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Riverine and early marine survival of stocked salmon smolts, *Salmo salar* L., descending the Testebo River, Sweden

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Abstract A combination of radio and acoustic telemetry was used to monitor the out-migration of hatchery-reared Atlantic salmon, *Salmo salar* L., in the River Testebo, its estuary and coastal system. As with many other Baltic rivers, the hydropower regulated River Testebo once had a self-sustaining salmon population that is now extinct. Substantial losses of smolts in the river (48–69%) and inner part of the estuary (43–47%) were found, but after leaving the estuary, the success of post-smolts moving out of the Bay was sufficiently high (83–89%) to conclude that habitat within the bay is not a factor limiting initial marine survival. The results suggest that hatchery-based recovery of a wild salmon population in the river will not be successful unless other actions, such as habitat improvement, are included.

KEYWORDS: Atlantic salmon, migration, smolt, stocking, tag.

Introduction

An unprecedented widespread decline in the abundance of Atlantic salmon, *Salmo salar* L., populations has been observed over the past decades (Parrish, Behnke, Gephard, McCormick & Reeves 1998). In North America and Europe, wild populations are endangered in one-third of the salmon rivers and natural stocks have disappeared from nearly 300 of the historically salmon-bearing river systems. In the Baltic Sea region, currently only about 40 out of the estimated original 80–120 rivers supporting salmon populations hold natural spawning runs (ICES 2000).

The current plight of Atlantic salmon is influenced by many casual factors acting in concert. Global processes, such as climate change (Friedland 1998), are superposed on regional and local influences, such as habitat degradation, hydroelectric development, overfishing and pollution (Armstrong, Grant, Forsgren, Fausch, DeGraaf, Fleming, Prowse & Schlosser 1998). Palliative efforts have been carried out to restore extinct and enhance declining salmon populations by supplementing the wild stock with hatchery-reared

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juveniles, but the overall success of these programmes is questionable (Thorpe 1998).

In the Baltic Sea, river releases of hatchery-produced salmon smolts started in the 1950s and currently about 5.5 million smolts are released annually (ICES 2007). Despite these massive releases, Atlantic salmon stocks continue to decline (ICES 2007). It appears that factors affecting survival during the smolt and initial post-smolt stage are associated with this decline (ICES 2007).

Ultimately, the survival of released smolts depends on the state of the fish at the time of release, and on the conditions in rivers, estuaries and the coastal environment (McCormick, Hansen, Quinn & Saunders 1998). Substantial deficits in behavioural and physiological traits have been reported for hatchery-reared individuals (Sundell, Dellefors & Bjornsson 1998; Poole, Nolan, Wevers, Dillane, Cotter & Tully 2003), which may decrease their post-release survival. Moreover, most of the river systems subjected to stocking are or have been adversely affected by different human perturbations, which have profoundly altered many of the characteristics of the migration corridors of smolts. While numerous studies illustrate the impact of single habitat alterations such as dams (Coutant & Whitney 2000), reservoirs (Koed, Jepsen, Aarestrup & Nielsen 2002), weirs (Aarestrup & Koed 2003) or impounded estuaries (Russell, Moore, Ives, Kell, Ives & Stonehewer 1998) on the survival and migration of released salmonids, integrated investigations are lacking. These should incorporate adequate monitoring of post-release survival of hatchery fish, assessment of the relative contribution of different factors on fish mortality, and identification of potential habitats for preservation and restoration (Cowx 1994).

To understand better the relative importance of different elements affecting the survival of hatchery-released fish in the River Testebo, its estuary and coastal environment, the downstream migration of salmon smolts was investigated in the spring of 2006 and 2007. The situation in the River Testebo is typical of many Baltic rivers, that of once having a self-sustaining salmon population now extinct or near extinction (Anonymous 2001). Before 1900, the river was used for timber floating and since the beginning of the last century it was regulated for hydroelectric purposes. Its estuary is confined by a railway bridge and its coastal environment has been influenced by port activities. The approach to migration and passage success of stocked Atlantic salmon smolts at the lower-most power station was investigated using radio telemetry. Information about their subsequent riverine, estuarine and marine migratory behaviour was obtained by acoustic telemetry. Fish were released to obtain overlapping migration routes, which allowed for calculations of combined mortality in the two studied areas.

