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Cormorants in the Finnish archipelago

Aleksi Lehikoinen

Lehikoinen, A., Dept.of Biological and Environmental Sciences, P.O Box 65 (Viikinkaari 1), FI-00014, University of Helsinki, Helsinki, Finland. Aleksi.Lehikoinen@helsinki.fi

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The Great Cormorant *Phalacrocorax carbo sinensis* started to breed in Finland in 1996 following rapid growth of the population in western Europe. The Finnish population increased very quickly in nine years from 10 pairs to 2,930 pairs in 2004. The growth of the breeding population and the spatial pattern of colonization and possible factors affecting it in Finland are discussed. Breeding success was studied in detail within a single colony on the southern coast of Finland. Breeding success was higher in central nests of the study colony than in nests at the edge of the colony. Survival rates of eggs and 0–5 day-old young were lower than older young (>5 days old). Fledging success was determined in a number of different sized colonies, and was highest in large colonies. Small colony size may reduce the reproductive output, because (1) small colonies could have a relatively large proportion of young and inexperienced breeders and (2) small colonies may have proportionally more edge nests than large colonies and therefore suffer relatively more from negative edge effects.

1. Introduction

The European population of the continental subspecies of the Great Cormorant (*Phalacrocorax carbo sinensis*) (hereafter referred to as Cormorant) has increased rapidly from a few 1,000 to more than 150,000 pairs during recent centuries (e.g. Bregnballe *et al.* 2003, Engström 2001, Marion & Suter 1997). The breeding distribution has also expanded since the 1960s, especially in a northern direction. In the 1960s there were only a few colonies in the Baltic Sea area in Sweden, Poland and Germany, but in the 1980s Cormorants had colonized most of the Baltic Sea countries, Russia, Estonia, Latvia and Lithuania (Baumanis *et al.* 1997, Lilleleht 1997, Rusanen *et al.* 1998, Zydelis *et al.* 2002). In 1996 the Cormorant finally colonized the northernmost Baltic Sea country – Finland. The increase of the European population of Cormorants is due to better protection status in European Union countries (Van Eerden & Gregersen 1995), and lower concentrations of environmental toxins has increased the breeding success since the 1980s (Boudewijn & Dirksen 1995). Additionally, the eutrophication of water systems like the Baltic Sea (e.g. Dahlberg & Jansson 1997, Wahlström *et al.* 1996) have increased the numbers of small fish and improved environmental conditions for Cormorants.

In the Baltic the historic distribution of Cormorants is best described in Sweden. Based on prehistoric bone records nominate subspecies of the Great Cormorant have bred widely in southern Sweden after the last glaciation. However, nominate subspecies disappeared between the 11th–17th centuries for some reason and there are no written observations of breeding Cormorants in Sweden until the 19th century, when *sinensis* subspecies established several colonies in southern Sweden. Nevertheless, probably due to hunting and human persecution, this population disappeared by 1909 (Engström 2001). In Estonia Cormorants started to breed at the end of the 18th century, but the population had disappeared by the beginning of the 20th century (Lilleleht 2004). Lehikoinen *et al.* (2003) suggested that, based on written historic descriptions, Cormorants have probably bred in southwestern Finland (Åland archipelago and Archipelago Sea) in the beginning of the 18th century and disappeared before the 19th century possibly because of persecution. However, confirmed records of breeding have not been documented in Finland before 1996. Rusanen *et al.* (2003) have reported population development of Cormorants in Finland until 2002. In that article the patterns of population are described only briefly and the situation has changed quickly due to rapid population growth. This paper describes the population development, immigration intensity, spatial distribution of colonization and breeding success of *sinensis* Cormorants in Finland until 2004.

2. Material and methods

2.1. Study area

The development of breeding numbers of Cormorants has been monitored by the Finnish Environmental Institute, with the help of volunteer ornithologists (Rusanen *et al.* 2003). Annual breeding populations are based on counts of nests containing eggs, usually at the peak of the breeding season, the method normally used for Cormorants and other sea birds (e.g. Engström 2001, Koskimies & Väisänen 1988). Empty nests were ignored.

The mortality rate of chicks and breeding success was studied in 2002 in Tammisaari, at that time the biggest colony in Finland and comprising 670 breeding pairs. The colony has spread onto two islands, Sköldharun and Lerharun (59°50' N, 23°38' E), situated 2 km from each other. Cormorants started to breed on Sköldharun in 1997 and a subcolony was established on Lerharun in 2001. Colonies were defined as separate when the distance between the islands was more than 2 km, otherwise close-by breeding islands were treated as subcolonies. Fledging success was also studied in eleven other colonies in the communes of Kotka, Inkoo, Tammisaari (3), Dragsfjärd, Nauvo, Kustavi, Merikarvia, Uusikaupunki and Maksamaa in 2002–2004. Young Cormorants (age >30 days) were considered as fledglings, since the mortality rate of younger birds is still notable (Krag 2003, see also section 3.3. and Discussion) and thus too early counts could overestimate the fledging success.

