

Capture probability of fishes in Central European (Hungary) wadeable lowland streams

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Abstract

Neglect of imperfect capture efficiency leads to biased inferences on population abundance, and correspondingly, seriously affects ecological research, bio-assessment, conservation, and fisheries management. To date, many research studies have studied capture efficiency of salmonid fishes, but the catchability of fishes living in non-salmonid streams has received much less attention. This paper estimates capture probability for seven fish species in densely vegetated lowland streams by using double-pass electrofishing data and an N-mixture removal model. Results show that capture probability can vary among species, and between-stream differences have a stronger influence on the abundance and the catchability than within-stream variability. Estimation uncertainty decreases with observed abundance, and the mean catchability tends to be the highest for the medium abundant species. These findings suggest that relative abundances from single-pass data are biased to a species- and habitat-specific degree. Therefore, plausible estimation of capture probability from double-pass electrofishing requires data collected from numerous sites that cover a wide range of the environmental gradient in lowland streams.

KEYWORDS

catchability, electrofishing, N-mixture model, removal sampling, sample representativeness

1 | INTRODUCTION

Effective protection of wild populations and their sustainable exploitation require reliable information on distribution and population size. However, even the assessment of these basic ecological variables can be loaded with bias from the imperfect detection of organisms (Kellner & Swihart, 2014). This could be especially the case for such elusive target animals as fish.

In wadeable streams, back-pack electrofishing is a common sampling method to survey fish assemblages. Researchers typically take one (single-pass), or repeated removal (multiple-pass) samples, with or without block nets. Because removal sampling is much more labor-intensive and time-consuming than single-pass electrofishing, surveys covering wide study areas with a large number of sites generally use single-pass electrofishing without blocking (e.g., Sály et al., 2011; Terra et

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al., 2016). Sampling effort for these surveys is usually standardized by the length of the sampled stream reach, and the catchability is assumed to be perfect for all species. However, several studies show that catchability and species detection can be imperfect (Bayley & Peterson, 2001; Deacon et al., 2017; Glover et al., 2019).

Previous studies on capture efficiency of fishes have commonly investigated salmonid species, and focused mainly for the estimation of population size (Glover et al., 2019; Mäntyniemi et al., 2005; Riley et al., 1993; Riley & Fausch, 1992; Ruiz & Laplanche, 2010; Wyatt, 2002). Trouts and juvenile salmonids typically live in clear cool water streams with no or little aquatic vegetation in the channel, which are different from the often densely vegetated, small (wetted width < ca. 7 m) lowland streams. Therefore, the transferability of the salmonid-centric results to lowland streams can be problematic, because environmental factors (e.g., water depth, turbidity, substratum, emergent vegetation) have commonly been found to influence capture efficiency of fish (Zalewski, 1983) and detection probability of other animals as well (Conway & Gibbs, 2011; Hamer, 2018; Kéry et al., 2009), and evidence also suggests that catchability differs among the species (Mollenhauer et al., 2018; Price & Peterson, 2010; Reid et al., 2009). This indicates a need to investigate capture probability in various stream types and for multiple species.

Neglect of imperfect detection can lead to improper inferences on populations, which may seriously influence bioassessment, conservation, and fisheries management outcomes (Williams et al., 2002). Increased noise-to-signal ratio in population estimates may hinder our ability to perceive subtle changes and trends in spatial and temporal population dynamics, which can be an issue in case of both imperiled species and spreading of non-native ones. Moreover, species can even remain completely undetected in severe cases (Deacon et al., 2017). Biased population estimates may involve erroneous knowledge on fish–habitat associations too. As a consequence, data with underestimated abundances or many false zeros for rare species can result in inadequate habitat restorations or improperly selected habitats for reintroductions. Biased catchability estimates may risk overexploitation of wild fish stocks, which makes uncertain the long-term survival of the economically important species. Capture probability is therefore an issue that needs to be addressed (Kellner & Swihart, 2014; Radinger et al., 2019).

1.1 | Aims

This study is a complement to the former investigation of Sály et al. (Sály et al., 2009), who compared the sampling efficiency of single-pass and double-pass

electrofishing. The primary aim of the present paper is to estimate capture probability for common fish species in wadeable lowland streams of the Pannonian Basin (Hungary). To do so, an N-mixture model is applied on the data of seven fish species caught by double-pass electrofishing. In addition to the estimation of capture probability, within-site and between-site stochastic variability in capture probability are also compared to indirectly assess the importance of environmental conditions at two spatial scales on catchability. Our model presented in this paper can easily be applied to any double-pass removal data to infer about abundance and imperfect detection. This estimation framework extends the application of former models (e.g., Dorazio et al., 2005; Wyatt, 2002) by adding random effects terms to account for unmeasured heterogeneity.

