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ORIGINAL ARTICLE

Great cormorant (*Phalacrocorax carbo sinensis*) predation on adult anadromous brown trout (*Salmo trutta*)

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Abstract

The increase in abundance of great cormorants (*Phalacrocorax carbo sinensis*) over the last decades has caused concern for the sustainability of fish populations. Cormorants are opportunistic piscivorous birds that eat fish from a wide range of species and sizes, in marine, lacustrine and riverine habitats. It has been documented that juvenile salmonids are under significant predation pressure by great cormorants, although knowledge on the predation of adult salmonids by cormorants is limited. In this study, adult anadromous brown trout (*Salmo trutta*) were tagged over multiple years with PIT tags during their spawning migration in a Danish lowland river. Two nearby cormorant colonies were subsequently scanned for PIT tags to estimate predation rate. It was estimated that by minimum 15.4% of tagged adult sea trout were predated by cormorants. The majority of the individuals were predated in the river, and females were more likely to be predated than males. Moreover, length had a significant effect on predation probability: individuals between 35 and 43 cm had the highest likelihood to be predated, while smaller and larger individuals were less likely to be predated. Our findings challenge the assumption that cormorants do not prey on reproductively mature salmonids. Furthermore, predation of mature individuals may have implications for the recruitment and sustainability of the population.

KEYWORDS

Passive Integrated Transponder (PIT) telemetry, predator-prey dynamics, *Salmo trutta*, spawning, species interactions

1 | INTRODUCTION

Salmonids undergo migrations between habitats to increase evolutionary fitness (Chapman et al., 2012; Klemetsen et al., 2003). However, migration between habitats also encompasses a level of risk, as increased mortality is often associated with such movements (Ferguson et al., 2019; Thorstad et al., 2016). Therefore, determining the causes of mortality and the factors that influence survival is essential for understanding population dynamics and assessing recruitment adequately (Armstrong, 2005; Fromentin & Powers, 2005).

Predation has been found to be one of the key causes of mortality (Strøm et al., 2019; Thorstad et al., 2016), especially in transition areas, where individuals may be more vulnerable to predation due to physiological constraints caused by changes in habitat conditions (Handeland et al., 1996; Klemetsen et al., 2003).

In recent decades, great cormorants (*Phalacrocorax carbo sinensis*, herein referred to as cormorants), which are opportunistic piscivorous birds, have increased significantly in abundance in different geographical areas, causing concern for many fish populations (Jepsen & Olesen, 2013; Vetemaa et al., 2010). Cormorants eat fish from a

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wide range of species and sizes (Östman et al., 2013), as well as in various environments, including marine, lacustrine and riverine habitats (Heikinheimo et al., 2015; Jepsen et al., 2018; Skov et al., 2014). Even though there are documentation of cormorants eating large amount of fish (Boström et al., 2012; Jepsen et al., 2019) and having negative implications to fish populations (Ovegård et al., 2021), the consequences of cormorant predation on fish populations in general are difficult to assess. This mainly stems from a lack of knowledge about the state of the population prior to the establishment of cormorant colonies in the area, which is further complicated by intricate ecosystem processes and life-history characteristics of the prey species. Within this context, further documentation about the possible impacts of cormorant predation on fish populations, including estimates on the rate of predation and the factors that may contribute to predation probability, is required.

Anadromous brown trout, also referred to as sea trout, hatch in freshwater and after some years in the river juveniles go through a metamorphosis, known as smoltification, and migrate to the sea, where growth opportunities are greater (Klemetsen et al., 2003). Although anadromy offers great benefits for growth and fecundity, it is also associated with costs, such as increased risks of mortality, resulting in a major life-history trade-off (Stearns, 1989). One major driver for the increased risk of mortality in anadromous fishes is predation, which can be relatively high in certain regions (Källo et al., 2020; Thorstad et al., 2016). During the migration between freshwater and the sea, the lower stretches of rivers as well as estuaries have been identified as predation bottlenecks for salmonids (Aarestrup et al., 2014; Flávio et al., 2020; Koed et al., 2006), which may include predation by predatory fish, mammals and piscivorous birds, including cormorants (Jepsen et al., 2006, 2018; Middlemas et al., 2009). Predation by great cormorants on salmonids has mainly been documented on juveniles, and appears to vary significantly depending on location (Jepsen et al., 2019).

