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Comparing the Diet of Harbour and Grey Seals in Scotland and Eastern England

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Comparing the diet of harbour and grey seals in Scotland and eastern England

Lindsay Wilson and Philip Hammond

Sea Mammal Research Unit
Scottish Oceans Institute,
University of St Andrews, St Andrews, Fife, KY16 8LB, UK

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1 Executive Summary

Harbour seal populations in some areas around Scotland have declined since around 2000 but the cause(s) of these declines are unknown. Reduced availability of prey is one potential contributory cause, including the possibility of competition between grey seals and harbour seals. To contribute new information regarding this question, regional and seasonal similarities and differences in the diet of harbour and grey seals in relation to regional differences in population trajectories of harbour seals, were examined.

Grey seal diet was dominated by sandeel in all regions of the North Sea. Sandeel were also dominant in the diet of harbour seals in the Moray Firth but, to the south, their diet was more varied and also included flatfish, sandy benthic and large gadid prey. In Orkney and Shetland, harbour and grey seal diet comprised mostly sandeel, large gadids and pelagic prey. The largest differences were in Orkney in spring/summer, where harbour seals ate more sandeel, and in Orkney in autumn/winter and all year in Shetland where harbour seals ate more pelagic fish. West of Scotland, large gadids were the main prey in the diet of both harbour and grey seals. Pelagic fish were also important in harbour seal diet and sandeel and sandy benthic prey in grey seal diet. Despite some differences in diet between grey and harbour seals, there was no clear evidence of seasonal variation in these differences that may be related to the different life cycles of these two species.

Although there was considerable seasonal and regional variation in the diet of both harbour and grey seals, there was no unequivocal pattern to explain differences in diet between species in regions where harbour seals have and have not declined.

However, there was some evidence that sandeel may play an important role in the diet of harbour seal populations in the North Sea and Northern Isles. In regions where harbour seals have declined (northern and eastern Scotland) sandeel stocks have also declined and, although their contribution to the diet has declined, they remain an important component. In regions where harbour seals have not declined (west coast of Scotland and southern North Sea), sandeel were and remain unimportant in the diet. Grey seal populations are stable or increasing, regardless of the importance of sandeel in the diet.

Overall, the diet of harbour seals was less diverse and at least partially reliant on declining sandeel stocks in regions where population declines have been observed, and was more diverse and not reliant on sandeels in regions where population declines have not been observed. A tentative conclusion is that declines in harbour seal abundance in northern regions may be linked to a decline in the abundance of sandeels.

More information is needed to improve the understanding of whether or not changes in prey availability, including any influence of competition between harbour and grey seals, may have led to changes in the ability of harbour seals to meet their nutritional requirements and, hence, ultimately to population declines. This information includes, at appropriate temporal

and spatial resolutions, prey distribution and abundance, the availability of that prey to seals, and the foraging behaviour of seals in relation to their life history.

2 Introduction

Grey (*Halichoerus grypus*) and harbour seals (*Phoca vitulina*) around Britain are sympatric along much of the coastline. These species differ in body size and annual life cycle (Bonner, 1972), and show some spatial partitioning in their distribution at sea (Jones *et al*., 2015). There is also a large difference in population abundance around Britain as a whole. Estimated total population sizes around Britain in 2012 were 112,300 (95% CI 90,600-142,900) grey seals and 37,300 (approximate 95% CI 30,500-49,700) harbour seals (SCOS, 2013).

Differences in annual cycles mean that during autumn and winter, grey seals spend more time on land and harbour seals spend more time away from haul-out sites, a pattern that is apparent throughout their range (Thompson *et al.* 1989, Boyd and Croxall 1996; Lowry *et al.* 2001, Reder *et al.* 2003, Simpkins *et al.* 2003). The reverse is true in spring and summer when harbour seals spend more time on land (e.g. Thompson *et al.* 1994, 1998) and grey seals more time at-sea (Russell *et al.* 2015). This difference in breeding and foraging chronology may partially reflect how these sympatric high level predators partition their niches on an annual basis.

Harbour seal populations in some areas around Scotland (Shetland, Orkney and eastern Scotland) have declined since around 2000 (Lonergan *et al.*, 2007; SCOS, 2013; 2015) but the cause(s) of these declines are unknown (Sea Mammal Research Unit 2012, 2014). Reduced availability of prey is one potential contributory cause, especially if this had an impact at a critical life history stage. One possible contributing reason for a reduction in the availability of prey to harbour seals is competition with grey seals. To contribute new information to help address this question, the similarities and differences in the diet of harbour and grey seals were examined, as described in detail by Hammond and Wilson (2016) and Wilson and Hammond (2016), with the aim of searching for any patterns in relation to regions where harbour seals are and are not declining.

Diet is the result of a combination of factors, including prey distribution, abundance and availability, and seal foraging distribution and behaviour. As such, a comparison of harbour and grey seal diet cannot directly answer the question of whether competition for prey may or may not be occurring. However, it might provide an indication. For example, if it were apparent that harbour seals consumed poorer diets than grey seals in areas where harbour seals have declined, but this was not the case in areas where no decline has been observed, this might be indicative of competition for prey.

In this report the work to address the following objectives is described:

- To compare harbour and grey seal diet composition, regionally and seasonally;
- To compare harbour and grey seal diet diversity;

with the aim:

- To investigate patterns of similarity or difference in harbour and grey seal diet in relation to regional differences in population trajectories of harbour seals around Scotland.

3 Methods

Methods of data collection, processing and analysis to estimate harbour and grey seal diet are described in Wilson and Hammond (2016) and Hammond and Wilson (2016), respectively.

In those studies, the seasonal stratification of data collection and analysis used was different between species because of differences in the life cycles. For harbour seals, winter, spring, summer, and autumn were defined as December-February, March-May, June-August, and September-November, after Sharples *et al.* (2009). For grey seals, these seasons were calendar quarters: January-March, etc., to facilitate comparison with fisheries data, after Hammond and Grellier (2006) and Hammond and Harris (2006).

For comparison of diets, the data were grouped into two seasons: spring/summer (harbour seals: March-August; grey seals: April-September) and autumn/winter (harbour seals: September-February; grey seals: October-March).

There were also differences in regional stratification between the studies of harbour and grey seal diet. For harbour seals, regions matched the Scottish Government designated Seal Management Regions (Baxter *et al.* 2011) and also included The Wash in southeast England. For grey seals, the regions were broader: Inner Hebrides, Outer Hebrides, Shetland, Orkney and the northern North Sea, central North Sea and Southern North Sea, allowing direct comparison with results from previous studies in 1985 and 2002 (Hammond and Grellier 2006; Hammond and Harris 2006).

