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Seals, sandeels and salmon: diet of harbour seals in St. Andrews Bay and the Tay Estuary, southeast Scotland

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ABSTRACT: Harbour seal populations have declined by up to 40% around northern and eastern Britain since 2000 due to unknown causes; prey availability is one important factor that could be contributing to the decline. We estimate the diet and prey consumption of a population of harbour seals in southeast Scotland, using analysis of hard prey remains recovered from scats, to investigate change in the importance of sandeels over 6 yr spanning the local sandeel fishery closure. The study site includes Special Areas of Conservation for harbour seals as well as vulnerable salmon stocks. We estimate the extent of harbour seal predation on salmon in the area. In St. Andrews Bay, harbour seal diet was heavily dominated by sandeels, especially in winter and spring. Gadoids (whiting, cod) and flatfish (dab, plaice, flounder) were the other main prey. The proportion of sandeels in the diet was remarkably consistent over time (71 to 77%), but the average size of sandeels consumed increased following the closure of the fishery. In the Firth of Tay, sandeels were prevalent in winter, but the diet in the rest of the year was dominated by salmonids: salmon comprised 64% of the diet in summer and sea trout comprised 40% of the diet in autumn. Thus marked differences in diet were evident at a fine spatial scale. The effects of the sandeel fishery closure on harbour seals were equivocal, but harbour seals that haul out in SE Scotland are clearly dependent on sandeels; re-opening the fishery could thus have a negative impact and be inadvisable. We found evidence that local harbour seal predation could be impacting salmon stocks but the high uncertainty in estimates of seal diet and salmon stock size preclude the provision of management advice at this time.

KEY WORDS: Faecal sampling · Fisheries · North Sea · Prey availability · *Phoca vitulina* · Special Area of Conservation

INTRODUCTION

Significant declines of up to 40% have been observed in harbour seal populations around Britain since 2000, particularly around the northern isles of Shetland and Orkney and along the east coasts of Scotland and England (Lonergan et al. 2007). The cause of these declines is unknown but changes in prey availability resulting from competition with other marine mammals, especially grey seals, or the impacts of fisheries or environmental change are important factors to assess. The North Sea is a highly productive sea, supporting abundant populations of cetaceans (Hammond et al. 2002), pinnipeds (SCOS 2007) and seabirds (Mavor et al. 2005). It is also one of the most strongly exploited shelf seas (Heath 2005); fish stocks of a number of species have been heavily overfished (ICES 2007) and it has been rated as one of the most highly impacted marine areas by humans on the planet (Halpern et al. 2008). The ability to understand the effects of fisheries-induced changes in the abundance and size structure of fish stocks on the distribution and abundance of marine mammal top predators is of great interest (DeMaster et al. 2001). Modelling studies have begun to incorporate interactions among species as well as the effects of environmental factors such as changes in ocean productivity (Guénette et al. 2006). However, such studies are often hampered at a basic

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level by a fundamental lack of information on predator diet. In the North Sea, there is good recent information on the diet of grey seals (Hammond & Grellier 2006) and some relatively recent information on cetacean diet (Pierce et al. 2004, Santos et al. 2004, Windsland et al. 2008). However, most information on harbour seal diet in the North Sea is at least 10 yr old (Tollit & Thompson 1996, Tollit et al. 1997, Brown & Pierce 1998, Hall et al. 1998, Brown et al. 2001, Middlemas et al. 2006).

One heavily exploited fish that is important to many predator species in the North Sea is the lesser sandeel *Ammodytes marinus* (Furness & Tasker 2000). North Sea landings of sandeels fluctuated between 700 000 and 1 110 000 tonnes (t) from 1994 to 2002 but declined to around 200 000 t in 2007 (ICES 2007). Some seabirds are heavily reliant on sandeels in summer for feeding their chicks while in the nest (Wanless et al. 1998), and concern has been expressed about the effects on predators of local concentrated fishing effort in areas where they congregate (Furness & Tasker 2000). This concern and poor breeding success in seabirds in the Firth of Forth area led to the closure in 2000 of the sandeel fishery off southeast Scotland (Rindorf et al. 2000, Greenstreet et al. 2006). This fishery has remained closed.

The population of harbour seals that hauls out in southeast Scotland shares its at-sea distribution with the area targeted by the sandeel fishery (Sharples 2005). This harbour seal population is estimated to have declined by 12% per year (95% CI: –14 to –9%) since 2000 (Lonergan et al. 2007). Elsewhere along Scottish North Sea coasts, sandeels have been shown to be an important component of the diet of harbour seals (Tollit & Thompson 1996, Tollit et al. 1997, Brown & Pierce 1998, Brown et al. 2001) and grey seals (Hammond & Grellier 2006). If sandeels are also important prey for harbour seals in southeast Scotland, local depletion of sandeel aggregations may adversely impact the population as has been reported with seabirds (Frederiksen et al. 2004). Knowledge of harbour seal diet is therefore important to inform investigations into causes of the decline in harbour seal numbers in this area and the management of local sandeel fisheries.

In addition to interactions with fish stocks and fisheries in the open sea, harbour seals prey on salmon in estuaries and around the mouths of rivers. Salmon stocks have declined throughout Scotland in recent years (Middlemas 2003, FRS 2006) and pinniped predation is one of a number of possible contributing causes (Harwood & Croxall 1988, Middlemas 2003, Butler et al. 2008). In the River Tay, southeast Scotland, spring salmon stocks have declined and are considered vulnerable (Youngson et al. 2002, FRS 2006). Harbour seals regularly haul out on sandbanks in the Tay Estuary and are known to prey on salmon. The Tay River and its estuary contain Special Areas of Conservation for both harbour seals and salmon (EU codes UK0030311 and UK0030312, respectively). Obtaining quantitative information on the amount of salmon consumed by harbour seals in the Tay estuary is thus important for the management of both SACs and is also relevant to the conservation of other salmon stocks throughout Scotland.

In the present study we investigate the importance of sandeels in the diet of harbour seals in southeast Scotland and, in particular, determine whether their contribution to the diet increased following the closure of the Firth of Forth sandeel fishery. Secondly, we investigate the importance of salmon in the diet of harbour seals in the Firth of Tay and surrounding areas and consider the extent to which predation by harbour seals could be impacting the vulnerable salmon stock in this area. Implications of the results for understanding the decline in harbour seal abundance and for management of the SACs in this area are discussed.

