Evidence of Atlantic salmon Salmo salar fry movement between fresh water and a brackish environment

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This study reports descent of Atlantic salmon Salmo salar fry from their natal streams to brackish waters of the Baltic Sea and their use of this environment as an alternative rearing habitat before ascending back to freshwater streams. To the authors’ knowledge, residency in a brackish environment has not previously been demonstrated in S. salar fry. Recruitment success and evolutionary significance of this alternative life-history strategy are presently not known.

Key words: early life-history; fry migration; otolith microchemistry; parr migration; Salmo salar; salmonids.

It is traditionally considered that juvenile Atlantic salmon Salmo salar L. 1758 stay in their native river from one to several years before descending to the sea as smolts in spring (Klementsen et al., 2003; Jonsson & Jonsson, 2011). Besides spring migration, autumn descent of S. salar parr has been noted in Canadian (Cunjak et al., 1989), British (Buck & Youngson, 1982; Youngson et al., 1983; Riley et al., 2002; McGinnity et al., 2007; Pinder et al., 2007; Riley, 2007; Ibbotson et al., 2013), Norwegian (Jensen et al., 2012) and Baltic (Taal et al., 2014) populations. This behaviour is also recorded, although less frequently, in anadromous brown trout Salmo trutta L. 1758 (reviewed in Winter et al., 2016). Anadromous S. trutta, however, can follow several alternative life-histories in coastal areas of the Baltic Sea as it has been reported that fry and parr of anadromous S. trutta may descend to sea soon after hatching in spring and early summer (Järvi et al., 1996; Limburg et al., 2001; Landergren, 2004; Taal et al., 2017) and migrate into non-natal streams before transforming into smolts (Taal et al., 2017). Similar mixed life histories have been also previously observed in various other anadromous salmonid populations [e.g. steelhead Oncorhynchus mykiss (Walbaum 1792) (Hodge et al., 2016); Dolly Varden Salvelinus malma (Walbaum 1792) (Armstrong, 1974; Bond et al., 2014); coho salmon Oncorhynchus kisutch (Walbaum 1792) (Koski, 2009; Roni et al., 2012)]. Still, residency in a brackish environment has

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not previously been demonstrated in *S. salar* fry. This study reports what are, as far as is known, the first observations of this alternative life history pattern in *S. salar*.

Four juvenile *S. salar* parr were electrofished from Lemmejõgi Stream and Loode Stream and one milt producing sneaker-male from Toolse River (Fig. 1) during an annual national salmonid parr density survey in 2015 and 2016. These streams are well-known nurseries for anadromous *S. trutta* (HELCOM, 2011; Järvekülg et al., 2015), but *S. salar* parr have only been found as single individuals during national salmonid parr density surveys (1996–2014). Lemmejõgi Stream (catchment 55.7 km²), Loode Stream (catchment 18.5 km²) and Toolse River (catchment 84.3 km²) are not classified as historical or potential *S. salar* rivers (HELCOM, 2011) due to their relatively small size and discharge (Jonsson et al., 1991). Loobu River (catchment 314 km²) and Vääna River (catchment 315 km²) are the smallest *S. salar* spawning rivers in Estonia, but still significantly larger than Lemmejõgi and Loode streams and Toolse River. Moreover, historical *S. salar* rivers in Estonia (except Narva River and Pärnu River) are among the smallest in terms of discharge and catchment area compared with other *S. salar* rivers in the Baltic Sea region (Kesler, 2015).

Loode and Lemmejõgi streams drain into the Gulf of Riga where surface-water salinity usually ranges between 4.5 and 6 (Leppäranta & Myrberg, 2009). Owing to high inflow from rivers and relative isolation from the open Baltic Sea, however, salinity in the coastal zone of the Gulf of Riga can be variable and occasionally fluctuate between...
0.5 and 2.0 during spring (reviewed in Ojaveer, 1997). The mouth of the nearest known *S. salar* spawning river (*i.e.* Salaca River; HELCOM, 2011) is situated 22 and 24 km from the Loode and Lemmejõgi streams, respectively (Fig. 1). Toolse River flows into Kunda Bay (Gulf of Finland) where surface-water salinity is usually <5 (Järvekülg, 1979). The closest neighbouring *S. salar* spawning stream (*i.e.* Kunda River; HELCOM, 2011) discharges to the sea c. 3.5 km eastwards from Toolse River’s mouth (Fig. 1). It was hypothesized that *S. salar* parr, caught from Lemmejõgi and Loode streams and Toolse River did not hatch in these waterbodies and may be immigrants from other rivers. This was tested by examining their otolith microchemical profiles for shifts that would co-occur with such movement through brackish water (Walther & Limburg, 2012). Otolith profile from a *S. salar* caught in Toolse River was compared with otolith profiles of parr caught from lower reaches of Kunda River (*n* = 10) to test this hypothesis.