The causes of mortality among adult sea trout have received less attention than the juvenile life stage, although the transition between freshwater and the sea appears to pose a similar bottleneck for adult migration as it does for juvenile out-migration with increased mortality documented to occur during river exit and the early marine migration (Aarestrup et al., 2015; Kristensen, Righton, et al., 2019). Often, a clear source of mortality cannot be determined, albeit predation and physiological constraints have been proposed to be the main causes for mortality for adult sea trout leaving the river postspawning (Birnie-Gauvin, Bordeleau, et al., 2021; Birnie-Gauvin, Koed, et al., 2021; Kristensen, Birnie-Gauvin, et al., 2019). To our knowledge, predation of adult sea trout by cormorants has not been quantified before, which consequently means that the extent to which they may be affected by cormorant predation is unknown. Moreover, there is often an assumption that cormorants do not prey heavily on larger adult salmonids due to gape-size limitations (Östman et al., 2013). To assess this, we aimed to estimate the predation rate of adult sea trout by cormorants, as well as the factors that may affect predation susceptibility, by PIT-tagging

returning adult sea trout during their spawning migration in river Villestrup, Denmark. Predation rate was estimated based on the number of tags that were subsequently recovered from two nearby cormorant colonies.

2 | METHODS

2.1 | Study area and tagging

River Villestrup is approximately 20km long, has an annual average discharge of 1.1 m³/s and flows into Mariager Fjord, which further exits to the Kattegat (Figure 1). The river holds the largest spawning population of sea trout in the proximate area. In years 2016–2020, 2443 adult sea trout were caught during the spawning season in the river Villestrup via electrofishing in October–November to be tagged with 23-mm PIT tags (Texas Instruments, RI-TRP-RRHP, half duplex, 134kHz, length 23.1 mm, diameter 3.85mm and weight 0.6 g in air) (Table 1). Upon capture the fish were transferred to a bin of fresh oxygenated water, and immediately measured, sexed (via visual assessment) and tagged by inserting the PIT tag in the back, just below the dorsal fin. Tagged fish were left to recover in the bin with fresh oxygenated water prior to release.

A double-antenna PIT station (to determine direction of movement) was mounted at the outlet of the river to infer location of the tagged fish at the time of the predation event (river vs. the sea). All sea trout were tagged and released upstream of the PIT-antenna, meaning predated sea trout were assumed to be eaten in the river if they were not detected out-migrating, or if they had returned to the river following a period at sea. The last download of the data from the PIT station was conducted on November 30, 2021. The effect of tagging and handling has been shown to have minimum effects on the survival and predation of salmonids (Acolas et al., 2007; Jepsen et al., 2008). The protocols used in this study were approved by the Danish Experimental Animal Committee (2017-15-0201-01164).

2.2 | Cormorant predation

Cormorants are opportunistic feeders that predate on fish in a variety of environments and from different taxa. During predation events cormorants can dive down to 30+ metres, while also having the ability to forage effectively in shallower waters (Grémillet & Wilson, 1999). Once a cormorant catches and eats a PIT-tagged trout, the tag from the predated fish will subsequently be expelled/regurgitated in a pellet, consisting of all indigestible parts of the fish. These pellets are deposited in the proximity of the resting and breeding colonies of cormorants, which provide an opportunity to subsequently try to recover the PIT tags by scanning the colonies.

