



**University of Dundee**

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*Published in:*  
Aquatic Conservation: Marine and Freshwater Ecosystems

*DOI:*  
[10.1002/aqc.2609](https://doi.org/10.1002/aqc.2609)

*Publication date:*  
2017

*Document Version*  
Peer reviewed version

[Link to publication in Discovery Research Portal](#)

*Citation for published version (APA):*  
Hanson, N., Thompson, D., Duck, C., Baxter, J., & Lonergan, M. (2017). Harbour seal (*Phoca vitulina*) abundance within the Firth of Tay and Eden Estuary, Scotland: recent trends and extrapolation to extinction. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 27(1), 268-281. <https://doi.org/10.1002/aqc.2609>

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**Harbour seal (*Phoca vitulina*) abundance within the Firth of Tay and Eden estuary, Scotland: recent trends and extrapolation to extinction**

Journal:	<i>Aquatic Conservation: Marine and Freshwater Ecosystems</i>
Manuscript ID:	AQC-15-0016.R1
Wiley - Manuscript type:	Research Article
Date Submitted by the Author:	n/a
Complete List of Authors:	Hanson, Nora; University of St Andrews, NERC Sea Mammal Research Unit, Scottish Oceans Institute Thompson, Dave; University of St Andrews, NERC Sea Mammal Research Unit, Scottish Oceans Institute Duck, Callan; University of St Andrews, NERC Sea Mammal Research Unit, Scottish Oceans Institute Lonergan, Mike; University of St Andrews, NERC Sea Mammal Research Unit, Scottish Oceans Institute; University of Dundee, School of Medicine
Broad habitat type (mandatory) select 1-2:	coastal < Broad habitat type, littoral < Broad habitat type
General theme or application (mandatory) select 1-2:	monitoring < General theme or application, Special Area of Conservation < General theme or application, conservation evaluation < General theme or application
Broad taxonomic group or category (mandatory, if relevant to paper) select 1-2:	mammals < Broad taxonomic group or category
Impact category (mandatory, if relevant to paper) select 1-2:	

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5 2 ***Harbour seal (*Phoca vitulina*) abundance within the Firth of Tay and Eden estuary,***  
6 3 ***Scotland: recent trends and extrapolation to extinction***  
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10 Running head: Rapid harbour seal decline and extrapolation to extinction  
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35  
36 20 **ABSTRACT**

- 37 21 1. Aerial surveys have detected alarming declines in the counts of harbour seals in  
38 22 several regions across Scotland.  
39 23 2. Demographic data and simple models were used to examine the recent decline in the  
40 24 numbers of harbour seals counted in one population within a Special Area of  
41 25 Conservation (SAC) on the east coast of Scotland. The models suggest that the  
42 26 continuation of current trends would result in the species effectively disappearing from  
43 27 this area within the next 20 years.  
44 28 3. While the cause of the decline is unknown, it must be reducing adult survival because  
45 29 the high rate of decline cannot be wholly accounted for by changes in other  
46 30 demographic parameters.  
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4 31 4. Recovery of the population to the abundance recorded at the time the SAC was  
5 32 designated (2005) is likely to take at least 40 years, even if the cause of the decline is  
6 33 immediately identified and removed.

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9 34 5. The models suggest that partial removal of the cause can have only limited benefits to  
10 35 population recovery, and there are unlikely to be any long-term benefits from  
11 36 introducing or reintroducing additional individuals while the underlying problem  
12 37 persists. Therefore, if the population of harbour seals in this area is to recover it is  
13 38 essential that the sources of the increased mortality are identified and measures are put  
14 39 in place to manage these.  
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21 41 KEYWORDS: coastal, littoral, monitoring, Special Area of Conservation, conservation  
22 42 evaluation, mammals  
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## 25 26 44 INTRODUCTION

27 45 The UK is home to around 30% of Europe's harbour seals (*Phoca vitulina*), with the  
28 46 majority of these hauling out at island and coastal sites in the north and west of Scotland  
29 47 (SCOS, 2013). Harbour seals in Scotland have been monitored on an approximately  
30 48 five-yearly cycle since the late 1980s. Two populations, in part of the Moray Firth and  
31 49 around the Firth of Tay, have been surveyed more frequently. The surveys have  
32 50 detected alarming declines in the number of harbour seals observed at haulout sites in  
33 51 several regions. This trend is most apparent in populations in Orkney and on the north  
34 52 and east coasts of Scotland, where numbers have declined by between 65% and 90%,  
35 53 respectively, since the 1990s (Duck and Morris, 2014). Importantly, the decline in  
36 54 number of seals counted is not simply a consequence of changes in seal behaviour  
37 55 altering the proportion of time seals spend hauled out during the moult. A recent  
38 56 telemetry study comparing harbour seals in the declining Orkney population and a  
39 57 stable population on the west coast of Scotland demonstrated that the proportion of  
40 58 animals hauled out during the survey window was high in both areas, and similar to  
41 59 previously published proportions for this species (Lonergan *et al.*, 2013). The declines  
42 60 in harbour seal counts are thus likely to represent real reductions in the numbers of  
43 61 animals present in the region.  
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4 63 Harbour seals are protected under the Marine (Scotland) Act 2010, which prohibits the  
5 64 killing of any seal except under a licence granted by the Scottish Government explicitly  
6 65 for the protection of fisheries or fish farms. There is also the capacity under the Marine  
7 66 (Scotland) Act 2010 to designate seal conservation areas where it is considered  
8  
9 67 necessary to further encourage the proper conservation of seals. Furthermore, a number  
10 68 of harbour seal Special Areas of Conservation (SAC) have been designated under the  
11 69 EU Habitats Directive (for a map of SACs in Scotland, see:  
12 70 <http://www.scotland.gov.uk/Publications/2011/03/16182005/54>). The Firth of Tay and  
13 71 Eden Estuary (FTEE; Figure 1) was designated an SAC in 2005 in part due to its  
14 72 importance as a breeding and haulout site for harbour seals. Between 1990 and 2002 the  
15 73 average aerial survey count in the FTEE was 640 harbour seals but annual aerial  
16 74 surveys since 2002 indicate a continuing and significant decline in this population: in  
17 75 2013 only 50 animals were counted within the FTEE (Duck and Morris, 2014).  
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27 77 To address this situation, the ultimate and proximate causes of the decline must be  
28 78 identified. This, in turn, requires a sound understanding of the population structure and  
29 79 its dynamics. For a number of reasons, estimating the structure of pinniped populations  
30 80 is not straightforward (Lonergan, 2014; see discussions in Matthiopoulos *et al.*, 2014).  
31 81 When the population of interest is critically small and in decline minimising disturbance  
32 82 to the population is particularly important, but in addition to aerial surveys, targeted –  
33 83 and repeated – land-based surveillance studies are necessary to estimate key  
34 84 demographic parameters such as adult survival rates, age structure, sex ratio and  
35 85 fecundity (Bowen *et al.*, 2003; Mackey *et al.*, 2008). Some age classes can be identified  
36 86 when observing harbour seals at a distance – for example, very small animals obviously  
37 87 are young and sub-yearlings can be identified by characteristically pale unpatterned  
38 88 pelage (Thompson and Rothery, 1987). Large mature adults may also be distinguishable  
39 89 from other age/sex classes. However, some one-year old animals are similar in length to  
40 90 small adults (Härkönen and Heide-Jørgensen, 1990) and the species is less sexually  
41 91 dimorphic than many other pinnipeds (Burns, 2008). This lack of obvious dimorphism  
42 92 means that visual identification of the sex of adult harbour seals from a distance is  
43 93 seldom possible, so assumptions about sex ratio of survey counts must be adopted. The  
44 94 sex of animals could be determined non-invasively from the DNA analysis of scats left  
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4 95 at haulouts, but obtaining a representative sample from the population is difficult and  
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6 96 moving from this to estimating the structure of the population is seldom practical.  
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8 97 Furthermore, harbour seals can haul out in sex-related groups so haulout groups may  
9  
10 98 not provide an unbiased estimate of sex ratio. Mass mortality events and strandings data  
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12 99 can provide information on the sex ratio, age structure and fecundity of affected  
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14 100 populations – but with the caveat that these data are likely to be biased towards  
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16 101 particular groups of animals (e.g. Härkönen and Heide-Jørgensen, 1990; but see also  
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18 102 Härkönen *et al.*, 2007). Relatively unbiased samples may be obtained where animals are  
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20 103 part of a subsistence hunt or culled for management purposes but there are no such  
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22 104 samples available for harbour seals in the UK. In the absence of direct estimates of  
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24 105 these demographic parameters, indirect estimates and information from other similar  
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26 106 populations must be adopted.  
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30 108 Here, available demographic information on the Firth of Tay and Eden estuary and  
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32 109 neighbouring harbour seal populations is pooled from across multiple sources to  
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34 110 characterize and contextualize decadal trends in abundance within the region, to explore  
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36 111 the potential proximate causes of the decline and to extrapolate to future population  
37  
38 112 sizes under various scenarios. Insights gained from this exercise are discussed in  
39  
40 113 relation to the future management and conservation of this population specifically, and  
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42 114 of harbour seals in the UK more generally. The results confirm a rapid decline in the  
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44 115 number of harbour seals hauled out in the FTEE and demonstrate that, if the problem  
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46 116 persists at its present rate, the population will become extinct from this area within 20  
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48 117 years.  
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#### 119 **DATA & ANALYSIS**

