

Scientific Advice on Matters Related to the Management of Seal Populations: 2003

Contents

Scientific Advice

ANNEX I Terms of reference and membership of SCOS

ANNEX II Briefing papers for SCOS 2003

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 2003. 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). 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 did not recover from the effects of over-exploitation for many decades. In this case, lack of recovery is probably because of reproductive failure caused by pollution.

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 between trips to forage for food at sea. Female grey seals give birth to a single white-coated pup, which moults and is abandoned by its mother following a lactation period of about 3 weeks.

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 southwest Britain. 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 2002, there were an estimated 42,000 grey seal pups born in Britain. This is estimated to equate to a total population of between 97,900 and 123,000 grey seals.

Adult male grey seals may weigh up to 350 kg and grow to over 2.3 m in length. Females are smaller, reaching a maximum of 250 kg in weight and 2 m in length. Grey seals are long-lived

animals. Males will live for over 20 years and begin to breed from about age 10. Females often live for over 30 years and begin to breed at about age 5.

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 oiliness of the prey but an average consumption estimate is 7 kg of cod or 4 kg of sandeels per seal per day.

Table 1. The status of grey seals in the North Atlantic region

Region	Population² size	Year when latest information was obtained	Type of data (see key¹)	Population status
Mainland Scotland & Shetland	12,000	1998-2002	1	Possibly increasing
Outer Hebrides	30,400	2002	2	Pup production stable, total population possibly still increasing
Inner Hebrides	7,500	2002	2	Pup production stable, total population possibly still increasing
Orkney	44,300	2002	2	Increasing but rate may be slowing
Scottish North Sea coast	5,900	2002	2	Increasing
Scotland	100,100			
English North Sea coast	4,400	2000	2	Increasing
Southwest (England/Wales)	5,000	1999	1	Stable
England & Wales	9,400			
Total (UK)	109,500			
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 1 – Estimates based upon occasional pup counts or counts of seals hauled out

² 2 - Estimates based upon systematic annual pup counts using aerial survey

² Counts are rounded to the nearest 100 seals.

Common 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 particular concentrations in The Wash, Firth of Tay and the Moray Firth

Between 1996 and 2001, about 33,800 common seals were counted in the whole of Britain, of which 29,800 (88%) were in Scotland and 4,000 (12%) were in England (Table 2). A total of 1,200 seals were counted in Northern Ireland (Table 2). The total British population cannot be estimated accurately because it is not possible to count all individuals in the population.

Accounting for those animals that are not seen during surveys 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 severely affected by the phocine distemper virus (PDV) epidemic in 1988 and 2002. Seal numbers in England increased following the 1988 epidemic and recovered to the pre-epidemic level. However, the epidemic in 2002 is likely to have had a similar impact to the one in 1988.

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 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 without a white coat and can swim almost immediately.

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

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

Table 2 Sizes and status of European populations of common seals. Numbers given predate the PDV epidemic of 2002. Those in parentheses show the estimated totals after subtraction of the number of carcasses found during the epidemic.

Region	Population size¹	Years when latest information was obtained	Population Status
Outer Hebrides	2,400	1996-2000	Possibly increasing
Scottish W coast	12,800	1996-2000	Possibly increasing
Scottish E coast	1,800	1996-97	Stable
Shetland	4,900	1996-2001	Possibly decreasing
Orkney	7,800	1996-2001	Possibly decreasing
Scotland	29,700		
England (E & S coast)	4,000	2001	Increasing
Northern Ireland	1,200	1997	Decrease since 1970s
UK	34,900 (31,000)		
Ireland	900	1978	
Wadden Sea (Germany)	11,500	2000	Declining ²
Wadden Sea (Netherlands)	3,300	2000	Declining ²
Wadden Sea (Denmark)	2,100	2000	Declining ²
Limfjorden (Denmark)	1,000, 495	1998-2000	Declining ²
Kattegat/Skagerrak	9,752	2000	Declining ²
West Baltic	315	1998	Small increase
Kalmarsund (East Baltic)	270	1998	Increasing
Norway S of 62°N	1,200	1996-98	Unknown
Norway N of 62°N	2,600	1994	Unknown
Iceland	19,000	?	Unknown
Barents Sea	660	?	Unknown
Europe excluding UK	52,600 (35,600)		
Total	87,300 (66,400)		

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

² – Thought to have declined as a result of the PDV epidemic.

Responses to questions raised by the Scottish Executive

In the past, the Advice from SCOS has contained annexes explaining the data about the status of UK grey and common seal populations. This year 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 seal populations

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 03/2.

Pup production

The total number of pups born in 2002 at all annually surveyed colonies was estimated to be 36,246. A further 5,500 pups were likely to have been born at other scattered sites. Regional estimates were 3,096 in the Inner Hebrides, 11,134 in the Outer Hebrides, 17,598 in Orkney, and 4,418 at North Sea sites.

Table: Grey seal pup production and total population size estimates for the main colonies surveyed in 2002

Location	2002 pup production	Change in pup production from 2001-2002	Change in pup production from 1998-2002	Total 2002 population (to nearest 1000)
Inner Hebrides	3,096	+2.1%	-0.9%	8,000
Outer Hebrides	11,134	-10.7%	-1.6%	30,000
Orkney	17,598	-1.9%	+3.0%	44,000
Isle of May + Fast Castle	2,509	+10.2%	+3.3%	6,000
All other colonies	3,765			11,000
Total (Scotland)	38,102			99,000
Donna Nook	709	+10.6%	+12.6%	2,000
Farne Islands	1,200	-3.9%	+2.2%	3,000

SW England & Wales (last surveyed 1994)	1,750			5,000
Total (England & Wales)	3,659			10,000
Total (UK)	41,761	-3.2%*	+1.4%	109,000

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

Trends in pup production

Between 1984 and 1996, estimates of the total number of pups born at regularly surveyed colonies increased year on year (SCOS-BP 03/2). In 1997, estimated pup production fell for the first time but recovered again in 1998 in line with the previously observed upward trend. However, there was a second temporary decline in 1999 followed by a recovery in 2000. Pup production remained nearly static between 2000 and 2001 and showed a small decline in 2002.

The differences in pup production between 2001 and 2002 are shown in the table above. This shows that, while the percentage change between 2001 and 2002 varied from -10% in the Outer Hebrides to +10% at the Isle of May (including Fast Castle) and at Donna Nook, the overall pup production at annually monitored colonies as a whole declined by 3.2%.

In recent years, the pup production at all annually monitored colonies appears to have been more variable than in preceding years (SCOS-BP 03/2). 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 whereas in the past 5 years it was less than 2% .

Population size

Pup production is used in a model of the grey seal population that provides an estimate of the total population size. While the pup production was increasing steadily year-on-year, it was possible to assume that the population was not being affected by density. However, there are now strong indications that the rate of increase in pup production is slowing and a new model that includes the likely effects of density is being developed to estimate the total population from the pup production (SCOS-BP 03/3). This supercedes the previous model used to estimate the total size of the grey seal population. The new model is described in SCOS-BP 03/3 and Table 3 within this paper shows the estimated population size using this model.

Based on the pup production in 2002, this model estimates a total UK grey seal population of between 97,900 and 123,000 with a point estimate of 109,500. The total population estimate is about 20% lower than the estimate produced by the modelling method used in the past (SCOS-BP 03/4). The majority of these seals, approximately 91% (99,100), are associated with breeding colonies in Scotland and the remaining 9% (9,400), with colonies in England and Wales.

Uncertainty in estimates

There is considerable uncertainty associated with the total population estimates. Each estimate of pup production could lie within a range of -10% to +13% of the values provided and there are similar levels of uncertainty associated with other factors used to calculate total population size. However, this does not take account of the unknown uncertainties associated with the estimates of pup production at colonies that are not surveyed annually and of adult male survival.

Additional uncertainties arise because we do not currently know which stages of the life cycle of grey seals are likely to be influenced by density. Lower fecundity or juvenile survival rate will have less effect on stabilizing the population than reduced survival in adult females. Studies of other long-lived mammals suggest that it is most likely that density will act initially on fecundity of females or juvenile survival rather than on adult female survival and it is assumed that this is the case with grey seals.

Trends in population size

There is now reasonable evidence for the stabilisation of pup production in some regions. However, even if these trends continue, the grey seal population as a whole is likely to continue increasing (SCOS-BP 03/3). This is especially the case if the observed changes in pup production are caused by reduced pregnancy rate or juvenile survival rather than by an increase in the death rate of adults (SCOS-BP 03/5). However, if the death rate of adults is contributing to the overall levelling off in pup production then the overall population size will be over-estimated.

Future trends

Assuming that conditions remain as they are at present, then the total population size is predicted to increase by about 1% per year over the next 10 years. As a result, the total population associated with annually monitored breeding sites is predicted to increase from 92,500 to 105,300 (SCOS BP 03/3, Table 3).

Current status of British common seal populations

Each year SMRU carries out surveys of common seals during the moult in August. Recent surveys and overall estimates are summarised in SCOS-BP 03/7. It is impractical to survey the whole of the coastline every year but current plans by the 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 uncertainties. The largest contribution to uncertainty is the proportion of the seals not counted during the survey because they are in the water. We cannot be certain what this proportion is and it is likely 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 35,000 common seals in the UK

is likely to indicate a total population of 50,000-60,000 seals before the outbreak of PDV in 2002. Apart from the population in The Wash, common seals in the UK were relatively unaffected by PDV in 1998 (SCOS-BP 03/10). The overall effect of PDV in 2002 on the common seal population in the UK may have been to reduce the total population by about 10%.

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

Region	1996-2001
Shetland	4,883
Orkney	7,752
Outer Hebrides	2,413
Highland (Nairn to Cape Wrath)	910
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)	159
Tayside (Newburgh to Montrose)	109
Fife (Kincardine Bridge to Newburgh)	635
Lothian (Torness Power Station to Kincardine Bridge)	40
Borders (Berwick upon Tweed to Torness Power Station)	0
TOTAL SCOTLAND	29,763
Blakney Point	489
The Wash	2,976 ¹
Donna Nook	341 ¹
Scroby Sands	75 ¹
Other east coast sites	117
South and west England (estimated)	20
TOTAL ENGLAND	4,018
TOTAL BRITAIN	33,781
TOTAL NORTHERN IRELAND	1,248
TOTAL BRITAIN & NORTHERN IRELAND	35,029

¹The numbers represent counts made before the PDV epidemic of 2002

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

Until recently, it was assumed that all of the grey seals breeding around the UK formed a single population that was distinct from populations breeding in northern Norway and the Baltic Sea. The genetic structure, and long-term observations using tagging and mark-recapture, of grey seal populations now suggests that there is a reasonably strong partitioning of animals between breeding sites. The components of this partitioning are (1) a strong tendency for females to return to breed at their birth site, dependent upon the availability of space at this site, and (2) an even stronger tendency to return to the same site year on year to give birth. A model is currently being developed to examine the movement patterns of grey seals between colonies and movement patterns are also an explicit component of the most recent population model (SCOS-BP 03/3). Preliminary results suggest that much of the colonization pattern shown by grey seals can be explained by the competing tendencies for animals to breed as close as possible to their birth site and the negative effects that occur because of the high densities this creates. Consequently, even when colonies fill up, new colonies are most likely to appear close to the originating colony and seal populations breeding in the Inner Hebrides, Outer Hebrides, Orkney and North Sea colonies have independent dynamics.

These results have consequences for how we might view the factors regulating grey seal populations. Inspection of coastlines reveal no apparent restriction in breeding habitat for grey seals. Based upon such an analysis there appears to be no effective barrier to a continued high rate of population growth. However, we are beginning to understand why this might be counteracted by behaviour associated with high levels of breeding site fidelity. Consequently, the detailed substructure of grey seal populations may be an important determinant of the population dynamics, both in terms of bringing about reduced rate of growth and in terms of the population's robustness to the effects of local declines in abundance.

Common seals

There is less information about common seals than for grey seals but information from the Kattegat / Skagerrak, Alaska and the UK using both genetics and tagging studies suggest that these seals also tend to show fidelity to specific regions and that there is a strong tendency to return to breed in the region of birth. An analysis of genetic variation suggests that there is a small exchange of breeding individuals between common seal populations in the North Sea. However, the rapid spread of PDV in both 1988 and 2002, and the results of telemetry studies in Scotland and the Netherlands indicate that there is regular movement of individuals and contact between these populations. Despite these movements, at the scale of the regions over which common seal numbers are surveyed and reported here, it is likely that the populations in these regions should be considered as relatively independent units.

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

Total fish consumption depends upon the type of fish being eaten and the proportion of the diet that is composed of fish. For the purposes of this calculation, it is assumed that alternative sources of food for UK seals, 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 93,000 and 117,000 tonnes of fatty fish, such as sandeels, herring or mackerel. Alternatively, if these seals ate only whitefish then the annual consumption would be between 173,000 to 218,000 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 142,000 to 318,000 tonnes. The greatest uncertainties in this calculation are caused by lack of knowledge of diet and uncertainties in the population estimates. If we use diet composition in the mid 1980s as an indication of diet composition today, the total annual fish consumption is likely to lie between 179,000 and 253,000 tonnes.

Current work

Projects funded by DEFRA, SEERAD and SNH will result in 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. Sample collection has been completed successfully. Analyses, data processing and experiments with captive animals to estimate prey-specific coefficients of digestion are ongoing. Preliminary results should be available to SCOS in 2004.

4. What information would be required to determine the effects of predation of seals on fish populations and fisheries? What types of modelling approaches are likely to be the most informative?

The amount of a particular fish species eaten by seals depends upon four factors. These are (1) the number of seals, (2) the energy requirements of these seals, (3) the number and quality of fish of the species of interest and (4) the number and quality of alternative prey available to the seals. Changes in any of these factors could lead to changes in the number of a particular species being eaten by the seals. The way in which other predators respond to changes in fish abundance will also affect fish populations and fisheries. At present there is no agreed framework for analysing these complex multispecies interactions. However, an EU-funded international modelling programme (Critical Interactions Between Species and their Implications for Precautionary Fisheries Management in a Variable Environment - BECAUSE), will attempt to develop such a framework.

Through studies involving surveys of the UK seal populations (SCOS-BP 03/2; SCOS-BP 03/7), estimation of total population size (SCOS-BP 03/3; SCOS-BP 03/4), studies of seal diet, energetics and foraging distribution (SCOS-BP 03/8; SCOS-BP 03/9), modelling of the way in which seals adapt their choice of prey depending upon prey availability (SCOS-BP 03/11) and estimates of fish population size (data from FRS, Aberdeen, and CEFAS, Lowestoft), there is now a body of science that is making progress in this field.

The type of modelling approach that is likely to be most informative is illustrated by SCOS-BP 03/11. This is the first attempt to define the degree to which grey seal diet is affected by changes in fish abundance and distributions.

5. What is known about the distribution of grey seals around the Scottish coast outside the breeding season?

Current knowledge of the distribution of grey seals around the Scottish coast outside the breeding season is summarized in SCOS-BP 03/8. This makes use of data about haulouts and from the tracking of seals at sea using satellite telemetry. The results suggest that the distribution at sea is patchy and there are particular areas that appear to be attractive to grey seals.

The method used to calculate the distribution of seals provides an estimate of the error associated with the distribution. These errors are relatively large at this stage because of the small sample size of animals involved. In addition, there are insufficient data at present to allow us to stratify the estimated distribution according to time of year and there may be biases caused by the sex and age composition of the sample. However, the methods presented in SCOS-BP 03/8 can assimilate more data as it becomes available and thereby it will provide an incrementally better estimate of distribution as time goes on. A substantial increase in sampling effort will take place during 2003-2004 and this will tend to cover regions, particularly in the southern Hebrides, where sampling effort has been poor in the past.

6. What is the impact on seal populations of accidental capture in fishing gear and fish farms? How is this impact estimated?

There has been little systematic collection of data about the accidental capture of seals in fishing gear and there is no information about capture in gear associated with fish farms. Based on observer programmes (established primarily to estimate cetacean bycatch) and mark-recapture of tagged seals the bycatch of seals in fishing gear is estimated to be in the low hundreds of animals per year. These appear to be mainly of grey seals and are currently associated with pelagic herring and mackerel fisheries. Anecdotal evidence suggests that many of these seals are males.

At this level, fisheries bycatch does not appear to present a significant threat to seal populations but more analysis of available data and new data is required in order to quantify this cause of mortality. The estimate of bycatch also does not include seals killed by fishermen around fishing gear and better data are also required in this area. Until these data are available, it is not possible to determine whether the additive effects of bycatch in fisheries, shooting and interactions with fish farms have significant effects upon the overall mortality of seals, or on localized populations of common seals. Preliminary calculations indicate that the observed reduction in the grey seal pup production could be explained by the deaths of an additional 4,000-8,000 juvenile or adult seals each year since the mid-1990s. We need to quantify the extent to which additional mortality of adults seals is caused by accidental capture in fishing gear, interactions with fish farms or shooting to protect fisheries.

7. What kind of information that fishermen, fish farmers and/or tourist operators might be able to collect would be useful to scientists in assessing the significance of interactions between seals and human activities?

Information collected by the public or even by those professionals directly involved in a particular activity, is often difficult to assimilate into scientific advice. There are several requirements of such information to be useful:

- The purpose needs to be clearly defined. The questions being addressed also need to be clearly defined in advance because these will determine data collection protocols. It is also important that those who are involved in collecting the data understand the objective and that methods for analyzing the information or assessing its significance have been considered in advance.
- Information needs to be verified using some form of quality control procedure.
- Information needs to be collected to specified levels of spatial and temporal precision

Assuming this can be achieved, the type of data that could be collected includes:

Fishermen

Frequency with which seals are captured in fishing gear expressed relative to a consistent measure of fishing effort according to fishing area, gear type and species targeted;
Frequency of seal damage to fish within fishing gear (noting that not all damage to fish is caused by seals) expressed as a proportion of the total fish caught;
Frequency with which seals are killed as a result of being around fishing gear and, where possible, information about the species, age class and sex of the seal involved. A system for collecting and analyzing the jaws from seals that are killed would provide much of this information.

Fishfarms

Frequency and extent of net damage (as a proportion of the net area in the water) caused by seals;
Loss of fish due to seals;
Frequency of killing of seals in the vicinity of fish farms together with provision of information about the species, age class and sex of the seal involved. This would require to be expressed relative to the amount of observation effort.
Use of seal scarers expressed in terms of the power and make of the scarer and the schedule of use; information about any other anti-predator methods.

Tour operators

Tour operators could maintain a log book of the number of seals of each species observed within a designated area that is visited regularly and, the number of visits made to each site. These data may be useful as a means of tracking trends in abundance.

8. To what extent may lack of data on numbers of seals shot outside the close seasons affect the predictions from models of seal population dynamics?

During the coming year, SMRU will use the mathematical model described in SCOS-BP 03/3 to investigate the effects of different levels of shooting of seals outside the close season on the dynamics of the British grey seal population. There are no data about the number of animals being killed, but preliminary calculations indicate that the observed reduction in the growth of the population could be explained by the killing of 4,000-8,000 juvenile or adult grey seals each year since the mid-1990s. If these deaths were the result of the deliberate killing and/or bycatch then the current size of the population is likely to be higher than estimated in SCOS-BP 03/3. Obtaining data about the number of seals being killed will reduce the uncertainty surrounding current estimates of the total population size.

9. To what extent is seal predation likely to delay or prevent the recovery of cod stocks in the North Sea and to the west of Scotland?

To understand the impact of seal predation on the recovery of cod stocks we need to know not only how many seals there are, but also how their diet is affected by the abundance of cod and other prey species. The functional response (SCOS-BP 03/11) is a convenient way of describing and predicting how diet and prey consumption vary with prey abundance. Some forms of functional response can result in predators holding a prey species at a low population level, sometimes known as a “predator pit”. It is not yet known if the correct circumstances exist for a “predator pit” to exist for cod.

