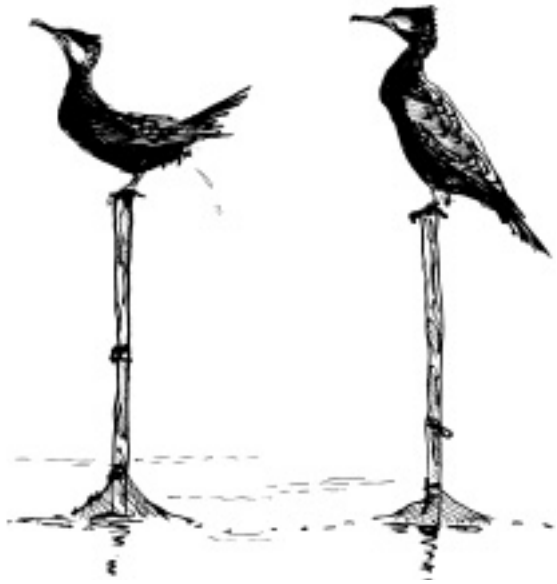
Post-breeding dispersal of Great Cormorants *Phalacrocorax carbo sinensis* from Danish breeding colonies



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(Med et dansk resumé: Danske Skarvers spredning efter yngletiden)

Introduction

Some species of birds migrate long distances soon after breeding, whereas others disperse in many directions or to specific nearby areas before initiating the actual migration. Several strategies seem to exist among and within species of the family Phalacrocoracidae (Coulson & Brazendale 1968, Galbraith et al. 1981, Galbraith et al. 1986, Furness & Monaghan 1987, Summers & Laing 1991, del Hoyo et al. 1992, Koshelev et al. 1997). The bulk of the European population of the continental subspecies of the Great Cormorant *Phalacrocorax carbo sinensis* is known to migrate 800-2500 km south in autumn to reach wintering areas along the Atlantic coast, in the Mediterranean and in central Europe (Siefke & Berger 1979, Nilsson 1980, van Eerden & Munsterman 1986, 1995, Larsson 1994, Bregnballe et al. 1997). However, little has been published about the movements of this subspecies immediately after breeding, at a time of the year when Great Cormorants are in conflict with fisheries in several parts of Europe (e.g. Zimmermann & Rutschke 1991, van Eerden & van Rijn 1997, Keller et al. 1996, Drobrowolski & Dejtrowski 1997, Bildsøe et al. 1998).

Like most seabirds, young cormorants often fledge in a condition that enables them to subsist on internal nutrient and fat reserves if they are unsuccessful in covering their daily demands immediately after fledging (own unpubl. data). Nonetheless, the survival of the young birds is likely to depend on their ability to locate good feeding areas during post-fledging. Likewise, the parents' ability to recover from the demands of breeding and put on reserves before the autumn migration probably depends on successful localisation of profitable feeding areas after breeding.

The distribution of areas rich in food is not the only factor likely to influence the distribution of cormorants during post-breeding. The birds may be genetically predetermined to disperse in a certain direction, and the routes followed during dispersal may be influenced by the connectivity of water bodies, the location of wintering areas and other factors.

Population control of colonies has been suggested and attempted as a management tool to reduce conflict between cormorants and fisheries (e.g. Bédard et al. 1995), but the success will depend on the relationship between geographical

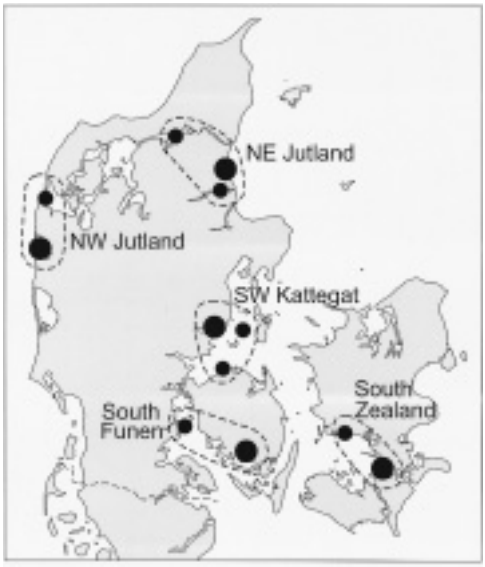


Fig. 1. Colonies and ringing regions. A large circle denote the colony where most Cormorants within each region were ringed (see Table 1).
De 12 mærkningskolonier og de fem ringmærkningsregioner. En stor cirkel angiver kolonien i den pågældende region, hvor flest unger blev ringmærket.

origin and distribution of the birds causing conflict. For example, cormorants may appear in large numbers in an area because it is situated along a migration route followed by the majority of cormorants from a few controlable colonies. However, cormorant numbers could also be high because individuals from a range of breeding areas concentrate in the same areas (e.g. Lewis 1937, Kozakiewicz et al. 1997).

Ringing studies can provide some of the information needed to understand how cormorants distribute themselves during post-breeding. In the present paper, we analyse approximately 1200 recoveries of cormorants ringed in 12 breeding colonies in Denmark in order to describe their post-breeding distribution in Danish and western Baltic waters. We also address the following questions:

I) Do Danish Cormorants disperse to food-rich areas prior to autumn migration?

II) Are Danish Cormorants attracted to certain areas, irrespective of the location of their colony?

III) Do areas of open sea or land masses constitute barriers for dispersal?

Material and methods

This study is based on 1217 recoveries from 17970 Great Cormorants (hereafter referred to as Cormorants) ringed as chicks in Denmark during 1972-91. Most chicks (>90%) were ringed between 15 May and 20 June at the age of 20-43 days. To study variation between colonies in the birds' dispersal patterns, we divided Denmark into five ringing regions (Fig. 1). In the 1970s ringing took place only in the Vorsø colony (22% ringed in the 1970s). In all ringing regions the majority of birds were ringed in the second half of the 1980s (Table 1). To avoid the effect of an unequal ringing effort after 1991 (ringing continued only in NW Jutland and SW Kattegat) and a change in the pattern of post-breeding dispersal during the 1990s, we excluded recoveries of birds ringed after 1991.

