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Variability in stream water chemistry and brown trout (*Salmo trutta* L.) parr otolith microchemistry on different spatial scales

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Abstract

Mixed-stock fishery of sea trout (*Salmo trutta* L.) in the Baltic Sea targets wild and stocked individuals, which could lead to over-exploitation of wild stocks. Studying the contribution of different spawning streams and hatcheries to the fishery would aid in more effective management and conservation of *S. trutta*. The aim of the present study was to explore whether and to what extent parr from different *S. trutta* spawning streams and hatcheries can be differentiated, using water chemistry and otolith microchemistry. Water chemistry samples demonstrated significant spatial variation between different study regions (Estonia and Finland); Sr, Mg, Fe, Zn, Ca and Cu contributed most to the separation. Parr collected from different sites showed a significant difference in otolith element:Ca and ^{87}Sr:^{86}Sr ratios on a smaller scale, including only Estonian samples ($n = 361$), and on a larger scale incorporating parr from Estonia, Latvia and Finland ($n = 564$). The reclassification rate of *S. trutta* parr was on average 73%, being highest in Finnish streams and hatcheries, followed by Latvia and Estonia. Otolith ^{87}Sr:^{86}Sr and Sr:Ca ratios were the most important in discriminating fish from different sampling sites. The present study demonstrates the potential of separating *S. trutta* on various spatial scales including different countries and neighbouring streams, making this the most extensive otolith microchemistry study to date in terms of streams and regions studied. The established reclassification rules form a basis for future work investigating the natal origin of adult *S. trutta* caught in the mixed-stock fishery in the sea.

KEYWORDS
Baltic Sea, natal origin, salmonids, trace elements, water chemistry

1 | INTRODUCTION

Diadromous fish is one of the most threatened animal groups in the world (Graham & Harrod, 2009). They are ecologically important and, in most cases, economically valued, both in freshwater and marine environments. In freshwater habitats, diadromous species, especially anadromous salmonids, can have well-defined and resilient populations due to natal philopatry (McDowall, 2001), although straying from the natal stream is also an important trait, ensuring gene flow and population genetic diversity (Ferguson, 2004; Santaquiteria et al., 2016). During sea residency, anadromous species/individuals can exhibit vast migrations and distribute over broad geographic scales (e.g. Klemetsen et al., 2003; Lehtonen & Himberg, 1992). As diadromous fish rely on freshwater and marine habitats during their life histories, they are influenced by a myriad of factors such as migration barriers, habitat loss (Limburg & Waldman, 2009), predation (Jepsen et al., 2006), climate change (Jonsson & Jonsson, 2009) and pressure from commercial and recreational fisheries. Due to their extensive migrations in the sea, diadromous species are often subjected to mixed-stock fishery. This means that within a specific location, multiple populations may be harvested at the same time, and this might result in over-exploitation of some populations, including populations that are threatened or in weak conditions. However, at the time of the fishing it is usually impossible to determine whether a fish originates from weak or strong population. Therefore, the best strategy for preventing the over-exploitation of threatened populations would be implementation of various measures at the "source", for example freshwater habitats. Such measures can include ban for fishing at certain times/locations and size/daily bag limit. However, before protection measures can be implemented it is vital to determine which populations are in a precarious state.

Sea trout, the anadromous form of brown trout (*Salmo trutta* L.), is an important predator and a valued catch in many areas around the world. In the Baltic Sea region, *S. trutta* constitutes a vital part in small-scale commercial and recreational fisheries. Currently, many *S. trutta* stocks in the Baltic Sea are in suboptimal state (ICES, 2018). Although the Gulf of Finland (GoF) is one of the few regions where the populations are thought to be in good condition, the conditions may vary largely by country and stream (ICES, 2018). While the recruitment status in Estonia is thought to be close to optimal, it has been estimated that about 20% of the streams draining to the GoF reach only about 5% of their potential smolt production level. Most of these streams are situated in the northern coast (Finland) and easternmost part (Russia) of GoF (ICES, 2020). Latvia belongs to the eastern part of main basin (MB) together with Lithuania and Poland. The overall recruitment status in the eastern part of MB is poor. In Latvia, it has been estimated that the smolt production level in the majority of the streams is uncertain and below 5% in the rest (ICES, 2020). To support wild populations, hatchery releases are used. In areas surrounding Estonia, these releases have been mostly done in the north and easternmost parts of GoF (Finland and Russia) and the MB of the Baltic Sea (Latvia) in the form of smolt releases (ICES, 2020). Estonia has previously released but a fraction of the fish compared with its neighbours, and as of 2018, Estonia has stopped hatchery releases of trout altogether (ICES, 2019). Fish of wild and hatchery origin can mix in the sea, which could lead to over-exploitation of wild populations (Koljonen et al., 2014; Lundqvist et al., 2007). As hatchery releases are still widely used and the fishing pressure on *S. trutta* is high, stocks of *S. trutta* in the Baltic Sea are still considered to be vulnerable (ICES, 2020).

One possible way to evaluate the stock structure in a mixed-stock fishery is to use the chemical information stored in otoliths (Elsdon et al., 2008). Otoliths are paired calcified structures located in the inner ear of all teleost fish. The composition of otoliths is dominated by calcium, oxygen and carbon that make up the calcium carbonate ($CaCO_3$) matrix, but minor trace- and microelements (e.g. Sr, Ba, Mg, Mn) are also incorporated into otoliths (Campana, 1999). The incorporation of elements to otoliths can be dependent on multiple environmental (Elsdon & Gillanders, 2004; Engstedt et al., 2012) and physiological factors (Sturrock et al., 2014; Walther et al., 2010). However, it has been demonstrated that the chemical composition of otoliths, mainly the concentrations of strontium (^{86}Sr) and barium (^{137}Ba), is mostly dependent on the elemental concentration of ambient water (Doubleday et al., 2013; Walther & Thorrold, 2006) and that Sr isotope ratios (^{87}Sr:^{86}Sr) are not fractionated biologically and are therefore incorporated into the otoliths in proportion to the ratios in aqueous habitat (Kennedy et al., 2000; Martin, Bareille, Berail, Pecheyran, et al., 2013). Stream water chemistry itself is mainly influenced by the underlying bedrock and sediments (Horton et al., 1999; Simm, 1975). Due to some of the unique properties of otoliths (reviewed in Campana & Thorrold, 2001), which also include continuous growth in time, the habitat-specific multi-elemental signatures (elemental fingerprints) are incorporated into the otoliths in a chronological manner. These natural tags can be used retrospectively in studying fish migration (Rohtla et al., 2012; Taal et al., 2014, 2018) and identifying nursery areas (Reis-Santos et al., 2012). Moreover, elemental fingerprints have become a powerful tool in identifying fish of natural or hatchery origin in a mixed sample (Arechavala-Lopez et al., 2016; Watson et al., 2018), delineating stock and/or population structure (Rohtla et al., 2017; Tanner et al., 2014), and studying the origin of adult fish (Martin, Bareille, Berail, Pécheyran, et al., 2013; Veinott et al., 2012). For example, this method has been used successfully in identifying the natal origin of adult *S. trutta* in Newfoundland and New Zealand (Mikheev et al., 2021; Olley et al., 2011; Veinott et al., 2012) and distinguishing Atlantic salmon parr (*Salmo salar* L.) between different streams in France (Martin, Bareille, Berail, Pecheyran, et al., 2013). In the Baltic Sea region, otolith elemental fingerprints have been used in studying the population structure of European whitefish (*Coregonus lavaretus* L.; Rohtla et al., 2017) and examining the natal homing of pike (*Esox lucius* L.; Engstedt et al., 2014). However, to our best knowledge there are no studies using otolith elemental fingerprints in order to study the natal origin of salmonids in the Baltic Sea and Nordic region. Considering the vulnerable state of salmonid stocks in the Baltic Sea (ICES, 2020), such studies are in great need.

Although the aforementioned studies demonstrate the usefulness of elemental fingerprints in studying stock structure, natal homing and natal origin (Engstedt et al., 2014; Olley et al., 2011; Rohtla et al., 2017; Veinott et al., 2012), it ought to be emphasised that one of the most important assumptions in using otolith elemental fingerprints as natural tags is that each baseline group (e.g. stream) studied ideally has a unique elemental fingerprint (Campana et al., 2000). Also, these elemental signatures should be stable in time as a temporal variation may limit the use of otoliths in studies aiming to differentiate between fish stocks and populations (Gillanders, 2002; Walther & Thorrold, 2009). Ambient water elemental composition is one of the most important influencers of otolith chemical composition (Doubleday et al., 2013; Walther & Thorrold, 2006). Additionally, in otolith microchemistry studies it is often expected that the otolith signatures reflect the water chemistry in which the fish resides (Martin, Bareille, Berail, Pecheyran, et al., 2013); therefore, spatial variation in water chemistry usually implies that fish that have grown up in these different environments could be discriminated also based on their otolith elemental fingerprints (Campana, 2005). Therefore, monitoring the spatial and temporal variability of stream water chemistry and the relationship between water and otolith microchemistry can add useful background information for understanding otolith microchemistry.

