

Contribution to the Theme Section 'Tracking fitness in marine vertebrates'

Comparison of the riverine and early marine migration behaviour and survival of wild and hatchery-reared sea trout *Salmo trutta* smolts

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ABSTRACT: The seaward migration of wild (n = 61) and hatchery-reared (n = 46) sea trout smolts was investigated in the Danish River Gudenaå and Randers Fjord (17.3 and 28.6 km stretch, respectively) using acoustic telemetry. Their riverine and early marine migration was monitored by deploying automatic listening stations (ALS) at 4 locations in the river and fjord. Migration speeds were approximately 3 to 11 times faster in the river than in the early marine environment. Hatchery-reared smolts migrated faster than wild smolts, but the difference was small, especially compared with the large differences in migration speeds among habitats. There was no difference in the diurnal activity pattern between wild and hatchery-reared smolts. Both the riverine and early marine migration activity were primarily nocturnal, although some individuals were also recorded by the ALSs during the daytime. The survival of the wild smolts from release in the river to the outermost marine ALS site, 46 km from the release site, was 1.8 and 2.9 times higher than that of the hatchery-reared smolts in the 2 study years, respectively. Overall, survival from release to the outermost ALS site was 79% for wild and 39% for hatchery-reared smolts. Since the lower survival of the hatchery-reared compared with the wild smolts could not be explained by differences in migration speeds or diurnal migration patterns, behavioural differences on a smaller scale than those recorded in the present study may explain the difference in survival.

KEY WORDS: Downstream · Ground speed · Telemetry · Postsmolt · Brown trout

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INTRODUCTION

The life cycle of anadromous salmonids includes a migration of immature fish from freshwater to the sea. This seaward migration is believed to be an adaptive strategy, with fish migrating to more favourable habitats in terms of feeding and growth, which may ultimately enhance their individual fitness (Gross 1987, Jonsson & Jonsson 1993). Individuals in many brown trout *Salmo trutta* populations undertake migrations between freshwater and the sea (hereafter termed sea trout). Juveniles grow for 1–5 yr in freshwater before undergoing a physiological, morphological and behavioural transformation termed smoltification, preparing them for life at sea (Høgåsen

1998). The physiological transformation is synchronised by photoperiod and temperature, and the downstream migration is ultimately initiated by environmental stimuli such as temperature and water flow in the spring (McCormick et al. 1998, Aarestrup et al. 2002). Timing of and behaviour during downstream migration may be influenced by the genetic origin, indicating a genetic component of the response to environmental factors (Aarestrup et al. 1999, 2000). Following successful downstream migration, trout may spend up to 4 yr (usually 1 or 2 yr) at sea before returning to spawn in their natal river (Klemetsen et al. 2003).

Many brown trout populations have become extinct or severely reduced due to anthropogenic fac-

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tors, such as habitat degradation and man-made migration barriers (Jepsen et al. 1998, Koed et al. 2002, Aarestrup & Koed 2003). Where still present, sea trout are of high economic importance, especially as a target species for recreational angling in both freshwater and seawater (Butler et al. 2009). To supplement wild brown trout populations and/or increase the economic potential of the associated recreational activities, several stocking programs are currently running in many nations. Some are large scale, such as the Baltic stocking programmes, which release about 3.9 million sea trout smolts per year (ICES 2008).

Based on mark-recapture studies, hatchery-reared salmonid smolts often have a reduced survival in nature compared with wild smolts (Finstad & Jonsson 2001). The hatchery environment and domestication may result in production of fish with less optimal behaviours in the wild, e.g. in terms of foraging (Fernö et al. 2011), risk-taking (Sundström et al. 2004) and predator avoidance (Jackson & Brown 2011). The rearing history of the fish also seems to affect the temporal responsiveness to environmental factors, such as temperature and discharge, which initiate downstream migration (Hansen et al. 1984). Aarestrup et al. (2002) found that wild trout smolts migrated faster than first-generation (F1) hatchery-reared smolts, and that the migration speed of wild smolts was positively related to water discharge, as opposed to hatchery-reared smolts. The downstream freshwater and early marine migrations have been suggested to be especially critical for survival (Thorstad et al. 2012a). Hence, the hatchery environment may lead to different migration patterns and timing, as well as less optimal behaviour, leading to reduced fitness compared with wild counterparts.

