

# Marine Mammal Scientific Support Research Programme MMSS/001/11

USD 5:  
Report

## Assessing the impact of the observed and estimated levels of mortality on seal populations at a local, national and international level

Sea Mammal Research Unit  
Report to  
Scottish Government

July 2015 [version F1]



marinescotland



Hanson, N.<sup>1</sup>, Baxter, J.<sup>2</sup>, Thompson, D.<sup>1</sup>, Duck, C.<sup>1</sup> & Lonergan, M.<sup>1</sup>

1. Sea Mammal Research Unit, Scottish Oceans Institute, University of St Andrews, St Andrews, Fife, KY16 8L.

2. Scottish Natural Heritage, Silvan House, 231 Corstorphine Road, Edinburgh EH12 7AT

Assessing the impact of the observed and estimated levels of mortality on seal populations at a local, national and international level

<b>Editorial Trail</b>			
<b>Main Author</b>	<b>Comments</b>	<b>Version</b>	<b>Date</b>
N. Hanson J. Baxter D. Thompson C. Duck M. Lonergan	authors	V1.0	20/01/2015
D. Thompson	review	V1.1	22/01/2015
P. Irving	review	V1.2	22/01/2015
Marine Scotland	comments	V2.0	24/04/2015
N. Hanson	response to comments	V3.0	20/06/2015
A. Hall	final editing	VF1	27/07/2015

Citation of report

Hanson, N., Baxter, J., Thompson, D., Duck C. & Lonergan M. (2015) Assessing the impact of the observed and estimated levels of mortality on seal populations at a local, national and international level. Sea Mammal Research Unit, University of St Andrews, Report to Scottish Government, no. USD 5, St Andrews, 20pp.

## Contents

Contents	3
1 Executive summary	4
2 Introduction	5
3 Data and Analysis	6
3.1 Harbour seal population in Firth of Tay and Eden Estuary	7
3.2 Neighbouring populations	8
3.3 Grey seal population in Firth of Tay and Eden Estuary	8
4 Results	9
4.1 Harbour seal population in Firth of Tay and Eden Estuary	9
4.2 Neighbouring populations	10
4.3 Grey seal population in Firth of Tay and Eden Estuary	10
4.4 Potential proximate causes	11
4.5 Future scenarios	12
4.5.1 'Business as usual'	12
4.5.2 Source of decline eliminated	13
4.5.3 Source of decline partially eliminated	14
4.5.4 Female shortage in recovering population	14
4.6 Extinction & recolonisation	14
5 Discussion	15
6 Acknowledgements	18
7 References	18

## 1 Executive summary

Aerial surveys have detected alarming declines in the counts of harbour seals (*Phoca vitulina*) in several regions across Scotland. Available demographic data and simple models are used to examine the recent declines in the numbers of harbour seals counted in one population within a Special Area of Conservation (SAC) on the east coast of Scotland. The models suggest that the continuation of current trends would result in the species effectively disappearing from this area within the next 20 years.

While the cause of the decline is unknown, it must be reducing adult survival because the high rate of decline cannot be wholly accounted for by changes in other demographic parameters. Recovery of the population to the abundance when the SAC was designated is likely to take at least 40 years, even if the cause of the decline is immediately identified and rectified.

The models suggest that partial removal of the cause will have only limited benefits to population recovery, and there are unlikely to be any long-term benefits from introducing or reintroducing additional individuals while the problem persists. Therefore, if the population of harbour seals in this area is to recover it is essential that the sources of the increased mortality are identified and measures are put in place to manage these.

A total of 36 harbour seal carcasses with characteristic spiral wounds have been recorded in the vicinity of the Firth of Tay and Eden estuary since 2010. This level of mortality is estimated to be unsustainable and likely to be a major factor in the decline.

Less information is available from other regions, but a comparison with potential biological removal (PBR) estimates suggests that the same mechanism of injury may become important in the Moray Firth and possibly Orkney if the level of reporting is low.

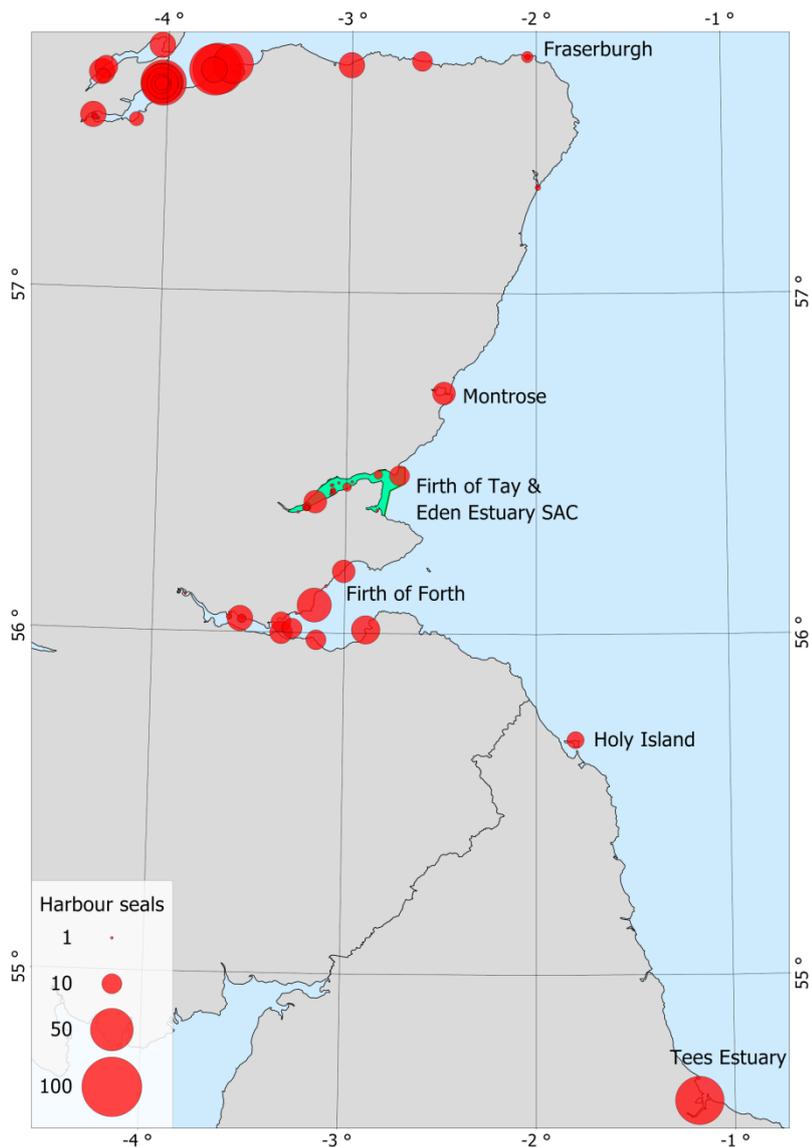
## 2 Introduction

The UK is home to around 30% of Europe's harbour seals (*Phoca vitulina*), with the majority of those being distributed at island and coastal sites in the north and west of Scotland (SCOS 2013). Harbour seals in Scotland have been monitored on an approximately five-yearly cycle since the late 1980s. Two populations, in part of the Moray Firth and around the Firth of Tay, have been surveyed more frequently. These surveys have detected alarming declines in the number of harbour seals observed at haulout sites in several regions. The trend is most apparent in populations in Orkney and on the north and east coasts of Scotland, where numbers have declined by between 65% and 90% since the 1990s (Duck & Morris, 2014). Importantly, the decline in number of seals counted is not a consequence of changes in seal behaviour, such as changes in the proportion of time seals spend hauled out during the moult. A recent telemetry study on harbour seals in Orkney has demonstrated that the proportion of animals hauled out during the survey window was high, and similar to another location where population growth has been stable (Lonergan *et al.*, 2013). The declines in harbour seal counts are thus likely to represent real reductions in the numbers of animals present in the region.

