

Connectivity and Age Distribution of the Baltic Common Guillemot *Uria aalge* Population: Evidence from Morphometry and Ringing Recoveries

Authors: Peterz, Mats, and Blomqvist, Sven

Source: *Ardea*, 98(2) : 169-178

Published By: Netherlands Ornithologists' Union

URL: <https://doi.org/10.5253/078.098.0206>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Connectivity and age distribution of the Baltic Common Guillemot *Uria aalge* population: evidence from morphometry and ringing recoveries

Mats Peterz¹ & Sven Blomqvist^{2,*}

Peterz M. & Blomqvist S. 2010. Connectivity and age distribution of the Baltic Common Guillemot *Uria aalge* population: evidence from morphometry and ringing recoveries. *Ardea* 98: 169–178.

In evolutionary ecology, environmental monitoring and conservation management, reliable information on phenotypic and demographic traits in marine seabirds is highly wanted, but difficult to acquire. Therefore, freshly dead Common Guillemots *Uria aalge* ($n = 149$) incidentally drowned in salmon drift gill nets in the Baltic Sea, during October–November, were studied. We noted age, sex, moult pattern and fat status, and took morphometric measurements to compare with data from the Northeast Atlantic population. Only minor phenotypic differences were found. The birds had slightly longer wings than expected at the latitude where they were collected, probably due to their newly grown primaries and/or observer differences, rather than a genetic divergence. The Baltic Guillemot appears not to be a distinct subspecies, but only the marginal member of a deme. Ringing recoveries also suggest intermittent exchange of birds between the Baltic and the North Sea. Young birds did not seem to be over-represented in gill net bycatches. Our found age distribution – with a heavy dominance of adult birds, but few immature/juveniles – deviated from that reported earlier, and suggests that the population is more vulnerable to adult mortality through bycatch in gill nets than previously believed.

Key words: Common Guillemot, *Uria aalge intermedia*, seabird, age distribution, deme, taxonomy, fishing net, bycatch, Baltic Sea

¹Avenue Félix-Cornu 36, CH-1802 Corseaux, Switzerland;

²Dept Systems Ecology, Stockholm University, SE-106 91 Stockholm, Sweden;

*corresponding author (sven.blomqvist@ecology.su.se)



Avian phenotypic and demographic traits are particularly difficult to investigate in marine seabird populations (Brooke 1990, Wooller *et al.* 1992, Ratcliffe 2004). This is unfortunate, since such information is crucial for understanding evolutionary avian ecology in general (Sæther & Bakke 2000, Bennett & Owens 2002), and for designing reliable environmental marine monitoring programmes, in particular (cf. Furness & Monaghan 1987, Einoder 2009). This applies also to the Common Guillemot *Uria aalge* (Camphuysen 2007), which in the non-breeding season is a largely pelagic seabird species (Halley *et al.* 1995).

Common Guillemots found dead can provide phenotypic data on biometrics and population characteristics useful for deducing their taxonomic status, demography and geographic origin. This applies to birds

found at wrecks (Jones *et al.* 1984), beached bird surveys (Camphuysen 1983), oil spills (Camphuysen & Leopold 2004) and bycatches in fishing net (Oldén *et al.* 1985). The dead birds can also be used for other studies, such as food selection (Lyngs & Durinck 1998), physical condition (Jones *et al.* 1984), moult pattern (cf. Thompson *et al.* 1998a), and pollutant burden (Stewart *et al.* 1994). The Common Guillemot is a polytypic species (Storer 1952), which makes such specimen studies particularly appropriate (e.g. Cadiou *et al.* 2004). However, to be useful in conservation management, the taxonomic status of the studied population needs to be established with the help of reliable biometric reference information. Also, we have to know that collected specimens are representative of the studied population, for instance, with respect to age

and sex distribution. Perhaps, adults are better than immature at avoiding entangling in fish nets (cf. Oldén *et al.* 1986, Strann *et al.* 1991, Murray *et al.* 1994, Österblom *et al.* 2002)?

The Common Guillemot shows geographical clines in several morphological characters (Storer 1952) and this might be used to deduce the origin of collected birds. From south to north the proportion of bridling, the colour darkness of upperwing, head and back, the degree of streaking on the flanks, and the wing length all increase in the Northeast Atlantic (Salomonsen 1944, Jones 1988, Camphuysen 2007, Barrett *et al.* 2008). These latitudinal phenotypic clines are continuous, without sharp boundaries between putative subspecies or colonies. However, a prerequisite for assigning individual Common Guillemot to subpopulations or morphs is that reliable comparative reference data from breeders in different geographical areas are available – including that of the Baltic Sea.

We therefore report extensive biometric data from freshly dead Common Guillemots drowned in salmon gill nets in the Baltic Sea. We give particular attention to comparing Baltic Common Guillemots with the North Atlantic population, and to the age distribution in relation to mortality, moult pattern and fat status. Such biometric data on bycaught Common Guillemot from the Baltic have not been published before, but are clearly needed.

METHODS

The Common Guillemot is a mainly piscivorous (pursuit diving) seabird species, found in northern continental shelf water environments (Brown 1985, Nettleship 1996). In the North Atlantic and adjacent waters, the Common Guillemot breeds from Labrador in the west, to Novaya Zemlya in the northeast, and Iberia in the southeast (Nettleship & Evans 1985). This population is estimated at 2.9 million pairs (Harris & Wanless 2004), with a small fraction breeding in the brackish Baltic Sea.

