Author(s): Mats Westerbom, Camilla Ekblad, Juhani Hopkins, Toni Laaksonen, Mikko Olin, Antti Ovaskainen, Veijo Jormalainen

Title: Cormorant predation in fyke net fishing: The direct effects of a protected bird on coastal commercial fishing

Year: 2025

Version: Published version

Please cite the original version:

Mats Westerbom, Camilla Ekblad, Juhani Hopkins, Toni Laaksonen, Mikko Olin, Antti Ovaskainen, Veijo Jormalainen, Cormorant predation in fyke net fishing: The direct effects of a protected bird on coastal commercial fishing, Fisheries Research, Volume 281, 2025, 107234, ISSN 0165-7836, https://doi.org/10.1016/j.fishres.2024.107234. .

Fisheries Research 281 (2025) 107234

Contents lists available at ScienceDirect

Fisheries Research

journal homepage: www.elsevier.com/locate/fishres

Cormorant predation in fyke net fishing: The direct effects of a protected bird on coastal commercial fishing

Mats Westerbom [a,*], Camilla Ekblad [b,c], Juhani Hopkins [c], Toni Laaksonen [b], Mikko Olin [c], Antti Ovaskainen [a,b], Veijo Jormalainen [b]

[a] Natural Resources Institute Finland, Itäinen Pitkäkatu 4 A, Turku 20520, Finland
[b] University of Turku, Department of Biology, Turku 20014, Finland
[c] Natural Resources Institute Finland, Latokartanonkaari 9, Helsinki 00790, Finland

ARTICLE INFO

Handled by B. Morales-Nin

Keywords:
Depredation
Fisheries
Fish traps
Human-wildlife conflict
Wildlife management
Wildlife damage
Baltic Sea

ABSTRACT

The population size of great cormorants, *Phalacrocorax carbo sinensis,* has risen steeply in the Baltic Sea over the past 40 years. The growing population has resulted in polarized conflicts between conservation and coastal fisheries due to the losses cormorants may inflict on fisheries. Mitigation of the conflicts requires objective estimates of true losses to fisheries, but quantitative research on losses has been scarce. We used continuous video-recordings to systematically quantify cormorant visits and their activity at 15 fyke nets during the 2022–2023 breeding and post breeding seasons. More than 2400 h of video footage were recorded, in which cormorants were found for 664 h. We also quantified the frequency of fish injured by birds in coastal fishing catches using data from the EU Fisheries Data Collection Program including data from fyke nets and gill nets. Our results show that cormorants frequently foraged in open, floating fyke nets but relatively rarely in submerged nets, leading to significantly higher losses in the former. Monitoring data from fyke and gill net catches covering the entire Finnish coast revealed that the proportion of bird-injured fish in catches is very modest (0.5 %) but can be considerable in individual catches. Finally, results indicate that cormorant visits and the proportion of injured fish in the catch tend to increase when distance to the nearest cormorant colony decreases. We conclude that the losses caused by birds are generally modest, except in open fyke nets where cormorants may conduct hundreds of dives and catch dozens of fish a day. Our study shows that cormorant depredation is highly variable in time and space, but also partly manageable by selecting gear that conforms to local cormorant pressures. We underline the importance of systematic scientific research when measuring damage caused by cormorants and ask for evidence-based political strategies to mitigate perceived cormorant problems.

1. Introduction

Global fish landings are declining (Watson et al., 2013) as many exploited fish are experiencing population drops (Pershing et al., 2015). The reasons for the declines in fish populations are many, including overfishing (Dulvy et al., 2014, Davidson et al., 2016), ecosystem degradation (Verschuren et al., 2002, Alvarez-Filip et al., 2011), changes in species-interactions in the food webs (Mills et al., 2003) and climate change (e.g., Pershing et al., 2015). While natural predators such as piscivorous birds and aquatic mammals consume fish, thus competing with human fisheries, their impact on fish populations is typically limited (Hansson et al., 2018). However, predators may exert considerable predation pressure on coastal fish populations, at least locally, as found in the coastal Baltic Sea (Hansson et al., 2018). Greater predation pressure caused by increased numbers of fish-eating birds and mammals may contribute to declines in some fish populations (Mills et al., 2003, Neuenhoff et al., 2019, Veneranta et al., 2020, Rossi et al., 2021). Resource competition between natural predators and coastal fisheries – and wildlife preying from fishing gear and aquaculture – generates human-wildlife conflicts and may result in negative attitudes towards wildlife (Dehnhard et al., 2021, Tixier et al., 2021). Although depredation is readily observed, we typically lack quantitative estimates about its importance in decreasing fish catches and causing costs to fisheries.

* Corresponding author.
E-mail addresses: mats.westerbom@luke.fi (M. Westerbom), camilla.ekblad@luke.fi (C. Ekblad), Juhani.hopkins@luke.fi (J. Hopkins), toni.laaksonen@utu.fi (T. Laaksonen), mikko.olin@luke.fi (M. Olin), veijo.jormalainen@utu.fi (V. Jormalainen).

https://doi.org/10.1016/j.fishres.2024.107234
Received 5 July 2024; Received in revised form 2 October 2024; Accepted 21 November 2024
Available online 29 November 2024

Across the Baltic Sea, the population size of great cormorants, *Phalacrocorax carbo sinensis*, has increased (Reusch et al., 2018). For example, the Finnish breeding population has expanded over the recent decades from only a few hundred breeding pairs at the turn of the millennium to almost 28,000 breeding pairs in 2023 (Suomen ympäristökeskus, 2023). Cormorants are obligate piscivorous birds, with a daily consumption of about 0.5 kg fish (Grémillet et al., 1995). As generalist opportunists, cormorants feed on a variety of fish species and adjust their diet and feeding areas in response to food availability (Lehikoinen, 2005, Boström et al., 2012). This flexibility has largely contributed to their rapid population growth, supported by the strict European bird conservation laws and regulations (EU Birds Directive - 2009/147/EC), and by banning the use of DDT and PCB since the 1970s (Beike, 2014).

The rapid expansion and population growth of cormorants has caused increased concern about their consequences for coastal fisheries and has brought these protected birds into widespread human-wildlife conflicts (Marzano et al., 2013, Bregnballe et al., 2014). The consequences of increased avian predation on Baltic Sea fish stocks and its potential influence on coastal fisheries have been a persistent and intense matter of debate (e.g., Saarikoski et al., 2024). It is evident that a large cormorant population consumes a large quantity of wild fish, but the current highly polarized debate is triggered by very different views regarding the extent of how cormorant predation affects wild fish populations and subsequent fish yields (Marzano et al., 2013).

Several different approaches have been used for estimating how cormorants affect fish stocks. Dietary studies have compared past and present cormorant population sizes and consequent fish yields (Vetemaa et al., 2010 Östman et al., 2012). Fish have been tagged and recoveries of tags have been used to estimate the mortality rate caused by cormorants (Jepsen et al., 2010, 2019, Veneranta et al., 2020, Källo et al., 2023, Säterberg et al., 2023). Studies based on stock assessment data combined with population models have indicated that the effects of cormorants on fish populations are relatively small (Heikinheimo et al., 2016, 2022). However, using the same data, Salmi et al. (2015) suggested that cormorant predation may affect catches and decrease the profitability of fishing. In some areas, cormorants have been implicated in weakening fish stocks and seriously harming the financial viability of commercial fishing (Hansson et al., 2018).

The losses experienced by fisheries may not only be due to smaller fish stocks. Foraging birds have been claimed to cause bite marks and scratches to fish that lower the market value of catches (Bryhn et al., 2023). According to questionnaires to fishermen, avian predators have also been said to disrupt fishing by scaring fish from fishing areas or by damaging fishing equipment (Svels et al., 2019, Nordberg and Salmi, 2019). The presence of predators may have forced fishermen to move elsewhere or work longer hours to compensate for lower catches or to visit their gear more frequently, increasing the labour and production costs of fishing (Nordberg and Salmi, 2019).

Despite a wealth of literature, research quantifying the direct impacts of cormorants on small-scale coastal fisheries is scant (Marzano et al., 2013, see however Bildsøe et al., 1998). This is particularly the case with fyke net fisheries along the Baltic Sea coast (Ovegård et al., 2021). We lack systematically collected, quantitative data on the direct costs of cormorants to fyke net fisheries and factors explaining variation in these costs (such as distance to cormorant colonies or the type of fyke net used). By direct costs, we refer to the costs from cormorants removing or damaging fish in the catch. Such data would be valuable in the moderation and management of the human-wildlife conflict e.g., by finding ways to mitigate bird-caused direct costs.

