Fish Predation by the Great Cormorant (*Phalacrocorax carbo sinensis*)

Analytical Basis for Ecosystem Approaches

Maria Boström
Faculty of Natural Resources and Agricultural Sciences
Department of Aquatic Resources
Uppsala

Licentiate Thesis
Swedish University of Agricultural Sciences
Uppsala 2013

Aqua Licentiate Theses
2013:1

Cover: Breeding cormorants in the bay Lövstabukten, 2005.
(photo: M. Boström)

ISBN (print version) 978-91-576-9153-8
ISBN (electronic version) 978-91-576-9154-5

Print: SLU Service/Repro, Uppsala 2013

Fish Predation by the Great Cormorant (*Phalacrocorax carbo sinensis*). Analytical Basis for Ecosystem Approaches

Abstract

This thesis concerns the diet of a piscivorus top predator, the Great Cormorant (*Phalacrocorax carbo sinensis*), in the Baltic Sea. The Great Cormorant has increased exponentially in numbers during the last decades. This has resulted in a human-cormorant conflict because of its perceived competition with fisheries and negative impact on ecosystems. Information about the diet of cormorant along the Swedish Baltic coast and knowledge about the appropriate methodology to use for investigating potential ecosystem impacts and predatory effects on fish populations is, however, lacking. This thesis therefore examined the diet at two coastal locations, in the Bothnian Sea and in the Baltic Proper. Diets were examined with different methodologies to enable evaluation of its uses and applications. For an overall diet, pellets, regurgitate material and stomach content were considered. By tagging fish, estimates of the predatory pressure could be achieved.

The predatory impact on stocked trout (*Salmo trutta*) and salmon (*Salmo sala*r) smolt migrating from the river Dalälven was estimated to 2.3 % in 2005 and 2006. This was achieved by tagging smolt with Coded Wire Tags and Carlin tags which were recovered in pellets, faeces and nest material. Common species in the diet of cormorants in Lövstabukten (southern Bothnian Sea) and around Mönsterås (Baltic Proper) were herring (*Clupea harengus*), European perch (*Perca fluviatilis*), eelpout (*Zoarces viviparus*), Cyprinidae and sticklebacks (Gasterosteidae), but the diets varied between locations and over time. One of the investigated areas, Mönsterås, has undergone substantial changes in the fish ecosystem structure over the last two decades, with decreasing numbers of large predatory fish and more sticklebacks and Clupeidae. These changes were reflected in the cormorant diet as this shifted from European perch and Cyprinidae in 1992, towards more herring and eelpout in 2009. Sticklebacks were the most commonly occurring prey in 2009, and this was probably due to the general increase in stickleback numbers. It could also partly be due to a difference in methodology. The study in 1992 was based on pellet material while the study covered in this thesis, in 2009, was based on stomachs, which better represents smaller fish individuals and species than pellets. In studies concerning ecosystem impacts, where it is important to attain the entire size spectra of prey throughout the year, stomach content was concluded the most applicable method.

Keywords: cormorant, diet, otolith, pellets, *Phalacrocorax carbo sinensis*, predator, regurgitate, stomach

Author's address: Maria Boström, SLU, Department of Aquatic Science, Skolgatan 5, 453 30, Lysekil, Sweden.
*E-mail:*maria.bostrom@slu.se

Dedication

I dedicate this thesis to Mikael who had to endure many hours of my mental absence during the process.

”The specialist knows more and more about less and less and finally knows everything about nothing”.
Konrad Lorenz

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., Karlsson L., Ragnarsson, B. (2009) Cormorant impact on trout (*Salmo trutta*) and salmon (*Salmo salar*) migrating from the river Dalälven emerging in the Baltic Sea. Fisheries Research 98: 16-21.

II 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.

III 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.

Publications are reproduced with the permission of the following publishers; Elsevier (papers I and III) and BirdLife Finland (paper II).

The contribution of Maria Boström to the papers included in this thesis was as follows:

I Conducted field work, collected and analyzed diet material, conducted the statistical analyses, wrote the manuscript and handled the review process.

II Participated in initiating planning and designing the study, analyzed diet material, conducted the statistical analyses, wrote the manuscript and handled the review process.

III Participated in initiating planning and designing the study, analyzed most of the diet material, wrote the manuscript and handled the review process.

1 Introduction

The Great Cormorant population in Europe has increased in numbers the last decades. This has led to a European wide human-wildlife conflict, mainly because they remove large quantities of fish from ecosystems (Klenke *et al.*, 2013; Steffens, 2010). Cormorants are often blamed for reducing commercial and recreational fish catches directly because they are assumed to eat fish of the same species and sizes as those targeted by fisheries. They are also blamed for reducing catches indirectly, by eating fish in lower trophic levels, i.e. the prey of commercially important fish. In the conflict reconciliation process and for successful management decisions, reliable estimates of cormorant predation, and an understanding of ecosystem functioning, are necessary tools (Klenke et al., 2013). In order to understand how a predator, such as the cormorant, affects its prey and the food web it interacts within it is essential to have the theoretical background on predation and foraging behaviour.

1.1 Theoretical framework of predator-prey interactions in food webs

Ecosystems are assemblages of species interacting with each other and their environment (Begon et al., 2002). Species sharing an environment are called communities and these are structured and defined by the species within them, their relative abundances and physical features. Species and individuals within a community have positive, negative or insignificant effects on each other and these might be direct or indirect. All these 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).

There are many examples of how predator and prey populations can interrelate. In some (simple system) cases the predator and prey population sizes are dependent on each other and thus linked together. An increase in the number of prey increases the number of predators, which in turn reduces the prey population, causing predator numbers to decline. As predators decline, prey can increase again and the predator-prey cycle continues with fluctuations in predator-prey abundances (Begon et al., 2002).

By predating within a limited size span, predators can alter the individual size structure of the prey population (Kneib, 1982). Depending on where in the prey life cycle the main predation occurs, predators have different effects on the population as a whole. Predation that predominantly is directed toward young prey individuals may have little effect on the survival of the prey population. On the other hand, if the reproductive individuals are preferred, the effect can be substantially larger (Boyd et al., 2006). The effects a piscivorus predator has on certain fish species is often related to the vulnerability of the prey population. A vulnerable species may not be the most commonly occurring prey in the diet, but even little predation may still harm the population if predation occurs within a vulnerable life stage (Fielder, 2008). Factors such as spatial heterogeneity in the environment and prey defence are important for the prey population survival (Gilinsky, 1984). Prey that can hide (Russell et al., 2008), escape (Skov et al., 2013) and/or defend themselves have higher probabilities of survival from predators. Availability of alternative prey is also important for the survival of a prey population. As a prey population decreases the predator might choose an alternative prey, more abundant and/or easier to catch. On the other hand, if one prey species is abundant and the predator is unable to reduce its numbers, the result might be the maintenance of a continuously high predator density which may have detrimental effects on alternative prey species that are more sensitive to predation (Begon et al., 2002).

Predatory competition can enhance the predation pressure on a given prey populations. Competition (perceived or real) for resources is the origin of the conflict between humans and cormorants. Compared to most predators, humans catch fish of variable sizes. In addition, capture fisheries have historically depleted species in a top-down manner, fishing down the food web by targeting the larger fish first (Pauly *et al.*, 1998; Trites *et al.*, 1997). Even though the prey species may not overlap between a predator and certain capture fisheries or between two predators, there may still be an indirect competition between them (Baum & Worm, 2009; Andersen *et al.*, 2007; Trites *et al.*, 1997). This occurs when there is an overlap of the trophic flows, or prey species, supporting a given group of species (e.g. marine piscivorous birds) with the trophic flows supporting another group (e.g. certain capture fisheries). Effects of such indirect competition can be detected all the way down the trophic flow to the primary producers.

In theory, foraging behaviour aims to maximize energy gain per unit effort (Smith & Smith, 2003). For example, predators may choose to eat fewer but fatter prey if this results in a larger energy gain than hunting for smaller or less energy rich prey. Predators also tend to forage in areas where their prey is abundant. When prey becomes scarce they move to the next area with more abundant prey, ignoring areas with low numbers of prey (MacArthur & Pianka, 1966). Some predators are specialists which only consume few prey species, while others, like the cormorants, are generalists and predate on a large variety of species (Nelson, 2005; Carss, 2003; Johnsgard, 1993). Because they can switch target prey (and size to a certain degree), they can forage in an area even though the most preferable prey is scares. Cormorants are also adaptable by being able to change foraging behaviour after environmental conditions, from solitary foraging to social foraging. Social foraging has been suggested to occur under turbid conditions (Van Eerden & Voslamber, 1995) and when pelagic fish species are targeted (Grémillet *et al.*, 1998).

