The diet of European Shag *Phalacrocorax aristotelis*, Black-legged Kittiwake *Rissa tridactyla* and Common Guillemot *Uria aalge* on Canna during the chick-rearing period 1981–2007

Swann, R. L.[1]*, Harris, M. P.[2] & Aiton, D. G.[3]

**Correspondence author. Email: robert.swann@homecall.co.uk*
[1] *14 St Vincent Road, Tain, Ross-shire IV19 1JR, UK;* [2] *Centre for Ecology and Hydrology, Hill of Brathens, Banchory, Aberdeenshire AB31 4BY, UK (current address: CEH Bush Estate, Penicuik, Midlothian EH26 0QB, UK);* [3] *14 Buckstone Howe, Edinburgh EH10 6XF, UK.*

Abstract
Chick diet of European Shags *Phalacrocorax aristotelis*, Black-legged Kittiwakes *Rissa tridactyla* and Common Guillemots *Uria aalge* at Canna was investigated over a 27-year period. The diet was mainly composed of Sprats *Sprattus sprattus*, Lesser Sandeels *Ammodytes marinus* and members of the Gadidae (a variety of species but mainly *Trisopterus* spp. and Whiting *Merlangius merlangus*). Other groups (ten families of fish, crustaceans, cephalopod molluscs and polychaete worms) were of minimal importance. Lesser Sandeels dominated the diet of young Black-legged Kittiwakes and European Shags, Sprats the diet of young Common Guillemots, whereas gadid otoliths were by far the commonest items found in pellets regurgitated by older European Shags. There were few significant temporal changes in species composition or the size of prey taken over the 27 years and the results confirm earlier findings that gadids are a normal and important part of the diet of seabirds at this colony.

Introduction

Over the last 40 years seabird populations in Britain have undergone major changes. Up to the late 1980s numbers were tending to increase, but since then major declines have been observed (Mavor *et al*. 2006). For some species, e.g. Black-legged Kittiwake *Rissa tridactyla*, changes in numbers are thought to be linked to changes in food supply, particularly sandeels (Ammodytidae, mainly Lesser Sandeels *Ammodytes marinus*) (Frederiksen *et al*. 2004). Several studies on seabird diet undertaken at colonies in the North Sea and Shetland have shown the importance of sandeels in the diets of seabirds in these areas (Pearson 1968; Monaghan 1992; Daunt *et al*. 2008), but relatively little information is available on the food of seabirds at colonies in the west of Britain. Swann *et al*. (1991) summarised information on the food of seabirds on Canna during the chick-rearing periods 1981–90, and showed that although sandeels were the main species taken by European Shag *Phalacrocorax aristotelis*, Black-legged Kittiwake and Common Guillemot *Uria aalge*, in contrast to some other places gadids (Gadidae, cod-fishes) and clupeids (Clupeidae, Herring *Clupea harengus* and Sprats

Sprattus sprattus) also featured highly in the diet. This paper updates information on the diet of these seabirds on Canna up to 2007 and compares the findings with information from other locations in northern Britain.

Methods

Canna (57°03'N, 6°32'W) is situated in the southern Minch in western Scotland and annual visits were made to the colony to ring and monitor seabirds in the period 1981–2007. Three visits were made each year, one for five days in late May, one for seven days in late June/early July and one for five days in late July/early August. Regurgitations were collected from young and adults feeding chicks of Black-legged Kittiwake (hereafter 'Kittiwake') and European Shag ('Shag'). Fish being carried back to chicks by adult Common Guillemots ('Guillemot') were also collected. Adult Guillemots returning with fish to the colony were targeted and captured and the fish they dropped were collected (Swann *et al*. 1991). Kittiwake and Guillemot samples were mainly collected between 28 June and 10 July, whilst Shag samples were collected, if available, on all visits. The contents of regurgitates and pellets were broken up in warm water or were digested in a warm solution of biological washing powder (biotex), fish present were identified, using otoliths where necessary (Härkönen 1986) and any intact specimens were measured. Sandeels, mostly if not all Lesser Sandeels, were classified as 0-group (young of the year) or older, based on the absence or presence of annual growth rings in otoliths (ICES 1995). Fish from Guillemots were identified, using otoliths where necessary, and the majority were measured (tip of snout to tip of tail) and weighed (to 0.1 g), although we are aware that these fish will have lost weight due to desiccation while being carried back to the colony held in the adult's beak (Montevecchi & Piatt 1987). Prior to 1990 gadids were measured and weighed but measurements were not always matched with species. Unless otherwise stated, all Clupeidae appeared to be Sprat, although the identification of very small specimens was problematic, so the name sprat is used for that family.

