




Development of northern pike (*Esox lucius*) populations in the Baltic Sea, and potential effects of grey seal (*Halichoerus grypus*) predation

Populationsutveckling hos gädda (Esox lucius) i Östersjön, och potentiella effekter av predation från gråsäl (Halichoerus grypus)

Rebecka Svensson

Degree project/Independent project • 60 hp
Swedish University of Agricultural Sciences, SLU
Faculty of Natural Resources and Agricultural Sciences
Öregrund 2021

A thick, bright yellow diagonal bar that starts from the bottom left corner and extends towards the top right corner of the page.

Development of northern pike (*Esox lucius*) populations in the Baltic Sea, and potential effects of grey seal (*Halichoerus grypus*) predation

Populationsutveckling hos gädda (Esox lucius) i Östersjön, och potentiella effekter av predation från gråsäl (Halichoerus grypus)

Rebecka Svensson

Supervisor: Ulf Bergström, SLU, Department of Aquatic Resources
Assistant supervisor: Örjan Östman, SLU, Department of Aquatic Resources
Assistant supervisor: Karl Lundström, SLU, Department of Aquatic Resources
Examiner: Rahmat Naddafi, SLU, Department of Aquatic Resources

Credits: 60 hp
Level: A2E
Course title: Master thesis in Biology
Course code: EX0900
Course coordinating dept: Department of Aquatic resources

Place of publication: Öregrund, Sweden
Year of publication: 2021

Keywords: diet analysis, marine mammals, predator-prey, socio-economic, sport fishing, recreational fisheries

Swedish University of Agricultural Sciences
Faculty of Natural Resources and Agricultural Sciences
Department of Aquatic Resources
Institute of Coastal Research

Publishing and archiving

Approved students' theses at SLU are published electronically. As a student, you have the copyright to your own work and need to approve the electronic publishing. If you check the box for **YES**, the full text (pdf file) and metadata will be visible and searchable online. If you check the box for **NO**, only the metadata and the abstract will be visible and searchable online. Nevertheless, when the document is uploaded it will still be archived as a digital file.

If you are more than one author you all need to agree on a decision. You can find more information about publishing and archiving here: <https://www.slu.se/en/subweb/library/publish-and-analyze/register-and-publish/agreement-for-publishing/>

YES, I/we hereby give permission to publish the present thesis in accordance with the SLU agreement regarding the transfer of the right to publish a work.

NO, I/we do not give permission to publish the present work. The work will still be archived and its metadata and abstract will be visible and searchable.

Abstract

Worldwide, marine mammal populations are increasing after considerable efforts to turn the downward trends caused by hunting, accidental mortality and pollution. The ecosystem effects from the increases of these top predators may be pronounced, but are in most cases poorly known. In the Baltic Sea, the grey seal (*Halichoerus grypus*) has been increasing by 5-9% annually since the middle of 1980, with potential effects on fish populations, food webs and fisheries. One possible prey for the grey seal is the northern pike (*Esox lucius L.*), a large, predatory fish abundant in the Baltic Sea archipelagos. Recreational fishers are experiencing declines in abundances of pike, and partly blame the decline on seal predation. To assess a potential influence of grey seal on pike population, I have analysed trends in pike abundance and size and correlate it with trends in seal abundance. In addition, I have analysed diet composition of grey seal to study what seals in the archipelago eat. To follow trends in pike abundance I have used data from the Swedish coastal fish monitoring programme and data from fishing competitions. For trends in seal abundance, I used data from the Swedish national grey seal survey. Grey seal diet was estimated from scats and stomach content collected during 2016-2020 from Uppsala County and Stockholm County, in the inner and central parts of the archipelago, i.e. the habitats where pike is most abundant.

Analyses were performed for five counties; Stockholm, Södermanland, Östergötland, Kalmar and Blekinge from 2000 to 2020. The fish monitoring data showed that the abundance of pike smaller than 40 cm has decreased significantly in all counties whereas the abundance of pike larger than 40 cm has decreased significantly in three counties, Stockholm, Östergötland, and Kalmar. The fishing competition data showed that both the abundance and the maximum size of pike have decreased significantly only in Stockholm County. Grey seal abundance has increased in all counties except Kalmar. In the grey seal diet, pike constituted 20% of the diet by weight, after perch (*Perca fluviatilis*) and herring (*Clupea harengus*). Overall, there was a negative relationship between the abundance of grey seal and the catch of both smaller and larger pike in the fish monitoring data. There was also a negative relationship between the abundance of grey seal and the maximum size of pike in Stockholm County, while no relationships between the abundance of grey seal and the maximum size of pike were observed in the other counties.

Taken together, the results from this study indicate that the increasing grey seal population is associated with the negatively development of pike population in the archipelagos of the western Baltic Sea. Management of coastal fish has traditionally only taken the effects of fishing into account. The results of this thesis emphasize the importance of a transition towards an ecosystem-based fisheries management, where the effects of increasing populations of top predators are also taken into account in the assessments, to maintain viable populations of fish.

Keywords: diet analysis, marine mammals, predator-prey, socio-economic, sport fishing, recreational fisheries

Populärvetenskaplig sammanfattning

Gäddan är en av Sveriges viktigaste fiskart för fritidsfisket. Tack vare den troféstorlek som gäddan kan nå, i kombination med Sveriges orörda natur, vallfärdar många européer årligen för att fånga just sin drömgädda. Men fisket efter gädda i skärgården, som en gång varit känt som världens bästa, har enligt gäddfiskarna förändrats. Fisket efter gädda flyttas mer och mer till sjöarna, och många gäddfiskare förknippar förändringen med predation från det växande gråsälsbeståndet. Syftet med min studie var att undersöka gäddbeståndens utveckling längs svenska kusten, och jämföra dessa med gråsälsbeståndets utveckling. Sälspillning från viloplattor och maginnehåll från skjutna och självdöda sälar analyserades också för att se vad gråsälen i skärgården äter.

För att få en bild av gäddbeståndens utveckling längs svenska kusten analyserade jag data från nätprovfiske. Data fanns tillgängligt från Stockholms län till och med Blekinge län. Min analys visar att antalet gäddor har minskat med mer än 90 % i provfisken under 2000-talet, och de troféfiskar som många historier så stolt berättar om finns inte kvar.

Samtidigt som bestånden av gädda minskat, breder gråsälen ut sig i skärgården och blir en allt vanligare syn i grunda innervikar, samma vikar som gäddan trivs i. Gråsälen är Östersjöns viktigaste toppkonsument och har just nu det största beståndet på länge med närmare 50000 individer, jämfört med mindre än 4000 individer när antalet var som lägst. När jag analyserar sambandet mellan gråsälens ökande antal och gäddans minskande antal finns ett samband, länsvisa analyser visar på ett samband i alla län förutom Blekinge. Samtidigt bekräftar mina dietanalyser att sett till vikt var gädda gråsälens tredje viktigaste bytesart efter abborre och strömming, i skärgården i Uppsala och Stockholms län.

Resultaten från min studie visar att nedgången av gädda har skett i takt med att sälbeståndet har ökat. Traditionellt sätt har fiskförvaltningen längs kusten endast räknat med fiskets uttag. Mina resultat visar på vikten av att ha med effekten av toppredatorer i förvaltningen, och övergå mer till att använda en så kallad ekosystembaserad fiskförvaltning. Kännedom om hur arter påverkar varandra är viktig för att kunna vidta effektiva åtgärder för att stärka bestånden av rovfisk i Östersjön.

Table of contents

1. Introduction.....	9
2. Materials and methods.....	12
2.1. Pike.....	12
2.1.1. Fish monitoring	12
2.1.2. Fishing competitions	13
2.1.3. Case study: Värtan cup	14
2.2. Grey seal	14
2.2.1. Diet analyses	14
2.2.2. Grey seal abundance data.....	18
2.3. Statistical analyses	18
3. Results.....	20
3.1. Pike.....	20
3.1.1. Fish monitoring	20
3.1.2. Fishing competitions	21
3.1.3. Case study: Värtan cup	21
3.2. Grey seal	23
3.2.1. Diet analyses	23
3.2.2. Grey seal abundance data.....	25
3.3. Analyses of the relationship between pike and seal	26
4. Discussion.....	29
References	33
Acknowledgements.....	39

1. Introduction

For decades, researchers and environmentalists have fought to reverse the downward abundance trend faced by populations of marine mammals worldwide (Heithaus et al. 2008; Estes et al. 2009). Hunting (Clapham & Baker 2009; Gero & Whitehead 2016), accidental mortality (Schipper et al. 2008) and pollution (Helle et al. 1976; Murphy et al. 2015), are the main pressures contributing to the abundance declines (Gibson et al. 2006), where some species have even been driven to extinction (Kenyon 1977; Mead & Mitchell 2012). Management plans, including marine protected areas, reducing pollutants and ban of hunting, have together contributed to reversing several negative trends of marine mammal populations (Jeffries et al. 2003; Brown et al. 2006; Gormley et al. 2012; Magera et al. 2013; Laake et al. 2018). However, with increased marine mammal abundance, already endangered predatory fish populations (Worm et al. 2006; Tanzer et al. 2015) will have more possible predators that may negatively affect them.

In the Baltic Sea, grey seal (*Halichoerus grypus*) is the main top predator (Ohlberger et al. 2019), primarily foraging on herring (*Clupea harengus*), sprat (*Sprattus sprattus*), cod (*Gadus morhua*) and flatfish (*Pleuronectidae*) in the outer archipelago (Lundström et al. 2010; Hansson et al. 2018), but also perch (*Perca fluviatilis*) and cyprinids (*Cyprinidae*) in some regions (Tverin et al. 2019). Previous studies describe grey seal as a generalist and opportunistic feeder, catching the most abundant species (Lundström et al. 2010; Suuronen & Lehtonen 2012). During the 1900s, grey seal was severely affected by hunting, causing a decline from close to 100.000 individuals in the beginning of the 20th century down to 3.600 grey seals in 1975 (Harding & Härkönen 1999). Along with the population decline, the recovery rate of grey seal was limited due to toxins such as PCB and DDT, which caused diseases and depressed pregnancy rates (Bergman & Olsson 1985; Bergman 1999). Today, more than 40 years after the historically low level in the late 1970s, the population of grey seal has recovered and has since then grown 5-8% annually (Harding et al. 2007; HELCOM 2018b). The number of grey seal individuals counted during the annual seal survey in 2019 in the Baltic Sea was 38000 (ICES 2020). However, along with the grey seal population increase, there are signs of decreased blubber thickness (Hermansson 2015; HELCOM 2018a), which may indicate that grey seal in the Baltic Sea is food limited (Kauhala et al. 2017).

At the same time, fishermen are reporting about decreasing catches of northern pike (*Esox lucius* L., henceforth pike) in the archipelago, both regarding size and abundance. Studies have shown local population declines in pike abundance (Lehtonen et al. 2009; Ljunggren et al. 2010; Olsson 2019), but information about the population status of pike in the Baltic Sea is limited (Olsson 2019). Pike is a freshwater species that has adapted to live in the brackish, shallow coastal waters of the Baltic Sea. The species consists of numerous local populations with a limited spatial mixture, most likely only migrating to the neighbouring populations as farthest (Wennerström et al. 2016). Pike is mostly found in inner bays along with cyprinids and perch. After perch, pike is the most common large predatory fish living in the coastal inner bays. It can grow up to around 140 cm (>20 kg), making it a highly valuable sport fish all over the Swedish east coast (SLU 2020).

