

Parr dispersal between streams *via* a marine environment: A novel mechanism behind straying for anadromous brown trout?

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Abstract

Otolith Sr:Ca profiles demonstrated that juvenile anadromous brown trout (ABT) *Salmo trutta* may descend to the brackish waters of the Baltic Sea from their natal streams as parr or fry and then migrate into non-natal streams before transforming into smolt. To our knowledge, no such published documentation exists for ABT. The ecological significance of this life-history strategy is presently not clear. However, stream shifting through the marine environment should to be considered with regard to stock management and the assessment and restoration of salmonid populations and their potential habitats.

KEYWORDS

life history, otolith microchemistry, parr migration, salmonids

1 | INTRODUCTION

Anadromous brown trout (ABT), *Salmo trutta*, display diverse habitat-use strategies as juveniles throughout the distribution area (e.g. Jonsson & Jonsson, 2011; Klements et al., 2003). Anadromous brown trout stay in the natal watershed usually for at least one to several years and descend to the sea in spring after parr–smolt transformation (e.g. Jonsson & Jonsson, 2011; Klements et al., 2003). However, seaward movements of ABT have also been documented at times of the year not associated with the spring parr–smolt transformation (e.g. Holmes, Hayes, Jiang, Quarterman, & Davey, 2014; Järvi et al., 1996; Jonsson & Jonsson, 2009; Limburg, Landergren, Westin, Elfman, & Kristiansson, 2001; Marine Institute 2014; Taal et al., 2014; Winter, Tummers, Aarestrup, Baktoft, & Lucas, 2016). Autumn descents of brown trout parr to the habitats where salinity is low enough for them to survive have been recorded in Irish (Marine Institute 2014), Norwegian (Jonsson & Jonsson, 2009), Baltic (Taal et al., 2014), New Zealand (Holmes et al., 2014), Great British and Danish (Winter et al., 2016) ABT populations. In the Baltic Sea, it has also been reported that fry and parr of ABT from small Gotland streams (with high number of spawners and decreasing water levels during spring and summer) move to sea soon after hatching in spring and early summer (e.g. Järvi et al., 1996; Landergren, 2004; Limburg et al., 2001). Those various seaward

movements of ABT parallel with various potamodromous movements of brown trout parr from tributaries (spawning and nursery grounds) into the main river or from inlet or outlet streams into freshwater lakes (reviewed in Jonsson & Jonsson, 2011). It is also known that immature juveniles of anadromous Dolly Varden *Salvelinus malma* may use the saline environment to colonise non-natal streams for wintering (e.g. Armstrong, 1974; Bond, Crane, Larson, & Quinn, 2014).

In the Baltic Sea, investigation on the origin of adult sea-caught trout (using individual otolith microchemistry profiles) from the Gotland area revealed that some individuals showed no evidence of freshwater history, thereby provoking a hypothesis that a proportion of this population may not depend on riverine spawning at all (Limburg et al., 2001). However, experiments by Landergren and Vallin (1998) demonstrated that successful development of brown trout is unlikely to occur at ambient salinity around Gotland (6–7‰). Thus, Landergren and Vallin (1998) concluded that the spawning grounds located at the stream outlets could, on account of the low salinity (<4‰), contribute to the recruitment. Still, eggs deposited in such areas always face the risk of being adversely influenced by storms (Landergren & Vallin, 1998).

Annual Estonian salmonid parr density surveys have detected the occurrence of brown trout parr in several years (Kesler, Taal, & Svirgsden, 2015) in a stream characterised by the absence (Järvekülg, 2001) of suitable spawning habitat (*sensu* Ottaway, Carling, Clarke,



FIGURE 1 Map of the study area. Asterisk = Ermespu Stream (coordinates of the river mouth = 58°25′8.3″N 22°6′39.4″E). All the other streams marked in the detailed part of the map are known to be ABT spawning streams (Kesler et al., 2015)

& Reader, 1981; Louhi, Mäki-Petäys, & Erkinaro, 2008; Jonsson & Jonsson, 2011). It has been observed that juvenile ABT (not transformed into smolt) can follow several alternative life histories in coastal areas of the Baltic Sea (e.g. Järvi et al., 1996; Landergren, 2004; Limburg et al., 2001; Taal et al., 2014). This study was undertaken to test whether ABT display stream shifting through the marine environment (SSME) before transformation into smolt as the brackish water of the Baltic Sea (6–7‰ and less) is not an unsurpassable barrier in terms of the physiological tolerance to salinity of early out-migrating ABT parr (Landergren, 2001; see also Limburg et al., 2001). Stream shifting through the marine environment among ABT has not to date been described.