MATERIALS AND METHODS

Scat collection. Scats were collected monthly within 2 h of low tide between February 1998 and June 2003 (no scats were collected February to October 2000, inclusive) from sand banks within St. Andrews Bay (Fig. 1). Harbour and grey seals haul out in these areas; scats were only collected from sites where only harbour seals were observed hauling out. Scats were collected from haul-out sites in the Firth of Tay (Fig. 1) from November 2000 to June 2003. Scats were collected in individual plastic bags, labelled and stored at –20°C until processed.

Sample processing. Scats were thawed and washed through a column of sieves with decreasing mesh size (5.0, 1.0, 0.5 and 0.25 mm) to collect the hard remains of prey. Prey species were identified from sagittal otoliths and cephalopod beaks using published identification guides (Clarke 1986, Härkönen 1986, Leopold et al. 2001) and an Intel Play QX3 computer microscope at either 10× or 60× magnification. Due to the level of erosion of otoliths, it was not always possible to identify them to species level, in which case they were identified to the lowest possible taxonomic grouping.

The length or width of each otolith was measured to the nearest 0.01 mm using digital callipers. Where large numbers of otoliths of a single species were found in a sample, a random subsample of 50 otoliths was measured. For cephalopod beaks the lower rostral lengths were measured.

Estimating diet composition and variability. Sample sizes in some months were small, so the data were

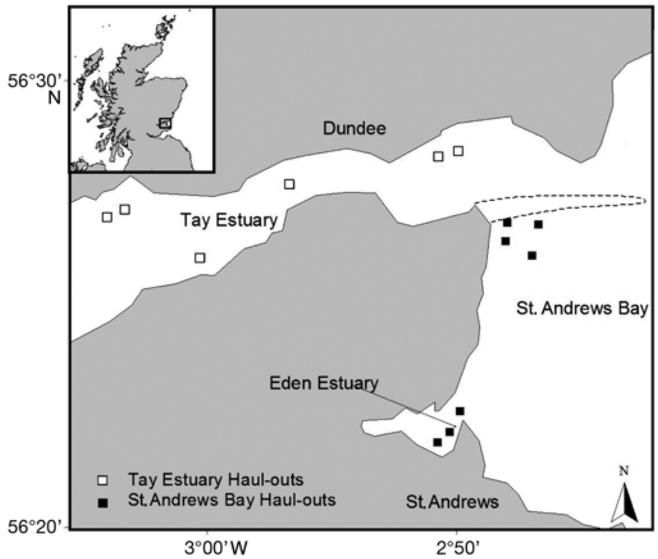

Fig. 1. Approximate locations of the main harbour seal haul-out sites in southeast Scotland. Dashed black line represents sandbar exposed at low tide

aggregated into quarters for analysis as follows: December (counted as part of first quarter of following year)–February (winter), March–May (spring), June–August (summer) and September–November (autumn). The numbers of scats containing hard remains ranged from 7 to 75 per quarter (Fig. 2).

Measurements of fish otoliths and cephalopod beaks recovered from scats were corrected for partial digestion using digestion coefficients derived experimentally for grey seals by Grellier & Hammond (2006). Digestion coefficients for salmonids were derived from similar experiments by Middlemas et al. (2004). Where species-specific digestion coefficients were not available, either group-specific values were taken (e.g. gadoid, flatfish), or the value of the most similar species with comparable otoliths. Fish or cephalopod weight was derived from estimated undigested otolith size using published species-specific regression relationships (Clarke 1986, Härkönen 1986, Leopold et al. 2001). For species where relationships were not available, relationships for the most similar prey were used. The unmeasured otoliths were assumed to be drawn from the same size distribution of the measured otoliths of that species within that scat. Prey length was estimated from undigested otolith size using published species-specific regression relationships (Leopold et al. 2001).

Species-specific numerical correction factors (NCFs) (Bowen 2000) derived for grey seals (Middlemas et al. 2004, Grellier & Hammond 2006) were used to correct for the proportion of structures that were completely digested. Grey seal NCFs were used because they were estimated from the most comprehensive captive experimental data available and little difference has been reported in the literature between harbour and grey seal NCFs (Bowen 2000). Where species-specific correction factors were not available, an average value for the taxonomic group was used. The weights of prey estimated for each otolith or beak were summed across species to give percentages in the diet, by weight, for each quarter in each year.

The variance of the estimated proportion of each prey species in the diet was estimated using non-

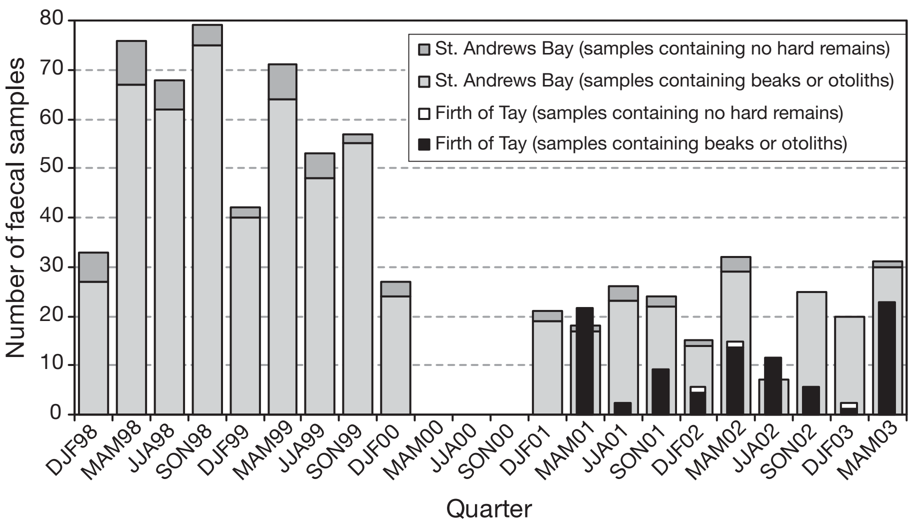

Fig. 2. Number of faecal samples collected from harbour seals in each quarter in St. Andrews Bay and the Firth of Tay, with and without hard remains present

