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Do sea trout *Salmo trutta* parr surveys monitor the densities of anadromous or resident maternal origin parr, or both?

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Abstract

Brown trout *Salmo trutta* L. parr were sampled from 21 Estonian and three Finnish streams to investigate whether national sea trout parr surveys sample the progeny of anadromous or resident maternal parents. Otolith Sr:Ca core values were used and validated as a tool for distinguishing between the progeny of the two forms. In Estonia (n = 283), 92% of the parr were the progeny of anadromous maternal parents, and 8% were the progeny of resident maternal parents, whereas in Finland (n = 24), the respective proportions were 79% and 21%. Variation in the maximum otolith Sr:Ca core values among progeny of anadromous maternal parents indicated that some adult females may enter fresh waters several months before spawning. It was concluded that easily accessible locations situated up to 30 km from the sea largely contain progeny of sea trout, whereas sites with poor connectivity with the sea can be dominated by progeny of resident trout. This study demonstrated that the method applied provided an effective means to distinguish between the progeny of sea trout and resident brown trout.

KEYWORDS
anadromy, brown trout, electrofishing, Estonia, Finland, otolith microchemistry

1 | INTRODUCTION

Economically important fish stocks often undergo a rigorous monitoring and management processes (e.g. Kuikka, Vanhatalo, Pulkkinen, Mantyniemi & Corander, 2014; Taylor, McAllister, Lawson, Carruthers & Block, 2011). Decisions are generally based on species-specific stock assessment models, which rely on the input obtained from various surveys, studies and expert knowledge. These models are assumed to provide the best management solution for the specific stock, although they are not flawless. Fortunately, such models can be perfected through time, so researchers are constantly looking for ways to improve the quality of the input data.

Stock assessment modelling (ICES 2015) of sea trout, *Salmo trutta* L., that inhabit the brackish Baltic Sea is based mainly on surveys of parr density (fish/100 m^2) to estimate smolt production. However, a shortcoming of such model building is that all parr are assumed to be the progeny of sea trout and not resident brown trout, which cannot be separated from the anadromous form based on morphological traits. To improve assessment of sea trout stocks, resident parr should be accounted for in stock assessment models, and thus, new methods are needed to distinguish between parr of anadromous and resident brown trout in electrofishing surveys (ICES 2015). Although it is known that resident brown trout can also produce sea trout (and vice versa; Jonsson, 1989; Limburg, Landergren, Westin, Elfman & Kristiansson, 2001), the extent of this in the wild has not been quantified.

Several methods have been applied to distinguish between anadromous and freshwater-resident brown trout. These include scale chemistry, carotenoid pigment, stable-isotope and genetic analyses (Bagenal, Mackereth & Heron, 1973; Briers, Waterman, Galt & Campbell, 2013; Charles, Roussel & Cunjak, 2004; Goodwin, King,

Jones, Ibbotson & Stevens, 2016; Youngson, Mitchell, Noack & Laird, 1997). However, apart from genetic analyses, all of these methods can be used only with the eggs and newly hatched fry, which in the case of sea trout progeny contain (for a limited time) marine-derived stable isotopes and pigments (Briers et al., 2013; Doucett, Hooper & Power, 1999); scale chemistry can be used with fish that have experienced the marine environment themselves (Bagenal et al., 1973). Unfortunately, such methods do not distinguish between the two brown trout forms in parr monitoring surveys, which are usually conducted late in the year when marine-derived stable isotopes and pigments in the tissues of young of year are dissolved and replaced with freshwater-derived stable isotopes and pigments. It is possible to identify the maternal and paternal origin of brown trout on the basis of sibling groups defined by microsatellite genotyping (Goodwin et al., 2016), but ideally this requires that all adults in the spawning population (resident and anadromous) are genotyped. Even then, one must first confirm visually the form an adult trout appears to be, and for this, genetics cannot provide an answer and morphological features are often inconclusive.