2 Cormorant predation on fish

From an ecological management perspective, the cormorant, *Phalacrocorax* spp., can on a global scale be considered a model genus for human-wildlife conflict, or a symbol of ecological conflict (Wild, 2012). The core of the conflict relates to the adaptability of cormorants to quickly inhabit new areas and exploit new food resources. In many cases they forage in large numbers and will consequently, in short time, consume large numbers of fish. They are present near salt, fresh and brackish waters on all continents (Sibley, 2001). Different areas of the world have similar conflicts with cormorants, although the particular species of cormorant differ (Doucette *et al.*, 2011; Wires *et al.*, 2003). For example, one of the most well-known conflicts is about the Double-Crested Cormorant (*Phalacrocorax auritus*) in the Great Lakes in North America. They have had a similar steep increase in numbers (Seefelt, 2012), almost during the same time period as the Great Cormorant increase in Europe.

2.1 The Cormorant - species description

Cormorants belong to the pelican family Phalacrocoracidae, traditionally within the single genus *Phalacrocorax*, (though there are discussions of 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. In Sweden there are two species of cormorants, the Great Cormorant (*Phalacrocorax carbo*, Linnaeus 1758) and the less common European Shag (*Phalacrocorax aristotilis*, Linnaeus 1761), found on the west coast. The Great Cormorant is the most widespread of all cormorants and can be found on all continents except South America and Antarctica (Johnsgard, 1993). In Sweden there are two subspecies of the Great Cormorant, *P.c. carbo* and *P.c. sinensis*, of which *P.c. sinensis* is the most common. The Great Cormorant where hunted down to extinction in Europe during the 19th century but have since then benefited from protection from human persecution (Steffens, 2010). During the last 30-40 years there has been a large increase in populations of *P.c. sinensis* across Europe (Steffens, 2010; Bregnballe *et al.*, 2003; Van Eerden & Gregersen, 1995). 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). Concerns about the European populations of the Great Cormorant (*P. c sinensis*) has increased markedly in the last decennium due to the increase in numbers (Keller & Visser, 1999). For an ornithologists and conservationist the increase might be considered good news as the cormorants now re-colonise their original habitats after being repressed. Though, for certain capture fisheries the cormorant increase relates to a competitor for fish resources. The Great Cormorant is subjected to debate since cormorants interact with human activities in several ways. Many fisherman and fish farmers claim that cormorants cause economic loss. They claim that cormorants deplete fish populations, cause damage (Engström, 1998) and drown in fishing gear (Żydelis *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).

Dietary studies on piscivorous top-predators are important not only in order to understand their economical and ecological interactions with certain capture fisheries but also to investigate the biology of the species, their role in the marine ecosystem and for conservation purposes (Pierce & Boyle, 1991). Though cormorant diet has been studied before there is insufficient knowledge about cormorant food habits and their effects on fish populations (Russell et al., 2003). Research results are not always consistent. Some studies have shown that cormorants can have negative effects 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.*, 1996; Barret *et al.*, 1990), while others show less or no effects of cormorant predation (e.g. Dalton *et al.*, 2009; Diana *et al.*, 2006; Engström, 2001; Suter, 1995).

2.2 Cormorant interaction within food webs in the Baltic Sea

Facts about foraging behaviour and diet are necessary ingredients in order to understand how cormorants, or any species, fit into a food web (Klenke et al., 2013). A daily food intake of around 500 grams is often assumed for the Great Cormorants, but requirements vary over seasons (Grémillet *et al.*, 1995). The Great Cormorant, *P.c. sinensis* has an energy requirement that represents between 238 grams to 588 grams of fish per day and adult during the breeding season. The energy requirement increases from incubation to the rearing of fledglings (Grémillet et al., 1995). During winters their energy requirement is on the higher end, around 539 grams per day and adult have been estimated for *P.c. sinensis* (Keller & Visser, 1999). Cormorants are generalists (Grémillet et al., 1995), which means that they can switch their diet in relation to environmental conditions. They are also opportunistic in that they are able to predate on several kinds of prey, including those which would result in less than the optimal energy intake. Basically, they eat the most common prey and the prey easiest to catch (Gremillet, 1997). Due to their flexibility they are able to quickly exploit new food resources and habitats and easily adapt to shifts in fish community structures.

Most predators feed within one or a few trophic levels (Boyd et al., 2006). However, even though cormorants feed on fish within a certain size span, as the size of their prey is limited by the size of their beak and the body height of the fish (personal observation), they tend to feed on fish individuals from several trophic levels. In the Baltic Sea, cormorant prey are both predatory fish, such as Northern pike (*Esox lucius*) and European perch (*Perca fluviatilis*), and planktivores, such as sprat (*Sprattus sprattus*) and sticklebacks (Gasterosteidae) (Lindell, 1997; Paper II; Paper III). This complicates theoretical modelling of the impact of cormorants on fish communities, as when individuals in one trophic level are reduced to low levels, cormorants feed on trophic levels with more common species. With this kind of foraging behaviour cormorants act as reducers of the most dominant species in a community (Smith & Smith, 2003). Thus, the impact cormorants have on a community is dependent on the community structure. Under the assumption that the controlling force is the most dominant species in the system and that the community is top-down controlled, i.e. where the abundance of organisms in lower trophic levels is dependent on the predation of top-predatory fish (Baum & Worm, 2009), a predation by cormorants on top-predatory fish, such as pike and perch, may have a positive effect on the lower trophic levels, but negative effect on the top-predator. On the other hand, if the system is bottom-up controlled and the species in lower trophic levels are more dominant

(Frederiksen et al., 2006), e.g. stickleback, cormorants may act as a stabilizer towards a top-down controlled system and thus support biological management (Dirksen et al., 1995) (Figure 1).

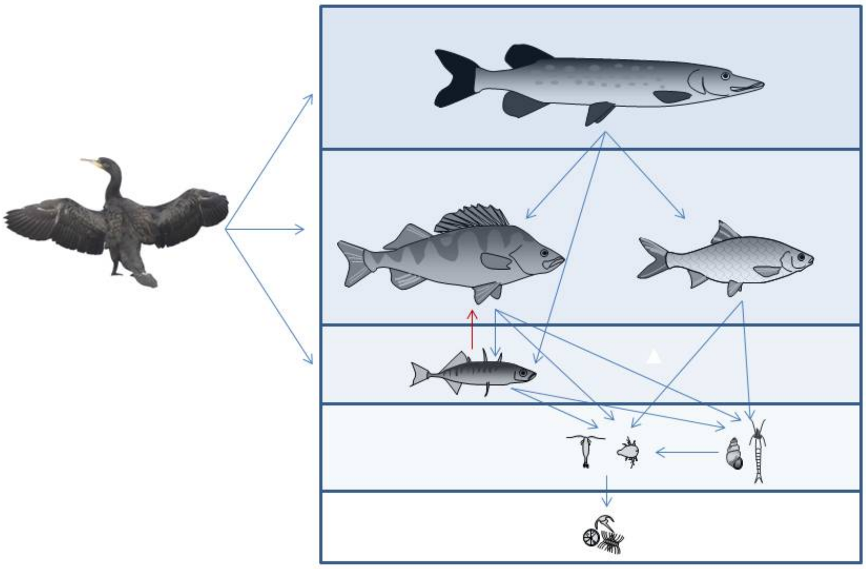

Figure 1. Cormorants within a Baltic Sea food web (very simplified in the figure) can affect the community on several trophic levels. Red arrow indicates predation on larvae. (Illustrations by Anna Gårdmark).

The Great Cormorant has been absent in European waters due to human persecution for about a century and during that time the food webs have likely adapted to the absence of this top predator. With the re-establishment of the cormorant population, theory states that they as a top predator should have started to change the interactions within ecological communities (Kraft et al., 2007). However, exactly how these changes have advanced is not known due to insufficient knowledge about the community as a whole. A complicating factor is that there were also other predators that increased in numbers during the expansion of cormorants. In some areas the prey choice of these predators may overlap and the predators can thus together affect community structures. E.g. both grey seals (*Halichoerus grypus*) (Harding & Härkönen, 1999) and the White-tailed Sea Eagle (*Haliaeetus albicilla*) (Herrmann et al., 2011) increased in numbers after the 1980s. Due to the predatory behaviour of cormorants and the variable community conditions, in space and time, the effects cormorants have on food web structure probably differs, as explained above, making it difficult to make generalizations on predatory effects.