We quantified the direct impacts of cormorants on coastal fyke net fishing. We replicated our sampling over the breeding and post breeding seasons across a wide geographic area off the coast of Finland. By using continuously operating surveillance cameras, we 1) determined how often cormorants visit fyke nets, 2) estimated how much fish cormorants take from different types of fyke nets and 3) estimated whether the level of damage can be predicted from the distance to the closest breeding colony. In addition, 4) we used coastal-wide monitoring data from the EU Fisheries Data Collection Program to determine the frequency of wounds and lesions caused by birds on commercially caught fish. Our hypotheses were: 1) different fyke net types are differently targeted by cormorants, 2) larger cormorant colony size and decreasing distance to active colonies increases fish losses in fishing gear. Indirect effects, such as reduction of wild fish stocks or scaring fish from fishing areas are beyond the scope of this study.

2. Material and methods

2.1. Study area and the focal species

The non-tidal, brackish Baltic Sea is characterised by shallow coastal and archipelagic areas with active coastal fisheries. The low salinity allows for a diverse fish community including both salinity tolerant freshwater species and euryhaline marine species. Marine species include Baltic herring (*Clupea harengus membras*) and sprat (*Sprattus sprattus*), whereas limnic species living in coastal areas include pike (*Esox lucius*), perch (*Perca fluviatilis*), pikeperch (*Sander lucioperca*), smelt (*Osmerus eperlanus*), whitefish (*Coregonus lavaretus*), vendace (*Coregonus albula*) and several species of cyprinids.

In 1996, cormorants nested in Finland for the first time in over a hundred years. Since then, the closely monitored population has increased to 28,000 breeding pairs in over 50 colonies across the entire Finnish coast (Suomen ympäristökeskus, 2023). The colony sizes in Finland range from eight to 6800 breeding pairs (median 172 pairs, data from Finnish Environmental Institute). Spring migration occurs from early March onwards. As cormorants feed almost exclusively on fish and the Finnish coasts freeze over winter months, they migrate to southern latitudes starting in late summer.

2.2. Video surveillance

Video surveillance is a cost-effective way to quantify feeding behaviour of birds in remote places where continuous direct observations are not possible (López-López, 2022). Unlike direct observations, video footage allows for repeated analysis by several specialists, making video observations more objective and accurate than on-site observations.

This project was conducted in cooperation with seven commercial fishermen, whose fyke nets and fishing events were recorded using surveillance cameras. The main goal in this study was to evaluate the direct effects of cormorant predation on commercial fishing. Within the technical limits of the equipment, we allowed each fisherman to decide where the fyke nets were positioned and which type of fyke nets were used. As all fishermen where experienced commercial fishermen, selection of sites was therefore based on years of experience for maximizing fish yields and catching target species.

Our video surveillance included data from 15 fyke nets covering a large portion of the south and west coast of Finland (Fig. 1). In 2022, cameras recorded cormorant activities at five fyke nets from 1st June to 17th October. In 2023, recordings took place at 10 fyke nets between 14th April and 24th August. We used continuously recording cameras for 24 h a day. In the autumn, when light conditions were insufficient to record at night, cameras were set to record from 4 am to 10 pm in September and 6 am to 8 pm in October. The cameras were mounted on the shore (approx. 1.2–1.5 m above the ground) as close as possible to the focal fyke net and providing a view over the fishing location. The recording period ranged from 7 to 83 days and averaged 40 days.

Video recordings were done with a SD49225XA-HNR-P Dahua PTZ Lite-AI IR 2 Mpx 25x IP camera system (4.8–120 mm). The cameras were powered by a 125 W solar panel and recordings were sent over a 4 G network to a server. The image stream recorded by each camera was set to be saved on the server as one hour video files (24 files/day). The

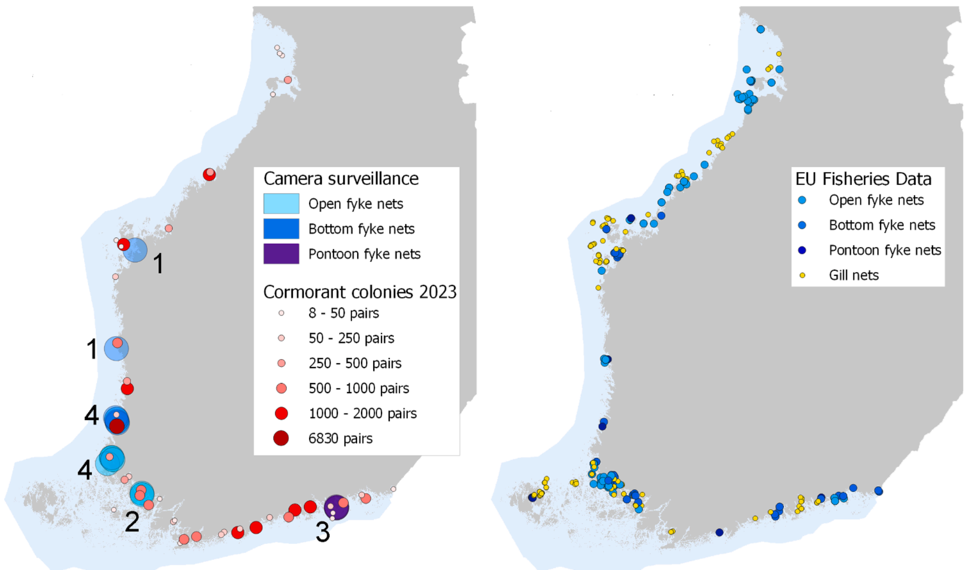

Fig. 1. Left: The locations of the video-surveyed fyke nets. Fyke net types are indicated by different shades of blue circles. Number next to the circle indicates the number of fyke nets used in each area. Position and size of cormorant colonies are shown with red dots. Right: The locations of the fish samples collected by the EU fisheries Data Collection Program. Blue circles indicate samples collected from fyke nets, and yellow dots samples collected from gill nets. Each catch site was sampled 1–17 times.

cameras recorded in 1280 ×720 p resolution at 12 frames per second. Altogether, recordings covered a total of 600 days (ca 14,000 h) and came from 6 open fyke nets, 6 bottom fyke nets and 3 pontoon fyke nets.

2.3. Data processing

Because of the amount of work, equivalent to more than 8 man-years if analysing the full material at normal speed, we subsampled our data, and analysed every 6th day, translating to 2420 h of recordings. Sampling every 6th day, instead of every 7th reduced the possibility of including any effects of systematic human behaviour that could have confounded results. Videos were manually analysed at 0.5–32 times the recording speed. Whenever there was bird activity, videos were rewatched and analysed at normal or half speed to quantify predation pressure caused by cormorants at fyke nets. We recorded the maximum number of birds present simultaneously each hour, the number of predation attempts (=dives), the duration of dives and the number of successful catches in cases when predation success was possible to determine. We defined successful predation as situations where a cormorant brought a fish to the surface or when the throat of the cormorant was swollen right after surfacing, indicating a recent catch.

Due to variation between cameras in their distance to the fyke net, and variable weather and lighting conditions, verifying predation success was not always possible. We therefore use the number of dives (predation attempts) as an indicator of predation pressure. The number of dives was possible to count with high accuracy in all conditions, while the number of successful attempts could only be counted reliably during times of excellent visibility and calm weather conditions. Dives were categorised according to whether they occurred inside or outside the fyke net. Observations where the bird dived outside the net but surfaced inside, or vice versa, or dived on one side of the fyke net and resurfaced on the other side, were counted as dives inside the fyke net.

2.4. Fyke nets

Fyke net fishing can be described as artisanal, family-based entrepreneurship, where fishermen operate from small boats that leave to sea at morning and return the same day. Fyke nets are commonly used in Baltic Sea coastal fisheries targeting salmon (*Salmo salar*), whitefish, herring, perch, and various species of cyprinids. Fyke nets are stationary fish traps that have one long lead net and wings that direct fish into a bag from where the fish are retrieved (He et al., 2021).

We compared three types of fyke nets: 1) bottom standing (n=6), 2) open (n=6) and 3) pontoon fyke nets (n=3). In bottom standing fyke nets, the trap is fixed to the bottom and the entire trap is covered by a net, preventing free access from the top. The only access for cormorants to the fish goes through the mouth of the trap. Open fyke nets are open at the top with floats keeping the top of the net at the surface, and there is free access from the surface for predators to enter the net. Pontoon fyke nets, which were originally developed to reduce damage from seals (Hemmingsson et al., 2008), are essentially bottom fyke nets, but with inflatable pontoons under the fish chamber and an additional double layer of netting to prevent seals and other predators from getting fish through the net from the outside of the trap. All three types of fyke nets are commonly used in the coastal waters of Finland.

