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Original Article

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

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Seals and fish-eating birds have increased in the Baltic Sea and there is concern that they compete with fisheries. Using data from around year 2010, we compare consumption of different fish species by seals and birds to the catch in the commercial and recreational fishery. When applicable this is done at the geographical resolution of ICES subdivisions. Predation by birds and mammals likely has limited impact on the populations of the commercially most important species (herring, sprat, and cod). 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 these species are important to the fishery (e.g. perch and whitefish) and competition between wildlife and the fishery is likely, at least locally. Estimated wildlife consumption of pike, sea trout and pikeperch varies among ICES subdivisions and the degree of competition for these species may differ among areas. 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 5000 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 3000 grey, 2000–3000 ringed and 200 harbour seals remained in the 1970–1980s (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 1980 s 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 20th century, the population of the great cormorant (*Phalacrocorax carbo sinensis*) has increased from some 6500 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 (cf. Davies *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 defined by the International Council for the Exploration of the Sea (ICES, 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 (Supplementary Document 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

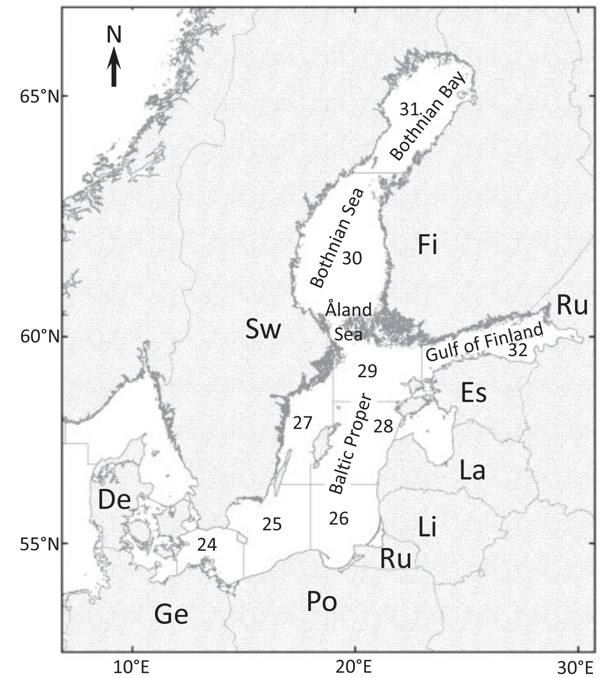

Figure 1. The Baltic Sea, with the subdivisions (SD) defined by the International Council for the Exploration of the Sea (ICES) and geographic names used in the article. Country abbreviations: De, Denmark; Es, Estonia; Fi, Finland; Ge, Germany; La, Latvia; Li, Lithuania; Po, Poland; Ru, Russia; Sw, Sweden.

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 $km^{2*}yr^{-1}$ 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 km^2 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 km^2 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 km^2 based on a primary production and a net allochthonous supply of 730 gC/m^2. Using the relationships between primary- and fish production reported in these ecosystem analyses, and a primary production of 165 gC/m^2 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 km^2.

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 3–4 times more fish than seals and birds combined. Among the marine mammals, the three seal species account for >95% of the consumption (Supplementary 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 (Supplementary 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% (Supplementary 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*, Supplementary 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.

Table 1. Distribution among ICES subdivisions 24–32 (Figure 1) of fishery catch (metric tons, based on Supplementary Table S3.4) and consumption by seals (Supplementary Table S1.7) and birds (Supplementary Table S2.7, only cormorant, razorbill, common guillemot, common, and red-breasted merganser).

