Migratory behavior and maternal origin of anadromous brown trout in the Baltic Sea

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ABSTRACT: In the Baltic Sea, brown trout have been shown to make extensive use of the marine ecosystem; however, little is known regarding their movements between freshwater and marine environments or the interactions between individuals at different life history stages within a population. First, we analyzed the otolith structure and chemistry of hatchery origin (n = 26) anadromous brown trout with known life history and maternal origin to evaluate the efficacy of otolith microchemistry to distinguish between freshwater habitat in northern Sweden and marine rearing in the northern Baltic Sea. We then described the maternal origin and migration patterns of wild anadromous brown trout (n = 59) originating from the Ume and Vindel River catchment in Northern Sweden. Otolith microchemistry revealed that the majority (73%) of fish made 3 or more (up to 5) migrations to the marine environment prior to capture, presumably to feed. We observed a high degree of life history diversity, where trout first migrated to sea from age-1 to age-4 and either migrated back to freshwater once each year (presumably to spawn) or spent more than 1 yr in the marine environment before returning to freshwater. While 42% of the wild anadromous trout were judged to be the progeny of a resident mother, sex ratio, age, and inter-habitat migrations were similar for resident and anadromous progeny, highlighting the role of resident life histories in producing anadromous adults. Results reported here provide managers with new information to support the protection and enhancement of brown trout populations in places where they have declined.

KEY WORDS: Brown trout · Otolith microchemistry · Life history diversity · Anadromy

1. INTRODUCTION

Anadromous salmonids are among the most threatened groups of fishes in the world, and there is a great need to better understand their behavior and ecology to mitigate the impact of anthropogenic activities and refine management and recovery strategies. In many rivers of the Baltic Sea, anadromous brown trout *Salmo trutta* have experienced a decline in abundance; this pattern has been particularly evident in Northern rivers draining into the Gulf of Bothnia (ICES 1994, 2006, Lundqvist et al. 2006,

Degerman et al. 2015, HELCOM 2018, Magnusson et al. 2020). Overfishing and habitat degradation are considered to be the main causes responsible for population decline, with special emphasis placed on reduced access to freshwater habitat as a result of hydropower operations (Pedersen 2009, Degerman et al. 2015). Reduced connectivity between freshwater and marine habitats is a cause for concern for all anadromous fish because they rely on both environments to complete their lifecycle. It is especially concerning for anadromous brown trout, given their reliance on a variety of life histories and complex

migratory patterns to maximize resilience within the dynamic environments that they occupy (Lobón-Cerviá & Sanz 2017, Arostegui & Quinn 2019, Jonsson et al. 2019, Duval et al. 2021). Given that increased life history diversity adds to the resilience and stability of salmonid populations (Schindler et al. 2010), it is important that movement patterns are understood by managers and conservation biologists.

Brown trout have the potential to exhibit a range of life history patterns after entering the marine environment (Thorstad 2016, Jonsson et al. 2019). For instance, anadromous brown trout have been shown to visit neighboring rivers as both juveniles (Taal et al. 2018) and adults (Degerman et al. 2012), spend winter months in freshwater, estuarine, or marine environments (Rikardsen et al. 2006, Etheridge et al. 2008, Jensen & Rikardsen 2008, Jensen & Rikardsen 2012, Rohtla et al. 2017), and produce both resident and anadromous offspring (Goodwin et al. 2016). However, descriptions of the relative rates of differing migratory patterns are lacking, especially while accounting for maternal origin (resident vs. anadromous). One specific area of uncertainty is the location where anadromous brown trout spend the winter months. The majority of descriptions of the anadromous brown trout lifecycle describe a fall migration to freshwater for spawning followed by a period of extended freshwater residency prior to entering marine waters again in the spring (Jonsson 1985, Jonsson & Jonsson 2011). Although this pattern has been demonstrated through high-resolution tagging studies (Birnie-Gauvin et al. 2021), alternative patterns of extended winter marine residence have been observed at the northern extent of the brown trout distribution (Sømme 1941, Jonsson & Jonsson 2002, Rikardsen et al. 2006), including immediate return to the marine environment following spawning and overwintering in marine waters. In the Baltic Sea, the behavior of trout during the winter months remains an important data gap, but the use of natal and neighboring rivers as well as overwintering in marine waters has been observed (Limburg et al. 2001, Klemetsen et al. 2003, Degerman et al. 2012). By clarifying this and other fine-scale patterns of migration, fishery managers may be better equipped to monitor changes in particular aspects of the life history of brown trout and work to restore life histories that may be at risk, in an effort to meet management objectives and ensure the long-term persistence of native populations.

