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Short sea migration and precocious maturation in reared Atlantic salmon post-smolts in the northern Baltic Sea

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Atlantic salmon (*Salmo salar* L.) display significant variation in life history traits, including migration patterns and age at maturity. Hatchery rearing has been shown to affect the life history, and rearing-induced changes may include unfavourable consequences, e.g. shortened sea migration period and smaller size at maturity. We report on a new phenomenon of life history of reared Atlantic salmon in the Baltic Sea area: small-sized salmon returning to freshwater only a few months after release as smolts. These "one-sea-summer (1SS)" salmon were ca. 35 cm in length and weighed ca. 400 g, being clearly larger than smolts, but substantially smaller than one-sea-winter (1SW) salmon from the same cohorts. Almost all 1SS salmon were mature males and, at release, had been longer than the overall mean. Stable isotope analysis suggested that the 1SS salmon had been feeding in different sea areas than 1SW and multi-sea-winter salmon, likely in nearby Bothnian Bay, which is typically not a salmon feeding area. If an increasing proportion of the released salmon are not undertaking a normal marine migration (≥1SW) and are returning to estuaries and rivers as 1SS fish, the success and profitability of the reared salmon releases will decline even more than the reduced post-smolt survival is suggesting. We suggest that alternative rearing practices (e.g. enriched rearing environments and advanced diets) should be considered in hatchery production for shaping the reared smolts towards a closer resemblance to wild smolts.

Keywords: life history, migration, regulated rivers, *Salmo salar*, sea-age at maturity, stocking.

Introduction

Atlantic salmon (*Salmo salar* L.) display significant variation in life history traits, including migration patterns and age at maturity, and extend from freshwater resident forms to anadromous populations characterized by extensive oceanic migrations (Klemetsen *et al.*, 2003; Jonsson and Jonsson, 2011). In anadromous Atlantic salmon populations, individuals may mature and return to freshwater after 1–5 years (sea-winters, SW) of feeding and growth at sea, and a proportion of adults survive to return to the sea post-spawning, recondition, and return to spawn again (Klemetsen *et al.*, 2003; Niemelä *et al.*, 2006). In some North American Atlantic salmon populations, individual fish have been documented to mature and return back to rivers only after a few months feeding migration in the estuarine or coastal areas (e.g. Koksoak River, Ungava Bay, Quebec; Robitaille *et al.*,1986, and Campbellton River, Newfoundland; Downton *et al.*, 2001). In Atlantic Europe, the only record on salmon returning within the year of smoltification has been reported from reared fish in the River Imsa, southern Norway (Jonsson *et al.*, 1993).

The Baltic Sea maintains a salmon population complex (Baltic group) that is genetically differentiated from the Northwest Atlantic (North America) and Northeast Atlantic (Western Europe) groups (Verspoor *et al.*, 2007). The Baltic salmon life history follows a typical anadromous cycle with individuals undergoing a feeding migration for 1–4 SW, while a proportion of juvenile males mature in freshwater (Karlsson and Karlström, 1994). During the past century, a majority of the most important and largest Baltic salmon rivers have been harnessed for hydropower development, and their naturally reproducing salmon populations have been lost; only some 30% of the historical salmon rivers still support naturally reproducing stocks (Rappe *et al.*, 1999). To compensate for the losses of natural salmon production and to maintain salmon fishing, hydropower companies are obliged to release reared smolts (e.g. Erkinaro *et al.*, 2011). Although wild salmon production has recently greatly increased in the northern Baltic Sea rivers (Romakkaniemi *et al.*, 2003; ICES, 2016), large-scale releases of reared smolts are still continuing, totalling 4–5 million individuals annually (ICES, 2016).

