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ARTICLE

Reduced rearing density increases postrelease migration success of Atlantic salmon (*Salmo salar*) smolts

Martin H. Larsen, Jörgen I. Johnsson, Joacim Näslund, Søren T. Thomassen, and Kim Aarestrup

Abstract: The overall aim of this study was to investigate the effect of rearing density on the postrelease survival of Atlantic salmon (*Salmo salar*) smolts during seaward migration. Fish were either reared at conventional hatchery density or at one-third of conventional density. Three hundred 1-year-old smolts from each density treatment were individually tagged with passive integrated transponder tags and released 3.2 km upstream of a stationary antenna array in a natural stream. There were no significant differences in length, body mass, or condition between fish from the two density treatments during rearing in the hatchery. However, individuals reared at reduced density had less eroded dorsal fins and opercula relative to those from the high-density treatment. In the stream, the downstream migration success was 16% higher for fish reared at reduced density than for conspecifics kept at high density, but the timing of migration was similar for both groups. These novel results suggest that conventionally high rearing densities may reduce welfare and the postrelease migration success of hatchery-reared Atlantic salmon.

Résumé : L'objectif global de l'étude consistait à étudier l'effet de la densité d'élevage sur la survie après le lâcher de saumoneaux de saumon atlantique (*Salmo salar*) durant la migration vers la mer. Des poissons ont été élevés soit dans des conditions de densité normale en alevinière ou à une densité égale à un tiers de la densité normale. Trois cents saumoneaux de 1 an issus de chacun des traitements de densité ont été marqués individuellement avec des radioétiquettes passives intégrées et relâchés 3,2 km en amont d'un réseau d'antennes stationnaires dans un cours d'eau naturel. Aucune différence significative n'a été observée en ce qui concerne la longueur, la masse corporelle et l'embonpoint entre les poissons issus des deux traitements de densité durant l'élevage en alevinière. Cependant, les individus élevés à moindre densité présentaient une nageoire dorsale et des opercules moins érodés que les individus issus du traitement à plus forte densité. Dans le cours d'eau, le succès de l'avalaison était de 16 % supérieur pour les poissons élevés à moindre densité que pour leurs congénères maintenus dans des conditions de forte densité, le moment de la migration étant toutefois semblable pour les deux groupes. Ces résultats originaux donnent à penser que les fortes densités d'élevage utilisées normalement pourraient limiter le bien-être et le succès de la migration après le lâcher des saumons atlantiques élevés en alevinière. [Traduit par la Rédaction]

Introduction

Hatchery supplementation programs are widely implemented to mitigate losses in declining or threatened populations of salmonids from anthropogenic factors, such as habitat degradation, damming of rivers, pollution, and overexploitation (Parrish et al. 1998; Fraser 2008; Jonsson and Jonsson 2009). However, because the postrelease survival of hatchery-reared salmonids is often considerably lower than that of their wild counterparts (e.g., Jonsson et al. 2003; Jonsson and Jonsson 2006; Aarestrup et al. 2014), the efficiency of such hatchery programs has been debated (Brannon et al. 2004). Saloniemi et al. (2004), for example, showed that wild Atlantic salmon (*Salmo salar*) smolts had a 4.5 times higher survival rate than cultured fish in a northern Baltic river. Changes in behavioural, physiological, and morphological phenotypes due to the artificial rearing environment have been recognized as major factors contributing to the poor survival of hatchery-reared fish in nature (Brannon et al. 2004; Huntingford 2004; Fraser 2008).

Several studies have evaluated the potential for improving postrelease performance of hatchery-reared salmonids by using a variety of different rearing methods (Brown and Laland 2001; Brown and Day 2002; Näslund and Johnsson 2016), but surprisingly few have tested and verified whether these methods are applicable on a larger scale to increase survival of released fish in nature (but see Brockmark and Johnsson 2010; Hyvärinen and Rodewald 2013; Kavanagh and Olson 2014). Recently, however, rearing at reduced hatchery density has shown promising results in increasing postrelease survival of hatchery-reared salmonids (Brockmark and Johnsson 2010; Barnes et al. 2013; Kavanagh and Olson 2014). For instance, studies on brown trout (*Salmo trutta*) parr demonstrated that reduced density facilitated development of behavioural life skills, including foraging abilities and predator avoidance response, resulting in increased survival in their natural stream environment (Brockmark and Johnsson 2010; Brockmark et al. 2010). Furthermore, altering rearing densities may have profound influence on growth, stress levels, and fin condition of hatchery fish (Ellis et al. 2002; Ashley 2007; Johnsson et al. 2014). In general, higher stocking densities in the hatchery will increase stress and degree of fin erosion and reduce growth (Ellis et al. 2002; Ashley 2007). These findings may also explain why salmonids reared at low densities often have higher percentages of postrelease survival than those reared at higher densities (Johnsson et al. 2014). Kavanagh and Olson (2014), for example, found that juvenile steelhead (*Oncorhynchus mykiss*) reared at low density were larger at release, had significantly better dorsal fin condition, and greater smolt-to-adult survival rate in nature when compared with individuals reared at higher densities. It should be emphasized that not all studies report positive effects of reduced

