# The Interactions between Cormorants and Wild Fish Populations

## Analytical Methods and Applications

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# The Interactions between Cormorants and Wild Fish populations. Analytical Methods and Applications

## Abstract

Predation is the core in ecology, as a function in food webs which regulate both populations and communities. Seabirds are at the top of the food chain and key players in many aquatic food webs. So are humans, and in certain cases conflicts of resources arise. Cormorant predation on fish is probably one of today's most well-known and wide spread human-wildlife conflict. Different species of cormorants have independently increased in numbers in several areas of the world. For some species, their predation has created a human conflict concerning resource competition (real or perceived competition) with both commercial and recreational fisheries. Though there is extensive research on cormorant diet we are far from reaching a consensus about how cormorant predation affects the environment.

The aim of this thesis was to investigate how cormorants interact with wild fish communities and human fisheries. This was achieved by investigating cormorant diet composition, changes in diet over time, and between areas. The thesis also includes the first meta-analysis on cormorant diet, in which previous research investigating the effects of cormorant abundance on fish parameters were analysed.

The results shows that cormorants generally have negative effects on fish populations, and control measures to limit predation generally have positive effects. Especially vulnerable to cormorant predation are species within the Percidae and Cyprinidae families. To some degree fish species and sizes in the diet overlap with those in fisheries catches (commercial and recreational). The predation on smaller sized fish however, is for some fish species more important in terms of competition with fisheries, as it results in less recruitment to commercial sizes. The diet analyses support earlier studies on temporal and spatial variation in the diet of cormorants.

Essential knowledge for the management of fish, fisheries and cormorants is how cormorants affect fish populations. A misdirected effort in cormorant research is emphasized. Most studies fail to identify effects as they don't relate diet with cormorant abundance and predation pressure. There is a need for systematically designed research, where cause and effects are studied. Future research should also consider an ecosystem approach, where indirect effects of predation are considered.

*Keywords:* cormorant, diet, fishery, meta-analysis, Phalacrocorax, tag, wildlife-conflict.

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# Dedication

To my supporting family and friends whom I love very much.

*And she gazed at the sky, the sea, the land,*
*The waves and the caves and the golden sand.*
*She gazed and gazed, amazed by it all,*
*And she said to the whale, "I feel so small"*
Julia Donaldson, The snail and the Whale

# Contents

# List of Publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I Boström, M.K., Lunneryd, S-G., Hanssen, H., Karlsson, L. and Ragnarsson, B. (2012). Diet of the great cormorant (Phalacrocorax carbo sinensis) at two areas in the Bay Lövstabukten, South Bothnian Sea, Sweden, based on otolith size-correction factors. *Ornis Fennica* 89, 157-169.

II Boström, M.K., Östman, Ö., Bergenius, M.A.J. and Lunneryd, S.G. (2012) Cormorant diet in relation to temporal changes in fish communities. *ICES Journal of Marine Sciences* 69(2), 175-183.

III Östman, Ö., Boström, M.K., Bergström, U., Andersson, J. and Lunneryd, S-G. (2013) Estimating competition between wildlife and humans-a case of cormorants and coastal fisheries in the Baltic Sea. *PLoS ONE* 8(12), 1-8. (DOI: 10.1371/journal.pone.0083763).

IV Ovegård, M.K., Öhman, K. and Mikkelsen J. S., and Jepsen, N. (2017) Cormorant predation overlaps with fish communities and commercial-fishery interest in a Swedish lake. *Marine and Freshwater Research* (DOI: 10.1071/MF16227).

V Ovegård, M.K., Jepsen, N., Bergenius, M., and Petersson E. (2017) A review and meta-analysis of the effects of cormorant predation on fish populations. *Manuscript.*

Publications I-IV are reproduced with the permission of the publishers.

The contribution of M. Ovegård to the papers included in this thesis was as follows:

I Participated in planning and designing the project that was initiated by Sven-Gunnar Lunneryd. Conducted field work with personnel at Älvkarleby field station and Hanna Ståhlberg, collected and identified pellet material, conducted the statistical analyses, primary author of the manuscript and handled the review process.

II Initiated, planned and designed the study with Sven-Gunnar Lunneryd, analysed most diet material, conducted the statistical analyses with support of Örjan Östman, primary author of the manuscript and review process.

III Planned and designed the field work with Sven-Gunnar Lunneryd, identified most diet material, wrote the manuscript as secondary author, Örjan Östman conducted the analyses and handled the review process

IV Initiated, planned and designed the study as project leader, participated in field work together with Kristin Öhman, Niels Jepsen, Jørgen Mikkelsen and Anders Nilsson (local fisherman), identified diet material with Kristin Öhman, conducted statistical analyses, primary author of the manuscript and handled the review process.

V Initiated the study with Erik Petersson, planned and designed the study with co-authors, managed the literature review and conducted the analyses with the support of Erik Petersson. Primary author of the manuscript.

# 1 Introduction

The cormorant, *Phalacrocorax* spp., can on a global scale be considered a model genus for human-wildlife conflict (Klenke *et al.*, 2013; Wild, 2012; Doucette *et al.*, 2011; Vetemaa, 1999). There is a wide spread conflict between humans where concerns for the conservation of a bird species stand against protection of harvestable natural fish resources. The core of the conflict regarding cormorants relates to its ability to quickly colonize new areas and exploit new food resources. In many cases they forage in large numbers and will consequently, in a short time, consume large numbers of fish. Cormorants are present in salt-, fresh- and brackish waters on all continents (Sibley, 2001). Different areas of the world have similar conflicts regarding cormorants, although the particular species of cormorant in question differ (Doucette *et al.*, 2011; Wires *et al.*, 2003).

The great cormorant (*Phalacrocorax carbo*) is one of the most studied and well-known conflict species, along with the double-crested cormorant (*Phalacrocorax auritus*) in North America. Both species have had a similar steep increase in numbers (Seefelt, 2012), almost during the same period of time. They are also considered to have similar feeding behaviour, and thus similar potential effects on fish communities. Despite a persistent belief that these species affect fish populations negative, there is relatively little known about their interactions in ecosystems and food webs (Doucette *et al.*, 2011). This thesis aims to contribute to that knowledge using the great cormorant as the study species.

## 1.1 Interaction in food-webs and predator hypotheses

Species interactions create food webs where predation plays a central role for the energy flow through the food chain, from primary producers to top predators (Smith & Smith, 2003). Capture fisheries have historically depleted species in a top-down manner, fishing down the food web by targeting the larger fish (Pauly *et al.*, 1998; Trites *et al.*, 1997). A top predator, in the top of the food chain, may (and will in most cases) in a similar manner supress the abundance of a prey, and thus releasing the next trophic level from predation, which then can increase in numbers. This is called a top-down trophic cascade, as it results in abundance changes down the food web. (Bottom-up cascades, on the other hand, occurs when a primary producer is removed (or boosted) and affects the whole food web from primary, up to top predators (Hunter & Price, 1992)). For example, in the Baltic Sea it has been suggested that seal predation on fish, together with human interactions, is an important component in driving the system by top-down control (Österblom *et al.*, 2007). After extensive seal hunting, resulting in population reduction, followed a shift from seal to cod domination. Human overfishing of cod later resulted in a shift towards clupeid domination in the Baltic Sea, which was the state it was in when cormorants increased in number. The cormorant is a generalist predator, able to predate on fish in various sizes and therefore their interaction act at several trophic levels. Cormorants forage mainly in shallow waters, close to the coast, compared to seals, which are also foraging in off shore systems (Boström *et al.*, 2016). Form an ecological management perspective, it is important to not only consider cormorant predation, but in association with other piscivorous predators (such as seals) and fishery catch, especially as there is a conflict around competition with fisheries.

Exactly how predation from one species affects individuals and populations of other species within an ecosystem is complicated as it depends on the community structure and other species interactions. Within communities there are interactions in the form of competition. The level of competition can be regulated by predators higher in the food-web because individuals or species benefit if a competitive species is reduced by a predator. Alternatively, removal of one competitor species may open up for increased competition between other species. The competitive interaction is based on a limitation of resources, which can be food supplies or habitats. There are both intraspecific and interspecific competitions, in which individuals compete within the same species respectively between species (Persson, 1983). Predators may alter such competitions and thus alter population structures.

By predating on a limited prey size span predators can alter the size structure of a prey population (Begon *et al.*, 2002). Predators may have different effects on a population depending on in which life stage predation is concentrated. Predation on predominantly young individuals may have relatively little effect on the population compared to predation on reproductive individuals (Boyd *et al.*, 2006).