Reared Atlantic salmon typically show various biological characteristics that are different from wild fish, both during the life stages in freshwater and at sea (e.g. Einum and Fleming, 2001). Typically, rates of somatic growth and precocious maturation in freshwater are higher in reared individuals than in wild fish (McGinnity *et al.*, 1997; Fleming *et al.*, 2002; Hutchings and Fraser, 2008). In reared salmon, a positive relationship between smolt size at release and survival (recovery rate of tagged adult fish) has been observed in several studies (e.g. Salminen *et al.*, 1995; Saloniemi *et al.*, 2004), and the benefits of larger size are generally assumed to be associated with improved predator avoidance (e.g. Skilbrei *et al.*, 1994). However, survival of reared smolts, despite their generally larger size, is typically much lower than that of wild individuals (e.g. Einum and Fleming, 2001; Chaput, 2012; ICES, 2016), and rearing-induced changes in life history traits may include unfavourable consequences, e.g. shortened sea migration and smaller size at maturity (Kallio-Nyberg *et al.*, 2011).

During the last few decades, a strong decline in survival rates of hatchery-reared salmon has been evident in the Baltic Sea (Mäntyniemi *et al.*, 2012; ICES, 2016). Similarly, recent studies in the Baltic Sea area have clearly indicated that hatchery-reared smolts tend to reach sexual maturity and return earlier, often as one-sea-winter (1SW) salmon, and at a smaller size than wild fish (Vainikka *et al.*, 2010; Kallio-Nyberg *et al.*, 2011, 2014).

In this article, we report a new phenomenon of life history of reared Atlantic salmon in the Baltic Sea area, i.e. small-sized salmon returning to a northern Baltic river after only a few months from release (one-sea-summer, 1SS), describe their biological characteristics, and use stable isotope analysis (SIA) to uncover their potential sea migration behaviour in relation to salmon with typical 1- or 2-year feeding migration at sea. Despite the large-scale release programmes of salmon smolts and comprehensive monitoring programmes (ICES, 2016), no documented information on reared salmon returning to freshwater during the year of release has so far been available from the Baltic Sea area.

Material and methods

Study area

The River Oulujoki is a large (drainage area 22 841 km^2, mean annual flow 259 $m^3 s^{-1}$) regulated river system draining into the Bothnian Bay, the northernmost part of the Baltic Sea (Figure 1a). The first hydroelectric power plant (HPP1) was constructed in 1948 at the river mouth, preventing the spawning migration

