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Swedish University of Agricultural Sciences

Department of Wildlife, Fish, and Environmental Studies

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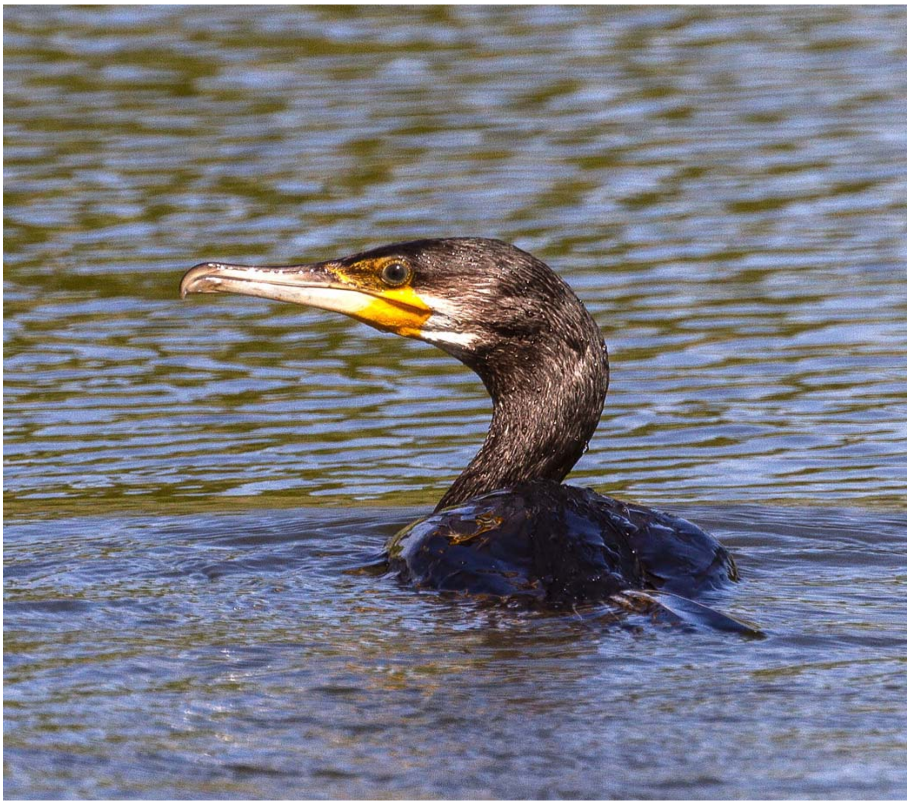

Master´s thesis • 30 credits

Jägmästarprogrammet
Examensarbete/Master's thesis, 2018:18
Umeå 2018

Impact of Great cormorant (Phalacrocorax carbo sinensis) on post-smolt survival of hatchery reared salmon (Salmo salar) and sea trout (Salmo trutta)

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Credits:	30 credits
Level:	Second cycle, A2E
Course title:	Master degree thesis in Forest Sciences at the department of Wildlife, Fish, and Environmental Studies
Course code:	EX0840
Programme/education:	Jägmästarprogrammet
Course coordinating department:	Department of Wildlife, Fish, and Environmental Studies

Place of publication:	Umeå
Year of publication:	2018
Cover picture:	Tobias Svensson
Title of series:	Examensarbete/Master's thesis
Part number:	2018:18
Online publication:	https://stud.epsilon.slu.se

Keywords:	Great cormorant, salmon, sea trout, grey seal, post-smolt survival

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Abstract

To compensate for the losses due to altered stream habitat large amounts of hatchery-reared Atlantic salmon (*Salmo salar*) and sea trout (*Salmo trutta*) are released into the Baltic Sea each year. During the last decades there have been an overall declining trend in the post-smolt survival of both hatchery reared and wild salmon in the Baltic Sea. During this period there has been a rapid increase of the piscivorous great cormorant (*Phalacrocorax carbo sinensis*) but also in the grey seal (*Halichoerus grypus*) population of the Baltic Sea. These two predators consume large amounts of fish in the Baltic Sea. This study investigated if the predation of great cormorants contributes significantly to the mortality of hatchery reared salmon and sea trout, together with the effects of the increasing grey seal population on hatchery reared salmon. Besides gut content analyses of cormorants, an index of return rate and post-smolt survival were estimated from data on salmon and sea trout smolt releases between 1989-2010 in river Dalälven, and the returning spawners from these releases.

The dietary study was performed on cormorants nesting in the Sundsvall bay, where the stomachs of 183 cormorants were examined. The cormorants were culled as a protective measure both in direct relation to smolt release right outside Bergeforsen hatchery, and later in the season at Alnö, further out in the Sundsvall bay. The dietary study showed a high number of sticklebacks (*Gasterosteidae*) in cormorants from both areas. For cormorants culled near Bergeforsen hatchery salmonoids (*Salmo spp.*) had the highest relative biomass (68.18 %) and the highest frequency of occurrence (48.1 %). For cormorants culled at Alnö the predation on salmonoids were lower in comparison with other fish species, sticklebacks had the highest frequency of occurrence (67.2 %) and fourhorn sculpin (*Triglopsis quadricornis*) the highest relative biomass consumed (27.4 %).

The estimated post-smolt survival of the Dalälven smolt did not differ from the overall estimates of hatchery reared smolt estimated by ICES. This suggests that the decline in post-smolt survival in river Dalälven is due to large-scale processes in the Baltic Sea rather than great cormorant predation. The analyses indicated a high level of co-variation between the two predators, great cormorant and grey seal in the study area, which can make it hard to separate the effects of these two predators. The dietary study indicated that the predation on salmon and sea trout smolts can be high especially during the smolt release, but it can be hard to draw any certain conclusion from the data in this dietary study.

Keywords: Great cormorant, salmon, sea trout, grey seal, post-smolt survival

1 Introduction

Atlantic salmon (Salmo salar) and sea trout (Salmo trutta) are faced with many challenges throughout their life span. Such as naturally occurring predators and human induced changes to their habitats (ICES, 2017). One example of human induced changes is the building of hydroelectric power dams. This change of habitat mainly affects the early life stages of anadromous fish species. To compensate for the loss of habitat for young salmonoids an extensive hatchery programme have been developed in Sweden (Montén, 1988). The first salmon smolt release was performed around 1950, followed by a rapid increase in smolt releases between the 1950s and 1960s (Ackefors et al., 1991, Eriksson and Eriksson, 1993). Today all Swedish hydropower companies are obligated to make compensatory releases of salmon and sea trout, to make up for the production losses caused by altered stream habitat (Svenskt vattenbruk 2016). By fin clipping hatchery reared salmon and sea trout they can easily be distinguished from wild stocks. According to the Swedish regulation of fisheries, aquaculture and the fishing industry (SFS 1994:1716) fin clipping is mandatory for all salmon and sea trout smolts released to the sea.

Wild salmon and sea trout utilize different habitats for different life stages. Spawning of wild salmon and sea trout is carried out in freshwater streams during the autumn or winter (Karlsson and Karlstrom, 1994, Jonsson and Jonsson, 2011, Kullander, 2012). After hatching in the following spring, the juvenile salmon and sea trout spend their first years in freshwater (Kullander, 2012, HELCOM, 2011). After a few years of growth in the river habitat the salmon and sea trout are beginning to adapt to a life at sea, so called smoltification (Kullander, 2012, Nielsen, 2010). The smolt migration from their natal river to the sea usually occur in spring (Jonsson and Jonsson, 2011, Karlsson and Karlstrom, 1994). The migration patterns differ between salmon and sea trout. Sea trout usually stay in the coastal areas close to their natal rivers (Kullander, 2012, Thorstad et al., 2016, Kallio-Nyberg et al., 2002, Degerman et al., 2012) while salmon migrate further out to pelagic areas

(Kullander, 2012). The Baltic Proper has been identified as the main feeding area used by Baltic salmon during their sea phase (Romakkaniemi et al., 2003, Eriksson and Eriksson, 1993, Salminen et al., 2001). In the beginning of the sea phase both salmon and sea trout mainly feed on terrestrial insects. With increasing size, they later shift to a piscivorous diet (Kullander, 2012). Due to their homing instinct salmon and sea trout return to their natal rivers to spawn after approximately 1- 4 years at sea (ICES, 2017, HELCOM, 2011).

The Baltic salmon and sea trout are important species in the aquatic food web, functioning as important top predators during their adult sea phase. They can also be considered key stone species during their juvenile stream residence when they utilize specific niches, such as the fast-flowing low-productive northern rivers and tributaries (ICES, 2017). Besides their ecological importance salmon and sea trout are important species for both commercial and recreational fisheries (HELCOM, 2011). Salmon fishing is carried out in most habitats such as rivers, along the coast and in the offshore areas of the Baltic Sea. While sea trout are caught mainly in river- and coastal areas (HELCOM, 2011). Salmon have a history of economic importance (Johansson, 1981) and are considered to be a prized food-fish (Nielsen, 2010). During the last decades there have been an overall declining trend in the post-smolt survival of both hatchery reared and wild salmon in the Baltic Sea. For sea trout a lot of the populations are considered weak (ICES, 2017).

Several factors are discussed in relation to salmon and sea trout survival. Factors like predation and prey availability during the sea phase is often discussed in relation to post-smolt survival (Friedland et al., 2017, Mäntyniemi et al., 2012, Kallio-Nyberg et al., 2006). Smolt size may also affect the survival (Kallio-Nyberg et al., 2011, Dieperink et al., 2001). It has been suggested that smaller smolts are more susceptible to predation than larger ones (Dieperink et al., 2001).

Salmon and sea trout are predated by both mammalian predators such as for example grey seal (Halichoerus grypus) (Mäntyniemi et al., 2012, Lundström et al., 2007, Suuronen and Lehtonen, 2012), avian predators such as sea birds (Dieperink et al., 2002, Degerman et al., 2012), but also by predatory fish species such as cod (Gadus morhua) and pike (Esox lucius) (Jepsen et al., 2006, Jepsen et al., 1998). According to previous studies it seems that hatchery reared smolts are more susceptible to predation than wild smolts (Dieperink et al., 2001, Saloniemi et al., 2004).

During the last decades there has been a rapid increase in both numbers and distribution of the piscivorous great cormorant in Europe. This rapid expansion has led to conflicts with the fisheries (Gagliardi et al., 2015, Carss, 2003). There are two subspecies of the great cormorant extant in Europe, the Phalacrocorax carbo carbo and the Phalacrocorax carbo sinensis (Gagliardi et al., 2015, Marion and Le Gentil, 2006). Both subspecies occur in Sweden but in general only the P. c. sinensis breed in the Baltic area (Grant et al., 1999, Ericson and Carrasquilla, 1997). Throughout this thesis the term cormorant will refer to the subspecies P. c. sinensis, when nothing else stated. In Sweden the number of nesting cormorants were kept low during the 19th century, even extinct around early 1900s. Human persecution is believed to have been one of the main factors explaining the low numbers (Engström, 2001). In the late 1940s the cormorant started to re-establish as a breeding bird in the south of Sweden (Engström, 2001, Lindell et al., 1995, Ottosson and Sveriges ornitologiska, 2012). However, it was not until the 1980s the population really started to expand. The Swedish cormorant population grew with approximately 24 % per year during the period 1980-1994, making the estimated population go from 940 breeding pairs in 1981 to 15 400 breeding pairs in 1995 (Bregnballe, 1996). According to the latest national inventory from 2012 the cormorant population in Sweden was estimated to approximately 40 600 breeding pairs (Herrmann et al., 2014).