Prey fish answer to predators by changing its behaviour, and on a population level such behavioural change may alter distribution and abundance (Skov *et al.*, 2013). Spatial heterogeneity in the environment and defence ability are important factors in population survival (Gilinsky, 1984). On an evolutionary scale prey may even change to antipredator patterns in their behaviour and morphology.

According to the predator hypothesis on a generalist and opportunistic predator, which prey on the most common and easily caught species, consumption rates should accelerate relative to prey density as the predator learn to recognise the more abundant prey item. At some point prey consumption reaches its maximum and the prey number decreases. If other prey is more abundant the predator should change its target prey. (For example, cormorants change target prey when a prey becomes scarce, so their predation is not likely to bring a population down to zero). In those cases consumption rate may be driven by variability in recruitment and may explain prey switching behaviour as fish community changes (Schultz *et al.*, 2013). This could lead to an eventual suppression of recruitment to older age classes, particularly those recruiting to fishery sizes. The predator thus regulates its own prey densities. Changes in predator diet may, however, also be caused by natural fluctuations in fish stocks, fish removal by other predators or by environmental changes which may affect fish assemblages.

## 1.2 The Cormorant

Cormorants belong to the pelican order, Pelecaniformis, and the family Phalacrocoracidae, traditionally within the single genus *Phalacrocorax*, (though there are discussions about dividing them further into three groups; flightless cormorants, long-tailed cormorants and other cormorants (Sibley, 2001)). Within the genus there are approximately 37 different species with a disputed number of subspecies. The great cormorant (*Phalacrocorax carbo*) is the most widespread of all cormorants and can be found on all continents except South America and Antarctica proper (Johnsgard, 1993). In Sweden, there are two species of cormorant, the great cormorant (*Phalacrocorax carbo*, Linnaeus 1758) and the less common European shag (*Phalacrocorax aristotilis*, Linnaeus 1761). The two subspecies of the great cormorant present in Europe are *P. c. sinensis* and *P. c. carbo* and about 90 % of the population is represented by *P. c. sinensis* (Klimaszyk & Rzymski, 2016).

The great cormorant were hunted to the brink of extinction in Europe during the 19th century, but have since the EU bird directive in 1980 benefited from protection from human persecution (Steffens, 2010) and highly productive, eutrophic, waters. During the last decades there has been a large increase of the population of *P.c. sinensis* across Europe (Steffens, 2010; Bregnballe *et al.*, 2003; Van Eerden & Gregersen, 1995). The population within the EU has increased from 3 500 pairs in 1960 to 220 000 pairs in 2012 (CorMan; http://ec.europa.eu/environment/nature/cormorants/home_en.htm, 2017-02-28).

The great cormorant is, like most cormorant species, an opportunistic piscivore, (Johnsgard, 1993) able to exploit most waters, and therefore the increases in numbers have led to conflicts with fisheries (Vetemaa *et al.*, 2010; Carss, 2003; Leopold *et al.*, 1998; Dieperink, 1995). Concern about the European population of *P. c. sinensis* has increased markedly in the last decennium due to their increase in number (Keller & Visser, 1999). From a bird conservation point of view the development is considered highly successful and cormorants are now colonising their original habitats, and are also possibly taking new ground (Bregnballe *et al.*, 2011). This success is on the other hand seen as a major problem for certain capture fisheries because the cormorant is perceived as a competitor for fish resources. Many fishermen and fish farmers claim that cormorants cause them economic loss. They claim that cormorants deplete fish populations, cause damage (Engström, 1998) (partly by drowning in fishing gear (Žydelis *et al.*, 2009; Bregnballe & Frederiksen, 2006)), reduce fisheries catch (Andersen *et al.*, 2007) and influence the local flora and fauna on islands they occupy (Kolb, 2010). They are also claimed to cause economic losses for fish farms, put and take lakes and pond aquaculture (Klenke *et al.*, 2013; Lekuona, 2002). There are several cases, where predation from cormorants has been thought to threaten the conservation of vulnerable fish stocks and cause ecosystem derogation in freshwater (Skov *et al.*, 2014; Ryan *et al.*, 2013; Steffens, 2011; Jepsen *et al.*, 2010; Ebner *et al.*, 2007).

During the first half of the 20th century the subspecies *P. c. sinensis* occurred only occasionally in Sweden. They established a colony in 1948 on an island in Kalmarsund, near the island Öland, and spread from there. Already in the 1980´s, when the numbers had increased to around 1 000 nesting pairs, the potential effect of cormorant predation was discussed at the local county, and measures to reduce the number were implemented (Lindell & Jansson, 1993). However, the population rapidly increased. The fast population growth was due to high survival and breeding success. Eutrophic waters, with high primary production and large amount of small fish, are believed to have offered good food resources (De Nie, 1995; Van Eerden & Gregersen, 1995). Protection areas were implemented in association with cormorant colonies. A decrease in the use of pesticides may also have contributed to a higher reproduction rate (Bregnballe *et al.*, 2011). The national counts in 2006 and 2012 indicate that the Swedish population is no longer increasing. The population reached its maximum at 42 000 nesting pairs in 2006 and around 40 000 pairs in 2012. Reasons for levelling off in numbers are most probably the limitation of food resources (Engström, 2001). Also the growing population of White-tailed eagle (*Haliaeetus albicilla*) that are predating on cormorants may keep numbers down in some areas (HELCOM, 2015; Sevastik, 2002). A reduction in breeding success may also be due to kleptoparasitism, that is, when other species steal prey from predators. Seagulls have learned to attack cormorants and steal fish when they surface to ingest prey (Klenke *et al.*, 2013), which impacts the net energetic gain for individuals and its nestlings. Seagulls have also learned to steal eggs from cormorants, when the adults leave the nest in response to disturbance (personal observation). Another reason for the reduced breeding success in some areas is human interference to reduce the number of cormorants. These are both legal and illegal disturbances. In extreme illegal cases cormorant nests are destroyed and young chicks killed.

## 1.3 *P. c. sinensis* - foraging behaviour and distribution

Cormorants are foot propelled divers that usually dive and forage in waters shallower than 10 meters, but they are able to dive more than 30 meters (Nelson, 2005). They are commonly submerged for around 20 seconds to a minute. They feed almost exclusively on fish. Crustaceans and Polychaetes (Niels Jepsen and personal observations and Lunneryd and Alexandersson (2005), have however, been observed in the diet. Targeted fish sizes range from a few cm to a maximum size being limited by what can fit in the cormorant beak, thus fish of one or two kilo are regularly eaten. This means that elongated fish can be consumed in larger sizes than high bodied fish or flat fish. Cormorants have been observed to attempt to eat too large fish, resulting in suffocation and mortal outcome (Fig. 1). This may be an effect of limiting food resources, making cormorants prone to eat what is available.

Cormorants undertake feeding bouts at least two to three times a day. They forage solitary or in large groups and may follow conspecifics to locate lucrative feeding areas (Nelson, 2005). It is thought that fishing in larger groups is an adaptation to murky waters with less visibility (Van Eerden & Voslamber, 1995). The group work effectively together by moving in a row and taking turns in diving to stir up the fish from the bottom so they can be seen and caught. However, exactly how cormorants locate food, visually, hearing or sensory, is not entirely known (Grémillet *et al.*, 2012). They are commonly surfacing to swallow prey but they may also swallow smaller prey under the water. During the breeding season cormorants have been shown to change their target prey. In the Gulf of Finland cormorants were observed to feed small chicks with smaller and more easily digested fish, such as eelpout (*Zoarces viviparus*), compared to more scaly roach (*Rutilus rutilus*) and perch (*Perca fluviatilis*) during the later phase of breeding (Lehikoinen, 2005). It has also been observed that foraging occurs closer to the colony when they rear small chicks and that they can forage at larger distance before and after. It is not uncommon that they forage 15 to 20 kilometres from the colony (Nelson, 2005), but a distance up to 40-60 kilometres has been documented (Van Eerden *et al.*, 2012). The theory of Ashmole´s halo may apply to cormorants (Andrews *et al.*, 2012), where the foraging distance from the colony increases due to a decrease in prey availability near the colony through the breeding season (Birt *et al.*, 1987).

*Figure 1.* A mortal outcome from a struggle between a cormorant and an eel. Usually the fish get stuck in the throat of the cormorant, but in this case the eel strangled the cormorant. Photo: Kristina Lager.

Cormorants are commonly said to consume around 500 grams of fish per day. The amount of food varies however, depending on gender, species, temperature and breeding state requirements (Carss, 1997). Cormorants overwintering in colder areas with cooler waters spend more energy and require more food. Details of energy demand and food requirements can be found in Carss *et al.* (2012), Ridgway (2010), Keller and Visser (1999), Carss

(1997), Feltham and Davies (1997), Grémillet *et al.* (1996), Gremillet *et al.* (1995), and Platteeuw and Van Eerden (1995), and will not be covered in this thesis.