For comparison of diets, the data were grouped into the following regions: southern North Sea, south east Scotland (Firth of Forth, Isle of May, Rivers Tay, Eden and Ythan), Moray Firth, Orkney, Shetland, Inner Hebrides and Outer Hebrides.

Table 1 shows the numbers of scats containing otoliths and or beaks collected in each region/season. Table 2 shows the number of otoliths/beaks of each prey species recovered by region.

Table 1

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

Region	Season	Scats containing otoliths / beaks		Otoliths / beaks recovered		Otoliths / beaks measured	
		Harbour	Grey	Harbour	Grey	Harbour	Grey
Southern North Sea	SS	145	86	4,148	4,401	2,790	1,899
	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

Table 2: Number of fish otoliths and cephalopod beaks recovered from (A) harbour seal scats in 2010/12 and (B) grey seal scats in 2010/11.

A) Harbour seal

Prey group	Prey species	Southern North Sea	SE Scotland	Moray Firth	Orkney	Shetland	Outer Hebrides	Inner Hebrides	TOTAL
	3-bearded rockling	0	0	0	0	1	0	12	13
	4-bearded rockling	0	0	0	1	0	0	3	4
	5-bearded rockling	1	0	0	0	0	0	0	1
	Blue whiting	0	0	0	1	0	0	1,219	1,220
	Cod	21	27	82	672	22	33	261	1,118
	Forkbeard	0	0	0	0	2	0	1	3
	Haddock	0	11	18	50	2	14	867	962
	Hake	0	0	1	0	1	0	15	17
	Ling	0	0	0	16	15	2	47	80
	Pollock	0	0	0	0	0	0	2	2
	Rockling	0	0	2	21	3	2	62	90
	Saithe	0	6	51	169	692	3	146	1,067
	Saithe or Pollock	0	0	0	0	0	0	9	9
	Seasnail	0	0	0	0	0	1	0	1
	Silvery pout	0	0	0	0	0	0	123	123
	Tadpole fish	0	0	0	0	2	0	0	2
	Unid. gadid	3	8	37	289	138	45	984	1,504
	Whiting	637	641	55	13	8	34	3,029	4,417
Gadid	**TOTAL**	**662**	**693**	**246**	**1,232**	**886**	**134**	**6,780**	**10,633**
	Norway pout	0	0	1	3	569	798	3,290	4,661
	Norway pout or Poor cod	0	0	0	0	0	19	612	631
	Poor cod	2	0	13	128	300	201	3,720	4,364
	Pout whiting	27	0	0	0	0	0	5	32
	Unid. *Trisopterus*	0	0	0	45	98	54	789	986
Trisopterus	**TOTAL**	**29**	**0**	**14**	**176**	**967**	**1,072**	**8,416**	**10,674**
Sandeel	**TOTAL Sandeel**	**829**	**1,261**	**18,311**	**4,506**	**2,507**	**250**	**924**	**28,588**

Prey group	Prey species	Southern North Sea	SE Scotland	Moray Firth	Orkney	Shetland	Outer Hebrides	Inner Hebrides	TOTAL
	Brill	10	0	1	0	0	0	0	11
	Dab	279	186	359	63	5	0	38	930
	Dover sole	122	0	0	0	0	0	3	125
	Flounder	41	23	67	12	0	0	0	143
	Flounder or Plaice	8	0	11	0	0	0	0	19
	Lemon sole	38	3	2	3	5	0	23	74
	Long rough dab	0	2	9	1	0	0	42	54
	Megrim	0	0	1	0	0	0	1	2
	Norwegian topknot	0	0	0	0	0	0	11	11
	Plaice	770	1,022	801	60	20	7	84	2,764
	Scaldfish	0	0	2	0	0	0	1	3
	Thickback sole	0	0	0	0	0	0	14	14
	Topknot	0	0	0	1	0	0	0	1
	Unid. flatfish	307	359	434	35	3	2	30	1,170
	Unid. sole	0	0	0	0	0	0	7	7
	Witch	0	0	0	0	0	0	74	74
Flatfish	**TOTAL**	**1,575**	**1,595**	**1,687**	**175**	**33**	**9**	**328**	**5,402**
	Butterfish	1	0	0	14	0	0	10	25
	Dragonet	684	10	4	51	131	28	683	1,591
	Goby	2,898	2,522	18	9	4	0	28	5,479
	Lesser weever	25	0	1	0	0	0	0	26
Sandy benthic	**TOTAL**	**3,608**	**2,532**	**23**	**74**	**135**	**28**	**721**	**7,121**
	Bullrout	0	1	25	6	0	0	6	38
	Grey gurnard	0	0	0	0	0	0	6	6
	Gurnard	0	0	0	0	0	0	7	7
	Hooknose	7	0	0	2	0	0	3	12
	Sea scorpion	20	0	0	41	0	0	2	63
	Unid. cottid	2	0	0	2	0	16	37	57
Scorpion fish	**TOTAL**	**29**	**1**	**25**	**51**	**0**	**16**	**61**	**183**

Prey group	Prey species	Southern North Sea	SE Scotland	Moray Firth	Orkney	Shetland	Outer Hebrides	Inner Hebrides	TOTAL
	Argentine	0	0	0	0	1	0	30	1
	Herring	18	1	6	189	160	17	492	391
	Horse mackerel	1	0	0	1	0	22	84	24
	Mackerel	0	3	2	34	28	20	279	87
	Smelt	13	0	0	0	0	0	0	13
	Sprat	106	96	168	0	1	0	1	371
Pelagic	**TOTAL**	**138**	**100**	**176**	**224**	**190**	**59**	**886**	**887**
	Sea trout	0	2	0	0	0	0	1	3
	Unid. salmonid	0	1	4	0	0	0	2	7
Salmonid	**TOTAL**	**0**	**3**	**4**	**0**	**0**	**0**	**3**	**10**
	Alloteuthis spp.	2	0	0	0	0	0	0	2
	Eledone	2	0	0	4	3	10	20	39
	Loligo	5	34	24	2	1	0	16	82
	Sepiolids	11	1	0	2	1	1	34	50
Cephalopod	**TOTAL**	**20**	**35**	**24**	**8**	**5**	**11**	**70**	**173**
	Ballan wrasse	0	0	0	3	0	0	4	7
	Bass	1	0	0	0	0	0	0	1
	Conger eel	0	0	0	0	0	0	1	1
	Cuckoo wrasse	0	0	0	2	0	0	5	7
	Eelpout	0	3	9	4	1	0	15	32
	Garfish	4	0	0	2	37	0	0	43
	Snake blenny	0	2	0	0	0	0	0	2
	Unid. roundfish	13	0	2	3	1	2	6	27
	Unknown fish species	8	1	0	0	4	0	0	13
	Wrasse	0	0	0	1	1	3	18	23
Other	**TOTAL**	**26**	**6**	**11**	**15**	**44**	**5**	**49**	**156**

