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Behaviour of trap-and-transported atlantic salmon spawners of hatchery origin in the Ogre river (Latvia) / Nyqvist, D.; Zagars, M.; Calles, O.; Comoglio, C.. - In: JOURNAL OF LIMNOLOGY. - ISSN 1129-5767. - ELETTRONICO. - 78:2(2019), pp. 210-219.

Availability:
This version is available at: 11583/2787918 since: 2020-01-31T14:11:00Z

Publisher:
Page Press Publications

Published
DOI:10.4081/jlimnol.2019.1871

Behaviour of trap-and-transported Atlantic salmon spawners of hatchery origin in the Ogre River (Latvia)

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ABSTRACT

Where migrating fish have to pass multiple dams, very high passage performance is required at the series of obstacles to avoid accumulated negative effects of multiple dam passage. In some rivers, migrating fish are trapped, transported past several obstacles, and released to continue their migration. Such trap-and-transport solutions, however, have seldom been evaluated. In the Daugava River, Latvia, several dams with no functional fishways block the river for migrating fish. A remnant Atlantic salmon population is being sustained by a sea ranching regime, where returning spawners are caught and artificially spawned, the juveniles raised in hatcheries, and smolts released in to the river in time for their seaward migration. Hatchery released fish, however, differ substantially from wild conspecifics, and in Latvia, as elsewhere throughout the range of salmon, reduced dependency on hatchery production and the re-establishment of wild salmon populations are being discussed. In the Daugava River system, suitable spawning and rearing habitat remains upstream two dams and an associated large reservoir in a mainstem tributary, the Ogre River, offering the potential to restore a wild salmon population. To explore the potential of a trap-and-transport solution to bring Atlantic salmon spawners in contact with remaining spawning grounds in the Daugava River system, spawners were caught, radio tagged, transported upstream of the two dams and the reservoir, and released to pursue their spawning migration in the tributary. Despite being unfamiliar with the river, some of the tagged spawners moved upstream, reaching areas up to 12 km from the release sites. Males were observed higher upstream in the river compared to females, and some males were tracked relatively close to potential salmon spawning habitat. Females, although displaying some movements in the lower parts of the river, did not move far upstream and were not observed close to any suitable spawning areas, highlighting potentially important sex differences in post trap-and-transport behaviour. Perhaps due to different responses to handling stress, between males and females such low post-transportation spawning success among females has the potential to negatively impact restoration efforts in the Daugava River system and elsewhere. The present study represents a first step towards the restoration of wild Daugava salmon, one of several unique Baltic Atlantic salmon populations, and a potential model for future restoration efforts.

INTRODUCTION

Atlantic salmon (*Salmo salar*) is a socially important migrating fish species with a life cycle consisting of a juvenile stage in rivers and streams, migration to feeding areas at sea or in large lakes, and a return migration to its river of origin to spawn (Klemetsen *et al.*, 2003; Jonsson and Jonsson, 2011). Similar to other river migrating fish species, Atlantic salmon has suffered population declines and local extinction in rivers throughout their range of distribution (MacCrimmon and Gots, 1979; Parrish *et al.*, 1998; Waldman, 2013). In many rivers connected to the Baltic sea, damming of the river for hydropower, together with dredging of juvenile and spawning habitat for log driving, have been the main causes behind salmon extirpations (Mannerla *et al.,* 2011).

While hydropower is an important source of electricity, associated dams block migration routes, break longitudinal connectivity, disrupt natural flow regimes, and inundate lotic habitat for riverine and migrating fish (Rudberg *et al.,* 2014; Olden, 2015; Birnie-Gauvin *et al.,* 2017). The need for fishways and other solutions to facilitate both upstream and downstream passage at dams and other migration barriers has been acknowledged for hundreds of years (Montgomery, 2004; Waldman, 2013). Despite this, fishways are lacking at many dams (Calles *et al.,* 2013; Nieminen *et al.,* 2017), and where fish passage solutions exist, their functionality is often relatively low or largely unknown (Bunt *et al.,* 2012, 2016; Noonan *et al.,* 2012).

Instead of building functional fishways, releases of hatchery-reared salmon smolts have been used to mitigate negative effects of dams and habitat loss, and to increase harvest (Brannon *et al.,* 2004; McClure *et al.,* 2008).

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Key words: Baltic salmon; reintroduction; fish passage; salmon migration; sex differences; Daugava River.

Edited by: Fabrizio Stefani, *CNR-IRSA Brugherio, Italy*

Received: 22 November 2018.
Accepted: 28 March 2019.

