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RESEARCH ARTICLE

Does wetland restoration create an ecological trap for migrating Brown trout smolts?

Lene K. Sortland[1,2], Kim Birnie-Gauvin[1], Robert J. Lennox[3], Hugo Flávio[3], Anders Koed[1], Kim Aarestrup[1]

Restoring wetlands is often used by management to boost ecosystem services like improving downstream water quality, but it may create ecological traps for migrating salmonids by increasing migration time and predation rates, potentially compromising self-sustaining populations. In River Gudenaa, Denmark, the wild Brown trout (*Salmo trutta*) population has declined over the past one to two decades, and it remains unclear whether this decrease is linked to higher mortality due to restored wetlands in the river's lower reaches. This study investigated the progression rates and survival of migrating wild Brown trout smolts through River Gudenaa and Randers Fjord before and after the wetland restoration using acoustic telemetry. In 2020 and 2021, 150 smolts were tagged and released, and their movements and survival were compared with those of 61 smolts tagged and released before the restoration, in 2003 and 2005. Smolt progression rates were significantly slower in the river and fjord after the restoration, with the greatest reduction in the river. Despite slower progression rates, restoration did not impact survival, suggesting the wetlands did not act as an ecological trap for smolts. However, it remains unknown whether the slower migration had carryover effects on sea survival by increasing energy expenditure and delaying sea arrival. The retention of a main river channel, with a directed albeit slower flow, likely kept smolts from venturing into the adjacent wetland lakes, where predation may be higher. By incorporating measures that support migrating fish, wetland restoration can remain a valuable management tool to secure ecosystem services while sustaining fish populations.

Key words: acoustic telemetry, management, migration, river, salmonid, survival

Implications for Practice

- Wetland restoration is a valuable management tool for enhancing ecosystem services, but it must consider *and* address the potential negative impacts on native species that rely heavily on river flow, such as migratory salmonids.
- Maintaining a defined river channel with consistent flow, and only allowing the upper layer of the river to flow into wetlands may help to minimize migratory fish entering wetland lakes where predation risks are higher, thereby lowering mortality rates and supporting fish populations while achieving restoration goals.
- Despite no effect on survival, such wetland restoration projects significantly affect the progression rates of smolts, and the consequences of this are not known but could include decreased energy reserves and carryover effects on survival at sea.

Introduction

Wetlands are vital ecosystems that host a variety of animal species (e.g. birds, insects, and fish), while also providing crucial ecosystem services to humans. By trapping sediments, filtering run-off, and providing habitat for nutrient assimilation, wetlands improve downstream water quality and help safeguard aquatic systems from upstream environments (Reddy & Gale 1994; Fisher & Acreman 2004; Ury et al. 2023). Moreover, wetlands play a key role in flood regulation by storing and gradually releasing water (Acreman & Holden 2013; Temmerman et al. 2013; Åhlén et al. 2022). Despite these benefits, extensive drainage for agricultural production has caused the loss of 50% of the world's wetlands since 1900 (Davidson 2014). Concerns about the adverse effects of wetland degradation have sparked a range of restoration and conservation efforts, such as the international Ramsar Convention of 1971 (Zedler & Kercher 2005) and Denmark's freshwater restoration program launched in 1998 (Hoffmann & Baattrup-Pedersen 2007; Graversgaard et al. 2021). In Denmark, wetland restoration projects have

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[1]Section for Freshwater Fisheries and Ecology, Technical University of Denmark, Vejlsøvej 39, 8600, Silkeborg, Denmark
[2]Address correspondence to L. K. Sortland, email lesor@aqua.dtu.dk
[3]Ocean Tracking Network, Dalhousie University, 6375 Edzell Castle Cir, Halifax, Nova Scotia, Canada

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primarily been motivated by the need to reduce nutrient run-off from heavily fertilized agricultural areas into marine environments (VMP I, VMP II, and VMP III plans).

A notable example of wetland restoration includes the lower River Gudenaa on the Jutland Peninsula, Denmark. Historically, the lower reaches of River Gudenaa were landscaped by floodplain wetlands, which were drained in the early 1900s to convert the land into agricultural fields. The drainage process involved building dikes to permanently dry out the wet meadows. From 2007 to 2012, a series of restoration projects were undertaken to revive these wetlands. The restoration efforts included removing dikes along the lower 8 km stretch of River Gudenaa, allowing natural flooding to form shallow lakes. Additionally, shallow channels were excavated through the remaining dikes to connect the river to adjacent wetlands. These channels allowed the river to naturally overflow into surrounding areas during high water levels (Gudenaaengene n.d.). However, the drainage has caused significant subsidence of the soil due to decomposition of peat layers when exposed to oxygen (Silins & Rothwell 1998; Pedersen et al. 2006). Consequently, the restored wetland lakes are deeper than the original floodplain wetlands and can support resident fish populations (e.g. pike and perch). Over time, deposition of organic material will rebuild the peat layers and fill the lakes so they more closely resemble their natural state (Pedersen et al. 2006; Björk 2010; Moreno-Mateos et al. 2012). Restored wetlands can also impact other downstream conditions such as water temperatures and dissolved oxygen contents (Hansen et al. 2016; Liu et al. 2016; Krochta & Chang 2024). Despite these changes, the 678 ha of restored wetlands now support diverse bird and insect species (Randers Kommune n.d.; Maagaard et al. 2008; Kjeldsen 2024).

While wetland restoration enhances biodiversity and ecosystem services (Peh et al. 2014; Mitsch et al. 2015), it can have unintended impacts on native fish species. For instance, the restoration of wetlands and shallow lakes in River Skjern (Denmark) led to increased predation on Atlantic salmon (*Salmo salar*) and Brown trout (*S. trutta*) smolts due to an increase in piscivorous birds (Koed et al. 2006; Pedersen et al. 2007). Studies have shown that migrating smolts can experience higher mortality rates when traversing lakes due to slower progression rates and therefore longer exposure to predators (e.g. Olsson et al. 2001; Schwinn et al. 2017), a risk that may apply to wetlands. The altered hydrological conditions in restored wetlands may mislead and delay migrating smolts, causing them to spend longer time in areas with high predation risk, effectively turning the wetland into an ecological trap (Ohms et al. 2022). The recognition of the potential risks posed by wetlands to migrating fish has prompted revisions in the restoration practices in Denmark. Namely, researchers have advised keeping the main river channel intact, spreading and reducing the water intake from the river, and only extracting water from the surface layer to ensure that fish stay within the main channel during migration (Schwinn 2018).