Chemical constituents of otoliths can provide a wealth of information on fish migrations, recruitment and stock structure (Campana, 1999; Walther & Limburg, 2012). The most straightforward application of otolith geochemistry is probably with respect to fish species that migrate between fresh and marine or brackish waters (Kafemann, Adlerstein & Neukamm, 2000; Rohtla et al., 2015; Secor, 1992). Calcium (Ca) is an essential life element and forms a major building block of otoliths, which undergo continuous growth throughout the life of the fish. In the meantime, non-essential trace elements such as strontium (Sr) and barium (Ba) are also incorporated to otoliths as mimics of Ca (Campana, 1999; Loewen, Carriere, Reist, Halden & Anderson, 2016). As marine and brackish waters usually contain several times higher levels of Sr than fresh waters, this difference will also be reflected in otoliths of fish that migrate between those biomes (Walther & Limburg, 2012). However, besides recording migrations, otolith cores of some fish species also contain useful information about the life history of the maternal parent. During vitellogenesis, fish deposit a suite of nutrients and essential life elements (e.g. Ca) along with the non-essentials (e.g. Sr) to the developing eggs. In anadromous salmonids (and some other fish, e.g. northern pike *Esox Lucius* L.; Engstedt, Stenroth, Larsson, Ljunggren & Elfman, 2010) that usually mature in the sea, the high concentrations of marine-derived Sr will eventually be incorporated into the otolith core of the developing embryo and will be visible as a distinctive strontium-to-calcium ($Sr:Ca_{core}$) peak in the elemental profile (Kalish, 1990). Height of the $Sr:Ca_{core}$ peak will depend on the stage of vitellogenesis at entry into fresh water, the time spent in fresh water before spawning, and freshwater Sr:Ca values (Donohoe, Adams & Royer, 2008; Volk, Blakley, Schroder & Kuehner, 2000). Progeny of freshwater-resident maternal parents, however, do not normally possess such a peak in $Sr:Ca_{core}$ values due to low Sr concentrations in fresh waters. Otolith $Sr:Ca_{core}$ values have been widely used to distinguish between progeny of resident and anadromous rainbow trout *Oncorhynchus mykiss* (Walbaum; e.g. McMillan et al., 2015; Riva-Rossi, Pascual, Babaluk, García-Asorey & Halden, 2007; Zimmerman & Reeves, 2000), while Limburg et al. (2001) and Taal et al. (2014) demonstrated the utility of such an approach with brown trout in the Baltic Sea.

The aim of this study was to demonstrate the use and validation of otolith chemistry to distinguish between the parr of resident brown trout and anadromous sea trout, a problem highlighted by the ICES Baltic Salmon and Trout Assessment Working Group (ICES 2015). The specific objective was to investigate whether national sea trout parr surveys sample the progeny of anadromous or resident forms, or both. This research is intended to inform the sea trout stock assessment modelling process for the Baltic Sea.

2 | METHODS

Brown trout parr (n = 283) were sampled from 27 sites located in 21 different streams from across Estonia (Figure 1; Table 1). Fish were collected during the annual national salmonid parr density surveys,

FIGURE 1 Map of the Estonian study region and the streams where brown trout parr were collected. Stream numbers correspond to the numbers given in Table 1. Note that some streams contain two-three sampling sites (see Table 1 for details)

TABLE 1 Brown trout parr sampling locations for maternal parent determination. Note that streams with the same identification (ID) number represent different sampling sites within one stream. ID numbers correspond to the numbers given in Figure 1. For each site, the number (*n*) and the mean total length (L_T, mm) of sampled parr together with ±*SD* and minimum (min) and maximum (max) values are given. Sampling location distance from the sea (Dist.; in rkm), parr densities/100 m^2 for 0+ (0 + dens.) and 1 + parr (1 + dens.), and number (*n* anadr.) and percentage (% anadr.) of anadromous maternal origin parr are also provided. Note that while most of the sites where sampled in 2012, there were two sites (Kolga and Tõrva) sampled in 2013 and one site (Kloostri) sampled in both of these years

