

BRIEF COMMUNICATION**Evidence of Atlantic salmon *Salmo salar* fry movement between fresh water and a brackish environment**I. TAAL*, M. ROHTLA, L. SAKS, R. SVIRGSDEN, M. KESLER, L. MATETSKI
AND M. VETEMAA*Estonian Marine Institute, University of Tartu, Vanemuise 46a, EE-51014 Tartu, Estonia**(Received 13 March 2017, Accepted 31 May 2017)*

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.

© 2017 The Fisheries Society of the British Isles

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 (Klementsens *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

*Author to whom correspondence should be addressed. Tel.: +372 5036048; email: imre.taal@ut.ee

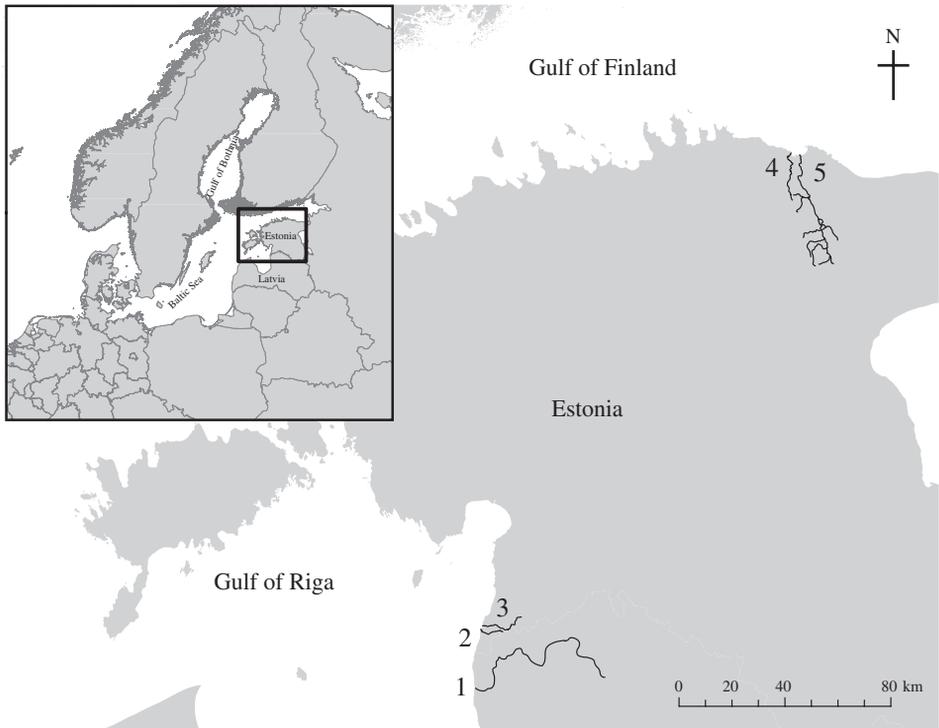


FIG. 1. Map of the study area. 1, Salaca River; 2, Loode Stream; 3, Lemmejõgi Stream; 4, Toolse River; 5, Kunda River.

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 (Järvekül, 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 , $\pm 1 \text{ mm}$) 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 = $0.12 \text{ mmol mol}^{-1}$; range = $0.11 - 0.17 \text{ mmol mol}^{-1}$) 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.