The majority of what is known regarding movement patterns of brown trout in the marine environ-ment comes from tagging studies whereby individual fish are captured, tagged, and either recaptured later in life or detected through stationary or mobile equipment (e.g. radio and acoustic telemetry). Though these tools have led to significant advances, they are often cost-prohibitive, result in a small sample size, and provide information for only the period of time during which fish were tagged and tracked. One alternative to physical tags to track movement patterns is the analysis of mineralized structures such as otoliths. Elemental analysis of otoliths is a valuable tool for reconstructing movements of anadromous fish between freshwater and marine waters (Secor et al. 1992, Leppi et al. 2022). Strontium (Sr) is most often used to differentiate movements between fresh and marine waters because its concentration generally varies between the 2 environments. (Kalish 1989, Zimmerman 2005, Miller et al. 2010, Miller 2011). Many species form otolith structures such as daily increments and winter annuli, and studies often combine patterns in otolith Sr with otolith structure to estimate the duration and timing of anadromous migrations (Volk et al. 2010, Tomaro et al. 2012). Because variation in Sr within the otolith primordia is related to the amount of maternal Sr supplied to the egg, Sr may also be used to determine maternal origin (Kalish 1989, Volk et al. 2010). In the Baltic Sea, Limburg et al. (2001), and more recently Rohtla et al. (2017), demonstrated the efficacy of otolith microchemistry to distinguish between progeny of resident vs. anadromous brown trout originating from Finnish and Estonian rivers and showed that it is not uncommon for resident brown trout to produce anadromous offspring. However, questions remain regarding the maternal origin of anadromous brown trout from other areas of the Baltic Sea and, specifically, the rate at which resident life histories contribute to the production of the anadromous forms.

In this study, we analyzed the chemistry and structure of otoliths to understand the life history variation of brown trout in the Baltic Sea. Our objectives were to (1) evaluate the efficacy of otolith microchemistry to distinguish between freshwater and brackish marine habitat use in the northern Baltic Sea, (2) describe the migration history of wild adult anadromous brown trout throughout their life through paired analysis of otolith chemistry and structure, and (3) use otolith chemistry at the primordia to determine the maternal origin (anadromous or resident) of wild anadromous adults and explore how maternal origin may affect life history patterns of the offspring.

2. MATERIALS AND METHODS

2.1. Study area

The Ume and Vindel rivers originate in the Scandinavian mountains on the border between Norway and Sweden and flow south-easterly for approximately 500 km, where they join 42 km upstream from the outlet in the Bothnian Bay at 63° 50′ N, 20° 05′ E (Fig. 1). The Bothnian Bay is a shallow part of the Baltic Sea (average depth: 55 m) with low salinity (3–5 ppm). The Ume River branch is affected by multiple dams that restrict fish passage. However, the lower-most dam, downstream of the confluence with the Vindel River, has a fish passage that annually allows upstream movement of thousands of wild adult Atlantic salmon *Salmo salar* and hundreds of anadromous brown trout that migrate up the unregulated Vindel River branch. The Vindel River catchment comprises 12 654 km² and is characterized by large seasonal variations in water flow, with high flows in May–June (ca. 1000 m³ s⁻¹) because of snowmelt and the lowest flows in March–April (ca. 40 m³ s⁻¹) right before the spring flood.

The spawning of brown trout commonly occurs in tributaries over a 2 wk period starting in mid-October. In addition to trout and salmon, the local composition of fish species is dominated by European grayling *Thymallus thymallus*, northern pike *Esox lucius*, Eurasian perch *Perca fluviatilis*, Eurasian minnow *Phoxinus phoxinus*, roach *Rutilus rutilus*, and burbot *Lota lota* as well as other species in low abundance.

A hatchery situated in connection with the lowermost dam annually releases 20 000 adipose-clipped 2 yr old brown trout smolts as mitigation for lost natural production due to the dam. Broodstock for these hatchery-produced brown trout are upstream-migrating, naturally produced (adipose fin intact) adults that are captured at the dam.

2.2. Sample collection

A total of 59 wild adult anadromous brown trout (mean ± SD total length [TL]: 60.71 ± 6.17 cm) and 26 hatchery-reared anadromous brown trout (63.36 ± 5.11 cm) were sampled in the lower Ume River in
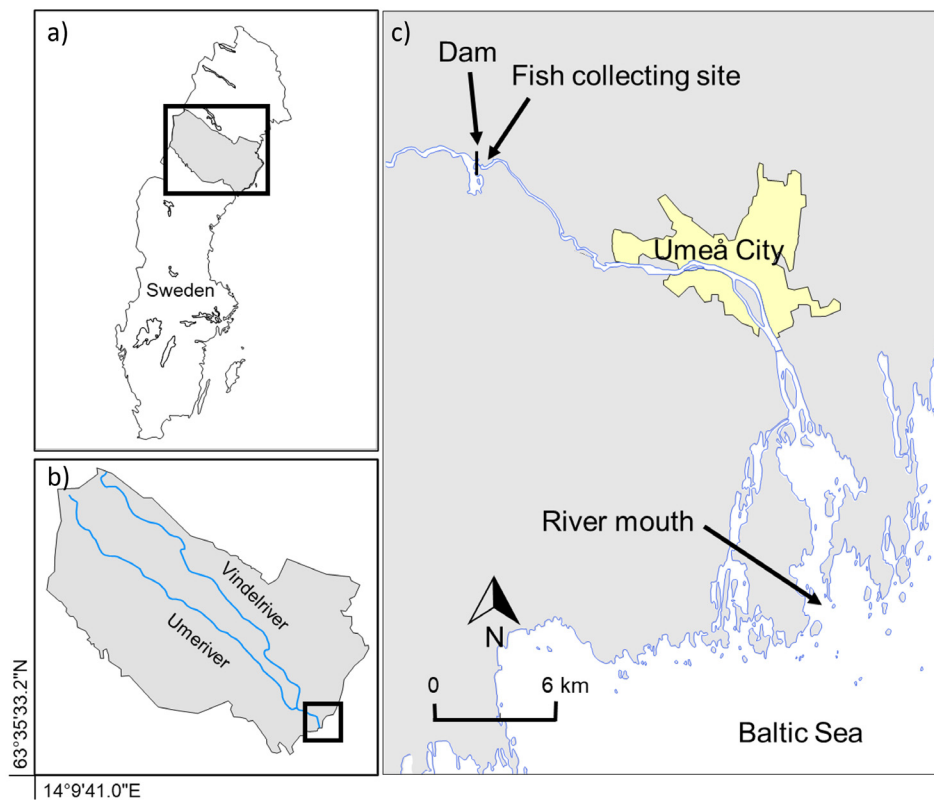

