Canadian Journal of Fisheries and Aquatic Sciences
Journal canadien des sciences halieutiques et aquatiques

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Journal:	<i>Canadian Journal of Fisheries and Aquatic Sciences</i>
Manuscript ID	cjfas-2015-0033.R1
Manuscript Type:	Article
Date Submitted by the Author:	12-Jul-2015
Complete List of Authors:	Heikinheimo, Outi; Natural Resources Institute Finland (Luke), Rusanen, Pekka; Finnish Environment Institute (SYKE), Korhonen, Katja; Turku University of Applied Sciences,
Keyword:	PREDATION < General, MORTALITY < General, COASTAL WATERS < Environment/Habitat, FISHERY RESOURCES < General, POPULATION DYNAMICS < General

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

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22 Abstract

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

35 Keywords: Great cormorant; *Phalacrocorax carbo sinensis*; pikeperch; *Sander lucioperca*; predation;
36 mortality; population dynamics; Baltic Sea

37

38 1. Introduction

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

52 The breeding of the great cormorant in the Finnish coast started in 1996 (Rusanen 2014). The number
53 of colonies and breeding pairs increased rapidly until 2009, after which the annual population growth
54 rate slowed. In the Archipelago Sea, the first colonies were established in the beginning of the 2000s,
55 and the population increased steeply until 2008. Due to cold winters in the wintering areas, illegal
56 disturbance and destruction of the nests and increased predation by white-tailed eagles (*Haliaeetus*
57 *albicilla*), the number of breeding pairs has been stable or fluctuating in the Archipelago Sea since
58 2009, but still increased in many other parts of the Finnish coast (Rusanen et al. 2012; Rusanen 2014).
59 According to diet studies, the cormorants are generalist predators that mainly consume shoaling
60 species, for instance perch (*Perca fluviatilis*), roach (*Rutilus rutilus*) and ruffe (*Gymnocephalus*
61 *cernuus*) in still waters (Cowx 2013), but the diet may consist of tens of different species (Lehikoinen
62 et al. 2011; Salmi et al. 2015).

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

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

78 Because the daily energy demand of the cormorants is high, the total fish biomass consumed by a
79 cormorant population annually is large (Cowx 2013 and references therein). In lakes and rivers,
80 studies on the potential impact of cormorants on fish stocks have produced varying results,
81 summarized by Cowx (2013). Only few studies so far have attempted to estimate cormorant predation
82 mortalities in the prey fish populations (Nielsen et al. 1999; Rudstam et al. 2004; Östman et al. 2013;
83 Skov et al. 2014). In several published studies from the Baltic Sea area conclusions about potential
84 effect of cormorant predation on fish stocks have been drawn on the basis of correlations between the
85 changes in the fish stocks and abundance of cormorants in the nearby area (Vetemaa et al. 2010;
86 Östman et al. 2012; Mustamäki et al. 2013). From the scientific perspective, such correlations cannot
87 be considered a valid evidence of cormorant impact if the effects of environmental and other factors
88 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 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 (Finnish Environment Institute, P. Rusanen), 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.

2. Material and methods

2.1. Study area and the pikeperch stock

The Archipelago Sea (60N, 21E) 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 sticklebacks (*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 viviparus*) 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 to the 1980s (Fig. 2). The minimum allowable landing size of pikeperch is 37 cm total length. Due to several strong year classes, the catches were at 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).

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

147 The fishing effort of commercial fishermen in the Archipelago Sea increased in the period from the
148 1980s to the mid-2000s. In recent years, the effort has decreased and many of the fishermen have
149 moved to the innermost archipelago, mainly due to the damage caused by the grey seals. On the
150 contrary, recreational rod fishery has become more popular and the share of the recreational catches
151 has grown during the 2000s (Heikinheimo et al. 2014) (Fig. 2).

152 2.2. Estimation of predation mortality caused by cormorants

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

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

$$160 \quad (1) \quad C = M_c / Z * N * (1 - \exp(-Z)),$$

161 where

162 N = number of pikeperch in the population in the beginning of the year, in those age groups that are
163 utilized by cormorants.

164 Z = total instantaneous mortality rate per year, i.e. $M_c + M_o + F$, where

165 M_c = annual mortality rate caused by cormorants; M_o = other natural mortality rate per year; F =
166 fishing mortality rate per year.