2 | METHODS

2.1 | Sampling design

Field data were gathered from seven wadeable lowland streams belonging to the catchment of Lake Balaton, Hungary, in spring of 2008. Detailed description of the streams and sampling procedure, and the raw fishing data can be found in the study by Sály et al. (Sály et al., 2009), but the design and the sampling method are briefly reiterated here. A total of eight sampling sites were selected on seven streams. At each site, a 200-m long stream reach was divided into ten 20-m long stream units, which were the basic sampling units of this study. Sampling units were block-netted (mesh size 2 mm) at both the downstream and the upstream end before fish sampling. Then, a double-pass removal (or depletion) sampling procedure with a back-pack gear (Hans-Grassl IG200/2B, PDC, 75–100 Hz) was conducted to catch fish. During the first pass, the gear operator caught the fish with a netted hand-held anode by wading, and another crew member helped to collect the stunned fishes with a hand dip net. Caught fish were temporarily collected in water filled plastic container boxes until identification and counting. After that, they were released back into their habitat a little downstream from the sampled unit. Having waited for at least 15 min, the second-pass electrofishing was carried out in the same way as the first one had been.

This sampling procedure yielded two data matrices accordingly to the first and second electrofishing passes. Both matrices had sampling units grouped by a site variable in its rows, and species in its columns. Entries contained the raw counts of the fish caught during the first or the second pass, respectively. Hence, the number of individuals of a species observed via the field sampling in

a given sample unit of a given site was the sum of the counterpart cell entries of the two matrices.

2.2 | Studied fish species

Out of the total 27 fish species caught during the field sampling, seven were assessed here. Prior to species selection, data of one sampling site were excluded because release of fish from a nearby fishery pond caused extreme and atypical variability in the composition of fish assemblages of this stream site. A species was selected to be assessed if it occurred in at least four sites and it was caught from a minimum of three sampling units at each of those sites. This criterion of selection screened out the species occurring commonly in small lowland Pannonian streams. Of the selected species, the rudd (*Scardinius erythrophthalmus* [Linnaeus, 1758]), the roach (*Rutilus rutilus* [Linnaeus, 1758]), and the European bitterling (*Rhodeus amarus* [Bloch, 1782]) are native water-column cyprinids; the Prussian carp (*Carassius gibelio* [Bloch, 1782]) is a non-native benthopelagic cyprinid; the Danubian spined loach (*Cobitis elongatoides* complex) is a native benthic fish; the European perch (*Perca fluviatilis* Linnaeus, 1758) is a native percid; and the pumpkinseed (*Lepomis gibbosus* [Linnaeus, 1758]) is a centrarchid non-native to Hungary (Table 1).

2.3 | Data analysis

To estimate catchability, a hierarchical multinomial N-mixture model was constructed and fitted on the double-pass removal data. N-mixture (or binomial mixture) models have a hierarchical structure that corresponds to the mechanism generating the ecological data (Dorazio et al., 2005; Joseph et al., 2009; Kéry & Royle, 2016; Kéry &

Schaub, 2012; Royle, 2004; Royle et al., 2005; Wyatt, 2002). The first level of our depletion model composes the distribution of individuals across sites. The unknown number of individuals in a sampling unit of a site (N) is supposed to follow a Poisson distribution. The expected value of the Poisson distribution, λ , has extra random variability across the sites ($\sigma_{\lambda_{SI}}^2$, sub-subscript SI stands for “site”) and sampling units within a site ($\sigma_{\lambda_{SU}}^2$, sub-subscript SU stands for “sampling unit”). The second level of the model incorporates the observation process, which is a double-pass sampling procedure. During the first pass, known number of individuals are captured (y_1) and removed from the sampling unit. As a result, an unknown of n individuals remain in the sampling unit. Subsequently, known number of additional individuals are caught (y_2) from the same unit during the second pass. Both y_1 and y_2 are modeled as binomially distributed random variables and have a common probability parameter, q that actually represents the individual capture probability (or catchability). Similarly to the abundance, capture probability also has extra random variability originating from the sites ($\sigma_{q_{SI}}^2$) and the sampling units ($\sigma_{q_{SU}}^2$). Extra random variations (i.e., random effects) account for the between-site and the within-site spatial differences in the distribution of the individuals, and in the capture probability, which differences can be termed as extrinsic (i.e., independent of the morphological and behavioral characteristics of the fish specimens) heterogeneity (Veech et al., 2016). A common ability of this type of N-mixture models is that they can estimate simultaneously both the unknown abundance (population size, N) and the capture probability (q) from the data, nonetheless, catchability is in the focus of this study. The formal description and a graphical representation of the model can be found in supporting information (S1).

