SELF-FEEDING AND CHICK PROVISIONING DIET DIFFER IN THE COMMON GUILLEMOT *URIA AALGE*

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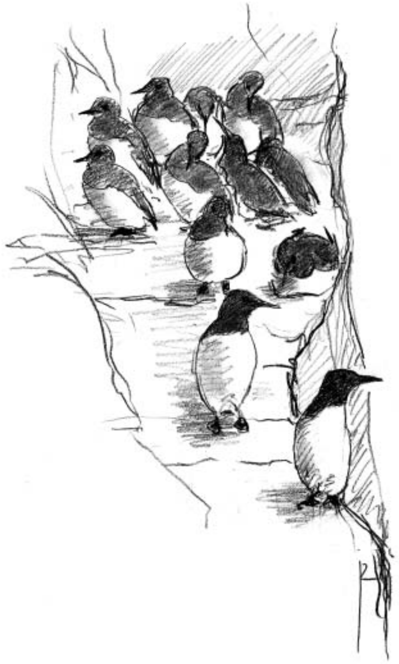

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The Common Guillemot *Uria aalge* is one of the most abundant seabird species in the North Atlantic. The diet delivered to the chicks by breeding adults is well known, since the food is carried in the bill and readily observed at colonies. Much less is known about the diet of adults during the breeding season and, in the absence of empirical data, the diet of adults and chicks has generally been assumed to be the same. However, foraging theory predicts that adults should select higher quality prey for chick provisioning. Furthermore, Common Guillemots are single prey loaders, and likely to deliver large prey items for their chicks, whilst feeding themselves on a much broader range of prey sizes. In this paper, we present the first detailed comparison of adult and chick Common Guillemot diet, using data collected concurrently on both age groups at the Isle of May, south-east Scotland. Our results strongly support the prediction that breeding adults select higher quality prey for chick provisioning than for self-feeding. Chicks were primarily fed energy rich Sprats *Sprattus Sprattus* and adult Lesser Sandeels *Ammodytes marinus*. In contrast, adults fed on smaller prey items, with young of the year Lesser Sandeels being the most frequently recorded. Seasonal variation in diet composition of both adults and chicks accorded well with our current understanding of the availability of different prey types, but the difference in prey size between self-feeding and chick provisioning persisted throughout the sampling period.

Key words: *Ammodytes marinus* – *Uria aalge* - feeding ecology – predator prey – central place foraging theory

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INTRODUCTION

Quantifying the diet of adult marine birds that swallow their prey underwater is challenging. In contrast, the diet of chicks is well documented in many species (Cramp & Simmons 1977, 1985; Gaston & Jones 1998). Given the lack of empirical data, the assumption has frequently been made that diet of breeding adults is the same as the diet they deliver to their chicks (e.g. Litzow *et al.* 2000; Sydeman *et al.* 2001; Barrett 2002). However, foraging theory predicts that, because of the associated costs of returning to the breeding site, adults will deliver prey of a higher energetic value to the offspring than they consume themselves (Orians & Pearson 1979; Lessells & Stephens 1983; Ydenberg *et al.* 1994). Furthermore, those species that deliver a single prey item in the bill to their chicks are expected to select a larger item than the average size ingested. The few primarily qualitative studies have shown that, in accordance with theory, adults feed themselves on prey of lower quality and smaller size than those they deliver to their offspring (Gaston & Nettleship

1981; Bradstreet & Brown 1985; Baird 1991; Davoren & Burger 1999; Ramos 2000; Butler & Buckley 2002; Hatch 2002).

