

Common Guillemot *Uria aalge* chick diet and breeding performance at Sumburgh Head, Shetland in 2007–09, compared to 1990–91

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Abstract

Chick diet of Common Guillemots *Uria aalge* was studied by direct observation at Sumburgh Head, Shetland during 2007–09. Lesser Sandeels *Ammodytes marinus* comprised 55% of prey items, the remainder being Gadidae, including Whiting *Merlangius merlangus* and Saithe *Pollachius virens*, and a few Snake Pipefish *Entelurus aequoreus*. This contrasts with 1990–91 when chicks were fed 80% sandeels, the remainder mostly being unidentified Gadidae. When this shift from a diet dominated by sandeels took place is unknown, but a similar shift in chick diet at Fair Isle (40 km southwest of Sumburgh Head) seems to have occurred some time during 2000–02. Since 2003, weights of chicks near fledging have been lower than during the 1990s, and average breeding success has been reduced.



Figure 1. Common Guillemots *Uria aalge* off Noss, Shetland, June 2006. © Hugh Harrop

Introduction

Nothing has been published on Common Guillemot *Uria aalge* chick diet in Shetland since the late 1980s and early 1990s, when parent birds at two colonies fed their young almost exclusively Lesser Sandeels *Ammodytes marinus* (Harris & Riddiford 1989; Uttley *et al.* 1994). These studies have continued to be cited as indicative of chick diet in Shetland (Österblom & Olsen 2002; Swann *et al.* 2008), although the intervening years have seen considerable fluctuation in the breeding performance of Common Guillemots and other seabird species that are considered to need sandeels for successful breeding (Kunzlik 1989; Wright & Bailey 1993). This paper presents three years of observations at a Shetland colony, and compares chick diet and various parameters of breeding performance with a study at the same colony in 1990–91 (Uttley *et al.* 1994).

Methods

Sumburgh Head (59°51'N 1°16'W), at the southern tip of Mainland Shetland, is an 80 m high headland flanked to the east and south by open sea and strong tidal races, and to the west by a shallow, sandy bay. It holds a multi-species seabird colony that includes c. 8,000 Common Guillemots (most recent count, 7,931 individuals, 16 June 2009). Seabird populations have been monitored there since 1978, with Common Guillemot (hereafter 'Guillemot') breeding success monitored since 1989 in a single study plot on the east side of the Head. Feeding watches were conducted here since the number of chicks present and their ages were known each day.

Chick diet: Observations were made in one-hour watches, either of a single hour in a day or in two one-hour watches interrupted by a five-minute break. Most (88%) observations were made after 12.00 BST in fine weather conditions. The observation point was c. 30 m above and c. 40 m from the plot. Incoming adults were spotted with the naked eye and as they landed were checked to see if they were carrying fish, using a 20–60x telescope. The breeding group is backed by a vertical rock wall and surrounded on the other sides by gently sloping rock (Figure 3). About three-quarters of birds entering the breeding group either landed on top of the rock wall or on the peripheral slopes first, which allowed time to confirm whether they were carrying a fish or not and if so, to identify it; the remainder crash-landed directly into the breeding group, which often allowed very little time for fish identification. Fish were identified to family using a photographic key, and ranked as small, medium, or large in size (Uttley *et al.* 1994). The time a fish-carrying adult landed at the colony, site number, fish type, and other relevant information was recorded onto a tape recorder, which allowed uninterrupted visual scanning of the breeding group. Fish brought in by non-breeders or failed breeders were recorded separately as 'display fish'. A few feeds of identified fish were missed, usually when several parents with fish were simultaneously making cautious approaches to their sites, and a few feeds by 'crash-landers' were identified to site but were too rapid to identify the fish.

Breeding performance: Breeding success was monitored by daily checks lasting 1–3 hours made from before first egg-laying until the last chick disappeared (Walsh *et al.* 1995) to obtain dates of laying, egg loss, relaying, hatching, chick loss

and fledging. Weights of chicks approaching fledging age (with wings 60 or more mm long) were obtained on 30 June 2007 and 1 July 2009 in a colony at Compass Head, 1.3 km north of Sumburgh Head.