2.2. Study nests

60 nests (two groups of 30 nests) and 56 (groups of 30 and 26 nests) nest were marked on Sköldharun and Lerharun, respectively. Nests were marked with iron rope and tape, on which the nest number was written, on 8 May 2002, before the young had hatched. On both islands the nests were on the ground or in juniper (*Juniperus communis*) and bird-cerry (*Prunus padus*) bushes. On Sköldharun the nesting area consisted of smaller patches of 20–50 nests, while in Lerharun the nesting area were more uniform. The nests were checked approximately every fourth day (range 2–6) from 16 May until 12 June, when the last young hatched in the study nests. The maximum number of eggs in each nest was treated as the full clutch. Weight of the newly hatched young was measured and that information used to calculate the hatching days. 75% of the chicks were aged 0–2 days, 23% were aged 3–4 days and 2% were aged 5–6 days old. The hatching dates of chicks and dates of vanished eggs and chicks were used to measure the survival rate of eggs during the incubation period (proportion of surviving eggs/incubation day) and the survival rate of chicks (surviving nestlings/day). Survival rate of chicks could be measured only during their first 15 days of life, when they started to run away from their nests when a human entered the colony. All 116 study nests on Sköldharun and Lerharun were classed as central or edge nests (Fig. 1.) and the failure rate of nests of these two nest groups were compared combining the data from both subcolonies.

The mortality rate of bigger juveniles is more difficult to measure, because of their tendency to

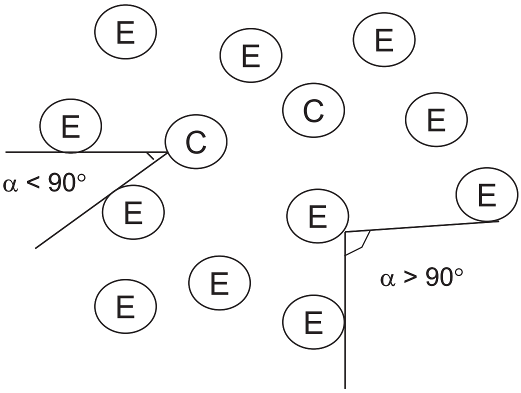

Fig. 1. Edge (E) and central nests (C). Central nests were surrounded by other nests so that their edge sector (α, angle between a nest and the two closest nests on the outer side of the colony) was < 90º. Nests with edge sectors more than 90º were edge nests.

run away when humans entered the colony. The number of nearly fledged juveniles (age more than 30 days) were counted at the end of the breeding season (at the end of June–beginning of July) to measure the breeding success of different colonies in 2002–2004. These numbers were treated as the number of fledglings, since according to Krag (2003) loss of young birds rarely occurs after the age of 40 days (see also section 3.3.). Fledging success was calculated by dividing the number of fledglings by the number of nests with eggs. Most of the juveniles on Sköldharun and Lerharun were ringed with metal rings when they were around 25 days old. Dead juvenile Cormorants were searched for during and after the breeding season by walking through the areas of both subcolonies during each visit. The mortality rate of nearly fledged juveniles was determined in two similar ways: number of dead ringed juveniles found in the colony was compared to the number of total ringed juveniles and number of all dead juveniles found was compared to the number of all nearly fledged juveniles in the colony. Fledging success in different sized colonies was estimated by a correlated model of univariate analysis of variance (ANCOVA) with the study year (2002–2004) as a fixed factor.

The proportion of immigration was estimated using the knowledge (a) that Cormorants do not start breeding until two years of age, and usually at three years of age (Fredriksen & Bregnballe 2001), (b) average fledging success of Finnish colonies was approximately 1.85 birds/nest of eggs (see section 3.3.), and of (c) mortality rates of different age classes (Fredriksen & Bregnballe 2000a, b).

Values are reported as mean ± 1SD unless mentioned otherwise.

3. Results

3.1. Population development

Numbers of observed Cormorants during the summertime increased in Finland during the 1980s and 1990s (Rusanen *et al.* 1998). Higher numbers in the summertime were already seen in the Åland archipelago in the beginning of the 1980s, and in 1981 an unfinished Cormorant nest was found in the northern part of the archipelago. However, since the end of the 1980s the numbers in summertime decreased in Åland for some reason (Rusanen *et al.* 1998). The first colony in Finland was established in 1996. Since then the Cormorant population of Finland has increased from a colony of 10 pairs to 2,830 pairs in 20 colonies in 2004 (Fig. 2). The average annual growth rate was 124% (16–408%) from 1997–2004 (Table 1). Based on the general population growth model $N_t = R^t N_0$ (e.g. Begon *et al*. 1996), where N_0 is the size of a population during the first year and t is number of study years, the annual average growth rate R was estimated as 1.17.