Fig. 1. (a,b) Study area in the Ume/Vindel River catchment, a tributary of the Baltic Sea in Northern Sweden, and (c) enlarged area highlighting study sites

northern Sweden (Fig. 1) at river kilometer 31 and at the mouth in early October of 2018 and 2019. Trout smolts released from the hatchery in the river, commonly at 2 yr of age, have their adipose fin removed; thus, we could easily differentiate between hatchery and wild returning adults. Sampling was conducted using gillnets immediately below the dam near the entrance to the upstream fish passage and using fyke nets further downstream at the mouth. Anadromous hatchery-origin fish are the progeny of anadromous mothers and were collected to provide validation for the otolith chemistry approach that we used to estimate maternal origin and migratory history of wild brown trout. As the hatchery uses water from the river, wild and hatchery-produced trout were exposed to the same water during their egg, fry, parr, and smolt stages.

2.3. Otolith preparation and microchemical analysis

One otolith per fish was mounted on a glass slide with thermoplastic resin (Crystalbond[TM] 509). Sagittal sections were prepared by grinding otoliths first in the distal (to provide a flat surface) and then proximal planes to expose the primordia while maintaining the otolith dorsal edge (Fig. 2), using a Buehler Meta Serv 250 with successive grits of sanding discs
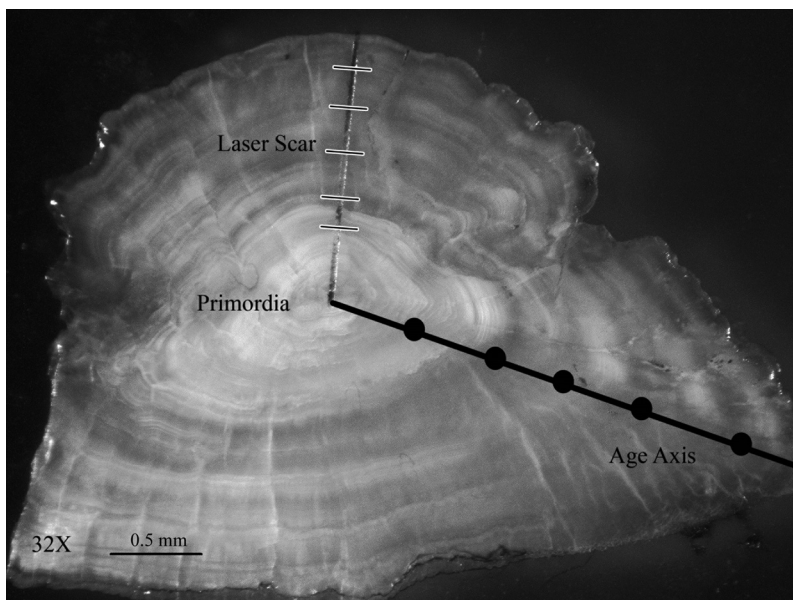

Fig. 2. Wild adult brown trout thin otolith section showing the age axis (thick black line), otolith annuli (black dots), laser path from the primordia to the dorsal edge, and corresponding annuli measurements (black line with white outline)

(Buehler[TM] P800, P1200) and then polished using an aluminum oxide slurry (Buehler[TM] 1 µm).

To determine maternal origin and migrations between freshwater and marine environments, we measured otolith Sr, Barium (Ba), and Calcium (Ca) using a Thermo X series II inductively coupled plasma mass spectrometer coupled with a Photon Machines G2 193 nm excimer laser at the Keck Collaboratory for Plasma Mass Spectrometry at Oregon State University. Laser ablation scans were completed from approximately 100 µm ventral of the otolith primordia (hereafter otolith core) to the dorsal edge at the widest point (Fig. 2). The laser was set at a pulse rate of 8 Hz traveling across the sample at $5 \, \mu m \, s^{-1}$ with a spot size of 30 µm. Normalized ion ratios to Ca were converted to elemental concentration using a glass standard from the National Institute of Standards and Technology (NIST 610), converted to molar ratios, and smoothed (10 point moving average) for analysis.