The interest in recreational fishing is rising, and pike is one of Sweden's most important species for recreational fishing and was the second most caught species after perch during 2013-2017 (Swedish Agency for Marine and Water Management 2019). Thus, it is important to maintain viable populations of pike because of its big socio-economical interest. But today, the pike populations are exposed to many different pressures. One factor that has caused local declines in pike populations is recruitment failure caused by predation from the mesopredator three-spined stickleback (*Gasterosteus aculeatus*) (Bergström et al. 2015; Nilsson et al. 2019; Eklöf et al. 2020). According to fishermen, they believe that another factor affecting pike populations is “a negative impact from seals due to their increased foraging in the inner and central parts of the archipelago”, where pike is most abundant today.

It is hard to determine how large impacts certain factors such as extraction from marine mammals, birds and fishing have on pike population abundances and its maximum size. Hansson et al. (2018) estimated that in total in the Baltic Sea, recreational and commercial fisheries, seals (grey seal, ringed seal (*Pusa hispida*) and harbour seal (*Phoca vitulina*)) and the great cormorant (*Phalacrocorax carbo sinensis*) were extracting 4610 metric tons of pike annually during 2012-2013. Seals and birds consumed about 20% each of the yearly pike removals, whereas fishing accounted for almost 60% (Hansson et al. 2018). But there is large variation of pike removal between sites, and the extraction over time are likely to increase with increased grey seal abundance.

The aim of my study was to illustrate the population development of pike along the Swedish Baltic Sea coast and to study the potential effects of grey seal predation. This was done by analysing abundance trends in pike smaller and larger than 40 cm along a 600 km stretch of the Swedish east coast, using data from coastal fish monitoring programmes. Also, I studied pike maximum size using data from fishing competitions. Moreover, my aim was to look for correlations between pike

population parameters and grey seal density by analysing the population indices of pike in relation to density estimates of grey seal. To examine to which extent the grey seal in the archipelago eats pike, I assessed the importance of pike in grey seal diet. I discuss the potential implications of the results for monitoring and management.

2. Materials and methods

2.1. Pike

2.1.1. Fish monitoring

To study changes in the abundance of pike over time I used data from annual monitoring of coastal fish. I downloaded the data from the Swedish national database KUL (<https://www.slu.se/en/departments/aquatic-resources1/databases1/database-for-coastal-fish-kul/>) 2020-11-23 and the fish monitoring areas were chosen if the catch of pike was more than one individual for at least six years annually between 2003-2020 (Table 1, Figure 1). The fish monitoring was performed during July-August using gillnets of two types, the Nordic coastal multi-mesh gillnets (K064) and net series (K053). K064 is 1.8 m deep and 45 m long and built up by nine different mesh size panels (10, 12, 15, 19, 24, 30, 38, 48 and 60 mm) whereas K053 is 1.8 m deep and 120-180 m long and built up by four nets with different mesh sizes (17, 21.5, 25 and 30 mm) (HELCOM 2015). The nets were set in the afternoon and lifted the following morning, once per station. For K064, each monitoring area consists of around 45 randomly distributed stations separated in four depth intervals (0-3 m, 3-6 m, 6-10 m or 10-20 m) (Söderberg et al. 2004). For the net series, the principle is the same but each area is fished with 6-10 stations.

The fish monitoring areas were separated into counties to be comparable with the other data. For each of the counties, catch per unit effort (CPUE) was calculated as the number of pike per net and night.

Table 1. The different counties investigated with information about fish monitoring area and gear type, as well as the name of the pike fishing competitions which provided data for the analyses.

County	Area	Gear type	Fishing competition
Stockholm	Lagnö	K064	Värtan cup
Södermanland	Asköfjärden	K064	-
Östergötland	Kvädöfjärden	K053	Sportfish masters Valdemarsvik
Kalmar	Mönsterås and Vinö	K053	Sportfish masters Oskarshamn
Blekinge	Torhamn	K064	Blekinge gäddfestival

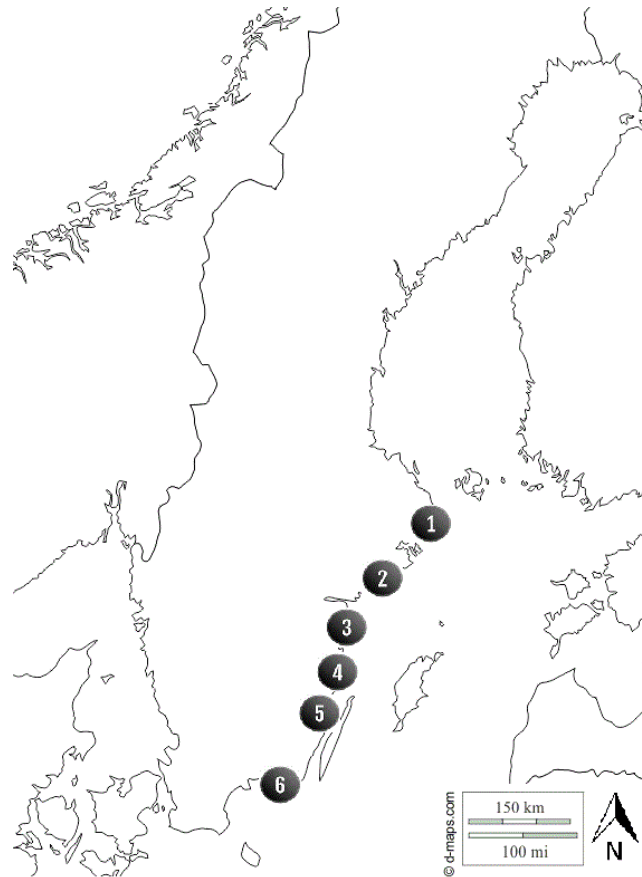


Figure 1. A map showing Sweden and the Baltic Sea, with markings of the fish monitoring areas numbered 1-6 from north to south. 1. Lagnö (Stockholm County), 2. Asköfjärden (Södermanland County), 3. Kvädöfjärden (Östergötland County), 4. Vinö (Kalmar County), 5. Mönsterås (Kalmar County), 6. Torhamn (Blekinge County). Map source: d-maps.com.

2.1.2. Fishing competitions

Fish monitoring mainly aim for fish smaller than 60 cm, and as pike can be much larger than that I complemented the fish monitoring data with data from fishing competitions to cover also larger pike. Information about abundance and maximum size was used to study changes in the pike maximal size.

I collected available data from rod fishing competitions with at least six years of results by extracting data from home pages, social media or by contacting organizers. All competitions were analysed separately and divided into counties (Table 1).

The data collected differed to some extent between competitions. For competitions that had registered individual weight instead of length (Värtan cup), weight was converted to length with a length-weight relationship available from the database KUL:

$$\text{length (cm)} = (\text{weight (kg)} / 5 * 10^{-6})^{\left(\frac{1}{3,0836}\right)}$$

Measured values of interest for each competition were:

- The largest pike
- The five largest pike
- Number of registered pike
- Number of participants

These measures were analysed to assess trends over time in both abundance and maximum size of the pike population in the Baltic Sea, divided into counties.

2.1.3. Case study: Värtan cup

Värtan cup is one of the world's largest pike fishing competition and takes place in the 'Stora Värtan' bay in Stockholm archipelago. Apart from other competitions, the competition has had the same rules and fishing area for each year 2003-2018, which makes the data comparable between years. All data is accessible at <http://info.sportfiskeboden.com/tavlingar.asp>. Every individual was weighted, and to be able to compare Värtan cup with other competitions, the weight was converted to length with the length-weight relationship presented above. The minimum size of the reported pike was 75 cm for 2003-2018, and 65 cm for 2019. Therefore, year 2019 was excluded from the analysis that investigates the number of caught pike per team.

2.2. Grey seal

2.2.1. Diet analyses

To assess the importance of pike in grey seal diet, faeces and stomach contents from hunted seals and seals found dead were sampled. Analyses of the diet were done to describe the frequency of occurrence for each species, the weight proportion for each species and the size structure of the species (Lundström et al. 2007). Based on recommendations from archipelago residents, 11 grey seal haul-out sites in the inner and central parts of the Stockholm archipelago were identified (Figure 2). The faeces were sampled during four collection trips in 2020, 4th of February, 6th of April, 20th of April and 5th of May. The collection days were chosen depending on the weather situation; the wind should not exceed 5 m/s either during the collection day or the day before, because the rocks where the seals rest are often exposed by waves potentially rinsing away the faeces. The faeces were sampled with a scraper and kept in plastic bags in the freezer at -20°C. Additionally, subsamples for DNA analysis were sampled from each of the faeces with a *Canvax Stool Sample*

Collection & Stabilization Kit pre-filled with 8 ml of DNA Stabilization Buffer. The DNA-samples have not been analysed yet and will therefore not be described further in this thesis.

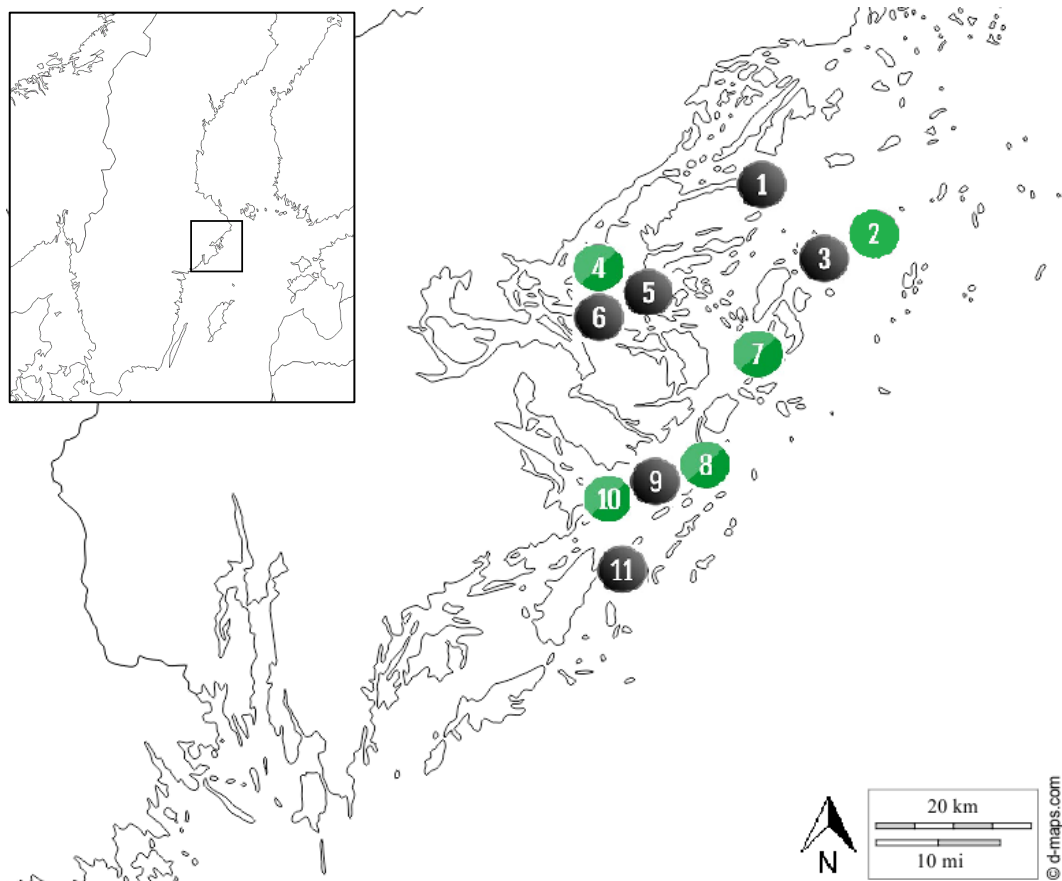


Figure 2. A map over Stockholm archipelago and the seal scat sampling areas, with green symbols denoting areas where scats were found (number 2, 4, 7, 8 and 10) and black symbols where no scats were found. 1. Östra Lagnö, 2. Angödrommen, 3. Småskäret, 4. Valöarna, 5. Allmäningsgrund, 6. Stinagrund, 7. Jällögrund, 8. Knallarna, 9. Nämdebåden, 10. Pannkaksgrunden, 11. Trollhättsgrunden. Map source: d-maps.com.