The ICES (International Council for the Exploration of the Sea) Study Group on Multispecies Assessment in the North Sea, met in Bergen, Norway in August 2003 to consider whether multispecies interactions (including those involving grey seals) might impact plans for cod recovery. The group used a multispecies modelling approach called MSVPA, developed in the 4M model, which considers predator-prey relationships among 13 species of commercially important fish (cod, haddock, whiting, saithe, norway pout, sandeel, sole, plaice, grey gurnard, starry ray, herring, mackerel, horse-mackerel), as well as grey seals and seabirds. The model generates estimates of the relative share of cod prey in predator stomachs. Multispecies assessments indicated that that, after fisheries, the most important predator of older cod age classes was seals. Younger cod age classes were predominantly preyed on by seabirds, whiting and cod itself. When used to investigate various cod recovery scenarios, the only trend predicted for 2002-2010 by the model was an increase in cod cannibalism.

However, the 4M model uses estimates of the diet of composition of grey seals obtained in 1985 and assumes that consumption by predators is directly proportional to prey abundance. Work currently underway will update data on grey seal diet and techniques are being developed for fitting a multispecies functional response to the available data on grey seal and prey abundance, and for investigating the implications of this for the dynamics of exploited fish stocks (SCOS-BP 03/11). However, we will not be able to come to any conclusions about the effects of seals on the recovery of cod until these studies are completed.

10. To what extent is seal predation likely to delay or prevent the recovery of salmonid stocks of early running salmon throughout Scotland and late running salmon on the north west coast of Scotland?

Seal predation is only one of many factors that could affect salmon populations. Until more is known about all factors, including other causes of salmon mortality at sea, it would be difficult to assess the extent to which seals are contributing to declines in the abundance of spring and autumn runs of salmon. Based on current analyses of diet, salmon do not appear to be an important component of the diet for the seal population as a whole but this may not be the case at local scales, especially in areas where salmon congregate before entering rivers. Where there is a large seal population and a small, aggregated salmon population it might be possible for seals to be an important cause of mortality in the later stages of the salmon life cycle, but it is unlikely that seals around the UK are responsible for the long term declines in the abundance of salmon.

11. *Considering the "favourable conservation status" of seals in SACs, what are the likely outcomes of local seal population control in the proximity of seal SACs, for example, in the Moray Firth?*

SACs are generally not sufficiently large to include all the critical habitat required by common seals. Consequently common seals will often move outside SACs and, in many cases, they may spend most of their time feeding outside the boundaries of SACs. Therefore, there is a high probability that population control carried out in the vicinity of SACs will effect the "favourable conservation status" of seals within SACs.

The population of seals in the Moray Firth has been in decline since the early 1990s (SCOS-BP 03/7, Table 2; SCOS-BP 03/16) and has also been subject to a degree of population control by the local salmon fishery boards. Studies of seal movements in the Moray Firth have also shown that seals move between the SAC and sites where shooting takes place. Given that equivalent levels of population decline have not been observed in other regions subject to regular surveys (e.g. The Wash, Wadden Sea, Kattegat and some regions in the Hebrides) and where there was little effect of PDV, it is possible that the recent decline in abundance is associated with shooting. The sensitivity of this population to this type of management is part of ongoing modelling studies and the results of these will be reported in future. Nevertheless, given the evidence of a decline in abundance in this region, further decline is the most likely outcome if population control is resumed at the level of effort applied before the Conservation of Seals (Scotland) Order 2002 came into effect.

12. *What, from a scientific perspective, might constitute a reasonable definition of "adjacent" to an SSSI or SAC in Section 3 of the SEERAD application form for a licence to shoot seals?*

In order to answer this question, it will be necessary to undertake a specific analysis of the movements of seals in relations to SACs. The meaning of "adjacent" cannot be defined until it is possible to estimate the probability that seals from particular SACs could be present in an area subject to an application for a licence to shoot seals. The probability of a seal from an SAC being present in an area where shooting takes place will probably differ between SACs. Some of the data needed to make an assessment already exists for grey seals (SCOS-BP 03/8) and data are currently being collected to allow this calculation to be done for common seals. Depending upon the distance that seals travel away from SACs it may be possible to specify the risk to seals from SACs being shot by those applying for licences. Assuming that this is possible with the data currently being collected, it would then be possible to include these risks within models of the population dynamics of seals in SACs. This could provide a framework within which a judgment could be made about the acceptable levels of shooting in regions adjacent to SACs.

13. Has the recent outbreak of PDV run its course and what is the likelihood of its recurrence in the future?

The recent outbreak has run its course because no confirmed cases of PDV have been reported from the UK in 2003. The prognosis is less clear. A preliminary analysis of blood samples collected this year suggests that only a small proportion of cases of PDV were reported from Scotland in 2002 (see SCOS-BP 03/10) because the mortality amongst those that were exposed was less than in other North Sea populations. The likelihood of future outbreaks will be assessed when current data analysis is completed.

14. What impact has the recent PDV outbreak had on seal populations across Europe, Scottish waters and in specific Scottish local areas? How does this compare to the previous outbreak?

Europe

The total number of common seals washed up dead around Europe (including the UK) during the epidemic was approximately 21,000. Table 1 shows the breakdown by area with an estimate of the minimum population size (Sources Wadden Sea Newsletter 2002 –2 and SMRU; see SCOS-BP 03/10 for further information)

Table 1

Region	First date of occurrence of unusual mortality	No. of dead common seals to 31 st October, 2002	Minimum population size (Date of count/survey)
Wadden Sea	16 th June	10,360	20,000 (2001) 25,000
Heligoland	11 th August	270	400
Kattegat/Skagerrak	7 th May	6,915	19,000 (2001)
Denmark – Limfjord	September	315	886 (2000)
Baltic Sea	August	102	270 (2000)
Belguim/France	July	21	N/A
UK	13 th August	3,557	34,625 (2001)

The total number found dead in the UK (August to October for comparison) by area are shown in Table 2.

Table 2

Region	Grey	Common	Unknown	Total
England				
Kent to Lincolnshire	19	349	2060	2428
Yorkshire to Northumberland	30	33	159	222
West coast England	5	1	10	16
South West coast England	10	0	11	21

Scotland				
Borders and Lothian	2	7	15	24
Fife and Tayside (Tay Firth)	11	8	22	41
Grampian	19	9	30	58
E. Highland (Moray Firth)	23	4	44	71
Orkney	41	3	33	77
Shetland	3	4	4	11
North and West Coast incl Western Isles	16	20	41	77
Northern Ireland	13	33	18	64
Wales	103	0	1	104

We do not yet know the true impact of the epidemic on the abundance of common seals because results from the 2003 aerial surveys of the major populations on the east coast are not yet available. Estimates of mortality based on numbers found dead in 1988 (SCOS-BP 03/10) were found to be a considerable underestimation.

How does this compare with the previous outbreak?

The total numbers found dead throughout Europe were nearly 30% higher in 2002 than in 1988. However, in the Waddensea it is estimated that 60% mortality occurred in 1988 compared with 40% in 2002. In the Kattegat/Skagerrak area PDV mortality is estimated at 50% in 2002 whereas it was around 40% in 1988.

In the UK estimated common seal mortality in areas where a significant number of carcasses were reported, the crude mortality measure from the number found dead as a proportion of the population size (adjusted for estimated growth rate and proportion not counted during surveys) were :

23% in The Wash in 1988 and 35% in 2002;
6% in the Tay estuary in 1988 and 4% in 2002 and
7% in the Moray Firth in 1988, 4.5% in 2002.

It is not possible to estimate similar mortality rates for grey seals (SCOS-BP 03/10) but from the number of carcasses washed ashore and the number found positive for PDV by molecular methods they were clearly less acutely affected by the virus.

15. What is the scientific case for retaining/lifting the additional protection offered to common seals by the Conservation of Seals (Scotland) Order 2002, either in Scotland as a whole or in specific local areas?

Information about the PDV outbreak in 2002 is still being gathered. However, based on the current data, there is little evidence that an outbreak is likely to recur in the next few years. Although the assessments of post-epidemic common seal population sizes have still to be completed, based upon carcasses recovered during the epidemic it appears that common seals in Scotland were not seriously affected by the disease. In addition, evidence from grey seals shows that the virus has infected seal populations throughout Scotland but has apparently had little effect. This means that a large proportion of the seals in Scotland are likely to be immune to the disease. With the evidence currently to hand, it appears that lifting the Conservation of Seals

(Scotland) Order 2002 would carry a low risk to Scottish seal populations, in relation to the effects of disease.

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 JR Beddington (Chairman), Imperial College, London;
Dr WD Bowen, Bedford Institute of Oceanography, Halifax, Nova Scotia, Canada;
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;
Dr EJ Millner-Gulland, Imperial College, London;
Dr J. Pinnegar, CEFAS, Lowestoft;
Professor W Sutherland, University of East Anglia;
Dr PM Thompson, University of Aberdeen;
Professor F Trillmich, University of Bielefeld, Germany;
Dr P Newton (Secretary), NERC, Swindon.

ANNEX II

Briefing papers for SCOS

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

This year, a new structure is used. 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 new structures for considering the Advice from 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 in its deliberations. Some of the *briefing papers* will be provided along with the Advice and that 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.

List of briefing papers submitted to SCOS 2003. Those shown bold have been released with the Advice.

1. Boyd, I.L. The management of seals in Scotland: new procedures introduced in 2002.
2. **Duck, C.D. Pup production in the British grey seal population.**
3. **Thomas, L. & Harwood, J. Estimating grey seal population size using a Bayesian state-space model**
4. **Hiby, A.R. & Duck, C.D. Grey seal total population estimate, 2002.**
5. **Hiby, A.R. Changes in UK grey seal demographic parameters and consequences for estimation of population size.**

6. Pomeroy, P.P. Parameters in the current grey seal pup production model: how variable is time to moult?
7. **Duck, C.D. & Thompson, D. The status of British common seal populations.**
8. **Matthiopoulos, J. The distribution of grey seals around the Scottish coasts outside the breeding season.**
9. **Sparling, C.E. & Smout, S.C. Population energy budget for UK North Sea grey seals.**
10. **Hall, A.J., Pomeroy P.P. & Lonergan, M. The phocine distemper virus outbreak.**
11. **Matthiopoulos, J., Smout, S., Asseburg, C. & Harwood, J. Modelling the functional response of British grey seals.**
12. Matthiopoulos, J., Harwood, J. & Thomas, L. Modelling the Short-Term Movements of Grey Seals between Breeding Colonies and their Long-Term Population Consequences.
13. Northridge, S.P. Seal bycatch in fishing gear
14. Sharples, R.J. and Hammond, P.S. Distribution of Harbour Seals from St Andrews Bay
15. Sharples, R.J. and Hammond, P.S. Estimating total population size of harbour seals. Case study - St Andrews Bay
16. **Thompson, P.M. & Barton T.R. Recent trends in the abundance of harbour seals in the Moray Firth.**
17. Bennett, K.A., McConnell, B.J. & Fedak, M.A. Dispersal of grey seal pups.
18. Additional data for assessing the size of the British grey seal population.
19. Participants in grey seal population dynamics research in the North Atlantic Region.

C.D. Duck

Pup Production in the British Grey Seal Population

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

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

1. Surveys conducted in 2002

Each year SMRU conducts aerial surveys of the major grey seal breeding colonies in Britain to determine the number of pups born. In addition, new sites where grey seal pups have been reported or which appear to be suitable for colonisation are visited regularly. During 2002, five surveys were flown over the main colonies in the Inner Hebrides, Orkney and in the Firth of Forth and six over the Outer Hebrides. Two recently formed colonies have been included in the full Orkney survey and one in the Inner Hebrides survey. Photographs from the last flight over the Orkney colonies that have breeding late in the year were uncountable so only four counts were available for their pup production estimation.

Ground counts of the numbers of pups born at the Farne Islands were made by National Trust staff. Similar counts at Donna Nook on the Humber Estuary were made by members of the Lincolnshire Wildlife Trust and at South Ronaldsay by Scottish Natural Heritage staff. Locations of the main British grey seal breeding sites are shown in Figure 1.

2. Estimated pup production

The number of pups born (pup production) at regularly surveyed colonies is estimated each year from counts from aerial survey photographs using a model of the birth process and the development of pups. The method used to obtain the estimates for this year's advice was similar to that used for the past several years.

Total pup production in 2002 at all annually surveyed colonies is estimated to be 36,246, a reduction of 1.9% from the 2001 pup production (37,419 pups). Estimates of the total pup production from all major breeding sites in England and Scotland (excluding Loch Eriboll, Helmsdale and Shetland) between 1984 and 2002 are shown in Figure 2. Pup production

estimates for the main island groups (the Inner Hebrides, the Outer Hebrides and Orkney) are shown in Figure 3a and for the North Sea colonies in Figure 3b. The time series of data for island groups are given in Table 1. For colonies not surveyed by air, pup numbers are counted directly on the ground either annually (Farne Islands and Donna Nook,) or less frequently (South Ronaldsay, SW England, Wales and Shetland). Pup production estimates for individual colonies are included in the Appendix.

Note that the pup production total for 2001 (37,419) differs from the value in last year's report (36,920). This is because three new colonies have been incorporated into the annual survey procedure, one in the Inner Hebrides (Oronsay mainland) and two in Orkney (Calf of Flotta and South Fara). These colonies were previously included in Table 2. Production at Oronsay has been monitored since 2001 and at the new Orkney colonies since 1996 and 1998. The totals in Table 1 have been adjusted accordingly.

3. Trends in pup production

Between 1984 and 1996 estimates of the total number of pups born at regularly surveyed colonies increased year on year. In 1997, estimated pup production fell for the first time but recovered again in 1998 in line with the previously observed upward trend. However, there was a second temporary decline in 1999 followed by a recovery in 2000. Pup production remained nearly static between 2000 and 2001 and showed a small decline in 2002.

The differences in pup production between 2001 and 2002 are shown in Text-table 1. This shows that, while the percentage change between 2001 and 2002 varied from -10% in the Outer Hebrides to +10% at the Isle of May (including Fast Castle) and at Donna Nook, the overall pup production at annually monitored colonies as a whole declined by 3.2%.

In recent years, the pup production at all annually monitored colonies has been more variable than in preceding years (Figure 2). Production increased between 1995 and 1996, decreased between 1996 and 1997, increased between 1997 and 1998, decreased between 1998 and 1999, increased between 1999 and 2000 and decreased between 2000 and 2001 and between 2001 and 2002. The reasons for this variability are not known. It is possible that, as the grey seal population begins to stabilise, breeding females become more susceptible to subtle changes in environmental factors such as food availability and this is reflected in the increased variation in pup production.

The overall annual percentage change in pup production for each region over the past five years is shown in Text-table 1. This shows that, apart from Donna Nook, which is the smallest of the regional groups considered with 709 pups born in 2002, the overall annual change in production ranged from -1.6% to +3.3%. The overall annual change in pup production for all annually monitored colonies between 1998 and 2002 was +1.4%

Text-table 1. The percentage change in grey seal pup production at annually surveyed colonies between 2001 and 2002, with the overall annual change between 1998 and 2002.

Location	Change 2001-2002	Overall annual change 1998-2002
Inner Hebrides	+2.1%	+0.9%
Outer Hebrides	-10.7%	-1.6%
Orkney	-1.9%	+3.0%
Isle of May + Fast Castle	+10.2%	+3.3%
Farne Islands	-3.9%	+2.2%
Donna Nook	+10.6%	+12.6%
Total	-3.2%	+1.4%

The results from 2002 support the trends observed in recent years. Firstly, the increased variability in pup production has continued. Secondly, production in the Hebrides continued

to remain unchanged since 1992 and may even be in slight decline. Thirdly, production in Orkney declined slightly in spite of the inclusion of two 'new' colonies. There is therefore, further support for the suggestion of a reduced rate of increase in pup production in Orkney. Fourthly, the North Sea colonies as a whole are showing a gradual overall decline in their rate of increase in pup production even though there has been a rapid increase at the small colony at Donna Nook on the Lincolnshire coast (Text-table 2). Overall, the trend in the rate of increase suggests a gradual decline has been taking place during the past 10 years. In the late 1980s, pup production was increasing at well over 6% per annum and this has declined to less than 2% in the past 5 years.

Pup production fluctuates between years, but in the last 5 years the fluctuations have been larger than previously (Figure 2). This is also reflected in the annual rate of change between years. It is difficult to be sure what causes these changes but they could indicate that the population is nearing its limits of size. To even out these fluctuations the average percentage rate of annual change in the pup production by region is shown in Text-table 2 for the past 5 years and this probably provides 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 site to site and year to year, but that those defining the time to moult and time to leave the colony remain constant. The pup production estimate is sensitive to the value used for the latter parameter and hence there is an argument for allowing this parameter to vary between colonies.

In the past versions of this advice, we have considered the effect of allowing the time-to-leave parameter to vary. However, although the pup production trajectory is slightly lower using the method with variable time-to-leave, the variations in pup production are consistent amongst the two methods. Since we are in the process of developing a new method for estimating pup production from production curves we will not present data using the method involving a variable time-to-leave. This is

consistent with the Advice provided in previous years.

6. Confidence limits

Ninety-five percent confidence limits on the pup production estimates at each colony are within 14% of the point estimate. The exact limits depend on a number of factors including the number of surveys flown in a particular year. Confidence limits can be seen in Figures 3a (Orkney, Inner and Outer Hebrides) and 3b (for Isle of May and Fast Castle only).

7. Pup production at sites surveyed less frequently

Less than 15% of all pups are born at these colonies each year. Confidence limits cannot be calculated for most of these estimates because they represent single counts. Loch Eriboll and Eilean and Ron (Tongue) were surveyed three times and production modelled using a normal rather than a lognormal distribution. South

Ronaldsay was counted four times by SNH and production modelled using a lognormal distribution. The resulting figures are given in Text-table 3.

Text-table 3 shows breeding colonies which are either not surveyed annually or have recently been included in the survey programme. These and other potential breeding colonies are checked when flying time, flying conditions and additional circumstances permit. Accumulated data from colonies that are surveyed on an *ad hoc* basis are given in Data-table 2. Taking all these additional colonies into account, about 6,000 pups are likely to be born at sites that are not part of the main annual survey. A survey of Shetland is overdue. In 1993 and 1994 a partial survey was carried out by E. Brown, Scottish Natural Heritage and SMRU. Compared with 1977, this survey showed increases in pup numbers at some locations with decreases at others.

Text-table 2. Pup production estimates for the main colonies surveyed in 2002. The overall annual changes over successive 5-year periods are also shown. These annual changes represent the exponential rate of change in the pup production. The total for the North Sea represents the combined estimates for the Isle of May, Fast Castle, Farne Islands and Donna Nook.

Location	2002 pup production	Overall annual change in pup production		
		1988-1992	1993-1997	1998-2002
Inner Hebrides	3,096	+9.8%	+2.4%	+0.9%
Outer Hebrides	11,134	+8.5%	+0.9%	-1.6%
Orkney	17,598	+12.5%	+7.6%	+3.0%
Isle of May + Fast Castle	2,509	+18.7%	+8.7%	+3.3%
Farne Islands	1,200	+4.3%	+4.4%	+2.2%
Donna Nook	709	+41.7%	+13.6%	+12.6%
Total (North Sea)	4,418	+12.9%	+7.5%	+4.4%
Total	36,246	+10.4%	+4.4%	+1.4%

Text-table 3. Pup production estimates for breeding colonies surveyed less regularly

Location	Date and location of last survey	Pup production (to nearest 100)
Mainland Scotland & South Ronaldsay	Helmsdale (including Berriedale) 2001	2,765
	Loch Eriboll, E. nan Ron 2002	
	South Ronaldsay 2002	
Shetland	1977	1,000
Southwest Britain	Southwest England 1973	1,750
	Wales 1994	

Data-table 1. Estimates of pup production for the North Sea, Orkney, Outer Hebrides and Inner Hebrides, 1960-2002.

