



**The diet of harbour and grey seals around Britain:
examining the role of prey as a potential cause of harbour
seal declines**

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3 1 **The diet of harbour and grey seals around Britain: examining the role of prey as a**
4 2 **potential cause of harbour seal declines**
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14
15 7 **Abstract**
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17 8 1. Harbour seal populations have declined over the last 20 years in some regions around
18 9 Britain. Causes are unknown but could include a reduction in prey availability which may
19 10 potentially be influenced by competition with grey seals. The diets of these two marine
20 11 predators overlap considerably, indicating that there could potentially be competition for
21 12 prey.
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25 13 2. In this study, the diets of harbour and grey seals in 2010/12 are compared regionally and
26 14 seasonally in relation to (a) regional variation in population trends around Britain; (b)
27 15 previous information on diet and (c) changes in the stock size of key prey to investigate
28 16 whether or not patterns could be consistent with reduction in prey availability or
29 17 competition.
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33 18 3. Diet was estimated from comprehensive sampling of scats around Scotland and eastern
34 19 England. In total, 65,534 otoliths and beaks were recovered from 1,976 harbour seal scats
35 20 and 68,465 otoliths and beaks were recovered from 2,205 grey seal scats collected in
36 21 2010/12. Results showed considerable seasonal and regional variability; overall sandeel and
37 22 large gadids were the two main prey types.
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41 23 4. Patterns in diet and trends in seal population size and prey stock size indicate that
42 24 harbour seals have declined in regions where they appear to be reliant on sandeel and
43 25 where sandeel stocks have declined, but not in regions where sandeel have never been an
44 26 important component of the diet. A possible contributing reason for the harbour seal
45 27 declines may therefore be a reduction in the availability of sandeel in these regions.
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49 28 5. Sandeel continue to be an important (although reduced) prey in the diet of grey seals in
50 29 regions where harbour seals have declined. If sandeel are a limiting resource, it is possible,
51 30 therefore, that grey seals may reduce prey availability to harbour seals and contribute to
52 31 their decline through competition.
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57 33 **Key words**
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59 34 coastal, ocean, sea loch, feeding, behaviour, predation, mammals
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36 1. Introduction

37 Grey seals (*Halichoerus grypus*) are sympatric with harbour seals (*Phoca vitulina*) over much
38 of their North Atlantic range but these species show some spatial partitioning in their
39 distribution on land and at sea (e.g. Jones, McConnell, Sparling, & Matthiopoulos, 2013).
40 Differences in the timing of annual breeding and moulting result in grey seals spending more
41 time on land and harbour seals spending more time at sea during autumn and winter
42 throughout their range (Boyd & Croxall, 1996; Lowry, Frost, Hoep, & Delong, 2001; Reder,
43 Lydersen, Arnold, & Kovacs, 2003; Simpkins, Withrow, Cesarone, & Boveng, 2003;
44 Thompson, Mackay, Tollit, Enderby, & Hammond, 1998). The reverse is true in spring and
45 summer when harbour seals spend more time on land (Thompson et al., 1998; Thompson,
46 Miller, Cooper, & Hammond, 1994) and grey seals more time at sea (Russell et al., 2015).
47 These differences in phenology may be one way in which these sympatric high level
48 predators partition their niches on an annual basis.

49 The abundance of grey seals around Britain has been increasing since the 1960s and the
50 total population was estimated at 141,000 (95% CI 117,500 - 168,500) in 2016 (SCOS, 2017).
51 Regionally, numbers have been more or less stable west of Scotland since the 1990s and in
52 Orkney since the 2000s, albeit with some inter-annual variation; however, numbers
53 continue to increase in the North Sea (SCOS, 2017).

54 In contrast, harbour seals around Britain are less numerous (total estimate 43,500; approx.
55 95% CI 35,600 - 58,000 in 2016) and have declined in some regions (Shetland, Orkney and
56 eastern Scotland) since around 2000 whilst remaining stable or having increased (Scottish
57 west coast and Western Isles and eastern England) in others (Lonergan et al., 2007; SCOS,
58 2017). The causes of the declines are unknown (Sea Mammal Research Unit, 2012, 2014)
59 but one possible contributing reason is competition with grey seals.

60 Aggressive interactions between individual grey and harbour seals have been observed at
61 mixed species haul-out sites in some areas. These direct inter-specific interactions may be a
62 form of interference competition with space on haul-out sites as a limiting resource.
63 Aggressive intra-specific interactions have been shown to be related to pinniped density at
64 haul-out sites. For example, Fernández-Juricic and Cassini (2007) found an increase in the
65 rate of agonistic interactions with density in female South American sea lions, and Kriebler
66 and Barrette (1984) found a positive relationship between the proportion of aggressive
67 interactions leading to animals leaving a site and the density of seals at the site.

68 Grey seals have also been observed preying on harbour seals and injuries on harbour seal
69 carcasses consistent with grey seal predation are well-documented (Brownlow, Onoufriou,
70 Bishop, Davison, & Thompson, 2016; ICES, 2017; van Neer, Jensen, & Siebert, 2015).
71 However, it is not possible with current information to assess the extent of such predation
72 nor, therefore, the population consequences of this predator-prey interaction (ICES, 2017).

73 Harbour and grey seals may also compete for food. Diet studies around Britain show that
74 the ranges of prey species consumed by harbour and grey seals overlap considerably. In
75 particular, sandeel and large gadids have been important prey groups in the diet of grey
76 seals for the last three decades (Hammond & Wilson, 2016) and these prey also feature
77 strongly in the diet of harbour seals around Britain (e.g. Brown, Pierce, Hislop, & Santos,
78 2001; Hall, Watkins, & Hammond, 1998; Pierce & Santos, 2003; Sharples, Arrizabalaga, &
79 Hammond, 2009; Tollit & Thompson, 1996; Wilson & Hammond, 2016).

80 This overlap in diet could lead to exploitation competition if prey are a limiting resource,
81 through which one or both species may be impacted indirectly by prey depletion.
82 Comparison of harbour and grey seal diets can provide some information on the extent of
83 the potential for these species to compete for prey. However, diet is the result of
84 interactions among prey distribution, abundance and availability, and seal foraging
85 distribution and behaviour, so comparison of diets can only ever provide part of the picture.
86 In addition, even detailed observations of a system can only show the “ghost of competition
87 past” (Connell, 1980), if such competition exists, and cannot directly address whether or not
88 competition for prey is occurring. To demonstrate competition typically requires
89 manipulative experiments (Connell, 1961; Paine, 1984; Paine, Castillo, & Cancino, 1985) or a
90 major natural change such as an extreme El Niño event (e.g. Paine & Trimble, 2004).