Materials and methods

Study area and salmon stock

The River Testebo, located in central Sweden, enters the Baltic Sea at 60º41′ N, 17°10′ E, about 85 km from its origin. The study area comprised the last 5 km of the River Testebo, its estuary and the Bay of Gävle (Fig. 1). Until very recently, two power stations were operating within the last 5 km of the

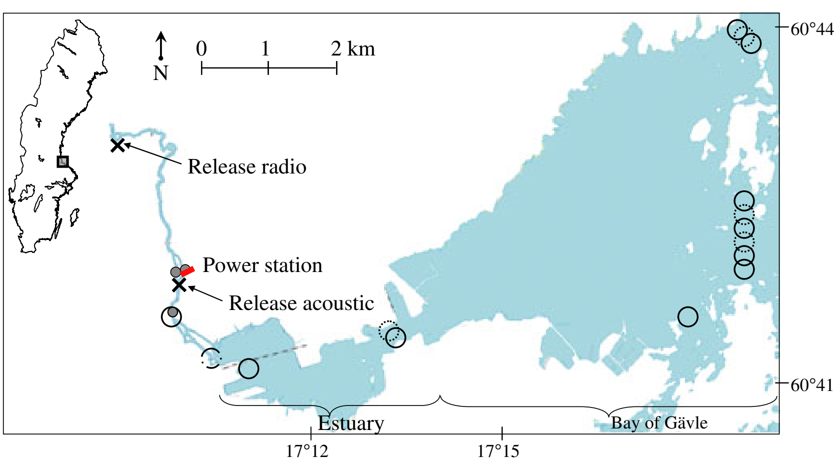

Figure 1. Locations of release sites for radio- and acoustic-tagged Atlantic salmon smolt in the Testebo River. Grey-shaded circles indicate the position of radio loggers. Circles with dashed line denote the position of acoustic receivers in 2006 not present in 2007. Circles with full line denote the location of acoustic receivers present both years.

river; in 2005, the uppermost dam was removed. The remaining station, located 1.7 km upstream from the river mouth, consists of two Francis turbine units and has a discharge capacity of 10 $m^3 s^{-1}$. Flow is diverted into the turbine intake channel by a dam located 200 m upstream from the power-station. The residual stream channel acts as a bypass route for migrating fish and joins the turbine outlet channel approximately 100 m downstream from the power-station. Minimum flow at the bypass channel is 1 $m^3 s^{-1}$.

The estuary of the River Testebo is divided in its middle section by a railway bridge that directs the flow through a 20 m wide channel into the outer part of the estuary. The inner part covers 25 ha and is characterised by shallow (< 3 m) and turbid (secchi-depths in May of 0.8–1.0 m) fresh water (0.005 psu). This section of the estuary has been protected for wildlife use under various jurisdictions since 1997. The outer part of the estuary is still largely influenced by human activities. This section exhibits higher marine influence (1.8–2.3 psu at 1–3 m). Three kilometres east of the river mouth the estuary opens into the Bay of Gävle, a relatively small and shallow (max depth 15 m) coastal system (non-tidal brackish water, 4.2–4.5 psu at 1–3 m), delimited by a belt of islands and islets with few, narrow passages connecting it to the open sea (Fig. 1).

Atlantic salmon was considered extinct in the river by 1960. Within the framework of the international Salmon Action Plan, recent attempts to re-establish a self sustaining salmon population have been carried out and large numbers of eggs and juveniles originating from the nearby River Dal (Dalälven in Swedish) have been introduced every year. However, the number of returning adults has remained low (0–9 per year, 1986–2006). In 2006, a rotary screw smolt trap (Thedinga, Murphy, Johnson, Lorenz & Koski 1994) was installed in the river during April to June and the wild salmon smolt-run was estimated to be between 1300 and 3600 smolts.

