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Competition for the fish - fish extraction from the Baltic Sea by humans, aquatic mammals and birds

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Abstract

Populations of fish eating mammals (primarily seals) and birds have increased in the Baltic Sea and there is concern that their consumption reduces fish stocks and has negative impact on the fishery. Based primarily on published data on fisheries' landings and abundances, consumption and diets of birds and seals around year 2010, we compare consumption of commercial fish species by seals $(1*10^5 \text{ metric tons per vear})$ and birds $(1*10^5 \text{ tons})$ to the catch in the commercial and recreational fishery $(7*10^5 \text{ tons})$, and when applicable at the geographical resolution of ICES subdivisions. The large populations of herring (Clupea harengus), sprat (Sprattus sprattus) and cod (Gadus morhua), primarily inhabit off-shore areas and are mainly caught by the fishery. Predation by birds and mammals likely has little impact on these stocks. For these species, seals and birds may be negatively impacted by competition from the fishery. In the central and southern Baltic, seals and birds consume about as much flatfish as is caught by the fishery and competition is possible. Birds and seals consume 2-3 times as much coastal fish as is caught in the fishery. Many of the coastal species are not much targeted by the fishery (e.g. eelpout Zoarces viviparus, roach Rutilus rutilus and ruffe Gymnocephalus cernua), while other species used by wildlife are important to the fishery (e.g. perch Perca fluviatilis and whitefish Coregonus spp.) and competition between wildlife and the fishery is likely, at least locally. Estimated wildlife consumption of pike (*Esox lucius*), sea trout (*Salmo trutta*) and pikeperch (*Sander lucioperca*) varies among ICES subdivisions and the degree of competition for these species will likely differ among areas. Our results indicate that competition between wildlife and fisheries need to be addressed in basic ecosystem research, management and conservation. This requires improved quantitative data on wildlife diets, abundances and fish production.

Keywords

Baltic Sea, bird, catch, competition, fisheries, food consumption, seal

Introduction

The exploitation of many fish stocks is intensive, and for many years overfishing has been on the political agenda (e.g. UN, 2002; EU, 2009). With recreational fishing as a fast growing component of the tourism-industry, increasing fishing pressure must be expected also on other species than those targeted by commercial fisheries (Coleman *et al.*, 2004; Lewin *et al.*, 2006; Ihde *et al.*, 2011).

There is increasing awareness that fish are vital to the functioning of aquatic ecosystems (Crowder *et al.*, 2008; Cury *et al.*, 2011; Jensen *et al.*, 2012; Morissette *et al.*, 2012; Östman *et al.*, 2016) and fish sometimes even impact terrestrial environments (Hilderbrand *et al.*, 1999; Moore and Schindler, 2004). Consequently, it has become generally accepted that fisheries need to be managed using an ecosystem approach (EU, 2009; Essington and Punt, 2011). Acknowledging that "stakeholders" other than humans play an important role, focus turns to the potential competition between humans and other fish consumers, such as marine mammals and birds. Numerous studies have addressed the possibility of increasing fishery by reducing abundances of competitors, as well as the impact of fisheries on the foraging conditions of top predators (e.g. Corkeron, 2004; Pikitch *et al.*, 2004; Cury *et al.*, 2011; Morissette *et al.*, 2012; Bowen and Lidgard, 2013; Hilborn *et al.*, 2017).

In the Baltic Sea, issues of competition between fishery and predatory (fish eating) wildlife have been considered for at least two centuries. When inexpensive Norwegian whale oil flooded the market in the end of the 19th century the production of seal oil became unprofitable, reducing hunting (Harding and Härkönen, 1999). As a consequence, seals became considered competitors rather than resources and bounty systems were initiated to reduce the seal populations (Sweden 1903-1967, Denmark 1889-1977, Finland 1909-1975).

Hunting reduced the ringed seal (*Pusa hispida*) population from about 180 000 in the beginning of the 20th century to about 25 000 in the 1940s. Grey seals (*Halichoerus grypus*) and harbour seals (*Phoca vitulina*) decreased from about 80 000 to 20 000 (Harding and Härkönen, 1999) and 5 000 to 500 (Härkönen and Isakson, 2010) individuals, respectively. After the closure of the bounty systems, organochlorine pollutants (mainly PCB and DDT) brought the populations close to extinction through diseases and sterility (Bergman and Olsson, 1985; Bergman, 1999). All Baltic seal species plunged and only some 3 000 grey, 2 000-3 000 ringed and 200 harbour seals remained in the 1970-80s (Harding and Härkönen, 1999; Härkönen and Isakson, 2010). Drastic reductions in the levels of these toxic substances have since improved the health of the seals (Bergman, 1999; Bäcklin *et al.*, 2011) and since the late 1980s populations have increased by 6-9% annually (Harding *et al.*, 2007).

Seals are not the only fish predators that have increased over the last decades. From being nearly absent from the Baltic in the beginning of the 20^{th} century, the population of the great cormorant (*Phalacrocorax carbo sinensis*) has increased from some 6 500 nesting pairs in 1981 to >150 000 pairs in 2006-2012 (Herrmann *et al.*, 2014). This rapid increase is parallel to that recorded across Europe (Carss, 2003; Bregnballe *et al.*, 2014).

With growing populations of seals and cormorants, their impacts on fish stocks and possible exploitative competition with commercial and recreational fisheries have become increasingly discussed. Public debates are sometimes heated. Some fisheries stakeholders demand culling to reduce cormorant and seal populations, while some conservationists advocate for sustained protection. One reason for the strong polarization in the debate is the lack of data on fish consumption by predators and the fishery catch, as well as of estimates of their effects on fish populations. The objective of this paper is to collate and present quantitative data on fish extraction by the fishery, mammals and birds – how much are caught in different parts of the Baltic Sea, and of which fish species. These quantitative data constitute the results section of this paper, and in the discussion we combine our data with estimates of fish production and published studies on the impacts of fishery, seals and birds on fish Baltic Sea fish stocks. This synthesis will hopefully support a more informed debate on resource competition between wildlife and humans and provide relevant information for resource management.

Material and Methods

The data used in the analyses have been derived from a multitude of sources: scientific publications, reports and unpublished information. Abundances of birds and aquatic mammals, and the fishery catch are from around year 2010, depending upon data availability. The full derivation of all data is described in three supplementary documents, each focusing on one of the three consumer groups (S1=mammals, S2=birds, S3=fishery). Due to data scarcity and uncertainties, consumption and catch estimates are coarse, but the data used are the best available given the geographical resolution and extent of the study, covering spatial scales from regional to whole basins.

Discards have not been included in the catch as data are uncertain or missing, in particular for coastal species. No assumptions have been made on the quantities of fish mortally wounded but not consumed by birds and seals (c.f. Davis *et al.* 1995; Adámek *et al.* 2007; Kortan *et al.* 2008; Bergström et al. 2016).

Estimates of fish consumption by mammals and birds were done in two steps. First, abundances of predatory birds and mammals were compiled for areas corresponding to subdivisions (SD24-32, Figure 1). Second, these abundance data were combined with consumption rates and diet compositions to derive estimates of the extraction of different fish species. Depending on the population structure of different fish species and the spatial resolution in the data on fishery catch, the geographic scale at which these extraction rates are presented vary from the entire Baltic to individual ICES subdivision.

Six predatory mammals were considered: grey seal, ringed seal, harbour seal, American mink (*Neovison vison*), harbor porpoise (*Phocoena phocoena*) and common otter (*Lutra lutra*). For birds, fish consumption was estimated for 21 species. Data on abundances, diets and estimated consumption rates for mammals and birds are in supplementary documents S1 and S2.

Fishery landings were estimated separately for the commercial and recreational fishery (S3). Data on the commercial catch were mainly based on information from ICES. Landings by anglers are not as well documented, but for Estonia, Finland, Russia and Sweden, covering most of the Baltic coast there are assessments available.

Exploitative competition between fisheries and wildlife occurs if the catch/consumption of a fish species by one group has adverse effects on another consumer group. Field observations of decreased abundance of a fish species in response to fisheries and/or predation by wildlife imply exploitative competition. Reduced catch caused by wildlife's interference with fishing gear is not considered in this paper.

Estimates of effects of predation and fishery on fish populations should ideally be based on consumption vs. production rates. Production rates are difficult to derive for fish as abundance measurement and age structure data often are of poor quality or missing, in particular for coastal species consisting of local populations. In addition, compensatory processes such as increased growth and/or survival of juveniles in response to increased fisheries/predation (Rose *et al.*, 2001) complicate analyses. Production in populations that are lightly exploited may increase as a result of increased fishery but at some point compensatory processes cannot compensate for further mortality increases. At this point production decreases and the decrease in population size accelerates (e.g. Hilborn and Walters, 1992).

If possible, and as described above, catch and consumption should be compared to production estimates. For sprat (*Sprattus sprattus*), herring (*Clupea harengus*) and cod (*Gadus morhua*) which together have been suggested to constitute some 80% of the Baltic Sea fish biomass (Elmgren, 1984; Thurow, 1984), there are production estimates based on ecosystem analyses. Elmgren (1984) proposed a fish production of 11-12 metric tons per km²*yr⁻¹ for the Baltic Proper (SD24-29) and the Gulf of Finland (SD32), and 7.6 and 2.8 tons for the Bothnian Sea (SD30) andthe Bothnian Bay (SD31). Of the production, landings in fisheries corresponded to 24-26%, 15% and 10% in the three regions respectively. Based partly on data from Elmgren (1984) but with more data on fish and fisheries, Harvey *et al.* (2003) reported production estimates of 3.7, 2.9 and 1.3 tons per km² for sprat, herring and cod in the Baltic Proper and Gulf of Finland (SD25-29+32). Fisheries on these populations extracted on average 16%, 29% and 47%, respectively, of the production. Tomczak *et al.* (2012) modified the model of Harvey *et al.* (2003) and calibrated it to a longer period (1974-2006). They estimated the total annual production by sprat, herring and cod to 16 tons per km² with the fishery extracting 20%, 15% and 43% of the production of these species. Wolnomiejski and Witek (2013)

presented a detailed ecosystem analysis on the Szczein Lagoon and derived at a fish production of ~45 tons per km² based on a primary production and a net allochthonous supply of 730 gC/m². Using the relationships between primary- and fish production reported in these ecosystem analyses, and a primary production of 165gC/m² in the Baltic Proper (Elmgren, 1984; consistent with intensive pelagic monitoring up to and including recent years, pers. comm. with U. Larsson, Dept. Ecology, Environment and Plant Science, Stockholm, Sweden), the fish production would be ~10 tons per km².