51  
52 120 All analyses were implemented within the R statistical framework (R Development  
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54 121 Core Team, 2013) and are based on the number of seals counted at haulouts. These  
55  
56 122 numbers can be converted into rough population estimates by multiplying the counts of  
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58 123 harbour seals by a factor of 1.4 (Lonergan *et al.*, 2013) and those of grey seals by a  
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60 124 factor of 3 (Lonergan *et al.*, 2011) to allow for those seals not hauled out at the time of  
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126 125 the survey.

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4 127 *Harbour seal population in Firth of Tay and Eden Estuary*

5 128 Aerial surveys during the moulting period are used to monitor the abundance of harbour  
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7 129 seals in the UK. Surveys are conducted from either a fixed-wing aircraft using  
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9 130 conventional photography or from a helicopter using thermal imaging during the first  
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11 131 three weeks of August, in the period two hours before and after low tide (Thompson *et*  
12  
13 132 *al.*, 2010b). These counts represent an index of the minimum population abundance.  
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15 133 Previous research suggests that the proportion of animals hauled out and available to be  
16  
17 134 counted is similar between sites, so persistent interannual changes in the counts are  
18  
19 135 unlikely to be due to changes in seal haulout behaviour (Lonergan *et al.*, 2013).  
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22 137 Counts were made in the FTEE region in most years from 1990 to 2000 and annually  
23  
24 138 from 2002 – 2013 (Table 1). Four previous counts in 1971, 1975 and 1984 were also  
25  
26 139 included in the analysis, although they used a different survey method. These were boat-  
27  
28 140 based survey counts made during the June/July breeding/pupping season and are likely  
29  
30 141 underestimates of the total population size. Thompson and Harwood (1990) counted  
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32 142 twice as many seals in Orkney using aerial surveys conducted during the moult period  
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34 143 than using boat-based surveys during the breeding/pupping season.  
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37 145 To investigate trends in the harbour seal counts, a generalized additive model (GAM)  
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39 146 (Wood, 2006), with quasipoisson errors and a log link function, was fitted to the data by  
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41 147 maximum likelihood. As the later part of the trajectory appeared to resemble an  
42  
43 148 exponential decay, a similar generalized linear model (GLM) was also fitted, with  
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45 149 different exponential rates of population growth up to 2000 and from 2001 onwards.  
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47 150 This initial transition point was chosen visually, and its suitability was checked by  
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49 151 fitting models with a range of transition dates. Model suitability was assessed by  
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51 152 examining residual dispersion and quasi-Akaike Information Criterion values (QAIC  
52  
53 153 Akaike, 1976; Burnham and Anderson, 2002).  
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56 155 Additional sources of information existed for this population and were included in the  
57  
58 156 assessment of the population trajectory. In 2010, 2011, and 2012 land-based counts of  
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60 157 harbour seal pups were conducted in the FTEE during the June/July breeding/pupping  
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159 season. These numbers, combined with the counts of adults during the August moult,  
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4 159 provide an estimate of the proportion of pups in the population. Additionally, since  
5 160 2008, harbour seal carcasses with distinctive 'spiral' or 'corkscrew' injuries have been  
6 161 found at various locations around the UK, including a total of 36 carcasses within or  
7 162 close to the Firth of Tay and Eden estuary (Table 2). The pathology of these injuries has  
8 163 been described elsewhere (Bexton *et al.*, 2012), and the potential causes were discussed  
9 164 in Onoufrinou *et al.* (2014) and Thompson *et al.* (2015). Recent observations of adult  
10 165 male grey seals preying on harbour seals and grey seal pups have demonstrated that  
11 166 the characteristic 'spiral' lesions can be inflicted by another seal (Thompson *et al.*,  
12 167 2015; van Neer *et al.*, 2015). The number of such harbour seal carcasses reported in the  
13 168 FTEE is likely to underestimate the total number of animals that are killed in this way  
14 169 because the data describe only animals that wash ashore and are reported. Carcasses of  
15 170 animals that are killed far from the shore are unlikely to wash ashore and will be  
16 171 underrepresented in this dataset. As with all marine mammal strandings data, it is  
17 172 extremely difficult to estimate the scale of under-reporting, but it is likely to be large for  
18 173 pinnipeds. Additionally, the relative buoyancy of animals of different sexes or ages is  
19 174 likely to affect the chance of their carcasses being recovered, and variation in this may  
20 175 make the sample unrepresentative. In the absence of more appropriate data, the sex ratio  
21 176 of these mortalities over the years 2008 to 2013 was investigated by fitting binomial  
22 177 GLMs.  
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### 178 179 *Neighbouring populations*