The Common Guillemot *Uria aalge* is widespread in the North Atlantic, and numbers in most regions have increased greatly in the last 30 years (Ainley *et al.* 2002; Harris & Wanless 2004). Data have been collected on chick diet, which consists primarily of small, shoaling fish such as Lesser Sandeel *Ammodytes marinus*, Sprat *Sprattus Sprattus* and capelin *Mallotus villosus* (Gaston & Jones 1998; Ainley *et al.* 2002). Differences in diet between adults and chicks are particularly likely in Common Guillemots because they are single prey loaders. However, there is only patchy information on adult diet during the breeding season (Blake *et al.* 1985; del Nevo 1990; Ainley *et al.* 1996; Camphuysen 2001; Mehlum 2001; Wilhelm *et al.* 2003), and no study has compared adult and chick diet concurrently at the same breeding colony. We compared adult and chick diet on the Isle of May, southeast Scotland, where the latter has already been described in detail (Harris & Wanless 1985, 1995; Finney *et al.* 1999; Rindorf *et al.* 2000). Typically, there is a gradual switch from adult (hereafter referred to as 1+ group) Lesser Sandeel to Sprats during chick-rearing. Smaller prey are potentially available during this period, notably young of the year (hereafter referred to as 0 group) Lesser Sandeels, which are common in the diet of other seabird species breeding in the region, such as Black-legged Kittiwake *Rissa tridactyla*, Atlantic Puffin *Fratercula arctica*, Razorbill *Alca torda* and Northern Gannet *Morus bassanus* (Lewis *et al.* 2001, 2003; Wilson *et al.* 2003; Wanless *et al.* 2004). Behavioural observations at sea close to the Isle of May suggest that 0 group Lesser Sandeels are an important component in the diet of adult Common Guillemots (Camphuysen & Webb 1999). However, these smaller prey are only rarely recorded in the diet of chicks (Harris & Wanless 1985; Finney *et al.* 1999). Thus, we aimed to test the prediction that adults bring large fish to their chick but have a broader range of prey types and lower mean prey size and quality in their own diet. We expected these differences to be maintained throughout the chick-rearing period, despite expected changes in prey composition, namely a decline in 1+ group Lesser Sandeels and an increase in Sprats in the diet (Harris & Wanless 1985; Finney *et al.* 1999).

METHODS

Adult diet

Ninety-one adult Common Guillemots were caught on breeding ledges on the Isle of May, Firth of Forth, southeast Scotland (56°11’N, 02º33’W) between 17 May and 29 June 2003, a period that spanned the late incubation and chick-rearing periods. Breeding status was determined by the presence of a brood patch, egg or chick. Diet samples were obtained by water off-loading (under UK Home Office Licence). A 15 mm diameter soft rubber tube was passed down the oesophagus and into the stomach and water gently pumped into the tube. When water started to seep through the gape, indicating that the stomach was full, the tube was removed, the bird inverted and the water and stomach contents offloaded into a sample flask. This process was repeated until the water was clear (one repeat flushing was necessary in almost all cases; maximum two) and the bird was then released.

One sample contained undigested whole fish; the remainder were almost completely digested. Thus, we scored presence or absence of prey species only. Prey were identified from hard parts (otoliths, vertebrae and other characteristic bones e.g. premaxillae and opercular bones), using a dissecting microscope and keys in Härkönen (1986), Watt *et al.* (1997) and Leopold *et al.* (2001). Sixty-two samples (68%) contained remains that could be identified, of which 48 (77%) contained identifiable otoliths.

Maximum otolith diameter (width for Sprats; length for all other species) was measured to within ± 27µm using a calibrated eyepiece graticule. Age class of Lesser Sandeels was determined using counts of annuli (ICES 1995). Fish lengths of all species were calculated from otolith length / fish length regression equations (see Appendix for Lesser Sandeels; Härkönen (1986) for other species). All goby Gobiidae otoliths were too small to give meaningful fish lengths since published regression equations from Härkönen (1986) were based on samples of larger fish. Goby vertebrae from one of the samples were used to calculate an average goby length, assuming that goby vertebrae lengths are 1.6-2.1% of fish length (Härkönen 1986).

