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Estimating the mortality caused by great cormorant predation on fish stocks: pikeperch in the Archipelago Sea, northern Baltic Sea, as an example

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Abstract: Estimates of the mortality rates caused by cormorants are needed to assess the impact on fish stock dynamics and fisheries. In this study, we calculated the annual instantaneous mortality caused by great cormorants (*Phalacrocorax carbo sinensis*) on young pikeperch (*Sander lucioperca*), using data from Archipelago Sea, southwestern coast of Finland. The pikeperch are vulnerable to cormorant predation mainly at the ages 2–4. The annual instantaneous mortality caused by cormorants was between 0.04 and 0.13, and the estimated effect on the pikeperch stock size at recruitment to the fishery ranged from 4% to 23%, respectively. The average annual cormorant-induced mortality accounted for 5%–34% of the total mortality in these age groups. The sensitivity analyses proved that the rates of mortality from other sources largely affect the estimated mortality from cormorant predation. In cases with strong fluctuations in the abundance of the prey fish stocks, ignoring the size and density dependence of the natural mortality may lead to overestimation of the importance of cormorants as competitors of fisheries.

Résumé : Des estimations des taux de mortalité causée par les cormorans sont nécessaires pour en évaluer l'incidence sur la dynamique des stocks de poissons et les pêches. Nous avons calculé la mortalité instantanée annuelle causée par les grands cormorans (*Phalacrocorax carbo sinensis*) chez de jeunes sandres (*Sander lucioperca*), en utilisant des données provenant de la mer de l'Archipel, au sud-ouest de la Finlande. Les sandres sont principalement vulnérables à la prédation par les cormorans à l'âge de 2 à 4 ans. La mortalité instantanée annuelle causée par les cormorans allait de 0,04 à 0,13, et l'effet estimé sur la taille de stock de sandres au moment du recrutement dans la pêche allait de 4 % à 23 %, respectivement. La mortalité annuelle moyenne induite par les cormorans expliquait de 5 % à 34 % de la mortalité totale dans ces groupes d'âge. Les analyses de sensibilité démontrent que les taux de mortalité d'autres sources ont une forte incidence sur l'estimation de la mortalité découlant de la prédation par les cormorans. Dans les cas de fortes fluctuations de l'abondance des stocks de poissons-proies, le fait de ne pas tenir compte de la dépendance de la mortalité naturelle sur la taille et sur la densité pourrait mener à une surestimation de l'importance des cormorans comme concurrents aux pêches. [Traduit par la Rédaction]

Introduction

Enlarged cormorant populations have led to major conflicts with fisheries and fish culture in many parts of Europe during the last three decades (van Eerden et al. 2012; Troynikov et al. 2013). While cormorants are protected under the Birds Directive (Directive 79/409/EEC), fishermen are worried about potential harm caused to their catches or to fish populations by cormorant predation. There are several published studies on the diet and food consumption of cormorants, but the problem has often been how to integrate these calculations to fish population dynamics; i.e., to express the impact of cormorant as mortality rates of the prey fish stocks (Cowx 2013 and references therein). Even if a decrease in fish catches was simultaneously observed with increasing abundance of cormorants, it is difficult to distinguish the potential effect of cormorants from other factors, natural year-class fluctuations in fish stocks, or environmental changes (Marzano et al. 2013). Incorporating predation mortality into fish population models would essentially increase the understanding about the state and dynamics of the fish stock and might affect, for instance, fisheries management decisions (Tyrrell et al. 2011).

The breeding of the great cormorant (*Phalacrocorax carbo sinensis*) in the Finnish coast started in 1996 (Rusanen 2014). The number of colonies and breeding pairs increased rapidly until 2009, after which the annual population growth rate slowed. In the Archipelago Sea, the first colonies were established in the beginning of the 2000s, and the population increased steeply until 2008. Owing to cold winters in the wintering areas, illegal disturbance and destruction of the nests, and increased predation by white-tailed eagles (*Haliaeetus albicilla*), the number of breeding pairs has been stable or fluctuating in the Archipelago Sea since 2009, but still increased in many other parts of the Finnish coast (Rusanen et al. 2012; Rusanen 2014). According to diet studies, the cormorants are generalist predators that mainly consume shoaling species, for instance perch (*Perca fluviatilis*), roach (*Rutilus rutilus*), and ruffe (*Gymnocephalus cernua*) in still waters (Cowx 2013), but the diet may consist of tens of different species (Lehikoinen et al. 2011; Salmi et al. 2015).

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Pikeperch (*Sander lucioperca*) is an important target species for both commercial and recreational fishery in the Archipelago Sea. Strong fluctuations in the annual catches are typical of the pikeperch fishery, due to wide variation in the year-class strength (Heikinheimo et al. 2014). The commercial fishermen's opinion is that the cormorants have caused a decrease in the pikeperch stock and their catches (Salmi et al. 2010). In recent years, in the most important pikeperch fishing area, delimited permissions have been allocated to the fishermen's association primarily to drive off the cormorants before egg-laying (Rusanen 2014).

The cormorants inhabiting the Finnish coast of the Baltic Sea feed on about 30 fish species, including economically valuable target species of commercial fishery, such as pikeperch and perch (Lehikoinen et al. 2011; Salmi et al. 2015). However, quantifying the effects of the predation on the fish stocks by cormorants is not straightforward because the rate of natural mortality from other sources is mostly unknown, compensative processes such as density dependence of growth and mortality may counteract the predation effect (Dekker and De Leeuw 2003), and changes in the composition of the fish assemblage reflect the diet of the generalist predator (Murdoch 1973; Turchin 2003; Smout et al. 2010).