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rearing density on survival of stocked salmonids in nature (Hopley et al. 1993; Clarke et al. 2013). This might have to do with differences in rearing facilities (e.g., ponds versus raceways), species-specific responses to crowding stress, and specific environmental conditions (Ewing and Ewing 1995; Tipping et al. 2004; Johnsson et al. 2014). Clearly, more work is required in this area to investigate the effects of rearing density on postrelease performance of salmonids.

Atlantic salmon reared for supplementary purposes are often released into rivers as smolts in spring, shortly before or at the time of seaward migration of their wild conspecifics (Jonsson and Jonsson 2009). Stocked fish have little time for adapting to the novel natural environment before migration should start, and therefore, any maladaptive traits may lead to mortalities at this stage (Jonsson and Jonsson 2006; Johnsson et al. 2014). Since mortality at the smolt stage contributes to determine the number of returning adult spawners, it is imperative to understand the potential effects of rearing density on behaviour and survival of stocked smolts during migration to the sea.

The objective of this study was to compare the seaward migration success of 1-year-old Atlantic salmon smolts reared at conventional hatchery density and one-third of conventional density. Fish were released during spring in a natural stream, and their decent was monitored using passive integrated transponder (PIT) telemetry. Based on previous work with salmonids discussed above, we hypothesize that fish reared at reduced density would be more successful of undertaking the migration to the sea than individuals from a high-density environment.

Materials and methods

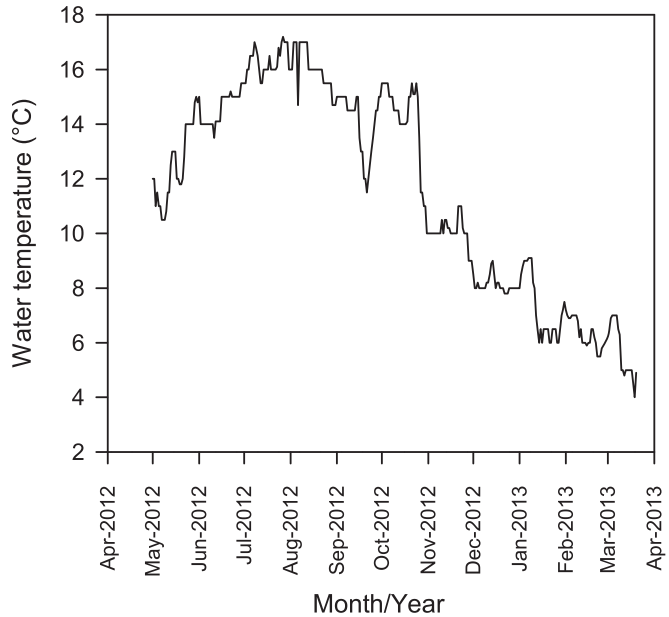
Experimental fish and rearing conditions

The fish used in this study were first-generation hatchery offspring (F_1) of Atlantic salmon originating from River Storå, Denmark. The parental fish were caught in late autumn 2011 by electrofishing and transported to the Danish Centre for Wild Salmon in Randers. The eggs from 47 females were stripped and fertilized by mixing with milt from 27 males. Fertilized eggs were incubated in egg trays and hatched in late March 2012. After yolk sac absorption, experimental fish were transferred to indoor conventional hatchery tanks (200 cm × 200 cm) for exogenous feeding at two rearing densities: high density (HD) and low density (LD). The HD treatment was set according to the local hatchery practice, and the LD treatment was set to one-third of standard density. The initial number of fish in each tank was 30 000 (7500 fish·m^{-2}) for the HD treatment and 10 000 (2500 fish·m^{-2}) for the LD treatment. As the fish grew larger through the summer, the number of fish was lowered in July 2012 to 6000 (1500 fish·m^{-2}) and 2000 (500 fish·m^{-2}) individuals per tank in the HD and LD treatment groups, respectively. Each density treatment was replicated in three hatchery tanks. Water depth in the tanks was kept at 35 cm, resulting in a water volume of 1400 L. The tanks were individually supplied with water from a recirculation system at a flow rate of 30 L·min^{-1}. Throughout the rearing period, the water temperature and indoor light regime followed the natural cycles. The water temperature ranged between 4.0 to 17.2 °C (Fig. 1). The fish were fed with commercial trout pellets (Aller Performa, Aller Aqua, Denmark), equivalent to 2% of body mass per day using automatic feeders. The pellet size was changed in accordance to the manufacturer's recommendations as the fish increased in size.