Finnish marine commercial fishermen caught 8.1 million kg of fish in 2023 with fyke nets, which accounts for 9.0 % of all commercial fishing (Natural Resources Institute Statistics, 2024). A large proportion of catches from fyke nets go directly to human consumption, whereas trawling catches are mostly used as industry products such as fishmeal. Excluding trawling, fyke nets produced 86.7 % of all commercial catches at sea (Natural Resources Institute Statistics, 2024).

2.5. EU Fisheries Data Collection Program and fishing protocols from fishermen

For analysing the frequency of bird bite marks in fish caught by fishermen, we used samples of the most important commercial fish species that regularly are collected as part of the EU monitoring program (EU Data Collection Framework; https://datacollection.jrc.ec.europa.eu). Samples are collected coast-wide from commercial fishermen and then analysed by professional public servants who compile the statistics. In addition to basic population ecological data (species, size, sex, age), any injury likely caused by predators are registered. The instructions by Kortan and Adámek (2009) were used for distinguishing bird generated marks (cormorants and other birds) from non-avian marks. We only included fish sampled between March and September, covering most of the time cormorants stay in Finland. We used wound information from perch, pike, pikeperch, salmons (pooled; brown trout (*Salmo trutta*), Atlantic salmon and rainbow trout *(Oncorhynchus mykiss)*), whitefish and herring from 2018 to 2023, and roach (*Rutilus rutilus*) and bream (*Abramis brama*), for which data was available for 2022 and 2023. This comprised 481 independent samples totalling 59 653 individual fish. Each sample included 1–370 fish (average 124) of 1–7 species. The number of species-specific samples were 1200. 233 samples were from fyke nets (41 084 fish) and 249 from gill nets (18 569 fish). Samples from fyke nets were divided into open, bottom and pontoon fyke nets, depending on the type of gear used for each sample. Any wounds were studied with the aim of identifying the cause (seal, cormorant, unknown bird) when possible and all wounds likely caused by any bird were included in this study.

In addition to the EU Fisheries Data Collection Program, the commercial fishermen who participated in this study collected and made notes on predator-damaged fish they caught. When visiting the fyke nets they counted the number of cormorants near the trap (within 100 m of the trap) and they also reported the biomass and species of their catch.

2.6. Modelling cormorant colony influences on wound frequency and diving visits

One of our goals was to determine the effect of the proximity of cormorant colonies on bird visits and the occurrence of bird-wounded fish in fyke nets. We used cormorant nesting data from the Finnish Environmental Institute, video surveillance data and frequencies of wounded fish in the EU Fisheries Data Collection Program. We calculated the distance to the nearest inhabited cormorant colonies for each fyke net in our study and fyke and gill net in the EU Fisheries Data Collection Program data as well as the number of cormorant nests within 5, 10 and 15 km from the fishing site in the year our fishing data came from. To account for the different sizes of the colonies, we calculated the ‘cormorant pressure’ at the three ranges by dividing the number of nests in each colony by the distance (km) from the fishing site up to 5, 10 or 15 km. If more than one colony existed within the radius, the pressures were added together. For example, a fyke net 4 km from a colony with 100 nests would have a cormorant pressure index of $100/4 = 25$. An additional colony with 50 nests 10 km away from the same fishing site would increase the pressure index to $100/4 + 50/10 = 30$.

All statistical analyses were performed with R version 4.2.0 (R Core Team, 2022). We analysed our video surveillance data with a generalized mixed model (GLMM) with negative binomial residual variation in the package glmmTMB (Brooks et al., 2017) to model the number of cormorant dives on each observation day ($n = 117$) as a function of the distance to the nearest cormorant colonies, cormorant pressure within a 5, 10 or 15 km radius, fyke net type, and observation month. The fyke net identity was included in the model as a random factor. As the distance to the cormorant colonies and the cormorant pressures partly modelled the same thing, the models were run separately for each of these variables. The models were compared by AICc (Burnham and Anderson, 2002). The variables in the models were tested for collinearity with the Variation Inflation Factor (VIF) and did not exceed the threshold of 3 (Zuur et al., 2010). Tukey’s test in the package emmeans was used for post-hoc comparisons (Lenth, 2023).

We analysed the data from the EU Fisheries Data Collection Program using a generalized linear mixed model (GLMM, using the glmmTMB package), but with binomial error distribution. The proportion of wounded fish of each species in a sample was the dependent variable. Explanatory variables were gear type (fyke or gill net), year, month, latitude and longitude, fish species, average size (length in mm) of the fish in the sample and the distance to the nearest cormorant colony or cormorant pressure within a 5, 10 or 15 km radius. As in the video surveillance models, the models were run separately for each of the cormorant variables. Sample ID and trap identities were included as random factors. Fyke nets within 100 m of similar nets (i.e., fyke net types or nets with the same mesh size), were considered the same trap ($n = 234$). Only perch, pikeperch and whitefish ($n = 28,457$) were used in this modelling, as there were only a few or no injured fish among the other species. All cormorant pressure variables were run in separate models, which were compared by AICc (Burnham and Anderson, 2002). The remaining variables did not exceed the VIF threshold of 3 (Zuur et al., 2010).

3. Results

3.1. Video surveillance

In all, we analysed 2420 h of video footage, from which cormorants were observed for 664 h. Cormorant sightings were made at all but one fyke net. On average, cormorant presence at the fyke nets was registered for 6.3 ± 6.5 (SD) hours per day, but the daily variation within, and spatial variation among fyke nets was large. At three fyke nets cormorants made visits practically every daylight hour of the day; on average during 17.0 ± 0.7 (SD) h. The largest number of cormorants recorded simultaneously at one fyke net was 13 individuals. The model containing the cormorant pressure (number of breeding pairs within a 15 km radius divided by the distance to the colony) had the lowest AICc (δAICc = –4.91 to −11.47) and was considered the best model. All results are reported according to this model.

Cormorants made on average 222 ± 379 (SD, range 0–1059, n=117) dives per day in the fyke nets. Fyke net type was the most significant predictor for the number of dives. There were significantly more cormorant dives in floating open fyke nets (98.3 % of all dives), compared to the two types of submerged and covered fyke (Table 1, Fig. 2). The average daily number of dives in open floating fyke nets was 547±437 (SD, range28–1059, n=40), compared to 5.0±7.2 (SD, range 0–14.6, n=47) in bottom fyke nets and 4.3±4.1 (SD, range 1.4–9, n=30) in pontoon fyke nets.

In addition to the fyke net type, the density of cormorants nesting in the proximity affected the number of dives (Fig. 3). The number of cormorant dives increased with the increasing cormorant pressures within 15 km radius, i.e., a higher number of nesting cormorants was associated with a higher number of dives in the fyke nets. The month was not associated with the number of dives (Table 1).

Cormorants usually dived several times during their visit to a fyke net. The number of dives per visit varied from 1 to a maximum recorded number of 33 dives. In fyke nets with small fish, cormorants typically dived several times and caught several fish during the same visit, but when they hunted at fyke nets with larger fish, they typically stopped hunting after one successful catch. The largest recorded catch by a single cormorant during one feeding event was seven fish.

Where we were able to quantify the number of predated fish in relation to the number of dives, an average of 20 dives resulted in one successful catch, but there was considerable difference in success rate

Table 1
Parameter estimates ± SD, Wald Z statistics (z) and probabilities (p) for the predictors used in the model explaining the number of cormorant dives at fyke nets (n = 117 days in 15 fyke nets) along the Finnish coast. The predictor ‘cormorant pressure within 15 km radius’ was standardized.

Predictor	Estimate (±SE)	z		*P*
Intercept	5.35 ± 1.23	4.36	<	0.0001 ***
Fyke net type				
Floating & Open – Bottom	8.52 ± 1.08	7.86	<	0.0001 ***
Floating & Open – Pontoon	4.78 ± 0.90	5.32		0.0001 ***
Bottom – Pontoon	−3.74 ± 1.11	−3.36		0.0022 **
Cormorant pressure within 15 km radius	1.94 ± 0.46	4.20	<	0.0001 ***
Month	0.23 ± 0.22	1.04		0.2970

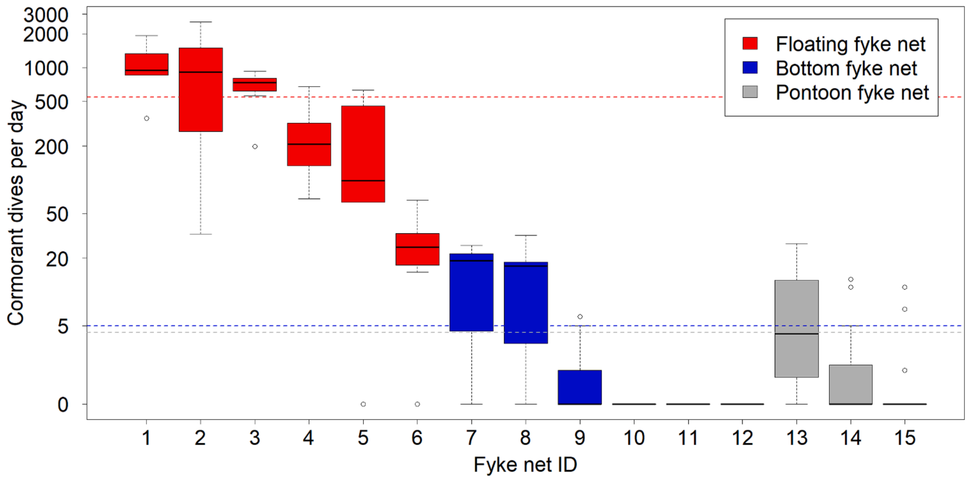

Fig. 2. Number of cormorant predation attempts (=dives) in different types of fyke nets. Each box represents the daily number of dives in the fyke net. The coloured box represents the 25–75 % interquartile range, the horizontal line in the box the median, and the scatter lines the maximum and minimum values, excluding possible outliers (> 1.5 x quartile interval), which are shown with circles. The coloured horizontal dashed lines depict the mean values of the fyke net types. Note the logarithmic scale of the Y-axis.

