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Species- and origin-specific susceptibility to bird predation among juvenile salmonids

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Abstract

Juvenile salmonids often experience high mortality rates during migration and bird predation is a common source of mortality. Research suggests that hatchery-reared salmonids are more prone to predation than wild salmonids, and that Atlantic salmon (*Salmo salar*) experience lower predation than Sea trout (*Salmo trutta*), yet telemetry studies have displayed equivocal results. Here, using a large data set on passive integrated transponder (PIT) tagged hatchery-reared and wild juveniles of Atlantic salmon and Sea trout (25,769 individuals) we investigate predation probability by piscivorous birds (mainly Great Cormorants *Phalarocorax carbo*) on salmonids originating from River Dalälven in Sweden. Bird colonies and roosting sites were scanned annually (2019–2021), and the temporal dynamics of bird predation on salmonids released in 2017–2021 was assessed. Hatchery-reared trout was clearly most susceptible to cormorant predation (0.31, 90% credibility interval [CRI] = 0.14–0.53), followed by wild trout (0.19, 90% CRI = 0.08–0.37), hatchery-reared salmon (0.13, 90% CRI = 0.07–0.23), and wild salmon (0.08, 90% CRI = 0.04–0.14), in subsequent order. This order in predation probability was consistent across all studied tag- and release-years, suggesting that the opportunistic foraging of cormorants affects the overall survival of juvenile salmonids, but that the inherent predation risk between different salmonid types differs systematically.

KEYWORDS

Atlantic salmon, avian predation, Great Cormorant, *Phalarocorax carbo*, PIT tag, *Salmo salar*, *Salmo trutta*, sea trout

INTRODUCTION

Salmonid populations have declined globally due to several anthropogenic pressures, such as dam building, habitat destruction, pollution, climate change, decreased food availability at sea, and an extensive fishery (Dadswell et al., 2022; Friedland et al., 2009; Limburg & Waldman, 2009). Population declines caused by predation from, for example, birds, are less well-studied (Steinmetz et al., 2003; Strøm et al., 2019). This is a major

shortcoming as some studies suggest that predation may be significant (Ovegård et al., 2021; Thorstad et al., 2012), even to the extent of threatening the viability of some salmonid populations (Jepsen et al., 2010, 2018; Koed et al., 2006). Thus, there is a general need to enhance the knowledge on predation effects on salmonids and if such pressure can cause significant adverse population impact. This is of relevance, not only for predation ecology as such, but also for the management and conservation of salmonid populations (Jonsson & Jonsson, 2011; Thorstad et al., 2012).

Behavioral and foraging patterns among different salmonid species may affect their relative risk of being predated (Hostetter et al., 2015; Jonsson & Jonsson, 2011). For example, as Atlantic salmon (*Salmo salar*) feed preferentially in the pelagic and sea trout (*Salmo trutta*) forage in coastal areas (Jacobson et al., 2020; Jonsson & Jonsson, 2011), and because salmon juveniles migrate faster through rivers and estuaries than sea trout juveniles (Thorstad et al., 2007), it may be expected that salmon should experience a lower predation risk than sea trout when migrating through river systems. However, studies have found that salmon juveniles may experience either higher predation risk than trout juveniles (Dieperink et al., 2002; Koed et al., 2006), predation risk of similar magnitude as trout juveniles (Jepsen et al., 2019), or lower predation risk than trout juveniles (Boström et al., 2009). Thus, whether juvenile salmon or trout are more susceptible to predation needs further exploration.

Another factor that may affect the susceptibility of a juvenile salmonid to predation is whether it is of reared or natural origin. To this end, it is generally believed that hatchery-reared fish are more prone to predation than wild fish due to lower levels of anti-predator behavior in the hatchery-reared fish (Einum & Fleming, 2001; Pedersen et al., 2008; Serrano et al., 2009). However, despite that a strong effect of origin (hatchery compared with wild) on juvenile to adult survival has been found in Baltic sea salmon (Kallio-Nyberg et al., 2006; Saloniemi et al., 2004; Siira et al., 2006), a difference in mortality and predation risk between hatchery-reared and wild fish during the juvenile life stages has generally not been documented for Atlantic salmon (Flávio et al., 2021; Gudjonsson et al., 2005; Hvidsten & Lund, 1988; Hyvärinen et al., 2006; Kennedy & Greek, 1988; Lacroix, 2008; Thorstad et al., 2007). For sea trout, on the other hand, a difference in juvenile survival between hatchery-reared and wild fish has been found, with wild juveniles often having a higher survival and lower predation mortality than hatchery-reared juveniles (Aarestrup et al., 2014; Dieperink et al., 2001; Serrano et al., 2009). Thus, it is unclear whether hatchery-reared or wild salmon juveniles are more at risk of being predated, whereas for sea trout, previous research suggests that hatchery fish are more prone to predation than wild fish.

Birds are potent consumers of fish (Hansson et al., 2018; Harris et al., 2008; Ovegård et al., 2021; Steinmetz et al., 2003; Wiese et al., 2008) and in European waters fish consumption by Great Cormorants, *Phalarocorax carbo*, has received specific attention (Harris et al., 2008; Ovegård, 2017). Great Cormorants consume approximately 400–600 g fish per day (Grémillet et al., 1995; Ridgway, 2010), they feed opportunistically (Ovegård, 2017), and as they form dense colonies they may cause severe mortality events in local fish populations (Koed et al., 2006; Östman et al., 2012; Ovegård et al., 2021). Further, as populations of cormorants have increased all over Europe since the 1980s–1990s and have reached record high population sizes (Bregnballe et al., 2014; Herrmann et al., 2018; Steffens, 2010) they have the potential to regulate the dynamics of many fish populations (Ovegård et al., 2021).