Cormorants are generalist predators, which means that their diet generally reflects the species available in their foraging area (Boström et al., 2012a, Keller, 1995, Gagliardi et al., 2015). They are skilled swimmers that forage mainly in the shallow parts of freshwater systems and coastal areas, often less than 10 meters deep. After diving down, they can search for and pursue their prey under water. Even if they usually forage in shallow waters they can dive down to at least 35 meters (Gremillet et al., 2006). In a review by Ridgway (2010) the daily estimated food intake for cormorants of the subspecies sinensis ranged between approximately 238 to 539 grams of fish per day. The energy demand appears to be higher during the breeding season than in the non-breeding season (Ridgway, 2010, Gremillet et al., 1995). The energy demand also fluctuates within the different phases of the breeding cycle (Gremillet et al., 1995), resulting in different effects on fish stocks depending on phase, in combination with different vulnerability for fish in different life phases. In earlier studies feeding distance have been estimated to within 15 km for nesting sites in coastal environment (Phalacorcorax carbo L). While cormorants nesting in a lake feeding in both coastal waters and lake environment showed a mean foraging distance of 17.5 km from the nesting site (Gremillet et al., 2004, Gremillet et al., 1995).

Earlier studies examining Cormorant (P. carbo sinensis and P. carbo L.) predation on salmon and sea trout smolts suggests that the majority of the predation occur during the early phase of the seawards migration, often within the first few days after reaching the estuaries (Dieperink et al., 2001, Dieperink et al., 2002). On the two islands Gistaholmarna close to Bergeforsen hatchery a large cormorant colony are nesting. During smolt release large numbers of cormorants have been seen foraging right outside Bergeforsen hatchery. Similar observations have been done earlier around river Dalälven in association with smolt releases from Älvkarleby hatchery. Whether salmon or sea trout are most vulnerable to cormorant predation differs between earlier studies (Boström et al., 2009, Dieperink et al., 2002). Boström et al. (2009) suggests that sea trout are more vulnerable to cormorant predation as when they reach the river delta they spread along the coast lines, where they are available for cormorants during a longer time span, than salmon, that swim out towards the deep sea fast after reaching the river delta. In contrast, another study suggests the direct predation in estuaries seems to be higher in salmon than sea trout (Dieperink et al., 2002).

Next to humans, cormorants and grey seal are the two fish predators that have the highest outtake of fish from the Baltic Sea (Hansson et al., 2017). Since there has been a rapid increase in both cormorants and grey seal in the Baltic Sea during the last decades (Havs och Vattenmyndigheten, 2012, SOF, 2013) it can be difficult to separate the effects of these two predators.

In this thesis I investigate the predation of great cormorants on hatchery reared salmon and sea trout, together with the effects of the increasing grey seal population on hatchery reared salmon.

The major aim was to examine if the presence of great cormorants significantly affects the mortality of compensatory released salmon and sea trout. And in relation to that examine a subsample of diets of the cormorants foraging in the Sundsvall bay area, and near the hatchery in Bergeforsen. In addition, I analysed if the growing grey seal population in the Baltic Sea might affect the survival of hatchery reared salmon from Dalälven, and to assess the correlation between cormorant and grey seal predation on hatchery reared salmon from Dalälven in comparison with all reared smolt in the Baltic.

2 Materials and methods

2.1 Study areas – smolt compensations and cormorant development

Cormorant smolt predation was examined at two different locations. A dietary study was performed on cormorants nesting in the Sundsvall bay, around Bergeforsen and Alnö, located on the Swedish east coast, near river Indalsälven (62°30 N, 17°27 E). At the other location, further south along the coast for Älvkarleby, near river Dalälven (60°38 N, 17°26 E) the effects cormorants may have on the survival of hatchery reared salmon and sea trout were examined.

2.1.1 Bergeforsen and Alnö

Bergeforsen hydropower plant is located 9 km upstream and is the lowest located hydropower station in river Indalsälven. Swedish hydropower company Vattenfall ordered a report in 2009 examining fish ways and hydropower. This report stated the potential for restoring upstream natural reproduction of salmon and sea trout above Bergeforsen hydropower station as very small (Larsson and Sparrevik, 2009). To compensate for the losses due to altered stream habitat approximately 330 000 salmon and 100 000 sea trout are released from Bergeforsen hatchery each year.

In the vicinity of the release site there has been a colony of Cormorant on the two islands Gistaholmarna since around 2008 (Norrgrann and Olofsson, 2009). The population has grown rapidly during the last years and were estimated to 1852 nesting adults during the latest count in 2017 (Artportalen 2017).

In Västernorrland County the first documented Cormorant breeding took place in 1993 (Engström, 2001). The County administrative board in Västernorrland has initiated five cormorant counts during the years 1999 to 2017 (table 1.). During this period the number of nesting colonies in Västernorrland county has varied between 6-8 colonies (Nilsson, 2017. pers. Comm.). Despite a lower national count in 2012 than in 2009 (SOF, 2013) the population is still growing in the northern part of Sweden (Nilsson, 2017 pers. comm.).

Table 1. *Number of cormorant pairs nesting in Västernorrland County, 1999-2017 (Nilsson, 2017 pers. comm).*

Year	Number of breeding pairs in Västernorrland County
1999	702
2002	1147
2008	2077
2012	1925
2017	3220

2.1.2 Älvkarleby

Älvkarleby hydropower plant is located 9 km upstream and is the lowest located hydropower station in river Dalälven. In contrast to river Indalsälven the Vattenfall report from 2009 examining fish ways and hydropower, stated that there is potential to restore some natural salmon and sea trout reproduction in river Dalälven, since there in contrast to Indavsälven still are some remaining fast-flowing river stretches left in Dalälven river (Larsson and Sparrevik, 2009). Well known for their prime salmon stock, Älvkarleby has been a historically important salmon fishing ground documented all the way back to the Middle Ages (Montén, 1988). Each year approximately 200 000 salmon and 70 000 sea trout are released into river Dalälven.

In the vicinity of the release site there are a number of cormorant colonies nesting both in the Gävle bay and in the Lövsta bay. The first successful coastal nesting in the Gävle bay, located in Gävleborg County took place in 2005 (Ageheim and Lindqvist, 2015). And in the Lövsta bay located in Uppsala County the first cormorant colony were recorded in 1992 (D. Brelin, 2018, pers. comm). Both diet and smolt predation has been studied earlier for cormorants nesting in the Lövsta bay (Boström et al., 2012a, Boström et al., 2009).

Even if the cormorants established around the same time in the Uppsala County as in Västernorrland County (Engström, 2001), the population development has differed between the two counties (Figure 1), with what seems to be a faster initial establishment in Uppsala county.

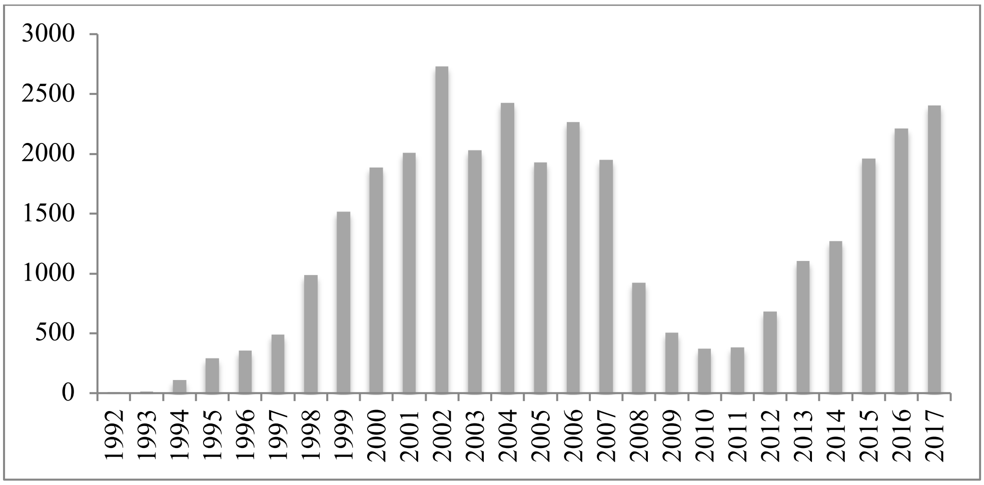

Figure 1. Number of cormorant nests in Uppsala County, 1992-2017 (Brelin, 2018, pers. comm).

2.2 Cormorant diet in the Sundsvall bay

Fish prey can be identified by examining the otoliths and skeletal remains in regurgitated pellets or stomachs of shot sea birds (Barrett et al., 2007). Since fish otoliths are somewhat more resistant to degradation compared to other tissues and usually have a very species-specific shape they are often used to identify fish species (Campana, 2004, Härkönen, 1986). Fishes have three different otoliths on each side of the head called Lapillus, Astersicus and the Sagitta. The otoliths help fishes to orientate under water but also work as sound receptors (Härkönen, 1986). The largest of the otoliths, the Sagitta, is the one used when identifying fish species (Härkönen, 1986, Hecht and Appelbaum, 1982). When further mentioned in the text the term otolith refers to the Sagittal otoliths.

To determine the dietary composition the stomach content of 183 cormorants were examined. The great cormorant is protected according to the EU Birds Directive (2009/147/EC), and may only be hunted as a protective measure if certain criteria are fulfilled. The criteria can be found in article 9 of the Birds Directive (2009/147/EC). This dietary study was performed on cormorants culled with permission of the County administrative board in Västernorrland (permit: 218-2039-17 and 218-3432-17). The culling took place at two different locations in the Sundsvall bay. During a two-week period, coinciding with the smolt release, 34 of the cormorants were shot right outside Bergeforsen hydropower plant. The other 149 Cormorants were shot at Alnö further out in the Sundsvall bay (figure 2). All salmon and sea trout were released as one-year old smolts during the night of June 15th (Sahlin, B. 2018).

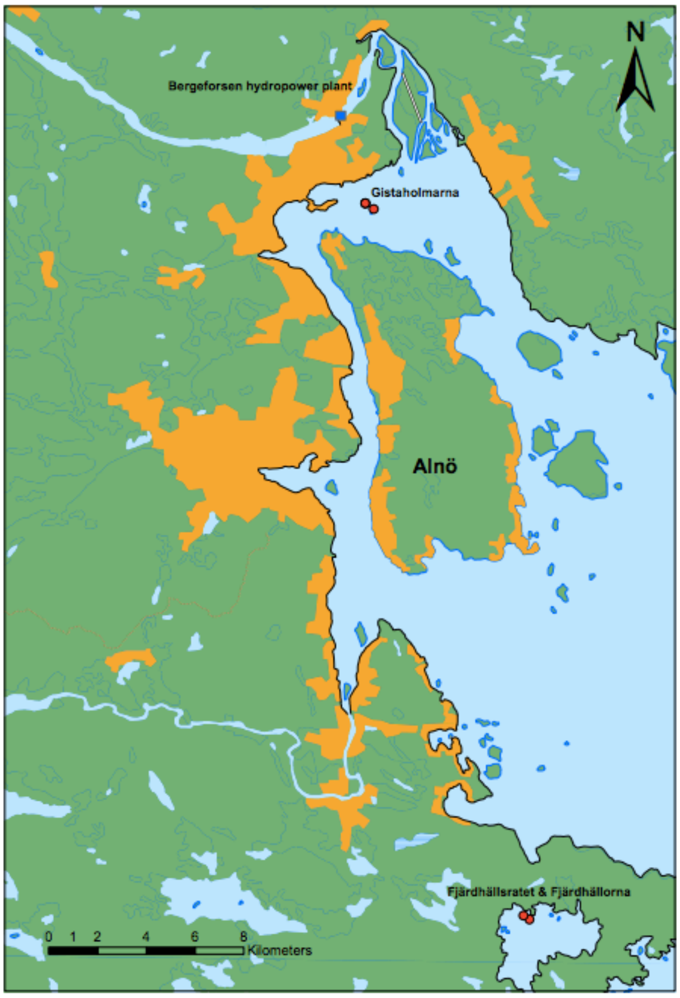

Figure 2. Map over Sundsvall bay Cormorant colonies are marked with red dots and Bergeforsen hydropower plant with a blue square. Urban areas are marked with orange. GSD- General map, vector ©Lantmäteriet.