2.4. Migratory history

To describe the life history of adult anadromous brown trout, we combined otolith structure analysis with patterns of otolith chemistry. We used visual interpretation of otolith Sr:Ca and Ba:Ca ratio patterns (inflections) with mean values for distinct regions of each otolith scan in order to identify freshwater and marine migrations. Laboratory and field studies on salmonid species indicate that the otolith Sr:Ca ratio for fish residing in brackish and marine waters (>5 ppt) is consistently $>1.5 \, mmol \, mol^{-1}$ (Zimmerman 2005, Miller 2011, Rohtla et al. 2020). In addition, the otolith Ba:Ca ratio during marine residence is consistently below $0.005 \, mmol \, mol^{-1}$ (Miller et al. 2010). Therefore, we determined that a fish resided in marine waters when the otolith Sr:Ca ratio was $>1.5 \, mmol \, mol^{-1}$ and otolith Ba:Ca ratio was $<0.005 \, mmol \, mol^{-1}$ (Claiborne et al. 2020). When these conditions were not met, fish were presumed to reside in freshwater. Using these criteria, we estimated that 100% (26 out of 26) of known anadromous hatchery fish had made at least one migration to marine waters before capture, corroborating that our approach was successful in

identifying at least the initial movement between freshwater and brackish/marine waters of the northern Baltic Sea.

After identifying freshwater and marine migrations, a digital image of each otolith thin section was captured using a Leica M80 dissecting scope and Leica DC450 camera (32× magnification). Two readers independently aged each otolith by counting the total number of annuli for each otolith thin section and then the readers resolved any discrepancies in annulus counts together. Annuli were assumed to form once each year from February to May (Jonsson 1976), and the number of annuli was equal to fish age. For example, a fish with 5 otolith annuli was 5 yr old. Each annulus was measured along the laser scar to the outer edge using Image Pro Plus (Fig. 2). To describe the timing and length of anadromous migrations, we overlayed annulus measurements on patterns of Sr:Ca and Ba:Ca ratios for each fish. We were also interested in exploring the relationship between the age of anadromous brown trout and fish size. For this investigation, we used correlation analysis to compare variation in fork length at capture to the number of years an individual had been anadromous (age at capture minus age at first marine migration).

2.5. Maternal origin

We classified a fish as having either a resident or an anadromous mother based on the mean Sr:Ca ratio within the otolith core (i.e. across primordia to barium inflection) and mean natal freshwater Sr:Ca ratio immediately after the otolith core to its first marine migration (Berejikian et al. 2013, Claiborne et al. 2020). We classified an individual as having an anadromous mother when an individual's core Sr:Ca ratio was greater than that individual's mean natal freshwater Sr:Ca ratio (see Fig. 3) by at least 2 standard deviations of its mean natal Sr:Ca ratio (Berejikian et al. 2013, Rohtla et al. 2017, 2020). If those conditions were not met, then we classified the fish as having a resident mother. We expected some Swedish river systems to have high freshwater Sr (Rohtla et al. 2017), which could result in the misclassification of some progeny. To evaluate the efficacy of our maternal origin assignments, we analyzed otolith cores and natal freshwater Sr:Ca ratios from n = 26 hatchery-origin individuals returning in 2018 that are known progeny of anadromous mothers. For all statistical analyses, we used R statistical software (v.4.1.2). We also compared median otolith core and natal freshwater Sr:Ca ratios for wild and hatchery brown trout using Wilcoxon rank sum tests corrected for multiple comparisons (Benjamini-Hochberg adjustment). A chi-squared test was used to test for differences in the maternal origin between fish with different ages at outmigration, age at capture, the number of marine migrations, life history, and sex. Yates' continuity correction was used in chi-squared tests where the degrees of freedom was 1 (i.e. sex, life history).

3. RESULTS

3.1. Migratory history

All wild adult brown trout (59 out of 59) captured at the river mouth and below the dam (Fig. 1) showed otolith Sr:Ca and Ba:Ca ratios indicative of anadromy. We observed that fish captured below the dam in October showed values of Sr:Ca and Ba:Ca ratios at the otolith edge consistent with recent freshwater residence (Fig. 3). Conversely, all adults (8 out of 8) captured in July at the river mouth had marine values of Sr:Ca and Ba:Ca ratios at the otolith edge (data not shown).

Overall, age at first outmigration ranged from 1 to 4 yr, and 58 and 34 % of fish outmigrated at 2 and 3 yr old, respectively. Age at capture of wild anadromous brown trout ranged from 3 to 6 yr old, with the majority (83 %) of fish being either 4 or 5 yr old. Length at capture was positively related to the number of years an individual had been in the sea (Pearson's correlation test r = 0.59, p < 0.001; Fig. 4). The number of annual migrations between freshwater and marine waters before capture ranged from 1 to 5 for adult brown trout. We observed that 73 % of individuals made 3 or more annual migrations between marine and freshwater habitats and only 13 % had made a single migration before capture.

