# COMPARATIVE BREEDING BIOLOGY OF GUILLEMOTS *URIA* SPP. AND RAZORBILLS *ALCA TORDA* AT A COLONY IN THE NORTHWEST ATLANTIC

## *VERGELIJKENDE BROEDBIOLOGIE VAN ZEEKOETEN EN ALKEN OP EEN KOLONIE IN HET NOORWESTELIJKE ATLANTISCHE GEBIED*

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*We compared various aspects of the breeding biology of Razorbills, Common Guillemots, and Brünnich's Guillemots (the "intermediate" auks) at the Gannet Islands, Labrador, Canada, in 1997. In all three species, laying followed a strongly right-skewed pattern, with median laying dates falling within a narrow window between 27-29 June. In comparison to previous years, laying was late, and relatively synchronous among species. Incubation periods were 2 days longer in Razorbills (median 35 days) than in either guillemot species (33 days), whereas Common Guillemots had longer nestling periods (mean 24 days) than Razorbills (19 days) or Brünnich's Guillemots (20 days). In all species, there was a tendency for late-laying pairs to contract their breeding periods, mainly by reducing the duration of the nestling period. Breeding success was high in Razorbills (73%) and Common Guillemots (85%), but low in Brünnich's Guillemots (51%), largely due to low hatching success. Late-breeding Brünnich's Guillemots were more likely to fail than were early pairs, but there was little indication of this in the other two species. Seasonal patterns of colony attendance suggested that there were many young, pre-breeding Brünnich's Guillemots and Razorbills present; populations of these species appear to be faring well at this colony. Despite a major shift in chick diets since the early 1980's, caused by a decline in the availability of capelin in Labrador, chicks of all three species grew relatively quickly and departed the colony at normal masses.*

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## .INTRODUCTION

The diversity of nestling developmental strategies found within the Alcidae (the auks) is unmatched by any other bird family (Sealy 1973). Three species, Razorbill *Alca torda*, Common Guillemot *Uria aalge*, and Brünnich's Guillemot *Uria lomvia,* employ a unique strategy that is 'intermediate' between the precocial and semi-precocial developmental modes of other auks. In the intermediate auks, the single chick is fed by both parents at the nest site for 15-30 days, leaves the colony at less than 30% of adult mass and covered in a transitional, mesoptile plumage, and subsequently is cared for at sea by its male parent for several weeks. Not surprisingly, there are broad ecological similarities between the three species, but they differ in important respects in morphology, feeding behaviour, nesting habitat, and distribution. Razorbills and Common Guillemots are mainly boreal and low-Arctic species, while Brünnich's Guillemot is an Arctic-nesting species (Gaston & Jones 1998). The breeding biology of these three species has rarely been studied at one time and place, in large part because there are few colonies where all three breed and are accessible. In this paper, we compare: (1) the timing of breeding; (2) the duration of incubation, nestling, and breeding periods; (3) seasonal trends in reproductive success; (4) seasonal patterns of colony attendance; and (5) egg size and chick growth, of the three intermediate auks breeding at the Gannet Islands, Labrador, Canada.

## METHODS

The Gannet Islands (53°57'N 56°31'W) support the largest Razorbill colony in North America, with *c.* 10 000 pairs, as well as *c.* 50 000 pairs of Common Guillemots and *c.* 3000 pairs of Brünnich's Guillemots (Lock *et al.* 1994; Chapdelaine *et al.* 1999; G.J. Robertson unpubl. data). Lying in the path of the Labrador current, the colony is part of a low-Arctic marine ecosystem (Nettleship & Evans 1985). All observations were made between mid-June and early September in 1997 on 'GC4', one of seven small islands comprising the Gannet Clusters (see Birkhead & Nettleship 1987a).

We used the Type I methods of Birkhead & Nettleship (1980) to monitor breeding chronology and breeding success. Common Guillemot pairs were observed from a blind situated 5 m above a 15 $m^2$ plot on which they nested densely on a gently sloping, boulder-strewn rock face, 5 m above sea level and 20 m from the sea. Razorbills and Brünnich's Guillemots occupied nest sites on narrow cliff ledges and steep rocky slopes, most of them > 10 m above sea level, and were monitored from a blind at distances of 5-30 m. Many Razorbill pairs also nested in crevices among boulders, but these birds could not be monitored without causing excessive disturbance. We included only sites for which we knew laying, hatching, and nest departure dates to within one day. Chicks were considered to have survived to departure if they were at least 15 days of age when last seen.