The wetland restoration projects in the lower River Gudenaa aimed to implement the aforementioned recommendations to protect native salmonid populations. Despite these efforts, the population of wild Brown trout has declined over the last one to two decades, prompting suggestions that the decline could be linked to higher mortality for Brown trout smolts migrating through the constructed wetlands. To investigate whether the restored wetlands act as an ecological trap for smolts, we compared the survival of seaward migrating Brown trout smolts in River Gudenaa before and after the restoration using acoustic telemetry. Wild smolts were captured, tagged, and released upstream from the wetlands in River Gudenaa in 2020 and 2021, and their downstream migration was monitored with acoustic receivers deployed in the river and fjord. The migration and survival of these smolts were then compared with a previous study on wild Brown trout smolts from before the wetland restoration, in 2003 and 2005 (Aarestrup et al. 2014). We hypothesized that (1) progression rates through the restored wetlands would differ following the restoration projects, with progression rates predicted to be slower and migration time longer post-restoration, and (2) the restored wetlands act as an ecological trap by increasing mortality rates, with mortality predicted to be higher post-restoration than before. The findings from this study will provide critical insights for managers on the effectiveness of wetland restoration measures designed to mitigate negative impacts on migrating fish, guiding future efforts to balance wetland restoration with the protection of native fish populations.

Methods

Study Area and Species

River Gudenaa is a lowland river system located in the Jutland peninsula and is the longest river in Denmark (149 km; mean annual discharge of 32 m^3/s; Aarestrup & Jepsen 1998). The river exits into Randers Fjord, which stretches 30 km in length and consists of a narrow inner section (12.2 km stretch; A2–A3 in Fig. 1) and a wider outer section (15.5 km stretch; A3 and A4), before reaching the Kattegat Sea. Randers Fjord is brackish, and salinity ranges from 0 to 30 ppt with increasing salinity toward the Kattegat Sea (Aarestrup & Jepsen 1998). Randers Fjord is a microtidal environment, wherein the height of the tide ranges from 0.2 to 0.3 m and is highest in the narrow inner section (Nielsen et al. 2001; Gazeau et al. 2005). River Lilleaa is the most important tributary to River Gudenaa and drains into River Gudenaa circa 15 km upstream from the river mouth (mean annual discharge of 2.6 m^3/s; Aarestrup et al. 2014). Aerial photos showing the river sections before and after the wetland restoration projects can be found in Figure 2.

Brown trout is a facultative migratory species, meaning individuals can remain as freshwater residents or migrate between the freshwater and marine environment (anadromy) (Birnie-Gauvin et al. 2019; Ferguson et al. 2019). The life history of anadromous Brown trout starts in the freshwater environment, where juveniles hatch from eggs deposited in gravel beds (Klemetsen et al. 2003). After spending 0–3 (or more) years in the river, juvenile Brown trout migrate to the ocean as smolts in search of richer food opportunities that can maximize growth (Gross et al. 1988; Birnie-Gauvin et al. 2019). Prior to their seaward migration, juvenile Brown trout undergo a series of

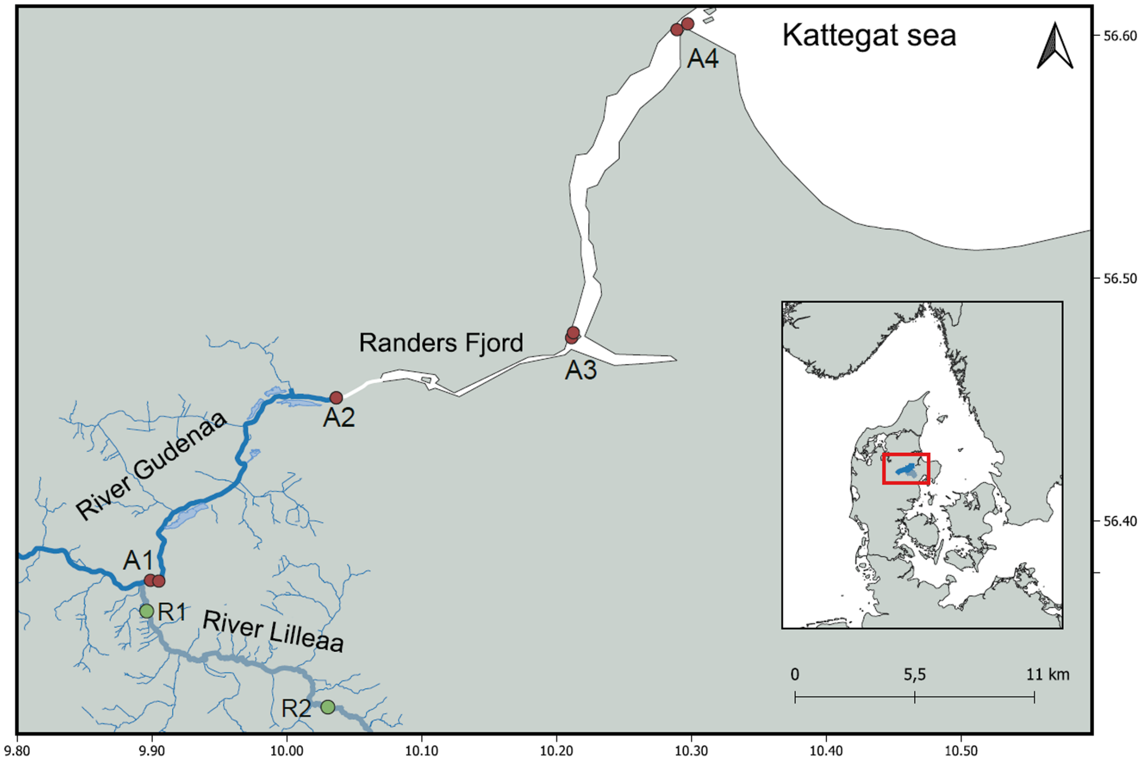

Figure 1. Map shows the River Gudenaa (dark thick blue) and its main tributary, River Lilleaa (light thick blue), which joins River Gudenaa at array A1 (15 km upstream of the river mouth). Red points represent acoustic arrays, and the green points denote release sites in River Lilleaa. The restored wetland lakes are located between array A1 and A2. Smolts were released at R1 in 2003 and 2005, and at R2 in 2020 and 2021. The color blue represents the freshwater part of the system, while white represents the marine part (i.e. after A2). Red box in the inset shows the location of River Gudenaa in Jutland, Denmark.

physiological, morphological, and behavioral changes that prepare them for a life in the marine environment, a process known as "smoltification" (McCormick & Saunders 1987). Once smolts venture into the marine environment, they are termed post-smolts. Some studies have found that post-smolts use tidal currents during their migration through estuaries and fjords, likely to conserve energy (i.e. ebb-tide transport pattern; Moore et al. 1995, 1998; Sortland et al. 2024a). Brown trout usually remain in coastal areas close to their natal rivers during marine residency (Eldøy et al. 2015; Flaten et al. 2016; Atencio et al. 2021), but large variations can occur with some individuals migrating long distances at sea (del Villar-Guerra et al. 2014; Kristensen et al. 2019; Strøm et al. 2021). After spending one or more summers feeding in the marine environment, mature adult Brown trout return to their natal rivers to spawn (Thorstad et al. 2016; Birnie-Gauvin et al. 2019; Ferguson et al. 2019) but straying to non-natal rivers also occurs (Källo 2023).