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39 180 There are a few, small, harbour seal groups neighbouring the FTEE population: in the  
40 181 Firth of Forth (~ 50 km to the south) and the Montrose basin (~50 km to the north) that  
41 182 could be potential sources of immigrants or destinations for emigrants (Figure 1). Until  
42 183 recently, far fewer animals were counted in those areas than in the FTEE. However, that  
43 184 difference is less clear now that the FTEE counts have decreased. Four counts are  
44 185 available from the Firth of Forth (Duck and Morris, 2014), but it is difficult to estimate  
45 186 trends from so few data points. Here, it was assumed that the uncertainty in these counts  
46 187 was similar to those from the FTEE. The counts were modelled using a GAM with  
47 188 quasipoisson error distribution and with the same overdispersion as was estimated from  
48 189 the FTEE data (scale = 13.3). GLMs were also fitted to the data collected after 2000,  
49 190 when the FTEE counts began to show a decline.  
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*Grey seal population in Firth of Tay and Eden Estuary*

7 193 Harbour seals share the FTEE with larger and more abundant grey seals (*Halichoerus*  
8 194 *grypus*). The only available information about the number of grey seals in this region  
9 195 comes from August harbour seal moult surveys, when grey seals are also counted.  
10 196 Seventeen counts of grey seals were made between 1990 and 2013 (Table 1), and one  
11 197 count was made during a boat-based survey in 1984. To investigate trends in the count  
12 198 data over this time period, a GAM was fitted with quasipoisson error distribution and a  
13 199 log link function.

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15 201

**RESULTS**

16 202 Harbour seal abundance in the Firth of Tay and Eden estuary showed positive growth  
17 203 prior to 2001 after which there was a clear transition to a rapid decline. Emigration of  
18 204 seals to nearby haulouts, or local redistribution, could not be ruled out, but seems  
19 205 unlikely based on available counts of neighbouring populations and distances to those  
20 206 populations. Potential proximate causes for the decline are explored in more detail,  
21 207 including changes to haulout behaviour, fecundity, survival and emigration.

22 208

*Harbour seal population in Firth of Tay and Eden Estuary*

23 209 The choice of the year 2000 as the transition point in the population trajectory was  
24 210 supported by the fact that models fitted with transitions in 1998, 1999, 2001 and 2002  
25 211 had greater residual overdispersion. Equivalent models fitted with Poisson errors also  
26 212 had higher AIC values than the model with a break point at year 2000. The results of  
27 213 the GAM and the GLM with a change in trajectory after 2000 were similar (Figure 2),  
28 214 especially for recent years. While the truth is probably somewhere between these  
29 215 extremes, a model where two exponential trajectories were fitted along with a shrinkage  
30 216 spline allowed the two representations to compete and produced results  
31 217 indistinguishable from the original GLM. A similar model containing two smooth  
32 218 functions and two exponential trajectories, all meeting between 2000 and 2001,  
33 219 produced identical results. These combined models therefore support a relatively sudden  
34 220 transition between two periods with different, but stable, rates of exponential population  
35 221 change.

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4 223 The population growth rate between 1970 and 2000 was estimated at 4.6% *p.a.* (95%  
5 224 Confidence Interval 3.5 - 5.7). This lies within the range of values that have been  
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7 225 observed in other harbour seal populations (Thompson *et al.*, 2005; Lonergan *et al.*,  
8  
9 226 2007), but is still far from the 12% intrinsic rate of increase for harbour seals (Härkönen  
10 227 *et al.*, 2002). The different methodology used for the early surveys may limit their  
11 228 comparability with the later ones, and the reliance that can be put on the estimate of  
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13 229 population growth prior to 2000. However, even if count data from the three years of  
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15 230 boat-based surveys were doubled (following Thompson and Harwood, 1990), estimated  
16 231 population growth was still positive (1.8% *p.a.*; 95% CI 0.9 - 2.8). This source of  
17 232 uncertainty does not affect the estimated annual rate of decline since 2000, which was  
18 233 19.9% (95% CI: 16.8 – 23.0). This is significantly faster than the estimated annual rate  
19 234 of decline in the harbour seal population around the Orkney Islands and northern  
20 235 Scotland (13% *p.a.*; 95% CI 10.8 - 14.8), another area where there are serious concerns  
21 236 for this species (Lonergan *et al.*, 2013). Detailed examination of the modelled  
22 237 trajectories showed that some recent counts (2009, 2011, 2013) and GAM predictions  
23 238 lie below the trajectory estimated by the GLM (Figure 2), suggesting that the decline of  
24 239 the FTEE population is unlikely to be slowing.  
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34 241 A total of 12 harbour seal pups were observed during onshore visual searches of the  
35 242 FTEE in 2010, 6 in 2011, and just one in 2012 (R. Milne, SMRU, *pers. comm.*). In those  
36 243 years 124, 77 and 88 adult harbour seals were observed during the moult aerial surveys,  
37 244 meaning roughly 1 pup was observed for every 10 animals counted in 2010 and the ratio  
38 245 was 1:13 in 2011, and 1:88 in 2012. These ratios are lower than those estimated for  
39 246 other populations. For example, in The Wash (~450 km south of the FTEE on the east  
40 247 coast of England) the ratio of peak pup numbers observed via aerial surveys during the  
41 248 breeding season to mean total moult counts of adult animals was much higher (1:1.6 to  
42 249 1:3.5; SCOS, 2012). The low proportion of pups in the area in recent years implies  
43 250 either a lower fecundity among adult females or that a smaller proportion of the  
44 251 population are adult females.  
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54 253 The sex ratio of the unusual mortality events caused by spiral lesions (based on  
55 254 recovered stranded carcasses) was modelled with binomial GLMs. If it is assumed that  
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4 255 there were no detection biases on the basis of sex, GLMs suggested that 29% (95% CI:  
5 256 16 – 47) of the animals killed in this way were male. An intercept-only model  
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7 257 performed worse than one including a year covariate ( $\Delta AIC = 5$ ) providing some  
8  
9 258 evidence to suggest the proportion had changed over the period. Unfortunately, it is not  
10  
11 259 possible to test whether the carcasses match the sex ratio of the surviving population, or  
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13 260 other populations under more normal conditions.  
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### *Neighbouring populations*

17 263 GAMs fitted to the four available counts from the Firth of Forth (116 in 1997; 280 in  
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19 264 2005; 148 in 2007; and 145 in 2013) showed no evidence of changes in abundance over  
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21 265 the period. A GLM fitted to the data from after 2000 ( $n = 3$ ), when the FTEE counts  
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23 266 were declining, suggested the population in the Firth of Forth may have been in decline  
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25 267 but the annual rate of change was in the range -0.21 to +0.05 (95% CI). The range in the  
26  
27 268 FTEE during the same period was -0.23 to -0.16. The uncertainty associated with small  
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29 269 samples in the Firth of Forth means that approximately 45 more surveys would be  
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31 270 required to match the precision of the current estimate of the trend in the FTEE.  
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33 271 Without this added precision, no firm conclusions can be made about trends in  
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35 272 abundance in the Firth of Forth area.  
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37 274 Over the last ten years, 36 harbour seals have been fitted with telemetry tags in and  
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39 275 around the FTEE. Inspection of their GPS tracks showed two of them hauled out at or  
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41 276 beyond Montrose to the north, and another two hauled out within the Firth of Forth to  
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43 277 the south. Other individuals swam beyond these places without coming ashore  
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45 278 there (Sparling *et al.*, 2012). It therefore seems unlikely that the abundance trajectories  
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47 279 in these areas will be wholly independent.  
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### *Grey seal population in Firth of Tay and Eden Estuary*

