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Effects of Great Cormorant Predation on Fish Populations and Fishery

BY

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Abstract

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The strong increase in number of Great cormorants *Phalacrocorax carbo* in Sweden in recent years has led to conflicts – particularly with fishery. This thesis focuses on the possible effects of cormorant predation on fish populations. In total, data from 15 lakes in South Sweden were included in this study while most studies were carried out in Lake Ymsen. The results suggest that the impact of cormorant predation on natural fish populations was small, and I observed no decline in fish mass after cormorants established. Cormorant predation on eel was difficult to evaluate because of several confounding factors.

Ruffe, roach and perch were the most important prey species to the cormorants and most fish taken were small. Cormorants do not seem to catch species and sizes in proportion to their occurrence in the fish community.

Total fish removal by cormorants varied considerably among lakes (0.2-15.0 kg/ha) and cormorant population sizes at the different lakes were significantly positively correlated with fishery catches, which in turn was significantly positively correlated with total phosphorous levels. Thus, cormorant densities in lakes, and perhaps elsewhere, seem to be governed chiefly by fish densities. The fact that cormorant predation appears not to reduce fish densities suggest cormorants to be regulated by other means than prey depletion. The mechanism behind population regulation could be a behavioural response of fish, making fish more difficult to catch for the cormorants.

In recent years, cormorant populations have been subjected to intensive legal and illegal actions with the aim to reduce cormorant numbers. However, the actions currently carried are well below the efforts needed to limit population sizes. To conclude, cormorants appear to compete little with fishery, with regards to free-living fish. The main problem is that cormorants sometimes damage and take away fish in fishing gears.

Key words: Great cormorant, *Phalacrocorax carbo sinensis*, predation, population regulation, diet, diet preferences, eel, behavioural responses, bird-fishery conflicts.

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This thesis is based on the following five papers, which will be referred to in the text by their Roman numerals.

I Engström, H. 2001. The occurrence of the Great Cormorant *Phalacrocorax carbo* in Sweden, with special emphasise on recent population growth. *Ornis Svecica* 11:155-170.

II Engström, H. 2001. Long term effects of cormorant predation on fish communities and fishery in a freshwater lake. *Ecography* 24:127-138.

III Engström, H & Jonsson, L. Great Cormorant *Phalacrocorax carbo* diet in relation to fish community composition in a freshwater lake. *Submitted*.

IV Engström, H & Olsén K. H. Roach *Rutilus rutilus* response to Great Cormorant *Phalacrocorax carbo* odour. *Submitted*.

V Engström, H. & Petersson, E. Great Cormorant *Phalacrocorax carbo* predation on commercial fish species – an evaluation based on long-term fishery statistics from 15 lakes in South Sweden. *Submitted*.

I have personally written, and collected the data for the papers. Erik Petersson performed most of the statistical tests in papers **II** and **V**. Håkan Olsén helped with the experimental set-up in paper **IV** and provided helpful comments on the manuscript. Leif Jonsson made the cormorant diet analysis for papers **II** and **III**.

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Introduction

Many animals interact with human interests and some cause conflicts, and, thus, are subjected to debate. In recent decades the population of great cormorants *Phalacrocorax carbo sinensis* has increased dramatically in Sweden, as well as in many other parts of Europe and, as a result, problems caused by cormorants on fishery have been brought into focus. The exceptionally strong increase and re-colonisation by cormorants of suitable areas have been met with mixed feelings. Many fishermen claim that cormorants have a negative effect upon fishery; i.e. fish populations become reduced and fish caught in fishing gears will be lost and/or damaged, which leads to economic loss. This has led to a number of calls to reduce cormorant numbers. However, conservation and animal welfare organisations have objected to such reductions on ecological and ethical grounds and in addition there is a debate among scientists if reductions of top predators actually lead to increased numbers of a target species (see Yodsis 2001).

Based on existing information, food is generally considered to be the most important factor in regulating seabird populations; the mechanism for such regulation, however, is not clearly understood. Lack (1966) argued, by using studies on seabirds, that populations are regulated by density dependence, mainly through density dependent mortality outside the breeding season. Ashmole (1963), however, suggested that seabirds are regulated during the breeding season and that this is due to depletion of food around breeding colonies. The arguments for food-based density-dependent regulation of colony size hinges on the ability of birds to substantially reduce food resources within the foraging range of the colony (Cairns 1992). Estimates of prey consumption around large seabird colonies suggest removal to amount to about 20-30 % of the local prey production (Cairns 1992). Because prey of most seabirds are very mobile and patchily distributed few attempts have succeed in testing Ashmole's prey depletion theory (but see Birt et al. 1987, Croxal & Rothery 1991). In Ashmole's prey depletion theory, populations become limited because of the successively longer distances individuals have to travel in search for food with growing colony size. Recently, Lewis et al. (2001) suggested that prey may become unavailable to birds because of disturbance when prey is attacked. Thus foraging may affect distribution of fish and thereby their local density. Apparently, food availability (either through depletion or disturbance) might be an ultimate factor behind population regulation of most seabird populations. The question still remains whether fish consumption, or disturbance of fish by foraging seabirds automatically leads to competition between fishery and fish eating birds?

There is no simple way to identify the potential for competitive interactions between fishery and seabirds. Seas and lakes are complex systems and it is usually difficult to separate effects of bird predation from other factors affecting the community. A simple way to look at "competitive" interactions between predators and fishery is as if it was symmetric. This means that if predators are removed from the system, prey they would have taken become available to fishery (the so called "surplus-yield calculation"). However, most aquatic systems are far more complicated than that. For example, if there is also a fish predator (or several predators) between the top predator (in this case the cormorant) and the target species, which is also eaten by the top predator, the outcome of a reduction is extremely difficult to predict (Yodzis 2001). For example, suppose that the top predator is reduced, this will also lead to fewer fish predators eaten, which in turn will lead to increasing pressure by the fish predator on the target species.

Modelling has been suggested as a possible tool to study predator-prey interactions when experiments cannot be used or are impractical (e.g. Yodzis 2001). However, the flexibility of cormorant feeding behaviour may greatly restrict the ability to use any model (e.g. Virtual Population Analysis or Multispecies Virtual Population Analysis) (Rice 1997).

Despite much effort to analyse and measure factors affecting population dynamics of seabirds and the impact of seabird predation on fish populations and fishery, much knowledge is still lacking. Variation in the surrounding environment makes it difficult to tease out the relative importance of different factors affecting fish populations.

Most attempts to assess effects of great cormorant predation on fish densities are based on theoretical, rather than actual data on fish numbers and biomass. For example, the potential for fish production and/or standing stock is compared against the consumption of the birds. Studies in marine environments (as opposed to small lakes) suffer from the weakness that fish can migrate in and out of the local area. There may be substantial predation effects, which cannot be detected if immigrants replace removed fish (cf. the 'depletion effect'). Likewise, fish immigrating out of a high-risk-area can mimic a predation effect (cf. the 'disturbance effect').

The recent increase and dispersal of cormorants to many inland lakes gave opportunities to follow changes in fish populations along with cormorant expansion. This also allowed for testing the hypothesis of prey depletion around colonies. I choose Lake Ymsen as my major study site. This lake was particularly well suited since it had a recently established cormorant colony, which was in the initial phase of its growth. Moreover, data on fish populations had been collected before the establishment of the cormorant colony. The possibility to make comparisons between conditions before and after the establishment of the colony provided opportunity to study the effects of cormorant predation.

One important question relative to the fisheries is whether cormorants have any preferences for particular species and/or size/age classes among prey. Such preferences could lead to changes in composition in the fish community. Fish are strongly dependent on available resources for growth; thus, removal of intra/inter specific competitors due to predation could lead to compensatory growth among surviving fish. This means that fish consumed by cormorants cannot be translated directly into decreased fish biomass.

Cormorants are likely to affect fish populations not only by removal of fish. Fish that live in the vicinity of cormorant colonies are frequently at a risk at being eaten. This exposure to cormorants could possibly elicit fish escape behaviours, and affect the distribution of fish, and thereby the local density of fish.

Main objectives and papers in brief

In this thesis, the main objective was to answer the question to what extent do cormorant affect fish populations, and in what respect numbers, biomass and composition? Therefor, it was essential to obtain data on fish populations, fishery catches, local cormorant population sizes and diet of cormorants.

Paper **I** summarises historical and present distributions of the great cormorant in Sweden. This paper also gives data on illegal persecution and management practises to control cormorant populations. The roles of these actions are evaluated in relation to population development. Paper **II** deals with long-term effects of cormorant predation on fish numbers and biomass in a freshwater lake. Fish removal by cormorants are estimated and compared to commercial catches. This paper also deals with the regulation of cormorant densities. In paper **III**, I examine cormorant diet in relation to fish community composition. This paper also evaluates effects of cormorant predation on size-frequency distribution of the main prey species taken. Cormorant predation on eel is given special attention by studies from recoveries of individually marked stocked eels. Paper **IV** explores if fish elicit escape behaviour when exposed to cormorant odour. In this laboratory experiment, cormorant odour was used as a cue for fish to perceive foraging cormorants. Paper **V** examines the role of cormorant predation on commercial fish species. Long-term fishery data from 15 lakes, holding important small-scale fisheries were evaluated in relation to cormorant population numbers and phosphorous levels.