Because the daily energy demand of the cormorants is high, the total fish biomass consumed by a cormorant population annually is large (Cowx 2013 and references therein). In lakes and rivers, studies on the potential impact of cormorants on fish stocks have produced varying results (summarized by Cowx 2013). Only few studies so far have attempted to estimate cormorant predation mortalities in the prey fish populations (Nielsen et al. 1999; Rudstam et al. 2004; Östman et al. 2013; Skov et al. 2014). In several published studies from the Baltic Sea area, conclusions about the potential effect of cormorant predation on fish stocks have been drawn on the basis of correlations between the changes in the fish stocks and abundance of cormorants in the nearby area (Vetemaa et al. 2010; Östman et al. 2012; Mustamäki et al. 2013). From the scientific perspective, such correlations cannot be considered valid evidence of cormorant impact if the effects of environmental and other factors cannot be discounted (Marzano et al. 2013). Östman et al. (2013) showed that the cormorant-induced mortality can be calculated without an estimate of the prey population size when the cormorants and fisheries exploit the same age groups of the prey and the fishermen's catches and fishing mortality are known. In many cases, however, the cormorants take mainly younger ages than those targeted by fisheries. In such cases, future catch losses caused to fishermen have been calculated using the numbers of fish eaten by cormorants as a starting point and natural and fishing mortality estimates for the fish species from the same or other areas (Östman et al. 2013; Skov et al. 2014; Salmi et al. 2015). Comparison of the catch losses calculated in this way to current fisheries catches incorporates an implicit assumption of an equilibrium state in the prey fish stock and that the cormorant-induced mortality was additive to other mortality agents. In fish stocks that exhibit wide fluctuations in recruitment due to environmental circumstances (Myers and Barrowman 1996), such as percids and cyprinids and many other species in the Baltic Sea (Lappalainen et al. 2009; Kallasvuo 2010), the predation effect calculated under these assumptions may be biased. Thus, a reliable estimate of cormorant-induced mortality and effect on the fish stock recruiting to the fishery can be achieved only on the basis of the prey population size. Still, there are several sources of uncertainty, as the same prey fish stocks are most probably preyed upon by other predators, the abundance and effect of which is not known. To distinguish the effect of a specific predator, estimates of instantaneous mortalities from other potential sources should be available (Matthiopoulos et al. 2008). Such information seldom exists, but it is known that the natural mortality in fish stocks is highly variable and often considerably higher than the commonly used estimates (Tyrrell et al. 2011). Moreover, the often unknown relationship between per capita predator consumption and prey density, i.e., the functional response, may play an important role in the predator–prey interaction (Hunsicker et al. 2011).

In this study we estimated the instantaneous mortality rate caused by the predation by cormorants on young pikeperch and examined the sensitivity of the results to the assumed rate of natural mortality from other sources. We used the data on the diet of the great cormorants in the Archipelago Sea (Korhonen 2010; Salmi et al. 2015), estimates of the abundance of cormorants in the area (P. Rusanen, Finnish Environment Institute, personal communication, 2015), and stock assessment of pikeperch based on long-term catch statistics and samples from the commercial catches (Heikinheimo et al. 2014). We compared the mortality in two different years, representing different stock sizes of pikeperch, to trace the effect of pikeperch abundance on the cormorant predation rate. The estimated mortality was used to assess the effect of cormorants on the size of the pikeperch population at recruitment to the fishery.

Materials and methods

Study area and the pikeperch stock

The Archipelago Sea (60°N, 21°E) is a brackish water area off the southwestern coastline of Finland in the northern Baltic Sea, characterized by numerous islands of different sizes (Fig. 1). The salinity of surface waters varies from 3 to >6 ppm (Pitkänen et al. 2001). The inner and outer archipelago areas largely differ in terms of salinity, turbidity, exposure, water temperature, and level of eutrophication (Kallasvuo 2010). The coastal fish communities consist of both marine and freshwater species. Some freshwater species such as perch, pike (*Esox lucius*), ruffe, three-spined stickleback (*Gasterosteus aculeatus*), roach, and bream (*Abramis brama*) are abundant in the whole archipelago area, whereas pikeperch and certain warm-water cyprinids inhabit the inner archipelago and shallow bays. Species adapted to marine environment such as sprat (*Sprattus sprattus*), flounder (*Platichthys flesus*), and eelpout (*Zoarces viviparous*) are common in the outer archipelago (Lappalainen et al. 2000). The Baltic herring (*Clupea harengus membras*) is a marine species that migrates to spawn to the inner archipelago.

Pikeperch has benefitted from the eutrophication of the Baltic Sea and warm summers (Pekcan-Hekim et al. 2011; Heikinheimo et al. 2014), and in the recent decades the catches have been on a high level compared with the 1980s (Fig. 2). The minimum allowable landing size of pikeperch is 37 cm total length. Because of several strong year classes, the catches were highest in the latter half of the 1990s and in the beginning of the 2000s and have leveled out after that (Heikinheimo et al. 2014). The reproduction areas of pikeperch are located in the innermost bays characterized by high turbidity (Veneranta et al. 2011).

The reproduction success of pikeperch is mainly regulated by summer temperatures (Lappalainen et al. 2009; Pekcan-Hekim et al. 2011; Heikinheimo et al. 2014). There are even tenfold differences in the year-class strength, warm summers producing very strong year classes, which are often followed by weak ones (Heikinheimo et al. 2014). Pikeperch is included in the diet of cormorants in the Archipelago Sea mainly in the inner archipelago, but is almost absent in the outer archipelago (Salmi et al. 2015).

The fishing effort of commercial fishermen in the Archipelago Sea increased in the period from the 1980s to the mid-2000s. In recent years, the effort has decreased and many of the fishermen have moved to the innermost archipelago, mainly because of the damage caused by grey seals (*Halichoerus grypus*). On the contrary, the recreational rod fishery has become more popular, and the share of the recreational catches has grown during the 2000s (Heikinheimo et al. 2014) (Fig. 2).

Fig. 1. Study area (ICES rectangles 47, 51, and 52) in the Archipelago Sea and the cormorant colonies (black dots) present in 2009–2010.