The susceptibility of fish to cormorant predation has mainly been studied using two types of methods (Jepsen et al., 2010). The first type considers dietary analyses of cormorant pellets (e.g., Boström et al., 2012), and the second method is based on tagging fish with different types of electronic or conventional tags and recovering those in cormorant colonies and roosting sites. While the former method gives a good qualitative understanding of cormorant predation ecology (e.g., which fish species are predated), the latter method is also feasible for estimating cormorant predation rates as the recovery (in bird colonies or roosting sites) of tags constitute a direct measure of predation (Jepsen et al., 2010). It should be noted, however, that predation rates derived through tagging should be considered minimum rates as not all tags from predated fish can be recovered. Some tags are deposited outside bird colonies and roosting sites, and the scanning of bird colonies and roosting sites is associated with errors (Hostetter et al., 2015; Osterback et al., 2013). Therefore, the pure recovery of tags in bird colonies and roosting sites represents absolute minimum predation rates. Minimum predation rates have often been estimated using passive integrated transponder (PIT) tags. These tags are relatively cheap, have an almost indefinite life, and can be detected using mobile scanning equipment. Due to these merits, tagging with, and recovery of, PIT tags is a useful method for studying cormorant predation ecology (Jepsen et al., 2010; Källo et al., 2020).

River Dalälven in Sweden is a feasible system for studying bird predation on salmonid juveniles as an extensive stocking program of salmonids, in conjunction with PIT tagging, is conducted in the river. River Dalälven is an important river for salmon and sea trout production and it has historically supported, and is still supporting, a large recreational fishery. However,

decreased post-juvenile survival of salmon in the Baltic region (ICES, 2021) and a concurrent increase in the number of cormorants in Europe (Bregnballe et al., 2014) has raised concerns about the potential impact of cormorants on the salmonid populations in River Dalälven (Boström et al., 2009). The first cormorant colony in the area was established in 1993 (Engström, 2001) and today (in 2017–2021) there are about 2000 nesting pairs within a 18-km distance from the river delta. With such high cormorant density, and given the fact that cormorants tend to alter their feeding behavior according to fish availability (Bugajski et al., 2013; Kennedy & Greek, 1988; Kumada et al., 2013), high predation rates within confined areas, such as the river mouth of River Dalälven are to be expected. Still, a previous study conducted in 2005–2006 suggests that the overall predation pressure on salmonid juveniles from cormorants in River Dalälven is low (Boström et al., 2009), but as the number of breeding cormorants in the area in 2005–2006 was about half of the current population counts (2017–2021), the extent to which cormorants currently consume salmonids in River Dalälven area needs a re-evaluation. Moreover, other bird species beside cormorants may also impose significant predation pressure on salmonids (Boström et al., 2009). One such species is the grey heron (*Ardea cinerea*), which is a common fish-eating bird often observed close to fish release sites in River Dalälven. As herons can consume an extensive amount of juvenile salmonids (Sherker et al., 2021), it is important to evaluate also the impact of grey herons in order to assess the overall impact of bird predation on juvenile salmonids.

Here, using a large data set on PIT tag recoveries in bird colonies and roosting sites, we investigate the temporal dynamics of bird predation on salmon and sea trout juveniles originating from River Dalälven in Sweden. Our objectives are to make the best possible estimates of minimum predation probability and investigate to what extent this predation probability depends on species (salmon or trout) and origin (hatchery-reared or wild) of juvenile salmonids.

METHODS

Study site

River Dalälven, with its outlet in the Baltic Sea, is about 557-km long with an overall catchment area of 28,920 km^2 and a mean annual discharge of 365 m^3/s (SMHI, 2022). Since 1915, the river has been regulated by hydropower and the lowermost hydropower station (~8 km from the river outlet) is located in Älvkarleby. The current study was conducted downstream of this hydropower station (Figure 1). As Älvkarleby hydropower station constitutes a migration barrier, the hydropower company is obligated to compensate for the extensive losses of fish. Stocking at Älvkarleby hydropower station began in 1915 and fry or 1-year-old nonsmoltified juveniles were released in the river annually. In 1955, the stocking program changed and 2-year-old smoltified salmon and trout were released in the river. From 1989, the river has been stocked extensively with approximately 220,000 salmon and 70,000 sea trout hatchery-reared juveniles being released annually. Since the beginning of the 1990s most salmons are released as 1-year-old smolts and their adipose fin have been removed prior to being released to enable visual determination of their origin. In addition, a significant amount of the hatchery-reared salmon and trout smolts were previously tagged with Carlin tags, but since 2017 salmonids have been tagged with PIT tags. As the migration barrier is located only 8 km from the river mouth and there is a general lack of suitable spawning and rearing habitats for salmonids below the station (expect for in a short section of the river stretch known as Kungsådran), natural production of salmon and trout is low (Petersson et al., 1996). Broodstock fishing has been conducted annually within River Dalälven, using a permanent trap located at the first migration barrier in Kungsådran.

Tagging and recovery of PIT tags

Hatchery-reared salmon and trout juveniles were PIT tagged and released in River Dalälven annually in April and May 2017–2021 (Tables 1–3). Wild salmonid juveniles were caught either using electrofishing gear in Kungsådran, which is a part of the river downstream the Älvkarleby hydropower station, or in a fish trap from an enclosed part of Kungsådran where free-ranging adult salmon and trout had been translocated from the free river to spawn. Wild fish were tagged and released from late April to early June 2019–2021. Lengths of individual fish are relatively similar for hatchery-reared and wild fish, but differ between species (Table 1). Hatchery-reared trout are heavier than wild trout (Table 1).

All fish were anesthetized with anesthetics in a bucket of water before tagging, length and mass were measured, and a 12-mm PIT tag (0.6 g) was inserted into the body cavity through an incision of 4–6 mm length. Post tagging, all fish were allowed to fully recover in freshwater before being released back into the river. Two types of PIT tags were used: Biomark (12 × 2 mm) and i-Tag 162 FDX-B (12 × 2 mm) from BTS Scandinavia. Independent trials revealed that the scanning efficiency for the two types of PIT tags is similar. Hatchery-reared fish were tagged approximately one month before they were released in the river and wild caught fish were

