Journal of the Marine Biological Association of the United Kingdom, 2012, 92(8), 1711–1722.
doi:10.1017/S0025315411002050

A review of spatial and temporal variation in grey and common seal diet in the United Kingdom and Ireland

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Knowledge about the diet of fish-eating predators is critical when evaluating conflicts with the fishing industry. Numerous primary studies have examined the diet of grey seals Halichoerus grypus *and common seals* Phoca vitulina *in a bid to understand the ecology of these predators. However, studies of large-scale spatial and temporal variation in seal diet are limited. Therefore this review combines the results of seal diet studies published between 1980 and 2000 to examine how seal diet varies at a range of spatial and temporal scales. Our results revealed extensive spatial variation in gadiform, perciform and flatfish consumption, likely reflecting variation in prey availability. Flatfish and gadiform consumption varied between years, reflecting changes in fish assemblages as a consequence of factors such as varying fishing pressures, climate change and natural fluctuations in populations. Perciform and gadiform consumption varied seasonally: in addition there was a significant interaction between season and seal species, indicating that grey and common seals exhibited different patterns of seasonal variation in their consumption of Perciformes and Gadiformes. Multivariate analysis of grey seal diet revealed spatial variation at a much smaller scale, with different species dominating the diet in different areas. The existence of spatial and temporal variation in seal diet emphasizes that future assessments of the impact of seal populations should not be based on past or localized estimates of diet and highlights the need for up-to-date, site specific estimates of diet composition in the context of understanding and resolving seal/fisheries conflict.*

Keywords: phocid, pinnipeds, diet analysis, scat analysis, fisheries interactions

Submitted 3 October 2011; accepted 8 November 2011;

INTRODUCTION

Overexploitation of commercial fish stocks following the industrialization of the fishing industry during the 19th and 20th Centuries caused many marine fish populations to decline and collapse (Jackson *et al*., 2001; Myers & Worm, 2003). As efforts to reduce exploitation and to manage fish stocks have increased, there have been continued calls from a number of stakeholders for populations of certain piscivorous predators to be reduced (Yodzis, 2001). In the seas surrounding the United Kingdom and Ireland, the grey seal *Halichoerus grypus* (Fabricius, 1791) and the common seal *Phoca vitulina* (Linnaeus, 1758) are two piscivorous predators that have long been the focus of attention from the commercial fishing industry, policy makers, conservationists and scientists with regard to their impact on fish stocks. There is a long history of conflict between both seal species and fisheries for Atlantic salmon *Salmo salar* (Linnaeus, 1758) (Butler *et al*., 2008), with consumption by these pinnipeds being postulated as a potential reason for the decline in salmon stocks around Scotland (Butler *et al*., 2008).

As large, conspicuous predators, with a high level of national and international protection, management of seal populations is extremely controversial. Culling of grey seals, for the purpose of controlling seal numbers and protecting fisheries, began in the UK in the early 1960s and became increasingly controversial. It was called off in the 1970s under mounting pressure from animal rights groups and the general public (Lambert, 2002). Controversial seal culls, and increased public interest in the conflict between seal populations and fishing interests, have led to the collection of detailed information on the biology, and specifically the feeding behaviour of seals, to generate an evidence base for understanding the impact of seals on fish populations (Lambert, 2002).

Increasingly, studies are attempting to model the impact of seal populations on commercial fish stocks and these studies are vital in assessing whether management of seal populations is necessary or likely to be effective. Estimates of impact are often sensitive to slight variation in model parameters (Hansen & Harding, 2006) and in particular to variation in the consumption rates of the prey species concerned (Mohn & Bowen, 1996); underpinning the importance of appreciating

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whether, and to what extent, seal diet varies spatially and temporally. Such information on diet variability is of particular importance when considering the impact of seal populations on commercial fish stocks (Harwood & Greenwood, 1985) and whether factors such as seasonal and spatial variation in seal diet could affect the recovery of commercial populations of species such as Atlantic cod *Gadus morhua* (Linnaeus, 1758) (Trzcinski *et al.*, 2006). Diet composition is also of relevance when considering the status of grey and common seal populations. In the UK the common seal population has undergone a sharp decline since 2000 (Lonergan *et al.*, 2007). Conversely, the grey seal population has continued to increase (Anonymous, 2009). The need to explore the role of changes in prey availability and dietary overlap, and therefore competition with grey seals, as possible drivers for the common seal decline has been recognized (Anonymous, 2009; Sharpes *et al.*, 2009).

Numerous studies of seal diet have been undertaken around the United Kingdom and Ireland. As well as estimating diet composition, these studies have examined spatial (e.g. Brown & Pierce, 1998; Hall *et al.*, 1998; Brown *et al.*, 2001) and temporal variation (e.g. Hammond *et al.*, 1994a, b; Pierce & Santos, 2003) in seal diet. The diet of Scottish seal populations, particularly those in the Moray Firth, has been studied extensively (Pierce *et al.*, 1991a, b; Thompson *et al.*, 1991; Tollit & Thompson, 1996), whilst other areas have been studied sporadically, e.g. Dundrum Bay (Wilson *et al.*, 2002). In general these studies span relatively short time-frames and cover small spatial scales. The present study aimed to review the results of these primary studies and combine them to provide an overview of the scale of spatial and temporal variation in seal diet around the United Kingdom and Ireland in a period spanning two decades. We hypothesized that the opportunistic nature of grey and common seals (Pierce & Santos, 2003) would result in considerable variation in seal diet across broad spatial and temporal scales. If this is the case, recognition of the scale of variation in the trophic ecology of these key predators is important for those attempting to make estimates of seal impact and subsequent management decisions.

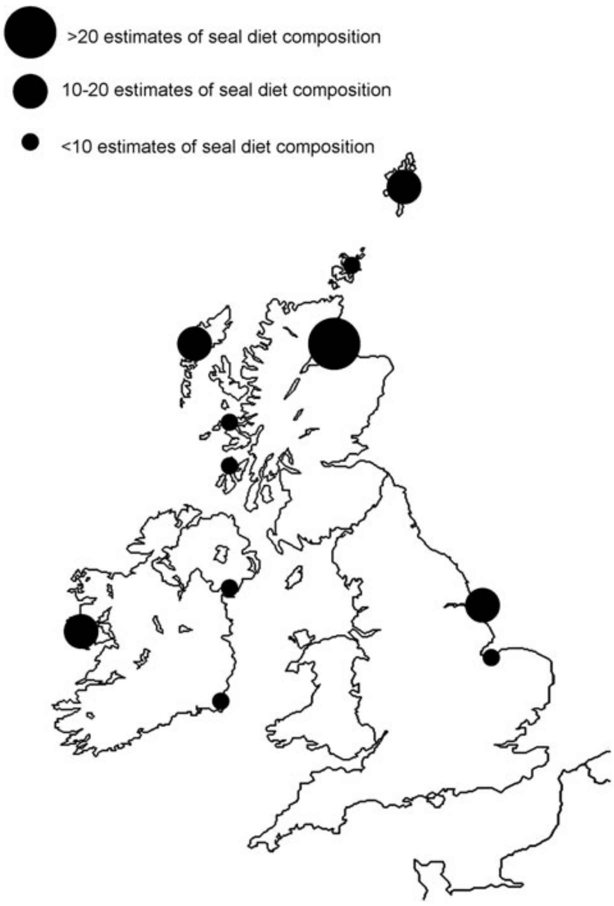

Fig. 1. Number of estimates of seal diet composition (reported in the studies listed in Table 1) for areas of the United Kingdom and Ireland used to examine spatial and temporal variation in grey and common seal diet.