49 282 Fitting a GAM to the counts of grey seals in the FTEE in August showed that there has  
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51 283 probably been a slow decline ( $\sim 1\%$  *p.a.*) in their numbers over the period since 1990  
52  
53 284 (Figure 3). While this change is not statistically significant (95% CI: -4.3 – +0.9), it  
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55 285 clearly shows that, at least in August, there has not been a substantial increase in grey  
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57 286 seal numbers in the FTEE. Grey seal pup production has been increasing at around 9%

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4 287 *p.a.* in the British North Sea breeding colonies (SCOS, 2013); though pup production at  
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6 288 the Isle of May (a SAC for grey seals), a breeding colony about 35km from the FTEE  
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8 289 harbour seal population, has been fairly stable (Duck and Morris, 2011). Grey seal and  
9  
10 290 harbour seal at-sea and haulout usage overlaps in the FTEE (Jones *et al.*, 2013) but the  
11  
12 291 observed stability in the number of grey seals in the area implies that any competitive  
13  
14 292 pressure they apply to the harbour seals is unlikely to have increased, unless there is a  
15  
16 293 total carrying capacity for pinnipeds in the area that has steadily reduced over this  
17  
18 294 period. Reductions in pinniped carrying capacity could be caused by a reduced prey  
19  
20 295 resources, or reductions in access to suitable haulout locations. The latter is not the case  
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22 296 as there are ample suitable haulout locations for both species in the FTEE; the former is  
23  
24 297 less easily determined. North Sea regime shifts (Beaugrand, 2004; Beaugrand *et al.*,  
25  
26 298 2014) and trends in pelagic fish communities (e.g. Shephard *et al.*, 2014) are well  
27  
28 299 documented but the impact of these changes on marine mammal diet and condition is  
29  
30 300 not well understood.  
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#### 302 ***Potential proximate causes***

303 There is one behavioural change, and four changes in the population's demographics,  
304 with the potential to produce the observed decline in harbour seal numbers in the FTEE.  
305 It is unlikely that a single factor is responsible for the dramatic decline in this  
306 population, but for the sake of clarity, each is discussed in isolation below.  
307

308 The counts of hauled out animals could decrease if haulout behaviour changed and the  
309 proportion of time animals spent out of the water during the survey window declined.  
310 Harbour seals tagged in the FTEE in 2001-2003 did not show significant interannual  
311 variation in haulout probability, but because seals lose their tags during the moult, no  
312 animals were tracked during August, when the counts used in the present study were  
313 made (Sharples *et al.*, 2009). However, a recent study in Orkney, where the harbour seal  
314 population is also declining rapidly, used flipper-attached satellite tags to track animals  
315 throughout their moulting period. The animals showed similar haulout behaviour to that  
316 previously reported elsewhere and to a control sample of individuals from a stable  
317 population on the west coast of Scotland (Lonergan *et al.*, 2013). Furthermore, to  
318 account for the magnitude of the reductions found in the FTEE population since 2000, a

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4 319 93% reduction in the proportion of time spent hauled out around daytime low tides  
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6 320 during the moult (and hence proportion of animals available to be counted) would be  
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8 321 required. The number of harbour seals hauled out peaks during their moult (Watts,  
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10 322 1996; Thompson *et al.*, 2005), so whilst interannual shifts in haulout behaviour are  
11  
12 323 possible, it is considered unlikely that they were the main cause of the observed  
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14 324 changes.

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16 325  
17 326 The decline could be caused by a reduction in pup and/or adult survival. If all pups die,  
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19 327 populations decline at a rate determined by the mortality rates among adults. There are  
20  
21 328 few adult survival estimates for harbour seals in the region. In the Kattegat-Skagerrak,  
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23 329 the annual survival rate of male harbour seals has been estimated at 0.91, while female  
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25 330 survival was slightly higher (Härkönen and Heide-Jørgensen, 1990). A higher rate 0.97  
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27 331 (95% CI 0.92 – 0.99) was estimated in the Cromarty Firth, in northeastern Scotland,  
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29 332 from photo identification mark-recapture of live animals (Mackey *et al.*, 2008); and in a  
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31 333 nearby population, recent estimates were 0.95 (95% CI 0.91-0.97) for females and 0.92  
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33 334 (95% CI 0.83-0.96) for males (Cordes and Thompson, 2014). The FTEE population is  
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35 335 therefore declining too rapidly for even a total failure in recruitment to provide a  
36  
37 336 complete explanation, though it could be a contributory factor. If adult female survival  
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39 337 is assumed to have been 0.92 before the decline, then a total failure of recruitment  
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41 338 would need to have been accompanied by a reduction in adult survival of at least 10%  
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43 339 to produce the observed changes.

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45 340  
46 341 The decline could simply be explained by a reduction in overall survival. Lower adult  
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48 342 survival would increase the proportion of juveniles in the population, and result in a  
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50 343 drop in the ratio of pup numbers to total abundance and an accelerating rate of decline  
51  
52 344 in abundance. A gradual decrease in the proportion of females in the population would  
53  
54 345 have similar effects. The female-bias in the recovered spiral-cut carcasses is difficult to  
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56 346 interpret due to incomplete information on the cause of the mortalities and potential  
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58 347 detection biases (e.g. due to differences in carcass buoyancy between sexes). However,  
59  
60 348 the low pup to adult ratio found in the population in recent years is consistent with  
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350 349 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

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4 351 years (Figure 2) hint at an accelerating rate of decline, but as such provide very limited  
5 352 evidence to support such a conclusion.

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9 354 The same argument that applies to pup/adult survival also means that reduced fecundity  
10 355 alone cannot entirely explain the decline. While reduced fecundity could contribute to  
11 356 the observed low pup to adult ratio, if fecundity were zero (which it cannot be given the  
12 357 observations of pups in 2010, 2011, and 2012) the adult mortality would have to equal  
13 358 the observed rate of decline, i.e. 19% *p.a.* An increase in the age at first reproduction  
14 359 would be equivalent to a reduction in fecundity, but again, there are no data available to  
15 360 test this hypothesis.

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18 362 Emigration and immigration are the last demographic parameters that must be  
19 363 examined. Emigration is only distinct from mortality if the animals arrive somewhere  
20 364 else. The Moray Firth contains the only harbour seal population in reasonable proximity  
21 365 that is sufficiently large that an immigration of tens of animals per year could possibly  
22 366 pass unnoticed (Duck and Morris, 2014). Emigration from the FTEE to smaller  
23 367 populations south of the Moray Firth or to the Firth of Forth would likely have been  
24 368 detected as substantial percentage increases in survey counts. A cessation of  
25 369 immigration to the FTEE population from neighbouring populations could possibly  
26 370 have contributed to the observed decline, but there is no evidence that the FTEE  
27 371 population received large numbers of immigrants in the years before the decline  
28 372 occurred. The Moray Firth population is again the most likely source of animals for  
29 373 such redistribution but it is > 250 km away from the FTEE and telemetry data suggests  
30 374 that harbour seal redistribution at this scale is likely to be minimal (Thompson *et al.*,  
31 375 1994; Cunningham *et al.*, 2009; Sharples *et al.*, 2009). While net immigration to the  
32 376 FTEE population in years prior to 2000 is possible, it is considered that reduced  
33 377 immigration is unlikely to explain the observed rapid population decline since 2000.

