Transactions of the American Fisheries Society 136:1453–1462, 2007

DOI: 10.1577/T06-245.1

[Article]

Effects of Rearing Density and Structural Complexity on the Pre- and Postrelease Performance of Atlantic Salmon

SOFIA BROCKMARK*
Animal Ecology, Department of Zoology, Göteborg University, Box 463, 405 30 Göteborg, Sweden

LENA NEREGÅRD
Fish Endocrinology Laboratory, Department of Zoology and Zoophysiology, Göteborg University, Box 463, 405 30 Göteborg, Sweden

TORGNY BOHLIN
Animal Ecology, Department of Zoology, Göteborg University, Box 463, 405 30 Göteborg, Sweden

BJÖRN THRANDUR BJÖRNSSON
Fish Endocrinology Laboratory, Department of Zoology and Zoophysiology, Göteborg University, Box 463, 405 30 Göteborg, Sweden

JÖRGEN I. JOHNSSON
Animal Ecology, Department of Zoology, Göteborg University, Box 463, 405 30 Göteborg, Sweden

Abstract.—Hatchery fish released for supplementation purposes often have difficulties adapting to wild conditions and, therefore, perform poorly in the wild. This can, at least partly, be explained by differences between hatchery and wild conditions. Our objective was to evaluate the effects of rearing density and structural complexity on the culture and postrelease performance of age-0 Atlantic salmon *Salmo salar*. By using a 2×2 factorial design, we manipulated density (standard density and one-third of standard density) and structure (standard rearing tanks with and without added rocks and plastic plants) in a conventional hatchery. After 3 months of rearing, 300 fish/treatment were individually tagged with passive integrated transponders, released in a nearby stream, and recaptured in late autumn (November) and summer (June). Fish not released were retained in the hatchery until smolting occurred during the next spring. In the stream, Atlantic salmon reared at reduced density grew faster during the first period after release, but there was no difference in June. The treatments had no effect on postrelease survival estimated by the recapture rates. In the hatchery, fish kept at low density with structure grew faster than conventionally reared fish. At smoltification, fish kept at low density had higher levels of insulin-like growth factor I than those reared at standard density. Independent of size, fish kept at low density were more silvery (smolt-like) and had a lower mortality rate than fish reared at high density. There was also a density effect on dorsal fin damage; Atlantic salmon at reduced density had less-damaged fins than those at standard density. These results collectively indicate that reduced rearing density may be more important than structural complexity for improving postrelease performance of juvenile Atlantic salmon.

Hatchery-reared fish are frequently released to compensate for losses in natural production or to sustain valuable populations. However, fish raised in captivity often have difficulties adapting to wild conditions, showing poor postrelease performance. This is largely a result of genetic and environmental effects on the phenotype caused by rearing (Price 1999). Genetic differences between wild- and captive-bred fish can arise through a number of processes, including alterations of natural selection pressures. For example, captive breeding results in relaxed selection pressure from predators (Johnsson et al. 1996, 2001; Sundström et al. 2004) or inadvertent selection for traits that are advantageous in captivity (Kohane and Parsons 1988). Also, the captive environment often lacks stimuli that promote development of essential life skills under wild conditions (Olla et al. 1998; Brown and Laland 2001; Huntingford 2004; Huntingford et al. 2006). Recent studies suggest that physical variation in the early environment can shape the expression of neural phenotype in juvenile salmonids (Lema et al. 2005; Kihslinger and Nevitt 2006) and that the ability to learn and adapt to new situations improves with increasing

* Corresponding author: sofia.brockmark@zool.gu.se

Received November 2, 2006; accepted April 30, 2007
Published online September 20, 2007

environmental variability (Odling-Smee and Braithwaite 2003; Braithwaite and Salvanes 2005).

For stream-living salmonid species, increased structural complexity can be linked to higher population density (Elliott 1994). One reason is the reduced interference competition and territory size as the visual field is reduced by physical structure (Basquill and Grant 1998; Imre et al. 2002). In contrast, most fish reared for conservation or supplementation are confined at high densities to a physical environment entirely lacking in structural complexity. This creates a social environment substantially different from that in natural waters (Brown and Laland 2001). Commonly reported effects of high stocking density are reductions in food conversion efficiency and growth and increases in fin damage (Ellis et al. 2002). High density in the hatchery has also been found to select for behaviors that are inefficient in nature, such as higher general activity level and use of higher-velocity areas (Weber and Fausch 2003). In addition, the frequent visual contact with conspecifics at high rearing densities may alter behavior patterns that are adaptive in the wild (Alanärä and Brännäs 1996; Ellis et al. 2002; Sundström et al. 2003; Kristiansen et al. 2004). Berejikian et al. (2000) demonstrated that submerged structures, overhead cover, and underwater feeders added to conventional hatchery tanks increased the ability of juvenile steelhead *Oncorhynchus mykiss* to win contests over size-matched competitors reared in tanks lacking these features. Furthermore, salmonids bred for supplementary purposes are usually released as smolts. During parr–smolt transformation, fish undergo extensive physiological, behavioral, and morphological changes to prepare them for sea migration. Relative to natural environments, hatchery conditions may impair the physiological development of smolting (McCormick and Björnsson 1994; Sundell et al. 1998; Munakata et al. 2000; McCormick et al. 2003). Depressed smolt development and inappropriate timing of release are suggested to contribute to poor return rates of hatchery-reared smolts (Virtanen et al. 1991; Staurnes et al. 1993).