91 Even in the absence of competition with grey seals for food, reduced prey availability could
92 be a contributory cause of the decline in harbour seals in some regions of Scotland,
93 especially if this had an impact at a critical life history stage. Fish assemblages have changed
94 markedly in the North Sea in recent decades because of over-exploitation of some fish
95 stocks and climate change (Christensen & Richardson, 2008; Heath, 2005; Perry, Low, Ellis, &
96 Reynolds, 2005). In south-east Scotland, Frederiksen, Wanless, Harris, Rothery, and Wilson
97 (2004) found temperature to influence plankton abundance and a positive correlation
98 between plankton and sandeel larval abundance resulting in reduced sandeel recruitment in
99 warm winters, suggesting that sandeel populations are driven by bottom-up effects. If such
100 changes have reduced the availability of key prey to harbour seals they could contribute to
101 the observed declines in Shetland, Orkney and south-east Scotland.

102 Interactions between sympatric marine predators and their prey are of interest in the
103 context of changes in the marine environment both cyclical (such as the North Atlantic
104 Oscillation) and unidirectional (ocean warming) but they are also of interest in a
105 conservation and management context. The harbour seal and the grey seal are both listed
106 under Annex II of the EU Habitats Directive requiring Member States to propose Special
107 Areas of Conservation (SACs) under Natura 2000 and to act if human activities are
108 threatening favourable conservation status (EEC, 1992). It is thus important to investigate
109 whether harbour seals are declining for natural reasons, such as reduced prey availability
110 driven by changes in hydrography or competition with grey seals for food, or directly as a
111 result of manageable human activities.

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3 112 In this paper, regional variation in population trends in harbour and grey seals around
4 113 Britain was used as a kind of natural experiment, within which patterns in the diet of these
5 114 two species were compared that they might provide indications of whether or not
6 115 competition for food may be occurring.

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9 116 The focus is on new information on the diet of harbour seals and grey seals from
10 117 comprehensive sampling throughout Scotland and eastern England in 2010/12 (Hammond &
11 118 Wilson, 2016; Wilson & Hammond, 2016). Equivalent results are available for grey seals
12 119 from 1985 and 2002 (Hammond & Grellier, 2006; Hammond, Hall, & Prime, 1994a, 1994b;
13 120 Hammond & Wilson, 2016; Harris, 2007). Earlier information on harbour seal diet is
14 121 available from previous studies that were more restricted in time and space and, in most
15 122 cases, analytical treatment (Brown et al., 2001; Hall et al., 1998; Pierce & Santos, 2003;
16 123 Sharples et al., 2009; Tollit & Thompson, 1996), which makes comparison with diet in
17 124 2010/12 more challenging.

18 125 These results on diet are considered in the context of information on changes over time in
19 126 the abundance of the main prey species, which have generally declined in the last few
20 127 decades (ICES, 2018a; 2018b; 2018c; 2018d; 2018e). This approach was used to evaluate
21 128 the indirect evidence for impacts of declines in prey availability and consider whether
22 129 competition for food between harbour and grey seals might play a role. It is important to
23 130 stress that this evaluation can only provide circumstantial evidence supporting only weak
24 131 inferences and that any conclusions, therefore, remain largely speculative. In particular, it is
25 132 not known whether one or more prey species act as a limiting resource, a necessary
26 133 requirement for competition. It is therefore not possible to define which patterns would or
27 134 would not be expected if competition were or were not occurring because of lack of key
28 135 information. Nevertheless, the aim is that by an examination of the various sources of
29 136 information some insight can be gained into the role that predation and competition may
30 137 play in the decline of harbour seals in some regions around Britain.

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42 43 139 **2. Methods**

44 45 140 2.1 Sample collection

46 141 Scats were collected in 2010/2012 within two hours of low water. All scats were placed into
47 142 separate plastic bags and stored at -20°C and were expected to be no more than two weeks
48 143 old (since the previous spring tide). Supplementary Material Figure 1 shows locations where
49 144 harbour and grey seal scats were collected.

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53 145 Seasonal stratification of sample collection and diet analysis was different between species
54 146 because of differences in the life cycles of the two species and to facilitate comparison of
55 147 grey seal results with earlier studies. For harbour seals, winter, spring, summer, and autumn
56 148 were defined as December-February, March-May, June-August, and September-November,
57 149 after Sharples et al. (2009). For grey seals these seasons were calendar quarters: January-
58 150 March, etc., to facilitate comparison with fisheries data, after Hammond and Grellier (2006).

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3 151 For this comparison of diets, data from the studies of Hammond and Wilson (2016) and
4 152 Wilson and Hammond (2016) were grouped for analysis into two seasons: spring/summer
5 153 (harbour seals: March-August; grey seals: April-September) and autumn/winter (harbour
6 154 seals: September-February; grey seals: October-March).

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9 155 There were also differences in regional stratification between the studies of harbour and
10 156 grey seal diet. For harbour seals, regions matched the Scottish Government designated Seal
11 157 Management Regions (Baxter et al., 2011) and also included The Wash in south-east
12 158 England. For grey seals, the regions were broader: Inner Hebrides, Outer Hebrides,
13 159 Shetland, Orkney and the northern North Sea, central North Sea and southern North Sea,
14 160 allowing direct comparison with results from previous studies in 1985 and 2002 (Hammond
15 161 & Grellier, 2006; Harris, 2007)

16 162 For regional comparison of diets, the data from Hammond and Wilson (2016) and Wilson
17 163 and Hammond (2016) were grouped into the following regions: southern North Sea, south
18 164 east Scotland (Firth of Forth, Isle of May, Rivers Tay, Eden and Ythan), Moray Firth, Orkney,
19 165 Shetland, Inner Hebrides and Outer Hebrides.

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27 166 Before approaching a haul-out site, the number of harbour seals was counted and any grey
28 167 seals were identified and counted. Haul-out sites were designated as a single species site if
29 168 the area contained $\geq 80\%$ of one species (based on a low misclassification rate of 3% in
30 169 molecular analyses to identify the species, Matejusová et al., 2013; Wilson, 2014) or if the
31 170 seals were spatially segregated at the haul-out site.

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35 172 2.2 Sample processing

36 173 Approximately 33 individual scats were defrosted, placed in nested mesh bags (inner 350
37 174 μm , outer 240 μm) and soaked in 40L warm water with 25 g Dreft detergent (P&G, UK) for
38 175 2-24 h. Scats were subsequently machine washed (Orr et al., 2004), in a 73 L capacity
39 176 machine following the protocol developed by S. Brasseur (pers. comm.); a 2 h 40°C pre-wash
40 177 with 50 g detergent and 0.5 h wool wash at 40°C with 50 g detergent, the spin cycle was
41 178 deactivated for all wash cycles. If pebbles had been picked up as part of an individual scat,
42 179 otoliths and beaks were extracted using running water through a nest of sieves (mesh sizes
43 180 1 mm, 600 μm , 335 μm and 250 μm) to avoid damage to prey hard remains. The presence of
44 181 other possible prey remains (e.g. feathers and crustacean carapaces) was noted.