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

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

174 (2)
$$A_c(t) = M_c / Z * (1 - \exp(-Zt)),$$

175

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

179 With the values of natural mortality (M_o) used in the stock assessment by Heikinheimo et al. (2014)
180 (the lowest option applied in the sensitivity analysis), the mortality caused by cormorants was
181 assumed to be additive, thus the VPA analysis was run with higher M at the ages vulnerable to
182 cormorant predation. The VPA then produces a larger estimate of population size, which again affects
183 the resulting mortality estimate M_c . The rate of additive mortality in the VPA was found by trial
184 repeating the VPA with different values of M until the additive mortality corresponded to the
185 predation mortality by cormorants. In the sensitivity analysis with higher values of M_o it was assumed
186 that the mortality caused by cormorants was included in the total natural mortality used in the VPA
187 runs. Thus the VPA was simply run with the alternative values of M to produce the corresponding
188 estimates of N and F , and M_c was solved from the Equation 1 in each case as described above. Finally,
189 to examine the sensitivity of the mortality estimates to the assumed consumption rate of cormorants,

190 the analysis with the most extreme assumptions of M was repeated using 500 g as the daily food
191 consumption (25% larger number of pikeperch individuals consumed by cormorants).

192

193 2.3. Diet of the cormorants and consumption of pikeperch

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

198 The colony islets Kalmanhohde and Aukkoletto are located in an inner bay with closed shoreline, and
199 turbid and shallow water. Äggskär, Måsgrund and Pohilainen are situated in the central part of the
200 archipelago, where the water area is greater than the land area, and waters are deeper than and not as
201 turbid as in the innermost archipelago. Kluppi is situated in the open sea, characterized by exposed
202 shores with deep and cool water. The colonies Kluppi and Äggskär were populated by cormorants in
203 2003 and other colonies in the late 2000s.

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

210 In the estimation of the food consumption in the cormorant colonies we assumed that the birds arrived
211 to the area in the beginning of April and the breeding season was ended by the end of July. However,
212 the arrival is dependent on the ice cover which probably caused a delay of some weeks in the years in
213 question, but this was not taken into account. The cormorants were assumed to leave the area in
214 August – September. Lowered breeding success caused by illegal destruction or legal handling of nests

215 was taken into account in the food consumption estimates (Tables 1 and 2). In most cases the birds did
216 not start new nesting after the nests were destroyed. However, in 2009 more than 400 pairs built new
217 nests at the Kluppi colony and had chicks, though less than normally. In this case it was assumed that
218 each pair had one chick (Table 1).

219 The food consumption of adult cormorants varies from 436 g to 542g per day depending on the season
220 (Ridgway 2010). The chicks need less food in the beginning compared to adults, but after about two
221 weeks from hatching the consumption equals that of the adults (Barrett et al. 2007). In the current
222 study, a mean consumption 400 g fish by an 'average cormorant' per day was used for the whole
223 population, both adults, subadults and chicks (Engström 1997), but sensitivity analysis was performed
224 using 500 g as a mean consumption. Two chicks per nest were assumed to survive and grow to
225 fledglings. The share of non-breeding individuals in the adult population was assumed at 25% in April
226 and 40% in the period from May to July (Lehikoinen 2003). To include the consumption in August and
227 September, when the breeding population gradually leaves the breeding area and migrate southward,
228 25% was added to the total consumption of the breeding season (Lehikoinen 2003). In the current study
229 the food consumption of the breeding population only was included. Already from late August onwards
230 migrants in the Archipelago Sea may be dominated by the nominate subspecies *P. carbo carbo*,
231 presumably originating from northern Norway (Rusanen et al. 2012).

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

239 The percentages of pikeperch in the diet in terms of biomass in each separate colony in 2009 and 2010
240 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 weight of the pikeperch in that colony. With the fresh regurgitates, the lengths of undigested pikeperch individuals and length/weight relationship from trap net samples were used to calculate the mean weight 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 previous case, the mean weight of consumed pikeperch for each colony was calculated using the length/weight equation (Salmi et al. 2015).

2.4. Abundance of pikeperch

The annual abundance of the pikeperch population by age group from the stock assessment (virtual population analysis 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.

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 in Lake Oulujärvi because the mortality of naturally born fish is probably lower than that of stocked individuals (Table 3).