Fish species	Consumer group	ICES subdivision SD24	SD25	SD26	SD27	SD28	SD29	SD30	SD31	SD32	Entire Baltic
Cod	Fishery	8900	50 000 (SD25–32)								59 000
	Birds	1100	530 (SD25–32)								1600
	Seals	1600	3400 (SD25–32)								4900
Herring	Fishery	15 000	150 000 (SD25–29)					72 000	2100	incl. in SD25-29	240 000
	Birds	500	2300 (SD25–29)					800	63		3600
	Seals	300	36 000 (SD25–29)					4200	7600		48 000
Sprat	Fishery	350 000 (SD24–32)									350 000
	Birds	22 000 (SD24–32)									22 000
	Seals	8300 (SD24–32)									8300
Flatfish	Fishery	3600	8600	3200	90	410	100	0	0	99	16 000
	Birds	130	180	84	150	30	0	0	0	0	570
	Seals	1600	220	18	740	800	0	0	0	0	3300
Salmon	Fishery	740 (SD24–31)								40	780
	Birds	1 (SD24–31)								0	1
	Seals	370 (SD24–31)								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	1800
Smelt	Fishery	0	0	37	0	1600	8	350	140	300	2400
	Birds	0	0	48	0	17	0	88	0	0	150
	Seals	0	0	0	0	8	11	120	210	23	370
Eel	Fishery	560 (SD24–32)									560
	Birds	340 (SD24–32)									340
	Seals	0 (SD24–32)									0
Perch	Fishery	980	41	280	270	1000	790	1500	350	990	6200
	Birds	290	1900	510	1500	810	2100	860	23	920	8900
	Seals	0	86	0	300	0	1700	120	25	130	2300
Northern pike	Fishery	54	75	9	400	140	410	450	150	1100	2700
	Birds	0	140	0	580	19	63	84	3	24	920
	Seals	0	130	0	440	0	420	0	0	0	990
Pike-perch	Fishery	180	22	500	130	78	240	120	9	310	1600
	Birds	0	0	190	0	180	380	0	0	110	860
	Seals	0	0	0	0	0	0	0	0	0	0
Whitefish	Fishery	30	36	0	140	4	190	370	490	210	1500
	Birds	0	0	0	0	0	0	98	20	0	120
	Seals	0	86	0	300	0	830	560	200	110	2100
Un-specified	Fishery	1400	130	860	210	610	420	410	1500	1700	7200
	Birds	4000	2200	5300	4600	3600	8900	4900	5300	5400	44 000
	Seals	860	820	8	2800	580	9200	680	10 000	520	25 000
All species	Fishery	–	–	–	–	–	–	–	–	–	690 000
	Birds	–	–	–	–	–	–	–	–	–	83 000
	Seals	–	–	–	–	–	–	–	–	–	98 000

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.

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 4×10^4 tons and seals 1×10^4 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 (2×10^4 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 7 of 12 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 30 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

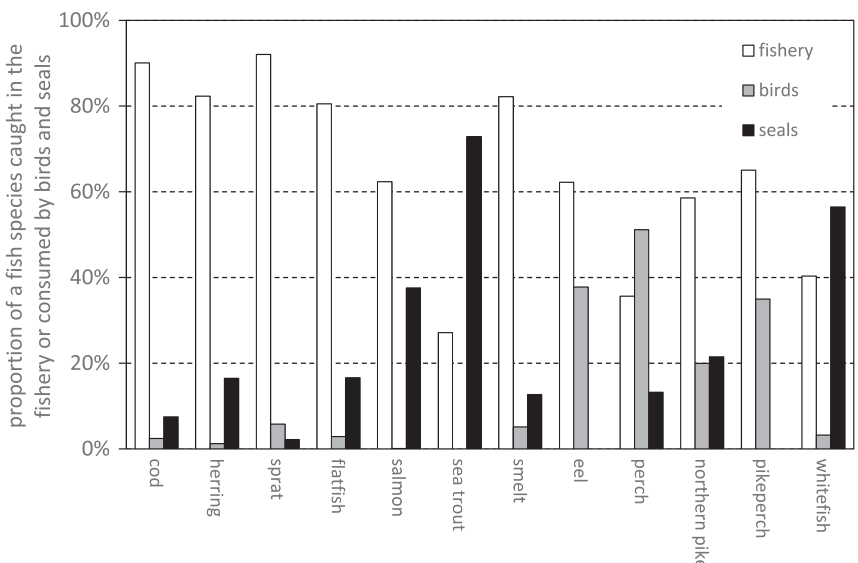

Figure 2. Proportions of different fish species extracted from the Baltic Sea through fishery catch and predation by birds and seals.

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 (cf. Middlemas *et al.*, 2006). This kind of focused predation is not captured by the broad-scale analyses of the current study. Our data (Supplementary Table S1.3), in combination with previous studies, suggest that the intensity of the competition varies among different local populations.

A 5 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 (Supplementary 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 summarized in Supplementary Document 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 (cf. 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/km^2 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/km^2 (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 support 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/km^2, resulting in an annual production of 700 kg/km^2 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 S7D25, 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 (cf. 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

Table 2. Perch and pike catch (Supplementary Table S3.4) and consumption by seals and cormorants (Supplementary 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).

		Catch and consumption, kg/km^2							
		Perch				Pike			
ICES SD	Area <10 m, km^2	Human	Seal	Cormorant	Total	Human	Seal	Cormorant	Total
24	3000	320	0	97	420	18	0	0	18
25	1400	29	62	1300	1400	54	94	100	250
26	3200	87	0	160	250	3	0	0	3
27	3200	84	94	490	670	130	140	180	450
28	3900	260	0	210	470	37	0	5	42
29	11 000	73	150	190	420	38	39	6	83
30	5700	260	21	150	440	78	0	15	93
31	6800	52	4	3	58	22	0	1	22
32	5600	180	24	170	370	190	0	4	190
Total	44 000	140	53	200	400	63	23	21	110

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 emphasized by Essington and Plagányi (2014), 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 (cf. 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, and 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 (cf. Lessard *et al.*, 2005) or to changes in local predator populations.

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Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

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