TEMPORAL COMPARISONS IN FEEDING ECOLOGY AND GROWTH OF YOUNG COMMON GUILLEMOTS *URIA AALGE*

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Wilhelm, S.I. & Storey, A.E. 2004. Temporal comparisons in feeding ecology and growth of young Common Guillemots *Uria aalge*. Atlantic Seabirds 6(2): 47-64. *Short and long-term changes in feeding ecology of Common Guillemots* Uria aalge *breeding in Witless Bay, Newfoundland, were investigated across three consecutive breeding seasons (1998-2000) and across decades (late 1970s to mid 1980s versus 1998-2000). The relationship between feeding rates and two chick growth parameters (mass and wing length) was also examined. From 1998-2000, observations were focused on the same subset of colour-ringed guillemots. Chick provisioning rates were highly variable within and across seasons. In all years, young guillemots were fed primarily medium-sized Capelin* Mallotus villosus. *In 1999 and 2000, their diets were supplemented with sandeel* Ammodytes *spp. Chick mass did not differ across years, however, a positive relationship existed between feeding rates and chick mass. Although no relationship was found between feeding rates and wing length, chicks reared in 2000 had longer wings than same aged chicks reared in 1998 and 1999. During unfavourable breeding conditions, wing growth may be prioritized to allow earlier departure. Overall, the diet and condition of Common Guillemot chicks reared in Witless Bay are similar to those reported in the 1970s and 1980s, despite important changes in Capelin biology and distribution in the Northwest Atlantic.*

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INTRODUCTION

In the spring, many seabirds return to land to breed, often in large dense colonies. Off the east coast of Newfoundland, this spatial and temporal clustering of birds is generally timed to coincide with the inshore arrival of spawning Capelin *Mallotus villosus*, the main prey fed to many seabird chicks (Massaro *et al.* 2000; Davoren & Montevecchi 2003). Prior to 1990, Capelin was the primary prey item for Common Guillemots *Uria aalge* breeding in Labrador (Birkhead & Nettleship 1987), but following a sharp decline in Capelin abundance, chicks were fed primarily Daubed Shannies *Lumpenus maculates* (Bryant *et al.* 1999). This diet shift had no apparent effect on chick

feeding rates and growth, although adults were exhibiting high foraging effort as shown by low co-attendance time at the colony (Bryant *et al.* 1999).

The impact of changes in Capelin biology is of growing concern on Common Guillemots and other seabirds breeding off the east coast of Newfoundland. There is evidence that Capelin abundance may have decreased since the 1980s while Capelin size and condition declined throughout the 1990s (reviewed in Carscadden *et al.* 2002). In 1991, inshore migration and spawning of Capelin was delayed due to unusually cold sea temperatures (Carscadden *et al.* 1997). Sea temperatures subsequently returned to normal, but delayed inshore spawning persisted at least to the 2000 season, presumably because of the smaller size of the fish since smaller Capelin spawn later (Carscadden *et al.* 1997; Carscadden *et al.* 2002).

The Witless Bay Ecological Reserve, off the south-east coast of Newfoundland, has approximately 100,000 breeding pairs of Common Guillemots on three islands: Gull, Green and Great Island (Robertson *et al.* 2004; Canadian Wildlife Service, unpubl. data). During the late 1970s, guillemot chicks on Gull Island were fed mostly Capelin (97%) with the remainder of their diet consisting of sandeel *Ammodytes* spp (Mahoney 1980), whereas in 1982-1985, chick diet while still primarily Capelin, included 9% Sandeel (Burger & Piatt 1990). In the latter study, hydroacoustic data showed that Capelin abundance varied during the chick-rearing period in two of the four years. Low Capelin abundance resulted in higher foraging effort and, in at least one year, to lower Capelin but higher Sandeel proportions in the chicks' diet. Chick feeding rates and breeding success did not vary across years, suggesting that parents were able to compensate for reduced Capelin abundance by increasing their foraging effort and/or bringing in more Sandeel to the chicks (Burger & Piatt 1990).

Common Guillemots breeding on Great Island, 7.5 km south of Gull Island, showed variable foraging effort and chick feeding rates within and between the 1998, 1999, and 2000 seasons (Wilhelm 2004). Despite high foraging effort, parents fed the chicks at low rates during early chick rearing in 2000, suggesting that prey availability was low, presumably due to the late arrival of spawning Capelin (Wilhelm 2004). In 1999, however, adults fed chicks at high rates with lower foraging effort compared to the other years, due to chicks hatching after the inshore arrival of spawning Capelin and/or higher Sandeel availability around the breeding colonies (Wilhelm 2004).

This study investigated changes in guillemot chick feeding rates, prey type and size across the chick-rearing period in three consecutive years (1998-2000). Our results were compared with those from earlier studies in the area. Chick growth is directly linked to the amount of food parents bring to their young (Harris 1978). The relationship between feeding rates and two chick

growth parameters (mass and wing length) was examined within and across years, and in comparison to other Common Guillemot colonies.