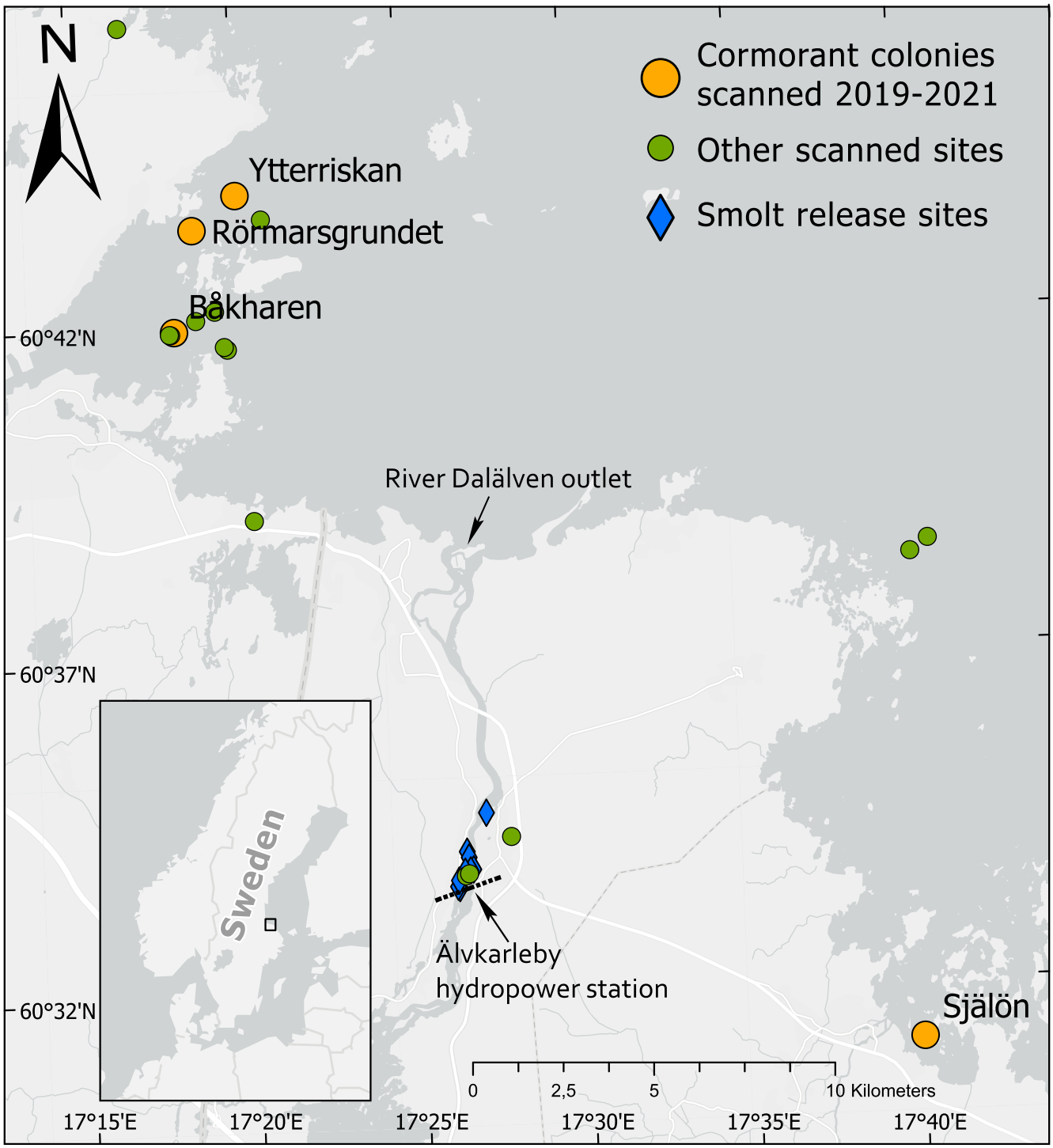

FIGURE 1 Map of River Dalälven and its surrounding area. Symbols refer to salmonid release sites (blue diamond), cormorant colonies scanned annually during the study period 2019–2021 (orange circles), and other bird sites that were also scanned although not annually (green circles).

released after a few hours in captivity. The care and use of experimental animals in this study complied with Swedish animal welfare laws, guidelines, and policies as approved by the Swedish Board of Agriculture (decision ethical permission numbers Dnr 5.8.18-02987/2018 and Dnr 5.8.18-05062/2021).

In total, 15 known cormorant and heron roosting sites and breeding colonies in the surrounding of the outlet of River Dalälven were scanned using a Biomark HPR Plus Handheld PIT tag reader with a BP Plus Portable antenna (Figure 1). Each annual scanning event, except one complementary scanning event

TABLE 1 Length and mass measurements of tagged fish (mean ± SD).

Species	Origin	Length (mm)	Mass (g)	n_{Length}	n_{Mass}
Salmon	Hatchery reared	137 ± 14	27 ± 9	13,421	5948
Salmon	Wild	151 ± 25	28 ± 16	1004	407
Trout	Hatchery reared	214 ± 34	166 ± 38	10,722	60
Trout	Wild	205 ± 41	65 ± 43	622	226

TABLE 2 Total number of passive integrated transponder tags recovered in bird colonies and roosting sites.

			Recovered sites	
Species	Tag year	Tagged	Cormorant	Heron
Salmon	2017	3281	365 (0.11)	186 (0.06)
	2018	2700	134 (0.05)	57 (0.02)
	2019	2805	200 (0.07)	95 (0.03)
	2020	3429	187 (0.05)	125 (0.04)
	2021	2210	81 (0.04)	0 (0)
Trout	2017	1499	547 (0.36)	58 (0.04)
	2018	1500	226 (0.15)	14 (0.01)
	2019	3135	928 (0.30)	73 (0.02)
	2020	3395	909 (0.27)	56 (0.02)
	2021	1815	257 (0.14)	2 (0)

Note: The columns "Recovered cormorant sites" and "Recovered heron sites" show the number (and proportions) of PIT tags recovered in cormorant and heron colonies and roosting sites.

conducted early fall 2022 of colonies not scanned in 2021, was conducted in the fall when migrating cormorants had left the area. Four major cormorant colonies (Själön, Båkharen, Ytterriskan, and Rörmarsgrundet) were scanned annually 2019–2021 (Figure 1). Most PIT tags were recovered in the cormorant colony situated on the Island Själön. This Island can be divided into two main types of areas: one area that is relatively flat with trees and numerous cormorant nests (an area considered relatively easy to scan) and another area with fallen trees and large stones (an area considered relatively difficult to scan). The major heron colony was not scanned in 2021 as it was too dangerous to scan this area due to an extensive number of fallen trees in the colony. All other bird colonies and roosting places were considered relatively easy to scan. Additional data on the number of breeding cormorants, from two coastal bays in the area: Gävlebukten (located west of the outlet of River Dalälven) and Lövstabukten (located east of the outlet of River Dalälven), were acquired from local ornithologists. Breeding cormorants typically migrate to the area in March–April every year and leave in late August–October.