Numbers of adults present were counted on five plots at 1600 h every two to three days. The count plots included those plots that we monitored for breeding chronology and success. Prior to hatching, length and maximum breadth (± 0.1 mm, with dial callipers) of eggs laid by all three species were

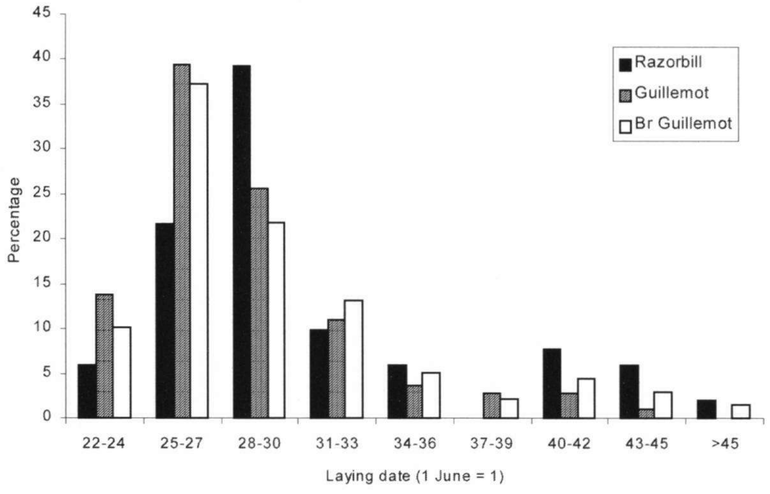



*Figure 1. Laying dates of Razorbills (n = 51), Common Guillemots (n = 109) and Brünnich's Guillemots (n = 137) at the Gannet Islands in 1997.*
*Figuur 1. Legdata van Alken (n = 51), Zeekoeten (n = 109) en Dikbekzeekoeten (n= 137) op de Gannet Islands in 1977.*

measured. An egg volume index (length x breadth$^2$) that has a strong linear relationship with fresh egg mass in all three species (Birkhead & Nettleship 1984) was used as a measure of egg size. We measured mass (± 1 g, with a 300 g Pesola) and wing length (maximum flattened cord excluding down tips, ± 1 mm, with a ruler) of the chicks that hatched from these eggs at two- or occasionally three-day intervals between hatching and nest departure. Chicks were assumed to have hatched on the day between consecutive checks, unless they were still wet after hatching or their down was still matted. For identification, chicks were marked with a binary code of nail clipping when first found, and banded when large enough, always within one week of hatching.

Data were analysed using SPSS (version 7.5) statistical software. Parametric statistics were used where residuals fit the assumptions of normality and equality of variances, otherwise non-parametric statistics were used. We used Tukey's tests to make pair-wise, multiple comparisons following significant ANOVAs, and non-parametric multiple comparisons following significant Kruskal-Wallis tests. A significance level of $_{crit}$ = 0.05 was used for all statistical tests.

## RESULTS

**Breeding chronology** Timing of laying differed among species (Kruskal-Wallis test, $H_2 = 8.1$, $P = 0.02$), but median laying dates for all three species fell between 27-29 June, and none of the pairwise comparisons were significant (Fig. 1). Timing of laying of first eggs followed a right-skewed pattern in all three species, with a sharp peak in the last week of June, and laying continued until mid-July (Fig. 1). Incubation periods differed among species (Kruskal-Wallis test, $H_2 = 63.6$, $P < 0.001$), being shorter in both guillemot species (medians = 33 days) than in Razorbills (median = 35 days).

The spread in incubation periods was similar in all species at 4-5 days (Fig. 2). Nestling periods also differed among species (ANOVA, $F_{2,154} = 89.5$, $P < 0.001$), and all pair-wise comparisons were significant: Razorbills had the shortest nestling periods (mean ± 1 SD = 18.9 ± 1.6 days), followed by Brünnich's Guillemots (20.0 ± 2.0 days), and Common Guillemots (23.5 ± 1.6 days). The spread in nestling periods was similar in all species at 8-10 days (Fig. 2). Breeding periods (i.e. incubation + nestling periods) also differed (Kruskal-Wallis test, $H_2 = 56.1$, $P < 0.001$), being similar in Razorbills and Brünnich's Guillemots (medians = 54 and 53 days, respectively), but longer in Common Guillemots (median = 56 days). Again, the spread in breeding periods was similar among species, at 8-10 days (Fig. 2).