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50 183 Sagittal otoliths were stored dry and identified to the lowest possible taxonomic group
51 184 based on morphological criteria using a reference collection and identification guides
52 185 (Härkönen, 1986; Leopold, van Damme, Philipart, & Winter, 2001). Beaks were stored in
53 186 70% IMS and identified to species using a reference collection and identification guide
54 187 (Clarke, 1986). Where prey remains could not be identified to species, they were recorded
55 188 at a higher level (e.g. sandeel, unidentified gadid).

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Otolith lengths and widths were measured for all fish species where possible and cephalopod lower rostral (squid species) or lower hood lengths (octopus species) were measured, all to the nearest 0.01 mm, using digital callipers (Mitutoyo) under binocular microscopes. Broken otoliths and beaks were counted and measured only if the widest/longest part of the otolith, or the lower beak, was unbroken. Fragments of otoliths or beaks which were not large enough to be measured were not counted or measured to avoid misidentification of species and double counting.

All counted otoliths and beaks were measured except where a large number of otoliths of a prey species were recovered from a scat. In such cases, 30 otoliths were randomly chosen with respect to size and measured if there were 30-120 otoliths of the same species in a scat, and 25% were randomly chosen and measured if there were greater than 120 otoliths of the same species.

The degree by which each measured otolith was digested was recorded after examination of individual morphological features (Leopold et al., 2001; Tollit et al., 1997). Three grades of digestion were allocated for grey seals following Leopold et al. (2001). Because of the high number of grade 3 otoliths recovered, and the high levels of digestion observed in this and other studies (Tollit et al., 1997) four grades of digestion were allocated for harbour seals ; grade 1 - pristine, grade 2 - moderately digested, grade 3 - considerably digested, and grade 4 - severely digested. The amount by which cephalopod beaks had been digested was not classified (Tollit et al., 1997).

2.3 Estimation of diet composition

All data processing and analysis was conducted using a suite of analysis programs written in software R (R Core Team, 2013).

Estimation of seal diet composition generally followed the methods used in previous assessments of seal diet by the Sea Mammal Research Unit. Measurements of the size of otoliths (corrected for partial digestion) and beaks recovered from scats were used to estimate the weight of prey ingested. These values were summed across all scats in the region for each species, corrected for complete digestion, and expressed as percentages of the diet by weight (Hall et al., 1998; Hammond & Grellier, 2006; Hammond et al., 1994a, 1994b; Hammond & Rothery, 1996; Harris, 2007; Prime & Hammond, 1990; Prime & Hammond, 1987; Sharples et al., 2009).

Measurements of partially digested otolith/beak size were converted to estimates of undigested otolith/beak size using experimentally derived grade-specific digestion coefficients estimated separately for each seal species (Grellier & Hammond, 2006; Tollit et al., 1997; Wilson et al., 2017). For each prey species (or higher taxon) the preferred measurement (otolith length or width, or lower rostral or lower hood length) was

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3 231 determined based on the availability of experimental data, the precision of the estimated
4 232 digestion coefficients (Grellier & Hammond, 2006; Tollit et al., 1997; Wilson et al., 2017), the
5 233 measurement available from recovered hard parts and the availability of regression
6 234 equations to estimate prey size. Where species-specific correction factors were not
7 235 available, group-specific values were used (e.g. gadids, flatfish) or values from prey species
8 236 with otoliths of similar size and robustness (Härkönen, 1986) were applied.
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13 238 For dragonet (*Callionymus lyra*) and Cottidae species, digestion coefficients were only
14 239 available for grey seals (Grellier & Hammond, 2006). Species-on-species comparison showed
15 240 that harbour seal digestion coefficients were generally smaller than grey seal digestion
16 241 coefficients (by 8.3%, on average). Grey seal digestion coefficients for dragonet and short-
17 242 spined sea scorpion (bullrout) were, therefore, multiplied by 0.917 to use for harbour seals.
18 243 For herring, estimated fish size was sensitive to the choice of DC for both harbour and grey
19 244 seals. Based on a comparison of available DCs for harbour seals, the species-specific DC
20 245 generated by Tollit et al. (1997) provided the most realistic estimates of fish size and was,
21 246 therefore, used in the analyses.
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27 248 For some prey species there was no suitable substitution and general “round fish” digestion
28 249 coefficients were used. The use of values from other species or the general “round fish”
29 250 value only occurred for prey species that were minor components of the diet.
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33 252 Estimates of fish/cephalopod weight were derived from the estimates of undigested
34 253 otolith/beak size using allometric equations (Clarke, 1986, GJ Pierce and MB Santos pers.
35 254 comm.; Härkönen, 1986; Leopold et al., 2001; Santos, Clarke, & Pierce, 2001). Where no
36 255 equations were available for prey species, equations for the closest matching species were
37 256 used; these species were all minor prey. For grey seals, grade-specific digestion coefficients
38 257 for herring led to an unacceptable proportion of estimated sizes (weights and lengths) that
39 258 were larger than the known size range of the species. There was no obvious explanation for
40 259 this anomaly. As an *ad hoc* solution to rectify this problem, the grade 1 digestion coefficient
41 260 was applied to all otolith measurements regardless of their assigned grade; this generated
42 261 sizes that were mostly within the known size range. This anomaly is discussed further in
43 262 Hammond and Wilson (2016).
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49 264 For scats in which a sub-sample of the otoliths identified for a species had been measured,
50 265 the fish weight represented by each unmeasured otolith was assumed equal to the mean
51 266 weight of all measured otoliths of that species in that scat. This was also assumed for
52 267 broken otoliths without an appropriate measurement. If there were no measured otoliths of
53 268 that species in that scat, the mean weight of that species over all scats was used.
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58 270 For each region/season, the estimated weights of prey represented by all fish otoliths and
59 271 cephalopod beaks were summed across all scats within species. To account for species-