Capture and Tagging

Before the restoration project, 31 and 30 wild Brown trout smolts were caught in screw traps, tagged, and released in River Lilleaa in 2003 and 2005, respectively (R1 in Fig. 1; Aarestrup et al. 2014). Following the restoration project, 75 wild Brown trout smolts were caught by electrofishing, tagged, and released in River Lilleaa, both in 2020 and 2021 (R2 in Fig. 1). There were significant differences in smolt length (cm) among years (Welch's Analysis of Variance test: $F = 54.9$, degrees of freedom [df] = 3, $p < 2.2e{-16}$), with smolts tagged in 2003 being significantly longer (mean = 20.51, SD = 1.63) than those in 2005 (mean = 16.92, SD = 0.70; Games-Howell post hoc, CI: −4.4 to −2.7, $p < 0.001$), 2020 (mean = 16.70, SD = 1.00; CI: −4.7 to −3.0, $p < 0.001$), and 2021 (mean = 16.50, SD = 1.00; CI: −4.9 to −3.2, $p < 0.001$). There was no difference in smolt length among the other years. Information on biometrics of tagged smolts is shown in Table 1.

Smolts were anesthetized using a benzocaine solution (300 ppm) until the operculum rate became slow and the fish lost equilibrium (circa 3 ± 2 minutes). Once anesthetized, fish were weighed (g) and total length measured (cm). An incision was made lateroventrally, and an acoustic transmitter was placed into the abdominal cavity of the fish. The incision was then sealed using one to two sutures (4–0 Vicryl absorbable sutures). Operation time was approximately 1–2 minutes. After tagging, smolts were transferred to a 60-L plastic container with well-oxygenated water for recovery. Once smolts resumed normal behavior (i.e. regained equilibrium and regular operculum rate, normally within 5–10 minutes), fish were released at the capture site (usually within 60 minutes of tagging). The total

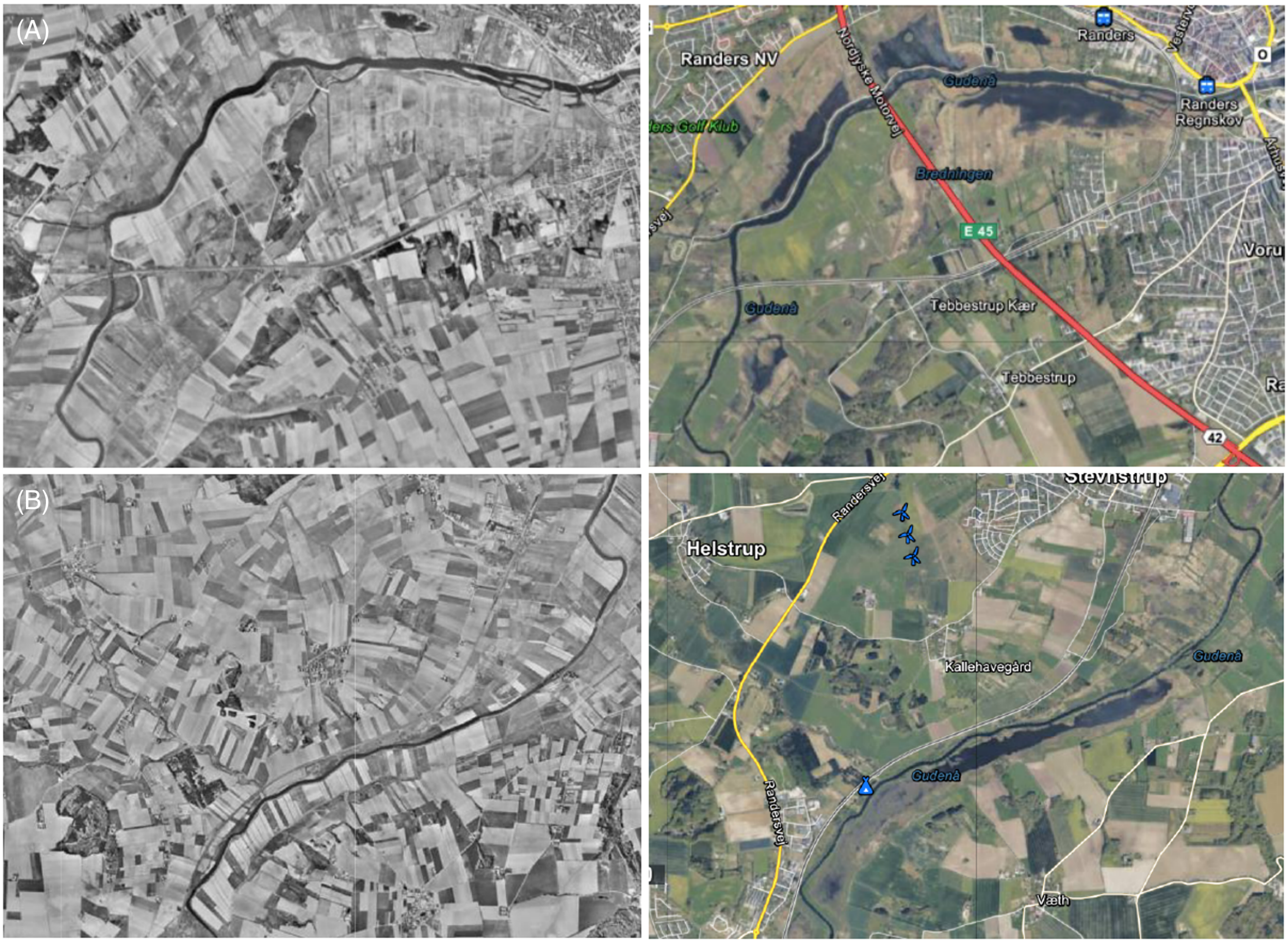

Figure 2. Aerial photos of the River Gudenaa, Denmark, taken in 1954 before the wetland restoration projects (gray) and in 2020 after the restoration projects (colored). Note the wetland lakes adjacent to the river in the colored photos. The top panel (A) shows the river section close to the river mouth (array A2) by Randers City, while the lower panel (B) shows the river section further upstream closer to where the tributary River Lilleaa drains into the River Gudenaa (array A1). Aerial photos were sourced from www.krak.dk.