The *S. salar* were anaesthetized and killed immediately after capture with an overdose 400 mg l\(^{-1}\) MS-222, with death confirmed by individual cervical dislocation. Total length (*L*\(_T\), ±1 mm) of all caught *S. salar* was recorded. Parr status of the caught *S. salar* was confirmed by visual analysis of their parr markings and the absence of any signs of smoltification (Jonsson & Jonsson, 2011). Sagittal otoliths were removed for age and microchemical analyses. Age was determined by counting the translucent zones from unstained otoliths using a stereomicroscope against dark and light background. Otolith Sr:Ca ratios (for methodological details see Taal *et al.*, 2017) were quantified to test whether parr otoliths revealed chemical patterns that indicated descent to brackish water and concurrent re-entry to fresh water (described as ‘stream shifting via marine environment (SSME)’ by Taal *et al.*, 2017). It was expected that individuals that underwent SSME would display otolith microchemical profiles where initial low Sr:Ca levels (characteristic of a freshwater environment) are followed by increase (indicating brackish water experience) and subsequent decrease (indicating freshwater environment again).

The otoliths of all the *S. salar* parr caught had microchemical patterns that indicated SSME (Fig. 2; for detailed individual biological and life-history variables of all *S. salar* see Table I). Three *S. salar* (ID1, ID4 and ID5 in Table I and Fig. 2) possessed a Sr:Ca profile consisting of distinct natal freshwater habitat values followed by a sudden increase, subsequent decrease and stabilization of Sr:Ca levels on the values different from the natal ones. This indicates fry or parr emigration from the natal stream during spring or summer, brief (<14 days) residency in the brackish waters and subsequent entry to a non-natal stream (*i.e.* Lemmejõgi and Loode streams and River Toolse). Two *S. salar* parr (ID2 and ID3 in Table I and Fig. 2) displayed a Sr:Ca profile with a disrupted Sr:Ca decrease in the maternally influenced otolith region that resulted in unstabilized natal value. This indicates that the specific individuals drifted or emigrated to brackish water soon after hatching, while even potentially possessing some remnants of the yolk sac. *S. salar* parr (*n* = 10) sampled from the Kunda River as controls possessed otolith Sr:Ca natal freshwater habitat values (median value = 0.12 mmol mol\(^{-1}\); range = 0.11–0.17 mmol mol\(^{-1}\)) similar to the natal freshwater habitat value of the parr caught from Toolse River (ID5 in Table I and Fig. 2).

The main result of this study is that the life-history patterns of *S. salar* may be more diverse than previously known. Otolith chemical profile of *S. salar* parr caught from Toolse River (ID5 in Table I and Fig. 2) demonstrated a clear Sr:Ca concentration shift from one stable plateau to another stable plateau with significantly different values.
This stage-shift was also divided by a clear brackish water signal. Such temporally stable shifts in otolith chemical profiles are only possible if a fish has migrated from one chemically stable environment to another (Miller, 2011). Moreover, *S. salar* parr caught from the Toolse River possessed otolith Sr:Ca natal freshwater habitat values (Table I) very similar to those *S. salar* that were caught from nearby Kunda River. Therefore, it is likely that *S. salar* parr resident in Toolse River originated from Kunda River (Fig. 1). Thus, it is safe to conclude that *S. salar* fry can undergo SSME. Similar
Table I. Recorded biological and life-history variables of *Salmo salar* parr