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3 272 specific differences in complete digestion, the weight estimated for each prey species was
4 273 adjusted using experimentally derived recovery rates, derived as a proportion of
5 274 otoliths/beaks fed that were recovered. (Grellier & Hammond, 2006; Wilson et al., 2017).
6 275 Where no experimental data were available, group-specific values (e.g. gadids, flatfish) or
7 276 values for the closest matching species were used. Diet composition was estimated as the
8 277 percentage that each species contributed to the total estimated weight consumed.
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10 279 Prey species were assigned to prey groups to facilitate general comparisons (see
11 280 Supplementary Material Table 1). Large gadids mainly included cod, haddock, ling, rockling,
12 281 saithe and whiting. Flatfish mainly included dab, Dover sole, flounder, lemon sole, plaice and
13 282 witch. Sandy benthic mainly included dragonet and goby. Scorpion fish mainly included
14 283 bullrout and sea scorpion. Pelagic mainly included herring, mackerel and sprat.
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16 285 95% confidence limits around estimates of diet composition were obtained using the
17 286 method described by Hammond and Rothery (1996) as described and presented in
18 287 Hammond and Wilson (2016) and Wilson and Hammond (2016). Non-parametric bootstrap
19 288 resampling was used to estimate sampling error, with scat as the sampling unit. Each data
20 289 set was resampled 1,000 times. Measurement error was estimated using parametric
21 290 resampling of the coefficients describing the relationships used to obtain estimates of diet
22 291 composition from otolith/beak measurements. All coefficients were resampled at each
23 292 bootstrap replicate. Variability in measurement error was associated with (i) estimating
24 293 undigested otolith/beak size from partially digested measurements via species- or grade-
25 294 specific digestion coefficients; (ii) estimating fish/cephalopod weight from estimated
26 295 undigested otolith/beak size via species-specific allometric relationships and (iii) accounting
27 296 for complete digestion of otoliths/beaks using estimated recovery rates. 95% confidence
28 297 limits were estimated as the 2.5%-ile and 97.5%-ile of the bootstrapped distributions.
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30 299 2.4 Diet Diversity

31 300 Diet diversity was estimated for each region within a season using estimates of prey species
32 301 richness and the relative abundance of prey species (species evenness). Species Richness (S)
33 302 was calculated as the total number of species identified in the sample and evenness was
34 303 measured using Pielou's evenness index (PEI). PEI provides a measure of how different the
35 304 abundances of the species in a community are from each other (Smith & Wilson, 1996).
36 305

37 306 Rarefaction analysis was used to standardize for sampling effort (number of scats collected)
38 307 and to adjust for differences in sampling intensity, allowing meaningful comparison of
39 308 datasets (Gotelli & Colwell, 2001; Gotelli & Colwell, 2011; Simberloff, 1978). This incurs loss
40 309 of information but this is necessary to allow valid comparison.
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42 311 To generate species richness, the rarefied (reduced) number of scats was randomly re-
43 312 sampled multiple times from the total number of scats and the number of species

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3 313 determined. The data were rarefied to the minimum number of scats across regions within a
4 314 season. Note that this means that species richness can only be compared across regions
5 315 within seasons not across seasons.
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9 317 PIE was calculated as $J = \frac{H'}{\log(S)}$ where H' is the Shannon-Weiner diversity index and S is the
10 318 rarefied total number of species in a sample. The value of J ranges from 0 to 1, with larger
11 319 values representing more even distributions in abundance among species.
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15 321 **3. Results**

16 322 In total, 65,534 otoliths and beaks were recovered from 1,976 harbour seal scats and 68,465
17 323 otoliths and beaks were recovered from 2,205 grey seal scats collected in 2010/12. Table 1
18 324 shows the breakdown of the number of scats collected in each region/season.
19 325 Supplementary Material Table 1 shows the number of otoliths/beaks of each prey species
20 326 recovered from scats, by region. Estimates of the percentage of the diet for each seal
21 327 species, by season, in each prey group and in each of the main prey species are given in
22 328 Table 2 and Supplementary Material Table 2, respectively.
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27 329 Estimated 95% confidence intervals are given in Supplementary Material Tables 3 and 4. The
28 330 intervals are wide for most prey species in most seasons and regions. Precision is greater for
29 331 prey groups than for prey species, and for major components of the diet, especially sandeel.
30 332 Because precision is generally poor, caution should be exercised when drawing quantitative
31 333 inferences about differences in the diet. In this comparison of diet, therefore differences are
32 334 primarily described qualitatively.
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36 335 3.1 Dietary comparison east of Britain / North Sea

37 336 Grey seal diet was dominated by sandeel in all regions of the North Sea (southern North
38 337 Sea, south-east Scotland and the Moray Firth). Although sandeel were also dominant in the
39 338 diet of harbour seals in the Moray Firth (>75% in both seasons), in the southerly regions
40 339 their diet was more varied in composition and included sandeel, flatfish, sandy benthic and
41 340 large gadid prey.
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45 341 In the southern North Sea, harbour seals ate mostly sandy benthic prey, flatfish and sandeel
46 342 in spring/summer (SS) and flatfish, large gadids and sandy benthic prey in autumn/winter
47 343 (AW) (Table 2 and Supplementary Material Table 2 for the main prey species). Grey seal
48 344 diet was dominated in both seasons by sandeel but also included large gadids and flatfish in
49 345 SS, with a change to scorpion fish, sandy benthic, large gadid and flatfish prey in AW (Table
50 346 2 and Supplementary Material Table 2). The number of prey species consumed by both
51 347 species was similar in the region; however, harbour seal diet was spread much more evenly
52 348 across the prey species (Table 3).
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57 349 In south-east Scotland, the diet of harbour seals was dominated by sandeel and flatfish in SS
58 350 with lesser contributions of large gadids. In AW, flatfish dominated with large gadids,
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3 351 pelagic and cephalopod prey making up the remainder of the diet (Table 2 and
4 352 Supplementary Material Table 2). Grey seal diet was dominated by sandeel in SS and to a
5 353 lesser extent in AW; other important prey in AW included large gadids and flatfish (Table 2
6 354 and Supplementary Material Table 2). Species richness in the diet was similar for both seal
7 355 species in SS but grey seals consumed fewer prey species in AW and grey seal diet was more
8 356 uneven in both seasons than harbour seal diet (Table 3).
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13 358 In the Moray Firth, the diet of both species was dominated by sandeel throughout the year
14 359 (minimum contribution 67% harbour seals in SS, Table 2 and Supplementary Material Table
15 360 2). Flatfish were also important in the diet of harbour seals in SS (Table 2 and
16 361 Supplementary Material Table 2). The dominance of sandeel in the diet is reflected in the
17 362 very low species diversity in the diet for both species (Table 3).
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21 363 3.2 Dietary comparison in the Northern Isles

22 364 The diet of harbour and grey seals in Orkney and Shetland comprised mostly sandeel, large
23 365 gadids and pelagic prey across both seasons and, for grey seals, scorpion fish in Shetland in
24 366 SS. The largest difference in the diet of the two species was in Orkney AW and all year in
25 367 Shetland, where harbour seals ate a higher estimated percentage of pelagic fish than grey
26 368 seals. In Orkney in SS, harbour seals also ate a higher estimated percentage of sandeel than
27 369 grey seals.
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31 370 In Orkney in SS, sandeel and pelagic prey dominated harbour seal diet while grey seal diet
32 371 comprised large gadids, sandeel and pelagic prey (Table 2 and Supplementary Material
33 372 Table 2). In AW, harbour seal diet was dominated by pelagic and large gadid prey, although
34 373 sandeel were also important, and grey seal diet comprised mostly large gadids, sandeel and
35 374 pelagic fish (Table 2 and Supplementary Material Table 2). Grey seal diet composition was
36 375 much more evenly spread across prey species with no contributions to the diet greater than
37 376 20% in SS or 30% in AW. Overall grey seal diet was more diverse, as reflected in the greater
38 377 species richness and evenness, than harbour seal diet (Table 3).
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43 378 The diet of harbour seals in Shetland in SS and AW was dominated by pelagic fish, sandeel
44 379 and large gadids (Table 2 and Supplementary Material Table 2). Grey seal diet was
45 380 dominated by large gadids and scorpion fish in SS and large gadids and sandeel in AW (Table
46 381 2 and Supplementary Material Table 2). Species richness was similar for harbour and grey
47 382 seals in SS, but much greater for grey seals in AW (Table 3); grey seal diet was more even
48 383 than harbour seal diet in both seasons (Table 3).
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53 384 3.3 Dietary comparison west of Scotland

