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Using PIT-tags and portable antennas for quantification of fish movement and survival in streams under different environmental conditions

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ABSTRACT

While PIT-tag tracking using mobile antennas is being increasingly used to study fish movement and survival in streams, little is known about the limitations of the method, especially over longer periods of time and under different environmental settings. We used six years of data combining tagging, mobile antenna tracking and recaptures of *Salmo trutta* in multiple small streams in the Lake Lucerne drainage in Switzerland to evaluate the relative importance of different environmental and intrinsic factors affecting the efficiency of the method. Our study system and experimental design allowed us to accurately verify continuous presence and survival of recaptured fish in the stream after tracking, which meant that we could estimate detection probability with high confidence. Mean detection probability of tagged trout was 43%, but we found that fish length had a strong negative effect on detection probability, especially in males. Multivariate axes of stream environmental features did not predict efficiency but stream width alone was significantly positively correlated with efficiency. Additionally, stream temperature when tracking had a positive effect on fish detectability. Tag loss at recapture was globally rare (< 8%) but common in large post-spawn females (>30 %). Based on escape response of fish after detection, we could estimate the proportion of ghost tags, which reached a plateau of around 80% two years after tagging. We finally showed that our models of tag loss, fish detection and escape response are needed to interpret detection events. Our results highlight that individual variation in detection probability and tag loss is high, and has to be considered for analysis.

INTRODUCTION

Movement is a defining behavior for animal life: where, when and why animals move can be a crucial determinant for many aspects of their life history, including survival and fitness (Rasmussen and Belk 2017). While some animals move over land or through the air and can be readily observed, tracking the movement of fish underwater has historically been more difficult. The earliest recorded attempts at marking fish go back to Walton (1653) and involve tying ribbons around the caudal peduncles of salmon. While tags and tracking techniques are continuously evolving, the scientific field of movement ecology is experiencing a paradigm shift towards more differentiation of different forms of movement and more quantitative rather than qualitative descriptions of movement (Nathan et al. 2008). This holds particularly true in fish ecology in which there is an increasing focus on differentiating different forms of movement (Radinger and Wolter 2014; Brodersen, Hansen, and Skov 2019) and quantifying differences among individuals and populations in response to environmental variables (e.g. Sousa et al. 2016; Kessel et al. 2018; Villegas-Ríos et al. 2018).

Passive integrated transponder (PIT) telemetry has been increasingly used in studying fish ecology and provided great insights into habitat use (Teixeira and Cortes 2007; Bottcher et al. 2013), survival (Weber et al. 2016), causes (Dermond, Melián, and Brodersen 2019) and consequences (Pärssinen et al. 2020) of migration, or movement in response to resource dynamics (Bentley et al. 2015). PIT telemetry uses the general mark-recapture framework, which consists in repeating observations of marked individuals over time and space to estimate survival and movements. Analysis of mark-recapture data relies on several assumptions (Pledger, Pollock, and Norris 2003). In particular, models must account for method artefacts, such as heterogeneity in detection probability (Pollock 1982) and tag loss (Arnason and Mills 1981). It is therefore necessary to understand method limitations to verify assumptions underlying mark-recapture models.

A PIT-tag consists of an electronic chip, a capacitor and an antenna coil encapsulated in a biocompatible glass that sends a unique alphanumeric code when energized by a scanning device. As they do not require an internal battery, PIT-tags offer a small, cheap and long life technology for barcoding individuals. Identification of individuals is commonly made during recaptures or *in situ* by an automated scanning device. For instance, stationary antennas can record fish passage in small streams, even when fish swim at ground speeds up to 3.6 $m.s^{-1}$ (Prentice 1990). For the past two decades, mobile antenna have been developed to actively track individuals, and are particularly suitable to detect small fish in shallow streams (Roussel, Haro, and Cunjak 2000), offering an interesting alternative to radio telemetry. However, limitation of the method has only been evaluated in enclosure set-ups (O'Donnell, Horton, and Letcher 2010; J. Cucherousset et al. 2010), in comparison with other methods such as electrofishing (Sloat, Baker, and Ligon 2011) or radio telemetry (Enders et al. 2007), and in natural systems but without retrospective information about the true presence of fish (Hodge et al. 2015). Thus, the potential of tracking with mobile antenna to study fish ecology has hitherto not been evaluated in natural conditions over the long term and with precise knowledge of the fate of tagged fish.

PIT-tag detection requires close proximity between the mobile antenna and the tag, typically less than 90 cm for a 23 mm tag (Linnansaari et al. 2007). Thus, detection efficiency, as defined as the probability of detection, depends on the interaction between the observer, behaviour of the tagged fish and the environment. The outcome efficiency of this complex interaction remains unclear although it has been partially explored in different studies using different approaches, either in closed systems or with undetermined fate of the tag. Observer experience obviously has a significant impact on detection, as demonstrated in an experimental set-up (O'Donnell, Horton, and Letcher 2010). Due to method limitation, efficiency depends on tag size as it increases detection range (Zentner et al. 2021), and can be negatively affected by physical parameters such as stream velocity (O'Donnell, Horton, and Letcher 2010) or depth (Burnett et al. 2017). All parameters being equal, fish species is a crucial determinant of detection efficiency, varying from near completely inefficient (<1%) in highly mobile species such as *Leuciscus leuciscus* (common dace), to 43% in territorial fishes such as salmonids (Cucherousset et al. 2010). In addition, environmental features have a species-dependent effect on detection efficiency. For instance, detection efficiency increases with boulder percentage in *Cottus cognatus* (slimy sculpin) (Keeler et al. 2007), while habitat complexity either increases detection in *Neogobius melanostomus* (round goby) (Cookingham and Ruetz III 2008) or decreases it in *Salmo trutta* (brown trout) (Weber et al. 2016). Habitat features such as deep holes or undercut banks that provide shelters to fish are expected to decrease detection, especially in salmonids (Hill et al. 2006). Within species, size or age also influence detection because of ontogenetic niche shifts (Kelly et al. 2017), likely in interaction with available habitats in the stream.

The high longevity of PIT-tags also leads to a potential accumulation of tags in the environment, which comes from fish dying or expelling their tags, also referred to as 'ghost tags'. This is particularly a concern in mobile antenna tracking, where tag movement is not necessary for detection, and the tag status thereby is uncertain (i.e. ghost or fish). Movement patterns can be used to discriminate ghost tags (Stout et al. 2019), although ghost tag displacements can mimic fish movements (Bond et al. 2019), as ghost tags can be displaced downstream by currents and carcasses can be carried over large distances both upstream and downstream by scavengers (Havn et al. 2017). In addition, accumulation of ghost tags can decrease the detection efficiency when tracking because of 'tag collision' and generate a source of error for future studies (Šmejkal et al. 2020).

Thus, it is crucial to understand exactly what is detected and what is not. For instance, detection of ghost tags and/or a bias in detection between individuals will bias interpretation of survival, movement pattern or habitat use. Here, we used a unique data set that combined six years of tagging, active tracking, stationary antenna monitoring and recapture of *Salmo trutta* (brown trout) to estimate the method limitation in natural conditions. The two main objectives were to evaluate the environmental and individual factors affecting detection efficiency, and how to interpret mobile antenna tracking detection events.

METHOD

All methods and the handling of live fish were assessed by the regional veterinary office regulating animal experimentation and approved under permit number LU08/17. The cantonal fisheries authorities gave all necessary electrofishing permits.

Data collection

Site description

We conducted the study in 14 streams of the Lake Lucerne drainage, Switzerland (Table 1). The streams are all ground-water fed streams, meaning that their flow regime stays stable over time even during moderately heavy rainfall events. We placed an automatic PIT-tag detection system, composed of dual loop antenna connected to a multiplex PIT-tag reader (Oregon RFID) that can detect fish leaving the system (Dermond, Melián, and Brodersen 2019), at the mouth of each stream. In June 2017 and 2018, we measured habitat features of streams. We divided each stream into sections (length mean 160 meters, sd=64), which we characterized by counting visually (1) the relative proportion of runs, fast runs, riffles, shallow water and pools, (2) the proportion of stream bank with vegetation and undercut banks, (3) the proportion of stream with overhead cover, and (4) the proportion of mud, sand, gravel, cobble and large stone by visual observations of the substrate (see Table 1 for description of environmental data). We measured depth, width and velocity at 50, 50 and 5 points linearly distributed in the sections, respectively. We calculated overall stream features as the mean of sections weighted by section length. In the streams, temperature loggers measured water temperature every hour for the time of the study. We calculated daily temperature as the mean of stream temperature during 24 hours. Daily mean temperature when tracking varied between 2°C and 15°C, with a mean of 9°C and a mean of standard deviation within streams of 1.4°C.

Fish tagging

Between 2015 and 2020, we caught wild *Salmo trutta* (brown trout) by electrofishing with a DC backpack (ELT 62-II from Hans Grassl) and tagged them using the method described in Dermond, Melián, and Brodersen (2019). We tagged 17.853 *Salmo trutta* in streams of the Lake Lucerne drainage, including 10.524 in the 14 streams where we carried out mobile antenna tracking (see Additional file 1: Table S1 for description of tagging per stream). We mainly tagged juvenile fish (80% fish < 180 mm). Fish were anesthetized (MS-222®, tricaine methanesulfonate, $0.067gl^{-1}$), measured and weighed to the nearest mm and 0.1 g, respectively, and photographed (standardized and cuvette pictures), and sampled for adipose fin clips and scales. Fish length refers to total length, meaning that we measured fish from the tip of the snout to the tip of the caudal fin. Sex was visually determined for mature individuals and genetically determined for a subset of juveniles caught in 2015 (Hunziker 2020). We surgically implanted PIT-tags (HDX 23 mm, 0.6 g, Oregon RFID, USA) in the fish's peritoneal cavity using a scalpel to incise fish skin. We treated the incision to prevent infection (Koi Med Wound Snow©). Fish recovered in oxygenated water tanks and we then released them in the original section where we caught them. Minimum tagged fish length was 101 mm (mean=162 mm) following experimental recommendations that resulted in 100% survival above this size (Larsen et al. 2013). Field surveys also indicate no long-term effects of PIT-tagging on fish body condition (Skov et al. 2020). We calculated body condition as: $K=10^5.W/L^3$, where K, W and L denote body condition, weight (g) and total length (mm), respectively (Bolger and Connolly 1989).

Mobile antenna tracking data collection

Over six years (2015-2020), we performed PIT-tag mobile antenna tracking in 14 streams in summer or late spring and fall (see Additional file 2: Table S2 for description of tracking per stream), with the potential to detect 5169 tags (i.e. number of unique tagged fish in streams that we tracked afterwards). Within a year, we tracked each stream twice on average (mean=2.3 min=1, max=5) with a one-week interval. We tracked all the streams for more than a year, and we tracked six streams continuously over six years from 2015 to 2020. When tracking had to be interrupted (e.g. due to heavy rain) or when the mobile antenna was malfunctioning, we repeated the tracking and did not include the data from the interrupted event in the subsequent analysis. We performed the tracking by walking through the stream in the upstream direction during daytime (between 08:23 and 17:44), from the downstream stationary antenna to the upstream natural boundary, hereafter defined as one-pass tracking. The operator used a mobile antenna (mobile reader kit, OregonRFID) to scan the stream bottom while walking and covered the whole stream area by moving the antenna left and right. For each detection, we recorded the tag ID, time, GPS waypoint and when possible habitat features around the detection event. After detection, the operator scanned the detection location a second time within a one-minute period and we recorded escape response (moved if the tag was not detected again, sometimes confirmed by visual observation of the fish swimming away). We made 8109 detections in total from mobile antenna tracking (including redetection and all tags, mean detection events of 3.0 per tag, S.D=2.4, median=2.0, maximum=17). We clearly identified 209 ghost tags while tracking when we detected them on the shore or in very shallow waters with no fish, and we therefore excluded those tags in the analysis.

Fish recapture

During tagging sessions, we made 1724 cumulated recaptures based on PIT-tag identification of 1328 individual resident fish (maximum number of recaptures per fish=6, see Additional file 1: Table S1 for description of recapture per stream). Based on a previous study in a comparable system that showed a high concordance between PIT-tag mobile antenna tracking and electrofishing under different environmental conditions (Sloat, Baker, and Ligon 2011), we assumed that the way fish were recaptured was not related to their PIT-tag detectability. We classified fish between resident and migrating fish based on their phenotype, as returners from the lake show a distinct phenotype (silvery body coloration and lack of red spots). We used the identification of recaptures to estimate the efficiency of active tracking (see Analyses). We also visually identified 128 tag losses by the observation of abdomen incision and/or cut adipose fin. All data were then processed and analysed in R (R Core Team 2020).

Analyses

Environmental factors

To avoid multi-collinearity between environmental variables (Johnston, Jones, and Manley 2018) (e.g. positive correlations between percentage of mud and vegetation r=0.75 or mean width and maximum depth r=0.71), we performed a principal component analysis (PCA) which included mean and maximum depth, mean width, total length, habitats, flowing regime and substrate composition (Table 1). We did not include velocity because of missing data. PCA composition of the three main axes can be found in Additional material: Table S3.

Logistic regression and model selection

We fitted three binary responses (PIT-tag detection, tag loss and escape response) to logistic regressions with the glm function in R. To select the best fit between different sets of explanatory variables, we performed a model selection based on the Akaike information criterion (AIC) (Burnham, Anderson, and Burnham 2002). We implemented model selection using the stepAIC function in *MASS* package (Venables, W.N. 2002) which is a stepwise algorithm to select for the best fit. We used a bidirectional approach (direction='both') which means that at each step the algorithm will add or remove a variable based on the lowest AIC. After model selection, we calculated McFadden's pseudo-R^2 (R^2_{McFadden}) which denotes the proportion of explained variation compared to the null model, using the package *pscl* (Jackman 2020). We also performed a Wald test to calculate the significance of the model. For significant models, we calculated variable effects using the package *effects* (Fox 2019). For all model selection, we did not include fish sex as a candidate variable at first because of missing data, but later tested the effect of sex on the best model using the subset data of sexed fish. In the subsequent sections, we describe the datasets and some hypothesis behind each of the five models. Summary of model selection can be found in Table 2.

Model 1: Fish detection efficiency

We evaluated the detectability of living fish in streams based on detection of tagged fish present in the stream in a one-pass tracking. Due to our experimental setup, we were able to precisely determine some of the tagged fish that were alive and present in streams during the tracking period. We considered that a fish was present in the stream if it was recaptured after the tracking in a one-year period and present in the stream. We were able to determine movements of fish outside the stream because each stream was limited by a natural barrier upstream and equipped with a stationary PIT-antenna downstream. Thus, we excluded all fish that were detected out migrating (fish that permanently left before returning to spawn, Dermond, Melián, and Brodersen 2019). We also excluded all fish that left and entered the stream but were detected only once (at entry or departure), because in that case we were not able to conclude on the time of presence in the stream. A recaptured fish that would not have been present during tracking implies that the fish was detected twice by the stationary antenna (at departure before tracking and entry after tracking). As the probability of a stationary antenna malfunctioning twice on different days in very low, we were confident that all fish considered in the analysis were indeed present during tracking. In addition, only nine fish considered in this model were detected by the stationary antenna, supporting that they showed little inter-creek movements.

The model selection included eleven candidate variables: fish length, fish somatic condition, day of the year, repetition, stream temperature and the three main PCA axes of environmental data as continuous variables, and year and stream as categorical variables. We did not include interaction of fish length and temperature because of skewed distribution of fish length relative to temperature (few fish >300 mm for low and high temperatures). The minimum number of potential detections in one stream was 12 (see Additional material: Table S2), and all streams showed comparable variation of fish length.

After model selection, we performed an additional regression adding sex as a variable to the best fit, and included interaction between sex and the other variables. We specifically hypothesized that sex would affect detectability in adult fish that are characterized by sex-specific life histories and behaviour.

Model 2: Tag loss

We evaluated individual probability to expel tag based on tag loss at recapture. This model included all recaptured resident fish from the Lake Lucerne drainage, even in streams that were not tracked (see Additional file 1: Table S1). The model selection included four variables: fish length, fish somatic condition, season (two levels: late summer-fall and winter when trout spawn) and streams (categorical). After model selection, we performed an additional regression adding sex as variable to the best fit, and included interaction between sex and the other variables. We hypothesized that mature females would be more likely to expel tags because of spawning behaviour (abdomen squeezing by males to release eggs).

Model 3: Escape response to detection of living fish

We evaluated individual propensity to escape after detection. A fish was classified as escaping based on the observations by the operators of fish swimming away after detection and/or by the absence of redetection in a one-minute period after the first detection. The model only included detected fish that were recaptured later, meaning that they were alive at the time of detection. By doing so, probability to escape was not biased by ghost tag detection and we could use phenotype at recapture as a proxy of phenotype at detection. The model selection included six variables: fish length, fish somatic condition, day of the year, stream temperature, stream and year. After model selection, we performed an additional regression adding sex as a variable to the best fit.