All cormorants in this thesis were shot during the summer months (June-September) and the hunters recorded date and time of the day when the birds been shot. The stomachs and oesophagus were removed and kept frozen until they were about to be analysed. Weight, sex and age (juvenile or adult) were recorded for all birds.

The stomachs and oesophagus were opened and rinsed with water in a sieve. Fish that had remained relatively intact in the stomachs were identified to species and fish length was recorded if possible. The hard parts remaining after the rinse were collected and dried in a heating cabinet. When dried, the stomach content from each bird were examined with a stereomicroscope. Each stomach counts as one sample (n= 183). To be able to count how many fishes each sample contained all otoliths were sorted to left or right, depending on which side of the fish they came from. By sorting them into left or right otoliths and only counting one of them from each fish it was made sure that the number of fish prey were not overestimated. After sorting them, all otoliths were classified by species if possible. Some of the otoliths could not be classified further than by family due to degradation. In some cases, the otoliths could not be classified at all and were then recorded as unknown. Length and width were measured for all otoliths that were classified to species or family. Empty stomachs (n =31) were excluded from the analysis.

All otoliths were classified on a scale ranging from 1-3, depending on the level of degradation. The classification was done in accordance with the criteria stated in Tollit et al. (1997); where the otoliths in wear class 1 show almost no sign of degradation with well defined structures such as distinct sulcus and clear lobes. Wear class 2 are more worn down with less distinct structures such as for example less clear lobes and sulcus. Wear class 3 has a high level of wear with no distinguishable lobes or sulcus.

Since the regressions used to calculate the weight and length of fishes from otoliths gives a more accurate size estimate for relatively uneroded otoliths i.e. wear class 1 (Suter and Morel, 1996, Tollit et al., 1997), size-correction factors were used to get an estimate of what size the otoliths would be with minimal erosion. Without correction, heavily eroded otoliths can lead to underestimations of fish size (Tollit et al., 1997). The same as in Boström et al. (2012a) otoliths of wear class 2 and wear class 1 were added together, due to a small number of uneroded otoliths. The size-correction factors for otolith width were calculated for Baltic herring, sandeel and fourhorn sculpin. Correction factors for otolith length were calculated only for sandeel and fourhorn sculpin since herring otoliths easily break on the length. The average of these correction factors was later used to correct for wear in all other species. The size-correction factors were calculated by dividing the mean length or widths of otoliths in wear class 3 with the mean for otoliths in wear class 1+2. After correcting the otoliths in wear class 3 all otoliths were assumed to be of original size. No corrections were calculated for otoliths for wear class 1+2.

After correcting the size of all otoliths in wear class 3 the widths or lengths of all otoliths were applied to species-specific regression slopes from Härkönen (1986), Lundström (unpublished) and Leopold et al. (2001) to calculate mass and length of each fish. In most species the otolith width was used except for salmon and fourhorned sculpin for which otolith length was used. All fishes intact enough for length to be measured directly, the mass was calculated using linear regression slopes from Leopold et al. (2001) and the Institute of Coastal Research, SLU using fish length instead of otolith size. A small amount of fish was identified by other skeletal structures such as parasphenoids, jaw bones and vertebras identified with the help of identification keys (Von. Busekvist, 2004, Watt and Boyle, 1997). For fish only identified by family the mean lengths and weights for all species within that family were used. Fish identified to the Coregonoidae family (n= 3) regressions for whitefish were applied.

Instead of otoliths the number of pelvic spines was used to estimate the amount of sticklebacks in each stomach. To avoid overestimations each spine was sorted as left, right or “other”. The side with most spines were used to estimate the number of sticklebacks in each sample. To estimate the mass of sticklebacks the mean weight was calculated from all the lengths of intact sticklebacks. For the otoliths that could only be classified by family, the mean length and mass of all fishes classified down to species within that family were used to estimate length and weight for that specific family.

Samples from Alnö and Bergeforsen were analysed separately to get an overview of the cormorant feeding regimes in the two areas. Diet indices FOi, Ni and Bi were calculated the same way as in Lundström et al. (2007). Where frequency of occurrence (FOi) was calculated for each species consumed, by dividing the number of cormorants containing the species (si) with the total amount of cormorants containing any prey species (st).

$FOi = (si/st) \cdot 100.$

The relative numerical contribution (Ni) for each prey species were estimated by dividing total number of individuals of a species (ni) with the total amount of individuals of all prey species (nt).

$Ni = (ni/nt) \cdot 100$

Contribution of relative biomass (Bi) was calculated for each species by dividing total weight from a species (bi) with the total biomass of all species consumed (bt). Since no measurements were made for the species European eel (Anguilla anguilla) and Eurasian minnow (Phoxinus phoxinus) they were excluded from the relative biomass calculations. Unidentified species recorded as unknown were also excluded.

$Bi = (bi/bt) \cdot 100$

To achieve a measure of confidence to the results the Bi % and Ni % data was bootstrapped with 1000 iterations using JMP Pro statistical software (12.2.0, 2015 SAS institute Inc.).

2.2.1 Estimated salmon and sea trout predation in the Sundsvall bay

As mentioned before the cormorant energy demand varies over time during the breeding season. In an energetic study by Gremillet et al. (1995) daily energy demand and the length of each phase were stated in the following way. During the

30 days of egg incubation each adult including its chicks consume 238 grams of fish per day. During the 10 days of rearing small chicks the daily food intake was estimated to 316 grams for each adult including its chicks. During the 40 days when raising larger downy chicks, the estimated food intake were 588 grams per day for each adult including its chicks.

In a field study near river Dalälven by Boström et al. (2012a) the timing of the different stages in the breeding season were defined to occur during the following periods. Egg incubation during the period 24 March – 4 May. Raising small chicks during the period 18- 23 May, and larger downy chicks during 2 June – 30 July. And during the period 6 August – 18 October, the chicks start to leave the nests but still remain close to the nesting site.

In this thesis each nest was assumed to contain two adults raising two chicks and one adult pre-breeder per nest. Cormorants were also assumed to stay in the area for approximately 180 days, based on the previous study in Lövsta bay by Boström et al. (2012a). During the post-breeding phase, the daily food intake was estimated to approximately 540 grams per day for both adults and juveniles (Ridgway, 2010). The post-breeding phase were estimated to 100 days, as in Östman et al. (2013). Pre-breeders were also assumed to consume 540 grams of fish per day during the whole period.

The predation per adult bird and its chicks was calculated by multiplying the number of days of each period with the estimated daily food intake. After calculating food intake for each breeding period, the total predation for the whole period were estimated by adding the periods together. Since there were estimated to be one pre-breeder per nest the food intake of the pre-breeding cormorants was divided in two and multiplied with the number of days (180) and number of nesting adults. To estimate the "outtake per bird" the predation per adult and its chicks were summed together with the food intake of half a pre-breeder.

Total predation for all birds during the whole period (180 days) were attained by multiplying the total number of adult cormorants within 20 km (figure 2), with the "outtake per bird". The maximum salmon and Salmo spp. predation was estimated by multiplying the relative biomass (Bi %) from cormorants culled at Alnö for each taxon with the total predated biomass, during a period of 14 days. The minimum outtake of salmon and Salmo spp. were calculated by multiplying the (Bi %) for the two prey species, with the total outtake during 1 day. These time periods were assumed since salmon were the most abundant and they usually migrate towards the sea quickly after release (Thorstad et al., 2004). Birds shot around Alnö were assumed to better represent the general diet of the birds feeding in the area than the birds shot in association to the smolt release.

To estimate the maximum and minimum number of smolts predated, the total biomass of all smolts predated within each time period were divided with the mean smolt weight. The mean smolt weight were 34.4 grams for salmon and 44.6 grams for sea trout (Sahlin, 2018, pers. comm). The mean smolt weight for salmonids not identified to species (Salmo spp.) were estimated to 39.5 grams.

2.3 Index of return rate for sea trout in river Dalälven

To estimate the return rate index of hatchery reared sea trout in river Dalälven a dataset of smolt releases and the returning adults from these for the year's 1989-2012 were obtained from the Fisheries Research Station in Älvkarleby. The data collection on upstream migrating salmon and sea trout have been carried out in a similar way during the study period 1990-2012. Between 1 May- 30 September up streams migrating salmon and sea trout were caught in a trap located approximately 14 km up streams from the river mouth. The trap was open 24 h per day and emptied when needed. All fishes caught were registered by species, sex, length and origin as hatchery reared or wild.

Since the amount of grilse is low among female salmon (McKinnell and Lundqvist, 1998) the return rates were calculated on hatchery reared females only. With the assumption that the sex ratio of smolts released were 50:50 the number of females was obtained by dividing the amount released each year by two. The return rate index for sea trout were obtained by dividing the number of returning hatchery reared females two years after the release with the estimated number of females released two years prior.

Return rate index = n_{2sw}/n_{t0}

Where n_{t0} is the number of sea trout females released each year and n_{2SW} is the number of sea trout females returning two years after the release.

Except for smolts that were released every year during the study period, parr and fry were also released in some years. The release of parr and fry were not taken into account in these calculations since they were not expected to have any major effects on the result.

The return rate index for sea trout were plotted against the number of cormorant nests within 20 km from river Dalälven estuary to look for correlations (figure 3). A regression was applied to get an estimated R^2 value.