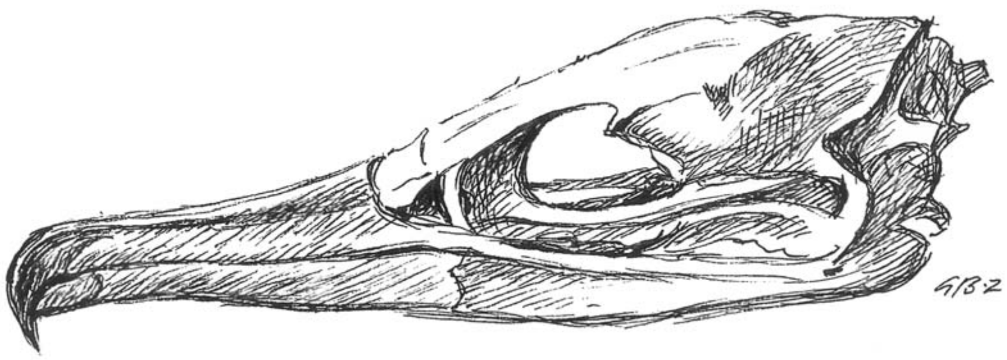
The species

There are about 40 species of cormorants (Phalacrocorasidae) in the world (Johnsgard 1993). The great cormorant is the most widespread species among cormorants and inhabits all continents except South America and Antarctica. Two subspecies breed in Europe: *Phalacrocorax carbo carbo* along coasts of Western Europe (France, Britain, Ireland and Norway) and *Ph. c. sinensis* in North-central Europe and locally across central Asia. The main countries inhabited by *Ph. c. sinensis* in Europe are Denmark (ca 42000 pairs), Sweden (ca 27000 pairs), the Netherlands (ca 19000 pairs) and Germany (ca 18000 pairs) (populations sizes are for 2000) (Bregnballe et al. in press). If not otherwise stated only *Ph. c. sinensis* are considered below.

Great cormorants are size dimorphic with males being larger than females (2612 vs. 2195g N=65, 86, own data). They breed in colonies, which occasionally may contain up to 8000 pairs (Bregnballe et al. in press). In Sweden maximum colony size is about 3000 pairs. The species is mainly migratory and birds breeding in Sweden over-winter in West and Central Europe south to coasts of North Africa.

Because of human persecution the great cormorant became extinct in many countries in Europe the 19th century or remained at low numbers (Zijlstra & Van Eerden 1989, Lindell et al. 1995). In the early 1970s only a handful of colonies existed in the Netherlands, Sweden and Denmark, and the total population in Europe consisted of no more than a few thousand pairs (Bregnballe 1996). However, due to several protective measures taken in various countries in the period 1965-1980 the population slowly started to recover. From about 1980, and in the following 10-15 years, populations of cormorants in several countries showed a spectacular population development with annual increases of 10-31% (Bregnballe 1996, Engström 2001b). In the Denmark, Sweden, The Netherlands and Germany a transition from high annual growth rates to a period of much slower growth occurred within a few years after 1992. This transition was caused by an almost simultaneous saturation within the core breeding areas, involving major declines in the largest breeding colonies (Bregnballe et al. in press).

In Sweden, the great cormorant has been an inhabitant of the Baltic region since the last ice age. Cormorant remains, found at archaeological excavations, have been recorded from more than 30 places in southern Sweden, including the provinces of Bohuslän, Skåne, Blekinge, Öland, Västergötland, Gotland and Uppland (see Ericson & Hernandez Carrasquilla 1997 for a full review). Some of the remains are from nestlings and juveniles (i.e. from Öland, Gotland and Uppland) which indicate the existence of breeding populations at that time. Based on bone sizes, the prehistoric Baltic cormorants appear all to have belonged to the nominate subspecies (*Ph. c. carbo*). When the former breeding subspecies *Ph. c. carbo* became extinct and replaced by present day *Ph. c. sinensis* is unknown, but the youngest remains of *Ph. c. carbo* found at archaeological excavations are from ca 800 – 975 AD (nestlings) and for adults ca 1300±50 AD. Probably, cormorants of the subspecies *Ph. carbo sinensis* became established for the first time in Sweden in the early 19th century. Cormorants established also in Denmark around this time (Jespersen 1949 in Berglund 1958). However, the 19th century population of *Ph. c. sinensis* of Southeast Sweden appear to have been small and probably due to systematic persecution the cormorant disappeared as a breeding species in Sweden sometime in the late 19th or early 20th century (Neander 1918).



Material and methods

In paper **I**, data on cormorant populations and illegal actions carried out against cormorants were collected from a great number of ornithologists throughout Sweden. Officials at various County Administrative Boards provided data on legally shot cormorants and colonies open for egg pricking. Answers to questions dealing with developments of fish populations in relation to increasing cormorant numbers, and diet of great cormorants (papers **II** & **III**) were collected during five years of field work (1995-1999) at Lake Ymsen (Fig. 1), located in the province of Västergötland and Lake Garnsviken, located in Uppland. Both lakes had been sampled at several occasions during the 1980s and early 1990s by the County Administrative Board of Skara and the Institute of Freshwater Research. To sample fish populations, I used multi-mesh gillnets (standardised test fishing), a method that permits comparisons of catch per unit of effort (Appelberg 2000). Cormorants established in Lake Ymsen probably in 1987 but the colony remained small until 1995 when it suddenly increased rapidly in size.

The birds' diet (paper **III**) was studied by examination of fish remains found in pellets. Pellets were collected during the breeding season on the ground at Lake Ymsen colony. Bones were measured and original fish lengths calculated from a series of allometric equations. Species identification and size determinations were made with help of a collection of fish skeletons from species of known size (all identifications made by Leif Jonsson from his own reference collection). To study food preferences of cormorants I compared results from diet studies with results obtained from test-fishings.

Cormorant fish removal among the different lakes was estimated by multiplying population size, number of bird days, daily food intake (DFI) and proportion of time spent by cormorants in the focal lake relative other lakes. In Lake Ymsen, foraging cormorants was observed from observation plots around the lake, at different times during the day and the breeding season.

Studies of behavioural responses of roach to great cormorant odour (paper **IV**) were carried out at the Department of Environmental Toxicology (Uppsala University). The behavioural reactions of roach to the test substance/controls were examined in an avoidance/preference aquarium. Fish was taken from two populations: one sample from a cormorant-free area in Lake Mälaren (near Drottningholm, Stockholm), as roe, and raised at the Institute of Freshwater Research, and the other population come from Lake Ymsen. We prepared cormorant odour from two semi-tame cormorants held at Skansen Zoo in Stockholm.

The test-water was prepared by letting a cormorant stay in a large plastic container holding 25 litres of water.

Data on commercial catches of fish (paper **V**) were collected from the Institute of Freshwater Research (Örebro) and from Fishery Officials at various County Administrative Boards. On average, lakes had 33 years of data (range: 7-87 years). Figure 1 shows locations of the lakes. We took personal contact with all fishermen presently known to be active in the lakes (except for those fishing in the four greatest lakes) to inform us about any major changes in fishing practices or fishing efforts over the time. Among the different lakes, cormorants established between 1989 and 1996. Using long-term fishery data meant that fish populations could be compared with and without foraging cormorants. Data on total phosphorus (TP) at the different lakes were collected from a database at the Faculty of Environmental Assessment (Agricultural University of Uppsala) and from County Administrative Boards.

Fig. 1. Locations of study lakes in South Sweden.

Results and discussion

RECENT POPULATION DEVELOPMENT IN SWEDEN (**I**)

The recent history of the cormorant in Sweden begins at Svartö in southern Kalmar Sound where cormorants established in the late 1940s (Berglund 1956; Berglund 1958). Until 1986, Svartö and Gåsö (established in the early 1960s) were the only cormorant colonies in Sweden. A dramatic change in the population development occurred at around mid 1980s when the population suddenly increased tremendously in size. For example, between 1986 and 1987, the population rose on average by 33 % and new colonies were founded in the provinces of Blekinge, Västergötland, and the year after also in Östergötland and at several sites in Småland (Fig. 1). During a period of almost exponential increase (i.e. 1986 to 1994) the number of pairs increased from 1800 to 15500 pairs. After the mid-1990s population increase levelled off in most of the core breeding areas located along the southern and eastern coasts in Sweden south of Södermanland (in particular in Skåne, Blekinge, Östergötland and Småland). These provinces held 59% of all nests recorded in Sweden in 1999. Growth levelled off mainly because some of the oldest and largest colonies ceased to grow or even declined in size. After 1995, population growth, at high annual rates, has taken place in more northern breeding areas along the East Coast (especially in Södermanland, Uppland, and on Gotland), and in many freshwater lakes far inland. The population size in Sweden in 1999 comprised of ca 25200-26000 pairs distributed over about 154 colonies (Fig. 2 and 3). The current size of great cormorant population means that Sweden holds about 25 % of the total Northwest European population of *Ph. c. sinensis*.

The success of the great cormorant in Europe, including Sweden, shows many similarities with the closely related and equally successful double crested cormorant *Phalacrocorax auritus* in North America (Hatch 1995). Several factors are though to have contributed to the recovery and strong increase of *Ph. c. sinensis* during the last decades. For example, recent studies indicate an exceptional high survival of immature and adult birds during the period of strong increase (i.e. 1970-90s), and in Denmark it was shown that first year survival was much higher (0.42-0.75) than for the fairly stable population of *Ph. c. carbo* breeding along the Norwegian coast (0.19-0.38) (Frederiksen & Bregnballe 2000). Protection is thought to have played a central role, and the European population of *sinensis* began to increase after the species had been protected in the Netherlands in 1965. In Denmark the cormorant was given partial (1971) and full protection in 1977. In 1980, the great cormorant was given full protection in all the member states of the European Union, according to the EU Birds

Directive. In Sweden, before the EU association in 1995, there was an open hunting season on cormorants, lasting from 21 August to 28 February. This hunting, however, probably had little effect on the population since a majority of the cormorants had left Sweden for their winter quarters at that time.

It has been suggested that foraging conditions have been exceptionally good in later decades and contributed to the strong population increase of great cormorants in Europe. Improved foraging conditions are partly due to increased productivity related to eutrophication and, thus, more fish have became available to the cormorants. Moreover observations suggest that great cormorants has changed habit from fishing mainly solitary to fishing mainly in groups. This change in foraging habit has been interpreted as a response to turbid underwater conditions with high stocks of pelagic fish (De Nie 1995; van Eerden & Voslamber 1995). To conclude, protection seems to be the most important factor behind the success of the great cormorant in recent decades, though its habit of feeding on a variety of fish species, at almost all kinds of waters, obviously also have contributed to the strong population expansion.

