Reproductive performance in Great Cormorants during colony expansion and stagnation

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Contents

Preface

This thesis reports the results of a project conducted on Great Cormorants during Part B of a Ph.D. study at the Institute for Biological Sciences, University of Aarhus. During Part A, a study of breeding success and colony development in Common Eiders was performed. The results of the Eider study have been reported separately. The present thesis deals with the influence of colony size and age of individual breeders on breeding parameters in Great Cormorants and includes chapters describing the development of the Danish and European breeding population and its distribution outside the breeding season. The thesis consists of an introductory chapter, three manuscripts and four papers in press or already published.

Acknowledgements

Summary

Breeding success, population development and distribution outside the breeding season of Danish-breeding Great Cormorants *Phalacrocorax carbo sinensis* was studied. Analyses of data on breeding success of known-age individuals showed that breeding success increased with parental age and that birds advanced timing of breeding with increasing age. Both breeding experience and age itself affected breeding success. Some parents raised large broods and had high survival whereas others performed poorly and had low survival.

Changes in breeding success with growth of the Vorsø colony was studied. The changes suggests that parents became food limited after colony growth had levelled off. It was not clear whether predation of fish stocks by the Cormorants caused the decline in food availability. Some of the birds from the Vorsø colony emigrated and founded new colonies. A study in one of the new neighbouring colonies suggested that food was more easily available here than in the old colony and that breeding success was higher. Hence those individuals which emigrated performed better than those which remained in the old saturated colony.

Since the mid 1960s the population of continental Great Cormorants breeding in Europe has increased markedly: from c. 4000 pairs in 1965 to c. 95 000 pairs in 1995. The Danish breeding population increased from 250 pairs in 1970 to 38 300 pairs in 1995. Decreasing disturbance and persecution by man, abundance of food near breeding colonies, and possible higher survival on the wintering grounds is suggested as being responsible for the expansion. The rate of expansion in the Netherlands and Denmark has slowed down in recent years.

A large number of areas are used by Danish Cormorants on their migration to and from the wintering areas. The most-used wintering areas in Europe for Danish-breeding Cormorants are the inner Danish coastal waters, and lakes and coastal areas in Germany, France, Switzerland, Italy and Tunisia.

Chapter 1

General introduction

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gør de nyankomne Stære.

General introduction

The Cormorants as a group (Phalacrocoracidae) are large to medium-sized, highly colonial, aquatic birds. They have a worldwide distribution, mainly in tropical and temperate regions. Most species inhabit coastal waters and estuaries, but some are found inland (del Hoyo 1992).

This chapter pays particular attention to factors affecting breeding success and regulation of breeding numbers of continental Great Cormorants *Phalacrocorax carbo sinensis*.

Background and perspective

Within a span of 30 years, the status of the continental Great Cormorant in Europe has changed from being threatened and in need of active protection to becoming an expanding species subject to local and regional control programmes (Chapter 5,7). Cormorants depend on fish and thus impinge on human interests, either commercial or social, giving the potential for both real and perceived conflicts amongst fishermen, fishery managers and bird/nature conservationists. A few countries have therefore developed national management plans for the species (Bregnballe & Asbirk 1995; Veldkamp 1996). These plans aim at maintaining a favourable conservation status at the same time as reducing the damage caused by Cormorants. Management policies have been under pressure from fishery interests and politicians (C. van Dam & W. Suter pers. comm.; example in Bregnballe & Asbirk 1995) and the authorities in several countries have now resumed actions to avoid presence of Cormorants and further increase in population size. The actions taken outside the breeding areas include scaring and shooting of birds when present in their foraging areas, on day roosts, and on night roosts (Van Eerden, et al. 1995; L. Marion, N. Baccetti & E. Staub pers. comm.). Rather large numbers of Cormorants (2000 or more) are now being shot per season in each of the countries France, Italy, Switzerland, Poland and Denmark (Lindell et al. 1995; L. Marion, N. Baccetti & E. Staub pers. comm.). Actions taken in breeding areas include scaring and shooting of continental Great Cormorants attempting to found new colonies, removal or spraying of eggs to reduce hatching success, and felling of nesting trees (e.g. Bregnballe & Asbirk 1995; Lindell & Jansson 1995; Lindell, et al. 1995, Veldkamp 1996).

In most European countries, management deals only with local human needs and concerns, with little regard for the requirements of the birds. Being migratory, the continental Great Cormorant moves across political boundaries, and Denmark and the Netherlands have, therefore, initiated work on developing a management plan for the European flyway of the continental Great Cormorant. Before cost-

effective management schemes on a flyway scale can be developed, two things are needed. First, characteristics of the environment and the bird's life-history and behaviour, which promote and limit population expansion have to be identified. Secondly, knowledge about population parameters, mechanisms of density-dependent regulation and carrying-capacity effects are needed. Thirdly, the distribution during autumn and winter of birds from different breeding areas should be identified.

Aim and approach

The aim of the work presented in this thesis was:

1. To describe the development and the distribution of the Danish breeding population of continental Great Cormorants.
2. To identify factors which may limit the population from expansion.
3. To quantify demographic parameters, especially breeding success, and investigate whether parameter values are related to population size.

To provide information about population expansion and population limitation, I collated data on the development of Cormorant colonies in Denmark (Chapter 5,6) and Europe (Chapter 7). To identify the areas that Danish Cormorants depend upon outside the breeding season, ring recoveries and resightings of colour-ringed individuals were organised and analysed (Chapter 8). To quantify demographic parameters and study the influence of bird density on population parameters, a large data set on individually marked Great Cormorants breeding in the colony on Vorsø, east Jutland, was organised and analysed. Results of analyses of changes in the production of young and effects of age on breeding success are included in the thesis (Chapter 2,3). The analyses of changes in age at first breeding, timing of breeding, frequency occurrence of non-breeding, return rate of immatures, and rate of recovery of dead birds are not included. To identify some of the environmental factors responsible for regional variation in population growth, young production in Danish and Dutch colonies was compared (Chapter 7). In 1993-1995, reproductive success in several Danish colonies was monitored, but only the results from the Stavns Fjord colony, Samsø, are included in the thesis.

Breeding success

Breeding success is an important parameter for population growth in continental Great Cormorants (Van Eerden & Gregersen 1995) and the influence of some of the factors potentially affecting breeding success has been studied and is discussed below.

Individual variation

Individual performance of continental Great Cormorants nesting in the colony on Vorsø was dependent on age, breeding experience and individual quality (Chapter 2). Timing of arrival to the colony turned out to be an important variable for breeding success (Chapter 2), suggesting that choice of wintering area might influence breeding success (Bregnballe unpublished). There was some indication that individuals which fledged in food poor years produced fewer fledglings when breeding than individuals which fledged in food rich years, but the year-class effects were small (Bregnballe unpublished).

Influence of predators, nesting sites and food availability

The influence of predation of eggs and young on breeding output was not studied, but predation seems to be of minor importance as long as Cormorants are undisturbed. Although, nesting site quality can influence breeding success and give rise to individual and subcolony variation in nesting success (cf. Van Eerden, et al. 1991), food availability seem to be the single most important factor regulating breeding success in continental Great Cormorants. This is seemingly the case for most seabirds (Furness & Monaghan 1987, Croxall & Rothery 1991, Anker-Nilssen 1992, Crawford & Dyer 1995).

Alternative prey

Availability of alternative prey may buffer seabirds against the effects of local fluctuations in a particular prey population but, where or when alternative prey is unavailable, seabirds are likely to be vulnerable to variation in the supply of their main prey (Furness & Monaghan 1987, Crawford & Dyer 1995, Monaghan 1992). This seems to hold true for the continental Great Cormorant. The Cormorants breeding in Denmark exploit a multitude of prey species (Hald-Mortensen 1994, Hald-Mortensen 1995) and this has a positive influence on the production of young, which has been high throughout the period of population growth (Chapter 7). The continental Great Cormorants breeding at Lake IJsselmeer, the Netherlands, have a more restricted diet than Danish Cormorants and fish availability varies considerably (Van Eerden, et al. 1991, Van Eerden and Voslamber 1995). Consequently, the production of young in the lake IJsselmeer area has shown large year-to-year fluctuations (Van Eerden, et al. 1991) and been lower than in Denmark (Chapter 7, Van Eerden & Gregersen 1995).

Influence of colony size

The production of young can be affected by colony size in several ways. Mean breeding success in a colony can decline as an increasing proportion of the sites where breeding success is poor are taken into

use (Potts, et al. 1980). Ecto and endo parasite load may build up with increasing colony size and affect chick survival (Feare 1976, Møller 1987, Brown, et al. 1990). The influence of these factors on breeding success was not studied.

Ashmole (Ashmole 1963, 1971) proposed a hypothesis to explain how colony size affects reproductive success in seabirds. The hypothesis predicts that when a colony is small, each pair will find plenty of food in the sea close to the colony, so the parents will not have to work hard to raise their chicks. As the colony increase in size, breeding birds will begin to deplete the food supplies close to the colony and will thus have to fly further out to sea to get food. With further increase in colony size, birds will be travelling so far they will not have time to make as many flights each day as needed to keep their chicks growing. Gradually, breeding success will fall and limit further recruitment to the colony. Some large seabird colonies do appear to deplete food resources in surrounding waters (Gaston, et al. 1983, Furness & Birkhead 1984, Wittenberger & Hunt 1985, Birt, et al. 1987, Hunt, et al. 1986) so that feeding conditions deteriorates with increasing colony size.

The pattern of changes in breeding success in the colony on Vorsø (Chapter 3) supports, but does not prove, the main predictions of Ashmole's model. Hence, we had evidence to suggest that the distance of foraging flights increased and that the number of daily feeds received by chicks declined as colony size increased. However, the production of young did not start to decline until a certain colony size was reached, and it was not clear whether declining fish availability was the result of predation by Cormorants.

Following year-to-year changes in breeding success in a single colony is not a strong method to study effects of increased colony size, because food availability may decline due to environmental change. To investigate further whether breeding success was related to the phase of a colony's development, breeding output was monitored in a number of other Danish Cormorant colonies and a tendency for lower production of young in saturated colonies than in colonies which were still in the phase of expansion, was found.

There is a need for further studies of the effects of colony size on breeding performance before it can be concluded that negative effects of colony size on breeding success are common in continental Great Cormorants. It seems likely that sedentary fish populations around colonies might become depleted, and some preliminary studies of fish densities around Cormorant colonies in Newfoundland suggest that depletion can happen (Birt et al. 1987). But it has yet to be proven that prey depletion regulates breeding output as proposed by Ashmole. This needs to be tested by observation and experiment.

Regulation of colony size

The production of potential recruits is not likely to be the only factor influencing colony size as predicted by Ashmole's model for regulation of colony size. Rather, the development of a colony will be determined by the balance between the demographic parameters: recruitment, survival, non-breeding and emigration.

Recruitment to a Cormorant colony can depend not only on the production of potential recruits, but also on factors affecting individual birds' choice of colony such as (a) the number and quality of nesting sites available, (b) the abundance of food around the colony, and (c) the type and frequency of disturbance by humans and mammalian predators (Kortlandt 1942, Lindell, et al. 1995).

Nesting sites

The number and quality of nesting sites available can limit recruitment in other ways than through its potential effect on breeding success. Firstly, if only low quality nesting sites are available, young individuals may abstain from settling and instead join other colonies, as demonstrated in Kittiwakes *Rissa tridactyla* (Porter & Coulson 1987). Thirdly, individuals may postpone breeding until they reach the age or social status where they are capable of obtaining nesting sites of 'acceptable' quality as shown for Oystercatchers (Ens 1992). In a review of population regulation in seabirds, Birkhead and Furness (1985) concluded that limitation by nesting sites appears to be an exceptional rather than a general situation. This seems to hold true for the continental Great Cormorant (e.g. Van Eerden & Gregersen 1995), however, convincing studies have not yet been performed.

Food availability

The amount of food available around colonies seems to play an important role for the size of continental Great Cormorant colonies. Hence, there appears to be a relation between the size of continental Great Cormorant colonies and the surface area and productivity of the nearby foraging areas (see Van Eerden & Gregersen 1995, Lindell, et al. 1995).

Furness and Birkhead (1984) demonstrated a negative relationship between the size of seabird colonies and the number of birds breeding in other colonies within a given range, and suggested that birds breeding in adjacent colonies competed for food. Cairns (1989) proposed a model to explain regulation of colony size, and suggested that seabirds would not feed regularly within the ranges of adjacent colonies. Cairns predicted that colony size was related to the surface area of feeding grounds within non-overlapping feeding zones near the colonies, denoted as 'hinterlands'. Support for this model was obtained from population analysis of British seabird colonies. Røv

(1994) studied colony size in Atlantic Great Cormorant *P. c. carbo* breeding in Norway. He found evidence to suggest that the area of shallow water and the spatial distribution of adjacent colonies (but not their sizes) regulated colony size, i.e. the findings were essentially in accordance with the predictions from the hinterland model.

The mechanism

Brown et al. (1990) suggested that colony size would be adjusted to resource availability within the breeding areas and to the number of conspecifics at other colonies through intercolony recruitment as predicted by the model of 'ideal free distribution' (Fretwell & Lucas 1970). It is common in seabirds that young individuals disperse from their birth place when they first breed (e.g. Chabrzyk & Coulson 1976, Serventy & Curry 1984, Kress & Nettleship 1988, Harris & Wanless 1991, Halley & Harris 1993, Aebischer 1995), and intercolony recruitment does explain some of the changes in colony growth and colony size in Danish Cormorant colonies (Chapter 4,6).

The tendency for experienced breeders to respond by emigration to changes in the costs and benefits of philopatry can greatly influence regulation of colony size in seabirds (Coulson & Nève de Mévergnies 1992, Danchin & Monnat 1992). Many of the Cormorants which had already settled as breeders in the Vorsø colony remained philopatric even though local food availability declined (Chapter 4). On the contrary, in Atlantic Great Cormorants breeding in Norway, Røv (1994) found a profound flexibility in colony choice also among experienced breeders. The reasons for this difference in philopatric behaviour is unknown but may relate to the difference between the two regions in density and physical structure of potential colony sites.

The size of the Vorsø colony

The observed change in breeding success in the Vorsø colony (Chapter 3) cannot explain the change from growth to stabilization of breeding numbers in that colony. Thus, preliminary analyses showed that the total number of young produced on Vorsø and the proportion of young returning to the colony before first breeding (an index for 'local survival') did not decline until after the colony had stopped growing (Bregnballe unpublished). Age at first breeding increased but not until after breeding numbers had stabilised. Resightings of adults on Vorsø did not suggest marked changes in adult survival and there was no increase in the proportion of old breeders which skipped breeding. Emigration from Vorsø, especially of first time breeders, has been extensive (examples in Chapter 5) and seems to be the main reason for the change from growth to stabilisation of the Vorsø colony. Changes in food availability around Vorsø combined with appearance of new colonies may have lead to increased natal dispersal. Subsequent decline in breeding success (Chapter 3) explains low recruitment in recent years.

Number and distribution of colonies

The number and distribution of many seabird colonies is limited by availability of safe sites (Furness & Monaghan 1987, Olsthoorn & Nelson 1990), and the results presented in Chapter 6 suggest that experience with safety plays an important role for the distribution and probably also the number of continental Great Cormorant colonies present in Denmark.

Limitation of population size

The size of the breeding population of the continental Great Cormorant may become limited mainly by a combination of (1) human control programmes affecting colony numbers and (2) density-dependence working in the breeding colonies. The overall population size may become limited by factors affecting immature and adult survival, e.g. the frequency occurrence of severe winters, human harassment and density dependent effects in some of the areas used by Cormorants in autumn, winter and spring.

Røv (1994) suggests (1) that density-dependent factors limit breeding numbers of Atlantic Great Cormorants in Norway both on a colony and a regional level, and (2) that the overall size of the Norwegian Cormorant population is partly regulated by winter conditions in a density-independent way.

Management of population size

Despite scarce documentation for competition between Cormorants and fisheries, the pressure to control continental Great Cormorant numbers at the national level is growing (C. van Dam, J. Kirby, E. Staub, N. Baccetti, L. Marion pers. comm.). Therefore, it is likely that actions will continue to be taken to reduce population size at local and regional levels. A range of actions can be taken, but some will be more cost-effective than others and some will better ensure that the species does not become extinct within regions than others.

I suggest that management strategies may take advantage of the process of natural density-dependent regulation by limiting the access that individual birds have to food resources. This can be done by artificially reducing the attractiveness of potential colony sites through scaring away those birds which attempt to settle in new areas. By hindering the foundation of new colonies, potential breeders will either join existing colonies or abstain from breeding, and if birds join existing colonies, density dependent effects can be expected to start to work on fledgling production and other population parameters sooner than if the birds settled in new colonies. This will advance the time of stabilisation of population size. Furthermore, since Cormorants are naturally limited from exploiting food resour-

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ces far from their breeding colonies, the population can be expected to stabilise at a lower level if potential breeders are unable to colonise sites near hitherto unexploited feeding areas.

The cost of limiting the number of colonies by scaring away birds is likely to be lower than the cost of reducing population size through shooting adults and spraying eggs to reduce breeding success (cf. Bédard, et al. 1995).

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Chapter 2

Age-related reproductive performance of Great Cormorants

Thomas Bregnballe

conspecifics (Raveling 1981; Rockwell, Findlay & Cooke 1983; Nol & Smith 1987; Sæther 1990; Perdeck & Cavé 1992; Fowler 1995), but there are many exceptions (Sæther 1990). The increase in reproductive success with age is generally largest over the first few years and often there is a decline in the oldest age-classes (Coulson 1984; Wooller et al. 1990).

Middle-aged and old individuals are expected to be more efficient foragers and have greater experience with foraging areas than younger individuals (Orians 1969; Morrison, Slack & Shanley 1978; Searcy 1978). The question arises whether all age-classes are affected to the same extent when food availability declines (Rockwell, Findlay & Cooke 1985; Boekelheide & Ainley 1989; Hamer & Furness 1991). In Brandt's cormorant (Phalacrocorax penicillatus Brandt) differences in reproductive performance between age-classes became larger as the availability of food diminished (Boekelheide & Ainley 1989) and in great skuas (Catharacta skua L.) age-related effects on reproductive success were evident only in a period of reduced food supply (Hamer & Furness 1991). This suggests that age-effects may depend on the accessibility of food.

Nol & Smith (1987) proposed four hypotheses to explain enhancement of reproductive performance with age. The breeding experience hypothesis states that reproductive performance improves with cumulative breeding experience. It predicts that birds entering the breeding population at older ages perform poorly in comparison to birds that already have achieved breeding experience by entering the breeding population at an earlier age. The age hypothesis states that with increasing chronological age, individuals improve their feeding skills, become more dominant, better competitors etc. and thus improve their reproductive performance. The restraint hypothesis states that young birds should withhold reproductive effort until they have achieved the size, status or experience necessary for successful reproduction (Curio 1983; Forslund & Pärt 1995; Fowler 1995; Pärt 1995). Restraint could be expected if young birds have little chance of breeding successfully, and if raising young incur a cost in terms of diminished survival or future fecundity. The differential survival hypothesis states that reproductive performance increases with age because young

birds, which perform poorly, disappear from the breeding population. The hypothesis predicts that reproductive performance differs between the young birds that subsequently do and do not survive. The hypotheses are not mutually exclusive (Wheelwright & Schultz 1994).

Young and inexperienced breeders often breed late in the season (Kortlandt 1942), and late breeders are often less successful than early breeders (see Perdeck & Cavé 1992). Therefore, to understand the reasons for age-related variation in reproductive performance, it is relevant to take the confounding effect of timing of breeding into consideration (Sydeman et al. 1991).

In this paper, breeding data from a long-term study of great cormorants (P. carbo L.) are used for examining age-specific differences in reproductive performance. In addition to describing the age-relation, I explore the effect of variation in timing of breeding, the influence of a change in food availability, and to what extent each of the hypotheses proposed by Nol & Smith (1987) can explain the age-related variation in breeding performance.

Methods

The continental subspecies of the great cormorant (P. c. sinensis L.) was studied on the island of Vorsø (55°52'N, 10°01'E), 34 km south-south-west of Aarhus, Denmark. The majority of birds nested in trees 3-14 m above the ground and nesting sites were not limited during the study period. Between 1977 and 1993, 9415 chicks were marked individually with an engraved plastic leg band on one leg and a metal ring on the other. Most of the breeding birds were observed from a blind overlooking a section of the colony holding 522-1097 pairs, constituting 11-63% of the total number of breeding pairs. Searches for ringed individuals breeding elsewhere in the colony were performed irregularly throughout the breeding season.

The data allowed analyses of the influence of age on date of arrival, timing of egg-laying, proportion successful of birds initiating clutches, brood size at fledging, total number of young fledged per clutch, the proportion of young returning to the colony as 1-3-year-old, and the

proportion recorded to join the colony as breeders. The number of young fledged per clutch, i.e. the product of the proportion successful of initiated clutches and brood size at fledging, was known for 3287 clutches (138-339 per year) of 1267 individuals (636 males, 631 females) breeding between 1983 and 1995. Not all parameters were recorded for all individuals. By 1-4 daily searches for ringed individuals throughout each year, the date of arrival was determined for 2927 bird-years. The date of laying was known or estimated for 1869 clutches. Absence/presence of eggs could be observed in only a few nests, making it difficult to precisely determine the laying date of the first egg. The timing of laying was therefore determined by back-calculation from observations of onset of incubation, hatching and/or from regular estimates of chick growth stages, assuming 2 days from laying of the first egg to start of incubation, and 29 days from start of incubation to hatching of the first egg. The young were scored as fledged (wings looked fully grown) when on average 49 d old (range 43-62 d).

Studies of feeding frequency, diet and breeding success suggest that food availability was higher during the first eight years of the study than during the last five years (unpublished). During the first period, 1983-1990, referred to as period I, the number of occupied nests increased from 1837 to 4642 nests, and the production of young ranged from 1.87 to 2.18 young per clutch. In the second period, 1991-1995, referred to as period II, breeding numbers varied between 4318 and 5048 nests with no trend, and the number of young raised per clutch declined from 1.64 in 1991 to 0.86 young per clutch in 1995. From period I to period II, the stock of at least two important prey species declined, the diet broadened, and the average distance that cormorants migrated on their foraging flights increased (Hald-Mortensen 1995; P. Hald-Mortensen & T. Bregnballe unpublished data).

To adjust for annual variation in mean arrival date, laying date, and number of young fledged, annual population means were subtracted from the variable and the residual was added or subtracted from the observed value for each individual bird before analyses. The population means were computed for each period (number of young fledged) or both periods (timing) after excluding birds younger than 5 years to avoid year-to-year variation in age structure of ringed birds.

The age of the female parent was known for 534 of the colour-ringed young and the age of the male parent for 617 young. The proportion of young returning to the colony at age 1, 2 or 3 years was calculated for the young raised between 1982 and 1990. The young raised after 1990 were excluded to avoid influence of low return rate of 1-3-year-olds in 1994-1995. The proportion of young later recorded as breeders (observed with eggs or chicks at the age of 2, 3 or 4 years) was computed for the young raised between 1981 and 1988. The young fledged after 1988 were excluded because the proportion of 2-4-year-olds recorded incubating declined after 1991.

In some years sample sizes were low and, therefore, proportional data were tested with χ^2-statistics and not with parametric statistics. To examine the relationship between parental age, date of arrival, date of egg-laying, brood size at fledging and number of young fledged per initiated clutch, I performed one-way analyses of variance (ANOVA), followed by a Scheffé multiple comparison test to determine differences between age-classes at the 0.05 level.

To test whether changes in breeding performance with increasing age could be related to intrinsic changes, a series of paired t-tests were performed on laying dates and number of young fledged by individuals seen breeding in two successive years. Since the analyses of single individuals did not allow me to distinguish between the effects of age and previous breeding experience, I used t-tests to compare (a) breeding performances of parents with and without previous breeding experience but of identical age (*breeding experience hypothesis*), and (b) birds with the same number of years of breeding experience but of varying age (*age hypothesis*). t-tests were applied to examine the *differential survival hypothesis* by comparing the reproductive performance of females and males that survived and bred in a subsequent breeding season with individuals which did not return to breed. Sequential Bonferroni (Rice 1989) was applied to reduce the probability of Type I error arising with the large number of comparisons. The potential effect of the duration of the pair-bond was not taken into account (Cézilly & Nager 1996), because few birds repaired (see

results). Multivariate tests were performed using factorial ANOVA and ANCOVA procedures with SPSSPC+ (Norusis 1990). Significance levels presented refer to two-tailed tests. Unless otherwise stated all tests refer to period I. For period I, 51% of the individuals were represented in more than one age-class, and for period II the proportion was 46%; i.e. not all data are independent.

Results

Age of partner

The age of both parents was known for 269 egg-laying pairs. Most males and females of 2-3 years of age had partners which were younger than would have been expected if pairing had occurred at random, and most 8-17-year-old males and females paired with mates older than expected (Fig. 1). Hence, age similarities within pairs were greater than would be expected through random assortment. Of the 2-3-year-old males, 75% were paired with 2-4-year-old females ($n = 61$). Of the 2-3-year-old females, 46% were paired with 2-3-year-old males ($n = 85$), whereas for 4-year-old females, only 16% were mated with 2-3-year-old males ($n = 45$). As found for other *Phalacrocoracidae* (Shaw 1985; Boekelheide & Ainley 1989; Aebischer, Potts & Coulson 1995), mate change between seasons was high (92.5%, $n = 817$ pairs).

Age-related reproductive performance

The percentage of egg-laying females successfully raising young to fledging increased linearly from 2 to 5 years of age in period I (Fig. 2a), as did brood size at fledging (Fig. 2c). The number of young fledged per initiated clutch increased by 0.76 young from age 2 to 5 and by 0.09 young per nest from age 5 to age 8-12 (Fig. 2e).

In period II, the number of young fledged per initiated clutch increased until females reached the age of 8-9 years (Fig. 2f). Of the females initiating a clutch, the percentage successful increased by 17% from 2-3 to 6-12 years of age in period I, and by 50% in period II (Fig. 2a,b).

In period I, a higher percentage of the 4-year-old and older males raised at least one young to fledging than did 2-3-year-old males (Fig. 2g),
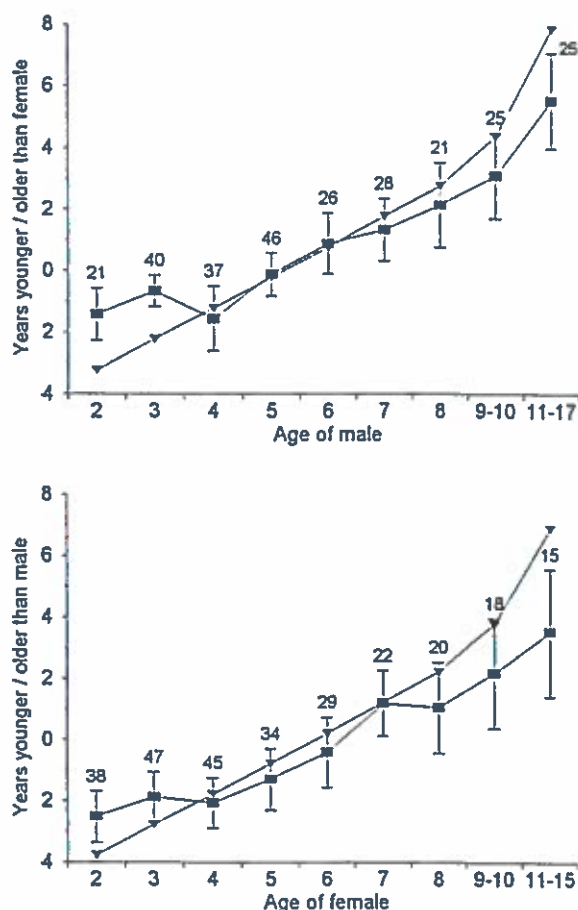
Figure 1. The mean age differences observed and predicted between members of great cormorant pairs in relation to male (upper) and female (lower) age; only pairs with eggs or young are included. Vertical bars indicate 95% confidence limits, and numbers above bars are sample sizes. The line connecting triangles is the predicted age-difference if birds had paired at random. It was calculated from the mean age of ringed birds with eggs or young, which was 5.23 for females ($n = 1574$) and 5.78 years for males ($n = 1743$).

whereas brood size at fledging showed only a slight increase with age (Fig. 2i). The number of young fledged per clutch increased linearly by 0.73 young from age 2 to age 4, and by 0.27 young from age 4 to age 9-12 years (Fig. 2k).

The form of the age-relation for males changed from period I to period II with a tendency for an increase until the age of 9 years and a tendency for a decline towards the oldest ages in period II (Fig. 2 h, l). The percentage of successful males increased by 21% from 2-3 to 6-12 years of age in period I, and by 111 % in period II. In period II, 4-year-old males raised 0.75 more young per nest than did 2-year-olds, and a further increase of 0.37 young was recorded

Female

Period I

Period II

(a)

(b)

(c) F = 7.70****

(d) F = 1.19 NS

(e) F = 12.74****

(f) F = 3.99****

Age

Age
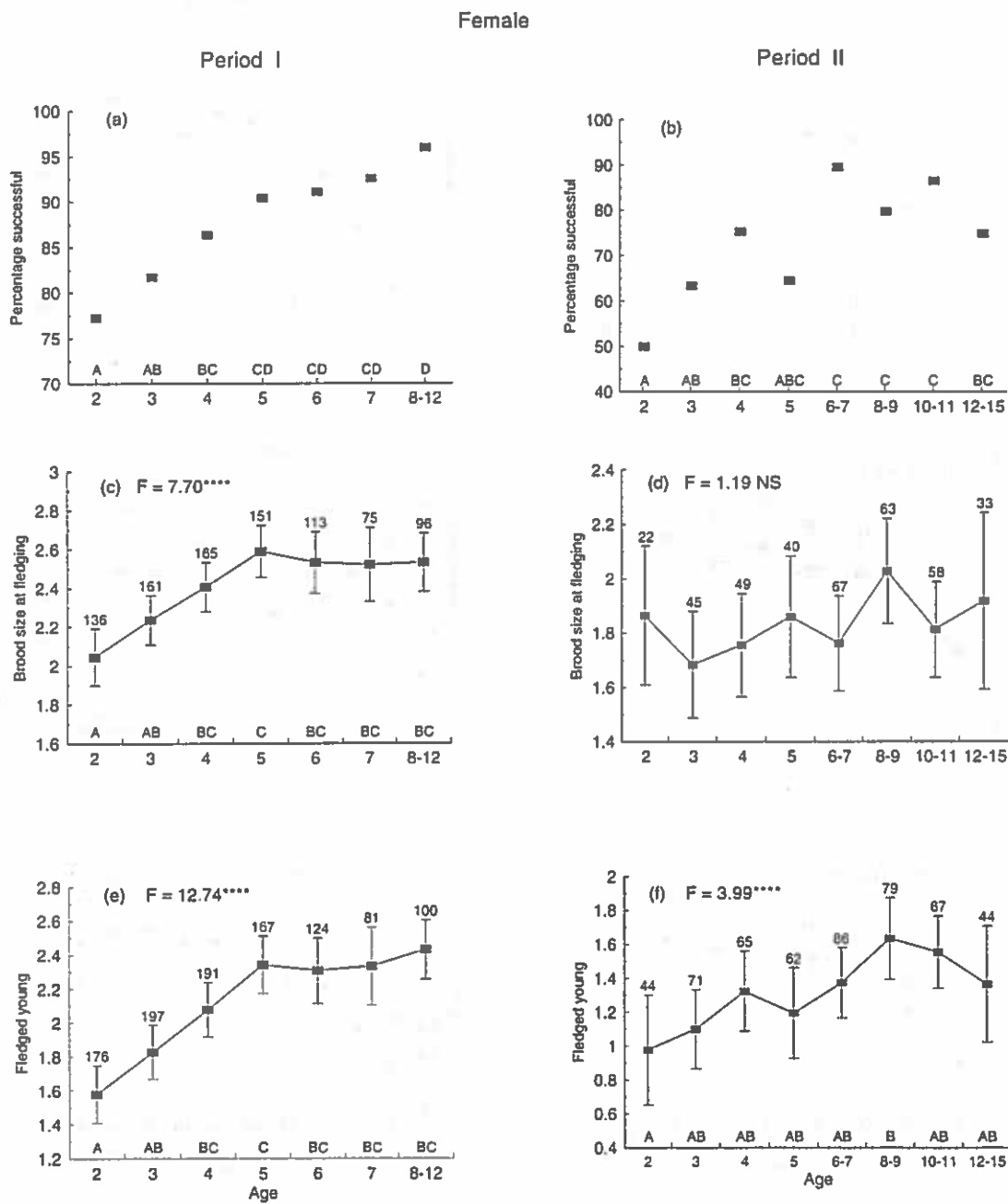
Figure 2. The mean age differences observed and predicted between members of great cormorant pairs in relation to male (upper) and female (lower) age; only pairs with eggs or young are included. Vertical bars indicate 95% confidence limits, and numbers above bars are sample sizes. The line connecting triangles is the predicted age-difference if birds had paired at random. It was calculated from the mean age of ringed birds with eggs or young, which was 5.23 for females (n = 1574) and 5.78 years for males (n = 1743).

from the age of 4 to the age of 9 (Fig. 2l). Hence, the number of young produced increased by 56 % from 2 to 4 years of age in period I, and by 123% in period II.

The proportion of fledged young returning to

the colony at the age of 1-3 years was independent of the age of parents (age-classes of parents, 2, 3, 4, 5-6, 7-8, 9-11; females, 23 < n < 143, χ^2 = 2.32, df = 5, P = 0.803; males, 20 < n < 138, χ^2 = 4.36, df = 5, P = 0.499). The probability of breed-

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Male

Period I

Period II
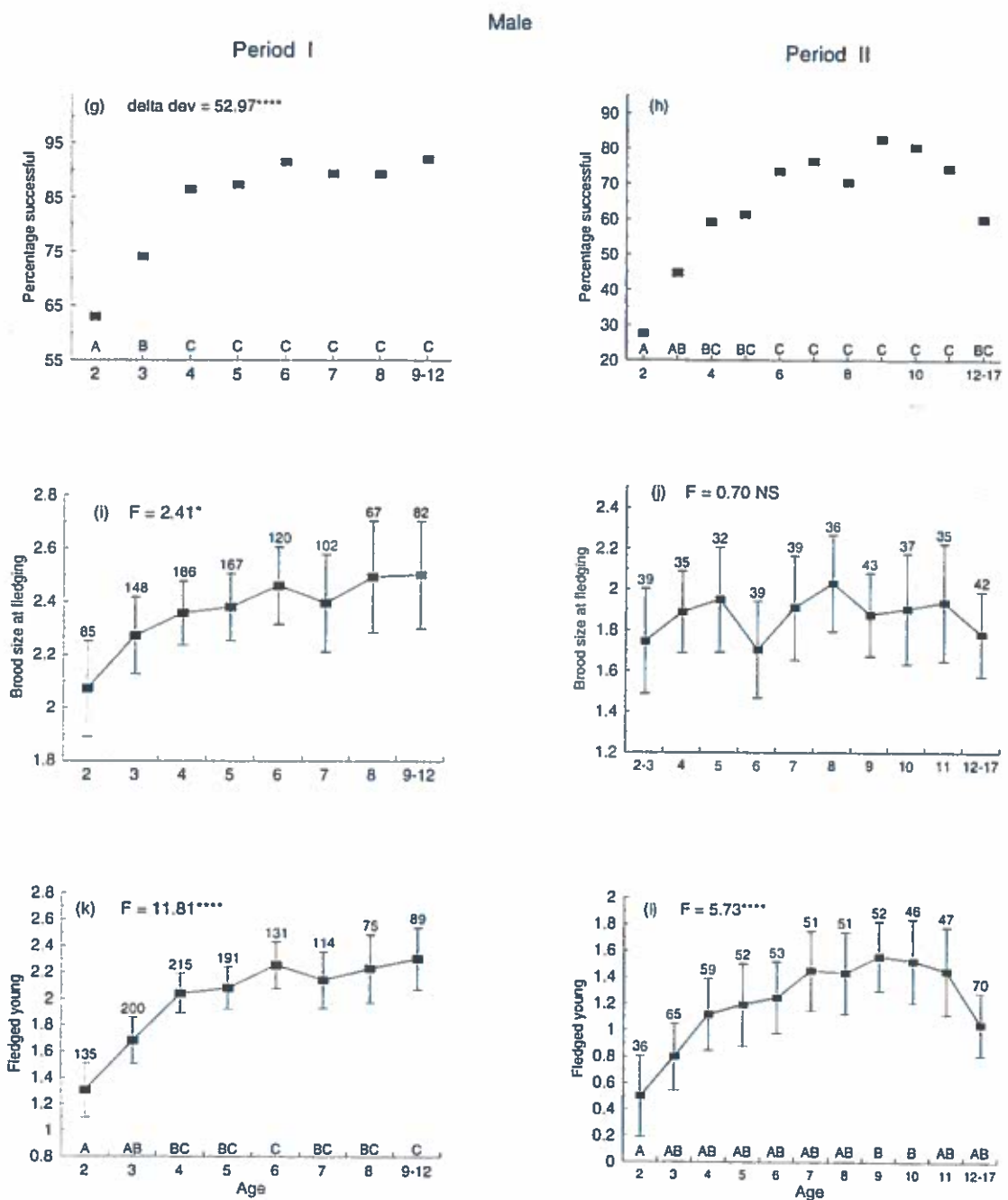
Figure 2. Continued.

ing in the study colony was the same for young raised by 2-4-year-old parents as for young raised by older parents (age-classes of parents, 2-3, 4-5, 6-11; females, $82 < n < 148$, $\chi^2 = 0.798$, $df = 2$, $P = 0.671$; males, $54 < n < 187$, $\chi^2 = 3.684$, $df = 2$, $P = 0.158$).

