

Biometrics as a determinant of the origins of seabirds killed in oil spills and other incidents

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Summary

Common Guillemots *Uria aalge* and Brünnich's Guillemots *U. lomvia* are common victims of oil spills, drowning in fishing nets and winter wrecks. Because the Norwegian population of Common Guillemots is classified as critically endangered and the Russian population of the Brünnich's Guillemot has declined greatly, it is important to be able to identify the origins of birds killed outside the breeding season. Measurements of birds made in nine colonies in the Barents and Norwegian Seas showed that although it is impossible to determine with reasonable accuracy the colony of origin from body measurements, the most likely sea of origin of Common Guillemots may be determined on the basis of wing and head + bill lengths, whereas there was no systematic variation in any measurement of Brünnich's Guillemots.

Introduction

With more than seven million pairs of some 40 species breeding in about 2,000 colonies, the Norwegian and Barents Seas are among the richest seabird areas in the world (Anker-Nilssen *et al.* 2000). The largest colonies are in Svalbard (including Bjørnøya [Bear Island] and Hopen), the west coast of Novaya Zemlya, the Murman coast, and the coast of northern Norway. Whereas many populations were heavily hunted and harvested for eggs, feathers and meat in the 19th and 20th centuries, fisheries and oil pollution are considered to be among the greatest threats today. Oil and gas production started in the North Sea in the 1960s and has since spread northwards into the Barents Sea. Huge reserves have also been found in the Russian sector of the Barents Sea as well as on land in Northwest Russia and there is already a large traffic of tankers carrying oil westwards into the North Atlantic and to European ports (Bambulyak and Frantzen 2005). Several assessments of the vulnerability of the environment, including seabirds, to oil pollution have been made for the region and all concluded that, in whatever area or season, many seabird populations of international conservation value will be in danger of being seriously affected in the event of an oil spill (e.g. Arctic Council Oil and Gas Assessment, in prep.).

Because auks spend most of their life at sea, are surface-divers, and tend to spend most of their time in dense flocks on the sea surface, they are among those most vulnerable to long-term effects of oil pollution at the population level (e.g. King and Sanger 1979, Anker-Nilssen 1987, Camphuysen *et al.* 1999). In Norway, Common Guillemots *Uria aalge* and Brünnich's Guillemots *U. lomvia* are among the most conspicuous casualties of oil spills. For example, a small oil spill in North Norway in March 1979 killed an estimated 10,000–20,000 Brünnich's Guillemots (Barrett 1979) and another in the Skagerrak in December 1980 killed more than 60,000 Common Guillemots (Anker-Nilssen and Røstad 1982). Similarly, outside Norwegian waters, Common Guillemots have been very common victims of oil spills (Grantham 2004). Guillemots are also often killed in winter 'wrecks', often as a result of starvation during a period of food shortage and/or bad weather, or sometimes in fishery by-catch incidents. For example, an

estimated 200,000 guillemots (mostly Common) drowned in an extraordinary fishing incident in North Norway in April 1985 (Strann *et al.* 1991).

When the Norwegian population (excluding the Svalbard archipelago) of Common Guillemot was first counted in the 1960s, it was already under increasing pressure from hunting, egg harvesting, drowning in fishing gear and oil spills (Brun 1969). Since then the numbers have collapsed from Brun's estimate of 120,000–160,000 pairs to the alarmingly low estimate of only 15,000 pairs today (Barrett *et al.* 2006). Although two thirds of these birds breed in the far north of Norway (Finnmark) where there are signs of a recovery in colonies east of the North Cape, there are fears that what were once among the largest colonies in Europe are now on the brink of extinction (Røst 16,000 pairs in 1960–63, Sør-Fugløy 10,000 pairs in 1940, Nord-Fugløy 15,000 pairs in 1963, and Hjelmsøya *ca.* 100,000 pairs in the mid-1960s) (Soot-Ryen 1941, Lütken 1965, Brun 1969, Tschanz and Barth 1978). This may be through a breakdown of the social structure on the breeding shelves and/or increasing disturbance pressure from White-tailed Eagles *Haliaeetus albicilla* (Barrett *et al.* 2006). As a result, the Common Guillemot population is now classified as 'Critically Endangered' (CR) on the Norwegian Red List (Kålås *et al.* 2006).

