

# Cormorant predation effects on fish populations: A global meta-analysis

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## Abstract

This paper provides the results from the first meta-analysis to examine the impact of cormorant (*Phalacrocoracidae*) predation on fish. It is based on a systematic search of literature, covering studies using significance-based hypotheses tests on the relation between fish parameters and cormorant abundance. The results show that extensive research on cormorant diet exists, but few studies use statistical hypotheses testing to examine the effect on fish populations. In total, 603 publications were identified from titles and abstracts, to include the interaction between cormorants and fish. From these, 27 articles tested fish population parameters against cormorant predation, whereof 22 could be included in analyses. The effect size was defined negative in cases when cormorant numbers or presence reduced fish numbers or biomasses, or when individual fish sizes decreased, and vice versa for a positive effect. In a hierarchical dependence model, the combined effect of cormorant predation on fish was negative, but the overall effect was not significant at the 95% confidence level ( $-0.169$ , 95% C.L.  $-0.505$  to  $0.167$ ,  $p = .256$ ,  $df = 5.26$ ). A covariate analysis revealed a difference in predatory effects between fish prey taxa ( $p = .006$ ,  $df = 5.73$ ), but no difference in effect sizes between study type, foraging habitat, or response variable measured. The meta-analysis reveals a complex interaction between cormorants and fish, but adds to the consensus on the importance of considering cormorant predatory effects in research, conservation actions, ecosystem-based management, and environmental monitoring.

## KEYWORDS

cormorant, effect, management, meta-analysis, *Phalacrocorax*, predation, wildlife-conflict

## 1 | INTRODUCTION

In ecology, predation and predatory behavior are central factors. In many cases, predator consumption affects prey populations by defining population size, community, and food web structures, and vice versa. However, the effect of a predator on a prey population in the wild is difficult to measure, as many variables, biotic and abiotic,

may correlate with prey (and predator) population trends (Domenici et al., 2007). Investigating predator effects on fish populations adds to the difficulty as the effects occur under the water surface.

The conflict between conservation and fisheries stakeholders concerning the piscivorous cormorant (*Phalacrocorax* spp., *Phalacrocoracidae*) is one of today's most widespread wildlife management issues. The human conflict is fueled both by the lack of

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documentation of whether cormorant predation affects fish population (i.e., number, biomass and size at age) and/or fishery catch, and the difficulty for the scientific community to communicate the uncertainties in scientific investigations (Klenke et al., 2013). Alongside the continued public debate about cormorants being a problem species or not, a substantial number of scientific studies on their effects on fish populations have been conducted. Some report on negative impacts and some on no impacts of predation on fish populations (see results section for references). Most conclusions are based on investigations of cormorant diet or recoveries of tags from fish in cormorant colonies, with both methods focusing on quantifying the mortality of fish caused by cormorant predation (Jepsen et al., 2018 offer a summary on the impact of cormorant predation on migrating Atlantic salmon (*Salmo salar*, Salmonidae) and brown trout (*Salmo trutta*, Salmonidae) smolt based on tagging studies in Denmark). Though these are important studies, a common critique against many diet and tagging studies is that they fail to adequately relate cormorant predation to responses in the fish population, such as changes in the total number of fish over time, size distribution in populations, or age at maturity. This is probably mainly a result of the lack of fish data (Coleman et al., 2016). In addition, studies on cormorants are limited in time and space, giving only a snapshot of predatory behavior and effects. Another criticism is that studies (naturally) do not cover all the environmental factors/variables, which may be the true reasons behind changes in fish populations. Therefore, despite extensive research (and debate) a consensus on the effects of cormorant predation on fish populations and fisheries has not been reached. Whether this is due to the variability of environmental responses, structure of the local ecosystems, variation in the methods used, or a general basic disagreement of what a tolerable impact is remains unclear.

Globally, there are about 40 species of cormorants and shags (Phalacrocoracidae) foraging in marine, fresh-, and brackish waters (Sibley, 2001). All species are predominantly piscivorous, but the conservation and fishery conflict has mainly involved the Great cormorant (*Phalacrocorax carbo*, Phalacrocoracidae) and Double-crested cormorant (*Phalacrocorax auritus*, Phalacrocoracidae; Nelson, 2005). The increasing populations of these two species in Europe (Bregnballe et al., 2003; Steffens, 2010) and North America (Wires & Cuthbert, 2006) are results of complex processes that are not fully understood. Both the Great cormorant and Double-crested cormorant were earlier (and still are) perceived competitors with fisheries which led to human persecution of the birds. In addition, in the early 1970s these top predators began to be severely affected by environmental contamination, which reduced the numbers. Later reduction of contaminants such as DDT, regulatory protection, and the birds' adaptability to anthropogenic environmental changes facilitated astonishing resurgence of the populations (Taylor & Dorr, 2003). Freezing temperatures limit the availability of fishing waters, and cold temperature has been identified as the main factor affecting the birds' distribution (distribution was considered in relation to average temperature in January when Cormorants have been counted at mid-winter roosts [van Eerden et al., 2012]). The change in climate, for example, warmer conditions, may consequently be

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beneficial for the cormorants, at least for the Great cormorant and Double-crested cormorant.

This paper presents the first systematic review of the impact of cormorant predation on fish populations and fisheries using a global meta-analysis of published scientific literature that has used significance based hypothesis testing. The strength of a meta-analysis is its ability to combine results from different studies that uses a variety of experimental methods (Koricheva et al., 2013). It is a quantitative method that increases the number of replicates by combining studies, addressing a common question, and thus increases the statistical power to answer the question. The crucial concept of meta-analysis is that of the *effect size*. An effect size is a statistical measure that portrays the degree to which a given outcome (or result, sometimes referred to as event) is present in a sample (Cohen, 1969). The effect sizes are combined to synthesize results from several studies. The meta-analysis in this paper covers all species of cormorants, all over the world. The aim was to assess the overall effect of cormorant predation on fish populations and examine the sources of variation in these effects, that is, variations between prey habitat, prey species, and fish responses.

## 2 | METHODS

### 2.1 | Selection criteria and data acquisition

The following procedure was used to reduce reviewer bias in the search for relevant literature. Searches were conducted through the

Web of Science-Cross Search (ISI Ver.3.0) and ASFA: Aquatic Sciences and Fisheries Abstracts (ProQuest) 1971-; which in total includes 21 databases (see Appendix S1). The search was conducted with a range of Boolean search terms in the English language. Two combinations of search terms were used per database group: (a)  $ts = \text{cormorant}^* \text{ AND diet}^*$ , (b)  $ts = (\text{cormorant}^* \text{ OR Phalacrocorax}) \text{ AND } (\text{fish}^* \text{ OR diet}^* \text{ OR prey}^*) \text{ AND } (\text{abundance}^* \text{ OR diversit}^* \text{ OR size}^* \text{ OR predat}^* \text{ OR populat}^* \text{ OR migrat}^* \text{ OR forag}^* \text{ OR stock}^*) \text{ AND } (\text{effect}^* \text{ OR affect}^* \text{ OR impact}^* \text{ OR compet}^* \text{ OR respon}^*)$ . The last search was made 2020-07-27, thus including all studies up to that date. A first screening process involved reading all the titles and abstracts to identify studies examining cormorant predation of fish (see Appendix S2 for ROSES flow diagram for systematic reviews [Haddaway et al., 2017]). Journal name, title, year of publication, and author names were recorded. In the second step of the screening process, texts were read in full to identify studies reporting values of cormorant predation on fish, that is, those presenting values for fish parameters (e.g., abundance and size distribution) in relation to cormorant abundance. When possible, the effect size was calculated from the information given in the articles. Defining which effects are positive or negative can be complicated as it may vary between fish species, populations, and ecosystem structures. The definition was therefore simplified, for comparability, by defining effects negative if the cormorant predation had negative effects on the fish parameters, for example, more cormorants result in less or smaller fish, and positive if cormorant predation had positive effects on the fish parameters, for example, more cormorants result in a greater number of, or larger, fish. The explanatory variables that may cause variations in effects, such as, foraging area/habitat type (i.e., lake, farm, estuary, and marine), bird species, fish species, and effect type were noted. For example, it was noted whether the effect was based on variations of fish parameters in relation to bird abundance (controlling bird numbers by, e.g., hazing or shooting) or the use of refuges for fish or behavioral changes in fish due to cormorant presence/predation, etc. All are listed in columns in the table in Data S3. Explanatory variables were not predefined but added during the reading process. Effect size is calculated using a test value and sample size or degrees of freedom. Sample sizes ( $n$ ) were either given as the number of fish, number of years, or number of study sites, over which the mean fish abundance, biomass, numbers, or size of prey were given. Data were extracted from tables or figures when not stated in the texts. The studies included reported differences in means, ratios, and correlations, but as they all address the same broad question, data were transformed to the most common effect size metric, the Pearson  $r$  correlation using Meta Win Version 2.1 (Rosenberg et al., 2010). To account for skewed distributions (Koricheva et al., 2013), a Fisher's  $Z$  transformation was conducted to convert the data from correlations to the effect size ( $Z_r$ ) and variance ( $\text{Var}(Z_r)$ ) before used in models. In the critical appraisal and synthesis process, effect values were excluded if the same data were presented in several articles. In a covariate model, effect values were excluded if an explanatory variable had a representation of less than three effect values.

