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– The influence of biological and ecological factors

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THE INFLUENCE OF BIOLOGICAL AND ECOLOGICAL FACTORS

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1. Common guillemots *Uria aalge*, ringed as chicks in 2000-2005, were studied when returning to their natal colony on Stora Karlsö (Baltic Sea) in 2002-2006. 390 ringed birds were observed visiting breeding ledges where their behaviour were studied in detail and used to define "early maturity". The effects of sex and condition as chick (using fledging weight as a proxy for condition) on maturity were tested. In addition, club attendance (i.e. attendance of immature individuals on rocks adjacent to the breeding colony) was studied in 2004-2006. Observations at breeding ledges and clubs, together with ring recovery data, were used to calculate minimum post-fledging survival.

2. There was a clearly distinctive pattern in how immature birds successively developed adult behaviour (finding a suitable breeding location, establishing a pair-bond and breeding). In contrast to findings elsewhere, 1-year-olds were observed at the colony, commonly on clubs and occasionally on breeding ledges. 2-year-olds were the most frequently observed age class at breeding ledges, possibly due to a high return rate and a tendency towards substantial mobility between ledges. Some 2-year-olds repeatedly visited one specific breeding ledge, but this behaviour was more common for older birds. Establishments of pair-bonds were first seen among 3-year-olds and the first observed breeding attempts occurred at age four. No differences were found between males and females in developing adult behaviour and thus speed of maturation.

3. The more recently born cohorts (from 2003 and 2004) appeared to survive better than cohorts 2000-2002. A cold winter experienced by the earlier (2000-2002) cohorts may explain this, but it is also possible that bycatches in fisheries has been reduced in recent years.

4. There was no evidence of a correlation between chick fledging weight and post-fledging survival.

5. Contrary to expectations, guillemots defined as "early maturity"-individuals were lighter at fledging than birds defined as "normal maturity"-individuals. There are two possible explanations for these counter-intuitive results. Low quality individuals have reduced life expectancy or reproductive performance and for them, early investments in reproduction (analogous to the "early maturity" individuals) are more likely to pay off rather than saving resources for the future. Assuming that fledging weight is positively correlated to quality, individuals with low fledging weight are thus expected to mature at younger ages. An alternative explanation is that fledging weight does not reflect individual quality, but that both weight and maturity are physiologically controlled by the same mechanism, for example an endocrine factor.

Introduction

Delayed breeding is a common feature in the life history of long-lived seabirds (Lack 1968, Cadiou et al. 1994 and references therein). It will be adaptive if the potential benefits of early reproduction are outweighed by the costs of breeding early in life (Lack 1968, Forslund & Pärt 1995, Pyle et al. 1997). In most seabirds immature birds visit the colony prior to first breeding and an array of explanations to this has been suggested. Young birds have been proposed to assess the quality of colonies and breeding sites (Cadiou et al. 1994, Oro & Pradel 2000, Dittmann et al. 2005), to achieve necessary competence for breeding, such as foraging techniques, knowledge of feeding areas, predator avoidance (Lack 1968, Marchetti & Price 1989, Forslund & Pärt 1995) and to develop behaviour and social skills essential for site acquisition and pair-bond formation (Harrington 1974, Porter 1988, Pickering 1989, Cadiou et al. 1994).

Development of behaviour is often directly related to age and/or experience (e.g Lloyd & Perrins 1977, Harris 1983, Porter 1988, Cadiou et al. 1994, Dittmann & Becker 2003). Sex may be an important factor, since males and females often have different reproductive roles and behaviour prior to first breeding (e.g. Pickering 1989, Dittmann & Becker 2003). This has been more rarely addressed, especially in sexually monomorphic species, for which sex determination in the field requires observations of copulations, hardly obtainable for a sufficient number of immature birds. However, with the recent improvements of molecular sex determination, this

problem has now diminished (Fridolfsson & Ellegren 1999).

Seabirds often display a large intraspecific variation in sexual maturation and age at first breeding. Variation in this respect can also be caused by environmental factors, such as food abundance, which in addition can affect males and females differently (Spear et al. 1995).

A change in food abundance or other environmental variable might, however, affect other aspects of population ecology and dynamics, e.g. survival, dispersal and reproductive success (Sydeman et al. 1991, Harris & Bailey 1992, Oro et al. 2004).

The common guillemot *Uria aalge* is a long-lived, piscivorous seabird. It is sexually monomorphic and both sexes invest heavily in reproduction, but especially after fledging of the chick the roles are different. The male parent takes the chick to sea and feeds it for a substantial period while the female continues to visit the breeding site (Harris & Birkhead 1985, Wanless & Harris 1986, Harris & Wanless 2003). Young guillemots can not be physically distinguished from adults after their first winter but breeding is delayed and is initiated several years later (Birkhead & Hudson 1977, Harris & Birkhead 1985).

Colony attendance in immature guillemots has been studied by Halley et al. (1995). They found that as birds gain experience arrival dates become earlier, more visits are made at the colony and the likelihood of attempting to breed increase. However, the behaviour during the visits is poorly studied and little is known about differences between males and females.

The common guillemot is a top-predator and can thus be affected by changes occurring in different parts of the food-web (Harris & Bailey 1992, Wanless et al. 2005). In the Baltic Sea, large-scale long-term changes in the ecosystem have affected the abundance of sprat *Sprattus sprattus*, the main prey for guillemots in the Baltic Sea (Hedgren 1976, Lyngs & Durinck 1998, Österblom et al. 2006). During the 1990's the sprat stock increased, leading to lower energy content of the fish, and the fledging weights of guillemot chicks decreased. The fledging weights have recovered in recent years when energy value of sprat has increased corresponding to a decrease in sprat numbers (Österblom et al. 2001, 2006, ICES 2005).

Little is known about the effects of these changes in chick fledging weights. A positive relationship between condition as young and post-fledging survival have been reported in a range of bird species (e.g. Perrins 1965, Perrins et al. 1973, Krementz et al. 1989, Tinbergen & Boerlijst 1990, Magrath 1991, Gaston 1997, Sagar & Horning 1998), but there are also species where no such relationships could be confirmed (e.g. Lloyd 1979, Kersten & Brenninkmeijer 1995, Olsson 1997).

Hedgren (1981), who studied the Baltic Sea guillemot population at Stora Karlsö during the 1970's, found no correlation between post-fledging survival and fledging weight. However, his study was conducted before the major ecosystem changes in the Baltic Sea, during a period when fledging weights showed less inter-year variation and were generally higher than during recent years (Österblom et al. 2006). No studies on guillemots (Hedgren 1981, Harris et al. 1992) have analysed the possibility of a critical weight in terms of post-fledging survival for chicks fledging at very low weights.

Conditions experienced as young can also have long-term fitness consequences. In the kittiwake *Rissa tridactyla* was length of the rearing period for the chick positively correlated with its reproductive performance as adult and first-hatched chicks started breeding earlier than their later-hatched siblings (Cam et al. 2003). Also in guillemots may conditions during the early stages in life affect sexual maturation and reproductive performance and the recent variation in fledging weight can thus have long-term effects.