Table 1. Information on tagged Brown trout smolts before (2003 and 2005) and after (2020 and 2021) the wetland restoration projects. All smolts were captured, tagged, and released in River Lilleaa, a tributary of River Gudenaa. Smolts were captured in screw traps before the restoration projects, while after the restoration, smolts were captured by electrofishing.

Year	*Restoration*	*Capture method*	*Number tagged*	*Release date*	*Total length ± SD (cm)*
2003	Before	Screw trap	31	01.04	20.51 ± 1.63
2005	Before	Screw trap	30	31.03	16.92 ± 0.70
2020	After	Electrofishing	75	23–24.03	16.7 ± 1.0
2021	After	Electrofishing	75	18.03 and 25.03	16.5 ± 1.0

handling time, including sedation, surgery, and recovery, was approximately 7–17 minutes. In 2003 and 2005, all smolts were tagged with acoustic transmitters from VEMCO (Model V7-2L, 7 mm diameter, 20 mm long, weight in air 1.6 g, weight in water 0.75 g, tag life 94 days), whereas in 2020 and 2021 smolts were tagged with acoustic transmitters from Thelma Biotel (Model LP7, 7.3 mm diameter, 17 mm long, weight in air 1.8 g, weight in water 1.10 g, tag life 110 days). The mean tag burden (tag weight [g]/fish weight [g]) was 4% (SD = 0.5%) in 2005, 5% (SD = 0.7%) in 2020, and 5% (SD = 0.8%) in 2021. In 2003, smolt weight was missing for 14 individuals, and the mean tag burden for the remaining 17 smolts was 2% (SD = 0.4%). Sampling and tagging were conducted according to the Danish experimental animal welfare board regulations (2017-15-0201-01164).

Acoustic Receiver Network

In 2003 and 2005, eight acoustic receivers (model VR2, VEMCO) were deployed in the river and fjord to track tagged smolts. The receivers were mounted either on poles driven into the river bottom or on existing infrastructure, such as buoys. Receivers were arranged into four arrays: one in River Gudenaa (A1), one in the estuary by Randers City (A2), one in Randers Fjord (A3), and one at the sea entry to the Kattegat Sea (A4). Each array comprised two receivers positioned one after the other. For more details on the acoustic receiver network in 2003 and 2005, see Aarestrup et al. (2014). In 2020 and 2021, eight acoustic receivers (Thelma Biotel; TBR 700) were deployed in four arrays (A1–A4) corresponding to the same locations as in 2003 and 2005. Note that the array names in this study (A1–A4) differ from previous studies in River Gudenaa (Aarestrup et al. 2014; Sortland et al. 2024b). The river stretch between array A1 and A2 features several restored wetland areas adjacent to the river (Figs. 1 & 2). Although the main river channel still exists, smolts can now enter and exit the wetlands through channels in the dikes (see Fig. S1).

Data Analysis

All statistical models and figures were made using R (R Core Team 2024), within Rstudio (version 2024.4.2.764, Posit Team 2024).

Data Filtering. Raw detection data were processed and checked for potential false detections using the function *migration* in the actel package with skipping arrays set to two and the speed limit between arrays set to 3 m/s (Flávio & Baktoft 2021). In other words, actel issued a warning if a smolt had a speed greater than 3 m/s or if it skipped two or more arrays. The speed limit of 3 m/s was chosen as this permitted the smolt to swim slightly faster than the river current in this system (circa 1 m/s; Aarestrup K. 2025, Technical University of Denmark, personal communication). Moreover, detection plots were manually inspected for atypical migration patterns, such as single detections followed by extended periods of non-detection, or extensive upstream movements—which might suggest the smolt had been ingested by a predatory fish and we were following the predator's movements. Prior to statistical model testing, data were explored using the protocol described in Zuur et al. (2010).

Progression Rates. We calculated the progression rates of smolts migrating through River Gudenaa (A1 and A2, 15.0 km), the narrow part of Randers Fjord (A2 and A3, 12.2 km), and the wide part of Randers Fjord (A3 and A4, 15.5 km) before (2003 and 2005) and after (2020 and 2021) the restoration project. Smolt progression rates were determined by calculating the time between the first detection at the first array and the first detection at the final array, divided by the shortest in-water distance between these two arrays. To determine the shortest distance between arrays, we made a transition matrix using the *transition* function and estimated the shortest path using the *shortestPath* function in the gdistance package (van Etten 2017). Next, the length of each path segment was measured using the *gLength* function in the rgeos package (Bivand & Rundel 2023).

To test whether progression rates through the river and fjord differed after the restoration project, we fit a generalized linear mixed-effects model (GLMM) with a gamma distribution and log link function. The response was progression rate (km/day), and the factors restoration (before and after) and array (A2–A4) were included as fixed effect covariates. Array A2 represents the progression rate in River Gudenaa (A1 to A2), array A3 the narrow part of Randers Fjord (A2 to A3), and A4 the wide part of Randers Fjord (A3 to A4). Because we expected the restoration might have impacted the progression rates in the river but not through the narrow and wide parts of Randers Fjord, we included an interaction between restoration and array ("Restoration: Array"). To account for temporal variation in arrivals at arrays, we included Julian arrival day-of-year at each array as a covariate ("yday") and allowed its effect to vary by array with an interaction term ("yday:Array") (Table 2). Year (2003, 2005, 2020, and 2021) and Fish ID were included as random effects to account for variability across years and multiple observations per individual. Candidate models also included water discharge (L/second) and tidal stage (rising or falling) as potential covariates, as high water discharge and ebb tides can increase progression rates of smolts (Aarestrup et al. 2002; Moore et al. 1998; Persson et al. 2019). Tidal stage was estimated based on water level (m) data recorded at the time of smolt arrival at A4 (www.vandportalen.dk), while water discharge was based on the daily mean water discharge at the time of smolt arrival recorded at a water logger located circa 7.6 km upstream from A1 in River Gudenaa (i.e. upstream from the restored wetlands; www.vandportalen.dk). This upstream water logger was used to assess if discharge trends driven by precipitation influenced progression rates. However, discharge conditions within the restored river section could not be evaluated due to the lack of a water logger in this area.

Model selection based on Akaike's Information Criterion (AIC) showed that water discharge and tidal stage did not improve model fit or explain variation in progression rates and

Table 2. Summary output from model testing the effects of restoration, array, and Julian day-of-year (yday) on progression rates of Brown trout smolts in River Gudenaa and Randers Fjord, Denmark. "Restoration:Array" and "yday:Array" represent interaction terms, while Year and FishID represent the random effects.