Surprisingly, studies of Atlantic salmon *Salmo salar* smolts in the initial marine phase have found few differences in survival and migration patterns between hatchery-reared and wild smolts. A possible explanation for this unexpected pattern is related to the larger size of hatchery-reared compared with wild salmon smolts, which may give rise to a faster migration speed and also limit the number of potential predators (Thorstad et al. 2007, Lacroix 2008). Serrano et al. (2009) found a lower survival of hatchery-reared compared with wild sea trout smolts, and suggested larger size, better condition and higher lipid concentrations to be the reasons for this. However, potential confounding effects exist. In such studies, the wild fish are usually captured for tagging in a trap in the river during the downstream migration, while the hatchery-reared fish are taken directly from the hatchery and released into the river. This

may give a potential bias due to different samples, with for instance different proportions of migrating and non-migrating fish in the wild and hatchery-reared groups (i.e. non-migrating wild fish are not included in the study, but an unknown proportion of hatchery-reared fish not motivated for migration may be included). However, the problems of potential genetic differences and different composition of migrating and non-migrating individuals can be overcome by comparing fish of the same genetic origin and migration propensity. This can be done by releasing F1 hatchery-reared fish of local origin upstream of the trap and allowing them to migrate into the trap together with the wild fish before tagging. With this study design, only actively migrating fish will be used in the comparison of hatchery-reared and wild smolts, and hence this will facilitate a more realistic comparison of survival and behaviour during migration, as done in the present study.

The purpose of the present study was to investigate (1) the behaviour and survival of the freshwater and early marine phase of the seaward migration of sea trout smolts, and (2) whether rearing history affects behaviour and survival in actively migrating smolts by comparing F1 hatchery-reared smolts and wild smolts from the same population and of a similar body size. This was done by capturing downstream migrating wild and hatchery-reared sea trout smolts in the same trap, equipping them with acoustic transmitters, and monitoring their behaviour and survival through the lower river and early marine migration in the fjord by use of automatic listening stations (ALSs).

MATERIALS AND METHODS

Study area

The River Gudenaå (mean annual discharge of $32 \text{ m}^3 \text{ s}^{-1}$; Fig. 1), located in the central part of the Jutland peninsula, is the major freshwater source to the narrow Randers Fjord, Denmark. The River Lilleå (mean annual discharge of $2.6 \text{ m}^3 \text{ s}^{-1}$) is the most important sea trout tributary of the River Gudenaå, and drains into the river 15 km upstream of the river mouth (Aarestrup & Jepsen 1998). The Randers Fjord (30 km long) is divided into a narrow inner section and a wider outer section, which exits into the Kattegat Sea. The salinity varies with water discharge in the River Gudenaå, but the fjord can generally be characterised as brackish. Salinity increases with depth and increasing distance from the river mouth.

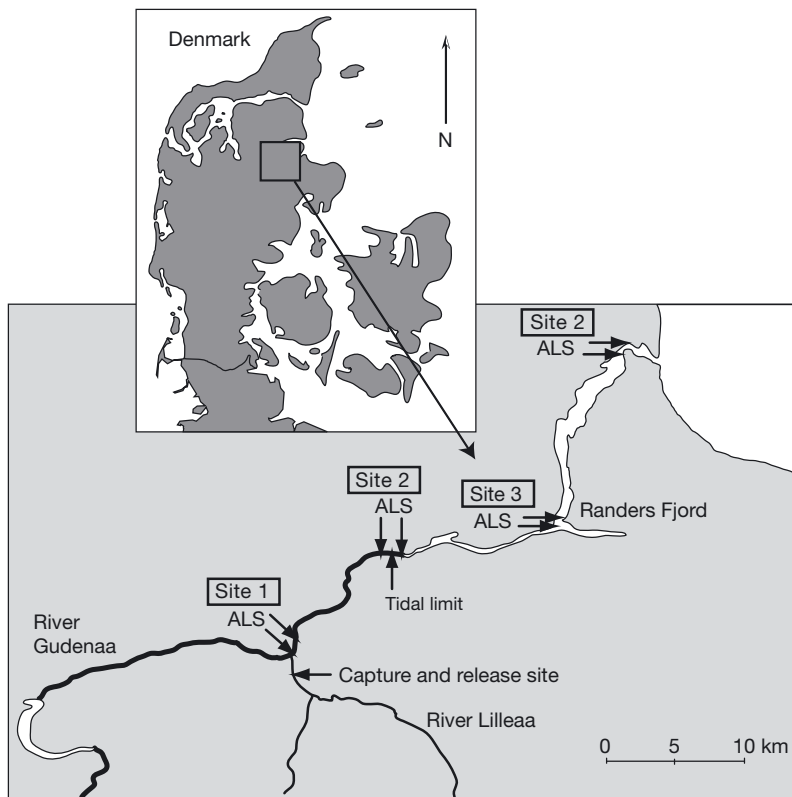


Fig. 1. Capture and release site of wild and hatchery-reared sea trout smolts in River Lilleaa in 2003 and 2005 with sites with automatic listening stations (ALSs) in the River Gudenaa and Randers Fjord. The different compartments are delineated by the capture and release site and the ALS sites; hence, compartment LilRiv is from the capture and release site to ALS 1, GudRiv is from ALS 1 to 2, InnerFj is from ALS 2 to 3 and OuterFj is from ALS 3 to 4. There are two ALSs (arrows) at each site