2 | MATERIALS AND METHODS

The study area consisted of the Ermespu Stream which is situated on Saaremaa Island and drains into Tagalaht Bay (Järvekülg, 2001), Baltic Proper (Figure 1), where surface water salinity ranges between 5 and

7‰ (Martin, Torn, Kotta, & Orav-Kotta, 2003). The influence of the fresh water is very low as Tagalaht Bay receives marginal freshwater inflow from a few small streams (Järvekülg, 2001). Ermespu Stream is spring fed and 3.4 km long. It has a catchment area of 4.9 km², no tributaries and no suitable spawning habitat for brown trout (*sensu* Ottaway et al., 1981; Louhi et al., 2008; Jonsson & Jonsson, 2011), as the substrate consists entirely of fine sediment (Järvekülg, Kesler, Pihu, & Lauringson, 2012). The closest neighbouring trout spawning stream (i.e. River Pidula) discharges to the Baltic Sea 0.5 km eastwards from Ermespu stream (Figure 1) and has viable ABT stock (Kesler et al., 2015). To test whether SSME occurs, 20 ABT were electrofished in the Ermespu Stream on 27 September 2015. The fish were killed immediately after capture by cervical dislocation. In the laboratory, total length (TL, ±1 mm) of all caught fish was recorded, and sex was determined by visual examination of the gonad (e.g. Uren Webster & Santos, 2015). Parr status of the caught fish was confirmed by visual analysis of their parr markings and the absence of any signs of smoltification (Jonsson & Jonsson, 2011). Otolith strontium-to-calcium (Sr:Ca) ratios were quantified to test whether parr otoliths revealed patterns that

indicated SSME. We aimed only to determine whether SSME occurs, and not how frequently it may occur or the possible specific sources of the parr. Thus, the number of captured individuals was limited to reduce the impact of research-induced mortality upon the local population. According to Miller (2011), otolith Sr:Ca can readily be used to identify individual movements among distinct water masses as for juvenile Chinook salmon *Oncorhynchus tshawytscha*, changes in otolith composition were detected 2–3 days after a change in ambient water chemistry. Similar methodology has been used in recent studies to examine juvenile movement patterns in coho salmon *Oncorhynchus kisutch*, Chinook salmon (Shrimpton et al., 2014) and sockeye salmon *Oncorhynchus nerka* (Walsworth, Schindler, Griffiths, & Zimmerman, 2015).

Sagittal otoliths were removed, cleaned and stored dry in microtubes. For the chemical analysis, one randomly chosen otolith from each fish was glued sulcus side down onto a coverslip, which was then partly glued to a standard glass slide. All otoliths were ground-down manually using silicon carbide sandpaper until the core became visible and finally polished. Each prepared otolith thin-section was glued onto a standard glass slide and stored in a clean plastic bag for later analysis. Before the chemical analyses, all otolith thin-sections were ultrasonically cleaned for 15 min in ultrapure water and subsequently dried in a laminar flow hood. ^{43}Ca and ^{88}Sr were quantified using laser ablation inductively coupled plasma mass spectrometry (LA-ICPMS). An Agilent 8,800x ICPMS with a Cetac LSX213 laser was used. The laser was set to 10 Hz, with a 40 μm ablation spot size, and a scan speed of 5 $\mu\text{m}/\text{s}$. A continuous line scan was traced from the core to the dorsal edge. Helium was used as the carrier gas. A reference glass material (NIST 612) and calcium carbonate standard (MACS-3) were analysed before and after all 20 otoliths. Data were handled following the methods of Miller (2007) as described in Rohtla et al. (2014). The precision (%RSD) of quantifying ^{43}Ca and ^{88}Sr for the NIST 612 glass was 15%. Precisions for Sr:Ca ratios were 2%; otolith Sr:Ca values were corrected for this drift. The age of the sampled fish, including during the SSME (as determined by shifts in otolith elemental profiles), was determined by counting the otolith annuli. In the Baltic basin the Sr:Ca as a tracker of fish migration is known to have positive relationship between salinity, water Sr:Ca and otolith Sr:Ca (e.g. Engstedt, Koch-Schmidt, & Larsson, 2012; Rohtla et al., 2014, 2015; Svirgdsen et al., 2016). Thus, we expected that individuals who underwent SSME show initial lower Sr:Ca levels, followed by increase and subsequent decrease in Sr:Ca levels.