Meta-regression models were used to synthesize and compare effect sizes. To alleviate, the problems introduced by dependent

effect sizes, a robust variance estimation model (RVE) was applied using the Robumeta package in R 1.2.5042 (R core Team, 2020). Effect values were categorized into being weighted either as hierarchical or correlated before choosing the final models. For example, effect sizes from studies with multiple measures taken on the same fish stock were assigned as correlated. In cases where effect sizes were derived from the same paper or scientist, and thus nested, they were assigned as hierarchical. The most common weighting type, which represented the most prevalent type of dependence, was subsequently chosen (according to Tanner-Smith et al., 2016). An average effect size was calculated in an intercept model, without conditioning on the study covariates and accounting for small sample sizes. A covariate model was used, again accounting for small sample sizes, to explore the heterogeneity in effect sizes by investigating the biological and methodological explanatory variables identified during the reading process (e.g., cormorant predation effects may differ depending on foraging habitats or some prey species may be more vulnerable to predation than others). Effect sizes are presented with 95% confidence intervals (CI). The effect size was considered significant if both values for the confidence limits were either positive or negative. The results extracted from the R script were used for drawing the figures in SigmaPlot<sup>®</sup> 11.0 (Systat, 2008).

## 2.2 | Exploration of bias

The quality of the results was evaluated for publication bias due to inaccurately reported or non-reported results by plotting the distribution of the effect size against sample sizes in a funnel plot. In the funnel plot, the variation around the mean effect size should decrease as sample size increase. Two plots were produced, one with all studies and one excluding  $n$  values  $>1,000$  to enable visualization of a funnel of studies with smaller  $n$  values.

It is important to note that the meta-analysis includes all studies, found in the search process based on the protocol described above, presenting results where an effect size can be obtained (either directly or by calculating, if essential information is presented). Thus, the meta-analysis includes both studies showing significant effects and studies with non-significant results (neutral effect or no impact studies). A publication was excluded from the analysis if it did not report effect size or the underlying values to calculate the effect size. It should be noted that there may be articles on cormorant predation missing from this meta-analysis, as some studies on the topic might not have been identified within the frames of the search criteria used.

## 3 | RESULTS

### 3.1 | Search results

The searching process yielded  $>4,000$  articles (of which many were found in both databases and with both search terms) of which all abstracts were read. Out of these articles, 603 contained information

on the interaction between cormorants and fish or fisheries (Listed in Data S3). Of these, 537 could be read in full while 66 articles could either not be retrieved or not translated. Read publications included studies on the diet of 40 cormorant species and subspecies, covering about 50 countries, from all seven continents. However, only 27 articles included cases from which the effect size on one or several fish responses could be obtained (articles are listed in Table 1). Of these, two articles were excluded from all models. Fielder (2008) was excluded because data on the same fish was presented in Fielder (2010). Gagnon et al. (2015) was excluded because they used colony age instead of cormorant abundance. In addition, three articles were excluded under the criteria that they had less than three effect values within their category. Thus, the final models included 22 articles with 135 effect values.

The selected articles were divided into those that were management related (10 studies in analysis) and those that were non-management related (12 studies in analysis). The first category included those studies where cormorant numbers had been reduced by hazing, shooting, or kept out by using fish refuges, with the aim to measure the effects on fish biomass, number, size, survival, and recruitment. The non-management related studies included those in which cormorant abundance or presence have been correlated to fish catch (biomass, number, or survival/mortality) in commercial fishery, recreational fishery, or scientific surveys. The common factor between these two categories is that they both correlate cormorant abundance to responses in fish parameters and thus could be combined for a common total effect size. Studies enabled the exploration of between-study variations concerning explanatory variables within the grouping variables, (a) study type (bird abundance, hazing, refuge, and shooting), (b) foraging area/habitat type (Baltic Sea coast, marine, estuary, river, lake, and experimental [i.e., in a captive/pond setting]), (c) prey taxa, and (d) fish response (biomass, number, recruitment size and age, and survival). Note that it was not possible to compare effects between cormorant species because there were less than three data points for many species. A minimum of three effect values per species was set as required for a covariate model.

### 3.2 | Meta-analysis/Quantification of effect sizes

The overall effect of cormorants on fish populations across the meta-data set was negative  $-0.169$  but the result was not significant (95% C.L.  $-0.505$  to  $0.167$ ,  $p = .256$ ,  $df = 5.26$ ; based on the intercept hierarchical effects model [i.e., all data, without grouping], with small sample corrections).

The covariate analysis revealed a difference in effects among prey taxa ( $p = .006$ , 95% C.L.  $-0.186$  to  $-0.049$ ,  $df = 5.73$ ; Figure 1). Cormorant numbers/presence seems to have the most negative effect on different cyprinid species (Cyprinidae), *Sander* spp. (Percidae), and European perch (*Perca fluviatilis*, Percidae). Cyprinidae includes common carp (*Cyprinus carpio*, Cyprinidae), common roach (*Rutilus rutilus*, Cyprinidae), silver bream (*Blicca bjoerkna*, Cyprinidae), and ide (*Leuciscus idus*, Cyprinidae). Cormorant predation had a smaller

negative effect, no effect, or positive effect on other species considered. The miscellaneous category includes species with a small number of effect sizes, such as European eel (*Anguilla Anguilla*, Anguillidae), smallmouth bass (*Micropterus dolomieu*, Centrarchidae), ruffe (*Gymnocephalus cernua*, Percidae), herring (*Clupea harengus*, Clupeidae), and Northern pike (*Esox Lucius*, Esocidae; Figure 2a–e). There was no significant difference in effects between study types ( $p = .127$ , 95% C.L.  $-0.320$  to  $0.051$ ,  $df = 6.34$ ), foraging area/habitat types ( $p = .726$ , 95% C.L.  $-0.150$  to  $0.200$ ,  $df = 5.04$ ), or fish response ( $p = .123$ , 95% C.L.  $-0.206$  to  $0.031$ ,  $df = 6.92$ ; Figure 1).

### 3.3 | Publication bias

The so-called publication bias must be taken into account, which can be due to an underrepresentation of insignificant results as publishing non-significant results may be difficult. This potential bias is unlikely to be of major concern for this meta-analysis, as both significant and non-significant effects of cormorant predation on fish communities are of interest for both scientists and the public, considering the diametrically opposing views among stakeholder groups. The funnel plot (Figure 3a,b) suggested no bias in the reporting/extraction of result values.

## 4 | DISCUSSION

The result from this meta-analysis indicates that cormorant predation does not have an effect on fish populations in general but can have significant negative effects on certain fish species. The effects did not differ between foraging habitats, study types, or response variables measured (see the results section for all explanatory variables within grouping variables). The most important take-home message from this study is that the literature search shows that there are few studies with statistical tests of cormorant predatory effects. This is probably one reason for the perpetual nature of the conflict. >50% of the 603 articles considered presented results on cormorant diet and concludes that cormorants either have negative or positive impacts on fish populations but without presenting results supporting such a conclusion. Around 3% of the articles used tagging to estimate predation on defined populations but did not test if the predation had an effect or not. Articles are mainly descriptive, presenting what, and how much, cormorants eat. The information on diet is in some cases discussed as effects of cormorant predation, evaluated in relation to commercial fishery, recreational catch, or fish survey results. With such descriptive data, however, it is only possible to discuss "indications" of effects as statistical tests and effect sizes are missing. In most cases, such studies leave the author and reader to interpret if the level of predation may affect fish populations, or fisheries catch. Another problem encountered during the literature search is the failure of authors in presenting statistical results adequately, for example, only  $p < .05$  is presented. To be able to calculate effect sizes, an exact  $p$ -value, or exact