To evaluate the variability of elemental fingerprints on different spatial scales, parr otoliths were collected from streams and hatcheries from Estonia, Latvia, and the southern Finland (hereafter referred to as Finland), whereas water samples were collected only from Estonia and Finland. The aim of the present study was to use *S. trutta* parr otolith elemental fingerprints and water chemistry data to: (i) explore the spatial and temporal (i.e. seasonal) variation in water chemistry and study which elements have the highest discriminating power among different waterbodies, (ii) test the relationship between water chemistry and otolith microchemistry and (iii) explore whether and to what extent *S. trutta* parr from different sea trout spawning streams and hatcheries (sensu stricto) and regions (sensu lato) can be distinguished from one another. We predicted that due to the differences in the composition of the bedrock between the study regions (Löfvendahl et al., 1990) and based on previous studies (Rohtla et al., 2017, 2021), these regions would also be separable based on the collected water samples, and as such, these differences would be reflected in *S. trutta* otoliths at least on a regional level. We further predicted that hatchery-origin *S. trutta* are distinguishable from wild *S. trutta* based on their otolith chemical composition.

2 | MATERIALS AND METHODS

2.1 | Study system

Streams draining to the Baltic Sea flow over bedrock and sediments with varying age and composition. For example, Estonian and Latvian bedrocks are mostly composed of carbonate rocks (e.g. limestone), clays and sandstones (Uścinowicz, 2011). Carboniferous limestones from the Ordovician era can be found predominantly in northern Estonia, clays and sandstones from the Silurian and Devonian eras are prevalent in western and central parts of Estonia to South-Estonia (Soesoo, 2010), and sedimentary rocks from the Devonian era also cover most of Latvia (Zelčs & Nartišs, 2014). Areas just north of Estonia, for example the south coast of Finland, are significantly older, from the Pre-Cambrian era with Proterozoic crystalline bedrock consisting of granitoids (Uścinowicz, 2011; Figure 1).

Streams in the Baltic States region feed mostly on precipitation (rain and snow) and groundwater (Kriauciuniene et al., 2012). The chemistry of stream water is largely determined by the underlying bedrock and sediment layers these waters go through before reaching the stream. Stream water chemistry in Estonia is mostly affected by the presence of Carboniferous rocks from different eras (Simm, 1975). Carboniferous rocks are closely related to the concentration of Ca, Ba and Mg in stream water (Jarvie et al., 2000). The higher concentration of Ca and Mg in stream water flowing over Carboniferous bedrock compared with granite has been demonstrated before (Horton et al., 1999; Ingri et al., 2005). As carbonate rocks are widely distributed in Estonian and Latvian bedrock, Estonian and Latvian freshwaters should also have relatively higher concentrations of Ca and Mg, compared with the areas north of Estonia. The composition of bedrock can also influence the concentration of Sr and the ^{87}Sr:^{86}Sr ratio. Acidic bedrocks contain higher ratios of ^{87}Sr:^{86}Sr, but this can also depend on the bedrock age (Löfvendahl et al., 1990). Older bedrock has higher ^{87}Sr:^{86}Sr values, but lower Sr concentrations. This means that the areas north of Estonia should have considerably higher ^{87}Sr:^{86}Sr ratios, but lower Sr concentrations, whereas areas south of Estonia have higher Sr concentrations, but lower ^{87}Sr:^{86}Sr ratios, which in some cases can be even as low as seawater value (0.709; Löfvendahl et al., 1990).

In Estonia, anadromous *S. trutta* is found in at least 75 different streams disemboguing to the GoF, Gulf of Riga (GoR) and Baltic Sea main basin (MB). Streams that produce the most smolts are found on the northern coast of Estonia (in GoF). Of the 75 streams, 74 are known to have wild populations. Finland has about 20 *S. trutta* streams, 13 of them flowing to the GoF, and 8 of these having wild populations. In Latvia, anadromous *S. trutta* are found in about 28 streams, with all of them flowing to the GoR and MB and half of them having wild populations. Russia has about 41 streams flowing to the GoF that have *S. trutta* populations. Of these streams, only one is known to have mixed populations, and the rest have wild populations (ICES, 2019).

2.2 | Water and fish sampling

Water samples were collected from 100 different sampling sites in Estonia and Finland (Figure 1; Table I in the Supporting Information). In Estonia, samples were collected from 63 different sea trout spawning streams during the annual national salmonid parr density monitoring surveys in August–September 2012. A total of 81

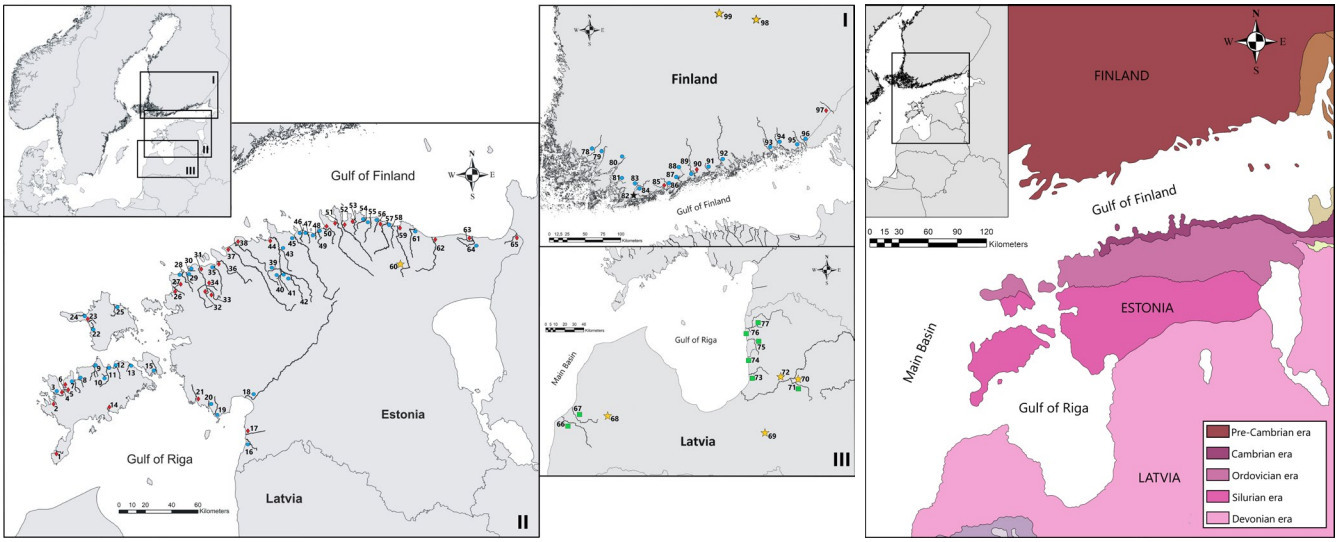

FIGURE 1 (a) Maps of the Finnish (I), Estonian (II) and Latvian (III) sampling locations where juvenile *Salmo trutta* and water samples were collected. Stream ID numbers correspond to the numbers provided in Table I in the Supporting Information. In Estonia and Finland, streams where both water samples and juvenile fish were collected are marked diamonds (♦). Streams where only water samples were collected are marked with circles (●). Fish hatcheries are marked with a star (★). In Latvia, all streams were sampled for S. *trutta* parr only and are marked with a square (■). The exact coordinates of all the stream and hatcheries sampled are found in the Supporting Information. (b) Bedrock geologic map of the study system. Estonian and Latvian bedrock are mostly composed of carbonate rocks, clays and sandstones from the Cambrian, Ordovician, Silurian, and Devonian era. Southern Finland is dominated by granitoids from the Pre-Cambrian era.

sampling sites were covered, with some of the streams having multiple sampling sites to evaluate the possible within-stream water chemistry variation. To characterise the seasonal change in water chemistry, additional samples were collected from 34 different sampling sites in February and June 2013. Water samples from Finland were collected in August 2013 from 19 different streams, with only one sampling site per waterbody.

Water samples were collected with a syringe and filtered through 45-μm nylon filter into sterile sampling containers. The syringe was rinsed with water from the sampling spot three times before filling it with 20 ml of water, after which the filter was attached to the syringe. 10 ml of water was filtered, and the remaining 10 ml was used to rinse the container. For the final sample, the syringe was filled again with 20ml water and filtered through the nylon filter into the container. To fix the samples, 2 ml of Carl Roth suprapure HNO_3 was added to every sample after the filtration. All samples were refrigerated until analysis.