3 | RESULTS

The otoliths of all the caught individuals had Sr:Ca patterns that indicated SSME; however, these patterns were not uniform as different strategies were employed. All the sampled trout were the progeny of ABT, as evidenced by the high Sr:Ca values in their otolith cores (Figure 2a,b,c,d). Natal values (pre-SSME in Table 1) were significantly lower ($Z = 3.57$; $p = .0004$; $N = 17$ Wilcoxon matched pairs test) than measurements indicating residence in the Ermespu Stream (post-SSME in Table 1). Three individuals had a Sr:Ca profile with distinct

natal stream values, followed by a sudden increase, subsequent decrease, and stabilisation of Sr:Ca at levels dissimilar to the natal value (Figure 2a). This suggests emigration from the natal stream, a brief (<14 days) residency in brackish waters, and subsequent entry to a non-natal stream (i.e. Ermespu Stream). Two individuals had a moderate Sr:Ca peak just next to the maternally influenced region (ID14 and ID19 in Table 1), which was interpreted as emigration from the natal stream before the environmental chemical signal reached a plateau in the otolith (Figure 2c). Otolith Sr:Ca profile revealed that another sampled individual (ID 9 in Table 1) can be also classified as early out-migrating fry (together with ID14 and ID19) due to unstabilised natal freshwater value (Figure 2a). The rest of the sampled ABT parr did not possess a peak in Sr:Ca values that would indicate prolonged brackish water residency (ID1, ID3-ID8, ID10-13, ID15-17 in Table 1), but a clear or subtle shift in Sr:Ca freshwater values was evident (Figure 2b,d). This suggested parr emigration from their natal stream, a minimal (up to 2 days) residency in brackish waters, and then entry to a non-natal stream. Parr movement to a non-natal stream through the marine environment occurred during the period between early spring and late autumn, but mostly during mid-summer (Table 1). Age at dispersal varied from early stage fry to 4-summer old individuals (all older individuals were milt producing sneaker-males with a parr phenotype; Table 1). Otolith Sr:Ca values revealed that some parr may have shifted between tributaries within their natal watershed (ID1, ID4, ID6, ID12, ID17, ID18 in Table 1), before a subsequent shift to the Ermespu Stream *via* the marine environment.

4 | DISCUSSION

The collected otolith microchemical profiles demonstrated that as a life-history strategy of ABT, SSME occurred with both fry and 1- to 4-year-old parr caught from the Ermespu Stream. These shifts were not restricted to spring, which is the typical sea descent season for ABT (e.g. Jonsson & Jonsson, 2011). Similar life histories have been previously observed in coho salmon populations (e.g. Koski, 2009; Roni et al., 2012).

As the timing of SSME differed in parr of the same age, we suggest that the changes in the otolith chemistry were due to migrations between streams with distinctive water chemistry, and not because of alternating chemistry of the waters inhabited by sedentary parr or other potential factors that could influence otolith chemistry (e.g. diet, ontogeny, temperature). Alternating water chemistry would imply that parr of the same age from the Ermespu Stream should have displayed similar otolith chemistry; however, this was not the case in the present study. Otolith chemical profiles demonstrate clear stage-shifts (i.e. concentrations shift from one stable plateau to another stable plateau with significantly different values). Such temporally stable “plateau shifts” in otolith chemical profiles are possible if the fish has shifted from one chemically stable environment to another as minor changes in otolith composition could be detected 2–3 days after a change in water composition (Miller, 2011). Same logic also applies for other potential confounding factors (e.g. diet, temperature). It is also important

