Sveriges lantbruksuniversitet
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Analysing the seal-fishery conflict in the Baltic Sea and exploring new ways of looking at marine mammal movement data

En analys av säl-fiske konflikten i Östersjön och ett utforskande av nya sätt att titta på marina däggdjurs rörelsemönster

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Examensarbete i ämnet biologi
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Abstract

A comprehensive analysis of the available data reveals that there is currently not enough information for making informed management decisions regarding the seal-fishery conflict in the Baltic Sea. Knowledge of hidden and visual damages is limited, which means that the actual cost to the fishing industry from damages is not known. No research has been carried out of the effects of culling seals, which has been one of the main conflict management strategies. As rising seal numbers are probably going to lead to increased damages, then the other main management tool – compensation payments, will not be a viable long-term strategy and does not ensure that coastal fishing industry will survive. I argue that governments should instead concentrate on technical innovations to reduce seal damages, as fish damaged in gear has currently been the main concern for fishermen. In the second part of the thesis, integrated step-selection function was successfully used to look at grey and ringed seal movements on a fine scale, which shows that such a method can be used on marine mammal data to obtain novel information for management. The results showed that both species select for deeper areas compared to what is available within the range of a single step. Previous studies have only shown that seals reside in shallower areas, but as iSSA defines availability more precisely, it was possible to see that although seals are bound to shallower areas due to haul-out sites, they seem to select for deeper water in those areas. Ringed seals had shorter step lengths in deeper areas and when further from coast, whereas grey seals had longer step lengths in deeper areas and away from coast. This might be explained by the difference in water depths that these species use for movement and for feeding. Grey seals selected for steps that were closer to coast and ringed seals selected for steps further from coast. Grey seals had shorter step lengths and directional persistence when slope of the seafloor was steeper, which could show the areas where grey seals prefer to feed and use for directional movement.

Keywords: Halichoerus grypus, Phoca hispida botnica, seal-fishery conflict, human-wildlife conflict, integrated step selection analysis

Preface

As conflicts between wildlife and humans become more prevalent, it is important to analyse how conflicts are being managed to improve results and to be able to replicate successes elsewhere. The first chapter explains the conflict between the fishing industry and grey and ringed seals in the Baltic Sea. I have divided this chapter into two parts: mapping the conflict and managing the conflict. In the first part, I describe how the conflict manifests itself and what is known of the biological and economic aspects. In the second part, I outline the approach that governments are using, as well as the management solutions that are available. Problems of the current management strategy have been outlined and recommendations are made regarding how governments should proceed.

The second chapter uses a relatively new habitat selection and movement decision analysis method called integrated step selection to describe grey and ringed seal movements in the Baltic Sea using GPS data. Such fine-scale analysis of seal movement has not been carried out in the Baltic previously, but has the potential to improve our understanding of seal distributions and movements that can be used in management.

Chapter 1: The Seal-Fishery Conflict in the Baltic Sea

1. Introduction

Conflicts between carnivores and humans often arise when they are both competing for the same resources (Graham et al., 2005), and the management of these systems becomes increasingly complicated if the species in question are either economically or socially valuable, threatened and/or protected by law (Thirgood et al., 2000; Graham et al., 2005). The conflict unravelling between the fishing industry and the seals in the Baltic Sea meets all of the aforementioned criteria. Both the grey seal (*Halichoerus grypus*) and the ringed seal (*Phoca hispida botnica*) are listed as Annex II and V species in the Habitats Directive (Council of Europe, 1992) and are the focus of the HELCOM Seal recommendation (HELCOM, 2006), which was ratified in all of the Baltic countries in 2006. These documents require the member states to ensure the "favourable conservation status" of seals and to work towards meeting the objectives of natural distribution and abundance of seals, and their persistence in the future. In addition, people in the area are fond of seals, especially in areas where seal populations are still low, and conservation organizations are concerned for their well-being. On the other hand, as seal populations have started recovering after near extinction in the 1970s (Harding & Härkönen, 1999; Ahola & Leskelä, 2014), fishermen are growing increasingly concerned due to the biological (potential competition for the same resource) and operational (conflicts during fishing operations) interactions with seals. Increased economic losses and concern for decreased catches and increased competition, has led to the introduction of culling in the Baltic. But, although some seal populations are increasing, others are decreasing, and the uncertainties regarding seal movements, diets, and their broader ecological role mean that the impacts that culling and by-catch have on the fisheries and seal populations are not known. Baltic coastal fisheries have been culturally and economically important, but in recent decades, this ancient tradition is disappearing. Although conflict is being managed and large compensations are being paid, many fishermen are retiring whilst few young people are taking over, and one of the cited reasons is increasing seal populations. Even though large sums of money are each year paid as compensation, local fishermen are still struggling, which raises the question of whether this money is used in the most efficient way and whether conflict management could be carried out differently.

At present, there are many uncertainties, leading to a "conflict of perspectives" and to discussions that are not based on scientific evidence. The aim of this chapter is to give an

a) overview of the interactions between seals and the fisheries in the Baltic Sea by analysing the extent of the impacts, both to the fisheries and to the seals;
b) to describe the current mechanisms of conflict mitigation and documentation;
c) to identify uncertainties and future research needs; and
d) to identify possible management solutions.

I aim to construct this study using the foundation of the roadmap created by Redpath et al. (2014) (Figure 1), which involves two main elements: 1) mapping of conflict and 2) managing conflict. Better understanding of the conflict can lead to more efficient management decisions, which could benefit all of the stakeholders. The aspects of mapping and management of conflict are not presented separately, but the text is an amalgamation of arguments that present the current state of mapping of conflict and its management. Mapping here contains the aspects known about seals and fishermen's behaviours and the management contains policy and active measures and steps taken by different stakeholders towards reducing seal populations, or reducing or diverting fishing effort, compensations paid and received and their relevance in moving towards solving the conflict, or accepting the status quo. An attempt has been made to include most of the aspects relevant to the conflict (Figure 2).

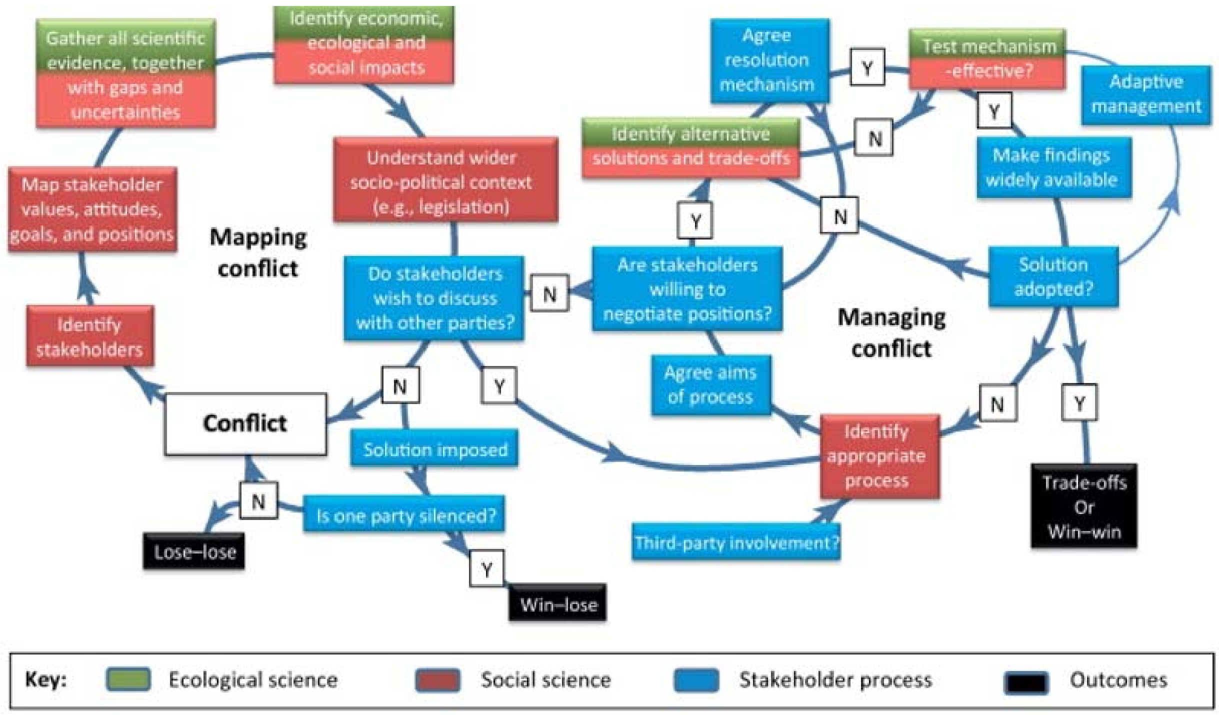

Figure 1. The framework of mapping and management of conflict, adapted from Redpath et al. (2014). It represents a roadmap intended to guide effective management of human wildlife conflicts and fits well with the seal-fishery conflict in the Baltic. Redpath et al. (2014) suggest two main elements (i) passive mapping of the conflict, garnering evidence, and considering the context; and (ii) more active attempts at conflict management involving engagement, often with a third party, exploring alternative solutions, and developing strategies within an adaptive management framework.

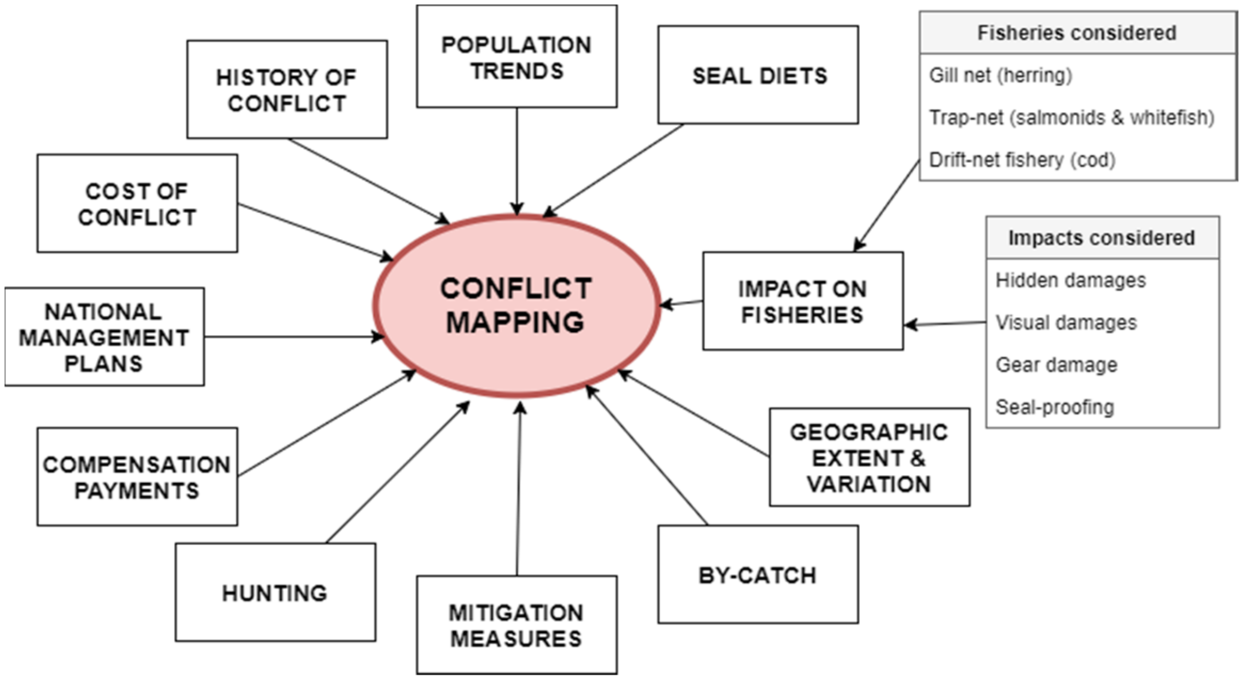

Figure 2. A flow chart giving an overview of the aspects considered in this review. The review starts with looking at the history of the conflict and moves clockwise; costs of the conflict have been covered in other sections when appropriate.

2. History of the conflict and changes in seal population size

The conflict between humans and seals in the Baltic dates back many centuries and has considerably changed during this time. Up to the 19th century, seals were considered a natural resource, which led to a severe reduction of many seal stocks, but as cheap mineral oils replaced seal oil, commercial sealing stopped (Harding & Härkönen, 1999). At the start of the 20th century, increasing seal stocks, which were estimated at between 190 000 and 220 000 for ringed seals and between 88 000 to over 100 000 for grey seals (Harding & Härkönen, 1999), led to a new type of conflict. The fishing industry started complaining about competition and damages caused by seals, which in turn led to the widespread introduction of culling and bounty systems during the beginning of the 20th century (Ylimaunu, 2000). These practices as well as disturbance from human development and environmental pollutants led to a reduction in seal populations with only a few thousand individuals of both species remaining by the 1970s (Harding & Härkonen, 1999). In the late 20th century, seals were protected in considerable parts of their distribution range due to pressure from conservation groups. Coupled with the reduction of organochlorine concentrations in their prey (Olsson et al., 2000) that caused reproductive failure and uterine occlusions in seals (Nyman, 2000; Routti, 2009), this has led to the populations recovering since the 1990s (Harding & Härkönen, 1999). Culling was prohibited in 1988 (Harding & Härkonen, 1999), but due to pressure from the fishing industry and for allowing the harvesting of a traditionally used resource, it was reinstated in Finland in 1997, Åland Islands in 2000, Sweden in 2001, and Estonia in 2015 (Jahiseadus, 2014, Anon, 2013) with certain country-specific differences and limitations in hunting methods. Seals are considered as one of the most difficult game animals to hunt, which leads to a situation where national quotas are not fulfilled (Härkonen, 2016).

From counts, it was estimated that in 2014, there were about 40,000–53,000 grey seals (Härkonen, 2016) and in 2015 about 23,000 ringed seals (Härkonen, 2015) in the Baltic Sea (Figure 3). The overall population of grey seals has been increasing at about 7.5% per year (Harding et al., 2007). Ringed seal population in the Bothnian Bay has been increasing at 4.6% per year between 1998 and 2013, whereas the subpopulations in the Gulf of Riga and Gulf of Finland have been decreasing (HELCOM, 2013). Ringed seals in Estonia are considered rare and in decline (Talvi, 2014). As ringed seal populations in the south are experiencing a decline and will probably be negatively impacted by climate change (Sundqvist et al., 2012), it is important that culling does not occur without solid scientific evidence of their negative effect on the fishery. Based on past population estimates, both species are far from reaching the carrying capacity of the system, which means that conflict is probably going to intensify with time as seal populations continue to increase. Grey seals' range includes most of the Baltic Sea and although they are more aggregated in the Gulf of Bothnia and Åland Sea (Sjöberg, 1999), they are increasingly colonizing southern parts of their historical range (HELCOM, 2015), which might lead to increasing damages further south.

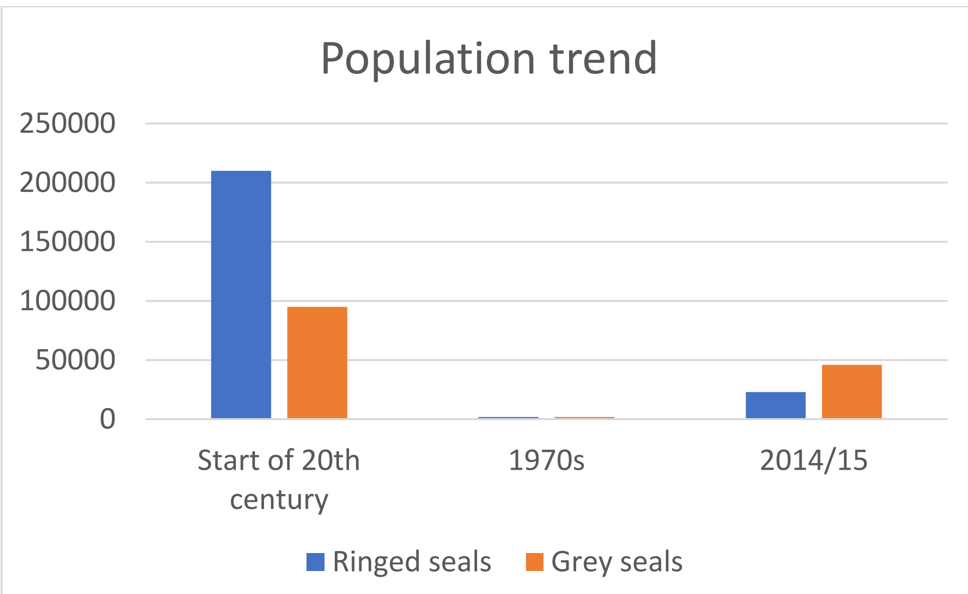

Figure 3. Number of seals in the Baltic Sea. Based on data from Harding & Härkonen, 1999; Härkonen, 2015 & 2016.

3. Seal diet

To be better able to formulate management plans for fishery and seal interactions, the ecological role of these seal species should be understood, in particular regarding their dietary habits and movement patterns (Lundström et al., 2010). However, estimating the diet of carnivores, especially of those living in marine environments, is difficult as feeding events are difficult to observe and therefore other methods, such as digestive system content analysis or fatty acid composition in the blubber, have to be used. Due to difficulties with using these methods, previous dietary studies have had limitations (Lundström et al., 2010), and only recently, more accurate information has become available. However, there is still very limited knowledge of the diet of ringed seals.

On average, grey seals consume 4.5–7.5 kg of fish per day (Innes et al., 1987; Ronald et al., 1984). Dietary studies have not been conducted in the Gulf of Finland and Gulf of Riga, but in the Gulf of Bothnia and the Baltic Proper, variation of their diet can best be predicted by geographic region and age group (Lundström et al., 2010). In those regions, Atlantic herring (*Clupea harengus*) is the most common prey species in all age groups, whereas the second most common prey species in the Baltic Proper is common whitefish (*Coregonus lavaretus*) and European sprat (*Sprattus sprattus*) in the Gulf of Bothnia. These species contribute an estimated 84.7% of the total biomass consumed (Lundström et al., 2010). Differences in diet between regions (Söderberg, 1972; Lundström et al., 2007; Karlsson, 2003) are attributable to the salinity gradient in the Baltic Sea (Ojaveer et al., 1981). Grey seals have been reported to consume over 20 different species (Söderberg, 1975; Lundström et al., 2010) as they take advantage of locally and seasonally abundant prey, and their diet is generally determined by the availability of potential prey species (Lundström et al., 2010). However, the number of prey species consumed by individual seals in the Baltic is generally low, with 41% of seals containing a single prey taxon and a further 51% containing two or three prey species (Lundström et al., 2010). Younger seals tend to feed more on small non-commercial species, such as viviparous blenny (*Zoarces viviparus*) and sandeel (*Ammodytes marinus*), which is probably caused by inexperience and incomplete development (Noren et al., 2005). According to Lundström et al. (2010), season and gender do not influence prey items found from the seals' digestive systems, which is contrary to the Atlantic Ocean, where season and gender has been reported to explain most of the observed diet variation in grey seals (Beck et al., 2007).