B) Grey seal

Prey group	Prey species	Southern North Sea	SE Scotland	Moray Firth	Orkney	Shetland	Outer Hebrides	Inner Hebrides	TOTAL
	3-bearded rockling	0	0	0	0	0	0	1	1
	4-bearded rockling	1	0	0	1	1	0	9	12
	Blue whiting	0	0	0	0	0	5	152	157
	Cod	40	68	44	503	70	48	97	870
	Forkbeard	0	0	0	1	0	13	0	14
	Haddock	1	26	92	387	5	30	56	597
	Hake	0	0	0	1	8	14	5	28
	Ling	0	1	3	120	36	40	102	302
	Pollock	0	0	0	1	1	7	0	9
	Rockling	99	5	49	338	25	28	57	601
	Saithe	0	4	22	777	550	71	72	1,496
	Seasnail	2	0	0	1	0	0	0	3
	Silvery pout	0	0	0	1	2	5	2	10
	Tadpole fish	0	0	3	5	8	6	2	24
	Torsk	0	0	0	0	0	4	0	4
	Unid. gadid	16	101	16	236	89	91	192	741
	Whiting	370	408	16	106	13	52	85	1,050
Gadid	**TOTAL**	**529**	**613**	**245**	**2,478**	**808**	**414**	**832**	**5,919**
	Norway pout	0	13	1	1,354	234	787	1,074	3,463
	Poor cod	21	18	97	1,045	310	446	643	2,580
	Pout whiting	26	0	0	1	0	0	1	28
	Unid. *Trisopterus*	3	27	25	519	50	323	378	1,325
Trisopterus	**TOTAL**	**50**	**58**	**123**	**2,919**	**594**	**1,556**	**2,096**	**7,396**
Sandeel	**TOTAL Sandeel**	**6,189**	**8,440**	**10,119**	**6,238**	**1,939**	**2,904**	**1,288**	**37,117**

Prey group	Prey species	Southern North Sea	SE Scotland	Moray Firth	Orkney	Shetland	Outer Hebrides	Inner Hebrides	TOTAL
	Brill	1	0	0	0	0	0	0	1
	Dab	18	49	14	95	39	4	7	226
	Dover sole	215	0	1	1	0	0	1	218
	Flounder	1	2	26	2	0	0	0	31
	Lemon sole	23	27	3	86	24	30	36	229
	Long rough dab	0	13	1	7	2	0	7	30
	Megrim	0	0	0	10	9	45	3	67
	Norwegian topknot	0	2	1	11	7	4	6	31
	Plaice	76	207	52	329	21	14	29	728
	Scaldfish	0	0	0	0	0	0	3	3
	Solenette	11	0	0	2	0	1	0	14
	Thickback sole	0	0	0	26	8	1	39	74
	Topknot	0	0	0	9	0	1	30	40
	Unid. flatfish	72	125	59	173	18	46	88	581
	Unid. sole	1	1	0	8	5	1	30	46
	Witch	0	2	0	13	7	10	41	73
Flatfish	**TOTAL**	**418**	**428**	**157**	**772**	**140**	**157**	**320**	**2,392**
	Butterfish	21	3	1	18	0	0	0	43
	Dragonet	166	13	16	71	147	59	217	689
	Goby	29	12	5	96	260	0	2	404
	Lesser weever	4	0	4	0	0	0	0	8
Sandy benthic	**TOTAL**	**220**	**28**	**26**	**185**	**407**	**59**	**219**	**1,144**
	Bullrout	41	40	30	241	58	0	21	431
	Grey gurnard	0	0	1	6	0	1	2	10
	Gurnard	0	0	0	6	0	0	2	8
	Hooknose	26	44	4	27	4	0	4	109
	Lumpsucker	0	0	7	1	0	1	0	9
	Sea scorpion	134	2	0	144	19	3	32	334
	Unid. Cottid	15	4	0	1	0	0	0	20

Scorpion fish	**TOTAL**	**216**	**90**	**42**	**426**	**81**	**5**	**61**	**921**
Prey group	**Prey species**	**Southern North Sea**	**SE Scotland**	**Moray Firth**	**Orkney**	**Shetland**	**Outer Hebrides**	**Inner Hebrides**	**TOTAL**
	Argentine	0	0	0	30	6	0	4	40
	Herring	14	9	1	202	14	83	26	349
	Horse mackerel	0	0	0	11	4	2	1	18
	Mackerel	0	1	2	44	8	21	3	79
	Pilchard	0	0	0	1	0	0	0	1
	Sprat	9	86	9	2	0	0	1	107
Pelagic	**TOTAL**	**23**	**96**	**12**	**290**	**32**	**106**	**35**	**594**
Salmonid	**TOTAL Unid. Salmonid**	**0**	**0**	**0**	**0**	**5**	**0**	**0**	**5**
	Alloteuthis spp.	0	0	0	2	0	0	0	2
	Eledone	0	0	0	33	9	34	73	149
	Loligo	2	5	2	106	15	26	23	179
	Ommastrephidae	1	0	0	1	1	1	0	4
	Rossia	1	0	0	1	10	0	0	12
	Sepietta spp.	0	0	0	7	4	1	4	16
	Sepiola spp.	0	3	1	20	45	3	5	77
	Sepiolids	0	0	0	32	13	1	1	47
	Unid. squid	0	5	1	29	17	5	8	65

Cephalopod	**TOTAL**	**4**	**13**	**4**	**231**	**119**	**71**	**114**	**556**
	Atlantic catfish	0	0	0	0	9	0	0	9
	Ballan wrasse	0	0	1	11	7	6	14	39
	Conger eel	0	0	0	1	0	5	11	17
	Cuckoo wrasse	0	0	0	8	0	4	6	18
	Eel	0	1	0	0	0	0	0	1
	Eelpout	3	5	2	30	0	0	0	40
	Garfish	0	0	0	3	2	0	0	5
	Snake blenny	0	0	0	13	0	0	0	13
	Unid. roundfish	13	0	0	0	1	0	0	14
	Unknown fish species	13	0	0	0	0	1	9	23
	Wrasse	0	0	0	19	0	12	3	34
Other	**TOTAL**	**29**	**6**	**3**	**85**	**19**	**28**	**43**	**213**

4 Results

4.1 Dietary Comparison Eastern UK/North Sea

Grey seal diet was dominated by sandeel in all regions of the North Sea (southern North Sea, south east Scotland and the Moray Firth). Although sandeel were also dominant in the diet of harbour seals in the Moray Firth (>75% in both seasons), in the southerly regions their diet was more varied in composition and included sandeel, flatfish, sandy benthic and large gadid prey.