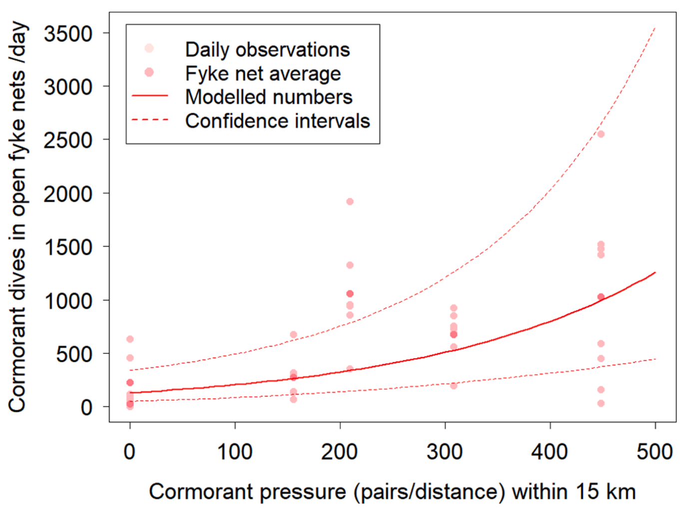

Fig. 3. Modelled daily number of dives in open fyke nets by cormorants in relation to the cormorant pressure (number of breeding pairs divided by the distance) within a 15 km radius (red lines). The dotted lines show the confidence intervals. The actual numbers of daily dives are plotted with light dots, while the darker dots show the average for each fyke net.

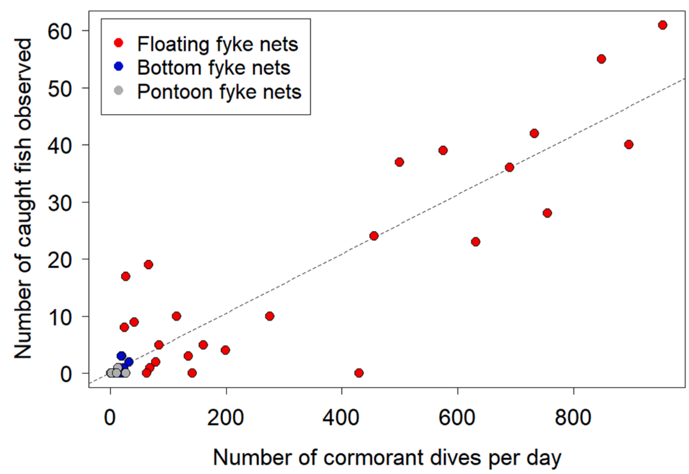

Fig. 4. Scatterplot of number of fish caught by cormorants in relation to the number of dives per day in 13 monitored fyke nets. Each point represents one day in one fyke net. The different fyke net types are shown with different colours.

among different birds and among the type of fyke net (Fig. 4). At the upper end, the average success rate in one open fyke net was 30 %, while at the other extreme we recorded a success rate of only 1.5 %. Interestingly, in some cases, cormorants continued diving persistently in fyke nets that had recently been emptied. In one case where the fyke net was emptied in the afternoon, cormorants dived 234 times and caught 44 fish (success rate of 18.8 %) during the three hours before the emptying of the net and they dived 172 times and caught 1 fish (success rate of 0.6 %) in the two hours after emptying.

3.2. *EU fisheries data collection program*

Out of a total of 59 653 individual fish in the EU Fisheries Data Collection Program, 285 fish carried wounds that were classified as caused by birds. This is 0.48 % of all sampled fish. There were no fish wounded in the smallest (0–100 mm) and largest (> 700 mm) size classes. The proportion of wounded fish peaked to 1.9 % among fish in the 400–500 mm class (Fig. 5). Even though the proportion of wounded fish in the overall data was very small, their proportion in individual samples was several percent, up to 30 % in the most affected size classes (Fig. 5). The species most often found wounded were pikeperch (143 individuals, 2.1 % of the total pikeperch catch), whitefish (70 individuals, 0.94 %), roach (6 individuals, 0.47 %) and perch (63 individuals, 0.44 %), whereas there were no wounded Baltic herring or salmons.

The results of the statistical models concerning the proportion of wounded fish (pikeperch, whitefish and perch, n = 733 species-specific samples and 28,457 individuals) in the EU Fisheries Data Collection Program revealed that the proportion of wounded fish was explained by fish size, fish species and the type of fishing gear (Table 2). AICc for the models containing the different cormorant variables did not differ significantly (δAICc max = 1.55). We report here the results for the model with the lowest AICc, which contained the cormorant variable ‘distance to cormorant colony’. Larger fish were more likely to have wounds than smaller fish, and perch and pikeperch had more wounds than whitefish (Fig. 6, Table 2). The was a higher proportion of wounded fish among fish caught by fyke nets than among those caught by gill nets (Table 2). There was also an indication that the proportion of injured

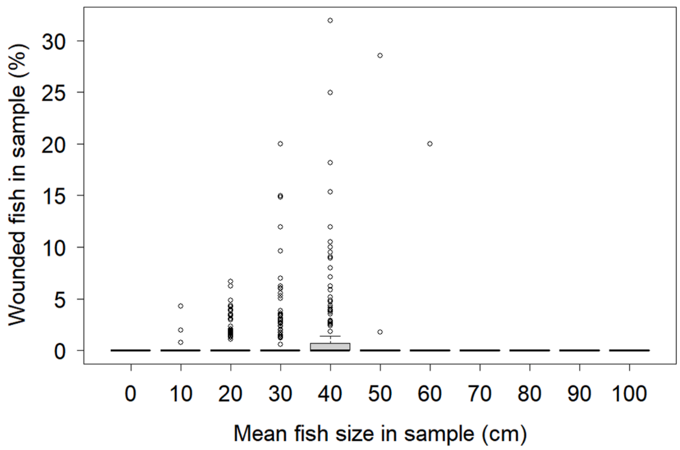

Fig. 5. Proportion (%) of fish of different size wounded by birds in the data from the EU Fisheries Data Collection Program. The box represents the 25–75 % interquartile range, the horizontal line in the box the median, the scatter lines show the 1.5 × quartile interval, and the observations exceeding that are shown with circles. N = 1205 species-specific samples.

Table 2
Parameter estimates ± SD, Wald Z statistics (z) and probabilities (*p*) for the predictors used in the model explaining the proportion of wounded fish in fyke nets and gill nets (n = 733 species-specific samples) along the Finnish coast. The predictors 'distance to cormorant colony', 'fish size', latitude and longitude were standardized.