In this study, a comparatively large number of common guillemots were observed when returning to their natal colony on Stora Karlsö (Baltic Sea) in 2002-2006. Observations of attendance and behaviour were used to describe how behaviour is affected by age and sex and to make assessments of post-fledging survival. I analyse the influence of fledging weight on maturation and survival and address the question whether fledging weight can measure individual quality in some aspect. Other factors potentially affecting survival are also considered, such as weather (i.e. sea surface temperature), food availability and bycatch mortality.

Methods

FIELD STUDY

Study area and study population

Field work was conducted at the island Stora Karlsö (57°17'N, 17°58'E) in the Baltic Sea in the 2002-2006 breeding seasons (May-July). About two thirds of the Baltic Sea population of Common Guillemots breed at Stora Karlsö, approximately 10 000 pairs (Österblom et al. 2004). Emigration from Stora Karlsö is likely important for the smaller colonies in the Baltic Sea, but the immigration rate to Stora Karlsö has not been studied whereby the role of Stora Karlsö as a source for the Baltic Sea metapopulation can not be fully assessed (Hario 1982, Lyngs 1993, Olsson et al. 2000).

Since the year 2000 guillemot chicks have been ringed with metal rings and individually coded colour rings (ProTouch ©). Each code consists of one letter and two digits, is 9 mm tall, engraved and contrast coloured, and is displayed three times on

the ring. A unique ring colour was used each year to facilitate identification of each cohort. At the time of ringing (immediately after fledging), chicks were weighed to the nearest 5 g.

Two growing feathers were taken from 7170 of the 7982 ringed chicks. The feathers were placed in paper envelopes, transferred to -18°C on the night of sampling and later kept in -30°C until analysis for sex determination.

The study is based on data from birds ringed 2000-2005 (994-1998 per year, total n = 7982).

Observations at breeding ledges

In 2006, three observation points were visited almost daily between May 31st and June 26th. The breeding ledges observed are situated above the beach where chicks are ringed and hence all guillemots included in this study were hatched in this part of the colony. Observations were made in daylight and all hours between 8 AM and 8 PM were covered, for each of the three observation points. Visits typically lasted 90-120 min per observation point, but ranged from 25 to 150 min due to unpredictable weather affecting observation possibilities and number of birds present. An additional observation point, situated approximately 650 m south of the ringing site, was visited six times, every third or fourth day, between 5th and 21st of June. Visits lasted 60-120 min. Total observation time, for all four observation points, was 99 hours.

Birds were observed from above the breeding ledges causing minimal disturbance, typically at distances of < 40 m using 10x binoculars and a 20-60x telescope. Often both the metal ring number and the colour ring code could be recorded. Metal ring number was used for identification if the coloured ring was missing. Less than 1% of the observations were discarded because of mis-match between metal ring number and colour ring code.

For every ringed immature bird present at each visit notes were made on:

(1) Time spent at the ledge: (i) present during the entire observation period, (ii) present during most of the observation period – at least more than 5 min or (iii) occasionally present – less than 5 min.
(2) Distance to breeding birds: dissociated, next to, or among.
(3) Acceptance by nearby breeding guillemots.
(4) Social interactions, e.g. grooming, fighting or copulating.
(5) Presence of egg or chick.

Studies were also made 2002-2005. These studies were performed in the same way and during the same period as described above, but with less observation effort (Observation time 2002: 53 h; 2003: 52 h; 2004: 51 h; 2005: 57 h).

Observations of clubs

Immature guillemots were also studied at clubs (sensu Birkhead & Hudson 1977), aggregations of birds on rocks in the water beneath the breeding ledges. Observations were restricted to two stones, each approximately 5 m in diameter, situated ca 70 m from the shore where ringing of chicks takes place. Birds were observed at a distance of approximately 100 m using a 20-60x telescope. At the beginning of each visit, and after 5, 10 and 15 min, birds were counted and ring colours noted. Using this information, the total number of present guillemots was estimated as well as the fraction of each age class. When possible, birds were also identified by their colour ring code. In 2006 observations were made on an almost daily basis during 3 – 20 June and 29 June – 4 July, in total 24 occasions. Some observations were made in mid-June 2004 (9 observation periods) and mid-June 2005 (6 observation periods).

CATEGORISATION OF BEHAVIOUR

All records from ledges during one season were compiled for each of the observed ringed individuals. Each bird was assigned one of the following categories:

(A) Observed at a breeding ledge, usually at the edge, maximum twice at the same spot.
(B) Observed at least three times at the same breeding ledge, usually at the same spot. More accepted by breeding birds. Occasional social interactions but no indication of pair-bond formation.
(C) Observed with a potential mate and showing behaviour indicating pair-bonding, e.g. grooming and copulations (observations clearly suggest that the pair-bond is stable). Mimicking adult behaviour such as brooding and feeding.
(D) Breeding. Egg or chick observed. Not necessarily successful breeding.

Immature birds observed in more than one season were assigned to a category for each season.

Some birds that were actually breeding (category D) may have been recorded as non-breeders (cat. A) as there is much more difficulty in observing rings in aggregations of breeding birds than at the edge or on ledges with few birds present. It is very unlikely that this affected the overall result since this situation may have occurred only for very few of the birds studied. First, it is unlikely that more than a few birds in this study were old enough to breed (Harris et al. 1994, 1996) and second, strong efforts were made to reduce this problem by carefully scanning for rings in the dense aggregations of breeding birds.

The categorisations and the age of the youngest birds in each category were used to define "early

maturation". Since this study included only birds born 2000 and later, late maturity was not possible to define.

SEX DETERMINATION

Birds were first sexed by copulation behaviour. Males were sexed from both successful and unsuccessful copulations, assuming males to be on top, as no studies have revealed the occurrence of reverse mounts (e.g. Wanless & Harris 1986, Sydeman 1993, Robertson et al. 2006). Females were sexed only when successful copulations were observed, as male-male mountings can occur (Henrik Österblom, pers. comm.) However, as most birds were not seen copulating, molecular sexing was also applied (Fridolfsson & Ellegren 1999). Provided that samples were available, sex was determined for birds assigned category A as 1-year-olds and for all individuals assigned category B-D.

DNA was prepared from pulp-containing feather shafts using the QIAamp® DNA Mini Kit (QIA-GEN®) according to the manufactor's instructions. Polymerase chain reactions were performed in 25 µl volumes using 5 pmol of primers 2550F and 2718R and PuReTaq™ Ready-To-Go PCR Beads (GE Healthcare). The thermal profile comprised an initial denaturing step of 95°C for 5 min, followed by a touch-down scheme starting with an annealing temperature of 60°C during 3 cycles, then 57°C during 3 cycles and 53°C during 3 cycles. Then 32 additional cycles were run at a constant annealing temperature of 50°C. The cycles consisted of a denaturation step at 95°C for 30 s, an annealing step for 30 s and an extension step at 72°C for 60 s. A final extension step of 8 min was added after the last cycle. Polymerase chain reaction products were visualised in UV light on agarose gel. DNA was successfully extracted from all 72 samples.

Molecular results were confirmed by correctly sexing 3 (2 females and 1 male) guillemots previously sexed upon copulation behaviour.

