Long-term study of mortality in the common guillemot in the Baltic Sea

Olof Olsson, Torbjörn Nilsson, Thord Fransson
Long-term study of mortality in the common guillemot in the Baltic Sea
Analysis of 80 years of ringing data

by

Olof Olsson¹
Torbjörn Nilsson²
Thord Fransson³

¹Swedish Council for Planning and Coordination of Research, Box 7101, SE-103 87 Stockholm, Sweden (e-mail: olof.olsson@frn.se)
²Department of Animal Ecology, Evolutionary Biology Centre, Uppsala University, Norbyvägen 18D, SE-752 36 Uppsala, Sweden
³Swedish Museum of Natural History, Bird Ringing Centre, Box 50007, SE-104 05 Stockholm, Sweden
FOREWORD

The common guillemot is a seabird that was almost extinct in the Baltic Sea at the end of the 19th century, due to hunting and collection of eggs. Only about 20 birds remained in 1880. Following legal protection of the species and its breeding areas, the population has increased to about 45,000 birds today. The common guillemot was on the 1996 Swedish Red List of threatened vertebrates, in the category “Care Demanding”. As guillemots are slow to reach maturity, are long-lived and produce only a few offspring each year, the population is particularly vulnerable to factors that affect adult survival.

Each summer, the fledglings jump from the nesting ledges to the beach or sea below, to swim out to sea with the males. What fate awaits them during their lifetime?

This report is a follow-up of the Swedish Action Plan on Biological Diversity, which was published in 1995: “Action 26” states the need to continue to study and analyse the habitat requirements of red-listed species and the need for measures to protect them.

Nearly 43,000 common guillemots were ringed in Sweden from 1912 to 1998, mainly on the island of Stora Karlsö in the southern Baltic proper. About 6% of the ringed birds have been recovered. Of the recovered birds, 50% were found entangled in fishing gear, mainly in the southern Baltic Sea. It appears that the main culprit is the commercial drift-net fishery for salmon. The proportion of oiled birds was smaller, and has decreased since the 1960s to less than 5% today.

It is alarming that so many guillemots meet a painful death by drowning in fishing gear. Moreover, many of the bycatches of birds caught in fisheries may never be reported. The results show that measures need to be implemented to prevent guillemots from drowning in commercial fisheries in the Baltic Sea.
The study was financed by the World Wild Fund for Nature (WWF Sweden) and the Swedish Environmental Protection Agency (Swedish EPA). The report was commissioned by Cathy Hill, then at the Research Secretariat of the Swedish EPA.

The manuscript was reviewed by Tycho Anker-Nilssen, Norwegian Institute for Nature Research, Trondheim, Norway; Pär Forslund, Swedish University of Agricultural Sciences, Uppsala; Risa Rosenberg, WWF Sweden; and Anders Wetterin, Swedish Environmental Protection Agency. The final manuscript was edited by Cathy Hill, WWF Sweden.

The authors are solely responsible for the contents of this report.

STOCKHOLM, JANUARY 2000
SWEDISH ENVIRONMENTAL PROTECTION AGENCY

Olof Olsson with a guillemot chick. Photographer: Ola Jennersten.
CONTENTS

FOREWORD 3
SVENSK SAMMANFATTNING 7
SUMMARY IN ENGLISH 9
INTRODUCTION 11
METHODS 14
Survival analysis – model selection procedure 17
RESULTS AND DISCUSSION 20
Temporal and age aspects of geographical distribution 20
Finding circumstances and geographical distribution of recoveries 26
Age of recovered birds 32
Conclusions about geographical distribution, finding circumstances and age 33
Survival analysis – estimates 36
Conclusions of survival analysis 40
ACKNOWLEDGEMENTS 40
REFERENCES 41
APPENDIX 43
Basic theory of survival analysis and model selection with ring recovery data 43
SAMMANFATTNING

LÄNGTIDSSTUDIE AV DÖDLIGHET HOS SILLGRISSLOR I ÖSTERSJÖN - ANALYS AV 80-ÅRS RINGMÄRKNINGSDATA

Denna studie är baserad på data från 42 824 sillgrisslor (Uria aalge) som ringmärkts i Östersjöområdet, främst ungar som ringmärkts vid Stora Karlsö mellan 1912–1998. Materialets storlek och långa tids-spann gör det unikt i världen. Av de ringmärkta fåglarna har 6 % rapporterats som återfynd, d.v.s. funnen död eller kontrollerad levande.

De rapporterade återfynden indikerar klart att i stort sett alla sillgrisslor som häckar i Östersjön stannar i området året runt. Vintertid (september–februari) fanns särskilt stora koncentrationer av återfynd rapporterade från områdena runt Gotland och Öland (inkluderande fiskebankarna söder om Gotland), Gdanskbukten, havet runt Bornholm, Hanöbukten, Rügen, Pommerska bukten samt de danska öarna. Vi fann signifikanta skillnader i den geografiska fördelningen av återfynden mellan fåglar upp till två års ålder och de som var äldre än två år; de yngre fåglarna övervintrade i genomsnitt längre från häckningsområdena jämfört med de äldre. Återfynden som rapporterades under sommaren (juni–juli) visade att fåglar som var fem år eller äldre var koncentrerade till häckningsplatserna medan yngre fåglar var mer utspridda. Detta styrker tidigare iakttagelser att sillgrisslor börjar häcka vid ungefär fem års ålder.

Majoriteten återfynden (50 %) utgjordes av fåglar som fastnat i fiske-redskap (bifängst). Andelen fåglar som rapporterats som oljedödade var endast 5 %. Ur vårt material går ej att utläsa vilka fiskeredskap som orsakat flest bifängster, men vi anser det troligt att flertalet sillgrisslor hade fastnat i drivgarn som används vid kommersiellt fiske efter lax (Salmo salar), bland annat eftersom både laxars och sillgrisslors huvudsakliga föda utgörs av skarpsill (Sprattus sprattus). Bifängster har även förekommit i nät som används vid fiske efter torsk (Gadus morhua).
De största koncentrationerna av bifångster var rapporterade från områdena runt Öland och Gotland, fiskebankarna söder om Gotland, Hanöbukten, havet runt Bornholm och Rügen, Pommerska bukten samt, inte minst, Gdanskbukten. Vi fann en signifikant skillnad i den geografiska fördelning mellan fåglar som fastnat i fiske-redskap och de fåglar som rapporterats som funna döda (i huvudsak utmed stränder, d.v.s. ej i fiske-redskap). Orsaken var framförallt att få bifångster, jämfört med andra återfynd, rapporterats från Danmark (Bornholm undantaget). En annan förklaring var det proportionellt stora antalet bifångster i Gdanskbukten och bankarna söder om Gotland. Dessa skillnader torde avspeglas var laxfisket bedrivs.