Coefficient	df	F	p *Value*
Restoration	1	36.15	4.20e–09
Array	2	13.88	1.50e–06
yday	1	13.94	0.0002
Restoration:Array	2	3.98	0.019
yday:Array	2	21.00	2.17e–09

	edf	*Ref.* df	F	p *Value*
Year	1.30	2.00	3.67	0.062
FishID	60.88	169.0	0.52	0.003

were therefore excluded from the final model. The final model with the lowest AIC had the following equation:

$$\text{Speed}_{ij} \sim \text{Gamma}\left(\text{mu}_{ij}, r\right)$$

$$\log\left(\text{mu}_{ij}\right) = \text{Restoration}_{ij} + \text{Array}_{ij} + \text{yday}_{ij} + \text{Restoration} : \text{Array}_{ij} + \text{yday} : \text{Array}_{ij} + \text{FishID}_i + \text{Year}_j$$

where the response variable speed_{ij} follows a Gamma distribution with mean mu_{ij}, representing the expected progression rate for individual *i* in year *j*, and shape parameter r, which controls the distribution's shape and variability in progression rates. The GLMM was fit using the *gam* function from the mgcv package (Wood 2017). Model assumptions were validated by plotting residuals against fitted values, and against covariates included and not included in the model (Zuur et al. 2010). To assess in which section (River Gudenaa, Narrow Fjord, or Wide Fjord) the progression rates differed after the restoration, we performed post hoc testing using the function *emmeans* in the emmeans package (Lenth 2024). *p* Values were adjusted for multiple comparisons (i.e. for the three sections) using the Bonferroni method (Bonferroni 1936). To determine the significance of each covariate term, we applied ANOVA (type III) testing using the function *anova.gam* from the mgcv package (Wood 2017).

To evaluate if water discharge differed among study years due to interannual variability in precipitation, we compared water discharge during the smolt run among years using ANOVA testing (*anova* function in the stats package; R Core Team 2024). Tukey post hoc testing was performed to determine which years differed from each other using the function *glht* in the multcomp package (Hothorn et al. 2008), where *p* values were adjusted with the single-step method. The period from when smolts were first and last detected at A1 in River Gudenaa was used to compare water discharges during river migration (Table 3).

Survival and Detection Probabilities. Detection probabilities for arrays (i.e. array forward efficiencies) were estimated using the *migration* function in actel (Flávio & Baktoft 2021), which is based on the mark-recapture models in Perry et al. (2012). For further information on detection probability calculations, see Flávio and Baktoft (2021).

To test if survival probability was lower after the restoration projects, we used a GLMM with the logit link function and Bernoulli distribution. Given the high array efficiencies (>96%; see Section 3.2), we estimated survival based on our observed detections. The response variable was survival (yes or no), quantified as a smolt being last detected on the final sea entry array A4. The factor restoration (before vs. after) was included as a fixed effect, while year (2003, 2005, 2020, and 2021) was included as a random effect to account for yearly variations. Smolts never detected after release were not included in the model to avoid including non-migratory individuals or tagging-related deaths. The GLMM was fit using the function *glmmTMB* in the glmmTMB package (Brooks et al. 2017), and had the following equation:

$$\text{Survival}_j \sim \text{Bernoulli}\left(Pi_j\right)$$

$$\text{logit}\left(Pi_j\right) = \text{Intercept} + \text{Restoration}_j + \text{Year}_j$$

where survival_j represents the survival to sea entry for year *j*. Model assumptions were validated by evaluating scaled quantile residuals using the function *plot* in the DHARMa package (Hartig 2022), and by plotting scaled quantile residuals against covariates included and not included in the model.

Results

Progression Rates

Progression rates of smolts were lower after the restoration project in River Gudenaa, and in the narrow and wide parts of Randers Fjord, compared to pre-restoration rates (Fig. 3). ANOVA testing (type III) of the GLMM revealed a significant effect of restoration ($F = 36.15$, $df = 1$, $p < 0.001$) and array ($F = 13.88$, $df = 2$, $p < 0.001$) on the progression rates of smolts, as well as a significant interaction between restoration and array ($F = 3.98$, $df = 2$, $p = 0.019$). The interaction between restoration and array indicated that progression rates (km/day) decreased significantly post-restoration, but the magnitude of reduction varied depending on section (Fig. 4A). Specifically, in the River Gudenaa (A1 to A2) progression rates were 2.85 times slower after the restoration (estimated marginal means [EMM] = 12.41 km/day) compared to before (EMM = 35.43 km/day; t.ratio = 6.012, SE = 0.50, $p < 0.0001$). In the narrow part of Randers Fjord (A2 to A3), progression rates were 1.88 times lower after the restoration (EMM = 6.51 km/day) compared to before (EMM = 12.27 km/day; t.ratio = 3.60, SE = 0.33, $p = 0.0004$). Finally, in the wide part of Randers Fjord (A3 to A4) progression rates were 1.91 times lower after

Table 3. Water discharges (L/second) experienced by Brown trout smolts during migration in River Gudenaa before (2003 and 2005) and after (2020 and 2021) the wetland restoration projects. Water discharge represents mean daily water discharge with corresponding standard deviations (SD). Letter in significant groups indicate significant differences in mean water discharge from Tukey post hoc testing: Years with a similar letter are not different, while years with a different letter indicate significant differences to other years.

Year	*Period*	*Water discharge (L/second)*	*Significance*
2003	April 16 to June 9	19,642 ± 2597	a
2005	April 6 to May 22	20,212 ± 3159	a
2020	March 24 to May 1	23,278 ± 4444	b
2021	March 29 to May 10	18,848 ± 2571	a

