



Presence and de-smolting of juvenile anadromous brown trout *Salmo trutta* in an off-channel diversion used in small-scale hydropower

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Abstract Rivers are frequently modified to help generate provisioning ecosystem services, but these modifications frequently affect fish movements. Small-scale hydropower schemes frequently incorporate off-channel diversions into which migrating fishes can be entrained, potentially delaying or preventing their migration. The aim here was to evaluate the presence of brown trout *Salmo trutta* (“trout”) in an off-channel diversion used for hydropower (480 m length) on an upland river in southwest England between September 2024 and August 2025. The focus was on trout smolts tagged with passive integrated transponder tags, but with tagged river-resident trout also considered. Across all sampling events, 696 individual brown trout were captured in the channel. During the smolt migration period (mid-March to late May), 160 trout were identified as a smolt. The number of days between smolt capture and recapture varied between 11 and 132 days; smolts captured early in the migration period remained in the diversion for significantly longer than those captured later. At the migration period conclusion, 3% of tagged smolts remained in the diversion versus 32% of tagged river-resident trout. These remaining smolts had reverted

to river-resident trout, indicating that trout smolts remaining within diversion channels will de-smoltify if they fail to emigrate.

Keywords PIT tag · Smolt run · Mark recapture · River-resident · Smolt migration

Introduction

The modification of river channels to enable the generation of important provisioning ecosystem services is now common across the world, but these modifications can form obstacles that impede the movements of many fish species (van Puijenbroek et al., 2019; Costa et al., 2021). These species include diadromous fishes, where anthropogenic barriers are recognised as a primary driver of population declines (Limburg & Waldman, 2009; Duarte et al., 2021). The consequences of these impoundments for upstream migrating fish are well recognised, with intensive efforts aiming to facilitate their upstream passage via, for example, the installation of various types of fish passes and ladders (Kemp, 2016).

Small-scale hydropower plants often operate by diverting water from the main river channel and into an off-stream diversion (Anderson et al., 2015). This diversion is often in the form of an artificial channel (“off-channel diversion”) that can run for several hundred metres before the water is passed through the turbine and then rejoins the main river channel

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further downstream, with the flow in the main river channel between the off-take and confluence being depleted (Kuriqi et al., 2021). The diversions are usually designed to accommodate a high proportion of the river discharge to ensure the turbine remains operational even when flows are low (Fjeldstad et al., 2018). Downstream migrating fishes generally follow the main river flow to conserve energy (Anderson et al., 2015) and so there is risk they become entrained in the diversion.

When downstream migrating fishes are entrained into such off-stream diversions, including those used in small-scale hydropower systems, they remain within this channel until they either move back out into the main channel through an upstream movement (e.g. through the open penstock) or they pass downstream (Mueller et al., 2017, 2022), unless they are lost to predation (Thorstad et al., 2012). Their downstream passage requires their movement either through the turbine or, if present, then some form of bypass or fish ladder that provides the fish with an alternative route around the turbine corridor and so transports the fish unharmed into the tailwater (Knott et al., 2023). Structures that divert debris or floodwater to the tailwater (e.g. spillways, sluices), and fish passes designed to assist upstream migration, are also known to be used by downstream moving fish in some contexts (e.g. Egg et al., 2017). A potential issue with these downstream routes is that fish must elect to use them, which might then depend upon their motivation to pass downstream (Goerig & Castro-Santos, 2017). This motivation might be inhibited, and their usual migration cues (e.g. temperature change, elevated river flow) can be diminished within the diversion due to its more regulated flow regime (Haraldstad et al., 2021). Fish that do move downstream through turbines can be killed or injured (e.g. Algera et al., 2020; Knott et al., 2023). Although turbine losses can be highly variable, they are often below 20%, such as the additional mortality of up 17% in smolts passing through hydropower units in a River Rhine tributary (Havn et al., 2018) and 6% in smolts in the River Kinzig, Germany (Thorstad et al., 2017). However, fish that are not killed while passing through the turbine can still be impacted physiologically (Ammar et al., 2020). Entrainment into off-channel diversions can also delay smolt emigration, with individuals often prevented from moving downstream for several days (Lauridsen et al., 2017; Moore et al., 2018).

Where emigrating juvenile salmonid fishes (“smolts”) are delayed in their passage for prolonged periods, then there is a risk that they are unable to emigrate. Rather than moving out into the marine environment, these smolts instead remain in freshwater and then de-smolt to enable them to tolerate the physiological demands of remaining in freshwater (Soivio et al., 1989; Nielsen et al., 2006). Silvering is usually used as an external indicator of smolt status, with clear differentiation from river-resident conspecifics (Birt et al., 1991). However, in wild salmonid smolts, physiological observations of the osmoregulatory functions of the gill suggest that de-smolting can commence during the smolt migration period, with smolt status tailing off after the peak migration period is reached (Nielsen et al., 2006). More specifically, in Atlantic salmon *Salmo salar* Linnaeus, 1758, this osmoregulatory activity can decrease by up to 66% in approximately one month and is related to the increased temperatures and number of degree-days (Duston et al., 1991; McCormick et al., 1999).