We considered recoveries from Denmark, South Sweden, NE Germany and NW Poland. To study the degree of overlap in the distribution of birds from different colonies and to explore whether certain areas had an overabundance of recoveries, the region was divided into 19 sub-areas (Fig. 5a). The sub-areas in NE Germany and NW Poland followed the borders of the EURING provinces Schwerin (sub-area no. 13 in Fig. 5a), Rostock (no. 14), Neubrandenburg (no. 15) and Szczecin (no. 16). All other sub-areas were defined as shown by the straight lines in Fig. 5a.

The analyses were based on recoveries of birds shot, found dead or drowned between July and November, 1972-1997, excluding those recovered inside breeding colonies and those where the finding details were uncertain. The recoveries from inside colonies were excluded to avoid inclusion of birds that had died before fledging and to avoid effects of variation among colonies in the timing and effort invested in finding dead birds with rings. Recoveries of first-year birds (i.e. birds recovered in their first autumn) were treated separately from recoveries of birds older than one year.

All older birds were assumed to be affiliated to a colony within the region where they had been ringed although some may have settled and bred in colonies located outside their natal region (Bregnballe & Gregersen 1995). We could not identify such individuals and assume that any bias introduced by emigration on the relationship between geographical origin and post-breeding distribution was minor.

The overlap in distribution of birds from different ringing regions was expressed by proportional similarity (Hurlbert 1978):

Table 1. Number of Cormorant young ringed within five ringing regions in Denmark (years with ringing in parentheses), and number of Cormorants recovered in their first year or as older birds in the main post-breeding area, July-November 1972-1997.
Antal skarvunger ringmærket i kolonierne i de fem mærkningsregioner i Danmark, og antal genmeldt som unge (i deres første efterår) hhv. som voksne i Danmark, Sydsverige og NØ-Tyskland, juli-november, 1972-1997.

Ringing region *Ringmærkningsregion* Colony (ringing period) *Koloni (mærkningsår)*	Numbers ringed *Antal ringmærket*	*Antal genmeldt* Numbers recovered First-year *Unge*	 Older *Voksne*
NW Jutland *NV-Jylland*		47	4
Fjandø (1986-91)	357		
Rønland Sandø (1990-91)	196		
NE Jutland *NØ-Jylland*		70	22
Toft Sø (1983-91)	1631		
Havnø (1984)	73		
Rønholm (1988-89)	101		
SW Kattegat *SV-Kattegat*		533	181
Vorsø (1972-91)	9749		
Måge øerne (1985-88)	736		
Svanegrunden (1987-90)	144		
South Funen *Sydfyn*		197	61
Brændegård (1980-88)	2969		
Bastholm (1987-88)	159		
South Zealand *Sydsjælland*		76	26
Ormø (1983-86)	446		
Dyrefod (1985-91)	1429		

$$O_{jk} = 1 - {}^1/_2 \sum |p_{ij} - p_{ik}|$$

where p_{ij} and p_{ik} is the relative abundance in subarea *i* of recoveries from the *j*th and *k*th ringing region, respectively.

Results

Timing, distance and direction of dispersal

In July-September the vast majority of birds were recovered in lakes and along coasts in Denmark, South Sweden and NE Germany (96% of the recoveries of first-year birds, n=791, and 81% of the recoveries of older birds, n=293). By November these proportions had declined to 38% (n=139) and 32% (n=111), respectively.

A large proportion of the Cormorants recovered in July were found within 60 km from the colonies (see Fig. 2 for the SW Kattegat colonies). This proportion had declined in August (Fig. 2, Table 2), suggesting departure from colonies during July-August.

Less than 12% of the first-year birds and less than 23% of the older birds were recovered further than 350 km from the ringing sites in SW Kattegat during July-September (Fig. 2). This suggests that when the SW Kattegat cormorants left the colonies, the major part dispersed to nearby areas and only a smaller proportion initiated migration immediately after the end of the breeding season.

The dispersal of birds from the other ringing regions, except NW Jutland, hardly differed from the pattern observed among the SW Kattegat birds

Table 2. Comparison using the Kolomogorov-Smirnov two-sample test of recovery distance from ringing site in different months (see Fig. 2).
Sammenligning af afstanden mellem mærkningssted og genfundssted i forskellige måneder (se Fig. 2) testet med Kolomogorov-Smirnovs two-sample test.

Age-group *Aldersgruppe* Period (sample size) *Periode (antal genfund)*	D
First-year birds *Unge*	
July (101) vs Aug. (242)	0.197 **
Aug. vs Sep. (205)	0.157 **
Sep. vs Oct. (135)	0.260 ***
Oct. vs Nov. (105)	0.333 ***
Older birds *Voksne*	
July (73) vs Aug./Sep. (98)	0.211 *
Aug./Sep. vs Oct. (63)	0.248 *
Oct. vs Nov. (64)	0.323 **