Harbour seals are protected under the Marine (Scotland) Act 2010 that prohibits the killing of any seal except under licence granted by the Scottish Government for the explicit protection of fisheries or fish farms. There is also the capacity under the Marine (Scotland) Act 2010 to designate seal conservation areas where it is considered necessary to further encourage the proper conservation of seals. Furthermore, there are a number of harbour seal Special Areas of Conservation (SAC) designated under the EU Habitats Directive (for a map of SACs in Scotland, see: <http://www.scotland.gov.uk/Publications/2011/03/16182005/54>); these include the Firth of Tay and Eden Estuary (FTEE; Figure 1). Between 1990 and 2002 the average aerial survey count in this area was 640 harbour seals and the area was designated as a SAC in 2005. Annual aerial surveys since 2002 indicate a continuing and significant decline in this population; in 2013, only 50 animals were counted within the FTEE (Duck & Morris, 2014).

To address this situation, the ultimate and proximate causes of the decline must be identified. This, in turn, requires a sound understanding of the population structure and its dynamics. For a number of reasons, estimating the structure of pinniped populations is not straightforward (see discussions in Lonergan, 2014; Matthiopoulos *et al.*, 2014). When the population of interest is critically small and in decline, minimising disturbance to the population is even more important but in addition to aerial surveys, targeted – and repeated – land-based surveillance studies are necessary to estimate key demographic parameters such as adult survival rates, age structure, sex ratio and fecundity (e. g. Bowen *et al.*, 2003, Mackey *et al.*, 2008). Some age classes can be identified when observing harbour seals at a distance – very small animals obviously are young, and large mature males may be distinguishable. However, some one-year old animals are similar in length to small adults (Härkönen & Heide-Jørgensen, 1990) and the species is less sexually dimorphic than many other pinnipeds (Burns, 2008). This lack of obvious dimorphism can complicate the visual identification of the sex of adult harbour seals from a distance, so assumptions about sex ratio of survey counts must be adopted. The sex of animals could be determined non-invasively from the DNA analysis of scats left at haulouts, but obtaining a representative sample from the population is difficult and moving from this to estimating the structure of the population is seldom practical. Mass mortality events and strandings data can provide information on the sex ratio, age structure and fecundity of affected populations – but with the caveat that these data are likely to be biased towards particular groups of animals (e. g. Härkönen & Heide-Jørgensen 1990; but see also Härkönen *et al.*, 2007). Relatively unbiased samples may be obtained where animals are part of a subsistence hunt or culled for management purposes but there are no such samples available for harbour seals in the UK. In the absence of direct estimates of these demographic parameters, indirect estimates and information from other similar populations must be adopted.

## Assessing the impact of the observed and estimated levels of mortality on seal populations at a local, national and international level



**Figure 1.** Map of north east England and eastern Scotland showing the location of the Firth of Tay & Eden estuary (FTEE) Special Area of Conservation (SAC) (marked in green) and neighbouring harbour seal population sites (red dots). Harbour seals counts from 2013 are presented.

In this report, available demographic information on the Firth of Tay and Eden estuary and neighbouring harbour seal populations is pooled from across multiple sources to characterise and contextualise decadal trends in abundance within the region, to explore the potential proximate causes of the decline and to extrapolate to future population size under various scenarios. The relevant insights gained from this exercise are discussed in relation to the future management and conservation of this population specifically, and of harbour seals in the UK more generally. The results confirm a rapid decline in the number of harbour seals hauled out in the FTEE and demonstrate that, if the problem persists at its present rate, the population will become extinct from this area within 20 years.

### 3 Data and Analysis

All analyses were implemented within the R statistical framework (R Core Development Team, 2014) and are on the number of seals counted at haul-outs. These numbers can be converted into rough population estimates by multiplying the counts of harbour seals by a factor of 1.4 (Lonergan *et al.*, 2013) and those of

grey seals by a factor of 3 (Lonergan *et al.*, 2011) to allow for those seals not hauled out at the time of the survey.

### 3.1 Harbour seal population in Firth of Tay and Eden Estuary

Aerial surveys during the moulting period are used to monitor the abundance of harbour seals in the UK. Surveys are conducted from either a fixed-wing aircraft using conventional photography or from a helicopter using thermal imaging during the first three weeks of August, in the period two hours before and after low tide (details of survey methods in Thompson *et al.*, 2010b). These counts represent an index of the minimum population abundance. Previous research suggests that the proportion of animals hauled out and available to be counted is similar between sites, so persistent interannual changes in the counts are unlikely to be due to changes in seal haulout behaviour (Lonergan *et al.*, 2013).

Counts were made in the Firth of Tay and Eden Estuary region in most years from 1990 to 2000 and annually from 2002 – 2013 (Table 1). Four previous counts in 1971, 1975 and 1984 also were included in the analysis, although they used a different survey method. These were boat-based survey counts made during the June/July breeding/pupping season and are likely underestimates of the total population size. Thompson and Harwood (1990) counted twice as many seals in Orkney using aerial surveys conducted during the moult period than using boat-based surveys during the breeding/pupping season.

**Table 1.** Counts of harbour seals and grey seals (*Halichoerus grypus*) hauled out during the annual moult in August in the Firth of Tay and Eden Estuary Special Area of Conservation. Prior to 1990, counts were made from boat-based surveys conducted during the breeding season (June/July). From 1990, counts were made from a fixed wing aircraft using standard photography, from a helicopter using thermal imaging, or using both of these methods ('both').

Year	Harbour seals	Grey seals	Survey method
1971	296		boat
1971	170		boat
1975	208		boat
1984	310	259	boat
1990	467	912	fixed wing
1991	670	1549	fixed wing
1992	773	1226	fixed wing
1994	575	1468	fixed wing
1997	633	1891	thermal imaging
2000	700	2253	fixed wing
2002	668	1593	fixed wing
2003	461	1663	fixed wing
2004	459		fixed wing
2005	335	843	both
2006	342	1379	fixed wing
2007	275	1559	both
2008	222	508	fixed wing
2009	111	450	fixed wing
2010	124	1555	fixed wing
2011	77	1322	fixed wing
2012	88	1202	fixed wing
2013	50	482	thermal imaging

To investigate trends in the harbour seal counts, a generalised additive model (gam) (Wood, 2006), with quasipoisson errors and a log link function, was fitted to the data by maximum likelihood. As the later part of the trajectory appeared to resemble an exponential decay, a similar generalised linear model (glm) was also fitted, with different exponential rates of population growth up to 2000 and from 2001 onwards. This transition point was chosen visually, but its suitability was checked by fitting models with a range of transition dates. Model suitability was assessed by examining residual dispersion and quasi-Akaike Information Criterion (QAIC; Akaike, 1976; Burnham & Anderson, 2002) values.

Additional sources of information existed for this population and were included in the assessment of the population trajectory. In 2010, 2011, and 2012 land-based counts of harbour seal pups were conducted in the FTEE during the June/July breeding/pupping season. These numbers, combined with the counts of adults during the August moult, provide an estimate of the proportion of pups in the population. Additionally, since 2008, harbour seal carcasses with distinctive spiral injuries have been found at various locations around the UK, including within or close to the Firth of Tay and Eden estuary. A total of 36 such harbour seal carcasses have been recovered from within or near the FTEE since 2008 (Table 2). This number is likely an underestimate of the total number of animals that are killed in this way because the data describe only animals that wash ashore and are reported. Carcasses of animals that are injured far from the shore are unlikely to wash ashore and will be underrepresented in this dataset. As with all marine mammal stranding data, it is extremely difficult to estimate the scale of under-reporting, but it is likely to be large for pinnipeds. Additionally, the relative buoyancy of animals of different sexes or ages is likely to affect the chance of carcasses being recovered, and variation in this may make the sample unrepresentative. In the absence of more appropriate data, the sex ratio of these mortalities over the years 2008 to 2013 was investigated by fitting binomial glms.