Results

Chick diet: Sandeels, most probably Lesser Sandeels although a few large individuals of possibly another species were seen in late 2009, and gadoids dominated the chick diet in each of the three years. A few Snake Pipefish *Entelurus aequoreus* were recorded in 2007, but with only one seen in 2008 and none in 2009 (Table 1). The ratio of gadoids to sandeels varied significantly between 2007 (0.48:1), 2008 (0.87:1) and 2009 (1.14:1) ($\chi^2 = 24.54, df = 2, P < 0.001$). Although medium-sized sandeels predominated in each year (Figure 2), the relative proportions of small, medium and large sandeels differed significantly between years with fewer small sandeels in 2008, and fewer large sandeels in 2009 ($\chi^2 = 17.21, df = 4, P < 0.01$).

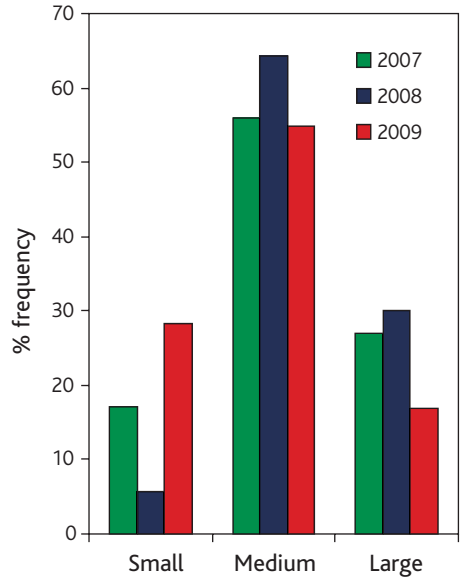


Figure 2. The percentage of sandeels in different size classes fed to Common Guillemot *Uria aalge* chicks at Sumburgh Head, 2007–09.



Figure 3. Common Guillemot *Uria aalge* breeding success and feeding watch study plot (highlighted), Sumburgh Head, May 2007. © Martin Heubeck

Table 1. Details of Common Guillemot *Uria aalge* chick feeding watches at Sumburgh Head, 2007–09.

	2007	2008	2009
Observation date range (n)	13/6–10/7 (15)	15/6–5/7 (15)	15/6–6/7 (12)
Total hours watched	25	29	24
Hours before/after mid-day	3.5/21.5	6/23	7.75/16.25
No. chicks (first date, peak, last date)	52, 82, 31	22, 46, 40	72, 86, 36
Chick-hours watched	1,589	1,196	1,668
Total fish brought	324	140	250
Sandeel sp. (% of total)	193 (59.6%)	70 (50.0%)	113 (45.2%)
Total gadoid sp.	92 (28.4%)	61 (43.6%)	129 (51.6%)
“Whiting”	Not recorded	31 (22.1%)	72 (28.8%)
“Saithe”	Not recorded	30 (21.4%)	55 (22.0%)
Pipefish sp.	23 (7.1%)	1 (0.7%)	0
Clupeid sp.	4 (1.2%)	0	3 (1.2%)
Unidentified	12 (3.7%)	8 (5.7%)	5 (2.0%)
Fish/chicks/hour (sum)	0.20	0.12	0.15
Fish/chicks/hour (mean daily rate)	0.22	0.11	0.14
Fish/chicks/hour (daily range)	0.11–0.37	0.07–0.25	0.10–0.23
Failed feeds (%)	18 (5.6%)	12 (8.6%)	6 (2.4%)

The gadoids brought to chicks were mainly two species, which, judging by fish collected from Compass Head in 2009 were Whiting *Merlangius merlangus* and Saithe *Pollachius virens*. These were recorded separately in 2008 and 2009 and there was no significant difference in their relative proportions in either year (Table 1).

Of 36 dropped fish collected on 1 July 2009, 10 (28%) were sandeels (c. 9–21 cm in length), 15 (42%) were Whiting (c. 12–15 cm in length), and 11 (31%) were Saithe (c. 9–12 cm in length). Lengths were mostly estimates as most specimens were headless. These dropped fish were as likely to have been used for display than for feeding to chicks, and the species and size composition of the two categories of fish can differ (Harris & Wanless 1985).