Taxonomic status of Baltic Common Guillemots

Sven Nilsson (1835) was first in proposing that the Baltic Common Guillemot population is separated from the rest of the North Atlantic population. Later it was given subspecies status as *U. a. intermedia*, an intermediate between the paler southern *albionis* and the darker nominate subspecies *aalge* (Salomonsen (1944). Also, two other subspecies have been distinguished, namely *spiloptera* in the Faeroe Islands and *hyperborea*

in the northern Northeast Atlantic (Salomonsen 1932). This view has persisted in the literature (Storer 1952, Tuck 1960, Vaurie 1965, Dementiev & Gladkov 1968, Harrison 1983, Brown 1985, Freethy 1987, Howard & Moore 1991, Morris-Pocock *et al.* 2008), but has also been called into question (e.g. Glutz von Blotzheim & Bauer 1982, Nettleship 1996) and a lumping of the subspecies *intermedia*, *spiloptera* and *aalge* in a single subspecies *aalge* has been proposed (Bédard 1985). Sequence analysis of mitochondrial DNA and multiple nuclear loci (microsatellite DNA) supports amalgamation of the Northeast Atlantic population (Moum & Árnason 2001, Riffaut *et al.* 2005, Morris-Pocock *et al.* 2008).

Baltic population studied

In the early 1970s, the total breeding population of the Common Guillemot in the Baltic Sea was estimated at about 8,800 pairs (Hedgren 1975), with the largest colony (c. 6,400 pairs) found at the island of Stora Karlsö (Fig. 1). Four other colonies of c. 1,000 pairs or more are now found in the Baltic Sea, i.e. on the islands of Lilla Karlsö, Källskären, Græsholmen and Bonden, respectively (SOF 2003, 2004, Hjernquist *et al.* 2005, Lyngs 2005). The total breeding population in the Baltic Sea has been estimated at 12,000–17,000 pairs (Österblom *et al.* 2002). The expansion of the Common Guillemot in the Baltic is to a large extent a result of emigration from the colony at Stora Karlsö. The colony at Stora Karlsö appears to be the major centre of emigration but there is also a substantial interchange between other colonies within the sea area (Hario 1982, Lyngs 1993, Fransson *et al.* 2008, Staav 2009).

Collection of birds

When comparing small morphological differences in wing and bill of birds, measurements can be made on dried museum skins, but these have the disadvantage that due to post-mortem shrinkage they cannot be directly compared with measurements on live or recently dead individuals (e.g. Harris 1980, Ewins 1985). Comparisons to museum skins can still be made with a correction factor for shrinkage, but corrections are specific for each species and shrinkage may vary due to differences in preparation of specimens (Ewins 1985, Winker 1993). Data measured on live or freshly dead birds – as reported in the present study – are therefore to be preferred when comparing records from different populations.

In the present study, birds incidentally drowned in salmon gill nets were collected by fishermen at the island of Öland, Sweden (Fig. 1). In total, 149 indivi-



Figure 1. Map of the Baltic Sea and adjacent sea areas, with geographical names mentioned in the text. Bd Bonden, Gh Gräsholmen, Gr Grän, Hl Helgoland, HV Hallands Väderö, LK Lilla Karlsö, SK Stora Karlsö and Ks Källskären.

duals were landed at five occasions; 11 November 1987 (13 specimens), 28 October 1988 (4), 2 November 1988 (10), 29 November 1988 (50) and 14 November 1989 (72), respectively.

The birds were kept chilled and sent to the National Veterinary Institute, at Uppsala, Sweden, where they were dissected and sexed by gonad inspection. External examination was carried out either on fresh birds, or after 3–5 months of freezing.

Biometric examination

The examination followed the proposal of Jones *et al.* (1982; see also review by Camphuysen 1995), but included some additional measurements (Table 1). Complete measurements were not made on all birds, as some were damaged when disentangled from the gill net. To avoid inter-measurement variability, a single person (MP) carried out all measurements, as recommended by Barrett *et al.* (1989). Throughout, the central values of mean refer to arithmetic mean (AM) \pm one standard deviation (SD). We used JMP[®] statistical software (version 3, SAS Institute Inc., Cary, North Carolina, USA). For details of the statistical tests used, see Zar (2009).

Table 1. Phenotypic characters recorded on Common Guillemots drowned in salmon gill nets in the Baltic proper 1987–89. For description of methodology used, see references.

Phenotypic character	Examination	Measured to nearest mm
Wing length	Maximum flattened cord, from the carpal joint to the tip of the longest primary (Jones <i>et al.</i> 1982)	1
Bill length, culmen	Straight distance between culmen tip and the proximal edge of the horny sheet of upper mandible (Jones <i>et al.</i> 1982)	0.1
Bill length to nostril	Straight distance between culmen tip and the distal edge of external naris (Gaston 1984)	0.1
Head + bill length	Length from the tip of the bill to the back of the head (Coulson <i>et al.</i> 1983)	1
Bill depth	Depth at the gonys perpendicular to the cutting edge (Jones <i>et al.</i> 1982)	0.1
Supraorbital ridge	Width across the supraorbital ridge (Gaston 1984)	0.1
Total tarsus and foot length	Distance from the “knee” of the flattened tarsometatarsus to the base of the nail of the middle toe of the flattened foot (Fox <i>et al.</i> 1981)	1
Cloacal bursa (bursa Fabricii)	Absence or length and width of cloacal bursa (Jones <i>et al.</i> 1982)	1
Plumage	Winter (basic ¹), summer (nuptial ¹) or intermediate (prenuptial ¹) head plumage (Jones <i>et al.</i> 1982; ¹ following Humphrey & Parks 1959)	–
Appearance of white tips on greater underwing coverts	Presence of white tips on greater underwing coverts (Kuschert <i>et al.</i> 1981)	–
Moult of greater upperwing coverts	Presence of unmoulted juvenile greater upperwing coverts (Kuschert <i>et al.</i> 1981)	–
Bridling polymorphism	Presence or absence of a bridle mark, i.e. white eye-ring and stripe (Jones <i>et al.</i> 1982)	–
Subcutaneous fat	Amount of visible fat under the abdominal skin ranked from 0 (no fat) to 3 (thick fat) (Jones <i>et al.</i> 1982)	–

Ageing

Birds were classified (Appendix 1) as follows:

- Adult, c. 5 calendar years of age or more. Absence of cloacal bursa (bursa Fabricii) and absence of white tips on the greater underwing coverts.
- Immature, 2– c. 4 calendar years of age. Presence of cloacal bursa, but absence of white tips on the greater underwing coverts.
- Juvenile, first calendar year. Presence of cloacal bursa and white tips on the greater underwing coverts.