Plots overlaying otolith annuli and otolith chemistry revealed that wild brown trout exhibited diversity in life history strategies. To compare age and maternal origin of these 2 behavioral strategies, we categorized trout as type 1 whereby after an initial marine migration, fish exhibited seasonal migrations between fresh and marine waters, returning to freshwater once each year. We observed that 79 % of wild anadromous brown trout exhibited the type 1 life history and otolith annuli were formed most closely to periods of freshwater residence (Fig. 3A). We defined life history type 2 as fish exhibiting periods of extended marine residence. We observed that 21 % of
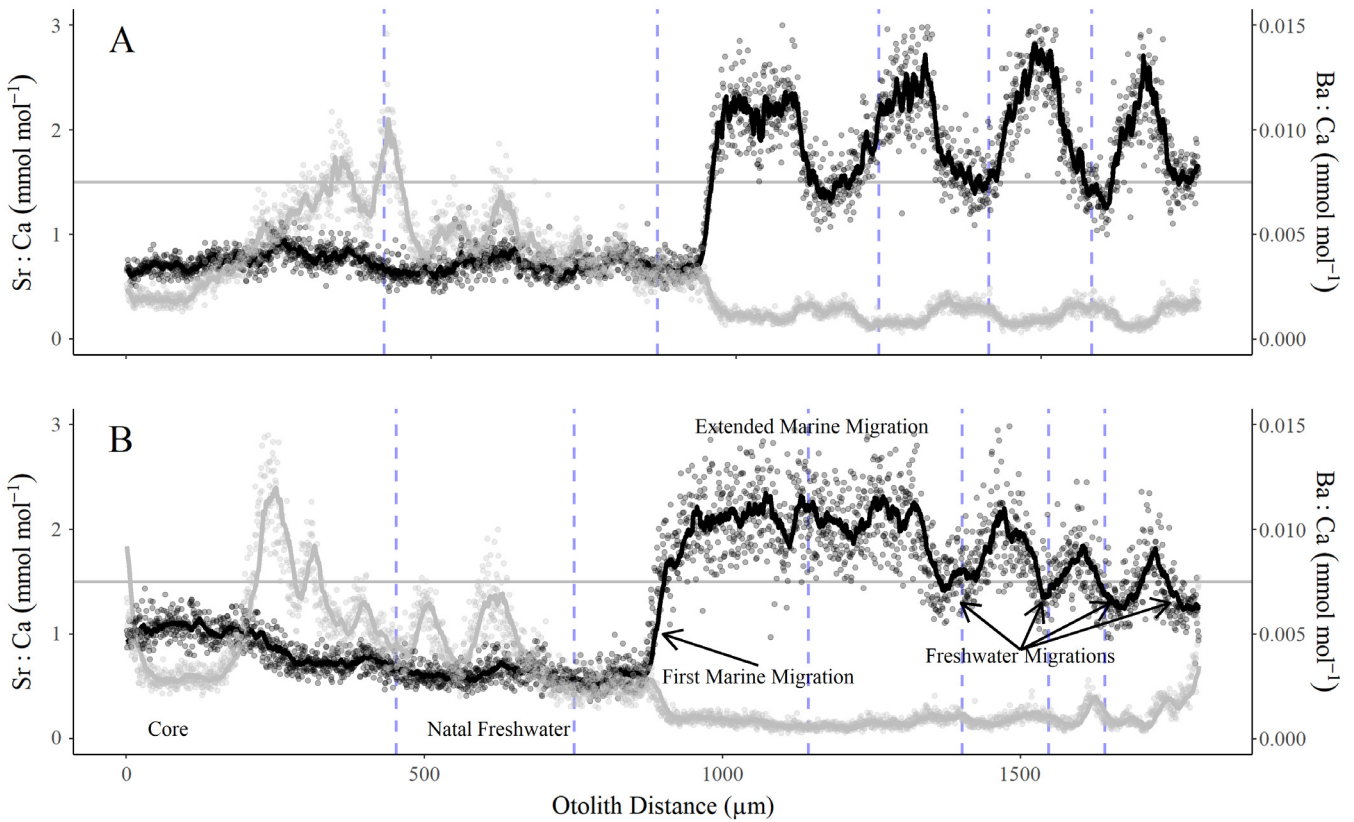
Fig. 3. Otolith chemistry transects (black line: Sr:Ca ratio; grey line: Ba:Ca ratio) from the core to the dorsal edge with annuli overlayed (vertical dotted lines) for 2 wild adult brown trout classified as life history (A) type 1 (makes seasonal migrations between freshwater and marine environments once each year) and (B) type 2 (extended period of marine residence occurring immediately after first marine migration followed by seasonal migrations between freshwater and marine environments once each year). Horizontal gray line: 1.5 Sr:Ca ratio (mmol mol^{-1}) threshold for reference
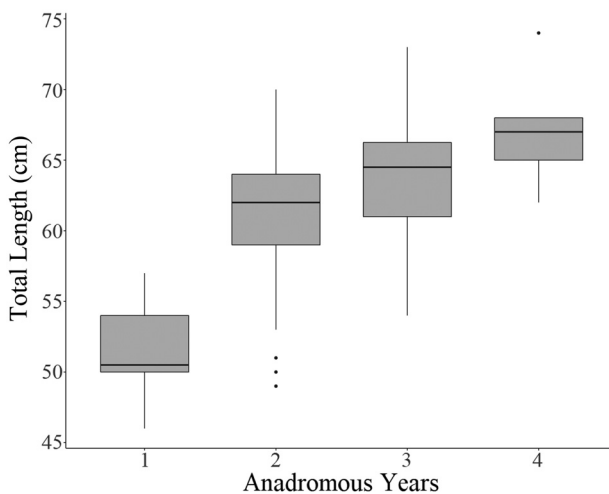

Fig. 4. Length at capture by the number of years an individual brown trout has been anadromous (age at capture minus age at first marine migration), determined from otolith chemistry and age analysis. Line: median; box: 1st and 3rd quartiles; whiskers: values outside those quartiles; dots: outliers

adults exhibited the type 2 life history whereby trout may spend more than 1 yr in the marine environment prior to migrating back to freshwater (Fig. 3B). For most (75%) type 2 trout, an extended period of marine residence occurred immediately after their first marine migration (fish formed one annuli in the marine environment) followed by freshwater migrations once each year (Fig. 3B). The remaining 25% of type 2 fish formed 2 annuli in marine waters and had not migrated back to freshwater before capture.