Sampling protocol

Fish were sampled at three occasions during the rearing period: 12 July 2012 (n = 600), 5 November 2012 (n = 300), and 20 March 2013 (n = 300). At each sampling, equal numbers of fish were netted at random from each replicate tank. Fish were anaesthetized with benzocaine (20 mg·L^{-1}) and individually measured for total length (±1.0 mm) and body mass (±0.1 g). These measurements were later used to calculate condition factor (CF = (100 × body mass (g))/(length (cm)^3)). In addition, during the final sampling event on 20 March 2013, erosion to the fins (dorsal, pectoral, and caudal) and opercula was visually quantified using an ordinal scale of 0, 1, 2, and 3, corresponding to no erosion (0% eroded), mild erosion (1%–24% eroded), moderate erosion (25%–49% eroded), and severe erosion (≥50% eroded), respectively (after Hoyle et al. 2007). Fin and opercula erosion were measured as important indicators of aggression and stress levels during rearing (Ellis et al. 2002; Latremouille 2003; Huntingford et al. 2006). Fish were also examined for other external lesions on their bodies as evidence of aggressive encounters with conspecifics. All fins and opercula were scored by the same observer to avoid bias. Fish were returned to their respective tanks after these procedures.

Fig. 1. Water temperature (°C) during rearing.

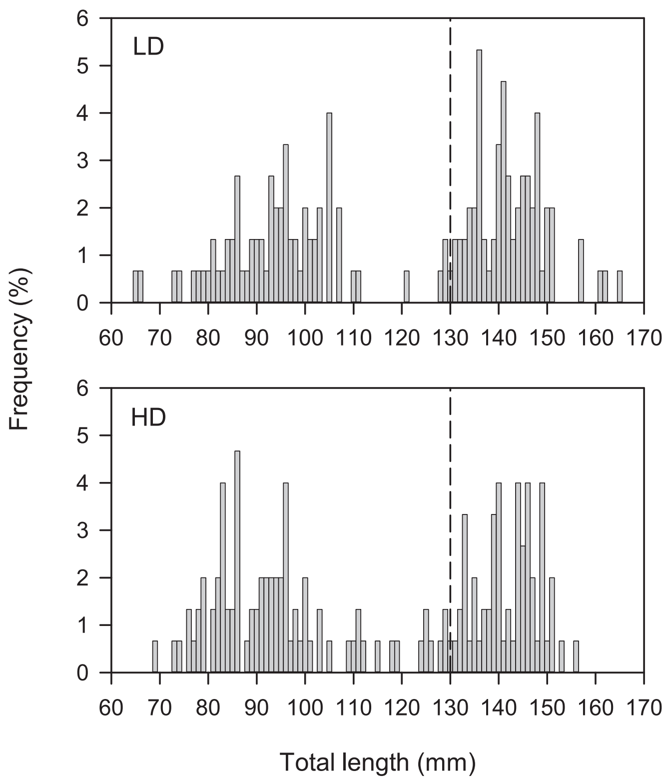


Released fish

In March 2013, the Atlantic salmon exhibited a bimodal size distribution regardless of density treatment (Fig. 2). The antimode separating the lower (LMG) and upper (UMG) modal group was approximately 130 mm for both density groups. Only UMG fish were selected for release in a nearby natural stream, since these individuals were expected to smoltify at 1 year old (Thorpe 1977). On 22 March 2013, 100 Atlantic salmon ≥130 mm in total length were randomly netted from each of the six hatchery tanks (i.e., 300 fish from each density treatment). These fish were anesthetized and measured for length and body mass as above. Next, fish were individually tagged by surgically implanting a 23 mm PIT tag (RI-TRP-RRHP, half duplex, 134 kHz, diameter 3.85 mm and mass 0.6 g in air; Texas Instruments, Plano, Texas, USA) into the peritoneal cavity through a small ventrolateral incision made slightly anterior to the pelvic fins. A recent evaluation of this marking technique with Atlantic salmon showed that retention of the tags is very high (97%) with no major effects on survival or growth (Larsen et al. 2013). Following tagging, smolts were kept in a tank for observation during 12 days. As expected, there were no mortalities or tag loss during this period.