SURVIVAL OF IMMATURE BIRDS

This study was not designed to provide absolute measures of immature survival. Firstly, the colony was only partially studied. Secondly, survival, measured as resightings of individuals, is a combined measure, which includes both true survival and resighting probability, and in addition emigration can be a source of bias (Krementz et al. 1989, Crespin et al 2006). Here neither resighting probabilities nor emigration were assessed.

However, as records refer to individually identifiable birds, minimum survival rates can be calculated. A bird was considered to have survived if it was known to be alive on 1 April following the year it was born (or later). Two datasets were used for survival analysis. When a measure of observation effort was desirable, records from observations at breeding ledges during 2002-2006 (n = 386) were used since observation effort was quantifiable for this dataset. Otherwise, records of all individuals identified on and near Stora Karlsö (n = 513) and ring recoveries, where "survival" was certain, reported to the Bird Ringing Centre until August 2006 (n = 149) were included in the dataset used (total n = 662). Cohort 2005 was excluded from all analysis concerning survival since the period when "survivors" could have been observed was considered too short.

STATISTICAL METHODS

Descriptive statistics and χ^2-tests were performed in Microsoft® Office Excel 2003 (© Microsoft Corporation). Mann-Whitney U-tests, Spearman rank correlation tests and Kruskal-Wallis ANOVA were conducted using Statistica 5.5 (© StatSoft, Inc.). All tests are two-tailed with the significance level set at $\alpha = 0.05$.

To test pooled data, the datasets were normalised to eliminate inter-annual variation. This was done by subtraction of the cohort mean value from each data followed by division with the standard deviation. This operation normalised each dataset to an average of 0 and standard deviation of 1.

Results

BEHAVIOUR AND FIRST BREEDING

The distribution of behaviour categories among different age classes of guillemots was significantly heterogenic ($\chi^2 = 120.7$, d.f. = 15, p < 0.001). 1-year-olds visited the breeding ledges only occasionally and all observed individuals were classified as category A (Fig. 1). Regular visits to the breeding ledges (category B) were made by 7 % of the 2-year-olds. The youngest birds interacting socially indicating stable pair-bonding (category C) were 3 years old and these birds constituted 5 % of the observed 3-year-olds. Breeding (category D) was first observed at the age of 4, when 10 % started to breed. Among the other 4-year-olds observed regularly on breeding ledges one third was interacting with a mate but not breeding (category C) and two thirds were without a stable partner (category B). The pattern for 5-year-olds was similar to that of 4-year-olds, but with a higher percentage (50%) of birds regularly observed at breeding ledges. A smaller proportion was assigned to category B and C and 19 % were breeding. Of the observed 6-year-olds 30 % were breeding, while category B and C constituted 10 % each and category A 50 %. However, the figures for birds aged 6 years should be interpreted cautiously; the number of observed individuals is low (n = 10) and misclassification might have occurred for two birds assigned category A due to the problem of
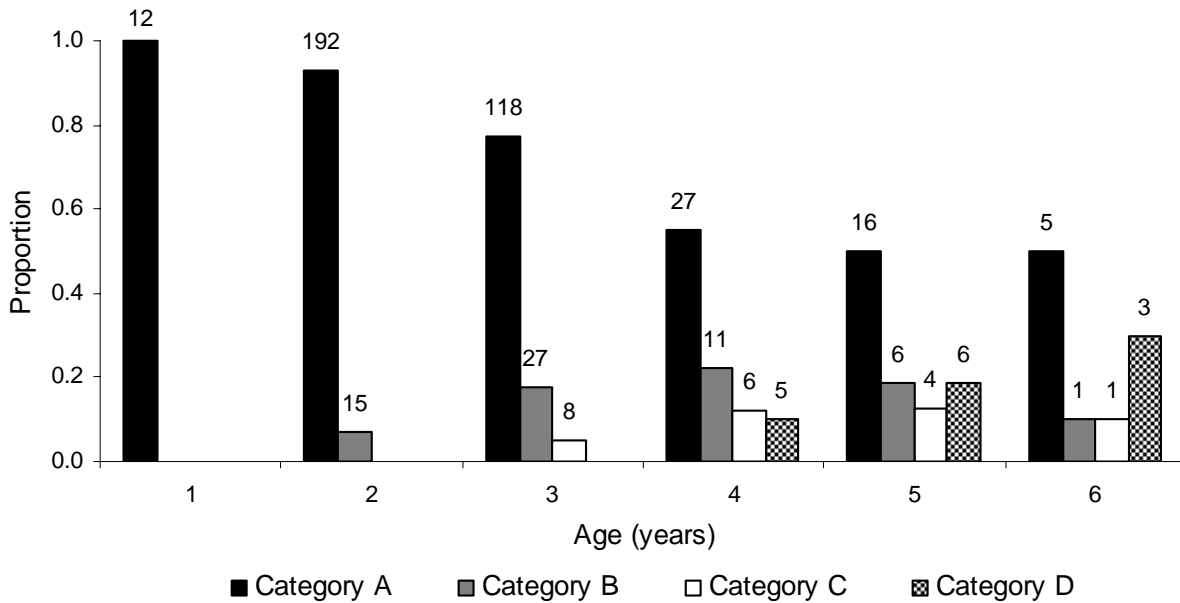
Fig. 1. Proportions of Common guillemots in behaviour categories for ages 1-6 years (all years pooled). Based on observations of individually identifiable birds. Number of birds given above each bar. For every bird and year observations were compiled and the bird was assigned a category. Definitions of categories: A. Observed at a breeding ledge, maximum twice at the same spot; B. Observed at least three times at the same breeding ledge. Occasional social interactions but no indication of pair-bond formation; C. Observed with a potential mate and showing behaviour indicating pair-bonding, e.g. grooming and copulations. Mimicking adult behaviour; D. Breeding. Note that individuals observed more than one year are included in all appropriate age classes.

observing rings in the dense aggregations of breeding birds.

The observation effort varied between years, which may have been a source of bias as data were pooled. However, the results from each specific year were very similar to results of the other years. Therefore it is unlikely that variation in observation effort has influenced the results.

The age distribution among birds visiting clubs was obtained by using the total number of observed birds of known age (n = 148). 1- to 4-year-olds were considered, since these were the age classes possible to observe in all seasons when clubs were studied (Birds were not colour-ringed before year 2000 and metal ring numbers can not be read at this long distance.). The majority of birds observed at clubs were aged 1 year (38 %) or 2 years (47 %), but 3-year-olds (13 %) and 4-year-olds (2 %) were also observed. The result is the same when the different numbers of chicks ringed each year are accounted for.

