

## BRIEF COMMUNICATION

# Quantifying an overlooked aspect of partial migration using otolith microchemistry

Mehis Rohtla<sup>1\*</sup>  | Lagle Matetski<sup>1\*</sup> | Imre Taa<sup>1</sup> | Roland Svirgsden<sup>1</sup> |  
Martin Kesler<sup>1</sup> | Päärn Paiste<sup>2</sup> | Markus Vetemaa<sup>1</sup>

<sup>1</sup>Estonian Marine Institute, University of Tartu, Tartu, Estonia

<sup>2</sup>Department of Geology, University of Tartu, Tartu, Estonia

## Correspondence

Mehis Rohtla, University of Tartu, Estonian Marine Institute, Vanemuise 46a, 51003 Tartu, Estonia.  
Email: mehis.rohtla@ut.ee

## Present address

Mehis Rohtla, Norwegian Institute of Marine Research, Austevoll Research Station, Storebø, Norway

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## Abstract

For the first time, an overlooked aspect of partial migration was quantified using otolith microchemistry and brown trout, *Salmo trutta*, as a model species. Relative contributions of freshwater resident and anadromous female brown trout to mixed-stock sea trout populations in the Baltic Sea were estimated. Out of 236 confirmed wild sea trout sampled around the coast of Estonia 88% were of anadromous maternal origin and 12% were of resident maternal origin. This novel finding underscores the importance of the resident contingent in maintaining the persistence and resilience of the migratory contingent.

## KEYWORDS

anadromy, Baltic Sea, brown trout, otolith microchemistry, resident

Partial migration is a phenomenon describing populations of animals that are composed of resident and migratory individuals that often co-occur sympatrically during certain time periods of their life histories. It is widespread among various animal taxa, including fish (e.g., Chapman *et al.*, 2011; Jonsson & Jonsson, 1993). A considerable amount of fundamental research has been conducted to understand the mechanisms driving partial migration in different fish species (e.g., Brodersen *et al.*, 2008, 2019; Hendry *et al.*, 2004; Jonsson & Jonsson, 1993). Far less is known about the population-level proportions of resident and migratory individuals at different spatio-temporal scales (e.g., Austin *et al.*, 2019; Kerr & Secor, 2012; Svirgsden *et al.*, 2018) and almost nothing is known about the absolute or relative contribution of resident individuals to the migratory contingent (and *vice versa*) (but see Zimmerman *et al.*, 2009; Courter *et al.*, 2013). The latter could be important for population persistence and resilience if significant resident contingent contribution to migratory contingent occurs.

Brown trout, *Salmo trutta* L., is a facultatively anadromous species typically displaying partial migration. Resident and migratory individuals can co-occur sympatrically and display a wide range of life histories (reviewed by, e.g., Birnie-Gauvin *et al.*, 2019; Nevoux *et al.*, 2019).

It is widely acknowledged that resident trout can also produce migratory offspring and *vice versa* (Dębowski & Dobosz, 2016; Jonsson, 1982; Jonsson & Jonsson, 2006), but so far this has not been quantified among subadults and adults that have recruited to the feeding areas or returned to spawn. Although it has been recently demonstrated that offspring of both resident and anadromous maternal parents can be present in various proportions in sympatric spawning and nursery grounds (Goodwin *et al.*, 2016; Rohtla *et al.*, 2017), these data cannot be used to quantify recruitment success to fresh and/or marine waters by these two forms. Such information could also be of wider interest as some other salmonids (e.g., Arctic charr, *Salvelinus alpinus* L., Jonsson *et al.*, 1989), and also pike, *Esox lucius* L. (Engstedt *et al.*, 2010), display similar life history variability and physiological traits relevant for the use of the presented methodology.

The aim of the present study was to sample wild sea trout from brackish coastal waters of the Baltic Sea in Estonia and quantify the proportion of sea trout spawned by freshwater resident and anadromous female brown trout using otolith microchemistry. Since anadromous maternal origin parr tend to dominate in Estonian brown trout streams accessible to anadromous individuals (Rohtla *et al.*, 2017), it was hypothesised that they will also dominate in the sea and therefore the contribution of resident trout is minuscule.

\* Mehis Rohtla and Lagle Matetski should be considered joint first authors.