On 3 April 2013, the PIT-tagged fish were transported in two oxygenated tanks (each 750 L) to Gudsø Stream located in east-central Jutland, Denmark (Fig. 3). The total transportation time was 1.5 h, and all fish were in good condition and showed no signs of abnormal behaviour. Including a series of tributaries, the stream flows approximately 16 km through primarily agricultural areas before reaching the sea at Kolding Fjord (Fig. 3). The width of the stream

Fig. 2. Length–frequency distribution of Atlantic salmon on 20 March 2013 reared at conventional hatchery density (HD) and one-third of conventional density (LD). Three hundred fish ≥ 130 mm in total length (indicated by dashed vertical lines) were randomly selected from each density treatment for release into a natural stream.



is mostly between 1 and 4 m, and the water depth is generally less than 1 m. The bottom substratum consists mainly of coarse sand, mud, and gravel. Atlantic salmon are not indigenous in Gudsø Stream, but it supports a wild population of partially migratory brown trout, wherein a portion of the individuals become resident and the remaining perform seasonal migrations between freshwater and seawater habitats. European eel (*Anguilla anguilla*) and brook lamprey (*Lampetra planeri*) are also found in the stream.

The fish were released on a 150 m stretch of the stream, 3.2 km upstream of a PIT antenna station (S1) consisting of two loop-shaped antennas spaced 5 m apart, each covering the entire cross-section of the stream (Fig. 3). The antenna station was installed 1.1 km upstream from the stream outlet to Kolding Fjord. The paired use of antenna allowed us to determine the swimming direction of migrating fish. When a tagged fish passed an antenna, the unique tag number with date and time of detection were recorded by a reading unit and stored on a memory card. If a fish was recorded at an antenna, it was considered a successful migrant. Conversely, fish not recorded at S1 were classified as unsuccessful migrants. These individuals may include mortality of fish, residual fish, tag lost by fish after release, and nondetected tags.

To evaluate the in situ tag detection efficiency of S1 (E_{S1}), a second antenna station (S2), which also consisted of two individual swim-through antennas, was positioned approximately 150 m downstream of S1 (Fig. 3). E_{S1} was estimated based on the number of Atlantic salmon that were detected at the PIT stations using the formula described in Zydlewski et al. (2006):

$$E_{S1} = (d_{\text{common to S1 and S2}}) \times (d_{\text{unique to S2}} + d_{\text{common to S1 and S2}})^{-1} \times 100\%$$

where d is the number of PIT-tagged fish decoded. This allowed us to estimate E_{S1} as 99.7%. The in situ detection efficiency could not be estimated for S2 because of the absence of downstream detections (Zydlewski et al. 2006). A marker tag (Oregon RFID, Portland, Oregon, USA) was mounted over the top of each antenna to verify that the antennae were operating continuously throughout the study period. The marker tags were set to emit a pulse every hour.

On 18 and 19 June 2013, after the smolt migration had finished, the stream was surveyed using single-pass backpack electrofishing from the antenna stations to 1.5 km upstream of the release site. Selected transects of all tributaries that flow into the main stem of the stream were also sampled. Electrofishing was performed to assess the survival status (i.e., dead or alive) of fish that were not detected at the PIT antennas. Handling, rearing, and tagging of fish were conducted in accordance to the guidelines described in permission (2012-DY-2934-00007) from the Danish Experimental Animal Committee.

Statistical analysis

Linear mixed effects models (LMMs) were used to analyze effects of rearing density on length, body mass, and CF for the three sampling occasions in the hatchery. The model used was as follows:

$$\text{(1)} \quad \text{Response variable} = \text{Intercept} + \text{Treatment} + \text{Tank(Treatment)}$$

with Treatment (LD and HD) as a fixed factor and replicate Tank nested within Treatment as a random effect variable. The model was fitted using restricted maximum likelihood. We used the same model to compare length, body mass, and CF of released smolts between density treatments. Differences in intensity of fin and opercula erosion between density treatments were assessed using generalized linear models (GLMs) with a multinomial probability distribution and cumulative logit link function according to model 1, but with Tank(Treatment) as a fixed factor to detect possible effects of specific tanks. Likelihood ratio tests (LRT) were used to evaluate overall model significance. Separate analyses on fin and opercula condition were also performed for fish ≥ 130 mm in total length, corresponding to the size range of fish that were released into Gudsø Stream. Fin and opercula erosion was not quantified for the released smolts to minimize handling time.