**Table 2.** Occurrence and sex of harbour seal mortalities from spiral injuries recorded on the east coast of Scotland south of Aberdeen.

	Male	Female	Unidentified
2008*		2	
2009*	1	3	
2010		8	1
2011	1	5	3
2012	4	2	
2013	3	2	1

\* Likely greater under-reporting of spiral seal strandings in these years as the significance of the injuries was not identified prior to 2010

### 3.2 Neighbouring populations

There are a few (small) harbour seal groups neighbouring the FTEE population: in the Firth of Forth (~ 50 km to the south) and the Montrose Basin (approx. 50 km to the north) that could be potential sources of immigrants or emigrant destinations (Figure 1). Until recently, far fewer animals were counted in those areas than in the FTEE. However, that difference is less clear now that the FTEE counts have decreased. There were four counts available from the Firth of Forth (Duck & Morris, 2014) but it is difficult to estimate trends from so few data points. Here, it was assumed that the uncertainty in these counts was similar to those from the FTEE. The counts were modelled using a gam with quasipoisson error distribution and with the same overdispersion as was estimated from the FTEE data (scale = 13.3). Glms were also fitted to the data collected after 2000, when the FTEE counts began to show a decline.

### 3.3 Grey seal population in Firth of Tay and Eden Estuary

Harbour seals share the FTEE with larger and more abundant grey seals (*Halichoerus grypus*). The number of grey seals hauled out during the August harbour seal moult surveys also is counted. Seventeen counts were made between 1990 and 2013 (Table 1), and one count was made during a boat-based survey in 1984.

To investigate trends in the count data over this time period, a generalised additive model was fitted with quasipoisson error distribution and a log link function.

## 4 Results

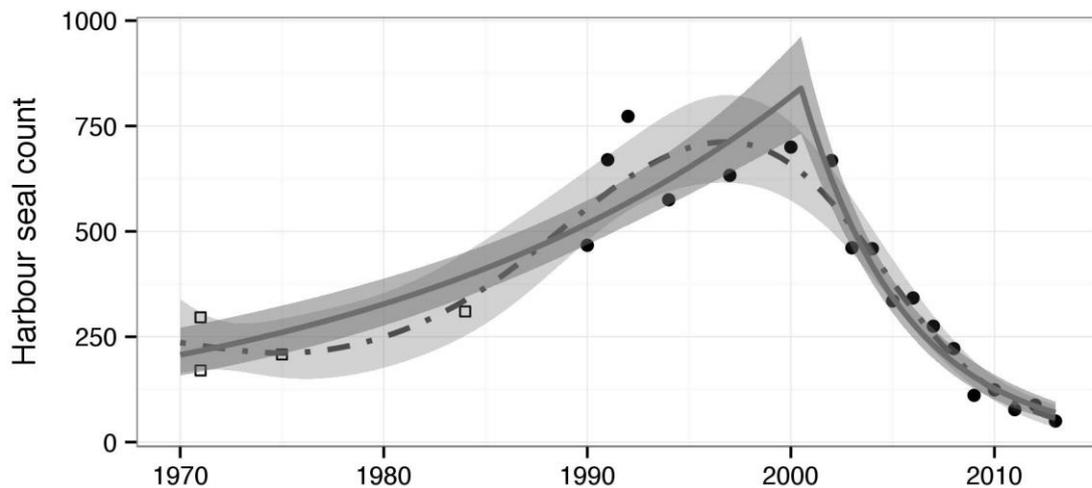
### 4.1 Harbour seal population in Firth of Tay and Eden Estuary

The choice of the year 2000 as the transition point in the population trajectory was supported by the fact that models fitted with transitions in 1998, 1999, 2001 and 2002 had greater residual over-dispersion. Equivalent models fitted with Poisson errors also had higher AIC values than the model with a break point at year 2000. The results of the gam and the glm with a change in trajectory after 2000 were similar (Figure 2), especially for recent years. While the truth is probably somewhere between these extremes, a model where two exponential trajectories were fitted along with a shrinkage spline allowed the two representations to compete and produced results indistinguishable from the original glm. A similar model containing two smooth functions and two exponential trajectories, all meeting between 2000 and 2001, produced identical results. These combined models therefore support a relatively sudden transition between two periods with different, but stable, rates of exponential population growth.

The population growth rate between 1970 and 2000 was estimated at 4.6% *p. a.* (95% Confidence Interval 3.5 - 5.7). This lies within the range of values that have been observed in other harbour seal populations (Thompson *et al.*, 2005, Lonergan *et al.*, 2007). However, the different methodology used for the early surveys may limit their comparability with the later ones, and the reliance that can be put on the estimate of population growth prior to 2000. However, even if count data from the three years of boat-based surveys were doubled (Thompson & Harwood, 1990), population growth was slower but still positive (1.8% *p. a.*; 95% CI 0.9 - 2.8). This source of uncertainty does not affect the estimated annual rate of decline since 2000, which was 19.9% (95% CI: 16.8 – 23.0). This is significantly faster than the estimated annual rate of decline in the harbour seal population around the Orkney Islands and northern Scotland (13% *p. a.*; 95% CI 10.8 - 14.8), another area where there are serious concerns for this species (Lonergan *et al.*, 2013). Detailed examination of the modelled trajectories showed that some recent counts (2009, 2011, 2013) and gam predictions lie below the trajectory estimated by the glm (Figure 2), suggesting that the decline of the FTEE population is unlikely to be slowing.

A total of 12 harbour seal pups were observed during onshore visual searches of the FTEE in 2010, six in 2011, and just one in 2012 (R. Milne, SMRU, pers. comm. ). In those years 124, 77 and 88 adult harbour seals were observed during the moult aerial surveys, meaning roughly 1 pup was observed for every 10 animals counted in 2010. In 2011 the ratio was 1:13 and 1:88 in 2012. These ratios are lower than those estimated for other populations. For example, in The Wash (~450 km south of the FTEE on the east coast of England) the ratio of peak pup numbers observed via aerial surveys during the breeding season to mean total moult counts of adult animals was much higher (1:1.6 to 1:3.5; SCOS, 2012). The low proportion of pups in the area implies either a lower fecundity among adult females or that a smaller proportion of the population are adult females.

The sex ratio of the unusual mortality events caused by spiral lesions (based on recovered stranded carcasses) was fitted with binomial glms. If it is assumed that there were no detection biases on the basis of sex, glms suggested that between 2008 and 2013, 2 to 68% of the animals killed in this way were male. An intercept-only model performed worse than one including a year covariate ( $\Delta\text{AIC} = 5$ ) providing some evidence to suggest the proportion had changed over the period. Unfortunately, it is not possible to test whether the carcasses match the sex ratio of the surviving population, or other populations under more normal conditions.



**Figure 2.** Numbers of harbour seals counted during surveys of the Firth of Tay and Eden Estuary. Solid circles indicate aerial surveys that were carried out during the annual moult in August. The hollow squares indicate an earlier boat-based survey method that counted animals hauled out during the breeding season in June/July, and therefore may not be truly comparable to counts post-1990. The solid line is an estimated trajectory from a glm where the rate of exponential population growth changed after 2000. The dark shaded region around it shows the associated 95% confidence intervals. The dashed curve (and 95% confidence interval) is the result of a gam that assumes changes in the population growth rate changed smoothly over the period.