The aim here was to assess the presence and consequences of the facultatively anadromous brown trout *Salmo trutta* Linnaeus, 1758 in an off-stream diversion that supplies water to a small-scale hydropower plant located on an upland river in Southwest England. The objectives were to assess how brown trout generally used this diversion (e.g. as river-resident trout or using it as migration pathway) and then, during the smolt migration period, identify those trout that smolted within the diversion versus those that smolted further upstream and were entrained during their migration, and the approximate duration that these smolts were present in the diversion. Note that due to the study design, the fate of the trout smolts that were no longer recorded as present in the diversion at the end of sampling period was unknown, only that they were no longer recaptured there after the conclusion of the smolt migration period.

Materials and methods

Study river and hydropower off-stream diversion

The study river was the River Teign, an upland spate river in Devon, southern England that flows approximately 50 km from its source (50° 38' 19.0" N; 3° 57' 31.0" W) to its tidal limit below Newton Abbot (50°

32° 10.8" N; 3° 35' 13.7" W; Fig. 1). The river has a fish assemblage largely dominated by brown trout (anadromous and non-anadromous forms; "trout" hereafter) and Atlantic salmon, although other fish species are present in relatively low abundance, including minnow *Phoxinus phoxinus* (Linnaeus, 1758), bullhead *Cottus gobio* Linnaeus, 1758 and stone loach *Barbatula barbatula* (Linnaeus, 1758).

The focal off-stream diversion was situated in the upper catchment (Fig. 1). This scheme diverts some of the river flow through this 480-m channel, with a difference in elevation between the intake and tail race of the channel being approximately 9 m (channel gradient: -1.86%). Although the diversion channel is constructed of concrete, a natural substrate has developed, with a mix of sand, gravel and cobble present throughout its length, with macrophytes also present (e.g. *Ranunculus* spp.). This contrasts with the main river channel that has a greater proportion of cobble and boulders present, with macrophytes largely absent. The diversion channel has a mean width of approximately 3 m (range 2 to 4 m) and depths ranged

from 0.5 m at the upstream end to over 1 m towards a hydropower unit located at the downstream end.

The proportion of diverted flow from the main river and into the channel is dependent on the extent to which manually operated penstock is open at the upstream end of the diversion and the flow conditions of the main river, with this penstock always at least partially open throughout the study period. The amount of flow diverted into the channel is dependent on the extent that the penstock is open, with this modified manually. Accordingly, the amount of river flow diverted into the channel is variable and could not be quantified accurately here. Note that as the hydropower unit is run as a private business then more specific operating details are not available. The water flow within the diversion was, however, permanent throughout the study. The hydropower unit is located at the downstream end of the diversion, with a single crossflow turbine that can generate up to 87,000 kWh per year, with screening to prevent debris ingress. Within the unit, there is bypass channel (bypass) that is designed to divert fish past the turbine