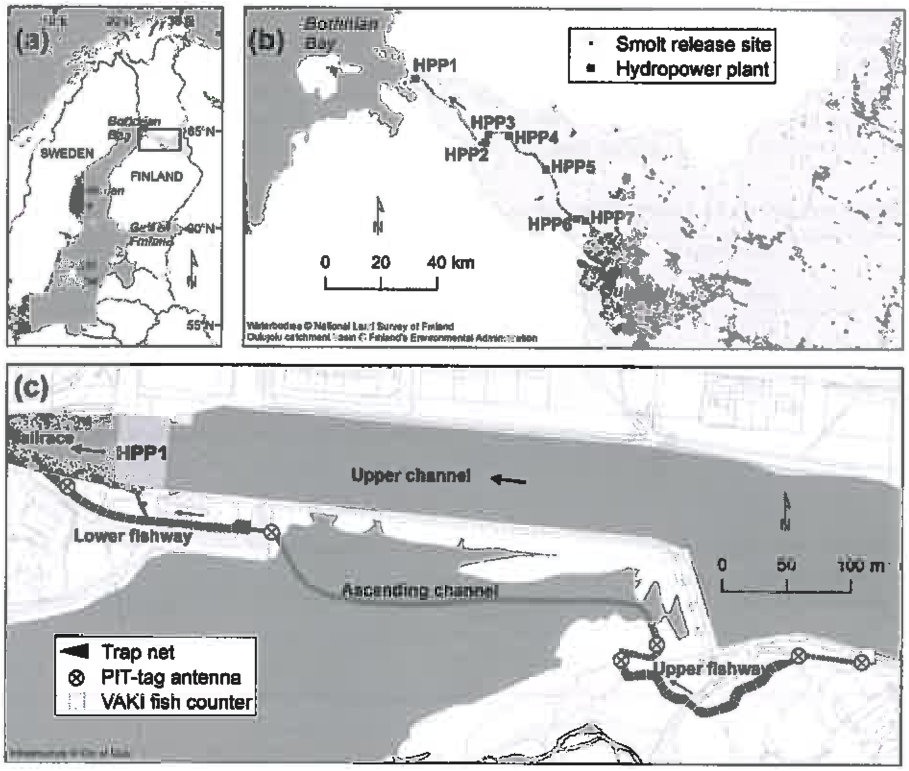

Figure 1. Map of the Baltic Sea and the River Oulujoki catchment (a), locations of the Oulujoki HPPs and smolt release sites (b), and locations of the Merikoski fishway, trapnet fishing site, PIT antennas and the Vaki counter (c).

and causing the extinction of the River Oulujoki salmon population. At present, there are seven HPPs and connecting impoundments within the 107-km long Oulujoki main stem (Figure 1b). A fishway was built at the HPP1 at Merikoski in 2003 creating 36.5 km of impounded river accessible for salmon, up to the HPP 2 (Figure 1b). However, only limited spawning habitats are available for salmon within this river stretch, and the Oulujoki salmon population and both commercial and recreational fishing are dependent on stocking of smolts.

Before the hydropower development, the River Oulujoki supported a viable population of large-sized salmon (mean size 7–11 kg; Lind, 1982) with average annual in-river catches of 46 t (Salojärvi, 1986). The present salmon returns originate from annual compensatory releases of ca. 250 000 2-year-old hatchery-reared smolts, stocked in the tailrace of HPP2 and the river mouth (Figure 1b, Table 1). The founding of the Oulujoki broodstock for compensatory stocking began in 1955. Salmon individuals from at least six other stocks in the Bothnian Bay area (rivers Tornionjoki, Kemijoki, and Iijoki in Finland, and rivers Indalsälven, Skellefteälven, and Umeälven in Sweden) were included in the broodstock to increase genetic diversity and to satisfy the need for eggs (Säisä *et al.*, 2003). The Oulujoki broodstock has since been supplemented at times by salmon individuals captured on their return to the river mouth.

Smolt releases, passive integrated transponder tagging, and monitoring of returning salmon

A large-scale PIT (passive integrated transponder) tagging and monitoring programme was conducted at the Merikoski fishway in 2010–2012. Salmon were PIT tagged in two different life history phases, as 2-year-old smolts (smolt cohorts 2011 and 2012) and as returning adults (captured in 2010–2012). PIT tags (Texas Instruments Inc., Dallas, TX, USA, size 23 × 4 mm) for both smolts and adult salmon were implanted into the body cavity through a small (ca. 5 mm) mid-ventral incision between the pectoral and pelvic fins. The incision was not closed as recommended by Larsen *et al.* (2013). Smolts ($n = 19\,996$) were tagged in the Montta hatchery, 35 km upstream of the Merikoski fishway, and released in 2011–2012 below the HPP2 and in the river mouth (Figure 1b, Table 1). Returning adults were caught with a trapnet situated below the HPP1 close to the Merikoski fishway entrance in 2010–2012 (Figure 1c). Spawning migration of the tagged individuals was monitored between 2010 and 2012 by multiple PIT antennas and readers installed in the fishway (Figure 1c). The PIT data in combination with scale analysis allowed defining the duration of sea residency and migration timing of tagged individuals entering the fishway.

Salmon caught with the trapnet were also used to collect morphological (length, weight) and growth data (scales) on returning fish in 2010–2012. Based on scale reading (Hiilivirta *et al.*, 1998), sampled individuals were assigned to three different sea-age categories (1SS, 1SW; multi-sea-winter, MSW). Length and weight of the 1SS salmon were compared with the characteristics of smolts and 1SW salmon from the same stocking cohorts (cohorts 2010 and 2011, see Table 2). In 2010 and 2012, samples of 37 and 14 individuals of 1SS salmon, respectively, were sacrificed for determining sex and maturation.