Age-related timing and its influence on reproductive performance

In period I, the date of return to the colony differed between female age-groups by up to 9 d (Fig. 3a). Date of egg-laying advanced linearly with increasing age of females; 8-12-year-olds laying on average 14 d earlier than 2-year-olds
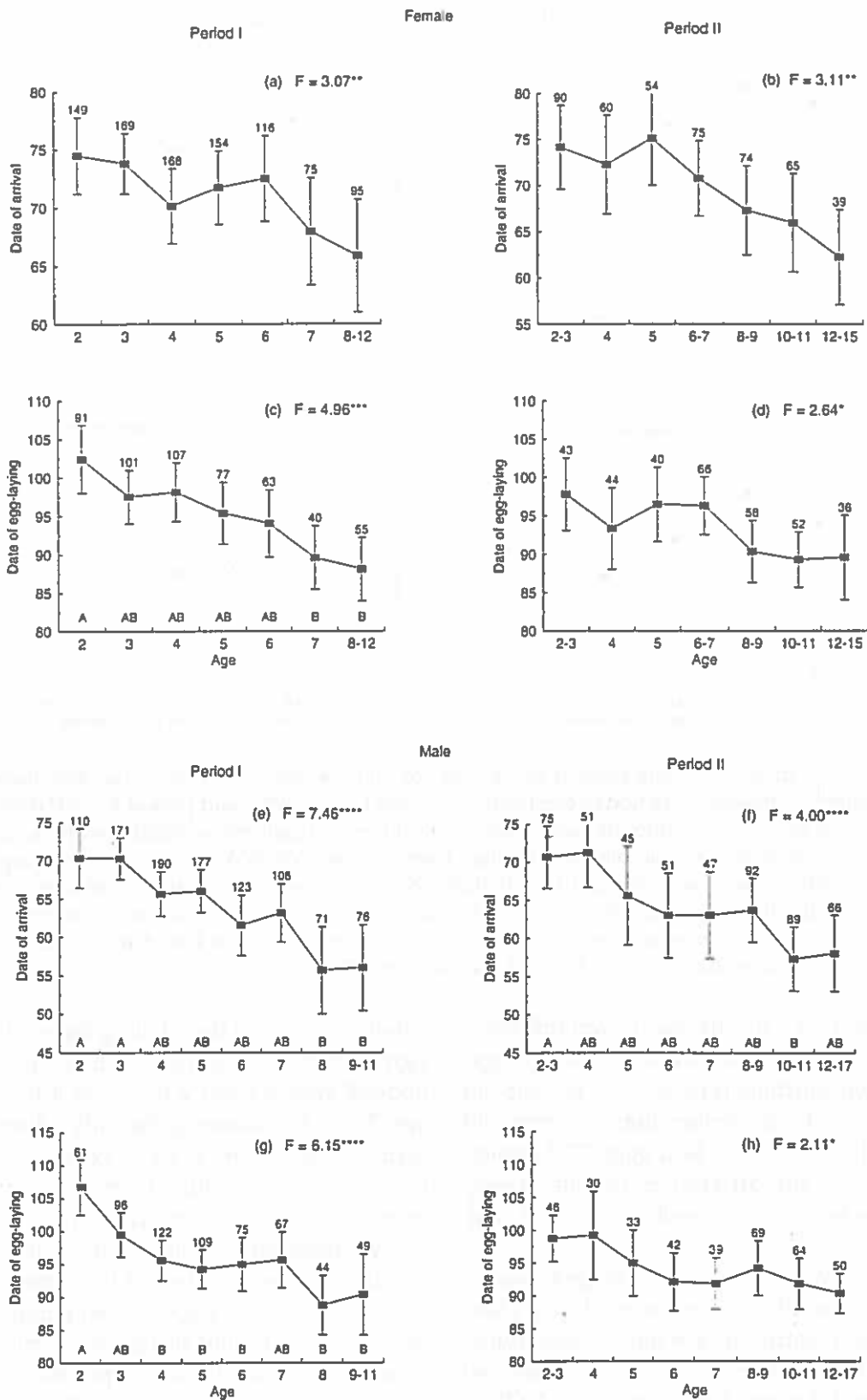
Figure 3. Date of arrival and date of egg-laying of 2 to 12-year-old (period I) or 15-year-old (period II) females and males given in Julian dates (Julian dates of 100 = 10 April). Vertical bars indicate 95% confidence limits, and numbers above bars are sample sizes. F-values from one-way ANOVA are given in each graph, with significance levels indicated (* $P<0.05$;** $P<0.01$; *** $P<0.001$). Mean values for age-classes with different capital letters differ significantly ($P<0.05$) from each other (Scheffé multiple comparison test).

25
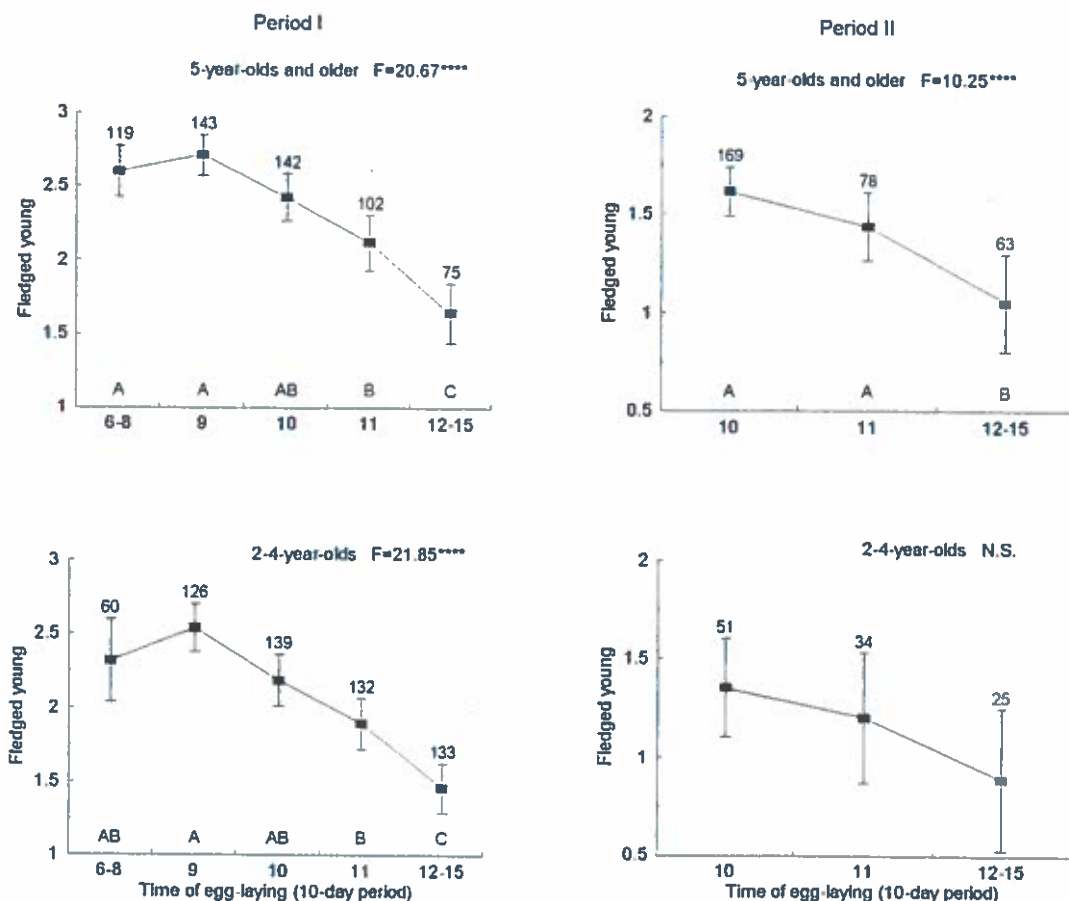
Figure 4. Number of young fledged by ≥5-year-old and 2-4-year-old great cormorants (sexes combined) in relation to period of egg-laying in period I (1983-1990) and period II (1991-1995). Abscissas are not drawn to the same scale. Vertical bars indicate 95%-confidence limits, and numbers above bars are sample sizes. *F*-values from one-way ANOVA are given in each graph, with significance levels indicated (**** *P*<0.001; N.S., non-significant). Mean values for age-classes with different capital letters differ significantly (*P*<0.05) from each other (Scheffé multiple comparison test). Sexes were pooled because no differences were found in the time-age relation (tested with a two-way ANOVA for each period).

(Fig. 3c). Age had a highly significant influence on date of arrival of males and on date of egg-laying of their partners (Fig. 3e,g); 8-12-year-old males arrived 14 d earlier than 2-3-year-old males and their partners laid eggs 17 d earlier. For both sexes, the differences in date of egg-laying were less pronounced in period II (Fig. 3d,h).

Reproductive performance changed seasonally in 2-4-year-old breeders as well as in older birds (Fig. 4). Controlling for date of egg-laying, birds older than 4 years produced more fledged young than 2-4-year-olds (two-way ANOVA, age-group: period I, $F_{1,1161}$ = 14.28, *P*<0.001; period II, $F_{1,414}$ = 5.94, *P*<0.001).

Influence of breeding experience and age
Females and males followed over successive years were compared showing that individual females advanced their laying dates, though not significantly, and increased their production of fledged young from 2 to 3 and 4 to 5 years of age (Table 1). Males significantly advanced their laying dates from 2 to 3 years of age, and the production of young increased significantly from 3 to 4 years of age (Table 1).

By comparing individuals with different breeding experience but of the same age, there was a tendency for experienced females to initiate egg-laying earlier and produce more fledged young per clutch than inexperienced females, but the differences were small (Table 2). Three-year-old females breeding for the second time produced significantly more young than did 3-year-old first-time breeders (Table 2). Mates of males with breeding experience did not lay earlier than the mates of inexperienced males (Table 2). Experienced 4- and 5-year-old males

Table 1. Within-individual, age-related changes in reproductive performance in great cormorants. The table presents mean values of between-year changes (± 1 SE; sample size), and significance levels from paired t-tests

	Mean change from		
Variable	2 to 3 years	3 to 4 years	4 to 5 years
Females			
Egg-laying date	-5.85 (4.08; 31) [a]	3.83 (2.99; 42) [a]	-5.79 (4.17; 37) [a]
Fledged young	0.39 (0.17; 66) *	0.05 (0.13; 105)	0.30 (0.13; 107)*
Males			
Egg-laying date	-10.82 (5.24; 28) *	-4.41 (3.37; 44) [a]	1.81 (2.46; 62)
Fledged young	0.32 (0.20; 60) [a]	0.43 (0.15; 109) **	0.05 (0.12; 124)

* $P<0.05$; ** $P<0.01$; [a] $0.05<P<0.20$

tended to fledge more young than inexperienced birds (Table 2).

The effect of age on timing of breeding and number of young fledged was tested within experience groups 0, 1, 2 and 3 years. No significant differences were found in the pairwise comparisons of 2- to 5-year-old females, except that 4-year-old first-time breeders produced significantly more young than did 3-year-old first-time breeders (t-test, $P = 0.016$; means, standard errors and sample sizes are given in Table 2). A comparison of males breeding for

Table 2. The effects of previous breeding experience on components of reproductive performance of female and male great cormorants. Values are means (± 1 SE), followed by sample sizes. Significance was determined with t-tests.

Sex	Age	Year as breeder		Date of egg-laying[1]	Young fledged per clutch
Female	3		First	99.5 (2.13), 84 [a]	1.62 (0.10), 148 ***
		Second		95.4 (2.26), 48	2.14 (0.11), 76
	4		First	98.8 (2,94), 53	1.99 (0.11), 89
		Second		96.2 (2.46), 66	2.13 (0.13), 77
		Third		94.5 (2.51), 32	2.08 (0.17), 38
	5		First	100.1(3.19), 27	2.04 (0.16), 47
		Second		96.6 (2.99), 36	2.22 (0.15), 54
		Third		93.1 (2.47), 38	2.33 (0.16), 57
		Fourth		92.9 (4.53), 16	2.63 (0.25), 24
Male	3		First	99.1 (1.67), 85	1.66 (0.10), 157
		Second		98.0 (2.32), 46	1.62 (0.15), 63
	4		First	98.0 (2.20), 60	1.87 (0.11), 110 [a]
		Second		96.3 (2.38), 56	2.12 (0.13), 77
		Third		93.5 (2.87), 36	2.18 (0.14), 40
	5		First	93.3 (3.22), 33	1.69 (0.14), 51 [a]
		Second		96.6 (3.03), 47	1.96 (0.15), 71 *
		Third		93.7 (2.43), 34	2.42 (0.13), 52
		Fourth		93.0 (2.58), 28	2.35 (0.17), 31

* $P<0.05$; ** $P<0.01$; *** $P<0.001$; [a] $0.05<P<0.2$; [1] Julian date

Table 3. Factorial ANOVA on number of young fledged by female and male great cormorants 1983-1990. Sample sizes are in parentheses.

Source	Female (n = 1187)		Male (n = 1315)	
	d.f.	F-value	d.f.	F-value
Main effects				
Age[1]	3	4.00**	3	11.97***
Breeding experience[2]	4	5.76***	4	2.94*
Two-way interactions				
Age x Breeding experience		N.S.		N.S.

[1] Birds older than 4 years were pooled;[2] Birds with more than 3 years of breeding experience were pooled.
* P<0.05; **P<0.01; ***P<0.001; N.S., not significant.

the first time at different ages showed that 3-year-olds nested earlier and raised significantly more young than did 2-year-olds (for age 3, see Table 2; age 2: date of egg-laying, $\bar{x}$ = 107.4, SE = 2.06, n = 73; young fledged, $\bar{x}$ = 1.22, SE = 0.10, n= 153. t-test, P = 0.002, P = 0.002, respectively). Four-year-old second-time breeders produced more fledged young than 3-year-old males of the same experience group (Table 2; t-test, P = 0.014). No significant effects of age were found when 4- and 5-year-olds were compared.

A two-way analysis of variance of the same data showed that both age and breeding experience affected the number of young fledged and that in males, age was of higher importance than breeding experience, and vice versa in females (Table 3). Entering timing of breeding as a covariate (possible for 56 % of the data), age and breeding experience no longer significantly affected fledgling production in males (two-way ANCOVA; date of egg-laying, $F_{1,634}$ = 73.47, P<0.001), whereas, in females, only the influence of age disappeared (two-way ANCOVA; breeding experience, $F_{1,533}$ = 2.78, P = 0.040; date of egg-laying $F_{1,533}$ = 73.00, P<0.001). Hence for both sexes, the increase with parental age in the production of fledged young arose mainly from earlier breeding of older individuals.

Reproductive performance and survival
Cormorants that returned to the studied sections of the colony and laid eggs in a subsequent year performed better in the previous season than the ones that did not return (Table 4). I do not know to what extent 'non-survivors' disappeared because they emigrated, skipped breeding or died.

The differences between 'survivors' and 'non-survivors' in timing of egg-laying were not significant after adjusting the significance level with a sequential Bonferroni (Table 4). Females disappearing from the breeding population after breeding in their third or fourth year fledged fewer young when breeding than the ones that survived and bred at least once more later in life (Table 4). In males, the lower production of young by non-surviving birds was pronounced at ages 4 and 5.

The differences depicted in Table 4 arose partly because 'survivors' tended to start breeding at an earlier age than 'non-survivors' and, therefore, had more breeding experience than 'non-survivors' (Table 5); the same was true for period II. However, in a series of t-tests, where breeding experience was controlled for, a significant difference remained between 'survivors' and 'non-survivors' in unexperienced 3 and 4-year-olds, and in 3-year-olds with one year of experience (0.006<P<0.008; also significant after adjusting with sequential Bonferroni). In males, significant differences remained in unexperienced 3-year-olds (P = 0.003), in unexperienced as well as experienced 4-year-olds (0.0004<P<0.003), and in 5-year-olds with one year of experience (P = 0.002).

The production of fledged young was age-related both among the individuals surviving to breed later and among individuals disappearing

Table 4. Reproductive performance of great cormorants that disappeared from the breeding population in the year that followed in comparison with those that returned to the colony and laid eggs in a subsequent year. Values are means ($\pm$ 1 SE), sample sizes. Significance was determined with *t*-tests. *P*-values are given when $P < 0.20$. Star denotes significance according to sequential Bonferroni.

Sex	Age	Date of egg-laying			Young fledged per initiated clutch		
		'Non-survivors'	'Survivors'	P	'Non-survivors'	'Survivors'	P
Female	2	107.0 (4.03), 31	102.4 (2.65), 62	N.S.	1.33 (0.14), 64	1.73 (0.11), 114	0.026
	3	101.1 (3.80), 30	97.0 (1.93), 72	N.S.	1.49 (0.13), 71	2.00 (0.10), 127	0.002*
	4	106.6 (3.14), 28	95.1 (2.14), 79	0.011	1.75 (0.15), 61	2.25 (0.09), 134	0.006*
	5	98.3 (3.37), 26	93.9 (2.51), 51	N.S.	2.23 (0.15), 60	2.40 (0.10), 107	N.S.
	6	102.1 (4.82), 18	90.8 (2.24), 45	0.018	2.09 (0.19), 35	2.39 (0.11), 89	0.168
Male	2	104.7 (3.39), 20	107.7 (2.66), 41	N.S.	1.17 (0.17), 46	1.37 (0.13), 89	N.S.
	3	106.0 (3.07), 20	97.8 (1.96), 76	0.050	1.40 (0.16), 57	1.80 (0.11), 142	0.042
	4	99.4 (3.74), 20	94.9 (1.71), 102	N.S.	1.49 (0.15), 55	2.23 (0.08), 161	0.000
	5	96.8 (2.73), 33	93.1 (1.74), 76	N.S.	1.66 (0.16), 67	2.29 (0.09), 125	0.001
	6	101.2 (4.33), 12	92.7 (2.04), 62	0.096	1.93 (0.23), 28	2.34 (0.10), 103	0.107

Table 5. Age at first breeding of great cormorants that disappeared from the breeding population the following year versus those that returned to the colony and laid eggs in a subsequent year. Values are means (± 1 SE), followed by sample sizes. Significance was determined with *t*-tests. *P*-values are given when $P<0.20$.

		Age at first breeding		
Sex	Age[1]	'Non-survivors'	'Survivors'	P
Female	3	2.80 (0.05), 71	2.62 (0.04), 127	0.008
	4	3.38 (0.10), 61	3.08 (0.07), 134	0.019
	5	3.77 (0.16), 60	3.16 (0.10), 107	0.001
	6	3.74 (0.24), 35	3.45 (0.15), 89	N.S.
Male	3	2.86 (0.05), 57	2.68 (0.04), 142	0.003
	4	3.67 (0.08), 55	3.12 (0.06), 161	<0.001
	5	3.76 (0.13), 67	3.35 (0.10), 125	0.015
	6	4.14 (0.32), 28	3.57 (0.13), 103	0.057

[1] Age before non-survivors disappeared.

Table 6. ANCOVA on number of young fledged by female and male great cormorants 1983-1990 in relation to age up to age 5 and whether the birds disappeared from the breeding population before age 6 or bred as 6-years-old or older. Sample sizes are in parentheses.

	Female (n =738)		Male (n =742)	
Source	d.f.	F-value	d.f.	F-value
Main effects				
Breeding experience (covariate)	1	41.69***	1	40.38***
Age	3	3.60*	3	6.39***
'Non-survivors' vs. 'survivors'[1]	1	9.79**	1	18.34***
Two-way interactions				
Age x 'non-survivors' vs. 'survivors'		N.S.		N.S.

[1] Birds not breeding as 6-years-old or older were defined as 'non-survivors'.
* $P<0.05$; **$P<0.01$; ***$P<0.001$; N.S., not significant.

Table 7. ANCOVA on number of young fledged by female and male great cormorants 1983-1990 in relation to age up to age 5, timing of breeding and whether the birds disappeared from the breeding population before age 6 or bred as 6-years-old or older. Sample sizes are in parentheses. All interactions had *P*-values above 0.40.

	Female (n =379)		Male (n =390)	
Source	d.f.	F-value	d.f.	F-value
Main effects				
Year (covariate)	1	58.04***	1	52.75***
Breeding experience (covariate)	1	20.39***	1	22.65***
Age	3	0.67	3	2.08[a]
Period of egg-laying[1]	5	7.72***	5	3.10**
'Non-survivors' vs. 'survivors'[2]	1	0.05	1	5.76*

[1] Date of egg-laying was divided into periods as given in Fig. 3.
[2] Birds not breeding as 6-years-old or older were here defined as 'non-survivors'.
*$P<0.05$; **$P<0.01$; ***$P<0.001$; [a] $0.05<P<0.20$.

from the breeding population (Table 6). The difference between 'surviving' females and 'non-surviving' females disappeared when correcting for date of egg-laying (Table 7). Hence, for females the difference between 'survivors' and 'non-survivors' arose because 'non-survivers' bred later in the season than 'survivors'.

Discussion

Reproductive output increased with age, but the survival of young during post-fledging and the rate of recruitment of young to the breeding population were unaffected by the age of parents. The influence of age on reproductive success was mainly mediated through the influence of age on arrival date and clutch initiation date. Of the unsuccessful breeders, most failed before hatching or before the chicks reached the age of 5-7 d (87.9%, n = 628). The causes for frequent failure in the phase of incubation and soon after hatching may include lack of foraging skills (affecting parental body condition and nest attendance) and in several aspects of the behaviour associated with breeding such as the quality of incubation, protection of the nest or its contents against intruding males, inclement weather or predation by crows (see also Coulson & White 1958; Nelson 1966; Ryder 1981; Shaw 1986; Weimerskirch 1990; Wooller et al. 1990). The age difference in the early phase of breeding was accentuated in the stagnant colony phase when food availability was poor. Foraging skills and experience with the foraging area may influence the birds' ability to replenish their body reserves after spring migration and during the early phases of breeding when fish availability is likely to be low (Voslamber & Van Eerden 1995) and egg and chick survival dependent on the parents' attendance (Gregersen 1982).

The relation between female age and the number of eggs laid was not measured in this study. Clutches laid by 2 and 3-year-old females of Brandt's cormorant were smaller than those laid by females older than 5 years (Boekelheide & Ainley 1989), and the age-related variation in brood size at fledging recorded in the present study is likely to be caused partly by an age-related variation in the number of eggs laid. Thus, if brood size varied only because of partial loss of eggs and chicks, equally large age-effects in brood size at fledging would have been expected in both sexes, and this was not the case. Potts et al. (1980) measured survival of common shag P. aristotelis chicks in nests of known-age parents and found that survival of young older than 5 days was not affected directly by age or experience of their parents. The disappearance of an age-effect in brood sizes at fledging in period II may be explained by the less marked age differences in timing of breeding which is likely to affect the number of eggs laid. Second, the daily number of feedings of young was lower in the food poor period than in the food rich period, and older breeders may have been forced to reduce the number of foraging flights to the level of young breeders, resulting in increased chick mortality.

In accordance with studies of other bird species, the largest increase in reproductive performance with age took place in the youngest age classes (Newton, Marquiss & Moss 1981; Nol & Smith 1987; Sæther 1990). The mean number of young fledged by male and female great cormorants studied in Japan, increased markedly between age 1 and 3, slightly between age 3 and 6, and declined again in 14-17-year-olds (Fukuda in press.). Boekelheide & Ainley (1989) reported that the number of Brandt's cormorant young fledged per nest was significantly lower for the youngest group of breeders (3- to 4-years-old), only. There was no significant variation beyond the first one or two breeding attempts in common shags (Potts, Coulson & Deans 1980), whereas in antarctic blue-eyed shags (P. atriceps King) the number of fledglings increased both between age 3 and 5 and between age 5 and 8-10 (Shaw 1986). These differences within the Phalacrocoracidae may, at least to some extent, have arisen through time-place variation in food availability. Thus the results of this study suggest that the attainment of maximum reproductive output occurs at an early age when food is abundant and easy to obtain early in the season, but becomes a gradual process spanning several seasons when or where food is scarce. This finding can easily complicate modelling aimed at predicting population growth (cf. Rockwell et al. 1983; Rockwell et al. 1985).

The four hypotheses

The prediction of the *breeding experience hypothesis* and the *age hypothesis*, i.e. that a within-individual change will occur through a maturation process (Forslund & Pärt 1995), was confirmed. Within-individual improvements in timing of breeding and reproductive output have been found in snow geese (*Anser caerulescens* L.) (Hamann & Cooke 1987), barnacle geese (*Branta leucopsis* Bechstein) (Forslund & Larsson 1992) and coots (*Fulica atra* L.) (Perdeck & Cavé 1992). The comparison of cormorants of the same age showed that breeding experience was important for breeding performance in females, but not in breeding performance in males. Similar sex differences were found in a study of western gulls (*Larus occidentalis* Audubon) (Pyle *et al.* 1991). The weak influence of breeding experience in males is unlikely to have been an artefact from males observed nesting for the first time having nested in another part of the colony in the previous year (cf. Hamann & Cooke 1987), because male cormorants were more site faithful than females (unpublished data). In Brandt's cormorant (Boekelheide & Ainley 1989) and blue-eyed shag (Shaw 1986) breeding experience had little influence on nesting and fledging success. In the present study, some component related with age, but not with breeding experience, was important for the breeding performance of males. The component of importance for males may be the date of return to the colony which advanced with age. Hence, early arriving males settled in the upper sections of the nesting trees, whereas later arrivers settled in the lower sections (Gregersen 1982), suggesting that early arrival gave older males an opportunity to select the most attractive nest-sites (cf. Thomas & Coulson 1988; M.R. van Eerden unpublished data). Possessing good territories may have affected the chances of attracting high 'quality' females of all ages, laying eggs early. Date of return of common shags to the colony on the Farne Islands, England was strongly age-related and date of return influenced the location of the nest in the colony, which was the main determinant of breeding success in that colony (Potts *et al.* 1980).

I am unable to reject the the *restraint hypothesis* which suggest that within-individual increase in breeding performance arise because of an increase with age in the investment in breeding rather than because of an increase in competence (Pärt 1995). Sæther (1990) reviewed the studies on effects of age on reproductive success and concluded that although there was evidence in support of both constraint and restraint hypotheses, there was more evidence in support of the constraint hypotheses (cf. Newton 1989). So, in general, young birds seem to be less capable rather than less willing (Fowler 1995).

The results presented here support the prediction of the *differential survival hypothesis*, suggesting progressive disappearance of phenotypes (Forslund & Pärt 1995). In a study of Kittiwakes (*Rissa tridactyla*) Coulson & Porter (1985) found that females which laid large clutches had a higher survival rate than those which laid small clutches, and the authors explained this with variation in individual quality. Surviving females followed in the present study produced more fledged young per year than females which disappeared from the breeding population, and did so mainly because they laid eggs earlier in the season (early breeders may perform well because they are of high 'quality'; Verhulst, van Balen & Tinbergen 1995). Also males of varying 'quality' differed from each other in the number of young they fledged, and the difference between males did not disappear when timing of breeding were controlled for.

The overall increase with age in the number of young fledged per initiated clutch amounted to 0.76 young between age 2 and 5 years in females and to 0.73 young between age 2 and 4 in males. The corresponding within-individual increases added up to 0.74 young in females and to 0.75 young in males. Hence, the within-individual changes were adequate to explain the overall increase in reproductive performance with age. This suggest that the gradual disappearance of inferior breeders had no or only minor influence on the overall increase in reproductive performance. The continued appearance of new inferior breeders may have counterbalanced the influence of differential in survival. Note that the overall mean number of young parents fledged by known age male parents only increased slightly between ages 4, 5 and 6 despite documented disappearance of inferior birds after ages 3, 4 and 5 (Table 4). Late recruitment of inferior birds is in accordance with what would be expected, because only individuals that have the opportunity and that can af-

ford to reproduce at an early age should do so (Pärt 1995).

To sum up, the difference between age-classes in reproductive performance was dependent on food availability, and most of the age-related differences in performance appeared in the early phases of breeding. The observed changes in reproductive performance with age arose through the influence of age itself, breeding experience and maybe through differential survival. Their effects were mediated mainly through their influence on timing of breeding.

Acknowledgements

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Chapter 3

Changes in reproductive performance with expansion of a Danish Great Cormorant *Phalacrocorax carbo sinensis* colony

Thomas Bregnballe, Jens Gregersen & Poul-Hald Mortensen

Changes in breeding success with expansion of a Danish Great Cormorant *Phalacrocorax carbo sinensis* colony

by

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Summary

We studied breeding success and dietary changes of Great Cormorants *Phalacrocorax carbo sinensis* as a colony quadrupled in number of breeding pairs. The average number of young fledged per initiated clutch remained unchanged as breeding numbers increased from 950 to 3300 nests over eight years. But an increasing proportion of egg-laying pairs failed when rearing chicks, and brood sizes at fledging and frequency of late clutches declined over the period. This suggests that the availability of food late in the breeding season declined as breeding numbers increased. Over a six-year-period with 4300-5050 pairs following a single year's increase of 1050 nests, the number of young fledged per initiated clutch declined by 56% in old breeders and 88% in young 2-4-year-old breeders. This decline was the result of an increase in the proportion abandoning nests during incubation and in the proportion of chicks dying. Changes in the early phases of breeding may relate to a decline in the Bull Rout *Myoxocephalus scorpius* stock, which formerly was exploited by the Cormorants during pre-laying and incubation. Increased chick mortality seems to be caused by a decline in feeding frequency of the chicks, the result of longer foraging flights and carry over effects from low food availability early in the season. Depletion of the local food resources by Great Cormorants may have added to the within and between year changes in food availability, affecting breeding success.

Introduction

Breeding success in a sea bird colony can affect the production of potential recruits (e.g., Anker-Nilssen 1987) and the decision made by individuals whether to join the colony or not (Danchin & Monnat 1992, Danchin & Boulinier in press.). Hence, a breeding colony's production of young can greatly influence its development (Bédard *et al.* 1995). Reproductive performance of birds may decline with increasing colony size (Coulson *et al.* 1982, Møller 1987), and studies of seabirds and colonial waterbirds have shown that in some species, individuals perform better in small colonies than in large colonies, e.g. chicks grow faster, survive better

and/or fledge at a greater mass (Coulson et al. 1982, Birkhead & Furness 1985, Hunt et al. 1986, Cairns 1989, Butler et al. 1995). These relationships are often believed to have arisen because of density-dependent competition for food (review in Croxall & Rothery 1991). The suggested mechanism is that, as competition for food increases with colony size birds are forced to travel further to forage, consequently, the chicks get less food and fewer of them survive to fledging (Ashmole 1971, Birkhead & Furness 1985). Seabirds foraging in social groups on prey that school may experience interference competition (Hunt et al. 1986), and fish standing stocks may decline over the season due to predation (Furness 1978, Furness & Cooper 1982, Gaston et al. 1983, Furness & Birkhead 1984, Birt et al. 1987). Comparisons of species and families of seabirds support the suggestion that distance to the foraging area influences feeding frequency and thereby brood size (Nelson 1977, Anderson & Ricklefs 1992). For example, Phalacrocoracids are able to produce large broods compared with Sulids, and it is believed they are able to do so only because they feed very near their breeding sites (Nelson 1977).

The food supply for breeding seabirds often varies greatly both within and between seasons independently of numbers breeding. Density-independent effects can influence breeding performance in an early phase of breeding in one year and in a late phase of breeding in another year (Harris & Wanless 1990), whereas effects from depletion initially will be expected to affect performance mainly in the late phases of breeding. Thus, assuming limited within-season recruitment to fish stocks, predation may reduce prey density as the season progresses, affecting parents' food provisioning rate and thereby chick survival. At a later stage of colony growth, food availability at the beginning of the season may be affected by the previous year's predation. This could lead to a decline in clutch size, an increase in nest desertion, a faster seasonal decline of food abundance and thereby an increasing chick mortality.

Great Cormorants *Phalacrocorax carbo* are inshore feeders. They produce large broods, their colonies may increase to large sizes and the fish species taken are in some regions fairly stationary. Hence, the premises for a within-

season and later a between-season decline in food availability with increasing colony size may be met in some of the colonies. To detect whether changes in breeding success occur in the suggested sequence, breeding success should, as far as possible, be divided into sub-units of time, i.e. the number of eggs laid, the proportion of eggs hatched, the proportion of nests deserted and the number of chicks dying (Cairns 1987).

This paper describes and discusses the changes in breeding success in a Great Cormorant colony where breeding numbers quadrupled in ten years and thereafter stabilized.

Methods

The present study of the continental subspecies of the Great Cormorant *P. c. sinensis* was carried out between 1980 and 1995 on the island of Vorsø (55°52'N, 10°01'E) located in a fjord on the east coast of Jutland, Denmark. Nesting began in 1944 and numbers varied between 5 and 525 nests until 1970 (then 250 nests), after which a long period of continuous increase began, reaching a maximum number of 5050 nests in 1991 (1980-1995, see Fig. 1).

The Great Cormorants nested in trees 1.5-25 m above the ground. Colony size was censused by counting all nests once a year. Ringing of young with inscribed colour-rings was performed annually between 1977 and 1995; 227-1144 young were ringed per year. Observations of foraging routes were made throughout the study period but quantified in 1983-1984 and 1993-1994 only.

In this paper, breeding success is the number of young fledged per initiated clutch. The percentage successful is the proportion of initiated clutches from which at least one young fledged. Brood size at fledging is the number of young present in the nest at the time when primaries have grown to a stage allowing the young to fly from the nest, usually when aged 43-55 days. Some broods could not be followed until fledging, and we included broods aged 35 days or more, assuming no mortality until fledging. These parameters were obtained by using different methods to monitor two different groups of

birds. One group of birds included all pairs nesting in one section of the colony, referred to as the "reference area". The reference area consisted of 19 to 67 trees. Nesting pairs were followed from establishment of the territory until fledging of young. Observations were made at irregular intervals (1980-1983, 1988, 1993-1995, mean 3-5 days; 1984-1985, 1990, mean 6-9 days; 1986-1987, 1989, 1991-1992, mean 9-21 days). We assume that pairs nesting in the reference area represented the whole nesting population quite well with a large proportion of young birds breeding in the early 1980s and in 1989-1991, but few between 1992 and 1995 (unpublished data). However, breeding success may vary between areas within a colony (e.g. Van Eerden *et al.* 1991) and we do not know how well breeding success in the reference area reflected the colony's breeding success. Therefore, we include a dataset on breeding success of ringed birds, which nested over a much larger area of the colony.

The other group of birds consisted of all the pairs of which one or both parents were ringed and the breeding success was known, including colour-ringed birds nesting in the reference area (one or both birds were ringed in 17% of the pairs monitored in the reference area). Notes about the progress of breeding in colour-ringed birds were made when seen in a territory or at a nest. However, during 1994-1995, the position of ringed breeders nets' were mapped and supplementary information on the fate of nests were collected also when the ringed parents were away from their nest or the ringcode was invisible, e.g. because the bird was incubating. Observations on most of the colour-ringed birds and all pairs in the reference area were made from a tower inside the colony (except 1980-83). Searches for ringed individuals from the tower were conducted one to several times per day throughout the breeding season. Searches for colour-ringed birds nesting in colony sections not visible from the tower were made from the ground outside the colony at irregular intervals of 3-23 days. Hence, colour-ringed birds were observed with a frequency ranging from about once every day to once in a breeding season (e.g. seen at a nest with nearly fledged young). Therefore, an unknown proportion of the unsuccessful breeding attempts of ringed birds were

never detected. In the reference area, all unsuccessful attempts were detected, except for a few years with low observation intensity.

Clutch size data were collected in only a few of the years covered by the study. Most pairs, 80-93%, started to incubate before 20 April, and we assume that clutches observed after this date were complete. The frequency of chick mortality in broods in the reference area could be quantified in years with frequent observations. The chick stage was divided into 7-day intervals and for each age interval, the proportion of broods in which one or more chicks died was calculated.

Young and old breeders were treated separately, and analysis of the relation between age and reproductive performance (Bregnballe M.S.) suggested that it was reasonable to define 2-4-year-old birds as "young breeders" and birds of 5 years and older as "old breeders". The probability that the partner of a ringed bird would be young was 45% for young breeders (n = 229) and 35% for old breeders (n = 209). Ringed birds constituted on average 17% of the nesters in the reference area.