During the periods studied by Harvey *et al.* (2003) and Tomczak *et al.* (2012) the abundance of seals was lower than today and their predation impact was found rather insignificant, while fisheries for at least herring and cod had adverse impacts on these populations (ICES, 2015). The calculations thus indicate that extractions by fishery and predators exceeding 20-40% of the production can significantly reduce a Baltic Sea fish stock. For lakes, it has been suggested that fishing is generally sustainable at catch rates corresponding to <15% of the biomass (Downing and Plante, 1993), and as production is usually around 50% of the biomass (Downing and Plante, 1993; Randall and Minns, 2000), this corresponds to an extraction level of 30%. An extraction of 20-40% of the production will be used as reference point when discussing impacts on fish populations and competition between fishery, mammals and birds.

Results

Annual fishery landings add up to $7*10^5$ tons (Table 1) and the combined predation by mammals and birds amounts to $2*10^5$ tons ($1*10^5$ tons for each group). Humans thus extract four times more fish than seals and birds combined. Among the marine mammals, the three seal species account for >95% of the consumption (Table S1.1). Five species of birds,

cormorant, razorbill (*Alca torda*), common guillemot (*Uria aalge*), common and red-breasted merganser (*Mergus merganser* and *M. serrator*) account for 80% of the consumption by birds (Table S2.1). Focus in this paper will be on humans, seals and these five bird species.

The fishery catch is dominated by sprat, herring and cod, which together contribute ~95% of the total landing. These three fish species constitute ~60% of the consumption by seals and ~30% of the consumption by birds (Table 1). With the exception for the Bothnian Bay, where the fishery for sprat, herring and cod is limited, consumption by birds and seals is small in comparison to the catch.

Predation by seals is dominated by the grey seal (~75% of the total consumption), followed by ringed seal (~20%) and harbour seal (~5%). The estimated food consumption of grey seal consists generally of about 50% herring and 10% sprat, while eelpout (*Zoarces viviparus*), cod and cyprinids each constitute ~5% (Table S1.6). In the diet of ringed seal, herring, vendace (*Coregonus albula*) and three-spined stickleback (*Gasterosteus aculeatus*) constitutes about 40%, 30% and 20% respectively. Harbour seals feed primarily on herring (40%), but also substantially on flatfish (20%) and sprat (10%).

Among the five bird species, consumption by the cormorant constitutes 50% of the combined consumption, while razorbill and common guillemot together consume 30% and the mergansers 20%. The cormorant's diet is diverse, consisting of mainly coastal species, with on average 25% perch (*Perca fluviatilis*) and 10-15% each of eelpout, roach (*Rutilus rutilus*) and ruffe (*Gymnocephalus cernua*, Table S2.6). Diets of razorbill and common guillemot is dominated by sprat (90%), with herring and other fish species each constituting 5%. Data on

merganser diets are poor, but they are still included in the analyses (100% unspecified fish) since they contribute substantially to birds' fish consumption.

Overall, on a Baltic Sea scale, the fishery catch is considerably larger than the predation by birds and seals combined (see above). The situation is different in coastal areas, however, where birds annually consume about 4*10⁴ tons and seals 1*10⁴ tons of coastal species (all species except for cod, herring, sprat, flatfish and salmon (*Salmo salar*)). The combined consumption by seals and birds is thus substantially higher than the catch of coastal species (2*10⁴ tons). To derive these numbers, razorbill and common guillemot were assumed to feed exclusively on off-shore species. Mergansers, for which diet data are lacking, were assumed to include 50% coastal fish species in their diet, which is a conservative estimate given that they are primarily residing and foraging in shallow coastal areas. Unspecified fish in cormorant and seal diets was split into offshore and coastal fish in proportion to the quantity of identified prey from these two categories in their diets. To avoid underestimating the fishery impact, all unspecified landings were assumed to be coastal species.

In a comparison for the entire Baltic Sea, the combined consumption by predators is in the same range as the fishery catch for seven of twelve fish species (salmon, sea trout, eel (*Anguilla anguilla*), perch, northern pike, pikeperch and whitefish, Figure 2). To evaluate if this implies resource competition, other factors and data need to be considered and this is done in the Discussion section.

Discussion

Our results show that both seals and birds consume large quantities of fish and should to be carefully considered in ecosystem analyses and stock assessment models. This is particularly true for local, coastal fish populations. These populations are often small, at the same time as they are overlapping spatially with the haul-out sites for seals and feeding areas for many avian predators (three of the five consumers considered here; cormorant and the mergansers). The impacts of wildlife on the larger, off-shore populations are small compared to the fishery. However, as these fish stocks are intensively exploited by the fishery, the additional mortality caused by growing seal populations also deserve to be accounted for in resource management.

In the following, we will first focus on the extraction of fish species with a single or few populations (cod, herring, sprat, eel, flatfish and salmon) and then shift to coastal species which are reasonably sedentary, consisting of local populations. If results differ substantially among ICES subdivisions, this indicate that care is necessary when interpreting our results. For example, the estimated consumption of sea trout by seals is equal or exceeds the catch in four subdivisions, while they appear to consume no sea trout at all in four other subdivisions (Table 1). The explanation is that total consumption by seals is large and even a small proportion (1%) of sea trout in the diet results in an estimated consumption that is substantial compared to the catch. Predation impact on species that are rare it the diet are thus associated with substantial uncertainties.

The largest fish stocks (cod, herring and sprat) are under a substantial pressure from commercial fishery (ICES, 2015) while predation by seals and birds are generally small in comparison (Table 1). The fishery for these species is not in substantial competition from birds and/or seals, whereas birds and seals may be subjected to competition from the fishery. However, since these fish populations are impacted by fisheries, increased mortalities caused by seals and birds, without reductions in the fishery, may contribute to a total mortality rate that exceeds the capacity of compensatory responses.

Recruitment of eel to European waters has decreased by 95-99% over the last thirty years and the species is classified as critically endangered by IUCN (Jacoby and Gollock, 2014). The reason for this decrease is unknown and it is thus not possible to conclude if fisheries, seals and/or birds reduce the population and compete for this species. From a conservation and management perspective it is noteworthy that the predation by cormorants is of the same magnitude as the landings (Table 1).

In the central Baltic Sea (SD27-28), populations of flounder (*Platichthys flesus*) and turbot (*Scophthalmus maximus*) are impacted by the fishery, as shown by changes in abundance and size composition in a no-take area (Florin *et al.*, 2013). In some areas seals and cormorants take at least as much flatfish as the fishery (Table 1) and it is likely that there is competition for flatfish. Theoretical analyses indicate competition between cormorants and fisheries in SD25 and 27 (Östman *et al.*, 2013). More to the south (SD24-26), the catch is substantially higher than the predation by seals and birds.

Salmon and sea trout are intensively fished by both commercial and recreational fishers, and the closure of commercial offshore fishery for salmon has resulted in increased returns of adults to spawning rivers (ICES, 2016). This shows that salmon has been impacted by the fishery. This is likely the case also for sea trout, which has many local populations that reproduce in small streams.

Salmon and trout can also be important prey for seals, as described by Suuronen and Lehtonen (2012) for grey seal in the Bothnian Bay (SD31), and increased grey seal population appears to have reduced the survival of salmon substantially (Mäntyniemi *et al.*, 2012). Furthermore, local sea trout populations consisting of some tens or hundreds of adults are prone to predation effects, as seals have been observed to patrol outside river mouths and also entering into rivers to hunt for ascending fish (c.f. Middlemas *et al.*, 2006). This kind of focused predation is not captured by the broad-scale analyses of the current study. Our data (Table S1.3), in combination with previous studies, suggest that the intensity of the competition varies among different local populations.

A five years closure of the fishery for common whitefish (*Coregonus* sp., excl. *C. albula*) in a coastal area of SD30 resulted in increased catch rates (Florin *et al.*, 2016), indicating that the whitefish stock had been influenced by the fishery. Verliin *et al.* (2013) also suggested that overfishing may explain some of the long-term catch variation in this species. In the Baltic Proper and Bothnian Sea, more whitefish is consumed by grey seals than caught in the fishery (Table 1) and predation by the seals is also substantial in the Bothnian Bay and Gulf of Finland. It is thus likely that fishery and seals compete whitefish in several areas. Vendace (*C. albula*) is primarily fished in the Bothnian Bay (SD31). The fishery is intensive and managed under the assumption that it impacts the population (Andersson *et al.*, 2015). As ringed seal consume more than landed by the fishery (Tables S1.7 and S3.4; Lundström *et al.*, 2014), competition is possible.

Perch is a common species with local populations around the Baltic. There are several studies on effects of cormorant predation on perch and these are summarised in Supplement S4. Even if apparently contradictory, the results from these field studies are rather conclusive. The current fishing intensity can be sufficient to impact perch populations (Bergström *et al.*, 2007) and cormorants and seals together consume twice as much as the fishery (Table 1). Locally, in areas where perch production can be assumed to be very high, no effects of cormorant predation can be detected (Pūtys, 2012). In less productive coastal areas, representative for larger areas of the Baltic Sea, decreases in perch in response to cormorant predation can be detected in long-term data series, provided that the variation in cormorant abundance is large (strong signal) and particularly if data from reference areas allows for background variation to be taken into account (Östman *et al.*, 2012). The local effect of cormorant predation on perch can be substantial (80-90% reduction in perch, Vetemaa *et al.*, 2010; Östman *et al.*, 2012; Gagnon *et al.*, 2015), but there are no data available on how far from nesting sites that effects from cormorant predation can be detected. This distance is likely to depend not only by the size of a colony, but also influenced by the age of the colony (c.f. Gagnon *et al.*, 2015).