**TABLE 1** Alphabetical list of references with the number of effect values extracted from each

Author(s)	Year	Title	Journal/Book	Country	Habitat	Short summary
Ainley et al.	2018	Ecosystem-based management affecting Brandt's Cormorant resources and populations in the central California Current region	Biological Conservation	USA	Marine	This study deals with Brandt's cormorant ( <i>Phalacrocorax penicillatus</i> ) and the study site was the coast of California, USA. They used multidecadal time series of cormorant colony size and fish abundance. Involved were increases and decreases of some prey species; northern anchovy ( <i>Engraulis mordax</i> ), sanddab ( <i>Citharichthys sordidus</i> ); and young-of-the-year rockfish ( <i>Sebastes</i> sp.). Colony size was achieved by direct counts of nests and data on fish abundance (catch-per-unit-effort) was extracted from surveys conducted by the National Marine Fisheries Service
Bacheler et al.	2011	Controls on Abundance and Distribution of Yellow Perch: Predator, Water Quality, and Density-dependent Effects	Transactions of the American Fisheries Society	USA	Lake	This study deals with <i>Phalacrocorax auritus</i> and its predation on yellow perch ( <i>Perca flavescens</i> ). The study site was Green Bay, Lake Michigan, USA. The authors used spatially explicit, varying-coefficient generalized additive models to relate summertime abundance and distribution of yellow perch to a variety of predatory, water quality, landscape, and density-dependent factors. The model used 25 years of fishery-independent trawling data for yellow perch. Cormorant abundance was measured as number of breeding pairs in the area. The study showed (among other results) that increased cormorant abundance was related to declines in local yellow perch catch-per-unit-effort, especially near cormorant nesting islands
Barbraud et al. <sup>b</sup>	2018	Density dependence, prey accessibility, and prey depletion by fisheries drive Peruvian seabird population dynamics	Ecography	Peru	Marine	This study focuses on how climate, population density, and the accessibility and removal of prey, the Peruvian anchovy ( <i>Engraulis ringens</i> ), by fisheries influence the population dynamics of the largest sedentary seabird community (Guanay cormorant ( <i>Phalacrocorax bougainvillii</i> ), Peruvian booby ( <i>Sula variegata</i> ) and Peruvian pelican ( <i>Pelecanus thagus</i> ) of the northern Humboldt Current System. The authors used Gompertz state-space models and found strong evidence for density dependence in abundance for the three seabird species. After accounting for density dependence, sea surface temperature, prey accessibility (defined by the depth of the upper limit of the subsurface oxygen minimum zone), and prey removal by fisheries were retained as the best predictors of annual population size across the three bird species
Barlow and Bock <sup>b</sup>	1984	Predation of fish in farm dams by cormorants, <i>Phalacrocorax</i> spp	Australian wildlife research	Australia	Farm	This experimental study deals with predation on fish in dams (with mixed fish species) by three species of cormorants ( <i>Phalacrocorax carbo</i> , <i>P. melanoleucos</i> , and <i>P. sulcirostris</i> ). Some dams were stocked with an alternative prey, a crayfish species. The result showed that (a) mean percentage survival for fish was significantly higher in dams that had not been fished by cormorants than in dams that had been, and (b) in dams containing abundant crayfish, the mean percentage survival was the same as in the unfished dams
Bayer	2000	Cormorant harassment to protect juvenile salmonids in Tillamook County, Oregon	Studies in Oregon Ornithology	USA	Estuary	This study was conducted as part of the plan to restore wild coho ( <i>Oncorhynchus kisutch</i> ) and wild steelhead ( <i>O. mykiss</i> ) runs. During several years at several sites attempts have been made to reduce the cormorants ( <i>Phalacrocorax auritus</i> ) predation with hazing (cracker shells by a fast boat; scarecrows, firearmed, hovercraft, chasing birds with boats). Hazing was not correlated with consistently improved hatchery returns
Brian et al.	2010	Evaluation of harassment of migrating double-crested cormorants to limit depredation on selected sport fisheries in Michigan	Journal of Great Lakes research—International Association for Great Lakes Research	USA	Lake	This study deals with double-crested cormorants ( <i>Phalacrocorax auritus</i> ) and its predation on the walleye ( <i>Sander vitreus</i> ) and the yellow perch ( <i>Perca flavescens</i> ). They used hazing (harassment methods (pyrotechnics) in order to deter cormorants from foraging. Cormorant foraging declined significantly at both studied locations. Overall harassment deterred 90% of cormorant foraging attempts. Cormorant foraging was estimated as number of birds within the study area, on the water, or flying. Fish abundance was based on estimates from trap-netting, gill-netting, and electrofishing

(Continues)

TABLE 1 (Continued)

Author(s)	Year	Title	Journal/Book	Country	Habitat	Short summary
Callaghan et al.	1998	Cormorant Phalacrocorax carbo occupancy and impact at stillwater game fisheries in England and Wales	Bird Study	England	Lake	This study provides an assessment of cormorant ( <i>Phalacrocorax carbo sinensis</i> ) occupancy and impact on put-and-take trout ( <i>Oncorhynchus mykiss</i> ) fisheries in UK. The study deals with several factors, and a regression model explaining autumn/winter cormorant numbers contained only one significant variable, fishery age. Fish data included number of angler visits and fish caught per year
Carss <sup>b</sup>	1993	Cormorants Phalacrocorax carbo at cage fish farms in Argyll, western Scotland	Seabird Group Newsletter	Scotland	Farm	This study deals with the predation of <i>Phalacrocorax aristotelis</i> at cage fish farms in Argyll, Western Scotland. The target fish species were rainbow trout ( <i>Oncorhynchus mykiss</i> ) and Atlantic salmon ( <i>Salmo salar</i> ). The cormorant did not take fish from farm cages but attacked them through the netting. Losses to cormorants were confined to 0.1% at one farm
Coleman et al.	2016	Evaluating the Influence of Double-crested Cormorants on Walleye and Yellow Perch Populations in Oneida Lake, New York	Oneida Lake: Long-term dynamics of a managed ecosystem and its fisheries	USA	Lake	The effect of predation by <i>Phalacrocorax auritus</i> on walleye ( <i>Sander vitreus</i> ) and yellow perch ( <i>Perca flavescens</i> ) was studied. Adult and juvenile cormorants were counted weekly, often multiple times per week, to monitor population growth, assess breeding success, and track the influx of migrants to the lake. Fish abundance was monitored at all life stages using multiple gears and techniques. For both fish species, the abundances were lower when cormorants were present compared to the period before the cormorant established at the lake
Crawford et al.	2019	Food habits of an endangered seabird indicate recent poor forage fish availability off western South Africa	ICES Journal of Marine Science	South Africa	Marine	This study deals with the relation between three bird species (one being the Cape cormorants <i>Phalacrocorax capensis</i> ) and the prey availability of several fish species (the most important being anchovy <i>Engraulis encrasicolus</i> and sardine <i>Sardinops sagax</i> ). In order to investigate this, they examined long-term dietary characteristics for gannets in the region in relation to acoustically derived biomass of prey. Based on the principal component analysis they found that Forage Availability Index was positively related to numbers of cormorants breeding each year. Thus, the availability of anchovy and sardine seemed to be insufficient to support the cormorant population
Fielder <sup>a</sup>	2008	Examination of Factors Contributing to the Decline of the Yellow Perch Population and Fishery in Les Cheneaux Islands, LakeHuron, with Emphasis on the Role of Double-crested Cormorants	Journal of Great Lakes research	USA, Canada	Lake	According to this study, <i>Phalacrocorax auritus</i> increased exponentially in the study area and at the same time the yellow perch ( <i>Perca flavescens</i> ) fishery and population declined. Regression analysis explored six possible independent variables to account for yellow perch trends. Mean perch age declined, which was consistent with a high mortality rate explanation. Total annual mortality rates determined by the cohort method were as high as 85% during much of this time and increased over the time series. Cormorant abundance accounted for a total of five significant relationships with the yellow perch data, more than any other independent variable. Fish abundance was retrieved from fishery statistics from creel surveys conducted by the Michigan Department of Natural Resources. Counts of nest numbers were used as an indicator of trends in cormorant abundance. This paper contains data 1979–2004
Fielder <sup>b</sup>	2010	Response of yellow perch in Les Cheneaux Islands, LakeHuron to declining numbers of double-crested cormorants stemming from control activities	Journal of Great Lakes research	USA, Canada	Lake	This study also deals with <i>Phalacrocorax auritus</i> that increased exponentially in the study area and at the same time the yellow perch ( <i>Perca flavescens</i> ) fishery and population declined. Regression analysis explored six possible independent variables to account for yellow perch trends. Mean perch age declined, which was consistent with a high mortality rate explanation. Total annual mortality rates determined by the cohort method were as high as 85% during much of this time and increased over the time series. Cormorant abundance accounted for a total of five significant relationships with the yellow perch data, more than any other independent variable. Fish abundance was retrieved from fishery statistics from creel surveys conducted by the Michigan Department of Natural Resources. Counts of nest numbers were used as an indicator of trends in cormorant abundance. This paper contains data 1979–2008

(Continues)

TABLE 1 (Continued)