EFFECTS OF CONTROL MEASURES ON CORMORANT POPULATIONS IN SWEDEN **(I)**

The return of the great cormorant has been so successful that conflicts have come into existence in many areas. This has led to a pressure from, mainly, fishery organisations to reduce cormorant numbers. In the management recommendations for the great cormorant in Europe, it is suggested that each country, or regional authority, should attempt to reduce these conflicts by local solutions (Anonymous 1997). In 1995, Sweden joined the European Community and the open hunting season on cormorants had to be abolished. Due to increasing conflicts between cormorants and mainly fishery interests, local authorities have in several areas decided upon widespread control actions during the last 10 years. In addition to management practises approved by local authorities, a number of illegal actions against cormorants have taken place in the last 10 years. Legal measures to control cormorants have involved mainly shooting of birds at or near standing fishing gears and egg pricking at colonies. Up to now, egg pricking is known to be carried out in at least 19 colonies in Sweden during the last 15 years, and reported shooting involved between 895 and 3864 birds per year (1994-2000).

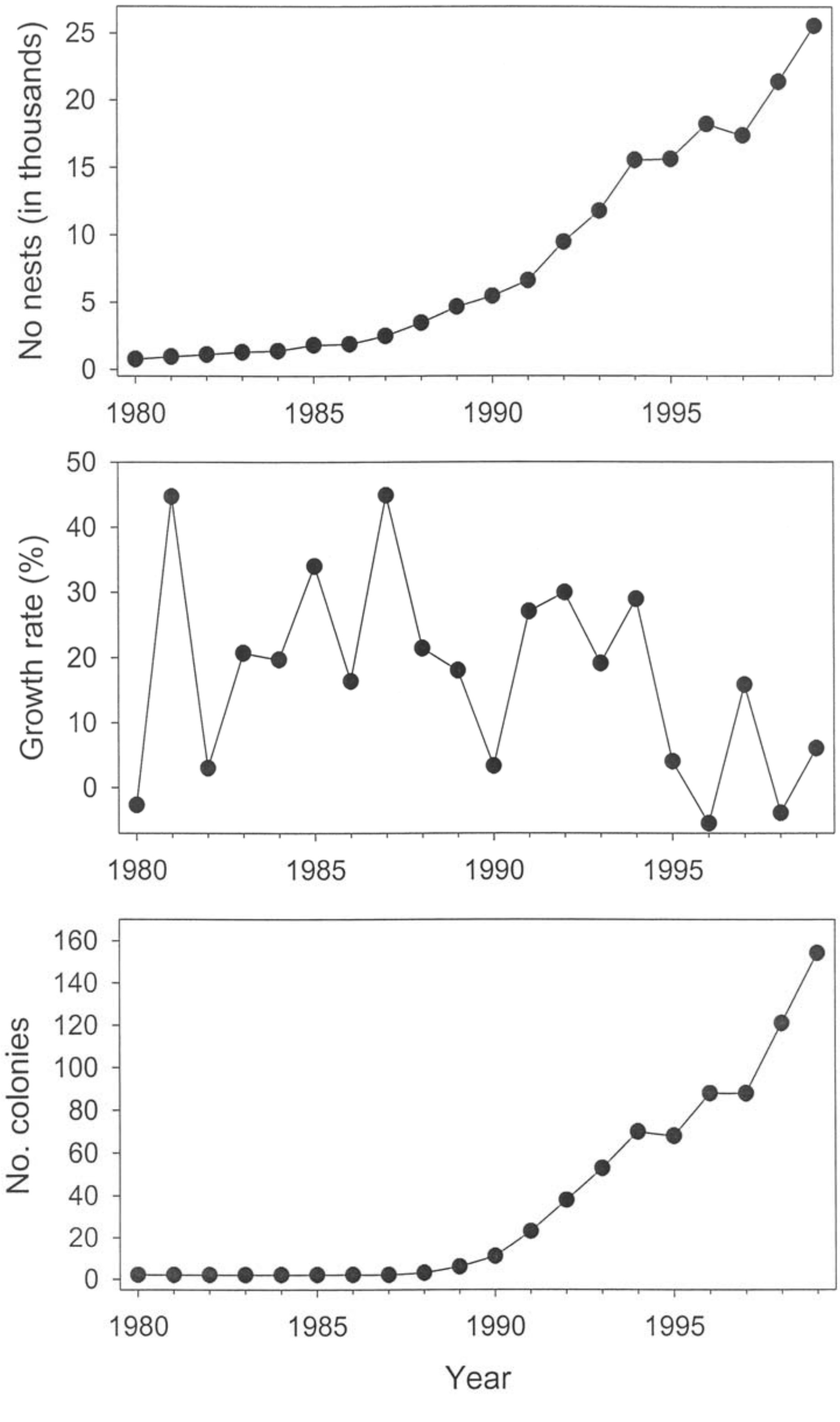


Fig. 2. Development of the breeding population of great cormorants *Phalacrocorax carbo* in Sweden, 1980-1999, expressed as number of assumed occupied nests, the annual rate of increase, and the number of colonies (including sites also with only single nests).

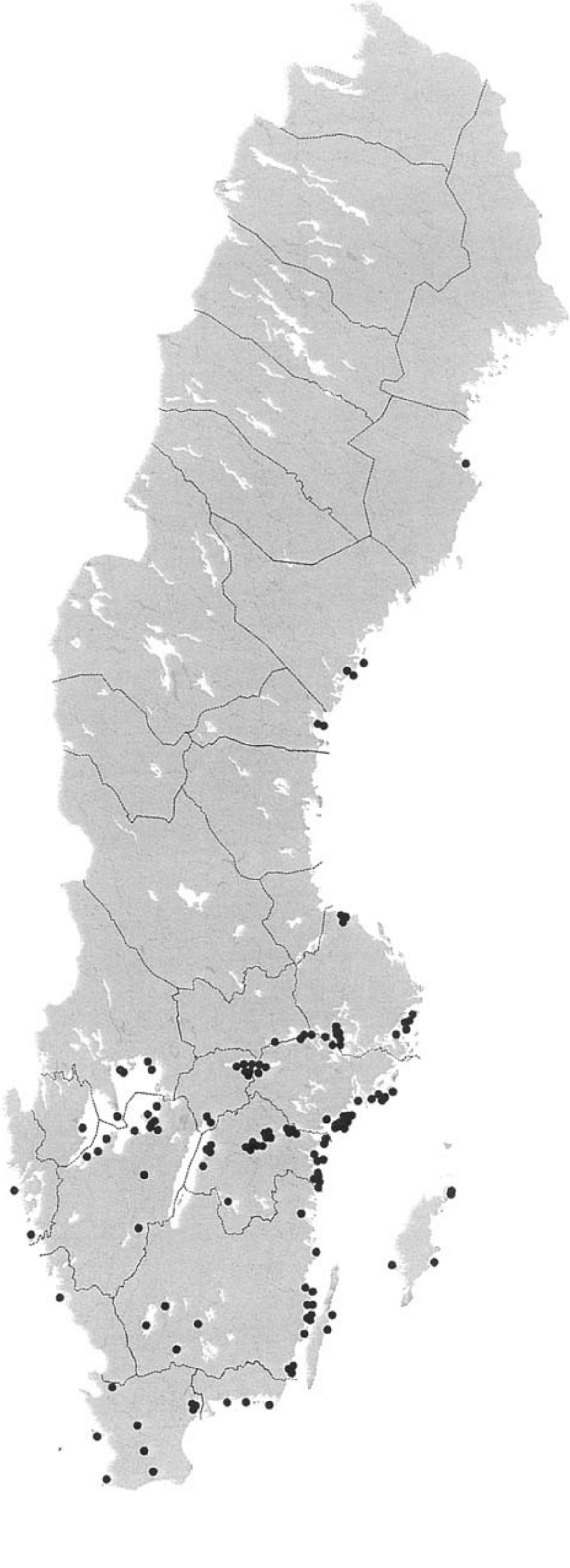


Fig. 3. Great cormorant *Phalacrocorax carbo sinensis* colonies in Sweden in 1999. Total population consisted of about 25 600 pairs distributed on about 154 colonies.

For many years, management actions against cormorants have been most intense in the provinces of Småland and Östergötland. However, with expanding cormorant populations legal and illegal actions have increased, and permits to shoot cormorants in order to protect fishing gears and fish therein, and/or egg pricking are currently issued by 11 of 16 local authorities where cormorants breed.

The effects of hunting, on the Northwest European population of great cormorants, have recently been studied by Frederiksen et al. (2001). In a model they studied the interaction between hunting and density-dependence in regulating population sizes. The most well-supported scenarios indicated that the effect of hunting at the present level (1998/99: 17000 cormorants reported shot) was small (<10% reduction in population size when they are at equilibrium). In their model the total European population was assumed to consist of 500000 individuals (100000 breeding pairs). When removal was increased to 65000 birds per year a critical level was reached and the population started to decrease in size. Converted to the Swedish situation, of an estimated 127000 individuals (25600 breeding pairs x correction factor 4.7-5.2 = 120000-133000 ind. [correction factor: personally from M. Frederiksen]) the critical level (13%) would be at 16000 - 17000 birds shot per year. Data from Sweden indicate the number of shot cormorants never have exceeded 4000 per year. Hence, it seems as if local reductions carried out, in terms of number of shot birds, so far only can have a marginal effect, when the whole Swedish population is considered.

What do we know about the effects of hunting and egg pricking on populations on a regional scale? When cormorants nest in trees and the trees are felled, the cormorants do not return, or return only by some few pairs in the following year(s). However, when cormorants nest on ground and eggs are pricked, the cormorants seem to be more reluctant to leave their sites (at least so for old colonies) and cormorants sometimes continue to use the sites for several more years. However, when colonies are subjected to repeated disturbance, year after year (e.g egg pricking), numbers are usually much reduced and sites finally abandoned. What happen to birds that are forced to leave a former breeding site, for example when nesting trees have been cut or after repeated egg pricking at ground breeding colonies? It seems as if the cormorants most likely will move to another site, as long as there are some protected and/ or undisturbed sites available to them. Only when such safe sites are limiting to the birds (or when cormorants are regulated by other means, e.g. by food availability) the number of birds within a region could be expected to level off or decline. At present, cormorants in Sweden appear, in general, not to be limited by the amount of suitable sites for breeding, and when disturbed cormorants can, more or less freely, move to other sites. Moreover, when areas with low disturbance (e.g. the coastal areas of Skåne and Blekinge) are compared with areas with extensive disturbance (e.g. the coastal areas of Småland Östergötland), populations stabilised at about the same time, and most likely other factors than hunting and disturbance are responsible for the stabilisation in population numbers.