Fish counter data

Data on upstream migrating salmon (numbers, migration timing, and size) were collected from the Merikoski fishway exit at HPP1 by a Vaki Riverwatcher Fish Counter (VAKI Aquaculture Systems Ltd, Kópavogur, Iceland; hereafter referred to as Vaki; Figure 1c) combined with an underwater video camera (Lamberg Bio-Marin, Trondheim, Norway) in 2009–2013. After species determination, salmon were classified into two size (age) categories based on the length estimates (with a fish height–length coefficient of 5.3) produced by the Vaki counter system: 1SS salmon (length ≤ 41 cm) and $\geq$1SW salmon (length >41 cm). This size limit was used because the largest 1SS salmon measured during the study period was 41 cm, and all the 1SW salmon were >41 cm

Table 1. Release dates/periods and release groups of hatchery-reared 2-year-old Atlantic salmon smolts in the River Oulujoki in 2009–2013.

	Stocking year				
Smolt releases	**2009**	**2010**	**2011**	**2012**	**2013**
Montta, compensatory	28 April	29 April–10 May	10 May	11 May	10–11 May
RM, compensatory	5–8 May	4–7 May	10–13 May	8–11 May	22–25 May
Montta, PIT-tagged			10 May–8 June	10 May–6 June	
RM, PIT-tagged			11 May	9 May–6 June	

Annual compensatory releases of ca. 250 000 smolts are stocked at river (Montta, below HPP2) and at river mouth (RM, see Figure 1b). PIT-tagged smolts ($n = 19\,996$) were stocked at the same release sites for this study in 2011–2012.

Table 2. Mean lengths (mm) and weights (g) of smolts ($n = 15\,009$), 1SS ($n = 137$), and 1SW ($n = 496$) salmon from smolt stocking cohorts 2010 and 2011 in the River Oulujoki.

	Smolt		1SS salmon		1SW salmon	
Cohort	**Length (mm)**	**Weight (g)**	**Length (mm)**	**Weight (g)**	**Length (mm)**	**Weight (g)**
2010	198 (188–261)	68 (23–142)	351 (315–396)	419 (297–572)	601 (420–750)	2140 (700–4200)
2011	215 (128–284)	–	342 (290–410)	–	591 (430–760)	2157 (650–4500)

Minimum and maximum values are indicated in parenthesis. No weight data on smolt and 1SS salmon were available for smolt stocking cohort 2011. Smolts were measured at the hatchery before the stocking and 1SS and 1SW measurements were conducted for the fish caught from the trapnet below the HPP1 in 2010–2012 (see Figure 1c).

(see e.g. Table 2). In addition, the Vaki data were used to infer the timing of migration in these two salmon categories.

Stable isotope analysis

SIA of salmon scales was used to infer the marine migration and feeding patterns of the River Oulujoki 1SS and 1SW salmon. In the Baltic Sea, the progressively north–south increase in marine influence (Kullenberg, 1981) leads to a divergence of stable isotope (SI) ratios [carbon (δ^{13}C) and nitrogen (δ^{15}N) in this study] of the biota between different sea areas (e.g. Rolff and Elmgren, 2000; Kiljunen *et al.*, 2008; Torniainen *et al.*, 2017), allowing inferences regarding salmon feeding in the different sea areas (Torniainen *et al.*, 2014, 2017). The first set of scales from the River Oulujoki included scale samples of returning 1SS (n = 54) and 1SW (n = 55) salmon caught from the trapnet below HPP1 (see Figure 1c) in 2010. The second set of scales was sampled from commercial fisheries at salmon feeding grounds in different areas of the Baltic Sea (Baltic Proper, Bothnian Sea, and Gulf of Finland; Figure 1a) during the preceding winter (2009–2010) feeding period (n = 63), providing a geographical reference against which the data from salmon ascending the River Oulujoki (1SS and 1SW) were compared. To ensure correct sea area for reference SI values, only scales from feeding salmon collected between 1 September 2009 and 31 March 2010 were used. Since predatory fish show a positive relationship between fish size and trophic level (e.g. Romanuk *et al.*, 2011), larger salmon tend to show higher δ^{15}N values (Satterfield and Finney, 2002; MacKenzie *et al.*, 2011a, b; Trueman *et al.*, 2012), which could lead to incorrect assignment to sea areas showing higher δ^{15}N values. This is especially true when returning salmon tend to be larger than those in the feeding phase. In contrast, δ^{13}C values in fish tissues do not show this bias (Vander Zanden and Rasmussen, 1999). To address the possible size effects, δ^{15}N values were tested with a linear regression between length and δ^{15}N. Statistically significant relationships were not observed, and hence no adjustments were made.