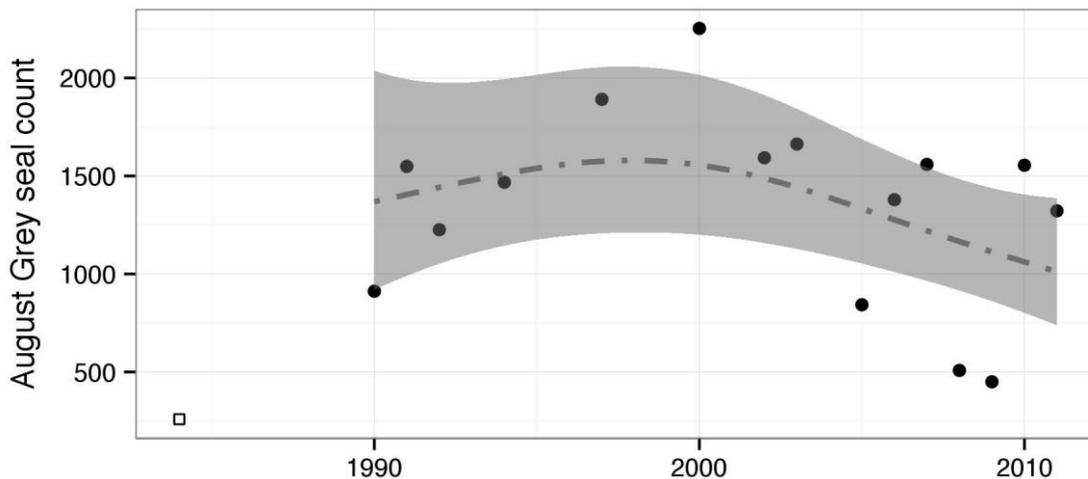
## 4.2 Neighbouring populations

Gams fitted to the four available counts from the Firth of Forth (116 in 1997; 280 in 2005; 148 in 2007; and 145 in 2013) showed no evidence of changes in abundance over the period. A glm fitted to the data from after 2000 ( $n = 3$ ), when the FTEE counts were declining, suggested the population in the Firth of Forth may have been in decline (7.5% p. a.;  $p = 0.13$ ), but the annual rate of change was in the range -0.21 to +0.05. The range in the FTEE during the same period was -0.23 to -0.16. The uncertainty associated with small samples means that approximately 45 more surveys of the Firth of Forth would be required to match the precision of the current estimate of the trend in the FTEE.

Over the last ten years, 36 harbour seals have been fitted with telemetry tags in and around the FTEE. Inspection of their GPS tracks showed two of them hauled out at or beyond Montrose to the north, and another two hauled out within the Firth of Forth to the south. Other individuals swam beyond these places without coming ashore there (Sparling *et al.*, 2012). It therefore seems unlikely that the abundance trajectories in these areas will be wholly independent.

## 4.3 Grey seal population in Firth of Tay and Eden Estuary

Fitting a gam to the counts of grey seals in the FTEE in August showed that there has probably been a slow decline (~1% p. a.) in their numbers over the period since 1990 (Figure 3). While this change is not statistically significant (95% CI: -4.3 – +0.9), it clearly shows that, at least in August, there has not been a substantial increase in grey seal numbers in the FTEE. Grey seal pup production has been increasing at around 9% p. a. in the British North Sea breeding colonies (SCOS, 2013); though pup production at the Isle of May (a SAC for grey seals), the nearest breeding colony to the FTEE harbour seal population, has been fairly stable (Duck & Morris, 2011). The stability in the number of grey seals in the area implies that any competitive pressure they apply to the harbour seals is unlikely to have increased, unless there is a total carrying capacity for pinnipeds in the area that has steadily reduced over this period.



**Figure 3.** Numbers of grey seals counted in aerial surveys of the Firth of Tay and Eden Estuary Special Area of Conservation. Solid circles indicate aerial surveys that were carried out during the annual moult in August. The hollow square indicates an earlier boat-based survey method that counted animals hauled out during the harbour seal breeding season in June/July, and therefore may not be truly comparable to counts post-1990. The dashed line is an estimated trajectory from a gam, and shows a steady exponential decline. The shaded region around the trajectory shows the associated 95% confidence intervals.

#### 4.4 Potential proximate causes

There is one behavioural change, and four changes in the population's demographics, that have the potential to produce the observed decline in harbour seal numbers in the FTEE. The counts of hauled out animals could decrease if haulout behaviour changed and the proportion of time animals spent out of the water during the survey window declined. Harbour seals tagged in the FTEE in 2001-2003 did not show significant inter-annual variation in haulout probability, but because seals lose their tags during the moult, no animals were tracked during August, when the counts used in the present study were made (Sharpley *et al.*, 2009). However, a recent study in Orkney, where the harbour seal population is also declining rapidly, used flipper-attached satellite tags to track animals throughout their moulting period. The animals showed similar haulout behaviour to that previously reported elsewhere and to a control sample of individuals from a stable population on the west coast of Scotland (Lonergan *et al.*, 2013). Furthermore, to account for the magnitude of the reductions found in the FTEE population since 2000, a 93% reduction in the proportion of time spent hauled out around daytime low tides during the moult (and hence proportion of animals available to be counted) would be required. The number of harbour seals hauled out peaks during their moult (Watts, 1996; Thompson *et al.*, 2005), so whilst inter-annual shifts in haulout behaviour are possible, it is considered unlikely that they were the main cause of the observed changes.

The decline could be caused by a reduction in pup and/or adult survival. If all pups die, populations decline at a rate determined by the mortality rates among adults. There are few adult survival estimates for harbour seals in the region. In the Kattegat-Skagerrak, the annual survival rate of male harbour seals has been estimated at 0.91, while female survival was slightly higher (Härkönen & Heide-Jørgensen, 1990). A higher rate 0.97 (95% CI 0.92 – 0.99) was estimated in the Cromarty Firth, in north-eastern Scotland, from photo identification mark-recapture of live animals (Mackey *et al.*, 2008) and in a nearby population, recent estimates were 0.95 (95% CI 0.91 – 0.97) for females and 0.92 (95% CI 0.83 – 0.96) for males (Cordes & Thompson, 2014). The FTEE population is therefore declining too rapidly for even a total failure in recruitment to provide a complete explanation, though it could be a contributory factor. If adult female survival is assumed to have been 0.92 before the decline, then a total failure of recruitment would need to have been accompanied by a reduction in adult survival of at least 10% to produce the observed changes.

The decline could simply be explained by a reduction in overall survival. Lower adult survival would increase the proportion of juveniles in the population, and result in a drop in the ratio of pup numbers to total abundance and an accelerating rate of decline in abundance. A gradual decrease in the proportion of females in the population would have similar effects. The female-bias in the recovered spiral-cut carcasses is difficult to interpret due to incomplete information on the cause of the mortalities and potential detection biases (e. g. due to differences in carcass buoyancy between sexes). However, the low pup to adult ratio found in the population in recent years is consistent with changes in the population structure and a shift towards fewer females than males. The counts and gam trajectory falling below the predicted values from the glm in recent years (Figure 2) hint at this accelerating rate of decline, but as such provide very limited evidence to support such a conclusion.

The same argument that applies to pup/adult survival also means that reduced fecundity cannot entirely explain the decline. If fecundity were zero (which it cannot be given the observations of pups in 2010, 2011, and 2012) the adult mortality would have to equal the observed rate of decline, i. e. 19% p. a. An increase in the age at first reproduction would be equivalent to a reduction in fecundity, but again, there are no data available to test this hypothesis.

