th June 2004*
Laid before the Scottish Parliament	*10th June 2004*
Coming into force - -	*4th September 2004*

The Scottish Ministers, in exercise of the powers conferred by section 3(1) of the Conservation of Seals Act 1970(**a**) and of all other powers enabling them in that behalf, and after consultation with the Natural Environment Research Council as required by that section, hereby make the following Order:

Citation, commencement and extent

1.—(1) This Order may be cited as the Conservation of Seals (Scotland) Order 2004 and shall come into force on 4th September 2004.

(2) This Order extends to Scotland only.

Prohibition on killing, injuring or taking of seals

2. The killing, injuring or taking of seals of the species known as–

(a) Phoca vitulina (common seals); and

(b) Halichoerus grypus (grey seals),

is prohibited in that area enclosed by a line beginning at a point on the coast of Scotland at Noss Head at 58°28.623'North latitude and 003°02.923'West longitude; then due east to the seaward limit of the territorial sea adjacent to Scotland; then in a generally southerly and easterly direction following the seaward limit of the territorial sea adjacent to Scotland to the point of intersection with a line drawn due north from the coast of Scotland at Troup Head at 57°41.652'North latitude and 002°17.744'West longitude; then due south to that point at Troup Head; then in a generally westerly and northerly direction, following the line of mean high water springs, to the point of beginning.

ALLAN WILSON
Authorised to sign by the Scottish Ministers

St Andrew's House,
Edinburgh
9th June 2004

(**a**) 1970 c.30. The functions of the Secretary of State were transferred to the Scottish Ministers by virtue of section 53 of the Scotland Act 1998 (c.46).

EXPLANATORY NOTE

(This note is not part of the Order)

In addition to the close seasons for seals provided for in section 2(1) of the Conservation of Seals Act 1970 (c.30) ("the 1970 Act"), this Order prohibits from 4th September 2004 the killing, injuring or taking of common seals and grey seals in a defined area within the Moray Firth (article 2).

Subject to general exceptions in section 9 of the 1970 Act and to actings under a licence issued under section 10 of that Act, any person who acts in contravention of this Order is guilty of an offence under section 3(2) of the 1970 Act and liable on summary conviction to a fine not exceeding level 4 on the standard scale.

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John Harwood

Some comments on the Moray Firth Seal Management Plan

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

Summary

Since 1994 nearly 3000 seals have been shot in the Moray Firth area to protect salmon fisheries and salmon farms. During the same period, harbour seal counts declined by 36% and the estimated numbers of salmon returning to the Spey declined by 50%. The Conservation of Seals (Scotland) Order 2004 will provide year-round protection for seals in the Moray Firth region. The District Salmon Fisheries Boards in that region have proposed that they should be issued with licences permitting the killing approximately 200 seals each year in Salmon Protection Areas. This paper discusses the merits of their proposal.

Introduction

Both grey and harbour seals in the Moray Firth region have been protected year-round by the Conservation of Seals (Scotland) Order 2002, which expires in September 2004. The Dornoch Firth, in the same region, was designated as a candidate Special Area for Conservation (cSAC) for harbour seals in 2000. Seventeen major Atlantic salmon rivers drain into the Moray Firth and are managed by 12 District Salmon Fisheries Boards (DSFBs). Six of these rivers were designated as cSACs for Atlantic salmon in 1999. In addition, 15 salmon netting stations operate within the region.

Substantial numbers of seals have been shot around the salmon rivers, netting stations and farms in the Moray Firth since at least the 1930s. Butler (2004) obtained information from DFSBs, netting stations and salmon farms on the numbers of seals that were shot between 1994 and 2003

In June 2004, the Conservation of Seals (Scotland) Order 2004 extended year-round protection for both seal species in the region indefinitely. As a consequence, Boards and netting stations will require licences to shot any seals away from the immediate vicinity of nets. The salmon interests in the region have proposed a Seal Management Plan (summarized in Butler, 2004) that would allow Boards and netting stations to kill up to 109 harbour seals and 78 grey seals each year in specified "Salmon Protection Areas".

Material and Methods

Seal counts were taken from figures in Mackey (2004), Butler (2004) and from Lonergan et al (submitted). Estimates of the numbers of harbour, grey and unidentified seals shot by Boards, farms and netting stations are provided in Table 1 of Butler (2004). Estimates of the numbers of salmon returning to the Spey each between 1980 and 2002 were taken from Fig. 4 of Butler (2004).

Results

According to the current draft Management Plan around 270 seals were shot each year in the Moray Firth region until 1999, when numbers being shot rose sharply to around 400. Numbers fell sharply after the introduction of the 2002 Order. Despite the fact that at least 2847 seals were shot between 1994 and 2003, the estimated number of salmon returning to the River Spey each year declined by 50%. At the same time, counts of harbour seals fell from around 900 to 630.

Discussion

The figures reported by Butler (2004) provide little or no support for the concept that reducing the number of seals in a region benefits local salmon stocks or fisheries. In fact, there appears to be a *positive* relationship between the estimated number of salmon returning to the Spey each year since 1988 and the numbers of harbour seals hauled out in the Moray Firth region (Figure 1). However, it would be unwise to read too much into this apparent relationship, because the main feature of Figure 1 is a steady and concurrent decline in both salmon and seal numbers.