A phase of colony growth (period I) and a phase of stabilization (period II) were defined (Fig. 1). In the statistical analyses the two phases were kept separate. To ensure large annual sam-
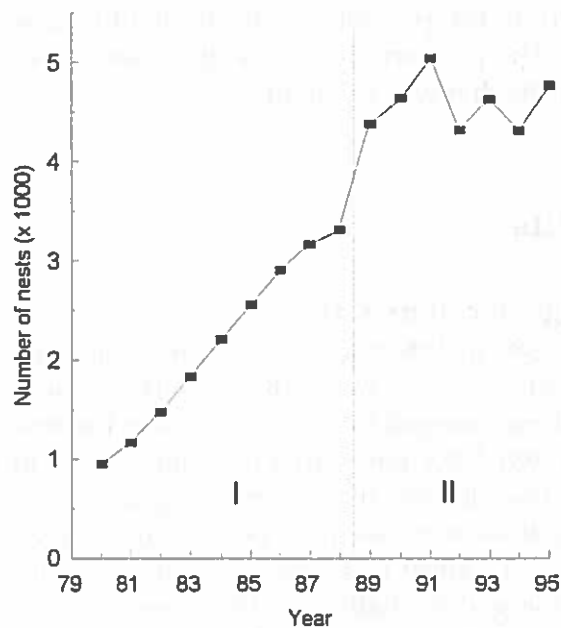

Figure 1. Number of occupied nests in the Great Cormorant colony on Vorsø, 1980-1995. Periods I and II are separated by a dashed vertical line.

ple sizes of known-aged breeders, individuals were allowed to appear in the data in more than one season. The proportions of these individuals were as follows: period I, 36% of the 2-4-year-olds (n = 636 individuals), 41% of the 5-17-year-olds (n = 333); period II, 28% of the 2-4-year-olds (n = 394); 53% of the 5-17-year-olds (n = 561). Pairs consisting of two ringed birds of the same age-group were included only once per season. One-way ANOVA was applied to analyse for annual variation in breeding parameters, except 'proportion successful'. The Scheffé multiple range test was performed as a post hoc test to detect whether declines from one year to the next were significant. The number of young fledged per initiated clutch and brood size at fledging declined over the season, and there was year-to-year variation in the mean date of egg-laying (Bregnballe unpublished analyses). This led us to include date of egg-laying as a covariate when analysing the subset of data (55%) where date of egg-laying was known or could be estimated. The correction affected the pattern of change in clutch size and brood size at fledging, and we report the corrected means and significance levels for these analyses.

Dietary research was performed by collecting regurgitated pellets. From the otoliths found in the pellets, prey species were determined and fish length and mass reconstructed (Berg 1985, Härkönen 1986, and unpublished reports); no correction for possible wear of otoliths was made. The proportions by weight of each species in the diet was calculated.

Results

Change in colony size
From 1980 to 1988 the Vorsø colony increased from 949 to 3321 nests (Fig. 1). The annual growth rate ranged from 23% to 27% in the first years, 1981-1983, whereafter it declined to 5% in 1988. The decline in growth suggests that a ceiling level was about to be reached in 1988 (see Fig. 1). Until this time, the Great Cormorants foraged in shallow (2-15 m deep) marine areas east of the fjord, and all foraging trips were made through the mouth of the fjord, ex-
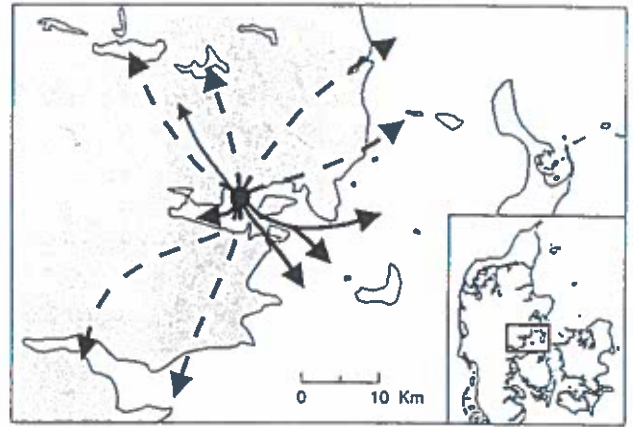
Figure 2. Routes taken by the Great Cormorants nesting Vorsø when migrating to foraging areas in period I (1980-1988, only unbroken lines), and in period II (1989-1995, unbroken and dashed lines).

cept for some migration to freshwater lakes north-west of the colony (Fig. 2).

In 1989, nest number increased by 1070 nests, a 32% increase. This was the first year with extensive migration over land to foraging areas northeast, south and southeast of the colony (Fig. 2). A further increase of 660 nests took place over the two following years, and the colony reached a maximum of 5050 nests in 1991 (Fig. 1). Between 1992 and 1995, nest numbers fluctuated between 4320 and 4540 nests (Fig. 1). The carrying capacity seemed to have been reached by then.

Based on this pattern of colony development, we treat the period 1980-1988 as a phase of growth and the period 1989-1995 as a phase of stabilization following an extraordinary increase in colony size in 1989. We refer to the two phases as period I and period II (Fig. 1).

Young fledged per initiated clutch
There was no significant decline in the mean number of young fledged per initiated clutch in period I (Fig. 3, Table 1). However, there was a slight decline in breeding success in the reference area between 1981 and 1986, followed by a slight increase. The breeding success of 2-4-year-old and 5-17-year-old parents showed a plateau at the high level of 1.6-1.9 and 2.3-2.4 young per initiated clutch respectively.

In period II there was a significant difference between years in the mean number of young fledged per initiated clutch and the decline was

Figure 3. Annual mean number of young Great Cormorants fledged per initiated clutch given for the reference area (A) and for known-aged parents (B), 1980-1995. Mean values plotted with standard error of the mean and sample size. Periods I and II are separated by a dashed vertical line.
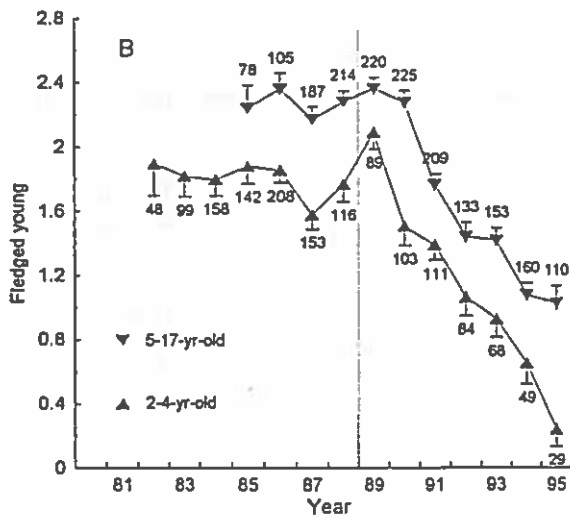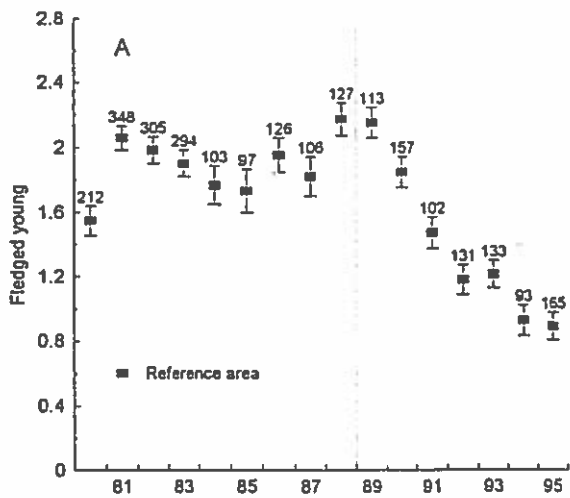
significant (Fig. 3, Table 1). In the reference area and in 2-4-year-old parents, the decline was recorded in the first year after 1989, whereas in 5-17-year-olds it was recorded in the second year after 1989. The decrease between 1989 and 1995 was 59% in the reference area, 56% in 5-17-year-olds, and 88% in 2-4-year-olds.

Proportion successful

It is evident from Fig. 4 that the proportion of pairs breeding successfully did not decline as
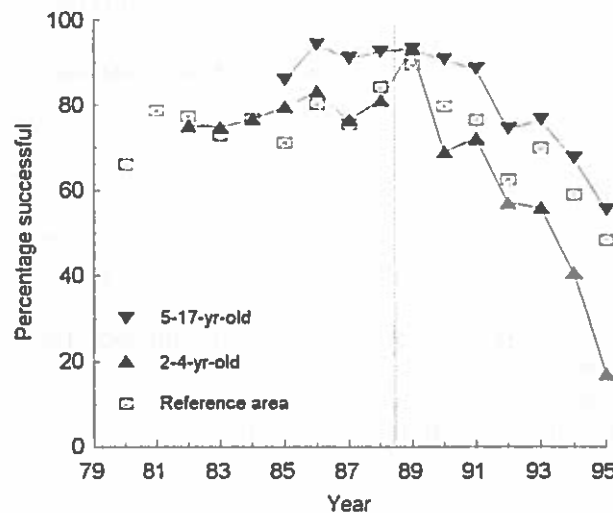
Figure 4. Percentage of clutches successful in Great Cormorants (i.e. at least one young fledged) in the reference area and for known-aged parents, 1980-1995. Sample sizes are as in Fig. 2.

the colony increased during period I. Between 66% and 84% of the pairs in the reference area were successful in raising at least one young to fledging. There was a high proportion of breeders which successfully raised young in 1989 and young and old breeders performed equally well (Fig. 4). 1989 was a year when old and young breeders laid eggs contemporaneously (t-test, $t_{113} = 0.79$, n.s.; timing of egg-laying differed significantly in the years 1985-1988, $P < 0.001$ for all). The proportion successful among 2-4-year-olds declined after the increase in colony size in 1989, whereas no decline was recorded in old breeders until after 1991 (Fig. 4). During 1993-1995, the decline was larger in young breeders than in old breeders.

Unsuccessful and "second clutches

The proportion of clutches failing during the chick stage increased from 10% in 1980 to 35% in 1988 (the reference area, $r^2_7 = 0.51$, $P = 0.031$, $22 < n < 108$ per year). Overall, 77% of all failures in period I and 72% of all failures in period II took place during the incubation phase. In some nests in the reference area, a new clutch was laid by the same pair or by a new pair, either because the first clutch or brood had been lost or, more rarely, after the young had fledged. Laying of these "second clutches" occurred in 9-19% of the nests in 1980-1984, but only in 0-2%

Table 1. One-way ANOVA on number of young fledged per initiated clutch and brood size at fledging in Great Cormorants in relation to year during period I (1980-1988) and II (1989-1995).

| | Young fledged per initated clutch | | | | | | Brood size at fledging | | | | | |
| | Period I | | | Period II | | | Period I | | | Period II | | |
	d.f.	F-value	n	d.f.	F-value	n	d.f.	F-value	n	d.f.	F-value	n
Reference area	8	3.62***[1]	1718	6	26.05****	894	8	n.s.	1300	6	18.56****	707
2-4-year-olds	6	n.s.[2]	923	6	20.36****	532	6	2.87**[2]	727	6	5.66****	344
5-17-year-olds	3	n.s.[3]	583	6	49.27****	1209	3	n.s.[3]	533	6	32.47****	978

[1] No significant difference between years 1981-1988.
[2] 1982-88.
[3] 1985-88.
** $P<0.01$; ***$P<0.001$; ****$P<0.0001$; n.s., not significant.

Table 2. ANCOVA on brood size at fledging in Great Cormorants 1989-1995 in relation to year and age-group. $n = 860$.

Source	d.f.	F-value
Timing of egg-laying (covariate)	1	71.65****
Age-group	1	4.75*
Year	6	14.46****
Age-group x year		n.s.

*$P<0.05$; ****$P<0.0001$; n.s., not significant.

Table 3. Mean clutch size recorded in Great Cormorant nests on Vorsø 20 April to 31 May, 1973-1995. Means adjusted for date of observation are given in parentheses. One-way ANOVA: 1973-1983, not significant; 1990-1995, $F_{2,517} = 7.21$, $P < 0.001$. Clutch size declined with observation date ($r^2_{839} = 0.03$, $P < 0.0001$). One-way ANCOVA with observation date as covariate: 1973-83, not significant; 1990-95, $F_{2,516} = 4.18$, $P = 0.016$.

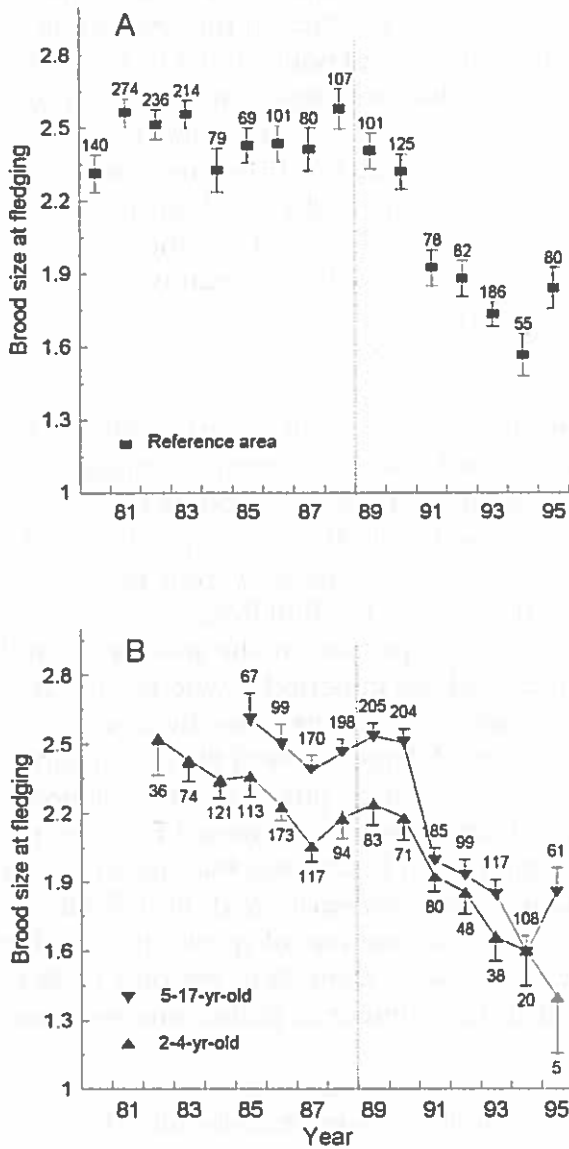| Year	Mean		s.e.	n
1973	3.15	(3.12)	0.12	101
1978	3.26	(3.40)	0.09	146
1980	3.29	(3.03)	0.29	24
1983	3.29	(3.13)	0.12	75
1990	3.12	(3.11)	0.14	50
1994	2.64	(2.68)	0.06	154
1995	2.94	(2.92)	0.06	316

Figure 5. Annual mean sizes of broods fledging of Great Cormorant given for broods raised in the reference area (A) and by known-aged parents (B), 1980-1995. Mean values plotted with standard error of the mean and sample size. Periods I and II are separated by a dashed vertical line.

of the nests in 1985-1988 (the lower frequency in 1985-1988 cannot be explained by later laying of first clutches). The frequency of "second clutches" in period II was low, 0-3.2% (data available from 1990 and 1993-1995).

Brood size at fledging: influence of clutch size and chick mortality

The size of broods raised in period I by pairs with at least one parent aged 2-4 years declined significantly over the years (Fig. 5, Table 2, $r^2_{727} = 0.02$, $P = 0.0013$) and with increasing colony
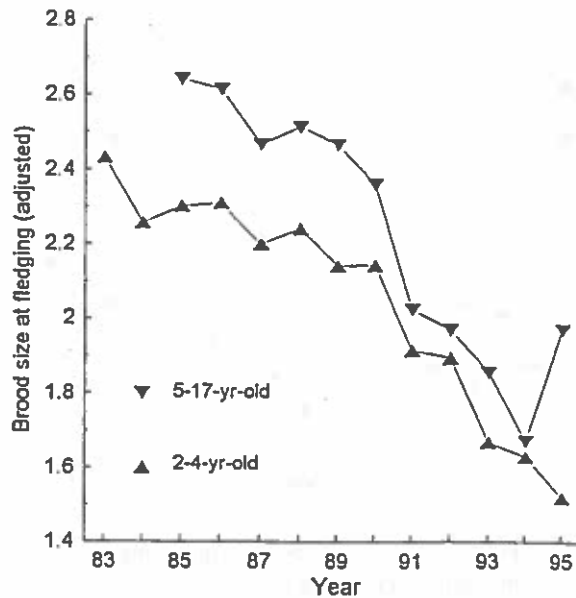
Figure 6. Annual mean brood sizes at fledging in Great Cormorants adjusted for variation in timing of egg-laying.

size ($r^2_{727} = 0.02$, $P < 0.001$). The decline remained significant after adjusting for variation in timing of egg-laying (Fig. 6, $r^2_{426} = 0.02$, $P = 0.0056$) and was not explicable by a change in year-class composition of the age group. Thus, the mean brood size of the relevant year-classes, 1979-1984, did not differ significantly in 1989-1990, i.e. when the birds aged 5 years or more (two-way ANOVA, year and year-class; 11-51 broods per cell).

The broods raised in period II varied significantly in size between years and there was a strong linear component in the decline (Fig. 5, Table 2). The decline was abrupt and significant in 5-17-year-olds and in the reference area in 1991 (Scheffé multiple range test, $P < 0.05$). To examine whether this decline arose through a systematic change in individual breeding success, we compared the sample of known-age females and males for which we had nesting records in both 1990 and 1991. The within-individual decrease from 1990 to 1991 amounted to 0.51 young in 5-17-year-olds (paired t-test, $t_{136} = 5.73$, $P < 0.001$, 13 year-classes represented), being close to the overall decline of 0.52 young observed in the 1990-1991-population of old breeders, suggesting that the observed decline reflected changes within individuals. The de-

Figure 7. Percentage of nests in which one or more Great Cormorant chicks died when 15- to 28-days-old (filled squares) and when 29- to 42-days-old (open cicles), 1980-1995. Only years and age-intervals where brood size were noted frequently for 32 nests or more are included (mean *n* = 101).

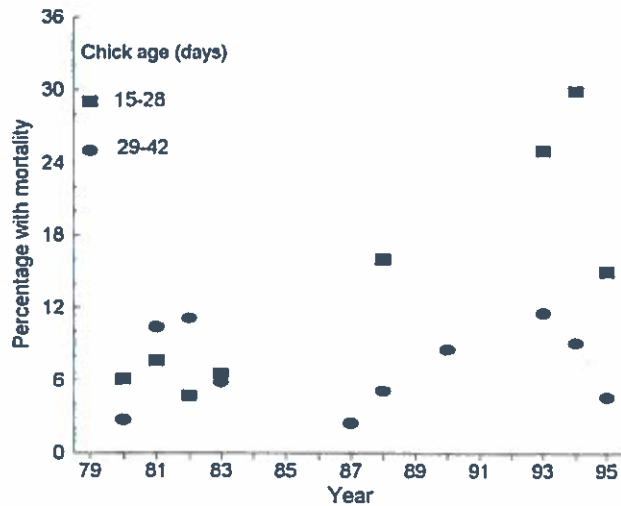cline in brood size may reflect a decline in clutch size, in the number of eggs hatched, and/or in the survival of young. Mean clutch size was 0.48 egg (15%) lower in 1994 than in 1990, and the decline was significant (Table 3; Scheffé multiple range test, $P < 0.05$). The difference was lower

(0.33 eggs; 11%) after adjusting for the influence of date. We have no data on the proportion of eggs that hatched but noticed that in 1991-1995 one to two unhatched eggs were present in several of the nests when chicks were ringed. The proportion of broods where one or more chicks died was low in period I and high in the last years of period II (Fig. 7). Thus the decline in brood size in period II was mainly due to an increase in chick mortality.

Diet

The relative importance of the main fish species taken by the Great Cormorants changed from the pre-laying and incubation phase to the chick rearing phase (Table 4). The composition of the diet in both phases changed from period I to period II (Table 4). The Bull Rout *Myoxocephalus scorpius* was important in the pre-laying and incubation phase in period I, whereas the Dab *Limanda limanda* and several freshwater species took up a much larger share of the diet in period II. In the chick rearing phase, the importance of Dab and 'other species' increased between period I and period II, whereas the importance of Eelpout *Zoarces viviparus* and Bull Rout declined. The total number of species included in the diet increased from 22 in period I to 38 in period II; the number of pellets analysed was

Table 4. Mean and range in parentheses (% by weight) of monthly occurrence of fishes in the diet of adult Great Cormorants during pre-laying and incubation (February-April), and during chick rearing (May-July), 1980-1983 and 1993-1994.

	February - April				May - July			
	1980-1983[1]		1993-1994[2]		1980-1983[3]		1993-1994[4]	
Bull Rout	39	(31-57)	5	(0-13)	17	(10-28)	2	(0-8)
Eelpout	15	(0-29)	8	(0-16)	24	(7-45)	4	(0-18)
Dab	21	(0-39)	47	(23-74)	29	(7-55)	53	(48-57)
Other saltwater species[5]	25	(10-40)	38	(28-49)	30	(20-40)	36	(23-52)
Freshwater species	0		4	(0-9)	2	(0-8)	7	(0-22)

[1] 18-116 pellets per month 1980 and 1983, and March 1981.
[2] 36-40 pellets per month 1993, and April 1994.
[3] 16-136 pellets per month 1980 and 1983, and June 1981 and May 1982.
[4] 29-45 pellets per month.
[5] Eel *Anguilla anguilla* and Stickleback *Gasterosteus aculeatus* included.

641 and 470 respectively. Species living in deeper water, e.g. Dab and *Lumpenus lampretaeformis*, were more frequent in the diet in period II than in period I.

Discussion

Declining brood sizes at fledging in young parents, increasing probability of failure during chick rearing, and declining occurrence of second clutches during the expansion of the colony from 950 to 3300 nests suggest that food availability late in the breeding season declined over the years of period I. These changes are in accordance with the predictions from Ashmole's hypothesis (Ashmole 1971, Birkhead & Furness 1985).

The extreme expansion of the colony in 1989 was followed by a marked decline in breeding success. This decline was mainly a result of an increase in the proportion failing during incubation. Towards the end of period II, but very rarely before, territories and nests were deserted for long periods of the day or even for several days during and after windy and cold periods. This suggests that the physical condition of individual birds had deteriorated at some point prior to or during incubation. The decline in the number of eggs laid supports this suggestion (cf. Birkhead & Nettleship 1981).

The Great Cormorants may have experienced food shortage already before returning to the colony, i.e. in the wintering areas or at some point during spring migration. Some of the Vorsø breeders overwintered in areas used by large numbers of Great Cormorants during autumn and winter (Reymond & Zuchuat 1995, Suter 1995, Bregnballe *et al.* in press.) and the build up of nutrient and energy reserves may have been constrained by a shortage of food in late winter. However, the only indication we have for changes of the annual cycle at this stage is a progressively later arrival to the colony during 1992-1994 (mean arrival date for breeding birds, $r^2_{530} = 0.15$, $P < 0.0001$), but this may, at least to some exent, relate to the weather conditions in February-March 1993-1994. The food availability after return to the colony is known to be an important parameter in many colonial waterbirds affecting nest attendance and nest abandonment (Barrett & Runde 1980, Galbraith 1983, Boekelheide & Ainley 1989, Cezilly 1993, Coulson & Johnson 1993, Hamer *et al.* 1993, Crawford & Dyer 1995). Mass abandonment of nests is most frequently observed in regions where seabirds depend on a single species of prey (see Croxall & Rothery 1991, Crawford & Dyer 1995). In period I, the Bull Rout was a keyspecies for the Vorsø Cormorants in the first months after returning to the colony (February - early April). The species was far less frequent in the diet in period II, suggesting a decline in stock. This may explain why the Cormorants increased their food spectrum to include more of the deep water species which were not utilized in period I. Many of the fish species exploited when rearing chicks are likely to be inactive and reside at relatively great depths in the first month(s) after the Great Cormorants return to the colony (cf. Voslamber *et al.* 1995). Therefore, the Great Cormorants may have been particularly sensitive to the 'disappearance' of the Bull Rout, which is present in relatively shallow areas in winter. Regurgitated pellets without otoliths or fish bones (but consisting of mucus) were more frequent in the February-March samples (8-10% of the pellets) than in the April-July samples (0.5-1.8%).

One consequence of low food availability early in the season in the last years of period II, may have been that some parents approached a lower threshold of body condition when rearing chicks (cf. Coulson & Porter 1985) affecting their willingness to invest in frequent long-distance foraging trips. Drent & Daan (1980) suggested the existence of an 'optimal working capacity' or a threshold below which parents would not permit their body condition to fall. Some studies support the idea that adults adjust their breeding effort so that they do not incur the risk of increased mortality (Monaghan *et al.* 1989, Sæther *et al.* 1993, Pons 1995, Weimerskirch *et al.* 1995).

There is circumstantial evidence which suggest that it was a decline in the amount of food brought to the chicks that caused the increase in chick mortality and thereby the decline in brood size at fledging. Thus when chicks were handled during ringing in 1991-1995 far fewer of them regurgitated food than was the case in previous

years; however, this was not quantified. Furthermore, in 1983-1984 large broods at the age of 6 weeks were fed every two hours (Hald-Mortensen 1988) but in 1994, feeding of chicks occurred at an interval of six hours (Bregnballe & Schjørring M.S.).

The proportion of Eelpout and Bull Rout in the diet declined from period I to period II. Both species are bottom dwelling, stationary and of no commercial interest. The local stock of Bull Rout may therefore have declined over the years because of, or partly because of, predation by Great Cormorants. Bull Routs, which would have reproduced later in the season, were taken early in the season and the preceding years' predation may, therefore, have affected recruitment to the stock during 1991-1995. The hinterland model (Cairns 1989) suggests that both food density and competition from conspecifics in other colonies contribute to the regulation of colony size in seabirds (cf. N. Røv, 1994, unpublished PhD thesis, University of Trondheim). Predation by cormorants breeding in four neighbouring colonies, located 25-40 km from Vorsø, may have added to a decline in food availability. These colonies increased from 120 nests in 1985 to 1330 nests in 1989, and to 6130 nests in 1995 (Bregnballe & Gregersen 1995). Information about the demography and regulation of the Bull Rout population is, however, not available and this makes it impossible to state that cormorant predation actually caused the decline in the local Bull Rout stock. A study of Double-crested Cormorants *P. auritus* in Newfoundland suggested that predation had led to low fish densities late in the chick rearing period. Thus densities of bottom dwelling species were significantly lower in the vicinity of the colony than 40 km away, i.e., outside the foraging range of breeding birds (Birt *et al.* 1987). However, several of the changes in diet composition and fish density are likely to have had no direct relation with predation from Great Cormorants. Long-term trends in the breeding performance of Kittiwakes *Rissa tridactyla* in Great Britain paralleled long-term changes in the marine environment (Coulson & Porter 1985, Harris & Wanless 1990).

Our interpretation of the changes in breeding success of Great Cormorants at the Vorsø colony can be summarized as follows: firstly, the amount of food available in the later phases of breeding began to decline influencing chick survival and the frequency occurrence of second clutches and late breeding. Secondly, predation on Bull Rout increased in period II causing or adding to a between-year decline in food availability in early spring. This limited the breeders from investing large amounts of energy and nutrients in reproduction leading to reduced clutch sizes. Thirdly, after the extreme increase in colony size at the beginning of period II, the parents searched for food further away from the colony affecting the daily number of foraging flights, and thereby the number of chicks surviving to fledging.

Acknowledgements

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Chapter 4

Breeding success in the Great Cormorant *Phalacrocorax carbo sinensis*: costs and lost opportunities associated with philopatry

Thomas Bregnballe & Solveig E. Schjørring

Breeding Success in the Great Cormorant *Phalacrocorax carbo sinensis*: Costs and Lost Opportunities Associated with Philopatry

by

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Abstract
The consequence of philopatric and dispersal behaviour was examined in Great Cormorants (*Phalacrocorax carbo sinensis*) in 1994 by studying colony reproductive performance and time spent on foraging trips in a saturated colony and in a new expanding colony, located 43 km apart in south-west Kattegat, Denmark. Clutch size, brood size and the proportion of initiated clutches from which at least one young fledged was determined. Choice of foraging area and duration of foraging trips was studied by recording directions of flights and counting birds flying to and from each colony. For 22 broods in the saturated colony and for 26 broods in the expanding colony, chick provisioning rates, chick time budgets, parental attendance and number of foraging trips were quantified from continuous observation for one 48 h period and one 24 h periods. Observations were made when chicks aged c. 30 days. Chick growth during a 7-9-day-period was determined for 16 chicks in the saturated colony and 20 chicks in the expanding colony. The body weight of 56-157 chicks per year was plotted against wing-length and used as a condition index. The expanding colony received more than 1600 immigrants over four years including some colour-ringed individuals from the saturated colony, where breeding success was declined. The large number of birds which remained philopatric towards the saturated colony, travelled further to find food, spent twice as much time on each trip and spent 20% more per day on food provisioning than birds in the expanding colony. In the saturated colony, feeding frequency of chicks was 50% lower than in the expanding colony, and chicks were less active and mortality was higher. No significant differences were detected in the growth rate of chicks between colonies, but more of the chicks in the saturated colony had low body weight for given wing-lengths. Overall, the gain from breeding in the expanding colony in comparison with the saturated colony amounted to a production of 148% more fledged young in the study year. Old breeders in the saturated colony may have been constrained by limited time to learn about the potential gain of moving to the expanding colony.

Introduction

Philopatry, the tendency of an individual to exhibit long term use of a certain area, such as a breeding colony, is commonly observed in colonial waterbirds (e.g. Rowan 1965, Greenwood 1980, Swann and Ramsay 1983, Harris and Wanless 1991, Coulson and Nève de Mévergnies 1992, Danchin and Monnat 1992, Aebischer 1995, Fairweather and Coulson 1995). It is thought to be an adaptive behavioural strategy to return to a colony with which one has experience, because it may reduce the costs associated with securing high quality territories and finding the most profitable feeding areas (Brown *et al.* 1990). However, philopatry is not likely to be an adaptive strategy in a rapidly changing environment (Røv 1994). Due to local environmental changes, food or nest sites may come in short supply (Porter and Coulson 1987, Cooch *et al.* 1989, Cooch *et al.* 1993, Fairweather and Coulson 1995) or predators may immigrate (Parker and Mehlum 1991, Coulson and Nève de Mévergnies 1992). A decline in food availability may force parents to work harder to meet the recuirements of the brood (Anker-Nilssen 1990, Platteuw and Van Eerden 1995) and if parents are unable or unwilling to do so, they may experience low breeding success. Under such circumstances, breeding and natal dispersal may become advantageous, unless food availability or predation risk changes simultaneously in all breeding areas (Levin *et al.* 1984, Danchin and Monnat 1992, Stenzel *et al.* 1995).

This study examines the costs of philopatry in Great Cormorants, measured as the time invested in providing food for the young, and the benefit that may be incurred, measured as breeding success, by settling in an expanding neighbouring colony.

Study area and methods

Two colonies in the south-west Kattegat were studied (Fig. 1). The largest and oldest of the two colonies is located in a fjord on the island of Vorsø (55°52'N, 10°01'E) surrounded by large areas of land, whereas the more recently established and smaller colony, Stavns Fjord (55°54'N, 10°39'E), is located in a fjord on a small islet from which there is a short distance to the sea in an almost 300 degrees arc. The main part of the study was carried out in 1994 and unless otherwise stated the results refer to 1994.

Parents

The minimum distance travelled between the colony and the foraging area was determined by studying directions of foraging flights. The proportion of birds taking various routes was quantified by simultaneous counts from four posts located at a distance of 0.4–1.9 km from the colony in various directions so that all outgoing as well as incoming birds could easily be followed and directions recorded. These counts were also used to estimate the average time spent on foraging trips. Thus, after plotting the curves for the cumulated numbers of departures and returns against time, the horizontal distance between the curves could be used as an estimate of the average duration of a foraging trip (an example is given in Van Dobben 1995). These observations, performed twice for each colony, started at 0240 h, i.e. before the first comorants left the colony, and ended at 0700 h. Knowing the duration of foraging trips and the number of trips (see below), the total time invested in food provisioning could be calculated. The time spent on a foraging trip is likely to vary from day to day according to feeding conditions and the cost
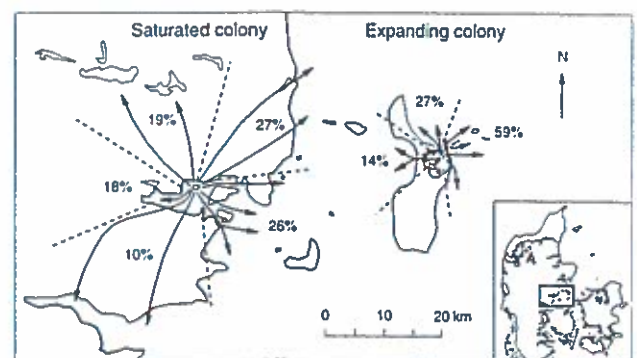

Figure 1. Map showing location of the saturated and the expanding colony of Great Cormorant in the south-west Kattegat, Denmark. Arrows show main foraging routes, and numbers denote percentage of outgoing birds in the sections, indicated by dashed lines.

of flight, e.g. wind force, wind direction and thermals (Cairns 1987, Platteeuw and Van Eerden 1995, Van Eerden and Voslamber 1995). When trip duration was measured, the wind was stronger in the expanding than in the saturated colony and the duration of foraging flights from the expanding colony may therefore have lasted longer than usual.

Parental attendance at the nest may greatly affect survival of Great Cormorant chicks especially in the first 22 days after hatching (Gregersen 1982; J. Gregersen unpublished observations). Parental attendance and the mean number of daily feeds received by broods was determined from continuous observations of 22 nests in the saturated colony and 26 nests in the expanding colony. The nests were kept under observation over one 48-hr period in each colony (13-14 and 17-18 June) and one 24-hr period in each colony (21 and 23 June) by two persons taking 4-hr stints in relay. All observations were made from hides located so that all nests being monitored could easily be seen without disturbing the birds. Mean brood sizes on the first day of observation were 1.59 chicks ± 0.73 SD in the saturated colony and 2.35 chicks ± 0.63 SD in the expanding colony, and the mean age was 27.4 d ± 7.9 SD (35 chicks) and 25.7 d ± 4.7 SD (61 chicks) respectively. The brood was here defined as being unattended if both parents were more than 4 m from the nest.

Chicks

Chicks in the surveyed nests and in a random sample of other nests were ringed and aged from wing-length measurements (estimated from data collected by K. Koffijberg & M.R. van Eerden in the Oostvaardersplassen colony in the Netherlands). Chick activity and behaviour may reveal whether chicks are emaciated or in a good nutritional state (Swiergel 1987, Klaassen et al. 1994). Chicks with excess energy may exercise their wing muscles, imitate feeding behaviour and perform other energy demanding activities. The activity of chicks in the nests studied was quantified by instantaneous records at 10-15 min intervals during several one hour periods distributed through the day between 0730 and 1900 h. In total, 3115 records of chick activity was obtained in the saturated colony

and 1525 records in the expanding colony. When the data were collected, we distinguished between 16 types of activities. These were subsequently grouped according to the activity level: 'active' (standing or lying combined with being aggressive, pecking branches in the nest, exercising wings etc.), 'passive I' (brooded by parent, sleeping when lying or standing), and 'passive II' (lying in the nest). Passive I and II are not mutually exclusive.

Growth of seabird chicks may provide an indicator of feeding conditions (Ricklefs et al. 1984, Anker-Nilssen 1987), and data on growth of chicks in broods of 2 or 3 were obtained from two weighing sessions in each of the study colonies, 7-9 days apart. The chicks, 16 in the saturated colony and 20 in the expanding colony, were 15-23 days saturated on the first day of weighing, i.e. growth was followed in the phase when body mass increases with an approximately fixed number of grams per day (cf. Platteeuw et al. 1995). All chicks were weighed to the nearest 25 g using a Pesola spring balance, and the wing-length was measured to the nearest mm. Body weights of chicks for given wing-lengths may be used as rough measures of 'body condition' (Beintema 1994), and 56-157 chicks were measured in each colony in 1993 (4-8 June) and in 1994 (5-16 June).

Reproductive parameters
To obtain a reasonably comparable estimate of clutch size, we recorded the number of eggs in a random sample of nests after the pairs had finished laying. Information on brood size was collected during ringing and on three other occasions by counting chicks in broods where all chicks were visible. Chicks were aged by measuring wing-length or by estimating age when observed standing in the nest. The proportion of pairs nesting successfully (at least one young fledged) was recorded by randomly selecting and numbering nests soon after incubation began and subsequently follow them until fledging. Nests in the saturated colony were checked twenty times (from an observation tower) and nests in the expanding colony were checked four times (by climbing trees and observing from the ground). To obtain an index of chick mortality, searches for dead chicks were
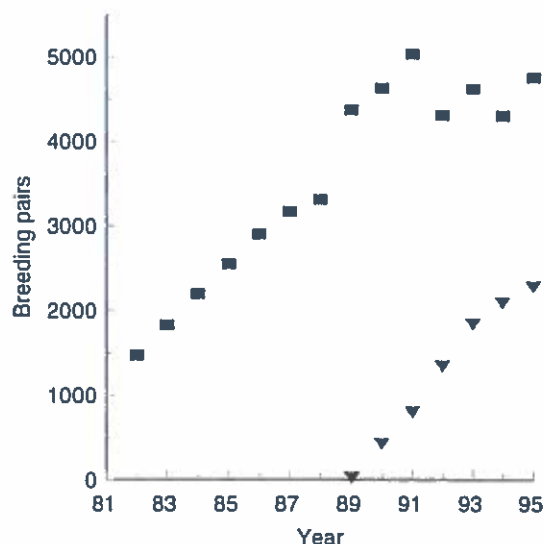
Figure 2. Development of the number of breeding pairs in the saturated colony (squares) and in the expanding colony (triangles), 1982-1995.
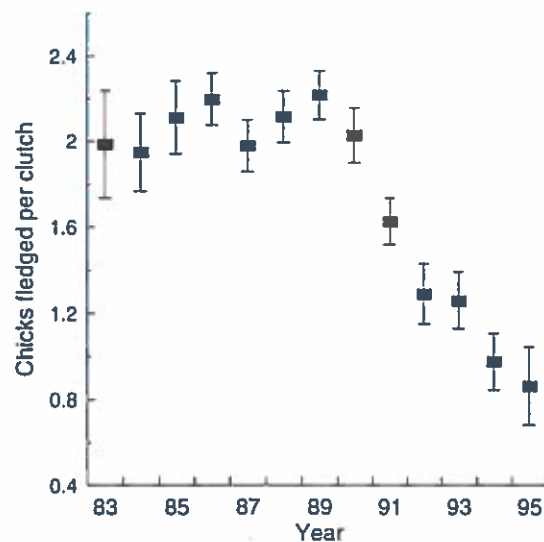
Figure 3. Mean number of chicks fledged per clutch in the saturated colony 1983-1995. Vertical lines denote 95%-confidence limits. Annual sample size ranged between 104 and 340 clutches.

performed below a known number of nests after almost all chicks had fledged.