The understanding of the interactions and transfer of energy between different trophic levels in food webs is crucial for the successful management and protection of nature habitats and ecosystems (Carey et al., 2013). In the Baltic Sea, large scale food web changes occurred about the same time as the cormorants re-established, however before cormorants started to expand and increase in numbers. Compared to other seas, the Baltic Sea ecosystem is young (8 000 years (Elmgren, 2001)), and has a uniquely low species diversity, due to its brackish environment and temperate climate (Casini et al., 2008). This means that each trophic level consists of fewer species compared both to marine and freshwater ecosystems in the same climatic region. As a consequence, if one species is reduced in numbers there are few, or none, species to compensate the role of that species. A trophic cascade occurred in the offshore ecosystem of the Baltic Proper in the 1980s (Casini et al., 2008). From a food web dominated by cod (*Gadus morhua*), a dramatic reduction of cod affected its main prey, sprat which increased in number to dominate the food web. Zooplankton, the main prey of sprat, decreased and thus the abundance of phytoplankton increased. Changes in the top of the food chain consequently changed the whole ecosystem. The decrease in the cod population was probably due to overfishing but may also have been related to recruitment failure. Changes also occurred in the coastal areas of the Baltic Proper at around the same time. The two dominating predators, Northern pike and European perch, decreased by 80 % in the 1990s, however no declines were observed in the Bothnian Sea (Ljunggren et al., 2010). The cause for the declines has also been suggested to be a recruitment failure (Ljunggren *et al.*, 2010; Nilsson *et al.*, 2004). As the large predators decreased, the smaller planktivorous, three-spine stickleback (*Gasterosteus aculeatus*) increased in numbers. The increase in mesopredatory fish species resulted in higher larvae predation which keep the recruitment of large predators to low levels (Ljunggren *et al.*, 2010).

2.3 Cormorant diet in Baltic Sea waters

Prior to the research within this thesis, cormorant diet on the Swedish Baltic coast has been studied at two occasions in the Kalmar Sound area. In 1975-1978 by Jonsson (1979) and in 1992 by Lindell (1997) Both studies used pellet material to examine cormorant diet and at both occasions European perch and roach (*Rutilus rutilus*) dominated the diet. Though these studies were limited in sample size, they confirmed that the diet partly consisted of commercially and recreationally important species, such as European perch and Northern pike. Later investigations of cormorant diet in other countries around the Baltic Sea have shown varying dominating prey species during the breeding season, e.g. roach, eelpout (*Zoarces viviparus*) and European perch in Finland, based on regurgitate material in 2002 to 2010 (Lehikoinen *et al.*, 2011; Lehikoinen, 2005). Roach and pike-perch (*Stizostedion lucioperca*) in the Curonian Lagoon in Lithuania, based on regurgitate material in 2001 (Žydelis et al., 2002). Roach and perch in the same area in the Curonian Lagoon, based on pellets in 2005-2007 (Pūtys & Zarankaitė, 2010). Ruffe (*Gymnocephalus cernua*) in the Vistula split in Poland, based on both pellets and regurgitate material in 1996 and 1997 (Martyniak et al., 2003).

Only a few studies have considered the effect of cormorant predation on fish populations and the potential consequences for different capture fisheries in the Baltic Sea. Focus in most of these studies has been on the direct effects of predation, i.e. removal of individuals of the prey species and sizes of investigation. Studies in Finland (Lehikoinen et al., 2011) and Lithuania (Žydelis & Kontautas, 2008) show no impacts of cormorants on commercial species, comparing diet of cormorants with standard multi-meshed monitoring gillnets data. While on the other hand a similar study in Estonia showed that cormorants indeed competed with fisheries in the Väinameri, and that certain capture fisheries and cormorants targeted the same sized fish. Unfortunately, studies based on standard multi-meshed monitoring gillnets are limited in the way that the nets do not capture fish individuals of smaller sizes. This limits the possibilities to look at effects on fish populations of which cormorants feed on smaller fish individuals. A Swedish study comparing cormorant diet to commercial catches shows that cormorants eat more than what capture fisheries land, but the direct impact was lowered by cormorants generally feeding on smaller individuals than the commercial fisheries catch. When accounting for the predation on smaller individuals however, the impact on certain capture fisheries became larger, up to 30 % of the fisheries catch for perch (Östman et al., unpublished). A difference in the size of the fish individuals targeted by cormorants, to those generally targeted by humans in the Baltic Sea, is a reason for local differences in the effects on capture fisheries.

In Swedish Baltic waters so far, European perch is the only species that has been considered in the investigation of the effects of cormorant predation on fish populations. Results indicate that cormorants can have negative effects on perch populations (Östman *et al.*, 2012; Saulamo *et al.*, 2001). Besides this, the effects cormorants have on fish populations and fisheries have only been considered in inland lakes (Engström, 2001). Considering that only one fifth of the cormorant colonies in Sweden can be found in inland lakes (Engström and Staav unpublished), the human conflict is likely to be more widespread around the coastal colonies, such as has been described in a Danish estuary (Jepsen *et al.*, 2010). It is therefore peculiar why the diet of cormorants in coastal colonies has not yet been properly investigated. In order to determine the role of cormorants on a fish population it is important to have information on not only their diet, but also their daily food intake (Barrett et al., 2007) and the fish population size. In inland lakes, which are smaller in size than coastal areas, the movements of the fish are restricted to a smaller water volume, making lake ecosystems easier to monitor. Investigating the role of predation on fish populations in marine environments requires a greater effort, but as most of the fisheries take place in marine habitats, research on the eventual effects of cormorant predation on coastal fish populations are needed. As the cormorants are blamed for causing dramatic declines of fish populations and thereby reducing or even removing the basis for economical sustainable fisheries, there is a need of further diet analyses combined with monitoring fishing results, population dynamics and fish behaviour, in order to get basis for both fishery management and cormorant action plans. The work of this thesis is therefore to contribute to the need for scientific valid data on cormorant diet by the use of different methodologies in the context of ecosystem research approaches, such as research regarding ecological and socio-economical effects of cormorants, important topics debated by different NGOs, governmental institutions (GO's) and researchers.

2.4 Major aims of the thesis

The major aim of this thesis was to gain knowledge about cormorant fish predation in Swedish Baltic waters. A secondary aim was to evaluate methods used to analyze their diet in relation to studies concerning ecosystem impact and effects on fish populations. The objectives were i) to determine cormorant predation on a defined, tagged, fish population, ii) to investigate temporal and spatial variation in diets, iii) investigate variations between sexes and life history stage, iv) to compare pellets and regurgitate materials, v) to evaluate the use of size correction factors on otoliths.

3 Methods

There are several ways of determining prey choice of a fish predator; observational studies, tagging prey, visually examining food remains in e.g. stomachs and faeces, biochemical methods such as DNA, stable isotope and fatty acid analysis (Barrett et al., 2007). The type of method to use depends on the hypothesis in question, e.g. if fish size estimates are necessary for quantitative measurement of predation. In other cases it might be enough with a presence/absence measurement of a prey. Understanding how and when in the life cycle predators impact their prey is important for the understanding of predator interactions in ecosystem functioning. It is therefore crucial to attain reliable estimates of prey size. For that reason, this thesis examines methods where size estimates can be attained.

3.1 Tagging of prey (Paper I)

Ecological complexities make it difficult to demonstrate predatory impacts (Carss, 2003; McKay *et al.*, 2003), but if the aim is to get reliable estimates on predation impact on certain fish populations, one possibility is to tag fish and search for the tags in excretions such as in faeces, pellets and vomits (Jepsen *et al.*, 2010). In field tagging experiments a subsample of the total fish population in an area become traceable, to a larger or smaller extent. It is also possible to collect additional information of the tagged fish, such as length, weight etc. The basic assumption is in most cases that the tagged fish should be a random sample of the total investigated population. There are several type and brands of tags available and the choice depends on the hypothesis and fish size. For example, the researcher can choose between tags for individual identification or just for identifying batches of fish. In this thesis both these types were used. Carlin tags were used for fish individual information (Feltham & MacLean, 1996) and Coded Wire Tags (CW-tags) for batch information (Jepsen *et al.*, 2010).

Figure 2. A CW-tag on the left and a Carlin tag on the right (Photo: M. Boström).

CW-tags and Carlin tags were used to estimate the predatory impact of cormorants on salmon (*Salmo salar*) and trout (*Salmo trutta*) smolt. The aim was to determine if the decline in return-rate of salmon and trout, within a sea-ranching programme, was due to cormorant predation around the river delta of Dalälven. We tagged fish in a hatchery in Älvkarleby. 4,000 salmon and 2,500 trout were tagged with carlin tags in 2005 and 2006. 31,650 trout were tagged with CW-tags in 2005 and 39,877 in 2006. In total 84,527 fish were tagged, released and searched for in cormorant faeces, pellets, vomits and nests. The map in figure 3 shows the major study areas in the thesis. Paper I and II considers the studies around the river Dalälven, with colonies in Lövstabukten.