Perch and pike (below), are demersal warm water species that inhabit waters above the thermocline (~10 m in coastal areas) during the growth (=production) season. For these species, catch and predation per bottom area shallower than 10 m is thus the relevant spatial unit. Based on our estimates (Table 1) the average extraction of perch exceeds 400 kg/km² in areas shallower than 10 m (Table 2). However, as a large proportion of these bottoms are located in the outer coastal zone and off-shore areas where perch is uncommon, the exploitation intensity in archipelagos is generally substantially higher. With an estimated perch production of 2 tons/km² (see S4) the local fishing/predation pressure can reach or exceed the level 20-40% of the production (Table 2), which for other Baltic fish stocks have resulted in adverse impacts on the populations (see Material and Methods). These calculations supports the field observations that perch populations are likely to be locally negatively

impacted by both fishery and predation from cormorants and in some areas possibly also by seals.

Pike (*Esox lucius*) is sedentary (Saulamo and Neuman, 2002) with genetic differences over relatively short distances (Aro, 1989; Laikre *et al.*, 2005). When quantifying pike in a sheltered bay on the Swedish coast, Adill and Andersson (2006) derived at an biomass estimate of 1000 kg/km², resulting in an annual production of 700 kg/km² based on an assumed production to biomass ratio of 0.7 (derived from Baltic cod, another fast growing piscivorous species; Harvey *et al.*, 2003). Compared to this production estimate, fishing and predation rates are high (Table 2). This is consistent with increased abundances and larger individuals in response to a local fishing closure (Bergström *et al.*, 2007). In SD25, 27 and 29, the predation by cormorants and seals are in the same order of magnitude as the catch (Table 1) and competition is likely (c.f. Östman *et al.*, 2013). There are also observations of high incidences of seal wounds on pike at spawning sites (Bergström *et al.*, 2016), indicating local effects which are not detected on the spatial scale of this study.

Pikeperch (*Sander lucioperca*) are unevenly distributed along the coast occurs in separate and restricted areas (Lehtonen and Toivonen, 1988; Lehtonen *et al.*, 1996; Saulamo and Thoresson, 2005) and genetic differences have been documented among such areas (Dannewitz *et al.*, 2010; Säisä *et al.*, 2010). Management is generally based on the assumption that populations are significantly impacted by fishery (Mustamäki *et al.*, 2014; Lappalainen *et al.*, 2016). In many areas, the catch have decreased over the last decades, and although under debate (Heikinheimo and Lehtonen, 2016; Heikinheimo *et al.*, 2016; Salmi *et al.*, 2016; Lehikoinen *et al.*, 2017) predation from cormorants has been suggested to contribute to this decline (Mustamäki *et al.*, 2014; Salmi *et al.*, 2015). Pikeperch constitute a small fraction in

cormorants' diet and predation estimates are uncertain (Table 1). With the patchy distribution of pikeperch, possible competition among seals, cormorants and fisheries cannot be captured by our large-scale study.

As seen above, competition with wildlife is primarily a potential problem to fisheries for coastal species. For cormorants in general, this is consistent with results from a meta-analysis of a large number of studies on interactions between cormorants and different fish species (Ovegård *et al.*, 2017). However, our results show that landings from the large offshore stocks of herring, cod and sprat, which quantitatively dominate Baltic Sea fishery, were not subject to significant competition from seals and birds. This difference in competition between coastal and off-shore areas, as well as differences among coastal sites, reflects spatial aspect of the issue of competition for the fish. Another spatial aspect is that "Baltic wildlife" can be involved in competition with fishery outside the Baltic Sea. Intensive fishing in the North Sea and other areas may have adverse effects on winter feeding conditions for migratory birds (however, see Hilborn *et al.*, 2017 on fishery effects on small forage fish), influencing their reproductive condition once back in the Baltic. On the other hand, predation by overwintering cormorants has adverse impacts on brown trout, salmon and grayling (*Thymallus thymallus*) in Danish rivers (Jepsen *et al.*, 2014).

Predation by seals and in particular by birds are often excluded from quantitative food web studies, including several of those published on the Baltic Sea (e.g. Elmgren, 1984; Ulanowicz and Wulff, 1991; Sandberg *et al.*, 2000; Worm *et al.*, 2000; Harvey *et al.*, 2003; Håkanson and Gyllenhammar, 2005; Sandberg, 2007; Tomczak *et al.*, 2012). Our results show that both seals and birds can consume large quantities of fish and deserve to be carefully considered in ecosystem analyses and stock assessment models. This is particularly important in areas where populations of fish predators are increasing, particularly in coastal areas where birds and seals concentrate and where many fish populations are local.

Predation by birds can also be an issue for the management of freshwater systems. From Lake Oneida in North American, Rudstam *et al.* (2004) and Coleman *et al.* (2016) reported significant reductions in both yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum*) abundances in response to predation by the double-crested cormorant (*Phalacrocorax auritus*). Another example is from Danish rivers, in which cormorant predation reduced salmon smolt output by 50 % in just few weeks (Jepsen *et al.* 2010, 2014). Such short time "predation events" can easily be overlooked in ecosystem models with focus on the large scale picture, but can be very significant to consider in management. As emphasised by Essington and Plaganyi (2013), it is important that models include the interactions that are critical to the questions that they are supposed to address. Straight forward and reasonably detailed calculations like ours, can produce insights that are difficult to derive from complex models where detailed aspects of trophic interactions may have to be sacrificed when constructing the models (c.f. Hilborn *et al.* 2017).

In the Ecopath with Ecosim (EwE) food–web model Harvey *et al.* (2003) assumed that herring sprat and cod together constituted 50% of the seal diet in SD25-29. This assumption was also used in the updated EwE model of Tomczak *et al.* (2012), who calculated seals to consume $1*10^4$ tons of herring sprat and cod in 2006. Our compilation of data suggests that these three fish species constitute ~70% of the seals diet and that they consumed $5*10^4$ tons in 2010 (Table 1). The five fold difference in consumption results from our use of a higher proportion of herring sprat and cod in the seal diet and a larger population of seal.

In conclusion, our results show that there are cases of competition between wildlife and fisheries in the Baltic Sea, although not for all species and not to the same extent everywhere. There are many uncertainties, e.g. how far from cormorant colonies perch abundances are adversely impacted and how much of marginal diet components (e.g. salmon, sea trout, eel, pikeperch) are actually consumed. There are also uncertainties regarding the potential for compensatory mechanisms in the fish populations, in particular if wildlife feed on smaller sizes than exploited by the fishery. Besides comprehensive and comparative analysis over large systems, such as our analyses, one way to improve our understanding of the importance of competition is to explore the responses in the fish community to changes in the management (c.f. Lessard *et al.*, 2005) or to changes in local predator populations.

Supplementary material

The following supplementary material is available at ICESJMS online:

- S1 Supplement 1, Fish consumption by aquatic mammals
- S2 Supplement 2, Fish consumption by birds
- S3 Supplement 3, Fishery catch
- S4 Supplement 4, Review of published studies on cormorant predation on perch

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Table 1. Distribution among ICES subdivisions 24-32 (Figure 1) of fishery catch (metric tons, based on Table S3.4) and consumption by seals (Table S1.7) and birds (Table S2.7, only cormorant, razorbill, common guillemot, common and red-breasted merganser). For some fish, primarily open sea species we assume a common population for the entire Baltic Sea and catch/consumption are summed over subdivisions, while catch/consumption for other species are divided into subdivisions. The fish species that are presented separately are of interest to commercial and recreational fisheries. The category "unspecified" may include species that are also reported separately. Total estimated consumption by e.g. mergansers is almost 19 000 tons and without diet composition data this quantity cannot be attributed to different prey species.

fish	consumer		ICES subdivision								
species	group	SD24	SD25	SD26	SD27	SD28	SD29	SD30	SD31	SD32	Baltic
cod	fishery	8 900	50 000 59								
	birds	1 100	530								1 600
	seals	1 600	3 400								4 900
	fishery	15 000	150 000 72 000 2 100 incl							incl in	240 000
herring	birds	500	2 300 800 63 SD						SD25-29	3 600	
	seals	300	36 000 4 200 7 600 ^{3D23-29}								48 000
sprat	fishery		350 000								
	birds		22 000								22 000
	seals	8 300									8 300
flatfish	fishery	3 600	8 600	3 200	90	410	100	0	0	99	16 000
	birds	130	180	84	150	30	0	0	0	0	570
	seals	1 600	220	18	740	800	0	0	0	0	3 300
salmon	fishery	740 40								780	
	birds	1 0								1	
	seals				3'	70				110	470
sea trout	fishery	15	160	260	44	6	20	97	48	23	670
	birds	0	0	0	0	0	0	0	0	0	0
	seals	0	170	0	590	0	830	91	86	0	1 800
	fishery	0	0	37	0	1 600	8	350	140	300	2 400
	birds	0	0	48	0	17	0	88	0	0	150
	seals	0	0	0	0	8	11	120	210	23	370
	fishery	560									560
eel	birds	340									340
	seals	000	0								
perch	fishery	980	41	280	270	1 000	/90	1 500	350	990	6 200
	birds	290	1900	510	1 500	810	2 100	860	23	920	8 900
	seals	54	80	0	300	140	1 /00	120	25	1.100	2 300
northern pike pike- perch	Insnery	54	/5	9	400	140	410	450	150	1 100	2 700
	birds	0	140	0	580	19	420	84 0	3	24	920
	febory	180	150	500	120	79	240	120	0	210	990
	hirds	180	0	100	130	180	240	120	9	110	860
	coole	0	0	190	0	100	0	0	0	0	0
whitefish	fishery	30	36	0	140	4	100	370	490	210	1 500
	birds	0	0	0	0	0	190	98	20	210	120
	seals	0	86	0	300	0	830	560	20	110	2 100
un- specified	fichary	1 400	130	860	210	610	420	410	1 500	1 700	7 200
	birds	4 000	2,200	5 300	4 600	3 600	8 900	4 900	5 300	5 400	44 000
	seals	860	820	8	2 800	580	9 200	680	10 000	520	25 000
all species	fisherv	000	020	<u> </u>	_ 000	200	200	000	10000		690 000
	birds										83 000
	seals										98 000