Pellets regurgitated by fully-grown Shags of unknown breeding status were collected between May and September and were digested in biotex until the mucous was dissolved. Otoliths were identified to family and when they were not too worn, and time allowed, to species level. Other items (crustacean fragments, polychaete jaws, cephalopod beaks) were assigned to the lowest possible taxa. Otoliths from sandeels fell obviously into two sizes. 'Large' were from older sandeels, but 'small' were a mixture of those from 0-group and those from older individuals that had their outer parts (and so growth rings) eroded away by the acid of the stomach (Johnstone *et al*. 1990) so no attempt was made to age these otoliths.

Results are expressed as frequency of occurrence in samples and, for otoliths and other hardparts, the actual numbers present. No attempt was made to pair up otoliths or mandibles of polychaete worms but fragments of crustacea and pairs of cephalopod beaks were treated as single items. A few regurgitates and many pellets contained more than one category of food so percentages of occurrence can total more than 100%. Some of the earlier data are described in Swann *et al*. (1991). Samples were collected on only a few days so we could not look for within-year variation in diet and we assume that what we report are representative of the chick-rearing season as a whole.

Results

Shag: Regurgitations were dominated by sandeels that were found in 67% of the 134 samples (Table 1). There was no significant trend in the proportion of samples with sandeels during the period (linear regression on arcsin transformed data: n = 24 years weighted by sample size, R^2 = 13.8%, P = 0.14). Of 40 regurgitations where sandeel size was assessed, 19 (48%) had small sandeels (0-group) and 24 (60%) large (older) sandeels. Gadids occurred in 36% of samples; 17 fish were identified to genus or species – *Trisopterus* spp. (8), Whiting *Merlangius merlangus* (7), Cod *Gadus morhua* (1) and rockling *Ciliata/Gaidropsarus* sp. (1). Two samples contained Sprat (1), two unidentified wrasse (Labridae), whilst single samples contained Herring, Butterfish *Pholis gunnellus* (Pholidae), Bull-rout *Myoxocephalus scorpius* (Cottidae), Viviparous Blenny *Zoarces viviparus* (Zoarcidae), pipefish (presumably Snake Pipefish *Entelurus aequoreus* (Syngnathidae)), unidentified fish, Sea Mouse *Aphrodite aculeate* (Polychaete worm) and small crab (Crustacea).

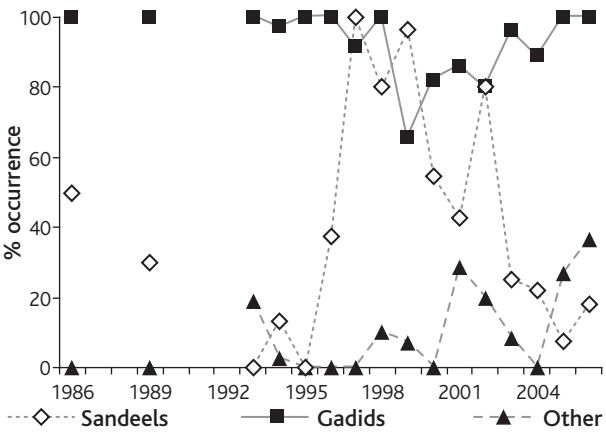

Figure 1. Annual frequency of occurrence of otoliths and other remains of sandeels (Ammodytidae), cod-fishes (Gadidae) and other prey groups in pellets of European Shag *Phalacrocorax aristotelis* on Canna.

Table 1. Contents of regurgitations from European Shags *Phalacrocorax aristotelis* on Canna. See text for details of other items.

Year	Sample size	% Sandeels	% Gadidae	% Other items	Year	Sample size	% Sandeels	% Gadidae	% Other items
1981	6	50	33	17	**1996**	3	33	67	0
1982	2	100	0	0	**1997**	14	85	14	7
1983	2	100	0	0	**1998**	11	82	36	0
1984	5	80	20	0	**1999**	4	75	50	0
1987	6	100	0	0	**2000**	1	100	0	0
1988	3	100	0	0	**2001**	8	25	75	25
1989	5	100	20	0	**2002**	5	100	0	0
1990	8	50	50	0	**2003**	11	55	45	0
1991	4	100	25	25	**2004**	3	100	0	0
1992	6	50	67	17	**2005**	0			
1993	2	0	50	50	**2006**	6	17	83	17
1994	7	86	14	0	**2007**	3	33	100	33
1995	9	44	44	22	**Total**	**134**	**67**	**36**	**8**

Table 2. Frequency of occurrence and total numbers of otoliths and other items in pellets regurgitated by European Shags *Phalacrocorax aristotelis* on Canna. See text for details of other items.