Author(s)	Year	Title	Journal/Book	Country	Habitat	Short summary
Gagnon et al. <sup>b</sup>	2015	Cormorant-induced shifts in littoral communities	Marine Ecology Progress Series	Finland	Baltic Sea coast	This study describes fish, invertebrate, and algal communities, as well as algal growth and biomass accumulation, around colony and control islands along the Finnish coast to determine how cormorants affect communities through top-down and bottom-up processes. While cormorants ( <i>Phalacrocorax carbo sinensis</i> ) did not affect the species richness or biodiversity of any trophic level, there were differences in the community composition of fish between colony and control islands. Perch ( <i>Perca fluviatilis</i> ) abundance decreased with colony age. Cormorant abundance was measured as number of breeding pairs and fish abundance by gill-netting
Glahn and Dorr	2002	Captive double-crested cormorant <i>Phalacrocorax auritus</i> predation on channel catfish <i>Ictalurus punctatus</i> fingerlings and its influence on single-batch cropping production	Journal of the World Aquaculture Society	USA	Farm	In this study, the authors investigated the effects of captive <i>Phalacrocorax auritus</i> predation on channel catfish ( <i>Ictalurus punctatus</i> ) inventories from research ponds with and without alternative prey. However, there was no preference for alternative prey over catfish. The average loss due to cormorant predation was 29.5% (measured as the number of fish harvested)
Haeseker et al.	2020	Avian Predation on Steelhead is Consistent with Compensatory Mortality	Journal of Wildlife Management	USA	River	The authors applied a random effects model to a long-term, mark-recapture-recovery data set on anadromous steelhead ( <i>Oncorhynchus mykiss</i> ) juvenile out-migration to assess whether avian predation mortality constitutes an additive or compensatory source of mortality. Average predation rates were 3.3% for the double-crested cormorant ( <i>Phalacrocorax auritus</i> ) and 17.0% for the Caspian tern ( <i>Hydroprogne caspia</i> ) colony. For both bird species, the estimated correlation between the predation rate and survival rate of steelhead was near zero, indicating that mortality due to avian predation is compensatory. Models that included variables for river flow, juvenile migration timing, and an index of forage biomass in the ocean accounted for 56%–59% of the variation in steelhead survival, whereas avian predation rates accounted for <1% of the variation
Knöesche	2003	The impact of cormorants on the eel fishery in the river Havel catchment area, Germany	Interactions between fish and birds: Implications for management	Germany	River	A long-term dataset on eel ( <i>Anguilla anguilla</i> ) stocking intensity, eel yield, and catch-per-unit-effort in River Elbe was used to assess the influence of different factors, for example, water flow, stocking rate, and the number of cormorants ( <i>Phalacrocorax carbo sinensis</i> ) on fishery yield. The number of cormorants present explained approximately 28% of the variability in yield of eels. Cormorant abundance was measured as numbers of breeding pairs
Lantry et al.	1999	The Relationship Between the Abundance of Smallmouth Bass and Double-crested Cormorants in the Eastern Basin of Lake Ontario	Journal of Great Lakes research	USA	Lake	First, it is stated that the catch-per-unit-effort of adult smallmouth bass ( <i>Micropterus dolomieu</i> ) from index gill-netting has declined steadily since the 1983 year-class hit the fishery in 1989. Analyses revealed that the number of <i>Phalacrocorax auritus</i> nests had a significant relationship with relative fish mortality. Fish abundance was estimated by gill-net surveys
Lehikoinen et al.	2017	The role of cormorants, fishing effort, and temperature on the catches-per-unit-effort of fisheries in Finnish coastal areas	Fisheries Research	Finland	Baltic Sea coast	The authors investigated potential connection of <i>Phalacrocorax carbo sinensis</i> abundance, fishing effort, and water temperature with perch ( <i>Perca fluviatilis</i> ) and pikeperch ( <i>Sander lucioperca</i> ) yields (measured as catches per unit of effort in gill-net fishing along the Finnish coastal areas). Despite a population increase of cormorants the yield of perch increased in 10 out of 29 areas, during the study period, and pikeperch yield increased in five out of 24 areas. The increasing yields in several areas indicate that stocks are more abundant than ten years ago, despite an increasing cormorant population

(Continues)

TABLE 1 (Continued)

Author(s)	Year	Title	Journal/Book	Country	Habitat	Short summary
Lemmens et al.	2016	Can underwater refuges protect fish populations against cormorant predation? Evidence from a large-scale multiple pond experiment	Fisheries Management and Ecology	Belgium	Pond	In this study, the authors conducted a large-scale field experiment, with 24 ponds stocked with differently composed fish communities, in order to investigate if the effect of artificial refuges on fish is species-specific and determined by the characteristics of the fish community. The study provides experimental evidence for artificial refuges protecting fish against predation from cormorants ( <i>Phalacrocorax carbo sinensis</i> ), even in the presence of submerged vegetation. The effect of refuges was, species-specific and depended on the composition of the fish community. Strong positive effects of refuges were observed for rudd ( <i>Scardinius erythrophthalmus</i> ), and roach ( <i>Rutilus rutilus</i> ). No effect of artificial refuges on other fish species was found
McKay et al.	2003	Pilot trials to assess the efficacy of fish refuges in reducing the impact of cormorants on inland fisheries	Interactions between fish and birds: Implications for management	England	Experimental	Artificial structures (wire mesh refuges) designed to protect fish from predators were studied. Two adjacent drainable ponds were stocked with three sizes of common carp ( <i>Cyprinus carpio</i> ). One pond was netted over to exclude piscivorous birds, the other was left open. Cormorant ( <i>Phalacrocorax carbo sinensis</i> ) dive duration was longer, and the percentage of large fish recovered with wounds was lower, when refuges were present. These results suggest that refuges may reduce the availability of carp to cormorants, particularly the larger size classes which are more sought after by anglers (>28 cm)
Mustamäki et al.	2014	Pikeperch (Sander lucioperca (L.)) in Decline: High Mortality of Three Populations in the Northern Baltic Sea	Ambio	Sweden, Finland	Sea	In this study, the abundance of pikeperch ( <i>Sander lucioperca</i> ) was estimated by gill-net monitoring, with standardized annual multimesh, at three sites. Cormorant ( <i>Phalacrocorax carbo sinensis</i> ) abundance was measured as number of breeding pairs. Declining trends in the abundances of pikeperch over 40 cm (total length), low numbers of individuals older than 6 years, and high mortality rates were observed in all sites. In the site with the largest commercial catches per unit area and a rapidly increased colony of cormorants also the abundance of pikeperch below 40 cm (total length) and year-class strength showed declining trends
Russell et al.	2008	Reducing fish losses to cormorants using artificial fish refuges: an experimental study	Fisheries Management and Ecology	England	Experimental	In this study, they investigated whether the introduction of artificial refuges might provide protection for fish and reduce the level of cormorant ( <i>Phalacrocorax carbo sinensis</i> ) predation. Two, paired-pond, cross-over trials were done. The results showed 77% fewer cormorant visits to the refuge pond than the control pond, on average. There was also a 67% fall in the mean mass of fish consumed per cormorant visit and 79% less fish mass lost in the refuge pond. At the start of each trial, the ponds were stocked with roach ( <i>Rutilus rutilus</i> ), perch, ( <i>Perca fluviatilis</i> ), and common carp ( <i>Cyprinus carpio</i> )
Schultz et al.	2013	Modeling Population Dynamics and Fish Consumption of a Managed Double-Crested Cormorant Colony in Minnesota	North American Journal of Fisheries Management	USA	Lake	In this case study, cormorant ( <i>Phalacrocorax auritus</i> ) colonies were evaluated under no, moderate, and intensive control (culling) rates and the observed population responses were compared. They noted a negative relationship between cormorants and most statistics of the fishery suggested cormorant management had positively affected the fishery. However, despite these differences and the observed increases in yellow perch ( <i>Perca flavescens</i> ) and cisco ( <i>Coregonus artedii</i> ) abundance, following the onset of cormorant management activities, variation in gill-net catch rates of these species, as well as changes in yellow perch growth rates, were not explained by cormorant predation pressure

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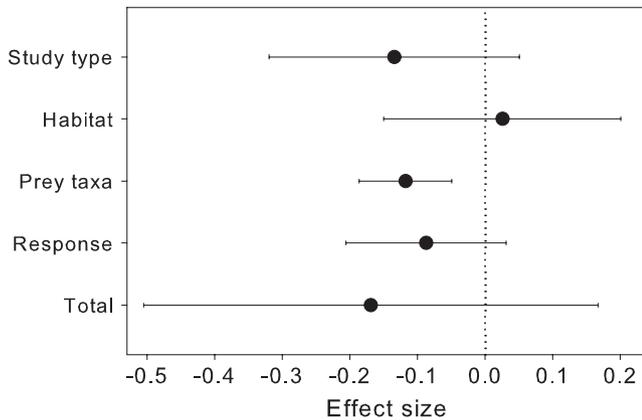
TABLE 1 (Continued)