Table 2. Perch and pike catch (Table S3.4) and consumption by seals and cormorants (Tables S1.7 and S2.7) in different areas, calculated for bottoms down to 10 m based on hypsographic data (Al-Hamdani and Reker, 2007).

	area	catch and consumption, kg/km ²									
0		perch				pike					
ICES SI	<10 m, km ²	human	seal	cormorants	total	human	seal	cormorants	total		
24	3 000	320	0	97	420	18	0	0	18		
25	1 400	29	62	1 300	1 400	54	94	100	250		
26	3 200	87	0	160	250	3	0	0	3		
27	3 200	84	94	490	670	130	140	180	450		
28	3 900	260	0	210	470	37	0	5	42		
29	11 000	73	150	190	420	38	39	6	83		
30	5 700	260	21	150	440	78	0	15	93		
31	6 800	52	4	3	58	22	0	1	22		
32	5 600	180	24	170	370	190	0	4	190		
total	44 000	140	53	230	420	63	23	21	110		



Figure 1. The Baltic Sea, with the subdivisions (SD) defined by the International Council for the Exploration of the Sea (ICES) and geographic names used in the article. Country abbreviations: De=Denmark, Es=Estonia, Fi=Finland, Ge=Germany, La=Latvia, Li=Lithuania, Po=Poland, Ru=Russia, Sw=Sweden



Figure 2. Proportions of different fish species extracted from the Baltic Sea through fishery catch and predation by birds and seals
Competition for the fish - fish extraction from the Baltic Sea by humans, aquatic mammals and birds

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Supplement 1 – Fish consumption by aquatic mammals

To make the calculations transparent, data are presented with an excessive number of significant figures, which are rounded off in the main text.

Abundances

Fish eating mammals in the Baltic, besides three seal species (grey seal *Halichoerus grypus*, harbour seal *Phoca vitulina* and ringed seal *Pusa hispida*), are common otter (*Lutra lutra*), American mink (*Neovison vison*) and harbor porpoise (*Phocoena phocoena*).

There are no available published data on the abundance of mink and otters. An estimate of the mink population was derived from a minimum home range area of 12 ha per mink in the Finnish archipelago (Salo et al., 2010). Converted to coastline, yields a maximum of 0.63 mink per kilometer of coast (Salo et al., 2010). Assuming the same mink density along the 38 628 km of the Swedish coastline (SCB Statics Sweden) results in an estimate of 24 300 minks. For a comparison, the highest annual hunting report of mink in Sweden was 48 200 individuals in 1988 including all freshwater habitats (Carlsson et al., 2010). The Swedish

mink population is assumed to constitute one third of the total Baltic population, which is thus 73 000 animals.

The otter has increased in the Baltic Sea area during the last two decades, and expanded from freshwater habitats towards the coasts in especially the eastern parts. Today the population is estimated to roughly 2 500 individuals in the entire Finland, the main part of the population occurring in the fresh water areas (HELCOM, 2013).We assume a population of at most 1 000 individuals in the Baltic.

Harbor porpoises in the Baltic have been surveyed from air twice over the last decades. In 1995 the estimated population amounted to 200-3300 specimens (95% confidence intervals, Berggren et al., 2002) whereas a survey in 2002 estimated the population to 10-460 individuals roughly in areas SD 24 and SD 25 (Berggren et al., 2004). The lower option is unrealistic, why we use the figure 460 individuals. The project SAMBAH – Static Acoustic Monitoring of the Baltic Sea Harbour Porpoise – has estimated the population abundance but final corrected data is not published yet. Especially in SD 24 the estimate will exceed earlier estimates considerably (SAMBHA, 2016). Several fish species is consumed by porpoises in western Baltic, but gadoids and clupeids dominate (Lockyer and Kinze, 2003; Sveegaard et al., 2012).

All three species of seals are surveyed during peak moulting season, when the largest proportion of the population is hauled out. Consequently, numbers of counted seals provide robust index data for trend analyses, but for estimates of true population size conversion factors have to be applied.

Moulting ringed seals are scattered on the ice in late April and are assessed using a strip survey technique, where north-southerly strips are flown such that a minimum of 13% of the total ice area is covered (Härkönen and Lunneryd, 1992). In the Bothnian Bay, counts increased from 4 900 in 2005 to 8 000 in 2013 (Härkönen et al., 2012; Härkönen et al., 2013). In the Finnish Archipelago Sea, the Gulf of Finland, and the Gulf of Riga, surveys have been sporadic due to variable ice conditions. In 2012, 150 ringed seals were recorded in the Archipelago Sea (Markus Ahola, Natural Resources Institute Finland, pers. comm.) and 100 specimens in the Gulf of Finland (Michail Verevkin, University of St. Petersburg, Russia, pers. comm.). In the Gulf of Riga and Estonian coastal waters ringed seal populations are stable or declining after 1996 (Mart Jussi, Estonian Fund for Nature, Estonia, pers. com.), when 1 500 were counted (Härkönen et al., 1998). Consequently, our best estimate of the hauled out population of Baltic ringed seals is 9 750. The hauled out fraction is not known, but surveys in 2015 showed that numbers of hauled out seals in the Bothnian Bay amounted to about 17 000, when winter lairs had collapsed (Härkönen unpublished data). Consequently, the haul-out fraction in earlier counts should have been below 50%. Thus the minimum true population size in this area should amount to 20 000 ringed seals in 2013, and at least 2 100 ringed seals in the Estonian coastal waters, and about 300 seals in the Archipelago Sea and 200 in the Gulf of Finland.

The peak haul-out season for grey seals occur in the last week of May and the first week of June, when coordinated international surveys are carried out in Estonia, Finland, Russia, and Sweden since year 2000. The haul-outs are generally surveyed twice during the two-week period and numbers are reported for each basin. Total numbers of counted seals have increased from about 18 000 in 2005 to 30 000 in 2013. However, the population in the Bothnian Bay is stagnant, whereas numbers increase in the Baltic Proper. As for ringed seals,

there is no accurate data on the fraction hauling out during surveys, but best available information (Hiby et al., 2007) suggest that 60-80% of the population is visible during surveys, and if a 70% correction factor is applied, the total Baltic grey seal population amount to about 43 000 seals in 2013.

The peak haul-out season for harbour seals occurs in mid-August in the Kalmarsund region and during the last two weeks of August in the southern Baltic (Heide-Jørgensen and Härkönen, 1988). During these periods, each area is surveyed three times. With more information on the harbour seals than for the other species, the fraction hauled out during surveys has been estimated 56% of the average count and 65% of trimmed mean values, where mean is based on the two highest counts. In 2005 there were at most 450 seals counted in the Kalmarsund region and in 2013 the corresponding number was 950 seals (Härkönen and Isakson (2010), Härkönen unpubl.). In the southern Baltic, the maximum numbers of counted harbour seals amounted to 581 in 2005, and 940 in 2013 (Härkönen unpubl.). From these observations we estimate the total harbour seal population in the Baltic to 2 900 individuals in 2013.

Abundances of mammals are shown in Table S1.1, and for seals we also give estimated numbers in different areas (Table S1.2).

Food consumptions

The daily energetic intake of phocid seals shows a strong seasonal flux, with reduced feeding during the moulting, lactation (females) and mating (males) periods (Härkönen and Heide-Jørgensen, 1990; Lydersen and Kovacs, 1999; Mellish et al., 2000; Lidgard et al., 2005). The mean daily consumption of seals thus only gives a coarse picture, where the weight consumed

also is influenced by the fat contents of the prey e.g. Winship et al. (2002). The mean daily consumption is estimated to 2.0-2.4 kg for a ringed seal (Ryg and Øritsland, 1991; Lundström et al., 2014), 3.7-4.6 kg for a harbour seal (Härkönen and Heide-Jørgensen, 1991), and 4.5-5.0 kg for a grey seal (Hammond and Grellier, 2006; Hammond and Harris, 2006). Using mean values of these estimates gives annual per capita consumptions at 800 kg for ringed seals, 1530 kg for harbour seals, and 1750 kg for grey seals.

Otter (Nolet and Kruuk, 1994; Kruuk, 2006) and harbour porpoise (Lockyer, 2003; Lockyer et al., 2003) are assumed to feed only on fish and have annual individual consumptions of 440 and 1450 kg respectively. The diet of mink is more mixed and we assumed 1/3 to be fish (Dunstone, 1993; Hammershøj et al., 2004; Salo et al., 2010), resulting in an annual individual fish consumptions of 18 kg.

Diets

Since seals consume at least 95% of the fish eaten by aquatic mammals based on the data in Table S1.1, only these three species are considered in further analyses. Seals are generally opportunistic feeders and their diets vary considerably by area, year, season and age group (Söderberg, 1975; Härkönen, 1987; Härkönen and Heide-Jørgensen, 1991; Lundström et al., 2010; Lundström et al., 2014). With reasonably many observations and good spatial and temporal coverage it is however possible to derive general patterns of diet compositions. Most of the diet samples were collected in coastal areas which may have introduced some bias in diets, overestimating the proportions of coastal fish species. Current information about seal diets in the Baltic has been determined from analyses of prey remains (mostly bones and otoliths) in digestive tracts and scats. We used results from Lundström et al. (2014) for ringed

seals in the Bothnian Bay (n=43, ICES SD31), supported by Suuronen and Lehtonen (2012), whereas the diet of ringed seals in other areas was assumed to be similar, except for the replacement of vendace by sprat (Tormosov and Rezvov, 1978). For harbour and grey seals in ICES SD24 we used results from Andersen et al. (2007) (n=26), assuming that harbour and grey seals have similar diets. For grey seals in ICES SD26 and SD28 we used unpublished data from a dietary study based on scats (n=112) collected off Gotland 2011-2012 (Lundström and Asp in prep). For grey seals in ICES SD27, SD29, SD30-32, we used data from digestive tract contents from hunted seals (n=624) between 2001 and 2013 (Lundström et al. in prep.). The recovery, identification and quantification of prey remains followed the procedures described in Lundström et al. (2007); Lundström et al. (2010). Grey seals and harbour seals in ICES SD25 were assumed to have the same diet as grey seals in SD27.