*p<0.05; **p<0.01; ***p<0.001

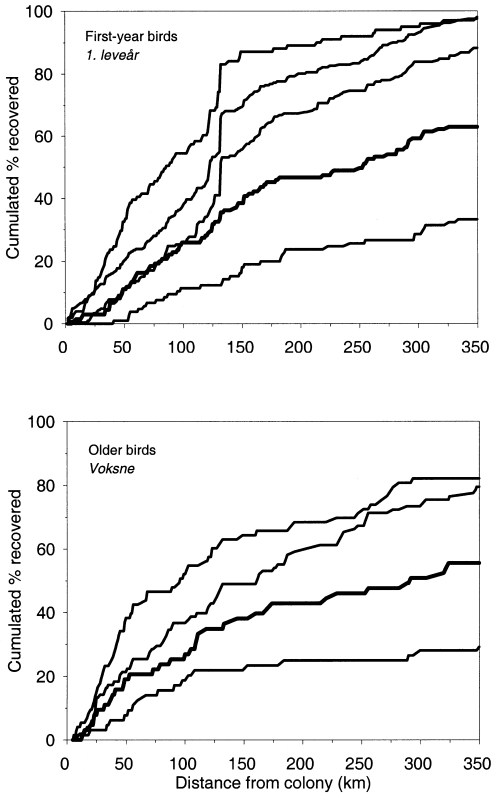


Fig. 2. Cumulated proportion of SW Kattegat cormorants recovered within the given distance from the colony in July (uppermost line) to November (lowermost line) for first-year birds and older birds (data from August and September pooled for older birds); October is denoted by a thick line. Recoveries from all of Europe are included. The number of recoveries per month is given in Table 2. Recoveries from inside the natal colonies were excluded. *Den kumulerede procent af genfundne Skarver ringmærket i SV-Kattegat, der blev genfundet inden for den givne afstand fra mærkningsstedet i juli (øverste linie) til november (nederste linie) (data fra august og september lagt sammen for voksne Skarver); den kumulerede fordeling for oktober er vist med tyk linie. Genfund fra hele Europa og Middelhavsområdet indgår, men genfund fra selve kolonierne er udeladt. Se også Tabel 2.*

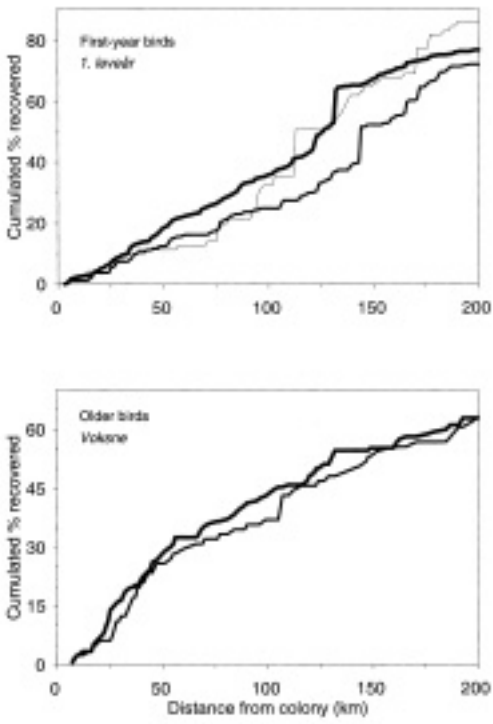


Fig. 3. Dispersal distance. As Fig. 2, but for Cormorants from different regions during July-September. First-year birds: SW Kattegat (thick line, n=544), South Funen (medium line, n=161), and South Zealand (thin line, n=71). Older birds: SW Kattegat (thick line, n=172), and South Funen and South Zealand combined (medium line, n=81).
Spredningsafstand. Som Fig. 2, men for Skarver fra forskellige regioner i juli-september. Unge Skarver: SV-Kattegat (tyk linie), Sydfyn (mellemtyk linie), Sydsjælland (tynd linie). Voksne Skarver: SV-Kattegat (tyk linie), Sydfyn & Sydsjælland (mellemtyk linie).

(Fig. 3). The only significant difference was between first-year birds from SW Kattegat and South Funen (Kolmogorov-Smirnov two-sample test: $D=0.276$, $p<0.001$; $0.046<D<0.124$, NS for the other comparisons; no statistical comparisons with NW Jutland because of small sample size). The step in the curves at 113-144 km distance was caused by differences in the distances from the colonies to the freshwater lake Arresø in North Zealand, where many first-year birds from all three ringing regions were recovered. Most of the first-year Cormorants from NW Jutland recovered inside the study area were recovered near the colony (Fig. 5b); but many dispersed south out of the study area (48% of all July-September recoveries were made more than 350 km south of the ringing site, n=86).

In the early post-breeding period, the net direction of dispersal was towards the east and south-east, but after September the net direction was towards the south or south-west (Fig. 4).

Dispersal in relation to area of origin

The distribution among sub-areas of recoveries of first-year birds and older birds is shown in Fig. 5 and described below for each of the five ringing regions.