DO CORMORANTS DEPLETE FISH POPULATIONS? (**II**)

Results from survey net samplings carried out in Lake Ymsen indicate that cormorant impact upon fish populations was small and probably in no case have led to declines of neither commercial nor non-commercial fish species (Engström 2001a). For example, there was no significant change in number or biomass over the study period (comparing periods with low, vs. high foraging pressure) of any of the five most commonly caught fish species (i.e. perch *Perca fluviatilis*, pikeperch *Stizostedion lucioperca*, bream *Abramis brama*, ruffe *Gymnocephalus cernuus* and roach *Rutilus rutilus*). Non of the correlations fish number - cormorant density and fish biomass - cormorant density, for any of the five fish species showed significant values (Table 1). Why was there no effect? First, it should be noted that given the large variation in survey-net catches between years it is difficult to obtain a significant result (Table 2). On the other hand, if the cormorants have had a profound effect on fish populations, such as dramatically altering fish densities (which was not the case), this would clearly have been discerned here.

Table 1. Pearsson correlation on cormorant number (pairs) and fish number and biomass of Lake Ymsen.

	corr. coeff.	P-Value
Bream number	-0.2	0.6
Bream biomass	-0.3	0.5
Perch number	-0.3	0.4
Perch biomass	-0.6	0.1
Roach number	-0.7	0.06
Roach biomass	-0.4	0.3
Ruffe number	0.3	0.5
Ruffe biomass	0.4	0.4
Pikeperch number	0.5	0.2
Pikeperch biomass	0.6	0.1

Table 2. Power analysis on fish number and biomass of Lake Ymsen.

	power %
Bream number	6
Bream biomass	11
Perch number	10
Perch biomass	7
Roach number	61
Roach biomass	5
Ruffe number	9
Ruffe biomass	8
Pikeperch number	46
Pikeperch biomass	7

The pattern of population development of the Lake Ymsen cormorant colony suggests that the colony is near its maximum size in relation to fish availability. The colony size corresponds to 6.4 breeding pairs km^{-2} (1998) which is among the highest values recorded for lakes in Sweden. However, it is lower than average of values found for in-land lake colonies in the Netherlands, i.e. 9.6 breeding pairs km^{-2} (van Eerden and Gregersen 1995). These differences probably most likely reflect local differences in fish productivity related to lake morphology, temperature regime and nutrient conditions. The high number of cormorants present in Lake Ymsen in relation to foraging area means that a considerable amount of fish is being withdrawn annually from the lake. Current out-take is estimated at 17 tons per year (ca 13 kg ha^{-1} $year^{-1}$) compared to 12 tons (ca 9 kg ha^{-1} $year^{-1}$) taken by the commercial fishery. Similar high figures, for fish out-take by cormorants, was found by Dekker (1997) at Lake Ijssel. Suter (1995) reported 18-22 % of the annually recruited stock of greyling *Thymallus thymallus* to be consumed by cormorants without hampering greyling populations. Linn & Campell (1992) considered a consumption of 17% of fish biomass by cormorants to be sustainable by the fish populations.

Lake Garnsviken (reference lake, without cormorants) and Lake Ymsen most fish species varied considerably in population size between years. Most likely, these variations reflect differences in the recruitment of fry, related mainly to water temperature, which may give rise to strong year-classes (Willemsen 1977, Mills et al. 1987, Buijse & Houthuijzen 1993, Dekker 1996). In Lake Ymsen, particularly large variation was recorded for pikeperch, which also showed a strong increase in both number and biomass towards the end of the test-fishing period. The increase of pikeperch in the survey net catches was also supported by a very strong increase in the commercial catch of pikeperch over the period 1994-1998. This increase most likely was due to stocking. Notable is the apparently stable population of ruffe, the most important species (by number) in the diet of the cormorant, which made up 47-75% (by number) of all fish consumed by Lake Ymsen cormorants. The seemingly unaffected population size of ruffe clearly suggest a high potential of this species, on the population level, to withstand extensive cormorant predation (see also Dirksen et al. 1995).

THE REGULATION OF CORMORANT DENSITIES (**II** & **V**)

As mentioned earlier food is generally regarded as a key factor behind distribution of cormorants as well as other piscivorous seabirds (Birkhead & Furness 1984, Furness & Birkhead 1984, Cairns 1989, Croxall & Rothery 1991, Lewis et al. 2001). Thus, because more fish are found in shallow and nutrient rich lakes, than in deep and nutrient poor lakes, more cormorants are likely to be found there. Data (**V**) support this idea, and cormorant densities (pairs/km^2) were much higher, for example, in the nutrient rich lakes Ymsen, Glan, Roxen than in the nutrient poor lakes Bolmen, Vänern and Vättern (Table 1). In some lakes, cormorants seem to forage almost entirely at the lake where they breed. For lakes where birds utilise several lakes, information on the proportions of time spent foraging at the different lakes were often missing and, hence, it is difficult to relate cormorant densities to food supplies at these lakes (**V**). However, from lakes with acceptable information a significant correlation was found (p=0.04) between number of cormorant pairs per lake-area and total phosphorous levels (Fig. 4). This correlation would probably have been even stronger if cormorants were at "equilibrium" with respect to food supplies at all lakes. For example, the populations at lakes Vänern, Mälaren and Hjälmaren are still growing while populations at lakes Roxen and Glan appear to be over-satiated in relation to food. The population at Lake Ymsen is probably satiated while the population in Lake Bolmen appears to be small relative food supplies. It would be unrealistic to think that food is the only important factor in determining cormorant densities. However, population control measures carried out in recent years appear in general not to have had any major impact upon population size (Engström 2001b, Frederiksen et al. 2001). So, based on results from this study, I propose that lake-productivity in terms of fish supplies (here measured as total phosphorus, or fishery yield per area unit), is the key-factor behind distribution of lake breeding cormorants in Sweden.

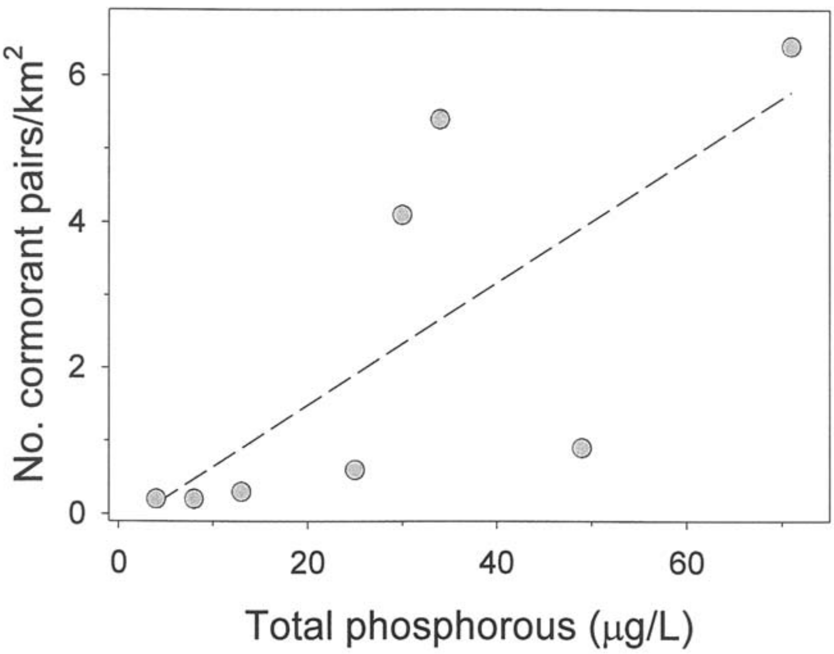


Fig. 4. Cormorant densities in relation total phosphorous (TP). Data on cormorant densities and TP are from lakes Ymsen, Roxen, Glan, Hjälmaren, Mälaren, Vänern, Vättern and Bolmen.

This mean that total phosphorous can be used as a rough measure to predict the potential for cormorant numbers at lakes hitherto unexploited, or at lakes with still expanding cormorant populations. The result from Lake Ymsen indicated no depletion of fish populations with increasing population size. This raises the question why the cormorant colony does not continue to grow in size, despite the seemingly good food conditions in the lake. For example, several other colonies in the surroundings of Lake Ymsen were still growing between 1995-1998, which indicate that the population as a whole not yet has reached carrying capacity. The question why cormorants breeding in Lake Ymsen regularly forage at other nearby lakes can also be asked. Nesting sites presumably do not regulate the colony size since there are still available trees on the island to build nests in. No data on breeding performance is available from Lake Ymsen colony, but data obtained at colonies in Denmark suggest density-dependence primarily to be operating at the summer grounds. For example, it has recently been demonstrated that young birds postpone first breeding to an older age after the colony had reached its maximum size (Frederiksen & Bregnballe 2001; Bregnballe & Gregersen in press). This may depend on (1) poorer feeding conditions during chick rearing, (2) poorer feeding conditions outside of the breeding season, or (3) lower food availability around the colony in early spring. The authors suggests a combination of the first two explanations, because the cormorants in their study area do now not attain full breeding plumage until older age as compared to the 1980s (J. Gregersen & T. Bregnballe unpublished in Bregnballe et al. in press).

