Survival of reared Atlantic salmon (Salmo salar) smolts during downstream migration and its timing: a case study in the Pirita River

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Downstream migration of 1- and 2-year-old reared Atlantic salmon (Salmo salar) smolts in the Pirita River was studied using a mark–recapture method. Age affected the migration duration. Majority of the 2-year-old fish reached the sea within a week after release, but younger, 1-year-old fish, descended later and reached the sea a few weeks after stocking. A few 1-year-old fish remained in the river for an additional year and migrated one year later, simultaneously with wild smolts. On average, 2-year-old smolts had higher survival (44%) than 1-year-old smolts (18.8%). Hence, the efficiency of stocking programs most probably depends not only on the number of stocked fish, but also on their age, timing of smoltification and on environmental conditions.

Introduction

Atlantic salmon (Salmo salar) stocks in the Baltic Sea started to decline in the 1950s, mainly due to damming and water pollution. Later, most stocks were overexploited by sea fisheries. To restore wild reproduction and sustain catches, extensive and costly enhancement programmes are carried out in several countries. In Estonia, the stocking programme for the Pirita River started in 1998. It is based on annual releases of 1- and 2-year-old smolts and young-of-the-year parr. During the last decade, however, recoveries of tagged fish in the commercial sea fisheries have been alarmingly low, which has given rise to serious doubts about the success of salmon stocking programmes. Carlin-tag recovery of 2-year-old smolts stocked in the Pirita River varies between 0.6%–1.6%, and for 1-year-old-smolt recovery has been as low as 0.1%–0.3% (Paaver et al. 2006). Some of the mortality causing the low recapture rates may occur during freshwater migration.

In spring, Atlantic salmon smolts migrate downstream from freshwater nursery areas to feeding areas in the sea. During migration, smolts encounter several bird and fish predators (Larsson 1985, Koed et al. 2002, Jepsen et al. 2006, Strand and Finstad 2007). Reared smolts do not survive during migration as well as their wild counterparts (Jonsson et al. 1991). The period between the release from the hatchery and
entering the sea is the most critical for survival (Larsson 1985). Finally, one of the most important factors influencing survival of reared smolts is the timing of migration (McKinnell and Lundqvist 2000, Kallio-Nyberg et al. 2004). Migration of wild smolts occurs during an ecological and physiological “migration window” (Jonsson and Ruud-Hansen 1985, Zydlewski et al. 2005), when conditions for migration are optimal. Most likely, these conditions differ between rivers, and wild smolts are adapted to their local environmental conditions. Therefore, it is recommended that reared smolts are released simultaneously with the migration of wild smolts, especially if stocked fish originate from other rivers (Kennedy et al. 1984, Strand and Finstad 2007), and despite the size and behavior differences between reared and wild smolts (Jonsson et al. 1991). Reared smolts that are released into rivers a few weeks before the beginning of migration season descend at the same time as wild smolts (Jokikokko and Mäntyniemi 2003). However, survival rates and timing of migration after release and before entering the sea are still poorly known, especially when several different age groups are simultaneously released.

In this study, timing of migration and survival rates during the freshwater period of reared 1- and 2-year-old smolts stocked in 2007–2010 were compared using a mark–recapture method. Some of the stocked 1-year-old fish did not migrate to the sea in the same year when they were released; they spent a year in the river as parr, and migrated to the sea one year later. These fish were also included in the mark–recapture study, and because these fish had smoltified in the wild, their migration timing was compared with that of the wild fish.

### Material and methods

The study was carried out in the lower reaches of the Pirita River (59°28’N, 24°29’E), which flows into the Gulf of Finland (Baltic Sea) (Fig. 1). The river is 105 km long; its catchment area is 799 km², and a mean annual runoff 6 m³ s⁻¹ (Järvekülg 2001). The lower 24 km of the river are accessible to anadromous fish, and the main rapids suitable for salmon spawning and growth of juveniles are situated in the lowest 16-km stretch (slope 2 m km⁻¹), with the total habitat area of 9–10 ha (Kangur and Viilman 2001). The reared fish were always released at the same site: 13 km upstream from the river mouth (Fig. 1).