YEAR	North Sea	Orkney	Outer Hebrides	Inner Hebrides
1960	1020	2048		
1961	1141	1846	3142	
1962	1118			
1963	1259			
1964	1439	2048		
1965	1404	2191		
1966	1728	2287	3311	
1967	1779	2390	3265	
1968	1800	2570	3421	
1969	1919	2316		
1970	2002	2535	5070	
1971	2042	2766		
1972	1617		4933	
1973	1678	2581		
1974	1668	2700	6173	
1975	1617	2679	6946	
1976	1426	3247	7147	
1977	1243	3364		
1978	1162	3778	6243	
1979	1620	3971	6670	
1980	1617	4476	8026	

Data-table 1 continued.

YEAR	North Sea	Orkney	Outer Hebrides	Inner Hebrides
1981	1531	5064	8086	
1982	1637	5241	7763	
1983	1238			
1984	1325	4741	7594	1332
1985	1711	5199	8165	1190
1986	1834	5796	8455	1711
1987	1867	6389	8777	2002
1988	1474	5948	8689	1960
1989	1922	6773	9275	1956
1990	2278	6982	9801	2032
1991	2375	8412	10617	2411
1992	2437	9608	12215	2816
1993	2710	10790	11915	2923
1994	2652	11593	12054	2719
1995	2757	12412	12713	3050
1996	2938	14195	13176	3117
1997	3698	14051	11946	3076
1998	3989	16352*	12373	3087
1999	3380	15455*	11683	2787
2000	4303	16281*	13396	3223
2001	4134	17928*	12325	3032**
2002	4418	17598*	11134	3096**

* *Production for Calf of Flotta and South Fara included in the Orkney total for first time*

** Production for Oronsay mainland included in the Inner Hebrides total for first time

These three colonies have been removed from Table 2 and included in the main production Tables for the appropriate island group in the Appendix.

Data-table 2. Scottish grey seal breeding sites that are not surveyed annually and/or have recently been included in the survey programme .

	Location	Survey method	Last surveyed, frequency	Number of pups
Inner Hebrides	Loch Tarbert, Jura	SMRU visual	1998, every 3-4 years	None seen
	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	1999, 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	1998, every 2-3 years	13
	Muck	SMRU photo	1998, every other year	45
	Rum	SNH ground	2001, annual	10-15
	Canna	SMRU photo	1998, every other year	54
	Rona	SMRU visual	1989, infrequent	None seen
	Ascrib Islands, Skye	SMRU photo	1998, 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	2001, 2002	102, 114
	Sound of Harris islands	SMRU photo	2002, every 2-3 years	358
	St Kilda	Warden's reports	Infrequent	Few pups are born
	Shiantas	SMRU visual	1998, every other year	None
	Flannans	SMRU visual	1994, every 2-3 years	None
	Berneray, Lewis	SMRU visual	1991, infrequent	None seen
	Summer Isles	SMRU photo	2002	50
	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	15, 7, 7, 10, 10
	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
Others	North Ronaldsay	SMRU visual	1994, every 2-3 years	None seen
	Eday mainland	SMRU photo	2000, 2002	8, 2
	Firth of Forth islands & Inchcolm	SMRU photo	Infrequent, 1997	<10, 4
	Forth Seabird Group	SMRU photo	2002	30

Figure 1 Map of the UK showing the locations of grey seal breeding colonies

Grey seal breeding sites
in Great Britain

Figure 1



Figure 2. Total estimated pup production for all major breeding colonies in Scotland and England (excluding Loch Eriboll, Helmsdale and Shetland) from 1984 to 2002.

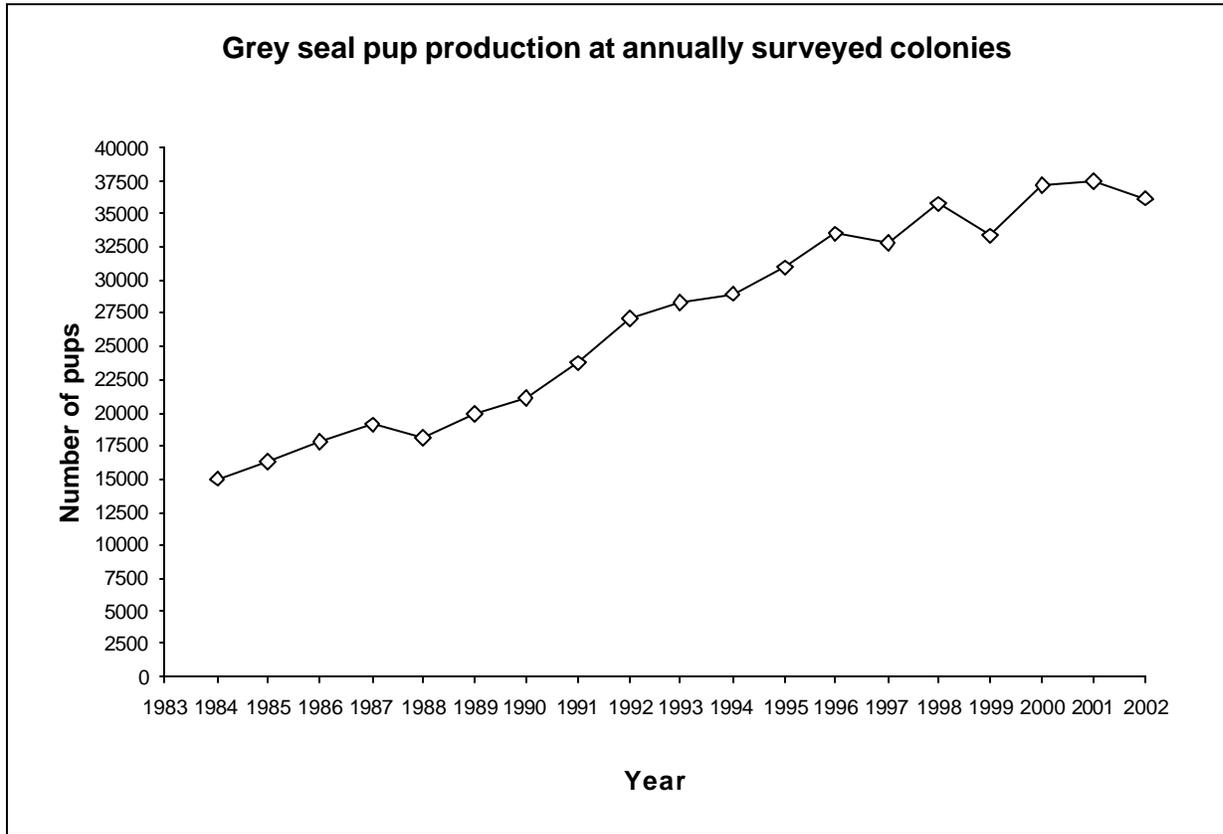
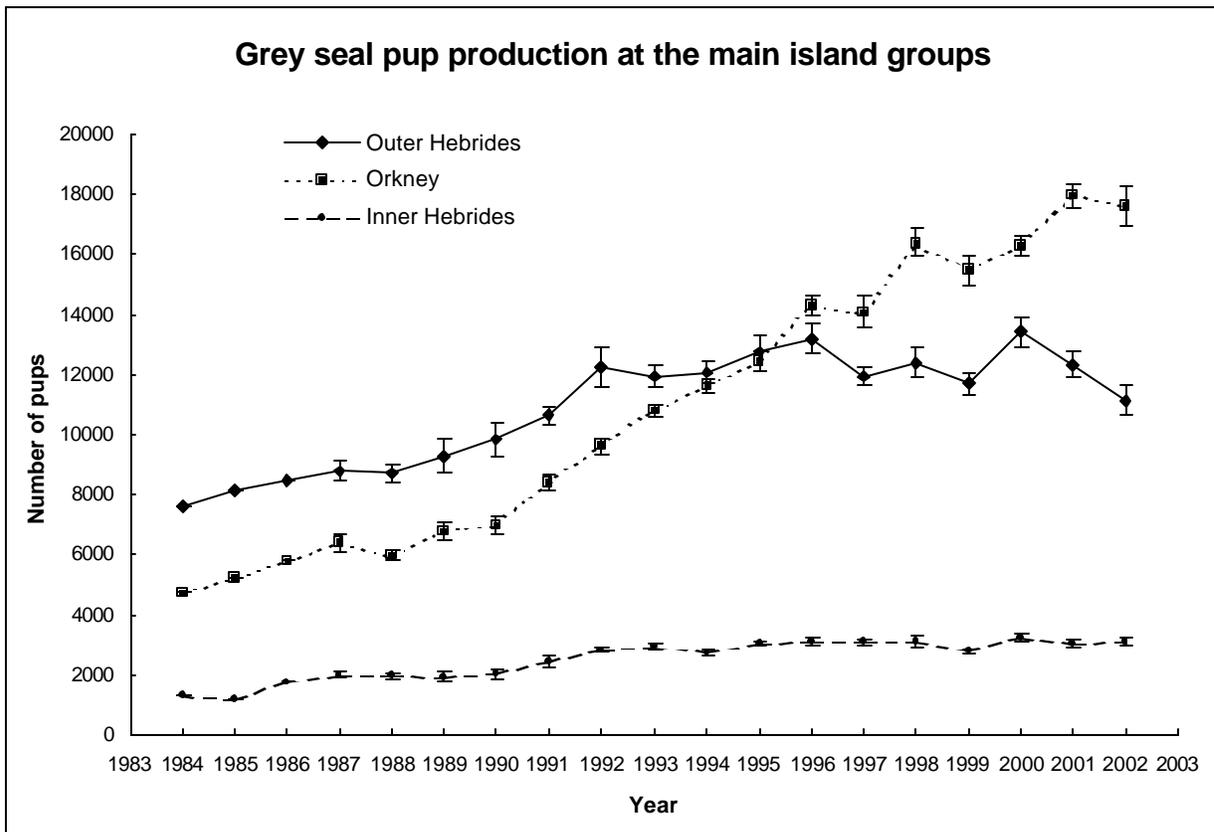
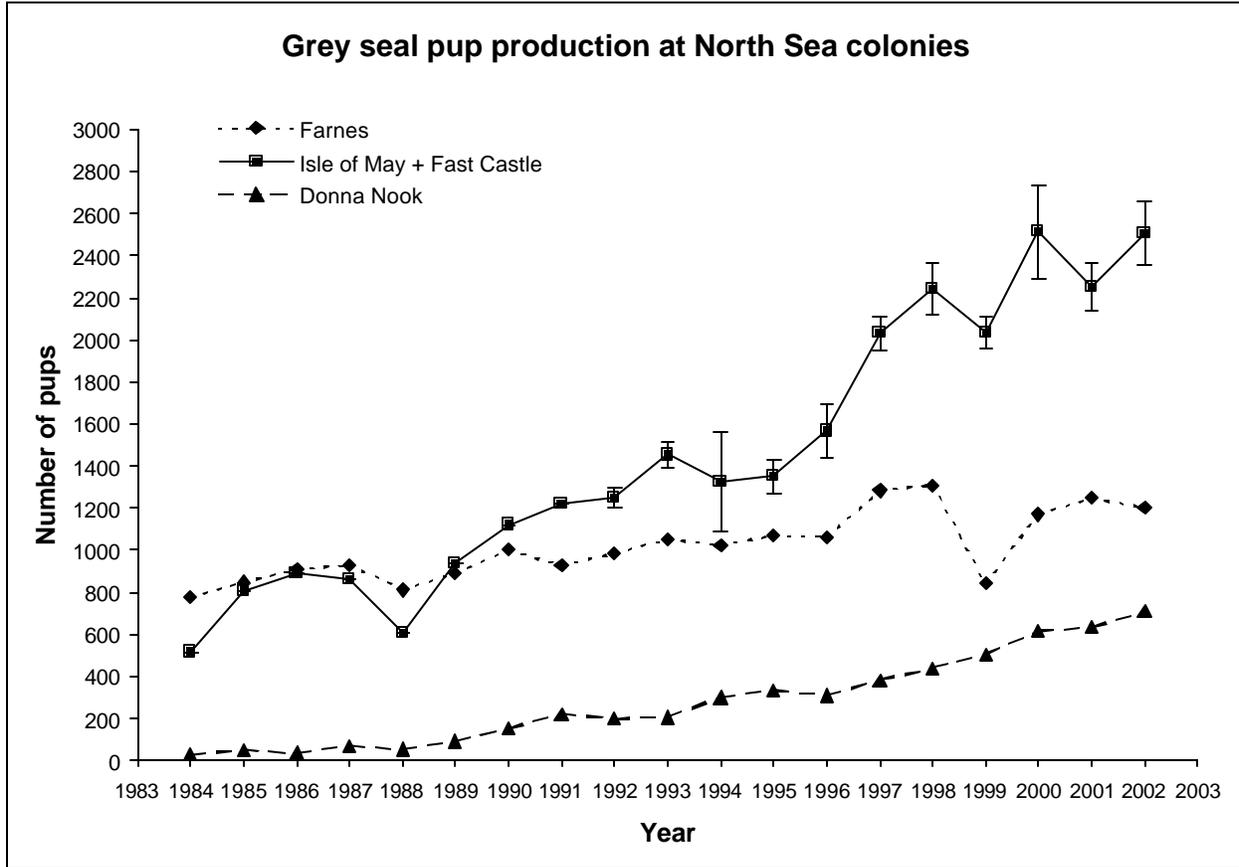


Figure 3 Trends in pup production at the major grey seal breeding areas since 1984. Production values are shown with their upper and lower 95% confidence limits where these are available. These limits assume that the various pup development parameters which are involved in the estimation procedure remain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

(a) Outer Hebrides, Orkney and Inner Hebrides



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



L. Thomas¹, J. Harwood^{1,2}

Estimating Grey Seal Population Size using a Bayesian State-Space Model

¹ Centre for Research into Ecological and Environmental Modelling, The Observatory, University of St Andrews, St Andrews KY16 9LZ

² NERC Sea Mammal Research Unit, Gatty Marine Laboratory, University of St Andrews, St Andrews KY16 8LB

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

Summary

We develop a spatially-explicit, stochastic model of the British grey seal population. We fit the model using a computer-intensive Bayesian technique, using the pup production estimates for each region from 1984-2002 as input data. We give estimates of population parameters, historical population sizes and projections of future populations.

By fitting simpler models, various hypotheses about population processes can be tested. We find evidence for both density dependent juvenile survival and density dependent movement at the regional level.

Introduction

A principal aim of collecting annual pup production data is as a means to monitor total population size of seals. To do this, we must make inferences about the adult population based on the pup data, and this requires a model for the population dynamics. Here, we develop such a model, based on the state-space modelling framework proposed by Buckland *et al.* (in press). Recent advances in computer-intensive statistical inference allow us to fit this kind of stochastic, nonlinear model to the pup production data.

Our model allows for two density-dependent processes: survival of pups and recruitment of adult females to different breeding sites. Although we believe that these processes probably operate at the level of individual colonies, technical considerations have – so far – prevented us from fitting the model at that level. Instead, we have aggregated colony data into four regions: North Sea, Inner Hebrides, Outer Hebrides and Orkney.

We can use the modelling framework to test for evidence of the density dependent processes at the level of the region. To do this, we fit models with the density dependent processes taken out, and compare their fit with that of the full model.

Material and Methods

Here we briefly summarize the model and fitting methods. A more detailed description is given in Thomas *et al.* (in press), although both the movement model and the fitting algorithm have been further refined since that paper was written.

Full Model

A state space model has two components: (1) the state process, which models the true but unknown state of the population; and (2) the observation process, which models how the survey data are generated given the true states.

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

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

Survival is modelled as a binomial random process. Following Harwood (1981), we assume that pup survival is density dependent, and follows a Beverton-Holt function of the form:

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

where $n_{0,r,t-1}$ is the number of pups born in region r in year $t-1$, $f_{p,r,t}$ is survival rate of these pups, $f_{p\max}$ is maximum pup survival

rate, and $1/b_r$ reflects the carrying capacity of the region. Since half of the pups born will be male, the expected number of female pups surviving will be $0.5f_{p,r,t}n_{0,r,t-1}$. We assume that adult female survival rate, f_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 expected survival of their future offspring is higher elsewhere, and the probability of movement is proportional to the expected survival difference. 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:

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

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

$$q_{r \rightarrow i,t} = \begin{cases} g_{sf} & : i = r \\ \frac{g_{dd} \max([f_{p,r,t} - f_{p,i,t}], 0)}{\exp(g_{dist} d_{r,i})} & : i \neq r \end{cases}$$

where g_{sf} , g_{dd} , and g_{dist} are three movement parameters that index the strength of the site fidelity, density dependence and distance effects respectively, 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).

We model breeding by assuming that the number of pups produced is a density independent function of the number of breeding females in the region, with binomial probability a .

For the observation process, we assume that pup production estimates follow a normal distribution with a constant coefficient of

variation (CV). This CV is a model parameter, y , which is estimated from the data.

In summary, the full model contains 11 parameters: adult survival f_a , maximum pup survival, f_{pmax} , one carrying capacity parameter for each region $b_1 - b_4$, three movement parameters g_{sf} , g_{dd} , and g_{dist} , fecundity a and observation CV y .

Reduced Models

We fitted two reduced models to the data. In the first, we assumed no movement between regions. This removed the movement parameters, leaving 8 parameters in the model. In the second we assumed no movement and density independent juvenile survival. This removed both the movement and carrying capacity parameters, leaving 4 parameters in the model.

In the results, we denote the full model M_{full} , the first reduced model M_1 and the second M_2 .

Fitting method

We used an implementation of a class of computer-intensive Bayesian techniques called sequential importance sampling (SIS) to fit the models. This technique is well suited to the analysis of time series data, as each data point is introduced one at a time into the algorithm, making it potentially much more efficient than other computer-intensive techniques such as Markov chain Monte Carlo (MCMC).

The basic idea is as follows. 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 large number of 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. We next resample according to the likelihood weights, so that particles with high likelihoods tend to be retained and those with low likelihood tend to be discarded. We then project forward to the second time period, calculate the likelihood of each particle given the second years’ pup production estimates, resample, and so on to the

end of the data. The distribution of particles at the end gives an estimate of the posterior of the parameters and states.

The basic method outlined above does not work well in practice because with a long enough dataset, we end up discarding almost all the particles: a problem known as ‘particle depletion’. A large number of strategies are available to combat this problem (see Lui 2001 and papers in Doucet *et al.* 2001). We used four strategies here: kernel smoothing of the parameter vectors, auxiliary particle filtering, residual sampling, and partial rejection control. The first three are described briefly in the context of the seal model by Thomas *et al.* (in press); the last is described in Lui (2001). For the record: for all runs shown here we used 400,000 particles, a kernel smoothing discount factor of 0.9 and a partial rejection criterion of the 99th percentile of the distribution of weights. The prior distributions for each parameter are given in Table 1, and are shown on Figure 4. We fit the models using pup production data for the four regions from 1984 to 2002. The first year of data was used to provide priors for the states (see Thomas *et al.* in press for details), and the SIS algorithm ran from 1985 to 2002.

Table 1. Prior parameter distributions

Param	Prior	Expected value
f_a	Beta(22.05,1.15)	0.95
f_{pmax}	Beta(14.53,6.23) Beta(5.45,3.38) ¹	0.7 0.62 ¹
b_1	Gamma(4,2.07x10 ⁻⁴)	8.29x10 ⁻⁴
b_2	Gamma(4, 2.96x10 ⁻⁴)	1.18x10 ⁻³
b_3	Gamma(4,7.40x10 ⁻⁵)	2.96x10 ⁻⁴
b_4	Gamma(4,5.76x10 ⁻⁵)	2.30x10 ⁻⁴
g_{sf}	Gamma(2.25,1.33)	3
g_{dd}	Gamma(2.25,0.49)	ln(3)
g_{dist}	Gamma(2.25,0.22)	0.5
a	Beta(22.05,1.15)	0.95
y	Gamma(4,0.025)	0.10

¹This prior on juvenile survival was used in model M₂, and comes from Hall *et al.* (2001).

Model comparison

For each model, we calculated the likelihood of the posterior pup production in all years, given the priors and all the data, averaged over all particles. We expect models with more

parameters to fit better *a priori*, so we also computed Akaike’s Information Criterion (AIC), a form of penalized likelihood, which adds a penalty proportional to the number of model parameters (Burnham and Anderson 1998). Models were compared using Akaike weights (Burnham and Anderson 1998, p124), which can be thought of in the Bayesian context as the posterior probability of each model being the best approximating model (Akaike 1981).