Licensee PAGEPress, Italy
J. Limnol., 2019; 78(2): 210-219
DOI: 10.4081/jlimnol.2019.1871

Hatchery reared salmon typically spend their first years in high densities, in a predator free environment, with fast growth as a consequence of an abundance of food. This results in hatchery released fish that substantially differ from wild conspecifics. Hatchery-reared salmon have, for example, been observed to have inferior swimming performance (Pedersen *et al.,* 2008), weaker anti-predator response (Jackson and Brown, 2011), and lower marine survival (Saloniemi *et al.,* 2004) compared to wild salmon. Continued hatchery releases risk spreading these, in nature inferior, traits into wild populations (Palmé *et al.,* 2012). At the same time, adding hatchery-reared salmon to the system also masks negative effects of dams and habitat destruction. Consequently, the conservation value of hatchery releases is currently questioned (Palmé *et al.,* 2012; Brown *et al.,* 2013). In the Baltic Sea, many salmon populations are completely dependent on hatchery releases, and the aim has been set to replace release programs with re-established, wild self-reproducing salmon populations (Mannerla *et al.,* 2011; Swedish Agency for Marine and Water Management, 2015).

Re-establishment of wild salmon populations in rivers where they have been extirpated requires available spawning and rearing habitat, as well as free migration routes. Hence, the successful termination of hatchery programsin impounded rivers involves habitat restoration and the construction of functional fishways (Mannerla *et al.,* 2011; Swedish Agency for Marine and Water Management, 2015). Wild salmon can then be allowed to naturally recolonize the river (Kesler *et al.,* 2011), although the process could potentially be made faster by implementing active reintroduction programs (Hesthagen and Larsen, 2003). Such Atlantic salmon reintroduction programs exist across the Atlantic salmon's range of distribution, and typically involves releases of eggs, fry or smolts (Bölscher *et al.,* 2013; Gustafsson *et al.,* 2015; Dirado *et al.,* 2017; Lyach and Čech, 2017; Nyqvist *et al.,* 2017a). Transportation of hatchery reared salmonid spawners has, at some places and with variable success, also been part of reintroduction studies or programs (Hagelin *et al.,* 2016b, 2018).

Where migrating fish have to pass multiple dams, with little suitable habitat available between these man-made obstacles, very high passage performance is required at the series of dams to avoid accumulated negative effects of multiple dam passages (Norrgård *et al.,* 2012; Greenberg *et al.,* 2017). Very high passage efficiency, (percent fish successfully passing), and little passage delay at dams can be difficult and costly to achieve (Bunt *et al.,* 2012, 2016; Noonan *et al.,* 2012). Instead, in some rivers where multiple dam passage is required, various trap-and-transport solutions have been applied. For example, in the River Klarälven, Sweden, and the Winooski River, USA, upstream migrating Atlantic salmon spawners are caught at the lowermost dam and transported by truck upstream, past a series of dams, and released to resume their migration (Piccolo *et al.,* 2012; Nyqvist *et al.,* 2017a). In the Columbia River, USA, downstream migrating Pacific salmon (*Onchorhynchus spp*.) smolts and steelhead (*Oncorhynchus sp.*) kelts are trapped on their downstream migration, transported downstream in barges and released downstream of the lowermost dam to continue their migration towards the sea (Zabel and Williams, 2002; Evans *et al.,* 2008).

The Daugava River is Latvia's largest river, and used to be home to a socially and economically important Atlantic salmon population (Askling, 2015). Development of hydropower during the 20th century created a great capacity to produce electricity, with Daugava hydropower plants supplying 50-100% of Latvia's electricity demand, but also led to the virtual extirpation of self-reproducing Atlantic salmon (Bolonina *et al.,* 2016). Hydropower dams inundated large former lotic habitats and blocked migration routes for Atlantic salmon and other migratory fish species such as brown trout (*Salmo trutta*), river lamprey *(Lampetra fluviatilis),* and vimba (*Vimba vimba).* No functional fishways are present in the river and the Atlantic salmon population has been sustained by a sea ranching regime including annual releases of hatchery reared smolts and collection of returning spawners as brood stock (Mannerla *et al.,* 2011; Bolonina *et al.,* 2016). Suitable spawning and rearing habitat, however, remains in the Ogre River, an upstream tributary to the Daugava River (Birzaks, 2013). The remaining salmon spawning and rearing habitats in the Ogre River, are located upstream of one main stem dam (Riga dam), a large reservoir, and one dam in the tributary itself. The lack of suitable salmon habitat between the dams, in combination with the high technical complexity and costs needed to retrofit the Riga dam and reservoir with a two-way fishway, suggests that a trap-and-transport solution might be an appropriate, short term, fish passage solution in the river system. Returning Atlantic salmon spawners would be caught downstream the lowermost hydropower dam (Riga dam), transported upstream, and released to continue their spawning migration in the river reach with suitable spawning habitat. To explore such a trap-and-transport solution, and to study the behaviour of trap-and-transported fish, returning male and female spawners of hatchery origin were caught, radio tagged, transported upstream past the two dams, and released to pursue their spawning migration to potentially suitable spawning habitat in the Ogre River. The radio tagged fish were tracked manually, and with one stationary receiver, in the river throughout the spawning season and fish movements in relation to sex and river habitat was evaluated.