To analyze the effect of rearing density and fish length at time of release on the probability of successful migration (yes or no), we used a generalized linear mixed model (GLMM) with a binomial error structure and logit link function according to the following model:

$$\text{(2)} \quad \text{Migration success} = \text{Intercept} + \text{Treatment} + \text{Length} + (\text{Treatment} \times \text{Length}) + \text{Tank(Treatment)}$$

with Treatment as a fixed factor, Length as a continuous covariate, and replicate Tank nested within Treatment as a random effect variable. Model 2 was also used to examine the influence of body mass and CF on migration propensity. A two-sample Kolmogorov–Smirnov (K–S) test was used to evaluate the influence of rearing density on migratory timing, which was calculated as the number of days from release until a migratory fish was first recorded at S1.

All statistical analyses were performed in R 3.0.1 (R Core Team 2013) and SPSS 20.0 (IBM Corporation, Armonk, New York, USA). Prior to the analyses, data explorations were applied following a protocol described by Zuur et al. (2010). To determine minimum adequate models, we used backwards stepwise elimination of nonsignificant predictors with a retention threshold of $P < 0.05$. Assumptions of homogeneity of variance and normality were assessed by graphical inspection of the residuals. Independence was verified by plotting residuals versus each explanatory variable. Length and body mass data were log-transformed prior to analy-

Fig. 3. Map of the Gudsø Stream and position of the two PIT antenna stations, S1 and S2. The arrow indicates the site of release of PIT-tagged Atlantic salmon.

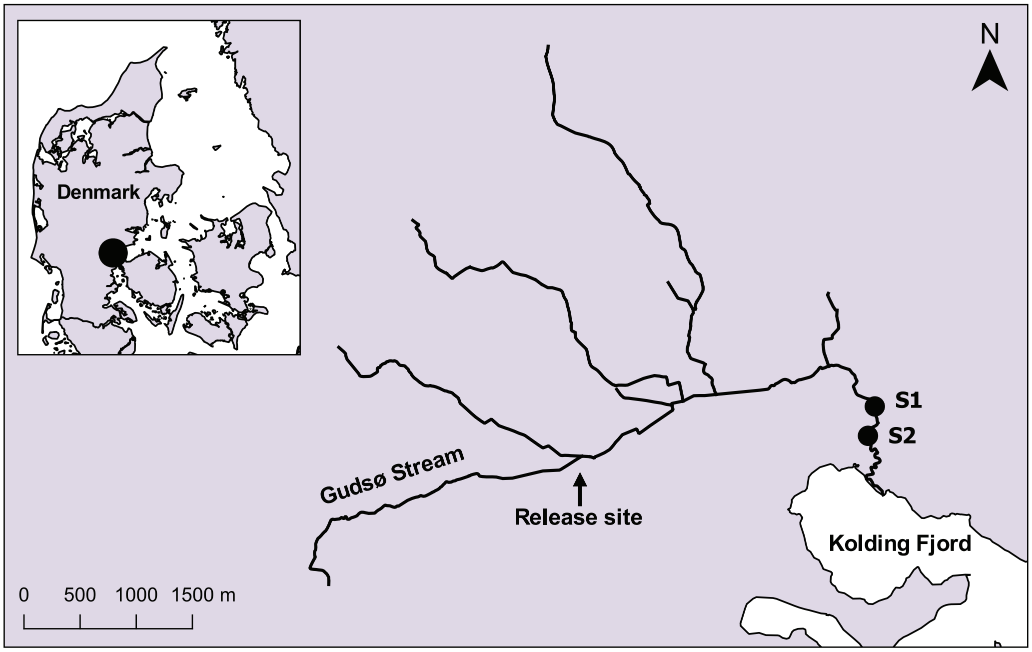


Table 1. Mean (±SD) total length (mm), body mass (g), and condition factor (CF) for Atlantic salmon reared at conventional hatchery density (HD) and one-third of conventional density (LD).