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#### *Future scenarios*

38 380 Attempts to predict the future trajectory of the FTEE population depend on assumptions  
39 381 about the underlying cause of the decline and any potential mitigation. This section  
40 382 attempts to project the future of the FTEE population under various possible scenarios.

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383

384 *'Business as usual'*

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

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

407

408 *Source of decline eliminated*

409 The GLM model fitted to survey counts after 2000 suggested that the 2013 survey was  
410 one where a low proportion of animals were hauled out, and that 70 animals could have  
411 been expected to be seen, rather than the 50 animals that were actually observed. Using  
412 a scaling factor of 1.4 to account for those animals not hauled out during the survey  
413 window (Lonergan *et al.*, 2013) the total population abundance was estimated to be 100  
414 animals. With this – perhaps over optimistic – number, and assuming the sex-ratio and

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4 415 age structure are stable and comparable to those for other harbour seal populations, and  
5 416 ignoring stochastic effects such as elimination of males, the time for abundance to  
6 417 return to 600 can be estimated. Table 3 contains some estimated recovery times based  
7 418 on different population growth rates. The additional years needed for population  
8 419 recovery per year of delay in eliminating the present cause of decline are also presented.  
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10 421 The population growth rates explored in Table 3 were chosen on the basis of existing  
11 422 empirical information on harbour seal population dynamics within the North Sea region.  
12 423 Twelve percent is the present growth rate for the Wadden Sea harbour seal population  
13 424 (TSEG, 2013) and is often considered to be around the maximum sustainable growth  
14 425 rate for pinniped populations (Härkönen *et al.*, 2002). This represents the most  
15 426 ‘optimistic’ scenario whereby the cause of the present situation is immediately resolved  
16 427 and the population reaches and maintains a maximum growth rate for at least 16 years.  
17 428 Perhaps more realistic are the projections from growth rates between 3% and 6%. The  
18 429 population in The Wash was growing at 3% *p.a.* prior to the 1988 phocine distemper  
19 430 epidemic. It then increased and was approximately 6% *p.a.* between the 1988 and 2002  
20 431 epidemics (Thompson *et al.*, 2005; Lonergan *et al.*, 2007). If the abundance estimates  
21 432 that were made for the Tay in the 1970s are believed to be consistent with the more  
22 433 recent ones, then this population was growing at around 4.5% *p.a.* up to the beginning  
23 434 of the recent decline. In these scenarios, the FTEE population could be expected to  
24 435 recover to its previous abundance in 30 – 60 years. Even in this ‘ideal’ scenario, there is  
25 436 no ‘quick fix’. In reality, the different survey method used in early counts was likely to  
26 437 have caused underestimation of abundances and therefore overestimation of the rate of  
27 438 population growth. Assuming that the underestimation was about half (Thompson and  
28 439 Harwood, 1990), this has the effect of decreasing the population’s rate of growth prior  
29 440 to 2000 to about 2%.

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#### 31 442 *Source of decline partially eliminated*

32 443 The accepted “normal” maximum growth rate for pinniped population is 12% *p.a.*  
33 444 (Härkönen *et al.*, 2002), but the FTEE population is declining by around 19% *p.a.* The  
34 445 impact of the problem is thus 31% (i.e. 12% - -19%= 31%); a halving of the impact of  
35 446 the problem to 15.5% could be expected to result in a population rate of decline of 3.5%  
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4 447 *p.a.* (i.e.  $-19\% + 15.5\% = -3.5\%$ ). Whatever is affecting this population would therefore  
5 448 need to be reduced by more than half of the total impact for the population to stabilize at  
6 449 its current level, and by more than that to permit it to begin to recover. A growth rate of  
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8 450 6% under optimal conditions similar to that observed in The Wash (Thompson *et al.*,  
9 451 2005; Lonergan *et al.*, 2007), would imply that population recovery would require at  
10 452 least  $\frac{3}{4}$  of the problem to be resolved. If the maximum achievable growth rate were 3%  
11 453 *p.a.* – which may be more representative of Scottish harbour seal populations – then  
12 454 recovery would depend on finding an almost complete solution to the problem.  
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#### 18 455 19 456 *Female shortage in recovering population*

20 457 Direct measurement of the true sex ratio in the FTEE population is neither feasible, nor  
21 458 advisable given its present state and the need to minimize disturbance. A project is  
22 459 underway to estimate the sex ratio of this population non-invasively via DNA testing of  
23 460 scats; however, recovery of suitable samples has proven difficult in this region.  
24 461 Additionally, the method requires many assumptions about patterns of haulout  
25 462 behaviour and defecation and is unlikely to produce an estimate of sex ratio that is truly  
26 463 representative of the population. However, if there is a shortage of females in the  
27 464 recovering population, this would both increase the risk of local extinction because of  
28 465 stochastic variation (i.e. all the females dying) and slow the initial stages of the  
29 466 recovery. Populations starting with more highly skewed sex ratios would initially grow  
30 467 more slowly and it would take longer for their growth rates to recover to more normal  
31 468 values.  
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#### 41 469 42 470 *Extinction & recolonization*

43 471 Though capable of long distance movement, harbour seals generally exhibit high site  
44 472 fidelity, generally using haulouts less than ~25 km apart (Thompson *et al.*, 1998;  
45 473 Cunningham *et al.*, 2009; Sharples *et al.*, 2012; Cordes and Thompson, 2015), and there  
46 474 is evidence that genetic diversity increases with distance (Stanley *et al.*, 1996;  
47 475 Goodman, 1998). Philopatry could thus limit their ability to recover from local  
48 476 extinctions. There is no indication that males and females of this species travel together  
49 477 (Thompson *et al.*, 1998), therefore the establishment of a population would seem to  
50 478 require multiple colonizing events.  
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6 480 There are two examples of UK harbour seal populations that became extinct and have  
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8 481 recovered to some extent, in the Tees and the Ythan Estuaries. The population in the  
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10 482 Ythan was removed by shooting in 1979 and 1980. It is not known when the first  
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12 483 animals returned, but by the mid 1990s harbour seals were seen regularly in the estuary.  
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14 484 The harbour seal population in the Tees disappeared at an unknown date in the mid 19<sup>th</sup>  
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16 485 century when large parts of the estuary were developed (Woods, 2012). Harbour seals  
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18 486 recolonized the Tees Estuary in the 1970s or early 1980s and the population has grown  
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20 487 slowly to reach around 20 to 50 seals (Woods, 2012). The first successful pupping was  
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22 488 recorded in 1994. The more rapid recolonization of the Ythan Estuary may be related to  
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24 489 the proximity of small harbour seal haulout groups on the coast 45km to the north  
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26 490 (Figure 1). In contrast, the nearest groups to the Tees are in the Firth of Forth, 200km to  
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28 491 the north, or in the River Humber, 170km to the south (Figure 1).

