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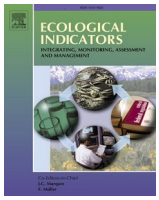

Original Articles

Environmental DNA surveys can determine in-stream dominance of non-native brook charr *Salvelinus fontinalis* over native brown trout *Salmo trutta*

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ABSTRACT

For effective management of established potentially invasive species it is important to find management target sites (e.g. for depletion or eradication measures). In Sweden, the brook charr is non-native and competes with the native brown trout. Hence, finding methods allowing for rapid screening for potential problem areas is important. Wading electrofishing is the main method used, but eDNA surveys have the potential to replace the former method. Here we evaluate the usage of quantitative single-species eDNA analyses to find sites where brook charr dominates over brown trout. Using the ratio of the estimated relative amount of eDNA for each species, we correctly detect the vast majority of the areas where brook charr is dominating brown trout in the electrofishing results (> 50 % of total abundance or biomass). Surveys using eDNA also have a higher chance to detect brook charr than electrofishing. We also show that quantitative comparisons between eDNA and electrofishing can be interpreted in very different ways depending on handling of outliers and inclusion/exclusion of sites without either catch or eDNA detections of a species in the analyses. Overall, however, even if relationships between catch results and eDNA results are found to be significantly positive under certain assumptions, the ability of eDNA results to predict electrofishing catches at the site level is associated with substantial uncertainties, at the scale of an order of magnitude. No environmental factors were found to clearly affect eDNA concentrations. In conclusion, eDNA is a promising tool to be used for cost-efficient screening of streams where brook charr is a potential ecological problem, but electrofishing still has a strong methodological position for follow-up studies quantifying their actual abundance. The two methods are complementary and one should not completely replace the other.

1. Introduction

Brook charr *Salvelinus fontinalis* (Mitchill 1814), also commonly called 'brook trout', has been intentionally introduced in many places outside its native range in north-eastern North America (MacCrimmon & Campbell 1969). In Sweden the interest for stocking brook charr was raised in the late nineteenth century, after successful hatchery- and stocking operations in e.g. Germany, France, and England (Lönnberg 1894). Introduction was promoted by fisheries managers, typically as a game fish, despite a clearly expressed lack of knowledge about how they affect native brown trout (Larsson 1922). Import started in the early 1890′s and it has been continually stocked in various places since then (Hammarström 1908; Nilsson 1983). Stocking attempts have often been successful and the species is today established in many catchments across Sweden (Hammarström 1908; Olofsson 1937; Nilsson 1983; Artdatabanken 2024).

The within-catchment distribution of brook charr and brown trout in Swedish streams often follow a pattern where brook charr live in allopatry in smaller headwaters, followed downstream by a section of sympatry, with brown trout being found in allopatry even further downstream (Nilsson 1967; Kjellberg 1969; Öhlund et al. 2008; Závorka et al. 2017). This pattern suggests a competitive advantage of brook charr in the smaller headwaters, and field studies suggest that brown trout are behaviourally affected by its presence in sympatric river sections (Cucherousset et al. 2007; Závorka et al. 2017, Závorka et al., 2020; Larranaga et al. 2019). While brown trout are often found to be

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stronger competitors, as noted in e.g. North America where the brown trout is the introduced species among the two (McKenna et al. 2013; Zorn et al. 2020; Olson et al. 2024), the presence of brook charr may still affect brown trout negatively (Dewald & Wilzbach 1992). The brook charr fry hatch earlier than the brown trout fry and thus have a size advantage during early life stages (Lovén Wallerius et al. 2022). Through competition with brown trout in running waters, the brook charr is also suspected to negatively affect the freshwater pearl mussel *Margaritifera margaritifera*, which uses the brown trout as a host for its glochidia (Salonen et al. 2016). Brook charr appears to be a low- to non-functional host for these glochidia (Salonen et al. 2016), making replacement of brown trout with brook charr potentially problematic for mussel recruitment. Brook charr also occur in some boreal lakes, where they can have a long-term negative effect on sympatric brown trout, sometimes leading to local extinction of the latter (Spens et al. 2007). Furthermore, hybridization between brook charr and native salmonids (Arctic charr and brown trout) is known to be possible (Cucherousset et al. 2008; Faulks & Östman 2016), but the extent and the ecological effects thereof are not investigated.

To ascertain healthy brown trout and freshwater pearl mussel populations, several brook charr depletion projects have been launched in Sweden in recent years. Hence, detecting sites where brook charr dominates over brown trout is an important part of these projects. While this can be done with high confidence using wading electrofishing, which is particularly suitable for salmonids in smaller streams (Bohlin et al. 1989), the usage of environmental DNA (eDNA) is attractive due to the possibility to sample more candidate areas per time unit. While eDNA surveys are good for detecting species presence (e.g. McKelvey et al. 2016), quantitative assessments have been questioned in terms of their precision (e.g. Sepulveda et al. 2020). Typically, positive correlations are found between the quantity of DNA and the estimated mass or abundance of target species, but at the site-specific level the match between eDNA and traditional sampling estimates can differ substantially (e.g. Yates et al. 2019; Sepulveda et al. 2020). Nevertheless, some of the more promising investigations relate to surveys of brook charr (e.g. Wilcox et al. 2016, Wilcox et al., 2018; Baldigo et al. 2017). These studies find clear positive correlations between eDNA reads and estimated abundance, although with substantial residual variation.

Here, eDNA quantification of brook charr and brown trout were conducted with a main aim to assess the relative abundance of brook charr and brown trout. The main focus of the study was to determine which sites that were dominated by brook charr (brook charr > brown trout) in terms of numerical abundance and biomass. As an auxiliary analysis, results from eDNA surveys were also quantitatively compared with traditional wading electrofishing to assess the how well eDNA surveys represent the electrofishing results (i.e. whether eDNA, at face value without additional sampling of environmental variables, could potentially replace electrofishing in Swedish streams and produce data meaningful to historical Swedish electrofishing time series). Finally, the species detection abilities of the two methods were also compared.