As a pretreatment for SIA analysis, scales were soaked in deionized water and cleaned with fine, non-lint, paper tissue to remove tissue other than scale material (e.g. mucus, pigment, guanine, adhered paper). The last year growth region (i.e. growth during spring/summer prior to river entry) was determined using a microfilm reader and was cut using a scalpel against a glass edge to sample a minimum of 0.2 mg of scale tissue. To prevent bias in SI values from extraneous carbonates, scale material was acidified for 2 min in 1.2 N HCl, rinsed four times in deionized water, and dried overnight at 60 °C (Perga and Gerdeaux, 2003).

SIA analysis was done at the University of Jyväskylä laboratory using a Thermo Finnigan DELTA^{plus}Advantage mass spectrometer (Thermo Electron Corporation, Waltham, MA, USA) connected to a FlashEA 1112 elemental analyzer. White muscle tissue of northern pike (*Esox lucius* L.) was used as an internal working standard. Results are expressed using the standard δ notation (δ^{13}C, δ^{15}N) as parts per thousand (‰) differences from the international standard. The reference materials used were International Atomic Energy Agency standards of known relation to the international standards of Vienna Pee Dee Belemnite (for carbon) and atmospheric N_2 (for nitrogen). Precision for each run was better than 0.35% for C and 0.20% for N based on the standard deviation of replicates of the internal working standards.

Results

Biological characteristics of 1SS salmon

The 1SS salmon in the River Oulujoki averaged 34–35 cm in total length and weighed ca. 400 g (Figure 2), being clearly larger than smolts, but substantially smaller that 1SW salmon of the same cohort (Table 2). There was no overlap in length distributions of these salmon groups. Except for one female, all sacrificed 1SS salmon (n = 51) were fully mature males with running milt. Based on information from the PIT-tagged smolts (n = 9999 and 9997 in 2011 and 2012, respectively), PIT-tagged fish returning to freshwater as 1SS fish (n = 12 and 14 in 2011 and 2012, respectively) had been significantly longer than the overall mean of the stocked smolts at release both in 2011 (mean length 234 vs. 215 mm, t-test, p <0.001) and 2012 (243 vs. 212 mm, t-test, p < 0.001). By contrast, this phenomenon was not evident among the returning PIT-tagged 1SW salmon in 2011 (n = 17; 215 vs. 215 mm) or 2012 (n = 34; 216 vs. 212 mm).

Numbers of 1SS migrants and their migration timing

The yearly numbers of 1SS migrants in the Merikoski fishway, documented by a Vaki counter, varied between 23 and 65 individuals in 2009–2013, constituting a mean of 11% of the overall annual numbers of ascending salmon (Table 3). Pooled data from 2009–2003 suggest that timing of the ascent of 1SS and ≥1SW salmon was rather similar, starting in August and peaking in September (Figure 3).

Scale SIs

Statistically significant differences were observed in average values of δ^{13}C and δ^{15}N in salmon scales sampled in different areas and at different life stages (Analysis of Variance, ANOVA, d.f. = 4, f = 343.6 (C), f = 254.4 (N), p < 0.001). The δ^{13}C values of 1SW salmon returning to the River Oulujoki differed from other salmon values except for those fish sampled from the Bothnian Sea (Tukey HSD, p > 0.05), whereas the values of δ^{15}N in 1SW salmon differed from other values except for those fish sampled from the Baltic Proper (Tukey HSD, p > 0.05) (Figure 4). In contrast, the average δ^{13}C and δ^{15}N values of 1SS salmon differed from all other life stages and geographical areas covered in this study (Tukey HSD, p < 0.001) (Figure 4).