Additionally, faeces collected from Stockholm Archipelago around Angödrommen in May and October 2016 and in September and October 2017 were analysed (Figure 2, Symbol 2). These samples had been collected using the same method as described above. Since the collection, the faeces samples have been stored in the freezer with ethanol and the DNA-samples with buffer. As above, the DNA-samples have not been analysed yet and will therefore not be described further in this thesis.

To sort out the hard part structures used to identify the species, the faeces were put into bottles with water and detergents for each sample separately. Under a microscope, the structures were identified using archived materials from SLU (Institute of Coastal Research), an identification key to otoliths (Härkönen 1986) and the software Bone Base Baltic Sea (Von Busekist 2004). The number of

individuals per species were counted in regard to the number of right and left side otoliths, right and left side spines (three-spined stickleback), chewing pads or pharyngeal teeth (cyprinids). All otoliths were then measured under a microscope and the level of erosion was assessed according to Tollit et al. (1997), where class 1 was minimally eroded with distinct shapes and a clear sulcus, class 2 had still a distinct sulcus but were eroded showing smoother shapes and class 3 were greatly eroded with rounded shapes and almost no sulcus (Figure 3). If no otoliths were found in the sample but other hard part structures were identifiable (such as scales, spines and pharyngeal teeth), the species were counted as one individual, which was assigned the mean length and biomass of the species in the whole sample.

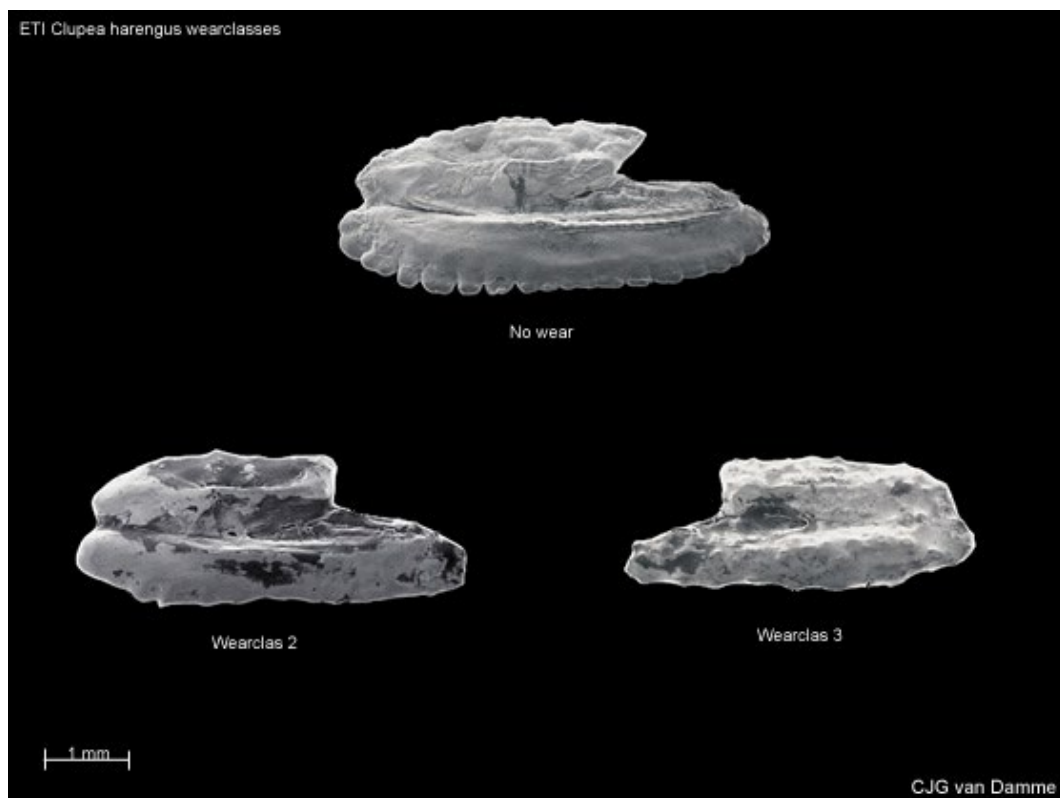


Figure 3. Otoliths from herring (*Clupea harengus*) showing the different erosion classes 1-3 used to describe the sampled otoliths and to back-calculate the original size. Figure: (Leopold et al. 2001)

To compensate for the assumed total erosion of otoliths through digestion, numerical correction factors from Lundström et al. (2007) were used for each species (Table 2). The numerical correction factors were calculated from otolith size and otolith recovery rates from experiments with captive seals (Tollit et al. 1997; Bowen 2000). The number of otoliths of each species in a sample was multiplied with species-specific numerical correction factor without caring for right or left otoliths.

Table 2. Numerical correction factors from Lundström et al. (2007) were used to multiply each otolith to correct for biases caused by total erosion of otoliths through digestion.

Scientific name	Common name	Numerical correction factors
<i>Gobiidae</i>	Gobies	6.3
<i>Sprattus sprattus</i>	Sprat	5.9
<i>Zoarces viviparus</i>	Eelpout	5.4
<i>Clupea harengus</i>	Herring	3.7
<i>Perca fluviatilis</i>	Perch	1.8
<i>Coregonus lavaretus</i>	Common whitefish	1.7
<i>Esox lucius</i>	Pike	1.4
<i>Cyprinidae</i>	Cyprinids	1.3
<i>Gadus morhua</i>	Cod	1.2

I used regression equations from the Baltic Sea to calculate the fish length from the size of the otoliths for pike (Engstedt et al. 2010), gobies (*Gobiidae*) and perch (Sapota & Dąbrowska 2019) and, herring and sprat (Lundström et al. 2007). Furthermore, I used the regression equations from Härkönen (1986) for common whitefish (*Coregonus lavaretus*) and from Leopold et al. (2001) for cod, cyprinids and eelpout. For otoliths and other hard part structures only identified to family level of cyprinids or gobies, I applied the regression equations for roach (*Rutilus rutilus*) and black goby (*Gobius niger*), as these were the most common species of the families in the diet samples.

The erosion class 1-3 was then used to back-calculate the original size of the otoliths, with size correction factors, and to correct for the assumed erosion through digestion (Tollit et al. 1997). The size correction factors are based on the ratio between the otolith sizes in erosion classes 1-3. I used the size correction factors that Lundström et al. (2007) estimated for the most abundant species in their study; herring, sprat and common whitefish (Table 3). For the rest of the species, an average of the three species was used. Then, to calculate weight from length for each species, I used SLU's length-weight relationships based on data from KUL.

Table 3. Size correction factors from Lundström et al. (2007) were used to multiply each otolith to correct for biases caused by erosion of otoliths through digestion.

Species	Otolith width Erosion class			Otolith length Erosion class		
	1	2	3	1	2	3
Herring	1.00	1.08	1.32	1.00	1.07	1.23
Sprat	1.00	1.09	1.23	1.00	1.10	1.32
Common whitefish	1.00	1.04	1.26	1.00	1.05	1.33
Average	1.00	1.07	1.27	1.00	1.07	1.29

Apart from grey seal diet analysis of faeces, five stomachs and intestines collected by hunters (3) and from seals found dead (2) were also used for the diet analysis. One from the Swedish Museum of Natural History (found close to Gålö, Stockholm), and the other four from different private persons (one found close to

Öregrund, Uppsala and three shot close to Östhammar, Uppsala). The stomachs and intestines were opened and rinsed, whole prey was identified and length measured, and the hard part structures were sorted out and identified under the microscope using the same method as described above for the faecal samples. No DNA was sampled.

2.2.2. Grey seal abundance data

To show the development of the abundance of grey seals during the 21st century in the Baltic Sea, data from Swedish national annual seal counts was used (data from 2003-2019 was downloaded from Sharkweb (*Swedish Agency for Marine and Water Management* and *Swedish Meteorological and Hydrological Institute*); data from 2020 was shared by M Ahola 2020 at NRM). Since year 2000, the survey is done internationally across the Baltic Sea (Finland, Estonia, Russia, Sweden) every late May-early June when the grey seal is spending more time ashore for moulting. Each haul-out site is surveyed 2-3 days each year and the date with the highest count per county was used for the analysis, with the assumption that the grey seals were not moving across counties between the survey days.

To estimate the grey seal density and be able to compare the counties, the abundance was divided with each county's water surface area from land out to the baseline, which defines the outermost part of the archipelago. The counts are estimated to cover 70-85% of the grey seal population in the Baltic Sea (Hiby et al. 2007), and thus do not represent the total number of seals in the population but rather look at trends in the population.

2.3. Statistical analyses

All statistical analyses were done with R 4.0.1 (R Core Team 2020). I log-transformed data as necessary to better fit the assumptions of normality and homoscedasticity and visually inspected the residuals of the models, and found them to meet model assumptions in a satisfactory way. I used the R-function 'glm' (generalised linear models) to correlated changes in pike CPUE and pike maximum size with grey seal density across years. 'County' was included as a fixed factor. Significance of fixed factors was assessed from an ANCOVA (R-function 'Anova' in package 'car' by Fox & Weisberg (2019)). Interaction terms between seal abundance and county were included in the model but removed if non-significant ($p > 0.1$)

In the cases where there was a significant interaction term between seal abundance and County I ran the same model (without county as a fixed factor) for each county separately.

To show how much of the variation was explained by the fixed factors, adjusted R-square and partial R-square values were calculated using the R-function 'rsq' and 'rsq.partial' in the 'rsq'-package (Zhang 2020). I visualized the data using 'ggplot2'-package v3.3.2 was used (Wickham 2016).

3. Results

3.1. Pike

3.1.1. Fish monitoring

During 2003-2020, the CPUE of pike decreased in the Baltic Sea, and there was no interaction between Year and County (Table 4). All counties assessed in this study exhibited a significant decline in CPUE for pike smaller than 40 cm ($p < 0.05$, Figure 4A) as well as for pike larger than 40 cm ($p < 0.05$, Figure 4B), except for Blekinge ($p = 0.74$) and Södermanland County ($p = 0.054$, Figure 4B).

Table 4. Results from the general linear models conducted with catch per unit effort for pike smaller and larger than 40 cm as the response variable, and year and county as the predictor variables.