Experimental fish

Hatchery-reared trout were released at the beginning of the normal smolt run (released 1 April in 2003 and 31 March in 2005) 3 km upstream of the trap and allowed to migrate down to the trap to ensure that only migrating smolts were selected for tagging. Downstream migrating smolts were captured in the spring of 2003 (13 April–24 May) and 2005 (4 April–21 April) in a wolf-type trap at Løjstrup Mill fish farm in the River Lilleaa (for details, see Aarestrup et al. 2002). Løjstrup Mill fish farm is situated 2 km upstream of the confluence with the River Gudenaa. A total of 107 smolts captured in the trap were tagged and identified as of either wild or hatchery-reared origin (Table 1). Hatchery-reared smolts were distinguishable from wild smolts

based on a small clip in the adipose fin. Additionally, hatchery fish were clearly separable based on fin damage and coloration. The hatchery-reared smolts were F1 offspring of wild returning sea trout captured in the River Lilleaa and reared at the Skibelund hatchery in outdoor tanks.

Acoustic tracking

Based on previous experiences (Aarestrup et al. 2008, 2010), 8 ALSs (model VR2, VEMCO) were deployed at 4 different locations in the River Gudenaa and Randers Fjord in groups of 2, separated by a few hundred metres (Fig. 1). The 4 groups of ALSs were placed 2.4 km (ALS 1), 17.3 km (ALS 2), 29.6 km (ALS 3) and 46.0 km (ALS 4) downstream of the release site (Fig. 1) to monitor the time of passage. This design enabled comparison of smolt survival and behaviour between 4 compartments with different physical characteristics: (1) the small River Lilleaa from the release site to the confluence with the River Gudenaa (2.4 km stretch, termed LilRiv in the 'Results'), (2) the lower part of the River Gudenaa (14.9 km stretch, termed GudRiv), (3) the narrow inner section of the Randers Fjord (12.3 km stretch, termed InnerFj), and (4) the outer wider section of the Randers Fjord (16.3 km stretch, termed OuterFj) (Fig. 1). Efficiency for the arrays is estimated to be 100%. For more information on the system setup, range and efficiency see Aarestrup et al. (2010). Manual tracking by boat was performed in both years over the complete study area from Randers to the outlet of the fjord in mid-June to assess whether there were any remaining fish and/or tags in the area.

Table 1. *Salmo trutta*. Number of tagged and released wild and hatchery-reared sea trout smolts in 2003 and 2005, mean (\pm SE) body length at release, and number and proportion of fish exiting Randers Fjord into the Kattegat

Group	Number tagged	Body length (cm)	Number (%) survived out of the fjord
Wild trout 2003	31	20.5 \pm 0.6	25 (81)
Hatchery-reared trout 2003	16	17.6 \pm 0.3	7 (44)
Wild trout 2005	30	15.7 \pm 0.1	22 (77)
Hatchery-reared trout 2005	30	15.5 \pm 0.4	8 (27)

Smolt tagging and release

The smolts were tagged with miniature acoustic transmitters (VEMCO, model V7-2L, 7 × 20 mm, weight in air 1.6 g, weight in water 0.75 g, lifetime 94 d) on the same day as captured in the trap, according to the method used by Aarestrup et al. (1999). The total length (to nearest 0.5 cm) and weight (to nearest gram) of each individual were recorded. When recovered (less than 10 min in all fish), the fish were released immediately downstream of the trap. No fish died prior to release, and all fish appeared to be in good physical condition with swimming behaviour in the recovery tank similar to that of untagged control fish in the field. For Atlantic salmon smolts, Moore et al. (2000) recommended tags to be <5% of fish mass to minimise effects on behaviour and survival. In the present study, this proportion (1.4–4.1%) was below the above recommendation.