Vi fann inte någon förändring i andelen återfynd rapporterade som bifångster i fiske-redskap, jämfört med andra återfyndsomständigheter, under perioden 1960-1998. Däremot fann vi en signifikant minskning av andelen återfynd som rapporterats som oljeskadade under samma period.

SUMMARY IN ENGLISH

This study is based on a uniquely large and long-term data set of ringed common guillemots (*Uria aalge*) in the Baltic Sea. We analysed recoveries of 42,824 common guillemots ringed in Sweden from 1912-1998. Most of the birds were juveniles ringed on the island of Stora Karlsö in the southern Baltic proper. Of the ringed birds, 6% were recovered (*i.e.* found dead or controlled alive).

Our data clearly indicated that almost all common guillemots that breed in the Baltic Sea area stay in the region all year round. Outside the breeding season, we found significant differences in the distribution of recoveries of birds up to two years old compared to older birds, which indicates that the younger birds tend to winter further away. In winter (September–February) birds of all age classes were recovered mainly in the central and southern parts of the Baltic proper: off the Swedish islands of Gotland and Öland (including the fishing banks south of Gotland), the Polish Gulf of Danzig, off the Danish island of Bornholm, in the Swedish Hanöbukten Bay, off the German island of Rügen and in the Pomarian Bay, and off the Danish islands.

The recoveries reported during the summer (June and July) indicated that as the birds grew older, their distribution became less spread-out: recoveries (including recaptures) of birds that were five years and older were concentrated to known breeding localities in summer. This supports previous suggestions that common guillemots do not start breeding until about five years of age.

The majority of recovered birds (50%) had been trapped in fishing gear. The proportion of birds reported as oiled was only 5%. It is likely that most of the common guillemots were caught in drift nets used in the commercial fishery for salmon (*Salmo salar*), since both salmon and common guillemots feed on sprat (*Sprattus sprattus*). Birds had also become trapped in gillnets used in the fishery for cod (*Gadus morhua*).
The largest concentrations of birds trapped in fishing gear were reported from the area around Öland and Gotland, the fishing banks south of Gotland, the Hanöbukten Bay, the sea around Bornholm and Rügen, the Pomarian Bay, and the Gulf of Danzig. There was a significant difference between the geographical distribution of birds reported as trapped in fishing gear and those found dead (mainly along shores, but not trapped in fishing gear). This difference can mainly be explained by geographical differences in the intensity of the salmon fishery, as only a small proportion of birds was recovered from fishing gear in the Danish area of the Baltic (excluding the island of Bornholm), while a larger proportion of birds was trapped in fishing gear in the Gulf of Danzig and the fishing banks south of Gotland.

There were no time trends in the proportion of birds reported as trapped in fishing gear in the period 1960-1998. However, in the sub-sample of birds that were found dead mainly on beaches during the same period, there was a significant decrease in the proportion of oiled birds, from about 25 % in the 1960s to about 10 % in the 1990s.

We also conducted an analysis of the survival rates of the birds, based on the ringing and recovery data from 1962 to 1998, using maximum-likelihood estimation techniques and the computer program MARK. The annual survival rates of the adult common guillemots were estimated to be 87-90 % in 1962-1989, and 78 % in 1989-1997. These figures are relatively low compared to other studies of the same species, and the decrease of the survival rate in the last decade was unexpected. We cannot rule out that this decrease in survival rates may be due to increased mortality in the commercial drift-net fishery for salmon, but further studies are required to confirm this.
INTRODUCTION

Typical life-history characteristics of seabirds are that they start breeding when relatively old, they produce few offspring each year and they are often very long-lived. According to the literature, common guillemots (*Uria aalge*) start breeding at an age of about five years, they lay only one egg, and many ringed individuals have been reported to have lived more than 20 years (Hudson 1985). These characteristics, which have evolved because they favour the lifetime reproductive success of the individual birds, also have consequences for the population ecology of the species. The small clutch and the delayed adulthood make the development of the population relatively more sensitive to changes in the probabilities of adult survival, than to changes in offspring production and survival of young birds.

Little is known about the survival rates of common guillemots in the Baltic. The analyses published so far concern chick survival up to fledging, survival of chicks when they jump from the nesting ledges, and recovery rates of ringed birds up to seven years after they were ringed as chicks (Hedgren 1980, 1981). For long-lived animals, it is highly desirable to base estimates of their demographic rates on long-term studies. The present data set, comprising common guillemots ringed in the Baltic every year from 1912-1998, provides a unique opportunity to do this.

Harris & Bailey (1992) reported that the minimum annual adult survival rate of common guillemots from the Isle of May in the North Sea varied from 92.6 % to 97.3 % between years. Due to very high resighting rates these figures may be good approximations for actual survival rates. Harris *et al.* (1992) similarly used the proportion of birds marked as young and known to be alive six months later as a measure of post-fledging survival. For different years, they reported these proportions to vary from 15 % to 47 %, but here one cannot exclude the possibility that true survival rates may be considerably higher.
The Baltic Sea population of common guillemots most likely has its origin in Atlantic populations, probably British, and it may have been established some 4,000 years ago (Løppenthin 1963; for a history of the population, also see Hedgren 1975). It is one of the smallest populations of common guillemots in the world, and it is considered to be a particular subspecies: *U. a. intermedia* (e.g. Salomonsen 1944).

The population was almost extinct at the end of the nineteenth century; the only known breeding locality was the Swedish island of Stora Karlsö (and perhaps also Lilla Karlsö), and only about 20 individuals were seen in 1880 (review in Hedgren 1975). The birds were protected at Stora Karlsö in the 1880s, and since then the population has increased to about 8,000-10,000 breeding pairs on Stora Karlsö and 1,100 on Lilla Karlsö. Today, there are also several other colonies in the Baltic Sea, most of them relatively small – the largest of these is Grøesholmen (near the Danish island of Bornholm) with 2,000-3,000 pairs. It is likely that the Stora Karlsö colony is the source of the entire Baltic Sea population, which today comprises about 15,000 pairs (corresponding to about 45,000 individuals). No complete or regular surveys of the Baltic Sea population of common guillemots have been carried out. A general impression is, however, that the number of pairs on Stora Karlsö has increased steadily throughout the entire century. Competition for breeding ledges has probably entailed a more pronounced dispersal of young birds, which are forced to settle in other breeding sites. The information available suggests that the number of pairs has also increased, more or less steadily, in other breeding localities in the Baltic Sea.