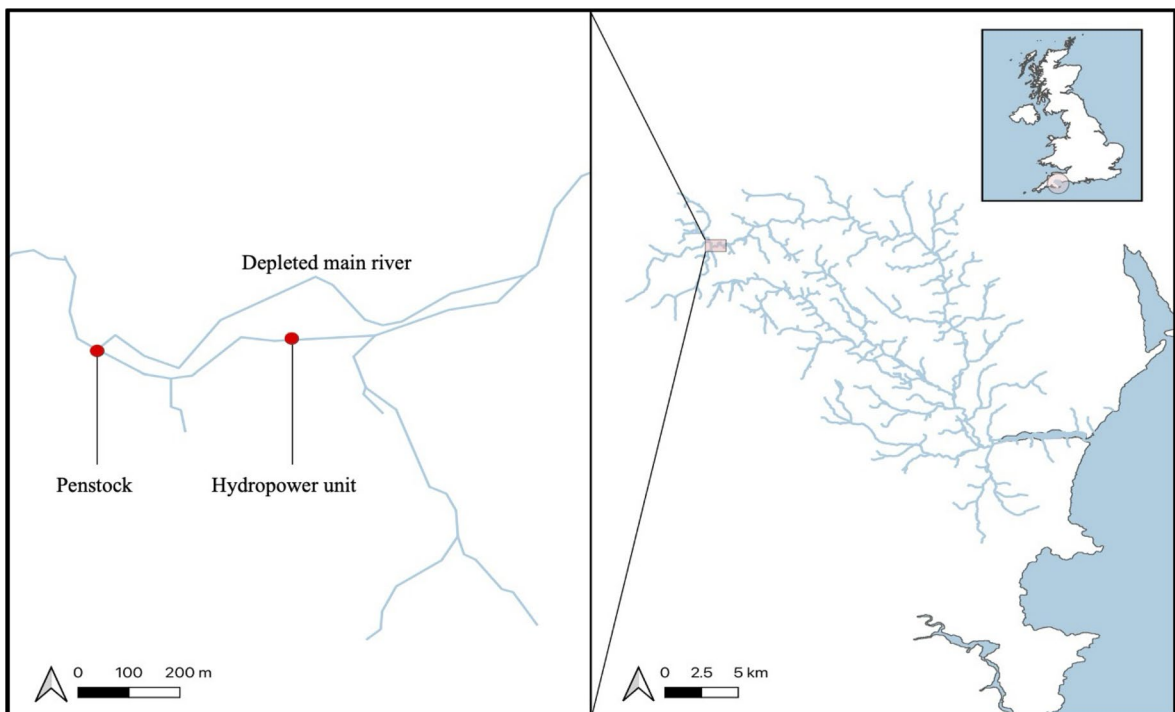


Fig. 1 Map of the River Teign study area, where (left): the off-channel diversion, running from the penstock, through the hydropower unit containing the turbine, before its confluence

with the main river; (right): location of the study area in the River Teign catchment; and (inset): location of the study area in the wider context of the UK

and into the tail race, from where they can rejoin the main river channel. There is no barrier upstream of the penstock and so fish movements within main river channel are not inhibited.

Fish sampling and tagging

Fish sampling was conducted in the off-channel diversion from September 2024, initially every 6 to 8 weeks to mid-March 2025, with sampling thereafter occurring every 2 to 3 weeks to late May 2025, before being reduced in frequency once more through to August 2025 (Table 1). All fishing used back-mounted electric fishing (SmithRoot LR-24) with single pass fishing used in an upstream direction, with the section closed by the placement of a stop-net across the channel at the downstream end and the penstock posing a fixed obstacle at the upstream end. Single pass fishing was used to minimise the risk of causing injury and trauma to fish subjected to the electric fishing on multiple occasions (Panek and Densmore 2013), with electric fishing once (or even twice) in cold water considered as not affecting salmonid growth rates (Clancy et al., 2022).

Following their capture, the fish were held in aerated river water prior to their processing. Due to previous studies on the upstream reaches of the river that involved PIT tagging of brown trout, tagged fish could have already been present in the channel from the initial sampling event from September 2024, where tagged fish were identifiable externally by their clipped adipose fin. Accordingly, the processing of each captured fish from the channel involved initial inspection for a clipped adipose fin and, if clipped, manual scanning for its PIT tag code. Trout without a clipped adipose fin were then anaesthetised (buffered tricaine methanesulfonate (MS222); approximately 100 mg l^{-1} , exposure generally $<3 \text{ min}$ for the required induction), identified to species and measured (fork length (FL), nearest mm), the adipose was fin clipped, and then, providing the tag length/body length ratio was $<17.5\%$ (Vollset et al., 2020). A 23-mm PIT tag (132.4 Hz, HDX) was implanted into the body cavity. If this ratio was $>17.5\%$ for 23-mm tags, then a 12-mm PIT tag was used instead. The exception to this was for river-resident brown trout captured in samples from 2nd May 2025. These fish were only fin clipped. This was because the air and water temperatures were now sufficiently high that

Table 1 The number (n) of sampled and recaptured brown trout ("trout") captured on each sampling occasion, the number and proportion of trout smolts per sample, and the number and proportion of trout that had de-smolted per sample

	Sample date									
	24/09/24	15/11/24	30/11/25	11/03/25	02/04/25	21/04/25	02/05/25	22/05/25	26/06/25	21/07/25
Trout sampled (n)	60	90	90	91	87	137	191	158	86	124
Recaptured trout (n)	1*	15	36	54	44	36	69	89	40	74
Trout smolt (n)	0	0	0	33	51	52	46	38	0	0
Recaptured trout smolts (n)	0	0	0	22	24	22	17	23	0	0
Proportion of smolts in sample (%)	0	0	0	36	59	38	24	24	0	0
Recaptured de-smolted trout (n)	0	0	0	0	0	0	0	0	3	3
Proportion of de-smolted trout (%)	0	0	0	0	0	0	0	0	3.5	2.4

*Initial capture and tagging of this fish was in a site further upstream of the diversion channel in July 2024

holding the fish prior to PIT tagging was no longer feasible on welfare grounds (Table 1). However, all newly captured smolts were still PIT tagged in this period (Table 1). Concomitantly, the fish were identified in all samples as either a river-resident brown trout or a smolt, where the differentiation was primarily through smolts having a very distinct silver/iridescent appearance (Birt et al., 1991). Following their recovery in river water (generally < 2 min), the fish were released back into the off-stream diversion. All procedures were conducted under UK Home Office licence PP5256306 (under the Animals (Scientific Procedures) Act (1983)) and following ethical review and approval.