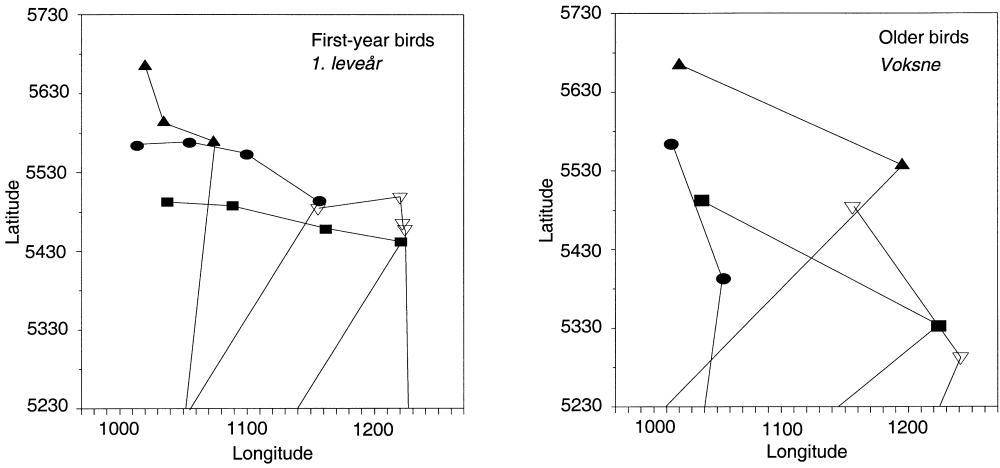
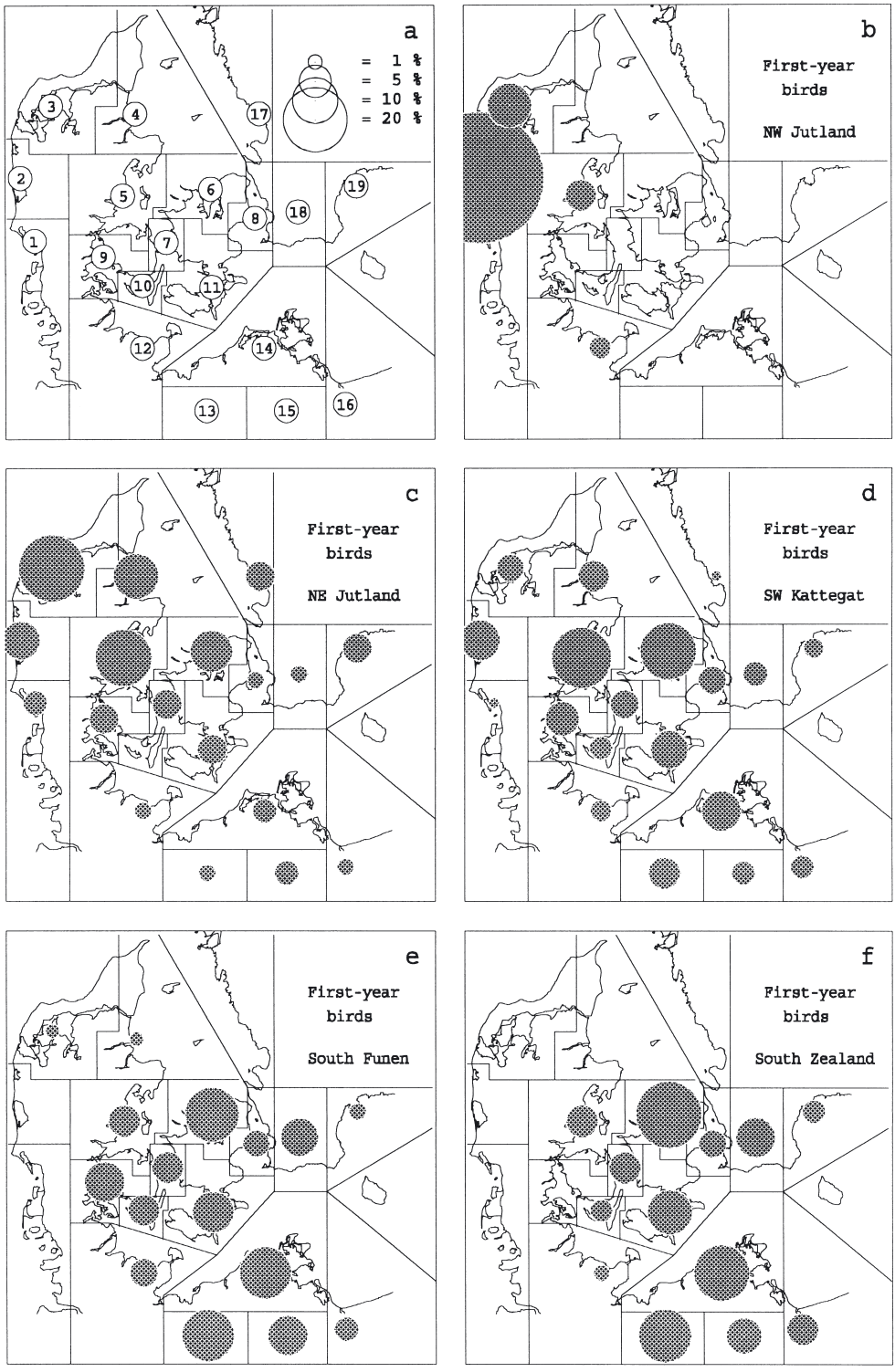


Fig. 4. Seasonal change in the average coordinate of recoveries of first-year Cormorants and older birds ringed in NE Jutland (▲), SW Kattegat (●), South Funen (■), and South Zealand (▽). The first point on each line denotes the average position of the ringing sites. For first-year birds, the subsequent points denote monthly averages from July to September, except for NE Jutland, where data from July and August were pooled. For older birds, the second point in each line denotes the average for August and September pooled. The mean coordinates for October (first-year birds) and October/November (older birds) are located outside of the shown area. All recoveries were included, also those from outside Denmark, South Sweden and NE Germany.
Den tidsmæssige ændring i gennemsnitskoordinaten for genfund af unge og voksne Skarver ringmærket i NØ-Jylland (▲), SV-Kattegat (●), Sydfyn (■) og Sydsjælland (▽). Det første punkt på hver linie angiver gennemsnitskoordinaten for ringmærkningsstedet. For unge Skarver gælder de næste punkter hhv. juli, august og september, og for voksne Skarver august-september (gennemsnitskoordinaterne for juli ikke vist). Gennemsnitskoordinaterne for oktober og oktober-november ligger uden for figuren.

First-year birds. The vast majority of the *NW Jutland* birds were recovered in West Jutland near the colonies (sub-area 2, Fig. 5b), mainly in Nissum Fjord, but a few birds dispersed east into Limfjorden and Kattegat. Some of the *NE Jutland* birds dispersed west into Limfjorden and to the fjords in West Jutland, and some dispersed in southerly or south-easterly directions, staying fairly close to NE Jutland, i.e. along coasts in SW Kattegat (sub-area 5) and in lakes in North Zealand (sub-area 6, Fig. 5c). The *SW Kattegat* birds dispersed in many directions, but most were recovered within SW Kattegat and in North Zealand, and a fair number of birds were recovered in SE Denmark (sub-area 11) and around Rügen (sub-area 14, Fig. 5d). Few of the birds from *South Funen* dispersed west but many moved in easterly directions, some to North Zealand and South Sweden, and a large number to NE Germany (Fig. 5e). The *South Zealand* birds dispersed to coasts and lakes in North Zealand and NE Germany and only a few birds dispersed in westerly directions (Fig. 5f). The distribution of birds from South Zealand was fairly similar to the distribution of South Funen birds.