		% of pellets containing				% of otoliths containing		
Period	**No. of Pellets**	**Sandeels**	**Gadidae**	**Other**	**No. of Otoliths**	**Sandeels**	**Gadidae**	**Other**
1986 early August	6	50	100	0	231	5	95	0
1989 early August	10	30	100	0	4195	5	95	0
1993 early July	5	0	100	40	547	0	98	2
1993 early August	8	0	100	0	3314	0	100	0
1993 mid Sept	3	0	100	33	475	0	100	<1
1994 early August	38	13	97	3	no count			
1995 early July	7	0	100	0	790	0	100	0
1996 early July	4	50	100	0	159	44	56	0
1996 late July	4	25	100	0	578	17	83	0
1997 early July	9	100	89	0	482	77	23	0
1997 late July	3	100	100	0	178	29	71	0
1998 early July	3	67	100	33	271	44	56	<1
1998 late July	17	82	100	6	1583	13	87	<1
1999 late May	7	100	43	14	no count			
1999 early July	22	95	73	5	2397	48	51	1
2000 late May	2	100	0	0	no count			
2000 early August	9	44	100	0	896	10	90	0
2001 late May	3	67	67	0	no count			
2001 early July	4	25	100	25	631	40	60	<1
2002 late May	1	100	100	0	no count			
2002 early July	1	100	0	0	513	5	95	0
2002 early Aug	3	67	100	33	156	14	85	1
2003 early July	4	100	75	50	207	66	32	1
2003 late July	20	10	100	0	1152	1	99	0
2004 late July	9	22	89	0	766	4	96	0
2006 early July	4	0	100	25	580	0	100	<1
2006 late July	22	9	100	27	2671	0	98	2
2007 early July	13	23	100	54	1388	4	95	1
2007 late July	20	15	100	25	2219	4	96	<1
Total	**261**	**38**	**93**	**12**	**26376**	**11**	**88**	**1**

Pellets were dominated by gadid otoliths which were present in 243 (93%) of the 261 pellets and made up 88% of the 26,376 otoliths and other items present (Table 2). Similar figures for sandeel otoliths were 38% and 11%. Other groups present in 12% of pellets were wrasse (9 pellets), gobies (Gobiidae (8)), Butterfish (4), flatfish (Pleuronectidae (4)), dragonets *Callionymus* spp. (Callionymiidae (3)), a bullhead (Cottidae (1)), pipefish (2), cephalopod beaks (3), and crustaceans (3), but contributed little to the total items. Although the occurrence of gadids in pellets remained consistently high, sandeels increased to a peak in the late 1990s before declining again (Figure 1). In eight years, samples were collected in both early July and in late July/early August. Pooling years, sandeels occurred in 21 (49%) of 43 pellets from the early period, a significantly higher proportion than the 27 (28%) of the 97 pellets in the later period ($\chi^2 = 5.83$, 1 df, $P = 0.02$).

No systematic attempts were made to identify gadid otoliths, but many species were present including *Trisopterus* spp. (25% of 3,621 that were assigned to genus), Saithe *Pollachius virens,* rockling, Whiting, Haddock *Melanogrammus aeglefinus*, Cod and Ling *Molva molva*. Most of these otoliths would have come from fish 50–150 mm long. Of the sandeel otoliths, 626 (67%) were 'small' (probably mainly 0-group but including some eroded otoliths from older fish) and 310 (33%) were 'large'.

Kittiwake: Sandeels were the commonest species found in regurgitations in 14 of the 20 years, and occurred in 60% of the 227 samples (Table 3), gadids were the commonest food in four years, sprat in one, and in one year the two families were equally represented. Gadids and sprat were present in 22% of samples and very large numbers of very small pelagic crustaceans were found in 5%. The 'other' category was made up of four Lumpsuckers *Cyclopterus lumpus* (Cyclopteridae), two pipefish (both in 2007), one Three-spined Stickleback *Gasterosteus aculeatus* (Gasterosteidae) and a wrasse. Of the 62 samples where sandeels were aged, 58 (94%) were 0-group. Due to the lack of a colony-specific otolith:fish length relationship we could not calculate the lengths of these fish, but the bulk of relatively intact 0-group were 60–80 mm. Other fish were mostly very digested but most gadids appeared to be 60–100 mm long, whereas sprats were smaller at 50–60 mm.