The duration of incubation showed little relationship with laying date in Razorbills or Common Guillemots, but declined significantly with date in Brünnich's Guillemots (Table 1; see Hipfner *et al.* in press). Nestling periods declined with hatching date in both guillemot species, and showed a similar, but non-significant, decline in Razorbills. Overall, breeding periods were negatively related to laying date in all species, although the decline was not significant in Razorbills (Table 1).

**Breeding success** Reproductive success (i.e. the proportion of eggs laid that produced chicks that survived to 15 days of age) differed among species, being lower in Brünnich's Guillemots than in either Razorbills ($\chi^2_1 = 6.3$, $P = 0.01$) or Common Guillemots ($\chi^2_1 = 29.3$, $P < 0.001$; Table 2). This was mainly due to lower hatching success (the proportion of eggs laid that hatched) in Brünnich's Guillemots than in the other two species (both $P \leq 0.05$). Nestling success (the proportion of eggs that hatched that produced chicks that survived to 15 days) was high in all three species.

Whereas reproductive success varied little with timing of breeding in Razorbills or Common Guillemots, both hatching and reproductive success declined with date among Brünnich's Guillemots (Table 2).

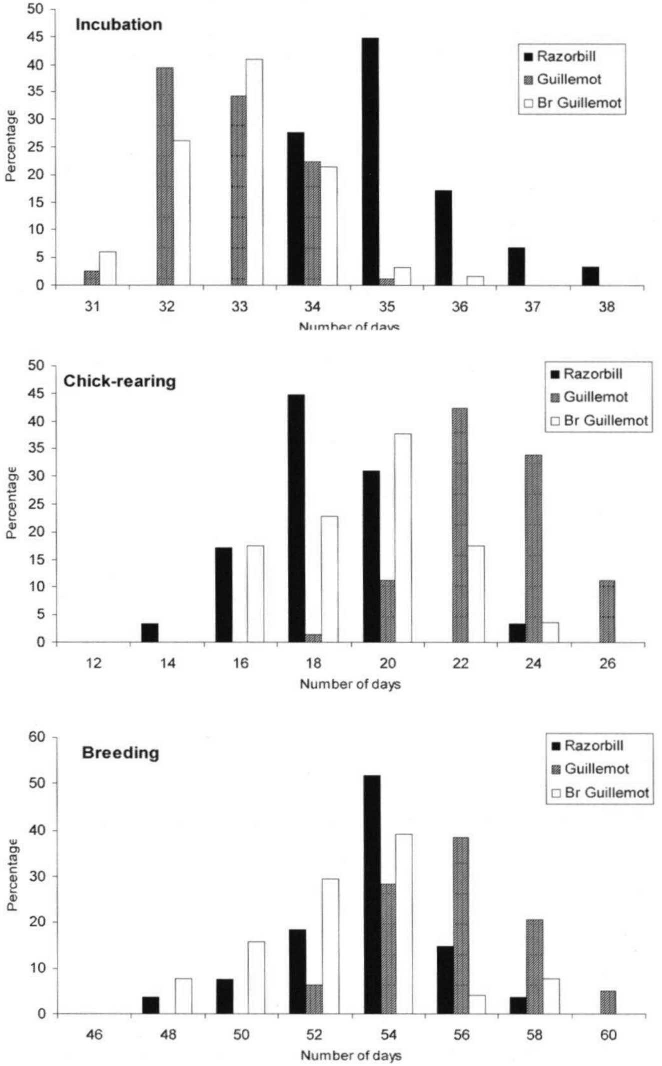



*Figure 2. Duration of incubation, nestling and breeding periods of Razorbills (n = 29, 29, and 27 respectively), Common Guillemots (n = 80, 71, 77), and Brünnich's Guillemots (n = 61, 57, and 51) at the Gannet Islands in 1997.*

*Figuur 2. Tijdsduur van broeden, kuikenfase en broedperiode van Alken (n = 29, 29, en 27), Zeekoeten (n = 80, 71, 77) en Dikbekzeekoeten (n = 61, 57 en 51) op de Gannet Islands in 1997*