Model 4: In-situ survival (Escape response to detection of all detected tags)

We evaluated survival response of tags that we detected. As we assumed that escape response to detection was a stochastic phenomenon (see Results), we used the proportion of escaping individuals to infer the proportion of fish alive that we detected, referred to as "*in-situ* survival". The response variable was the escape response of tag at detection (see above). The model selection included six variables: stream, three main PCA axes of environmental data, fish length, time after tagging and its interaction with fish length. After model selection, we performed an additional regression adding sex as variable to the best fit, and included interaction between sex and the other variables.

We then estimated the overall proportion of ghost tags that we detected through time (e.g. proportion of ghost tags after 3 years include detection in 2018 and 2019 of tags from fish tagged in 2015 and 2016, respectively). To do so, we measured the confidence interval of living fish for each cohort of time after tagging, using the proportion of tags that moved and the probability of moving when alive (P=0.13, see Results).

Model 5: Tag detection

We evaluated the probability of tag detection, also referred as "apparent survival" in other studies, based on tag detection on a one-pass tracking. The model included only tags potentially present in streams (i.e. excluding migrants) and all detections (i.e. also including ghost tags). The model selection included six variables: stream, three main PCA axes of environmental data, fish length, time after tagging and its interaction with fish length. Because most detections were comprised of ghost tags (see Results), we did not include stream temperature in this model, as we did not expect it to affect ghost tag detectability and ghost tag retention in streams. After model selection, we performed an additional regression adding sex as variable to the best fit, and included interaction between sex and the other variables. We hypothesized that sex would have no effect on survival, irrespective of length, and thus no effect on tag detectability.

Depletion curves

To visualize how inter-individual variability in detectability affected estimate of the number of tags detected, we simulated depletion curves (i.e. cumulated proportion of detected tags with passes). In a homogeneous population, the proportion of detected tags (D) follows $D=1-(1-P)^N$, where P and N denote the detection probability and the number of passes, respectively. In a heterogeneous population, $D=\sum_i \mathrm{xi}.[1-(1-\mathrm{Pi})^N]$ where xi and Pi are the proportion and probability of detection in the sub-group i, respectively. For illustration, we fitted depletion curves with tracking data from 2020 in which we had three passes for six streams (see Additional material: Table S1). To do so, we calculated the cumulated number of detected tags for all combinations of visit orders. We then fitted the values to a logistic function of three parameters.

Results

Fish detection efficiency

Among fish that were present in the streams, average detection efficiency was 43% (95% confidence interval [40% - 46%]). Detection was best predicted by fish length, stream and year (Table 2). Fish length had a drastic influence on detection. For instance, a 500 mm fish was three times less likely to be detected than a 200 mm fish (Fig. 1A). Within sexed fish, detection was best predicted by adding sex and its interaction with fish length (Table 2). At larger sizes, males were less likely to be detected (Fig. 1B). Slight effects were observed between years (Fig. 1C), and with stream temperature when tracking (Fig. 1D). The model that included the day of the year had a slight AIC difference (Table 2), suggesting that the time of year could also affect efficiency.

The 14 streams where we carried out active tracking formed a continuum along the first PCA axis (26% of variation), from on average deep, muddy and with more vegetation and area of shallow slowly running water to streams with more riparian vegetation cover and riffles. The second PCA axis (19% of variation) differentiated streams mainly according to length and proportion of undercut banks and sand (Fig. 2A). Detection was best predicted when adding streams as categorical factors, rather than considering environmental variables resulting from the PCA analysis (Table 2). Six streams had high uncertainty around the estimate because of limited data (see Additional material: Table S2, for recapture-tracking design). Among the eight other streams, the estimates of effect varied in less than a one-to-two ratio except for Lochrütibach, which has a high efficiency determined with high confidence. We found a significant positive correlation with width (Fig. 2C). We did not find correlations with other stream features (Table 1).

Tag loss

Individual tag loss was best predicted by fish length and somatic condition (Table 2). Larger individuals with lower somatic condition were more likely to expel their tags (Fig. 3A & B). Within sexed fish, detection was best predicted by adding sex as variable (Table 2), with no interactive effects between sex and either length or somatic condition. Sex had a strong effect on tag loss probability, with females being around four times more likely to have lost their tag at recapture (Fig. 3C). Altogether, the results showed that tag loss mainly occurred in large females. For instance, fish <200 mm (juveniles) with average somatic condition had low probability of tag expulsion (2.1%), while females >400 mm in low somatic condition (0.8) had more than 30% chance to have expelled their tags at recapture, suggesting that female spawning behaviour induces tag loss.

Escape response at detection of living fish

Escape response at detection was low with an average of 0.13 (55/427, 95% confidence interval [0.10 – 0.16]), and best predicted by a null model (Table 2). The model on sexed fish including fish sex had a slightly higher AIC, but this model was not statistically significant. Habitat recorded at detection did not differ between escaping and not moving individuals (chi-square test d.f = 5, P=0.83, X-squared = 2.15), suggesting that escape response did not differ between habitats (mainly vegetation 43%, under banks 25%, and stones 13%). Thus, we modelled escape response as a stochastic event with a probability of 0.13 in order to estimate the proportion of living fish.

In-situ survival (Escape response at detection of all detected tags)

The escape response at detection for all detected tags was best predicted by streams (Table 1) and time after tagging (Table 2) reflecting *in-situ* mortality and tag loss (i.e. increase of ghost tag detection probability), with no interactive effect of fish length and time. This estimate of *in-situ* survival only includes tags that we detected in the streams, thereby omitting avian predation or out-migrating individuals, for instance. The logistic intercept at t=0 matched the probability of escape response that we found with living individuals (13% ± 3%, see above). Among sexed individuals, escape response was best predicted by adding sex and its interaction with fish length (Table 2). Based on this probability, the estimate of ghost tags showed a linear accumulation within two years after tagging before it reached a plateau of around 80% (Fig. 4C). This means that around 80% of tags that we detected two years post-tagging were ghost tags.

Tag detection

Overall detection probability of resident fish tags was best predicted by streams (Table 1), time after tagging (Fig. 5A) and its interactive effect with fish length (Fig. 5B, Table 2). Fish length had no effect alone on overall fish detection (P=0.06). After only one spring, we estimated a detection probability of 0.15, which then decreases by around 20% per year, meaning that after five years the detection probability was around 0.05 (Fig. 5A).

Among sexed fish, the model was best predicted by adding sex and its interactive effect with time after tagging (Fig. 5C), and fish length (Fig. 5D, Table 2).

Depletion curves

Theoretical depletion curves with inter-variability of detection probability (but same average detection probability) showed different growth with the number of passes (Fig. 6A, blue and green lines). Our empirical depletion curves showed similar growth to heterogeneous populations with easily detectable tags and tagged fish with low detection probability (Fig. 6B).

Discussion

Factors influencing fish detection

We determined detection efficiency of mobile PIT-Tag antennas under natural conditions with inclusion of recapture data and stationary PIT-antennas, which allowed us to monitor continuous presence of some individuals in the investigated streams. Using this methodology, we evaluated the potential of mobile antennas in multiple natural streams over a long period of time (>5 years) across a range of variation in time, space and individual variability that greatly exceeds that of previous literature in the field (Kelly et al. 2017; Breen et al. 2009). We determined average detection efficiency to be 43% with a very narrow confidence interval of only ± 3%. This value is in line with previous studies on *Salmo trutta* under similar conditions that reported efficiency of 43% (Cucherousset et al. 2010) or 39% (Enders et al. 2007).

The strongest effect we found on detection probability was fish size, with large individuals being up to five times less likely to be detected than small ones. As we were able to confirm the presence of fish during active tracking, we suggest two non-exclusive hypotheses that could account for the size effect. First, *Salmo trutta* prefer deeper habitats with increasing size (Ayllón et al. 2010), which may decrease detection ability. Second, larger trout may have higher tendency and/or ability to flee the operator, potentially as an alternative to hiding. We did not find that size predicted escape response after detection, but larger fish likely have the ability to escape the operator before first detection, as suggested in a previous study (Cucherousset et al. 2005). Additionally, our results indicate a sex effect on detection, in interaction with fish length. With increasing size, males are less likely to be detected than females. Again, this is likely due to differences in behaviour between sexes. For instance, a previous study in an enclosure set-up has shown that *Salmo trutta* males tend to spend much more time in deep pools than females (Greenberg and Giller 2001).

Our model also showed that efficiency depended to a lesser extent on streams, which were better explanatory variables than environmental variables. Yet, the low number of potential detections in some streams might have affected our ability to identify environmental variables associated with tracking efficiency, and resulted in a large confidence interval for some stream effects. Streams that clustered together on the PCA analysis had distinct efficiency estimates, suggesting that our environmental data did not encompass the main factors influencing fish detection. In particular, we expect that the number of artificial structures that we did not measure (e.g. bridges and pipes) decrease efficiency by providing refuge to fish or by creating metal interference with the detector. In addition, the mean of an environmental variable might not be representative of the local effects of a parameter (e.g. deep ponds), which interacts with other variables (e.g. deep ponds with vegetation that decrease detection efficiency). We nonetheless found that efficiency increases with river width. On one hand, narrower streams may facilitate scanning by the operator, as fish cannot easily move away from the antenna. On the other hand, narrower streams in our system were sometimes hard to access for the operators due to abundant overhanging riparian vegetation. Within streams, temperature on the day of tracking had a positive effect on fish detectability. *Salmo trutta* can change their behaviour in response to different temperatures (Vehanen et al. 2000), and the commonly increasing use of microhabitat with more cover at lower temperature may decrease our ability to detect them.

Escape response of fish to infer in-situ survival

Another limitation of PIT telemetry is to deal with the presence of ghost tags that come from either tag loss or fish death. Our results show that tag retention is high in juveniles, consistent with laboratory experiments (Hanson et al. 2020). However, our results show that tag loss is most common in large females. We hypothesize that the squeezing of female abdomen to release their eggs is a cause of tag loss. This result is also supported by our observation of ghost tags in spawning pits and similar findings in a cyprinid fish (Šmejkal et al. 2019). While it is sometimes possible to either visually detect ghost tags (O'Donnell, Horton, and Letcher 2010; Breen et al. 2009) or identify them by their movement patterns (Hodge et al. 2015; Zydlewski et al. 2001), this can be difficult for species or individuals that are highly sedentary (Rodríguez 2002) or that live in environments that facilitate movement of ghost tags (Bond et al. 2019). We therefore used a novel approach, based on the escape response of living fish, which we found to be stochastic. The low probability of escape response at detection (0.13) was in line with a previous experiment that showed little escape response to trout scanned by mobile antennas (Hill et al. 2006), suggesting that trout are more inclined to stay under cover than try to escape from a potential predator.

By calculating the proportion of known living fish that showed an escape response, we were able to estimate the number of total detected tags that should have moved given that they were all living fish, and thus the proportion of ghost tags. Our results clearly show that detection more than two years after tagging is mainly explained by ghost tags (>80% of detections). Given that most of tagged fish were juveniles and that tag loss is rare (especially in juveniles <2.1%), those ghost might come from birds that represent the main predators. Despite the fact that they are terrestrial predators; we hypothesize that a substantial amount of tags ends in the streams when birds are predating. Ghost tags also probably contribute disproportionally to detections because they might be easier to detect (see high detection rates with tags alone, O'Donnell, Horton, and Letcher 2010). We also found that streams differed in their *in-situ* survival (i.e. proportion of ghost tag). This result is likely biased by differences in ghost tag dynamics, determined by flow regime, storm events and substrate composition (Bond et al. 2019; Stout et al. 2019). Each stream has a different population structure and unique ghost tag dynamic. As a result, our simulation of depletion curves indicates that it is hard to predict the total number of tags based on asymptotic inference from few passes. More experiments using seeded tags would be required to correctly interpret ghost tag detections, and thus survival.

Interpretation of detection events

We showed that fish length had an effect on detection probability, which was however not reflected in the absolute number of tag detections. After one spring, overall detection probability of resident fish (i.e. not classified as migrant by the downstream antenna) was around 15% with no significant effect of fish size. Using a different experimental setup than ours, one might infer that detection probability is merely globally low. However, our use of recapture data suggests that small and large fish remain undetected for different reasons. We suggest that around 70% of resident small fish (<200 mm) are missing from the streams after one spring, and are therefore no longer present to be detected. Large resident fish (>300 mm) show a very high survival, but are more difficult to detect even when present. In addition, larger fish expel more tags, which are interpreted as dead fish by the escape response model. As we did not observe differences in *in-situ* survival among sizes (i.e. no difference in escape responses), the true survival of larger fish is even more underestimated. The low survival of smaller fish could be attributed to two non-exclusive hypotheses. First, it is possible that some migrants were not recorded at the stationary antenna (efficiency typically between 96-100%, Connolly et al. 2008). Secondly, it suggests that predation by terrestrial predators is stronger on smaller trout, partially supported by heron colony tracking (data not shown) and past studies that showed the strong effect of salmonid size on avian predation susceptibility (Osterback et al. 2014; Hostetter et al. 2012). This estimate of survival also includes migrating individuals that are more vulnerable to predation (Thorstad et al. 2012), and were eaten before they could reach the downstream antenna.

We also found an interactive effect of length and time after tagging on the probability of detection, suggesting that size at tagging has long-term effects on survival. However, the increase of tag detection in large females that we observed over time is likely an artefact of ghost tags that were expelled, as shown by the escape response model. Our results highlight the importance of considering individual effects on detection probability and ghost tag accumulation to correctly interpret tag detection events.

Implications of method artefacts for modelling movement and survival

Movement and survival of wild population are commonly studied by mark-recapture models applied to several methods. Despite the advance of new technologies, such as PIT-tags, each method is associated with artefacts that affect model estimates. Heterogeneity in probability of detection, such as the length effect found in our study, is particularly problematic in standard mark-recapture models (Link 2003). This artefact is ubiquitous among methods (e.g. classic recapture or observation Ogutu et al. 2006, telemetry Keeler et al. 2007, feces sampling Cubaynes et al. 2010, camera trap Noyce 2021) and among taxa, from large organisms to plants (e.g. seed dormancy, Shefferson et al. 2001). In addition, habitat (e.g. streams in our study) and environment variability (e.g. temperature in our study) also have the potential to affect detectability, with consequences on movement and survival estimates (Bailey, Simons, and

Pollock 2004). Several models have been developed to deal with these biases (Pollock 1982; Pledger, Pollock, and Norris 2003), but they may require *a priori* knowledge on detectability. For instance, our study showed that spawning females were more likely to expel tags, creating detection artefacts from expelled ghost tags. This effect would not have been detected with *a posteriori* model analysis alone (i.e. the model would have predicted higher *in-situ* mortality in large females).

Altogether, our data highlight that a thorough understanding of the method is required to characterize survival and movements over long term and make comparison across different environmental conditions.

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CONTRIBUTIONS

JB supervised the study. JB conceived and designed the field study and data collection. JB and PD led the fieldwork and data collection. GS analysed and interpreted the data with substantial input from JB and input from PD. GS led the writing of the manuscript with inputs from JB and PD. All authors reviewed and agreed upon the final version of the manuscript.

REFERENCES

Arnason, A. N., and K. H. Mills. 1981. “Bias and Loss of Precision Due to Tag Loss in Jolly–Seber Estimates for Mark–Recapture Experiments.” *Canadian Journal of Fisheries and Aquatic Sciences* 38 (9): 1077–95. https://doi.org/10.1139/f81-148.

Ayllón, D., A. Almodóvar, G. G. Nicola, and B. Elvira. 2010. “Ontogenetic and Spatial Variations in Brown Trout Habitat Selection: Plasticity of Brown Trout Habitat Selection.” *Ecology of Freshwater Fish* 19 (3): 420–32. https://doi.org/10.1111/j.1600-0633.2010.00426.x.

Bailey, Larissa L., Theodore R. Simons, and Kenneth H. Pollock. 2004. “SPATIAL AND TEMPORAL VARIATION IN DETECTION PROBABILITY OF PLETHODON SALAMANDERS USING THE ROBUST CAPTURE–RECAPTURE DESIGN.” *Journal of Wildlife Management* 68 (1): 14–24. https://doi.org/10.2193/0022-541X(2004)068[0014:SATVID]2.0.CO;2.

Bolger, T., and P. L. Connolly. 1989. “The Selection of Suitable Indices for the Measurement and Analysis of Fish Condition.” *Journal of Fish Biology* 34 (2): 171–82. https://doi.org/10.1111/j.1095-8649.1989.tb03300.x.

Bond, Rosealea M., Colin L. Nicol, Joseph D. Kiernan, and Brian C. Spence. 2019. “Occurrence, Fate, and Confounding Influence of Ghost Passive Integrated Transponder Tags in an Intensively Monitored Watershed.” *Canadian Journal of Fisheries and Aquatic Sciences* 76 (2): 286–98. https://doi.org/10.1139/cjfas-2017-0409.

Bottcher, Jared L., Timothy E. Walsworth, Gary P. Thiede, Phaedra Budy, and David W. Speas. 2013. “Frequent Usage of Tributaries by the Endangered Fishes of the Upper Colorado River Basin: Observations from the San Rafael River, Utah.” *North American Journal of Fisheries Management* 33 (3): 585–94. https://doi.org/10.1080/02755947.2013.785993.