Statistical methods

Overall approach

The proportion of PIT tags recovered in bird colonies or roosting sites out of the total number of tagged individuals constitutes a direct measure of predation, a metric often referred to as minimum predation rate (Hostetter et al., 2015; Källo et al., 2020). This metric was calculated as a measure of predation on salmon and trout, from heron and cormorants, during the period 2017–2021. Because cormorants are the major piscivorous avian predators in the area, and the major heron colony was not scanned in 2021, we made a detailed statistical analysis on cormorant predation only. There are two additional factors beside the actual PIT tag recoveries that should be considered in order to better estimate predation quantitatively. First, the deposition probability, which is the probability that a PIT tag from a predated fish ends up in a scanned area (colony or roosting site). Second, scanning efficiency, which is the probability of detecting a PIT tag when it is there. Assuming that deposition probability, scanning efficiency, and predation probability are independent, the probability of detecting a PIT tag can be calculated from (see Hostetter et al., 2015; Osterback et al., 2013):

$$\theta = \vartheta \times \gamma \times p, \tag{1}$$

where θ is the probability of detecting a PIT tag in a cormorant colony or resting spot, ϑ is the deposition probability, γ is the scanning efficiency, and p is the predation probability. As there is currently no information available on the deposition probability, ϑ, for cormorants in colonies and roosting sites in the River Dalälven area, predation probability, p, was estimated accounting for scanning efficiency only ($0 < \gamma < 1; \vartheta = 1$). The predation probabilities estimated in the current study should hence be considered minimum predation probabilities as a substantial proportion of tags most likely are deposited in other areas besides cormorant colonies and roosting places. All models were fitted in a Bayesian framework and weakly informative priors (Lemoine, 2019) were used for model parameters, except for scanning efficiencies for

TABLE 3 Total number of passive integrated transponder tagged juvenile salmonids and recoveries of these in cormorant colonies and roosting sites.

Salmonid type	Tag year	Tagged	Scanning year		
			2019	2020	2021
Hatchery-reared salmon	2017	3281	240 (0.07)	89 (0.03)	36 (0.01)
	2018	2700	84 (0.03)	31 (0.01)	19 (0.01)
	2019	2712	124 (0.05)	51 (0.02)	20 (0.01)
	2020	2923		111 (0.04)	60 (0.02)
	2021	1805			66 (0.04)
Wild salmon	2019	93	3 (0.03)	2 (0.02)	0 (0)
	2020	506		12 (0.02)	4 (0.01)
	2021	405			15 (0.04)
Hatchery-reared trout	2017	1499	352 (0.23)	129 (0.09)	66 (0.04)
	2018	1500	145 (0.10)	56 (0.04)	25 (0.02)
	2019	3019	577 (0.19)	218 (0.07)	118 (0.04)
	2020	2994		514 (0.17)	327 (0.11)
	2021	1710			248 (0.15)
Wild trout	2019	116	8 (0.07)	4 (0.03)	3 (0.03)
	2020	401		47 (0.12)	21 (0.05)
	2021	105			9 (0.09)

Note: This table shows which year salmonid juveniles were tagged and released, and the year at which the tags were first detected in cormorant colonies and roosting sites. Values refer to numbers and proportions (in parentheses).

which priors based on posterior modes from scanning efficiency trials were used (see next paragraph). The models were implemented in STAN (Stan Development Team, 2023) through the open software CMDSTANR (Gabry & Češnovar, 2022), which makes efficient use of Hamiltonian Markov chain sampling. We let each model burn-in for 1000 iterations, and thereafter extracted 1000 samples per chain for posterior analysis. All models were checked for convergence using the Gelman–Rubin statistics, which compares within and across chain variability (Gelman & Rubin, 1992), and a posterior predictive check was conducted in order to investigate model fit (Appendix S1: Figure S1). Code and data for reproducing the analyses in this study are available in an open repository (Säterberg, 2023).

Scanning efficiency

Scanning efficiency, that is, the probability of detecting a PIT tag known to be there, was estimated by scanning two different areas (hereafter area A and area B) on the cormorant colony Själön, which is located approximately 18 km southeast of the outlet of River Dalälven (Figure 1). Area A is relatively flat without much complexity due to vegetation or stones, making it relatively easy to scan. Area B is an area with large stones and fallen trees, which makes it relatively difficult to scan. Each area (~250 m^2) was scanned independently six times by three persons, that is, twice per person. Data from these scanning trials were used as independent data to estimate scanning efficiencies.

A closed population mark–recapture model, using data augmentation (Kéry & Schaub, 2011), was used to estimate scanning efficiency. The model assumes heterogeneity in scanning efficiency. Hence, in the model, every tag is assumed an individual detection probability, which is drawn from a beta distribution. The reason for this is that the probability of success (the probability of detecting a tag which is there) likely varies due to differences in detection probability depending on where a tag is located on the ground. The model reads:

$$z \sim \text{Bern}(\psi), \tag{2}$$

$$X_i \sim \text{Bin}(n, eff_i \times z), \tag{3}$$

$$eff_i \sim \text{Beta}(\alpha, \beta), \tag{4}$$

where z is a latent variable indicating whether a tag, with probability ψ, is a "true" tag or a simulated nonexisting tag (a large number of nonexistent tags [$n_{\text{augmented}} = 200$]

were added to the data sets prior model fitting (Kéry & Schaub, 2011), X_i is the number of times an individual PIT tag was detected during the n scanning events ($n = 6$), eff_i is the scanning efficiency for PIT tag i, that is, the probability of detecting a tag known to be there, and α and β are shape parameters for the beta distribution.

The scanning efficiency model was fitted to data from each area individually, that is, the model was fitted to data from either area A or area B. Model fitting was conducted using a penalized maximum likelihood approach in order to find the posterior modes of the parameters. Priors and posterior modes for the parameters are given in Appendix S1: Table S1.