*Table 1: Linear regressions showing seasonal trends in duration of incubation (inc), nestling (nest), and total breeding periods (tot) for auks at the Gannet Islands in 1997.*
*Tabel 1. Resultaten van lineaire regressie analyse ter illustratie van trends in de duur van het bebroeden van het ei (inc), de kuikenfase (nest) en van de totale broedduur (tot) voor alkachtigen op de Gannet Islands in 1997.*

| | *Alca torda* | | | *Uria aalge* | | | *Uria lomvia* | | |
|---|---|---|---|---|---|---|---|---|---|
| Parameter | inc | nest | tot. | inc | nest | tot. | inc | nest | tot |
| $n$ = | 29 | 29 | 27 | 80 | 71 | 77 | 61 | 57 | 51 |
| $R^2$ = | 0.002 | 0.09 | 0.07 | 0.003 | 0.19 | 0.40 | 0.10 | 0.30 | 0.37 |
| $P$ = | 0.81 | 0.12 | 0.20 | 0.61 | <0.001 | <0.001 | 0.02 | <0.001 | <0.001 |
| Slope | 0.05 | -0.30 | -0.26 | -0.06 | -0.34 | -0.52 | -0.08 | -0.23 | -0.35 |

*Table 2: Logistic regressions showing seasonal trends in hatching (hatch), nestling (nestl), and reproductive success (repr) for auks at the Gannet Islands in 1997.*
*Tabel 2. Resultaten van logistische regressie ter illustratie van seizoenpatronen in het uitkomen van de eieren (hatch), de overleving van nestjongen (nestl) en van het totale broedsucces (repr) voor alkachtigen op de Gannet Islands in 1997.*

| | *Alca torda* | | | *Uria aalge* | | | *Uria lomvia* | | |
|---|---|---|---|---|---|---|---|---|---|
| Parameter | hatch | nestl | repr | hatch | nestl | repr | hatch | nestl | repr |
| $n$ = | 51 | 37 | 51 | 108 | 79 | 102 | 136 | 67 | 136 |
| success (%) | 75 | 97 | 73 | 87 | 98 | 85 | 57 | 89 | 51 |
| Wald $\chi^{\bullet\bullet}$ | 0.26 | 0.92 | 1.02 | 0.007 | 0.57 | 0.67 | 8.40 | 0.51 | 6.51 |
| $P$ = | 0.61 | 0.34 | 0.31 | 0.93 | 0.45 | 0.41 | 0.004 | 0.48 | 0.01 |
| Slope | -0.02 | -0.05 | -0.05 | -0.005 | 0.38 | -0.06 | -0.10 | 0.06 | -0.09 |

**Colony attendance** Numbers of Razorbills attending the colony were high during the pre- and early-laying period, then declined sharply after median laying (Fig. 3). Numbers then built up to a peak in early-to-mid chick-rearing, before dropping off late in the season. Common Guillemot attendance was low during pre- and early-laying, then increased after median laying. Numbers were more or less stable through the incubation period, with a small peak in early chick-rearing, then dropped off late in the season. Brünnich's Guillemot numbers increased steadily between pre-laying and late incubation/early chick-rearing, then doubled to mid chick-rearing, before dropping off (Fig. 3).

**Chick growth and development** The smallest of the three species, the Razorbill, laid smaller eggs than either guillemot species; as a result, 2 day old Razorbill chicks were lighter in mass (Table 3). Razorbill chicks also gained

*Table 3. (A) Growth parameters (mean ± SD) for auks. % values are percentages of adult measurements taken during incubation. (B) Post-hoc comparisons that are the results of Tukey's tests at P = 0.05 following ANOVAs on measurements as absolute values, and as percentages of adult measurements (% adult). Values that are not significantly different are underlined together.*

*Table 3. (A) Groeivariabelen (gemiddelde ± SD) voor alkachtigen. De getallen tussen haakjes zijn percentages van maten van adulte vogels genomen in de broedtijd. (B) Post-hoc vergelijkingen als resultaten van Tukey's test bij P = 0.05 op grond van ANOVAs op biometrische gegevens als absolute getallen en als percentage van afmetingen bij adulte vogels (% adult). Resultaten die niet significant verschillen zijn door onderstreping verbonden.*

| (A) Parameter | Species (*n*) *Alca torda* (14) | (%) | *Uria aalge* (8) | (%) | *Uria lomvia* (8) | (% |
|---|---|---|---|---|---|---|
| Egg volume index (cm$^3$) | 185.1 ± 15.7 | | 198.0 ± 16.0 | | 201.7 ± 12.9 | |
| Two day mass (g) | 72.0 ± 7.2 | 10.0 | 84.4 ± 6.4 | 8.6 | 83.0 ± 9.4 | 8. |
| Growth 2-14 d: | | | | | | |
| mass (g) | 103.1 ± 15.5 | 14.3 | 125.3 ± 16.0 | 12.8 | 130.0 ± 34.6 | 13 |
| wing (mm) | 34.9 ± 4.5 | 16.8 | 20.9 ± 6.3 | 9.8 | 30.3 ± 7.2 | 13 |
| Departure mass (g) | 186.7 ± 19.8 | 25.9 | 223.1 ± 20.8 | 22.8 | 221.1 ± 25.1 | 23 |
| Departure wing (mm) | 72.5 ± 8.0 | 34.8 | 62.4 ± 4.4 | 29.4 | 72.8 ± 33.3 | 33 |