2. Materials and methods

2.1. Survey sites

Surveys were conducted between June 30 and September 8, 2022, at 45 sites, in 18 streams, within 5 tributary catchments to the river Piteälven (Fig. 1). At three of the sites, only eDNA samples were taken (sites: 27 – RÖ3, 30 – ST3, 45 – VA3). The survey area is located in Norrbotten County, Sweden, where several brook charr populations are established. Currently, no systematic monitoring of brook charr population dynamics or spread is conducted. The selection of the survey sites were based on anecdotal and previously documented occurrence of brook charr. In addition, some closely situated streams with similar size and characteristics, but without historical indications of brook charr being present, were selected. An additional selection criterion was the presence of freshwater pearl mussels, since these are target species for conservation measures (including potential brook charr reduction/removal).

2.2. Electrofishing

Wading electrofishing was conducted using gear powered by a bank-side gasoline-driven generator (Hans Grassl ELT60II, adapted for Nordic conditions; Hans Grassl GmbH, Schönau am Königssee), with a 30-m anode cable. The whole widths of the streams were fished in a single pass, for as long distance as the cable allowed at a given site (mean fished area: 196 m^2; SD: 168 m^2; range: 30 – 675 m^2). All brown trout and brook charr individuals caught were anesthetized (MS-222), measured for maximal total body length (mm), and thereafter released back into the stream. Body mass was not recorded, but calculated based on average length-mass relationships registered in FishBase (Froese & Pauly 2024), using the formula:

$$M = a \cdot L^b$$

where M = mass in grams, L = total length in centimetres, and a and b are species specific constants (brown trout: $a = 0.0102$; $b = 3.02$; brook charr: $a = 0.0102$; $b = 3.04$).

2.3. eDNA

Water samples for eDNA were taken prior to electrofishing, just downstream of the electrofishing site. The water samples were taken using eDNA sampling rod (Sylphium Molecular Ecology, Groningen), to avoid disturbing the bottom sediments in the streams. The end of the rod is equipped with a remotely operated syringe, fitted with a closed capsule filter (0.8 µm, 108 × 52 × 130 mm; 69 cm^2 effective area, polyethylene sulfon membrane; Dual eDNA Filter, Sylphium Molecular Ecology, Groningen) and a check valve (all of which were replaced for each sample). At each site, water was sampled at 6–10 points, covering the whole stream width, using a single filter. Filtration proceeded as long as water could be passed through the filters (mean total volume: 664 mL; SD: 172 mL; range: 240 – 1200 mL). Filters were preserved in buffer ATL (QIAGEN N.V., Hilden) (Wu & Minamoto 2023). Molecular analyses were run at the Center for Genetic Identification (CGI) at the National Museum of Natural History in Stockholm.

Extraction of DNA was done using a KingFisher Flex automated extraction instrument (Thermo Fisher Scientific Inc., Waltham, MA) and the Omega Mag-Bind Blood and Tissue extraction kit (Omega Bio-tek, Inc., Norcross, GA), following the user manual. Species-specific mtDNA primers and probes were used for amplification (Table 1). The brook charr primers were derived from Thalinger et al. (2021b), complemented by a newly developed probe. Brown trout primers and probe were derived from Carim et al. (2016). Prior to analyses the samples were tested for PCR inhibition by qPCR. All analyses were run on a Bio-Rad CFX96 instrument (Bio-Rad Laboratories AB, Hercules, CA). Three technical replicates of each sample were analysed and averaged for statistical evaluation. The qPCR protocols were run with known concentration samples for each species and blank samples, to allow translation of qPCR C_q values from field samples to an approximate concentration of DNA (ng/µL), through linear regression. Each plate run contained negative (water as template) and positive controls. Efficiency of qPCR was 97.1 % ($R^2 = 0.991$) for brown trout and 97.1 % ($R^2 = 0.983$) for brook charr. Limits of detection (LOD) and quantification (LOQ) were not calculated, due to the main analysis being focussed at relative abundance in terms of dominance of one species over the other (non-detection and detection near the LOD would lead to similar conclusions). These limits are important for detailed quantitative comparisons and species detection evaluation (Klymus et al. 2020), which means that our auxiliary results relating to these analyses should be evaluated in light of the limitations set by the lack of LOD and LOQ estimation.