Feeding rates and failed feeds: The rate at which fish were brought to chicks varied considerably, both within the season (Table 1), and between consecutive days, e.g. in 2008 six fish were brought to 46 chicks during 09.00–11.05 BST on 1 July (0.07 hr^{-1}), and 25 fish were brought to the same 46 chicks during 13.30–15.35 BST on 2 July (0.25 hr^{-1}). There was no significant correlation between the number of fish brought to chicks per hour and either date or the mean age of chicks in the plot in any year, apart from a positive correlation with chick age in 2007 (Pearson correlation: $r = 0.552$, $P < 0.05$). The mean daily feeding rate in 2008 was half that in 2007 (Student’s *t*-test: $t = 4.02$, $P < 0.001$), was not significantly different between 2008 and 2009, but was slightly higher in 2007 than in 2009 (Student’s *t*-test: $t = 2.36$, $P < 0.05$).

What was not quantified was the incidence of parental non-brooding, which potentially allowed both parents to forage and provision their chick simultaneously. An example of this was a 16-day-old chick being brooded off-site on 25

June 2007 that was fed a medium sandeel on-site by one presumed parent at 14.52 BST and another medium sandeel by the other presumed parent at 14.54 BST; after eating the second fish the chick returned to the foster bird and both presumed parents departed their site.

In 2007 there were 40 instances during watches of a chick being brooded on-site by one presumed parent and fed more than once by the other presumed parent, 13 in 2008, and 29 in 2009 (these figures are obviously minima as some such feeds will have been missed during breaks in two-hour watches). The shortest intervals between these feeds was 12 minutes for both a sandeel and a gadoid in 2007, 41 minutes for a sandeel and 13 minutes for a gadoid (Saithe) in 2008, and 18 minutes for a sandeel and 19 minutes for a gadoid (Saithe) in 2009. While these data are admittedly sparse, they do suggest that some Guillemots (at least) were foraging close to the colony.

Intended feeds failed for a variety of reasons. Incoming adult Guillemots risked having their fish stolen while in flight by Arctic Skuas *Stercorarius parasiticus*, and by Common Gulls *Larus canus* and Herring Gulls *L. argentatus* after having landed. They also risked having their fish stolen by conspecifics while approaching their site, feeding their chick, or waiting for a chick that was offsite to return. A few feeds also failed because a chick would not, or could not, eat the fish, which was then stolen. The proportion of feeds that failed because of interference by conspecifics, because the fish was an inappropriate size, or because the parent could not find its chick was highest in 2008 (Table 1), when levels of interspecific aggression were (albeit subjectively) particularly high.

Breeding performance: Median laying date was five days later in 2008 than in 2007, but then advanced six days between 2008 and 2009 (Table 2). Incubating birds were clearly under stress in 2008, with at least 10% of eggs being abandoned

Table 2. Comparison of Common Guillemot *Uria aalge* breeding performance at Sumburgh Head in 1990 and 1991 (Uttley *et al.* 1994) and 2007–09 (this study), and chick weights at 50–59 mm and 60+ mm wing lengths at Compass Head (Shetland Ringing Group). Hatching dates are days from 1 May for first egg chicks only.

	1990	1991	2007	2008	2009
Egg-laying pairs	133	117	142	137	144
Median lay date			11 May	16 May	10 May
Mean hatching date (SE)	53.3 (0.7)	49.2 (0.7)	44.6 (0.5)	48.8 (0.8)	44.8 (0.8)
First/relay hatching success	0.76	0.72	0.65/0.44	0.49/0.20	0.65/0.48
First/relay fledging success	0.78	0.98	0.80/0.75	0.58/0.67	0.90/0.64
Mean fledging age (SE)	24.3 (0.4)	21.5 (0.5)	24.0 (0.3)	24.0 (0.7)	22.9 (0.3)
Breeding success	0.59	0.70	0.56	0.28	0.63
Mean 50–59 mm weight (g)	200.6	249.3	207.8		241.9
(n, SE)	(5, 10.6)	(23, 4.4)	(12, 8.5)		(17, 5.4)
Mean 60+ mm weight (g)		280.4	225.5		243.6
(n, SE)		(38, 5.6)	(13, 6.6)		(21, 5.4)

in situ, and hatching success of first eggs was significantly lower than in 2007 and 2009 ($\chi^2 = 9.86$, $df = 2$, $P < 0.01$). Similarly, fledging success of chicks from first eggs was significantly lower in 2008 than in 2007 and 2009 ($\chi^2 = 32.10$, $df = 2$, $P < 0.001$). The only difference between years in fledging age of first-egg chicks was between 2007 and 2009 ($t = -2.53$, $P < 0.05$).