Table 3. Frequency of occurrence of fish families, crustacea and other items in regurgitations of Black-legged Kittiwakes *Rissa tridactyla* on Canna. See text for details of other items.

		% regurgitations with				
Year	**No. of Samples**	**Sprats**	**Sandeels**	**Gadidae**	**Crustacea**	**Others**
1987	7	0	14	86	0	0
1988	6	0	0	83	17	17
1989	17	0	94	12	0	0
1990	6	0	100	0	0	0
1991	3	0	100	33	0	0
1992	8	25	25	63	13	0
1993	3	0	67	33	0	0
1994	6	0	100	0	17	0
1995	5	0	40	40	40	0
1996	9	33	67	11	0	0
1997	20	5	70	15	0	15
1998	4	50	25	50	50	0
1999	22	36	59	18	0	0
2000	32	16	81	0	13	3
2001	12	0	67	42	0	0
2002	22	27	73	0	0	0
2003	11	9	82	27	0	0
2004	21	95	5	5	0	0
2005	9	11	22	67	11	11
2006	0					
2007	4	0	75	50	0	50
Total	**227**	**22**	**60**	**22**	**5**	**4**

Guillemot: Of the 1,562 fish collected, 753 (48%) were Clupeidae (three Herring and the rest Sprat), and 416 (27%) were Gadidae including 314 Whiting, 52 *Trisopterus* spp. (mostly unidentified but including Poor Cod *T. minutus,* Bib *T. luscus* and Norway Pout *T. esmarkii*), 25 Haddock, 10 Saithe, two Blue Whiting *Micromesistius poutassou* and two Cod; the rest of the gadids were not identified to species level. Sandeels (24%) made up the remainder (Table 4). There were large variations in the fish taken from year to year (Figure 2), but generally sprats were less important in the 1980s and 2000s than during the 1990s (χ^2 = 57.5, 2 df, P < 0.001). On an annual basis, sprats were the most important, making up on average 47 ± 4% of the fish. Sandeels and Gadidae contributed 26 ± 3% and 27 ± 3%, respectively.

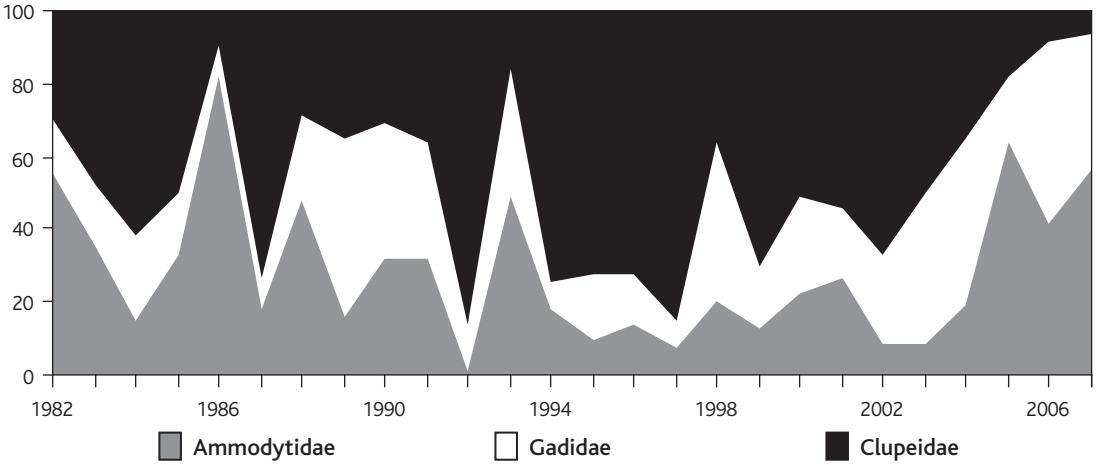

Figure 2. Fish family composition (% by number) of prey taken by Common Guillemots *Uria aalge* on Canna. Excludes 1981 when sample size < 10.