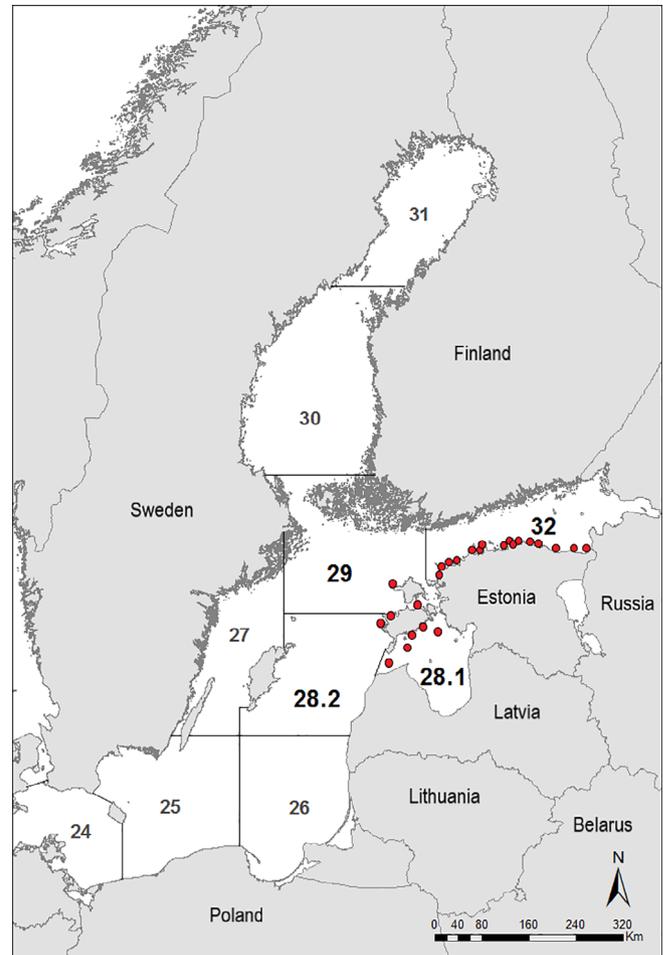
The state of Estonian sea trout populations has been improving lately as parr densities in spawning rivers and fisheries yields have increased (Kesler *et al.*, 2020). This has been the result of various managemental and conservational actions, mostly directed to freshwater habitats. The state of Estonian resident brown trout populations are mostly unknown as the stocks are only occasionally and non-systematically monitored.

The premise of using otolith microchemistry to infer the maternal origin of the sampled specimens depends on the species' ecology and vitellogenesis process, and therefore cannot be applied to all species. In species where yolk formation in the egg is completed before the anadromous fish enter fresh water (*e.g.*, salmonids, anadromous pike) the otolith nuclei of the embryo will contain elements (*e.g.*, Strontium) from the marine environment (Engstedt *et al.*, 2010; Kalish, 1990). As marine water usually contains higher concentrations of Sr compared to fresh water, this difference is also reflected in the otolith nuclei of anadromous and resident specimens. This has been previously validated for brown trout in the Baltic Sea (Limburg *et al.*, 2001; Rohtla *et al.*, 2017).

Sea trout used in the present study ( $n = 236$ ) were mostly obtained from commercial and recreational fishers in the period 2013–2017. The study area covered the entire coast of Estonia and encompassed all seven counties that border the sea (Figure 1 and Table 1). The heads of the sampled fish were frozen and later thawed in the laboratory for otolith removal. Details of the otolith microchemistry analyses and data interpretation are described fully in Rohtla *et al.* (2017) and Taal *et al.* (2018). Briefly, otoliths were ground down in the sagittal plane using different size silicon carbide sandpapers until the core became visible and were then polished.  $^{43}\text{Ca}$  and  $^{88}\text{Sr}$  were then quantified in ultrasonically cleaned otolith thin sections using laser ablation inductively coupled plasma mass spectrometry. The laser was set to 10 Hz, with a 40  $\mu\text{m}$  ablation spot size and a scan speed of 5  $\mu\text{m s}^{-1}$ . A line of at least 700  $\mu\text{m}$  was traced from the core towards the dorsal edge. A reference glass material (NIST 612) and calcium carbonate standard (MACS-3) were analysed before and after every 10 otoliths to monitor precision and accuracy. Raw counts were corrected for instrument drift using NIST 612 and converted to Sr:Ca in  $\text{mmol mol}^{-1}$ . Finally, a five-point running mean followed by a five-point running median was applied to the profiles to smooth the data for presentation.