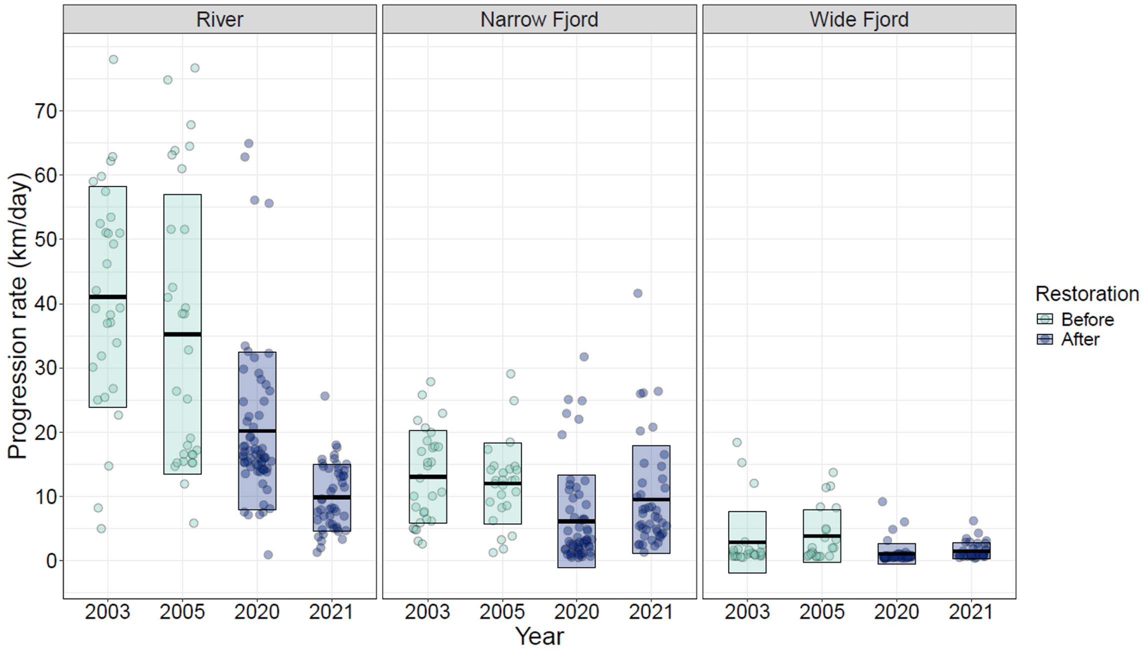

Figure 3. Mean progression rates (km/day) in River Gudenaa (A1 to A2), the narrow part of Randers Fjord (A2 to A3), and the wide part of Randers Fjord (A3 to A4) for smolts tagged before (light blue; 2003 and 2005) and after the wetland restoration project (dark blue; 2020 and 2021). Horizontal line represents the mean progression rate, the box represents the range of one standard deviation above and below the mean (mean ± SD), and the points represent raw data.

the restoration (EMM = 2.32 km/day) compared to before (EMM = 4.43 km/day; t.ratio = 3.56, SE = 0.35, $p = 0.0004$). Additionally, migration time in days from entering River Gudenaa (A1) to entering the sea (A4) was longer post-restoration: the median migration time was 16 days in 2003 and 15 days in 2005, compared to 32 days in 2020 and 21 days in 2021. See Table 2 for summary output from model testing covariate effects on smolts' progression rates.

Julian day-of-year significantly influenced progression rates of smolts ($F = 13.94$, $df = 1$, $p = 0.0002$), with the effect varying depending on the section (i.e. Restoration:Array; $F = 21.00$, $df = 2$, $p < 0.001$). Specifically, in River Gudenaa (A1 and A2) and the wide part of Randers Fjord (A3 and A4), progression rates were slower later in the year (Fig. 4B). Progression rates did not vary with day-of-year in the narrow part of Randers Fjord (A2 and A3; Fig. 4B).

Mean daily water discharge (L/second) during river migration was significantly higher in 2020 compared to 2003 ($t = 5.42$, SE = 671.4, $p < 0.001$), 2005 ($t = 4.41$, SE = 694.7, $p < 0.001$), and 2021 ($t = -6.25$, SE = 709.2, $p < 0.001$; Table 3). There were no differences in water discharge among the other years ($p > 0.05$).

See Table S1 for mean progression rates in kilometers per day and body lengths per second, and Figure S2 for trends in daily water discharges (L/second) in River Gudenaa across study years.

Survival and Detection Probabilities

After the restoration, nine smolts in 2020 and 23 smolts in 2021 were not detected after release. Of the smolts detected entering River Gudenaa on A1 (or downstream arrays), 81% (25/31) in 2003, 77% in 2005 (23/30), 77% in 2020 (51/66), and 73% in 2021 (38/52) were detected on the final sea entry array (A4; Table 4). Detection probabilities (i.e. array efficiencies) were 100% for all arrays in 2020 and 2021. Detection probability was 98% for array A1 in 2003 and 97% for array A3 in 2005 due to one smolt skipping the array. For the remaining arrays, detection probability was 100% in 2003 and 2005 (Table S2). Survival probability to sea entry was 78.7% (CI: 67–87%) before the wetland restorations and 75.4% (CI: 67–82%) after the restorations (Fig. 5), and restoration did not influence the survival probability of smolts ($p = 0.63$; Table 5).

Discussion

The wetland restoration led to a significant reduction in smolt progression rates in the river, with rates three times slower than pre-restoration rates. Smolts may have entered the wetlands through the channels in the dikes and spent time in the lakes before returning to the river, leading to slower river progression rates after the restoration (Olsson et al. 2001; Schwinn et al. 2017, 2019). More likely, the slower progression rates were due to changes in water discharge dynamics of River Gudenaa, as the upper layers, where flow speed typically is greatest, now flow into the restored wetlands. The progression rate relative to the ground depends on both the smolts' movements and the speed and direction of water currents (Aarestrup et al. 2002, 2014; Thorstad et al. 2004). Hence, the reduced river progression rate could be attributed to slower water velocity in