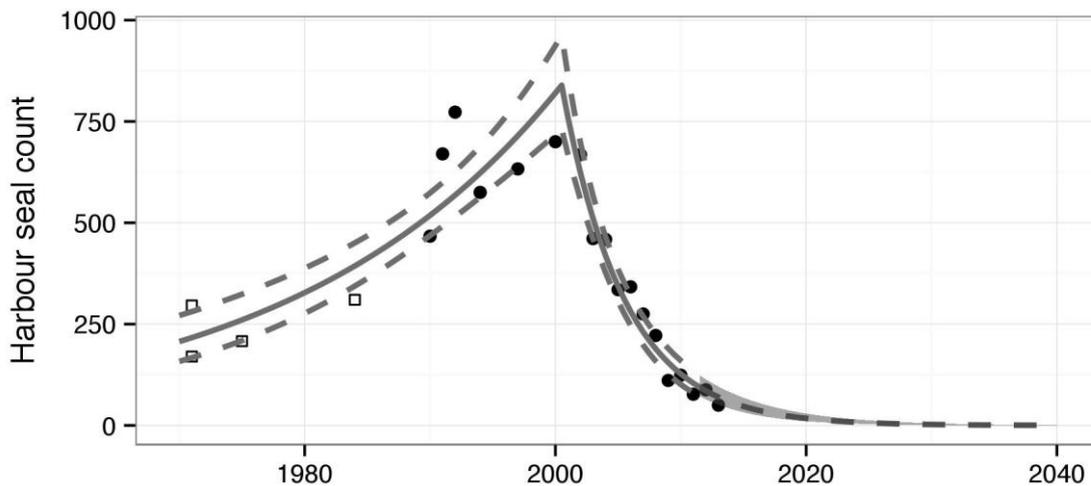
Emigration and immigration are the last demographic parameters that must be explored. Emigration is only distinct from mortality if the animals arrive somewhere else. The Moray Firth contains the only harbour seal population in reasonable proximity that is sufficiently large that an immigration of tens of animals per year could possibly pass unnoticed (Duck *et al.*, 2012). Emigration from the FTEE to smaller populations south of the Moray Firth or to the Firth of Forth would likely have been detected. A cessation of immigration to the FTEE population from neighbouring populations could possibly have contributed to the observed decline, but there is no evidence that the FTEE population received large numbers of immigrants in the years before the decline occurred. The Moray Firth population is again the most likely source of animals for such redistribution but it is > 250 km away from the FTEE and telemetry data suggests that harbour seal redistribution at this scale is likely to be minimal (Thompson *et al.*, 1994, Cunningham *et al.*, 2009, Sharples *et al.*, 2009). While net immigration to the FTEE population in years prior to 2000 is possible, reduced immigration is considered as an unlikely explanation for the observed rapid population decline since 2000.

## 4.5 Future scenarios

Attempts to predict the future trajectory of the FTEE population depend on assumptions about the underlying cause of the decline and any potential mitigation. This section attempts to project the future of the FTEE population under various possible scenarios.

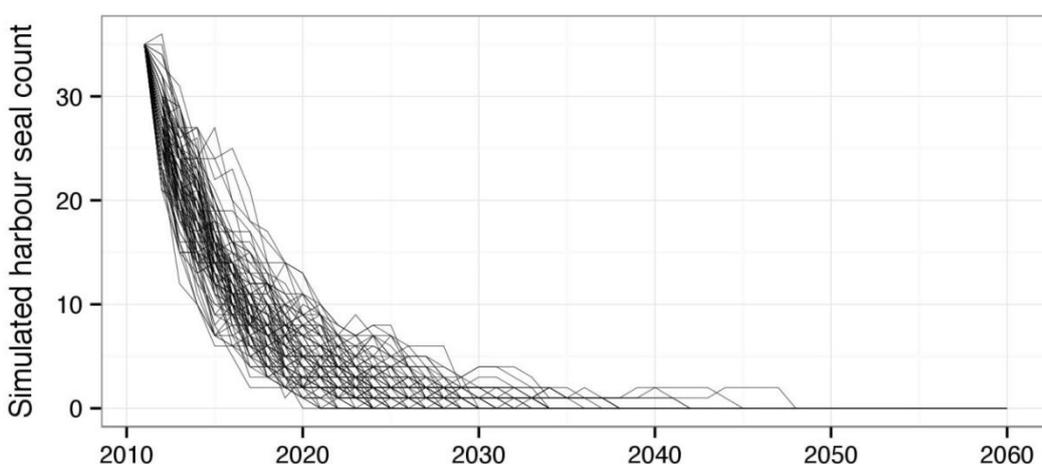
### 4.5.1 'Business as usual'

If no management actions are taken to identify and rectify the cause of decline in this population, and if it continues at the rate established since 2000 (19% p. a.), effective population extinction is likely. Even ignoring stochastic effects, this can be expected to occur before 2040 (Figure 4). In practice, random variations in the sex ratio of births and timings of deaths are likely to make this occur much sooner.



**Figure 4.** Projection of the glm model of the harbour seal counts in the Firth of Tay and Eden estuary is shown in the shaded region after 2013. Dashed lines give the 95% confidence intervals.

A simple stochastic model of the female component of the FTEE harbour seal population assuming 92% annual survival of non-pups (Mackey *et al.*, 2008), 40% survival of pups (Harding *et al.*, 2005), 90% of females older than 3 years old pup each year (Härkönen & Heide-Jørgensen, 1990) and a 50:50 sex ratio, produces a population growth rate of 5% p.a. Introducing an additional 25% mortality, affecting adults and non-pup juveniles, changes this to an 19% p.a. decline. Treating each birth and each individual's annual mortality risk as an independent draw from binomial distributions, and starting with a population of 35 non-pup females, suggests extinction is likely to occur after 20 years (95% CI, from 1000 replicates: 12 – 34 yrs). Figure 5 shows the trajectories of 100 replicate simulated populations. The starting population size of 35 animals was chosen on the assumption that more than half of the 50 animals counted in 2013 were female, but that some of those were pups. This starting estimate may be slightly low to account for the proportion of animals missed from the moult count because they were in the water, but the model also neglects the counteracting possibility that extinction occurs as a result of all males dying or that individual deaths are not independent.



**Figure 5.** Simulated trajectories for the decline of the Firth of Tay and Eden estuary harbour seal population. Each line shows the numbers of females aged at least 1. Populations that appear to recover from zero abundance are those that were reduced to contain only juveniles. By neglecting the possibility of extinction through total loss of males, this model is likely to overstate the length of time this population will survive.

#### 4.5.2 Source of decline eliminated

The glm model fitted to survey counts after 2000 suggested that the 2013 survey was one where a low proportion of animals were hauled out, and that 70 animals could have been expected to have been seen, rather than the 50 animals that were actually observed. Using a scaling factor of 1.4 to account for those animals not hauled out during the survey window (Lonergan *et al.*, 2013) the total population abundance was estimated to be 100 animals. With this – perhaps over optimistic – number, and assuming the sex-ratio and age structure are stable and comparable to those for other harbour seal populations, and ignoring stochastic effects such as elimination of males, the time for abundance to return to 600 can be estimated. Table 3 contains some estimated recovery times based on different population growth rates. The additional years needed for population recovery per year of delay in eliminating the present cause of decline are also presented.