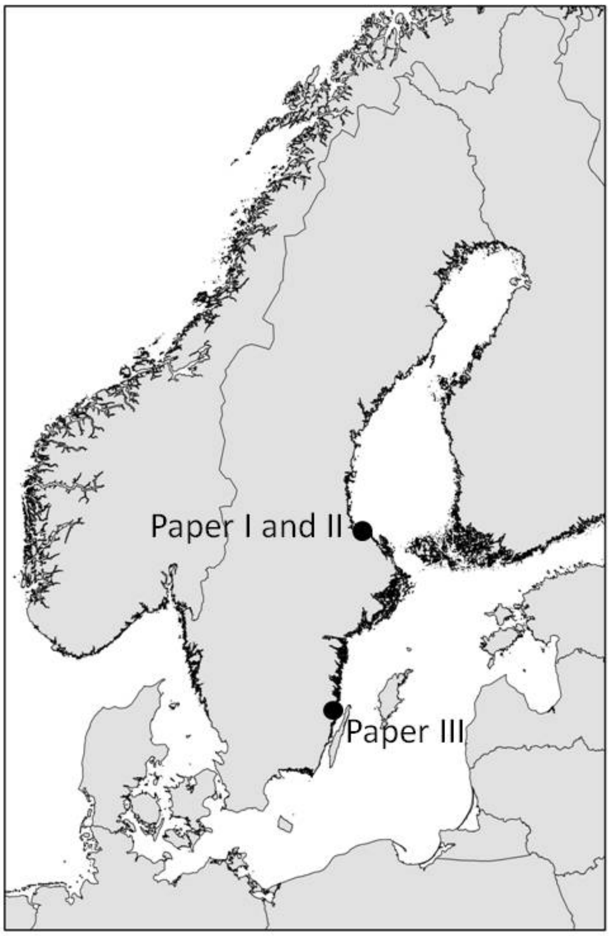

Figure 3. Study areas in which the diets of cormorants were examined. Paper I and II includes studies around colonies in the bay Lövstabukten. Paper III includes a diet study of cormorants in the archipelago outside Mönsterås, northern Kalmar Sound.

3.2 Prey remains from pellets and regurgitates (Paper II)

Cormorant prey remains can be found by investigating their pellets, regurgitates or stomach contents. Cormorants produce mucus coated pellets, about once a day, as a mean of getting rid of excess hard parts they don't digest (Barret *et al.*, 1990; Duffy & Laurenson, 1983). Pellets are easiest to find in colonies or roosting areas, where also regurgitates are found. Cormorants often empty their pharynx and regurgitate their last meal when disturbed.

Disturbance occurs naturally in colonies by e.g. sea eagles, but can also be provoked by human activity, e.g. visits in colonies or chase by boat. This thesis includes a comparison between the diets remains found in pellets with the remains in regurgitates (Figure 4).

Figure 4. Pellet (on the left) and regurgitate (on the right) collection in the bay Lövstabukten. The regurgitate contained eelpout (*Zoarces viviparus*), herring (*Clupea harengus*) and a trout (*Salmo trutta*) (Photo: M. Boström).

3.3 Prey remains from stomachs (Paper III)

Pellets and regurgitates both has the advantage of being non-lethal methods compared to investigating stomach contents (Barrett et al., 2007). However, there are at least three advantages with examining stomachs. Firstly, culled birds is the only means of collecting enough samples during the non-breeding period, when birds are dispersed along the coast (Barrett et al., 2007). Secondly, individual information of the bird can be collected, such as weight, age and gender of the bird. Thirdly, diet remains are less digested in stomachs than in pellets (Barrett et al., 2007), making identification and size estimates easier (Figure 5).

Figure 5. Prey remains in a cormorant stomach (Photo: Sven-Gunnar Lunneryd).

3.4 Size estimates accounting for erosion on otoliths (Paper II, III)

When assessing the diet of piscivorous species it is important to attain not only reliable estimates of diet composition but also on prey size (Klenke et al., 2013). Size estimates can be obtained by measuring the size of the fish found whole, but also by measuring bones and relating sizes to the size of the fish. The most commonly used bone structure is the otolith, or ear bone (Leopold *et al.*, 2001; Härkönen, 1986). Otoliths are part of the balance and hearing organ of the fish, and which are assumed to grow proportionally to the growth of the fish. Their calcareous structure make them more resistant to digestion than other bone structures (Härkönen, 1986). Otoliths are morphologically species specific and can thus be used both to identify the species and estimate the size of the predated fish. However, in pellets otoliths are often partially digested and to various degrees eroded by gastric acids. Their lengths and widths are thus underestimated and consequently the fish sizes will be underestimated (Barrett *et al.*, 2007; Pierce & Boyle, 1991; Jobling & Breiby, 1986; da Silva & Neilson, 1985). Past studies have suggested various methods to reduce biases concerning otoliths with digestion damage, which has been discussed by Tollit et al. (2004). Methods include such as using only uneroded otoliths (Johnson *et al.*, 2006; Suter & Morel, 1996). The disadvantage of this method is a reduced sample size, as the majority of otoliths are eroded. It will also favour species with larger and more robust otoliths while species with small, fragile otoliths will be underrepresented in both number and mass (Ross *et al.*, 2005; Tollit *et* *al.*, 1997; Harvey, 1989; Jobling & Breiby, 1986). To reduce this bias a possibility is to use species specific Digestion Correction Factors (DCF's). These factors are attained through the use of captive feeding trials were predators are fed with fish of known sizes, and otoliths are subsequently recovered, measured and correction factors are calculated for each species of fish (Casaux *et al.*, 1997; Suter & Morel, 1996; Casaux *et al.*, 1995), and also for different size classes of each species (Tollit et al., 1997). Although species specific DCF methods improves the accuracy, it is costly and time consuming as predators in different localities feed on different species, and each would have to be captured and fed to captive predators. To overcome this, grade-specific correction factors or Size Correction Factors (SCF's) have been used. These are based on defined losses of morphological features, where a grading of worn otoliths is used as a base for correction factors. This method does not account for size specific wear of otoliths, as DCF's, but the method of SCF's has been extensively used in diet studies of marine mammals (*e.g.* (Lundström *et al.*, 2007; Grellier & Hammond, 2006; Prime & Hammond, 1990; Harvey, 1989). Prior to the studies in this thesis, as far as I know, this process had only been applied to cormorant research in an impact study performed by Leopold et al. (1998) and a diet study on the Swedish west coast by Lunneryd and Alexandersson (2005).

3.5 Spatial and temporal differences in diet and difference between gender and age (Papers II and III)

Because cormorants are opportunistic predators there is a need to investigate spatial and temporal variability in their diet (Barrett et al., 2007). The difference in diet between time periods during breeding and different colonies was examined on three islands in the bay Lövstabukten in paper II. Paper III, with diet based on culled birds, made it possible to further include and consider differences between gender and age. In both studies the time period examined was that of the cormorant breeding cycle; when they were incubating, had nestlings, had small chicks and when they had fledglings. Species specific relative biomass proportions of fish per pellet or stomach were used to analyze diet variability.

4 General Results and Discussion

4.1 Cormorant diet in two areas in the Swedish Baltic Sea

Paper II and III investigated the diet composition of the Great Cormorant in two areas in the Baltic Sea (Figure 3). The area considered in paper II is in the bay Lövstabuken, which has a maximum depth of about 20 m. The bay has many shallow areas suitable for recruitment of European perch, Northern pike and Cyprinidae. Compared to other areas along the coast this area is considered to have experienced little eutrophication (Hjelm et al., 2009). Cormorant diet was investigated during the breeding season in 2005, on three islands, one in the northern area and two in a southern area of Lövstabukten. Overall, herring, European perch and eelpout dominated the diet but the dominating species differed somewhat between periods of the breeding cycle and between colonies. During the incubation period the diet in the northern colony was characterized by more European perch while the southern colonies by European smelt (*Osmerus eperlanus*) and ruffe. During the nestling and chick rearing periods, the diet in both areas was characterized by herring and eelpout respectively. In the northern colony cormorants shifted towards Cyprinidae during the fledgling period. Observational studies indicated that the cormorants in the northern colony foraged in deeper waters, further out from the coast, while cormorants from the two islands in the southern area foraged in the shallower part of the bay. Most likely, the difference in foraging areas explains the difference in prey choice between the northern and southern colonies.

Unlike the study area in paper II, the area in paper III, northern Kalmar Sound, has undergone substantial changes in fish community structure during the last decades. Even though the area has many suitable places for recruitment of European perch and Northern pike the recruitments of these species have been low in the 1990s (Ljunggren et al., 2010). The fish community shifted from being dominated by roach and European perch in the mid 1990´s to Cyprinidae species like bleak (*Alburnus alburnus*), rudd (*Scardinius erythrophthalmus*) and white bream (or silver bream) (*Abramis bjoerkna*). Over time, the abundance of herring and sticklebacks also increased (Ljunggren et al., 2010). The dissimilar community structure was reflected in the diet of cormorants in Mönsterås, between the 1990s and 2009. In the 1990s, perch and roach dominated cormorant diet and in 2009 sticklebacks dominated.

