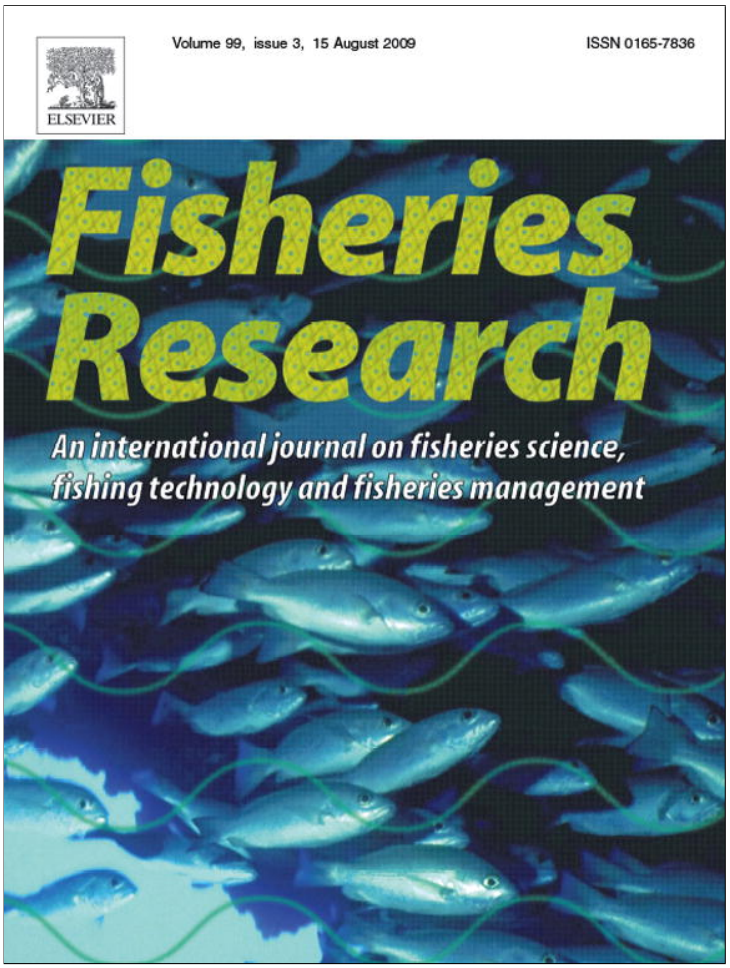

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Migration performance of wild and hatchery sea trout (*Salmo trutta* L.) smolts—Implications for compensatory hatchery programs

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ABSTRACT

Migration success of hatchery-reared and wild sea trout smolts through the lower stretches and the estuary of a Baltic Sea river were studied. During 3 years, wild and hatchery trout smolts were implanted with acoustic transmitters and released 14 km upstream from the river mouth. In order to monitor their out-migration pattern, acoustic receivers were deployed along the migratory route. Data on number of fish detected and date and time of detections were analysed and the migratory performance of wild and hatchery-reared fish was compared. A significantly higher proportion of wild fish (80%) successfully migrated to the coast compared to fish of hatchery origin (27.5%) and migration was faster in wild smolts. Hatchery fish were larger and had a higher condition factor and lipid concentrations, which are proposed as possible reasons for the poorer migratory performance of the hatchery-reared fish.

1. Introduction

In a majority of the rivers draining into the Baltic Sea, fish migration has been negatively affected by anthropogenic activities. Many of the rivers have been excavated to enhance timber floating efficiency and construction of hydroelectric-power dams has impaired or completely restricted migratory routes of descending and ascending anadromous fish, e.g. Atlantic salmon (*Salmo salar* L.) and brown trout (*Salmo trutta* L.) (henceforth referred to as sea trout). To compensate for the lost production of salmon and sea trout, large stocking programs of hatchery produced fish are in effect. Baltic Sea stocking programs release about 3.9 million sea trout (2006) smolts and about 5.4 million salmon smolts (2007) into the Baltic Sea every year (ICES, 2008). Stock assessments indicate a 10–15-year-long decline in sea survival of both salmon and trout in the Baltic Sea, but the cause for this is not known (ICES, 2008).