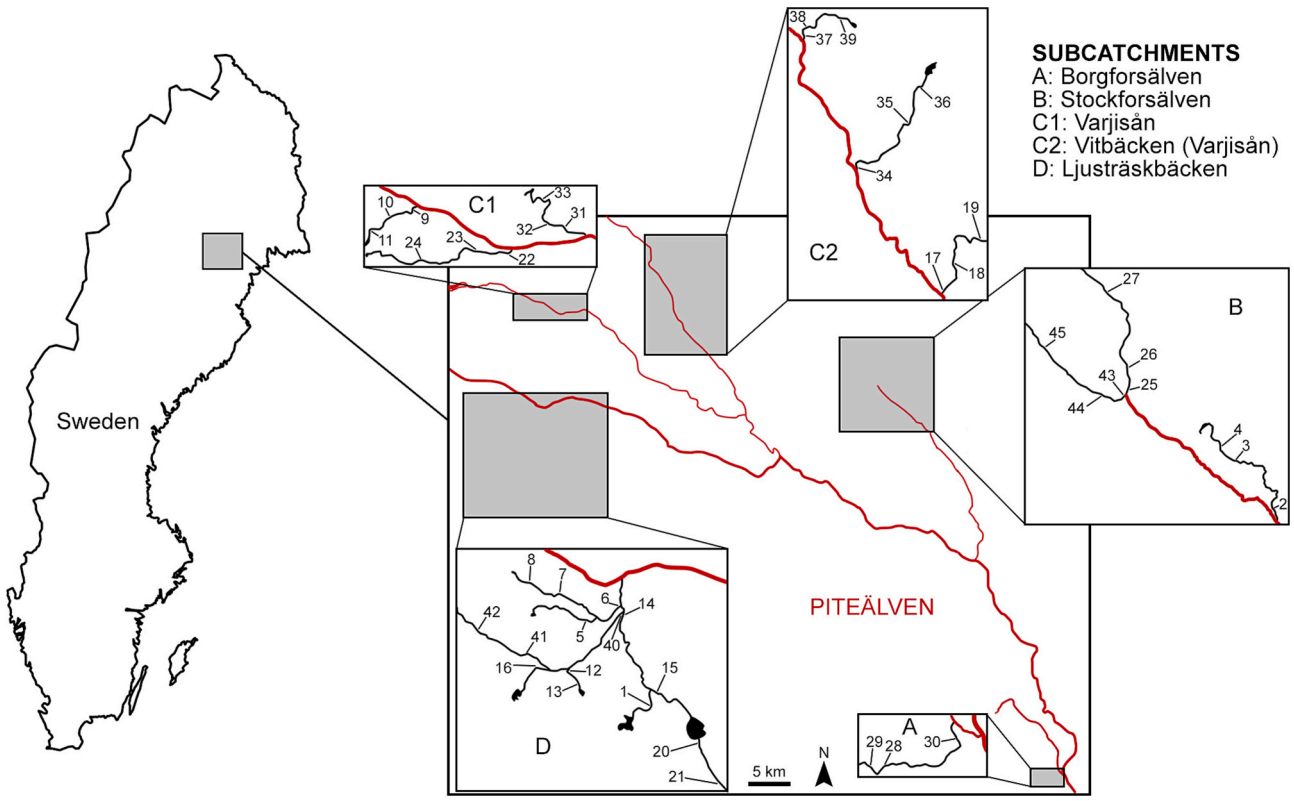

Fig. 1. Overview of the survey area in the river Piteälven main catchment. Survey sites in subcatchments (A-E) to Piteälven are marked 1 – 45 (alphabetical based on tributary name). Site names (name code within parenthesis): 1 – Abborrbäcken 1 (AB1); 2 – Brännmyrbäcken 1 (BR1); 3 – Brännmyrbäcken 2 (BR2); 4 – Brännmyrbäcken 3 (BR3); 5 – Fräkentjärnsbäcken 1 (FR1); 6 – Gardetjärnsbäcken 1 (GA1); 7 – Gardetjärnsbäcken 2 (GA2); 8 – Gardetjärnsbäcken 3 (GA3); 9 – Gäddträskbäcken 1 (GÄ1); 10 – Gäddträskbäcken 2 (GÄ2); 11 – Gäddträskbäcken 3 (GÄ3); 12 – Laxtjärnsbäcken 1 (LA1); 13 – Laxtjärnsbäcken 2 (LA2); 14 – Ljusträskbäcken 1 (LJ1); 15 – Ljusträskbäcken 2 (LJ2); 16 – Luossabäcken 1 (LU1); 17 – Njallebäcken 1 (NJ1); 18 – Njallebäcken 2 (NJ2); 19 – Njallebäcken 3 (NJ3); 20 – Pilträskbäcken 1 (PI1); 21 – Pilträskbäcken 2 (PI2); 22 – Rundtjärnsbäcken 1 (RU1); 23 – Rundtjärnsbäcken 2 (RU2); 24 – Rundtjärnsbäcken 3 (RU3); 25 – Rödkallkällmyrbäcken 1 (RÖ1); 26 – Rödkallkällmyrbäcken 2 (RÖ2); 27 – Rödkallkällmyrbäcken 3 (RÖ3); 28 – Storträskbäcken 1 (ST1); 29 – Storträskbäcken 2 (ST2); 30 – Storträskbäcken 3 (ST3); 31 – Suorkebäcken 1 (SU1); 32 – Suorkebäcken 2 (SU2); 33 – Suorkebäcken 3 (SU3); 34 – Svanaträskbäcken 1 (SV1); 35 – Svanaträskbäcken 2 (SV2); 36 – Svanaträskbäcken 3 (SV3); 37 – Säpmurimbäcken 1 (SÄ1); 38 – Säpmurimbäcken 2 (SÄ2); 39 – Säpmurimbäcken 3 (SÄ3); 40 – Tjartsebäcken 1 (TJ1); 41 – Tjartsebäcken 2 (TJ2); 42 – Tjartsebäcken 3 (TJ3); 43 – Varvlidbäcken 1 (VA1); 44 – Varvlidbäcken 2 (VA2); 45 – Varvlidbäcken 3 (VA3).

2.4. Statistical analyses

In the quantitative statistical analyses, sites without any catch of brown trout or brook charr ($N = 6$) and sites where only eDNA was sampled ($N = 3$) were excluded (analysed: $N = 36$ sites). The relative abundance (both numerical and biomass) in electrofishing surveys and the relative concentration (ng/μL) from eDNA assays were compared both graphically in scatter plots and analytically using standard major axis regressions ('SMA'), which has residuals perpendicular to the regression line, hence accounting for natural variability in both *x* and *y* variables (Sokal & Rohlf 1995). For these analyses we analyse fish density based on fished area (m^2), which was judged to be the most appropriate density measure for assessments of dominance. Stream-dwelling salmonid fish (especially brown trout) are generally territorial (e.g. Elliott 1990) and the streams are shallow, leading the fish to distribute themselves mainly in two dimensions.

The ability of eDNA to match electrofishing survey data was analysed separately for each species, using linear models where the estimated eDNA concentration was the independent variable and electrofishing data was the dependent variable. In these analyses we used volume-based densities [number of individuals and biomass per 1 m^3 of stream water (total fishing site volume estimated as fished area multiplied by average depth)], since volume based estimates of densities are more relevant for direct comparisons with eDNA concentration (in effect comparing 'concentration of fish' in the fished stream sections with concentration of eDNA in the water samples). Both electrofishing variables were $\log_{10}$–transformed, after adding 1 to each data point to make zero-values transformable. Evaluations were based on parameter estimates with 95 % confidence intervals (average fit), as well as 95 % prediction intervals (predictive precision for individual sites). We primarily analyse eDNA concentrations at face value, i.e. without any consideration of environmental factors such as discharge-dependent DNA transport distance, to contribute to the body of literature that has previously taken this approach (e.g. Wilcox et al. 2016).

Detection of species was evaluated based on the percentage of sites with positive and negative detections, with false negatives for one method being indicated by failure to detect a species detected by the other method. False positives for eDNA could not be assessed and are

Table 1
Species specific sequences for primers and probe, and annealing temperature for PCR reaction.