Predicting future abundances

By projecting the models forward from the posterior distribution of states and parameters it is possible to generate predictions of future numbers of pups and adult females. The models do not include adult males, so it is not possible to say anything about their numbers without making additional assumptions. Here, we followed Hiby and Duck (unpublished) in assuming that the number of adult males is 73% of the number of adult females.

Results

Posterior estimates of true pup production for the three models are shown in Figures 1, 2 and 3 (these estimates are known technically as smoothed estimates; see Thomas *et al.* in press). Both the full model (M_{full}) and the no-movement model (M₁) provide reasonable representations of the observed changes in pup production. M_{full} is slightly better at capturing the very rapid levelling off of pup production in the Inner and Outer Hebrides in the mid-1990s, but neither M_{full} nor M₁ completely capture this feature of the data. Without density dependence (model M₂) the fit to the Hebridean post-1995 data is very poor. This is supported by AIC statistics (Table 2), which show that model M₂ has very little support relative to M_{full} and M₁. In addition, M_{full} is favoured over M₁, providing evidence that density-dependent movement plays a role in regional population dynamics.

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

Model	LnL	AIC	Akaike weight
M _{full}	-527.6	1077.4	0.915
M ₁	-533.1	1082.1	0.085
M ₂	-576.8	1161.6	0.000

Focussing on the full model alone, we give posterior parameter estimates in Figure 4 and an estimate of the 2002 pre-breeding population

size in Table 3. Projecting the estimates from this model forward, we predict that abundance will continue to rise over the next 10 years (Figures 5 and 6, Table 3), but at a decreasing rate (2.4% in 2003-4, down to 1.8% in 2012-13). There is a moderate level of uncertainty about these predictions (95% posterior confidence intervals for the 2003 growth rate are 1.0-3.7% and for 2012 are 0.8-2.5%) and the results are also conditional on the model being correct and on the prior parameter distributions. The increases are predicted to be less in the Inner and Outer Hebrides than in the North Sea and Orkney. Indeed, in the Inner and Outer Hebrides there is a small chance of the population declining slightly (posterior probabilities of a decline are 8.1% and 3.1% respectively).

Table 3. Estimated population size, in thousands, of British grey seals from model M_{full} at the start of the 2002 breeding season and predicted population size before breeding in 2012. Numbers are posterior means with 95% confidence limits in brackets.

Region	2002	2012
North sea	10.2 (9.2-11.5)	11.3 (9.0-14.1)
Inner Hebrides	7.5 (6.9-8.5)	8.1 (6.5-10.1)
Outer Hebrides	30.4 (27.4-34.3)	33.2 (26.5-41.5)
Orkney	44.3 (40.1-50.4)	52.8 (42.7-64.8)
Total	92.5 (83.5-104.8)	105.3 (84.6-130.6)

Discussion

The full model is heavily favoured by the AIC statistic, but there is some Monte-Carlo variation in our results – repeat runs of the models produces slight differences in outputs. We therefore regard our conclusions as tentative at this stage, pending further methodological investigation and tuning of the SIS algorithm.

Our results are also conditional on the prior distributions used for the parameters. The posterior estimates for the movement parameters are similar to the priors (Figure 4), implying that there is relatively little information in the data to inform them. We anticipate that colony-level data will provide more information about movement, and plan on running an analysis at this level in the next year. A NERC/EPSRC funded PhD student is working on providing

independent estimates of migration rates using genetic and mark-recapture information.

Although the current movement model encapsulates the main features we believe influence the dispersal behaviour of breeding females, it is over-simplistic in only allowing recruiting females to choose where to breed based on the previous year's pup production. This produces over-compensatory behaviour, so we are working on an improved movement model that operates in continuous time (Matthiopoulos 2003).

An initial sensitivity analysis shows that the fit of M_{full} is not sensitive to reasonable variations in the assumed prior distribution of \mathbf{f}_a , \mathbf{f}_{pmax}

or \mathbf{a} . However the estimates and predictions of total population size (Table 3, Figures 5 and 6) are sensitive to these assumptions. One way to combat this is to expand the observation model to include independent estimates of adult survival and age structure (Harwood and Prime 1978) and pregnancy rates (Boyd 1985) from culled seals, and of adult survival (Pomeroy, unpublished) and juvenile survival (Hall et al. 2001) from tagged seals. An assumption must be made that these data are representative of the population they are applied to, and this is not necessarily valid as seal data is rarely collected from a random sample.

Hiby and Duck (unpublished) give an estimate of the total pre-breeding population size for 1999 of 109,000 with 95% CI 93,000-126,000. For comparison, our estimate for the same year (to the nearest thousand) is 85,000 with 95% CI 79,000-96,000 – about 20% lower. The main difference between Hiby and Duck's model and the one used here is that their model is density independent while ours includes density dependent pup survival (ours also includes movement, but that does not change the total population figures appreciably). Our estimates of pup survival are considerably lower (mean posterior estimates for 1999 in the 4 regions are 0.17, 0.15, 0.16 and 0.19, compared with Hiby and Duck's overall estimate of 0.39), which results in fewer non-breeding adult females. Hiby and Duck considered a model where pup survival showed a linear decline since 1989, but found insufficient evidence to support it in the data. They point out that such a model leads to significantly fewer females (their Figure 2). Hall et al. (2001) estimated first year female pup survival at the Isle of May (a North Sea colony) to be 0.617 (SE 0.155). This data could be incorporated into our observation model, but

more information about juvenile survival in other regions will be needed to improve the overall reliability of the model predictions.

Other planned improvements include: addition of a random effect for fecundity, allowing it to vary each year around a pre-defined mean (c.f. unexplained dip in pup production in all regions in 1999 in Figures 1-3); possible inclusion of covariates such as the North Atlantic Oscillation; and a more flexible form for density dependent survival that would allow survival to remain high until colonies become very crowded.

One strength of the Bayesian fitting method is that we can make projections of future population sizes that incorporate both uncertainty in parameter values and also uncertainty about which model is correct. If, for example, two models have posterior Akiake weights of 0.5 each, then we can project forward using equal numbers of particles from the two models. In the current case, with M_{full} getting a 91.5% posterior weight, this was not thought necessary – but this could change in the future as more models are considered.

The SIS algorithm is a relatively recent tool for fitting complex biological models to different sources of data, and there are a number of research avenues to be followed there. The model M_2 is linear and approximately normal, so could be fit using the well-established Kalman filter method, building on recent work by Besbeas et al (2002). The more complex models could be compared with the outputs from a MCMC analysis, although an efficient way to perform such an analysis would have to be devised. We also plan to investigate other strategies to avoid particle depletion in SIS, such as simulated tempering and multiple time-step look-ahead, and to further explore the optimum level of kernel smoothing.

References

Akiake, H. 1981. Likelihood of a model and information criteria. *Journal of Econometrics* 16:3-14.

Besbeas, P., J. Harwood, B.J.T. Morgan and P. Pomeroy. 2002. Integrated analysis of grey seal data. Report UKC/IMS/02/36, IMS, University of Kent, UK.

Boyd, I.L. 1985. Pregnancy and ovulation rates in grey seals *Halichoerus grypus* on the British coast. *Journal of Zoology* 205: 265-272.

Buckland, S.T., K.B. Newman, L. Thomas, and N. Kösters. In press. State-space models for the dynamics of wild animal populations. *Ecological Modelling*.

Burnham, K.P. and D.R. Anderson. 1998. *Model Selection and Inference: A Practical Information-theoretic Approach*. Springer-Verlag, New York.

Doucet, A., N. de Freitas and N. Gordon [eds.]. 2001. *Sequential Monte Carlo Methods in Practice*. Springer-Verlag, New York.

Hall, A.J., B.J. McConnell and R.J. Barker. 2001. Factors affecting first-year survival in grey seals and their implications for life history strategy. *Journal of Animal Ecology* 70: 138-149.

Harwood, J. 1981. Managing grey seal populations for optimum stability. Pp 159-172 in: C.W. Fowler and T.D. Smith. (Eds.) *Dynamics of Large Mammal Populations*. Joun Wiley & Sons, New York.

Harwood, J. and J.H. Prime. 1978. Some factors affecting the size of British grey seal populations. *Journal of Applied Ecology* 15: 401-411.

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

Lui, J.S. 2001. *Monte Carlo Strategies in Scientific Computing*. Springer-Verlag, New York.

Matthiopoulos, J. 2003. Modelling the between-year movement of grey seals and their population consequences. SCOS Briefing Paper.

Ruxton, G.D. and P. Rohani. 1998. Fitness-dependent dispersal in metapopulations and its consequences for persistence and synchrony. *Journal of Animal Ecology* 67: 530-539.

Thomas, L., S.T. Buckland, K.B. Newman, and J. Harwood. In press. A unified framework for modelling wildlife population dynamics. *Australian and New Zealand Journal of Statistics*.

Figure 1. Estimates of pup production from the full model, M_{full} . Input data are shown as circles, and the lines represent the mean of the particle values bracketed by 2.5th and 97.5th percentiles, which can be thought of as posterior 95% confidence intervals..

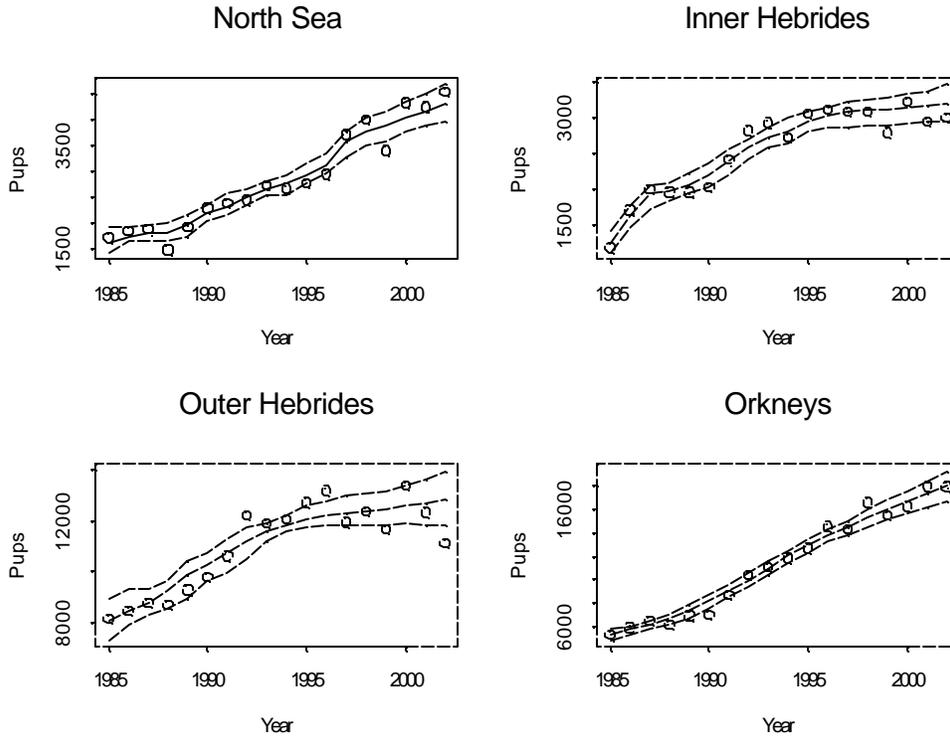


Figure 2. Estimates of pup production from the no-movement model, M_1 .

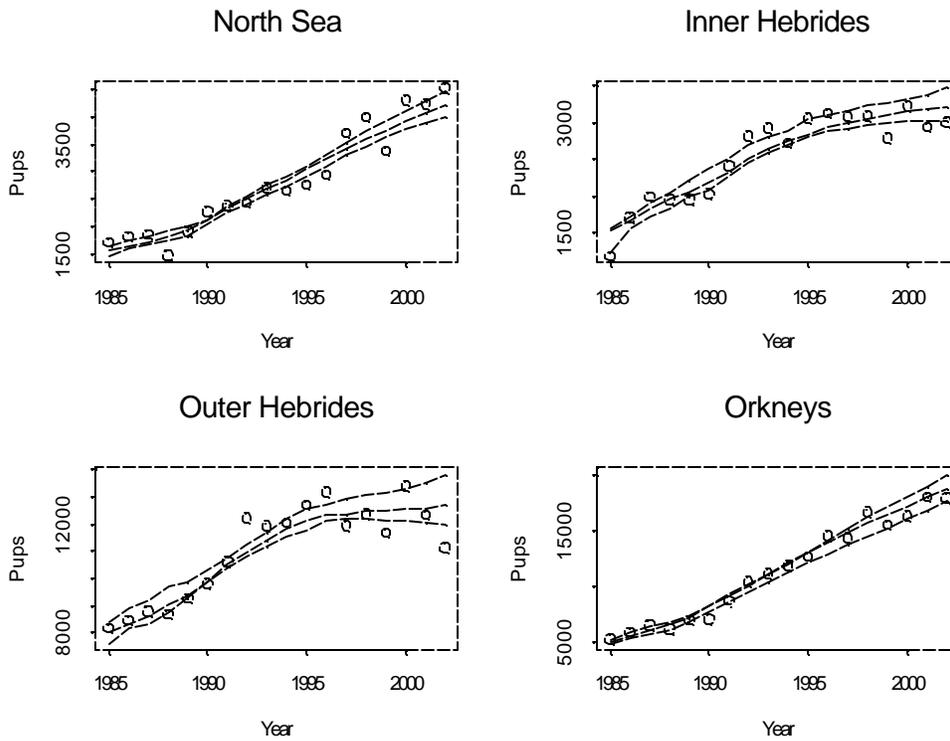


Figure 3. Estimates of pup production from the no-movement and no density dependence model, M_2 .

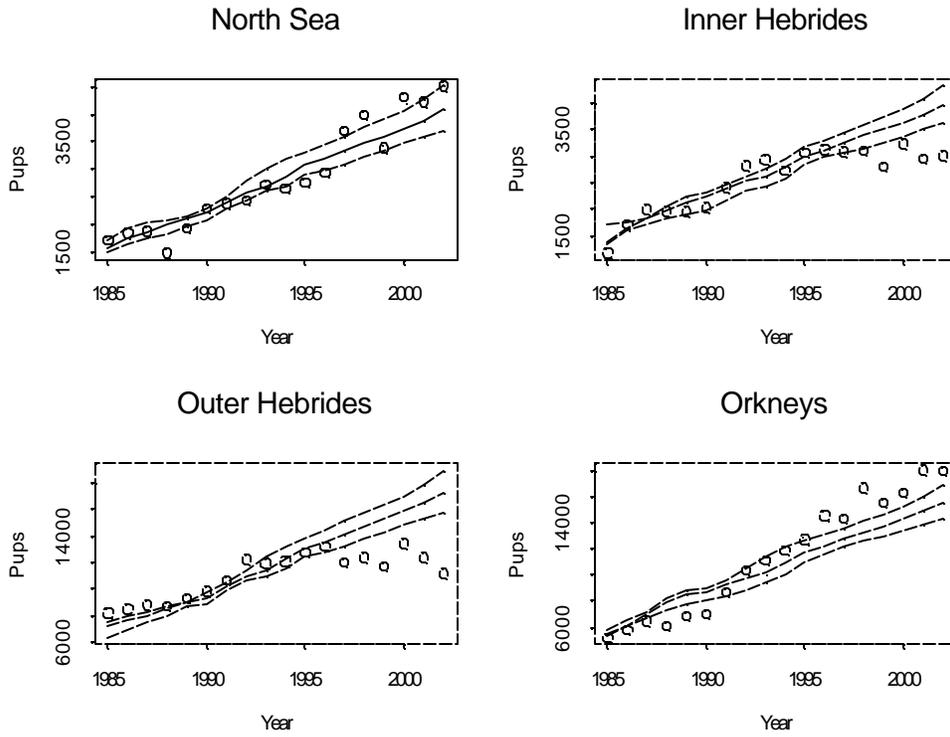


Figure 4. Posterior parameter estimates (histograms) and priors (solid lines) from M_{full} . Vertical line shows posterior mean, and this value is given in the title of each plot after the parameter name.

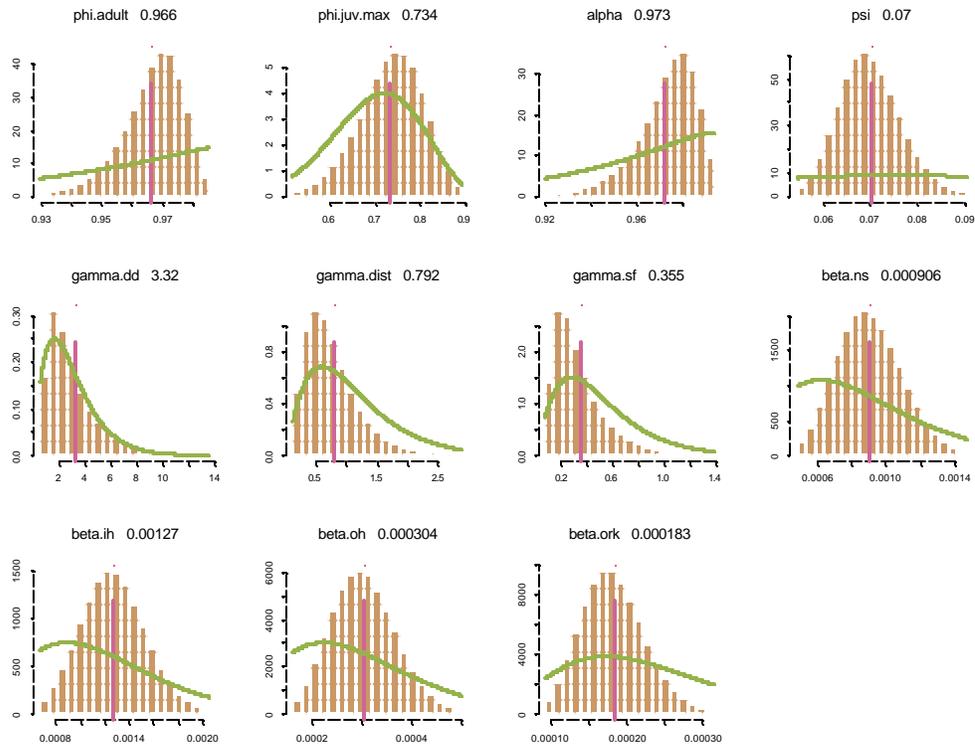


Figure 5. Predicted regional pre-breeding population size of British grey seals 2003-2012 from model M_{full} .