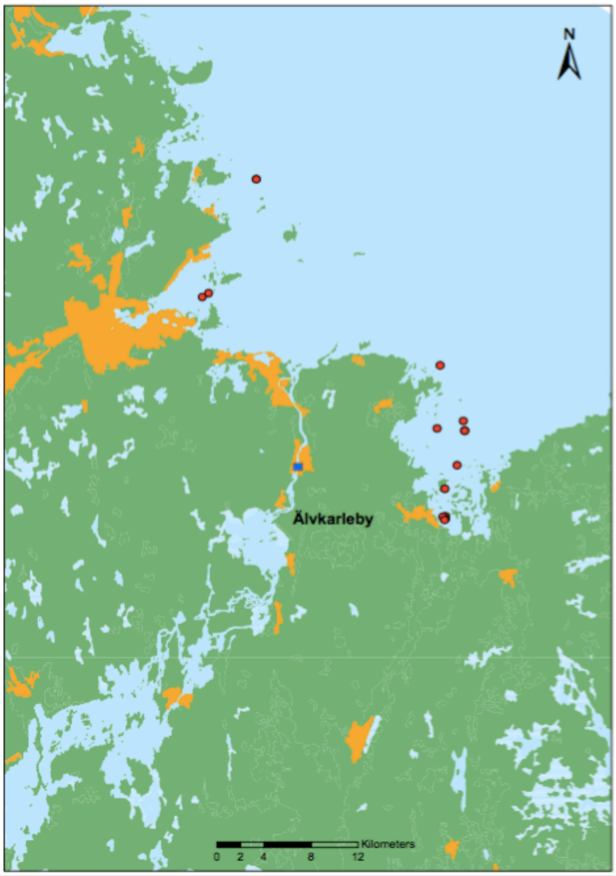

Figure 3. Map over cormorant colonies located within 20 km from Älvkarleby estuary, during the period 1992-2010. Cormorant nesting colonies are marked with red (Aspenberg pers. comm. 2018, Brelin 2018 pers. comm. and Ageheim and Lindqvist, 2015). Älvkarleby hydropower plant is marked with a blue square and urban areas are marked with orange. GSD-General map, vector ©Lantmäteriet

2.4 Post-smolt survival of salmon released in river Dalälven

The post-smolt survival was calculated for female salmon smolts released between 1989- 2010. The same dataset obtained from the Fisheries Research Station in Älvkarleby were used to estimate the number of salmon smolts released and adult females returning each year. No finclipped salmon females were recorded prior to 1996, so the quota of hatchery reared salmon females before 1996 were assumed to be the same as the average for the years after. Corrections were made for the fluctuation in fishing pressure during the study period, using data from (ICES 2010, ICES 2011). This is important since the cumulative fishing pressure in the beginning of the study period were estimated to be almost twice as high as in the end of the study period.

The assumptions were made that all salmon females reached sexual maturity and returned to their natal river after two (2SW) or three winters at sea (3SW). Since the proportion of females reaching sexual maturity after two sea winters (p_{2SW}) and three sea winters (p_{3SW}) were unknown the quotas were calculated. Due to the low number of returning salmon and the high estimated fishing pressure during the previous years these calculations were done for the years 2005-2009. Since the proportion of females reaching sexual maturity after two and three years respectively were assumed to be relatively constant during the study period the mean value for the period 2005-2009 were used for all years.

Since the number of females reaching sexual maturity after two and three sea winters is not the same amount that is expected to return to the river due to fishing pressure and natural mortality. The proportion of salmon females returning after two sea winters were calculated for each year. And the proportion of females returning after three sea winters were attained by subtracting the proportion of salmon females returning after two sea winters from 1.

The following formula was used to calculate the proportion of females returning after two winters at sea.

$$(1). \qquad P_{2SW} = \frac{(\mathrm{HR}_2\ -1)\cdot p_{2SW}}{(\mathrm{HR}_3 + M - \mathrm{HR}_3 \cdot M + p2sw\ \cdot (\mathrm{HR}_2 - \mathrm{HR}_3 - M + \mathrm{HR}_3 \cdot M) - 1}$$

Where:
P_{2SW} = Proportion 2SW females of returning adult females
HR_2 = Cumulative harvest rate after two winters at sea
M = Natural mortality
p_{2SW} = probability of reaching sexual maturity after two sea winters
HR_3 = Cumulative harvest rate after three winters at sea

The probability of sexual maturity after two sea winters was solved from equation 1, when P_{2SW}=2/3 as an approximation of the proportion of 2SW females of returning females in the Norrfors fish ladder during the period 2005-2009.

$$(2). \qquad p_{2SW} = 1 + \frac{1 - \mathrm{HR}_2}{-3 + \mathrm{HR}_2 - 2 \cdot \mathrm{HR}_3(-1 + \mathrm{M}) + 2\ \cdot \mathrm{M}}$$

Where HR_2 is the cumulative harvest rate after two winters at sea, HR_3 is the cumulative harvest rate after three winters at sea and M is the natural mortality.

Due to the fact that all females were assumed to reach sexual maturity after two or three winters at sea the probability of females reaching sexual maturity after three sea winters were set to 1, assuming that all females still remaining in the Baltic sea after three years would reach sexual maturity after three years. In the WGBAST report from 2003 the quota of females reaching sexual maturity after three years was estimated to 0.83 (ICES 2003).

After calculating the quotas for females returning after two and three sea winter the post-smolt survival were calculated by using the following formulas where the denominator is the number of released smolt times their survival, maturation probability, and capture probability upon return to the river:

$$S_{postsmolt2SW} = \frac{N_{2SW,returing}}{N_{0t-2} \cdot (1 - HR_2\,) \cdot (1 - M) \cdot p_{2SW} \cdot q}$$

$$S_{postsmolt3SW} = \frac{N_{3SW,returing}}{N_{0t-3} \cdot (1 - HR_3\,) \cdot (1 - M)^2 \cdot p_{3SW} \cdot q}$$

Where:
$N_{2SW, returning}$ = Number of females returning after two sea winters
$N_{3SW, returning}$ = Number of females returning after three sea winters
N_{0t-2} = Number of females released, two years earlier
N_{0t-3} = Number of females released, three years earlier
HR_2 = Cumulative harvest rate after two winters at sea
HR_3 = Cumulative harvest rate after three winters at sea
M = Natural mortality
q = recapture rate in fish trap
p_{2SW} = the probability of salmon females reaching sexual maturity after two sea winters
p_{3SW} = the probability of salmon females reaching sexual maturity after three sea winters

The cumulative harvest rates HR_2 and HR_3 were assumed to be the same as for wild salmon in assessment unit 3 (AU3) of the Baltic Sea, the areas are defined by the International Council for the Exploration of the Sea (ICES).

The cumulative harvest rate HR_2 for salmon returning after two sea winters were estimated from the WGBAST report of 2011 (ICES 2011). Containing the cumulative harvest rate for salmon released between 1989-2008. For the years not included in this graph the mean value of the cumulative harvest rate for the last three years was used to estimate harvest rate, assuming that the harvest rate was relatively constant during the last years.

The cumulative harvest rate HR_3 for salmon returning after three sea winters were obtained from the WGBAST report from 2010 (ICES 2010). For the years not included in this report (2008-2010) the mean cumulative harvest rate for the last three years was used to estimate harvest rate, assuming that the harvest rate was relatively constant during the last years.

The annual natural mortality, M was estimated to 0.083 from the WGBAST report from 2007 (ICES 2007). Natural mortality was assumed to be constant during the whole study period.

The recapture rate, q for the years 2004- 2011 were received from a previous capture-recapture study in river Dalälven (Dannewitz and Palm 2018, pers.comm). The mean value was used for the years that were not included in this study. The total post-smolt survival each year was attained by adding together the weighted means for salmon returning after two and three sea winters. The weighted means were calculated for each year by multiplying the post-smolt survival for females after two sea winters with the proportion of salmon females returning after two sea winters and the post-smolt survival after three sea winters multiplied with the proportion of salmon returning after three sea winters and then adding them together. For the last year 2010, the post-smolt survival was calculated for only 2 SW females, since the proportion of 2SW were higher than 3SW females this was considered to give a relatively good view of the post-smolt survival for the last year. To include the last year were considered to give a better overall view of the period than excluding it.

After calculating the post-smolt survival the result was plotted in a graph containing the cormorant population within 20 km from the Dalälven estuary to visually analyse correlations between the two parameters. A linear-regression curve with post-smolt survival as response variable was used to analyse the correlation between cormorant population within 20 km and post-smolt survival for river Dalälven. Due to the lack of harvest and recapture data no post-smolt survival could be calculated for sea trout.

2.5 Grey seal predation

Salmon and sea trout seems to be important prey species for grey seals in some parts of the Baltic Sea and accumulations of grey seals in estuaries can cause problems when predating on aggregations of salmonoids (Suuronen and Lehtonen, 2012). The grey seal population in the Baltic Sea has shown a steady increase during the study period, with a mean rate of increase of 15.5 % each year from 1990 (Havs och Vattenmyndigheten, 2012). There has been no coordination of grey seal inventories between countries surrounding the Baltic Sea before year 2000 (Havs och Vattenmyndigheten 2012). This makes it difficult to attain data for the whole Baltic Sea before year 2000. Due to the lack of data the grey seal population index before year 2000 data were attained in two ways. The years 1989- 1996 were attained both from (Hårding and Härkönen 1999 see Svärd et al., 2015) based on hunting bag statistics. It was also calculated backwards from the dataset from 2000 and forward, received from Naturvårdsverket et al., (2016) calculated with the assumption that 70 % of the population were counted in accordance with (Hilby et al., 2007). By assuming a population increase of 15.5 % from the year 1989 the grey seal population were attained by dividing the year before with 1.155 for each year before 2000.

The estimated grey seal population in the Baltic Sea were also plotted against the post-smolt survival to look for correlations between the two.

In ICES WGBAST report from 2010 the following formula were presented to calculate grey seal predation on wild salmon smolts in the Baltic. Where the calculated Et is the biomass of predated smolts and Nt the number of grey seals.

$$\mathrm{E_t = N_t \cdot pt \cdot \frac{6kg}{day} \cdot 60days}$$

In ICES (2010) the following formula were presented to calculate the proportion of wild salmon smolts predated by grey seal. With the assumptions that each grey seal eats 6 kg of fish per day and that salmon smolts are available for predation during 60 days, in June and July. The probability that a smolt will be eaten (pt) is based on the assumption that the seals only eat salmon and herring, that both salmon and herring have the same availability and that none of these prey species are preferred over the other.

$$\mathrm{pt} = \frac{\mathrm{B_t}}{\mathrm{H_{t,BB}t + H_{t,BS} + B_t + R_t}}$$

Where Bt = smolt biomass, Ht, BB = herring spawning biomass in Bothnian Bay, Ht,BS = herring spawning biomass in Bothnian Sea and Rt = biomass of hatchery reared smolts.

A rough estimate of how grey seal predation may affect hatchery reared smolts released into river Dalälven were calculated by modifying the formula to better fit the hatchery reared population. The risk of predation was calculated by dividing the total biomass of released smolts for year 2005, with the estimated spawning biomass of herring, released smolt biomass and sprat in the Baltic areas near river Dalälven in 2005. The spawning biomass of herring and sprat were received from ICES (2016a) and ICES (2016b). The biomass of wild smolts and other released smolts were not included since the amount was estimated to be negligible to the biomass of sprat and herring. The two areas were identified as Bothnian Sea (ICES subdivision 30) and the Baltic south of Bothnian sea (ICES subdivision 23-29 + 32) for herring. For sprat the spawning biomass were presented for subdivision 22-

32, although the biomass for subdivision 30-31 were assumed to be low (ICES 2006, Jacobson et al., 2018). Due to the assumed low biomass of sprat in the Bothnian Sea this area was only calculated on biomass herring and biomass of smolts released. The grey seal count in 2005 for the two areas were collected from HELCOM (2018), where the grey seal count of Central Sweden, containing western Åland sea, Northern Baltic proper and western Gotland basin were 4462 individuals. For the Bothnian Sea the grey seals were counted to 606 individuals (HELCOM 2018). The number of counted grey seals were divided with 0.7, to get an estimate of the population size in accordance to Hilby et al., (2007). Due to the fact that grey seal commonly feed on fish up to approximately 30 cm in length (Ridoux et al., 2007) the period that smolts are available to seal predation were estimated to 90 days ranging from June-August, instead of 60 days. The expected predated biomass was calculated separately for the two areas.