Data analysis

Net ground speed was calculated as the time from the first registration on the first ALS group and the first registration on the next ALS group divided by the shortest possible migration distance between. Speed was modelled as a function of compartment, e.g. InnerFj (Comp), year (Year), group (Group) and fish length (Length) using linear mixed effects models (LMM) following Zuur et al. (2009). Comp, Year, Group, and Length were entered as fixed effects. FishID was entered as a random effect, thereby accommodating the repeated measures on each fish. Additionally, the 2-way interactions Group:Year, Group:Comp, Year:Comp, and Group:Length were entered. Finally, a variance structure was included to allow variance heterogeneity between compartments. The optimal model was found using backwards elimination using $p = 0.05$ as threshold for elimination. Significance of model terms was estimated by likelihood ratio tests and single term deletion. Validation plots of model residuals showed no signs of violation of model assumptions. Survival between each compartment was measured as the number of smolts detected at the downstream group of ALSs divided by the number of smolts detected at the upstream group of ALSs. Individual mortality probabilities in each compartment (LilRiv, GudRiv, InnerFj, OuterFj; Fig. 1) were analysed using binomial generalised linear models (GLM) with a logit link function. Separate models were fitted for each compartment, such as $\text{MortLilRiv} = \text{Year} + \text{Length} + \text{Group} + \text{Group:Year}$,

where MortLilRiv is the individual mortality probability modelled as a function of year, length, group, and the interaction between group and year. Significance of model terms was tested using single term deletion, and non-significant terms were removed. Visualization of the models was based on back-transformed mean (\pm SE) values predicted on the logit scale. The LMM and GLM models were performed in R version 2.15.0 (R Development Core Team 2013) using the nlme 3.1-103 package (Pinheiro et al. 2013). Circular statistics were applied to assess the diurnal behaviour of the 2 groups of smolts using the statistical software Oriana 4 (www.kovcomp.co.uk/oriana/). All results presented are based on Watson's U^2 -tests (Zar 1999), which compares the distributions of 2 samples using mean squares deviations under the null hypothesis that the 2 distributions are identical. Input values were the first registration on each ALS group.

RESULTS

Behaviour

The mean (\pm SD) migration speed in wild smolts varied between $36.8 \pm 19.1 \text{ km d}^{-1}$ (range = 5.1–77.5; 0.23 ± 0.12 body lengths [BL] s^{-1} , range = 0.03–0.51) in the River Gudena and $3.2 \pm 4.4 \text{ km d}^{-1}$ (range = 0.51–16.2; $0.020 \pm 0.028 \text{ BL s}^{-1}$, range = 0.003–0.12) in the outer part of the fjord (Fig. 2). The mean migration speed in hatchery-reared smolts varied between $32.0 \pm 15.0 \text{ km d}^{-1}$ (range = 4.2–55.3; $0.22 \pm 0.11 \text{ BL s}^{-1}$, range = 0.02–0.39) in the River Gudena and $4.1 \pm 3.9 \text{ km d}^{-1}$ (range = 0.62–13.7; $0.023 \pm 0.029 \text{ BL s}^{-1}$, range = 0.004–0.10) in the outer part of the fjord (Fig. 2). The wild smolts spent on average 21.4 d (SD = 9.3, range = 5.5–37.5) and the hatchery-reared smolts on average 16.6 d (SD = 9.4, range = 4.4–32.0) from release to the outermost ALS (ALS 4), 46 km from the release site.

Although between-compartment variation existed, the LMM revealed an overall effect of Group on migration speed, indicating that hatchery-reared smolts migrated faster than wild smolts ($p = 0.0038$; Fig. 2). However, compared with the effect of compartment, this difference was small (Fig. 2). The Year:Comp interaction was significant ($p = 0.033$), indicating that net ground speed differed between years, but this difference was compartment dependent.

There was no significant difference in the migration timing at ALS locations between wild and hatchery-reared smolts at any ALS location (Watson's U^2 -tests, $p > 0.05$ in all cases). Additionally, no significant overall change in the diurnal pattern was

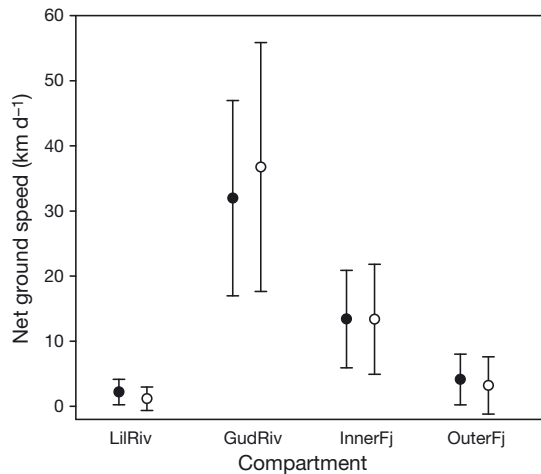


Fig. 2. *Salmo trutta*. Net ground speed of wild (open circles) and hatchery-reared (closed circles) sea trout smolts in each compartment (LilRiv: River Lilleaa; GudRiv: River Gudena; InnerFj: inner Randers Fjord; OuterFj: outer Randers Fjord). Data are means \pm SD

found as migration progressed downstream (Watson's U^2 -tests comparing migration timing at sequential ALS locations, $p > 0.05$ in all cases). The diurnal migration pattern was mainly nocturnal, but only significantly so in hatchery-reared smolts at ALS 1 and ALS 4 (Watson's U^2 -tests comparing migration timing at each ALS location against a uniform distribution; $p < 0.005$ for hatchery smolts at ALSs 1 and 4; $p > 0.05$ for all others; Fig. 3).