Baltic ringed seals have been reported to consume around 1.7 kg of fish per day (Innes et al., 1987) and their diet consists of at least 12 smaller fish species. In the northern part of the Bothnian Bay, the most abundant prey species from May to November are three-spined sticklebacks (*Gasterosteus aculeatus*), Baltic herring (*Clupea harengus*), smelt (*Osmerus eperlanus*), and vendace (*Coregonus albula*), but unlike grey seals, they also consume crustaceans in addition to fish (Suuronen & Lehtonen, 2012). A study conducted in the northern part of Bothnian Bay during the salmon migration, when salmonids are very vulnerable to predation, found no salmon or trout in ringed seal's diet (Suuronen & Lehtonen, 2012). This suggests that although there has been high concern from fishermen regarding the impact of both seal species on the stocks of salmon and trout, ringed seals might not be feeding on these species, at least not to a large extent.

As seal diets can somewhat vary in space and time, then extrapolations based on a few studies must be treated with caution. On a larger scale, for example, the factors influencing the diet of grey seals in the Atlantic Ocean, such as season and gender (Beck et al., 2007), do not coincide with the variables that influence grey seal's diet in the Baltic (Lundström et al., 2010). On an intermediate scale, grey seal's diets have been shown to vary between the northern and the southern part of the Baltic (Lundström et al., 2010) as well as possibly within the northern part of the Baltic Sea depending on prey availability (Suuronen & Lehtonen, 2012). On a smaller scale, it has been shown that within the same locality, ringed seal's diet varies during the breeding season between genders and between females depending on the individual's breeding stage (Sinisalo et al., 2008). The differences mean that whenever possible, knowledge from other areas should not be used for making inferences and management decisions.

4. Mapping and management of the conflict

Seals break fishing gear and their diet overlaps with fishery catches, creating economic and psychological hardship for the fisherman, but at the same time, seals can get trapped or injured in fishing gear and are culled. There are many uncertainties associated with these interactions and to a large extent, discussions are based on beliefs rather than solid scientific evidence. Ideally, we would like to achieve several seemingly conflicting goals, which include improving seal's conservation status, the resilience of the Baltic Sea ecosystem to cope with climate change and other stressors; as well as reducing unnecessary suffering of seals, economic damages to the fishing industry, psychological stress to those involved in the conflict, and economic cost to the society as a whole, whilst guaranteeing sustainable harvesting of natural resources. However, these goals are not necessarily mutually inclusive as with increasing scientific knowledge of the interactions and better management and mitigation measures, it should be possible to reduce the conflict and arrive at a win-win outcome where different stakeholders can gain from changes.

Population growth of seals has led to increasing interactions between seals and fisheries, with increased damage since the 1990s. Already decades back, seal-induced economic losses were considered to be at least 10–15% of the total catch value of the coastal fisheries (Westerberg et al., 2000) and the poor viability, low recruitment, and a continued decline in the number of active fishermen has also been attributed to seal damages (Anon, 2001). For example, in Sweden, damages to gear and catches increased from approximately EUR 2.65 million in 1997 (Westerberg et al., 2000) to over EUR 5 million in 2004 (Westerberg et al., 2008), and to EUR 5.55 million in 2006, which that year constituted 15–20% of the yearly catch value of the coastal fisheries in Sweden (Westerberg et al., 2006). However, in 2010, the government only paid compensations in the amount of EUR 1.8 million, which means that a significant amount of the costs are borne by fishermen. The situation in Finland has shown a similar trend (Kauppinen et al., 2005). Westerberg et al. (2006) estimated that additional costs relating to lost and damaged gear and reduced fishing opportunities are probably of the same magnitude, but are very difficult to quantify. In Estonia, damages in 2009 amounted to about EUR 0.37 million, which constituted 10.6% of the EUR 3.47 million total profit of the coastal fisheries (Anon, 2013). Out of this, 26% was due to damages to gear, 60% due to damaged fish and 14% due to lowered fishing effort or interruption of fishing (Anon, 2013). However, in Estonia most of these damages are sustained by fishermen as they don't claim compensation from the government, which in turn may lead to a situation where the government is not motivated to invest in mitigation measures.

When it comes to biological interactions in the form of potential competition for the same resource then there is limited knowledge of the effect of seals. It is evident that seals' diet overlaps with commercial fish species to a certain extent and that the amount of fish consumed by seals can be quite large. According to Elmgren (1989), at the beginning of the 20th century, marine mammals consumed about 5% of the primary production and the fishery only 1%. By 1990 seal populations had collapsed and fishing had intensified, leading to a situation where they required 0.1% and 10% of the primary productivity, respectively. Eutrophication in the Baltic has increased productivity and allowed for larger catches on the whole (Thurow, 1997), but it has also reduced cod reproduction in certain areas due to hypoxia and anoxia in their breeding grounds (Fonselius & Valderrama, 2003).

Functioning of marine environments is not well understood because of the large amount of interactions and mechanisms of which many are either badly understood or not yet identified, which means that cascading effects are difficult to predict. It is difficult to understand the relative effect that seals have on the availability of fish for the fishing industry in the Baltic Sea. This is in part because various environmental variables affect fish abundance and because commercial fish species prey on each other at different life stages (Figure 4); cod preys on herring and sprat (Sparholt, 1994), herring and sprat prey on cod (Köster & Möllmann, 2000), and herring preys on sprat (Patokina and Feldman, 1998). It is not known whether seals prefer to prey on certain age classes of these species, but this could indirectly influence commercial fish stocks as different age classes feed on different fish species. Due to complex interactions, fish not consumed by seals do not automatically translate into fish available for the fishing industry, for example due to being consumed by other fish species or due to fish populations being limited by habitat availability. Additionally, it is well known that there is substantial natural variation in fish stocks (e.g. Butterworth & Hardwood, 1991), and that fishing can significantly increase population variability (Hsieh et al., 2006). Considering the natural and human exacerbated fluctuations, it seems unlikely that fishermen could accurately quantify all losses, especially as their judgement can be influenced by emotions. Modelling study by Hansson et al. (2007) predicts that if fishery catches were kept at sustainable levels, densities of herring and cod would be as high or higher than in the period of 1996–2000 even if there were 100 000 seals in the Baltic. It is important to keep in mind that the Baltic Sea used to support a larger biomass of both marine mammals and fish than at present.

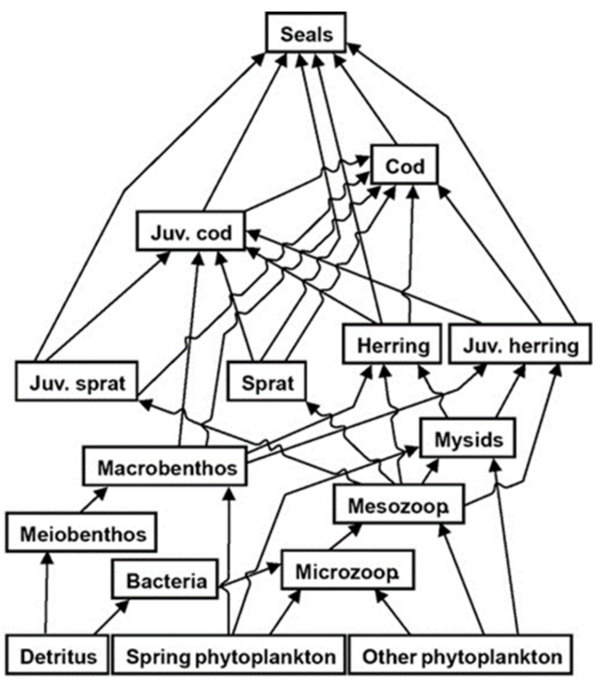

Figure 4. A representation of the food web with seals and main commercial fish species included. The figure does not include all the possible links in the food web and is for illustrative purposes. Adapted from Hansson et al. (2007).

The operational damages from seals can be divided into hidden and observed damages. Hidden damages can occur in various ways and these include: seals taking whole fish from the gear without leaving fish remains or holes behind; fish remains falling off; fish escaping through holes in the gear; seals scaring fish away due to their presence in the vicinity of fishing gear; and the so-called “goal-keeper seals” preventing fish from entering or taking fish as they are about to enter. Visual damages can be seen by fishermen as damage to gear or as fish remains left behind. For obvious reasons, hidden damages are much more difficult, if nearly impossible, to quantify at this point. Therefore, catch damages estimated by counting damaged fish and remains only give the lowest extent of the real damage as some damage might not be detected. There is some evidence that hidden damages can be even larger than visual damage, and therefore, they should be taken into account when calculating the true cost of seals to the fishing industry. The few studies that have attempted to look into hidden damage from taking entire fish (e.g., Sundqvist, 2005; Königson et al., 2005), have used the method of leaving marked entangled fish in the nets when resetting them and counting the marked fish that remain when the gear is lifted the next time. However, these marked fish may not be representative of the average picture as they spend more time in the water than caught fish as they are lowered in with the gear, and also, they are the first ones in, meaning seals might not have any other fish to choose from. An additional problem is that already dead entangled but undamaged fish from the previous fishing occasion are used and this may not give a representative sample to begin with, although it might counteract the previous problem, leading to negative selection by seals. Modelling damages by using a model that compares catches on consecutive days or day-pairs (e.g., Fjälling, 2005) is a more sophisticated method as it takes into account changes in catches over the season and also enables to analyse the amount of fish that escape through holes. It would also allow for the determination of seal preferences pertaining to fish species, sex, size, etc (Fjälling, 2005). Sadly, this method has not been widely used in the Baltic Sea. Fishermen have also been suggesting that the presence of seals can lower catches, and there is some evidence from the herring gillnet fishery to support that (Königson et al., 2005). Another type of damages occurs when fishermen choose to not fish or reduce their fishing effort because of the abundance of seals. Calculating the monetary loss from such actions is also difficult as it requires the prediction of potential catches had the seals not been in the area.

5. Impact on different fisheries

The following section gives an overview of the different types of damages for the most used gear and species over the entire Baltic Sea. An attempt has been made to include information from all of the studies that have been carried out, but the very limited number of studies has meant that only certain areas and aspects could be looked at.

5.1 Trap-net fishery

Damage to the trap-net fishery, which is a passive coastal fishery that mainly targets salmon, sea-running brown trout, and whitefish (Kauppinen et al., 2005), increased significantly during the 1990s in the northern Baltic Sea (Lehtonen & Suuronen, 2010; Kreivi et al., 2002; Westerberg et al., 2000), with most damage being inflicted by grey seals (Westerberg et al., 2000; Kreivi et al., 2002; Lunneryd et al., 2003). Ringed seals that are common in the Gulf of Bothnia are not known to feed at the traps although they are sometimes found drowned in the gear. Damage by grey seals to the coastal trap-net fishery has been identified as a significant problem throughout the Gulf of Bothnia (Kauppinen et al., 2005), and fishing has even been stopped in some areas. Damage by grey seals varies between areas and here an overview is given of the variation, and the most affected areas and gear types/materials are identified.

Visual damage

Most of the visual damage reported in this section is based on a study from the Gulf of Bothnia by Kauppinen et al. (2005) where 90% of the data was collected by fishermen. Kauppinen et al. (2005) found that during the comparison time, visual damages reported by volunteering fishermen were in accordance with their own observations and Helle (1999) has also found that fishermen's reporting was similar to their own observations; therefore, there is some indication that the damages reported by fishermen could be close to the actual damage rates.

In the Gulf of Bothnia, in 2002, the largest losses of salmon were recorded from the Bothnian Sea, where seals damaged 37% (by number) of the salmon caught, and seal-damaged salmon or remains were found in almost half of the emptyings when there were fish in the nets (Kauppinen et al., 2005) (Table 1). In other areas of the Gulf of Bothnia, the recorded damage was significantly lower varying between 3–9% (Kauppinen et al., 2005). Overall, the damages to salmon in 2002 can be considered quite low in all areas apart from the Bothnian Sea. It is unclear whether the low catch size is the result of high hidden damages in the Bothnian Sea, or whether the low catch leads to high damages. It is however interesting to note that the damage frequencies in the Northern Bothnian Bay are the same as in the Botnian Sea, but the number of damaged fish there is much lower at only 7% and the average catch is much higher at 11.5 (Table 1), leading to believe that the higher catch helps to lower the number of damaged salmon. With salmon, the number of damaged fish has been shown to correlate with the number of individuals caught in the trap, whereas the proportion of damaged salmon correlates negatively with total catch number (Kauppinen et al., 2005). It would be interesting to see how the damages have changed with increasing seal numbers.

Observed catch losses (by number) in the whitefish fishery varied from 5 to 7%, but did not differ between regions (Kauppinen et al., 2005) (Table 1). Gulls can also damage whitefish with the damage accounting for up to 5% of the total catch in a Swedish study (Lunneryd & Westerberg, 1997), but differentiating between seal and gull induced damage is difficult (Kauppinen et al., 2005) so it is not known how much of the damage was caused by seals. Brown trout catches in the Gulf of Bothnia were minor compared with salmon and whitefish catches (Kauppinen et al., 2005) (Table 1). Trout catches were most damaged in the southern Bothnian Bay and the Bothnian Sea, where losses amounted to 14% and 15% (by number), respectively, whereas in the Central Bothnian Bay and Northern Bothnian Bay, damaged fish only accounted for 1% and 2%, respectively; however, there was no significant difference in catch losses between regions (Kauppinen et al., 2005). The results show that the damages to whitefish and brown trout were quite minor.

In addition to the geographic variation, temporal variation in damages can also be observed. The fishing season in the Finnish coast of the Gulf of Bothnia is between May and October. Each salmon stock has a genetically determined stock-specific temporal and spatial marine distribution, which is also influenced by environmental factors (e.g., Kallio-Nyberg et al., 2000). The salmon of northern Gulf of Bothnia is far-migrating, spending their feeding years in the Southern Gulf of Bothnia, and maturing salmon leave their feeding area in April–June and move up rivers in June–September (Ikonen & Kallio-Nyberg, 1993). The peak in catches in different areas therefore depends on the timing of the migration, on the abundance of maturing salmon of different genetic stocks, and on the number of individuals already removed by fishing, to name a few. On the Swedish coast of the Gulf of Bothnia, set-trap catches of salmonids generally peak for a short period in early summer; however, seal-damages increase in extent and severity towards autumn (Fjälling, 2005). Data from the Swedish and Finnish coasts points to the fact that there seems to be temporal variation in catches and damages between the two coastlines (Kauppinen et al., 2005; Fjälling, 2005). A temporal pattern in salmon catch losses in all five regions of the Gulf of Bothnia has been previously identified, with peaks in most areas occurring around July, and in the Bothnian Sea, another peak has been seen in May (Kauppinen et al., 2005) (Figure 5). There is also temporal variation in whitefish catch damage, which peaks in October (Kauppinen et al., 2005) (Figure 5). However, these observations were made in a single year, and it is possible that different patterns might be observed in other years.

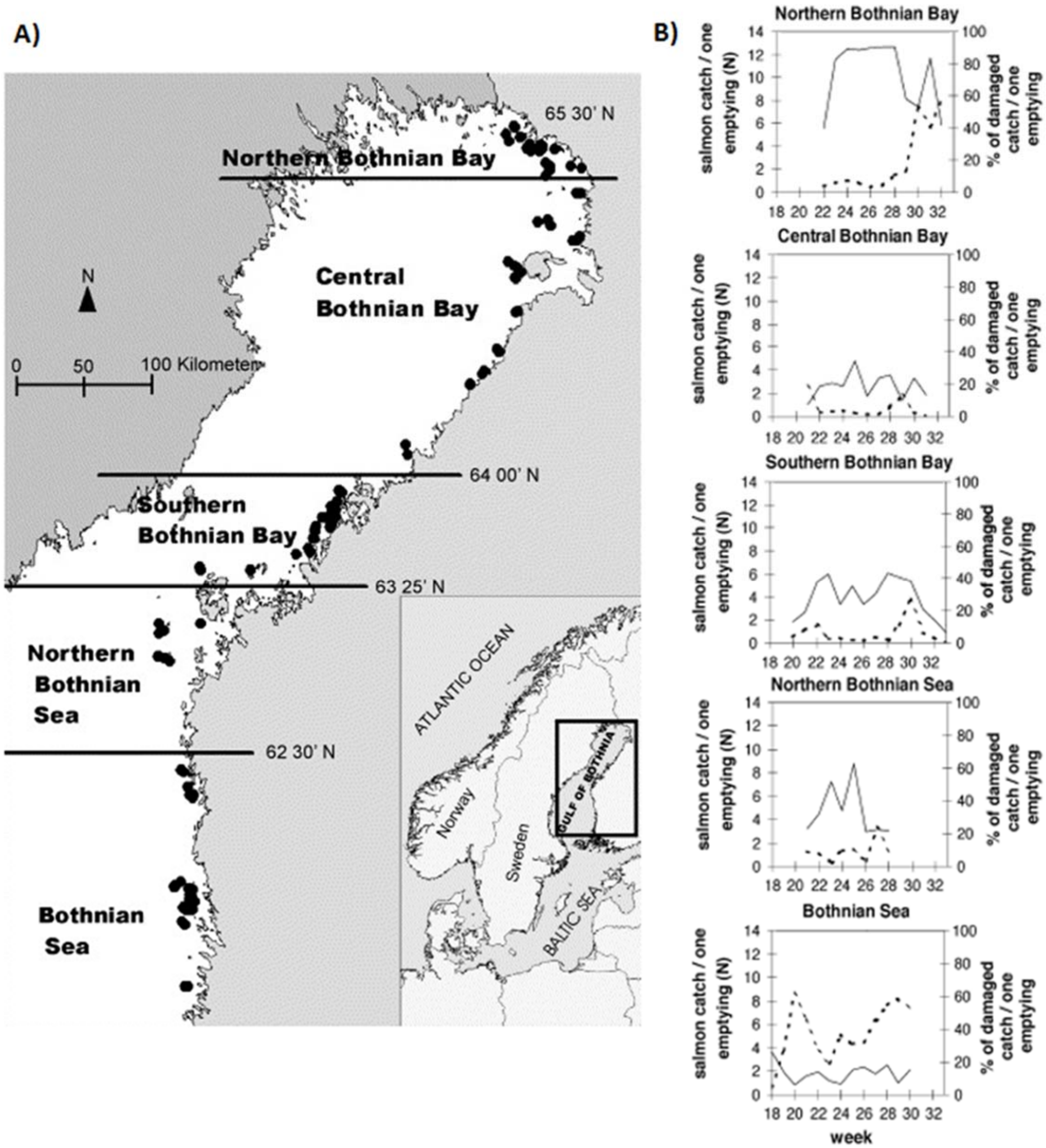

Figure 5. A) Different regions of the Gulf of Bothnia with black dots representing fishing sites where damage was measured. B) Temporal patterns of catch (solid line) and % of damaged catch (dashed line) in the areas shown on the map. Adapted from Kauppinen et al., 2005.