Table 1. List of studies of grey and common seal diet included in the temporal and spatial analysis of diet. The studies varied in the number of estimates of seal diet they reported. The estimates of diet composition also varied in the number of scat or stomach samples they were based on.

Reference	Species	Location
Anonymous, 1997	Grey	Ireland
Anonymous, 2001	Grey	Ireland
Brown & Pierce, 1997	Common	Shetland
Brown & Pierce, 1998	Common	Shetland
Brown *et al.*, 2001	Common	Shetland
Hall *et al.*, 1998	Common	Humber
Hammond *et al.*, 1994a	Grey	Orkney
Hammond *et al.*, 1994b	Grey	Hebrides
Kiely *et al.*, 2000	Grey	Ireland
Pierce & Santos, 2003	Common	Hebrides
Pierce *et al.*, 1989	Grey and common	Moray Firth
Pierce *et al.*, 1991a	Grey	Moray Firth
Pierce *et al.*, 1991b	Common	Moray Firth
Prime & Hammond, 1990	Grey	Humber
Thompson *et al.*, 1991	Common	Moray Firth
Thompson *et al.*, 1996a	Common	Moray Firth
Tollit & Thompson, 1996	Common	Moray Firth
Tollit *et al.*, 1997	Common	Moray Firth
Wilson *et al.*, 2002	Common	Ireland

MATERIALS AND METHODS

Data collection

Estimates of grey and common seal diet composition were compiled from the literature (Table 1). In these primary studies, diet composition was estimated through identification of otoliths removed from seal scats, stomachs or digestive tracts. The relationship between otolith size and fish size allowed the percentage contribution by biomass of the fish species in predator diet to be determined (Leopold *et al.*, 2001).

A database of published studies of seal diet was compiled and comprised the following variables: seal species (grey or common seal); date of sample collection; location of sample collection (Figure 1); type of sample collected (stomach or scat); number of samples collected; and species identified in the diet and their estimated percentage contribution to the diet by biomass. Of the prey items identified in seal diets, neither the nomenclature nor level of taxonomic resolution was consistent across studies (e.g. flounder, plaice, flounder/plaice, and flatfish). To address this issue, standard prey

Table 2. Mean composition of grey and common seal diet (% contribution by biomass) from estimates of common seal (N = 42) and grey seal (N = 34) diet composition (based on estimates using more than 30 scat samples to determine diet composition) across all locations, years and seasons.

Prey		REML group	Common N = 42 Mean ± SE	Grey N = 34 Mean ± SE
Sandeel	*Ammodytes tobianus*	Perciformes	27.9 ± 4.2	23.1 ± 3.7
Whiting	*Merlangius merlangus*	Gadiformes	16.3 ± 2.4	9.6 ± 2.0
Herring	*Clupea harengus*	Clupeiformes	8.4 ± 1.9	0.6 ± 0.3
Flounder/plaice	*Pleuronectidae*	Flatfish	8.4 ± 3.0	7.8 ± 1.8
Cephalopods		Cephalopods	4.5 ± 2.0	2.8 ± 1.4
Sprat	*Sprattus sprattus*	Clupeiformes	3.6 ± 2.4	
Ling	*Molva molva*	Gadiformes	3.4 ± 0.9	9.3 ± 1.8
Cod	*Gadus morhua*	Gadiformes	3.0 ± 0.7	10.4 ± 1.3
Dragonet	*Callionymus lyra*	Perciformes	2.9 ± 1.4	1.4 ± 0.5
Other gadids	*Trisopterus* spp.	Gadiformes	2.8 ± 0.8	2.3 ± 0.6
Garfish	*Belone belone*	Other fish[1]	2.5 ± 1.1	
Pollack	*Pollachius pollachius*	Gadiformes	2.4 ± 0.8	5.0 ± 1.1
Others[2]		Other fish	2.4 ± 0.6	1.1 ± 0.4
Goby spp.	*Gobius* spp.	Perciformes	2.1 ± 1.0	
Sole	*Solea solea*	Flatfish	1.5 ± 0.7	4.1 ± 2.1
Bib	*Trisopterus luscus*	Gadiformes	1.4 ± 0.7	
Bullrout	*Notesthes robusta*	Other fish	1.3 ± 0.7	1.4 ± 1.0
Haddock	*Melanogrammus aeglefinus*	Gadiformes	1.3 ± 0.5	2.4 ± 0.5
Dab	*Limanda limanda*	Flatfish	1.2 ± 0.4	2.8 ± 1.2
Scad	*Trachurus trachurus*	Perciformes	1.0 ± 0.9	2.1 ± 1.0
Lemon sole	*Microstomus kitt*	Flatfish	0.4 ± 0.1	0.9 ± 0.4
Salmon	*Salmo salar*	Other fish	0.3 ± 0.3	
Turbot	*Psetta maxima*	Flatfish	0.2 ± 0.2	
Eelpout	*Zoarces vivparus*	Perciformes	0.2 ± 0.2	
Witch	*Glyptocephalus cynoglossus*	Flatfish		2.6 ± 1.0
Sculpin	*Myoxocephalus scorpius*	Other fish		1.1 ± 0.4
Megrim	*Lepidorhombus whiffiagonis*	Flatfish		2.6 ± 1.0
Forkbeard	*Phycis phycis*	Gadiformes		0.7 ± 0.3
Conger eels	*Conger conger*	Other fish		1.8 ± 0.9
Brill	*Scophthalmus rhombus*	Flatfish		1.3 ± 0.6
Black sea bream	*Brama brama*	Perciformes		0.3 ± 0.2
Bass	*Dicentrarchus labrax*	Perciformes		0.4 ± 0.3

[1] 'Other fish' includes the following species *Chimaera monstrosa, Anguilla anguilla, Cyclopterus lumpus, Maurolicus muelleri, Taurulus bubalis, Lumpenus lampretaeformis, Alepisaurus ferox*, which belong to families other than those defined for the REML analysis.

[2] 'Others' denotes prey species contributing less than 5% to the diet in published estimates in addition to prey which were not classified in the published study including 'other fish', 'other Gadiformes', 'unknown' etc.)