Mackey (2004), who did not have access to Butler's (2004) figures, analysed the changes in the numbers of harbour seals counted in the Moray Firth between 1988 and 2002. She concluded that these could be explained by a 25% mortality as a result of the 1988 phocine distemper epidemic, and the deliberate killing of 0-84 seals each year from 1989 to 1993 and 158-250 per year after 1993. Butler's (2004) estimates are not very different from this (120-230 harbour seals were shot per year after 1993, if it is assumed that harbour seals make up the same proportion of the unidentified seals as they do the identified). It therefore seems that most of the observed decline in harbour seal numbers since 1994 was a result of deliberate killing.

It will be hard to justify the indiscriminate killing of more seals on the basis of the evidence presented in Butler (2004). If predation by "rogue" seals is, at least in part, responsible for the continuing decline in the numbers of salmon returning to the Spey, then killing has to be targeted more precisely at these animals. The research proposed in Butler (2004), which the Scottish Executive has agree to fund, should help determine whether or not such rogue animals exist and how they can be identified.

If the Scottish Ministers decide to licence the killing of harbour and grey seals within the Moray Firth region, how can an upper limit on numbers be set? One possibility is to use the formula implemented under the US Marine Mammal Protection Act for licencing the numbers of animals that can be taken from a depleted population. The Potential Biological Removal (PBR) is defined (Wade 1998) as:

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

where N_{MIN} is a minimum population estimate (usually the lower 20th percentile of the distribution of the population estimate), R_{MAX} is the maximum rate of increase of the population (often set at a default value of 0.12 for seals), and F_R is a correction factor which is normally set at 1.0, but can be descreased for populations that are considered to be particularly at risk. The PBR is designed to ensure that there is a very low probability that the managed population will decline.

Mackey's (2004) estimate of the potential rate of increase of the Moray Firth population before 1988 (0.10) provides a useful basis for R_{MAX}. The mean haul out count of the Inner Moray Firth in 2003 was 634 (SCOS-BP 03/16) with a standard error of 36 (Lonergan et al, submitted). This can be converted to a population estimate by taking account of the proportion of time that radio tagged animals spend hauled out at low tide at the time of the surveys (Thompson et al. 1997). This gives a current population size using the Inner Moray Firth of 1040 with a standard deviation of 76. If we set F_R to 1, the PBR is 49. Using the number of seals for the Inner Moray Firth as the basis of this estimate is more conservative than using estimates for the Moray Firth as a whole. This conservatism is justified on the grounds that better data exist for the number of seals in the Inner Moray Firth and the extent to which counts for the Inner Moray Firth are representative of the Moray Firth as a whole appears to vary between years (SCOS-BP 04/5, Table 2).

Approximately one third of all the seals shot in previous years were not identified to species. The PBR should therefore be decreased to take account of harbour seals that are shot but not identified. A simple rule would be to assume that all seals that are shot but not identified are harbour seals. Proposals for improved monitoring in Butler (2004) should result in a progressive reduction in the proportion of unidentified seals and this would allow an increase in the number of harbour seals that can be taken.

There does not appear to be a grey seal population that is confined to the Moray Firth region. Satellite telemetry data indicate the region is likely to be used by grey seals from the wider North Sea. The North Sea grey seal population is still increasing, and there seems to be no reason to calculate a PBR for grey seals. Licencing the killing of 78 grey seals per year, as requested in the Moray Firth Management Plan, is unlikely to have any detectable effect on the North Sea grey seal population.

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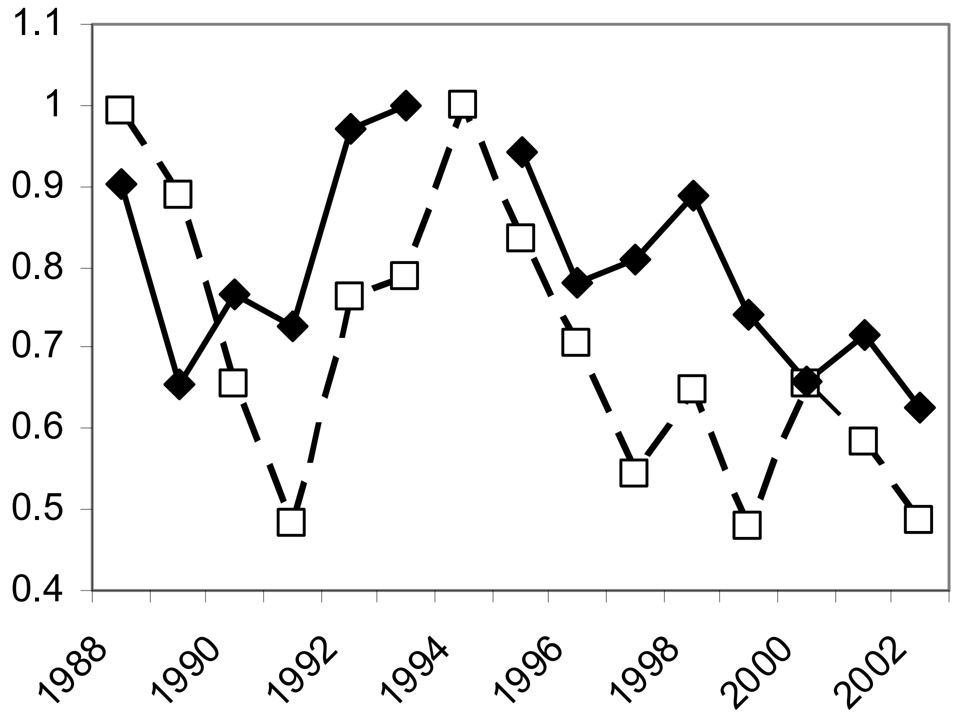
Figure 1. Standardised counts of harbour seals made during the moult in the Moray Firth area (data provided by Dr P Thompson, University of Aberdeen) and estimates of the numbers of salmon returning to the River Spey (data from Butler 2004).