Lower survival of hatchery fish than in their wild counterparts is suggested to be a result of, for instance, domestication and lack of experience of the natural environment (Huntingford, 2004; Jonsson and Jonsson, 2006). Recent findings suggest that the adaptation of salmonids to hatchery environments is much faster than thought before, causing a rapid cumulative fitness decline for hatchery fish in the wild (Araki et al., 2007a,b). Fish reared under hatchery conditions are relieved of selective factors present in the wild, which might make them less adapted to avoid predators and obtaining food in the natural environment. Furthermore, as a result of improved hatchery-rearing techniques and feed formulas, size and lipid content of salmon and trout smolts in the Baltic Sea has increased (Eriksson et al., 2008; Lundqvist et al., 2008). Sustained higher growth rates at the hatcheries may translate into higher propensity to residency, especially among trout (Jonsson and Jonsson, 1993; Forseth et al., 1999).

Comparisons of hatchery and wild smolt sea survival performance are to a large extent based on recapture data of tagged fish or on data from studies on either solely wild or hatchery fish. Besides a few good exceptions (e.g. Hvidsten and Mokkelgjerd, 1987; Hvidsten and Lund, 1988), tag-recapture data give valuable information mainly on long-term sea survival. However, survival data during the transition from freshwater to sea, which is suggested to be an especially critical period (Gross et al., 1988), is more difficult to obtain using a tag-recapture study design. Using telemetry instead, important results on survival rate of salmon and trout smolts during freshwater-to-sea transition have been obtained (e.g. Dieperink et al., 2002; Finstad et al., 2005), but further knowledge on this important event of the salmonid life-cycle is still warranted.

The main objective of this study was to compare the migratory success of wild and hatchery-reared sea trout smolts. Ultrasonic telemetry was used to track the movement of smolts during their descent through the lower stretches, the estuary and in to the coastal area of a northern Baltic river. Data on survival rate and migration behaviour were compared over 3 years.

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2. Materials and methods

2.1. Study area

The Sävar River is about 142 km long and drains in to the brackish water of the Gulf of Bothnia (N63°54′38.6″, E20°33′56.5″), which constitutes the northern part of the Baltic Sea. The Sävar River has a drainage area of 1161 km^2, including 6.5% lake surface. The calculated mean flow rate at the river mouth is about 12 m^3 s^{-1}, with maximum low and high peaks of 0.7 and 98.5 m^3 s^{-1}, respectively (IBSFC, 1999). The river was formerly used for timber floating and parts of its channel were excavated for that purpose. Today, these areas have been restored. In the 1930s, a canal was built about 3.0 km north of the natural river outlet, connecting the estuary and the coastal area, and providing the fish with two alternative routes to enter the sea (Fig. 1). The lower stretches of the Sävar River and its estuary, which comprise the present study area, are slow flowing with no rapids and are renowned as a good pike fishing area. To compensate for negative anthropogenic factors and fishery-induced low return rates of spawners, salmon and trout fry and smolts have been released in the river during the latest 20-year period. However, the result regarding returning adult spawners has been poor (Anonymous, 2004) and no significant genetic impact of these stockings has been detected in wild fish (Nilsson et al., 2008).

2.2. Tagging and tracking study fish

Hatchery trout were obtained from a compensatory stocking hatchery (Norrfors Hatchery, Umeå, Sweden), 28 km from the release site in the Sävar River, and were the progeny of wild anadromous trout (>10 males and females) from River Vindelälven. Wild trout were caught in rotary screw traps in the Sävar River about 14 km upstream from the river mouth (for details see Lundqvist et al., 2008). Prior to tagging, the length (L) and weight (W) of the hatchery and wild smolts were measured to the nearest mm and g, respectively. These measurements were later used to calculate the condition factor (Fulton, 1904) by applying the formula: $CF = 10^5 \times W/L^3$. Subsequently, all fish were surgically implanted with coded acoustic transmitters (2005 and 2006: VEMCO, V7-2L-R256, 7 × 18.5 mm, mass in air 1.6 g, nominal delay: 45 s. 2007: VEMCO, V7-4L-R256, 7 mm × 22.5 mm, mass in air 1.8 g, nominal delay: 45 s). During surgery, fish were anaesthetized in a 0.5 g L^{-1} solution of benzocaine (MS222) and placed ventral side up on a surgery table. An incision was made anterior to the pelvic girdle and the transmitter was inserted into the body cavity. The incision was closed with two interrupted sutures. Hatchery fish were kept at the hatchery for at least 3 days prior to transportation to the release site. Wild fish were tagged over several days (May 23–27) between 9.00 and 10.00 a.m., and on each single day of fish releases a similar number of hatchery fish were transported from the hatchery. After tagging of wild smolts, hatchery and wild smolts were kept in a net pen positioned in a slow flowing eddy in a rapid just below the capture site until they were released at 7.00 p.m. the same day. In 2005, only hatchery fish were released (Table 1).