Both wings were lacking on 14 birds with a cloacal bursa, and these were aged using the width of the supraorbital ridge (Gaston 1984). In the initial stage of classification, the supraorbital ridge of whole juvenile birds was estimated at 8.8 ± 0.7 mm (maximum 10.2 mm), and of the immature group to 11.3 ± 0.6 mm (minimum 10.3 mm). From these reference records, specimens without wings, but with a supraorbital ridge of 9.2 mm or less, were counted as juveniles ($n = 10$), and those with a supraorbital ridge of 11.1 mm or more as immature birds ($n = 3$). One Common Guillemot (a male), with a supraorbital ridge of 10.2 mm was classified as immature, since its length of head and bill were in the upper range of this age group.

To validate ageing records one wing was collected from 57 birds. The wings were checked for moult in the upper greater wing coverts, after being dried in the air at ambient/room temperature. The presence of unmoulted greater wing coverts was compared with the presence of white tips on the greater underwing coverts, as both are found to be an almost infallible character of juvenile birds (Kuschert *et al.* 1981). With the exception of three birds, the two criteria agreed perfectly (Appendix 2). Among the three birds showing deviating patterns, one was a juvenile (with a bursa and a supraorbital ridge of 10.0 mm) lacking unmoulted greater wing coverts. The other two were adults (absence of bursa and supraorbital ridge 11.9 and 13.4, respectively) showing white tips on the greater underwing coverts.

Ringling data for recovered birds were received from the Bird Ringing Centre at the Swedish Museum of Natural History, Stockholm. Nine individuals classified as adults were ringed as fledglings of the Stora Karlsö colony. Among these, one was in its 5th calendar year, seven in their 11th to 14th year, and one in its 20th year, all well in line with the age classification.

Table 2. Biometric measurements (mm) of Common Guillemots drowned in salmon gill nets in the Baltic proper 1987–89. For each parameter, mean, SD, range and number of records (n) are given.

Age		Male				Female			
		Mean	SD	Range	n	Mean	SD	Range	n
Adult	Wing length	207.0	3.9	199–215	31	207.8	4.6	197–215	47
	Bill length, culmen	50.3	2.2	45.5–55.5	45	47.8	2.3	43.0–54.2	62
	Bill length to nostrils	43.0	1.9	38.6–47.6	45	41.0	2.0	36.9–48.2	62
	Head + bill length	116.8	2.7	112–124	45	113.0	2.9	107–120	62
	Bill depth	13.7	0.6	11.8–14.8	45	13.1	0.7	11.7–14.5	63
	Supraorbital ridge	12.6	0.9	10.7–14.8	45	12.2	1.0	9.5–14.0	64
	Tarsus + foot	96.8	3.3	91–104	25	94.1	2.7	88–100	43
Immature	Wing length	204.5	7.8	199–210	2	203.7	2.8	201–209	6
	Bill length, culmen	52.0	1.8	49.0–53.4	5	47.9	1.5	45.7–50.3	6
	Bill length to nostrils	43.7	2.2	39.9–45.3	5	40.3	1.4	38.0–41.9	6
	Head + bill length	117.4	2.1	114–119	5	112.2	2.5	108–115	6
	Bill depth	12.6	0.5	12.0–13.3	5	12.7	0.7	11.3–13.3	6
	Supraorbital ridge	11.3	0.8	10.2–12.2	5	11.5	0.8	10.3–12.7	6
	Tarsus + foot	97.0	2.3	94–99	5	93.8	2.4	90–97	6
Juvenile	Wing length	199.1	3.1	194–206	13	200.0	6.1	196–207	3
	Bill length, culmen	48.6	2.7	43.8–52.6	18	49.6	1.9	45.9–51.6	8
	Bill length to nostrils	40.8	2.2	36.5–44.0	18	41.5	2.0	37.1–44.0	8
	Head + bill length	112.8	4.2	106–119	18	113.5	2.2	109–117	8
	Bill depth	12.2	0.7	10.5–13.8	18	11.8	0.3	11.4–12.2	8
	Supraorbital ridge	8.7	0.7	7.5–10.2	18	8.8	0.3	8.4–9.3	8
	Tarsus + foot	94.9	3.0	90–99	11	93.3	1.6	91–95	6

RESULTS

Demography

Age distributions were not different in the three years studied (Chi-square test; $\chi^2 = 7.93$, $df = 4$, $P = 0.094$) (Appendix 1). Most were adults (74.5%), followed by juveniles (17.4%) and immature birds (8.1%). Females dominated among the adults, males among the juveniles. The overall sex ratio did not differ from parity 1:1 ($\chi^2 = 0.812$, $df = 1$, $P = 0.368$).

Biometric measurements

An overlap between age and/or sex groups was recorded for all measured parameters (Table 2). Significant differences were found in wing length, bill depth and supraorbital ridge between age groups, but not between sexes (Table 3). Bill length at culmen and nostrils, as well as tarsus plus foot length were significantly different between sex, but not between age classes. Only head plus bill length was significantly different between both age and sex groups.

Pooled wing lengths for all adult females and males averaged 207.5 mm (SD = 4.3, range 197–215, $n = 78$). Birds originating from the colony at Stora Karlsö (57.3°N) are expected to have a wing length of approximately 203 mm (Jones 1988, Barrett *et al.* 2008). Hence, our average wing length is significantly longer than predicted (one-sample t -test; $t = 9.30$, $P < 0.001$).

The wing lengths of our birds are also significantly longer ($t = 8.06$, $P < 0.001$) than those measured in June in the colony at Græsholmen (201 ± 4.4 , range 192–210, $n = 46$, Lyngs 1992). This difference might be the result of inter-measurer variability (Barrett *et al.* 1989), and/or a consequence of difference in undergone feather abrasion.