R. J. Sharples and P.S. Hammond

Distribution and movements of harbour seals around Orkney, Shetland and the Wash.

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

Introduction

Recent research conducted at SMRU and in Denmark and the Netherlands using satellite telemetry to study harbour seal ecology has highlighted that this species can forage much further offshore than previously shown. As a result of these studies there has been further investment to identify the possible impacts that developments relating to oil, gas and renewable energy industries may have on harbour seal foraging areas. The preliminary results described and discussed here look at whether this pattern holds for Orkney, Shetland and the Wash. Prior to this study there was very limited information about how frequently harbour seals use offshore areas around the UK. All the locations collected from harbour seals in the North Sea by SMRU to date are summarised, a total of 65 deployments.

Material and Methods

Satellite relay data loggers (SRDLs) were deployed on 15 animals in Orkney, 15 in Shetland and 10 in the Wash, between October 2003 and March 2004. Two deployments were made at each study site to improve data coverage over the year.

The SRDL's were attached to the back of the neck behind the head using fast setting epoxy resin as described in Fedak *et al*. (1983). Animals were captured at haul-out sites or in the water near haul-out sites in two areas in Orkney, one on the east and one on the west of the islands, and two sites in Shetland, one on the north coast and one on the southeast coast of the mainland. Seals were captured in one area in the Wash.

Results

Orkney and Shetland

A total of 4157 days of data from 30 seals (17 females; 13 males) have been collected from harbour seals captured in Orkney and Shetland to date. All animals weighed more than 45 kg, this being the minimum size considered for a SRDL of this size.

Figure 1 shows the densities of location fixes obtained from these tagged animals; warmer colours illustrate higher densities. Locations are unfiltered (and thus include any errors in location) and are displayed as densities of locations per 100 m^2. Orkney animals tagged on the west appeared to be foraging in a concentrated area 30 to 40 km offshore from their haul-out area. Animals on the east of Orkney seemed to be foraging in all directions around the tagging area with slightly higher densities of locations obtained to the south. In Shetland animals captured in the north remained largely within the confines of Yell Sound with some further ranging movements. Animals tagged in the southeast of Shetland used an area approximately 40 km east of their haul-out area for foraging.

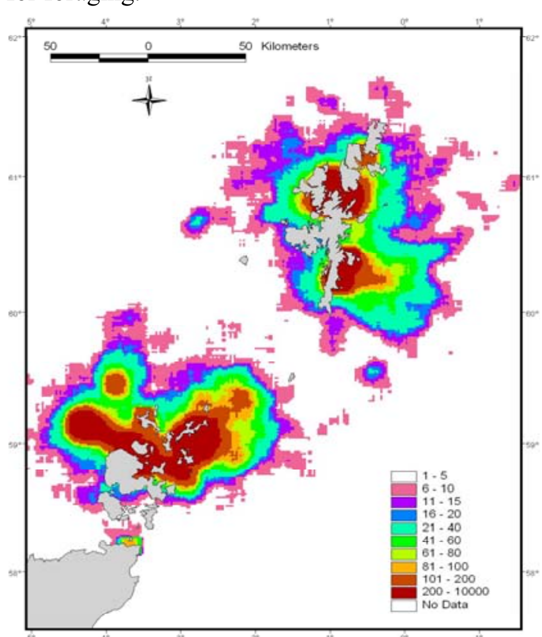


Figure 1: Density of locations from 30 harbour seals tagged in Orkney and Shetland.

Animals caught in both Orkney and Shetland have shown longer distance movements in addition to repetitive short distance trips. One female tagged on Sanday, Orkney travelled repeatedly between Orkney and Shetland, a distance of over 220 km, hauling out in both island groups. An adult male caught in Orkney travelled approximately 75 km south, to the north coast of Scotland, again hauling out at both sites. In Shetland, animals from Yell Sound appear to be making longer distance trips, travelling to areas over 100 km from where they haul-out. Other changes in haul-out areas were over a smaller scale; for example, animals often used different haul-out sites within roughly a 40 km radius.

The majority of movements recorded from harbour seals tracked in Shetland seem to consist of repeated trips to within 50 km of a haul-out, presumably to where foraging is taking place. There are however longer distance movements being made. Three out of the 15 animals tracked made trips of more than 100 km from haul-outs.

The Wash

A total of 1474 days of data have been collected to date from 10 harbour seals (7 females; 3 males) captured in The Wash.

Seals tagged in The Wash tended to make repeated trips of relatively long distance and duration. With the exception of one animal that remained within 20 km of the haul-out, seals travelled repeatedly between 75 and 120 km offshore to assumed foraging patches (*Fig 2*). With the exception of the seal that only foraged locally, foraging trips averaged approximately 10 days in duration.

All seals tagged in The Wash were highly consistent in their individual foraging habits, repeatedly travelling to the same areas. No seasonality in behaviour was apparent. All but one of the seals tagged, which used a haul-out site 60 km north of The Wash, remained faithful to the haul-out site at which they were captured.