4.1.1 Southern North Sea

In the southern North Sea, harbour seals ate mostly sandy benthic prey, flatfish and sandeel in spring/summer (SS) and flatfish, large gadids and sandy benthic prey in autumn/winter (AW) (Tables 3 and 4). Grey seal diet was dominated in both seasons by sandeel but also included large gadids and flatfish in SS, with a change to scorpion fish, sandy benthic, large gadid and flatfish prey in AW (Tables 3 and 4). The number of prey species consumed by both species was similar in the region; however, harbour seal diet was spread much more evenly across the prey species (Table 5)

4.1.2 Southeast Scotland

In southeast Scotland, the diet of harbour seals was dominated by sandeel and flatfish in SS with lesser contributions of large gadids. In AW, flatfish dominated with large gadids, pelagic and cephalopod prey making up the remainder of the diet (Tables 3 and 4). Grey seal diet was dominated by sandeel in SS and to a lesser extent in AW; other important prey in AW included large gadids and flatfish (Tables 3 and 4). Species richness in the diet was similar for both seal species in SS but grey seals consumed fewer prey species in AW and grey seal diet was more varied in both seasons than harbour seal diet (Table 5).

4.1.3 Moray Firth

In the Moray Firth, the diet of both species was dominated by sandeel throughout the year (minimum contribution 67% harbour seals in SS, Tables 3 and 4). Flatfish were also important in the diet of harbour seals in SS (Tables 3 and 4). The dominance of sandeel in the diet is reflected in the very low species diversity in the diet for both species (Table 5).

4.2 Dietary Comparison in the Northern Isles

The diet of harbour and grey seals in Orkney and Shetland comprised mostly sandeel, large gadids and pelagic prey across both seasons and, for grey seals, scorpion fish in Shetland in SS. The largest differences in the diet of the two species were in Orkney in SS where

harbour seals ate more sandeel, and in Orkney AW and all year in Shetland where harbour seals ate more pelagic fish.

Orkney: In Orkney in SS, sandeel and pelagic prey dominated harbour seal diet while grey seal diet comprised large gadids, sandeel and pelagic prey (Tables 3 and 4). In AW, harbour seal diet was dominated by pelagic and large gadid prey, although sandeel were also important, and grey seals ate mostly large gadids, sandeel and pelagic fish (Tables 3 and 4). Grey seal diet composition was much more evenly spread across prey species with no contributions to the diet greater than 20% in SS or 30% in AW. Overall grey seal diet was more diverse than harbour seal diet in Orkney, as reflected in the greater species richness and a less varied diet in grey seals (Table 5).

Shetland: The diet of harbour seals in Shetland in SS and AW was dominated by pelagic fish, sandeel and large gadids (Tables 3 and 4). Grey seal diet was dominated by large gadids and scorpion fish in SS and large gadids and sandeel in AW (Tables 3 and 4). Species richness was similar for harbour and grey seals in SS, but much greater for grey seals in AW (Table 5), but grey seal diet was more even than harbour seal diet in both seasons (Table 5).

Table 3

Seasonal variation in the diet of harbour and grey seals, expressed as the percentage of each species in the diet by weight. Prey species listed are those contributing >5% in any season for either seal species.

A) Southern North Sea

	Spring/Summer		Autumn/Winter	
Species	**Harbour**	**Grey**	**Harbour**	**Grey**
Cod	2.3	5.3	1.2	2.4
Whiting	1.5	5.9	28.4	6.2
Sandeel	20.8	70.6	6.5	47.0
Plaice	8.3	4.1	8.2	1.3
Lemon sole	1.8	0.4	6.0	1.6
Dover sole	8.2	3.8	7.7	6.4
Dragonet	38.1	4.2	16.6	11.0
Goby	5.1	0.0	2.0	0.0
Bullrout	0.8	1.0	5.0	5.8
Sea scorpion	0.1	0.4	1.6	12.7

B) South east Scotland

	Spring/Summer		Autumn/Winter	
Species	**Harbour**	**Grey**	**Harbour**	**Grey**
Cod	2.4	0.5	4.8	5.7
Whiting	7.9	0.8	8.6	4.4
Sandeel	44.5	89.1	0.0	60.7
Plaice	18.4	2.0	34.9	6.1
Flounder	7.4	0.0	3.9	0.1
Dab	9.7	0.0	5.6	2.8
Bullrout	0.0	0.6	1.3	6.3
Mackerel	0.0	0.1	6.1	0.0
Sprat	0.8	0.0	7.3	2.1
Loligo	4.2	0.2	11.4	0.5

C) Moray Firth

	Spring/Summer		Autumn/Winter	
Species	**Harbour**	**Grey**	**Harbour**	**Grey**
Haddock	0.7	0.0	0.0	7.3
Sandeel	67.1	97.6	72.7	75.6
Plaice	7.6	0.6	1.4	0.9
Dab	10.5	0.3	2.0	0.6

D) Orkney

	Spring/Summer		Autumn/Winter	
Species	**Harbour**	**Grey**	**Harbour**	**Grey**
Cod	19.0	9.1	28.9	16.3
Haddock	0.6	5.6	3.7	5.7
Saithe	7.0	20.8	2.2	6.9
Norway pout	0.0	8.3	0.0	1.6

Sandeel	53.2	21.9	17.6	34.3
Bullrout	0.8	7.6	0.0	8.1
Mackerel	1.2	0.7	8.2	0.3
Herring	3.1	2.5	22.7	3.1