Table 1. Number of otoliths recovered from each prey species by quarter from samples collected from St. Andrews Bay (excluding Firth of Tay). Species with less than 5 otoliths found in total are not included in the table; these include Norway pout *Trisopterus esmarki*, rockling *Ciliata mustela*, *Enchelyopus cimbrius*, *Gaidropsarus vulgaris*, hooknose *Agonus cataphractus*, unidentified Cottidae, smelt *Osmerus eperlanus*, eelpout *Zoarces vivaparus*, sea trout *Salmo trutta* and squid *Loligo* spp. n: number of scats

Common name	Scientific name	Year:	1998				1999				2000	2001				2002				2003		
		Quarter:	DJF	MAM	JJA	SON	DJF	MAM	JJA	SON	DJF	DJF	MAM	JJA	SON	DJF	MAM	JJA	SON	DJF	MAM	Total
		n =	27	67	62	75	40	64	48	55	24	19	17	23	22	14	29	7	25	20	30	668
Sandeel	*Ammodytes marinus*		5641	3947	2356	7978	12148	3630	2571	5385	7593	2302	1789	1959	2063	1676	5117	32	1651	5106	4032	76976
Cod	*Gadus morhua*		0	32	1	40	11	3	52	128	10	3	22	4	2	1	3	2	7	0	0	321
Haddock	*Melanogrammus aeglefinus*		1	9	7	16	20	10	0	2	15	0	1	0	0	0	4	0	6	2	1	94
Pollock	*Pollachius pollachius*		0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	1	0	0	6
Saithe	*Pollachius virens*		0	0	0	0	0	0	0	0	0	0	0	0	21	0	0	1	4	0	25	51
Whiting	*Merlangius merlangus*		8	241	321	535	69	151	46	987	28	420	192	14	40	3	58	2	41	11	41	3208
Bib	*Trisopterus luscus*		0	4	0	1	0	3	0	1	0	0	0	0	0	0	0	1	0	0	3	13
Dab	*Limanda limanda*		0	42	54	107	4	13	107	178	2	14	11	27	39	2	121	1	8	3	44	777
Dover sole	*Solea solea*		0	5	2	3	0	1	0	18	0	0	0	0	0	0	0	0	0	0	0	29
Flounder	*Platichthys flesus*		0	7	4	10	0	20	59	8	0	4	6	48	81	2	52	1	4	0	59	365
Plaice	*Pleuronectes platessa*		0	26	19	69	1	23	78	248	0	19	4	21	14	1	18	0	18	9	15	583
Plaice/flounder			3	60	33	70	0	9	56	58	0	4	1	2	0	0	0	2	2	0	4	304
Lemon sole	*Microstomus kitt*		0	0	2	5	0	3	4	4	0	0	0	0	0	0	0	0	0	0	0	18
Turbot	*Scophthalmus maximus*		0	0	1	0	0	0	3	0	0	0	0	1	0	0	0	0	0	0	0	5
Unid. flatfish			0	2	23	13	2	3	154	117	1	25	28	47	46	0	663	0	103	5	22	1254
Witch	*Glyoptocephalus cynoglossus*		0	0	0	0	1	1	0	1	0	0	1	0	11	0	0	0	4	1	5	25
Herring	*Clupea harengus*		0	10	1	23	1	4	2	5	0	0	0	2	0	1	1	186	0	0	0	236
Sprat	*Sprattus sprattus*		1	0	0	2	4	3	4	0	4	0	0	0	0	0	0	0	1	5	0	24
5-bearded rockling	*Ciliata mustela*		1	0	0	0	20	0	0	1	20	0	0	0	0	0	0	0	0	0	0	42
Bullrout	*Myoxocephalus scorpius*		0	2	6	3	5	2	2	7	0	0	0	0	0	0	0	0	0	0	0	27
Butterfish	*Pholis gunnellus*		3	56	371	87	1	15	151	6	1	30	0	0	0	0	0	0	0	0	0	721
Dragonet	*Callionymus lyra*		0	2	4	16	1	3	0	63	0	1	0	0	1	1	2	0	1	0	0	95
Goby	*Pomatoschistus microps*		0	7	0	19	4	2	0	14	4	0	12	13	47	0	33	1	2	2	58	218
Lesser octopus	*Eldone cirrhosa*		0	0	0	0	0	0	0	0	0	2	2	0	0	0	0	0	6	1	0	11
Poor cod	*Trisopterus minutus*		0	0	0	0	6	7	0	0	6	0	4	0	0	0	4	0	1	0	0	28
Salmon	*Salmo salar*		0	0	0	3	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	5

parametric bootstrap resampling, with replacement, of species weights to estimate sampling variability, and parametric resampling of all conversion and correction coefficients to estimate measurement error (Hammond & Rothery 1996). The 95% confidence limits were obtained as the 2.5th and 97.5th percentile of the distribution of estimates from 1000 bootstrap resamples.

Estimating prey consumption. To estimate prey consumption of each prey species *j*, the energy represented in the sample of scats was equated with harbour seal energy requirements for the population over that period. For each quarter of the year, estimated weights for each prey species, w_j (g), were converted to their energy value, e_j (cal), using published energy densities E_j (cal g^{-1}) (Murray & Burt 1977):

$$e_j = w_j \times E_j$$

which were expressed as the proportion of total energy represented in the sample:

$$P_j = \frac{e_j}{\sum e_j}$$

The weight consumed of each prey species, C_j, (t) was then estimated as:

$$C_j = \frac{P_j \times R \times d \times \mathrm{N}}{E_j \times 1000}$$

where *R* is the estimated daily energy requirement of an average harbour seal (4680 kcal, Härkönen & Heide-Jørgensen 1991), *d* is the number of days in the quarter, and N is the estimated number of seals in the population: 544 (95% CI: 493–630) in St. Andrews Bay (excluding Tay estuary) and 301 (95% CI: 273–348) in the Tay estuary (Sharples et al. 2009).

To obtain totals across seasons, bootstrapped estimates of consumption from each replicate were summed and percentiles taken from the resulting values.