Stream (site)	ID	Dist.	n	L_T	±*SD*	Min–max	0 + dens.	1 + dens.	*n* anadr.	% anadr.
Estonia (reference sites)										
Jõelähtme	14	–	5	90	14	73–105	–	–	0	0
Jänijõgi	15	–	5	101	6	96–108	–	–	0	0
Estonia (survey sites)										
Pidula	1	0.3	11	64	8	54–74	30.4	64.3	10	91
Vanajõgi	2	2.1	11	93	18	86–118	34.9	31.5	11	100
Timmkanal	3	15.3	11	72	8	58–86	27.4	2.4	11	100
Kolga[2013]	4	3.4	11	132	25	94–168	19.5	24.6	11	100
Riguldi	5	1.8	11	74	8	60–86	16.0	5.1	11	100
Höbringi	6	3.5	5	86	9	73–99	23.7	2.7	4	80
Vihterpalu	7	0.9	11	84	8	71–97	1.6	1.3	11	100
Piirsalu	8	29.7	11	73	8	57–81	59.7	19.1	11	100
Kloostri[2012]	9	7.4	10	120	40	77–184	4.4	15.6	0	0
Kloostri[2013]	9	7.4	5	75	7	66–83	44.6	0.6	1	20
Vasalemma	10	4.6	11	80	8	64–90	15.3	2.1	11	100
Keila	11	1.1	11	81	15	61–104	3.4	0.5	11	100
Vääna (Vääna-Jõesuu)	12	2.0	11	87	20	68–139	13.6	4.3	11	100
Vääna (Naage)	12	6.8	11	73	8	60–92	12.6	3.4	11	100
Pirita (Veneküla)	13	13.6	11	90	7	75–99	8.2	0.5	11	100
Pirita (Vaskjala)	13	24.2	10	71	8	59–83	6.1	0	10	100
Pudisoo	16	6.5	11	70	7	55–77	6.5	10.4	11	100
Valgejõgi (Loksa)	17	2.0	8	78	10	58–92	2.8	5.3	7	88
Valgejõgi (Kotka)	17	9.5	7	85	8	76–96	2.2	1.7	7	100
Loobu (Vihasoo)	18	2.2	10	71	5	64–80	8.6	3.7	10	100
Loobu (Porgaste)	18	5.4	10	60	8	50–81	26.3	0.9	10	100
Loobu (Joaveski)	18	10.0	10	87	7	74–97	7.7	1.3	9	90
Selja (Rutja)	19	3.5	10	79	14	60–106	17.8	1.0	9	90
Selja (Varangu)	19	17.7	11	83	14	60–106	29.3	0.3	11	100
Kunda	20	1.2	11	80	9	66–93	5.9	2.0	11	100
Purtse	21	0.6	11	85	9	73–103	1.1	0	8	73
Pühajõgi	22	1.7	11	86	13	66–103	27.7	19.1	11	100
Tõrva[2013]	23	13.9	11	73	10	55–89	159.9[a]	0	11	100
Finland (survey sites)										
Ingarskilanjoki	–	14.0	7	92	8	83–102	10.0	–	7	100
Longinoja	–	3.5	8	88	10	75–101	94.0	–	5	63
Mustanjoki	–	26.7	9	88	20	67–113	19.0	–	7	78

[a]Inflated densities due to low water levels (pool refugium).

which target stream reaches accessible to anadromous salmonids. The majority of parr were sampled in autumn 2012 as young of year, however, occasionally 1+ parr were sampled, and in three sites, parr were also sampled in 2013 (Table 1). To obtain reference samples for the progeny of resident brown trout, parr from two streams (*n* = 10) that are inaccessible to anadromous fish were sampled in 2015 (Figure 1; Table 1). Parr originating from three Finnish streams that discharge to the Gulf of Finland were also sampled in 2013 for comparative

purposes (n = 24; Table 1). All fish sampled were frozen for later analysis in the laboratory, where specimens were thawed and otoliths subsequently removed, cleaned and stored dry in microtubes. For each fish, one randomly chosen otolith was glued (sulcus side down) onto a coverslip, which was then partly glued onto a standard glass slide. Otoliths were manually ground down using silicon carbide sandpaper until the core became visible and then polished. Individual thin sections were glued onto standard glass slide and stored in clean plastic bags for later analysis. Prior to chemical analyses, all otolith thin sections were ultrasonically cleaned for 15 min in ultrapure water and then dried in laminar flow hood. Otoliths were analysed for ^{86}Sr and ^{43}Ca in the WM Keck Collaboratory of Plasma Spectrometry, Oregon State University. The laser was set at 7 Hz with a 40-μm ablation spot size and a scan speed of 5 μm/s. A continuous line scan was traced from core to edge. Data reduction to Sr:Ca in mmol/mol was achieved following the methods of Miller (2007) as described in Rohtla et al. (2014).