Breen, Matthew J., Carl R. Ruetz, Kurt J. Thompson, and Steven L. Kohler. 2009. “Movements of Mottled Sculpins (Cottus Bairdii) in a Michigan Stream: How Restricted Are They?” *Canadian Journal of Fisheries and Aquatic Sciences* 66 (1): 31–41. https://doi.org/10.1139/F08-189.

Brodersen, Jakob, Joan H. Hansen, and Christian Skov. 2019. “Partial Nomadism in Large-bodied Bream (*Abramis Brama*).” *Ecology of Freshwater Fish* 28 (4): 650–60. https://doi.org/10.1111/eff.12483.

Burnett, N. J., S. G. Hinch, N. N. Bett, D. C. Braun, M. T. Casselman, S. J. Cooke, A. Gelchu, et al. 2017. “Reducing Carryover Effects on the Migration and Spawning Success of Sockeye Salmon through a Management Experiment of Dam Flows.” *River Research and Applications* 33 (1): 3–15. https://doi.org/10.1002/rra.3051.

Burnham, Kenneth P., David Raymond Anderson, and Kenneth P. Burnham. 2002. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. 2nd ed. New York: Springer.

Connolly, Patrick J., Ian G. Jezorek, Kyle D. Martens, and Earl F. Prentice. 2008. “Measuring the Performance of Two Stationary Interrogation Systems for Detecting Downstream and Upstream Movement of PIT-Tagged Salmonids.” *North American Journal of Fisheries Management* 28 (2): 402–17. https://doi.org/10.1577/M07-008.1.

Cookingham, M. N., and C. R. Ruetz III. 2008. “Evaluating Passive Integrated Transponder Tags for Tracking Movements of Round Gobies.” *Ecology of Freshwater Fish* 17 (2): 303–11. https://doi.org/10.1111/j.1600-0633.2007.00282.x.

Cubaynes, Sarah, Roger Pradel, Rémi Choquet, Christophe Duchamp, Jean-Michel Gaillard, Jean-Dominique Lebreton, Eric Marboutin, et al. 2010. “Importance of Accounting for Detection Heterogeneity When Estimating Abundance: The Case of French Wolves.” *Conservation Biology* 24 (2): 621–26. https://doi.org/10.1111/j.1523-1739.2009.01431.x.

Cucherousset, J., J. R. Britton, W. R. C. Beaumont, M. Nyqvist, K. Sievers, and R. E. Gozlan. 2010. “Determining the Effects of Species, Environmental Conditions and Tracking Method on the Detection Efficiency of Portable PIT Telemetry.” *Journal of Fish Biology* 76 (4): 1039–45. https://doi.org/10.1111/j.1095-8649.2010.02543.x.

Cucherousset, Julien, Jean-Marc Roussel, Rachel Keeler, Richard A. Cunjak, and Roland Stump. 2005. “The Use of Two New Portable 12-Mm PIT Tag Detectors to Track Small Fish in Shallow Streams.” *North American Journal of Fisheries Management* 25 (1): 270–74. https://doi.org/10.1577/M04-053.1.

Dermond, Philip, Carlos J. Melián, and Jakob Brodersen. 2019. “Size-Dependent Tradeoffs in Seasonal Freshwater Environments Facilitate Differential Salmonid Migration.” *Movement Ecology* 7 (1): 40. https://doi.org/10.1186/s40462-019-0185-1.

Enders, Eva C., Keith D. Clarke, Curtis J. Pennell, L. M. Neil Ollerhead, and David A. Scruton. 2007. “Comparison between PIT and Radio Telemetry to Evaluate Winter Habitat Use and Activity

Patterns of Juvenile Atlantic Salmon and Brown Trout." *Hydrobiologia* 582 (1): 231–42. https://doi.org/10.1007/s10750-006-0562-9.

Fox, John, Sanford Weisberg. 2019. *An R Companion to Applied Regression*. 3rd Edition. CA: Thousand Oaks. <http://tinyurl.com/carbook>.

Greenberg, Larry A., and Paul S. Giller. 2001. "Individual Variation in Habitat Use and Growth of Male and Female Brown Trout." *Ecography* 24 (2): 212–24. https://doi.org/10.1034/j.1600-0587.2001.240212.x.

Hanson, Barry J., Jacob L. Davis, Jill M. Voorhees, Nathan Huysman, and Michael E. Barnes. 2020. "Long-Term Passive Integrated Transponders (PIT) Tag Retention in Juvenile Rainbow Trout and Brown Trout." *Open Journal of Marine Science* 10 (03): 110–15. https://doi.org/10.4236/ojms.2020.103008.

Havn, T. B., F. Økland, M. A. K. Teichert, L. Heermann, J. Borcherding, S. A. Sæther, M. Tambets, O. H. Diserud, and E. B. Thorstad. 2017. "Movements of Dead Fish in Rivers." *Animal Biotelemetry* 5 (1): 7. https://doi.org/10.1186/s40317-017-0122-2.

Hill, Megan S., Gayle B. Zydlewski, Joseph D. Zydlewski, and James M. Gasvoda. 2006. "Development and Evaluation of Portable PIT Tag Detection Units: PITpacks." *Fisheries Research* 77 (1): 102–9. https://doi.org/10.1016/j.fishres.2005.08.001.

Hodge, Brian W., Richard Henderson, Kevin B. Rogers, and Kyle D. Battige. 2015. "Efficacy of Portable PIT Detectors for Tracking Long-Term Movement of Colorado River Cutthroat Trout in a Small Montane Stream." *North American Journal of Fisheries Management* 35 (3): 605–10. https://doi.org/10.1080/02755947.2015.1012280.

Hostetter, Nathan J., Allen F. Evans, Daniel D. Roby, and Ken Collis. 2012. "Susceptibility of Juvenile Steelhead to Avian Predation: The Influence of Individual Fish Characteristics and River Conditions." *Transactions of the American Fisheries Society* 141 (6): 1586–99. https://doi.org/10.1080/00028487.2012.716011.

Hunziker Y. 2020. "Influence of Sex on Juvenile Brown Trout Migratory Patterns." Master thesis.

Jackman, Simon. 2020. "Pscl: Classes and Methods for R Developed in the Political Science Computational Laboratory. United States Studies. Centre, University of Sydney. Sydney, New South Wales, Australia. R Package Version 1.5.5." https://github.com/atahk/pscl/.

Johnston, Ron, Kelvyn Jones, and David Manley. 2018. "Confounding and Collinearity in Regression Analysis: A Cautionary Tale and an Alternative Procedure, Illustrated by Studies of British Voting Behaviour." *Quality & Quantity* 52 (4): 1957–76. https://doi.org/10.1007/s11135-017-0584-6.

Keeler, Rachel A., AndréR. Breton, Douglas P. Peterson, and Richard A. Cunjak. 2007. "Apparent Survival and Detection Estimates for PIT-Tagged Slimy Sculpin in Five Small New Brunswick Streams." *Transactions of the American Fisheries Society* 136 (1): 281–92. https://doi.org/10.1577/T05-131.1.

Kelly, Brett B., Joshua B. Cary, Alisha D. Smith, Kasey C. Pregler, Seoghyun Kim, and Yoichiro Kanno. 2017. "Detection Efficiency of a Portable PIT Antenna for Two Small-Bodied Fishes in a Piedmont Stream." *North American Journal of Fisheries Management* 37 (6): 1362–69. https://doi.org/10.1080/02755947.2017.1388886.

Kessel, Steven T., Darryl W. Hondorp, Christopher M. Holbrook, James C. Boase, Justin A. Chiotti, Michael V. Thomas, Todd C. Wills, Edward F. Roseman, Richard Drouin, and Charles C. Krueger. 2018. "Divergent Migration within Lake Sturgeon (*A Cipenser Fulvescens*) Populations: Multiple Distinct Patterns Exist across an Unrestricted Migration Corridor." Edited by Jason Chapman. *Journal of Animal Ecology* 87 (1): 259–73. https://doi.org/10.1111/1365-2656.12772.

Larsen, Martin H, Aske N Thorn, Christian Skov, and Kim Aarestrup. 2013. "Effects of Passive Integrated Transponder Tags on Survival and Growth of Juvenile Atlantic Salmon Salmo Salar." *Animal Biotelemetry* 1 (1): 19. https://doi.org/10.1186/2050-3385-1-19.

Link, William A. 2003. “Nonidentifiability of Population Size from Capture-Recapture Data with Heterogeneous Detection Probabilities.” *Biometrics* 59 (4): 1123–30. https://doi.org/10.1111/j.0006-341X.2003.00129.x.

Linnansaari, Tommi, Jean-Marc Roussel, Richard A. Cunjak, and Jo H. Halleraker. 2007. “Efficacy and Accuracy of Portable PIT-Antennae When Locating Fish in Ice-Covered Streams.” *Hydrobiologia* 582 (1): 281–87. https://doi.org/10.1007/s10750-006-0546-9.

Nathan, R., W. M. Getz, E. Revilla, M. Holyoak, R. Kadmon, D. Saltz, and P. E. Smouse. 2008. “A Movement Ecology Paradigm for Unifying Organismal Movement Research.” *Proceedings of the National Academy of Sciences* 105 (49): 19052–59. https://doi.org/10.1073/pnas.0800375105.

Noyce, Karen V. 2021. “Differential Vulnerability of Black Bears to Trap and Camera Sampling and Resulting Biases in Mark-Recapture Estimates,” 16.

O’Donnell, Matthew J., Gregg E. Horton, and Benjamin H. Letcher. 2010. “Use of Portable Antennas to Estimate Abundance of PIT-Tagged Fish in Small Streams: Factors Affecting Detection Probability.” *North American Journal of Fisheries Management* 30 (2): 323–36. https://doi.org/10.1577/M09-008.1.

Ogutu, J. O., H.-P. Piepho, H. T. Dublin, R. S. Reid, and N. Bhola. 2006. “Application of Mark-Recapture Methods to Lions: Satisfying Assumptions by Using Covariates to Explain Heterogeneity.” *Journal of Zoology* 0 (0): 060423083931002-??? https://doi.org/10.1111/j.1469-7998.2006.00058.x.

Osterback, Ann-Marie K., Danielle M. Frechette, Sean A. Hayes, Morgan H. Bond, Scott A. Shaffer, and Jonathan W. Moore. 2014. “Linking Individual Size and Wild and Hatchery Ancestry to Survival and Predation Risk of Threatened Steelhead (*Oncorhynchus Mykiss*).” Edited by Bror Jonsson. *Canadian Journal of Fisheries and Aquatic Sciences* 71 (12): 1877–87. https://doi.org/10.1139/cjfas-2014-0097.

Pärssinen, Varpu, Kaj Hulthén, Christer Brönmark, Christian Skov, Jakob Brodersen, Henrik Baktoft, Ben B. Chapman, Lars-Anders Hansson, and P. Anders Anders Nilsson. 2020. “Maladaptive Migration Behaviour in Hybrids Links to Predator-mediated Ecological Selection.” *Journal of Animal Ecology*, August, 1365-2656.13308. https://doi.org/10.1111/1365-2656.13308.

Pledger, Shirley, Kenneth H. Pollock, and James L. Norris. 2003. “Open Capture-Recapture Models with Heterogeneity: I. Cormack-Jolly-Seber Model.” *Biometrics* 59 (4): 786–94. https://doi.org/10.1111/j.0006-341X.2003.00092.x.

Pollock, Kenneth H. 1982. “A Capture-Recapture Design Robust to Unequal Probability of Capture.” *The Journal of Wildlife Management* 46 (3): 752. https://doi.org/10.2307/3808568.

Prentice. 1990. “Feasibility of Using Implantable Passive Integrated Transponder (PIT) Tags in Salmonids.”

R Core Team. 2020. *R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing*. Vienna, Austria. https://www.R-project.org/.

Radinger, Johannes, and Christian Wolter. 2014. “Patterns and Predictors of Fish Dispersal in Rivers.” *Fish and Fisheries* 15 (3): 456–73. https://doi.org/10.1111/faf.12028.

Rasmussen, Josh E., and Mark C. Belk. 2017. “Individual Movement of Stream Fishes: Linking Ecological Drivers with Evolutionary Processes.” *Reviews in Fisheries Science & Aquaculture* 25 (1): 70–83. https://doi.org/10.1080/23308249.2016.1232697.

Rodríguez, Marco A. 2002. “RESTRICTED MOVEMENT IN STREAM FISH: THE PARADIGM IS INCOMPLETE, NOT LOST.” *Ecology* 83 (1): 1–13. https://doi.org/10.1890/0012-9658(2002)083[0001:RMISFT]2.0.CO;2.

Roussel, J -M, A Haro, and R A Cunjak. 2000. “Field Test of a New Method for Tracking Small Fishes in Shallow Rivers Using Passive Integrated Transponder (PIT) Technology.” *Canadian Journal of Fisheries and Aquatic Sciences* 57 (7): 1326–29. https://doi.org/10.1139/f00-110.

Shefferson, Richard P., Brett K. Sandercock, Joyce Proper, and Steven R. Beissinger. 2001. “ESTIMATING DORMANCY AND SURVIVAL OF A RARE HERBACEOUS PERENNIAL USING

MARK–RECAPTURE MODELS.” *Ecology* 82 (1): 145–56. https://doi.org/10.1890/0012-9658(2001)082[0145:EDASOA]2.0.CO;2.

Skov, Christian, Joan H. Hansen, Henrik Baktoft, Christer Brönmark, Jakob Brodersen, Ben B. Chapman, Lars-Anders Hansson, Kaj Hulthén, and P. Anders Nilsson. 2020. “A Field Evaluation of Long-term Effects of PIT Tagging.” *Journal of Fish Biology* 96 (4): 1055–59. https://doi.org/10.1111/jfb.14292.

Sloat, Matthew R., Peter F. Baker, and Franklin K. Ligon. 2011. “Estimating Habitat-Specific Abundances of PIT-Tagged Juvenile Salmonids Using Mobile Antennas: A Comparison with Standard Electrofishing Techniques in a Small Stream.” *North American Journal of Fisheries Management* 31 (5): 986–93. https://doi.org/10.1080/02755947.2011.635486.

Šmejkal, Marek, Daniel Bartoň, Vilém Děd, Allan T. Souza, Petr Blabolil, Lukáš Vejřík, Zuzana Sajdlová, Milan Říha, and Jan Kubečka. 2020. “Negative Feedback Concept in Tagging: Ghost Tags Imperil the Long-Term Monitoring of Fishes.” Edited by Johann Mourier. *PLOS ONE* 15 (3): e0229350. https://doi.org/10.1371/journal.pone.0229350.

Šmejkal, Marek, Petr Blabolil, Daniel Bartoň, Jindřich Duras, Lukáš Vejřík, Zuzana Sajdlová, Luboš Kočvara, and Jan Kubečka. 2019. “Sex-Specific Probability of PIT Tag Retention in a Cyprinid Fish.” *Fisheries Research* 219 (November): 105325. https://doi.org/10.1016/j.fishres.2019.105325.

Sousa, Lara L., Nuno Queiroz, Gonzalo Mucientes, Nicolas E. Humphries, and David W. Sims. 2016. “Environmental Influence on the Seasonal Movements of Satellite-Tracked Ocean Sunfish Mola Mola in the North-East Atlantic.” *Animal Biotelemetry* 4 (1): 7. https://doi.org/10.1186/s40317-016-0099-2.

Stout, J. Benjamin, Mary M. Conner, Phaedra Budy, Peter D. Mackinnon, and Mark C. McKinstry. 2019. “We Ain’t Afraid of No Ghosts: Tracking Habitat Interactions and Movement Dynamics of Ghost Tags under Differing Flow Conditions in a Sand-Bed River.” *North American Journal of Fisheries Management* 39 (6): 1337–47. https://doi.org/10.1002/nafm.10371.

Teixeira, Amílcar, and Rui M. V. Cortes. 2007. “PIT Telemetry as a Method to Study the Habitat Requirements of Fish Populations: Application to Native and Stocked Trout Movements.” *Hydrobiologia* 582 (1): 171–85. https://doi.org/10.1007/s10750-006-0551-z.

Thorstad, E. B., F. Whoriskey, I. Uglem, A. Moore, A. H. Rikardsen, and B. Finstad. 2012. “A Critical Life Stage of the Atlantic Salmon Salmo Salar: Behaviour and Survival during the Smolt and Initial Post-Smolt Migration.” *Journal of Fish Biology* 81 (2): 500–542. https://doi.org/10.1111/j.1095-8649.2012.03370.x.

Vehanen, T., P. L. Bjerke, J. Heggenes, A. Huusko, and A. Maki-Petays. 2000. “Effect of Fluctuating Flow and Temperature on Cover Type Selection and Behaviour by Juvenile Brown Trout in Artificial Flumes.” *Journal of Fish Biology* 56 (4): 923–37. https://doi.org/10.1111/j.1095-8649.2000.tb00882.x.

Venables, W.N., Ripley, B. D. 2002. *Modern Applied Statistics with S*. New York: Springer.

Villegas-Ríos, David, Denis Réale, Carla Freitas, Even Moland, and Esben M. Olsen. 2018. “Personalities Influence Spatial Responses to Environmental Fluctuations in Wild Fish.” Edited by Niels Dingemanse. *Journal of Animal Ecology* 87 (5): 1309–19. https://doi.org/10.1111/1365-2656.12872.