3. Results

The total food consumption of the cormorant population in the breeding season in the study area was 704 tonnes in 2009 (Table 1) and 576 tonnes in 2010 (Table 2). The proportion of pikeperch in weight 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 tonnes in 2009 and 44–46 tonnes in 2010. The number of pikeperch consumed was about 1.12 million and 0.36–0.38 million, respectively. According to the trapnet catch samples from the same area, the length classes used by cormorants included mainly 2–4 year old pikeperch. However, according to Salmi et al. (2014) the cormorants also utilized one-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 one-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, due to the

291 strong year classes 2005–2006 (Heikinheimo et al. 2014). In the 1990s and earlier 2000s, the
292 abundance varied between 3 and 9 million, estimated using the lowest values of natural mortality (Fig.
293 3).

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

305 With the high daily food consumption (500 g), the annual cormorant-induced mortality was 0.11–
306 0.16. The total percentage mortality caused by cormorants during three years would be 13–26%; i.e.
307 25–13% larger than with the lower assumed food consumption, respectively.

308 In 2010, the number of cormorants in the study area was lower and the percentage of pikeperch in the
309 diet was smaller compared to the data from 2009. The estimate of cormorant-induced mortality ranged
310 from 0.04–0.07 per year, and the total mortality from 0.34–0.70 (Table 3). The mortality caused by
311 cormorant predation was 5–20% of the total annual mortality. According to the results from 2010, the
312 total mortality in three years (ages 2–4) would be 64–88%, and the mortality caused by cormorants
313 (effect on the pikeperch stock at the recruitment to the fishery) 4–13% (Fig. 4). In 2010, the fishing
314 mortality of young pikeperch was slightly higher than in 2009, with the percentage effect during three
315 years being 4–8%.

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

319 As a comparison of the predation effect of one cormorant between years, the number of pikeperch
320 consumed by one cormorant in one day (average daily consumption estimate 400 g) was 0.5 in 2009
321 and 0.2 in 2010. The corresponding rates of instantaneous mortality were 2.8×10^{-8} – 5.0×10^{-8} in 2009
322 and 1.4×10^{-8} – 3.2×10^{-8} in 2010, depending on the estimated abundance of pikeperch in age groups 2–4.
323 The mortality rate of pikeperch caused by one cormorant per day in 2010 was about half of that in
324 2009 (50–63%).

325 4. Discussion

326 The annual instantaneous mortality of young pikeperch caused by cormorant predation was estimated
327 to range from 0.04 to 0.13 in the years 2009–2010, depending on the assumed rate of total natural
328 mortality in the analysis. In total, during the period of life when the pikeperch are most vulnerable to
329 predation, assuming that the annual mortality rate was constant, the cormorant-induced mortality was
330 4–23%, which can be interpreted as the effect on the pikeperch stock at recruitment to the fishery. The
331 rate of cormorant-induced mortality varied largely between years. According to sensitivity analyses,
332 using high daily food consumption (500 g) of cormorants in the calculation raises the upper range of
333 the percentage effect to 26%. The mortality estimates were most sensitive to the natural mortality rate
334 from other sources, such as other predators, diseases and parasites. The other predators that could
335 cause mortality in young pikeperch are mainly pike, which is common in the same habitats as
336 pikeperch, and larger pikeperch (cannibalism) (Lappalainen et al. 2006). However, it remains
337 uncertain to which extent the mortality caused by cormorants is additive to other natural mortality
338 (Hilborn and Walters 1992). On the basis of the density-dependence of natural mortality (Houde
339 2009) and compensatory processes acting in fish stocks (Rose et al. 2001), it seems reasonable to
340 assume, that the denser the prey population, and the higher the other natural mortality, the less
341 plausible it is that the cormorants could cause significant additive mortality.