Survival

Wild smolts had a within-river mortality of 0.19% km⁻¹ in 2003 and 0% km⁻¹ in 2005, whereas the corresponding numbers for hatchery-reared smolts were 1.65% km⁻¹ and 2.61% km⁻¹, respectively. Fjord mortality for wild smolts was 0.63% km⁻¹ in 2003 and 0.92% km⁻¹ in 2005. Corresponding num-

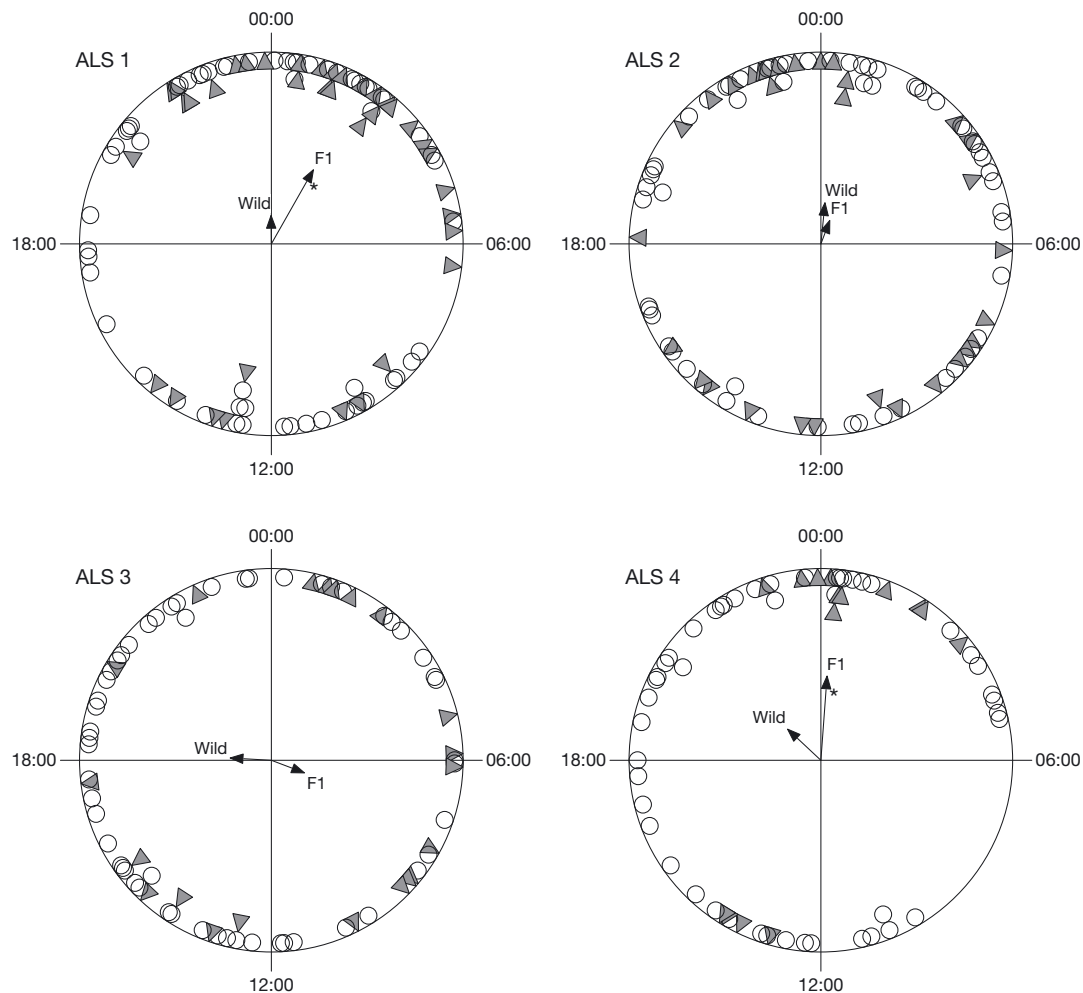


Fig. 3. Migration timing at the 4 automatic listening station (ALS) sites. Arrows indicate mean time of recordings of wild (open circles) and hatchery-reared (F1; filled triangles) sea trout smolts. Lengths of arrows indicate clustering of values, i.e. a long arrow indicates a high degree of clustering while a short arrow indicates a more uniform distribution. No significant differences in migration timing at each ALS group between wild and hatchery-reared smolts were found. The distributions of migration timing of hatchery-reared smolts at ALS 1 and 4 were significantly different from uniform ($p < 0.05$)