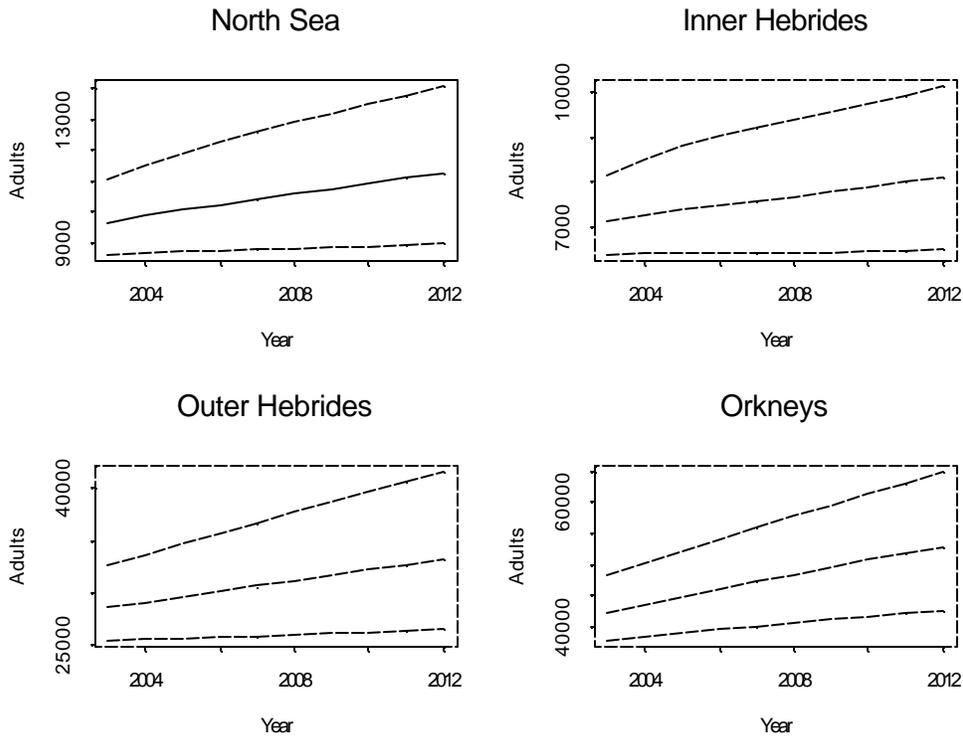
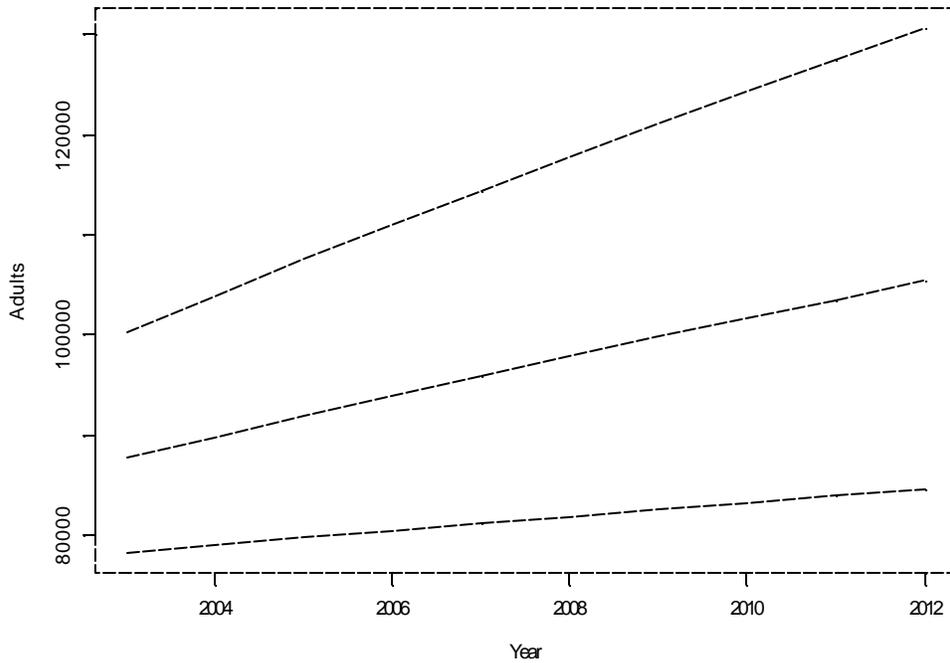


Figure 6. Predicted total pre-breeding population size of British grey seals 2003-2012 from model M_{full} .



A.R. Hiby¹ & C. D. Duck²
Grey seal total population estimate, 2002

¹Conservation Research Ltd., 110 Hinton Way, Cambridge CB2 5AL; ²NERC Sea Mammal Research Unit, Gatty Marine Laboratory, University of St Andrews, St Andrews KY16 8LB

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

Summary

This document presents the estimates of the size of the total British grey seal population and the size of the female population. These estimates were derived from the model developed by A R Hiby. This is the ‘traditional’ model which has been used to estimate these numbers in previous years. The document should be considered in conjunction with a second analysis using the same model, investigating whether effects of density dependence are influencing the population trajectories (SCOS-BP 03/5).

seal breeding colonies, a reanalysis investigating the effect of altering one of the density dependent parameters incorporated in the model was carried out. The results of this analysis are documented elsewhere (SCOS-BP 03/5).

Methods

The method (model) used here to estimate size of the total grey seal population and the total female grey seal population is the same as used in previous years.

Results

The estimate of the total grey seal population at annually monitored colonies was 116,000. The 95% confidence limits for the entire female population are within 13% of the point estimate (58,000 to 75,000). According to these estimates, there were 117,300 grey seals associated with Scottish breeding colonies and 11,300 associated with colonies in England and Wales. Figure 5 shows these population trajectories.

Introduction

This document presents the results of the estimation of the size of the total female grey seal population and of the total grey seal population using the Hiby model. The pros and cons of this model have been discussed in detail in previous SCOS documents. For consistency and comparability, the results from this model should be presented in parallel with those from alternative models, most of which are still ‘under construction’.

Following the recent changes in the trajectory of pup production at the annually monitored grey

Table 1. Estimated size of the grey seal population associated with all the major, annually monitored, breeding colonies around Scotland and eastern England with the exception of Loch Eriboll, Helmsdale, South Ronaldsay and Shetland. The female and total population estimates refer to the number of seals aged 1 and over at the start of the 2002 breeding season.

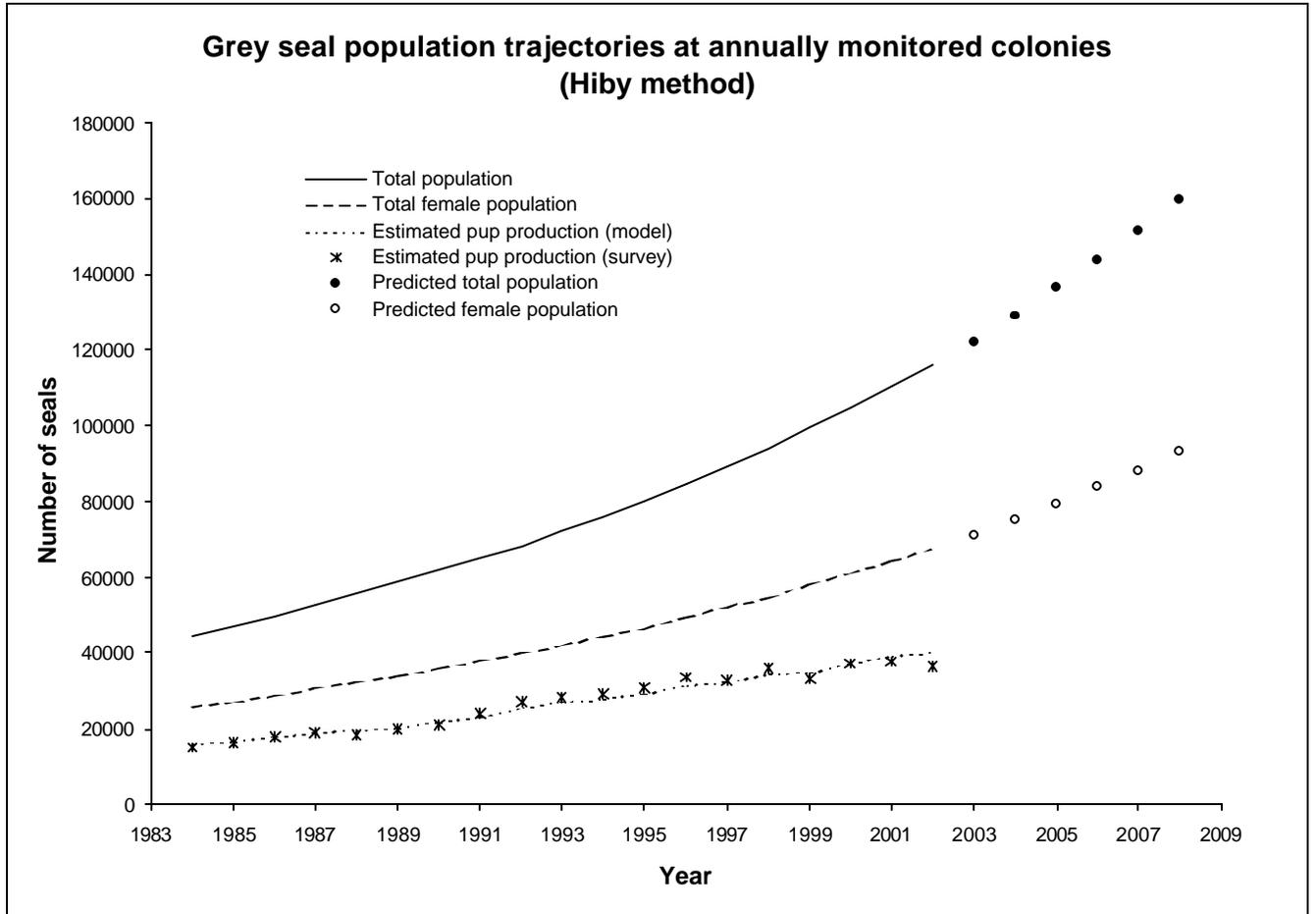
Year	Estimated pup production (survey)	Total female population	Total population
1984	14,992	25,781	44,401
1985	16,265	27,254	46,920

1986	17,796	28,826	49,616
1987	19,035	30,549	52,592
1988	18,071	32,401	55,798
1989	19,926	34,105	58,683
1990	21,093	35,924	61,767
1991	23,815	37,838	65,008
1992	27,075	39,905	68,514
1993	28,338	42,010	72,072
1994	29,018	44,298	75,966
1995	30,932	46,668	79,993
1996	33,504	49,325	84,559
1997	32,771	52,085	89,295
1998	35,801	54,778	93,857
1999	33,305	58,054	99,544
2000	37,203	61,113	104,743
2001	37,419	64,343	110,234
2002	36,246	67,737	116,008

Table 2. Pup production and associated population size for the annually monitored colonies and for colonies monitored less frequently.

Location	2002 pup production	Change in pup production 2001-2002	Total 2002 population (to nearest 100) aged =1
Inner Hebrides	3,096	+2.1%	9,900
Outer Hebrides	11,134	-10.7%	35,600
Orkney	17,598	-1.9%	56,323
Isle of May + Fast Castle	2,509	+10.2%	8,000
Farne Islands	1,200	-3.9%	3,800
Donna Nook	709	+10.6%	2,300
Subtotal	36,246	-3.2%	116,000
SW England & Wales	1,750		5,600
All other colonies (in Scotland)	3,765		12,000
Total	41,761		133,600

Figure 1. Grey seal population trajectories at the annually monitored colonies around Britain. These data have been generated using the Hiby & Duck method and can be compared with results presented to SCOS in previous years. Predictions for the years 2003 to 2008 are included.



A.R. Hiby

Changes in UK grey seal demographic parameters and consequences for estimation of population size

A report to SCOS 2003 by Conservation Research Ltd under contract to the Sea Mammal Research Unit. Conservation Research Ltd, 110 Hinton Way, Cambridge CB2 5AL, UK, email: hiby@ntlworld.com

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

The Sea Mammal Research Unit has used a consistent technique to monitor grey seal pup production on all major UK breeding sites since 1984. Aerial survey pup counts are used to derive maximum likelihood estimates of birth curve parameters and the number of pups born at each site. Those numbers are then summed each year over all sites to generate a trajectory of total pup production estimates (illustrated as the “pest” sequence in the figure below).

To estimate the number of female grey seals aged one year and over at the time of the breeding season, a stochastic model has been used to generate the likelihood of this trajectory of production estimates (plus data from the Farne Islands on pregnancy rate, age structure and age at first pregnancy) as a function of a vector of demographic parameters. Having maximised the likelihood with respect to those parameters, the probability density for the all-age female population size, conditional on the “pest” trajectory and other data, can be derived from the stochastic model and used to provide point and interval estimates in each year. Revised estimates of the annual pup production can also be obtained by conditioning on the full “pest” trajectory and other data. The model is described in the manuscript “Point and interval estimates of the size of the British grey seal population ...”, which has been provided at previous SCOS meetings. The manuscript has been accepted for publication with revisions but has not been revised and resubmitted.

The figure shows two sets of point estimates for pup production and all-age female population size. The “fixfem” and “fixpup” estimates were produced by the stochastic model used routinely, in which juvenile survival and age at first pregnancy fluctuate independently from year to year about constant mean levels. Adult survival and pregnancy rate are assumed to be subject to less variability and are constants in the model. The “freefem” and “freepup” estimates were

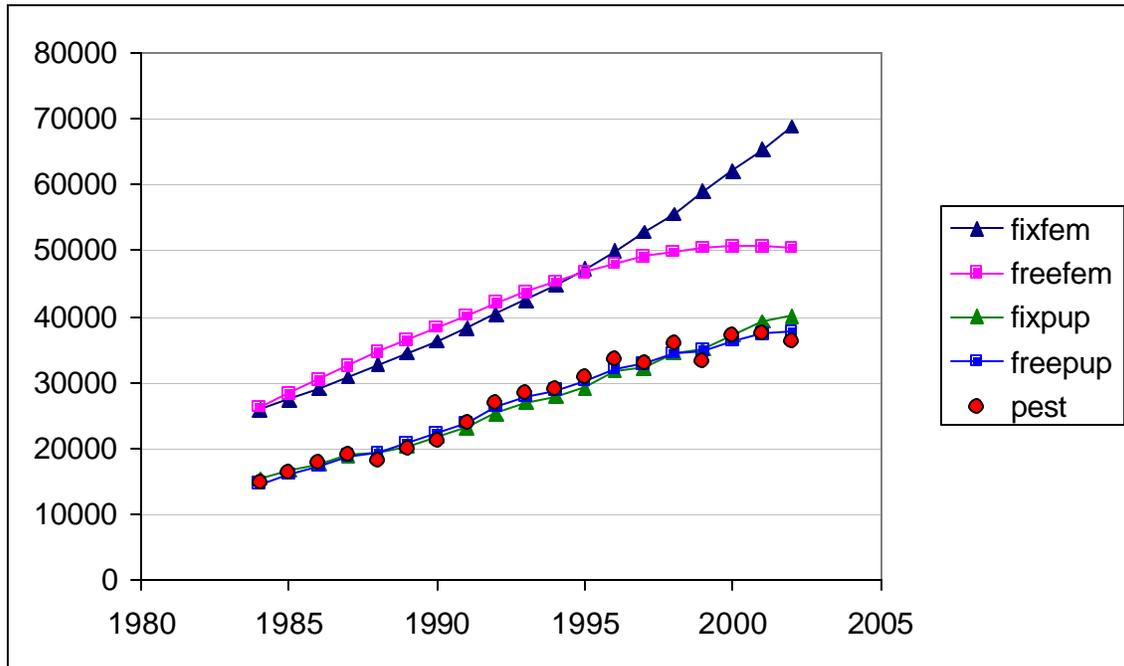
produced by allowing the mean level about which juvenile survival fluctuates to change over time. The resulting trajectory of all-age female population estimates differs markedly from the “fixfem” series and the point estimate for 2002 is below the lower 95% confidence limit calculated using the routine model. The sensitivity of population size estimates to possible trends in the demographic parameters was mentioned in the manuscript but at that time the improvement in fit to the data on allowing mean levels to change was not significant. With the addition of the 2002 “pest” estimate to the trajectory the increase in the likelihood is significant at the 5% level.

If the 19 years of “pest” data were a random selection these results would allow us to reject the hypothesis that mean levels of all demographic parameters remain unchanged. However, by re-assessing the question of change in demographic parameters at each SCOS meeting we are effectively carrying out a “sequential testing” experiment which will have a different test size from one based on a single, randomly selected sequence of years. It is not clear (to me) how the size of the test should be modified to allow for this sequential testing. However, it is also unclear why point and interval estimates from one model should be accepted anyway when an equally plausible model generates markedly different estimates, even if the fit of the second model is not significantly better than the first. Choosing the simpler model is merely a convention. To have confidence in the “confidence intervals” requires that equally plausible models produce similar estimates.

It is unlikely that revising the stochastic model will resolve this issue. The “pest” trajectory alone is not sufficient to determine the current status of the all-age population and the additional

data from the Farne Islands are now two decades out of date. Possible sources of additional data that could reduce the uncertainty about current trends are: recent mark/recapture estimates of survival to age one (though survival to recruitment is the critical parameter for the model); return rates of branded pups as breeding

females at the Isle of May (though unknown rates of dispersal to other sites is a problem); haul-out counts of grey seals obtained during thermal survey of common seal moulting haul-outs; photo-id work to match flank patterns on weaned pups and breeding females after a minimum four-year interval.



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

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

Summary

In August 2002, SMRU conducted surveys of common seals in Lincolnshire, Norfolk, Essex and Kent in England; in part of the Outer Hebrides, the Firth of Tay and the Moray Firth in Scotland; and for the first time, in Northern 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 2001 and within 1% of the pre-Phocine Distemper Virus (PDV) 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 2002 were substantially lower than in previous years, particularly in the Inner Moray Firth (at Ardersier and Beaully, Cromarty and Dornoch Firths). In the Firth of Tay, numbers were similar to previous counts.

The Sounds of Barra and Harris were surveyed for Scottish Natural Heritage for additional data relating to the selection of a Special Area of Conservation for common seals in the Western Isles. Numbers of common seals in both of these areas were lower than in any previous August survey.

Following the outbreak of PDV in August 2002, we anticipate a marked decline in numbers in 2003. The effects will likely be more pronounced in East Anglia as large numbers of seals were found dead in the southern North Sea. Relatively small numbers of dead seals were reported from Scotland and mortality appeared to be more confined to the south-east coast of Britain than in 1988.

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. Mortality was greatest in colonies in south-east England. 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.

Results

1. Common seals surveys 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 2002 (Table 1). Bad weather prevented surveying at Donna Nook on the second flight and at Scroby Sands on both flights. The mean count for The Wash (2,976)

was 6.8% lower than the 2001 count (3,194). The higher of the two counts obtained (3,037) was 5% lower than the 2001 count. The average annual rate of increase in the number of seals counted in The Wash since 1989 is 6.1% (SE = 0.50%). This is significantly greater than the average annual rate of increase between 1968 and 1988 of 3.5% (SE = 0.29%) (figure 1). The higher of the 2002 counts of common seals in The Wash was similar to the 1988 pre-epidemic count. It has taken 13 years for the population to recover from the effects of the PDV epidemic. This is in contrast to populations on the east and south sides of the North Sea, which recovered more rapidly and were similar to or exceeded their pre-epidemic levels by 1996.

The highest count at Blakeney in 2002 was 18% lower than the 2001 count, while the count at Donna Nook was 46% higher than in 2001 (Table 1). The average annual rates of increase in the number of seals counted at these sites since 1989 were 12.5% (SE=2.7%) and 19.4% (SE=3.9% respectively. These rates of increase are significantly higher than in The Wash. However, there has been no significant increase at either Blakeney or Donna Nook since 1997.

Overall, the English east coast population increased at an average annual rate of 7.2% (SE=0.49%) between

1989 and 2002.

2. Common seals in Scotland

In August 2002, areas surveyed for common seals included part of the Outer Hebrides, the Firth of Tay and the Inner Moray Firth. 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 common seals under the European Union's Habitat's Directive. The Firth of Tay and the Moray Firth were surveyed for DEFRA to provide baseline information in anticipation of increased mortality due to the PDV epizootic which was affecting colonies in the southern North Sea.

SMRU's aerial surveys of this area began in August 1992 and counts are in Table 2. Numbers of common seals in the Moray Firth appear to have declined in the Inner Moray Firth, an area where a bounty system has been in operation at least between 2000 and 2002. 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. More detailed counts of common seals in the Moray Firth have been made by Paul Thompson from Aberdeen University's Lighthouse Field Station, in Cromarty, since 1988.

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

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

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

SMRU's aerial surveys of common seals in the Firth of Tay began in August 1990. 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).

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

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

The Sound of Barra and the Sound of Harris, in the Outer Hebrides, were surveyed for common seals for Scottish Natural Heritage, as part of the investigation into suitable sites for designation as Special Areas of Conservation. The numbers of common seals counted

in these two areas are in Table 4. The 2002 counts for both the Sound of Barra and the Sound of Harris were the lowest moult counts recorded. These areas will be resurveyed in August 2003.