Author(s)	Year	Title	Journal/Book	Country	Habitat	Short summary
Sherley et al.	2017	Defining ecologically relevant scales for spatial protection with long-term data on an endangered seabird and local prey availability	Conservation Biology	South Africa	Marine	The authors investigated the local population response (number of breeders) of the Bank Cormorant ( <i>Phalacrocorax neglectus</i> ) to the availability of its prey, the heavily fished west coast rock lobster ( <i>Ianus lalandii</i> ). Using Bayesian state-space modeled cormorant counts at 3 colonies, 22 years of fisheries-independent data on local lobster abundance, and generalized additive modeling, it was determined that Cormorant numbers responded positively to lobster availability
Suter	1995	The Effect of Predation by Wintering Cormorants Phalacrocorax carbo on Grayling Thymallus and Trout (Salmonidae) Populations: Two Case Studies from Swiss Rivers	Journal of Applied Ecology	Switzerland	River	The effect of cormorant ( <i>Phalacrocorax carbo sinensis</i> ) predation on one trout ( <i>Salmo trutta</i> ) and two grayling populations ( <i>Thymallus thymallus</i> ) was examined in two rivers. Cormorant densities were among the highest recorded on Swiss rivers. Fishery yield was used as a means of detecting fish population changes, because population size could not be measured directly. No evidence was found to support predictions of a negative effect on fish population dynamics by cormorants. Predation intensity on grayling was positively correlated with yield in the largest grayling population. However, there were some effects due to cormorant predation on fish population, such as lower weight
Wright	2003	Impact of cormorants on the Loch Leven trout fishery and the effectiveness of shooting as mitigation	Interactions between fish and birds: Implications for management	England	Lake	In this study, cormorants ( <i>Phalacrocorax carbo sinensis</i> ) were shot in large numbers in order to reduce the potential effects of cormorant predation of brown trout ( <i>Salmo trutta</i> ). There was little evidence of any beneficial effect of shooting cormorants for fishery protection purposes. Catch-per-unit-effort remain relatively stable despite the cormorant increase, and the main determinant of angling catch was angling effort
Östman et al.	2012	Do cormorant colonies affect local fish communities in the Baltic Sea?	Canadian Journal of Aquatic Sciences	Sweden	Sea	In this study, the authors used both a paired design and time series analysis, in order to investigate associations between colony size of <i>Phalacrocorax carbo sinensis</i> and local fish community composition. Overall, cormorant colony size (number of breeding pairs) showed few associations with local fish communities. Most evident was a negative association between colony size and perch ( <i>Perca fluviatilis</i> ) abundances in some areas. However, for other species results were non-significant or variable among areas

Note: Details of original values for calculation of effect values and *n* for each are provided in Data S3.

<sup>a</sup>Fielder (2008) was considered but not used in the models as the same fish population was analyzed in Fielder (2010). Fielder (2010) was chosen as analyses included studies covering more years than Fielder (2008).

<sup>b</sup>Gagnon et al. (2015) was also excluded from models, as they used colony age instead of colony abundance. Other articles with <sup>b</sup> were excluded only in the covariate model based on having <3 effect values within categories.



**FIGURE 1** Effect sizes with 95% CI. Total is based on the intercept hierarchical effects model (i.e., all data, without grouping). Effect sizes for Study type, Habitat, Prey taxa, and Response are based on results from the covariate model for hierarchical data. If CI range over the zero line, the difference between categories within groups is non-significant. There was a significant difference in cormorant predation effects between prey taxa ( $p = .006$ , 95% C.L.  $-0.186$  to  $-0.049$ ,  $df = 5.73$ ).

outcome value from the original test (i.e.,  $t$ - or  $F$ -test value), together with the sample size ( $n$ ), is needed at a minimum. It is also possible to extract effect values from mean and variance values from normally distributed data (sample sizes are also required).

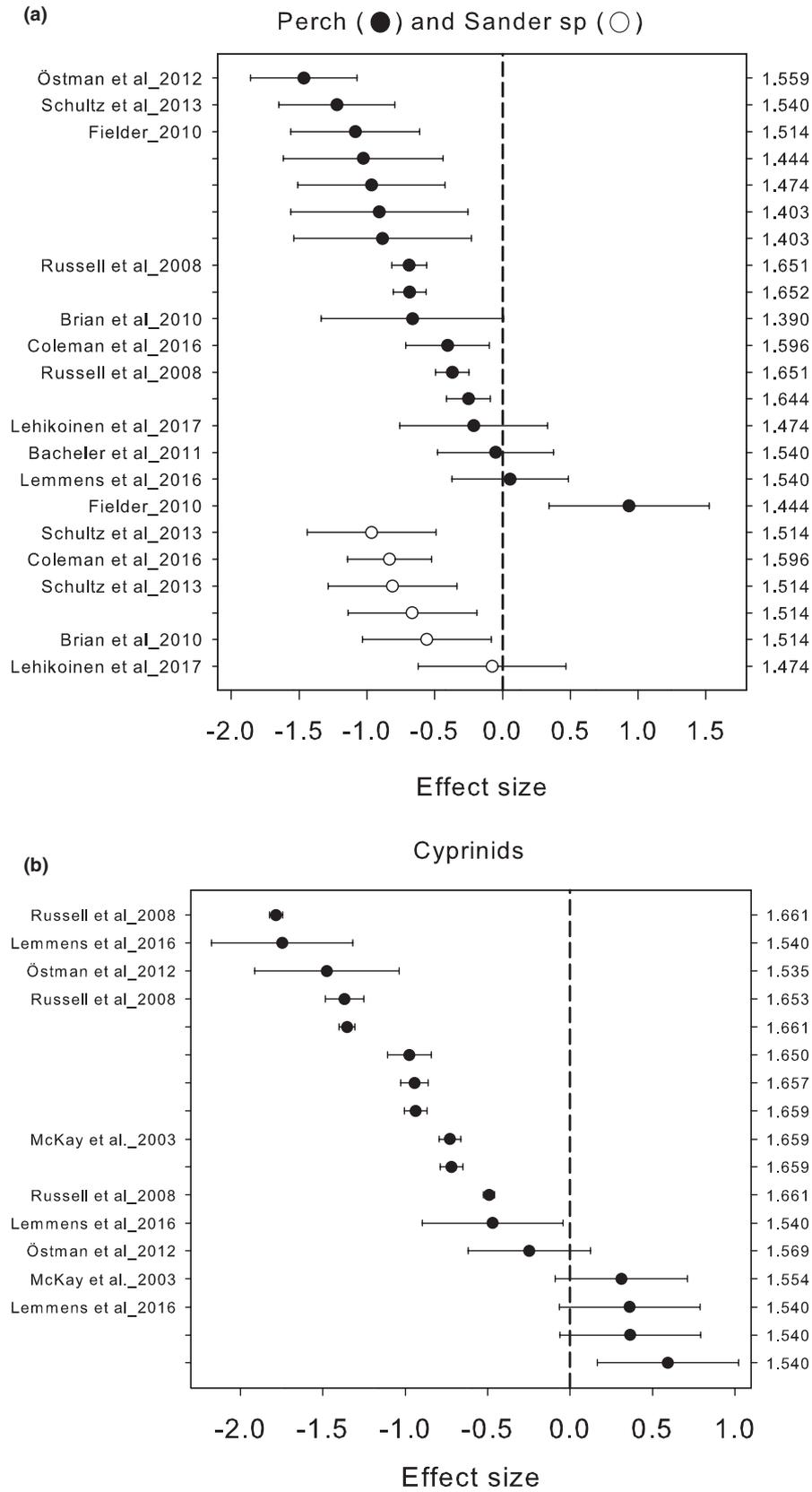
The meta-analysis is based on an extensive and structured literature search with degrees of freedoms in the models being  $<4$  signifying high confidence in the results, despite a complexity in covariates. Note that the analysis was based on effects of all cormorant species and covers several fish species, habitats, and responses, which complicates the picture of effects and increases the risk of type I error. However, the focus in this study was to reach a consensus of a general impact of cormorants on fish and thus the complexity in the data was accepted. The weakness is the low number of studies that could be included for many of the cormorant species. Because some cormorant species were only represented with few effect values it was assumed that cormorants have similar foraging behaviors and affect fish populations in similar ways. Similarities in the negative predation effects of the Great cormorant (*Phalacrocorax carbo sinensis*, Phalacrocoracidae) on European perch in Europe (Östman et al., 2012; Skov et al., 2014) and the Double-crested cormorant on yellow perch (*Perca flavescens*, Percidae) in Oneida Lake in North America (Rudstam et al., 2004) can be seen, but whether this holds for other cormorant species and other areas needs to be further investigated. With more future studies, it may be possible to do stronger meta-analyses and explore the variations in effects. In addition, few studies acknowledge a functional response of the cormorants, that is, the intake rate of a consumer as a function of food density (see Holling, 1959). Studies and field experiments of merganser (*Mergus merganser*, Anatidae) conducted by Wood and co-workers (Wood & Hand, 1985) indicated a functional II response (i.e., decelerating intake rate which follows from the assumption that the

consumer is limited by its capacity to process food), but also that mergansers continue food searching even at low prey densities (see also Wood, 1985). Mergansers were less successful at capturing coho salmon (*Oncorhynchus kisutch*, Salmonidae) smolt or fry in the enclosures with cover from undercut banks. A similar result was obtained for the Great cormorant *P. c. sinensis* by Russell et al. (2008). The work by Wood and co-workers also showed an aggregative response of the mergansers related to fish availability (Wood, 1985, 1986, 1987). Similar results have been obtained for the Cape cormorant (*Phalacrocorax capensis*, Phalacrocoracidae; Crawford et al., 2019); their Forage Availability Index, was positively related to numbers of cormorants breeding each year. The lack of good studies on fish responses (numbers and/or biomass) to cormorant predation makes it hard in each case to identify evidence for compensatory or additive mortality. However, fish responses to predation or exploitation might depend on species and age (size) of the fish individuals. For example, Allen et al. (1998) showed that crappies (*Pomoxis nigromaculatus*, Centrarchidae and *Pomix annularis*, Centrarchidae) and small ( $<40$  cm) Northern pike appeared to show compensatory mortality (populations compensate for predation/harvest mortality by reducing rates of natural mortality), whereas largemouth bass (*Micropterus salmoides*, Centrarchidae) and large Northern pike ( $>40$  cm) showed additive mortality (predation/harvest and natural mortalities operate additively (additive hypothesis).