Estimation of predation mortality caused by cormorants

The annual numbers of individuals in each age group in the pikeperch stock, resulting from the virtual population analysis (VPA) estimation (Heikinheimo et al. 2014), were used to calculate the share utilized by cormorants, and the predation mortality, in 2009 and 2010. The numbers of pikeperch consumed by each colony, including the nonbreeding cormorant individuals, were summed to get the total number of pikeperch consumed (Tables 1 and 2).

The number of pikeperch taken by cormorants in 1 year (C) is related to the pikeperch abundance in the sea through the equation

$$(1) \qquad C = M_c/Z \times N \times [1 - \exp(-Z)]$$

where N is number of pikeperch in the population in the beginning of the year in those age groups that are utilized by cormorants; Z is total instantaneous mortality rate per year, i.e., $M_c + M_o + F$, where M_c is annual mortality rate caused by cormorants; M_o is other natural mortality rate per year; and F is fishing mortality rate per year.

In this case, C was known, M_o was assumed an age-specific constant, F was estimated by the VPA, and M_c and Z were unknown; thus, the value for M_c could be found by iteration (the Solver tool in Excel), searching the value that produces C (the number of pikeperch consumed). Z was calculated by summing $M_c + M_o + F$. A similar iterative procedure has been used in the multispecies VPA (MSVPA; Sparre 1991).

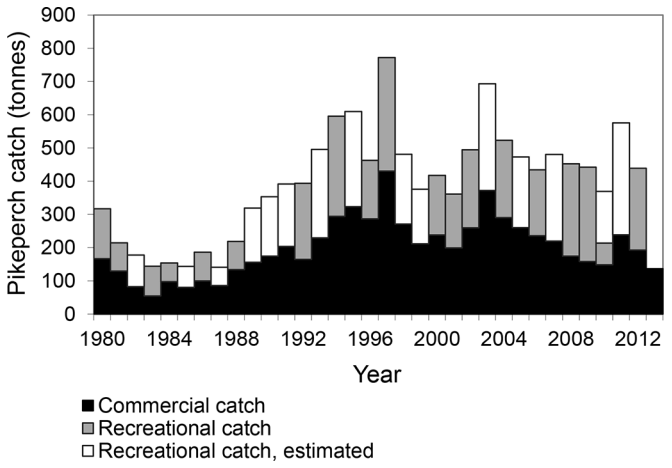
Finally, the total mortality in percentages caused by cormorants on pikeperch before recruitment to the fishery ($A_c(t)$), assuming that M_c is constant between years, was calculated as

$$(2) \qquad A_c(t) = M_c/Z \times [1 - \exp(-Z \times t)]$$

where t is the time in years during which the pikeperch are vulnerable to the cormorant predation. The pikeperch mainly recruit to the fishery at the ages 5–8 as they reach the legal catchable size (37 cm total length). Thus, $A_c(t)$ represents the effect of cormorants on the catchable pikeperch stock.

With the values of natural mortality (M_o) used in the stock assessment by Heikinheimo et al. (2014) (the lowest option applied in the sensitivity analysis), the mortality caused by cormorants was assumed to be additive; thus, the VPA analysis was run with higher M at the ages vulnerable to cormorant predation. The VPA then produces a larger estimate of population size, which again affects the resulting mortality estimate M_c. The rate of additive mortality in the VPA was found by trial repeating the VPA with different values of M until the additive mortality corresponded to the predation mortality by cormorants. In the sensitivity analysis

Fig. 2. Pikeperch catches in the Archipelago Sea (ICES rectangles 47, 51, and 52) from 1980 to 2013 according to the official fisheries statistics (Finnish Game and Fisheries Research Institute, currently Natural Resources Institute Finland (Luke)). Estimates of recreational catches in the years between recreational fishery surveys were produced by interpolation, using the recreational catch–commercial catch relationship. In 2010, both survey result and estimate are shown because of different sampling schedule and low number of responses in the survey (Heikinheimo et al. 2014). The recreational catch in 2013 was not estimated.



with higher values of M_o, it was assumed that the mortality caused by cormorants was included in the total natural mortality used in the VPA runs. Thus, the VPA was simply run with the alternative values of M to produce the corresponding estimates of N and F, and M_c was solved from eq. 1 in each case as described above. Finally, to examine the sensitivity of the mortality estimates to the assumed consumption rate of cormorants, the analysis with the most extreme assumptions of M was repeated using 500 g as the daily food consumption (25% larger number of pikeperch individuals consumed by cormorants).

Diet of the cormorants and consumption of pikeperch

Cormorant diet samples were collected from six cormorant breeding colonies in the study area in 2009 and from four colonies in 2010 (Korhonen 2010; Salmi et al. 2015). The number and location of the colonies with the numbers of breeding pairs were provided by the Finnish Environment Institute SYKE (P. Rusanen, unpublished data) (Tables 1 and 2).

The colony islets Kalmanhohde and Aukkoletto are located in an inner bay with closed shoreline and turbid and shallow water. Äggskär, Måsgrund, and Pohilainen are situated in the central part of the archipelago, where the water area is greater than the land area, and waters are deeper than and not as turbid as in the innermost archipelago. Kluppi is situated in the open sea, characterized by exposed shores with deep and cool water. The colonies Kluppi and Äggskär were populated by cormorants in 2003 and other colonies in the late 2000s.

Pellets and regurgitates were collected from the colonies during the nesting period. The remnants of fish were identified to species or genus level, and the fish lengths were calculated, using pharyngeal teeth and chewing pads (cyprinids), otoliths, or vomer bones. Detailed description of the handling of the samples in 2010 is presented by Salmi et al. (2015). In 2009, the masses of partly digested prey fish in the regurgitates were not corrected, but in 2010 this was done by estimating the original lengths of the prey and using the species-specific length–mass relationships (Salmi et al. 2015).

In the estimation of the food consumption in the cormorant colonies, we assumed that the birds arrived to the area in the beginning of April and the breeding season was finished by the end of July. However, the arrival is dependent on the ice cover, which probably caused a delay of some weeks in the years in question, but this was not taken into account. The cormorants were assumed to leave the area in August–September. Lowered breeding success caused by illegal destruction or legal handling of nests was taken into account in the food consumption estimates (Tables 1 and 2). In most cases the birds did not start new nesting after the nests were destroyed. However, in 2009 more than 400 pairs built new nests at the Kluppi colony and had chicks, though fewer than normal. In this case it was assumed that each pair had one chick (Table 1).