Energy content was derived for Sprats and Lesser Sandeels from fish length / energy density regression equations in Hislop *et al.* (1991). For gadids Gadidae, energy content was derived by converting length into mass using the equation: Mass(g) = 0.00626 x length(cm)$^{3.109}$ (Harris & Hislop 1978), and using an energy density of 3.06 kJ g^{-1} (Sidwell 1981). Energetic values for gobies were not available.

Chick diet

Observations of the prey fed to chicks were made between 0600 - 0800 each day from 2 - 30 June from a hide ca.15 m from an undisturbed group of ca.200 pairs of Common Guillemots. All the breeding sites were individually numbered and each item fed to a chick was identified where possible and assigned to one of five size categories (very small, small, medium, large and very large), using the bill length of the adult as a guide. Fish dropped by adults were collected to estimate proportions of clupeids that were either Sprat or Herring *Clupea harengus*, separated using the roughness of ventral scales and vertebra counts, and to calibrate the lengths of fish in each size category (Lesser Sandeels: very small = 6 cm, small = 9 cm, medium = 12 cm, large = 14 cm; clupeids: small = 10 cm, medium = 13 cm, large = 15 cm; very large = 17 cm; gadids and squid *Loligo* spp.: small = 5 cm, medium = 7 cm, large = 10 cm). All clupeids collected from breeding ledges were Sprats, so it was assumed that all clupeids delivered to chicks were of this species. 0 group Lesser Sandeels were distinguished from 1+ group Lesser Sandeels by their extremely small size and length (0 group were those in the smallest size category of 6 cm, 1+ group were those in the larger size classes; within a season fish length is a reliable method of distinguishing 0 group and 1+ group Lesser Sandeels, Wanless *et al.* 2004) and most were carried crosswise, rather than lengthwise, in the bill. An estimate of energy content of fish was determined in the same way as adult diet.

Statistical analysis

To establish frequency of occurrence through the season in the adult diet, we ran a Generalized Linear Model (GLM) with a binomial error and logit link function for each prey type, fitting the following fixed effects additively: linear Julian date, quadratic Julian date, cubic Julian date (we included three forms of Julian date to test for non-linear effects of season). For each prey type, we generated predicted values of frequency of occurrence at five day intervals throughout the study period (20 May – 24 June). We carried out a second GLM on each prey type to compare frequency of occurrence during incubation and chick-rearing, with breeding stage as a fixed effect (1 = incubation; 2 = chick-rearing).

To compare frequency of occurrence between prey types, we carried out a GLM with binomial errors and logit link function, with Julian date, quadratic Julian date, cubic Julian date, prey type and an interaction term between prey type and Julian date added sequentially. To further clarify prey occurrence through the season, we carried out paired tests between prey types (five prey types gave 10 pairwise comparisons) on three dates spread evenly through the sampling period (25 May, 9 June and 24 June). For each paired test, differences in predicted values divided by the standard error of the difference were compared against the Z distribution.

To compare the size of prey taken by adults with that delivered to chicks, we categorised prey in the adult diet during chick-rearing (2 - 29 June) into the size categories used for chick diet. This was carried out initially on each prey type, and we had to define a new length class for 0 group Lesser Sandeels (less than 6 cm) and Sprats (less than 10 cm). We then merged the different length classifications for each prey type into a single classification for all prey types: class 1: < 6 cm; class 2: 6 / 7 cm; class 3: 8 / 9 / 10 cm; class 4:

12 / 13 cm; class 5: 14 / 15 cm; class 6: 17 cm. Many prey deliveries were made to the same chick. Therefore, we ran a Generalized Linear Mixed Model (GLMM) with poisson errors and a log link function on number of fish, with age class and length class as fixed effects and site number as a random effect. All adult diet data were statistically independent, so we assigned a sequential list of dummy site numbers to ensure that the model could run.