Data analysis

The timing of when smolts were initially present in the electric fishing samples was determined from either their tagging date if captured for the first time during the smolt run period or their first recapture as a smolt within the channel. This was coupled with calculation of their proportional contribution to samples throughout the smolt run period, with comparison of the lengths of the river-resident trout versus smolts (Mann Whitney U test). The recapture history of each smolt was then determined, including their date of last capture, enabling the determination of the proportion of smolts that were no longer being captured in the diversion at the end of the smolt migration period. The number of days between initial smolt capture and final recapture within the diversion was also calculated. For PIT tagged river-resident trout that were also captured during the smolt migration period, their capture–recapture history was also determined to provide comparative data to the smolts.

Analysis of the temporal pattern of smolt and river-resident trout presence in the diversion following their initial capture during the smolt run period used the Survival Analysis R package (Therneau et al., 2026). The smolt migration period was taken as 11/03/2025 (the first sample in which trout identified as smolts were present) to 22/05/2025 (the final sample when tagged smolts were present). When a tagged smolt was captured in samples after 22/05/2025, then their actual survival time in the channel was not known but was longer than the smolt run period and they had de-smolted. For each of the five sampling/tagging occasions during the smolt migration period

(11/03/2025 to 22/05/2025; Table 1), a Kaplan–Meier plot estimated the proportion of tagged smolts and tagged river-resident trout remaining in the channel until the conclusion of the smolt migration period. A log-rank test tested the null hypotheses that: (i) there was no difference in the time that the tagged smolts were present within the diversion across each tagging event, and (ii) there was no difference in the time that tagged smolts and river-resident trout were present within the diversion across each tagging event.

The remaining analyses then focused only on the smolt data. Assessing the factors influencing the time that each smolt was present in the channel (taken as the time between their initial capture and final recapture) used a Cox proportional hazard model, where four smolt groups sampled between 02/04/2025 and 22/05/2025 were compared to the reference group sampled on 11/03/2025. The factors tested in the model were smolt length at tagging or initial capture (if already tagged when captured as a smolt), their date of initial capture and the mean river level during their time period within the channel. For mean river level, data were used from the main river, which was sourced from Clifford Bridge, located a short distance downstream of confluence of the channel with the main river (<https://check-for-flooding.service.gov.uk/station/3214>). As the Schoenfeld residuals initially revealed the proportional hazards assumptions were violated in the model, then the final version incorporated a time-varying effect of river level (log-transformed time interaction). All analysis were performed in R (R Core Team, 2026).

Results

Brown trout smolt numbers, lengths and capture efficiencies

Across all the sampling events, 696 individual brown trout were captured, of which 395 were implanted with a PIT tag (57%). The lengths of the PIT tagged fish ranged between 98 and 389 mm, with a mean length of 165 ± 5 mm (0.14). There were 186 PIT tagged fish recaptured at least once (47%), with individuals recaptured between 1 and 8 occasions (median (inter-quartile range, IQR): 2 (1–3) events).

Trout that were visually identified as smolts were present in samples between 11/03/2025 and

22/05/2025, with 160 individual smolts captured and PIT tagged (23% of all captured trout) (Table 1). There were also 100 river-resident trout captured and PIT tagged between 11/03/25 and 21/04/2025. The peak proportion of smolts within a sample occurred on 2nd April (59%). Median (IQR) smolt length was 167 (157–178) mm, whereas for river-resident trout was 129 (120–141) mm, with these length differences being significant (Mann–Whitney: $z = -12.16$, $P < 0.001$) (Fig. 2).

Smolt capture/ recapture

During the five sampling events completed during the smolt migration period, 41 of the smolts had been PIT tagged prior to smolting (26%), with 38 of these captured within the channel and tagged between September 2024 and January 2025. The other three fish were tagged in July 2023 ($n = 1$) and July 2024 ($n = 2$). The other 119 smolts (74%) were captured for the first time as a smolt during the migration period and tagged (Table 2). The proportion of smolts that

were recaptured was highest on 11/03/25 (54%) and declined across subsequent sampling events. During the two sampling events after the conclusion of the smolt migration window (26/06/25 and 21/07/25), there were 5 recaptured smolts that were now visually identified as a river-resident trout but had previously been captured and identified as a smolt, indicating that 3% of the tagged smolts had remained in the diversion after the conclusion of the smolt migration window and de-smolted (Table 2). These de-smolted individuals were all of lengths within the typical range of smolts (156 to 194 mm; Fig. 2). By comparison, 32 of the 100 tagged river-resident trout that were captured during the smolt migration period were recaptured after its conclusion (Table 3). Of these 100 river-resident trout, 66 had been tagged prior to the smolt migration period, with the earliest tagging date being in July 2024 at a site approximately 2 km upstream of the diversion. The other 34 river-resident trout were tagged in the diversion channel on 11/03/25 ($n = 4$), 02/04/25 ($n = 11$) and 21/04/25 ($n = 19$).