Species	Forward primer	Reverse primer	Probe	Temperature
Salmo trutta (target gene: Cyt b)	CGCCCCGAGGACTCTACTATGGT	GGAAGAACGTAGCCCACGAA	CGGAGTCGTACTGCTAC	60 °C
Salvelinus fontinalis (target gene: COI)	TGCCAGCTAAATGTAGGGAAAAA	CCTCCCGCCTCCTTTCTA	TCCTGGCTTCGTCCGGAGTTGA	60 °C

impossible for electrofishing given that species determination is assumed to be correct.

Finally, the variability in eDNA concentration was evaluated using linear models. The aim here was to identify potentially important environmental parameters that influence the eDNA concentration at a site. Global models (one for each species) were constructed using estimated eDNA concentration (log-transformed as above) as the dependent variable and the following variables as independent variables: $\log_{10}$(density per 1 m^3 + 1), $\log_{10}$(biomass per 1 m^3 + 1), filtered water volume (ml), water temperature (°C), water velocity (m/s), mean depth (m), mean wet width of the stream at the sampling site (m), $\log_{10}$[discharge (m^3/s)] (, and vegetation cover (%); no interactions were included as the sample size was evaluated to be too low to draw robust conclusions about interactive effects. The included independent variables were evaluated by dredging the global models (comparing model fit for all subsets of independent variables), using the MuMIn package (Bartoń 2023). While all subsets variable selection comes with the risk of overfitting data (Dahlgren 2010), the aim here is only to identify potentially influencing factors. Since the aim is not to test any specific hypotheses, collinearity among independent variables was disregarded. Assessment of which of the included environmental factors might be of importance was based on ranks of models, using the small-sample corrected Akaike Information Criterion (AICc). Models with AICc-values within 2 units from the top-ranked models (ΔAICc < 2) were evaluated to be of approximate equal explanatory power, and from the list of equivalent models the principle of parsimony (stronger belief in the simplest model) was used as the main principle for drawing conclusions.

All analyses were run in R (R Core Team 2024). Standard major axis regression was applied using the lmodel2 package for R (Legendre 2018); linear models were run through the stats package (R Core Team 2024); graphics were produced using ggplot2 (Wickham et al. 2019) and cowplot (Wilke, 2024) packages, or draw.io (https://app.diagrams.net/).

3. Results and discussion

3.1. Predicting brook charr dominance by eDNA

In terms of predicting the proportion of brook charr at a given site, the eDNA surveys produced results on average comparable to electrofishing catches. Both SMA regressions had parameter estimates close to the 1:1 relationship (95 % confidence intervals including intercept = 0.0 and slope = 1.0 in both cases; Fig. 2A-D, Table 2). For comparisons against the proportion of brook charr in terms of number of individuals, four sites were predicted to have more than 50 % brook charr by eDNA assessment when the electrofishing indicated less than 50 % brook charr (Fig. 2A). Of these four sites, three were low-density sites with less than

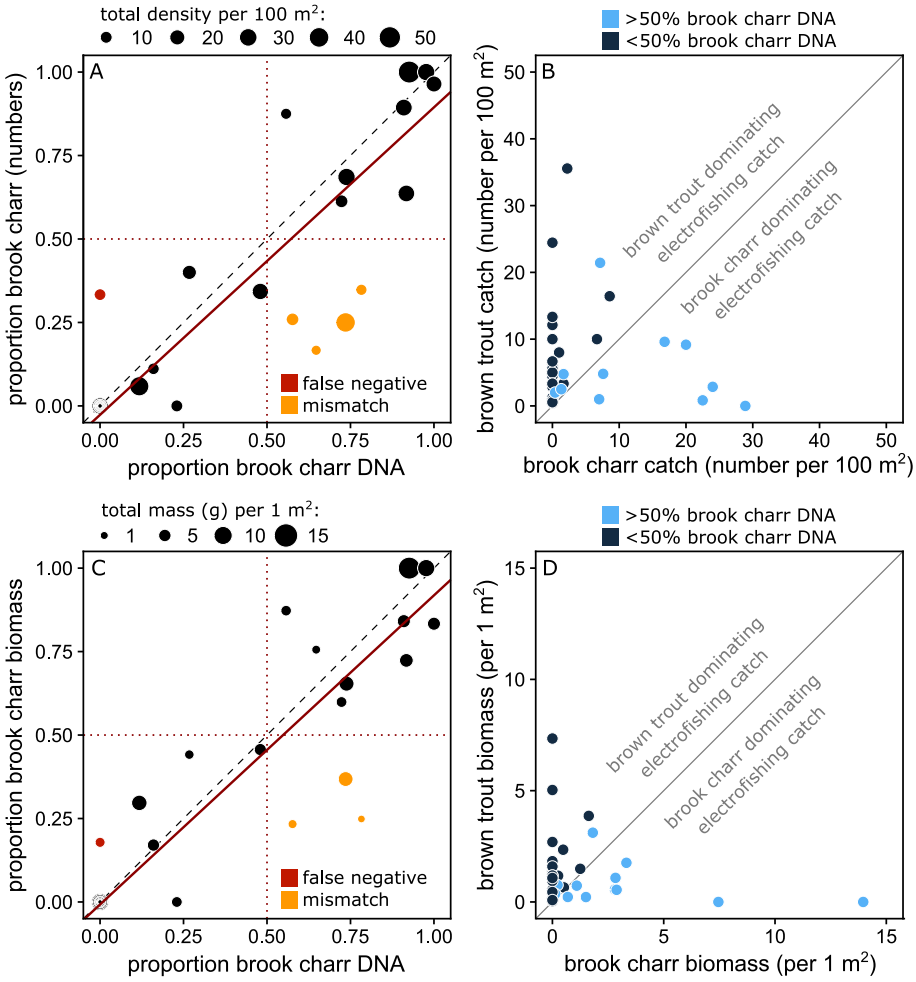

Fig. 2. Comparison of proportion brook charr DNA in water samples (based on eDNA concentration; ng/μL) and proportion of brook charr A) abundance in numbers of individuals (individuals per 100 m^2), and C) biomass [mass (g) per 1 m^2]. Panels B) and D) show data from electrofishing catches [B) number; D) biomass], with proportion of DNA categorised in different colour (light blue: > 50 % brook charr DNA; dark blue: < 50 % brook charr DNA). Dark red lines in A) and C) show the standard major axis regression; hatched black line show the 1:1 prediction of a perfect match; red dotted lines show the 50 % limits. False negative detections for brook charr with eDNA are plotted as red dots; mismatches, in terms of eDNA and electrofishing data not falling in the same 50 % bin, are plotted with orange dots.