To compare the occurrence of prey taken by adults and chicks, only 1+ group Lesser Sandeels and Sprats were compared statistically as only these were present in sufficient numbers in both diets for formal analysis. We ran a GLMM with binomial errors and logit link function with site number (dummy site number for adults) as a random effect. Julian date, quadratic Julian date, cubic Julian date, age class and age class * Julian date interaction were fitted additively as fixed effects. Predicted values of frequency of occurrence of Sprats and 1+ group Lesser Sandeels were generated for adult and chick diet at five day intervals (4 June to 24 June). The predicted values for adult diet differed very slightly from those obtained in the first analysis because the incubation period was excluded.

Non-significant effects were dropped from all models, with the condition that if any higher power of Julian date was significant all lower powers were retained. The significance of each variable or interaction was determined by comparing Wald statistics with percentiles of chi-squared (Elston *et al.* 2001). Goodness of fit tests were carried out on final models of seasonal patterns, by comparing residual deviance over residual degrees of freedom with percentiles of chi-squared. A non-significant result confirmed a good fit of the final model to the data. All models were run in Genstat6.

RESULTS

Adult diet

Lesser Sandeels, Sprats, gobies, gadids, squid, polychaetes and copepods were recorded. Fish prey items varied in mean length from 9.7 cm (1+ group Lesser Sandeels) to 2.5 cm (gadids, Table 1). These differences were even greater in energetic terms (Table 1) due to the non-linear relationship between length and mass in all species (Hislop *et al.* 1991) and because Sprats have a very high energy content for their length (more than twice that of 1+ group Lesser Sandeels).

The most frequently occurring prey were 0 group Lesser Sandeels (59% of samples); the remaining prey types were present in less than a quarter of samples (Table 2; GLM: between-species difference: $W = 7.62$, $P < 0.01$). There were also significant seasonal patterns in the frequency of occurrence (GLM: interaction between species and Julian date: $W = 5.20$, $P < 0.01$). Whilst there was no seasonal pattern in 0 group occurrence, the other species all showed seasonal changes in occurrence. Thus, 1+ group Lesser Sandeels showed an initial increase prior to a strong decline, Sprats and gobies showed a linear increase, while gadids showed an increase fol-

Table 1. Mean length (±SD) and mean energetic value (±SD) of each fish prey type recorded in adult Common Guillemot diet on the Isle of May in 2003. Goby lengths were estimated from vertebrae; no energetic value was available for gobies.

	Length (mm)	Energy value (kJ)	*n*
0 group Lesser Sandeel	52.53 ± 9.39	2.72 ± 1.77	272
1+ group Lesser Sandeel	96.60 ± 8.66	19.88 ± 6.73	45
Sprat	88.80 ± 10.97	45.97 ± 25.70	8
Goby	51.80	n/a	30
Gadid	24.97 ± 8.67	0.47 ± 0.56	13

Table 2. Frequency of occurrence of prey types in adult Common Guillemot diet samples. Note that the number of samples containing Lesser Sandeel remains is higher than the sum of the two age classes because non-otolith remains could not be aged. Invertebrates consisted of small copepods, squid beak remains and polychaete jaw remains.

	Samples with remains (*n*)	% samples containing prey type	Samples with otoliths (*n*)
Lesser Sandeel (all)	59	95	44
Lesser Sandeel (0 group)	35	56	35
Lesser Sandeel (1+ group)	14	23	14
Sprat	14	23	6
Goby	13	21	6
Gadid	10	16	7
Invertebrates	13	21	n/a
Total number of samples	62		48

Table 3. Deviance ratios for each parameter fitted sequentially for each prey type in the adult diet. Retained parameters are shown in bold.