The subspecies *P.c. sinensis* range from Europe and east/south east through central Asia to Serbia, China and India (Nelson, 2005). They breed in colonies, sometimes several hundred pairs, in trees, bushes or on the ground near shallow marine or fresh water systems. In northern Europe breeding occurs between April and August. European cormorants tend to have a south/south-western winter migration. Birds tagged in Sweden have been found as far south as Africa (Bird Ringing Centre, Fig. 2). The distribution of the great cormorant during winter has been correlated with a mean winter temperature warmer than -5.5ºC (Van Eerden *et al.*, 2011). As cormorants move long distances the conflict of cormorant predatory effect can be argued to be a European rather than a local concern. And this has led to the EU to fund several pan-EU cormorant projects; Redcafe, Intercafe and CorMan.

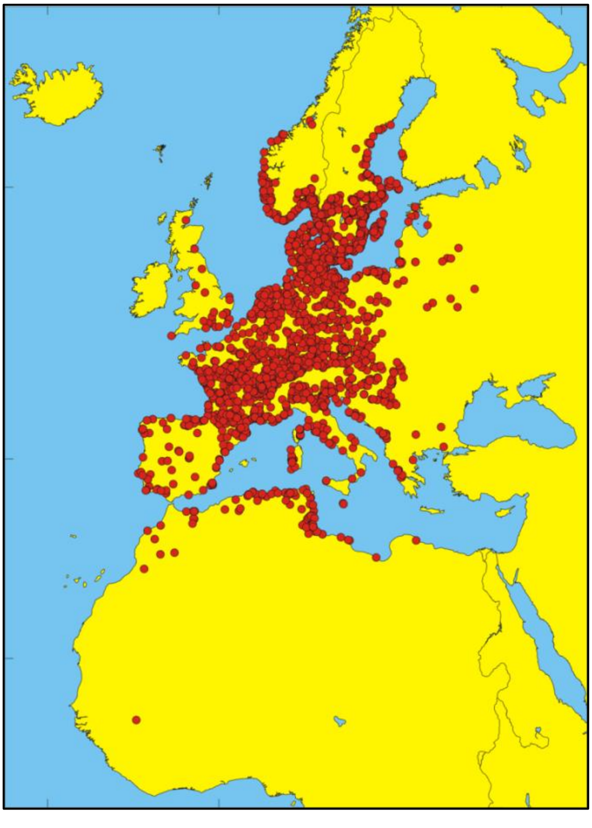

*Figure 2.* Recoveries of tags from cormorants tagged in Sweden, up until 2016 (n=3711). Source: Bird Ringing Centre, Swedish Museum of Natural History.

## 1.4 Scientific dilemma – how can the effect of predation be measured?

Though cormorant diet has been studied for decades there is insufficient knowledge about cormorant food habits, and in particular how they affect wild fish populations (Russell *et al.*, 2003). Conclusions from research results are not consistent. Some studies conclude that cormorants can have negative effect on fish stocks (e.g. Čech & Vejřík, 2011; Fielder, 2010; Vetemaa *et al.*, 2010; Fielder, 2008; Rudstam *et al.*, 2004; Leopold *et al.*, 1998; Kirby *et al.*, 1996b; Barret *et al.*, 1990), while others conclude less or no effect of cormorant predation (e.g. Dalton *et al.*, 2009; Diana *et al.*, 2006; Engström, 2001; Suter, 1995). The inconsistent results between studies partly relate to the ability of cormorants to make use of most fish communities, and that fish community structure differ spatially and temporally. There are many factors affecting fish communities, beside predation (Heikinheimo *et al.*, 2016). Both abiotic and biotic processes cause natural fluctuations in fish stocks or environmental change, which in turn may influence stocks. The significance of cormorant predation on natural fish populations is difficult to estimate because the true fish population size and structure is often unknown, or the knowledge incomplete. Fish surveys are useful in identifying changes in fish communities over time, but as no fishing method captures all fish and sizes representatively they are limited in that they cannot be used to identify exactly how the community is structured. There are too many variables to measure and account for, when attempting to identify effects of predation.

Though the highly various and complex ecological systems are one reason for the inconsistency between studies on the effects of cormorant predation, the main reason probably relates to differences in perceptions of what an effect is. How “large” should a predation effect be to be considered significant, and how can this be measured? A large quantity or even proportion of predated fish does not necessarily mean that cormorants affect a fish population, in terms of damage of human resources, as compensatory mechanisms may set in.

There are several methods available and used to quantify cormorant predation (see section 3.1). The most direct way to quantify predation on a known fish stock is to tag fish and recover tags in cormorant residues (Skov *et al.*, 2014; Jepsen *et al.*, 2010). Even though these methods results in the knowledge of how large a proportion of a given fish population the cormorants consume, the question of effects on the fish not eaten by cormorants remain. (Note that there is a possibility to model cormorant predation and abundance in relation to fish population parameters). A combination of tagging studies, preferably by telemetry, and good survey data on the fish population can provide very precise estimates of effects, but naturally this works best in small, restricted waterbodies like lakes or streams.

From a strict scientific point of view the significance of effects are best studied by using carefully designed experiments, with treatments and controls. As ecological systems are highly variable, it is important to conduct studies with replication in several waters and, preferably, to study fish communities before, during and after cormorant predation. But in most cases it is practically impossible to predict areas where cormorants will establish in the future. What can be done is to relate fish community changes to cormorant abundance, or manipulate the number of predating cormorants, either by using fish refuges or, more drastically, move cormorants from a fish community by e.g. hazing or shooting. The latter options infer cormorant population disturbance, in one way or another, which calls for legal consent. With cormorants being a source for a human-wildlife conflict such research project first needs to be considered on the political agenda. In Denmark, the negative effect of cormorants is documented and treated as a fact in the national management plan. A study is being conducted at present (2016-2018), where salmon smolt survival is related to lowered levels of cormorant predation. Radio-, PIT- and acoustic telemetry is used to monitor the survival of smolt and relate this to efforts to reduce predation, by shooting cormorants in the river and the estuary as well as destroying colonies.

## 1.5 Controversial predator under management and political debate

Managers and stakeholders are irresolute in decision processes around cormorant management, partly because of the difficulty in collecting scientific data on true effects of cormorant predation on fish population, communities and fisheries, but mainly because of the human-wildlife conflict and a difficulty in interpreting the legal frames.

Human-wildlife conflicts are in reality not conflicts between humans and wildlife, but conflicts between humans around a wildlife species issue (Dickman, 2010; Madden, 2004). The source of the conflict is often the consumption of resources by wildlife that is of value for humans (Chamberlain *et al.*, 2013; Madden, 2004). The social aspect may be a more important driver in such conflicts than the actual effect on prey of the wildlife (Dickman, 2010). Effects may be perceived and not even real, for such conflicts to arise (Klenke *et al.*, 2013). Deeply rooted attitudes and strong opinions are difficult to alter, even with scientific proof. When cormorants started to increase in number in Europe, they were a welcomed and exotic sight for many. As they increased further people relying on fish catch as an income started to become concerned. Fishery representatives in Europe consider cormorant predation harmful to their business and believe there is a need for a reduction of cormorant predation on a European scale (Marzano *et al.*, 2013). This viewpoint is shared by EIFAAC (European Inland Fisheries and Aquaculture Advisory Council) and EAA (European Anglers Alliance).

The subspecies *P. c sinensis* is not assessed for the IUCN Red List but is included in the species *P. carbo*, which is now listed as LC (Least Concern), due to its large range and extremely large population size (www.iucnredlist.org, 2016-12-19). In Europe cormorants are protected under international laws and treaties such as the EEC Directive 2009/147/EC (codified version of 79/409/EEC) on the Conservation of Wild Birds 1979, the Bern Convention on the Conservation of European Wildlife and Natural Habitats 1979, and the Bonn Convention on the Conservation of Migratory Species of Wild Animals 1979 (CMS). Originally the subspecies *P. c. sinensis* was listed under Annex 1 in the directive of Conservation of Wild Birds, which includes bird species on which special conservation measures, by protecting their habitats, are needed (Article 4). In 1997 it was removed from that list (commission directive 97/49/EC) because *P. s. sinensis* had reached favourable conservation status. It means that the level of protection is no more than for most other bird species. Member states can decide on measures to manage cormorants under conditions stated in Article 9. Article 9 can be used if it is in the interest of public health and safety, air safety, to prevent serious damage to crops, livestock, forests, fisheries and water, and for the protection of flora and fauna (Article 9 in the Directive 2009/147/EC on the conservation of wild birds).