Table 2
Model parameters for standard major axis regression of A) brook charr proportion in eDNA samples and B) proportion of brook charr in electrofishing (abundance or biomass). Intercepts and slopes are presented with 95 % confidence intervals within parentheses. Angle indicates the angle of the best-fit regression line (see dark red lines in Fig. 2). Perfect average fit (for comparison of parameters): intercept = 0.0; slope = 1.0; angle = 45.0).

Model	Intercept	Slope	Angle
A) Prop. eDNA vs. Prop. abundance	−0.027 (−0.075 – 0.014)	0.922 (0.785 – 1.083)	42.7
B) Prop. eDNA vs. Prop. biomass	−0.008 (−0.051 – 0.029)	0.926 (0.801 – 1.071)	42.8

10 fish being caught in total (Fig. 2B). There is no way of knowing which method is actually correct without further surveying. In electrofishing surveys, either some individuals could have been missed in the fished section, or there may be more brook charr upstream of the fished area. Regarding eDNA, there may be higher than expected concentrations due to the position or activity of the fish. In the comparison of eDNA and body mass, there was one less mismatch (Fig. 2C) and the observed mismatches were three of the same sites as for the comparison with proportion of fish individuals caught (Fig. 2A,C), suggesting that the biomass might play part in the fourth mismatch in the previously discussed analysis.

All sites where brook charr dominated in electrofishing catches (> 50 %) were also detected as such sites when looking at eDNA ($N = 8$ for abundance; $N = 9$ for biomass; Fig. 2A-D). However, eDNA also identified some extra sites as brook charr dominated ($N = 4$ for abundance; $N = 3$ for biomass), characterized by low densities and biomass (< 10 individuals per 100 m^2; < 2.5 g biomass per 1 m^2; Fig. 2B-D). Given the assumption that the electrofishing provides a good estimate of the relative abundance, no sites were falsely detected to have brown trout dominance (Fig. 2A,C). Overall, these analyses suggest that eDNA surveys can be suitable for use in screening surveys with an aim to identify streams where brook charr dominates over brown trout. Many previous studies show that eDNA, at least roughly, correlates positively with fish abundance assessed using standard capture methods (e.g. Lacoursière-Roussel et al. 2016; Thalinger et al. 2018; Rourke et al. 2022). While accuracy of quantitative eDNA assessments or relative abundance is still under active investigation, with several open questions (Rourke et al. 2022), the coarse-scale assessment of dominance appears to be a useful and resource-efficient method for initial detection and prioritisation of target sites for invasive species counter-measures, requiring less staff and allowing for more sites being covered per day as compared to electrofishing. Follow-up surveys using electrofishing can still refine the assessment.

3.2. Predicting species abundance and biomass

With respect to the hypothetical possibility to replace electrofishing with eDNA surveys, the quantitative analyses of single species did not provide any strong support for the idea, given that the data are taken at face value (i.e. not taking any environmental factors into consideration). For brown trout, an initial linear model including all data returned a very weak and non-significant positive relationship between eDNA and density (individuals caught per m^3) (Table 3A, Fig. 3A). Based on inspection of the graphed results, a potential outlier was detected and the model was re-run without this data point, resulting in a significantly positive relationship (Table 3B, Fig. 3B). However, to promote the replacement of electrofishing with eDNA in surveys, the eDNA should have the ability to predict the abundance of the target species with a high precision for each given site. The reason for this is that electrofishing gives a fairly accurate picture of the true abundance within target area (especially for salmonids in small streams; Bohlin et al. 1989), and given the large amount of electrofishing survey data available in Sweden

Table 3
Summary tables for models analysing how well electrofishing catches (A-D: fish density per m^3; E-F: fish biomass per m^3) are described by eDNA analyses. SE: standard error of the parameter estimate; *t*: *t*-value; *p*: *p*-value. The six model results are visualized in Figs. 3-4.

Model	Parameter	Estimate	SE	*t*	*p*
A) Brown trout $\log_{10}$(density + 1): all data	Intercept	0.196	0.043	4.553	< 0.001
	$\log_{10}$(eDNA conc. + 1)	232.9	217.8	1.069	0.292
B) Brown trout $\log_{10}$(density + 1): outlier removed	Intercept	0.109	0.044	2.471	0.019
	$\log_{10}$(eDNA conc. + 1)	1832	474.7	3.859	< 0.001
C) Brook charr $\log_{10}$(density + 1): all data	Intercept	0.038	0.042	0.902	0.374
	$\log_{10}$(eDNA conc. + 1)	2855	541.9	5.270	< 0.001
D) Brook charr $\log_{10}$(density + 1): 'null-null' sites removed	Intercept	0.144	0.116	1.249	0.229
	$\log_{10}$(eDNA conc. + 1)	2077	1053	1.973	0.066
E) Brown trout $\log_{10}$(biomass + 1): outlier removed	Intercept	0.680	0.121	5.609	< 0.001
	$\log_{10}$(eDNA conc. + 1)	3477	1310	2.653	0.012
F) Brook charr $\log_{10}$(biomass + 1): 'null-null' sites removed	Intercept	0.887	0.268	3.314	0.004
	$\log_{10}$(eDNA conc. + 1)	2890	2438	1.185	0.253

(> 80 000 surveys; Näslund et al. 2023) there is a need for any replacement method to be comparable with electrofishing results. The accuracy of eDNA to predict brown trout abundance at individual sites was low, as indicated by 95 % prediction intervals spanning approximately an order of magnitude (Fig. 3B).