Model	Lesser Sandeel														
	0-group			1+ group			Sprat			Goby			Gadid		
	W	*P*	df	*W*	*P*	df	*W*	*P*	df	*W*	*P*	df	*W*	*P*	df
Julian	1.26	0.26	1	**4.16**	**0.04**	1	**4.48**	**0.03**	1	**6.27**	**0.01**	1	**2.54**	**0.11**[a]	1
Julian[2]	1.59	0.21	1	**4.13**	**0.04**	1	0.01	0.93	1	0.79	0.38	1	**5.81**	**0.02**	1
Julian[3]	0.02	0.87	1	0.45	0.50	1	1.27	0.26	1	0.51	0.48	1	1.08	0.30	1

[a]Non-significant lower power of Julian date retained because higher power significant – see Methods

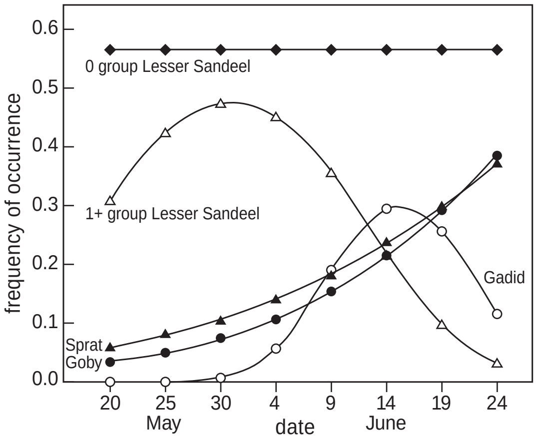

Fig. 1. Predicted values of frequency of occurrence of different prey types in adult Common Guillemot diet through the season.

lowed by a decrease (Table 3; Fig. 1). Goodness of fit tests confirmed the strength of the seasonal patterns in occurrence of 1+ group Lesser Sandeels (χ^2 = 0.98, *P* = 0.32), Sprats (χ^2 = 1.02, *P* = 0.31), gobies (χ^2 = 0.96, *P* = 0.33) and gadids (χ^2 = 0.79, *P* = 0.38). Pairwise comparisons revealed that, at the beginning of the sampling period, 0 group and 1+ group Lesser Sandeels were the most frequently recorded prey in the diet. During early June, 0 group Lesser Sandeel occurrence remained high, whilst 1+ group Lesser Sandeels were replaced by Sprats, gobies and gadids. By late June, 1+ group Lesser Sandeels were absent from the diet, whilst there was no significant difference in the occurrence of Sprats, gobies and 0 group Lesser Sandeels (Fig. 1; Table 4). Differences in frequency of

Table 4. Z statistics for pairwise comparisons between predicted values of prey types on three dates through the season. ** $P < 0.01$.

		Lesser Sandeel			
Date	Prey typ	0 group	1+ group	Sprat	Goby
25 May	1+ group Lesser Sandeel	1.03			
	Sprat	**5.71	**2.60		
	Goby	**6.76	**2.95	0.43	
	Gadid	**8.95	**3.54	1.39	1.13
9 June	1+ group Lesser Sandeel	1.73			
	Sprat	**4.49	1.48		
	Goby	**4.91	1.77	0.41	
	Gadid	**3.23	1.19	-0.04	-0.32
24 June	1+ group Lesser Sandeel	**7.58			
	Sprat	1.59	**-3.20		
	Goby	1.43	**-3.20	-0.10	
	Gadid	**4.04	-0.89	1.87	1.93

occurrence between incubation and chick-rearing matched the seasonal patterns very closely. Thus, there was no difference in occurrence of 0 group Lesser Sandeels, significantly higher occurrence of 1+ group Lesser Sandeels during incubation and significantly higher occurrence of Sprats, gobies and gadids during chick-rearing (GLM: 0 group Lesser Sandeels: $W = 0.59$, $P = 0.44$; 1+ group Lesser Sandeels, $W = 4.89$, $P = 0.03$; Sprats: $W = 5.07$, $P = 0.03$; goby: $W = 4.18$, $P = 0.04$; gadids: $W = 4.87$, $P = 0.03$).

Comparison of adult and chick diet

Of 2017 prey items delivered to chicks, 1663 (82.5%) could be identified to species and assigned to a size class. The commonest prey was Sprats (79%), with the rest of the diet composed primarily of 1+ group Lesser Sandeels (20%). 0 group Lesser Sandeels and gadids accounted for less than 1% of prey delivered to chicks (Table 5). Sprats were the most energetically rich prey item, followed by 1+ group Lesser Sandeels, gadids and 0 group Lesser Sandeels (Table 5). Prey ingested by adults were significantly smaller than

Table 5. Number, mean length and mean energy value of each prey type delivered to Common Guillemot chicks, 2-30 June 2003.