Water flow, temperature and salinity

Average water discharge at the river mouth in Testebo is about12 $m^3 s^{-1}$, and can vary from 1 to 160 $m^3 s^{-1}$, with a peak from April to May. During the study period (May to June 2006 and 2007) average daily flows were 28 and 7 $m^3 s^{-1}$ respectively. The trial in 2006 began on the falling limb of the spring flood, when discharge in the river was 58 $m^3 s^{-1}$. Water flow at the power station intake was 10 $m^3 s^{-1}$and the average spill during the experimental period was 19 $m^3 s^{-1}$. In 2007, the flow was substantially lower with a maximum discharge of about 8 $m^3 s^{-1}$ and a constant spill of 1 $m^3 s^{-1}$. Average daily temperatures for May in the river, estuary and Bay of Gävle (1–3 m depth) did not differ substantially between years (ranges for river, estuary and bay: 12.0–15.0, 9.2–10.3 and 5.5–9.1 °C, respectively).

Fish tagging

The study was carried out over 2 years, between 8 May–1 June 2006 and 9 May–8 June 2007. Altogether, 100 hatchery-reared Atlantic salmon smolts were tagged with uniquely pulsed radio transmitters (ATS, model 1540, mass of 2 g in air) and acoustic transmitters (VEMCO Ltd, Canada, V7–1L and V7–2L, mass in air of 1.4–1.6 g) at Älvkarleby Hatchery and Fishery Research Station (Table 1). Smolts were 2 years old and originated from the brood stock of returning adults. The fish were anaesthetized using a 0.5 g L^{-1} solution of MS222 (Jolly, Mawdesley-Thomas & Bucke 1972) until the opercular rate became slow and irregular (2–4 min), weighed to the nearest 0.1 g and measured to the nearest mm (total length). Prior to implantation, all tags were sanitized in 95% ethanol. A mid-ventral incision about 1 cm long was made just anterior to the pelvic girdle and the transmitter gently inserted. The antenna (only in radio tags) was run through a hole from the body cavity, pierced with a needle. The incision was closed with two separate

Table 1. Atlantic salmon post-smolts tagged with radio and acoustic transmitters and released in the Testebo River in 2006 and 2007

Group	*N*	Mean body length (L_T), mm (range, SE)	Mean body mass, g (range, SE)	Mean transmitter mass in air to fish mass ratio (%) (range, SE)	Release dates
2006 Radio	24	223 (205–249, 11.8)	113.4 (84.1–150.9, 19.0)	1.8 (1.3–2.4, 0.3)	8, 10 May
2006 Acoustic	21	214 (202–235, 9.5)	97.6 (82.8–133.8, 13.9)	1.7 (1.2–1.9, 0.2)	9 May
2007 Radio	34	207 (176–240, 15.8)	81.3 (53.2–121.9, 17.7)	2.5 (1.6–3.8, 0.5)	7, 8 May
2007 Acoustic	21	210 (185–245, 17.7)	88.6 (56.6–135.0, 22.9)	1.7 (1.0–2.5, 0.4)	8 May*

*Fish were released on two occasions (00:00 and 01:00 hr).