Though a shift in cormorant diet during breeding was not as obvious in Mönsterås, as in Lövstabukten, a tendency of a shift was revealed. During the incubation period cormorants mainly predated on stickleback and Cyprinidae. Later, while rearing chicks, eelpout and right-eye flounders (Pleuronectiformes) were more prominent in the diet. Herring were abundant in the diet during the fledging period. A similarity between the two study areas during the time frame of the study was the frequent occurrence of eelpout during the chick rearing period. This result corresponds to cormorant diet studies from the Tammisaari archipelago, in the western Gulf of Finland in 2002 (Lehikoinen, 2005), where roach and white bream dominated the diet (in biomass) during the incubating period and roach and European perch while rearing large chicks. When rearing small chicks 49 % of the diet consisted of eelpout. Also, a diet study in a colony in North East Poland, in 1996 and 1997, showed a temporal variability in the diet over time, with the greatest weight share of eelpout in June to July (based on regurgitates) (Martyniak et al., 2003). There may be a selection of eelpout during the rearing of small chicks (Lehikoinen, 2005). There is also a possibility that eelpout is easier to catch during that period as they are present in shallower waters when water temperature reaches 4-12 °C (Vetemaa, 1999), which occurred about the time when eelpout were the most abundant in cormorants diets in both paper II and III. Thus, the Great Cormorant does indeed seem to be an opportunistic predator and the changes in diet is probably mostly associated with changes in fish behaviour during the breeding season (Neuman et al., 1997).

4.2 Critical evaluation of methods; what to sample and when?

In Paper I and II the diet of cormorants were examined by tagging prey and examining prey remains in pellets and regurgitates. The aim of the tagging study was to determine if cormorants predate on trout and salmon smolt during the smolt run (when smolt leave the river). Because considerable predation on smolt was estimated in an estuary in Denmark, based on investigating pellets for CW-tags, and because cormorants were seen predating around the river delta the years before, we expected a significant predation. Defining a fish population by tagging gives reliable estimates of total predation on the defined population (Jepsen *et al.*, 2010) but for our aim we encountered an uncertainty in between year differences.

No tags which had been used for salmon were recovered and the predation on trout was only estimated to 0.8-2.3 %. The tags were all recovered in the colonies closest to the river delta. Thus, the study indicated that cormorants were the minor mortality factor during the smolt run. However, this single observation does not make it possible to conclude that this is the general circumstance. Cormorants were almost absent around the river delta during the study period, while reports from previous years indicated high numbers. The opportunistic cormorants may have predated on other fish species available closer to their colonies. In paper II, where the diet of the cormorants was examined, the results showed that the diet of cormorants in the colonies closest to the river delta was characterized by European perch and herring during the smolt run. An availability of European perch and herring closer to the colony than the available smolt around the river delta, might have led to cormorants neglecting the smolt run, or not even discovering the sudden congregation of a new food resource. The impact cormorants have on the smolt run is likely to depend on the availability of other prey species in their foraging range, but also on the behaviour of the tagged fish population. The majority of salmon smolt migrates during night, when cormorants roost (Olsén et al., 2004). Also, when salmon reach the delta they swim straight out to the open sea, outside the cormorant foraging range. Predation on salmon was therefore only expected if cormorants would have aggregated around the river delta, which they did not. Trout on the other hand move along the cost after reaching the delta (Finstad *et al.*, 2005; Thorstad *et al.*, 2004) and are thus more vulnerable to cormorant predation. My conclusion from these experiences is that although tagging studies is a useful tool to get estimates of predation it is important to consider the temporal aspect in the study design. In studies where fish only is available within the predators foraging range for a short period of time there might be temporal (or between year differences) that need to be considered.

The predation of cormorants in the bay of Lövstabukten was examined by using a combination of pellets and regurgitated fish, found in the nesting area. The most dominating species were the same by the two methods, but the methods gave varying results for smaller and less common species. Regurgitated fish contained more species compared to pellets, but pellets revealed more fish individuals compared to regurgitates. (It has also been shown that pellets reveal more individuals than stomachs (Johnson *et al.*, 2010)). The difference between the methods concur with earlier comparisons between pellets and regurgitates (Martyniak *et al.*, 2003; Derby & Lovvorn, 1997), where for example, regurgitates generated more species and regurgitates had species not present in pellets (32 %) and vice versa (20 %) (Martyniak et al., 2003). Most of the species that were present in regurgitates but not in pellets were species with smaller individuals and/or smaller otoliths, more prone to complete digestion. If the aim is to investigate the ecological significance of cormorant predation it is important to use a method that also reveals the smaller species and smaller individuals. Among these two methods, our study therefore recommends examining regurgitates, or regurgitates in combination with pellets. Also because of a risk of including secondary consumed individuals in pellets (i.e. fish in the stomach of cormorant prey) (Leopold *et al.*, 1998).

Paper III considers the diet of culled birds. These were shot during the breeding season; local fishermen had permission from the local county administration for protective hunting. Sticklebacks constituted 92 % of the number of fish found in total in stomachs. Because many of the sticklebacks were found more or less intact, we concluded that it was not a matter of secondary consumption. If we compare this to pellets and regurgitates, pellets did not reveal sticklebacks in the diet at all, while regurgitates did. Even though stomachs generate less fish individuals, they have been shown to cover more species than pellets (Lunneryd & Alexandersson, 2005) and also, secondary consumption is lower in stomachs than in pellets (Casaux et al., 1997). Therefore stomachs give a more reliable picture of prey species. Comparisons of diet data, in terms of relative frequency and biomass, have shown to concur between stomachs and regurgitated fish (Seefelt & Gillingham, 2006). It is therefore likely that stomach and regurgitate material are more comparable to each other than to results based on pellets. Moreover, stomach material has the advantage of being collectible throughout the year, even when the birds disperse.

Another interesting result was that when comparing the diet of culled birds with the catch of fish species in an annual gill net monitoring program, more fish species were found in cormorant stomach than in the gill nets, especially of the smaller sized species and species with eel like body shape. Because cormorants are opportunistic generalists their diet may represent the fish community better than gill net monitoring, which is limited in catching smaller individuals.

The tagging of fish populations is a cost effective method to determine the direct effects of cormorant predation on valuable fish populations. It does not involve the time consuming investigations of diet material and identification of fish remains. Moreover, because the size of the tagged population is known, there is no need for extensive monitoring fisheries to estimate population sizes. Number and biomass estimates of fish predation can also be investigated for species with large and robust otoliths by investigating diet material in the form of pellets, regurgitates or stomach material. If the indirect effects on predation and ecological aspects are to be considered, stomach content data gives the most reliable estimates of prey proportion in diet as it includes smaller species and individuals. However, due to the ethical aspects of killing the birds, the collection of regurgitates should be considered as an alternative.

4.3 Correction for gastric acid erosion

In paper II the application of size correction factors on worn otoliths was evaluated by comparing fish sizes, estimated based on otoliths, with estimates corrected and not corrected for wear. Figure 2 in paper II shows that the correction factors were correctly applied, even though there was a lack of otoliths in wear class 1, i.e. uneroded otoliths. To solve this correction factor 1 and 2 were pooled and wear class 3 corrected to wear class 2, with the consequence of somewhat underestimated original fish sizes. However, though not presented in the papers within this thesis, we did a comparison of fish lengths based on otoliths corrected for wear and those not corrected for wear with the length of fish found whole from regurgitates. For herring and eelpout, correction of wear resulted in a mean length closer to the mean length of regurgitated fish than not correcting for wear. For European perch on the other hand, regurgitated fish estimates gave a lower mean length than length based on uncorrected otoliths; i.e. the regurgitated European perch were smaller in size than the European perch found in pellets (Figure 6). If regurgitates represent the diet of both adults and chicks this is probably due to a selection of smaller individuals fed to chicks. Therefore, I conclude that the application of size correction factors on otoliths should be used to obtain as precise fish size estimates as possible.

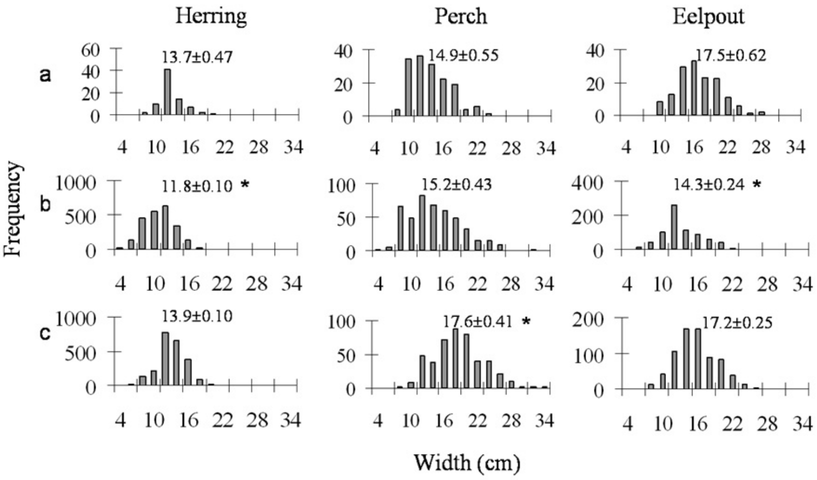

Figure 6. Histograms of fish lengths of herring, perch and eelpout based on a) regurgitated fish, b) calculated lengths from otoliths uncorrected for wear, and c) otoliths corrected for wear. Presented is also the mean length and 95 % C.I. Significance (ANOVA, $p < 0.05$) is indicated with an asterix for histogram that differs for each species.