Table 1. Catch and gear damages, and salmon catches in different areas of the Gulf of Bothnia in 2002. Adapted from Kauppinen et. al. (2005)

	Catch damage			Gear damage	Average salmon catch (no.)/emptying
	Salmon	Whitefish	Trout		
Northern Bothnian Bay					11.5
Damaged fish (by number) (%)	7	7	2		
Damage frequency/emptyings (%)	30	4		25	
Range fisherman (%)	0–80	0–48		0–66	
Central Bothnian Bay					2.8
Damaged fish (by number) (%)	3	6	1		
Damage frequency/emptyings (%)	3	1		2	
Range fisherman (%)	0–67	0–11		0–17	
Southern Bothnian Bay					4.3
Damaged fish (by number) (%)	6	5	14		
Damage frequency/emptyings (%)	9	8		7	
Range fisherman (%)	0–58	0–47		0–37	
Northern Bothnian Sea					6.1
Damaged fish (by number) (%)	9	7	6		
Damage frequency/emptyings (%)	21	12		15	
Range fisherman (%)	2–46	0–100		0–41	
Bothnian Sea					1.7
Damaged fish (by number) (%)	37	6	15	15	
Damage frequency/emptyings (%)	30	3		23	
Range fisherman (%)	1–90	0–8		1–84	

Kauppinen et al. (2005) analysed their data based on fish numbers and did not take fish biomass into account, which means that the actual lost weight and therefore the monetary value of losses can't be inferred, but the value of their study relies in that they did not use surveys that can bias the reporting of damage (Lunneryd & Westerberg, 1997; Cairns et al., 2000).

Hidden damage
In the Swedish coastal fishery in the Gulf of Bothnia, Fjälling (2005) found that over the fishing season, on average, salmonid catches were significantly lower on days when seals had visited nets. But, because catches and seal damages vary throughout the year; it is not known to what extent the figures reflect seal damages or environmental variation. For example, larger salmon usually migrate earlier in the season and because the weight of caught and damaged fish matters, it is important to also consider the timing of damages. Because of these variations, it is better to use a model that compares catches in consecutive days with and without seal visits. Using that method, Fjälling (2005) found that hidden losses were significant, and that looking only at visual damage underestimated damages by at least 37% (Figure 6). As there seems to be a correlation of seal attacks with rising trend in catch figures, then correcting for that led to an underestimation of damage by at least 46% (Fjälling, 2005). Both types of losses varied over time but increased at the end of the season (Fjälling, 2005). An interesting finding by Fjälling (2005) is that there are also negative after-effects of seal visits, with catches being significantly lower on days when a seal has visited gear in the previous day. Although Bonner (1982) has attributed negative after-effects to scent, then an explanation that fitted the data was that lower catches were due to unrepaired structural damage to the traps, as traps with Dyneema netting did not show any effect on catch (Fjälling, 2005). Another interesting finding is that mean salmon weights are higher on days with seal visits which could indicate that seals prefer to take smaller fish, or that smaller fish escape from broken gear more easily (Fjälling, 2005). It is not known whether seals prefer smaller fish; therefore, both explanations could be possible.

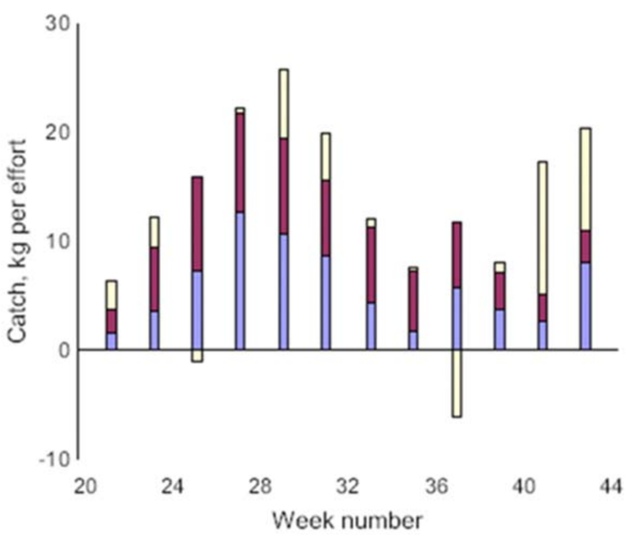

Figure 6. Salmon and sea trout hidden losses (yellow) and observed losses (red) compared to landed catch (blue) per two-week period. The total height of the bar indicates potential total catch. (The negative figures are due to sudden weather shifts and insufficient data.) Adapted from Fjälling (2005).

Gear damage
Gear damage in the northern Baltic Sea varies between 2–25% of trap-net landings, being largely dependent on region and peaking in October, with the highest damages in the Northern Bothnian Bay and the Bothnian Sea (Kauppinen et al., 2005) (Table 1). This variation has been suggested to depend on the number of seals in the area, fishing gear type, and netting material (Kauppinen et al., 2005). Trap-net material impacts gear-damage frequency, with nylon and monofilament being more susceptible than Dyneema and polythene netting (Kauppinen et al., 2005). Different parts of the trap-net can be made of different materials, which affects salmon entanglement, and therefore, affects gear damage. Traps with wings and middle chambers made of nylon and monofilament entangle salmon more than polythene meshes (Kauppinen et al., 2005) (Figure 7). This makes choice of gear material important because the minimum total damage to gear has a positive correlation with the total number of salmon entangled in meshes per trap as seals are more likely to damage areas where fish are entangled (Kauppinen et a., 2005). As can be expected, thick and strong netting materials get less damaged (Kauppinen et a., 2005). There is a temporal pattern in gear damage. The increase in damage later in the season can be due to a higher prevalence of smaller salmon, which are more easily entangled in nets (Kauppinen et a., 2005).

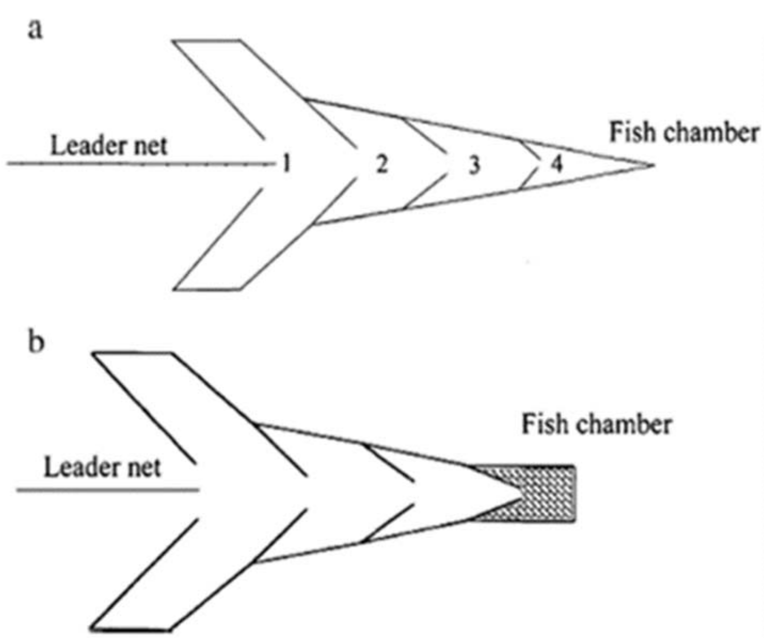

Figure 7. Two common designs of set traps for salmonids: a) soft fish chamber for caught fish, b) reinforced fish chamber giving more protection from seal damage. Adapted from Kauppinen et al., 2005.

Mitigation
Kauppinen et al. (2005) identified that trap-net damage was dependent on fish entanglement in the gear, and that salmon entanglement and gear-damage frequencies were significantly dependent on netting material. Trap-nets can either catch fish by guiding them into the fish-bag or by gilling which means that fish get entangled in the netting of the “wings” and “middle chambers” (Figure 7). This means that switching to netting gear that mainly catches by guiding fish to the fish-bag could limit damage to gear. For example, the conventional monofilament

traps designed to catch mainly by gilling and entangling should be avoided. The same holds for conventional traps made of twisted nylon with certain mesh sizes as they also catch mostly by gilling. It has also been shown that Dyneema netting removes the losses due to unrepaired holes and therefore should be used to reduce losses. Additionally, as trap type and netting material affects the intensity of gear and catch damage, then netting materials that are stronger and thicker and that catch mostly by trapping should be used. Estonian Environmental Protection Agency recommends the use of fish traps that are improved by seal-proof netting material Dyneema, especially for the fish bag, and the use of a metal or large-meshed net in front of the entrance to the trap (Talvi, 2014). The added benefit of using Dyneema nets is that algae does not grow on them (Talvi, 2014). Although the Dyneema netting is much more expensive than conventional netting materials, then according to the Estonian Environmental Protection Agency, it is cost-effective due to increased catch, quality, and reduced by-catch (Talvi, 2014). Fjälling (2006) has shown that acoustic harassment devices reduce seal interactions in the Baltic salmon-trap net fishery and may be a complementary mitigation tool.

5.2 Cod drift-net fishery

Conflict between seals and the cod fishery has been increasing in past decades (Swedish Board of Fisheries, 2009). For example, in Öland, the decrease in the number of fishing boats from over a 100 to 40 in the period of 2001–2012 was coupled with an increase in the proportion of days with seal damage from less than 20% to over 80% (HELCOM, 2016a). This suggests that the increase in seal damages might have led to a decrease in the number of fishermen.

The Atlantic cod (*Gadus morhua*) inshore fishery in Sweden operates from early fall till late spring, and there is a temporal pattern in catches per week (Sundqvist, 2005) (Figure 8). According to fishermen, there is also a temporal pattern of seal damages, which are highest from December to the end of February, decrease in March when seals are giving birth, and then rise again (Fiskeriverket, 2001). Cod in the drift-net fishery is caught by fishermen setting consecutive nets that form links that can be up to 1km in length. The small-scale coastal cod fishery is a passive fishery operation that uses stationary nets, which only exploit the swimming activity of the fish and catch fish of certain species and of larger size than trawlers and longlines (Huse et al., 2000). Therefore, this type of cod fishery is environmentally friendlier than alternatives as it uses less energy, causes minimal damage to the seabed, and is more selective. Unfortunately, passive gear is much more prone to damage from seals than active gear such as trawls (Westerberg et al., 2000).

Visual damage

Studies from the cod fishery are limited, but a study conducted in Öland has shown that damages can be substantial (Köningson et al., 2009). As the study in question had a very limited geographical extent, then these results only serve as a pointer to possible damages and might not necessarily reflect the situation elsewhere. Near Öland, seals have damaged 55% of the links set out, and visual damage was 41.2% on average in occasions when links were damaged (Sundqvist, 2015). However, significantly higher average catch per effort between damaged and undamaged links was only found in one of the two fishing areas (Sundqvist, 2005), which could be due to underlying environmental variation or small sample size. It has also been shown that the larger the cod catch, the smaller proportion of it is damaged (Sundqvist, 2015). However, when looking at the total number of cod caught in all links, only

16.3% of the caught cod were damaged (Sundqvist, 2015). As the size of cod was not considered, it is difficult to calculate the exact monetary loss.

Hidden damage

According to a study by Sundqvist (2005), carried out in Öland, 64.3% of the marked cod left into nets were removed and an additional 10.1% were damaged in occasions when seals visited the nets/damaged the catch. In the experimental links with marked fish, 64.5% of the time the fish were either damaged or missing (Sundqvist, 2005). Although the study only lasted for 3 months and had low sample sizes with only 2 fishermen being used, it indicates that damage to the cod fishery by seals in Kalmar, Sweden was large during 2005, and that hidden damage could be significant as 64.3% of the marked cod was missing (Sundqvist, 2005). However, the visible damage recorded in experimental and regular nets contrasted as it was 10.1% in experimental links compared to 41.2% in the non-experimental links indicating a possible problem with the methodology. Two fishing areas on opposite sides of Öland with locations about 15–30km apart showed no significant difference in visible or hidden damage recorded (Sundqvist, 2005).

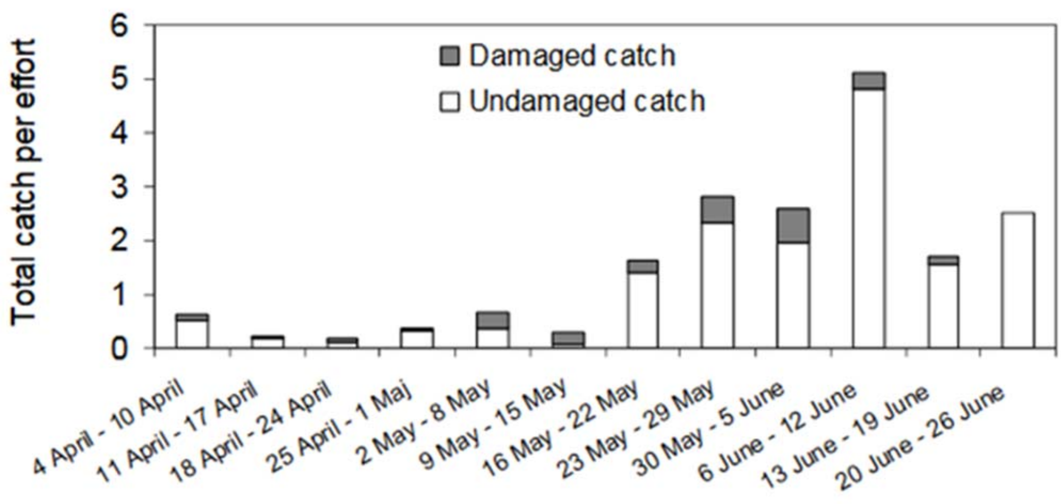

Figure 8. Average weekly cod catch and the amount of damaged catch in grey. Adapted from Sunqvist (2005).

The mean hidden losses accounted for 44.2% of the marked fish (Königson et al., 2009). Königson et al. (2009) found that 4.1 fish and 2.7 fish were lost for every damaged fish in 2005 and 2006, respectively. Based on their findings, they extrapolated the hidden losses to constitute 36% of the potential catches and 67% of the landed catches in 2005, whereas the values were 15% and 19% in 2006 (Königson et al., 2009). These results shed light to the possible high hidden losses, but also highlight the inherent variability in losses in the same region during consecutive years. The data is from a study that used two fishermen in consecutive years, with a total of 425 entangled fish used, and therefore, it is possible that the overall variability in damage is lower. Whereas the hidden losses help to understand the scale of the pressure to the industry from seals, it is clear that compensating for these losses is not possible due to the possible high cost and due to the high variability, which makes calculating real hidden losses extremely difficult. In addition, the method used has methodological problems, and therefore, the results might not be accurate.

Mitigation

It has been shown that damages in the cod fishery increase if fishing is carried out at the same location for a longer time (Königson, 2001), which could indicate that changing fishing locations more often might help with reducing damages. But otherwise, mitigation in the drift-net fishery is difficult as several nets are put out in a row, forming a link of up to 1km in length. Therefore, using acoustic deterrents that have a limited range is tricky, as many deterrents would be needed for a single link. It is also difficult to use other methods to limit access to seals.

Hidden damage should be taken into account when considering the damages inflicted to the fishing industry, but compensating the fishermen for hidden damages seems unrealistic considering the already high compensation payments. Compensation also interferes with market forces, creating a situation where fishermen are less interested in avoiding damages. Compensation can be seen as a relatively short-term mechanism to help the fishermen cope with the fast increase of seal populations. The aim should be to adapt so that damages can be reduced while the industry remains profitable. As the passive coastal cod fishery is important for the local areas, and as the alternative of trawling and long-lining has higher environmental costs, these should also be taken into account to find a balance that prefers fishing methods that inflict less overall damage. There is also the convoluted question of whether fishermen fishing in the natural system should be compensated for damages and for how long, as this distorts the market and lowers incentives for adapting.

In the period 2005–2006, when the study by Königson et al. (2009) was carried out, the cod population had declined (ICES, 2010) due to a shift from a cod-dominated to a clupeid-dominated ecosystem (MacKenzie et al. 2007) that was triggered by climate-induced hydrographic changes (Möllmann et al., 2008), and additionally driven by overfishing and eutrophication (Österblom, 2010). This new state was thought to be „cod-hostile“ due to the co-occurrance of several drivers that were negatively affecting the recruitment of cod (Möllmann et al., 2008). However, between 2005–2009, the cod biomass tripled (ICES, 2010) after more than two decades of low biomass and productivity, which is thought to be a result of large reduction in fishing mortality (Cardinale & Svedäng, 2011). Although, the new regime was thought to be a low recruitment period for cod, this assumption was falsified when the stock was fished at or around FMSY, and according to Cardinale & Svedäng (2011), the fishery seems to be the primary regulator of the population dynamics of cod in the Baltic Sea. As the cod stocks in the Baltic recovered, this could mean higher yield per effort for fishermen and if catches in nets are higher and the relationship of a lower proportion of cod damaged as catches increase, it could mean that relative damages might have dropped. Although it has been hypothesised that a larger seal population would inhibit the recovery of the cod stock (e.g., Köningson et al., 2009), it has been shown that despite an increasing seal population, reduced fishing mortality led to a very fast recovery of the cod stock (Cardinale & Svedäng, 2011). This should lead to a reduction in the conflict between seals and the fisheries, and turn attention to the significant detrimental effects that unsustainable management has on fish stocks.