In total 116 individuals were identified at clubs. A small fraction of these individuals were also observed at breeding ledges (Fig. 2). None of the club-visiting birds aged three years and older were observed on breeding ledges in the same breeding season. However, these age classes visited clubs more rarely (13 observations).
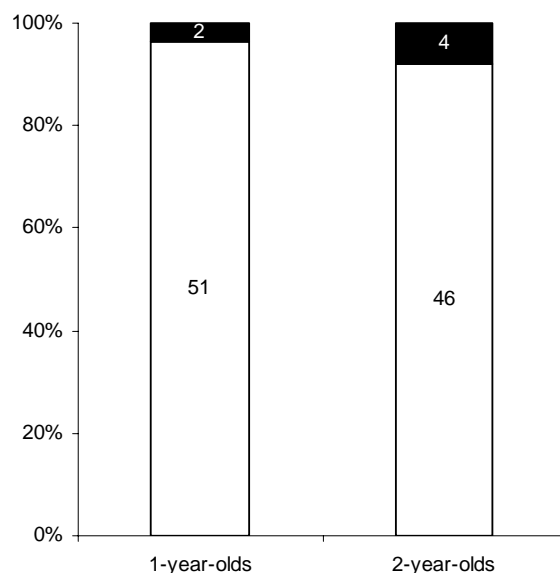

Fig. 2. Proportion of immature Common guillemots observed at clubs also attending breeding ledges. Based on observations of individually identifiable birds: (■) Observed at clubs and breeding ledges, (□) Observed only at clubs. Number of birds indicated.

Table 1. Number of Common guillemots in behaviour categories B, C and D by age and sex, based on observations of individually identifiable birds. None of the age classes had a heterogenic distribution between the sexes (χ^2-test; 2-year-olds: $\chi^2 = 0.077$, d.f. = 1, p > 0.75; 3-year-olds: $\chi^2 = 0.064$, d.f. = 1, p > 0.80; 4-year-olds: $\chi^2 = 0.038$, d.f. = 2, p > 0.98; 5-year-olds: $\chi^2 = 0.533$, d.f. = 2, p > 0.75). Note that individuals observed more than one year are included in all appropriate age classes.

| Age | 2 | | 3 | | 4 | | 5 | |
| Sex | ♂ | ♀ | ♂ | ♀ | ♂ | ♀ | ♂ | ♀ |
Category								
B	7	6	12	14	4	5	2	3
C	-	-	2	3	2	3	1	1
D	-	-	-	-	2	3	2	1

Table 2. Minimum return rates of Common guillemots, in percent, based on records of individually identifiable birds at Stora Karlsö.

Age Cohort	1	2	3	4	5
2000	*	3.3	3.2	1.7	1.0
2001	0.6	1.7	2.1	1.5	2.6
2002	0.1	3.0	2.2	2.3	
2003	1.3	4.6	7.7		
2004	0.9	7.8			
2005	1.6				

* No observations were made in 2001.

BEHAVIOUR AND MATURITY IN RELATION TO SEX

Males and females were evenly distributed among behaviour categories B-D (Table 1). For 6-year-old birds sex was known for only two specimens (both breeding males, category D). All 12 observations of 1-year-olds at breeding ledges were assigned category A (7 females, 5 males).

In consistency with the results from the observations at breeding ledges, birds were defined as early maturing individuals or with normal maturity as follows: Guillemots with early maturity are 1-year-olds visiting the breeding ledges (cat. A), 2-years-olds assigned category B, 3-year-olds assigned category C and/or breeding 4- and 5-year-olds. All other birds are regarded as of normal maturity.

There was no sex bias among "early-maturing" birds (18 males : 19 females).

10 birds of known age were observed breeding and sex was possible to determine only for six of these individuals. Two males started to breed at the age of 4 and one at the age of 5. The three females were all 4 years old at first breeding.

MATURATION AND CHICK CONDITION

In all studied cohorts, guillemots defined as "early maturity"-individuals weighted less at fledging than normally maturing birds (Fig. 3). The differences were non-significant for individual years (Mann-Whitney U-test; 2000: p = 0.16; 2001: p = 0.08; 2002: p = 0.12; 2003: p = 0.24; 2004: p = 0.44), but after pooling the data the difference became significant (Mann-Whitney U-test on normalised values; $n_{\text{"early"}} = 36$, $n_{\text{"normal"}} = 316$, p < 0.01).

RETURN RATES OF IMMATURES

A small proportion, on average 1%, of the guillemots returned to their natal colony when 1 year old. This is a minimum figure as only individually identified birds were included. In addition, only a fraction of the sites occupied by immatures were searched for rings. Return rates for
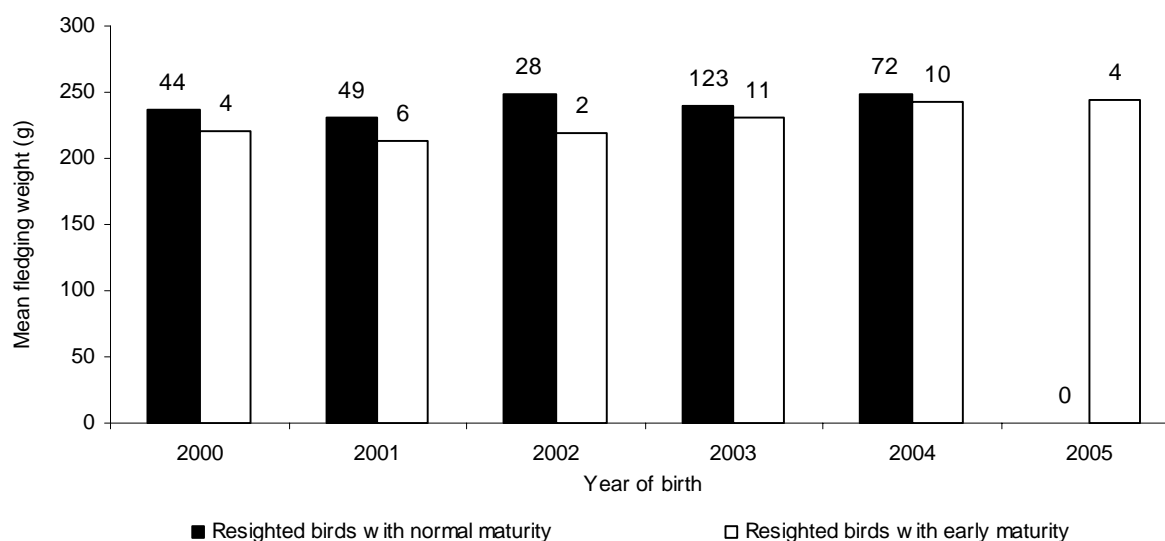
Fig. 3. Mean fledging weights of Common guillemots resighted at their natal colony on Stora Karlsö. Birds are separated in two groups by maturity criteria based on observations of individually identifiable birds 2002-2006. Number of birds indicated.
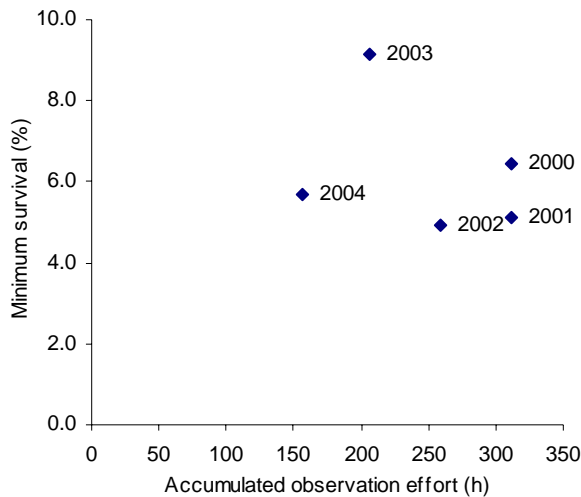
Fig. 4. Minimum post-fledging survival of Common guillemots, based on observations at breeding ledges of individually identifiable birds, in relation to accumulated observation effort (total observation hours/cohort).

older birds were at least twice the rate for 1-year-olds in all cohorts (Table 2). There was a large annual variation, possibly to some extent due to annual differences in observation effort, and therefore no statistical tests were used to compare age classes.