MATERIALS AND METHODS

This study was conducted on a group of Common Guillemots nesting on Great Island (47°11'N, 52°49'W), Newfoundland, Canada, from June to August 1998-2000. Continuous observations from dawn (first light after 04:30 h) to dusk (last light before 21:30 h), were made on 11 days in 1998 (175.8 hr total), 15 days in 1999 (238 hr total) and 12 days in 2000 (190.8 hr total). Guillemots were individually colour-ringed and breeding sites were easily viewed from the blind. Some adults had been previously marked with a Canadian Wildlife Service metal band in the 1980s (D. Cairns, *pers. comm.*) and were observed to be rearing chicks up to 2003. Breeding success (fledged chicks/eggs laid) was monitored in 1999 and 2000 and was generally high (75% and 79% respectively; Wilhelm & Storey 2002).

Chick provisioning rates and diet composition Number of daily chick feeds, type and size of prey were determined by direct observation of fish being carried in the bill by adults and delivered to the chick. In 1998, fish species were identified as "Capelin" or "other". During the second half of the 1998 chick-rearing period, "other" fish were primarily identified as Sandeel. In 1999 and 2000, fish species were identified as "Capelin" or "Sandeel". Fish sizes were estimated by the length of fish (including tail) protruding from the bird's bill tip upon its arrival at the nest site and designated to one of three size classes: small (< 3 cm of fish length protruding from bird's bill), medium (3-6 cm) and large (> 6 cm). Diet composition was investigated across Julian date and in relation to age of chick.

Chick body mass and wing length Body mass (±1 g, with a 300 g Pesola spring scale) and wing length (±1 mm, from the carpal joint to the tip of the longest primary covert, with a ruler) were obtained once from chicks aged 12-20 d in each year (1998: $n = 13$, 1999: $n = 14$, 2000: $n = 18$). The hatching date of a chick was determined by observing the actual hatching ($n = 15$), by seeing a chick at a site where there had not been a chick on the previous observation day ($n = 24$) or by counting forward the mean incubation period (33 days, *pers. obs.*; $n = 7$) from the date the egg was laid.

Data analysis Chick feeding rates were analysed for 23 pairs in 1998, 20 pairs in 1999, and 26 pairs in 2000. However, sample sizes varied across the chick-rearing period as a function of hatch dates, colony departure dates, and the fate

of individual chicks. Daily provisioning rates (mean total number of fish received by both parents per day) were compared across Julian dates (grouped into 7d categories: Julian date 178-184, 185-191, 192-198, 199-205, and 206-212) among years using a mixed within-subjects ANCOVA with nest site as the repeated subject variable and hatch date as the covariate, to control for age, as there is evidence that parents may modify frequency of daily feeds depending on the age of the chick (Harris & Wanless 1985, 1995; Hatchwell 1991). The Tukey-Kramer Method (Sokal & Rohlf 1995) was applied to make pair-wise comparisons for significant ANOVAs. All interactions were examined, however, none were significant.

Chi-squared tests were applied to assess if prey species differed within each year across Julian date. Chi-squared tests were also used to investigate differences in type and size of prey delivered to chicks across years for three age categories separately (1-8d, 9-16d and 17d to departure) and within each year across the three age categories. If a significant difference was found, pairwise comparisons were made using the Yates' correction (Sokal & Rohlf 1995).

To quantify differences in chick growth parameters between years, an ANCOVA with age as a covariate was conducted on each growth parameter separately. Chicks were randomly selected and matched by age across years (mean = 15.2 d and $n = 10$ for each year) to ensure that age of chick was not a confounding factor. Wing lengths were log-transformed to homogenize the variance. Pairwise comparisons were adjusted using the Bonferroni correction.

To assess if provisioning rates were related to chick growth, mean daily chick feeding rates prior to measuring the chick was calculated for all chicks. These means were then grouped into three age categories: 12-14d, 15-17d, and 18-20d, and averaged. A Pearson's correlation was subsequently applied to examine the relationship between chick feeding rates with chick mass and wing length (all years combined). All values are reported as means ± SE. Statistical significance was set at $\alpha = 0.05$.

RESULTS

Chick provisioning rates Provisioning rates differed across years ($F_{2,35} = 14.18$, $P < 0.0001$) and across Julian date ($F_{4,88} = 11.10$, $P < 0.0001$; Fig. 1). Overall, mean daily chick-feeding rates were significantly lower in 2000 (3.44 ± 0.24 fish d-1, $n = 26$) compared to 1999 (5.30 ± 0.21 fish d-1, $n = 20$; Tukey-Kramer Method, $P< 0.05$), with chicks being fed on average two extra fish per day in 1999. In all years, provisioning rates were lowest during the first week of chick rearing and peaked between Julian dates 192-198 (Fig. 1).