Statistical analyses

The annual mean number of young fledged per clutch in the saturated colony, 1983-1995, was calculated by weighting the annual mean for the group of 2-4-year-olds and 5-17-year-olds by the estimated proportion of the two age-groups nesting in the population (Bregnballe unpublished data). Data on the number of feeds per brood per day were square-root transformed before analyses and we controlled for the influence of weather and age of chicks (cf. Léger and McNeil 1985, Platteeuw and Van Eerden 1995) by having day as a factor in a two-way ANOVA. The proportion of each observation period that chicks were left unattended by both parents simultaneously was calculated separately for each nest, and then combined to produce mean values for all nests. The number of nests observed was too small to control statistically for weather, brood size and chick age, all of which influenced parental attendance on the young. Therefore, we decided to present only the data on variation with age and colony for broods with two chicks followed on two days which

had similar weather conditions. Before analyses of differences in chick activity, chick ages were grouped into 5-day intervals. All chick activities were recorded as proportions of scans and arcsin transformed before analysis. The influence of sun, wind, rain and chick age on each chick activity group was revealed by plotting the relationships and selecting those intervals of age (5-day-intervals), sun (four intervals), wind (Beaufort scale) and rain (three intervals), when there was no marked increase or decline and both colonies were well represented. One-way and two-way ANOVA were used to test for differences in chick activity between colonies. All tests were two-tailed and we used 5% as the level of significance.

Results

The colonies

The growth of the saturated colony levelled off after a large increase in 1989 (Fig. 2) and breeding success began to decline thereafter (Fig. 3).

Table 1. Number of birds originating from the saturated colony observed and minimum number estimated to breed in the expanding colony in the years 1992-1995.

Year-class	Individuals breeding	Estimated to breed[1]
1980-84	4	23
1986-88	4	67
1989	6	106
1990-93	4	58

[1] A minimum, estimated from proportions ringed of chicks fledged in the saturated colony corrected for influence of mortality on resighting probabilities. No corrections for the proportion of breeders checked for rings.

The expanding colony increased from 25 pairs in the first year 1989 to 804 pairs two years later (Fig. 2). Eighteen of the Great Cormorants ringed as chicks in the saturated colony were later seen breeding in the expanding colony (Table 1). This corresponds to a minimum number of 254 immigrants from the saturated colony of which most originated from the 1989 year-class. We estimated that c. 30% af the nesting birds were checked for colour-rings, and correcting for this, the observed birds corresponded to c. 880 individuals. At least eight of the identified immigrants had formerly been nesting (here defined as having had a partner) in the saturated colony.

Table 2. Number of feeds of broods in the saturated colony and in the expanding colony in 1994. Given are $\bar{x} \pm$ SD for each of the three days with continous observations (day, $F_{2,120} = 1.20$, n.s.; colony, $F_{1,120} = 36.45$, P < 0.001; interaction, $F_{2,120} = 0.44$, n.s.; two-factor ANOVA).

	Day 1	Day 2	Day 3
Old colony	2.2 ± 1.4	2.2 ± 1.2	2.9 ± 1.4
New colony	4.4 ± 1.8	3.9 ± 1.7	4.6 ± 2.0

The parents

Most of the Great Cormorants breeding in the saturated colony foraged in the Kattegat east of the colony, an area reached by some of the birds by travelling at least 12 km over land (Fig 1). Birds foraging in Vejle Fjord south of the colony or in the freshwater lakes north-west of the colony covered distances of at least 16-20 km. By contrast, Great Cormorants breeding in the expanding colony had a much shorter distance to the sea in almost all directions, but we do not know how far they travelled, except that some larger flocks were observed come down on the sea 6-8 km from the colony.

Parents nesting in the saturated colony delivered food to the chicks only half as frequently as parents nesting in the expanding colony (Table 2). The foraging trips performed by birds nesting in the saturated colony lasted twice as long as the foraging trips in the expanding colony (157 vs 72 min). Although nesters in the saturated colony left the colony earlier in the morning than nesters in the expanding colony, the first feeding of chicks in the morning took place 52 min later in the saturated colony than in the expanding colony (median for all three days 0930 vs 0838 h). The total time spent on food provisioning per day per parent was 184.2 min ± 15.2 SD in the saturated colony and 153.8 min ± 14.1 SD in the expanding colony. Hence, the parents in the saturated colony spent 30 min (20%) more on foraging trips than parents in the expanding colony.

Parents in the saturated colony attended the nest for a shorter proportion of the day than parents in the expanding colony (example in Fig. 4). Our data did not allow for tests of significance after having controlled for effects of brood size, chick age and weather.

The chicks

The variation within and between broods in daily weight increase of chicks was considerable (range: saturated colony, 21.4-92.9 g/d; expanding colony, 25.0-102.8 g/d), but there was no difference between the two colonies in mean weight increase when chicks were 16-31-day-old (63.0 g/d ± 21.7 SD in the saturated colony vs 68.5 g/d ± 23.7 SD in the expanding colony, t_{34} = 0.331). The weights of a larger sample of
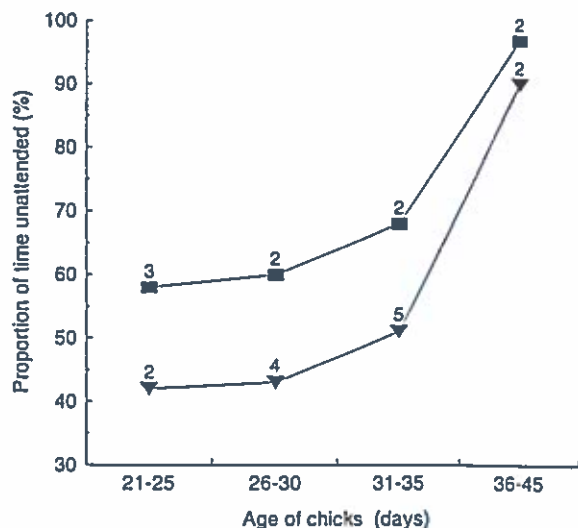
Figure 4. Proportion of time in which chicks in the saturated (upper line) and expanding colony (lower line) were left alone as a function of chick age. The figure gives data for broods with two chicks only (number of broods denoted) followed continuously 0240-2300 h on day 2.

chicks are shown in Fig. 5, plotted against their wing-length. In 1993, body weight of chicks were generally lower in the saturated compared to the expanding colony for chicks with wing-lengths between 180 and 240 mm (24-34-day-old). Body weights were almost similar in the two colonies in 1994, but underweight chicks were observed only in the saturated colony (Fig. 5). Chicks in the saturated colony were passive for a larger proportion of the day than chicks in the expanding colony. ('Passive I', compared for 31-45-day-old chicks, $t_{32} = 5.44$, $P < 0.001$. 'Passive II': colony, $F_{1,52} = 27.42$, $P < 0.001$; age-class (21-35 day-old and 36-50-day-old), $F_{1,52} = 16.72$; $P < 0.001$; interaction $F_{1,52} = 0.11$, n.s.; two-factor ANOVA).

Breeding success

Clutch size did not differ significantly between the two colonies (Fig. 6). Mean brood size declined over the first period of chick rearing in both colonies (Fig. 6). The decline was more rapid in the saturated than in the expanding colony and brood size continued to decline in the old colony until fledging (Fig. 6). The difference in brood size between the colonies amounted to 0.80 young when close to fledging.
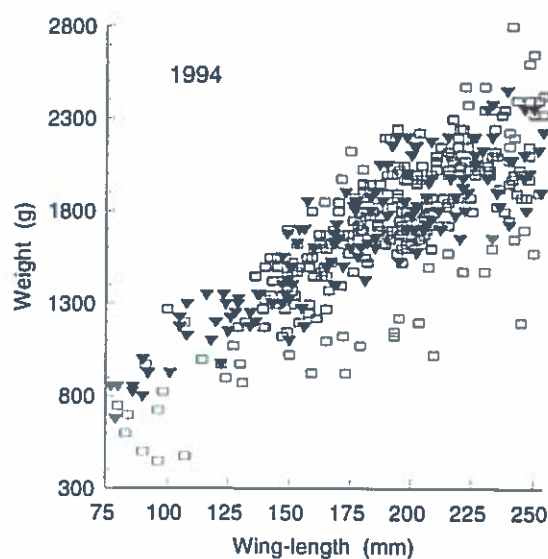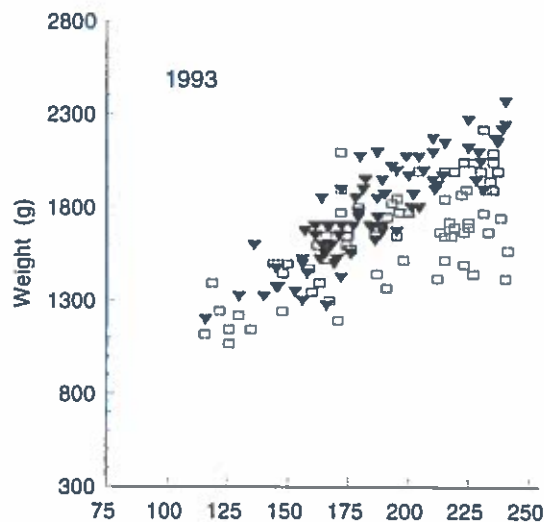
Figure 5. Weight and wing-length relationship for Great Cormorant chicks in the saturated (open squares) and expanding (triangles) colony in 1993 (upper figure; 18-34-day-old) and 1994 (lower figure; 11-37-day-old).

The proportion of pairs raising at least one chick to fledging was smaller in the saturated colony than in the expanding colony (59% vs 98% for 93 and 51 nests monitored from incubation to fledging; $X^2_1 = 25.24$; $P < 0.0001$). After the breeding season, ten times more dead chicks were found per nest in the saturated colony than in the expanding colony (0.203 vs 0.026 chick per nest, comprising searches below 655 and 699 nests; $X^2_1 = 96.87$; $P < 0.0001$). Compared with the expanding colony, a larger proportion of the chicks found dead in the saturated colony were older than 28 days (56% vs
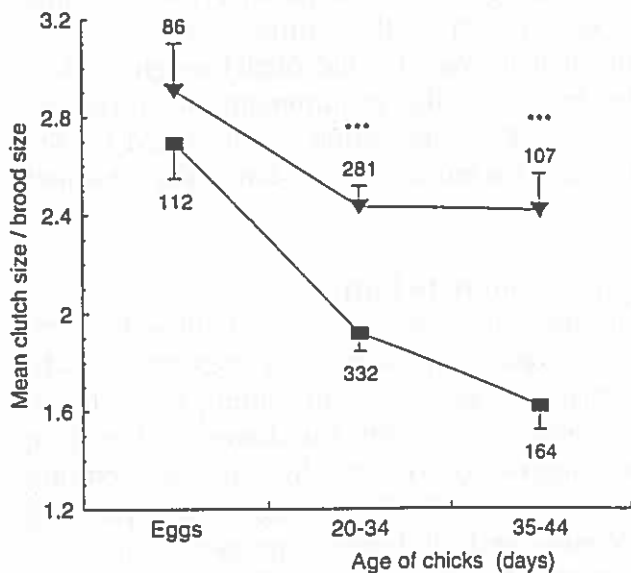
Figure 6. Mean clutch and brood size in the saturated (squares) and expanding colony (triangles), 1994. Vertical lines denote 95%-confidence limits. Sample sizes and level of significance are given (***P<0.001; t-test).

39%, 124 and 18 chicks; $X^2_1 = 16.94$; $P < 0.0001$). The total reproductive output per clutch was 2.5 times higher in the expanding colony than in the saturated colony (2.37 vs 0.96 young per clutch).

Discussion

Parental investment: costs and limitations

In the saturated colony Great Cormorants performed few but long foraging trips whereas, in the expanding colony, more but shorter trips were performed. Each parent in the saturated colony spent on average 30 min (20%) more per day on food provisioning than parents in the expanding colony, but it is uncertain whether this also meant that more energy was invested in food provisioning. Time spent away from a colony may not be a good measure of energy expenditure because time spent on foraging (Monaghan *et al.* 1994), flapping flight, soaring, roosting and on digesting the birds' own food requirements before returning to the colony (Wanless *et al.* 1993) might vary and affect energy expenditure (Cairns *et al.* 1987). However, if the parents nesting in the saturated colony had attempted to provide chicks with food at the same rate as the parents in the expanding

colony did, they would have had to invest more energy because of the greater distances to the foraging areas.

Platteeuw and Van Eerden (1995) found that the daily sum of time spent on foraging flights (2 trips), swimming and diving of Great Cormorants nesting at Lake IJsselmeer in the Netherlands, amounted to 5.4 h in one colony and to 5.7 h in a neighbouring colony. In the saturated colony in this study, the total time spent on foraging trips by a single parent was estimated as 3.1 h per day, i.e. 2.3-2.6 h less than in the Dutch colonies. The difference is due to the higher frequency of foraging trips in the Dutch colonies (2.0-3.5 trips/d/parent) than in the saturated Danish colony (1.2 trips/d/parent; chicks of similar ages). The use of different methods to record the number of foraging flightst in the two studies may explain the large differences in foraging flight distances. In our study, we assumed that each foraging trip by a parent would be followed by bringing food to the chicks, and this may not be true. Platteeuw and Van Eerden (1995) assumed that parents which were absent for at least half an hour performed a foraging trip, and this may not be true either. On several occasions, we observed one of the studied (colour-ringed) parents feed the chicks whereafter it left and sat passively elsewhere in the colony for more than half an hour and then returned to the nest. More stringent methods (e.g. Hamer *et al.* 1993, Monaghan *et al.* 1994) should be adopted to quantify the number of foraging flights.

Chicks in the saturated colony were fed approximately half as often as chicks in the expanding colony. This raises the question whether lack of time or lack of energy limited the parents from performing more foraging flights. Most of the parents studied in the Netherlands were dependent on joining social fishing flocks (Platteeuw and Van Eerden 1995, Van Eerden and Voslamber 1995), and the authors suggested that this lead to a time constraint. The parents in our saturated study colony distributed their foraging trips over 19.5 h of the day, so with 2 trips per day per parent (total time 3.1 h), there would have been ample time with daylight to carry out more fishing trips. The upper limit of time allocated to foraging trips by parents nesting in our saturated colony may

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instead have been set by a ceiling on daily energy expenditure (cf. Drent and Daan 1980) rather than by the requirements for other activities such as sleep, digestion or preening (see Cairns 1987, Cairns et al. 1987). That birds do not work hard for more than 4 h per day for long periods of time has been observed in several bird species (Drent and Daan 1980), though there are exceptions also among seabirds using flapping flight (Anker-Nilssen 1987). We find it likely that some of the Great Cormorants in the saturated colony were approaching a critical low level of condition in the last weeks before their chicks fledged and were therefore unwilling to work. Greater foraging efforts due to low food availability when breeding may result in declining adult body condition, as observed in Arctic Terns *Sterna paradisaea* (Monaghan et al. 1989).

Chicks: importance of food

There was no significant difference between the two colonies in chick growth rate. Parents in the saturated colony may thus have compensated for the lower provisioning rates by bringing back heavier loads (cf. Dunn 1975). Wanless et al. (1993) found that Shags *P. aristotelis* brought back heavier loads when feeding farther away from the colony. The food requirement of chicks varies with growth rate, the amount of fat deposits, cost of thermoregulation, activity and other maintenance costs (Dunn 1979). Chicks in the saturated study colony were inactive for a larger proportion of the day than chicks in the expanding colony, suggesting that they attempted to save energy for growth and maintenance (cf. Swiergel 1987, Klaassen et al. 1994). Dunn (1975, 1980) found that the daily energy intake of single Double-crested Cormorant *P. auritus* chicks reached maximum values between the age of 24 and 35 days, and the period of maximum food requirement of chicks may have represented an important bottleneck (cf. O'Connor 1978, Klaassen and Bech 1992) for the parents in the saturated colony. Thus, shags and cormorants increase the number of fishing trips and/or bring back larger loads as chicks grow older (Dunn 1975, Léger and McNeil 1985, Wanless et al. 1993, Platteeuw et al. 1995). The plots of body weight for given wing-lengths

(Fig. 5) suggest that most parents (1993) or some parents (1994) in the saturated colony were unable to increase the fish catch brought back to the brood as the requirement of chicks increased. This suggestion is supported by the higher chick mortality recorded in the saturated colony.

Which colony to join?

Moving from a decreasing or stabilized colony to an expanding colony may increase an individuals prospects of contributing genes to future generations. Thus the chances of breeding with high success early in life without impairing own survival will often be highest in expanding colonies and philopatric progeny will have opportunities for settling and reproducing successfully. Hence, even though, dispersal and migration may result in a short-term decrease in reproductive output because of missing experience with a new area, a substantial improvement of an individuals lifetime reproductive success is to be expected if it joins the 'right' colony. Since 804 Great Cormorant pairs settled in the expanding colony in its second year of existence, at least 1600 birds must have immigrated (Great Cormorants very rarely start breeding before the age of 2 years (Kortlandt 1942, del Hoyo 1992, Grieco 1994, Bregnballe and Gregersen in press.)). An unknown proportion of these individuals originated from colonies other than our saturated study colony (four colour-ringed individuals from three other Danish colonies were observed breeding). The birds which moved from the saturated to the expanding colony are most likely to have gained from doing so. Thus, on average, pairs nesting in the expanding colony raised 1.4 (148%) more chicks to fledging than pairs breeding in the saturated colony. This difference cannot be attributed to differences in age structure of the two breeding populations. Furthermore, age at first breeding increased in the saturated colony during the 1990s (Bregnballe, unpublished) suggesting that young potential breeders which attempted to nest in the old colony performed poorly.

The choice between philopatric and dispersal is likely to be influenced by the relationship between the pattern of environmental variation,

both spatially and temporally, and the relative costs associated with obtaining information. It is difficult to see the overall benefits of philopatry in the scenario of the present study. Immediate advantages of remaining (experience with safety against predators, ability to obtain a good territory early in the season, etc.) and difficulties with predicting future food abundance may have kept experienced breeders from emigrating (Brown *et al.* 1990). In addition, obtaining information about food availability and breeding success in other colonies may be difficult for parents engaged in chick rearing. Experienced breeders may have been unaware of the reproductive success they could gain by joining the expanding colony (cf. Brown *et al.* 1990) .

Recruitment of Great Cormorants to colonies may in some area follow a pattern of ideal free distribution (Fretwell and Lucas 1970, Røv 1994) where individual birds settle among available colonies in densities so that fitness of nesting becomes independent of colony (Furness and Birkhead 1984, Brown *et al.* 1990). Great Cormorants are generally prone to disperse (Røv 1994, Bregnballe and Gregersen 1995, Lindell *et al.* 1995, Van Eerden and Gregersen 1995) and large numbers of breeders may regularly move between colonies (e.g. Røv 1994). However, for several reasons, ideal free distribution may not develop (see Brown *et al.* 1990, Brown and Rannala 1995) and our study indicates that if it develops, it may take several years. As pointed out by Coulson and Nève de Mévergnies 1992), further studies are clearly required to elucidate the process of choosing breeding colony.

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Chapter 5

Udviklingen i ynglebestanden af Skarv *Phalacrocorax carbo sinensis* i Danmark 1938-1994

With a summary in English: Development of the breeding population of Cormorant Phalacrocorax carbo sinensis *in Denmark, 1938-1994*

Thomas Bregnballe & Jens Gregersen

Udviklingen i ynglebestanden af Skarv *Phalacrocorax carbo sinensis* i Danmark 1938-1994

THOMAS BREGNBALLE og JENS GREGERSEN
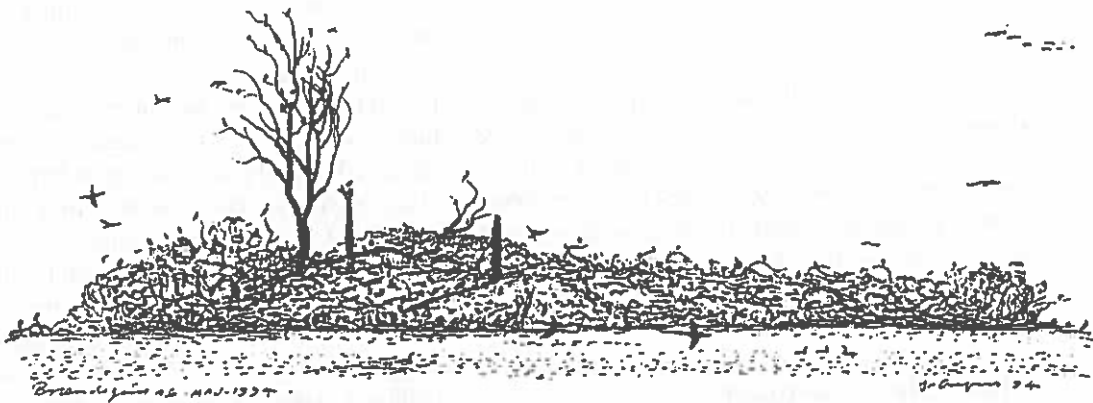
(With a summary in English: Development of the breeding population of Cormorant
Phalacrocorax carbo sinensis *in Denmark, 1938-1994)*

Indledning

Mellemskarven *Phalacrocorax carbo sinensis* er udbredt fra Japan og Philippinerne i sydøst til Europa i nordvest (del Hoyo et al. 1992). I Nord- og Vesteuropa har underarten haft sin hovedudbredelse i Holland, langs den vestlige og sydlige del af Østersøen (Sverige, Polen, Tyskland) og omkring de danske bælter (Hansen 1984, Suter 1989). Her har tilstedeværelsen af træbevoksninger ved søer, floder og lavvandede kystområder givet Skarven gode muligheder for at yngle nær rige føderessourcer og i sikkerhed for prædatorer. Betegnelsen Skarv henviser fremover til Mellemskarven.

I de sidste århundreder har Skarven været opfattet som en konkurrent til fiskeriet, hvilket har ført til talrige forsøg på at fordrive arten (Helms 1940, Brouwer 1954, Coomans de Ruiter 1966, Løppenthin 1967, Gregersen 1982, Andersson et al. 1984, Hansen 1984). Disse forsøg har ofte været vellykkede, bl.a. fordi Skarven yngler koncentreret i kolonier og er følsom over for forstyrrelser. Indgrebene har omfattet forsøg på bortskræmning, ødelæggelse af æg og reder samt beskydning af voksne og unger (Kortlandt 1942, Brouwer 1954, Coomans de Ruiter 1966, Gregersen 1982, Andersson et al. 1984, Veldkamp 1986). Indgrebene har i perioder været så effektive, at udbredelsen af den nord- og mellemeuropæiske bestand flere gange i 1700-, 1800- og 1900-tallet indskrænkedes til ganske få kolonier (Brouwer 1954, Gregersen 1982). Under intensive forfølgelser ophørte arten sent i 1800-tallet med at yngle i Danmark (Helms 1940, Løppenthin 1967), men genindvandrede i 1938, efter at vilkårene i nabolandene mod syd var forbedret i århundredets begyndelse. Alligevel var arten i en årrække truet af udryddelse, ikke blot i Danmark, men også i det øvrige Europa. Som en konsekvens af tilbagegangen øgedes beskyttelsen af Skarven gradvist fra 1965 til 1981, og i løbet af 1970erne og 1980erne mangedobledes antallet af ynglepar i Nord- og Mellemeuropa (Suter 1989). I de senere år er væksten i hovedudbredelsesområdet, dvs. Holland og Danmark, aftaget og i flere af kolonierne helt ophørt (van Eerden & Gregersen 1995).

Denne artikel beskriver vækstmønsteret i den danske skarvbestand i det 20. århundrede. Udviklingen i de enkelte kolonier og inden for seks større vandområder forsøges forklaret ud fra menneskelige indgreb, fuglenes føderessourcer og ud- og indvandring fra/til kolonierne og landet som helhed. I beskrivelsen er der skelnet mellem tre perioder:

1938-1971 Efter genindvandringen blev forfølgelserne genoptaget, og alle kolonier på nær én forsvandt.

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1972-1981   To nye kolonier blev grundlagt; for-
            følgelserne indskrænkedes, og bestan-
            den begyndte at vokse.
1982-1994   Nye kolonier dannedes hvert år; de få
            indgreb, der fandt sted, havde kun lo-
            kal betydning, og den samlede be-
            stand voksede hastigt til sidst i perio-
            den, hvor vækstraten aftog.

Vi lægger størst vægt på sidstnævnte periode; ko-
loniernes udvikling i de foregående perioder er be-
skrevet i Helms (1940), Madsen (1946), Madsen &
Spärck (1950), Løppenthin (1967), Hald-Morten-
sen (1974), Hansen (1980, 1984) og Gregersen
(1982). Gregersen (1990, 1992) giver detaljerede
oplysninger om status for de enkelte kolonier i pe-
rioden 1989-1991.

Materiale og metoder

I denne artikel defineres koloni- og bestands-
størrelse som antallet af reder, der er registreret
omkring det tidspunkt på året, hvor redeantallet
kulminerer. Efter skøn har vi valgt at henføre to el-
ler flere grupper af reder til én koloni, hvis de lå
mindre end 2000 m fra hinanden. Tilfælde, hvor
Skarver har forsøgt at yngle, men ikke har bygget
rede, er ikke medregnet som kolonier.
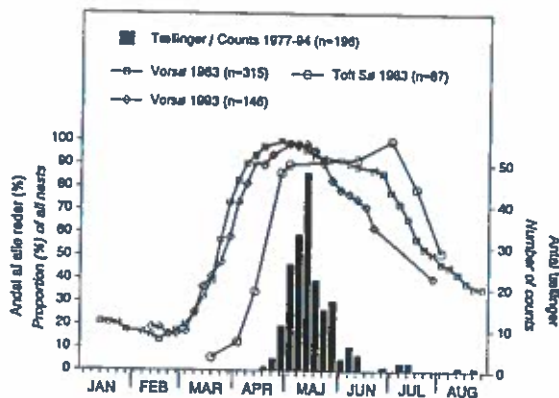
Fig. 1. Den tidsmæssige fordeling af optællingerne af
danske kolonier 1977-1994 (søjler, højre akse) og for-
løbet af etableringen af reder i procent af alle reder (ven-
stre akse) i et afsnit af den gamle Vorsø-koloni i 1983 og
1993 samt i kolonien ved Toft Sø, der var nyetableret i
1983.
*Frequency distribution of counts of colonies in Denmark
1977-1994 (columns, right axis) and seasonal change in
nest numbers given as the percentage of all nests in a
section of the old Vorsø colony 1983 and 1993 and the
newly established Toft Sø colony 1983 (left axis).*

I den første periode, 1938-1971, benyttedes for-
skellige optællingstidspunkter og -metoder, og i
enkelte tilfælde blev antallet af reder snarere an-
slået end egentlig talt. I perioden 1972-1994 sør-
gede Naturfredningsrådet og senere Skov- og Na-
turstyrelsen for, at alle reder taltes under én årlig
gennemgang af hver koloni. J. Gregersen foretog
hovedparten af tællingerne fra og med 1977. Dob-
beltregistrering blev undgået ved, at placering af
træer og afgrænsning af sektioner blev indtegnet
på detaljerede kort. Kolonierne optaltes normalt
mellem den 5. og 25. maj. I dette tidsinterval er de
fleste reder færdigbyggede, og rederne er nemme
at se, fordi løvet endnu ikke er fuldt udsprunget.
Antallet af yngleforsøg vil normalt være lidt høje-
re end antallet af registrerede reder, fordi reder kan
blive overtaget af nye par (jf. Harris & Forbes
1987), og fordi reder kan forsvinde før eller blive
bygget efter optællingstidspunktet, også selv om
tællingen udføres i den periode, hvor redeantallet
kulminerer. Dette sker tidligst i de ældste kolonier
og senest i nyetablerede kolonier. Således har an-
tallet af reder i skarvkolonien på Vorsø toppet mel-
lem midten af april og slutningen af maj, mens til-
gangen af reder aftog tre uger senere i den dengang
nyetablerede koloni ved Toft Sø (Fig. 1). Hvis Fig.
1 viser ekstremerne i den sæsonmæssige udvikling
i antallet af reder i danske kolonier, er skarvkolo-
nierne generelt optalt umiddelbart efter, at antallet
af reder er kulmineret i de gamle kolonier, og før
eller under kulminationen i de yngre kolonier. En-
kelte nye kolonier blev etableret så sent som i maj-
juni, men disse er talt senere end de andre.

Enkelte mindre kolonier kan have eksisteret
uden at være blevet registreret, i det mindste før
1969. Fra tre lokaliteter har vi usikre oplysninger
om kolonier eller yngleforsøg. På Ormø var der
muligvis en koloni mellem 1950 og 1953 samt i
1958 (greve U. Holstein pers. medd.). I hejrekolo-
nien på Bognæs i Roskilde Fjord ynglede der Skar-
ver i 1965 og 1966 og muligvis også i 1967 (F.
Jensen pers. medd.), men der vides intet om antal-
let af ynglepar. På Fænø i Lillebælt forsøgte Skar-
ver at etablere sig i en hejrekoloni i 1985.

For Vorsø er der tidligere offentliggjort tal for
1960erne, der var lavere end det faktiske antal par
(Hald-Mortensen 1974). Eksempelvis blev det an-
givet, at der i 1969 og 1970 yngiede 150 par, men
samme år talte J. Gregersen hhv. 260 og 250 reder.
Der foreligger ikke lignende uafhængige tællinger
fra Vorsø før 1969, så for 1960erne benyttes de tid-
ligere offentliggjorte tal.

Genmeldinger og aflæsninger af farveringmær-
kede Skarver har givet viden om ud- og indvan-

En fuldt besat poppel i den gamle koloni på Vorsø, fotograferet i maj, hvor de fleste par ruger eller har små unger. Træet har nået den fase, hvor Skarverne har optimale rede- og siddemuligheder. Smågrenene er fjernet, og ind- og udflyvning kan foregå uhindret. Foto: John Sandberg.

dring. Bl. a. er skarvunger ringmærket i Tyskland (1932-37), på Vorsø (1967-1976) og på Ormø (1948) senere genmeldt som voksne i forbindelse med beskydninger i kolonierne. Fra 1977 til 1992 blev skarvunger ringmærket med individuelt nummererede farveringe i følgende antal: Vorsø 8919 (1977-1992); Brændegårdssøen 2369 (1982-1988); Toft Sø 1612 (1983-1991); Dyrefod 1348 (1985-1991); Mågeøerne 732 (1985-1988); Ormø 445 (1983-1986). I seks andre kolonier er mellem 73 og 356 unger mærket i årene 1984-1991. Af de i alt 16 457 farveringmærkede individer er 723 siden registreret som ynglende eller sandsynligvis ynglende i andre danske kolonier end dér, hvor de blev mærket, mens et langt større antal er registreret i de kolonier, hvor de klækkede. Søgningen efter farveringmærkede ynglefugle har været størst på Vorsø, Mågeøerne, Rønland Sando, Ormø og Dyrefod, samt ved Toft Sø og Brændegårdssøen.

Resultater
Udviklingen frem til 1938

For fuldstændighedens skyld gives her et resumé af udviklingen for Skarvens genindvandring i 1938, baseret på oplysninger givet i litteraturen (Helms 1940, Madsen 1946, Spärck 1952, Løppenthin 1967, Coomans de Ruiter 1966, Hansen 1980, Knief & Witt 1983).

De to underarter *sinensis* og *carbo* har antagelig optrådt i Danmark gennem de sidste 7000 år. Knoglerester af begge er fundet i køkkenmøddinger fra (især) yngre stenalder. Fra midten af 1500-tallet har vi skriftlige vidnesbyrd om ynglende Skarver i Danmark (formodentlig *sinensis*). Tilsyneladende ynglede Skarven ikke i landet gennem en længere periode i 1700-tallet, men omkring 1775 indvandrede den igen. Faber (1826, i Løppenthin 1967) angav, at Skarver ynglede i stor mængde ved Svendborg i 1780 og 1790, men at

Fig. 2. Beliggenhed af skarvkolonier etableret i Danmark 1938-1994 og afgrænsningen af regioner. Kolonierne er nummererede i den rækkefølge, de er opstået; numrene refererer til teksten og Tab. 1.
Position of Cormorant colonies established in Denmark 1938-1994, and boundaries of regions. Numbers refer to Tab. 1.
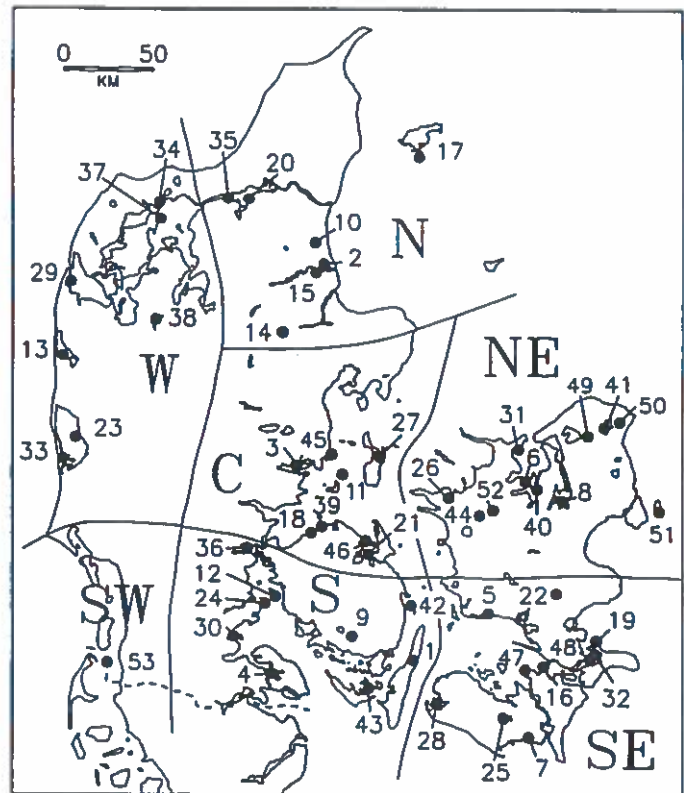
Tab. 1. Antal reder registreret i skarvkolonier i Danmark 1938-94. T, rederne i høje træer; K, i krat; J, på jorden. +: antallet af reder ukendt. De angivne tal stammer fra upublicerede optællinger og fra Helms (1940), Madsen (1946), Madsen & Spärck (1950), Behrends (1945), Hansen (1950, 1962), Spärck (1952), Løppenthin (1967 og referencer heri), Harritz (1982), Brun (1987).
Size of Danish Cormorant colonies (nests), 1938-94. T, nests in high trees; K, in scrub; J, on the ground. +: present, number unknown.

Nr	Koloni, område	1937	1938	1939	1940	1941	1942	1943	1944	1945	1946	1947	1948	1949	1950	1951
1	Tranekær, Langeland	–	14	36	24	31	37	100	300	400	–	–	–	–	–	–
2	Lovnkær, Mariager Fjord	–	–	–	–	–	–	–	6	–	–	–	–	–	35	125
3	Vorsø, Horsens Fjord	–	–	–	–	–	–	–	50	233	400	525	340	5	326	284
4	Arnkil, Als	–	–	–	–	–	–	–	4	–	–	–	–	–	–	–
5	Ormø, Holsteinborg	–	–	–	–	–	–	–	–	–	–	–	100	25	–	–
6	Hønsehals, Isefjord	–	–	–	–	–	–	–	–	–	–	–	–	75	–	–
7	Ålholm, Lolland	–	–	–	–	–	–	–	–	–	+	–	–	300	268	140
Total		0	14	36	24	31	37	100	360	630	400	525	440	405	621	549

Nr	Koloni	1952	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962	1963	1964	1965	1966
2	Lovnkær, Mariager Fjord	320	250	250	250	10	–	–	–	–	–	–	–	–	–	–
3	Vorsø, Horsens Fjord	85	70	63	82	136	110	125	175	210	175	150	250	200	250	170
5	Ormø, Holsteinborg	–	–	292	320	365	87	+	158	45	–	–	–	–	–	–
7	Ålholm, Lolland	135	210	150	250	223	–	–	–	–	–	–	–	–	–	–
8	Bognæs, Roskilde Fjord	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+
Total		540	530	755	902	734	197	125	333	255	175	150	250	200	250	170

Nr	Koloni	1967	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981
3	Vorsø, Horsens Fjord	175	250	260	250	280	370	520	580	640	705	801	811	869	949	1169
5	Ormø, Holsteinborg	–	–	–	–	–	35	50	110	250	323	250	215	269	420	959
8	Bognæs, Roskilde Fjord	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–
9	Brændegård, Sydlige Fyn	–	–	–	–	–	–	5	35	50	75	145	349	559	668	663
Total		175	250	260	250	282	405	575	725	940	1103	1196	1375	1697	2037	2791

kolonien var udryddet i 1826.