E) Shetland

	Spring/Summer		**Autumn/Winter**	
Species	**Harbour**	**Grey**	**Harbour**	**Grey**
Cod	0.1	8.5	1.7	8.5
Saithe	8.8	19.9	23.3	17.5
Ling	8.4	0.8	0.8	3.9
Poor cod	1.4	2.6	5.4	1.8
Norway pout	6.9	1.9	0.5	1.1
Sandeel	23.7	18.8	31.5	33.3
Dragonet	10.1	0.3	0.9	11.4
Bullrout	0.0	28.5	0.0	5.2
Sea scorpion	0.0	5.2	0.0	0.7
Mackerel	1.4	0.0	10.9	0.6
Herring	29.8	0.0	9.1	0.7
Garfish	0.0	0.0	9.9	0.1

F) Outer Hebrides

	Spring/Summer		**Autumn/Winter**	
Species	**Harbour**	**Grey**	**Harbour**	**Grey**
Cod	3.6			10.7
Ling	2.6			8.0
Norway pout	19.8			4.2
Sandeel	13.1			38.2
Unid. *Cottidae*	16.2			0.0
Mackerel	12.6			0.9
Eledone	3.8			1.2

G) Inner Hebrides

	Spring/Summer		**Autumn/Winter**	
Species	**Harbour**	**Grey**	**Harbour**	**Grey**
Cod	9.2	0.0	5.6	11.3
Whiting	12.3	5.0	5.8	1.3
Haddock	9.5	3.4	9.4	1.6
Ling	4.4	27.2	3.1	8.9
Blue whiting	9.1	0.0	3.7	1.5
Poor cod	6.0	3.7	5.8	2.4
Norway pout	7.1	10.7	1.8	4.9
Sandeel	3.2	8.0	4.2	22.2
Dragonet	3.7	32.0	15.7	11.2
Mackerel	10.6	2.8	15.4	0.0
Herring	4.9	0.0	10.6	0.8
Ballan wrasse	0.0	0.0	0.1	7.9

4.3 Dietary Comparison West of Scotland

Large gadid prey were important in the diet of both harbour and grey seals west of Scotland. Pelagic fish were also important in harbour seal diet and sandeel and sandy benthic prey in grey seal diet.

Outer Hebrides: In the Outer Hebrides, diet could only be estimated in SS for harbour seals and AW for grey seals, so no comparison within seasons is possible. Harbour seal diet in SS was split across five main prey groups; *Trisopterus* species, pelagic fish, large gadids, scorpion fish and sandeel. Grey seal diet in AW was dominated by sandeel and large gadids with the remaining prey groups individually contributing less than 10% to the diet.

Inner Hebrides: In SS in the Inner Hebrides, harbour seals ate mostly large gadids, and some pelagic fish and *Trisopterus* species. Grey seal diet was dominated by large gadids and sandy benthic prey with important contributions from *Trisopterus* species. In AW, harbour seals ate predominantly large gadids and pelagic fish while grey seals ate mostly large gadids and sandeel. Harbour seals had greater species richness in the diet in SS and dietary species richness was similar in both species in AW. The diet of both species was diverse (high evenness), reflected in the diet composition estimates in which no one prey species dominated the diet in either seal species or season.

4.4 Overall Comparison of Harbour and Grey Seal Diets

A summary comparison of the diet of harbour and grey seals in 2010/11 in relation to regional population trends is given in Table 6. In terms of diet composition, in the southern North Sea, sandeel strongly dominates grey seal diet but flatfish, gadid and sandy benthic prey are much more important for harbour seals. In southeast Scotland, grey seal diet is also dominated by sandeel, which is also an important prey for harbour seals together with flatfish and gadids. In the Moray Firth, the diet of both species is strongly dominated by sandeel. In Orkney and Shetland, sandeel and gadids are the mainstay of harbour and grey seal diets, with pelagic prey also important for harbour seals. Gadids are the main prey of both seal species in the Inner Hebrides.

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

Overall, the qualitative comparison summarised in Table 6, supported by the detailed results given in Wilson and Hammond (2016) and Hammond and Wilson (2016), shows that differences in diet between harbour and grey seals did not vary greatly between Spring/Summer and Autumn/Winter. There is thus no evidence that any such diet differences may be related to seasonal differences in the life cycles of the two species.

Table 4

Harbour and grey seal diet listed according to prey group for each region and season, expressed as the percentage of each prey group in the diet by weight.

A) Southern North Sea

	Spring / Summer		Autumn / Winter	
Prey type	**Harbour**	**Grey**	**Harbour**	**Grey**
Gadid	3.8	11.5	29.6	11.0
Trisopterus	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

	Spring / Summer		Autumn / Winter	
Prey type	**Harbour**	**Grey**	**Harbour**	**Grey**
Gadid	10.3	1.7	16.9	13.7
Trisopterus	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

	Spring / Summer		Autumn / Winter	
Prey type	**Harbour**	**Grey**	**Harbour**	**Grey**
Gadid	2.2	0.2	5.9	11.6
Trisopterus	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

	Spring / Summer		Autumn / Winter	
Prey type	**Harbour**	**Grey**	**Harbour**	**Grey**
Gadid	30.8	42.3	39.2	34.0
Trisopterus	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

	Spring / Summer		Autumn / Winter	
Prey type	**Harbour**	**Grey**	**Harbour**	**Grey**
Gadid	23.9	35.3	27.6	31.9
Trisopterus	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

	Spring / Summer		Autumn / Winter	
Prey type	**Harbour**	**Grey**	**Harbour**	**Grey**
Gadid	17.2			32.4
Trisopterus	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

G) Inner Hebrides

	Spring / Summer		Autumn / Winter	
Prey type	**Harbour**	**Grey**	**Harbour**	**Grey**
Gadid	54.5	38.2	35.0	32.4
Trisopterus	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

Table 5

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

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	0.30

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	0.10
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				
Harbour seal	140	34	24	0.30
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

Table 6: Summary comparison table of harbour and grey seal diets. Harbour seals are annotated as Pv and grey seals as Hg. Trend displays the population trajectory of seals in each region (SCOS, 2013): ↗ = population increasing, -- = population stable and ↘ = population declining. SS = spring/summer; AW = autumn/winter. For species evenness: H = high (PIE > 0.75), -- = intermediate (PIE = 0.3-0.75) and L = low (PIE < 0.3). Under Diet composition, prey groups are listed in order of dominance and include those that together comprise at least two-thirds of the diet, by weight. Strongly dominant prey are in bold.

