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Breeding biology and population dynamics of a colonial seabird: The Razorbill

A long-term study of an expanding Razorbill colony on Græsholmen in the central Baltic Sea, 1983-2011

Peter Lyngs*

(Med et dansk resumé: Ynglebiologi og populationsdynamik hos en kolonirugende havfugl: Alken – et langtidsstudie af en ekspanderende alkekoloni på Græsholmen i den centrale del af Østersøen, 1983-2011)

*) Peter Lyngs passed away on 14. November 2019 only 12 days after his submission of the present monograph. We have done our best to produce it according to his wishes and spirit.

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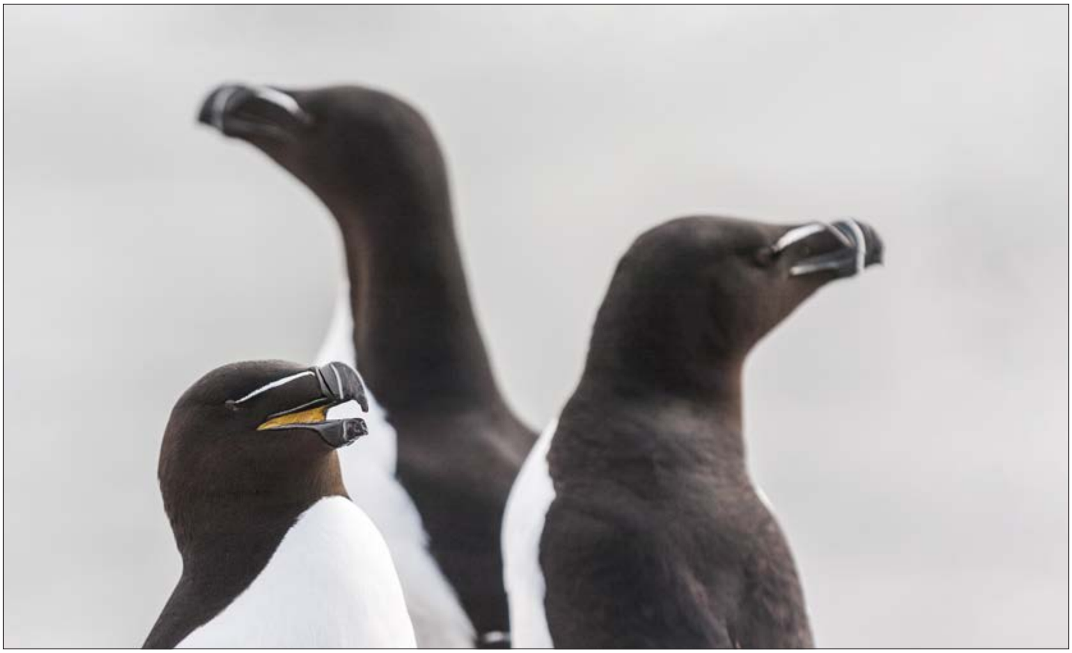

Abstract

This paper presents the results of a 29-year study (1983-2011) of the biology and population dynamics of Razorbills *Alca torda* breeding on Græsholmen in the central Baltic Sea. During the study years, the breeding population increased from c. 250 pairs in 1983 to 1200 pairs in 2011 (380%). Though variable, the mean annual survival was high (93-95%) for breeding adults, as was the overall survival of immature birds (57.7% up to the age of four years) returning to breed on Græsholmen. Mean age of first breeding was 4 years, but around 23% of the birds started to breed when 3 years old. First and second year birds visited the colony regularly but did not breed. Generally, older females laid larger eggs earlier in the breeding season and had a higher breeding success than females breeding for the first time. Overall, breeding success averaged 71-75% in seven study plots. Mean hatching date was 19 June (23 May – 6 August). Fledging chicks were recorded in the period 22 June – 15 August and the mean fledging age was 19 days. Chicks fledging early in the season were significantly larger and heavier than late fledging chicks, but no difference was found in post-departure survival. Sprats *Sprattus sprattus* were the main food (90%) supplied to the chicks. Average rate of non-breeding among adult birds with previous breeding experience was 3%. Average divorce rate was 14.5% and was highest (26%) among the youngest and lowest (3.1%) among the oldest breeding birds. Around 50% of the ringed chicks returning to breed on Græsholmen did so in their natal subcolony. Once settled, local nest-changes over the years occurred among 44% of the birds, but <2% moved to a completely different subcolony. Some young birds, perhaps a few percent, emigrated to other Razorbill colonies, mainly in the Baltic. Inter-colony movement of immature birds was a regular feature, and 37 Razorbills ringed as chicks in other Baltic countries were resighted on Græsholmen, 15 of these as breeders. Most of the adult breeding birds from Græsholmen wintered in the southern Baltic, while some first and second year birds entered the Kattegat and the North Sea.

Key-words: Razorbill, *Alca torda*, breeding biology, population dynamics, survival, demography, Græsholmen, Baltic Sea

Contents

Introduction

The Razorbill *Alca torda* is a stocky, black and white fish-eating seabird, an alcid of the Alcini tribe. Its closest extant relatives are the Common Guillemot *Uria aalge* and the Brünnich's Guillemot *Uria lomvia*. The Razorbill, which starts to breed at the age of 3-6 years, displays high site fidelity and has a single-egg clutch that may be replaced if lost. The egg is large, constituting about 10-15% of adult body mass. After hatching, the chick can thermoregulate at an age of about nine days (Barrett 1984a). The Razorbill has biparental care, but 2-3 weeks after hatching, the male follows the chick out to the sea, caring for it alone until it becomes independent a month or so later. At the time of nest departure, the chick cannot fly and weighs around 25% of the adult (Nettleship & Birkhead 1985).

The Baltic Razorbill belongs to the large nominate subspecies *A. t. torda*, which elsewhere primarily breeds in colonies along the coasts of northern Norway, western Russia, western Greenland, and eastern North America. Smaller and more numerous, the subspecies *A. t. islandica* breeds northward from northern France, the British Isles, the Faeroe Islands, and Iceland which holds the largest part of the total world population (Lloyd 1976a, Nettleship & Evans 1985, Hipner & Chapdelaine 2002).

This study is the first long-term study of the Baltic Razorbill and one of the most detailed studies of the species worldwide. By coincidence, the study covered a period of 29 years of continuous colony growth, where the breeding population on Græsholmen increased from about 250 pairs in 1983 to at least 1200 pairs in 2011. When the study was initiated in 1983, the main purpose was to record the size of the breeding population and collect information on breeding success. However, the introduction of triangular metal rings on Græsholmen in 1986 opened new possibilities. Using telescopes, these rings were easy to read in the field, which made it possible to record several demographic factors. From 1987, the aim of the study was simply to collect as much data as possible given the equipment and time available.

In many ways, the study on Græsholmen was old-fashioned: telescopes, metal rings, rulers, scales, portable hides, notebooks and a lot of time were the main instruments used. In addition, the study was primarily driven by enthusiasm, as little funding was received through the years. For a number of reasons, the study was terminated after the 2011 season. Still, spending 29 seasons with the Razorbills was a remuneration in itself. Additionally, this study presents information on breeding bi-

The middle of the breeding bird sanctuary of Græsholmen (the Grass Islet) with the inhabited islands of Christiansø og Frederiksø seen in the background.

ology and demography that only becomes available through long-term studies such as survival, age at first breeding, mortality of immature birds, divorce rate and site fidelity.

Throughout the text, SM-Figs and SM-Tabs refer to figures and tables found in the Supplementary Material published as an appendix on the net (see address in the end).

Study area

Situated 18 km northeast of Bornholm in the central Baltic Sea, Græsholmen (55°19’N, 15°11’E) is the second largest island in the archipelago of Ertholmene (often referred to as Christiansø after the main island which together with Frederiksø is inhabited; Fig. 1). Græsholmen is 425 by 293 m, covers an area of 89 700 m² (nine ha) and has a coastline of c. 2000 m. The central part of the island forms a plateau c. 9 m a.s.l. with 12 m as the highest elevation (Fig. 2). The surrounding sea depths range from 20 to 120 m and the water is brackish (0.8% salinity). Due to the low salinity, only relatively few fish species occur around Ertholmene, with sprat *Sprattus sprattus*, herring *Clupea harengus* (apparently mostly older age-classes), cod *Gadus morhua,* sandeel (mostly *Ammodytes tobianus),* goby (mostly black goby *Gobius niger)* and blenny *Zoarces viviparus* as the most numerous species. Occasionally, large schools of sprat surface during the day around the archipelago in June – mid-July, sometimes within a few metres of the coast.

In June 1926, Græsholmen was declared a fully protected bird reserve and all public admittance, including a 100 m zone of sea around the island, was banned (Lyngs 1992). Regular counts of breeding birds on Græsholmen started in 1925. Since then, the bird fauna has undergone marked changes: in the 1920s and 1930s the most numerous species were Common Eider *Somateria mollissima*, Common Gull *Larus canus* and Lesser Black-backed Gull *Larus fuscus*, while the dominating species during the present study were Herring Gull *Larus argentatus*, Common Guillemot and Razorbill (Tab. 1). The Common Guillemots on Græsholmen typically started breeding two weeks earlier than the Razorbills. Razorbills apparently colonised Græsholmen around 1910-1920 (Paludan 1947). The breeding population increased rapidly, and 318 active nests were found in 1939. After the severe winters of 1939-40 and 1941-42, the population was reduced to some 75 pairs (Paludan 1947), slowly increasing to about 250 pairs by 1983 (Lyngs 1992).

Græsholmen is a flat granite island with many areas of boulders. The vast majority of the Razorbills

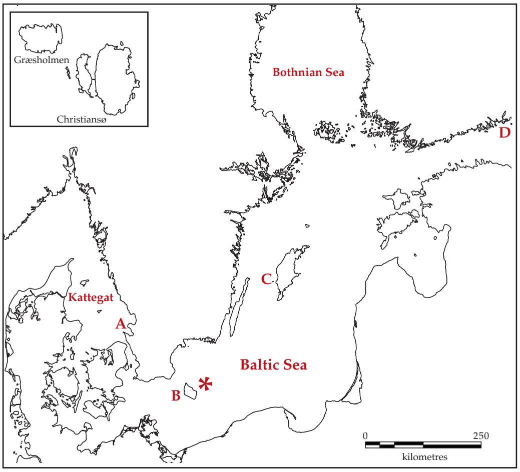

Fig. 1. Location of Græsholmen (star) in the central Baltic Sea. Insert shows the three main islands in the Ertholmene archipelago. Localities mentioned in text: A = Hallands Väderö (Sweden; SE), B = Bornholm (Denmark; DK), C = Stora Karlsö (SE), D = Aspskär (Finland; SF). *Græsholmens (stjerne) placering i Østersøen* (Baltic Sea). *Det lille kort viser de store øer blandt Ertholmene. I teksten nævnes følgende lokaliteter: A = Hallands Väderö (Sverige), B = Bornholm, C = Stora Karlsö (Sverige), D = Aspskär (Finland).*

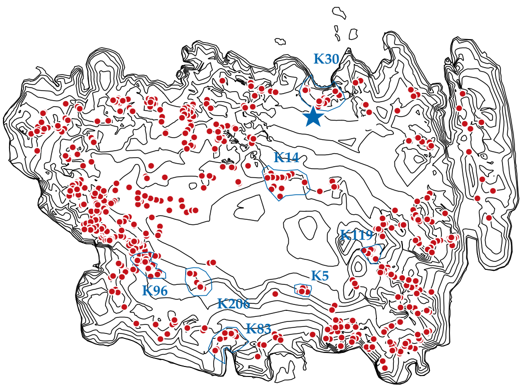

Fig. 2. Map of Græsholmen showing position of the main study-plot K30 (blue star = permanent hide) and six plots used for recording breeding success 1987-2007. Red dots denote the distribution of Razorbill nests 1996. The island extends 425 by 293 m. Contours are at 1 m intervals. *Kort over Græsholmen med de mest brugte studieområder. K30 er det vigtigste, og den blå stjerne viser placering af et permanent skjul her. Desuden ses yderligere seks studieområder, hvor ynglesuccesen blev undersøgt 1987-2007. Røde prikker viser fordelingen af alkereder i 1996.*

Tab. 1. Population estimates of the most numerous seabirds breeding on Græsholmen, 1925-2015, given as the approximate number of pairs per decade. Data from Lyngs (1992) and https://chroe.dk/viden-data.
Bestandsudvikling hos de talrigest ynglende havfugle på Græsholmen 1925-2015. Data fra Lyngs (1992) og https://chroe.dk/viden-data.

Species	**1925**	**1935**	**1945**	**1955**	**1965**	**1975**	**1985**	**1995**	**2005**	**2015**
Common Eider *Somateria mollissima*	200	500	1000	850	600	700	700	450	200	200
Common Gull *Larus canus*	5000	5000	350	5	0	0	0	0	0	0
Lesser Black-backed Gull *Larus fuscus*	300	600	1000	1100	300	50	7	7	5	2
Herring Gull *Larus argentatus*	25	200	700	2500	4500	11.000	5500	8000	8400	5500
Great Black-backed Gull *Larus marinus*	0	0	0	0	0	0	1	6	17	30
Common Guillemot *Uria aalge*	0	50	250	600	1000	1200	1500	2000	2500	4300
Razorbill *Alca torda*	50	250	70	100	110	150	325	580	890	1500

were breeding in crevices between or under boulders; of 1227 nests, 3% were completely in the open, 43% between boulders, and 54% under boulders or other cover (including under human artefacts since old fish boxes and pallets washed ashore were also used to provide sheltered nesting sites). The mean elevation a.s.l. of 1202 nests was 5.4 ± 2.2 m (1.1–11.7 m).

During the Razorbill study, some 5000-9000 pairs of Herring Gulls also bred on Græsholmen. Though most of the predation during nest-time (of eggs and chicks) were done by Herring Gulls, the Razorbills generally coped well with the Herring Gulls, and won many of the interspecific conflicts. When fledging, the chick was accompanied by its adult male all the way to the sea and predation from large gulls, especially the Great Black-backed Gull *Larus marinus*, constituted the main threat to the fledging chick. A few adults (5 found) were also killed by Great Black-backed Gulls as well as by other Razorbills (4 found; immatures intruding into a nest with only one exit were caught by the owner).

Influenced by the high number of breeding birds, the vegetation on Græsholmen was generally low and dominated by nitrophilous herb species, mainly *Holcus lanatus* and *Atriplex prostrata* (Abrahamsen *et al.* 1993).

A population of more than a thousand pairs of Lesser Black-backed Gulls on Græsholmen in the middle of the 20th century has decreased to just a few pairs in recent years.

Methods and material

This study of the Razorbills of Græsholmen was initiated in 1983 and terminated in 2011. Fieldwork was usually carried out from early April to mid-August, with most of the work done in June-July (Tab. 2 and 3; see also Appendix Tab. 1-2 for details on the material). Of the 4197 h used in the field 1984-2011, 2290 (55%) were used for resightings in the years 1989-2011. These work hours are fieldwork only and do not include transportation, painting of nest numbers in autumn, paperwork etc.

During 1983-2008, all Razorbill nests found were marked by a large red number (e.g. 96A), painted near the entrance of the nest. As this paint rarely lasted more than four years, it was refreshed during autumn at least every third year. In 2009-2011, only nests in the study plot K30 were numbered and painted. Using a theodolite, Niels-Christian Clemmesen and Peter Lyngs (PL) mapped all nests including height a.s.l. to an accuracy of 2 cm (centre of nest) in 1990-91. In the following years, the positions of new nests were established by triangulation. All marked and new nests were visited at least 1-5 times during the breeding seasons of 1983-2008 and their contents noted.

In 1985, the main study plot K30 (Fig. 2) was established and in 1990, a permanent hide was erected there. This study plot (a subcolony numbering 10 active nests in 1985 and 52 in 2011) was followed closely through the years, and records were taken of breeding success, adult survival, divorces etc. Every year, practically all chicks and many of the new adults entering the plot were ringed, and some older adults were re-ringed. K30 was a coastal boulder plot of 621 m², c. 40 m wide and 18 m broad. Two large loafing areas situated some 35 m NW (C30) and NE (C29) from the permanent hide were much used by the birds from K30 (see Appendix section Græsholmen).

Six other study plots were used in 1987-2007 to monitor breeding success (Fig. 2) and visited 5-10 times per season. In these plots, a chick was considered fledged if it disappeared from the nest at an age and/or stage of development at which it would be expected to have fledged. Fledging is here defined as when the chick leaves the nest not to return (though, in a strict sense, fledging does not take place before the chick gains its ability of flight a month or so later out at sea). In this paper, breeding success is expressed as the success (chicks fledged) per pair laying. When referring to specific cases of breeding (e.g. age at first breeding), the status was always confirmed by the presence of an egg or chick in a nest.

Captured birds were weighed to the nearest 2-5 g with a spring balance (300 g balance for chicks, 1 kg for adults) and wing length (flattened and straightened) was measured to the nearest mm with a metal ruler. The maximum length and width of eggs were measured to the nearest 0.1 mm using Vernier callipers. PL measured all eggs, adult birds and c. 98% of the chicks. The birds were ringed with a metal ring, and from 1986 triangular rings were used with the address of the Danish Bird Ringing Centre stamped on top of the ring and a large identification number stamped on both sides. To reduce the chance of these rings falling off, all triangular rings used on chicks were fitted with a small lump of wax inside the ring, adjusting the amount used to the actual size of the chick's leg (Lyngs 2006).

Hatching dates were either directly observed or estimated (in 94% of the cases) by comparing chick wing length (WL, mm) to the wing length of 49 chicks measured daily from hatching to fledging, calculating the chick age in days as $0.3 \times WL - 4.5$ ($r^2 = 98\%$). An index of egg volume was calculated (length × width²) and used as a proxy for egg size (see Birkhead and Nettleship 1984), while fresh egg weight was calculated as 0.48 × egg volume index + 10.51 (see Hipfner & Chapdelaine 2002). A total of 756 eggs were photographed from the blunt end and from the side. These eggs were balanced on a Kodak Gray Card with appropriate cut holes and then put back in the nest.

Adult birds were sexed by observing copulations and in some cases by deducing the sex after a mate change. For birds ringed as chicks and seen in later years, the age is given as xY, i.e. the number of years after ringing. Thus, 3Y refer to birds three years old, while 3Y+ refer to birds three years old or older. Birds of unknown age ringed as adults (i.e. 4Y+) in the colony are referred to as adults. The term cohort is used for all chicks ringed in a given year.

Græsholmen was considered as one large colony with several more or less well-defined subcolonies. Practically every subcolony on Græsholmen had one or more loafing areas, typically large patches of flat rock or large stones, used by birds breeding close by (mostly by off-duty breeders during brooding and early chick rearing), non-breeders (primarily immature birds) and 'guests' (breeding birds from other areas on short visits). Most of the resighting effort was done at these loafing areas and at K30, where considerable amounts of time were also used to assign ringed birds to a nest and/or partner.

Using 20×60 zoom telescopes, all resightings of rings (Tab. 4; see also Appendix Tab. 2) were done by PL, Lars Abrahamsen (LA) and Gitte Christensen Lyngs (GCL), either from portable hides or from the permanent hide at K30. With telescopes, the triangular rings could be read at ranges of up to 60 m, but the resighted birds were typically 10-30 m away or less. For each resighted bird, a minimum of ring-number, date and resighting spot (nest/loafing area) was noted. During the fieldwork, social behaviour of the Razorbills was not recorded systematically, but over the years, several notes were recorded in the Razorbill database. To minimise resighting errors (misreading of one or more of the inscribed digits on a 'field-readable' ring; see Lavers & Jones 2008), the following precautions were taken: observers were instructed that only absolutely certain ring readings were recorded and even then that the ring had to be read at least twice with 100% certainty during the session; additionally, all ring-readings were entered in a custom-made database the same day as the observations were made – this database instantly provided information of the ring in question, i.e. if used, if the bird had been reported dead, if the bird had been re-ringed and when last resighted; if the actual record then appeared dubious, it was either deleted or used only if the bird was resighted again.

As mentioned, 2290 hours were spent exclusively for resightings of rings on Græsholmen. Additionally, to search for emigrated Razorbills ringed as chicks on Græsholmen, two other Baltic colonies were visited: Stora Karlsö (Sweden; 57° 17′ N, 17° 57′ E) 6-11 May 1996 (PL, GCL), 8-11 June 1997 (PL, GCL, LA) and 13-16 July 2000 (PL) and Haverören (Aspskär, Finland; 60° 15′ N, 26° 25′ E) on 12-15 June 1996 (PL).

Græsholmen had to be reached by dinghy, and the dinghy had to be anchored in one of the small bays while working on the island (see Appendix section Græsholmen). We soon realized that the best weather to work in was wind of 6-13 m/s from the S-WNW sector and preferably overcast with no rain. High winds from the NW-ESE sector produced a high sea which washed around the island, mak-

Tab. 2. Fieldwork (h) per month on Græsholmen, 1984-2011. Resighting = hours of total work used for resighting Razorbills.
Feltarbejde angivet i antal timer (Total work) *pr. måned på Græsholmen, 1984-2011. Resighting = heraf timer brugt til aflæsning af ringmærkede Alke.*

Month	Total work	Resighting
April	137	137
May	254	152
June	1412	607
July	2267	1329
August	127	58
Total	4197	2283

Tab. 3. Overview of the Razorbill data from Græsholmen, 1983-2011.
Oversigt over alke-materialet fra Græsholmen, 1983-2011.