Trods forfølgelser var der skarvkolonier adskillige steder herhjemme i første halvdel af 1800-tallet, hvor bestandens størrelse kulminerede i 1830-erne. I århundredets anden halvdel intensiveredes ydryddelseskampagnerne både i Danmark og i Tyskland og Holland, og alt tyder på, at det lykkedes at udrydde arten som ynglefugl i Danmark midt i 1870erne. Et af de sidste yngleforsøg fandt sted ved Roskilde Fjord i 1876. Arten forsvandt også fra Schleswig-Holstein og Niedersachsen, så sidst i 1800-tallet var udbredelsen stort set begrænset til Holland. Niethammer (1938) angiver, at der endnu i 1905 var enkelte ynglepar på Als, men herudover er der ingen oplysninger om, at Skarver skulle have ynglet eller forsøgt at yngle i Danmark i perioden 1877 til 1937.

Bestandens udvikling 1938-1971

I årene før Skarvens genindvandring i 1938 sås et stigende antal fugle i farvandene syd for Fyn og omkring Lolland/Falster (Helms 1940, Løppenthin 1967). Stigningen i antallet af observationer hang formentlig sammen med en fremgang i Holland, fra 1200 par i 1926 til 4622 par i 1940 (van IJzendoorn 1950), samt inddæmningen af et stort område ved IJsselmeer i 1942, der resulterede i en nedgang i bestanden her (van Eerden & Gregersen 1995).

Fra midt i 1940erne til midt i 1950erne dannedes flere nye kolonier i Danmark (Fig. 2 og 3, Tab. 1). Genmeldinger i Danmark i årene 1944-51 af fugle fra Pulitz-kolonien på Rügen tyder på, at beskydningen her i 1940erne bidrog til væksten i både Tranekær-kolonien på Langeland og Vorsø-

|	Region	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994
3 Vorsø, Horsens Fjord, TK	C	1479	1837	2207	2560	2911	3173	3321	4385	4642	5048	4321	4634	4318
5 Ormø, Holsteinborg, T	SE	1423	2129	2320	2437	2655	3351	3555	4216	5263	4985	5009	4720	4522
9 Brændegård, Sydlige Fyn, TKJ	S	766	836	1251	1578	1866	2603	2787	4080	5064	6943	7087	5874	5732
10 Toft Sø, Lille Vildmose, TK	N	8	90	135	396	595	681	712	785	1019	1300	1480	2149	2253
11 Svanegrund, Endelave, J	C	12	40	64	–	4	20	35	250	404	674	847	1142	1161
12 Bågø, Lillebælt, KJ	S	25	–	–	–	–	–	–	–	70	–	–	–	–
13 Fjandø, Nissum Fjord, J	W	–	10	–	–	170	253	15	252	309	380	680	690	773
14 Fussing Sø, Randers, T	N	–	2	–	–	–	–	3	–	–	–	–	–	–
15 Havnø, Mariager Fjord, T	N	–	–	120	–	–	–	–	–	–	–	–	–	–
16 Dyrefod, Storstrømmen, TKJ	SE	–	–	175	474	668	896	1126	1365	1668	1658	1646	1780	1746
8 Bognæs, Roskilde Fjord, T	NE	–	–	–	1	–	15	30	34	145	381	645	450	515
17 Søndre Rønner, Læsø, J	N	–	–	–	1	–	–	–	–	–	–	–	–	–
18 Mågeøerne, Bogense, J	C	–	–	–	120	452	708	946	1057	1500	1982	1860	2170	2648
19 Ægholm, Mon, J	SE	–	–	–	18	120	200	351	436	351	61	2	3	–
20 Rønholm, Nibe Bredning, J	N	–	–	–	–	45	127	239	160	81	5	40	–	30
21 Roholm, Odense Fjord, J	C	–	–	–	–	15	13	–	–	–	–	–	–	–
22 Søtorup, Haslev, T	SE	–	–	–	–	2	–	–	–	–	–	–	–	–
23 Klægbanken, Ringkøbing Fj., J	W	–	–	–	–	–	29	60	–	–	–	–	–	90
24 Bastholm, Lillebælt, KJ	S	–	–	–	–	–	100	675	1012	355	204	–	5	–
25 Søholt, Maribo, T	SE	–	–	–	–	–	19	213	617	1415	1587	2167	2185	2034
26 Saltbækvig, Sejrø Bugt, T	NE	–	–	–	–	–	–	48	220	222	548	520	766	952
27 Stavns Fjord, Samsø, JK	C	–	–	–	–	–	–	–	25	430	804	1350	1848	2100
28 Nakskov Fjord, Lolland, JTK	SE	–	–	–	–	–	–	–	7	37	266	450	741	602
29 Rønland Sandø, Harboor, J	W	–	–	–	–	–	–	–	–	207	467	775	1196	1185
30 Hupsø, Genner Bugt, T	S	–	–	–	–	–	–	–	–	30	379	881	383	435
31 Hovvig, Isefjord, TJ	NE	–	–	–	–	–	–	–	–	3	–	88	428	882
32 Tyreholm, Mon, J	SE	–	–	–	–	–	–	–	–	342	1183	2743	3161	2633
33 Olsens Pold, Ringkøbing Fj., J	W	–	–	–	–	–	–	–	–	–	95	226	814	988
34 Melsig, Limfjorden, J	W	–	–	–	–	–	–	–	–	–	8	77	228	1009
35 Troldholmene, Limfjorden, J	N	–	–	–	–	–	–	–	–	–	177	240	–	–
36 Kidholmene, Kolding Fj., TK	S	–	–	–	–	–	–	–	–	–	6	85	162	218
37 Ejerslev Røn, Limfjorden, J	W	–	–	–	–	–	–	–	–	–	–	7	60	–
38 Flyndersø, Skive, T	W	–	–	–	–	–	–	–	–	–	–	9	1	240
39 Dræet, Bogense, JKT	C	–	–	–	–	–	–	–	–	–	–	158	586	122
40 Rønø, Isefjord, J	NE	–	–	–	–	–	–	–	–	–	–	164	125	180
41 Esrum Sø, Hillerod, T	NE	–	–	–	–	–	–	–	–	–	–	3	1	75
42 Vresen, Knudshoved, J	S	–	–	–	–	–	–	–	–	–	–	–	38	23
43 Lille Græsholm, Ærø, J	S	–	–	–	–	–	–	–	–	–	–	–	4	–
44 Skarresø, Jyderup, T	NE	–	–	–	–	–	–	–	–	–	–	–	52	7
45 Hov Røn, Hov, J	C	–	–	–	–	–	–	–	–	–	–	–	–	8
46 Hofmansgave, Odense Fj., J	C	–	–	–	–	–	–	–	–	–	–	–	–	43
47 Suderø, Storstrommen, J	SE	–	–	–	–	–	–	–	–	–	–	–	–	50
48 Lindholm, Stege Bugt, T	SE	–	–	–	–	–	–	–	–	–	–	–	–	1
49 Solbjerg Engsø, Arresø, T	NE	–	–	–	–	–	–	–	–	–	–	–	–	67
50 Gurre Sø, Helsingor, T	NE	–	–	–	–	–	–	–	–	–	–	–	–	16
51 Saltholm, Øresund, J	NE	–	–	–	–	–	–	–	–	–	–	–	–	27
52 Hallehy Åmose, Jyderup, T	NE	–	–	–	–	–	–	–	–	–	–	–	–	48
53 Jordsand, Vadehavet, J	SW	–	–	–	–	–	–	–	–	–	–	–	–	15
Antal kolonier *Number of colonies*		6	7	7	9	12	15	16	16	21	23	28	30	37
Total		3713	4944	6272	7585	9503	12188	14116	18901	23557	29141	33560	36396	37748

Antal reder / Number of nests
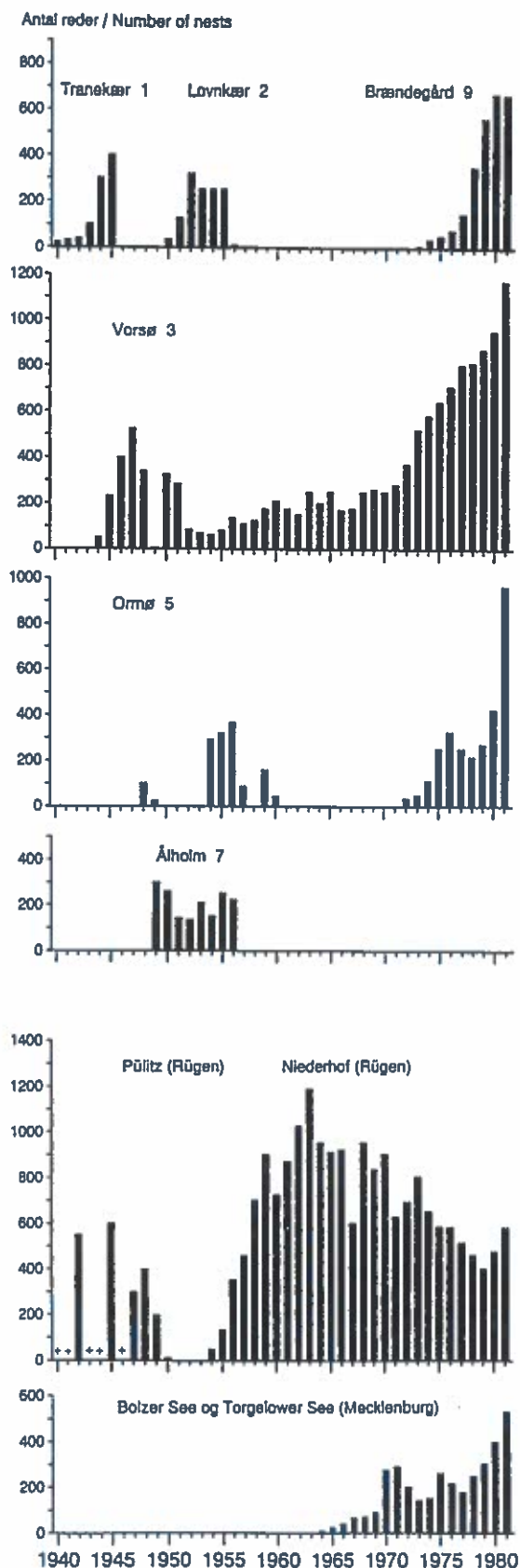
Fig. 3. Udviklingen i antallet af reder i seks danske og fire nordtyske skarvkolonier 1940-1981. Oplysningerne om de tyske kolonier fra Schulz (1947) og Zimmermann (1985, 1986).
Development of breeding numbers in six Cormorant colonies in Denmark and in four colonies in northern Germany, 1940-1981.

kolonien i Horsens Fjord, og til etableringen af kolonien i Lovnkær skov ved Mariager Fjord (kolonierne 1, 2 og 3 i Fig. 2 og Tab. 1). Det vides også, at der indvandrede Skarver til Vorsø fra Tranekær. Formentlig bidrog bekæmpelsen af Tranekær-kolonien i 1946 og de første års beskydning i kolonien på Vorsø til dannelsen af kolonierne Lovnkær (2), Ormø (5), Hønsehals (6) og Ålholm (7). Eksempelvis blev der i 1950 genmeldt Skarver i kolonien ved Ålholm, som var ringmærket på Vorsø.

Koloniernes udvikling var præget af hurtig vækst. Tranekær, Vorsø og Lovnkær havde under 50 par i deres første år, men mellem 300 og 525 par få år senere, og på både Ålholm og Ormø var der 300 par allerede i det første år. Da kolonien ved Tranekær nåede 400 par i 1945, begyndte man at beskyde fuglene, og allerede året efter forsvandt kolonien. På Vorsø indledtes beskydning af voksne Skarver og muligvis også unger, da kolonien nåede 525 par i 1947. I 1948 blev der skudt 600 gamle fugle, og året efter ynglede der kun fem par. Også i kolonierne på Ormø og Lovnkær førte beskydning til stagnation og udvandring allerede få år efter etableringen.

Den fortsatte bekæmpelse i 1950erne medførte, at antallet af ynglepar faldt fra 902 par i 1955 til 125 par i 1958; samtidig voksede Niederhof-kolonien i Nordtyskland fra 134 par til 700 par (se også Fig. 3). Fra 1961 til 1971 var Vorsø den eneste tilbageværende koloni i Danmark, og den nåede ikke op over 250 par i 1960erne (Fig. 3), hvilket skyldtes årlig nedskydning af op til 300 unger og et ukendt antal gamle fugle.

Skarven bekæmpedes således med held i perioden, og ingen koloni voksede til mere end 530 par.

Bestandens udvikling 1972-1981

I 1972 genetableredes skarvkolonien på Ormø i Sydsjælland (5), få år efter at beskydningen i Niederhof-kolonien på Rügen blev genoptaget. Kun et år senere etableredes kolonien i Brændegårdssøen på Sydfyn (9). Dermed havde Skarven udvidet sit udbredelsesområde i Danmark til udover det sydvestlige Kattegat også at omfatte farvandene syd

for Fyn og Sjælland. I de samme år begyndte Vorsø-kolonien at vokse (Fig. 3), og den samlede danske bestand gik frem fra 280 par i 1971 til 940 par i 1975 (Fig. 4 og Tab. 1), svarende til en årlig vækst på 35% (Fig. 5). Beskydningen af unger på Vorsø ophørte efter 1970, men da væksten i Danmark var meget hurtig allerede de første år herefter, forekommer det sandsynligt, at udenlandske (tyske) fugle etablerede sig i landet og medvirkede til væksten først i 1970erne. Ved Brændegårdssøen voksede antallet af ynglepar fra 5 i 1973 til 668 i 1980 (Fig. 3), hvilket både tilskrives høj ynglesucces og indvandring fra Vorsø. I 1980 havde mindst 8% af de ynglende Skarver i Brændegårdssøen farveringe, der viste, at de stammede fra Vorsø (Hansen 1980). Ynglende Skarver med Vorsø-ringe blev også set på Ormø, samt i Østtyskland og i Kalmarsund i Sverige. Udvandring er den sandsynlige grund til, at vækstraten på Vorsø var lav i årene 1974-1980 (9% om året, se også Fig. 3). På Ormø steg antallet af ynglepar fra 20-30 par i 1972 til 320 par i 1976, men mellem 1977 og 1979 ynglede der ikke over 269 par (Fig. 3). Tilbagegangen var givetvis et resultat af, at mindst 300-350 unger blev skudt i kolonien i hvert af de tre år 1976-1978, efter tilladelse fra Naturfredningsrådet. Fra 1980 til 1981 gik Ormø-kolonien markant frem, fra 420 til 959 par (Fig. 3), hvilket ud fra aflæste farveringe kan tilskrives indvandring fra Brændegårdssøen, hvor de fleste redetræer blev fældet umiddelbart

Fig. 5. Årlig vækstrate (%) i antal ynglepar af Skarver i Danmark 1972-1994.
The annual rate of increase (%) in the Danish breeding population of Cormorants, 1972-1994.

før ynglesæsonen i 1979. Den ekstraordinært store fremgang i den danske bestand i 1981, på 37% i forhold til året før (Fig. 5), kan skyldes, at unge Skarver, der under normale forhold ville have etableret sig i Brændegårdssøen i 1979 eller 1980, udskød ynglestart fordi redetræerne var fældet.

Bestandens udvikling 1982-1994

Den samlede bestand voksede fra 3713 par i 1982 til 37 748 par i 1994 (Fig. 4, Tab. 1). Fra 1982 til 1989 forøgedes antallet af ynglepar med 16-36% om året (gennemsnit 26%), men efter 1989 er vækstraten faldet og var det sidste år (1994) nede på 3,7% (Fig. 5).

Fra 1982 til 1986 dannedes nye kolonier både nær de eksisterende på Vorsø og Ormø og langt fra disse, f.eks. i Ålborg Bugt, Limfjorden og Nissum Fjord. I 1987 bredte Skarven sig yderligere til Ringkøbing Fjord, Lillebælt, Roskilde Fjord og Maribosøerne, og senere til den vestlige Limfjord, Langelandsbæltet, Vadehavet og flere lokaliteter i det nordlige Sjælland (Tab. 1, Fig. 2). Ikke alle kolonier slog dog an. Af 36 dannet mellem 1982 og 1993 blev 17 endeligt eller midlertidigt opgivet efter ét til ni år med yngleforsøg; 13 af dem nåede aldrig op over 200 reder. I flere af de opgivne kolonier forstyrredes Skarverne regelmæssigt af menneskelig færdsel. I hovedparten af de kolonier, der slog an, var vækstraten særdeles høj i de første år, hvorefter den gradvist aftog, hvilket viser, at indvandring var af stor betydning for koloniernes tidlige vækst. De gamle kolonier Vorsø, Brændegård
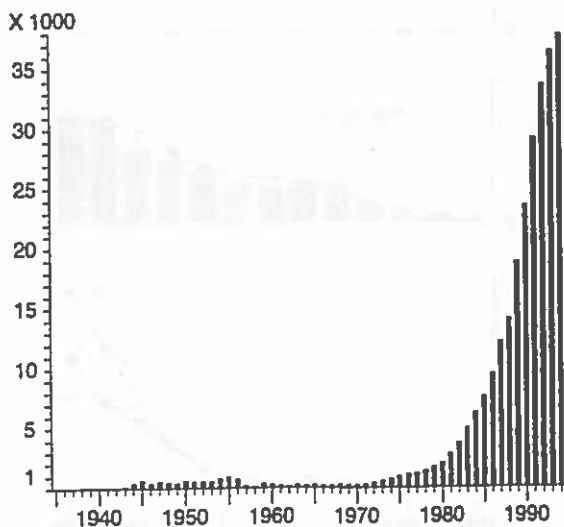

Fig. 4. Udviklingen i antallet af ynglepar af Skarv i Danmark 1938-1994.
Development of the number of breeding pairs of Cormorants in Denmark, 1938-1994.

Antal reder / Number of nests
X 1000

Vorsø 3 C

Mågeøerne 18 C

Stavns Fjord 27 C

Region C

Brændegård 9 S

Ormø 5 SE

Dyrefod 16 SE

Søholt 19 SE

Tyreholm 26 SE

Region SE

Toft Sø 4 N

W

NE

Fig. 6. Antallet af reder i regionerne og i de ni største skarvkolonier (>1700 reder i 1994) i Danmark 1982-1994. *Number of Cormorant nests in the regions and in the nine largest colonies (>1700 nests in 1994) in Denmark, 1982-1994.*

og Ormø fortsatte med at vokse til 1989-1991, hvorefter antallet af ynglepar stabiliseredes eller gik tilbage; en stabilisering er også sket i enkelte andre store kolonier (Fig. 6).

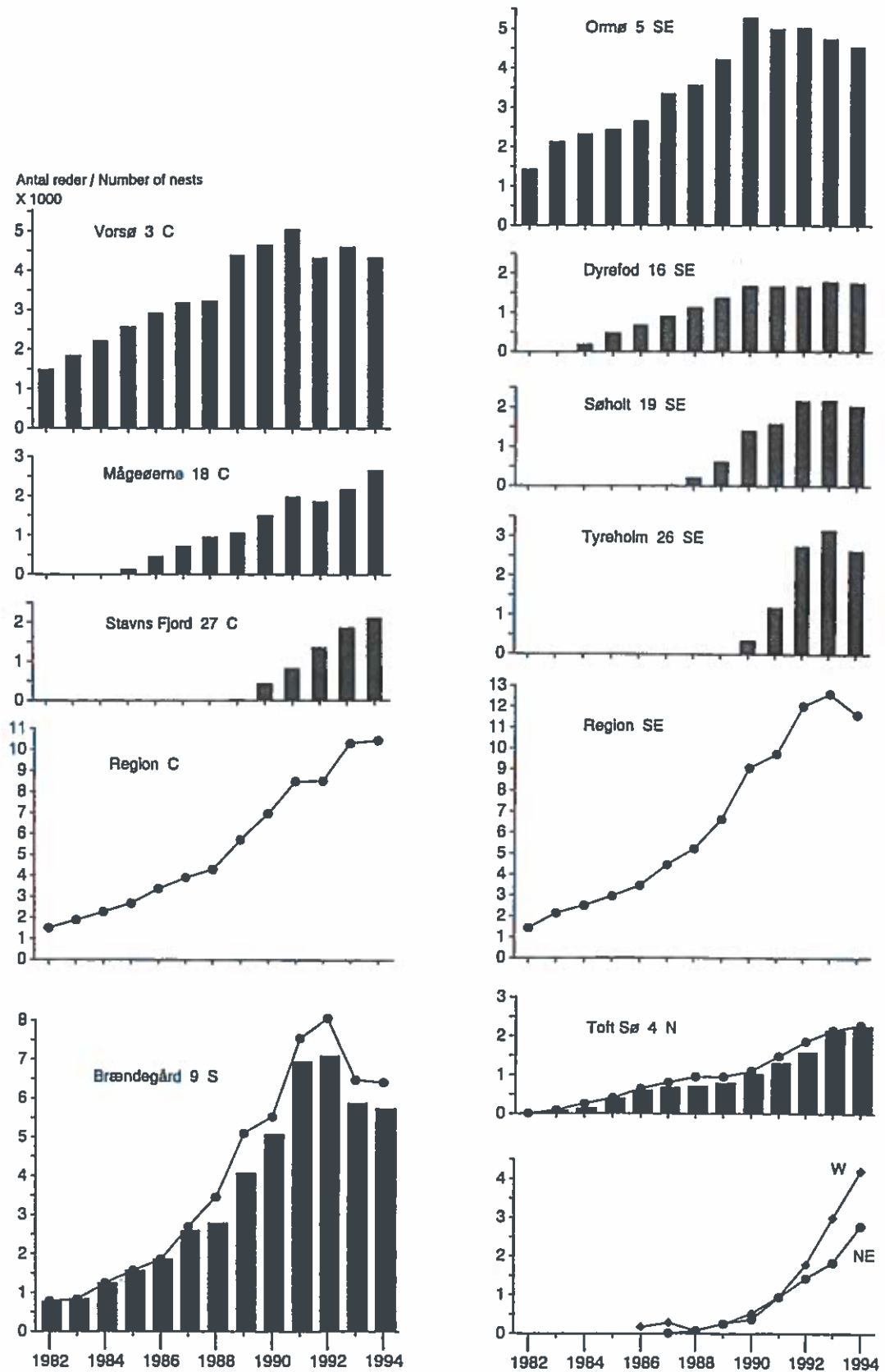I 1982 ynglede 99% af den samlede bestand i de tre gamle kolonier, men med væksten i de nye kolonier faldt denne andel jævnt til 39% i 1994. I 1994 ynglede 83% af Skarverne i 12 kolonier med mellem 1000 og 6000 par, mens de resterende 17% var fordelt på 25 kolonier med under 1000 par. Næsten alle kolonier lå i 1994 i fjorde eller ved kyster nær store åbne vandflader (Fig. 7). Kun Brændegård og Søholt ligger forholdsvis langt inde i landet (hhv. 8 og 9 km fra kysten). Endnu i 1994 ynglede hovedparten af bestanden i den sydvestlige del af Kattegat, ved det Sydfynske Øhav og omkring Smålandsfarvandet (Fig. 7). Afstanden mellem nabokolonier varierer betydeligt, men alle kolonierne med over 1000 par lå i 1994 mere end 25 km fra hinanden.

Fordelingen af bestanden på kolonityper ændredes i periodens løb (Fig. 8). Da redetræerne på øen i Brændegårdssøen blev fældet i 1979, begyndte nogle af Skarverne at yngle i de fældede træer, og enkelte par byggede rede direkte på jorden (se Hansen 1980). Desuden er flere kolonier etableret direkte på jorden på småøer, med Svanegrunden (11) og Mågeøerne (18) som de første. I 1994 ynglede 38% af bestanden på jorden, og 30% ynglede i krat 1-7 m over jorden (Fig. 8).

Udviklingen i regionerne 1982-1994

Antallet af ynglepar udviklede sig nogenlunde ens i de tre regioner (C, S, SE; Fig. 2 og 6) omkring de gamle kolonier Vorsø, Brændegård og Ormø. I disse regioner, hvor 75% af bestanden ynglede i 1994, stagnerede antallet i 1991-1994. I region N aftog vækstraten efter 1986. I de senest koloniserede regioner, Vestjylland (W) og Nordsjælland (NE), har bestandene været i hastig vækst frem til i dag (Fig. 6).

I den sydvestlige del af Kattegat (C) voksede bestanden forholdsvis jævnt med ca 19% pr år frem til 1993. Når væksten var stabil trods aftagende vækstrate og stagnation i den store koloni på Vorsø, skyldtes det dannelsen af fire nye kolonier og hurtig vækst i disse (Fig. 6). På Mågeøerne voksede bestanden kraftigt i 1990 og 1991, men efter at der illegalt var udsat mår *Martes* sp. i april 1992, udvandrede mange af Mågeø-fuglene til den nærliggende ø Dræet (39). Her mislykkedes yngleforsøget det følgende år, da rederne blev ødelagt af mennesker. Aflæsning af farveringe viser, at væksten i de nydannede kolonier bl.a. skyldtes ind-
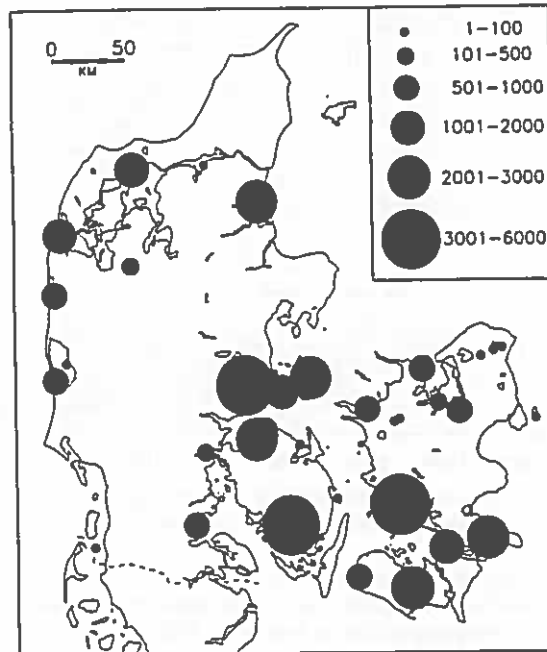
Fig. 7. Fordelingen af skarvbestanden i Danmark i 1994.
Distribution of breeding Cormorants in Denmark 1994.

vandring fra Vorsø. På Mågeøerne var fugle fra Vorsø således 10 gange hyppigere end fugle fra Brændegårdssøen i 1987, givetvis fordi afstanden til Vorsø er kortere (30 km mod 70 km), og fordi Mågeøerne ligger i et vandområde, som i yngletiden udnyttes til fødesøgning af Vorsø-fugle, men formentlig ikke af Brændegård-fugle. Der optrådte også fugle fra fjerne kolonier som Fjandø i Nissum Fjord, Toft Sø nær Ålborg Bugt, Ormø syd for Sjælland og Oostvaardersplassen i Holland.

Det fremgår af Fig. 9, at i tre ud af fire år var hovedparten af de 67-112 årligt aflæste Vorsø-skarver på Mågeøerne 3 eller 4 år gamle, og at 1984-årgangen dominerede.

Der var ingen fremgang i regionen fra 1993 til 1994 (Fig. 6).

I Lillebælt og farvandet syd for Fyn (S) voksede bestanden gennemsnitligt med 26% om året frem til 1992. Udviklingen var mere uregelmæssig end i region C. I Brændegårdssøen voksede antallet af reder med næsten 2000 fra 1990 til 1991, hvilket til dels kan tilskrives ødelæggelse af kolonien på Bastholm (24). Tilbagegangen i regionen fra 1992 til 1993, med ca 1600 par, skyldtes bl.a. udvandring fra Brændegårdssøen og Hopsø-kolonien (30) til Pugum ved Flensborg Fjord. I denne koloni steg antallet fra 290 par i 1992 til 990 par i 1993, og blandt de ynglende Skarver sås fugle fra Bræn-
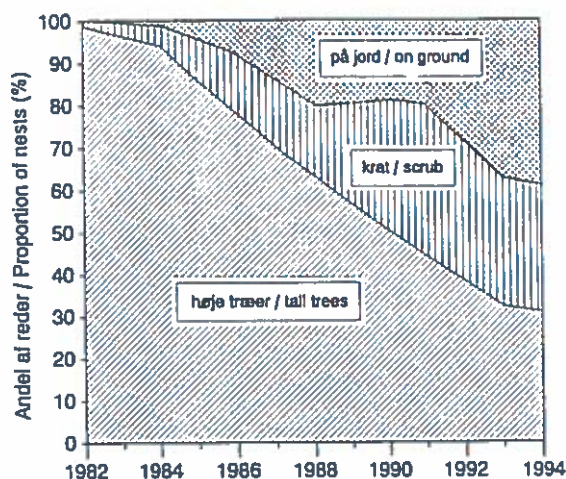
Fig. 8. Andelen af bestanden, der yngler i høje træer, i krat og på jorden i procent af det totale antal reder i Danmark 1982-1994.
Proportion of the population breeding in high trees, in scrub and on the ground given as the percentage of the total breeding population in Denmark, 1982-1994.

degårdssøen og Bastholm (J.J. Kieckbusch pers. medd.). Udvandringen fra Bastholm var et resultat af illegal ødelæggelse af reder og redetræer i 1990 og 1991, og også udvandringen fra Hopsø faldt sammen med fældning af redetræer.

I farvandene syd for Sjælland og omkring Lolland-Falster og Møn (SE) voksede bestanden med 25% om året, indtil antallet stabiliseredes i 1993. Den høje vækst fandt sted til trods for, at 5500 unger blev skudt på Ormø i perioden 1982-1986. Vækstraten var dog noget lavere (17%) mellem 1984 og 1986, og for Ormø-kolonien blot 8% (Fig. 6). Formentlig var beskydningerne på Ormø medvirkende til dannelsen af kolonien på Dyrefod (16) i 1984; denne koloni voksede lineært (med 200-300 par pr år) indtil 1990, hvor den stabiliserede sig omkring 1700 par (Fig. 6). Kolonien på Ægholm nord for Møn (19) voksede også lineært (med 80-150 par pr år); den lineære vækst kan hænge sammen med øernes udforming, der hindrede Skarverne i at ekspandere i alle retninger. Efter 1989 udvandrede Skarver fra Ægholm til den nærliggende ø Tyreholm (32), hvor antallet voksede fra 342 par i 1990 til 3161 par i 1993 (Fig. 6). Også kolonierne ved Søholt (25) og i Nakskov Fjord (28) voksede hurtigt (Fig. 6, Tab. 1). Bestanden i regionen nåede 12 590 ynglepar i 1993, men aftog så med ca 1000 par i 1994.

I det nordlige Jylland (N) opstod der allerede i 1982 en koloni i Toft Sø i Lille Vildmose (10). I modsætning til andre nye kolonier etableredes den langt fra eksisterende kolonier, og formodentlig derfor var væksten langsom; først efter otte år nåede kolonien over 1000 par. Trods den lave indvandringsrate til Toft Sø er der i yngletiden registreret fugle fra syv af de 13 danske skarvkolonier, hvor der er ringmærket unger, flest fra Vorsø. I anden halvdel af 1980erne opstod der desuden to kolonier i Limfjorden (20 og 35), men de blev begge ødelagt gennem ulovlige indgreb.

I den vestlige del af Jylland (W), hvor alle Skarver yngler på jorden, voksede bestanden fra 252 par i 1989 til 4188 par i 1994 (75% pr år, Fig. 6). *I det nordlige Sjælland (NE)*, hvor alle kolonier undtagen to er i træer, voksede bestanden fra 254 par i 1989 til 2769 par i 1994 (61% pr år, Fig. 6). Ved Saltbækvig var væksten uregelmæssig (Tab. 1), formentlig fordi der blev fældet redetræer hvert år efter 1988. Omfanget af indvandring afhænger tilsyneladende af skarvbestanden i den pågældende region. I begge regionerne W og NE var indvandringen til de først grundlagte kolonier moderat, mens den var høj til de senere etablerede kolonier (f.eks. 31, 33, 34).

For at forhindre dannelsen af nye skarvkolonier i Danmark, og for at reducere ungeproduktionen, indførte Miljøministeriet en ny forvaltningspraksis i 1994. Ifølge denne kan lodsejere efter ansøgning få tilladelse til at nedlægge enkelte fugle og derved skræmme resten af Skarverne bort, når de forsøger at etablere nye kolonier. For visse jordrugende kolonier kan der desuden gives tilladelse til, at nogle eller alle æg hindres i at klække; det må alene ske under det lokale statsskovdistrikts kontrol. I overensstemmelse med denne forvaltningspraksis blev der givet tilladelse til at fordrive Skarverne fra seks lokaliteter i det vestlige Jylland og nordlige Sjælland (i alt "reguleredes" ca 90 Skarver). Desuden fik skovdistrikterne tilladelse til at begrænse klækningssuccesen i to kolonier: på Drættegrund nord for Fyn blev æggene prikket i ca 25 reder, og på Fjandø i Nissum Fjord omfattede indgrebet ca 95% af ialt 773 reder, eller ca 3000 æg. På Fjandø betød indgrebet og en efterfølgende forstyrrelse, at Skarverne forlod kolonien.

Diskussion

Betydningen af regulering

I 1931 blev Skarven fredet i månederne maj, juni og juli, men blev ikke desto mindre bekæmpet med stor effekt. Fra genindvandringen i 1938 til 1971 blev kolonierne udsat for mange indgreb, og pånær én forsvandt alle efter mindre end 10 år. Især i årene 1944-1955 var der et tydeligt mønster, hvor be-

skudte kolonier gik tilbage, samtidig med at nye opstod og i begyndelsen tiltrak mange ynglefugle. Tendensen var, at hele kolonier flyttede mellem landsdelene. I 1960erne var rekrutteringen til bestanden lav pga. beskydning af unger i Vorsø-kolonien. Samlet førte de menneskelige indgreb til lav ynglesucces og i visse år formentlig også til lav overlevelse, og bestanden lå under 300 par i hele tiåret.

Kolonien på Vorsø gik markant frem allerede i 1973, som var det første år, hvor unger fra en sæson uden regulering nåede yngledygtig alder (Fig. 3). Reguleringen af ungeproduktionen på Ormø 1976-1978 svarede til næsten 20% af den samlede ungeproduktion i Danmark (J. Gregersen upubl.), og vækstraten steg et par år efter at beskydningen ophørte, både på Ormø selv og i landet som helhed. Den senere beskydning på Ormø 1982-1986, som svarede til ca 9% af ungeproduktionen i Danmark, samt de indgreb, der fandt sted i andre kolonier i årene 1988-1993, havde ikke nogen målelig effekt på væksten i landsbestanden. Den hurtige vækst startede og fortsatte på grund af øget fred med kun begrænset regulering i kolonierne, og især efter 1981 også pga. udvidet beskyttelse mod beskydning uden for kolonierne. I 1977 blev fredningstiden udvidet til også at omfatte marts og april, så Skarverne ikke længere kunne skydes, mens de havde æg eller små unger (Hansen 1980). I 1978 blev Skarven totalfredet, men en jagttid fra oktober til december genindførtes i 1979. Endelig totalfredning i Danmark indførtes i 1980 og i de øvrige EU-lande i 1981.

En tilsvarende effekt af øget beskyttelse kendes fra flere områder i Nordamerika, hvor forbud mod jagt og forstyrrelser (samt brug af DDT og DDE) resulterede i, at bestanden af Totoppet Skarv *Ph. auritus* nåede en vækstrate som den, Skarverne havde i Danmark i 1980erne (Scharf & Shugart 1981, Hatch 1984, Price & Weseloh 1986, del Hoyo et al. 1992).

Betydningen af føde, ynglesteder og udvandring

Væksten i skarvbestanden var generelt højere i Danmark end i andre europæiske lande i årene fra 1972 til 1992, hvilket især tilskrives en høj ungeproduktion (Bregnballe in press, van Eerden & Gregersen 1995). Hvor Skarver yngler beskyttet mod forstyrrelser og prædatorer, bestemmes ynglesuccesen først og fremmest af fødeudbudet (Boekelheide & Ainley 1989) og afstanden mellem kolonien og fødeområdet (Platteeuw 1991, Platteeuw & van Eerden 1995, Platteeuw et al. 1995).

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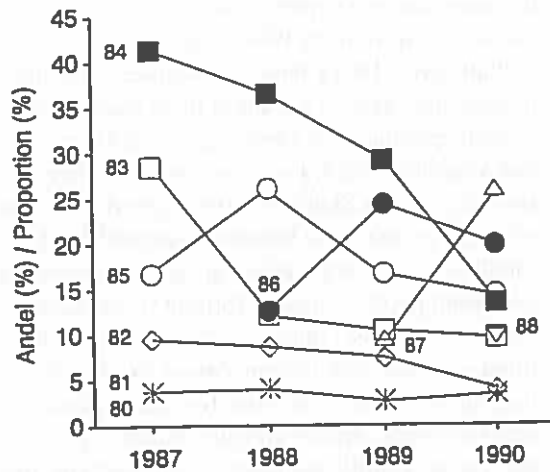
Fig. 9. Forekomsten af forskellige årgange af Vorsø-skarver i kolonien på Mågeøerne. 1987-90. I de fire år registreredes henholdsvis 67, 43, 112 og 103 Vorsø-skarver ynglende på Mågeøerne. For hvert år er vist de aflæste ringes fordeling på ringmærkningsår, korrigeret for andelen af Vorsø-unger, der blev mærket i de pågældende år (1980-88).