REML, restricted maximum likelihood analysis; SE, standard error.

categories were used for analyses (see Table 2). Where analysis of seal diet was repeated in discrete time periods (e.g. May, June, July or spring/summer), each time period was treated as a separate estimate of diet composition, though their interdependence was accounted for in statistical analysis.

Analysis of broad scale spatial and temporal variation in seal diet

Dietary data were both non-orthogonal and unbalanced and therefore broad scale spatial and temporal variation in grey and common seal diet were analysed by fitting linear mixed models in a restricted maximum likelihood (REML) analysis (Patterson & Thompson, 1971), in SPSS/PASW (Version 17).

The diet studies recorded 79 different prey categories: for the purposes of REML analysis, these were pooled into 4 prey groups (flatfish, Perciformes, Gadiformes and Clupeiformes: see Table 2), which were treated as separate dependent variables. The remaining prey species, including cephalopods, were grouped into 'other fish' and were not included in the REML analysis. With one exception (Hall *et al.*, 1998), error associated with estimates of diet composition was not recorded in the primary studies. Therefore, in an attempt to account for this unquantified source of variation three estimates of consumption were produced for each of the prey groups. The mean estimate of consumption was produced by averaging the % biomass contribution across the species within the prey group. The upper and lower estimates of consumption were calculated from the 95% confidence intervals around the mean estimate.

Recognizing the potential for bias resulting from primary studies based on small sample sizes, analyses were restricted to primary studies where diet estimates were based on >30 samples. The percentage consumption of each prey category was arcsine square-root transformed. Data describing the consumption of Clupeiformes, the least prevalent prey group in the diet, could not be transformed to normality and were not analysed further.

Of the 76 estimates of diet composition based on >30 samples, two were based on stomach contents analysis, whilst the remainder were based on scat analysis. Whilst it was unlikely that such a small number of stomach analysis studies would influence diet composition, 'analysis type' was included as a factor in a preliminary analysis. Although the small sample size meant that the statistical power to detect differences between the two analytical approaches was low, 'analysis type' had no significant effect on diet composition and the results of both methods were pooled in the final analysis.

Location and timing of sample collection were grouped to reduce the number of levels of factors in the model. Locations of sample collection were grouped into five areas: Irish Sea; Atlantic; the Moray Firth; the North Sea Islands (Shetland and Orkney); and the southern North Sea (the Humber Estuary and the Wash). The resulting variable LOCATION was treated in the model as a repeated measure. Time of sample collection was classified into season, i.e. January–March, April–June, July–September and October–December, and SEASON was treated as a fixed factor. To examine differences in diet between years, rather than trends in diet across years, we treated year of sample collection as a factor in the model, rather than a covariate. The primary studies analysed diet during 15 different years and therefore to reduce the number of levels within the factor, and improve model fit, we condensed the year of sample collection into six blocks of 3 years (1983–1985, 1986–1988, 1989–1991, 1992–1994, 1995–1997 and 1999–2000). The resulting factor 'YEAR GROUP' was treated as a fixed factor. Where a study spanned more than one year or season, the year or season that covered the longest period of sample collection was taken as the YEAR GROUP or SEASON of the study. Alternatively, when this did not resolve the issue, the first year or season of sample collection was taken as the year or season of the study. Seal species was treated as a fixed factor (SPECIES). Diet composition estimates were available for both seal species in each of the four seasons and therefore the interaction SPECIES*SEASON was included in the model. However, data on diet composition was not available for both species in every year group or in every location. In instances where estimates of diet composition were available for both species, the number of estimates was too small, or too unbalanced between the species, to permit analysis. Therefore it was not possible to include the interactions SPECIES*YEARGROUP and SPECIES*LOCATION in the analysis.

All possible model combinations were computed for the mean, upper and lower estimates of consumption of each of the three transformed prey categories (flatfish, Perciformes and Gadiformes). Model parsimony was assessed by Akaike's information criterion (AIC) (Akaike, 1983). AIC and change in AIC (ΔAIC) were calculated, and the model with the lowest AIC value and a ΔAIC value greater than 2 units was considered the most parsimonious within the suite of models. For each of the prey groups, the influence of each of the terms within the most parsimonious model was described by the F statistic. Estimated marginal means were calculated for each of the significant factors remaining in the most parsimonious models and compared through Bonferroni *post-hoc* tests. The estimated marginal means are reported in the following section for the mean estimate of diet and the upper and lower estimates of diet.

Spatial and seasonal variation in grey seal diet—a 1985 case study

Recognizing the potential loss of variation through the data pooling required by the REML analysis, multivariate analysis was carried out in PRIMER v6 (Clarke & Warwick, 2001) to examine spatial and seasonal variation in seal diet. Substantial data on grey seal diet were available from the 1980s, for example 26 estimates of grey seal diet composition were available for 1985 permitting multivariate analysis of diet composition at higher taxonomic resolution. Again, as with the broad scale analysis, the analysis focused on studies based on 30 or more samples to reduce the influence of diet studies based on small sample sizes.

Bray–Curtis similarity matrices were constructed on untransformed species biomass data (% contribution to the diet by biomass) (Clarke & Gorley, 2006) and species ordination through multidimensional scaling was performed on the resulting data. Spatial and seasonal variation in grey seal diet was examined using a two-way crossed non-parametric analysis of similarity (ANOSIM) and where such variation occurred prey species contributing to variation were identified via similarity of percentages (SIMPER) (Clarke & Warwick, 2001).

RESULTS

General diet

Estimates of diet composition were collated from 19 studies of grey and common seal diet published between 1980 and 2000, relating to 18 locations from the around the United Kingdom and Ireland (Table 1; Figure 1). The studies recorded 122 estimates of diet composition and identified 79 different prey items in the diet of the grey and common seal. Three studies were reported by statutory bodies in non-peer reviewed reports (Anonymous, 1997, 2001; Kiely *et al.*, 2000). All remaining studies were from peer reviewed articles.

In studies based on more than 30 scats ($N = 76$), sandeels *Ammodytes tobianus* (Linnaeus, 1758) contributed most to common seal diet with a biomass contribution of 28% ± 4.2 (mean biomass contribution ± standard error) (Table 2), whilst whiting *Merlangius merlangus* (Linnaeus, 1758) was the second most abundant species (16% ± 2.4). Sandeels were also the most prominent species in grey seal diet albeit making a slightly lower mean biomass contribution of 23% ± 3.7. Cod was the second most prevalent species in grey seal diet contributing a mean biomass of 10% ± 1.3. Salmon contributed 0.3% to the biomass of the diet of the common seal and was not recorded in the diet of the grey seal.

Broad scale spatial and temporal variation in common and grey seal diet

The most parsimonious model of variation in consumption of each prey type was the full model (SPECIES, LOCATION, SEASON, YEAR GROUP and SPECIES*SEASON interaction) and this was the case for the mean, lower and upper estimated consumption models. The models revealed spatial, seasonal and inter-annual variation in prey consumption. The pattern of variability was broadly similar for the mean, lower and upper estimates of consumption but varied between the prey groups. Estimated marginal mean % contribution to the biomass of the diet, produced when the most parsimonious model was fitted, are reported for the mean, lower and upper estimated consumption models (mean and lower–upper).