In the Baltic Sea region, *S. trutta* parr have been shown to exhibit various alternative migration strategies (Limburg et al., 2001; Taal et al., 2014, 2018). However, on average, juvenile *S. trutta* spend 1–3 years in their natal stream before descending to sea (reviewed in Klemetsen et al., 2003). Therefore, natal fingerprints of juvenile *S. trutta* otoliths should reflect the elemental signature of the stream they originate from. By creating a baseline library of the otolith elemental signatures from known *S. trutta* spawning streams, it is later possible to retrospectively assign adults caught from the sea back to their natal stream. In order to see whether juvenile *S. trutta* of different stream origin may be distinguished from one another and to create a database of juvenile natal fingerprints, *S. trutta* parr (n = 564) were collected from anadromous *S. trutta* spawning streams and hatcheries in Estonia, Latvia and Finland (Figure 1). In Estonia, parr were sampled from one hatchery and 28 streams during the annual national salmonid parr density monitoring survey in 2012 (n = 361; seven to 11 individuals per site; Figure 1; Table I in the Supporting Information). In total, parr were collected from 34 different sites with some of the streams having multiple sampling sites to test the possible intra-stream variation in otolith microchemistry. From Latvia, fish were collected from 8 streams and four hatcheries in 2013 (n = 132; 11 per site; Figure 1; Table I in the Supporting Information). In Finland, three streams and three hatcheries were sampled in 2013 (n = 71; 10–14 per site; Figure 1; Table I in the Supporting Information). The exact coordinates of all the sampled streams and hatcheries and distances of the sampling sites from the river mouths (including Latvia and Finland) are found in Table I in the Supporting Information. All fish were kept frozen until subsequent analyses in the laboratory.

To better visualise the differences between streams and hatcheries, different *S. trutta* parr sampling sites were divided into five groups according to their geographic location. Gulf of Finland North (GOFN; n = 6) includes three Finnish streams (all flowing to the GoF) and three hatcheries from Finland. Gulf of Finland South (GOFS; n = 19) includes 18 Estonian streams (all flowing to the GoF) and one Estonian hatchery. Saaremaa and Hiiumaa (SAHI; n = 8) includes eight streams from Estonia´s largest islands Saaremaa and Hiiumaa in West Estonian Archipelago (all flowing to GoF, GoR, MB and Väinameri). GoR (n = 11) includes two Estonian and six Latvian streams (all flowing to GoR) and three hatcheries from Latvia. MB (n = 3) includes two streams from Latvia (both flowing to the MB) and

one Latvian hatchery. The streams were divided into groups based on their watershed location and not on the Baltic Sea region (e.g. gulf or bay) a particular stream flow into. For this reason, streams from islands Saaremaa and Hiiumaa are placed into one group (SAHI) although their streams disembogue into three different Baltic Sea regions. For exact coordinates and group divisions, see Table I in the Supporting Information.

2.3 | Sample preparation and analysis

Water samples were analysed in the Tallinn University of Technology's Geology Institute's ICP-MS laboratory and Tartu University´s Department of Geology. In the former, water samples were analysed with X series II ICP-MS and in the latter with Agilent 8800 QQQ ICP-MS. NIST water standards 1643e and 1643f were used for precision and accuracy assessment in Tallinn and Tartu respectively. Thirty two elements were measured from the water samples; these also included rare earth metals and two actinides (^{7}Li, ^{23}Na, ^{24}Mg, ^{39}K, ^{43}Ca, ^{45}Sc, ^{52}Cr, ^{55}Mn, ^{56}Fe, ^{63}Cu, ^{66}Zn, ^{85}Rb, ^{88}Sr, ^{89}Y, ^{111}Cd, ^{137}Ba, ^{139}La, ^{140}Ce, ^{141}Pr, ^{146}Nd, ^{147}Sm, ^{153}Eu, ^{157}Gd, ^{159}Tb, ^{163}Dy, ^{165}Ho, ^{166}Er, ^{169}Tm, ^{172}Yb, ^{175}Lu, ^{232}Th and ^{238}U).

For otoliths, the collected fish samples were thawed in the laboratory, measured (for the average total length of parr in each sampling site, the reader is referred to the Supporting Information) and dissected to extract a pair of sagittal otoliths. Otoliths were cleaned, air-dried and stored in Eppendorf tubes. One otolith per fish was randomly chosen and prepared for microchemical analysis as described in Rohtla et al. (2017). Before the microchemical analyses, all otolith thin sections were ultrasonically cleaned for 15 min in NANO-pure water and dried in laminar flow hood.

For trace elements, otoliths were analysed with laser ablation inductively coupled plasma mass spectrometry (LA-ICP-MS) in the University of Tartu, Department of Geology (UT), and in Oregon State University's WM Keck Collaboratory for Plasma Spectrometry (OSU). Analyses were conducted in two separate laboratories due to the long course of the study. Inter-compatibility of the results was assured by running a smaller number of same otoliths in both laboratories. In OSU, a VG PQ ExCell ICMPS (Thermo Scientific) with a New Wave DUV193 excimer laser (New Wave Research) was used. In UT, LA-ICP-MS analysis was conducted using Cetac LSX-213 G2+ laser equipped with HelEx II ablation cell connected to Agilent 8800 QQQ ICP-MS. The laser was set with 40 μm spot size and 5 μm/s scan speed both in UT and in OSU, while the pulse rate was set at 10 Hz in UT and 7Hz in OSU. A continuous line scan was traced from core to edge. A glass reference material (NIST 612) and calcium carbonate standard (MACS-3) were analysed at the beginning and end of every run and between every 10 and 20 otoliths. Otoliths were analysed for ^{43}Ca, ^{55}Mn, ^{85}Rb, ^{86}Sr, ^{138}Ba, ^{208}Pb and ^{66}Zn after which element:Ca ratios in mmol/mol were calculated following the methods of Rohtla et al. (2014). The average precisions of quantifying ^{43}Ca, ^{86}Sr, ^{137}Ba, ^{25}Mg and ^{55}Mn for NIST 612 glass varied between different sampling days from 8% to 17%, 5% to 12%, 4% to 12%, 7% to 14% and 6% to 15% respectively. From MACS-3, absolute accuracy was estimated, the mean values in different sampling days for Sr:Ca, Ba:Ca, Mg:Ca and Mn:Ca were 7%–22%, 15%–41%, 1%–32% and 1%–2% higher than reported for the standards. In data treatment, all the data values were corrected for the drift in measurements.

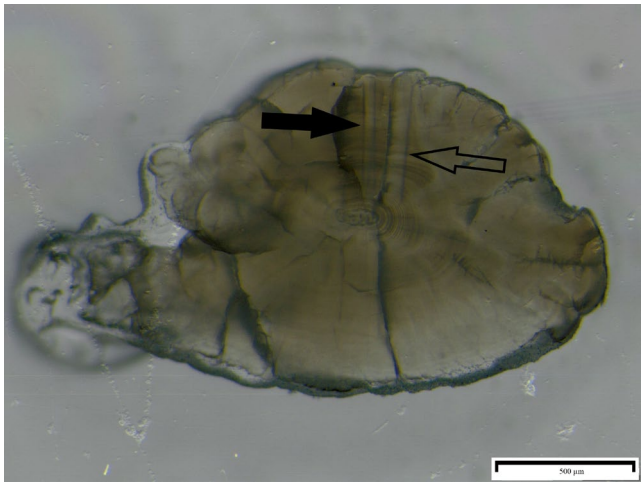

FIGURE 2 Otolith of *Salmo trutta* parr showing laser ablation transects of trace element (filled arrow) and Sr isotope (empty arrow) analysis on the dorsal side of the otolith. Both transects begin after the yolk absorption mark that is visible as a dark band around the primordia

After the elemental analysis, the same otoliths were used to quantify ^{87}Sr:^{86}Sr. Due to the long course of this study, otoliths from 25 locations were analysed in OSU and 23 at the Vegacenter at the Swedish Museum of Natural History in Stockholm. In the former, a Nu-Plasma MC-ICP-MS with a New Wave DUV193 excimer laser system was used, and in the latter, a Nu-Plasma (II) MC-ICP-MS together with ESI NWR193 ArF exclaimer laser ablation system was used. The isotope transect was set parallel to the elemental scan with the laser set at spot size 65 μm, scan speed of 5 μm/s and a pulse rate of 10 Hz in OSU and 15 Hz at the Vegacenter. To monitor instrument precision and accuracy, a marine gastropod was used in OSU and a brachiopod shell ("Ecnomiosa gerda"; TIMS value: 0.709181 ± 0.000004; Kiel et al., 2014; primary reference material) and a modern oyster shell from Western Australia (secondary reference material) at the Vegacenter, which were measured repeatedly every 2–10 otoliths. In OSU, a mean value (±2SE) of 0.70911 ± 0.00021 (n = 220) was consistently obtained. At the Vegacenter, all isotope ratios were normalised to the primary reference material value using a linear drift correction. The resulting average ^{87}Sr:^{86}Sr value for the modern oyster shell was 0.70911 ± 0.00016 (n = 29), which agrees with the expected value of modern seawater (^{87}Sr:^{86}Sr = 0.7091792 ± 0.000 0021; Mokadem et al., 2015).