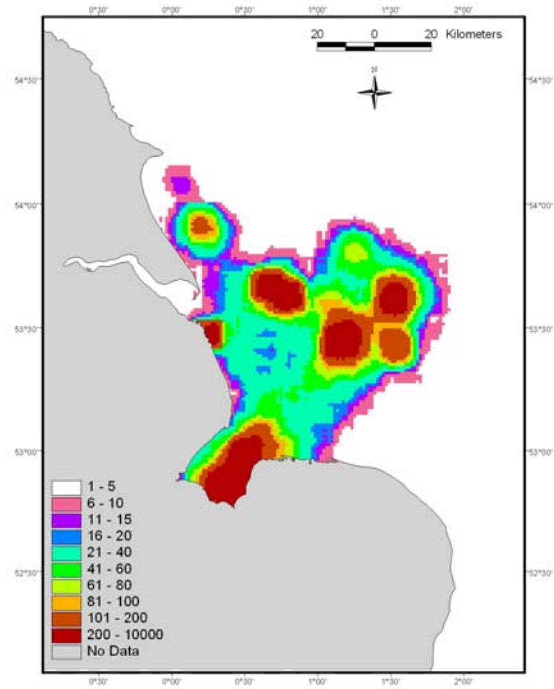


Figure 2*: **Density of locations from 10 harbour seals tagged in the wash.***

South East Scotland

Data from southeast Scotland were collected from 25 harbour seals captured in St Andrews Bay between November 2001 and July 2003. Distance travelled to areas where seals were assumed to be foraging ranged from 10 km to 120 km, with a mean of 46 km. Duration of trips ranged from less than a day to 23 days, with a mean of 4.5 days. These animals were site faithful, repeatedly returning to within 3km of the haul-out site where they were tagged. No seals hauled out outside St Andrews Bay except one young male that travelled to Leith Docks where it remained for 3 weeks, and then to the docks in Newcastle-upon-Tyne where it remained for several months.

UK harbour seal distribution

Figure 3 illustrates all the SRDL data SMRU have collected on harbour seal distribution in the North Sea and adjacent waters to date. Data from southeast Scotland are displayed as well as the data from Orkney, Shetland and the Wash. Additional data have recently started to accumulate from the west coast of Scotland.

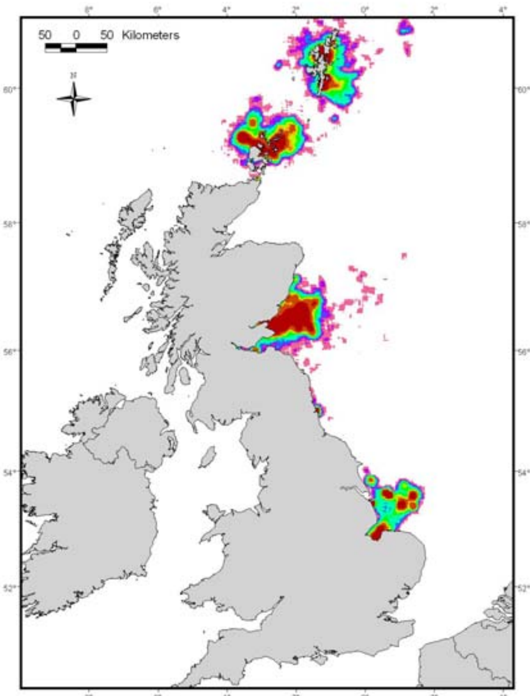


Figure 3: Distribution of harbour seals captured in Orkney, Shetland, southeast Scotland and the Wash.

Discussion

The data collected in this study and presented here are greatly improving the knowledge of harbour seal ecology in UK waters. The information will not only provide an insight to the at-sea distribution of the species but will also permit many other aspects of harbour seal ecology, such as foraging and haul-out behaviour as well as spread of disease to be studied. In addition, the data will be valuable in the context of considering the location and effectiveness of Special Areas of Conservation (SACs) for harbour seals under the EU Habitats Directive.

In Orkney and Shetland there were local, relatively short distance movements to assumed foraging areas but there were also movements at a much larger scale. In contrast, in the Wash, the majority of animals travelled repeatedly to offshore sites 75-120 km from the haul-out and the animals were much more site faithful in both the areas used to forage and the areas used to haul-out. This latter behaviour may have important implications for the proposed development of wind farms in the Wash. In St Andrews Bay animals were site faithful and traveled shorter distances to forage than animals from the Wash, traveling 45 km on average.

Despite the advance in our knowledge of the at-sea distribution of this species from these studies, there are still a number of gaps in our knowledge. For example, we have not sampled harbour seals in the Moray Firth, northeast Scotland and still rely on earlier VHF telemetry studies in this area (e.g. Thompson and Miller, 1990) that may not fully describe the offshore distribution of this population. Further tagging of harbour seals the Wash, Moray Firth and Thames is planned for October 2004.

The data collected here will be further analysed using a modelling framework developed at SMRU which predicts where seal populations spend their time at sea using additional information on the numbers of animals counted at haul-out sites throughout the area (Matthiopoulos, 2003 a, b; Matthiopoulos et al., 2004)

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Cunningham, L., Sharples, R.J. & Hammond, P.S.

Harbour seal diet in the UK

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

Introduction

Studies of harbour seals on Northern European coasts indicate that they are largely piscivorous (Pierce *et al.*, 1991). However, there is wide variation in the reported importance of different prey species, reflecting the diverse geographical and seasonal origins of samples, different sampling methods and, probably, changes in diets over 55 years. Diets of harbour seals in UK waters have been described in The Wash, the Moray Firth, Orkney, Shetland, the west coast of Scotland and Northern Ireland. There are also unpublished results from the Firth of Tay.

Material and Methods

All recent published results on harbour seal diet around the UK have been derived from analyses of hard prey remains (mainly fish otoliths) recovered from faeces (scats). Collection of scats has occurred at a range of spatial and temporal scales around the British coast.