sutures of coated Vicryl absorbable suture (Ethicon Ltd, Sweden) through the entire body wall. Handling time lasted between 2 and 3 min. Tagged smolts were allowed to recover overnight in the tanks to reduce any possible post-tagging effects in 2006. In 2007, the fish were observed for a period of 3 days. During this period, all fish were judged to be in good condition. In 2007, three radio-tagged fish jumped out of the holding tank at the hatchery 24 h after tag implantation. These fish were dissected and examined visually for gross morphological effects from surgery (damage to internal organs, bleeding), appearing to be unaffected. The radio transmitters were sanitized and re-implanted in other fish. After the recovery period at the hatchery, fish were transported to the release site in aerated tanks, where they remained in cages for 12 h to recuperate from transport without being prone to predation. All releases took place at late evening (19:00–01:00 hours) together with non-tagged hatchery-reared Atlantic salmon smolts to dilute possible predator pressure on the tagged fish. In total, fish were allowed 24 h for recovery in 2006 and 24–84 h in 2007. Radio-tagged fish were released in two groups in 2006 and 2007, whereas acoustic-tagged smolts were released in one group in 2006 and in two groups in 2007 (Table 1). Mean transmitter mass ranged from 0.8% to 2.5% of fish mass ratio.

Fish tracking

Both acoustic and radio telemetry are suitable methods for tracking animals in aquatic systems. The use of one or the other of these methods is mainly determined by water depth, turbulence and conductivity (reviewed by Priede 1992). In general, a radio signal is effective in fresh water and has considerable advantages over an ultrasonic signal in relation to positioning and power usage. Radio waves are however, severely attenuated at high water conductivity and depth. To overcome this limitation, a combination of ultrasonic and radio tags was used in this investigation.

Radio-tagged fish were followed manually from boat and shore, covering the whole study area, with ATS-receivers (R2100) connected to 4-element Yagi antennas and also repeatedly fine scale positioned to areas of about 5-m radius with a Televilt RX8910 receiver. Tagged fish were followed immediately after the releases and intensively for about 10–15 h per day during the first week. After this manual tracking was carried out regularly every second day for 3 weeks. Besides manual tracking, archival data-logging receivers (LOTEK SRX_400, aerial 4-element Yagi antenna) that continuously recorded tags were used. These were calibrated and tested for precise transmitter registrations to specify the exact migration route for individual fish. One archival receiver was placed in the bypass spillway 3.2 km downstream of the fish release site; a second one was located in the turbine intake channel (3.3 km downstream from release site). A third archival receiver was installed 0.7 km downstream of the power station and a fourth was situated at the river mouth (5.5 km downstream of the release site) (Fig. 1).

Acoustic-tagged fish were manually tracked from a boat and the land using a VEMCO VR100 receiver. Fourteen Vemco Inc., VR-2 acoustic receivers were used to create an automatic detection array from the lower section of the river to the outer limits of the Bay of Gävle (Fig. 1), which recorded identification number and time from transmitters as fish travelled through the receiver detection range. Receiver range testing at each station was determined by submerging a continuous transmitter at known distances from a receiver. Detection range exceeded 250 m, which assured that no fish could pass the monitored passages undetected. Mean distance between adjacent receivers in an array was 275 m (range 90–382 m) in 2006 and 340 m (range 160–490 m) in 2007.

Na^+, K^+-ATPase analyses

In 2007, gill Na^+, K^+-ATPase activity was used to evaluate the development of smoltification. Gill samples were taken from smolts from the same batches as the tagged fish on three occasions (11 April, 23 April and 3 May). A small gill biopsy (four to five tips of filaments) was taken from the first gill arch of each fish and frozen in SEI buffer (300 mm sucrose, 20 mm Na_2EDTA, 50 mm imidazole, pH 7.3) using the non-lethal gill biopsy method described by Schrock, Beeman, Rondorf & Haner (1994). Gill samples were stored in a −80 °C freezer until Na^+, K^+-ATPase activity was analysed according to Schrock *et al.* (1994).

Data analysis and model

Non-parametric tests were employed to analyse the data. Results of tests were considered statistically significant at $P \leq 0.05$. Analysis of data was performed with the statistical package SPSS for Windows v. 16.0.