Chicks with wing lengths of 60+ mm were significantly heavier in 2009 than in 2007 ($t = 2.11$, $P < 0.05$) (Table 2). Guillemot chicks have been measured at this colony since 1986, and chick weights in 2007 were towards the lower end of the range recorded, while those in 2009 were towards the middle of the range (Figure 4).

Breeding success has been recorded at this plot for 21 years in more or less the same manner, although less intensively during 1989–95 when a few early egg losses may have been overlooked (Figure 5). There was no significant difference between average breeding success in 1989–1995 (mean = 0.72, $SE = \pm 0.03$) and 1996–2002 (mean = 0.65, $SE = \pm 0.03$), but a significant reduction between 1996–2002 and 2003–09 (mean = 0.42, $SE = \pm 0.08$, $t = 2.74$, $P < 0.05$), with particularly poor seasons in 2003, 2004 and 2008.

Comparison with 1990 and 1991: Sandeels comprised 80% of 1,124 identified prey items fed to Guillemot chicks at Sumburgh Head in 1990 and 1991 (Uttley *et al.* 1994), but only 55% of 689 items in 2007–09, a highly significant dietary shift ($\chi^2 = 137.58$, $df = 1$, $P < 0.001$). The remainder of prey items in 1990–91 were largely gadoids. Fish dropped by Guillemots at Compass Head (i.e. probably including display fish) comprised 85% large (> 160 mm) sandeels over three years old and 15% Whiting (> 120 mm) in 1990, and 30% 0-group (young of the year) and 60% 1-group sandeels in 1991, the remainder being gadoids (Wright & Bailey 1993).

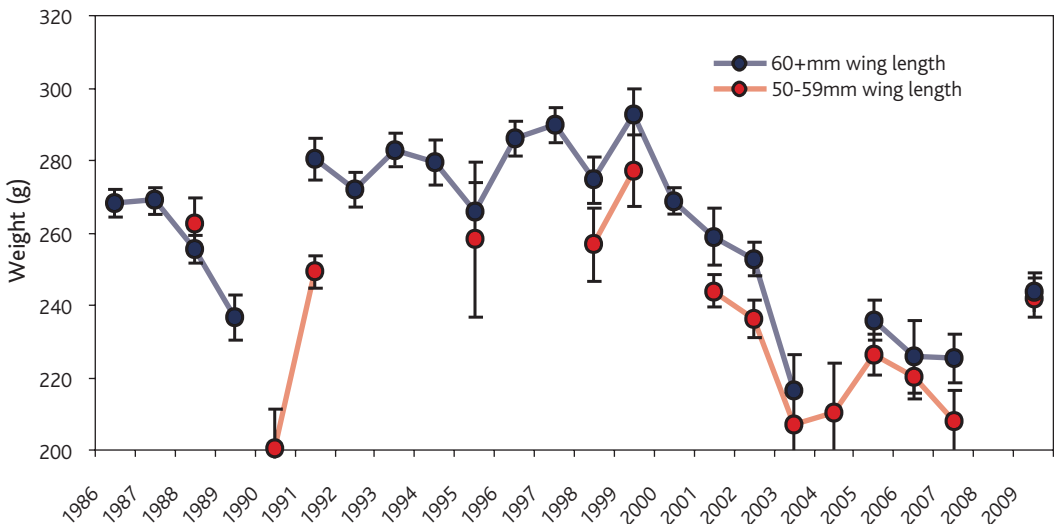


Figure 4. Mean weights ± 1 SE of Common Guillemot *Uria aalge* chicks with wing lengths of 50–59 mm (inclusive) and 60 mm or over at Compass Head, Shetland, 1986–2009. Sample sizes of < 5 are excluded.