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

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

368 There seems to be an inconsistency in the results of different studies on cormorant effects from the
369 coastal waters of the Baltic Sea or lakes in the nearby area. Some studies demonstrate large amounts
370 of fish consumed by cormorants and suggest declines in the expected catches of fishermen (Östman et
371 al. 2013; Salmi et al. 2015). On the contrary, some authors found no evidence that the prey fish stocks
372 would have declined in the presence of cormorants (Engström 2001; Lehtikoinen et al. 2011; Östman
373 et al. 2012). The differences are at least partly explained by the issues described above. In some
374 studies in the Baltic Sea area, decline in the prey fish stocks of cormorants was assumed on the basis
375 of simultaneous changes occurring in both populations, but environmental factors or changes in the
376 fish assemblage could explain the decline in the prey fish as well (Vetemaa et al. 2010; Mustamäki et
377 al. 2013). For instance, according to Vetemaa et al. 2010, simultaneously with the decline of roach
378 stock in the Käina Bay there was a marked increase in the abundance of ruffe, which is regarded as a
379 serious competitor and egg predator of several fish species (Winfield 1992). The data on
380 environmental variables presented in the article by Mustamäki et al. (2013) reveals that the low mean
381 temperature in August (17 °C) in Galtfjärden compared to the other study areas (20 °C) could alone
382 explain the weak pikeperch year classes which were assumed to be caused by the cormorant predation
383 (see Pekcan-Hekim et al. 2011; Heikinheimo et al. 2014). Moreover, the potential large variation in
384 natural mortality, and the compensative processes counteracting the predation effect (Rose et al. 2001)
385 may explain the situations where no effect of cormorants could be detected by monitoring the fish
386 stocks. In the studies where cormorant-induced catch losses were estimated to be caused to the
387 fisheries, the rate of other natural mortality was mainly assumed to be low (Östman et al. 2013; Skov
388 et al. 2014; Salmi et al. 2015) and in the study by Skov et al. (2014), the fishing mortality was not
389 taken into account. Several studies have been based on tagging the potential prey fish (Jepsen 2010;
390 Skov et al. 2014), where the handling stress may affect the vulnerability of the fish to predation even
391 if the fish survived when kept in a sheltered place after tagging. Also, the cormorant-induced
392 mortality based on tag returns may be overestimated because part of the ingested fish would have died
393 from other causes in the absence of cormorants.

394 It seems not plausible that our analysis would have underestimated the cormorant-induced mortality
395 of pikeperch. Because the cormorants in the Archipelago Sea utilize about 30 prey species, and the
396 most common species in the diet are perch, roach and eelpout (Salmi et al. 2015), the cormorants
397 seem not to particularly select pikeperch. If the functional response is of type III, the resulting
398 mortality of the prey decreases when the prey density is at a low level (Murdoch 1973). As the natural
399 mortality is generally density-dependent (Murdoch 1973; Matthiopoulos et al. 2008; Houde 2009;
400 Smout et al. 2010), it would probably be high at large pikeperch densities regardless of the presence
401 of cormorants. This is also suggested by the dome-shaped stock-recruitment curve (Heikinheimo et al.
402 2014). In general, the effect of compensative processes is emphasized at high population densities of
403 the prey (Rose et al. 2001), and density-dependence is of crucial importance in understanding the
404 dynamics of predator-prey systems (Dekker and De Leeuw 2003). Thus the lower values from the
405 range of cormorant-induced mortality estimates produced by the current study can be considered
406 more plausible than the high values, as the warm summers in the 2000s have produced dense
407 pikeperch year classes such as 2005 and 2006 (Pekcan-Hekim et al. 2011; Heikinheimo et al. 2014).

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

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

419

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 two 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 vs. the commercial catches has been relatively stable (around 1) but 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 (Moilanen, P. 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

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

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

465 The predation rate by cormorants on a given prey fish species depends not only on their abundance
466 but also on the density of other potential suitable-sized prey, and to accurately predict the effect of
467 cormorants on the commercially valuable fish species, a multispecies functional response should be
468 incorporated in the predation model (Matthiopoulos et al. 2008; Smout et al. 2010). However, the
469 results of the current study produce new information of the cormorant effect on pikeperch in terms of
470 mortality, and on the ranges of uncertainty connected to the assumptions commonly applied in the
471 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 significant 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 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.

Acknowledgements

We wish to thank Juhani A. Salmi for providing the cormorant diet data and Jari Raitaniemi for constructive comments on the manuscript.

References

- Barrett R.T., Camphuysen K.C.J., Anker-Nilssen T., Chardine, J.W., Furness R.W., Garthe S., Hüppop O., Leopold M.F., Montevecchi W.A., and Veit R.R. 2007. Diet studies of seabirds: a review and recommendations. *ICES J. Mar. Sci.* 64: 1675–1691.
- Carss D. (ed.), 2003. Reducing the conflict between Cormorants and fisheries on a pan-European scale, REDCAFE. Final report of Concerted Action Q5CA- 2000-31387, 169 pp. Available at: <http://www.intercafeproject.net/>
- Carss, D.N., Parz-Gollner, R., and Trauttmansdorff, J. 2012. The INTERCAFE Field Manual: research methods for cormorants, fishes, and the interactions between them. INTERCAFE COST Action 635 Final Report II. http://www.intercafeproject.net/pdf/Field_Manual_web_version.pdf (accessed 16 October 2013).