The pooled bill depth for adult females and males averaged 13.4 mm (SD = 0.7, range 11.7–14.8,

$n = 108$), which is less than reported from the Græsholmen colony (14.1 ± 0.6 , range 13.0–15.8, $n = 46$; Lyngs 1992). This difference is statistically significant ($t = 6.30$, $P < 0.001$), and fits with the shed of bill plates reported in the Common Guillemot before and after breeding (Grandjean 1972). A similar decrease (0.7 mm) in June to November was found in Northwest Scotland (Furness *et al.* 1994).

Plumage and fat status

Most birds (68%) were in winter (basic) plumage. All birds in summer (nuptial) plumage were adults. Among birds in intermediate (prenuptial) plumage, one was a juvenile in winter plumage with some facial streaks of black, all others were adults. In adult birds, the proportion in summer plumage increased during autumn (Fig. 2). In the first ten days of November all adult birds were in winter plumage. By the end of the month only 27% were in winter plumage, and the rest had either started the prenuptial moult or attained summer plumage.

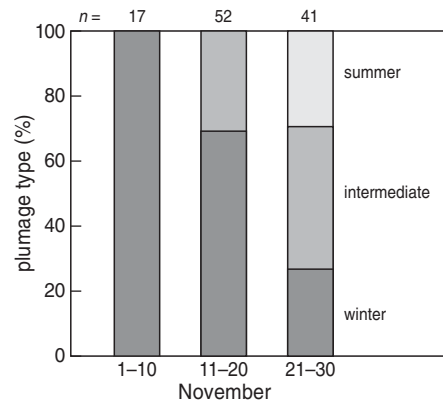


Figure 2. Moult status of bycaught adult Common Guillemot, classified by summer (nuptial), intermediate (prenuptial) and winter (basic) plumage.

Table 3. Statistical tests for differences in morphometric characters between age and sex groups by two-way ANOVA of Common Guillemots drowned in salmon gill nets in the Baltic proper 1987–89.

	Age			Sex			Age x Sex		
	F	df	P	F	df	P	F	df	P
Wing length	16.2	2,96	<0.001	0.04	1,96	0.843	0.11	2,96	0.897
Bill length, culmen	0.86	2,138	0.427	10.6	1,138	0.002	6.80	2,138	0.002
Bill length to nostrils	1.71	2,138	0.185	9.28	1,138	0.003	5.20	2,138	0.007
Head + bill length	3.13	2,138	0.047	13.5	1,138	<0.001	5.84	2,138	0.004
Bill depth	50.4	2,139	<0.001	3.35	1,139	0.070	1.90	2,139	0.153
Supraorbital ridge	148.8	2,140	<0.001	0.03	1,140	0.860	0.913	2,140	0.404
Tarsus + foot	1.42	2,90	0.247	10.22	1,90	0.002	0.323	2,90	0.725

The proportion of the bridled morph found in the present study (2.7%, $n = 147$) was neither significantly different (χ^2 with Yates correction) from earlier reports for the two Karlsö islands (3.8%, $n = 425$; Birkhead 1984), nor the colony at Græsholmen (6.5%, $n = 46$; Lyngs 1992).

The subcutaneous fat status showed that most birds were in good condition (Table 4). A fat score of 2 or 3 was recorded for about 75% of the birds, while only two birds (1.3%) totally lacked subcutaneous fat reserves (fat score 0). This is a much higher fat status than reported from a wreck in the North Sea, where 69% of the Common Guillemots had a fat score of zero (Jones *et al.* 1984). Among our adults, females carried significantly more subcutaneous fat than males ($\chi^2 = 9.40$, $df = 3$, $P = 0.024$), but no difference was found between the age groups ($\chi^2 = 9.17$, $df = 6$, $P = 0.164$).

Table 4. Subcutaneous fat score of Common Guillemots drowned in salmon gill nets in the Baltic proper 1987–89.

Age	Sex	Fat score				Total
		0	1	2	3	
Adult	Female		11	28	26	65
	Male	1	16	22	7	46
Immature	Female		1	2	4	7
	Male		3	1	1	5
Juvenile	Female		2	1	5	8
	Male	1	3	5	9	18
Total		2	36	59	52	149

DISCUSSION

Findings reported above demonstrate the usefulness of biometric data from drowned Common Guillemots to determine demography, age specific mortality rate, moult pattern and nutritional status. Strong evidence on taxonomic status and geographic origin is obtained when these data are combined with ringing recoveries and genetic analysis. This is information concerned, for instance, in reliable conservation management and marine environmental monitoring.

Flight feathers and moult

The wing length of adult Common Guillemots found in our study deviates from a previously reported European latitudinal cline. However, the wing length is not a fully distinctive character, since Baltic birds overlap consid-

erably with Common Guillemots reported from the Northeast Atlantic gradient (Cadiou *et al.* 2004, Barrett *et al.* 2008). This is similar to the Razorbill *Alca torda* in the Norwegian–Barents seas gradient, where wing length likewise overlaps considerably in the subspecies of *torda*, *islandica* and *pica*, and often makes it virtually impossible to assign an individual bird to a geographical origin with certainty (Barrett *et al.* 1997).

Guillemots moult their flight feathers in late summer to early autumn, and wear freshly grown primaries in October–November (Birkhead & Taylor 1977, Bédard 1985, Harris & Wanless 1990). This coincides with the season in which our specimens were collected, whereas the length of wings in the European cline studies (Jones 1988, Barrett *et al.* 2008; the latter included samples of dried museum specimens) and at Græsholmen (Lyngs 1992) were measured on birds in colonies during the breeding season. This is just before moulting, when primaries are worn, and might be shorter than when freshly moulted. Longest primaries in Common Guillemots are frequently abraded, losing several millimetres in length by end of chick-rearing period (Ainley *et al.* 2002).

Our observation that moulting of flight feathers could influence wing length warrants further studies of the Common Guillemot to clarify whether this character can be used as a reliable criterion of geographical origin throughout the year. This is particularly important as wrecks and oiling incidents often occur in the winter. If wing measurements are compared between autumn–winter and spring–summer, inferences of the birds’ origin will be uncertain.