Recently, there has been a growing interest in preparing naïve hatchery fish for a life in the wild by creating more natural rearing conditions (Maynard et al. 1996; Berejikian et al. 2000, 2001; Brown et al. 2003; Zydlewski et al. 2003; Berejikian and Tezak 2005; Braithwaite and Salvanes 2005; Kelley et al. 2005). However, there is still a lack of studies evaluating these methods at full scale in hatcheries and in the wild.

The objective of this study was to evaluate the effects of rearing density and in-water structure on the culture and postrelease performance of young-of-the-year (hereafter, age-0) Atlantic salmon *Salmo salar*. We manipulated density (standard hatchery density or one-third of standard density) and habitat structure (standard rearing tank or tank enriched with rocks and plastic plants) in an Atlantic salmon hatchery. After 3 months in the hatchery, 300 fish from each treatment were individually marked, released in a nearby stream in early September, and recaptured on two occasions (November and June). The remaining fish were kept in the hatchery until the next spring, when their parr–smolt transformation was studied by use of seawater challenge tests and a silvering index. We predicted that fish reared under more natural conditions (i.e., at lower density in a structurally complex environment) should have higher postrelease survival rates and faster growth in the natural environment than fish reared under standard hatchery conditions. Additionally, fish kept at reduced densities with structure should be better adapted to seawater during smoltification.

Methods

Study population.—Atlantic salmon were obtained from hatchery-spawned, sea-ranched parents originating from River Lagan on the west coast of Sweden. Because of the construction of hydroelectric facilities, River Lagan now lacks natural Atlantic salmon reproduction, and the fish have been hatchery spawned for 16 generations at the power plant hatchery. We released some experimental fish into the tributary, River Smedjeån, 7 km downstream of the power plant, where there is still some natural reproduction of Atlantic salmon.

Rearing treatments.—The experiments were carried out between June 2004 and April 2005 at the E.on fish farm in Laholm, Sweden. On 7 June 2004, first-feeding Atlantic salmon were placed in indoor conventional hatchery tanks (2×2 m). The experimental fish were subjected to four treatments; each treatment was replicated in three tanks until mid-September 2004. Thereafter, two replicates per treatment were used until termination of the experiment on 15 April 2005. Tanks were randomly assigned the following treatments: (1) high density (HD); (2) low density (LD); (3) high density with in-water structure (HDS); and (4) low density with in-water structure (LDS). In total, 35,000 fish (total weight $\sim$ 32 kg) were distributed among the 12 tanks. The HD treatment was 3.75 kg/m^3 according to local standard hatchery practice, and the LD treatment was approximately one-third of the standard density, or 1.35 kg/m^{-3}. In-water structure was provided by 10 green plastic bags (17 L) per tank. A stone was placed in each bag to keep it in place, increase flow variation, and provide additional protective cover for the fish. Each bag was sliced to make

them flutter in the water, resembling water plants. To prevent dirt, bacteria, and parasites from attaching, the bags were changed every third day until the end of October and then once per week during the remaining experimental period. Concurrently, the tanks were cleaned with a brush. During the study period, fish were fed ad libitum rations of commercial salmon food. In each tank, feed was delivered at 30-min intervals during daylight by an automatic feeder fixed at one side of each tank. The hatchery was provided with freshwater from the nearby river. Rearing tanks had a mean water depth of 0.26 m and a mean water flow of 0.2 L/s. The rearing units had natural lighting.

Sampling.—Fish were sampled on four occasions: 30 July 2004, 1 September 2004, 9 October 2004, and 15 April 2005 (53, 86, 123, and 311 d, respectively, after being placed in experimental tanks). Before each sampling, the fish were fasted for 24 h; 40 fish/tank were then randomly removed, anesthetized with 2-phenoxyl-ethanol (0.5 mL/L), and measured for wet weight and fork length. In addition, directly after the September, October, and April measurements, the left side of each fish was photographed with an Olympus C-5060 camera (Olympus Corporation, Tokyo, Japan) to document fin damage and silvering. The 40 fish were returned to the tank after measurements.