Estimating minimum predation probabilities for different salmonid types

Minimum predation probabilities for different salmonid types were estimated assuming that fish are consumed the same year as being released in the river. This assumption was deemed plausible for salmon as they migrate fast through rivers and estuaries as juveniles (Thorstad et al., 2007) and feed in the pelagic when at sea (Jacobson et al., 2020). As most trout remain in the coastal areas when at sea (Jonsson & Jonsson, 2011), and are therefore susceptible to predation during their whole life at sea, until reaching a size refuge, this assumption was corroborated by an analysis showing that trout experience an approximately 2.4-fold (2.39 [2.12, 2.71]; posterior median [5th percentile, 95th percentile]) higher risk of being predated by cormorants the same year as being released in the river, rather than during any of the two thereafter consecutive years at sea (see Appendix S1: Figures S2 and S3, Table S2, and text therein).

Now, assuming that predation only takes place the year of release, and scanning efficiency is equal and independent across years (i.e., for each scanning event), the probability of detecting a PIT tag during a specific scanning event can be described by:

$$\theta_{r_{T,j}}^{d_{t+i-1}} = p_j \gamma_{i,j}, \tag{5}$$

where $\theta_{r_{T,j}}^{d_{t+i-1}}$ is the probability that a fish j, released year T (indexed $r_{T,j}$), is detected in a cormorant colony or roosting site year $t+i-1$ (indexed d_{t+i-1}), t is the first year of scanning and i is the ith scanning event for PIT tag j, p is the minimum predation probability for fish j, and $\gamma_{i,j}$ is the expected PIT tag detection efficiency for a previously undetected tag:

$$\gamma_{i,j} = \left(1 - \mathrm{eff}_j\right)^{i-1} \mathrm{eff}_j, \tag{6}$$

where eff_j is the scanning efficiency, i is the number of scanning events conducted (number of years), and j is the id of the PIT tag (see Appendix S1: Figure S2a for an illustration of $\gamma_{i,j}$).

The probability of detecting a PIT tag during a specific scanning event (year) (Equation 5) was assumed to follow a categorical distribution:

$$\begin{bmatrix} y_{r_{T,j}}^{d_{t+n-1}} \\ \vdots \\ y_{r_{T,j}}^{d_t} \\ y_{r_{T,j}}^{\text{not detected}} \end{bmatrix} \sim \text{Categorical} \begin{bmatrix} \theta_{r_{T,j}}^{d_{t+n-1}} \\ \vdots \\ \theta_{r_{T,j}}^{d_t} \\ 1 - \sum_{i=1}^{n} \theta_{r_{T,j}}^{d_{t+i-1}} \end{bmatrix}, \tag{7}$$

where $y_{r_{T,j}}^{d_{t+i-1}}$ are the observed data, that is, whether a PIT tag from a fish j released year T (index $r_{T,j}$) was recovered (coded as 1), or not recovered (coded as 0), in a cormorant colony or roosting site year $t+i-1$ (index d_{t+i-1}); t corresponds to the first year at which a tag could theoretically have been detected, and n is the total number scans during which a PIT tag theoretically could have been detected during the study period.

Predation probability was modeled as a function of origin (wild or hatchery-reared), species identity (trout or salmon) and release year:

$$\mathrm{logit}(p_j) = \alpha + \alpha_S S_j + \alpha_W W_j + \alpha_Y Y_j + \alpha_{SY} S_j Y_j, \tag{8}$$

where α is the model intercept representing the average predation probability for hatchery-reared salmon, α_S is a linear contrast describing the difference in trout and salmon predation probability, α_W is a linear contrast describing the difference in predation probability between wild and hatchery-reared fish, α_Y is a categorical variable representing the yearly variation in predation risk for juvenile salmonids, and α_{SY} is a linear contrast describing difference in yearly predation probability between trout and salmon. S_j, W_j, and Y_j are all indicator variables, indicating whether fish j is a salmon or trout, whether fish j is wild or hatchery-reared, and whether fish j was released a given year, respectively. Priors for the model are given in Appendix S1: Table S3.

As scanning efficiency affects the estimate of predation probability, p_j, we modeled three different scanning efficiency scenarios using different priors for scanning efficiency, specifically assuming that:

1. All colonies and roosting places are easy to scan (i.e., eff_j is based on area A).
2. All colonies and roosting places are difficult to scan (i.e., eff_j is based on area B).

3. The relative proportion of areas that are easy and difficult to scan, respectively, are based on the observed proportion of PIT tags found in difficult and easily scanned areas (based on a map). This scenario, which could be deemed the most plausible scenarios, assumes a mixture of scanning efficiencies from area A and area B:

$$\mathrm{eff}_j = \varphi \mathrm{eff}_{j,\text{area A}} + (1-\varphi)\mathrm{eff}_{j,\text{area B}}. \tag{9}$$

Differences in predation probability for hatchery-reared salmon, wild salmon, hatchery-reared trout, and wild trout were tested using model predictions (Equation 8):

$$p_{\mathrm{HS}} = \mathrm{logit}^{-1}(\alpha), \tag{10a}$$

$$p_{\mathrm{WS}} = \mathrm{logit}^{-1}(\alpha + \alpha_W), \tag{10b}$$

$$p_{\mathrm{HT}} = \mathrm{logit}^{-1}(\alpha + \alpha_S), \tag{10c}$$

$$p_{\mathrm{WT}} = \mathrm{logit}^{-1}(\alpha + \alpha_W + \alpha_S), \tag{10d}$$

$$p_{\mathrm{HS},Y} = \mathrm{logit}^{-1}(\alpha + \alpha_Y), \tag{10e}$$

$$p_{\mathrm{WS},Y} = \mathrm{logit}^{-1}(\alpha + \alpha_W + \alpha_Y), \tag{10f}$$

$$p_{\mathrm{HT},Y} = \mathrm{logit}^{-1}(\alpha + \alpha_S + \alpha_Y + \alpha_{SY}), \tag{10g}$$

$$p_{\mathrm{WT},Y} = \mathrm{logit}^{-1}(\alpha + \alpha_S + \alpha_W + \alpha_Y + \alpha_{SY}), \tag{10h}$$

where HS, WS, HT, and WT stand for hatchery-reared salmon, wild salmon, hatchery-reared trout, and wild trout, respectively, and index Y indicates year Y.