Model	df	R ²	R ² partial	Parameter	p-value	F-value
<40 cm	86	0.81	0.55	County	<0.001	17
				Year	<0.001	149
				County × Year	0.48	0.75
≥40 cm	86	0.67	0.58	County	<0.001	20
				Year	<0.001	16
				County × Year	0.63	0.65

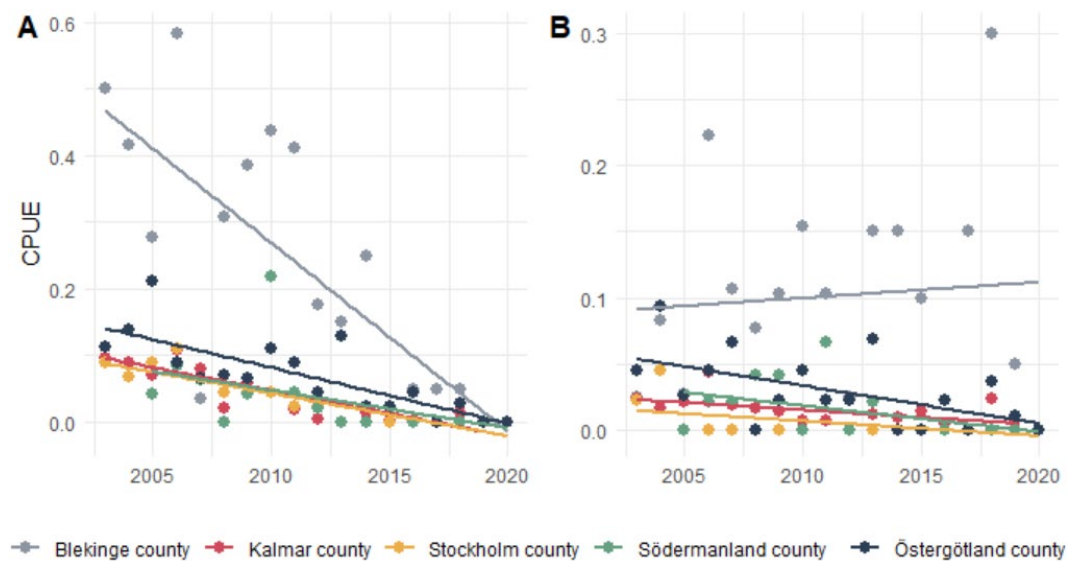


Figure 4. Catch per unit effort (CPUE) of pike caught in fish monitoring during 2003-2020; A<40 cm, B≥40 cm in the different counties.

3.1.2. Fishing competitions

The length of the largest pike caught in fishing competitions did not change during 2003-2020 (Figure 5A, Table 5), and there was no interaction between County and Year (Table 5) There was no data available for Södermanland County.

For the length of the five largest pike, there was an interaction between County and Year (Table 5). The mean length of the five largest pike decreased in Stockholm County during 2003-2020 ($p<0.001$, Figure 5B) while it was stable in Blekinge County ($p=0.30$, Figure 5B). There was no corresponding data available for Kalmar, Södermanland or Östergötland County.

Table 5. Results from general linear models conducted with The largest pike and The five largest pike as response variable, and year and county as predictor variables.

Model	df	R ²	R ² partial	Parameter	p-value	F-value
The largest pike	44	0.60	0.40	County	<0.01	6.5
				Year	0.79	5.4
				County × Year	0.43	0.92
The five largest pike	28	0.84	0.68	County	<0.001	24
				Year	<0.001	38
				County × Year	<0.01	8.9

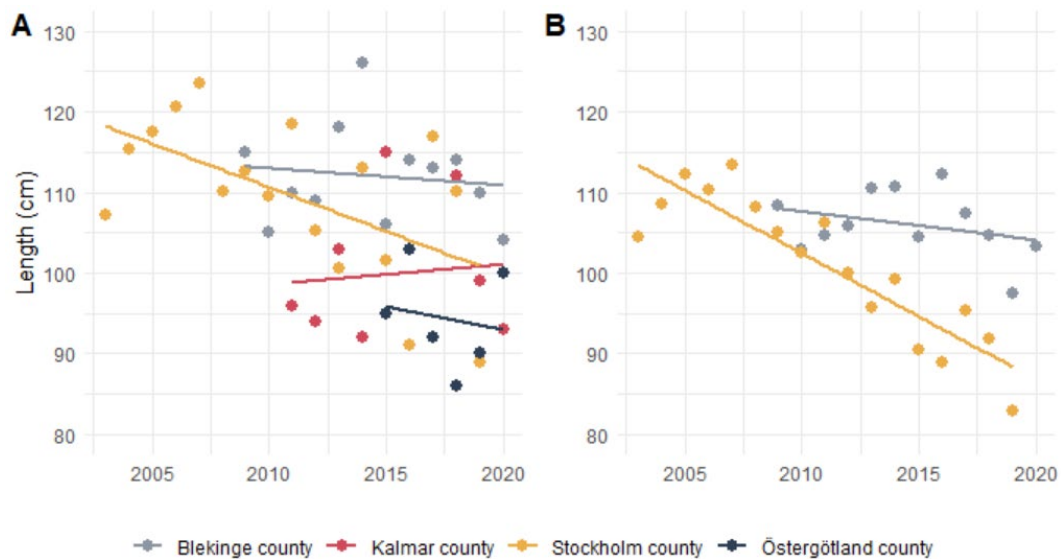


Figure 5. Differences in length (cm) of pike caught in fishing competitions during 2003-2020 for; A=Mean length of the largest pike, B=Mean length of the five largest pike, separated into counties.

3.1.3. Case study: Värtan cup

During 2003-2018, the number of pike caught per team in the fishing competition Värtan cup decreased significantly, from almost one pike over 75 cm per team in

mid 2000-ies to only one per seven teams catching a pike over the minimum size in 2018 ($F=38$, $p<0.001$, $df=15$, $R^2=0.71$, Figure 6).

The length of the largest pike caught during Värtan cup has fluctuated, but decreased significantly from around 120 cm in the beginning of 2000s, to around 100 cm in the end of 2010s ($F=7.0$, $p<0.05$, $df=16$, $R^2=0.27$, Figure 7). Also the mean length of the five largest pike caught during Värtan cup decreased significantly from around 115 cm the beginning of 2000s, to around 90 cm the end of 2010s ($F=55$, $p<0.001$, $df=16$, $R^2=0.77$, Figure 7).

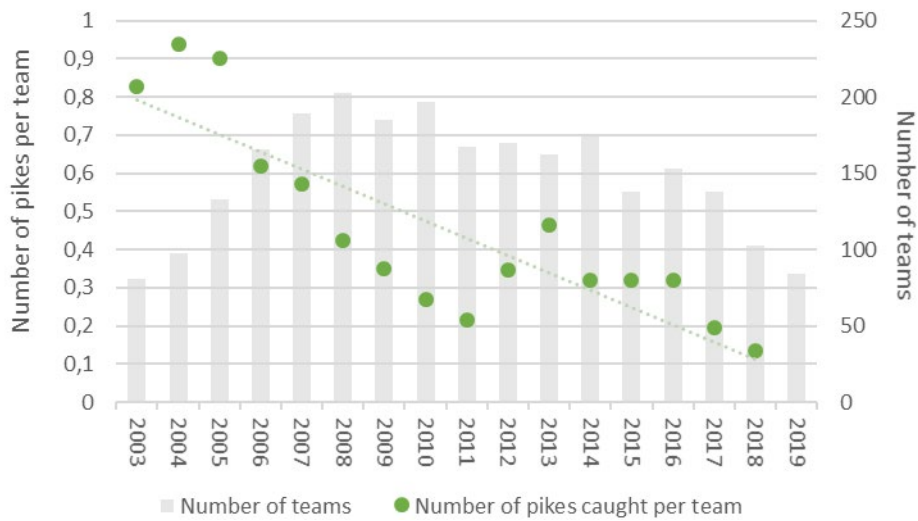


Figure 6. Mean number of pike over 75 cm length caught per team (green dots) with a regression line (green line) and number of teams (grey bars) annually from 2003-2019 caught during Värtan cup in Stockholm archipelago. 2019 was excluded because the minimum length was changed from 75 cm to 65 cm.

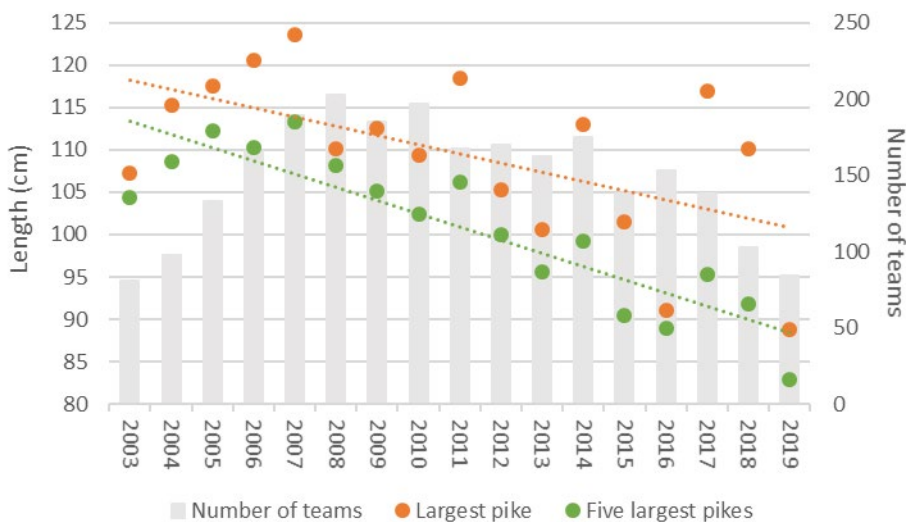


Figure 7. Length of the largest pike (orange dots), mean length of the five largest pike (green dots) and number of teams (grey bars) caught during Värtan cup in Stockholm archipelago during 2003-2019. Dashed lines show regressions.

3.2. Grey seal

3.2.1. Diet analyses

Scats were found at four of the eleven surveyed haul-out sites in 2020. A total of 17 grey seal faecal samples were found (Figure 2, green numbers). Additionally, 35 faecal samples collected from Stockholm archipelago in 2016-2017 were analysed. Also, four grey seal stomachs and intestines from Uppsala County and one from Stockholm County were examined. Totally within the 57 samples, 657 otoliths were found from 11 different taxa. Two of these otoliths were not possible to identify because of extensive erosion.

Hard-part structures from pike were found in 20% of the samples, and those from perch, herring and cyprinids were found in 54%, 39% and 28%, respectively (Figure 8). Sprat, gobies, three-spined stickleback, eelpout, cod and common whitefish occurred in less than 7% of the samples.

Out of the 657 otoliths, 24 were from pike, which was the fourth most abundant species after herring (n=381), perch (n=192) and cyprinids (n=28). When applying numerical correction factors (Table 2), which correct abundance estimates for the total loss of otoliths due to erosion in the seal stomachs, there was a total of 1994 otoliths. Pike was then the sixth most abundant species with 34 otoliths after herring (n=1428), perch (n=346), gobies (n=57), sprat (n=47) and cyprinids (n=39).

For the weight proportion, pike (20%) was the third most important prey species for grey seal after perch (46%) and herring (24%) (Figure 9).

When applying size correction factors (Table 3), correcting for the erosion of otoliths through digestion, the length of pike ranged from 28 cm to 73 cm (median=41 cm, Figure 10), whereas the whole sample ranged from a 5.8 cm three-spined stickleback to the 73 cm pike (median=19 cm, Figure 11). The length of perch ranged from 12 cm to 42 cm (median=22 cm) and herring ranged from 10 cm to 30 cm (median=19 cm).