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32 493 In the event of harbour seal extinction in the Firth of Tay and Eden Estuary, the most  
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34 494 likely source of colonizing animals would be the small populations in the Firth of Forth,  
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36 495 50 to 60 km away, or the animals that haul out north of Montrose, about 40km from the  
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38 496 FTEE haulouts. However, it is not clear that these groups of animals actually are  
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40 497 sufficiently separated to follow different population trajectories. Telemetry tags  
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42 498 attached to harbour seals in the FTEE have recorded some of these individuals hauling  
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44 499 out in the Firth of Forth and around Montrose (SMRU, *unpublished data*). Beyond these  
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46 500 areas, and the few animals now on the Ythan Estuary, the next nearest potential sources  
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48 501 of immigrants to the FTEE would be the Moray Firth or the Tees and Humber Estuaries  
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50 502 (Figure 1). These areas are > 200km away, so reestablishment of the FTEE population  
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52 503 would be unlikely to occur rapidly.

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## 505 **DISCUSSION**

506 The data available to assess the extent of, and potential mechanisms for, the decline in  
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508 507 harbour seal numbers in the Firth of Tay and Eden Estuary are diffuse and often sparse.  
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510 508 Nevertheless, analysis of these limited data provides insights into the potential  
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512 509 proximate causes for the rapid decline. Furthermore, they provide an avenue to explore  
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514 510 possible scenarios for the future of this population and the likely impact of specific

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4 511 management policies. Such an approach may also be useful in other studies of  
5 512 populations where demographic data are limited or non-existent.  
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9 514 Using such data, the present study demonstrates that if the trends identified here  
10 515 continue at the present rate, harbour seals are likely to effectively disappear from the  
11 516 FTEE within the next 20 years. Exploration of the demographic parameters that could  
12 517 produce such changes indicate that the, presently unidentified, cause of the decline must  
13 518 be reducing adult survival (potentially in addition to reducing fecundity and/or pup  
14 519 survival). Simple projections and simulations demonstrate that, if the cause is  
15 520 immediately identified and removed, recovery of the population to the abundance when  
16 521 the SAC was designated is likely to take at least 40 years and that partial removal of the  
17 522 problem would have limited benefits. Thus there are unlikely to be any long-term  
18 523 benefits from introducing or reintroducing additional individuals while the problem  
19 524 persists.  
20 525  
21 526 Globally, harbour seals are classified as a species of ‘least concern’ on the IUCN Red  
22 527 List; however, the rapid population declines such as the one described here and in  
23 528 Orkney and Shetland (Thompson *et al.*, 2001; Lonergan *et al.*, 2007, 2013) represent  
24 529 significant regional losses of a large and iconic predator. In the FTEE population, a  
25 530 reduction in overall survival must be invoked to account for the rate of decline – but the  
26 531 potential causes of an increase in mortality are various and often inter-linked.  
27 532  
28 533 Substantial declines in food availability or accessibility could increase competition for  
29 534 limited resources between conspecifics, and with grey seals. Harbour seals tagged in the  
30 535 area foraged primarily in an area ~ 25-100 km from the haulout site (Sharples *et al.*,  
31 536 2009, 2012), but there are few simultaneous telemetry data to assess whether grey seals  
32 537 actively exclude harbour seals from some areas. Given that there is a high degree of  
33 538 dietary overlap between the species and that both use the FTEE to haul out, there is  
34 539 considerable potential for overlap in foraging areas. If inter-specific competition is  
35 540 indeed hastening the demise of the FTEE harbour seal population, the question of any  
36 541 relevant management action remains. However, a reduction in harbour seal condition as  
37 542 a result of increased competition for resources would most likely be manifest in the  
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4 543 population as reduced fecundity and/or pup survival. In addition to natural mortality  
5 544 from predators, this has been proposed as an explanation for the decline of the harbour  
6 545 seal population on Sable Island, Canada (Bowen *et al.*, 2003). Reduced fecundity and/or  
7 546 pup survival could be a factor in the decline of the FTEE population but neither of these  
8 547 can wholly account for the rapid rate of decline observed. A substantial reduction in  
9 548 adult survival must also be invoked.  
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15 550 A notable recent phenomenon has been the discovery of multiple carcasses with  
16 551 'corkscrew' or 'spiral' injuries on the east coast of Scotland and England (Thompson *et*  
17 552 *al.*, 2010a; Bexton *et al.*, 2012). The majority of these have been adult female harbour  
18 553 seals, or juvenile male grey seals. The pathology of these characteristic injuries is  
19 554 consistent with the animals being pulled through a ducted propeller (Bexton *et al.*,  
20 555 2012), but there now exists unequivocal evidence that such injuries can be, and in some  
21 556 cases are being, inflicted by adult male grey seals (Thompson *et al.*, 2015; van Neer *et*  
22 557 *al.*, 2015). Investigations into the prevalence of this behaviour and its impact on harbour  
23 558 seal populations are ongoing. While the numbers of 'corkscrew' harbour seals recorded  
24 559 in the FTEE since 2008 are fairly low ( $n = 36$ ), these are likely to underestimate total  
25 560 numbers because not all carcasses will be washed ashore, detected, or reported.  
26 561 Furthermore, the 6 corkscrew mortalities reported in 2013 represent >10% of the total  
27 562 number of animals counted at the FTEE that year. Clearly, mortality at this rate is not  
28 563 sustainable for this population.  
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41 565 Each year of delay in addressing the cause of the decline seems likely to both increase  
42 566 the risk of local extinction and further delay any recovery to historical abundances by  
43 567 several years. Future management actions should be focused on unequivocally  
44 568 identifying and ameliorating this, and other, potential sources of additional harbour seal  
45 569 mortality if the population is to be conserved.  
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#### 51 571 **ACKNOWLEDGEMENTS**

52 572 Aerial surveys were funded by SNH and NERC. We thank colleagues at SMRU for  
53 573 their help conducting surveys. Preparation of this work benefited from discussions with  
54 574 C. Morris and A. Hall at the SMRU.  
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710 **TABLES**

711 **Table 1:** Counts of harbour seals (*Phoca vitulina*) and grey seals (*Halichoerus grypus*)  
 712 hauled out during the annual moult in August in the Firth of Tay and Eden Estuary  
 713 Special Area of Conservation since regular surveys began. Prior to 1990, counts were  
 714 made from boat-based surveys conducted during the breeding season (June/July). From  
 715 1990, counts were made from a fixed wing aircraft using standard photography, from a  
 716 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

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4 718 **Table 2:** Occurrence and sex of harbour seal (*Phoca vitulina*) mortalities from  
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6 719 corkscrew injuries recorded on the east coast of Scotland south of Aberdeen.  
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	Male	Female	Unidentified
2008*		2	
2009*	1	3	
2010		8	1
2011	1	5	3
2012	4	2	
2013	3	2	1

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19 720 \* Likely under-reporting of corkscrew strandings in these years  
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4 725 **Table 3:** The number of years required for a population to increase from 100 to 600  
5 726 individuals, at various annual growth rates. The final column is the number of additional  
6 727 years required to balance out the present population decline continuing at 19% for one  
7 728 additional year.