Though the directive of Conservation of Wild Birds is rather clear in that it now opens up for regulating cormorant predation, the level of evidence is not stated. There is an attempt to describe the directive in relation to cormorants in the EU derogation report (Great cormorant, Applying derogations under Article 9 of the Birds Directive 2009/147/EC). It is up to the member states to decide on the level of evidence of cormorant predation effects, before regulation measures can be implemented. Most member states have management plans on national level and in some instances also local level.

Cormorant damage on fisheries is easiest to measure and report by estimating wounded fish in fishing gear. It is more difficult to measure and prove if cormorants induce changes in fish communities to the degree that they cause damage to fisheries catch and income, a concern that for some fishermen is considered more worrying than damage in fishing gear (Strömberg *et al.*, 2012). This damage may be of even higher importance than damage of fish catch. The same challenge is found in seal management in Sweden, where the fishery gets compensated for seal damaged catch, but the degree of damage on fish stocks is not considered. However, there is relatively new evidence, based on models, showing an importance of fish predation on fish populations. Seal predation can prevent the recovery of overexploited fish stocks (Cook *et al.*, 2015; Swain & Benoit, 2015). In Denmark, where the nesting cormorant population used to be the highest in Europe, it is stated in their national management plan (2016) that cormorant predation can prevent recovery of coastal fish populations and even drive populations of freshwater fish to an unsustainable level.

# 2 Goals and outline of the thesis

The objective of this thesis was to achieve further understanding of cormorant predation and predatory effects on fish population and community structures. The thesis work had two main focuses:

1. Investigate the diet of cormorants on the Swedish Baltic Sea coast (papers I and II).
   - Examine spatial and temporal differences in diet.

2. Investigate how cormorant predation effect fish populations and fisheries. (papers III, IV and V)
   - Explore the competition between cormorants and humans (papers III and IV)
   - Summarize previous research measuring the effects of cormorants on fish and examine the variations in those effects (paper V).

In the process of my thesis work I encountered several methodological challenges and difficulties. Diet analysis methodology was discussed in my licentiate thesis (Boström, 2013). In this thesis I discuss the challenges in research related to the identification of effect of cormorant predation on fish populations (see discussion and paper V).

# 3 Methods

To complete this thesis, the diet of the great cormorant (*Phalacrocorax carbo sinensis*) was examined in four areas, whereof three in the Baltic Sea (I, II, III) and one freshwater lake (IV). Patterns of change in diet between areas and periods were analysed (I, II). The results from diet studies could then be used to estimate the competition between cormorants and coastal fisheries (III). The direct competition on fish of the same sizes were accounted for, as well as the indirect competition by cormorant predating on smaller sized fish, resulting in a decrease in the number of fish recruiting to catchable sizes (for fishery). As coastal systems are open, and fish move over long distances, it is a challenge to relate cormorant predation to response in fish populations. Therefore a study was conducted in a freshwater lake (IV). To quantify predation, fish were tagged and tags were recovered in colonies and roosting areas. In both the lake and the coastal areas trends in fish community structure were examined and related to cormorant predation (II, III, IV). For this, fish survey data (II, III), collected by the Swedish Board of Fisheries[1], were used, and an own survey was conducted (IV). Finally, cormorant predatory effects on fish and fisheries were evaluated, based on published literature. This was achieved by a structured literature search and meta-analysis (V).

## 3.1 Diet analyses – sampling and description of diet

Bird diet composition can be determined with several methods; observational studies, tagging prey, visually examining food remains in stomachs, pellets, regurgitates or faeces, and biochemical methods such as analysis of DNA,

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[1] Before 1 July 2011 The Swedish Board of Fisheries was responsible for these fish surveys, but after that date the Department of Aquatic Resources at the Swedish University of Agricultural Science has this responsibility. The section of the board dealing with research and monitoring were simply incorporated to the university as a new department.

stable isotopes and fatty acids (Barrett *et al.*, 2007). The type of methods to use depends on the hypothesis in question. If the size of prey is important, visual analysis of food remains or tagging prey is a necessity. Biochemical methods have the advantage that a large sample can be analysed with little effort, compared to visual methods. However, these methods have their limitations. With DNA you can get semi-quantitative proportions of prey, but it is not possible to measure prey size, and the application to quantify prey is in its developmental phase (e.g. Huang *et al.* (2016). With stable isotopes you can identify which trophic level(s) and geographical area a predator feed in. Fatty acids can also give a semi-quantitative estimate of prey proportions, but with the advantage that you can investigate diet over longer time spans (time span depends on which structure you sample). If your objective is a deeper understanding of predator interaction with prey and food webs, it is advisable to complement biochemical methods with visual analyses. Though not studied in this thesis, with visual analysis it is possible to examine the life stage of prey.

In this thesis diet was investigated through visual analysis of pellets (paper I), regurgitated fish (paper I) and from stomach content from shot birds (papers II, III, IV) (For study areas, see map in Fig. 3). The methods, limitations, application of size correction factors on otoliths, regression use on otolith size to attain fish sizes and methodological differences in relation to questions of ecosystem impacts and effects on fish populations, are described in Boström (2013) and will not be covered in detail in this thesis.

Diet composition can be described as frequency of occurrence, numerical or biomass contribution. Either the total contribution of prey for all samples examined or the contribution of prey can be weighted per sample. The later method was used in papers I, II and IV. It has the advantage that the contribution of prey in each sample is considered to be equally large, with each sample containing 100 % prey. If one diet sample contains only a little amount of prey it is equally weighted as a diet sample with large amount. For example, if one sample contains 10 prey items of which 1 is species A and another sample contain 100 prey items of which 10 items are species A, both samples contain 10 % of the species within each sample; and thus species A has the same weight in both samples though it was found in less amount in the first sample. The method accounts for a potentially skewed distribution in diet composition and also allows estimating uncertainties due to random processes by bootstrapping (Haddon, 2001).

With complex predator and prey dynamics it is of importance to take into account, that short term studies only give a short term picture of the diet and effect of a predator. As cormorants are opportunistic generalists they can adapt to variable sources of food. Fish can be dynamic in behaviour and movement during its life time and move long distance to reproduce or feed. Migration behaviour may also be a response of predator presence (Skov *et al.*, 2013; Kortan & Adámek, 2011). In paper I, II and IV the diet of cormorants were investigated during the entire breeding season. In paper III sample collection was spread out over the entire year to identify the predation in the non-breeding season. Spatial and temporal differences in the diet were examined with one-way non-parametric permutational multivariate analyses of variance Permanova by using Bray-Curtis similarity indices on relative biomass or number of prey. Variations were examined with constrained canonical analysis of principal coordinates (CAP) biplots using the Bray-Curtis similarity index. Differences between breeding phases (Paper I and II), gender and age (Paper II) were examined.

## 3.2 Fish community – gillnet fish surveys

National gillnet fish surveys were used to examine the degree of change in fish communities between years, in relation to cormorant abundance and diet (Paper II and IV). Fish surveys were conducted by the Swedish Board of Fisheries as part of the national and regional monitoring programme. The survey along the coast is conducted annually (Paper II and III), while in Lake Roxen (paper IV) the data was limited to only a few years. Therefore an additional survey in Lake Roxen was conducted in 2013. Procedures in the field are explained for coastal survey in Söderberg *et al.* (2004) and Thoresson (1996), and for lake survey in (Kinnerbäck, 2001) and Appelberg *et al.* (1995).

It is important to note that gillnet survey methodology relies on the active movement of fish into nets and therefore sedentary species are poorly represented. Also smaller sized fish and elongated fish, like eel and eelpout, are not caught representatively.

Gillnet catches were examined by using catch per unit effort (numbers or biomass) with principal coordinate analysis (PCO) (Paper II) and Student´s t-test (Paper IV). Differences in fish sizes, among surveys, were investigated using one-way ANOVA (paper IV).

## 3.3 Direct and indirect predatory effects on fishery catch

Cormorants may prey on fish of the same species and sizes as those targeted by the fishery. They may also add to the natural mortality of fish in earlier life stages, before recruiting to commercial size (as seen for perch Gagliardi *et al.* (2015)). These kinds of direct and indirect competitions were investigated in paper III, using length distribution of fish in cormorant diet and commercial fishery catch, together with total cormorant predation and total fishery catch. A model to measure competition between human catch and cormorant predation was constructed, based on consumption levels and mortality rates, where both commercial and recreational fishery were accounted for. Published literature was used for estimates on the natural mortality, which were included in the equations. For details of equation modifications see paper III.

However, it is important to note that aquatic systems are more complex and these estimates do not include all indirect effects of predation on fisheries. For example, cormorants may injure fish and also force fish to use sub-optimal feeding strategies (like shown by, amongst others, Skov *et al.* (2013)), and cormorant predation may affect piscivorous fish by removing their prey.