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
Sound of Barra pSAC	762	287	510	94	140	127
Sound of Barra, remainder	123	45	97	43	169	156
Sound of Barra Total	885	332	607	137	309	255
Sound of Harris	375	107	471	184	323	180
Outer Hebrides total	2329		2820		2413	

*Breeding season surveys, remainder during August moult. The surveys in July 1996, July and August 2000 and August 2002 were funded by Scottish Natural Heritage.

Table 5. Numbers of common and grey seals in subregions of Northern Ireland. The two adjacent subregions in the Irish Republic are included (Carlingford Lough West and Lough Foyle West).

Date	Region	Subregion	Unknowns	Harbour seals	Grey seals
15 Aug 2002	Louth (S. Ireland)	Carlingford Lough W	0	56	4
15 Aug 2002	Antrim	Carlingford Lough E	0	201	0
	Antrim	Newcastle	0	2	0
	Antrim	Dundrum	1	299	0
	Antrim	Strangford Lough	0	180	0
	Antrim	The Ards	1	264	35
	Antrim	Copelands	0	65	46
	Antrim	Belfast Lough S	0	63	0
	Antrim Total		2	1074	81
15 Aug 2002	Down	Belfast Lough N	0	3	0
16 Aug 2002	Down	Madman's Window	0	40	11
	Down	Red Bay	0	0	0
*14 Aug 2002	Down	Rathlin Island	0	(34)	(4)
16 Aug 2002	Down	Rathlin Island	0	128	1
14Aug 2002	Down	Ballycastle	0	0	7
	Down Total		0	171	19
14Aug 2002	Londonderry	Port Rush	0	0	0
	Londonderry	Lough Foyle East	0	3	0
	Derry Total		0	3	0
14Aug 2002	Donegal (S. Ireland)	Lough Foyle west	0	2	0
14-16 Aug 2002	Northern Ireland total		2	1,248	100
14-16 Aug 2002	Survey total		2	1,306	104

* First survey of Rathlin Island not used in totals as surveyed early in the low tide

3. Common seals in Northern Ireland

The Environment and Heritage Service of Northern Ireland commissioned a survey of harbour seals in August 2002. This is the first complete survey of harbour seals in the Province since the 1978 breeding season (Summers *et al.* 1980) and was carried out using a helicopter equipped with a thermal imaging camera. This survey coincided with a more-or-less simultaneous series of ground counts of the main haulout sites by Heritage Service staff and others. Counts are presented in Table 5. 1248 seals were counted in Northern Ireland (Table 5). This total was considerably more than the Heritage Service had expected. This, in part, reflects the advantage of using the helicopter and thermal imager system that enabled all of the coast used by 86% of the common seals seen in Northern Ireland to be surveyed within the same low tide.

4. 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 29,763 from surveys carried out in 1996, 1997, 2000, 2001 and 2002. The most recent minimum estimate for England is 4,018. This comprises 3,882 seals in Lincolnshire and Norfolk in 2002 plus 117 seals in Northumberland, Cleveland, Essex and Kent between 1994 and 2002 and an estimated 20 seals from the south and west coasts.

Table 6 contains counts by region for the period 1996 - 2002. 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.

5. Common seal surveys proposed for 2003

Common seals in the Outer Hebrides (full island survey), Orkney, the Republic of Ireland and the east coast of Britain between the Moray Firth and Thames Estuary are due to be surveyed in August 2003. The east coast and Orkney surveys will provide the data required to assess the impact of the 2002 PDV epizootic. There was a large mortality in south-east England but mortality in Scotland appeared to be considerably lower than in 1988. These surveys will be funded by SNH, DEFRA and Duchas (Ireland). We propose to conduct a series of surveys on consecutive days in the Firth of Tay and Moray Firth to estimate the variability in numbers of seals ashore during their annual moult.

References

Summers C.F., Warner, P.J., Nairn, R.G.W., Curry, M.G. & Flynn, J. 1980. An assessment of the common seal *Phoca vitulina vitulina* in Ireland. *Biological Conservation*. **17**:115-123.

Table 6. Minimum estimates of the UK common seal population by region

Region	Year of survey	1996-2002
Shetland	2001	4,883
Orkney	2001	7,752
Outer Hebrides	2000	2,413
Highland East & North (Nairn to Cape Wrath)	1997, 2002	910
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, 2002	159
Tayside (Newburgh to Montrose)	1997, 2002	109
Fife (Kincardine Bridge to Newburgh)	1997, 2002	635
Lothian (Torness Power Station to Kincardine Bridge)	1997	40
Borders (Berwick upon Tweed to Torness Power Station)	1997	0
TOTAL SCOTLAND		29,763
Blakeney Point	2002	489
The Wash	2002	2,976
Donna Nook	2002	341
Scroby Sands	2001	75
Other east coast sites	1994, 2000, 2002	117
South and west England (estimated)		20
TOTAL ENGLAND		4,018
TOTAL BRITAIN		33,781
TOTAL NORTHERN IRELAND	2002	1,248
TOTAL BRITAIN & N. IRELAND		35,029

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	11.8.90	2.8.91	1.8.92	8.8.93	6.8.94	5.8.95	2.8.96	2.8.97	7.8.98	3.8.99	4.8. 00	4.8.01	11.8.02
		12.8.89		11.8.91	16.8.92		12.8.94	15.8.95		8.8.97	14.8.98	13.8.99	12.8.00		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
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
Donna Nook	173	- 126	57	- -	18 -	88	60 146	115 36	162	240 262	294 201	321 286	435 345	233	341 -
Scroby Sands	-	- -	-	- -	- -	-	61 -	- 49	51	58 72	52 -	69 74	84 9	75	-
The Tees	-	- -	-	- -	- -	-	- 35	- -	-	- -	- -	- -	- -	-	- -
Holy Island	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Northumberland	-	-	-	-	-	-	13	-	-	12	-	-	10	-	-
Essex & Kent	-	- -	-	- -	- -	-	- -	90 -	-	- -	- -	- -	- -	-	- 72

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

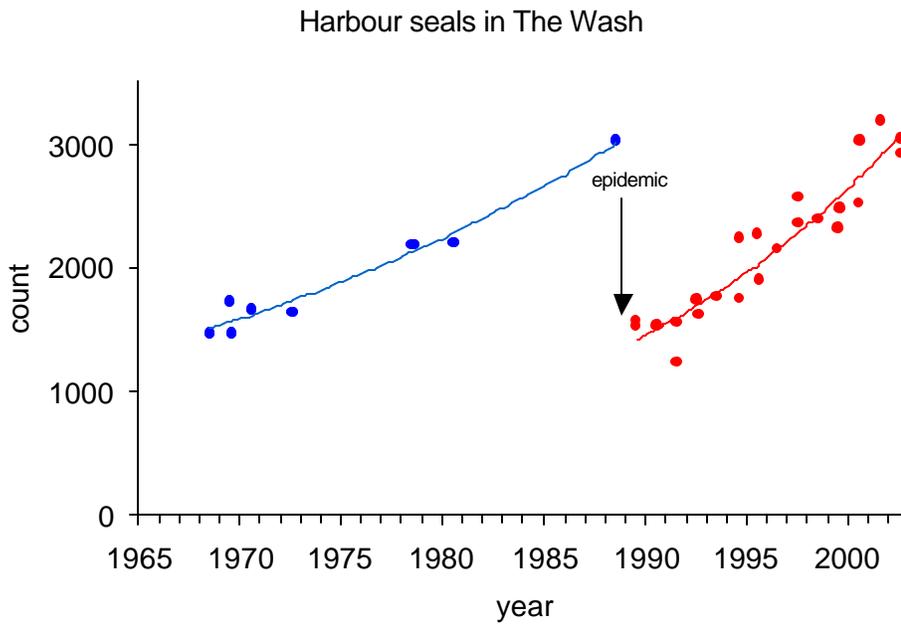


Figure 1. Counts of common seals in The Wash in August. These data are an index of the population size through time. Fitted lines are exponential growth curves (growth rates given in text).

J. Matthiopoulos**The distribution of grey seals around the Scottish coasts outside the breeding season**

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

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

Summary

In the UK, conservation of the population of grey seals and management of fish stocks have often come into conflict. The consensus is that this can only be resolved with detailed knowledge of the seals' distribution on the coast and at sea, outside the breeding season. We present here, a large-scale, high-resolution analysis and synthesis of telemetry and aerial survey data on the marine movements and coastal distribution of grey seals. Our approach is a combination of modelling and interpolation based on these diverse data.

1. Introduction

The requirements of seal conservation and fisheries management can, and have in the past, come into conflict. Given that the extent of overlap between seal foraging and human activity depends on the fine-scale spatial distribution of the seals' foraging effort UK government bodies have invested in studies aimed at obtaining and analyzing data on the coastal and marine distribution of the species. Here, we present the data collected by these studies and synthesise them into a reliable map of the use of space by those grey seals associated with the UK coasts and waters. The quantity, diversity and scale of the data used and the statistical robustness of the estimation procedures make this study unique to aquatic animals in general, marine mammals, and grey seals in particular.

2. Distribution of grey seals around the UK

As grey seals are central-place foragers with close associations to particular coastal sites (the haulouts) our approach firstly subdivides the population into subpopulations associated with 24 haulout regions. We then use auxiliary information on seal movement (speed, trip duration, locations of haulouts, obstacles to movement) to estimate the relative accessibility (Matthiopoulos 2003a) of marine locations from each haulout region.

Maps of accessibility are used to supervise non-parametric surface-fitting (Matthiopoulos 2003b) on

satellite telemetry data hence providing a map of the marine usage radiating from each haulout region.

The number of animals associated with each haulout and the corresponding uncertainty in these numbers are obtained from aerial survey data via a simple Bayesian calculation (Matthiopoulos *et al.* In prep).

Finally, maps of usage from each haulout region are weighted by the numbers of animals associated with it. These are then superimposed to yield the aggregate map of usage for the whole of the British isles (Fig. 1).

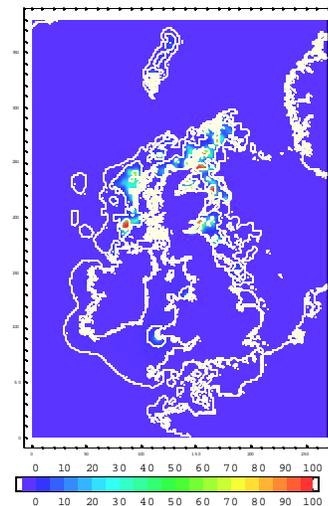


Figure 1: Distribution of the UK population of grey seals

3. Sampling effort

The satellite tagging effort at different haulout regions was not balanced. Consequently, the estimate of usage at different points at sea is made on the basis of a variable number of tags and therefore estimates of usage at different points at sea would be subject to variable degrees of sampling error. An informative map of relative effort can be obtained by quantifying the number of tagged animals that use a location as a proportion of the total number of animals using that location (Matthiopoulos *et al.* In prep).

Plotting this index in our spatial grid (Fig. 2) reveals that less effort is associated with the south and

east of the British Isles. We would therefore expect the usage estimates made about these regions to be less precise compared to predictions for the north and east.

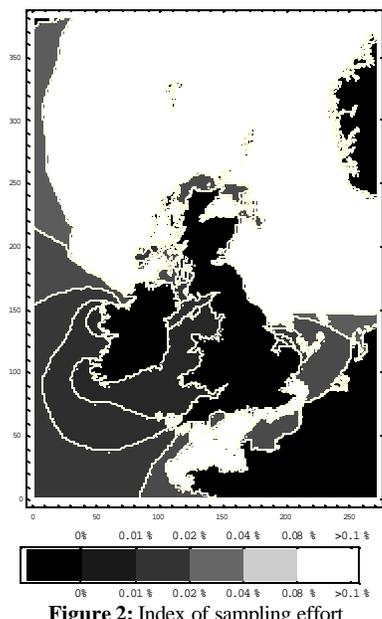


Figure 2: Index of sampling effort

4. Focus on the Scottish coasts

As the majority of the grey seal population is concentrated around the Scottish coasts, data collection has been focused in this region. For the data-rich North, we have been able to quantify not only mean usage of different locations at sea (Fig. 3a), but also, the uncertainty in these estimates.

We have dealt with two types of uncertainty, 1) sampling error in the satellite tag data and 2) uncertainty in the numbers of animals associated with different haulout regions. Using the individual tagged animal as our sampling unit, we have quantified sampling error for all 16 haulout regions for which we had two, or more, tagged animals. Using a simple Bayesian model we have quantified uncertainty in haulout population numbers.

By combining these two types of uncertainty, we derived an expression for the standard error in our estimates (Matthiopoulos et al. In prep). Wherever possible, we have plotted this in space (Fig.3b).

5 Discussion

Human-wildlife interactions are best studied in a spatial context as it is difficult to quantify co-occurrence if the spatial distribution of one or the other are unknown. Our approach to the estimation of grey seal usage has the advantages of 1) using auxiliary information

external to the aerial or satellite data and 2) accounting for different sources of uncertainty in the estimates. We should, however, stress that it is not a correlational approach. It tells us where the seals go but not why. Relating grey seal distribution to environmental covariates is the objective of ongoing work. Further, the distribution depicted here is not representative of all age classes as the satellite data were obtained exclusively from adults. Conservation efforts are often focused on juvenile classes which are important for population viability. Data collection on juveniles is currently under way and should provide an interesting comparison with adults. Finally, further tagging in the south west of Scotland (currently under way) should reduce our uncertainty about seal usage in these areas.

References

- Matthiopoulos, J. (2003a) The use of space by animals as a function of accessibility and preference. - *Ecological Modelling* 159: 239-268.
- Matthiopoulos, J. (2003b) Model-supervised kernel smoothing for the estimation of spatial usage. *Oikos* 102: 367-377.
- Matthiopoulos, J., McConnel, B., Fedak, M. & Duck, C. (In prep) The spatial distribution of grey seals in Britain

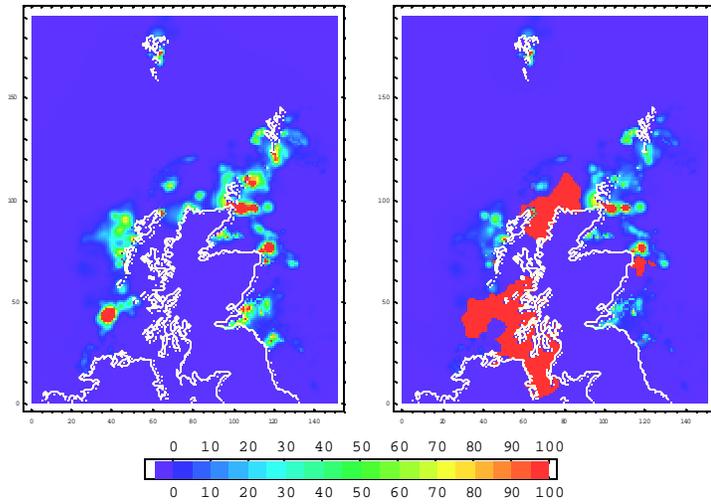


Figure 3: Usage estimates for marine locations around Scotland (a), and the corresponding standard errors (b). The colour red in part (b) indicates large standard errors as well as regions where limited data prevented us from calculating uncertainty.

C.E. Sparling and S.C. Smout

Population Energy Budget for UK North Sea grey seals.

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

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

Summary

This paper presents a summary of a model that predicts the energy requirement, by quarter and by sex and age class, of the UK North Sea grey seal population. Error in model predictions was calculated using uncertainty in parameter values and Monte Carlo simulation methods. Final estimates of annual energy requirement are most sensitive to changes in estimates of population size and estimates of metabolic rate. Uncertainty surrounding estimates of population size had a disproportionate effect on the uncertainty surrounding the final estimate of energy requirement, particularly the error associated with estimates of the size of the male component of the population. Final estimates are less sensitive to changes in parameters relating to males, suggesting that it is the female component of the population that is the largest single determinant of overall population energy requirements.

Introduction

The energy requirements of animals are the major determinants of how much food they eat. Predicting how much energy a population expends in its current state is a crucial task if we are to predict how much prey a population consumes. Bioenergetic models have frequently been used to estimate the energy consumption of marine mammals (e.g. Olesiuk 1993, Mohn and Bowen 1996, Stenson *et al.* 1997, Winship *et al.* 2002). The first objective of this research was to develop a generalized bioenergetic model for the North Sea population of grey seals, and to apply this model to ask such questions as: how do energy requirements vary with age and sex? How do energy requirements vary seasonally? How much energy does the entire North Sea (UK) grey seal population consume on an annual basis? Our second objective was to calculate confidence limits for these estimates using the errors in input variables. Thirdly we attempted to examine how sensitive our estimates were to changes in input

variables. We also assessed how much uncertainty in each variable contributed to the error in our final estimate.

Material and Methods

The energy costs of activities (rest, foraging, reproduction) were empirically derived from a combination of lab and field studies (Anderson and Fedak 1985, Reilly and Fedak 1996, Sparling 2003). A time-activity budget was constructed from satellite tagged free-living grey seals around the UK (n=14) from McConnell *et al.* (1999). These were combined to produce an estimate of energy expenditure throughout the year. Information on the population size and composition (2001 figures) from the Hiby and Duck model (in press) were used to predict the energy requirement of different sex and age classes of the population, (pups <1yr; sub-adult males, sub-adult females, adult males and adult females). Confidence limits of these estimates were derived by Monte Carlo simulations (1000 runs) using the error distributions of input parameters. A sensitivity analysis was carried out to determine the effect of changing the input parameters by 10% on the total estimate of annual energy requirement. A second analysis was carried out to see which variables had the largest effects on the uncertainty surrounding this final estimate by only incorporating uncertainty in one variable at a time, holding the rest at their mean values and iterating the model 1000 times.

Results

Individual daily energy expenditure

i) Pups

The model predicted that pups in their first year exhibited a gradual rise in daily individual energy expenditure from 6.1 (4.7-7.8) MJ.day⁻¹ to 8.7 (6.7-10.7) MJ.day⁻¹. This change was mainly due to an increase in mass throughout the year given that they were assumed to spend a fairly constant

proportion of time in the water.

ii) Sub-adults

Predicted mean daily energy expenditure of sub-adult males and females changed very little seasonally. Males have a slightly higher requirement due to a higher mass. Predicted daily energy expenditure, averaged across all quarters increased for both sexes between age 1 and 5.

iii) Adults

Predicted adult female daily energy expenditure was fairly constant throughout the first two quarters of the year, at an average of 25.5 MJ.day⁻¹ over the first 2 quarters. The model predicted a decline in daily expenditure in the third quarter to 20.1 MJ.day⁻¹, which then increased to 42.4 (30.6-56.6) MJ.day⁻¹ in the 4th quarter. Males showed a similar pattern, although during the first three quarters, average male daily expenditure was 23% higher than expenditure of females. In the 4th quarter this difference was reduced to 7%.

Total energy expenditure

i) Pups

Predicted total energy expenditure of pups decreased throughout the year from 1.2 x 10⁷ (9.3 x 10⁶ – 1.5 x 10⁷) MJ in the first quarter, to 6.8 x 10⁶ (5.3 – 8.7 x 10⁶) MJ in the fourth quarter. Although individual energy expenditure increased due to mass increase throughout the year, high mortality of young animals was reflected in decreasing total requirements.

ii) Sub-adults

As with daily energy expenditure, predicted total energy expenditure of the sub-adult part of the population changed very little throughout the year. Total annual expenditure increased from age 1 to age 3 (change in mass was greater than mortality). After this, mortality cancelled out the increase in mass throughout the year and annual expenditure did not change.

iii) Adults

Total energy expenditure of the adult male and female segment of the population followed similar trends to individual energy requirements. Total requirements of the male component of the population were lower than that of females throughout the year. This difference was greatest in the 4th quarter, when total male expenditure was 60 (44-73) % of female expenditure.

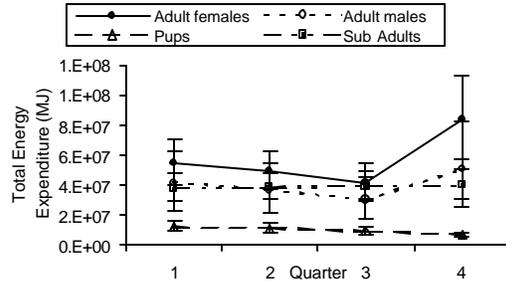


Figure 1. Total population energy requirements, by quarter and by sex/age class. Error bars are 95% confidence limits generated by Monte Carlo simulations (1000 runs).