The food consumption of adult cormorants varies from 436 to 542 g·day^{-1} depending on the season (Ridgway 2010). The chicks need less food in the beginning compared with adults, but after about 2 weeks from hatching the consumption equals that of the adults (Barrett et al. 2007). In the current study, a mean consumption 400 g fish by an "average cormorant" per day was used for the whole population, including adults, subadults, and chicks (Engström 1997), but sensitivity analysis was performed using 500 g as a mean consumption. Two chicks per nest were assumed to survive and grow to fledglings. The share of nonbreeding individuals in the adult population was assumed at 25% in April and 40% in the period from May to July (Lehikoinen 2003). To include the consumption in August and September, when the breeding population gradually leaves the breeding area and migrate southward, 25% was added to the total consumption of the breeding season (Lehikoinen 2003). In the current study the food consumption of the breeding population only was included. From late August onwards, migrants in the Archipelago Sea may be dominated by the nominate subspecies *Phalacrocorax carbo carbo*, presumably originating from northern Norway (Rusanen et al. 2012).

In 2009 six colonies and in 2010 three colonies were illegally destroyed, probably by local people who consider the cormorant an undesirable species. In these cases it was assumed that the adult birds remained in the adjacent area, i.e., only the consumption of the chicks was subtracted. In 2010, as part of experiments aiming at mitigating the contradictions with fisheries, the cormorants were driven away from two colonies when they tried to start nesting, and these birds were assumed to have joined other nearby colonies (Table 2). In one colony (Kalmanhohde), the breeding success was lowered by 90% by egg-pricking.

The percentages of pikeperch in the diet in terms of biomass in each separate colony in 2009 and 2010 were used to calculate the biomass of pikeperch consumed by cormorants (Tables 1 and 2). For those colonies from which no samples were available, the diet data from an adjacent colony was applied, or if the colony was situated in a different environment than the adjacent colony, the share of pikeperch was roughly estimated using an average value of the outer and inner archipelago (Tables 1 and 2).

The number of pikeperch taken by cormorants in each colony was calculated by dividing the biomass consumed by the mean mass of the pikeperch in that colony. With the fresh regurgitates, the lengths of undigested pikeperch individuals and length–mass relationship from trap net samples were used to calculate the mean mass of the pikeperch. For pellet data, the length of each individual pikeperch was estimated on the basis of the length of the otoliths, and as in the previous case, the mean mass of consumed pikeperch for each colony was calculated using the length–mass equation (Salmi et al. 2015).

Abundance of pikeperch

The annual abundance of the pikeperch population by age group from the stock assessment (VPA) by Heikinheimo et al. (2014) was used to estimate the number of pikeperch available for the predation by cormorants. For the sensitivity analyses, the VPA was run with higher values of natural mortality to achieve estimates for the corresponding population sizes.

Table 1. Estimation of the biomass and numbers of pikeperch consumed in each cormorant colony in the ICES rectangles 47, 51, and 52 in 2009.

Colony island	No. of nests in 2009	Disruption of nesting	Food consumption (t)	Pikeperch (%)	Pikeperch (t)	Pikeperch (numbers)
Skrakaskär E	49	Nests destroyed	7.4	10.0	0.74	8 096
Tvåkobbarna	320	Nests destroyed	48.6	10.0	4.86	52 870
Måsgrund	186	—	37.2	**17.0**	6.32	68 739
Äggskär	1 355	—	271.0	**15.8**	42.82	465 413
Svartbådan	170	Nests destroyed	25.8	15.8	4.08	44 377
Stengrund	0	—	—	—	—	—
Äijäkari	0	—	—	—	—	—
Mäntykari	0	—	—	—	—	—
Iso Mustiletto E	29	Nests destroyed	4.4	12.7	0.56	6 085
Tupaletto	69	Nests destroyed	10.5	12.7	1.33	14 478
Aukkoletto	16	—	3.2	**12.7**	0.41	4 417
Kalmanhohde	342	—	68.4	**12.7**	8.69	94 422
Kluppi	890	Nests destroyed*	145.7	**1.4**	1.98	21 538
Kallioriutta	0	—	—	—	—	—
Pohilainen	406	—	81.2	**13.1**	10.64	115 622
Urpoinen	0	—	—	—	—	—
Total			703.52	11.72	82.44	896 056
25% added to represent the time in the area after breeding					103.05	1 120 070

Note: The percentages in bold are based on samples from the colony in question; others are estimated. In six colonies, the nests were illegally destroyed.

*In Kluppi, 434 new nests were built after the destruction of the original nests and are estimated to have produced one chick per nest.

Table 2. Estimation of the biomass and numbers of pikeperch consumed in each cormorant colony in the ICES rectangles 47, 51, and 52 in 2010.

				Regurgitated fish			Pellets		
Colony island	No. of nests in 2010	Disruption of nesting	Food consumption (t)	Pikeperch (%)	Pikeperch (t)	Pikeperch (numbers)	Pikeperch (%)	Pikeperch (t)	Pikeperch (numbers)
Skrakaskär E	0	—	—	—	—	—	—	—	—
Tvåkobbarna	0	—	—	—	—	—	—	—	—
Måsgrund	425	—	85	**15.1**	12.84	104 376	7.8	6.63	52 453
Äggskär	1 436	—	287.2	**5.8**	16.66	135 462	**7.8**	22.40	177 228
Svartbådan	0	—	—	—	—	—	—	—	—
Stengrund	10	Nests destroyed	1.52	5.8	0.09	717	7.8	0.12	938
Äijäkari	5	Nests destroyed	0.76	15.1	0.11	933	7.8	0.06	469
Mäntykari	24	Nests destroyed	3.65	15.1	0.55	4 480	7.8	0.29	2 251
Iso Mustiletto E	0	Nesting prevented	—	—	—	—	—	—	—
Tupaletto	0	—	—	—	—	—	—	—	—
Aukkoletto	0	—	—	—	—	—	—	—	—
Kalmanhohde	325	Most eggs handled	49.4	**2.3**	1.14	9 240	**11.3**	5.58	50 020
Kluppi	717	—	143.4	**2.4**	3.44	27 988	**1.0**	1.43	13 144
Kallioriutta	0	—	—	—	—	—	—	—	—
Pohilainen	0	Nesting prevented	—	—	—	—	—	—	—
Urpoinen	25	—	5	5.8	0.29	2 358	7.8	0.25	3 575
Total			575.93	6.1	35.11	285 553	6.4	36.90	300 077
25% added to represent the time in the area after breeding					43.89	356 941		46.13	375 096