METHODS

Study area

The Daugava River (Fig. 1) originates in the Valdai Hills, Russia, and runs through Russia, Belarus and Latvia before emptying into the Gulf of Riga, in the Baltic Sea. The river is 1020 km long, with a catchment of 87,900 km^2, and a mean annual discharge of 678 m^3/s. It is Latvia's largest river, and the confluences of two major Latvian tributaries, the Ogre and Aiviekste rivers, are situated about 50 km and 120 km from the river mouth (Vogt *et al.,* 2007; Bolonina *et al.,* 2016). Historically, the Daugava River supported large populations of migrating fish with Atlantic salmon, brown trout, vimba, and river lamprey migrating from the Baltic Sea to river reaches higher up the system. With the development of hydropower in the mid-1900s migrating fish populations were substantially reduced. To compensate for losses caused by hydropower dams, juveniles and fry of Atlantic salmon, brown trout, vimba, river lamprey, whitefish (*Coregonus sp.),* pikeperch (*Sander lucioperca),* and pike (*Esox lucius)* are stocked in the river (Bolonina *et al.,* 2016).

The Atlantic salmon population is currently sustained by releases of hatchery reared smolts and collection of returning spawners as brood stock. The sea ranched Atlantic salmon population has its origin in the historical wild Daugava salmon population (Mannerla *et al.,* 2011). Compared to the historical wild salmon population, the sea ranched population matures at a younger age, and has become dominated by late-run spawners. Currently, 400,000 - 600 000 hatchery reared smolts are stocked annually in the Daugava River (Bolonina *et al.*, 2016; ICES, 2017; ICES, 2018).

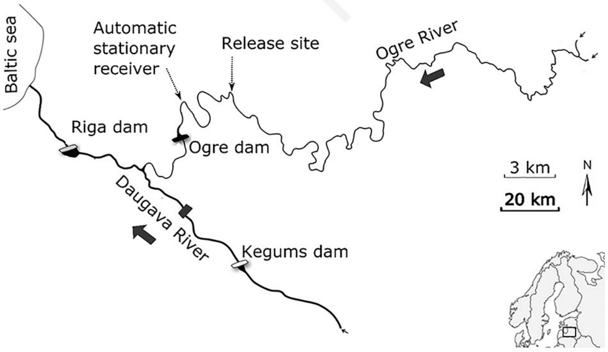

Fig. 1. The Daugava River with the tributary Ogre River, with hydropower dams, the release site and the automatic stationary receiver. Hydropower dams are denoted by black bars and flow direction with large arrows. Note that separate scales apply to the larger Daugava River (thick scale, 20 km) and the smaller Ogre River (thin scale, 3 km).

The Ogre River is 188 km long, with a catchment of 1730 km^2 and a mean annual discharge of 18 m^3/s (Askling, 2015). During the study period, river level (a proxy for variation in discharge) varied from 52 cm to 135 cm (mean=83 cm) and temperature from 1.8 to 11.5°C (Fig. 2; Latvian Environment, Geology and Meteorology Centre). The riverbed consists mainly of sand substrate, and the river is primarily surrounded by mixed forest and agricultural land. A total of 223 potential Atlantic salmon spawning areas, covering an area of 29.6 ha, has been reported (Birzaks, 2013; Askling, 2015). The potential spawning areas most relevant for re-introduction purposes are located between the lowermost hydropower dam (Ogre dam), 5 km upstream from the confluence with the Daugava River, and a hydropower dam located 80 km upstream Ogre dam.