54 385 Large gadid prey were important in the diet of both harbour and grey seals west of Scotland.
55 386 Pelagic fish were also important in harbour seal diet, and sandeel and sandy benthic prey in
56 387 grey seal diet (Table 2 and Supplementary Material Table 2).
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388 In the Outer Hebrides, diet could only be estimated in SS for harbour seals and AW for grey
389 seals, so no comparison within seasons is possible. Harbour seal diet in SS was split across
390 five main prey groups; *Trisopterus* species, pelagic fish, large gadids, scorpion fish and
391 sandeel. Grey seal diet in AW was dominated by sandeel and large gadids with the
392 remaining prey groups individually contributing less than 10% to the diet.

393 In SS in the Inner Hebrides, harbour seal diet mostly comprised large gadids, and some
394 pelagic fish and *Trisopterus* species. Grey seal diet was dominated by large gadids and
395 sandy benthic prey with additional contributions from *Trisopterus* species. In AW, the diet
396 of harbour seals was predominantly large gadids and pelagic fish while the diet of grey seals
397 was mostly large gadids and sandeel. Dietary species richness was greater for harbour seals
398 than grey seals in SS but similar between species in AW. The diet of both species was
399 diverse (high evenness), reflected in the diet composition estimates in which no one prey
400 species dominated the diet in either seal species or season (Table 3).

401 3.4 Overall comparison of harbour and grey seal diets

402 A summary comparison of the diet of harbour and grey seals in 2010/12 in relation to
403 regional population trends is given in Table 4. In terms of diet composition, in the southern
404 North Sea, sandeel strongly dominates grey seal diet but flatfish, gadid and sandy benthic
405 prey are much more important for harbour seals. In south-east Scotland, grey seal diet is
406 also dominated by sandeel, which is also an important prey for harbour seals together with
407 flatfish and gadids. In the Moray Firth, the diet of both species is strongly dominated by
408 sandeel. In Orkney and Shetland, sandeel and gadids are the mainstay of harbour and grey
409 seal diets, with pelagic prey also important for harbour seals. Gadids are the main prey of
410 both seal species in the Inner Hebrides.

411 Prey evenness, a measure of how diverse the diet is and how evenly it is spread among
412 multiple prey species, for harbour seals is greater than or equal to that of grey seals in all
413 regions and seasons except in spring/summer in Orkney and Shetland, where harbour seals
414 have declined. However, in south-east Scotland, where harbour seals have also declined, the
415 evenness of harbour seal diet is greater than that of grey seals.

416 Overall, the qualitative seasonal comparison summarized in Table 4, supported by the
417 detailed results given in Wilson and Hammond (2016) and Hammond and Wilson (2016),
418 shows that differences in diet between harbour and grey seals did not vary greatly between
419 Spring/Summer and Autumn/Winter. There is thus no evidence that diet differences are
420 related to seasonal differences in the life cycles of the two species.

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422 **4. Discussion**

423 This study compared new and previous information on harbour and grey seal diets in the
424 context of regional variation in recent trends in population size with the primary aim of

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3 425 investigating whether or not any patterns that emerged could be consistent with reduction
4 426 in prey availability or competition for prey. Table 4 summarizes a comparison of current
5 427 (2010/12) diet composition and evenness together with an indication of regional population
6 428 trends.

9 429 Overall, the 2010/12 results confirm the regional and seasonal variation in diet observed in
10 430 previous studies and that some prey types are more important in the diet than others.
11 431 Sandeel and large gadids have consistently been the most important prey groups in the diet
12 432 of grey seals for the last three decades (Hammond & Grellier, 2006; Hammond et al., 1994a,
13 433 1994b; Hammond & Wilson, 2016; Prime & Hammond, 1990) and are also important in the
14 434 diet of harbour seals both currently (Wilson & Hammond, 2016) and previously (Brown et
15 435 al., 2001; Hall et al., 1998; Pierce & Santos, 2003; Sharples et al., 2009; Tollit & Thompson,
16 436 1996). Below, regional, seasonal and temporal variation in the contribution of these two
17 437 prey types to the diets of harbour and grey seals are considered in the context of available
18 438 information on fish stock sizes.

23 439 4.1 Importance of sandeel in the diet of harbour and grey seals

24 440 Sandeel is an important prey of many marine predators including large gadids, seabirds and
25 441 mammals (Harwood & Croxall, 1988). Estimated sandeel stock biomass in the North Sea
26 442 declined from the 1980s in the southern/central North Sea and from the 1990s in the
27 443 central/northern North Sea through the 2000s, but has been higher, although highly
28 444 variable since 2010 (ICES, 2018a; 2018b). Seabird breeding failure in the north-west North
29 445 Sea has been linked to a reduction in the availability of sandeel (Wanless, Harris, Redman, &
30 446 Speakman, 2005) and to reduced sandeel recruitment in warm winters (Frederiksen et al.,
31 447 2004). There are no sandeel stock assessments west or north of Scotland but catches in the
32 448 Orkney/Shetland area declined steeply in the 1980s and have been zero since the early
33 449 2000s (ICES 2018c).

34 450 Overall, the results for 2010/12 show that sandeel remains a very important prey for
35 451 harbour and grey seals (Table 4). There is considerable variability in the results but there is a
36 452 tendency for sandeel to be more dominant in the diet of both species in the North Sea and
37 453 Northern Isles than west of Scotland. Sandeels tend to be more important in the diet of grey
38 454 seals in autumn/winter in the Northern and Western Isles, but in spring/summer in the
39 455 southern/central North Sea. In some regions there is a weak tendency for sandeel to be
40 456 more dominant in the diet of harbour seals in spring/summer than in autumn/winter.
41 457 Overall, however, there is no strong evidence for a consistent seasonal difference in the
42 458 importance of sandeel in the diet of either seal species.