	N
Chicks ringed	8467
Adults ringed	185
Number of resightings	27219
Individual birds resighted (indv.)	3153
Sexed birds	342
Recoveries	343
Chicks, wings and mass	3792
Chicks, wings measured	7588
Fledging chicks (w + m)	188
Eggs measured	3076
Food loads	359

Tab. 4. Resightings of Razorbills ringed on Græsholmen, 1983-2011.
Aflæsninger (resightings) *på Græsholmen 1983-2011 af Alke ringmærket hhv. som unger* (chicks) *og voksne* (adults) *på Græsholmen og som unger i udenlandske kolonier.* Resightings = *totalt antal aflæsninger,* Indvidual birds resighted = *totalt antal aflæste individer.*

	Ringed	Resightings	Individual birds resighted
Ringed as chicks	8467	24629	2986
Ringed as adults	184	2590	167
Ringed abroad	Not available	87	38
Total		27306	3191

ing it impossible to anchor. In low winds (< 4 m/s), the Razorbills were very reluctant to return to their sites after disturbance, so we avoided working on Græsholmen in calm weather. The large number of breeding Herring Gulls on Græsholmen (Tab. 1) was a mixed pleasure. Since the Razorbills clearly used the gulls as 'extended vision', any disturbance affecting the gulls also affected the Razorbills – but this also meant that when the gulls relaxed, the Razorbills did so too. On windy days, when sitting quietly in a portable hide to do resightings, we often had numbers of Razorbills a few meters from the hide – and occasionally a gull sitting on top of our (hidden) head.

Overall, the study can be divided into three main (but overlapping) periods: finding of nests and ringing of chicks (1983-1989), resighting and checking of nests on the whole of Græsholmen (1990-2008) and resighting and checking of nests at K30 (1990-2011). Harald Kjøller recorded daily sea surface temperatures at Christiansø in 1985-2000. All times are given as local summertime (UTC+2), and all distances as loxodrome distances. Means are given ± the standard deviation (SD). Statistical tests were done using SigmaPlot 12 (Systat), Prism 6 (GraphPad) and R 3.5 (R Core Team 2018). Wherever applicable, two-tailed tests were used.

Rune S. Tjørnløv estimated the survival of Razorbills from the whole of Græsholmen for the period 1986-2009 based on the life histories of 7932 birds ringed as chicks and 147 birds ringed as adults. Throughout the study period, 285 and seven birds ringed as chicks and adults, respectively, were recovered dead. In addition, survival of Razorbills within the intensively surveyed study plot K30 was also estimated during the period 1986-2011 using 100 individuals ringed as chicks and 23 individuals ringed as adults. Survival was estimated using the Burnham model parameterization as implemented in program MARK, i.e. true survival (S), recapture probability (p), recovery rate (r) and site fidelity (F) (White & Burnham 1999). To accommodate for estimation of survival of several age-classes (a), a classical age-structure was implemented for all parameters, which allowed immature individuals to age. For the whole of Græsholmen, 1Y, 2Y and 3Y survival were estimated to be constant over time, whereas adult survival was estimated to be time dependent. Due to the much smaller sample-size from the study plot K30, the same set of parameters were all estimated to be constant over time. As immature individuals are much less likely to occur in the colony than adult breeders, three immature age-classes (1Y, 2Y and 3Y) were specified for recapture probability. The recovery probability (r) was structured with either one or two age-classes (1Y and 2Y+) because the probability of 1Y individuals to be found dead and reported was assumed to be different from the older age-classes. A similar presumption was applied to the site fidelity parameter (F). Different constraints i.e. constancy (c) and a linear Trend (T) were implemented with specific parameters, and Akaike's Information Criterion (AICc) adjusted for small sample sizes was then used to select between competing candidate models (Burnham & Anderson 2002). The option 'simulated annealing' was used for a more robust optimization procedure, and 'Profile likelihood' was used to derive meaningful confidence limits around boundary values. The Median C-hat method was applied to test for a potential lack of fit of the most general model. Confidence limits of model estimates were then adjusted accordingly.

Rune S. Tjørnløv then combined survival estimates from the best model with other demographic data in a population matrix model with a pre-breeding census that tracks the Razorbill population just before the start of the breeding season (Caswell 2006). The transition matrix of the population model was structured as a Lefkovitch matrix with five age-classes to accommodate age-related differences in survival and reproduction, for instance in age-specific breeding probabilities (see section Natal fidelity). The proportion of breeders was estimated from data collected on Græsholmen: 2Y: 0%, 3Y: 23%, 4Y: 76% and 5Y: 97%. The hatching success from Græsholmen was 0.73 per breeding female, which implies that not every egg hatched. Rune then computed age-specific fertility parameters based on the proportion of breeders in each age-class, first year survival, hatching success, and the sex ratio (assumed to be equal) at birth. Finally, we conducted a life-table response experiment by using the lower and upper confidence limits of breeding success and age-specific survival to explore how changes in these parameters could affect the population growth rate.

Typical nest site in study area K30 with nest ID painted on a rock.

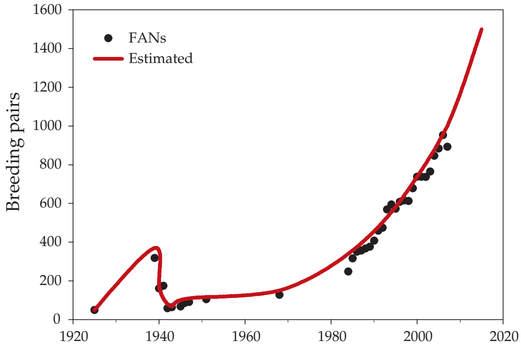

Fig. 3. Development of the breeding population of Razorbills on Græsholmen, 1925-2015. FANs = Found Active Nests.
Udviklingen i ynglebestanden af Alke på Græsholmen, 1925-2015. FANs = *Fundne aktive reder.*

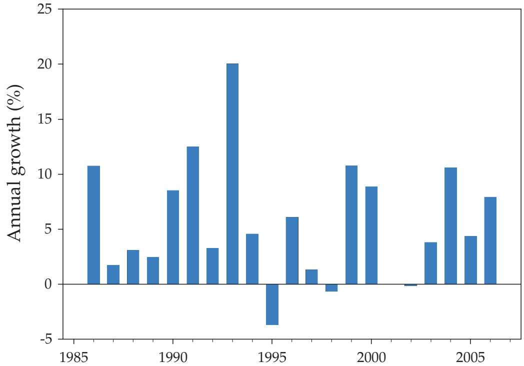

Fig. 4. Annual growth in the number of active Razorbill nests on Græsholmen, 1986-2006.
Årlig vækst (Annual growth) *i antallet af fundne aktive Alkereder på Græsholmen, 1986-2006.*

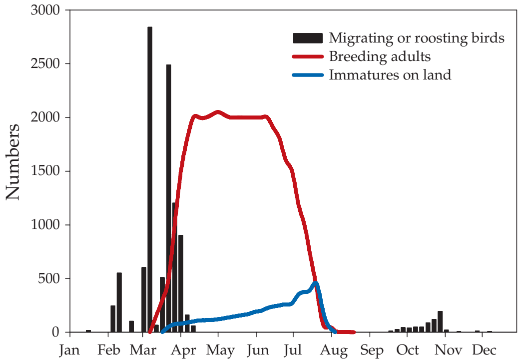

Fig. 5. The yearly phenology of Razorbills on Græsholmen and in surrounding waters. The phenology of breeding adults and of immature birds (1-3Y) visiting the colony is based on a population of 1000 breeding pairs. Migrating or roosting birds are estimates from the seas around Ertholmene.
Den årlige fænologi blandt Alkene på Ertholmene. De adulte (Breeding adults) *og yngre fugles (1-3Y) (Immatures on land) fænologi er baseret på en bestand på 1000 ynglepar.* Migrating or staging birds = *Trækkende og rastende fugle omkring øerne.* Number = *antal.*

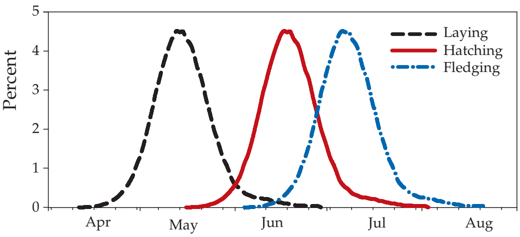

Fig. 6. Schematic representation of the breeding phenology of Razorbills on Græsholmen, 1983-2011.
Model over ynglefænologien for Alkene på Græsholmen, 1983-2011. Laying = *æglægningsperiode,* Hatching = *klækningsperiode,* Fledging = *udflyvningsperiode.* Date = *dato.*

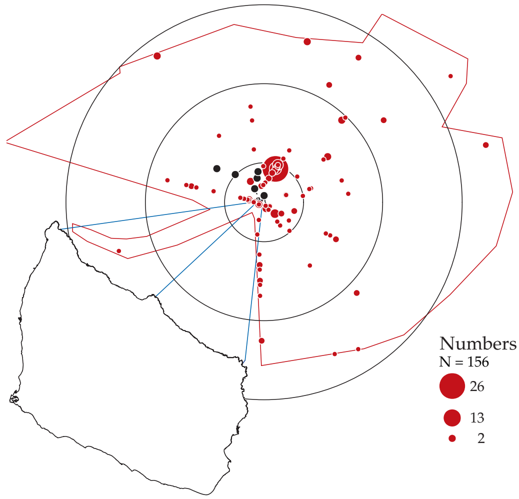

Fig. 7. Presumed diurnal foraging area of Razorbills breeding on Græsholmen. Red dots denote positions and numbers of birds recorded on ship-based transects covering the area indicated by red lines. Black dots denote six feeding positions of a bird fitted with a directional recorder. Thin circles at sea indicate 5, 15 and 25 km distances from Græsholmen. Strait blue lines denote diurnal ferry-routes to Ertholmene.
Formodet fourageringsområde i dagtimerne for Alke ynglende på Græsholmen. Røde prikker viser positionen og antallet af Alke observeret fra skib under sejlads inden for de røde linjer. De sorte prikker viser seks positioner, hvor fugle forsynet med dataloggere fouragerede. Tynde cirkler på havet angiver 5, 15 og 25 km afstand fra Græsholmen. Rette blå linjer angiver sejlruterne til og fra Christiansø, hvorfra der er set efter Alke.

Results

Population development

From the early 1980s, the Razorbill breeding population on Græsholmen increased rapidly (Fig. 3). When the study started in 1983, c. 250 pairs were breeding, while the number of found active nests increased by 160% during 1986-2006. In 2007, the breeding population reached an estimated 1000 pairs, and 1200 pairs in 2011. The overall growth 1983-2011 was estimated at 380%. During the intensive search for nests in 1986-2006, the number of found active nests on average increased by 5.5% per year (Fig. 4), ranging from -3.7% to 20%. The negative growth in 1995 was caused by an oil spill incident in June 1994, whereas another oil spill in June-July 2003 had no discernible influence on the population development (Lyngs 2005). In 1996, Razorbills colonised Bornholm and in 2014, the first Razorbills (two pairs) started to breed on the inhabited island of Christiansø.

Phenology

Based on observations of migrating and staging Razorbills recorded in the bird-database of Christiansø Field Station 1976-2018 as well as breeding data from this study, a model of Razorbill occurrence and breeding phenology on Ertholmene is presented here:

Few Razorbills occurred around the islands during winter (Fig. 5). Depending on the weather, more and more birds arrived from late January-February, but numbers varied considerably from day to day. In March and April in particular, high numbers occurred on some days, occasionally exceeding the numbers of local breeding birds – probably due to the arrival of birds *en route* to northern Baltic colonies. The breeding birds started to visit the colony from early – mid-March, and from early April their presence in the colony was more or less permanent.

In the average year (Fig. 6), the first eggs were laid around 24 April (15 April – 5 May) and mean laying occurred around 15 May (9-28 May). Mean hatching took place around 19 June (13 June – 2 July) and mean fledging was around 8 July (2 –21 July). The last fledgings occurred around 11 August (1 –21 August), and the period between the first laid egg and the last fledging chick spanned 109 days (97-119 d; 128 d using extreme dates from all years).

By early August, most of the Razorbills had left the colony and by mid-August, only a few late breeders remained (latest observation 28 August). The first migrating Razorbills were recorded in late September (the earliest on 17 September), but apart from a small peak of migrating birds in mid-late October, relatively few birds were seen in autumn and early winter. In contrast to the Common Guillemot (Lyngs 1992), no Razorbills were recorded visiting the colony during winter.

Foraging areas

This basic information of the diurnal and nocturnal foraging areas used by the Razorbills breeding on Græsholmen was extracted from a combination of different datasets (data-loggers, recoveries and ship-based counts) collected during the study years. In June 1998, nine breeding Razorbills were fitted with data loggers operating for 48 h. Data were retrieved from seven birds (for details, see Benvenuti *et al*. 2001). In 41 foraging trips (33 diurnal and 8 nocturnal), the birds returned from the foraging sites either in a single nonstop flight or in two flights (34 and 7 cases, respectively). The distance of the return flights to Græsholmen were calculated by dividing the time spent flying by an assumed flight speed of 58 km/h. From a bird fitted with a directional recorder, the approximate positions of the main foraging sites in seven trips (six diurnal and one nocturnal) were obtained. Additional information on nocturnal foraging came from 13 recoveries of breeding Razorbills (five dead, eight released alive), caught during late April – early July 1990-1999 in salmon drift nets operated at night by local fishermen. Five of these had precise recovery coordinates, while eight were reported as caught 'some six nautical miles' east of Christiansø.

In 2008, seven standardised (Webb & Durinck 1992) ship-based diurnal transects in calm weather were carried out between 17 May – 31 July. Each transect lasted an average of 11:30 h and consisted of 9-10 legs reaching as far as up to 29 km from Græsholmen, to cover in total an area of 1565 km².

On the diurnal transects, 55% of the Razorbills resting at sea were noted at <5 km, 31% at 6-15 km and 13% at 16-23 km off Græsholmen (Fig. 7). This distribution fits well with the data from the loggers and with non-systematic visual observations carried out during more than 30 years of ferry crossings to Christiansø, in suggesting that Razorbills were considerably less frequent to the south of the colony than in other directions (pers. obs.). For birds equipped with data loggers, the median foraging distance for birds on short trips (79% of the diurnal trips) was 3.3 km and for birds on long trips was 12.2 km (Tab. 5). Around 12% of the time of the diurnal trips was spent flying, 74% resting on the sea, 14% diving; the deepest dives were recorded around midday. Overall, the data loggers recorded 1202 dives, of which 47% took place at 1-10 m depth, 16% at 10-19 m, 14% at 20-29 m and 24% at 30-43 m depth (Benvenuti *et al*. 2001).

With a median distance of 13.5 km (range 9-35 km) recorded by the data loggers, nocturnal foraging apparently took place further off Græsholmen than diurnal foraging (Fig. 8), as was also suggested by the distribution of the nightly recoveries (Fig. 9). Nocturnal trips on average lasted 8.9 h (N = 7). Around 80% of the time was spent resting on the sea, and 12% diving. Most of the diving was concentrated around sunset and sunrise and stopped completely around midnight; the diving depth never exceeded 20 m during these periods (Benvenuti *et al*. 2001). This pattern reflects the vertical migration and dispersion of the sprat, the primary food of the Razorbills on Græsholmen. Baltic sprat typically form schools during the day, which at dusk migrate vertically upward and disperse. At dawn, the reverse happens (Nilsson *et al*. 2003).

Tab. 5. Calculated flight distance from main foraging sites to Græsholmen of Razorbills fitted with data loggers in 1998.
Beregnet flyveafstand fra fourageringsområderne til Græsholmen hos Alke udstyret med dataloggere i 1998.
Short diurnal trips = *korte ture om dagen.* Long diurnal trips = *lange ture om dagen.* Nocturnal trips = *ture om natten.* Median distance = *gennemsnitsafstand.* SD = *standardafvigelse.* Range = *korteste og længste tur.* Duration = *varighed.*

	Short diurnal trips	Long diurnal trips	Nocturnal trips
Median distance (km)	3.3	12.2	13.5
SD	1.9	3.0	6.3
Range (km)	0.8-8.8	10.5-19.4	9.1-26.9
Duration (min)	75	230	535
N	26	7	8

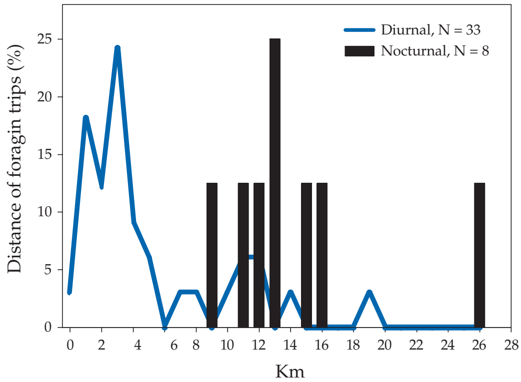

Fig. 8. Distribution of ranges (%) of 33 diurnal and eight nocturnal foraging trips of Razorbills breeding on Græsholmen, 1998.
Den procentuelle fordeling af længderne på 33 fourageringstogter (Distance of fouraging trips) *om dagen* (Diurnal) *og otte om natten* (Nocturnal) *for Alke ynglende på Græsholmen, 1998.*

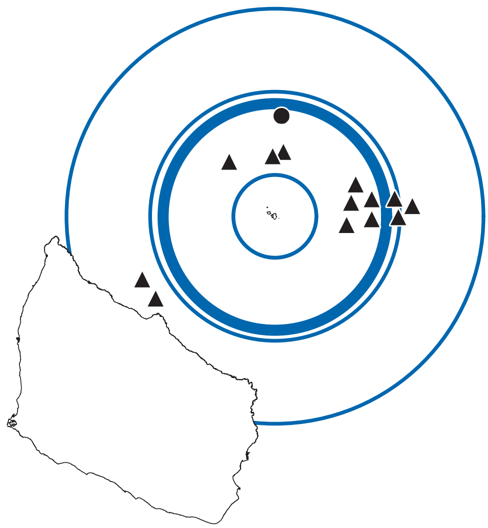

Fig. 9. Nocturnal foraging area of Razorbills breeding on Græsholmen. The black dot denotes nocturnal feeding position of a bird fitted with a directional logger, black triangles denote recoveries of 13 Razorbills caught during night in salmon drift nets. Thin circles indicate 5, 15 and 25 km distances from Græsholmen, while the thick circle indicates the mean distance (13.5 km) of eight nocturnal foraging trips recorded by data-loggers.
Natligt fourageringsområde for Alke ynglende på Græsholmen. Sorte prikker viser positionen af en fugl forsynet med en datalogger med kompas. Sorte trekanter viser positionen af 13 Alke fanget om natten i laksedrivgarn. Tynde blå cirkler viser afstande på 5, 15 og 25 km fra Græsholmen. Den tykke blå cirkel viser gennemsnits-afstanden for otte natlige fourageringstogter registeret med datalogger.

The egg

General characteristics

A total of 3129 Razorbill eggs were measured during the study, including two runt eggs and 53 replacement eggs. The runt eggs (both from 2000) measured 49.0 × 33.6 mm (vol. 55.3 cm³) and 52.3 × 36.9 mm (vol. 71.2 cm³). Excluding these and measurements of eggs known to be replacements for eggs lost earlier in the season, the average egg measured 75.8 × 48.2 mm and had a volume of 175.9 cm³ (Tab. 6) – the smallest egg (vol. 124.4 cm³) was 48.9% smaller than the largest (vol. 243.5 cm³) and both these eggs hatched. The distribution of the calculated egg volume was almost perfectly bell-shaped (Fig. 10). The calculated mean fresh egg weight was 94.9 ± 7.4 g (70.2 – 127.4), corresponding to 13.4 ± 1.0% (9.9-18%) of adult body mass.

Replacement eggs

On average, replacement eggs were significantly smaller in all measurements than the first egg (Tab. 7). The calculated egg volume was 14.9 ± 9.2 cm³ (i.e. 8.2%) smaller.

Variation of eggshell coloration and pigmentation

Egg colouration and pigmentation varied considerably on Græsholmen (Fig. 11), but the most common type of egg was off-white with specks and patches of black, grey and brown pigment (Fig. 12).

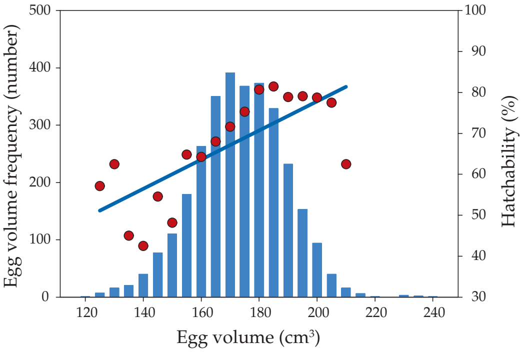

Fig. 10. Proportion of eggs hatching (Hatchability) in relation to egg volume (cm³) based on 3072 measured eggs (egg volume frequency), Græsholmen 1984-2008. The blue trend line indicates the relationship between the proportion of eggs hatching (Hatchability) and egg volume. *Klæknings-andel* (Hatchability) *i relation til æggenes volumen* (cm³) *baseret på 3072 målte æg* (egg volume frequency), *Græsholmen 1984-2008. Den blå trendlinje angiver forholdet mellem andelen af klækkede æg* (Hatchability) *og æggenes volumen.*

Inspired by the sentence "*The pattern of pigmentation on eggs laid by the same female in successive years was very similar*" in Lloyd (1976a), a total of 756 eggs (501 from K30) were photographed and analysed visually to establish if year-to-year comparisons of egg pigmentation patterns could be used to identify the female breeding in a given nest.

Tab. 6. Measurements of Razorbill eggs on Græsholmen, 1984-2011 (N = 3074).
Mål og volumen på alkeæg fra Græsholmen, 1984-2011 (N = 3074).

Variable	Mean ± SD	Median	Max.	Min.
Egg length (mm)	75.8 ± 0.29	75.9	87.1 (x 46.8)	62.7 (x 44.8)
Egg width (mm)	48.2 ± 0.16	48.1	55.1 (x 80.2)	41.9 (x 79.1)
Egg volume (cm³)	175.9 ± 15.42	176.1	243.5 (80.2 x 55.1 mm)	124.4 (68.2 x 42.7 mm)

Tab. 7. Characteristics of first (1) and replacement (2) Razorbill eggs on Græsholmen, 1984-2010.
Mål og volumen på det førstlagte æg og omlægsæg hos Alke fra Græsholmen, 1984-2010.