In several other parts of the breeding range of the species, common guillemots have experienced dramatic population decreases in recent years (e.g. in the Norwegian Sea and the Barents Sea regions) (Mehlum & Bakken 1994, Mendenhall & Anker-Nilssen 1996, Anker-Nilssen et al. 1997). Thus, analyses of spatial and demographic parameters of the Baltic population may prove essential for the future management of the species.
On Stora Karlsö in the southern Baltic Sea, common guillemot chicks have been ringed since 1912. Up to 1998, more than 90 % of the 42,824 common guillemots marked in Sweden were ringed as chicks on Stora Karlsö. Of these ringed birds, 2,509 have been reported as recovered to the Ringing Centre at the Swedish Museum of Natural History. The reported recoveries include the following three categories of birds: found dead; trapped and released alive (recapture); and resighted alive. According to practice among ornithologists, we will use the term recovered for all three categories in this report. At the Ringing Centre the recoveries have been processed and computerised. This long-term and extensive data set is unique in the world, and has previously been explored scientifically only to a minor extent (e.g. Olsson et al. 1999).

The aim of this report is to investigate (i) causes of mortality (recovery circumstances), (ii) geographical distribution, and (iii) survival rates, based on ringed birds. This report is part of an overall study, funded mainly by WWF, that investigates the conditions for long-term survival of common guillemots in the Baltic Sea.

The cliffs at Stora Karlsö are home to the largest colony of common guillemots in the Baltic Sea. Photographer: Olof Olsson.
METHODS

The vast majority of the marked birds on which this study is based were ringed on the Swedish island of Stora Karlsö (57°17'N, 17°58'E), west of the island of Gotland, in the Baltic Sea (see Figure 1). At Stora Karlsö, common guillemots are ringed in summer when the chicks have jumped from the ledges and landed on the beach. Only a few adults have been ringed at Stora Karlsö. This study also includes birds that were ringed at a few other localities along the Swedish coast (their positions are indicated in Figure 1). Among those birds, a larger proportion were adults, compared to those marked at Stora Karlsö.

Figure 1. Swedish colonies (circles) of common guillemot in the Baltic Sea where ringing has been carried out. The Danish common guillemot colony at Græsholmen (square) is also shown.
In this report, different subsets of the entire data set of ringed birds and recoveries were included in the different analyses, mainly due to differences in the details given in the recovery reports (e.g. the accuracy of the recovery date). Generally, the analyses of geographical distribution and recovery circumstances included recoveries from 1915 to 1998 of birds marked only on Stora Karlsö.

In the analysis of survival rates, the data set was restricted to birds that were ringed from 1 June 1962 to 1 June 1998 (ringing figures prior to 1962 are not separated according to age categories). This data set contains 31,652 ringed juveniles and 2,395 adults. Most juveniles were ringed at Stora Karlsö, whereas the adults had mainly been ringed at other Swedish breeding localities along the coast. Because juveniles were ringed after jumping from the ledges at an age of about 20 days, the estimates of first-year survival concern those that survived both the nestling period and the jump from the cliffs.

Among the birds ringed after 1 June 1962, 1,918 juveniles and 52 adults have been recovered (6.1 % and 2.2 %, respectively). Birds for which the date of death was uncertain by three months or more were not included. Hence, the recoveries used in the analysis were of 1,521 birds ringed as juveniles and 48 birds ringed as adults.

In modern analyses of survival rates in free-ranging animals, maximum-likelihood estimation techniques are used to separate survival rate from resighting or recovery probabilities. Various models have been developed for analysis of recapture/resighting of live animals and for recoveries of dead individuals. The basic theory for analysis of ring recovery data was summarised by Brownie et al. (1985), and the analysis presented here is based on this theory (see Appendix for a short summary of the theory). For this analysis we used the computer programme MARK, a programme package that provides a range of sub-programmes for analysis of various types of re-encounter data, e.g. one sub-programme for analysing ring recovery data in accordance with Brownie et al. (1985).

The birds were marked with metal rings on one leg. A variety of ring types was used, and generally the quality, and thus ability to withstand oxidation in salt water and wear on the cliffs, has improved.
throughout time. We have no estimates of ring loss, but in this kind of analysis ring loss should influence recovery rate rather than the estimated survival rate.

The breeding phenology of the common guillemots on Stora Karlsö is roughly the following: egg-laying starts in early May, and the peak period when the chicks jump from the cliffs and depart, escorted by adult males, occurs in late June and early July (Hedgren & Linman 1979, Hedgren 1980, personal observations). The chicks and males leave the breeding area and start immediately swimming together (but without the females) to wintering grounds in the southern Baltic Sea (Olsson et al. 1999). The adult birds often start to visit the colony occasionally in January or February, but do not visit regularly until April. Throughout July, many immature birds and adult females are still present in the colony, but in August the colony eventually becomes empty. Based on this phenology, we have defined the winter as the period when birds are mainly in the wintering areas: i.e. September – February. The breeding season starts in the second half of April, prior to laying, and ends in the first half of July, when most chicks have left.
Survival analysis - model selection procedure

The basic theory of survival analysis with ring recovery data and of model selection is summarised in Appendix 1. The primary goal of model selection is to find, among a vast number of possible models, a model which is biologically reasonable, fits the data, and is as parsimonious as possible.

Since the birds start breeding at an age of about 5 years, it is biologically sensible to separate them into three age classes: juveniles (in their first year of life), immatures (from 1 to 5 years old) and adults (from 5 years of age and older). We started with a model in which both survival and recovery rates varied independently between these three age classes and between all years (Model 1 in Table 1). Then we simplified this model, first by making recovery rate vary between years concurrently for the three age classes (no interaction between age and time variation in recovery rates; Model 2), then by pooling the years arbitrarily into four periods of nine years each (Model 3), and then by making recovery rate constant over time (Model 4).

Of these four models, Model 3 had the lowest QAICc (a measure of the fit of a model), so we started from this model when simplifying survival rates. This was done in a similar way, by first removing the interaction between time and age variation in survival rate (Model 5), then pooling the years into four periods (Model 6), and finally by making survival constant over time (Model 7).

Subsequently, we explored whether age variation could be simplified by pooling the age classes with regard to recovery rates. We tried pooling juveniles and immatures (Model 8), immatures and adults (Model 9) and making recovery rate equal for all age classes (Model 10). Accepting Model 9 but rejecting Models 8 and 10, we continued by trying the same simplifications for survival rates (Models 11, 12 and 13).
Table 1. Description, deviance, number of parameters, and QAICc for the models used to calculate survival rates of common guillemots (see the text). Subsequently lower QAICc values are indicated by bold figures. The QAICc values presented here are calculated using the c-hat value of Model 14, which is 2.131.