The age structure of the population was not taken into account in estimating consumption because energetic requirement has been found to be proportional to the total population size despite changes in population structure (Härkönen & Heide-Jørgensen 1991). The present study was based on a branding study before and after the 1988 phocine distemper virus outbreak, based on measurements of seasonal changes in mass and estimates of the energy required for maintenance and growth. Average daily energy requirement was calculated as 4680 kcal per seal in both 1979 and 1989, despite considerable changes in the population structure.

RESULTS

Faecal samples collected and hard parts recovered

Harbour seal haul-out sites in St. Andrews Bay and the Firth of Tay were visited 162 times between February 1998 and July 2003. A total of 809 scats were collected, 749 (92.6%) of which contained fish otoliths and/or cephalopod beaks: 88 401 otoliths and beaks were recovered and 31 different prey species identified (Tables 1 & 2). In the Firth of Tay, scats were collected only in the second half of the study period and were analysed separately.

Table 2. Number of otoliths recovered from each prey species by quarter from samples collected from the Firth of Tay. Species with less than 5 otoliths found in total are not included in the table, these include: cod, saithe, pollack, dragonet, brill (*Scophthalmus rhombusc*), turbot, witch and haddock/saithe. n: number of scats

Species	2001			2002				2003		Total
	MAM n = 19	JJA n = 2	SON n = 8	DJF n = 4	MAM n = 12	JJA n = 10	SON n = 5	DJF n = 1	MAM n = 20	n = 81
Sandeel	152	0	50	350	168	317	197	546	222	2002
Haddock	5	0	0	0	12	0	0	0	7	24
Whiting	101	0	1	0	110	0	5	0	17	234
Dab	0	0	1	0	0	2	0	0	8	11
Plaice	3	7	8	0	8	3	0	0	19	48
Flounder	29	3	4	0	6	66	3	0	58	169
Plaice/flounder	4	0	5	0	0	0	0	0	0	9
Unid. flatfish	5	0	0	0	8	3	1	0	7	24
Herring	2	0	21	0	7	36	0	0	0	66
Mackerel	8	0	0	0	0	0	0	0	0	8
Butterfish	9	0	4	0	2	0	27	0	123	165
Eelpout	0	0	0	0	0	0	15	0	0	15
Goby	4	2	0	0	0	14	0	0	34	54
Salmon	1	0	0	0	0	7	0	0	39	47
Sea trout	0	0	1	0	15	0	0	0	0	16
Smelt	53	0	0	0	20	0	0	0	0	73

Sandeel otoliths were by far the most numerous (78 978 recovered in total) prey items, followed by whiting (3442) and otoliths from flatfish that were too small and too digested to identify to species level (1278) (Tables 1 & 2). Cephalopod beaks were rare; only 2 squid beaks and 11 octopus beaks were recovered (Table 1). A total of 52 salmon and 18 sea trout otoliths were recovered (Tables 1 & 2).

Harbour seal diet in St. Andrews Bay

Ten prey species made up more than 95% of the total prey consumed by mass in any year or season (Tables 3 & 4). Sandeels were the dominant prey across all quarters and years, contributing 71 to 77% by weight in each year. The contribution of sandeels was highest in winter and spring (81 to 94% of the diet) and lower in summer and autumn (63%). The reduced sandeel consumption in summer and autumn was compensated for primarily by higher percentages of gadoids in autumn, flatfish in summer and autumn and pelagic fish (herring) in summer (Fig. 3).

The mean length of sandeels recovered increased from 12.57 ± 0.03 cm (±SE) before 2000 (the year of the fishery closure) to 13.31 ± 0.04 cm after 2000. The difference in the distributions of the lengths of sandeels consumed by harbour seals before and after the sandeel fishery closure was highly significant (Kolmogorov-Smirnov, $D = 0.104$, $p < 0.001$) (Fig. 4).

The dominant gadoid in the diet was whiting, followed by cod (Tables 3 & 4). Flatfish consumed were

Table 3. Estimated annual percentage by mass in the diet of main prey species (contributing >5% by weight within any quarter) for harbour seals in St. Andrews Bay, averaged across seasons for each year (95% CI). n: total number of samples

Species	1998 n = 231	1999 n = 207	2001 n = 81	2002 n = 75
Sandeel	76.9 (72.9–86.8)	72.7 (60.9–80.7)	71.2 (53.7–83.9)	75.5 (60.4–91.4)
Cod	3.4 (1.05–5.79)	5.41 (2.36–8.81)	1.31 (0.03–5.17)	2.06 (0.04–7.1)
Whiting	3.94 (1.68–5.41)	4.93 (1.73–7.88)	16.5 (3.36–28.7)	1.89 (0.73–8.99)
Dab	1.38 (0.53–2.38)	3.07 (1.23–4.87)	1.69 (0.5–6.3)	1.15 (0.19–2.46)
Flounder	0.98 (0.30–1.46)	2.18 (0.76–4.4)	2.14 (0.9–5.13)	0.56 (0.07–1.4)
Plaice	1.40 (0.46–2.08)	1.66 (0.39–3.39)	1.81 (0.14–6.14)	0.93 (0.01–3.98)
Plaice/flounder	2.35 (0.76–3.36)	1.8 (0.44–3.15)	0.02 (<0.01–0.09)	1.34 (<0.01–9.9)
Unid. flatfish	0.56 (0.04–1.19)	0.88 (0.22–1.39)	0.93 (0.35–3.27)	2.21 (0.16–7.85)
Herring	0.36 (0.11–0.76)	0.65 (0.06–1.65)	0.26 (<0.01–1.47)	13.2 (<0.01–22.7)
Bullrout	1.71 (0.32–3.92)	0.26 (0.08–1.14)	0	0
Butterfish	2.37 (0.3–5.17)	1.06 (0.17–2.9)	0.41 (<0.01–2.94)	0
Salmon	0.68 (<0.01–1.89)	1.9 (<0.01–6.87)	2.15 (<0.01–7.3)	0
Other	3.97 (1.26–11.13)	3.5 (1.02–21.50)	1.58 (0.16–13.64)	1.16 (0.03–10.67)