There is a cormorant resting colony called Villestrup and a breeding colony called Kielstrup in Mariager Fjord. Birds from these two sites are considered to be the main sources of cormorant predation

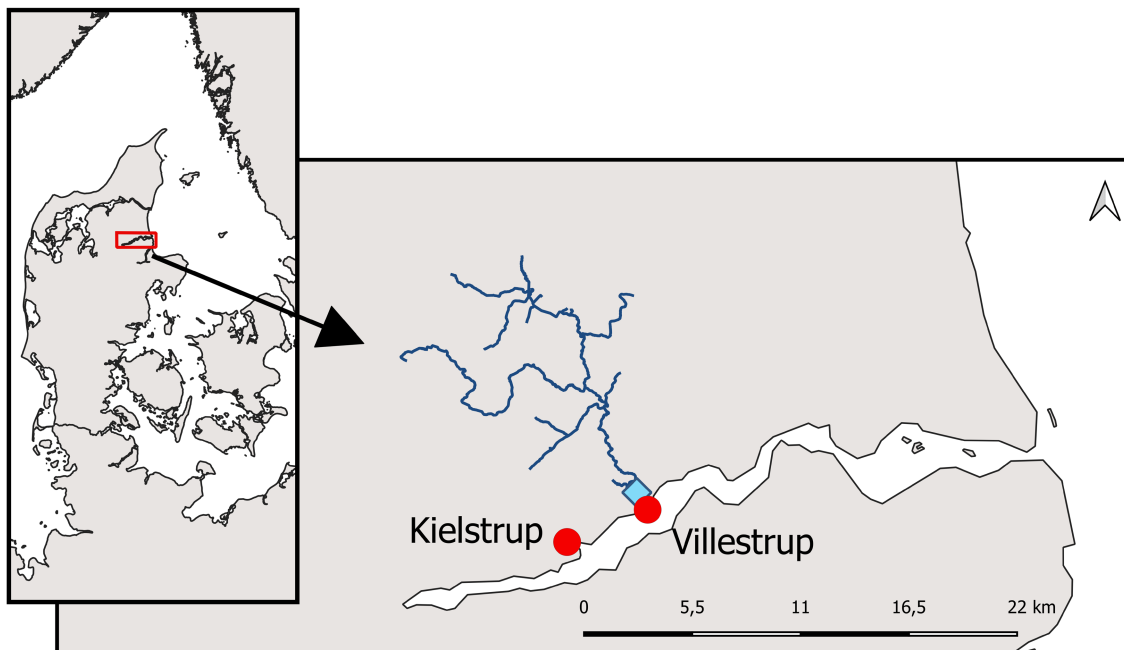


FIGURE 1 Adult sea trout were tagged with PIT tags during the spawning season in the river Vilestrup in 2016–2020. To estimate the rate of predation by cormorants, two nearby cormorant colonies, Kielstrup and Vilestrup (red spots), were scanned for PIT tags. There was a PIT station (blue diamond) mounted at the outlet of the river to determine the location (river vs. the sea) of the individuals during predation.

for sea trout in river Vilestrup (Källo et al., 2020). The Vilestrup resting colony is situated approximately 700 metres from the river mouth, while the Kielstrup breeding colony is situated near Kielstrup lake, approximately 4.3 km from the river. In the Kielstrup colony between 193 and 350 nests have been counted over the study period (Sterup & Bregnballe, 2019). Both colonies were scanned twice since 2017, with a portable scanner (Skov et al., 2014), with the last scanning taking place in March 2022.

2.3 | Data handling and analyses

To estimate predation rate, raw tag counts were corrected with site-specific scanning efficiencies, by calculating the percentage of tags that were detected in the colony during the second scanning that were also present during the first scanning. Scanning efficiencies in the Kielstrup and Vilestrup colonies were 69% and 80% respectively (Källo et al., 2020). To further explore the factors that may affect predation susceptibility, the effect of length (L_T) and sex on individual probability of predation by cormorants (P) were explored using a Bernoulli distributed (predated vs. non-predated) generalised additive model (GAM), with logit link function (Wood, 2011). The initial model included the main effects and interaction of the aforementioned variables, although the interaction was excluded from the final model after parsimonious model selection using Akaike information criterion (AIC) (Table 2; Zuur et al., 2009). To allow for potential non-linear patterns, the effect of length was modelled using a smoothing function $f(L_T)$, which was independent of sex. The final model fitted to the data was the following:

$$P_i \sim \text{Bern}(\pi_i).$$

$$\text{Logit}(\pi_i) = \text{Sex}_i + f(L_{Ti}).$$

Data were analysed using R (v. 4.0.5) (R Core Team, 2021).