## 3.4 Effect of predation on fish populations

In chapter 3.1 the methods in describing cormorant diet were explained. It is one thing to measure and estimate predation (in numbers or biomass) and another thing to estimate the “effect” of predation on wild fish populations, communities or ecosystems. Effect is here defined as change in fish parameters e.g. size, number, biomass, survival etc. in relation to cormorant abundance or presence. It is measurements on the effect on the surviving fish population that is of importance in effect studies, not “only” measurements of mortality caused by cormorants, (though survival and mortality are correlated).

Several studies in Denmark (e.g. Jepsen *et al.* (2010), Koed *et al.* (2006), Dieperink *et al.* (2001), Dieperink (1995)) and North America (e.g. Hawkes *et al.* (2013), Sebring *et al.* (2013), Lovvorn *et al.* (1999)) have used tags on fish to estimate predation by cormorants. As mentioned in section 1.4., tag fish and recover tags in cormorant colonies or roosting areas is considered the most direct way of measuring predation (Jepsen *et al.*, 2010). Tag studies give precise estimates on which fish individuals cormorants have eaten, but not direct information on the effects of the fish population surviving cormorant predation. However, predation effect, as defined above, can be measured with tag studies if designed to consider cormorant abundance/predation pressure in relation to fish parameters of the individuals surviving cormorant predation. For applications on a wild fish population the available size range of fish must be covered and tagged respectively, which may be challenging as fishing gear don’t catch all sizes.

Most research on cormorant diet is descriptive diet studies, which do not prove or disprove the effect of cormorant predation, in a clear statistical sense. In paper V a systematic search for published articles on cormorant predation was conducted. From these, articles including a statistical setup, where effect sizes and direction (positive or negative) of effect could be extracted, was identified and used in a meta-analysis. A meta-analysis enables to combine results from different studies as long as they address a similar question. This means that studies that are variable in; what fish parameter they measured (individual size, numbers, biomass, size at age etc.), in which habitat type studies were conducted and on what cormorant and fish species studies targeted, can be used. An overall quantitative estimate between all studies, the effect size, can be calculated. Increased sample size provides an increased statistical power. A meta-analysis also enables the exploration of sources of variation in effects. The meta-analysis included in this thesis is the first ever attempted on cormorant predatory effects.

# 4 General Results and Discussion

## 4.1 Cormorant interactions with wild fish populations

The results from this thesis (papers I and II) support earlier findings (e.g. Lehikoinen *et al.* (2011), Lehikoinen (2005) and Neuman *et al.* (1997)) that diet of cormorants vary both spatially and temporally (Fig. 3). In Lövstabukten the diet differed between colony islands only 6 km apart (Paper I), which probably was a result of birds foraging in different areas. The diet changed more (Paper I) or less (Paper II) during the breeding season, which can be the result of varying demands during different stages of chick rearing (Lehikoinen, 2005). While rearing small chicks, smaller, more easily digestible fish species may be preferred. Or, as proposed in paper I, the change in the diet over time may be due to fish prey availability in relation to fish behaviour and abundance. For example, the timing of eelpout present in cormorant diet, in both paper I and II, matched the migration of eelpout into shallower waters.

Changes in diet between years were also identified (papers II, IV). The clearest change was the large amount of sticklebacks in the diet of cormorants in the Mönsterås area observed in 2009 (92 % in numbers). A study in the same area in 1992 found no sticklebacks in the cormorant diet (Lindell, 1997). Instead perch dominated the diet in 1992 (Table 1). The fish community, based on net surveys, indicate a change from a dominance of roach and perch in the mid 1990´s towards dominance by herring and species of cyprinids, other than roach. However, survey nets used in coastal areas do not catch sticklebacks representatively, because the smallest mesh sizes, 17 mm, are too large to catch sticklebacks. But stickleback presence has increased in the coastal area of the Baltic proper since the early 1990´s (Ljunggren *et al.*, 2010). Perch on the other hand has decreased (Vetemaa *et al.*, 2010).

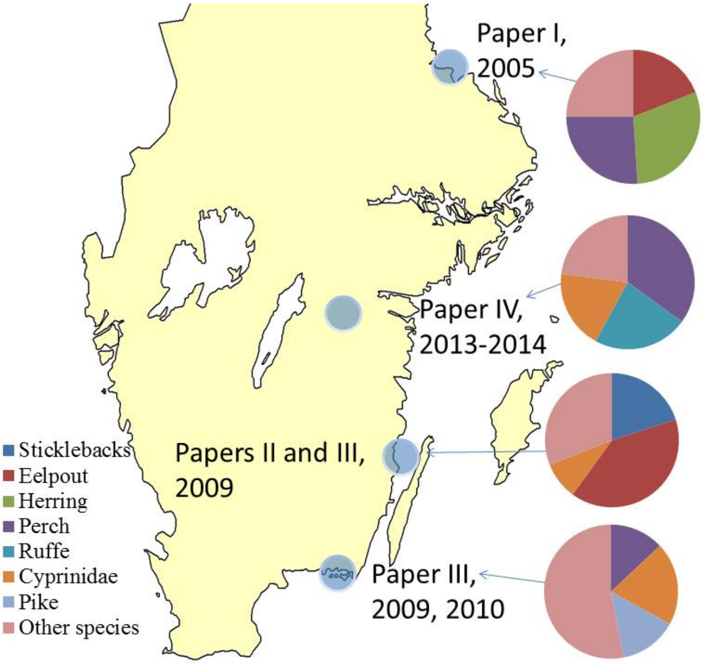

*Figure 3.* The three most commonly occurring species in the diet of cormorants in the four study areas (Paper I-IV). In all areas samples were collected throughout the breeding seasons and during the time of cormorant presence (in such numbers that sample collections were possible). In paper III collections were made all year round.

Table 1. *The diet of cormorants in the archipelago close to Mönsterås in 1992 (Lindell, 1997) and 2009 (paper II) in numerical percentage. For 2009 estimates included and excluded sticklebacks to get an idea of the importance of sticklebacks compared to other species. Other fish preys of importance in 2009 were gobies and flatfish which, with stickleback removed, contributed 23.6 and 7.3%, respectively (modified from paper II).*

| Species | Sticklebacks included 1992 | Sticklebacks excluded 2009 | Sticklebacks included 2009 |
|---|---|---|---|
| Perch | 41 | 0.2 | 0 |
| Cyprinids | 36 | 8.7 | 0.7 |
| Ruffe | 6 | 0.2 | 0 |
| Eelpout | 7 | 50.8 | 3.9 |
| Sticklebacks | - | excluded | 92.3 |
| Other Species | 10 | 40.1 | 3.1 |

A coastal trophic cascade (Ljunggren *et al.*, 2010) may have followed a shift in the offshore system (Casini *et al.*, 2008), (the shift in the offshore system is described in section 1.1) which may be the reason for the change in cormorant diet. Cascades may, in turn, be due to overharvesting by humans, and maybe to some degree also the predation from predators, that during the same time period increased in numbers (seals (Harding & Härkönen, 1999), mainly in the offshore system and cormorants (Bregnballe *et al.*, 2003), mainly in the coastal system).

Long term changes in cormorant diet were also suspected in cormorants foraging in Lake Roxen (paper IV). Net surveys conducted in 1990, 2001, 2010 and 2013 show a change in the fish community structure, and the fishery catch decreased during the same time. Cormorants inhabited the lake in 1992 and have been blamed for these changes. As the eutrophic state of the lake has improved during the years (paper IV) an increase in the number of larger piscivore fish predators was expected. But generally, there were fewer but larger piscivorous individuals in 1990 than in the following surveys. The number of perch, ruffe and roach decreased from 2001. The only species with a significant continuous decrease (table 2 paper IV) in both biomass and number was ruffe, belonging to the Percidae family. In the last survey however, in 2013, perch were larger in individual size, but still caught in smaller number, i.e. more piscivorous perch (Fig. 4).

Piscivorous predators have been shown to enhance growth and size structure of prey populations, which is probably a result of decreased density and intra specific competition (Pierce *et al.*, 2006). For example, Dorr and Engle (2015) found that harvest loss of catfish (*Ictalurus punctatus*) due to cormorant predation occurred, but was to some degree mitigated by compensatory growth of individual catfish.