	LD				HD			
	n	Length (mm)	Mass (g)	CF	*n*	Length (mm)	Mass (g)	CF
Hatchery								
12 July 2012	300	53.7±4.73	1.7±0.49	1.04±0.066	300	52.6±4.65	1.6±0.45	1.04±0.060
5 November 2012	150	85.8±20.16	8.1±5.87	1.07±0.090	150	79.8±15.09	6.0±4.04	1.05±0.078
20 March 2013	150	118.9±26.05	20.7±12.04	1.07±0.077	150	114.9±26.46	18.9±11.99	1.06±0.075
Released fish								
22 March 2013	300	152.2±8.05	31.9±5.44	0.90±0.056	300	147.3±7.12	29.4±4.75	0.91±0.064

Note: Fish were measured at three occasions during the rearing period in the hatchery: 12 July 2012, 5 November 2012, and 20 March 2013. The fish released into Gudsø Stream were PIT-tagged and measured on 22 March 2013.

ses. Variation in association with recorded mean values is given as standard deviation throughout. Statistical significance for all analyses was set at $P < 0.05$.

Results

Effect of treatment during rearing

The mean length, body mass, and CF did not differ between fish in the two density treatments at any of the three sampling occasions (LMM, $F \leq 1.914$, df = 1, $P \geq 0.239$; Table 1). However, fish reared at high density had higher frequency and more severe dorsal fin and opercula erosion than those reared at reduced density (GLM, LRT ≥ 4.871, df = 1, $P \leq 0.027$; Table 2). We observed no damage to the caudal and pectoral fins in either of the two density treatments (Table 2). Analyses on fish ≥ 130 mm in total length showed similar results, except that erosion to the right operculum could not be distinguished statistically among density treatments (GLM, LRT = 1.988, df = 1, $P = 0.159$). There were no significant differences in the level of fin and opercula erosion among replicate tanks within each treatment (GLM, LRT ≤ 9.429, df = 4, $P \geq 0.051$).

Downstream smolt migration

A total of 359 out of 600 released smolts were detected at S1 in Gudsø Stream, giving an overall migration rate of 60%. The downstream migration success was significantly higher (16%) for Atlantic salmon reared at reduced density than for individuals reared at high density (GLMM, LRT = 4.517, df = 1, $P = 0.034$; Fig. 4). The migration rate was 64% ($n = 193$ of 300) and 55% ($n = 166$ of 300) for the LD and HD treatment groups, respectively. The mean length of released smolts differed between density treatments, with LD fish being slightly larger (4.9 mm on average) than HD individuals (LMM, $F = 24.300$, df = 1, $P = 0.008$; Table 1). However, length as well as the interaction between treatment and length had no significant effect on the probability of successful migration and were thus excluded from the final model (GLMM, Length: LRT = 0.171, df = 1, $P = 0.679$; Treatment × Length: LRT = 0.418, df = 1, $P = 0.518$). HD fish also had significantly lower body mass than LD individuals (LMM, $F = 16.121$, df = 1, $P = 0.016$), but there was no significant difference in CF between density treatments (LMM, $F = 1.613$, df = 1, $P = 0.273$; Table 1). Migration propensity was not related to body mass (GLMM, LRT = 0.242, df = 1, $P = 0.623$) or CF (GLMM, LRT = 0.045, df = 1, $P = 0.832$).

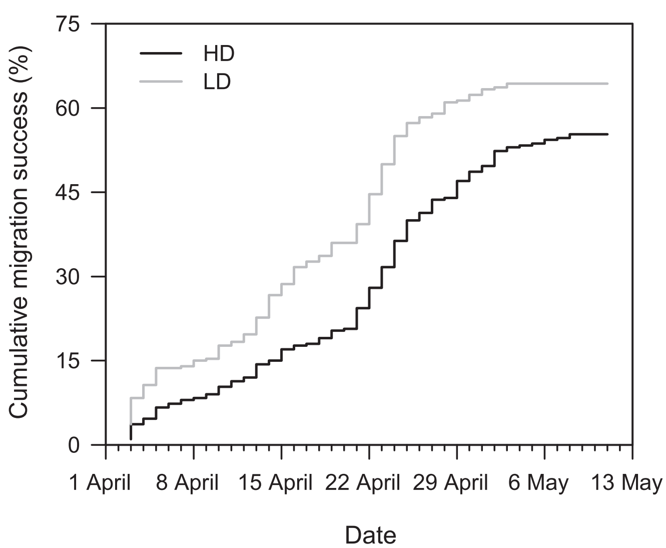
The migratory timing (i.e., time in days since release it took the fish to reach S1) did not vary significantly between density treatments, although smolts reared at high density, on average, were delayed by 4 days (K–S test, $Z = 1.279$, $P = 0.076$). LD fish were detected moving downstream from 3 April to 4 May 2013, whereas HD individuals migrated from 3 April to 9 May 2013 (Fig. 4). None of the released fish were caught during subsequent electrofishing in the stream that occurred on 18 and 19 June 2013.