3 | RESULTS

Tagged sea trout ranged in length between 25 and 87 cm (Figure 2). Of the 2443 tagged fish, 299 unique tags were detected in the two nearby cormorant colonies (283 and 16 from Vilestrup and Kielstrup respectively) situated in Mariager fjord. When correcting raw tag count with scanning efficiencies, the total number of individuals estimated to have been predated was 377, representing 15.4% of all the tagged individuals. The length of the predated individuals ranged between 29 and 53 cm (Table 3). When only accounting for the individuals in the size range available for cormorants (max 53 cm, $n = 1995$), predation rate was estimated to be 18.9%.

Females were more likely to be predated than males (GAM, Sex; $p < .001$; Figure 3), with estimated predation rates of 18% and 9% respectively (Table 1). Length at tagging had a significant effect on individual likelihood of predation (GAM, length; $p < .001$), with the highest predation probability for individuals between 35 and 43 cm (Figure 3). Predation probability decreases relatively fast for individuals larger and smaller than that range.

All the individuals included in this study were tagged in the river Vilestrup upstream of the double-antenna PIT station that is mounted at the outlet of the river. As such, we can assess if these

TABLE 1 Total number of tagged adult sea trout, number of tags recovered and minimum estimated predation rates in total and grouped by year of tagging and sex.

Year	Tagging period	No. of individuals tagged	No. of tags recovered from colonies			Minimum estimated predation rate			Length (cm)
			Male ^a	Female ^a	Total ^a	Male ^b	Female ^b	Total ^a	
2016	29.11–1.12	868	223 (25.7%)	645 (74.3%)	131 (15.1%)	27 (12.1%)	104 (16.1%)	167 (19.2%)	47 ± 9
2017	28.11–30.11	65	15 (23.1%)	50 (76.9%)	0	0	0	0	58 ± 8
2018	26.11–30.11	793	217 (27.4%)	576 (72.6%)	113 (14.2%)	11 (5.1%)	102 (17.7%)	141 (17.8%)	46 ± 9
2019	28.10–1.11	245	55 (25.6%)	160 (74.4%)	15 (7.0%)	2 (3.6%)	13 (8.1%)	19 (8.8%)	48 ± 9
2020	26.10–30.10	502	148 (29.5%)	354 (70.5%)	40 (8.0%)	5 (3.4%)	35 (9.9%)	50 (10.0%)	47 ± 5
Total		2443	658 (26.9%)	1785 (73.1%)	299 (12.1%)	45 (6.8%)	254 (14.2%)	377 (15.4%)	47 ± 9

Note: Also shown is the mean length (cm) ± SD across all years and grouped by the year of tagging.

^aPercentages are calculated based on the total number of individuals tagged in a given year.

^bPercentages are calculated based on the total number of individuals tagged in a given year and sex.

TABLE 2 Models included in the model selection process, during which the most parsimonious model was selected based on AIC values.

Model	df	AIC	ΔAIC
Predation likelihood ~ Sex+ Length × Sex ^a	7.9	1512.2	2.1
Predation likelihood ~ Length + Sex	5.3	1510.1	0.0
Predation likelihood ~ Sex	2.0	1792.8	282.7
Predation likelihood ~ Length	4.3	1523.2	13.1
Predation likelihood ~ Intercept	1.0	1817.9	307.8

Note: The most parsimonious model is highlighted in bold.

^aModel included separate smoothing functions $f(L_T)$ dependent on sex.

individuals were likely predated prior to (in freshwater) or after migrating out of the river (at sea) by following their migration between the river and the sea. The majority of predated sea trout (65%) were either not detected out-migrating, or were detected returning to river Villestrup prior to the time of predation, suggesting that predation by cormorants largely occurs in the river (Chi sq.; $\chi^2 = 17.2$, $df = 1$; $p < .001$).