Fig. 2 Box plots of lengths of river-resident brown trout (clear) versus brown trout smolts (grey) from electric fishing sampling conducted during the smolt migration period. Horizontal lines are 25th, 50th and 75th percentiles, vertical lines are 10th and 90th percentiles, x are mean lengths and circles are tagged fish lengths

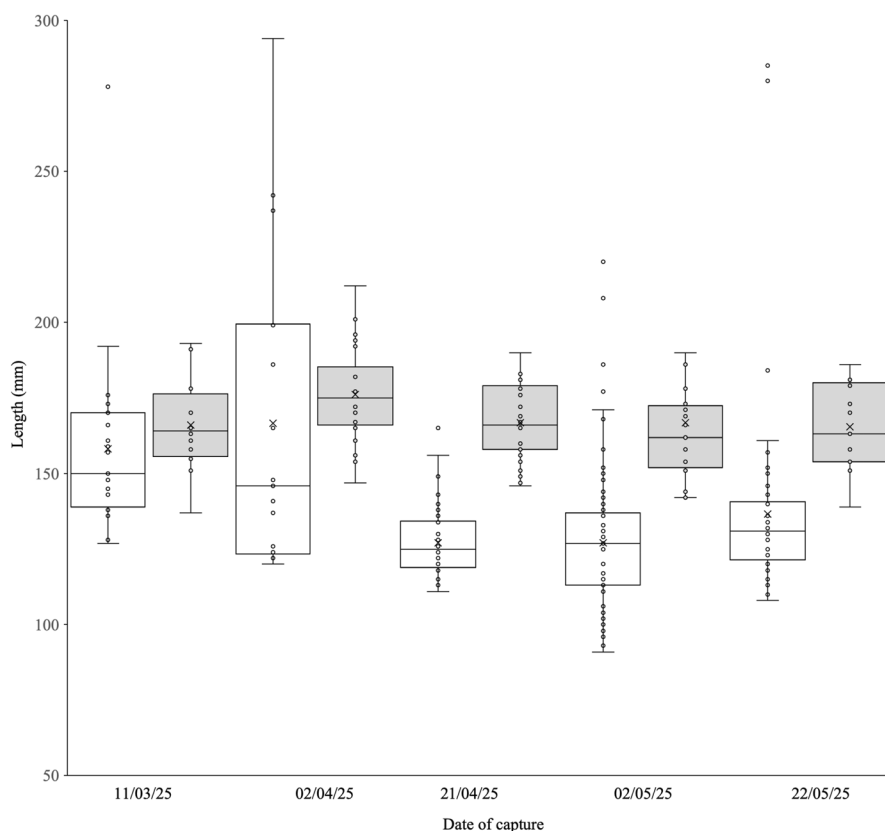


Table 2 The number (n) of brown trout smolts implanted with a PIT tag on each sampling event (*captured and tagged before smoltification and recaptured as a smolt at least once between

11/03/25 and 22/05/25), and the number of these smolts that were recaptured during subsequent sampling events (**de-smolted brown trout)

	Date of PIT tagging							
	24/09/2024 (Day 0)	15/11/2024 (Day 52)	30/01/2025 (Day 128)	11/03/2025 (Day 168)	02/04/2025 (Day 190)	21/04/2025 (Day 209)	02/05/2025 (Day 220)	22/05/2025 (Day 240)
Smolts tagged (n)	10*	15*	16*	18	26	32	28	15
Recaptured 11/03/25 (n)	4	11	7					
Recaptured 02/04/25 (n)	4	5	9	7				
Recaptured 21/04/25 (n)	3	1	6	6	6			
Recaptured 02/05/25 (n)	1	2	3	1	3	9		
Recaptured 22/05/25 (n)	3	2	1	4	1	5	6	
Recaptured 26/06/25** (n)	1	1	1	0	0	0	0	0
Recaptured 21/07/25** (n)	1	0	1	0	1	0	0	0

Table 3 Numbers of brown trout smolts (“smolts”) and river-resident trout (“resident trout”) detected for the first time in the diversion channel during the smolt migration period (“start”) and that were recaptured in the channel after the smolt migration periods (“end”), plus the results of log-rank tests (χ^2 , p) comparing temporal patterns in the proportions of smolts and resident trout remaining in the channel by their initial capture date (cf. Fig. 3)

Initial capture date	n smolts start/ end	n resident trout start/ end	χ^2	P
11/03/2025	36/ 3	32/ 7	3.11	0.08
02/04/2025	34/ 1	12/ 7	15.77	<0.001
21/04/2025	32/ 0	16/ 6	17.36	<0.001
02/05/2025	29/ 0	19/ 7	9.71	<0.002
22/05/2025	29/ 1	21/ 5	4.69	0.03