<table>
<thead>
<tr>
<th>Model</th>
<th>Description</th>
<th>Deviance</th>
<th>Number of parameters</th>
<th>QAICc</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Both survival and recovery rates: three age classes, all time-steps independent.</td>
<td>545.16</td>
<td>211</td>
<td>9538.23</td>
</tr>
<tr>
<td>2</td>
<td>Survival rates as in Model 1. Recovery rates: no interaction between age and time variation.</td>
<td>652.58</td>
<td>142</td>
<td>9451.06</td>
</tr>
<tr>
<td>3</td>
<td>As Model 2, but for recovery rates: time-steps pooled into four periods.</td>
<td>731.51</td>
<td>110</td>
<td>9423.70</td>
</tr>
<tr>
<td>4</td>
<td>Survival rates as in Models 1-3. Recovery rates: constant over time, varying only between age classes.</td>
<td>763.46</td>
<td>107</td>
<td>9432.66</td>
</tr>
<tr>
<td>5</td>
<td>Survival rates as in Model 1. Recovery rates: no interaction between age and time variation.</td>
<td>785.36</td>
<td>43</td>
<td>9314.46</td>
</tr>
<tr>
<td>6</td>
<td>As Model 5, but time-steps pooled into four periods also for survival rates.</td>
<td>847.69</td>
<td>12</td>
<td>9281.62</td>
</tr>
<tr>
<td>7</td>
<td>Recovery rates as in Model 3. Survival rates: constant over time, varying only between age classes.</td>
<td>882.51</td>
<td>9</td>
<td>9291.96</td>
</tr>
<tr>
<td>8</td>
<td>Survival rates as in Model 6. Recovery rates: juveniles and immatures pooled.</td>
<td>872.97</td>
<td>11</td>
<td>9291.48</td>
</tr>
<tr>
<td>9</td>
<td>Survival rates as in Model 6. Recovery rates: immatures and adults pooled.</td>
<td>848.21</td>
<td>11</td>
<td>9279.86</td>
</tr>
<tr>
<td>10</td>
<td>Survival rates as in Model 6. Recovery rates: equal across age classes, varying only between time periods.</td>
<td>885.27</td>
<td>10</td>
<td>9295.25</td>
</tr>
<tr>
<td>11</td>
<td>As Model 9, but survival rates for juveniles and immatures pooled.</td>
<td>871.56</td>
<td>10</td>
<td>9288.82</td>
</tr>
<tr>
<td>12</td>
<td>As Model 9, but survival rates for immatures and adults also pooled.</td>
<td>950.57</td>
<td>10</td>
<td>9325.90</td>
</tr>
<tr>
<td>13</td>
<td>Recovery rates as in Model 9. Survival rates: equal across age classes, varying only between time periods.</td>
<td>951.57</td>
<td>9</td>
<td>9324.37</td>
</tr>
<tr>
<td>14</td>
<td>Survival rates: Two age classes: juveniles (0-1 year), older than 1 years; Two time periods: 1962-90, 1990-97; No time-age interaction. Recovery rates: Three age classes: 0-2 years, 2-3 years, and older than 3 years; Three time periods: 1962-72, 1972-90, 1990-98; No time-age interaction.</td>
<td>816.11</td>
<td>8</td>
<td>9258.60</td>
</tr>
</tbody>
</table>
In a separate series of analyses, we relaxed the assumption that all birds from 1 to 5 years of age should belong to the same age class, and tried a wide range of models in which these birds were separated into different age classes or pooled with juveniles and/or with adults. Then we also tried many different ways of grouping the years into two, three or four periods. This may be considered to over-fit the model (which is not recommended by Lebreton et al. 1992), and in the most parsimonious model found in this way the age classes are not easy to interpret biologically, but we present this model too (Model 14) just for the sake of comparison.

Photographer: Olof Olsson.
RESULTS AND DISCUSSION

TEMPORAL AND AGE ASPECTS OF GEOGRAPHICAL DISTRIBUTION

Our data clearly indicate that almost all common guillemots stay in the Baltic Sea all year round. The monthly mean positions of recovered birds ringed on Stora Karlsö were concentrated to the central and southern Baltic Sea (Figure 2). The general pattern was that recoveries were reported S to SW of the Karlsö area outside the breeding season, with the southernmost positions in mid winter.

To investigate if there were differences between the wintering areas of young and old birds, we compared the number of birds in four age classes (first, second, third, fourth year and older birds) in six different areas (Figure 3). We found significant differences between birds in the first two year-classes and those that were older, indicating that the younger birds tended to winter further away from the colony. Of those birds found among the Danish islands (Sjælland, Fyn, Lolland) and also among the few that were found outside the Baltic Sea, the proportion of young birds was much higher (Figure 3). Nevertheless, the vast majority of all age categories were reported from the central and southern parts of the Baltic Sea in winter. In particular, in winter (September–February) birds were concentrated in the following areas: around Gotland and Öland (including the fishing banks S of Gotland); the Gulf of Danzig; the sea around Bornholm; Hanöbukten; Rügen and the Pomarian Bay; and the Danish islands.

Our findings differ considerably from the conclusions of Durinck et al. (1994), who suggested the Karlsö area (i.e. SW Gotland) to be the most important wintering area. However, their short-term survey by aircraft and ship covered only late winter. At this time of year, large numbers of birds can appear sporadically, but simultaneously, on the breeding grounds. However, they seem to be very mobile, and may perhaps move around in the central and southern Baltic Sea during the winter. Thus, one can argue that the survey conducted by Durinck et al. happened to take place when the birds were close
Figure 2. Monthly mean positions of recoveries of common guillemots of all age classes ringed at Stora Karlsö (indicated by star) from 1912 to 1998 (sample sizes: Jan, n=108; Feb, n=84; Mar, n=108; Apr, n=108; May, n=171; Jun, n=128; Jul, n=63; Aug, n=46; Sep, n=132; Oct, n=268; Nov, n=136; and Dec, n=115). The mean positions were calculated according to formula 2 in Perdeck (1977). Birds controlled at breeding sites and recoveries for which the uncertainty of the finding date was greater than one month are not included.

to Stora Karlsö. Our data may, on the other hand, suffer from not being based on observed living birds, and may be biased by an uneven distribution of human activities, e.g. the salmon fishery. The strength of our report is that the data include all months of the year and a vast number of years.
It is important to note that a large proportion of the recovered birds were juvenile or immature (younger than five years). These birds are not tied to the breeding localities in spring and summer, but it is known that immature birds appear in colonies at the end of the breeding season. This may explain why the mean position of recoveries was closer to the Karlsö area in September-November compared to February-May (Figure 2).

The data set used in this study contains recoveries of birds marked at other locations that were further north than the Karlsö area. These birds also spend winter in the central and southern parts of the Baltic Sea (Figure 4) and, consequently, mix with the birds from the Karlsö area.