43 459 Comparing the 2010/12 results with those from previous studies, estimates of the
44 460 proportion of sandeel in the diet have increased for both harbour and grey seals in the
45 461 southern North Sea, where both seal species are increasing, and they have also increased
46 462 for grey seals in the central North Sea, where they are increasing (Hall et al., 1998;
47 463 Hammond & Grellier, 2006; Hammond & Wilson, 2016; Wilson & Hammond, 2016). Sandeel
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3 464 has consistently remained the dominant prey in the diet of harbour seals in the Moray Firth
4 465 (Pierce, Miller, Thompson, & Hislop, 1991; Wilson & Hammond, 2016), where seal numbers
5 466 have been variable. In south-east Scotland, where harbour seals numbers have declined
6 467 sharply, the importance of sandeel in their diet remains high but appears to have decreased,
7 468 while that of flatfish has increased (Sharples et al., 2009; Wilson & Hammond, 2016).

10 469 In Orkney and Shetland, where grey seal populations are stable, the proportion of sandeel in
11 470 their diet has declined (Hammond & Grellier, 2006; Hammond & Wilson, 2016; Harris,
12 471 2007). Inferring changes in the importance of sandeel in the diet of harbour seals, which
13 472 have declined in these regions, requires accounting for the fact that these studies did not
14 473 incorporate correction for complete digestion of otoliths (Brown & Pierce, 1998; Brown et
15 474 al., 2001; Pierce, Boyle, & Thompson, 1990). It is straightforward to calculate how the
16 475 percentage of sandeel in the diet changes when complete digestion is taken into account,
17 476 depending on the overall species composition in the diet. For diets covering the range of
18 477 species composition observed in these earlier studies, the percentage of sandeel in the diet
19 478 increases by a few percent when it is already high to by around 50% when the diet is
20 479 dominated by gadids. From these approximate corrections it is clear that estimates of the
21 480 amount of sandeel in harbour seal diet in Orkney and Shetland were higher in earlier years
22 481 (late 1980s to late 1990s) than in 2010/12. The conclusion can therefore be drawn that
23 482 while sandeel remain an important prey for harbour seals in these areas, their contribution
24 483 has declined.

32 484 Although there are gaps in the available information, a general pattern emerges from these
33 485 results. In regions where harbour seals have declined (northern and eastern Scotland)
34 486 sandeel stocks have also declined and, although estimates of their contribution to the diet
35 487 have declined, they remain an important prey. In contrast, in regions where harbour seals
36 488 have not declined (west coast of Scotland, southern North Sea), sandeel remain relatively
37 489 unimportant in the diet, which is more diverse (higher evenness) than in regions where they
38 490 have declined. For grey seals, the dominance of sandeel in the diet has been maintained
39 491 year-round in the southern/central North Sea, where populations are still increasing. In
40 492 other regions, where populations are stable, estimates of the importance of sandeel have
41 493 declined (Northern Isles) or remained low (West of Scotland).

46 494 Harbour seals have thus declined in regions where they appear to be reliant on sandeel and
47 495 where sandeel stocks have declined, but not in regions where sandeel have never been an
48 496 important component of the diet. A possible contributing reason for the declines may
49 497 therefore be because of a reduction in the availability of sandeel in these regions. Sandeel
50 498 continue to be an important (although reduced) prey in the diet of grey seals in regions
51 499 where harbour seals have declined. If sandeel are a limiting resource, it is possible,
52 500 therefore, that grey seals may reduce prey availability to harbour seals, and contribute to
53 501 their decline through competition.

58 502 4.2 Importance of large gadids in the diet of harbour and grey seals

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3 503 Large gadid fish have been heavily exploited for human consumption world-wide and the
4 504 seas around Britain are no exception. The main demersal fisheries around Scotland are for
5 505 cod, haddock and whiting. In 2002, the west of Scotland cod and whiting stocks were
6 506 considered to be outside safe biological limits, as was the haddock stock to the west and
7 507 north of Scotland (Gordon, Magill, Sayer, & Barrington, 2002). In the same year, these
8 508 species were shown to be major components of grey seal diet west of Scotland, with the
9 509 likelihood that grey seals may be inflicting significant predation mortality on cod stocks
10 510 (Hammond & Wilson, 2016; Harris, 2007).

11 511 Current ICES stock assessments show that over the period for which there is seal diet
12 512 information (1985-2010/12), the estimated size of the haddock stock in the North Sea and
13 513 west of Scotland fluctuated considerably with generally lower stock sizes in the 1990s than
14 514 in the 1980s and 2000s (ICES, 2018d). In contrast, cod declined steadily in the greater North
15 515 Sea until 2005, since when it has recovered somewhat (ICES, 2018e), and also declined
16 516 sharply west of Scotland with no sign of recovery (ICES, 2018f) – but see below. Whiting has
17 517 remained more or less stable in the North Sea (ICES, 2018e) but declined sharply between
18 518 1996 and 2006 west of Scotland with only recent signs of recovery (ICES, 2018h).

19 519 Cook and Trijoulet (2016) and Trijoulet, Holmes, and Cook (2017) incorporated grey seal
20 520 predation in fish stock assessment models of west of Scotland cod, which indicate that the
21 521 stock is not as depleted as shown in ICES assessments (e.g. ICES, 2018f). A revised
22 522 assessment has found similar results generated by alternative assumptions about fish
23 523 selectivity without incorporating seal predation (Cook, in press). A multispecies assessment
24 524 model including grey seals, cod, haddock and whiting west of Scotland found little evidence
25 525 that seal predation mortality affected fish stock dynamics (Fallon et al., In prep).

26 526 Results for 2010/12 show that these species of large gadid fish are important prey for both
27 527 grey and harbour seals in the Northern Isles and west of Scotland. In these regions, large
28 528 gadids comprise around one-third of the diet overall; this proportion is remarkably
29 529 consistent considering the inherent variability in the estimates. There is no indication of any
30 530 seasonal variation in the contribution of large gadids to the diet of either harbour or grey
31 531 seals. In the central and southern North Sea, large gadids are more minor components of
32 532 both harbour and grey seal diet, but are more important in autumn/winter than in
33 533 spring/summer (Table 4).

34 534 Comparing the 2010/12 results with those from previous studies, since 1985 the estimated
35 535 contribution of large gadids to the diet of grey seals has increased in the Northern Isles,
36 536 where harbour seals are declining, but stayed approximately the same in the southern
37 537 North Sea and west of Scotland, where harbour seals are not declining (Hammond &
38 538 Grellier, 2006; Hammond et al., 1994a, 1994b; Hammond & Wilson, 2016; Harris, 2007). For
39 539 harbour seals, the available information from the temporally, spatially, and in most cases,
40 540 analytically restricted limited previous studies shows no evidence that the importance of
41 541 large gadids in the diet has changed west of Scotland since 1993-94, in the Moray Firth since
42 542 1988-92, in Shetland since 1994-96, in the southern North Sea since 1990-92 and in south-

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3 543 east Scotland since 1998-2002 (Brown & Pierce, 1998; Hall et al., 1998; Pierce & Santos,
4 544 2003; Sharples et al., 2009; Tollit & Thompson, 1996).