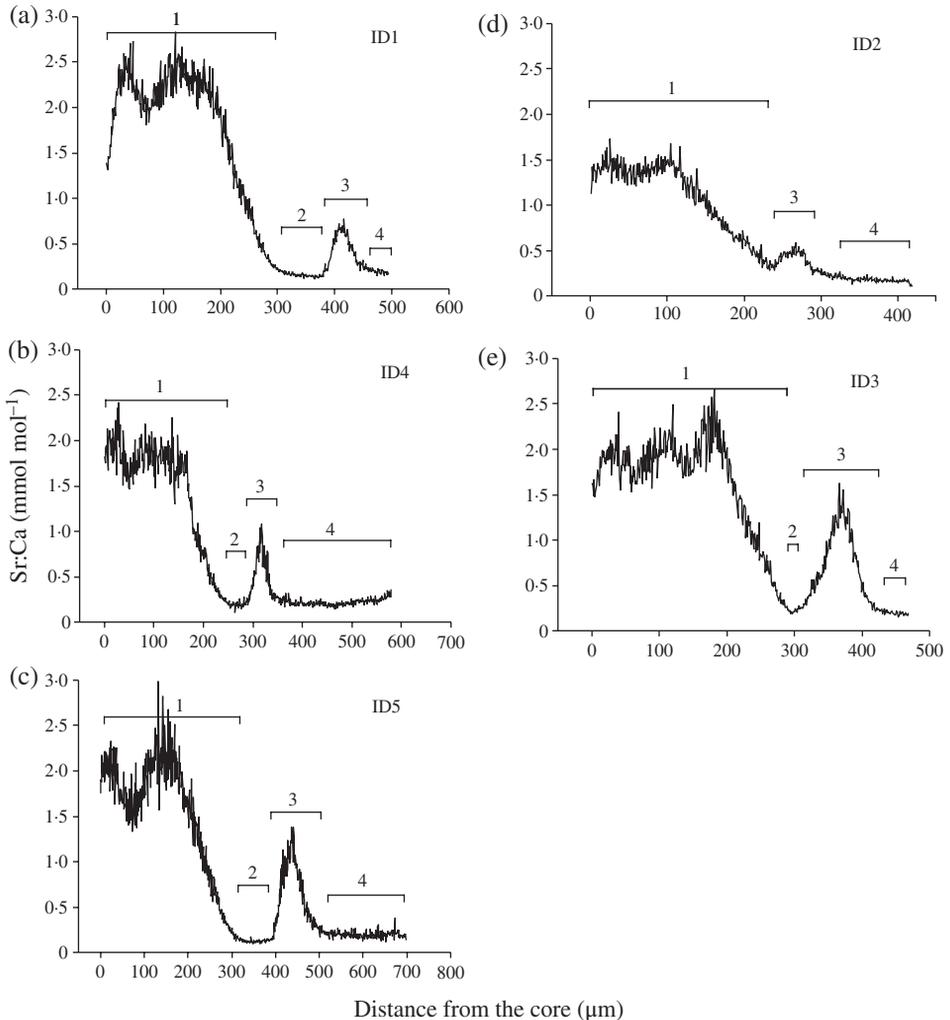


FIG. 2. Otolith Sr:Ca profiles of *Salmo salar*. (a, b, c) parr with distinct natal values followed by a clear marine signal and subsequent decrease and stabilization of values different from the natal ones; (d, e) parr that descended–drifted to the sea immediately after yolk-sac resorption, or even during it, and subsequently entered the non-natal freshwater habitat. Numbered parentheses represent distinct stages in the chemical profiles: 1, maternally influenced region (*sensu* Kalish, 1990); 2, natal freshwater habitat; 3, brackish water experience; 4, non-natal freshwater habitat. The Sr:Ca freshwater threshold is $<0.5 \text{ mmol mol}^{-1}$ in the fresh waters of Estonia (Matetski, 2014).

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

| ID | Stream | L_T (mm) | Age (years) | SSME event | Pre-SSME | Peak | Post-SSME | Date |
|----|--------|---------------|----------------|---------------|-------------|------|-----------|------------------|
| 1 | Lemme | 82 | 0 | I spr. | 0.14 | 0.7 | 0.19 | 19 August 2015 |
| 2 | Lemme | 75 | 0 | I spr. | Early-stage | 0.55 | 0.17 | 19 August 2015 |
| 3 | Loode | 79 | 0 | I spr. | Early-stage | 1.3 | 0.19 | 19 August 2015 |
| 4 | Loode | 113 | 1 | I spr. | 0.19 | 1.1 | 0.22 | 21 May 2016 |
| 5 | Toolse | 153 | 1 | Mid I sum. | 0.11 | 1.3 | 0.21 | 8 September 2016 |

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 Salaca (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* (Klementsens *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.

We thank all the people who were involved in the fieldwork and P. Paiste for helping with chemical analyses. We also thank anonymous reviewers for their thorough and constructive criticism which greatly improved the quality of the manuscript.