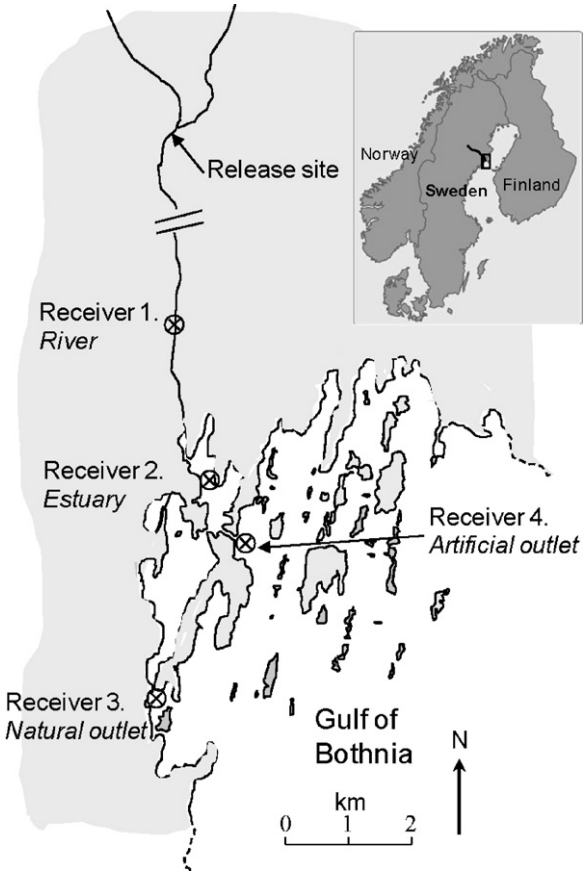

Fig. 1. Map of the river Sävarån and its estuary and archipelago. The release site, about 14 km upstream the estuary, and the receiver sites (⊗) are indicated. Note that in text, receivers 3 and 4 are defined as *Coast*.

In order to monitor the out-migration pattern of the hatchery and wild smolts, acoustic receivers (VEMCO, VR2) were submerged half-way between the bottom and the water surface at three stations along the migratory route, by attaching them to a rope, a weight and surface buoy (Fig. 1). From here on, the receiver stations are referred to as *River* (receiver 1), *Estuary* (receiver 2) and *Coast* (receivers 3 and 4). Due to physical barriers (e.g. river width) at each receiver station, fish could not pass a receiver further away than on a distance of 60 m. Receiver range testing at each station was determined by submerging a continuos transmitter at known distances from the receiver. Detection range exceeded 100 m, which assured that no fish could pass the monitored passages undetected.

For all years, the receivers were in place for at least 45 days. No coastal receivers were deployed in 2005 and thus, analyses including fish reaching *Coast* were conducted only on data from 2006 and 2007.

2.3. Smolt gill Na^+, K^+-ATPase activity and body composition

In 2007, gill Na^+, K^+-ATPase activity was used to evaluate the development of smoltification. Gill samples were taken from hatchery and wild smolts of the same batches as the tagged fish. A gill biopsy (four to five tips of filaments) was taken from the first gill arch of 10 hatchery and 10 wild smolts and frozen in SEI buffer (300 mm sucrose, 20 mm Na_2EDTA, 50 mm imidazole, pH 7.3), using the gill biopsy method described by Schrock et al. (1994). Gill samples were stored in a −80° C freezer until Na^+,K^+-ATPase activity was analysed (Schrock et al., 1994).

The 10 wild and 10 hatchery fish used for Na^+, K^+-ATPase activity analyses in 2007 and an additional 48 hatchery and 51 wild fish from 2005 were lethally sampled and analysed for lipid and protein concentration in muscle tissue. From each fish, 3–10 g from the mid section of the left fillet was removed and homogenized in a food processor together with an alkaline detergent and thereafter, the solution was analysed using a Mid-Infrared-Transmission (MIT) spectroscopy method (MIRIS AB, Uppsala, Sweden), according to the protocol by Elvingson and Sjaunja (1992). For comparisons of lipid and protein, the mean MIT value of three sub-samples of each homogenized fillet was used.

Table 1
Morphological fish characteristics (±SE) for wild and hatchery fish used in the telemetry component. For the pooled data, unequal letters between parameters indicate a significant difference at the $P < 0.0001$ level.