3.2. Maternal origin

We correctly classified the maternal origin of 92% of hatchery-origin fish with known anadromous mothers. Using the same criteria, we found that 58% of wild adult brown trout had an anadromous mother while 42% were the progeny of a resident mother. The median otolith core Sr:Ca ratio was greater than

the natal freshwater Sr:Ca ratio for hatchery fish and wild brown trout classified as anadromous progeny (Wilcoxon rank sum test, p < 0.001; Fig. 5). However, median otolith core and natal freshwater Sr:Ca ratio was not different for wild brown trout classified as resident progeny (Wilcoxon rank sum test, p = 0.251; Fig. 5). Median otolith natal freshwater Sr:Ca ratio was significantly less (Wilcoxon rank sum test, p < 0.001) for wild brown trout classified as anadromous compared to that of known anadromous progeny (hatchery fish) or wild brown trout classified as resident progeny (Fig. 5).

Sex ratio was similar for resident and anadromous progeny and, overall, 65% of wild adults were female while 35% were male (chi-squared test, p = 0.737). Age at outmigration, age at capture, and the number of marine migrations were similar for resident and anadromous progeny (chi-squared test, p > 0.115; Fig. 6A–C). Similarly, the proportion of life history type 1 and type 2 was similar among progeny of anadromous and resident mothers (chi-squared test, p = 0.523; Fig. 6D).

4. DISCUSSION

We examined the age structure and chemistry of otoliths of brown trout in the Baltic Sea to clarify life history diversity and migration patterns. Overall, age at first outmigration, age at capture, and size at age corroborated previous work with initial outmigration
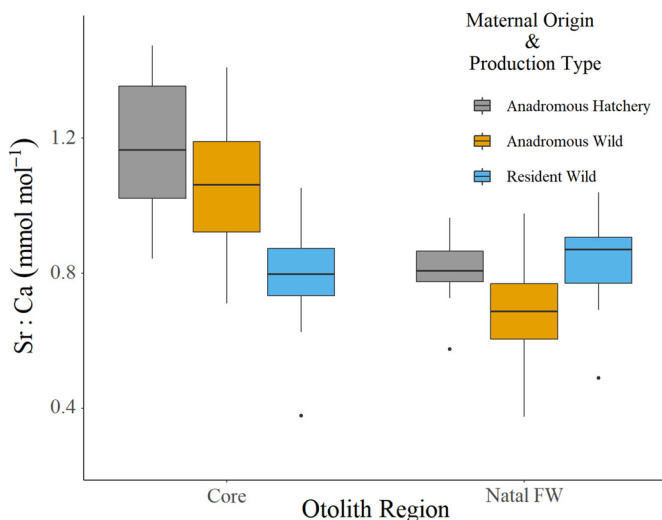

Fig. 5. Ratio of otolith strontium to calcium (Sr:Ca) in the core and natal freshwater region (natal FW) of brown trout by maternal origin (anadromous vs. resident) and production type (hatchery vs. wild). Line: median; box: 1st and 3rd quartiles; whiskers: values outside those quartiles; dots: outliers

primarily occurring at age 2 or 3 yr, with a maximum observed age of 4 yr. However, analysis of otolith microchemistry, in combination with estimates of age for adult trout of hatchery and natural origin, revealed new insights. We demonstrated that trout in the Baltic Sea are the progeny of both resident and anadromous mothers and may migrate back to fresh waters each year or stay in marine waters all year, regardless of maternal life history. These results provide important new information on the behavior of brown trout in the Baltic Sea and highlight for managers the array of life histories expressed by anadromous brown trout.