Table 3. Results of restricted maximum likelihood analysis for each of the variables in the most parsimonious model of the mean, upper and lower consumption of (A) flatfish, (B) Perciformes and (C) Gadiformes (mean % contribution to the diet by biomass) by grey and common seals in the United Kingdom. For prey items in each prey category see Table 2.

A						
	Lower flatfish		**Mean flatfish**		**Upper flatfish**	
Factor	**F_{df}**	**P**	**F_{df}**	**P**	**F_{df}**	**P**
SPECIES	$8.08_{1,59}$	0.01	$1.20_{1,59}$	0.28	$3.18_{1,59}$	0.08
LOCATION	$11.32_{4,59}$	<0.0001	$23.46_{4,59}$	<0.0001	$23.11_{4,59}$	<0.0001
SEASON	$2.27_{3,59}$	0.09	$2.73_{3,59}$	0.05	$2.41_{3,59}$	0.08
YEAR GROUP	$3.84_{5,59}$	0.004	$7.51_{5,59}$	<0.0001	$7.72_{5,59}$	<0.0001
SPECIES*SEASON	$1.19_{3,59}$	0.32	$1.42_{3,59}$	0.25	$1.26_{3,59}$	0.29
B						
	Lower Gadiformes		**Mean Gadiformes**		**Upper Gadiformes**	
Factor	**F_{df}**	**P**	**F_{df}**	**P**	**F_{df}**	**P**
SPECIES	$3.57_{1,59}$	0.06	$1.78_{1,59}$	0.19	$0.94_{1,59}$	0.34
LOCATION	$8.56_{4,59}$	<0.0001	$9.53_{4,59}$	<0.0001	$9.19_{4,59}$	<0.0001
SEASON	$5.25_{3,59}$	0.003	$8.12_{3,59}$	<0.0001	$8.92_{3,59}$	<0.0001
YEAR GROUP	$3.08_{5,59}$	0.015	$2.37_{5,59}$	0.05	$2.01_{5,59}$	0.09
SPECIES*SEASON	$1.69_{3,59}$	0.18	$3.25_{3,59}$	0.03	$3.75_{3,59}$	0.02
C						
	Lower Perciformes		**Mean Perciformes**		**Upper Perciformes**	
Factor	**F_{df}**	**P**	**F_{df}**	**P**	**F_{df}**	**P**
SPECIES	$1.23_{1,59}$	0.27	$0.96_{1,59}$	0.33	$0.79_{1,59}$	0.38
LOCATION	$6.03_{4,59}$	<0.0001	$5.51_{4,59}$	0.001	$5.12_{4,59}$	0.001
SEASON	$4.95_{3,59}$	0.004	$5.1_{3,59}$	0.003	$5.14_{3,59}$	0.003
YEAR GROUP	$0.73_{5,59}$	0.61	$0.74_{5,59}$	0.59	$0.83_{5,59}$	0.54
SPECIES*SEASON	$3.34_{3,59}$	0.03	$3.79_{3,59}$	0.02	$4.07_{3,59}$	0.01

There was significant spatial variation in flatfish, perciform and gadiform consumption (Table 3 A, B, C; Figure 2A). The pattern of spatial variation in perciform consumption was consistent for the models of mean, upper and lower estimated consumption. In each case, (mean and lower–upper) estimated consumption in the Atlantic Ocean (11%, 10–13%) was significantly lower than in the North Sea Islands (20% and 13–23%) and Moray Firth (24% and 21–26%). Perciform consumption was highest in the Moray Firth and consumption in that area also exceeded that in the southern North Sea (14% and 11–16%). Gadiformes contributed least to seal diet in the Moray Firth (4% and 3–5%) compared with all other areas (Atlantic = 14% and 11–17%; Irish Sea = 15% and 12–17%; North Sea Islands = 16% and 13–18%; and southern North Sea = 11% and 8–14%). The contribution to the diet in the North Sea Islands also exceeded that in the southern North Sea. This pattern was significant for the mean and lower estimated consumption models but the difference between the North Sea Islands and the southern North Sea was not significant in the upper consumption model. Flatfish contributed more to the diet of seals in the Irish Sea (13% and 5–18%) than in all other areas (Atlantic = 2% and 0.4–3%; North Sea Islands = 0.1% and 0–1.6%; Moray Firth = 5% and 4–6%; and southern North Sea = 6% and 5–7%). This pattern was significant for both the mean and upper estimated consumption models. The lower estimated consumption model indicated that flatfish contributed significantly more to the diet in the Irish Sea than in the Atlantic, but the difference was not significant for any of the other areas. This model also indicated, along with the upper estimate of consumption model, that consumption in the southern North Sea exceeded that in the Atlantic, whilst the three models indicated that consumption in the Moray Firth and southern North Sea exceeded that in the North Sea Islands.

Gadiformes and Perciformes exhibited seasonal variation and again the pattern of variation was similar for the models of mean, upper and lower estimated consumption (Figure 2B). The pattern in seasonal variation in perciform consumption was evident for the mean, lower and upper estimates of consumption. Perciformes contributed less to the diet between October and December (10% and 9–12%) than between April and June (19% and 16–21%) and July and September (18% and 16–21%). The seasonal pattern of gadiform consumption was slightly different between the three diet estimates. Gadiformes formed a greater proportion of the diet between October and December (14% and 10–16%) and January and March (15% and 12–18%) than between April and June (10% and 7–12%) and July and September (10% and 8–12%). The differences were significant for the mean and upper estimated consumption models but the lower estimated consumption model indicated that the consumption of Gadiformes in October–December was not significantly different from the other seasons.

Flatfish were estimated to contribute more to the biomass of seal diet in 1983–1985 (12% and 4–16%) than in any other year group (1986–1988 = 4% and 2–15%; 1989–1991 = 5% and 5–6%; 1992–1994 = 6% and 4–7%; 1995–1997 = 4% and 3–5%; and 1998–2000 = 0.1% and 0.3–0.4%). This difference was significant for both the mean and upper estimated consumption models but not for the lower estimated consumption model. In addition, the model of upper estimated consumption indicated that flatfish contributed more to the biomass of the diet in 1992–1994 than in 1998–2000. The model of lower estimated consumption indicated that the contribution to the biomass of the diet in 1983–1985, 1989–1991 and 1992–1994 was significantly higher than in 1998–2000. The lower estimate