Ogre dam, the lowermost hydropower dam on the Ogre River, is located about 50 km from the Baltic Sea, by the town of Ogre (Fig. 1). The hydropower station at the Ogre dam (Fig. 3) has a production capacity of 630 kW (Askling, 2015). The turbine intake is protected by a rack with 2 cm bar spacings, and water not used for electricity production is spilled via spill gates located at the water surface.

Radio telemetry

Returning Atlantic salmon spawners of hatchery-reared origin were caught with fyke-nets by local fishermen at the mouth of the Daugava River during their

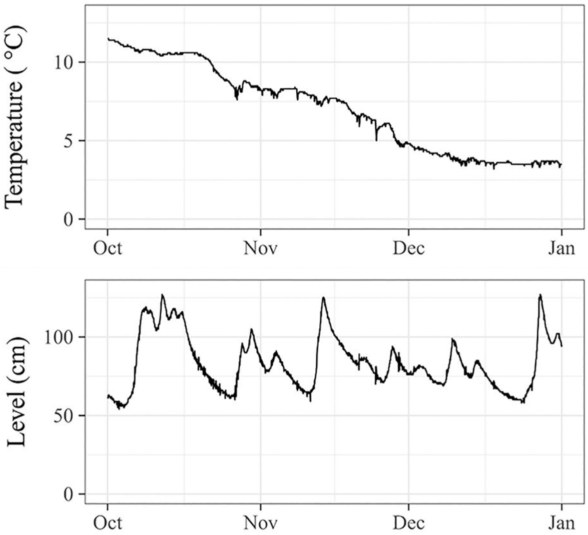

Fig. 2. River temperature (°C) and level in Ogre River during the study period. Data from LVGMC -Latvijas Vides, ģeoloģijas un meteoroloģijas centrs (Latvian Environment, Geology and Meteorology Centre).

spawning migration in late October 2017. The captured fish were transported to a hatchery where they were kept for 3 to 5 days before tagging. After tagging, the fish recuperated in well aerated water for about 1 h before being transported to the Ogre River (about 1 h drive). Fish were released in the Ogre River, approximately 5 km upstream of the Ogre dam on 30-31 October 2017. The fish were individually inspected before release, and only healthy looking, actively swimming fish, were released into the river. Fish were tagged and released in two groups, on two subsequent days.

The fish were tagged with external radio transmitters (model F2120; 16 g; 21 × 52 × 11 mm; 55 ppm; Advanced Telemetry System ATS, USA), each transmitting on a unique frequency (151.000-151.640 MHz). The tags were attached below the dorsal fin, using wires inserted horizontally through the upper part of the musculature. The fish were tagged in water-filled tubes, with their head covered and without use of anaesthetics, following Thorstad *et al*. (2000). Transmitter weight was considerably less than the recommended maximum for natural behaviour of tagged fish (Winter, 1983; Brown *et al.,* 1999).

After release, fish were tracked manually in the Ogre River, from the confluence with the Daugava River up to the second hydropower dam (from car and walking along the shore and on the Ogre dam) with handheld antennas and receivers (R4000 & R410, ATS, USA) every 1-3 days, until the presumed end of spawning activity (*i.e.* cessation of significant movements due to mortality, fish leaving the system, or over-wintering inactivity). After the spawning season, in December and early January, fish were tracked approximately once a week. Fish position and time was noted in GISPro (Garafa LLC, Provo, UT, USA).

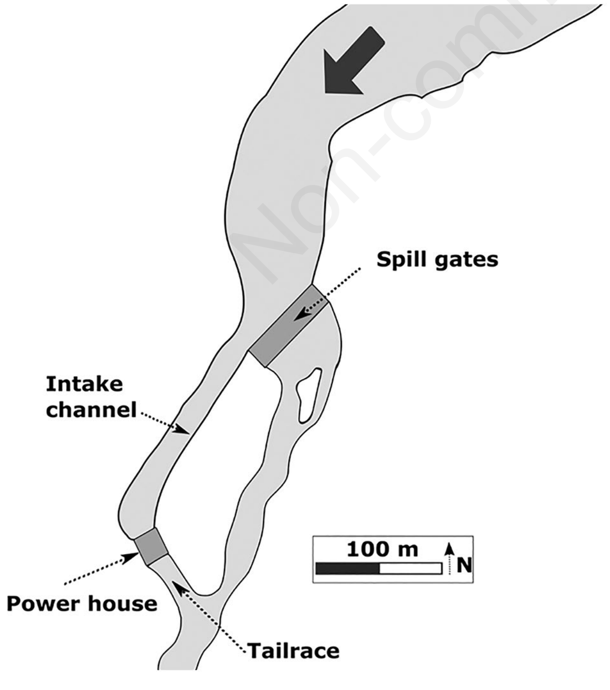

Fig. 3. The Ogre dam with the hydropower plant (Power house), turbine intake channel and spill gates. The thick arrow shows the direction of flow. The depicted area upstream of the dam constitute the forebay.