Annual growth rate	Approximate recovery time	Additional years per year of delay
3%	60	7
4.5%	40	5
6%	30	4
12%	16	2

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4 732 **Figure 1:** Map of northeast England and eastern Scotland showing the location of the  
5 733 Firth of Tay & Eden estuary (FTEE) Special Area of Conservation (SAC) and  
6 734 neighbouring harbour seal population sites. Harbour seals counts from 2013 are  
7 presented.  
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4 737 **Figure 2:** Numbers of harbour seals counted during surveys of the Firth of Tay and  
5 738 Eden Estuary. Solid circles indicate aerial surveys that were carried out during the  
6 739 annual moult in August. The hollow squares indicate an earlier boat-based survey  
7 740 method that counted animals hauled out during the breeding season in June/July, and  
8 741 therefore may not be truly comparable to counts post-1990. The solid line is an  
9 742 estimated trajectory from a GLM where the rate of exponential population growth  
10 743 changed after 2000. The dark shaded region around it shows the associated 95%  
11 744 confidence intervals. The dashed curve (and 95% confidence interval) is the result of a  
12 745 GAM that assumes changes in the population growth rate changed smoothly over the  
13 746 period.  
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4 748 **Figure 3:** Numbers of grey seals counted during summer surveys of the Firth of Tay  
5 and Eden Estuary Special Area of Conservation. Solid circles indicate aerial surveys  
6 749 that were carried out during the annual harbour seal moult in August. The hollow square  