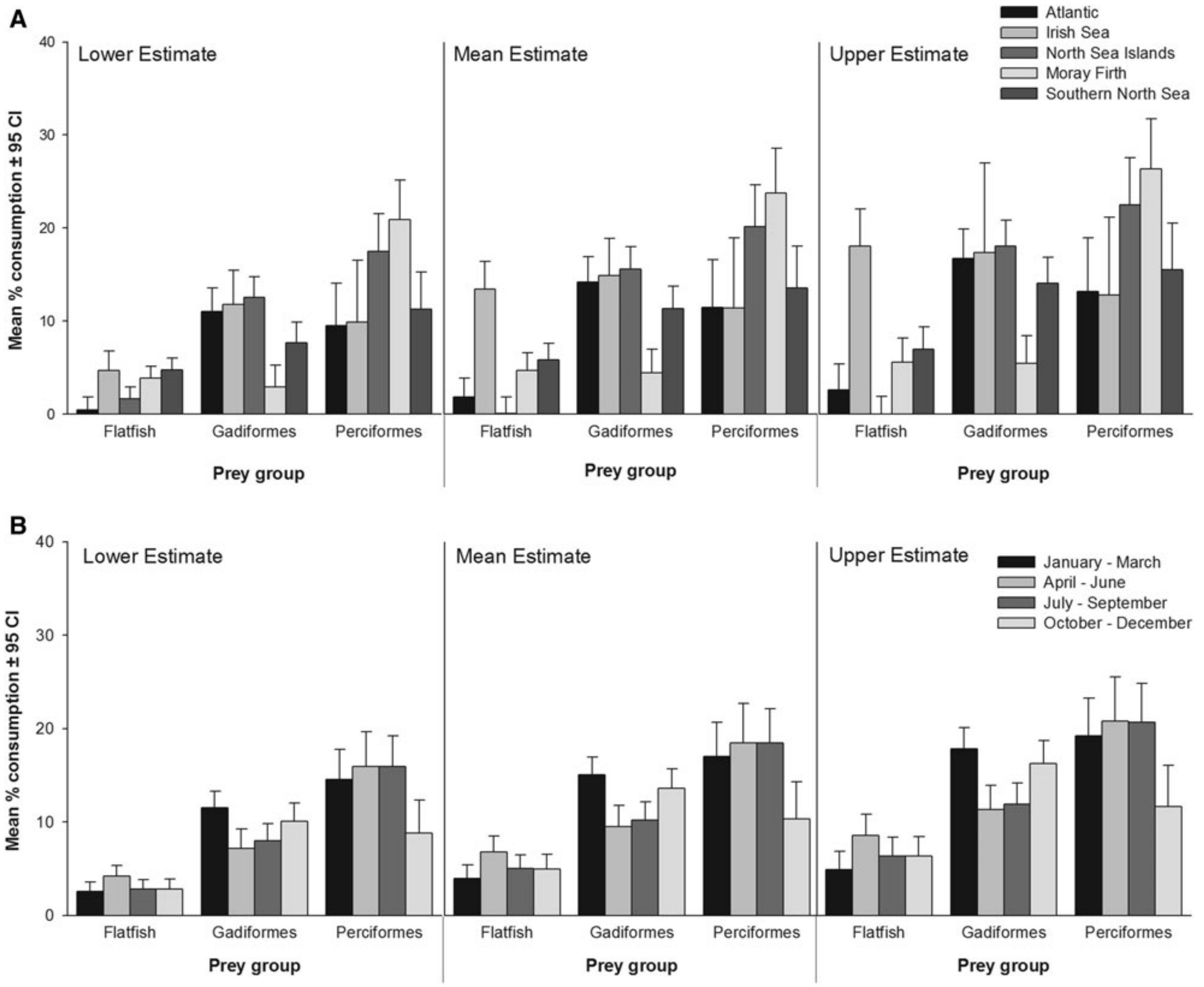

Fig. 2. (A, B) The mean, upper and lower estimated marginal mean consumption by seals in the United Kingdom and Ireland (mean % contribution to the diet by biomass ± 95% confidence intervals) of (A) each prey group at each location and (B) each prey group in each season, produced when the most parsimonious model was fitted; (C, D) the mean, upper and lower estimated marginal mean consumption by seals in the United Kingdom and Ireland (mean % contribution to diet by biomass ± 95% confidence intervals) of (C) each prey group in each year group and (D) of Gadiformes and Perciformes in each season and for each seal species, produced when the most parsimonious model was fitted.

of gadiform consumption was the only model to indicate inter-annual variation in the consumption of this prey group. Gadiformes contributed more to the diet in 1992–1994 (13%) than in 1983–1985 (6%). The mean and upper estimates of consumption did not indicate significant inter-annual variation.

There was no evidence for consistent differences in the diet of the two seal species, with the exception of the lower estimate of flatfish consumption, where grey seals (6%) consumed significantly more flatfish than harbour seals (3%). However, a significant interaction between species and season (Table 3) revealed that grey and common seals showed different patterns in seasonal variation in the consumption of perciform and gadiform fish. Grey seals consumed a greater proportion of Perciformes than common seals in each season, with the exception of April–June where the opposite was true (Figure 2D). This pattern was apparent for mean, upper and lower estimated consumption models. Grey seals ate more Gadiformes than common seals in every season, with the exception of October–December when the pattern was reversed (Figure 2D). This pattern was present in the mean and upper estimated consumption models but was absent in the lower estimate.

Spatial and seasonal variation in grey seal diet—a 1985 case study

Multidimensional scaling ordination indicated segregation in grey seal diet composition between the Humber Estuary, Orkney Islands and Hebridean Islands (Figure 3) and was supported by ANOSIM (global R = 0.477, $P = 0.001$). The greatest segregation in diet occurred between the Humber Estuary and Orkney Islands (pairwise R = 0.681, $P = 0.008$). SIMPER analysis revealed that grey seal diet was characterized by sandeel in both the Humber Estuary and the Orkney Islands but with differing levels of consumption (Table 4). Sandeel contributed 42% to the diet of the grey seal in Orkney and 29% in the Humber, contributing 21% to the 67% dissimilarity between the two areas. There was no significant seasonal variation in grey seal diet between the three locations (R = 0.025, $P = 0.4$).