4 | DISCUSSION

Bottlenecks to survival and the underlying factors that determine why some individuals die in such bottlenecks during different life stages are not fully understood. They are, however, necessary to identify in order to understand population dynamics and ensure long-term sustainability. This is a complicated task, however, a significant amount of information on bottlenecks of mortality have been produced through the use of telemetry for migratory species. In the present study, PIT telemetry was used to investigate predation rate of adult sea trout by cormorants, which to our knowledge has not been quantitatively estimated previously. It was found that predation of adult sea trout by cormorants can be high, particularly in freshwater, possibly during the spawning season.

We estimated that 15.4% of adult sea trout tagged in river Villestrup were predated by cormorants, with the estimated predation rate being even higher (18.9%) when only accounting for individuals within the size range vulnerable to cormorant predation. These proportions represent minimum predation estimates, as not all tags in the colonies may have been detected due to “tag collision” (inability to detect tags due to their adjacent position), deposition of tags in areas that were difficult or impossible to scan, or excretion of tags by cormorants outside of these two colonies (Bugajski et al., 2012; Källö et al., 2020). For example, Hostetter et al. (2015) documented among PIT-tagged steelhead (*Onchorhynchus mykiss*) predated by double crested cormorants (*Phalacrocorax auritus*) in the Columbia River basin (USA), that approximately only half of the tags were deposited in the cormorant colony. Knowledge about tag deposition probability is not available for this system nor the species included in this study, so no such estimate could be added to the predation rates calculated in this study.

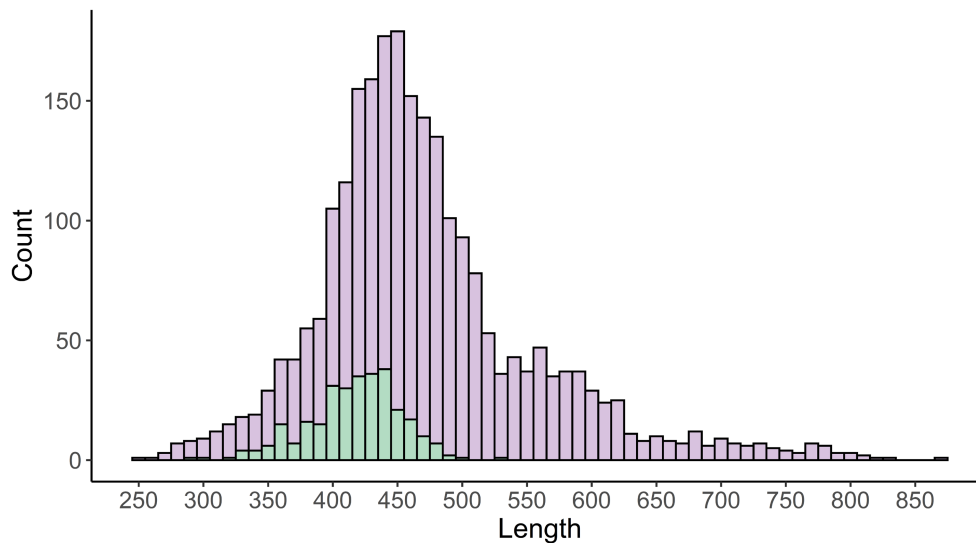


FIGURE 2 Frequency distribution of tagged sea trout lengths that were predated (green) or not (purple).

TABLE 3 Average length (cm) \pm SD (min–max) of tagged sea trout, among all individuals and grouped by sex, that were predated by cormorants or not.

	Length \pm SD (min–max) (cm)		
	All	Male	Female
Not predated	48 \pm 9 (25–87)	47 \pm 8 (25–82)	48 \pm 9 (27–87)
Predated	42 \pm 4 (29–53)	41 \pm 4 (30–49)	42 \pm 4 (29–53)