Until 1999, Cormorants bred only on the southern coast of Finland, but since 2000 the Gulf of Bothnia has also been colonized, when one colony was established in Bothnian Bay, in the commune of Ii. In 2002 Cormorants bred in all sea areas of Finland (Table 1) and all the colonies were situated on islands or islets: no inland breeding colonies have been reported. None of the colony islands have been inhabited by humans and the nearest settlements or official sailing waterways are situated on average 1.9 ± 1.3 km (0.3–5.4 km) from the colonies. Most of the colonies could be reached by the American Mink (*Mustela vison*), the most common ground predator in the archipelago. Colonies were usually established on islands with rich colonial avian fauna e.g. gulls, terns,

Fig 2. The distribution and size of Cormorant colonies of Finland in 2004. Arrow shows the study colony of Sköldharun–Lerharun (616 pairs in 2004).

razorbills, grey herons. 70% of the colonies were established on islands with Herring Gulls (*Larus argentatus*). The colonies were established on fairly small islands, with average size of 1.3 ± 0.9 ha (0.2–3.4 ha). In general, nesting sites of Cormorants occupied only a few percent of the whole land area of the islands (maximum 30% of the total area).

One or two years before establishment of a colony, small numbers of non-breeding Cormorants were usually roosting on the islands during the breeding season or migration periods. Illegal persecution against Cormorant colonies has been reported in 10 colonies out of a total of 23 (43%). Persecution was rarer on protected islands (20%, 10 islands) than on non-protected islands (67%, 12 islands) (Table 1).

Six cases of persecution (60%) occurred during the establishing year and four during later years. Population development in each sea area is described below and the yearly development of each colony is shown in Table 1.

Gulf of Finland

The first colony was established in 1996 on a small rocky islet of Blekharun near Tammisaari in the western part of the Gulf of Finland, including ten pairs. The next year the colony moved 2 km to the bigger islet of Sköldharun. In 1997 one colony was also established in the eastern part of the Gulf of Finland near the Finnish town of Pernaja on the islet Haverören, including two nests of eggs. These two colonies have been until 2004 the biggest colonies in Finland. In 2004, 616 pairs bred on Sköldharun–Lerharun and 652 pairs on Haverören, while the remainder of the colonies were no larger than 230 pairs.

In 2004 the population contained seven colonies, six in the outer and one in the inner archipelago. In five of these Cormorants have been mostly breeding on the ground on rocky islands, but two have been established in trees within a colony of Grey Herons *Ardea cinerea*.

Illegal persecution was reported in two colonies. The most persecution in Finland so far was reported in 2001, when around 1,100 eggs were removed from the islet of Sköldharun. Eggs were also removed from 15 nests from the other colony near Tammisaari in 2002.

Archipelago Sea

The first Cormorant colony was established near Dragsfjärd including three nests with eggs in 1998. The colony was illegally destroyed the same year by breaking the nests and eggs and Cormorants have not bred there since. The next colony was established near Nauvo on the islets of Tvåkobbarna in 2000. In 2000 and 2001 the population was only a few pairs, but in 2002 it increased to 52 pairs, when it was also destroyed in the same way as the colony near Dragsfjärd. Unlike on Dragsfjärd, small numbers of Cormorants returned to Nauvo in 2003, when nine pairs bred. More colonies were established in 2002 (three) and 2003 (three), but in 2004 the population consisted of six colonies, since one colony was rejected after nest destruction by humans. Seven of the all established colonies were ground breeding, mostly in the inner archipelago, and one colony was situated in trees (Common Alder *Alnus*

Table 1. Number of pairs (nests with eggs) in each colony of Cormorants in different Finnish sea areas in 1996–2004 including annual growth percents. Habitat (Hab.: T = tree, B = bush, G = ground) and protection status (PS: P = protected area, common landing the island during the breeding season prohibited, N = island, includes the Natura 2000 network) of colonies. Sub-colonies of Tammisaari 1 are shown in 1A–C. A = Blekharun, B = Sköldharun and C = Lerharun, mentioned in the text.