Age distribution

Based on ringing data, first-year Common Guillemots killed in fishing nets have previously been reported in higher numbers than other age groups (Peterz & Oldén 1987, Heubeck *et al.* 1991, Lyngs & Kampp 1996, Harris & Swann 2002, Österblom *et al.* 2002). Likewise, young birds are over-represented in biometric examinations of dead birds collected from fishing nets in the Kattegat and the Skagerrak (Oldén *et al.* 1985, 1986, Anker-Nilssen & Lorentsen 1995), as well as in northern Norway (Strann *et al.* 1991) and northeast Scotland (Murray *et al.* 1994). As a corollary, it has been suggested that adult birds are more skilled at avoiding nets (Oldén *et al.* 1986, Strann *et al.* 1991, Murray *et al.* 1994, Österblom *et al.* 2002). The present study contrasts with this notion, since 74% of our drowned birds were adults, whereas less than 10% were adults in the studies mentioned above, with up to 70% first-year birds. A similarly high proportion of

adult birds (63%) entangled in gill nets is reported from Washington State, USA (Thompson *et al.* 1998b).

The breeding success of Common Guillemots at Stora Karlsö has been estimated to be 0.80 fledged chicks/ pair (Hedgren 1980), and the survival rate for the Baltic Guillemots (mostly ringed at Stora Karlsö) is 0.65 for immature birds, and 0.89 for adults (Olsson *et al.* 2000). So far, no estimate has been provided on survival rate in first-year birds, but a survival rate estimate of 0.56 is reported from a Scottish colony (Harris *et al.* 2007). Based on these estimated age-specific survival rates, and assuming a constant mortality rate during the year, we calculated (see example by Pianka 2000) that approximately 54% adults, 27% immature and 19% juveniles are expected in October–November among Common Guillemots in the Baltic Sea. This age structure differs significantly ($\chi^2 = 21.7$, $df = 2$, $P < 0.0001$) from what we have recorded in birds drowned by fishing nets (Appendix 1).

Ringling recoveries have shown that juvenile and immature birds disperse farther away from their natal colony than adults (Harris & Swann 2002). In the Baltic, most juveniles are reported recovered in the very south or southwest and the adults largely around the island of Gotland during winter months (Olsson *et al.* 1999, Fransson *et al.* 2008). Also, adult birds may start to return to their breeding colony from October, and onwards (Halley *et al.* 1995). As the birds examined are collected off Öland, not far from their presumed natal colony at the Karlsö islands, this may easily explain the deviation from the expected age distribution. Hence, the age distribution found in bycatch studies probably reflects the true at-sea distribution in the fishing area rather than age-specific differences related to fishing net vulnerability. Therefore, the notion that adults are better at avoiding fish nets than young birds may be questioned.

Ringling recoveries

Earlier ringling recoveries have shown that the Baltic Guillemot is fairly resident, and that most birds remain in this sea area throughout the year (Fransson *et al.* 2008). All our recovered birds were ringed at Stora Karlsö, and the proportion of bridled morphs was likewise in agreement. Hence, it appears safe to state that our biometric data represent the Baltic Sea population, and probably breeders from the Karlsö islands in particular.

Although the Common Guillemot is highly philopatric, there are examples of emigration to non-natal sea areas. Since 1993, three British Guillemots were captured in colonies of the Baltic Sea. A Scottish (Isle of

May) bird in its fourth calendar year was observed in the colony at Græsholmen (Mead *et al.* 1995), and another, ringed at Fair Isle, Shetland, was found breeding at the island of Bonden (Staav 1997), i.e. the northernmost colony in the Baltic Sea (Fig. 1). The third bird ringed as chick at Sule skerry, Orkney, was captured in the colony at Grän (Fig. 1) in 1999, and once again nine years later (Staav 2009). Also, there is one bird ringed as a chick in the Baltic (Stora Karlsö) that has been found breeding in a Northeast Atlantic colony, namely at Skomer Island, Wales (Staav 1997).

Before 1980, only a few Common Guillemots ringed in the North Sea area were recovered in the Baltic Sea. Since then, more than 20 birds from northeast British colonies have been recovered in the Baltic and a few from Helgoland (Staav 1997, Lyngs & Kampp 1996, Harris & Swann 2002). The Baltic records coincide with a large general increase in Common Guillemots wintering in the Kattegat, where ringling recoveries of birds entangled in fishing gear suggested an origin mainly from Scottish colonies and Helgoland (Peterz & Oldén 1987).

Conclusions

Our phenotypic records in combination with previous genetic studies provide strong evidence in favour of the Baltic Common Guillemot population being a marginal deme of the North Atlantic population, rather than a distinct subspecies. Ringling recoveries (referred above) suggest intermittent exchanges of birds between the two areas, and the reality of these interchanges has been supported by genetic analysis (Riffaut *et al.* 2005). Our biometric measurements (Table 2) are in full agreement with this view.

The common notion (e.g. Österblom *et al.* 2002) that Baltic Common Guillemots bycaught in gill nets are over-represented by young individuals may well be questioned. Our recorded age distribution with a heavy dominance of adult birds, but few immature/juveniles (Appendix 1), deviates from that reported earlier. It implies that the Baltic population of the Common Guillemot is more vulnerable to adult mortality through bycatch in gill nets than previously suggested (cf. Österblom *et al.* 2002).

ACKNOWLEDGEMENTS

We are grateful to fisherman Reine Johansson and to Seppo Ekelund for the collecting of birds. Roland Staav provided valuable information on ringling recoveries from Swedish Common Guillemot colonies. Ragnar Elmgren and Emma Karlsson kindly improved the linguistics. Umeå Marine Sciences Centre, Umeå University, provided favourable opportunity for manuscript preparation.