Fish in the Percidae family are from other studies known to be vulnerable to cormorant predation. Cormorants may have been, together with high fishery catches before cormorants arrived, and the improved eutrophic state, one of the factors for changes observed in Lake Roxen. In Oneida Lake in New York, USA, cormorant predation caused an increase in sub-adult mortality and caused declines in the Percidae species walleye (*Sander vitreus*) and yellow perch (*Perca flavescens*) (Coleman *et al.*, 2016; Rudstam *et al.*, 2004). There are some contradicting conclusions about cormorants being the reason for declines in yellow perch in Les Cheneaux Islands region, of northern Lake Huron discussed in Diana (2010). Conclusions and indifferences are mainly based on different perceptions of importance of level of predation. Despite this, an increase in abundance of perch followed cormorant control efforts, strengthening the fact that cormorants had a negative effect. In Lake Ontario there has been a decrease in fish abundance of the Percidae species smallmouth bass (*Micropterus dolomieui*). The high mortality of age 3 to 5 year old fish has been related to cormorant abundance (Lantry *et al.*, 1999). Gagnon *et al.* (2015) found that perch and ruffe were less abundant near cormorant colonies along the Finish coast in the Baltic Sea. As ruffe in Lake Roxen is not targeted by the fishery, cormorants are probably the main reason for their continuous decrease in both number and biomass.

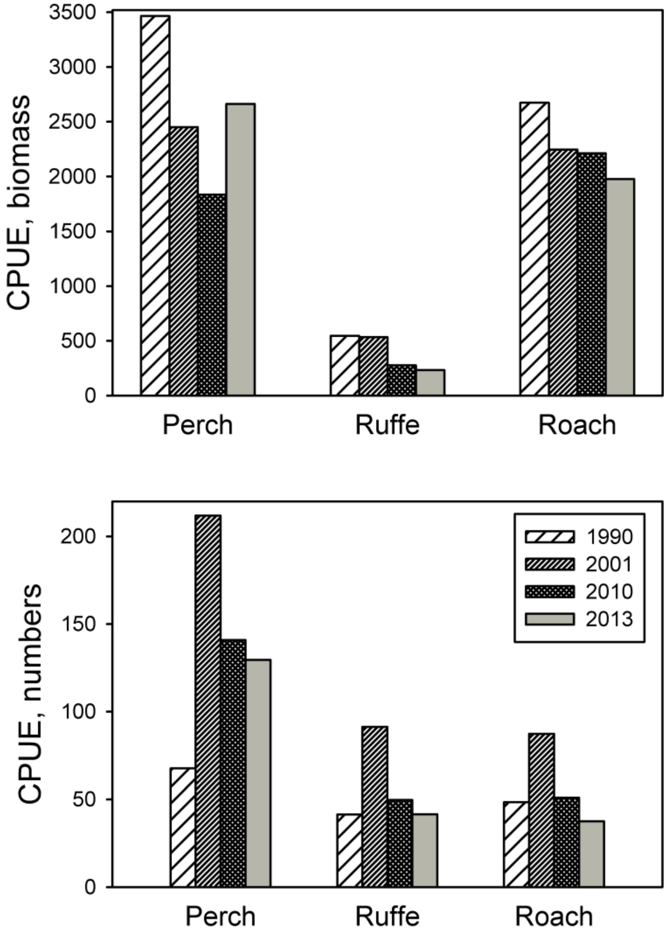

*Figure 4.* CPUE of perch, ruffe and roach in net surveys conducted in Lake Roxen (Paper IV).

Considering that cormorants eat around 500 grams (+/- depending on life stage and energy demand) of fish per day, are central foragers during breeding, and breed in large numbers, it is difficult to argue that a significant number of cormorants don't have an effect on a local fish community level. Effect are especially likely in lakes, where fish movement is limited, and foraging in other lakes mean an extra energy loss for cormorants due to a larger flight distance. Cormorants in Lake Roxen were observed to have foraged further than 21 kilometres away, as Baltic fish species were found in diet samples. There were also cormorants foraging both in Lake Roxen and in the nearby Lake Glan. This change in foraging areas opens up the question of at which prey density level cormorants change foraging strategy and target species. Enstipp *et al.* (2007) studied prey capture rate in relation to prey density for double crested cormorants and juvenile rainbow trout (*Oncorhynchus mykiss*) and found that the capture rate decreased disproportionately at a level below 2 $g \times m^{-3}$. The study was undertaken in captivity, but if it occurs in a natural setting that might be the level at which cormorants move to other foraging areas (or change prey species).

## 4.2 Cormorant interaction with fish of human interest

The process of a predator eating a prey means an interaction in the form of removal of an individual from a prey population. Depending on how many individuals, and at what life stage the prey individuals are removed, the effects can be more or less important on a population level. Cormorants are likely to impact fish communities, but the effects do not have to impact fishery catches negatively. Cormorants are known to prosper in eutrophic waters and it is argued that eutrophic waters are the very reason for the fast increase in cormorant number (De Nie, 1995; Van Eerden & Gregersen, 1995). They often eat fish of smaller sizes than what is targeted by the fishery (Östman *et al.*, 2012), but are able to feed on as large fish individuals as can fit in their beak and thus sizes which may overlap with commercial and recreational fishery catch.

When comparing cormorant predation on fish with commercial and recreational fishery catches some overlap in fish species and size was identified (paper III). This can be considered a direct competition on resources. Cormorants were estimated to consume the equivalent of 44 % in Karlskrona archipelago and 10 % in Mönsterås archipelago of the commercial and recreational fishery catch in biomass, of cod, flounder (*Platichthys flesus*), herring (*Clupea harengus*), perch, pike (*Esox lucius*) and whitefish (*Coregonus lavaretus*) combined. The cormorant consumption estimates of harvestable sized fish were 14 % respective 5 % for Karlskrona and Mönsterås. The direct competition did not result in large decreases in catchable sized individuals, < 10 % for all species. But when accounting for indirect effects, by consuming smaller individuals, the estimated removal of fish that could have reached catchable size at least doubled. The results stress the importance to include the predation (or removal) of fish individuals of smaller sizes in predation estimates, that has not yet reached maturity and therefore not reproduced (paper III). The impact on fisheries catches more than four folded compared to the estimated direct competition for perch, pike and whitefish.

The estimated competition with fisheries differed between areas, mainly as a result of differences in target species between fisheries. In Karlskrona archipelago the commercial fishery targeted herring and cod, while in Mönsterås the targeted species were herring and eel. Recreational fishery in Karlskrona targeted pike and perch while in Mönsterås they targeted pike and flounder. In general, results showed that the estimated impact of cormorant predation was higher for stocks important for recreational fishery (perch and pike) than for commercial (cod, herring and eel), which seems reasonable as most commercial species are more offshore species and cormorants forage closer to the coastline.

Results in paper III show that competition between human catch and cormorant predation is very dynamic in relation to predation pressure, fisheries pressure, natural mortality, competition etc. Not accounted for in study III was the removal of available prey for commercial fish species, and sizes, caused by cormorants. This is another indirect way, in which cormorant predation may affect the survival and condition of fish available for the fishery.

## 4.3 A Global Perspective on conflicts - in short

Cormorant predation has been studied on all continents and for most cormorant species. The literature search for the meta-analysis covered all cormorant species, except four species; the red-faced (*P. urile*), Socotora (*P. nigrogularis*), red-legged (*P. gaimardi*) and the flightless cormorant (*P. harrisi*), of which the first three are considered vulnerable or near threatened.

Of the 448 articles found, around 50 % was based on studies in Europe, mainly England, Italy and Germany and concerned primarily the great cormorant in fresh water, lakes or ponds. Freshwater aquaculture ponds have been identified as the main area of conflict by the INTERCAFE project (Seiche *et al.*, 2012), in particularly with carp (*Cyprinus carpio*) pond areas in Central Europe. But the literature search reveal that most studies in Europe are diet analysis on cormorants related to sea and lake areas, not ponds.

Around 30 % of the articles concerned cormorants in North America and most of them studied the double crested cormorant, which has increased in number in a similar manner as the great cormorant has in Europe. Most research seem to originate from the Great Lakes and the Mississippi channel cat fish (*Ictalurus punctatus*) aquaculture in the Mississippi delta area, the two areas where cormorants seem to be causing the most conflict (Wild, 2012).

About 4 % of the articles were studies from South America and most on the imperial cormorant (*P. atriceps*) in marine systems and the neotropical cormorant (*P. brasilianus*) in freshwater environments. The predation of the South American cormorant species do not seem to cause major human conflict, as most studies concern their diet and no identified studies showed predatory effect on fish.

Most of the literature from Africa (5 %) was based on studies in South Africa on the cape cormorant (*P. capensis*) in marine systems and the white breasted cormorant (*P. c. lucidus*) in both lakes and sea areas. Studies related to the cape cormorant mainly concern the welfare of the species in relation to fisheries depleting food resources. Linn and Campbell (1992) identified no effect of predation on fisheries as white breasted cormorant foraging areas and diet did not overlap with fisheries catch in Lake Malawi. Most probably there is no large cormorant conflict in Africa, or research is lacking.