TABLE 1 Fish species assessed for catchability

Common name	Scientific name	k	Freq	Mean	SD
Prussian carp	<i>Carassius gibelio</i>	5	37	5.28	8.72
Danubian spined loach	<i>Cobitis elongatoides</i> complex	4	31	4.23	4.61
Pumpkinseed	<i>Lepomis gibbosus</i>	4	24	2.80	4.28
European perch	<i>Perca fluviatilis</i>	5	36	2.84	4.41
European bitterling	<i>Rhodeus amarus</i>	5	43	17.58	21.22
Roach	<i>Rutilus rutilus</i>	6	46	15.73	15.53
Rudd	<i>Scardinius erythrophthalmus</i>	4	29	13.08	26.53

Note: Note that the total number of the sampling units in each species data was $k \times 10$. See section 2.1 and 2.2 for more details. k , the number of sites where the species was observed in at least three 20-m sampling units; Freq, the number of sampling units from which the species was caught (i.e., observed occurrence frequency); Mean and SD , the average and the standard deviation of the number of individuals per sampling unit.

The model makes the assumptions that the species is present at the sampled site, but can be undetected from one or more sampling units of the site (incidence at site); the taxonomic identification of the caught individuals is without error (perfect identification); sampling units are closed (no emigration and immigration) during the double-pass sampling (closure); capture events among the individuals are independent from each other, that is all individuals have equal chance to be caught (independence between individuals); catchability is the same for both the first and the second electrofishing (equal capture probability for both passes); differences between the sites, and between the sampling units of a specific site cause random variation in real abundance and catchability (random space effects).

The model was applied in a Bayesian framework using JAGS v4.3.0 (Plummer, 2003) for Markov chain Monte Carlo (MCMC) algorithm via R (R Core Team, 2020) and the package “rjags” (Plummer, 2019). For each species data, the model was run with three chains, uninformative priors, a burn-in length of 100,000 steps, 200,000 iterations, and a thinning rate of 100, after 5,000 adaptation steps. This setting led to a sample size of $3 \times 2,000$ (from the three chains) from the posterior distribution, for there is no MCMC simulation during the adaptation phase, and the burn-in period is dropped away. Convergence of the chains was evaluated by Gelman and Rubin’s diagnostic convergence statistic (Gelman & Rubin, 1992). Goodness-of-fit was assessed with a posterior predictive checking procedure (Gelman et al., 1996; Kéry & Schaub, 2012) providing a lack-of-fit ratio. The closer this value is to one, the better the model fits on the data, whereas deviation from one in either directions suggests poor fit.

Capture probability was monitored after averaging the q parameters across the sites and sampling units (hereafter \bar{q}) to get the estimation supposed to be typical

for the streams of the study region. In contrast, estimated abundances were monitored after averaging the latent ecological variables N across only the sampling units of each site, which yielded a mean abundance estimate for a 20-m stream reach separately for the sites. Finally, we were interested in comparison of between-site and within-site variances of the capture probability and the abundance, so the corresponding model parameters ($\sigma_{q_{SI}}^2$, $\sigma_{q_{SU}}^2$, $\sigma_{\lambda_{SI}}^2$, $\sigma_{\lambda_{SU}}^2$) were monitored as well. These variances of the random terms (sites, sampling units) can handle the overdispersion of the data, and make the model estimation robust (Harrison, 2014; Kéry & Royle, 2016), although many other options can be applied to model ecological count data (e.g., (Joseph et al., 2009; Wenger & Freeman, 2008)). Model source code in BUGS language can be found in supporting information S2.

3 | RESULTS

3.1 | Capture probability

Posterior predictive checking procedure showed the model fitted well on the observed data: lack-of-fit ratios spread closely around one (Table 2), with deviation not more than 0.048 (in case of the European perch).

The lowest expected individual capture probability uninfluenced by random effects was estimated for the pumpkinseed ($\hat{\alpha}_q = -1.337$ [logit], 0.208 [probability]), and the highest one for the Prussian carp ($\hat{\alpha}_q = 0.850$ [logit], 0.701 [probability]). The ratios of the between-site variance estimates to the within-site variance estimates in the logit-scaled capture probability ($\hat{\sigma}_{q_{SI}}^2 : \hat{\sigma}_{q_{SU}}^2$) ranged between 0.768 and 12.50 (mean and SD: 4.480 ± 3.827), and were greater than one for six but one species, the bitterling (Table 3).