Diet compositions used in our calculations are summarized in Tables S1.3-S1.5

Table S1.1. Abundances of mammals in the Baltic Sea in 2013 and annual individual and population food consumption.

Species	Total number in	Individual fish	Total annual fish
	the Baltic Sea	consumption	consumption
		per year (kg)	(metric tons)
grey seal	43000	1750	75250
harbour seal	2900	1530	4437
ringed seal	22600	800	18080
common otter	1000	440	440
American mink	73000	18	1314
harbor porpoise*	460	1450	667
total			100188

* SD24 and SD25

Table S1.2. Seal abundances in different parts of the Baltic Sea in 2013, referring to ICES subdivisions (SD) shown in Figure 1.

	U		
Aron ICES	Abund	lance, number	per SD
subdivisions	grey seal	harbour seal	ringed seal
24	2400+	2000+	0
25	2400†	29001	0
26	50	0	0
27 and 29 Swedish area	16900‡	0	0
29 Finnish area	13050	0	300
28 and islands in southeastern 29	4500 φ	0	2100ф
30	3500	0	300
31	1400	0	19700
32	1200	0	200
total	43000	2900	22600

† in consumption analyses, equal distribution assumed between SD24 and 25

‡ in consumption analyses, equal distribution assumed between SD27 and 29

 ϕ in consumption analyses, equal distribution assumed between SD28 and 29

bea. I iguies in staene	to marea	le sampi	e bille in	anaenym	ig alot brad	1051				
Prey species	ICES subdivision (number of analysed seals)									
	SD24*	SD25	SD26	SD27	SD28	SD29	SD30	SD31	SD32	
				(n=59)	(n=112)	(n=92)	(n=223)	(n=218)	(n=32)	
Herring	7%			43%	29%	56%	67%	74%	45%	
Clupea harengus										
Sprat	1%			13%	4%	10%	3%	0%	10%	
Sprattus sprattus										
Unknown	0%			0%	1%	3%	0%	0%	4%	
Clupeidae										
Cod	36%			10%	36%	0%	0%	0%	0%	
Gadus morhua										
Burbot	0%			0%	0%	0%	0%	1%	0%	
Lota lota										
Salmon	0%			0%	0%	0%	3%	1%	2%	
Salmo salar										
Sea trout	0%			1%	0%	1%	1%	1%	0%	
S. trutta										
Salmo spp	0%			2%	0%	1%	1%	2%	0%	
Unknown	0%	-		1%	0%	0%	1%	3%	3%	
Salmonidae		027	028							
Common white-	0%	SI	SI	2%	0%	2%	9%	7%	5%	
fish Coregonus sp.		.in	in							
Vendace	0%	e as	e as	0%	0%	0%	0%	2%	0%	
Coregonus albula		me	me							
Coregonus spp	0%	Ss	S	0%	0%	0%	0%	1%	0%	
Smelt	0%			0%	0%	0%	2%	2%	1%	
Osmerus eperlanus										
Perch	0%			2%	0%	2%	2%	1%	6%	
Perca fluviatilis										
Unknown Percidae	0%			0%	0%	2%	0%	0%	0%	
Eelpout	2%]		6%	0%	9%	4%	1%	7%	
Zoarces viviparus										
Gobiidae	0%			0%	0%	1%	1%	0%	0%	
Ammodytidae	10%			3%	0%	0%	1%	0%	0%	
Pike	0%			3%	0%	1%	0%	0%	0%	
Esox lucius										
Flatfish	36%	1		5%	20%	0%	0%	0%	0%	
Sculpins	0%	1		0%	2%	0%	2%	1%	0%	
Cyprinidae	3%	1		8%	0%	6%	1%	0%	7%	
Unspecified	5%	1		2%	7%	5%	1%	2%	8%	
Chopouniou	570	1	1	- /0	1 /0	570	1/0	- /0	0/0	

Table S1.3. Grey seal diet proportional compositions by weight in different parts of the Baltic Sea. Figures in brackets indicate sample size in underlying diet studies.

*Assumed to be similar to the diet of harbour seals in SD24

	1	20
Prey species	SD28-30, 32	SD31 (n=43)
Herring	37%	37%
Sprat	36%	0%
Vendace	0%	36%
Smelt	1%	1%
Eelpout	3%	3%
Fourhorned sculpin	2%	2%
Three-spined stickleback	21%	21%
Unspecified	1%	1%

Table S1.4. Ringed seal diet proportional compositions in different parts of the Baltic Sea. Figures in brackets indicate sample size in underlying diet studies

Table S1.5. Harbour seal diet proportional compositions in different parts of the Baltic Sea

ICES	SD24‡	$SD25^*$
subdivision	(n=26)	
Prey species		
Herring	7%	43%
Sprat	1%	13%
Cod	36%	10%
Sea trout	0%	1%
Salmo spp	0%	2%
Unknown Salmonidae	0%	1%
Common whitefish	0%	2%
Perch	0%	2%
Eelpout	2%	6%
Ammodytidae	10%	3%
Pike	0%	3%
Flatfish	36%	5%
Cyprinidae	3%	8%
Unspecified	5%	2%

‡ averaged from (Andersen et al. 2007)

*Assumed to be similar to the diet of grey seals in SD27

	•dds	595	112	371	908	25	256	692	908	389	061	660	25	373	495	831	995	477	066	989	327	589	349	761	514
	All three	8 46	5 8		5 4			2	4	2	4	У			4		7 5		8 1	4	0 3		4		5 3
tal	Harbor	109	30		101			2	4	2	4				4		17		28	9	91		24		15
Tot	seal	5617	826									5611		181			542					362		3761	181
	Ringed	30 e	31	1	33	5	99	0,	14	27	9	6	5	33	0	31	15	1	18	12	7	8	5		8/
	Grey	3888	369	137	386		25	67	8	36	201	7		16	145	83	527	47	77	62	24]	22	41(317
2	seal	59	826											2			5					3		33	2
SD32	Ringed Binged	55	19	28	~~~~	~~~~	42		~~~~	63	05		~~~~	21	34	~~~~	47	~~~~	~~~~	~~~~	~~~~		53		76
	Grey	6	2								1				1		1						1		-
1	seal	5768										5611		158			473					315		3278	158
SD3	seal Binged	25				25	25	25	49	74	79	49	25	49	25		25					25			54
	Grey	18									1														
	seal	88	85											5			7					5		50	7
SD3(Seal Binged	34	96				906	61	61	61	64			23	23		46	61	61			23	61		61
	Grey	41	1				1				5			1	1		2					1			
	seal	395	384											11			32					22		225	11
3D29	Ringed	52	39	L1				91	9		31				31	31)3	91		9			4		11
01	Grey	2346	423	12^{2}				4]	4]		×				8	83	38(4]		4			249		216
	seal	307	299											8			25					17		175	8
SD28	Ringed	54	58	39	33	~~~~	~~~~						~~~			~~~~	~~~	~~~~			66	61			16
01	Grey	112	15		143																5L	(*			27
027	seal	5285	878		464			148	296	148	296				296		887		444	444	739		168		296
5 SL	Grey	90	4	1	:2																8	2			9
SD2(Grey	0			<i>a</i> ,																1				
	lsəz	943	283		216			22	44	22	4				44		133		67	67	111		177		4
3D25	Harbor	33	27		8			21	12	21	12				12		56		53	53	5		90		5
01	Grey	8	26		2(7		7				7		12		Ŷ	V	1(16		7
	lsəz	155	22		799												44		222		799		67		111
D24	Harbor	L	L.		9												12		0		9		33		5
S	Grey	14	(1		75												4		21		75		Q		10
										e														back	
				eidae						onida	fish					idae								icklel	
	es			Clup						Salm	vhite		dds (Perc			idae					ned st	ğ
	speci	ing		nwo		ot	uo	L.	o spp	nwo	non v	lace	sunog	t		uwo	Jut	dae	odyti		sh	ins	inidae	e-spir	ecifie
	Prey	Herr	Sprat	Unkr	Cod	Burb	Salm	Trou	Salm	Unkr	Com	Venc	Core	Smel	Perc	Unkr	Eelop	Gobii	Amn	Pike	Flatfi	Scult	Cypr.	Thre(Unsp

Table S1.6. Summary of estimated consumptions (tons) by seals, derived by combining information is Tables S1.1 - S1.5

Table S1.7. To compare seal consumption (tons) with human catch, Table S1.6 has been condensed to the same structure as Table S3.4

Grey seal

SD SD	24	25	26	27	28	29	30	31	32		
fish species											
cod	756				31	37					
herring ¹	147		32910 4134 1825								
sprat ¹		7192									
flatfish	756	105	18	739	799						
salmon ²				30	58				105		
sea trout ²		84		592		831	91	86			
smelt							123	49	21		
eel											
perch ³		42		296		1663	123	25	134		
northern pike		63		444		416					
pikeperch											
whitefish ⁴		42		296		831	564	198	105		
unspecified	420	397	8	2795	354	8874	613	182 ⁵	477		

Ringed seal

	SD	24	25	26	27	28	29	30	31	32			
fish species	/												
cod													
herring			703 88 5768										
sprat			826										
flatfish													
salmon													
sea trout													
smelt						8	11	2	158	2			
eel													
perch													
northern pike													
pikeperch													
whitefish													
unspecified						225	289	64	9834 ⁶	43			

Harbor seal

	SD	24	25	26	27	28	29	30	31	32		
fish species	/											
cod		799				2	16					
herring		155		943								
sprat				305								
flatfish		799	111									
salmon												
sea trout ²			89									
smelt												
eel												
perch			44									
northern pike			67									
pikeperch												
whitefish			44									
unspecified		444	422									

1 - for each SD separately, the mass of unknown clupeidae is split between herring and sprat proportionally to their masses

2 - for each SD separately, the masses of Salmo spp and unknown Salmonidae are split between salmon and trout proportionally to their masses

3 - perch is the totally dominating Percidae in seal stomachs and all unknown Percidae are assigned to perch

4 - for each SD separately, the mass of Coregonus spp is split between common whitefish and vendace proportionally to their masses

5 - of which 54 tons vendace

6 - of which 5611 tons vendace

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Competition for the fish - fish extraction from the Baltic Sea by humans, aquatic mammals and birds

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Supplement 2 – Fish consumption by birds

To make the calculations transparent, data are presented with an excessive number of significant figures, which are rounded off in the main text.