Walton, Izaak. 1653. *The Compleat Angler*. London and New York: John Lane: The Bodley Head. This edition reprints the 5th edition of 1676.

Weber, Christine, Hannes Scheuber, Christer Nilsson, and Knut T. Alfredsen. 2016. “Detection and Apparent Survival of PIT-Tagged Stream Fish in Winter.” *Ecology and Evolution* 6 (8): 2536–47. https://doi.org/10.1002/ece3.2061.

Zentner, Douglas L., Skylar L. Wolf, Shannon K. Brewer, and Daniel E. Shoup. 2021. “A Review of Factors Affecting PIT-tag Detection Using Mobile Arrays and Use of Mobile Antennas to Detect PIT-tagged Suckers in a Wadeable Ozark Stream.” *North American Journal of Fisheries Management*, February, nafm.10578. https://doi.org/10.1002/nafm.10578.

Zydlewski, Gayle B., A. Haro, K. G. Whalen, and S. D. McCormick. 2001. “Performance of Stationary and Portable Passive Transponder Detection Systems for Monitoring of Fish Movements.” *Journal of Fish Biology* 58 (5): 1471–75. https://doi.org/10.1111/j.1095-8649.2001.tb02302.x.

Table

Stream	Physical parameters						
	Total length (m)	Slope(m.km-1)	Width mean (m)	Depth mean (cm)	Depth minimum (cm)	Depth maximum (cm)	Velocity mean (cm.m-1)
Dorfbach LU	1750	6	192	20	0	81	0.19
Giebelbächli North	1780	59	93	12	0	40	
Giebelbächli South	1970	37	135	11	0	55	
Giessen	1400	3	482	35	0	132	0.22
Klosterbach SZ	1790	3	275	39	2	100	0.32
Klosterbach UR	1391	2	306	35	0	103	0.18
Lochrütibach	1170	12	458	24	0	80	
N2 Entwässerungskanal	1210	6	251	29	2	59	0.40
Polenschachen	890	9	294	21	0	115	0.17
Rossträkekanal	1450	4	276	29	0	96	0.32
Scheidgraben	2380	4	325	28	0	100	0.16
Schützenbrunnen	668	5	299	32	0	89	
Würzenbach	1280	8	283	13	0	92	0.14
Würzenbach reference	2790	25	304	14	0	70	0.17

Special habitat			Flow regime composition						
Undercut bank (%)	Vegetation (%)	Overhead cover (%)	Riffles	Run	Fast run	Shallow water	Pool	Mud	Sand
4.5	3.6	7.2	24	46	27	2	2	16	0
2.2	0.0	57.1	13	61	26	0	0	0	26
10.2	0.0	70.1	12	87	1	0	0	0	9
2.0	18.5	66.2	3	49	43	3	2	11	16
9.6	33.2	30.6	2	63	35	0	1	10	22
6.1	26.4	26.0	2	83	9	5	1	29	14
0.3	20.8	3.0	0	38	62	0	0	8	4
5.7	29.4	25.4	5	29	63	1	2	12	19
15.2	3.7	58.6	13	57	28	1	1	3	45
2.5	46.2	50.4	0	80	19	0	1	19	5
8.1	47.5	26.1	5	65	16	11	3	30	6
27.7	1.8	33.5	2	68	29	0	0	8	33
0.9	1.3	70.2	14	83	3	0	0	5	20
1.0	1.3	70.0	47	43	0	2	9	3	16

Substrate composition				Environment PCA			Fish detection (i.e. efficiency)		Escape res *in-situ* s
Gravel	Pebble	Cobble	Large stones	PCA 1 (26 %)	PCA 2 (19 %)	PCA 3 (12 %)	Mean	Standard error	Mean
38	19	22	4	0.2	2.5	1.6	0.14	0.10	0.11
18	30	13	12	3.3	-0.9	1.0	0.30	0.13	0.04
36	35	15	5	3.2	-0.2	-0.1	0.33	0.11	0.01
23	38	7	4	-1.4	-1.0	-0.6	0.46	0.06	0.03
21	27	13	7	-1.3	-0.8	0.2	0.33	0.06	0.04
24	20	12	1	-2.7	0.6	-1.5	0.36	0.06	0.04
39	23	23	4	-1.7	1.2	3.4	0.70	0.06	0.04
24	30	7	9	-0.5	-0.7	2.3	0.29	0.04	0.07
14	20	16	2	-0.2	-2.5	-1.1	0.49	0.15	0.06
26	29	12	9	-0.9	0.1	0.0	0.42	0.14	0.06
14	23	24	4	-2.7	3.1	-2.2	0.36	0.04	0.06
15	30	12	3	-0.9	-3.3	-0.6	0.43	0.06	0.05
22	32	17	4	1.7	-0.8	-1.0	0.52	0.04	0.10
25	33	17	7	3.9	2.6	-1.4	0.33	0.10	0.04

ponse (i.e. survival)	Tag detection (i.e. overall detection)	
Standard error	Mean	Standard error
0.02	0.16	0.01
0.01	0.20	0.02
0.01	0.14	0.01
0.01	0.07	0.00
0.01	0.11	0.01
0.01	0.10	0.01
0.01	0.24	0.01
0.01	0.10	0.01
0.01	0.08	0.01
0.02	0.11	0.01
0.01	0.10	0.00
0.01	0.08	0.00
0.01	0.17	0.01
0.01	0.13	0.01

Table

Response variable	Dataset	Model	AIC
Model 1: Fish detection efficiency			
Tag detection on a one-pass tracking	Fish present in the stream	**~ Stream + Year + TL + Temperature**	1325
		~ Stream + Year + TL + Temperature + DOY	1326
		~ Stream(PCA1 + PCA2 + PCA3) + Year + TL + Temperature	1351
		~ Stream(PCA1) + Year + TL + Temperature	1351
		~ Year + TL + Temperature	1349
	♀♂	**~ Stream + Year + TL + Temperature + Sex*TL**	549
		~ Stream + Year + TL + Temperature	555
		~ Stream + Year + TL + Temperature + Sex	557
Model 2: Tag loss			
Tag loss at recapture	Recapture fish	**~ TL + K**	664
		~ TL + K + Season	665
	♀♂	**~ Sex + TL + K**	266
		~ Sex + TL + K + Season	267
		~ Sex*TL + K	268
Model 3: Escape response at detection of living fish			
Escape after detection	Detected recapture fish	**~ 1**	316
		~ TL	329
		~ TL + Temperature	331
	♀♂	**~ 1**	114
		~ Sex	116
		~ Sex*TL	116
Model 4: *In-situ* survival (Escape response at detection of all dete			
Escape after detection	Detected tags	**~ Delay + Stream**	3264
		~ Delay + Stream + K	3266
		~ Delay + Stream + TL	3266
		~ Delay*TL + Stream	3267
	♀♂	**~ Delay + Stream + Sex*TL**	592
		~ Delay + Stream + Sex	595
		~ Delay + Stream	595
Model 5: Tag detection			
Tag detection on a one-pass tracking	Alll potential detection	**~ Stream + TL*Delay**	23462
		~ Stream + TL + Delay	23489
		~ TL*Delay + Stream(PCA1 + PCA2 + PCA3)	23819
	♀♂	**~ Stream + TL*Delay + Sex*TL + Sex*Delay**	5626
		~ Stream + TL*Delay + Sex*TL	5637
		~ Stream + TL*Delay + Sex	5649
		~ Stream + TL*Delay	5754

ΔAIC	d.f.	P	R^2 McFadden
0	1041	< 10E-10	0.11
0.3	1040	< 10E-10	0.11
26.0	1051	< 10E-10	0.08
26.0	1053	< 10E-10	0.08
24.1	1054	< 10E-10	0.08
0.0	427	< 10E-4	0.15
6.0	429	< 10E-4	0.13
7.3	428	0.002	0.13
0	1435	< 10E-10	0.07
1.0	1434	< 10E-10	0.08
0	653	< 10E-5	0.16
1.7	652	< 10E-5	0.16
1.8	652	< 10E-5	0.16
0	404		
12.7	403	0.5	0.001
14.4	402	0.7	0.002
0	131		
1.5	130	0.5	0.004
1.8	128	0.3	0.04
ected tags)			
0	7147	< 10E-10	0.06
1.6	7146	< 10E-10	0.06
2.0	7146	< 10E-10	0.06
2.5	7145	< 10E-10	0.06
0	1206	0.0002	0.10
3.2	1208	0.0004	0.09
2.4	1209	0.0004	0.09
0	33346	< 10E-10	0.05
27	33347	< 10E-10	0.05
358	33356	< 10E-10	0.03
0	8083	< 10E-10	0.08
11	8084	< 10E-10	0.08
23	8085	< 10E-10	0.08
128	8086	< 10E-10	0.06

TABLE AND FIGURES CAPTIONS

Table 1. Environmental data of 14 streams of the Lake Lucerne drainage where the study was carried out. Special habitats refers the proportion of stream bank with vegetation and undercut banks, and the proportion covered by terrestrial vegetation (Overhead cover). Flow regime describes the relative portion of the stream with slack deep water (pool), smoothly running water in shallow (shallow water) or deeper water (run), and fast running water in shallow water agitated by stones (riffle) or deeper water (fast run). Substrate composition describes the proportion of each type of substrate in the stream. PCA axes from 18 of environmental variables (see additional material: Table S3) ae reported. Model estimates of tracking efficiency, tag detection and *in-situ* survival are reported for each stream.

Table 2. The results from candidate generalized logistic regression models. For each model, we report the two best fits (two lowest AIC), and all models with ΔAIC <2. Models are described by Aikake information criteria (AIC), ΔAIC (the difference between the model and the lowest AIC), degree of freedom (d.f.), associated p-values (P) and McFadden's pseudo-R^2 (R^2_{McFadden}). We report for each fit a secondary model selection, which includes sexed fish dataset (♀♂). Variables are categorical factors: streams, year, fish sex (Sex) and season (two levels: spawning season/summer), and continuous variables: fish length (TL), day-of-the-year of the day of tracking (DOY), stream temperature of the day of tracking (temperature), PCA axis of stream environmental variables (PCA1, PCA2, PCA3), fish condition factor (K) and time since tagging (Delay).

Figure 1. Effect of total length (A), years (C) and temperature (D) on fish detection probability during a one-pass tracking from the best logistic regression, in *Salmo trutta* from the Lake Lucerne drainage. (B) shows the interactive effect of sex and fish length when adding sex in the prediction. Grey area (A,D) shows 95% confidence limits. (A,B,D) Bars (above) show

potential detection and histograms (below) show densities of detection. (C) Bars show show 95% confidence intervals.

Figure 2. (A) Main environmental variables of the PCA projection of the 14 streams where tracking was carried out. Size of dots show to the predicted probability from the best logistic regression on fish detection probability, for each stream denoted by colours (ranked by hue according to efficiency) (B). (C) shows correlation between stream effects and mean width.

Figure 3. Effects of condition factor (A), total length (B) and sex (C) from the best logistic fit on probability of tag loss in *Salmo trutta* from the Lake Lucerne drainage. Grey area (A-B) and bars (C) show 95% confidence intervals. Bars (above A-B) show distribution of fish considered in the analysis and histograms (above A-B) show densities of tag loss.

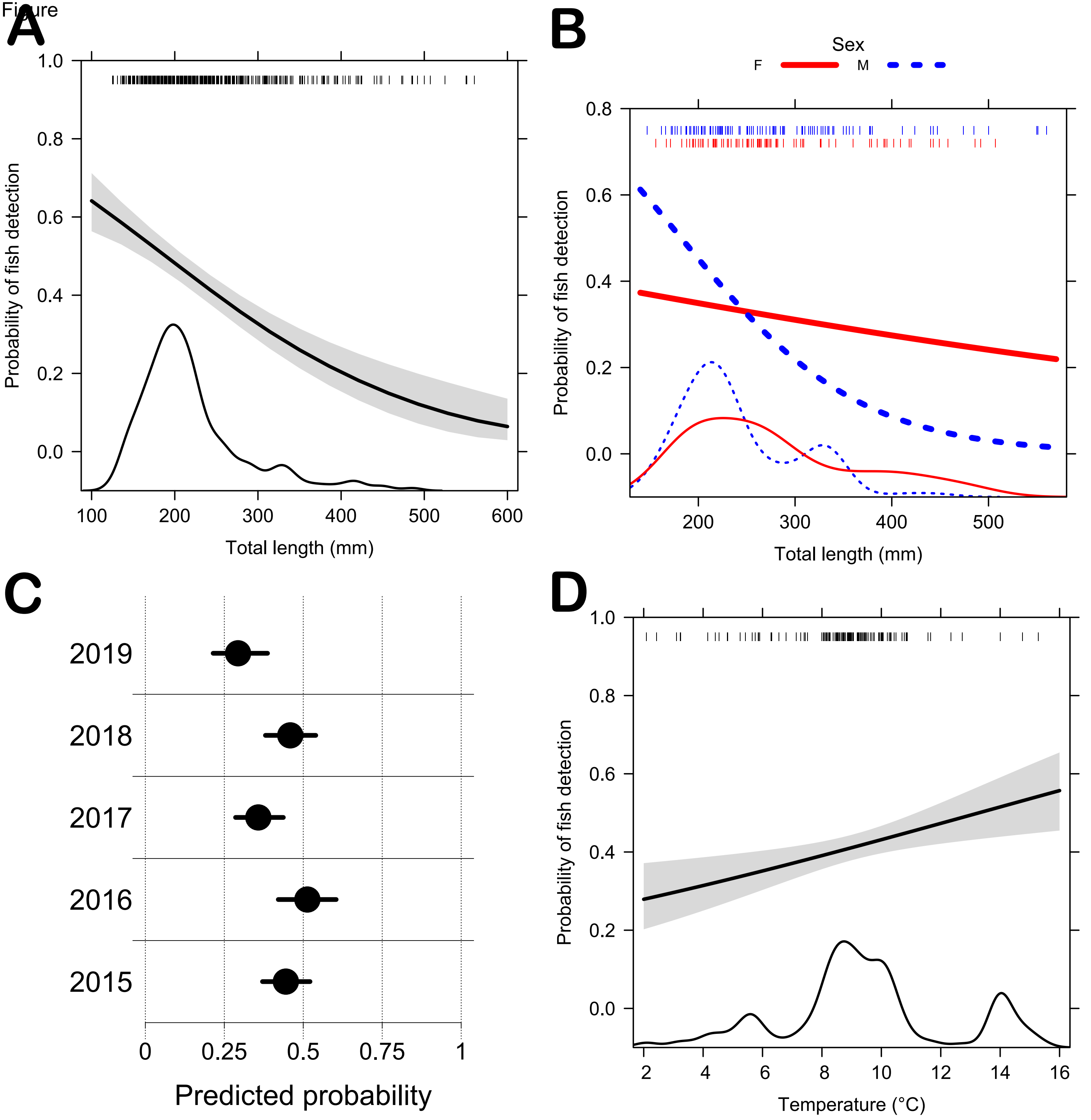
Figure 4. Logistic fit of probability of escape response of *Salmo trutta* at detection from all detected tags of (A-B). (A) shows the effect of time after tagging. (B) shows the interactive effect of fish length and sex on escape response, for all detected tags. (C) Estimated proportion of ghost tags during tracking against time after tagging. Bars (above A-B) show distribution of fish considered in the analysis and histograms (below A-B) show densities of fish that moved after detection. Grey area (A) and bars (C) show 95% confidence intervals.

Figure 5. Logistic fit of overall detection probability of all tags from resident *Salmo trutta* for a one-pass tracking. (A) shows the effect of time after tagging. (B) shows the interactive effect of fish length and time after tagging. (C) shows the interactive effect of sex and time after

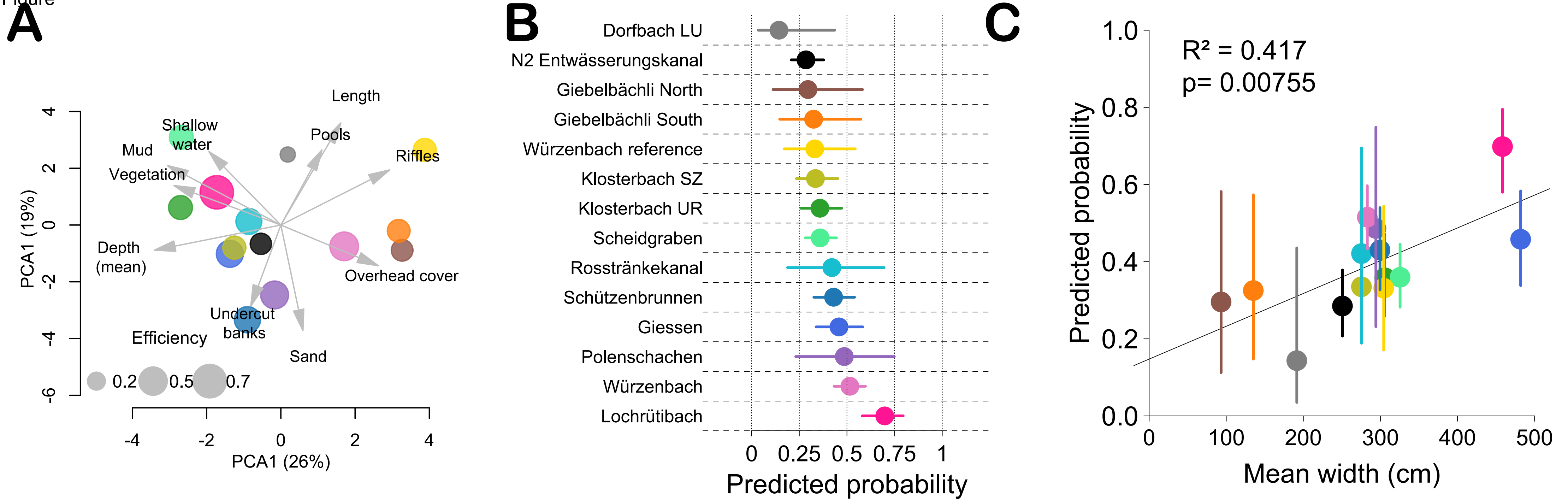
tagging on tag detection. (D) shows the interactive effect of sex and fish length on tag detection. Bars (below A, above B-D) show distribution of fish considered in the analysis and histograms (below A-D) show densities of tags that were detected.