The combined losses of radio- and acoustic-tagged smolts were modelled using survival analysis. Survival of tagged smolts was estimated using an analogue of the staggered-entry Kaplan–Meier formula (Pollock, Winterstein, Bunck & Curtis 1989), with 'distance from release to death' as the variable of interest (equation 1). This staggered-entry procedure allows for animals to be entered into the survival analysis at different times throughout the study.

$$\hat{S}(t) = \prod_{x \le t} \left(1 - \frac{d(x)}{n(x)}\right), \tag{1}$$

where $d(x)$ denotes the number of losses at time x, and $n(x)$ the number of individuals at risk just prior to time x; i.e. number of individuals that were neither lost nor censored prior to time x.

The calculations used for this model were based on apparent survival. In the context of this study, apparent survival is defined as the joint probability that the animal is both alive and migrates through the study area. As such, fish that stop migrating counted as mortalities. Fish remaining within the study area after their transmitters ceased operating were also counted as mortalities. All references to survival when presenting or discussing the Kaplan–Meier model refer to apparent survival. A log-rank test statistic for two samples (Pollock *et al.* 1989) was used to compare survival functions for 2006 and 2007.

Results

Na^+, K^+-ATPase

A significant increase in the level of gill Na^+, K^+-ATPase activity of the hatchery fish was observed between April (2.27 ± 0.24 µmol P_i g^{-1} h^{-1}, $n = 16$) and the time of release in May (3.03 ± 0.26 µmol P_i g^{-1} h^{-1}, $n = 16$) (t-test = −2.146, $P = 0.04$, d.f. = 30).

Radio and acoustic tracking

Automatic monitoring of the tagged fish at fixed receivers combined with the detection of fish during manual tracking accounted for nearly all tagged smolts (99%), thus providing an accurate measure of migration success of the smolts out of the river and of post-smolts through the estuary and out of the Bay (Table 2).

In 2006, most of the radio-tagged smolts initiated downstream movement shortly after release, but at the end of the experimental period, only 13 (54%) smolts had reached the dam. Of the remaining 11 smolts, nine were tracked to a lentic area 1 km downstream of the release site, while two tagged smolts suddenly disappeared from the study area (presumably eaten by avian predators). The assumption that sudden and permanent loss of a signal was caused by bird predation is based on the considerable range of the signals, the reliability of the transmitters and the intensive tracking. One of the nine transmitters was detected in a moving pike, *Esox lucius* L., while the tags of the remaining smolts ($n = 8$) were found on the river bottom (generally along the riverside at depths < 1 m). Presumably, these smolts were eaten and digested by predatory fish and the transmitters expelled thereafter.

Initial movements of radio-tagged smolts in 2007 were similar to those in the previous year. In 2007, 22 smolts (65% of the 34 tagged) remained in the lentic area 1 km downstream of the release site. They were also detected in moving pike ($n = 8$) or found stationary for several days at the river bottom ($n = 14$). No difference in length or condition factor was observed between the smolts that approached the dam or remained upstream from the power station (t-test, $P_{Length} = 0.57$ $P_{CF} = 0.26$, d.f. = 55). In 2006, eight of the 13 smolts that arrived at the power station descended via the spillway, while five entered the turbine intake. In 2007, all 12 migrating smolts entered the turbines. Turbine mortality was recorded to be 60% (three of five) and 75% (nine of 12) for 2 years. No size-related mortality could be established (t-test,

Table 2. Summary of results of tracking programme and Kaplan–Meier model

		Number of fish registered per section according to Fig. 1					Relative loss (%)	
		Radio	Acoustic	Radio	Acoustic			
Place	Km	2006	2006	2007	2007	Section	2006	2007
Release site radio	0.0	24		34		River	48	69
Power Station Intake	3.1	13		12				
Turbine Outlet	3.3	11	21	3	21			
E4-bridge	3.9	11	20	3	17			
River mouth	5.0	11	17	3	14	Estuary	47	43
Railway bridge	5.5	8?	13		8			
Fredriksskans (sea entry)	8.5		9		6	Sea	11	17
Outer limit of Bay of Gävle	13.5		8		5			

$P = 0.88$, d.f. = 15). Overall, 14 (11 in 2006 and 3 in 2007) of the radio-tagged smolts were recorded moving downstream from the power station and entering the inner part of the estuary.