<table>
<thead>
<tr>
<th>ID</th>
<th>Stream</th>
<th>$L_T$ (mm)</th>
<th>Age (years)</th>
<th>SSME event</th>
<th>Pre-SSME</th>
<th>Peak</th>
<th>Post-SSME</th>
<th>Date</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Lemme</td>
<td>82</td>
<td>0</td>
<td>I spr.</td>
<td>0·14</td>
<td>0·7</td>
<td>0·19</td>
<td>19 August 2015</td>
</tr>
<tr>
<td>2</td>
<td>Lemme</td>
<td>75</td>
<td>0</td>
<td>I spr.</td>
<td>0·55</td>
<td>0·17</td>
<td>0·19</td>
<td>19 August 2015</td>
</tr>
<tr>
<td>3</td>
<td>Loode</td>
<td>79</td>
<td>0</td>
<td>I spr.</td>
<td>Early-stage</td>
<td>1·3</td>
<td>0·19</td>
<td>19 August 2015</td>
</tr>
<tr>
<td>4</td>
<td>Loode</td>
<td>113</td>
<td>1</td>
<td>I spr.</td>
<td>0·19</td>
<td>1·1</td>
<td>0·22</td>
<td>21 May 2016</td>
</tr>
<tr>
<td>5</td>
<td>Toolse</td>
<td>153</td>
<td>1</td>
<td>Mid I sum.</td>
<td>0·11</td>
<td>1·3</td>
<td>0·21</td>
<td>8 September 2016</td>
</tr>
</tbody>
</table>

ID, individual fish identification. Lemme, Lemmejõgi Stream; Loode, Loode Stream; Toolse, Toolse River. $L_T$, total length; SSME event, the estimated age and season when stream shifting via the marine environment occurred (Mid, Middle; I, first; spr., spring; sum., summer). Pre-SSME, mean otolith Sr:Ca natal value before the SSME event. Peak, occurrence of a clear Sr:Ca peak indicating exposure to marine waters during an SSME event. Post-SSME, mean otolith Sr:Ca freshwater value after the SSME event. Early-stage, a *S. salar* that descended to the sea shortly after or even before yolk-sac resorption, but definitely before the ambient values of the natal stream were incorporated to the otolith.

Behaviour has been previously observed in other salmonids, e.g. anadromous *S. trutta* in the Baltic Sea (Taal et al., 2017) and *O. kisutch* in North America (Koski, 2009; Roni et al., 2012).

Owing to logistical reasons, it was not possible to determine the specific sources of the parr caught from Lemmejõgi and Loode streams (ID1, ID2, ID3 and ID4 in Table I and Fig. 2). The most plausible source population of those parr could be the nearest known *S. salar* spawning river, River Šalaca (HELCOM, 2011). Nevertheless, possible immigration from nearby streams with possible irregular *S. salar* reproduction or the hypothesis that these parr, in fact, originated from Loode (ID2 in Table I) and Lemmejõgi streams (ID3 in Table I) cannot be conclusively excluded. In both cases, however, (i.e. possible SSME and possible *S. salar* reproduction in Loode and Lemmejõgi streams) observed Sr:Ca profiles indicated fry movement between brackish and freshwater environments shortly after hatching. Brackish influxes caused by storm surges are also highly unlikely in the case of the Lemmejõgi Stream sampling area as it is >4 m a.s.l. In the case of the Loode stream, short-time brackish influxes during strong westerly winds could be possible as the sampling area is only 1 m a.s.l. Such storm surges would need to last for at least a week to be detectable from otolith micro-chemical profiles (Miller, 2011). Favourable conditions for brackish water influxes to Loode and Lemmejõgi streams, however, were not met (the sea level was constantly low) during April and May 2015 (EWS, 2017).

High river discharges together with various wind conditions in this region may also affect the salinity regime in coastal areas of the Gulf of Riga and hence explain relatively high variation in maximum peak values of observed otolith Sr:Ca profiles (ID2 v. ID1, ID3 and ID4 in Table I). The coastal zone of the Gulf of Riga is characterized by low and variable salinity 0·5–2·0 in spring due to relative isolation from the open Baltic and high and variable river discharge (Ojaveer, 1997). Moreover, high rainfall was observed (184% of average April values for the region) during April 2015 in the Salaca basin (LEGMC, 2017). Thus, *S. salar* fry may have been passively washed out from Salaca River during high flow events. Also in this context, SSME seems to be the most parsimonious explanation for the observed otolith Sr:Ca profiles of *S. salar*.
parr caught from Loode and Lemmejõgi streams (if compared with hypotheses about occasional spawning in those streams), especially as SSME of *S. salar* fry has been previously shown in the Toolse River. In the case of *S. salar* parr caught from the Toolse River the SSME event occurred in the middle of the summer and, therefore, it is possible that this individual moved actively to a non-natal stream. The possible SSME event of *S. salar* parr caught from Loode and Lemmejõgi streams occurred shortly after hatching. Thus, wind and wave induced drifting is the most plausible explanation behind this particular case.