4.4 Concluding remarks and future considerations

Because of the variable diet of cormorants an active adaptive management approach should be considered. If cormorants are found to have severe effect, on certain fish species or on an ecosystem, in one area it does not mean they have the same effect elsewhere. Future research should therefore address the role of cormorants in different environments and ecosystems to identify type of areas of special concern for sustainability of diverse ecosystems and viable socio-economy. The reason for this is that it is unfeasible to investigate the diet of cormorants everywhere. A precautionary approach may be to adapt management actions towards culling and use the stomachs for dietary analysis before continual management decisions.

In this thesis it was also concluded that stomach content, in combination with the use of SCF's on otoliths, is the most applicable methodology for scientific valid data on cormorant diet in the context of ecosystem research approaches. Not only because stomachs better reveal the true prey composition, but also because cormorant stomach material can be attained throughout the year. This is important as cormorants tend to feed their chicks with smaller individuals during breeding (Lehikoinen, 2005), while consuming larger fish during wintertime (Čech *et al.*, 2008). Though not considered in this thesis I want to highlight the importance of investigating diet outside the breeding season as it might differ considerable from what cormorants eat and feed their chicks with during the breeding season, both in terms of species composition and fish sizes. In areas where cormorants are present also when not breeding, estimates of cormorant effects based on cormorant diet only during breeding should be regarded as a minimum estimate.

In order to progress in the reconciliation process of the human-cormorant conflict more research is needed and it is essential to consider both ecological and socio-economic aspects. A closer collaboration between seabird biology and fisheries science is urgently required.

References

Andersen, S.M., Teilmann, J., Harders, P.B., Hansen, E.H. & Hjøllund, D. (2007). Diet of harbour seals and great cormorants in Limfjord, Denmark: interspecific competition and interaction with fishery. *ICES Journal of Marine Science: Journal du Conseil* 64(6), 1235-1245.

Barret, R.T., Røv, N., Loen, J. & Montevecchi, W.A. (1990). Diets of shags *Phalacrocorax aristotelis* and cormorants *P. carbo* in Norway and possible implications for gadoid stock recruitment. *Marine Ecology Progress Series* 66, 205-218.

Barrett, R.T., Camphuysen, K., Anker-Nilssen, T., Chardine, J.W., Furness, R.W., Garthe, S., Hüppop, O., Leopold, M.F., Montevecchi, W.A. & Veit, R.R. (2007). Diet studies of seabirds: a review and recommendations. *ICES Journal of Marine Science: Journal du Conseil* 64(9), 1675-1691.

Baum, J.K. & Worm, B. (2009). Cascading top-down effects of changing oceanic predator abundances. *Journal of Animal Ecology* 78(4), 699-714.

Begon, M., Harper, J.L. & Townsend, C.R. (2002). *Ecology*. 3rd edition. ed. Oxford.

Boyd, I.L., Wanless, S. & Camphuysen, C.J. (2006). *Top Predators in Marine Ecosystems, Their Role in Monitoring and Management*. Cambridge: Cambridge University Press.

Bregnballe, T., Engström, H., Knief, W., Mennobart, R., Van Eerden, S., Van Rijn, J., Kieckbusch, J. & Eskildsen, J. (2003). Development of the breeding population of Great Cormorants *Phalacrocorax carbo sinensis* in The Netherlands, Germany, Denmark and Sweden during the 1990s. *Vogelwelt* 124, 15-26.

Bregnballe, T. & Frederiksen, M. (2006). Net-entrapment of great cormorants Phalacrocorax carbo sinensis in relation to individual age and population size. *Wildlife Biology* 12(2), 143-150.

Carey, M.P., Levin, P.S., Townsend, H., Minello, T.J., Sutton, G.R., Francis, T.B., Harvey, C.J., Toft, J.E., Arkema, K.K., Burke, J.L., Kim, C.-K., Guerry, A.D., Plummer, M., Spiridonov, G. & Ruckelshaus, M. (2013). Characterizing coastal foodwebs with qualitative links to bridge the gap between the theory and the practice of ecosystem-based management. *ICES Journal of Marine Science: Journal du Conseil*.

Carss, D. (2003). Reducing the conflict between cormorants and fisheries on a pan-European scale (REDCAFE). *Final Report to European Union DG Fish*.

Casaux, R., Favero, M., Coria, N. & Silva, P. (1997). Diet of the imperial cormorant Phalacrocorax atriceps: comparison of pellets and stomach contents. *Marine Ornithology* 25, 1-4.

Casaux, R.J., Favero, M., E.R., B.O. & Silva, P. (1995). Feeding trial on an imperial cormorant Phalacrocorax atriceps: preliminary results on fish intake and otolith digestion *Marine Ornithology* 23, 101-106.

Casini, M., Lövgren, J., Hjelm, J., Cardinale, M., Molinero, J.C. & Kornilovs, G. (2008). Multi-level trophic cascade in a heavily exploited open marine ecosystem. *Proceedings of the Royal Society of London Series B-Biological Sciences* 275, 1793-1801.

Čech, M., Čech, P., Kubečka, J., Prchalová, M. & Draštík, V. (2008). Size Selectivity in Summer and Winter Diets of Great Cormorant (Phalacrocorax carbo): Does it Reflect Season-Dependent Difference in Foraging Efficiency? *Waterbirds* 31(3), 438-447.

Čech, M. & Vejřík, L. (2011). Winter diet of great cormorant (Phalacrocorax carbo) on the River Vltava: estimate of size and species composition and potential for fish stock losses *Folia Zoologica* 60(2), 129-142.

da Silva, J. & Neilson, J.D. (1985). Limitations of using otoliths recovered in scats to estimate prey consumption in seals. *Canadian Journal of Fisheries and Aquatic Sciences* 42, 1439-1442.

Dalton, C.M., Ellis, D. & Post, D.M. (2009). The impact of double-crested cormorant (Phalacrocorax auritus) predation on anadromous alewife (Alosa pseudoharengus) in south-central Connecticut, USA. *Canadian Journal of Fisheries and Aquatic Sciences* 66(2), 177-186.

Derby, C.E. & Lovvorn, J.R. (1997). Comparison of pellets versus collected birds for sampling diets of double-crested cormorants. *Condor* 99(2), 549-553.

Diana, J.S., Maruca, S. & Low, B. (2006). Do Increasing Cormorant Populations Threaten Sportfishes in the Great Lakes? A Case Study in Lake Huron. *Journal of Great Lakes research - International Association for Great Lakes Research* 32(2), 306-320.

Dieperink, C. (1995). Depredation of commercial and recreational fisheries in a Danish fjord by cormorants, Phalacrocorax carbo sinensis, Shaw. *Fisheries Management and Ecology* 2(3), 197-207.

Dirksen, S., Boudewijn, T.J., Noordhuis, R. & Marteijn, E.C.L. (1995). Cormorants Phalacrocorax carbo sinensis in shallow eutrophic freshwater lakes: Prey choise and fish consumption in the non-breeding period and effects of large-scale fish removal. *Ardea* 83(1), 167-184.

Doucette, J.L., Wissel, B. & Somers, C.M. (2011). Cormorant–fisheries conflicts: Stable isotopes reveal a consistent niche for avian piscivores in diverse food webs. *Ecological Applications* 21(8), 2987-3001.

Duffy, D.C. & Laurenson, L.J.B. (1983). Pellets of Cape Cormorants as Indicators of Diet. *Condor* 85, 305-307.

Elmgren, R. (2001). Understanding Human Impact on the Baltic Ecosystem: Changing Views in Recent Decades. *AMBIO: A Journal of the Human Environment* 30(4), 222-231.

Engström, H. (1998). Conflicts between cormorants (Phalacrocorax carbo L.) and fishery in Sweden. *Nordic Journal of Freshwater Research* 64, 148-155.

Engström, H. (2001). *Effects of Great Cormorant predation on fish populations and fishery. PhD Thesis.* Diss. Uppsala:University of Uppsala.

Feltham, M.J. & MacLean, J.C. (1996). Carlin tag recoveries as an indicator of predation on salmon smolts by goosanders and red-breasted mergansers. *Journal of Fish Biology* 48(2), 270-282.

Fielder, D.G. (2008). Examination of Factors Contributing to the Decline of the Yellow Perch Population and Fishery in Les Cheneaux Islands, Lake Huron, with Emphasis on the Role of Double-crested Cormorants. *Journal of Great Lakes Research* 34(3), 506-523.