With the assumption that each released salmon smolt weigh approximately 118 gram, estimated from Alanärä et al. (2017), the number of smolts released in Dalälven river predated in each area were calculated by dividing the biomass with 118. A graph was made to estimate the number of smolts expected to be predated in the areas depending on how long time they spend in each area, assuming the released smolts only stay within those two areas.

2.6 Post-smolt survival in river Dalälven vs. salmon populations in the Baltic Sea

To look for correlations due to large-scale processes that affects all salmon populations in the Baltic Sea, the estimated post-smolt survival for river Dalälven were plotted against ICES estimates of post-smolt survival 1989-2010 with data received from (Dannewitz. 2018, pers. comm). Both wild and hatchery reared salmon were taken into account. A linear-regression with river Dalälven as response variable were made to estimate correlation between ICES estimated post-smolt survival for hatchery reared smolts with the post-smolt survival for river Dalälven. A paired t-test with the confidence level of 95 % was performed using JMP Pro statistical software (12.2.0, 2015 SAS Institute Inc.), to evaluate if there was any significant difference in the post-smolt survival of salmon smolts released into river Dalälven and ICES estimates of the post-smolt survival for hatchery reared salmon smolts. A p-value < 0.05 was considered significant.

2.7 Cormorant numbers near Dalälven vs. the grey seal numbers in the Baltic Sea

Due to the fact that both grey seal and cormorants predate on salmonoids it can be difficult to separate the effects of these two predators when predating on the same fish stock. The correlation between grey seal population in the Baltic Sea and the number of cormorant nests near river Dalälven were attained by a linear-regression curve. Using the R^2-value to estimate if the two variables were correlating.

3 Results

3.1 Dietary study

Out of the 183 stomachs analysed, 31 were empty and therefore excluded from analysis. Making the total sample size 152 for both areas, 27 for Bergeforsen and 125 for Alnö. In both areas sticklebacks was the most common prey, with 43 individuals at Bergeforsen and a total of 1992 individuals at Alnö (table 2 and 3). The second most predated prey type were salmonoids (27 individuals) for Bergeforsen, and sandeel (599 individuals) at Alnö. The third most predated species for Bergeforsen were unidentified fish species (n= 9) and herring (n= 70) at Alnö.

The species most frequently found (FOi %) in cormorants culled near Bergeforsen fish farm were salmonoids (48.1 %), followed by unidentified species (29.6 %) and salmon (22.2 %). For cormorants culled at Alnö sticklebacks were the most frequently found prey species (67.2 %) followed by sandeel (38.4 %) and herring (22.4 %).

The relative numerical contribution (Ni %) at Bergeforsen was highest for sticklebacks (38.4 %) and salmonoids (24.1 %) and unknown (8.04 %). At Alnö the numerical contribution was highest for stickleback sp. (69.1 %), sandeel (20.8 %) and herring (2.4 %).

The relative biomass (Bi %) at Bergeforsen were dominated by Salmo spp. (68.2 %), salmon (18.1 %) and herring (3.6 %). For Alnö fourhorn sculpin (27.4%), sandeel (17.3 %) and Cottidae sp. (11.9 %) had the highest relative biomass.

Table 2. *Prey species consumed by cormorants culled outside Bergeforsen hatchery (n= 27). Displaying the number of fish individuals consumed by species or family (n), frequency of occurrence (Foi %), relative numerical contribution (Ni %) and relative biomass (Bi %). See methods for calculations.*

Family	Species	Common name	individuals (n)	Foi %	Ni %	95 % CI-	95 % CI+	Bi %	95 % CI-	95 % CI+	Total predation biomass (kg)	Regression source
Ammodytidae	Ammodytes sp.	Sandeel	2	3.7	1.79	0.000	0.044	0.29	0.000	0.012	0.018	Leopold et al. (2001)
Anguilidae	Anguilla anguilla	European Eel	1	3.7	0.89	0.000	0.022					
Clupeidae	Clupea harengus	Herring	6	11.1	5.36	0.000	0.100	3.65	0.000	0.090	0.219	Lundström et al. (unpublished)
Cottidae	Cottidae sp.	Sculpin	1	3.7	0.89	0.000	0.028	2.13	0.000	0.052	0.127	
Gasterosteidae	Gasterosteidae sp.	Stickleback	42	18.5	37.50	0.037	0.320	1.23	0.040	0.352	0.074	
Gasterosteidae	Gasterosteus aculeatus	Three-spined stickleback	1	3.7	0.89	0.000	0.009	0.04	0.000	0.012	0.002	Leopold et al. (2001)
Percidae	Gymnocephalus cernuus	Ruffe	3	11.1	2.68	0.000	0.148	1.36	0.000	0.183	0.081	Leopold et al. (2001)
Percidae	Perca fluviatilis	Perch	2	7.4	1.79	0.000	0.031	1.25	0.000	0.023	0.075	Leopold et al. (2001)
Cyprinidae	Rutilus rutilus	Roach	1	3.7	0.89	0.000	0.022	0.14	0.000	0.003	0.008	Leopold et al. (2001)
Salmonidae	Salmo salar	Atlantic salmon	8	22.2	7.14	0.023	0.174	18.12	0.037	0.262	1.084	Härkönen (1986)
Salmonidae	Salmo sp.	Salmonid	27	48.1	24.11	0.199	0.512	68.18	0.305	0.659	4.078	
Salmonidae	Salmo trutta	Sea trout	4	11.1	3.57	0.000	0.093	1.65	0.000	0.053	0.098	Leopold et al. (2001)
Cottidae	Taurulus bubalis	Longspined bullhead	1	3.7	0.89	0.000	0.037	0.07	0.000	0.002	0.004	Härkönen (1986)
Unidetified	unknown	unknown	9	29.6	8.04	0.050	0.264					
Zoarcidae	Zoarces vivparus	Eelpout	4	11.1	3.57	0.000	0.074	1.89	0.000	0.045	0.113	Leopold et al. (2001)
Total:			**112**								**5.981**	

Table 3. *Prey species consumed by cormorant culled at Alnö (n= 125). Displaying the number of fish individuals consumed by species or family (n), frequency of occurrence (Foi %), relative numerical contribution (Ni %) and relative biomass (Bi %). See methods for calculations.*

Family	Species	Common name	individuals (n)	Foi %	Ni %	95 % CI-	95 % CI+	Bi%	95 % CI-	95 % CI+	Total predation biomass (kg)	Regression source
Ammodytidae	Ammodytes sp.	Sandeel	599	38.4	20.77	0.136	0.252	17.29	0.135	0.259	4.627	Leopold et al. (2001)
Anguilidae	Anguilla anguilla	European Eel	1	0.8	0.03	0.000	0.000					
Clupeidae	Clupea harengus	Herring	70	22.4	2.43	0.022	0.078	8.44	0.044	0.116	2.259	Lundström et al. (unpublished)
Clupeidae	Clupeidae sp.		1	0.8	0.03	0.000	0.024	0.11	0.000	0.024	0.028	Lundström et al. (unpublished)
Coregonus	Coregonus sp.		3	0.8	0.10	0.000	0.004	0.18	0.000	0.003	0.048	Lundström et al. (unpublished)
Cottidae	Cottidae sp.	Sculpin	25	7.2	0.87	0.014	0.058	11.90	0.018	0.083	3.184	
Cyprinidae	Cyprinidae sp.		5	1.6	0.17	0.000	0.006	0.10	0.000	0.003	0.026	
Gasterosteidae	Gasterosteidae sp.	Stickleback	1696	64.0	58.81	0.331	0.477	11.10	0.261	0.404	2.972	
Gasterosteidae	Gasterosteus aculeatus	Three-spined stickleback	213	23.2	7.39	0.029	0.083	1.64	0.024	0.074	0.439	Leopold et al. (2001)
Percidae	Gymnocephalus cernuus	Ruffe	3	1.6	0.10	0.000	0.008	0.60	0.000	0.011	0.159	Leopold et al. (2001)
Cottidae	Myoxocephalus scorpius	Shorthorn sculpin	6	3.2	0.21	0.001	0.034	2.45	0.000	0.035	0.657	Leopold et al. (2001)
Osmeridae	Osmerus eperlanus	European smelt	2	1.6	0.07	0.000	0.002	0.24	0.000	0.007	0.064	Leopold et al. (2001)
Percidae	Perca fluviatilis	Perch	4	2.4	0.14	0.000	0.002	0.55	0.000	0.005	0.148	Leopold et al. (2001)
Cyprinidae	Phoxinus phoxinus	Eurasian minnow	1	0.8	0.03	0.000	0.000					
Gobiidae	Pomatoschistus minutus	Sand goby	10	4.8	0.35	0.001	0.012	0.06	0.000	0.003	0.015	Leopold et al. (2001)
Gasterosteidae	Pungitius pungitius	Ninespine stickleback	83	16.0	2.88	0.011	0.044	0.22	0.002	0.008	0.059	Institute of Coastal Research, SLU
Cyprinidae	Rutilus rutilus	Roach	2	1.6	0.07	0.000	0.001	0.04	0.000	0.002	0.010	Leopold et al. (2001)
Salmonidae	Salmo salar	Atlantic salmon	2	0.8	0.07	0.000	0.001	3.48	0.000	0.021	0.932	Härkönen (1986)
Salmonidae	Salmo sp.	Salmonid	4	2.4	0.14	0.000	0.030	2.26	0.000	0.043	0.604	
Clupeidae	Sprattus sprattus	Sprat	11	4.0	0.38	0.000	0.016	0.14	0.001	0.015	0.037	Lundström et al. (unpublished)
Cottidae	Triglopsis quadricornis	Fourhorn sculpin	57	21.6	1.98	0.074	0.179	27.47	0.105	0.221	7.352	Härkönen (1986)
Unidetified	unknown	unknown	23	11.2	0.80	0.006	0.023					
Zoarcidae	Zoarces vivparus	Eelpout	63	21.6	2.18	0.028	0.083	11.75	0.040	0.111	3.146	Leopold et al. (2001)
Total:			**2884**								**26.766**	

Predation per adult bird and its chicks plus one sub adult pre-breeder per nest was estimated to approximately 760 grams per day and 136 kg for the whole period (180 days). There was a small amount of salmon otoliths in the stomachs as late as in the end of August. The total predated biomass during the whole period for all cormorants within 20 km from Alnö (n= 2289) were estimated to approximately 314 tons of fish.

With the assumption that all salmonid smolts unidentified to species (Salmo spp.) weigh 39.5 gram and all salmon smolts weigh 34.4 gram, the maximum number of predated smolts were estimated to approximately 38 600, during a period of 14 days. The minimum number of smolts predated were estimated to approximately 2760 (1 day). Assuming that the ratio of salmon and Salmo spp. predated remained constant during the whole period.

3.2 Return rate index for sea trout in river Dalälven,1989-2010

The return rate index for sea trout ranged between 0.05 and 2.93 for females released between 1989- 2010 (figure 4). For both salmon and sea trout the return rate fluctuated during the study period (tables in appendix 1 and 2). Sea trout had the highest estimated return rate index in 1993. The return rate index for sea trout females were plotted against the number of cormorant nests within 20 km from river Dalälven estuary (figure 5). The linear-regression indicated that the return rate index for sea trout released in river Dalälven seems to have a very low correlation with the cormorant population nesting in the area (R^2= 0.01, p= 0.649, df= 20).