Review of Results

Initial diet studies in The Wash were based on a small sample of stomachs from culled harbour seals which mainly contained common whelks, flatfish and whiting (Sergeant, 1951). Subsequently Hall, Watkins & Hammond (1998) showed that whiting was the overall dominant prey species by weight in The Wash (24%), with sole (15%), dragonet (13%) and sand goby (11%) other major contributors to the diet. Lesser contributions were made by flatfish: (dab, flounder and plaice); the gadoids: (bib and cod); bullrout and sandeels (3%). In addition it was apparent that whiting, bib and bullrout dominated from late autumn through early spring; sand goby peaked during winter and early spring; sole peaked in spring and again to a lesser extent in autumn; and dragonet, sandeels and flatfish (except sole) dominated from late spring to early autumn.

In the Moray Firth, Tollit & Thompson (1996) found the key prey by weight during 1989 – 1992 to be sandeels (47%), lesser octopus (27%), whiting (6%), flounder (5%), and cod (4%). Sandeels were less important during the summer than the rest of the year and whiting and cod were preyed upon more frequently in the winter. Pierce *et al.* (1991) found that clupeids dominated the diet during the winter, with both herring and sprat being eaten in large numbers. Sandeels were the most important prey during much of the early spring and summer. Gadids, especially whiting and cod, were prominent in samples from early spring, and flatfish, especially flounders, were important in some of the summer samples. Octopus appeared in the diet in several months. Overall, clupeids (sprat and herring) formed 28% of the diet by weight, flatfish 15% (mainly flounder), and 13% of gadids (especially cod and whiting).

Significant between-year and seasonal fluctuations were evident. In another study in the same area, Tollit, Greenstreet & Thompson (1997) compared the diet composition of harbour seals feeding in the Moray Firth with the abundance of their fish prey estimated from dedicated fishery surveys in 1992 and 1994. Diet composition was almost totally dominated by either pelagic species or species dwelling on or strongly associated with the seabed, depending upon the relative abundance of pelagic schooling prey.

Seasonal patterns in Shetland were similar to those in the Moray Firth. Brown & Pierce (1998) found that sandeels were important in spring and early summer, and gadids in winter. Pelagic species (mainly herring, garfish and mackerel) were important in late summer and autumn. Gadids (mainly whiting and saithe) accounted for an estimated 53.4% of the annual diet by weight in Shetland, sandeels 28.5% and pelagic fishes 13.8%.

Harbour seals in the Inner Hebrides consumed a wide range of species, the most important of which were scad, herring and whiting (Pierce & Santos, 2003). Fish from the gadid family comprised between 50% and 90% of prey biomass. However sandeels formed a very minor part of the diet, even in the summer months. Although this differs from other harbour seal studies, it is consistent with previous studies on grey seals in the Inner Hebrides (Hammond, Hall & Prime, 1994).

In the Firth of Tay, unpublished SMRU data from 1998 – 2003 show that the diet comprised primarily sandeels, gadids and flatfish. Gadid prey were dominated by whiting, followed by cod and haddock. Plaice was the main flatfish consumed followed by dab, flounder and lemon sole. Strong seasonal patterns in prey consumption were evident.

The main constituents of the diet of harbour seals in north-east Ireland between 1995 – 2000 were small flatfish and gadid fish, with the emphasis shifting from the beginning to the end of the study period from flatfish to gadids (principally whiting, haddock, pollock and saithe). The diet of juvenile seals consisted almost entirely of small gadid fish (Wilson *et al.*, 2002).

Elsewhere in Europe, studies in Skagerrak and Kattegat found that gadoids made up 50% and flatfish over 25% of harbour seal diet by weight (Härkönen, 1987). A similar study ten years later found a similar domination by gadoids but with herring displacing flatfish as the prey type of secondary importance (Härkönen & Heide-Jorgensen, 1991).

Summary

Harbour seals feed on a variety of prey including sandeels, whitefish, flatfish, herring and sprat, octopus and squid. Their diet is often dominated by just a few key species and varies both seasonally and from region to region. Given the marked geographical variation in harbour seal diets it is clear that results from one area should not be extrapolated to seals in other areas.

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S.J.Middlemas, S.Mackay

The occurrence of salmonids in harbour seal scat samples collected in the Moray Firth

FRS Freshwater Laboratory, Faskally, Pitlochry, PH16 5HB

Summary

Scat samples were collected from two sites in the Moray Firth during May and July 2003 in order to investigate the occurrence of salmonids in the diet of harbour seals. Sea trout otoliths were found in 3 of the 171 scats collected, with vertebrae found in a further 7 samples. Sea trout remains were significantly more prevalent in July than May. The contribution of sea trout to the diet was highly uncertain, and the choice of analytical model introduced a large potential bias into this estimate.

Introduction

The declines in salmon and sea trout returning to Scottish rivers have prompted increasing concern about the impact of predation in both the freshwater and marine environments (Middlemas *et al.* 2003).

Salmonids are likely to make up a very small part of the prey biomass available to seals in the marine environment. Seals are therefore likely to be exposed to greater numbers of salmonids in estuaries and rivers and predation on salmonids may be more prevalent in these areas than in the open sea.

In this study we investigate the diet of seals using two estuarine haulout sites (Findhorn and Cromarty) in the Moray Firth. The aim of this work is to quantify seasonal and geographic changes in the contribution of salmonids to pinniped diets, based on otoliths and bones found in scats.

Material and Methods

Scat samples were collected during May and July 2003 from tidal sandbars in the Cromarty Firth and in the Moray Firth at Findhorn. The abundance of salmon in the coastal zone is seasonal and the sampling regime was designed to coincide with the seaward migration of salmon smolts and the return of one sea winter salmon (grilse) during July. Where an area contained >90% of one species the scats collected were attributed to a single seal species.