For otolith element:Ca and ^{87}Sr:^{86}Sr values representing the natal area, an average ratio was calculated from a region starting after the yolk absorption mark (dark band) and ending at or near the otolith edge. This yolk absorption mark indicates the start of exogenous feeding (Marshall & Parker, 1982) after what the elemental fingerprint of the natal stream begins (Figure 2). Before the

yolk absorption mark and before fish have fully started exogenous feeding, the elemental composition of otoliths can be a mixture of natal signature and maternal influence (Bacon et al., 2004). Otolith Mn:Ca, Mg:Ca, Sr:Ca, Ba:Ca and $^{87}Sr:^{86}Sr$ were in the final data analysis. Otolith Zn:Ca, Pb:Ca and Rb:Ca were excluded because no significant differences were detected among sampling sites. It has been shown previously that several elements, such as Zn, Cu and Pb, might be under physiological control and the uptake of these elements is strongly regulated (Bury et al., 2003; Sturrock et al., 2014). In addition, the concentration of some elements, for example Zn and Rb, can be influenced by diet (Friedrich & Halden, 2008; Ranaldi & Gagnon, 2008).

2.4 | Data analysis

To test whether different streams are separable from one another by water chemistry, and to identify which elements contribute the most to this separation, a principal component analysis (PCA) was run on element concentrations of water samples collected from Estonia and Finland ($n = 100$). To meet the PCA assumptions, all data were log ($x + 1$)-transformed and normalised. Seasonal differences in element:Ca ratios in water samples collected from Estonian streams were tested with nonparametric Friedman's ANOVA, because the assumptions of parametric repeated-measures ANOVA were not met due to non-normal distribution.

As *S. trutta* can shift between streams (Taal et al., 2018), all otolith profiles were monitored for such movements. The possible intra-stream variation in otolith microchemistry was tested with nonparametric Kruskal–Wallis and Mann–Whitney *U* test on *S. trutta* samples from rivers with multiple sampling sites. Differences in otolith element:Ca and $^{87}Sr:^{86}Sr$ ratios among streams and hatcheries in Estonia, Latvia and Finland were investigated with Kruskal–Wallis tests. The canonical discriminant analysis (CDA) was used to test which elements are the most important in discriminating different groups of fish (different streams) and to visualise the differences. To determine the accuracy, each juvenile fish can be assigned back to their original stream, a quadratic discriminant function analysis (QDFA) with leave-one-out cross-validation was used. The prior probabilities of class membership were set equal between classes, and data were log-transformed before the analysis. Using the whole original data to determine classification accuracy has been a regular practice in multiple studies (Gahagan et al., 2012; Martin, Bareille, Berail, Pecheyran, et al., 2013; Nazir & Khan, 2019).

The relationship in element:Ca values between otoliths and water samples was tested with the Spearman rank correlation. For this, element:Ca values of *S. trutta* parr otoliths were compared with the values in Estonian water chemistry summer and autumn samples collected in June and August–September. Although the first feeding season during spring and summer months is the most important for the somatic and otolith growth of the fish (Folkvord & Johannessen, 2004), we included autumn samples also to the analysis as our autumn samples were collected in early autumn at a time when fish were probably still eating and growing. Finnish water and otolith samples were not tested as only three sampling sites from Finland had both water and fish samples.

Differences in the otolith microchemistry of wild- and hatchery-origin *S. trutta* were tested with the nonparametric Kruskal–Wallis *U* test.

3 | RESULTS

3.1 | Water chemistry

All stream water chemistry results, including in streams with multiple sampling sites, clear variation in within-stream water chemistry was not observed. In the PCA that included all water samples from Estonia and Finland, the first three principal components explained 77.8% of the total variation (54.2%, 15.0% and 8.6% respectively). The first principal component was mostly loaded by rare earth metals (i.e. lanthanides). Rare earth metals are usually below a detection limit in otoliths (Lara et al., 2008) and thus are usually not pertinent in the otolith microchemistry field. In the second test, only the elements that have found wider use in otolith microchemistry studies (i.e. Li, Na, Mg, K, Ca, Cr, Mn, Fe, Cu, Zn, Rb, Sr and Ba) were included. In the new test, the first three principal components explained 71.3% of the total variation (36.0%, 22.3% and 13.0% respectively). According to the PC1 and PC2 values, Estonian and Finnish streams formed clearly separable groups based on their water samples (Figure 3). Variations in Sr, Mg, K, Fe, Cr, Zn and Ba concentrations in water samples contributed the most to separation along the PC1, while Cu, Na, Cr, Rb, Li and Ca contributed the most to separation along the PC2 (Table 1). Based on the sign of the principal component loadings and principal component scores of each stream, this can be translated into somewhat lower Ca, K, Mg and Sr but higher Cr, Cu, Rb and Na concentrations in Finnish streams, compared to Estonian streams, with Ca being one of the most important elements in separating the two regions. All water chemistry data are found in the Supporting Information (Table IV).

Sr, Ba, Mg, Mn and Rb were selected in order to study the element:Ca differences in water samples between seasons collected from Estonian streams. Although Rb:Ca was excluded from the otolith microchemistry analysis, the seasonal variation of Rb:Ca was still studied in water chemistry. Summer, autumn and winter water samples had significantly different Sr:Ca ($F_{2,102} = 46$; $p < .001$), Ba:Ca ($F_{2,102} = 12$; $p < .01$), Mg:Ca ($F_{2,102} = 14$; $p < .01$), Mn:Ca ($F_{2,102} = 3$; $p < .01$) and Rb:Ca ($F_{2,102} = 36$; $p < .001$) ratios in water samples. Sr:Ca, Mg:Ca and Mn:Ca ratios were the highest in summer water samples (Figure 4). Ba:Ca levels were somewhat higher in winter water samples (Figure 5) and Rb:Ca in autumn samples. In terms of Rb:Ca levels, River Pühajõgi stood out with extremely high ratios compared to other streams, having Rb:Ca ratios of 1.4 (ppb) in autumn water samples compared to the average of 0.03 (ppb) of other streams. If River Pühajõgi was excluded, Rb:Ca levels were similar to other elements highest in the summer samples.

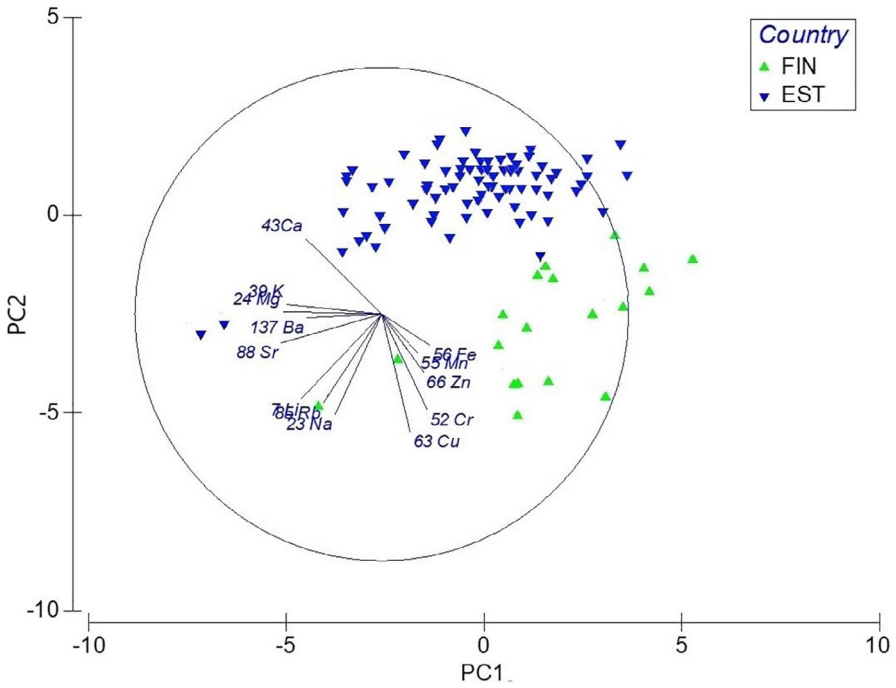

FIGURE 3 Plot of the principal component scores of the first two principal components (PCs) based on water samples collected from Estonian and Finnish streams. According to PC1 and PC2 values, Estonian and Finnish streams form two clearly separable groups

TABLE 1 Principal component loadings of the first two principal components (PC1 and PC2) from the principal component analysis (PCA). PCA was performed on element concentrations in water samples collected from different streams in Estonia and Finland. The PCA loadings demonstrate the contribution of each element to the separation of streams along the PC1 and PC2

Variables	PC1	PC2
Li	−0.328	−0.345
Na	−0.189	−0.407
Mg	−0.400	0.010
K	−0.387	0.039
Ca	−0.309	0.306
Cr	0.184	−0.388
Mn	0.147	−0.159
Fe	0.193	−0.125
Cu	0.115	−0.479
Zn	0.169	−0.234
Rb	−0.236	−0.360
Sr	−0.409	−0.118
Ba	−0.306	−0.015