Perhaps the most important finding in this study is the relatively high proportion of anadromous trout that were the progeny of resident females and their similarity in life history expression with those that originated from anadromous mothers. Previous studies of brown trout using genetics, physical tags, and otolith microchemistry have highlighted the close relationship between anadromous and resident life histories and the potential for resident individuals to produce anadromous offspring (Hindar 1991, Jonsson & Jonsson 2009, Duval et al. 2021). However, the proportion of anadromous populations that are the offspring of resident mothers has generally been found to be low. For instance, Rohtla et al. (2020) reported only 12% of wild anadromous brown trout captured in brackish marine waters near the Estonian coast had otolith chemistry indicative of a resident mother. This contrasts with the current study, in which 42% of adult anadromous trout were the product of resident mothers. This is especially noteworthy given that the fitness and rates of survival of anadromous trout produced by resident parents may be low relative to those produced by the anadromous form based on reports in the literature (Goodwin et al. 2016, Mottola et al. 2020, Duval et al. 2021), and the current study investigated individuals that had survived to adulthood and did not account for those produced by males, which are likely an important source of production. The high rates of contribution from resident mothers that we observed relative to previous studies could be the result of numerous factors, including barriers to fish passage associated with dams for anadromous individuals, a high abundance of resident brown trout in the Vindel watershed, or habitat limitations favoring migration to sea. Regardless, factors driving the rate at which resident parents (mothers and fathers) produce anadromous offspring and the relative survival of the 2 groups is an area ripe for future research. The similarity in age, size, and migratory patterns between trout with different
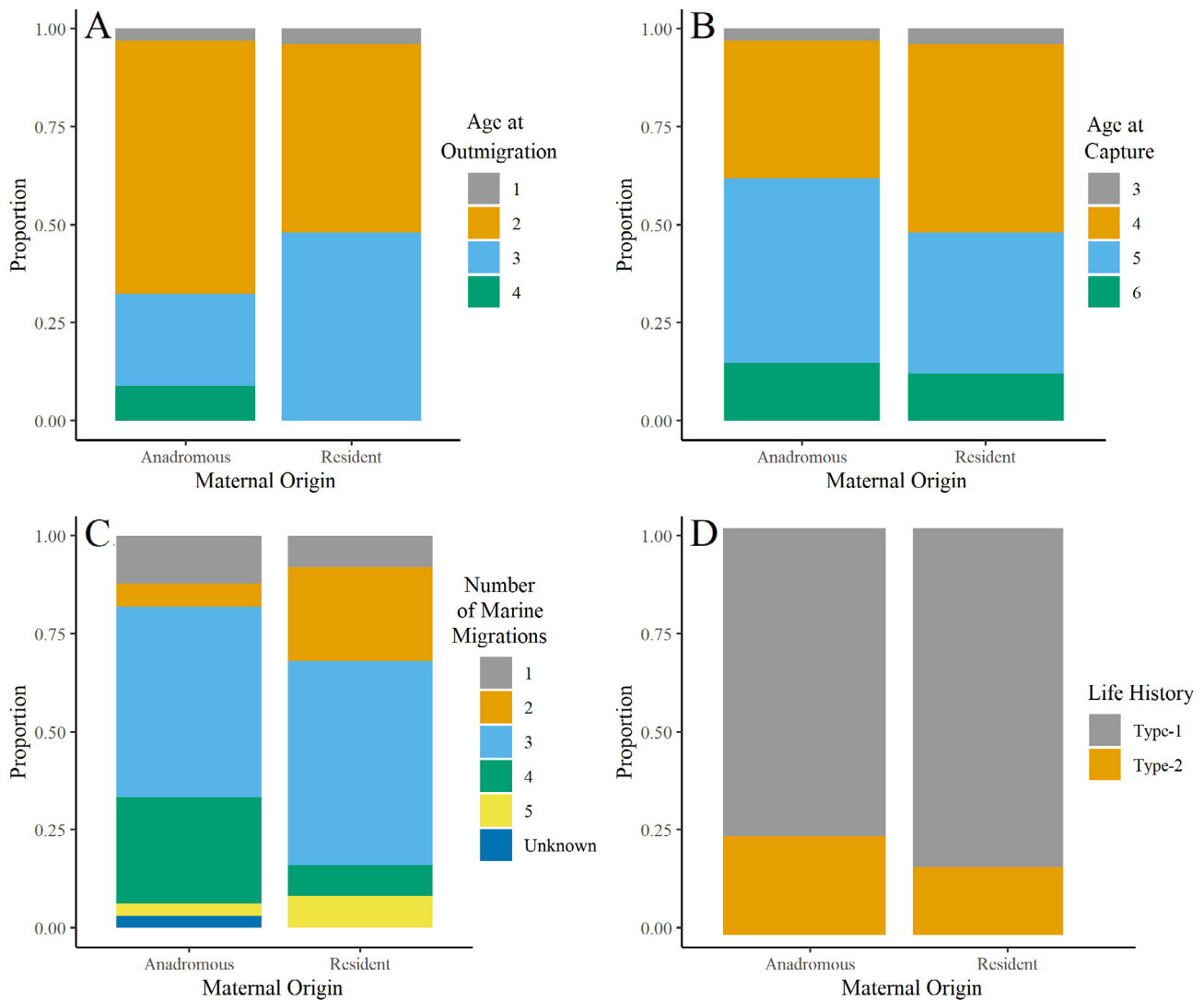
Fig. 6. Proportion of age at outmigration, age at capture, number of annual marine migrations, and life history types (1 and 2) by maternal origin for wild anadromous brown trout. Life history type 1 is defined as making seasonal migrations between freshwater and marine environments once each year; life history type 2 is defined as fish exhibiting an extended period of marine residence occurring immediately after first marine migration followed by seasonal migrations between freshwater and marine environments once each year

maternal origins (resident vs. anadromous) further highlights the importance of freshwater resident parents in producing viable anadromous offspring. Together, these fine-scale patterns in behavior and life history provide fisheries managers with important biological parameters to consider when designing management objectives and recovery plans, particularly the contribution that residents make. For conservation of anadromous brown trout, the contribution of resident trout may constitute a valuable buffer to the detrimental effects of migration barriers and periods of low marine survival, as shown previously (Duval et al. 2021).