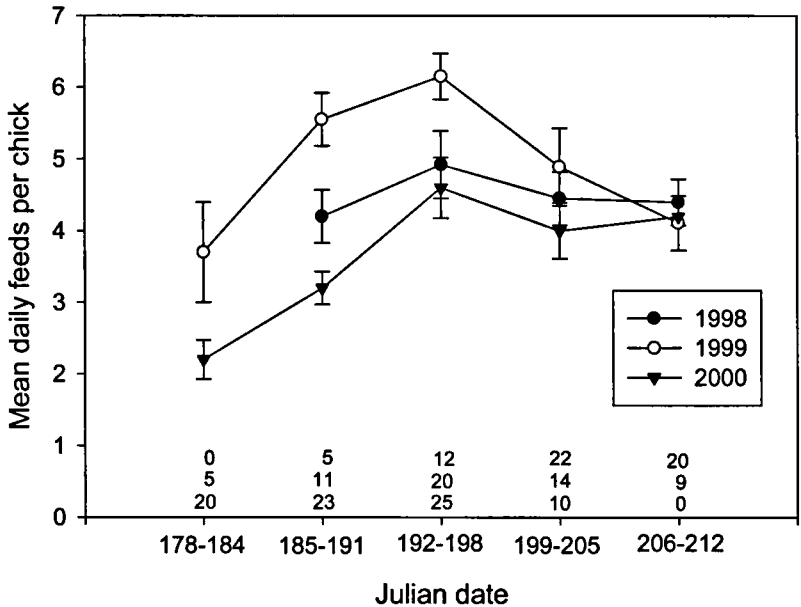

Figure 1. Mean number of daily feeds (± SE) received by Common Guillemot chicks across five Julian date categories (178-184, 185-191, 192-198, 199-205, and 206-212) during the 1998-2000 chick rearing periods. Numbers above x-axis represent sample sizes for each year in each age category (top row = 1998; middle row = 1999; bottom row = 2000).

Figuur 1. Gemiddeld aantal dagelijkse voedselafdrachten (± SD) aan zeekoetkuikens gedurende vijf Juliaanse datumcategorieën (178-184, 185-191, 192-198, 199-205 en 206-212).

Species and size of fish fed to chicks Capelin dominated the diet in all years (Tables 1 and 2). However, type of prey fed to chicks across Julian date varied differently in each year. In 1998, chicks were fed almost exclusively Capelin throughout chick rearing, with the exception of the first week (Table 1). In 1999, chicks were fed exclusively Capelin during the first week of chick rearing. However, by the end of the season, Sandeel made up 29% of the diet (Table 1). In 2000, chick diet did not vary significantly. Chicks were fed mostly Capelin, however, their diets were consistently supplemented with Sandeel (Table 1).

Table 1. Fish species fed to Common Guillemot chicks across Julian dates grouped into 7-d categories (178-184, 185-191, 192-198, 199-205, and 206-212) during three chick-rearing periods (1998-2000) on Great Island, Newfoundland. Chi-squared analyses examine diet shifts across Julian dates.

Tabel 2. Vissoorten die gevoerd werden aan zeekoetkuikens per zevendaagse periode (in Juliaanse data) gedurende drie kuikenperiodes (1998-2000) op Great Island, Newfoundland. Chi-kwadraat analyses vergelijken een verschuiving in dieet.

	Capelin		Other[1]				
	No.	%	No	%	Total	χ^2	*P*
1998							
185-191	20	80	5	20	25	18.81	<0.001
192-198	145	96	6	4	151		
199-205	153	94	10	6	163		
206-212	135	93	10	7	145		
1999							
178-184	21	100	0	0	21	40.26	<0.001
185-191	167	87	25	13	192		
192-198	205	92	18	8	223		
199-205	201	82	43	18	244		
206-212	61	71	25	29	86		
2000							
178-184	74	86	12	14	86	4.51	> 0.10
185-191	205	85	36	15	241		
192-198	181	92	16	8	197		
199-205	79	82	17	18	96		

[1]For 1999 and 2000, fish species were identified as sandeel.

Chick diet composition varied significantly among years in all three age groups (Table 2). Chicks were fed a higher proportion of sandeel in 2000 compared to 1998, regardless of chick age (1- 8 d: $\chi^2_1 = 9.40$, $P < 0.01$; 9-16 d: $\chi^2_1 = 5.80$, $P < 0.05$; 17 d to departure: $\chi^2_1 = 9.26$, $P < 0.01$; Table 2). In 1999, chicks were also fed more sandeel compared to 1998 at ages 9-16 d ($\chi^2_1 = 4.94$, $P < 0.05$) and 17 d to departure ($\chi^2_1 = 13.64$, $P < 0.01$; Table 2). Prey composition did not vary within any given year across age of chick (1998: $\chi^2_2 = 0.8$, $P > 0.10$; 1999: $\chi^2_2 = 2.6$, $P > 0.10$; 17 d to departure: $\chi^2_2 = 1.5$, $P > 0.10$; Table 2). Overall, sandeel or other fish (most likely sandeel) made up 3% of a chick's diet in 1998, 15% in 1999 and 14% in 2000.

Table 2. Fish species fed to Common Guillemot chicks across three age categories (1-8 d, 9-16 d and 17 d to departure) during three chick-rearing periods (1998-2000) on Great Island, Newfoundland. Chi-squared analyses examine diet shifts between years.

Tabel 2. Vissoorten die gevoerd werden aan zeekoetkuikens per leeftijdscategorie (1-8, 9-16 en 17 dagen voor 'uitvliegen') gedurende drie kuikenperiodes (1998-2000) op Great Island, Newfoundland. Chi-kwadraat analyses vergelijken een verschuiving in dieet.