If the Lake Ymsen cormorant colony is “prevented” from further increase during the breeding period, this must be so due to some mechanism(s) other than depletion of prey numbers or biomass. A potential candidate would be a behavioural response of fish, making them more difficult to catch for the cormorants. Such a mechanism has recently been suggested for gannet populations in the North Atlantic (Lewis et al. 2001). Data on cormorant foraging patterns showed that cormorants breeding at Lake Ymsen (at which site they spent about 79% of their foraging time) regularly also use other lakes for foraging. One explanation for such movements may be that food can be obtained at an equal cost at other lakes despite increased distance of flying. For example, the nearby Lake Östen, 7 kilometres south of Lake Ymsen, is known to hold very dense populations of several fish species (J. Swahn pers. comm.). The reason for moving to another lake may be that cormorants induce changes in fish behaviour at their breeding lake, which may make fish more difficult to catch, for the cormorants (see also van Eerden and Voslamber 1995). To conclude, based on data from Lake

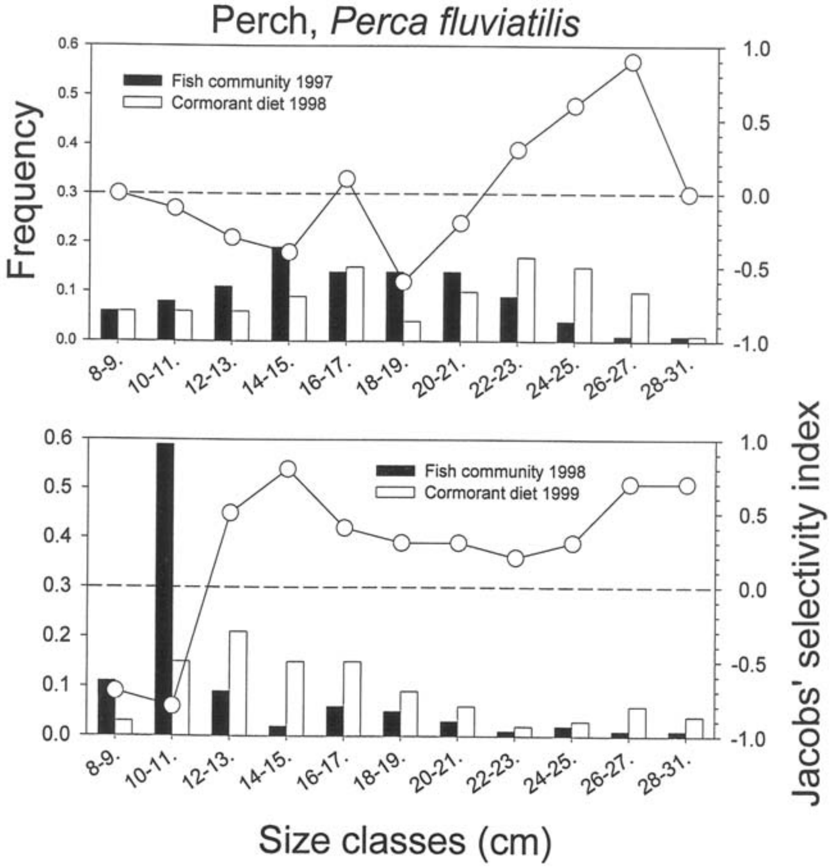
Ymsen, I found no evidence for major changes in fish populations due to cormorant predation.

DO CORMORANTS PREFER CERTAIN SPECIES AND SIZES OF PREY? (**III**)

It is not merely fish numbers or biomass that may change as an effect of cormorant predation. Predation could affect species composition of the fish community and size structure of different species. In that respect it is important to test if cormorants show preferences for any particular species and sizes. A total of 2789 fish individuals belonging to 10 fish species were identified from 132 pellets during the three sampling years. By numbers, the cormorant diet was clearly dominated by ruffe in all years, followed by roach and perch. Except for these three species no other species made up any significant part in the diet, and these three species comprised between 85 and 96 % of the total diet (by number) during the three sampling years. On the basis of weight, the species composition deviated somewhat from that based on numbers. Based on mass cormorant diet consisted mainly of perch (28-46%) followed by pike (13-30%), ruffe (14-25%) and roach (8-20%). Ruffe made up a higher proportion in the diet than in the fish community in all three years comprising 57% of the diet vs. 47% in the fish community in 1995/96, 75% vs. 14% in 1997/98 and 47% vs. 20% in 1998/99 (Table 1). In contrast, roach (all years) was less (sometimes much less) common in the diet than found in the survey-net catches. Perch was, in two out of three sampling years, less common in the diet than in the survey-net catches. On the other hand, perch weighed more than ruffe and roach and hence contributed to a larger proportion of the biomass.

The presence of the different size-classes of ruffe, roach and perch in the cormorant diet and size-curves of the same species in the fish community are shown in Figure 5. The overall pattern for the three species point at a miss-match for most size-classes; i.e. cormorants do not take them in proportion to their occurrence. This miss-match was most obvious for the smallest size-classes, and particularly pronounced for perch (<120 mm) but also present for ruffe and roach, which occurred in lower (sometimes much lower) frequencies in the cormorant diet than found in the fish community.

Why was ruffe caught to such a high degree although roach and perch were of larger size (more energy gained by per capture) and constituted a larger portion of the fish community? One explanation may be related to the fact that Lake Ymsen cormorants forage almost exclusively solitary and not in-groups.



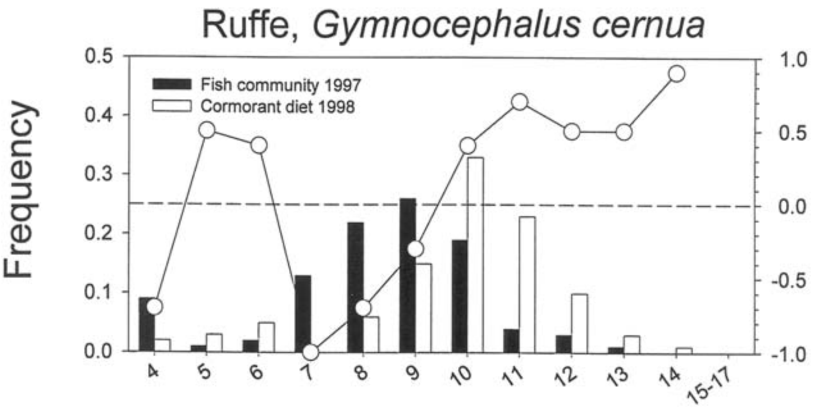
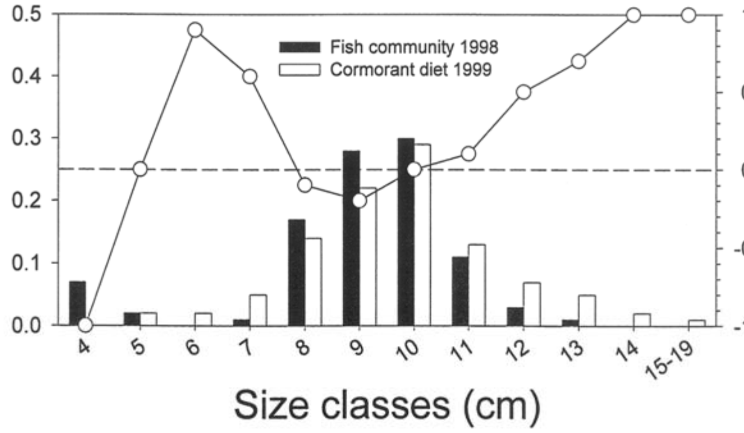
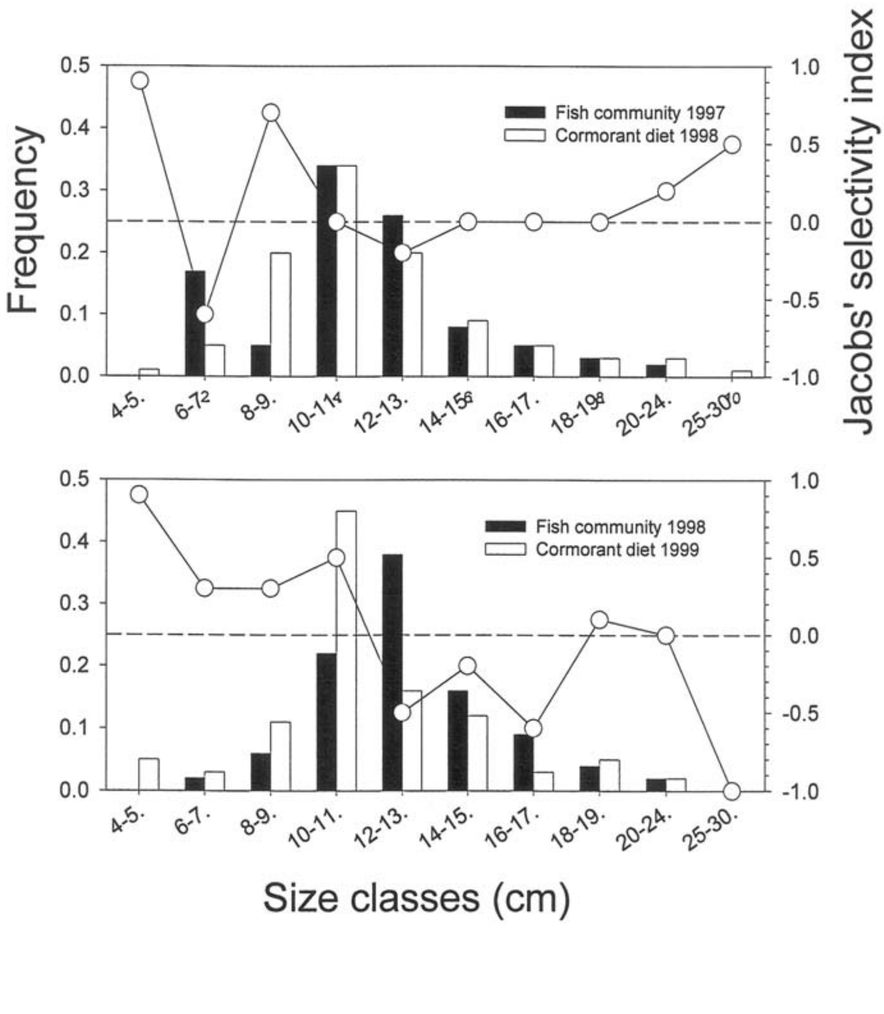


Fig. 5. Great cormorant diet in relation to fish community composition of Lake Ymsen. The left y-axis shows fish community composition in relation cormorant diet. The right y-axis shows Jacob's selectivity index. Values larger than 0 (dotted line) indicate preference. Values smaller than 0 indicate avoidance. Range - 1(complete avoidance) to + 1 (complete preference). Cormorant diet is based on pellet analysis and fish community data is based on multi-mesh gillnet sampling. To allow comparisons of fish size class distributions of ruffe, perch and roach in the cormorant diet (data collected in April and May) with size curves obtained from test fishing (August), data from pellet analysis in one year were compared with the previous year test fishing data. This was done to minimise discrepancies of fish sizes related to somatic growth between the two sampling occasions. Test-fishing data corrected for species and size selectivity.