Most of the Norwegian and Russian Brünnich's Guillemots breed much further north in the Barents Sea, mainly in Svalbard, Franz Josef Land and on Novaya Zemlya where populations have recently been estimated to be *ca.* 850,000, 25,000 and 850,000 pairs respectively (Bakken and Pokrovskaya 2000). There have also been large declines in this population. For example, in the largest colony on Novaya Zemlya numbers have dropped from >1.5 million individuals in the 1930s to 100,000–150,000 individuals in the early 1990s. A second colony of 200,000 individuals in 1920 is now abandoned (Krasnov and Barrett 1995, Bakken and Pokrovskaya 2000). Long-term monitoring in Svalbard since 1986 has so far indicated a stable population (Strøm 2006). At the southern edge of their distribution, on the mainland coast of North Norway and the Kola Peninsula, the population has recently been estimated at 3,000–5,000 individuals although little is known about recent developments (Krasnov *et al.* 2007).

Both species also breed along the coasts of many North Atlantic seaboard countries and are very faithful to their breeding site, but outside the breeding season, birds from many regions may gather at sea in large flocks such that any 'incident' may involve birds from several breeding populations simultaneously (Strann *et al.* 1991, Bakken *et al.* 2003, Cadiou *et al.* 2004). In these cases, to be able to assess the scale of the impact through the identification of the source populations is of utmost importance for the management of those populations.

With the present focus on oil and gas exploration, production and transport from the Barents Sea, the possibility of the northern populations of guillemots being directly affected by a spill is increasing. Furthermore the direct and indirect pressures on individuals by fishing activity in the region are ever-present such that the possibility of a mass mortality incident is always present. Because at least the Common Guillemot population in the Barents Sea is already seriously threatened, there is a need to be able to identify the origin of birds killed in oil incidents in order to document effects at the population level and identify any mitigating post-event management actions.

Traditionally, the recovery of ringed birds and the examination of structural size has been used to identify the origins of the victims of wrecks or oil spills (Anker-Nilssen *et al.* 1988, Camphuysen and Leopold 2004, Cadiou *et al.* 2004, Grantham 2004) through the fact that body size often increases with latitude (e.g. Anker-Nilssen *et al.* 1988, Jones 1988a, Barrett *et al.* 1997). Other characteristics such as slight changes in plumage colour and, among Common Guillemots, a north-south cline in the proportion of bridled birds (Birkhead 1984) have proved to be of limited value in such studies. Recently much effort has been put into population genetic studies, partly in the hope that there is enough genetic differentiation among colonies to be able to identify the geographical origins of birds found outside the breeding season. For both guillemot species, however, the populations were found to be so weakly structured that any clear assignment of birds to their origin is impossible using this method alone (Moum *et al.* 1991,

Birt-Friesen *et al.* 1992, Moum and Arnason 2001, Riffault *et al.* 2005). Another approach has been through the use of stable-isotope analyses of feathers but this method is also limited in its precision (Cherel *et al.* 2000). Thus, as yet, the use of biometrics still produces the best management advice.

Jones (1988a) documented a clear latitudinal cline in Common Guillemot wing length based on measurements made in 13 colonies from Skomer in West Wales in the south to Vardø in Northeast Norway in the north, while Gaston *et al.* (1984) found a small but significant inter-colony phenotypic variation among Brünnich's Guillemot colonies in the Hudson Strait, Canada. Until now, the only systematic data published from Norway were based on museum skins (Pethon 1967), but these are of limited value in this context due to e.g. shrinkage (Harris 1980, Jones 1988b) and often unknown measuring techniques.

To facilitate the identification of the origins of birds killed by oil spills, fishing gear or starvation outside their breeding areas, we here present recent measurements of live Common Guillemot from eight Norwegian colonies, one from Iceland and one from Northwest Russia (Figure 1) and compare them to published measurements from other colonies in the Northeast Atlantic. We also present for the first time biometrical data of Brünnich's Guillemots from eight breeding colonies in the Barents Sea.

Material and methods

One Russian and seven Norwegian Common Guillemot colonies (Figure 1) were visited either once (Runde), twice (Bleiksøya, Hjelmsøya, Syltefjord) or over several years (Røst, Hornøya, Bjørnøya, Kharlov) and measurements were made of birds caught on the breeding sites (open ledges or natural cavities inside boulder scree). At a ninth colony, Loppa, measurements were taken of birds drowned in fishing nets under the cliff. Measurements of Brünnich's Guillemots were also made of birds caught in the breeding colonies during single or repeated visits to eight