Figure 2. 1SS salmon from the River Oulujoki, length 35 cm and weight 440 g. Photo: Timo Kanniainen.

Table 3. Numbers and proportions (%) of 1SS and older (≥1SW) salmon ascending through the Merikoski fishway in 2009–2013.

	2009		2010		2011		2012		2013		Total	
Age	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%
1SS	54	33.1	65	18.8	36	6.5	29	6.7	23	7.6	207	11.5
≥1SW	109	66.9	281	81.2	519	93.5	404	93.3	281	92.4	1 594	88.5
Total	163	100.0	346	100.0	555	100.0	433	100.0	304	100.0	1 801	100.0

Figures are based on video-verified Vaki counter data.

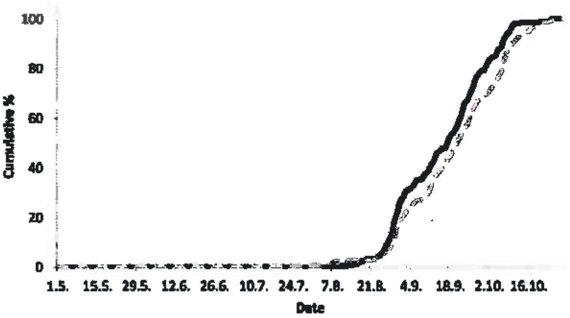

Figure 3. Cumulative timing of fishway passing of 1SS (solid black line) and ≥1SW (dashed grey line) salmon at the Merikoski power plant in 2009–2013. Results are based on video-verified Vaki counter data.

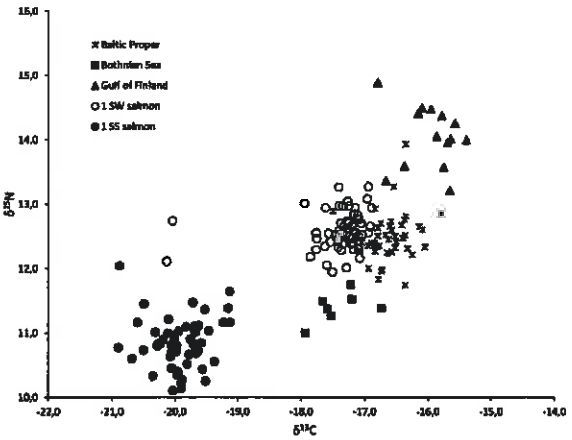

Figure 4. SI values (%) of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) in Baltic salmon scales. Baltic Proper, Bothnian Sea, and Gulf of Finland SI-values represent the values of salmon caught from those sea areas during winter 2009–2010. 1SS and 1SW salmon SI-values represent the values of salmon returning to the River Oulujoki in 2010.

SI values of 1SW salmon ascending the River Oulujoki seemed to resemble values of those reference salmon sampled from the Baltic Proper, with the exception of two individuals whose $\delta^{13}C$ values resembled those of 1SS salmon, but the $\delta^{15}N$ values were more enriched than those of 1SS salmon (Figure 4).

Discussion

In this study, we documented reared mature male Atlantic salmon in the northern Baltic Sea that return to freshwater after only a few months feeding at sea, i.e. as a 1SS salmon. To the best of our knowledge, this is the first record of returning 1SS salmon in the Baltic Sea. Generally, hatchery-reared salmon have been shown to mature earlier and at a smaller size than wild fish (Kallio-Nyberg *et al.*, 2011, 2014), but only one earlier observation on reared 1SS salmon has been reported from Europe (Atlantic coast in Norway), although without detailed information (Jonsson *et al.*,1993).