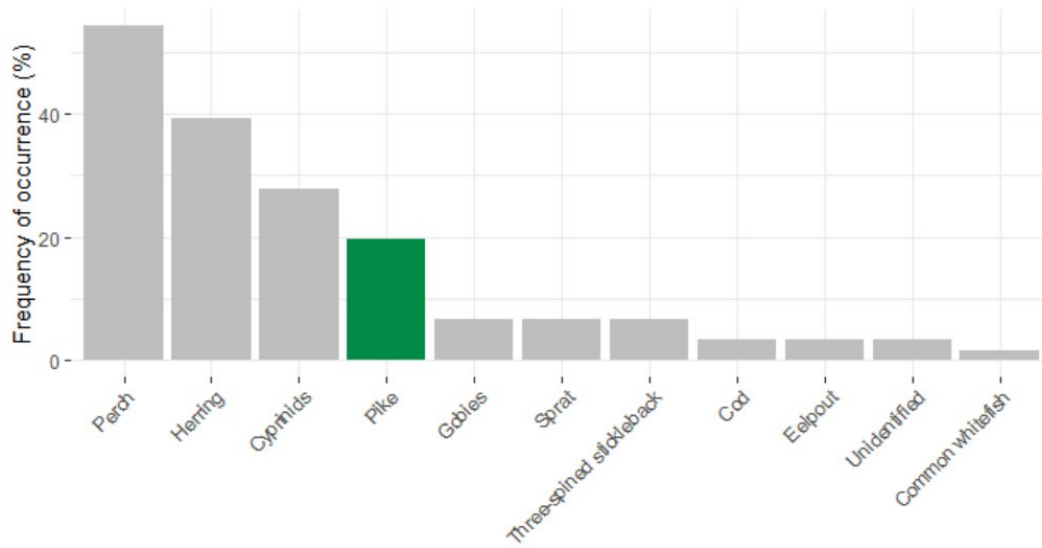


Figure 8. Frequency of occurrence (number of samples that contains the species divided by the total number of samples) for the different species found in the grey seal diet.

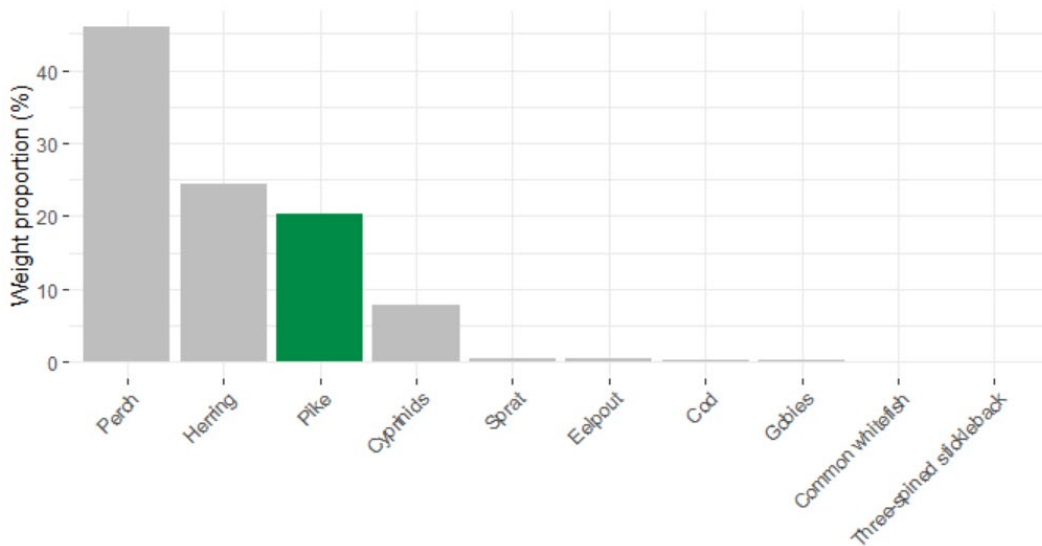


Figure 9. The weight proportion of the species found in the grey seal diet, calculated from otolith size.

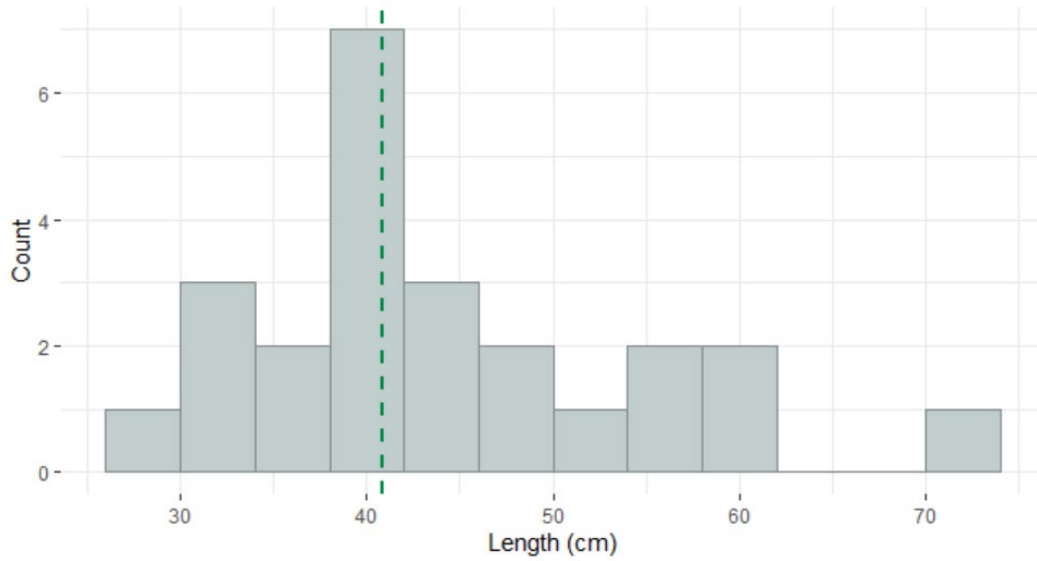


Figure 10. The length distribution of pike found in the grey seal diet, calculated based on otolith width, divided in 4 cm length classes. The dashed line describes the calculated median length of pike found in the samples.

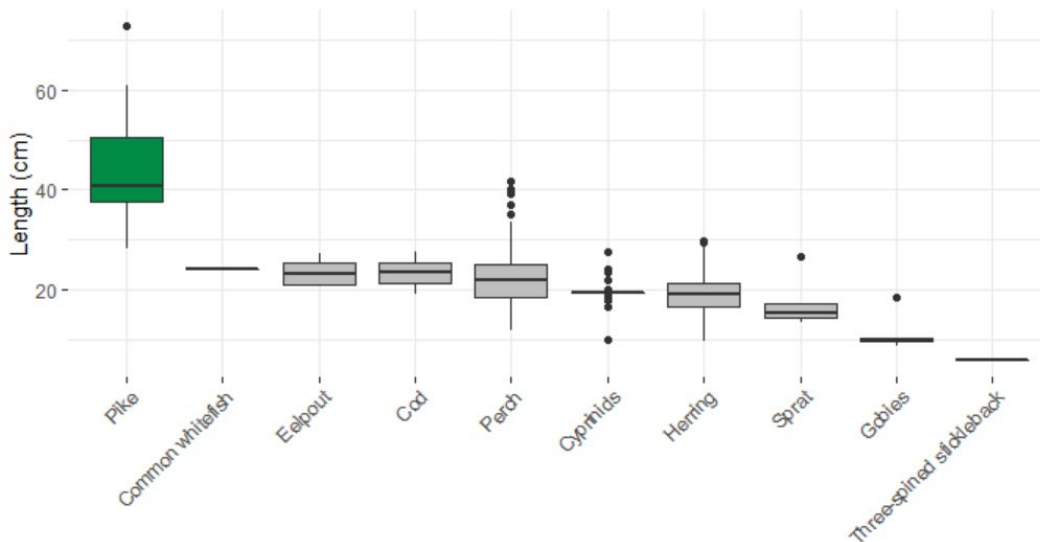


Figure 11. The length distribution of the different species found in the grey seal diet, calculated based on otolith width. The horizontal line describes the median length, the box shows the interquartile range, the vertical line shows the data range excluding outliers and the points show potential outliers.

3.2.2. Grey seal abundance data

The density of counted grey seals increased significantly in all counties except Kalmar during 2003-2020 ($F=6.8$, $p<0.001$ for County \times Year, Figure 12). In Kalmar County the density increase was marginally insignificant ($p=0.058$ for Year). The density of counted grey seals had the greatest rate of increase in Södermanland County (slope=0.20) followed by Östergötland County (slope=0.11).

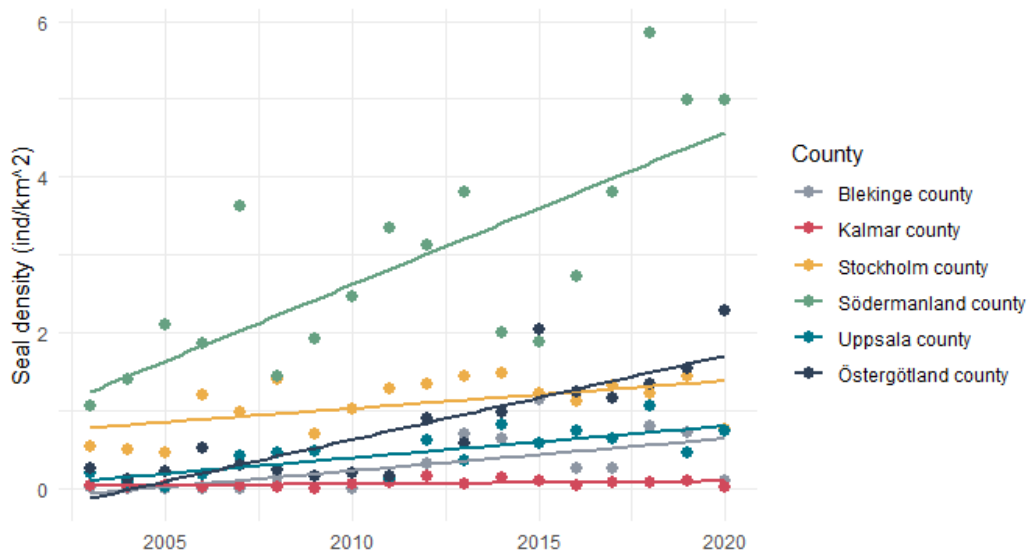


Figure 12. The density of grey seals by county in 2003-2020, based on the national survey performed in May-June each year.

3.3. Analyses of the relationship between pike and seal

All counties combined, there was a negative relationship between CPUE for small pike and seal density, with seal density explaining 29% of the variation (Table 6; Figure 13A), and there was no interaction between County and Seal density (Table 6).

For larger pike, there was a tendency for interaction between County and the log-transformed seal density (Table 6). Blekinge was the only county that showed no relationship between CPUE and seal density ($p=0.25$, Figure 13B). When excluding Blekinge from the analysis, there was a negative relationship between CPUE for larger pike and seal density, with seal density explaining 34% of the variation (Table 6).

Table 6. Results from general linear models conducted with catch per unit effort for pike smaller and larger than 40 cm as response variable, and county and seal density as predictor variables.