	Trend		Evenness		Diet composition			
			SS	AW	SS		AW	
Region	**Pv**	**Hg**	**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	↘	↗	-- > L	-- > L	sandeel flatfish	**sandeel**	flatfish gadid	**sandeel** gadid
Moray Firth	↘	↗	L = L	L = L	**sandeel**	**sandeel**	**sandeel**	**sandeel**
Orkney	↘	--	L < --	-- = --	sandeel gadid	gadid sandeel *Trisopterus*	gadid pelagic	sandeel gadid
Shetland	↘	--	-- < H	-- = --	pelagic gadid sandeel	gadid scorpion fish	sandeel gadid pelagic	sandeel gadid sandy benthic
Outer Hebrides	↗	--	--	--	*Trisopterus* 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

5 Discussion

The overall aim of this study was to compare harbour and grey seal diets in the context of regional variation in recent trends in population size. The population of grey seals around Britain as a whole is three times greater than that of harbour seals (SCOS, 2013) but there is considerable regional variation in population size and trend. Grey seals are increasing in the North Sea but are stable elsewhere. Harbour seals are increasing in the southern North Sea, decreasing in southeast Scotland, Moray Firth, Orkney and Shetland, and approximately stable west of Scotland. Table 6 summarises these regional trends as context for comparing regional variation in diet composition and evenness.

Our results show clearly that some prey are, and in some cases remain, more important in the diet than others. Sandeel and large gadids have been important prey groups in the diet of grey seals for the last three decades (Hammond and Grellier 2006, Hammond and Harris 2006, Hammond and Wilson 2016). These prey are also important in the diet of harbour seals around Britain (Wilson and Hammond 2016) and were previously, as shown in earlier studies (Pierce *et al.* 1991, Thompson *et al.* 1996, Tollit and Thompson 1996, Tollit *et al.* 1997, Brown and Pierce 1997, 1998, Hall *et al.* 1998, Brown *et al.* 2001, Pierce and Santos 2003, Sharples *et al.* 2009). It is, therefore, relevant to consider these two prey groups in more detail in the context of how the diets of harbour and grey seals vary seasonally and over time.

5.1 Regional Variation in Major Prey in Harbour and Grey Seal Diet

5.1.1 Sandeel in the North Sea and Northern Isles

Sandeel is an important prey of many marine predators including large gadids, seabirds and mammals (Harwood and Croxall 1988). Around Britain, the majority of sandeel stock biomass is in the central and southern North Sea (ICES 2012); however, sandeel are also found in abundance around Orkney and Shetland, and in the north east and north west of the Outer Hebrides (SNH 2014). Fish assemblages in the North Sea have changed markedly in recent decades because of large scale fisheries removals and the influence of decadal scale oceanic changes (Heath 2005, Christensen and Richardson 2008). In particular, sandeel biomass in the northern and central North Sea has declined (ICES Advice 2015) and seabird breeding failure in the north west North Sea has been linked to a reduction in the availability of sandeel (Wanless *et al.* 2004) and to reduced sandeel recruitment in warm winters (Frederiksen *et al.* 2004). In contrast, sandeel biomass has increased in the southern North Sea since 2000 (ICES Advice 2015).

Overall, the results presented in Hammond and Wilson (2016) and Wilson and Hammond (2016) show that sandeel remains an important prey for both grey and harbour seals in the North Sea and Northern Isles but is much less important and one of several prey types contributing to varied diets west of Scotland.

Sandeel has increased in importance in the diet of both harbour and grey seals in the southern North Sea, where both seal species are increasing, and it has increased in the diet of grey seals in the central North Sea, where they are increasing (Hall *et al*. 1998; Hammond and Grellier 2006, Hammond and Wilson 2016, Wilson and Hammond 2016). Sandeel has remained consistently important in the diet of harbour seals in the Moray Firth (Pierce *et al.* 1991, Wilson and Hammond 2016), where numbers have declined. However, in southeast Scotland, where harbour seals numbers have declined sharply, the importance of sandeel in their diet has decreased, while that of flatfish has increased (Sharples *et al.* 2009, Wilson and Hammond 2016).

In Orkney and Shetland, where grey seal populations are stable, the proportion of sandeel in their diet has declined (Hammond and Grellier 2006, Hammond and Harris 2006, Hammond and Wilson 2016). It is difficult to infer changes in the importance of sandeel in the diet of harbour seals, which have declined in these regions, because previous studies either did not account for complete digestion of otoliths (Brown and Pierce 1997, 1998, Brown *et al.* 2001) or did not estimate percentage diet composition (Pierce *et al.* 1990). However, it is likely that the contribution of sandeel to the diet has declined in harbour seals in Shetland, particularly in spring and summer (Wilson and Hammond 2016).

Although there are gaps in the relevant information, a general pattern emerges from these results, as described in Wilson and Hammond 2016). In regions where harbour seals have declined (northern and eastern Scotland) sandeel stocks have also declined and, although their contribution to the diet has declined, they remain an important component. In regions where harbour seals have not declined (west coast of Scotland, southern North Sea), sandeel were and remain unimportant in the diet and, in the southern North Sea, sandeel stocks have increased. Grey seal populations are stable or increasing regardless of the importance of sandeel in the diet.

Overall, the diet of harbour seals is less diverse and at least partially reliant on declining sandeel stocks in regions where population declines have been observed, and is more diverse and not reliant on sandeels in regions where population declines have not been observed. A tentative conclusion is that declines in harbour seal abundance in northern regions may be linked to a decline in the abundance of sandeels.

5.1.2 Large Gadids West and North of Scotland

Large gadid fish have been heavily exploited for human consumption world-wide and the seas around Britain are no exception. The main demersal fisheries around Scotland are for cod, haddock, whiting and saithe. In 2002, the west of Scotland cod and whiting stocks were considered to be outside safe biological limits, as was the haddock stock to the west and north of Scotland (Gordon *et al.* 2002). In the same year, cod, whiting and haddock were shown to be major components of grey seal diet in the Western Isles, with the likelihood that grey seals may be inflicting significant predation mortality on cod stocks (Hammond and Harris 2006).

The results show that these species of large gadids are important prey for both grey and harbour seals in the Northern Isles and west of Scotland. This is especially so in the Inner Hebrides, where the diet of both seal species was dominated by large gadid prey, although not by any particular species. In the Outer Hebrides, large gadids were equally as important as sandeel in the diet of grey seals but were part of a diverse diet for harbour seals. Populations of harbour and grey seals are stable west of Scotland.