The reasons for the unusually short time at sea and return as small, mature males may be connected to several factors, including artificial breeding effects and large size of the reared smolts. Modern, improved hatchery-rearing techniques and feed formulas have increased the size and lipid content of salmonid smolts in the Baltic Sea (Eriksson *et al.*, 2008), significantly exceeding those of wild smolts (Larsson *et al.*, 2012). For a comparison with our results, the mean length of wild Atlantic salmon smolts in the nearest salmon river (River Simojoki draining into Bothnian Bay about 70 km north of River Oulujoki) was only 145 mm, with a mean weight of 21.7 g (Kallio-Nyberg *et al.*, 2015). Large size and high condition factor of hatchery-reared smolts is typically linked with high prevalence of early maturation in males, but in brown trout (*Salmo trutta*), this may also result in a large proportion of individuals losing their migration motivation and remaining resident in freshwater (Jonsson *et al.*, 1995; Ugedal *et al.*, 1998). The large initial size of the 1SS salmon individuals compared with the average size of the stocked smolts further supports the concept that large size of reared smolts induces precocious maturation and early migration back to the river.

Captive breeding has been suggested to result in an evolutionary divergence between reared and wild salmonid fish (Fleming *et al.*, 2000; Blanchet *et al.*, 2008) and also to decrease genetic diversity of the reared population over time (Säisä *et al.*, 2003). The breeding regime of the Finnish hatchery populations, including the River Oulujoki, includes continuous broodstock breeding where the stocks are maintained in hatcheries of the Natural Resources Institute Finland (Luke) and, at times, complemented from nature (Säisä *et al.*, 2003). This has been continuing for the Oulujoki salmon since 1955 (Säisä *et al.*, 2003). In a recent study by Vainikka *et al.* (2010), consistent phenotypic differences between reared and wild salmon stocks of the Bothnian Bay area were found, and increased growth rate in hatchery and early maturation were linked with a long captivity breeding history. The long history of the River Oulujoki broodstock was linked with the largest divergence from the wild populations of the same area (Vainikka *et al.*, 2010). Given that the 1SS salmon have never been documented in the wild salmon rivers of the Bothian Bay area, despite intensive, long-term monitoring programmes at several rivers (Romakkaniemi *et al.*, 2003), the occurrence of such a life history form in a stock with the longest captive breeding history may indicate evolutionary changes in this population.

Precocious maturation of Atlantic salmon, i.e. reaching sexual maturity at an early life stage before the return migration of anadromous individuals, is a common phenomenon in both wild and reared fish (e.g. Klemetsen *et al.*, 2003). Increased growth and nutritional status of juvenile salmon is inducing early maturation. Therefore, hatchery rearing is typically resulting in higher maturation rates, up to 50–90% in male parr compared with those in natural populations (e.g. Lundqvist, 1983; Heinimaa and Erkinaro, 2004 and references therein). Given that the brackish water of the northern Baltic Sea has been experimentally shown to reduce or inhibit sexual maturation of young salmon

(Lundqvist and Fridberg, 1982), it is interesting that virtually all 1SS salmon that had likely remained in the Bothnian Bay (see below) in very low salinity for 2–4 months, and thereafter sampled at the Oulujoki river mouth, were mature males. Their maturity status as smolts at release a few months earlier is not known, however; thus, the onset and development of their sexual maturity remains unknown. It is possible that the gonadal development of 1SS salmon was in progress at the time of release as smolts and that their gonad development had not ceased, but further continued in brackish water until their return to freshwater.