Predictor	Estimate (±SE)	z	*P*
Intercept	−0.001 ± 131.2	0.00	1.0000
Fish mean size in sample	1.21 ± 0.22	5.50	< 0.0001 ***
Distance to nearest cormorant colony	−0.31 ± 0.16	−1.86	0.0628.
Latitude	0.11 ± 0.16	−0.68	0.4995
Longitude	−0.07 ± 0.14	−0.46	0.6459
Month	0.00 ± 0.06	−0.03	0.9761
Year	−0.00 ± 0.06	−0.03	0.9734
Fish trap: gill net	−0.62 ± 0.27	−2.28	0.0229 *
Fish species		4.10	0.0002 ***
Perch – pikeperch	0.25 ± 0.40	0.63	0.8038
Perch – whitefish	1.51 ± 0.41	3.71	0.0006 ***
Pikeperch – whitefish	1.26 ± 0.38	3.35	0.0024 **

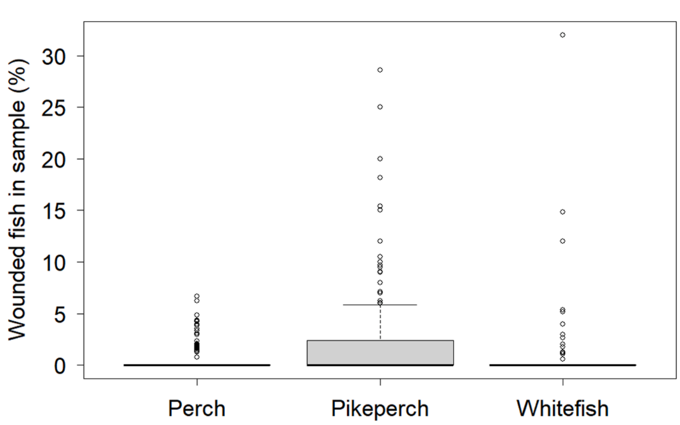

Fig. 6. The proportion of wounded fish among different species.

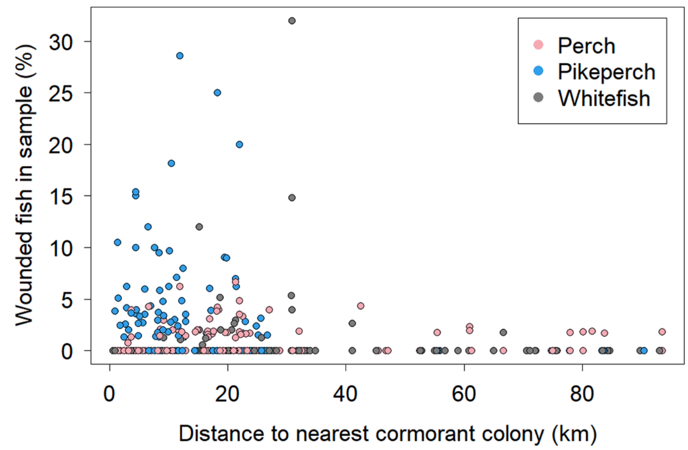

Fig. 7. The proportion of wounded fish in individual samples of the EU Fisheries Data Collection Program 2018–2023. The predictor 'distance to cormorant colony' was not statistically significant in the full model, but indicative (p=0.06).

fish was greater in fish traps that were closer to cormorant colonies (Fig. 7, p=0.063, Table 2), where very few observations of wounds were observed when the distance to the nearest cormorant colony exceeded ca 30 km (Fig. 7). In the full model, the proportion of wounded fish was not associated with latitude, longitude, month or year (Table 2). The full model explained 23 % of the variation in the proportion of wounded fish in the samples.

3.3. *Fishing protocols by fishermen*

Two fishermen who participated in the project in 2022 (data from 3 fyke nets, 41 samples and 171 fishing days) reported that they discarded a total of 187 kg of the catch due to injuries presumably caused by cormorants (4.7 % of the total catch). The average discard was 4.6 kg with a maximum of 6.7 kg. Of the discarded biomass, 78.6 % were roach and 21.4 % were bream. No fish of other species were reported as discarded. In 2023, (7 fishermen, 9 fyke nets, 68 samples and 256 fishing days), the catch presumably damaged by cormorants totalled 83 kg, equalling 0.4 % of the total catch. Discarded fish mass per sample was on average 1.2 kg with a maximum of 15.0 kg. Pikeperch (30.0 %), bream (25.2 %) and perch (22.2 %) had the most bite marks followed by roach (15.2 %) and whitefish (7.2 %). No fish of other species were reported to be damaged. Fishermen observed an average of 7 individual cormorants per fishing event (maximum 60 individuals) in the vicinity of the fishing gear. Cormorants were observed in 40 % of the fishing events. Damage to fishing gear, assumed to be caused by cormorants (holes in the fyke nets) was reported once.

4. Discussion

Determining the extent and impact of depredation on fisheries is critically important for resolving human-wildlife conflicts (Tixier et al., 2021). Quantification of impacts using scientific methods has further been called for (Marzano et al., 2013). We quantified cormorant activity in three types of fyke nets, aiming at defining the effect of gear type on the level of damage. We also assessed how cormorant colony size and the distance to colonies affects cormorant presence and activity in the adjacent fyke nets. Cormorants readily visited, made predation attempts, and caught fish in fyke nets. Our results from camera surveillance analysis showed that fyke net type had a major effect on the number of cormorant feeding visits and consequent depredation rates. Depredation can be a significant factor in open fyke nets, whereas losses in fully covered, submerged fyke nets are much rarer. Predation activity increased with higher cormorant pressures within 15 km to the fyke nets. The variation in predation success rate among birds and fyke nets was large, partly attributable to the emptying interval of the fyke nets. Studies detailing cormorant effects on fish and fisheries have been criticized for their low spatial and temporal coverage (Ovegård et al., 2021). Our study encompassed nearly the entire Finnish coastline, spanned two years, and included both the breeding and post-breeding seasons of cormorants.

Feeding patch quality, prey predictability, prey type and food intake rate all play an important role in bird feeding behaviour (Sponza et al., 2010 with references). Piscivorous birds that forage by diving are faced with trade-offs between time and energy spent reaching the foraging site, time and energy spent foraging underwater, time and energy spent handling the prey and breathing at the surface (Sponza et al., 2010). When diving to catch prey, prey density exerts the strongest influence on cormorant foraging success (Enstipp et al., 2007). According to optimal foraging theory, the diet and feeding behaviour of cormorants is expected to reflect foraging profitability in terms of prey abundance, food quality and ease of capture.

Different types of fyke nets vary in their accessibility to birds and potentially in the amount and/or quality of prey. Floating open fykes congregate fish from a large area into a small, condensed space close to surface, reducing search time and pursuit costs for the predator, providing them with easy access to food. Floating fyke nets therefore provide a rewarding hunting opportunity for piscivorous birds, because prey density may be very high. Further, diving in open fyke nets close to the surface allows for many more dives per unit of time and is energetically less costly as energy is not spent on travel from the surface to the seafloor. Light conditions in floating fyke nets are also better, particularly in the turbid coastal waters of the Baltic Sea, possibly improving hunting success in low light conditions and prolonging daytime foraging time (White et al., 2008).

We found significantly fewer cormorant predation attempts in the submerged bottom and pontoon fyke nets than in floating fyke nets. Although cormorants are occasionally found entrapped in bottom fyke nets (Engström, 1998, Bregnballe and Frederiksen, 2006), showing that they do dive inside them, our surveillance suggested that depredation in submerged closed fyke nets is relatively rare. As single dives by cormorants typically last less than 30 seconds (Cosolo et al., 2010), bottom fyke nets with several chambers and narrow throats probably prevent cormorants from finding and entering the fish chamber, explaining lower depredation rates in these nets. Floating and submerged fyke nets also target different fish species: the latter nets typically target demersal fish such as pikeperch, perch, and roach whereas floating open fyke nets typically target pelagic species such as whitefish and herring. Herring may be particularly profitable as they occur in large shoals, are within a suitable prey size range, easy to handle owing to their soft body and rich in energy due to their high fat content. Although we cannot fully separate the effects of fish species assortment in the fyke net and the accessibility of the fyke net type on cormorant predation attempts, we consider accessibility more important mainly because cormorants appear to be opportunist generalist feeders with widely varying diet composition (e.g. Lehikoinen, 2005, Boström et al., 2012).

The small proportion of bird-injured fish in the EU fisheries Data Collection Program data closely matched the accounts provided by fishermen who participated in this study, but is markedly lower than indicated by fishermen in questionnaire surveys and in fish landing reports (Salmi et al., 2010, Svels et al., 2019, Söderkultalahti and Rahikainen, 2023). For example, one third of Finnish commercial fishermen reported catching fish damaged by cormorants (Salmi et al., 2010). On average, 10 % of all commercial fishermen in the Finnish sea region report annually, as part of the obligatory catch reports, that cormorants have disturbed their fishing by damaging catches or reducing fish stocks. The reported total mass of damaged fish in the fish catches was 18 tonnes. The value of the reported damage caused by cormorants was estimated to be 35,000 euros, where the largest damage, in terms of value, was caused to perch (Söderkultalahti and Rahikainen, 2023). Our extensive data show that the overall proportion of fish wounded by birds is very small, but some individual catches can bear a high frequency of wounded fish. Interestingly, wounded fish were more common in fyke nets than in gill nets indicating the possibility of higher bird predation in fyke nets. This may arise due to birds learning to associate the relatively long-term locations of the fyke nets as rewarding preying sites, while the location of the short-term gill net sites may remain unpredictable. Such learning could also explain why cormorants continued diving in fyke nets that had been emptied recently.