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6 545 In summary, there is a negative correlation between the change in contribution of large
7 546 gadids to the diet of grey seals and the population trend in harbour seals, but otherwise no
8 547 signal emerges from the spatio-temporal patterns in the available information. Considering
9 548 the changes in stock size of the main species of large gadids together with the patterns in
10 549 the importance of these species in the diet of harbour and grey seals regionally and over
11 550 time, there is no evidence that harbour seal declines in some regions may be caused by
12 551 reduced large gadid prey availability or possible competition for prey with grey seals.

13 552 4.3 Dietary and prey comparison in a wider context

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15 553 Generally speaking, the overall increase in the numbers of seals in British waters (SCOS,
16 554 2017) and the historically low stock levels of some of their main prey species (ICES, 2018d,
17 555 2018e, 2018f, 2018g, 2018h) provide potential for intra-specific and inter-specific
18 556 competition between harbour and grey seals for food.

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20 557 There has been a general increase in non-commercial prey species in the diet of grey seals
21 558 over the last 30 years (Hammond & Grellier, 2006; Hammond et al., 1994a, 1994b;
22 559 Hammond & Wilson, 2016; Harris, 2007) and these prey, including sandy benthic species,
23 560 primarily dragonet, and scorpion fish, are also a major part of current harbour seal diet in
24 561 some regions (Wilson & Hammond, 2016). Thus, both grey and harbour seals may have
25 562 responded to the changing fish assemblage around Britain by consuming more of those
26 563 species that may have become more available relative to other species that have declined.

27
28 564 Measures of diet provide information on the types and relative amounts of prey consumed
29 565 but provide no information on the costs of acquiring that prey. Information on diet alone is
30 566 insufficient to determine whether changes in the relative abundance and availability of prey
31 567 may have led to changes in the ability of seals to meet their nutritional requirements,
32 568 including any influence of competition. Sharples, Moss, Patterson, and Hammond (2012)
33 569 found no evidence for a relationship between harbour seal regional population trend and
34 570 foraging trip duration or distance. Similarly, Russell et al. (2015) found that the relationship
35 571 between time spent resting (at sea and on land) and population trend was the opposite of
36 572 that expected if harbour seals were spending more time at sea foraging in areas where
37 573 populations were declining.

38
39 574 These studies focused on seal foraging and haul-out behaviour. Smout, Rindorf, Hammond,
40 575 Harwood, and Matthiopoulos (2014) fitted multispecies functional response models to data
41 576 on the diet of grey seals and prey availability based on measures of the overlap between the
42 577 distribution of foraging seals and their prey. Applying such modelling approaches to harbour
43 578 seals around Britain, at appropriate spatial and temporal scales, could provide an important
44 579 additional dimension to investigation of whether reduction in prey availability could be a
45 580 contributing cause of declines in harbour seals in some regions. Assessing whether grey
46 581 seals may influence the relationship between harbour seals and their prey will require

582 extension of this model framework to include other predators, such as harbour porpoise, as
 583 well as multiple prey.

584

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790 **viii. Tables**

791 Table 1: Number of harbour and grey seal scat samples containing hard prey remains (fish
 792 otoliths and cephalopod beaks), the total number of hard prey remains recovered and the
 793 number of otoliths/beaks measured for each region and season (SS = spring/summer; AW =
 794 autumn/winter).

Region	Season	Scats containing otoliths/beaks		Otoliths/ beaks recovered		Otoliths / beaks measured	
		Harbour	Grey	Harbour	Grey	Harbour	Grey
Southern	SS	145	86	4,148	4,401	2,790	1,899
North Sea	AW	143	75	2,790	3,277	1,919	1,548
SE Scotland	SS	22	107	2,018	4,667	716	1,998
	AW	17	162	4,208	5,105	1,419	2,516
Moray Firth	SS	192	29	17,037	2,740	6,452	865
	AW	73	90	3,484	7,991	1,506	2,905
Orkney	SS	140	57	4,932	1,332	2,813	767
	AW	117	563	1,529	12,292	986	7,872
Shetland	SS	75	45	2,145	492	1,233	465
	AW	111	206	2,622	3,647	1,642	2,472
Outer Hebrides	SS	99		1,584		1,180	
	AW	13	274	799	5,300	385	3,419
Inner Hebrides	SS	438	18	10,627	104	8,804	103
	AW	391	314	7,611	4,904	5,384	4,056

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797 Table 2: Seasonal variation in the diet of harbour and grey seals, expressed as the
798 percentage of each prey group in the diet by weight.

A) Southern North Sea

Prey type	Spring / Summer		Autumn / Winter	
	harbour	grey	harbour	grey
Gadid	3.8	11.5	29.6	11.0
<i>Trisopterus</i>	1.1	0.9	0.5	0.2
Sandeel	20.8	70.6	6.5	47.0
Flatfish	29.0	10.7	31.3	10.0
Sandy benthic	43.5	4.4	18.7	11.2
Scorpion fish	1.0	1.5	6.9	19.6
Pelagic	0.3	0.0	3.5	1.0
Salmonid	0.0	0.0	0.0	0.0
Cephalopod	0.0	0.5	2.9	0.0
Other	0.4	0.1	0.2	0.0

B) Southeast Scotland

Prey type	Spring / Summer		Autumn / Winter	
	harbour	grey	harbour	grey
Gadid	10.3	1.7	16.9	13.7
<i>Trisopterus</i>	0.0	0.1	0.0	0.4
Sandeel	44.5	89.1	0.0	60.7
Flatfish	38.7	6.3	49.7	12.5
Sandy benthic	0.0	1.0	5.9	1.1
Scorpion fish	0.0	0.6	1.3	8.3
Pelagic	1.0	1.0	13.4	2.1
Salmonid	1.4	0.0	0.2	0.0
Cephalopod	4.2	0.2	11.4	0.5
Other	0.0	0.0	1.3	0.7

C) Moray Firth

Prey type	Spring / Summer		Autumn / Winter	
	harbour	grey	harbour	grey
Gadid	2.2	0.2	5.9	11.6
<i>Trisopterus</i>	0.0	0.0	0.2	0.5
Sandeel	67.1	97.6	72.7	75.6
Flatfish	24.5	1.1	7.6	4.1
Sandy benthic	0.1	0.1	1.0	1.8

Scorpion fish	2.3	0.0	3.4	6.0
Pelagic	1.6	0.7	5.1	0.1
Salmonid	0.5	0.0	3.0	0.0
Cephalopod	1.7	0.0	0.5	0.1
Other	0.1	0.2	0.5	0.1