In addition, fish approaching or returning upstream from the Ogre dam were automatically tracked by a stationary automatic receiver (model R4500S; ATS, USA), connected to a unidirectional antenna, on the shore of the river, 3 km upstream of the Ogre dam, and 2 km downstream of the release site.

Data analysis

Manual radio tracking was used to position fish in the river. Maximum river distance ascent was defined as the highest position where the individual fish was manually positioned, constituting a conservative measure of distance ascended.

For fish tracked downstream of the Ogre dam, time from release to passage was calculated as the time from release to the first time the fish was positioned downstream of the dam. Our estimated time to passage is therefore per definition longer (the interval between tracking occasions) than the actual duration of time. Fish positions were compared to the locations of suitable spawning habitat (mapped by Latvian Institute of Food Safety, Animal Health and Environment; Birzaks, 2013), and the number of fish present in the vicinity (<600 m) of or on suitable spawning habitat was quantified. The automatic stationary receiver placed between the release site and Ogre dam tracked fish visiting this reach of the river, a specific reach of the river of about 500 m long. Typically, a visit means that the fish passed the reach, moving towards or away from the dam. It can also, however, mean that the fish visited the reach, and, for some reason, turned back up- or downstream. Number of visits to the river reach covered by the receiver was used to quantify movement taking place in the time between tracking events. For fish detected within this reach, periods of >2 h without radio detection defined departure from the area (either in an upstream or downstream direction), and subsequent detections constituted a new visit.

Wilcoxon-tests were used to test for sex related differences in maximum river distance of ascent and number of visits to the reach covered by the automatic stationary receiver between males and females. Data analysis was performed with software QGIS ver. 2.18.14 (https://qgis.org/ en/site/) and R (https://www.R-project.org/). In R, the following packages were used:

ggplot2 (for plots and visual movement analysis; Wickham, 2016), plotly (for visual movement analysis; Sievert *et al.,* 2017), dplyr (for data management; Wickham and Francois, 2015), plyr (for data management; Wickham and Wickham, 2017), and sqldf (for data management; Grothendieck and Grothendieck, 2017).

RESULTS

Twenty Atlantic salmon spawners were tagged and released in the Ogre River on 30 October (n=15) and 31 October (n=5) 2017. The tagged fish had a mean length and weight of 76 cm (SD=8 cm, range=62-92 cm) and 4.8 kg (SD=1.9 kg, range=3.1-8.9 kg). Of the tagged fish, 7 fish were females, and 13 were males. Females were significantly larger than males (length and weight; *t*-test, t=6.0 and 7.6, P<0.01). Fish were manually tracked in the river on 22 separate occasions. Individual fish were positioned on 4-22 times (median=18.5 times), constituting 20-100 % (median=84%) of tracking occasions. All fish moved after release. Sixteen fish (80%) showed some upstream movement, with maximum river distance of ascent ranging from 50 m to 12,300 m (median=1700 m). Eight fish moved more than 1000 m upstream (Fig. 4).

Males ascended higher than females (Wilcoxon Test, W=18.5, P=0.03), and no female ascended higher than 150 m (Fig. 5). There was no observed difference in maximum river distance of ascent between fish in the two release groups (Wilcoxon Test, W=11.5, P=0.84).

Individual fish visited the river reach covered by the stationary automatic receiver from one to eight times (median=3), displaying a more intense localized search behaviour than what was immediately visible from the manual tracking data. Even though males were detected further upstream than females no statistically significant sex difference was found in the number of visits to the receiver station reach of the river (Wilcoxon Test, W=19.5, P=0.27; Fig. 6).

Four fish (all males) were positioned in relative proximity (<600 m) to known suitable spawning ground, but no fish was repeatedly tracked in or close to suitable spawning habitat.