Populations of many salmonid fish species consist of migratory and stationary individuals, a trait often referred to as partial migration (cf. Jonsson and Jonsson, 1993). It has been suggested that the physical environment of fish and its changes may dictate the benefits, costs, and ultimately the tendency and onset of migration (Näslund *et al.*, 1993; Olsson *et al.*, 2006). Although Atlantic salmon can be considered a nearly obligate anadromous species, the duration of migration, i.e. maturation and return to freshwater, varies considerably. Life history theory predicts that increased mortality at potential ages and sizes at maturation selects for an earlier onset of maturation (e.g. Ernande *et al.*, 2004) and thus earlier return of an anadromous fish. Although earlier maturation may simply reflect phenotypic plasticity (cf. Olsen *et al.*, 2004), recent research on Atlantic salmon has revealed strong evidence of genetic basis for age at maturity (Johnston *et al.*, 2014; Barson *et al.*, 2015). In reared fish, individual trait selection in a hatchery environment may strongly differ from selection in the wild (e.g. Niva and Jokela, 2000). Interactions between genetics and environment (both in hatchery and in the wild) of the 1SS vs. ≥1SW salmon with a relatively narrow genetic background, but with a large difference in their migration behaviour, could provide an interesting future field of research from both scientific and management perspectives.

Progressive northward increase in freshwater influence creates distinctive gradients in isotope ratios ($\delta^{13}C$, $\delta^{15}N$, and $\delta^{18}O$) in the water and in the biota of the Baltic Sea (Rolff and Elmgren, 2000; Kiljunen *et al.*, 2006, 2008; Torniainen *et al.*, 2014, 2017), less saline areas having more depleted values. These gradients have proven very useful in the identification of salmon feeding areas in the Baltic Sea from SIs of salmon scales (Torniainen *et al.*, 2014) and otoliths (Torniainen *et al.*, 2017). The results of our analysis suggest that the 1SS salmon have been feeding at different sea areas compared with 1SW and MSW salmon. Due to their depleted values, the most plausible candidate for their marine feeding area is the the Bothnian Bay (see Figure 1a) in the northernmost part of the Baltic Sea, which has typically not been considered as a feeding area for anadromous salmon (cf. Siira *et al.*, 2006). The distance between the mouth of the River Oulujoki and the northern limit of the known salmon feeding grounds in the Bothnian Sea is ca. 300 km. Post-smolts of the nearest salmon river (River Simojoki) had reached an average distance of 181 km from the river mouth in July and about 400 km in August (Jutila *et al.*, 2009). Therefore, it can be assumed that 1SS salmon have insufficient time at sea to migrate outside the Bothnian Bay and return to River Oulujoki between the stocking in May–June (Table 1) and their return to the river in August–September.

The $\delta^{13}C$ values of two 1SW salmon resembled those of 1SS salmon, but the $\delta^{15}N$ values were more enriched than those in 1SS salmon (i.e. similar as other 1SW salmon). The $\delta^{13}C$ values suggest that those two 1SW salmon had been feeding in the Bothnian Bay like 1SS salmon. Higher $\delta^{15}N$ values are apparently a result of larger size and thus foraging on a slightly higher trophic level (i.e. higher proportion of fish in diet) compared with 1SS salmon (still largely on an invertebrate diet). Interpretation of foraging on a higher trophic level is supported by the sizes of these two individuals—550 mm and 1200 g, and 520 mm and 1100 g—which fall between the average sizes of 1SS and 1SW salmon (Table 2). Further, this suggests that the Bothnian Bay is a poor foraging and growing area for salmon.

More than one million hatchery-reared salmon smolts are released yearly in the Bothnian Bay area (ICES, 2016). If an increasing proportion of the released salmon are not undertaking a normal marine migration (≥1SW) and return to the estuaries and rivers as 1SS fish, the success and profitability of the compensatory releases will decline even more than the reduced post-smolt survival is presently suggesting (ICES, 2016). Although the life history of 1SS salmon after their first ascent to the river remains unknown, it could be anticipated that the premature return migration is further decreasing the success of hatchery-reared salmon in the northern Baltic Sea. New hatchery practices such as rearing of smolts with endurance training (Anttila *et al*., 2011), enriched rearing environment (Hyvärinen and Rodewald, 2013), and feeding an advanced diet for lower, more natural energetic status (Larsson *et al.*, 2012) have shown the potential for improved swimming capacity, migration motivation, and, ultimately, survival of stocked smolts. It is concluded that these alternative rearing practices should be carefully considered in routine hatchery production in order to ensure that reared smolts more closely resemble wild smolts.

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