There was a great overlap in the distribution of recoveries of first-year birds from different ringing regions, the proportional similarity being highest between birds from South Zealand and South Funen (Table 3). There was little overlap between first-year birds from NW Jutland and birds from other ringing regions (Table 3). The mean coordinates of July-September recoveries of first-year birds differed significantly among ringing regions (Mardias $U>21.32$, $p<0.0001$), except that there was no difference between first-year birds from South Funen and South Zealand (Mardias $U=1.25$, $p=0.535$; see Batschelet 1981 for a description of the 'Mardia-test').

Older birds. Birds from *NE Jutland* dispersed in many directions, some moved west into Limfjorden and others to the south and south-east, though not as far as to NE Germany (Fig. 5g). A large proportion of the *SW Kattegat* birds remained within SW Kattegat during the post-breeding period but some moved towards the south-east and were recovered in SE Denmark (sub-area 11) and NE Germany (Fig. 5h). Birds from *South Funen* dispersed mainly in southerly and easterly directions, with a fair number of recoveries from SE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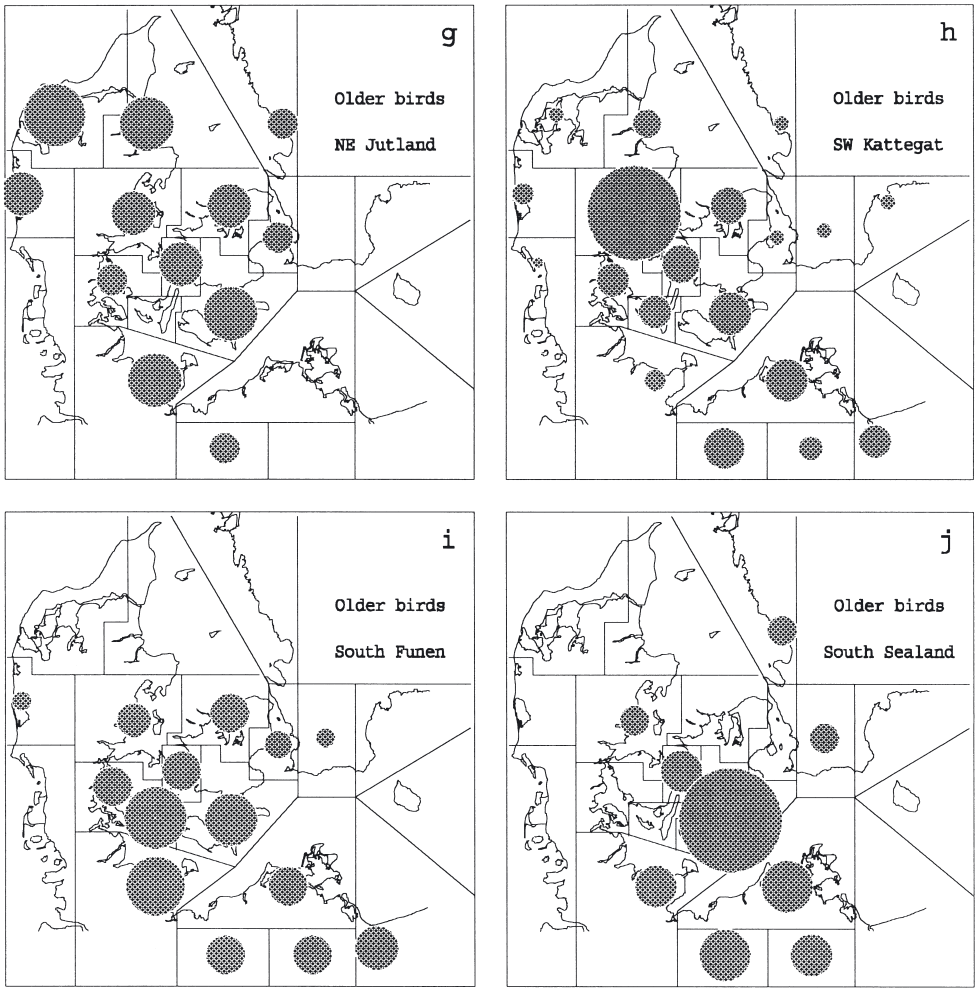

Fig. 5. The distribution of Cormorants recovered as first-year birds (b-f) or as older birds (g-j) in Denmark, NE Germany and South Sweden, July-November, in relation to region of origin in Denmark. The area of the circles is proportional to the percentage recovered in the given sub-area. Sub-areas are defined in (a).
Den procentuelle fordeling af genfund af unge (b-f) og voksne (g-j) Skarver i Danmark, Sydsverige og NØ-Tyskland, juli-november, i relation til mærkningsregion. Hver cirkels areal er proportionalt med procenten genfundet i delområdet. Delområderne er defineret i (a).

Denmark and NE Germany (Fig. 5i). A large proportion of the *South Zealand* birds were recovered in areas near the colonies, but some were found in NE Germany (Fig. 5j).

The comparisons of distributions of recoveries among sub-areas showed a fairly high degree of overlap among older birds from different ringing regions, except that South Zealand birds showed only a moderate degree of overlap with birds from NE Jutland and SW Kattegat (Table 3). The mean coordinates of recoveries of older birds from NE Jutland and SW Kattegat differed significantly from those originating from South Funen and South Zealand (Mardias $U>22.44$, $p<0.0001$, 4 comparisons), but these were the only significant differences in mean coordinates among older birds.

First-year birds vs older birds

A higher proportion of older birds than of first-year birds was recovered in July (28.5% vs 12.8%, n=294 and 917, respectively). One reason is that first-year birds were not recovered before they began foraging on their own or dispersed from the

Table 3. Overlap in distribution of Cormorants from different ringing regions expressed by proportional similarity in distribution among sub-areas (see Fig. 5). Overlap values for first-year birds are given above the diagonal, values for older birds in italics below the diagonal; a value of 1 corresponds to identical distributions. Number of recoveries are given in Table 1.
Overlapindekser for fordelingen af genfund af Skarver fra forskellige ringmærkningsregioner. Værdierne over diagonalen gælder unge fugle, værdierne under diagonalen (i kursiv) voksne fugle; en værdi på 1 svarer til identiske fordelinger. Antal genfund fremgår af Tabel 1.