SURVIVAL AND MORTALITY

There was considerable variation in the percentage of each cohort known to have survived until 1 April the year following ringing. In the dataset of records from breeding ledges, minimum estimated survival ranged between 4.9 % for cohort 2002 and 9.1 % for cohort 2003 (Fig. 4). Inter-cohort comparisons should be used cautiously due to the potentially large errors caused by annual differences in observation effort and the number of years each cohort had been observed. Therefore no statistical tests were used to compare survival between cohorts. However, despite the uncertainty of the exact magnitude of these errors, the lack of a positive relationship between observation effort and estimated minimum survival (Fig. 4) suggests that observation effort can not explain all variation in minimum survival rates. It appear that guillemots born in 2003 and possibly also those born in 2004 survived better than cohorts born 2000-2002.

THE INFLUENCE OF FLEDGING WEIGHT ON POST-FLEDGING SURVIVAL

There was significant difference in mean fledging weight between cohorts, ranging from 230.8 in 2001 to 251.4 g in 2002 (Kruskal-Wallis

ANOVA, $p < 0.001$). This variation appeared to have no effect on survival on cohort level (Fig. 5).

There was no difference in mean fledging weight for survivers (S) (survival based upon all records from Stora Karlsö and ring recoveries reported 2001-2006) and other birds (O) (Mann-Whitney U-test for cohorts separately; 2000: $n_S = 90$, $n_O = 698$, $p = 0.66$; 2001: $n_S = 107$, $n_O = 889$, $p = 0.50$; 2002: $n_S = 61$, $n_O = 617$, $p = 0.91$; 2003: $n_S = 200$, $n_O = 1293$, $p = 0.69$; 2004: $n_S = 132$, $n_O = 1354$, $p = 0.79$). To further examine possible effects of fledging weight on survival, data were split into 10 weight classes (Table 3, including > 95% of chicks ringed 2000-2004), and the proportion of known survivors in each class was calculated. No correlation between survival and weight was found (Spearman Rank test, $p = 0.78$). Data did neither suggest an optimal fledging weight, as the differences in proportions of known survivors per weight class were non-significant ($\chi^2 = 11.2$, d.f. = 9, $p = 0.26$). To examine the possibility of a threshold for survival of very light chicks, the survival of individuals weighing less than 200 g at fledging was assessed. The differences between weight classes were non-significant ($\chi^2 = 3.15$, d.f. = 3, $p = 0.37$) and without trend (Table 4).

Table 3. Post-fledging survival of Common guillemots ringed as chicks on Stora Karlsö 2000-2004. Based on all records from Stora Karlsö and ring recoveries reported 2001-2006.

Fledging weight	n_r	n_s	Survival
200-209 g	287	31	0.108
210-219 g	430	59	0.137
220-229 g	703	77	0.110
230-239 g	823	83	0.101
240-249 g	909	104	0.114
250-259 g	785	80	0.102
260-269 g	541	55	0.102
270-279 g	366	40	0.109
280-289 g	252	20	0.079
290-299 g	86	16	0.186
Total	5182	565	0.109

Table 4. Post-fledging survival of the lightest Common guillemot chicks ringed on Stora Karlsö 2000-2004. Chicks lighter than 200 g constituted only 2.4% (n = 130) of the ringed chicks. The small number of individuals made a division in equal intervals inappropriate and neither were intervals with similar samples sizes possible. Based on all records from Stora Karlsö and ring recoveries reported 2001-2006.

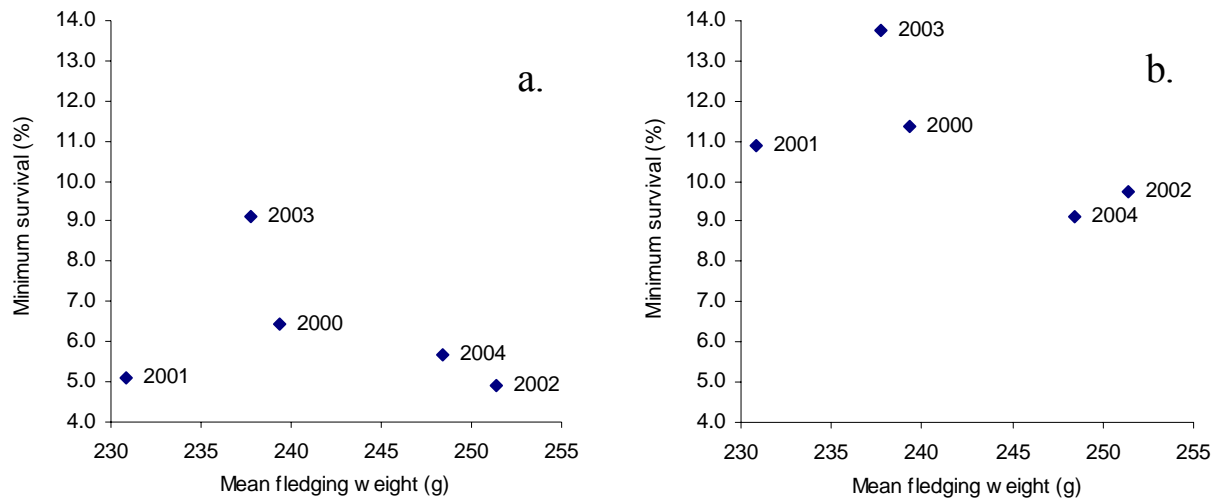| Fledging weight	n_r	n_s	Survival
110-179 g	20	2	0.10
180-189 g	29	4	0.14
190-194 g	53	2	0.04
195-199 g	28	4	0.14

Fig. 5. Minimum cohort survival of Common guillemots in relation to mean fledging weight, based on a) observations at breeding ledges on Stora Karlsö 2002-2006 b) all records from Stora Karlsö and ring recoveries reported 2001-2006.

FACTORS POTENTIALLY AFFECTING POST-FLEDGING SURVIVAL

85 % (304 of 356) of the ring recoveries came from bycatches in fisheries. There was no apparent trend in the monthly number of bycatches of the guillemots ringed 2000-2004 (Fig. 6). Neither did an analysis of monthly deviation from the mean, for each month, reveal a trend. However, this result should be interpreted cautiously bearing in mind that the number of birds possible to catch, at each given moment, increased each summer as more chicks were ringed. The proportion of ringed guillemots entangled in fishing gear and found dead during their first year in life showed a tendency to decrease over time (Table 5).

Sprat stock biomass and spawning stock biomass in the Baltic Sea 1999-2004 were well above the average for 1974-2004 (Table 6), which were 1267 000 tonnes and 991 000 tonnes respectively (ICES 2005).

The mean sea surface temperature in the central and southern Baltic Sea was lower during the winter 2002/03 than during the other winters experienced by the guillemots in this study (Fig. 7).

Table 5. Minimum first-year-mortality for Common guillemots ringed as chicks on Stora Karlsö 2000-2004. Based upon ring recoveries of dead birds until 31 March the year following ringing.