Our findings indicate that predation mostly occurs in the river, as 65% of the predated individuals had not been detected (by the double-antenna PIT station) migrating out of the river prior to predation. Although the exact timing of predation events could not be determined, they must have taken place between October and November, when the individuals were tagged, and late spring, by which time postspawned individuals (kelts) are expected to migrate back to sea (Kristensen, Birnie-Gauvin, et al., 2019; Kristensen, Righton, et al., 2019). For sea trout from river Villestrup, most individuals appear to leave shortly after spawning, in December and January (Birnie-Gauvin, Bordeleau, et al., 2021; Birnie-Gauvin, Koed, et al., 2021), suggesting that most individuals were likely predated during a narrow window of time, which to a large extent overlaps with the spawning season. This indicates, that cormorants target adult sea trout during a vulnerable time, when fish are energetically depleted (Berg et al., 1998; Birnie-Gauvin et al., 2023), and may have a reduced ability to avoid predators (Svendsen et al., 2004). Within the scope of this study, it was not possible to determine when or where predation occurred for the remaining 35% of predated individuals that had migrated out of the river. However, increased mortality of kelts has commonly been documented to occur early in the marine phase (Aarestrup et al., 2015; Kristensen, Righton, et al., 2019; Thorstad et al., 2016), so at least some of the sea trout tagged in this study were likely predated shortly after migrating back to sea.

We found that female sea trout were more likely to be predated than males. Females and males have different reproductive strategies (Berg et al., 1998; Serbezov et al., 2010), which may explain the difference in their predation probabilities. Females invest a lot of energy into egg development and spawning, which is further expressed in high postspawning mortality (Bendall et al., 2005; Berg et al., 1998), meaning severe energy depletion in females may increase their vulnerability to predation. However, as males may also display high energetic expenditures during spawning (Jonsson et al., 1997), additional factors, possibly related to behavioural differences between the sexes, may have an effect as well. Females may be more visible to cormorants than males during spawning as they spend significant amounts of time digging redds, ovipositing and covering, often in the centre of the riverbed (Evans, 1994; Jonsson & Jonsson, 2011). Males may also be conspicuous during aggressive encounters, but are perhaps less constrained in their movements as they do not need to protect the redds in the same way females do, which as a result may decrease their predation probability (Jonsson & Jonsson, 2011).

Predation of females is likely to have more important implications for recruitment and consequently for the sustainability of the population, compared to males, as the number of offspring produced among salmonids is largely limited by the abundance of females, and the number of eggs they produce (Fleming, 1996; Fleming & Einum, 2010). Unfortunately, it is unclear whether predation in the river occurred prior to or subsequent to spawning, which impedes the full assessment of the possible implications of these results. However, in either case there are potential negative implications to the recruitment of the population. Predation of sea trout prior to spawning means these individuals had not contributed to recruitment, either during the spawning season they were tagged in, or at all if they were maiden spawners. Predation after spawning means these individuals were seized from the opportunity to spawn the following season and to potentially significantly increase their lifetime

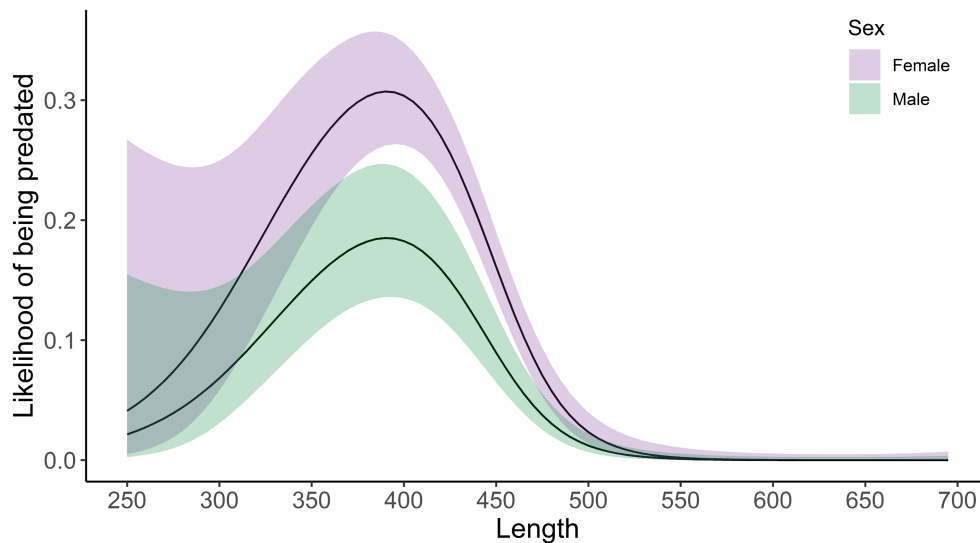


FIGURE 3 Modelled output of the likelihood of tagged adult sea trout to be predated by cormorants as a function of length at tagging. Females and individuals between 35 and 43 cm were more likely to be predated. Different colours represent different sexes.