5.3 Herring gillnet fishery

Herring is the most important commercial fish species in the Baltic Sea and the Gulf of Bothnia, with the largest value and catch in many areas (Commercial fishing in the Sea, 2009). During the recent three decades, herring fishery has moved from trap-net dominated gear to a trawl dominated fishery (e.g., Stephenson et al., 2001), and about 90% of total landings are from trawls (ICES, 2001a). This can be problematic as most of the herring that escape through trawl selection devices die shortly after, mainly due to exhaustion and physical damage (Suuronen et al., 1996a, 1996b). As the effort by trawls has increased (ICES, 2001b), it is expected that the fraction of herring stocks encountering trawls has increased, and as the size-at-age of herring has decreased, it is thought that the amount of „underwater discarding" has increased, creating substantial unaccounted mortality in the fishery. According to Rahikainen et al. (2004), trawling causes significant waste of biological resource in the Bothnian Sea herring fishery as more herrings between age 0–1 years are discarded underwater than landed. It is believed that herring stocks have been sustainably harvested in the past decades, with fishing mortality being below the threshold since 1970s (Swedish Board of Fisheries, 2010), however there is some concern as herring has become much smaller in size in the past two decades (Lundmark, 2010). One of the explanations for that is strong fishing pressure but also climate change or changes in plankton composition (Lundmark, 2010). If the decrease was due to fishing pressure, it would be important to use highly selective gear.

The problem with trawls, purse seine nets, and traps is that they catch herring indiscriminately, and survival of young herring escaping from selection devices is low (Suuronen et al., 1996a, 1996b). Minimizing the bycatch of juvenile and undersized herring is important because it reduces the productivity of stocks and causes waste of natural resources; this is also one of the Swedish Board of Fisheries priority objectives (Swedish Board of Fisheries, 2004). As fish caught in passive gear experience less stress, it is expected that survival of escaped individuals is higher, but as herring have strong school cohesion, achieving as high escape success as in cod for example, is difficult.

Fishing for herring with gillnets in the Baltic Sea is usually carried out by single fishermen from small boats (Königson et al., 2007), and this has been the main coastal fishery in the northern Baltic Sea (Königson et al., 2007). The fishery is size-selective and as a passive fishery, it is less environmentally harmful than active gear. However, the fishery is vulnerable to damages from seals as herring is the main prey species of grey seals (Lundström et al., 2005). Fishermen have for generations used steeply sloped areas of the seabed where herring schools concentrate (Hessle, 1925), and these areas have also been suggested by Sjöberg & Ball (2000) as areas where grey seals prefer to feed to maximise their feeding effort. This overlap in the fishing and seal's feeding areas might be one of the reasons for large damages to the industry.

Fishing mainly takes place during spring and autumn and is severely damaged by grey seals (Königson et al., 2005). Herring spawns during spring and aggregates in the shallower waters near the coast for about 3 months (Lundin, 2011, Rajasilta, 1993) where the main coastal fishing activity takes place. After spawning, they migrate to the deeper waters, where they can be found for the rest of the year (Rajasilta et al., 1997), and therefore, during autumn, fishing mostly takes place in the deeper waters (Königson et al., 2007). During winter, fisheries' activity is low (Köningson et al., 2005). Grey seals prefer larger sized herring which can affect the size-distribution in a herring stock (Östman, unpublished, 2010), but this preference has not been extensively studied.

According to both the EU compulsory logbook and a voluntary logbook scheme, seal attacks are lowest from May to July, with a minimum in June, and most frequent in October to December (Köningson et al., 2005). This is reflective of the life history of both species. When herring aggregates to spawn in the spring, it provides seals with an abundant food source and the motivation to raid gear is probably lower, as well as the damages will be less noticeable with high catches. In spring, adult grey seals mate, and as capital breeders, they don't feed during this time; in May and June they moult, which means that they spend most of their time on land and their food consumption is low (Söderberg, 1974; Bonner, 1994). In autumn, grey seals concentrate on feeding to restore their energy stores. Due to the high damages in late autumn, fishing during this part of the year has mostly disappeared.

Visual damages

Visual damage has not been shown to differ depending on whether seals are seen during setting and lifting of the nets or not (Köningson et al., 2007). In the voluntary log book scheme, which aims to obtain seal damage data, seal interference was recorded 60% of the time compared to the official EU log book, which only showed seal interference 30% of the time (Köningson et al., 2007). This highlights that when such data is not specifically required, fishermen avoid extra reporting; therefore, the EU log book scheme underestimates seal interference. It is however possible to get the temporal patterns of seal interference from the EU logbooks, which have shown that seal attacks are fewest in June and most frequent in October to December.

Hidden damages

Köningson et al. (2007) used a day-pairs method to look at damages in the herring gillnet fishery in the Gulf of Bothnia. Hidden damages were calculated by analysing losses from experimental nets with entangled fish lowered in. Catch per unit effort (CPUE) was 34–51% lower when fishermen reported interference from seals; the pattern remained the same when day-pair method was used for analysing data and was in the same range (41.6%) as when the day-pair method was not used (Köningson et al., 2007).

Field studies with 19 net settings revealed that in total, 70% of the marked fish left into nets went missing (Köningson et al., 2007). Seals were observed 74% of the time when nets were set, and in these cases, more than 86% of the marked fish went missing and an additional 5% were damaged (Köningson et al., 2007). In 58% of cases, more than 95% of the marked fish went missing (Köningson et al., 2007). Care must be taken because this data is from a single fisherman from the Bothnian Sea during September and October when damages to the fisheries are supposed to be the highest. The hidden damages in the whole Baltic might differ and the amount of damages in spring has, to my knowledge, not been studied. During field studies, the mean CPUE was 70% lower for links where seals had been observed during the setting or lifting of nets (Köningson et al., 2007). Interestingly, the CPUE was only 61% lower when fishermen's log book data was analysed, leading to believe that fishermen underestimate the losses to seals, which could be a result of seals being missed due to non-systematic seal observations.

As fishermen have observed herring disappearing from around nets with echo-sounders when seals have been present, it is a possibility that the mere presence of seals significantly reduces the catch. According to Köningson et al. (2007), the decrease in catch per metre net per day was 1.3 kg, which made the loss 240 kg per 180 m fleet of net. They question whether the observed seals (maximum 2 at any one time) could consume that many fish, as grey seals consume 4.5–7.5 kg of fish per day on average (Innes et al., 1987; Ronald et al., 1984). Even if we assumed the seals to consume 7.5 kg of fish per day, it would take 32 seals to consume 240 kg of herring. Köningson et al. (2007) believe that a more likely explanation is that seals patrolling around the nets are able to feed on some herring that get caught in the nets, but that large part of the losses is due to herring being scared away from the nets. Herring anti-predator behaviour consists of schooling, continual change of position, and rapid response to stimuli; however, they don't disperse from the school when a predator is encountered (Baxter, 1990; Pitcher et al., 1996; Pitcher & Parrish, 1993; Similä, 1997), and therefore, it seems that whole schools will be avoiding the nets patrolled by seals. A clever hunting adaptation by seals would be to push herring schools into the nets for easier feeding, but evidence to support that has not been found (e.g., Köningson et al., 2007).

Mitigation

Evidence shows that damages, especially hidden damages from seals in the traditional coastal herring gillnet fishery are very high. In the trap-net fishery, developing seal-safe gear has seen some success, but unfortunately, no progress has been made in the herring gillnet fishery. The problem is that protecting long nets, where fish are easily accessible to seals, is difficult, and novel solutions are needed to either transform the gear into a more sophisticated set-up, where seals can't access caught fish, or by using deterrents to keep seals away from the nets in the first place. Acoustic harassment devices (AHDs) can be costly for protecting long nets as they have a limited working range, and maintaining them at sea also requires extra investment of time and money. Acoustic deterrents have been shown to reduce losses in the trap-net fishery, however there have also been problems with acoustic deterrents working as "dinner bells" inviting seals to the gear (Carretta & Barlow, 2011). Information on whether moving gear more often would limit damages is not available. Köningson et al. (2007) hypothesise that a lot of the reduction in CPUE could be due to herring schools keeping away from patrolling seals. In this case, it would be better to either use sophisticated gear to deprive seals from a "reward" so that gear becomes uninteresting for seals, or to stop seals from getting close to the gear by using deterrents. Seals have successfully been deterred from entering bays by using acoustic deterrents (Anon, 2013). Such systems could be employed in areas mostly surrounded by islets or islands, where a limited number of deterrents could protect a larger area. This would however require a coordinated effort to make it economical and sustainable in the long run.

The benefit of the gillnet fishery is that compared to its alternative, trawling, it is much more environmentally friendly as it uses less energy, is more size-selective, catches less of unwanted by-catch species, and does not damage the seabed. Other methods of catching herring in an environmentally friendly way are being tested. For example, the herring trap fishery has been used in Finland since the 19th century for catching spawning herring in the spring (Parmanne 1989). It seems to be a good sustainable solution for the future, but more development is still needed (Lundin, 2011). The income from the coastal fisheries is also important to the communities, and this social perspective should also be taken into account when considering the spending for mitigation measures.

6. Geographic variation and extent of conflict

Conflicts between seals and commercial fisheries have increased dramatically in recent decades as can be seen from the increasing compensation payments. Conflict has been moving southward as seal populations have been slowly expanding from the north towards the south. For example, in Öland, damages have increased from 20% to 80% in the period 2001–2012, and the number of fishing boats has more than halved (HELCOM, 2016a). Although conflict is moving southwards, the monetary damages do not follow a uniform gradient, but can vary significantly between geographically close areas (Figure 9). Additionally, damages and catches vary throughout the year making calculating damages difficult. There are also hidden damages and financial losses from stopping fishing in certain areas.

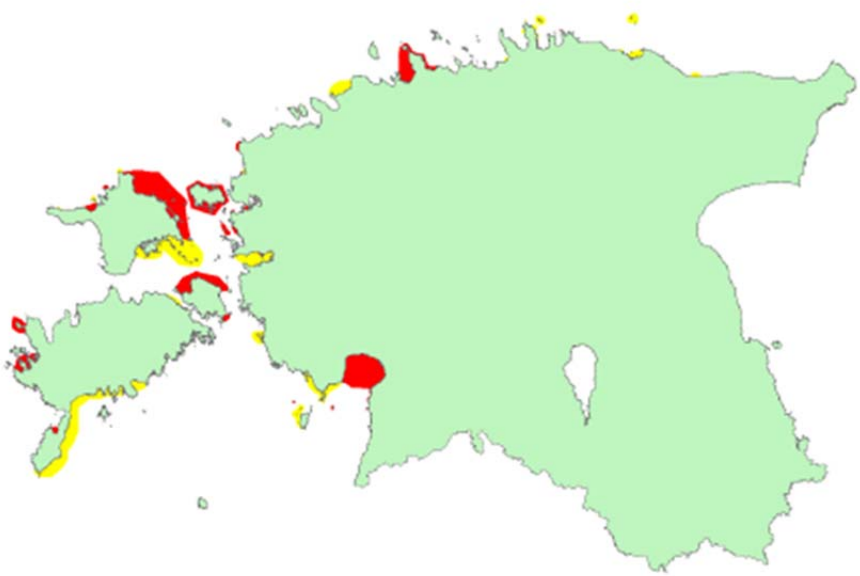

Figure 9. Results from an Estonian questionnaire study showing areas that are most affected by seals. Red areas show places where some fishermen have had to stop fishing and yellow areas indicate where disturbance from seals is common. Adapted from Anon (2013).

An analysis of both hidden and visual as well as gear damage shows that damages can be significant. But studies looking at hidden damage are very rare, and care should be taken when extrapolating data from a few fishermen to the entire Baltic. Data is also missing on the preferences of seals regarding fish taken from the gear. Even when looking at visual damage, data is mostly missing on the monetary value of lost catches as the weight of lost fish is usually not considered.

A questionnaire study conducted in Estonia that looked at the damages caused by seals to the fishermen, found that 95% of the fishermen thought that seals cause a problem for them and 75% felt that the problem frequency had increased (Anon, 2013). 94% noted that one of the main damaging factors is taking fish from the nets, and 85% noted breaking the traps as one of the main concerns, which was followed by damage to fish in the nets and scaring away the fish (Anon, 2013). Additionally, it was revealed that most of the fishermen are emotionally affected by the current situation – an aspect rarely considered (Anon, 2013). When estimating the danger to fishing as a source of income, 15% thought it was a very large danger and 39% noted it as a large danger. Interestingly, 5% believed that seals posed no danger to their income (Anon, 2013).

Out of the estimated damages, 60% were caused due to damage to fish, 26% due to damaged gear, and 14% due to reduction in effort or interruptions to fishing (Anon, 2013) (Figure 10). The most damaged gear type was nets (Anon, 2013). Relative losses compared to profits differed between gear types, being highest for trap nets, followed by nets and were the lowest for pound nets (Anon, 2013). The total damage to the Estonian coastal fishing industry from seals, extrapolated based on questionnaire data, was estimated at 0.86 million euros in 2009, which accounted for approximately 25% of the profits (Anon, 2013).

The largest total damages were recorded from the areas where the most profits were also made (Anon, 2013). However, there were large differences in the relative damage vs profits in many areas, which depended on the types of gear, target species, and possibly to a lesser extent on the distribution of seals (Anon, 2013). Namely, areas that used nets and targeted high value species had larger damages than for example areas that used nets but targeted European flounder (Platichthys flesus) that seals do not like to eat (Anon, 2013).

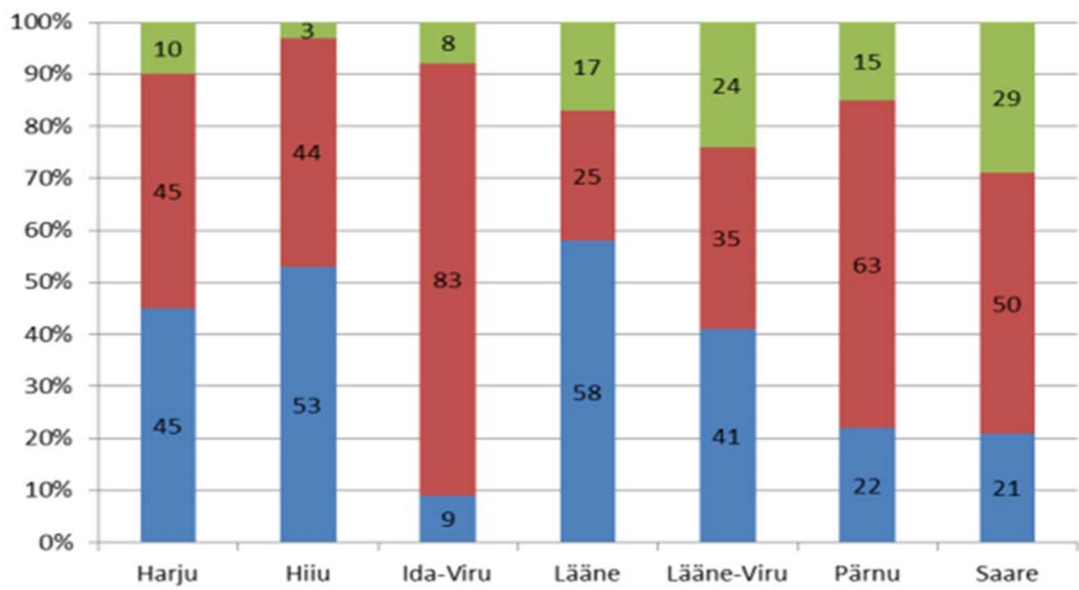

Figure 10. The proportion of monetary loss from different types of damages in different areas of Estonia. Losses due to reduced or abandoned fishing in green, losses due to damaged fish in red, and losses due to damage to gear in blue. As can be seen, types of losses vary between areas due to fishing methods, target species, and seal abundance. The data is based on a retrospective questionnaire study, and therefore, should be viewed critically.

83% of the fishermen thought that seal attacks had a temporal pattern (Anon, 2013). 58% of fishermen thought that seals are everywhere and it does not matter where to fish, whereas 35% thought that in some areas fishing is more intensely disturbed (Anon, 2013). 62% of fishermen had not had to stop fishing in any of their fishing grounds, whereas 32% had had to stop fishing in certain areas (Anon, 2013). Despite frequent damages to the gear, 56% of the Estonian fishermen had not seal-proofed their gear noting the high cost as a deterrent, even though partial compensation from the government is available (Anon, 2013). 37% of fishermen had tried various seal-proofing methods and most of those thought that it had helped, whereas 18% thought it wasn't economically justified, and 11% said that it depended on the conditions (Anon, 2013).

7. By-catch

Monitoring the by-catch of marine mammals in coastal small-scale fisheries is extremely difficult because by-catch events are rare in relation to fishing effort; having independent monitoring on boats would be too expensive and would not produce enough data for extrapolating for the entire Baltic Sea. An alternative to independent observations are either interviews or log-book schemes. Both have inherent problems associated with them as retrospective interviews can produce inaccurate information, and in both cases fishermen can either under or overreport by-catch to hide the negative effect on seals or to make the problem with seals seem more severe. Usually, it seems that fishermen tend to underreport by-catch as for example in Estonia, in most years, officially registered by-catch is zero (Vanhatalo et al., 2014).

Largest by-catch in Estonia is in Pärnumaa, where according to the Estonian Environmental Board, the abundance of fish has attracted grey seals to the area, but the number of by-caught individuals in Estonia is unknown (Jüssi & Jüssi, 2011). A questionnaire survey conducted for fishermen in Estonia revealed that 68% of the fishermen had bycaught seals (Anon, 2013). Out of these, 24% thought that these incidences had increased, 19% that the frequency had not changed in the past years, and 15% thought that the frequency had decreased (Anon, 2013). Extrapolating to the entire Swedish coastal fishing industry using the by-catch numbers from log book keepers showed that by-catches were in the range of 300–500 grey seals and 50 for ringed seals in 2004 (Lunneryd et al., 2005), which matches with the results of a telephone survey that estimated that over 400 grey and 50 ringed seals were by-caught during the year 2001. A more recent study suggests that nowadays, around 2,000 grey seals are by-caught each year (Vanhatalo et al., 2014), whereas numbers of by-caught ringed seals are not know (HELCOM, 2015). It is evident that by-caught seals are in worse condition than hunted seals (Bäcklin et al., 2011), and according to Bäcklin et al. (2011) the blubber thickness in grey seals has been significantly reducing over the last decade, which could point to food limitation in the population. By-catches as a relative proportion of the seal populations seem to be decreasing.