| (B) | Post-hoc comparisons: Absolute | | | % Adult | | |
|---|---|---|---|---|---|---|
| Egg volume index (cm$^3$) | RZ | G | BG | | | |
| Two day mass (g) | RZ | BG | G | G | BG | R |
| Growth 2-14 d: | | | | | | |
| mass (g) | RZ | G | BG | | n.s. | |
| wing (mm) | G | BG | RZ | G | BG | R |
| Departure mass (g) | RZ | BG | G | G | BG | R |
| Departure wing (mm) | G | RZ | BG | G | BG | R |

mass more slowly than guillemot chicks, and were less heavy at nest departure (Table 3, Fig. 4). Chicks of the two guillemot species gained mass at similar rates, and departed to sea at similar masses. Conversely, the rate of wing growth did not differ between Razorbill and Brünnich's Guillemot chicks, but Common Guillemot chicks grew their wings more slowly. Razorbill and Brünnich's Guillemot chicks departed with wings of similar length, and longer than those of Common Guillemots.

In relation to adult masses during incubation in 1997, Razorbill chicks actually were heavier at 2 days of age than were chicks of either guillemot species (Table 3), presumably because Razorbill eggs are c. 2% heavier as a proportion of adult mass (M. Hipfner unpubl. data). The three species differed

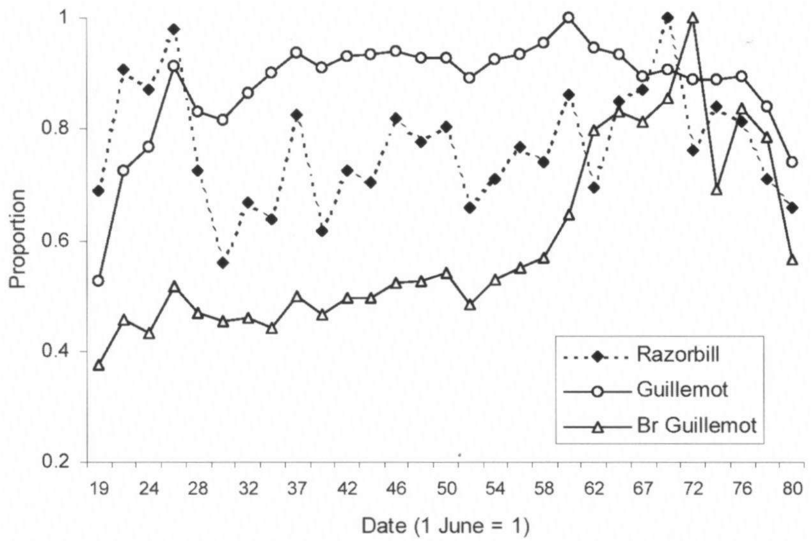



*Figure 3. Colony attendance of Razorbills, Common Guillemots, and Brünnich's Guillemots at the Gannet Islands in 1997. Values are proportions of the single highest count.*
*Figuur 3. Aanwezigheid op de kolonie door Alken, Zeekoeten en Dikbekzeekoeten op de Gannet Islands in 1997. De gepresenteerde waarden zijn proportioneel ten opzichte van de hoogste waargenomen presentie.*

little in the relative rate at which they gained mass, but Razorbill chicks were somewhat heavier than Common Guillemot chicks at departure. Relative to adult wing lengths, neither rates of wing growth nor wing lengths at nest departure differed between Razorbills and Brünnich's Guillemots, but both were greater in these species than in Common Guillemots (Table 3).