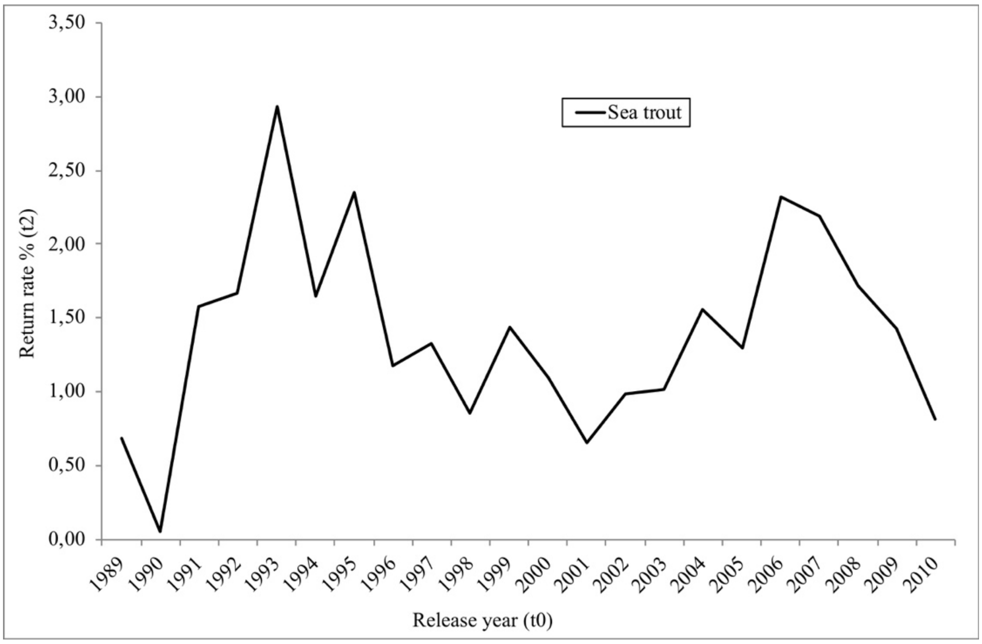

Figure 4. Index of return rate for sea trout released in river Dalälven (1989-2010). The return rate is calculated by dividing the number of sea trout females returning after two years at sea with the number of sea trout females released two years earlier.

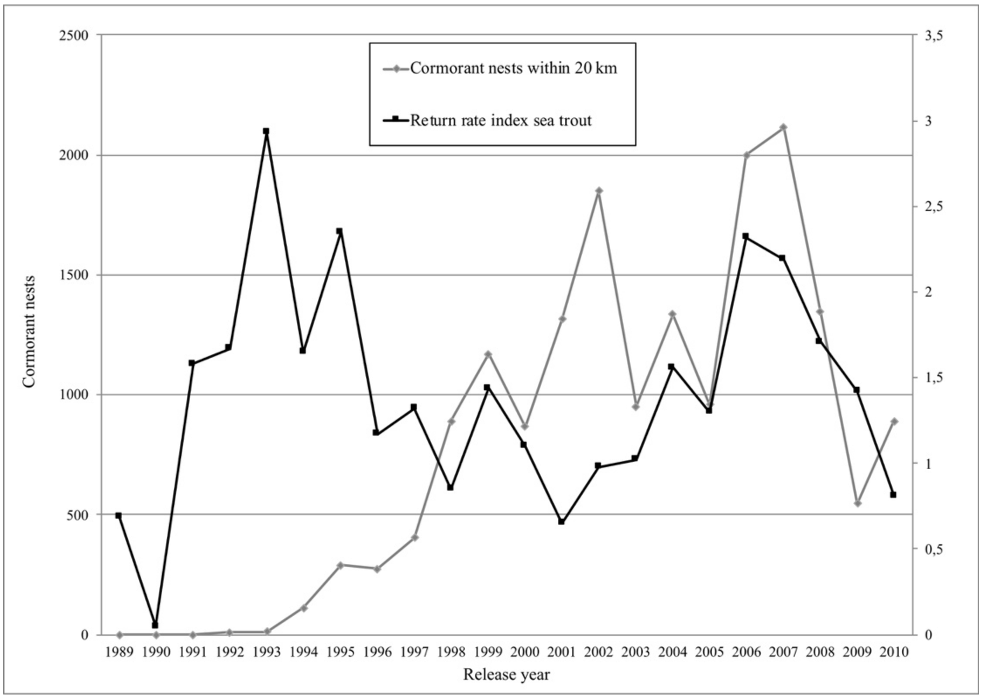

Figure 5. Index of return rate for female sea trout released in river Dalälven 1989-2010 and the number of cormorant nests within 20 km from river Dalälven estuary.

3.3 Cormorant impact on salmon post-smolt survival

There has been an increase in the cormorant population near river Dalälven during the study period. At the same time there has been a decline in the post-smolt survival in salmon females released into river Dalälven, with the exception for the last years in the study period where there seems to have been a decline in the cormorant population. During the last year of the study period both post-smolt survival and the number of cormorants seems to increase (figure 6). The linear regression curve showed a correlation between the two parameters with $R^2= 0.37$, ($p < 0.05$, df = 20).

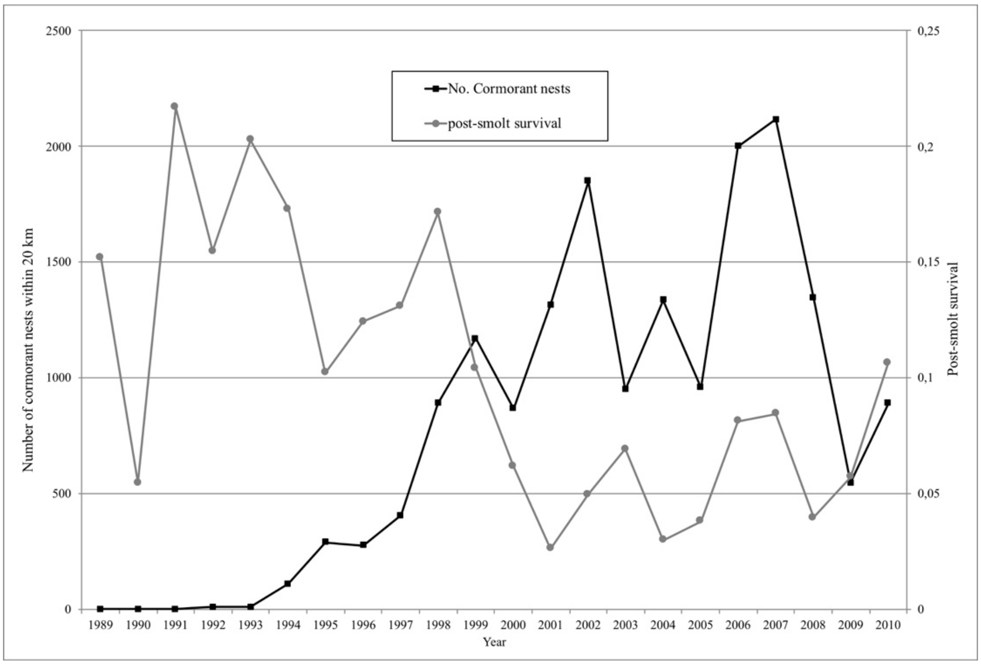

Figure 6. Number of cormorant nests within 20 km from river Dalälven estuary (black line) and estimated post-smolt survival for hatchery reared salmon females in river Dalälven (grey line), released between 1989-2010.

3.4 Grey seal population in the Baltic Sea

When comparing the grey seal population in the Baltic Sea with the post-smolt survival of salmon females in river Dalälven there seems to be a correlation with the rapid increase of the grey seal population and the decrease in post-smolt survival (figure 7). The logarithmic regression line showed a correlation between the grey seal population development and the decline in post-smolt survival with an R^2-value of 0.44. The grey seal predation index is showing a higher expected salmon predation in the area south of Bothnian Sea than in the Bothnian Sea (figure 8). With an expected predation of approximately 137 salmons if the salmon smolts spend all of their time in the Baltic south of Bothnian Sea and an expected predation of approximately 33 salmons if they spend all of their time in the Bothnian Sea.

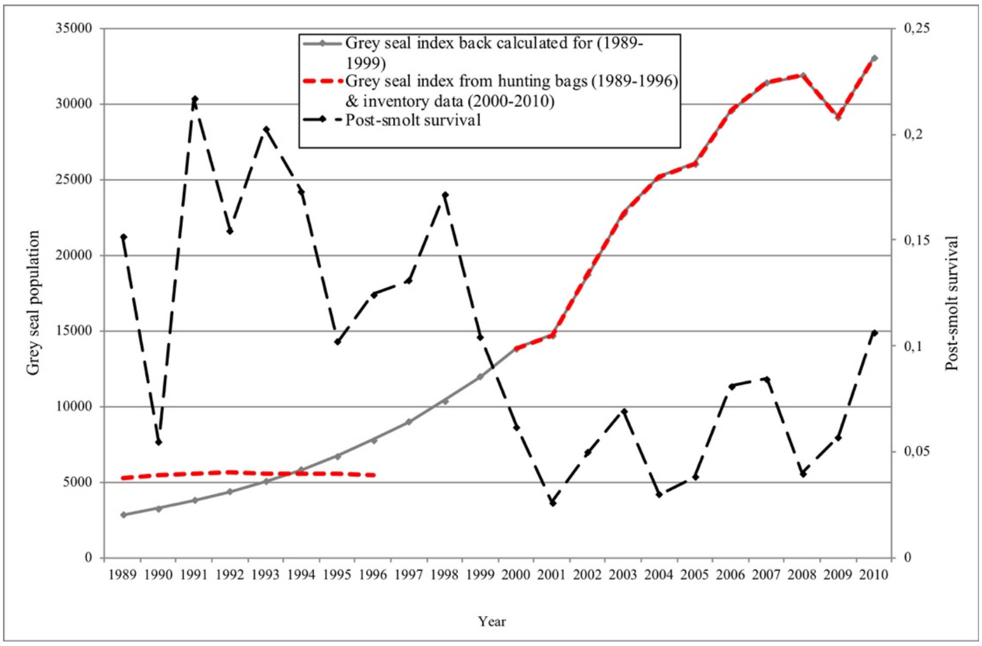

Figure 7. Estimated post-smolt survival for hatchery reared salmon females in river Dalälven released between 1989-2010 and estimated index of Grey seal population in the Baltic Sea. Grey seal index from hunting bag statistics for the years 1989-1996 (red dashed line) (Hårding and Härkönen 1999 see Svärd et al., 2015). From year 2000 the grey seal population is based on inventory data from Naturvårdsverket et al. (2016) with the assumption that 70 % of the population is counted (Hilby et al., 2007)