Kaplan–Meier survival, log-rank test and Cox proportional hazard model

The time between tagged initial smolt capture and final recapture in the diversion channel varied between 11 and 132 days. Individuals initially captured as a smolt on 11/03/25 and 02/04/25 generally had longer durations between their capture–recapture periods than those initially captured on 21/04/25 (Fig. 3). The log-rank test revealed the differences in the time of smolts within the diversion were significant between the five groups ($\chi^2 = 9.9$, $P = 0.04$), with smolts that were present in the channel earlier in the smolt migration window then present for significantly longer. This result was supported by the

Cox proportional hazards model, which revealed that smolts tagged/ captured for the first time later in the smolt run window had a significantly higher probability of not being recaptured within the channel (Table 4). The model revealed that smolts first detected on 02/05/2025 and 22/05/2025 had a significantly higher likelihood of not being recaptured within the diversion channel than those on 11/03/2025 (02/05/2025: HR = 2.72, $P = 0.001$; 22/05/2025: HR = 3.06, $P = 0.01$) (Table 4). River level had a significant and positive effect on departure rate (HR = 1.34, $P = 0.05$), with this effect increasing over time (time-varying HR = 1.60, $P = 0.01$). Fish length was, however, not significant ($P = 0.17$).

Kaplan–Meier survival curves also revealed that in general, tagged river-resident trout had a higher probability of remaining the diversion channel at the end of the smolt migration period than tagged smolts (Fig. 3). Log-rank tests indicated that these differences were significant between smolts and river-resident trout for all initial capture dates other than 11/03/25 (Table 3).

Discussion

Small-scale hydropower plants have the potential to cause a range of issues for migrating fish, including the entrainment of migrants within their off-take channels. The results here demonstrated that the smolts that were present in an off-channel diversion that supplies water to hydropower unit were a

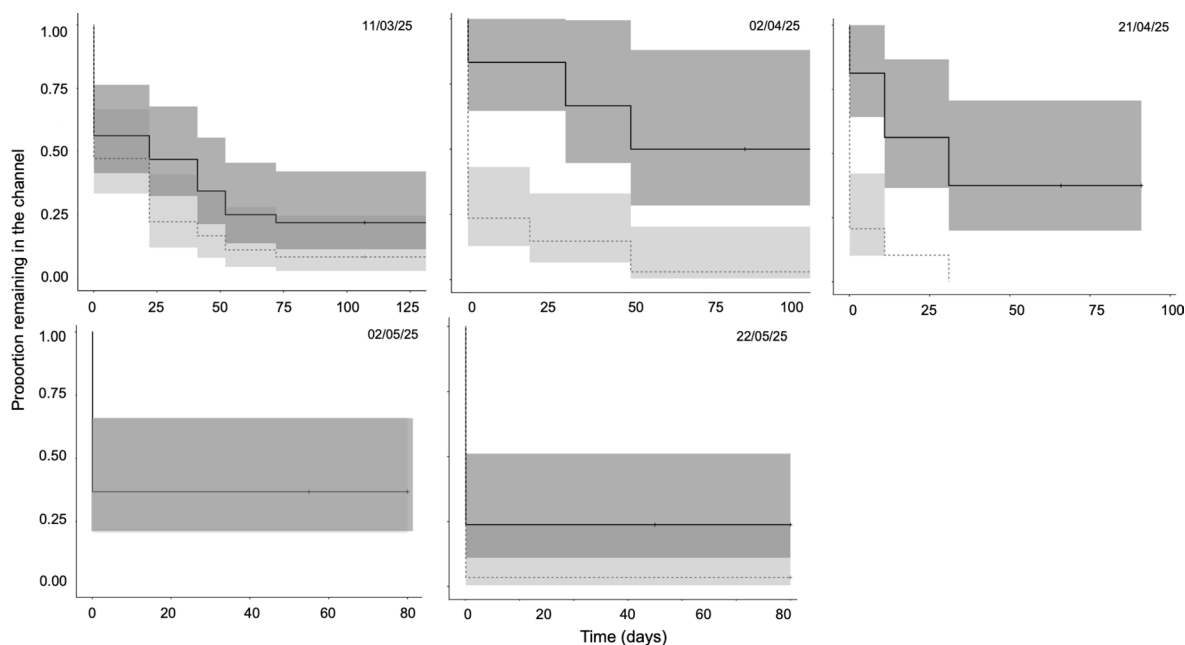


Fig. 3 Kaplan–Meier survival plots estimating the probability of a tagged fish remaining in the hydropower diversion channel according to the data of first detection during the smolt migration period, where the solid line represents river-resident trout

and dark shading their 95% CI, and the dashed line represents trout smolts, with light shading representing 95% CI. Note that no tagged trout smolts captured for the first time on 02/05/25 were recaptured

Table 4 Outputs of the Cox proportional hazards model, where the smolt reference group was the fish captured/ tagged at the start of the smolt migration period (11/03/2025)