References

- Armstrong, R. H. (1974). Migrations of anadromous Dolly Varden (*Salvelinus malma*) in south-eastern Alaska. *Journal of the Fisheries Research Board of Canada* **31**, 435–444. <https://doi.org/10.1139/f74-071>.
- Bond, M. H., Crane, P. E., Larson, W. A. & Quinn, T. P. (2014). Is isolation by adaptation driving genetic divergence among proximate Dolly Varden char populations? *Ecology and Evolution* **4**, 2515–2532. <https://doi.org/10.1002/ece3.1113>.
- Buck, R. J. G. & Youngson, A. F. (1982). The downstream migration of precociously mature Atlantic salmon, *Salmo salar* L. parr in autumn; its relation to the spawning migration of mature adult fish. *Journal of Fish Biology* **20**, 279–288. <https://doi.org/10.1111/j.1095-8649.1982.tb04709.x>.
- Cunjak, R. A., Chadwick, E. M. P. & Shears, M. (1989). Downstream movements and estuarine residence by Atlantic salmon parr (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* **46**, 1466–1471. <https://doi.org/10.1139/f89-187>.
- Degerman, E., Leonardsson, K. & Lundqvist, H. (2012). Coastal migrations, temporary use of neighbouring rivers and growth of sea trout (*Salmo trutta*) from nine northern Baltic Sea rivers. *ICES Journal of Marine Science* **69**, 971–980. <https://doi.org/10.1093/icesjms/fss073>.
- Hansen, L. P. & Jonsson, B. (1994). Homing in Atlantic salmon: effects of juvenile learning on transplanted post-spawners. *Animal Behaviour* **47**, 220–222. <https://doi.org/10.1006/anbe.1994.1027>.
- Hodge, B. W., Wilzbach, M. A., Duffy, W. G., Quiñones, R. M. & Hobbs, J. A. (2016). Life history diversity in Klamath River steelhead. *Transactions of the American Fisheries Society* **145**, 227–238. <https://doi.org/10.1080/00028487.2015.1111257>.
- Ibbotson, A. T., Riley, W. D., Beaumont, W. R. C., Cook, A. C., Ives, M. J., Pinder, A. C. & Scott, L. J. (2013). The source of autumn and spring downstream migrating juvenile Atlantic salmon in a small lowland river. *Ecology of Freshwater Fish* **22**, 73–81. <https://doi.org/10.1111/eff.12003>.
- Järvekülg, A. (1979). *The Bottom Fauna of the Eastern Part of the Baltic Sea (in Russian)*. Tallinn: Valgus.
- Järvi, T., Holmgren, K., Rubin, J. F., Petersson, E., Lundberg, S. & Glimsäter, C. (1996). Newly-emerged *Salmo trutta* fry that migrate to the sea – an alternative choice of feeding habitat? *Nordic Journal of Freshwater Research* **72**, 52–62.
- Jensen, A. J., Finstad, B., Fiske, P., Hvidsten, N. A., Rikardsen, A. H. & Saksgård, L. (2012). Timing of smolt migration in sympatric populations of Atlantic salmon (*Salmo salar*), brown trout (*Salmo trutta*) and Arctic char (*Salvelinus alpinus*). *Canadian Journal of Fisheries and Aquatic Sciences* **69**, 711–723. <https://doi.org/10.1139/f2012-005>.
- Jonsson, B. & Jonsson, N. (2011). *Ecology of Atlantic Salmon and Brown Trout. Habitat as a Template for Life Histories*. Dordrecht: Springer.