Variable	Mean ± SD	Median	Max.	Min.	N	t-test, P
1 egg length (mm)	75.7 ± 0.29	75.9	82.8	68.5	53	
2 egg length (mm)	73.6 ± 0.28	73.4	80.9	67.2	53	< 0.001
1 egg width (mm)	48.6 ± 0.16	48.3	53.0	45.7	53	
2 egg width (mm)	47.2 ± 0.17	47.5	50.3	42.0	53	< 0.001
1 egg volume (cm³)	179.2 ± 16.10	178.1	217.4	152.2	53	
2 egg volume (cm³)	164.3 ± 15.29	164.4	201.4	127.5	53	< 0.001

Fig. 11. Variation in colour and shell pigmentation of Razorbill eggs laid by 10 ringed females on Græsholmen - a selected series of more unusual eggs.
Variation i farve og skalpigmentering blandt Alkeæg fra Græsholmen – en serie af mere usædvanlige æg (udvalgte æg fra 10 hunner).

Fig. 12. Eggs from four female Razorbills with a commonly occurring colour and shell pigmentation (selected eggs and years from K30).
Alkeæg fra Græsholmen med almindelig farve- og skalpigmentering. Fra fire hunner (udvalgte æg og år fra område K30).

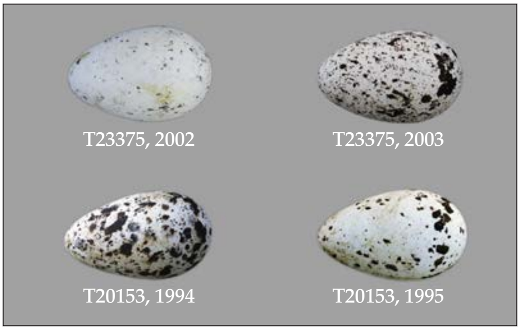

Fig. 14. Eggs from two female Razorbills from K30 with variable shell pigmentation. The eggs with the most extreme pigmentation differences were selected from records for six and 13 years, respectively.
Alkeæg fra to hunner i område K30. De mest forskellige æg udvalgt fra serier på henholdsvis seks og 13 år. Der ses indimellem stor variation i pigmenteringen fra år til år.

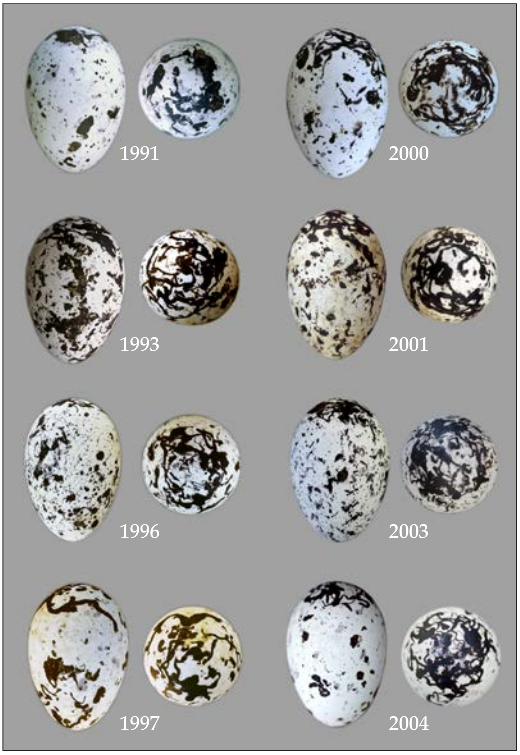

Fig. 13. Eggs from female 5037413 (hatched 1984) selected from eight years between 1991 and 2004.
Æg fra Alkehun 5037413 (klækket i 1984), 1991-2004 (udvalgte år, område K30).

Fig. 15. Eggs from four mothers and their daughters (selected years, K30).
Æg fra mødre og deres døtre (udvalgte år, fra område K30).

From this analysis, the following results appear:
1. Some females laid eggs where the pattern of pigmentation was very similar over many years (Fig. 13).
2. Other females laid eggs where the pattern of pigmentation occasionally was highly variable (Fig. 14).
3. Egg colour and pigmentation were not inherited from mother by daughter (Fig. 15)
4. Replacement eggs generally had the same pattern of pigmentation as the first egg (Fig. 16).
5. Two-egg clutches were the product of two females competing for the same nest (Fig. 17).

Overall, the main conclusion was that though many females were easily identified from year to year based on egg pigmentation patterns, others were not – and that ringing of the birds generally was a better method for individual recognition. However, in study plots with a high number of ringed birds (such as K30), egg photos proved useful for identifying new un-ringed females (Fig. 18) in the year they entered the plot as breeders.

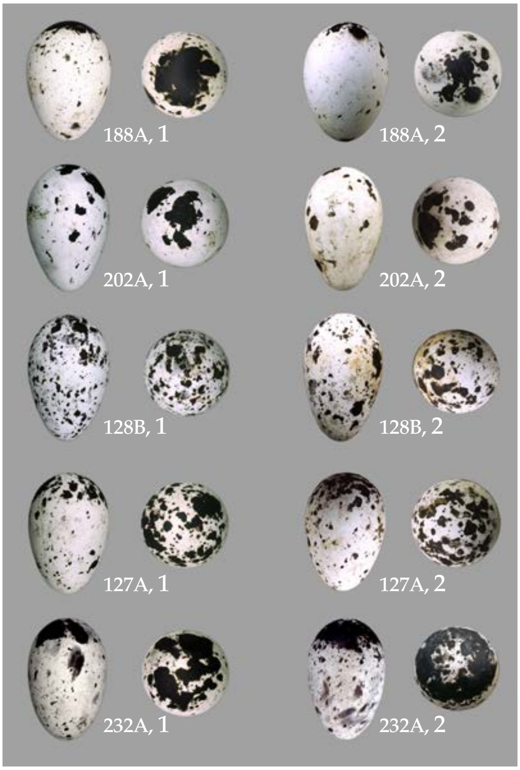

Fig. 16. First egg and replacement egg from five relaying females, Græsholmen, 1990.
Første (1) og andet æg (2) fra fem hunner, der omlagde i 1990.

Fig. 17. Eggs from two different females found in nest 38F in 1993. Female T21524 left and female 5037446 right.
Æg fra to forskellige hunner fundet i samme rede, 38F, 1993. Hun T21524 til venstre og hun 5037446 til højre.

Egg volume and fate of egg

Eggs that hatched had a significantly greater volume than eggs that did not, and chicks that fledged came from eggs with a significantly greater volume than chicks that did not fledge (Tab. 8, Fig. 10).

Egg volume and time of hatching

The mean egg volume decreased during the last part of the hatching period (July; Fig. 19), and eggs hatching in May-June had a significantly greater volume than eggs hatching in July (Mann-Whitney U = 123341.0, P = <0.001). On average, the earliest hatched chicks (end May – early June) came from the largest eggs, but there was no significant difference in egg volume between these and eggs from mid to end June (Mann-Whitney U = 118955.5, P = 0.134).

Tab. 8. Calculated egg volume in relation to fate of the egg, Græsholmen, 1984-2008.
Beregnet rumfang af æg sammenholdt med æggets skæbne, Græsholm, 1984-2008.

Variable	Mean Vol. ± SD	Median	Max.	Min.	N	Mann-Whitney U, P
None-hatched eggs	170.8 ± 15.95	170.4	212.8	128.1	691	
Hatched eggs	177.6 ± 14.87	178.0	243.5	124.4	2217	<0.001
Hatched, chick not fledged	171.6 ± 17.46	173.1	243.5	124.4	295	
Hatched, chick fledged	178.6 ± 14.11	178.9	238.1	126.1	1852	<0.001

Fig. 18. Eggs laid in nest 38K by Female T22509 in 2003-2009 and an unringed female in 2010.
Æg fundet i rede 38K, 2003-10. Hun T22509 i perioden 2003-09, ikke-mærket hun i 2010.

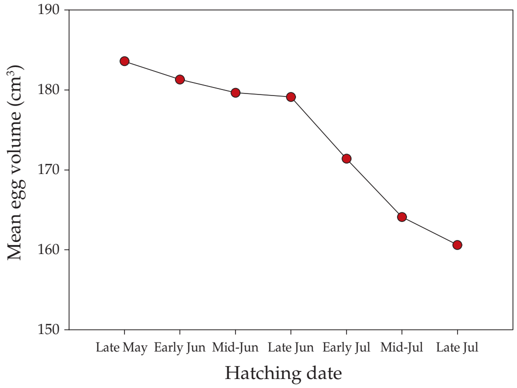

Fig. 19. Relation between egg volume and hatching date for Razorbills on Græsholmen (N = 1885).
Sammenhæng mellem æggets størrelse (rumfang; Mean egg volume*) og klækkedato* (Hatching date) *hos Alke fra Græsholmen (N = 1885).*

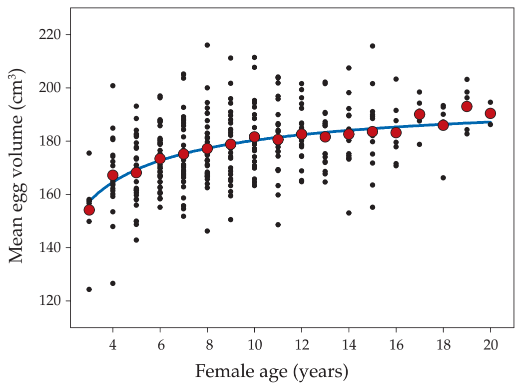

Fig. 20. Egg volume in relation to female age for Razorbills on Græsholmen. Red dots = mean egg volume, blue line = nonlinear regression fitted using standard curves (four parameter logistic). Based on measurements of 337 eggs from 85 females of known age.
Sammenhæng mellem hunners alder i år (Female age, years) *og deres ægs rumfang* (Mean egg volume) *for Alke på Græsholmen. Røde prikker = gennemsnitligt rumfang, blå kurve = non-lineær regression. Baseret på 337 æg fra 85 hunner med kendt alder.*

Egg volume and female age

Comparing the egg volume of 16 eggs laid by females breeding for the first time at an age of 3-5 years (3Y 3 eggs, 4Y 9 eggs, 5Y 4 eggs) showed no significant difference (one-way ANOVA, $F = 0.285$, $P = 0.756$). Among these 16 birds, the egg volume on average increased by 5.1% (4.6-5.3) the year after the first breeding attempt and on average by 1.8% the following two years.

Egg volume increased during most of the female's life, with the largest increase occurring during the first 10 years of life. Among 337 eggs laid by 85 females of known age (3-20 years), the mean egg volume increased by 8.5% from age 3 years to age 4 years, by 1.4% annually from age 5-10 years, and by 0.5% annually for age 11-20 years (Fig. 20; see also Appendix Tab. 3). However, there was considerable individual variation: some females consistently laid larger eggs than others and an annual variation in the egg volume was recorded (Fig. 21). There was also annual variation in egg volume recorded at the colony level. For example, 332 eggs measured in 1993 had a significantly lower volume than 300 eggs measured in 1996 (t-test, $t = -2.959$, $P = 0.003$).

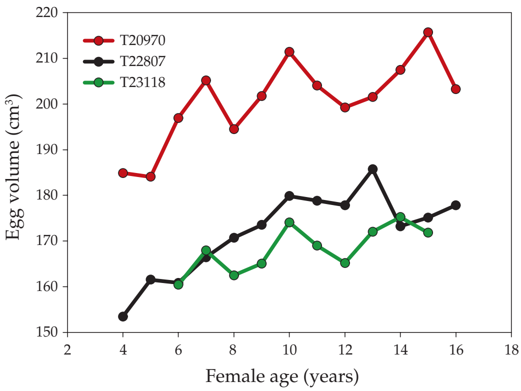

Fig. 21. Egg volume of three ringed female Razorbills: T20970, breeding for the first time in 1993, consistently laid large eggs, while T22807 and T23118, breeding for the first time in 1999 and 2001, respectively, consistently laid smaller eggs.
Æggets rumfang (Egg volume*) hos tre alkehunner fulgt gennem flere år. T20970 (ynglede første gang 1993) lagde altid store æg. T22807 (ynglede første gang 1999) og T23118 (ynglede første gang 2001) lagde altid mindre æg.* Female age *= hunnens alder.*

The chick

Hatching

Hatching chicks were recorded from 23 May – 6 August (mean hatching date 19 June; Appendix Tab. 4) with an average span of 56 d (43-69) between the

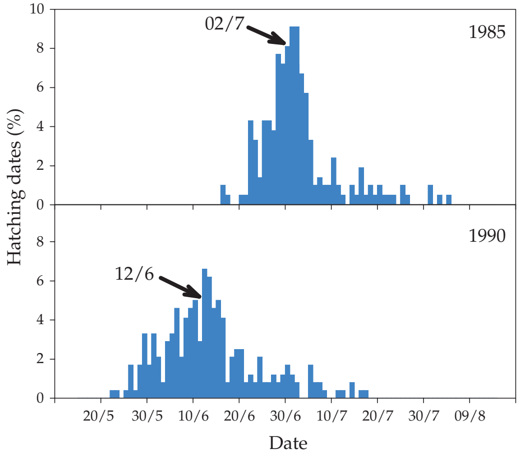

Fig. 22. Daily distribution of hatching dates (%) for Razorbills on Græsholmen in a late year (1985, mean date 2 July; N = 207) and an early year (1990, mean date 12 June; N = 241).
Fordeling af klækningsdatoer (Hatching dates) *i procent på Græsholmen et sent år (1985, gennemsnitsdato 2. juli; N = 207) og et tidligt år (1990, gennemsnitsdato 12. juni; N = 241).* Date = *dato.*

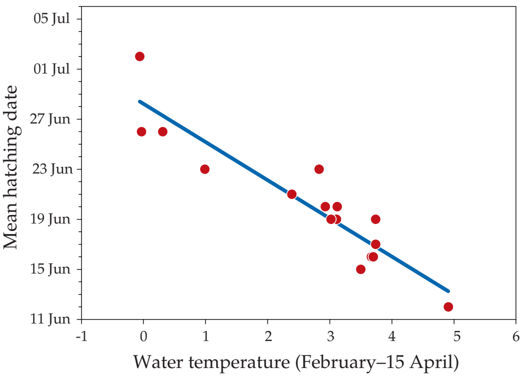

Fig. 23. Correlation between average sea surface temperature at Christiansø in February – 15 April 1985-2000 and mean hatching dates for Razorbills on Græsholmen.
Sammenhæng mellem havoverfladens gennemsnitstemperatur (Sea temperature) *ved Christiansø i perioden februar til 15. april 1985-2000 og gennemsnitlig klækningsdato* (Mean hatching date) *samme år for alkeæg på Græsholmen.*

earliest and latest hatching. Mean annual hatching date varied considerably between years, with 19 d between the earliest and the latest year (1990 vs 1985; Fig. 22). The right-skewed pattern of hatching seen in these two years occurred in all years, presumably due to some pairs laying replacement eggs. Most of the variation in mean annual hatching dates was coupled with the average sea surface temperature in late winter-early spring (1 February – 15 April) in as much as low sea temperatures in this period were followed by late mean hatching dates and vice versa (Spearman $r = 0.9104$, $P = < 0.001$; Fig. 23). During 1985-2000, the average sea temperature in the three years with the latest mean hatching dates (1985-1987) was 0.1 °C, while in the five years with hatching dates close to the overall mean hatching date (1991-1993, 1997, 1999) it was 3.2 °C, and in the earliest hatching date year (1990) it was 4.9 °C. It is, however, most likely that the sea temperature was a proxy for the accessibility of the Razorbills' main prey – sprats – for which no data are available.

Food

During the study, 359 food items, all fish, were recorded (Tab. 9 and Appendix Tab. 5); 189 were found inside sheltered nests with chicks and 170 were observed during actual feedings. Clupeids (most likely all sprats, see Lyngs 2001) constituted 89.7%, sandeels 7.5% and gobies 2.8% by number of the fish recorded. Using the median mass (Tab. 10) obtained for 18 sprats (12 g) and three sandeels (14 g) and a mass of 2 g for gobies (based on an estimated length of 4-6 cm of the observed fish), and assuming the same size distribution for all 359 fish, clupeids (sprats) constituted 90.7%, sandeels 8.9% and gobies 0.4% by wet weight. Using the calorific content of sandeels (6.5 kJ/g wet weight) and sprat

Tab. 9. Species and numbers of fish brought to Razorbill chicks on Græsholmen, 1985-2009.
Art og antal af fisk bragt til Alkeunger på Græsholmen, 1985-2009.

	Observed	Found in nest	Total
Clupeid	153		153
Sprat		169	169
Sandeel	7	20	27
Goby	10		10
Total	170	189	359

Ninety percent of the food supplied to chicks were sprat.

Tab. 10. Length and mass of fish found in Razorbill nests on Græsholmen 1985-2000.
Længde og vægt af henholdsvis brisling og tobis fundet i alkereder på Græsholmen 1985-2000.

	Sprat	Sandeel
Median length (mm)	131.5	181
Range	28-151	80-200
N	48	6
SD	24.8	19.0
Median mass (g)	12	14
Range	8-16	13-15
N	18	3
SD	1.8	1.0

(10.9 kJ/g wet weight) presented by Harris & Hislop (1978), the mean value for sandeels becomes 91 kJ per fish and the calorific content per sprat is 131 kJ. If all clupeids delivered were sprats, then about 94% of the total calorific content of the 349 clupeids/sandeels recorded was derived from these species.

Except for a load with two small gobies and one load with two sprats, all observed feedings consisted of one fish carried crossway in the bill (98%; average load 1.02 fish). The daily schedule of adult birds fitted with data loggers in 1998 suggested that the chicks received on average 4-5 feeds per day (Benvenuti *et al*. 2001). When opportunity was there, however, the number of daily feeds could be higher. For example, when a large school of sprats surfaced just offshore from K30 in the afternoon of 16 June 2009, some chicks were fed every 16 min (for up to five times).

Intraspecific kleptoparasitism (see Lavers & Jones 2007) was only observed on very few occasions, whereas Herring Gulls regularly tried to steal the fish from Razorbills returning with food.

Growth

The growth of 49 chicks hatched 13 June – 8 July was measured daily in 1985 (15 chicks), 1986 (19 chicks) and 1994 (15 chicks; see Appendix Fig. 1 and Appendix Fig. 2). Mean body mass of 44 chicks weighed within 24 h of hatching was 65.8 ± 5.7 g (52 – 78 g); the mass was strongly correlated to egg volume (Spearman r = 0.782, P = <0.001). From d 4 to d 13 (Fig. 24), the gain of body mass averaged 11.3 g/d (7.8%/d), and from d 14 to d 21 the gain was 2.8 g/d (1.9%/d). The increase in wing length (Fig. 25) averaged 3.1 mm/d (5.4%/d) during d 4-13 and 3.0 mm/d (5.3%/d) during d 14-21; the highest increase occurred during d 7-18 (3.6 mm; 6.2%/d). Although the chicks from 1994 were lighter (on average 9.7%) than those from 1985-86 (Fig. 26), the difference between years was not significant (Mann-Whitney U = 172.0, P = 0.227).

When the body mass of 1035 chicks having a wing length of 55-70 mm (i.e. aged 12-15 days and after the main period of rapid growth) measured in

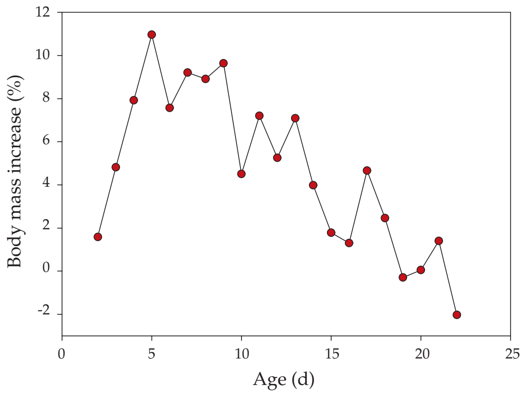

Fig. 24. Daily percent increase in body mass increase of 49 Razorbill chicks on Græsholmen, 1985-86 and 1994.
Daglig forøgelse af vægt (Body mass increase) *i procent blandt 49 Alkeunger på Græsholmen, 1985-86 og 1994.* Age (d) = *alder (dage).*

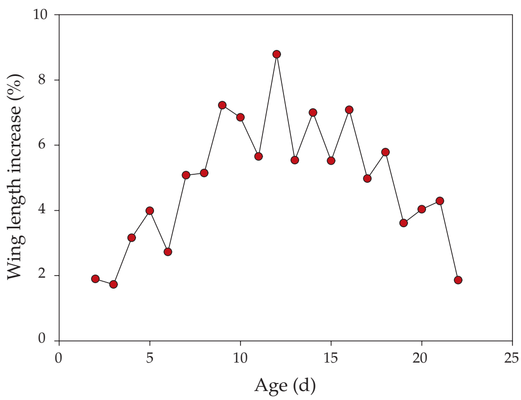

Fig. 25. Daily percent increase in wing length of 49 Razorbill chicks on Græsholmen, 1985-86 and 1994.
Daglig forøgelse i vingelængde (Wing length increase) *i procent blandt 49 alkeunger på Græsholmen, 1985-86 og 1994.* Age (d) = *alder (dage).*

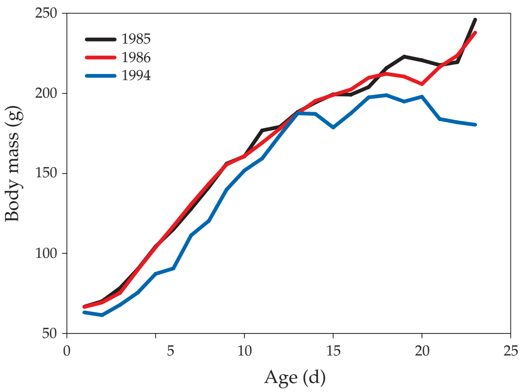

Fig. 26. Daily mean body mass of Razorbill chicks on Græsholmen, 1985 (N = 15), 1986 (N = 19) and 1994 (N = 15).
Daglig vægt (Body mass) *af alkeunger på Græsholmen, 1985 (N = 15), 1986 (N = 19) og 1994 (N = 15).* Age (d) *= alder (dage).*

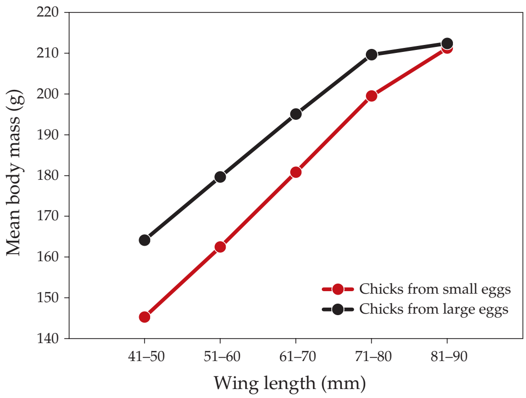

Fig. 27. Mean body mass in relation to wing length of Razorbill chicks from small (red dots) and large (black dots) eggs on Græsholmen, June-July 1985-2008 (N = 750).
Gennemsnitlig kropsvægt (Mean body mass) *i relation til vingelængde* (Wing length) *blandt Alkeunger fra små (røde prikker) og store (sorte prikker) æg på Græsholmen, juni-juli 1985-2008 (N = 750).*

June-July 1990-1999 was compared, no annual difference could be found (Kruskal-Wallis, H = 16.197, 9 df, P = 0.063).