RESULTS

In total, 4500 PIT tags (~17% of all 25,769 tags) were recovered (detected) in bird colonies and roosting sites during the study period (2019–2021). Fewer PIT tags were recovered in heron (666 tags) compared with cormorant sites (3834), especially for trout (Table 2). The majority of the PIT tags (3830 out of 3834) recovered in cormorant sites were recovered from sites being scanned annually (Figure 1), and most PIT tags were recovered in the eastern colony Själön (93% of the PIT tags). By contrast, the number of breeding pairs of cormorants displayed a less distinct spatial pattern with respect to western and eastern colonies than PIT tag recoveries (Appendix S1: Table S4). For 2017–2021, ~65% of the breeding cormorant pairs in the area were nesting on the Island Själön. The number of PIT tag recoveries varied among years (Table 2) and the highest proportion of recoveries was found for hatchery-reared trout tagged in 2017 (40% of all tags were recovered). In cormorant sites, recovery rates from hatchery-reared trout were highest, followed by wild trout, hatchery-reared salmon, and wild salmon, in subsequent order (Table 3). Moreover, the number of recovered PIT tags from fish released a given year always decreased with the number of years that an area was scanned (Table 3), indicating that predation preferentially occurs the same year as fish is released in the river (see also Appendix S1: Figure S2 and text therein).

Scanning efficiency

As expected scanning efficiency at Själön was higher in area A (a relatively flat area with cormorant nests in high trees) than in area B (an area with fallen trees and large stones) (Figure 2; see Appendix S1: Table S1 for prior and posterior parameter values). The models further suggest that there is a larger variability in scanning efficiency in

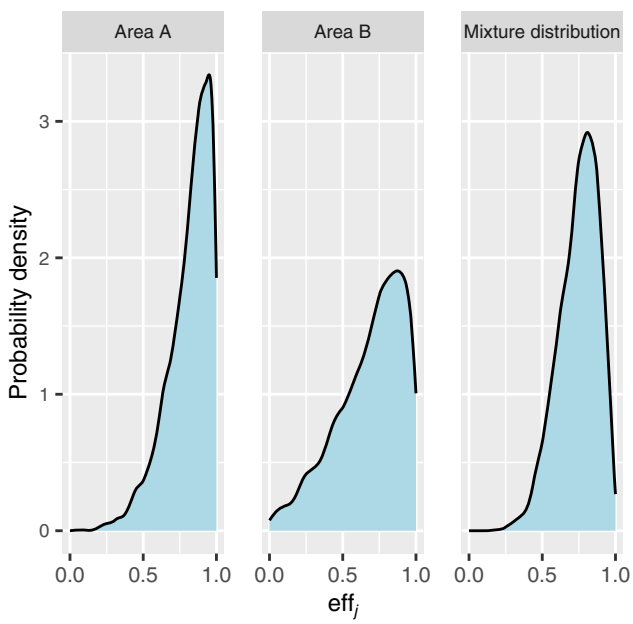

FIGURE 2 Scanning efficiency. This figure shows scanning efficiency for area A ($\mathrm{eff}_j = \mathrm{eff}_{j,\text{area A}}$), an area that was considered relatively easy to scan, area B ($\mathrm{eff}_j = \mathrm{eff}_{j,\text{area B}}$), an area that was considered relatively difficult to scan, and a mixture of the two ($\mathrm{eff}_j = \varphi\mathrm{eff}_{j,\text{area A}} + (1-\varphi)\mathrm{eff}_{j,\text{area B}}$, where $\varphi = 0.48$ [based on the relative proportion of PIT tags recovered in area A and area B, respectively]). These distributions were used as priors for scanning efficiencies in the three different predation risk scenarios that were modeled (scenarios 1–3).

area B as compared with area A (Figure 2). For the case that could be deemed the most plausible, that is, mixture distribution case, scanning efficiency is in between the two cases estimated from area A and area B, respectively (Figure 2).

Difference in predation probability between salmonid types

The best estimate of minimum predation probability illustrates that there has been considerable variation in cormorant predation on juvenile salmonids from River Dalälven during 2017–2021 (Figure 3; see also Appendix S1: Figures S4 and S5 for the low and high scanning efficiency scenarios, respectively). The highest predation occurred in 2017, with an estimated predation risk of hatchery-reared trout of 42% ($p_{HT,2017} = 0.42$, 90% credibility interval [CRI] = 0.42–0.44), and the lowest predation occurred in 2018, with an estimated predation risk of hatchery-reared trout of 17% ($p_{HT,2018} = 0.17$, 90% CRI = 0.15–0.18) (Figure 3). As can be seen in Figure 3, the corresponding predation risk for hatchery-reared salmon was 17% in 2017 ($p_{HS,2017} = 0.17$, 90% CRI = 0.16–0.18) and 7% in 2018 ($p_{HS,2018} = 0.07$, 90% CRI = 0.06–0.08). Further, the model suggests that there is a consistent order in susceptibility to predation among the different juvenile salmonid types (Figure 3, Table 4). Hatchery-reared trout are most susceptible to predation ($p_{HT} = 0.31$, 90% CRI = 0.14–0.53), followed by wild trout ($p_{WT} = 0.19$, 90% CRI = 0.08–0.37), hatchery-reared salmon ($p_{HS} = 0.13$, 90% CRI = 0.07–0.23) and wild salmon ($p_{WS} = 0.08$, 90% CRI = 0.04–0.14), in subsequent order. The predation risk among juvenile salmonid types is statistically clearly discernable (Table 4), except wild trout and hatchery-reared salmon where the model suggests that there is a 17% probability that the predation probability on hatchery-reared salmon is higher than the predation probability on wild trout. Further, the estimates of predation probability are insensitive to the choice of scanning efficiency priors, with only minor differences in predation estimates depending on the scanning efficiency prior used (Appendix S1: Table S5).