An individual fish was classified as being of anadromous maternal origin if the mean $Sr:Ca_{core}$ value (before the abrupt decrease; Figure 2b) was higher than the mean + 2 *SD* of the Sr:Ca natal value ($Sr:Ca_{natal}$) for the same specimen (Berejikian, Campbell & Moore, 2013). A specimen was classified as being of resident maternal origin if the mean $Sr:Ca_{core}$ value was lower or within two standard deviations of the mean $Sr:Ca_{natal}$ value for the same specimen. Although different statistical techniques have been used for aiding the anadromous versus resident maternal parent distinction (e.g. Donohoe et al., 2008; Hart, Bond, May-McNally, Miller & Quinn, 2015; Zimmerman & Reeves, 2000), no universal method exists. Pearson correlation analysis was used to study the relationship between parr density, distance from the sea and percentage of parr with anadromous maternal parents.

3 | RESULTS

All parr sampled from the rivers Jänijõgi and Jõelähtme (i.e. the reference sites) possessed otolith $Sr:Ca_{core}$ values similar to natal values with no accompanying Sr:Ca peak (Figure 2a). Parr with mean $Sr:Ca_{core}$ values lower or within 2 *SD* of mean $Sr:Ca_{natal}$ values were therefore classified as progeny of resident maternal parents (Figure 2d). Parr with mean $Sr:Ca_{core}$ value greater than mean + 2 *SD* of $Sr:Ca_{natal}$ value were classified as progeny of anadromous maternal parents (Figure 2b,c,e,f). Ninety-two percent of parr sampled in the Estonian national survey sites (n = 283) were progeny of anadromous maternal parents (Table 1). Only 8% of parr sampled in Estonia were classified as progeny of resident maternal parents, and most (n = 14) originated from the River Kloostri, where only one individual had an anadromous maternal parent. Seventy-nine percent of parr sampled in the Finnish national survey (n = 24) were the progeny of anadromous maternal parents, and 21% were the progeny of resident maternal parents (Table 1).

$Sr:Ca_{core}$ values in Estonian parr with anadromous maternal parents (n = 261) varied considerably, with 78% possessing a peak of 1.50–2.80 mmol/mol (Figure 2b), 21% possessing a peak of 0.50–1.49 mmol/mol (with large majority > 1 mmol/mol), and only 1% possessed a peak of 0.39–0.49 mmol/mol (Figure 2c). All mean $Sr:Ca_{core}$ values ≤1.11 mmol/mol were from parr (n = 14) that originated from larger streams in which Atlantic salmon, *Salmo salar* L., also spawn. Otolith $Sr:Ca_{natal}$ values in brown trout parr sampled from Estonian streams were <0.5 mmol/mol (freshwater threshold), with most of the $Sr:Ca_{natal}$ values being 0.1–0.3 mmol/mol.

Visual distinction of parr from anadromous or resident maternal parents was less obvious among Finnish trout because they displayed considerably higher otolith $Sr:Ca_{natal}$ values (Figure 2e,f). Finnish fresh waters run on granitic bedrock and are characterised by relatively low concentrations of Ca (2.9–17 ppm, mean = 6.5 ppm) and Sr (15–77 ppb, mean = 39 ppb), which resulted in relatively high freshwater (>0.004 mg/L) and otolith (0.6–1.5 mmol/mol) Sr:Ca ratios (Löfvendahl, Åberg & Hamilton, 1990; the present study). Estonian fresh waters, on the other hand, run on carbonate bedrock and are characterised by relatively high concentrations of Ca (9.5–147 ppm, mean = 78 ppm) and Sr (25–232 ppb, mean = 94 ppb), which result in relatively low freshwater (<0.003 mg/L) and otolith (<0.5 mmol/mol) Sr:Ca ratios (Matetski, 2014; the present study). Otolith Sr:Ca ratios are therefore mostly driven by freshwater Sr:Ca ratios (see also Brown & Severin 2009), but freshwater Ca concentration seems to be the most influential factor in extremely hypocalcemic environments due to the positive effect this environmental setting has on Sr uptake kinetics (Loewen et al., 2016). Consequently, the dilution effect (i.e. marine Sr:Ca is diluted with low freshwater Sr:Ca values in developing eggs) is weaker in Finnish fresh waters, but high marine-derived $Sr:Ca_{core}$ values may still go unnoticed if freshwater Sr:Ca values are high and the female enters fresh waters several months prior to spawning.