Most wounded individuals in our data were found among 20–40 cm-sized fish. Cormorants typically predate on fish less than 20 cm in length (Čech et al., 2008, Lehikoinen et al., 2011, Salmi et al., 2015), but occasionally also bigger fish may be predated upon (Salmi et al., 2015). Davies et al. (1995) found that cormorants inflict wounds on a variety of cyprinid fish including 33–53 cm carp. Källo et al. (2023) found similar results among sea trout, where the length of the predated individuals ranged between 29 and 53 cm, and predation was most heavy on 35–43 cm fish. It is important to note that the wounded fish represent fish which managed to escape from the predator, or which were discarded by the predator, e.g., because of their large size (Adámek et al., 2007). Data on wounded fish doesn't represent cormorant prey size preferences. The most common species of fish in the fykes, herring, bore no wounds, nor did we find wounds on the biggest fish, mainly salmon. The escape rate among smaller fish in a pursuit is probably much smaller and the dying rate of injured individuals that have escaped pursuit is likely much higher than among larger fish, explaining the lack of observed wounds among the smallest fish: small fish are simply eaten if caught or die soon after escape and do not end up in the fishing gear (Grémillet et al., 2006). This may also explain why the distance to the cormorant colony was only indicatively significant in the EU-data, as we could not detect wounded herring. The surveillance data often showed Baltic herring being eaten by cormorants.

In our surveillance data, fyke nets with higher predation pressure indexes experienced more cormorant dives, indicating a distance and colony size effect on fish losses. Similar results were shown by Adámek and Kajgrová (2022) who demonstrated that the distance from cormorant breeding colonies to inland aquaculture ponds were important predictors for the presence of cormorants at the ponds. Dorr et al. (2008), showed that double-crested cormorant (*Phalacrocorax auritus*) roost counts and counts on ponds correlated positively, but only 24 % of the total counts for night roosts were found near catfish ponds. This was explained by the fact that most of the cormorants feed elsewhere at any point in time. In our study area, there are vast areas of available shallow natural habitats offering feeding grounds for cormorants, spreading the predation pressure over a large area. Our data also included the post-breeding period during which the distribution patterns are less linked to active breeding colonies. Burr et al. (2023) found no relationship between the number of nearby roosts and double-crested cormorant presence, but findings were seasonally dependent and suggested shifts in resource selection over the season. It is possible, that cormorants change their optimal target fish as their offspring grow, potentially leading to season-dependent changes in the predation pressure they elicit.

Our study design places some limits on interpreting the results. Firstly, we cannot evaluate other effects than predation pressure, which was based on the number of dives cormorants made in each fyke. Predation pressure and actually catching a fish probably correlate but may also depend on factors that we couldn't control. Secondly, we did not monitor each site for the entire season cormorants were present - mostly because the commercial fishing of coastal fish mainly occurs in spring. The main target in this study was to evaluate the direct effects of cormorant predation on commercial fishing. Given this research framework, we collaborated with commercial fishermen and allowed them to decide where the fyke nets were positioned, and which fyke nets were used. Fishermen also decided how long the fishing lasted. Therefore, our study was designed to measure the effects of cormorants within the conditions that prevail during coastal commercial fishing. Thirdly, as cormorants also swallow small fish while diving, only calculating catches seen at the surface may underrate the true predation effect they exert. In this study, our statistical analyses were therefore based on the number of dives, not documented catches.

5. Conclusions

Fyke net fishing is currently experiencing several challenges. Many fishermen have transitioned to more expensive types of fyke nets to mitigate catch losses to seals. In addition, fishing quotas for many species are limited, some fish stocks have dropped from the former years and production expenses (e.g., fuel) have increased (Raitaniemi and Sairanen, 2021). The rapid increase in the number of cormorants during the past 25 years has been a new challenge to coastal fisheries leading to an escalating human-wildlife conflict. Developing strategies to minimize damage is therefore important.

Our results suggest that fish losses in fyke nets are not strictly dependent on the number of birds present (see also Engström, 1998). The video surveillance data frequently showed large cormorant flocks flying by or swimming and foraging in the vicinity of fyke nets without making any predation attempts in the gear. In some cases, predation effort may be high, but actual predation loss is low or moderate. Direct costs to the fish catch in fyke nets caused by cormorants can be mitigated by moving from open floating fyke nets to submerged, enclosed fyke nets where possible considering the targeted prey species. This could be particularly useful in fishing close to cormorant breeding colonies where the cormorant pressure may be very high. A means to reduce depredation in open floating fyke nets could be to cover the fish chamber with a protective net. Covering open fyke nets with nets reduces direct accessibility to the catch and the number of fish lost to cormorants (Cornelisse and Christensen, 1993, Bildsøe et al., 1998). Similar findings are commonly found from the fish aquaculture, where losses to avian predation are a concern and where netting enclosures over fish ponds or bags are efficient at reducing depredation by cormorants (e.g. Dieperink, 1995, Lemmens et al., 2016).

Where state funded compensation strategies are adopted, colony size and distance to colonies should be taken into consideration, as cormorant damages correlated with predation pressure. However, while predation pressure indicated damage size, variability among fyke nets was high, suggesting that there are also other factors affecting the size of fish losses. Damage prevention decisions and adopted mitigation strategies should therefore be based on systematic scientific research that incorporates the impact of variability. Observational data on only presence and absence, without quantifying impact, may cause ineffective management decisions. This study shows that cormorants are highly flexible, their direct effects on fisheries are context dependent and highly localised in time and space, but not always as dramatic as commonly outlined in the political discussion (see Marzano et al., 2013 for further reading).

Funding information

The study was financed by the Ministry of Environment in Finland and the European Fisheries, European Maritime, Fisheries and Aquaculture Fund (EMFAF).

Ethical statement

All procedures were performed in compliance with relevant laws and institutional guidelines and that the appropriate institutional committee (s) have approved them.

CRediT authorship contribution statement

Mats Westerbom: Writing – review & editing, Writing – original draft, Project administration, Methodology, Funding acquisition, Conceptualization. **Camilla Ekblad:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis, Data curation. **Juhani Hopkins:** Writing – review & editing, Writing – original draft. **Toni Laaksonen:** Writing – review & editing, Funding acquisition, Conceptualization. **Mikko Olin:** Writing – review & editing, Methodology, Funding acquisition. **Antti Ovaskainen:** Writing – review & editing, Methodology. **Veijo Jormalainen:** Writing – review & editing, Writing – original draft, Project administration, Methodology, Funding acquisition, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We are grateful to Henry Hietanen and Eino Nousiainen (EN) for help in building and maintaining the video surveillance system, and to EN, Valtteri Arkko, Roope Lehmonen, Matti Kylmäaho, Mikko Kytökorpi, Satu Metsola and Tarja Wiik for participating in analysing the video footage. Pekka Rusanen from the Finnish Environmental Institute provided the cormorant nesting data. We are highly grateful to the commercial fishermen who participated in the study, also assisting in the field. Two reviewers provided constructive comments that helped us to improve this paper. The study was funded by the Ministry of the Environment in Finland. Funding from the European Maritime, Fisheries and Aquaculture Fund (EMFAF) facilitated the writing process of the article.

Data availability

Data will be made available on request.

References

Adámek, Z., Kajgrová, L., 2022. Great cormorant (Phalacrocorax carbo sinensis) occurrence in carp aquacultural ponds: a case study from the South Bohemia (Czech Republic) pond region. Aquacult. Int. 30, 2541–2556. https://doi.org/10.1007/s10499-022-00917-4.

Adámek, Z., Kortan, J., Flajšhans, M., 2007. Computer-assisted image analysis in the evaluation of fish wounding by cormorant [Phalacrocorax carbo sinensis (L.)] attacks. Aquacult. Int. 15, 211–216. https://doi.org/10.1007/s10499-007-9087-0.

Alvarez-Filip, L., Cote, I.M., Gill, J.A., Watkinson, A.R., Dulvy, N.K., 2011. Region-wide temporal and spatial variation in Caribbean reef architecture: Is coral cover the whole store? Glob. Change Biol. 17, 2470–2477. https://doi.org/10.1111/j.1365-2486.2010.02385.x.

Beike, M., 2014. Phalacrocorax carbo sinensis in Europe – indigenous or introduced? Ornis Fenn. 91, 48–56. https://doi.org/10.51812/of.133843.

Bildsøe, M., Jensen, I.B., Vestergaard, K.S., 1998. Foraging behaviour of cormorants Phalacrocorax carbo in pound nets in Denmark: the use of barrel nets to reduce predation. Wildl. Biol. 4 (3), 129–136. https://doi.org/10.2981/wlb.1998.015.