7 750 indicates an earlier boat-based survey method that counted animals hauled out during  
8 751 the harbour seal breeding season in June/July, and therefore may not be truly  
9 752 comparable to counts post-1990. The dashed line is an estimated trajectory from a  
10 753 GAM, and shows a steady exponential decline. The shaded region around the trajectory  
11 754 shows the associated 95% confidence intervals.  
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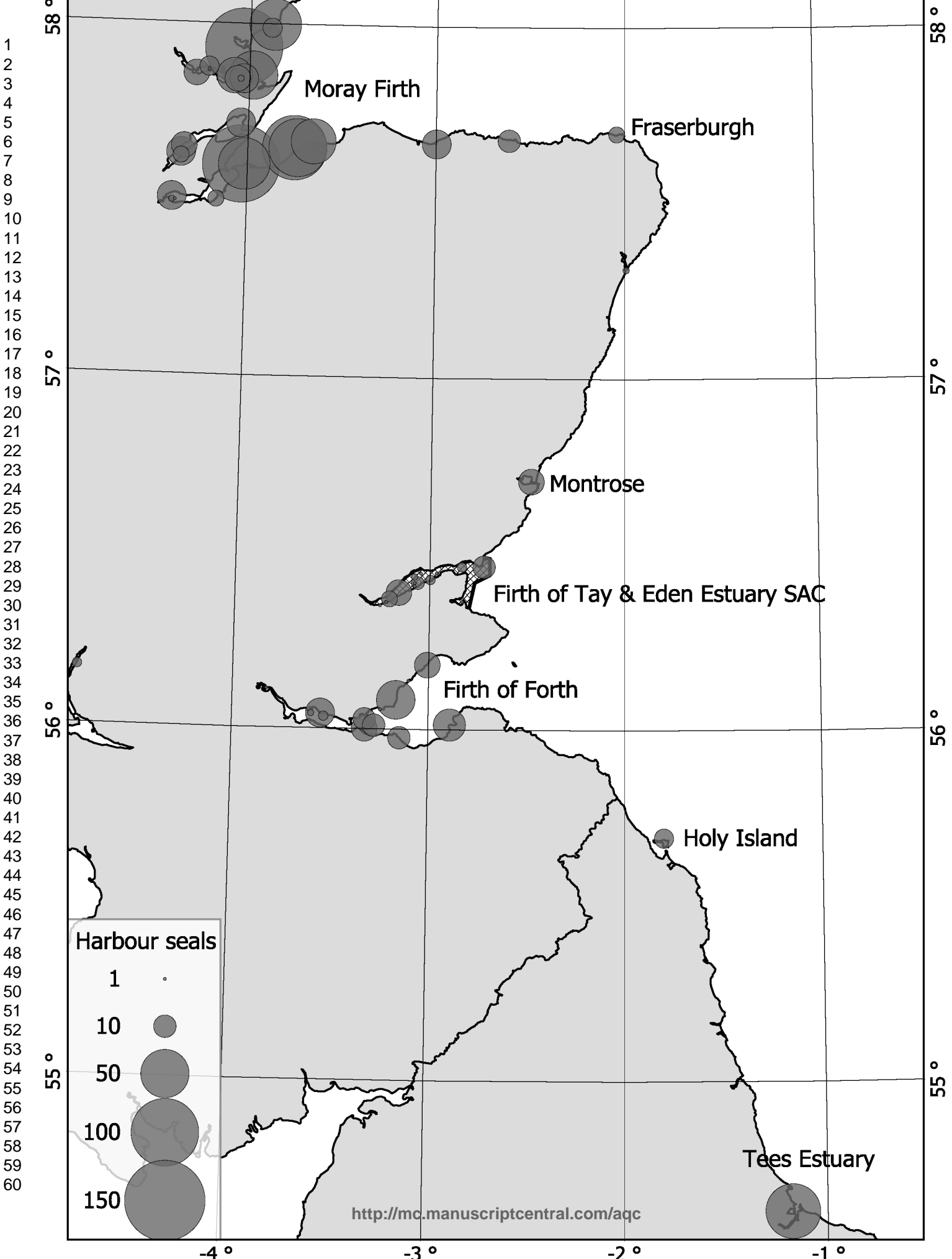
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4 757 **Figure 4:** Projection of the GLM model (and 95% confidence intervals) of the harbour  
5 758 seal counts in the Firth of Tay and Eden estuary shown in the red shaded region after  
6 759 2013.  
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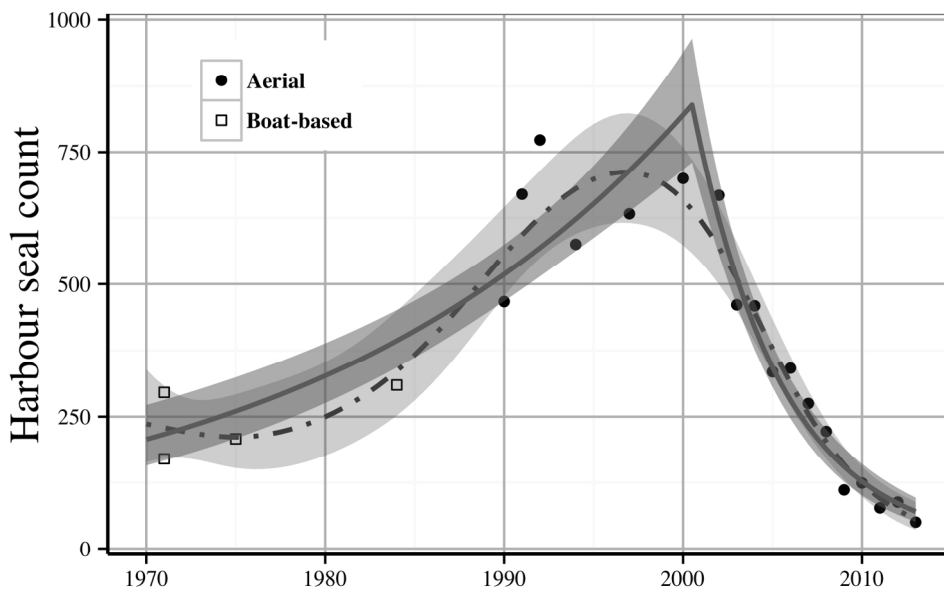
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4 761 **Figure 5:** Simulated trajectories for the decline of the Firth of Tay and Eden estuary  
5 harbour seal population. Each line shows the numbers of females aged at least 1.  
6 762  
7 763 Populations that appear to recover from zero abundance are those that were reduced to  
8 contain only juveniles. By neglecting the possibility of extinction through total loss of  
9 764 males, this model is likely to overstate the length of time this population will survive.  
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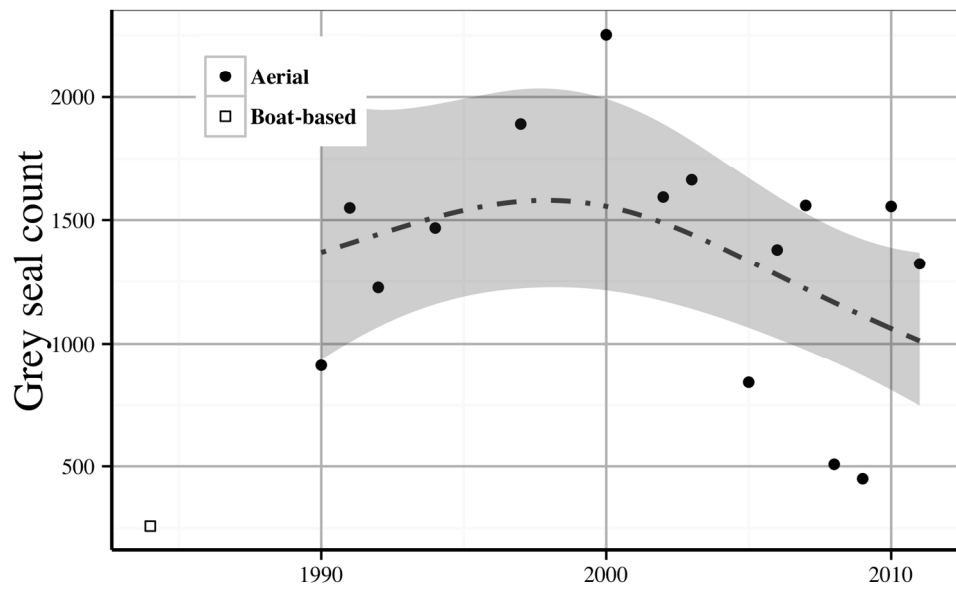
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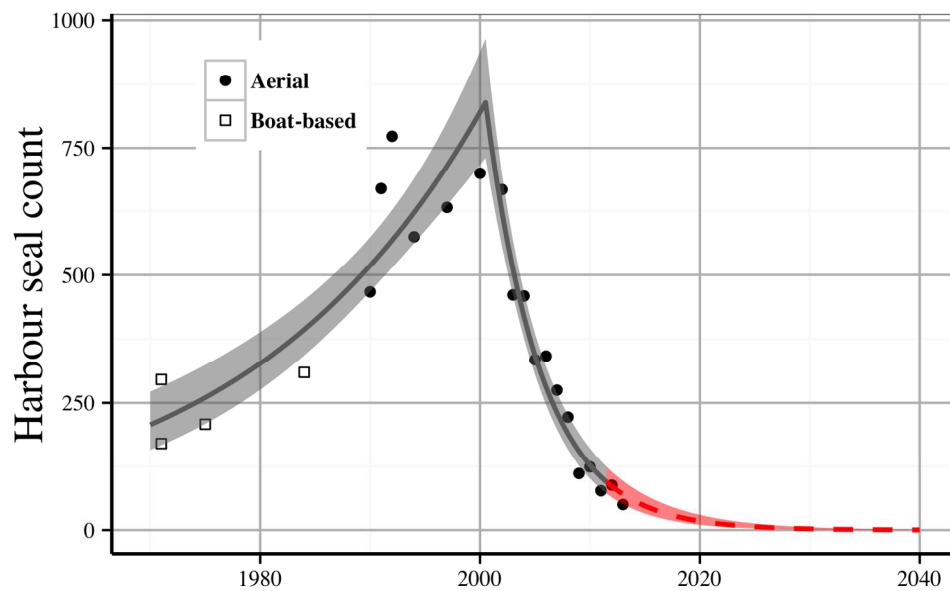
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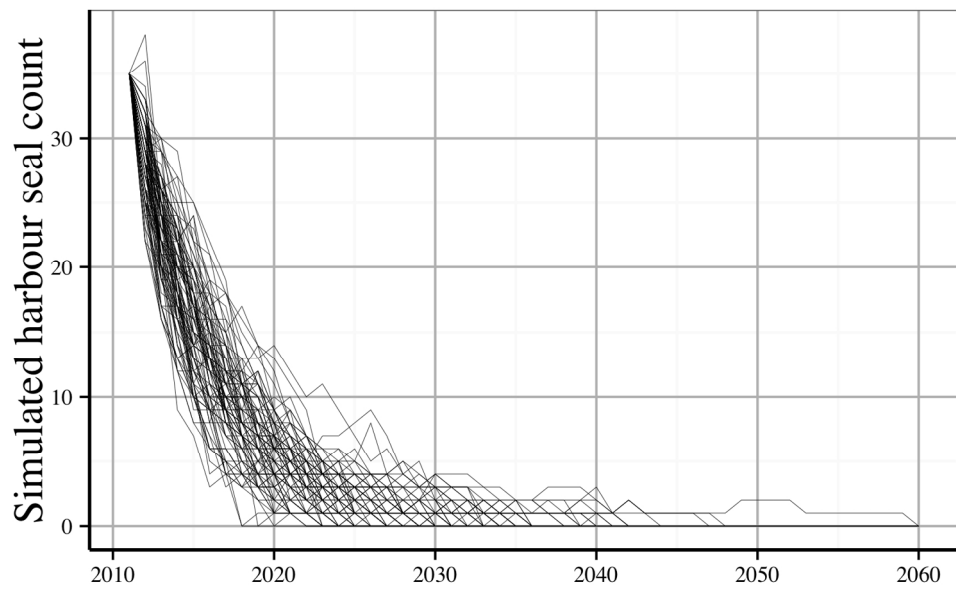
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