The overall picture from the voluntary logbooks is that most seals are by-caught in trap nets for salmon and eels, in the cod and flatfish fisheries, and in yellow eel fyke nets along the west coast. By-catches of seals in the salmon trap fishery remained the same during the period when a large part of traps were replaced with "push-up traps" that should make it harder for seals to get to the catches. Seals observed near gear decreased, but by-catch figures did not decrease (Lunneryd et al., 2005).

Honest reporting of by-catch numbers is always under threat as political decisions and changes in regulations can infuriate fishermen, and if they assume that the negative changes were due to data provided by fishermen, they can refuse to provide information or deliberately misreport by-catch numbers. Examples of such changes are for example the EU-regulation requiring the phasing out of salmon drift-netting in the Baltic Sea and the compulsory use of pingers for bottom-set nets (Anon, 2004) to prevent by-catch of harbour porpoises, and the "Environmental Objective" of limiting seal by-catch numbers to at most 1% of the population size (Anon, 2005). Articles questioning whether it was a good idea for fishermen to cooperate with scientists have been published in various magazines (e.g., Yrkesfiskaren, 2005). Before the introduction of the voluntary logbook scheme, there was a serious lack of data, and therefore, it is vital that cooperation between scientist and fishermen takes place.

It is clear that by-catch is not viewed as a significant threat to seal numbers either by the fishing community or the general public, but rather as an unfortunate consequence of a conflict. This may be the main reason for the readiness with which fisherman have (until recently) provided information to researchers. There is a genuine effort being made by the fishing community to avoid by-catches as it usually causes gear damage, lost catches, and wasted time. Fishermen also know that this issue can stop them from receiving certificates for environmentally friendly fisheries.

8. Mitigation options

8.1 AHDs (Acoustic harassment devices)

Effectiveness of AHDs has had mixed results in the scientific literature (e.g., Quick et al., 2004; Sepulveda & Oliva, 2005). This could be due to varying conditions and differences in AHDs used. Several attempts have been made trying to scare seals away from fishing gears using AHDs with varying levels of sound (Fjälling et al., 2006, Graham et al., 2009). When using an AHD in connection to a salmon trap, the amount of caught salmon has initially increased, but a recurring fact is that the seals get used to the sound and return to the fishing gear. Seals have been known to learn the frequency of the noise and to avoid diving at these periods, and to swim to gear with their head out of the water to minimise exposure to noise. However, seals should not be able to get used to AHDs with a varying sound interval (Anon, 2013). In bays and around traps, AHDs have been shown to be effective in keeping seals away, though some seals can have reduced hearing and are able to enter the areas. These seals can then be removed through hunting (Anon, 2013). The equipment is unfortunately expensive and requires regular maintenance. Acoustic deterrents have a working range of a few hundred meters which means that they are effective for fish traps but not for long nets. Considering their effect and range, currently it is practical to use them for protecting fish farms and at fish trap locations that give large catches (Talvi, 2014). Pingers, although cheap and long-lasting with a single charge, scare seals only for a short period as seals get used to them (Talvi, 2014).

The effectiveness of deterrents depends on the local maritime conditions, seal abundance, and distribution patterns (Anon, 2013). Compared to Finland and Sweden, the coast of Estonia has a lower water depth and the coast is much more open (Anon, 2013). If in Sweden and Finland, fishing gear is often protected by archipelagos and fjords, then in Estonia, most of the fishing is conducted at open sea meaning that there is a possibility of strong waves and therefore using deterrents is much more difficult in Estonia (Anon, 2013). In addition, the main gear types and target species in Estonia differ from those of Sweden and Finland (Anon, 2013).

One of the main problems with these devices is lack of innovation. The only company producing them is focused on fish farms that have high returns and access to the electrical grid. Apparently, they sell enough deterrents, and are not interested in reducing the energy consumption of these devices to make them more suitable for coastal fishermen that must use batteries (Anon, 2013).

8.2 Seal-safe fishing gears

For salmonids, using the pontoon trap, also known as a push-up trap, has been a successful way of minimizing seal damages (Lunneryd et al., 2003; Kauppinen et al., 2005; Lehtonen & Suuronen, 2010). Developing the trap was a long process as seals learnt to adjust to the modifications. In the end, the most successful strategy seemed to be to deprive seals from a reward by letting hunted prey escape. This makes the gear uninteresting to seals and they stay away (Lunneryd et al., 2003). As an additional benefit, the gear that was developed is faster and easier to empty than the regular traps used previously (Lunneryd et al., 2003). This type of gear is now commonly used for e.g., in the Bothnian Sea, however, take-up is still low in Estonia, where fishermen see the high costs as a strong deterrent (Anon, 2013).

Unfortunately, no progress has been made in the herring gillnet fishery. The problem is that protecting long nets where fish are easily accessible to seals, is difficult and needs novel solutions to either transform the gear into a more sophisticated set-up, where seals can't access caught fish, or by using deterrents to keep seals away from the nets in the first place. The trap-net gear, which is used for herring in spring in Finland still needs development, but seems promising.

8.3 Seal catching devices and feeding stations

Attempts have been made to catch seals either adjacent to fishing gear (Lunneryd & Fjälling, 2004), or by using the so-called "seal sock" attached straight to a pontoon trap (Lehtonen & Suuronen, 2010). This would serve to catch the "problem seals", and remove them from the population in a humane way, and to use the seals for research. However, success has been poor as seals do not go to baited traps often, whereas grey seals tend to drown in the modified gear as they seem to not exhibit the same behaviour of swimming to the surface as ringed seals, who are used to using breeding holes in ice. Experiments with feeding seals close to fishing gear have had promising results, attracting seals to feeding stations and showing increases in catches, however more research is needed.

8.4 Hunting seals near fishing gear

Although fishermen seem to believe that hunting seals next to gear reduces damages for a while, then a study monitoring damages between areas with hunting and no hunting failed to show any beneficial effects of hunting on catch damages (Bäcklin et al., 2011). A review by Bowen & Lidgard (2011) has shown that effects of seal hunt have rarely been documented, and that it is probable that significant beneficial effects would only be seen when seal populations are significantly reduced. Despite that, many scientific articles have claimed that removing the "nuisance" seals might be necessary for the survival of the coastal fishery (eg., Lehtonen & Suuronen, 2010). It is possible that further studies, perhaps in different areas, or with different environmental conditions, would show a beneficial effect of hunting. But, as it currently stands, the theory of "problem seals" does not have much grounding. It seems that male grey seals in good condition seem to be mainly caught near fishing gear, whereas by-caught animals tend to be males of poorer condition, possibly signifying increased risk-taking by weaker individuals (Bäcklin et al., 2011). However, it is not known how large of a proportion these "problem seals" constitute of the whole population. If it is a large proportion of the population, then culling near gear would have little effect, unless it was done at a large enough scale as to reduce the population size. Another justification for hunting is to make seals scared of humans and to deter them from approaching gear, but if this is not done at a large scale, there would always be naïve animals moving into the area to take advantage of the feeding opportunity. Additionally, developing seal-safe gear has shown that seals are very smart and adaptable, and it might be the case that seals would learn to only approach gear when humans are not close-by, which still leaves them plenty of time to empty the nets.

It could be argued that although hunting provides a psychological benefit to fishermen, making them feel that they have a way of protecting their livelihood, it might be more beneficial to conduct further scientific studies of the benefits of hunting. If only limited benefits were to be found, then a better option might be to use resources to develop seal-safe gear, acoustic deterrents, and other types of negative conditioning techniques. At present, policy documents often list culling as a mitigation measure, however for e.g., the Estonian seal hunting policy specifically notes that hunting will not reduce damages to the fishing industry. Culling seems to be more effective as a conflict mitigation tool between fishermen and parties protecting seals, than in reducing actual damages, and an easy mitigation method to list in policy documents that relieves pressure from having to develop better mitigation measures but that will leave fishermen worse off in the long run.

9. Hunting

Hunting was reintroduced in 1997 in Finland, in 2000 in Åland Islands, in 2001 in Sweden, and in 2015 in Estonia (Jahiseadus, 2014, Anon, 2013). Hunting ringed seals is allowed in Finland (Hunting Act, 2013) but not in other countries. Differences in hunting legislation exist between the countries bordering the Baltic Sea. For example, in Estonia, grey seals are only allowed to be hunted from land, not from boats next to fishing traps, and not during the breeding season (Jahiseadus, 2014). But in Sweden, hunting is only allowed 200 m from fishing gear where seal damage has occurred.

The Estonian hunting quota will be decided yearly by the Environmental Board based on the findings of the game monitoring report (Jahiseadus, 2014); in 2015, the proposed quota was at 1% of the counted animals at haul-outs in Estonia, which amounted to 53 individuals (Keskkonnaagentuur, 2014). The low quota does not follow regular game population control principles, being very cautious at the beginning of the reinstatement of hunting (Keskkonnaagentuur, 2014). In the future, the quota will probably rise to around 200 animals (Jüssi & Jüssi, 2011).

In other countries, the quota is higher; for e.g., in 2011 it was 1,050 in Finland, 230 in Sweden, and 450 in Åland Islands. However, limitations in the form of a limited hunting season and only certain hunting methods being allowed mean that hunting seals is considered as one of the most difficult types of hunting and quotas are not fulfilled; in 2011, less than 1/3 of the total quota was used (Jüssi & Jüssi, 2011).

10. Compensation payments

Compensation payments vary significantly between countries. According to the Estonian Environmental Protection agency, compensation is paid to all who make a claim (Pärnu Postimees, 2016). Partial compensation has been paid since 2009 to fishermen for damages by both grey and ringed seals (Riigiteataja, 2008). However, in Estonia, fishermen are very reluctant to make claims, whereas the procedure for making claims is not overly complex, and follows the same principles as compensation claims for damages by other animals such as bears or wolves. The Republic of Estonia Environmental Board compensated wolf and brown bear inflicted damages in the sum of a little over EUR 200,000 in 2015 (Keskonnaamet, 2016). However, when it comes to damages for seals, then annual damages between 2009–2013 were only paid to 3–8 subjects and totalled about EUR 5,000 (Jüssi & Jüssi, 2011). According to a study by Jüssi & Jüssi (2011), the annual damages by seals already amounted to EUR 0.37 million in 2009 (Anon, 2013). The reason for the mismatch between claims made and estimated damages is not known. The Estonian government reimburses 50% of the expenditure spent on seal-proofing gear, up to 3,200 per individual per year (Nature Conservation Act, 2014). Damages to traps are compensated up to 30% and damages to gillnets and entangling nets are compensated up to 70% of replacement cost to the extent of up to 320 euros per fishing gear set out in the fishing permit annually (Nature Conservation Act, 2014). In Sweden, fishermen can claim compensation for the visible damage from the county's administrative board. For example, in 2004, the administrative board in Kalmar paid out about EUR 100,000 (Lst Kalmar, 2005). In 2015, Sweden paid out about EUR 2.2 million out of which about 25% was for preventing damage, and 75% for compensating damages (Havs- och vattenmyndigheten, 2016).

I would argue that without a clear aim of finding quick ways to reduce the conflict, governments are wasting money that could be used for other conservation projects. Compensation payments are not a long-term solution. As fishermen give up their work, the cost to governments will slowly decline, but at the same time, the spending will in a way be wasted as it can't stop the decline of the industry unless innovative solutions can improve returns.

11. Management plans

HELCOM Contracting Parties committed themselves to complete national management plans in the Baltic Sea Action Plan to protect the long-term viability of the Baltic seal populations in the Baltic Sea Action Plan (HELCOM, 2016b). As of 2016, Denmark has a management plan (MP) for grey seals but not for ringed seals that was adopted in 2005, and they are carrying out surveys of seals (HELCOM, 2016b). In Finland an MP for grey and ringed seals is valid since 2007. In Sweden, an MP for grey seals was adopted in 2012 but the MP for ringed seals is still being reviewed (HELCOM, 2016b). The grey seal MP is Under development in Poland (HELCOM, 2016b). In Russia there are no MPs, whilst the numbers of grey seals are increasing but the numbers of ringed seals are still very low with only about a 100 animals in the Gulf of Finland (HELCOM, 2016b). Germany, Latvia and Lithuania currently have no plans of creating MPs for seals (HELCOM, 2016b).

The management plan from Estonia is especially promising. Estonia adopted an MP for grey and ringed seals in 2015 (HELCOM, 2016b). In Estonia, the number of individuals lost due to by-catch is unknown, moreover, the number of seals is at the moment a rough estimate, but the government intends to improve and modernise the monitoring (HELCOM, 2016b). The aim of the MP is to maintain the grey seal population in a good state, which would mean 3,500–4,000 individuals (Jüssi & Jüssi, 2011). The cost of actions outlined in the management plan for the period 2015–2019 is almost 200,000 euros (Jüssi & Jüssi, 2011), and the main protection measures are reduction of pollution, reduced disturbance in times when seals are most vulnerable, and reduced by-catch. Seal monitoring will continue and breeding success will be monitored as well (Jüssi & Jüssi, 2011). Further research into by-catch and damages to the fishery will be conducted and methodology for reporting both in reliable ways will be developed (Jüssi & Jüssi, 2011). Results from these will in turn be used for planning management in the future (Jüssi & Jüssi, 2011). There is also a plan of increasing public awareness (Jüssi & Jüssi, 2011). The main argument for wanting to re-introduce hunting of grey seals in other countries has been to reduce their abundance and thereby reduce damages to the fishing industry (Jüssi & Jüssi, 2011). However, the authors admit that a reduction in damages to the fishery is unlikely (Jüssi & Jüssi, 2011). The Estonian seal MP states that the reasons for reinstating the seal hunt are mainly for allowing the coastal communities to regain access to a resource that they have been exploiting in the past and that the communities have been interested in exploiting in the future (Jüssi & Jüssi, 2011). It also mentions the fact that as other Baltic countries are already hunting seals and only filling part of their quota, then hunting by Estonia should not negatively affect the populations. With the counted population of about 3,600 individuals in 2011, the quota that would allow the maintenance of a stable population or a slight increase could be 216 animals (Jüssi & Jüssi, 2011).

12. Synthesis

There are many gaps in data for successful and science-based management to be possible. As has been highlighted in this review, there is not enough information regarding the ecosystem level effect of seals and how they affect the fish communities. However, one modelling study that was available, concluded that if fisheries were sustainably managed, catches could be maintained at as high or higher levels than in the past even with 100,000 seals. The problem, however comes from the large amount of fish that are damaged by seals and that fishermen are unable to sell. Information is also very limited when it comes to seal diets – only a few temporally and geographically localised studies exist. Although in Sweden samples exist in the National History museum, there is not enough financing to analyse them. Some researchers have suggested that the seal populations in the Baltic should be managed at a sub-population level, but there is not enough information available to decide whether that is necessary or achievable. Most importantly, even the scale of damages in different regions is largely unknown. A few studies have attempted to measure the percentage of damaged fish but monetary calculations have rarely been made. Even more surprisingly, there is no evidence and measurements done to calculate the beneficial effect of the cull. Gear improvement has also been slow as damages are still high and 2,000 seals still drown in fishing gear each year.

There is little information regarding damages from each country and studies are carried out at small scales and are difficult to compare and to use for making inferences. As far as I know, there are no dietary studies from the Gulf of Finland or from the Estonian coast, and no published studies about damages from Estonia. However, there is a good questionnaire-based study trying to estimate total damages to the fishing industry, which is thought to amount to 25% of the total profit.

Sweden, Estonia, and Finland all have differences when it comes to the management and characteristics of the conflict. Damages and profits depend on local fish resources, catching method, and on occurrence of seals. In Estonia deterrents are most difficult to use as the coastline is open and waves can get high, meaning that deterrents can get damaged. Estonia has also only recently started compensating for seal damages, but a lot of the fishermen have found the system too complicated to take advantage of. Additionally, Estonian fishermen have relatively smaller incomes than those of Finland and Sweden, meaning that they find it more difficult to purchase deterrents and are at a disadvantage when it comes to protecting catches. Estonia was the last to reinstate seal hunt, and whereas Finland and Sweden consider it as one of their main management options, then Estonian government has made it clear that they do not expect seal damages to fall due to a hunt, rather it has been allowed to bring back an old tradition.

Even though the Baltic Sea could be able to support both a high population of seals and commercial fish, then this does not help with the problem of seals damaging fish without even fully eating them. Seals damage a large portion of the catch as it is their instinctive behaviour, and as a result, fishermen lose a lot of money as they can't sell the fish and discard it. As seal populations increase, there might be enough food for seals in the sea, but they will also be damaging fish, and therefore, protecting gear from seals is one of the most important management options. Governments should also make an effort to utilise the damaged fish in other industries as to reduce the biomass of fish taken from the sea and to provide income for fishermen. Another issue is with trawlers wasting a huge number of herring as small fish that are meant to escape die shortly afterwards. Coastal fisheries are by far the better option for catching herring and governments should invest into developing seal-proof gear or into creating seal-free areas using deterrents in bays or between islands.

Governments paying for damages and allowing seal hunt, does very little for developing a sustainable fishery. Developing seal-proof gear takes time, but currently, governments have not done enough to carry out such projects. Creating innovative gear solutions would surely be possible if governments made it their priority. As fishermen are quitting and retiring, and there will be less and less fishermen left, if governments do not take action quickly, there will not be a coastal fishing tradition left to save.

Chapter 2: Using integrated step selection analysis to understand seal movements in the Baltic Sea

1. Introduction

Conflicts between humans and wildlife are intensifying in many parts of the world as human populations are increasing and many previously over-exploited wildlife populations are recovering (Berger 2006; Woodroffe & MacDonald 1995). One such conflict is unfolding in the Baltic Sea, where an increase in grey seal (*Halichoerus grypus*) and ringed seal (*Phoca hispida botnica*) numbers has led to an increasing interaction between seals and fisheries, with increased damage being observed since the 1990s. Damages to the fishing industry have been climbing; for e.g., in Sweden, damages to gear and catches increased from approximately EUR 2.65 million in 1997 (Westerberg et al., 2000) and already reached EUR 5.55 million in 2006, which constituted 15–20% of the yearly catch value of the coastal fisheries in Sweden (Westerberg et al., 2006). Governments and other agencies and organisations are trying to manage the conflict, but this is done with limited knowledge of many aspects of the conflict, such as seal diets, effects of culling, monetary value of total losses, and the distribution and movement of seals, besides many others.