3.2 | Otolith microchemistry

Individual otolith microchemistry profiles of all *S. trutta* parr included in this study were examined, and all parr were determined of not being stream shifters, meaning they originated from the stream they were caught. Three streams with multiple sampling sites exhibited variation in stream otolith microchemistry. For Loobu and Selja streams, only Sr:Ca showed variation ($p = .003$ and $p = .04$ respectively) between the sites. Riguldi stream showed a significant variation in Sr:Ca, Ba:Ca and $^{87}Sr:^{86}Sr$ between the two sites ($p < .05$). For all other streams, in all the element:Ca ratios significant variation was not found between the multiple sampling sites ($p > .05$). Despite three streams showing variation between the sampling sites, we decided to combine the data in streams with multiple sampling sites as two streams out of the three exhibited variation only in one element:Ca ratio out of five that were included in the analysis. Tests on variation in otolith microchemistry of juvenile *S. trutta* originating from different streams and hatcheries were done twice, firstly to study the otolith microchemistry variation on a smaller scale, including only the juvenile *S. trutta* that were sampled from Estonian streams and one hatchery ($N = 361$); and secondly to study the variation on a larger spatial scale, including all the samples from Estonia, Finland and Latvia ($N = 564$). On both occasions, the nonparametric Kruskal–Wallis ANOVA showed a significant difference in *S. trutta* parr otolith Sr:Ca ($F_{28,361} = 278$, $p < .001$; $F_{46,564} = 513$, $p < .001$), Ba:Ca ($F_{28,361} = 300$, $p < .001$; $F_{46,564} = 498$, $p < .001$), Mg:Ca ($F_{28,361} = 167$, $p < .001$; $F_{46,564} = 329$, $p < .001$), Mn:Ca ($F_{28,361} = 246$, $p < .001$; $F_{46,564} = 472$, $p < .001$) and $^{87}Sr:^{86}Sr$ ($F_{28,361} = 322$, $p < .001$; $F_{46,564} = 543$, $p < .001$) ratios.

Canonical discriminant analysis demonstrated the differences among the *S. trutta* parr, based on their otolith elemental fingerprints, originating from different streams and hatcheries from Estonia, Latvia and Finland (Figure 6). The first two canonical variables explained 94.2% of the variation, with the first explaining 74.9% and the second one 19.3% respectively. According to the CDA, $^{87}Sr:^{86}Sr$ and Sr:Ca are the most important in discriminating groups of fish from different streams and hatcheries, followed by Ba:Ca, with Mg:Ca and Mn:Ca contributing the least (Table 2). The QDFA reclassification accuracy was on average 73% ranging from 27 to 100% among streams. The highest reclassification accuracy of 100% was detected in all Finnish streams. Estonian and Latvian

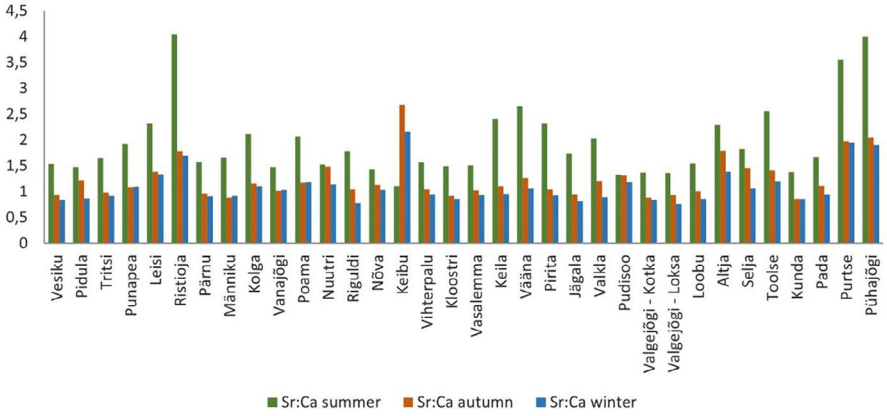

FIGURE 4 Sr:Ca ratios (ppb) in summer, autumn and winter water samples collected from Estonian streams. Streams are arranged according to their geographic location from west to east. Note that Sr:Ca ratios in winter and autumn samples are relatively similar compared to summer water samples that have significantly higher Sr:Ca ratios, apart from Keibu

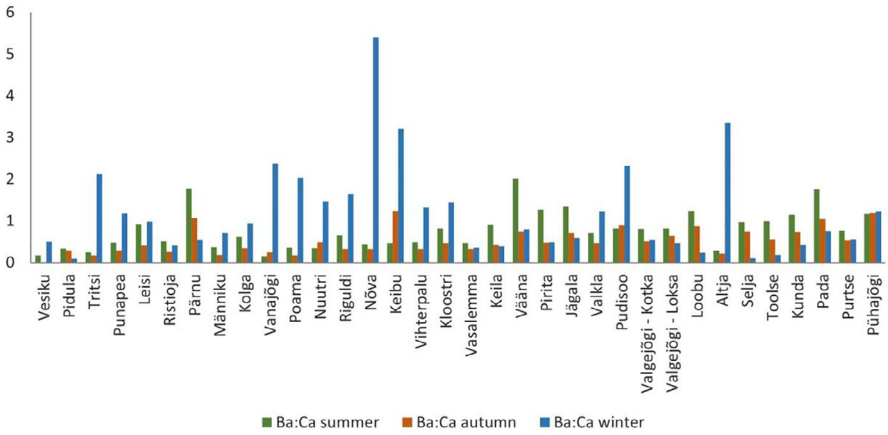

FIGURE 5 Ba:Ca ratios (ppb) in summer, autumn and winter water samples collected from Estonian streams. Streams are arranged according to their geographic location from west to east. Note that Ba:Ca ratios are highest in the winter samples

streams displayed average reclassification rates of 67% and 73% respectively (Table III, Supporting Information).

3.3 | Relationship between water chemistry and otolith microchemistry

Significant positive correlation was observed between water samples and *S. trutta* parr otoliths collected from Estonian streams for both Sr:Ca ($Rs = .49$; $n = 18$; $p < .05$) and Ba:Ca ($Rs = .64$; $n = 18$; $p < .05$) ratios (Figure 7). Mg:Ca and Mn:Ca showed no significant correlation between water samples and *S. trutta* parr otoliths ($Rs = .18$; $n = 18$; $p = >.05$ and $Rs = .14$; $n = 18$; $p = >.05$ respectively; Figure 7).

3.4 | Otolith microchemistry of hatchery- and wild-origin juveniles

All the element:Ca and $^{87}Sr:^{86}Sr$ ratios in Estonian and Latvian *S. trutta* otoliths were significantly different between wild- and hatchery-origin fish ($p < .05$). For example, both Estonian and Latvian hatchery fish had low $^{87}Sr:^{86}Sr$ (average in both 0.710) but high Sr:Ca ratios (average 0.6 and 0.84 mmol/mol respectively; Figure 8). Estonian wild fish had, on the contrary to hatchery fish, low average Sr:Ca (0.2 mmol/mol) but medium $^{87}Sr:^{86}Sr$ (0.712) ratios (Figure 8). However, Latvian wild *S. trutta* had either low (0.709) or medium $^{87}Sr:^{86}Sr$ average ratios (0.714) and low or medium Sr:Ca average ratios (0.2 and 0.9 mmol/mol respectively). Similar to Latvian hatchery fish, wild fish from Amata, Riva and Tebra streams that had the lowest average $^{87}Sr:^{86}Sr$ also had high Sr:Ca values. However, juvenile *S. trutta* in the Amata stream are likely stocked fish from Brasla or Kārļi FF. This is probably also the case with *S. trutta* from Riva and Tebra streams that were very similar to juveniles from Pelči FF and might actually originate from there. Finnish hatchery and wild fish had significantly different Sr:Ca and Mn:Ca ratios ($p < .05$). Wild fish from Finnish streams had average Sr:Ca values of 0.9 mmol/mol compared with the average of 1.8 mmol/mol of hatchery-origin juveniles (Figure 8). However, otolith $^{87}Sr:^{86}Sr$, Ba:Ca and Mg:Ca did not show significant difference between Finnish hatchery and wild *S. trutta* ($p > .05$; Figure 8).