Sea area	Commun	Estab.	1996	1997	1998	1999	2000	2001	2002	2003	2004	Hab.	PS
Gulf of Finland	Tammisaari 1	1996	10	22	105	130	229	436[A]	670	605	616	B,G	N
	Tammisaari 1A	1996	10	0	0	0	0	0	0	0	0	G	
	Tammisaari 1B	1997		22	105	130	229	380	176	39	3	B,G	
	Tammisaari 1C	2001						56	494	566	613	B,G	
Gulf of Finland	Pernaja	1997	0	2	14	31	75	228	439	489	652	B,G	P
Gulf of Finland	Kotka	2001	0	0	0	0	0	1[B]	10	2	9	G	P
Gulf of Finland	Kirkkonummi	2002	0	0	0	0	0	0	10	73	192	T,G	P
Gulf of Finland	Tammisaari	2002	0	0	0	0	0	0	17[C]	20	70	T,G	
Gulf of Finland	Tammisaari	2002	0	0	0	0	0	0	11[D]	8	9	B,G	P
Gulf of Finland	Inkoo	2003	0	0	0	0	0	0	0	80	228	T,B,G	P
Gulf of Finland	Hamina	2004	0	0	0	0	0	0	0	0	1	G	P
Gulf of Finland	Total		10	24	122	161	304	665	1,157	1,277	1,777		
Archipelago Sea	Dragsfjärd	1998	0	0	3[E]	0	0	0	0	0	0	G	
Archipelago Sea	Nauvo	2000	0	0	0	0	1	9	51[F]	9	30	G	
Archipelago Sea	Brändö	2002	0	0	0	0	0	0	18	9	10G	T	
Archipelago Sea	Dragsfjärd	2002	0	0	0	0	0	0	46	65	140	G	
Archipelago Sea	Tammisaari	2002	0	0	0	0	0	0	48[H]	99	142	G	
Archipelago Sea	Tammisaari	2003	0	0	0	0	0	0	0	1[I]	0	G	
Archipelago Sea	Kustavi	2003	0	0	0	0	0	0	0	14	208	G	N
Archipelago Sea	Nauvo	2003	0	0	0	0	0	0	0	5	50	G	N
Archipelago Sea	Total		0	0	0	0	1	9	163	202	580		
Bothnia Sea	Merikarvia	2002	0	0	0	0	0	0	20	60	181	T	N
Bothnia Sea	Luvia	2003	0	0	0	0	0	0	0	15[J]	130	B,G	P
Bothnia Sea	Total		0	0	0	0	0	0	20	75	311		
Quark	Maksamaa	2001	0	0	0	0	0	10	3[K]	1	4	G	P
Quark	Maksamaa	2002	0	0	0	0	0	0	6	6	4[L]	G	N
Quark	Uusikaarlepyy	2003	0	0	0	0	0	0	0	14	100	T,B,G	P
Quark	Total		0	0	0	0	0	10	9	20	108		
Bothnia Bay	Ii	2000	0	0	0	0	31	25	42	43	129	G	P
Bothnia Bay	Kokkola	2004	0	0	0	0	0	0	0	0	4[M]	G	N
Bothnia Bay	Total		0	0	0	0	31	25	42	43	133		
Number of pairs			10	24	122	161	336	709	1,391	1,618	2,909		
Number of colonies			1	2	3	2	4	6	14	20	21		
Annual growth rate (%)				140	408	32	109	111	96	16	80		

A 1,100 eggs were removed from nests in 2001, B Poor breeding success (colony situated next to a sailing course), C 15 nests were destroyed, only two tree nests were not persecuted, D Poor breeding success, but no persecution, E All nests were destroyed in 1998, F All nests were destroyed in 2000, G All nests were destroyed 2004, H Eggs of a few nests were perforated in 2002, since then no persecution, I All nests were destroyed in 2003, J All nests were destroyed in 2003, K Poor breeding success (possibly persecution in 2002), L Poor breeding success, all nests were destroyed in 2004, M All nests were destroyed in 2004.

glutinosa) in the western Archipelago Sea. In 2002, eggs of a few nests were perforated on the island near Tammisaari and in another small colony near Tammisaari nests were destroyed in 2003, which led to rejection of the colony in 2004.

Bothnian Sea

The first colony was established off Merikarvia in 2002 and in 2003 two colonies were founded near Luvia and Kustavi. All the colonies were in outer archipelago. The colony near Merikarvia (181

Table 2. Daily average survival rate of eggs during hatching period and of Cormorant nestlings in the study nests of Sköldharun and Lerharun in 2002. Based on daily survival rate the survival rates of the whole incubation period (25 days, Lindell & Jansson 1994) and different chick ages are shown.

Breeding period	Daily survival rate (%)	Survival rate of whole period (%)	Number of study ind.
Eggs laying and incubation	97.7	55.9	419
Chicks 1–5 days	93.6	71.8	241
Chicks 6–10 days	98.6	93.4	152
Chicks 11–15 days	99.4	97.4	108

pairs in 2004) was built on coniferous trees, while two were on the ground. On Luvia all 15 nest of eggs were destroyed in 2003, but Cormorants returned next year and population of the colony grew up to 130 pairs.

Quark Archipelago

In the Quark, Cormorants started to breed in 2001 near Maksamaa. In 2003 there were three colonies including only 21 breeding pairs, but in 2004 the population increased rapidly to 108 pairs. All the colonies were on the ground and situated quite close to each other.

Bothnian Bay

For several years the only colony in the area was situated in the commune of Ii in the outer archipelago. This colony is the most northern in the Baltic Sea and highly likely the most northern colony of subspecies *sinensis* in Europe. In 2004 another small colony was established near Kokkola, but it was destroyed the same year in the egg stage.

3.2. Breeding success in study nests

In 2002, average clutch size was 3.70 ± 0.98 (n = 60) in Sköldharun and 3.55 ± 0.87 (n = 52) in Lerharun. The median hatching date of the whole Sköldharun–Lerharun colony was 22 May. Hatching was earliest in the older sub-colony of Sköldharun (20 May ± 3.3 days, n = 46) than in Lerharun (25 May ± 5.6 days, n = 39) (Mann-Whitney U-test Z = –5.10, P < 0.001). The first young hatched on 14 May in Sköldharun. Breeding failed in the edge nests more frequently than in the central nests during the one month study period. Breeding failed in almost half (45%, n = 64) of the edge nests during the incubation and small young period, but in only 15% (n = 48) of the central nests ($\chi_1^2 = 6.39$, P > 0.001). Although the clutch size did not differ in these two groups (central 3.84 ± 0.72; edge 3.55 ± 1.06; Mann-Whitney U-test Z = –1.21, P = 0.22), more young hatched in central nests (2.59 ± 1.34) than in edge nests (1.68 ± 1.50; Mann-Whitney U-test Z = –3.12, P = 0.002).