Table 4. Estimated seasonal (quarterly) percentage by mass in the diet of main prey species (contributing greater than 5% by weight within any one quarter) for harbour seals in St. Andrews Bay, averaged across years for each season (95% CI). n: number of samples

Species	DJF n = 144	MAM n = 207	JJA n = 140	SON n = 177	Mean annual percentage
Sandeel	94.4 (86.6–97.8)	80.9 (68.9–88.9)	62.5 (48.3–80.2)	63.1 (49.5–75.6)	69.5 (75.3–85.6)
Cod	0.51 (0.21–2.06)	1.86 (0.49–3.26)	1.28 (0.26–3.66)	8.12 (3.01–14.2)	3.44 (0.99–5.80)
Whiting	3.17 (0.42–9.29)	6.92 (2.18–10.7)	2.81 (0.86–10.3)	11.5 (2.95–19.7)	7.12 (1.60–12.5)
Dab	0.19 (0.02–0.85)	1.31 (0.55–4.02)	2.53 (0.77–6.04)	3.08 (1.39–4.48)	2.08 (0.68–3.84)
Plaice	0.11 (0.01–0.25)	0.47 (0.18–0.83)	2.47 (0.47–6.74)	2.63 (0.59–5.96)	1.66 (0.31–3.44)
Flounder	0.02 (<0.01–0.08)	1.27 (0.57–4.35)	2.73 (1.11–5.2)	2.02 (0.85–3.85)	1.76 (0.63–3.37)
Plaice/flounder	0.02 (<0.01–0.2)	1.19 (0.23–2.02)	2.9 (0.77–11.43)	1.1 (0.19–1.98)	1.52 (0.30–3.91)
Unid. flatfish	0.16 (0.01–0.72)	1.64 (0.2–6.54)	1.28 (0.42–2.62)	1.12 (0.21–2.07)	1.05 (0.21–2.99)
Herring	0.51 (<0.01–2.16)	0.12 (0.02–0.27)	13.07 (0.22–22.7)	0.45 (0.12–0.91)	4.14 (0.09–6.50)
Bullrout	0.07 (<0.01–0.19)	0.03 (<0.01–0.06)	1.47 (0.2–3.31)	0.35 (0.12–1.62)	0.56 (0.08–1.19)
Butterfish	0.28 (<0.01–1.98)	0.19 (0.01–0.41)	3.07 (0.57–6.2)	0.12 (0.01–0.35)	1.07 (0.15–2.24)
Salmon	0	1.52 (<0.01–5.5)	0	2.82 (<0.01–8.05)	1.27 (<0.01–3.39)
Other	0.56 (0.07–2.65)	2.58 (0.63–13.02)	3.89 (0.63–21.01)	3.59 (1.3–23.22)	4.83 (0.44–14.98)

primarily common dab, flounder and plaice; however, a large number of flatfish otoliths were too small or eroded to identify to species. Salmon contributed little to the diet during spring, autumn and summer, averaging 1.27 % (range = <0.01 to 3.39) (Table 4).

Estimates of annual consumption highlight the importance of sandeels in the diet, which, at an average of 548 t (95 % CI: 457–678 t), was an order of magnitude greater than any other species (Table 5). Gadoid consumption was estimated at 50 t (95 % CI: 13–125 t) of whiting and 26 t of cod (95 % CI: 8–51 t) (Table 5). Approximately 34 t of plaice and founder were estimated to be consumed annually. Salmon consumption in this area was estimated at 7 t yr^{-1} with a very wide confidence interval (95 % CI: <0.01–30 t).

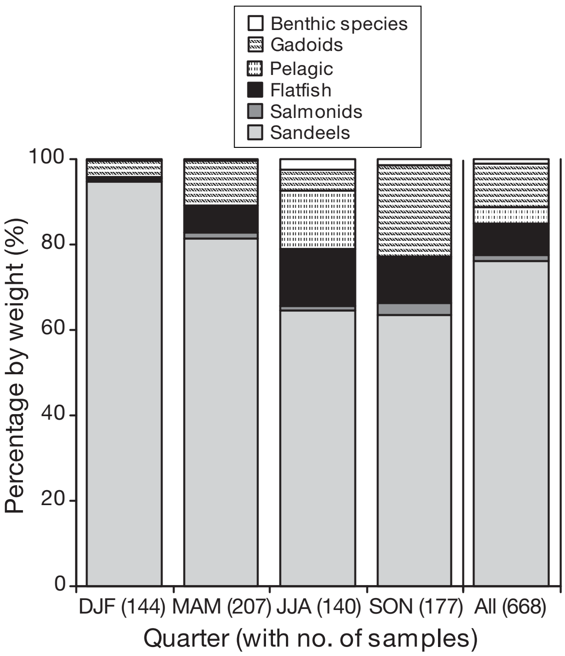

Fig. 3. Average seasonal percentage by mass of each prey type in the harbour seal diet for St. Andrews Bay

Harbour seal diet in the Firth of Tay

The diet of harbour seals that hauled out in the Firth of Tay was markedly different to that in St. Andrews Bay (Table 6, Fig 5). Salmonids were the dominant prey type, except in winter, comprising an estimated 78 % of the diet in spring (salmon 32 %, smelt 17 % and sea trout 28 %), 47 % in summer (salmon only) and 40 % in autumn (sea trout only), but all with very wide confidence intervals (Table 6).