TABLE 2 Estimates for the average capture probabilities of the observation process (double-pass removal sampling)

Common name	Scientific name	\bar{q}				Lack-of-fit ratio
		Mean	Std err	95%lwr	95%upr	
Prussian carp	<i>Carassius gibelio</i>	0.630	0.092	0.425	0.778	0.998
Danubian spined loach	<i>Cobitis elongatoides</i> complex	0.409	0.108	0.201	0.614	1.010
Pumpkinseed	<i>Lepomis gibbosus</i>	0.325	0.120	0.123	0.585	0.976
European perch	<i>Perca fluviatilis</i>	0.313	0.106	0.109	0.533	0.952
European bitterling	<i>Rhodeus amarus</i>	0.410	0.054	0.316	0.528	1.014
Roach	<i>Rutilus rutilus</i>	0.501	0.073	0.332	0.618	1.008
Rudd	<i>Scardinius erythrophthalmus</i>	0.653	0.090	0.440	0.803	0.997

Note: Arithmetic-scaled values (probabilities), except “Lack-of-fit ratio.” \bar{q} , average capture probability; 95%lwr and 95%upr, the 2.5th and 97.5th percentile of the posterior distribution (i.e., limits of a 95% credible interval); Lack-of-fit ratio, a goodness-of-fit statistics, the closer it is to one, the better the fit of the model is on the data.

TABLE 3 Estimates for the model parameters of the observation process (double-pass removal sampling)

Common name	Scientific name	$\hat{\alpha}_q$		$\hat{\sigma}_{q_{SI}}^2$		$\hat{\sigma}_{q_{SU}}^2$	
		Mean	Std err	Mean	Std err	Mean	Std err
Prussian carp	<i>Carassius gibelio</i>	0.850	1.149	4.492	5.448	1.218	1.359
Danubian spined loach	<i>Cobitis elongatoides</i> complex	-0.527	1.012	2.529	4.134	1.157	1.052
Pumpkinseed	<i>Lepomis gibbosus</i>	-1.337	1.652	6.338	6.137	1.373	1.500
European perch	<i>Perca fluviatilis</i>	-1.129	1.157	4.266	5.018	0.341	0.391
European bitterling	<i>Rhodeus amarus</i>	-0.650	0.758	2.099	3.584	2.732	1.022
Roach	<i>Rutilus rutilus</i>	-0.080	0.727	1.830	3.084	0.706	0.709
Rudd	<i>Scardinius erythrophthalmus</i>	0.715	0.910	2.092	3.906	0.417	0.694

Note: Logit-scaled values. $\hat{\alpha}_q$, overall expected individual capture probability (i.e., without random effects); $\hat{\sigma}_{q_{SI}}^2$, between-site variance in capture probability; $\hat{\sigma}_{q_{SU}}^2$, within-site variance in capture probability.

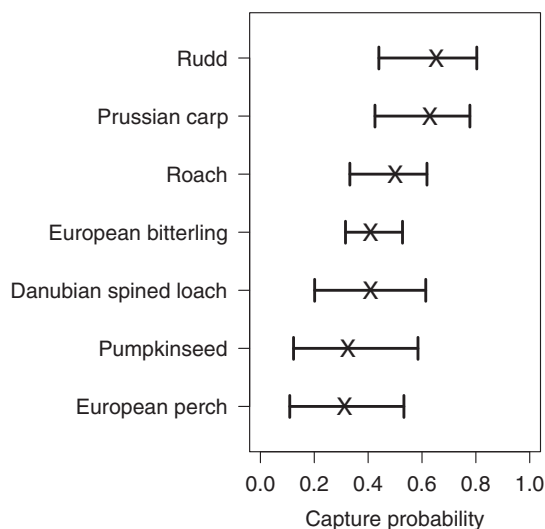


FIGURE 1 Estimated average capture probabilities (\hat{q}). Horizontal ranges delineate 95% credible intervals; “X”s indicate the mean of the posterior distribution

Average capture probability encompassing the random site and sampling unit effects (\hat{q}) was moderate and similar to each other for the European perch and the pumpkinseed, relatively high and similar also for the rudd and the Prussian carp, and medium for the other three species (Table 2). Despite the remarkable contrasts in the means of the posterior distributions of capture probability, the pairwise overlaps of the 95% credible intervals suggested no statistically significant differences in catchability between the species (Figure 1).

Estimation uncertainty expressed as the width of the 95% credible interval of \hat{q} showed a negative linear relationship with the mean of the observed abundance (i.e., number of individuals captured in the sampling units via the two electrofishing passes). Catchability

estimation was less precise for the species with low average density (Figure 2).