	Capelin		Other[1]				
	No.	%	No	%	Total	χ^2	*P*
1-8d							
1998	179	97	6	3	185	10.99	<0.01
1999	194	89	24	11	218		
2000	207	83	42	17	249		
9-16d							
1998	223	96	9	4	232	11.17	<0.01
1999	136	86	22	14	158		
2000	248	89	31	11	279		
17d to departure							
1998	120	98	2	2	122	15.06	<0.01
1999	53	81	12	19	65		
2000	168	85	30	15	198		

[1]For 1999 and 2000, fish species were identified as sandeel.

Chicks were fed primarily medium-sized Capelin (48%), and there was no significant difference in size between years at any of the age categories (Table 3). Within each year, chicks were also fed primarily medium-sized Capelin across all age groups (1998: $\chi^2_4 = 3.81$, $P > 0.10$; 1999: $\chi^2_4 = 8.31$, $P > 0.05$; 2000: $\chi^2_4 = 4.56$, $P > 0.10$; Table 3). In 1998 and 1999, other researchers collecting chick diet at another guillemot colony on Great Island reported that chicks were mostly fed Capelin measuring 100-150 mm in length, which they classified as medium-sized; no difference in fish sizes were found between years (Davoren & Montevecchi 2003).

Size of sandeel varied across years with chicks aged 1-8 d being fed a higher proportion of large sandeel and lower proportion of medium sandeel in 2000 compared to 1999 (Table 4). Conversely, chicks aged 17 d or older were fed more small sandeel in 2000 compared to 1999 (Table 4), although most sandeel fed to chicks in both years were medium and large. Size of sandeel did

Table 3. Number (%) of small, medium, and large Capelin fed to Common Guillemot chicks across three age categories (1-8 d, 9-16 d and 17 d to departure) during three chick-rearing periods (1998-2000) on Great Island, Newfoundland. Chi-squared analyses examine diet shifts between years.

Tabel 3. Aantal (%) kleine, medium en grote Lodde dat aan zeekoetkuikens gevoerd werd per leeftijdscategorie (1-8, 9-16 en 17 dagen voor 'uitvliegen') gedurende drie kuikenperiodes (1998-2000) op Great Island, Newfoundland. Chi-kwadraat analsyes vergelijken een verschuiving in dieet.

	Small	Medium	Large	Total	χ^2	*P*
1-8d						
1998	38 (18)	114 (54)	59 (28)	211	5.43	>0.10
1999	62 (28)	107 (48)	53 (24)	222		
2000	36 (23)	65 (42)	53 (34)	154		
9-16d						
1998	31 (21)	64 (43)	55 (37)	150	3.00	>0.50
1999	38 (16)	129 (54)	72 (30)	239		
2000	39 (19)	93 (45)	75 (36)	207		
17d to departure						
1998	15 (23)	27 (42)	22 (34)	64	5.49	>0.10
1999	22 (14)	83 (51)	56 (35)	161		
2000	12 (12)	53 (51)	39 (38)	104		

not differ across years in chicks aged 9-16 d (Table 4). Size of Sandeel fed to chicks varied across age in 1999 ($\chi^2_4 = 20.43$, $P < 0.001$) but not in 2000 ($\chi^2_4 = 3.91$, $P > 0.01$; Table 4). In 1999, older chicks (17 d to departure) were fed a higher proportion of large Sandeel compared to younger chicks (1-8 d; $\chi^2_1 = 6.24$, $P < 0.025$; Table 4).

Chick growth parameters and provisioning rates Chick body mass did not differ across years ($F_{2,26} = 0.92$, $P = 0.41$). However, inter-annual differences were found in wing length ($F_{2,26} = 9.87$, $P = 0.01$), with chicks reared in 2000 having longer wings compared to the other two years (Fig. 2). A significant correlation was found between chick feeding rates and chick mass for chicks aged 12-14 d ($r = 0.49$, $P = 0.05$, $n = 14$). A similar relationship was found in the other two age categories, although correlations were not statistically significant (Fig. 3). No relationship was found between chick feeding rates and wing length in any of the age groups (Fig. 4).

Table 4. Number (%) of small, medium, and large sandeel fed to Common Guillemot chicks across three age categories (1-8 d, 9-16 d and 17 d to departure) during two chick-rearing periods (1999-2000) on Great Island, Newfoundland. Chi-squared analyses examine diet shifts between years.

Tabel 4. Aantal (%) kleine, medium en grote Zandspiering dat aan zeekoetkuikens gevoerd werd per leeftijdscategorie (1-8, 9-16 en 17 dagen voor 'uitvliegen') gedurende twee kuikenperiodes (1998-2000) op Great Island, Newfoundland. Chi-kwadraat analyses vergelijken een verschuiving in dieet.