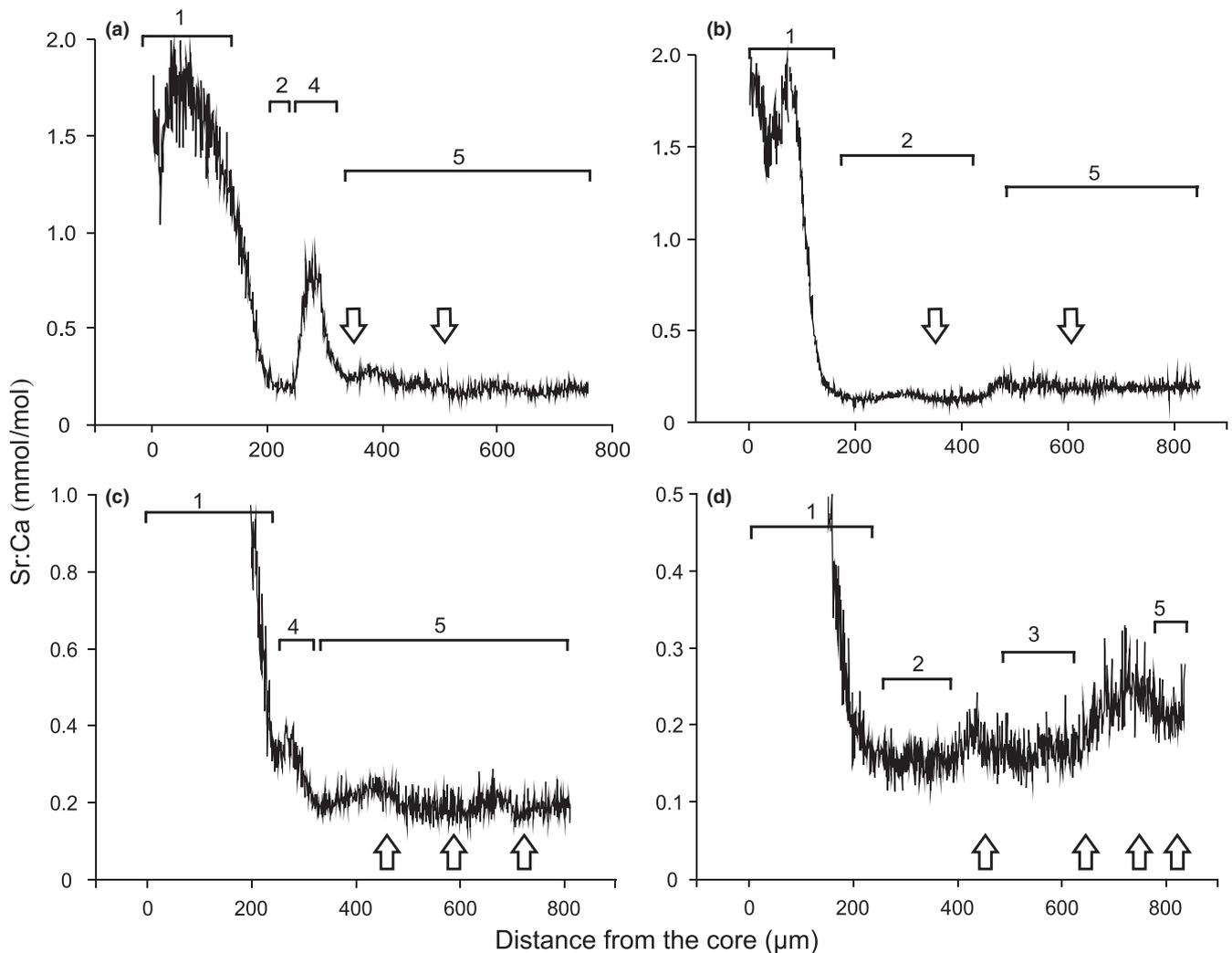


FIGURE 2 Representative otolith profiles (Sr:Ca) of brown trout from the Ermespu Stream: (a) parr (ID 9) with a clear Sr:Ca marine signal (note that pre-SSME natal freshwater Sr:Ca value is not stabilised); (b) parr (ID 15) with a clear shift in Sr:Ca values; (c) parr (ID 14) that descended/drifted to the sea immediately after yolk sac resorption or even during it and subsequently entered the Ermespu Stream; (d) parr (ID 1) that possibly migrated between tributaries within its natal watershed and subsequently migrated to the Ermespu Stream via the marine environment, as evidenced by increased Sr:Ca values. Numbered brackets represent distinct stages in the chemical profiles: (1) maternally influenced region (*sensu* Kalish, 1990), (2) natal freshwater habitat, (3) possible migration between tributaries in the natal watershed, (4) brackish water experience and (5) non-natal freshwater habitat (Ermespu Stream). The Sr:Ca freshwater threshold is <0.5 mmol/mol in the freshwaters of Estonia (Matetski, 2014). Note the different scales of Sr:Ca profiles. Arrows denote the annuli