Otoliths were used to estimate the proportion by weight of the different prey species in the diet through standard methods (including the use of digestion and numerical correction factors). In addition the remaining hard parts were examined to determine the presence of salmonid bones.

There are several different mathematical models that can be used for estimating the contribution of prey species in predator diets (Laake *et al.* 2002). Here we use a bootstrapping approach with ratio and split sample estimators to estimate the contribution of salmonids to the diet (Middlemas 2003).

Results

In total 143 harbour seal scats were collected during the study, 79 from Cromarty (May: 31, July: 48) and 64 from Findhorn (May: 35, July: 29). 19 species were identified from otoliths recovered from both sample sites. In general the diets in Cromarty and Findhorn are similar, with flatfish and sandeels being key components by weight in both May and July

Sea trout otoliths were found in 3 out of the 48 scats collected from Cromarty during July (6.25%). Their estimated contribution to the diet is dependent on the estimation model used (Table 1).

Table 1. Estimated contribution of sea trout in the diet of harbour seals using the Cromarty Firth in July 2003.

Estimation	Proportion by weight of sea trout

Method	Lower 95% CL	median	Upper 95% CL
ratio	0	0.336	0.600
split-sample	0	0.064	0.149
combined	*0*	*0.116*	*0.559*

When bones were included in the Cromarty analysis the overall occurrence of salmonids increased from 3 (7.3%) to 7 (15.6%) in the July samples although none were found in May (Figure 1). Although salmonid otoliths were absent from Findhorn samples, bones were present in harbour seal samples collected in both months sampled, 1 (2%) for May and 3 (6%) during July. The results of a logistic regression suggested that there were no differences in the probability of a scat containing salmonid remains between the two sites. There was however a significant difference between the two study months.

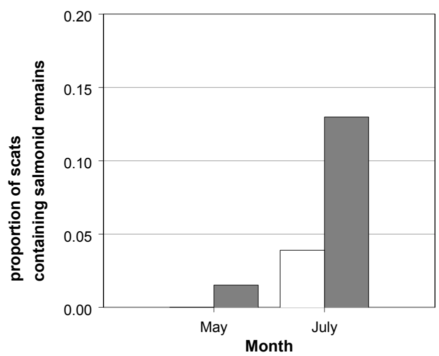

Figure 1: The monthly occurrence of salmonid remains in scats collected in the study. Results are presented on the percentage of samples containing otoliths and those containing vertebrae in each month

Discussion

There were seasonal differences in the occurrence of salmonids in the seal scats in the study. The peak during July coincides with the return of adult salmon and sea trout to the rivers and agrees with the view of harbour seals as generalist predators, whose diet reflects, in part, the availability of prey. Although there were differences between the two sites, they were not found to be significantly different, possibly as a result of the relatively low sample sizes and the rarity of salmonids in the scats.

A proportion of the otoliths ingested by seals is lost during digestion, and this can be corrected for by the application of experimentally derived correction factors (Bowen 2000). Application of such correction factors only works when there is a large enough sample size to ensure the detection of at least one otolith. This can be problematic for rare species in the diet such as salmonids. For example, even with a reasonably large sample (66 scats) identifying otoliths alone found no evidence of salmonids in the diet of harbour seals using Findhorn in this study. The use of both otoliths and key skeletal structures, although a lengthy process, is recommended as it provides evidence for salmonids that might otherwise be overlooked or undetected from otolith-based diet studies. However, this approach may only give a non-quantifiable indication of a presence or absence of species, unless unique, or paired, bone structures such as the atlas are present (Browne *et al*. 2002).

The estimated contribution of salmonids to the July Cromarty diet is highly variable. In addition, a sizable bias can be introduced by the choice of estimation model. It is not possible to determine which of the two approaches is valid (Laake *et al*. 2002; Middlemas 2003). In order to fully represent the uncertainty in such estimates we suggest that combining the outputs of the different estimation models by giving each equal weighting.

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S.J.Middlemas[1], K.Grellier[2], S.Mackay[1], S.E.W.Moss[2], J.D.Armstrong[1] & P.S.Hammond[2]

Results of Feeding Experiments to Determine the Effect of Digestion on the Recovery and Reduction of Salmon Otoliths

[1]Fisheries Research Services Freshwater Laboratory, Faskally, Pitlochry, PH16 5LB
[2]NERC Sea Mammal Research Unit, Gatty Marine Laboratory, University of St Andrews, St Andrews KY16 8LB

Summary

Feeding experiments with captive grey seals were undertaken in order to investigate the recovery and reduction of salmon otoliths. A total of 173 (18%) of the 968 otoliths fed during the experiments was recovered. The loss rate was positively correlated with initial otolith size with few smolt otoliths being recovered. Otoliths were reduced in size by an average of 37.5%, and this, together with the high loss rate, agrees with the view that salmonid otoliths are more fragile than most prey species. It was found that grading the morphological characteristics of recovered otoliths according to degree of digestion improves the accuracy and precision of estimating ingested otolith size.

Introduction

Studies of scats have generally reported Atlantic salmon either to be absent or to constitute a minor component of seal diet. However, it has been suggested that salmonid otoliths may be underrepresented in scat samples because they are fragile (Boyle *et al.* 1990) and because seals may discard the heads of some large prey (Pitcher 1980). Indeed, of the 24 Atlantic salmon heads presented to an adult male grey seal, 19 were consumed and only one otolith out of a possible 38 (~3%) was recovered (Boyle *et al.* 1990).