Although there was a high complexity of cormorant and fish interactions among the studies included in the meta-analysis, it was possible to identify a broad general pattern of how effect sizes differ between fish species (prey taxa). When searching for articles, no evaluations on study quality were done prior to the analysis as a mean to minimize author influence. Instead, the discussion includes a review of the papers included, within each grouping variable, as a mean to evaluate the results and identify future research needs.

#### 4.1 | Study type

Of the 22 publications in the models, 10 studied the change in fish communities after controlling cormorant predation, in the type category "Management related," and 12 studies were "non-management" related. Management method did not affect the results. A report on the use of cormorant harassment, under grouping variable "hazing," to protect juvenile salmonids by Bayer (2000) included values indicating both positive and negative effects of cormorants, that is, an overall effect could not be identified. The effects were measured on the fish returning to spawning areas (adults or jacks) or caught in recreational fishing. The author assumes cormorant predation during the smolt migration is the most important factor for return rates, but there are other key factors, such as sea temperature, availability of food, or other predators affecting return rates, which may mask potential effects of cormorant predation on smolts. From a cormorant predation management perspective, hazing may be a good method to protect smolt during migration, but the positive effects on the



**FIGURE 2** Effect sizes for (a) Perch and Sander spp. (b) Cyprinidae, (c) Coho salmon, (d) Catfish, Rainbow trout, and Brown trout, and (e) Miscellaneous (including several taxa as explained in the text), with 95% CI from Robust Variance Hierarchical Effects Model with Small Sample Corrections. The effect is non-significant if CI range over the zero line. Sources for each effect size are presented as author and year on the first y-axis (lines without author refers to the author above) and the weighing of each effect on the second y-axis

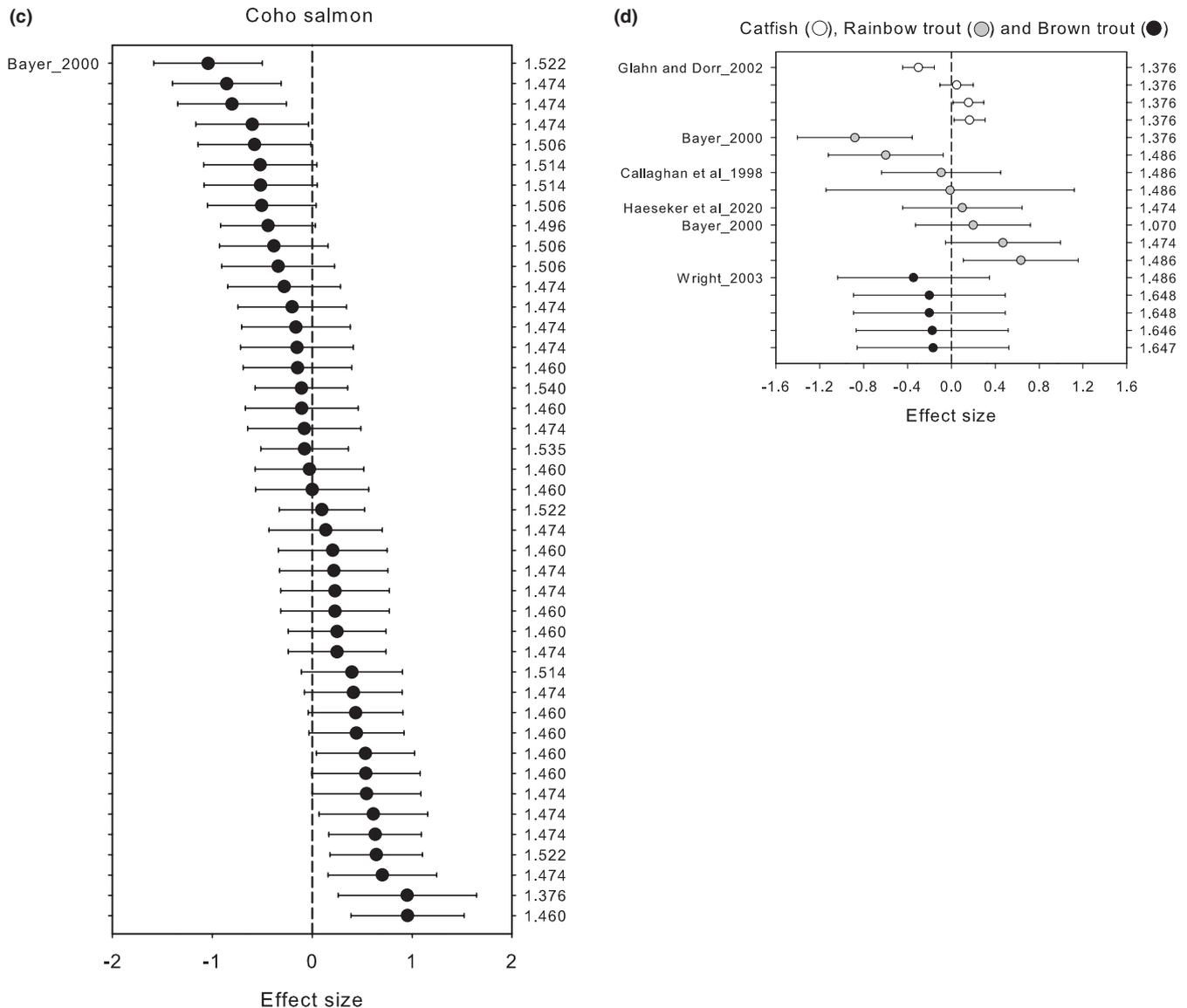


FIGURE 2 (Continued)

population may be less than expected as other mortality factors may be as, or more, important than cormorant predation on the population level. Non-lethal deterrents against predators are often used for terrestrial animals (e.g., Young et al., 2015).

The "refuge" studies were based on the methodology of totally covering a body of water (Glahn & Dorr, 2002) or underwater refuges in the form of cages (Lemmens et al., 2016; McKay et al., 2003; Russell et al., 2008). Positive effects of predation on fish populations were identified in Glahn and Dorr (2002), but these represent individual fish being larger, in mass, in depredated versus control ponds. Larger fish was in the meta-analysis considered a positive response to predation, from a human consumption point of view. If cormorant predation reduces fish numbers, compensatory growth among surviving fish may lead to larger individuals (c.f. Engström, 2001; see also Rose et al., 2001). Thus, in some cases cormorant predation may have a positive effect on fishery catch if the desired outcome is larger (but less) fish (Glahn

et al., 1995; Östman et al., 2012). Most studies on underwater cages as refuges for fish show positive effects on fish. Lemmens et al. (2016), however, conclude that effects are highly species specific with large positive effects on common rudd (*Scardinius erythrophthalmus*, Cyprinidae) and common roach (both as Cyprinidae/cyprinids in analyses) but smaller effects on European perch, ide, common carp, and European pike. The study by Wright (2003) investigated the effects on fish populations by "shooting" cormorants. All effect values were negative, but the result of shooting is based on only one paper.