However, the number of hatched young in successful central (2.89 ± 1.06, n = 42) and edge nests (2.56 ± 1.15, n = 43) did not differ (Mann-Whitney U-test Z = –1.56, P = 0.12). The average first hatching date was slightly earlier in central nests (21 May ± 4.6 days, n = 42) than in edge nests (24 May ± 5.3, n = 43), but this was only marginally significant (Mann-Whitney U-test Z = –1.92, P = 0.054).

The daily survival rates of eggs during the hatching period and of nestlings during the first 15 days are shown in Table 2. Survival was clearly lower during incubation and small nestling periods than when the nestlings were older than five days ($\chi_3^2 = 46.7$, P < 0.0001). In total, 5.7% of all eggs (n = 419) never hatched.

3.3. Fledging success

In 2002, altogether 810 nestlings were ringed in Sköldharun and Lerharun on 5–12 June, and 1050 more than 30 day-old nestlings (estimated fledging success 1.57 young/nests with eggs) were counted in the colony on 25 June. During summer (June–August), 16 dead big Cormorant nestlings

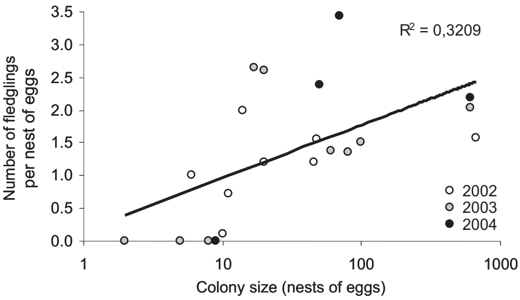

Fig. 3. Fledging success of different sized, unpersecuted Cormorant colonies (logarithmic scale) in Finland in 2002–2004.

(older than 20 days) were found, half of them ringed. Hence, the mortality rate of bigger nestlings was estimated at 1.0% for ringed nestlings and, when based on all nestlings, the mortality rate was estimated at 1.5%. Fledging success increased with the size of the colony on a logarithmic scale without significant effect between study years (ANCOVA correlated model $F = 3.51$, $P = 0.038$; colony size: $F = 7.32$, $P = 0.015$; year: $F = 0.85$, $P = 0.45$) (Fig. 3). The average fledging success was 1.85 fledglings/nest with eggs in 2002–2004.

3.4. Immigration

Immigration estimates assumed that the complete production of Finnish Cormorants were recruited back to Finland and that birds that previously bred in Finland continued to breed in Finland in later years if they have not died during the non-breeding season. Based on these (highly conservative) assumptions, the average proportion of immigrants for population growth has been 84% in 1996–2004 (Table 3).

4. Discussion

4.1. Population development

The expansion of Cormorants in Finland has been very rapid. In seven years the species has colo-

Table 3. Number of breeding Cormorants and estimates of the proportions of immigration and breeding production for population growth.

Year	1996	1997	1998	1999	2000	2001	2002	2003	2004
Number of nests with eggs[1)]	10	24	122	161	336	703	1,392	1,619	2,931
Number of breeding individuals[2)]	20	48	244	322	672	1,406	2,784	3,238	5,862
Fledging production[3)]	18	44	225	297	620	1,297	2,569	2,988	5,409
Number of breeding adults, which have bred last year[4)]		18	42	215	283	591	1,237	2,450	2,849
Number of first-time-breeders[5)]	20	30	202	107	389	815	1,547	788	3,013
Number of first-time-breeders of Finnish fledging production[6)]				8	20	101	133	279	583
The fledging production of Finland in mature age[7)]				8	27	125	243	493	1,016
Number of immigrated first-time-breeders[8)]	20	30	202	99	369	714	1,413	510	2,430
Proportion of Finnish fledging production of first-time-breeders	0%	0%	0%	8%	5%	12%	9%	35%	19%
Proportion of immigration of first-time-breeders	100%	100%	100%	92%	95%	88%	91%	65%	81%
Proportion of Finnish fledglings of all breeders	0%	0%	0%	3%	4%	9%	9%	15%	17%

1) See Table 1, 2) Number of pairs * 2, 3) Number of pairs * average fledging success 1.85 4) Number of individuals bred last year * survival rate of adults (based on survival rate estimates of Fredrikson & Bregnballe (2000b); 88%), 5) Number of first-time-breeders = number of all breeding individuals minus number of adults (section 2), which have already bred one year before (section 4), 6) Number of first-time-breeders (at the age of three years) of Finnish fledging production based on Fredriksen & Bregnballe (2000a,b) estimates of survival rates of young birds (average survival rate of 1st year 58% and adults 88%), 7) Total number of breeders of Finnish fledging production based on Fredrikson & Bregnballe (2000b) estimates of survival rate of adult birds, 8) Number of immigrant first-time-breeders = number of all first-time-breeders (section 5) minus number of first-time-breeders of Finnish fledging production (section 6).