A dataset consisting of 1419 records from June-July 1985-2008 with known egg volume, hatching date and a subsequent measure of chick wing length and body mass was analysed to examine whether chicks from small eggs were on average lighter than chicks from large eggs (Tab. 11). The data were grouped according to wing length and sorted on egg volume. For the three groups with more than 300 records, the records of the 100 smallest and the 100 largest egg volumes were used for comparisons. For the two groups with 130 and 98 records, respectively, the first and last 50 and 25 records were used, in total 750 records. For wing lengths between 41-80 mm (corresponding to chicks c. 10-17 d of age), chicks hatched from small eggs were significantly lighter than chicks hatched from large eggs (Fig. 27). For the oldest chicks (wing length 81-90 mm, c. 21 d of age, i.e. close to fledging), however, no difference was found. Likewise, no significant difference in the egg volume/body mass relation were found among fledging chicks (see section Fledging below).

Tab. 11. Mean egg volume in relation to wing length (age) of Razorbill chicks on Græsholmen, June-July 1985-2008 (N = 750). MA = mean age in days, MEVS = mean volume of small eggs, MEVL = mean volume of large eggs, MEMAS = mean mass of chicks from small eggs, MEMAL = mean mass of chicks from large eggs. Mann-Whitney U test used in all volume and mass comparisons.
Gennemsnitlig ægvolumen sammenholdt med vingelængde (Wing), som udtryk for deres alder, blandt Alkeunger på Græsholmen, juni-juli 1985-2008 (N = 750). MA = gennemsnitsalder i dage, MEVS = gennemsnitlig ægvolumen af små æg, MEVL = gennemsnitlig ægvolumen af store æg, MEMAS = gennemsnitsvægt af unger fra små æg, MEMAL = gennemsnits vægt af unger fra store æg. Mann-Whitney U test benyttet ved sammenligninger.

Wing (mm)	MA (d)	MEVS (cm^3)	MEVL (cm^3)	U	P	MEMAS (g)	MEMAL (g)	U	P	N
41-50	10	163,9	191,0	0	<0.001	149,0	167,5	699,5	<0.001	100
51-60	12	162,1	193,0	0	<0.001	162,5	179,5	2744,5	<0.001	200
61-70	15	161,1	195,2	0	<0.001	185,5	196,0	3140,5	<0.001	200
71-80	17	165,8	194,9	0	<0.001	200,5	210,5	3793,5	<0.003	200
81-90	21	167,1	193,2	0	<0.001	210,0	217,0	296,5	0,764 (ns)	50

Plumage variation

For 3294 large chicks, the plumage variation of cheeks, chin and throat were noted: of these chicks, 112 (3.4%) were classed as 'white throated' (resembling adult winter plumage, see Hudson 1984 and Birkhead & Nettleship 1985), 642 (19.5%) as 'intermediate', and 2540 (77.1%) as 'black throated' (resembling adult summer plumage). Additionally, for 640 of these chicks, the variation of the white line running from the eye to the base of the upper mandible of 266 (28.3%) chicks was classed as '3' (well-defined, see Birkhead & Nettleship 1985), for 237 (25.2%) chicks this line was classed as '2' (incomplete), for 241 (25.6%) chicks the as '1' (trace), and for 196 (20.9%) chicks as '0' (absent).

Fledging

In this section, a fledging chick is defined as a chick of known age and at the stage of development where it would be expected to have fledged, and could be found in the nest one day but not the following day. Thus, 211 fledging chicks were recorded in the period 22 June – 15 August (span 55 d; 21 years).

Overall, the median fledging age was 19 d (range 13-27 d; N = 202). Chicks fledging in the early part of the fledging period (end June – early July; fledging age 21 d) were, however, on average four days older than chicks fledging in the late part (August; fledging age 17 d, see Appendix Tab. 6). The difference in fledging age between these two periods was significant (t-test, t = 6.639, 112 df, P = <0.001). On average, chicks fledging late in the season had shorter wings and lower body mass than early fledging chicks (Tab. 12, Fig. 28). Thus the mean wing length at fledging in August (71 mm) was significantly

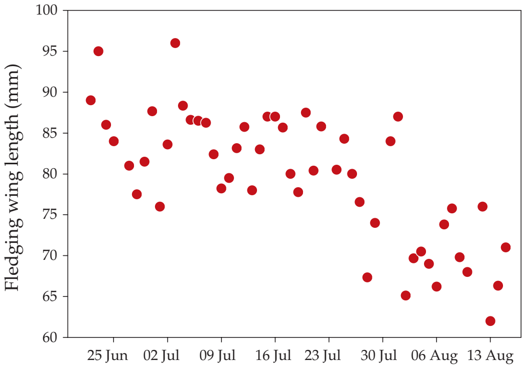

Fig. 28. Wing length of fledging Razorbill chicks in relation to fledging date, Græsholmen 1984 -2005 (N = 193). *Vingelængde* (Fledging wing length) *hos udgangsunger i relation til udgangsdatoen, Græsholmen 1984-2005 (N = 193).* Date = *Dato.*

shorter (15%) than in June (84 mm; t-test, t = 5.851, 56 df, P = <0.001) and the mean body mass in August (160 g) was significantly lower (25%) than in June (214 g; t-test, t = 6.024, 56 df, P = <0.001).

Though on average lighter, no significant difference in body mass was found when comparing the fledging mass of chicks from the smallest 25 eggs with the mass of chicks from the largest 25 eggs from a group of 96 chicks with known egg volume and fledging mass (Tab. 13). Fledging mass of chicks subsequently resighted on Græsholmen on average was slightly higher than among fledging chicks not seen again, but the difference was not statistically significant (χ^2 = 0.305, 4 df, P = 0.989; Tab. 14). Likewise, no significant difference in the resighting probability was found among chicks fledging in different parts of the season (χ^2 = 3.994, 4 df, P = 0.407).

Tab. 12. Mean wing length and body mass of Razorbill chicks fledging in different periods of the breeding season, Græsholmen 1984 -2005 (N = 193).
Gennemsnitlig vingelængde og kropsvægt hos udgangsunger på forskellige tidspunkter af ynglesæsonen, Græsholmen 1984-2005 (N = 193).

	Late June	Early July	Mid- July	Late July	August
Mean wing length (mm)	84	84	83	79	70
Min. length (mm)	76	70	62	65	56
Max. length (mm)	98	96	95	96	90
Mean mass (g)	214	206	205	186	157
Min. mass (g)	170	130	136	114	92
Max. mass (g)	251	260	270	251	222
N	17	47	39	38	52

Tab. 13. Egg volume in relation to fledging mass for Razorbills on Græsholmen, 1985-2005 (N = 50). Group A = smallest eggs, group B = largest eggs.
Ægvolumen (Egg vol.) i relation til udgangsvægten (Fledging mass) hos alkeunger på Græsholmen, 1985-2005 (N = 50). Group A = mindste æg, group B = største æg.

Group		Mean	SD	t-test,	P=
A	Egg vol. small (cm^3)	160.8	8.3		
B	Egg vol. large (cm^3)	196.0	7.0	-16.234, 48 df	<0.001
A	Fledging mass (g)	190.6	34.0		
B	Fledging mass (g)	205.5	27.8	1.6698, 48 df	0.096 (ns

Tab. 14. Resighting rates and body mass of 158 Razorbills ringed as fledging chicks in different periods of the breeding season, Græsholmen 1986-2005.
Aflæsningsrate og kropsvægt hos 158 Alke ringmærket som udgangsunger i forskellige perioder af ynglesæsonen, Græsholmen 1986-2005.

	Resighted		Not resighted		
Period	Mean mass	N	Mean mass	N	Resighted %
Late Jun	216	11	210	6	64.7
Early July	217	24	197	23	51.1
Mid - July	209	15	194	14	51.7
Late July	187	11	175	18	37.9
Early August	169	15	154	21	41.7

Recoveries

Among 8107 birds ringed as chicks in 1986-2011, 284 (3.5 %) were subsequently recovered, mostly reported as dead. In total, 121 (42.6%) of these were reported as caught in fishing gear, 82 (28.9%) were found as chick remains on Græsholmen (often as rings found in gull pellets), 62 (21.8%) were found dead on beaches, 17 (6%) were reported as oiled (11 during the oil spills of 1994 and 2003) and two (0.7%) as shot. Among the birds reported as caught in fishing gear, 63 (52%) were from just four years (1998-2001; 35 from Poland, 19 from Denmark, with 12 of the latter reported as rings found in a fishing harbour, and nine from other Baltic countries). Overall, the recoveries probably provide only little information on the fate of the birds; even among the 1989 cohort where 60% of the ringed chicks were subsequently resighted alive, only 3% were recovered while 37% of the birds were never reported in any way (see Appendix Tab. 7)

Full-grown Razorbills

Immature birds

In this study, immature Razorbills are defined as 1-3Y birds, i.e. birds less than four years old. On Græsholmen, no 2Y birds but several 3Y birds bred. The shape of the bill easily identified 1Y and 2Y birds visually (Appendix Fig. 3), whereas older birds in many cases were difficult or impossible to age visually due to individual variation of bill shape, including the number of vertical grooves. Based on resightings of ringed birds of known age, the phenological pattern of occurrence of 3Y birds was close to that of older age-classes (Fig. 29), with some notable differences, especially in latest part of the breeding period (August).

First year birds (1Y)

1Y birds on the water around Ertholmene were seen in low numbers from mid-April, while the first few birds actually on Græsholmen island were noted on 30 May. In the period 13 June – 2 August, 196 resightings of 164 birds ringed as chicks on Græsholmen were recorded. Practically all 1Y birds were resighted on loafing areas close to the coast (Fig. 30) and did not generally participate much in the social life of the Razorbills. 1Y birds from other Baltic colonies (three birds resighted) also visited Græsholmen – see section Intercolony movements.

Most of these birds (87%) were resighted between 20 June and 16 July (27 d; Fig. 29), i.e. from around mean hatching to early fledging (see Phenology, p 69). The majority (140; 83%) of 1Y birds were recorded only on a single day (Tab. 15), and only 5% (9) of the birds were resighted over a period spanning more than 10 d (13-24 d). Expressed as resighted birds (1992-2001) as a percentage of a given cohort, the proportion of 1Y birds ranged between 0.5% and 6.9% (Tab. 16).

During summer (May-July), recoveries of ringed 1Y birds (Tab. 17, Fig. 31) were widely scattered, ranging from the eastern North Sea and Skagerrak to the Finnish coast of the Bothnian Sea, and the mean distance of these birds from Græsholmen was 514 (49-906) km. In winter (November-April), most of the recoveries were from the southern Baltic Sea with a few from Kattegat (Fig. 32), and the mean distance of the birds from Græsholmen was 235 (18-380) km, significantly shorter (Mann-Whitney U = 186.5, P = 0.017) than during summer.

Second year birds (2Y)

On the water around Ertholmene, 2Y birds were seen from late March, with the first birds resighted on Græsholmen on 13 April. During the period 13 April – 8 August 2084 resightings of 1183 birds ringed as chicks on Græsholmen were recorded.

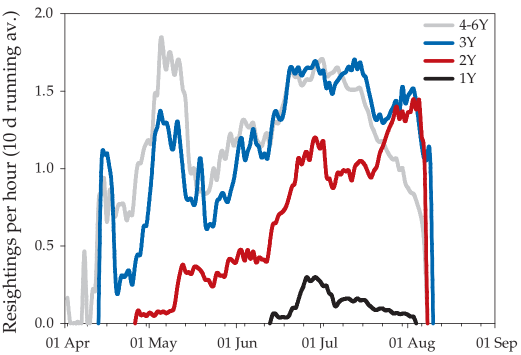

Fig. 29. Phenology of sightings of different age-classes of Razorbills on Græsholmen, 1988-2011, expressed as mean number (10 d running average) of resightings per hour of birds ringed as chicks. 1Y N = 196, 2Y N = 2084, 3Y N = 3156, 4-6Y N = 8878 resightings. See also Fig. 33.
Fænologien hos forskellige aldersklasser af Alke på Græsholmen, 1988-2011. Udtrykt som gennemsnitligt antal aflæsninger pr. time (Resightings per hour) *af fugle ringmærket som redeunger. 1Y N = 196, 2Y N = 2084, 3Y N = 3156, 4-6Y N = 8878 aflæsninger. Se også Fig. 33.*

Fig. 30. Spatial distribution of resighted 1Y and 2Y Razorbills ringed as chicks on Græsholmen. Red dots with green filling denote resighting locations of 1Y birds (N = 196 resightings of 164 birds), red dots denote resighting locations of 2Y birds (N = 1959 resightings of 1112 birds).
Rumlig fordeling af aflæste 1Y og 2Y Alke ringmærket som redeunger på Græsholmen. Røde prikker viser aflæsningssteder for 1Y-fugle (N = 196 aflæsninger af 164 fugle), røde prikker med grøn fyldning af 2Y-fugle (N = 1959 aflæsninger af 1112 fugle).

The observation hide at study area K30.

Though many (711; 60%) 2Y birds were recorded only on a single day, others were recorded throughout most of the breeding season (Tab. 15), and 27% (317) of the birds were resighted over a period spanning more than 10 d (11-98 d). The number of 2Y birds increased throughout the breeding season, reaching its maximum in late July – early August (Fig. 29). The percentage of a given cohort seen back at the colony as 2Y birds ranged between 3.9 and 35.7% (Tab. 16).

To test if 2Y birds staying for a long period were more likely to breed on Græsholmen in the following years than birds recorded only once, a group of birds (G1) with a span of >40 attendance days was compared to a group of randomly selected birds (G2) with only one attendance day. G1 consisted of 44 birds of which 33 were found breeding in subsequent years, and G2 consisted of 49 birds of which 30 were found breeding in subsequent years. The difference between the two groups was not statistically significant (Fisher's exact test, $P = 0.625$).

Contrary to 1Y birds, 2Y birds were resighted throughout the colony (Fig. 30) and did participate much more in the social life of the Razorbills. For example, copulations were recorded and in two cases two 2Y birds stayed together as a pair for more than 30 d while holding a nest site. No 2Y birds, however, were recorded breeding. 2Y birds from other Baltic colonies (12 birds resighted) also visited Græsholmen – see section Intercolony movements.

During summer (May-July) there were only four recoveries of 2Y birds (Tab. 17 & Fig. 31), three from the Baltic Sea and one from Kattegat, and the mean distance from Græsholmen was 343 (153-861) km. In winter (November-April), most of the 19 recoveries were from the southern Baltic Sea with a single bird from the Wadden Sea (Fig. 32), and the mean distance of these birds from Græsholmen was 244 (62-431) km.

Third year birds (3Y)

3Y birds were seen on the water around Ertholmene from at least mid-March. During the period 14 April - 14 August, 3156 resightings of 1519 birds ringed as chicks on Græsholmen were recorded. Though many (798; 53%) 3Y birds were recorded only on a single day, others were recorded throughout the breeding season (Tab. 15), and 36% (548) of the birds were resighted over a period spanning more than 10 d (11-108 d). The number of 3Y birds was highest in late June/July and remained high in early August, but otherwise the phenological pattern of occurrence was close that of older age-classes (Fig. 29). Expressed as resighted birds (1992-2001) as a percentage of a given cohort, the proportion of 3Y birds ranged between 24.9 – 42.7% (Tab. 16).

In total, 147 local 3Y birds were recorded breeding (nest with egg or chick found) and of these, 23 were sexed (10 females, 13 males). 3Y birds from other Baltic colonies (7 birds resighted, one breeding) also visited Græsholmen – see section Intercolony movements.

Seven 3Y birds were recovered during summer (May-July), all from the Baltic Sea (Tab. 17, Fig. 31), and the mean distance from Græsholmen for these birds was 265 (18-794) km. In winter (November-April), 11 of the 12 recoveries were from the southern Baltic Sea and a single bird was from the inner Danish waters (Fig. 32), and the mean distance of these birds from Græsholmen was 193 (20-313) km.

Tab. 15. Span of attendance days (d) of 1-3Y Razorbills ringed as chicks and subsequently resighted on Græsholmen, 1990-2011.
Tidsmæssigt spænd (Span) i antal opholdsdage hos 1-3Y Alke ringmærket som unger og senere aflæst på Græsholmen, 1990-2011.

Span (d)	1Y N	2Y N	3Y N
1	140	711	798
2-9	14	144	153
10-19	7	116	192
20-29	3	106	149
30-39		62	82
40-108		44	145
Total	164	1183	1519

Tab. 16. Return rates of 1-5Y Razorbills on Græsholmen 1992-2001, expressed as percentage of chicks ringed and seen in subsequent years.
Aflæsningsrater hos 1-5Y Alke på Græsholmen 1992-2001, udtrykt som procentdel af de ringmærkede unger, som i efterfølgende år blev aflæst på Græsholmen.

	1Y	2Y	3Y	4Y	5Y
1992	1.8	18.9	28.3	29.2	26.8
1993	2.1	23.0	42.7	47.5	38.5
1994	0.5	35.7	36.5	37.9	38.1
1995	4.7	17.8	33.8	38.0	39.7
1996	4.6	28.3	28.7	35.9	35.8
1997	3.0	35.6	24.9	22.5	25.6
1998	6.9	22.9	39.7	29.5	20.4
1999	6.7	20.5	38.9	40.9	32.5
2000	2.2	12.8	29.9	32.1	32.3
2001	4.3	3.9	27.9	23.4	26.5
Mean	3.7	21.9	33.1	33.7	31.6
Max	6.9	35.7	42.7	47.5	39.7
Min	0.5	3.9	24.9	22.5	20.4
SD	2.0	9.2	5.7	7.5	6.2

Tab. 17. Recoveries of Razorbills ringed as chicks on Græsholmen after 1980 (N = 197).
Genfund fordelt på årstider af Alke ringmærkede som redeunger på Græsholmen efter 1980 (N = 197).

	1Y	2Y	3Y	4Y+
Autumn (Aug - Oct)	15	9	4	5
Winter (Nov - Apr)	38	19	12	25
Summer (May - Jul)	17	4	7	42
Total	70	32	23	72

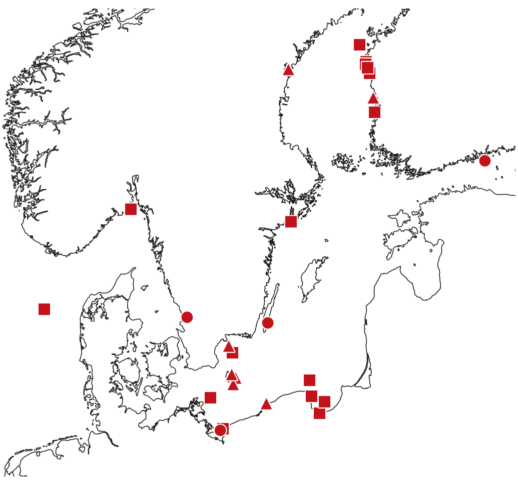

Fig. 31. Recoveries in May-July of 1Y (square), 2Y (dot) and 3Y (triangle) Razorbills ringed as chicks on Græsholmen.
Genfund i maj-juli af 1Y (firkant), 2Y (prik) og 3Y (trekant) Alke ringmærket som redeunger på Græsholmen.

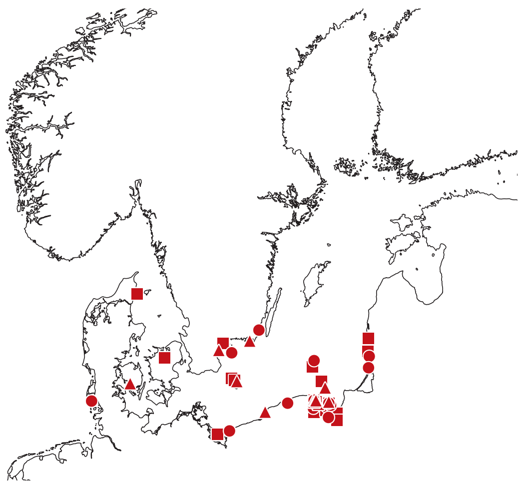

Fig. 32. Recoveries in November-April of 1Y (square), 2Y (dot) and 3Y (triangle) Razorbills ringed as chicks on Græsholmen.
Genfund i november-april af 1Y (firkant), 2Y (prik) og 3Y (trekant) Alke ringmærket som redeunger på Græsholmen.