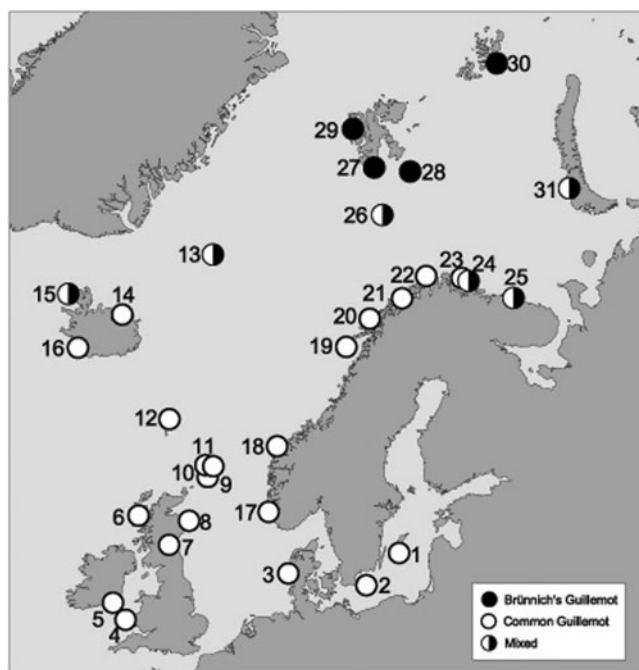


Figure 1. Approximate positions of the colonies mentioned in the text. Numbers by each symbol are colony numbers in Tables 3 and 4.

colonies in the Barents Sea. Samples of both species were measured during a visit to Latrabjarg, Northwest Iceland.

The following measurements were taken: body mass (± 2.5 g), wing length (maximum flattened chord ± 0.5 mm), culmen length (from tip of bill to proximal edge of horny sheath of the upper bill, ± 0.05 mm), gonys depth (vertical depth of bill at gonys perpendicular to cutting edge of bill ± 0.05 mm) and head + bill length (± 0.05 mm). 95% confidence limits (cl) of the means were calculated taking inter-observer variability of measurements into account using the equation $cl = \pm t\sqrt{[(SD)^2/2 + (S_R)^2]}$ where t = student's t when probability $P = 0.05$, SD = standard deviation of mean and S_R = inter-observer variability of wing measurements of large auks (Barrett *et al.* 1989).

In an attempt to assign individuals to population, we used not only colony-based measurements but also grouped the Norwegian and Russian Common Guillemots by region - Svalbard (1 colony), North Norway and Russia (7 colonies), and South Norway (1 colony) (Table 3) - and by sea area: Barents Sea (6 colonies - nos. 21–26 in Table 3) and Norwegian Sea (3 colonies - nos. 18–20 in Table 3). To test the accuracy of the method, we used the discriminant function of SPSS (ver. 15.0, SPSS Inc.) to predict the group membership of each bird according to colony, region and sea area.

Mean sea surface temperatures in May–July were taken from Levitus (1982) and Steffánsson (1969).

Results

Common Guillemot

The biometric characteristics of Common Guillemots examined were significantly different across the eight Norwegian and one Russian colony (ANOVA tests, $P < 0.001$ in all cases) and indicates a clear increase in size from southwest to northeast (Table 1). This is reflected in positive correlations between body mass (mass) and latitude (lat) (mass = $-48.4 + 15.112 \times \text{lat}$, $r^2 = 0.78$, $P = 0.004$) and wing length (wing) and latitude (wing = $160.9 + 0.737 \times \text{lat}$, $r^2 = 0.71$, $P = 0.003$). Correlations of gonys depth, culmen or head + bill lengths with latitude were, however, insignificant.

When all published wing length data from other NE Atlantic colonies are included (Fig. 1), there is a clear correlation between mean wing length and latitude throughout the range of the

Table 1. Body mass (g) and morphometric measurements (mm) of adult Common Guillemots in Norwegian, Northwest Russian and Icelandic breeding colonies. The geographic coordinates of each colony are given in Table 3.

Colony	Mass			Wing			Culmen			Gonys			Head + bill		
	Mean	SE	<i>n</i>	Mean	SE	<i>n</i>	Mean	SE	<i>n</i>	Mean	SE	<i>n</i>	Mean	SE	<i>n</i>
Runde	922.3	8.7	40	207.1	0.7	40	46.9	0.4	40	13.6	0.1	40	113.8	0.5	40
Røst	935.9	6.3	114	209.2	0.4	173	46.1	0.2	107	13.4	0.1	172	114.0	0.3	121
Bleikøya	988.7	7.5	94	210.9	0.6	89	45.2	0.2	89	13.9	0.1	89	112.9	0.4	89
Loppa	—	—	0	208.5	1.5	13	46.3	0.6	15	13.7	0.2	15	113.3	0.9	15
Hjelmsøya	995.1	5.7	198	212.9	0.3	159	46.0	0.2	199	14.1	0.1	159	114.3	0.3	159
Syltefjord	1,016	11.1	46	213.6	0.5	110	47.9	0.2	109	14.2	0.1	110	116.9	0.3	109
Hornøya	1,055	3.9	422	213.2	0.3	412	47.7	0.1	403	14.2	0.0	405	116.6	0.2	332
Kharlov	976.8	8.9	48	213.4	0.7	89	47.4	0.2	89	14.5	0.1	41	116.2	0.5	89
Bjørnøya	1,103	7.9	57	219.8	0.6	57	48.7	0.3	77	14.4	0.1	74	115.9	0.4	57
ANOVA ^a <i>F</i>	60.0			31.3			21.9			28.5			18.4		
<i>P</i>	< 0.001			< 0.001			< 0.001			< 0.001			< 0.001		
Latrabjarg	941.1	9.7	31	206.6	0.6	38	45.0	0.3	37	13.2	0.1	33	111.1	0.5	36

^aAmong Norwegian and Russian colonies.