Model	df	R ²	R ² partial	Parameter	p-value	F-value
<40 cm	86	0.46	0.29	County	<0.001	8
				log(Seal density)	<0.001	34
				County × log(Seal density)	0.24	1.4
≥40 cm	86	0.47	0.28	County	<0.001	9
				log(Seal density)	0.97	0.001
				County × log(Seal density)	0.082	2
≥40 cm without Blekinge	68	0.40	0.33	County	<0.001	11
				log(Seal density)	<0.001	32
				County × log(Seal density)	0.89	0.21

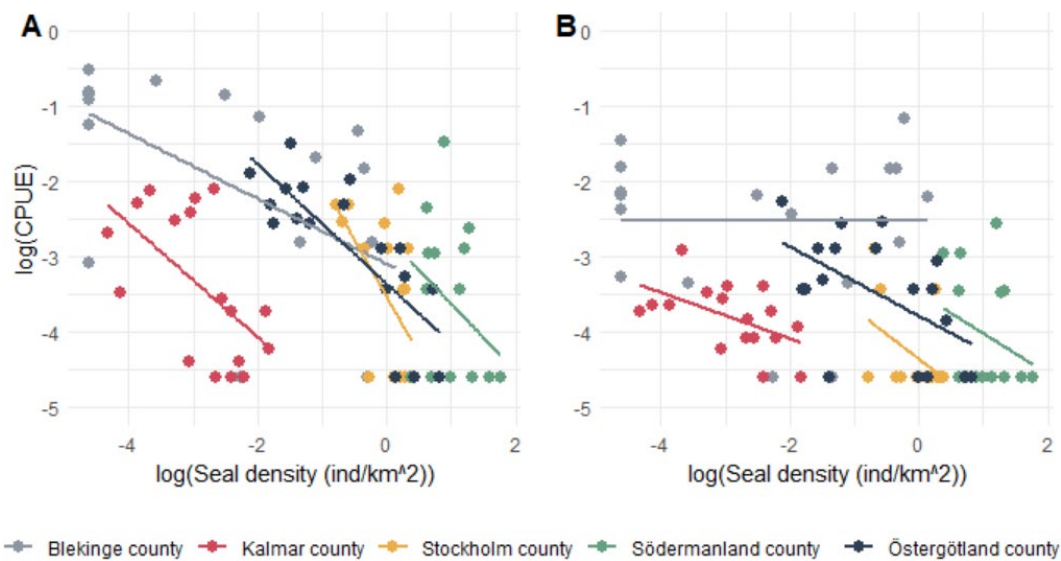


Figure 13. Log-transformed catch per unit effort (CPUE) of pike caught in fish monitoring during 2003-2020; A < 40 cm, B ≥ 40 cm compared with log-transformed grey seal density, separated into counties.

In the fishing competition data there was no relationship between mean length of *The largest pike* and grey seal density (Table 7, Figure 14A), and there was no interaction between County and Seal density (Table 7). Between *The five largest pike* and grey seal density there was a significant negative relationship, with seal density explaining 15% of the variation (Table 7, Figure 14B), and there was no interaction between County and Seal density (Table 7).

Table 7. Results from general linear models conducted with *The largest pike* and *The five largest pike* as response variable, and county and seal density as predictor variables.

Model	df	R ²	R ² partial	Parameter	p-value	F-value
The largest pike	44	0.40	0.40	County	<0.001	8.8
				log(Seal density)	0.67	0.18
				County × log(Seal density)	0.23	1.4
The five largest pike	28	0.25	0.00034	County	0.93	0.0088
				log(Seal density)	<0.05	4.6
				County × log(Seal density)	0.10	2.9

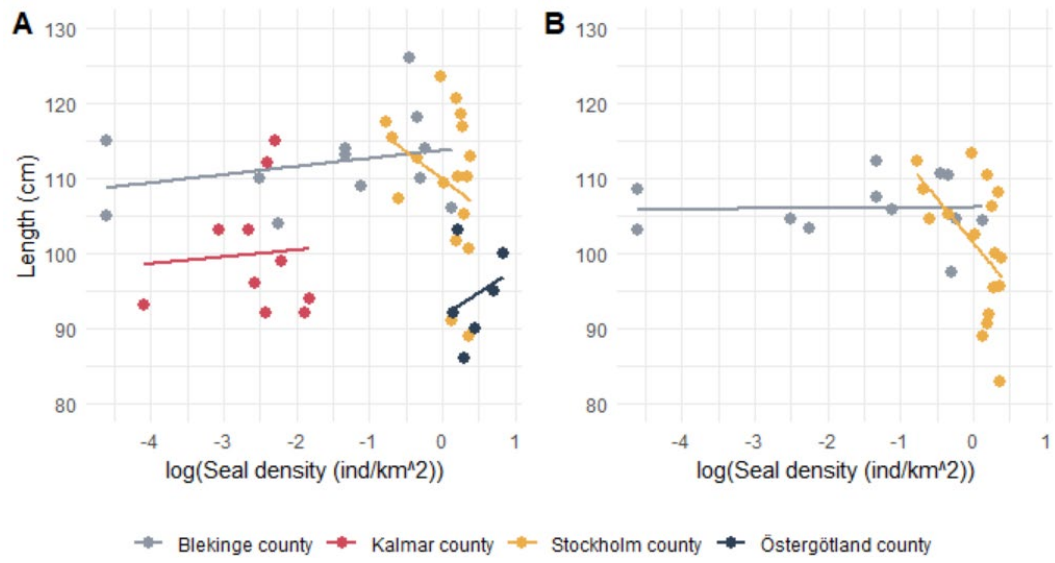


Figure 14. Differences in length (cm) of pike caught in fishing competitions in relation to log-transformed grey seal density per county during 2003-2020 for; A=Mean length of the largest pike, B=Mean length of the five largest pike.

4. Discussion

This study shows that the abundance of pike along the Swedish Baltic Proper coast has declined during fish monitoring data 2003-2020 both regarding pike smaller and larger than 40 cm, except for larger pike in Blekinge and Södermanland. In 2019, the mean catch per unit effort of pike was on average 6% of the mean in 2003. Also, in the longest time series from pike fishing competitions, the catch of pike larger than 75 cm has declined in Stockholm County. Altogether, these results indicate a general declines in the pike population in the western Baltic Sea from 2000.

Along with declining pike abundances, the maximum size of pike in competitions has decreased in Stockholm County by more than 20 cm (~5 kg), from around 120 cm (~11 kg) to 100 cm (~6 kg), while the maximum size has been stable in the other investigated counties. In Blekinge, which also has a longer time series from pike fishing competitions, there was no decline, which matches with the pattern from the fish monitoring data for larger pike in Blekinge. Blekinge has had the strongest populations of pike, which may explain why the larger pike is still abundant in the county.

During the same period, the abundance of grey seal has increased significantly in all investigated counties, except Kalmar where it was marginally significant. There was a strong negative relationship between the abundance of grey seal and the catch of both smaller and larger pike in the coastal fish monitoring programme, except for Södermanland County and larger pike in Blekinge County (Figure 13). In Södermanland, the catches of pike has been low compared to the other counties, which may possibly explain why there was no relationship between pike abundance and grey seal abundance. There was a negative relationship between the abundance of grey seal and the maximum size of pike in pike fishing contests in Stockholm County. This indicates that the pike populations especially in Stockholm County, may be affected by the increasing grey seal population.

This study is based on correlations over time, and it is always statistically challenging to infer interactions between species from long-term trends in population data. Thus, this study cannot establish any causal relationship between pike and seals as there is always risk of spurious correlations. However, data was

split up on a county level with independent dynamics of pike (Wennerström et al. 2016; Östman et al. 2017) and partly independent dynamics of seals (Figure 12). Despite the partly independent dynamics, the pattern between pike and seal is similar between counties with the exception of Kalmar that had a generally lower pike abundance given the seal abundance. For pike larger than 40 cm, Blekinge stands out with consistent abundance over time. Notably, seal densities in Blekinge have been high only during the last years of the study period. The similar pattern in different counties strengthen the conclusion that grey seals may impact pike and is not a results of a spurious correlation. In addition, adjusted r^2 -values for seal abundance was relatively high, often above 50% supporting my conclusion that seals have an impact on pike population abundance.

When examining grey seal diet from the haul-out sites in the inner and central part of Stockholm archipelago, pike appeared in 20% of the samples and was the fourth most abundant species after herring, perch and cyprinids. Pike also constitutes 20% of the diet by weight, after perch and herring. Probably, these proportions may be underestimated because seal may not always consume the head of larger fish (Skóra et al. 2014 in Keszka et al. 2020; observations from the project Refisk and fishing guides). Thus, if a grey seal has eaten only the soft parts of the larger pike, this would not be accounted for. This complicates the manual diet analysis and indicates that when looking for pike in seal scats and stomachs, a DNA-analysis would probably show a more accurate picture of the content. What can be confirmed, is that pike is an important prey species for grey seal foraging in the inner and central parts of the archipelago.

The diet analysis of grey seal scat and stomach content, however, is a rough estimate of the actual diet (Lundström et al. 2007, 2010). There are many potential sources of error such as erosion and sampling methods that only cover when the fish is eaten as a whole. The erosion was corrected for using size correction factors and numerical correction factors to calculate the original size and number of otoliths in each sample (Tollit et al. 1997; Lundström et al. 2007, 2010). Also, pike length estimated from otolith width measured between 28-73 cm and the mean length was 44 cm.

The diet samples in this study were sampled in the inner and central parts of the archipelago, which differs from other grey seal diet studies (Lundström et al. 2007; Strömberg et al. 2012; Hansson et al. 2018). When comparing the results, the proportion of pike in the diet of grey seal foraging in the inner and central archipelago was 20%, compared to less than 5% in the outer archipelago (Lundström et al. 2007; Strömberg et al. 2012; Hansson et al. 2018). In a report by Bergström et al. (2016), they also point out the grey seal as a predator of pike probably affecting the population negatively.

As the grey seal population has increased in general, the abundance of grey seal in the inner and central parts of the archipelago, which also is the pike's core habitat, has probably also increased. Generally in the Baltic Sea, the condition of grey seal is assessed to be poor and the species does not achieve good nutritional status in assessments by HELCOM (2018a). Results from Kauhala et al. (2017) indicated that grey seal in the Baltic Sea may be food limited, which also can force the grey seal further into the archipelago.

Seals are not the only predators on pike. Also, the cormorant may feed on especially smaller pike (Östman et al. 2013). Another species that may impact the pike population negatively from increasing abundance is the three-spined stickleback, through predator-prey reversal (Bergström et al. 2015; Byström et al. 2015; Nilsson et al. 2019; Eklöf et al. 2020). Three-spined stickleback can forage on juvenile pike, and thereby reduce the reproductive outcome of pike. Predation by sticklebacks will clearly only directly affect smaller pike, but loss of recruits may translate in reduced abundance of larger pike after a couple of years. Fishing will mainly affect larger pike. Recreational fishing is a contributing factor for fish population declines (Lewin et al. 2006; Bergström et al. 2016; Hansson et al. 2018) and may also affect the population of pike negatively. After angling was made open access along the Swedish coast in 1985, the catches of larger pike soon declined, likely as a consequence of the extensive catch-and-kill fisheries (Bergström et al. unpublished). In 2010, new restrictions were implemented regarding size and bag limits for pike, and since then, the majority of the fishermen are applying catch and release (Thörnqvist et al. 2006; Ferter et al. 2013). However, the populations of pike are still decreasing. Hansson et al. (2018) estimated that fishing in subdivision 27 (which covers most of the analysed area) accounted for almost 30% of the total removal of pike during 2012-2013, dominated by recreational fishing.