Adult birds (4Y+)

During the period 2 April – 14 August, 21782 resightings of 2432 individuals ringed as adults and chicks and resighted as 4Y+ on Græsholmen were recorded (Fig. 33). The lowest numbers of resighted birds per hour of observation were recorded in the last half of April (just before laying started), and again on 13-26 May (around mean laying date; males more numerous than females). During the nesting period, one adult bird always guarded the nest, but some large chicks were left unattended for a couple of hours around sunrise while the adult departed to feed during the latest part of the chick-rearing period. The non-guarding partners mostly returned to the colony during 0700-1100 h and 1500-2100 h (Fig. 34). The daily schedule of birds fitted with data loggers in 1998 suggested that pairs of chick-rearing adults on average spent 6.2 h together in the colony between sunrise and sunset (Benvenuti *et al*. 2001). From mid-July to early August (during the main fledging period), the number of resighted adult females exceeded the number of males (Fig. 34 4Y+), which was a reflection of many females remaining in their subcolony a week or two after the male had departed to sea with the fledging chick.

Among 23 ringed and sexed pairs from K30 (1993-2005; 47 pair-years) where the fledging chick was seen back the colony in later years, the females on average remained in their subcolony 16 ± 11.4 days (-2 – 48 d, N = 47) after the male departed with the chick. Two males that lost their chick during fledging (chick known to be taken by Great Black-backed Gulls) remained 10-19 days longer than their female. Observations from K30 over the years showed that the females that stayed usually engaged in social associations ('summer flirts') with males that were not their partner of the year. Generally, these associations were temporary, involved one or more males, and lasted anything from a day to a week or two (though one association continued for three breeding seasons). Most of the males that participated in these non-sexual activities were either local failed breeders or young birds (2-4Y) that had not bred yet, but occasionally local males that still had a chick in the nest also participated. Five ringed females from K30 followed for 2×2 h on 19 & 24 July 2005 represent a typical example of this (Tab. 18): the females all bred with ringed males that had successfully led the fledging chick to the sea some 18 days (7-29 d) earlier; during the two watches, the five females spent their time with (six) males that were not their breeding partner, allopreening, walk-

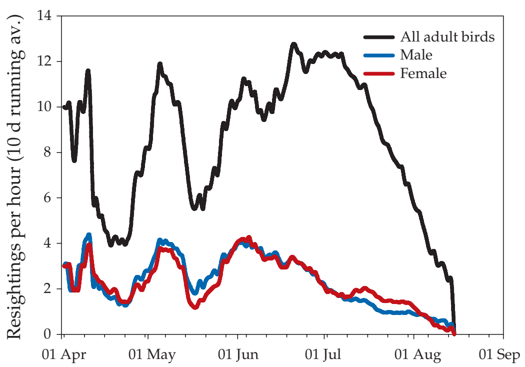

Fig. 33. Phenology of sightings of adult (4Y+) Razorbills on Græsholmen, 1988-2011, expressed as mean number (10 d running average) of resightings per hour of birds ringed as adults or chicks (black line, N = 21782 resightings) and of birds sexed as males (blue line, N = 4159 resightings) and as females (red line, N = 4587 resightings). See also Fig. 29.
Fænologien hos adulte (4Y+) Alke på Græsholmen, 1988-2011. Udtrykt som gennemsnitligt antal aflæsninger per time (Resightings per hour) *af fugle ringmærket som adulte eller redeunger (sort streg, N = 21782 aflæsninger), af hanner (blå streg, N = 4159 aflæsninger) og af hunner (rød streg), N = 4587 aflæsninger). Se også Fig. 29.*

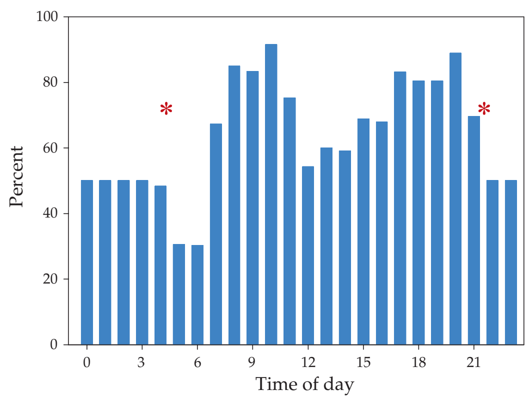

Fig. 34. Colony attendance (% of time) by chick-rearing Razorbills fitted with dataloggers on Græsholmen in late June 1998. The data is from six birds sampled during 48 h (12 bird-days) during which they had 5-13 d old chicks. Asterisks denote sunrise and sunset. See Benvenuti *et al.* 2001 for details.
Tilstedeværelsen af ynglende Alke forsynet med datalogger på Græsholmen i slutningen af juni 1988. Data er fra seks fugle fulgt gennem 48 timer (12 fugledage) mens de havde 5-13 dage gamle unger. Stjerner angiver solopgang og -nedgang. Time of day = *klokkeslet.*

Tab. 18. Information on five Razorbill females followed 19 and 24 July 2005, Græsholmen, K30. RiW = Ringed where (nest), Appr. age = Approximate age of female, Breeding nest = Breeding nest used, Chick hatching = hatching date of chick, Chick fledging appr. = approximate date of chick fledging. Status of partner: B = Breeder, FB = Failed breeder, Imm = young bird that had not yet bred.
Oplysninger om fem alkehunner fulgt den 19. og 24. juli 2005, Græsholmen område K30. Ringed as = *alder på fugl ved mærkning,* RiW = *reden fuglen er ringmærket i.* Appr. age = *ca. alder på fuglen,* Breeding nest = *reden benyttet til at yngle i,* Mate ring = *magens ringnummer,* Chick hatching = *unges klækkedato,* Chick fledging appr. = *ca. dato for unges udgang,* Temporary partner = *midlertidig partner,* Days after fledging = *dage efter ungens udgang.*

	5AL02	T21524	5AT17	T21611	T21611	5AN79
Ringed as	Adult	Adult	Chick	Chick	Chick	Adult
RiW	35A	38F	84F	157A	157A	38A
Appr. age (years)	8	19	4	13	13	8
Breeding nest	35B	38B	38F	33C	33C	38J
Mate ring	T22855	T21159	5A386	5AC76	5AC76	T22435
Chick hatching	05 June	28 June	20 June	15 June	15 June	12 June
Chick fledging appr.	25 June	16 July	08 July	03 July	03 July	29 June
Date obs.	24 July	24 July	24 July	19 July	24 July	19 July
Temporary partner	Unringed	Unringed	5AN37	T23298	5AL09	5AR84
Status of partner	?	?	Imm (4Y)	B (9Y)	FB (13Y)	Imm (4Y)
Days after fledging	29	7	16	16	21	20

ing around together and lying side by side resting; four of the 'temporary' males were ringed; two were 4Y birds that never had bred, one was a 13Y bird whose chick was dead, and one was a 9Y bird that still had a large chick in the nest.

During summer (May-July) 42 4Y+ birds were recovered, all but three from the Baltic Sea (Tab. 17, Fig. 35) at a mean distance from Græsholmen of 111 (19-376) km. In winter (November-April), 23 of the 24 recoveries were from the southern Baltic Sea and a single bird was from Kattegat (Fig. 35) while the mean distance from Græsholmen was 194 (23-379) km. Though the recoveries do not reflect the at-sea-distribution of Razorbills (10 of the winter recoveries were found dead on beaches, 14 were caught in mostly coastal fishing nets), most of the adult birds from Græsholmen apparently wintered in the Baltic Sea south of 58 degrees north and east of 13 degrees east.

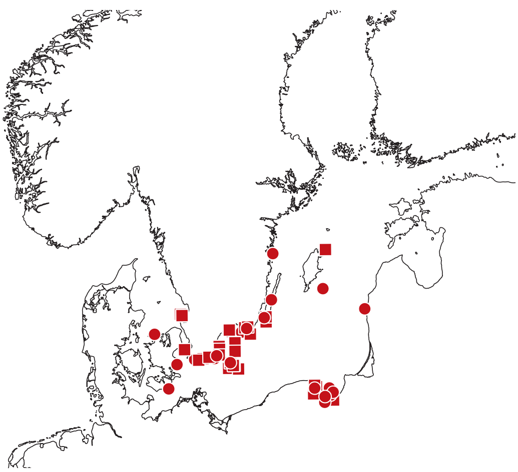

Fig. 35. Recoveries in August-April (dots) and May – July (squares) of 4Y+ Razorbills ringed as chicks on Græsholmen.
Genfund i august-april (prik) og maj-juni (kvadrat) af adulte (4Y+) Alke ringmærket som redeunger på Græsholmen.

Tab. 19. Measurements of adult Razorbills on Græsholmen.
Forskellige mål på adulte Alke fra Græsholmen.

	Mean	Range	SD	N
Wing (mm)	208	190-221	5.8	34
Wingspan (mm)	724	721-726	2.6	3
Bill length (mm)	33.7	30.1 - 38.1	1.8	33
Bill height (mm)	23.3	18.6 - 25.3	1.3	33
Tarsus (mm)	43.6	40.5 - 46.5	1.6	17
Mass (g)	716	645 - 805	40.7	23

Age of first breeding

Estimating age of first breeding of alcids can be difficult. The most likely source of bias is failure to detect an individual on its first breeding attempt, either because the egg was lost soon after laying (and no relaying occurred) or because the bird bred elsewhere and subsequently moved to another site (see Harris *et al*. 1994).

To reduce this bias as much as possible, only data for birds breeding in the study plot K30 were used. In this plot, the age of first breeding of 89 birds from the 1987-2008 cohorts was recorded (nest with egg or chick found). Among these birds, 78 were sexed. Mean age at first breeding was 4.0 years for males and 4.2 years for females; the difference in age was not significant (χ^2 = 2.50, 2 df, P = 0.285). Overall, the mean and median age at first breeding was 4.1 and 4.0 years, respectively (Tab. 20), and at first breeding 22.5% of these birds were three years old, 51.7% were four years, 22.5% were five years, and 3.4% were 6-7 years. During 1990-2008, 3-5-year-old first-time breeders constituted 7.9 ± 5.5% of the birds breeding annually in K30.

Of the 89 birds breeding for the first time, 63 (71%) were recorded as prospectors in the study plot for 1-3 seasons before actually breeding (Tab. 21).

Age and timing of breeding

Generally, the mean hatching dates of Razorbills breeding for the first time were later than the hatching dates of birds with previous breeding experience (Tab. 22). On average, the mean hatching date for 3Y birds occurred 10 days later than among 4-5Y birds breeding for the first time, but the difference was not statistically significant (Mann-Whitney U = 23.5, P = 0.189). Hatching dates of all birds breeding for the first time (3-5Y) occurred significantly later (Mann-Whitney U = 122.5, P = 0.002) than with 4-5Y birds that had previous breeding experience.

Overall, the median age of females whose eggs hatched late (period E in Tab. 23) was significantly lower than in all the other groups (A-E; Kruskal-Wallis, H = 13.2, 4 df, P = 0.01; D vs E Mann-Whitney U = 323.5, P = 0.003). Likewise, the egg volume of the females breeding latest (period E) was significantly smaller than the mean volume in all other groups (A-D; one-way ANOVA, F = 8.91, P = < 0.001).

After the first breeding attempt, the mean hatching date did not change as a function of female age (Fig. 36; Kruskal-Wallis, H = 9.168, 12 df, P = 0.674). Though most older females (53%; Tab. 24) had eggs hatching around the mean annual hatching date, some birds consistently bred up to a week earlier, others a week later and a few up to three weeks later. Over the years, some older females were known to consistently lay late in the season. This is exemplified by T20237 (latest bird in Tab. 24) which even at an age of 8-17 years laid relatively small eggs (170 cm^3) that hatched about three weeks later than the mean annual hatching date.

Tab. 20. Age at first breeding of 89 Razorbills from K30, Græsholmen.
Alder ved første yngleforsøg af 89 Alke fra K30, Græsholmen.

Age (years)	Male	Female	Not sexed	Total
3	10	7	3	20
4	24	20	2	46
5	5	10	5	20
6			1	1
7	1	1		2
Total	40	38	11	89
Mean age	4	4.2	4.4	4.1
Median age	4	4	5	4
SD	0.8	0.8	1.0	0.9

Tab. 21. Number of prospecting Razorbills in relation to age of first breeding, K30, Græsholmen.
Antal og alder hos prospekterende Alke i forhold til alder ved første yngleforsøg, K30, Græsholmen.

Age (years)	Number of First-time breeders	Number prospecting in previous year(s)	Percent prospecting
3	20	9	45.0
4	46	35	76.1
5	20	16	80.0
6	1	1	100.0
7	2	2	100.0

Tab. 22. Mean hatching dates of eggs from different age groups of younger female Razorbills, Græsholmen 1990-2011. FB = first breeding attempt, BE = previous breeding experience.
Gennemsnitlige klækningsdatoer af æg fra forskellige alders-klasser af yngre alke-hunner, Græsholmen 1990-2011. FB = første yngleforsøg, BE = fugle med tidligere yngleerfaring.

	3Y FB	4-5Y FB	4-5Y BE
Mean Hatching	6 July	26 June	19 June
SD	15.9	6.2	8.9
Latest Hatching	6 Aug.	5 July	13 July
Earliest Hatching	11 June	20 June	3 June
N	11	7	30

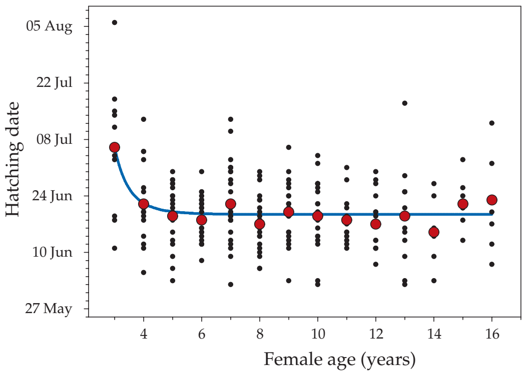

Fig. 36. Hatching dates in relation to female age based on 221 hatching dates from 82 females of known age (3-16Y), Græsholmen 1990-2011 (with known replacement eggs excluded). Red dots = mean hatching date, blue line = nonlinear regression fitted using standard curves (four parameter logistic).
Klækkedatoer sammenholdt med hunnens alder. Baseret på 221 klækkedatoer (Hatching date) *fra 82 hunner* (Female age) *af kendt alder (3-16 år), Græsholmen 1990-2011 (omlagte æg udeladt). Røde prikker = gennemsnitsklækkedato, blå streg = non-lineær regression.*

Tab. 23. Mean age of females in relation to the seasonal period where their eggs hatched. Based on 242 hatching dates for 96 females of known age (3-25Y; hatching of known replacement eggs excluded), Græsholmen 1989-2011. Mean egg volume for these birds also given (N = 210).
Gennemsnitlig alder hos alke-hunner i relation til den periode i ynglesæsonen hvor deres æg klækkede, Græsholmen 1989-2011. Tabellen er baseret på 242 klækningsdatoer hos 96 hunner af kendt alder (3-25Y; kendte omlæg ikke medtaget). Den gennemsnitlige ægvolumen er ligedes vist (N = 210).

	Mean age (years)	SD	Birds	Egg vol. (cm³)	SD	Eggs
2-10 June (A)	10.5	5.1	22	180.0	14.3	19
11-15 June (B)	9.0	3.5	51	177.6	12.1	49
16-24 June (C)	9.3	4.6	98	181.1	13.0	87
25 June - 2 July (D)	9.1	3.7	47	176.2	14.7	37
3-27 Jul (E)	6.6	4.7	24	159.9	19.6	18

Tab. 24. Difference between individual hatching dates and mean annual hatching date of 19 adult females of known age (3-25Y) followed for at least six breeding seasons. Based on 138 breeding attempts, Græsholmen 1989-2011 (hatching of known replacement eggs excluded). Days* = average deviation from mean annual hatching date in days (mean hatching = 0 ± 2 d).
Forskelle mellem individuelle og den gennemsnitlige årlige klækningsdato hos 19 adulte hunner med kendt alder (3-25Y) der er fulgt i mindst seks ynglesæsoner. Tabellen er baseret på 138 yngleforsøg på Græsholmen, 1989-2011. Days = gennemsnitlig afvigelse fra gennemsnitlig årlig klækningsdato i dage.*

Hatching	Days*	Age (years)	SD	Seasons	Birds	Birds (%)
Early (E)	7	9.3	2.7	15	2	10.5
Little early (LE)	3	10.1	4.2	14	2	10.5
Mean (M)	-0.08	11.3	4.6	77	10	52.6
Little late (LL)	-3	9.4	4.6	13	2	10.5
Late (L)	-7	11.1	3.6	13	2	10.5
Very late (VL)	-20	12.2	3.7	6	1	5.3

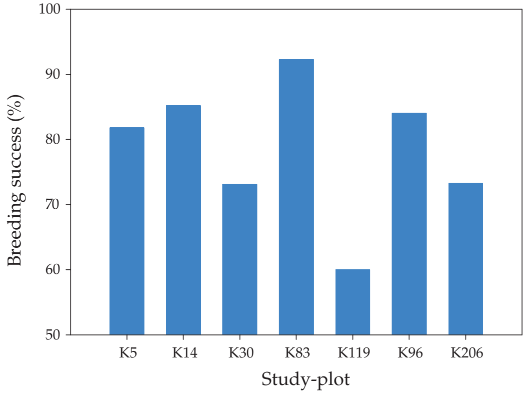

Fig. 37. Breeding success of Razorbills (fledged chicks per pair) in seven study plots, Græsholmen 2001 (N = 152 pairs).
Ynglesucces (Breeding success) *udtrykt som udgangsunger pr. par i syv forskellige studieområder* (Study-plot), *Græsholmen 2001 (N = 152 par).*

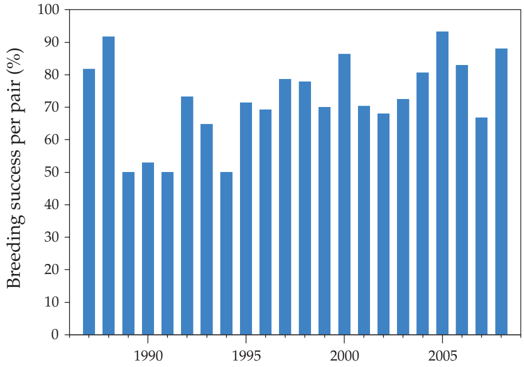

Fig. 38. Annual variation in breeding success of Razorbills (fledged chicks per pair) in study plot K30, Græsholmen 1986-2008 (N = 493 pair-years, 23 years).
Årlig variation i Alkenes ynglesucces (Breeding success per pair) *udtrykt som antal udgangsunger pr. par i studieområde K30, Græsholmen 1986-2008 (N = 493 par-år, 23 år).*

Tab. 25. Overall breeding success (%) per pair laying eggs in six study plots on Græsholmen, 1987-2007 (N = 1937 pair-years, 21 years).
Gennemsnitlig ynglesucces pr. par i seks studie-områder på Græsholmen, 1987-2007 (N = 1937 par-år, 21 år).

	K83	**K14**	**K206**	**K96**	**K5**	**K119**	**Mean**
Mean	69.1	77.8	79.5	79.0	63.8	82.3	75.2
Median	70.0	80.0	80.0	78.5	72.7	85.7	77.6
Max.	94.4	100.0	100.0	94.1	100.0	100.0	92.9
Min.	41.7	46.2	50.0	58.3	12.5	50.0	56.2
SD	13.2	12.8	13.4	10.0	26.4	14.4	9.1
Pair-years	306	384	215	670	163	199	

Tab. 26. Breeding success (%) in the K30 study plot on Græsholmen, 1986-2008 (N = 493 pairs, 23 years).
Ynglesucces i studieområdet K30, Græsholmen, 1986-2008 (N = 493 par, 23 år).

	Eggs hatched per pair	**Chicks fledged per hatched eggs**	**Chicks fledged per pair**
Mean	80.5	88.8	71.3
Median	83.3	91.3	72.4
Maximum	100.0	100.0	93.5
Minimum	56.3	50.0	41.7
SD	12.1	11.4	14.0

Non-breeding

In the study plot K30 (1990-2011), 26 instances of non-breeding involving 11 birds were recorded. Taken as a proportion of all instances of breeding birds in the plot (928 cases, 125 birds), non-breeding birds corresponded to 3% of the cases and 9% of the birds. The average age of the non-breeders was 19 (7-31) years, five were females, and six were males. In nine (35%) instances the bird was not seen during the entire season, while in the remaining 17 instances the bird was seen in the colony but did not breed. Among 10 birds, the non-breeding was linked to changes in 'mate status' (divorce 9 [previous mate still alive], widow 1 [mate disappeared]). One bird apparently had some illness, and in at least two seasons, all the outer primaries were broken, rendering that bird flightless. Only three (27%) of the 11 non-breeders had successfully reared a chick the previous breeding season, which was a considerably lower result than the 71% mean annual breeding success found in K30 (1985-2008).

Using only birds recorded for more than nine seasons in the study plot (569 bird-years, 42 birds), 19 (3%) instances of non-breeding were recorded. Among these 42 birds, six (14%) did not breed in at least one year while two birds (5%) accounted for 10 (53%) of the 19 cases of non-breeding.