A subtle but important finding reported here was the difference in natal freshwater chemistry of those fish originating from wild resident mothers vs. those of wild anadromous mothers. This result suggests that the progeny of resident mothers likely came from a common source in the watershed or from locations with similar water chemistry that were different than the area(s) producing fish originating from wild anadromous mothers. This highlights potential natural variability in the watershed that favors anadromy vs. residency and potential fish passage challenges in the study area. For instance, areas that restrict upstream fish passage for anadromous spawners but al-

low for downstream passage of the progeny of residents could be sources of production of anadromous fish from resident mothers. In streams draining a fjord in Washington State, USA, Berejikian et al. (2013) documented stream flow and the presence of barriers as important determinants of maternal origin. Increased production of juvenile *Oncorhynchus mykiss* from resident parr was observed where mean annual stream flows were high and barriers were present that restricted upstream movement. The Ume and Vindel River catchments, where this study took place, is a tributary-rich system with numerous large, highly productive lakes and manmade and natural barriers that could restrict passage permanently or seasonally. Future studies analyzing water chemistry and the otolith chemistry of juvenile brown trout throughout the catchment could help to identify 'hotspots' of resident production to better understand the factors that stimulate this important component of the brown trout life history and perhaps identify places where anadromous adults are not contributing to the spawning population as a result of anadromous barriers.

Results from this study also provide important insights into the migratory patterns during the winter months in the Baltic Sea. Specifically, 21% of trout exhibited extended periods of marine residence (commonly upon their first marine migration), supporting previous work documenting overwintering in marine waters by anadromous trout. For instance, Jonsson & Jonsson (2002) observed that approximately two-thirds of adult fish tracked between 1976 and 1999 in Norway migrating downstream in the fall and winter months, suggesting an immediate return to marine waters following spawning. Furthermore, Rikardsen et al. (2006) documented rapid growth and intense feeding in the marine environment during winter months when anadromous trout were assumed to be occupying freshwater and starving. We detected a diverse use of the marine environment and classified anadromous trout into 2 life history types: one in which fish exhibited seasonal migrations between fresh and marine waters, returning to freshwater once each year, and those that showed at least one season of marine overwintering patterns. While effective at comparing 2 important differences in migratory pattern, this grouping likely masks numerous, fine-scale patterns of movement that were not detected, particularly in the marine environment, highlighting important limitations of otolith microchemistry in characterizing finer scale movements in brackish and marine habitats (Sturrock et al. 2012, Hüssy et al. 2021). Degerman et al. (2012) showed that most brown trout tagged in the Baltic Sea re-

mained within 150 km of their natal stream, utilizing neighboring rivers. This was consistent with the restricted migration patterns reported by Kallio-Nyberg et al. (2002) for fish released in the Gulf of Bothnia and the Gulf of Finland, which had a tendency to remain in coastal areas near release sites. However, both studies observed some migrations greater than 800 km from the release locations, including some individuals that left the Baltic Sea for the Atlantic Ocean. It is worth mentioning that both studies relied on hatchery fish and may not mirror patterns observed for wild fish investigated in the current study. With this information in mind, we would encourage studies designed to track fine-scale movements during the winter period to close an important information gap in the life history of brown trout.

The use of otolith chemistry to describe maternal origin and anadromous migrations for salmonids has become a regularly used tool, but the application of this tool on adult trout in the Baltic Sea has been limited. In this study, we used previously established methods of determining maternal origin that compare Sr:Ca ratios in the otolith core and natal freshwater regions (Berejikian et al. 2013, Rohtla et al. 2017, 2020) and found that this approach categorized hatchery fish with known anadromous mothers correctly 92% of the time. This suggests that our estimates of the proportion of wild anadromous and resident progeny are largely accurate but also indicates that a few wild fish may have been misclassified as resident when they are in fact the progeny of anadromous mothers. The efficacy of determining maternal origin is, in part, dependent on relatively low Sr in freshwater (Donohoe et al. 2008) and the length of freshwater residence before spawning (Volk et al. 2010). We suspect freshwater Sr in the Vindel basin did not impact our results significantly, as the natal freshwater otolith Sr:Ca ratios we observed were within the range shown for brown trout from rivers in Estonia and Finland (Rohtla et al. 2017) and well below marine values. However, we did observe lower Sr:Ca ratios on average in the otolith core and during marine migrations compared to values shown for brown trout in the central Baltic Sea (Rohtla et al. 2017, Taal et al. 2018, Rohtla et al. 2020). We suspect that a longer residence in freshwater prior to spawning and the relatively low salinities of the northern Baltic Sea experienced by mothers may have influenced the lower Sr:Ca ratio core values we observed for their progeny. The low salinities of the Baltic Sea relative to salinity values in the Atlantic Ocean experienced by anadromous trout in neighboring regions may have influenced patterns of migration and

maternal origin and represents an area for future research.

Our results highlight important aspects of the life history of brown trout in the Baltic Sea. We show the frequency at which resident life histories produce surviving anadromous trout and the frequency at which trout overwinter in the marine environment. These expressions of life history appear to be common and of considerable importance relative to the set of life histories expressed by brown trout. With new information presented here and the growing body of work describing the movement patterns of anadromous brown trout, fisheries managers are better equipped to support the protection and enhancement of brown trout populations in places where they have declined, like the Baltic Sea.

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