Abundances and Food consumption

For birds, food consumption were based on assumed daily rations equivalent to 20% of the birds' bodyweight (Carss, 1997) and D. N. Carss pers.comm. in (Engström, 2001)). Some of the species redistribute themselves over the Baltic between summer and winter, while others completely or partially leave the area in the autumn and spend winter outside the Baltic Sea. During summer, reproduction results in substantial increases in population numbers. Based on data and assumptions on these factors for 21 bird species (Table S2.1) annual fish consumption were estimated.

The five top species in the table (great cormorant (*Phalacrocorax carbo sinensis*), razorbill (*Alca torda*), common guillemot (*Uria aalge*), common merganser (*Mergus merganser*) and red-breasted merganser (*M. serrator*) were estimated to consume 80% of all fish eaten by

birds in the Baltic and details on assumptions for these species and their consumption are presented in detail in Tables S2.2 - S2.4.

Diets

Razorbills (Lyngs, 2001) and common guillemots (Hedgren, 1976; Lyngs and Durinck, 1998; Österblom and Olsson, 2002; Enekvist, 2003; Kadin et al., 2012) feed almost exclusively on clupeids, primarily on sprat and to a minor extent herring. Based on these studies we assume that sprat and herring constitute 90% and 5% of diets while other species contribute 5%.

There are only a few diet studies on merganser diets in the Baltic Sea. From Finnish archipelago areas, Bagge et al. (1973) and Lemmetyinen and Mankki (1975) reported that three-spined stickleback (*Gasterosteus aculeatus*) constituted the dominant fish prey in both red-breasted and common merganser. The other fish that they found were also primarily species that are not targeted in fisheries (e.g. roach, *Rutilus rutilus* and eelpout, *Zoarces viviparous*) although occasional pike and herring were also recorded. For common merganser in the Lithuanian section of the Curonian Lagoon, Zydelis and Kontautas (2008) reported that >80% of identified prey fish biomass was smelt (*Osmerus eperlanus*) with an average size of 17 cm. Birds are also known to feed substantially on smelt during their spawning in the eastern Gulf of Finland (SD32, Dmitry Sendek pers. obs.). Studies on diets of mergansers outside the Baltic Sea shows that red-breasted merganser feed primarily on smaller fish (mainly <10 cm, (Feltham, 1990; Feltham, 1995; Bur et al., 2008; Craik et al., 2011)) than common merganser (prey fish up to 25-30 cm, (Kålås et al., 1993; McCaw III et al., 1996)). With the limited diet data availability for the mergansers, we were unable to split their consumption among different prey species.

The size of cormorant prey is considerably larger than those of the other piscivorous birds, with some studies reporting prey regularly exceeding 30 cm (Pūtys, 2012; Östman et al., 2013; Salmi et al., 2015) and preference for fish larger than 25 cm have been reported (Skov et al., 2014). The diet of the cormorant varies substantially among the numerous studies that has been conducted (Figure S2.1, Table S2.5). Based on Table S2.5, we derived diets for different areas of the Baltic (Table S2.6) and from these diets and area specific consumption (Table S2.7), consumption of different fish species were calculated.

Table S2.1. Summary of fish eating birds in the Baltic Sea and their annual consumption of fish (metric tons). Birds born during the year are referred to as young-of-the-year (YOY) individuals. The table was compiled by Henri Engström and can be referred to as 'H. Engström in Hansson et al. 2017, Table S2.1 in Supplement 2'

Species	Daily food consumption (kg, 20% of body weight)	Proportion of fish in diet, in weight %	Number of non-YOY birds	Number of nesting pairs	Number of YOY birds	Species annual fish consumption (tons)
great cormorant Phalacrocorax carbo sinensis	0.5	1	272229	90743	181486	39971
razorbill Alca torda	0.14	1	244055	34865	34865	13516
common merganser Mergus merganser	0.28	1	68933	22978	114889	11393
common guillemot Uria aalge	0.2	1	134141	19163	19163	10612
red-breasted merganser Mergus serrator	0.22	1	74981	24994	124968	7470
black guillemot Cepphus grylle	0.08	0.75	155616	25936	25936	5980
herring gull Larus argentatus	0.22	0.2	327404	81851	245553	5512
great crested grebe Podiceps cristatus	0.18	0.9	48792	16264	48792	2134
common gull Larus canus	0.08	0.25	319154	79789	239366	1532
white-tailed sea eagle Haliaeetus albicilla	1.1	0.5	5983	855	1710	1431
great black-backed gull Larus marinus	0.36	0.2	40460	10115	15173	941
arctic tern Sterna paradisaea	0.02	0.9	181654	90827	272481	834
grey heron Ardea cinerea	0.28	0.75	15536	3884	11652	783
lesser black-backed gull Larus fuscus	0.16	0.4	44933	14978	44933	604
common tern Sterna hirundo	0.02	0.9	44290	22145	66435	203
caspian tern Sterna caspia	0.2	1	3350	1675	3350	141
osprey Pandion haliaetus	0.4	1	978	489	1467	100
sandwich tern Sterna sandvicensis	0.06	0.9	2908	1454	4362	40
parasitic jaeger Stercorarius parasiticus	0.1	0.75	2060	1030	3090	39
red-throated loon Gavia stellata	0.3	1	555	185	370	38
little tern Sterna albifrons	0.02	0.75	4256	2128	6384	16
estimated total consumption by birds						103290

Data sources:

Abundances: Ottosson et al. (2012.), Tucker et al. (1994), Bregnballe et al. (2014), Skov et al. (2011) pers. comm. with Martin Green, Swedish Bird Survey, Lund University, Sweden; Kjell Larsson, Linneaus University, Kalmar, Sweden; Christof Herrmann, Agency for Environment, Germany; Thomas Bregnballe, Aarhus University, Denmark; Kalev Rattiste, Estonian University of Life Sciences, Estonia; <u>http://www.luomus.fi/en/bird-monitoring</u>, Finland.

Proportions of fish in diets: Snow and Perrins (1997), H. Engström unpubl.

Migration: Fransson and Pettersson (2001); Fransson et al. (2008) Skov et al. (2011)

Table S2.2. Duration of the summer period and proportions of the populations in the different ICES subdivisions during summer/winter periods. Based on references cited in Table S2.1. The table was compiled by Henri Engström and can be referred to as 'H. Engström in Hansson et al. 2017, Table S2.2 in Supplement 2'

	Summer		Proportion per SD, summer/winter									
Species	period	SD24	SD25	SD26	SD27	SD28	SD29	SD30	SD31	SD32		
great cormorant	Mar 16 Cap 15	0.11	0.11	0.13	0.16	0.10	0.16	0.11	0.003	0.12		
great cormorant	War. 16 - Sep. 15	0.52	0.06	0.22	0.07	0.02	0.11	0.00	0.00	0.00		
razorbill	Mar 1 Jul 21	0.03	0.00	0.00	0.27	0.00	0.36	0.11	0.17	0.06		
	Wal. 1 - Jul. 31	0.15	0.30	0.20	0.15	0.20	0.00	0.00	0.00	0.00		
common morgans or	Apr. 1 Oct. 21	0.00	0.00	0.00	0.05	0.02	0.41	0.14	0.27	0.11		
common merganser	Apr. 1 - Oct. 51	0.20	0.05	0.24	0.17	0.15	0.16	0.00	0.00	0.03		
aamman guillamat	Mar 1 Jul 21	0.14	0.00	0.00	0.69	0.00	0.10	0.01	0.06	0.00		
common guillemot	War. 1 - Jul. 31	0.15	0.30	0.20	0.15	0.20	0.00	0.00	0.00	0.00		
red-breasted merganser	Apr 1 Oct 21	0.00	0.01	0.01	0.02	0.01	0.21	0.20	0.39	0.15		
	Apr. 1 - Oct. 31	0.23	0.09	0.01	0.09	0.52	0.05	0.00	0.00	0.01		

Table S2.3. Number of birds in the Baltic Sea during different periods. The period 'Jan. 1st spans Jan. 1st up to and including Jan. 15th. The birds are distributed differently during summer and winter (see Table S2.2) and winter periods are indicated with a gray background. Birds born during the year are in the 'YOY' (young-of-the-year) columns, where also assumed date of birth are indicated. The table was compiled by Henri Engström and can be referred to as 'H. Engström in Hansson et al. 2017, Table S2.3 in Supplement 2'

Species	great co	rmorant	razo	orbill	common	nerganser	common	guillemot	red-br merg	easted anser	
Age group Date	older	YOY	older	YOY	older	YOY	older	YOY	older	YOY	
Jan. 1 st	26554		244055		55350		134141		16815		
Jan. 16 th	26554		244055		55350		134141		16815		
Feb. 1 st	26554		244055		55350		134141		16815		
Feb. 15 th	26554		244055		55350		134141		16815		
Mar. 1 st	26554		244055	244055			134141	134141			
Mar. 16 th	272229		244055		55350		134141		16815		
Apr. 1 st	272229		244055		68933		134141		74981		
Apr. 16 th	272229		244055		68933		134141		74981		
May 1 st	272229	181486	244055		68933		134141		74981		
May 16 th	272229	181486	244055		68933		134141		74981		
Jun. 1 st	272229	181486	244055	34865	68933	114889	134141	19163	74981		
Jun. 16 th	272229	181486	244055	34865	68933	114889	134141	19163	74981		
Jul. 1 st	272229	181486	244055	34865	68933	114889	134141	19163	74981	124968	
Jul. 16 th	272229	181486	244055	34865	68933	114889	134141	19163	74981	124968	
Aug. 1 st	272229	181486	278	920	68933	114889	153	304	74981	124968	
Aug. 16 th	272229	181486	278	920	68933	114889	153	304	74981	124968	
Sep. 1 st	272229	181486	278	920	68933	114889	153	304	74981	124968	
Sep. 16 th	26	554	278	920	68933	114889	153	304	74981	124968	
Oct. 1 st	26	554	278	920	68933	114889	153	304	74981	124968	
Oct. 16 th	26	554	278	920	68933	114889	153	304	74981	124968	
Nov. 1 st	26	554	278	920	553	350	153	304	168	815	
Nov. 16 th	26	554	278	920	553	350	153	304	16815		
Dec. 1 st	26	554	278	920	553	350	153	304	16815		
Dec. 16 th	26	26554		278920		350	153	304	16815		