nized nearly all the sea areas of Finland. Although fledging success is (especially in large colonies) at the same level as in western European colonies (Bregnballe *et al.* 1997, Krag 2003, Van Eerden & Gregersen 1995), the observed growth rate of the Finnish Cormorant population critically depends on immigration. The average growth has been 123% (R = 1.17), which is the highest recorded population growth of Cormorants when compared to other countries bordering the Baltic Sea. Maximal growth in Denmark was 43% in 1972, with an average growth of 23.8% during 1978–1992 (Bregnballe & Gregersen 1997, Van Eerden & Gregersen 1995). The maximal growth rate in Sweden was 43% in 1992, with an average growth around 30% during 1987–1994 (Engström 2001, Lindell 1997). In western Germany the maximal growth was 79%, with average growth of 45% during 1986–1992 (Menke 1997), in Poland the average growth was 55% during 1988–1992 (Przybysz *et al.* 1997), while in Estonia the average growth was 92% during 1989–1993 (Lilleleht 2004).

As in Finland, the population has increased intensively in neighbouring countries. In the Russian part of the Gulf of Finland, Cormorants were estimated to have started breeding between 1985–1990, when in 1994 two colonies (of 144 and 850–1,150 pairs) were found only a few kilometres east of the Finnish border (Rusanen & Gaginskaya 2003). These colonies have not been monitored since, but in 2000 the smaller one contained 790 pairs (Rusanen & Gagiskaya 2003). In Estonia, Cormorants bred for the first time since beginning of 20th century in 1983. In 1994 the population increased to over thousand pairs (1,425) for the first time, and in 2004 the population contained 8,010 pairs (Lilleleht 2004). In Latvia, Cormorants bred the first time 1989 (16 pairs) and in 1999 the population was 400–500 pairs (Baumanis *et al.* 1997, Latvian management plan for Cormorants). In Sweden, the second appearance of Cormorants started in the middle of 20th century and the most rapid increase of population occurred from 1,861 pairs in 1986 to 15,536 pairs in 1994 (Engström 2001). In 2000, the Swedish population was estimated at 27,300 pairs (Bregnballe *et al.* 2003). Although the growth rates of the Russian population are not known, the highest population growth rates of the Baltic Sea are found in the most northeastern countries in Finland and Estonia, indicating very high immigration intensity from other areas of the Baltic Sea (see also Table 3). Suitable breeding areas in the southern Baltic Sea area are probably getting filled and additional Cormorants are forced to disperse north to search for new breeding areas. This is supported by the results of Fredriksen & Bregnballe (2000a), who noted a clear decline in the return rate of 1-year-old birds (from 0.40–0.10) in a Danish colony from 1990–1997. This decline was partly explained by increased emigration. Since the 1990s Cormorant populations of a few western European countries (e.g. Netherlands, Denmark, Germany, Sweden) have started to become saturated (Bregnballe *et al.* 2003, Engström 2001).

Finland has a wide archipelago and even though Finnish ornithologists are searching every year around nearly all sea-areas a few colonies may not have been found during their first year. However, most of the colonies are well documented and their establishing year can be exactly determined by the observations of ornithologists and local laymen.

The spatial distribution of the colonization in Finland is interesting. In particular, it is puzzling that the colonization started from the eastern sea areas of Finland, although the Swedish side of the Åland Sea was colonized already in the 1980s. In Södermanland, in the province of Stockholm, Cormorants bred for the first time in 1989 (50 pairs) and in 1996 the population consisted of 1,615 pairs (Engström 2001). One unfinished Cormorant nest was found in the Åland Archipelago in 1981, but no observations indicating breeding in the area have been made since.

There are at least two reasons which may explain the low numbers of breeding Cormorants in the Åland archipelago and in the western Archipelago Sea. Firstly, the breeding population of White-tailed Eagles (*Haliaeetus albicilla*), essentially the only natural predator of older Cormorants, has increased rapidly in Finland since the 1980s. Eagles have been most abundant in the Åland archipelago and in the Archipelago Sea, increasing from around 30 pairs in 1990 to 130 pairs in 2002, constituting two-thirds of the Finnish population (Stjernberg *et al.* 2003). There are a few direct or indirect observations (feathers of Eagles or eaten Cormorants) that White-tailed eagles have visited Cormorant colonies during the breeding season in the colonies near Tammisaari (A. Lehikoinen & M. Kilpi unpublished), even though the White-tailed eagle is a scarce breeding bird in the Gulf of Finland compared to the Åland archipelago and Archipelago Sea (Stjernberg *et al.* 2003). The reason why colonies have been often established on the same islands as Herring gulls could be that Herring gulls actively protect their nests against avian predators (e.g. eagles) (Cramp 1985) and at the same time also protect nests of Cormorants. Eagles have also been noted to have an effect on the Common Eider population in the Gulf of Finland (Kilpi & Öst 2002).

Secondly, the spring hunting of waterfowls has been allowed only in Åland (from 15 March) and some areas of the Archipelago Sea (from 10 April). Although the Cormorant is protected by law and the spring hunters are shooting only diving ducks (see Tiainen *et al.* 2001), the disturbance of the hunters' boating and shooting noises may have caused Cormorants to choose breeding areas elsewhere.