Occurrence 1987-90 at the colony Mågeøerne of different cohorts of Cormorants ringed in the Vorsø colony. A total of, respectively, 67, 43, 112 and 103 Vorsø Cormorants were recorded as breeding on Mågeøerne in the four years. For each of these years the distribution on ringing years is shown, corrected for the proportion of Vorsø young ringed each year during 1980-88.
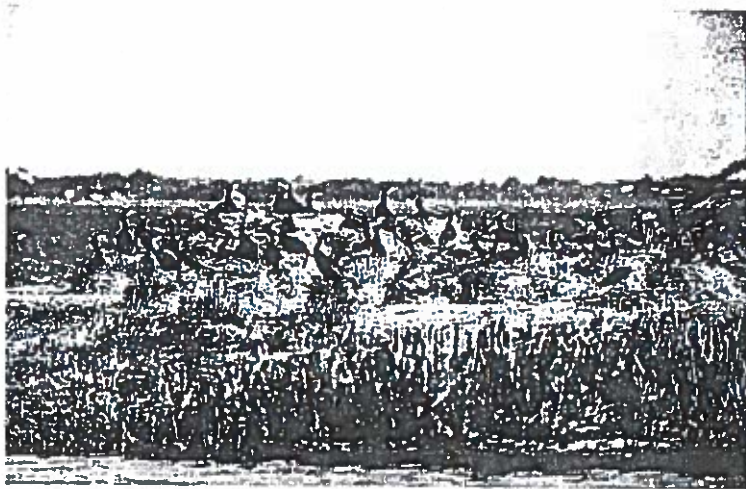
Udsnit af Fjandøkolonien. Billedet er fra 1989, hvor Skarverne byggede reder på den lille ø Kollingø. I overensstemmelse med ny forvaltningspraksis blev æggene sprøjtet i 1994, og Skarverne er udvandret til andre kolonier. Foto: Jens Overgaard Christensen.

I Danmark har Skarverne haft adgang til rige føderessourcer over en lang periode af året, idet ålekvabber *Zoarces viviparus*, ulke *Myoxephalus scorpius* og isinger *Limanda limanda*, der udgør en væsentlig andel af fuglenes føde (Hald-Mortensen 1994), forekommer talrigt i de indre danske farvande og i mange af fjordene (f.eks. Hoffmann 1975). I kolonier som Brændegård og Ormø har Skarverne desuden haft adgang til småtorsk *Gadus morhua*, og i april-maj har Skarverne i nogle af kolonierne kunnet supplere med sild *Clupea harengus* (Hald-Mortensen 1994, in press).

Platteeuw (1991) fandt, at Skarver, som måtte trække mere end 20 km for at nå et fødesøgningsområde, producerede færre unger end Skarver, der kun ynglede 8 km fra samme område. I flere danske regioner har Skarven haft mulighed for at danne kolonier nær store fødesøgningsområder. De to satellitkolonier Svanegrunden og Mågeøerne ligger eksempelvis centralt i forhold til de store lavvandede områder i det sydvestlige Kattegat, hvorimod oprindelseskolonien Vorsø er omgivet af land til flere sider. At store fourageringsområder nær kolonierne spiller en rolle underbygges af, at der var en signifikant positiv sammenhæng mellem vandarealet omkring 10 nydannede kolonier i Sydøstdanmark og koloniernes vækstrate i de første fire år (vandarealet defineret som areal med en dybde ned til 20 m inden for en radius af 20 km; van Eerden & Gregersen 1995).

Udvandring kan i nogle tilfælde have været forårsaget af ændrede betingelser med voksende kolonistørrelse, f.eks. øget konkurrence om føden eller de bedste redepladser (jf. Porter & Coulson 1987). Kolonidannelsesmønsteret i den centrale og sydøstlige region synes at afspejle, at tilgængeligheden af føden omkring nogle kolonier aftog, når kolonierne voksede. De nye kolonier grundlagdes således i periferien af eller uden for de allerede udnyttede fødesøgningsområder. De første satellitkolonier dannedes 26-40 km fra hovedkolonierne Vorsø og Ormø, og efterfølgende kolonier dannedes længere borte (typisk 70 km fra hovedkolonierne). Mønsteret kan dog skyldes præference for lokaliteter nær oprindelseskolonien kombineret med, at ingen velegnede kolonisteder lå mindre end 25 km fra denne.

I de kolonier og regioner, hvor hovedparten af bestanden yngler, er udviklingen stagneret, og da ekspansionen i Vestjylland og det nordlige Sjælland kun omfatter en ringe andel af den samlede bestand, er vækstraten i Danmark faldet (Fig. 4, 5 og 6). Ophør af vækst trods fravær af forfølgelse eller sygdomsudbrud indikerer en begyndende mangel på ressourcer af en eller anden art.

Velegnede kolonisteder synes at være en sådan begrænsende ressource. I de senere år er der ikke dannet nær så mange nye succesfulde kolonier som i 1980erne, måske fordi de ubenyttede potentielle kolonisteder er forstyrrede eller er omgivet af mindre attraktive fourageringsområder. Udviklingsmønsteret i regionerne tyder på, at stabilisering hænger sammen med manglende mulighed for at etablere nye kolonier. I den sydlige region forsvandt de nye kolonier pga. forstyrrelser og indgreb, mens hovedkolonien Brændegård (af samme grund?) fortsatte med at vokse til den nåede ca 7000 par. Herefter faldt yngleantallet med ca 1100 par, hvilket tyder på at kolonien var vokset ud over det, som på længere sigt kunne oppebæres med fødetilgangen inden for Brændegård-fuglenes fourageringsområde. Da Skarverne ikke udvandrede til nye kolonier i nærheden, gik bestanden i hele regionen tilbage. Nogle af Brændegård-skarverne

udvandrede dog til fjerntliggende kolonier, mens andre formentlig undlod at yngle. Det er påvist, at hollandske ungskarver ofte undlader at yngle i perioder, hvor der var mangel på nærliggende nye kolonier (Zijlstra & van Eerden 1991).

I modsætning til den sydlige region fortsatte bestanden med at vokse i den centrale og sydvestlige region, efter at væksten i hovedkolonierne var ophørt, fordi Skarverne her udvandrede og dannede nye kolonier (Fig. 6).

I enkelte kolonier på jorden er det foretrukne areal (de højest beliggende områder) begrænset, og det kan være årsagen til at nogle af dem er ophørt med at vokse. Men langt flere kolonier er formentlig begrænset af fødeudbudet. Det er således påfaldende, at de stabiliserede kolonier har nået forskellig størrelse til trods for, at de stadig rummer ubenyttede egnede redesteder. Betydningen af fødeudbudet underbygges også af, at næsten alle de store europæiske kolonier (>1000 par) findes nær vidtstrakte foureringsområder, hvorimod kolonier ved søer og floder typisk er små (se van Eerden & Gregersen 1995, Lindell et al. 1995). Hvis fødekonkurrence regulerer kolonistørrelsen, vil der muligvis kunne måles et lavere fødeudbud omkring store kolonier end omkring små og nydannede kolonier, i lighed med hvad der er konstateret omkring canadiske kolonier af Totoppet Skarv (Birt et al. 1987).

I overensstemmelse med Ashmole's model for regulering af størrelsen af havfuglekolonier (Ashmole 1963, Furness & Monaghan 1987) kan mekanismen være, at nedgang i fødeudbudet tvinger forældrefuglene til at gennemføre længere og dermed færre foureringstræk, hvorved et lavere antal unger overlever. Denne hypotese understøttes af feltstudier. Ungeproduktionen er således aftaget på Vorsø og tilsyneladende også i andre danske kolonier. På Vorsø faldt antallet af flyvefærdige unger pr rede fra 1,6-2,2 i perioden 1981-1989 til 1,1 i 1994 (inklusive ikke-produktive reder; Bregnballe & Gregersen upubl.). Den aftagende ungeproduktion i danske kolonier er dog utilstrækkelig til at forklare det bratte fald i bestandens årlige vækstrate (Fig. 5) (Bregnballe upubl. data). Den lavere rekruttering skyldes formentlig også en lavere ungfugleoverlevelse og et fald i andelen af fugle, der får opbygget tilstrækkelige reserver til at påbegynde eller fuldføre ynglen. Blandt unger opfostret på Vorsø i 1993 var den lokale dødelighed i det første leveår større end i 1980erne (kun 18% af 496 unger ringmærket i 1993 blev genset i kolonien i det efterfølgende år, mod 33-49% af ungerne mærket 1985-1992; årgangene 1983-92 vs 1993:

χ_1^2=67,0, P<0,0001; 375-1144 unger mærket pr år). Samtidig er et betydeligt større antal Skarver end forventet ud fra antallet af reder blevet set i bl.a. Nissum Fjord (J. Overgaard Christensen pers. medd.). Vi har ingen indicier for et pludseligt fald i voksenoverlevelsen, og selv om farveringmærkede danske Skarver er set ynglende i bl.a. Nordtyskland, er udvandring næppe en væsentlig forklaring på den lavere vækstrate i ynglebestanden. Derimod er det sandsynligt, at et fald i andelen af fugle, der yngler, har været en vigtig faktor for den aftagende vækst.

Fremtidig udvikling i Danmark

Trods faldet i væksten vil skarvbestanden formentlig blive noget større. Enkelte af de nye kolonier er således i kraftig vækst, og der er stadig uudnyttede fødesøgningsområder i det nordlige Kattegat samt i kystområderne langs Nord- og Østsjælland og langs Sydjyllands østkyst. Men Miljøministeriets nye forvaltningspraksis vil gøre det vanskeligt for Skarverne at finde uforstyrrede ynglesteder. Tilmed er bærekapaciteten sandsynligvis lav i flere af de endnu uudnyttede fourageringsområder, f.eks. sammenlignet med områderne omkring bælterne. Vi forudser, at mange koloniers størrelse indstilles efter de lokale fourageringsområders bæreevne, der er bestemt af fiskeforekomsterne, og formodentlig også af arealet af lavvandede områder og af antallet af ynglepar i nabokolonierne (jf. Furness & Birkhead 1984, Røv 1994).

Konklusion

Mellem 1938 og 1973 var menneskelige indgreb af stor betydning for dannelsen af nye kolonier, og for hvordan de udvikledes og hvor længe de eksisterede. Den hurtige vækst i den danske bestand i begyndelsen af 1970erne (26-44% om året 1972-1975) og fra 1980 til 1992 (15-36%) forklares med færre indgreb i kolonierne, indførelse af fredninger og adgang til uforstyrrede ynglelokaliteter nær føderige områder. Væksten formodes at være aftaget fordi tæthedsafhængige mekanismer er begyndt at virke i de vigtigste kolonier, og fordi der nu er færre attraktive områder, som kan koloniseres med succes.

Summary

Development of the breeding population of Cormorant *Phalacrocorax carbo sinensis* in Denmark, 1938-1994

The present paper describes and discusses the population development of the Cormorant in Danish breeding colonies during the 20th century with emphasis on the influence of human interference and movements of individuals between colonies. Nests were counted in all colonies once a year. The timing of counts is shown in Fig. 1 in relation to the seasonal development of nest numbers in one old and one young colony. Between 1977 and 1992 16457 Cormorants were ringed with inscribed colour rings at 12 colonies. Of these, 723 were recorded breeding or possibly breeding at colonies away from their natal site.

No Cormorants bred in Denmark between 1877 and 1937, and from the reappearance of a colony in 1938 till 1971 the breeding population remained small, up to 902 pairs (Tab. 1). All colonies existing in this period, except one, disappeared after one to nine years due to shooting of adults and young in the colonies. Recoveries of ringed birds being shot, and changes in colony sizes during the 1940s and 1950s, indicate exchange of individuals between colonies in Denmark and colonies in the former GDR (Fig. 3). The Vorsø colony (see Fig. 2 for location of colonies) was established in 1944 and was the only colony where Cormorants were protected throughout most of the year; shooting was limited to a maximum of 300 young per year.

Vorsø was the only existing colony between 1961 and 1971, but after the shooting of young stopped in 1971, and shooting in the Niederhof colony at Rügen was reassumed, breeding numbers increased in Denmark (Fig. 3). The Ormø colony reappeared in southeast Denmark in 1972 and a colony was founded at Brændegård, south Funen, in 1973. Although, total numbers increased during the 1970s, shooting of young at Ormø 1976-1978 (approximately 20% of the total Danish production of young) hampered the rate of increase (Fig. 5). Felling of nesting trees at Brændegård in 1979 probably forced young Cormorants to delay breeding, which may explain the 37% increase in the population two years later (Fig. 5) and the sudden increase at Ormø in 1981. Sightings of colour-ringed breeders confirm that Cormorants emigrated from Brændegård to Ormø in 1981.

During 1982-1994, breeding numbers increased from 3700 to 37748 nests (Tab. 1). The yearly increase ranged from 16% to 36% (avr.=26.2%) between 1982 and 1989, but from 1989 to 1994 the annual increase declined from 33.9% to just 3.7% (Fig. 5). The temporary decline in the overall growth rate after 1983 is thought to be due partly to the shooting of 5500 young at Ormø 1982-1986 (approximately 9% of the young production in Denmark). From 1982 onwards new colonies were established every year (Tab. 1). The majority of new colonies increased in size at a decelerating rate, indicating effects of immigration on initial growth. Three- and four-year old Cormorants originating from large neighbouring colonies predominated among immigrants (e.g., Fig. 9). In 11 out of 14 colonies where colour-ringed immigrants were observed as breeders or possible breeders, one or more individuals came from a colony situated more than 150 km away. The fastest growing colonies were situated close to large colonies and were surrounded by extensive areas of shallow water (cf. van Eerden & Gregersen 1995). In some colonies recruitment was seemingly affected by human disturbance and availability of attractive nesting sites. Out of 36 colonies established during 1982-1993, 17 were abandoned permanently or temporarily one to nine years after first breeding; 13 of the sites were abandoned before numbers reached 200 pairs. Several of these colonies suffered from illegal destruction of nests or nesting trees.

Up until the 1980s, Cormorants established colonies in trees on small islets situated in lakes or fjords, but since 1982 some colonies were established on the ground, leading to a decline in the proportion of Cormorants breeding in trees (Fig. 8). The highest number of colonies and the largest colonies are situated in fjords, inlets or in near-coastal areas close to large water bodies (Fig. 2 and 7); being located 8 and 9 km from the coast, Brændegård and Søholt are exceptions. In 1994, 83% of the population nested in 12 colonies holding 1000 to 6000 breeding pairs.

On a regional scale, numbers developed in a similar manner around the three old colonies Vorsø, Ormø and Brændegård (Fig. 6). Establishment of new colonies allowed regional numbers to continue to increase despite stabilisation at Vorsø and Ormø (Fig. 6). However, in the region around Brændegård very few colonisations were successful and the rate of recruitment to Brændegård continued to be high until 1991, whereafter the increase stopped and numbers declined (Fig. 6); some Brændegård birds emigrated to Flensborg Fjord, Germany. In the regions around Vorsø and Ormø numbers stabilized in 1992-1993. In the recently colonised regions of west and northeast Denmark, the breeding population is still in an early phase of growth and expansion (Fig. 6).

The two main reasons for the rapid expansion in the Danish Cormorant population during 1972-1975 (26-44% per year) and 1980-1992 (15-36%) are suggested to be (1) increased protection leading to increased survival and production of young, and (2) availability of undisturbed potential colony sites located close to rich feeding areas. The decline in overall growth rate is explained by the change from growth to stabilization in the three regions where most Cormorants breed. Cessation
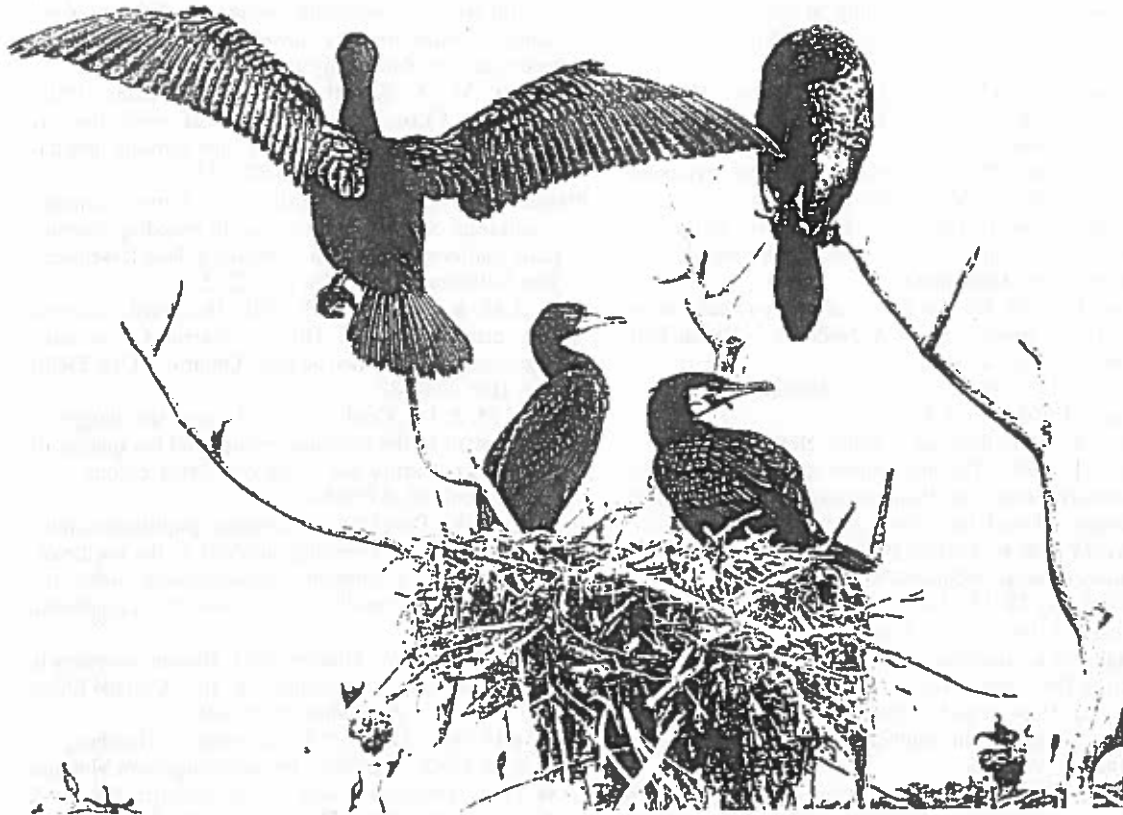
Den høje vækstrate i den danske bestand skyldes bl.a. høj ungeproduktion. Her en voksen med tre flyvefærdige unger, Vorsø, 1977. Foto: Erik Thomsen.

of growth in these regions despite no outbreak of disease suggests a beginning shortage of resources such as available food and undisturbed colony sites. A decline in the production of recruits and in the proportion of birds able to breed seems to be the major reason for the fast decline in growth rate (Fig. 5).

We expect many colonies to become limited in size by the carrying capacity of the surrounding feeding areas, i.e. the amount and availability of fish, area of shallow water and distance to and size of neighbouring colonies (cf. Furness & Birkhead 1984, Røv 1994). Further expansion of the breeding population in Denmark will be constrained by a new management practice implying scaring of Cormorants trying to settle in new areas.

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Chapter 6

Changes in growth of the breeding population of Cormorants
Phalacrocorax carbo sinensis in Denmark

Thomas Bregnballe & Jens Gregersen

Changes in growth of the breeding population of Cormorants *Phalacrocorax carbo sinensis* in Denmark

by

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Summary

In 1995 Denmark had 38 301 pairs of Great Cormorants nesting in 35 colonies. This population level was reached after 17 years of an average annual increase of 26% followed by a decline in growth from 34% in 1989 to 1.4% in 1995. The suggested reasons for the rapid reduction in annual growth rate are (1) that the very large 'mother colonies' stopped growing and that growth levelled off a few years later in the satellite colonies, (2) that reproductive output declined, (3) that a minor proportion of the potential recruits produced in the 'saturated regions' dispersed to colonies in unsaturated regions, and (4) that the overall rate of colonization of new sites declined early in the phase of expansion.

The total breeding population has not reached its potential maximum and will probably not do so in near future. The still expanding colonies are generally located far from very attractive feeding areas and/or recruitment to the colonies is hampered by human interference. A new management strategy includes scaring of birds attempting to found new colonies, so few new colonies will be founded.

Introduction

Numbers of breeding Cormorants *Phalacrocorax carbo sinensis* increased by 11% per annum in The Netherlands and 26% in Denmark between 1971 and 1991 whereafter growth levelled off (Bregnballe, in press.). Numbers in Sweden, Germany and Poland began expanding in the early 1970s (Sweden) and early 1980s (Germany and Poland; Lindell *et al.*, 1995) and the subspecies has extended its breeding range in central Europe and along the Baltic Sea (Bregnballe, in press., Lindell *et al.*, 1995).

The conflict with human interests has intensified causing an increase in the pressure for action to halt further expansion. Scaring at roosts or of birds attempting to establish new colonies, as well as egg destruction, killing of young and shooting of adults is now taking place over most of Europe (Lindell *et al.*, 1995, Lindell, in press., W. Suter, L. Marion & N. Baccetti pers. comm.).

Our ability to assess impacts of control measures depends on our understanding of: i) factors and resources limiting growth and geographical expansion of the population, ii) the mechanisms involved in the transition from expansion to stabilization, and iii) how decisions taken by individual birds are affected by human
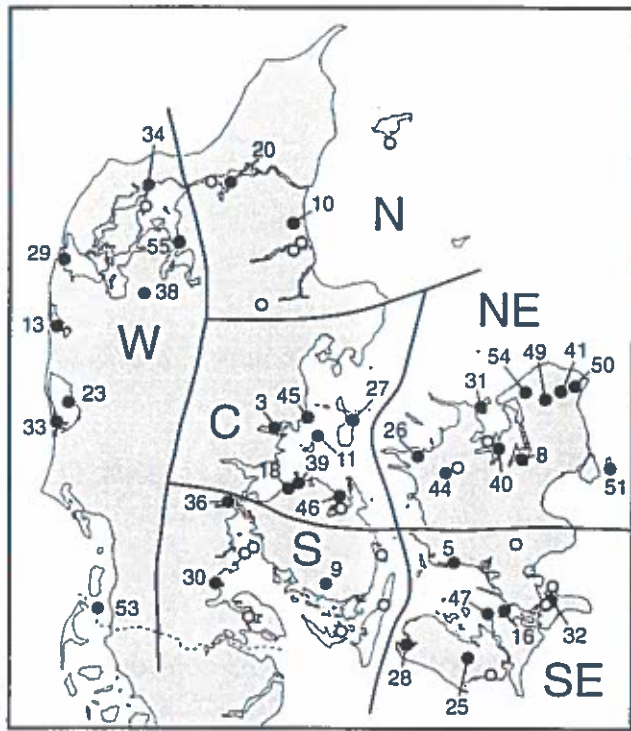
Figure 1. Distribution of Cormorant colonies in Denmark 1995 and boundaries of the six regions. Colonies existing in 1995 are shown as filled circles with numbers referring to Table 1. The colonies are numbered in order of foundation. Colonies founded and disappearing 1938-1956 are shown as encircled dots, and colonies founded after 1981 and disappearing before 1995 are shown as open circles.

interference. The reasons behind cessation of growth may not be the same in all countries and it is still unclear to what extent numbers in different areas are limited by the same factors and the same resources.

This paper presents data on breeding numbers in Denmark in 1995 and reviews and discuss dispersal and colonization patterns and the implications of these patterns for the observed change in propulation growth.

The development of the breeding population in Denmark before 1995 is described in detail by Bregnballe & Gregersen (1995, in press.) and van Eerden & Gregersen (1995).

Methods

Since 1980, the number and distribution of colonies in Denmark has been known from
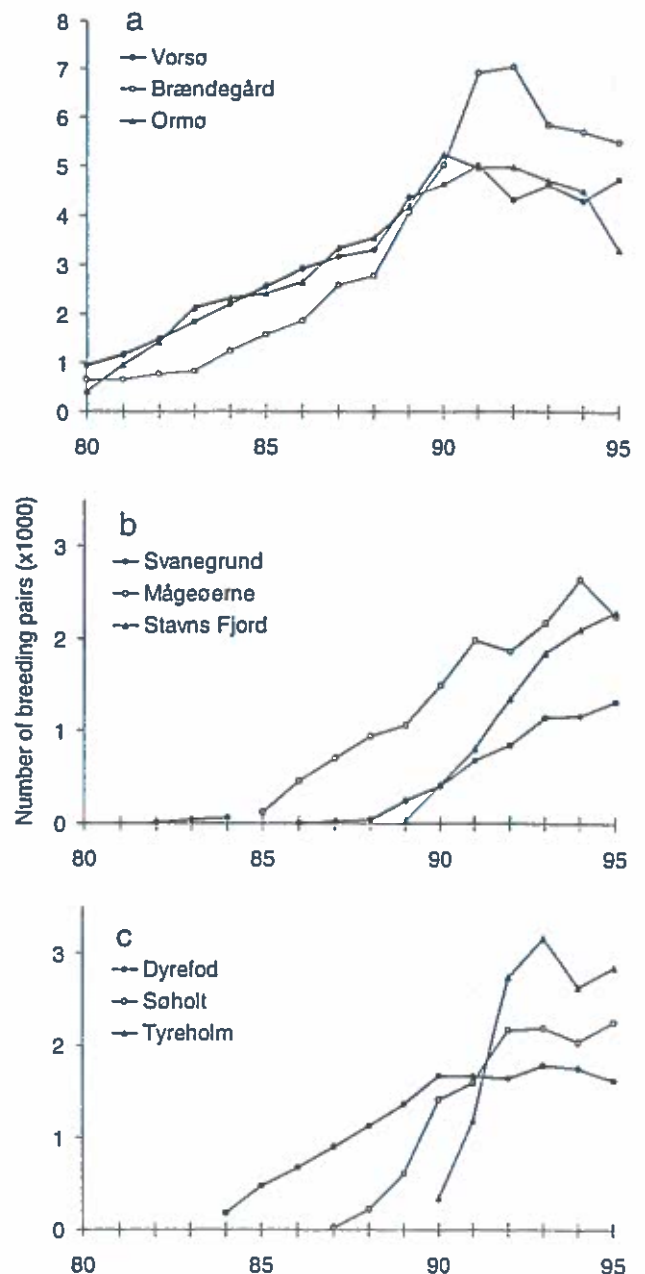
Figure 2. Development of number of breeding pairs in the three 'mother colonies' Vorsø, Brændegård and Ormø (a), in the main satellite colonies around Vorsø, i.e. region C (b), and around Ormø, region SE (c), 1980-1995. Only colonies increasing to at least 1000 pairs in 1985-1995 are included. One satellite colony near Brændegård, i.e. region S, increased to more than 1000 pairs but disappeared due to illegal nest destruction. Boundaries of regions are shown in Fig. 1.

visits to former and existing colony sites and from observations made by ornithologists, landowners, and state forest personnel. Many potential Cormorant breeding sites have been overflown by ornithologists during aerial surveys in the breeding season or visited by persons likely

to report Cormorant breeding attempts. None the less, some new breeding attempts (especially unsuccessful attempts) may have been missed. All active nests have been counted at least once; most colonies were counted in early May. Maximum numbers were used from the colonies censused two or three times in a year. Sub-colonies located less than 2000 m apart were aggregated as one colony. Lowest inter-colony distance beyond this limit was 3500 m. 'Colony' refers to a site where at least one whole nest was built. 'Number of pairs' equates to 'number of nests', even though the number of pairs attempting to breed is higher than the number of nests counted. The same methods and defini-

tions have been used throughout the period 1980-1995.

For the purpose of studying differences in development of breeding numbers at a regional level, the country was divided into five regions (see Fig. 1).

Results

From growth towards stabilization
In 1980 Denmark had three Cormorant colonies: Vorsø, Brændegård and Ormø. These colonies, which we refer to as the 'mother colonies', ex-
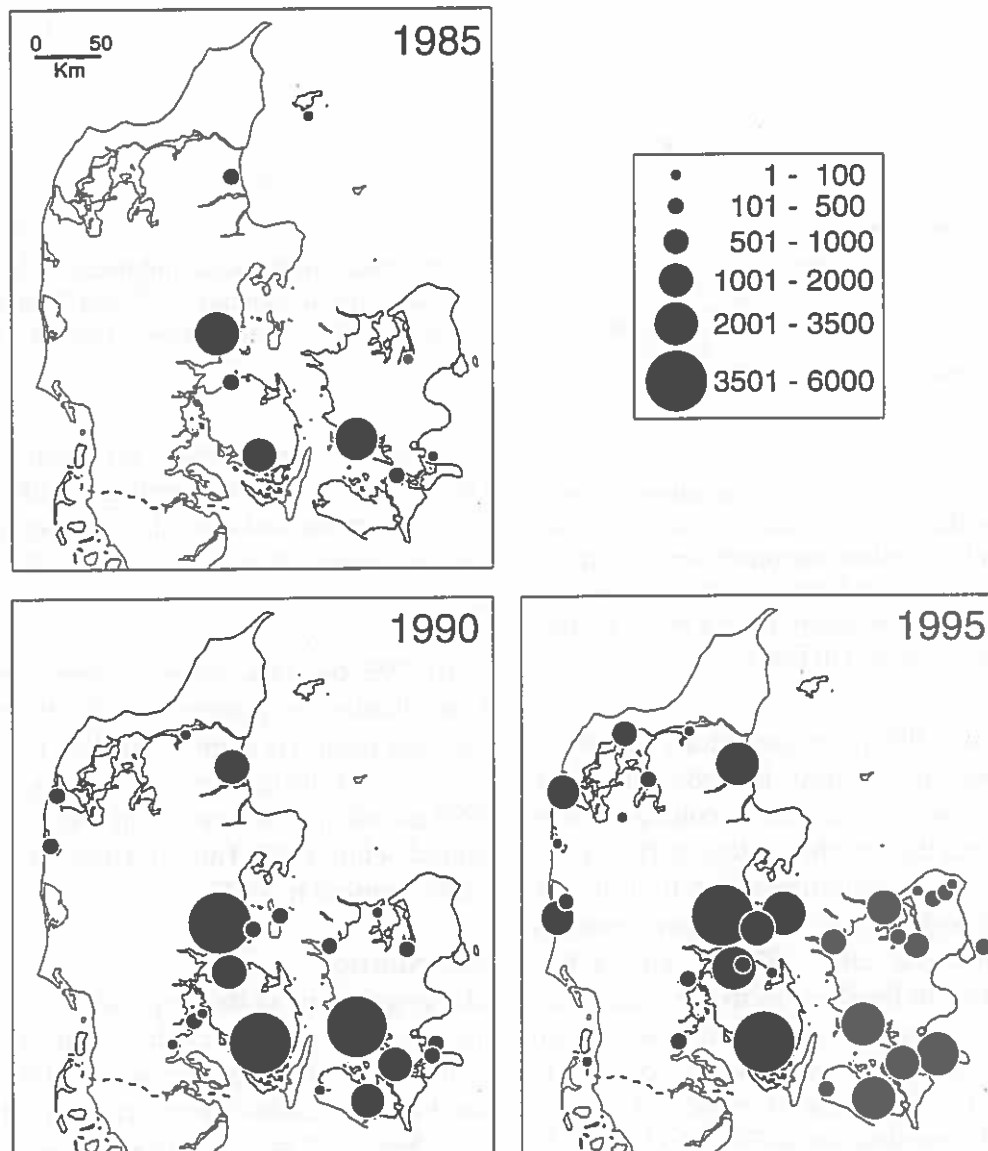
Figure 3. Distribution and size of Cormorant colonies given as the number of breeding pairs in Denmark in 1985, 1990 and 1995.
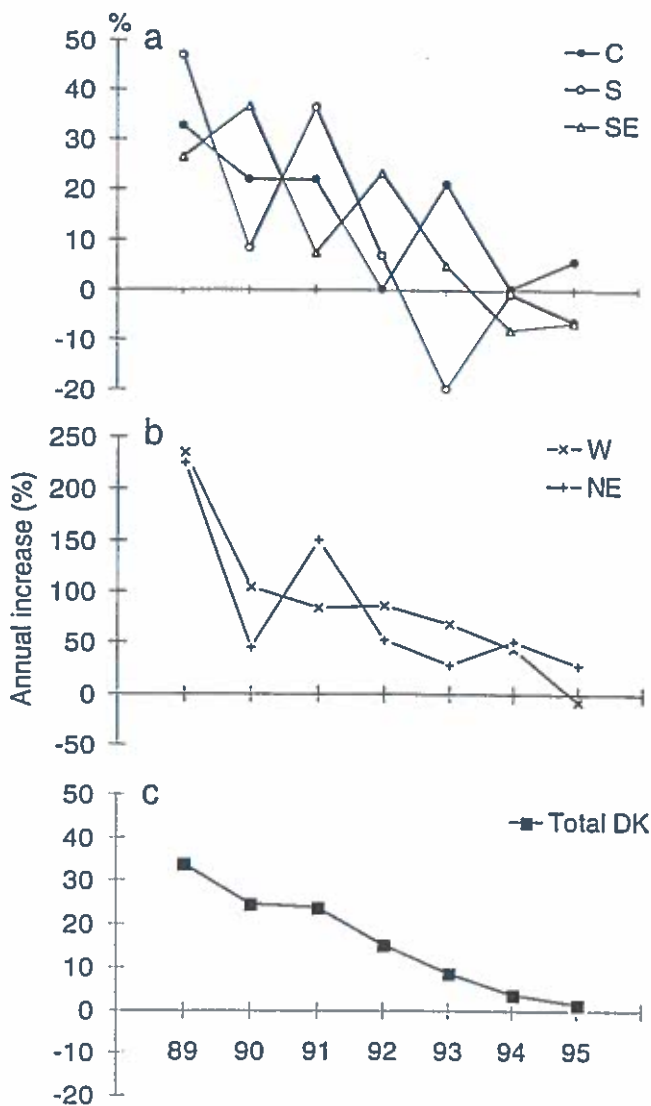
Figure 4. Annual rate of increase in number of breeding pairs in the three old regions C, S and SE (a), the two most recently colonized regions W and NE, and in total in Denmark (c), 1989-1995. Note that the ordinate in b is drawn to a scale different from a and c. Boundaries of regions are shown in Fig. 1.

panded from 420-950 pairs per colony in 1980 to 4080-4385 pairs per colony in 1989 (Fig. 2 a). From 1982 onwards, satellite colonies were founded around the 'mother colonies' (Fig. 2 b,c, 3), and later more colonies were founded in neighbouring regions (Fig. 3). The three 'mother colonies' stabilized after 1989-91, and a few years later, growth levelled off in the large satellite colonies, most evident in the region around Ormø (Fig. 2 c). This pattern lead to a decline in the annual rate of increase in regions C, S and SE (Fig. 4 a; the regions are defined in Fig. 1). In the latest colonized regions, W and NE, recruitment was high during 1989-95 (Fig. 4 b) but
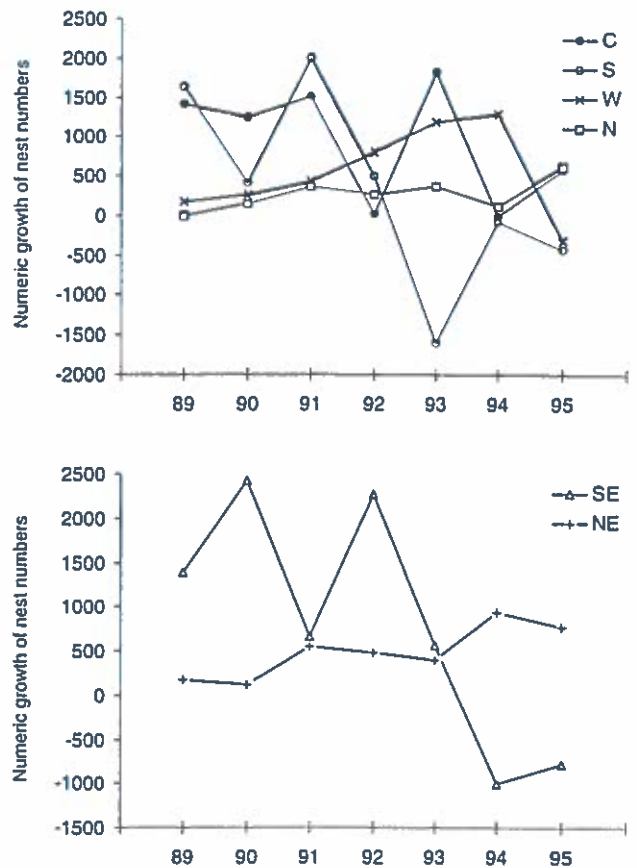
Figure 5. Numeric increase and decrease in number of breeding pairs in regions C, S, N and W (a) and SE and NE (b), 1989-1995. Boundaries of regions are shown in Fig. 1.

relatively few birds were involved (Fig. 5). In Denmark as a whole, breeding numbers continued to increase, but the rate of increase declined steadily from 34% in 1989 to 1.4% in 1995 (Fig. 4 c).