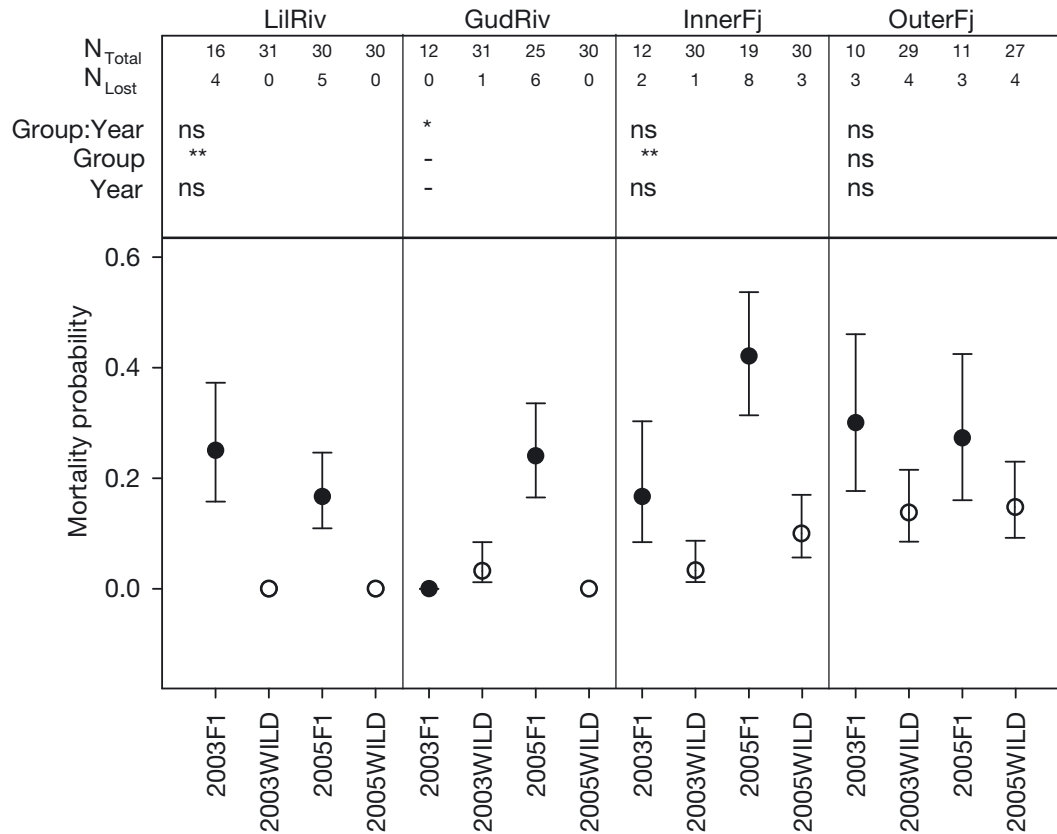


Fig. 4. Visualization of generalised linear models testing for differences between Group and Year in individual sea trout smolt mortality probabilities (means \pm SE) in the 4 compartments (see Fig. 2 legend for compartment definitions). Statistical significance levels (**: $p < 0.01$; *: $p < 0.05$; ns: $p \geq 0.05$) of model terms are indicated for each compartment; -: not tested due to significant interaction

bers for hatchery-reared smolts were $1.86\% \text{ km}^{-1}$ and $2.91\% \text{ km}^{-1}$, respectively.

With one exception (GudRiv in 2003), all results indicate that the mortality was considerably higher in hatchery-reared than wild fish (Fig. 4). In compartments LilRiv and InnerFj, the main effect of Group was highly significant ($p < 0.01$), whereas no significant effect of Group was found in the outer marine compartment OuterFj ($p = 0.17$). The main effect of Year was non-significant in compartments LilRiv, InnerFj, and OuterFj. The Group:Year interaction was significant in the compartment GudRiv ($p = 0.028$). Although non-significant in the other compartments, this interaction was maintained when producing the visualization of all models to facilitate direct comparison between compartments. Length was non-significant ($p > 0.05$) in all compartments and was thus removed from the final models. The manual tracking detected no acoustic tags when performed in mid-June and the ALSs detected no tags after this time, indicating that all tagged smolts had either died or left the fjord before mid-June.