## DISCUSSION

**Breeding chronology** Both the timing and the pattern of laying by Razorbills, Common Guillemots, and Brünnich's Guillemots were quite similar at the Gannet Islands in 1997. The right-skewed laying pattern is typical for these species, and in Brünnich's Guillemots occurs mainly because older, more experienced females lay early, while young, inexperienced females continue to lay for extended periods after the peak (de Forest & Gaston 1996; Hipfner *et al.* 1997). Common Guillemots laid 3-12 days later in 1997 than they had in 1981-1983, while Brünnich's Guillemots laid 2-9 days later (cf. Birkhead &

Nettleship 1987a). In Birkhead and Nettleship's study, delayed and synchronous laying by the two guillemot species in one year (1982) were attributed to heavy spring ice cover in waters around the Gannet Islands. Ice conditions are known to affect timing of laying by Brünnich's Guillemots (Gaston & Hipfner 1998), but ice maps obtained from Environment Canada (and our own observations) showed that there was little sea ice around the Gannet Islands during early June of 1997. We can only speculate on what other factors might have caused the late and synchronous laying. Total breeding failure by Black-legged Kittiwakes *Rissa tridactyla* at the Gannet Islands in 1997, due mainly to failure to lay eggs (pers. obs.), suggests that food availability was low early in the season. This might have been caused by the recent, anomalously cold oceanographic conditions in the Northwest Atlantic (Drinkwater 1996).

Incubation and nestling periods of Razorbills and Brünnich's Guillemots were similar to those reported previously at this colony (Birkhead & Nettleship 1987a), and at others (Lloyd 1979; Harris & Wanless 1989). Common Guillemot incubation periods also were typical, but their nestling periods were long compared to other colonies (cf. Murphy & Schauer 1994). As growth rates of Common Guillemot chicks appeared normal, it seems unlikely that the long nestling periods were consequences of developmental constraints; they may have been due to low predation pressure that would select for rapid departure of young from the nest site (Ydenberg 1989).

There was a tendency in all species for late-laying birds to contract their breeding seasons, mainly by reducing the nestling period (cf. Murphy 1995). Seasonal declines in departure age increase the colony-wide synchrony of nest departure, which reduces the predation risk for individual departing chicks (Daan & Tinbergen 1979), and they lessen the predation risk for late-hatched young at the colony (Hatchwell 1991). On GC4, Herring Gulls *Larus argentatus* and Great Black-backed Gulls *L. marinus* preyed heavily on departing chicks, but we saw few predation attempts on nestlings.

**Breeding success** Despite a decrease in capelin availability to marine birds at the Gannet Islands, reproductive success of both guillemots in 1997 was similar to that in the early 1980s (Bryant *et al.* 1999). Common Guillemots had higher success than Brünnich's Guillemots, and their breeding success at the Gannet Islands (85%) was high compared to that at other Atlantic colonies (70-80% is typical, Gaston & Jones 1998). Conversely, success of Brünnich's Guillemots (51%) was at the low end of the range compared to other colonies (48-82%; Gaston *et al.* 1994). Reproductive success of Razorbills (73%) was similar to that at other colonies (70-76%; Gaston & Jones 1998), even though all monitored pairs laid on exposed ledges, habitats where success is sometimes low (Hudson 1982).