- 495 Cowx, I.G. 2013. Between fisheries and bird conservation: The cormorant conflict. Note. EU,
496 Directorate-General for Internal Policies, Policy Department B: Structural and Cohesion Policies.
497 Fisheries. IP/B/PECH/IC/2012-046. 62 pp. doi: 10.2861/13262.
- 498 Dekker, W., and De Leeuw, J.J. 2003. Bird–fisheries interactions: the complexity of managing a
499 system of predators and preys. *In* Cowx, I.G. (Ed.), *Interactions Between Fish and Birds: Implications*
500 *for Management*. Blackwell Science Ltd, Oxford, pp. 3–13.
- 501 Engström, H. 1997. Mellanskarvens ekologi och effekter på fisk och fiske. Sammanställning av
502 nuvarande kunskap om Mellanskarven *Phalacrocorax carbo sinensis*. Fiskeriverket rapport 1.
503 Fiskeriverket, Sötvattenslaboratoriet, Drottningholm (in Swedish).
- 504 Engström, H. 2001: Long-term effects of cormorant predation on fish communities and fishery in a
505 freshwater lake. *Ecography* 24: 127–138.
- 506 Grémillet, D., Enstipp, M., Boudiffa, M., and Liu, H. 2006. Do cormorants injure fish without eating
507 them? An underwater video study. *Mar. Biol.* 148: 1081–1087. doi: 10.1007/s00227-005-0130-2.
- 508 Heikinheimo, O., Setälä, J., Saarni, K., and Raitaniemi, J. 2006. Impacts of mesh-size regulation of
509 gillnets on the pikeperch fisheries in the Archipelago Sea, Finland. *Fisheries Research* 77: 192–199.
- 510 Heikinheimo, O., Pekcan-Hekim, Z., and Raitaniemi, J. 2014. Spawning stock – recruitment
511 relationship in pikeperch, *Sander lucioperca*, in the Baltic Sea, with temperature as environmental
512 effect. *Fisheries Research* 155: 1–9.
- 513 Hilborn, R., and Walters, C.J., 1992. *Quantitative Fisheries Stock Assessment. Choice, Dynamics and*
514 *Uncertainty*. Chapman and Hall, London.
- 515 Houde, E.D., 2009. Recruitment variability. *In* Jakobsen, T., Fogarty, M.J., Megrey, B.A., and
516 Moksness, A. (Eds.), *Fish Reproductive Biology. Implications for Assessment and Management*. John
517 Wiley & Sons, Chichester, pp. 91–171.

- 518 Hunsicker, M.E., Ciannelli, L., Bailey, K.M., Buckel, J.A., White, J.W., Link, J.S., Essington, T.E.,
519 Gaichas, S., Anderson, T.W., Brodeur, R.D., Chan, K.-S., Chen, K., Englund, G., Frank, K.T., Freitas,
520 V., Hixon, M.A., Hurst, T., Johnson, D.W., Kitchell, J.F., Reese, D., Rose, G.A., Sjodin, H.,
521 Sydeman, W.J., van der Veer, H.W., Vollset, K., and Zador, S. 2011. Functional responses and
522 scaling in predator–prey interactions of marine fishes: contemporary issues and emerging concepts.
523 Ecology Letters (2011) doi: 10.1111/j.1461-0248.2011.01696.x
- 524 Jepsen, N., Klenke, R., Sonnesen, P., and Bregnballe, T. 2010. The use of coded wire tags to estimate
525 cormorant predation on fish stocks in an estuary. Marine and Freshwater Research 61: 320–329.
- 526 Kallasvuo, M. 2010. Coastal environmental gradients. Key to reproduction habitat mapping of
527 freshwater fish in the Baltic Sea. PhD thesis, University of Helsinki. Available from
528 <http://urn.fi/URN:ISBN:978-952-10-6392-3>.
- 529 Korhonen, K. 2010. Merimetson (*Phalacrocorax carbo sinensis*) poikasajan ravinnonkäyttö
530 Saaristomerellä kesinä 2009–2010. (Diet of the great cormorant nestlings in the Finnish archipelago
531 during summers 2009–2010). Bachelor's thesis. Turku University of Applied Sciences. (In Finnish
532 with English summary). Available from <http://urn.fi/URN:NBN:fi:amk-2010120517165>.
- 533 Lappalainen A., Shurukhin A., Alekseev G., and Rinne J. 2000. Coastal fish communities along the
534 northern coast of the Gulf of Finland: responses to salinity and eutrophication. Internat. Rev.
535 Hydrobiol. 85: 687–696.
- 536 Lappalainen, J., Olin, M., and Vinni, M. 2006. Pikeperch cannibalism: effects of abundance, size and
537 condition. Ann. Zool. Fenn. 43: 35–44.
- 538 Lappalainen, J., Milardi, M., Nyberg, K., and Venäläinen, A. 2009. Effects of water temperature on
539 year class strengths and growth patterns of pikeperch (*Sander lucioperca* (L.)) in the brackish Baltic
540 Sea. Aquat. Ecol. 43: 181–191.