In 1995, two new colonies were founded and four colonies disappeared, so that the number of colonies declined from 37 in 1994 to 35 in 1995. Fig. 1 shows the location of the sites occupied in 1995 as well as the location of colony sites abandoned before 1995. Table 1 gives the number of nests counted in 1995.

Distribution

The greater part of the population is still breeding around the Belts, i.e. in regions C, S and SE (Fig. 3), but the proportion breeding in north, west and northeast Denmark is slowly increasing (Fig. 6). The proportion breeding in the largest colonies (>4000 pairs) has declined, whereas that in large colonies (1000-4000 pairs)

Table 1. Number of breeding pairs in Cormorant colonies in Denmark 1995 including regional and country totals. 't' denotes trees; 's' scrub; 'g' ground; '*' founded in 1995. Numbers refer to Fig. 1.

Region	No.	Colony, habitat	Colony size	Region total
C	3	Vorsø, t,s	4771	
	11	Svanegrund, g	1315	
	18	Mågeøerne, g	2251	
	27	Stavns Fjord, s,g	2288	
	39	Dræet, g	272	
	45	Hov Røn, g	39	
	46	Hofmansgave, g	61	10 997
S	9	Brændegård Sø, t,s,g	5543	
	30	Hopsø, t	203	
	36	Kidholmene, t,s	250	5 996
SE	5	Ormø, t	3317	
	16	Dyrefod, t,s,g	1623	
	25	Søholt, t	2250	
	28	Nakskov Fjord, t,s,g	464	
	32	Tyreholm, g	2847	
	47	Suderø, g	320	10 821
N	10	Toft Sø, t,s	2901	
	20	Rønholm, g	20	2 921
W	13	Fjandø, g	17	
	23	Klægbanken, g	155	
	29	Rønland Sandø, g	1140	
	33	Olsens Pold, g	1296	
	34	Melsig, g	890	
	38	Flyndersø, t	92	
	53	Jordsand, g	3	
	55	Rotholmene, g *	392	3 985
NE	8	Bognæs, t	750	
	26	Saltbækvig, t	900	
	31	Hovvig, t,g	1101	
	40	Rønø, g	118	
	41	Esrum Sø, t	125	
	49	Solbjerg Engsø, t	403	
	50	Gurre Sø, t	23	
	51	Saltholm, g	116	
	54	Arresø, t *	45	3 581
Total				38 301

has increased (Fig. 7), partly a consequence of the decline from 4522 pairs in 1994 to 3317 pairs in 1995 in the Ormø colony.

Pattern of growth and dispersal
For many years, most birds settled in the three long-established colonies of Vorsø, Brændegård and Ormø. As late as in 1989, 63% of the annual increase occurred in these colonies. After 1989, the Vorsø colony more or less stabilized and Ormø reached its maximum one year later (Fig. 2 a). However, growth continued for some years in the satellite colonies (Fig. 2 b,c) so for these regions, numbers continued to increase at the
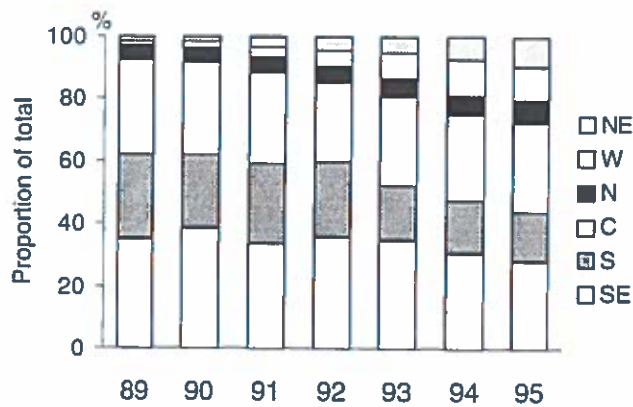
Figure 6. Development of Cormorant breeding populations in six regions in Denmark, 1989-1995, given as the proportion of total numbers breeding. Boundaries of regions are shown in Fig. 1.

Figure 7. Total number of Cormorant pairs breeding in colonies holding 1-300, 301-1000, 1001-4000 and 4001-7100 breeding pairs in 1989, 1992 and 1995.

regional level (see Bregnballe & Gregersen, 1995). The third 'mother colony', Brændegård, continued to receive large numbers of recruits and increased to 7087 pairs in 1991 whereafter numbers declined (Fig. 2 a). Few new colonies were successful in this region, and trends in regional numbers followed the trends in Brændegård (see Bregnballe & Gregersen, 1995 or van Eerden & Gregersen 1995).

Northern Denmark was first colonized in 1982. Immigration to the Toft Sø colony lead to an increase in region N from 8 to 596 pairs during the first four years. Thereafter, the rate of increase has been moderate at Toft Sø (maximum 36%). There has been no tendency for an increase in growth in nest numbers in region N in years without growth in the neighbouring region C (1992 and 1994, Fig. 5 a).

West and northeast Denmark were first colonized in 1986 and 1987, respectively. The yearly increase in breeding numbers in region W did not rise when there was no growth in regions S and C (Fig. 5 a). In region NE, numeric growth increased slightly in 1991 and 1994 when there was no, respectively low recruitment to region SE (Fig. 5 b).

Table 2. Number of colonies founded and disappeared (in brackets) per year in six regions and in total in Denmark, 1982-95. Breeding numbers had stabilized in regions C, S and SE in 1993.

| Region | Number of colonies founded (disappeared) | | | | | | | | | | | | | |
	82	83	84	85	86	87	88	89	90	91	92	93	94	95
C	1			1(1)	2[1]		(1)	1				1	2	
S	1	(1)				1			2[1]	1(1)	(1)	3[1]	(2)	(1)
SE			1	1	1	1(1)		1	1				2(1)	(1)
N	1	1	1(1)	1(1)	1(1)		1[1]	(1)		1		(2)	1[1]	
W		1	(1)		1[1]	1		(1)	1	2	2		2[1](1)	1
NE				1[1]	(1)	1[1]	1		1	(1)	3	1	4	1(2)
Total founded	3	2	2	4	5	4	2	2	5	4	6	4	11	2

[1] one colony founded on a former colony site

Table 3. Characteristics of sites colonized by Cormorants in Denmark 1938-81, 1982-93 and 1994-95.

Status of site before colonisation	Colonies established		
	1938-81	1982-93	1994-95
Used as a roost by Cormorants	0	22	5
Presence of heronry	13	8	0
No roost and no heronry	0	6	4
Colony within the last 6 years	3	6	2
Colony more than 6 years back	1	2	0
Unknown	0	2	2

Colonizations

Overall, the number of attempts to found new colonies has increased only slightly; maximum was 11 in 1994 (Table 2). Hence, the rate of colonization of new sites slowed down in the early phase of expansion. Attempts to colonize new sites have continued in region C, S and SE after growth levelled off in these regions. After 1991, most colonizations have taken place in northeast Denmark (Table 2).

Most sites where Cormorants attempted to found a colony had been used by i) roosting Cormorants up until the year before colonization, ii) by breeding herons in the year of colony formation, or iii) by breeding Cormorants two to six years earlier (Table 3). For the period before 1994, 57 of 63 sites (90%) had at least one of these three characteristics, whereas, in 1994-95, 9 of 13 sites (69%) had the characteristics.

Of 24 colonies which disappeared out of 52 established during 1982-1995, two disappeared after illegal intervention (destruction of nests), ten after disturbance, two after legal intervention and ten for unknown reasons. The probability that a colony would disappear during 1994-1995 was not different fromt the probability in the years 1983-1993: a 10.4% chance in the earliest period compared with 10.9% chance in 1994-1995 (calculated as 'number of colony sites abandoned in year x' / 'number of colonies present in year x-1').

Discussion

Annual growth rate of the overall Danish Cormorant breeding population declined due to progressive stabilization in breeding numbers in the first colonized regions. The change towards stabilization was first observed in the 'mother colonies', where most birds bred, and was followed by stabilization in several satellite colonies a few years later. Some colonies, particularly those in the most recently colonized parts of the country, continue to expand, although numbers involved are relatively low and have only a small effect on overall growth rate.

Limitation of colony size: the importance of food

The three 'mother colonies' did not stabilize because of limited access to potential nesting sites (Gregersen, unpubl. data). Observed declines in reproductive output (Bregnballe, in prep.) suggest that stabilization is related to a decline in the amount of food available around colonies. Changes in food availability are likely to affect not only chick survival but also decisions taken by birds early in the season about whether to recruit, emigrate, postpone breeding or skip breeding.

The cessation of growth of the satellite colonies at lower levels than the 'mother colonies' could be due to: (1) restriction on physical expansion, (2) overlap in feeding range (i.e. interference or exploitative competition with birds breeding in neighbouring colonies; cf. Furness &

Birkhead, 1984, Røv, 1994, van Eerden & Gregersen, 1995), (3) smaller area of shallow water within the foraging range (Røv 1994), (4) smaller fish stocks and/or (5) lower recruitment to local fish stocks.

Presumably, few of the colonies founded in northeast and west Denmark will expand to become large colonies, because the feeding potential of these areas are likely to be low compared with the Belts (Hald-Mortensen, 1995). Although two colonies in northeast Denmark (Saltbækvig and Hovvig) are located close to rich and extensive feeding areas and have the potential for expansion, their growth has been hampered by felling of nesting trees (Saltbækvig) and more recently by disturbance (Hovvig). Most of the other new colonies in region NE are located near freshwater lakes, more than 6 km from extensive marine feeding areas, and such colonies rarely grow large (Lindell et al., 1995, van Eerden & Gregersen, 1995).

Rate of geographical expansion: importance of dispersal behaviour

The transition from a period of expansion of breeding numbers to a phase of stabilization has occurred within a few years. One reason seems to be that only a minor proportion of the potential recruits produced in the saturated regions dispersed to colonies in unsaturated regions.

There are indications that for regions C and SE more potential breeders were produced in the years before stabilization than actually started to breed. For example, in the Vorsø colony reproductive output and survival from fledging till one year old continued to be high or relatively high until four years after breeding numbers stabilized (Bregnballe & Gregersen in prep.). Some of these birds settled in the Stavns Fjord colony (unpubl. data) but also this and other satellite colonies have increased at low rates in recent years despite high reproductive outputs (unpubl. data). Hence, many potential recruits have seemingly abstained from settling in their region of origin. A similar pattern is observed in region SE.

It seems that emigration to neighbouring regions is not an option which has been taken by many birds during the declining growth in regions C, S and SE. The rate of increase was only slightly higher in the newly colonized regions W and NE than could be expected from local reproduction except for the first years (unpublished data). The large year-to-year changes in annual increase in nest numbers in regions S, SE and C (Fig. 5) and the absence of equally large complementary year-to-year variations in population growth in neighbouring regions is further evidence that immediate exchange of large numbers of birds between regions is not taking place. We suggest, therefore, that at least for some years an increasing number of birds abstained from recruiting to the breeding population.

Immigration of Danish birds to northern Germany and southern Sweden has not been quantified, but growth patterns do not indicate large scale immigration of Danish Cormorants (Menke, pers comm., Lindell et al., 1995, Lindell, in press.).

Year-to-year fluctuations in numeric growth has also been observed in The Netherlands (van Eerden & Zijlstra, 1995), Germany (Menke, pers. comm.), Poland (Mellin & Mirowska-Ibron, pers. comm.) and Sweden (Lindell, in press.). Year-to-year variation in access to food is likely to be a main factor affecting the number of Cormorants breeding (cf. Boekelheide & Ainley, 1989, Røv, 1994, van Eerden & Zijlstra, 1995).

Limitation of colony distribution: importance of safe sites

The continued high rate of increase at Brændegård until 1991 is likely to be related to the absence of satellite colonies associated with Brændegård: only two of five new colonies in the region around Brændegård (region S) were successful and they developed slowly because of disturbance and felling of trees. Despite the presence of extensive foraging areas in this region, total numbers breeding remain low compared with the regions C and SE (Table 1). This difference may be related to the failure to found new successful colonies.

There are still many sites in Denmark where Cormorants could breed close to unexploited or only partly exploited feeding areas, but Cormorants have attempted to breed on only few of the sites despite a supposed pressure in the saturated colonies. Most colonized sites have either been used as roosting sites, had breeding

herons and/or were located in trees or on islets difficult to reach for mammalian predators, i.e. the Cormorants knew or had reasons to expect that the sites were safe for breeding. Many roosting sites suitable for breeding have already been colonized and most of the remaining roosts are offshore sites which are flooded temporarily (S. Pihl & I.K. Petersen pers. comm.). It may be that Cormorants are constrained by a combination of attempting to breed only on sites they 'judge' as being safe and by lack of information about where they can breed safely outside roosts.

Few individuals were involved in each of the attempted colonizations in northeast Denmark during 1994-95. We speculate whether this may indicate low attractiveness of the sites or that only few individuals had experienced that the sites were safe (only one of the four new sites had been used for roosting before colonization was attempted).

A new management practice was introduced in Denmark in 1994 (Bregnballe & Asbirk, 1995). Because it includes disturbance and scaring of Cormorants on new sites, only a few of the future colonizations are likely to be successful.

From estimates of sizes of potential Cormorant feeding areas in Denmark, van Eerden & Gregersen (1995) and Bregnballe (unpubl.) estimated that the Danish breeding population could increase to around 60 000 pairs, i.e. 20 000 more pairs than present in 1995. The observed levelling off of growth suggests that the breeding population will stabilize below its potential maximum.

Conclusions

The rapid reduction in annual growth rate of breeding Cormorant numbers can be partly explained by the absence of emigration of large numbers of birds from 'saturated' to unsaturated regions. Future population expansion in Denmark is likely to become limited mainly by limited availability of food around existing colonies, 'absence' of safe sites with the 'right' characteristics (e.g. cues for safety), and human interference at new colonies limiting the number of successful colonization attempts.

Acknowledgements

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Udviklingen i bestanden af Mellemskarv *Phalacrocorax carbo sinensis* i Nord- og Mellemeuropa 1960-1995

With a summary in English: Development of North and Central European breeding population of Cormorant Phalacrocorax carbo sinensis, *1960-1995*

Thomas Bregnballe

Udviklingen i bestanden af Mellemskarv i Nord- og Mellemeuropa 1960-1995
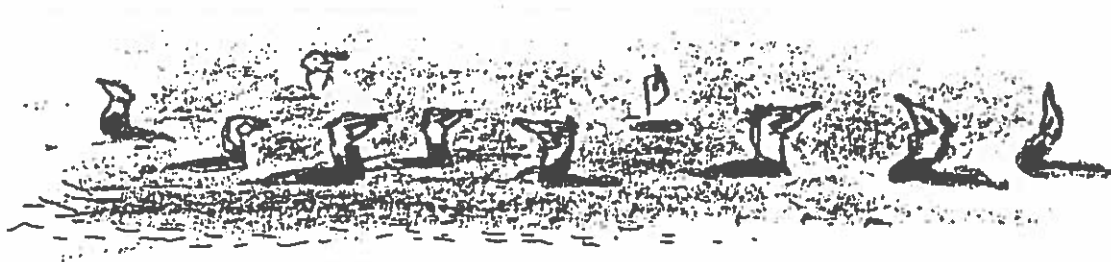
THOMAS BREGNBALLE

(With a summary in English: Development of the North and Central European breeding population of Cormorant Phalacrocorax carbo sinensis, 1960-1995)

Indledning

Mellemskarven *Phalacrocorax carbo sinensis*, der yngler i flere bestande i Europa og Asien (del Hoyo et al. 1992), har i de sidste 25 år formået at opbygge en stor ynglebestand i Nord- og Mellemeuropa og har nu bredt sig til de fleste lande i Europa. Her beskrives fremgangen og de første tegn på stabilisering. I beskrivelsen og diskussionen er der lagt særlig vægt på forløbet af udviklingen i hovedudbredelsesområdet, som omfatter Danmark, Holland, Tyskland, Polen og Sverige.

Metoder

I det følgende er bestandsstørrelser opgivet som antal ynglepar, skønt det i praksis er antallet af beboede reder, der registreres. Med gennemsnitlig vækstrate menes årlig vækst på den udglattede vækstkurve over de pågældende år (og ikke gennemsnittet af væksten i de enkelte år). Oplysninger om antal ynglepar hidrører fra van IJzendoorn (1950), Przybysz & Przybysz (1975), Goethe et al. (1978), Knief & Witt (1983), Jonsson (1986), Zimmermann (1986), Hashmi (1988), Przybysz et al. (1988), Suter (1989), Lindell (1991, 1993), Menke (1991, in press), Gromadzka & Przybysz (1991), Zijlstra & van Eerden (1991). Zimmermann & Rutschke (1991), Ossipov & Gaginskaja (1994). Knief (1994), Bregnballe & Gregersen (1995), Lilleleht (1995), Lindell et al. (1995). Marion (1995a), Žalakevičius (1995), van Eerden & Gregersen (1995), Bregnballe & Gregersen (in press), Carpegna (in press) og Menke (in press). Supplerende oplysninger er indhentet fra den Tredje og Fjerde Europæiske Skarvkonference, afholdt i hhv. Polen 1993 og Italien 1995, fra M. R. van Eerden & M. Zijlstra (pers. medd., for Holland), L. Lindell (pers. medd., for Sverige), J. Przybysz, M. Mellin & I. Mirowska-Ibron (pers. medd., for Polen), T. Menke, J. J. Kieckbusch, W. Knief & T. Keller (pers. medd., for Tyskland), P. Ulenaers & K. Devos (pers. medd., for Belgien), R. Sellers & J. Kirby (pers. medd., for England), G. Debou (pers. medd., for Frankrig), P. Musil (pers. medd., for Tjekkiet og Slovakiet), I. Samusenko (pers. medd., for Hviderusland), V. Lilleleht (pers. medd., for Estland), og J. Viksnes og V. Smislov & J. Baumanis (pers. medd., for Letland).

Resultater

I 1960erne havde Mellemskarven vanskelige forhold i Europa (Coomans de Ruiter 1966, Gregersen 1982, Knief & Witt 1983, Hansen 1984). I Holland faldt antallet af ynglepar fra et maksimum på ca 4622 par i 1940 til 800 par i 1962 pga. inddæmning, forstyrrelser og forurening (Koeman et al. 1972). I Belgien forsvandt de sidste kolonier i 1964, i Tyskland var der mellem 920 og 1260 par i 1961-64 (heraf kun 50-60 par i Vesttyskland), i Polen 1800 par i 1959 og 1500 par i 1965, i Danmark 150-255 par i 1960-65, og i Sverige 100-150 par i 1965. Så i begyndelsen af 1960erne ynglede i alt 3500-4300 par Skarver i disse lande. I 1971 talte bestanden stadig kun ca 4900 par.

I 1970erne begyndte bestanden at vokse i Holland, Danmark og Sverige, og trods tilbagegang i det tidligere DDR og Polen var det samlede antal

Tab. 1. Bestandsudviklingen for Mellemskarv (ynglepar) i fem europæiske lande. For 1991 er bestanden i Holland. Polen og Sverige skønnet af forfatteren ud fra optællingsresultater i det foregående og/eller efterfølgende år. For Polen 1995 er estimatet en ekstrapolation på grundlag af en optælling i en del af landet (M. Mellin & I. Mirowska-Ibron pers. medd.).
Breeding pairs of P. c. sinensis in five European countries. Numbers given for 1991 for the Netherlands, Poland and Sweden are estimated by the author from counts in a previous or following year. The number given for Poland 1995 is extrapolated from partial counts.

	1971	1981	1991	1995
Holland *The Netherlands*	2500	7028	19232	15200
Danmark *Denmark*	282	2791	29141	38301
Tyskland *Germany*	667	1149	7269	14819
Polen *Poland*	1100	1470	7300	11000
Sverige *Sweden*	200	940	6600	15400
Total	4749	13378	69542	94720

øget til ca 9100 ynglepar i 1979. Allerede i 1981 kunne bestanden opgøres til ca 13400 par (Tab. 1), hvoraf 53% ynglede i Holland, og med fortsat vækst i alle fem lande nåede bestanden ca 26000 par i 1985 og 94720 par i 1995.

Den samlede tilvækst steg fra i gennemsnit 11% pr år i 1971-1981 til 18% pr år i 1981-1991, men faldt så fra 17% i 1992 til 3% i 1994. Fig. 1 viser udviklingen i de enkelte lande. Den logaritmiske skala gør det muligt at aflæse vækstraterne fra kurvernes hældning, og det fremgår tydeligt, at den årlige tilvækst var højere i Danmark (26%) end i Holland (11%) i den tyveårige periode fra 1971 til 1991. Derved kom Danmark til at huse en stigende andel af den samlede bestand, fra 6% i 1971 til 40-42% i 1991-95, så Danmark nu er det vigtigste yngleområde. I de senere år er væksten i Danmark aftaget fra 36% i 1989 til 1,4% i 1995, og i Holland registreredes en tilbagegang på over 6000 par i 1994 (se van Eerden & Zijlstra 1995). Den hollandske bestands andel af den samlede bestand svandt derved yderligere, fra 31% i 1990 til 16% i 1994. I Sverige og Tyskland voksede bestanden årligt med hhv. 24% og 23% i perioden 1980-94 og havde i begge lande nået samme størrelse som i Holland i 1994 (Fig. 1). Fra 1994 til 1995 var fremgangen svag i både den svenske og tyske bestand, hhv. 2,2% og 3,0%. I kystkolonierne i det nordøstlige Polen registreredes en vis fremgang igen i 1995 efter stilstand i 1993 og 1994.

I 1995 var der 35 kolonier i Danmark, 59 i Tyskland og 56 i Sverige, mens Polen havde 32 og Holland 18 i 1992. De største kolonier findes nær de danske bælter (op til 7087 par), ved den holland-

ske indsø IJsselmeer (op til 8380 par), og ved Østersøkysterne i Tyskland (op til 2402 par), Sverige (op til 3500 par) og Polen (op til 3650 par). Kolonier ved floder og søer er gennemgående små (50-500 par).

I takt med væksten i det nordlige Europa udvidede Skarven sit udbredelsesområde, og antallet af kolonier i hele det nord- og mellemeuropæiske område voksede fra ca 15 i begyndelsen af 1960erne til ca 176 i 1992. Mellem 1982 og 1992 genindvandrede Mellemskarven til mindst 11 lande. Følgende bestandsstørrelser er indtil videre registreret: England (1100 par i indlandet i 1995), Frankrig (950 par i indlandet i 1995), Belgien (272 par i 1995), Italien (493 par i 1995), Tjekkiet og Slovakiet (712 par i 1991, 425-490 par i 1995), Estland (1390 par i 1994), Letland (mindst 205 par i 1995), Litauen (800-1000 par i 1995), Rusland (1400 par i Finske Bugt i 1994) og Hviderusland (850 par i 1995). I England og Frankrig er det endnu uklart hvor stor en andel fugle af underarten *P. c. carbo* udgør blandt de ynglepar, som har etableret sig inde i landet, men meget tyder på, at *P. c. sinensis* dominerer (Marion 1995b).

I flere tilfælde er ekspansionen mod syd og vest sket på den måde, at Skarver er forblevet i et overvintringsområde og har etableret koloni på en lokalitet benyttet til dagrast eller overnatning. Aflæsninger af farveringe har vist, at danske Skarver har medvirket til dannelsen af kolonier i Italien, Sydtyskland, England og Frankrig. De fugle, som etablerede sig her, havde høj ynglesucces (Grieco 1994), og flere af fuglene ynglede allerede efter første eller anden vinter (Carpegna et al. in press).
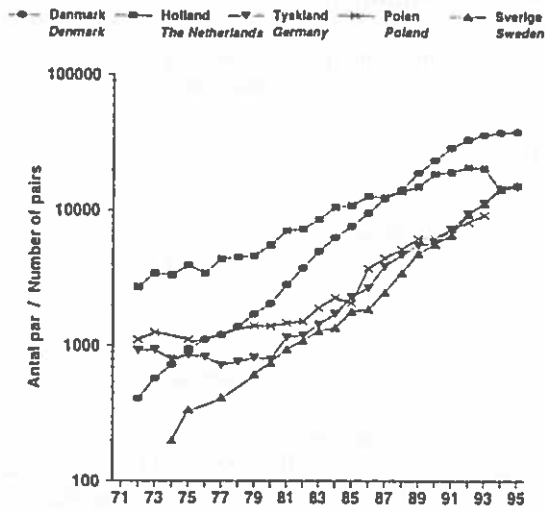
Fig. 1. Udviklingen af skarvbestanden i Holland, Danmark, Sverige, Polen og Tyskland i 1972-1995. Kilderne er angivet i teksten.
Population development of Cormorants in the Netherlands, Denmark, Sweden, Poland and Germany, 1972-1995. References are given under methods in the Danish text.

Diskussion

Den markante vækst, der har bragt den nord- og mellemeuropæiske bestand af Mellemskarv op på over 40% af verdensbestanden (del Hoyo et al. 1992, Rose & Scott 1994), var i hvert fald delvist forårsaget af aftagende bekæmpelse og fredninger. Skarven blev fredet i Holland i 1965 og i andre europæiske lande i 1970erne (Coomans de Ruiter

1966, Hansen 1984). I Danmark indstilledes beskydningerne af unger på Vorsø i 1971, og i 1977 udvidedes den generelle fredningstid fra maj, juni, juli til også at omfatte månederne marts og april. I 1980 blev Skarven totalfredet i Danmark, og i 1981 i alle landene i den Europæiske Union. Herved blev den nord- og vesteuropæiske skarvbestand beskyttet i mange af de lande, som benyttes uden for yngletiden (Gregersen 1982, van Eerden & Munsterman 1986, Bregnballe et al. i manus). Den lave vækst i Polen og i det tidligere DDR i 1970erne (Fig. 1) forklares med indgreb i kolonierne, bl.a. aflivning af et betydeligt antal unger (Osieck 1991, Lindell et al. 1995).

Medvirkende årsager til bestandsfremgangen kan have været forbedrede fødesøgningsmuligheder som følge af overfiskning af visse fiskearter og eutrofiering af kystområder og søer (Hald-Mortensen 1988, 1994, de Nie 1995, Suter 1995).

At den hollandske bestand voksede langsommere end den danske kan bl.a. tilskrives en lavere ungeproduktion i Holland (van Eerden & Gregersen 1995). I de to kolonier Oostvaardersplassen og Naardermeer registreredes mellem 0,6 og 2,5 (gennemsnit 1,3) unger pr yngleforsøg i årene 1982-87 (25-40 dage gamle unger; data fra van Eerden et al. 1991). I de samme år produceredes 1,6-2,0 (gennemsnit 1,8) flyvefærdige unger pr yngleforsøg i den danske skarvkoloni på Vorsø. For andre danske kolonier haves kun oplysninger om antallet af 20-40 dage gamle unger (dvs. 5-30 dage før de bliver flyvedygtige). I disse kolonier var der i gennemsnit 3,1 unger pr rede (excl. mis-

Tab. 2. Gennemsnitligt antal unger pr rede registreret under ringmærkning af 20-40 dage gamle skarvunger i seks danske og én hollandsk koloni. Baseret på 196-764 reder på Vorsø ($\bar{x}$=551), 62-458 reder i de andre danske kolonier ($\bar{x}$=196), og 72-150 reder i Oostvaardersplassen ($\bar{x}$=117). Kun oplysninger indsamlet mellem 13. maj og 20. juni er inkluderet. Pga. manglende data kan tallene ikke omregnes til ungeproduktion pr rede. Data fra Holland fra M. R. van Eerden (upubl.).
Average brood size of Cormorants recorded during ringing of 20-40 day old young in six Danish and one Dutch colony. Based on 196-764 nests in Vorsø ($\bar{x}$=551), 62-458 nests in the other Danish colonies ($\bar{x}$=196), and 72-150 nests in Oostvaardersplassen. Only data collected between 13 May and 23 June are included. Data do not permit a recalculation into breeding output per nest. Figures from the Netherlands from M. R. van Eerden (unpubl. data).

	1983	1984	1985	1986	1987	1988	1989	1990	1991
Danmark									
Vorsø	2,8	2,9	3,0	2,9	3,0	2,9	2,9	3,0	2,5
Brændegård	2,9	3,0	3,4	3,2	3,2	3,3	-	-	-
Toft Sø	-	3,0	3,1	3,4	3,1	3,6	3,5	3,5	3,2
Dyrefod	-	-	3,3	3,5	-	3,3	3,2	-	2,9
Mågeøerne	-	-	-	2,6	3,1	2,9	-	-	-
Fjandø	-	-	-	-	3,2	-	3,4	-	-
Holland									
Oostvaardersplassen	1,7	1,9	2,3	1,5	1,4	2,0	1,8	2,7	1,7

lykkede yngleforsøg), mod 1,9 unger (30-40 d) i Oostvaardersplassen i 1983-91 (Tab. 2). Ynglesuccesen er mere fluktuerende og gennemgående lavere i Holland, fordi hovedparten af fuglene er henvist til at fouragere i ferskvandssøen IJsselmeer. Skarvernes mulighed for at fange fisk i IJsselmeer falder markant i perioder med megen vind, fordi finkornet sediment opslemmes i vandet og reducerer sigtbarheden (van Eerden et al. 1991, Voslamber & van Eerden 1991).

Den påviste forskel i ungeproduktion mellem Danmark og Holland kan imidlertid kun delvist forklare den mere end dobbelt så høje vækstrate i Danmark. Et stort fødeudbud gennem en større del af året i Danmark end i Holland kan have bidraget til den højere vækstrate i Danmark. I 1980erne fodrede Vorsø-koloniens Skarver unger over en fem-måneders periode (Bregnballe & Gregersen upubl.), hvilket er længere end i de hollandske kolonier (Boudewijn & Dirksen 1995, M. R. van Eerden pers. medd.), og grundet den langvarige ynglesæson opfostrede nogle af de danske Skarver to kuld pr sæson (Gregersen 1982). Store sensommerforekomster af migrerende og stationære fisk i de danske farvande har givetvis også haft en positiv effekt på overlevelsen af juvenile danske Skarver. At danske farvande er et attraktivt fødesøgningsområde afspejles af sensommer- og efterårsgenmeldinger af Skarver fra Polen (Gromadzka 1986), Sverige (Larsson 1994), Tyskland (Heckenroth & Voncken 1970), Holland (M. R. van Eerden pers. medd.) og Tjekkiet (P. Musil pers. medd.).

Den begyndende stabilisering i ynglebestandene i Holland og Danmark skyldes tilsyneladende en kombination af (a) ændringer i forekomsten og tilgængeligheden af føde, der både påvirker ynglesuccesen og andelen af fugle, som yngler, og (b) manglende muligheder for at finde sikre ynglepladser (van Eerden & Zijlstra 1995, Bregnballe & Gregersen in press). Det sidstnævnte forhold forstærkes af, at legale og illegale tiltag i stigende grad prøver at forebygge dannelsen af nye kolonier (Bregnballe & Asbirk 1995). Årsagerne til den manglende fremgang i Tyskland, Sverige og Polen i de senere år er ukendte, men er sandsynligvis knyttet til fødeforholdene. På mange efterårs- og vinterrastepladser er Skarverne desuden udsat for en stigende grad af beskydning og bortskræmning (W. Suter, L. Marion & N. Baccetti pers. medd.). hvilket kan have mindsket fuglenes overlevelse eller muligheder for at opbygge fedtreserver for forårstrækket og ynglestarten.

Summary

Development of the North and Central European breeding population of Cormorant *Phalacrocorax carbo sinensis*, 1960-1995

The present paper reviews the expansion and recent change towards stabilization of the main populations of the Great Cormorant *Phalacrocorax carbo sinensis* in Europe.

Breeding numbers in Poland, Germany, the Netherlands, Sweden and Denmark were at their lowest in the early 1960s (3500-4300 breeding pairs). The populations then began to increase and reached a total number of about 4900 pairs in 1971, after the species had been protected in the Netherlands. Annual growth rates increased in the 1970s and averaged about 11% between 1971 and 1981, when the population had reached 13400 pairs (Tab. 1). By 1985 it had increased to 26000 pairs, and in 1995 there were 94700 pairs. Between 1981 and 1991 growth rates were as high as 18% per year but thereafter declined, from 17% in 1992 to c. 3% in 1994. The annual increase during the period 1971-91 was much higher in Denmark (26%) than in the Netherlands (11%) (Fig. 1). Recently the growth rate in Denmark has declined, from 36% in 1989 to 1.4% in 1995, and a crash in the Dutch Cormorant population in lake IJsselmeer occurred in 1994 (van Eerden & Zijlstra 1995). Breeding numbers increased rapidly in Sweden and Germany until 1994 (24% and 23% per year, respectively, during 1980-94), but in 1995 the growth was very slight (2% and 3%, respectively).

The proportion of the total population breeding in Denmark increased from 6% in 1971 to 42% in 1991 and varied between 40% and 42% thereafter. The proportion breeding in the Netherlands was 50-55% during the 1970s but subsequently declined to 16% in 1994. The proportion breeding in Sweden and Germany increased during the early 1990s so that each country held 16% of the population in 1994. Less than 15% bred in Poland during 1980-1995.

Immigration to former breeding areas has occurred during 1982-1992, with recent breeding numbers being: England (1100 pairs inland, 1995), France (950 pairs inland, 1995), Belgium (272 pairs, 1995), Italy (493 pairs, 1995), the former Czechoslovakia (690-710 pairs in 1991, 425-490 in 1995), Estonia (1390 pairs, 1994), Latvia (205 pairs, 1995), Lithuania (800-1000 pairs, 1995), Belarus (850 pairs, 1995), and Russia (1400 pairs, 1994). From the early 1960s till 1992, the number of known colonies increased from 15 to 176.

The lower growth rate in the Netherlands, compared with the Danish Cormorant population, was apparently caused by a lower production of young in the Netherlands (van Eerden & Gregersen 1995), see Tab. 2. The average production of fledged young in two major Dutch colonies was 1.3 per breeding attempt during 1982-87 (van Eerden et al. 1991), compared with 1.8 in the Danish Vorsø colony.

The tendency towards a stabilization of Cormorant populations in the Netherlands and Denmark in recent years appears to be related to a combination of (a) the amount
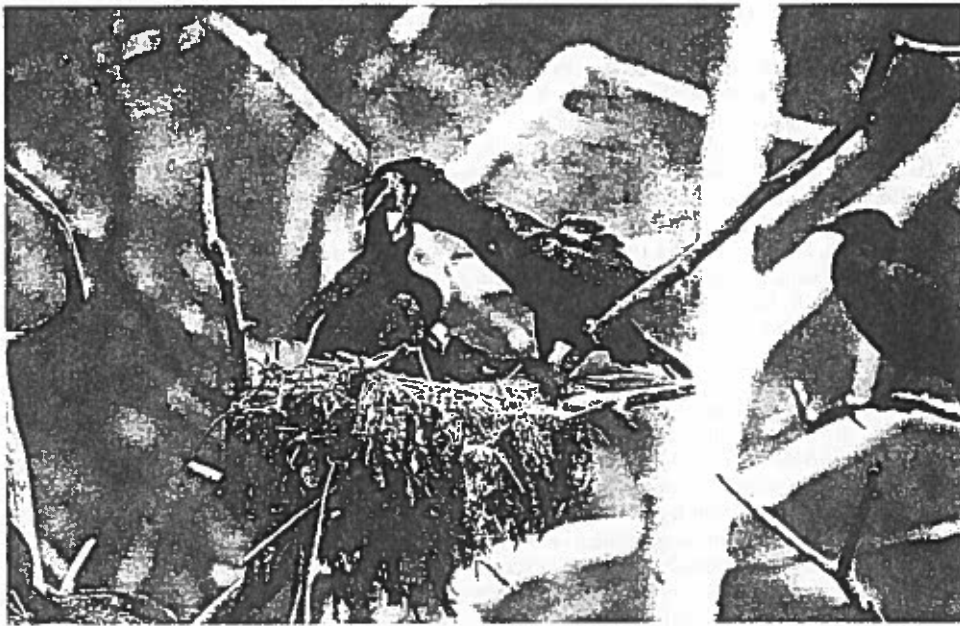
Foto: Morten Strange.

and availability of fish around the existing colonies, affecting the number of birds that breed and the breeding success, and (b) human interference and disturbance hampering the establishment of new colonies (Bregnballe & Asbirk 1995, Van Eerden & Zijlstra 1995, Bregnballe & Gregersen in press). The failing growth in Germany and Sweden in 1995 is unexplained but may have been caused by low food availability.

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Timing of migration and seasonal distribution of Cormorants *Phalacrocorax carbo sinensis* breeding in Denmark

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Timing of migration and seasonal distribution of Danish-breeding Cormorants *Phalacrocorax carbo sinensis*

by

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Summary

The recent expansion of the continental Cormorant *Phalacrocorax carbo sinensis* population has led to management conflict throughout Europe, hence it is important to identify migration patterns and distribution for different breeding populations. The timing of movements and distribution of Danish-breeding Cormorants outside the breeding season are presented here based upon recoveries and upon resightings of colour-ringed birds.

Birds disperse after breeding to coastal areas and freshwater lakes in the southwestern Baltic. From July and August onwards, they move slowly south, many stopping over in The Netherlands and Central Europe, reaching the Mediterranean mainly from October. Wintering occurs from the Baltic to North Africa; at least half the Danish population winters in the Mediterranean. In spring most birds migrate north in March.