Although catches of pike in gillnet fishing are generally low because of its passive behaviour, all available trends are indicating declining abundances. To support the fish monitoring data for the pike population, usage of citizen science and e.g. data from fishing competitions would be useful. Pike angling data has been found useful for monitoring abundance trends and evaluating the effects of management measures (Edgren 2005; Lehtonen et al. 2009; Niemi 2020; Bergström et al. unpublished). Fishing competitions for pike are arranged all over the year in Sweden, both in the coastal areas and in lakes. In some parts of the archipelago, the fishing competitions accounts for a fourth of the total estimated recreational catch of pike (County Administrative Board, 2019). In Stockholm and Blekinge, there are competition data available from the beginning of 2000s with the same competition rules and fishing area, which makes the trends more comparable over time than in other counties. Consistent competition rules are important to be able to use the collected data in research. A strategy to share catch data when arranging fishing

competitions could be letting each of the County Administrative Boards to handle a permission for arranging fishing competitions, with an obligatory data share. The important measures are date, fishing hours, fishing area, minimum length (preferably the same for all competitions, at least county-wise), length of registered pike, number of teams and number of participants. Some competitions have even created an online application for registration of pike, so maybe it is possible to design an online application that transfers all collected data automatically to a database. Then it is also possible to use GPS-data of catches. Photo-identification of each pike is required for approved registration of the catches in the competitions, which could be used for identification of individual pike (Kristensen et al. 2020; Lavenius 2020).

Taken together, the results from this study indicate that the increasing grey seal population is associated with the negatively development of pike population in the archipelagos of the western Baltic Sea. Management of coastal fish has traditionally only taken the effects of fishing into account. The results of this thesis emphasize the importance of a transition towards an ecosystem-based fisheries management, where the effects of increasing populations of top predators are also taken into account in the assessments, to maintain viable populations of fish.

References

- Ahola, M. (2020). Data from the grey seal survey 2020 in the Baltic Sea, Swedish Museum of Natural History. Unpublished data. Swedish Museum of Natural History.
- Arlinghaus, R., Klefoth, T., Gingerich, A.J., Donaldson, M.R., Hanson, K.C. & Cooke, S.J. (2008). Behaviour and survival of pike, *Esox lucius*, with a retained lure in the lower jaw: CONSEQUENCES OF RETAINED LURES ON PIKE. *Fisheries Management and Ecology*, 15 (5–6), 459–466. <https://doi.org/10.1111/j.1365-2400.2008.00625.x>
- Bergman, A. (1999). Health condition of the Baltic grey seal (*Halichoerus grypus*) during two decades. Gynaecological health improvement but increased prevalence of colonic ulcers. *APMIS: acta pathologica, microbiologica, et immunologica Scandinavica*, 107 (3), 270–282. <https://doi.org/10.1111/j.1699-0463.1999.tb01554.x>
- Bergman, A. & Olsson, M. (1985). Pathology of Baltic grey seal and ringed seal females with special reference to adrenocortical hyperplasia: Is environmental pollution the cause of a widely distributed disease syndrome? *Finnish Game Research*, (44), 47–62
- Bergström, U., Fredriksson, R., Boström, M., Florin, A.-B., Lundström, K. & Andersson, H.C. (2016). *Ett fiskefritt område för skydd av gös, gädda och abborre i Stockholms skärgård. In: Bergström m fl 2016. Ekologiska effekter av fiskefria områden i Sveriges kust- och havsområden.* (Aqua reports, 2016:20). Department of Aquatic Resources.
- Bergström, U., Olsson, J., Casini, M., Eriksson, B.K., Fredriksson, R., Wennhage, H. & Appelberg, M. (2015). Stickleback increase in the Baltic Sea – A thorny issue for coastal predatory fish. *Estuarine, Coastal and Shelf Science*, 163, 134–142. <https://doi.org/10.1016/j.ecss.2015.06.017>
- Bowen, W.D. (2000). Reconstruction of pinniped diets: accounting for complete digestion of otoliths and cephalopod beaks. *Canadian Journal of Fisheries and Aquatic Sciences*, 57 (5), 898–905. <https://doi.org/10.1139/f00-032>
- Brown, R., Wright, B., Riemer, S. & Laake, J. (2006). Trends in abundance and current status of harbor seals in Oregon: 1977–2003. *Marine Mammal Science*, 21, 657–670. <https://doi.org/10.1111/j.1748-7692.2005.tb01258.x>
- Burkholder, A. (1992). *Mortality of Northern Pike Captured and Released with Sport Fishing Gear.* (Fishery Data Series, 92–3). Anchorage, Alaska: Alaska Department of Fish and Game, Division of Sport Fish.
- Byström, P., Bergström, U., Hjalten, A., Ståhl, S., Jonsson, D. & Olsson, J. (2015). Declining coastal piscivore populations in the Baltic Sea: Where and when do sticklebacks matter? *AMBIO*, 44 (S3), 462–471. <https://doi.org/10.1007/s13280-015-0665-5>
- Clapham, P. & Baker, C. (2009). Whaling, Modern. *Encyclopedia of Marine Mammals*, 1239–1243. <https://doi.org/10.1016/B978-0-12-373553-9.00283-2>
- DuBois, R., Margenau, T., Stewart, R., Cunningham, P. & Rasmussen, P. (1994). Hooking Mortality of Northern Pike Angled through Ice. *North American*

- Journal of Fisheries Management*, 14, 769–775.
[https://doi.org/10.1577/1548-8675\(1994\)014<0769:HMONPA>2.3.CO;2](https://doi.org/10.1577/1548-8675(1994)014<0769:HMONPA>2.3.CO;2)
- Edgren, J. (2005). *Effects of a no-take reserve in the Baltic Sea on the top predator, northern pike (Esox lucius)*. (Degree project). Stockholm University.
- Eklöf, J.S., Sundblad, G., Erlandsson, M., Donadi, S., Hansen, J.P., Eriksson, B.K. & Bergström, U. (2020). A spatial regime shift from predator to prey dominance in a large coastal ecosystem. *Communications Biology*, 3 (1).
<https://doi.org/10.1038/s42003-020-01180-0>
- Engstedt, O., Stenroth, P., Larsson, P., Ljunggren, L. & Elfman, M. (2010). Assessment of natal origin of pike (*Esox lucius*) in the Baltic Sea using Sr:Ca in otoliths. *Environmental Biology of Fishes*, 89 (3–4), 547–555.
<https://doi.org/10.1007/s10641-010-9686-x>
- Estes, J.A., Doak, D.F., Springer, A.M. & Williams, T.M. (2009). Causes and consequences of marine mammal population declines in southwest Alaska: a food-web perspective. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364 (1524), 1647–1658.
<https://doi.org/10.1098/rstb.2008.0231>
- Ferter, K., Weltersbach, M.S., Strehlow, H.V., Vølstad, J.H., Alós, J., Arlinghaus, R., Armstrong, M., Dorow, M., De Graaf, M., Van Der Hammen, T., Hyder, K., Levrel, H., Paulrud, A., Radtke, K., Rocklin, D., Sparrevoorn, C.R. & Veiga, P. (2013). Unexpectedly high catch-and-release rates in European marine recreational fisheries: implications for science and management. *ICES Journal of Marine Science*, 70 (7), 1319–1329.
<https://doi.org/10.1093/icesjms/fst104>
- Fox, J. & Weisberg, S. (2019). *An R Companion to Applied Regression*. Third. Thousand Oaks CA: Sage.
<https://socialsciences.mcmaster.ca/jfox/Books/Companion/> [2021-01-06]
- Gero, S. & Whitehead, H. (2016). Critical Decline of the Eastern Caribbean Sperm Whale Population. (Li, S., ed.) *PLOS ONE*, 11 (10), e0162019.
<https://doi.org/10.1371/journal.pone.0162019>
- Gibson, R., Atkinson, R. & Gordon, J. (eds.) (2006). *Oceanography and Marine Biology: An Annual Review*. CRC Press.
<https://doi.org/10.1201/9781420006391>
- Gormley, A.M., Slooten, E., Dawson, S., Barker, R.J., Rayment, W., du Fresne, S. & Bräger, S. (2012). First evidence that marine protected areas can work for marine mammals: *Protected areas for marine mammals*. *Journal of Applied Ecology*, 49 (2), 474–480. <https://doi.org/10.1111/j.1365-2664.2012.02121.x>
- Hansson, S., Bergström, U., Bonsdorff, E., Härkönen, T., Jepsen, N., Kautsky, L., Lundström, K., Lunneryd, S.-G., Ovegård, M., Salmi, J., Sendek, D. & Vetemaa, M. (2018). Competition for the fish – fish extraction from the Baltic Sea by humans, aquatic mammals, and birds. (Hunsicker, M., ed.) *ICES Journal of Marine Science*, 75 (3), 999–1008.
<https://doi.org/10.1093/icesjms/fsx207>
- Harding, K. & Härkönen, T. (1999). Development in the Baltic grey seal (*Halichoerus grypus*) and ringed seal (*Phoca hispida*) populations during the 20th century. *Ambio*, (28), 619–627
- Harding, K.C., Härkönen, T., Helander, B. & Karlsson, O. (2007). Status of Baltic grey seals: Population assessment and extinction risk. *NAMMCO Scientific Publications*, 6, 33. <https://doi.org/10.7557/3.2720>
- Härkönen, T. (1986). *Guide to the otoliths of the bony fishes of the northeast Atlantic: with 74 tables*. Hellerup: Danbiu ApS.
- Härkönen, T. & Isakson, E. (2010). Status of harbour seals (*Phoca vitulina*) in the Baltic proper. *NAMMCO Scientific Publications*, 8, 71.
<https://doi.org/10.7557/3.2673>