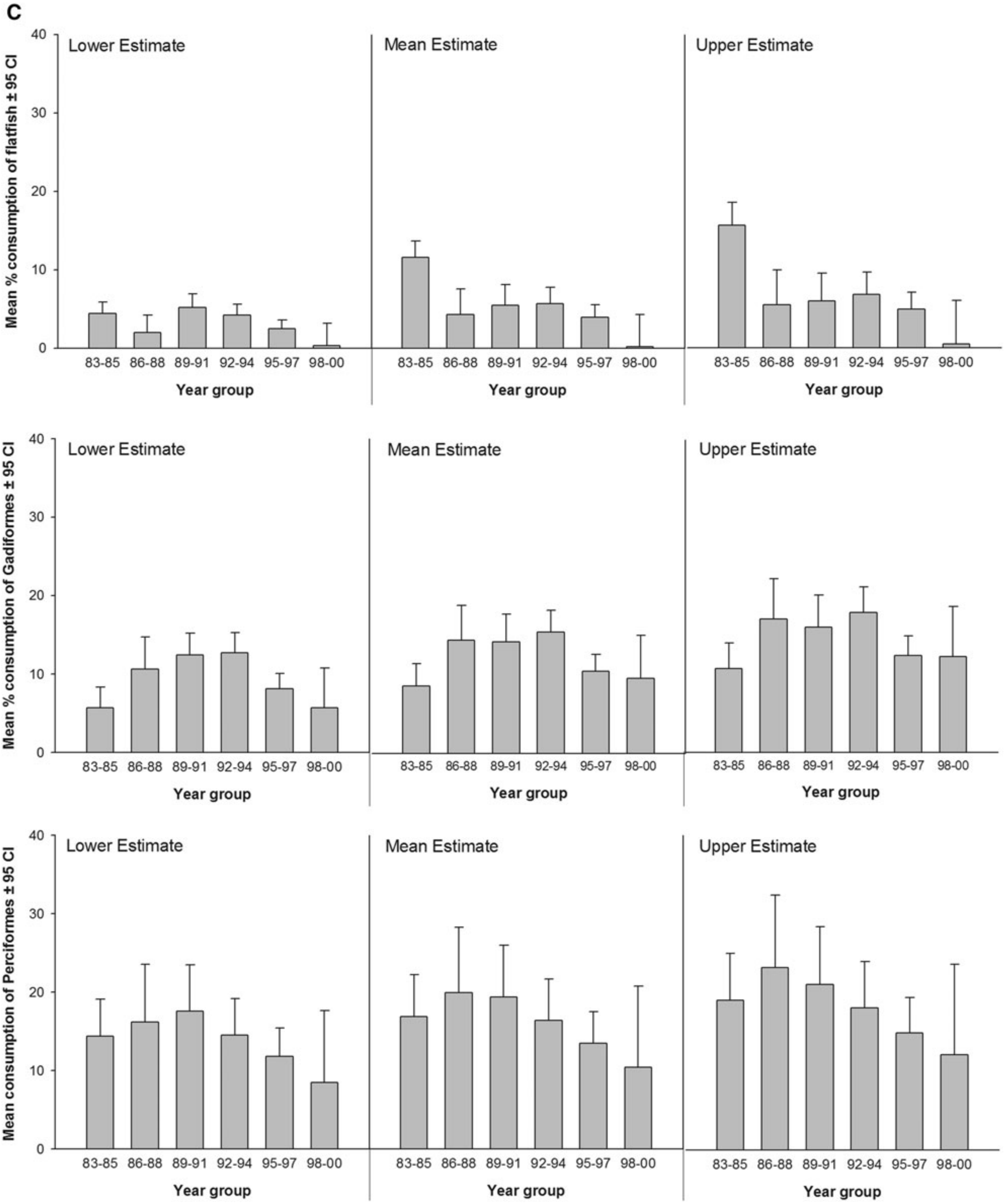

Fig. 2 *Continued*

DISCUSSION

Perceived conflict between seals and the fishing industry has resulted in a large body of work investigating the composition of seal diet and estimating the impact of seals on populations of commercial fish species. This study combined the results of primary studies of seal diet and revealed little evidence of difference in diet between seal species. However, seal diet was very variable, both spatially and temporally, with spatial variation being evident across broad spatial scales and temporal variation being apparent over long time periods. These findings have implications in the context of ecosystem-based fishery management, contributing to our understanding of the role of seals in the marine foodweb.