The mean of the observed abundance, that is the mean density of the species, was associated with the average catchability (\hat{q}) too. The quadratic relationship suggested lower average capture probability for the species with both low (e.g., Danubian spined loach) and high average density (e.g., roach), and relatively high capture probability for species with medium density (e.g., rudd) (Figure 3).

3.2 | Abundance

Ignoring random effects, the mean of the estimates for the overall log-scaled abundance varied from $\hat{\alpha}_\lambda = 0.665$ (log), 1.94 (arithmetic) (rudd) to $\hat{\alpha}_\lambda = 2.926$ (log), 18.56 (arithmetic) (bitterling). Similarly to capture probability, the variance in the log-scaled abundance across the sites ($\hat{\sigma}_{\lambda_{SI}}^2$) was definitely greater than the variance across the sampling units within the sites ($\hat{\sigma}_{\lambda_{SU}}^2$) (Table 4).

Taking into consideration the random effects, estimates for the mean abundance of one sampling unit (\hat{N}) were larger than the mean observed abundances (i.e., number of the captured individuals during two electrofishing passes: $N_{obs} = y_1 + y_2$) for each species, but the degree of the difference varied by species. The two highest relative differences between the predicted and the observed mean abundance were found for the pumpkinseed ($d = 2.06$) and the European perch ($d = 2.04$), and lowest one for the rudd ($d = 0.20$). In contrast to the means, the standard errors of the predicted abundances were quite similar to observed ones (Table 5).

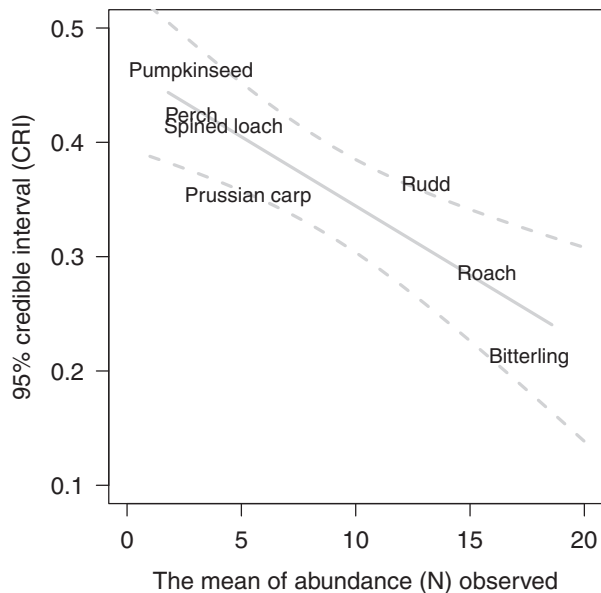


FIGURE 2 Relationship between estimation uncertainty of catchability measured by the width of 95% credible interval and the mean of abundances observed (total number of caught individuals via double-pass sampling) in 20-m long stream reaches. Solid gray line represents expected value (mean), and dashed gray lines represent 95% confidence interval for the mean. Equation of the function and coefficient of determination: $y = 0.465 - 0.012 \cdot x$, $R^2 = 0.823$

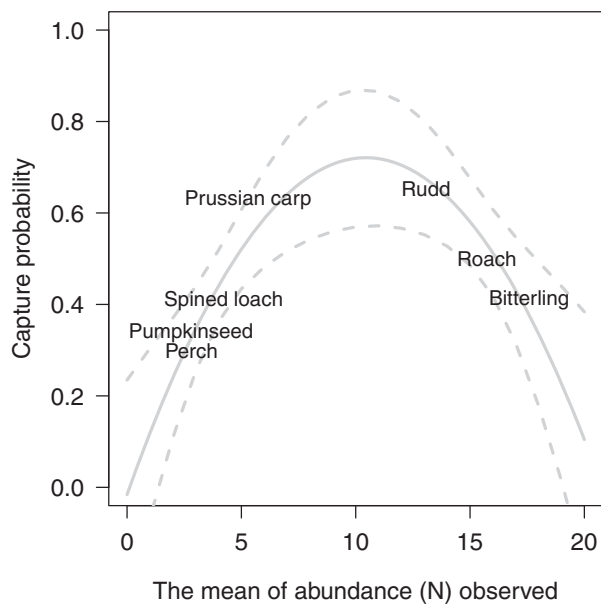


FIGURE 3 Relationship between average capture probability (\hat{q}) and the mean of abundances observed (total number of caught individuals via double-pass sampling) in 20-m long stream reaches. Solid gray line represents expected value (mean), and dashed gray lines represent 95% confidence interval for the mean. Equation of the function and coefficient of determination: $y = -0.016 + 0.141 \cdot x - 0.007 \cdot x^2$, $R^2 = 0.813$