Note: The percentages in bold are based on samples from the colony in question; others are estimated. The mean masses of pikeperch consumed were 126.4 g in Äggskär, 111.6 g in Kalmanhohde, and 109.1 g in Kluppi (used also for Urpoinen). Mean mass of the pikeperch was 122.9 g according to the whole pellet material, and this was also used for the regurgitated fish.

The values of instantaneous natural mortalities (M) used in the VPA stock assessment were 0.5 for pikeperch of age 1, 0.3 for age 2, 0.2 for ages 3–5, and 0.1 for ages ≥ 6 (Heikinheimo et al. 2014). This was based on the commonly used basic value 0.2 for M in fish stock assessments (Pauly 1980) and on the assumption that the natural mortality is negatively size-dependent (e.g., Houde 2009; Vainikka and Hyvärinen 2012). There is wide variation in the individual growth rates of pikeperch in the Archipelago Sea (Heikinheimo et al. 2006), and thus the estimates of natural mortality were rough average values. In reality, there are large uncertainties in the natural mortality. For instance, according to Vainikka and Hyvärinen (2012), the natural mortality in young pikeperch in Lake Oulujärvi was much higher, 1.5 at the age 1 and 1.0 at the age 2. These values were based on a stock assessment using the VPA and the recapture rate from pikeperch stocking in Lake Oulujärvi. To examine the effect of the uncertainty in the natural mortality rate on the results, we performed sensitivity analysis using different combinations of age-specific mortality values. However, the highest values used were lower than that in Lake Oulujärvi because the mortality of naturally born fish is probably lower than that of stocked individuals (Table 3).

Table 3. Effect of cormorant predation on the mortality of 2- to 4-year-old pikeperch in 2009 and 2010 (pellets) under different assumptions (a–e) on instantaneous natural mortality rates (*M*) in the pikeperch stock assessment.

	M values at different ages (years) assumed in the pikeperch stock assessment			No. of pikeperch eaten by cormorants, the number of 2- to 4-year-old pikeperch in the population, and mean instantaneous mortality rates per year					
	Ages ≥6	Ages 3–5	Age 2	Eaten by cormorants	*N*	*F*	*Z*	M_c	M_o
2009									
(a)	0.1	0.33	0.43	1 120 070	10 189 632	0.03	0.39	0.13	0.23
(b)	0.1	0.4	0.6	1 120 070	12 609 574	0.03	0.49	0.11	0.35
(c)	0.1	0.5	1	1 120 070	18 273 132	0.02	0.69	0.08	0.58
(d)	0.2	0.4	0.6	1 120 070	13 729 139	0.02	0.49	0.10	0.36
(e)	0.2	0.5	0.7	1 120 070	18 138 799	0.02	0.59	0.08	0.49
2010									
(a)	0.1	0.27	0.37	375 096	6 570 613	0.04	0.34	0.07	0.24
(b)	0.1	0.4	0.6	375 096	9 679 008	0.04	0.50	0.05	0.42
(c)	0.1	0.5	1	375 096	14 875 572	0.03	0.70	0.04	0.63
(d)	0.2	0.4	0.6	375 096	10 463 152	0.04	0.50	0.05	0.42
(e)	0.2	0.5	0.7	375 096	13 930 327	0.03	0.60	0.04	0.53

Note: *M* is the total natural mortality rate per year, *N* is the number of 2- to 4-year-old pikeperch in the population, *F* is mean annual fishing mortality at ages 2–4, *Z* is annual total mortality, M_c is the annual natural mortality caused by cormorants, and $M_o$is other natural mortality per year.

Results

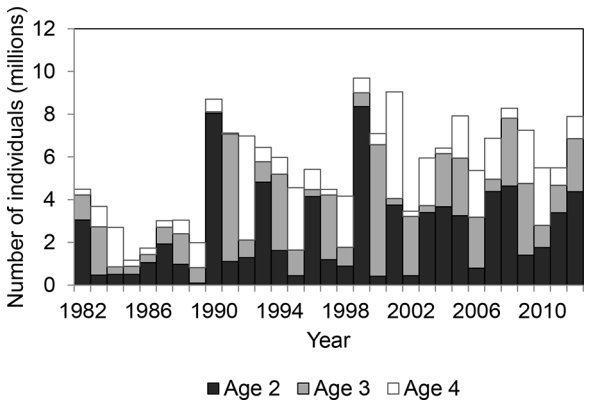
The total food consumption of the cormorant population in the breeding season in the study area was 704 tonnes (t) in 2009 (Table 1) and 576 t in 2010 (Table 2). The proportion of pikeperch in mass was 11.7% in 2009 (range 1.4%–17% in different colonies) and 6.1% or 6.4% in 2010, based on regurgitates or pellets (range 2.3%–15.1% or 1%–11.3%, respectively; Tables 1 and 2; Korhonen 2010; Salmi et al. 2015). The proportion of pikeperch varied greatly between colonies and even daily in the same colony.