- Jonsson, N., Hansen, L. P. & Jonsson, B. (1991). Variation in age, size and repeat spawning of adult Atlantic salmon in relation to river discharge. *Journal of Animal Ecology* **60**, 937–947. <https://doi.org/10.2307/5423>.
- Jonsson, B., Jonsson, N. & Hansen, L. P. (2003). Atlantic salmon straying from the river Imsa. *Journal of Fish Biology* **62**, 641–657. <https://doi.org/10.1046/j.0022-1112.2003.00053.x>.
- Kalish, J. M. (1990). Use of otolith microchemistry to distinguish the progeny of sympatric anadromous and non-anadromous salmonids. *Fishery Bulletin* **88**, 657–666.
- Klements, A., Amundsen, P.-A., Dempson, J. B., Jonsson, B., Jonsson, N., O'Connell, M. F. & Mortensen, E. (2003). Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.): a review of aspects of their life histories. *Ecology of Freshwater Fish* **12**, 1–59. <https://doi.org/10.1034/j.1600-0633.2003.00010.x>.
- Koski, K. V. (2009). The fate of coho salmon nomads: the story of an estuarine-rearing strategy promoting resilience. *Ecology and Society* **14**, 4. Available at <http://www.ecologyandsociety.org/vol14/iss1/art4/>.
- Landergren, P. (2001). Survival and growth of sea trout parr in fresh and brackish water. *Journal of Fish Biology* **58**, 591–593. <https://doi.org/10.1006/jfbi.2000.1460>.
- Landergren, P. (2004). Factors affecting early migration of sea trout *Salmo trutta* parr to brackish water. *Fisheries Research* **67**, 283–294. <https://doi.org/10.1016/j.fishres.2003.10.005>.
- Leppäranta, M. & Myrberg, K. (2009). *Physical Oceanography of the Baltic Sea*. Berlin and Heidelberg: Springer.
- Limburg, K. E., Landergren, P., Westin, L., Elfman, M. & Kristiansson, P. (2001). Flexible modes of anadromy in Baltic Sea trout: making the most of marginal spawning streams. *Journal of Fish Biology* **59**, 682–695. <https://doi.org/10.1111/j.1095-8649.2001.tb02372.x>.
- McGinnity, P., de Eyto, E., Cross, T. F., Coughlan, J., Whelan, K. & Ferguson, A. (2007). Population specific smolt development, migration and maturity schedules in Atlantic salmon in a natural river environment. *Aquaculture* **273**, 257–268. <https://doi.org/10.1016/j.aquaculture.2007.10.008>.
- Miller, J. A. (2011). Effects of water temperature and barium concentration on otolith composition along a salinity gradient: implications for migratory reconstructions. *Journal of Experimental Marine Biology and Ecology* **405**, 42–52. <https://doi.org/10.1016/j.jembe.2011.05.017>.
- Pinder, A. C., Riley, W. D., Ibbotson, A. T. & Beaumont, W. R. C. (2007). Evidence for an autumn downstream migration and the subsequent estuarine residence of 0+ year juvenile Atlantic salmon *Salmo salar* L., in England. *Journal of Fish Biology* **71**, 260–264. <https://doi.org/10.1111/j.1095-8649.2007.01470.x>.
- Riley, W. D. (2007). Seasonal downstream movements of juvenile Atlantic salmon, *Salmo salar* L., with evidence of solitary migration of smolts. *Aquaculture* **273**, 194–199. <https://doi.org/10.1016/j.aquaculture.2007.10.022>.
- Riley, W. D., Eagle, M. O. & Ives, S. J. (2002). The onset of downstream movement of juvenile Atlantic salmon, *Salmo salar* L., in a chalk stream. *Fisheries Management and Ecology* **9**, 87–94. <https://doi.org/10.1046/j.1365-2400.2002.00287.x>.
- Riley, W. D., Ibbotson, A. T., Lower, N., Cook, A. C., Moore, A., Mizuno, S., Pinder, A. C., Beaumont, W. R. C. & Privitera, L. (2008). Physiological seawater adaptation in juvenile Atlantic salmon (*Salmo salar*) autumn migrants. *Freshwater Biology* **53**, 745–755. <https://doi.org/10.1111/j.1365-2427.2007.01933.x>.
- Riley, W. D., Ibbotson, A. T. & Beaumont, W. R. C. (2009). Adult returns from Atlantic salmon, *Salmo salar*, parr autumn migrants. *Fisheries Management and Ecology* **16**, 75–76. <https://doi.org/10.1111/j.1365-2400.2008.00643.x>.
- Roni, P., Bennett, T., Holland, R., Pess, G., Hanson, K., Moses, R., McHenry, M., Ehinger, W. & Walter, J. (2012). Factors affecting migration timing, growth and survival of juvenile coho salmon in two coastal Washington watersheds. *Transactions of the American Fisheries Society* **141**, 890–906. <https://doi.org/10.1080/00028487.2012.675895>.
- Taal, I., Kesler, M., Saks, L., Rohtla, M., Verliin, A., Svrigsdén, R., Jürgens, K., Vetemaa, M. & Saat, T. (2014). Evidence on autumn migrating parr of Atlantic salmon *Salmo salar* (Linnaeus) and anadromous brown trout *Salmo trutta* (Linnaeus) in the Baltic Sea. *Helgolander Marine Research* **68**, 373–377. <https://doi.org/10.1007/s10152-014-0395-2>.