Boström, M.K., Östman, Ö., Bergenius, M.A.J., Lunneryd, S.-G., 2012. Cormorant diet in relation to temporal changes in fish communities. ICES J. Mar. Sci. 69 (2), 175–183. https://doi.org/10.1093/icesjms/fss002.

Bregnballe, T., Frederiksen, M., 2006. Net-entrapment of great cormorants Phalacrocorax carbo sinensis in relation to individual age and population size. Wildl. Biol. 12 (2), 143–150. https://doi.org/10.2981/0909-6396(2006)12[143:NOGCPC]2.0.CO;2.

Bregnballe, T., Hyldgaard, A.M., Clausen, K.K., Carss, D.N., 2014. What does three years of hunting great cormorants, Phalacrocorax carbo, tell us? Shooting autumn-staging birds as a means of reducing numbers locally. Pest. Manag. Sci. 71, 173–179. https://doi.org/10.1002/ps.3782.

Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Machler, M., Bolker, B.M., 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R. J. https://doi.org/10.3929/ethz-b-000240890.

Bryhn, A.C., Lunneryd, S.G., Königson, S., 2023. Predator damaged eel caught in coastal fisheries of the Baltic Sea. Fish. Res. 267, 106827. https://doi.org/10.1016/j.fishres.2023.10682.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. Springer-Verlag, New York. https://doi.org/10.1007/b97636.

Burr, P.C., Dorr, B.S., Avery, J.L., Street, G.M., Strickland, B.K., 2023. Long term changes in aquaculture influence migration, regional abundance, and distribution of an avian