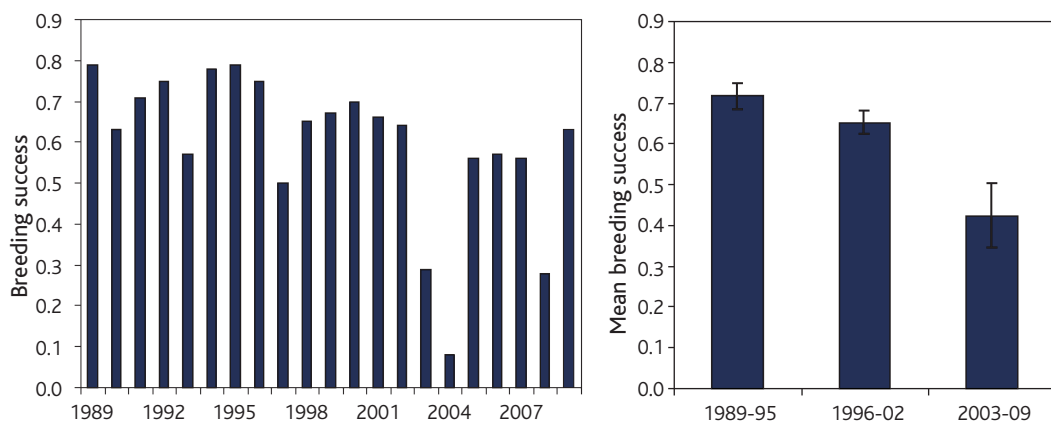


Figure 5. Common Guillemot *Uria aalge* breeding success (chicks fledged per egg-laying pair) at Sumburgh Head, 1989–2009 (left), and average success during three seven-year periods (right, including standard error bars).

Monitoring in my plot was not as rigorous in 1990 and 1991 as in 2007–09, and comparison of breeding performance is therefore made with data in Uttley *et al.* (1994), obtained from a plot on the west side of Sumburgh Head (Table 2). Mean hatching dates advanced by 4.1 days between 1990 and 1991, similar to the 4.0 days between 2008 and 2009, but hatching success was higher in both 1990 and 1991 than in 2007–09. For chicks with wing lengths of 50–59 mm, there was no difference in weights between 1990 and 2007, or 1991 and 2009, but chicks were significantly lighter in 2007 than in 1991 ($t = 4.79$, $P < 0.001$), and heavier in 2009 than in 1990 ($t = 3.61$, $P < 0.01$). Chicks with wing lengths of 60 mm or greater were lighter than in 1991 in both 2007 ($t = 5.33$, $P < 0.001$) and 2009 ($t = 4.33$, $P < 0.001$).

Discussion

Around the British Isles and the North Sea, Guillemots preferentially feed their chicks sandeels or clupeids. Chick diet can vary between years at the same colony, and between colonies on a regional and local scale. In southwest Britain, chicks on Skomer Island were fed 99% Sprats *Sprattus sprattus* and 1% sandeels by number during 1972–75 (Birkhead 1977), and 79% Sprats and 21% sandeels during 1985–87 (Hatchwell 1991), while at Lundy Island, 75 km southeast of Skomer, chicks were fed the same species during 1985–86 but in significantly different proportions to those on Skomer (Hatchwell *et al.* 1992). On the Isle of May, Firth of Forth, Guillemot also switched between the two species, but fed their chicks, on average, 59% sandeels and 39% Sprat by number during 1981–2003 (Wanless *et al.* 2005). In the southeast North Sea, chick diet on Helgoland, Germany in 1990 was 95% clupeids (Sprat and Herring *Clupea harengus*) and 5% sandeels (Leopold *et al.* 1992). On the west coast of Scotland, chick diet on Canna during 1981–2007 comprised, in total, 48% Sprat, 24% sandeels and 20% gadoids (by number), with the percentage of gadoids in any year ranging from 7–51% (Swann *et al.* 2008). Around Shetland, however, there is apparently no abundant, appropriate-sized clupeid alternative to sandeels. A spawning population of Sprat existed in the late 1960s and 1970s, centred on the Fair Isle area (40 km southwest of Sumburgh Head), but largely disappeared after 1977 as the species' range contracted southwards (Kunzlik 1989; Corten 1990).