	Similarity in distribution *Lighed i fordeling*			
Ringing region *Mærkningsregion*	NE Jutland	SW Kattegat	South Funen	South Zealand
NW Jutland *NV-Jylland*	0.262	0.192	0.082	0.071
NE Jutland *NØ-Jylland*		0.689	0.431	0.387
SW Kattegat *SV-Kattegat*	*0.469*		0.687	0.629
South Funen *Sydfyn*	*0.538*	*0.571*		0.810
South Zealand *Sydsjælland*	*0.367*	*0.375*	*0.484*	

Table 4. Overlap in distribution of first-year Cormorants and older birds expressed by proportional similarity in distribution among sub-areas (see Fig. 5), including and excluding birds recovered less than 45 km from the natal colonies. A value of 1 corresponds to identical distributions. Numbers of recoveries are given in Table 1 and in parentheses (first-year birds, older birds).
Overlapindekser for fordelingen af genfund af unge og gamle Skarver (se Fig. 5), inklusive hhv. eksklusive fugle genfundet nærmere end 45 km fra hjemkolonierne. En værdi på 1 svarer til identiske fordelinger. Antal genfund fremgår af Tabel 1 og af parenteserne (unge, voksne).

	Similarity in distribution *Lighed i fordeling*		
Ringing region *Mærkningsregion*	All recoveries *Alle genfund*	Excluding <45 km *Eksklusive <45 km*	
NE Jutland *NØ-Jylland*	0.675	0.619	(61, 18)
SW Kattegat *SV-Kattegat*	0.722	0.747	(480, 140)
South Funen *Sydfyn*	0.652	0.644	(170, 45)
South Zealand *Sydsjælland*	0.511	0.522	(67, 16)

Table 5. Percentage of Cormorants recovered in freshwater lakes in the main post-breeding area, July-November, in relation to geographical origin in Denmark.
Procent af de genmeldte Skarver genfundet i ferskvandssøer i juli-november.

	% in freshwater lakes *% i ferskvandssøer*	
Ringing region *Mærkningsregion*	First-year birds *Unge*	Older birds *Voksne*
NW Jutland *NV-Jylland*	4.2	-
NE Jutland *NØ-Jylland*	30.0	19.2
SW Kattegat *SV-Kattegat*	31.8	21.8
South Funen *Sydfyn*	45.4	34.3
South Zealand *Sydsjælland*	60.2	34.5

colony, whereas older birds were recovered also before the young fledged. Despite the higher proportion of older birds affiliated to the breeding colony at the time of recovery, the degree of overlap in distribution between first-year birds and older birds was fairly high (Table 4). Furthermore, the proportional overlap bewteen age classes changed little when only recoveries of birds assumed to have dispersed were included (Table 4).

Occurrence in freshwater lakes

Between 82% and 100% of the recoveries in North Zealand (sub-area 6), Scania interior (18), Neubrandenburg (13) and Schwerin (15) were from freshwater lakes. The tendency to occur in freshwater lakes as opposed to coasts was highest among South Zealand first-year birds (Table 5) which predominantly visit North Zealand and NE Germany. Most birds from these regions were recovered in lakes.

Overall, the proportion of first-year birds recovered in lakes increased from 30% in July to 45% in September and then declined (27% in November). Among older birds, the proportion was 22% in July, 33% in August, and 23% in November. Freshwater lakes thus appeared to be an important habitat for Cormorants throughout the period July-November.

Discussion

Dispersal prior to autumn migration?

Most Cormorants dispersed progressively further from their colonies during July-September, but few had dispersed further than 350 km by September (Fig. 2). In July-September, the net direction of movements was towards the east and south-east whereas during October-November movements were towards the south and south-west, i.e. towards the wintering areas (Fig. 4; Bregnballe et al. 1997). From these findings we conclude that many Cormorants of Danish origin move to nearby areas after the breeding season and remain in Danish and NE German waters for one to three months before initiating autumn migration. Presumably it is attractive to remain in Danish and western Baltic waters during post-breeding because eel *Anguilla anguilla*, herring *Clupea harengus* and cod *Gadus morhua* are abundant in late summer and autumn (Nørrevang & Lundø 1979, Hald-Mortsensen 1995, Anon 1998, Nielsen et al. 1999, E. Nielsen pers. comm.).

The dramatic increase of the Cormorant population in Denmark, Sweden and NE Germany in the 1970s and 1980s (Bregnballe & Gregersen 1995, Lindell et al. 1995, van Eerden & Gregersen 1995) is believed to be related both to a high production of young (Bregnballe 1996) and to a high first-year survival. Between 50% and 75% of the chicks ringed in the Vorsø colony during 1977-1992 survived until the age of one year (Frederiksen & Bregnballe in press). Presumably, such a high first-year survival was possible because the birds had easy access to food in Danish and NE German waters.

Were certain areas preferred?

Cormorants dispersed to most parts of Denmark, NE Germany and South Sweden during the post-breeding period, though very few older birds appeared in South Sweden (Fig. 5). Most first-year birds were recovered in North Zealand and most older birds near the colonies or in SE Denmark and NE Germany. This does not necessarily mean that most individuals moved to these areas, because the distribution of recoveries does not directly reflect the distribution of Cormorants. First, the distributional pattern of all recoveries (Table 6) was dominated by Vorsø birds (59%, Table 1). Secondly, recovery probabilities were not equally high in all areas, partly because the probability of drowning in pound nets was high in some areas but low in others (see Bregnballe 1999). For example, 82% of the first-year birds (n=92) in North Zealand were recovered drowned in pound nets, compared with only 32% (n=50) in Fynske Øhav (sub-area 10).