Breeding success

Breeding success on Græsholmen varied considerably, both between subcolonies (Fig. 37) and within years (Fig. 38). When the years 1986-2008 and data from seven study plots were combined, the overall breeding success was 0.73 (73%) fledged chick per pair. In six study plots followed in 1987-2007 (Tab. 25), the mean breeding success ranged from 63.8 to 82.3% (overall mean 75.2%). Among these six plots, some consistently had a lower breeding success than others (Kruskal-Wallis, H = 14.759, 5 df, P = 0.011) and in some years the breeding success was significantly lower than in other years (see Appendix Tab. 8; e.g. in 1995 64.0% and in 2005 93.1%; t-test, t = -3.991, 10 df, P = 0.003). The reason for this is unknown. In the main study plot K30 which was followed more intensively in 1986-2008, annual breeding success ranged from 41.7 to 93.5% with an overall mean of 71.3% (Tab. 26, Fig. 38; see also Appendix Tab. 9).

In K30 (1989-2011), 336 breeding attempts of 45 female Razorbills of known age were recorded. Among 38 3-5Y females breeding for the first time,

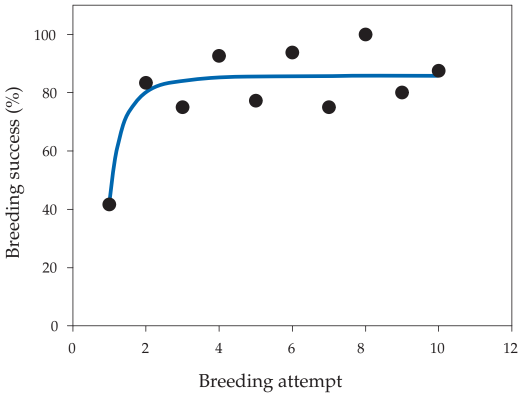

Fig. 39. Breeding success in relation to number of breeding attempts for female Razorbills on Græsholmen. Blue line = nonlinear regression fitted using standard curves (four parameter logistic). Based on 213 breeding attempts from 36 birds of known age followed for 1-10 years from their first breeding attempt.
Ynglesucces (Breeding success) *sammenholdt med antallet af yngleforsøg* (Breeding attempt) *hos Alke på Græsholmen. Blå streg = non-lineær regression. Baseret på 213 yngleforsøg hos 36 fugle med kendt alder fulgt gennem 1-10 år efter deres første yngleforsøg.*

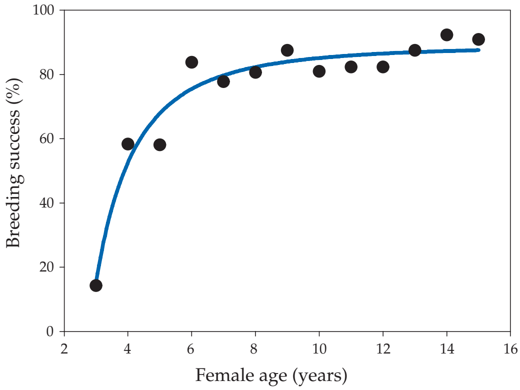

Fig. 40. Breeding success in relation to age for female Razorbills on Græsholmen. Blue line = nonlinear regression fitted using standard curves (four parameter logistic). Based on 214 breeding attempts from 36 birds of known age followed for 1-15 years from their first breeding attempt.
Ynglesucces (Breeding success) *sammenholdt med hunners alder* (Female age) *på Græsholmen. Blå streg = non-lineær regression. Baseret på 214 yngleforsøg hos 36 Alke af kendt alder fulgt gennem 1 til 15 år efter deres første yngleforsøg.*

the mean fledging success was 39.5%, which was significantly lower than the success during the second breeding attempt (83.3%, N = 30; Fisher's exact test, P = <0.001; Fig. 39). 3Y females had the lowest breeding success (14.3%), but the success of 4Y (52.6%) and 5Y (33.3%) females breeding for the first time was not significantly higher (χ^2 = 4.292, 2 df, P = 0.117). Individuals breeding for the first time and/or when 3-5 years old tended to have low breeding success (Fig. 39, Fig. 40), but regardless of age some birds consistently had a higher breeding success than others. For example, 15 females with 10-16 known breeding attempts produced 192 fledging chicks. Dividing these 15 experienced birds in three groups ranked after breeding success, the groups consisted of:

Four females with 10-14 (mean 12.5, N = 50) breeding attempts produced 26 fledging chicks in total. Mean breeding success 52%, mean age at last recorded breeding attempt 15.8 (12-18) years.

Seven females with 10-16 (mean 12.7, N = 89) breeding attempts produced 77 fledging chicks. Mean breeding success 77.5%, mean age at last recorded breeding attempt 16.8 (14-19) years.

Four females with 11-15 (mean 13.3, N = 53) breeding attempts produced 47 fledging chicks. Mean breeding success 88.7%, mean age at last recorded breeding attempt 16.6 (13-20) years.

The breeding success between these three groups was significantly different (one-way ANOVA, F = 42.66, P = <0.001). Among 180 ringed chicks from the nests of 27 females of known age and with at least four prior breeding attempts, 51 (28%) were subsequently resighted on Græsholmen. The resighted chicks came from 18 nests/females (67%) and 27 (53%) of these chicks came from just six nests/females (22%).

Expressed as chicks fledged of chicks hatched, the overall fledging success on Græsholmen (1986-2007; Tab. 27) decreased as a function of time (one-way ANOVA, F = 44.17, P = <0.001). A post-hoc Tukey HSD test showed that while the fledging success during the early stages of the season (before 26 June; A and B) was equally high, success in the later stages of the season (after 25 June; C and D) was significantly lower. Likewise, the mean egg volume in D was significantly smaller than in A (Mann-Whitney U = 707.5, P = <0.001).

Tab. 27. Mean fledging success (%) on Græsholmen in different periods of the breeding seasons 1987-2007, calculated as chicks fledged of chicks hatched. Mean hatching date for these years was 18 June (12-26 June). Mean egg volume also given.
Gennemsnitlig ynglesucces (her beregnet som andel udgangsunger af antal klækkede unger) på Græsholmen i forskellige perioder af ynglesæsonerne 1987-2007. Den gennemsnitlige klækningsdato for disse år var 18. juni (12.-26. juni). Den gennemsnitlige æg-volumen er også vist.

Period of season	**A** 23 May - 4 June	**B** 5-25 June	**C** 26 June - 9 July	**D** 10 July - 6 Aug
Mean fledging success	98.1	98.6	94.9	89.8
Number of nests	215	6067	1312	225
Mean egg volume (cm^3)	178.1	180.1	175.0	163.6
SD	13.4	13.2	15.8	21.2
Number of measured eggs	213	6093	1320	229

Tab. 28. The fate of Razorbill eggs that did not hatch in study plot K30 (N = 87) and on the whole of Græsholmen (N = 2036), 1986-2008.
Årsager til at æg ikke klækkede i studieområdet K30 (N = 87) og på hele Græsholmen (N = 2036), 1986-2008.

	K30		**Græsholmen**	
Fate of egg	N	%	N	%
Chick died in egg during hatching	6	7.1	118	5.8
Egg predated/disappeared	28	32.9	953	46.8
Egg infertile/deserted	28	32.9	527	25.9
Egg damaged in nest	11	12.9	365	17.9
Egg drowned (rain or sea)	14	16.5	73	3.6

During the study period, between 5500 and 8400 pairs of Herring Gulls bred on Græsholmen.

In K30 (1986-2008), the mean hatching success (chicks hatched per pair laying) was 80.5% and the proportion of chicks fledging per hatched egg was 88.8% (Tab. 26). Among 87 eggs that did not hatch, roughly one third disappeared (most probably predated by Herring Gulls), one third were infertile or deserted for other reasons, and one third had shell damage or drowned in the nest due to flooding by rain or seawater (Tab. 28). Among 38 chicks that did not fledge, 13 (34%) disappeared (probably predated; 10 at an age of <7 days), four (11%) drowned in the nest after heavy rain/gales, and 21 (55%) were found dead in the nest (17 at an age of <7 d).

Over the years and on the whole of Græsholmen, 356 chicks were found dead in the nest and 116 chicks of known age disappeared (most likely predated) before fledging. Among the dead chicks, 340 (96%) were <7 d old, and of the disappeared chicks 99 (85%) were also <7 d – the remaining were 10+ d. Thus, the first five to six days of life are the most critical period for Razorbill chicks until the actual fledging takes place. After the mid-1990s, where the breeding population of Great Black-backed Gulls increased (Tab. 4), the remains (legs, wings and ring) of 82 fledging chicks were found in pellets regurgitated by gulls around their nesting area. A minimum of 43 of these had been eaten by Great Black-backed Gulls, which occasionally were seen catching fledging chicks shortly after they reached the sea. The highest numbers of remains of ringed fledging chicks in gull pellets were found in 2002 (16, 3.4% of chicks ringed that year) and in 2004 (21, 3.7% of ringed chicks).

In 1994, when c. 8100 pairs of Herring Gulls and 600 pairs of Razorbills were breeding on Græsholmen, the mean distance between a Razorbill nest and the nearest Herring Gull nest was 100 ± 62.9 cm (20-400 cm, N = 368) with 71% of the nests situated 50-120 cm from each other. Apparently, the distance was not important for the outcome of the Razorbills breeding success. For example, no difference (Mann-Whitney U = 638.0, P = 0.845) was found in the distances to the nearest Herring Gull nest between a group of 32 Razorbill nests where the egg was predated (or disappeared) and a group of 41 nests where the egg did not hatch of other reasons (infertile or shell damage).

More than half the Razorbills rested and fed within 5 km of the colony when at sea in the daytime.

Divorces and widows

Data on divorces (partner did not die) and widows (partner died or disappeared) from the study-plot K30 relate to 73 birds of known age and sex followed for an average of 16 years (4-22 years; 465 pair-years; 1990-2011). Movers refer to birds that relocated to another nest after a divorce or death of a partner (widow), while stayers refer to birds that remained at the original nest.

In all divorces, one bird from the original pair stayed at the nest and bred there with a new partner and the other bird moved to another nest. A significantly higher proportion of females (53.8%) than males (13.9%) stayed at the original nest after a divorce (Fisher's exact test, P = <0.001; 75 cases involving 53 birds). In 26 cases (17 birds), the breeding success the year before a divorce was 46.2%, which was significantly lower than the breeding success a year after the divorce (95.7%; Fisher's exact test, P = <0.001).

Tab. 29. Change of partner (Divorce or No divorce) and of nest site (Moved or Stayed) of Razorbills from K30 (%). Widow = partner died. Only birds of known age and sex, followed from the first breeding attempt, are included. *Partnerskifte (skilsmisse* [Divorce] *eller ej) og redeskifte (flyttet* [Moved] *eller forblevet* [Stayed]*) blandt Alke fra studieområdet K30 (%) fordelt på aldersklasser.* Widow = *partneren død.* Divorce rate = *skilsmisseandel*, Divorce + widow rate = *samlet andel af skilsmisser og partnerdød.*

Male	Female	Divorce?	3-7 Y	8-12 Y	13-22 Y	All
Moved	Moved	No divorce	6.8	1.8	0.0	2.9
Moved	Stayed	Divorce	15.8	10.1	3.1	10.4
Stayed	Moved	Divorce	10.3	3.0	0.0	4.5
Stayed	Stayed	No divorce	67.1	85.2	96.9	82.6
Divorce rate			26.0	13.0	3.1	14.5
N			146	169	127	442
Divorce + Widow rate			29.4	17.4	8.2	18.8
N			153	178	134	465

When widowed, 78.3% (23 cases, 19 birds) stayed at the original nest; slightly more males (43.5%) than females (34.8%) remained but the difference was not statistically significant (Fisher's exact test, P = 0.122). In 465 pair-years, 23 birds were widowed, corresponding to an average annual mortality of 4.9%.

The overall yearly divorce rate was 14.5% and the overall rate of partner change (including widows) was 18.8% (Tab. 29). However, the divorce rate was highest (26%) among the youngest birds (3-7 years) and lowest (3.1%) among the oldest (13-22 years). The difference between the three age-classes was highly significant (3-7Y, 8-12Y and 13-22Y; χ^2 = 36.7, 6 df, P = <0.001). The risk of becoming a widow increased from 3.4% among the youngest birds to 5.1% among the oldest birds.

Overall, some pairs were very stable, and in K30 10 pairs bred together in the same nest for 10-13 consecutive years (10 years for six pairs, 11 years for two pairs, 13 years for two pairs). Other birds were more unstable in their pair bonds: one bird had five different mates in 12 years, another had four mates in 11 years.

Age structure in subcolony K30

Razorbills may live for more than 40 years (Fransson *et al*. 2010), and in that sense a study only lasting 29 years is not really a long-term study. Additionally, due to wear, the loss of the triangular metal rings used in this study was calculated to be 50% at the age of 14 years (Lyngs 2006). These circumstances may add a considerable bias when presenting an age structure of a subcolony, even in this case where four out of six of the oldest (>16 Y) birds had been re-ringed.

Nevertheless, among 61 birds ringed as chicks and breeding in K30 in 2011, the mean age was 10.3 ± 5.2 years (3-25 years; Fig. 41). Four (6.6%) of the birds were 3-4 years old, 43 (70.5%) 5-13 years, eight (13.1%) 14-18 years and six (9.8%) 19-25 years old – four of the latter had been re-ringed. A bird ringed as adult and also breeding in the plot was at least 29 years old. The oldest Razorbill resighted on Græsholmen was 32 years old (ringed as chick in 1979, re-ringed 1989, still alive in 2011 at the end of the study).

Among 18 pairs breeding in 2011 where both members were ringed as chicks, the mean age difference between each member of the pair was 1.8 ± 1.5 years (0-17 years). Overall, for the majority (11; 61%) of pairs, the age difference was 0-2 years (0 years 28%, 1 year 11%, 2 years 22%) - and 17% were 11-17 years older than their partner (see Appendix Fig. 4).

Survival

Among 107 Razorbills ringed as adult breeders on Græsholmen in 1989-2006, 102 (95.3%) were resighted in consecutive years (see Appendix Tab. 10). In the study plot K30, ringed breeding birds resighted between 1990 and 2011 had a mean annual survival rate of 94.8% (89.7-100%; Tab. 30). An analysis of survival of adult breeders over the same period conducted in program MARK suggested a slightly lower average survival rate of 93.7% (Tab. 31). Including the period 1986-1989 resulted in a mean adult survival rate of birds in K30 of 94.8% (95% CI: 86.1-98.1). For the whole of Græsholmen, mean annual survival of adult breeders in 1986-2009 was estimated as 93.2% (Tab. 31, Fig. 42).

The mean resighting probability of adult breeders (4Y+) on Græsholmen in 1986-2009 was estimated as 66.3% (Tab. 31) but was considerably higher (82%) throughout the years 1993-2000. The resighting probability was strongly correlated with the number of hours spent resighting (Spearman r = 0.953, P = <0.001; see Appendix Tab. 11). Overall, the resighting probability of immature birds on the whole of Græsholmen was 5.5% for 1Y birds, 32.3% for 2Y birds and 55.2% for 3Y birds (Tab. 31).

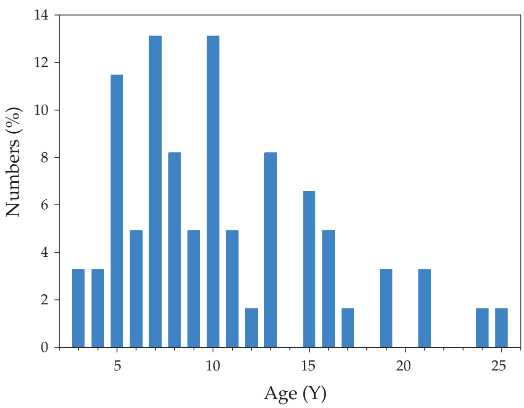

Fig. 41. Age composition of Razorbills breeding in study-plot K30, Græsholmen in 2011. Only birds ringed as chicks included (N = 61).
Alderssammensætning blandt Alke ynglende i studieområde K30, Græsholmen 2011. Kun fugle ringmærket som redeunger medtaget (N = 61). Age = *alder,* Number = *antal.*

Year	No. of birds	Alive next year	%
1990	11	9	81.8
1991	14	14	100.0
1992	16	16	100.0
1993	19	18	94.7
1994	19	18	94.7
1995	18	15	83.3
1996	21	21	100.0
1997	23	23	100.0
1998	30	27	90.0
1999	36	34	94.4
2000	40	38	95.0
2001	54	53	98.1
2002	54	51	94.4
2003	55	51	92.7
2004	54	51	94.4
2005	59	54	91.5
2006	60	57	95.0
2007	66	63	95.5
2008	68	65	95.6
2009	66	62	93.9
2010	69	66	95.7

◁ Tab. 30. Resightings of ringed breeding Razorbills at K30, Græsholmen 1990-2011, including two birds that moved to another subcolony.
Aflæsninger af ringmærkede ynglende Alke i K30, Græsholmen 1990-2011. To fugle, der flyttede til en anden subkoloni, er inkluderet.

Tab. 32. Resighting rates of Razorbills ringed as chicks with known hatching dates subsequently seen on Græsholmen, 1987-1998 cohorts.
Aflæsningsrate af Alke ringmærket som unger med kendt klækningsdato og senere aflæst på Græsholmen (1987-1998 kohorterne).

Period	Hatched	Resighted	%
Late May	41	22	53.7
Early June	465	233	50.1
Mid-June	1640	821	50.1
Late June	1207	549	45.5
Early July	282	118	41.8
Mid-July - Early August	104	36	34.6

Tab. 31. Survival estimates and resighting probabilities of Razorbills ringed as chicks in study plot K30 and on the whole of Græsholmen (GH). Age-dependent survival (S) and resighting probabilities (p) were estimated in program MARK. Due to data limitations the recovery probability (r) of birds from K30 was estimated as constant over time, whereas QAICc model selection selected a model with a linear trend on the recovery probability (r) of birds from the whole of Græsholmen. Both models had two age-classes for site fidelity (F). Parameter notation: S_{1Y} = survival from ringing to first year, S_{2Y} = survival from first to second year, S_{3Y} = survival from second to third year, S_{Ad} = survival of adult birds, p_{1Y} - p_{Ad} = resighting probability of different age-classes, Est. = estimate, SE = standard error, L CI and U CI = lower and upper 95% confidence interval.
Overlevelse (Survival) *og sandsynlighed for at genfinde* (resighting probability) *Alke ringmærkede som redeunger i studieområdet K30 og på hele Græsholmen. S (aldersafhængig overlevelse) og p (aflæsningssandsynlighed) beregnet i programmet Mark. På grund af begrænset datamængde blev genfundssandsynligheden (r) af fugle fra K30 estimeret som konstant over tid, mens QAICc valgte en model med en lineær udvikling af genfundssandsynligheden (r) for fugle fra hele Græsholmen. Begge modeller benyttede to aldersklasser for stedtrohed (F). De forskellige parametre: S_{1y} = overlevelse fra ringmærkning til første leveår, S_{2y} = overlevelse fra første til andet leveår, S_{3y} = overlevelse fra andet til tredje leveår, S_{Ad} = overlevelse af adulte fugle, p_{1Y} - p_{Ad} = aflæsningssandsynlighed for de forskellige aldersklasser.* EST = *estimat*, SE = *standardfejl*, L CI *og* U CI = *nedre og øvre 95 % konfidensinterval*, GH = *hele Græsholmen.*

Study plot	Survival					Resighting probability					
	Est.	SE	L CI	U CI		Est.	SE	L CI	U CI	Area	Period
S_{1Y}	0.786	0.066	0.630	0.888	p_{1Y}	0.013	0.007	0.005	0.035	K30	1990-2011
S_{2Y}	0.840	0.069	0.659	0.935	p_{2Y}	0.316	0.033	0.255	0.384	K30	1990-2011
S_{3Y}	0.848	0.055	0.708	0.928	p_{3Y}	0.587	0.038	0.511	0.659	K30	1990-2011
S_{Ad}	0.937	0,028	0.854	0.974	p_{Ad}	0.959	0.006	0.945	0.970	K30	1990-2011
					Whole island						
S_{1Y}	0.700	0.054	0.584	0.794	p_{1Y}	0.055	0.004	0.048	0.063	GH	1986-2009
S_{2Y}	0.877	0.021	0.829	0.912	p_{2Y}	0.326	0.009	0.309	0.344	GH	1986-2009
S_{3Y}	0.893	0.018	0.853	0.923	p_{3Y}	0.530	0.010	0.510	0.550	GH	1986-2009
S_{Ad}	0.932	0.012	0.905	0.953	p_{Ad}	0.663	0.005	0.654	0.672	GH	1986-2009

For the whole of Græsholmen, overall survival was 63.1% (95% CI: 57.9-67.8) to the third year (3Y), 57.7% (95% CI: 52.8-62.3) to the fourth year (4Y), and 55.4% (95% CI: 48.5-59.0) to the fifth year (5Y). First-year survival (1Y) was estimated as 70.0%, second-year (2Y) survival as 87.7%, and third year survival as 89.3% (Tab. 31). Goodness-of-Fit tests suggested a slight, but not critical, lack of fit with an estimated median c-hat value of <1.45 for both K30 and the whole of Græsholmen.

Generally, there was a tendency that resighting rates were lower for birds hatched late in the breeding season (Tab. 32), but this was not significant even when comparing birds hatched in May with those hatched in mid-July/August (Fisher's exact test, P = 0.184).

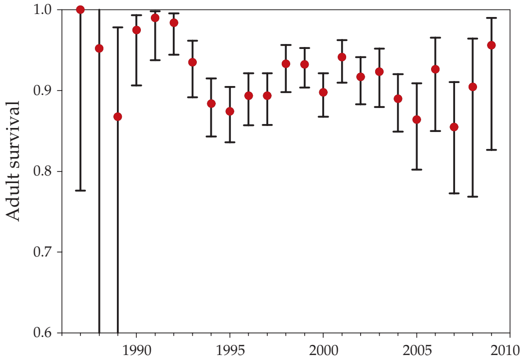

Fig. 42. Mean annual survival ± 95% CI of adult breeding birds on Græsholmen, 1989-2009, as calculated in programme MARK.
Gennemsnitlig overlevelse (± 95 % CI) blandt adulte ynglefugle på Græsholmen, 1989-2009. Beregnet med programmet MARK.