species. PLoS ONE 18 (4), e0284265. https://doi.org/10.1371/journal.pone.0284265.
Čech, M., Čech, P., Kubečka, J., Prchalová, M., Draštík, V., 2008. Size selectivity in summer and winter diets of great cormorant (Phalacrocorax carbo): does it reflect season-dependent difference in foraging efficiency? Waterbirds 31, 438–447. 〈https://www.jstor.org/stable/25148353〉.
Cornelisse, K., Christensen, K.D., 1993. Investigation of a cover net designed to reduce southern cormorant (Phalacrocorax carbo sinensis) fisheries depredation in a pound net. ICES J. Mar. Sci. 50 (3), 279–284. https://doi.org/10.1006/jmsc.1993.1030.
Cosolo, M., Ferrero, E.A., Sponza, S., 2010. Prey ecology and behaviour affect foraging strategies in the Great Cormorant. Mar. Biol. 157 (11), 2533–2544. https://doi.org/10.1007/s00227-010-1517-2.
Davidson, L.N.K., Krawchuk, M.A., Dulvy, N.K., 2016. Why have global shark and ray landings declined: improved management or overfishing? Fish Fish. 17, 438–458. https://doi.org/10.1111/faf.12119.
Davies, J.M., Feltham, M.J., Walsingham, M., V., 1995. Fish wounding by cormorants, Phalacrocorax carbo L. Fish. Manag. Ecol. 2, 321–324. https://doi.org/10.1111/j.1365-2400.1995.tb00123.x.
Dehnhard, N., Langset, M., Aglen, A., Lorentsen, S.H., Anker-Nilssen, T., 2021. Fish consumption by great cormorants in Norwegian coastal waters-a human-wildlife conflict for wrasses, but not gadids. ICES J. Mar. Sci. 78 (3), 1074–1108. https://doi.org/10.1093/icesjms/fsab004.
Dieperink, C., 1995. Depredation of commercial and recreational fisheries in a Danish fjord by cormorants, Phalacrocorax carbo sinensis, Shaw. Fish. Manag. Ecol. 2 (3), 197–207. https://doi.org/10.1111/j.1365-2400.1995.tb00112.x.
Dorr, B.S., Burger, L.W., Barras, S.C., 2008. Evaluation of aerial cluster sampling of double-crested cormorants on aquaculture ponds in Mississippi. J. Wildl. Manag. 72, 1634–1640. https://doi.org/10.2193/2007-308.
Dulvy, N.K., Fowler, S.L., Musick, J.A., Cavanagh, R.D., Kyne, P.M., Harrison, L.R., Carlson, J.K., Davidson, L.N., Fordham, S.V., Francis, M.P., Pollock, C.M., 2014. Extinction risk and conservation of the world's sharks and rays. eLife 3, e00590. https://doi.org/10.7554/eLife.00590.
Engström, H., 1998. Conflicts between cormorants (Phalacrocorax carbo L.) and fishery in Sweden. Nord. J. Freshw. Res. 74, 148–155.
Enstipp, M.R., Grémillet, D., Jones, D.R., 2007. Investigating the functional link between prey abundance and seabird predatory performance. Mar. Ecol. Prog. Ser. 331, 267–279.
Grémillet, D., Enstipp, M.R., Boudiffa, M., Liu, H., 2006. Do cormorants injure fish without eating them? An underwater video study. Mar. Biol. 148 (5), 1081–1087. https://doi.org/10.1007/s00227-005-0130-2.
Grémillet, D., Schmid, D., Culik, B., 1995. Energy requirements of breeding great cormorants Phalacrocorax carbo sinensis. Mar. Ecol. Prog. Ser. 121, 1–9. https://doi.org/10.3354/meps121001.
Hansson, S., Bergström, U., Bonsdorff, E., Härkönen, T., Jepsen, N., Kautsky, L., et al., 2018. Competition for the fish – fish extraction from the Baltic Sea by humans, aquatic mammals, and birds. ICES J. Mar. Sci. 75, 999–1008. https://doi.org/10.1093/icesjms/fsx207.
He, P., Chopin, F., Suuronen, P., Ferro, R.S.T., Lansley, J., 2021. Classification and illustrated definition of fishing gears. FAO Fisheries and Aquaculture Technical Paper No. 672. FAO, Rome. https://doi.org/10.4060/cb4966en.
Heikinheimo, O., Marjomäki, T.J., Olin, M., Rusanen, P., 2022. Cormorant predation mortality of perch (Perca fluviatilis) in coastal and archipelago areas, northern Baltic Sea. ICES J. Mar. Sci. 79, 337–349. https://doi.org/10.1093/icesjms/fsab258.
Heikinheimo, O., Rusanen, P., Korhonen, K., 2016. Estimating the mortality caused by great cormorant predation on fish stocks: pikeperch in the Archipelago Sea, northern Baltic Sea, as an example. Can. J. Fish. Aquat. Sci. 73, 84–93. https://doi.org/10.1139/cjfas-2015-0033.
Hemmingsson, M., Fjälling, A., Lunneryd, S.G., 2008. The pontoon trap: description and function of a seal-safe trap-net. Fish. Res 93, 357–359. https://doi.org/10.1016/j.fishres.2008.06.013.
Jepsen, N., Flavio, H., Koed, A., 2019. The impact of Cormorant predation on Atlantic salmon and Sea trout smolt survival. Fish. Manag. Ecol. 26 (2), 183–186.
Jepsen, N., Sonnesen, P., Klenke, R., Bregnballe, T., 2010. The use of coded wire tags to estimate cormorant predation on fish stocks in an estuary. Mar. Freshw. Biol. 61, 320–329.
Kalakantojen tila vuonna 2020 sekä ennuste vuosille 2021 ja 2022: Silakka, kilohaili, turska, lohi, meritaimen, siika, kuha, ahven ja hauki. Luonnonvara- ja biotalouden tutkimus 61/2021. Luonnonvarakeskus. Helsinki. 137 p. http://urn.fi/URN:ISBN:978-952-380-267-4 [In Finnish].
Källo, K., Birnie-Gauvin, K., Jepsen, N., Aarestrup, K., 2023. Great cormorant (Phalacrocorax carbo sinensis) predation on adult anadromous brown trout (Salmo trutta). Ecol. Freshw. Fish. 32, 488–495. https://doi.org/10.1111/eff.12701.
Kortan, J., Adámek, Z., 2009. How to distinguish between fish wounding caused by fish predatory birds—Examples from Czech Republic. Finn. Game Fish. Res. Inst. 13 (in Finnish).
Lehikoinen, A., 2005. Prey-switching and diet of the great cormorant during the breeding season in the Gulf of Finland. Waterbirds 28, 511–515. 〈https://www.jstor.org/stable/4132633〉.
Lehikoinen, A., Heikinheimo, O., Lappalainen, A., 2011. Temporal changes in the diet of great cormorant (Phalacrocorax carbo sinensis) on the southern coast of Finland—Comparison with available fish data. Boreal Environ. Res. 16, 61–70, 2011.
Lemmens, P., De Meester, L., Declerck, S.A.J., 2016. Can underwater refuges protect fish populations against cormorant predation? Evidence from a large-scale multiple pond experiment. Fish. Manag. Ecol. 23 (2), 89–98. https://doi.org/10.1111/fme.12157.
Lenth, R., 2023. emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.9.0, 〈https://CRAN.R-project.org/package=emmeans〉.
López-López, P., 2022. Potential negative effects of the installation of video surveillance cameras in raptors' nests. Sci. Rep. 12, 21969. https://doi.org/10.1038/s41598-022-26153-7.
Marzano, M., Carss, D.N., Cheyne, I., 2013. Managing European cormorant-fisheries conflicts: problems, practicalities and policy. Fish. Manag. Ecol. 20, 401–413. https://doi.org/10.1111/fme.12025.
Mills, E.L., Casselman, J.M., Dermott, R., Fitzsimons, J.D., Gal, G., Holeck, K.T., Hoyle, J.A., Johannsson, O.E., Lantry, B.F., Makarewicz, J.C., Millard, E.S., Munawar, I.F., Munawar, M., O'Gorman, R., Owens, R.W., Rudstam, L.G., Schaner, T., Stewart, T.J., 2003. Lake Ontario: food web dynamics in a changing ecosystem (1970–2000). Can. J. Fish. Aquat. Sci. 60, 471–490. https://doi.org/10.1139/F03-033.
Natural Resources Institute Statistics. https://statdb.luke.fi/PxWeb/pxweb/fi/LUKE/LUKE accessed 24.9.2024.
Neuenhoff, R.D., Swain, D.P., Cox, S.P., McAllister, M.K., Trites, A.W., Walters, C.J., Hammill, M.O., 2019. Continued decline of a collapsed population of Atlantic cod (Gadus morhua) due to predation-driven allee effects. Can. J. Fish. Aquat. Sci. 76 (1), 168–184. https://doi.org/10.1139/cjfas-2017-0190.
Nordberg, K., Salmi, P., 2019. Addressing the gap between participatory ideals and the reality of environmental management: the case of the cormorant population in Finland. Environ. Policy Gov. 29 (4), 251–261. https://doi.org/10.1002/eet.1850.
Östman, Ö., Bergenius, M., Boström, M.K., Lunneryd, S.-G., 2012. Do cormorant colonies affect local fish communities in the Baltic Sea? Can. J. Fish. Aquat. Sci. 69, 1047–1055. https://doi.org/10.1139/f2012-042.
Ovegård, M.K., Jepsen, N., Bergenius Nord, M., Petersson, E., 2021. Cormorant predation effects on fish populations: a global meta-analysis. Fish Fish 22 (3), 605–622. https://doi.org/10.1111/faf.12540.
Pershing, A.J., Alexander, M.A., Hernandez, C.M., Kerr, L.A., Le Bris, A., Mills, K.E., Nye, J.A., Record, N.R., Scannell, H.A., Scott, J.D., 2015. Slow adaptation in the face of rapid warming leads to collapse of the Gulf of Maine cod fishery. Science 350, 809–812. https://doi.org/10.1126/science.aac98.
R Core Team, 2022. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria (URL https://www.R-project.org/).
Reusch, T.B., Dierking, J., Andersson, H.C., Bonsdorff, E., Carstensen, J., Casini, M., Czajkowski, M., Hasler, B., Hinsby, K., Hyytiäinen, K., Johannesson, K., Jomaa, S., Jormalainen, V., Kuosa, H., Kurland, S., Laikre, L., MacKenzie, B., Margonski, P., Melzner, F., Zandersen, M., 2018. The Baltic Sea as a time machine for the future coastal ocean. Sci. Adv. 4 (5), eaar8195. https://doi.org/10.1126/sciadv.aar81.
Rossi, S.P., Cox, S.P., Hammill, M.O., Den Heyer, C.E., Swain, D.P., Mosnier, A., Benoît, H.P., 2021. Forecasting the response of a recovered pinniped population to sustainable harvest strategies that reduce their impact as predators. ICES J. Mar. Sci. 78, 1804–1814. https://doi.org/10.1093/icesjms/fsab088.
Saarikoski, H., Vikström, S., Peltonen, L., 2024. Knowledge co-production around the cormorant-fishing conflict using a joint fact-finding approach. Environ. Sci. Policy 151, 103628. https://doi.org/10.1016/j.envsci.2023.103628.
Salmi, J.A., Auvinen, H., Raitaniemi, J., Kurkilahti, M., Lilja, J., Maikola, R., 2015. Perch (Perca fluviatilis) and pikeperch (Sander lucioperca) in the diet of the great cormorant (Phalacrocorax carbo) and effects on catches in the Archipelago Sea, Southwest coast of Finland. Fish. Res. 164, 26–34. https://doi.org/10.1016/j.fishres.2014.10.011.
Salmi, J., Salmi, P., Moilanen, P.(2010). Ammattikalastus ja merimetso. Riista- ja kalatalous -selvityksiä. [In Finnish with English Abstract].https://jukuri.luke.fi/bitstream/handle/10024/531236/rks2010_1.pdf?sequence=1.
Säterberg, T., Jacobson, P., Ovegård, M., Rask, J., Östergren, J., Jepsen, N., Florin, A.-B., 2023. Species-and origin-specific susceptibility to bird predation among juvenile salmonids. Ecosphere 14 (12), e4724. https://doi.org/10.1002/ecs2.4724.
Söderkultalahti, P., Rahikainen, M., 2023. Kaupallisten kalastajien ilmoittamat hylkeiden ja merimetsojen aiheuttamat saalisvahingot 2021. Luonnonvara- ja biotalouden tutkimus 28/2023. Luonnonvarakeskus, Helsinki, p. 17 http://urn.fi/URN:ISBN:978-952-380-650-4.
Sponza, S., Cimador, B., Cosolo, M., Ferrero, A., F., 2010. Diving costs and benefits during post-breeding movements of the Mediterranean shag in the North Adriatic Sea. Mar. Biol. 157, 1203–1213. https://doi.org/10.1007/s00227-010-1400-1.
Suomen ympäristökeskus, 2023 Merimetsoseuranta. (last accessed 24.9. 2024) [In Finnish].https://www.ymparisto.fi/fi/luonto-vesistot-ja-meri/luonnon-monimuotoisuus/lajien-monimuotoisuus/lajien-seuranta/merimetsoseuranta.
Svels, K., Salmi, P., Mellanoura, J., Niukko, J., 2019. The impacts of seals and cormorants experienced by Baltic Sea commercial fishers. Nat. Resour. Bioeconomy Stud. 48. http://urn.fi/URN:ISBN:978-952-326-854-8.
Tixier, P., Lea, M.A., Hindell, M.A., Welsford, D., Mazé, C., Gourguet, S., Arnould, J.P.Y., 2021. When large marine predators feed on fisheries catches: Global patterns of the depredation conflict and directions for coexistence. Fish Fish. 22 (1), 31–53. https://doi.org/10.1111/faf.12504.
Veneranta, L., Heikinheimo, O., Marjomäki, T.J., 2020. Cormorant (Phalacrocorax carbo) predation on a coastal perch (Perca fluviatilis) population: estimated effects based on PIT tag mark-recapture experiment. ICES J. Mar. Sci. 77 (7–8), 2611–2622. https://doi.org/10.1093/icesjms/fsaa124.
Verschuren, D., Johnson, T.C., Kling, H.J., Edgington, D.N., Leavitt, P.R., Brown, E.T., Talbot, M.R., Hecky, R.E., 2002. History and timing of human impact on Lake Victoria, East Africa. Proc. R. Soc. B 269, 289–294. https://doi.org/10.1098/rspb.2001.1850.
Vetemaa, M., Eschbaum, R., Albert, A., Saks, L., Verliin, A., Jürgens, K., Kesler, M., Hubel, K., Hannesson, R., Saat, T., 2010. Changes in fish stocks in an Estonian estuary: overfishing by cormorants? ICES J. Mar. Sci. 67, 1972–1979. https://doi.org/10.1093/icesjms/fsq113.

Watson, R.A., Cheung, W.W.L., Anticamara, J.A., Sumaila, R.U., Zeller, D., Pauly, D., 2013. Global marine yield halved as fishing intensity redoubles. Fish Fish. 14, 493–503. https://doi.org/10.1111/j.1467-2979.2012.00483.x.

White, C.R., Butler, P.J., Grémillet, D., Martin, G.R., 2008. Behavioural strategies of cormorants (Phalacrocoracidae) foraging under challenging light conditions. Ibis 150, 231–239. https://doi.org/10.1111/j.1474-919X.2008.00837.x.

Zuur, A., Ieno, E., Elphick, C.S., 2010. A protocol for data exploration to avoid common statistical problems. Methods Ecol. Evol. 1, 3–14. https://doi.org/10.1111/j.2041-210X.2009.00001.x.