The length of sprats ranged from 68–155 mm, with a peak at 110–14 mm (Figure 3a). Most of these fish will have been 1-group or older. There was a significant decline in mean length over the period (linear regression: Length (mm) = 765 – 0.328 year, n = 717, P < 0.001); however since the overall decrease was only 5 mm, and year explained only 3% of the variation, this decline was unlikely to be biologically meaningful. The mean length of gadids varied from 42–147 mm with a peak at 80–84 mm (Figure 3b). The length of Whiting, the commonest gadid, showed no significant change in size over the study period (linear regression: R^2 = 0.0%, n = 274, P = 0.903), though there were marked annual variations in the size of fish taken (Appendix 1). Sandeels varied in length from 66–231 mm, with peaks around 90, 130 and 160 mm (Figure 3c). Fish were not aged but, given that most 0-group sandeels in samples from Kittiwakes were 60–80 mm long, it is unlikely that many of these from Guillemots were 0-group. There was no significant change in the size of sandeels taken over the period (linear regression: n = 315, R^2 = 0.1%, P = 0.66). Overall the mean weights of individual sprats, gadids, and sandeels were 10.7 ± 0.1 g (n = 669), 6.7 ± 0.2 g (339) and 7.8 ± 0.3 g (280), respectively; assuming that each of these fish had lost equal weight due to desiccation, then 59%, 20% and 21% of the biomass of food fed to chicks came from these fish families.

Table 4. Fish collected from Common Guillemots *Uria aalge* on Canna.

Year	Number	% Sandeels	% Sprats	Gadidae % Whiting	Gadidae % other species	Gadidae % unknown
1981	5	20	40	0	40	0
1982	27	56	26	0	15	0
1983	23	35	48	9	4	4
1984	34	15	62	6	12	6
1985	24	33	50	4	13	0
1986	72	69	17	4	8	0
1987	22	18	73	9	0	0
1988	64	48	28	13	9	2
1989	74	16	35	31	18	0
1990	72	32	31	28	8	1
1991	106	32	35	20	12	1
1992	77	1	86	10	3	0
1993	76	16	49	32	4	0
1994	66	18	74	6	2	0
1995	87	10	71	17	1	0
1996	78	14	71	10	4	1
1997	27	7	85	7	0	0
1998	81	20	36	40	5	0
1999	76	13	70	16	1	0
2000	89	21	49	26	1	1
2001	113	27	52	12	7	3
2002	24	8	67	25	0	0
2003	56	9	50	39	2	0
2004	119	19	35	45	1	0
2005	11	64	18	18	0	0
2006	40	40	8	13	38	3
2007	19	47	5	16	16	16
Total	**1562**	**24**	**48**	**20**	**7**	**1**

Discussion

The finding that sandeels were the main constituent (62%) of regurgitations from young Shags and adults feeding chicks accords well with numerous studies in Britain and Europe, although most reported higher frequencies (Pearson 1968; Harris & Riddiford 1989; Barrett *et al*. 1990; Guyot 1990; Harris & Wanless 1991; Harris & Wanless 1993). However, the frequency of gadids (37%) was unexpectedly high when compared with none in 57 and 141 regurgitates from Fair Isle, Shetland in 1986-1989 and the Isle of May, Firth of Forth in 1985–1990, respectively (Harris & Riddiford 1989; Harris & Wanless 1991). There are problems in describing the diet of Shags using otoliths, arising from the differential rates of digestion of otoliths of different sizes and from different families. For instance, otoliths from gadids are much more robust than those from sandeels and particularly sprats, whereas Butterfish and gobies have notably small otoliths for fish of their size (Härkönen 1986; Johnstone *et al*. 1990). However, gadids were represented in more than twice as many pellets as were sandeels and the total numbers recovered were over seven-times greater, so it seems likely that the diet of these individuals, full-grown but of unknown breeding status, that produced the pellets