that several brown trout (ID2, ID9, ID14, ID18, ID19, ID20 in Table 1) had a clear brackish water signal in their otolith chemical profiles and it had merely taken them longer to reach Ermespu Stream. Our hypothesis is also supported by Matetski (2014) who analysed 257 brown trout parr otoliths from 19 streams from different regions of Estonia. All the analysed otolith profiles were stable without such clear stage-shifts (Matetski, 2014). Moreover, Ermespu Stream is a small spring-fed stream with a total length of ca 3 km and has no tributaries. It is unlikely that spatial and/or temporal variability of water chemistry in such a marginal stream has this kind of effect on otolith chemical profiles. Altogether, this evidence coupled with the fact that there are no suitable spawning grounds in the Ermespu Stream suggests that all the sampled brown trout had hatched elsewhere and immigrated to the Ermespu Stream via the Baltic Sea. There are several streams

with viable ABT populations and spawning grounds in the vicinity of the Ermespu Stream (Kesler et al., 2015; Figure 1) that could be the sources of such immigration. To the best of our knowledge, this is the first empirical evidence of such a life-history pattern among ABT, that is immigration to non-natal streams via the marine environment.

Although two ABT individuals (ID14 and ID19 in Table 1) did not show natal freshwater values, the possibility that these fish may be offspring of brown trout spawning in the Baltic Sea (*sensu* Landergren & Vallin, 1998; Limburg et al., 2001) is unlikely in our case as ambient surface water salinity in Tagalaht Bay (5–7‰; Martin et al., 2003) is too high for egg survival (Landergren & Vallin, 1998). Moreover, the coastal area of Tagalaht Bay near stream outlets is sandy and also exposed to northerly winds which may displace the bottom substrate during stormy weather. These conditions (Landergren & Vallin, 1998)

TABLE 1 Recorded biological and life-history parameters of brown trout parr from the Ermespu Stream

ID	TL	Sex	Maturity	Age	SSME event	Sr:Ca pre-SSME	Sr:Ca peak	Sr:Ca post-SSME
1	193	M	Mature	4	Start III sum.	0.16 & 0.18	Absent	0.22
2	182	F	Juvenile	3	End III sum.	0.18	0.35	0.22
3	173	F	Juvenile	2	Mid II sum.	0.14	Absent	0.19
4	195	M	Mature	2	Mid III sum.	0.14 & 16	Absent	0.23
5	154	M	Mature	1	I aut./II spr.	0.14	Absent	0.20
6	153	F	Juvenile	1	I aut./II spr.	0.14 & 0.18	Absent	0.21
7	184	M	Mature	2	II aut./III spr.	0.17	Absent	0.23
8	189	M	Mature	3	IV spr.	0.15	Absent	0.19
9	169	F	Juvenile	2	Start I sum.	NS	0.88	0.20
10	168	M	Mature	2	II aut./III spr.	0.14	Absent	0.19
11	151	F	Juvenile	1	Start II sum.	0.13	Absent	0.19
12	160	M	Juvenile	1	I aut./II spr.	0.14 & 0.17	Absent	0.19
13	204	M	Mature	3	Mid III sum.	0.14	Absent	0.20
14	190	M	Mature	3	I spr.	Early stage	0.40	0.20
15	180	F	Juvenile	2	Mid II sum.	0.14	Absent	0.19
16	167	F	Juvenile	2	Mid II sum.	0.22	Absent	0.19
17	160	F	Juvenile	2	III spr.	0.15 & 0.18	Absent	0.20
18	87	F	Juvenile	2	II aut./III spr.	0.17 & 0.14	0.43	0.20
19	90	F	Juvenile	0	I spr.	Early stage	0.78	0.21
20	70	M	Juvenile	0	Mid I sum.	0.16	0.47	0.22

TL, total length in mm. Age, age at capture in years. SSME event, the estimated age and season when stream shifting via the marine environment occurred (spr., spring; sum., summer; aut., autumn; I, first; II, second; III, third). Estimations with a forward slash indicate that the exact season could not be established because the shift occurred at the annulus. Sr:Ca pre-SSME, the mean Sr:Ca natal values before the SSME event. Two values indicate that habitat shifting within tributaries of natal watersheds occurred. Sr:Ca peak, the occurrence of a clear Sr:Ca peak indicating exposure to brackish waters during an SSME event. Sr:Ca post-SSME, mean Sr:Ca values after the SSME event. NS, an unstabilised Sr:Ca pre-SSME value owing to the fish having descended to the sea soon after hatching. Early stage denotes a fish that descended to the sea shortly after yolk sac resorption, but before the ambient values of the natal stream reached a plateau in the otolith Sr:Ca profile.