Table S2.4. Annual consumption (ton) by the five major fish eating birds in different subdivisions (SD, Figure 1) of the Baltic Sea. Calculations based on individual daily consumption (Table S2.1), their distributions over the sea (Table S2.2) and the number of birds during different periods of the year (Table S2.3). The table was compiled by Henri Engström and can be referred to as 'H. Engström in Hansson et al. 2017, Table S2.4 in Supplement 2'

	Annual fish consumption per SD											
Species	SD 24	SD 25	SD 26	SD 27	SD 28	SD 29	SD 30	SD 31	SD 32			
great cormorant	5382	4277	5412	6123	3805	6219	4132	113	4508			
razorbill	1364	2397	1598	2690	1598	1989	608	939	332			
common merganser	468	117	562	850	532	4086	1267	2444	1066			
common guillemot	1548	1882	1255	3935	1255	434	43	260	0			
red-breasted merganser	128	119	75	189	360	1479	1382	2696	1042			

Table S2.5. Summary of feeding data for cormorant, expressed as weight percentages in the diet. Based on analyses of stomachs from dead birds (s), more or less intact regurgitated fish (f) and regurgitated pellets with fish remains (p).

Area	А	В	С	С	0	0	P	Q	D	E	F	К	G	1	J	Н	L, M	М	Ν
ICES SD	24	25	25	25	26	26	26	26	27	27	27	29	30	30	30	31	32	32	32
number of observations (s=stomachs, p=pellets,						4.000		2089p			75kg of	1196p 103s			469p 8s				124p
	96p	624S	120p	430p	220p	1032p	?p	42011	279p	1955	iisn	32091	333p	зор	21//1	60p	286p	30461	1285
coa Gadus morhua	20%	13%		4%						5%	9%								
herring																			
Clupea harenaus	7%	2%				1%		4%		9%	7%	8%	33%	4%	19%	3%	5%		5%
sprat		-				-												2%	
, Sprattus sprattus		<.5%								<.5%			<.5%						
flounder + plaice, <i>Platichthys</i>																			
flesus, Pleuronectes platessa;	2%	12%				3%	3%			7%								<.5%	<.5%
salmon																			
Salmo salar																1%			
sea trout																			
S. trutta																			
smelt																			
Osmerus eperlanus						3%		1%					4%		2%				1%
eel																			
Anguilla anguilla	5%	3%	2%	<.5%				1%		1%	<.5%								<.5%
perch																			
Perca fluviatilis	5%	15%	55%	59%	17%	16%		5%	45%		30%	33%	21%	24%	17%	20%	41%	17%	3%
pike																			
Esox lucius		9%		1%					3%		25%	1%	1%	4%	1%	3%			2%
pikeperch																			
Sander lucioperca					6%	5%		4%			1%	6%	<.5%		1%			4%	3%
whitefish																			
Coregonus sp. excl. C. albula		<.5%									1%		1%	4%	2%	18%	1%		L
eelpout																			
Zoarces viviparus	19%	9%	3%	3%		2%	12%	5%	4%	28%	14%	9%	19%		15%		5%	24%	32%
roach																			
Rutilus rutilus	9%	9%	35%	12%	42%	37%		9%	34%	2%	3%	15%		4%	18%		17%	43%	31%
other cyprinids		5%	3%	4%	6%	10%		3%	3%	10%	1%	12%	5%	8%	3%	3%	12%	4%	3%
rutte																			
Gymnocephalus cernua		2%	1%		14%	1/%		69%	3%	<.5%	5%	6%	/%	30%	19%	35%	8%	2%	1%
sticklebacks	201	6 94										4.04			404		404		-
Gasterosteus aculeatus	3%	8%	201	4.001	450/	<i>C</i> 24	11%	. 50(001	30%	<.5%	1%	001	3%	1%	2%	1%	<.5%	2%
unspecified	29%	13%	2%	16%	15%	6%	/5%	<.5%	8%	8%	3%	8%	9%	19%	2%	15%	9%	4%	16%
References	1	2,3	4	5	6	7	8	9	4	2,10	3	11-13	14	13,15	12,13	13,15	13,15	16	17

References: 1= Hald-Mortensen (1995); 2= Östman et al. (2013); 3= Ovegård, M. unpublished,; samples kindly provided by Claes Kyrk; 4= Lindell (1997), proportions calculated from numbers of fish and their average size, as given by Lindell; 5= Jonsson (1979); 6= Švažas et al. (2011); 7= Pūtys (2012);8= Bzoma and Meissner (2005); 9= Stempniewicz et al. (2003); 10= Boström et al. (2012); 11= Salmi et al. (2015); 12= Salmi et al. (2013); 13= Salmi, J.A. unpublished; 14= Bostrom et al. (2012); 15= Salmi (2011), recalculated with length-weight equation from Salmi et al. (2015); 16= Lehikoinen et al. (2011); 17= Eschbaum et al. (2003)

ICES SD								
Prey	24	25	26	27	29	30	31	32
cod	20%	6%		5%				
herring	7%	1%	1%	5%	8%	19%	3%	/10/
sprat		<.5%		<.5%		<.5%		470
flounder + plaice	2%	4%	2%	2%				
salmon							1%	
sea trout								
smelt			1%			2%		
eel	5%	2%	<.5%	<.5%				
perch	5%	43%	9%	25%	33%	21%	20%	20%
pike		3%		9%	1%	2%	3%	1%
pikeperch			4%	<.5%	6%	<.5%		2%
whitefish		<.5%		<.5%		2%	18%	
eelpout	19%	5%	5%	15%	9%	11%		20%
roach	9%	19%	22%	13%	15%	7%		30%
other cyprinids		4%	5%	5%	12%	5%	3%	6%
ruffe		1%	25%	3%	6%	19%	35%	4%
sticklebacks	3%	3%	3%	10%	1%	1%	2%	1%
unspecified	29%	10%	24%	6%	8%	10%	15%	9%

Table S2.6. Cormorant proportional diets in different ICES subdivisions, calculated as mean values from Table S2.5

Table S2.7. Annual consumption (tons) in different areas of the Baltic, expressed as ICES subdivisions). To compare bird's consumption with human catch, the table has been condensed to the same structure as Table S3.4

Cormorant									
SD	24	25	26	27	28¹	29	30	31	32
fish species									
cod	1060				53	32	-		-
herring ²	359			1096			767	3	187
flatfish	130	175	84	147	30				
salmon									
smelt			48		17		88		
eel					337		-		-
perch	294	1850	514	1548	813	2073	857	23	923
northern pike		143		582	19	63	84	3	24
pikeperch			193		183	377			105
whitefish							98	20	
unspecified	3278	1764	4512	3223	2568	3204	2238	62	3269
Razorbill									
SD fish species	24	25	26	27	28	29	30	31	32
herring	68			514			30	47	17
sprat					12164				
unspecified	68	120	80	135	80	99	30	47	17
Common guill	emot								
SD fish species	24	25	26	27	28	29	30	31	32
herring	77			438			2	13	0
sprat					9551				
unspecified	77	94	63	197	63	22	2	13	0
Common merg	anser								
SD fish species	24	25	26	27	28	29	30	31	32
unspecified	468	117	562	850	532	4086	1267	2444	1066
Red-breasted m	nerganse	er							
SD fish species	24	25	26	27	28	29	30	31	32
unspecified	128	119	75	189	360	1479	1382	2696	1042

1 - diet in SD28 assumed to be the average of those in SD26 and SD29

2 - all clupeids in SD32 assumed to be herring, since sprat generally contributes only marginally to the diet



Figure S2.1. Sites from where cormorant diet data have been compiled in Table S2.5

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Competition for the fish - fish extraction from the Baltic Sea by humans, aquatic mammals and birds

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Supplement 3 – Fishery catch

To make the calculations transparent, data are presented with an excessive number of significant figures, which are rounded off in the main text.

Data on commercial catch per subdivision for year 2010 were extracted from the official national catch statistics collated by ICES (www.ices.dk) and are summarized in Table S3.1. For recreational fishing there are no complete catch statistics, but various assessments are available, primarily from areas with archipelagos where there are local populations of reasonably sedentary species. From Finland and Sweden data based on postal questionnaires are available from 2010. For Finland the methods and results are described in Anon. (2011). Data for Sweden were obtained from the Swedish Agency for Marine and Water Management and the methodology is described in Thörnqvist (2009). However, these recreational catch were merged for SD24-SD25 and SD27-SD29 respectively. To allocate catch to different subdivisions they were split proportionally to Swedish commercial catch in corresponding areas. Russian data from the Gulf of Finland are averages from 2003-2008 (Anon., 2009) and are relevant also for the current situation (D. Sendek, unpubl.). For Estonia data were

available from 2012, for gillnet catch from mandatory catch reports and for other types of gears estimates from a telephone-based survey (Ender et al., 2013).

To compare catch with consumption by other marine mammals and birds, all human catch are merged in Table S3.3 and S3.4. It should be recalled, however, that these data underestimates catch in the southeastern parts of the Baltic, from where we lack data on recreational fisheries for several countries. The number of significant digits is excessive given the data uncertainty but it is kept to allow readers to follow how we have merged data.