- 541 Lehtikoinen, A. 2003. Merimetson kannankehitys Suomessa – pesintämenestys, ravinto ja vaikutus
542 muuhun pesimälinnustoon. Master's thesis. University of Helsinki, Department of Ecology and
543 Systematics. (In Finnish).
- 544 Lehtikoinen, A., Heikinheimo, O., and Lappalainen, A. 2011: Temporal changes in the diet of great
545 cormorant (*Phalacrocorax carbo sinensis*) on the southern coast of Finland — comparison with
546 available fish data. Boreal Env. Res. 16 (suppl. B): 61–70.
- 547 Marzano, M., Carss, D.N., and Cheyne, I. 2013. Managing European cormorant-fisheries conflicts:
548 problems, practicalities and policy. Fisheries Management and Ecology 20: 401–413. doi:
549 10.1111/fme.12025
- 550 Matthiopoulos, J., Smout, S., Winship, A.J., Thompson, D., Boyd, I.L., and Harwood, J. 2008.
551 Getting beneath the surface of marine mammal - fisheries competition. Mammal Rev. 38, Nos. 2-3, p.
552 167–188.
- 553 Murdoch, W.W. 1969. Switching in generalist predators: experiments on predator specificity and
554 stability of prey populations. Ecological Monographs 39: 335–354.
- 555 Murdoch, W.W., 1973. The functional response of predators. J. Appl. Ecol. 10: 335–342.
- 556 Mustamäki, N., Bergström, U., Ådjers, K., Sevastik, A., and Mattila, J. 2013. Pikeperch (*Sander*
557 *luciperca* (L.)) in decline: high mortality of three populations in the Northern Baltic Sea. AMBIO
558 42, <http://dx.doi.org/10.1007/s13280-013-0429-z>.
- 559 Myers, R.A., and Barrowman, N.J. 1996. Is fish recruitment related to spawner abundance? Fish.
560 Bull. 94: 707–724.
- 561 Myers, R.A., and Worm, B. 2003. Rapid worldwide depletion of predatory fish communities. Nature
562 423: 280–283. doi:10.1038/nature01610.

- 563 Nielsen, E., Neuenfeldt, S., and Vinther, M. 1999. Betydningen af skarvens prædation på torsk
564 vurderet ved hjælp af flerartsmodellen (MSVPA) (The predation of cormorant on cod in the Baltic
565 using the multispecies model MSVPA). Danmarks Fiskeriundersøgelser, Afd. for Hav- og
566 kystøkologi, Charlottenlund. DFU-Rapport nr. 68-99. 13 pp. (In Danish with English abstract).
- 567 Östman, Ö., Bergenius, M., Boström, M.K., and Lunneryd, S.-V. 2012. Do cormorant colonies affect
568 local fish communities in the Baltic Sea? Can. J. Fish. Aquat. Sci. 69: 1047–1055.
- 569 Östman, Ö., Boström, M.K., Bergström, U., Anderson, J., and Lunneryd, S.-V. 2013. Estimating
570 competition between wildlife and human – a case of cormorants and coastal fisheries in the Baltic
571 Sea. PLOS ONE 8, <http://dx.doi.org/10.1371/journal.pone.0083763>.
- 572 Pauly, D. 1980. On the interrelationships between natural mortality, growth parameters, and mean
573 environmental temperature in 175 fish stocks. J. Cons. Int. Explor. Mer. 39: 175–192.
- 574 Pekcan-Hekim, Z., Urho, L., Auvinen, H., Heikinheimo, O., Lappalainen, J., Raitaniemi, J., and
575 Söderkultalahti, P. 2011. Climate warming and pikeperch year-class catches in the Baltic Sea. Ambio
576 40, 447–456.
- 577 Pitkänen, H., Kauppila, P., and Laine, Y. 2001. Hydrography and oxygen conditions. In: Kauppila, P.,
578 Bäck, S. (Eds.), The State of Finnish Coastal Waters in the 1990, vol. 472. Finnish Environment
579 Institute, The Finnish Environment, Helsinki, pp. 30–36.
- 580 Ridgway, M.S. 2010. A review of estimates of daily energy expenditure and food intake in
581 Cormorants (*Phalacrocorax* spp.). J. Great Lakes Res. 36: 93–99.
- 582 Rose, K.A., Cowan Jr J.H., Winemiller, K.O., Myers, R.A., and Hilborn, R. 2001. Compensatory
583 density dependence in fish populations: importance, controversy, understanding and prognosis. Fish
584 and Fisheries 2: 293–327.