To avoid the bias from unequal probability of net-entrapment, we calculated the relative distribution excluding all birds found drowned in nets (Table 6). Following this procedure, North Zealand no longer appeared particularly attractive to first-year birds whereas sub-areas 5, 9-10, 11 and 13-14 were still identified as areas with high numbers of recoveries during July-September. Since most of these were not areas used mainly by Vorsø birds, we conclude that parts of southern and south-eastern Denmark, and Schwerin and Rostock, were much exploited by Danish Cormorants during post-breeding.

Little is known about the seasonal and geographical variation in the abundance of fish in shallow areas in Danish and western Baltic waters (E. Nielsen & J. Tomkowitch pers. comm.) but some fish species are known to concentrate temporarily in certain areas. For example, western Baltic herring becomes highly concentrated in the Sound (Øresund) from (late) August onwards (e.g., approximately 1125 million herring were

Table 6. Percentage of Cormorants recovered in each sub-area, with or without inclusion of those recovered drowned in fishing gear.
Genfundenes procentuelle fordeling på delområder, når druknede Skarver hhv. medtages og ikke medtages.

		First-year birds *Unge*		Older birds *Voksne*	
No. *Nr*	Sub-area *Delområde*	Excluding *Eksklusive* (n=279)	Including *Inklusive* (n=828)	Excluding *Eksklusive* (n=166)	Including *Inklusive* (n=295)
3,4	Northern Jutland *Nordlige Jylland*	14.0	8.9	6.3	5.4
5	SW Kattegat *SV-Kattegat*	24.0	15.1	32.0	24.8
6	North Zealand *Nordl. Sjælland*	2.9	17.1	1.7	6.4
7	Great Belt *Storebælt*	4.3	4.7	8.6	7.0
8	Sound *Øresund*	2.9	3.3	2.3	1.7
9,10	Fynske Øhav, Little Belt *Fynske Øhav, Lillebælt*	16.1	9.6	13.1	11.1
11	SE Denmark *SØ-Danmark*	10.7	8.1	14.3	11.4
12	E Schleswig-Holstein *Østlige Slesvig-Holsten*	1.8	2.7	7.4	5.7
13,14	Schwerin & Rostock	16.8	18.0	10.9	14.8
15,16	Neubrandenburg & NW Poland	4.7	8.0	2.9	10.1
18,19	Scania (excl. Halland) *Skåne*	1.8	4.5	0.6	1.7

estimated to be present in the Sound in autumn 1997; Nielsen et al. 1999). Another example is that the 0-group and 1-group of cod, which Cormorants are known to prey upon in southern Denmark in July-September (Hald-Mortensen 1995), appear in fairly high concentrations in Mecklenburger Bucht in late summer-early autumn (E. Nielsen & J. Tomkowiztch pers. comm.). A third example is that pound net fishermen in the Sound and in SE Denmark catch more fish per net (especially many more eel) than pound fishermen in other parts of Denmark (Anon 1998). The ability of older Cormorants to localise areas rich in food may explain their tendency to move to southern Denmark and NE Germany irrespective of geographical origin. The distribution of older Cormorants during post-breeding may thus to some extent conform to the distribution of fish (of the right size and in shallow areas) in Denmark and northern Germany.

Influence of barriers

Coulson & Brazendale (1968) and Galbraith et al. (1986) found that cormorants and shags do not normally cross stretches of open sea. The "absence" of recoveries of NE Jutland birds from the west coast of Sweden may likewise indicate that birds from this area rarely disperse across Kattegat where they would have to cross 100-150 km of open sea. Movements from the west coast of Jutland to areas east of Jutland and vice versa were also uncommon, except for movements through Limfjorden, suggesting that Jutland constitute another barrier for dispersing Cormorants. This barrier effect may partly explain the easterly to south-easterly net direction of dispersal among birds from NE Jutland, SW Kattegat and South Funen (Fig. 4).

Implications for management

Knowledge about the geographical origin of the cormorants causing problems for fisheries is a prerequisite if culling in colonies is to be a successful tool in reducing intensities of conflict. For example, it needs to be established whether areas near colonies are also exploited by birds from non-local colonies, and if so, at what time of the year the non-local birds appear. We have shown that areas near colonies will be exploited mainly by local birds until the end of July, but that non-local birds will make up an increasing proportion from July/August onwards in many parts of Denmark.

The present results suggest that West Jutland is exploited mainly by local birds and birds from northern Jutland, and that culling of colonies in these areas could lead to measurable reductions in the number of cormorants appearing in West Jutland in late summer and autumn. Likewise, the distributional patterns show that SW Kattegat is exploited by local birds and by birds from NE Jutland, although Norwegian birds also appear from September onwards (Mogstad & Røv 1997, own unpubl. data). On the other hand, SE Denmark and NE Germany are exploited by cormorants from most Danish breeding colonies and by birds from Sweden, North Germany, Poland and to a smaller extent Norway, Russia, the Netherlands and even the Czech Republic and northern Croatia Siefke & Berger 1979, Nilsson 1980, Sirotic 1988, Gromadzka & Przybysz 1991, Larsson 1994, Mogstad & Røv 1997, Musil et al. 1997). Therefore no measurable reductions in conflicts with fisheries can be expected in late summer and autumn in these areas if only local breeding colonies are culled.

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Resumé

Danske Skarvers spredning efter yngletiden

På baggrund af 1217 genfund af Skarver mærket i 12 danske kolonier 1972-1991 (Tabel 1) undersøger vi de danske Skarvers spredning efter ynglesæsonen, før det egentlige efterårstræk. Vi belyser sammenhængen mellem oprindelseskoloniernes beliggenhed (Fig. 1) og Skarvernes fordeling i Danmark, Sydsverige og NØ-Tyskland i perioden juli til november, og vi diskuterer betydningen af faktorer, der indvirker på Skarvernes spredning efter yngletiden. Vi grupperer de 12 kolonier efter deres beliggenhed (Fig. 1) og skelner mellem individer genfundet i første (unge) hhv. senere efterår (voksne).