Common Guillemot (wing = 158.8 + 0.763 x lat, $r^2 = 0.78$, $P < 0.001$, Figure 2). Excluding the Icelandic birds, which are outside the main SW-NE axis, increases the correlation to 88 %. There is also a slightly weaker correlation with the mean summer sea surface temperature (sst) around the colonies (wing = 220.2 - 1.530 x sst, $r^2 = 0.71$, $P < 0.001$, Figure 2). Again excluding the Icelandic birds increases the correlation to 81 %. There is, however, considerable overlap of the 95% confidence intervals of the means along the SW-NE cline when inter-observer variability is taken into account (Figure 2).

Based on wing length alone, the discriminant function only classified 15% of the birds to the correct colony, whereas 51% were classified to the correct region and 64% to the correct sea

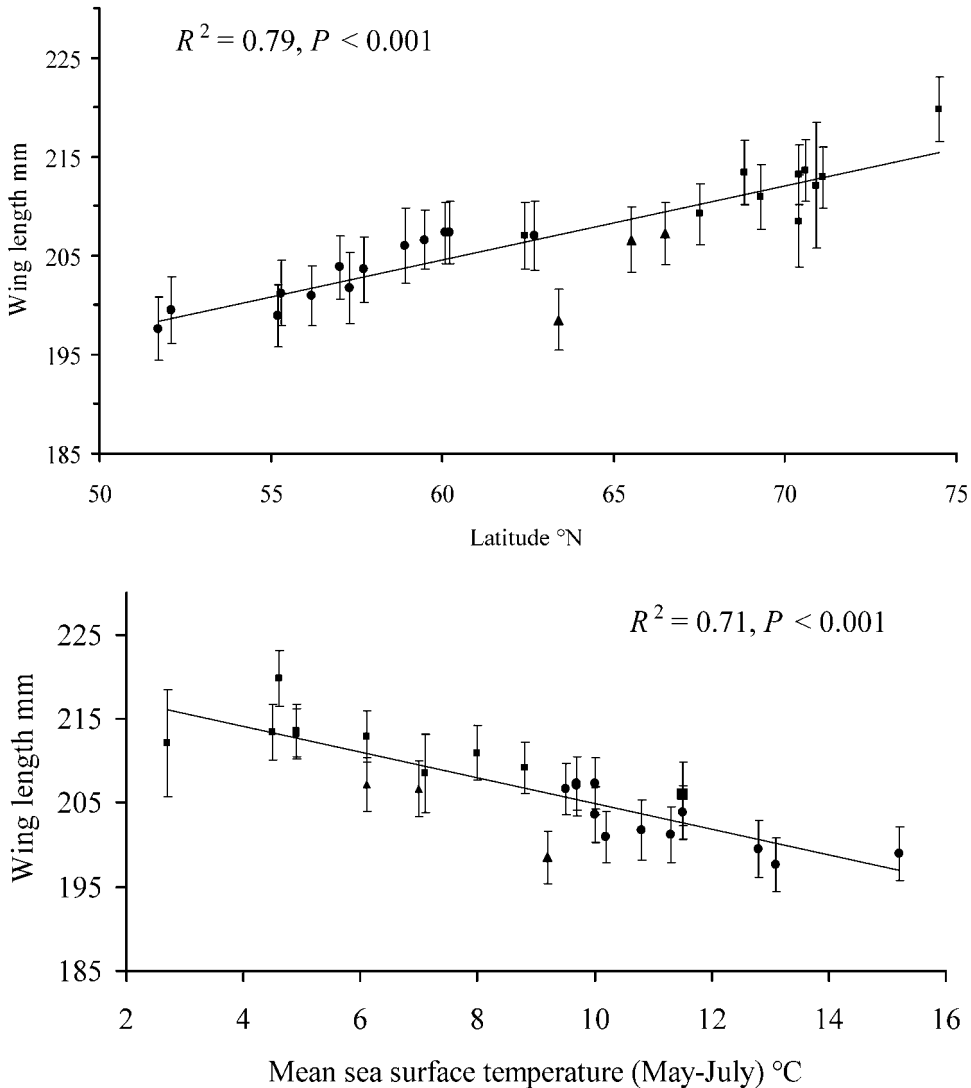


Figure 2. Plots of mean wing lengths of East Atlantic Common Guillemots in relation to latitude of colony and mean sea surface temperature. 95% confidence limits of means taking into account inter-observer variability of measurements (see methods) are shown. Data from Table 3. Square symbols = Norway and Russia, triangles = Iceland, dots = UK; from Jones (1988).