4 | DISCUSSION

4.1 | Relationship between estimation uncertainty and density

Using a hierarchical multinomial N-mixture model on double-pass electrofishing data, the study estimated the magnitude and uncertainty of capture probability and abundance for seven common fish species in wadeable Pannonian lowland streams. Similarly to many other studies (Benejam et al., 2012; Harris et al., 2016; Hedger et al., 2018; Peterson & Cederholm, 1984; Riley et al., 1993; Riley & Fausch, 1992), data showed that efficacy of electrofishing is not perfect, single-pass sampling resulted in a catch less than the true population size, and capture probability varied across the species (Mollenhauer et al., 2018; Price & Peterson, 2010; Reid et al., 2009; Stewart et al., 2019), although its stochastic fluctuations were too wide to identify sharp differences between the species. Stochastic fluctuation of capture probability is likely enhanced when stream reaches with very different environmental characteristics are sampled. In general, discharge, channel width, depth, width–depth ratio, boulders, emergent vegetation, and turbidity are among the most common environmental variables that affect capture probability, mostly in a negative way (Mollenhauer et al., 2018). On the other hand, environmental circumstances can influence efficiency with effect sizes varying from site to site (or region to region), and interactions between the abiotic variables also can happen (Mollenhauer & Brewer, 2017). This kind of heterogeneity of the influential environmental variables involves that some stream reaches can be sampled more efficiently than others. Moreover, influence of the environmental factors on catchability can depend on the species sampled, that is species–environment interactions exist (Mollenhauer et al., 2018; Price & Peterson, 2010; Reid et al., 2009), which makes the sample taken from a particular site more representative for one species and less representative for others. Our model did not contain abiotic covariates in an explicit way, instead random terms were charged to surrogate the environmental differences among the study sites. Because the precision of the capture probability was significantly affected by the random variances originated from between-site and within-site heterogeneity, we believe that the linear relationship shown in Figure 2 suggests that the influential role of the environmental variables are related to the density of the species as well. Accordingly, the catchability of low density species can be estimated with greater uncertainty than that of the more abundant species, which is highly likely due to latent abiotic covariates.

TABLE 4 Estimates for the model parameters of the ecological process (latent abundances)

Common name	Scientific name	$\hat{\alpha}_\lambda$		$\hat{\sigma}_{\lambda_{SI}}^2$		$\hat{\sigma}_{\lambda_{SU}}^2$	
		Mean	Std err	Mean	Std err	Mean	Std err
Prussian carp	<i>Carassius gibelio</i>	1.053	1.009	4.244	4.350	0.800	0.338
Danubian spined loach	<i>Cobitis elongatoides</i> complex	1.631	0.945	2.922	4.011	0.461	0.294
Pumpkinseed	<i>Lepomis gibbosus</i>	1.234	1.132	3.256	4.455	1.000	0.669
European perch	<i>Perca fluviatilis</i>	1.394	0.886	2.771	3.486	0.387	0.223
European bitterling	<i>Rhodeus amarus</i>	2.926	0.736	2.542	3.352	0.258	0.170
Roach	<i>Rutilus rutilus</i>	2.230	0.936	4.481	4.166	0.690	0.292
Rudd	<i>Scardinius erythrophthalmus</i>	0.665	1.312	7.903	5.672	0.781	0.357

Note: Log-scaled values (base e). $\hat{\alpha}_\lambda$, overall expected abundance (i.e., without random effects); $\hat{\sigma}_{\lambda_{SI}}^2$, between-site variance in abundance; $\hat{\sigma}_{\lambda_{SU}}^2$, within-site variance in abundance.

TABLE 5 Observed and estimated mean abundances for a 20-m long stream unit

Common name	Scientific name	k	N_{obs}			\hat{N}		d
			Freq	Mean	Std err	Mean	Std err	
Prussian carp	<i>Carassius gibelio</i>	5	37	5.28	5.31	7.08	5.76	0.34
Danubian spined loach	<i>Cobitis elongatoides</i> complex	4	31	4.23	3.34	8.36	5.86	0.98
Pumpkinseed	<i>Lepomis gibbosus</i>	4	24	2.80	2.89	8.57	3.37	2.06
European perch	<i>Perca fluviatilis</i>	5	36	2.84	3.08	8.62	5.10	2.04
European bitterling	<i>Rhodeus amarus</i>	5	43	17.58	16.82	30.16	18.79	0.72
Roach	<i>Rutilus rutilus</i>	6	46	15.73	12.71	23.80	18.15	0.51
Rudd	<i>Scardinius erythrophthalmus</i>	4	29	13.08	24.15	15.74	28.20	0.20