In the Northern Isles, grey seals are also stable but the diet has shifted from being heavily dominated by sandeel in 1985 and 2002 to one in which large gadids play a more important role (Hammond and Grellier 2006, Hammond and Wilson 2016). Gadids are also an important part of harbour seal diet in both Orkney and Shetland, where harbour seal populations have declined. The importance of gadids in the diet of harbour seals and their increased importance in the diet of grey seals may be linked to the declines in sandeel in the northern North Sea and Northern Isles.

5.2 The Bigger Picture

Generally speaking, the overall increase in the numbers of seals in British waters (SCOS 2013) and the historically low stock levels of some of their main prey species (ICES Advice 2015) suggests that competition among individuals of the same seal species (intra-specific competition) and/or between seal species (inter-specific competition) for fewer such prey could be occurring. The results show that there has been a general increase in non-commercial prey species in the diet of grey seals over the last 30 years (Hammond and Grellier 2006, Hammond and Harris 2006, Hammond and Wilson 2016) and that these prey, including sandy benthic species and scorpion fish, are also a major part of current harbour seal diet in some regions (Wilson and Hammond 2016). Both grey and harbour seals consume a wide variety of prey and they may have responded to the changing prey field around Britain by consuming more of those species that have become more available relative to other species that have declined.

Measures of diet provide information on the types and relative amounts of prey consumed. They do not provide information on the acquisition of prey leading to that diet. Information on diet alone is insufficient to determine whether changes in the relative abundance and availability of prey may have led to changes in the ability of seals to meet their nutritional requirements, including any influence of competition. Studies on the foraging behaviour of seals in relation to local prey distribution and abundance are required to explore, for example, whether there is regional variation in the amount of energy that seals expend foraging in relation to prey availability.

Regional and seasonal variation in seal diet must be strongly influenced by the distribution and abundance of potential prey. At an appropriate regional/seasonal level, harbour and grey seals effectively share a common prey field, so differences in diet are likely to be most influenced by differences in their life cycles and their foraging behaviour/distribution in relation to this prey field. There was no clear evidence of seasonal variation in differences in

diet between grey and harbour seals that may be related to the different life cycles of these two species. Information on the distribution and abundance of prey that are also fished commercially is available at a relatively large spatial and temporal scale from ICES stock assessment work. However, such information is mostly lacking at spatial and temporal resolutions likely to be important to foraging seals.

Information on foraging distribution of harbour and grey seals around Britain is quite good when viewed over a large spatial and temporal scale but the source data are patchy in time and space limiting the ability to investigate fine scale variation in time and space (Matthiopoulos *et al.* 2004, Sharples *et al*. 2012, Russell *et al*. 2013, 2015, Jones *et al*. 2015). This lack of sufficiently detailed data means that it is currently not possible to link differences in the diet of harbour and grey seals to differences in their foraging distributions as influenced by the distribution of their prey.

6 References

Baxter, J. M., Boyd, I., Cox, M., Donald, A. E., Malcolm, S. J., Miles, H., Miller, B. and Moffat, C. F. (2011). Scotland's Marine Atlas: Information for the national marine plan. Marine Scotland, Edinburgh.

Bonner, W. N. (1972). The grey and common seal in European waters. In: *Oceanography and Marine Biology. An Annual Review* (Barnes, H., ed.), pp. 461-507.
Boyd, I. and Croxall, J. P. (1996). Dive durations in pinnipeds and seabirds. *Canadian Journal of Zoology* **74**, 1696-1705.

Brown, E. and Pierce, G. (1997). Diet of harbour seals at Mousa, Shetland, during the third quarter of 1994. *Journal of the Marine Biological Association of the United Kingdom* **77**, 539-555.

Brown, E. G. and Pierce, G. J. (1998). Montly variation in the diet of harbour seals in inshore waters along the south east Shetland (UK) coastline. *Marine Ecology Progress Series* **167**, 275-289.

Brown, E. G., Pierce, G. J., Hislop, J. R. G. and Santos, M. B. (2001). Interannual variation in the summer diets of harbour seals *Phoca vitulina* at Mousa, Shetland (UK). *Journal of the Marine Biological Association of the United Kingdom* **81**, 325-337.

Christensen, J.T., and Richardson, K. (2008). Stable isotope evidence of long-term changes in the North Sea food web structure. *Marine Ecology Progress Series.* **368**, 1–8.

Frederiksen, M., Wanless, S., Harris, M.P., Rothery, P. and Wilson, L.J. (2004). The role of industrial fisheries and oceanographic change in the decline of North Sea black legged kittiwakes. *Journal of Applied Ecology.* **41**, 1129–1139.
Gordon, J. C. D., Magill, S., Sayer, S. and Barrington, J. (2002). DTI Strategic Environmental Assessment Area 7. SEA7: Fish and Fisheries. SAMS, Oban, UK.

Hall, A. J., Watkins, J. and Hammond, P. S. (1998). Seasonal variation in the diet of harbour seals in the south-western North Sea. *Marine Ecology Progress Series* **170**, 269-281.

Hammond, P. S. and Grellier, K. (2006). Grey seal diet composition and prey consumption in the North Sea. Final Report under project MF0319, Department for Environment Food and Rural Affairs, 54 pp.

Hammond, P. S. and Harris, R. N. (2006). Grey seal diet composition and prey consumption off western Scotland and Shetland. Final report to Scottish Executive Environment and Rural Affairs Department and Scottish Natural Heritage, 41pp.

Hammond, P.S. and Wilson, L.J. (2016). Grey seal diet composition and prey consumption. Sea Mammal Research Unit, Report to Scottish Government, no. CSD 3.3, St Andrews, 40pp.

Harwood, J. and Croxall, J. P. (1988). The assessment of competition between seals and commercial fisheries in the North Sea and the Antarctic. *Marine Mammal Science* **4**, 13-33.

Heath, M.R. (2005). Changes in the structure and function of the North Sea fish foodweb, 1973–2000, and the impacts of fishing and climate. *ICES Journal of Marine Science.* **62**, 847–868.

ICES (2012). Report of the Working Group on the Assessment of Demersal Stocks in the North Sea and Skagerrak (WGNSSK), ICES CM 2011/ACOM:13.. ICES Headquarters, Copenhagen, 1197pp.

ICES Advice (2015). http://www.ices.dk/community/advisory-process/Pages/Latest-Advice.aspx.