Besides SSME, current results are also the first documentation that *S. salar* fry may move to a saline environment shortly after hatching. In the Baltic Sea, similar early out-migrating behaviour has been previously described for anadromous *S. trutta* from small streams (Järvi *et al.*, 1996; Limburg *et al.*, 2001; Landergren, 2004). It has been hypothesized that this early out-migration phenomenon may be forced by competition (e.g. food, space) or promoted by variable hydrological conditions (e.g. decreasing water levels during dry periods in summer and early autumn) together with spawning ground distance from the sea (Limburg *et al.*, 2001; Landergren, 2004). Observed springtime out-migration of *S. salar* under yearlings in this study hint that the fry or young parr may disperse downstream from their natal habitat during high flows. Such effect of high flows could be further supported by the spawning site preferences of *S. salar*; this species prefers to spawn in relatively larger rivers (Jonsson *et al.*, 1991) in terms of flow volume and catchment area, if compared to e.g. anadromous *S. trutta*.

In the case of anadromous *S. trutta* it has been experimentally demonstrated (Landergren, 2001) that brackish environment in the Baltic Sea (salinity 6–7) does not require marine level osmoregulatory competency for survival. This may also be relevant for *S. salar* as phylogeny and life history of this species are similar to *S. trutta* (Klemmentsen *et al.*, 2003; Jonsson & Jonsson, 2011). Nevertheless, Riley *et al.* (2008) demonstrated that autumn descending *S. salar* parr are physiologically not sufficiently adapted to full-strength seawater (35). A low proportion of those *S. salar*, however, are reported to return as adults during the spawning run (Riley *et al.*, 2009). Thus, a proportion of *S. salar* may use residency in brackish coastal areas of the Baltic Sea directly after hatching as an additional alternative life-history pattern besides autumn descent (Taal *et al.*, 2014) and SSME. This has to be investigated in the future.

All observed early movements in *S. salar* fry were restricted to spring and summer during the first year of life. In the case of anadromous *S. trutta* in the Baltic Sea it has been reported that early out-migration occurs with both fry (Järvi *et al.*, 1996; Limburg *et al.*, 2001; Landergren, 2004) and 1–4 year old parr (Taal *et al.*, 2014, 2017). Moreover, anadromous *S. trutta* SSME occurred during the period between early spring and late autumn, but mostly during mid-summer (Taal *et al.*, 2017). Thus, the essence of this life history pattern may substantially differ between *S. salar* and anadromous *S. trutta*. The exact mechanisms that trigger SSME of *S. salar* and also anadromous *S. trutta* parr (Taal *et al.*, 2017) in the Baltic Sea are currently unknown. Taal *et al.* (2017) suggested that anadromous *S. trutta* parr which undergo SSME may become smolts in non-natal streams and thus fixate their homing to those new waterbodies. This hypothesis is in accordance with an experiment by Hansen & Jonsson (1994) who demonstrated that *S. salar*, regardless of genetic origin returned to the river they left as smolts. Furthermore, SSME is hypothesized (Taal *et al.*, 2017) to be a possible factor behind the straying behaviour documented during the spawning run of anadromous *S. trutta* in the Baltic Sea (Degerman *et al.*, 2012). This implication may also hold true.
for *S. salar* resulting in gene flow between closely situated spawning rivers and thus complement the known implications of straying behaviour for this species (Jonsson et al., 2003).

The findings of this study provide new information on the ecology of *S. salar*. Still, the ecological significance of early out-migration and SSME of *S. salar* fry remains unclear. Future studies are needed to assess the recruitment success and the proportion of such alternative life-histories in the adult population as well as during spawning runs. This might also provide implications for management and conservation of *S. salar* in the Baltic Sea.

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References


Electronic References