On 15 April 2005, 20 fish from each replicate were anesthetized. Weight and length were measured as above, blood was taken from the caudal vessels, and plasma was obtained through centrifugation of the blood samples (3,000 $\times$ *g* for 5 min). After blood was drawn, fish were sacrificed by a blow to the head. To determine branchial Na^+,K^+-ATPase (enzyme number 3.6.1.36; IUBMB 1992) activity, the gill arches were dissected out. Gill biopsies were separated from the arch in ice-cold sucrose–EDTA–imidazole buffer (150 mM sucrose, 10 mM Na_2-EDTA, and 50 mM imidazole; pH 7.3). Plasma and tissues were immediately frozen on dry ice and kept at -80°C until analysis.

Seawater challenge test.—On 13 April 2005, the hypoosmoregulatory capacity was assessed with a 24-h seawater challenge (Blackburn and Clarke 1987). Twenty fish randomly netted from each tank were transferred to two separate aquaria (20 $\times$ 30 cm; 9-cm water depth) containing either aerated seawater (25 mg/L; 10 fish) or freshwater (10 fish) kept at 9°C. After 24 h, the fish were sampled for blood and plasma was obtained as described above. The seawater challenge test was replicated on the subsequent day.

Analysis of plasma insulin-like growth factor I, plasma Na^+, and gill Na^+,K^+-ATPase activity.—Plasma levels of insulin-like growth factor I were determined through a validated radioimmunoassay as outlined by Moriyama et al. (1994).

Plasma Na^+ levels were measured with a flame emission photometer (Eppendorf AG, Hamburg, Germany; Model ELEX 6361). Samples and plasma standard (Na^+, 143.5 mmol/L) for calibration were diluted in 5 mM LiCl.

The gill Na^+,K^+-ATPase activity was measured according to a microassay protocol (McCormick 1993). Before homogenization of the gill filaments in a glass–glass tissue grinder (Contes, Vineland, New Jersey), the storage buffer was replaced with 1 mL of SEI buffer containing 0.1% sodium deoxycholate. Samples were centrifuged (3,000 $\times$ *g* for 30 s), whereupon duplicate 10-μL samples of the supernatant were analyzed in a Na^+,K^+-ATPase activity assay. The total protein concentration of each sample was assessed with a bicinchoninic acid protein assay kit (Pierce, Rockford, Illinois).

Release of fish.—On 2 September 2004, 100 individuals from each of the 12 tanks (e.g., 1,200 fish total, 300 fish/treatment) were randomly netted. Fish were anesthetized with 2-phenoxyl-ethanol (0.5 mL/L), measured for wet weight and fork length, fin clipped (adipose fin), and tagged with ID100 passive integrated transponder (PIT) tags (Trovan Ltd., United Kingdom). The tags were inserted into the body cavity through an incision made in the body wall. Individuals smaller than 65 mm in length were excluded, as they were too small to tag (average percentage of fish $<$ 65 mm in each treatment was 4.0% for HD, 5.5% for HDS, and 0.0% for LD and LDS). Before release, fish were kept in two tanks for observation during 1–2 nights. All fish were in good condition after tagging and showed no signs of abnormal behavior. Fish then transported in oxygenated tanks to River Smedjeån, 15–20 km from the hatchery, and released in groups of 600 fish at each of two sites located 6 km apart. Release sites were chosen based on good quality for small Atlantic salmon and suitability for subsequent electrofishing. At the lower site, wild Atlantic salmon (age-0) population density was 30 fish/100 m^2; at the upper location, only a few wild individuals were found, probably because of downstream dams with inefficient fish ladders. The density of fish predators was generally low at both locations. The area contained several predatory species, including the northern pike *Esox lucius*, European eel *Anguilla anguilla*, pike perch *Lucioperca lucioperca*, resident brown trout *S. trutta*, American mink *Mustela vison*, and grey heron *Ardea cinerea*.

The release sections were sampled on two occasions (15 November 2004 and 7 June 2005; 74 and 278 d, respectively, after release) using two electrofishing runs. A 150-m stretch that included 75 m downstream and 75 m upstream of the release site was fished, resulting in a total recapture area of 787 and 725 m^2,

TABLE 1.—Mean (±SE) weight (*W*) and length (*L*) of four hatchery-spawned Atlantic salmon treatment groups at release (1 Sep 2004) and at 74 and 278 d post release (15 Nov 2004 and 7 Jun 2005, respectively) in the River Smedjeån, Sweden. Number of released and recaptured fish is indicated by *N*.