All salmon otoliths were recovered from only 5 scats and all sea trout otoliths from only 2 scats. Of the 52 salmon otoliths recovered, 21 were estimated to come from fish no greater than 11 cm in length; these were likely to be salmon smolt leaving the river (Fig. 6). The 29 otoliths from fish with estimated lengths between 30 and 65 cm were likely to be returning one-sea-winter grilse. Two otoliths were estimated to be from fish >85 cm; these were likely to be returning multi-sea-winter adults. The weights estimated from otoliths in these size classes were in the proportions <2, 75 and 23 %, respectively. These are equivalent to the proportions of each size class

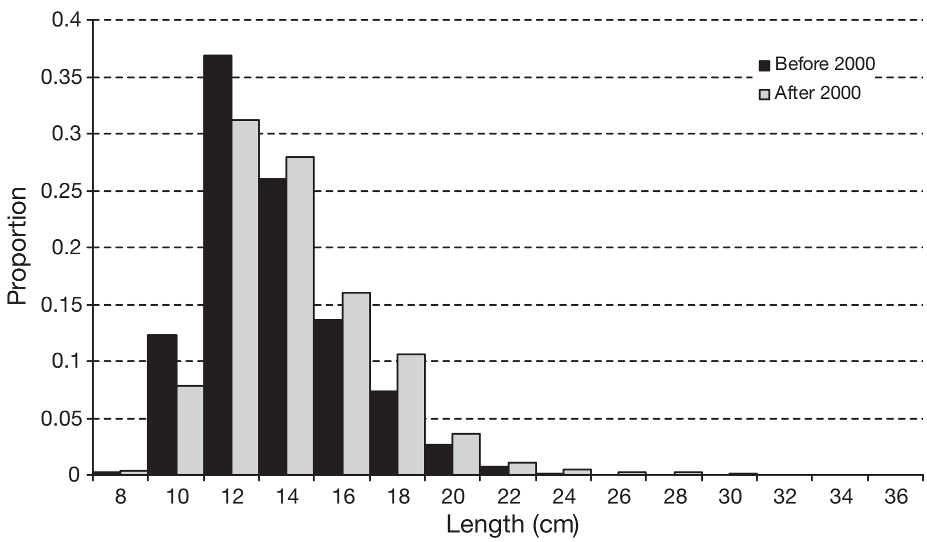

Fig. 4. Lengths of sandeels estimated from otoliths recovered in harbour seal scats before and after the 2000 sandeel fishery closure

Table 5. Estimated average quarterly and annual fish consumption (tonnes) by harbour seals in St. Andrews Bay (95% CI)

Species	DJF	MAM	JJA	SON	Mean annual consumption
Sandeel	163 (124–197)	148 (135–183)	116 (95.6–169)	121 (103–161)	548 (457–678)
Cod	0.9 (0.34–3.9)	3.5 (0.95–6.95)	2.42 (0.5–8.09)	19.3 (6.23–31.9)	26.2 (8.02–50.9)
Whiting	5.86 (0.75–24.3)	13.1 (4.29–24.1)	5.15 (1.77–26.4)	25.5 (6.16–50.5)	49.6 (13.0–125)
Dab	0.34 (0.02–1.95)	2.4 (1.07–9.11)	4.64 (1.61–12.4)	8.38 (3.02–10.7)	15.7 (5.74–34.1)
Plaice	0.17 (0.02–0.47)	0.9 (0.36–1.74)	4.62 (0.93–14.9)	6.11 (1.27–13.2)	11.8 (2.57–30.3)
Flounder	0.03 (<0.01–0.22)	2.33 (1.1–9.82)	5.18 (2.21–11.2)	3.75 (1.71–9.2)	11.3 (5.03–30.4)
Plaice/flounder	0.03 (<0.01 0.37)	2.24 (0.43–4.14)	5.25 (1.50–30.1)	3.28 (0.41–4.87)	10.8 (2.34–39.4)
Unid. flatfish	0.25 (0.02–1.51)	2.93 (0.41–14.2)	2.42 (0.86–5.41)	2.85 (0.47–4.52)	8.47 (1.77–25.6)
Herring	0.85 (<0.01–1.17)	0.24 (0.05–0.54)	21.9 (0.44–42.3)	1.02 (0.24–1.97)	24.0 (0.74–44.9)
Bullrout	0.12 (<0.01–0.36)	0.04 (<0.01–0.14)	2.91 (0.38–7.43)	0.53 (0.24–3.71)	3.6 (0.63–11.6)
Butterfish	0.51 (<0.01–4.14)	0.36 (0.02–0.85)	5.99 (1.12–14.0)	0.27 (0.01–0.78)	7.13 (1.14–19.7)
Salmon	0	2.84 (<0.01–12.4)	0	4.64 (<0.01–17.8)	7.48 (<0.01–30.2)

Table 6. Estimated seasonal (quarterly) percentage by mass in the harbour seal diet of the main prey species (contributing >5% by weight) in the Firth of Tay (95% CI). n: number of scats

Species	DJF n = 5	MAM n = 51	JJA n = 12	SON n = 13	Mean annual percentage
Sandeel	100	11.4 (4.04–42.2)	19.9 (1.14–47.1)	48.4 (29.6–80.4)	44.93 (33.7–67.4)
Whiting	0	3.76 (1.68–12.5)	0	2.66 (<0.01–21.4)	1.61 (0.42–8.47)
Flounder	0	2 (0.65–16.6)	13.8 (0.08–46.5)	1.1 (0.04–7.76)	4.23 (0.19–17.7)
Salmon	0	32.3 (<0.01–46.2)	64.3 (<0.01–87.0)	0	24.15 (<0.01–33.3)
Sea trout	0	17.1 (<0.01–28.8)	0	40.0 (<0.01–48.1)	14.28 (<0.01–19.2)
Smelt	0	28.4 (0.64–48.3)	0	0	7.1 (0.16–12.1)
Other	0	5.04 (0.63–34.52)	2.0 (<0.01–36.4)	7.84 (<0.01–48.4)	3.72 (<0.01–29.8)

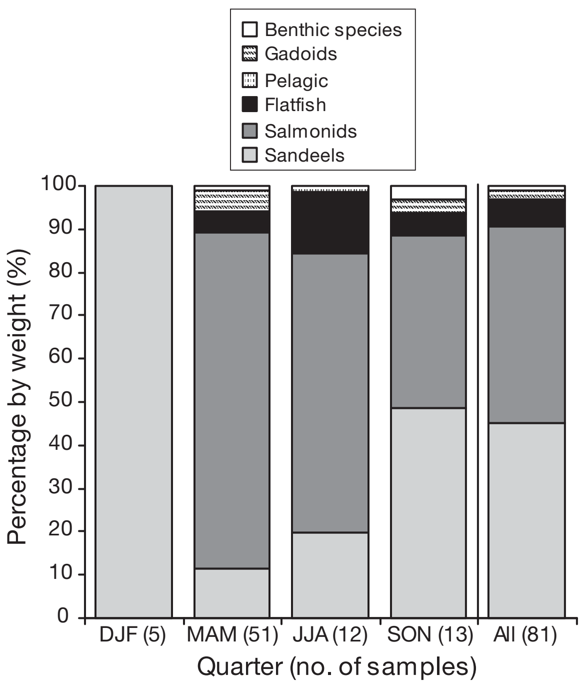

Fig. 5. Average seasonal percentage by mass of each prey type in the harbour seal diet for all samples collected in the Firth of Tay

consumed. Note that estimates of length and weight are subject to uncertainty so the above calculations are approximate only. However, consumption of smolts, which have a low survival rate (8.9%, Jonsson et al. 2003), is clearly minor; most of the salmon consumed were in the size range taken by the rod and line fishery for mature fish.