Factor/ smolt group	Hazard ratio (HR)	SE	<i>P</i>
02/04/2025	1.37	0.27	0.24
21/04/2025	1.15	0.26	0.59
02/05/2025	2.72	0.31	<0.01
22/05/2025	3.06	0.38	<0.01
Smolt length	0.90	0.07	0.17
River level	1.34	0.15	0.05
River level × time	1.60	0.17	0.01

combination of trout that were already present prior to their smolting, plus trout that had smolted further upstream in the river catchment and had entered the diversion during their downstream migration. Some of these smolts were present in the diversion for sustained periods, with these smolts likely to have incurred additional energetic migration costs that could have impacted their subsequent fitness (Nielsen et al., 2006). This is likely to have increased their vulnerability to predation, reduced their growth rates

and resulted in these fish being less likely to return as adults (Thorstad et al., 2012; Armstrong et al., 2018). By the end of the sampling period (several weeks after the conclusion of the smolt run period), 3% of tagged smolts had been recaptured within the channel, all of which had de-smolted and had thus reverted to their river-resident form. By comparison, 32% of tagged river-resident trout captured in the channel during the smolt migration period were recaptured after its conclusion.

The presence of some trout smolts in the off-channel diversion in multiple electric fishing samples collected during their migration period suggests they were either unwilling or unable to easily move back out into the main river. This is because once developed into a smolt, their motivation to migrate downstream (and so move through the channel quickly) would be assumed as strong (Goerig & Castro-Santos, 2017). This is because the survival of salmonid smolts is affected by a limited period of readiness—a physiological smolt window—with their timing of entry into the marine environment needing to coincide with environmental conditions that provide appropriate temperatures and prey resources for their

recovery and then growth (McCormick et al., 1998). Brown trout lifecycles are highly flexible, where individuals can undergo smolting within a broad time-scale, with migrating smolts capable of de-smolting and thus assume river-residency once more (Birnie-Gauvin et al., 2019). The smolts that remained in the off-channel diversion after the conclusion of the smolt migration period were all identified as a river-resident brown trout. This reversion to river-resident fish was most likely a response to increased water temperatures, as these accelerate the process of de-smolting through physiological changes that result in reduced osmoregulatory capability and so decreased tolerance for seawater that reduces the motivation to migrate (Schwinn et al., 2017). De-smolting tends to be more common in landlocked or lacustrine salmonid populations due to the lack or loss of migration cues (Wedemeyer et al., 1980). It has been hypothesised that anthropogenic structures (such as dams and or weirs) that cause delays in the downstream migration of trout smolts will also result in increased de-smolting if the fish fail to reach the marine environment during their physiological window (Aarestrup & Koed, 2003). However, there is a paucity of empirical evidence demonstrating this de-smolting in the wild and the extent to which it occurs in populations that are not impacted by anthropogenic activities.

In general terms, the channel provided an environment of relatively consistent environmental conditions (e.g. a regular depth and discharge due to the flow regulation provided by the penstock). This is a contrast to the main river that is subject to rapidly changing conditions, including periods of low flows in summer and large spates following high precipitation events (Centre for Hydrology and Ecology, 2025). Accordingly, these conditions potentially provided the fish with relatively favourable conditions versus the main river channel, which might help explain the relatively high proportion of river-resident trout recorded in the channel prior, during and after the smolt migration period, with almost 700 trout recorded in the channel across the 11-month sampling period. Moreover, with only 23% of all sampled trout being a smolt then this indicates that this diversion channel could be an important habitat in regulating the partial migration of the population (Chapman et al., 2011), in which only some individuals from a population migrate (Chapman et al., 2012). The proportion of smolts remaining in the diversion channel

after the conclusion of their migration period was 3% versus 32% for tagged river-resident trout in the same period, which further suggests the diversion channel provided a relatively stable environment that was not selecting strongly for river-resident trout movements back into the main river. Although it was determined that 23% of captured trout in the channel underwent smolting, it is not known whether this was a low or high proportion versus trout in the main river channel due these habitats not being able to be sampled in the smolt migration period.

This decision of remaining as a river resident versus smolting and migration in trout populations that exhibit partial migration is a balance between the enhanced foraging opportunities potentially provided by migration and the costs of potentially greater mortality and energy expenditure (Chapman et al., 2011, 2012; Ferguson et al., 2019). The initial decision threshold of whether an individual will migrate or remain river resident occurs early in life and relates to the individual's physiological condition (e.g. energy status) (Ferguson et al., 2019). For those trout that do decide to migrate, there is likely to be a further, later threshold that determines their age and timing of migration, with these decisions then resulting in the transformation of parr into smolts, as well as the timing of their sexual maturity and phenology of their return migration (Ferguson et al., 2019). Testing of individuals in the autumn prior to the smolt migration period has also revealed that individuals that migrated had higher antioxidant capacity than those remaining resident and that the future migration date was negatively correlated with both autumn antioxidant capacity and body length (Birnie-Gauvin et al., 2017). The energetic state of individual fish also has been suggested as providing a possible mechanism underpinning this partial migration in brown trout (Boel et al., 2014). Thus, the decision to migrate in brown trout involves some decisions early in life, involving physiological and energetic considerations and thresholds. This would suggest that where trout have transformed into a smolt but have not migrated—such as those individuals detected as de-smolting here—they incur considerable physiological and energetic consequences resulting from both the processes involved and their failure to acquire the resources they were seeking in their destination habitat. However, the issue of de-smolting is not well covered in the literature and so the implications for individuals

that undergo the process and the fitness costs remain unclear and requires further work.