- Heithaus, M.R., Frid, A., Wirsing, A.J. & Worm, B. (2008). Predicting ecological consequences of marine top predator declines. *Trends in Ecology & Evolution*, 23 (4), 202–210. <https://doi.org/10.1016/j.tree.2008.01.003>
- HELCOM (2015). *Guidelines for Coastal Fish Monitoring Sampling Methods of HELCOM*. <http://www.helcom.fi/helcom-at-work/publications>
- HELCOM (2018a). *Nutritional status of seals*. (HELCOM core indicator report)
- HELCOM (2018b). *Population trends and abundance of seals*. (HELCOM core indicator report). <https://helcom.fi/wp-content/uploads/2019/08/Population-trends-and-abundance-of-seals-HELCOM-core-indicator-2018.pdf> [2020-11-17]
- HELCOM (2018c). *Population trends and abundance of seals*. Helsinki, Finland: Baltic Marine Environment Protection Commission (Helsinki Commission - HELCOM).
- Helle, E., Olsson, M. & Jensen, S. (1976). DDT and PCB Levels and Reproduction in Ringed Seal from the Bothnian Bay. *Ambio*, 5 (4), 188–189
- Hermansson, A. (2015). *Blubber thickness variation in grey, harbour and ringed seals - A proxy for seal health and an indicator of energetic constraints*. (Master project). University of Gothenburg, Department of Biological and Environmental Sciences.
- Hiby, L., Lundberg, T., Karlsson, O., Watkins, J., Jüssi, M., Jüssi, I. & Helander, B. (2007). Estimates of the size of the Baltic grey seal population based on photo-identification data. *NAMMCO Scientific Publications*, 6, 163. <https://doi.org/10.7557/3.2731>
- ICES (2020). Working Group on Marine Mammal Ecology. <https://doi.org/10.17895/ICES.PUB.5975>
- Jeffries, S., Huber, H., Calambokidis, J. & Laake, J. (2003). Trends and Status of Harbor Seals in Washington State: 1978-1999. *The Journal of Wildlife Management*, 67. <https://doi.org/10.2307/3803076>
- Kauhala, K., Bäcklin, B.-M., Raitaniemi, J. & Harding, K.C. (2017). The effect of prey quality and ice conditions on the nutritional status of Baltic gray seals of different age groups. *Mammal Research*, 62 (4), 351–362. <https://doi.org/10.1007/s13364-017-0329-x>
- Kenyon, K.W. (1977). Caribbean Monk Seal Extinct. *Journal of Mammalogy*, 58 (1), 97–98. <https://doi.org/10.2307/1379738>
- Keszka, S., Panicz, R., Stepanowska, K., Biernaczyk, M., Wrzeczionkowski, K. & Zybała, M. (2020). Characteristics of the grey seal (*Halichoerus grypus*) diet in the Vistula River mouth (Mewia Łacha Nature Reserve, southern Baltic Sea), based on the osteological and molecular studies of scat samples. *Oceanologia*, 62 (3), 387–394. <https://doi.org/10.1016/j.oceano.2020.04.005>
- Kristensen, E., Sand-Jensen, K., Martinsen, K.T., Madsen-Østerbye, M. & Kragh, T. (2020). Fingerprinting pike: The use of image recognition to identify individual pikes. *Fisheries Research*, 229, 105622. <https://doi.org/10.1016/j.fishres.2020.105622>
- Laake, J., Lowry, M., Delong, R., Melin, S. & Carretta, J. (2018). Population growth and status of California sea lions: Status of California Sea Lions. *The Journal of Wildlife Management*, 82. <https://doi.org/10.1002/jwmg.21405>
- Lavenius, A. (2020). *Automatic identification of northern pike (Exos Lucius) with convolutional neural networks*. (Degree project). Uppsala University.
- Lehtonen, H., Leskinen, E., Selén, R. & Reinikainen, M. (2009). Potential reasons for the changes in the abundance of pike, *Esox lucius*, in the western Gulf of Finland, 1939-2007: CHANGES IN PIKE ABUNDANCE IN THE GULF OF FINLAND. *Fisheries Management and Ecology*, 16 (6), 484–491. <https://doi.org/10.1111/j.1365-2400.2009.00701.x>

- Leopold, M.F., van Damme, C.J.G., Philippart, C.J.M. & Winter, C.J.N. (2001). *Otoliths of North Sea Fish*. https://otoliths-northsea.linnaeus.naturalis.nl/linnaeus_ng/app/views/species/nsr_taxon.php?id=76743&cat=CTAB_MEDIA [2020-11-17]
- Lewin, W.-C., Arlinghaus, R. & Mehner, T. (2006). Documented and Potential Biological Impacts of Recreational Fishing: Insights for Management and Conservation. *Reviews in Fisheries Science*, 14 (4), 305–367. <https://doi.org/10.1080/10641260600886455>
- 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*, 67 (8), 1587–1595. <https://doi.org/10.1093/icesjms/fsq109>
- Lundström, K., Hjerne, O., Alexandersson, K. & Karlsson, O. (2007). Estimation of grey seal (*Halichoerus grypus*) diet composition in the Baltic Sea. *NAMMCO Scientific Publications*, 6, 177. <https://doi.org/10.7557/3.2733>
- Lundström, K., Hjerne, O., Lunneryd, S.-G. & Karlsson, O. (2010). Understanding the diet composition of marine mammals: grey seals (*Halichoerus grypus*) in the Baltic Sea. *ICES Journal of Marine Science*, 67 (6), 1230–1239. <https://doi.org/10.1093/icesjms/fsq022>
- Magera, A.M., Mills Flemming, J.E., Kaschner, K., Christensen, L.B. & Lotze, H.K. (2013). Recovery Trends in Marine Mammal Populations. (Stergiou, K. I., ed.) *PLoS ONE*, 8 (10), e77908. <https://doi.org/10.1371/journal.pone.0077908>
- Mead, J. & Mitchell, E. (2012). Atlantic Gray Whales. *The Gray Whale: Eschrichtius Robustus*, 33–53. <https://doi.org/10.1016/B978-0-08-092372-7.50008-X>
- Murphy, S., Barber, J.L., Learmonth, J.A., Read, F.L., Deaville, R., Perkins, M.W., Brownlow, A., Davison, N., Penrose, R., Pierce, G.J., Law, R.J. & Jepson, P.D. (2015). Reproductive Failure in UK Harbour Porpoises *Phocoena phocoena*: Legacy of Pollutant Exposure? (Lehmler, H.-J., ed.) *PLOS ONE*, 10 (7), e0131085. <https://doi.org/10.1371/journal.pone.0131085>
- Naturvårdsverket (2003). *Förvaltningsplan för mellanskarv och storskarv*. Stockholm: Naturvårdsverket. <http://www.naturvardsverket.se/Documents/publikationer/620-5261-6.pdf> [2020-12-26]
- Niemi, N. (2020). *Influence of reed (Phragmites australis) belts in the Baltic Sea archipelago on pike (Esox lucius) –and other coastal fish species*. (Master project). SLU Department of Aquatic Resources.
- Nilsson, J., Flink, H. & Tibblin, P. (2019). Predator–prey role reversal may impair the recovery of declining pike populations. (Prugh, L., ed.) *Journal of Animal Ecology*, 1365-2656.12981. <https://doi.org/10.1111/1365-2656.12981>
- Ohlberger, J., Schindler, D.E., Ward, E.J., Walsworth, T.E. & Essington, T.E. (2019). Resurgence of an apex marine predator and the decline in prey body size. *Proceedings of the National Academy of Sciences*, 116 (52), 26682–26689. <https://doi.org/10.1073/pnas.1910930116>
- Olsson, J. (2019). Past and Current Trends of Coastal Predatory Fish in the Baltic Sea with a Focus on Perch, Pike, and Pikeperch. *Fishes*, 4, 7. <https://doi.org/10.3390/fishes4010007>
- Östman, Ö., Boström, M.K., Bergström, U., Andersson, J. & Lunneryd, S.-G. (2013). Estimating Competition between Wildlife and Humans—A Case of Cormorants and Coastal Fisheries in the Baltic Sea. (Margalida, A., ed.) *PLoS ONE*, 8 (12), e83763. <https://doi.org/10.1371/journal.pone.0083763>

- R Core Team (2020). *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Sapota, M.R. & Dąbrowska, V. (2019). Shapes of otoliths in some Baltic fish and their proportions. *Oceanological and Hydrobiological Studies*, 48 (3), 296–304. <https://doi.org/10.2478/ohs-2019-0027>
- Schipper, J., Chanson, J., Chiozza, F., Cox, N., Hoffmann, M., Katariya, V., Lamoreux, J., Rodrigues, A., Stuart, S., Temple, H., Baillie, J., Boitani, L., Lacher, T., Mittermeier, R., Smith, A., Absolon, D., Aguiar, J., Amori, G., Bakkour, N. & Young, B. (2008). The Status of the World's Land and Marine Mammals: Diversity, Threat, and Knowledge. *Science (New York, N.Y.)*, 322, 225–30. <https://doi.org/10.1126/science.1165115>
- SLU Aqua (2020). *Fish and seafood stocks in the sea and fresh water 2019*. Department of Aquatic Resources.
- Söderberg, K., Forsgren, G. & Appelberg, M. (2004). *Samordnat program för övervakning av kustfisk i Bottniska viken och Stockholms skärgård – utveckling av undersökningstyp och indikatorer*. (2004:7). Fiskeriverket.
- Strömberg, A., Svärd, C. & Karlsson, O. (2012). *Dietstudier av gråsäl (Halichoerus grypus) i Östersjön och knobbsäl (Phoca vitulina) i Skagerrak och Kattegatt insamlade 2010*. (5:2012). Swedish Museum of Natural History.
- Suuronen, P. & Lehtonen, E. (2012). The role of salmonids in the diet of grey and ringed seals in the Bothnian Bay, northern Baltic Sea. *Fisheries Research*, 125–126, 283–288. <https://doi.org/10.1016/j.fishres.2012.03.007>
- Swedish Agency for Marine and Water Management (2019). *Fritidsfisket i Sverige - En inblick i fritidsfiskets omfattning under åren 2013-2017*. (2019:5). Gothenburg, Sweden.
- Tanzer, J., Phua, C., Jeffries, B., Lawrence, A., Gonzales, A., Gamblin, P., Roxburgh, T., WWF (Organization), & Zoological Society of London (2015). *Living blue planet report: species, habitats and human well-being*. Gland, Switz.: WWF International. http://ocean.panda.org/media/Living_Blue_Planet_Report_2015_Final_LR.pdf [2020-12-09]
- Thörnqvist, S., Norlin, J., Ulmestrand, M., Petersson, E., Aho, T. & Asp, A. (2006). *Fritidsfiskets utövare 2006*. 196
- 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 pinniped diet composition. 54, 15
- Tverin, M., Esparza-Salas, R., Strömberg, A., Tang, P., Kokkonen, I., Herrero, A., Kauhala, K., Karlsson, O., Tiilikainen, R., Vetemaa, M., Sinisalo, T., Käkälä, R. & Lundström, K. (2019). Complementary methods assessing short and long-term prey of a marine top predator – Application to the grey seal-fishery conflict in the Baltic Sea. *PLOS ONE*, 14 (1), e0208694. <https://doi.org/10.1371/journal.pone.0208694>
- Von Busekist, J. (2004). *'Bone Base Baltic Sea', a computer supported identification system for fish bones*. Version: 1.0. University of Rostock, Germany. <http://www.bioarchiv.de>
- Wennerström, L., Olsson, J., Ryman, N. & Laikre, L. (2016). Temporally stable, weak genetic structuring in brackish water northern pike (*Esox lucius*) in the Baltic Sea indicates a contrasting divergence pattern relative to freshwater populations. *Canadian Journal of Fisheries and Aquatic Sciences*,. <https://doi.org/10.1139/cjfas-2016-0039>
- Wickham, H. (2016). *ggplot2: Elegant Graphics for Data Analysis*. 2nd ed. 2016. Cham: Springer International Publishing: Imprint: Springer. (Use R!). <https://doi.org/10.1007/978-3-319-24277-4>
- Worm, B., Barbier, E.B., Beaumont, N., Duffy, J.E., Folke, C., Halpern, B.S., Jackson, J.B.C., Lotze, H.K., Micheli, F., Palumbi, S.R., Sala, E., Selkoe,

K.A., Stachowicz, J.J. & Watson, R. (2006). Impacts of Biodiversity Loss on Ocean Ecosystem Services. *Science*, 314 (5800), 787–790

Zhang, D. (2020). *R-Squared and Related Measures*. 2.1.

Acknowledgements

My greatest thanks go to my supervisor Ulf Bergström, for being so engaged in my project and for his knowledge about the subject. Also, I would like to thank my assistant supervisors Örjan Östman and Karl Lundström for their help with specific questions and guidance.

Without help from the foundation Voice of the Ocean, VOTO, my sampling would not have been possible to do in the same extent. Thank you!

Thank you Alf Anderin and Erik Isakson, for the sampling of grey seal faeces.

Thanks to Markus Ahola at NRM for sharing data from the national seal counting survey in 2020 that was not accessible at Sharkweb.

And lastly, thank you, everyone, at *The Institute of Coastal Research* for involvement in the otolith identification and your never-ending encouragement.