The summer (June–July) distribution of recoveries indicates that as the immature birds got older they became less spread-out, and recoveries of fifth-year and older birds were concentrated to known breeding localities (see Figure 5). During the breeding season, ringers control living adult birds to a larger extent in some of the smaller colonies than in the Karlsö colonies. This may explain the high figures for recoveries at some localities (see Figure 5d). Moreover, the concentration of summer recoveries of fifth-year and older birds in known colonies supports previous suggestions that common guillemots do not start breeding until an age of about five years, as suggested by Hudson (1985).
Figure 3a-d. Distribution of recoveries in winter (September–February) of common guillemots ringed at Stora Karlsö from 1912 to 1998, separated into different age groups: a) first-year birds (n=378); b) second-year birds (n=157); c) third-year birds (n=52); and d) birds older than three years (n=256). The maps also show the number of recoveries in six different areas. The combined distribution of birds from the first two age groups is significantly different from that of older birds (Chi-square Test, $c^2 = 38.27$, df=5, p<0.001).
Figure 4. Recoveries in winter (September–February) of common guillemots ringed at small colonies along the Swedish east coast from 1980 to 1997. Adults and juveniles were pooled (n=31).
Figure 5a-d. Recoveries in summer (June–July) of common guillemots ringed at Stora Karlsö from 1912 to 1998, separated into different age classes: a) second-year birds (n=88); b) third-year birds (n=37); c) fourth-year birds (n=21); and d) birds older than four years (n=181). Birds controlled at breeding sites are also included and numbers indicate when several birds were reported from the same place. It is notable that one bird ringed as a chick on Stora Karlsö was found breeding in Wales (UK).
FINDING CIRCUMSTANCES AND GEOGRAPHICAL DISTRIBUTION OF RECOVERIES

Details of the reports of recovered common guillemots that had been ringed from 1912-1998 show that 50 % of the recovered birds were trapped in fishing gear (Figure 6). Surprisingly, about 8 % of these birds were reported to have been released alive (although some were injured) after the ring number was recorded. Birds that had been hunted were reported mainly from Denmark, but after the protection of common guillemots there in 1980, there were almost no reports of shot birds. Birds reported as oiled constituted 5 % of the recoveries.

![Pie chart showing reported recovery details of common guillemots ringed in Swedish colonies in the Baltic Sea from 1912 to 1998 (n=2,509).](image)

**Figure 6.** Reported recovery details of common guillemots ringed in Swedish colonies in the Baltic Sea from 1912 to 1998 (n=2,509).

The largest concentrations of birds found dead (mainly along shores, but not trapped in fishing gear, hunted or controlled by ringers) were reported from Gotland, Öland, Bornholm, the southernmost coast of Sweden (Skåne/Blekinge), the easternmost parts of the Danish islands, Rügen, the Pomarian Bay, and the Gulf of Danzig (Figure 7). A sub-sample of these, birds found dead and reported as being affected by oil spills, differed mainly in that relatively few birds were
reported from the Danish islands and the S and SE coasts of the Baltic Sea (Germany, Poland, Russia (Kaliningrad), Lithuania and Latvia). Oiled birds were instead mainly reported from the shores of Gotland, Öland, Bornholm, and the SE tip of the Swedish mainland (Skåne) (Figure 8). We cannot see any obvious explanation for this divergence in the distribution of oiled birds. On the contrary, because westerly winds prevail, one would expect concentrations of birds in the SE parts of Baltic Sea. Sea currents may also influence the result, but all these factors deserve further investigation before any firm conclusions can be drawn.

Figure 7. Distribution of recoveries of common guillemots ringed in Sweden from 1912 to 1998 and reported as found dead (n=626). Birds that had been hunted or trapped in fishing gear are not included. The map also shows the number of birds found in six different geographical areas.
Figure 8. Common guillemots ringed in Sweden from 1912 to 1998 and found dead and reported to be oiled (n=132).

The largest concentrations of birds trapped in fishing gear were reported from the area around Öland and Gotland, the fishing banks S of Gotland, Hanöbukten, the sea around Bornholm and Rügen, the Pomarian Bay, and the Gulf of Danzig (Figure 9). Comparatively few birds were reported from Danish waters (except Bornholm), but relatively many were reported from both the Finish and Swedish coasts of the Gulf of Bothnia (Figure 9). Unfortunately, the types of fishing gear involved were only reported to a lesser extent and such information is not available in the computerised data base of recoveries (to manually search the archive for various details given in the recovery reports was beyond the scope of this study). However, because both salmon *Salmo salar* and common guillemots feed to a great extent on sprat *Sprattus sprattus* (Lyngs & Durinck 1998), it is likely that many common guillemots were caught in drift nets used in the commercial salmon fishery. This assumption was verified in interviews with a few fishermen on Gotland. However, common guillemots are also known to be trapped in gill nets for cod *Gadus morhua* in the Baltic Sea (Lyngs & Durinck 1998, Roland Staav, pers. comm.). Reports sometimes include information about the depth at which birds were trapped in the nets, and the maximum depth reported is 80 m (Staav 1983).
Figure 9. Distribution of recoveries of common guillemots ringed in Sweden from 1912 to 1998 and reported as entangled in fishing gear (n=1,264). The map also shows the number of birds found in six different areas.

To investigate if there were differences in the geographical distribution of ringed birds reported as trapped in fishing gear and those found dead (mainly along shores) we compared these two categories in six different areas (i.e. Figure 9 vs. Figure 7). There was a significant difference in the distribution (Chi-square Test, $c^2=121.6$, df=5, $p<0.001$). This can be mainly explained by the relatively few birds recovered in fishing gear in the Danish area (Bornholm excluded), and the relatively larger numbers of birds caught in fishing gear in the Gulf of Danzig and the fishing banks S of Gotland. This may reflect a corresponding geographical difference in the concentration of the salmon fishery.
We investigated whether there were any time trends in the proportion of birds reported as trapped in fishing gear, in the periods from 1960 to 1998 (divided into 5-year periods), but no statistically significant trends were detected (Figure 10). On the other hand, there was a significant negative correlation between the proportion of oiled birds and time in 1960–1998 (divided into 5-year periods) (Figure 11). Hence in the sub-sample of birds reported as found dead mainly along shores (e.g. birds trapped in fishing gear not included) the proportion of oiled birds decreased from about 25% in the 1960s to about 10% in the 1990s.

Figure 10. The proportion of recoveries of common guillemots ringed in Sweden and reported as entangled in fishing gear for different 5-year periods during 1960-1998 ($r_s=0.36$, $p=0.39$). The proportion is based on all recoveries excluding only those controlled alive at breeding sites. The number of birds entangled in fishing gear for each 5-year period are indicated in the figure.
Figure 11. The proportion of recoveries of common guillemots ringed in Sweden and reported as oiled among those found dead in different 5-year periods during 1960-1998 ($r_s=-0.95$, $p<0.001$). The number of birds found oiled in each 5-year period are indicated in the figure.
**Age of Recovered Birds**

Sixty-nine percent of the recovered birds were younger than five years, and only about 2% were 20 years or older (Table 2). The oldest birds were two individuals ringed as juveniles more than 26 years before they were recovered dead.