	High density only			High density plus structure			Low density only		
Date	*N*	*W* (g)	*L* (mm)	*N*	*W* (g)	*L* (mm)	*N*	*W* (g)	*L* (mm)
1 Sep 2004	300	5.60 ± 0.55	79.00 ± 2.27	300	4.69 ± 0.54	74.41 ± 2.08	300	5.43 ± 0.52	78.31 ± 2.56
15 Nov 2004	16	8.04 ± 0.76	92.56 ± 2.78	17	6.92 ± 0.68	87.65 ± 2.66	15	8.56 ± 0.78	94.25 ± 3.16
7 Jun 2005	9	22.71 ± 2.60	124.00 ± 4.20	8	20.65 ± 1.67	120.00 ± 3.00	9	19.34 ± 2.55	118.00 ± 2.60

respectively. At recapture, the fish were anesthetized (2-phenoxyl-ethanol: 0.5 mL/L), and wet weight and fork length were measured. Fish recaptured in November were released after measurements were taken; those recaptured in June were killed with an overdose of 2-phenoxyl-ethanol, and their sex was determined by visual inspection of the gonads. Discharge in the stream was unusually high throughout autumn because of heavy rainfall, so the November sampling resulted in very low recapture rates.

Data treatment and statistical analysis.—All continuous variables were tested for normal distribution using Kolmogorov–Smirnov tests; except for size distribution, no variable deviated from expectations.

To analyze effects of rearing conditions on body size, growth, and condition factor (CF; calculated with Fulton's formula), a mixed analysis of variance (ANOVA) was used according to model (1):

$$\text{Response variable} = \text{structure} + \text{density} + (\text{structure} \times \text{density}) + \text{replicate tank}(\text{structure} \times \text{density}).$$

To increase statistical power, the replicate tank factor (random factor) was excluded from final analyses when nonsignificant. Model (1) was also used to analyze plasma IGF-I, plasma Na^+ levels, and gill Na^+,K^+-ATPase activity (length was a covariate).

Differences in growth, CF, and number of fish recaptured after release were analyzed with a factorial ANOVA according to model (2):

$$\text{Response variable} = \text{structure} + \text{density} + (\text{structure} \times \text{density}) + \text{section} + \text{initial body size}.$$

Initial body size was used as a continuous covariate. Because there was no interaction between section and treatment, sections were pooled to increase statistical power.

Dorsal fin damage was assessed by use of digital photos taken on 1 September 2004, 9 October 2004, and 15^t April 2005. Fin damage was scored on a three-point scale: low damage (category 1), less than 50% erosion (category 2), and more than 50% fin erosion (category 3). Fin damage was analyzed with a multinomial logistic regression analysis, including the same independent factors as in model (1).

Visual assessment of body coloration was performed using digital photos taken on 15 April 2005. Silvering index was assessed based on a four-grade scale from 1 (indicating a state of fully developed parr marks and no silvering) to 4 (indicating full silvering and no visible parr marks). Silvering was analyzed with a multinomial logistic regression analysis, including the same independent factors as in model (1). All the fin damage and silvering scores were made by the same person (S.B.) to avoid bias.

Survival rate in the seawater challenge test was analyzed with Pearson's chi-square test. Because the survival rate of control fish in freshwater was 100%, these fish were not included in the analysis.

All analyses were conducted with the Statistical Package for the Social Sciences. To simplify presentation, *P*-values that exceeded 0.25 are not reported.

Results

Effects of Treatment during Rearing

Growth.—Initial weight and length did not differ among treatments (Table 1), and there were no significant treatment effects on size after 53 and 86 d of rearing in the experimental tanks (30 June and 1 September 2004). After 123 d (9 October 2004), however, there was a density effect on size and CF; fish in the LD treatments were larger and had a higher CF (length: $P = 0.032$, $F_{1,76} = 5.72$; weight: $P = 0.046$, $F_{1,76} = 4.92$; CF: $P = 0.051$, $F_{1,76} = 3.89$). The interaction between structure and density was significant for CF ($P = 0.029$, $F_{1,76} = 4.82$), indicating that the effect of LD was more pronounced in tanks containing structure. The structure main effect was not significant.

After 311 d of rearing (15 April 2005), density treatment had a significant effect on size and CF (length: $P = 0.011$, $F_{1,76} = 6.50$; weight: $P = 0.016$, $F_{1,76} = 5.92$; CF: $P < 0.001$, $F_{1,76} = 18.66$). There were also significant but less-pronounced effects of

TABLE 1.—Extended.