Ten fish eventually moved to and passed (or fell back) over the hydropower dam and were tracked downstream in the Ogre River. Time from release to downstream dam passage ranged from 8.8 - 19.9 days (median=14.3 days). No difference (Wilcoxon Test, P=0.83) in time from release to downstream passage between males (n=7) and females (n=3) was observed. Downstream passage

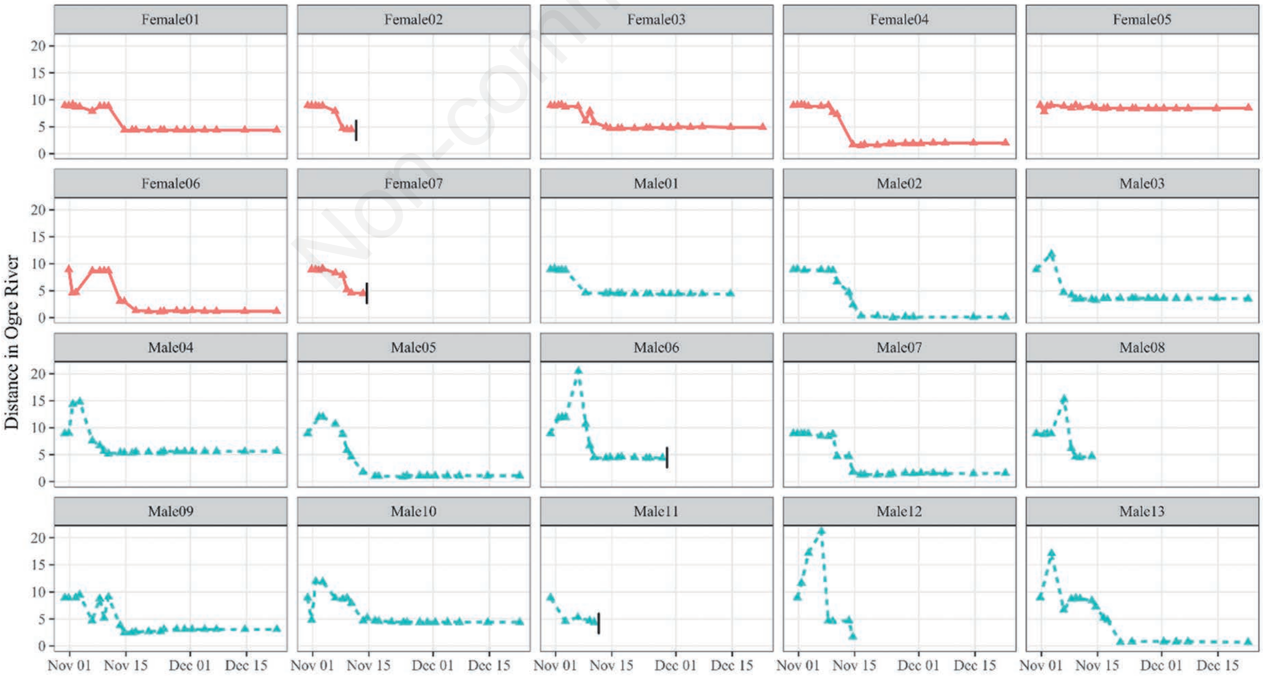

Fig. 4. Individual movements of radio tagged female (solid, red lines) and males (dashed, blue lines) in the Ogre River (rkm from the confluence with the Daugava River) as positioned by manual tracking November and December 2016. Black bars represent time of recapture of weak fish close to the hydropower dam. The release site is located at a distance of 9 km, and the dam at around 4.5-5 km from the confluence.

coincided with the highest river water levels during the study period (Fig 3), and most fish presumably passed downstream via temporarily opened spill gates. One fish, was tracked repeatedly, and until the end of the study, in the tailrace of the hydropower plant. Reportedly, it was lifted over the dam by workers at the hydropower station as they were cleaning the intake rack. Of the ten fish downstream the Ogre dam, seven were tracked in the intake channel of the hydropower dam, one in the forebay of the dam, and one within 500 m of the dam. In total, eight fish were tracked visiting the turbine intake channel.

By the end of the study, 14 fish had been repeatedly tracked at the same place in the river, assumed dead or inactive over winter. Four fish were found in bad condition in the Ogre dam forebay, captured and sacrificed. Two fish disappeared from the system after showing previous movements, including presence in the turbine intake channel, indicating that they were heading in a downstream direction. These two fish may have successfully left the Ogre River and entered the Daugava River (Fig. 3).

DISCUSSION

For the first time in decades, Atlantic salmon spawners migrated upstream in the Ogre River, a Daugava River tributary. Despite being unfamiliar with the tributary, some of the tagged spawners moved upstream, reaching areas up to 12 km from the release sites. Males were observed further upstream compared to females, and some males were tracked relatively close to potential spawning habitat. Females, although displaying some movements in the lower parts of the river, were not observed close to any suitable spawning areas, making successful spawning among these transported fish unlikely.