The population growth rates explored in Table 3 were chosen on the basis of existing empirical information on harbour seal population dynamics within the North Sea region. Twelve percent is the present growth rate for the Wadden Sea harbour seal population (TSEG, 2011) and is often considered to be around the maximum sustainable growth rate for pinniped populations (Härkönen *et al.*, 2002). This represents the most ‘optimistic’ scenario whereby the present situation is immediately ameliorated and the population reaches and maintains a maximum growth rate for at least 16 years. Perhaps more realistic are the projections from growth rates between 3% and 6%. The population in The Wash was growing at 3% *p.a.* prior to the 1988 phocine distemper epidemic. It then increased and was approximately 6% *p.a.* between the 1988 and 2002 epidemics (Thompson *et al.*, 2005, Lonergan *et al.*, 2007). If the abundance estimates that were made for the Tay in the 1970s are believed to be consistent with the more recent ones, then this population was growing at around 4.5% *p.a.* up to the beginning of the current decline. In these scenarios, the FTEE population could be expected to recover to its previous abundance in 30 – 60 years. Even in this ‘ideal’ scenario, there is no ‘quick fix’. In reality, the different survey method used in early counts was likely to have caused underestimation. Assuming that the underestimation was about half (Thompson & Harwood, 1990), this has the effect of decreasing the population rate of growth prior to 2000 to about 2%.

**Table 3.** The number of years required for a population to increase from 100 to 600 individuals, at various annual growth rates. The final column is the number of additional years required to balance out the present population decline continuing at 19% for one additional year.

Annual growth rate	Approximate recovery time	Additional years per year of delay
3%	60	7
4.50%	40	5
6%	30	4
12%	16	2

#### 4.5.3 Source of decline partially eliminated

The accepted “normal” maximum growth rate for pinniped population is 12% *p.a.* (Härkönen *et al.*, 2002), but the FTEE population is declining by around 19% *p.a.* The impact of the problem is thus 31% (i.e. 12% - 19% = 31%); a halving of the impact of the problem to 15.5% could be expected to result in a population rate of decline of 3.5% *p.a.* (i. e. -19% + 15.5% = -3.5%). Whatever is affecting this population would need to be reduced by more than half of the total impact for the population to stabilise at its current level, and by more than that to permit it to begin to recover. The situation is much worse if the maximum growth rate is lower. A growth rate of 6% under optimal conditions similar to that observed in The Wash (Thompson *et al.*, 2005; Lonergan *et al.*, 2007), would imply that population recovery would require at least ¾ of the problem to be resolved. If the maximum achievable growth rate were 3% *p.a.* – which may be more representative of Scottish harbour seal populations – then recovery would depend on finding an almost total solution to the problem.

#### 4.5.4 Female shortage in recovering population

Direct measurement of the true sex ratio in the FTEE population is neither feasible nor advisable given its present state and the need to minimise disturbance. A project is underway to estimate the sex ratio of this population non-invasively via DNA testing of scats; however, recovery of suitable samples has proven difficult in this region. Additionally, the method requires many assumptions about patterns of haulout behaviour and defecation and is unlikely to produce an estimate of sex ratio that is truly representative of the population. However, if there is a shortage of females in the recovering population, this would both increase the risk of local extinction because of stochastic variation (i.e. all the females dying) and slow the initial stages of the recovery. Populations starting with more highly skewed sex ratios would initially grow more slowly and it would take longer for their growth rates to recover to more normal values.

#### 4.6 Extinction and recolonisation

Though capable of long distance movement, harbour seals generally exhibit high site fidelity (~25 km from haulout sites; Thompson *et al.*, 1998; Cunningham *et al.*, 2009; Sharples *et al.*, 2012) and there is evidence that genetic diversity increases with distance (Stanley *et al.*, 1996; Goodman, 1998). Philopatry could thus limit their ability to recover from local extinctions. There is no indication that males and females of this species travel together (Thompson *et al.*, 1998), therefore the establishment of a population would seem to require multiple colonising events.

There are two examples of UK harbour seal populations that became extinct and have recovered to some extent, in the Tees and the Ythan Estuaries. The population in the Ythan was removed by shooting in 1979 and 1980. It is not known when the first animals returned, but by the mid-1990s harbour seals were seen regularly in the estuary. The harbour seal population in the Tees disappeared at an unknown date in the mid-19<sup>th</sup> century when large parts of the estuary were developed (Woods, 2012). Harbour seals recolonised the Tees Estuary in the 1970s or early 1980s and the population has grown slowly to reach around 20 to 50 seals (Woods, 2012). The first successful pupping was recorded in 1994. The more rapid recolonisation of the Ythan Estuary may be related to the proximity of small harbour seal haulout groups on the coast 45km to the north. In contrast, the nearest groups to the Tees are in the Firth of Forth, 200km to the north, or in the River Humber, 170km to the south (Figure 1).

In the event of harbour seal extinction in the Firth of Tay and Eden Estuary, the most likely source of colonising animals would be the small populations in the Firth of Forth, 50 to 60 km away, or the animals that haul out north of Montrose, about 40km from the FTEE haul-outs. However, it is not clear that these groups of animals actually are sufficiently separated to follow different population trajectories. Telemetry tags attached to harbour seals in the FTEE have recorded some of these individuals hauling out in the Firth of Forth and around Montrose (SMRU, *unpublished data*). Beyond these areas, the next nearest potential sources of immigrants to the FTEE would be the Moray Firth or the Tees and Humber Estuaries (Figure 1). These areas are > 200km away, so reestablishment of the FTEE population would be unlikely to occur rapidly.

## 5 Discussion

The data available to assess the extent of, and potential mechanisms for, the decline in harbour seal numbers in the Firth of Tay & Eden Estuary are diffuse and often sparse. Nevertheless, these limited data and analyses provide insights into the potential proximate causes for the rapid decline. Furthermore, they provide an avenue to explore possible scenarios for the future of this population and the likely impact of specific management policies.

Using such data, the present study demonstrates that if the trends identified here continue at the present rate, harbour seals are likely to effectively disappear from the FTEE within the next 20 years. Exploration of the demographic parameters that could produce such changes indicate that the, presently unidentified, cause of the decline must be reducing adult survival. Simple projections and simulations demonstrate that if the cause is immediately identified and rectified, recovery of the population to the abundance when the SAC was designated is likely to take at least 40 years and that partial removal of the problem would have limited

benefits. Thus there are unlikely to be any long-term benefits from introducing or reintroducing additional individuals while the problem persists.

Globally, harbour seals are classified as a species of ‘least concern’ on the IUCN Red List; however, the rapid population declines such as the one described here and in Orkney and Shetland (Thompson *et al.*, 2001; Lonergan *et al.*, 2007; 2013) represent significant regional losses of a large and iconic predator. In the FTEE population, a reduction in overall survival must be invoked to account for the rate of decline – but the potential causes of an increase in mortality are various and often inter-linked.

Substantial declines in food availability or accessibility could increase competition for limited resources between conspecifics, and with grey seals. Harbour seals tagged in the area foraged primarily in an area ~ 25-100 km from the haulout site (Sharples *et al.*, 2009; 2012), but there are few simultaneous telemetry data to assess whether grey seals actively exclude harbour seals from some areas. Given that there is a high degree of dietary overlap between the species and that both use the FTEE to haul out, there is considerable potential for overlap in foraging areas. If inter-specific competition is indeed hastening the demise of the FTEE harbour seal population, the question of any relevant management action remains. However, a reduction in harbour seal condition as a result of increased competition for resources would most likely be manifest in the population as reduced fecundity and/or pup survival – neither of which can account for the rapid rate of decline observed, without also invoking substantial reduction in adult survival.

A notable recent phenomenon has been the discovery of multiple carcasses with ‘corkscrew’ injuries on the east coast of Scotland and England (Thompson *et al.*, 2010a; Bexton *et al.*, 2012). The majority of these have been adult female harbour seals, or juvenile grey seals. The exact cause of the characteristic injuries is unknown, although the pathological findings are consistent with the animals being pulled through a ducted propeller (Bexton *et al.*, 2012). While the numbers of ‘corkscrew’ harbour seals recorded in the FTEE since 2008 are fairly low ( $n = 36$ ), these are likely to underestimate total numbers because not all carcasses will be washed ashore, detected, or reported. Furthermore, the six corkscrew mortalities reported in 2013 represent >10% of the total number of animals counted at the FTEE that year. Clearly, anthropogenic mortality at this rate is not sustainable for this population. Future management actions should be focused on unequivocally identifying and ameliorating this, and other, potential sources of additional harbour seal mortality if the population is to be conserved.