Ruffe, *Gymnocephalus cernua*



Roach, *Rutilus rutilus*



Van Eerden & Voslamber (1995) described social fishing with cormorants as concentrating and exhausting the fish at the same time as fish are pushed from the dark zone into the top layer where they are caught. This type of fishing would presumably be equally effective regardless of fish size. On the other hand fishing solitary (probably based more on surprise attack or short chasing than by exhaustion of prey) possibly would be less efficient on relatively large shoaling fish (i.e. perch & roach) with higher swimming speed, than hunting for relatively small slow moving prey (i.e. ruffe). For example, the maximum swimming speed (m/s) of fish is roughly estimated to be ten times its body length in metres (Van Eerden & Voslamber 1995) and consequently escape speed would on average be slower for ruffe than for perch and roach.

The number of breeding cormorants in Lake Ymsen is well below the size that is considered to be minimum level to make group fishing profitable (Van Eerden & Voslamber 1995). Then, if pelagic shoaling fish cannot be exploited efficiently by solitary fishing cormorants the only fish of numerical importance that remains to feed upon is the ruffe. Furthermore, if populations of roach and perch would have been easy to exploit to the cormorants those species should have been taken to a still larger extent than observed here, both because they are more numerous than ruffe and because their mean weights are higher. A large share of ruffe in cormorant diet has been demonstrated also in other studies (e.g. Dirksen et al. 1995, Adams & Maitland 1998) and possibly this species is easy to exploit for cormorants.

The importance of eel *Anguilla anguilla* as a prey to the cormorants is among the most intensively debated questions related to cormorants and their diet. Based on results from Lake Ymsen eel seem to be a rare prey in the cormorant diet and was represented by only 0.07 % by number (0.7 % by weight). Since eel cannot be caught in survey nets, I was not able to relate its presence in the diet to its presence in the fish community. The importance of eel in the cormorant diet in this lake was studied also by PIT-tag-marking (Passive Integrated Transponders) of stocking eels. One year after the majority of the marked eels (1717 ind.) had been released into the lake, the ground at the cormorant colony-island (containing 60-70% of the nesting trees) was searched and 3 PIT-tags were found. To what extent the proportions of eel found in the cormorant diet in this lake can be considered representative for Swedish lakes in general is difficult to say, but if also considering samples also from lakes Vänern, Ivösjön and Ringsjön, the eel appears overall, to be represented only by small numbers in the bird's diet (Lindell 1997, Engström 1998, Engström unpubl.).

If data on cormorant diet collected half a century ago is compared with recent data, the proportion of eel has declined markedly (see Madsen & Spärck 1950, Van Dobben 1952). This decline of eel in the cormorant diet is much larger than changes in the populations of eel. Van Dobben (1995) suggested this change to be partly related to eutrophication, which makes the eel difficult to see for the cormorants (Van Dobben 1995).

I examined possible long-term effects of cormorant predation on the size-frequency distribution of ruffe, roach and perch populations. Only for these species net-selectivity correction factors (see Appelberg 2000) are presently available and reliable size-curves can be constructed. Data from Lake Ymsen indicate that cormorant removal did not seriously affect the population structure of these species. For example larger size-classes were not absent when cormorant foraging pressure was strong (Fig. 6).

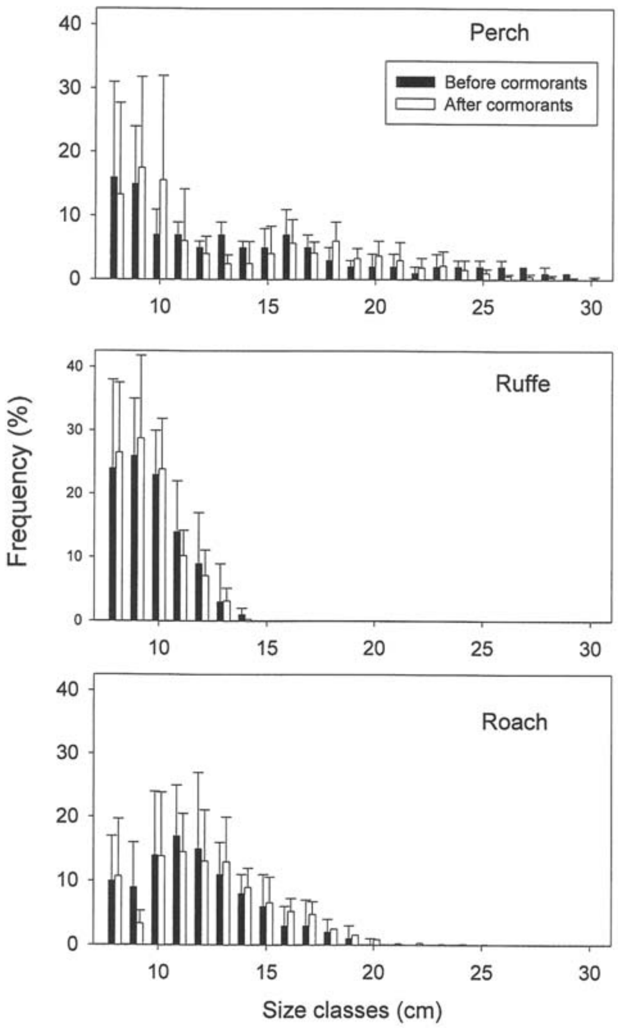


Fig. 6. Size-frequency distribution of perch, ruffe and roach in Lake Ymsen during years with no- or low cormorant foraging pressure (period 1; open bars) and years with extensive cormorant foraging pressure (period 2; solid bars). Data based on multi-mesh gillnet sampling.

BEHAVIOURAL RESPONSES OF FISH TO CORMORANT PREDATION (**IV**)

The cormorant is a bird that lives in colonies and in the vicinity to colonies fish will perceive frequent encounters with their predators. This exposure to cormorants could potentially elicit escape behaviour of fish. Many studies have shown that animals, fish included, respond behaviourally upon the risk of predation (Lima & Dill 1990). In this paper cormorant odour was tested as a possible cue for roach to perceive foraging cormorants. To separate possible genetic factors from experience roach were collected from two populations; one lake harbouring cormorants and one lake without cormorants. In this experiment roach did not respond to water treated with cormorant odour. Moreover, there was no major difference in the response of naive fish compared to fish with possible experience of cormorants. To our knowledge, chemoreception of fish to cormorants has not been studied before, and it is unknown if fish are able to perceive the presence of cormorants by chemical cues. Martel and Dill (1993) found that salmon responded to a stimuli-mixture of red-breasted mergenser *Mergus mergenser* and Mergenser's diet (coho salmon *Oncorhynchus kisutch*). However, this study did not discriminate bird odour, alone, from other chemicals, such as alarm substances released upon skin damage from consumed fish. Alarm substances are present in the skin of cyprinids, and, has recently been shown to be present also in Salmonides (Brown and Smith 1997), and several other fish, and is released upon mechanical damage of the skin. Residues of the alarm substances may also "leak" from piscivores and allow prey to associate odour of fish with the risk of predation (Mathis & Smith 1993; Mathis et al. 1996). In this study the cormorants were not fed for 24 hours prior to odour preparation of water, to reduce the risk of contamination of stimuli-water with alarm substances, which otherwise could come from recently consumed fish. By giving the cormorants roach (their normal diet consists of herring) we also tested if cormorants can be scented by this diet. Thus, our experimental set-up enabled us to study the effect of chemicals emitted from cormorants, alone, on roach, and not alarm substances. Krill odour was used as control, to which roach from Lake Ymsen (the cormorant lake) responded significantly by increased locomotor activity, while naive roach from Lake Mälaren did not respond to krill odour.

Several factors may explain the absence of response of roach to cormorant odour. First, other cues, such as vision, noise or currents created by diving birds may be more important, and efficient, for fish to detect attacking cormorants. The encounter rate of different prey species to predators may possibly also matter. For example, the cormorants are present mainly in spring and summer while predatory fish, such as e.g. pike, *Esox lucius,* and pikeperch, constitute potential risks to prey-fish more or less the year around. Differences in foraging technique of predators may possibly also influence the value of chemical cues to prey for risk assessment.

DO CORMORANTS COMPETE WITH FISHERIES FOR VALUABLE FISH? (**V**)

The effects of cormorant predation on commercially valuable fish is debated, and many fishermen claim that fish consumption by cormorants is detrimental to fish populations. In this paper cormorant predation on commercial fish species was examined by using long-term fishery statistics from 15 lakes in South Sweden. For most species we found no evidence for declines in catches related to cormorant predation. However, in few lakes, eel catches have declined, almost simultaneously with increasing cormorant numbers and cormorant predation most likely is the primary cause behind these declines. A significant negative correlation between increasing cormorant numbers and decreasing catches of vendace *Coregonus albula* most likely did not depend on cormorant predation. In several of the lakes, a long-term decline in catches could be observed, which started long before cormorants established, and probably is due to an overall decrease in productivity related to decreasing levels of total phosphorous.

Cormorant numbers, and thus fish removal by cormorants, varied considerably among lakes (0.2-15 kg/ha), and cormorant removed on average 0.4-4.2 times the amount of fish taken by fisheries. The highest estimates of fish removed by cormorants relative to fisheries were found at eutrophic lakes.

Fishery catches in this study varied considerably between years. The variations which normally differed a lot between species and lakes, often followed a wavelike pattern with peaks appearing at intervals of about one decade or more. Large natural variations make it difficult to tease out the importance of cormorant predation on fish stocks.

In some lakes populations of pikeperch and vendace apparently have “crashed” in recent decades and thereafter remained at low levels. The reason(s) for these declines are unknown, but cannot depend on cormorant predation, since populations usually crashed long before cormorants established in these lakes. If cormorant predation were important on vendace, it is hard to see why no clear decline occurred in Lake Roxen since cormorant foraging pressure appear to be exceptionally high in this lake. As for several other fish species, catches of pikeperch has varied considerable between years. However, for this economically important species we found no support for a decline related to increasing cormorant populations.