**Table 2.** Age distribution of recovered common guillemots of known age (i.e. ringed as chicks from 1912 to 1998). Recoveries with a large uncertainty concerning the finding date, (e.g. finding year), and recoveries where only the ring was found have been excluded.

<table>
<thead>
<tr>
<th>Year of life</th>
<th>Number</th>
<th>%</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>697</td>
<td>37.7</td>
</tr>
<tr>
<td>2</td>
<td>332</td>
<td>17.9</td>
</tr>
<tr>
<td>3</td>
<td>146</td>
<td>7.9</td>
</tr>
<tr>
<td>4</td>
<td>100</td>
<td>5.4</td>
</tr>
<tr>
<td>5-9</td>
<td>305</td>
<td>16.5</td>
</tr>
<tr>
<td>10-14</td>
<td>160</td>
<td>8.6</td>
</tr>
<tr>
<td>15-19</td>
<td>72</td>
<td>3.9</td>
</tr>
<tr>
<td>20-24</td>
<td>33</td>
<td>1.8</td>
</tr>
<tr>
<td>25-29</td>
<td>5</td>
<td>0.3</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>1,850</td>
<td>100.0</td>
</tr>
</tbody>
</table>
Our results show some differences in the geographical distribution between birds of different age classes and recovery circumstances, respectively. Nevertheless, the data suggest that outside the breeding season almost all Baltic common guillemots of all age categories spent their time in the central and southern parts of the Baltic Sea: very few migrated out of the Baltic Sea. On the other hand, birds from the Atlantic populations do not seem to migrate into the Baltic Sea. In a study of ringed common guillemots that had been recovered in Danish waters (*i.e.* including both the Atlantic Ocean and the westernmost Baltic Sea) birds from Atlantic populations (mainly British) reached the Baltic Sea only to a minor extent, and the majority of these were immature birds (Lyngs & Kampp 1996). In our study of Baltic guillemots the immature birds were also more dispersed than adults and hence, mixing of the populations in winter mainly involved immature birds.

From 1912 to 1998, most (50 %) of the reported recoveries of common guillemots were of birds trapped in fishing gear whereas oiled birds only constituted 5 %. However, due to differences in the probabilities of detection and the willingness of people to report different categories of recovered birds, it is not possible to draw any firm conclusions concerning which mortality factors were the most important (see also below). Moreover, to estimate how many birds that die annually due to anthropogenic causes would require information of a magnitude that was not available in the data set we analysed.

We believe that large numbers of ringed birds trapped in fishing gear were never reported. It may not be in the interest of the fishery to draw attention to accidental bycatches of birds because this could lead to restrictions in the fishery. This awareness may have increased with time among fishermen and hence, they may have become less willing to report bycatches of ringed birds. If so, the constant proportion of recovered birds trapped in fishing gear from the 1960s to the 1990s (*Figure 10*) may actually hide an increase.
Considering that only a small fraction of the entire population of common guillemots is ringed and that only a few of the trapped birds are probably reported, the fact that about 1,250 birds were reported as trapped in fishing gear during 60 years reveals a conflict between bird conservation and some fishing activities. We found the proportion of recovered birds trapped in fishing gear from the 1960s to the 1990s (Figure 10) to be more or less constant. We do not know whether the willingness to report bycatches of ringed birds has remained unchanged during the same period, but the constant proportion found may well hide an increase. The results also urge us to reflect on the ethical aspect of the considerable numbers of birds that drown in agony in fishing gear each year. We conclude that considerable numbers of common guillemots are probably trapped in fishing gear in the Baltic Sea every year, and we can not exclude the possibility that this extra mortality caused by humans affects the development of the population.

Surprisingly few of the ringed birds that were recovered were reported as oiled. The explanation for this may be that few birds are oiled. However, even in this category the number of undetected birds can be large. The main reason for this is that oiled birds can die at sea and never reach land and may thus never be detected by humans. Compared to those birds trapped in fishing gear, it is likely that a larger proportion of oiled birds found by humans are actually reported, because there are no conflicts with personal economic interests. Hundreds of small oil spills, mainly along the shipping route E and S of Gotland in international water, are detected every year by the Swedish Coast Guard (surveys from aircraft are done daily). In order to gain more insights on the potential risk from these more or less everyday spills, more detailed data are required on the geographical and temporal distribution of the birds. Our data show, however, a decrease in the proportion of recoveries of common guillemots reported as oiled during the last three decades (Figure 11). We have no reason to suspect a diminished probability of finding and reporting oiled birds, and therefore we conclude that this reflects a factual decrease.
To our knowledge, there are no reports of large-scale oil spills that have caused large numbers of oiled common guillemots in the Baltic Sea during the 20th century. However, if a large-scale oil accident/spill were to take place in an area with large concentrations of common guillemots, this could be devastating for the Baltic population. For example, if an oil spill occurred when the chicks leave the colony swimming together with the males, in late June/early July, this could wipe out not only the chicks, but also many of the adult males in the population (see also Olsson et al. 1999). Obviously, oil spills near colonies in the breeding season or in wintering areas could also be devastating. We believe that an important task for research in the near future is to carry out a risk analysis of larger oil accidents in relation to the distribution of guillemots and other seabirds in the Baltic Sea.

Despite the additional mortality due to anthropogenic causes (e.g. from fishing gear and oil), the Baltic population of common guillemots has increased throughout the twentieth century. The main reasons for this increase are probably the good availability of food (sprat) and the legal protection of the species.
Survival analysis - estimates

Of Models 1-13 (see Table 1), which all modelled age variation in a manner that can be motivated on biological grounds, the most parsimonious model (lowest QAICc) was Model 9. Therefore we regard this model to be the most appropriate for the data at hand. In Model 9, birds were divided into three age classes (juvenile, immature, and adults) and four time-steps (1962-71, 1971-80, 1980-89, and 1989-97).

According to Model 9, the annual survival rate of adult common guillemots in the Baltic was 87-90 % in the first three time periods (1962-89), but only 77 % in the last period (1989-97) (Table 3). Annual survival rates estimated for immatures are about 20-30 percentage units lower than for the adults (Table 3). The confidence intervals for juvenile survival rates are too wide for any interpretations to be made (Table 3).

Table 3. Survival rates and recovery rates (%) of common guillemots in the Baltic Sea from 1962 to 1998, estimated according to Model 9 (Table 1), with 95% confidence intervals.