Table 2. Percentage and absolute number (in parentheses) of Atlantic salmon with fin and opercula erosion reared at conventional hatchery density (HD) and one-third of conventional density (LD).

	Degree of erosion			
	0	1	2	3
Left operculum				
LD	44.7 (67)	54.0 (81)	1.3 (2)	0.0 (0)
HD	27.3 (41)	52.0 (78)	20.7 (31)	0.0 (0)
Right operculum				
LD	84.0 (126)	16.0 (24)	0.0 (0)	0.0 (0)
HD	64.0 (96)	34.0 (51)	2.0 (3)	0.0 (0)
Dorsal fin				
LD	57.3 (86)	31.3 (47)	11.3 (17)	0.0 (0)
HD	50.7 (76)	20.0 (30)	28.7 (43)	0.7 (1)
Left pectoral fin				
LD	100.0 (150)	0.0 (0)	0.0 (0)	0.0 (0)
HD	100.0 (150)	0.0 (0)	0.0 (0)	0.0 (0)
Right pectoral fin				
LD	100.0 (150)	0.0 (0)	0.0 (0)	0.0 (0)
HD	100.0 (150)	0.0 (0)	0.0 (0)	0.0 (0)
Caudal fin				
LD	100.0 (150)	0.0 (0)	0.0 (0)	0.0 (0)
HD	100.0 (150)	0.0 (0)	0.0 (0)	0.0 (0)

Note: The intensity of fin and opercula erosion was quantified using an ordinal scale of 0 (0% eroded), 1 (1%–24% eroded), 2 (25%–49% eroded), and 3 (>50% eroded).

Fig. 4. The cumulative migration success (%) in Gudsø Stream for Atlantic salmon reared at conventional hatchery density (HD) and one-third of conventional density (LD). Fish were released into the stream on 3 April 2013.



Discussion

The present results clearly demonstrate that lowering conventional rearing density can improve postrelease survival of Atlantic salmon smolts during riverine migration to the sea. This finding is in line with results obtained for other salmonid species, where reduced rearing density usually has been shown to increase survival of fish after stocking into nature (e.g., Brockmark and Johnsson 2010; Barnes et al. 2013; Kavanagh and Olson 2014).

Body size is often a key determinant influencing survival of hatchery-reared Atlantic salmon smolts when released into nature (Hansen and Jonsson 1989; Saloniemi et al. 2004). While a majority of studies have found negative effects of increased rearing density on growth of salmonids (e.g., Refstie and Kittelsen 1976; Ellis et al. 2002; Brockmark et al. 2007), some argue that rearing density has no or little effect on growth as long as water quality is maintained at adequate levels and food ratios are within the recommended standards (Hosfeld et al. 2009). In our study, rearing density had no significant effect on growth and condition of fish based on the results obtained from the three sampling occasions in the hatchery (Table 1). However, the mean length and body mass of smolts released into the stream differed significantly between treatments, with fish from the high density being slightly smaller than individuals reared at low density (Table 1; Fig. 2). Regardless, smolt size at release did not influence migration success per se.

The primary goal of the present study was not to identify the mechanisms underlying the observed difference in seaward migration success between density treatments. However, it is important to keep in mind that none of the released fish were caught during the electrofishing surveys that occurred after the smolt migration had finished, implying that unsuccessful migrants in our study may be mortalities. The mortality of smolts was probably mainly caused by predation from grey heron (*Ardea cinerea*), cormorants (*Phalacrocorax carbo*), American mink (*Neovison vision*), and adult trout, which are common in the area. Mortality from starvation is less likely to have occurred, as fish were released into the stream shortly before migrating downstream to the sea (Fig. 4). It has recently been suggested that reduced density may promote development of important behavioural life skills in salmonids, including anti-predator response (Brockmark and Johnsson 2010; Brockmark et al. 2010). As such, it is possible that the lower survival of HD fish during seaward migration was a result of reduced anti-predator behaviour. We cannot exclude that predation on the tagged smolts by adult trout resulted in "false" detections at the PIT antennas. That being said, the anadromous part of the trout population typically migrates back downstream to the sea shortly after spawning (i.e., before the release data of the smolts in the present study (M.H. Larsen, personal observation). Hence, trout predation on the smolts was probably mainly form resident individuals. Resident trout defend territories and are relatively stationary (Höjesjö et al. 2007), decreasing the likelihood of "false" tag detections.