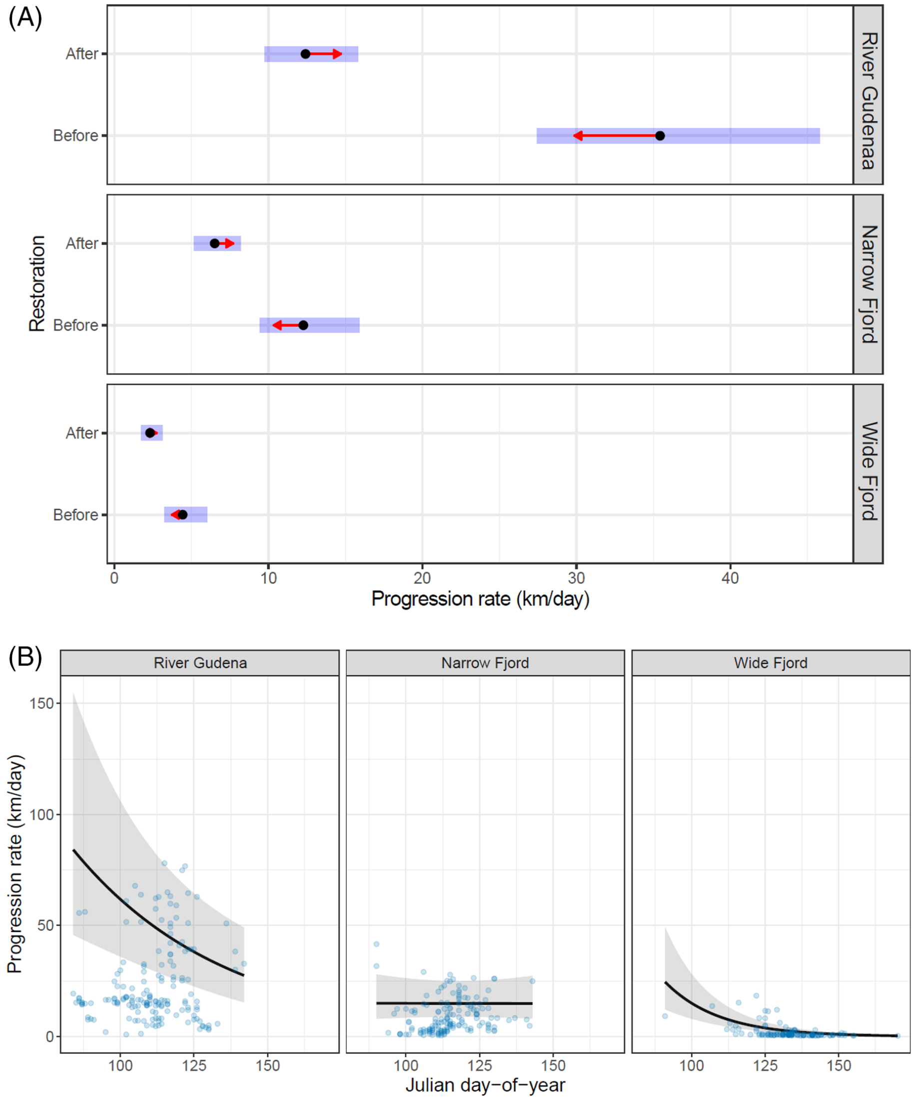

Figure 4. (A) Model estimated marginal means (EMM) of Brown trout smolt progression rates in River Gudenaa (A1 to A2), the narrow part of Randers Fjord (A2 to A3), and the wide part of Randers Fjord (A3 to A4) before and after the wetland restoration. Points represent EMM with corresponding 95% CI as shaded areas. Red arrows indicate pairwise comparisons between before- and after restoration rates, with the direction of the arrow indicating the direction of change between groups; non-overlapping arrows denote statistically significant differences. (B) Model predictions for progression rates (km/day) as a function of Julian day-of-year in River Gudenaa, the narrow part of Randers Fjord, and the wide part of Randers Fjord, assumed to be the same before and after the restoration projects. In other words, (B) shows the model predictions for the interaction between day-of-year (yday) and sections (Array). Black line shows fitted values with corresponding confidence bands as shaded areas, and blue points represent raw data.

Table 4. Number of Brown trout smolts released and detected at acoustic arrays in River Gudenaa (A1), the estuary (A2), and Randers Fjord (A3 and A4). Numbers in parentheses represent smolts that were not detected at an array but were detected at downstream arrays. Study years 2003 and 2005 were before the wetland restoration projects, while 2020 and 2021 were after.

Year	*Released*	*A1*	*A2*	*A3*	*A4*
2003	31	30 (1)	30	29	25
2005	30	30	30	26 (1)	23
2020	75	66	64	58	51
2021	75	52	47	43	38

River Gudenaa due to the restored wetlands, but we cannot confirm this for certain due to the lack of water logger in the river sections adjacent to the restored wetlands. Although water discharge (recorded at the upstream water logger) during river migration was significantly higher in 2020, there were no differences in water discharge among the other years, suggesting the reduced river progression rate was likely due to the restored wetlands rather than consistently higher precipitation and water discharge in pre-restoration years. The slower river progression rates could also be attributed to greater food availability (e.g. aquatic and terrestrial insects) generated by the restored

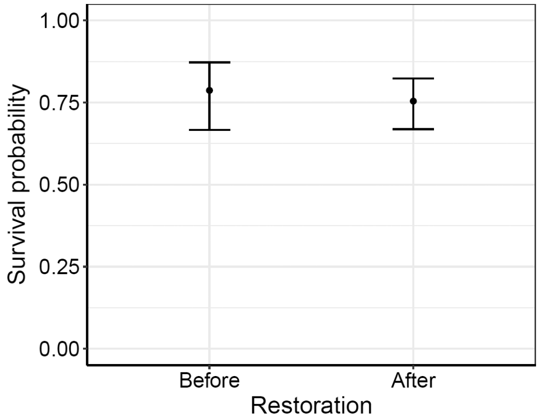

Figure 5. Effect of wetland restoration on the probability of Brown trout smolts surviving to sea entry (A1–A4). A value of 1 represents high probability of surviving, while 0 indicates low probability. There was no difference in survival probability between smolts tagged before and after the wetland restoration projects in River Gudenaa, Denmark.

Table 5. Summary output for Bernoulli GLMM testing the effect of restoration on the probability of surviving to sea entry array A4, including the random effect covariate Year. Intercept represents the log-odds of survival before the wetland restorations, while RestorationAfter represents the log-odds of survival after the restoration.

Fixed effects	*Estimate*	*SE*	*Z value*	*Pr(>|z|)*
Intercept	1.31	0.31	4.18	2.94e−05
RestorationAfter	−0.18	0.38	−0.49	0.63
Random effects	*Variance*		*SD*	
Year	5.902e−10		2.429e−05	

wetlands (Maagaard et al. 2008; Batzer & Wu 2020; Kjeldsen 2024), resulting in smolts spending more time feeding instead of actively migrating. Collectively, our findings support our hypothesis that smolt progression rates in the river were slower after the wetland restoration.

Similarly to the river, smolt progression rates through the narrow and wide parts of Randers Fjord were roughly two times slower following the wetland restoration. The slower river progression rates, likely caused by reduced water velocity in River Gudenaa, may have increased smolt energy expenditure and depleted energy reserves (Baktoft et al. 2020; Wilson et al. 2021a), contributing to slower swim speeds in Randers Fjord (Persson et al. 2018). Moreover, Brown trout post-smolts often stay in or spend time in fjords and coastal areas to feed (Thorstad et al. 2007; Middlemas et al. 2009; Sortland et al. 2024b), so smolts tagged after the restoration may have spent more time feeding in Randers Fjord to recover from greater energy depletion compared to pre-restoration tagged smolts. Supporting this, Boel et al. (2014) found that lipid-depleted Brown trout smolts were more likely to terminate migration early at the first feeding opportunity. Lastly, the slower fjord progression rates could have been due to unknown changes in the environment or ecological conditions of Randers Fjord.