Figure 6. (A) Theoretical depletion curves of cumulated detected tags against number of tracking passes. Line colours denote different populations composed of tags with different probability of detection P (see legends). (B) Empirical depletion curves of tracking in 2020 in six streams (see colours). Curves were fitted with a three-parameter logistic function based on three passes in each stream. The asymptotic values of the fits are scaled to one for visualization.

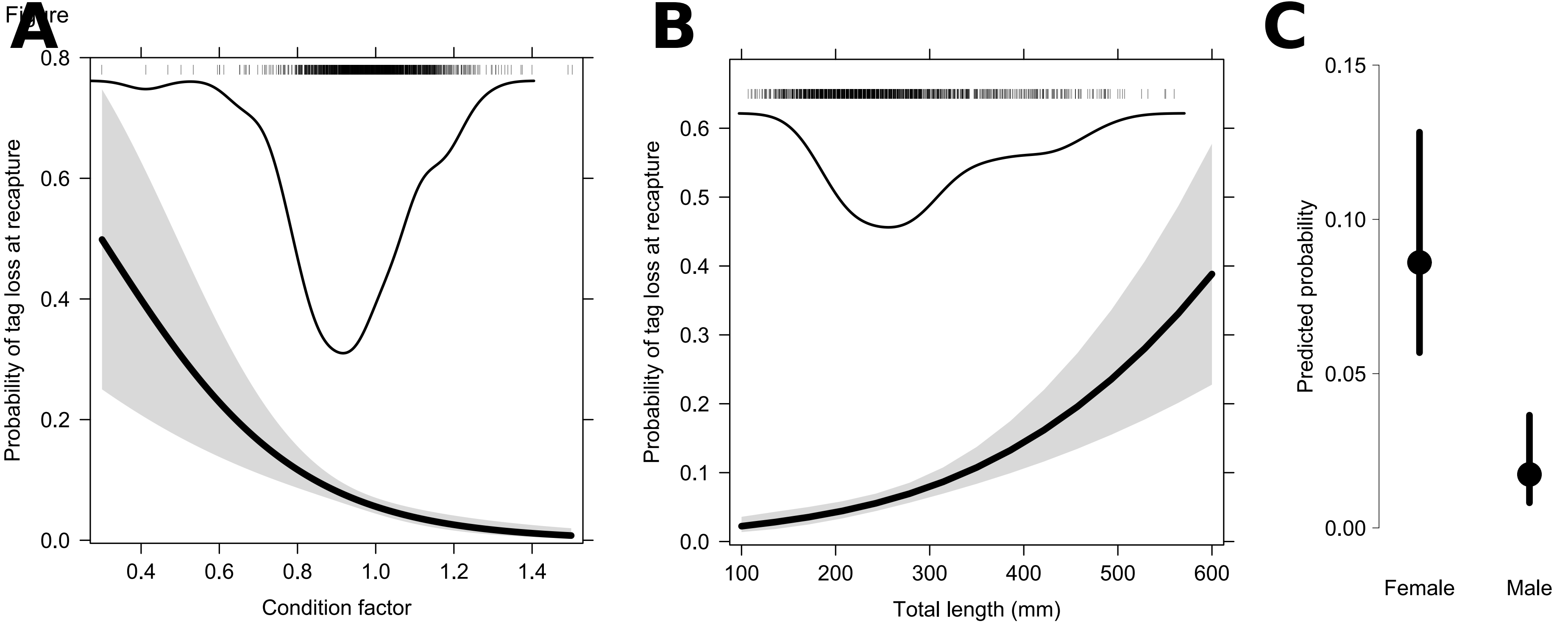
Figure


A
1.0
0.8
0.6
0.4
0.2
0.0
Probability of fish detection
100
200
300
400
500
600
Total length (mm)
B
Sex
F
M
0.8
0.6
0.4
0.2
0.0
Probability of fish detection
200
300
400
500
Total length (mm)
C
2019
2018
2017
2016
2015
0
0.25
0.5
0.75
1
Predicted probability
D
1.0
0.8
0.6
0.4
0.2
0.0
Probability of fish detection
2
4
6
8
10
12
14
16
Temperature (°C)

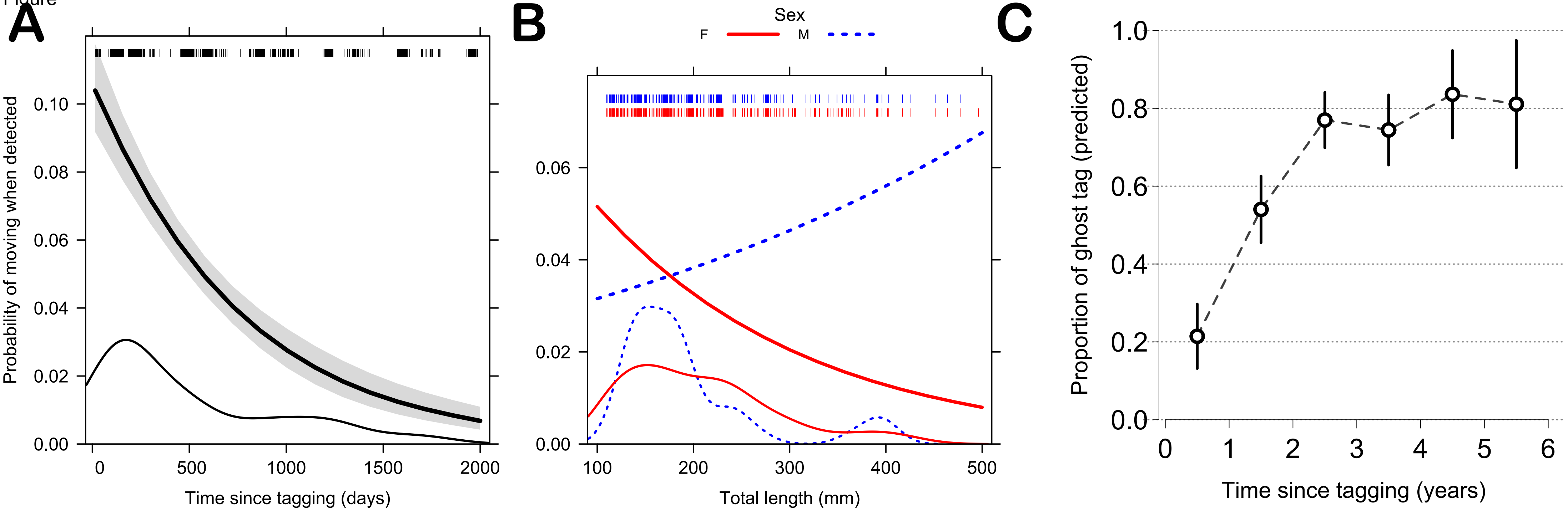
Figure


A
Length
Shallow water
Pools
Mud
Riffles
Vegetation
Depth (mean)
Overhead cover
Undercut banks
Efficiency
Sand
0.2
0.5
0.7
PCA1 (19%)
PCA1 (26%)
4
2
0
-2
-4
-6
-4
-2
0
2
4
B
Dorfbach LU
N2 Entwässerungskanal
Giebelbächli North
Giebelbächli South
Würzenbach reference
Klosterbach SZ
Klosterbach UR
Scheidgraben
Rossränkekanal
Schützenbrunnen
Giessen
Polenschachen
Würzenbach
Lochrütibach
0
0.25
0.5
0.75
1
Predicted probability
C
R² = 0.417
p= 0.00755
Predicted probability
1.0
0.8
0.6
0.4
0.2
0.0
0
100
200
300
400
500
Mean width (cm)

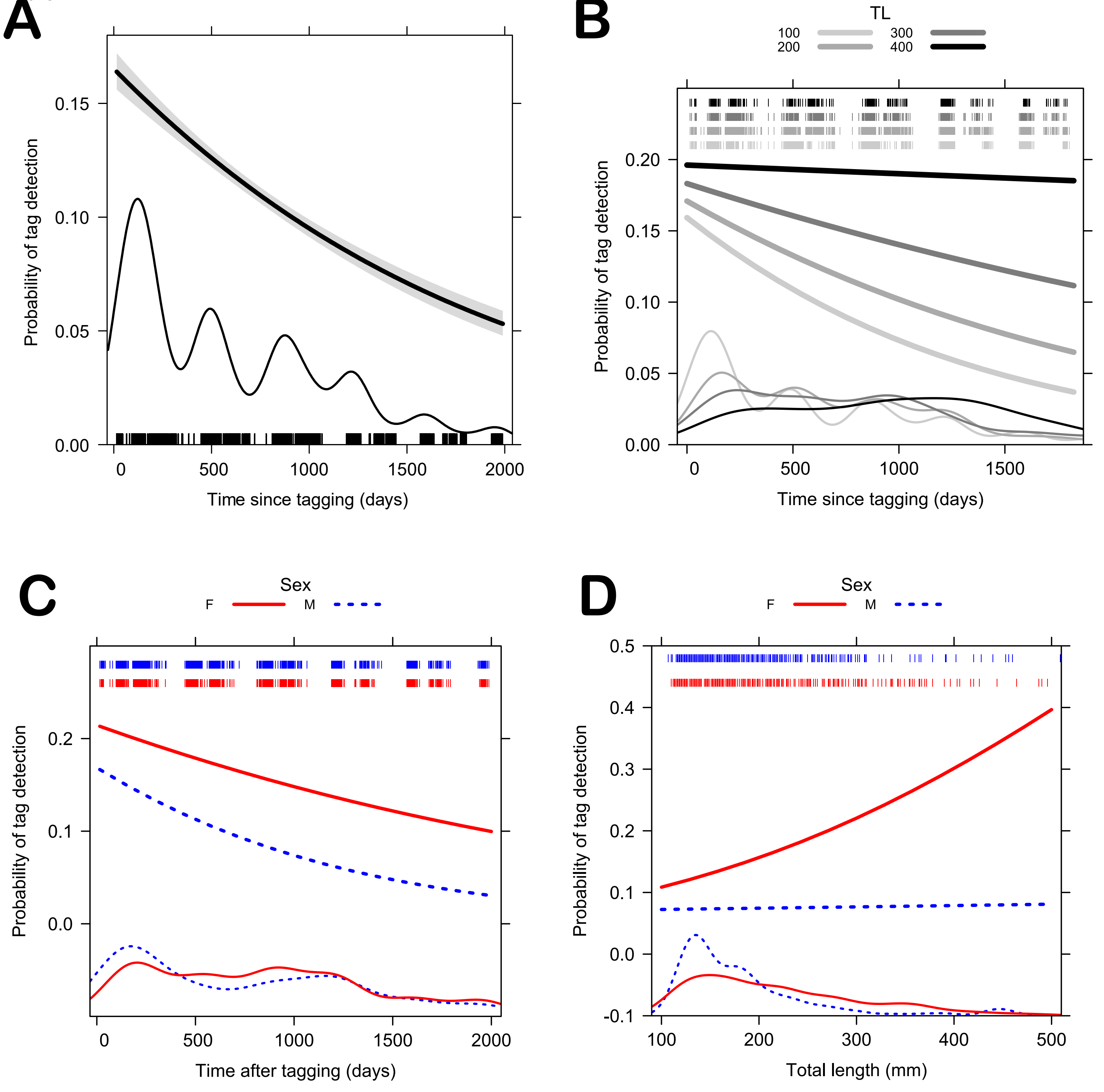
Figure


A
Probability of tag loss at recapture
0.0
0.2
0.4
0.6
0.8
0.4
0.6
0.8
1.0
1.2
1.4
Condition factor
B
Probability of tag loss at recapture
0.0
0.1
0.2
0.3
0.4
0.5
0.6
100
200
300
400
500
600
Total length (mm)
C
Predicted probability
0.00
0.05
0.10
0.15
Female
Male

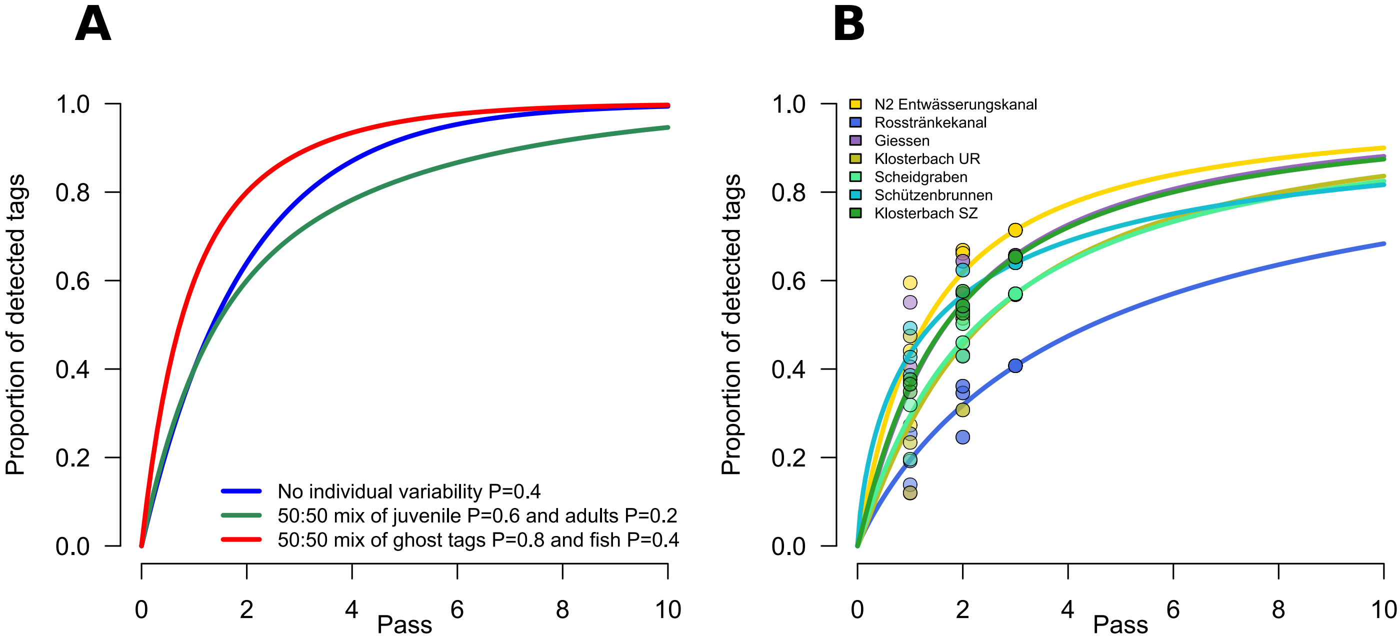
Figure


A
Probability of moving when detected
0.00
0.02
0.04
0.06
0.08
0.10
0
500
1000
1500
2000
Time since tagging (days)
B
Sex
F
M
0.00
0.02
0.04
0.06
100
200
300
400
500
Total length (mm)
C
Proportion of ghost tag (predicted)
0.0
0.2
0.4
0.6
0.8
1.0
0
1
2
3
4
5
6
Time since tagging (years)

Figure


A
Probability of tag detection
0.00
0.05
0.10
0.15
0
500
1000
1500
2000
Time since tagging (days)
B
TL
100
200
300
400
Probability of tag detection
0.00
0.05
0.10
0.15
0.20
0
500
1000
1500
Time since tagging (days)
C
Sex
F
M
Probability of tag detection
0.0
0.1
0.2
0
500
1000
1500
2000
Time after tagging (days)
D
Sex
F
M
Probability of tag detection
-0.1
0.0
0.1
0.2
0.3
0.4
0.5
100
200
300
400
500
Total length (mm)

Figure


A
1.0
0.8
0.6
0.4
0.2
0.0
Proportion of detected tags
0
2
4
6
8
10
Pass
No individual variability P=0.4
50:50 mix of juvenile P=0.6 and adults P=0.2
50:50 mix of ghost tags P=0.8 and fish P=0.4
B
1.0
0.8
0.6
0.4
0.2
0.0
Proportion of detected tags
N2 Entwässerungskanal
Rossträngkekanal
Giessen
Klosterbach UR
Scheidgraben
Schützenbrunnen
Klosterbach SZ
0
2
4
6
8
10
Pass