Danish Cormorants dominate wintering populations in eastern Central Europe, in the central Mediterranean (Italy) and Tunisia, however, Dutch birds dominate over Danish birds along Atlantic coasts.

Introduction

The European breeding population of the Eurasian subspecies of the Cormorant *Phalacrocorax carbo sinensis* has its stronghold in Denmark, The Netherlands and along southern Baltic coasts.[1-3] In this region breeding numbers increased from ca 4900 pairs in 1971 to ca 94 640 pairs in 1995.[3] After the breeding season Cormorants disperse to shallow coastal areas, to estuaries, lagoons, freshwater lakes and to rivers over most of Europe including the coast of North Africa.[4,5] The increase in Cormorant numbers in these habitats[6-8] have led to intensified conflict between conservational and fishery interests, the latter demanding control of Cormorant numbers at breeding as well as staging sites. How control measurements will affect the development of breeding populations and how measures taken in breeding colonies to control numbers will affect the occurrence of Cormorants at staging and wintering sites will depend largely on how each country's breeding population migrates.

Earlier information on distribution of recoveries[5,9-11] showed that Danish-breeding birds disperse widely, but concentrate in central Europe and the central Mediterranean. Since then many more recoveries have been received and a large number of colour-ringed individuals have been resighted on staging sites. These recoveries and resightings are used in this paper to i) identify the areas of importance for Danish Cormorants, ii) describe timing of migration and seasonal use of regions. The temporal variation in recoveries and resightings is related to published data on seasonal changes in numbers counted. From this the function of areas in the birds' annual cycle is discussed. We further discuss where in Europe Danish birds are likely to dominate over Cormorants from other breeding areas.

Material and methods

Of 19 963 Cormorant nestlings ringed in Denmark between 1946 and 1994, 229 were ringed 1946-1950, 109 in 1967 and 19 625 during 1972-1994. Between 1977 and 1994, 17 513 nestlings were also fitted with a coloured plastic leg ring bearing a three character code. Most young (57.4%) were ringed at the Vorsø colony (55°56'N 10°01'E) and the remaining 42.6% were ringed at 11 other colonies (Fig. 1; see also Bregnballe & Gregersen[12]).

To describe the dispersal of Danish Cormorants in Europe and North Africa we used 3326 recoveries of Cormorants reported as found dead before 31 December 1994. We here use the term 'recoveries' to refer only to Cormorants found dead.

The description of timing of occurrence is based upon the temporal distribution of recoveries and resightings of colour-ringed individuals in staging areas. In analysing the recoveries, we excluded young which died before leaving the colony, and recoveries where finding details were uncertain, only the ring was found, or the bird was recorded as long dead, leaving 2279 recoveries. 'First year birds' are defined as birds recovered up to 1 year and 20 days after ringing date, i.e. when one year of fledging.
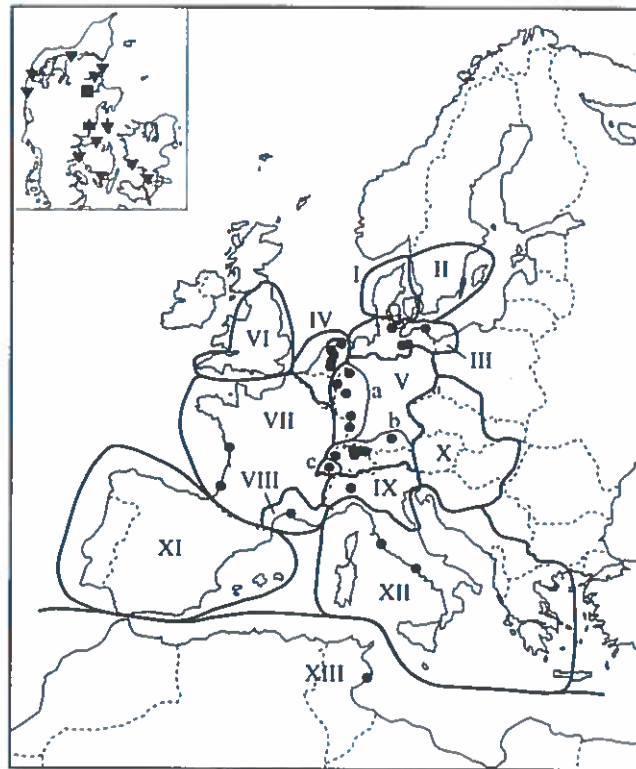
Colour-ring codes were identified by observ-

Figure 1. Boundaries of regions and location of sites (filled circles) where between 21 and 351 different individuals have been resighted. The small map shows locations of ringing sites (triangles; the star denotes Vorsø) and of the roost Fussing Sø (square). Areas a, b (both shaded) and c in region V refer to Fig. 4.

ers searching for individually marked birds at roosts in central, western, and, to a small extent, southern Europe. The resighting analyses were based on 16 769 resightings of 4735 individuals seen outside of Denmark between 1 June 1977 and 31 December 1993, the majority between 1985/86-1989/90.[13] The numbers of different individuals resighted is presented along with numbers of observation days per 10-day period or month. We did not use the number of individuals seen per observation day, because the number of new individuals resighted per observation day declined after a variable number of extra observation days depending on area and time of year. Numbers of observation days were defined as numbers of dates on which attempts to find and read rings resulted in reading the ring of at least one bird. To avoid pseudo-replications, individuals seen in the same period over two or more years counted only once.

Provinces defined by the European Union of Bird Ringing (EURING) were lumped into 13 regions (Fig. 1, Appendix I). Seasonal variation

in numbers of ringed individuals resighted is described for six of these regions (III-V, VII-IX). In region V phenology differed between the Rhine, Lac Léman and other Swiss lakes, so these areas are treated separately (a-c in Appendix I and Fig. 1).

Departure and arrival at Danish colonies are described using data from the Vorsø colony (Fig. 1), where night-roosting individuals were counted on one to five evenings per five-day-period between 1982 and 1994. Counts of numbers night roosting at Fussing Sø were used to describe occurrence at a Danish post-breeding site.

Results

Overall dispersal and timing of movements

The Cormorants dispersed widely outside the breeding season, occurring from France, Portugal and Morocco in the west to the Danube delta, Greece and Libya in the east (Fig. 2). Between August and April, 84.2% of 2537 birds recovered were found in Denmark, Sweden, northern Germany, The Netherlands, the Alpine lakes, the Po area, Mediterranean France, and along the coast of Tunisia and eastern Algeria (Fig. 2). Overall, in autumn and winter the Atlantic regions (England, west and central France
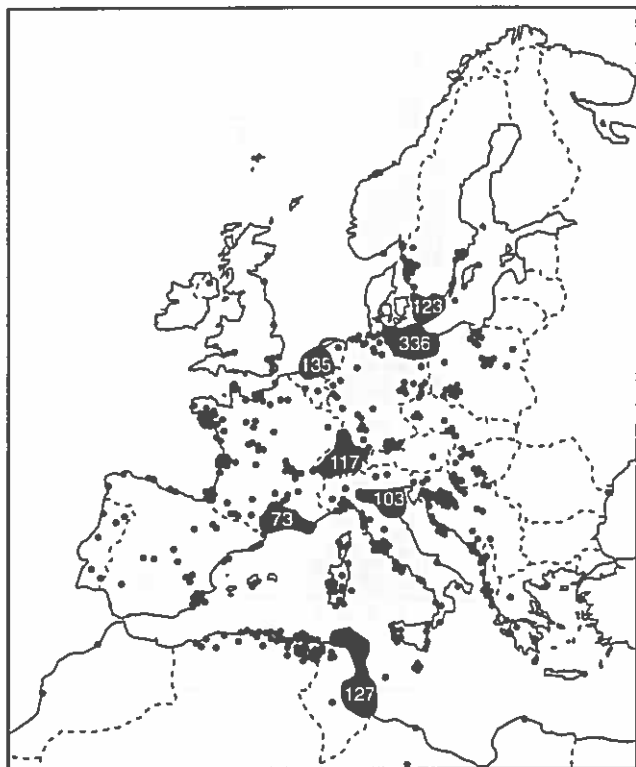

Figure 2. Distribution of recoveries of Danish-ringed Cormorants found dead outside Denmark.

and the Iberian Peninsula) were used by fewer birds than were the more central parts of Europe: 7.6% of all September - February recoveries in the Atlantic regions versus 37.2% recovered in Germany, Benelux, Switzerland, Mediterranean France and northern Italy (n=1731). The major wintering areas were the central Mediterranean and the coast of North Africa (Table 1).

After breeding and fledging Danish-ringed Cormorants dispersed to Danish waters and to coasts and freshwater lakes in southern Sweden, northern Germany and north-western Poland (Figs 3, 4); a few individuals moved to coasts and lakes in eastern Poland (Fig. 2). In August larger numbers began to depart from the Baltic and departure continued into early November, with a small proportion remaining to winter (Fig. 3). In northern Germany and The Netherlands most individuals staged in September, whereas at the Rhine and the Alpine lakes, main passage took place between early October and early November (Fig. 4). Wintering areas in France and the Mediterranean were reached mainly mid October - mid December with latest arrivals in North Africa (Figs 3, 5, 6). Some birds

Table 1. Regional distribution of recoveries in mid-winter (Dec-Jan) given as the percentage (%) of all winter recoveries of Danish Great Cormorants (n= 371).

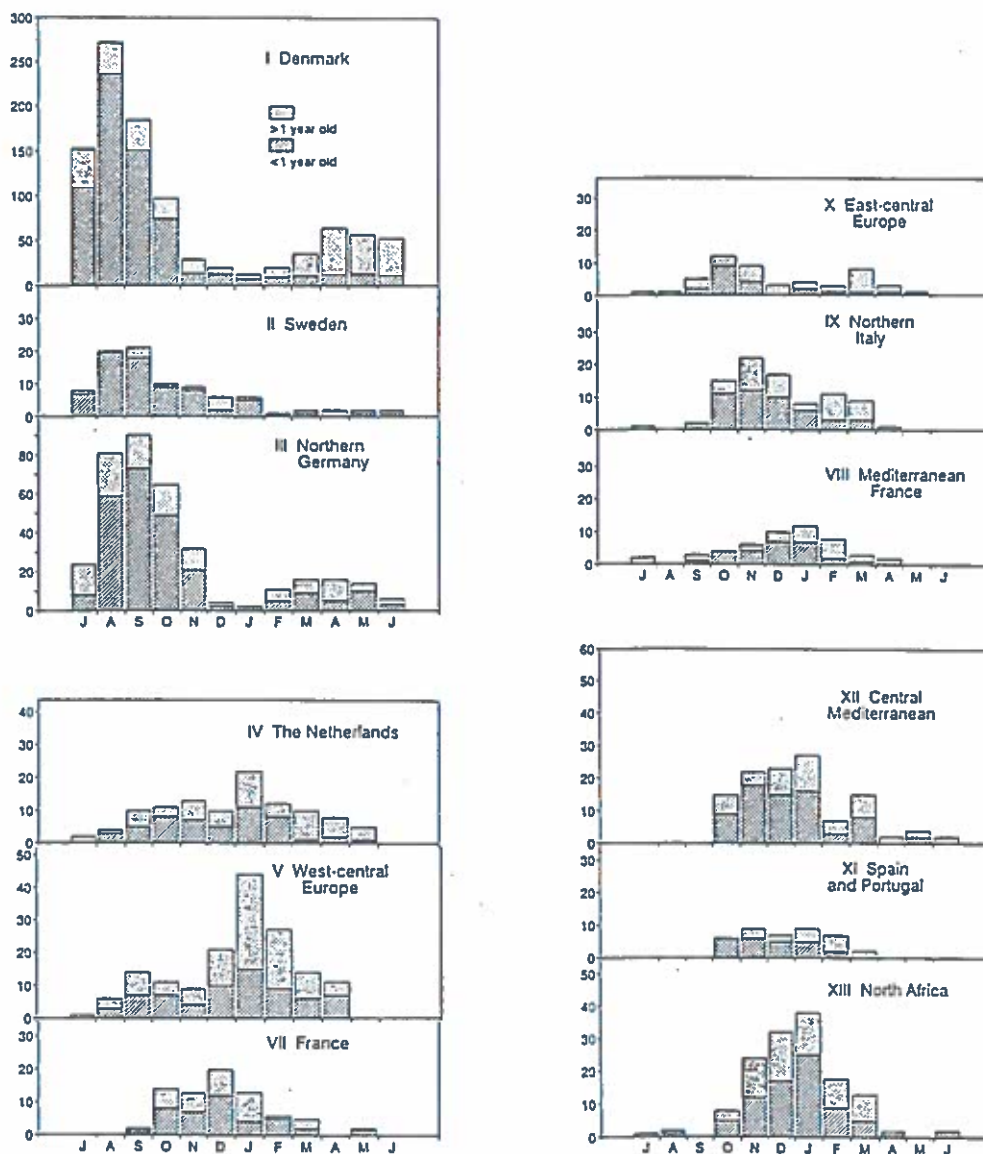| Region		% recovered Dec-Jan
I-III	Denmark and Baltic Sea	13.7
IV	Benelux	8.6
V	Central Europe	17.5
VII	West and central France	8.9
VIII	Mediterranean France	5.9
IX	Northern Italy	6.7
X	East-central Europe	1.9
XI	Portugal and Spain	4.3
XII	Central Mediterranean	13.5
XIII	North Africa	18.9

Figure 3. Temporal distribution of Danish Cormorants found dead in their first year of life (hatched) or later (shaded) by month in 12 of the regions shown in Fig. 1. Note that the ordinates are drawn to different scales.

left their wintering area in late winter, but many were still present in the Mediterranean in February and first half of March.

Occurrence in regions
Autumn - winter
Breeding birds arrived at Vorsø in small numbers in January - February, with the majority arriving 10 March - 10 April (Fig. 7). Most adults and juveniles left the colony mid July - mid August, but some remained in the local area (Fig. 7). At the post-breeding roost Fussing Sø numbers increased from July and declined between mid September and mid October (Fig. 8).

In north German freshwater lakes colour-ringed Cormorants occurred in highest numbers 10 August - 10 October with a peak 1-20 September, and few were resighted after 10 November (Fig. 4). In mid-winter some birds were recovered in the Baltic area, mainly in Denmark (Fig. 3).

The first birds arrived in The Netherlands in July - August, but most individuals stopped over 1 September - 20 October (Fig. 4). Numbers resighted at the Alpine lake Lac Léman increased sharply between 20 September and 10 October and many different individuals were resighted till late November (Fig. 4). Compared
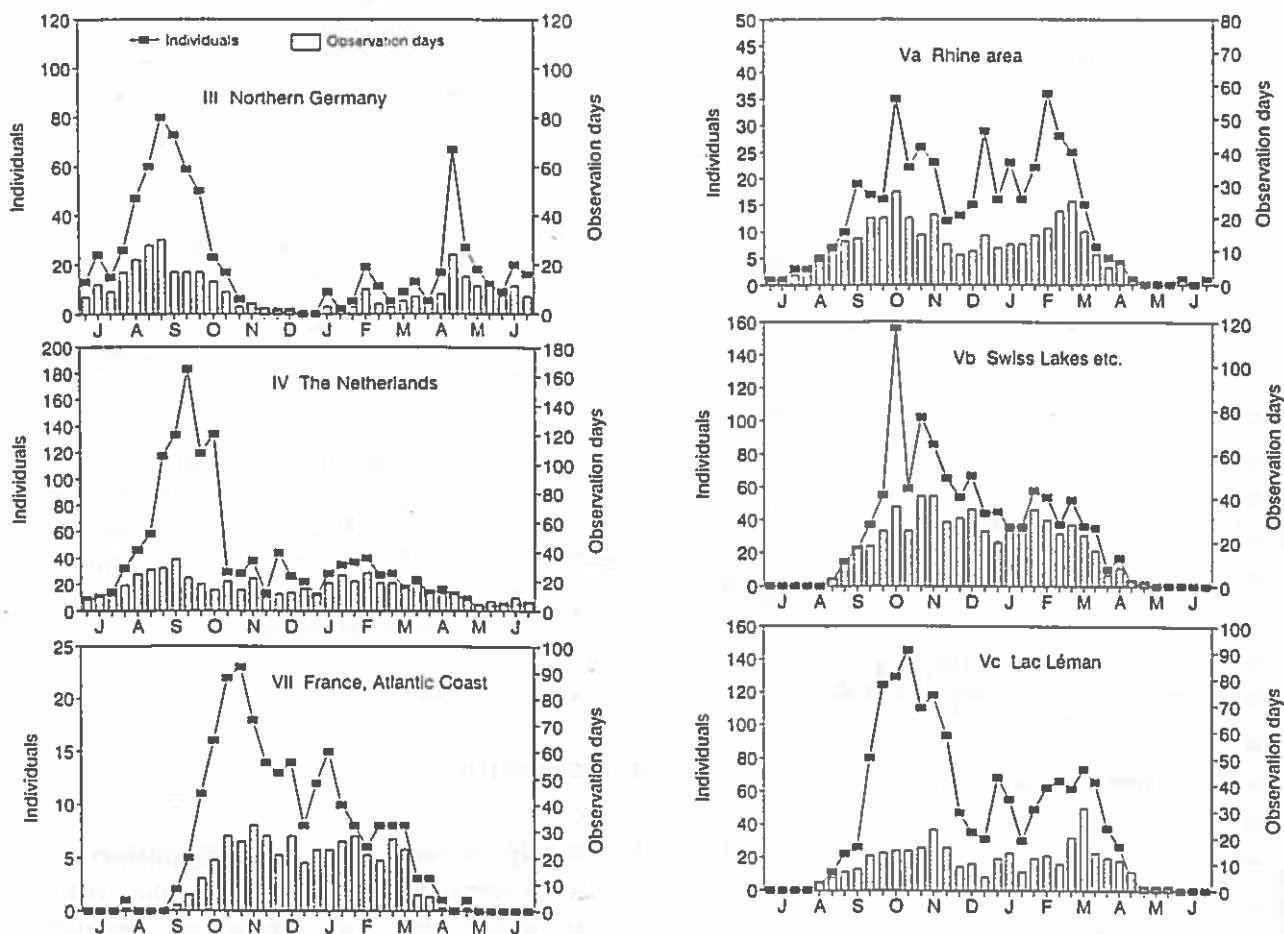
Figure 4. Numbers of individuals resighted and observation days per 10-day period in northern Germany, The Netherlands, western France, and in the Rhine area, the Swiss lakes, and Lac Léman. Ordinates are not drawn to the same scale.

with Lac Léman, arrival at the central and eastern Alpine lakes occurred 10-20 days later and numbers resighted declined slightly earlier, between mid October and late November (Fig. 4). Danish birds were present along the Rhine throughout autumn and winter (Fig. 4). A relatively large number of birds were recovered in Central Europe in mid-winter (Fig. 3, Table 1).

Eight recoveries and 81 resightings of 27 individuals showed main arrival to southern England October - November. Major arrival to coastal and inland France took place in October (Figs 3, 4). In Spain and Portugal presence was recorded from October till March (Fig. 3 and 23 resightings).

Both recoveries and resightings peaked in Camargue and the Rhône Valley during winter-early spring (Fig. 3, 5). Recoveries from northern Italy indicates passage of Danish birds October -

December (Fig. 3). Resightings at Orbetello (130 km north-east of Rome) and at a few other places along the Tyrrhenian coast showed arrival and stop-over October - November with some birds staying for the winter (Fig. 5). In East-central Europe, Danish birds were recovered from early September onwards (most October - November). Arrival in Tunisia and Algeria occurred between mid October and mid December (Fig. 3).

Spring

Fig. 3 suggests that some Cormorants had already left North Africa by January. The high number of individuals resighted in northern Italy in February and March (Fig. 5) suggests arrival and stop-over of birds which had spend the winter further south; peak in numbers resighted occurred during the first 10 days of
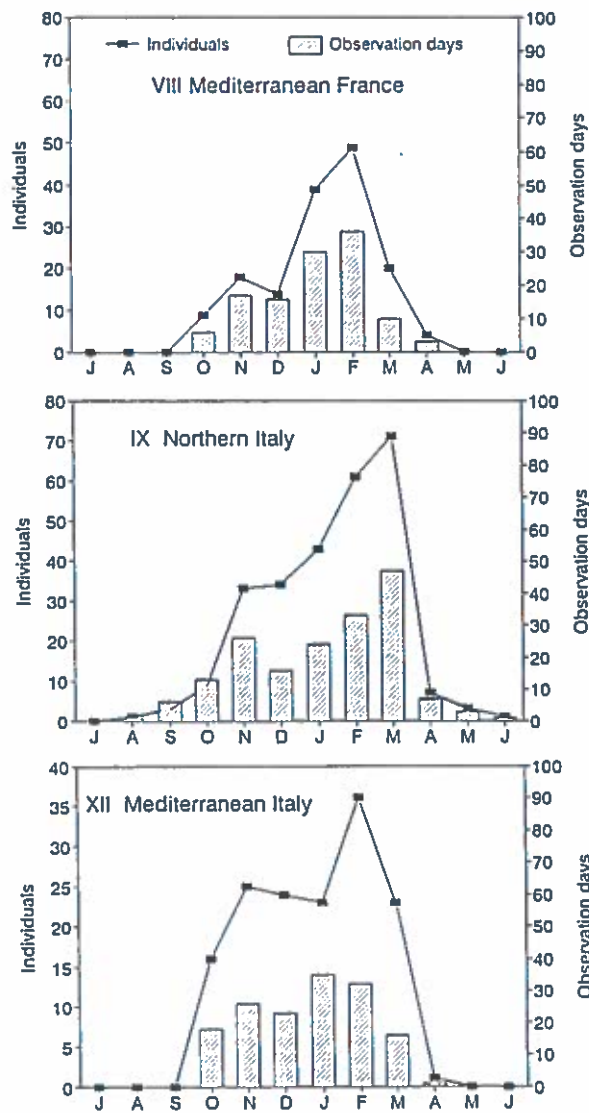
95

Figure 5. Numbers of individuals resighted and observation days per month in Mediterranean France, northern Italy, and Mediterranean Italy.

March. Spring migrating birds stopped over in Alpine lakes February - March (Fig. 4). In East-central Europe spring passage occurred seemingly 10 March - 20 April (Fig. 3), i.e. later than in West and Central Europe. Due to emigration to northern German colonies, many colour-ringed individuals were seen here in late spring.
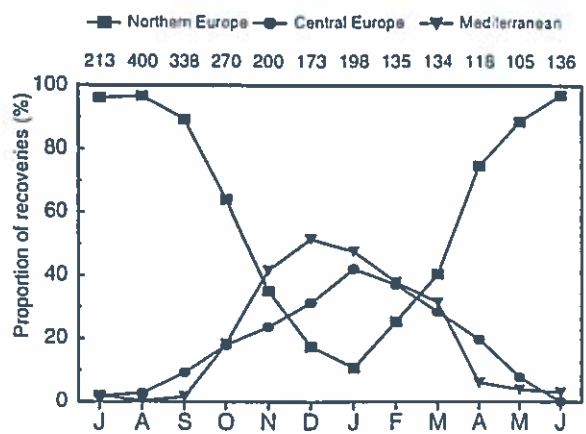

Figure 6. Seasonal distribution of Danish Cormorants recovered in northern Europe (regions I-III), central Europe (regions IV-VII, X) and in the Mediterranean (regions VIII, IX, XI-XIII) in percent of all Cormorants found dead per month, except those long dead. Monthly total of recoveries are given.

Discussion

Uncertainties with interpreting patterns

For some regions, analysis of seasonal changes in numbers of resighted individuals is possible only for a few sites, and patterns at these sites are not necessarily representative of overall occurrence in a region. For example, in France seasonal changes in Cormorant numbers differ between coastal and inland areas and between inland sites as well as between sites along the coast.[14] However, compared with recoveries and counts of numbers, resightings can more precisely unveil the time of passage of birds, and the extent of use of areas over the year.

Mortality and recovery rates are likely to vary with season and between areas and, therefore, spatio-temporal variation in occurrence of recoveries can easily be misinterpreted. The increases in numbers of recoveries of Cormorants in Swiss lakes and The Netherlands in January are likely to reflect an increase in mortality, not an increase in numbers present. Thus, both the pattern of resightings and counts of numbers of Cormorants do not indicate an increase in the use of these areas in January (Fig. 4 and Suter[15]).
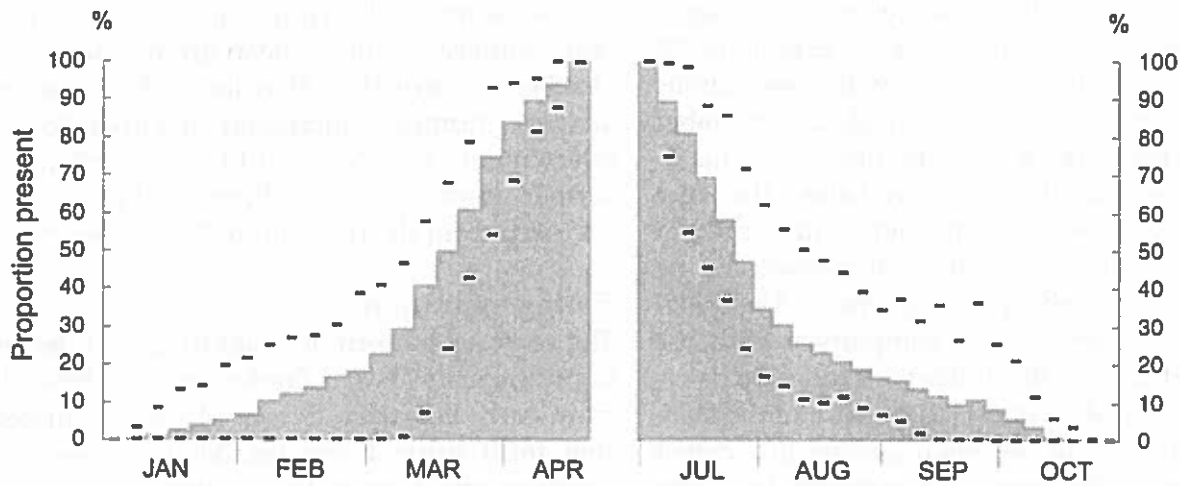
Figure 7. Average and range of arrival and departure recorded in the Vorsø colony 1982-94, presented as the percentage of maximum numbers counted 16-20 April and 30 June - 4 July, respectively. Annual maximum ranged from 1932 to 2854 individuals in spring and from 1820 to 3442 individuals in autumn.

The proportion wintering in North Africa may have been underestimated because mortality and recovery rates are likely to have been lower in North Africa than in Western Europe. Nevertheless, the proportion of Danish Cormorants recovered in southern Europe and North Africa in December-January is similar to the estimate of van Eerden & Munsterman[16] based on actual numbers: 51% vs. 47%. The proportion wintering in the Mediterranean is likely to increase in cold winters, where ice cover can push Cormorants further to the south[17,18] especially first year birds, and to a lesser extent, females.[16,17]

Figure 8. Seasonal change in numbers of Cormorants roosting at Fussing Sø 1988-1990. Of 847 colour-ringed individuals observed at the roost, 502 originated from the Vorsø colony.

Autumn - winter: areas of importance and seasonal occurrence

After breeding, coastal waters and freshwater lakes in Denmark, Sweden and Germany constitute very important feeding areas for Danish, Swedish, German and Polish Cormorants (this study,[19-22]). For Danish Cormorants the inner Danish waters are of greatest importance along with lakes and coastal sites in northern Germany. For Sweden the seasonal pattern of recoveries of Danish Cormorants is in accordance with changes in numbers present: an increase from the second half of July to a peak in August or September and a decline till late October.[23-25] Counts at German roosts have indicated a change in phenology with increasing population size. In 1984 and 1985 Danish birds arrived to Großer Plöner See and Selenter See between July and September, and numbers declined abruptly in late October.[26,27] The pattern had changed in 1992: in Großer Plöner See and Heidensee peak numbers occurred in late August and main departures had already occurred by late September.[28] A similar shift in peaks and departures occurred along the Baltic coast, where Menke[26,27] in 1984 and 1985 recorded an increase in numbers from August onwards and a peak in October, whereas in 1992 the peak of 40,000 occurred late summer.[28]
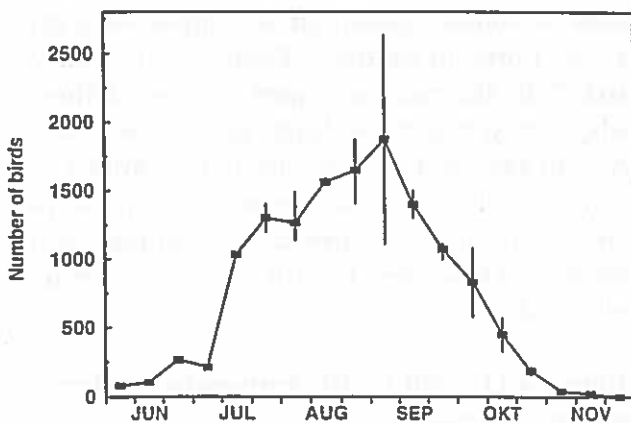
Lakes, rivers and coastal areas in The Netherlands are, along with the Alpine and southern German lakes, the most important autumn stop

over areas for Danish Cormorants. Stopover of Danish Cormorants in The Netherlands August - October with main passage 1 September-20 October (Fig. 4) corresponds with observations of direct migration, which peak in September and October (K. Koffijberg pers. comm.). In France, peak numbers occurred along the Loire river in October,[14] but further to the south, at Marais d'Olonne, numbers increased during October - December peaking between December and early March.[29,30] A comparison with the seasonal change in numbers of individuals resighted (Fig. 4) suggests that many of the Danish birds seen at Marais d'Olonne in October and November were on passage (see also Yésou[30]). In southwestern France and northern Spain, Campos & Lekuona[31] recorded high numbers during the whole period October - March with small peaks in October and February. Hence, overall, Cormorants taking western routes migrate mainly in October, but movements occur from August through December.

The occurrence of colour-ringed Danish Cormorants in the Alpine lakes is similar to the seasonal change in numbers present (maxima in October and November;[32-36]), but the high autumn peak in numbers of individuals resighted suggests that very large numbers of birds spend time at the lakes before migrating over the Alps. Repeated resightings show that some Danish Cormorants migrated southwest to The Netherlands and followed the Rhine to the Alpine lakes, whereas others migrated there directly south over Germany (Bregnballe & Gregersen unpubl.). After several years of increase, Cormorant numbers in the Alpine lakes have recently stabilized,[6,34] with presumably an increasing proportion of late arriving birds now moving on to more southerly areas, after only short stops north of the Alps.

Resightings and recoveries suggest arrival in the northern Mediterranean October - December (Figs 3, 5) corresponding to counts showing arrival to the northern part of Italy from October or early November until early December.[17,18,37,38] The absence of clear autumn peaks in numbers resighted (Fig. 5) and numbers counted in the upper Po, the Po delta and the lagoon of Venice[17,18,37,38] may suggest that many autumn migrating Cormorants pass northern Italy without stopping. Numbers are usually lower here in winter than in autumn and spring, especially in cold winters.[17,18] Wintering areas in central and southern Mediterranean are reached from October onwards (Fig. 3) as shown by counts in Toscana: numbers increased at Orbetello between mid October and mid December;[39] while further south, at Laghi Pontini, the increase occurred from the first half of November.[40]

Spring migration

The seasonal pattern of resightings and declining numbers at Laghi Pontini and at Orbetello from early February to late March[39,40] suggest that most birds leave the Mediterranean in February and March. This contrasts somewhat with information presented by van Eerden & Munsterman,[5] who suggested that large numbers of Cormorants were present in Tunisia until late March and that main departures from Sardinia took place in late March - early April. However, the spring peak at the Venice lagoon[17,18] and upper Po[38] points towards a main passage in the first half of March. From counts and resightings, it seems that the northern Mediterranean is used more extensively in spring, before passage over the Alps, than in autumn.

In Central Europe absolute numbers decline during March,[34-36] confirming the decline in numbers of individuals resighted after late March (Fig. 6). In the Ulm area, upper Danube, a small but distinct peak in spring passage was observed in late March.[41]

Departures from the Atlantic regions seemed to start in January with major movements in February and March.[31,42,43] At the Marais d'Olonne, Danish birds stopped over on the way north in January, February and early March.[44] In the northern part of The Netherlands, spring migrating birds were mostly observed in March (K. Koffijberg pers. comm.).

To conclude, some Cormorants move to more northern areas already in January and especially in February, but the majority migrate north in March.

Where do Danish birds dominate wintering populations?

Recoveries and resightings indicate a tendency towards segregation between birds breeding in the western part of the breeding range (The Netherlands, west Denmark), the central part

(the rest of Denmark, northwest Germany) and the eastern part (Sweden, east Germany, Poland).[4,5,10,16,23,45,46] However, large proportions of birds from all breeding populations are present in the central parts of the Mediterranean in winter.[5,19,21,22] The proportion of the north-central European population of *P. c. sinensis* breeding in Denmark increased during the 1980s, from 21% in 1981 to 41-43% in 1991-1995.[3] Hence, Cormorants of Danish origin are likely to have come to dominate staging and wintering populations in some areas since the mid 1980s.

Numbers wintering in Denmark and the Baltic Sea have increased since the 1970s: 14 697 individuals were counted during an aerial survey in 1993[47] compared with 888 in 1968; the last mentioned count covered the major wintering area, only, i.e. the Danish waters.[47] Norwegian Cormorants of the North Atlantic subspecies *P. c. carbo* used to dominate this winter population.[48] However, the higher rate of growth of the breeding population of *P. c. sinensis*[1-3,49] than of Norwegian *carbo*[50] suggests that Danish *sinensis* birds have made up an increasing proportion of this wintering population. The Dutch winter population (10 610 counted in January 1993[51]) is likely to be dominated by Dutch and not Danish birds (cf. Fig. 3). Kirby et al.[52] suggested that a few thousand continental *sinensis* winter in Britain dominated by Dutch, not Danish, birds.[7] The French national census in January 1992 produced about 66 000 Cormorants,[7] with Danish birds comprising slightly more than 10% of the foreign Cormorants (based on resightings and recoveries;[7]). In Spain and Portugal fewer Danish than Dutch birds occur ([5] and data given in[31] corrected for proportions ringed).

In the Swiss lakes resightings of 634 colour-ringed individuals during 1977/78-1987/88[46] gave recovery rates (number of recoveries/number of ringed X 100) of 4.8% from Denmark, 3.7% for The Netherlands, 2.9% from north-east Germany and 2.0% from Sweden. The proportion of Danish birds increased from west to east Switzerland,[46] and further east, at Ismaninger-Speichersee in southern Germany, only one Dutch but 87 Danish Cormorants were reported.[34]

Resightings and comparisons of maps with distributions of recoveries (Fig. 2, [5,19,21,22]) indicate that Danish birds mix with Dutch, German,

Swedish and Polish Cormorants in north-east Italy and along rivers and coasts in the former Yugoslavia, Albania and Greece. Danish birds seem to dominate over Dutch birds in these areas.[5] Cormorants from all breeding populations in North-central Europe, including Poland, winter in Tunisia,[5,19,21,22,53] but Danish birds are likely to dominate both because of the large population and because they make extensive use of the staging areas directly north of Tunisia.

Acknowledgements

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Appendix I

The 13 regions are defined as follows:

I *Denmark.*

II *Sweden.* The area south of Uppsala, Västmanland and Värmland.

III *Northern Germany.* Schleswig-Holstein, Mecklenburg-Vorpommern, Szczecin, Lüneburg, Bremen & Stade, and Aurich & Oldenburg. Main resighting localities are Selenter See, Gr. Plöner See, Hemmelmarker See, Heidensee, Culpinersee, Wittensee, Insel Tollow, and northwest Poland.

IV *Benelux.* All resightings are from The Netherlands with most resightings and recoveries from Lake IJsselmeer and the adjacent lakes, the rivers Rhine and Waal, and the Delta area.

V *Central Europe.* Germany (except III), Switzerland, west Austria (Voralberg), and north-east France (Bas Rhin, Haut-Rhin and Belfort). The three resighting areas are: (a) the Rhine area, including the German federal states Nordrhein-Westphalen, Rheinland-Pfalz, Hessen, Baden-Württemberg; (b) lakes in Switzerland (except Lac Léman) and neighbouring countries, including the Austrian province Vorarlberg and the German federal state Bayern; (c) Lac Léman, including the EURING province 'Fribourg, Vaud' in Switzerland.

VI *England.*

VII *West and central France.* All provinces in France except those included in the regions V and VIII. We use resightings from the EURING region 'Atlantic Coast' where most resightings were made at Marais d'Olonne and Bassin d'Arcachon.

VIII *Mediterranean France.* The EURING region 'Mediterranean' and the provinces Drôme and Ardéche. Most resightings are from Camargue and Rhône.

IX *Northern Italy.* The EURING regions 'Alpine Area', 'North Adriatic', and 'Po Area' with most resightings from Oldenico.

X *East-central Europe.* Wroclaw in south-west Poland, Czech Republic, eastern Austria, Hungary, Vojvodina, and Slovenia and Croatia (except coast).

XI *Portugal and Spain.*

XII *Central Mediterranean.* The region includes Italy (except IX), Corsica, the coast of Croatia and Slovenia, Bosnia-Hercegovina, Montenegro, Macedonia, Albania and Greece. The resighting area includes the EURING regions 'North Tyrrhenian' and 'South Tyrrhenian', the main sites being Orbetello and Lago Caprolace.

XIII *North Africa.*

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