4 | DISCUSSION

The present study demonstrated that there is considerable inter-stream variation in otolith microchemistry among and within the study systems, which was also supported by variation in water chemistry between regions. All this enabled to reclassify 73% of the sampled parr to their natal site. Elements such as Sr, Cu, Na, Mg, K, Rb, Ca, Li and Ba contributed the most to water chemistry variation, while otolith $^{87}Sr:^{86}Sr$ and Sr:Ca ratios were the best markers delineating streams and hatcheries. Although fish from Finland and most hatcheries were reclassified with 100% accuracy, misclassification of parr was observed

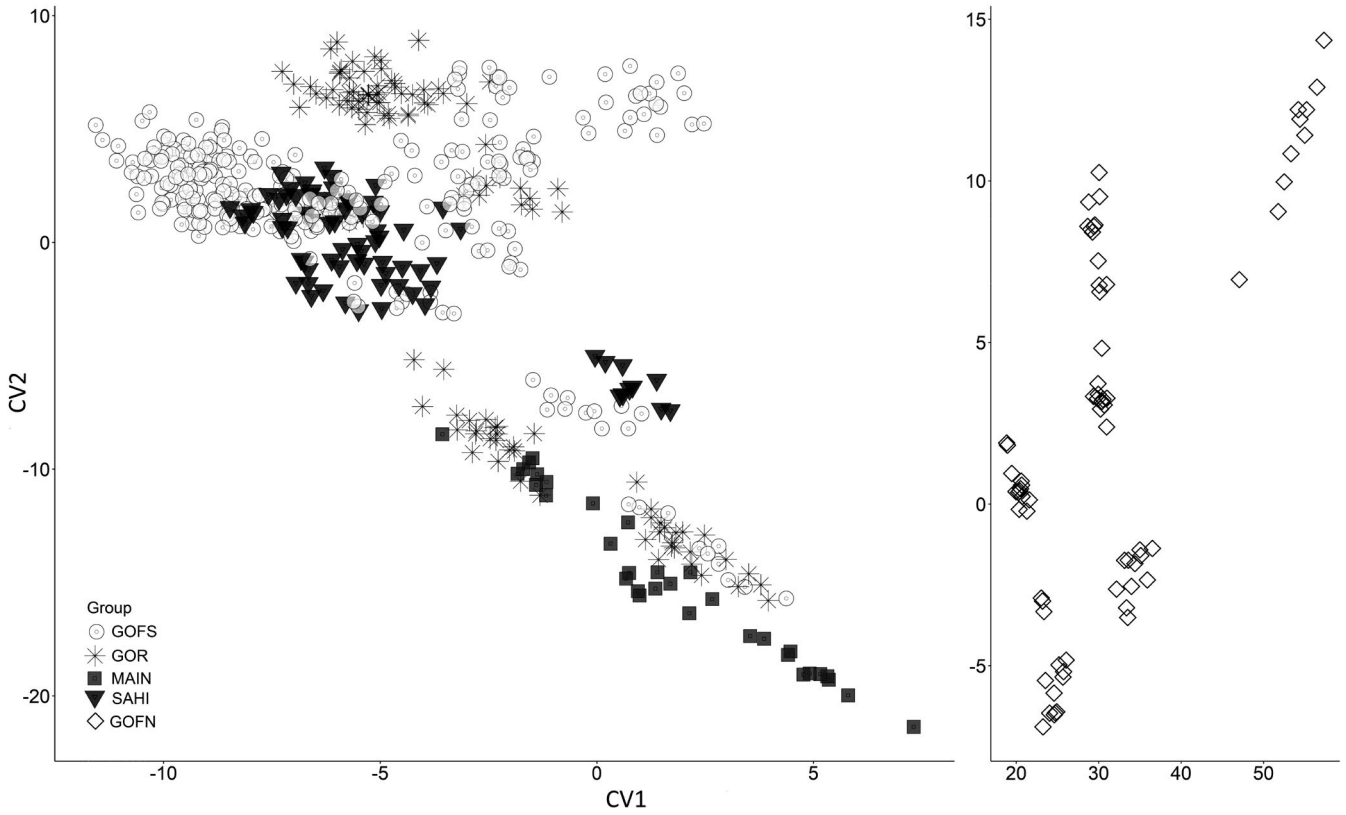

FIGURE 6 Results of canonical discriminant analysis (CDA) demonstrating the differences in *Salmo trutta* parr originating from different streams and hatcheries from Estonia, Latvia and Finland. The symbols represent individual fish in a specific group/area (GOFS, Gulf of Finland South; GOR, Gulf of Riga; MAIN, Main Basin; SAHI, Saaremaa and Hiiumaa Island; and GOFN, Gulf of Finland North). Note the difference in *x*- and *y*-scale between the left and right graph

TABLE 2 Total canonical structure coefficients for canonical discriminant analysis performed on ^{87}Sr:^{86}Sr, Sr:Ca, Ba:Ca Mg:Ca and Mn:Ca ratios measured from *Salmo trutta* parr otoliths collected from Estonian, Latvian and Finnish streams and hatcheries. Each coefficient demonstrates the relative importance of each element:Ca ratio in fish separation along canonical variate 1 (CV1) and canonical variate 2 (CV2)

Ratios	CV1	CV2
Mg:Ca	−0.112	0.288
Mn:Ca	−0.113	0.312
Sr:Ca	0.813	−0.536
Ba:Ca	0.187	0.296
^{87}Sr:^{86}Sr	0.894	0.447

in wild parr in Estonia and Latvia and between the regions. The present study exemplifies the potential of using otolith microchemistry to study natal origin of fish on different spatial scales, while also including high number of closely situated sampling sites.

4.1 | Water chemistry

The present study indicates that water chemistry of Estonian and Finnish streams displays considerable spatial variation, especially in the concentration of different rare earth metals and actinides (e.g. Y, Pr, Nd, Sm). These, however, have not been used widely in otolith microchemistry studies because the concentrations of these elements are usually below detection limits (Lara et al., 2008). When excluding rare earth metals and actinides, different alkaline earth, transition and alkaline metals (e.g. Sr, Mg, Ca, Ba, K, Fe, Mn, Cr, Cu) contributed the most to stream separation. Estonian and Finnish streams were clearly distinguishable based on the concentrations of these elements. For example, the two regions had clearly different Cr, Cu and especially Ca concentrations in stream water; Finnish streams have higher Cr and Cu but lower Ca concentrations. These results are in accordance with Löfvendahl et al. (1990) who showed that due to the crystalline bedrock, the surface waters of Finland have lower Ca and Sr concentrations compared with surface waters in areas south of Finland. As otolith chemical composition is influenced by ambient water chemistry (Doubleday et al., 2013; Walther & Thorrold, 2006), the spatial variation in water chemistry demonstrated in the present study indicates that *S. trutta* parr originating from different waterbodies and regions should also be separable based on their otolith elemental fingerprints.

Although Estonian and Finnish streams displayed differences in the concentrations of several elements, not all these are usable in otolith microchemistry studies. The elements used in discriminating different groups of fish should be deposited to the otoliths in

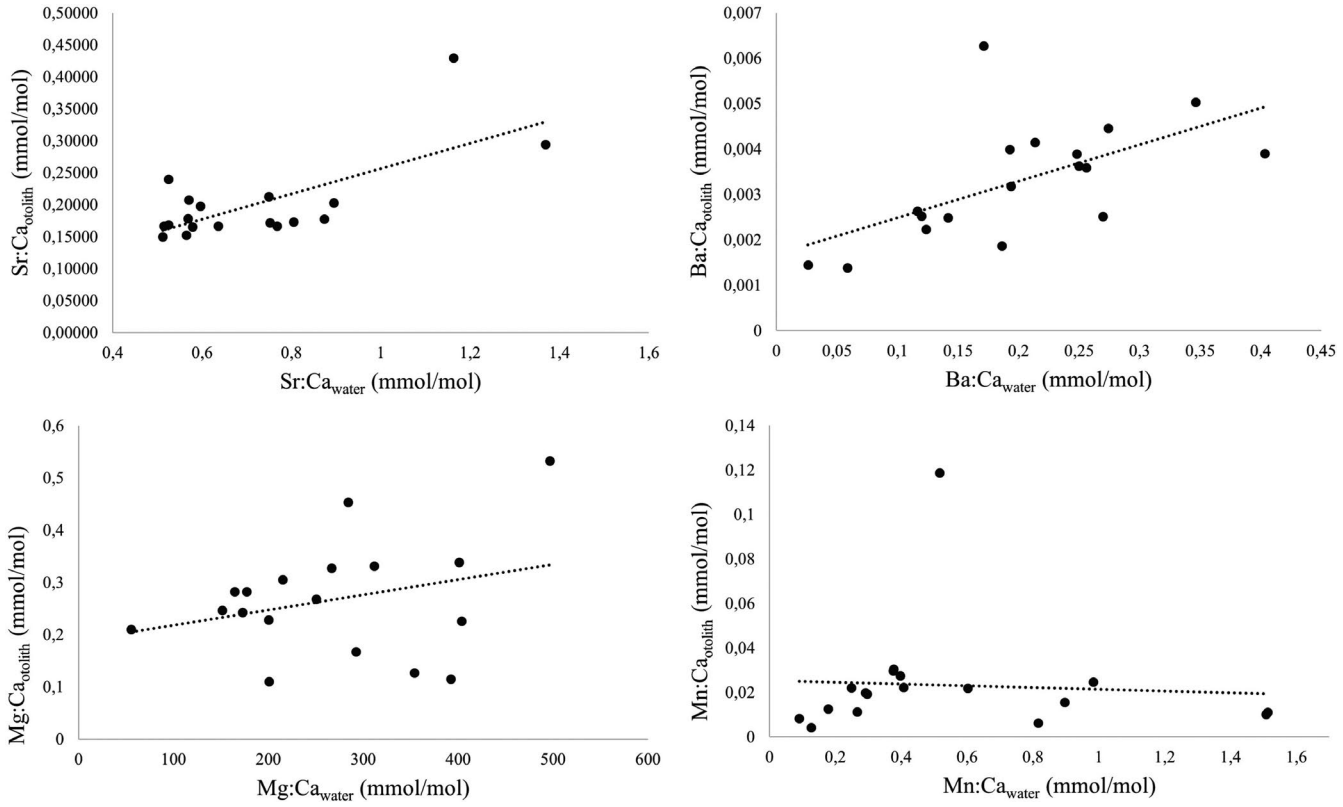

FIGURE 7 Correlations between Sr:Ca, Ba:Ca, Mg:Ca and Mn:Ca ratios in summer and autumn water samples and *Salmo trutta* parr otoliths collected from Estonian sample sites. Sr:Ca and Ba:Ca demonstrated significant positive correlation, and significant correlation was not observed in Mg:Ca and Mn:Ca ratios