2/18/2015	Dorfbach LU	52	0
8/31/2015	Dorfbach LU	79	12
10/6/2015	Dorfbach LU	23	1
11/30/2015	Dorfbach LU	2	7
3/17/2016	Dorfbach LU	31	3
10/17/2016	Dorfbach LU	4	2
2/21/2017	Dorfbach LU	77	2
3/8/2017	Dorfbach LU	16	1
11/16/2017	Dorfbach LU	3	2
2/15/2018	Dorfbach LU	58	0
3/8/2018	Dorfbach LU	12	0
3/14/2016	Giebelbächli No	83	0
11/21/2016	Giebelbächli No	4	3
2/20/2017	Giebelbächli No	80	9
3/9/2017	Giebelbächli No	26	1
2/16/2018	Giebelbächli No	65	8
3/9/2018	Giebelbächli No	35	0
12/14/2018	Giebelbächli No	0	1
3/14/2016	Giebelbächli So	75	0
2/20/2017	Giebelbächli So	83	1
3/9/2017	Giebelbächli So	28	3
11/20/2017	Giebelbächli So	5	0
2/16/2018	Giebelbächli So	44	5
3/9/2018	Giebelbächli So	48	0
11/20/2018	Giebelbächli So	0	2
12/14/2018	Giebelbächli So	0	3
2/20/2015	Giessen	16	0
3/5/2015	Giessen	53	0
3/13/2015	Giessen	9	0
8/17/2015	Giessen	21	3
9/4/2015	Giessen	43	2
10/15/2015	Giessen	11	2
11/17/2015	Giessen	11	12
12/10/2015	Giessen	0	5
2/16/2016	Giessen	34	9
3/1/2016	Giessen	27	3
3/9/2016	Giessen	7	0
11/14/2016	Giessen	0	1
12/12/2016	Giessen	1	2
2/7/2017	Giessen	73	1
2/24/2017	Giessen	58	1
11/13/2017	Giessen	2	4
12/11/2017	Giessen	1	2
2/5/2018	Giessen	12	0
2/6/2018	Giessen	95	1
2/9/2018	Giessen	12	0
2/12/2018	Giessen	13	0

2/14/2018	Giessen	10	0
2/16/2018	Giessen	10	0
2/19/2018	Giessen	13	0
2/20/2018	Giessen	13	0
2/22/2018	Giessen	73	11
2/23/2018	Giessen	12	0
2/26/2018	Giessen	20	0
2/27/2018	Giessen	13	0
2/28/2018	Giessen	10	0
3/2/2018	Giessen	12	0
3/6/2018	Giessen	12	0
3/7/2018	Giessen	12	0
11/13/2018	Giessen	5	6
12/11/2018	Giessen	0	1
2/18/2019	Giessen	122	1
3/4/2019	Giessen	107	5
3/12/2019	Giessen	160	0
11/21/2019	Giessen	0	2
2/14/2020	Giessen	76	0
2/24/2020	Giessen	27	0
3/4/2020	Giessen	28	0
2/26/2015	Klosterbach SZ	45	0
3/6/2015	Klosterbach SZ	53	0
8/20/2015	Klosterbach SZ	28	5
8/28/2015	Klosterbach SZ	48	15
10/8/2015	Klosterbach SZ	14	3
11/10/2015	Klosterbach SZ	1	10
12/4/2015	Klosterbach SZ	8	9
2/26/2016	Klosterbach SZ	56	0
3/3/2016	Klosterbach SZ	64	11
10/6/2016	Klosterbach SZ	2	3
11/7/2016	Klosterbach SZ	0	2
2/17/2017	Klosterbach SZ	41	4
3/7/2017	Klosterbach SZ	80	11
11/6/2017	Klosterbach SZ	3	5
12/4/2017	Klosterbach SZ	1	4
2/5/2018	Klosterbach SZ	12	0
2/6/2018	Klosterbach SZ	13	0
2/9/2018	Klosterbach SZ	12	0
2/12/2018	Klosterbach SZ	13	0
2/14/2018	Klosterbach SZ	74	4
2/16/2018	Klosterbach SZ	10	0
2/19/2018	Klosterbach SZ	13	0
2/20/2018	Klosterbach SZ	13	0
2/22/2018	Klosterbach SZ	13	0
2/23/2018	Klosterbach SZ	12	0
2/26/2018	Klosterbach SZ	20	0

2/27/2018	Klosterbach SZ	13	0
2/28/2018	Klosterbach SZ	10	0
3/2/2018	Klosterbach SZ	12	0
3/5/2018	Klosterbach SZ	99	7
3/6/2018	Klosterbach SZ	12	0
3/7/2018	Klosterbach SZ	12	0
11/21/2018	Klosterbach SZ	7	12
12/6/2018	Klosterbach SZ	1	10
2/8/2019	Klosterbach SZ	123	4
2/26/2019	Klosterbach SZ	107	6
3/8/2019	Klosterbach SZ	160	0
11/14/2019	Klosterbach SZ	9	0
12/11/2019	Klosterbach SZ	0	9
2/17/2020	Klosterbach SZ	77	2
3/2/2020	Klosterbach SZ	77	7
2/20/2015	Klosterbach UR	62	0
3/3/2015	Klosterbach UR	38	0
8/26/2015	Klosterbach UR	33	3
9/4/2015	Klosterbach UR	28	4
10/13/2015	Klosterbach UR	3	3
11/9/2015	Klosterbach UR	3	5
12/1/2015	Klosterbach UR	3	3
2/17/2016	Klosterbach UR	36	4
3/9/2016	Klosterbach UR	26	3
3/11/2016	Klosterbach UR	41	3
10/14/2016	Klosterbach UR	0	2
11/15/2016	Klosterbach UR	1	2
12/13/2016	Klosterbach UR	1	5
2/13/2017	Klosterbach UR	141	3
11/14/2017	Klosterbach UR	1	6
12/15/2017	Klosterbach UR	1	3
2/20/2018	Klosterbach UR	34	2
3/6/2018	Klosterbach UR	59	1
3/7/2018	Klosterbach UR	32	0
11/6/2018	Klosterbach UR	2	11
12/7/2018	Klosterbach UR	1	4
2/11/2019	Klosterbach UR	89	3
2/28/2019	Klosterbach UR	169	2
11/12/2019	Klosterbach UR	0	3
12/9/2019	Klosterbach UR	1	0
2/18/2020	Klosterbach UR	60	0
3/9/2020	Klosterbach UR	95	3
2/16/2015	Lochrütibach	30	0
3/12/2015	Lochrütibach	55	0
8/27/2015	Lochrütibach	84	23
10/9/2015	Lochrütibach	25	30
11/11/2015	Lochrütibach	11	14

12/9/2015	Lochrütibach	12	26
2/23/2016	Lochrütibach	49	31
3/8/2016	Lochrütibach	52	12
10/7/2016	Lochrütibach	5	10
11/8/2016	Lochrütibach	3	3
12/6/2016	Lochrütibach	0	3
2/14/2017	Lochrütibach	48	7
3/2/2017	Lochrütibach	60	17
11/7/2017	Lochrütibach	8	14
12/5/2017	Lochrütibach	0	1
2/8/2018	Lochrütibach	68	13
3/12/2018	Lochrütibach	48	13
11/15/2018	Lochrütibach	1	3
12/13/2018	Lochrütibach	0	2
2/19/2015	N2 Entwässerur	38	0
3/4/2015	N2 Entwässerur	52	0
2/24/2016	N2 Entwässerur	63	0
3/2/2016	N2 Entwässerur	43	2
10/18/2016	N2 Entwässerur	6	1
11/18/2016	N2 Entwässerur	10	3
12/16/2016	N2 Entwässerur	2	4
2/15/2017	N2 Entwässerur	50	7
3/3/2017	N2 Entwässerur	95	11
11/9/2017	N2 Entwässerur	7	3
12/7/2017	N2 Entwässerur	5	8
2/5/2018	N2 Entwässerur	12	0
2/6/2018	N2 Entwässerur	13	0
2/9/2018	N2 Entwässerur	54	3
2/12/2018	N2 Entwässerur	13	0
2/14/2018	N2 Entwässerur	10	0
2/16/2018	N2 Entwässerur	9	0
2/19/2018	N2 Entwässerur	76	2
2/20/2018	N2 Entwässerur	13	0
2/22/2018	N2 Entwässerur	13	0
2/23/2018	N2 Entwässerur	12	0
2/26/2018	N2 Entwässerur	20	0
2/27/2018	N2 Entwässerur	13	0
2/28/2018	N2 Entwässerur	10	0
3/2/2018	N2 Entwässerur	12	0
3/6/2018	N2 Entwässerur	12	0
3/7/2018	N2 Entwässerur	12	0
11/12/2018	N2 Entwässerur	3	9
12/13/2018	N2 Entwässerur	12	15
2/19/2019	N2 Entwässerur	123	2
3/5/2019	N2 Entwässerur	116	5
3/21/2019	N2 Entwässerur	160	0
12/2/2019	N2 Entwässerur	3	15

2/6/2020	N2 Entwässerur	79	0
2/28/2020	N2 Entwässerur	79	10
9/8/2015	Polenschachen	96	0
10/19/2015	Polenschachen	1	0
11/6/2015	Polenschachen	3	0
12/8/2015	Polenschachen	3	1
2/22/2016	Polenschachen	24	12
3/4/2016	Polenschachen	9	6
10/21/2016	Polenschachen	2	1
11/22/2016	Polenschachen	0	2
2/10/2017	Polenschachen	28	0
2/28/2017	Polenschachen	60	0
2/5/2018	Polenschachen	12	0
2/6/2018	Polenschachen	13	0
2/9/2018	Polenschachen	12	0
2/12/2018	Polenschachen	13	0
2/13/2018	Polenschachen	27	0
2/14/2018	Polenschachen	10	0
2/16/2018	Polenschachen	10	0
2/19/2018	Polenschachen	13	0
2/20/2018	Polenschachen	13	0
2/22/2018	Polenschachen	34	7
2/23/2018	Polenschachen	12	0
2/26/2018	Polenschachen	20	0
2/27/2018	Polenschachen	13	0
2/28/2018	Polenschachen	10	0
3/2/2018	Polenschachen	99	14
3/6/2018	Polenschachen	12	0
3/7/2018	Polenschachen	12	0
12/7/2018	Polenschachen	1	2
2/21/2019	Polenschachen	36	0
3/8/2019	Polenschachen	6	0
3/15/2019	Polenschachen	160	0
2/19/2015	Rossträнkekana	39	0
3/4/2015	Rosstränkekana	46	0
2/24/2016	Rosstränkekana	36	1
3/2/2016	Rosstränkekana	11	3
3/10/2016	Rosstränkekana	16	0
2/15/2017	Rosstränkekana	26	7
3/3/2017	Rosstränkekana	31	0
2/9/2018	Rosstränkekana	20	6
2/19/2018	Rosstränkekana	32	7
2/11/2015	Scheidgraben	51	0
2/27/2015	Scheidgraben	52	0
8/24/2015	Scheidgraben	92	3
10/12/2015	Scheidgraben	7	0
11/19/2015	Scheidgraben	5	10

12/7/2015	Scheidgraben	1	10
2/23/2016	Scheidgraben	84	6
3/8/2016	Scheidgraben	51	4
10/7/2016	Scheidgraben	0	2
11/8/2016	Scheidgraben	2	4
12/6/2016	Scheidgraben	0	4
2/14/2017	Scheidgraben	81	5
3/2/2017	Scheidgraben	70	7
11/7/2017	Scheidgraben	7	12
12/5/2017	Scheidgraben	0	2
2/8/2018	Scheidgraben	84	3
3/12/2018	Scheidgraben	67	4
11/15/2018	Scheidgraben	6	9
2/12/2019	Scheidgraben	127	3
2/27/2019	Scheidgraben	147	5
11/15/2019	Scheidgraben	1	11
2/28/2020	Scheidgraben	63	4
2/6/2020	Scheidgraben	80	6
2/17/2015	Schützenbrunne	30	0
3/5/2015	Schützenbrunne	35	0
3/13/2015	Schützenbrunne	24	0
8/21/2015	Schützenbrunne	18	4
9/1/2015	Schützenbrunne	54	1
10/19/2015	Schützenbrunne	5	2
11/16/2015	Schützenbrunne	3	7
12/14/2015	Schützenbrunne	2	4
2/19/2016	Schützenbrunne	50	6
3/4/2016	Schützenbrunne	84	16
10/21/2016	Schützenbrunne	13	4
11/22/2016	Schützenbrunne	16	1
2/10/2017	Schützenbrunne	64	2
2/28/2017	Schützenbrunne	102	2
11/21/2017	Schützenbrunne	3	4
12/18/2017	Schützenbrunne	1	0
2/5/2018	Schützenbrunne	12	0
2/6/2018	Schützenbrunne	13	0
2/9/2018	Schützenbrunne	12	0
2/12/2018	Schützenbrunne	13	0
2/13/2018	Schützenbrunne	51	1
2/14/2018	Schützenbrunne	10	0
2/16/2018	Schützenbrunne	10	0
2/19/2018	Schützenbrunne	13	0
2/20/2018	Schützenbrunne	13	0
2/22/2018	Schützenbrunne	13	0
2/23/2018	Schützenbrunne	75	7
2/26/2018	Schützenbrunne	20	0
2/27/2018	Schützenbrunne	13	0

2/28/2018	Schützenbrunne	10	0
3/2/2018	Schützenbrunne	12	0
3/6/2018	Schützenbrunne	12	0
3/7/2018	Schützenbrunne	12	0
11/22/2018	Schützenbrunne	0	9
12/4/2018	Schützenbrunne	3	5
2/21/2019	Schützenbrunne	64	0
3/7/2019	Schützenbrunne	115	3
3/21/2019	Schützenbrunne	160	0
11/25/2019	Schützenbrunne	1	3
2/19/2020	Schützenbrunne	56	1
3/4/2020	Schützenbrunne	78	2
2/25/2015	Steinibach	75	0
3/11/2015	Steinibach	41	0
3/17/2016	Steinibach	89	0
3/8/2017	Steinibach	45	5
2/15/2018	Steinibach	73	3
2/18/2015	Würzenbach	30	0
3/11/2015	Würzenbach	61	0
8/18/2015	Würzenbach	70	13
10/6/2015	Würzenbach	3	23
11/5/2015	Würzenbach	2	3
11/30/2015	Würzenbach	5	9
2/15/2016	Würzenbach	15	18
2/29/2016	Würzenbach	44	20
10/10/2016	Würzenbach	1	3
11/10/2016	Würzenbach	8	4
12/7/2016	Würzenbach	1	4
2/6/2017	Würzenbach	71	10
2/22/2017	Würzenbach	11	2
3/10/2017	Würzenbach	27	10
11/10/2017	Würzenbach	0	4
12/6/2017	Würzenbach	1	1
2/7/2018	Würzenbach	25	7
2/21/2018	Würzenbach	33	7
2/22/2018	Würzenbach	0	2
11/19/2018	Würzenbach	1	5
12/17/2018	Würzenbach	0	2
2/15/2016	Würzenbach re	59	0
2/29/2016	Würzenbach re	71	0
10/10/2016	Würzenbach re	12	4
12/7/2016	Würzenbach re	1	1
2/6/2017	Würzenbach re	61	0
2/22/2017	Würzenbach re	124	4
11/10/2017	Würzenbach re	2	1
12/6/2017	Würzenbach re	2	7
2/7/2018	Würzenbach re	22	12

2/21/2018	Würzenbach re	62	0
11/19/2018	Würzenbach re	0	1
12/17/2018	Würzenbach re	1	0
2/23/2015	Alpbach	39	0
3/9/2015	Alpbach	25	0
2/14/2020	Dorfbach	41	9
2/24/2020	Dorfbach	45	8
2/17/2015	Dorfbach UR	30	0
3/3/2015	Dorfbach UR	4	0
3/13/2015	Dorfbach UR	26	0
8/17/2015	Dorfbach UR	5	0
8/26/2015	Dorfbach UR	4	1
9/7/2015	Dorfbach UR	28	7
10/15/2015	Dorfbach UR	5	6
11/17/2015	Dorfbach UR	8	6
12/10/2015	Dorfbach UR	5	8
2/16/2016	Dorfbach UR	29	6
3/1/2016	Dorfbach UR	28	6
10/13/2016	Dorfbach UR	3	3
11/14/2016	Dorfbach UR	1	0
12/12/2016	Dorfbach UR	0	2
2/7/2017	Dorfbach UR	78	3
2/23/2017	Dorfbach UR	39	3
11/13/2017	Dorfbach UR	4	6
12/11/2017	Dorfbach UR	4	6
2/5/2018	Dorfbach UR	12	0
2/6/2018	Dorfbach UR	55	6
2/9/2018	Dorfbach UR	12	0
2/12/2018	Dorfbach UR	13	0
2/14/2018	Dorfbach UR	10	0
2/16/2018	Dorfbach UR	11	0
2/19/2018	Dorfbach UR	13	0
2/20/2018	Dorfbach UR	13	0
2/22/2018	Dorfbach UR	33	9
2/23/2018	Dorfbach UR	12	0
2/26/2018	Dorfbach UR	20	0
2/27/2018	Dorfbach UR	13	0
2/28/2018	Dorfbach UR	10	0
3/2/2018	Dorfbach UR	12	0
3/6/2018	Dorfbach UR	53	12
3/7/2018	Dorfbach UR	12	0
11/13/2018	Dorfbach UR	10	11
12/11/2018	Dorfbach UR	0	3
2/22/2019	Dorfbach UR	37	9
3/8/2019	Dorfbach UR	22	3
3/12/2019	Dorfbach UR	140	0
11/21/2019	Dorfbach UR	4	9