For brook charr, the initial model returned a significant positive relationship (Table 3C; Fig. 3C). However, in this case, there was a relatively high number of sites ($N = 18$) with 'null-null' detections (no brook charr caught and no eDNA detected). For the analysis, this means an accumulation of highly precise data, which improves the fit of the model without contributing much meaningful data in the evaluation. In theory, as long as the eDNA is detected at any level at sites where brook charr is also caught by electrofishing, enough sampling of 'null-null' sites will eventually lead to a statistically significant positive relationship. Hence, the 'null-null' sites were removed in a follow-up analysis. This analysis should still provide a statistically significant positive relationship in case eDNA is actually predicting the electrofishing results, but this was not the case here (Table 3D, Fig. 3D). Regarding the precision of the eDNA to predict electrofishing catches at individual sites, even the significant model including 'null-null' results indicated that the precision was low, with 95 % prediction intervals spanning approximately an order of magnitude, similar to the analysis of brown trout.

Analyses of the eDNA predictability of biomass caught in electrofishing surveys (biomass per m^3) yielded results very similar to the results above. Brown trout data were analysed without one outlier and results indicated a positive relationship, but without good precision (Table 3E, Fig. 4A). Brook charr data was analysed without 'null-null' sites, and the results were non-significant (Table 3F, Fig. 4B).

Overall, these analyses show that there are indeed some general patterns showing positive relationships between eDNA concentration and abundance estimated by electrofishing (given some assumptions regarding which data should be included in a conceivably proper analysis). This is in line with previous studies on brook charr (Wilcox et al. 2016, Wilcox et al., 2018; Baldigo et al. 2017) as well as other species (e.g. Sepulveda et al. 2020; Chin et al. 2021). However, we obtain no good support for the specific idea of replacing Swedish electrofishing surveys with eDNA surveys, given the large prediction intervals observed. The relatively low accuracy of the eDNA in predicting electrofishing catches for specific sites means that the continuity of long electrofishing time-

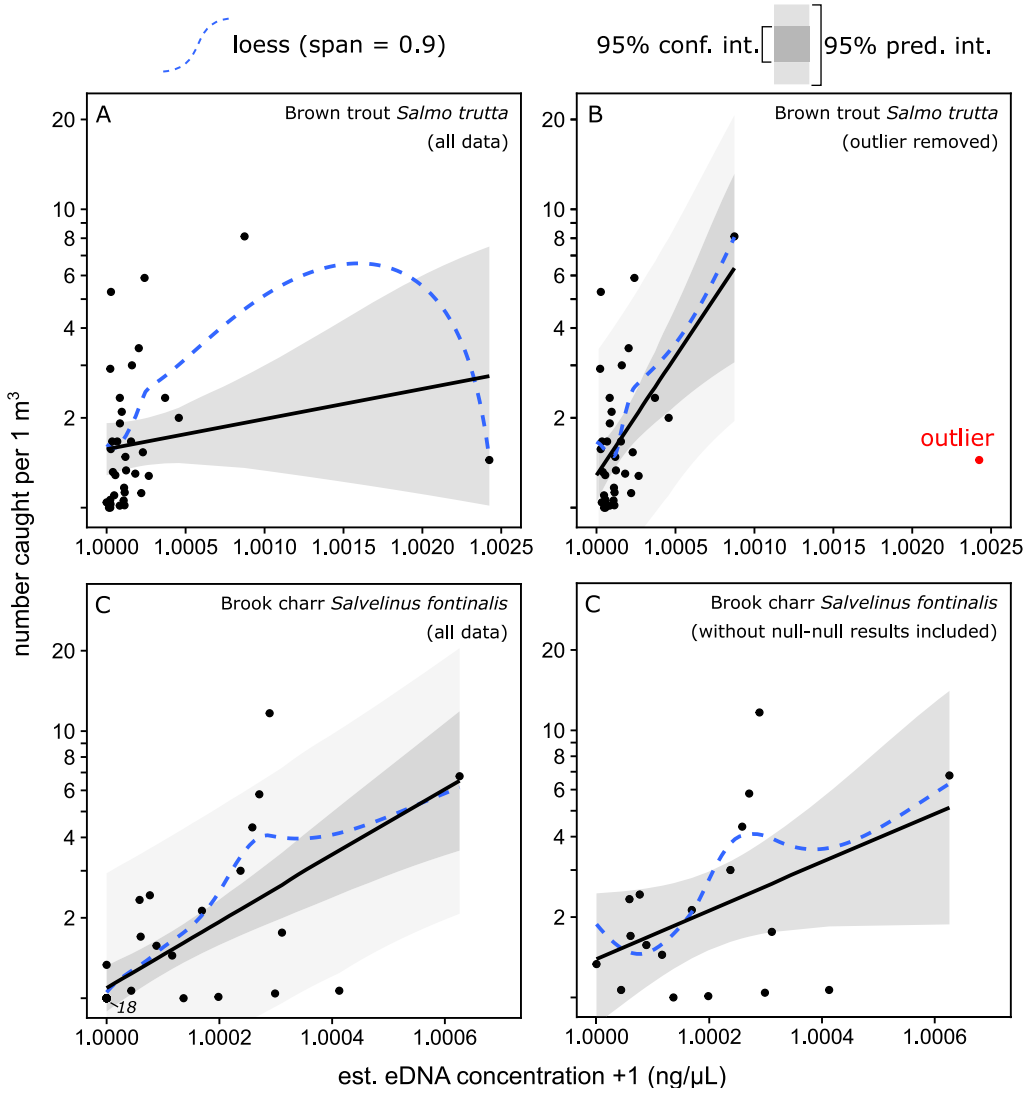

Fig. 3. Relationship between estimated concentration of DNA in water samples and the number of individuals caught per m^3 in a single-pass electrofishing survey; A) brown trout (all data); B) brown trout (one outlier removed; marked in red colour); C) brook charr (all data; note the 18 data points accumulating at the origin at x = 1, y = 1); D) brook charr ('null-null' sites removed; 'null-null' = no captured individuals and no eDNA detection). Black line show linear regression, darker grey area show 95 % confidence interval, lighter grey area show 95 % prediction interval (only presented in B and C), hatched blue line show non-linear regression (loess; span = 0.95).

series would be lost if replaced. The accuracy largely mirrors the result of e.g. Sepulveda et al. (2020), which hypothesized that more detailed environmental characterization could help to build more accurate models of abundance estimation from eDNA assays. This is supported by a review identifying a number of biotic and abiotic characteristics that may influence the eDNA concentration in the water (Rourke et al. 2022). Each added environmental characterization survey that is needed for increased precision in quantitative eDNA analyses will, however, reduce the relative efficiency of eDNA, as compared to electrofishing. While some environmental factors are quick and easy to measure, others may be more costly in terms of time and resources.