REFERENCES

- Ainley D.G., Nettleship D.N., Carter H.R. & Storey A.E. 2002. Common Murre (*Uria aalge*). In: Poole A. & Gill F. (eds) The Birds of North America, No. 666, The Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.
- Anker-Nilssen T. & Lorentsen S.H. 1995. Size variation of Common Guillemots *Uria aalge* wintering in the northern Skagerrak. *Seabird* 17: 64–73.
- Barrett R.T., Peterz M., Furness R.W. & Durinck J. 1989. The variability of biometric measurements. *Ring. Migrat.* 10: 13–16.
- Barrett R.T., Anker-Nilssen T. & Krasnov Y.V. 1997. Can Norwegian and Russian Razorbills *Alca torda* be identified by their measurements? *Mar. Ornithol.* 25: 5–8.
- Barrett R.T., Anker-Nilssen T., Bakken V., Strøm H., Krasnov Y.V. & Aarvik T. 2008. Biometrics as a determinant of the origins of seabirds killed in oil spills and other incidents. *Bird Conserv. Int.* 18: 229–241.
- Bédard J. 1985. Evolution and characteristics of the Atlantic Alcidae. In: Nettleship D.N. & Birkhead T.R. (eds) The Atlantic Alcidae. Academic Press, London, pp. 1–51.
- Bennett P.M. & Owens I.P.F. 2002. Evolutionary ecology of birds: Life histories, mating systems, and extinction. Oxford University Press, Oxford.
- Birkhead T.R. 1984. Distribution of the bridled form of the Common Guillemot *Uria aalge* in the North Atlantic. *J. Zool. (Lond.)* 202: 165–176.
- Birkhead T.R. & Taylor A.M. 1977. Moults of the Guillemot *Uria aalge*. *Ibis* 119: 80–85.
- Brooke M. 1990. The Manx Shearwater. Poyser, London.
- Brown R.G.B. 1985. The Atlantic Alcidae at sea. In: Nettleship D.N. & Birkhead T.R. (eds) The Atlantic Alcidae. Academic Press, London, pp. 383–426.
- Cadiou A., Riffaut L., McCoy K.D., Cabelguen J., Fortin M., Gélinaud G., Le Roch A., Tirard C. & Boulinier T. 2004. Ecological impact of the “Erika” oil spill: Determination of the geographic origin of the affected Common Guillemots. *Aquat. Living Resour.* 17: 369–377.
- Camphuysen C.J. 1983. Review of seabird mortality at The Netherlands coast, winter 1982/83. *Nieuwsbrief NSO* 4: 97–122. (In Dutch with English summary)
- Camphuysen C.J. 1995. Ageing Guillemots and Razorbills in the hand. *Sula* 9: 1–22. (In Dutch with English summary)
- Camphuysen C.J. 2007. Alcidae: auks. Technical documents 4.1, Handbook on oil impact assessment, version 1.0. Online edition, www.oiledwildlife.eu
- Camphuysen C.J. & Leopold M.F. 2004. The *Tricolor* oil spill: Characteristics of seabirds found oiled in The Netherlands. *Atl. Seabirds* 6: 109–128.
- Coulson J.C., Thomas C.S., Butterfield J.E.L., Duncan N., Monaghan P. & Shedden C. 1983. The use of head and bill length to sex live gulls Laridae. *Ibis* 125: 549–557.
- Dementiev G.P. & Gladkov N.A. (eds) 1968. Birds of the Soviet Union, Vol. 2. Israel Program for Scientific Translations, Jerusalem.
- Einoder L.D. 2009. A review of the use of seabirds as indicators of fisheries and ecosystem management. *Fish. Res.* 95: 6–13.
- Ewins P.J. 1985. Variation of Black Guillemot wing lengths post-mortem and between measurers. *Ring. Migrat.* 6: 115–117.
- Fox G.A., Cooper C.R. & Ryder J.P. 1981. Predicting the sex of Herring Gulls by using external measurements. *J. Field Ornithol.* 52: 1–9.
- Fransson T., Österblom H. & Hall-Karlsson S. 2008. Swedish bird ringing atlas, Vol. 2. Swedish Museum of Natural History and Swedish Ornithological Society, Stockholm. (In Swedish with English summary)
- Freethy R. 1987. Auks. Blandford Press, Poole.
- Furness R.W. & Monaghan P. 1987. Seabird ecology. Blackie, Glasgow.
- Furness R.W., Thompson D.R. & Harrison N. 1994. Biometrics and seasonal changes in body composition of Common Guillemots *Uria aalge* from north-west Scotland. *Seabird* 16: 22–29.
- Gaston A.J. 1984. How to distinguish first-year murrelets, *Uria* spp. from older birds in winter. *Can. Field Nat.* 98: 52–55.
- Glutz von Blotzheim U.N. & Bauer K.M. 1982. Handbuch der Vögel Mitteleuropas. Band 8/II. Charadriiformes (3 Teil). Akademische Verlagsgesellschaft, Wiesbaden.
- Grandjean P. 1972. Some morphological observations on the Guillemot (*Uria aalge* aalge Pont.) on Ellidaey, Westman Islands. *Dansk Orn. Foren. Tidsskr.* 66: 51–56.
- Halley D.J., Harris M.P. & Wanless S. 1995. Colony attendance patterns and recruitment in immature Common Murres (*Uria aalge*). *Auk* 112: 947–957.
- Hario M. 1982. On the size and recruitment of a peripheral breeding colony of the Guillemot *Uria aalge*. *Ornis Fenn.* 59: 193–194.
- Harris M.P. 1980. Post-mortem shrinkage of wing and bill of Puffins. *Ring. Migrat.* 3: 60–61.
- Harris M.P. & Swann B. 2002. Common Guillemot (Guillemot) *Uria aalge*. In: Wernham C., Toms M., Marchant J., Clark J., Siriwardena G. & Baille S. (eds) The Migration Atlas: Movements of the Birds of Britain and Ireland. Poyser, London, pp. 397–400.
- Harris M.P. & Wanless S. 1990. Moults and autumn colony attendance of auks. *Brit. Birds* 83: 55–66.
- Harris M.P. & Wanless S. 2004. Common Guillemot *Uria aalge*. In: Mitchell P.I., Newton S.F. Ratcliffe N. & Dunn T.E. (eds) Seabird Populations of Britain and Ireland. Results of the Seabird 2000 Census (1998–2002). Poyser, London, pp. 350–363.
- Harris M.P., Frederiksen M. & Wanless S. 2007. Within- and between-year variation in the juvenile survival of Common Guillemots *Uria aalge*. *Ibis* 149: 472–481.
- Harrison P. 1983. Seabirds: an identification guide. Croom Helm, Beckenham.
- Hedgren S. 1975. The breeding population of Guillemot *Uria aalge* in the Baltic Sea. *Vår Fågelvärld* 34: 43–52. (In Swedish with English summary)
- Hedgren S. 1980. Reproductive success of Guillemots *Uria aalge* on the island of Stora Karlsö. *Ornis Fenn.* 57: 49–57.
- Heubeck M., Harvey P.V. & Okill J.D. 1991. Changes in the Shetland Guillemot *Uria aalge* population and the pattern of recoveries of ringed birds, 1959–1990. *Seabird* 13: 3–21.
- Hjernquist M.B., Hjernquist M., Hjernquist B. & Hjernquist K.A.T. 2005. Common Guillemots *Uria aalge* differentiate their niche to coexist with colonizing Great Cormorants *Phalacrocorax carbo*. *Atl. Seabirds* 7: 83–89.
- Howard R. & Moore A. 1991. A complete checklist of the birds of the world, second edn. Academic Press, London.