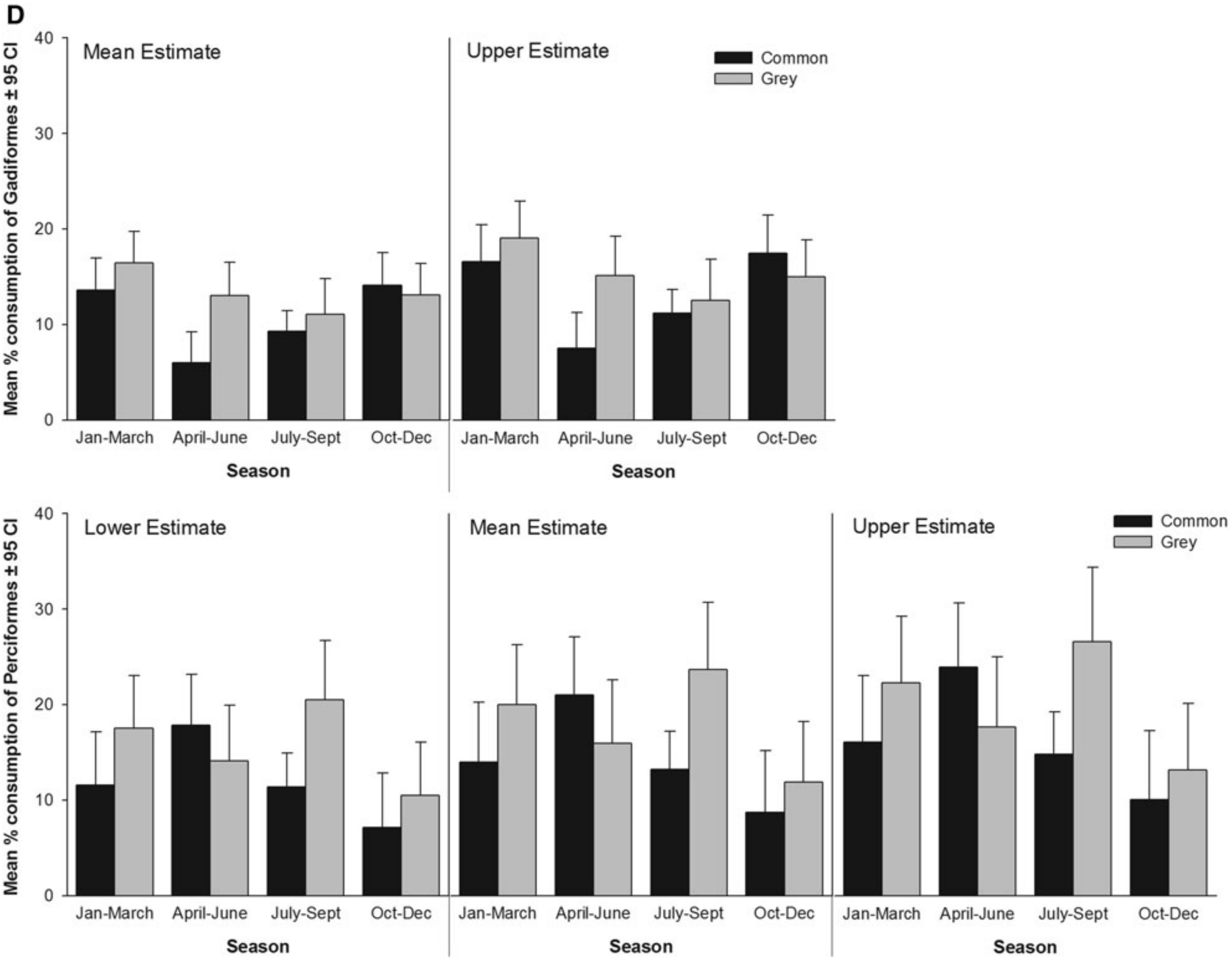

Fig. 2 *Continued*

Variation in seal diet is principally influenced by seals foraging as opportunistic predators, feeding according to prey availability and abundance (Pierce & Santos, 2003). Both flatfish and Gadiformes showed inter-annual variation in consumption with flatfish consumption peaking in the early 1980s before dropping considerably in subsequent years. Conversely the consumption of Gadiformes was high between 1986 and 1994 before decreasing from 1995 onwards. Climate change and fishing pressure are drivers of change in composition, abundance and distribution of fish communities (Graham & Harrod, 2009; Hofstede & Rijnsdorp, 2011). As such, it is likely that the inter-annual variation in consumption detailed here reflects variation in the availability of prey driven by these processes. Examining the diet at higher taxonomic resolution could shed light on how variation in prey species availability may affect diet annually, particularly for commercial species, whose stock sizes are generally well documented.

Prey distribution drives prey selection and therefore diet composition (Prime & Hammond, 1990; Härkönen & Heide-Jorgensen, 1991; Thompson *et al.*, 1996b) and consumption patterns depend on a variety of factors including habitat. Sandeels dominated the diet of common seals foraging over sandy habitats in the Inverness Firth, but were less important in the diet of seals in the Dornoch Firth where such habitat was rarely used (Tollit *et al.*, 1998). Variation in diet as a result of varying habitat use was reported in other studies including Hammond *et al.* (1994a, b) and Tollit & Thompson (1996). The abundance of prey in the local area also drives variation in the diet (Tollit *et al.*, 1997; Berg *et al.*, 2002). Spatial variation in grey seal diet illustrated here, between the Humber Estuary and the Orkney Islands, is probably a consequence of the differing prey assemblages supported by islands and tidal estuaries. Likewise, habitat differences and consequently differences in prey assemblages, between the five areas examined by the broader analysis, likely drive the spatial variation in consumption between flatfish, Perciformes and Gadiformes. Gadiform consumption was lower in both of the estuarine systems examined, the Moray Firth and the Humber and Wash (southern North Sea), and higher in the North Sea Islands of Shetland and Orkney. Based on the primary studies the principal gadiform in seal diet was whiting, which occurs in large aggregations, of both juveniles and adults, around the coast of Scotland and Shetland (Tobin *et al.*, 2010). These aggregations potentially influence the importance of Gadiformes in seal diet in these areas, as identified by the broad analysis. Similarly consumption of flatfish was higher in estuarine areas potentially because flounder, the most abundant flatfish in seal diet according to the primary studies, is most prevalent in shallow brackish coastal waters (Hemmer-Hanson *et al.*, 2007).

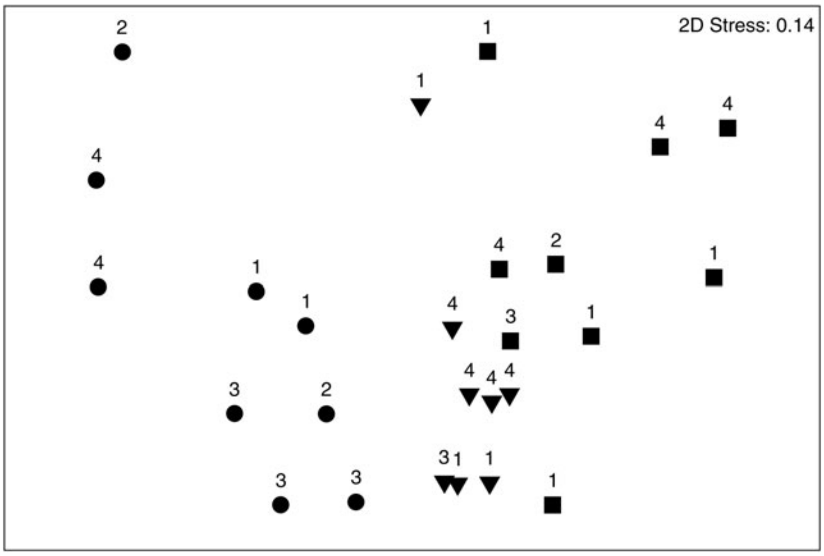

Fig. 3. Multidimensional scaling ordination of the 26 studies of grey seal diet carried out in 1985 in the United Kingdom. The plot is dimensionless, the closer the points the more similar the species composition of the grey seal diet. The plot shows apparent differences in grey seal diet between different areas of their range (■ Hebridean Islands, ▼ Orkney Islands and • Humber Estuary). The figures above the markers indicate the season of the study ((1) January–March; (2) April–June; (3) July–September; and (4) October–December). Area differences in diet appear to be of greater importance than seasonal differences in diet.

Seasonal foraging and spawning movements of prey also influence diet composition. Using telemetry, Thompson *et al.* (1991) demonstrated that common seals moved into the inner Moray Firth during the winter in response to the movement of clupeids. Variation in diet related to prey movement was also demonstrated by Brown & Pierce (1998) and Hauksson & Bogason (1997). Conversely, Berg *et al.* (2002) examined the diet of common seals in Norway and found that saithe *Pollachius virens* (Linnaeus, 1758) consistently dominated the diet throughout the year, as the saithe population in the area was stable. The results of the present study indicated that the seasonal variation shown in the consumption of Perciformes and Gadiformes was not apparent in the consumption of flatfish. Whiting exhibit seasonal movements, with juvenile whiting moving to shallow inshore waters from July and peaking in November and December (Gordon, 1977). This seasonal movement may explain the seasonal pattern in consumption of Gadiformes which indicated that consumption was highest between October and March. The movement of whiting into shallow waters during this period coincides with the decline in the consumption of Perciformes during the same period. It has been demonstrated that the availability of the prey item itself (Tollit & Thompson, 1996; Brown & Pierce, 1997) and the availability of other species (Hall *et al.*, 1998) leads to variation in the diet and it is possible that the increased availability of whiting during this period led to the decline in consumption of Perciformes. Perhaps more likely is that the seasonal variation in perciform consumption stemmed from the movements of the dominant species in this prey group—sandeels. Sandeels are dependent on specific substrate types (Reay, 1970) and therefore seasonal movements are largely restricted to movements into and out of

Table 4. Results of similarity of percentages analysis listing the prey species and their contribution to the mean dissimilarity of 66.8% between the diet compositions of grey seals in the Humber Estuary and the Orkney Islands. Diss/SD is the ratio of average dissimilarity to standard deviation and a good differentiating species is one with a high ratio indicating a consistent difference in the species across the sites. Sandeels contributed most to the mean dissimilarity in diet composition between the two locations, occurring in both locations but to different extents.