area. When including head + bill length the corresponding accuracy estimates for colony and sea area increased to 20% and 69%, respectively, whereas that for region dropped only slightly to 48%. It should be noted that the Box's M test for homogeneity of population covariances tested unequal in most cases. However, this test is particularly sensitive to deviations from multivariate normality, which we could expect from differences in sample sizes and measuring techniques among the observers (Barrett *et al.* 1989), as well as from probable natal dispersal of birds between the colonies (Nikolaeva *et al.* 1996).

Brünnich's Guillemot

There were again clear and significant ($P < 0.001$ in all cases) differences in mean measurements among the Barents Sea colonies (Table 2), but no obvious pattern with regards to geographical location within the Barents Sea. Furthermore, there were no significant correlations between any of the measurements and latitude or mean summer sea surface temperature with or without the inclusion of the Iceland and Jan Mayen colonies (Table 4, Figure 3). There was again considerable overlap of the 95% confidence intervals of the means.

Discussion

One major problem faced when comparing body measurements of birds is the inconsistency of repeat measurements among and between observers (Gaston *et al.* 1984, Ewins 1985, Barrett *et al.* 1989). Mass is probably the easiest and thus the most consistent to determine, but because body mass varies considerably throughout the year, it is useless as a parameter by which to determine a bird's origin. Of the others measured in this study, wing and head + bill have previously been shown to be most consistently measured (Barrett *et al.* 1989).

Furthermore, only slight variations in parameter definitions can preclude direct comparisons of measurements. For example, while culmen length is now generally measured from the bill tip to the proximal edge of the sheath, Storer (1952) measured from the bill tip to the "base of the anteriormost feathers", thereby presumably including the small patch of bare skin just behind the sheath. Likewise, gony's depth, as measured here, is not the same as Storer's measurement of bill depth (he measured vertically at the level of the anteriormost feathers), again precluding direct comparisons.

Table 2. Body mass (g) and morphometric measurements (mm) of adult Brünnich's Guillemots in Norwegian, Northwest Russian and Icelandic breeding colonies. The geographic coordinates of each colony are given in Table 4.

Colony	Mass			Wing			Culmen			Gonys			Head + bill		
	Mean	SE	n	Mean	SE	n	Mean	SE	N	Mean	SE	n	Mean	SE	n
Hornøya	999.6	3.7	323	222.2	0.3	322	37.5	0.2	312	14.6	0.1	312	105.5	0.2	298
Kharlov	936.9	27.1	8	219.0	0.7	43	37.8	0.3	43	14.5	0.1	35	105.8	0.5	43
Bjørnøya	1,068	9.5	51	224.4	0.6	51	37.3	0.3	82	14.3	0.1	82	103.5	0.4	51
Hopen	987.1	9.2	68	222.2	0.5	77	36.3	0.2	74	14.2	0.1	76	104.1	0.4	75
Kovalskifjellet	929.6	12.6	25	220.7	0.9	35	33.8	0.5	33	15.0	0.3	35	99.4	0.5	35
Ny-Ålesund	891.1	31.4	14	219.3	1.1	32	38.0	0.1	32	14.0	0.1	31	104.5	0.4	31
Rubini Rock	923.0	12.2	30	220.5	0.9	30	37.7	0.4	30	–	–	0	107.1	0.6	30
Bezmyannaya Bay	969.4	6.8	81	217.0	0.6	81	37.7	0.2	81	14.3	0.1	50	107.6	0.4	81
ANOVA ^a F		23.3			14.1			11.4			8.0			28.4	
P		< 0.001			< 0.001			< 0.001			< 0.001			< 0.001	
Latrabjarg	897.4	14.1	35	217.7	0.6	42	35.5	0.3	42	13.8	0.1	42	102.5	0.5	42

^aAmong Barents Sea colonies.

Table 3. Wing lengths (mm) of Common Guillemots breeding in the Northeast Atlantic. The positions of each colony are shown by number in Fig. 1. ucl, lcl = upper and lower 95% confidence limits (see methods), n = sample size.