11/11/2015	Engelberger Aa	8	0
11/13/2018	Engelberger Aa	2	0
11/16/2018	Engelberger Aa	2	0
11/22/2018	Engelberger Aa	1	1
2/22/2016	Eyreussli	18	0
3/15/2016	Färndlibach	69	0
2/24/2015	Gangbach	39	0
3/9/2015	Gangbach	44	0
8/25/2015	Gangbach	20	2
9/1/2015	Gangbach	50	5
10/16/2015	Gangbach	7	3
11/13/2015	Gangbach	4	8
12/3/2015	Gangbach	11	9
2/18/2016	Gangbach	34	9
3/7/2016	Gangbach	69	14
10/11/2016	Gangbach	2	4
12/9/2016	Gangbach	0	1
2/8/2017	Gangbach	77	4
2/23/2017	Gangbach	35	0
11/3/2017	Gangbach	3	2
2/5/2018	Gangbach	12	0
2/6/2018	Gangbach	13	0
2/9/2018	Gangbach	12	0
2/12/2018	Gangbach	13	0
2/14/2018	Gangbach	10	0
2/16/2018	Gangbach	10	0
2/19/2018	Gangbach	13	0
2/20/2018	Gangbach	43	2
2/22/2018	Gangbach	13	0
2/23/2018	Gangbach	12	0
2/26/2018	Gangbach	20	0
2/27/2018	Gangbach	13	0
2/28/2018	Gangbach	10	0
3/2/2018	Gangbach	12	0
3/6/2018	Gangbach	12	0
3/7/2018	Gangbach	78	28
11/5/2018	Gangbach	2	4
12/3/2018	Gangbach	0	1
2/20/2019	Gangbach	50	3
3/6/2019	Gangbach	40	0
3/12/2019	Gangbach	160	0
11/25/2019	Gangbach	0	1
2/18/2020	Gangbach	81	2
2/27/2020	Gangbach	52	1
2/17/2016	Gangbach refer	67	0
12/9/2016	Gangbach refer	2	2
2/8/2017	Gangbach refer	52	5

10/5/2015	Kärstelenbach	12	0
11/6/2015	Kärstelenbach	10	0
12/8/2015	Kärstelenbach	2	3
10/4/2016	Kärstelenbach	3	0
11/4/2016	Kärstelenbach	1	3
11/16/2018	Kärstelenbach	3	0
2/26/2015	Leewasser	48	0
3/6/2015	Leewasser	35	0
8/20/2015	Leewasser	50	3
8/28/2015	Leewasser	24	1
10/8/2015	Leewasser	7	7
11/10/2015	Leewasser	3	4
12/4/2015	Leewasser	2	10
2/26/2016	Leewasser	49	11
3/3/2016	Leewasser	44	0
10/6/2016	Leewasser	5	0
11/7/2016	Leewasser	3	0
12/5/2016	Leewasser	0	3
2/17/2017	Leewasser	67	3
3/7/2017	Leewasser	79	1
11/6/2017	Leewasser	1	2
11/20/2017	Leewasser	0	1
2/5/2018	Leewasser	24	0
2/6/2018	Leewasser	13	0
2/12/2018	Leewasser	13	0
2/14/2018	Leewasser	69	3
2/16/2018	Leewasser	10	0
2/19/2018	Leewasser	13	0
2/20/2018	Leewasser	13	0
2/22/2018	Leewasser	13	0
2/23/2018	Leewasser	12	0
2/26/2018	Leewasser	20	0
2/27/2018	Leewasser	13	0
2/28/2018	Leewasser	10	0
3/2/2018	Leewasser	12	0
3/5/2018	Leewasser	74	6
3/6/2018	Leewasser	12	0
3/7/2018	Leewasser	12	0
11/21/2018	Leewasser	1	1
12/6/2018	Leewasser	4	6
2/13/2019	Leewasser	141	1
2/25/2019	Leewasser	112	2
2/26/2019	Leewasser	160	0
11/14/2019	Leewasser	2	9
12/11/2019	Leewasser	1	3
2/17/2020	Leewasser	69	2
3/2/2020	Leewasser	83	4

2/11/2015	Mühlibach	18	0
2/16/2015	Mühlibach	14	0
2/27/2015	Mühlibach	8	0
3/12/2015	Mühlibach	24	0
3/16/2015	Mühlibach	50	0
9/3/2015	Mühlibach	45	7
10/12/2015	Mühlibach	2	7
11/19/2015	Mühlibach	0	9
12/7/2015	Mühlibach	2	6
2/25/2016	Mühlibach	95	9
3/10/2016	Mühlibach	59	6
10/18/2016	Mühlibach	4	5
11/18/2016	Mühlibach	1	2
12/16/2016	Mühlibach	0	2
2/16/2017	Mühlibach	98	5
3/6/2017	Mühlibach	80	7
11/9/2017	Mühlibach	8	8
11/24/2017	Mühlibach	1	2
12/7/2017	Mühlibach	0	1
2/5/2018	Mühlibach	86	6
2/6/2018	Mühlibach	13	0
2/9/2018	Mühlibach	12	0
2/12/2018	Mühlibach	13	0
2/14/2018	Mühlibach	11	0
2/16/2018	Mühlibach	10	0
2/19/2018	Mühlibach	13	0
2/20/2018	Mühlibach	13	0
2/22/2018	Mühlibach	13	0
2/23/2018	Mühlibach	12	0
2/26/2018	Mühlibach	20	0
2/27/2018	Mühlibach	13	0
2/28/2018	Mühlibach	10	0
3/2/2018	Mühlibach	12	0
3/6/2018	Mühlibach	12	0
3/7/2018	Mühlibach	12	0
3/14/2018	Mühlibach	89	23
11/12/2018	Mühlibach	8	9
12/10/2018	Mühlibach	1	8
12/11/2015	Muota	36	0
11/15/2016	Muota	0	1
12/14/2018	Muota	0	1
2/16/2015	Obbürgenbach	13	0
10/13/2015	Palangenbach	7	1
11/16/2015	Palangenbach	10	4
12/1/2015	Palangenbach	0	3
2/25/2015	Schlimbach	59	0
3/18/2016	Schlimbach	39	0

10/17/2016	Schlimbach	1	0
2/21/2017	Schlimbach	15	0
3/8/2017	Schlimbach	17	10
3/10/2017	Schlimbach	16	1
3/17/2016	Schlundbach	43	1
3/18/2016	Schlundbach	30	1
11/17/2016	Schlundbach	0	9
12/21/2016	Schlundbach	0	1
2/21/2017	Schlundbach	27	2
3/8/2017	Schlundbach	12	8
11/16/2017	Schlundbach	2	4
3/8/2018	Schlundbach	46	4
2/24/2015	Stille Reuss	43	0
3/10/2015	Stille Reuss	66	0
8/25/2015	Stille Reuss	38	4
9/2/2015	Stille Reuss	9	1
10/24/2015	Stille Reuss	0	1
2/18/2016	Stille Reuss	78	0
10/13/2016	Stille Reuss	3	0
10/29/2016	Stille Reuss	2	0
11/11/2016	Stille Reuss	7	2
12/1/2016	Stille Reuss	0	1
2/9/2017	Stille Reuss	70	1
2/27/2017	Stille Reuss	45	0
11/11/2017	Stille Reuss	0	7
11/30/2017	Stille Reuss	0	3
2/13/2018	Stille Reuss	59	2
3/1/2018	Stille Reuss	81	1
11/3/2018	Stille Reuss	0	1
11/16/2018	Stille Reuss	1	1
2/20/2019	Stille Reuss	92	4
3/6/2019	Stille Reuss	59	0
2/13/2020	Stille Reuss	66	2
2/19/2020	Stille Reuss	39	0
3/7/2016	Stille Reuss	50	5
10/5/2015	Urner Reuss	6	0
11/17/2017	Urner Reuss	1	0
2/23/2015	Walenbrunnen	46	0
3/10/2015	Walenbrunnen	52	0
8/21/2015	Walenbrunnen	54	0
9/2/2015	Walenbrunnen	48	1
10/16/2015	Walenbrunnen	6	3
11/13/2015	Walenbrunnen	5	2
12/3/2015	Walenbrunnen	1	6
2/19/2016	Walenbrunnen	30	4
3/11/2016	Walenbrunnen	81	4
10/3/2016	Walenbrunnen	1	1

11/3/2016	Walenbrunnen	1	2
2/9/2017	Walenbrunnen	53	0
2/27/2017	Walenbrunnen	70	0
11/2/2017	Walenbrunnen	5	1
2/6/2018	Walenbrunnen	13	0
2/9/2018	Walenbrunnen	24	0
2/12/2018	Walenbrunnen	13	0
2/13/2018	Walenbrunnen	34	0
2/14/2018	Walenbrunnen	10	0
2/16/2018	Walenbrunnen	10	0
2/19/2018	Walenbrunnen	13	0
2/20/2018	Walenbrunnen	13	0
2/22/2018	Walenbrunnen	13	0
2/23/2018	Walenbrunnen	12	0
2/26/2018	Walenbrunnen	20	0
2/27/2018	Walenbrunnen	13	0
2/28/2018	Walenbrunnen	10	0
3/1/2018	Walenbrunnen	58	5
3/2/2018	Walenbrunnen	43	0
3/6/2018	Walenbrunnen	12	0
3/7/2018	Walenbrunnen	12	0
11/5/2018	Walenbrunnen	5	2
12/3/2018	Walenbrunnen	1	1
2/15/2019	Walenbrunnen	82	0
2/22/2019	Walenbrunnen	19	0
3/1/2019	Walenbrunnen	145	0
3/15/2019	Walenbrunnen	160	0
2/13/2020	Walenbrunnen	63	2
2/27/2020	Walenbrunnen	66	1
11/8/2019	Walenbrunnen	0	3

Stream	Dorfbach LU											Giebelbächli North						
Date	2/18/2015	8/31/2015	10/6/2015	11/30/2015	3/17/2016	10/17/2016	2/21/2017	3/8/2017	11/16/2017	2/15/2018	3/8/2018	3/14/2016	11/21/2016	2/20/2017	3/9/2017	2/16/2018	3/9/2018	12/14/2018
Tagged	52	79	23	2	31	4	77	16	3	58	12	83	4	80	26	65	35	0
Recapture	0	12	1	7	3	2	2	1	2	0	0	0	3	9	1	8	0	1

Stream	Giebelbächli South																									
Date	3/14/2016	2/20/2017	3/9/2017	11/20/2017	2/16/2018	3/9/2018	11/20/2018	12/14/2018	2/20/2015	3/5/2015	3/13/2015	8/17/2015	9/4/2015	10/15/2015	11/17/2015	12/10/2015	2/16/2016	3/1/2016	3/9/2016	11/14/2016	12/12/2016	2/7/2017	2/24/2017	11/13/2017	12/11/2017	2/5/2018
Tagged	75	83	28	5	44	48	0	0	16	53	9	21	43	11	11	0	34	27	7	0	1	73	58	2	1	12
Recapture	0	1	3	0	5	0	2	3	0	0	0	3	2	2	12	5	9	3	0	1	2	1	1	4	2	0

Giessen																								Klosterbach SZ																									
2/6/2018	2/9/2018	2/12/2018	2/14/2018	2/16/2018	2/19/2018	2/20/2018	2/22/2018	2/23/2018	2/26/2018	2/27/2018	2/28/2018	3/2/2018	3/6/2018	3/7/2018	11/13/2018	12/11/2018	2/18/2019	3/4/2019	3/12/2019	11/21/2019	2/14/2020	2/24/2020	3/4/2020	2/26/2015	3/6/2015	8/20/2015	8/28/2015	10/8/2015	11/10/2015	12/4/2015	2/26/2016	3/3/2016	10/6/2016	11/7/2016	2/17/2017	3/7/2017	11/6/2017	12/4/2017	2/5/2018	2/6/2018	2/9/2018	2/12/2018	2/14/2018	2/16/2018	2/19/2018	2/20/2018	2/22/2018	2/23/2018	2/26/2018
95	12	13	10	10	13	13	73	12	20	13	10	12	12	12	5	0	122	107	160	0	76	27	28	45	53	28	48	14	1	8	56	64	2	0	41	80	3	1	12	13	12	13	74	10	13	13	13	12	20
1	0	0	0	0	0	0	11	0	0	0	0	0	0	0	6	1	1	5	0	2	0	0	0	0	0	5	15	3	10	9	0	11	3	2	4	11	5	4	0	0	0	0	4	0	0	0	0	0	0

															Klosterbach UR																											Lo							
2/27/2018	2/28/2018	3/2/2018	3/5/2018	3/6/2018	3/7/2018	11/21/2018	12/6/2018	2/8/2019	2/26/2019	3/8/2019	11/14/2019	12/11/2019	2/17/2020	3/2/2020	2/20/2015	3/3/2015	8/26/2015	9/4/2015	10/13/2015	11/9/2015	12/1/2015	2/17/2016	3/9/2016	3/11/2016	10/14/2016	11/15/2016	12/13/2016	2/13/2017	11/14/2017	12/15/2017	2/20/2018	3/6/2018	3/7/2018	11/6/2018	12/7/2018	2/11/2019	2/28/2019	11/12/2019	12/9/2019	2/18/2020	3/9/2020	2/16/2015	3/12/2015	8/27/2015	10/9/2015	11/11/2015	12/9/2015	2/23/2016	3/8/2016
13	10	12	99	12	12	7	1	123	107	160	9	0	77	77	62	38	33	28	3	3	3	36	26	41	0	1	1	141	1	1	34	59	32	2	1	89	169	0	1	60	95	30	55	84	25	11	12	49	52
0	0	0	7	0	0	12	10	4	6	0	0	9	2	7	0	0	3	4	3	5	3	4	3	3	2	2	5	3	6	3	2	1	0	11	4	3	2	3	0	0	3	0	0	23	30	14	26	31	12

Streams where tracking with mobile antenna was carried out																																																	
chrütibach											N2 Entwässerungskanal																																						
10/7/2016	11/8/2016	12/6/2016	2/14/2017	3/2/2017	11/7/2017	12/5/2017	2/8/2018	3/12/2018	11/15/2018	12/13/2018	2/19/2015	3/4/2015	2/24/2016	3/2/2016	10/18/2016	11/18/2016	12/16/2016	2/15/2017	3/3/2017	11/9/2017	12/7/2017	2/5/2018	2/6/2018	2/9/2018	2/12/2018	2/14/2018	2/16/2018	2/19/2018	2/20/2018	2/22/2018	2/23/2018	2/26/2018	2/27/2018	2/28/2018	3/2/2018	3/6/2018	3/7/2018	11/12/2018	12/13/2018	2/19/2019	3/5/2019	3/21/2019	12/2/2019	2/6/2020	2/28/2020	9/8/2015	10/19/2015	11/6/2015	12/8/2015
5	3	0	48	60	8	0	68	48	1	0	38	52	63	43	6	10	2	50	95	7	5	12	13	54	13	10	9	76	13	13	12	20	13	10	12	12	12	3	12	123	116	160	3	79	79	96	1	3	3
10	3	3	7	17	14	1	13	13	3	2	0	0	0	2	1	3	4	7	11	3	8	0	0	3	0	0	0	2	0	0	0	0	0	0	0	0	0	9	15	2	5	0	15	0	10	0	0	0	1