Sex differences in response to fisheries management actions, such as fish passage solutions, are often overlooked, but may have important implications for management and conservation (Hanson *et al.*, 2008; Roscoe *et al.*, 2011). In this study, males migrated further upstream compared to females. In contrast to females, males continued their spawning migration and, at least some males, located suitable spawning habitat. Even in natural free flowing rivers, males and females often display different migratory patterns. Females have been reported to migrate in a more step-wise manner (Karppinen *et al.,* 2004), but also to take longer to pass natural barriers (Kennedy *et al.,* 2013) compared to males. Also in passage of technical fishways, females have been seen to pass at lower rates and with longer delays (Lundqvist *et al.,* 2008; Nyqvist *et al.,* 2017b). Lower female fish passage success has, in sockeye salmon (*Oncorhynchus nerka)*, been attributed to behavioural differences and higher sensitivity to environmental stressors as an effect of higher investment in gonadal development in females compared to males (Burnett *et al.,* 2014a, 2014b). Our transported fish were caught in fyke nets, transported to a hatchery, tagged and transported to the river, before being released to continue their migration. It is plausible that females, as in Pacific salmon, were more negatively affected by the stress, here associated with substantial and repeated handling. A less stressful route to the Ogre River, may result in females continuing their migration towards suitable spawning grounds.

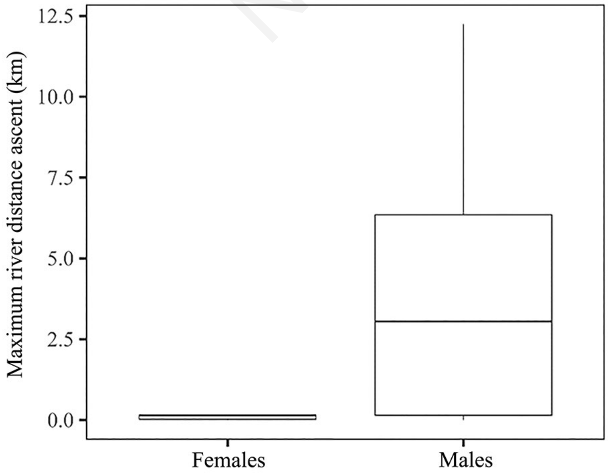

Fig. 5. Maximum river distance ascended by female and male Atlantic salmon (n=20).

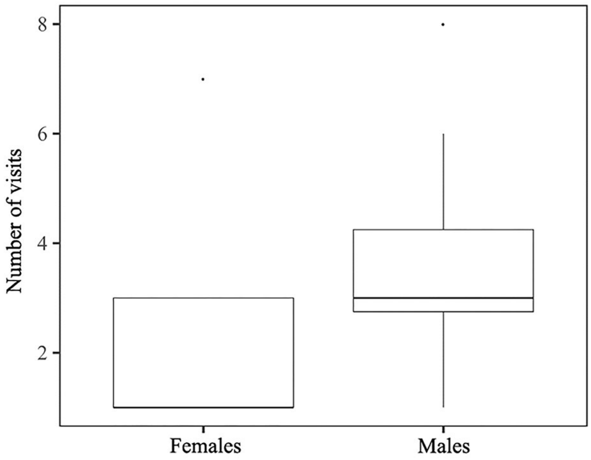

Fig. 6. Number of visits, or passages, of the river reach, located between the release site and the Ogre dam, and covered by the stationary automatic receiver (n=20).

A potential problem in trap-and-transport fish passage solutions is that fish may fall back downstream of the dam over which they were transported (Naughton *et al.,* 2006; Hagelin *et al.,* 2016a). If no spawning grounds are present downstream of the dam, falling back is equal to failed spawning. The risk of falling back depends on local river and dam characteristics, such as spill regimes and location of downstream passage routes (Reischel and Bjornn, 2003; Nyqvist *et al.,* 2017b). In our study, fish moving downstream did not immediately pass the dam, but remained for some time in its forebay, and the stationary automatic receiver showed that most fish that had dropped down to the dam made several upstream excursions before passing downstream. This indicates that the dam, to some extent, deters fish from falling back even when spill is being discharged. A few years ago, in a pilot study, Atlantic salmon spawners of hatchery origin were also transported upstream in the Daugava River system. In that year, however, all fish released in the Ogre River fell back behind the hydropower dam relatively shortly after release, whereas most fish in our study displayed at least some upstream movement. The difference could be explained, at least partly, by exceptionally high flows during the pilot study, providing downstream passage routes through wide open spill gates as well as potentially displacing recently transported fish during that year (Askling, 2015). High fallback percentages of transported spawners of hatchery and wild origin transported to river reaches not previously experienced have been seen elsewhere (Hagelin *et al.,* 2016b). In the River Klarälven, many of the transported hatchery spawners, presumably looking for their river reach of origin not to be found in these reaches of the river, displayed extensive ("erratic") search behaviour and eventually fell back behind the downstream hydropower dam, and were lost from the system (Hagelin *et al.,* 2016b). Spawning success among transported Atlantic salmon of hatchery origin has, however, also been observed (Scott *et al.,* 2005). Late transportation of fish, leaving little time for extensive search behaviour before spawning, has been suggested to contribute to spawning success of spawners of hatchery origin (Hagelin *et al.,* 2016a).