- 585 Rudstam L.G., VanDeValk A.J., Adams C.M., Coleman J.T.H., Forney J.L., and Richmond M.E.
586 2004. Cormorant predation and the population dynamics of walleye and yellow perch in Oneida lake.
587 Ecol. Appl. 14: 149–163.
- 588 Rusanen, P. 2014: Status of the breeding population of Great Cormorants in Finland in 2012. – In:
589 Bregnballe, T., Lynch, J., Parz-Gollner, R., Marion, L., Volponi, S., Paquet, J.-Y., Carss, D.N. and
590 van Eerden, M.R. (eds.): Breeding numbers of Great Cormorants *Phalacrocorax carbo* in the Western
591 Palearctic, 2012-2013. – IUCN-Wetlands International Cormorant Research Group Report. Scientific
592 report from DCE – Danish Centre for Environment and Energy, Aarhus University. No. 99, pp. 103-
593 107. Available from <http://dce2.au.dk/pub/SR99.pdf>
- 594 Rusanen, P., Mikkola-Roos, M., and Rytteri, T. 2012: Population development of cormorant and
595 effects in Finland. – The yearbook 2011 of the Linnut magazine, pp. 116–123. (In Finnish with
596 English summary). Available from [http://www.birdlife.fi/suojelu/lajit/ladattavat/merimetso-](http://www.birdlife.fi/suojelu/lajit/ladattavat/merimetso-vuosikirja-2011.pdf)
597 [vuosikirja-2011.pdf](http://www.birdlife.fi/suojelu/lajit/ladattavat/merimetso-vuosikirja-2011.pdf)
- 598 Salmi, J., Salmi, P., and Moilanen, P. 2010. Ammattikalastus ja merimetso. Merestä elantoon
599 hankkivien näkemyksiä. (Commercial fishing and the cormorant – fishers’ perspectives.) Finnish
600 Game and Fisheries Research Institute. Riista- ja kalatalous — Selvityksiä 1/2010. 18 pp. (In Finnish
601 with English abstract).
- 602 Salmi, J.A., Auvinen, H., Raitaniemi, J., Kurkilahti, M., Lilja, J., and Maikola, R. 2015. Perch (*Perca*
603 *fluviatilis*) and pikeperch (*Sander lucioperca*) in the diet of the great cormorant (*Phalacrocorax*
604 *carbo*) and effects on catches in the Archipelago Sea, Southwest coast of Finland. Fisheries Research
605 164: 26–34.
- 606 Skov, C., Jepsen, N., Baktoft, H., Jansen, T., Pedersen, S., and Koed, A. 2014. Cormorant predation
607 on PIT-tagged lake fish. J. Limnol. 73: 177–186.