Note: Arithmetic-scaled values (# of individuals). Note that the total number of the sampling units in each species data was $k \times 10$. N_{obs} , observed mean abundance (i.e., total number of individuals caught during the double-pass sampling); \hat{N} , estimated mean abundance; k the number of sites whose data were used for analysis, and abundance predictions were made for; Freq, the number of sampling units that the species was caught from (i.e., observed occurrence frequency); Std Err, standard error (i.e., standard deviation) of the observed and predicted mean abundances for the k sites which the species was caught from and predicted; d , difference between the predicted and the observed mean abundance relative to the observed: $\frac{N - N_{obs}}{N_{obs}}$.

4.2 | Issue of equal catchability

A possible weakness of the double-pass removal models including the one which was used in this study is that the assumption of equal catchability during the first- and the second-pass electrofishing is often violated. A decrease in catchability during the second and subsequent passes is possible in densely vegetated lowland streams. Aquatic vegetation impedes wading and becomes trampled after completing the first pass. In the subsequent passes the trampled vegetation might increase the chance of the fish getting stuck and remain undetected. On the other hand, decline of capture probability across the subsequent passes of a removal sampling is not always justified. Constant catchability across the passes also occurs (Benejam et al., 2012; Peoples & Frimpong, 2011; Reid et al., 2008; Riley et al., 1993; Riley & Fausch, 1992), which suggests that variation in catchability during removal sampling

can be context dependent. The model used in this study can be extended for allowing separate estimations of capture probability for the passes of a data set with three or more passes, and then testing of the decline in catchability becomes possible. In that case, even if the catchability proved to be constant, the increased number of passes would likely improve the estimations of the model (Riley & Fausch, 1992; Stewart et al., 2019).

4.3 | Benefits of random effects

Incorporation of extra variances via random effects into ecological models provides several benefits. Observation-level random effects can remedy the lack of statistical independence (Millar & Anderson, 2004; Price & Peterson, 2010) arising from spatial autocorrelation or pseudoreplication between study objects, mitigate the

overdispersion (Harrison, 2014) originating from spatial aggregation of individuals in count data, and represent the effects of variables unmeasured in the field (Kéry & Schaub, 2012). In our study design, sampling units within the sites were spatially adjacent to each other along the stream. Thus, neighboring sampling units usually had somewhat more similar habitat characteristics than non-neighboring ones, which could cause spatial autocorrelation. On the other hand, sampling units, even the neighboring ones, differed from one another in their environmental features affecting the catchability of fishes to a certain extent. That kind of environmental differences (e.g., in vegetation cover, mean depth) leads to extrinsic heterogeneity in individual capture probability, which can be modeled by appropriate covariates ((Veech et al., 2016), p. 1020). Because the main goal of this study was to estimate the extent of capture probability and not the investigation of the factors influencing that, random effects were used as surrogates for the environmental covariates. Nonetheless, our model can easily be developed by merging covariate terms into the log-linear and the logit-linear regression equations to assess the influential role of habitat features or sampling circumstances on capture probability and abundance (Joseph et al., 2009; Kéry & Schaub, 2012; Mollenhauer & Brewer, 2017; Smith et al., 2012; Som et al., 2018; Stewart et al., 2019). In such cases, one might expect more precise (i.e., narrower credible intervals) estimates, all else being equal.

4.4 | Between-site vs. within-site variance

Between-site differences appear to have larger influence on both abundance and catchability of the species than differences between the sampling units of a particular site. Other studies also found the sampling site being a relevant factor in the variation of capture probability (Benejam et al., 2012; Glover et al., 2019; Hedger et al., 2018; Stewart et al., 2019). The smaller within-site variance compared with the between-site variance might be explained by the modified status of the streams. Small lowland streams in Hungary are channelized and constrained between dykes, so they are quite homogeneous in comparison with highland or submountain streams. The most prominent agent that can cause some environmental variability within the mostly straight running lowland streams is the aquatic vegetation, whereas the hydrogeomorphological variety is practically absent. Therefore, the variability between the sampling sites of this study actually emphasizes, at least in part, a stream effect because our sites were located on different water

courses with the exception of one water course on which two sites were located. Maintenance of a kind of uniqueness of the modified lowland streams, via, for example, vegetation control and flow regulation, might promote the preservation of fish assemblage variability at regional scale.