The biomass of pikeperch consumed by the cormorant population in the whole season was estimated at 103 t in 2009 and 44–46 t in 2010. The number of pikeperch consumed was about 1.12 million and 0.36–0.38 million, respectively. According to the trap net catch samples from the same area, the length classes used by cormorants included mainly 2- to 4-year-old pikeperch. However, according to Salmi et al. (2015), the cormorants also utilized 1-year-old pikeperch in 2010, but the age distribution was from trap net catches and not based on age determination from the otoliths in pellets. Generally, the size classes of pikeperch found in the diet of cormorants (13–29 cm) mainly correspond to the age groups 2–4, even if there may be occasionally younger or also older, in most cases slow-growing fish included. In the mortality estimation we did not assume the age 1 to be included because the mortality at this age is large and varying, and thus the number of 1-year-old fish in the population is highly uncertain.

In 2009, the number of pikeperch in the population in the age groups 2–4 was estimated at 10–18 million depending on the assumptions on the natural mortality rates (Table 3). In 2010 the number was lower, 7–15 million. The abundance of young pikeperch was high in 2008–2010 because of the strong year classes 2005–2006 (Heikinheimo et al. 2014). In the 1990s and earlier 2000s, the abundance varied between 3 and 9 million, estimated using the lowest values of natural mortality (Fig. 3).

On the basis of the 2009 data, the instantaneous mortality of young pikeperch caused by cormorants was 0.08–0.13 per year on average, covering all alternative patterns assumed for natural mortality (Table 3). The share of cormorant-induced mortality from all mortality was 12%–34%, the total mortality (*Z*) ranging from 0.39–0.69. If we assume that the mortality was constant over the period when the young pikeperch were exposed to cormorant predation, the share of young pikeperch that died during those three years was 69%–87%, and the mortality caused by cormorants was 23%–11%, respectively (Fig. 4). The latter is the estimated effect of cormorants on the abundance of pikeperch recruiting to the fishery at the age of 5–8 years. According to the stock assessment, the mortality caused by fishing was low at the ages 2–4, only 3%–5% in total, even if the fishing pressure is high, and occasionally considerable numbers of young pikeperch are caught as bycatch in trap nets, gill nets, and with rods.

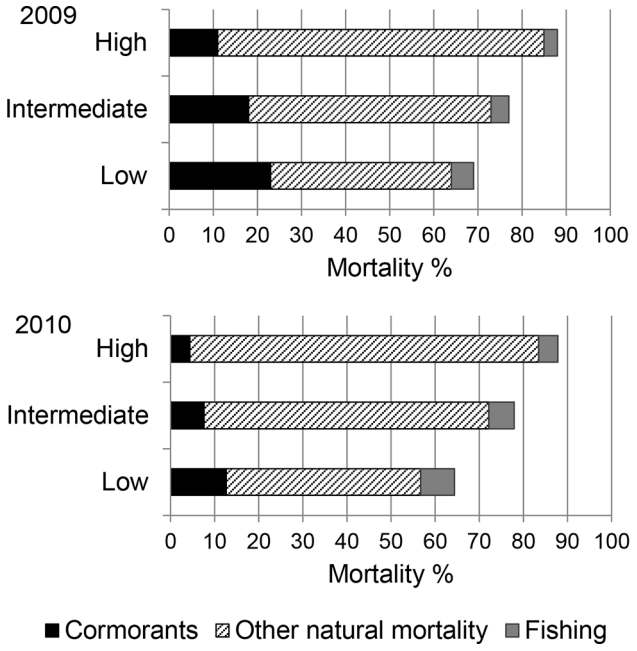
Fig. 3. Estimated numbers of pikeperch vulnerable to cormorant predation (ages 2–4) in the Archipelago Sea (ICES rectangles 47, 51, and 52) in 1982–2012, according to the stock assessment updated from Heikinheimo et al. (2014), with constant values of natural mortality (0.2–0.3 year^{-1}). Assuming additive mortality caused by cormorants would yield higher numbers of young pikeperch in the 2000s.



With the high daily food consumption (500 g), the annual cormorant-induced mortality was 0.11–0.16. The total percentage mortality caused by cormorants during 3 years would be 13%–26%; i.e., 25%–13% larger than with the lower assumed food consumption, respectively.

In 2010, the number of cormorants in the study area was lower and the percentage of pikeperch in the diet was smaller compared with the data from 2009. The estimate of cormorant-induced mortality ranged from 0.04 to 0.07 per year, and the total mortality from 0.34 to 0.70 (Table 3). The mortality caused by cormorant predation was 5%–20% of the total annual mortality. According to

Fig. 4. Mortality (%) caused by cormorants and other causes during 3 years in a pikeperch year class (ages 2–4), assuming that the annual instantaneous mortality rates are equal to those in 2009 (upper panel) or 2010 (lower panel). The three different options are low, intermediate, or high values of the natural mortality rate *M* in the stock assessment of pikeperch, which affect the estimates of population size of pikeperch (alternatives a, b, and c, respectively, in Table 3).



the results from 2010, the total mortality in 3 years (ages 2–4) would be 64%–88%, and the mortality caused by cormorants (effect on the pikeperch stock at the recruitment to the fishery) would be 4%–13% (Fig. 4). In 2010, the fishing mortality of young pikeperch was slightly higher than that in 2009, with the percentage effect during 3 years being 4%–8%.

The higher daily food consumption (500 g) yields annual cormorant-induced mortality estimates for the year 2010 ranging from 0.04 to 0.08, and in this case the mortality caused by cormorants in 3 years would be 5%–15%.

As a comparison of the predation effect of one cormorant between years, the number of pikeperch consumed by one cormorant in 1 day (mean daily consumption estimate 400 g) was 0.5 in 2009 and 0.2 in 2010. The corresponding rates of instantaneous mortality were 2.8×10^{-8} to 5.0×10^{-8} in 2009 and 1.4×10^{-8} to 3.2×10^{-8} in 2010, depending on the estimated abundance of pikeperch in age groups 2–4. The mortality rate of pikeperch caused by one cormorant per day in 2010 was about half of that in 2009 (50%–63%).