In agreement with previous work on salmonids, assessment of fish during rearing showed a higher degree of dorsal fin and opercula erosion among individuals reared at high density (e.g., Latremouille 2003; Brockmark et al. 2007; Branson 2008). Since damaged fins and opercula can decrease swimming performance and increase susceptibility to predation, this observation may also provide an explanation for the lower migration success of HD fish (Arnold et al. 1991; Ellis et al. 2002; Petersson et al. 2013). Aggressive acts between individuals have been recognized as the primary cause of dorsal fin damage in hatchery-reared salmonids, making it a useful indicator of aggression levels in hatchery environments (Abbott and Dill 1985; Turnbull et al. 1998; Latremouille 2003). Indeed, bites to the dorsal fin and attacks directed at this area were frequently observed in the present study. The definitive cause of the shortened opercula is less clear (Kazlauskieė et al. 2006), but aggressive interactions might represent an important factor as well. Agonistic encounters with conspecifics can be an important source of stress to hatchery fish (Schreck 1982; Wedemeyer 1997; Ellis et al. 2002). It should also be noted that stress has been implicated in causing fin damage by increasing susceptibility to bacterial and fungal infections (Pickering and Pottinger 1985; Branson 2008). Taken together, this may suggest that individuals reared at high density experienced increased stress during rearing relative to those at reduced density. This interpretation is supported by several other studies, which demonstrated that high stocking densities in the hatchery can increase stress levels (Ellis et al. 2002; Ashley 2007). Elevated stress has previously been shown to decrease survival of smolts during seaward migration and could provide an explanatory factor in the lower migration success of HD individuals in the present study (Midwood et al. 2014). It is therefore highly recommended that future studies include physiological stress indicators, such as circulating levels of plasma cortisol.

Another possible explanation for the higher migration success of LD fish could be that they were at a more advanced stage of smoltification compared with individuals in the HD treatment. However, since all released fish appeared to be fully smoltified as judged from morphological features (i.e., a silvery appearance, darkened fins, and slim body shape), this scenario is questionable. Previous studies have also been unable to detect effects of rearing densities up to 86 kg fish·m^{-3} on gill Na^+,K^+-ATPase activity in Atlantic salmon (Brockmark et al. 2007; Hosfeld et al. 2009), which is widely used as a physiological indicator of smolt status (Hoar 1988; Aarestrup et al. 2000). Nonetheless, Brockmark et al. (2007) found a higher survival of Atlantic salmon that were reared at reduced density after being exposed to a seawater challenge test, and visual assessment of body coloration showed that these individuals had a more silvery appearance than those reared at high density. This indicates that rearing density may influence smolt development (see also Schreck et al. 1985). Thus, further studies involving physiological and morphological indices of smolt status are required to resolve whether the observed difference in migration success among density treatments was mediated by differences in level of smoltification.

In conclusion, our study shows that the postrelease survival of hatchery-reared Atlantic salmon smolts along their migratory pathway to the sea can be substantially improved by reducing rearing density. Density reduction is a simple method to practice in supplementation hatcheries, but some important considerations must be made before implementation. An obvious limitation of the present study is that the adult return rate was not evaluated. The socioeconomic benefits of lowering rearing densities will ultimately depend on whether the increased production costs in the hatchery are compensated by increased number of adult returns. Answering such a question requires long-term studies investigating the smolt-to-adult return ratio and development of economic models. Aside from the economic aspects, there is also a growing public concern, as well as increasingly strict legislation, concerning animal welfare in many countries (Huntingford et al. 2006; Ashley 2007). In this context, the ultimate goal should be to minimize stress and allow natural behaviour to be expressed (Ashley 2007; Johnsson et al. 2014). Additional studies are also required to determine the generality of the present findings. These studies should ideally be conducted throughout the native distribution of Atlantic salmon and involve a range of different hatchery facilities and natural systems. Considering that only one of many variables was manipulated in the present study, our results highlight the scope for improving rearing methods of supplementation and (or) conservation hatcheries to optimize outcomes of releases.

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