No.	Colony	Country/Area	°N	°E	Mean	ucl	lcl	n	Source
1	Stora Karlsö	Baltic Sea	57.3	18.0	201.7	191.8	211.6	28	Salomonsen 1944
2	Graesholm	Baltic Sea	55.3	15.7	201.2	191.8	210.6	46	Jones 1988a
3	Helgoland	North Sea	55.2	7.9	198.9	195.0	202.8	25	O Hüppop pers. comm.
4	Skomer	SW Wales	51.7	-5.2	197.6	187.8	207.4	84	Jones 1988a
5	Great Saltee	SE Ireland	52.1	-6.7	199.5	191.3	207.7	35	Jones 1988a
6	Canna	NW Scotland	57.0	-6.5	203.8	193.8	213.8	91	Jones 1988a
7	Isle of May	SE Scotland	56.2	-2.6	200.9	190.9	210.9	351	Jones 1988a
8	Troop Head	NE Scotland	57.7	-2.3	203.6	195.7	211.5	39	Jones 1988a
9	Fair Isle	Shetland	59.5	-1.5	206.6	197.7	215.5	252	Jones 1988a
10	Foula	Shetland	60.1	-2.1	207.3	204.1	210.5	38	Jones 1988a
11	Noss	Shetland	60.2	-1.0	207.3	199.3	215.3	65	Jones 1988a
12	Eysturoy	Faeroes	62.7	-6.9	207.0	199.8	214.2	19	Jones 1988a
13	Jan Mayen	Norwegian Sea	70.9	-8.7	212.1	197.9	226.3	7	Camphuysen 1989
14	Grimsey	NE Iceland	66.5	-18.0	207.2	199.6	214.8	60	Jones 1988a
15	Latrabergr	NW Iceland	65.5	-24.4	206.6	198.5	214.7	38	This study
16	Ellidaey	SW Iceland	63.4	-20.2	198.5	188.4	208.6	150	Grandjean 1972
17	Rott	S Norway	58.9	5.5	206.0	198.5	213.5	13	Pethon 1967
18	Runde	S Norway	62.4	5.6	207.1	197.5	216.7	40	This study
19	Røst	N Norway	67.5	12.1	209.2	198.7	219.7	173	This study
20	Bleiksøya	N Norway	69.3	15.9	210.9	199.4	222.4	89	This study
21	Loppa	N Norway	70.4	21.4	208.5	196.3	220.7	13	This study
22	Hjelmsøya	N Norway	71.1	24.7	212.9	204.2	221.6	159	This study
23	Syltefjord	N Norway	70.6	30.3	213.6	202.6	224.6	110	This study
24	Hornøya	N Norway	70.2	31.1	213.2	202.1	224.3	412	This study
25	Kharlov	NW Russia	68.8	37.3	213.4	200.5	226.3	89	This study
26	Bjørnøya	Svalbard	74.5	19.0	219.8	216.7	222.9	57	This study

Among Common Guillemots, only wing length, with two exceptions, showed a clear geographic pattern in this study. Within the Norwegian samples, birds from Loppa had somewhat shorter wings than expected at the given latitude (Figure 2). Whereas the birds caught in all the other colonies were breeding adults, the Loppa birds were caught in nets below the cliffs. Eight of the 13 birds whose wings were measured had cloacal bursae of Fabricius and were thus immature and hence probably shorter winged than adults (Glick 1983). Similarly, the Icelandic outlier in Figure 2 (from Ellidaey) may also be due the inclusion of immature birds in the sample as Grandjean (1972) did not specify that the birds caught were only breeding adults and further suggests that the shorter wings may have been due to feather wear as the birds were caught late in the breeding season.

The increase in wing length with latitude in Common Guillemots in the East Atlantic is similar to that in the East Pacific where Californian birds have shorter wings than those in Alaska (Storer 1952). However, while the cline continues to the northeastern limit of distribution in the Atlantic (thus supporting de Wijs' (1978) suggestion to merge the race *hyperborea* with the nominate race), those from North Alaska and the Bering Sea are smaller in all measurements than those from southern Alaska (Storer 1952). Among Brünnich's Guillemots, this north-south cline seems to be reversed in eastern Canada with longer-winged birds breeding in the Gulf of St. Lawrence than in Arctic Canada (Storer 1952). There is, however, considerable variation in body size among colonies e.g. within the Hudson Strait (Gaston *et al.* 1984, Gaston and Jones 1998), suggesting factors other than the physical environment (SST, latitude) are operating.

Table 4. Wing lengths (mm) of Brünnich's Guillemots breeding in the Northeast Atlantic. The positions of each colony are shown by number in Fig. 1. ucl, lcl = upper and lower 95% confidence limits (see methods), n = sample size.