Prey type	very small	small	medium	large	very large	Total	Mean length (mm)	Mean energy value (kJ)
0 group Lesser Sandeel	9					9	60	3.76
1+ group Lesser Sandeel		239	74	11		324	99	22.70
Sprat		1286	26	8	1	1321	101	71.36
Gadid		4	1	2		7	67	9.83
Squid		2				2	50	n/a
Unknown species/length						354		
Total						2017		

Table 6. Number of fish in each length class in adult and chick diet during chick-rearing (2-30 June 2003).

Age class	Prey length class						
	1	2	3	4	5	6	Total
Chick	6	10	1527	100	19	1	1663
Adult	145	49	39	1	0	0	234

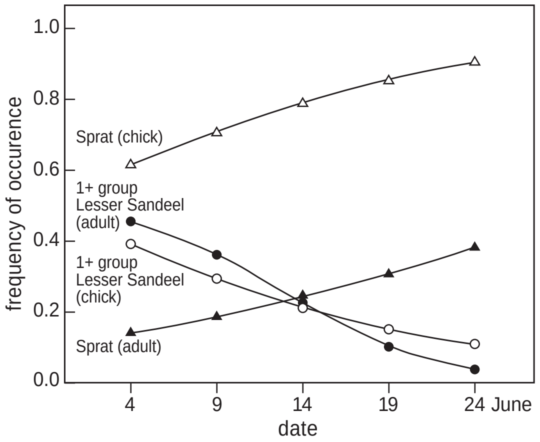

Fig. 2. Predicted values of frequency of occurrence of Sprat and 1+ group Lesser Sandeels in adult and chick Common Guillemot diet.

those delivered to chicks (Table 6; GLMM: interaction between age class and length class: $W = 20.58$; $P < 0.001$). The occurrence of 1+ group Lesser Sandeels was similar between adult and chick diet, declining from ca 40% in early June to < 10% at the end of June. In contrast, Sprats were more than twice as frequent in the diet of the chicks than adults, although both followed a similar increase in occurrence from early to late June (Table 7; Fig. 2). Goodness of fit tests confirmed the effect of season and age class on the occurrence of these two prey types (1+ group Lesser Sandeels: $\chi^2 = 2.99$, $P = 0.08$; Sprats: $\chi^2 = 2.93$, $P = 0.09$).

DISCUSSION

There was a marked difference in the diet of adult and young Common Guillemots, in accordance with our prediction. Throughout the sampling period, 0 group Lesser Sandeels were the most frequently recorded prey item in adult Common Guillemot diet. The remainder of the diet consisted of 1+ group Lesser Sandeels, gobies and, to a lesser extent, gadids and Sprats. In contrast, 79% of prey deliveries to chicks were Sprats and 20% were 1+ group Lesser Sandeels, with an almost complete absence of 0 group Lesser Sandeels, gadids and gobies. In addition to differences in species composition, we found that prey quality also differed between adult and chick diet. Not

Table 7. Deviance ratios for each parameter fitted sequentially for 1+ group Lesser Sandeels and Sprats in the diet of adult and chick Common Guillemots.

	1+ group Lesser Sandeel			Sprat		
Model	W	*P*	df	W	*P*	df
Julian	84.16	< 0.001	1	73.58	< 0.001	1
$Julian^2$	0.09	0.75	1	0.01	0.93	1
$Julian^3$	0.14	0.71	1	0.02	0.89	1
Age	1.27	0.26	1	28.01	< 0.001	1
Julian x age	0.68	0.41	1	0.04	0.84	1

only were chicks fed larger prey on average than the adults themselves ingested, they were also fed a higher proportion of Sprats, the most energy rich species. Together, these differences in species composition and prey quality between self feeding and provisioning diet confirm that breeding Common Guillemots, as obligate single prey loaders and central place foragers, show very strong selection of high quality prey for their chicks.