About 4 % of the articles were based on studies in Asia which included several species with low number of publications on each. Most studies were conducted in Japan on the great cormorant subspecies *P. c. hanedae*. They have since the 1970´s increased rapidly in numbers and distribution, and caused conflicts with fishery interests (Takahashi *et al.*, 2006). Most of the conflict occur in the inland recreational fishery and are about the ayu (*Plecoglossus altivelis*), which is one of the most popular recreational and commercial species (Kameda & Tsuboi, 2013). But there are also positive associations between human and cormorant. The Japanese and Chinese have, and are still to some degree, utilized cormorant guano as fertilizer and trained cormorants to catch fish.

About 3 % of the articles covered studies conducted in Australia, of which most concerned lakes or rivers and the little pied cormorant (*P. melanoleucus*). Negative effects of cormorant predation have been seen on stocked fish and farm fish, but conclusions from studies in open sea areas vary (Barlow & Bock, 1984).

In Antarctica there are no cormorants and thus no conflict with humans, but the closely related shags are present in the Antarctic peninsula and about 2 % of the articles found concerned these, mainly the blue-eyed shag (*P. atriceps*) and the Antarctic shag (*P. a. bransfieldensis*). Most studies described the diet of cormorants and one related fish abundance to declining number of birds (Casaux & Barrera-Oro, 2016).

Though cormorants are widespread in distribution and research on cormorant diet has been carried out on all continents and most cormorant species, the conflict is, at least today, limited to a few cormorant species. Most studied areas concern smaller sized systems, such as ponds, lakes and rivers.

## 4.4 Meta-analysis

As discussed in chapter 1.4., the way to answer if cormorants have an effect on fish or fishery is to relate fish population change to cormorant abundance. The meta-analysis of cormorant predation effect revealed that, in modern times, since the cormorant started to increase in numbers, their food habits have been extensively studied. The underlying reason for studying cormorant diet has in most cases been to get a picture of how their diets overlap with human catch. Research has mainly focused on quantifying predation, but quantities do not necessarily provide information on effect. Studies on diet mainly present percentage of fish, either by number, biomass or frequency of occurrence. Diet composition may be compared to fishery catch, but is seldom compared to known fish populations, (except in tagging studies), as there is a lack of cormorant diet studies in relation to independent fish monitoring.

Studies where effect sizes (Koricheva *et al.*, 2013) could be extracted were those which studied fish parameters in relation to cormorant presence or abundance. In some cases cormorant abundance was due to human induced limitations of number of foraging birds by the use of refuges, hazing or shooting. If the response was more or larger fish in relation to cormorant abundance the effect was considered positive. If less and smaller fish was a result of more cormorants the effect was considered negative.

Only 22 articles were identified where effect size could be extracted and the combined effect of those was negative -0.3103, 95 % C.I. -0.4260 to -0.1952). Thus, cormorant predation in general has a negative effect on fish and decreasing predation has a positive effect on a prey population. There was no significant difference in effect size between, cormorant species, study type, effect type or habitat/foraging area. But there was a significant difference in effect sizes between fish species. The most vulnerable species was perch, walleye and a combined effect for species in the Cyprinidae family. This further supports that species in the Percidae family are the most vulnerable to cormorant predation (as discussed in chapter 4.1.).

Though the meta-analysis covered cormorant predation on a global scale the identified studies only included great cormorants (*P. c. carbo and P. c.*

*sinensis*) and double crested cormorants (*P. c. auritus*). This, per se, is an indication that these two species are the source for most human-cormorant conflicts. It also mainly covers small enclosed systems, such as farms, dams, rivers and lakes where experimental manipulation with test and controls are relatively easy to apply. Such habitats often lack suitable refuges for fish and may thus be more vulnerable to cormorant predation (Gagliardi *et al.*, 2015) than other systems. There is still a lack of evidence for cormorants damaging wild fish populations and fisheries in open aquatic systems, because appropriate experiments have not been conducted to demonstrate cause and effect (Hustler, 1995).

## 4.5 Managing animals or human conflicts - personal reflections

There are many feelings and personal opinions around cormorant management, especially from persons whose livelihood or recreation depend on fish resources. During my work with cormorants I have encountered people with views all from “exterminate all cormorants”, “cormorants are natural predators that are back in our environment and should be left alone”, to “what is a cormorant”. Well, working with such a conflict species is, and has been, a challenge.

From an ecologist point of view I believe we should aim for sustainable populations and manage species from an ecosystem perspective (ecosystem based management). Increasing the commercial or recreational fishery catch alone is not incitement enough to deplete populations of cormorants. To maintain and protect a small scale local fishery, an occupation traditionally handed down in generations, may be a reason to mitigate cormorant predation (not exterminate cormorants). Or the economic and social benefits from recreational fishing may be another reason to discuss mitigation measures. It is essential to consider top predator consumption when formulating advice for fishery management (Cook *et al.*, 2015), as well as general wildlife management. The overall objective should be sustainable fishery and viable populations of both fish populations and all kinds of piscivorus predators.

However, there is a sociological concern in cormorant management that cannot be ignored. Management implementation in the form of reducing cormorant predation can reduce the animosity towards cormorants and might be a method to reduce unethical illegal actions (such as killing chicks). The great cormorant has the potential of fast reproduction, if conditions are right and if the population not yet has reached the point of food resources limiting reproduction. This theoretically means that if cormorants decrease in number from a food limited state, they will increase their reproduction (as each cormorant gets more available food). Controlling populations in some areas will not affect the population as a whole.

A reasonable strategy would be to identify where, when and with which species conflict occur and implement predation limitation in vulnerable areas. In some circumstances sacrificing fish to cormorants in some areas can be beneficial to protect fish in vulnerable areas (Kirby *et al.*, 1996a). Predation limitation in an area can be achieved by modifying cormorant behaviour, instead of killing, e.g. by scaring them from foraging in vulnerable areas.

At all times ethical considerations should be taken into account. Illegal actions, such as destroying nests with young and killing chicks should be publically unacceptable. Not only is it ethically questionable, but it impedes cormorant research and makes it problematic to evaluate effect of both cormorant predation and implemented limitations of cormorant predation. There is a need to "manage" the human view of cormorants and turn the negative picture around and, by all stake holders, start regard cormorants as a valued and respected species in our nature.

## 4.6 Conclusions and main results

From the results in this thesis it can be concluded that cormorant predation on fish has a negative effect on fish populations and fishery catch, (both direct and indirect). Successful management actions to reduce cormorant predation have positive effect on fish populations. These effects vary between study area and fish species, as cormorant diet and fish community structure vary.

In the meta-analysis in paper V it was identified that cormorants generally have negative effects on fish populations and that management actions to reduce predation are very probable to have positive effect on fish populations. Paper V, together with results from paper IV, show that fish in the Percidae family are the most vulnerable to cormorant predation. In paper III it was shown that the cormorant can compete with fishery. Smaller sized fish, which have not yet recruited to catchable sizes in fishery, are more important in terms of competition with fishery, than the predation of the same sizes the fishery catch. There are also strong indications from results in paper IV and V that cormorant predation can restructure the size distribution of a fish population by predating on a limited size span. This can affect recruitment to larger sizes and reproduction.

Studies demonstrate variations in diet (paper I, II, IV) and effect (III, V), due to differences in fish community structure and target species in fishery.

## 4.7 Future perspectives

Though there is an extensive number of research articles concerning cormorant predation there is a need of further research. A clearer picture of the interaction of cormorants in ecosystems, their function in food webs and effect in fishery catch, especially in open aquatic systems is needed. Research should focus on the effect of cormorant predation and test hypothesis with experimental set ups, instead of conducting elaborate, extensive and descriptive studies. The reason for this is that only using percentages of predation per species, or on a fish population, may not be considered to be enough proof of an effect. For example, though a tagging study manages to identify 60 % mortality of a fish species due to cormorant predation, it may still be argumentations about what the effects are on the fish not eaten by cormorants (unless the study is taken further). In conservation biology today we urgently need effective mitigation strategies in order to resolve human conflicts (Dickman, 2010). Increased knowledge and awareness are important tools in the process. The meta-analysis in this study was conducted to accommodate the requests from stake holders to investigate predation effect with hypothesis testing.

Another way to mitigate the conflict, and increase knowledge of predation effect could be to implement cormorant predation limitations and study the effect in fish response. Reducing wildlife damage alone may fail to produce long-term conflict resolution (Dickman, 2010). Therefore, close monitoring, evaluation of effect and an adaptive management, with fast decision and action process, is necessary, together with open and continuous communication between stake holders and the public. With an increased concern of the conservation of aquatic ecosystems and to sustain fishing efforts, conservation would benefit from close collaboration between seabird and fishery science.