Jones, E. L., McConnell, B. J., Smout, S. C., Hammond, P. S., Duck, C. D., Morris, C. D., Thompson, D., Russell, D. J. F., Vincent, C., Cronin, M., Sharples, R. J. and Matthiopoulos, J. (2015). Patterns of space use in sympatric marine colonial predators reveals scales of spatial partitioning. *Marine Ecology Progress Series* **534**, 235–249.

Lonergan, M., Duck, C., Thompson, P. M., Mackey, B. L., Cunningham, L. and Boyd, I. L. (2007). Using sparse survey data to investigate the declining abundance of British harbour seals. *Journal of Zoology* **271**, 261-269.

Lowry, L. F., Frost, K. J., Hoep, J. M. and Delong, R. A. (2001). Movements of satellite-tagged subadult and adult harbour seals in Prince William Sound, Alaska. *Marine Mammal Science* **17**, 835-861.
Matthiopoulos, J., McConnell, B., Duck, C. and Fedak, M. (2004). Using satellite telemetry and aerial counts to estimate space use by grey seals around the British Isles. *Journal of Applied Ecology* **41**, 476-491.

Pierce, G., Boyle, P. and Thompson, P. (1990). Diet selection by seals. In *The European Marine Biology Symposium: Trophic Relationships in the Marine Environment* (Barnes, M. and Gibson, R. N., eds.), Aberdeen University Press, Aberdeen, pp. 222-238.

Pierce, G. J., Miller, A., Thompson, P. M. and Hislop, J. R. G. (1991). Prey remains in grey seal (*Halichoerus grypus*) faeces from the Moray Firth, north-east Scotland. *Journal of Zoology* **224**, 337-341.

Pierce, G. J. and Santos, M. B. (2003). Diet of harbour seals (*Phoca vitulina*) in Mull and Skye (Inner Hebrides, western Scotland). *Journal of the Marine Biological Association of the United Kingdom* **83**, 647-650.

Reder, S., Lydersen, C., Arnold, W. and Kovacs, K. M. (2003). Haulout behaviour of High Arctic harbour seals (*Phoca vitulina vitulina*) in Svalbard, Norway. *Polar Biology* **27**, 6-16.

Russell, D. J., McConnell, B., Thompson, D., Duck, C., Morris, C., Harwood, J. and Matthiopoulos, J. (2013). Uncovering the links between foraging and breeding regions in a highly mobile mammal. *Journal of Applied Ecology* **50**, 499-509.

Russell, D. J. F., McClintock, B. T., Matthiopoulos, J., Thompson, P. M., Thompson, D., Hammond, P. S., Jones, E. L., Mackenzie, M. L., Moss, S. and Mcconnell, B. J. (2015). Intrinsic and extrinsic drivers of activity budgets in sympatric grey and harbour seals. *Oikos* **124**, 1462-1472**.**

SCOS (2013). Special Committee on Seals: Scientific Advice on Matters Related to the Management of Seal Populations 2013 Sea Mammal Research Unit, University of St Andrews, St Andrews, 211pp*.*

SCOS (2015). Special Committee on Seals: Scientific Advice on Matters Related to the Management of Seal Populations 2015 Sea Mammal Research Unit, University of St Andrews, St Andrews, 211pp*.*

Sea Mammal Research Unit. (2012). Workshop report on the decline in abundance of harbour seals around the coast of Scotland and discussion of mitigation and management measures, 28 August, 2012. Report to Scottish Government, 30pp.

Sea Mammal Research Unit. (2014). Harbour Seal Decline Workshop II, 24th April, 2014. Report to Scottish Government, 14pp.

Sharples, R. J., Arrizabalaga, B. and Hammond, P. S. (2009). Seals, sandeels and salmon: diet of harbour seals in St Andrews Bay and the Tay Estury, south east Scotland. *Marine Ecology Progress Series* **390**, 265-276.

Sharples, R. J., Moss, S. E., Patterson, T. A. and Hammond, P. S. (2012). Spatial variation in foraging behaviour of a marine top predator (*Phoca vitulina*) determined by a large-scale satellite tagging program. *PLoS ONE* **7**, e37216.

Simpkins, M. A., Withrow, D. E., Cesarone, J. C. and Boveng, P. L. (2003). Stability in the proportion of harbor seals hauled out under locally ideal conditions. *Marine Mammal Science* **19**, 791-805.

SNH. (2014). Sandeels. http://www.snh.gov.uk/docs/B989125.pdf.

Thompson, P. M., Fedak, M. A., Mcconnell, B. J. and Nicholas, K. S. (1989). Seasonal and sex-related variation in the activity patterns of common seals (*Phoca vitulina*). *Journal of Applied Ecology* **26**, 521-535.

Thompson, P. M., Mackay, A., Tollit, D. J., Enderby, S. and Hammond, P. S. (1998). The influence of body size and sex on the characteristics of harbour seal foraging trips. *Canadian Journal of Zoology* **76**, 1044-1053.

Thompson, P. M., Miller, D., Cooper, R. and Hammond, P. S. (1994). Changes in the distribution and activity of female harbour seals during the breeding season: implications for their lactation strategy and mating patterns. *Journal of Animal Ecology* **63**, 24-30.

Thompson, P. M., Tollit, D. J., Greenstreet, S. P. R., Mackay, A. and Corpe, H. M. (1996). Between-year variations in the diet and behaviour of harbour seals, *Phoca vitulina* in the Moray Firth; causes and consequences. In *Aquatic predators and their prey* (Greenstreet, S. P. R. and Tasker, M. L., eds.), pp. 44-52. Oxford, England: Blackwell Science Pulications.

Tollit, D.J., Greenstreet, S.P.R., and Thompson, P.M. (1997) Prey selection by harbour seals, *Phoca vitulina*, in relation to variations in prey abundance. *Canadian Journal of Zoology*, **75**, 1508-1518.

Tollit, D. J. and Thompson, P. M. (1996). Seasonal and between-year variations in the diet of harbour seals in the Moray Firth, Scotland. *Canadian Journal of Zoology,* **74**, 1110-1121.

Wanless, S., Harris, M.P., Redman, P. and Speakman, J.R. (2004). Low energy values of fish as a probable cause of a major seabird breeding failure in the North Sea. *Marine Ecology Progress Series.* **294**, 1–8.

Wilson, L.J. and Hammond, P.S. (2016). Harbour seal diet composition and diversity. Sea Mammal Research Unit, Report to Scottish Government, no. CSD 3.2., St Andrews, 78pp.