Fielder, D.G. (2010). Response of yellow perch in Les Cheneaux Islands, Lake Huron to declining numbers of double-crested cormorants stemming from control activities. *Journal of Great Lakes Research* 36(2), 207-214.

Finstad, B., Okland, F., Thorstad, E.B., Bjorn, P.A. & Mc Kinley, R.S. (2005). Migration of hatchery-reared Atlantic salmon and wild anadromous brown trout post-smolts in a Norwegian fjord system. *Journal of Fish Biology* 66, 86-96.

Frederiksen, M., Edwards, M., Richardson, A.J., Halliday, N.C. & Wanless, S. (2006). From plankton to top predators: bottom-up control of a marine food web across four trophic levels. *Journal of Animal Ecology* 75(6), 1259-1268.

Gilinsky, E. (1984). The Role of Fish Predation and Spatial Heterogeneity in Determining Benthic Community Structure. *Ecology* 65(2), 455-468.

Grellier, K. & Hammond, P.S. (2006). Robust digestion and passage rate estimates for hard parts of grey seal (Halichoerus grypus) prey. *Canadian Journal of Fisheries and Aquatic Sciences*, 1982-1998.

Gremillet, D. (1997). Catch per unit effort, foraging efficiency, and parental investment in breeding great cormorants (Phalacrocorax carbo carbo). *ICES Journal of Marine Science* 54(4), 635-644.

Grémillet, D., Argentin, G., Schulte, B. & Culik, B. (1998). Flexible foraging techniques in breeding Cormorants Phalacrocorax carbo and Shags Phalacrocorax aristotelis: benthic or pelagic feeding? *Ibis* 140(1), 113-119.

Grémillet, D., Schmid, D. & Culik, B. (1995). Energy requirements of breeding great cormorants *Phalacrocorax carbo sinensis Marine Ecology Progress Series* 121, 1-9.

Harding, K.C. & Härkönen, T.J. (1999). Development in the Baltic Grey Seal (Halichoerus grypus) and Ringed Seal (Phoca hispida) Populations during the 20th Century. *Ambio* 28(7), 619-627.

Härkönen, T. (1986). *Guide to the otoliths of the bony fishes of the northeast Atlantic*. Hellerup: Danbiu ApS. ISBN 87-982290-2-8.

Harvey, J.T. (1989). Assessment of errors associated with harbour seal (*Phoca vitulina*) faecal sampling. *Journal of Zoology (London)* 219, 101-111.

Herrmann, C., Krone, O., Stjernberg, T. & Helander, B. (2011). Population Development of Baltic Bird Species: White-tailed Sea Eagle (Haliaeetus albicilla). *HELCOM Baltic Sea Environment Fact Sheets 2011. Online. 2013-05-02, http://www.helcom.fi/environment2/ifs/en_GB/cover/*.

Hjelm, M., Johansson, G. & Persson, J. (2009). Naturvärden i södra Lövstabuktens grunda havsmiljöer. *Upplandsstiftelsen* 6, 1-40.

Jepsen, N., Klenke, R., Sonnesen, P. & Bregnballe, T. (2010). The use of coded wire tags to estimate cormorant predation on fish stocks in an estuary. *Marine and Freshwater Research* 61(3), 320-329.

Jobling, M. & Breiby, A. (1986). The use and abuse of fish otoliths in studies of feeding habits of marine piscivores. *Sarsia* 71, 265-274.

Johnsgard, P.A. (1993). *Cormorants, darters, and pelicans of the world*. Washington: Smithsonian Institution Press.

Johnson, J.A., Ross, M.R., McCullough, R.D. & Mathers, A. (2010). A Comparative Analysis of Double-Crested Cormorant Diets from Stomachs and Pellets from Two Lake Ontario Colonies. *Journal of Freshwater Ecology* 25(4), 669-672.

Johnson, J.H., Ross, R.M., Mc Kenna, J.E. & Lewis, G.E. (2006). Estimating the size of fish consumed by double-crested cormorants: considerations for better understanding cormorant-fish interactions. *Journal of Great Lakes research - International Association for Great Lakes Research* 32, 91-101.

Jonsson, B. (1979). Skarvarna och yrkesfisket i Kalmarsund. *Calidris Supplement* 8(3), 171-220.

Keller, T.M. & Visser, G.H. (1999). Daily energy expenditure of great cormorants Phalacrocorax carbo sinensis wintering at Lake Chiemsee, Southern Germany. *Ardea* 87(1), 61-69.

Kirby, J.S., Holmes, J.S. & Sellers, R.M. (1996). Cormorants *Phalacrocorax carbo* as Fish Predators: an Appraisal of their Conservation and Management in Great Britain. *Biological Conservation* 75, 191-199.

Klenke, R.A., Ring, I., Kranz, A., Jepsen, N., Rauschmayer, F. & Henle, K. (Eds.) (2013). *Human-Wildlife Conflicts in Europe, Fisheries and Fish-eating Vertebrates as a Model Case*. Berlin Heidelberg: Springer. (Environment Science and Engineering.

Kneib, R.T. (1982). The effects of predation by wading birds (Ardeidae) and blue crabs (Callinectes sapidus) on the population size structure of the common mummichog, Fundulus heteroclitus. *Estuarine, Coastal and Shelf Science* 14(2), 159-165.

Kolb, G. (2010). *The impact of cormorant nesting colonies on plants and arthropods, PhD thesis.* Diss. Stockholm:Stockholm University.

Kraft, N.J., Cornwell, W.K., Webb, C.O. & Ackerly, D.D. (2007). Trait evolution, community assembly, and the phylogenetic structure of ecological communities. *The American Naturalist* 170(2), 271-283.

Lehikoinen, A. (2005). Prey-switching and Diet of the Great Cormorant During the Breeding Season in the Gulf of Finland. *Waterbirds* 28(4), 511-515.

Lehikoinen, A., Heikinheimo, O. & Lappalainen, A. (2011). Temporal changes in the diet of great cormorant (Phalacrocorax carbo sinensis) on the southern coast of Finland - comparison with available fish data. *Boreal Environment Research* 16 (subbl. B), 61-70.

Leopold, M.F., van Damme, C.J.G., Phillippart, C.J.M. & Winter, C.J.N. (2001). *Otoliths of the North Sea: Interactive guide of identification of fish from the SE North Sea, Wadden Sea and adjacent fresh waters by means of otoliths and other hard parts* World Biodiversity Database.

Leopold, M.F., van Damme, C.J.G. & van der Veer, H.W. (1998). Diet of cormorants and the impact of cormorant predation on juvenile flatfish in the Dutch Wadden Sea. *Journal of Sea Research* 40(1-2), 93-107.

Lindell, L. (1997). Food composition of Cormorants Phalacrocorax carbo sinensis in Sweden. *Supplemento alle Ricerche di Biologia della Selvaggina* XXVI, 163-171.

Ljunggren, L., Sandström, A., Bergström, U., Mattila, J., Lappalainen, A., Johansson, G., Sundblad, G., Casini, M., Kaljuste, O. & Eriksson, B.K. (2010). Recruitment failure of coastal predatory fish in the Baltic Sea coincident with an offshore ecosystem regime shift. *ICES Journal of Marine Science: Journal du Conseil 67 (8): 1587-1595.*

Lundström, K., Hjerne, O., Alexandersson, K. & Karlsson, O. (2007). Estimation of grey seal (Halichoerus grypus) diet composition in the Baltic Sea. *NAMMCO Scientific Pubication Series* 6, 177-196.

Lunneryd, S.-G. & Alexandersson, K. (2005). Födoanalyser av storskarv Phalacrocorax carbo i Kattegatt-Skagerak. *Fiskeriverket informerar* 2005:11, 1-20.

MacArthur, R.H. & Pianka, E.R. (1966). On Optimal Use of a Patchy Environment. *The American Naturalist* 199(916), 603-609.

Martyniak, A., Wziatek, B., Szymanska, U., Hliwa, P. & Terlecki, J. (2003). Diet composition of Great Cormorants *Phalacrocorax carbo sinensis* at Kąty Rybackie, NE Poland, as assessed by pellets and regurgitated prey. *Vogelwelt* 124, 217-225.

McKay, H.V., Robinson, K.A., Carss, D.N. & Parrott, D. (2003). The limitations of pellet analysis in the study of cormorant Phalacrocorax spp. diet. *Vogelwelt* 124, 227-236.

Nelson, J.B. (2005). *Pelicans, Cormorants, and their Relatives The Pelecaniformes*: Oxford University press ISBN 0198577273

Neuman, J., Pearl, D., Ewins, P., Black, R., Weseloh, D., Pike, M. & Karwowski, K. (1997). Spatial and temporal variation in the diet of double-crested cormorants (Phalacrocorax auritus) breeding on the lower Great Lakes in the early 1990s. *Canadian Journal of Fisheries and Aquatic Sciences* 54(7), 1569-1584.