Although annual censuses of seals in the Baltic Sea have been conducted for a long time, these only take place during the breeding season and very little is known about the location of seals during the rest of the year. Evidence from GPS studies shows that seals can move over large distances over a few days whereas at other times they can exhibit feeding-site fidelity (Sjörberg & Ball, 2000; Oksanen, 2014), but what affects these movement decisions is not known. There is not enough data available from the Baltic to know where and how seals move. Such data, however, would be very important for understanding their effect in the food web and interaction with other species, and especially, how these interactions affect the fishing industry. This knowledge could be used for designing international management plans covering the whole Baltic Sea, to design measures for reducing damages, and to evaluate the effects of various management measures (such as use of culling or acoustic deterrents). For e.g., one of the premises the culling is based on, is the belief of the existence of individuals that are specialised on raiding fishing gear (Graham et al., 2011), but information to back such beliefs in the Baltic Sea is limited. Surge in GPS data availability and novel spatial data analysis methods have opened up the possibility for using such analysis techniques for conflict management (Ogburn et al., 2017). One such method, step selection analysis (SSA) has already for e.g., been used to understand effects of roads (Roever et al., 2010) and for designing movement corridors (Squires et al., 2013).

My study concentrates on the conflict between coastal fishermen and seals in the Baltic Sea and tests whether integrated step selection analysis (iSSA) could in the future be used for understanding seal movements in the Baltic Sea better, which could in turn assist with developing management options that could potentially benefit all of the stakeholders.

Resource selection functions have been used in the past to model the likelihood of an available spatial unit being used, but the problem has been with defining availability (Matthiopoulos, 2003; Northrup et al., 2013; McDonald et al., 2013). Step selection analysis (SSA) developed by Fortin et al. (2005) is a type of conditional resource selection analysis that tries to get around this problem by defining availability based on the empirical distribution of "used steps" (a line drawn between two consecutive observed positions of the monitored individual) and infers selection by contrasting the characteristics of used and "available steps" that are randomly sampled from a distribution defined from the characteristics of observed steps. Integrated step-selection analysis (iSSA) extends that approach by recognising that selection and movement are strongly linked – an animal's ability to move in certain habitats will influence its habitat selection (Avgar et al., 2015) whereas habitat-use will be affected by selection for habitats (Avgar et al., 2013). This can for example happen when an animal might be selecting for less snow, but is willing to go through deep snow to reach a better habitat. In case the animal moves slower through the snow, and if we are not taking into account its change of movement speed and destination, then we might falsely conclude that the animal selects for deeper snow/or is not affected by snow depth as it has spent more time in there due to slower movement. SSA uses a sequential approach to estimate movement and resource-selection parameters, whereas in iSSA, these are simultaneously estimated in the same conditional logistic regression model (Avgar et al., 2016). Such approach can avoid biased habitat selection estimates that can incur when movement processes are not taken into account (Forester et al., 2009).

To my knowledge, all of the published papers so far using SSA or iSSA have looked at terrestrial species. Using iSSA on marine mammals adds complexity as one of the requirements of such analysis is that all location fixes should be equally spaced in time. However, this is not the case with the location data obtained from seals in the Baltic Sea as their location data is only sent when the animal surfaces. As marine mammals can make long dives, fixes are often not equally spaced in time. To save battery time, the tags also use a sensor to identify when an animal is hauled out, and switches to a schedule where location data is sent much more infrequently. However, as can be seen from our data, these sensors can malfunction and thereby introduce an additional error of sending very infrequent locations when a seal is moving. Another problem is to do with the limited amount of data available in terms of individuals and fixes per individuals. This is caused by malfunctioning or premature falling off of trackers; for e.g., a lot of the trackers used on seals in Sweden have only produced limited amounts of data. Devices are expensive, but are currently glued on seals' fur and lost each year when seals molt; this means that available data is quite limited and inter-annual movement data from same individuals is not available. This contrasts sharply with for e.g., golden eagle location data that can already be obtained at an interval of 1 second (Singh et al., 2017).

Additionally, as Baltic Sea countries do not share data, datasets available for institutions to make management decisions are limited. I used the data available from the Swedish National History Museum to carry out an iSSA to test whether the method could be successfully used for analysing marine mammal movement decisions with a limited dataset.

The aim of this study is to use iSSA to explore how the movement of grey and ringed seals is affected by some key environmental variables, such as depth, distance to coast, and incline as knowledge from previous studies suggests that these factors should influence the presence and behaviour of seals.

2. Materials and methods

2.1 Study area and study species

The Baltic Sea is a large brackish water body with an average depth of 55 m that stretches from 53°N to 66°N latitude and from 10°E to 30°E longitude (Leppäranta & Myrberg, 2009). Limited water exchange with the Atlantic Ocean creates a salinity gradient that leads to differences in prey species composition (Ojaveer et al., 1981). Grey seals and ringed seals differ in their diet (Lundström et al., 2010; Suuronen & Lehtonen, 2012) and possibly in their movement extent, which means that differences in their movement preferences should exist. It has previously been believed that ringed seals are more local and move little (Härkonen et al., 2008), but a recent study has shown that this might not hold in the Baltic Sea (Oksanen, 2015). Grey seals move extensively throughout the Baltic Sea and are considered as a single management unit, whereas ringed seals are believed to have separated populations (HELCOM, 2017).

2.2 GPS data and study animals

Data was obtained from the Swedish National History Museum, who was responsible for the capture of seals and the attachment and retrieval of GPS transmitters. The dataset contained usable GPS locations from 2 grey seals and 6 ringed seals (Figure 11). All of the individuals were males, and half of the ringed seals were juveniles (Table 2). Grey seal data was collected in 2012–2013, and ringed seal data in 2015–2016. The dataset included 18 916 grey seal and 2 544 ringed seal locations. Relocations were filtered in R using a script tailored for cleaning argos data (Freitas et al., 2008) and still remaining errors were removed visually.

Table 2. Details of grey and ringed seals equipped with GPS transmitters. Ringed seal age class was determined from weight.

Species	ID	Sex	Tracking start	Tracking end	Length	Weight	Adult/ juvenile
ringed seal	RS1	male	09 Oct 2015	16 Jan 2016	105	62	adult
ringed seal	RS2	male	8 Oct 2015	14 Oct 2015	87	32.5	juvenile
ringed seal	RS3	male	8 Oct 2015	23 Oct 2015	89	33	juvenile

Species	ID	Sex	Tracking start	Tracking end	Length	Weight	Adult/ juvenile
ringed seal	RS4	male	8 Oct 2015	11 Jan 2016	85	32.5	juvenile
ringed seal	RS5	male	9 Oct 2015	10 Jan 2016	105	62	adult
ringed seal	RS6	male	10 Oct 2015	14 Oct 2015	118	72	adult
grey seal	GS1	male	26 Mar 2012	22 Aug 2012	-	-	-
grey seal	GS2	male	15 Mar 2012	08 Jan 2013	-	-	-

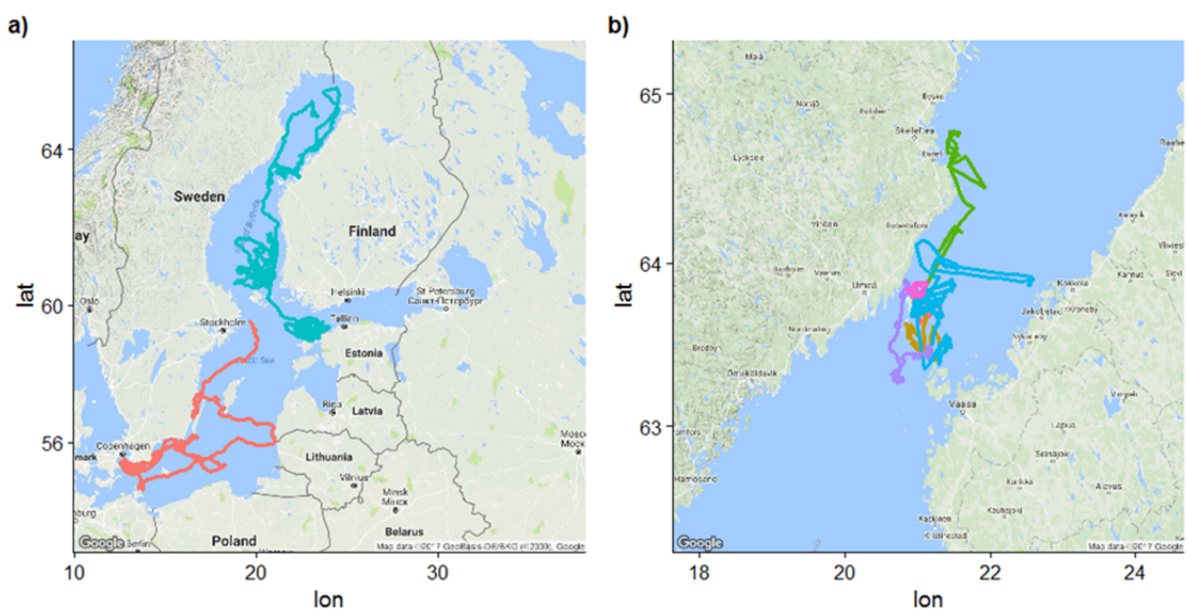

Figure 11. GPS paths of individual a) grey seals (red is individual GS1) and b) ringed seals

2.3 Integrated step selection analysis

When conducting integrated step selection analysis, I followed the method outlined in Avgar et al. (2016). A step in SSA is defined as the straight line between two consecutive observed locations. Steps are described by their length (distance between consecutive locations) and turning angle (angular deviation between consecutive steps). These values are used to parameterise distributions of step lengths and turning angles that are used for drawing available steps. Each available step (case) is then matched with random steps (controls) that start from the same geographic location (Figure 12). By comparing the properties of selected steps with those of random steps, it is possible to infer selection.

Steps two days after tag deployment and two days before tags stopped working were excluded to limit effects of such events. Due to diving and uneven fix rates, data was resampled to obtain fixed step durations that could be used in iSSA. Resampling interval was chosen based on the observed location fix intervals and differed between the species. Tracks were resampled to gain fix rates of 15 ± 2 minutes (range of ± 13%) for grey seals and 10 ± 2 minutes (range of ± 20%) for ringed seals. A variation in step duration of ± 16.7% has been regarded as a suitable range (Avgar et al., 2016), but there is also theoretical reasons to believe that iSSA would be robust to a fix rate variation of ± 20%, though it hasn't been tested (T. Avgar, pers. comm.). Due to small sample size, I felt that larger fix rate variability was necessary for carrying out the analysis. Only bursts with a minimum length of 3 consecutive locations were included as this was required to obtain the turning angle of the step using the preceding step. Step lengths were drawn from a gamma distribution as it matched the data and was also recommended by Avgar et al. (2016). Turning angles were drawn from a uniform distribution varying from $-\pi$ to π (-pi to pi), but this does not mean that a uniform distribution of turning angles was assumed as this is corrected for later in the analysis. After filtering, 544 ringed seal steps and 5 499 grey seal steps were available for analysis. Each of these steps was coupled with 8 randomly generated available steps using the created turning angle and step length distributions. Conditional logistic regression models were fitted separately for grey seal and ringed seal data in R (R Core Team, version 3.4.1) using clogit function. Movement coefficients were adjusted after coefficient estimates were obtained.

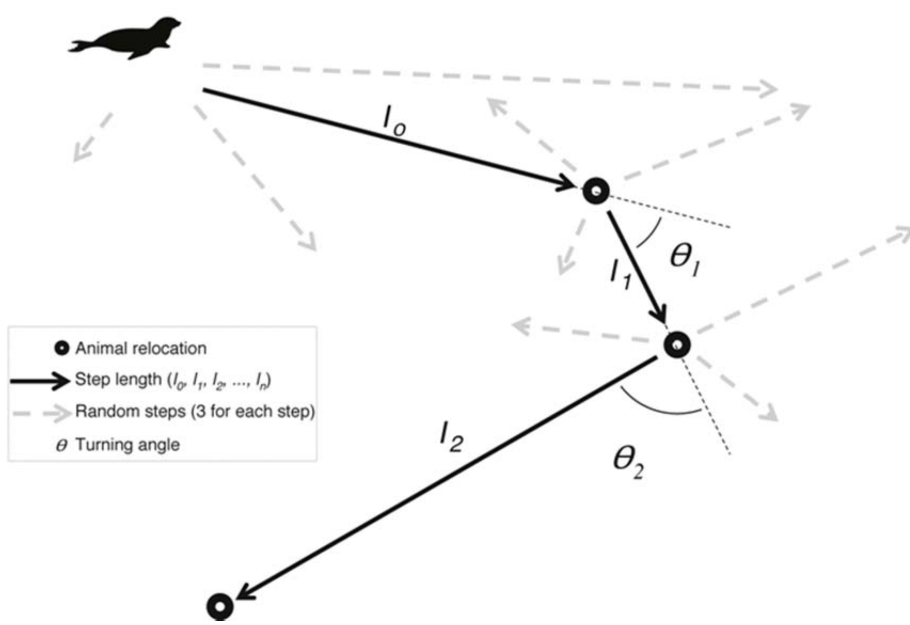

Figure 12. An illustration of how a movement path of an animal can be divided into consecutive steps, and how step attributes are obtained for analysis. Grey lines 3 randomly generated steps. Adapted from Thurfjell et al. (2014).

2.4 Model covariates

Main covariates included in the model that were expected to influence seal movement were depth (depth, m), distance from coast (dist2coast, m), and slope (slope, degree) of the seafloor.

Rasters with these values were obtained from HELCOM (HELCOM Map and Data service, http://maps.helcom.fi/website/mapservice/index.html). There wasn't significant correlation between these variables, and therefore, all of them were included in the model. Depth was used because it was expected that seals would prefer to feed at certain depths (Sjöberg & Ball, 2000; Oksanen et al., 2014). Distance to coast was included because it was expected that seals would prefer areas closer to coast as has been seen from previous studies (Sjöberg & Ball, 2000; Oksanen et al., 2014. Squared distance to coast was used in the model to look for non-linear relationship, but as it did not improve the model, it was discarded and not used in the final models. Distance to coast and step length (sl) were scaled because these variables had a very large scale. Incline was used because seals were expected to feed near steep slopes as it might provide better feeding opportunities (Sjöberg & Ball, 2000; Thompson et al., 1991; Hessle, 1925). Log of step length log(sl) that was used in models is the shape parameter modifier of the gamma distribution that was used for generating random steps (Avgar et al., 2016). I have also included a distance function scale(sl) in the model as it has been shown to reduce bias in habitat-selection models Forester et al. (2009). Turning angle is widely used to show directional persistence in animal movement (e.g., Avgar et al. 2013, Gurarie et al. 2009, Turchin 1998). To use it in the model, a cosine of the turning angle cos(ta) can be used to change it into a correlation factor ranging from -1 to 1 as it is a circular variable (Benhamou, 2006) to get an unbiased estimate of the von Mises distribution concentration parameter from the model (Avgar et al. 2016). Covariate values for each available and used step were obtained from the endpoints of the steps.

The grey seal model included 12 parameters, but due to a large amount of missing values in the slope data, this variable could not be used for the small sample size of ringed seals. Therefore, the maximal/base models between the species varied (Table 3). A dredge function was run on the grey seal model to identify the best model using AIC (Akaike's Information Criterion, Burnham & Anderson, 2003) that explained the presence of seals in relation to predictors considered. When comparing models for ringed seal, the model with interactions had a higher AIC score than a model without interactions and was therefore used as a basis for model selection, which was done by updating the model manually.

2.4.1 Interactions

It was assumed that depth would influence step length and turning angle due to seals preferring to feed at certain depths and due to moving larger distances when in deeper waters. Feeding behaviour would manifest itself by short step lengths and large turning angles, whereas longer directional movements would be seen as longer step lengths and smaller turning angles. To see whether seal movements differ at different water depths, interactions depth : scale(sl) and depth : cos(ta) were included. It was also believed that seals would move larger distances when away from coast, which would be manifested in longer step lengths, and hence, we included the interaction scale(dist2coast) : scale(sl). It was also hypothesised that seals would tend to turn less when further from the coast, which would be shown by the interaction scale(dist2coast) : cos(ta). There was reason to believe that seals might prefer to feed near steeper slopes, which would lead to shorter step lengths in these areas. To test that hypothesis the interaction slope : scale(sl) was included. As feeding behaviour in these areas would also lead to larger turning angles, the interaction slope : cos(ta) was included to explore that behaviour. As the variable slope was not used in the ringed seal model then interactions with this variable were also not included.

Table 3. Maximal models used in grey and ringed seal analysis.

Model	Covariates
Grey seal maximal model	depth + scale(dist2coast) + slope + scale(sl) + log(sl) + cos(ta) + depth : scale(sl) + scale(dist2coast) : scale(sl) + slope : scale(sl) + depth : cos(ta) + scale(dist2coast) : cos(ta) + slope : cos(ta)
Ringed seal maximal model	depth + scale(dist2coast) + scale(sl) + log(sl) + cos(ta) + depth : scale(sl) + scale(dist2coast) : scale(sl) + depth : cos(ta) + (dist2coast) : cos(ta)

3. Results

3.1 Grey seals

Out of the 10 best models for grey seals, the top two models had much higher AIC weights (w) than the following models (Table 4). The coefficient values of these two models were averaged and these values are used for making inferences of seal movements (Table 5). The best model for grey seals included 12 parameters. A positive selection for deeper areas was observed for grey seals (0.035 ± 0.005, z = 7.557) (Table 5). The negative coefficient for the cosine of turning angle indicates that no directional persistence was observed within the steps that were used in the model (Table 5). Grey seals selected for deeper areas (0.035 ± 0.005, z = 7.557) and had longer step lengths in deeper areas (0.006 ± 0.001, z = 7.333) (Table 5), meaning they moved faster in deeper waters. Grey seals also had longer step lengths when further from coast (0.05 ± 0.023, z = 2.139) (Table 5). The model showed that grey seals had shorter step lengths when slope of the seafloor was steeper (-20.4 ± 3.96 , z = - 5.157), and they exhibited directional persistence when they were around steeper slopes (15 ± 6.09, z = 2.455) (Table 5).