Perch and pike are important species to both cormorants and to the fishery. However, our data suggest no apparent competition between cormorants vs. fishery as has been suggested to be occurring, for example, along the Swedish East Coast (Saulamo et al. 2000). Rather, the data suggest that catches of perch in most lakes (8 out of 14) have remained largely stable, or in some lakes increased over the last one to two decades. Catches of pike, however, have declined in several lakes, but in some other lakes remained stable or increased over the last decade(s).

The whitefish *Coregonus* sp., which is present in five of the study lakes, is of high economic value to the fishery in lakes Vänern, Vättern and Bolmen. In this species, high yields coincided with increasing cormorant densities and there is no evidence, at the moment, for competition between cormorants and fishery for this species.

This study revealed an overall significant negative correlation between cormorant densities and eel catches. However, the importance of cormorant predation on eel populations was difficult to evaluate, partly because of an overall downward trend in eel abundance, changes in stocking programs, impact of the swimbladder parasite *Anguillicola crassus* and because of restricted knowledge of the importance of eel as prey to the cormorants. Moreover, when considering eel catches at the different lakes the pattern is contradictory. For example, catches have remained largely stable in some lakes where the presence of cormorants evidently has been high. The most pronounced declines in catches of eel occurred at lakes Ellestadsjön and Krageholmssjön where eel catches have decreased almost simultaneously with the rapidly expanding cormorant colony at Lake Ellestadsjön. Based on existing data the eel appears to be uncommon in the diet of the cormorant (paper **II**), though it might be possible for cormorants to affect eel densities locally. This depends, partly, on the number of eels present in the lakes, relative cormorant eel consumption and other mortality factors. No data exists on the total amount of eels present in the different lakes included in this study. For the eight lakes with reasonable data on cormorant fish consumption, we calculated the number of eels consumed by the cormorants, relative to the amount caught by the fishermen. If the cormorant diet consists of 0.7-1.5 % eel, by weight, (the 1.5-% value is used for oligotrophic lakes), the birds may take a median of 6% relative to the commercial fishery (range: 1-37 %). These figures may at best give a rough idea on eel consumption, in lakes with low or no natural eel immigration. However, in lakes with naturally immigrating eels, consumption may be even less important relative to the total number of eels present in the lakes.

In recent years, the swimbladder parasite *Anguillicola crassus* has spread to eels at many lakes (Wickström et al. 1998). This spread appears to be linked to the stocking of yellow eels in the early 1990s, and currently about 60-70% of the eels in South Swedish lakes are infected (Wickström et al. 1998). The parasite is mostly thought not to be deleterious to the eels, though, when affected by large number of parasites, eels may probably suffer considerably, and even die (Wickström pers. comm.). Other studies have further shown that fishes harbouring parasites are more vulnerable to bird predation than uninfected fish (Van Dobben 1989, Hald-Mortensen 1995).

To summarise, catches of most fish species did not decline in connection to the presence of cormorants. In a few lakes, however, cormorants might be the primary cause behind declines in catches of eel. In other lakes the observed declines of eel catches seem to be part of an already ongoing decline or fluctuation, that begun before cormorants established. The importance of the sudden change in stocking material in several of the lakes, from mainly yellow eels to elvers (1993/1994), is unknown. Moreover, more attention should be paid the susceptibility of eels harbouring *Anguillicola crassus* to cormorant predation.

FISH CATCHES IN RELATION TO TOTAL PHOSPHOROUS (TP)

Phosphorous is a common growth-limiting factor in lakes because it is often present in low concentrations (Horne & Goldman 1994). We found a strong relationship ($p<0.001$), over the whole range of lakes, between total amount of fish withdrawn by fisheries and TP (Fig. 7). Hence, a change in phosphorous loading, as has been observed over the years in several of the lakes, is expected to be followed by a decease in fish production, thus decreasing fishery yields. However, because of large between-year variations in both TP and fishery yields it was difficult to evaluate the significance of changes in total TP on fishery yields. Nevertheless, pronounced long-term decreases in TP were recorded, for example, in lakes Roxen, Glan and Vättern and it appears highly plausible that these decreases have had implications on the fish communities and thus fishery yields at these lakes. The role of phosphorous explaining fish abundance also means that a further decrease in phosphorous loads, as now seem to be the trend in many lakes, may have future implications on both fishery-yields as well as on cormorant densities.

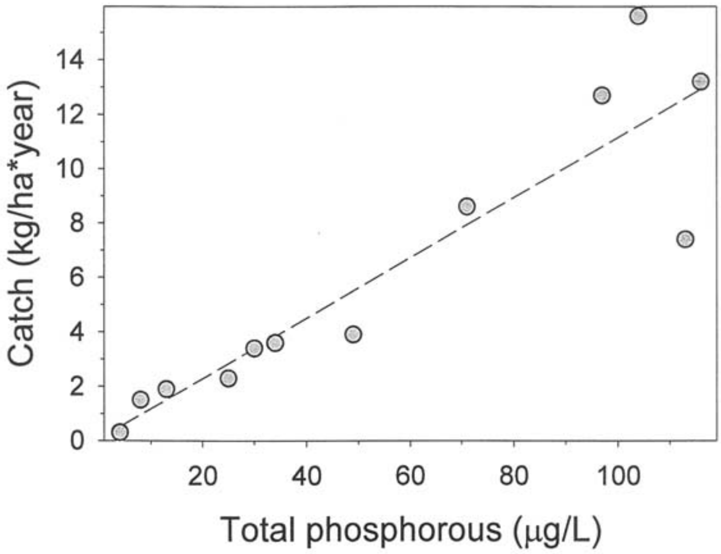


Fig. 7. Commercial catches of fish in relation to total phosphorous (TP) for 12 lakes of South Sweden (mean values for 1996-2000). Only lakes with sufficient data on catches of both commercial fish species and "coarse" fish were included. Data are from lakes Snogeholmssjön, Sövdesjön, Vombsjön, Ringsjön, Bolmen, Glan, Roxen, Ymsen, Hjälmaren, Mälaren, Vänern and Vättern.

CONCLUSION

For a long time the great cormorant was absent, or kept at low numbers, in most of Europe due to systematic persecution. Mainly because of protection the species was allowed to recover. The recovery, mediated partly by improved foraging conditions, has been so successful that the population now seem to be larger, and cover a wider area, than at any time before in the history. In line with this massive increase, conflicts between cormorant and fishery have emerged. The results presented here gives little support for major changes in fish populations related to cormorant predation, and cormorant predation seem to work within the range of compensatory mortality. Most fish taken by cormorants consist of small individuals, which are of non-economic value to the fishery.

Cormorant predation on eel is dubious because of several confounding factors. In most lakes cormorant predation seem not have had any major impact upon eel populations. However, in lakes with exceptionally high cormorant densities, cormorants are presumably capable of affecting eel densities. In several lakes, a long-term decline in fish catches could be observed. These declines most likely are linked to an overall decrease in productivity related to decreasing levels of phosphorous.

Since no obvious threat, appear to exist, to natural fish populations caused by cormorants, current actions to control cormorant populations can be questioned.

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Svensk sammanfattning

BAKGRUND

Som få andra fågelarter har den svenska beståndet av mellanskarv genomgått en anmärkningsvärd populationstillväxt och spridning under senare år. Populationsutvecklingen har varit så kraftfull att beståndet idag, med stor sannolikhet, är större och täcker ett vidare geografiskt områden än någonsin tidigare i historien. I spåren av den kraftiga ökningen har uppkommit ett flertal konflikter – till exempel, bland många yrkesfiskare anses fåglarna inverka negativt på fiskerinäringen. Som problem åberopas även skador på vegetationen vid skarvarnas häckningsplatser och störningar på friluftsintressen. Denna avhandling har haft som främsta mål att studera effekter av skarvens fiskkonsumtion på fisksamhällen och fiske. Avhandlingen redogör också för skarvens populationsutveckling och effekter av senare års jakt och illegala förföljelse på skarvbeståndet. Avhandlingen behandlar också skarvens föda, populationsreglerande faktorer samt beteendesvar hos fisken mot skarvpredation.

Data har insamlats från total 15 sjöar i Södra Sverige, men huvudundersökningarna har ägt rum i sjön Ymsen i Västergötland. Data över häckande skarvar i Sverige och jaktstatistik har insamlats från ett stort antal ornitologer och länsstyrelser.

HISTORISK OCH NUVARANDE FÖREKOMST

Storskarv av rasen *Phalacrocorax c. carbo* har funnits i Östersjöområdet sedan minst 9000 år – och förmodligen även häckat här under större delen av den tiden. När exakt storskarven försvann som häckfågel och ersattes av nuvarande mellanskarven *Ph. c. sinensis* går inte att fastställa. Från omkring början av 1800-talet finns säkra belägg för häckande mellanskarv i Skåne och Blekinge. De små och geografiskt begränsade populationerna i Skåne och Blekinge utsattes regelmässigt för sabotage och motverkade troligen spridning och mot slutet av 1800-talet, eller möjligen något senare, försvann arten som häckfågel i Sverige. Mot slutet av 1940-talet började skarven ånyo häcka i Sverige, på Svartö i Södra Kalmarsund. Ökat skydd genom fridlysning i kärnområdena i Nederländerna (1965) och Danmark (1971), samt att arten uppfördes på EU:s så kallade Fågeldirektiv 1979 är huvudorsaken till skarvens starka återhämtning. Vid sidan om skydd antas förbättrade födoförhållande varit avgörande för skarvbeståndets gynnsamma utveckling.

I Sverige var beståndsökningen särskilt kraftfull mellan 1986 och 1994 (31% per år) och antalet par ökade från 1800 till 15500. Efter 1994 har en uppbromsning skett i kärnområden i Skåne, Blekinge, Småland och Östergötland. Kring mitten av 1990-talet nådde skarven i princip sin nuvarande geografiska utbredning. Under andra halvan av 1990-talet har ökningen fortsatt att vara kraftig i glest besatta och perifera områden, dvs. kustområden i Södermanland, Uppland och Gotland samt i flera insjöar. År 1999 hade beståndet stigit till ca 25 600 par fördelade på omkring 154 kolonier.