	Low density plus structure		
Date	*N*	*W* (g)	*L* (mm)
1 Sep 2004	300	6.31 ± 0.81	81.31 ± 3.43
15 Nov 2004	14	9.55 ± 0.92	97.62 ± 3.47
7 Jun 2005	10	22.52 ± 2.29	124.00 ± 4.10

structure on length ($P = 0.052$, $F_{1,76} = 6.14$), weight ($P = 0.046$, $F_{1,76} = 4.92$), and CF ($P = 0.051$, $F_{1,76} = 3.61$). Hence, fish in LD tanks had reached a larger size by this date than did fish in HD tanks (Figure 1). There were no density × structure interaction effects on length or weight for any growth period.

After 311 d of rearing, fish reared in the LD treatment had higher plasma IGF-I levels ($P = 0.013$, $F_{1,76} = 6.73$) than fish reared in the HD treatment (LD mean ± SE = 21.6 ± 0.13 ng/mL; HD = 15.8 ± 0.19 ng/mL). Length was positively correlated with the IGF-I levels ($P = 0.044$, $F_{1,76} = 4.29$), such that larger fish had higher levels. However, structure had no effect on the IGF-I level ($P = 0.244$, $F_{1,76} = 1.39$).

Fin damage.—The number of fish with eroded fins increased with time and density. The sampling occasions before 9 October 2004 during rearing (length mean ± SE = 78.6 ± 0.86 mm) showed no significant difference in fin damage between treatments. In October (after 123 d) and in the final sampling on 15 April 2005 (Figure 2), LD and LDS fish had a lower proportion of fin damage than did HD and HDS fish ($\chi^2 = 22.19$, df = 3, $P < 0.001$). Structure exhibited neither a significant main effect nor a significant interaction effect (density × structure). After 123 and 311 d, there was a strong positive relationship between fin damage and body size (fin damage: $\chi^2 = 149.2$, df = 3, $P = 0.010$; body size: $\chi^2 = 168.1$, df = 3, $P = 0.014$). Large Atlantic salmon were significantly more likely to have eroded fins than small fish.

Size distribution.—Structure in tanks affected size distribution in October (Levene's test; length: $P = 0.054$, $F_{3,76} = 5.65$; mass: $P = 0.021$, $F_{3,76} = 7.06$) and April (length: $P = 0.028$, $F_{3,76} = 4.22$; mass: $P = 0.009$, $F_{3,76} = 9.58$). The LD and HD fish had a bimodal size distribution (Kolmogorov–Smirnov test: $P = 0.76$), whereas LDS and HDS fish had a unimodal size distribution (Kolmogorov–Smirnov test: $P = 0.89$; Figure 3). Neither density nor the density × structure interaction had a significant effect on size distribution.

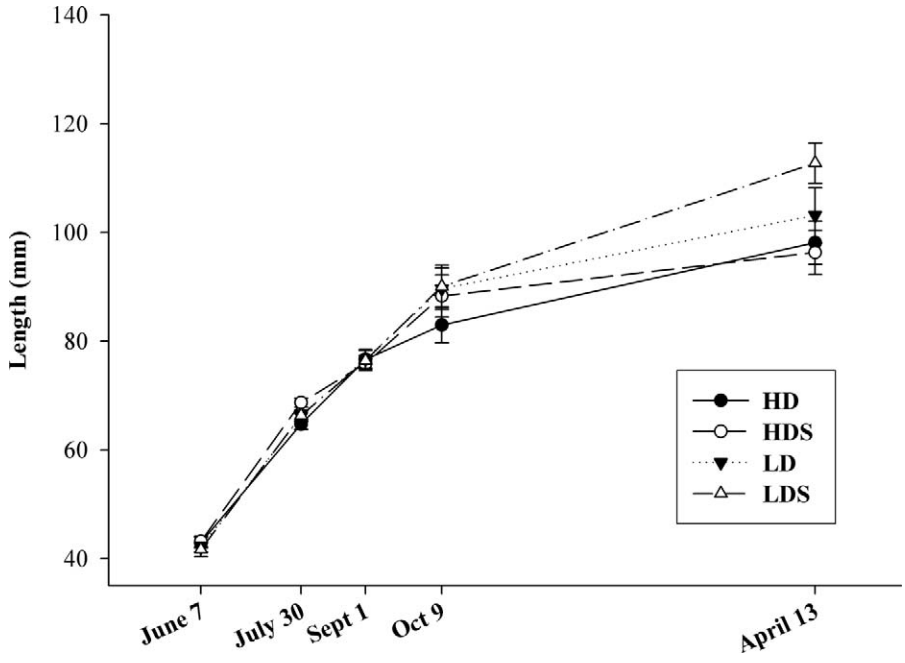

FIGURE 1.—Mean fork length (±SE) of juvenile Atlantic salmon reared at the E.on fish farm in Laholm, Sweden, from June 2004 to April 2005 under standard high-density (HD) hatchery conditions, one-third of standard hatchery density (low density, LD), HD conditions with in-water structure (HDS), and LD conditions with in-water structure (LDS). After 135 d (2 Sep 2004), 1,200 PIT-tagged fish were released into River Smedjeån.