Table 4. The variables included in the top 10 models for grey seals with degrees of freedom, AIC values, and model weights. The top 2 models in bold have higher weights than other models and were used for the final model

Model	Integer	Cos(ta)	Depth	Log(sl)	Scale(distance)	Scale(sl)	Slope	Str(step_id)	Cos(ta):depth	Cos(ta):scale(distance)	Cos(ta):slope	Depth:scale(sl)	Scale(distance):scale(sl)	Scale(sl):slope	df	AICc	Weight
1	+	**-0.1**	**0.03**		**-1.26**	**0.32**	**-5.34**	+		**0.06**	**14.86**	**0.01**	**0.05**	**-19.79**	**10**	**18453**	**0.19**
2	+	**-0.1**	**0.03**	**0.06**	**-1.26**	**0.28**	**-5.52**	+		**0.06**	**14.99**	**0.01**	**0.05**	**-20.45**	**11**	**18453**	**0.18**

Model	Integer	Cos(ta)	Depth	Log(sl)	Scale(distance)	Scale(sl)	Slope	Str(step_id)	Cos(ta):depth	Cos(ta):scale(distance)	Cos(ta):slope	Depth:scale(sl)	Scale(distance):scale(sl)	Scale(sl):slope	df	AICc	Weight
3	+	-0.09	0.03		-1.23	0.32	-5.14	+			12.99	0.01	0.05	-19.83	9	18454	0.11
4	+	-0.09	0.03	0.06	-1.24	0.28	-5.32	+			13.12	0.01	0.05	-20.48	10	18454	0.11
5	+	-0.15	0.03		-1.25	0.31	-5.46	+	0		13.59	0.01	0.05	-19.74	10	18455	0.09
6	+	-0.15	0.04	0.06	-1.25	0.28	-5.64	+	0		13.72	0.01	0.05	-20.4	11	18455	0.09
7	+	-0.11	0.03		-1.26	0.31	-5.37	+	0	0.06	14.81	0.01	0.05	-19.78	11	18455	0.07
8	+	-0.11	0.03	0.06	-1.26	0.28	-5.55	+	0	0.06	14.95	0.01	0.05	-20.44	12	18455	0.07
9	+	-0.1	0.03		-1.25	0.28	-5.16	+		0.06	14.79	0		-21.27	9	18456	0.05
10	+	*-0.1*	*0.04*	*0.06*	*-1.25*	*0.24*	*-5.34*	+		*0.06*	*14.93*	*0*		*-21.95*	*10*	*18456*	*0.05*

Table 5. Averaged coefficient values of model parameters of the two best models for grey seals

Model parameters	Coef.	Exp(coef)	SE(coef)	Z
Depth	0.035	1.04	0.005	7.557
Scale(distance)	-1.26	0.28	0.675	-1.866
Slope	-5.55	0.004	6.51	-0.853
Scale(sl)	0.280	1.32	0.046	6.088
Log(sl)	0.06	1.06	0.044	1.362
Cos(ta)	-0.11	0.895	0.074	-1.491
Depth : scale(sl)	0.006	1.01	0.001	7.333
Scale(distance) : scale(sl)	0.05	1.05	0.023	2.139
Slope:scale(sl)	-20.4	0.000	3.96	-5.157
Depth:cos(ta)	-0.000	1.00	0.001	-0.141
Scale(distance) : cos(ta)	0.058	1.06	0.048	1.211
Slope:cos(ta)	15	3110000	6.09	2.455

3.2 Ringed seal

A positive selection for deeper areas was observed for ringed seals (0.051 ± 0.02, z = 2.572) (Table 6). The negative coefficient for the cosine of turning angle (-0.068 ± 0.091, z = -0.739) indicates that no directional persistence was observed within the steps that were used in the model (Table 6). Ringed seals selected for areas further from coast (2.839 ± 1.838, z = 1.545) and had shorter step lengths in deeper areas (-0.022 ± 0.978, z = -3.16) (Table 6), meaning they moved less in deeper waters. Ringed seals also had shorter step lengths when further from coast (-0.807 ± 0.185, z = -4.352) (Table 6).

Table 6. Coefficient values of model parameters of the best model for ringed seals

Model parameters	Coef.	Exp(coef)	SE(coef)	Z
Depth	0.051	1.053	0.02	2.572
Scale(sl)	-0.968	0.380	0.285	-3.399
Log(sl)	0.124	1.132	0.095	1.309
Cos(ta)	-0.068	0.935	0.091	-0.739
Scale(distance)	2.839	17.093	1.838	1.545
Depth : scale(sl)	-0.022	0.978	0.007	-3.16
Scale(sl) : scale(distance)	-0.807	0.446	0.185	-4.352

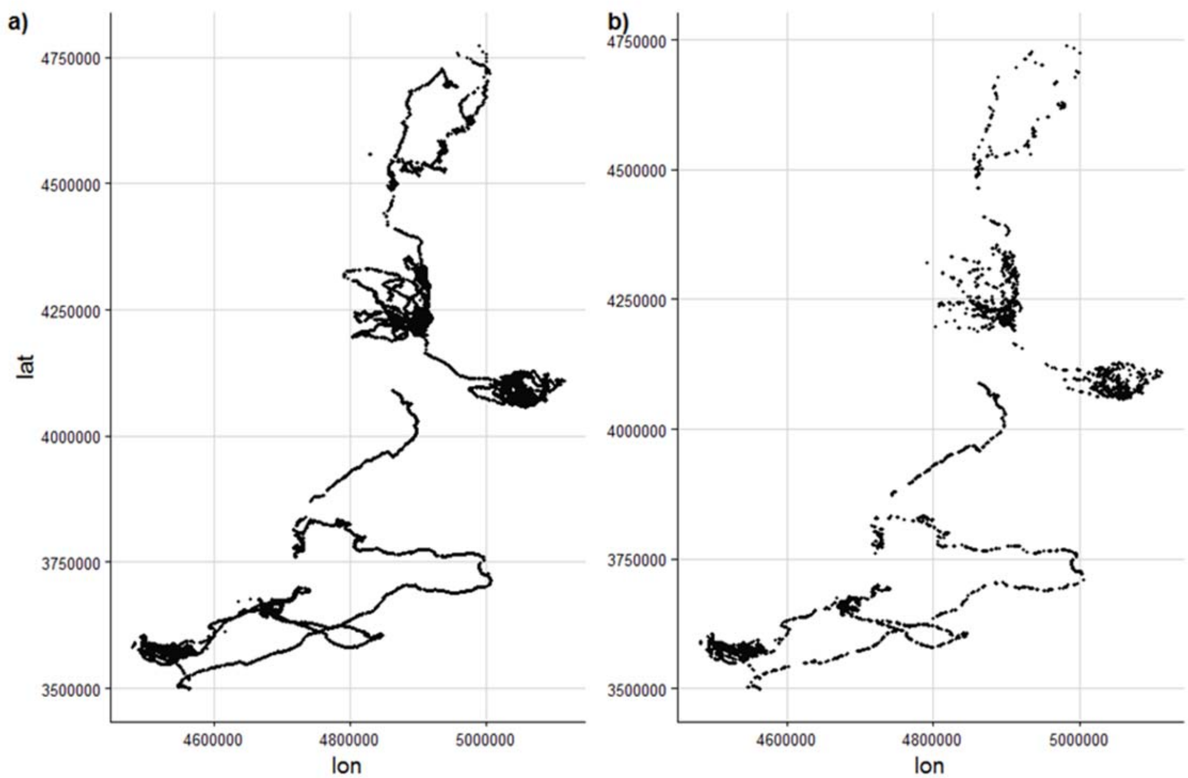

Figure 13. a) All grey seal location fixes after cleaning tracks, b) grey seal fixes used in step selection analysis (only burst length of at least 3).

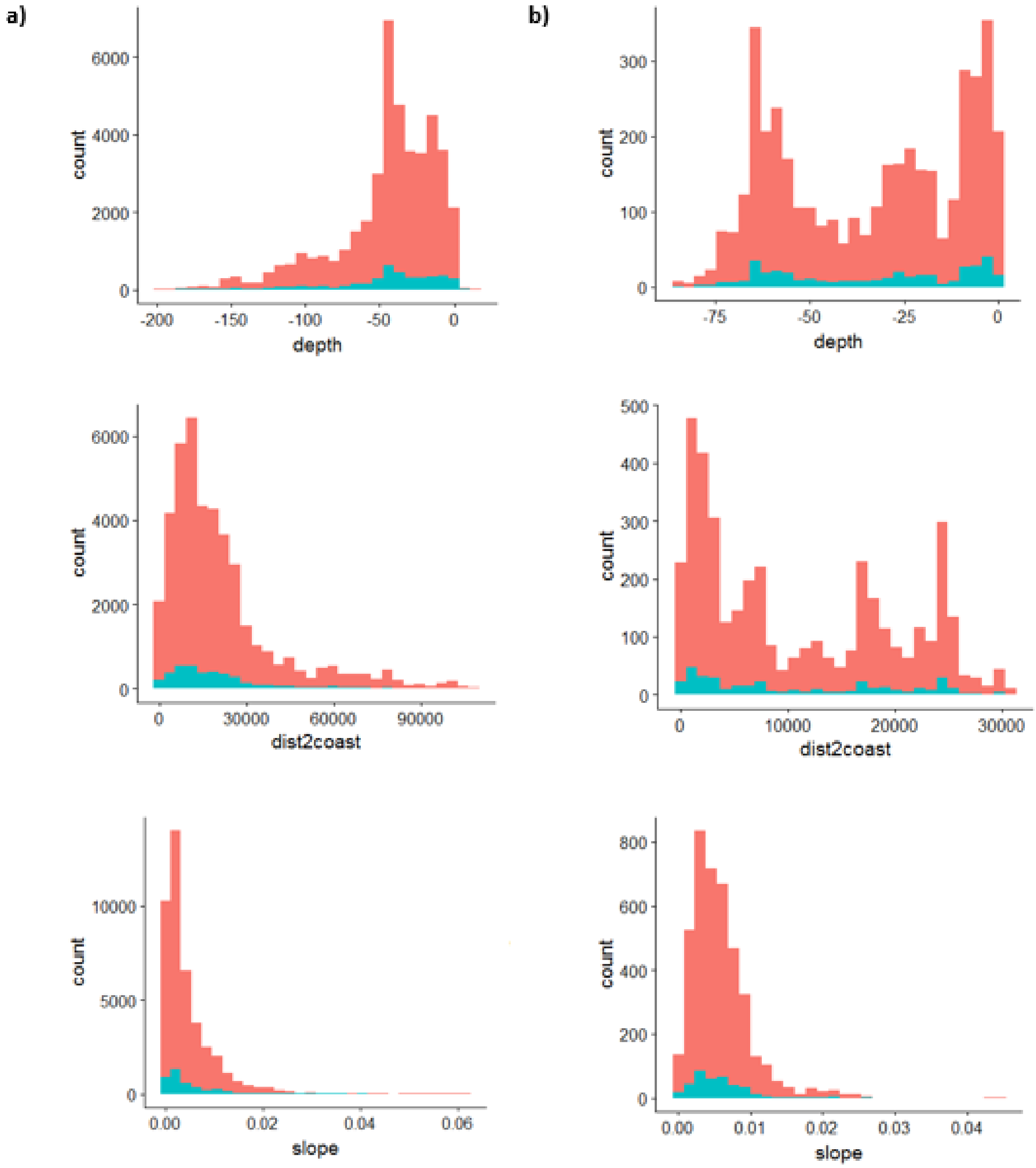

Figure 14. Distributions of variable values for used steps (blue) and random steps (red) in step selection analysis. a) grey seals, b) ringed seals.

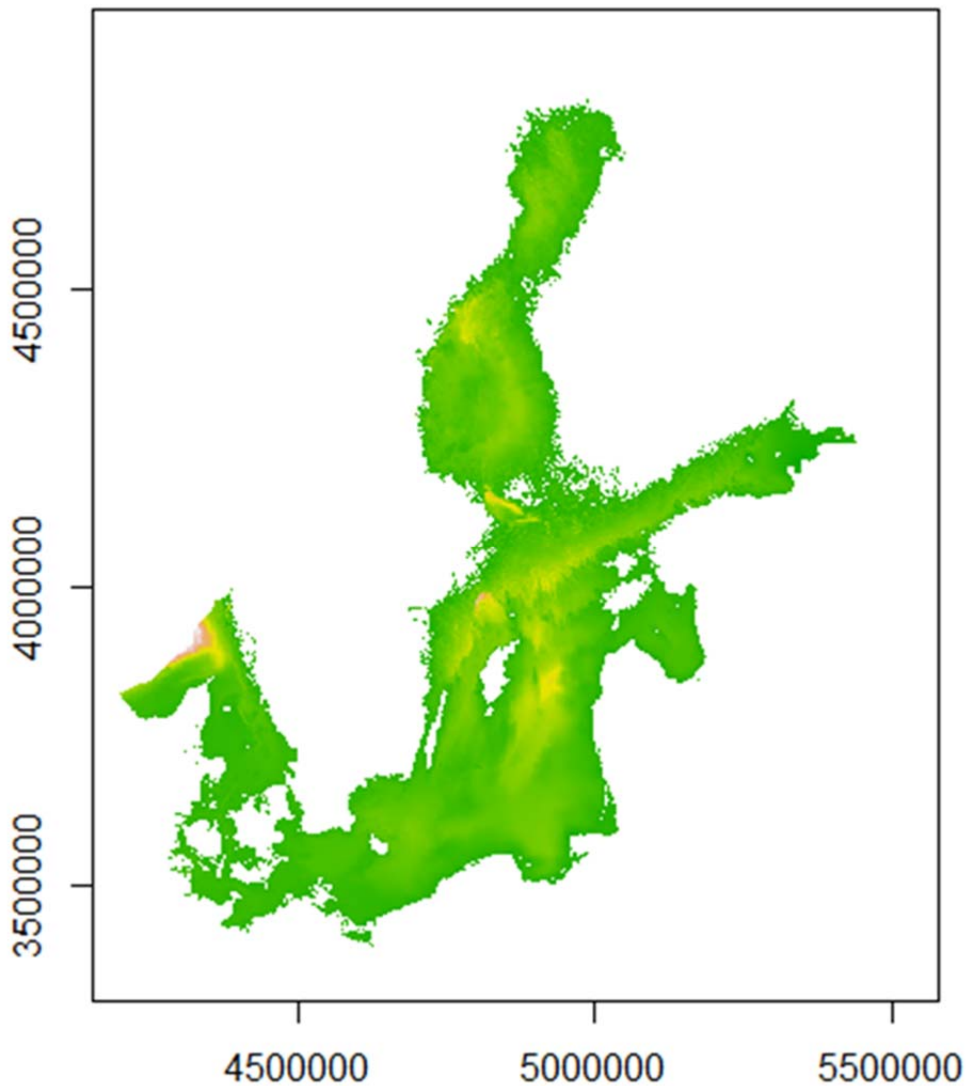

Figure 15. Bathymetric map of the Baltic Sea (HELCOM Map and Data Service, http://maps.helcom.fi/website/mapservice/index.html).

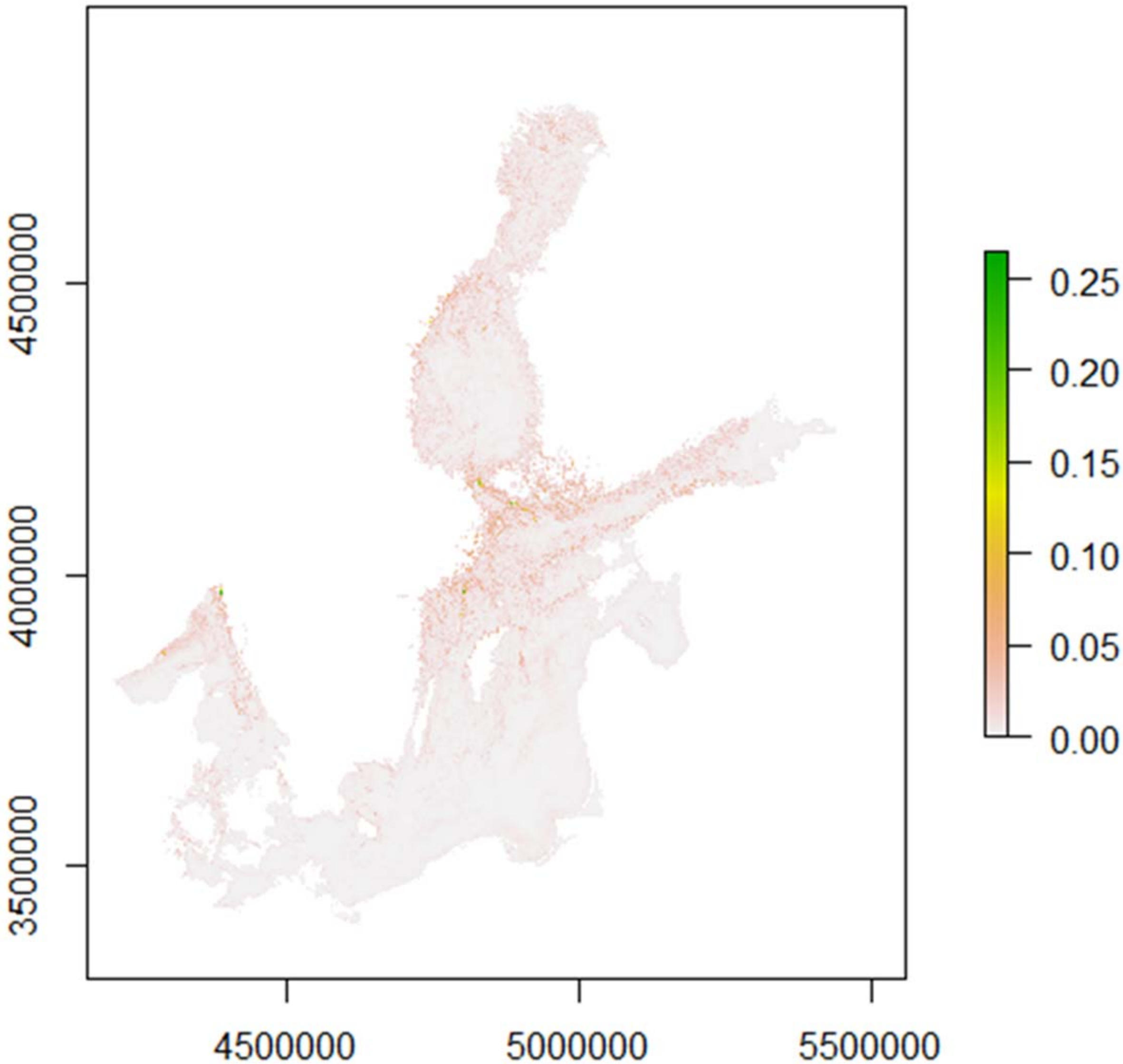

Figure 16. Incline map of the Baltic Sea. As can be seen, steeper slopes are concentrated close to the coastlines and near the Åland Islands (HELCOM Map and Data Service, http://maps.helcom.fi/website/mapservice/index.html).