Cohort	Recovered dead[a] (n)	Entangled in fishing gear[b] (n)
2000	3.9 % (39)	95 % (37)
2001	4.9 % (49)	100 % (49)
2002	2.8 % (28)	79 % (22)
2003	2.3 % (35)	80 % (28)
2004	1.1 % (17)	82 % (14)

[a] Percentage of all ringed chicks.
[b] Percentage of all birds recovered dead until 31 March the year following ringing.

Table 6. Sprat in the Baltic Sea 1999 – 2004. Data from ICES (2005).

Year	SB[a] (thousand tonnes)	SSB[b] (thousand tonnes)
1999	1959	1680
2000	1921	1527
2001	1691	1457
2002	1324	1052
2003	1573	1155
2004	1861	1405

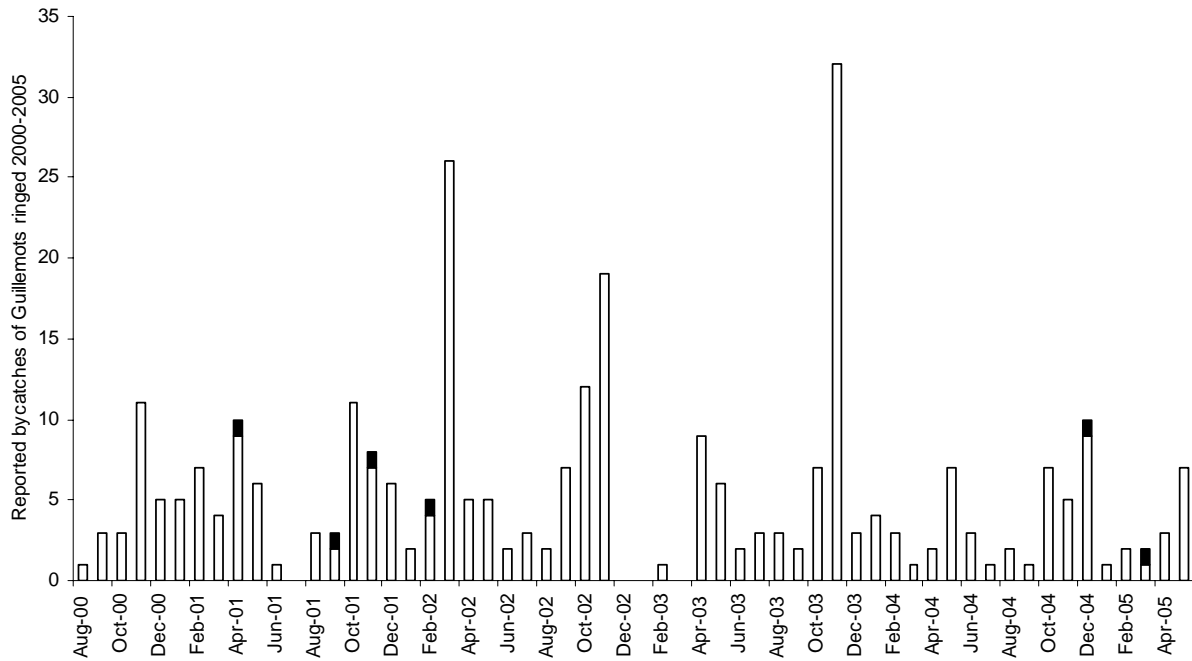[a] SB = Stock biomass
[b] SSB = Spawning stock biomass

Fig. 6. Bycatches of Common guillemots ringed as chicks on Stora Karlsö 2000-2004, found dead (□), alive (■)

Discussion

BEHAVIOUR AND MATURITY

The results indicate that there is a general pattern in how immature birds develop adult behaviour. The returning 1-year-olds rarely visited breeding ledges and if so, only occasionally. 2-year-olds were in all years the most observed age class at breeding ledges, which was possibly caused by a high return rate combined with a tendency towards substantial mobility between ledges (unpubl. data). Some 2-year-olds made repeated visits to one breeding ledge, but this behaviour was more common for older birds. Establishments of pair-bonds were first seen among 3-year-olds and first observed breeding occurred at the age of four.

Colony visits by immature birds and the recruitment process have been studied in many seabird species (see Introduction), but focus have in most cases been where and when the birds visit colonies. The behaviour of immatures, when at the breeding sites, has more rarely been addressed. Cadiou et al. (1994) studied squatting (i.e occupation of unattended nests or nests with unattended chicks belonging to other birds) in kittiwakes and found that the successive stages (non-squatting, squatting on nests, squatting on chicks) agreed with the ontogeny of recruitment, i.e. the choice of a colony, a breeding site and a partner. Pickering (1989) found similar stages in the wandering albatross *Diomedea exulans*. Albatross males, with experience from some seasons ashore, hold a nest site while similarly experienced females move around the colony, displaying with established males, which allows both sexes to assess potential partners. A stable pair-bond is formed one to three seasons prior to first breeding. My study suggests that common guillemots also experiences successive stages, although the timing of pair-bond formation is still poorly known. Pairing in first-time breeders can be assessed with breeding pairs of two identifiable birds of known ages, but to reveal when pair-bonds are established observations from the years before breeding are also required.

To some extent, the results from Stora Karlsö can be compared with results from other colonies. Colony visits made by immature birds have been studied on Isle of May, Scotland (Halley et al. 1995) and on Skomer Island, Wales (Birkhead & Hudson 1977). As expected, the general patterns are similar, although Stora Karlsö guillemots made the first return to the colony when younger and seem to abandon clubs for breeding ledges at an earlier age. Age at first breeding at Isle of May ranged from 3 to 9 years with a median age of 6 years (Harris et al. 1994, 1996). At Canna, Scotland, the median was 7 years (Harris et al. 1994). This study indicates that median age at Stora Karlsö could be higher than 6 years, but, as suggested by Harris et al. (1994), variation in survival between cohorts may affect the recorded ages at first breeding. Survival seemed to be lower for the older cohorts (see below) whereby it is necessary to follow additional cohorts to first breeding before conclusions can be made for Stora Karlsö guillemots.
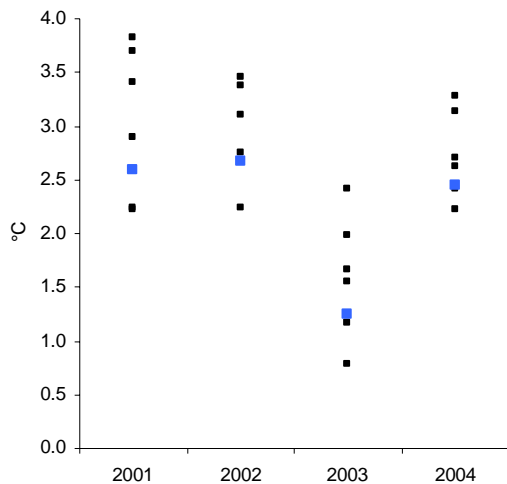
Fig. 7. Mean sea surface temperature (SST) in the sea area between Bornholm and Gotska Sandön (54-58°N, 15-22°E) during January-March (■). SST in rectangular subareas (■) are shown to illustrate the geographical variation. Data provided by the Institute of Marine Research and the Institute of Coastal Research, Swedish Board of Fisheries; Swedish Meteorological and Hydrological Institute; Sea Fisheries Institute, Poland and Bornholms Amt, Denmark.