The analysis presented above suggests that the observed level of harbour seal mortality in and around the FTEE due to corkscrew injuries is unsustainable at current population size. However, in other seal management regions around Scotland the numbers of recorded corkscrew injuries in harbour seals are lower relative to the current population estimates.

As argued earlier in USD 1&6 there is not any information on the true extent or scale of the corkscrew injury problem. It is possible that most of the animals that are being killed as being seen, but it may be that recording rate is low in other areas or that there is substantial mortality further offshore that does not result in stranded carcasses which would not be recorded. In the absence of information to differentiate between these two scenarios it is only possible to compare the observed mortality with the estimated population size and status in each region.

The simplest way to assess the importance of this phenomenon is to compare the observed mortality due to corkscrew lesions with the potential biological removals (PBR) estimate for each region. The PBR estimate is used by Scottish Government to set the maximum permissible anthropogenic levels of removals from the regional seal populations. PBR values and their calculation including the rationale for selecting the appropriate value for the recovery factor (FR) are presented elsewhere (e.g. SCOS, 2014). Table 4 shows the minimum population estimates (approximately the lower 20th percentiles of the distributions of population estimates) and PBR estimates for harbour seals in the seven Scottish seal management regions together with the total number of corkscrew carcasses seen since systematic recording began in 2010. There has clearly been a wide variation in recording rates in different regions at different times and it is therefore difficult to interpret this information. Notwithstanding the possible/likely general under-recording the maximum number of records in any 12 month period was compared with the PBR in each region.

**Table 4.** Details of PBR estimates and minimum estimated population sizes for harbour seals and the total and maximum annual rate of recording of corkscrew seals in Scotland.

<b>Harbour seal</b>						
<b>Management Region</b>	<b>N<sub>min</sub></b>	<b>F<sub>r</sub></b>	<b>PBR</b>	<b>Total number of CS recorded</b>	<b>Max number in one year</b>	<b>% of PBR</b>
South-west Scotland	834	0.7	35	2	1	3%
West Scotland	11057	0.7	464	0	0	0
Western Isles	2739	0.5	82	0	0	0
North coast and Orkney	1938	0.1	11	3	2	18%
Shetland	3039	0.1	18	0	0	0
Moray Firth	898	0.3	16	9	8	50%
East Coast	215	0.1	1	37	10	1000%

For the East Coast region, including the FTEE, where the population is both severely depleted and continuing to decline the PBR is currently set to one; the minimum allowed under the assumptions of the PBR method. The observed corkscrew mortality has exceeded the PBR in every year since 2008 and in 2010 it was ten times higher than the PBR. Exceeding the PBR by such a degree would be expected to cause a rapid population decline, as confirmed by the analysis detailed above.

In the Orkney and North Coast region the PBR is set at a precautionary level of 11 animals to reflect the continuing decline from unknown causes. The maximum number of harbour seals recorded in one year was two seals, and was in fact the first observation of corkscrew mortality in the UK in 1985. This occurred at a time when the harbour seal population was an order of magnitude higher than now, but if this is taken as the maximum annual rate it represents almost 20% of the estimated PBR. If the background cause of the Orkney decline is unrelated to the corkscrew seals then the removal of an extra two seals from the estimated minimum population of around 2000 seals would reduce the population by 0.1%. The average rate of decrease of the Orkney population has been 9.4% p.a. (95% c. i. 7.5-11.3%) over the past decade (SCOS, 2014) so the observed corkscrew mortality would have only a small and probably un-detectable effect on the dynamics of the Orkney population.

In the Moray Firth the situation is less clear. Until 2014 there had only been one confirmed corkscrew case but between December 2013 and December 2014 a total of eight harbour seals were found dead in the Moray Firth, one near Dunbeath and seven in the inner Firth. The observed corkscrew mortality therefore represents 50% of the PBR, which is itself less precautionary than the value for Orkney or the East Coast. The removal of an extra eight seals from the estimated minimum population of around 900 seals would reduce the population by almost 1%. The fact that these mortality events were apparently rare in the region before 2014 suggests that this may be a novel mortality factor. This situation needs to be closely monitored and this mortality will need to be accounted for in the implementation of the Moray Firth Management Plan.

Only one corkscrew case has been confirmed in harbour seals in the other seal management regions and this suggests that it is not a major factor in determining the population status in those areas.

**Table 5.** Details of PBR estimates and minimum estimated population sizes for grey seals and the total and maximum annual rate of recording of corkscrew seals in Scotland.

Grey seal						
Management Region	$N_{\min}$	$F_r$	PBR	Total number of CS recorded	Max number in one year	% of PBR
Southwest Scotland	957	1	57	2	1	2%
West Scotland	6912	1	414	1	1	<1%
Western Isles	6446	1	386	1	1	<1%
North coast and Orkney	20682	1	1240	12	4	<1%
Shetland	3932	1	235	0	0	<1%
Moray Firth	3356	1	201	1	1	<1%
East Coast	4954	1	297	47	19	6%

Table 5 shows the e population, PBR and corkscrew mortality data for grey seals in Scottish management regions. As for harbour seals the majority of carcasses have been recorded in the Firth of Tay and the Firth of Forth area. Even here the maximum number of reported cases in any one year represents less than 0.4% of the estimated minimum population. In addition, the grey seal population in the central North Sea is continuing to increase at an exponential rate. In all other areas the number of reported cases represents less than 0.1% of the estimated minimum population and overall in Scotland the total of the individual yearly maximum for each region represents less than 0.02% of the total population. This suggests that the corkscrew mortality is unlikely to have any noticeable impact on population trajectories of grey seals.

These comparisons are based on the numbers of corkscrew seal carcasses reported. This is likely to be an underestimate of the total number being killed. If for example only 10% of such events were recorded the mortality rate for grey seals due to such events would be around 3% p.a. in the East Coast management region. In all other regions the rate would still be less than 1% p.a. However, significant under-reporting of harbour seal mortality could mean that this could be an important driver of population trends in the Moray Firth as well as the East Coast management regions.

## 6 Acknowledgements

Aerial surveys were funded by SNH and NERC. We thank colleagues at SMRU for their help conducting surveys. Preparation of this work benefited from discussions with C. Morris and A. Hall at the SMRU.

## 7 References

- Akaike, H. 1976. An information criterion (AIC). *Journal of Mathematical Science*, **14**,5-9.
- Bexton, S., Thompson, D., Brownlow, A., Barley, J., Milne, R. & Bidewell, C. (2012) Unusual mortality of pinnipeds in the United Kingdom associated with helical (corkscrew) injuries of anthropogenic origin. *Aquatic Mammals*, **38**, 229-240.
- Bowen, W.D., Ellis, S.L. Iverson, S.J. & Boness, D.J. (2003) Maternal and newborn life-history traits during periods of contrasting population trends: implications for explaining the decline of harbour seals (*Phoca vitulina*), on Sable Island. *Journal of Zoology*, **26**, 155-163.
- Burnham, K. P. & Anderson, D. R. (2002) *Model Selection and Multi-Model Inference*. Springer, New York.
- Burns, J. J. (2008) Harbor Seal and Spotted Seal (*Phoca vitulina* and *P. largha*). in W. F. Perrin, B. Würsig, and J. G. M. Thewissen, editors. *Encyclopedia of Marine Mammals*. Academic Press, Burlington, MA.