In contrast to St. Andrews Bay, harbour seals that hauled out in the Firth of Tay were estimated to consume substantial quantities of salmon in spring and summer — 50 and 96 t, respectively — but with very wide confidence intervals (Table 7).

Sandeel, flounder and whiting were the only other prey species recovered. Estimated sandeel consumption was highest in winter and lowest in spring and summer (Table 7).

DISCUSSION

Methodology

The advantages and disadvantages of using fish otoliths and cephalopod beaks collected from scats to

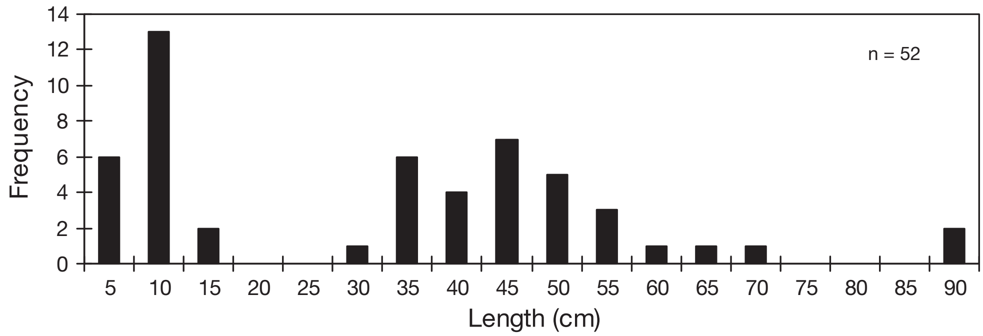

Fig. 6. Lengths of salmon estimated from otoliths recovered in harbour seal scats. n: number of otoliths recovered

Table 7. Estimated average quarterly and annual fish consumption (tonnes) by harbour seals in the Firth of Tay (95% CI)

Species	DJF	MAM	JJA	SON	Mean annual consumption
Sandeel	114 (79.3–128)	18.1 (5.88–53.0)	29.8 (1.47–49.7)	59.0 (31.0–91.1)	221 (118–322)
Whiting	0	5.97 (2.32–17.3)	0	3.93 (0–31.6)	9.9 (2.32–48.9)
Flounder	0	3.14 (0.89–25.3	20.7 (0.09–71.1)	1.34 (0.04–10.1)	25.2 (1.02–106)
Salmon	0	50.4 (<0.01–64.6)	96.4 (<0.01–137)	0	14 (<0.01–203)
Sea trout	0	27.0 (<0.01 –44.2)	0	61.6 (<0.01 –80.5)	88.5 (<0.01–125)
Smelt	0	45.3 (0.74–73.9)	0	0	45.3 (0.74–73.9)

assess diet have been discussed extensively in the literature (Jobling & Breiby 1986, Harvey 1989, Pierce & Boyle 1991, Cottrell et al. 1996). One important issue is the need to account appropriately for partial and complete digestion of hard prey remains (Bowen 2000, Grellier & Hammond 2006). Studies that fail to do this are prone to substantial bias.

In the present study we used NCFs and digestion coefficients derived from captive experiments with grey seals (Middlemas et al. 2004, Grellier & Hammond 2006) and assumed that these NCFs are applicable to harbour seals. We preferred these to the limited available information on harbour seals for a number of reasons. First, the grey seal experiments provided robust, consistent information for a wide range of fish found around Britain, including all major prey of harbour seals. Second, except for the salmonids (Middlemas et al. 2004), these experiments did not use a carrier species to deliver otoliths, which has been found to bias the resultant NCFs and digestion coefficients for some prey species (Grellier & Hammond 2005). Third, in a review of pinniped digestion rate studies, Bowen (2000) suggested that there was little difference in NCFs between harbour and grey seals. Ideally, similar experiments should be conducted with harbour seals to eliminate potential bias. Until these can be undertaken, the digestion coefficients and NCFs for grey seals are acceptable and the best proxies.

The confidence intervals around our estimates of diet composition and annual consumption are wide in most cases. This is especially true for results from the Firth of Tay, which are based on a relatively small number of scats. The results are precise only for sandeels in the diet of harbour seals foraging from St. Andrews Bay. This is because effective sample size is a function not only of the number of scats but also the number of recovered hard remains of each species. The confidence intervals are also wide because we have included all of the several known sources of variability in our estimates, including interannual and interseasonal variation. Whilst aiming to provide precise information on seal diet to inform conservation and management, it is essential that we convey the true extent of uncertainty in our knowledge.

Harbour seal diet composition in the North Sea

Studies of harbour seal diet in the northwestern North Sea have shown regional variation, but sandeels and whiting were dominant prey species in all regions. In the Moray Firth, Tollit & Thompson (1996) found the diet to be dominated by sandeels (47%), lesser octopus (26%) and whiting (6%). In Shetland, Brown & Pierce (1998) found that the diet mainly comprised sandeels (29%), whiting (25%), saithe (11%) and pelagic fishes (14%). These studies were conducted in different years and some of the variation observed may thus be temporal rather than regional. Our results accord well with other estimates of harbour seal diet in eastern and northern Scotland in terms of dominant prey species (sandeel and whiting). However, the percentage of sandeels in the diet of harbour seals off southeast Scotland was considerably greater at an average of 73%. Elsewhere in the North Sea, off eastern England (Hall et al. 1998) and in the Skagerrak (Härkönen & Heide-Jørgensen 1991), whiting also featured strongly in the diet of harbour seals but sandeels did not.