There were no differences between males and females in behaviour or maturity. To my knowledge, no other studies of immature common guillemots have found sexual differences (Halley et al. 1995). In Brünnich's guillemot *Uria lomvia*, the closest relative to the common guillemot, the age at first breeding was lower for females than for males (Gaston & Hipfner 2000 in Hipfner 2001). However, no differences between the sexes were detected in the related razorbill *Alca torda* (Lloyd & Perrins 1977). As samples sizes were small, both in this and the other studies were no difference was found, it can still not be ruled out that a difference between the sexes exists.

RETURNING 1-YEAR-OLDS

In all years covered by this study, 1-year-olds were observed at Stora Karlsö. This is surprising as no 1-year-olds have ever been seen at other colonies (Birkhead & Hudson 1977, Crespin et al. 2006).

It is unclear why Stora Karlsö guillemots are different in this aspect. However, the spatial distribution of Stora Karlsö guillemots and the seasonal change in this distribution is worth considering. Ring recoveries of Stora Karlsö guillemots in their first year indicate that dispersal outside the Baltic is very unusual (Olsson et al. 2000); most 1-year-olds stay within the Baltic, although they winter further away from the colony than older birds (Österblom et al. 2002). Ring recoveries from the breeding season indicate that younger guillemots (1-5-year-olds) are found closer to breeding colonies during these months than

during the rest of the year (Olsson et al 2000, unpubl. data, Swedish Bird Ringing Centre). One possible explanation is the location of foraging areas. If good foraging areas are not widespread in the Baltic, but especially in the summer situated close to Stora Karlsö birds will gather there and some 1-year-olds may visit the colony. Other colonies, where the return of immatures has been studied, are situated in or next to much larger seas, where there potentially is a smaller probability that foraging 1-year-olds encounter their natal colony.

THE EFFECTS OF FLEDGING WEIGHT ON POST-FLEDGING SURVIVAL

The fledging weights of guillemots decreased at Stora Karlsö during the 1990's, probably due to lower energy content in sprat, which likely was related to high sprat abundance in the Baltic Sea (Österblom et al. 2006). Still in the first years of the 2000's, three cohorts (2000, 2001, 2003) had notably lower mean fledging weights than cohorts born in the 1970's (Hedgren 1981). During recent years, 2004-2006, fledging weights increased to the level of the 1970's (Fig. 5 and unpubl. data).

Hedgren (1981) found no relationship between chick fledging weight and post-fledging survival for the 1970's cohorts. In my study, the effects of a wider range of fledging weights were possible to examine. Still no correlation was found. Even the very lightest chicks had a survival rate corresponding to the average. This indicates that the observed drop in fledging weights did not affect post-fledging survival.

Growth at sea is considered to be of greater importance for the chick than at the ledge, since a higher growth rate is possible at sea where food is more easily accessed than at the colony (Sealy 1973, Ydenberg 1989). For the guillemots in the Baltic Sea, the decrease in fledging weight was related to high sprat abundance (Österblom et al. 2006) and therefore food was most likely easily available at their fishing sites. The lower fledging weights were then probably possible to be compensated for at sea.

Except for the common guillemot, there are two other species in the family Alcidae which have the same 'intermediate' (termed by Sealy [1973]) fledging strategy: Brünnich's guillemot and razorbill. In the 'intermediate' strategy chicks are cared for by both parents at the nesting site for 15-35 days before fledging at 11-30 % of adult body mass. After departure to sea the male parent provides care for the chick during 3-6 weeks (Sealy 1973, Hedgren & Linnman 1979, Gaston 1998, Hipfner & Gaston 1999, Kylberg 2006, this study). Fledging weight has been studied in razorbill chicks, but no relationship between fledging weight and post-fledging survival was found (Lloyd 1979). It is likely that the 'intermediate' strategy, with an

accompanying parent, further facilitates compensation of a low fledging weight at sea.

The chicks of these species remain on the breeding ledge instead of leaving when very young (like the 'precocial' species in the Alcidae [Sealy 1973]), despite that their fledging weight will not affect the chances of subsequent survival and the potential for better growth at sea. Several explanations have been proposed to elucidate this strategy. One is Ydenberg's model, which states that fledging age and weight reflect a trade-off between potential growth and survival chances. This is caused by both growth rate and mortality being higher at sea than at the breeding site (Ydenberg 1989). Both the latter assumption and the model's predictions have been much debated (Gaston 1998, Ydenberg 1998, Hipfner & Gaston 1999). Contrary to this model are the constraint hypotheses. Birkhead (1977), Hedgren (1981) and Hipfner & Gaston (1999) all stressed the importance of wing growth. The chick uses its "flight feathers" to glide, rather than fall, from the breeding ledge to the beach during fledging and it has been suggested that feathers grow at a constant rate (Hedgren 1981) and continue to grow when growth in mass ceases (Gaston et al. 1985 in Hipfner & Gaston 1999).

This study only concerns post-fledging survival, since all birds studied were ringed after surviving both the time on the ledge and the fledging. The relationship between chick condition prior to fledging or during fledging and subsequent survival has not been addressed here.

A positive correlation between pre-fledging chick growth rate and post-fledging survival has been observed in Brünnich's guillemot (Steiner in Gaston & Hipfner 2006), so the ability to gain weight can be important. Such a relationship was not found in common guillemots (Harris et al. 1992). However, changes in food energy value have been shown to affect reproductive success in common guillemots. Wanless et al. (2005) demonstrated that the greatly reduced breeding success in North Sea guillemots in 2004 was related to the low energy content in sprat and lesser sandeel *Ammodytes marinus*. The chicks that fledged were severely underweight, but further effects of this remains to be studied.

Despite the potential importance of food quality and chick condition before fledging, a change in these variables does not necessarily imply that this affects post-fledging survival. If growth at sea is substantially greater than at the ledge a low fledging weight can be compensated for after fledging. Such a relationship has been suggested for the oystercatcher *Haematopus ostrelegus*, a shorebird with similar post-fledging dependence on parents as in the 'intermediate' alcids. A slow growth rate severely reduces fledging success in oystercatchers but post-fledging survival was not affected by size or weight at fledging (Kersten & Brenninkmeijer 1995).

THE RELATIONSHIP BETWEEN MATURATION AND FLEDGING WEIGHT

A range of non-exclusive explanations have been proposed for delayed breeding and age-related improvements of reproductive performance in birds (Forslund & Pärt 1995, Oro & Pradel 2000). Some of these can be applied to the counter-intuitive result of this study: Guillemots with early maturity were lighter at fledging than birds with normal maturity.

First, fledging weight is assumed to reflect some aspect of individual quality. Achievements of competence are regarded as important prerequisites of breeding (see Introduction) and it is likely that better quality individuals, birds with higher weights, then will achieve the required competence easier or earlier. This would result in earlier maturity for those individuals – the opposite to my findings.