DISCUSSION

The net ground speed during migration varied considerably among compartments, for both wild and hatchery-reared trout smolts. The slower migration speed in the River Lilleaa than that subsequently in the River Gudenaas may be related to the smolts having a slower migration speed in the first period after capture, tagging and release, but it may also be that the migration speed in general is higher in the much larger, more uniform and faster-flowing River Gudenaas. Migration speeds relative to the ground depend on the active movement of the smolts, but also on the speed and direction of the water currents (e.g. Økland et al. 2006). The slower migration speeds in the marine environment compared with the river, for both wild and hatchery-reared smolts, was also observed by Serrano et al. (2009), and may be due to slower water currents in the migration direction in the fjord than in the river because of tidal influence. In Atlantic salmon, there is evidence of a selective ebb-tide transport compo-

ment to estuarine migrations, with the smolts moving within the upper water column and in the fastest-moving section of the water channel (Moore et al. 1995, Lacroix et al. 2004). This may increase the effectiveness of fjord migration, but may still not be as effective as migrating downstream with the current in a large river. It is not known to what extent sea trout smolts use a selective ebb-tide transport. A further reduction in migration speeds in the outer marine compartment of the Randers Fjord before entering the Kattegat compared with the innermost and less saline marine compartment was surprising based on results in studies on Atlantic salmon smolts. In general, Atlantic salmon smolts increase their migration speed as they move from the river towards the ocean (Finstad et al. 2005, Davidsen et al. 2009, Kocik et al. 2009). Further, Hedger et al. (2008) found that exposure to more saline waters increased swimming speeds. Similarly, Martin et al. (2009) found that even small increases in salinity in an estuary induced a shift in smolt behaviour to an increasingly active and seaward-oriented migration. The discrepancy between the results in the present study and the studies referred to above may be due to species-specific differences between Atlantic salmon and brown trout, and there are few studies on brown trout from similar environments to compare our results with. One obvious difference between the 2 species is the generally much shorter migration distance in sea trout compared with salmon (Klemetsen et al. 2003). Sea trout predominantly stay within 200 km of the river whereas salmon migrate up to several thousand kilometres. Hence, the motivation to leave the fjord fast may be less in trout if the conditions are otherwise suitable in terms of food, etc. If this is a correct assumption, salmon smolts should leave the fjord faster than trout, and we recommend future studies comparing salmon and trout behaviour in similar systems. As pointed out by Thorstad et al. (2012a), there is huge variation among estuaries and early marine habitats, and different characteristics among study sites may also explain differences in results among studies. For example, Randers Fjord is microtidal and hence reversing current speeds will be smaller than in areas with a higher tidal amplitude (e.g. Moore et al. 1995), potentially affecting the net ground speed of smolts migrating through the fjord.

Net ground migration speeds in the river in the present study were within the range previously reported in studies of Atlantic salmon and sea trout smolts (Serrano et al. 2009, Thorstad et al. 2012a). The net ground speeds recorded in the marine en-

vironment were also within the range reported in studies of Atlantic salmon and sea trout smolts (Finstad et al. 2005, Thorstad et al. 2007, Serrano et al. 2009), but were among the slower speeds in the range. Variation in migration speeds among studies is generally large (Thorstad et al. 2012a).

Overall, the migration speeds were higher for hatchery-reared than wild smolts. In studies of Atlantic salmon, it has also been found that hatchery-reared smolts migrate faster than wild smolts, but this was mainly attributed to the larger size of the hatchery-reared smolts (Thorstad et al. 2007, Lacroix 2008). In a study of sea trout, wild smolts migrated faster than hatchery-reared smolts both in absolute terms and when corrected for the larger size of the hatchery-reared fish (Serrano et al. 2009). As opposed to other studies comparing wild and hatchery-reared smolts (Thorstad et al. 2007, Lacroix 2008, Serrano et al. 2009), hatchery-reared smolts in the present study were of approximately the same size as (or smaller than) the wild smolts, and there was no effect of fish length on migration speeds. On closer inspection of the results, the difference in speed was small, especially compared with the large differences in migration speed among compartments.

Most of the migration was nocturnal (~60%), but with a considerable amount of migration during daytime. A predominantly nocturnal migration is in concordance with the results of Aarestrup et al. (2002) and also with the general description of smolt migration. We have no obvious explanation for the relatively large number of fish moving during the daytime, and it may be related to yearly varying external factors such as rapid flow increases or temperature rises, also shown to stimulate smolt migration during the day (Aarestrup et al. 2002). However, both hatchery-reared and wild smolts were subjected to the same environmental stimuli and there was no difference in the diurnal migration pattern between wild and hatchery-reared smolts. According to Thorstad et al. (2012a), nocturnal migration at low temperatures is thought to be an adaptive behaviour to avoid predation by visual predators. Daytime migration using visual cues may in other respects be advantageous for the smolts, and daytime migration may be safer at higher water temperatures when smolt escape responses are faster (Ibbotson et al. 2006). Hence, whether a diurnal or nocturnal migration is the overall most advantageous strategy may depend on water temperature, in combination with water depth, predator regime and river size. The results in the present study indicate that adaptations to migration during the night were not influenced by hatch-

ery environment, since there were no differences in the behavioural pattern between the wild and the hatchery-reared fish.