This study aimed to investigate the effect of digestion on the recovery and erosion of otoliths from smolts and adult salmon.

Material and Methods

Experiments were undertaken with grey seals at the Sea Mammal Research Unit, St Andrews. Experimental constraints meant that otoliths were presented in both carrier fish (herring) and also *in situ* in salmon. Small (3mm diameter) indigestible plastic beads were used to investigate the potential for losses due to the experimental procedure.

For each trial the percentage of otoliths recovered was calculated. Morphological features were used to produce an objective method with which to grade each otolith for the apparent degree of digestion. The relationship between initial and digested otolith size was investigated by estimating digestion correction factors (dcf). Bootstrap simulation was used to estimate the error associated with the digestion correction factors. For each recovered otolith a length was drawn at random from those fed to the seal in that trial. For the *in situ* trials otolith length was estimated from fish length using an allometric equation, which incorporated normally distributed error around the regression line ($OL=0.0084FL+1.4655+e$, $n= 59$, $p<0.001$, e: mean=0, $SD=0.092$).

Results

Recovery rates

In the six experimental trials, 173 (18%) of the 968 otoliths and 100% of the plastic beads ingested by the seals were recovered. Percentage recovery was related to the mean original length of the ingested otoliths with larger otoliths giving a higher recovery rate (Spearman correlation, $R = 0.88$, $n = 8$, $p = 0.022$). There did not appear to be any consistent differences between adult and juvenile seals (Table 1).

Reduction in size

The mean dcf for all salmon otoliths recovered in the experiment was calculated as 1.6, i.e. otoliths were reduced by an average of 37.5% of their initial size. As expected the digestion correction factors increased as the digestion grade increased (Table 2). Categorising otoliths by grade decreased the variability in the degree of digestion of individual otoliths within each grade when compared to using a single dcf (i.e the cvs were smaller in all cases – Table 2). This suggests that using graded digestion correction factors rather than a single dcf is likely to increase the accuracy and precision of estimated undigested otolith size.

Table 1: Summary table showing the recovery rates of salmon otoliths in the different trials. C carrier, S in situ; A and J refer to adult and juvenile seals and the numbers identify individuals; OL mean length of ingested otoliths; n number of ingested otoliths; dcf digestion correction factor.

Type	Seal	OL	N	% recovery	dcf
C	J1	6.0	76	18	1.70
C	J1	5.2	81	53	1.54
C	J2	3.3	143	9	1.27
C	J2	3.8	127	8	1.97
C	A1	6.5	147	61	1.62
C	A1	3.2	202	0	-
S	A2	2.8	96	2	1.51
S	A2	2.8	96	2	1.35

Table 2: Estimated digestion correction factors for salmon otoliths graded by apparent degree of digestion. Data from all of the feeding trials have been treated together.

Grade	N	Dcf (se)	C.v. (se)
1 (low)	24	1.26 (0.008)	16.09% (0.57)
2 (med)	120	1.50 (0.003)	18.32% (0.22)
3 (high)	20	2.32 (0.015)	17.48% (0.70)
ALL	164	1.60 (0.003)	27.95% (0.27)

Discussion

In general the pattern of returns in this study (greater recovery for larger otoliths) is consistent with that of previous feeding experiments (e.g. Tollit *et al*. 1997). The results also support the view that salmon otoliths are more fragile (i.e. have higher loss rates and reduction) than most other prey species examined (e.g. Prime & Hammond 1987; Marcus *et al.* 1998; Bowen 2000).

The application of a single correction factor is inadvisable when there is a high degree of variation in otolith digestion between otoliths of a single fish species (e.g. Tollit *et al.* 1997). For salmon the application of a single correction factor is likely to introduce bias into estimates of original length for those otoliths that are either heavily or lightly digested. The results of the bootstrap simulations indicate that the use of grade-specific dcfs is likely to increase both the precision and accuracy of estimates compared to a single average correction factor.

Because of the small sample sizes we were not able to test for differences between the *in situ* and carrier experiments. However, such differences have been shown for other prey species fed to grey seals (Grellier & Hammond in review). Ideally all feeding trials would use *in situ* otoliths as this more accurately mimics the real life situation. However there are a number of additional factors that are likely to affect the digestion of otoliths including the species and size of experimental animal, meal size and captive conditions (active/non-active) (e.g. Marcus *et al.* 1998; Bowen 2000). It is unlikely that truly wild conditions will be replicated in feeding experiments and the results are likely to be biased in some form. There is ultimately a trade off between the potential bias in applying the results of carrier based feeding experiments with that involved in using average, instead of species specific, values for digestion and recovery.

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P.M. Thompson & T.R. Barton

RECENT TRENDS IN THE ABUNDANCE OF HARBOUR SEALS IN THE MORAY FIRTH

University of Aberdeen, School of Biological Sciences, Lighthouse Field Station, Cromarty, Ross-shire, IV11 8YJ.

Summary

Annual surveys of harbour seals in the Moray Firth, NE Scotland were made between 1987 and 2004. This briefing paper updates the time-series of counts presented previously to SCOS. Following the 1988 Phocine Distemper virus (PDV) outbreak, abundance increased for the next 4-5 years. Subsequent surveys indicate that this local population of approximately 1500 seals declined at 2.5-5% p.a. after 1993. There was no detectable impact of the 2002 PDV outbreak, but this may be balanced against a reduction in shooting resulting from the Conservation Order introduced during the epizootic. Initial data from 2004 indicate that pupping season counts were slightly higher, possibly also in response to continued protection in this area.