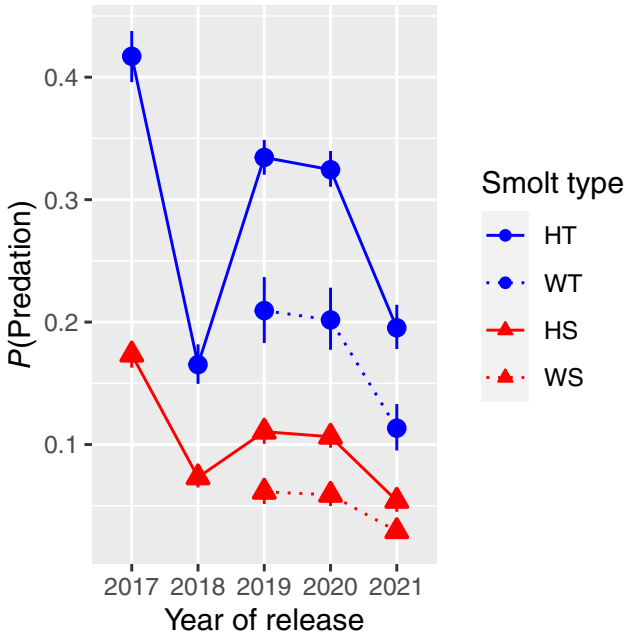

FIGURE 3 Annual variation in cormorant predation probability for different juvenile salmonid types. The different lines correspond to model predictions for: HT, hatchery-reared trout; WT, wild trout; HS, hatchery-reared salmon; and WS, wild salmon. Small symbols (circles, trout; triangles, salmon) represent medians of the posterior distributions and vertical bars illustrate 90% credibility intervals. Solid lines represent hatchery-reared fish and dotted lines represent wild fish. Colors represent trout (blue) and salmon (red), respectively. Model predictions correspond to scenario 3, the mixed distribution case (for the low and high scanning efficiency scenarios see Appendix S1: Figures S4 and S5, respectively).

Model diagnostics

Model diagnostics suggest that all parameters of all models (i.e., scenarios 1–3) had converged during the burn-in phase of the Hamiltonian Markov chain sampling. All parameters had Gelman–Rubin R statistic values smaller than 1.01, indicating that across and

TABLE 4 Difference in cormorant predation risk among juvenile salmonid types.

Salmonid types	Odds (ω) (q5–q95)	$P(\omega > 1)$
P(HT):P(WT)	1.61 (1.37–1.91)	1
P(HT):P(HS)	2.25 (1.36–3.53)	0.995
P(HT):P(WS)	4.00 (2.35–6.49)	1
P(WT):P(HS)	1.41 (0.77–2.34)	0.829
P(WT):(WS)	2.48 (1.4–4.14)	0.995
P(HS):P(WS)	1.77 (1.53–2.07)	1

Note: This table shows estimated odds, ω, comparing how much more (values larger than one) or less likely (values smaller than one) it is that juveniles of different types are predated by cormorants. For example, the odds, ω, presented in the first row of the table (P(HT):P(WT)) suggests that it is 1.61 (90% CRI = 1.36–1.91) times more likely that a hatchery-reared rather than a wild trout is predated by cormorants. The estimated odds, ω, are represented by posterior medians with 90% credibility intervals. The last column, $P(\omega > 1)$, displays the posterior probability that a given juvenile salmonid type is more likely to be predated by cormorants than another type.
Abbreviations: HS, hatchery-reared salmon; HT, hatchery-reared trout; WS, wild salmon; WT, wild trout.

within-chain variance was similar for all parameters. Further, posterior simulations (a posterior predictive check) suggest a plausible model fit, illustrating that there was no severe model-miss specification (Appendix S1: Figure S1).

DISCUSSION

In this study, we investigated the predation probability by piscivorous birds (cormorants and herons) on wild and hatchery-reared juvenile salmonids originating from River Dalälven by analyzing recoveries of PIT tags from tagged fish in bird colonies and roosting sites. As the total predation by heron on juvenile salmonids was much lower than cormorant predation, the statistical analyses were based on PIT tag recoveries from cormorant sites only. The remainder of the discussion is therefore focused on cormorant predation. Still, it should be noted that heron predation might be of importance for salmonid survival and should hence be further investigated.

Overall, we found a clear effect of species identity (trout or salmon) and origin (hatchery-reared or wild fish) on predation probability, an order that was consistent across all studied tag- and release-years. Trout juveniles were clearly more susceptible to predation than juvenile salmon, and hatchery-reared fish was more susceptible to predation than wild fish. Although these results are expected due to differences in behavior and life history between salmon and trout (Jonsson & Jonsson, 2011) and differences in, for example, phenotypic plasticity and natural selection between hatchery-reared and wild fish (Einum & Fleming, 2001), telemetry studies display less clear results. In fact, equivocal results with regard to differences in migration mortality and predation risk between trout and salmon juveniles (Boström et al., 2009; Dieperink et al., 2002; Jepsen et al., 2019; Koed et al., 2006), and no difference in mortality between hatchery-reared and wild salmon juveniles (Flávio et al., 2021; Gudjonsson et al., 2005; Hvidsten & Lund, 1988; Hyvärinen et al., 2006; Kennedy & Greek, 1988; Lacroix, 2008; Thorstad et al., 2007), have been found. Thus, no consensus concerning differences in predation risk between different salmonid types (hatchery-reared and wild, salmon, and trout, respectively) has so far been reached. In this regard, the current study contributes to an enhance understanding as it clearly proposes an order in predation probability between different salmonid types, an order that was consistent across the whole study period.

It has been found that mortality rates during migration depend on the size of migrating individuals, with large juvenile salmonids often being less prone to predation than small juveniles (Dieperink et al., 2002; Källo et al., 2020; but see Jepsen et al., 2018). As hatchery-reared salmon juveniles are often larger than their wild conspecifics this has led researchers to suggest that the nonsignificant difference often observed in mortality rate between hatchery-reared and wild salmon, may have been caused by a size effect (Thorstad et al., 2012). Hence, if wild and hatchery-reared salmon juveniles were of similar size, rather than hatchery fish being larger than wild fish (as often been the case when these juvenile salmonid types have been compared), higher mortality rates on hatchery-reared than wild fish would be found. In the current study, it was no difference in length and mass between hatchery-reared and wild salmon juveniles (Table 1), strengthening the result that hatchery-reared juvenile salmon are more susceptible to cormorant predation than wild juvenile salmon. In addition, released hatchery-reared and wild trout juveniles were of similar length (Table 1), but hatchery-reared trout was clearly heavier than wild trout (Table 1), inferring a higher body condition of hatchery-reared than wild juveniles. Such a difference in body condition between hatchery-reared and wild trout has been suggested as a major cause behind the lower survival rate observed in hatchery-reared than wild juveniles (Serrano et al., 2009). The higher body condition of hatchery-reared trout than wild trout tends to increase their residence time in the river (Serrano et al., 2009) and makes them migrate slower (Pedersen et al., 2008). Hence, hatchery-reared trout are exposed to predation during a longer time window than their wild conspecific. Our results are in line with this assertion as it suggests that hatchery-reared fish are more susceptible to cormorant predation than wild fish.