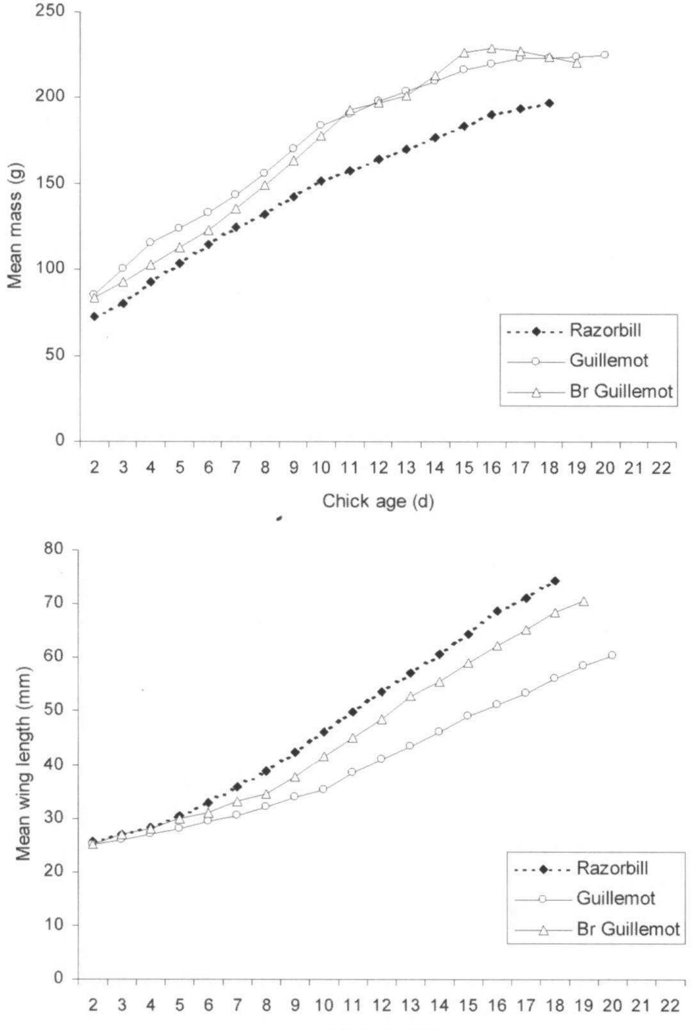
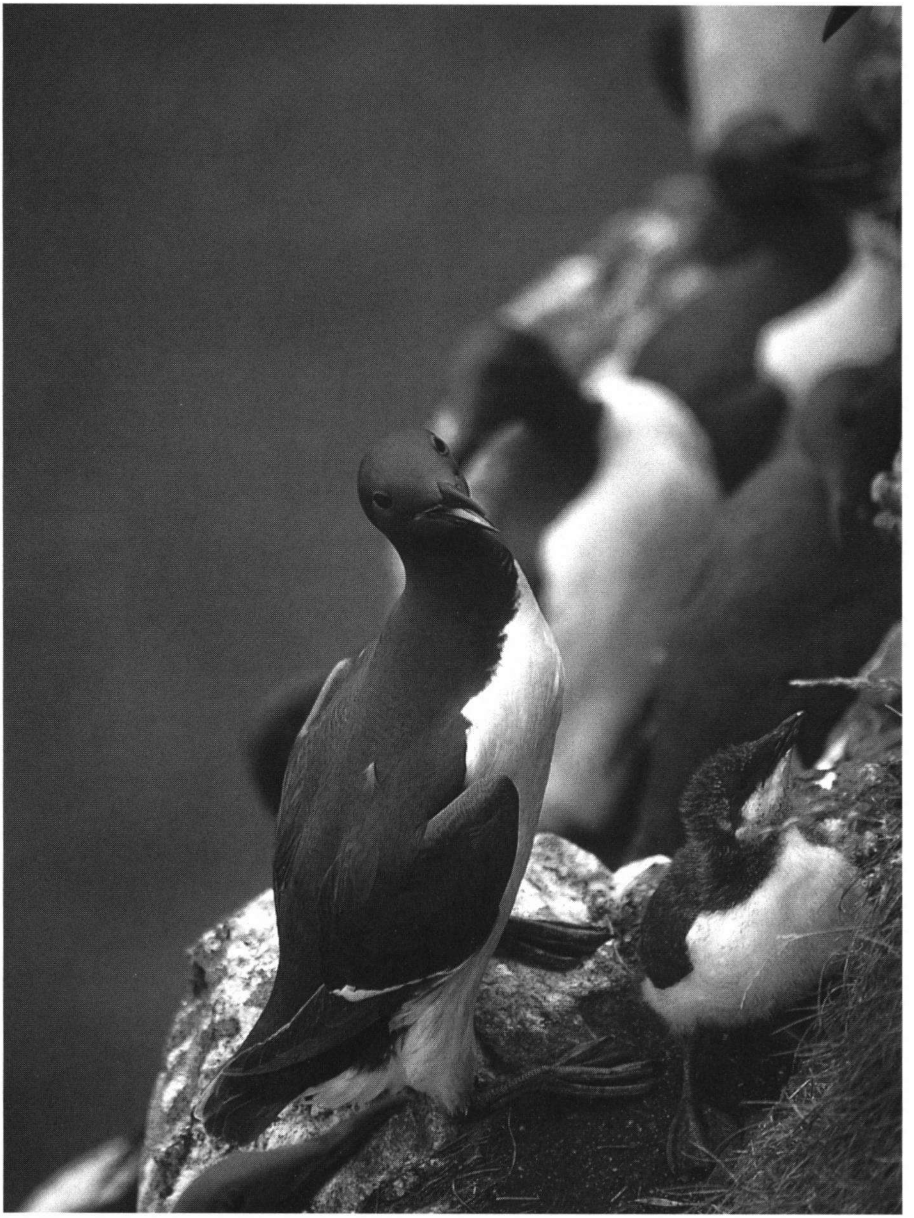



*Figure 4. Growth in mass and wing length of Razorbill (n = 14), Guillemot (n = 8), and Brünnich's Guillemot (n = 8) chicks at the Gannet Islands in 1997.*
*Figuur 4. Groei in massa en vleugellengte van Alk, Zeekoet en Dikbekzeekoetkuikens op de Gannet Islands in 1997.*