The fish were reared in the Põlula Fish Breeding Centre and were released as 1- (1Y) and 2-year-olds (2Y). The fish released in 2007 and 2008 originated from the Neva River, and in 2009 and 2010 from the Kunda River. Details about the reared fish and natural conditions on the release dates are presented in Table 1. All stocked fish had the adipose fin clipped. Both age groups were reared under the same temperature and light conditions. One hundred fish of every release group were visually examined for smoltification (i.e. silver colorization; Hoar 1988; Table 1). Smoltified fish may loose the instinct to migrate downstream when kept too long in the hatchery (Zydlewski et al. 2005), so in 2007 the majority (82%) of the 2Y old smolts were released (23 Apr. 2007) before 1Y old fish (5 May 2007) and in 2009 all of the 2Y smolts were released before 1Y old fish (5 and 9 May 2009, respectively). Water level data for the study area was obtained from the Estonian Meteorological and Hydrological Institute (www.emhi.ee).

A trap net was placed 1 km from the river mouth and 12 km downstream from the stocking site. Trapping began in mid-April and lasted until no smolts migrated for three days. Daily aver-
age water temperature at the start of the trapping period was below 5 °C and at the end it ranged from 12.5 to 19 °C. At the trapping site, the river was approximately 100 m wide, of which the trap net covered 1/3. The trap net was attended daily.

The number of smolts reaching the sea was calculated using Petersen’s mark–recapture method (Schwarz and Dempson 1994). During the entire study period (2007–2010), 2805 reared smolts were caught, and they were marked with a Visible Implant Elastomer (VIE, Northwest Marine Technology Inc.) tag in the post-ocular tissue (Table 1). To ensure recovery from the handling, tagged fish were held in a tank for 15 minutes, and then released 2 km upstream from the trap. The release site was located on the lowest rapid, which provided a good habitat for released smolts. Fish with visible injuries were not tagged.

Reared 1-year-old fish which had remained in the river for an additional year after their release were also included in the trapping and tagging study (migration of these fish occurred in 2008 and in 2010). This allowed us to compare the timing and duration of downstream migration of reared and wild smolts (Table 1). Freshly released fish were distinguished from the stocked ones that had remained in the river for a year, by their eroded fins with unhealed wounds, and at least some degree of scale loss. Coloration of the freshly released fish was bright green and resembled the color of the tanks in which they were reared. The fish stocked one year earlier had fully healed fins, although in some cases earlier fin deformations that healed could be detected. Their scale cover was also fully regenerated and the coloration was identical to that of the wild smolts.

For this mark–recapture study to be valid, it was assumed that (i) the fishing efficiency of the trap net did not change over the annual fishing period, and the probability of capture of all smolts (marked and unmarked) remained equal throughout the spring, (ii) all marked (VIE) smolts migrated downstream after tagging and release, (iii) there was no tag loss between release and recapture, (iv) there was no mortality between release and recapture site, (v) marked and unmarked smolts had equal migration and aggregation patterns.

<table>
<thead>
<tr>
<th>Age group</th>
<th>Release date</th>
<th>Water temp. (°C)</th>
<th>Total weight stocked (g) ± SD</th>
<th>Total length range (mm)</th>
<th>Number captured by trap</th>
<th>Number tagged</th>
<th>Survival rate (%)</th>
<th>Estimated number ± SE reaching the smolt</th>
</tr>
</thead>
<tbody>
<tr>
<td>2Y</td>
<td>2 Apr. 2007</td>
<td>6.1</td>
<td>90 ± 33.6</td>
<td>170–300</td>
<td>100</td>
<td>1550</td>
<td>598</td>
<td>141 ± 23.6</td>
</tr>
<tr>
<td>1Y</td>
<td>2 May 2007</td>
<td>7.5</td>
<td>77.8 ± 31.7</td>
<td>122–165</td>
<td>91</td>
<td>280</td>
<td>184</td>
<td>24 ± 13</td>
</tr>
</tbody>
</table>

Table 1. The characteristics of stocked, tagged and recaptured fish.
Day of the release was considered the null day of migration. In 2007, the second release group of 2Y smolts was too small, so it was excluded from the migration analyses. The two sets of released 2Y smolts were clearly distinguishable; migration of the first group ended well before the second group was released (Fig. 2). For the survival estimate, however, both 2Y groups released in 2007 were combined (see Table 1). The effect of the age of stocked fish on their survival during migration was estimated with a chi-square ($\chi^2$) test on smolt counts of different age groups. Separate general linearized models (GLM) with logit link were used to test the effect of origin (released 1Y fish which had stayed for additional year vs. wild smolts) and age (1Y vs. 2Y) on the individual descent time.