- Humphrey P.S. & Parkes K.C. 1959. An approach to the study of molts and plumages. *Auk* 76: 1–31.
- Jones P.H. 1988. The European cline in wing-length of Guillemots *Uria aalge*. *Seabird* 11: 19–21.
- Jones P.H., Blake B., Anker-Nilssen T. & Røstad O.W. 1982. The examination of birds killed in oil spills and other incidents – a manual of suggested procedure. NCC, Aberdeen.
- Jones P.H., Barrett C.F., Mudge G.P. & Harris M.P. 1984. Physical condition of auks beached in eastern Britain during the wreck of February 1983. *Bird Study* 31: 95–98.
- Kuschert H., Ekelöf O. & Fleet D.M. 1981. New criteria for the age determination of the Guillemot and Razorbill. *Seevögel* 2: 58–61. (In German with English summary)
- Lyngs P. 1992. Breeding birds on Græsholmen, Ertholmene in the Baltic Sea, 1925–1990. *Dansk Orn. Foren. Tidsskr.* 86: 1–93. (In Danish with English summary)
- Lyngs P. 1993. Colony interchange in Baltic Guillemots *Uria aalge*. *Dansk Orn. Foren. Tidsskr.* 87: 247–250.
- Lyngs P. 2005. Efter olieforureningen fra *Fu Shan Hai*. En to-årig undersøgelse af olieforureningens eftervirkninger på Ertholmens yngefugle. Christiansø Naturvidenskabelige Feltstation. Gudhjem, Danmark.
- Lyngs P. & Durinck J. 1998. Diet of Guillemots *Uria aalge* in the central Baltic Sea. *Dansk Orn. Foren. Tidsskr.* 92: 197–200.
- Lyngs P. & Kampp K. 1996. Ringing recoveries of Razorbills *Alca torda* and Guillemots *Uria aalge* in Danish waters. *Dansk Orn. Foren. Tidsskr.* 90: 119–132.
- Mead C.J., Clark J.A. & Peach W.J. 1995. Report on bird ringing in Britain and Ireland for 1993. *Ring. Migrat.* 16: 16–64.
- Morris-Pocock J.A., Taylor S.A., Birt T.P., Damus M., Piatt J.F., Warheit K.I. & Friesen V.L. 2008. Population genetic structure in Atlantic and Pacific Ocean Common Murres (*Uria aalge*): natural replicate tests of post-Pleistocene evolution. *Mol. Ecol.* 17: 4859–4873.
- Moum T. & Árnason E. 2001. Genetic diversity and population history of two related seabird species based on mitochondrial DNA control region sequences. *Mol. Ecol.* 10: 2463–2478.
- Murray S., Wanless S. & Harris M.P. 1994. The effects of fixed salmon *Salmo salar* nets on Guillemot *Uria aalge* and Razorbill *Alca torda* in northeast Scotland in 1992. *Biol. Conserv.* 70: 251–256.
- Nettleship D.N. 1996. Family Alcidae (auks). In: del Hoyo J., Elliott A. & Sargatal J. (eds) *Handbook of the Birds of the World*, Vol. 3, Hoatzin to Auks, Lynx Edicions, Barcelona, pp. 678–722.
- Nettleship D.N. & Evans P.G.H. 1985. Distribution and status of the Atlantic Alcidae. In: Nettleship D.N. & Birkhead T.R. (eds) *The Atlantic Alcidae*. Academic Press, London, pp. 53–154.
- Nilsson S. 1835. *Skandinavisk fauna*. Foglarna, Vol. 2, second edn, Lund.
- Oldén B., Peterz M. & Kollberg B. 1985. Seabird mortality in the gill-net fishery, southeast Kattegat, south Sweden. *Anser* 24: 159–180. (In Swedish with English summary)
- Oldén B., Kollberg B. & Peterz M. 1986. Seabird mortality in the gill-net fishing, southeast Kattegat, south Sweden the winter 1985/86. *Anser* 25: 245–252. (In Swedish with English summary)
- Olsson O., Fransson T. & Larsson K. 1999. Post-fledging migration of Common Murres *Uria aalge* in the Baltic Sea: management implications. *Ecography* 22: 233–239.
- Olsson O., Nilsson T. & Fransson, T. 2000. Long-term study of mortality in the Common Guillemot in the Baltic Sea. Report 5057, Swedish Environmental Protection Agency, Stockholm.
- Österblom H., Fransson T. & Olsson O. 2002. Bycatches of Common Guillemot (*Uria aalge*) in the Baltic Sea gillnet fishery. *Biol. Conserv.* 105: 309–319.
- Peterz M. & Oldén B. 1987. Origin and mortality of Guillemots *Uria aalge* on the Swedish west coast. *Seabird* 10: 22–27.
- Pianka, E.R. 2000. *Evolutionary ecology*, sixth edn, Benjamin/Cummings, San Francisco.
- Ratcliffe N. 2004. Causes of seabird population changes. In: Mitchell P.I., Newton S.F., Ratcliffe N. & Dunn T.E. (eds) *Seabird Populations of Britain and Ireland. Results of the Seabird 2000 Census (1998–2002)*. Poyser, London, pp. 407–437.
- Riffaut L., McCoy K.D., Tirard C., Friesen V.L. & Bouludier T. 2005. Population genetics of the Common Guillemot *Uria aalge* in the North Atlantic: geographic impact of oil spills. *Mar. Ecol. Prog. Ser.* 291: 263–273.
- Sæther B.-E. & Bakke O. 2000. Avian life history variation and contribution of demographic traits to the population growth rate. *Ecology* 81: 642–653.
- Salomonsen F. 1932. Description of three new Guillemots (*Uria aalge*). *Ibis* 13(2): 128–132.
- Salomonsen F. 1944. The Atlantic Alcidae. The seasonal and geographical variation of the auks inhabiting the Atlantic Ocean and the adjacent waters. Göteborgs Kungl. Vetenskaps- och Vitterhets-samhälles Handl. Sjätte Följden, Ser. B, Vol. 3: 1–138.
- SOF 2003. Fågelåret 2002. *Swed. Ornithol. Soc.*, Stockholm.
- SOF 2004. Fågelåret 2003. *Swed. Ornithol. Soc.*, Stockholm.
- Staav R. 1997. Utbyte av sillgrisslor mellan Östersjön och Atlanten. *Ringinform* 20(2): 22.
- Staav R. 2009. Sillgrisslan allt vanligare i Stockholms skärgård. *Fåglar i Stockholmstrakten* 38(3): 105–111.
- Stewart F.M., Thompson D.R., Furness R.W. & Harrison N. 1994. Seasonal variation in heavy metal levels in tissues of Common Guillemots, *Uria aalge* from northwest Scotland. *Arch. Environ. Contam. Toxicol.* 27: 168–175.
- Storer R.W. 1952. A comparison of variation, behavior, and evolution in the sea bird genera *Uria* and *Ceppus*. *Univ. Calif. Publ. Zool.* 52: 121–222.
- Strann K.-B., Vader W. & Barrett R.T. 1991. Auk mortality in fishing nets in north Norway. *Seabird* 13: 22–29.
- Thompson C.W., Wilson M.L., Melvin E.F. & Pierce D.J. 1998a. An unusual sequence of flight-feather molt in Common Murres and its evolutionary implications. *Auk* 115: 653–669.
- Thompson C.W., Wilson M.L., Pierce D.J. & DeGhetto D. 1998b. Population characteristics of Common Murres and Rhinoceros Auklets entangled in gillnets in fisheries in Puget Sound, Washington, from 1993 to 1994. *Northwest. Nat.* 79: 77–91.
- Tuck L.M. 1960. The Murres. *Can. Wildl. Ser.* 1, Canadian Wildlife Service, Ottawa.
- Vaurie C. 1965. The birds of the Palearctic fauna: A systematic reference. Non-Passeriformes. Witherby, London.
- Winker K. 1993. Specimen shrinkage in Tennessee Warblers and “Trail’s” flycatchers. *J. Field Ornithol.* 64: 331–336.
- Wooller R.D., Bradley J.S. & Croxall J.P. 1992. Long-term population studies of seabirds. *Trends Ecol. Evol.* 7: 111–114.
- Zar J.H. 2009. *Biostatistical analysis*, fifth edn. Pearson Education, Upper Saddle River, NJ.