All the sea trout used in the present study were confirmed to be wild anadromous trout using otolith microchemistry (L. Matetski, in prep.). An individual sea trout was classified as being of anadromous maternal origin if the mean otolith Sr:Ca<sub>core</sub> value was higher than the mean + 2S.D. of the Sr:Ca<sub>natal</sub> value (Figure 2a). An individual sea trout was classified as being of resident maternal origin if the mean Sr:Ca<sub>core</sub> value was lower or within two standard deviations of the mean Sr:Ca<sub>natal</sub> value (Figure 2b).

Eighty-eight percent of all the sampled sea trout ( $n = 236$ ) were of anadromous maternal origin (Figure 2a) and 12% were of freshwater resident maternal origin (Figure 2b). The latter had a mean total length ( $\pm$ S.D.) of 502 ( $\pm$ 108) mm and a female to male ratio of 17:4 (six specimens were juveniles and sex was unrecorded in one



**FIGURE 1** Study area and approximate sampling locations of anadromous brown trout, *Salmo trutta* (red dots), distributed over ICES subdivisions (those relevant to the present study are marked in bold). Sample sizes in each subdivision are shown in Table 1

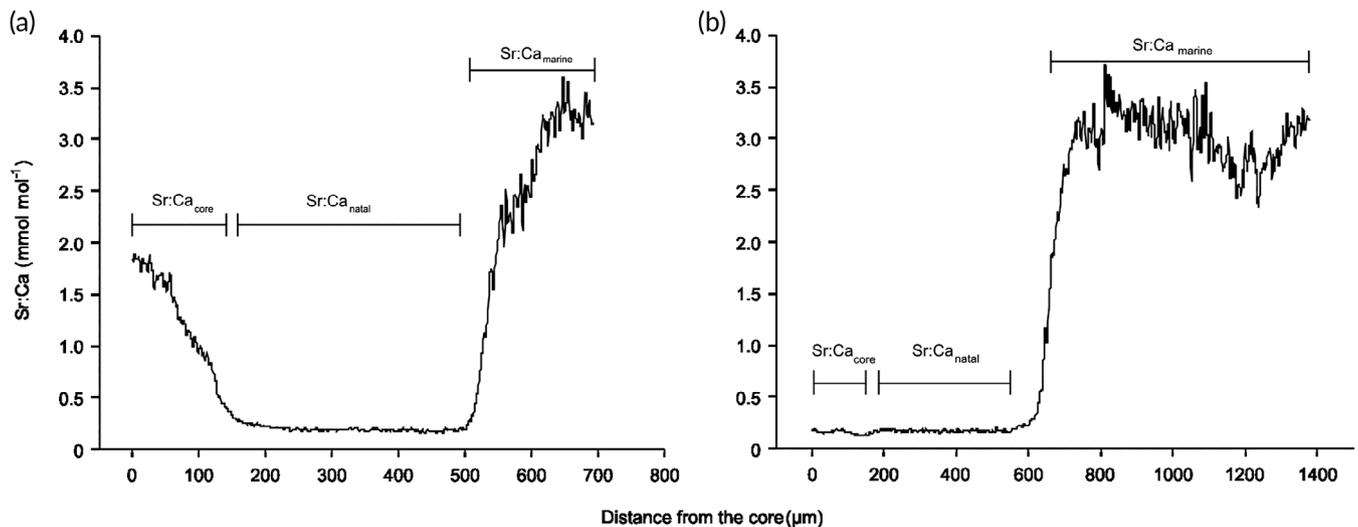
specimen). There were also some proportional differences among subdivisions, with half as many resident maternal origin sea trout sampled in the Gulf of Riga compared to the Gulf of Finland (Table 1). Strong dominance of anadromous maternal origin sea trout is of no surprise as Estonian sea trout populations in general are currently in relatively good condition, especially when compared to other Baltic Sea regions (ICES, 2020). However, to our knowledge nothing was known about the relative contribution of resident female parents to the migratory contingent in the entire brown trout native and introduced range.