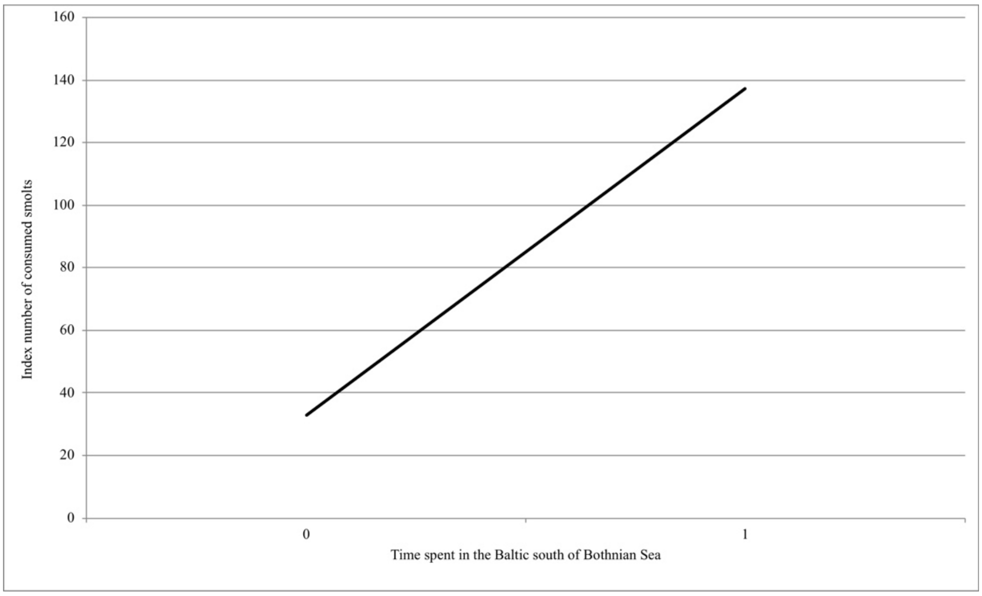

Figure 8. Grey seal predation index for hatchery reared salmon released in river Dalälven 2005. Divided by time spent in the Baltic south of Bothnian Sea and Bothnian Sea. Where 1= all time spent in the Baltic south of Bothnian Sea and 0 = all time spent in the Bothnian Sea.

3.5 Post-smolt survival in river Dalälven vs. salmon populations in the Baltic Sea

Estimated post-smolt survival for river Dalälven follow the same declining pattern as ICES estimate for the whole Baltic Sea (figure 9). With a lower post-smolt survival than for wild salmon in the Baltic Sea. The linear regression between hatchery reared salmon females in river Dalälven and ICES estimated post-smolt survival for all hatchery reared salmon in the Baltic sea showed the highest estimated correlation with an R^2- value of 0.50 ($p < 0.001$, df = 20). According to the paired t-test there was no significant difference in the post-smolt survival for salmon smolts from river Daläven and ICES estimates for hatchery reared salmon smolts (p= 0.6716) during the study period.

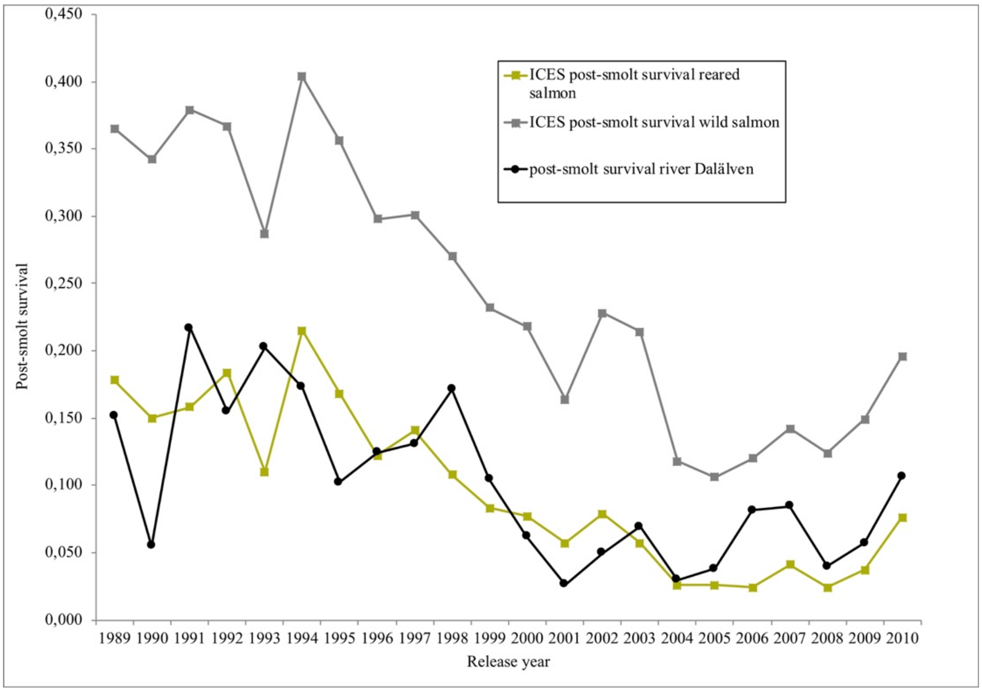

Figure 9. Estimated post smolt survival for salmon females released in river Dalälven (black line) and whole Baltic Sea. Estimated post-smolt survival for wild (grey line) and reared salmon (yellow line) in the Baltic Sea, estimated made by ICES (Dannewitz pers comm. 2018).

3.6 Grey seal population and cormorant population

There has been a steady increase in the grey seal population of the Baltic Sea during the study period, with a high increase during the same period as the cormorant population nesting near Dalälven river (within 20 km). The linear-regression examining the correlation between grey seal population development in the Baltic Sea and the number of cormorant nests within 20 km from Dalälven showed a correlation between the two variables with an R^2-value of 0.58 ($p < 0.001$, df= 20) (figure 10). There seems to have been a shift in the trend during the last three years (marked as red), when the cormorant population within 20 km from river Dalälven decline.

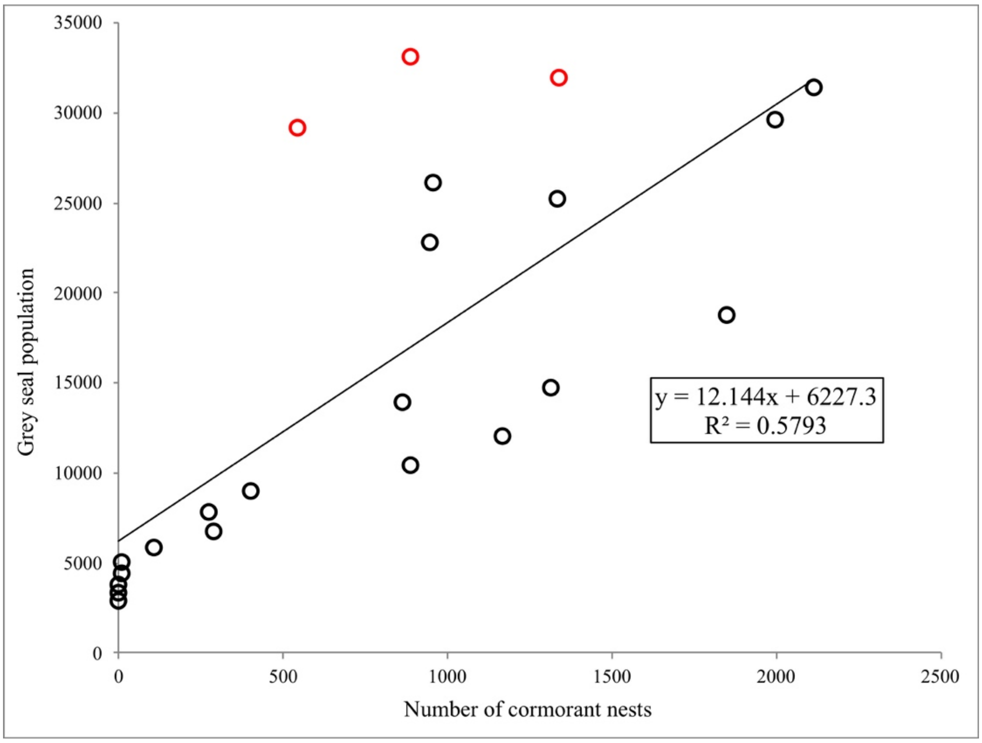

Figure 10. Graph showing the relation between the population development of grey seal in the Baltic Sea and the number of cormorant nests within 20 km of river Dalälven estuary (1989-2010). Displaying the number of cormorant nests on the x-axis and the grey seal population on the y-axis.

4 Discussion

According to the study carried out in river Dalälven cormorants do not seem to have any major effect on the mortality of hatchery reared salmon and sea trout. The post-smolt survival in river Dalälven follows the same pattern as post-smolt survival for the whole Baltic Sea. The high correlation with all hatchery reared salmon in the Baltic Sea suggests that the decline in post-smolt survival in river Dalälven during this period is caused by large scale processes in the Baltic Sea rather than local cormorant predation. Friedland et al. (2017) argued that it is important to consider all aspects both biotic and abiotic when trying to identify correlations between salmon survival and various factors. In this study, no abiotic factors were taken into account in the survival calculations. The fact that the post-smolt survival were not significantly lower for salmon smolts released into river Dalälven than for all hatchery reared salmon released into the Baltic Sea suggests that cormorants do not have any large effects on the mortality of salmon from the river Dalälven.

The return rate index for both salmon and sea trout varied over the study period. For most of the years the return rate is higher for sea trout than for salmon, indicating a higher post-smolt survival for sea trout. It has been suggested that high abundance of salmon may help reduce the predation pressure on sea trout (Jonsson and Jonsson, 2011). However, there seems to be no correlation between the return rate of sea trout and the cormorant population development near river Dalälven.

When comparing the cormorant population nesting near river Dalälven with the estimated post-smolt survival there seemed to be a significant correlation. But the same magnitude of correlation was present between the post-smolt survival and the grey seal population in the Baltic Sea. When using regressions, one need to keep in mind that they only point out the magnitude of the statistical relationship not the underlying causes to the correlation. When correlating the cormorant population near river Dalälven with the grey seal population in the Baltic Sea there seemed to be a co-variation between the two ($R^2 = 0.58$). This makes it hard to separate the effects the two might have on the post-smolt survival. The estimated number of consumed smolts from river Dalälven by grey seals depending on time spent in the Bothnian Sea or in the Baltic south of Bothnian Sea points to a relatively low salmon predation by grey seal. This estimate has high uncertainties and builds on the assumptions that salmon, herring and sprat has the same distribution over the areas. This might not be the case during for example smolt release. As mentioned before grey seals can cause problems when feeding on aggregations of salmonoids. Grey seals can also affect salmon stocks by (specialized) predation on salmon aggregating in salmon traps (Königson et al., 2013). Another factor to keep in mind is that there are large populations of grey seal south of the Bothnian Sea that may forage in the Bothnian Sea as well.

In the dietary study performed in Sundsvall bay the high predation of salmonoids in Bergeforsen indicate a high initial cormorant predation during the early smolt migration, which is in accordance with earlier studies (Dieperink et al., 2001, Dieperink et al., 2002). The fact that a small number of cormorants culled as late as in August contained salmon indicates that the predation period is much longer than during the actual smolt release. Although predation during the end of the period is expected to be less extensive than in the beginning of the smolt releases since the number of smolts remaining in the area are presumably low and scattered across the area.