<table>
<thead>
<tr>
<th>Age class</th>
<th>Time period</th>
<th>Estimate</th>
<th>Lower CI</th>
<th>Upper CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Survival</td>
<td>Adults</td>
<td>1962-71</td>
<td>87.1</td>
<td>84.1</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1971-80</td>
<td>90.1</td>
<td>87.8</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1980-89</td>
<td>88.7</td>
<td>86.1</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1989-97</td>
<td>76.8</td>
<td>70.9</td>
</tr>
<tr>
<td></td>
<td>Immatures</td>
<td>1962-71</td>
<td>61.6</td>
<td>57.3</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1971-80</td>
<td>68.2</td>
<td>64.9</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1980-89</td>
<td>65.0</td>
<td>58.2</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1989-97</td>
<td>43.9</td>
<td>36.4</td>
</tr>
<tr>
<td></td>
<td>Juveniles</td>
<td>all periods</td>
<td>100.0</td>
<td>0.0</td>
</tr>
<tr>
<td>Recovery</td>
<td>Adults &amp; immatures</td>
<td>1962-71</td>
<td>1.11</td>
<td>0.97</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1971-80</td>
<td>0.75</td>
<td>0.68</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1980-89</td>
<td>0.64</td>
<td>0.54</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1989-98</td>
<td>0.60</td>
<td>0.50</td>
</tr>
<tr>
<td></td>
<td>Juveniles</td>
<td>1962-71</td>
<td>1.95</td>
<td>1.72</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1971-80</td>
<td>1.33</td>
<td>1.20</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1980-89</td>
<td>1.13</td>
<td>0.96</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1989-98</td>
<td>1.06</td>
<td>0.89</td>
</tr>
</tbody>
</table>
The confidence intervals for the adult survival rates are satisfactorily narrow. It should be remembered, however, that these confidence intervals were calculated according to the specific model that produced the estimates. When several different models fit the data reasonably well, inspecting the estimates provided by different models gives a better idea of the robustness of these estimates. In the present case, the estimates of adult survival rates provided by alternative models are very similar (Table 4). This table shows the adult survival rates estimated both according to Model 6 which is similar, and Model 14, which is very different. The comparison of these alternative models shows that our estimates of the adult survival rates and also the decrease in adult survival in the last decade are very robust.

<table>
<thead>
<tr>
<th>Model</th>
<th>Description</th>
<th>Period</th>
<th>Estimate</th>
<th>Lower CI</th>
<th>Upper CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>6</td>
<td>Both survival and recovery rates: Three age classes: juveniles (0-1 year); immatures (1-5 years), 5 years and older; Four time periods: 1962-71, 1971-80, 1980-89, 1989-97/98; No time-age interaction.</td>
<td>1962-71</td>
<td>87.5</td>
<td>84.3</td>
<td>90.2</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1971-80</td>
<td>90.4</td>
<td>87.9</td>
<td>92.4</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1980-89</td>
<td>89.0</td>
<td>86.3</td>
<td>91.2</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1989-97</td>
<td>77.1</td>
<td>71.1</td>
<td>82.2</td>
</tr>
</tbody>
</table>

| 14    | Survival rates: Two age classes: juveniles (0-1 year), older than one year; Two time periods: 1962-90, 1990-97; No time-age interaction. Recovery rates: Three age classes: 0-2 years, 2-3 years, older than three years; Three time periods: 1962-72, 1972-90, 1990-98; No time-age interaction. | 1962-90      | 86.8     | 85.1     | 88.3     |
|       |                                                                              | 1990-97      | 78.2     | 70.6     | 84.3     |

The adult survival rates estimated here are low compared to those found in studies of the common guillemot in the North Sea (e.g. Hudson 1985, Harris & Bailey 1992). One explanation for this could be that annual survival rate increases with age, up to a much higher age than 5 years. This problem will affect the model when the age of birds marked as adults is not known. Although their actual age may differ widely, these birds must be assumed to have the same survival rate. For instance, if the true survival rates of adult birds increase up
to the age of 10–20 years, then birds that die at the age of 5–10 years will make up a somewhat larger proportion of the recovered birds than their proportion in the live population. Hence, the estimated overall survival rate may then be biased by the lower survival at younger ages.

On the other hand, birds caught as adults and followed in live-resighting studies are also likely to constitute a somewhat biased sample. The adults are most easily caught on the breeding ledges, and therefore birds of lower quality that fail to establish a territory on the ledges are less likely to be included in such studies. Considering this, our estimates may be more representative for the entire population.

Nevertheless, until we have other estimates for comparison, we cannot rule out the conclusion that the adult survival rates in the Baltic really are lower than those in e.g. the North Sea. An ongoing resighting study of ID-marked breeding adults at Stora Karlsö, which was initiated in 1997, will shed more light on this issue within a few years.

To our knowledge, there are no changes in non-anthropogenic ecological conditions that correspond to the decreased survival rate of common guillemots in the Baltic in the 1990s, shown by our analysis. The abundance of sprat, which is a major food item for these birds (Hedgren 1976, Lyngs & Durinck 1998, personal observations), has instead been higher than in previous decades, and the levels of known toxic substances in fish have decreased. Increased predation pressure e.g. by birds of prey could be a plausible explanation, but we have no such indications. However, very little is known so far about predation on these birds. One possible explanation is that more birds were trapped in fishing gear during the last decade. As mentioned above, we can not rule out the possibility that the constant proportion of recovered birds that were reported as trapped in fishing gear in the last four decades (Figure 10) actually hides an increase, due to a diminished willingness to report bycatches of birds.
Our analysis may be affected by the fact that a larger proportion of the ringed adult birds were ringed at locations other than Stora Karlsö, where nearly all of the juveniles were ringed. However, if this caused some serious heterogeneity in the data, this should have been revealed as an unacceptably high c-hat value. More important than this mathematical argument is the fact that birds born and ringed at Stora Karlsö spend a great part of their lives in the same areas and under the same ecological conditions as birds from other Baltic colonies. Controls of ringed birds at various localities indicate that a significant proportion of adults originate from Stora Karlsö. Hence, the birds marked as adults are to a large extent a sample of the same population as those marked as juveniles.

If only juveniles have been marked, it becomes very difficult to estimate recovery data (Brownie et al. 1985, Anderson et al. 1985). Catchpole et al. (1995) discuss how this problem can be dealt with in some models and with some data sets. In our data set, birds marked as adults comprised only 7% of the marked birds and 3% (48 individuals) of the recovered birds. This relatively low proportion may be a weakness in our data set, and we suspect, although it may sound counter-intuitive, that this may be why juvenile survival rates could not be estimated. At present, up to 500 juvenile guillemots are ringed at Stora Karlsö each year, but almost no adults. To produce better estimates of age-specific survival rates in the future, it would be desirable to also ring about 100-200 adult guillemots each year.
CONCLUSIONS OF SURVIVAL ANALYSIS

This study, which is based on a large sample from a unique long-term data set of ringed birds, leads us to three conclusions: (i) Estimated adult survival rates of common guillemots from the Baltic Sea were lower than earlier estimates for the same species in the North Sea. Further research may show whether this reflects a true geographical difference or is due to methodological differences. (ii) The results show an unexpected decrease in survival rate of the common guillemot in the Baltic in the last decade. Further investigation is required to find out the cause of this decrease. We speculate, however, that it may be caused by a hidden increase in the number of birds trapped in fishing gear. (iii) To produce better estimates of age-specific survival rates in the future, it is desirable to ring not only chicks, but also a certain number of adult guillemots each year.