Previous studies with brown trout have quantified the relative reproductive contributions of each life history strategy in the pre-migratory juvenile stages in lotic spawning and nursery areas. For example, in an English chalk stream Goodwin *et al.* (2016) demonstrated an overwhelming contribution to fry production from a small number of anadromous parents, despite the numerical dominance of resident adults in the spawning ground. In a study conducted in 24 Estonian and Finnish sea trout spawning streams progeny of anadromous maternal parents were the sole occupants in most of the study sites, but sites with presence or even dominance of

**TABLE 1** Biological characteristics of wild anadromous brown trout, *Salmo trutta*, sampled from different ICES subdivisions in the Estonian coastal sea

ICES subdivision	Assessment area	n	TL ± S.D.	Sex ratio (F:M)	% RMO	% AMO
32	Gulf of Finland	185	542 ± 90	116:33	12	88
29	Main Basin	10	556 ± 56	8:1	10	90
28.1	Gulf of Riga	18	511 ± 130	7:4	6	94
28.2	Main Basin	23	529 ± 64	17:5	9	91
	Total	236	539 ± 89	148:43	12	88

Note: TL ± S.D., total length ± standard deviation (mm); F:M, female to male sex ratio (specimens not included to the ratio were juveniles or with unrecorded sex); % RMO, proportion of anadromous brown trout with resident maternal origin; % AMO, proportion of anadromous brown trout with anadromous maternal origin.

**FIGURE 2** Representative otolith Sr:Ca profiles of wild anadromous brown trout, *Salmo trutta*, with (a) anadromous and (b) resident maternal origin. Sr:Ca<sub>core</sub>, maternally influenced region (*sensu* Kalish, 1990); Sr:Ca<sub>natal</sub>, natal freshwater habitat; Sr:Ca<sub>marine</sub>, brackish water habitat

progeny of resident maternal parents also existed (Rohtla *et al.*, 2017). These results, although useful in quantifying the initial reproductive contribution of resident and anadromous parents, do not provide information about the life history strategy undertaken by juvenile fish in the future. While there seems to be a tendency to track the parental life history in both anadromous and resident brown trout (Dębowski & Dobosz, 2016; Jonsson, 1982), the latter has only been quantified in unidirectionally land-locked populations, where anadromous phenotypes are not selected for owing to migration obstacles blocking the spawning migration to natal areas. For conservation and management of fully sympatric and semisympatric (unidirectionally land-locked) populations, it is important to know how many juveniles proportionally from each parental life history will descend to the sea (and contribute to coastal commercial and recreational fisheries) and how many will stay in fresh water (and contribute to freshwater recreational fisheries). Such information will improve our knowledge of population dynamics and recruitment processes, and will ultimately improve the stakeholder decision-making process.

Our results demonstrate the importance of the resident brown trout contingent in supporting sea trout stocks and

emphasise the need for incorporating this new information in conservation and management plans. Working towards a healthy resident contingent will help brown trout populations in general to hedge against variable environmental conditions and provide a low but stable output of migratory individuals even if sea trout spawners are less abundant or have no access to the spawning grounds.

The otolith microchemistry method used in the present study cannot be used to determine the paternal (*i.e.*, anadromous and resident male) contribution, and therefore some caution is warranted in drawing wider conclusions. However, the maternal contribution to reproduction is most often the limiting factor for population persistence, and therefore more vital for conservation and management. It has also been previously demonstrated that a small number of anadromous females can drive reproduction in brown trout populations (Goodwin *et al.*, 2016). Whether the sea trout with resident maternal origin identified in the present study originated from fully sympatric or semisympatric (unidirectionally land-locked) populations is currently unknown and warrants future study. Although we have quantified the contribution of freshwater resident origin maternal parents to

mixed-stock populations in the sea, the realized reproductive contribution of these specimen is also yet to be studied.

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## CONTRIBUTIONS

M.R. and M.K. conceived the presented study. M.R., L.M., I.T., R.S., M.K. and M.V. carried out the fieldwork. L.M. carried out otolith dissection and preparation, and data processing. L.M. and P.P. carried out the otolith analyses. M.R. drafted the first version of the manuscript. All authors discussed the results and contributed to the final manuscript.

## ETHICAL STATEMENT

The care and use of experimental animals complied with Estonian animal welfare laws, guidelines and policies as approved by the Ministry of Rural Affairs.

## ORCID

Mehis Rohtla  <https://orcid.org/0000-0002-7587-5552>

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