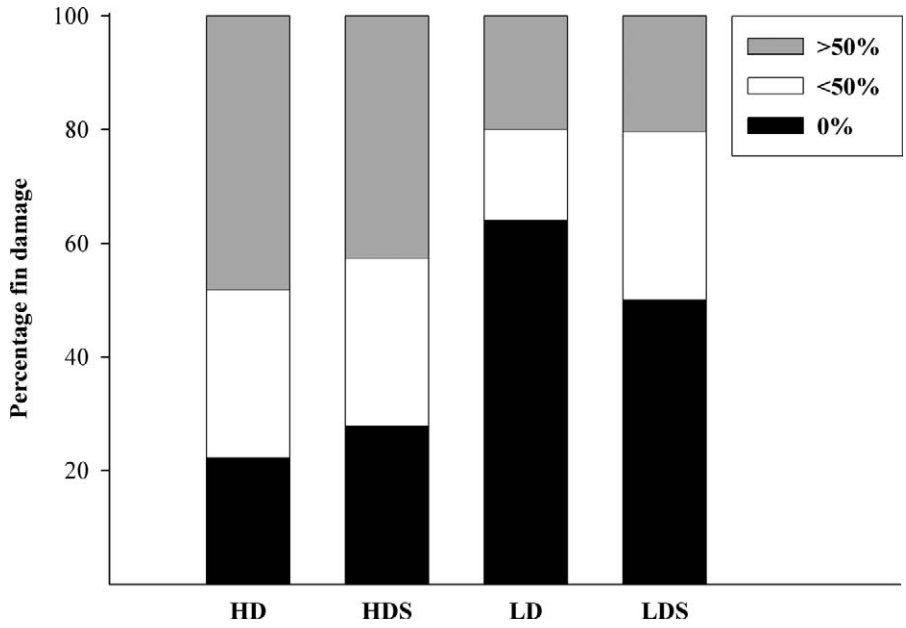

FIGURE 2.—Percent of juvenile Atlantic salmon exhibiting dorsal fin damage (scored as undamaged [0%], mild [<50%], or severe [>50%]) after 311 d of rearing (15 Apr 2005) at the E.on fish farm in Laholm, Sweden, under standard hatchery conditions of high density (HD), one-third of standard hatchery density (low density, LD), HD conditions with in-water structure (HDS), and LD conditions with in-water structure (LDS).

Smolt status.—There was no significant difference in Na^+,K^+-ATPase activity between treatments (mean ± SE = 3.37 ± 0.20 μmol P_i • mg protein^{-1} • h^{-1}, where P_i is inorganic phosphate) in the final sampling on 15 April 2005. There was no difference in plasma Na^+ levels between treatments after the seawater challenge test (196.2 ± 1.40 mmol/L^{-1}), but there was a significant difference in survival rate between treatments ($\chi^2 = 10.45$; df = 1, 54; $P = 0.015$): LDS fish had the highest survival rate and fish in the HD treatment had the lowest survival rate (Figure 4). Length did not significantly affect survival rate ($\chi^2 = 1.72$; df = 1, 54; $P = 0.19$). However, there was a positive correlation between length and plasma Na^+ levels in the freshwater controls ($P < 0.001$, $F_{1,54} = 16.30$). Mortality was negligible in control fish.

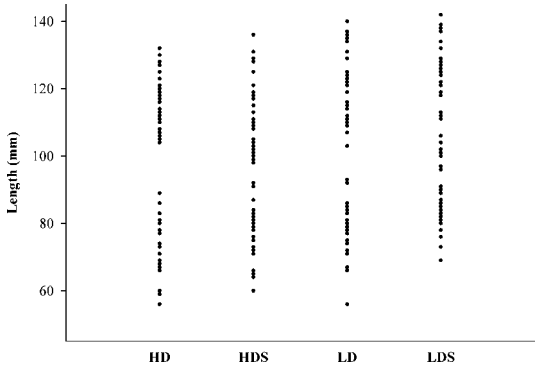

FIGURE 3.—Length distribution of juvenile Atlantic salmon after 311 d of rearing (15 Apr 2005) at the E.on fish farm in Laholm, Sweden, under standard hatchery conditions of high density (HD), HD conditions with in-water structure (HDS), one-third of standard hatchery density (low density, LD), and LD conditions with in-water structure (LDS). Fish reared in common tanks had a unimodal size distribution, whereas fish reared in tanks containing in-water structure were bimodally distributed.