### Results

Both age groups of reared smolts migrated from the release site to the smolt trap faster in 2007 than in 2009; however during both years, the 2Y fish reached the trap earlier than 1Y fish (association of age with descent time: $\chi^2 = 3285.02, p < 0.0001$, year: $\chi^2 = 0.65, p = 0.419$ and year $\times$ descent time interaction $\chi^2 = 107.36, p < 0.0001$; $n = 4399$). In 2007 and 2009, the 2Y smolts reached the smolt trap 16.9 ± 6.6 and 27.4 ± 2.8 days after their release, respectively. In 2007, the first 1Y smolt was caught in the river mouth 6 days, and the last specimen 36 days after their release (Fig. 2). In 2009, the first 1Y smolt was caught 12 days and the last specimen 34 days after their release (Fig. 3).

In 2008, released 1Y fish, which remained for an additional year in the river (released in 2007), migrated slightly earlier than the wild fish, but no such difference was apparent in spring 2010 (origin and year $\times$ descent time interaction $\chi^2 = 96.78, p < 0.0001$ in the model with main effects of year: $\chi^2 = 75.08, p < 0.0001$ and descent time: $\chi^2 = 0.10, p = 0.757; n = 1421$). Migration timing did not differ significantly between the two age groups of the wild fish, but there was a weak but not statistically significant tendency for 2Y smolts to descend later during 2008 (age group association with year: $\chi^2 = 0.16, p = 0.692$, descent time: $\chi^2 = 2.91, p = 0.088$, year $\times$ descent time interaction $\chi^2 = 0.05, p = 0.820; n = 1228$). Therefore, for comparisons of migration timing with reared fish that had remained in the river for one year, different age groups of the wild fish were pooled (Fig. 3). Characteristics of the wild smolts are presented in Table 2.

Out of the stocked 2Y fish, 33%–58.6% reached the smolt trap in 2007–2010 (Petersen’s mark–recapture method estimates; Table 1).
In 2007, out of 11050 stocked 1Y smolts, 2146 ± 239 (mean ± SE) (19.4%) reached the smolt trap and 136 ± 18 migrated one year later. In 2009, out of 15112 stocked 1Y smolts, only 1799 ± 87 (11.9%) reached the smolt trap and 770 ± 159 migrated one year later (Petersen’s mark–recapture method estimates; Table 1). As compared with the older age group (data pooled from both years), the proportion of 1Y smolts reaching the river mouth was significantly smaller ($\chi^2 = 939.31, p < 0.001$).

Discussion

The timing of smolt migration is crucial for later survival in the sea. Migrating too early results in higher mortality; sea-surface temperatures of < 9 °C are associated with low smolt survival (Jutila et al. 2005). The majority of the 2Y reared smolts migrated to the sea just a few days after their release. This took place in the beginning of May, when the water temperature in the Gulf of Finland is usually below 9 °C. In contrast, migration of the 1Y reared smolts, which were stocked slightly later (Fig. 2), took significantly longer. Still, we cannot ignore that in 2007 and in 2009 different age groups were released on slightly different dates and at different water temperatures. However, these differences in temperature were only between 0.8 and 1.4 °C, and the water level changed less than 10 cm. Therefore, even though we cannot rule out that some environmental factor may also have affected our results, we believe that the age and size of smolts were the most important factors affecting duration of migration and fish survival.

Temperature and photoperiod are the main factors determining the initiation and duration of migration. Zydlewski et al. (2005) suggested that the start and the end of the downstream movement are affected more by the cumulative temperature (degree days) than by a certain temperature threshold. Once the temperature requirements are met, an increase in day length triggers smoltification (McCormick et al. 2000). Much earlier smoltification of the released 2Y

<table>
<thead>
<tr>
<th>Year</th>
<th>Age group</th>
<th>Total weight ± SD (g)</th>
<th>n</th>
</tr>
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<tbody>
<tr>
<td>2008</td>
<td>1-year-old</td>
<td>12.3 ± 2.2</td>
<td>112</td>
</tr>
<tr>
<td></td>
<td>2-year-old</td>
<td>23.4 ± 6.3</td>
<td>558</td>
</tr>
<tr>
<td></td>
<td>3-year-old</td>
<td>55.4 ± 5.1</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>Average</td>
<td>21.7 ± 7.6</td>
<td>674</td>
</tr>
<tr>
<td>2010</td>
<td>1-year-old</td>
<td>13 ± 2.6</td>
<td>87</td>
</tr>
<tr>
<td></td>
<td>2-year-old</td>
<td>27.8 ± 5.9</td>
<td>467</td>
</tr>
<tr>
<td></td>
<td>Average</td>
<td>25.5 ± 7.7</td>
<td>554</td>
</tr>
</tbody>
</table>
fish in our study indicates that the threshold levels of environmental factors that trigger smol- tification may be different for different age and/or size groups. This result is in accordance with some previous studies on wild Atlantic (Jonsson et al. 1990) and Baltic salmon smolts (Jutila and Jokikokko 2008), which suggested that younger and smaller smolts migrate later. Bohlin et al. (1996) also reported this pattern for wild smolts of brown trout (Salmo trutta).