Year	N	Origin	Release dates (in May)	Numbers rel. on each date	Mean length (mm)	Mean weight (g)	Condition factor
2005	24	Hatchery	26	24	230 ± 2.4	116 ± 4.2	0.95 ± 0.01
2006	20	Wild	23, 24, 25, 27	4, 7, 2, 7	185.7 ± 4.2	54.8 ± 4.5	0.83 ± 0.02
2006	20	Hatchery	23, 24, 25, 27	4, 7, 2, 7	223.3 ± 3.9	119.5 ± 5.8	1.06 ± 0.01
2007	20	Wild[a]	23, 24	10, 10	166.7 ± 3.5	39.4 ± 2.3	0.82 ± 0.01
2007	20	Hatchery	23, 24	10, 10	242.5 ± 2.4	128.3 ± 4.7	0.89 ± 0.01
Pooled	64	Hatchery	–	–	231.8 ± 1.9A	121.2 ± 2.8A	0.97 ± 0.01A
Pooled	40	Wild	–	–	176.2 ± 2.9B	42.2 ± 3.6B	0.82 ± 0.01B

[a] The weight and condition factor of 5 fish could not be obtained.

2.4. Data analyses

For comparisons of fish morphology (length, weight and condition factor CF) and physiology (gill Na^+, K^+-ATPase activity, lipid and protein concentration) the Student's *t*-tests were used. In comparisons of the proportion of hatchery and wild trout successfully reaching *Coast* the Pearson's Chi-square test was used. The time in hours for an individual fish to migrate from the release site to the first receiver station or the time between two adjacent receiver stations was calculated as the time interval between the time of release and the time of the median detection at the receiver or the median detection at two adjacent receivers (Table 3). For comparisons of migration times between wild and hatchery fish, the non-parametric Wilcoxon signed-rank test was used. For analyses of the effect of length, weight and CF on migration time within groups, linear regression was used. Calculations on migration time from release until logger station *River* includes the possible event of fish staying resident for a period of time at the release site and thus, it is not a good indicator of swimming performance. However, such comparison is still relevant when discussing plausible explanations for differences in out-migration success of hatchery and wild smolts. Net ground speed was calculated as the migration time (days) from the site of release until logger station *River,* or the time between two adjacent receiver stations, divided by the distance between the stations (Table 3). Since fish differed in size, comparisons were also made on migration times corrected for body length. In cases of unequal variance, Wilcoxon signed-rank test was used, otherwise parametric tests were conducted.

3. Results

Overall, there were large individual differences in migration times but in general, the variation was larger among hatchery fish. Especially large variation was found in migration time for hatchery fish from the release site to *River,* which ranged from 9 to 495 h. The equivalent migration time for wild fish ranged from 7 to 148 h. Probably, this large individual variation was due to differences in initial post-release behaviour (i.e. some fish hesitated to migrate immediately after being released). No effect of fish length (*L*), weight (*W*) or CF on migration time for the defined stretches *River* and *Estuary*, was observed for wild (Wilcoxon, *River*: *L*; $P = 0.93$, *W*; $P = 0.54$, CF; $P = 0.13$. *Estuary*: *L*; $P = 0.75$, *W*; $P = 0.93$, CF; $P = 0.80$. *Coast*: *L*; $P = 0.99$, *W*; $P = 0.78$, CF; $P = 0.46$) or hatchery fish (Wilcoxon, *River*: *L*; $P = 0.10$, *W*; $P = 0.27$, CF; $P = 0.23$. *Estuary*: *L*; $P = 0.43$, *W*; $P = 0.24$, CF; $P = 0.55$). Due to the low number of detections, no analysis for hatchery fish migrating to *Coast* was conducted.

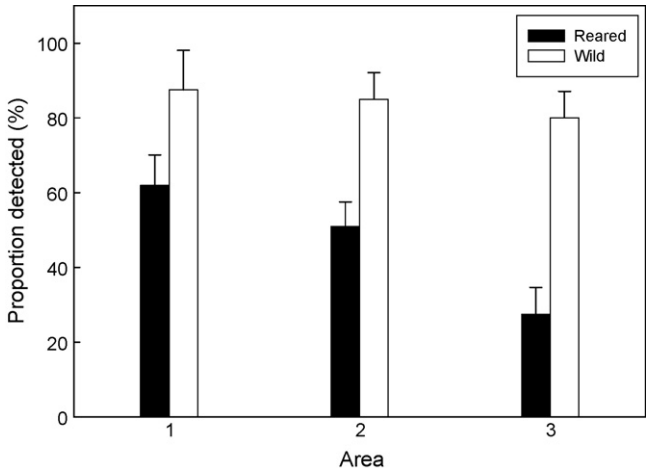

Fig. 2. Proportion of wild (open bars) and hatchery (filled bars) detected at each receiver station; *River*, *Estuary* and *Coast*. The data are pooled for three study years. However, the bar for Coast represents 2 years only (2006 and 2007), since no coastal loggers were deployed in 2005. Whiskers denote standard deviation (SD).