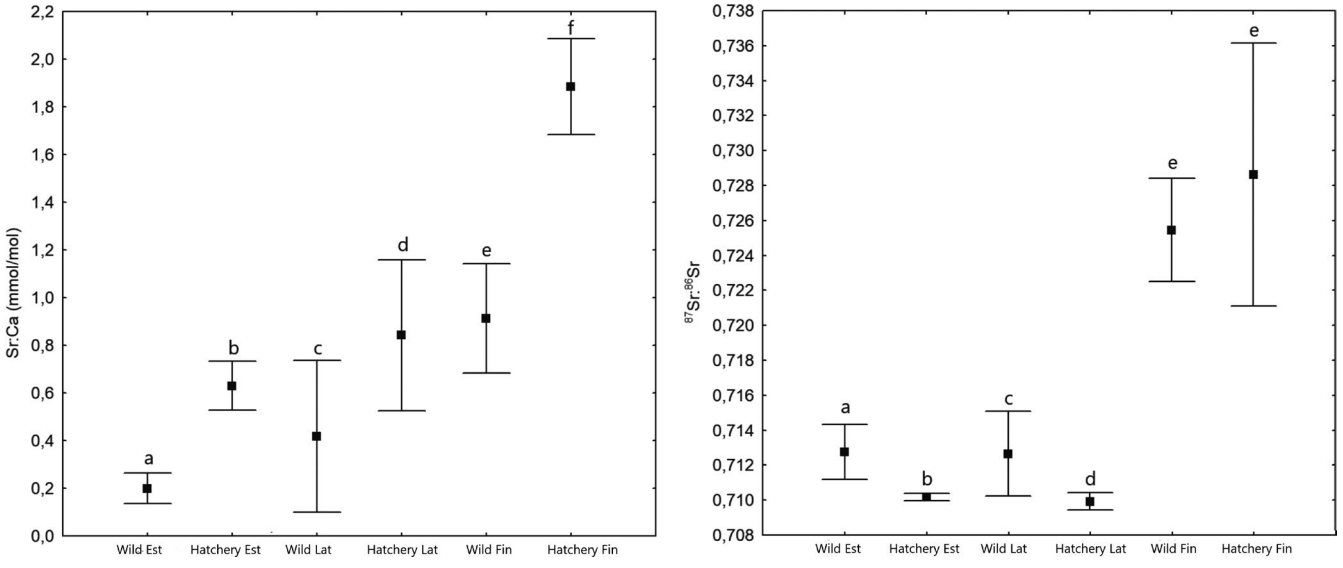

FIGURE 8 Mean ± SD ^{87}Sr:^{86}Sr and Sr:Ca ratios in the otoliths of juvenile *Salmo trutta* in Estonian (Est), Latvian (Lat) and Finnish (Fin) streams and hatcheries. Different letters indicate significance between hatchery and wild parr ($p < .05$)

proportion to ambient environment (Campana, 1999) and be stable over time (Campana et al., 2000). This means that in order to avoid temporal variation in otoliths, elements used in discriminating different fish groups should also be temporally stable in water, as a majority of the elements are incorporated into the otoliths from aquatic environment (Campana, 1999). The concentration of Mn, K, Cr and Cu in stream water has been shown to be influenced by anthropogenic factors (Jarvie et al., 2000) and potentially vary over time. Cu together with Fe has also been found to be under physiological control (Bury et al., 2003) and might not be deposited in otolith

equivalent to the surrounding environment. Mg is usually quite stable in time and not influenced by anthropogenic factors (Nikanorov & Brazhnikova, 2009). However, Mg together with Mn has shown temporal instability in otoliths (Veinott et al., 2014). For Mg:Ca and Mn:Ca levels in this study, no correlation was observed between water samples and the otolith microchemistry of *S. trutta*, indicating that these elements were not incorporated into the otoliths in proportion to ambient water. Although similar results have been reported before (Martin, Bareille, Berail, Pecheyran, et al., 2013; Nazir & Khan, 2019), these two elements might still add some value to the separation of fish (Mohan et al., 2012; Watson et al., 2018). Overall, Sr and Ba are considered to be the most useful elements in otolith microchemistry research, because of limited physiological control (Bath et al., 2000; Collingsworth et al., 2010) and strong positive relationship between water and otolith Sr:Ca and Ba:Ca values (Bath et al., 2000).

In this study, both Sr:Ca and Ba:Ca ratios in *S. trutta* parr otoliths were found to be well correlated with ambient water chemistry (Figure 7), which has also been demonstrated before (Gahagan et al., 2012; Martin, Bareille, Berail, Pecheyran, et al., 2013; Nazir & Khan, 2019), indicating that these elements are taken up into the otoliths in proportion to ambient water concentrations. Sr, Ba and Ca together with Mg have found a lot of use in separating different groups of fish (Gahagan et al., 2012; Martin, Bareille, Berail, Pecheyran, et al., 2013; Olley et al., 2011; Rohtla et al., 2017). As Estonian bedrock is dominated by Carboniferous limestone and Finnish by crystalline granitoids (Soesoo, 2010; Uścinowicz, 2011), and there are clear differences in water chemistry between Estonia and Finland (as demonstrated in the present study), Sr:Ca, Ba:Ca and Mg:Ca should also be usable in distinguishing fish between the two regions.

Intra- and/or interannual variations in otolith chemistry may limit the use of otoliths as a method to study fish population and discriminate stocks (Gillanders, 2002; Walther & Thorrold, 2009). In the present study, Sr:Ca, Ba:Ca, Mg:Ca, Mn:Ca and Rb:Ca levels in the water demonstrated some seasonal variation with most of the element:Ca ratios being higher during the summer period. Intra- and interannual variation in water element:Ca ratios has been demonstrated before, and this has been related to varying discharge rates with Sr:Ca and $^{87}Sr:^{86}Sr$ ratios being higher during the low flow period in summer and autumn (Martin, Bareille, Berail, Pecheyran, et al., 2013; Turner & Limburg, 2014). It has been also found, that during low flow conditions, surface water chemistry is dominated by groundwater and water from lower soil layers where the weathering is more intense, resulting in higher ion concentrations in surface water (Jarvie et al., 2000).

Although the relationship between flow regime and element:Ca ratios in the water was not examined in the present study, it is likely that alternating flow regimes cause the variations of element:Ca ratios among different seasons. The more extreme flow conditions usually do not last for a long time and might not affect otolith microchemistry significantly. Although it might take only 2–3 days for changes in water chemistry to be detectable in the otoliths, it may take at least several weeks before the concentrations reach a stable level and reflect the ambient water chemistry (Macdonald & Crook, 2010; Miller, 2011). Additionally, the base flow conditions during the ice-free months might be considered the norm of stream hydrology, and this period is also the most important for salmonid growth (Kennedy et al., 2000). Otolith natal fingerprints are usually extracted from an otolith region that is formed during the spring and summer months as the (body-proportional) growth rate of the fish and otolith is the highest during the first feeding season (Folkvord & Johannessen, 2004). This means, that even if there are some seasonal variations in stream water chemistry that in turn can be reflected in otoliths, these might not be significant enough to affect accurate reclassification of fish.

4.2 | Otolith microchemistry

One of the premises of using the otolith elemental fingerprints in distinguishing between different groups of fish is a site-specific chemical mark in the otolith. The present study shows significant variation in otolith Sr:Ca, Ba:Ca, Mn:Ca, Mg:Ca and $^{87}Sr:^{86}Sr$ ratios in *S. trutta* parr sampled from different streams and hatcheries. Finnish fish were clearly separable from Estonian and Latvian fish by their higher $^{87}Sr:^{86}Sr$ and Sr:Ca ratios in otoliths. Finnish bedrock is dominated by acidic igneous rocks that have been shown to have relatively high Sr:Ca and $^{87}Sr:^{86}Sr$ levels compared with Carboniferous and other basic rocks (Löfvendahl et al., 1990). For this reason, both streams located and *S. trutta* parr originating from the northern coast of GoF (i.e. Finland) have Sr:Ca and Sr isotope values considerably higher compared with the streams and fish samples from the southern coast of GoF (i.e. Estonia). This creates a very good premise for discriminating fish for evaluating the stock structure of mixed-stock fishery in the sea that incorporates fish originating from those regions.