3.3. Species detection

Out of the 42 sites where both methods were applied, eDNA detections (yes or no) corresponded with electrofishing at 37 sites (88 %; Fig. 5). Assuming that all eDNA indications of presence were true, electrofishing missed brook charr at one site and brown trout at two sites (Fig. 5). Environmental DNA failed to detect each of the species once, at sites where presence was definitely verified by the electrofishing (Fig. 5).

Six sites had congruent lack of detections for any of the species, all being located in three of the upstream-most sections of the investigated stream systems (Fig. 1, Fig. 5; subcatchment Ljusträskbäcken: 15 – LJ2, 20 – PI1, 21 – PI2; subcatchment Vitbäcken: 35 – SV2, 36 – SV3; subcatchment Varjisån: 33 – SU3). This pattern suggest that neither of the species may had yet been established in these locations. However, the two sites where eDNA failed to detected a species (13 – LA2, 24 – RU3), were also located in the upstream-most sampled sites in their respective tributaries (Fig. 1, Fig. 5). At these sites, only a single individual of the species missed by eDNA were caught in the electrofishing. Hence, at low densities eDNA might still miss detecting a species, which is expected based on previous studies in similar stream systems in North America (Wilcox et al. 2016). Discharge is related to the transport distance of eDNA, as revealed by a *meta*-analysis (Jo & Yamanaka 2022), and discharge declines the further upstream in a catchment a site is located, meaning that the overall area 'sampled' by eDNA is relatively small at such sampling points. Furthermore, caged-fish experiments in fish-free streams suggest that DNA dispersal at close distance to the target individuals is heterogeneous, which could also contribute to missed

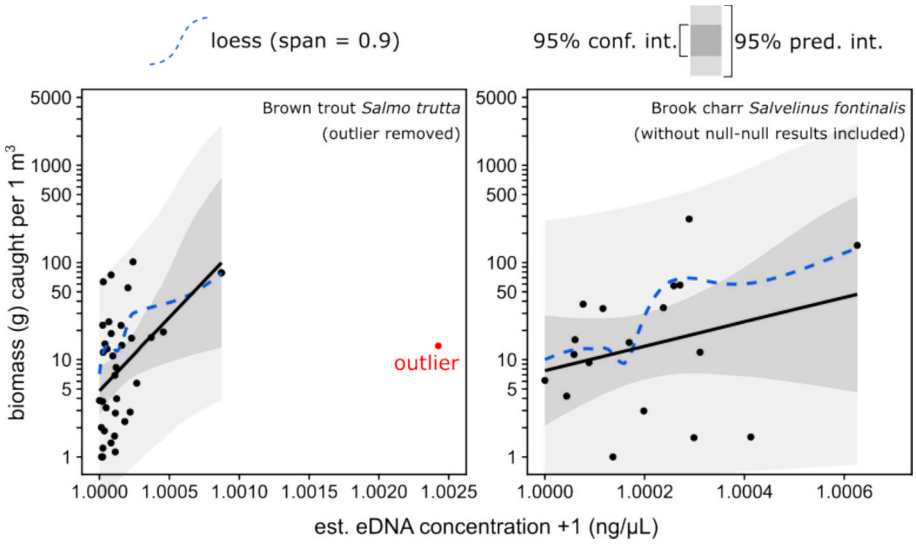

Fig. 4. Relationship between estimated concentration of DNA in water samples and the biomass (g) of individuals caught per 1 m^3 in a single-pass electrofishing survey; A) brown trout (one outlier removed; marked in red colour); B) brook charr ('null-null' sites removed; 'null-null' = no captured individuals and no eDNA detection). Black line show linear regression, darker grey area show 95 % confidence interval, lighter grey area show 95 % prediction interval, hatched blue line show non-linear regression (loess; span = 0.9).