A high number of the acoustic-tagged smolts entered the estuary (85% and 67% for 2006 and 2007 respectively), and most (80% and 83%) of post-smolts that left the estuary survived the passage through the bay. However, as a result of high losses in the estuary (41% and 57%), the overall migration success of acoustic-tagged smolts was low (40% and 24% in 2006 and 2007 respectively). There was no difference between 2 years in the proportion of salmon reaching any of the three sections (Fisher's exact test on difference between two proportions; $P = 0.28$, $P = 0.21$ and $P = 0.65$ for river, estuarine and sea respectively). There were no differences in body length or condition factor between individuals recorded and those not recorded either leaving the river, entering the sea or leaving the bay in both years (Mann–Whitney non-directional *U*-tests, $P_{Length} = 0.86$, 0.69, and 0.34; $P_{CF} = 0.86$, 0.95, and 0.35).

The combined losses: Kaplan–Meier

Relative mortality values extrapolated from the Kaplan–Meier model (Table 2) indicated that the highest loss rates in 2006 took place during the first kilometres after release of the radio-tagged smolts (46%) and during estuarine migration (47%). In 2007, smolts suffered the highest losses (65% and 75%) before reaching the power station and during its passage. Estuarine losses (especially in the inner section) were high (53%) and similar to the previous year. Loss rates for the marine section were low and relatively consistent between years (11% and 17% respectively for 2006 and 2007 respectively). By the end of the migration, the survival curves differed greatly between years (log-rank test $\chi^2 = 2.76$, $P < 0.05$); survival in 2006 was nearly 10 times higher than for 2007 (Fig. 2).

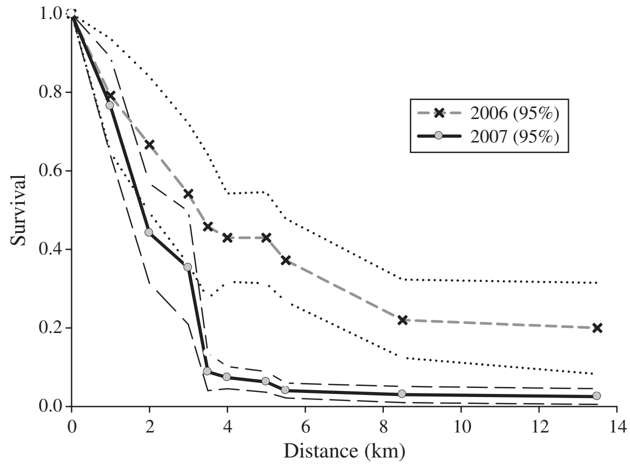

Figure 2. Kaplan–Meier cumulative survival estimates plotted together with 95% confidence intervals.

Discussion

The combined results of the radio and acoustic tracking programme revealed that overall, the migration success of the stocked smolts was low (21% and 3% for 2006 and 2007 respectively). Different water flows and the associated variation in the number of fish guided towards the turbines were seen as potential reasons for the discrepancy in survival between 2 years. The reduced water flows in 2007 might have been inadequate to trigger the downstream movement of the released radio-tagged smolts (Allen 1944; Österdahl 1969; Hesthagen & Garnås 1986). This, coupled with a higher proportion of fish guided towards the turbines, accounted for 53% of all losses observed in the system during the 2007 trial.

Some of the losses among the smolts that remained in the section of slack water 1 km upstream of the power station could be attributed to predation by pike (28–53% of all released fish). These values should, however, be treated with caution because they originate in part from indirect evidence. Analogous figures have been reported for smolts passing through lakes and reservoirs, habitats with high risk of predation for migrating salmonids (Menzies & Pentelow 1965; Jepsen, Aarestrup, Okland & Rasmussen 1998; Jepsen, Pedersen & Thorstad 2000). It appears that weak currents associated with areas of slow flow disorient smolts, delaying their migration and thereby prolonging their exposure to predators (Olsson, Greenberg & Eklöv 2001).