SAMENVATTING

Dit onderzoek gaat in op de vraag in hoeverre de Zeekoet *Uria aalge* die in de Oostzee voorkomt, verschilt van soortgenoten van de Noordoost-Atlantische populatie. Van 149 Zeekoeten, die in de maanden oktober–november in zalmnetten (staand want) waren verdronken, werden sekse, leeftijd, rui en vetscore genoteerd en werden allerlei lichaamsafmetingen bepaald. De Zeekoet uit de Oostzee blijkt in uiterlijk niet te verschillen van de populaties uit het Atlantische gebied. Alleen de vleugels waren iets langer dan verwacht werd op grond van de breedtegraad waarop de vogels voorkwamen, maar dit werd toege-

schreven aan de wijze van meten en niet aan genetische verschillen. Er wordt daarom verondersteld dat de Zeekoeten in de Oostzee deel uitmaken van een grote populatie zonder dat er sprake is van een aparte ondersoort. Ook op basis van ringonderzoek blijkt er geregeld uitwisseling van vogels tussen de Oostzee en Noordzee te bestaan. In de bijvangsten werden vooral veel volwassen vogels aangetroffen. Dit wijst erop dat de sterfte van volwassen vogels door de visserij met staand want groter is dan tevoren werd vermoed. (NJD)

Corresponding editor: Niels J. Dingemanse
Received: 8 August 2009; accepted 9 June 2010

Appendix 1. Age and sex distribution of Common Guillemots drowned in salmon gill nets in the Baltic proper in different years.

Year	Age	Female	Male	Total
1987	Adult	2	6	8
	Immature			0
	Juvenile		5	5
	Total	2	11	13
1988	Adult	30	20	50
	Immature	2	1	3
	Juvenile	4	7	11
	Total	36	28	64
1989	Adult	33	20	53
	Immature	5	4	9
	Juvenile	4	6	10
	Total	42	30	72
Total	Adult	65	46	111
	Immature	7	5	12
	Juvenile	8	18	26
	Total	80	69	149

Appendix 2. Moults status on greater upperwing coverts and white tips on greater underwing coverts of Common Guillemots drowned in salmon gill nets in the Baltic proper 1987–89. The number of birds with bursa Fabricii is within parentheses.

Presence of white tips on greater underwing coverts	Presence of unmoulted greater upperwing coverts		Total
	Yes	No	
Yes	11 (11)	3 (1)	14 (12)
No	0	43 (2)	43 (2)
Total	11 (11)	46 (3)	57 (14)