Introduction

Since 1987, the University of Aberdeen has been studying the behavioural and population ecology of harbour seals in the Moray Firth. As part of this programme, annual surveys have been carried out at the main breeding areas in the inner Moray Firth. Occasional surveys have also been made along the northern and southern shores of the Moray Firth where smaller non-breeding groups can be found. Although carried out over a limited geographical area, these studies therefore provide a dataset with high temporal resolution that complements the larger scale aerial surveys of harbour seals carried out by SMRU.

The aim of this briefing paper is to update SCOS with a summary of recent trends in the abundance of harbour seals in the Moray Firth.

Material and Methods

Annual surveys have been made at sites in the inner Moray Firth. These include the three main pupping areas in the Beauly, Cromarty and Dornoch Firth, and sites used predominantly by non-breeding seals at the mouth of the Inverness Firth and in Loch Fleet. Earlier radio-tracking and marking studies indicate that seals rarely move between the main pupping areas within a season, but that there is mixing between all breeding sites and the Inverness Firth site, particularly during winter (Thompson *et al.* 1996).

Annual estimates of abundance are based on the methodology outlined in Thompson *et al.* (1997a), and involve making 2-10 shore-based counts during both pupping (15 June – 15 July) and moult (1 – 31 August) periods. These data provide an index of abundance which equates to approximately 60 % of the population (Thompson *et al.* 1997a).

Results

Between 1987 and 2003, mean annual estimates from the time-series of counts made during the pupping and moult periods were highly correlated ($r = 0.83$, $n=15$, $p<0.001$). Following a slight reduction in numbers resulting from the 1988 PDV outbreak, there was an increase in annual mean counts between 1989 and 1993.

Year-to-year variation in mean counts can be high, but overall there has been a significant 2.5-5% decline in annual mean counts in the period 1993 – 2004 (Pupping: $F_{1,10} = 14.78$, $r^2 = 0.6$, $p<0.005$; Moult: $F_{1,8} = 48.5$, $r^2 = 0.86$, $p<0.001$).

known changes in food availability and impacts at the individual level (eg. Thompson et al. 1997b, 1998) mean that other bottom–up factors may also have influenced recent dynamics. Better data on the species and numbers of seal shot now need to be integrated into modeling and monitoring studies to assess the full impact of shooting upon the dynamics of this population.

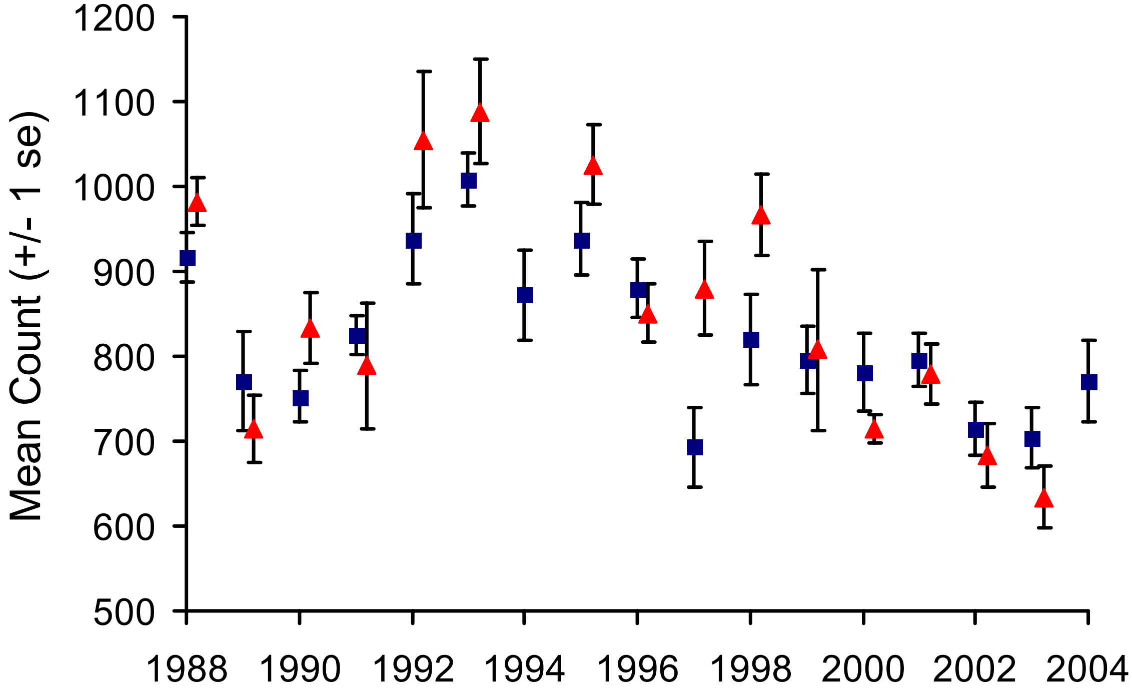

Fig. 1. Mean annual haul-out counts of Moray Firth harbour seals made during the pupping season (blue squares) and the moult (red

Discussion

As suggested from counts of dead seals, the 2002 PDV epizootic did not appear to cause major mortality within this population. However, a reduction in additional mortality from shooting (due to the Conservation Order introduced during the PDV outbreak) may have masked the impact of the outbreak on this population. Reductions in shooting during the period 2002-2004, may have also contributed to the apparent increase in haul-out counts observed during the 2004 pupping season. These preliminary data, together with recent modeling studies (Mackey 2003), suggest that levels of shooting during the period 1993-2004 may have made a significant contribution to the observed decline. However,

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