The population of White-tailed Eagles of Finland has been estimated to increase so it may also slow down the increase of the Cormorant population. On the other hand, spring hunting may end soon because it is against the laws of the European Union (e.g. Tiainen *et al.* 2001). The effect of White-tailed Eagles on the breeding success of Cormorants should be studied in the future.

Cormorants have not yet bred inland in Finland, even though in Sweden 24% (including 73 colonies) of the Cormorant population bred on lakes in 1999 (Engström 2001). However, none of colonies were situated north of latitude 60º N (approximately at the same level as the city of Helsinki). Engström (2001) suggested that the reason could partly be a longer period of ice-cover on northern lakes, which makes it difficult for birds to accomplish the long breeding cycle. Nevertheless, Cormorants have already spread into the Bothnian Bay, where ice-cover breaks usually more than a month later than in southern Finland (e.g. Seinä *et al.* 2001), so there may not be climatic barriers for Cormorants to spread inland. Finland is a land with thousands of lakes and there are many suitably large lakes for Cormorants in southern Finland.

4.2. Breeding success

Central nests had a higher survival rate than edge nests. Central nest breeders bred earlier and were probably more experienced adults in better condition than edge breeders, who were possibly breeding for the first time. Coulson (1968) found that breeding success of central nests of colony breeding Kittiwakes (*Rissa tridactyla*) was higher than that of edge nests. He explained this difference in that males in good condition (heavier weight) are capable of occupying better central nest places first. Wittenberger & Hunt (1985) proposed that central nests are more sheltered from predators than edge nests.

In Sköldharun and Lerharun, the difference between central and edge nests could be explained by the higher proportion of late breeding, inexperienced first-time breeders on edge nests and the predation by Herring gulls. During the study year the colony was still growing rapidly, and thus a huge proportion of breeders were probably first-time breeders. The breeding success of young breeders has been noted to be lower than older and more experienced Cormorants (Bregnballe, in press). Late breeding in edge nests probably decreased the survival rate, since early breeders have higher breeding success (Daan & Tibergen 1997). In the study colony Herring gulls reduced the breeding success in edge nests, while central nests were safe in the middle of nests patches. In Sweden, Herring Gulls and Hooded Crows (*Corvus corone cornix*) have also been reported to be quite usual predators of Cormorant eggs and small young (Lindell & Jansson 1994).

The rate of loss of eggs or chicks was highest during the incubation and small chick (age 0–5 days) periods. After that the young are probably harder to catch, because of their bigger size. The mortality rate of Shags' chicks has also been reported to be higher during the first 10 days (especially the first four) (Snow 1960), when the chicks are totally or nearly featherless and dependent partly on the warmth of their parents (Ostnes *et al.* 2001).

The study method of determining fledging success differed from Newson & Bregnballe (2003) and Newson *et al.* (2005), who minimized the disturbance after clutch determination during the incubation time and counted fledglings from a distance using a telescope. In Finnish ground-breeding islet colonies such a method is impractical since it is not possible to count fledglings from the nests outside of the colony islet. Since one of the aims of this study was to estimate the mortality of different sized Cormorant young, the results could not be attained without occasional visits during the breeding season. During the study period Herring Gulls were seen a few times stealing eggs from the Cormorants nests during our visits. Thus study visits may have increased the natural predation rate of Herring gulls, even though Cormorants usually returned fairly quickly (after 1–5 minutes) to their nests when humans left the colony. The failure rate of edge nests was around the same as that noted in the Danish Vorsø colony (31–46%), an old study area (Bregnballe & Gregersen 2003). Additionally, the estimated fledging success of both sub-colonies was not remarkably low (1.57) compared to other studies in western Europe (range 0.2–3.8, usually between 1.0–2.5) (Bregnballe *et al.* 1997) and other colonies in Finland (see section 3.3., Fig. 3), thus the study visits have probably not markedly affected the mortality rate results.

After ringing the mortality was quite low, 1–1.5%, based on dead juvenile Cormorants found on the islets. Even though the study colonies were checked thoroughly during every visit, all the dead juveniles were probably not found, so the mortality rate of young birds (from 25-day-old to fledging) was probably higher than 1.5%. Nevertheless, mortality rate of older Cormorant young was much lower than that of small nestlings. In the Danish Vorsø colony, loss of young occurred rarely between the ages of 40 days and fledging (Krag 2003). Based on results, the number of young birds (25 days or older) available for ringing gives a good estimate of the number of fledglings.