Despite no large differences detected in behaviour between wild and hatchery-reared smolts, the fitness of the hatchery-reared smolts was poorer than that of wild smolts based on a lower survival of the hatchery-reared fish in both the river and early marine environments. From release to recording at the outermost ALS site (46 km from the release site, immediately before entering the Kattegat), the survival of the wild smolts was 1.8 times higher than that of the hatchery-reared smolts in one study year, and 2.9 times higher in the other study year. It should be noted that in studies such as the present, it is the behaviour of the surviving individuals that is recorded and compared. This behaviour per se might not be representative of those not surviving. The results are in accordance with those of Serrano et al. (2009), who found a similar reduction in survival in hatchery-reared sea trout smolts.

The survival of wild smolts from release to the open coast was similar between this study and that of Serrano et al. (2009), with a survival of 81% and 77% in the 2 study years in this study, and 80% survival recorded by Serrano et al. (2009). These high survival rates were recorded despite the fact that trapping, handling and tagging may influence the fish negatively. The survival rates recorded must therefore be regarded as minimum survival compared with untagged fish. According to Peake et al. (1997), hatchery-reared Atlantic salmon smolts may be less affected by tagging than wild smolts. Further, Jepsen et al. (2008) found that tagging with dummy transmitters did not affect the predation rate by a fish predator in hatchery-reared brown trout compared with untagged control fish. Hence, potential tagging effects are therefore not expected to influence the validity of the conclusions in the present study regarding the lower survival of the hatchery-reared smolts relative to the wild smolts. Mortalities for the wild smolts in this study were within the range reported for wild Atlantic salmon smolts, given as mortality per kilometre migration (Thorstad et al. 2012a).

Since there were only small differences in migration speeds between hatchery-reared and wild smolts, and none in diurnal activity patterns, the considerably lower survival of the hatchery-reared smolts compared with wild smolts may be caused by behavioural differences on a smaller scale than those recorded in the present study, e.g. behaviour related to avoiding a predator attack. Studies of hatchery-

reared Atlantic salmon indicate that a considerable proportion of hatchery-reared smolts released in rivers might be lost due to predation before they actually leave the fjords (Thorstad et al. 2011, 2012b). In general, hatchery fish demonstrate poor anti-predator behaviour compared with wild fish, perhaps due to the lack of exposure to predators under hatchery conditions and relaxed selection on antipredator traits in hatchery populations (Einum & Fleming 2001). In the River Gudena, predators such as pike *Esox lucius*, pikeperch *Stizostedion lucioperca* and grey heron *Ardena cinerea* have been demonstrated to cause substantial mortality on migrating smolts (Koed et al. 2002). Other predators, such as cormorants *Palacrocorax carbo*, American mink *Neovision vison* and otter *Lutra lutra*, are also present in the area. However, none of the potential predators would resemble a smolt migration in this study, as birds would move the tagged smolt away from the water and pike and pikeperch are unable to survive in the outer fjord due to high salinities (so none would be detected at ALS 4). Consequently, ground speed of the surviving smolt will reflect true smolt behaviour. Hence, poor anti-predator behaviour of hatchery-reared smolts offers a potential explanation, but we advocate further research into possible behaviour differences between surviving and non-surviving fish. Alternatively, a lower survival of the hatchery-reared smolts could be explained by reduced smolt quality, impaired seawater tolerance and thereby increased mortality (Järvi 1989). However, the results do not support that the difference in survival was caused by a reduced seawater tolerance of hatchery-reared smolts. If this were the case, the difference in survival would likely have been larger in the outer saline marine compartment, where no significant difference was found, and smaller in the riverine and innermost marine compartments, where the largest differences were in fact recorded (Fig. 4).

The present results of poor survival, coupled with other reported negative effects of hatchery-reared salmonids (Einum & Fleming 2001), suggest a considerably lower fitness of hatchery reared smolts compared with wild smolts, and question the value of smolt releases as a means for supplementary stocking in brown trout.

CONCLUSIONS

This study demonstrated a large immediate loss of hatchery-reared sea trout smolts after release in the river, with a reduced survival compared to wild

smolts during both the downstream riverine migration and the early marine migration. The difference in survival between wild and hatchery-reared smolts could not be explained by behavioural differences such as migration speeds in different compartments and diurnal variation in migration behaviour, but could have been caused by differences in smaller-scale behaviour than that recorded in the present study, and thereby an increased predation rate in hatchery-reared smolts. The results of this study emphasise that there is scope for improving hatchery production and stocking strategies in order to optimise the outcome of releases.

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