Polenschachen	2/22/2016	24	12
	3/4/2016	9	6
	10/21/2016	2	1
	11/22/2016	0	2
	2/10/2017	28	0
	2/28/2017	60	0
	2/5/2018	12	0
	2/6/2018	13	0
	2/9/2018	12	0
	2/12/2018	13	0
	2/13/2018	27	0
	2/14/2018	10	0
	2/16/2018	10	0
	2/19/2018	13	0
	2/20/2018	13	0
	2/22/2018	34	7
	2/23/2018	12	0
	2/26/2018	20	0
	2/27/2018	13	0
	2/28/2018	10	0
	3/2/2018	99	14
	3/6/2018	12	0
	3/7/2018	12	0
	12/7/2018	1	2
	2/21/2019	36	0
	3/8/2019	6	0
	3/15/2019	160	0
Rossträнkekanal	2/19/2015	39	0
	3/4/2015	46	0
	2/24/2016	36	1
	3/2/2016	11	3
	3/10/2016	16	0
	2/15/2017	26	7
	3/3/2017	31	0
	2/9/2018	20	6
	2/19/2018	32	7
Scheidgraben	2/11/2015	51	0
	2/27/2015	52	0
	8/24/2015	92	3
	10/12/2015	7	0
	11/19/2015	5	10
	12/7/2015	1	10
	2/23/2016	84	6
	3/8/2016	51	4
	10/7/2016	0	2
	11/8/2016	2	4
	12/6/2016	0	4
	2/14/2017	81	5
	3/2/2017	70	7
	11/7/2017	7	12

n									Schützenbrunnen																																																								
12/5/2017	2/8/2018	3/12/2018	11/15/2018	2/12/2019	2/27/2019	11/15/2019	2/28/2020	2/6/2020	2/17/2015	3/5/2015	3/13/2015	8/21/2015	9/1/2015	10/19/2015	11/16/2015	12/14/2015	2/19/2016	3/4/2016	10/21/2016	11/22/2016	2/10/2017	2/28/2017	11/21/2017	12/18/2017	2/5/2018	2/6/2018	2/9/2018	2/12/2018	2/13/2018	2/14/2018	2/16/2018	2/19/2018	2/20/2018	2/22/2018	2/23/2018	2/26/2018	2/27/2018	2/28/2018	3/2/2018	3/6/2018	3/7/2018	11/22/2018	12/4/2018	2/21/2019	3/7/2019	3/21/2019	11/25/2019	2/19/2020	3/4/2020
0	84	67	6	127	147	1	63	80	30	35	24	18	54	5	3	2	50	84	13	16	64	102	3	1	12	13	12	13	51	10	10	13	13	13	75	20	13	10	12	12	12	0	3	64	115	160	1	56	78
2	3	4	9	3	5	11	4	6	0	0	0	4	1	2	7	4	6	16	4	1	2	2	4	0	0	0	0	0	1	0	0	0	0	0	7	0	0	0	0	0	0	9	5	0	3	0	3	1	2

Würzenbach																				
2/18/2015	3/11/2015	8/18/2015	10/6/2015	11/5/2015	11/30/2015	2/15/2016	2/29/2016	10/10/2016	11/10/2016	12/7/2016	2/6/2017	2/22/2017	3/10/2017	11/10/2017	12/6/2017	2/7/2018	2/21/2018	2/22/2018	11/19/2018	12/17/2018
30	61	70	3	2	5	15	44	1	8	1	71	11	27	0	1	25	33	0	1	0
0	0	13	23	3	9	18	20	3	4	4	10	2	10	4	1	7	7	2	5	2

Würzenbach reference											
2/15/2016	2/29/2016	10/10/2016	12/7/2016	2/6/2017	2/22/2017	11/10/2017	12/6/2017	2/7/2018	2/21/2018	11/19/2018	12/17/2018
59	71	12	1	61	124	2	2	22	62	0	1
0	0	4	1	0	4	1	7	12	0	1	0

Alpbach																
2/23/2015	3/9/2015	2/14/2020	2/24/2020	2/17/2015	3/3/2015	3/13/2015	8/17/2015	8/26/2015	9/7/2015	10/15/2015	11/17/2015	12/10/2015	2/16/2016	3/1/2016	10/13/2016	11/14/2016
39	25	41	45	30	4	26	5	4	28	5	8	5	29	28	3	1
0	0	9	8	0	0	0	0	1	7	6	6	8	6	6	3	0

2	0	12/12/2016	Dorfbach UR
3	78	2/7/2017	
3	39	2/23/2017	
6	4	11/13/2017	
6	4	12/11/2017	
0	12	2/5/2018	
6	55	2/6/2018	
0	12	2/9/2018	
0	13	2/12/2018	
0	10	2/14/2018	
0	11	2/16/2018	
0	13	2/19/2018	
0	13	2/20/2018	
9	33	2/22/2018	
0	12	2/23/2018	
0	20	2/26/2018	
0	13	2/27/2018	
0	10	2/28/2018	
0	12	3/2/2018	
12	53	3/6/2018	
0	12	3/7/2018	
11	10	11/13/2018	
3	0	12/11/2018	
9	37	2/22/2019	
3	22	3/8/2019	
0	140	3/12/2019	
9	4	11/21/2019	
0	8	11/11/2015	Engelberger Aa
0	2	11/13/2018	
0	2	11/16/2018	
1	1	11/22/2018	
0	18	2/22/2016	
0	69	3/15/2016	Färndlibach
0	39	2/24/2015	
0	44	3/9/2015	
2	20	8/25/2015	
5	50	9/1/2015	
3	7	10/16/2015	
8	4	11/13/2015	
9	11	12/3/2015	
9	34	2/18/2016	
14	69	3/7/2016	
4	2	10/11/2016	
1	0	12/9/2016	
4	77	2/8/2017	
0	35	2/23/2017	
2	3	11/3/2017	
0	12	2/5/2018	
0	13	2/6/2018	
0	12	2/9/2018	

Gangbach																						Gangbach reference	
2/12/2018	2/14/2018	2/16/2018	2/19/2018	2/20/2018	2/22/2018	2/23/2018	2/26/2018	2/27/2018	2/28/2018	3/2/2018	3/6/2018	3/7/2018	11/5/2018	12/3/2018	2/20/2019	3/6/2019	3/12/2019	11/25/2019	2/18/2020	2/27/2020	2/17/2016	12/9/2016	2/8/2017
13	10	10	13	43	13	12	20	13	10	12	12	78	2	0	50	40	160	0	81	52	67	2	52
0	0	0	0	2	0	0	0	0	0	0	0	28	4	1	3	0	0	1	2	1	0	2	5

Kärstelenbach						Leev																			
10/5/2015	11/6/2015	12/8/2015	10/4/2016	11/4/2016	11/16/2018	2/26/2015	3/6/2015	8/20/2015	8/28/2015	10/8/2015	11/10/2015	12/4/2015	2/26/2016	3/3/2016	10/6/2016	11/7/2016	12/5/2016	2/17/2017	3/7/2017	11/6/2017	11/20/2017	2/5/2018	2/6/2018	2/12/2018	2/14/2018
12	10	2	3	1	3	48	35	50	24	7	3	2	49	44	5	3	0	67	79	1	0	24	13	13	69
0	0	3	0	3	0	0	0	3	1	7	4	10	11	0	0	0	3	3	1	2	1	0	0	0	3

Streams where only tagging was carried out																																																	
wasser																					Mühlibach																												
2/16/2018	2/19/2018	2/20/2018	2/22/2018	2/23/2018	2/26/2018	2/27/2018	2/28/2018	3/2/2018	3/5/2018	3/6/2018	3/7/2018	11/21/2018	12/6/2018	2/13/2019	2/25/2019	2/26/2019	11/14/2019	12/11/2019	2/17/2020	3/2/2020	2/11/2015	2/16/2015	2/27/2015	3/12/2015	3/16/2015	9/3/2015	10/12/2015	11/19/2015	12/7/2015	2/25/2016	3/10/2016	10/18/2016	11/18/2016	12/16/2016	2/16/2017	3/6/2017	11/9/2017	11/24/2017	12/7/2017	2/5/2018	2/6/2018	2/9/2018	2/12/2018	2/14/2018	2/16/2018	2/19/2018	2/20/2018	2/22/2018	2/23/2018
10	13	13	13	12	20	13	10	12	74	12	12	1	4	141	112	160	2	1	69	83	18	14	8	24	50	45	2	0	2	95	59	4	1	0	98	80	8	1	0	86	13	12	13	11	10	13	13	13	12
0	0	0	0	0	0	0	0	0	6	0	0	1	6	1	2	0	9	3	2	4	0	0	0	0	0	7	7	9	6	9	6	5	2	2	5	7	8	2	1	6	0	0	0	0	0	0	0	0	0

0	20	2/26/2018	
0	13	2/27/2018	
0	10	2/28/2018	
0	12	3/2/2018	
0	12	3/6/2018	
0	12	3/7/2018	
23	89	3/14/2018	
9	8	11/12/2018	
8	1	12/10/2018	
0	36	12/11/2015	Muota
1	0	11/15/2016	
1	0	12/14/2018	
0	13	2/16/2015	Obbürgenbach
1	7	10/13/2015	Palangenbach
4	10	11/16/2015	
3	0	12/1/2015	
0	59	2/25/2015	Schlimbach
0	39	3/18/2016	
0	1	10/17/2016	
0	15	2/21/2017	
10	17	3/8/2017	
1	16	3/10/2017	
1	43	3/17/2016	
1	30	3/18/2016	Schlundbach
9	0	11/17/2016	
1	0	12/21/2016	
2	27	2/21/2017	
8	12	3/8/2017	
4	2	11/16/2017	
4	46	3/8/2018	
0	43	2/24/2015	Stille Reuss
0	66	3/10/2015	
4	38	8/25/2015	
1	9	9/2/2015	
1	0	10/24/2015	
0	78	2/18/2016	
0	3	10/13/2016	
0	2	10/29/2016	
2	7	11/11/2016	
1	0	12/1/2016	
1	70	2/9/2017	
0	45	2/27/2017	
7	0	11/11/2017	
3	0	11/30/2017	
2	59	2/13/2018	
1	81	3/1/2018	
1	0	11/3/2018	
1	1	11/16/2018	
4	92	2/20/2019	
0	59	3/6/2019	

2	66	2/13/2020	
0	39	2/19/2020	
5	50	3/7/2016	
0	6	10/5/2015	Urner Reuss
0	1	11/17/2017	
0	46	2/23/2015	Walenbrunnen
0	52	3/10/2015	
0	54	8/21/2015	
1	48	9/2/2015	
3	6	10/16/2015	
2	5	11/13/2015	
6	1	12/3/2015	
4	30	2/19/2016	
4	81	3/11/2016	
1	1	10/3/2016	
2	1	11/3/2016	
0	53	2/9/2017	
0	70	2/27/2017	
1	5	11/2/2017	
0	13	2/6/2018	
0	24	2/9/2018	
0	13	2/12/2018	
0	34	2/13/2018	
0	10	2/14/2018	
0	10	2/16/2018	
0	13	2/19/2018	
0	13	2/20/2018	
0	13	2/22/2018	
0	12	2/23/2018	
0	20	2/26/2018	
0	13	2/27/2018	
0	10	2/28/2018	
5	58	3/1/2018	
0	43	3/2/2018	
0	12	3/6/2018	
0	12	3/7/2018	
2	5	11/5/2018	
1	1	12/3/2018	
0	82	2/15/2019	
0	19	2/22/2019	
0	145	3/1/2019	
0	160	3/15/2019	
2	63	2/13/2020	
1	66	2/27/2020	
3	0	11/8/2019	
0	75	2/25/2015	Steinibach
0	41	3/11/2015	
0	89	3/17/2016	
5	45	3/8/2017	
3	73	2/15/2018	

Total
17530
1716

Supporting information e.g. additional data

Stream	Dorfbach LU								Giebelbächli North				Giebelbächli South									
Date	9/15/2015	9/22/2015	5/22/2016	9/18/2016	6/19/2017	7/5/2017	6/11/2018	6/18/2018	6/20/2017	7/11/2017	6/21/2018	7/12/2018	6/20/2017	7/11/2017	6/21/2018	7/12/2018	9/23/2015	6/1/2016	6/23/2016	10/1/2016	6/22/2017	7/13/2017
Number of unique detection	47	60	15	48	43	55	29	38	60	46	52	51	47	33	28	27	61	20	13	27	34	37
Number of recaptures within [0:365[days	1	1	5	5	2	2	0	0	7	7	1	1	4	4	5	5	21	3	3	3	1	1
Number of fish detected	0	1	0	0	0	1	0	0	1	2	1	0	2	2	2	0	14	3	3	0	1	0

Giessen										Klosterbach SZ									Klosterbach UR												
10/5/2017	6/15/2018	6/25/2018	7/4/2018	7/11/2019	7/18/2019	7/23/2019	6/26/2020	7/2/2020	7/9/2020	6/21/2018	6/29/2018	7/11/2018	7/3/2019	7/5/2019	7/9/2019	7/14/2020	7/20/2020	7/28/2020	6/22/2015	6/26/2015	6/30/2015	9/21/2015	9/25/2015	7/10/2016	8/8/2016	6/22/2017	6/30/2017	7/20/2017	6/19/2018	7/26/2018	7/11/2019
51	32	54	57	31	19	35	53	72	16	88	98	100	99	97	82	54	58	59	8	9	9	27	27	11	21	24	22	45	49	49	35
1	10	10	10	2	2	2				19	19	19	14	14	14				7	7	7	13	13	3	3	6	6	6	11	11	2
0	1	5	5	0	0	0				4	7	11	6	3	4				2	2	2	5	3	0	0	0	0	1	5	8	1

					Lochrütibach						N2 Entwässerungskanal													Polenschachen							
7/18/2019	7/23/2019	7/1/2020	7/9/2020	7/21/2020	6/21/2016	7/3/2017	7/13/2017	6/14/2018	6/26/2018	6/28/2018	6/29/2016	7/5/2016	5/23/2017	6/26/2017	7/10/2017	6/14/2018	6/28/2018	7/8/2019	7/12/2019	7/15/2019	6/25/2020	7/6/2020	7/22/2020	7/6/2014	10/5/2015	6/23/2016	7/6/2016	6/27/2017	7/6/2017	6/19/2018	7/3/2018
15	49	60	14	30	85	102	111	113	102	76	28	18	18	35	86	50	61	89	49	77	150	112	64	4	60	9	1	10	16	32	38
2	2				24	26	27	4	4	4	12	12	9	9	9	17	17	15	15	15				0	9	1	1	0	0	1	1
0	1				15	18	22	3	3	3	6	6	2	1	4	3	5	5	2	3				0	6	0	0	0	0	1	1

			Rosstränkekanal										Scheidgraben																		
7/2/2019	8/8/2019	8/9/2019	6/29/2016	7/14/2017	6/22/2018	6/28/2018	7/8/2019	7/18/2019	8/8/2019	6/25/2020	7/6/2020	7/22/2020	6/30/2015	9/29/2015	10/2/2015	10/6/2015	7/5/2016	7/19/2016	6/26/2017	7/7/2017	7/14/2017	6/17/2018	6/22/2018	7/16/2019	7/24/2019	8/6/2019	7/7/2020	7/14/2020	7/21/2020	9/16/2015	9/21/2015
1	18	11	16	40	36	25	14	28	16	31	18	24	29	64	59	60	58	27	28	35	32	85	81	64	27	69	30	51	46	39	38
0	0	0	5	10	0	0	0	0	0				4	9	9	9	9	9	13	13	13	11	13	15	15	15				24	24
0	0	0	1	4	0	0	0	0	0				4	6	3	3	7	1	2	2	3	6	8	4	1	3				10	11

Schützenbrunnen														Würzenbach									Würzenbach reference					
9/25/2015	6/28/2016	7/8/2016	6/22/2017	7/6/2017	6/15/2018	6/25/2018	7/4/2018	7/2/2019	7/4/2019	7/9/2019	7/10/2020	7/20/2020	7/28/2020	6/24/2014	9/15/2015	9/18/2015	9/22/2015	6/6/2016	7/4/2017	7/12/2017	6/20/2018	7/18/2018	6/24/2014	6/7/2016	7/5/2017	7/12/2017	6/20/2018	7/18/2018
50	19	28	33	42	28	44	58	44	60	37	44	40	52	16	64	65	65	58	20	38	29	33	1	19	27	37	20	30
25	5	6	4	4	10	9	9	3	3	3				0	47	47	47	25	15	15	7	7	0	7	10	10	1	1
14	0	4	2	3	3	3	4	2	1	1				0	33	26	32	21	1	4	2	3	0	1	4	3	0	0

TOTAL
6427
1089
464

Supporting information e.g. additional data

	Variable	PC1	PC2	PC3
Physical	Total length	0.18	0.41	-0.18
	Width (mean)	-0.27	0.03	-0.02
	Depth (mean)	-0.39	-0.10	-0.03
	Depth (maximum)	-0.30	-0.08	-0.28
Special features	Overhead cover (%)	0.30	-0.16	-0.33
	Vegetation	-0.33	0.16	-0.02
	Undercut bank (%)	-0.09	-0.31	-0.17
Substrate	Mud	-0.35	0.24	-0.16
	Sand	0.07	-0.42	-0.17
	Gravel	0.07	0.22	0.39
	Pebble	0.22	-0.15	-0.07
	Cobble	0.00	0.34	0.03
	Large stone	0.21	0.00	0.21
Flowing regime	Riffle	0.33	0.22	-0.12
	Run	0.02	-0.11	-0.35
	Fast run	-0.21	-0.12	0.47
	Pool	0.12	0.29	-0.20
	Shallow water	-0.22	0.29	-0.32

SUPPLEMENTARY TABLE CAPTIONS

Table S1. Summary of tagging data collection of *Salmon trutta* in streams of the Lake Lucerne drainage. The collection includes juvenile fish and resident adults (fish >250 mm that do not show a lacustrine phenotype), meaning that none of the fish had migrated to the lake prior to tagging. The collection comprised 14 streams in which PIT-tag mobile antenna tracking was carried out, and 18 other streams, which were only used in this study for modelling tag loss at recapture.

Table S2. Summary of tracking data collection of *Salmon trutta* from 14 streams in the Lake Lucerne drainage. For each pass, we reported the number of individual tags detected, the number of resident fish recaptured in a one-year period after the tracking and the number of them that were detected during the tracking.

Table S3. Three main vector compositions of the principal component analysis (PCA) of the environmental data from 14 streams in the lake Lucerne drainage where the study was carried out. We performed the PCA on 18 environmental variables (see Methods and Table 1).