Discussion

The annual instantaneous mortality of young pikeperch caused by cormorant predation was estimated to range from 0.04 to 0.13 in the years 2009–2010, depending on the assumed rate of total natural mortality in the analysis. In total, during the period of life when the pikeperch are most vulnerable to predation, assuming that the annual mortality rate was constant, the cormorant-induced mortality was 4%–23%, which can be interpreted as the effect on the pikeperch stock at recruitment to the fishery. The rate of cormorant-induced mortality varied largely between years. According to sensitivity analyses, using high daily food consumption (500 g) of cormorants in the calculation raises the upper range of the percentage effect to 26%. The mortality estimates were most sensitive to the natural mortality rate from other sources, such as other predators, diseases, and parasites. The other predators that could cause mortality in young pikeperch are mainly pike, which is common in the same habitats as pikeperch, and larger pikeperch (cannibalism; Lappalainen et al. 2006). However, it remains uncertain to what extent the mortality caused by cormorants is additive to other natural mortality (Hilborn and Walters 1992). On the basis of the density dependence of natural mortality (Houde 2009) and compensatory processes acting in fish stocks (Rose et al. 2001), it seems reasonable to assume that the denser the prey population and the higher the other natural mortality, the less plausible it is that the cormorants could cause substantial additive mortality.

According to the current study, the daily predation mortality caused by one cormorant was considerably lower in 2010 when there were less suitable-sized pikeperch in the population compared with 2009. This may indicate a functional response of type III in the predator–prey relationship, which is typical for generalist predators that tend to shift from one prey species to another depending on the abundance and availability of the given prey (Murdoch 1969; Smout et al. 2010). A decrease of predation mortality at low densities of the prey helps to prevent a collapse of the prey stock. For the estimation of the parameters of the functional response, data from more than 2 years should be available.

Estimating the mortality caused by cormorants to assess the influence of the predation on fish stocks or the potential competition with fisheries has some clear advantages compared with calculation of the potential loss of future catches (e.g., Salmi et al. 2015), because the size of the prey population will be accounted for. On the contrary, the catch losses estimated on the basis of the number of prey eaten by the predator will be largest when the prey stock is densest, even if the predation mortality was constant. This leads to erroneous conclusions especially in cases with a high density of the prey. Many coastal fish stocks in the Baltic Sea experience strong fluctuations in year-class strength and consequently in population density, owing to environmental circumstances. In particular, the reproduction of percids such as pikeperch and perch is greatly affected by summer temperatures (Lappalainen et al. 2009; Pekcan-Hekim et al. 2011; Heikinheimo et al. 2014). Comparing the number of fish eaten by cormorants or calculated catch losses caused to fisheries from the same period of time (Östman et al. 2013; Salmi et al. 2015) might not correctly signify the cormorant effect. For instance, at the same time when the predators exploit the young individuals from a strong year class, the fishermen's catch may be low if the fish of catchable size originate from earlier weak year classes. Moreover, the cormorants harvesting a dense prey stock may have no negative effect on the fishermen's catches. For instance, the stock–recruitment analysis on the pikeperch stock in the Archipelago Sea in 1981–2004 revealed a negative effect of density on the recruitment per spawning stock biomass (Heikinheimo et al. 2014).

There seems to be an inconsistency in the results of different studies on cormorant effects from the coastal waters of the Baltic Sea or lakes in the nearby area. Some studies demonstrate large amounts of fish consumed by cormorants and suggest declines in the expected catches of fishermen (Östman et al. 2013; Salmi et al. 2015). On the contrary, some authors found no evidence that the prey fish stocks would have declined in the presence of cormorants (Engström 2001; Lehikoinen et al. 2011; Östman et al. 2012). The differences are at least partly explained by the issues described above. In some studies in the Baltic Sea area, decline in the prey fish stocks of cormorants was assumed on the basis of simultaneous changes occurring in both populations, but environmental factors or changes in the fish assemblage could explain the decline in the prey fish as well (Vetemaa et al. 2010; Mustamäki et al. 2013). For instance, according to Vetemaa et al. (2010), simultaneously with the decline of roach stock in the Käina Bay there was a marked increase in the abundance of ruffe, which is regarded as a serious competitor and egg predator of several fish

species (Winfield 1992). The data on environmental variables presented in the article by Mustamäki et al. (2013) reveals that the low mean temperature in August (17 °C) in Galtfjärden compared with the other study areas (20 °C) could alone explain the weak pikeperch year classes, which were assumed to be caused by the cormorant predation (see Pekcan-Hekim et al. 2011; Heikinheimo et al. 2014). Moreover, the potential large variation in natural mortality and the compensative processes counteracting the predation effect (Rose et al. 2001) may explain the situations where no effect of cormorants could be detected by monitoring the fish stocks. In the studies where cormorant-induced catch losses were estimated to be caused to the fisheries, the rate of other natural mortality was mainly assumed to be low (Östman et al. 2013; Skov et al. 2014; Salmi et al. 2015); in the study by Skov et al. (2014), the fishing mortality was not taken into account. Several studies have been based on tagging the potential prey fish (Jepsen et al. 2010; Skov et al. 2014), where the handling stress may affect the vulnerability of the fish to predation even if the fish survived when kept in a sheltered place after tagging. Also, the cormorant-induced mortality based on tag returns may be overestimated because part of the ingested fish would have died from other causes in the absence of cormorants.

It seems not plausible that our analysis would have underestimated the cormorant-induced mortality of pikeperch. Because the cormorants in the Archipelago Sea utilize about 30 prey species, and the most common species in the diet are perch, roach, and eelpout (Salmi et al. 2015), the cormorants seem not to particularly select pikeperch. If the functional response is of type III, the resulting mortality of the prey decreases when the prey density is at a low level (Murdoch 1973). As the natural mortality is generally density-dependent (Murdoch 1973; Matthiopoulos et al. 2008; Houde 2009; Smout et al. 2010), it would probably be high at large pikeperch densities regardless of the presence of cormorants. This is also suggested by the dome-shaped stock–recruitment curve (Heikinheimo et al. 2014). In general, the effect of compensative processes is emphasized at high population densities of the prey (Rose et al. 2001), and density dependence is of crucial importance in understanding the dynamics of predator–prey systems (Dekker and De Leeuw 2003). Thus, the lower values from the range of cormorant-induced mortality estimates produced by the current study can be considered more plausible than the high values, as the warm summers in the 2000s have produced dense pikeperch year classes, such as 2005 and 2006 (Pekcan-Hekim et al. 2011; Heikinheimo et al. 2014).