EFFEKTER AV JAKT OCH ILLEGAL FÖRFÖLJELSE PÅ POPULATIONEN

Efter att Sverige blev medlem i EU 1995 upphörde den allmänna jakten på skarv. Länsstyrelserna kan dock bevilja undantag från det generella jaktförbudet enligt Artikel 9 i Fågeldirektivet. På grund av ökade populationstätheter och de skador skarven anses orsaka på fisket, och skador i vissa fall på naturmiljön, tillåter ett flertal länsstyrelser (11 av 16, med häckande bestånd av skarv) idag skyddsjakt i någon form. Mest omfattande har jakten hittills varit i kustområden i Småland och Östergötland, men i takt med att bestånden ökat har jakt på skarv kommit att beröra allt fler områden. Till exempel har omfattande jakt bedrivits i Hjälmaren under 1999 och 2000. Utöver legal jakt är skarven utsatt för omfattande illegal förföljelse främst genom sabotage på skarvarnas häckningsplatser. Till exempel, mellan 1985 och 1999 utsattes inte mindre än 17 kolonier i Kalmar län för störning varav 10 illegalt. I Östergötland var motsvarande siffra 22 varav 16 illegalt. Den mest omtalade störningen ägde rum 1993 på Gåsö i Norra Kalmarsund då några upprörda yrkesfiskare sågade ner samtliga boträd med omkring 3000 häckande par. Hur stor påverkan störningar haft på lokala bestånden är svårbedömt då störningarnas omfattning i många fall inte varit möjliga att kvantifiera. Likaså är kunskapen om täthetsreglerande mekanismer på populationsnivå begränsad. Populationsutvecklingen för de olika områdena antyder dock att påverkan varit förhållandevis liten. I flera fall finns tydliga indikationer på att skarvarna vid störning(ar) flyttat till närliggande kolonier och påbörjat häckning där.

Frederiksen et al. (2001) har använt en populationsmodell för att studera effekterna av jakt på populationsnivå och först vid en avskjutning av omkring 13% nåddes en kritisk gräns och beståndet började minska. Omräknat till det svenska beståndet, omfattande en sommarpopulation av ca 120000- 133000 individer, krävs en årlig avskjutning av minst ca 16000-17 000 individer för att långsiktigt minska beståndet. Den rapporterade jakten av skarv i Sverige har inget år överstigit 4000 fåglar och effekterna av nuvarande jakt är troligen små. Då problemen med skarvar generellt är störst under sommaren (skador på fisk i redskap) är min bedömning att åtgärder för att begränsa häckande bestånd (i form av äggprickning och jakt) vanligen är av liten betydelse eftersom de fåglar som orsakar problemen delvis härrör från andra bestånd. Populationsutvecklingen i Sverige under de senaste åren antyder att beståndet som helhet nu är nära mättnad. Omkring en fjärdedel Nordvästeuropas Mellanskarvar häckar i Sverige som näst efter Danmark (42000 par 2000) har flest häckande skarvar i Europa.

EFFEKTER AV SKARVENS FISKKONSUMTION PÅ FISKSAMHÄLLEN

Att skarvens konsumtion av fisk i närheten av stora kolonier är omfattande är givet men vilka effekter ett stort fiskuttag kan få på fiskbestånden är hittills inte väl kända. En vanlig uppfattning är att det skulle ett råda ett direkt samband mellan skarvarnas uttag av fisk och motsvarande förändringar av fiskbeståndets biomassa och numerär. Jag har studerat effekter av skarvens predation på fiskbestånd i sjön Ymsen i Västergötland. Långa tidsserier i Ymsen (provfisken: 1983-1998) har möjliggjort jämförelse av fisksamhällets utveckling före och efter skarvarnas etablering. Effekter av skarvens predation på fiskbestånden har studerats med avseende på biomassa, numerär och storleksfördelning och avser arterna abborre, gös, mört, braxen och gärs. Trots omfattande fiskuttag av skarvarna (ca 13 kg per ha, 1998) antyder såväl provfiskedata som kommersiell fångststatistik (inkluderande även ål och gädda) att skarven sannolikt inte påverkat beståndsstorlekarna av skilda fiskarter negativt. Yrkesfiskets uttag under senaste femårsperioden motsvarade omkring 9 kg per ha och år. I förhållande till den vattenareal skarvarna potentiellt kan utnyttja vid fiske (här räknat på en maximal aktionsradie på 20 km och ett vattendjup grundare än 20 m) är tätheten skarvar i Ymsen under häckningstiden bland det högst noterade för sjöar i Sverige.

SKARVENS FÖDA

Det är väsentligt att känna till skarvens val av föda då konsumtion av, till exempel, stora individer skulle kunna innebära konkurrens med yrkesfisket. Preferenser för vissa arter och storlekar skulle långsiktigt kunna påverka även fisksamhällets sammansättning. Skarvens födoval undersöktes genom att jämföra skarvarnas föda med resultat från provfisken (fisksamhällets sammansättning). Skarvens föda bestämdes genom identifiering av benrester funna i så kallade spybollar (uppkastade osmälta rester efter konsumerade fiskar). Vid undersökningar av skarvarnas föda i Ymsen påträffades i 132 spybollar totalt 2789 fiskindivider tillhörande 10 arter. Antalsmässigt dominerade gärs (47-75 %) följt av mört (11-32 %) och abborre (11-24 %). Vad vikt beträffar dominerade abborre (28-46 %) följd av gädda (13-30 %), gers (14-25 %) och mört (8-20 %). Ål och gös är för yrkesfisket de mest betydelsefulla arterna och förekom endast i enstaka exemplar i skarvarnas föda (0.07 respektive 0.1 antalsprocent). Ålens andel i skarvarnas föda undersöktes också genom utsättning av ålar märkta med mikrochip. Resultat visar även här på mycket låg konsumtion av ål.

Gärs, i motsats till mört och abborre, förekom i högre antal i skarvarnas föda än förekomsten i fisksamhället. Detta förhållande är sannolikt kopplat till skillnader mellan arter i beteenden och levnadssätt vilket påverkar deras grad av exponering och därmed tillgänglighet för skarvarna. Medelvikten på de av skarvarna konsumerade fiskarna var 24 g (SD±56g) vilket motsvarar en längd av 14 cm. Dygnskonsumtionen fisk, baserat på innehållet i en spyboll, var 512g (SD±220g).

BETEENDESVAR HOS MÖRT MOT SKARVPREDATION

Skarvar häckar i kolonier vilket innebär att fiskar som lever invid skarvkolonier regelbundet utsätts för predationsrisker. Ett flertal studier visar att djur, inklusive fiskar, balanserar predationsrisk mot intag av föda. I ett laboratorieförsök testades om mört reagerar på lukt av skarv. Mört insamlades från två populationer (med och utan skarv) för att studera om skillnader förelåg i eventuell nedärvt respektive inlärt beteendesvar. Resultaten visade att mört inte reagerar på lukt av skarv. Det är troligt att fiskar uppfattar attackerande skarvar på annat sätt; till exempel med hjälp av synen eller genom at uppfatta vibrationer/ljud i vattnet från simmande skarvar.

SKARVENS EFFEKTER PÅ KOMMERSIELLT VIKTIGA ARTER

Effekter av skarvens predation på ekonomiskt vikiga fiskarter har debatterats flitigt under senare år. Jag har använt fångststatistik för att undersöka skarvens effekter på kommersiellt viktiga arter i 15 sjöar i Södra Sverige. Långa tidsserier (medel 33 år, max 87 år) har möjliggjort jämförelse av fiskbeståndens utveckling före och efter skarvarnas etableringar. Skarvarnas uttag av fisk varierade kraftigt (0,2-15 kg) bland sjöarna och det fanns ett statistiskt positivt samband mellan antalet skarvpar per sjöyta och yrkesfiskets fångster, vilka i sin tur var statistiskt kopplade till totalfosfornivåerna i sjöarnas. Något samband mellan ökade skarvtätheter och minskade fångster kunde inte påvisas för flertalet arter. Ålen har visserligen minskat i flera sjöar under senare år men kopplingen till ökade skarvbestånd är oklar då åltätheterna påverkats av flera faktorer. Till exempel, för att motverka minskade fångster, på grund av minskad naturlig ålinvandringen, har omfattande utsättningar ål ägt rum i många sjöar. Utsättningarna har dock varierat kraftigt över tiden och bestått av olika utsättningsmaterial. En stor andel av ålarna är bärare av simblåsemask *Anguillicola crassus* och det kan inte uteslutas att infekterade ålar är särskilt exponerade för predation. I två sjöar har dock ålfångsterna minskat kraftigt ungefär samtidigt som antalet häckande skarvar ökat. Predationstrycket från skarvarna förefaller vara mycket stort i de båda sjöarna och det är troligt att skarvpredation är huvudorsaken bakom de observerade fångstminskningarna.

För ett flertal fiskarter, i ett flertal sjöar, kunde konstateras en allmänt nedåtgående trend i fångster, som påbörjades långt innan skarvarna etablerade sig. Den troliga förklaringen bakom dessa fångstminskningar är en minskad produktion relaterad till minskade nivåer av totalfosfor.

SLUTORD

Minskat jakttryck och exceptionellt goda födoförhållanden är huvudorsakerna bakom skarvbeståndets gynnsamma utveckling under senare decennier. I takt med att skarvbeståndet expanderat har konflikter med det småskaliga fisket ökat. Mina undersökningar har visat att skarvens effekter på naturliga fiskbestånd förefaller vara små. Dock, i små sjöar, med höga skarvtätheter, och omfattande ålutsättningar, kan skarvarna sannolikt påverka ålfångsterna negativt. Det stora problemet med skarvar är att de skadar och plockar bort fisk i redskap, vilket orsakar problem för yrkesfiskare flera områden. Nyttan med senare års jakt och äggprickning, med syftet att minska populationens storlek, kan dock ifrågasättas, och denna jakt förefaller påverkat populationen endast marginellt.

TACK!

(Se den tryckta versionen.)