fitness (Bordeleau et al., 2020). However, as postspawning mortality among iteroparous salmonids is naturally high (Berg et al., 1998; Källo et al., 2022), it cannot be excluded that cormorants targeted individuals that were energetically depleted, so these individuals may have had reduced survival regardless of if they had been predated or not by cormorants.

We found that in addition to sex, length was an important predictor of predation probability, with the highest probability for sea trout between 35 and 43 cm. Predation probability decreases quickly for individuals larger and smaller than this interval. Larger sea trout most likely escape predation due to gape-size limitations, which prevent cormorants from eating larger fish. The largest predated sea trout in this study are close to the upper limit of the size of fish cormorants have previously been documented to eat (Östman et al., 2013).

In contrast, most studies to date have documented cormorants targeting significantly smaller fish than the ones tagged in this study (Fonteneau et al., 2009; Lyach et al., 2018; Magath et al., 2016). Although the present study did not compare predation probability across life stages, a previous study on juvenile sea trout from river Villestrup found that smaller individuals were more likely to be predated (Källo et al., 2020). Consequently, it is unclear why the smallest individuals tagged in this study had relatively low predation rates, although examples of similar dome-shaped predation probabilities have been documented among other species, for example roach (*Rutilus rutilus*) and bream (*Abramis brama*; Skov et al., 2014). The diet of cormorants may, however, differ over the breeding season (Lehikoinen, 2005) and throughout the year, with larger prey being consumed during winter (Čech et al., 2008; Lyach et al., 2018). Changes in fish community and/or cormorant foraging ecology may be the cause behind these patterns (Čech et al., 2008; Lyach et al., 2018). Similar factors may also be involved in this system

and thus explain why smaller juveniles (Källo et al., 2020), but not smaller adults are more likely to be predated. More specifically, in the current study, the majority of predated tags were found in the Villestrup colony, which is a resting place for overwintering birds, while the majority of the tags from predated juvenile sea trout were found in the Kielstrup breeding colony (Källo et al., 2020). These findings suggest that adult sea trout from river Villestrup may be targeted by overwintering birds, and juveniles by breeding cormorants. It is also possible that cormorants would target adults more frequently if they had the opportunity, but given that mature adult sea trout spend relatively short periods in freshwater—and are thus only accessible by cormorants during fall/winter—the birds revert to foraging on the available prey item during other periods of the year, for example juvenile trout or other available fish species.

It remains unclear if the documented cormorant predation has, or will have, long-term implications on the recruitment and population dynamics of sea trout in river Villestrup. To truly assess the ecological consequences of a 15.4% minimum predation rate on reproductively mature fish, long-term data are required on the spawning population, recruitment and predation rate, as well as population estimates of cormorants. In addition, further research is needed to determine whether sea trout were predated prior to or after spawning. However, the finding that females were more likely to be predated elevates the risk of negative consequences on recruitment. In combination with our previous finding that a minimum of 27% of juveniles from this population are predated by cormorants (Källo et al., 2020), these results suggest that this sea trout population is under strong predation pressure by cormorants at different life stages. Although the sea trout population in the river Villestrup is the largest in the area, other smaller populations may be more significantly affected by similar predation rates, particularly if they depend on few successful spawners to persist.

AUTHOR CONTRIBUTIONS

All authors contributed to the conception and design of the study. KK contributed to analysing the data and writing the primary draft of the manuscript. All authors contributed significantly to the interpretations of the results and have given their final approval for the manuscript to be published.

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CONFLICT OF INTEREST

The authors have no conflict of interests to declare.

DATA AVAILABILITY STATEMENT

Data will be available by the authors upon reasonable request.

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