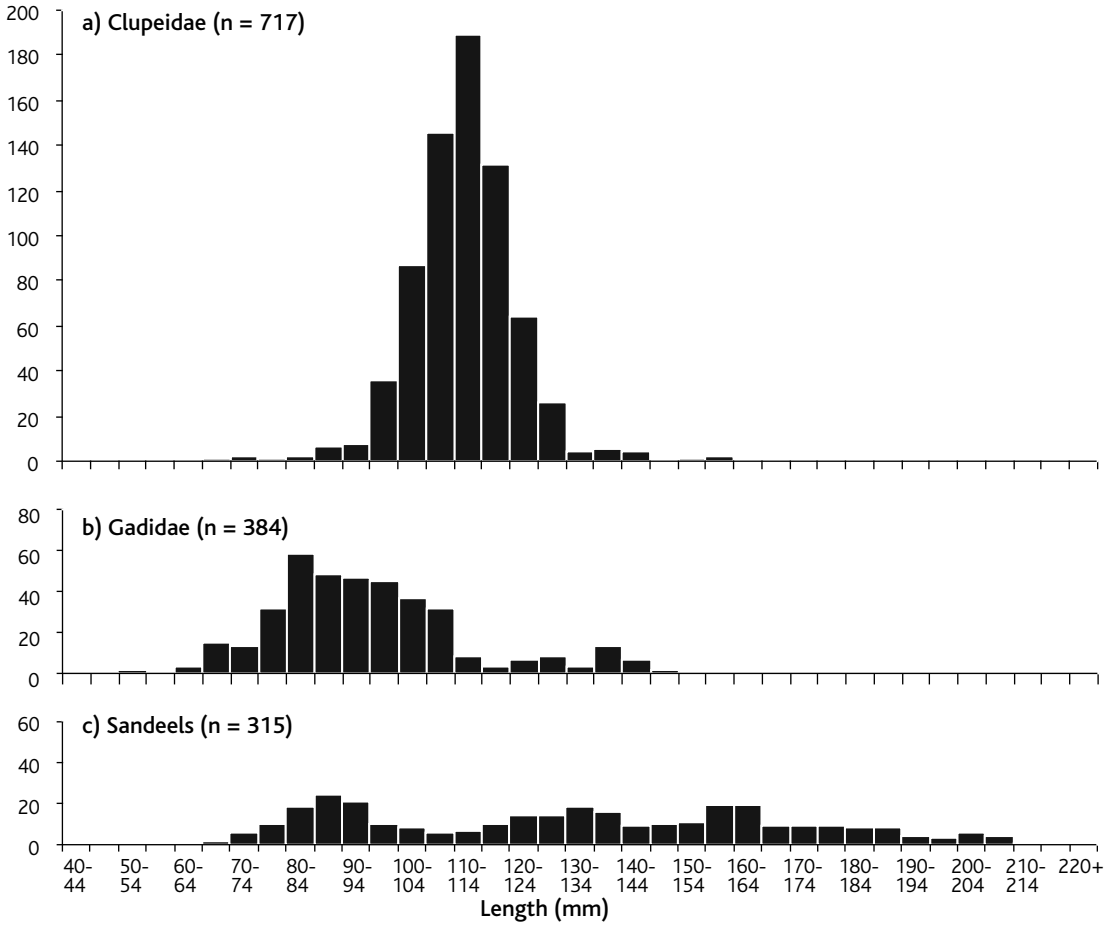

Figure 3. Distribution of lengths (mm) of fish from Common Guillemots *Uria aalge* on Canna.

was substantially different to that of the chicks. Such a difference in the diet of chicks and full-grown Shags has been recorded elsewhere (Harris & Wanless 1993). The significant lower proportion of pellets later in the season that had sandeels present was possibly the result of sandeels leaving the water column and burying themselves in the sand, where they spend most of the rest of the summer and winter (Macer 1966).

Although sandeels occurred in 60% of regurgitations from Kittiwakes and was the commonest family in 14 of the 20 years, these figures were low compared to many other British colonies. Sandeels made up an average of 83% of the biomass fed to chicks on the Isle of May over 18 years, were present in all 66 regurgitates on Fair Isle 1986–88, and in 98 of 100 regurgitates on Farne Islands, Northumberland 1998–2000 (Harris & Riddiford 1989; Lewis *et al*. 2001; Bull *et al*. 2004; Wanless *et al*. 2007). Gadids have been recorded at several other colonies, e.g. Farne Islands, Inchkeith, Inchcolm and Isle of May off northeast Britain (Bull *et al*. 2004), but not at such a high rate as on Canna. In contrast Sprats are regular in the diet and sometimes made up the bulk of the food at Inchkeith and Inchcolm.

Figure 1. Common Guillemots *Uria aalge* with gadids, Canna, July 2006 © *Kenny Graham*.

By number, approximately half the diet of young Guillemots was sprat, a quarter sandeels and a quarter gadids, and in biomass terms sprats contributed 59%. These are the normal constituents of the diet of young Guillemots in northern Britain. However, normally sandeels make up the bulk of the diet with sprats the usual alternative. On the Isle of May between 1981 and 2004 the relative mean annual percentages of these two families (by number) were 56% and 42% with the remainder being made up by a variety of other families (Wanless *et al*. 2005). Among 303 fish brought to Fair Isle in 1986-89, only four (two Sprat and two gadids) were not sandeels (Harvey *et al*. 1990). Gadids have been recorded from the stomachs of Guillemots shot during the summer in the 1980s in Shetland (11/83 birds with food remains), the Summer Isles (5/27), the Sound of Jura (1/5), the Clyde Front (1/5) and St Kilda (11/19) (Blake *et al*. 1985; Halley *et al*. 1995). However, it is difficult to compare these with fish brought to chicks since there are differences in the diet of parent birds and their chicks even at the same time at the same colony (Wilson *et al*. 2004).