The studies under the category "bird abundance" were the non-management related studies. A study on Brandt's cormorant (*Phalacrocorax penicillatus*, Phalacrocoracidae) by Ainley et al. (2018) generated the most effect values for the category "bird abundance," but this study was mainly concerned with the effect of prey availability on cormorants rather than vice versa. Brandt's cormorant is considered to be of least concern, but globally considered be decreasing

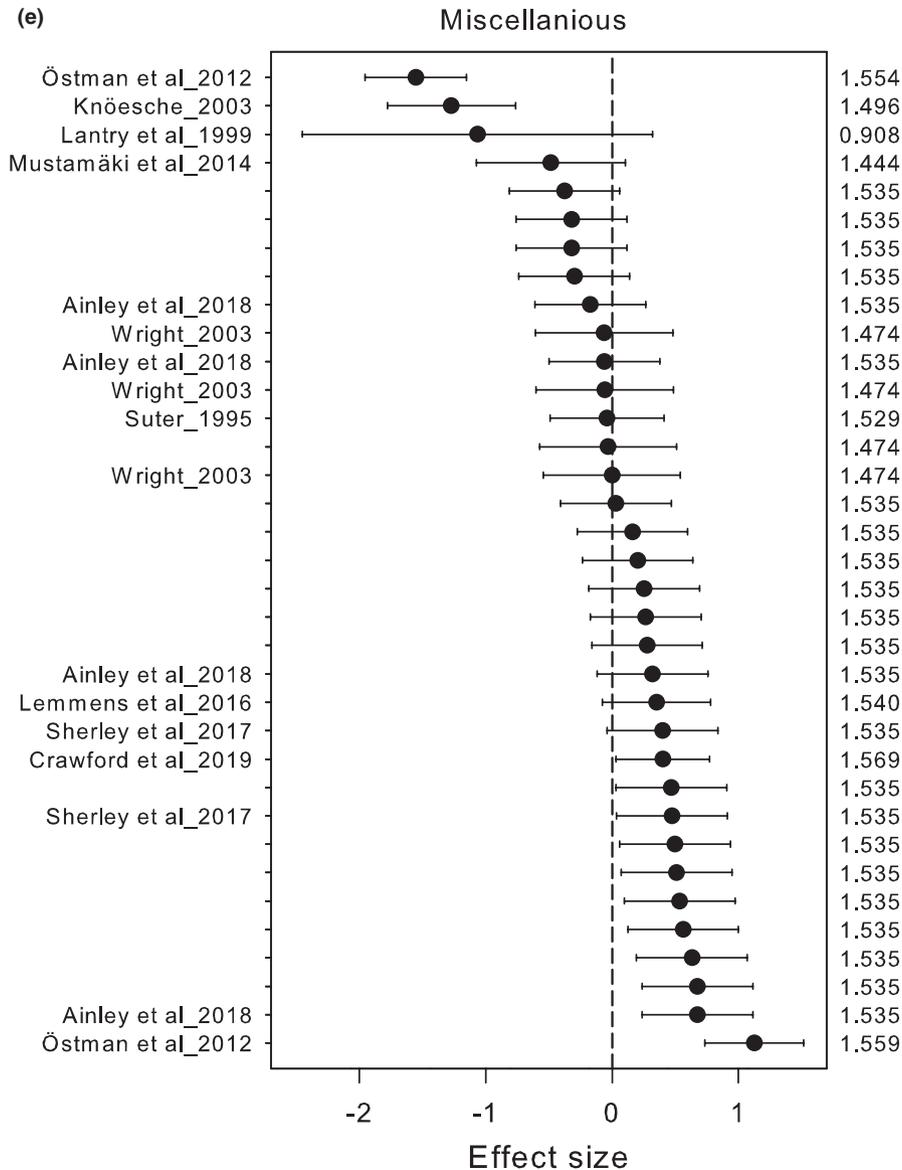


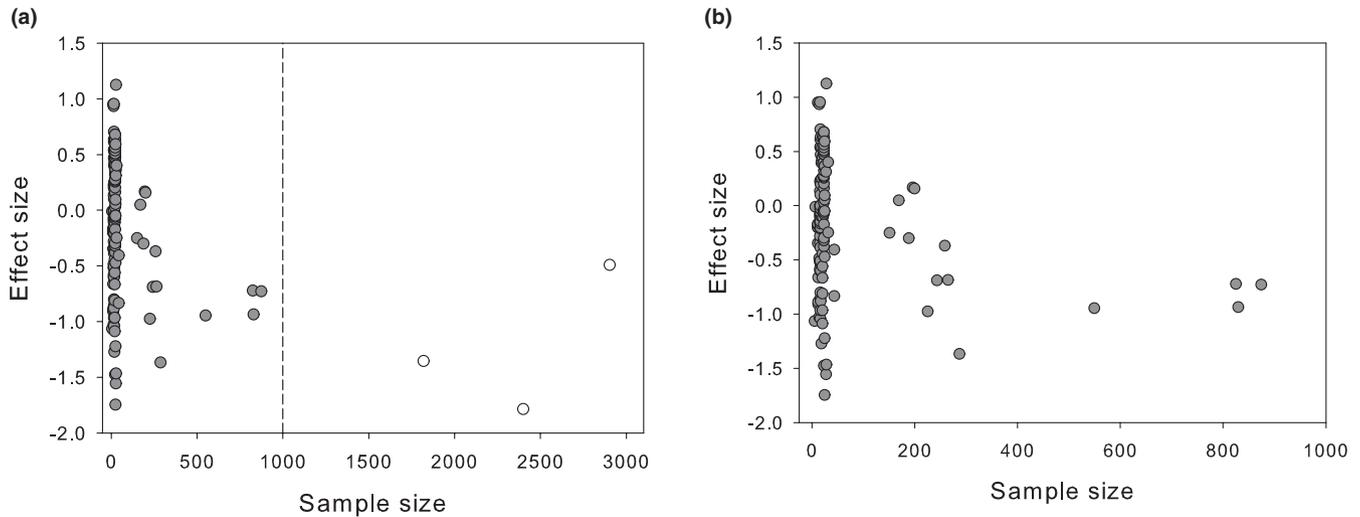
FIGURE 2 (Continued)

(BirdLife International, 2018, IUCN red list). It could be that the low number of cormorants does not have an effect on prey numbers and that other factors are involved, or that prey abundance rather reflects cormorant numbers and thus drive correlations.

#### 4.2 | Foraging area/habitat type

It must be noted that the majority of articles included concerned restricted aquatic systems, mainly inland water, such as lakes, rivers, or ponds (under experimental). Although the number of data points is large for marine and brackish environments, the number of studies is few. Naturally, large systems are more difficult to study than smaller systems, making studies in large systems less common. In larger systems, prey are able to move longer distances and more replicates are necessary for finding significant effects of

cormorants on fish populations. All the management-related studies are from lakes or ponds (as “experimental” in analyses) except Bayer (2000) which is the only article in the explanatory variable “estuary” (article discussed above). Of the non-management-related studies, six out of twelve have been conducted in an open marine settings. Three of these were in the Baltic Sea, with brackish water, on the Great cormorant *P. c. sinensis*, which is of least concern and increasing. Two studies were from the west coast of South Africa on the Cape cormorant, which is endangered and decreasing, and one from the Californian coast in America on the Brandt's cormorant which is of least concern but decreasing (statuses referred to BirdLife International, 2018, IUCN red list). The differences in the populations’ developments may drive differences in effects on fish between the studies in open marine settings. That is, a decreasing cormorant population may not have as big effect on fish populations as an increasing population.



**FIGURE 3** Funnel plots to illustrate bias in reporting of results. A large spread in effect size at the smallest sample sizes and less at the larger sample sizes indicate that the variation around the mean effect size decreases as sample size increases. Note that three studies with  $N > 1,000$  (marked with empty circles in Figure 3a) were excluded in Figure 3b as they masked the funnel plot of the other effect sizes

### 4.3 | Prey species

There was a significant difference among fish taxa; some taxa (perch, sander, and cyprinids) appear to have more negative effect size values than positive, catfish (*Ictalurus punctatus*, Ictaluridae) more positive than negative and remaining taxa about equal numbers of positive and negative values (see Figure 2a–e). However, the combined effect of cormorants on fish was non-significant. In particular cyprinids, *Sander* spp. and perch seem to be negatively affected (see Figure 2a–e for effect sizes on all prey taxa), in varying habitats. Wright (2003) studied brown trout and found no significant correlation between the catch-per-unit-effort data from gill-nets (variable mesh sizes between 5 and 55 mm knot to knot and thus catching smaller sized fish) and the number of cormorants before and after a cormorant population increase. Though results are not presented in the article, they mention a 90% decline in perch catch-per-unit-effort during the same period. The question is whether cormorants have preference species or whether predation risk depends on species abundance and/or behavior and size and thus catchability. An issue of confounding environmental variables masking the effects of cormorants needs to be considered for both Haeseker et al. (2020), studying rainbow trout (*Oncorhynchus mykiss*, Salmonidae), and Bayer (2000), regarding both coho salmon and rainbow trout, as both articles consider return rates. For most of the studies on rainbow trout (including the anadromous steelhead), effects were measured on recreational catches (Bayer, 2000), which again considers effect on larger sized fish, >40 cm. Also, Callaghan et al., 1998 based their study on rainbow trout on recreational catches. This meta-analysis does not cover the question about which sizes of fish or what life stages are more vulnerable to predation. The literature suggests, however, that fish of smaller sizes are more predated on, for example, less than 100 g (Grémillet et al., 2006) or 20 cm (Čech et al., 2008; Lorentsen et al., 2004, and more) and whether this is due to preference or abundance, or a combination, is unknown.