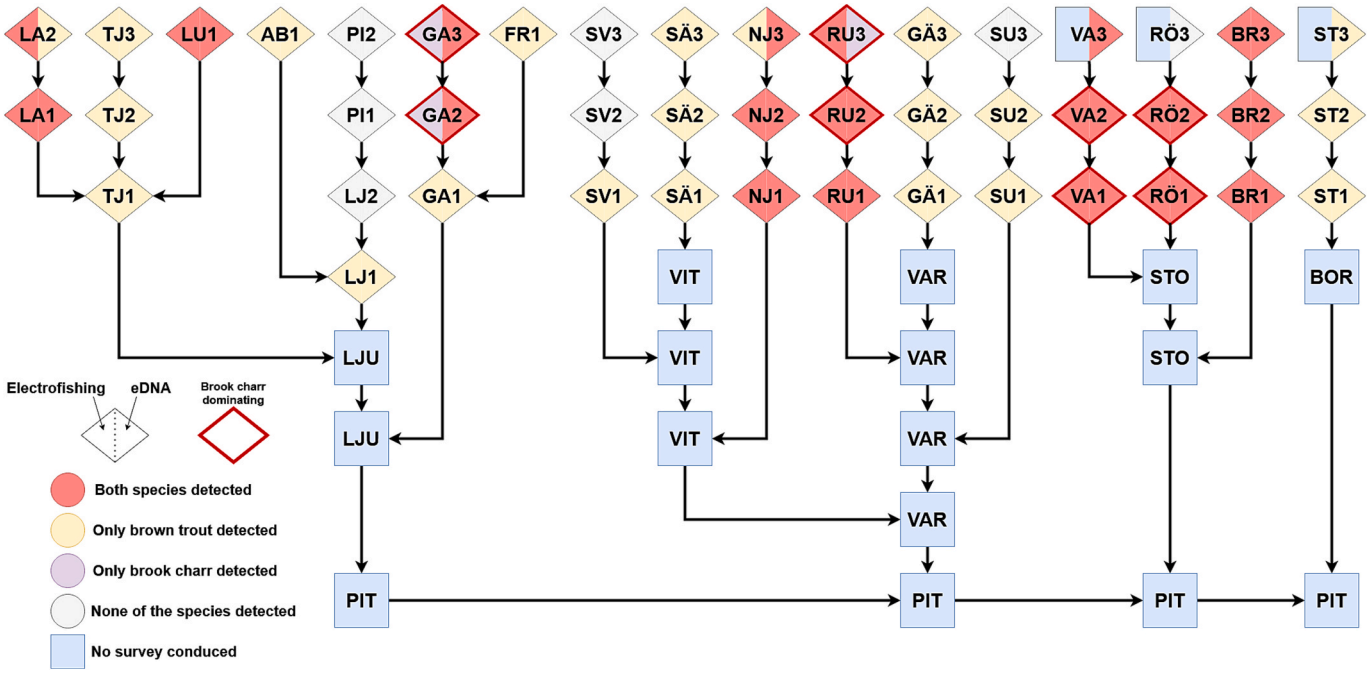

Fig. 5. Schematic overview of the detections of brown trout and brook charr in the Piteälven (PIT) catchment [subcatchments: Borgforsälven (BOR), Stockforsälven (STO), Varjisån (VAR), Vitbäcken (VIT), Ljusträskbäcken (LJU)]. Surveyed sites (for key to site codes, see Fig. 1) are connected in a network based on their relative position in the catchment (see map in Fig. 1). For sampled each site, detection is marked using coloured triangles (electrofishing to the left, eDNA to the right; colour codes in the figure); note that three sites lack electrofishing data (VA3, RÖ3, ST3). A thick red border marks sites where brook charr are dominating in abundance (> 50 %).

detections (Thalinger et al. 2021a).

As initially noted in this section, electrofishing failed to detect a species detected by eDNA, at three sites (brown trout missed at 7 – GA2 and 8 – GA3; brook charr missed at 19 – NJ3). This result is not unlikely a consequence of water samples containing eDNA transported from areas upstream of the electrofishing sampling area (as observed in e.g. David et al. 2021). However, it is also possible to miss fish during electrofishing since catchability typically lies substantially below 100 % even in easy-to-fish streams (e.g. Näslund et al. 2017). In addition, given the limited electrofished area it is expected to occasionally fail to catch fish when abundance is low. Both eDNA- and electrofishing sampling accuracy could likely increase with increased sampling effort, but for screening purposes of large geographic areas there is a trade-off between sampling effort at individual sites and the total number of sites sampled.

Overall, the detection probability of eDNA was slightly better than that of electrofishing. While the LOD was not assessed, the results indicate that detection probability of the eDNA assay was good. In total (for both species) there were only two false negatives for the eDNA, both

occurring at sites with apparent low fish densities, while a total of 30 negative assays were congruent with lack of catches in the electrofishing (Fig. 5).

3.4. Assessment of environmental factors influencing variability in eDNA concentration

Within the encountered range of the environmental factors included in the model evaluations (Table S1), there were no clear indication of any factor other than density of fish having a significant influence on the eDNA concentration.

For brown trout, the top-ranked model included density (as did all of rest of the models within ΔAICc < 2) and mean depth, but the latter factor was non-significant (Table S2, Table S4A). Discharge was included in the second ranked model, along with density and mean depth; in this model, mean depth was a significant factor, but not discharge (Table S2, Table S4A). For brook charr the top-ranked model also included density (significant) and mean depth (non-significant) (Table S3, Table S4B). The second ranked model included only density (non-significant). The intercept-only model was included among the models within ΔAICc < 2 for brook charr, suggesting that no model outperformed this factor-free model in a substantive way.

With respect to the results above, a brief discussion about discharge effects is warranted. Previous studies have indicated that discharge should have an effect on the eDNA transport distance (Carraro et al. 2018; Jo & Yamanaka 2022). In the present study, discharge varies with several orders of magnitude (min: 0.0008 $m^3 \cdot s^{-1}$; max: 2.0 $m^3 \cdot s^{-1}$; Table A1), but the majority of the streams are small (mean: 0.23 $m^3 \cdot s^{-1}$). Discharge effects on transport distance empirically follow a power-law relationship, but there is also order-of-magnitude variation in empirical results in smaller streams included in a recent *meta*-analysis (Jo & Yamanaka 2022). Hence, while we cannot find a relationship in our study, we do not consider our results disproving discharge as an important factor and we believe it should still be considered in future studies given previous investigations (see e.g. Carraro et al. 2018; Carraro & Altermatt 2024). Our results merely point to a conclusion that environmental effects on eDNA concentration may not always be detectable.

4. Conclusion

For the main aim of this study, to investigate whether electrofishing can be replaced by eDNA surveys to screen for streams with brook charr dominance over brown trout, we conclude that eDNA is a good and resource efficient replacement method. With respect to single species quantification of these salmonid species (abundance or biomass), at a local scale, electrofishing is judged to be the better choice. Electrofishing has consistently been found to have high accuracy in determining salmonid fish abundance in smaller streams (Bohlin et al. 1989), and allows for assessments of size structure in the surveyed populations. Furthermore, it has the additional benefit of providing direct evidence of presence when a species is caught (but detection probability is naturally related to sampling effort). However, while not investigated here, eDNA-based modelling approaches (Carraro & Altermatt 2024) may be applicable. Environmental DNA has a higher species detection ability and is more resource efficient in large screening projects where absolute abundance estimation is not required. Hence, the two survey methods are largely complimentary within fisheries management assessments and environmental monitoring.

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CRediT authorship contribution statement

Andreas Broman: Conceptualization, Methodology, Validation, Investigation, Resources, Data curation, Writing – review & editing, Supervision, Project administration, Funding acquisition. **William F. Englund:** Visualization, Writing – review & editing, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation. **Niclas Gyllenstrand:** Methodology, Resources, Writing – review & editing, Supervision. **Joacim Näslund:** Formal analysis, Data curation, Writing – original draft, Visualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2025.113407.

Data availability

Data and R code are available at the open figshare repository: https://doi.org/10.6084/m9.figshare.27915606. All electrofishing data are also available through the Swedish electrofishing register: https://www.slu.se/elfiskeregistret/.

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