	Small	Medium	Large	Total	χ^2	*P*
1-8d						
1999	3 (11)	19 (70)	5 (19)	27	30.42	<0.001
2000	5 (16)	10 (32)	16 (52)	31		
9-16d						
1999	6 (15)	21 (53)	13 (33)	40	3.54	>0.10
2000	4 (16)	10 (40)	11 (44)	25		
17d to departure						
1999	2 (5)	18 (49)	17 (46)	37	7.38	<0.05
2000	3 (17)	8 (44)	7 (39)	18		

DISCUSSION

Inter and intra-annual variation in chick provisioning rates and diet (1998-2000) Provisioning rates were unusually low during early chick rearing in 2000. During this time, chicks were being fed primarily medium-sized Capelin. Adults were presumably foraging at long distances from the breeding colony or allotting longer search times per prey item, reflected in the low chick feeding rates. Common Guillemots presumably feed well away from the breeding area in May and early June, as shown by low colony attendance during this time (Wilhelm & Storey 2002). However, they forage in the vicinity of the breeding colonies (< 5 km; Davoren *et al.* 2003) when spawning Capelin arrive inshore (Cairns *et al.* 1987; Piatt 1990). Hence, low chick feeding rates during first half of chick rearing in 2000 was likely due to a mismatch between Capelin arrival and chick hatching (Wilhelm 2004). During this time, however, chicks were fed higher proportions of large sandeel compared to other years. Although adults appeared to be partially compensating for potentially low Capelin availability by selecting large sandeel, feeding rates were still lower compared to other years and other colonies (see Wilhelm 2004). These results suggest that guillemots breeding in Witless Bay do not have a suitable alternate prey to Capelin, as seen

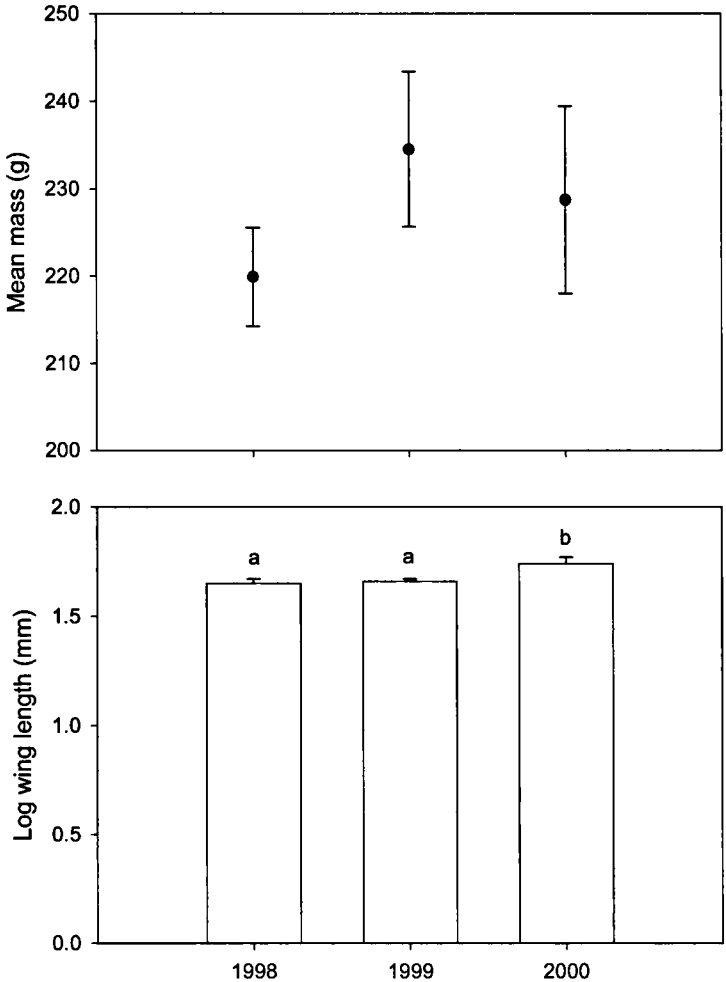

Figure 2. Analysis of covariance on body mass and wing length of Common Guillemot chicks aged 13 to 20 d during three consecutive chick-rearing periods (1998-2000). n = *10 for each group. Letters above bars show significant differences among groups.*

Figuur 2. Covariantie-analyse van lichaamsgewicht en vleugellengte van zeekoetkuikens in de leeftijd van 13 tot 20 dagen gedurende drie achtereenvolgende kuiken-periodes (1998-2000). n = *10 voor iedere groep. Letters boven de staafjes geven significante verschillen tussen groepen aan.*