The prey size differences between adult and chick diet were consistent throughout the period despite a strong seasonal pattern in prey composition in line with our current understanding of the availability of different prey types. Thus, adults appear to maintain a consistent strategy throughout the season of foraging on all available prey types for themselves, but bringing only large fish to the chicks. The seasonal patterns of prey composition in both diets accorded well with previous work on the diet of Common Guillemot chicks and other seabird species breeding in the region (Harris & Wanless 1985; Finney *et al.* 1999; Lewis *et al.* 2001, 2003; Wilson *et al.* 2003; Wanless *et al.* 2004). In the adult diet, 1+ group Lesser Sandeels were important at the beginning of the season, before declining strongly during chick-rearing, as they were replaced by Sprats, gobies and gadids, while the presence of 0 group Lesser Sandeels was consistently high throughout the study period. A similar pattern for 1+ group Lesser Sandeels and Sprats was also apparent in the chick diet, with the former decreasing in importance and being replaced by the latter, as previously recorded at this colony (Harris & Wanless 1985; Finney *et al.* 1999).

A shift away from 1+ group Lesser Sandeels during June is likely to reflect changes in prey behaviour. In early summer, these fish are active in the water column but, as the season progresses, they spend an increasing amount of time buried in the sediment (Winslade 1974), and therefore probably become less available to predators such as Common Guillemots. 0 group Lesser Sandeels were recorded in the adult diet from the start of the sampling period (17 May). There is considerable annual variation in the first appearance of 0 group Lesser Sandeels in the diet of Black-legged Kittiwakes (range 12 May to 2 June across 7 years, Lewis *et al.* 2001, pers. comm.; 12 May in 2003), which is believed to depend on the timing of metamorphosis from the larval to the juvenile fish stage (Winslade 1974). Thus, the seasonal pattern of 0 group presence in Common Guillemot adult diet is likely to be strongly dependent on conditions in the year of study. The reason for the increase in gadids and gobies as the season progressed is unclear; there are no appropriate data on these species to establish whether this pattern accords with their seasonal availability.

Seasonal trends in adult Common Guillemot diet have been demonstrated at other colonies, but not on such a fine scale. In California, Ainley *et al.* (1996) described a switch in the diet from euphausiids in March and April, to juvenile rockfish or anchovies in May. Blake *et al.* (1985) described seasonal changes in the diet of adult birds feeding in the North Sea and concluded that sandeels were generally dominant from March to August, with clupeids and gadids taken more often in September and October. Sampling was not continuous in their study, but it was suggested that there was a change from reliance on older sandeels to 0 group when they became abundant.

The water off-loading method has been used successfully in species that regurgitate (Duffy & Jackson 1986) but not, to our knowledge, on species that do not. It provides a useful non-destructive method of obtaining diet samples, and birds showed no visible adverse effects to the procedure. As with diet sampling of auks from dissection, the food present in the stomach was highly digested and many otoliths were fragmented, implying that recent meals had been almost completely digested. Thus, our data will have been affected by different rates of otolith digestion (Gaston & Nettleship 1981; Bradstreet & Brown 1985). In general the time taken for an otolith to digest increases with increasing size, and clupeid otoliths are more readily digested than sandeel otoliths (Johnstone *et al.* 1990). Thus, the frequency of Sprats and the smaller prey types (0 group Lesser Sandeels, gobies and gadids) are likely to be underrepresented in the adult samples. Occurrence of invertebrates may also be underestimated because of their short retention time in the stomach. Some groups have hard parts that are resistant to digestion, such as the polychaetes whose jaws were detected in this study and by Blake *et al.* (1985). Other groups such as crustacea are small and relatively soft-bodied. However, if such groups formed an important component of adult diet this would tend to make the difference between adult and chick diet even more extreme. We minimised the impact of these biases on our conclusions by quantifying frequency of occurrence only. Methods that estimate numerical abundance and biomass of different prey types in adult and prey diet would provide a much more detailed diet description, although we do not expect that these would impact on our main findings.