Only two fish seem to have successfully passed the Ogre dam and continued downstream to the Daugava River. Even so, this study can advise on downstream passage behaviour and potential fish passage solutions. Many fish did visit the turbine intake channel. Here, the volume of water is restricted and fish can be trapped or bypassed using relatively proven technology. At a similar setting at a dam in River Ätran, Sweden, a low sloping turbine intake rack, connected to a bypass, successfully guided Atlantic salmon kelts and smolts, as well as eels, past the hydropower dam (Nyqvist *et al.,* 2017b, 2018). In the present study, some fish probably eventually passed via the spill gates. When large amounts of water are spilled, fish passage rate through the spill gates is likely to increase, with more fish passing directly via the spill gates (Wertheimer and Evans, 2005; Nyqvist *et al.,* 2016). High occurrence of spill passage was also seen during high levels of spill in the previous pilot study in the Ogre River (Askling, 2015). For transported spawners, downstream passage is undesirable before spawning. But even for downstream migrating smolts and post-spawners, for spill passage to be preferred over collection in the intake channel, passage solutions at downstream dams are required (Greenberg *et al*., 2017).

Efforts to reintroduce wild Atlantic salmon populations are ongoing or discussed in many former Atlantic salmon rivers around the Baltic Sea (Mannerla *et al.,* 2011) and elsewhere (Bölscher *et al.,* 2013; Dirado *et al.,* 2017; Lyach and Čech, 2017). Despite a low sample size, which should be remembered when interpreting the presented results, this study represents a first step towards restoration of salmon in the Daugava River system. Trap-and-transport of spawners of hatchery origin can teach us about fish behaviour in the river (Hagelin *et al.,* 2018) but also contribute to the in-river production of salmonids (Piccolo *et al.,* 2012), and raises enthusiasm about reestablishment of wild salmon populations. The restoration of wild salmon to the Daugava River, however, will require much more. Longitudinal connectivity between the Baltic Sea and available spawning grounds in the Ogre River needs to be restored, through an efficient and fish friendly trap-and-transport solution, and/or multiple fishways. Even though Atlantic salmon, given two-way connectivity, can recolonize available habitat on their own (Kesler *et al.,* 2011), release of egg, fry or smolts by the spawning and nursery grounds might speed up the reestablishment process (Hesthagen and Larsen, 2003). Also, additional habitat restoration, and even the construction of artificial spawning grounds could be part of the restoration effort (Bolonina *et al.,* 2016).

CONCLUSIONS

This study is part of wide ranging efforts to re-establish wild Atlantic salmon in Baltic rivers. The results document upstream migration of transported fish and highlight sex differences in post-transportation behaviour related to potential spawning success. Lower post-transportation spawning success among females, perhaps due to different responses to handling stress, could have detrimental effects on the success of trap-and-transport programs as part of salmon re-introduction projects in the Daugava River system and elsewhere. This highlights the importance of evaluating fish passage solutions, and that any trap-and-transport solution needs to assess the migration and spawning success of transported fish.

ACKNOWLEDGMENTS

This research was funded by Latvenergo AS, the main hydropower company in Latvia. The authors wish to thank Dr. Alona Bolonina and Marta Utane, reference officers of Latvenergo AS, for their support during the study, Linda Buholce, Marta Dievina, Marta Utane, and Armands Roze for assistance in the field, and John Piccolo. We also thank fish farm “Tome” for providing tagging facilities.

The study was performed with permission from Institute of Food Safety, Animal Health and Environment “BIOR”, The Food and Veterinary Service and The Nature Conservation Agency, Latvia.

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