- Taal, I., Rohtla, M., Saks, L., Kesler, M., Jürgens, K., Svirgsden, R., Matetski, L., Verliin, A., Paiste, P. & Vetemaa, M. (2017). Parr dispersal between streams *via* a marine environment: a novel mechanism behind straying for anadromous brown trout? *Ecology of Freshwater Fish*. <https://doi.org/10.1111/eff.12338>.
- Walther, B. D. & Limburg, K. E. (2012). The use of otolith chemistry to characterize diadromous migrations. *Journal of Fish Biology* **81**, 796–825. <https://doi.org/10.1111/j.1095-8649.2012.03371.x>.
- Winter, E. R., Tummers, J. S., Aarestrup, K., Baktoft, H. & Lucas, M. C. (2016). Investigating the phenology of seaward migration of juvenile brown trout (*Salmo trutta*) in two European populations. *Hydrobiologia* **775**, 139–151. <https://doi.org/10.1007/s10750-016-2720-z>.
- Youngson, A. F., Buck, R. J. G., Simpson, T. H. & Hay, D. W. (1983). The autumn and spring emigrations of juvenile Atlantic salmon, *Salmo salar* L., from the Girnock Burn, Aberdeenshire, Scotland: environmental release of migration. *Journal of Fish Biology* **23**, 625–639. <https://doi.org/10.1111/j.1095-8649.1983.tb02942.x>.

Electronic References

- EWS. (2017). *Sea Weather: Water Level Observations*. Tallinn: Estonian Weather Service. Available at <http://www.ilmateenistus.ee/meri/vaatlusandmed/kogu-rannik/kaart/?lang=en#/> (last accessed 8 March 2017).
- HELCOM. (2011). Salmon and sea trout populations and rivers in the Baltic sea – HELCOM assessment of salmon (*Salmo salar*) and sea trout (*Salmo trutta*) populations and habitats in rivers flowing to the Baltic Sea. *Baltic Sea Environment Proceedings No. 126A*. Helsinki: Baltic Marine Environment Protection Commission (HELCOM). Available at <http://www.helcom.fi/Lists/Publications/BSEP126A.pdf/> (last accessed 8 March 2017).
- Järvekülg, R., Pihu, R., Sinimets, A., Kesler, M. & Taal, I. (2015). Eesti meriforelli kudejõgede taastootmispotentsiaali hindamine 2015. EMÜ PKI limnoloogiakeskus, TÜ Eesti Mereinstituut, MTÜ Trulling. Tartu (in Estonian). Available at http://www.envir.ee/sites/default/files/meriforelli_aruanne_2015_avalik.pdf/ (last accessed 8 March 2017).
- Kesler, M. (2015). Biological characteristics and restoration of Atlantic salmon *Salmo salar* populations in the rivers of Northern Estonia. PhD Thesis, University of Tartu, Tartu. Available at http://dspace.ut.ee/bitstream/handle/10062/47494/kesler_martin.pdf?sequence=1&isAllowed=y/ (last accessed 8 March 2017).
- LEGMC. (2017). *Hidroloģiskā režīma apskats: 2015 (in Latvian)*. Riga: Latvian Environment, Geology and Meteorology Centre. Available at <http://www.meteo.lv/lapas/noverojumi/hidrologija/hidrologiska-rezima-apskats/2015/?nid=963/> (last accessed 8 March 2017).
- Matetski, L. (2014). Distinguishing juvenile sea trout (*Salmo trutta*) from different natal streams based on otolith elemental fingerprints. Master's Thesis, University of Tartu, Tartu. (in Estonian with English summary). Available at <http://dspace.ut.ee/bitstream/handle/10062/42129/LagleMatetski.pdf?sequence=1&isAllowed=y> (last accessed 19 June 2017).
- Ojaveer, H. (1997). Composition and dynamics of fish stocks in the Gulf of Riga ecosystem. PhD Thesis, University of Tartu, Tartu. Available at http://dspace.ut.ee/bitstream/handle/10062/43097/ojaveer_composition_1997.pdf?sequence=1/ (last accessed 8 March 2017).