D) Orkney

Prey type	Spring / Summer		Autumn / Winter	
	harbour	grey	harbour	grey
Gadid	30.8	42.3	39.2	34.0
<i>Trisopterus</i>	1.1	11.4	0.2	3.6
Sandeel	53.2	21.9	17.6	34.3
Flatfish	6.0	3.6	6.1	8.3
Sandy benthic	1.1	2.5	3.4	2.0
Scorpion fish	2.8	8.8	0.2	10.1
Pelagic	4.4	5.3	30.9	4.1
Salmonid	0.0	0.0	0.0	0.0
Cephalopod	0.4	2.3	1.8	3.4
Other	0.3	1.9	0.6	0.3

E) Shetland

Prey type	Spring / Summer		Autumn / Winter	
	harbour	grey	harbour	grey
Gadid	23.9	35.3	27.6	31.9
<i>Trisopterus</i>	8.6	4.5	5.9	3.0
Sandeel	23.7	18.8	31.5	33.3
Flatfish	1.3	6.5	3.9	5.4
Sandy benthic	10.1	0.3	0.9	11.5
Scorpion fish	0.0	33.6	0.0	6.0
Pelagic	31.4	0.0	20.0	1.9
Salmonid	0.0	0.0	0.0	1.4
Cephalopod	0.9	0.9	0.2	1.9
Other	0.0	0.0	10.0	3.6

F) Outer Hebrides

Prey type	Spring / Summer		Autumn / Winter	
	harbour	grey	harbour	grey
Gadid	17.2			32.4

<i>Trisopterus</i>	24.5		6.8
Sandeel	13.1		38.2
Flatfish	2.0		6.6
Sandy benthic	2.8		3.5
Scorpion fish	16.2		0.5
Pelagic	20.3		3.9
Salmonid	0.0		0.0
Cephalopod	3.8		3.3
Other	0.3		4.8

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G) Inner Hebrides

Prey type	Spring / Summer		Autumn / Winter	
	harbour	grey	harbour	grey
Gadid	54.5	38.2	35.0	32.4
<i>Trisopterus</i>	14.0	14.6	8.2	7.6
Sandeel	3.2	8.0	4.2	22.2
Flatfish	2.7	3.1	5.0	8.3
Sandy benthic	3.8	32.0	15.7	11.2
Scorpion fish	3.0	0.0	1.6	4.9
Pelagic	16.5	2.8	28.8	1.0
Salmonid	0.1	0.0	0.0	0.0
Cephalopod	2.2	1.2	1.0	4.0
Other	0.1	0.0	0.4	8.3

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802 Table 3: Number of scats containing hard prey remains, observed and rarefied species
 803 richness, and species evenness. Data were rarefied within region/season combinations, so
 804 comparisons of species richness or evenness should only be made between seal species
 805 within seasons, not across regions, or across seasons within a region.

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A) Southern North Sea

	No. scats	Observed No. prey species	Species richness (S)	Species Evenness (PIE)
Spring/Summer				
Harbour seal	145	26	21	0.77
Grey seal	86	28	24	0.14
Autumn/Winter				
Harbour seal	143	29	23	0.81
Grey seal	75	24	22	0.3

B) South east Scotland

	No. scats	Observed No. prey species	Species richness (S)	Species Evenness (PIE)
Spring/Summer				
Harbour seal	22	12	10	0.38
Grey seal	107	18	8	0.04
Autumn/Winter				
Harbour seal	17	22	19	0.51
Grey seal	162	31	14	0.24

C) Moray Firth

	No. scats	Observed No. prey species	Species richness (S)	Species Evenness (PIE)
Spring/Summer				
Harbour seal	192	28	14	0.1
Grey seal	29	10	9	0.01
Autumn/Winter				
Harbour seal	73	21	18	0.12
Grey seal	90	32	27	0.07

D) Orkney

	No. scats	Observed No. prey species	Species richness (S)	Species Evenness (PIE)
Spring/Summer				

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Harbour seal	140	34	24	0.3
Grey seal	57	35	31	0.71
Autumn/Winter				
Harbour seal	117	25	23	0.41
Grey seal	563	61	42	0.57

E) Shetland

	No. scats	Observed No. prey species	Species richness (S)	Species Evenness (PIE)
Spring/Summer				
Harbour seal	75	25	17	0.54
Grey seal	45	24	20	0.77
Autumn/Winter				
Harbour seal	111	24	21	0.45
Grey seal	206	47	40	0.56

F) Outer Hebrides

	No. scats	Observed No. prey species	Species richness (S)	Species Evenness (PIE)
Spring/Summer				
Harbour seal	99	22	20	0.73
Autumn/Winter				
Grey seal	274	46	41	0.46

G) Inner Hebrides

	No. scats	Observed No. prey species	Species richness (S)	Species Evenness (PIE)
Spring/Summer				
Harbour seal	438	49	19	0.82
Grey seal	18	13	11	0.82
Autumn/Winter				
Harbour seal	391	52	46	0.87
Grey seal	314	53	49	0.77

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808 Table 4: Summary comparison table of harbour seal (Pv) and grey seal (Hg) diets. Trend is the population trajectory of seals in each region since 2000 (SCOS,
 809 2013): ↗ = population increasing, -- = population stable and ↘ = population declining. SS = spring/summer; AW = autumn/winter. Species evenness: H =
 810 high (PIE > 0.75), M = moderate (PIE = 0.3-0.75) and L = low (PIE < 0.3). Diet composition: prey groups are listed in order of dominance and include those
 811 that together comprise at least two-thirds of the diet, by weight. Strongly dominant prey groups (in **bold**) are defined as top ranked prey groups
 812 contributing > 45% to the diet and a greater % than the sum of prey groups ranked 2, 3 and 4.
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Region	Trend		Species evenness				Diet composition			
	Pv	Hg	SS		AW		SS		AW	
			Pv	Hg	Pv	Hg	Pv	Hg	Pv	Hg
Southern North Sea	↗	↗	H > L	H > L	sandy benthic flatfish	sandeel	flatfish gadid sandy benthic	sandeel scorpion fish		
SE Scotland	↘	↗	M > L	M > L	sandeel flatfish	sandeel	flatfish gadid	sandeel gadid		
Moray Firth	--	↗	L = L	L = L	sandeel	sandeel	sandeel	sandeel		
Orkney	↘	--	L < M	M = M	sandeel gadid	gadid sandeel <i>Trisopterus</i>	gadid pelagic	sandeel gadid		
Shetland	↘	--	M < H	M = M	pelagic gadid sandeel	gadid scorpion fish	sandeel gadid pelagic	sandeel gadid sandy benthic		
Outer Hebrides	↗	--	M	M	<i>Trisopterus</i> pelagic gadid scorpion fish			sandeel gadid		
Inner Hebrides	--	--	H = H	H = H	gadid pelagic	gadid sandy benthic	gadid pelagic sandy benthic	gadid sandeel sandy benthic		

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