Natal fidelity

Among 98 birds hatched and ringed in K30 (1984-2006) and subsequently resighted as breeding on Græsholmen, 49 (50%) returned to breed in this plot, while 49 bred elsewhere (Fig. 43). Of 42 sexed returning birds, 21 (50%) were males and 21 were females. During the same period, 50 birds ringed as chicks elsewhere on Græsholmen plus a female ringed as a chick in Finland (840 km NE) entered K30 as breeders. Of these, 46 were sexed and 21 (45%) were males, 25 were females. Thus, excluding the Finnish bird, the sex ratio of all the returning Græsholmen birds was almost equal (male 42, female 45; Fisher's exact test, P = 0.831).

The local birds returning to breed in K30 (area = 621 m²) bred in a nest 11 ± 6.3 m (1-27 m) from their natal (hatching) nest, while the mean distance from the natal nest on Græsholmen of birds entering to breed in K30 was 134 ± 59.7 m (18-245 m). Excluding one bird found breeding on Stora Karlsö (Sweden,

Off duty Razorbills in study area K30.

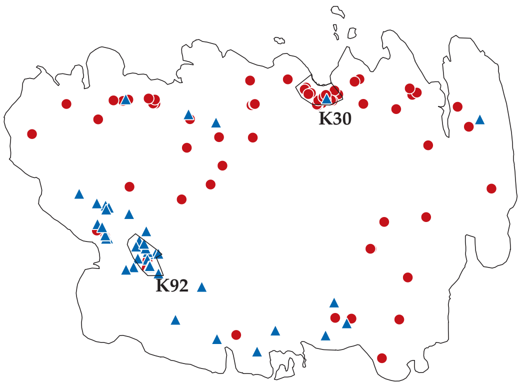

Fig. 43. Spatial distribution of nest sites for Razorbills hatched in K30 (red dots; 98 birds) and in K92 (blue triangles; 63 birds), which subsequently bred on Græsholmen. *Fordeling af redesteder hos Alke klækket i område K30 (røde prikker; 98 fugle) og i område K92 (blå trekanter; 63 fugle) og som efterfølgende ynglede på Græsholmen.*

280 km NE), the mean distance from hatching nest to breeding nest of the birds hatched in K30 and breeding elsewhere on Græsholmen was 132 ± 59 m (18-245 m).

For comparison, among 63 birds hatched in the far less closely monitored study plot K92 (area = 592 m^2, 200 m SW of K30), 32 (51%) returned to breed in a nest less than 26 ± 6.7 m (mean 16 m, 5-25.9 m) from their hatching-nest while 15 (24%) were inside the plot. The mean distance of 31 birds that bred elsewhere was 108 ± 74.9 m (31-315 m). The spatial distribution on Græsholmen of the two groups was not random (χ^2 = 59.4, 5 df, P = <0.001).

Generally, nest fidelity of breeding birds was high (88.5%). In K30 (1990-2011), 949 cases (or bird-years) involving 131 birds with known status of change in breeding nest were recorded. Change of breeding nest occurred in 81 cases involving 57 birds, i.e. 8.6% of the total number of cases and 43.5% of the birds. In 79 (97.5%) of the cases, the birds remained as breeders in K30, while two birds moved to breed in other areas of Græsholmen. One of these birds bred once (as 3Y) in K30 and then moved to another subcolony 155 m away, while the other moved from nest 72 (219 m away) to K30 and bred there for three years – after which it returned to breed in nest 72. Most of the cases of nest change (58; 72%) occurred during a change in 'mate-status', and 17 (21%) of the cases related to pairs moving to a new nest. The average distance moved within K30 was 5.4 ± 6.3 m. Nest fidelity among males (87%) was significantly lower than among females (92%; Fisher's exact test, P = 0.008).

On a larger scale, among 750 birds from the whole of Græsholmen, where both the natal hatching-nest and the subsequent breeding-nest were known, 274 (37%) bred in a nest situated <30 m from their hatching-nest, 379 (50%) bred 30-50 m away, 82 (11%) bred 51-199 m away and 15 (2%) bred 200-350 m from their hatching-nest (see Appendix Fig. 5). Eight birds (1.1%) bred in the same nest they were hatched in. The median age of these 750 birds was 5.0 ± 2.3 years (3-14 years).

Among 103 birds ringed as adults in a nest and resighted or re-caught in subsequent years, 34 (33%) were found in the nest they were ringed in, 68 (66%)

The boat *Alken* (the Razorbill) used during the study on Græsholmen.

were found in their natal subcolony and only one (1%) adult had moved more than 30 m (230 m).

Summing up, around 50% of the birds ringed as chicks and returning to breed on Græsholmen did so in their natal subcolony. Once settled, local nest-changes (typically within a radius of 10 m) occurred among 44% of the birds, but <2% moved to an entirely different subcolony.

A high degree of natal fidelity was also found among non-breeding 2Y Razorbills. Around 62-78% of the resightings were recorded less than 60 m from the centre of the plot the birds were hatched in (Tab. 33, Fig. 44), and their distribution on Græsholmen was not random (χ^2 = 282.6, 10 df, P = <0.001).

Intercolony movements

During 1984-2008, 87 resightings of 37 Razorbills ringed as chicks in other countries were recorded on Græsholmen (Fig. 45, see Appendix Tab. 12). Most of the birds (35) were from 14 colonies in the Baltic Sea, while two (1 3Y visitor, 1 breeding) came from Hallands Väderö (56° 27′ N, 12° 34′ E) on the Swedish west coast (Kattegat). The mean distance from Græsholmen to the natal colonies was 621 km (range: 205-930 km). Twenty-two birds were recorded as visitors/prospectors (1-3Y, 17 birds; 4-6Y, 5 birds), while 15 birds were recorded as breeding (nest with egg or chick found) on Græsholmen. Breeding birds ringed in other colonies were on average resighted for a period of six years (range: 1-10 years). The oldest bird was 19 years when last seen. All three breeding birds that were sexed were females.

Four birds ringed as chicks on Græsholmen were resighted as breeders in other Baltic colonies: three on Stora Karlsö (age 8-11Y) and one on NW

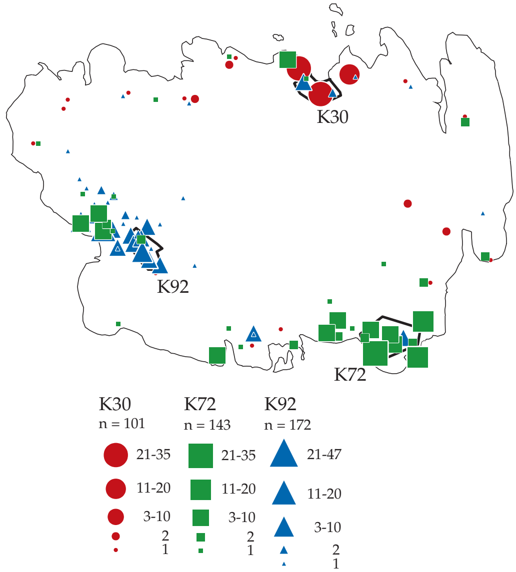

Fig. 44. Spatial distribution of resightings of 2Y Razorbills ringed as chicks in three different plots on Græsholmen. Blue triangle = birds ringed in K92, red dot = birds ringed in K30, green square = birds ringed in K72. See also Tab. 33.
Fordeling af aflæsninger af unge Alke (2Y) ringmærket som redeunger i tre forskellige studieområder på Græsholmen. Blå trekanter = unger mærket i K92, rød prik = K30, grønt kvadrat = K72. Se også Tab. 33.

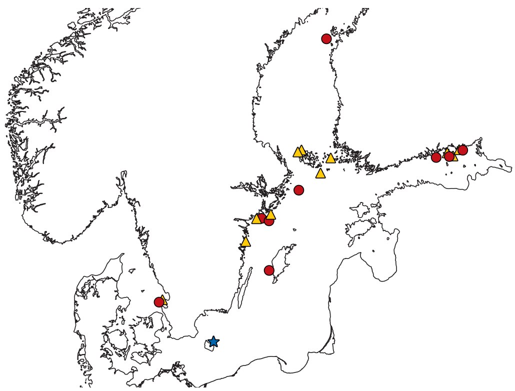

Fig. 45. Ringing locations of Razorbills ringed as chicks abroad and resighted on Græsholmen (star), 1984-2008. Red dot = ringing locations for birds subsequently breeding on Græsholmen, yellow triangle = ringing locations for birds recorded as visitors on Græsholmen.
Oprindelsen af Alke ringmærket som unger i andre kolonier og aflæst på Græsholmen (stjerne), 1984-2008. Rød prik = oprindelsessted for fugle der ynglede på Græsholmen, gul trekant = oprindelsessted for fugle som kun gæstede Græsholmen.

Tab. 33. Razorbills ringed as chicks in different plots and resighted as 2Y on Græsholmen. * = resighted <60 m from centre of natal plot (see Fig. 44).
*Alke ringmærket som unger i forskellige studie-områder og aflæst som 2Y på Græsholmen. * = aflæst <60 m fra centret af det område hvor de klækkede (se Fig. 44).*

	K30	K92	K72
Number of 2Y birds	72	63	78
Resightings, total	102	172	143
Resighted <60 m*	79	120	89
Resighted <60 m %	77.5	69.8	62.2

Bornholm (DK; 4Y). In addition, three birds ringed as chicks on Græsholmen were recovered in May-July very close to the colony at Hallands Väderö (SW Sweden) at an age of 5-10 years, suggesting that they had emigrated from Græsholmen. None of these birds were ever resighted on Græsholmen.

The efforts made to resight Razorbills in the other Baltic colonies were relatively modest, nevertheless a bird ringed on Græsholmen was resighted as a 2Y in June-July 1995 on Græsholmen, as a 3Y on Stora Karlsö in 1996, and again on Græsholmen in 1997 and 1998 (4-5Y, May-July). Another bird was resighted on Græsholmen as a 2Y in 1995 and as a 3Y 1-11 May 1996, and 17 days later it was caught in a fishing net in the Bothnian Sea, 767 km NE of Græsholmen. In June 1996, on Aspskär (Finland), PL resighted six immature (2-3Y) Razorbills ringed as chicks in other Finnish colonies (mean distance 144 km, range 38-376 km) and one 6Y breeding bird ringed as chick in a colony 271 km away.

The probability of birds remaining in the colony where they were ringed (Græsholmen 1986-2009) was calculated in program MARK as 78% (95% CI: 0.644-0.875) for 1Y birds and as 95% (95% CI: 0.916-0.966) for adults. These rates indicate that young birds are far more likely to emigrate than adult birds that have settled as breeders in the colony.

In July 2000, 218 large Razorbill chicks (mean age 16 d; 4-25 d) were ringed with triangular rings and yellow colour rings on Stora Karlsö. One of these chicks was later found breeding on Græsholmen at an age of four years. Using a fledging success of 85% (since the chicks were large) and a survival rate of 50% to age four years, this emigrated chick corre-

Tab. 34. Possible annual rates of population growth (%) under varying rates of breeding success (BS) and survival (S) of five different age-classes of Razorbills ringed in the study plot K30 on Græsholmen. Parameters that were changed to either lower or higher boundary values are shown in red. Constant, Age-dependent survival rates were estimated in program MARK and extracted from the best model {S(3 age, c) p(3 age, c) r(c) F(c)} which had four age-classes for survival (S) and recapture probability (p) and only one age-class for recovery probability (r) and site fidelity (F). Estimates of survival (S) of different age-classes (1Y, 2Y, 3Y, 4Y, AD) calculated in program MARK. S1Y = survival from ringing to first year, S2Y = survival from 1st to 2nd year, S3Y = survival from 2nd to 3rd year, S4Y = survival from 3rd to 4th year, SAd = adult survival from 4th of life, B1-2Y = birds breeding as 1-2Y, B3Y = birds breeding as 3Y, B4Y = birds breeding as 4Y, BAd = proportion of adults breeding, BS = breeding success expressed as the number of fledged chicks per laying pair recorded in the study-plot (mean, min. and max.; see section Breeding Success), CI = 95% confidence interval. Resulting growth rates λ under varying values of survival and breeding success were calculated using a matrix population projection model with a pre-breeding census and five age-classes.

Mulig årlig bestandsvækst (%) ved forskellige mål for ynglesucces (BS) og overlevelse (S) blandt fem forskellige aldersklasser af Alke ringmærket som redeunger i studieområde K30 på Græsholmen. Parametre, der blev ændret til enten højere eller lavere grænseværdier, er vist med rødt. Konstant aldersafhængig overlevelse blev estimeret i programmet MARK og udvalgt fra den bedste model. S = overlevelse, p = genfangstsandsynlighed, r = aflæsningssandsynlighed, F = stedtrofasthed. S1Y = overlevelse fra ringmærkning til første leveår, S2Y = overlevelse fra første til andet leveår, S3Y = overlevelse fra andet til tredje leveår; S4Y = overlevelse fra tredje til fjerde leveår, SAd = overlevelse af adulte fugle (fra 4Y), B1-2Y = fugle ynglende som 1-2Y, B3Y = fugle ynglende som 3Y, B4Y = fugle ynglende som 4Y, BAd = andel af adulte der yngler, BS = ynglesucces udtrykt som antal udgangsunger pr. par, der lagde æg i studieområdet, λ = vækstrater (%), CI = 95 % konfidensinterval.

	Mean	BS		SAd		S1Y		S2Y		S3Y		All age	
	Estim.	Low	High	Low CI	High CI	Low CI	High CI	Low CI	High CI	Low CI	High CI	Low CI	High CI
S1Y	0.786	0.786	0.786	0.786	0.786	0.630	0.888	0.786	0.786	0.786	0.786	0.630	0.888
S2Y	0.840	0.840	0.840	0.840	0.840	0.840	0.840	0.659	0.935	0.840	0.840	0.659	0.935
S3Y	0.848	0.848	0.848	0.848	0.848	0.848	0.848	0.848	0.848	0.708	0.928	0.708	0.928
S4Y	0.937	0.937	0.937	0.854	0.974	0.937	0.937	0.937	0.937	0.937	0.937	0.854	0.974
SAd	0.937	0.937	0.937	0.854	0.974	0.937	0.937	0.937	0.937	0.937	0.937	0.854	0.974
B1-2Y	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
B3Y	0.230	0.230	0.230	0.230	0.230	0.230	0.230	0.230	0.230	0.230	0.230	0.230	0.230
B4Y	0.750	0.750	0.750	0.750	0.750	0.750	0.750	0.750	0.750	0.750	0.750	0.750	0.750
Bad	0.970	0.970	0.970	0.970	0.970	0.970	0.970	0.970	0.970	0.970	0.970	0.970	0.970
BS	0.713	0.417	0.935	0.713	0.713	0.713	0.713	0.713	0.713	0.713	0.713	0.713	0.713
λ (%)	**7.9**	**3.0**	**10.9**	**1.1**	**10.8**	**5.7**	**9.2**	**5.5**	**9.0**	**6.1**	**8.8**	**-4.9**	**14.5**

sponded to 1.1% of the surviving birds. Using the same demographic parameters for the three birds ringed as chicks (of the 1986, 1987 and 1989 cohorts) on Græsholmen, which emigrated to Stora Karlsö, the mean emigration rate also corresponded to 1.1%.

Population dynamics

Annual nest counts on Græsholmen between 1986 and 2006 indicated an average annual growth rate of 5.5 %, but with growth >10% in five of the years (range 10.6-20%; see Fig. 4). In comparison, the population growth rate estimated from the population model based on demographic rates from Græsholmen was on average 7.9% (Tab. 34). The discrepancy in estimated growth from the nest censuses and the demographic model suggests a net emigration of Razorbills from Græsholmen to other colonies in the Baltic Sea. The very high annual growth of 10-20% based on nest counts could simply be the result of observation error because nest censuses can be extremely challenging.

The life table response experiment "LTRE" showed that growth >10% could be attained by elevating either the hatching success (BS, Tab. 34) or survival of birds older than four years (Sad, Tab. 34) to the value of the 95% upper confidence limits. Elevating the survival rate of one of the three immature age-classes (S1Y, S2Y, S3Y) to the value of their 95% upper confidence limits also resulted in a considerable increase in the population growth rate, whereas a decrease in hatching success (BS) to the lower 95% limit resulted in annual population growth of 3%. It appears that there was no correlation either between the annual population growth rate and adult survival (1988-2006; Spearman r = 0.225, P >0.050) nor between the annual population growth and sea temperature (1987-2000; Spearman r = 0.015, P >0.050).

Breeding Razorbills on Græsholmen spent about 12 percent of the day flying.

Tab. 35. Mean annual Razorbill survival estimates (Est. S) for Græsholmen and some other colonies across the breeding range. * = overall survival from ringing to the third to fifth summer.
*Gennemsnitlige estimater af årlig overlevelse (Est. S) hos Alke fra Græsholmen og fra andre kolonier gennem hele udbredelsesområdet. * = gennemsnitlig overlevelse fra ringmærkningen af redeunger til den 3.-5. sommer.*

Age-class	Age	Est. S (%)	Place	Country	Study	Years of observation	Reference
Adult		88.8	Isle of May	Scotland	1982-1987	5	Harris & Wanless 1989
Adult	3Y+	89.0	Gannet Island	Canada	1996-2006	10	Lavers et al. 2008
Adult	4Y+	89.0	Skokholm	Wales	1960-1970	10	Lloyd 1974
Adult		90.0	Gulf of St. Lawrence	Canada	1989-1994	5	Chapdelaine 1997
Adult		90.5	Isle of May	Scotland	1986-1997	11	Harris et al. 2000
Adult		90.5	Skomer	Wales	1970-2000	30	Brown et al. 2004
Adult	3Y+	91.2	Machias Seal Island	Canada	1999-2006	7	Lavers et al. 2008
Adult		91.9	Hornøy	Norway	1995-2003	8	Sandvik et al. 2005
Adult		92.1	Shiant Island	Scotland	1970-1978	8	Steventon 1979
Adult	3-21Y	93.2	Græsholmen	Denmark	1986-2009	23	Present study
Adult	3-20Y	94.8	Græsholmen K30	Denmark	1990-2011	21	Present study
Adult	4Y+	95.3	Græsholmen	Denmark	1989-2006	17	Present study
Adult	3-11Y	97.0	Gannet Island	Canada	1996-2006	10	Lavers et al. 2008
Adult	3-8Y	97.6	Machias Seal Island	Canada	1999-2006	7	Lavers et al. 2008
Immature	0-2Y	48.2	Gannet Island	Canada	1996-2006	10	Lavers et al. 2008
Immature	0-2Y	77.8	Machias Seal Island	Canada	1999-2006	7	Lavers et al. 2008
Immature	0-1Y	70.0	Græsholmen	Denmark	1986-2009	23	Present study
Immature	1-2Y	87.7	Græsholmen	Denmark	1986-2009	23	Present study
Immature	2-3Y	89.3	Græsholmen	Denmark	1986-2009	23	Present study
Immature	0-3Y*	63.1	Græsholmen	Denmark	1986-2009	23	Present study
Immature	0-4Y*	57.7	Græsholmen	Denmark	1986-2009	23	Present study
Immature	0-5Y*	55.4	Græsholmen	Denmark	1986-2009	23	Present study
Immature	0-4Y	18.0	Skokholm	Wales	1963-1973	10	Lloyd & Perrins 1977

Discussion

This study with its 29-year data series that exceeds the average life expectancy of a Razorbill gives a detailed picture of the life and dynamics of a seabird colony in the central Baltic. The Razorbills on Græsholmen generally lived under very good conditions during the study years (1983-2011). Annual survival rates for adult breeding birds (93-95%) and for young birds to the age of first breeding (4Y, 57.7%) were among the highest recorded in any study (Tab. 35 and references therein). Mean annual breeding success (73%) was also high (see Lavers *et al*. 2009 and references therein). The rate of annual adult nonbreeding was low (3%). The only other study on adult nonbreeding also found a rate of 3% in an increasing population (Isle of May; Harris & Wanless 1989). The high number of 1-2Y birds visiting Græsholmen and the relatively high numbers of birds starting to breed at an age of 3Y also suggest good conditions for the breeding population. In a stable or slightly declining colony at Skokholm, Wales, no 1Y birds and only small numbers of 2Y birds visited the colony, no 3Y birds bred and the mean age of first breeding attempt was five years (Lloyd & Perrins 1977). Decreasing age of first breeding appears to be a typical trait in increasing seabird populations (e.g. Coulson *et al.* 1982, Votier *et al.* 2008). In addition, much of the diurnal foraging of chick-rearing birds took place within a few kilometers from Græsholmen, enabling a breeding pair to spend around six hours together in the colony. At the very large colony at Latrabjarg, Iceland, the mean foraging distance of chick-rearing birds was 50 km and breeding pairs were only able to spend a few minutes together (Dall'Antonio *et al*. 2001).