The study design meant that the fate of the trout smolts that were no longer being recaptured in the off-channel diversion remained unknown, such as whether they died in the channel or main river, or emigrated to sea. Fixed PIT antennas had been operational previously in the river to track smolt emigration, but these had been rendered inoperable by the extreme flood conditions that affect this upland river (e.g. river levels rising rapidly at high velocity and carrying substantial debris, e.g. trees, that damaged equipment). Some smolts might have been predated by piscivorous fauna as, for example, Koed et al. (2006) reported that a doubling of in-river smolt mortality between years was primarily due to bird predation, with 12% losses in brown trout smolts. A potential source of smolt mortality could have been their movement through the hydropower turbine (Algera et al., 2020; Knott et al., 2023), although this was unable to be measured and so remains highly speculative and uncertain. However, fish protection screens and provision of alternative downstream routes around the turbine can reduce this source of additional mortality (Tomanova et al., 2018). Had some of these tagged trout smolts managed to migrate into the marine environment successfully, then there might have been some carry-over effects of their entrainment, as a long-term Norwegian study indicated that survival was highest for smolts entering the sea relatively early in the smolt run, especially for larger smolts (Jensen et al., 2022), so any delays in their marine entry could decrease their survival probability. This lack of knowledge on smolt survival following their final recapture in the off-channel diversion here is thus a study limitation that future studies should aim to overcome by incorporation of other detection and tracking methods.

The study design was also based on the application of regular electric fishing events, with the frequency of events being increased during the smolt run period. It is well established that electric fishing has the capacity to injure fish during its application (Snyder et al., 2003). Injury probability in salmonids increases with fish length, where the injury is caused by the strong voltage gradient present close to the anode (Pottier et al., 2020), but with pulsed direct current (as used here) being less injurious than alternating current (Sharber & Carothers, 1988). In an

86 day study where fish were captured on between two and seven occasions, the relationship between the number of electric fishing capture events and growth rates in Columbia River Redband trout *Oncorhynchus mykiss gairdneri* (Richardson, 1836) was not significant, and with conclusions that electric fishing in cold waters could be completed at least once per month, and potentially twice per month, without negatively affecting the growth rate of captured fish (Clancy et al., 2022). However, there was a significant relationship between the number of electrical shocks and the frequency and severity of haemorrhagic and spinal trauma in several fish species, including rainbow trout *Oncorhynchus mykiss* (Walbaum, 1792) and brook trout *Salvelinus fontinalis* (Mitchill, 1814) (Panek & Densmore, 2013). Accordingly, the study design here was limited to single run fishing on each sampling occasion. Although this prevented the derivation of estimates of the trout smolt abundance using multi-pass fishing during each sampling event (Peterson et al., 2004), the application of PIT telemetry and mark recapture using single run fishing was considered an acceptable trade-off between electric fishing frequency and smolt injury risk. Moreover, the study design also involved the insertion of PIT tags into smolts during their migration window. In juvenile salmonids, there are increased incidences of mortality and decreased growth rates when the ratio of tag size to fish size increases, and with an estimated minimum threshold of 131 mm total length for tagging salmonids with 23 mm PIT tags (Vollset et al., 2020). All the smolts tagged during the study were larger than this threshold and so the application of this PIT telemetry method was also considered as appropriate for the study design and not detrimental to the migrating trout smolts.

In conclusion, river-resident trout and trout smolts were present in this off-channel diversion across the smolt migration period, with some smolts captured and then recaptured over 100 days apart. At the end of the smolt migration period, 3% of the smolts remained in the channel versus 32% of the river-resident trout, with these remaining smolts now transformed to a river-resident fish. The fate of those smolts that were no longer recaptured in the channel could not be determined, including whether they successfully migrated downstream. Nevertheless, these results suggest that where smolts do remain within these diversion channels until after the conclusion of

their migration periods then they will de-smolt, with this failure to emigrate being despite their high motivation to reach the marine environment.

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Data availability Any raw data used in the manuscript that are not already provided are available from the corresponding author at reasonable request.

Declarations

Competing interests The authors have no competing interests to declare that are relevant to the content of this article.

Ethical approval All aspects of data collection were completed following ethical approval and were licenced under the U.K. Animals (Scientific Procedures) Act (1986) (project licence number: PPL PA2C7C4E6).

Consent to publication This is not applicable.

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