Hatchery smolts were significantly longer (*t*-test; $P < 0.0001$), heavier (*t*-test: $P < 0.0001$) and had higher CF than wild smolts (*t*-test: $P < 0.0001$) (Table 1). The lethally sub-sampled wild and hatchery-reared smolts did not differ in their gill Na^+,K^+-ATPase activity (wild: 2.88 μM ADP mg protein^{-1} h^{-1} ± 0.45, hatchery: 3.24 μM ADP mg protein^{-1} h^{-1} ± 0.28; *t*-test, $P = 0.507$), but differed significantly in muscle lipid (*t*-test; $P < 0.0001$) and muscle protein (*t*-test; $P < 0.0001$) concentration (Table 2).

At each logger station (*River*, *Estuary* and *Coast*) fewer hatchery fish than wild fish were detected. The proportion of smolts successfully migrating to the coast in 2006 and 2007 was consistent for both wild [2006; 17 (85%), 2007; 15 (75%), $P = 0.43$] and hatchery trout [2006; 4 (20%), 2007; 7 (35%), $P = 0.29$] (Fig. 2). The data on migration success for wild and hatchery fish from both years were therefore pooled. Out of 40 tagged and released wild sea trout smolts, 32 (80%) successfully migrated to *Coast* (i.e. were detected on either receiver 3 or 4, positioned outside the artificial and natural outlet) (Fig. 2). A significantly lower proportion of the 40 released hatchery smolts (27.5%) was detected on the same receivers ($P < 0.0001$; Fig. 2). Within the groups of wild

Table 2
Length, weight, condition factor and body composition of lethally sampled wild and hatchery trout smolts. No samples were taken for 2006.

Year	N	Origin	Mean length (mm) ± SE	Mean weight (g) ± SE	Condition factor ± SE	Lipid conc. (%) ± SE	Protein conc. (%) ± SE
2005	48	Hatchery	217 ± 2	114 ± 3	1.10 ± 0.01	6.13 ± 0.2	16.6 ± 0.6
2005	51	Wild	160 ± 2	46 ± 2	0.83 ± 0.07	0.99 ± 0.1	17.6 ± 0.1
2007	11	Hatchery	240 ± 4	131.0 ± 8	0.94 ± 0.02	5.06 ± 0.2	17.5 ± 0.1
2007	5	Wild	164 ± 9	38.4 ± 8	0.82 ± 0.05	0.74 ± 0.1	16.5 ± 0.4