SD	24	25	26	27	28	29	30	31	32
fish species									
cod									
Gadus morhua	8850	31115	18822	45	96	49	1	0	2
herring									
Clupea harengus	15062	24090	22737	14539	52303	24729	71694	2090	12451
sprat									
Sprattus sprattus	2116	35476	98543	35052	92309	45256	3345	2	35375
flounder									
Platichthys flesus	3159	8168	3216	37	385	91	1	0	99
plaice Pleuro-									
nectes platessa	441	402	3	0	0	0			
salmon									
Salmo salar	55	236	59	2	4	11	83	219	38
sea trout									
S. trutta	15	110	257	2	6	10	40	22	21
smelt									
Osmerus eperlanus	0		37	0	1564	8	345	142	245
eel									
Anguilla anguilla	253	129	35	124	2	9	2	0	1
perch									
Perca fluviatilis	982	24	282	12	869	226	473	67	256
northern pike									
Esox lucius	54	8	9	8	7	57	105	30	58
pikeperch									
Sander lucioperca	180	22	498	5	78	121	100	5	156
whitefish									
Coregonus sp.	30	6	0	17	4	98	287	330	60
unspecified	1408	106	855	5	170	174	273	1258‡	1082
(of which cyprinids)	(91%)	(33%)	(93%)	(0%)	(68%)	(96%)	(89%)	(7%)	(63%)

Table S3.1. Annual commercial catch (metric tons) in the Baltic Sea 2010

‡ = 1163 tons of vendace (*Coregonus albula*)
SD									
fish species	24	25	26	27	28	29	30	31	32
cod	11	87		31	2	37	0	0	2
herring	3	8		138	122	193	178	55	175
sprat	0	0		0	0	0	0	0	10
Flounder + plaice	8	23		53	22	9	0	0	0
salmon	2	21		18	0	9	8	10	2
sea trout	0	46	ta	42	0	10	57	26	2
eel	0	0	o da	0	0	0	0	0	0
perch	0	17	nc	254	130	563	1040	282	734
pike	0	67		396	138	354	342	118	996
pikeperch	0	0		127	0	123	17	4	157
whitefish	0	30		121	0	94	88	159	151
unspecified	7	27		207	443	247	136	216	656†
(of which cyprinids)	(0%)	(0%)		(0%)	(10%)	(83%)	(95%)	(50%)	(66%)

Table S3.2. Annual catch (tons) in recreational and household fisheries 2010 in Sweden and Finland, average 2003-2008 in Russia and 2012 in Estonia.

+=of which 56 tons of smelt

Table S3.3. Combined catch (tons) in commercial, recreational and household fisheries derived by combining Tables S3.1 and S3.2. When catch in the recreational/household fisheries were merged for two or more subdivisions, or when species were merged, these catch data were split in proportions proportional to catch in the commercial fishery.

SD	24	25	26	27	28	29	30	31	32	24-32
fish species						_>	20	01	0-	2.02
cod	8861	31202	18822	76	98	86	1	0	4	59150
herring	15065	24098	22737	14677	52425	24922	71872	2145	12626	240567
sprat	2116	35476	98543	35052	92309	45256	3345	2	35385	347484
flounder	3166	8190	3216	90	407	100	0	0	99	15268
plaice	442	403	3	0	0	0	0	0	0	848
salmon	57	257	59	20	4	20	91	229	40	776
sea trout	15	156	257	44	6	20	97	48	23	666
smelt	0	0	37	0	1564	8	345	142	301	2397
eel	253	129	35	124	2	9	2	0	1	555
perch	982	41	282	266	999	789	1513	349	990	6210
northern pike	54	75	9	404	145	411	447	148	1054	2747
pikeperch	180	22	498	132	78	244	117	9	313	1593
whitefish	30	36	0	138	4	192	375	489	211	1475
unspecified	1415	133	855	212	613	421	409	1474	1682	7214
total	32636	100217	145353	51236	148654	72478	78615	5034	52729	686951

Table S3.4. For some fish, primarily open sea species, it is realistic to assume that there is a common population for the entire Baltic Sea, while other species are divided into more or less sedentary subpopulations. This difference among species are of relevance when evaluating competition between man and beasts, since local fish populations may be impacted by local predation, while the impact on basin wide populations must be analyzed based on the total predation on the species. Based on this approach, Table S3.3 has been modified to better represent catch of different populations. The merging of catch is based on the population structures applied by ICES, except that flatfish and sea trout are kept as single SD values since these species may reproduce locally and are relatively sedentary. Values represent estimated annual consumption in tons.

	i										
SD SD	24	25	26	27	28	29	30	31	32		
fish species											
cod	8861		50289								
herring	15065		151484 71872 2145						**		
sprat			347484								
flatfish	3608	8593	3219	90	407	100	0	0	99		
salmon		736									
sea trout	15	156	257	44	6	20	97	48	23		
smelt	0	0	37	0	1564	8	345	142	301		
eel		555									
perch	982	41	282	266	999	789	1513	349	990		
northern pike	54	75	9	404	145	411	447	148	1054		
pikeperch	180	22	498	132	78	244	117	9	313		
whitefish	30	36	0	138	4	192	375	489	211		
unspecified	1415	133	855	212	613	421	409	1474†	1682		

 \ddagger = catches in SD32 merged with those in SD25-29

 \ddagger of which 1163 ton of vendace

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Competition for the fish - fish extraction from the Baltic Sea by humans, aquatic mammals and birds

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Supplement 4 – Review of published studies on cormorant predation on perch

Perch is a common coastal species about which much has been published, including articles addressing possible effects of predation by cormorants.

Perch forms local populations along the coast, with genetic, growth and condition differences over short distances (Hansson, 1985; Bergek and Björklund, 2009; Bergek *et al.*, 2010; Ahlbeck Bergendahl *et al.*, 2017). These local populations are potentially responsive to changes in local exploitation pressure. Bergström *et al.* (2007) showed that perch in a 4 km² area closed to fisheries where both larger and more abundant than in neighbouring fished areas. This implies that coastal fisheries can be intensive enough to impact local populations to such an extent that compensatory mechanisms are insufficient to buffer this impact. With cormorants and seals in some subdivisions consuming twice as much perch as caught in fisheries (Table 1), competition is likely to occur at least locally.

Adill and Andersson (2006) quantified fish >10 cm in a typical perch habitat (depth <10m) and concluded that perch constituted 43-55% of the biomass. The perch proportion of the total fish biomass is smaller, given the high abundance of fish <10 cm (Aneer and Nellbring, 1977;

Hansson, 1984; Nellbring, 1985; Thorman, 1986). Assuming that perch still constitute a large proportion (20%) of the total fish production on bottoms <10 m, this would equal 2 tons/km² (assumed fish production 10 tons per km², see Material and Methods).

Based on our consumption estimates (Table 1) the average extraction of perch exceeds 400 kg/km² in potential perch habitat (Table 2). However, as a large proportion of these bottoms are located in the outer coastal zone and off-shore areas where perch is uncommon, the exploitation intensity in the archipelagos is generally substantially higher.

With an estimated perch production of 2 tons/km², the local fishing/predation pressure can reach or exceed the level 20-40% of the production (Table 2), which for other Baltic fish stocks have resulted in adverse impacts on the populations (see Material and Methods). Thus perch populations in the Baltic are likely to be locally negatively impacted by both fisheries, predation from cormorants and in some areas possibly also by seals.

Several field studies have addressed the possible effects of cormorant predation on the abundance of perch. Some of these publications are based on long-term data, but these sampling programs were not designed to study interactions between cormorants and fish, compromising the statistical power of analyses. Based on 15 years of fish monitoring data from the Baltic Proper, Östman *et al.* (2012) reported ~80% lower catch of perch in an area with cormorant colonies compared to a reference area that had no colonies within 50 km. In time series analyses they also found a negative association between perch abundance and the size of the cormorant colonies. Their findings are supported by modelling results presented by Östman *et al.* (2013). During the period 1998-2011, commercial perch catch in the Finnish Archipelago Sea area decreased by about 50% and Salmi *et al.* (2015) proposed that this was

caused by predation by cormorants, as they increased from zero to 4000-5000 nesting pairs during the same period (see also Heikinheimo and Lehtonen, 2016; Salmi *et al.*, 2016). Using data from all Finnish coastal areas during 2002-2014, when cormorants were well established and abundant, Lehikoinen *et al.* (2017) reported generally increased perch catch. They analysed changes in catch rates in commercial fisheries vs. dynamics in cormorant numbers and found no significant relationship. Results from a short (6 years, 2005-2010) monitoring fishery in the entrance to the Gulf of Finland showed increased perch catch while the number of nesting cormorants in the area showed modest fluctuation (700-1400 nesting pairs, Lehikoinen *et al.*, 2011). A strong negative impact on perch by cormorants was suggested by Vetemaa *et al.* (2010), reporting a 90% abundance decrease in perch after the establishment of a cormorant colony in a small (~9 km²) Estonian bay.

In a study designed specifically to explore possible effects of cormorant predation on the fish community, Gagnon *et al.* (2015) compared catch at pairs of islands with and without cormorant colonies and reported three times larger catch at islands without colonies. At islands that had been colonised for seven years or more, catch were reduced by 90%. Pūtys (2012) analysed perch catch at two monitoring stations, located 7 and 25 km from a cormorant colony in the Curonian Lagoon. During the study period the colony increased from 200 to 3800 nesting pairs, but there was no temporal trend in catch. Further, there was no correlation between catch of perch and distances (<1 to ~23 km) from the cormorant colony. The Curonian Lagoon has a maximum depth of 5 m (Paldavičiené *et al.*, 2009), which makes the entire area (1600 km²) perch production habitat and applying the same production assumptions as above this results in a total perch production of 3200 tons, compared to 118 tons consumed by cormorants and 48 tons caught in fisheries (Pūtys, 2012). The total extraction of perch was thus only 5-6% of the estimated production. This proportion may even

be overestimated, as the primary productivity in the lagoon is 2-4 times higher than in the Baltic Proper (Elmgren 1984; Aleksandrov, 2010), probably also resulting in a higher fish production. The high productivity in the Curonian Lagoon may explain the absence of a detectable impact of cormorant predation.

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