Total population energy requirements

Total energy requirements by age/sex class are disproportional to population composition. 41% of total population energy requirement is accounted for by the adult female segment of the population, but adult females consist of only 30% of total population numbers. Similarly adult males account for only 17% of population numbers, yet account for 28% of population energy requirements. Pups make up only 7% of total population energy requirement, yet account for 21% of population numbers.

Dividing the total annual energy expenditure of 5.8 x 10⁸ MJ by the number of individuals in the population and by 365 gives an average daily energy expenditure for an ‘average’ grey seal of 20.2 (18.3-22.2) MJ.day⁻¹. Dividing these values by an efficiency of 0.8 gives a total annual energy consumption of the population of 7.25 x 10⁸ (6.1-8.4 x 10⁸) MJ and an average daily energy consumption for an ‘average’ grey seal of 25.3 (22.8-27.8) MJ.day⁻¹, or 5497 (4964-6042) Kcal.day⁻¹.

Estimation of errors and uncertainty

In the analysis shown in Table 1, a direct linear relationship between the magnitude of the variable and the magnitude of the estimate was found for total population size, cost of activities and basal metabolic rate. A change in variables relating to adult females has the largest effect on total population estimates.

A change in activity budget parameters has the least effect on total population estimates. The analysis in Table 2 shows that uncertainty in population size estimates contribute most to uncertainty in our estimate of total population energy requirement, whereas error in other

variables relating to metabolism and activity budget, contribute least to total variance.

parameter, when present in the model as the only variable with uncertainty.

Parameter(s)	D%
Population size	10
Adult females	4.4
Adult males	3
Sub adults	1.9
Pups<1	0.7
	7.4
Mass	
Adult females	3.2
Adult males	2.2
Sub adults	1.4
Pups<1	0.5
Cost of activity	10
Resting	4.2
At-sea	4.1
Reproduction	1.7
	10
BMR	
Adult females	4.4
Adult males	3.2
Sub adults	1.4
Pups<1	0.7
Activity budget	
Increased proportion resting, decreased at-sea	0.1
Increased proportion at-sea, decreased resting	-0.1
Duration of reproduction	1.2

Table 1. The effect on the total estimate of energy requirement of a 10% increase in the values of the input variables.

Parameter(s)	CV% of total estimate
Complete model	18
Population size – all	17.4
Adult females	6.1
Adult males	11.4
Sub adults	1.5
Pups<1	0.7
	4.2
Mass – all	
Adult females	0.5
Adult males	4.4
Sub adults	0.1
Pups<1	0.1
Cost of activity – all	2.8
Reproduction	2.0
Resting	1.6
At-sea	1.5
Activity budget – all	4.3
Reproduction	2.3
Resting	2.5
At-sea	2.5

Table 2. Uncertainty in the estimate of total population annual energy requirement associated with each

Discussion

The overall energy requirements of life in the wild are extremely difficult to measure in phocid seals. The best approach to quantify this is likely to be the development of quantitative models that make use of empirical data on the costs of various activities coupled with information on the extent of those activities in the wild populations, together with detailed information on the size and composition of the population. The model presented here uses estimates of the combined costs of activity of wild grey seals in captivity under similar thermoregulatory and behavioural regimes to those in the wild, in tandem with data derived from telemetry studies of the activity of wild grey seals. In this model bioenergetic parameters were calculated based on these empirical data wherever possible. Information on the cost of reproduction was also derived from empirical studies on wild grey seals.

This study tried to include as many parameters as possible in the model. This however, can lead to error in the resulting estimates as a result of inaccurate approximations of unknown parameters. One way of addressing inaccuracies in this type of model is to include error terms for all estimates of model parameters. Most model inputs had error estimates associated with them and using the error distributions allowed us to calculate upper and lower confidence limits on our estimates of energy requirements. Monte Carlo simulation techniques have been used in a similar manner by Mohn and Bowen (1996), Stenson *et al.* (1997) and Winship *et al.* (2002). Given that some input parameters were unknown and there may be a high degree of model error due to some of the assumptions made, these limits represent minimum error.

We have shown that final estimates of annual energy requirement are most sensitive to changes in estimates of population size and estimates of metabolic rate. Changes in variables relating to activity budgets and mass had a much smaller effect on total population energy requirement. Uncertainty surrounding estimates of population size had a disproportionate effect on the uncertainty surrounding the final estimate of energy requirement, particularly the error associated with estimates of the size of the male component of the population. Similarly, uncertainty associated with variables relating to male mass and male metabolism also contribute

more to overall variance than female mass and female metabolism. This is because so few data exist for all aspects of male grey seal biology. However our final estimates are less sensitive to changes in parameters relating to males, suggesting that it is the female component of the population that is the largest single determinant of overall population energy requirements.

It is important to note that the results of this model are estimates of energy requirements and not estimates of food consumption. On an annual basis, food consumption would probably equal energy requirements, but on a daily, or even seasonal basis, animals do not always consume the food they need to meet their energy demands. Mature seals undergo a period of starvation during the breeding season, and lose up to 40% of their body weight. Therefore estimates of energy requirement by quarter will not be reflected equally in consumption. Estimates of requirement will translate into consumption (by sexually mature animals at least) over truncated periods, between the end of the breeding season and before the moult, and then between the moult and the beginning of the next breeding season. Estimating actual energy expenditure coupled with time spent at sea and changes in the body energy content of seals during these periods can be used to follow actual food consumption at these times of year. This is a task that is currently being addressed by the authors.

Estimated energy required by each segment of the population is not proportional to the composition of the population. This has implications for predicting what will happen with projected changes in population structure. For example there has been speculation that the UK grey seal population is undergoing density dependent changes (Boyd, 2002). If this density dependence is operating at the level of pup survival, this will have little effect on total population energy requirements in the immediate future, given that pups only account for 7% of population energy requirements. However if density dependence effects are operating at the level of adult mortality or fecundity, their effects on population energy requirements may be more significant. The model presented here can be used to predict the outcome of changes in many parameters related to density dependence, and not only those directly related to demographic changes. For example, foraging patterns may change as prey becomes scarce, seals may spend longer at sea, or switch to alternative prey that require greater energy expenditure to capture. This model would allow the assessment of these types of effects on

population and individual energy requirements.

An assessment of population consumption broken down by fish species relies on detailed information on the diet composition of the population and the energetic density of each prey species. However, to put the model predictions of energy consumption into context, to satisfy a daily requirement of 24.5 MJ.day⁻¹, a seal would need 7.2kg of fish per day if it were feeding on cod alone. However, it could satisfy the same energy requirements with a daily consumption of about 3.9kg of sandeels. (These calculations are based on energy densities of 3.4 and 6.3 KJ per kilo for cod and sandeels respectively, taken from Hammond *et al.* (1994)).

The model presented here, like all models of biological systems, is a simplified representation of the real system. Nevertheless, models such as this can aid in predicting properties of the real system that are difficult or impossible to measure. A large amount of information is required to fill the gaps present in the data needed to completely parameterise this model. It is hoped that the approach started here can be developed and used in conjunction with information on diet composition and the energetic density of prey to model interactions between UK grey seals and their prey.

References

- Anderson, S.S. & Fedak, M.A. (1985) Grey seal males: energetic and behavioural links between size and sexual success. *Animal Behaviour*, **33**, 829-838.
- Boyd, I.L. (2002). Population dynamics of grey seals. SCOS 2002, Annex IV. Sea Mammal Research Unit.
- Hammond, P.S., Hall, A.J., & Rothery, P. (1994). Consumption of fish prey by grey seals. In: *Grey seals in the North Sea and their interactions with fisheries* (eds P.S. Hammond & M.A. Fedak). Final Report to the Ministry of Agriculture, Fisheries and Food Under Contract MF0503, Sea Mammal Research Unit.
- Hiby, A.R. & Duck, C.D. ((In Press)) Point and interval estimates of the size of the British grey seal population and their implications for management. *Journal of Applied Ecology*.
- McConnell, B.J., Fedak, M.A., Lovell, P., & Hammond, P.S. (1999) Movements and foraging areas of grey seals in the North Sea. *Journal of Applied Ecology*, **36**, 573-590.
- Mohn, B. & Bowen, D.W. (1996) Grey seal predation on the eastern Scotian Shelf: modelling the impact on Atlantic cod.

Canadian Journal of Fisheries and Aquatic Science, **53**, 2722-2738.

- Olesiuk, P.F. (1993) Annual prey consumption by harbour seals (*Phoca vitulina*) in the Strait of Georgia, British Columbia. *Fishery Bulletin*, **91**, 491-515.
- Reilly, J.J., Fedak, M.A., Thomas, D.H., Coward, A., & Anderson, S.S. (1996) Water balance and the energetics of lactation in grey seals (*Halichoerus grypus*) as studied by isotopically labelled water methods. *Journal of Zoology*, **230**, 157-165.
- Sparling (2003) *Causes and consequences of variation in the energy expenditure of grey seals (Halichoerus grypus)*. PhD Thesis, University of St Andrews.
- Stenson, G.B., Hammill, M.O., & Lawson, J.W. (1997) Predation by Harp seals in Atlantic Canada: preliminary consumption estimates for Arctic cod, capelin and Atlantic cod. *Journal of North West Atlantic Fisheries Science*, **22**, 137-154.
- Winship, A.J., Trites, A.W., & Rosen, D.A.S. (2002) A bioenergetic model for estimating the food requirements of Steller sea lions *Eumetopias jubatus* in Alaska, USA. *Marine Ecology-Progress Series*, 229, 291-312.

A.J. Hall¹, P.P. Pomeroy¹ and M. Lonergan²

The Phocine Distemper Virus Outbreak

¹NERC Sea Mammal Research Unit, Gatty Marine Laboratory, University of St Andrews, St Andrews KY16 8LB

²The Centre for Research into Environmental and Ecological Modelling, University of St Andrews, St Andrews, KY16 9LZ

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

Summary

In 2002 a second major phocine distemper virus (PDV) epidemic occurred, largely among European and UK harbour seal (*Phoca vitulina*) populations (Jensen et al., 2002). Between May and December over 21,000 carcasses washed up on the shores around the Kattegat/Skagerrak, Waddensea and North sea

(<http://www.waddensea-secretariat.org/news/publications/Wsnl/Wsnl02-2/articles/1-seal-epidemic.pdf>). The first cases in the UK were reported in the Wash in July and by the end of December 3,854 carcasses had been found around the UK, 72% of which were in England. Aerial surveys to determine mortality rates and studies on the role of the grey seal as a vector, together with epidemiological modelling of the spread of the virus are continuing.

Introduction

The impact of PDV on the UK harbour seal populations has important implications for the abundance and distribution of this species. The 1988 outbreak became one of the best-documented wildlife disease events (Harwood & Hall, 1990) but many questions about the true origin of the virus and the vector by which it spreads remained unanswered. DEFRA funded the UK response to the disease and SMRU was involved in disseminating information on numbers found dead by region and in the diagnosis of the disease using molecular methods. Just prior to the outbreak aerial surveys of the major east coast populations in the Wash, Tay and Moray Firth had been conducted by SMRU. Orkney had been surveyed by thermal imagery in 2001. These data provide minimum population estimates that can be compared with post-epidemic survey results. Although the number of carcasses found washed ashore gave some indication of the extent of the outbreak, these provide a biased estimate of

mortality because the origin and species of the carcasses is often not known. Indeed three harbour seals tagged in the Netherlands were found on the east coast of England at the height of the outbreak. Although PDV positive animals were found dead all around Scotland, including the Inner Hebrides, the disease there did not reach epidemic proportions. Of the 24 dead seals that were found to be PDV positive by PCR in Scotland, 11 were harbour seals and 13 were grey seals. Unfortunately the carcasses were often too decomposed for viral RNA to survive. As in 1988, there were no reports of large numbers of grey seals carcasses, particularly in Scotland, although a large proportion of the population was exposed to the virus (see section on virus neutralizing antibodies in breeding females).

Following the initial response to the outbreak there are now three studies on PDV continuing within SMRU.

- Aerial surveys of the Wash, Thames and Essex; Tay estuary; Moray Firth and thermal survey of Orkney in August 2003. These will be compared with the abundance and distribution data from 2002.
- Assessment of exposure to PDV in breeding grey seals.
- Modelling the spread of the disease between individuals, local populations and species to estimate the contact between them; and to attempt to assess the range of patterns and intensities of future outbreaks that are consistent with the available information.

Material and Methods

Estimated mortality

Seal carcasses washed ashore and reported to the central seal 'hotline' at the Institute of Zoology (IoZ) were logged and as many as possible were

post-mortemed by the vets at IoZ or the Scottish Agricultural College in Inverness. Samples of lung, spleen, lymph node and brain from freshly dead animals were examined for viral antigen using RT-PCR or immunoperoxidase methods.

Aerial surveys of harbour seals in the Wash and Tay were carried out by SMRU using large format photographs in a fixed wing aircraft. Counts were made in the Moray Firth from the ground during the breeding season (P.M. Thompson, University of Aberdeen). Counts used were the mean of all those carried out during the survey period and assumed to represent 65% of the total population size.

Exposure in Grey seals

CDV virus neutralization tests were carried out on serum samples collected at the start and end of lactation from grey seal mother/pup pairs at North Rona and Isle of May in NW and SE Scotland, respectively.

Modelling spread

Simple mathematical models of disease transmission are being made and parameterised using both the information on carcasses collected by IoZ and serological data collected at SMRU. As information on individual animal movements becomes available from satellite and phone tags this will also be incorporated.

Results

Estimated mortality

The number of seals (both species and unknown) found dead by week in England, Scotland and Wales is shown in Fig. 1. The peak mortality in England occurred during mid-September and the epidemic was largely over by the end of October. In Scotland a late peak in mortality was reported at the end of November, although many of the dead seals reported from this month were grey seal pups which had probably died from natural causes.

Mortality estimates based on pre-and post-epidemic survey data are not currently available. However, the mortality estimates for harbour seals, based on the number of carcasses washed ashore are shown in Table 1. Although almost 4,000 carcasses were reported around the UK

only 30% were identified to species. Because the proportion of grey to harbour seals found varied by region and season we used ratios calculated regionally and monthly to estimate the true number of dead harbour seals.

There was considerable uncertainty about the identification of carcasses found in the remoter areas of Scotland. In addition, it is difficult to determine 'population' groups for grey seals outside the breeding season, due to their large scale movements between haulout sites. It has therefore not been possible to use the data reported on dead animals to estimate PDV-related grey seal mortality. Relatively few individuals in total were identified as grey seals (<500), a similar number to that reported in 1988.

The mortality estimates have been restricted to the east coast of the UK since the disease did not appear to cause wide spread mortality either on the west coast of Scotland or in Northern Ireland.

Exposure in Grey seals

Using a threshold titre of 64, 50 out of 57 samples from the Isle of May and 40 out of 52 from North Rona tested positive to CDV. These figures are not significantly different; giving a maximum likelihood estimate of 83% for the proportion of individuals within these groups recently exposed to the disease, and suggests the true value lies in the range 74-88% (Bayesian 95% confidence interval with flat prior).

Mothers (aged by counting growth layers in an incisor tooth, or by reading flipper tags applied as pups), were classified into 2 groups: those of breeding age in 1988 and therefore likely to have been exposed during the 1988 epizootic (OLD), and those born after 1989 (YOUNG).

The proportion of seropositives in OLD and YOUNG mothers was similar (titre64: NR OLD=78%, YOUNG=71%: IoMOLD=85%, YOUNG=91%).

Mean log₁₀ antibody titres were higher for IoM mothers in 2002 (IoM 2.318±0.051, NR 2.079±0.057, p=0.002). Nearly half of pups were seropositive by the end of lactation

(positive titre₆₄: NR=36%, IoM=54%, n=33,48). Mean log₁₀ antibody titres in pups were larger towards the end of lactation (start=1.728±0.493, n=92, end=2.015±0.058, n=73, p<0.001).

Modelling spread

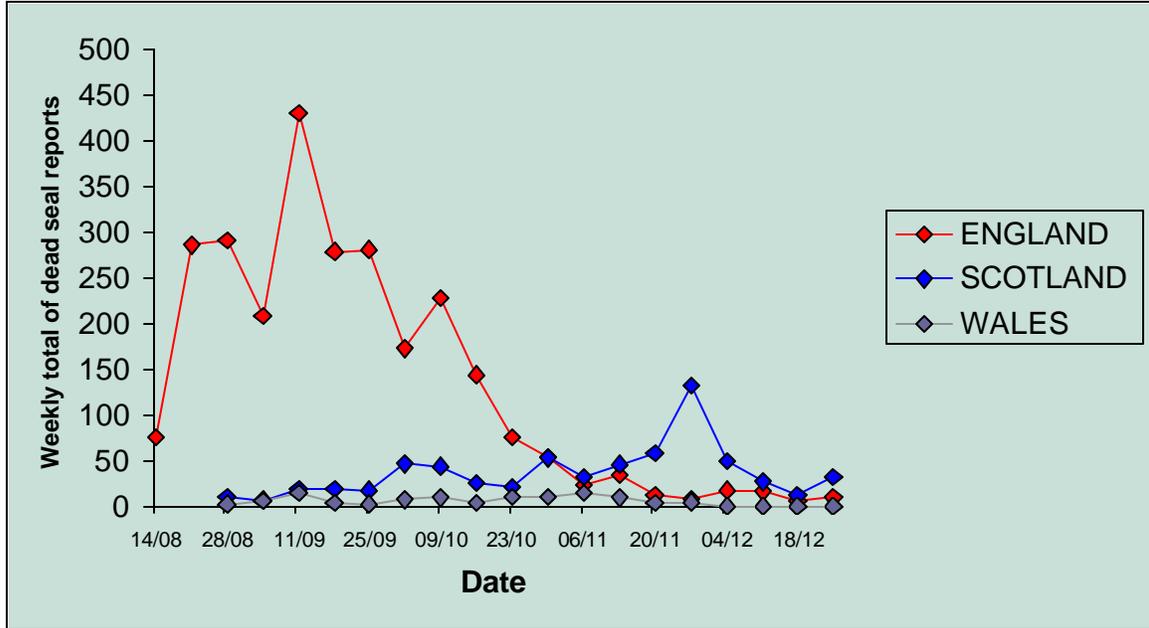
The absence of PDV from European harbour seals between 1988 and 2002 suggests that the disease is very unlikely to persist in this population, under current conditions. Preliminary analysis suggests that, for PDV to become a major threat to harbour seal populations, another species in close contact with them would have to regularly reinfect the majority of young animals (Loneragan and Harwood, 2003).

Discussion

The highest mortality estimates were reported among the Wash harbour seal population. Mortality estimates from carcass data reported in 1988 (Hall et al., 1992) (Thompson & Miller, 1992) when compared to estimates obtained from pre- and post-epidemic aerial surveys show that the rates reported here are likely to underestimate the true mortality. However, it can be concluded that the Scottish harbour seal populations were much less affected than the English population. PDV related mortality was also probably lower in Scotland than it was in 1988 but it was about the same or higher in England (Fig. 2).

CDV antibody titres measured in grey seal mothers during the 1988 epizootic had a similar distribution to those measured in 2002. As titres in harbour seals had fallen over the same period, the high prevalence of seropositives in geographically separated colonies suggests widespread recent exposure. The role for grey seals as PDV vectors is being investigated.

Fig. 1. No. carcasses reported during the epidemic by region.