Seasonal variation in harbour seal diet has typically been attributed to variation in prey availability (Tollit & Thompson 1996, Brown & Pierce 1998, Hall et al. 1998, Middlemas 2003, Wilson & McMahon 2006). In the present study, sandeels were the dominant prey throughout each year, but significantly more were consumed in winter and spring. In the Moray Firth, northeast Scotland, sandeels were the overall dominant prey species with annual and seasonal differences, and octopus were dominant prey in some summers (Tollit & Thompson 1996). Clupeids dominated in winter when they were locally abundant (Pierce et al. 1991, Thompson et al. 1991).

Seasonality in the diet of seals aggregating in rivers in response to abundance of salmon has been observed previously in the Moray Firth (Middlemas et al. 2006). Sample sizes were insufficient to characterise seasonal patterns in salmon consumption in the present study.

Interactions with fisheries for sandeels

The average estimated annual consumption of sandeels by harbour seals hauled out in St. Andrews Bay and the Tay estuary was around 770 t (Tables 5 & 7). The fishery on the southeast Scotland aggregation of sandeels caught a total of between 20000 and 100000 t annually over the course of its operation between 1990 and 1999 (Rindorf et al. 2000). Studies of the life-history characteristics of different sandeel aggregations throughout the North Sea have shown that sandeels in the southeast Scotland aggregation are relatively slow-growing—approximately half the mean weight-at-age of other aggregations in the North Sea (Wright & Bailey 1996). Because fecundity scales with size, the southeast Scotland aggregation has a lower age-specific fecundity making it more susceptible to collapse (Wanless et al. 2004).

We found no change in the contribution of sandeels to the diet from 2 yr before to 2 yr after the closure of the local fishery; indeed, it was remarkably consistent from year to year at 71 to 77% of the diet (Table 3). Studies of sandeel biomass prior to and after the fishery closure in this area found an increase in abundance of age 1+ fish, especially Greenstreet et al. (2006). We did find a significant increase of about 6% in the length of sandeels recovered in scats after the fishery closure. The energy value of the sandeel increases at approximately the 4th power of length (Wanless et al. 2004), equating to a 26% increase in the total energy per fish. The large proportion of sandeels in the diet of harbour seals in this area means that this could have a substantial effect on the balance between the costs and benefits of foraging in this population. In studies of grey seal diet in 1985 and 2002, a reduction in the size of sandeel consumed was found across the whole North Sea (Hammond & Grellier 2006).

The effects of the sandeel fishery closure on harbour seals were thus equivocal, but could the decline in harbour seals observed in this area and more widely (Lonergan et al. 2007) still be linked to sandeel abundance? Sandeel stocks in the North Sea declined to historically low levels in 2004–2006 (ICES 2007). In addition, it has been suggested that the southeast Scotland sandeel aggregation is driven by bottom-up effects; there is a positive correlation between the abundance of sandeel larvae and plankton, and an influence of temperature on plankton abundance resulting in reduced sandeel recruitment in warm winters (Frederiksen et al. 2004). Harbour seals that haul out in southeast Scotland are clearly dependent on sandeels; re-opening the fishery could thus have a negative impact and be inadvisable. Competition with other top predators could also be adversely impacting the population. Grey seals in particular have increased in recent years and there is a strong dietary overlap with harbour seals, sandeels being the dominant prey of grey seals on the east coast of Scotland (Hammond & Grellier 2006).

Importance of salmon in harbour seal diet

Salmon made up a substantial component of the diet of harbour seals hauled out in the Tay estuary (Table 7), but not of those outside the estuary where consumption was an order of magnitude lower (Table 5), showing marked differences in diet at a fine spatial scale. This pattern of localised foraging on salmon within rivers has also been observed in harbour seals in Oregon (Wright et al. 2007). Our results imply that seals are foraging on salmon within the Tay River or estuary in close proximity to the haul-out sites. Our method assumes that the sample of scats is representative of the overall diet. If the remains of some prey species are less likely to be found because scats containing them are less likely to be collected, this could lead to bias. We are unable to investigate this for harbour seals, but Smout (2006) found no bias in estimates of grey seal diet as a result of foraging offshore and species-specific differences in passage times of prey remains through the gut.

There are no robust estimates of salmon stock size but estimates can be made from the rod and line catches and assumptions of the catchability of salmon by fishermen in different seasons. Rod and line catches of salmon are available for the Rivers Tay, Earn and Eden combined (the Tay being the main salmon fishing river). Stock size can be estimated by assuming that 30% of spring fish are caught by anglers (Youngson et al. 2002) and 11% during autumn and summer (Crozier & Kennedy 2001). Based on these assumptions, the average stock size estimate for 2001 to 2003 for the Rivers Tay, Earn and Eden combined was 226 t (S. Middlemas pers. comm.). Annual consumption of salmon by harbour seals in this area was estimated to be 147 t (95% CI: <0.01–203). However, our sample sizes were small—only 81 scats were collected across 3 yr in the Tay estuary—and salmon otoliths were found in only 5 scats (mostly in 2 scats collected in the summer of 2003), resulting in the very wide confidence intervals associated with the estimates of consumption by harbour seals. Thus, although the estimate of consumption is high relative to the estimate of stock size, the uncertainty in this comparison is also very high.

Almost all of the estimated consumption is likely to be of mature fish that are also targeted by the rod and line fishery, a result which has implications for the impact of harbour seal predation on the local stocks and for how it is perceived in the context of the fishery. The high statistical uncertainty associated with the results precludes the provision of any management advice. However, the present study does provide evidence that harbour seal predation on mature salmon is likely non-trivial in this area and could have the potential to impact the stock; this information should be of some interest to the management group of the SAC for salmon in the River Tay. Further work to increase sample sizes would decrease the uncertainty in the results of the present study, and similar studies in other areas are necessary to determine the generality of these results.

Grey seals are also present in the St. Andrews Bay area, particularly during summer, but the diet of grey seals estimated for the east coast of Scotland does not feature salmon (Hammond & Grellier 2006). A small number (approximately 30) of grey seals have been observed to haul out within the Tay estuary in spring and summer (R. J. Sharples pers. obs.). These animals could be targeting salmon but scat samples have not been collected from this site.

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