Although previous research has observed post-smolts migrate through estuaries and fjords during falling tide (i.e. ebb tide; *Salmo trutta*; Moore & Potter 1994; Moore et al. 1998; *Salmo salar*; Sortland et al. 2024a), we found no evidence for this pattern in the present study, as model selection found that tidal stage did not explain variations in smolt progression rates. The lack of ebb-tide transport pattern in our study could have been due to (1) Randers Fjord being a microtidal environment, with tidal ranges of only 0.2–0.3 m (Nielsen et al. 2001; Gazeau et al. 2005), offering limited benefit for post-smolts to exploit tidal currents; (2) Brown trout post-smolts possibly spending time feeding in Randers Fjord, ignoring tidal patterns; or (3) the sample size being too small to detect a signal.

Day-of-year significantly influenced progression rates of smolts, where rates decreased later in the year closer to summer in the river and wide part of Randers Fjord. This decline could be due to more abundant or favorable food options later in the season and closer to summer (e.g. surface insects, zooplankton, fish larvae; Lyse et al. 1998; Andreassen et al. 2001), resulting in smolts spending more time feeding. Moreover, metabolic costs increase with water temperature, so the propensity to feed might have been stronger closer to summer when temperatures are higher (Jonsson & Jonsson 2009). Since post-restoration years were 15–18 years after pre-restoration years, warmer temperatures due to climate change may have slowed progression rates by increasing metabolic demands (Salinger & Anderson 2006; Elliott & Elliott 2010), though we lack temperature data to evaluate this. There was no trend between day-of-year and progression rates in the estuary, that is, the narrow part of Randers Fjord. Estuaries can be high-risk environments with elevated predation rates (Jepsen et al. 2006; Thorstad et al. 2012; Halfyard et al. 2013); therefore, post-smolts likely prioritized predator avoidance and migration over feeding in the narrow part of Randers Fjord across all years.

In contrast to our hypothesis, survival was not lower in years following the wetland restoration, and thus we found no evidence that the wetlands create a bottleneck for smolt survival in River Gudenaa. Although smolt progression rates were slower after the restoration project, this did not translate into reduced survival. The high survival of smolts through the restored wetlands contrasts with other studies, which reported low survival of migrating smolts through artificial lakes designed to reduce nutrient run-off (Olsson et al. 2001; Schwinn et al. 2017, 2019). The preservation of River Gudenaa's main channel after the restoration, with only surface waters flowing into the wetlands and a slower but seaward-directed flow, likely minimized straying of smolts into the wetland lakes, where predation risk can be higher.

Although our findings suggest that the restored wetlands did not act as an ecological trap for migrating smolts, we cannot exclude the possibility that the restored wetlands had carryover effects on post-smolt survival after they left Randers Fjord. The slower progression rates in the river and fjord post-restoration could have led to greater energy depletion and lower energy reserves upon arrival to sea (Baktoft et al. 2020; Wilson et al. 2021a), potentially impacting post-smolt marine behavior and survival (Tucker et al. 2016; Bordeleau et al. 2018; Furey et al. 2021). The prolonged duration of their river-to-sea migration likely also delayed their arrival at sea, which could have negative effects on post-smolt survival if it resulted in a mismatch with the timing of optimal sea conditions (Marschall et al. 2011; Thorstad et al. 2012; Wilson et al. 2021b). Delayed impacts on post-smolt marine survival and growth could diminish the benefits of anadromy, potentially leading Brown trout to adopt freshwater residency over anadromy and resulting in the loss of the anadromous population (Thorstad et al. 2016; Ferguson et al. 2019). As anadromous Brown trout are important vectors of marine nutrients into freshwater systems, loss of anadromy would reduce these nutrient-rich marine subsidies, impacting trophic production and overall ecosystem productivity (Näslund et al. 2015; Samways & Cunjak 2015; Samways et al. 2018). Ultimately, the decline of the wild Brown trout population in River Gudenaa is likely linked to increased mortality at other life stages than the smolt stage, either in freshwater during the pre-smolt or adult spawning stages, or at sea during the post-smolt or adult stages.

Despite being a valuable tool to track migrating fish, there are some limitations to consider when interpreting telemetry data. One important consideration is the possibility of a tagged smolt being consumed by a predator and subsequently recording the movements of the predator (Gibson et al. 2015; Daniels et al. 2019). If a predator's movements are distinguishable from a smolt, e.g. long upstream movements, skipping arrays undetected, and pausing at certain locations (Melnychuk et al. 2013; Flávio et al. 2021; Waters et al. 2024), the smolt's fate can be correctly assigned as a mortality. In this study, movement records from the tagged smolts were manually inspected for such unexpected behaviors. However, if a predator's movements are similar to a migrating smolt (e.g. adult Brown trout; Nash et al. 2022), the predation event would not be identified and result in the smolt being incorrectly assigned as a survivor. These incorrect fate assignments would result in an overestimation of survival (termed "predation bias"; Gibson et al. 2015). Hence, the survival estimates in this study should be considered tending toward the upper bound of the likely range. Future studies can reduce the risk of predation bias by using tags with mortality or predation sensors (Halfyard et al. 2017; Lennox et al. 2021, 2023).

Restoring wetlands is a valuable management tool for securing ecosystem services like nutrient cycling and flood mitigation (Fisher & Acreman 2004; Temmerman et al. 2013). However, restoration projects often overlook the needs of migrating fish, leading to unintended negative impacts on native fish populations by increasing passage time and avian predation risk (e.g. Koed et al. 2006). This study demonstrates that preserving the main river channel with a directed flow and avoiding lentic waters can help avoid the reduced survival rates often observed when smolts migrate through lakes. Nonetheless, potential carryover effects on sea survival cannot be ruled out. Future restoration projects should prioritize maintaining a well-defined river channel to support the conservation of anadromous salmonid populations.

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Supporting Information

The following information may be found in the online version of this article:

Table S1. Mean progression rates with corresponding standard deviations before (2003 and 2005; white) and after (2020 and 2021; gray) the restoration projects in River Gudenaa, the narrow part of Randers Fjord, and the wide part of Randers Fjord.

Table S2. Array efficiency (%) for acoustic arrays in River Gudenaa (A1), the estuary (A2), Randers Fjord (A3), and entry to Kattegat Sea (A4).

Figure S1. Red circles indicate channels excavated through the dikes in the River Gudenaa, Denmark, thereby connecting the river to the adjacent wetland lakes.

Figure S2. Daily mean water discharge (L/second) in River Gudenaa during the smolt run from March to June in 2003 (brown), 2005 (blue), 2020 (yellow), and 2021 (green).

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