The current study indicates that the predation pressure by cormorants on salmonid juveniles in River Dalälven has increased substantially since 2005–2006 when a previous bird predation study was conducted (Boström et al., 2009). In fact, predation estimates suggest that cormorant predation mortality on hatchery-reared sea trout has increased more than 10-fold since 2005–2006 (31% in 2017–2021 vs. 2.3% in 2005–2006). As the number of breeding cormorants in the area only doubled since 2005 (~1000 breeding cormorants in 2005–2006 vs. ~2000 breeding cormorants in 2017–2021) the increased impact by cormorants on sea trout in the area, is likely not solely caused by the increasing bird population per se. The spatial mismatch between the number of breeding cormorants and the number of PIT tags recovered, and a preliminary analysis showing no association between the annual number of breeding cormorants and annual predation mortality across the study period (Appendix S1: Figure S6) further corroborates this assertion. Thus, this suggests that other factor besides cormorant density alone have contributed to the observed

difference in salmonid predation risk between the two studies. To this end, two factors may specifically have contributed to the observed difference. First, different tags and a different tag recovery technique were used in Boström et al. (2009) compared with the current study. Second, as the availability of alternative prey for cormorants has been shown to affect predation risk for juvenile salmonids (Good et al., 2022), differences in availability of alternative prey between the two time periods may have contributed to the difference. For example, in 2005–2006 it was generally more herring (a common prey in the diet of cormorants; Boström et al., 2012; Östman et al., 2013) in the area than in 2017–2021 (Olin et al., 2022). As herring assemble in coastal areas for spawning during the same time of the year as salmonids migrate to the sea (late spring–early summer), cormorants may have assembled to forage in areas with large schools of herring to a larger extent in 2005–2006 than during the most recent years (2017–2021). The decreased densities of herring may thus have led to a spatial redistribution in cormorant foraging. Such a change in foraging, from coastal to more inland waters, has also been discussed as a potential driver of high cormorant predation rates observed in Danish inland waters (Jepsen et al., 2018). Yet, whether the predation risk of juvenile salmonids in River Dalälven has increased due to decreases in other local fish populations needs further exploration.

Here, we accounted for scanning efficiency when estimating cormorant predation probability. In this regard, we are confident that the minimum predation probabilities presented are robust estimates as they are insensitive to the specific scanning efficiency priors being used. The reason for this is that the cumulative scanning efficiency increases with the number of scanning events, inferring that the cumulative number of tags detected increases with the number of scanning events. Thus, if an area was scanned an infinite number of times all tags would be found and the specific assumption regarding scanning efficiency would, at least theoretically, not matter. Therefore, the largest uncertainty in our estimates of predation probability is caused by the fact that it is unknown how likely it is that a tag from a fish being eaten, ends up in a bird colony or roosting site, rather than somewhere else in the surrounding. Previous studies indicate that this bird deposition probability can be substantial (Hostetter et al., 2015; Osterback et al., 2013). Hostetter et al. (2015), for example, showed in a study conducted in the Columbia River basin that the deposition probability clearly differed between double-crested cormorants *Phalacrocorax auritus* 0.50 (95% CRI 0.34–0.70), Caspian terns *Hydroprogne caspia* 0.71 (95% CRI 0.51–0.89), and California gulls *Larus californicus* 0.15 (95% CRI 0.11–0.21). Further, Hostetter et al. (2015) found a low variability in deposition probability between years and trials, suggesting that the deposition probability is mainly determined by bird species identity. However, deposition probabilities are likely site-specific, and a site and bird species-specific estimate of tag deposition probability is needed in order to estimate predation probability quantitatively. Unfortunately, a tag deposition estimate for cormorants in the River Dalälven area is currently not available. It would therefore be useful if future studies could derive an estimate of tag deposition probability for the River Dalälven area. A straightforward approach would be to feed cormorants with PIT-tagged fish, and determine the proportion of the PIT tags recovered in colonies and roosting sites (Hostetter et al., 2015; Osterback et al., 2013). When such an experiment has been conducted a quantitative measure of predation probability, rather than a minimum predation probability, can be derived.

In the current study, we found relatively high predation levels (up to 40% annual predation probability on released hatchery-reared trout) by birds on migrating juvenile salmonids in a Swedish river. As similar bird predation levels have been documented in other systems (e.g., Jepsen et al., 2019; Källo et al., 2020), this suggests that birds have the potential to regulate salmonid populations. However, it should be noted that high predation rates on salmonids have been documented also for other piscivorous predators, such as seals and predatory fish (Carter et al., 2001; Hvidsten & Lund, 1988; Sepulveda et al., 2013; Thorstad et al., 2012). Further, if bird consumption was reduced (e.g., through hunting), other predators may fill their ecological nice and consume the migrating salmonids that would otherwise have been lost to bird predation (e.g., Wiese et al., 2008). Hence, although it is clear that cormorants currently have a significant direct impact on salmonid juveniles via predation (at least so for hatchery-reared trout) in River Dalälven, whether bird predation constitutes a compensatory or additive source of mortality remains to be rigorously explored (Haeseker et al., 2020; Payton et al., 2020).

AUTHOR CONTRIBUTIONS

Ann-Britt Florin, Jörgen Rask, and Maria Ovegård initiated and designed the study. Jörgen Rask collected the data. Torbjörn Säterberg analyzed the data and conceived the analysis methodology. Philip Jacobson created the maps. Philip Jacobson and Niels Jepsen gave input on model setups and analysis methodology. All authors took part in interpreting the results. Torbjörn Säterberg wrote the initial draft. All authors contributed to revising the manuscript and approved the final draft.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Novel code and data (Säterberg, 2023) are available from Zenodo: https://doi.org/10.5281/zenodo.7549782.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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