Species		Orkney Mean abundance	Humber Mean abundance	Mean dissimilarity	Diss/SD	% contribution to dissimilarity	Cumulative %
Sandeel	*Ammodytes tobianus*	41.9	28.5	14.3	3.0	21.4	21.4
Dab	*Limanda limanda*	0	10.1	6.8	1	10.1	31.5
Flounder	*Platichthys flesus*	0	10.2	6.6	1.4	9.9	41.4
Sole	*Solea solea*	0	15.2	4.9	1.4	7.3	48.7
Bullrout	*Notesthes robusta*	0.9	4.2	4.2	0.6	6.2	54.9
Whiting	*Merlangius merlangus*	6.6	6.3	4.0	1.1	6.0	60.9
Plaice	*Pleuronectes platessa*	8.9	3.7	3.9	0.7	5.9	66.8
Cod	*Gadus morhua*	11.7	13.8	3.5	1.3	5.3	72.1
Ling	*Molva molva*	7	0	3.5	1.4	5.3	77.3
Dragonet	*Callionymus lyra*	0	5.3	2.7	1.4	4.0	81.3
Pollack	*Pollachius pollachius*	5.2	0	2.5	1.1	3.7	85.0
Witch	*Glyptocephalus cynoglossus*	4	0	1.9	1.0	2.8	87.8
Sculpin	Unidentified	3.9	0.5	1.8	1.2	2.7	90.5

the substrate. The activity of sandeels in the water column peaks during the summer months (Winslade, 1974). Sandeels are least active between September and March, when they remain in the substrate, emerging in December and January to spawn (Macer, 1966; Wright, 1996). The seasonal pattern in perciform consumption, revealed by the analysis, reflects this pattern in sandeel movement. It is possible that loss of resolution, through data pooling, contributed to the lack of seasonal variation in flatfish consumption. Conversely, it is possible that the populations of these flatfish are more seasonally stable.

Considering that grey seals have been demonstrated to travel further than common seals to forage (Thompson *et al.*, 1996a), inter-specific differences in consumption were anticipated for each prey group. Interspecific variation was detected to some degree in flatfish where the lower estimate of consumption indicated that grey seals consumed more than common seals. As revealed by the significant interaction between species and season Perciformes and Gadiformes also displayed inter-specific variation in consumption. In both cases variation corresponded to the seal breeding season indicating that it may be driven by different energetic requirements during this period, or by changes in foraging range during this period influencing the prey species available. Evidence from tracked male harbour seals suggests an increase in time spent foraging in inshore waters, during the breeding season, at the expense of offshore foraging (Coltman *et al.*, 1997), whilst female common seals reduce the range of their foraging trips during a portion of the lactation period (Thompson *et al.*, 1994). Tracked grey seals also display changes in movements prior to the breeding season with males foraging closer to haulouts during this period (McConnell *et al.*, 1999). Grey seal consumption of Perciformes exceeded common seal consumption in every season with the exception of April–June when the opposite was true. The common seal pupping season runs through June and July (Anonymous, 2003) and it is possible that Perciformes are a prevalent component of the diet of breeding common seals. Likewise grey seal consumption of Gadiformes exceeded that of common seals during every season, bar October–December when the opposite was true. The lack of inter-specific differences in the consumption of the remaining prey groups, examined in this study, is suggestive of similarities in diet, raising the potential for trophic competition between grey and common seals (Sharples *et al.*, 2009) in the prey species they target. Partitioning of resources through other means, such as size selection, should also be explored.

Scat analysis became a popular and widely used method for analysing the diet of seals during the 1980s (e.g. Härkönen, 1987; Prime & Hammond, 1990) and is a useful way of qualitatively assessing diet composition. Like other means of estimating consumer diet, such as stable isotope analysis, there are several sources of potential bias involved in using this technique (Pierce & Boyle, 1991). Otoliths undergo erosion during digestion and the degree of erosion differs between species (Hall *et al.*, 1998). A number of primary studies, used in this review, did not correct for this variation (Anonymous, 1997, 2001; Pierce *et al.*, 1989, 1991a, b; Thompson *et al.*, 1991; Tollit & Thompson, 1996; Tollit *et al.*, 1997; Kiely *et al.*, 2000; Wilson *et al.*, 2002), whilst a variety of digestion coefficients were used in the remaining studies to account for erosion during digestion. Experimentally derived digestion coefficients published by Tollit *et al.* (1997) were used in the majority of primary studies which corrected for variation (Brown & Pierce, 1998; Hall *et al.*, 1998; Brown *et al.*, 2001; Pierce & Santos, 2003). The remaining studies (Prime & Hammond, 1990; Hammond *et al.*, 1994a, b) used correction factors published in Harvey (1989) and Prime & Hammond (1987). With the exception of one study (Hall *et al.*, 1998) diet compositions were reported as point estimates of the % contribution to the biomass of the diet by each prey species, and no estimate of error, or variation around this point estimate, was given. As not all studies applied the same digestion coefficients, and as the majority of studies did not report the statistical error associated with the estimates of diet composition, it was necessary to pool individual prey species into taxonomic groups. This allowed the mean, upper and lower estimates of diet composition for these categories to be calculated and analysed. Pooling of factors and prey categories prior to analysis undoubtedly reduced resolution and masked some variation in the dataset. Hall *et al.* (1998) found that monthly variation in the diet of common seals was lost when the months were grouped into seasons. Whilst pooling prey species may have obscured some of the variation in the diet, clear spatial and temporal differences in diet were still apparent.

The importance of robust information on seal diet composition and variation in diet is clear when considering the impact of seal populations on fisheries. Our findings support the classification of grey and common seals as opportunist predators whose diet varies with fish availability (Hall *et al.*, 1998). This variability makes understanding, predicting and resolving the conflict with commercial fisheries particularly difficult. The results described above are based on information from studies which primarily used scat analysis as a tool for dietary analysis. The limitations of scat analysis are well documented (Jobling & Breiby, 1986). However, scat analysis remains the only method available to determine the size-class of consumed prey and therefore their commercial relevance.

The existence of temporal variation in seal diet highlighted by this review has great significance for the estimation of seal impacts and the management of populations. Inter-annual variation in seal diet illustrates the highly variable nature of fish stocks and, as a consequence, the highly variable nature of the impact of seals. In short, temporal variation highlights the unsuitability of predicting long-term future impacts of seal populations from past short-term estimates of seal diet. Analysis of seal diet either through scat analysis or other techniques must be carried out in a routine rather than a reactive manner especially in the case of contentious seal populations which may be subject to management regimes. This will become of even greater importance in the future given the rise in ecosystem-based fisheries management, the changes in fishing pressures, as well as the continuing influence of climate change on fish stocks (Perry *et al.*, 2005; Graham & Harrod, 2009).

ACKNOWLEDGEMENTS

We thank Sue Wilson for access to data and literature. This work was supported by a studentship to Susie Brown (reference 2500121) from the Department of Agriculture and Rural Development, Northern Ireland.

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