Breeding success of bigger colonies was higher than smaller ones. The reason for this could be that smaller colonies have proportionally more edge nests that bigger ones. In smaller, just-established colonies the proportion of young and inexperienced breeders is probably higher than in bigger colonies (Bregnballe & Gregersen 1995) and young breeders have lower breeding success than older and more experienced Cormorants (Bregnballe, in press). Additionally, nearly all the study colonies were situated on the same islet with Herring Gull colonies (A. Lehikoinen unpubl.), so possible predators were present during the whole breeding season. In general, the most common results in avian studies of the interaction between colony size and breeding success have been that breeding success increases due to increasing colony size (27/54 cases) or that colony size has no effect on breeding success (25 cases) (Brown & Brown 2001). However, a few studies have noted a curvilinear trend in breeding success due to colony size with a peak in middle size colonies (Brown & Brown 2001). The effect of density dependence has been noted in large Cormorant colonies in western Europe. According to Van Eerden & Gregersen (1995), when a Cormorant colony grows big enough the food resources start to control the size of the colony and breeding success will decrease. Finally the growth of the colony will stop and the population may even decrease as has been observed in some Dutch and Danish Cormorant colonies (Van Eerden & Gregersen 1995). Since nearly all of the Finnish Cormorant colonies were fairly small and still growing during this study, the possible collapse in breeding success of large colonies could not be noted. So far, only one colony (Sköldharun-Lerharun, Table 1.) has shown signs of a saturated population, having been around the same size (about 600 pairs) since 2002.

4.3. Persecution

Illegal persecution was reported at least once in 43% of the colonies until 2004. This is remarkable, because in 2004 the species had bred for only nine years in Finland and most of the colonies have existed only a year or two. Human attitudes are negative against Cormorants in many areas and persecution occurred in all sea areas except the eastern part of the Gulf of Finland. Persecution has so far been more intensive than in Sweden, where during the period 1985–1999 19% of the Cormorant colonies were affected by occasional or repeated illegal actions (Engström 2001). In Finland these illegal actions have barely affected the growth of population. Only two colonies have vanished because of human disturbance, but illegal actions may have increased the establishment of new colonies. In Cormorants, uncontrolled persecution has been found to lead more rapid spreading to new breeding areas (Bregnballe & Eskildsen 2002, Veldkamp 1997).

All known persecutions have been reported during the hatching time, consisting of egg perforation, destruction of nests and eggs and egg removal. Illegal actions against young or adult birds have not been reported. In Finland most of the colonies have been established on the ground or in low bushes, but if persecution continues in the future Cormorants may start to settle more frequently in trees, where the nests are safer.

4.4. Studies for the future

Cormorant expansion to the northern Baltic Sea has occurred rapidly and the species has colonized vast areas, where it has probably bred before or at least for a few centuries. In Finland the population is still growing strongly. Cormorants interest humans as a potential threat to fishery and fish-farming and since this kind of colonization of large vertebrates is very rare and highly interesting from a population biological point of view, the expansion should be documented as accurately as possible in the future. This would give a unique opportunity to study nest site selection and density dependence of the population on the whole Baltic Sea scale. It would also give a tool for decision-makers to measure the economical losses caused by Cormorants. The possible controlling influence of White-tailed Eagles to the growth and colonization of Cormorant populations should be studied in the future.

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Merimetso kannankehitys ja pesintämenestys Suomessa

Merimetson *Phalacrocorax carbo sinensis* populaatio on runsastunut voimakkaasti Länsi-Euroopassa 1970-luvulta alkaen. Laji pesi ensimmäistä kertaa Suomessa vuonna 1996, jonka jälkeen populaatio kasvoi nopeasti yhdeksässä vuodessa kymmenestä parista 2 930 pariin. Kannankasvu on ollut voimakkaampaa kuin missään muussa Euroopan maassa perustuen hyvin pitkälti immigraatioon. Lajin lentopoikastuottoa tutkittiin useissa erikokoisissa yhdyskunnissa ja pesintämenestystä selvitettiin tarkemmin Tammisaaressa sijaitsevassa yhdyskunnassa. Pesintämenestys oli korkeampi kolonian sisäosissa olevissa pesissä kuin reuna-pesissä. Munien hävikki ja korkeintaan viisi päivää vanhojen poikasten kuolleisuus oli suurempi kuin vanhempien, yli viisi päivää vanhojen, poikasten. Lentopoikastuottoa oli korkein suurimmissa yhdyskunnissa. Tämän oletetaan johtuvan siitä, että pienemmissä yhdyskunnissa oli suhteessa suurempi osuus (1) nuoria kokemattomia pesijöitä ja (2) saalistukselle alttiimpia reunapesiä kuin suuremmissa yhdyskunnissa.

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Appendix 1. Breeding data collectors for each sea area.

Gulf of Finland: Tatu Hokkanen, Mikael Kilpi, Aleksi Lehikoinen, Juhana Niittylä, Jörgen Palmgren, Jarmo Ruoho, Pekka Rusanen, Henri Selin, Timo Tallgren, Veikko Tarsa, Aatu Vattulainen, Mikael Wickman.

Archipelago Sea: Esko Gustafsson, Esko Joutsamo, Kaius Hedenström, Mikael Kilpi, Aleksi Lehikoinen, Mikael Nordström, Tapani Ormio, Seppo Pekkala, Kalle Rainio.

Bothnia Sea: Pekka Alho, Mia Rönkä, Antti. J. Lind.

Quark: Tuukka Pahtamaa and Kari Pihlajamäki.

Bothnian Bay: Jorma Pessa and Jyrki Pynnönen.