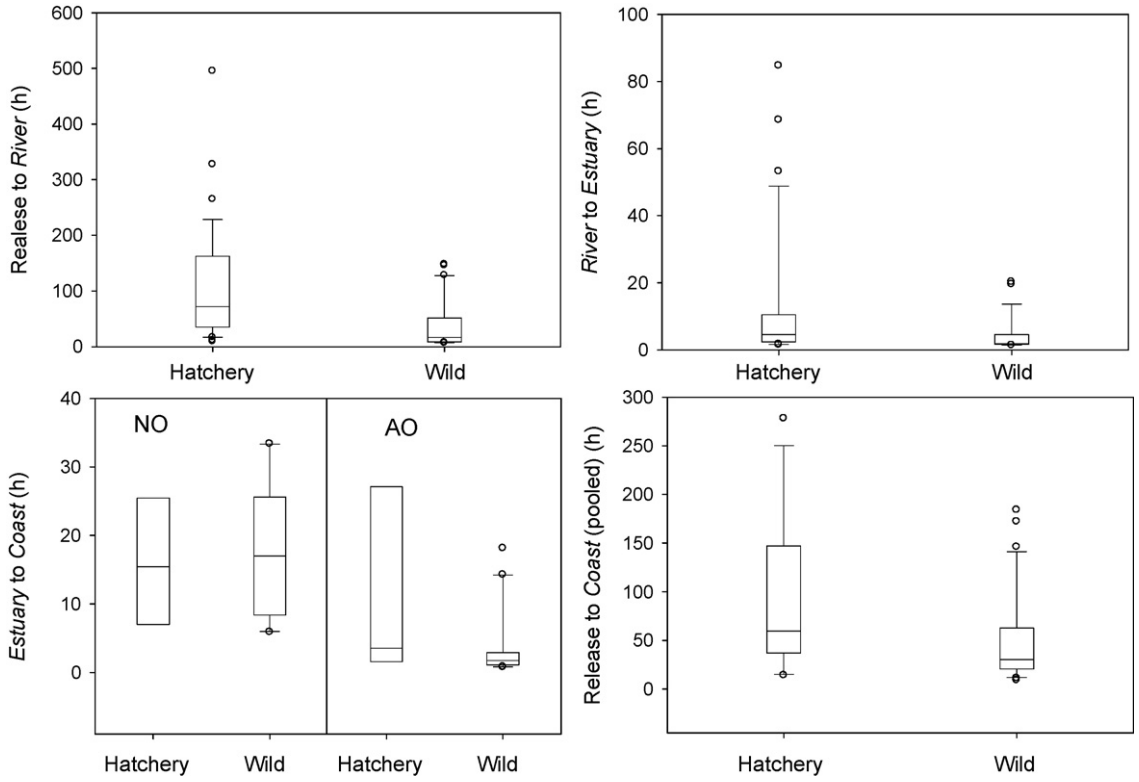

Fig. 3. Migration time (h) for wild and hatchery brown trout smolts in different stretches in river Sävarån. River Sävarån has two outlets; a natural (NO) and an artificial outlet (AO) (Fig. 1). Boundaries of the boxes indicate the 25th percentile and the 75th percentile. The line within the box shows the median value. Whiskers indicate the 90th and 10th percentiles. Open circles show outliers.

and hatchery smolts, no effect of fish length (wild: *t*-test; $P = 0.80$, hatchery: *t*-test; $P = 0.95$), weight (wild: *t*-test; $P = 0.87$, hatchery: *t*-test; $P = 0.42$) or CF (wild: *t*-test; $P = 0.45$, hatchery: *t*-test; $P = 0.12$) on the proportion of fish successfully migrating to *Coast* could be observed. For each year, the mean CF was consistently higher for non-successful migrants (mean CF, 2005: NM = 0.97, SM = 0.93; 2006: NM = 1.08, SM = 1.04; 2007: NM = 0.91, SM = 0.88).

No differences in migration time (h) between years could be detected for wild and hatchery smolts (Wilcoxon; wild; $P = 0.94$, hatchery; $P = 0.16$), and the data were therefore pooled. Wild smolts showed significantly shorter migration times from the site of release to *River* (wild = 37.4 h ± 43.2, hatchery = 114.1 h ± 115.0, Wilcoxon; $Z = -4.24$, $P < 0.0001$) and from *River* to *Estuary* (wild = 4.3 h ± 5.1, hatchery = 14.6 h ± 22.5. Wilcoxon; $Z = 2.63$, $P = 0.009$) than hatchery smolts. No difference in migration time was found for the stretch between *Estuary* and the artificial outlet (receiver 4) (wild = 3.96 h ± 5.12, hatchery = 10.8 h ± 14.8, Wilcoxon; $Z = 1.60$, $P = 0.11$) (Fig. 3.). Only 3 hatchery fish (16.0 h ± 9.3) migrated through the natural outlet, compared to 11 wild smolts (24.8 h ± 24.6). Therefore, no statistical analysis was conducted for the stretch between *Estuary* and the natural outlet.

Net ground speed (NGS; km day^{-1}) did not differ between years for wild or hatchery smolts (Wilcoxon; wild; $P = 0.99$, hatchery; $P = 0.14$) and data were pooled. Wild smolts showed higher NGS than hatchery smolts from the release site to *River* (Wilcoxon; $P < 0.0001$) and from *River* to *Estuary* (Wilcoxon; $P < 0.003$) (Table 3). No significant difference in NGS was found for *Estuary* to the artificial outlet or for *Estuary* to the natural outlet. Since hatchery smolts were significantly larger than wild smolts (*t*-test; $P < 0.0001$, Table 1), comparisons of size adjusted swim speeds were also

Table 3
Migration speed expressed as body length per second (BL s^{-1}) ± SE and Net Ground Speed (NGS km day^{-1}) ± SE of wild and hatchery-reared brown trout smolts (pooled over years).