Fish in the LD treatment were more silvery than fish in the HD treatment ($\chi^2 = 25.24$, df = 9, $P = 0.003$). Structure had no effect on silvering. The silvering index was not significantly correlated with size.

Postrelease Effects of Treatment

First recapture.—On 15 November 2004 (74 d after release), 62 of 1,200 Atlantic salmon were recaptured. The recapture rate did not differ among treatments or between the two sections (section 1 = 33 fish; section 2 = 29 fish). Fish reared in LD tanks tended to grow faster in the wild (weight: $P = 0.034$, $F_{1,58} = 4.63$, observed power = 0.56; length: $P = 0.056$, $F_{1,58} = 4.18$, observed power = 0.61), but structure had no significant effect on growth (Figure 5A). Fish generally experienced lowered CF after release into the wild

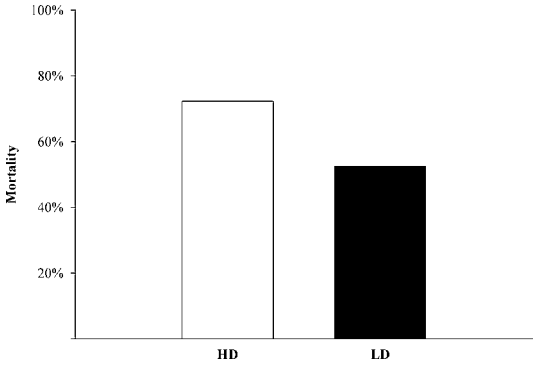

FIGURE 4.—Percent mortality (±SE) of Atlantic salmon after a seawater challenge administered on 13 Apr 2005 at 309 days of rearing under standard high-density (HD) hatchery conditions and one-third of standard density (low density, LD) at the E.on fish farm in Laholm, Sweden.

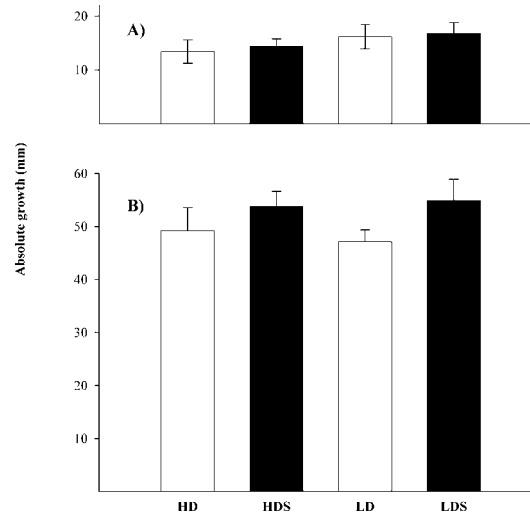

FIGURE 5.—Length increase in juvenile Atlantic salmon between release on 2 Sep 2004 and **(A)** 75 d after release (15 Nov 2004; $N = 62$) and **(B)** 279 d after release (7 Jun 2005; $N = 36$) among four rearing treatments at the E.on fish farm in Laholm, Sweden: standard high-density (HD) hatchery conditions (HD), HD conditions with in-water structure (HDS), one-third of standard hatchery density (low density, LD), and LD conditions with in-water structure (LDS).

($P = 0.008$, $F_{1,58} = 7.12$, observed power = 0.57), but there was no treatment effect on CF.

Second recapture.—On 7 June (278 d after release), 36 of 1,200 fish were recaptured. The recapture rate did not differ among treatments or between the two sections (section 1 = 16 fish; section 2 = 19 fish). Neither treatment (Figure 5B) nor sex affected growth or fish recapture.

Discussion

This study is the first to investigate the interactive effects of rearing density and structural complexity under full-scale rearing conditions on the pre- and postrelease performance of Atlantic salmon. Low rearing densities increased growth rate during the first period after release into the wild. This response should be noted, as there were no treatment effects on growth or fin damage in the hatchery at time of release. One possibility is that fish in the HD treatments experienced prolonged crowding stress, which may have reduced initial postrelease growth. In June, there was no longer a difference in body size among the treatment groups, which may indicate a compensatory growth response in the HD groups. Such compensatory growth responses have recently been demonstrated in free-ranging salmonid populations (Álvarez and Nicieza 2005; Johnsson and Bohlin 2005). Unfortunately, the low recapture rates reduced the statistical power for detecting treatment effects on postrelease performance. A probable explanation for the poor recapture was the extreme flow conditions in autumn. The recapture rate was, however, also low the next spring when sampling conditions were better, indicating either that the flood increased dispersal from the sites or that overwinter survival was low regardless of treatment. In contrast to our results, Berejikian et al. (2000, 2001) found postrelease effects of structural enrichment on growth; juvenile steelhead reared in structurally enriched tanks grew faster than fish reared in conventional tanks after release into a simulated natural stream. Environmental enrichment has also been found to improve instream survival in seaward-migrating juvenile Chinook salmon *O. tshawytscha* in some studies (Maynard et al. 1996; an exception was a study by Berejikian et al. 1999). Maynard et al. (1996) suggested that the differences in survival rate may be the result of adjustments in cryptic body coloration promoted by the natural substrates added to rearing tanks. Our data show no treatment effects on postrelease survival as estimated by recapture rates.