Figure 6. Common Guillemots *Uria aalge*, off Noss, Shetland, June 2009. © Hugh Harrop

It is not known when, during 1992–2006, gadoids became a significant element of Guillemot chick diet at Sumburgh Head, or whether the recent diet there is reflected at other Shetland colonies. The only other data for a Shetland colony come from Fair Isle. During 1992–99, feeding watches were carried on 5–7 days per year and sandeels comprised 91–99% of identified items brought to chicks, the remainder being gadoids or Sprat (Fair Isle Bird Observatory Trust annual reports to the Joint Nature Conservation Committee). During these years the mean hourly feeding rate ranged from 0.17 fish per hour (1997 and 1998) to 0.39 (1993). A single 20-hour feeding watch carried out annually during 2000–02 recorded feeding rates of 3.4, 1.5 and 2.1 fish per day, respectively, but the identity of fish was not reported; in those years dropped fish collected in the colony comprised 81% ($n = 27$), 71% ($n = 17$), and 100% ($n = 2$) sandeels, respectively. One-day feeding watches in 2003 and 2005–07 recorded a much lower proportion of sandeels in the diet than during the 1990s, 53% of identified items in 2003, 55% in 2005, 48% in 2006 and 61% in 2007, the remainder being a varying proportion of gadoids and Sprat, although including 9% pipefish in 2007. The reduction of sandeels in Guillemot chick diet at Fair Isle therefore occurred sometime between 1999 and 2003.

The 1990–91 studies found that in a year of low sandeel abundance (1990), adult Guillemots spent less time at the colony, made longer and more distant foraging trips, and fed their chicks larger prey items (albeit still 82% sandeels) than in 1991 when sandeels were more abundant (Wright & Bailey 1993; Monaghan *et al.* 1994; Uttley *et al.* 1994). This ability to alter time budgets to compensate for food scarcity meant there was no difference in breeding success in the two years, and while chicks fledged significantly lighter in 1990 this need not necessarily have compromised their post-fledging survival since the chick is accompanied and fed

by the male parent for up to two months after leaving the colony, and Harris *et al.* (2007) found no significant association between fledging weights of Isle of May chicks and subsequent survival.

Given the preponderance of sandeels in chick diet at both Sumburgh Head in 1990–91 and Fair Isle throughout the 1990s, it is reasonable to assume that they are the preferred prey of Guillemots at those colonies, and that sandeels were less available around Sumburgh Head in 2007–09 than in 1990. The 2007 breeding season in Shetland was generally 'moderate to poor' for those seabird species that normally rely on sandeels for successful breeding, 'poor' in 2008, yet in 2009 reasonable numbers of Arctic Skuas, Arctic Terns *Sterna paradisaea* and Black-legged Kittiwakes *Rissa tridactyla* fledged from some colonies; in all three years, however, breeding success was described as patchy within the islands (Heubeck 2007, 2008, 2009). During June and July 2009, a variety of seabird species were seen feeding in large numbers on sandeels in Mousa Sound, 16 km north of Sumburgh Head (pers. obs., supported by numerous reports from fishermen), and it perhaps surprising that the proportion of sandeels fed to Guillemot chicks at Sumburgh Head in 2009 was not higher. However, using radio telemetry Monaghan *et al.* (1994) found that Guillemots at Sumburgh Head foraged within 10 km of the colony, at a mean distance of 7.1 (SE = ± 0.5.) km in 1990 and 1.2 (SE = ± 0.2.) km in 1991. Such close foraging is consistent with observations in 2007–09 of some chicks brooded by a parent receiving feeds just 12–13 minutes apart. Perhaps the higher proportion of gadoids in these frequent feeds (at least in 2007) was due to some parents choosing to utilise a less energy-rich prey that was more readily available close to the colony rather than extend their foraging range too far in order to exploit a local source of sandeels, but this is speculation. Chick diet was unknown in the poor breeding seasons of 2003 and 2004, but the 2009 data suggest that Guillemots at Sumburgh Head are capable of achieving moderate breeding success on a chick diet of 50% gadoids, although chicks may fledge at a lighter weight than when fed largely sandeels.