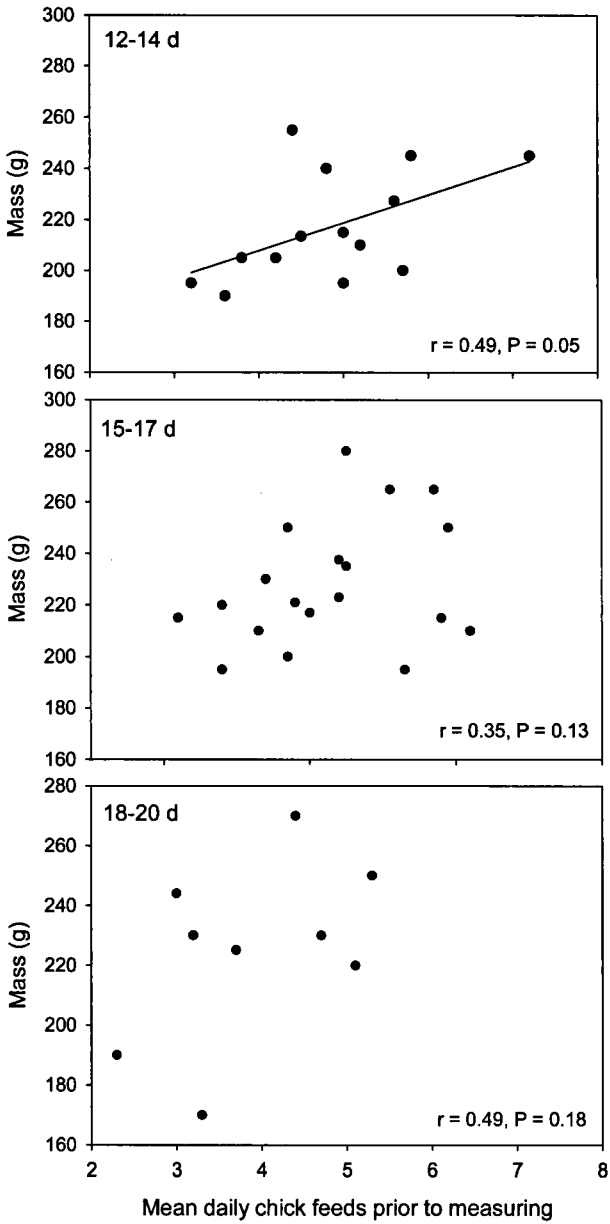

Figure 3. Relationship between chick mass (g) and provisioning rates (mean number of chick feeds per day) across three age categories: 12-14 d (n = 14), 15-17 d (n = 20), and 18-20 d (n = 9).
Figuur 3. Relatie tussen kuikengewicht (g) en voerfrequentie (gem. aantal dagelijkse voerbeurten per kuiken) per leeftijdscategorie: 12-14 d (n = 14), 15-17 d (n = 20), and 18-20 d (n = 9).

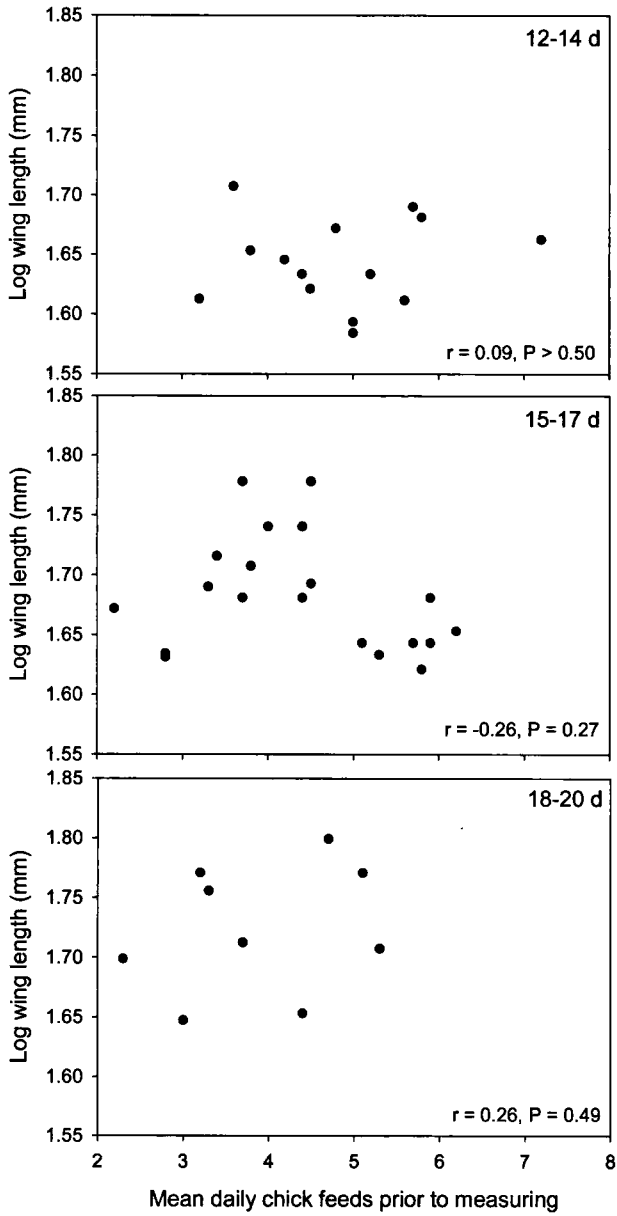

Figure 4. Relationship between wing length (mm; log-transformed) and provisioning rates (mean number of chick feeds per day) across three age categories: 12-14 d (n = 14), 15-17 d (n = 20), and 18-20 d (n = 9).

Figuur 4. Relatie tussen vleugellengte (mm; na log-transformatie) en voerfrequentie (gem. aantal dagelijkse voerbeurten per kuiken) per leeftijdscategorie: 12-14 d (n = 14), 15-17 d (n = 20), and 18-20 d (n = 9).

elsewhere (Harris & Wanless 1985; Hatchwell 1991; Bryant *et al.* 1999; but see Burger & Piatt 1990).