- Cordes, L.S. & Thompson, P. M. (2014) Mark-recapture modeling accounting for state uncertainty provides concurrent estimates of survival and fecundity in a protected harbor seal population. *Marine Mammal Science*, **30**, 691–705.
- Cunningham, L., Baxter, J. M., Boyd, I. L., Duck, C. D., Lonergan, M., Moss, S. E. & McConnell, B. (2009) Harbour seal movements and haul-out patterns: implications for monitoring and management. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **19**, 398-407.
- Duck, C. D. & Morris, C. D. (2011) Grey seal pup production in Britain in 2010. Sea Mammal Research Unit, St Andrews, Scotland.
- Duck, C. D. & Morris, C. D. (2012) Surveys of harbour (common) and grey seals in the Outer Hebrides and the Moray Firth in August 2011, Report to Scottish Natural Heritage, Sea Mammal Research Unit, University of St Andrews, St Andrews.
- Duck, C. D. & Morris, C. D. (2014) Surveys of harbour (common) and grey seals on the east, north and north-west coast of Scotland and in Orkney, including the Moray Firth and the Firth of Tay, in August 2013. Report to Scottish Natural Heritage, Sea Mammal Research Unit, University of St Andrews, St Andrews
- Goodman, S. J. (1998) Patterns of extensive genetic differentiation and variation among European harbor seals (*Phoca vitulina vitulina*) revealed using microsatellite DNA polymorphisms. *Molecular Biology and Evolution*, **15**, 104-118.
- Harding, K. C., Fujiwara, M., Axberg, Y. & Härkönen, T. (2005) Mass-dependent energetics and survival in harbour seal pups. *Functional Ecology*, **19**, 129-135.
- Härkönen, T., Harding, K.C. & Heide-Jørgensen, M.-P. (2002) Rates of increase in age-structured populations: a lesson from the European harbour seals. *Canadian Journal of Zoology*, **80**, 1498-1510.
- Härkönen, T., Harding, K., Rasmussen, T.D., Teilmann, J. & Dietz, R. (2007) Age- & sex-specific mortality patterns in an emerging wildlife epidemic: the phocine distemper in European harbour seals. *PLoS One*, e887.
- Härkönen, T., & Heide-Jørgensen, M.-P. (1990) Comparative life histories of east Atlantic and other harbour seal populations. *Ophelia*, **32**, 211-235.
- Lonergan, M. (2014) Modelling beyond data is uninformative: a comment on "State-space modelling reveals proximate causes of harbour seal population declines" by Matthiopoulos et al. *Oecologia*, **175**,1063-1067.
- Lonergan, M., Duck, C.D., Moss, S., Morris, C. & Thompson, D. (2013) Rescaling of aerial survey data with information from small numbers of telemetry tags to estimate the size of a declining harbour seal population. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **23**,135-144.
- Lonergan, M., Duck, C. D., Thompson, D., Mackey, B. L., Cunningham, L. & Boyd, I. L. (2007) Using sparse survey data to investigate the declining abundance of British harbour seals. *Journal of Zoology*, **271**, 261-269.
- Lonergan, M., Duck, C. D., Thompson, D, Moss, S. & McConnell, B. (2011) British grey seal (*Halichoerus grypus*) abundance in 2008: an assessment based on aerial counts and satellite telemetry. *ICES Journal of Marine Science*, **68**, 2201-2209.
- Mackey, B. L., Durban, J. W., Middlemas, S. J. & Thompson, P. M. (2008) A Bayesian estimate of harbour seal survival using sparse photo-identification data. *Journal of Zoology*, **274**, 18-27.
- Matthiopoulos, J., Cordes, L., Mackey, B., Thompson, D., Duck, C., Smout, S., Caillat, M. & Thompson, P. (2014) State-space modelling reveals proximate causes of harbour seal population declines. *Oecologia*, **174**,151-162.
- R\_Core\_Development\_Team. (2014) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.
- SCOS (2012) Scientific advice on matters related to the management of seal populations: 2012. Natural Environment Research Council, Sea Mammal Research Unit, University of St Andrews, St Andrews.
- SCOS (2013) Scientific advice on matters related to the management of seal populations: 2013. Natural Environment Research Council, Sea Mammal Research Unit, University of St Andrews, St Andrews.
- SCOS (2014) Scientific advice on matters related to the management of seal populations: 2013. Natural Environment Research Council, Sea Mammal Research Unit, University of St Andrews, St Andrews.

Assessing the impact of the observed and estimated levels of mortality on seal populations at a local, national and international level

- Sharples, R. J., Mackenzie, M. L. & Hammond, P. S. (2009) Estimating seasonal abundance of a central place forager using counts and telemetry data. *Marine Ecology Progress Series*, **378**, 289-298.
- Sharples, R. J., Moss, S., Patterson, T. A. & Hammond, P. S. (2012). Spatial variation in foraging behaviour of a marine top predator (*Phoca vitulina*) determined by a large-scale satellite tagging program. *PLoS One* **7**:e37216.
- Sparling, C. E., Russell, D. F., Lane, E., Grellier, K., Lonergan, M. E. , McConnell, B. , Matthiopoulos, J. & Thompson, D. (2012) Baseline seal information for the FTOWDG area. SMRUL-FDG-2012-0 to FTOWDG.
- Stanley, H. F., Casey, S., Carnahan, J. M., Goodman, S., Harwood, J. & Wayne, R. K. (1996) Worldwide patterns of mitochondrial DNA differentiation in the harbor seal (*Phoca vitulina*). *Molecular Biology and Evolution* ,**13**, 368-382.
- Thompson, D., Bexton, S., Brownlow, A., Wood, D., Patterson, T., Pye, K., Lonergan, M. & Milne, R. (2010a) Report on recent seal mortalities in UK waters caused by extensive lacerations October 2010. Report to Scottish Government, Sea Mammal Research Unit, University of St Andrews, St Andrews.
- Thompson, D., Duck, C.D. & Lonergan M. E. (2010b). The status of harbour seals (*Phoca vitulina*) in the United Kingdom. *NAMMCO Scientific Publications*, **8**,117-128.
- Thompson, D., Lonergan, M. & Duck., C. (2005) Population dynamics of harbour seals *Phoca vitulina* in England: monitoring growth and catastrophic declines. *Journal of Applied Ecology*, **42**, 638-648.
- Thompson, P. M. & Harwood, J. (1990) Methods for estimating the population-size of common seals, (*Phoca vitulina*). *Journal of Applied Ecology*, **27**, 924-938.
- Thompson, P. M., Kovacs, K. M. & McConnell, B. J. (1994) Natal dispersal of harbour seals (*Phoca vitulina*) from breeding sites in Orkney, Scotland. *Journal of the Zoology*, **234**, 668-673.
- Thompson, P. M., Mackay, A., Tollit, D.J ., Enderby, S. & Hammond, P. S. (1998) The influence of body size and sex on the characteristics of harbour seal foraging trips. *Canadian Journal of Zoology*, **76**, 1044-1053.
- Thompson, P. M., v. Parijs, S. & Kovacs, K. M. (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.
- TSEG. (2011) Aerial surveys of harbour seals in the Wadden Sea in 2010: Strong increase in pups, slight increase in total number? Common Wadden Sea Secretariat, Wilhelmshaven.
- Watts, P. (1996) The diel hauling-out cycle of harbour seals in an open marine environment: correlates and constraints. *Journal of Zoology*, **240**, 175–200.
- Wood, S.N. (2006). *Generalized Additive Models: An Introduction with R*. Chapman & Hall/CRC, Boca Raton.
- Woods, R. (2012) The State of the Natural Environment of the Tees Estuary (SONET): A review of the seal chapter. Industry Nature Conservation Association, Redcar.