Whilst our results are based on a single year only, we suggest that prey consumption models should not, as up to the present (e.g. Furness 1978; Tasker & Furness 1996; Wanless *et al.* 1998), assume that diets of Common Guillemot adults and chicks are similar. As Common Guillemots are one of the main seabird consumers of fish in the North Sea, the importance of 0 group Lesser Sandeels in their diet has implications for assessing the interaction between top marine predators, fish prey and fisheries. The Lesser Sandeel fishery in the North Sea primarily targets 1+ group Lesser Sandeels (ICES 2001), but a more complex relationship between Common Guillemots and sandeel fisheries is more likely than previously thought.

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SAMENVATTING

De Zeekoet *Uria aalge* is een van de talrijkste zeevogels van het Noord-Atlantische gebied. De prooien die volwassen vogels aan hun jongen in de kolonie voeren, zijn goed bekend, omdat de vis goed zichtbaar is bij de overdracht van oudervogel naar jong. Een stuk minder goed bekend is wat adulte vogels zelf eten. Waarnemingen van foeragerende Zeekoeten op volle zee leken vaak niet te kloppen met gegevens (zichtwaarnemingen van prooioverdrachten) die tegelijkertijd over het voedsel van deze dieren werden verzameld in de kolonie. In veel geval werd eenvoudigweg verondersteld dat het voedsel van de jongen wel hetzelfde zou zijn als het voedsel dat de oude dieren voor zichzelf vingen. De voedseltheorie voorspelt echter dat oudervogels een zo hoog mogelijke kwaliteit voedsel aanvoeren voor hun jongen. Voor vogels zoals Zeekoeten, die met een enkele vis in de snavel komen aanvliegen, geldt vermoedelijk eens te meer dat het verstandig is om een prooi van hoge kwaliteit voor hun nageslacht te selecteren. Zelf zouden deze vogels hun kwaliteitseisen wat lager kunnen stellen. In dit artikel wordt het voedsel van kuikens en oudervogels vergeleken. De gegevens werden verzameld op Isle of May, Schotland. De

oudervogels werden gevangen en met water leeggespoeld om te zien wat er zich in de maag bevond. Inderdaad bleken de dieren met andere prooien aan te komen vliegen dan die zij zelf juist geconsumeerd hadden. En inderdaad was de kwaliteit van de voor de jongen aangevoerde prooi relatief hoog. De jonge Zeekoeten werden vooral met vette Sprot *Sprattus Sprattus* en volwassen Zandspieringen *Ammodytes marinus* gevoerd. In de maag van de adulte vogels werd een veel grotere verscheidenheid aan vissen aangetroffen, vooral wat betreft de grootte van de vissen; in het algemeen waren de visjes die aan de kuikens werden gevoerd, echter groter en energierijker. De adulte vogels aten vooral veel 0-groep Zandspieringen, aanmerkelijk kleinere vissen dan de jaarklasse waarmee de jongen vooral werden gevoerd. De resultaten brachten de gegevens die op zee werden verzameld en het materiaal dat in de kolonie werd vergaard, weer prachtig op één lijn. (CJC)

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APPENDIX

Regression equations used to calculate fish length (FL, in mm) from otolith length (OL, in mm) for 0 group and 1+ group Lesser Sandeels, calculated from otoliths from known length fish collected from 1 June – 4 July 2003 on the Isle of May from food loads dropped by puffins during mist-netting (see Wanless *et al.* in press for details).

Lesser Sandeel age	Regression equation	Fish length (range)	Otoliths (*n*)
0 group	FL = 14.96 + (55.47 OL)	37-92 mm	376
1+ group	FL = 11.29 + (48.14 OL)	77-122 mm	98