Chicks were fed a higher proportion of Sandeel during the entire chick rearing periods of 1999 and 2000 compared to 1998. Large increases of juvenile Sandeel abundance were recorded over the Grand Banks in 1998 and 1999 (Anderson 2001), which may have contributed to the increase in adult Sandeel fed to guillemot chicks in subsequent years. However, it does not appear that the observed increase in Sandeel abundance was related to the high chick feeding rates in 1999. When chick-feeding rates peaked during mid-chick rearing in 1999, chicks were being fed primarily Capelin (92%). Sandeel proportions did, however, increase seasonally as chick feeding rates declined, suggesting that Capelin became less available as the chick-rearing period progressed.

During both instances of apparent low Capelin availability (early chick rearing in 2000 and late chick rearing in 1999), birds were returning to the colony with a higher proportion of large Sandeel. Sandeel have a higher energy density (7.3 kJ per g) than ovid female Capelin (4.6 kJ per g) and adult male Capelin (3.8 kJ per g; reviewed in Cairns *et al.* 1990), thereby making Sandeel a higher quality prey for growing chicks. When Capelin abundance in surrounding waters is low, guillemots spend more time away from the colony, presumably searching for prey (Burger & Piatt 1990). Therefore, if schools of Capelin were not as predictably found or were located far from the colony, and guillemots were required to increase their foraging time, then a more effective strategy may have been to spend extra time searching for the higher quality large Sandeel.

Diet comparison with Gull Island 1977-1978 and 1982-1985 The current diet of Common Guillemot chicks reared in Witless Bay has changed little since the late 1970s. The proportion of Capelin ingested by guillemot chicks from 1977-1985 ranged from 89-97%, with the remainder of the diet consisting primarily of Sandeel (Mahoney 1980; Burger & Piatt 1990). In 1998-2000, the proportion of Capelin fed to chicks ranged from 85-97%, with the remainder being Sandeel. Fish sizes also appear to have remained similar since the 1980s. From 1982-85, most fish delivered to chicks measured between 106-141 mm in length (estimated from Burger & Piatt 1990). The majority of fish delivered to chicks in this study (1998-2000) and at another guillemot colony on Great Island (1998-99) were medium-sized, and estimated to measure 100-150 mm (Davoren & Montevecchi 2003).

Chick mass, wing length, and provisioning rates Chick mass did not differ across years, although analyses were restricted to a sub-set of chicks sampled to control for age. However, at the individual level, a positive relationship was

Table 5. See opposite page for legend.
Tabel 5. Zie tegenoverliggende pagina voor bijschrift.

chick age (d)	year	mean mass ± SE (g)	mean wing ± SE (mm)	*n*
Great Island, Newfoundland, Canada. Source: this study				
12-14	1998	216.0 ± 6.5	41.9 ± 1.3	6
	1999	231.0 ± 10.9	45.8 ± 1.2	5
	2000	212.0 ± 10.2	54.2 ± 5.6	5
15-17	1998	220.5 ± 7.7	46.4 ± 2.5	5
	1999	236.9 ± 10.5	45.1 ± 0.8	7
	2000	227.9 ± 9.1	52.8 ± 1.8	8
18-20	1998	234.5 ± 9.5	48.0 ± 3.6	2
	1999	260.0 ± 10.0	48.0 ± 3.0	2
	2000	208.0 ± 12.0	57.6 ± 2.1	5
Gull Island, Newfoundland, Canada. Source: Mahoney & Threlfall (1981)				
13	1977-78	193.3	n.d.	?
17		223.0	n.d.	?
19		236.0	n.d.	?
Isle of May, Scotland. Source: Harris & Wanless (1995)				
13	1983-92	236[1]	n.d.	?
16		248[1]	n.d.	?
19		250[1]	n.d.	?
Gannet Islands, Newfoundland, Canada. Source: Hipfner & Bryant (1999)				
13	1997	205[1]	43[1]	8
16		215[1]	50[1]	8
19		220[1]	58[1]	8
Hornøya, Norway. Source: Barrett et al. (1997)				
12-14	1990	240[1]	46[1]	15
15-17		250[1]	56[1]	15
18-20		250[1]	66[1]	12
Skomer Island, Wales. Source: Hatchwell (1991)				
12-13	1985-87	180[1]	43[1]	25
16-17		200[1]	53[1]	35
18-19		198[1]	57[1]	30

[1]Values estimated from graphs

Opposite page: table 5. Inter-annual differences in mass and wing length of Common Guillemot chicks of three age groups (12-14 d, 15-17 d, and 18-20 d) reared on Great Island, Newfoundland, and in comparison to Common Guillemot chicks of similar ages reared in other colonies.

Tegenoverliggende pagina: tabel 5. Jaarlijkse verschillen in gewicht en vleugellengte van zeekoetkuikens in drie leeftijdscategorieën (12-14, 15-17 en 18-20 dagen) op Great Island, Newfoundland, vergeleken met zeekoetkuikens van dezelfde leeftijd in andere kolonies.

found between provisioning rates and chick mass: individuals that were fed more frequently also had higher body mass. This linear relationship between amount of food received and chick mass has been observed in other auks, including Atlantic Puffins *Fratercula arctica* (Harris 1978; Barrett *et al.* 1987; Øyan & Anker-Nilssen 1996) and Cassin's Auklets *Ptychoramphus aleuticus* (Hedd *et al.* 2002).