The estimated direct mortality of smolts descending through the Francis turbines at the hydropower-station varied from 40% to 75% for 2006 and 2007 respectively. Even if these figures originate from a small number of fish, they fall within the mortality range reported for small Francis units (Collins & Ruggles 1982) and pinpoint the power-station as a potential source of major in-river mortality during smolt migration. The disparity observed between 2 years was probably caused by the different flow distribution. In 2007, most of the water (80% of river flow) was directed to the turbines, whereas in 2006 turbine flows represented only 33% of the total river flow. As smolts usually travel with bulk flows (Coutant

& Whitney 2000), the reduced bypass flows in 2007 were probably insufficient to guide the fish.

Substantial mortality took place in the confined inner part of the estuary, with values being consistent over the 2 years (40–35%). In comparison, relative losses in the outer section were lower (11–18%). Delayed migration of salmonid smolts through impounded estuaries, with the subsequent additional potential dangers arising from factors such as predation, has been reported previously (Gough 1996; Russell *et al*. 1998). Despite the high losses registered in the inner section, overall migratory success through the estuary is similar to the values reported for unmodified river estuaries. In some northern Baltic rivers, 29–50% of hatchery-reared smolts were found to be predated by pike and burbot, *Lota lota* L, during estuarine passage (Larsson 1985; Kekäläinen, Niva & Huuskonen 2008). Examples from the Atlantic Ocean provide similar values (Hvidsten & Mokkelgjerd 1987), although studies indicating high estuarine survival also exist (Lacroix, McCurdy & Knox 2004; Gudjonsson, Jonsson & Antonsson 2005). It appears that the estuarine migration success of smolts can vary greatly between systems and is governed by a multitude of factors, such as the degree of human impact, estuary morphometry, environmental heterogeneity and abiotic conditions (Mather 1998; Lacroix 2008).

Whereas the fish tagged in the present study appeared to be fully smoltified, as judged by morphological features (i.e. coloration, body shape, darkened fins) (Wedemeyer, Saunders & Clarke 1980), behaviour in the tanks (negative rheotaxis) and physiological tests (increased gill Na^+, K^+-ATPase activity), it is possible that a subset of them did not constitute actively migrating fish. This may account for part of the losses reported. Predisposition of Atlantic salmon to migrate after their release as smolts seems to be associated with the rearing environment and the physiological status of the fish at the time of release (Stefansson, McGinnity, Björnsson, Schreck & McCormick 2003), but knowledge on the factors influencing the migration tendency in cultured smolts is scarce (Ugedal, Finstad, Damsgard & Mortensen 1998). There is a need for further research linking the freshwater rearing conditions, smolt physiology and migratory performance for the smolt release programmes.

Releases of salmon to re-establish rare or extinct stocks are currently on-going in over a third of all salmon rivers in the Baltic Sea region (ICES 2000). However, despite massive stocking programmes and other rebuilding efforts, natural reproduction has not increased (ICES 2007). Stocking can be an important tool in the management of salmonid populations. However, artificial reproduction will not lead to recovery unless the underlying problems that cause the population to decline are addressed (i.e. overexploitation, habitat degradation, dam building and pollution, in the case of the Baltic Sea).

Anthropogenic activity can severely affect the environmental conditions in the migration habitats of smolts. As observed in this investigation, these factors may result in increased mortality by delaying smolt migration and making them more likely to encounter predators. The altered habitats in the River Testebo and its estuary imposed severe constraints to the migration of stocked smolts. By contrast, the proportion of post-smolts surviving the passage through the Bay of Gävle was high enough to conclude that habitat within the bay is not a factor limiting initial marine survival.

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