Canna seabirds fed their chicks on a wide variety of fish species but the bulk of the diet was made up of sprats, sandeels and gadids (a variety of species but mainly *Trisopterus* spp. and Whiting). Other groups were of minimal importance. There are no data available on the numbers of small fish in the waters around Canna to allow a meaningful discussion as to whether the birds were selecting these species or were just eating the main species available to them. Over the period of the study there were few significant changes in species composition or the size of prey taken by Canna seabirds and the results confirm earlier findings that gadids are a normal and important part of the diet of seabirds at this colony.

Acknowledgements

We thank the many people who have helped collect the field data over many years, in particular Andrew Call, Simon Foster, Alan Graham, Kenny Graham, Kathryn Mackinnon, Andrew Ramsay and Alastair Young. John Hislop gave invaluable help with fish and otolith identification, and JNCC provided financial support through their seabird monitoring programme. Rob Barrett and Kees Camphuysen improved the manuscript with their criticisms.

References

Barrett, R. T., Røv, N., Loen, J. & Montevecchi, W. A. 1990. Diets of Shags *Phalacrocorax aristotelis* and Cormorants *P. carbo* in Norway and possible implications for gadoid stock recruitment. *Marine Ecology Progress Series* 66: 205–218.

Blake, B. F., Dixon, T. J., Jones, P. H. & Tasker, M. L. 1985. Seasonal changes in the feeding ecology of Guillemots (*Uria aalge*) off north and east Scotland. *Estuarine, Coastal and Shelf Science* 20: 559–568.

Bull, J., Wanless, S., Elston, D. A., Daunt, F., Lewis, S. & Harris, M. P. 2004. Local-scale variability in the diet of Black-legged Kittiwakes *Rissa tridactyla*. *Ardea* 92: 43–82.

Daunt, F., Wanless, S., Greenstreet, S. P. R., Jensen, H., Hamer, K. C. & Harris, M. P. 2008. The impact of the sandeel fishery closure in the northwestern North Sea on seabird food consumption, distribution and productivity. *Canadian Journal of Fisheries and Aquatic Sciences* 65: 362–391.

Frederiksen, M., Wanless, S., Harris, M. P., Rothery, P. & Wilson, L. J. 2004. The role of the industrial fishery and climate change in the decline of North Sea Black-legged Kittiwakes. *Journal of Applied Ecology* 41: 1129–1139.

Guyot, I. 1990. Le Cormoran Huppé en Corse: Biologie et interactions avec la pêche profesionnelle. *Travaux Scientifiques du Parc Naturel Regional et des Réserves Naturelles de Corse* 28: 1–40.

Halley, D. J., Harrison, N., Webb, A. & Thompson, D. R. 1995. Seasonal and geographical variations in the diet of Common Guillemots *Uria aalge* off western Scotland. *Seabird* 17: 12–20.

Härkönen, T. 1986. *Guide to the Otoliths of Bony Fishes of the Northeast Atlantic*. Danbiu ApS, Hellerup, Denmark.

Harris, M. P. & Riddiford, N. J. 1989. The food of some young seabirds on Fair Isle in 1986–88. *Scottish Birds* 15: 119–125.

Harris, M. P. & Wanless, S. 1991. The importance of the Lesser Sandeel *Ammodytes marinus* in the diet of the Shag *Phalacrocorax aristotelis*. *Ornis Scandinavica* 22: 375–882.

Harris, M. P. & Wanless, S. 1993. The diet of Shags *Phalacrocorax aristotelis* during the chick-rearing period assessed by three methods. *Bird Study* 40: 135–139.

Harvey, P. V., Harris, M. P., Osborn, K., Riddiford, N. & Silcocks, A. F. 1990. The breeding success and diet of Fair Isle's seabirds in 1986–1989. *Fair Isle Bird Observatory Report* 42: 47–54.

ICES 1995. *Report of the ICES workshop on sandeel otolith analysis: Review of sandeel biology*. ICES, CM 1995/G:4.