# 5 Sammanfattning

Fiskätande sjöfåglar i toppen av näringskedjan kan påverka ekosystem genom att reglera fiskpopulationer och förändra fisksamhällens struktur. Eftersom människan också nyttjar fisk i toppen av näringskedjan uppstår ibland konflikter om resurser.

Det finns omkring 40 arter av skarv i världen. Framför allt två av dessa har under slutet av 1900-talet oberoende av varandra ökat snabbt i antal, vilket orsakat konflikter om resurser. I Europa gäller det storskarven av underarten mellanskarv (*Phalacrocorax carbo sinensis*), och i Nordamerika gäller det öronskarv (*P. auritus*). Båda arter är så kallade generalister, vilket innebär att de snabbt anpassar sig till tillgängliga resurser. Beroende på vilket livsstadium skarvar befinner sig i äter de olika mängd fisk, men generellt brukar man säga att dessa två arter äter omkring 500 gram per dag per skarvindivid.

Denna avhandling gjordes för att öka kunskapen om skarvars interaktion med fisk och fiske. När projektet satte igång saknades det kvalitativ information om mellanskarvens föda på den svenska kusten i Östersjön, och till viss del i sjöar. Tidigare studier var begränsade till ett lågt antal undersökta spybollar. Födovalet studerades på tre platser, (Lövstabukten, utanför Mönsterås och Karlskrona) och förändringar i föda över tid undersöktes. För att få bättre kunskap om hur skarv konkurrerar med yrkes- och fritidsfisket beräknades, utifrån födovalsstudierna, hur mycket skarvar äter av storlekar som fångas av fisket (fångstbar fisk). Dessutom undersöktes en indirekt konkurrens i och med att skarvar också äter mindre fiskindivider än vad fisket fångar. Detta gjordes genom att beräkna hur skarvarnas predation på mindre fiskar påverkar överlevnaden till fångstbar storlek.

I sjön Roxen hade man sett att det skett förändringar i fisksamhället, och en del av förändringarna skedde under en period då antalet häckande skarvar ökade. Skarvföda undersöktes i relation till provfiskefångster, yrkesfiskefångster och näringshalter (fosfor och kväve) för att beskriva variabler i relation till förändringar i fisksamhället. Dessutom märktes fisk för att kvantifiera predationen på definierade populationer av abborre, gös och ål, vilka är några av de kommersiella arterna i sjön.

Den övergripande mängden forskning på skarv beskriver födoval och kvantifierar andelen fisk de tagit från fiskpopulationen i antal eller biomassa. Få studier baseras på uppställningar där man testar en hypotes och undersöker påverkan av predation på de fiskar som inte ätits av skarv, vilket egentligen är vad man vill veta för att identifiera effekten av skarvpredation. Alltså studier som undersöker påverkan på fiskparametrar, så som fångst per ansträngning, biomassa, antal, storlekar på fisk individer etc., i relation till skarvabundans. Ett exempel är att jämföra fiskparametrar i områden med skarv (försök) med områden utan skarv (kontroll). Fördelen med den sortens studier är att man statistiskt kan utvärdera skarvens effekter på fisk, och bortse från andra variabler som kan påverka fisken, eftersom de variablerna agerar på båda områdena. För en sådan studie kan man beräkna effekten, eller storleken av påverkan, d.v.s. hur positiv eller negativ effekten är.

För att få en övergripande global bild av skarvars påverkan på fisk gjordes en litterär sökning efter studier som statistiskt undersökt effekter av skarvpredation. Dessa användes i en meta-analys, vilken är den första som gjorts på skarvpredation. En meta-analys innebär att man inkluderar alla effektstudier för att ta fram en total övergripande effekt. Fördelen med meta-analyser är att man kan lägga samman effekter från undersökningar som varierar i studiedesign, eg. olika habitat, skarvart, fiskart, fiskparametrar som mätts etc. och skillnader i effektstorlekar mellan dessa kan undersökas.

Resultaten visar att skarvars föda varierar mellan områden (så kort som 6 km mellan kolonier) och de byter föda över tid. Förmodligen som ett resultat av ändrat fiskbeteende men det kan till viss del också bero på att skarvar aktivt väljer föda beroende på behov. När de föder små ungar kanske de väljer mindre och mera lättsmält fisk att föda ungar med. De äter allt från små spiggar till gäddor i, för fisket, fångstbara storlekar. Det är gapstorleken som avgör hur stora fiskar de maximalt kan äta.

Undersökningarna visar att det för vissa arter sker konkurrens med yrkes- och fritidsfisket. Skarvarna tog 10 % och 44 % av den mängd och storlekar som yrkesfisket fångster av ål, flundra, strömming, abborre, gädda och sik i Mönsteås respektive Karlskrona skärgårdar. Denna direkta konkurrens beräknades minska fiskets fångster med mindre än 10 % för alla arter, förutom flundra (>30%) och abborre (2-20 %). När predationen av mindre fisk inkluderades i beräkningarna minskades fångsterna för abborre med 13-34 % och för gädda 8-19 %. Konkurrensen mellan skarv och fiske varierade mellan de två områdena och för olika arter av fisk, men studien visar att skarvars predation lokalt kan konkurrera och ha negativ påverkan på vissa fisken.

Övergödning tillsammans med högt fisketryck kan ha bidragit till att fisksamhället i Roxen initialt förändrades. Från att försörja ett gynnsamt yrkesfiske med flera fiskare återstår bara en aktiv fiskare i sjön. I och med att både fisketryck och övergödning minskat förväntades fisksamhället gått från små planktonätande fiskar mot flera större fiskätande fiskar, men så var inte fallet. Gärs och mört har minskat i både antal, biomassa och individstorlek. Däremot visade fångster av abborre 2013 en ökning i individvikt. Skarvarna åt främst mindre storlekar av abborre och gers. Trenden med färre men större abborrar kan bero på att fiskproduktionen är stor, men skarvens predation på mindre fisk gör förmodligen att färre fiskar uppnår reproduktiv ålder. De fiskar som överlevt förbi den längden skarven främst fokuserar på, kan växa och bli större och därmed bli tillgänglig för fisket. Märkningen av fisk visade en skarvdödlighet på över 10 % för gös, 8 % för abborre och 3 % för ål. (Är man intresserad av att läsa mera om Roxenstudien på svenska hänvisas till skriften av Boström and Öhman (2014)).

Meta-analysen visade att skarvar generellt har en negativ effekt på fisk och att förvaltningsåtgärder för att minska predationen har positiva effekter på fisk. Statistiskt är det inga stora skillnader i effekter mellan undersökningsområden, olika fiskparametrar som mätts, hur skarvarnas abundans mätts, länder eller mellan skarvarter (mellanskarv och öronskarv var de enda arterna som det gjorts studier som uppfyllde kriterier för att kunna inkluderas i analysen). Däremot var det en signifikant skillnad i effekter av skarvpredation mellan fiskarter. Abborrfiskar (inkluderar t.ex. abborre, gös och gers) och arter inom familjen karpfiskar (t.ex. mört) är extra känsliga för skarvpredation. Skarvpredation på dessa arter hade större negativ effekt än för andra fiskarter.

Från resultaten kan man dra dessa huvudslutsatser:

1. Skarvens predation kan vara i den kapaciteten att fisk populationer påverkas negativt (paper V).
2. Skarvpredation kan påverka fisket negativt genom att direkt konkurrera om fiskar i samma storlekar (paper III, VI).
3. Den indirekta konkurrensen, där skarv äter fiskar innan de rekryteras till fångstbar storlek, kan ha större betydelse för fisket än den direkta konkurrensen (III).
4. Eftersom skarvföda, fisksamhällen och fiske varierar i tid och rum är påverkan mer eller mindre på olika platser och vid olika tider på året (I-V).

Studierna visar också starka indikationer på att skarvarpredation kan omforma strukturen på en fiskpopulation. Genom att äta specifika storlekar kan skarvar ändra storleksfördelningen och påverka reproduktion och rekrytering (III, V).

Med ytterligare belägg och vetskap om att skarven faktiskt kan ha en negativ påverkan på fisk och fiske yrkar jag på att man tar, inte bara den mänskliga konflikten om skarv på allvar, men även skarven som predator. Reduceringar av skarvpopulationer behöver i sig inte innebära att den mänskliga konflikten minskar. Därför behöver man kontinuerlig övervakning av effekter på både fisk och skarv efter reduktionsåtgärder. Det krävs en tät och öppen kommunikation och samarbete mellan allmänheten, politiker, forskare, och beslutsfattare för att snabbt kunna agera i en adaptiv förvaltningsstrategi med målsättning av hållbara bestånd av både fisk, skarv och naturresurser.

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