We had diet data from part of the colonies only, and the share of pikeperch had to be estimated for other colonies. However, as the composition of the diet depends on the availability of the prey species, it can be assumed that the diet did not considerably deviate in nearby areas where the fish assemblage was similar. The largest colonies were sampled in both years. In 2010, the diet samples were taken using two different methods and partly from different colonies, but the resulting estimated numbers of pikeperch consumed were close to each other (357 000 and 375 000).

There are also other uncertainties arising from the sampling, e.g., large fish and large otoliths may be better preserved in the stomachs (Carss et al. 2012), and therefore the share of large individuals or species with large otoliths may be overestimated. Further, the cormorants might take pikeperch that were released from the fisheries catches, such as trap nets, which occasionally take large amounts of undersized pikeperch. These sources of error could have caused some overestimation of the share of pikeperch in the diet.

The main sources of error in the pikeperch stock assessment originate from the catch data and from the VPA method that typically incorporates uncertainty in the estimates for the most recent years, which are affected by the input values of terminal fishing mortality (e.g., Hilborn and Walters 1992). However, the strong year classes mainly preyed upon by cormorants in the studied years, 2005 and 2006, were already recruited to the fishery in the assessment year (2012), which largely reduces the potential uncertainty, especially as the fishing mortality is high. The catch data from commercial fishery is based on annual official statistics, but the recreational catches are based on surveys that are carried out every 2 years and the uncertainty is clearly larger (Heikinheimo et al. 2014). The potential error could be in any direction. However, during the 1990s and 2000s the relationship recreational pikeperch catches versus the commercial catches has been relatively stable (around 1) but has increased since the latter half of the 2000s. Still, there may be some systematic underestimation of the recreational catches in the Archipelago Sea, as the catches of the rod fishers coming from other parts of the country are mostly not included (P. Moilanen, Natural Resources Institute Finland, personal communication, 2014).

An important question is whether removing the predator would lead to expected increase in the catches of the fishermen (Östman et al. 2013; Skov et al. 2014; Salmi et al. 2015). The answer is not easy to find in the case of complex ecosystems, such as the coastal waters considered in the current study, without extensive data and modeling (Matthiopoulos et al. 2008). Ignoring the biological complexity in models of competition between fisheries and natural predators may lead to erroneous conclusions concerning the effect of the predators on fish stocks (Matthiopoulos et al. 2008). In nature, slow-growing or weakened individuals are most vulnerable to predation (Houde 2009), and thus the fish preyed upon may experience a high probability of mortality in the first place (Hilborn and Walters 1992). In some cases, removing a top predator could even cause unexpected cascading effects in the food web (Yodzis 2001).

The cormorants have benefitted from the eutrophication of the coastal waters of the Baltic Sea and from the fisheries-induced change in the fish stocks towards dominance of small size classes, which is a well-known consequence of high fishing pressure (Carss 2003). Even if the cormorants are regarded as efficient predators, in reality a large proportion, about half of the trials, end up to losing the prey (Grémillet et al. 2006). Thus, it seems plausible that the cormorants are dependent on dense prey fish stocks to be able to satisfy their energy demand. The low abundance of large predator fish in the waters effectively exploited by fishing enables the cormorants to occupy the top-predator niche in the ecosystem (Marzano et al. 2013). Generally, large predator fish are considered an essential part of the ecosystem in coastal waters and lakes to maintain a balance in the fish assemblage (Myers and Worm 2003). On the contrary, the cormorants that utilize a similar species and size spectrum of prey fish are often regarded as harmful by the fishermen (Salmi et al. 2010, 2015). This contradiction is difficult to justify from the ecological perspective.

Our results support the conclusion by Cowx (2013) that the impact of cormorant predation on economically valuable fish species is most probably small where food webs are diverse with abundant prey species, as in the Archipelago Sea. The distribution, abundance, recruitment, and growth of fish populations are controlled by several abiotic and biotic factors, of which predation by cormorants is but one (Cowx 2013; Marzano et al. 2013). In commercially exploited fish populations, the fishing itself causes high mortality in the recruited size classes (Myers and Worm 2003), which should not be forgotten when discussing the role of natural predators (Marzano et al. 2013). For instance, in the Archipelago Sea the fishing mortality of pikeperch exceeds the optimum at which the yield would be highest (Heikinheimo et al. 2006).

The predation rate by cormorants on a given prey fish species depends not only on their abundance but also on the density of other potential suitable-sized prey, and to accurately predict the effect of cormorants on the commercially valuable fish species, a multispecies functional response should be incorporated in the predation model (Matthiopoulos et al. 2008; Smout et al. 2010).

However, the results of the current study produce new information of the cormorant effect on pikeperch in terms of mortality and on the ranges of uncertainty connected to the assumptions commonly applied in the studies on cormorant–fisheries competition. Estimates of the instantaneous mortality caused by cormorants enable the inclusion of the cormorant effect in fish population models and, assuming no major shifts in the fish assemblage, can be used when modeling scenarios with a growing cormorant population or with the effect of potential management measures aimed at reducing the cormorant–fisheries conflict. However, the complexity of the interactions in the ecosystem should be kept in mind when interpreting the modeling results (Matthiopoulos et al. 2008; Yodzis 2001; Marzano et al. 2013). Without taking any stand on the question of whether the cormorant populations should be reduced or not, it is important that usable biological information on the effects of cormorants in the ecosystem will be available as a basis for the management decisions.

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