Johnstone, I. G., Harris, M. P., Wanless, S. & Graves, J. A. 1990. The usefulness of pellets for assessing the diet of adult Shags *Phalacrocorax aristotelis*. *Bird Study* 37: 5–11.

Lewis, S., Wanless, S., Wright, P. J., Harris, M. P., Bull, J. & Elston, D. A. 2001. Diet and breeding performance of Black-legged Kittiwakes *Rissa tridactyla* at a North Sea colony. *Marine Ecology Progress Series* 221: 277–284.

Macer, C. T. 1966. Sandeels (Ammodytidae) in the southwestern North Sea; their biology and fishery. *MAFF Fishery Investigations 2*. 24: 1–51.

Mavor, R. A., Parsons, M., Heubeck, M. & Schmitt, S. 2006. *Seabird numbers and breeding success in Britain and Ireland, 2005*. Joint Nature Conservation Committee, Peterborough. (UK Nature Conservation No. 30.)

Monaghan, P. 1992. Seabirds and sandeels: the conflict between exploitation and conservation in the northern North Sea. *Biodiversity and Conservation* 1: 98–111.

Montevecchi, W. A. & Piatt, J. F. 1987. Dehydration of seabird prey during transport to the colony: effects on wet weight energy densities. *Canadian Journal of Zoology* 65: 2822–2824.

Pearson, T. H. 1968. The feeding biology of seabird species breeding on the Farne Islands, Northumberland. *Journal of Animal Ecology* 37: 521–552.

Swann, R. L., Harris, M. P. & Aiton, D. G. 1991. The diet of some young seabirds on Canna, 1981-90. *Seabird* 13: 54–58.

Wanless, S., Frederiksen, M., Daunt, F., Scott, B. E. & Harris, M. P. 2007. Black-legged Kittiwakes as indicators of environmental change in the North Sea: Evidence from long-term studies. *Progress in Oceanography* 72: 30–38.

Wanless, S., Harris, M. P., Redman, P. & Speakman, J. 2005. Low fish quality as a probable cause of a major seabird breeding failure in the North Sea. *Marine Ecology Progress Series* 294: 1–8.

Wilson, L. J., Daunt, F. & Wanless, S. 2004. Self-feeding and chick provisioning diets differ in the Common Guillemot *Uria aalge*. *Ardea* 92: 197–208.

Appendix 1. The mean lengths (and their standard error, SE) of fish from collected from Common Guillemots *Uria aalge* on Canna.

	Sandeels			Sprats			Whiting		
Year	**Number**	**Mean (mm)**	**SE**	**Number**	**Mean (mm)**	**SE**	**Number**	**Mean (mm)**	**SE**
1983				10	112.2	0.8			
1984				21	114.1	1.7			
1985	7	147.6	8.7	11	111.1	1.5			
1986	48	112.7	4.3	12	126.0	3.6			
1987				16	106.4	1.7			
1988	20	149.2	6.5	16	111.6	2.3			
1989	12	154.0	9.1	26	112.2	1.8			
1990	23	125.6	7.5	22	114.4	1.0			
1991	34	134.8	6.4	36	112.3	1.2	21	86.0	1.8
1992	1	143.0		64	113.1	1.3	8	84.8	3.3
1993	12	157.9	8.5	36	113.5	1.2	24	83.0	2.0
1994	12	141.3	11.3	49	110.6	1.5	4	89.0	6.5
1995	8	162.1	7.2	62	111.2	0.8	15	92.7	2.2
1996	11	132.5	13.7	55	111.2	0.7	8	94.4	3.4
1997	2	162.5	37.5	23	111.8	2.3	2	92.0	12.0
1998	16	126.6	8.3	29	116.8	1.5	32	90.2	3.7
1999	10	97.2	8.5	53	105.6	1.2	12	86.8	5.1
2000	19	126.8	11.4	42	112.8	1.5	22	103.1	2.5
2001	23	103.3	6.7	47	106.5	1.4	13	93.4	2.9
2002	2	105.0	12.0	16	108.7	1.6	6	100.2	5.0
2003	5	143.6	27.9	22	115.4	2.4	22	92.1	2.1
2004	23	127.8	6.5	42	102.4	1.6	52	88.7	1.8
2005	7	148.9	10.9	2	110.5	0.5	2	82.0	11.0
2006	16	153.9	6.7	3	110.7	5.3	5	75.6	9.2
2007	4	151.8	9.4	1	119.0		3	66.0	8.1