When using the cormorants culled outside Alnö to calculate the maximum and minimum predation one limitation is that the cormorants containing salmonids were culled late in the season, when the presence of salmonids is expected to be low in the area. My assumption is that both maximum and minimum predation is higher than the values calculated in this thesis. It is hard to make any certain conclusions from the data used to calculate this since the dietary study only provides a momentary picture of the total predation. On the other hand, if assuming that all salmonoids predated are one-year old smolts from the latest smolt release, there is an overestimation in the salmon weight while the sea trout is underestimated. Since no smolts were tagged in this study there is no way of knowing the size of the smolt during the predation. Ideally the cormorants used for calculating maximum and minimum values should have been culled closer in time with the smolt release. Considering the fact that smolts may swim together in small schools during seawards migration (Jonsson and Jonsson, 2011). I would assume that this behaviour makes it easier for cormorants to both detect and catch smolts when they occur in aggregations soon after release from the hatchery. Another thing that I think might affect the catchability of the released smolt is the age during release.

A study by Kesler et al., (2013) examining the migratory behaviour of hatchery reared salmon smolt in Pirita river indicated that there seems to be some behavioural differences between one- and two-year-old smolts during seawards migration. They found that most two-year old smolt migrated downstream and reached open sea within a week after the release, that was conducted 13 km upstream. While most of the one-year old smolt migrated downstream for a longer time period and reached the sea as late as a few weeks after the release. Some of the one-year old smolt even stayed in the river habitat for an additional year before migrating out to the sea. I think that further studies comparing the migratory behaviour of one- and two-year old smolt is needed to gain a better understanding if they differ in other populations as well, and how the smolt age during the release might affect the cormorant predation on different fish stocks. In theory the longer the salmonids stay in the estuaries and river habitats before migrating out to sea the longer they could be available for cormorant predation. Another factor to consider is the distance from the cormorant colonies to the smolt release site. Boström et al. (2009) argued that that both the distance from cormorant colonies to the river delta and the migratory behaviour of the released fish might be determining factors when studying the impact of cormorants on hatchery reared smolt. When comparing the distance from the release site and estuaries the cormorant colonies at Gistaholmarna in the Sundsvall bay is located closer than the colonies located near Älvkarleby. In future studies it would be interesting to count the number of foraging cormorants during smolt release to get a better understanding of the predation pressure in the different areas.

One thing to keep in mind is that the otoliths of salmon and sea trout are very similar in shape, especially when eroded so there might also be some errors when trying to specify which of the two species that have been consumed.

The fact that cormorants shot right outside Bergeforsen hatchery contained more salmonoids than cormorants shot at Alnö was expected, as cormorants shot at Bergeforsen were shot when foraging in the area during the smolt release. The time of the hunt may also be a factor contributing to the difference in prey species between the two areas, since most of the cormorants culled at Alnö were shot later in the summer and for a longer time period than the cormorants shot at Bergeforsen. The dietary study also showed a high numerical contribution of sticklebacks in cormorants culled in both areas. This result is consistent with previous studies that also has shown a high numerical contribution of sticklebacks in cormorant diet (Boström et al., 2012b). In Bergeforsen a larger amount of cormorants predated on salmon and unidentified salmonoids than sticklebacks but the ones that preyed on sticklebacks seems to eat a higher number of sticklebacks. Besides sticklebacks the cormorants culled at Alnö also contained a large amount of sandeel. The large amount of sandeel found might be due to the fact that they can occur in large aggregations along the coastline during the summer months (Kullander, 2012). The dietary study only provides a minimum of fish predated, since it can be easy to miss otoliths during the washing and sorting process and some otoliths might even have been completely eroded. The fact that the cormorants were shot during early morning might also affect the result since they might not have been able to forage for long before culled.

To make a more certain estimate of the proportion salmon and sea trout consumed I would recommend a study performed with tagged salmon and sea trout in the area. Combined with collection of diet samples. That way it could also be determined which one of the species that is most affected by cormorant predation. Due to the high number of salmonoids only classified by family it could not be determined in this study. What could be determined though is that both species were predated in the area. Further studies are also needed to compare post-smolt survival trends for different rivers containing hatchery reared salmon to investigate if the trends differ within areas, with and without cormorants present. It is possible that the time period considered in this study is too short to be able to see any clear trends and a study over a longer period of time might help to get a better view of the population trends.

4.1 Conclusion

According to the study in river Dalälven the decline in salmon post-smolt survival during the study period seems to be due to large-scale processes in the Baltic Sea rather than cormorant predation. The data suggests a high level of co-variation between the cormorant colonies nesting close to river Dalälven and the grey seal population in the Baltic Sea, which can make it difficult to separate the effects of the two predators. It is hard to draw any certain conclusions on the large-scale predatory effects of cormorants from the dietary study due to the high levels of uncertainty, but the data indicates that the level of predation can be high especially during smolt release. From a salmon and sea trout management perspective my results indicate that protective hunting measures would have best effect if applied in direct connection to smolt releases.

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Acknowledgements

First of all, I would like to thank my supervisors Maria Ovegård, Kjell Leonardsson and Karl Lundström for all the help and support during this thesis. Maria and Karl thank you for all your patience and dedication during the dietary study. Who would have guessed that learning to identify otoliths would be so much fun! A special thanks to Maria and her family for their hospitality during my week in Lysekil. Kjell thank you for always taking the time to share your extensive knowledge!

A huge thanks to Lars Bergman at Bergeforslax and his family for all the help during this summer with storing and collecting cormorants, I could not have done it without your help!

I would also like to thank the hunters for all of their hard work during this summer, as well as Jörgen Rask, Johan Dannewitz, Stefan Palm, Daniel Brelin, Per Aspenberg, Börje Sahlin, Peter Nilsson, Ulf Bergström and Anders Alanärä. Last but not least a huge thanks to my supporting family and friends.

Appendix 1

Estimated return rate index of hatchery reared salmon females released in river Dalälven, release year (1989-2010). No hatchery reared salmon females were recorded before 1996, bold numbers are estimated hatchery reared salmon of returning salmon females. Assuming that the quota of hatchery reared salmon was the same as the average for the years after.

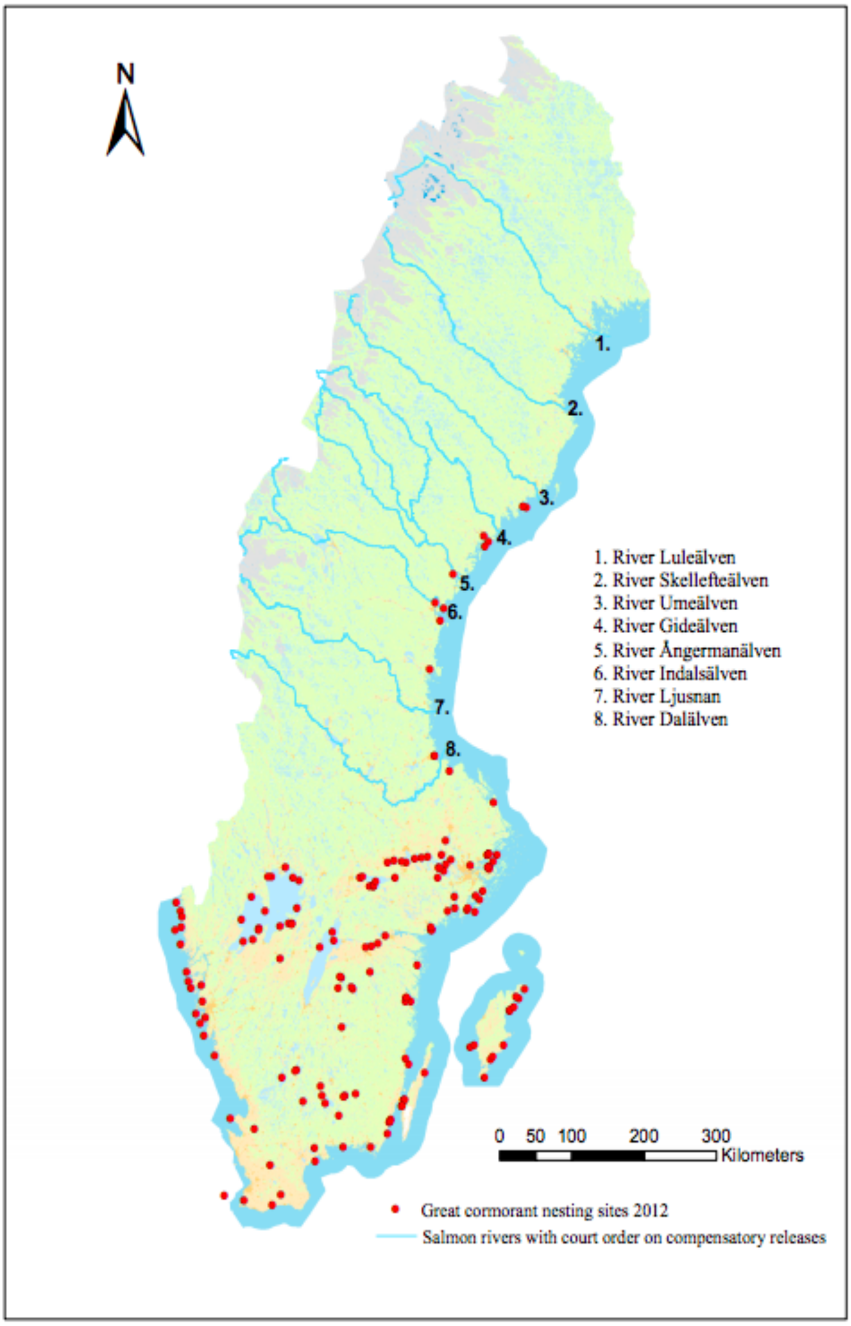
Year	Salmon females relesaed	Returning females (t+2)	Return rate %
1989	88020	**199**	0,23
1990	80858	**22**	0,03
1991	41848	**187**	0,45
1992	65223	**120**	0,18
1993	87284	**823**	0,94
1994	37615	**439**	1,17
1995	74352	**116**	0,16
1996	119406	1198	1,00
1997	111404	870	0,78
1998	119778	1491	1,24
1999	115096	784	0,68
2000	113503	500	0,44
2001	114626	206	0,18
2002	87852	226	0,26
2003	105881	346	0,33
2004	113110	254	0,22
2005	112738	250	0,22
2006	118034	1017	0,86
2007	101663	974	0,96
2008	133382	675	0,51
2009	115843	514	0,44
2010	104669	1033	0,99

Appendix 2

Estimated return rate index of hatchery reared sea trout females released in river Dalälven. Release year (1989-2010).

Year	**Released sea trout females**	**Returning females (t+2)**	**Return rate %**
1989	16477	113	0,69
1990	23690	11	0,05
1991	29307	463	1,58
1992	30581	511	1,67
1993	25292	742	2,93
1994	32748	541	1,65
1995	31618	742	2,35
1996	35792	420	1,17
1997	40878	540	1,32
1998	37033	316	0,85
1999	39886	574	1,44
2000	43476	478	1,10
2001	38366	249	0,65
2002	26660	262	0,98
2003	20881	212	1,02
2004	23048	359	1,56
2005	34297	445	1,30
2006	39495	917	2,32
2007	28547	624	2,19
2008	25329	434	1,71
2009	42932	611	1,42
2010	32014	260	0,81

Appendix 3



Appendix 3. Map over Swedish salmon rivers with court order on compensatory releases redrawn and modified from Palmé et al. (2012). Red dots represent cormorant nesting sites in 2012 (Bergström, 2018, pers. comm). GSD-General map, vector ©Lantmäteriet.

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