	Distance (km)	Origin	*N*	Mean BL s^{-1}	*P*	NGS (km day^{-1})	*P*
Release site *River*	9.5	Wild	30	1.03 ± 0.14	<0.0001	15.6 ± 1.6	<0.0001
		Hatchery	39	0.25 ± 0.04		5.0 ± 1.4	
River to *Estuary*	3.0	Wild	29	2.05 ± 0.20	<0.0001	33.1 ± 3.1	<0.003
		Hatchery	32	0.98 ± 0.13		20.2 ± 2.8	
Estuary to NO	3.2	Wild	11	0.39 ± 0.09	=0.67	5.7 ± 1.2	–
		Hatchery	3	0.32 ± 0.17		6.5 ± 2.5	
Estuary to AO	0.8	Wild	20	0.80 ± 0.11	=0.05	12.0 ± 1.7	=0.10
		Hatchery	8	0.39 ± 0.17		7.8 ± 2.6	

Speeds (± SE) are given for four migrated distances; from release site to the first receiver (*River*), from the first receiver (*River*) to the second receiver (*Estuary*) and from the second receiver (*Estuary*) to sea entry either through the natural (NO) or the artificial outlet (AO). *n* is the number of migrating fish in each migrated distance. In total, 40 wild and 64 hatchery fish were released. For statistical comparisons, Wilcoxon signed-rank test was used.
Note. Five wild fish passed receiver 1 (*River*) undetected, probably due to transmitter code collision, and could thus not be included in migration speed calculations for the first two distances.

conducted (i.e. expressed as body length s^{-1}). Between years, no differences in size adjusted swim speeds were observed and the data within wild and hatchery fish were pooled over years (Wilcoxon; wild; $P = 0.19$, hatchery; $P = 0.44$). Wild fish demonstrated significantly higher swim speeds in all stretches but from *Estuary* to the natural outlet (Table 3).

4. Discussion

A few studies, based on tag-recapture or smolt-to-adult data, put forward survival rates of sea trout on large temporal and spatial scales (e.g. Lundqvist et al., 1994; Kallio-Nyberg et al., 2007), but to our knowledge, this is the only study on survival rate during the important and high-risk transition from freshwater to sea conducted on wild and hatchery sea trout smolt in the Baltic Sea. The results of this study revealed that a much higher proportion of the wild sea trout smolts (80%) than smolts of hatchery origin (27.5%) successfully migrated from the release site to the coastal area. The migration route consists of about 12 km of slow flowing river water and of a large shallow estuarine environment (4 km long) with dense macrophyte stands, characteristic of a good quality pike habitat (Craig, 2008). Thus, the migration survival rate of wild sea trout (80%) in this study must be considered as high. For instance, Jepsen et al. (1998) found that >50% of the migrating wild trout smolts in a Danish river were predated. Similar predation rate was found for trout in the River Skjern (Denmark) (Koed et al., 2006). It is reasonable to assume that migration survival rates of trout smolts vary naturally between systems according to river specific abiotic (e.g. water flow, number of pools, turbidity, etc.) and biotic factors (e.g. type and density of predators), and thus, the comparatively high survival rate of wild fish found in this study is likely a result of favourable migration conditions (e.g. low predator abundance) in the lower part of the Sävar River, rather than smolt performance *per se*.

Several studies have demonstrated higher sea survival rate for wild salmonids than for fish of hatchery origin (Jonsson et al., 2003; Poole et al., 2003; Saloniemi et al., 2004; Chittenden et al., 2008). For Atlantic salmon, the sea survival of wild fish is suggested to be 2–4.5 times that of hatchery fish (Jonsson et al., 1991; Saloniemi et al., 2004). For sea trout, no equivalent data are available. In this study, the proportion of wild fish successfully migrating from the point of release to the coastal area was 2.7 times higher than for hatchery fish. Assuming that this reflects survival, this must be viewed as a large difference, considering that the equivalent comparisons for salmon include the entire sea phase from smolt release until adult returns. There is likely more than one reason to the inferior out-migration survival of hatchery trout in this study. Highly important is the almost complete absence of selective mortality in the hatchery environment. Accordingly, hatchery fish are suggested to have a naïve anti-predator behaviour, both due to lack of experience and domestication (Olla et al., 1994; Álvarez and Nicieza, 2003; Weber and Fausch, 2003). Furthermore, the hatchery fish in this study migrated slower than wild fish, both in absolute terms and when speeds were corrected for body length. Such pattern was recently shown for coho salmon smolts (*Oncorhynchus kisutch* Walbaum) (Chittenden et al., 2008). Pedersen et al. (2008) found that wild sea trout had approximately 25% higher swimming speed (U-burst) than hatchery trout. Hence, the time of exposure to predators in the lower stretches of the river and in the estuary was significantly longer for hatchery fish, likely making them more susceptible to predation.