Although underlying bedrock is considered to be one of the main factors influencing stream water chemistry and the resulting otolith microchemistry, in some cases, anthropogenic factors may outweigh the environmental effects. In Estonia, fish originating from rivers Purtse, Pühajõgi and Tõrvajõgi had the highest Sr:Ca levels. All these streams are located in North-East Estonia. It is plausible that the high Sr:Ca level in these streams is caused by the geology. Juveniles from River Kunda (that is geographically very close to River Purtse) had one of the lowest Sr:Ca ratios (0.15 mmol/mol vs. 0.39 mmol/mol respectively). It has been shown that that oil shale mining and the subsequent mine water release to the streams can raise the Sr levels in stream sediments (Szava-Kovats, 2001), possibly also elevating the Sr concentration in stream water over its natural level. Oil shale mining and the subsequent pollution have had a devastating effect on Purtse River and its fish fauna in the past. Although the fish fauna has since recovered (Kesler et al., 2011), Purtse River is still surrounded by different oil shale mines, along with Pühajõgi and Tõrvajõgi. Therefore, although geology is one of the main factors influencing Sr in stream water, this study also highlights the importance of the recent history of the streams and

possible anthropogenic effects on surface water chemistry, which in turn might be relevant to similar studies.

The present study demonstrated good separation of Estonian, Finnish and Latvian fish (Figure 6). ^{87}Sr:^{86}Sr was the most important marker in discriminating fish from different streams, followed by Sr:Ca and Ba:Ca. Mg:Ca and Mn:Ca contributed the least. The average reclassification rate of juvenile *S. trutta* to their natal stream/hatchery ranged from 27% to 100% with a mean of 73%. This can be considered a good result given the high number of relatively densely situated sampling locations. Otolith microchemistry-based reclassification accuracies tend to vary among studies (Gahagan et al., 2012; Vasconcelos et al., 2007; Veinott et al., 2012; Walther & Thorrold, 2008).

For example, Gahagan et al. (2012) showed relatively low reclassification rates (39%) for 0+ blueback herring (*Alosa aestivalis*, Mitchill), collected from ten different sites in seven streams, while Veinott et al. (2012) reclassified juvenile *S. trutta* from four streams back to their natal stream with 97% rate. Vasconcelos et al. (2007) showed that species sampled from a smaller number of sites showed a higher reclassification rate than species collected from larger set of sites. It is evident that the reclassification rate is dependent not only on water chemistry variability and the methodology used but also on study aims and scope. The more the sampling sites are included in reclassification models, the higher is the probability of having sites with similar water chemistry that in turn might create similar otolith fingerprints and lower the reclassification rate.

In addition to the number of sampling sites, spatial scale can also influence reclassification rate. Sampling sites that are spread over large spatial scale are more likely to have different underlying geology, and subsequently result in better reclassification. Turner and Limburg (2014) demonstrated with blueback herring and alewife that the incorrect classification of fish was less likely to happen between distant watersheds and most of the reclassification errors occurred between watersheds of proximity. Although Walther and Thorrold (2008) showed very good reclassification (93%) with 20 sampling sites, the spatial scale of their study was over 2700 km. The present study tested the otolith microchemistry separation power with even higher number of sampling sites (i.e. 39 different streams and eight hatcheries on a relatively small spatial scale) and demonstrated that it is possible to reclassify juvenile *S. trutta* with a good success rate. While the sampling locations in Finland were not so densely situated, some sampling locations in Estonia and Latvia were only few kilometres apart.

Anadromous *S. trutta* populations in Estonia are found in about 75 different streams (ICES, 2019) which means that present work includes approximately 40% of all the streams in Estonia where anadromous *S. trutta* is found, including the ones considered to be the most important for *S. trutta* spawning. Although there was some misclassification of juvenile fish between different study areas, mainly Estonia and Latvia, juvenile *S. trutta* are reasonably well separable between Estonia, Finland and Latvia based on their otolith microchemistry. The misclassification of Estonian and Latvian fish was mostly between Estonian stream Timmkanal and four Latvian streams. All these streams are located on the eastern coast of GoR, and these misclassifications were probably caused by similar geology between the north-western coast of Latvia and Estonian south-west coast as both are covered by similar sedimentary rocks from the Devonian era (Soesoo, 2010; Zelčs & Nartišs, 2014).

Out of the eight fish farms sampled in this study, six demonstrated reclassification accuracies of 100%. These included all Finnish fish farms, the only Estonian and two Latvian fish farms (Pelči and Brasla). Two Latvian fish farms that did not demonstrate so high accuracies (Tome and Kārļi 64% and 55% respectively) exhibited misclassification only with each other. No wild *S. trutta* juvenile was misclassified to any of the sampled fish farms and vice versa. Based on their elemental fingerprints, Estonian, Finnish and Latvian hatchery fish were separable from wild fish. Both in Estonia and Latvia, hatchery fish exhibited very low average ^{87}Sr:^{86}Sr but high Sr:Ca ratios (Figure 8). The reason behind this might be linked to their artificial diet. Although it has been previously shown that water is the main source of elements in otoliths (Walther & Thorrold, 2006), effect of diet has also been demonstrated (Engstedt et al., 2012; Kennedy et al., 2000). Albeit the chemical composition of pellets used as feed in sampled fish farms was not analysed, it is mostly of marine origin and would explain the very low average ^{87}Sr:^{86}Sr but high Sr:Ca values in the otoliths of hatchery-origin fish from Latvia and Estonia.

Streams that had lower reclassification than 100% were in some cases classified to a stream relatively far away. For example, brook Kõrtsioja that is located on the Estonian north coast had the lowest reclassification rate (20%; Table III, Supporting Information) with only two fish out of ten reclassified correctly to their natal stream. All other fish were misclassified to two streams located in Saaremaa Island. Using otolith microchemistry together with other methods, such as genetics, might help to overcome this issue. It has been shown that although genetic markers (microsatellite DNA markers) might not be able to classify fish back to their stream of origin, these natural markers might still help to distinguish fish on a larger spatial scale (Koljonen et al., 2014). This means that in a mixed-stock analysis, an individual from a specific spawning stream might be classified back to the region of origin using genetics, after which natal stream will be assigned with the help of otolith microchemistry. Otolith microchemistry together with genetic markers have been used before to separate different groups of fish with good results (Barnett-Johnson et al., 2010; Turner et al., 2015).

5 | CONCLUSIONS

Our study revealed the inter-region variability in stream water chemistry and inter-stream variability in *S. trutta* parr otolith microchemistry in the studied systems. It was demonstrated that the methods used are sufficient to distinguish individual fish with different origins over variable spatial scales, encompassing different Baltic Sea regions, catchment areas and neighbouring streams. Although the results demonstrated some overlapping otolith natal signatures

among some Estonian and Latvian streams, and consequently some misclassification of juvenile fish, this problem could be solved in the future by coupling otolith microchemistry with other methods (e.g. genetics). The results of the present study form a basis for future work to investigate the natal origin of adult *S. trutta* caught in the mixed-stock fishery in the sea. Albeit adult fish were not used in this work, our results based on juvenile fish indicate that finding natal origins of adults could be determined relatively accurately. Such studies are in acute demand for application in stream-based conservation measures for salmonids.

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CONFLICT OF INTEREST

The authors report no conflict of interest. This was not an invited submission.

AUTHOR CONTRIBUTION

Lagle Matetski, Mehis Rohtla and Roland Svirgsden designed the study, performed fieldwork and laboratory work, analysed the otoliths and interpreted the results. Martin Kesler, Lauri Saks, Imre Taal, Jānis Birzaks, Ari Saura, Mārcis Ziņģis, Matti Vaittinen and Markus Vetemaa performed fieldwork. Lagle Matetski, Lauri Saks and Kristiina Hommik analysed the data. Päärn Paiste, Melanie Kielman-Schmitt and Ellen Kooijman performed otolith analyses. Lagle Matetski drafted the manuscript. Mehis Rohtla, Roland Svirgsden, Martin Kesler, Lauri Saks, Imre Taal, Kristiina Hommik, Päärn Paiste, Melanie Kielman-Schmitt, Ellen Kooijman, Jānis Birzaks, Ari Saura, Mārcis Ziņģis, Matti Vaittinen and Markus Vetemaa were engaged in manuscript preparation and revision.

DATA AVAILABILITY STATEMENT

Data are available from the authors upon a reasonable request.

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