Acknowledgements

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References

- Birkhead, T. R. 1977.** The adaptive significance of the nestling period of Guillemots *Uria aalge*. *Ibis* 119: 544–549.
- Corten, A. 1990.** Long-term trends in pelagic fish stocks of the North Sea and adjacent waters and their possible connection to hydrographic changes. *Netherlands Journal of Sea Research* 25: 227–235.

- Harris, M. P., Beare, D., Torenson, R., Nøttestad, L., Kloppmann, M., Dörner, H., Peach, K., Rushton, D. R. A., Foster-Smith, J. & Wanless, S. 2007.** A major increase in snake pipefish (*Entelurus aequoreus*) in northern European seas since 2003: potential implications for seabird breeding success. *Marine Biology* 151: 973–983.
- Harris, M. P., Frederiksen, M. & Wanless, S. 2007.** Within- and between-year variation in the juvenile survival of Common Guillemots *Uria aalge*. *Ibis* 149: 472–481.
- 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. 1985.** Fish fed to young Guillemots, *Uria aalge*, and used in display on the Isle of May, Scotland. *Journal of Zoology, London (A)* 207: 441–458.
- Hatchwell, B. J. 1991.** The feeding ecology of young Guillemots *Uria aalge* on Skomer Island, Wales. *Ibis* 133: 153–161.
- Hatchwell, B. J., Birkhead, T. R., Goodburn, S. F., Perrins, J. M. & Jones, S. E. 1992.** Chick diets and food intake of nestling Common Guillemots *Uria aalge*: an inter-colony comparison. *Seabird* 14: 15–20.
- Heubeck, M. 2007.** 2007 breeding season news: Shetland (excluding Fair Isle). *Seabird Group Newsletter* 106: 16–17.
- Heubeck, M. 2008.** 2008 breeding season news: Shetland (excluding Fair Isle). *Seabird Group Newsletter* 109: 9–11.
- Heubeck, M. 2009.** 2009 breeding season news: Shetland (excluding Fair Isle). *Seabird Group Newsletter* 112: 9–10.
- Kunzlik, P. A. 1989.** Small fish around Shetland. In: Heubeck, M. (ed.) *Seabirds and Sandeels: Proceedings of a seminar held in Lerwick, Shetland, 15–16th October 1988*: 38–49. Shetland Bird Club, Lerwick.
- Leopold, M. F., Wolf, P. A. & Hüppop, O. 1992.** Food of young and colony attendance of adult guillemots *Uria aalge* on Helgoland. *Helgoländer Meeresunters* 46: 237–249.
- Monaghan, P., Walton, P., Wanless, S., Uttley, J. D. & Burns, M. D. 1994.** Effects of prey abundance on the foraging behaviour, diving efficiency and time allocation of breeding Guillemots *Uria aalge*. *Ibis* 136: 214–222.
- Österblom, H. & Olsson, O. 2002.** Changes in feeding behaviour and reproductive success in the Common Guillemot *Uria aalge* on the island of Stora Karlsö. *Ornis Svecica* 12: 53–62.
- Swann, R. L., Harris, M. P. & Aiton, D. G. 2008.** 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. *Seabird* 21: 44–54.
- Uttley, J. D., Walton, P., Monaghan, P. & Austin, G. 1994.** The effects of food abundance on breeding performance and time budgets of Guillemots *Uria aalge*. *Ibis* 136: 205–213.
- Walsh, P. M., Halley, D. J., Harris, M. P., del Nevo, A. J., Sim, I. M. W. & Tasker, M. L. 1995.** *Seabird monitoring handbook for Britain and Ireland*. JNCC / RSPB / ITE / Seabird Group, Peterborough.
- Wanless, S., Harris, M. P., Redman, P. & Speakman, J. R. 2005.** Low energy values of fish as a probable cause of a major seabird breeding failure in the North Sea. *Marine Ecology Progress Series* 294: 1–8.
- Wright, P. J. & Bailey, M. 1993.** *Biology of sandeels in the vicinity of seabird colonies at Shetland*. The Scottish Office Agriculture and Fisheries Department. Marine Laboratory, Aberdeen.