Wing length differed across years, with chicks reared in 2000 having overall longer wings than those reared in 1998 and 1999. Although no relationship was found between provisioning rates and wing length, a trend toward a negative relationship was found at age 15-17 d. The relationship between wing growth and nutrition has been studied in other auk chicks, including Razorbills *Alca torda*, Black Guillemots *Cepphus grylle* and Atlantic Puffins (reviewed in Gaston 1985; Øyan & Anker-Nilssen 1996). Most report no relationship between wing length and food supply (but see Øyan & Anker-Nilssen 1996). The results in this study suggest that during unfavourable breeding conditions, such as low Capelin availability, wing growth can perhaps be prioritized in Common Guillemots. Rapid wing growth can benefit chicks as well as parents by allowing earlier departure, thereby bringing the chick to the food source rather than adults depleting their reserves by bringing the food to the chick (Sealy 1973). This strategy is used by intermediate auk species, including the Common Guillemot, where the male parent brings the chick to sea and continues to provide parental care for several weeks (Harris & Birkhead 1985).

Growth parameters of Great Island chicks in comparison to other colonies

Chick mass and wing length from this study and of chicks of similar age from other Common Guillemot colonies are summarized in Table 5. Although growth parameters in this study showed considerable intra-colony variation across years, the weights of chicks reared on Great Island from 1998-2000 fell within the range of chick masses reported at other colonies, and are similar to chicks reared on Gull Island in the late 1970s. Furthermore, relative to other guillemot colonies, the seemingly low mass of chicks reared on Great Island in 2000 (208 g) that were close to fledging (18-20 d) were comparable to chick weights on

Skomer Island in Wales (198 g), and higher than fledging masses of chicks on Funk Island (192 g; Davoren & Montevecchi 2003), 60 km away.

Similarly, the apparent long wings of chicks reared in 2000 on Great Island resembled those reported in Labrador and Wales. However, Great Island chicks reared in 2000 had considerably shorter wings compared to guillemot chicks reared in Norway and to fledging Funk Island chicks (estimated at 66.1 mm; Davoren & Montevecchi 2003). Chick feeding rates on Funk Island are among the lowest of any reported (Davoren & Montevecchi 2003) as a result of parents travelling approximately 45 km each way to find predictable food sources (Davoren *et al.* 2003). The low mass and long wings of these chicks are consistent with the view that wing growth is maintained or may be prioritized when feeding conditions are poor (Harris 1966).

Prey type and size brought back to chicks by breeding Common Guillemots in Witless Bay did not appear to have changed since the late 1970s. Furthermore, there is no indication that fish fed to chicks were of lower quality/condition, as chick growth parameters were similar between the late 1970s and the late 1990s. These results do not corroborate with the view that Capelin abundance and size have decreased since the 1980s (Carscadden *et al.* 1997). However, Common Guillemots do not sample the ocean randomly (Davoren *et al.* 2003), but may instead selectively choose high quality fish for their chicks. Mean daily chick feeding rates prior to measuring appeared to be a good predictor of chick mass, although the relationship with wing length was unclear. Wing growth may be more plastic than previously thought, as wing lengths of chicks were highly variable within and between colonies. Caution is warranted when using wing measurement as a single indicator of chick body size or age.

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TEMPORELE VERANDERINGEN IN DE VOEDSELECOLOGIE EN GROEI VAN KUIKENS BIJ DE ZEEKOET *URIA AALGE*

Veranderingen op korte en lange termijn in de voedselecologie van Zeekoeten *Uria aalge* broedend in Witless Bay, Newfoundland werden onderzocht in drie opeenvolgende broedseizoenen (1998-

2000) en in twee verschillende decaden (eind jaren zeventig tot halverwege jaren tachtig vergeleken met 1998-2000). Daarnaast werden fluctuaties in voedselafdrachten in verband gebracht met variaties betreffende de groei van kuikens (massa en vleugellengte). In 1998-2000 concentreerden de waarnemingen zich op dezelfde, individueel herkenbare (gekleurringde) Zeekoeten. De frequentie van voedselafdrachten wisselde enorm, zowel binnen elk seizoen als in vergelijking tussen de broedseizoenen onderling. Elk jaar werden de jonge kuikens vooral met Lodde *Mallotus villosus* gevoerd, maar in 1999 en 2000 werd daarnaast ook zandspiering *Ammodytes* spp. aangebracht. De gemiddelde massa van de kuikens met leeftijd verschilde niet van jaar tot jaar, maar er was een positief verband tussen de frequentie van voedselafdrachten en kuikengewicht. Ofschoon er geen verband werd gevonden tussen het aantal voedselafdrachten en de groei van de vleugels, vertoonden de kuikens in 2000 een sneller groei dan in 1998 en 1999. Verondersteld wordt dat de groei van de vleugels prioriteit krijgt over het lichaamsgewicht in jaren met ongunstige omstandigheden rond de kolonie, zodat de jongen eerder de kolonie kunnen verlaten. Over het algemeen waren dieet, groei en conditie van de kuikens in Witless Bay goed vergelijkbaar met de in eerdere jaren vergaarde gegevens, ondanks dat er belangrijke veranderingen zijn geweest in de groei en verspreiding van Lodde in het Noordwest Atlantische gebied in deze periode.

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