The difference in timing of migration of wild smolts and 2Y fish that were released as 1Y and remained in the river for one year was not always the same. In 2008, both groups started to migrate at the same time, however the last reared fish was captured on 26 May and by that time only about 65% of the wild fish had migrated. The wild-smolt migration was completed by the end of June which was exceptionally late (cf. 2008 and 2010 in Fig. 3). Hence, the median migration date of the wild smolts in 2008 was significantly later. This difference may be explained by several factors. The reared smolts which had been stocked as 1Y a year earlier and the wild smolts were of different origins and may have experienced different environmental conditions prior to the 2008 migration. However, 1Y fish that remained in the river for a year had themselves different origins in 2008 and 2010. Therefore, the origin of the stocked fish alone cannot fully explain why the reared fish completed their migration earlier in 2008. Furthermore in 2008, the size difference between the stocked fish that had remained for a year in the river and the wild fish was greater than in 2010. Size-induced segregation in the timing of smolt migration (Jutila and Jokikokko 2008) could also explain this discrepancy.

With only one exception (2010), the wild and the stocked 2Y smolts migrated at the same time, which agrees with the results of Jokikokko and Mäntyniemi (2003), who showed that migration timing of 2Y smolts stocked into the Simojoki (Gulf of Bothnia, Baltic Sea) was similar to that of wild smolts. However their study was carried out in a much larger river, so the results may not be directly comparable.

Judging from the mark–recapture experiment results, both age groups experienced substantial mortality after release. However, 2Y smolts had still much higher survival rates. Keeping in mind the high mortality in both age groups during their 12-km-long migration, it cannot be ruled out that some mortality occurred also during the 2-km-long migration between the release and recapture sites. If that is the case, some tagged fish were not caught by the trap net not because they passed the gear, but because they were caught by predators before reaching the site for the second time. Therefore, if the true catching efficiency of the trap net was higher than the estimation used in our calculations, then in reality even a smaller share of the released smolts reached the river mouth as compared with what we present in our results. Hence, the actual survival of the reared smolts in the Pirita River during their 12-km-long migration from the stocking site to the sea may have been slightly overestimated.

Not all released 1Y fish migrated in the same year. However, the number of non-migrating fish was not high enough to explain the low proportion of 1Y smolts reaching the sea. Most likely, higher mortality of the 1Y smolts was due to the delay in migration after the release and their smaller size making them more susceptible to predators. The Pirita River has a variety of predators: northern pike (Esox lucius), burbot (Lota lota), herring gull (Larus argentatus), grey heron (Ardea cinerea), goosanders (Mergus merganser) and terns (Sterna sp.). Northern pikes alone caused 29% mortality of stocked smolts in the Pyhäjoki (Kekäläinen et al. 2008). Goosanders consumed up to 16% of total smolt run in the North Esk River, which flows into the North Sea (Feltham 1995, Feltham and MacLean 1996). Also grey herons and gulls were found to feed on salmon smolts (Koed et al. 2002, Ruggerone 1986). Therefore in our study, predation might be the main reason for the high mortality of 1Y smolts that remained in the river, since prolonged exposure to predators usually determines survival during freshwater migration (Wood 1987, Jepsen et al. 2006). Also territorial competition within the 1Y group and with the wild conspecifics could contribute to low survival (Romakkaniemi 2008).

We demonstrated differences in the timing of migration and the river-phase survival of reared smolts of different ages. It is also possible that 1Y smolts, which are 3–4 times lighter than the older ones, suffer greater mortality at the very
beginning of their sea phase (Kallio-Nyberg et al. 2004, 2006). On the other hand, the larger 2Y smolts that migrate earlier than wild smolts may be exposed to colder seawater which weakens their chances of survival (Jutila et al. 2005).

The main purpose of salmon stocking in the Pirita River is to increase the number of returning adults to enhance wild reproduction. During the last decade recapture rates of tagged stocked smolts in the Baltic Sea commercial catches were low (Paaver et al. 2006). This alarming information indicates the low success of stock programs depends not only on the number of stocked fish, but also on other factors such as their age, timing of smoltification, and environmental conditions.

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References