There was no correlation between parr density or distance from the sea and percentage of parr with anadromous maternal parent (p > 0.6 in all cases). These relationships are outside the scope of the present study and require further investigation, especially with regard to distance from the sea and the percentage of parr with anadromous maternal parents (Bohlin, Pettersson & Degerman, 2001).

4 | DISCUSSION

The proportion of parr that were spawned by anadromous maternal parents varied among locations. In most Estonian survey sites, all parr sampled were of anadromous maternal origin, and only some sites contained one or few parr of resident maternal origin. However, all but one parr were of resident maternal origin at the River Kloostri survey site, illustrating a potential pitfall for stock assessment modelling; this site was assumed to act as a spawning ground for sea trout, but was inhabited by progeny of resident brown trout. Extensive reed bed exists in the mouth of River Kloostri, and it is therefore plausible that this natural obstruction impairs the spawning migrations of anadromous salmonids at least in some, if not all, years. Data from such survey sites should be re-evaluated when sea trout recruitment is assessed. The overall situation was more or less the same in the three Finnish survey sites that were sampled, although the total share of parr with resident

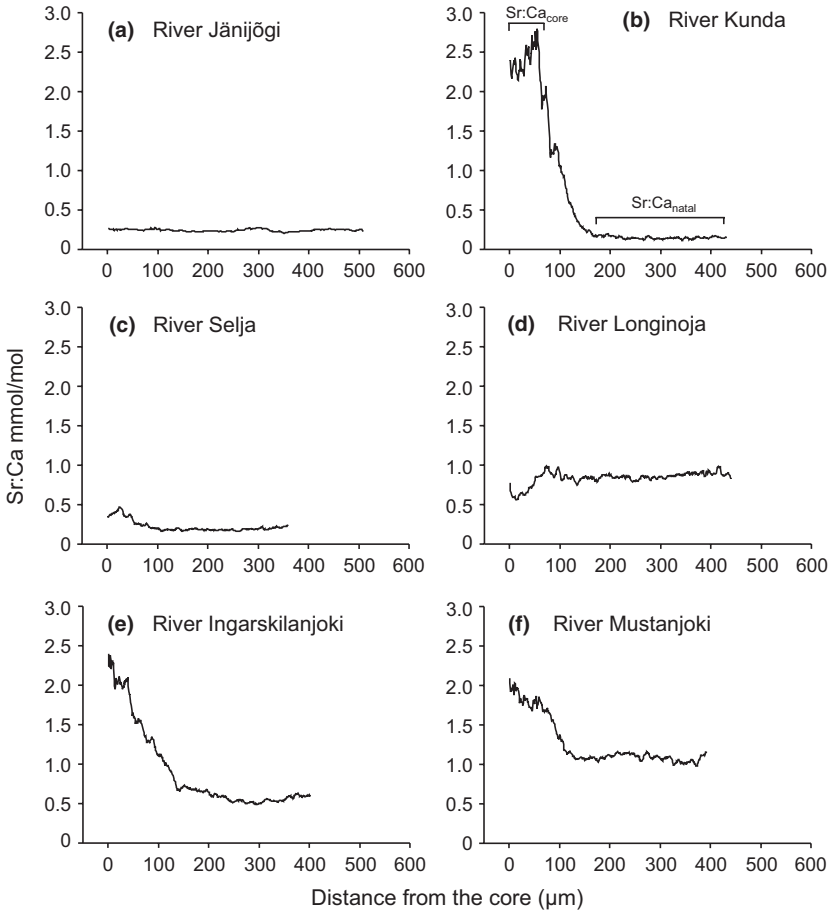

FIGURE 2 Representative otolith Sr:Ca profiles of brown trout parr with resident (a, d) and anadromous maternal parent (b, c, e, f). Indicative regions on Sr:Ca profile where the maternal (Sr:Ca$_{core}$) and natal (Sr:Ca$_{natal}$) chemical information was extracted are also denoted (b)