Guillemot and chick shortly prior to fledging *Zeekoet met jong, kort voor het 'uitvliegen'* (C.J. Camphuysen)

Reproductive success of Brünnich's Guillemots declined with date, due mainly to a seasonal decline in hatching success. However, early-laying pairs that were induced to lay replacement eggs bred as successfully as unmanipulated early-laying pairs, suggesting that the population-wide declines were not caused by seasonal environmental effects (Hipfner *et al.* 1999). At another Brünnich's Guillemot colony, such declines were caused by late laying of young, inexperienced pairs (de Forest & Gaston 1996), and this seems a likely explanation for the observed declines at the Gannet Islands. Seasonal declines in success are often reported for Razorbills and Common Guillemots as well (Lloyd 1979; Hatchwell 1991); it is not apparent to us why this did not occur at our study colony.

**Colony attendance** The seasonal patterns of colony attendance by Razorbills and Common Guillemots were generally similar to other published observations (Lloyd 1975; Birkhead & Nettleship 1987a), but attendance by Brünnich's Guillemots was unusual in showing a very marked increase late in incubation. Peaks in numbers of birds attending the colony occur then mainly because this is when many non-breeding birds begin to visit (Bédard 1969; Gaston & Nettleship 1982), and probably young, pre-breeding birds in particular (Halley *et al.* 1995). The peak was pronounced in Razorbills, and very pronounced in Brünnich's Guillemots, consistent with recent surveys that indicate that populations of these species are increasing at the Gannet Islands (Bryant *et al.* 1999; Chapdelaine *et al.* 1999).

**Chick growth and development** The diets of guillemot chicks included lower proportions of capelin and higher proportions of benthic fish (especially daubed shanny *Lumpenus maculatus*) in 1997 than in 1981-1983; however, this appeared to have little affect on growth rates and departure masses (Bryant *et al.* 1999). Razorbills chicks also grew normally compared to other colonies (Bédard 1969; Lloyd 1979). After controlling for variation in adult mass, the three species gained mass at similar rates, but Razorbills and Brünnich's Guillemots grew their wings more quickly (see also Barrett *et al.* 1997). As wing growth mainly measures growth of the primary coverts, this suggests that Razorbill and Brünnich's Guillemot chicks grew their wing feathers more quickly than did Common Guillemot chicks. This was seen in growth of the contour feathers as well, because Common Guillemot chicks retained natal down longer than Razorbills or Brünnich's Guillemots. The cliff-nesting habit of and Razorbills may place an evolutionary premium on wing feather growth, because success at departure may depend on the chick's ability to glide a long distance (Gilchrist & Gaston 1997; Hipfner & Gaston 1999). At many colonies, including the Gannet Islands, many Common Guillemot chicks simply walk from the nest site to sea. An evaluation of how chick development varies at colonies where ecological conditions differ (e.g. where most guillemots nest on cliffs) might be enlightening.

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SAMENVATTING

*Verschillende aspecten van de broedbiologie van Alk* Alca torda, *Zeekoet* Uria aalge *en Dikbekzeekoet* U. lomvia *werden onderzocht in een vergelijkende studie op de Gannet Islands in Labrador (Canada) in 1997. De mediaan van de eileg voor elk van deze soorten viel in een opmerkelijk korte periode, tussen 27 en 29 juni, en kon worden gekarakteriseerd als 'laat' in vergelijking tot eerdere jaren van onderzoek. Vermoedelijk als gevolg van deze uitgestelde eileg was de broedsynchronisatie tussen de onderzochte soorten erg groot. Alken bebroedden de eieren iets langer (mediaan 35 dagen) dan de beide zeekoeten (33 dagen), terwijl de Zeekoet de jongen het langst op het nest hield (gemiddeld 24 dagen, tegen gemiddeld 19 dagen bij de Alk en 20 dagen bij de Dikbekzeekoet). Bij alle soorten werd van relatief 'late' broedvogels de neiging waargenomen om de nestperiode te bekorten, door eerder met het kuiken naar zee te vertrekken. Het broedsucces was hoog bij de Alk (73%) en de Zeekoet (85%), maar laag bij de Dikbekzeekoet (51%), vooral als gevolg van een laag percentage uitkomende eieren. Ondanks een belangrijke verschuiving in het voedsel van de kuikens sinds het begin van de jaren tachtig, hoofdzakelijk veroorzaakt door een afgenomen aanbod van Lodde* Mallotus villosus *in Labrador, groeiden de kuikens bij alle soorten relatief snel en verlieten de kuikens de kolonie met een normaal gewicht.*

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