### 4.4 | Fish response variable

Effects did not vary between the response variables studied. For the explanatory variable “recruitment,” there was only one data point though, for coho salmon, that showed a positive effect (Bayer, 2000), while all other data points, including coho salmon, *Sander* spp., and yellow perch, showed lower recruitment to the adult stage with cormorant predation (Bayer, 2000; Coleman et al., 2016; Schultz et al., 2013). Fielder (2010) showed that yellow perch at age 3 were larger after cormorants had predated on the population compared to when they had not, indicating density-dependent effects, or that faster-growing individuals were selected for (Sogard, 1997). The study of Glahn and Dorr (2002; excluded from the models in this study) supports this theory as individual fish mass, and total mass of all fish, were larger in predated versus control ponds. Thus, cormorant predation may in some cases have positive effects on fishery catch if the desired outcome is larger (but less) fish (Glahn et al., 1995; Östman et al., 2012). Bachelier et al. (2011), however, found that the number of yellow perch at age 1 caught in trawl surveys was lower with increased predation pressure by cormorants. The number of age 0 was also lower, however, not significantly. Predation on smaller individuals may decrease the number of individuals growing to large size. On the other hand, cormorant predation on smaller sized planktivorous fish may mitigate or suppress eutrophication effects (Mehner et al., 2002), which may be considered as a positive effect. The responses in a fish population due to cormorant predation seem to be complex and variable depending on the ecosystem and food web structure.

### 4.5 | Non-consumptive effects

The result of the meta-analysis on the effects of cormorants on fish was non-significant, but it cannot be ruled out that cormorant

predation does not alter fish populations and behavior. Kortan and Adámek (2011) identified a predatory avoidance in the form of movements of carp toward the littoral zone, crowding, and hiding in littoral plant beds when cormorants were present. Though the response is not directly lethal for the fish, the presence of foraging cormorants may infer lower foraging success of the fishes, suboptimal foraging, and/or lower growth rate. It is important to consider these types of secondary effects of foraging cormorants, which may result in changed fish stock structure and alter food webs and whole communities (for a review of indirect effects read Klenke et al. (2013)). Another effect of cormorant predation is injury, that is, that the fish is not caught by the bird, but injured, and this may affect fish differently depending on the species. Kortan et al. (2008) show that two-year-old common (mirror) carps injured by cormorants have significantly lower condition than non-wounded carps, but for scaly common carp in the same age and size there was no significant difference in condition. Fish with large scales have a tougher skin surface to break through, but there may also be a difference in predatory avoidance behavior between the two carp varieties. Several studies have indicated multiple cascade pathways induced by removal or lethal control of an apex predator, which will drive unintended shifts in, for example, forest ecosystem structure. Apex predators usually are viewed as having a vital role in the functioning of ecosystems, and their importance has been underestimated because their effects often only become evident after they have been removed from ecosystems (Colman et al., 2014; Estes et al., 2011; Myers et al., 2007). One effect from removing (or introducing) an apex predator is that the larger predators can affect their prey, which may be smaller predators (meso-predators), in two different ways. First, by consumptive (i.e., lethal) effects that occur through direct killing and, second, non-consumptive (i.e., non-lethal) effects that become manifest as prey and competitors shift their phenotypes and habitat use in response to risks associated with predation (Gordon et al., 2015; Lima, 1998; Schmitz, 2008). The cormorant most likely plays a role as apex predators in marine, brackish, and freshwater ecosystems and fish species have to be regarded as meso-predators (feeding on smaller fish species or individuals, phytoplankton and zooplankton). However, little is known about their long-term effects on the ecosystems, their effects have to be analyzed together with effects of pollutants, fisheries, and other apex predators (such as other piscivorous birds and mammals). There is, to our knowledge, no comprehensive information on effects on (for example) zooplankton populations. Thus, the meta-analysis presented in this paper gives no additional understanding of these cascading effects, simply because such studies are missing or too few. Another aspect is that some empirical studies and theoretical models suggest that predators selectively prey on a certain part of the prey population (such as infected, wounded, weak, old, and/or young individuals (Emlen, 1966; Genovart et al., 2010; Krumm et al., 2010; Miller et al., 2014; Temple, 1987). This is however hard to study for cormorants, as they consume their prey in one piece and therefore there is little left for veterinary examination.

## 4.6 | Robustness of results

The results of the meta-analyses presented are confident, as the degrees of freedoms in models are  $>4$  (see Fisher & Tipton, 2015). Further studies are needed, however, to better evaluate the relationship between cormorant numbers/presence and measures on fish populations. The inclusion of several cormorant and fish species in one meta-analysis incorporates an uncertainty in model results. More studies will make it easier to account for complexity in the dataset and to reveal the influence of different types of effects. For example, in the future it may be possible to look into the effects of certain cormorant species and differences between species.

## 4.7 | Lessons learned for future focus for research and management

There was a high number of scientific papers covering cormorant predation but not testing the effects on fish statistically and thus not able to satisfactory (in the sense of statistical proof) answer the main question of the effects of cormorants on fish. Actions or programs to minimize cormorant predation have been and are proceeding with or without this statistical evidence. Therefore, there is a need from the scientific community to engage to make sure actions to minimize cormorant predation are researched rigorously to be able to give advice on how to evaluate, refine, and end actions if they are not effective. There are several ways to study the effect of cormorant predation of fish populations. An effective and accepted method is by using a BACI design (Before-After-Control-Impact), which is when you measure variables before cormorant predation and with cormorant predation using controls in areas with the same environmental prerequisites but no cormorant predation. However, with established colonies the before data is often missing. Here we outline two approaches for those instances. First, correlate cormorant presence (e.g., breeding pairs and roosting numbers) with fishery-independent data on fish population, such as catch-per-unit-effort, size of different species, and fish age estimates. Unfortunately, this approach will need data for at least several years, and the number of years depends on the actual effect of cormorant on fish population. Second, field experiments where areas either are protected from cormorant predation or left unaffected, that is, open for cormorant predation. Due to practical reasons, this method will mainly be possible to apply to smaller areas (pond or sections of rivers) and scaling up these results to open natural habitats might be questionable. However, with appropriate experimental designs such studies can generate valuable results, especially over longer timeframes.

The meta-analysis did not find a significant difference between methods to reduce cormorant predation but some may be more or less effective and more studies in the future may enable to reveal differences by post doc tests. Lehtikoinen (2005) noted that the adult birds feed small chicks with smaller and more easily digested fish, such as eelpout (*Zoarces viviparus*), compared to more scaly roach

(*Rutilus rutilus*) and perch (*Perca fluviatilis*) during the later phase of breeding. Our analyses give a slightly different view, because the "Fish taxa" was significant this indicates that the composition of fish species in the ecosystem might change. As cyprinids appear to be more sensitive to cormorant predation, they might decrease as cormorants increase (and the other way round), allowing other fish species to increase in number. This is speculative but needs to be taken into account in research and management decisions. Future meta-analyses, including more studies, will give a more conclusive answer concerning the effects of cormorant predation.

## 5 | CONCLUSIONS

The results published so far show that cormorant predation effects differ between fish species. Most vulnerable to cormorant predation are species within the Cyprinidae and Percidae families, which may be a result of prey selection. Effect sizes could only be extracted from 27 out of 603 publications on cormorant predation on fish, which stresses the importance of focusing future research on studies that includes a design with statistical hypothesis testing to further add to the knowledge of cormorant predatory effects. Especially studies investigating the effects of cormorant predation along the coasts and natural ecosystems (i.e., not artificial pond settings) are lacking. This is probably due to the difficulty in isolating the effects of cormorant predation among all the other biotic and abiotic pressure variables acting on fish populations in a variety of challenging habitats and complex systems. Also, further studies on fish responses are recommended regarding all methods to alleviate cormorant predation. Supported by the non-significance in the total result, it is recommended to monitor the effects in any attempts to alleviate predation. Hopefully, these results will inspire researchers to (a) focus on effects on fish populations rather than conducting diet analyses solely, (b) publish results in such a way that it can be used in meta-analyses, and (c) conduct studies on before–after or treatment–control.

The results in this study show that the interaction is complex but stresses that cormorant predation must be considered as a source of fish mortality in ecosystem-based management approaches and environmental monitoring, as cormorant predation affect certain fish species.

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### AUTHOR CONTRIBUTION

MO and EP conceived the ideas, designed the methodology, and analyzed the data. MO led the writing of the manuscript. All authors

contributed to data acquisition and critically evaluating scientific studies, contributed critically to the drafts, and gave final approval for publication.

### DATA AVAILABILITY STATEMENT

All data used in the analysis are available without limitation as supplementary Data S3.

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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