maternal parents was higher than the Estonian average. In general, Estonian surveys of sea trout parr capture the progeny of sea trout; however, progeny of resident brown trout is relatively common and can be numerous or even dominate in some survey streams. This same conclusion may also apply to Finnish survey sites, but with the caveat that only three Finnish streams were included to the present study. It has to be stressed that sample size per site was relatively low in the present study (i.e. mostly 10–11 randomly chosen specimens from a 100 m^2 reach of stream), and therefore, slightly different results may be reached with a larger sample.

Sr:Ca$_{core}$ values of the sampled brown trout parr varied considerably, demonstrating that the utility of identifying the maternal origin of anadromous salmonids using otolith Sr:Ca$_{core}$ values will ultimately depend on (1) the time sea-run females spend in fresh waters before completing yolk deposition and spawning; and (2) ambient Sr:Ca (or Ca; sensu Loewen et al., 2016) values in the spawning stream (Donohoe et al., 2008; Volk et al., 2000). Donohoe et al. (2008) demonstrated that if the migratory difficulty (index based on elevation and distance from the sea) for anadromous rainbow trout females is low and they spawn within 1–4 months of entering fresh waters, discrimination between the two forms was still good. However, discrimination was poor if migratory difficulty was high and females entered fresh water >6 months before spawning. It is known that sea trout can enter larger streams up to 6 months prior to spawning, whereas for reproduction in small streams, trout generally ascend a short period before spawning (reviewed in Klemetsen et al., 2003). In Estonia, sea trout can already enter streams in June, although the main spawning migration occurs in late August and September; spawning usually takes place in the second half of October, but may extend even to December in warm autumns (Kangur, Paaver, Drevs & Turovski, 2003). Hence, although it seems that sea trout generally do not enter the streams >6 months before spawning, the present study demonstrated that greatly diluted Sr:Ca$_{core}$ values exist in Estonia. This is probably due to the combination of early stream entry and low freshwater Sr:Ca values. Alternatively, the observed low Sr:Ca$_{core}$ values could be a methodological artefact (as a result of over or under grinding the primordium or slight misplacement of the laser track), but this is unlikely. In cases where no or little dilution occurs, but freshwater and thus otolith natal Sr:Ca values are higher or otherwise (i.e. in hypocalcemic environments; sensu Loewen et al., 2016) approach seawater Sr:Ca values (e.g. in Finland and most of Sweden), otolith ^{87}Sr:^{86}Sr$_{core}$ values can probably be used to distinguish between progeny of anadromous and resident brown trout. This has already been successfully applied with Chinook salmon *Oncorhynchus tshawytscha* (Walbaum; Bacon et al., 2004) and rainbow trout (Hodge, Wilzbach, Duffy, Quiñones & Hobbs, 2016).

Brown trout parr densities can be considerably higher in sites where anadromous individuals spawn compared with sites inhabited only by resident individuals (Bohlin et al., 2001). Parr densities in anadromous populations were negatively related with migration

distance (altitude) and as such associated with migration cost (Bohlin et al., 2001). No such trends were revealed in the present study. The prevalence of anadromy did not correlate with parr density or the distance from the sea. The farthest site from the sea was 29.7 km, and all fish sampled had anadromous maternal origin. Therefore, the cost of migration to the sampled sites may be relatively small due to the relatively short migration distance.

In conclusion, the present study has demonstrated that the chemical information stored in the otolith core can be used to distinguish between progeny of anadromous and resident brown trout and thus represents a relatively simple means to provide more accurate inputs to the modelling and management of sea trout stocks in the Baltic Sea (e.g. ICES 2015). Although this method may not be applicable in a routine manner, that is to all survey sites due to resource limitations and/or for conservation reasons, it could be used as a general screening method to identify sites with a high proportion of resident individuals. Screening should be undertaken along a relatively long length of stream to minimise the bias that could occur when parr from only one or two redds are sampled.

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