No.	Colony	Country/Area	°N	°E	Mean	lcl	ucl	n	Source
13	Jan Mayen	Norwegian Sea	70.9	-8.7	224.5	214.5	234.5	7	Camphuysen 1989
15	Latraberg	NW Iceland	65.5	-24.4	217.7	209.3	226.1	38	This study
24	Hornøya	N Norway	70.2	31.1	222.2	211.2	233.2	322	This study
25	Kharlov	NW Russia	68.8	37.3	219.0	209.2	228.8	43	This study
26	Bjørnøya	Barents Sea	74.5	19.0	224.4	215.3	233.5	51	This study
28	Hopen	SE Svalbard	76.6	25.3	222.2	213.0	231.4	77	This study
27	Kovalskifjellet	S Svalbard	77.1	17.1	220.7	209.5	231.9	35	This study
29	Ny-Ålesund	NW Svalbard	78.9	11.9	219.3	206.2	232.4	32	This study
30	Rubini Rock	Frans Josef Land	80.3	52.8	220.5	210.0	231.0	30	This study
31	Bezmyannaya Bay	Novaya Zemlya	72.9	53.1	217.0	205.4	228.8	81	This study

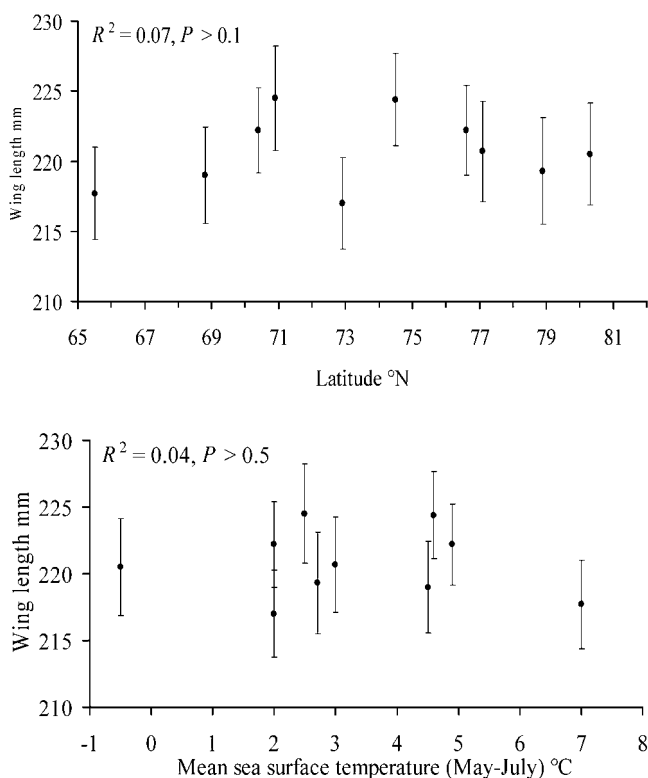


Figure 3. Plots of mean lengths of East Atlantic Brünnich's Guillemots in relation to latitude of colony and mean sea surface temperature. 95% confidence limits of the means taking into account inter-observer variability of measurements (see methods) are shown. Data from Table 4.

Whereas there was no consistent pattern of geographical variation among Brünnich's Guillemots in the NE Atlantic (this study), a comparison with data from the NW Atlantic substantiates Gaston and Jones' (1988) suggestion that North American birds are smaller than European birds (Fig. 4). Our data also place the Icelandic birds in the North American group,

whereas those from Jan Mayen are similar in size to those from Europe (Fig. 4). The only exception in this pattern were birds from Kovalskifjellet, Spitsbergen whose wings were long but whose culmens (and head + bill) were much shorter than their European counterparts (Table 2, Fig. 4). With the winter movements of Spitsbergen and probably also other Barents Sea Brünnich's Guillemots across to Greenland and Newfoundland (Nikolaeva *et al.* 1996, Bakken and Mehlum 2005), this size differentiation provides a means of detecting any European birds among those shot during the annual *turr* hunt in the Northwest Atlantic and hence evaluating the effect of the hunt on the mortality of adult European birds.

The absence of any phenotypic pattern among the Barents Sea Brünnich's Guillemots may be due to the northerly restriction of their breeding distribution. Furthermore, Friesen *et al.* (1996) found no genetic variation among North Atlantic Brünnich's Guillemots and suggested that this may be due to the establishment of all colonies from a single refugial population that survived the Pleistocene glaciation and that was so recent that there has been insufficient time for the evolution of colony-specific markers. This is further enhanced by the mixing of the whole Barents Sea population outside the breeding season, with large numbers of birds remaining in the area both at sea, near the coast and in ice-covered waters after the breeding season and over winter (Fauchald *et al.* 2004, Bakken and Mehlum 2005 and references therein). This probably also applies to an unknown proportion of the population that moves out of the region and winters off Iceland, Greenland and Northeast Canada (Nikolaeva *et al.* 1996, Bakken and Mehlum 2005). As a result, the chances of birds from different colonies joining recruits to other colonies and thus returning to non-natal colonies throughout the region are high. Such lack of philopatry has been documented through observations of ringed adult and immature birds (Nikolaeva *et al.* 1996) and would contribute to the low genetic and phenotypic variation demonstrated for this species (Birt-Friesen *et al.* 1992, this study)