ACKNOWLEDGEMENTS

We thank the Swedish Environmental Protection Agency and the Swedish World Wide Found for Nature (WWF Sweden) for financial support, and Bo Sällström at the Swedish Bird Ringing Centre at the Swedish Museum of Natural History for making the data set available. We also thank Stellan Hedgren, Göran Hoas, Roland Staaav and many others that have ringed common guillemots throughout time, and we thank Gary C. White at Colorado State University for valuable advice on the use of the programme MARK. Finally, we thank the referees and the editor for useful suggestions on the manuscript.
REFERENCES


APPENDIX

BASIC THEORY OF SURVIVAL ANALYSIS AND MODEL SELECTION WITH RING RECOVERY DATA

The basic idea of modelling ring recoveries is that in each time-step (year) each ringed individual has a probability of surviving up to the end of the time-step (S), a probability of dying during the time-step and being recovered (f), and a probability of dying during the time-step without being recovered (1-S-f). If all individuals have the same survival rate S and recovery rate f, then these rates can be estimated from the proportion of ringed individuals that are recovered in different years.

The following example is simplified from Brownie et al. (1985): Suppose that S and f are constantly 50% and 10%, respectively, and that in three successive years 2,000, 400 and 1,200 individuals are ringed, then the following numbers of recoveries would be expected:

<table>
<thead>
<tr>
<th>Year ringed</th>
<th>Number ringed</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>2,000</td>
<td>200</td>
<td>100</td>
<td>50</td>
<td>25</td>
</tr>
<tr>
<td>2</td>
<td>400</td>
<td>40</td>
<td>20</td>
<td>10</td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>1,200</td>
<td>120</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

More generally speaking, if S and f are constants and N₁, N₂, N₃ etc individuals are ringed in the different years, then the following number of recoveries are expected:

<table>
<thead>
<tr>
<th>Year ringed</th>
<th>Number ringed</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>N₁</td>
<td>fN₁</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>N₂</td>
<td>fN₂</td>
<td>fN₂</td>
<td></td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>N₃</td>
<td>fN₃</td>
<td></td>
<td>fN₃</td>
<td></td>
</tr>
<tr>
<td>etc.</td>
<td></td>
<td>fN₄</td>
<td></td>
<td></td>
<td>fN₄</td>
</tr>
</tbody>
</table>
On the other hand, it is equally plausible that survival and recovery rates are constant between years, but vary depending on the age of the animals. If juveniles are ringed and if survival and recovery rates are age dependent, then the expected number of recoveries will be:

<table>
<thead>
<tr>
<th>Year ringed</th>
<th>Number ringed</th>
<th>Expected recoveries in year</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>N₁</td>
<td>f₁N₁</td>
</tr>
<tr>
<td>2</td>
<td>N₂</td>
<td>f₁N₂  S₁f₁N₁</td>
</tr>
<tr>
<td>3</td>
<td>N₃</td>
<td>f₁N₃  S₁f₂N₂  S₁S₁f₁N₁</td>
</tr>
<tr>
<td>etc.</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

With the knowledge of numbers of birds ringed each year and how many of these were recovered in different years, the most likely values of year- or age-specific survival and recovery rates can be calculated. Computer programs like MARK do this iteratively, by testing various combinations of values for the parameters to find the combination of parameter values that would be most likely to generate the data at hand.

As can be seen in the example above, with four years of recovery, reporting rate can be estimated for all these four years, but survival rate can only be estimated for the first three years, since the estimate of survival rate in a certain year is based on those individuals that survive this year but are recovered in a later year. This is the reason why in some models discussed in this study, reporting rate is estimated for the years 1989-98 while survival rate can be estimated only for the years 1989-97.

The most general model would be one in which each age class has its own survival and recovery rates each year. To produce meaningful estimates, such a model would require huge amounts of data. However, simpler models can also be constructed that combine age effects and time effects, e.g. a model where for each time step separate survival and recovery rates are estimated for the youngest age class and the older birds.

The task for the researcher is to find the model that is most suitable for the data set at hand. Model selection is important, because different models applied to the same data set may sometimes produce very
different survival estimates. Hence, for estimates to be reliable, we must be confident that the model is appropriate for the data. The model chosen should be both biologically plausible and statistically supported by the data.

Model selection in the context of mark-recapture studies is discussed in detail by Lebreton et al. (1992) and developed further by Andersson et al. (1994), and the same principles are applicable to the analysis of ring recovery data.

Two statistics are important in selecting the right model. One is called c-hat, and is a measure of goodness-of-fit. The value for c-hat may be high if the model does not fit the data, or if the data themselves violate general assumptions of the modelling approach, e.g. the assumptions that individuals are identical and independent. Ideally, c-hat should be 1. In practice, it often ranges from 1 to 3. Andersson et al. (1994) recommend that a model should be dismissed if c-hat exceeds approximately 4.

The other important statistic is AIC (or modifications of AIC), which is a measure of how parsimonious a model is. AIC is the deviance of a model plus twice its number of identifiable parameters. The deviance is minus two times the log-likelihood of a model. Complex models with many parameters generally have lower deviance than comparable simpler models. The model with the lowest AIC is the model in which the model structure and the number of parameters best account for the significant variation present in the data.

Andersson et al. (1994) discuss modifications of AIC, and recommend the use of one correction term for small sample sizes, giving the statistic AICc. They also recommend a correction for values of c-hat that exceed 1 by calculating quasi-AICc (QAICc). The programme MARK calculates QAICc, so we based our model selection on this recommended statistic.

When c-hat exceeds 1, the standard errors and confidence intervals for the estimated survival and recovery rates should also be corrected for this. A higher c-hat leads to wider confidence intervals around the estimates.
Long-term study of mortality in the common guillemot in the Baltic Sea

The population of common guillemots in the Baltic Sea was nearly extinct at the end of the 19th century. Following legal protection of these seabirds and their breeding sites, the Baltic population has recovered, and it numbers about 45,000 at present.

This report follows up the fate of common guillemots that were ringed in Sweden, mainly on the island of Stora Karlsö in the southern Baltic proper, during the 20th century. Nearly 43,000 guillemots were ringed from 1912 to 1998, and 6% of these have been recovered. The results from this unique, long-term set of data show that half of the recovered birds were found entangled in fishing gear.