render trout spawning in the marine environment near the Ermespu stream outlet highly unlikely. Still, we cannot conclusively exclude the possible immigration from more distant stream outlet with suitable spawning substrate and more sheltered location. However, this scenario is highly unlikely as SSME event of disputable ABT trout individuals (namely ID14 and ID19 in Table 1; see also Figure 2c) occurred during spring shortly after hatching and distance between Ermespu stream and closest trout stream outside the Tagalaht Bay is approximately 26 km. Thus, it is safe to conclude that aforementioned ABT individuals descended to the sea immediately after yolk sac resorption or even during it and subsequently entered the Ermespu Stream. Our results do not contradict the possibility that offspring of brown trout spawning in the Baltic Sea (Landergren & Vallin, 1998; Limburg et al., 2001) may enter “non-natal” streams in less saline parts of the Baltic Sea where suitable spawning substrate and shelter against storms may be found. It is known that salmonids [e.g. Atlantic salmon and brown trout (e.g. Klemetsen et al., 2003; Jonsson & Jonsson, 2011)]; coho salmon, Chinook salmon, sockeye salmon, steelhead *Oncorhynchus mykiss* (e.g. Hodge, Wilzbach, Duffy, Quiñones, & Hobbs, 2016; Koski, 2009; Roni et al., 2012; Shrimpton et al., 2014; Walsworth et al., 2015) and charrs e.g. Dolly Varden (e.g. Armstrong,

1974; Bond et al., 2014; Hart, Bond, May-McNally, Miller, & Quinn, 2015) and Arctic charr *Salvelinus alpinus* (e.g. Klemetsen et al., 2003) exhibit a vast array of life histories, which differ in duration of freshwater and/or marine rearing, age at maturation and incidence of repeat spawning etc.

It is widely accepted that salmonids imprint to their natal stream during transformation to a smolt and are known to return there to spawn (“homing”) (e.g. Hansen & Jonsson, 1994; Quinn, 1993). Therefore, it is likely that ABT parr that become smolts in non-natal streams (e.g. Ermespu Stream), may fixate their homing to those new waterbodies. This hypothesis is also supported by Hansen and Jonsson (1994) who experimentally demonstrated that Atlantic salmon, regardless of their genetic origin returned the river they left as smolt. This would imply that SSME may result in adult spawning migrations to streams that are non-natal to these particular individuals. Thus, in the current study, SSME would have resulted in adult trout spawning migration to a stream unsuitable for spawning, indicating to a possible ecological trap. However, it remains to be determined whether SSME has an overall positive effect on recruitment by allowing to colonise unused nursery grounds in closely situated rivers or results in an ecological dead end (Kokko & Sutherland, 2001).

Although the ecological significance of SSME is unclear, it may partly explain the straying behaviour documented during the spawning runs of ABT populations in the brackish Baltic Sea basin (e.g. Degerman, Leonardsson, & Lundqvist, 2012). Our results, combined with those of previous studies (Järvi et al., 1996; Landergren, 2001; Landergren & Vallin, 1998; Landergren, 2004; Limburg et al., 2001; Taal et al., 2014), suggest that the importance of viable ABT spawning rivers may be underestimated during parr density surveys, as these populations may function as source populations (*sensu* Pulliam, 1988) for neighbouring streams and shallow brackish littoral zones (see also Bond et al., 2014). Furthermore, SSME of unsmolted ABT (as of adults; e.g. Jonsson & Jonsson, 2011) may result in gene flow between closely situated streams suitable for salmonids. Parr dispersal between streams through the marine environment may therefore further increase straying behaviour during adult spawning runs, at least in the Baltic Sea region.

In conclusion, our findings provide new information on the life history of ABT. However, as the extent and ecological significance of this behaviour remains unclear, future studies are warranted to clarify the potential impact of SSME on overall straying rates, as well as the ecological and physiological mechanisms behind this phenomenon. Stream shifting through the marine environment should to be considered in the context of the restoration and management of salmonid populations and their habitats, as it may affect population quality characteristics in different spawning streams.

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