Nilsson, J., Andersson, J., Karås, P. & Sandström, O. (2004). Recruitment failure and decreasing catches of perch (Perca fluviatilis L.) and pike (Esox lucius L.) in the coastal waters of southeast Sweden. *Boreal Environment Research* 9, 295-306.

Olsén, K.H., Petersson, E., Ragnarsson, B., Lundqvist, H. & Järvi, T. (2004). Downstream migration in Atlantic salmon (Salmo salar) smolt sibling groups. *Canadian Journal of Fisheries and Aquatic Sciences* 61(3), 328-331.

Östman, Ö., Bergenius, M., Boström, Maria K. & Lunneryd, S.-G. (2012). Do cormorant colonies affect local fish communities in the Baltic Sea? *Canadian Journal of Fisheries and Aquatic Sciences* 69(6), 1047-1055.

Pauly, D., Christensen, V., Dalsgaard, J., Froese, R. & Torres, F. (1998). Fishing Down Marine Food Webs. *Science* 279(5352), 860-863.

Pierce, G.J. & Boyle, P.R. (1991). A review of methods for diet analysis in piscivorous marine mammals. *Oceanography and Marine Biology: An Annual Review* 29, 409-486.

Prime, J.H. & Hammond, P.S. (1990). The diet of grey seals from the South-westen North Sea assessed from analyses of hard parts found in faeces. *Journal of Applied Ecology* 27, 435-447.

Pūtys, Ž. & Zarankaitė, J. (2010). Diet of the Great Cormorant (Phalacrocorax carbo Sinensis) at the Juodkrantė Colony, Lithuania. *Acta Zoologica Lituanica* 20(3), 179-189.

Ross, R.M., Johnson, J.H. & Adams, C.M. (2005). Use of Fish–Otolith-Length Regressions to Infer Size of Double-Crested Cormorant Prey Fish from Recovered Otoliths in Lake Ontario. *Northeastern Naturalist* 12(2), 133-140.

Rudstam, L., G, VanDeValk, A., J, Adams, C., M, Coleman, J., T. H, Forney, J., L & Richmond, M., E (2004). Cormorant Predation and the Population Dynamics of Walleye and Yellow Perch in Oneida Lake. *Ecological Applications* 14(1), 149-163.

Russell, I., Parrott, D., Ives, M., Goldsmith, D., Fox, S., Clifton-Dey, D., Prickett, A. & Drew, T. (2008). Reducing fish losses to cormorants using artificial fish refuges: an experimental study. *Fisheries Management and Ecology* 15(3), 189-198.

Russell, I.C., Kinsman, D.A., Ives, M.J., Finney, J. & Murrell, M. (2003). The use of coded-wire microtags to assess prey selectivity and foraging behavior in Great Cormorants *Phalacrocorax carbo*. *Vogelwelt* 124, 245-253.

Saulamo, K., Andersson, J. & Thoresson, G. (2001). Skarv och fisk vid svenska Östersjökusten. *Finfo Fiskeriverket Informerar* 7, 21 pp.

Seefelt, N. & Gillingham, J. (2006). A comparison of three methods to investigate the diet of breeding double-crested cormorants (Phalacrocorax auritus) in the Beaver Archipelago, northern Lake Michigan. *Hydrobiologia* 567(1), 57-67.

Seefelt, N.E. (2012). Comparing Decadal Census Trends and Yearly Variation in Abundance and Distribution of Breeding Double-Crested Cormorants: Importance of Monitoring a Managed Species. *Waterbirds* 35(sp1), 40-49.

Sibley, D.A. (2001). *The Sibley guide to bird life and behavior*. New York: Chanticleer Press Inc.

Skov, C., Chapman, B.B., Baktoft, H., Brodersen, J., Brönmark, C., Hansson, L.-A., Hulthén, K. & Nilsson, P.A. (2013). Migration confers survival benefits against avian predators for partially migratory freshwater fish. *Biology Letters* 9(2).

Smith, R.L. & Smith, T.M. (2003). *Elements of Ecology*. 5th edition. ed. San Francisco.

Steffens, W. (2010). Great cormorant—substantial danger to fish populations and fishery in Europe. *Bulgarian Journal of Agricultural Science* 16, 322-331.

Suter, W. (1995). The Effect of Predation by Wintering Cormorants *Phalacrocorax carbo* on Grayling *Thymallus thymallus* and Trout (Salmonidae) Populations: Two Case Studies from Swiss Rivers. *Journal of Applied Ecology* 32(1), 29-46.

Suter, W. & Morel, P. (1996). Pellet Analysis in the Assessment of Great Cormorant Phalacrocorax carbo Diet: Reducing Biases from Otolith Wear When Reconstructing Fish Length. *Colonial Waterbirds* 19(2), 280-284.

Thorstad, E., kland, F., Finstad, B., Sivertsgrd, R., Bjorn, P. & McKinleyd, R. (2004). Migration speeds and orientation of Atlantic salmon and sea trout post-smolts in a Norwegian fjord system. *Environmental Biology of Fishes* 71(3), 305-311.

Tollit, D.J., Heaslip, S.G., Zeppelin, T.K., Joy, R., Call, K.A. & Trites, A.W. (2004). A method to improve size estimates of walleye pollock (*Theragra chalcogramma*) and Atka mackerel (*Pleurogrammus monopterygius*) consumed by pinnipeds: digestion correction factors applied to bones and otoliths recovered in scats. *Fisheries Bulletin (Dublin)* 102, 498-508.

Tollit, D.J., Steward, M.J., Thompson, P.M., Pierce, G.J., Santos, M.B. & Hughes, S. (1997). Species and size differences in the digestion of otoliths and beaks: implications for estimates of pinneped diet composition. *Canadian Journal of Fisheries and Aquatic Sciences* 54, 105-119.

Trites, A.W., Christensen, V. & Pauly, D. (1997). Competition between fisheries and marine mammals for prey and primary production in the Pacific Ocean. *Journal of Northwest Atlantic Fishery Science* 22, 173-187.

Van Eerden, M.R. & Gregersen, J. (1995). Long-term changes in the northwest European population of cormorants *Phalacrocorax carbo sinensis*. *Ardea* 83, 61-79.

Van Eerden, M.R. & Voslamber, B. (1995). Mass Fishing by Cormorants Phalacrocorax carbo sinensis at Lake Ijsselmeer,the Netherlands: A Recent and Successful Adaptation to a Turbit Environment. *Ardea* 83(1), 199-212.

Vetemaa, M. (1999). Reproduction biology of the vivipaorus blenny (*Zoarces viviparus* L.) *Fiskeriverket Rapport* 2, 81-96.

Vetemaa, M., Eschbaum, R., Albert, A., Saks, L., Verliin, A., Jürgens, K., Kesler, M., Hubel, K., Hannesson, R. & Saat, T. (2010). Changes in fish stocks in an Estonian estuary: overfishing by cormorants? *ICES Journal of Marine Science: Journal du Conseil 67 (9): 1972-1979.*

Wild, D. (2012). *Double-Crested Cormorant Symbol of Ecological Conflict*. United States of America: The University of Michigan Press.

Wires, L.R., Carss, D.N., Cuthbert, F.J. & Hatch, J.J. (2003). Transcontinental connections in relation to cormorant - fisheries conflicts: perceptions and realities of a "bête noire" (black beast) on both sides of the Atlantic. *Vogelwelt* 124, 389-400.

Žydelis, R., Bellebaum, J., Österblom, H., Vetemaa, M., Schirmeister, B., Stipniece, A., Dagys, M., van Eerden, M. & Garthe, S. (2009). Bycatch in gillnet fisheries – An overlooked threat to waterbird populations. *Biological Conservation* 142(7), 1269-1281.

Žydelis, R., Gražulevič, G., Zarankaitė, J., Mečionis, R. & Mačiulis, M. (2002). Expansion of the Cormorant (Phalacrocorax Carbo Sinensis) Population in Western Lithuania. *Acta Zoologica Lituanica* 12(3), 283-287.

Žydelis, R. & Kontautas, A. (2008). Piscivorous birds as top predators and fishery competitors in the lagoon ecosystem. *Hydrobiologia* 611(1), 45-54.

Acknowledgements

Sven-Gunnar Lunneryd, Erik Petersson, Niels Jepsen, Mikaela Bergenius, Karl Lundström, Örjan Östman, Mikael Ovegård, Annika Strömberg, Alf Sevastik, Arne Fjälling. Thanks to all the personnel at Älvkarleby and Öregrund and thanks to the fishermen and ornithologists who have helped in the process.

Studies were financed by funds from the European Structural Fund for Fisheries, Swedish Board of Fisheries and through Program Sälar och Fiske with funding from the Swedish Environmental Protection Agency and the Swedish Agency for Marine and Water Management.

Version 1, June 2013.