I de første måneder efter ynglesæsonen opsøgte hovedparten af Skarverne søer og kystområder i Danmark, NØ-Tyskland og Sydsverige. Således kom 96% og 81% af juli-september genfundene af hhv. unge og voksne Skarver fra denne region (n=791 hhv. 293). Skarverne spredte sig gradvist længere væk fra hjemkolonierne, men endnu i september blev de fleste genfundet mindre end 350 km fra deres mærkningskoloni (Fig. 2). I juli-september var afstanden mellem mærkningssted og genfundssted stort set uafhængig af hvor i landet, Skarverne var blevet ringmærket (Fig. 3). Hovedparten af Skarverne fra NØ-Jylland, SV-Kattegat og Sydfyn spredte sig i østlig og sydøstlig retning, men fra septem-

ber til november, hvor mange Skarver forlod regionen, trak fuglene overvejende i sydlige og sydvestlige retninger (Fig. 4). Fordelingen af genfund i relation til mærkningsområde er vist i Fig. 5. De *unge* Skarver fra *NV-Jylland* blev genfundet tæt på deres mærkningssted, og fuglene spredte sig kun i ringe grad mod øst. Fra *NØ-Jylland* spredte halvdelen af de unge Skarver sig mod vest ind i Limfjorden og til Vestjylland, mens resten søgte mod syd og sydøst og blev genfundet ved kyster i SV-Kattegat og i søer i det nordlige Sjælland. Fra kolonierne i *SV-Kattegat* spredte fuglene sig hovedsagelig mod øst og sydøst; nogle blev genfundet i NØ-Tyskland. Hovedparten af de unge Skarver fra *Sydfyn* og *SØ-Danmark* blev genfundet i Nordsjælland, Sydsverige, det syddanske øhav og især i NØ-tyskland; ganske få spredte sig mod vest. Det var karakteristisk for de unge Skarver fra Sydfyn og SØ-danmark, at der stort set ikke var nogen genfund fra Vestjylland og kun få fra østkysten af Jylland. Der var stort overlap i fordelingen af genfund af unge Skarver ringmærket i forskellige egne af landet, dog ikke mellem Skarver fra NV-Jylland og det øvrige Danmark (Tabel 3).

Voksne Skarver fra *NØ-Jylland* spredte sig i mange retninger, men forholdsvis mange blev genfundet i SØ-Danmark og det nordøstlige Slesvig-Holsten. Hovedparten af de voksne fugle fra *SV-Kattegat* genfandtes i det sydvestlige Kattegat, mens en mindre andel spredte sig til SØ-Danmark og NØ-Tyskland. Blandt de voksne fugle fra *Sydfyn* var der mange genfund fra det syddanske øhav og Slesvig-Holsten og en del fra NØ-Tyskland. Mange voksne Skarver fra *SØ-Danmark* blev genfundet nær kolonierne og en del i NØ-Tyskland. Der var et forholdsvis stort overlap i fordelingen af unge og voksne Skarver fra de enkelte mærkningsområder (Tabel 4).

Mange Skarver blev genfundet i ferskvandssøer (27-45% af de unge og 22-33% af de voksne pr måned fra juli til november). En væsentlig andel (82%-100%) af fuglene genfundet i det nordlige Sjælland, det indre Skåne, Neubrandenburg og Schwerin blev genfundet i ferskvandssøer. Især unge fugle fra SØ-Danmark optrådte i søer (Tabel 5), hvilket stemmer overens med, at disse fugle i vid udstrækning blev genfundet i ovennævnte områder (Fig. 5f).

Vi konkluderer, at hovedparten af unge såvel som voksne danske Skarver følger et mønster karakteriseret ved en spredning i sensommeren over forholdsvis korte afstande til søer og kystområder i Danmark, NØ-Tyskland og i mindre omfang Sydsverige. Her opholder de sig i nogle uger eller måneder før de påbegynder efterårstrækket i september-november. Vi formoder, at Skarverne under opholdet i danske og nordøsttyske farvande drager fordel af forholdsvis høje forekomster af bl.a. torsk, sild og blankål. Nem fødeadgang umiddelbart efter ynglesæsonen formodes at have bidraget til den hurtige bestandsfremgang i 1970erne og 1980erne.

Fiskere i Danmark, Sverige og Nordtyskland har ønsket at få reguleret størrelsen af lokale skarvkolonier for at reducere den skade, Skarverne forårsager i bundgarn. De fordelingsmønstre, vi har fundet, tyder på, at konflikten mellem Skarverne og fiskeriet i de vestjyske fjorde formentlig ville kunne reduceres ved vedvarende regulering eller fjernelse af kolonier i det vestlige og nordlige Jylland, fordi de vestjyske fjorde kun i ringe grad udnyttes af Skarver fra indre danske farvande og andre lande. Men i områder som det nordlige Sjælland, det syddanske øhav og NØ-Tyskland vil en regulering af lokale kolonier næppe resultere i en målelig nedgang i den skade, Skarverne påfører fiskeriet i sensommeren og efteråret. I disse områder optræder der Skarver fra de fleste danske kolonier og fra kolonier i Sverige, Nordtyskland og Polen.

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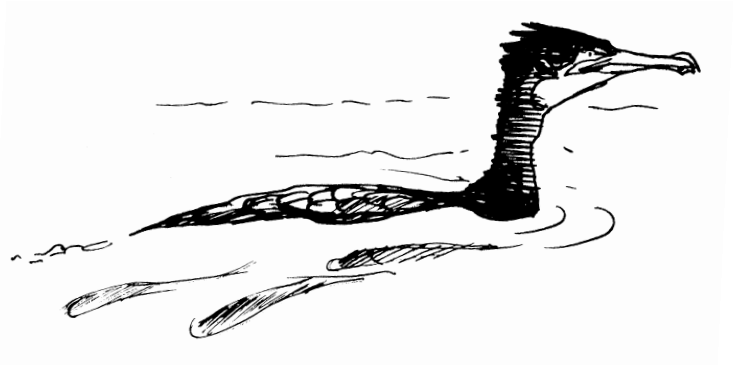

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