4. Discussion

Using iSSA allowed to understand which variables seals select for and using movement parameters such as step length and turning angle in the model helped to see how environmental variables lead to changes in their movement behaviour. The models do not allow for an interpretation of the relative strength of variables without further analysis, because of transformations and the differences in scales of the parameters. Therefore, the effects of parameters can vary in strength, and this should be considered when drawing any conclusions.

I expected positive directional persistence to be manifested in grey seal movement as this seal species is more long-ranging. My data and previous studies show that they can travel over 500 km during 1 or 2-week trips, but they can also spend long periods of time around the same haul-outs (Sjöberg et al., 1995; Karlsson, 2003). One grey seal in the study moved from Sweden to Lithuania, Germany, Denmark and back to Sweden in 5 months, whereas the other moved from northern Sweden to western Estonia in 10 months (Figure 11). However, the best models did not give support for directional persistence as the coefficient for the cosine of turning angle was negative. Positive directional persistence is often observed at high fix rates and tends to decrease with increasing time between GPS locations (Morales et al. 2004; Haydon et al. 2008). It is difficult to say, why directional persistence was not seen at the used fix rate of 15 ± 2 minutes. It could perhaps be that even when moving between opposite coasts of the Baltic Sea, they change direction due to feeding opportunities often enough to not show directional persistence. It has been proposed that the habit of grey seals diving to the bottom during travelling allows for opportunistic feeding (Thompson et al., 1991). No directional persistence could point to seals being opportunistic feeders that might stop a directional movement to chase after prey as they are encountered. It has also been proposed that directional persistence can help herbivores avoid resource depletion (Prokopenko et al., 2017). As seals feed on many species that all have somewhat different movement patterns, seals might not have to be concerned about depletion of resources and can chase after and feed on prey as they are encountered. Another option is that if seals stayed underwater for longer periods when making long directional movements, these steps could have been filtered out from our data as movement fix rates had to be between 13 and 17 minutes for 3 steps in a row to be included in the analysis. This could be checked by plotting the steps that remained after filtering and looking at whether such movements have been filtered out. A visualisation of remaining steps indicates that many points have been filtered out from the parts of the track where seals seemed to be moving in a straight line (Figure 13). However, it is difficult to visually tell whether such filtering has lost relatively more possibly consecutive directional movements. Sjöberg et al. (1995) have shown that grey seals' mean dive duration is about 3.12 ± 1.87 minutes; only rarely were dives longer than 10 minutes, which suggests that seals in our study probably also didn't spend longer time on a single dive than was the fix rate used in the study, but due to resampling and 3 consecutive steps having to be in the correct range, longer dives could still affect which steps were used in the analysis. If there was a pattern of longer dives at certain locations, then this could introduce a bias by filtering out relatively more of such steps. Further analysis might give a better explanation for the seen pattern. Directional persistence near steeper slopes could be explained by seals following steep slopes when making some of the long directional movements. It was also checked whether this pattern could have been explained by seals crossing sharp depth contours when moving over the deeper waters of the open sea, but this does not seem to be the case as the incline map shows that steeper slopes are concentrated near the coasts (Figure 16). It seems that seals might like following the coastline where steep incline can be found, and maintain directional persistence in these areas. Habitat use in phocids has been shown to depend on underwater trenches (Thompson et al., 1991). Sjöberg & Ball (2000) hypothesized that grey seals might concentrate their feeding to steep slopes to take advantage of herring schools being more stationary in these areas (Hessle, 1925). As seasonal movements of herring are also dependent on bathymetry (Hessle, 1925), there should be an interaction between bathymetry and grey seal feeding behaviour. The raster used in this analysis was constructed from a 500 meter pixel resolution depth map, which might be too low resolution to identify use of ridges and underwater structures that might influence seal movement. Depth contour maps with better resolution should be used in the future to see whether seals are attracted to such features. Directional persistence was also not present for ringed seals, but that is in line with the original prediction as ringed seals are more sedentary (Härkonen et al., 1998). The ringed seals in my sample were all located in vicinity of each other and stayed near the same haul-outs for the entire data collection period (Figure 11). It seems that the fix rate of 10 ± 2 minutes was long enough to not show directional persistence.

Both grey and ringed seals selected for deeper areas than were available in the vicinity. This might point to the fact that although these seals spend time in shallow areas due to using haul-outs, they might choose to spend their feeding and travelling time in deeper waters. Studies have shown that ringed seals like to forage in shallow areas (Oksanen, 2015), although information is not available on decisions made at such fine scales as in this study. In my data, there were two peaks in ringed seal depth distribution, one close to zero and another around 60 m (Figure 14). Previous studies have also indicated that grey seals select for certain depths. In identified home ranges, they have been shown to select for depths of 11–40 m and to avoid areas of >51 m (Sjöberg & Ball, 2000; Oksanen et al., 2014). Similar pattern was evident in my study as grey seals spent most of their time in areas of <50 m, though there seems to be a peak at just before 50 m depth. However, when previous studies showed that seals spend time in shallow areas (Sjöberg & Ball, 2000; Oksanen et al., 2014), then my study showed that both seal species select for deeper areas compared to what is available within the range of a single step. As iSSA defines availability more precisely, comparing the bathymetry of the selected step with what is available in its vicinity, it was possible to see that although seals are bound to shallower areas (or to ice) due to haul-out sites, they seem to select for deeper water in those areas. Correctly defining availability has always been an issue in habitat selection studies, and iSSA shows that when precise availability of depth in the vicinity is defined, then seals select for deeper areas. This could be due to prey availability or ease of travelling without obstacles. In the Baltic Sea, choosing for deeper areas does not automatically mean selecting areas further from coast as the bathymetry is complex and does not follow a uniform pattern of increase in depth with distance to coast (Figure 15). This is also evident from the fact that correlation between depth and distance to coast was not significant. Therefore, the relationship is more complex.

When it comes to step length, grey seals had longer step lengths in deeper areas and further from the coast, whereas ringed seals showed an opposite pattern. This means that grey seals moved further between two consecutive GPS fixes, and therefore, also moved faster, when they were in deeper waters. Ringed seals, however moved less and slower when in deeper waters. This trend is somewhat contradictory, but could perhaps be explained by the difference in water depths that these species use (Figure 14). Grey seals in the study made long-distance movements crossing the Baltic Sea and at times, were even over 100 km away from the coast. Ringed seals stayed much closer to the coast and spent half their time within 10 km of the coast (Figure 14). Thompson et al. (1991) inferred from dive profiles that short duration trips in grey seals were foraging dives. During these dives, seals are known to spend time motionlessly at the bottom, possibly to ambush prey (Thompson et al., 1991), and to swim at speeds between 1–2 m/s, which is lower than when travelling (Fedak & Thompson, 1993). If it is correct to assume that feeding behaviour would be seen as shorter step lengths due to slower swim speed, non-directional chasing movement, and handling time, then it might be hypothesised that grey seals show long step lengths when they are moving longer distances in deeper waters. If they feed and rest closer to the coast, their step lengths would be shorter in these areas as they move between resting and feeding areas, and also whilst they spend time at feeding areas. Grey seals might be swimming faster in deeper areas, perhaps due to feeding less or because they choose to go to deeper waters to make longer movements. As ringed seals spend their time mostly in shallow areas, then their behaviour of making shorter steps in deeper water and further from coast could be due to them going to deeper areas to feed.

Water currents could also affect seal's step lengths. Water currents in the Baltic Sea are not permanent, but irregular currents still form in certain areas, especially in open sea due to changes in sea level, wind strength and direction (SMHI). Currents are the strongest in the sounds, and can move at up to 9,260 m/h (SMHI), which would transport seals 2,315 meters in 15 minutes. If grey seals spent time at open sea and in sounds, then the mere effect of currents could add to their movement rate in these areas. Additionally, currents might also either lower directional persistence by taking seals in another direction when they stopped for short periods, or increase directional persistence by taking them in the same direction when seals were resting for longer periods. However, as currents in the Baltic Sea are irregular, then their effect in the study is difficult to predict.

Grey seals had shorter step lengths when slope of the seafloor was steeper. As steeper slopes can be found near the coastline and near the Åland Islands, then it seems that grey seals might be feeding in these areas. Grey seal's diet consists of many commercially important fish, such as Atlantic herring (*Clupea harengus*), common whitefish (*Coregonus lavaretus*), and European sprat (*Sprattus sprattus*) (Lundström et al., 2010). These three species contribute an estimated 84.7% of the total biomass consumed (Lundström et al., 2010). It can therefore be expected that grey seal's feeding behaviour is closely linked with the occurrence and behaviour of these species. During foraging dives, grey seals swim slowly, mostly on or near the seabed as they are known to mainly feed on demersal and benthic fish (Thompson et al., 1991). Herring and sprat make diel vertical migrations – they are dispersed on the surface at night and form schools at the bottom after dawn (Cardinale et al., 2003), when grey seals seem to be doing most of their feeding dives (Sjöberg et al., 1995). Therefore, grey seals seem to be taking advantage of the aggregated fish schools. These schools are more stationary in areas with steep slope and as seasonal movements of herring are also dependent on bathymetry (Hessle, 1925), there should be an interaction between bathymetry and grey seal feeding behaviour. Therefore, it is possible that shorter step lengths over steeper slopes represent grey seals feeding on the stationary herring schools. Additionally, directional movements following the coastline and short step lengths over these steep areas could be explained by grey seals following migrating salmonids. Both of the explanations could be better looked at by including dive types, prey availability, and time of day in the iSSA.

Ringed seals in the Baltic Sea have been believed to be sedentary (Härkonen et al., 2008), but more recent data shows that they range over large distances during open water season (Oksanen et al., 2015). Ringed seals in this study stayed around the same islands for the duration of the study period. This species is known to be limited in its movements during ice-covered times when individuals maintain breeding holes in ice (Kelly et al., 2010). However, this can't explain their limited range in this study as there was no ice cover in the area during the tracking period (CHNL Information Office). As ringed seals tracked by Oksanen et al. (2015) ranged over large distances compared to the ones in this study, it can be hypothesised that individual ringed seals' movement ranges vary, or that their behaviour can change during their lifetime.

Grey seals in the study were wide-ranging. One of them moved from Sweden to Lithuania, Germany, Denmark, and back to the Swedish coast in a few months. Karlsson (2003) has said that because the individuals they studied liked to stay in the vicinity of one or a few haul-outs, the seals in the Baltic Sea should not be managed as a single management unit. It is difficult to make conclusions from only the two grey seals in the study, but it seems that these individuals travel around quite a lot, with the exception of one of them staying in the vicinity of the north-west coast of Estonia and near the Åland Islands for longer times. Without yearly tracking records, it is unknown whether the same seals make the same journeys each year and at same times of the year, though there is indication of female grey seals exhibiting site fidelity during the summer for more than a single season (Karlsson, 2005). Genetic studies can show whether individual management units are necessary. But, with the current knowledge, it seems impossible to design separate management units as seals can travel thousands of kilometres and between many countries. Obtaining enough inter-annual records to design separate management units will take time and it would be costly. Additionally, taking it into account during culling seems infeasible as hunters would need to separate between local and travelling seals.

Oksanen et al. (2014) classified most of the grey seals in their study as residents as they remained within 120 ± 62 km from their capture sites during the ice-free period, and based on that, recommended that selective removal of seals could be a method for reducing seal-fishery interactions locally. The seals in my study moved extensively during the same time, and based on that, I can't recommend selective culling as a local management measure. It is unknown, how long it would take for new seals to colonize the area and replace the killed seals. As the habitat of grey seals strongly overlaps with coastal fishing activities, resident seals can visit the vicinity of trap-nets on 30% of the days (Oksanen et al., 2014), meaning that a large proportion of grey seals could be hunted in Sweden, where hunting is allowed to be conducted within 200 m from fishing gear. Which seals are actually visiting gear, will be difficult to tell without further studies. Although hunting has been a wide-spread management option, almost never has an attempt been made to evaluate the benefit of such interventions (Bowen & Lidgard, 2011). Additionally, a large part of catch is lost because seals damage fish in nets barely eating them, meaning that their damages are not in direct relationship with seals' food intake needs. This means that even one seal could do a lot of damage, and therefore, interventions that concentrate on protecting catches with deterrents or by seal-proofing, would be better in the long term. As the conservation goal is to let seal numbers in the Baltic Sea increase, hunting cannot have a large or long-lasting impact and attention should be put into gear development. This is a costly and long-term undertaking that is out of reach for individual fishermen; therefore, I encourage governments and research organizations to focus their attention on this management option. Hunting works to decrease fishermen's frustration as they feel like they have control over the damages, but in reality, it is not an effective long-term mitigation measure. On the other hand, this paper adds support to the belief that a portion of the ringed seal population exhibits strong site fidelity (Härkonen et al., 1998; Kelly et al., 2010; Oksanen et al., 2015), and therefore, local management interventions for ringed seals could be more effective and seem to be easier to implement. The proportion and distribution of ringed seals with strong site fidelity is however not known, and without this knowledge, it is difficult to say how effective local management would be. Another problem is the very limited knowledge of ringed seals' diet, which means the exact overlap and conflict with the fishing industry is not known.

5. Conclusion

As the relative effects of environmental variables were not identified, it is not possible to say which variables affect seal movement decisions the most. This study has shown that iSSA can be used on limited marine mammal data to simultaneously infer movement patterns and habitat selection. This furthers knowledge of seal movements and distributions in the Baltic Sea and can aid conflict management with the fishing industry. Currently, gaining such knowledge is difficult as technical problems with the GPS devices and lack of cooperation between different research teams and Baltic Sea countries lead to small sample sizes and geographically limited data. For example, with small samples it is not possible to identify patterns or differences in movement between different sexes, populations and times of the year or to look at the influence of underlying factors such as salmon migrations. However, as seals are creating problems for all the coastal nations, and as HELCOM is advocating joint management of seals, then I believe that in the future, such cooperation would be vital to be better able to understand seal movements in the Baltic Sea. I also hope to have demonstrated that data from more individuals could be analysed with iSSA to look at the effect of variables such as presence of fishing gear, aquaculture, acoustic deterrents, catch sizes, prey migrations, and culling.

Overall Conclusion

Currently, the seal-fishery conflict is being managed without full information of almost any of the aspects of the conflict, and this is limiting the effectiveness of management actions. Only a few studies have attempted to look at the amount of damaged fish and the frequency of fishing gear damage, but the seasonal and year-to-year variability in catch and damages means that a few studies can't be used to extrapolate damages for the entire Baltic Sea. Therefore, total monetary damages caused by seals in the Baltic Sea have never been fully calculated. Another unknown part of the equation is the value of environmental damages caused by active fishing gear such as trawls. Such negative effects should be taken into account when designing a sustainable fishery in the Baltic Sea. There is evidence that trawling for herring can be very environmentally damaging, whereas the coastal gillnet fishery is an environmentally friendly option. Additionally, there is value to the broader society from having thriving coastal communities. Without knowing a monetary figure behind all these positive and negative aspects of the conflict, it is difficult to decide, how much governments should invest into solving the conflict.

I would argue that governments have not been doing enough to solve the conflict, but have instead used monetary compensation and hunting to reduce the anger from fishing communities. As more and more fishermen stop fishing, compensation payments will be reduced, and therefore, governments might think of compensation payments as a temporary cost that they can afford. However, this money could be better used for other conservation projects if gear development was faster. If profitability of coastal fisheries was to increase, then coastal fishing communities could co-exist with high seal numbers. Although, the number of fishermen in the future would also depend on large scale societal changes, then it is probable that the number of fishermen would be higher if profitability was higher. Compensation goes against market forces in that it reduces fishermen's motivation to reduce damages, and it is only justified as a short-term measure to ease fishermen's financial losses as new gear is being developed. However, governments have not done enough to help with the development of such gear, or in helping to create affordable solutions for fishermen. Governments have to make a choice of whether a viable coastal fishery is in their interest, and if it is, they should divert their attention to developing gear and creating seal-free areas as has been shown to work in Norafjärden. Developing seal-proof fishing gear is also important because seals damaging fish causes both significant monetary loss as well as loss of biological resources that could be avoided.

Many studies from the Baltic, including this one, have shown that grey seals stay in smaller home ranges for parts of the year (Oksanen et al.,2014, Sjöberg et al., 1995). It has been suggested that hunting grey seals could be a viable management option, especially if there were so called "problem seals", support for which has sometimes been weak. For example, Oksanen et al. (2014) support the problem seal hypothesis by the mere fact that males get trapped in fishing gear and are shot near fishing gear more often than females, and that they eat larger fish compared to females. Additionally, it has been shown that grey seals that get trapped in fishing gear have thinner blubber and are in worse condition. These seals might be taking risks due to their poor condition, but there is no information regarding the condition of seals that raid nets or that wait by traps, behaviours that do not entail large risk of getting trapped. Even if we assumed that mostly only weak males were raiding traps, then we still do not have an overview of how large of a proportion of the seals were in sufficiently bad condition and whether we were removing enough of the right individuals to have a significant impact. Culling has been used as a management option for a very long time in many parts of the world to reduce damages from seals to the fishing industry, but the effects of culling have almost never been measured. For culling to work, there should be estimates and certain plans so that the right amounts of right individuals could be targeted and the effects should be measurable. It is believed that for culling to have an impact, populations of seals should be significantly reduced, and kept at a lower level as the effects of a cull will fade quickly as populations start increasing. In the Baltic Sea, seal populations will increase as seals are protected. In such a situation, it is difficult to believe that seal cull is having a significant positive impact. How low would the population have to be, or how widespread should hunting be for there to be significantly less individuals raiding gear is not known. The Estonian government has reinstated seal hunt to bring back an old tradition for the communities, but their official stand is that it will not reduce seal damages. This seems to be the correct assumption as reducing the population growth just by a little bit does not seem to be an actual mitigation measure against seal damages, rather a measure that might make fishermen feel less frustrated.

More needs to be known to be able to manage seal populations, especially in the face of climate change that is thought to negatively impact ringed seal populations. Integrated step selection analysis of seal tracks is a step closer to understanding fine scale decisions by seals. Such research can in the future be used to model the distributions of seals throughout the year, to reduce conflict with fishing and other industries, as well as in designing protected areas.

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Chapter 1

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