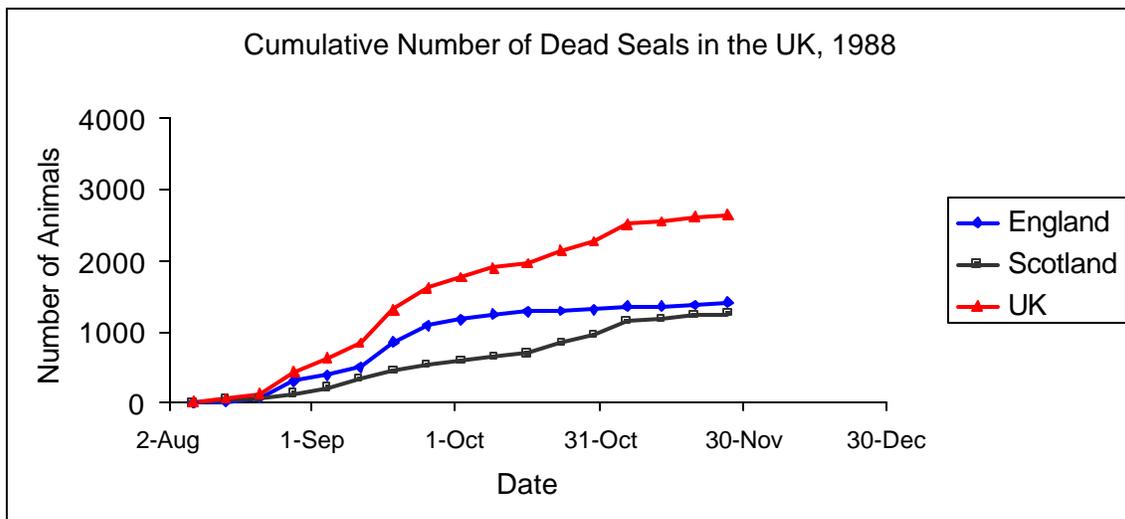
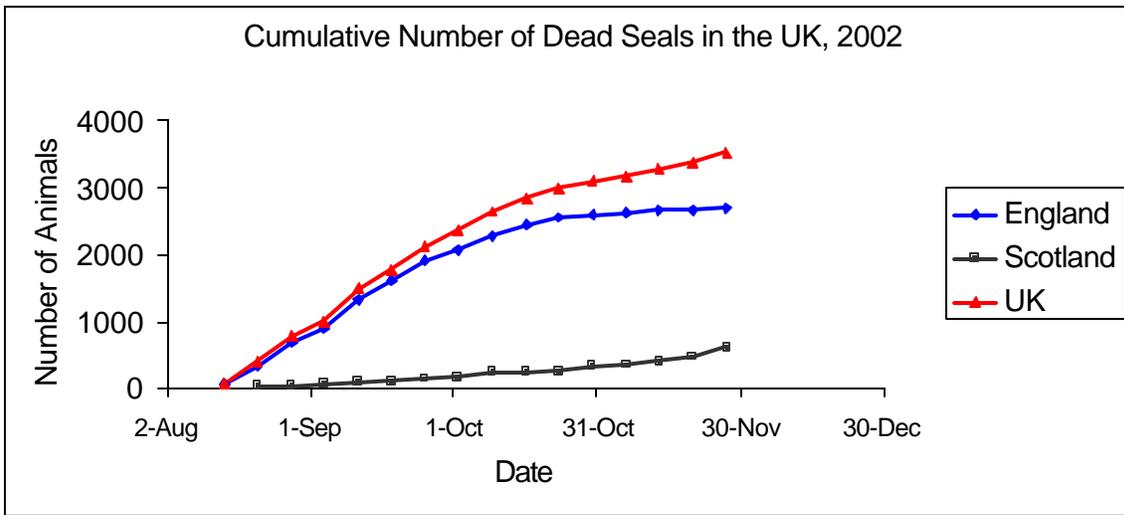


Fig. 2 Cumulative number of dead seals in England, Scotland and the UK as a whole during the 2002 and 1988 outbreaks of PDV.

Table 1. PDV mortality estimates for harbour 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 Deaths (all species)	Total No Deaths (harbour 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 harbour seals estimated from the proportion identified to species on a monthly pro-rata basis

³ No. identified as harbour 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

References

Hall, A.J., Pomeroy, P., & Harwood, J. (1992) The descriptive epizootiology of phocine distemper in the UK during 1988/89. *Science of the Total Environment*, 115, 31-44.

Harwood, J. & Hall, A. (1990) Mass mortality in marine mammals: its implications for population dynamics and genetics. *Trends in Ecology and Evolution*, 5, 254-257.

Jensen, T., van de Bildt, M., Dietz, H., Andersen, T., Hammer, A., Kuiken, T., & Osterhaus, A.D.M.E. (2002) Another phocine distemper outbreak in Europe. *Science*, 297, 209.

Lonergan M and Harwood J (2003/ in press September) The potential effects of repeated outbreaks of phocine distemper among harbour seals: a response to Harding et al. 2002. *Ecology Letters*.

Thompson, P.M. & Miller, D. (1992) Phocine distemper virus outbreak in the Moray Firth common seal population: an estimate of mortality. *Science of the Total Environment*, 115, 57-65.

J. Matthiopoulos, S Smout, C Asseburg & J Harwood
Modelling the functional response of British grey seals

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

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

Summary

We used Bayesian techniques to estimate the parameters of a generalized multispecies functional response relating the consumption by grey seals of groups of prey species to their availability in the environment. A preliminary analysis of diet information collected mostly in the 1980s, provided little evidence that grey seals switch between different prey categories. However, we will be able to provide more reliable parameter estimates when diet samples collected in 2002 have been analysed.

Introduction

The impact of a predator on the dynamics of its prey depends to a large extent on the nature of its functional response. This function relates per capita prey consumption to prey density. In the case of a generalist predator, such as the grey seal, consumption of one prey species is likely to be influenced by the availability of all its prey species – ie its multispecies functional response. There have been few attempts to fit multispecies functional responses to laboratory data and none, that we know of, to fit such a response to data from free-ranging individuals. This is probably because of the statistical and logistic problems involved. However, we have developed Bayesian techniques for estimating a generalized function of the form:

$$F_i(N_i) = \frac{a_i N_i^{m_i}}{1 + \sum_j a_j t_j N_j^{m_j}}$$

to field data (Asseburg et al., submitted). $F_i(N_i)$ is the mass of prey species i consumed per unit time, and a_i , t_i and m_i are prey-specific parameters. The parameter a_i is related to the attack rate on the i th prey by the predator, and the parameter t_i is related to the handling time of a single prey item by the predator. The parameter m_i determines how strongly sigmoidal the

response of the predator to the i th prey is. Sigmoidal (or type III) functional responses are usually evidence of switching of the predator away from that particular prey when it is relatively rare. Predators with a type III functional response can hold some of their prey species at a low density equilibrium, sometimes referred to as a “predator pit”. The multispecies functional response can be used to predict seal diet in areas or combinations of prey abundances for which no feeding data are available. It is therefore an essential component of any model of the interactions between seals and commercial fish species.

Material and Methods

In principle, estimating the parameters of a functional response requires two types of data, 1) the density of prey available to the predator and 2) the consumption of prey by each predator at these densities. Local prey densities can be estimated from fish surveys and prey consumption can be estimated from seal diet data. FRS, Aberdeen, and CEFAS, Lowestoft, kindly provided us with raw, survey data for Cod, Whiting, Haddock, Saithe, Pollock, Pout whiting, Poorcod, Norway pout, Ling, Tusk, Plaice, Lemon sole, Mackerel, Herring, Sandeels, Dover sole, Sprat, Hooknose, Blue whiting, Dab, Bullrout and Horse mackerel.

To estimate prey consumption for seals from different parts of the UK we used data from scat samples collected around the UK between 1984 and 2000, although most samples were collected in the 1980s. Fish otoliths in individual scats give us information of the proportion of different fish species in the seals’ diet, because the size of these otoliths, corrected for reduction in size as a result of partial digestion, can be used in allometric relationships to estimate the size (weight) of the prey.

We initially subdivided the prey field into 53 prey types. The trawl data were disaggregated into these categories. Using kernel smoothing estimation, in combination with least-squares

cross-validation, we used the trawl data to produce a map of the spatial distribution for each prey type.

To calculate fish consumption from the seals' diet we first calculated the proportion by mass of each prey type in each scat sample. Using known energetic values for different prey species, we converted these into proportions by energy. We subsequently scaled these proportions up to the average, daily energetic requirements of grey seals. Finally, we converted these back into biomass per prey type consumed daily by each seal.

In order to bring the fish abundance and seal diet data together we needed to ensure an exact correspondence between consumption and prey density. This is because the prey densities used for the functional response must be those actually experienced by the seals. As the availability of different prey types (species and size) is expected to change with season, to ensure that our prey distributions would be relevant, we produced different maps for winter and summer. Also, relative accessibility and usage of points at sea by seals will rely heavily on the haulout of reference. We therefore subdivided our diet data into the 6 haulout regions (Orkney, Inner Hebrides, Donna Nook, Farne Islands & Isle of May, Outer Hebrides South, Outer Hebrides North) at which they were collected. Finally, we calculated prey availability by weighting the estimated prey abundance at every point in space by the estimated usage of that point by seals from particular haulouts.

The functional response equation we used does not possess the property of additivity, so we had to identify which prey types are treated as identical by the seals. We used the ratio of consumption over availability for different prey types at different prey densities as the similarity criterion in a cluster analysis of prey. This analysis resulted in 28 prey groupings (Table 1).

Model fitting was done by using Markov chain Monte Carlo simulation with a Random Walk Metropolis-Hastings sampler, sampling each parameter in turn.

Results

Fitting the functional response gave us posterior distributions for each of the 84 parameters of the model. In general, we observed a reduction in variance which indicated that the data were able to refine the prior information on the parameters. The changes in the parameter means (from prior to posterior) were small, but most notably, all the m parameters took values close to 1, indicating no switching behaviour between prey types.

To inspect the goodness of fit of the functional response we used it to predict the diet of seals under conditions identical to those in our data. We therefore used observed prey availabilities as the input to the functional response, obtained consumption of each prey type and hence the proportion of each prey in the seals' diet and compared that to the observed diet. The results are shown in Figure 1.

Discussion

These results should be treated as preliminary. Once diet samples collected in 2002 are processed, we will have information on the quantities of prey consumed by grey seals over a much wider range of prey densities. This should substantially reduce the uncertainties associated with the estimates of the parameters of the grey seal's functional response.

Acknowledgements

Most of this work was carried out under contract for DEFRA, but Sophie Smout was supported by a NERC quota studentship and Christian Asseburg by a studentship from SHEFC to the Centre for Conservation Science.

References

Asseburg, C, Smout, S., Matthiopoulos, J, Fernandez, C., Redpath, S., Thirgood, S. & Harwood, J. (submitted) The functional response of a generalist predator. *Nature* (Lond.)

Table 1: The 28 groupings of prey types used to fit the functional response.

1	Cod(0.000kg)	15	Plaice(0.047kg)
2	Cod(0.027kg)	16	Plaice(0.111kg)
3	Cod(0.238kg)	17	Plaice(>0.373kg)
4	Cod(1.000kg)	18	Lemon sole(0.250kg)
5	Cod(2.863kg)	19	Lemon sole(>0.593kg)
6	Saithe(0.000kg)	20	Herring(0.091kg)
7	Saithe(0.238kg)	21	Sandeels(>0.000kg)
8	Saithe(0.779kg)	22	Dover sole(>0.000kg)
9	Saithe(1.953kg)	23	Hooknose(>0.000kg)
10	Saithe(>3.796kg)	24	Bullrout(>0.000kg)
11	Pollock(0.000kg)	25	Cod(>6.434kg),Whiting(>0.275kg)
12	Norway pout(0.000kg)	26	Whiting(0.000kg), Haddock(0.003kg), Haddock(0.032kg), Poor cod(0.000kg)
13	Ling(>0.000kg)	27	Whiting(0.091kg), Whiting(0.216kg), Haddock(>0.531kg), Norway pout(>0.047kg), Blue whiting(>0.000kg)
14	Tusk(>0.000kg)	28	Whiting(0.003kg), Whiting(0.027kg), Haddock(0.000kg), Haddock(0.157kg), Poor cod(>0.070kg), Norway pout(0.002kg), Norway pout(0.014kg), Plaice(>0.000kg), Lemon sole(0.000kg), Lemon sole(0.074kg), Mackerel(>0.000kg), Herring(>0.000kg), Herring(>0.250kg), Sprat(>0.000kg), Dab(0.000kg), Dab(>0.047kg), Horse mackerel(0.000kg), Horse mackerel(>0.091kg)

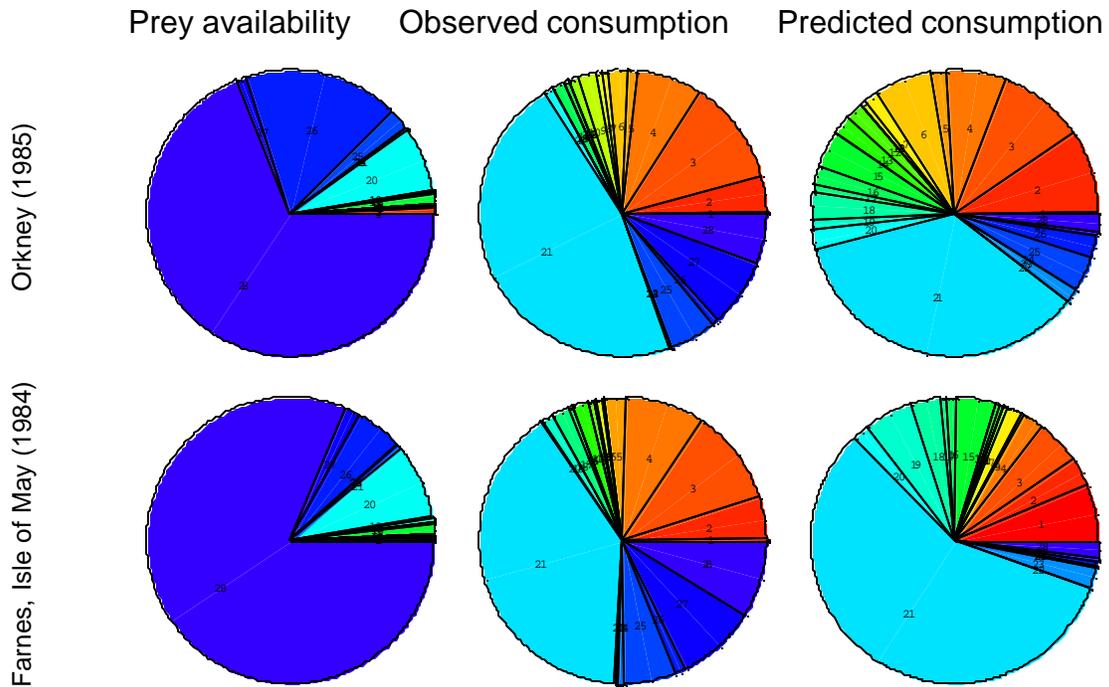


Figure 1: Two examples of the functional response's goodness of fit. The two pie charts on the left indicate the availability (by mass) of each prey grouping in the seal's environment. The two pie charts in the middle are observed proportions of consumption (i.e. diet by mass). The two pie charts on the right are proportions of consumption as predicted by the functional response. The numbers correspond to the prey groupings in Table 1.

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.

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

Summary

Annual surveys of harbour seals in the Moray Firth, NE Scotland were made between 1987 and 2003. 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 has declined at 3-5% p.a. since 1993. There are currently insufficient data to assess the extent to which similar trends have occurred in other UK populations. However, these data contrast markedly with the sustained increases in harbour seal abundance recorded in other parts of the North Sea.

Introduction

Increases in the overall abundance of UK grey seals have been well documented, but much less is known about the current status of UK harbour (common) seals.

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 provide 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 Beaully, 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.* (1997), and involve making 2-10 shore-based counts during both pupping (15 June – 15 July) and moult (1 – 31 August) periods. These data therefore provide an index of abundance of seals in this study area in each year of the study which account for approximately 60 % of the population (Thompson *et al.* 1997).

Results

The resulting data on changes in this index of the abundance of Moray Firth seals are presented in Fig. 1. Between 1987 and 2002, mean annual estimates from the time-series of counts made during the pupping and moult periods were highly correlated ($r = 0.6$, $n=13$, $p<0.01$). 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 3-5% decline in annual mean counts in the period 1993 – 2002 (Pupping: $F_{1,8} =$

11.93, $r^2 = 0.6$, $p < 0.01$; Moulting: $F_{1,7} = 30.7$, $r^2 = 0.81$, $p < 0.001$).

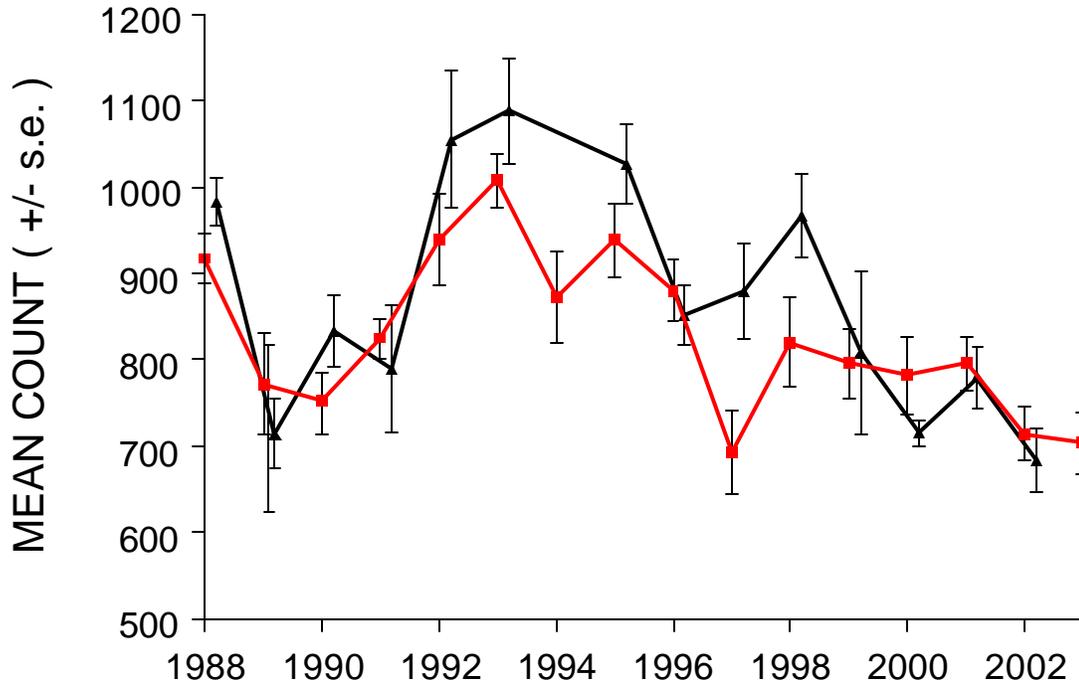


Fig. 1. Mean annual haul-out counts of Moray Firth harbour seals made during the pupping season (squares) and the moult (triangles)

Data from the 2003 pupping season suggest this trend has continued but that, as suggested from counts of dead seals, the 2002 PDV epizootic did not cause major mortality within this population.

Discussion

The recent decline in abundance of Moray Firth harbour seals over the last decade is in marked contrast to the sustained increase seen in other North Sea populations following the 1988 PDV outbreak (Hardin et al. 2003). Declines in abundance have been reported from another small areas within Orkney (Thompson et al. 2001), but further work integrating data from surveys made at different spatial and temporal scales is now required to determine whether or not the trends observed within the Moray Firth are representative.

References

Harding, K.C. et al. (2003) The 2002 European seal plague: epidemiology and population consequences. *Ecology Letters*, 5: 727-732.

Thompson, P.M. et al. (1996). Comparative distribution, movements and diet of harbour and grey seals from the Moray Firth, N.E. Scotland. *Journal of Applied Ecology*, 33: 1572-1584.

Thompson, P.M. et al. (1997). Estimating harbour seal abundance and distribution in an estuarine habitat in N.E. Scotland. *Journal of Applied Ecology*, 34: 43-52.

Thompson, P.M., et al. (2001) Local declines in the abundance of harbour seals; implications for the designation and monitoring of protected areas. *Journal of Applied Ecology*, 38: 117-125.