That the North Atlantic Common Guillemot colonies constitute a largely panmictic population with a low level of genetic differentiation (Moum and Arnason 2001, Cadou *et al.* 2004, Riffault *et al.* 2005) is corroborated by the lack of consistent variation in most of the body measurements presented here. There is, however, evidence that it is derived from two or more Pleistocene refugia, one in the far Northeast Atlantic (possibly Barents Sea) and one further south. Secondary contact between these genetically differentiated populations could result in a

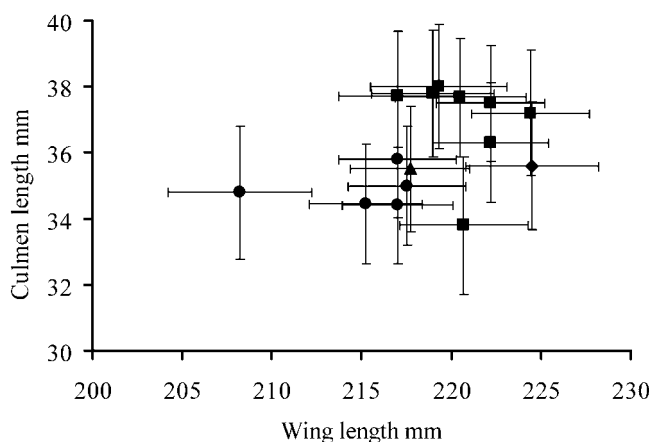


Figure 4. Plot of culmen length versus wing length for Brünnich's Guillemot populations. 95% confidence limits of means taking into account inter-observer variability of measurements (see methods) are shown. Squares = Norway and Russia, triangle = Iceland, diamond = Jan Mayen (all from Table 4); dots = East Canada (from Gaston and Nettleship (1981), Gaston *et al.* (1984) and Birkhead and Nettleship (1987)).

cline between the two (Friesen *et al.* 1996). Such secondary contact is common among European Common Guillemots whose post-breeding migratory/dispersal patterns, although somewhat differentiated (Harris and Swan 2002), does result in some mixing of populations along the coast of the North Sea and Norway (Strann *et al.* 1991, Bakken *et al.* 2003). Many young birds also recruit into non-natal colonies (Harris *et al.* 1996) and there is repeated documentation of long-distance dispersal of Common Guillemots from one colony to another (Halley and Harris 1993, Lyngs 1993, Nikolaeva *et al.* 1996, Harris and Swann 2002). Such contact between the two populations may, in time, have led to the clinal variations in wing length (this study) and the frequency of bridling (Birkhead 1984).

There is a clear south-north phenotypic cline in wing length among Common Guillemots, but the large confidence intervals that result from data being collected by different observers precludes more than a rough identification of the origins of birds found away from their colonies (Fig. 2). This is corroborated by our discriminant analyses, which indicated that although our method of identifying the origin of Common Guillemots based on their biometrics is not very accurate at the colony level, it performs relatively well at the region and sea area level, provided one has a reasonably large sample of adult birds. This assumes that the variance among those taking part in Barrett *et al.*'s (1989) study was similar to that among those who measured birds in the present study. This is a reasonable assumption as most of the measurements were made by experienced researchers. A reduction in the confidence intervals is possible only by a large increase in the sample sizes for each colony when several measurers are involved. An alternative is that all measurements are made by one observer in all colonies (Barrett *et al.* 1989) although this is obviously very impractical as it would also entail that same observer would need to measure all the birds examined in an 'incident'.

Despite this limitation, however, and until other genetic markers are found (Riffault *et al.* 2005), careful measurements of wing and head + bill lengths are still the only simple direct determinant of the origin of unringed adult Northeast Atlantic Common Guillemots, as is also the case for Atlantic Puffins *Fratercula arctica* and Razorbills *Alca torda* (Barrett *et al.* 1985, 1997, Anker-Nilssen *et al.* 2003). It is thus likely that if, for instance, such a series of measurements had existed for Common Guillemots or Rhinoceros Auklets *Cerorhinca monocerata* breeding in the North Pacific, the origins of the birds caught in gill nets in Washington in the early 1990s might have been easier to determine than through observations of incubation patch refeathering (Thompson *et al.* 1998). Although we succeeded only in differentiating the origins of one of the two *Uria* guillemot species in the Northeast Atlantic, we recommend exploring further the use of biometrics as determinants of the breeding areas of seabirds or any other bird species with a wide latitudinal distribution range.

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