- 608 Smout, S., Asseburg, C., Matthiopoulos, J., Fernández, C., Redpath, S., Thirgood, S., and Harwood, J.
609 2010. The functional response of a generalist predator. PLoS ONE 5(5): e10761.
610 doi:10.1371/journal.pone.0010761
- 611 Sparre, P. 1991. Introduction to multispecies virtual population analysis. ICES Mar.Sci. Symp. 193,
612 12–21.
- 613 Troynikov, V., Whitten, A., Gorfine, H., Pūtys, Ž., Jakubavičiūtė, E., Ložys, L., and Dainys, J. 2013.
614 Cormorant catch concerns for fishers: Estimating the size-selectivity of a piscivorous bird. PLoS ONE
615 8(11): e77518. doi:10.1371/journal.pone.0077518
- 616 Turchin, P. 2003. Complex Population Dynamics. A Theoretical/Empirical Synthesis. Monographs in
617 Population Biology, vol. 35. Princeton University Press, Princeton and Oxford, 450 pp.
- 618 Tyrrell, M.C., Link, J.S., and Moustahfid, H. 2011. The importance of including predation in fish
619 population models: Implications for biological reference points. Fisheries Research 108: 1–8.
- 620 Vainikka, A., and Hyvärinen, P. 2012. Ecologically and evolutionarily sustainable fishing of the
621 pikeperch *Sander lucioperca*: Lake Oulujärvi as an example. Fisheries Research 113: 8– 20.
- 622 van Eerden, M., van Rijn, S., Volponi, S., Paquet, J.-Y., and Carss, D.N. 2012. Cormorants and the
623 European Environment; exploring cormorant status and distribution on a continental scale.
624 INTERCAFE COST Action 635 Final Report I.
- 625 Veneranta, L., Urho, L., Lappalainen, A, and Kallasvuo, M. 2011: Turbidity characterizes the
626 reproductions areas of pikeperch (*Sander lucioperca* (L.)) in the northern Baltic Sea. Estuarine,
627 Coastal and Shelf Science 95(1): 199–206.
- 628 Vetemaa M., Eschbaum R., Albert A., Saks L., Verliin A., Jürgens K., Kesler M., Hubel K.,
629 Hannesson R., and Saat T. 2010. Changes in fish stocks in an Estonian estuary: overfishing by
630 cormorants? ICES J. Mar. Sci. 67: 1–8.

- 631 Winfield, I.J. 1992. Threats to the lake fish communities of the U.K. arising from eutrophication and
632 species introductions. *Neth. J. Zool.* 42: 233–242.
- 633 Yodzis, P. 2001. Must top predators be culled for the sake of fisheries? *Trends Ecol. Evol.* 16: 78–84.

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

Colony island	Number of nests in 2009	Disruption of nesting	Food consumption (tonnes)	Pike- perch %	Pikeperch tonnes	Pikeperch in numbers
Skrakaskär E	49	Nests destroyed	7.4	10	0.74	8 096
Tvåkobbarna	320	Nests destroyed	48.6	10	4.86	52 870
Måsgrund	186	-	37.2	17	6.32	68 739
Äggskär	1355	-	271.0	15.8	42.82	465 413
Svartbådan	170	Nests destroyed	25.8	15.8	4.08	44 377
Stengrund	0	-	-	-	-	-
Äjäkari	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
Kallioriota	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

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

642 Table 2. Estimation of the biomass and numbers of pikeperch consumed in each cormorant colony in
643 the ICES rectangles 47, 51 and 52 in 2010. The percentages in bold are based on samples from the
644 colony in question, others are estimated. The mean weights of pikeperch consumed were 126.4 g in
645 Äggskär, 111. 6 g in Kalmanhohde, and 109. 1 g in Kluppi (used also for Urpoinen). Mean weight of
646 the pikeperch was 122.9 g according to the whole pellet material, and this was used for the
647 regurgitated fish, too.

648

Colony island	Number of nests in 2010	Disruption of nesting	Food consumpt- ion (tonnes)	Regurgitated fish				Pellets	
				Pikeperch %	Pikeperch tonnes	Pikeperch in numbers	Pikeperch %	Pikeperch tonnes	Pikeperch in numbers
Skrakaskär E	0	-	-	-	-	-	-	-	-
Tvåkobbarna	0	-	-	-	-	-	-	-	-
Måsgrund	425	-	85	15.1	12.84	104 376	7.8	6.63	52 453
Äggskär	1436	-	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
Äjjäkari	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	1.43	13 144
Kallioriota	0	-	-	-	-	-	-	-	-
Pohilainen	0	Nesting prevented	-	-	-	-	-	-	-
Urpoinen	25	-	5	5.8	0.29	2 358	7.8	0.25	3 575
Total	2967	0	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

649

650

Table 3. Effect of cormorant predation on the mortality of 2–4 -year-old pikeperch in 2009 and 2010 (pellets) under different assumptions a) – e) on instantaneous natural mortality rates in the pikeperch stock assessment. M is the total natural mortality rate per year, N = the number of 2–4-year-old pikeperch in the population, F = average annual fishing mortality at ages 2–4, Z = annual total mortality, M_c = the annual natural mortality caused by cormorants, and M_o is other natural mortality per year.

2009

Natural mortality (M) values at different ages (years) assumed in the pikeperch stock assessment				Number of pikeperch eaten by cormorants, the number of 2-4 -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
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

658

2010

Natural mortality (M) values at different ages (years) assumed in the pikeperch stock assessment				Number of pikeperch eaten by cormorants, the number of 2-4 -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
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

660

661 Figure captions

662

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

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

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

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