Age at first breeding reflects a trade-off between lifetime reproduction and survival, as breeding early in life can increase mortality (Lack 1968, Forslund & Pärt 1995, Pyle et al. 1997) but a too late start will result in a reduced lifetime reproduction. For normal or high quality birds, delayed breeding would be adaptive as life expectancy is long for guillemots. For low quality individuals; birds with low fledging weights, the situation will be different if their intrinsic quality reduces life expectancy or reproductive performance, which may be the case in long-lived species (Cam et al. 2003 and references therein). Breeding is expected at younger ages, as early investments in reproduction are more likely to pay off than saving resources for the future. This is in accordance with the pattern observed among Stora Karlsö guillemots.

If fledging weight is assumed to have no influence on individual quality, the explanations for delayed breeding mentioned above may still be true for some other aspect of individual quality. In addition there is a possibility of one mechanism, directly or indirectly, regulating both fledging weight and maturation, which will result in the observed relationship. A likely such mechanism would be an endocrine function. Hector et al. (1990) found that in the wandering albatross sexual maturity requires production of oestradiol and colony attendance prior to maturity does not influence the time taken to start breeding. A similar mechanism is most likely operating in guillemots and as weight and/or growth also is under hormonal control, there may be one single function regulating both fledging weight and maturation. Although, the influence of other factors, e.g. colony visiting, on

the maturation process can not be dismissed for guillemots.

It is also possible that fledging weight reflects quality and an endocrine function is the mechanism of selection causing this relationship.

In conclusion, the observed relationship between fledging weight and sexual maturation does not reveal if fledging weight is a measure of individual quality. However, it indicates that long-term effects of different fledging weights deserve further attention. A correlation between fledging weight and life expectancy can be investigated using ring recovery data of adult guillemots that were ringed and weighed as fledglings. To study the potential effects of fledging weight on reproductive performance immense efforts are required, as individuals need to be followed from fledging, at first breeding and during many consecutive years. A study of reproductive hormones in guillemots of varying ages and reproductive stages, with respect to different fledging weights, would also be of interest.

VARIATION IN SURVIVAL AND POTENTIAL EXPLANATIONS

There seems too have been a difference in survival between cohorts, where the 2003 and 2004 cohorts appeared to survive better (Fig. 4). This pattern was seen both in records from Stora Karlsö and ring recoveries of guillemots found dead during their first year of life. Despite the non-quantitative analysis of survival, the influence of a few, potentially important, factors can be assessed.

A large part of the ring recoveries came from birds found entangled in fishing gear, which confirms the picture given by Österblom et al. (2002), that bycatch poses a serious threat to the Baltic Sea guillemot population. However, it is possible that the situation has improved during recent years. Among birds recovered dead during first year of life were the proportion entangled in fishing gear lower in 2002-2004 than in 2000-2001. As Österblom et al. (2002) showed that 1- and 2-year-olds are more likely to get entangled in fishing gear than adult birds, this may indicate an overall decease in bycatch. In addition, the number of ringed birds that could be caught increased each summer, as an additional cohort was ringed, but despite this, there was no apparent trend in number of bycatches (Fig. 6). Therefore, the individual risk may actually have decreased. It is tempting to conclude that bycatch has decreased during this study, which can be either a result of changed fishing practices or caused by decreased fishing intensity. However, as Olsson et al. (2000) and Österblom et al. (2002) pointed out, a majority of the trapped birds are probably not reported and it is possible that the report rate has been further reduced in recent years when the fishery has been much debated. These factors need consideration when ring recovery data are used to calculate survival, but further assessment of their importance was beyond the scope of this study.

Sprat abundance influenced first-year survival of guillemots born on Isle of May, Scotland (Harris & Bailey 1992). Baltic Sea guillemots depend even more on sprat as a food resource than their Scottish conspecifics (Lyngs & Durinck 1998) why it can be expected that sprat abundance is at least equally important to this population. The lowest sprat abundance in the Baltic during this study occurred in 2002, when the cohort with lowest post-fledging survival was born. However, the abundance in 2002 was well above the average for the last decades (ICES 2005) and therefore it is doubtful that sprat abundance was a limiting factor for guillemots during this study.

The winters experienced by the guillemots in this study were in general mild (SMHI), but the winter 2002/03 was an exception with sea surface temperatures more than 1° lower than in the other years. The cohorts born before this winter (2000-2002) had lower post-fledging survival than those born in the later years (2003-2004). The proportions resighted at Stora Karlsö were similar for cohorts 2000-2002, despite that there were relatively fewer ring recoveries of cohort 2002 during their first winter compared to cohorts 2000 and 2001. This indicates that cohort 2002 had a mortality rate similar to 2000 and 2001, but that this was not fully captured in the ring recovery figures. This is also what to expect if the cause of mortality is not directly related to human activities. Altogether, the resighting and ring recovery rates indicate that winter sea surface temperature in the Baltic affects survival and that 1-year-olds can be more sensitive. Colder temperatures can affect the guillemots directly, when more energy is required to maintain body temperature and functions. In addition, there may be indirect effects. The vertical distribution of sprat is limited by water temperature since sprat very rarely is found in water colder than 4°C (Rechlin 1967 and Grauman 1980 in Karasiova & Zezera 2000, Gröhsler et al. 2000). During colder winters sprat will then be found at larger depths. There are also indications that sprat shoals are more aggregated when water is colder (Dahl 2004). This implies that foraging will be more demanding and require more energy during cold winters. In total, the extra energy requirements caused by cold water temperatures may be a challenge for inexperienced guillemots.

It is possible that survival assessments have been influenced by emigration. Emigration from Stora Karlsö have been found important for some of the smaller Baltic Sea colonies (Hario 1982, Lyngs 1993) and it is likely that there are guillemots born on Stora Karlsö breeding in almost all Baltic colonies (Olsson et al. 2000). In addition, the emigration rate is probably variable. The number of

breeding pairs at Stora Karlsö, and hence available breeding sites there, is likely an important factor. Pre-breeding survival in a cohort will possibly also affect its emigration rate. Emigration and specially variation in emigration rate have not been assessed for the cohorts included in this study, whereby its influence can not be dismissed.

Sophisticated modelling is required to properly assess the importance of the factors mentioned above. However, the results here suggest that these factors, and how they are interconnected, can give further insight into the variation in survival rates.

Acknowledgements

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Appendix

Chicks ringed at Stora Karlsö since 2000.

Cohort	No. of chicks ringed	No. of chicks weighted	Mean weight ± S.D. (g)	Median ringing date
2000	994	788	239.3 ± 26.1	June 30
2001	999	996	230.8 ± 23.3	June 26
2002	997	678	251.4 ± 26.6	June 29
2003	1499	1493	237.8 ± 23.3	June 30
2004	1495	1486	248.4 ± 25.0	June 26
2005	1998	1991	249.6 ± 26.7	June 30
Total	7982	7432	243.6 ± 26.2	

Observations at breeding ledges at Stora Karlsö 2002-2006.

Cohort	No. observed 2002	No. observed 2003	No. observed 2004	No. observed 2005	No. observed 2006	No. observed in total
2000	28	26	17	10	10	64
2001	1	16	18	14	24	51
2002		0	21	21	18	49
2003			3	59	88	137
2004				4	83	85
2005					4	4
Total	29	42	59	108	227	390