4.5 | Relationship between capture probability and density

Results showed that observed abundance of the species can affect the expected value of catchability as well, or in other words, density differences between the species can lead to species-specific catchability. The quadratic relationship between the average capture probability and the observed abundance found in this study predicts that catchability can be expected to be the highest for the medium abundant species of a local assemblage, and somewhat lower for the low abundant and the most dominant ones. In a study on the Atlantic salmon parr (*Salmo salar*, Linnaeus, 1758), Riley et al. (1993) reported a nonlinear relationship between capture probability and density, which was similar to the relationship in Figure 3, and showed that capture probability was low when density of parr was low too. Experience of Harris et al. (2016), who sampled known number of size-classed larval lampreys in enclosures, partially supports our catchability–abundance relationship. Albeit the proportion of larval lampreys caught during the first pass was the lowest at high larval density, the highest proportion was caught at low larval density, and in between at medium density.

Inefficient sampling of low abundant species can arise mainly from the lack of detection by the sampling crew. For instance, as a reaction to the pulsating direct current, loaches such as the Danubian spined loach usually wriggle, and dash themselves into the fine sediment as soon as the current ceases; the perch and the pumpkinseed tend to hide, become immobilized, and get stuck in the underwater vegetation. In contrast, the individuals of high abundant species are usually well seen, but simply the large number of fish present makes difficult to catch each stunned specimen (gear saturation). In the studied lowland streams, the dominant species of the fish assemblages are usually small-bodied cyprinids like the roach, the rudd, and the bitterling. These species generally shoal, which lead to more or less aggregated distribution within the stream reach. When the sampling crew encounter a shoal and try to catch the numerous fish the nets used to collect the stunned specimens get full soon, and netting new specimens becomes practically impossible without losing some already captured individuals.

As a consequence of the capture probability varying by species, abundance estimates obtained from the model appear to depict somewhat different density relationships than can be inferred from the observed data for the studied streams. More specifically, observed data indicated that mean density of the Danubian spined loach (4.23 individuals per a 20-m long stream unit) is slightly higher than that of the pumpkinseed (2.80 individuals) and the perch (2.84 individuals), but predicted mean abundances suggested quite similar densities for these three species.

4.6 | Conclusions

This study provides estimates for the capture probability of fishes in densely vegetated lowland streams, and highlights the possibility that the relative abundances in the CPUE samples of single-pass electrofishing are biased to varying degrees due to differences in catchability of the fish species. Applicability of CPUE single-pass electrofishing therefore should be considered with regard to the aim of data collection. Many papers have emphasized the need for gear calibration or adjustment of catch data (Bayley & Peterson, 2001; Glover et al., 2019; Mollenhauer et al., 2018; Price & Peterson, 2010) in order to obtain more realistic data to monitor population sizes, for example, of endangered species. Nevertheless, if researchers aim to compare data sampled from the same multiple sites and repeated in time to investigate changes within the time extent of the survey period, for example, for bioassessment purposes, single-pass electrofishing with reasonable effort can be an acceptable cost-effective method. Similarly, single-pass electrofishing can be proper sampling method in small streams as well when the aim of the survey is the estimation of species richness (i.e., presence of species), because detection probability of a species can be high even in cases if individual capture probability is low (Peoples & Frimpong, 2011).

On the other hand, bias in abundance estimates can also vary within a species, depending on survey time and sites selected to be sampled (Benejam et al., 2012; Dauphin et al., 2019; Glover et al., 2019; Hedger et al., 2018; Stewart et al., 2019). Hence, monitoring protocols operated to record trends in true population sizes should involve gear calibration of single-pass electrofishing regularly and regionally (or in a water body type-specific way), and also an effort–result survey (e.g., rarefaction curves). Alternatively, monitoring systems may also consider the so-called robust design (Williams et al., 2002) and appropriate models to estimate capture probability and abundance (Kéry & Schaub, 2012).

As a rule, the estimation procedure requires such models that fit to the ecological and observational

processes generating the observed data (Joseph et al., 2009). Nevertheless, it clearly stands out from the previous studies that no single best model exists to estimate capture probability (Benejam et al., 2012; Veech et al., 2016), and even models supposed to be well structured can underperform with poor observed data. So, estimation of capture probability from double-pass electrofishing should be conducted with data collected from numerous sites covering the environmental heterogeneity of the water courses to be studied.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

Péter Sály: Conceptualization, Methodology, Software, Formal analysis, Investigation, Writing – original draft, Visualization; **Péter Takács:** Investigation, Writing – review and editing; **András Specziár:** Investigation, Writing – review and editing; **Tibor Erős:** Investigation, Resources, Writing – review and editing.

DATA AVAILABILITY STATEMENT

The complete data set can be found in Sály et al. (2009).

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