The level of gill Na^+,K^+-ATPase activity is generally regarded as a good indicator of smolting status in salmonids (Hoar, 1988) and high migratory tendency in sea trout appears to be associated with a well-developed hypoosmoregulatory capacity (Ugedal et al., 1998). Thus, poor gill Na^+,K^+-ATPase activity in hatchery fish could further explain their lower out-migration rate but in this study, the gill Na^+,K^+-ATPase activity did not differ between wild and hatchery-reared smolts. Despite the general correlation between smolt migration and gill Na^+,K^+-ATPase activity (e.g. Aarestrup et al., 2000; Nielsen et al., 2004), this is not necessarily always the case (e.g. Ewing and Birks, 1982; Pirhonen and Forsman, 1998). Instead, migration tendency and elevated Na^+,K^+-ATPase activity may not take place simultaneously, which might explain the lack of correlation between migration tendency and enzyme activity in this study. Another possible reason for the observed poor agreement between enzyme activity and migratory performance is that the physiological component of the smoltification process may be an adaptive response to local conditions. The salinity of the brackish Baltic Sea is as low as 4–5 ppm. Thus, the importance of high enzyme activities of migrating smolts might be less than that for smolts in systems with higher seawater salinity.

An additional explanation to the lower migration rate of hatchery trout smolts could be the partial migration strategy of many trout populations (Jonsson and Jonsson, 1993; Olsson et al., 2006). As noted by Olsson et al. (2006), migratory trout dominated when fish densities were high and their growth rates low. Vice versa, under conditions of low fish density and high individual growth rates, the proportion of residents increased. Due to sustained high growth rates in hatcheries, cultured fish generally have higher CF and lipid concentrations than wild fish (Bergström, 1989; Poole et al., 2003; this investigation). This may result in a higher propensity to residency and might be the reason to why a larger fraction of the released hatchery fish (*c.* 40%) than wild fish (*c.* 10%) was not detected at any station. The observed apparent negative correlation between migration tendency and high CF in the hatchery smolts (0.93 in migrants vs. 0.99 in supposed residents) confers further support to this hypothesis. Moreover, early sexual maturation, in sea trout males has been found to inhibit smoltification, which will constitute a part of the resident fish (Dellefors and Faremo, 1988). Wild fish were caught during their downstream migrating phase and thus, a majority of them constitute active migrants. Hence, in order to make an unbiased comparison of migration survival between wild and hatchery smolts, resident fish should be excluded. Nonetheless, even when removing non-migrants (i.e. fish not detected on the first logger), the proportion of wild fish reaching the sea was still significantly higher (about 2 times) than for hatchery fish. Thus, the partial migration theory cannot solely explain the inferior migration performance of hatchery trout in this study. The mechanisms responsible for this deficit are unknown. We suspect that altered physiological traits, on top of domestication effects (Álvarez and Nicieza, 2003; Araki et al., 2007a,b) and deficits in anti-predator behaviour (Jonsson et al., 1991; Johnsson et al., 1996; Álvarez and Nicieza, 2003), are probable explanations.

Whether an individual smolt gains any advantages from the migration depends on the balance between the growth opportunities in the marine environment and the freshwater habitat, and the increased mortality risk associated to the migration (Gross et al., 1988). Hence, the gain of migration to sea is higher for a wild smolt with low energy reserves than for a hatchery fish with high lipid concentration. Indeed, a difference in swimming speed from *River* to *Estuary* between migratory hatchery and wild smolts was observed but if this was due to lower motivation to migrate among hatchery fish or to inferior swimming capacity could not be assessed.

Concurrently with the increase in size and energetic status of stocked salmon and sea trout smolt in the Baltic Sea in recent year, post-stocking survival has gone down (ICES, 2008; Kallio-Nyberg et al., 2009). The aim of the Swedish compensatory stocking programs is to compensate for lost production of sea-running trout. Today however, fewer sea trout are recaptured than in previous

years. Efforts should therefore be made to reduce the likelihood of hatchery fish staying resident, which by this study is suggested largely to be a result of high CF, indicative of high lipid levels. Migratory studies of trout smolts of different energetic status are therefore needed, preferably designed for future implementation in large-scale hatchery environments.

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