During the study years, the breeding population on Græsholmen increased on average by 5.5% annually. The same development appears to have taken place among the entire Baltic population. In the early 1970s, the Baltic Razorbill breeding population was estimated to be in the order of 5000 pairs (Lloyd 1976b). The observed increase of the breeding population on Græsholmen was paralleled in the largest Baltic colony on Stora Karlsö, Sweden, where the number of Razorbills counted on the water increased by 925% between 1973 and 2016, corresponding to a mean increase of 5.6% p.a. (Olsson & Hentati-Sundberg 2017). Based on data from the present study, Herrman *et al*. (2013) and Olsson & Hentati-Sundberg (2017), the Baltic Razorbill breeding population around 2013 was of the order of 40 000 breeding pairs. Assuming the population contained 1.4 immature (1-3Y) birds per breeding pair, the total Baltic population at that time numbered in the order of 135 000 birds. The Baltic breeding population of Common Guillemots also increased during this period: on Stora Karlsö, the population increased by 175% during 1973-2016 (Olsson & Hentati-Sundberg 2017) and on Græsholmen it increased by around 160% during 1992-2018 (pers. obs.). This study suggests that the main driver behind the long-term increase of the Baltic Razorbill population was high survival rates of both adult and immature birds combined with a high breeding success. There are, however, no life history data available to pinpoint any one particular reason for the high survival. Food availability is essential for any (seabird) population growth. As the largest biomass in the open Baltic Sea, the sprat is one of the most important fish species in the marine food web there (Eero 2012) – and is the most important prey for both Razorbill (this study) and Common Guillemot (Lyngs & Durinck 1998, Evans *et al*. 2013). Overall, the Baltic sprat spawning stock biomass (SSB) was relatively high in the 1970s, low in the early 1980s, and increased to very high levels in the mid-1990s (ICES 2016; Fig. 46) due to reduced cod *Gadus morhua* predation and favourable climatic conditions (Eero 2012). At

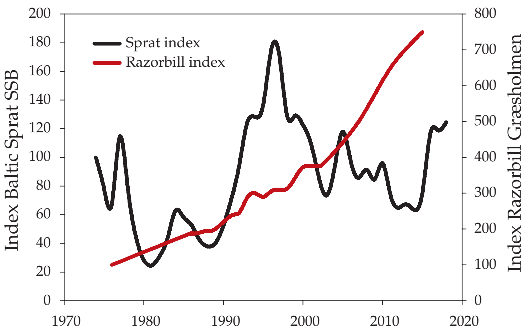

Fig. 46. Indices of sprat spawning stock biomass (SSB) in the Baltic (blue line; data from ICES 2016) and Razorbill breeding population on Græsholmen (red line) over recent decades.
Indeks for gydebestandens biomasse hos brisling (Index Baltic Sprat, SSB) *i Østersøen (blå streg) og for ynglebestanden af Alk på Græsholmen* (Index Razorbill Græsholmen) *(rød streg) gennem de senere årtier.*

least in this large-scale scenario, there was no correlation between the development in sprat SSB and the growth of the Razorbill breeding population on Græsholmen (Pearson $R^2 = 0.0193$, $P = 0.538$). In other words, food for the Baltic Razorbills appears to have been abundant at least since the 1970s. Since the 1970s, several environmental parameters have changed, which theoretically could have influenced Razorbill survival. For example, the Common Guillemot and the Razorbill became legally protected in Denmark (as the last country around the Baltic to do so) in 1978-1980. In 1975/76, the Danish bag of Razorbills was estimated at 1200 birds (Lyngs & Kampp 1996). The levels of some contaminants (e.g. DDE and PCBs) in Common Guillemot (and Razorbill) eggs both on Græsholmen and Stora Karlsö have dropped considerably since the 1970s (Lyngs 1992, Bignert & Helander 2015). In addition, some changes in commercial fishing policies – primarily the ban on drifting gillnets introduced in the Baltic in 2008 (ICES 2018) – may potentially have considerably reduced by-catches of auks (see Österblom *et al*. 2002). Furthermore, immigration could theoretically influence population development. Adult breeders exhibit a high degree of natal fidelity, but among both the Razorbill and the *Uria* guillemots some intercolony movements of visiting/prospecting immature birds as well as some permanent emigration of first-time breeders do occur (Ainley *et al*. 2002, Gaston & Hipfner 2000, Lavers *et al.* 2009 and references therein). The data from Græsholmen suggest that intercolony movements of visiting/prospecting immature Razorbills are relatively common in the Baltic, whereas permanent emigration among birds breeding for the first time apparently only involves a few percent of the population (as found among the Baltic Common Guillemot; Lyngs 1993). This emigration may influence local population development in the smaller receiving Baltic colonies but not the overall population development in the region. There are no indications of immigration to the Baltic from nearby Razorbill populations breeding in southwestern Norway and the British Isles (of the subspecies *A. t. islandica*).

Apart from the demographic parameters mentioned above, the study on Græsholm provided information on several aspects of Razorbill breeding biology, such as the influence of egg size (volume) and female age on breeding success and the timing of laying. Overall, breeding success was related to egg size, and eggs that produced fledging chicks were significantly larger than eggs that did not. Egg size decreased with laying date, and breeding success decreased during the season. Relative to mean annual laying date, laying date advanced for young breeders, while it remained relatively constant between years for older females. In addition, egg size increased with female age/breeding experience, especially during the first years after commencing breeding. In a given season, late breeding birds thus consisted of a mix of first-time breeders, some birds that replaced lost eggs and a few experienced females that consistently laid late (and laid small eggs). Finally, the overall timing of the annual laying period was correlated to early spring sea surface temperature. Similar characteristics have also been shown in several other studies of both Razorbill and the two *Uria* guillemots (Ainley *et al*. 2002, Gaston & Hipfner 2000, Lavers *et al*. 2009 and references therein) and all should probably be considered as general traits among the three large Alcinis. The study on Græsholmen

During recent decades, a population of Great Black-backed Gulls has begun breeding on Græsholmen.

The Razorbills share Græsholmen with several thousand pairs of Common Guillemots breeding in open colonies.

also showed that some older experienced females consistently laid larger eggs, had a higher breeding success and kept their partners for a longer time than others, suggesting that individual female quality was also a key factor in the overall reproduction success. Variation in individual quality of older females has also been shown in Brünnich's Guillemot (Hipfner *et al.* 1999) while in a detailed behavioural study on the variation of individual quality in the Common Guillemot, Lewis *et al.* (2006) found that quality operated most strongly at the level of the breeding pair. Apparently, variation in individual quality of older breeding birds is also a common trait in the three large Alcinis. Divorce rates among Razorbills have not previously been described, but on Græsholmen the average yearly divorce rate was 14.5%. In all divorces, one bird from the original pair stayed at the nest and bred there with a new partner, while the other bird moved to another nest. A significantly higher proportion of females than males stayed at the original nest after a divorce. The divorce rate was highest (26%) among the youngest birds (3-7 years), lower (13%) among 8-12-year-old birds and lowest (3%) among the oldest (13-22 years). A generally high breeding success and high nest site fidelity in older birds suggest that age and/or experience influence the divorce rate – and perhaps that older birds had more time to find a suitable mate. Among Common Guillemots, Moody *et al*. (2005) found an average divorce rate of 8.2% in Newfoundland and Jeschke *et al.* (2007) found a rate of 10.2% on Isle of May, but in neither case was the divorce rate of different age-classes known.

Variation of throat colour was noted for a number of large chicks. Chicks with a black throat (like adult summer) constituted 77.1%, while 3.4% had a white throat (like adult winter). There was some variation between colonies in the proportion of these parameters (Hudson (1984) found 49% white throated chicks on Skomer in Wales, while Birkhead & Nettleship (1985) found only 1.5% on Gannet Clusters in Canada) but the biological significance is unknown.

In conclusion, this study emphasises that long-term studies is the only way to obtain a number of important demographic parameters of long-lived seabirds, which reflect environmental constraints (see e.g. Dunnet 1989, Bradley *et al.* 1991) and that the continuity of long-term-studies is best ensured by anchoring them in institutions with an ample supply of money and students (Nisbet 1989). Further, this study provides a unique baseline for future studies to focus on detailed ecosystem linkages at different temporal and spatial scales in the Baltic ecosystem. The use of modern techniques such as data loggers and bioindicators could greatly improve such studies.

Acknowledgements

The present work was inspired by Knud Paludan's (1947) book *Alken* [The Razorbill] presenting the results of his studies of Razorbills on Græsholmen in 1944 (we actually inherited his dinghy and used it for the first years of the study) and by the study of Clare Lloyd (1976b) on Skokholm in Wales. Our study was initiated in 1983 by Flemming Rath Christensen and PL. Flemming perished in August 1984, but from 1990 Lars Abrahamsen and from 1992 Gitte Christensen Lyngs participated in the study, spending countless unpaid hours on Græsholmen, driven by their love for the island and its seabirds.

Over the years, Lene Tysk Andersen and Jørgen 'Pjøk' Harder-Hansen of Ertholmene provided much appreciated logistic support and good company during our stay. Through an energetic effort, Niels-Christian Clemmesen plotted the position of the Razorbill nests and made the basic maps of Græsholmen. Silvano Benvenuti braved gales to use his data-loggers in connection with the ongoing study. Jens Bagger, Oluf Lou and several others helped with the fieldwork in shorter periods. A number of other people helped in different practical ways: Torben Andersen, Ina Jørgensen, Lars Juul, Harald Kjøller, Henning Noer, Jan Kidholm Christensen, Poul Erling Stigfeldt, Lars Gundersen, Jan Tandrup, Niels-Erik Franzmann and the inhabitants of Ertholmene. Jan Durinck from Marine Observers kindly allowed use of the data from the ship-based surveys of 2008. Henrik Österblom and Olof Olsson helped us during our visits to Stora Karlsö, Sweden.

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To all: Thank you very much.

Resumé

Ynglebiologi og populationsdynamik hos en kolonirugende havfugl: Alken – et langtidsstudie af en ekspanderende alkekoloni på Græsholmen i den centrale del af Østersøen, 1983-2011

I årene 1983-2011 gennemførte Christiansø Feltstation et langtidsstudie af Alkene på Græsholmen ved Christiansø (Fig. 1), og denne artikel beskriver resultaterne. Der blev brugt over 4000 timers feltarbejde (Tab. 2), og materialet bestod blandt andet af 3000 målte æg, 8400 ringmærkede unger og 27 000 aflæsninger af Alke ringmærket på Græsholmen (Tab. 3). Desuden optaltes antallet af brugte reder hvert år, med meget grundige optællinger 1986-2006, og ynglebestanden steg gennem hele undersøgelsesperioden (Fig. 3).

Formålet med studiet var at indsamle så mange demografiske og populationsdynamiske data som muligt med de hjælpemidler, der var økonomisk tilgængelige: teleskoper med zoomlinser som kunne bruges til at aflæse de anvendte trekantede ringe på op mod 60 m afstand, flytbare skjul (et stort stykke vand- og vindtæt lærred) og et stationært skjul, linealer, skydelærer, notesbøger samt frivillig arbejdstid. Selvom studiet på mange måder må kaldes gammeldags – fx blev dataloggere kun brugt én gang, i 1998, og de kunne kun logge tre døgns dykkedata – er resultatet blevet et af de mest detaljerede studier over Alken nogensinde og det eneste langtidsstudie fra Østersøen.

Først nogle generelle informationer om Alken, en kolonirugende, fiskeædende havfugl som kun kommer på land for at yngle. Dens nærmeste slægtninge er Lomvie og Polarlomvie, og disse tre store alkefugle deler en række ynglebiologiske træk: De lever længe, yngler først i en alder af 3-6 år, er monogame, lægger kun et æg og udviser en høj grad af stedtrohed, når de først er begyndt at yngle. Når ungen er 2-3 uger gammel og langt fra flyvefærdig (Appendix s. 22), følger hannen den ud på det åbne hav, hvor de to bliver sammen, indtil ungen er selvstændig hen på efteråret. Denne vigtige hændelse kaldes her ungens udgang, og betegnelsen 'udgangsunger' referer til unger, som har forladt reden på vej ud på det åbne hav sammen med hannen.

På Græsholmen startede Alkenes æglægning omkring 24. april i et gennemsnitligt år. Den gennemsnitlige klækningsdato faldt 19. juni, og de sidste unger forlod reden 11. august (Fig. 6), svarende til en yngleperiode på 109 dage. Yngletidens fænologi det enkelte år var korreleret med havets overfladetemperatur i det tidlige forår, og i kolde forår kunne den gennemsnitlige klækningsdato falde op til 19 dage senere end i varme. Formentlig er havtemperaturen dog nok et udtryk for, hvor dybt Alkenes vigtigste føde, brisling, står i vandsøjlen, og hvornår hunnerne kan få samlet energi nok til at danne deres ene store æg – som udgør omkring 15 % af hunnens kropsvægt. Efter yngletiden overvintrede Græsholmens Alke hovedsageligt i den centrale og sydøstlige del af Østersøen øst for 18° E, med nogle få – især yngre fugle – i de indre danske farvande.

Det meste af yngletiden fouragerede Alkene inden for små 5 km fra Græsholmen i dagtimerne (Fig. 7-8, Tab. 5), og især midt på dagen dykkede de ned til omkring 43 m dybde. Deres tidsskema gjorde, at parret i ungefodringstiden kunne bruge omkring seks timer sammen i kolonien. I de mørke timer (Fig. 8-9, Tab. 5) blev én af magerne i reden, mens den anden fløj 10-30 km ud på havet og fulgte brislingernes vertikale vandringer. I skumringen stiger brislingerne stimevis opad og spreder sig derefter, mens de i lysningen atter samler sig i stimer og trækker nedad. Alkene fulgte brislingernes rytme i serier af dyk, der ikke var dybere end 20 m. Disse natlige togter varede omkring otte timer, hvoraf 80 % af tiden blev brugt til at hvile på havoverfladen. Til sammenligning fouragerede ynglende par ved den meget store koloni Latrabjarg på Island i snit 50 km væk og kunne kun tilbringe et par minutter sammen i kolonien.

Alke af alle aldersklasser sås på land på Græsholmen, men fænologien hos de yngre aldersklasser (1-3-årige) afveg fra de ældre aldersklassers. Således blev hovedparten af de et-årige fugle registreret i perioden 20. juni til 16. juli, svarende til den periode, hvor klækningen kulminerede, og frem til de første af årets unger begyndte at tage til havs. De et-årige Alke sås kun inde på land i nogle få dage, og stod næsten udelukkende nær vandkanten. I øvrigt spredtes de om sommeren over et stort geografisk område, fra den Botniske Bugt til ud i Nordsøen. De to-årige fugle begyndte at dukke op i kolonien i midten af april, og antallet steg gennem ynglesæsonen for at kulminere i slutningen af juli og de første dage af august. Selvom mange kun opholdt sig få dage i kolonien, blev andre der gennem næsten hele ynglesæsonen. De deltog ivrigt i de ældre Alkes sociale liv, og nogle få dannede par med andre to-årige og parrede sig, dog uden at lægge æg. De to-årige sås på hele Græsholmen, men fordelingen i kolonien var ikke tilfældig – hovedparten sås især i de områder, hvor de selv klækkede to år før. Tre-årige fugles forekomst mindede mest om de adultes (4 Y+) forekomst, og 23 % af dem ynglede, om end oftest sent på sæsonen. Den gennemsnitlige alder ved første yngleforsøg var fire år (fra 3 til 7 år) både hos hanner og hunner. I en alkekoloni i tilbagegang på Skomer, Wales, var den gennemsnitlige alder ved første yngleforsøg fem år og ingen tre-årige fandtes ynglende. Samtidig sås der ingen et-årige og kun få to-årige inde i kolonien. At alderen ved første yngleforsøg falder, synes at være et typisk træk hos mange havfugle, hvor bestanden er i fremgang.

Alkene på Græsholmen udviste en høj grad af lokal stedtrofasthed og 88,5 % vendte tilbage til den rede, de ynglede i året før, og 97,5 % til deres subkoloni. 72 % af redeskiftene skete i forbindelse med en ændring i 'parstatus' i forbindelse med skilsmisse eller partnerens død. Den gennemsnitlige årlige skilsmisserate var 14,5 %, men var signifikant højere hos yngre fugle (26 %; 3-7 y) end hos ældre (3,1 % 13-22 y). Blandt de unger, som vendte tilbage til Græsholmen for at yngle, havde 50 % rede i den subkoloni, de var klækket i, med en lige fordeling mellem hanner og hunner.

Alkenes årlige overlevelse var 93-95 % hos adulte ynglefugle, og en samlet overlevelse på 57,7 % for ungfugle frem til yngledygtig alder (4 år). Begge værdier er blandt de højeste fundet i nogen alkekoloni. De fleste adulte Alke ynglede hvert år, kun 3 % sprang et år over. Den gennemsnitlige ynglesucces var 0,73 udgangsunge per par, hvilket også er i den høje ende sammenlignet med andre kolonier. Ynglesuccesen faldt gennem sæsonen og var signifikant lavere i juli-august end i maj-juni. Det samme gjaldt ægstørrelsen.

Alkenes æg var nøglen til en række spændende oplysninger (Fig. 11-18). En del hunner kunne genkendes fra år til år, da pigmenteringen og farven på deres æg ikke ændrede sig meget, selv over en lang årrække. Udseendet på andre hunners æg ændrede sig dog så meget fra år til år, at man ikke nødvendigvis kunne genkende disse hunner fra år til år. Æggets størrelse og hunnens alder havde stor indflydelse på ynglesuccesen, og overordnet var æg, der producerede udgangsunger, statistisk signifikant større end æg, der ikke gjorde (Tab. 8). Hos unge hunner faldt lægningsdatoen de første 2-3 år, de ynglede, tidligere og tidligere i forhold til den gennemsnitlige årlige klækningsdato, mens ægstørrelsen øgedes med i alt omkring 10 %. Hos ældre hunner med større erfaring lå læggedatoen fast i forhold til årets gennemsnitlige årlige klækningsdato, og ægstørrelsen øgedes kun ganske lidt. I en given ynglesæson var mange af de sent ynglende hunner derfor førstegangsynglende med mindre æg og dårligere succes end blandt tidligt ynglende hunner. Samtidig viste det sig, at nogle ældre hunner konsekvent lagde større æg, havde højere ynglesucces og færre rede- og partnerskift end andre – hvilket indebærer, at den individuelle kvalitet af den enkelte ældre hun har betydning for den overordnede reproduktionssucces. Lignende resultater er fundet hos Polarlomvien, og i et grundigt adfærdsstudie over Lomvie blev det vist, at fuglenes kvalitet spillede en rolle på parniveau, således at højkvalitetsfugle dannede par.

Alke fra andre kolonier (Fig. 1) sås jævnligt på Græsholmen, og i alt aflæstes 37 mærket som unger i andre kolonier. De fleste (35) var mærket som unger i 14 kolonier i Østersøen og to på Hallands Väderö på den svenske vestkyst; den gennemsnitlige afstand mellem klækningssted og Græsholmen var 621 (205-930) km. Hovedparten (22) blev aflæst som gæstende ungfugle (hovedsagelig i deres 1-3 leveår), mens 15 ynglede på Græsholmen. Tre Alke mærket som unger på Græsholmen, blev aflæst som ynglende på Bornholm og Stora Karlsö, og to som unge gæster på Stora Karlsö (der var dog i det store hele ikke aflæsningsaktiviter andre steder end Græsholmen). Aflæsningerne og genfund tyder på, at det er ret almindeligt, at Alke fra Østersøen besøger andre kolonier i deres yngre år, og man kan forsigtigt beregne, at en mindre del (måske 2 % af en årgang) begynder at yngle i andre kolonier end deres klækningskoloni.

I løbet af undersøgelsen steg bestanden af ynglende Alke på Græsholmen fra omkring 250 par i 1983 til 1200 par i 2011, svarende til en vækst på 380 %. I årene 1986-2006 blev der foretaget meget grundige optællinger af reder, og her steg bestanden i snit 5,5 % (-3,7 – 20 %) om året. I fem af disse år steg bestanden med mere end 10,6 %, hvilket tyder på en vis indvandring fra andre baltiske kolonier. Hele den baltiske bestand steg i disse år. Ved den største koloni i Østersøen, Stora Karlsö, steg antallet af Alke på vandet ud for kolonien med 925 % mellem 1973 og 2016, svarende til en årlig vækst på 5,6 %. I starten af 1970erne blev den samlede baltiske bestand anslået til 5000 par og i 2013 til 40 000 par. Den meget høje overlevelse hos både adulte og unge fugle har været drivkraften bag bestandsvæksten, men hvorfor overlevelsen har været højere fra 1980erne og frem end i årene før, vides ikke. Fiskeriundersøgelserne i Østersøen viser, at der har været mange brislinger – Alkenes vigtigste føde – i hvert fald siden 1970erne, og der er ingen direkte kobling mellem alkebestandens størrelse og brislingebestandens størrelse. Siden 1970erne er der fx sket ændringer i jagttrykket (Alken blev jagtfredet i Danmark i slutningen af 1970erne – som det sidste land rundt om Østersøen), mængden af miljøgifte i æggene er faldet og bifangsten af alkefugle i især laksedrivgarn er faldet for at stoppe helt ved forbuddet mod drivgarn i 2008. Det er dog ikke muligt at koble nogen af disse forandringer direkte til alkebestandens udvikling. Ind- og udvandring mellem baltiske kolonier har haft lokal betydning, især for mindre eller nye kolonier (Fig. 35 og 45). Således er fx den lille bestand på selve Bornholm opstået som følge af indvandring bl.a. fra Græsholmen. Men den overordnede bestandsudvikling i Østersøen kan ikke forklares ud fra indvandring, da denne i så fald skulle være kommet fra kolonier i Nordsøen, fx fra De Britiske Øer eller det vestlige Norge. Og der er ingen indicier på, at en sådan indvandring skulle være sket.

Studiet på Græsholmen understreger, at langtidsstudier er den eneste måde at skaffe en række vigtige demografiske og ynglebiologiske parametre hos havfugle, der lever i lang tid. Desværre er langtidsstudier ikke særligt udbredte, hovedsageligt fordi det tager mange år, før resultaterne kommer. Adskillige langtidsstudier rundt om har været drevet af private, men som arbejdet på Græsholmen også viser, kan det være svært at skaffe penge og forskere til virkelig lange studier. Ideelt burde langtidsstudier af denne art være forankret i institutioner med en rigelig tilgang af midler og studerende. Trods disse begrænsninger foreligger der nu en basisundersøgelse over Alkene på Græsholmen, og det er fristende at lege med tanken om, hvad der kunne være kommet ud af endnu 30 års studier med brug af avanceret udstyr som dataloggere og bioindikatorer. Under alle omstændigheder var det en fornøjelse at tilbringe 29 feltsæsoner sammen med Alkene på Græsholmen.

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Appendix 1:
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