Body size is known as a critical factor in determining postrelease survival in freshwater (Quinn and Peterson 1996) and at sea (Holtby et al. 1990). Also, body size and enhanced growth during smoltification are considered to promote seawater adaptation in salmonids (Beckman and Dickhoff 1998; Beckman et al. 2000). In our study, Atlantic salmon reared in LDS tanks grew faster and reached a larger body size at smoltification than fish reared in conventional tanks. Therefore, these more natural rearing methods would probably increase postrelease survival. Density-dependent growth in hatcheries has been demonstrated in several previous

studies (Ellis et al. 2002). The growth suppression at high densities has been attributed to stress through deterioration in water quality, overcrowding, and adverse social interactions, but the actual mechanisms have not been further studied. However, very low rearing salmonid densities may also result in poor feeding response and increased aggression (Ellis et al. 2002).

Our physiological and morphological data indicate that fish reared at reduced densities were at a more advanced stage of smoltification than fish reared under standard hatchery conditions. These results are similar to those reported by Zydlewski et al. (2003); however, in contrast to our study, their experimental design could not separate density-dependent effects from effects of physical structural and natural food in the rearing environment.

Fish sampled from LD tanks had higher plasma levels of IGF-I. This hormone is believed to play a central role in promoting the growth stimulatory actions of growth hormone in anadromous fish (Duan 1997). Plasma levels of IGF-I increase during spring in response to seasonal changes in photoperiod and temperature, and such increases coincide with parr–smolt transformation (Beckman et al. 2000), particularly the peak in gill Na^+,K^+-ATPase activity (Beckman and Dickhoff 1998; Ágústsson et al. 2001).

No difference in gill Na^+,K^+-ATPase activity was found between fish exposed to a seawater challenge test and fish kept in freshwater. Although salinity is known to increase the gill Na^+,K^+-ATPase activity in most fish (Evans 1998), our results support earlier findings that 24 h of seawater exposure is not long enough to increase gill Na^+,K^+-ATPase activity in salmonids (e.g., Sundell et al. 1998). No treatment differences in plasma Na^+ levels could be demonstrated after the seawater challenge test, but mortality rates were significantly lower in LD fish than in HD fish. This effect was independent of fish size. The mortality may be attributable to higher chronic stress levels caused by visual and physical impacts on fish reared at high densities (Ellis et al. 2002). Furthermore, one of the most indicative morphological characters associated with smolting is silvering. We found that fish reared at reduced densities had a more silvery coloration than those reared at standard densities.

Aggression is a major factor influencing fin damage, making it a useful indicator of aggressive behavior in larger groups of fish (McLean et al. 2000). Previous studies have shown that conventional hatchery rearing often promotes agonistic behavior while preventing the fish's ability to settle territorial conflicts (Metcalfe et al. 2003; Sundström et al. 2003; Weber and Fausch 2003). Our results suggest that fin damage mediated by aggression can be reduced by lowering the rearing density; lower fin damage may in turn reduce susceptibility to a range of opportunistic pathogens (Ellis et al. 2002).

When studying juvenile Atlantic salmon, Kalleberg (1958) noticed that agonistic encounters between small fish mainly involved frontal attacks with the dorsal fin folded, while larger fish tended to use lateral displays with the dorsal fin erect. We first observed fin damage when juveniles reached a mean size of approximately 80 mm, but at that time, there were no size differences between treatments. However, after a year, the probability of fin damage was strongly correlated to body size; large fish were significantly more likely to have eroded fins than small fish. These results are consistent with those by McLean et al. (2000), who suggested that large, dominant fish compete aggressively among themselves rather than against subordinate individuals, while less-aggressive individuals adopt alternative feeding strategies, resulting in lower food intake and growth and reduced risk of injury.

Our results indicate that structurally complex rearing tanks produce Atlantic salmon with a unimodal size distribution, whereas rearing in conventional tanks leads to a bimodal size distribution. Bimodality is commonly observed in hatchery-reared fish (Ellis et al. 2002) but is seldom observed in nature. It may therefore be speculated that a unimodal distribution is a result of a more natural environment that allows greater variation in behavioral strategies than conventional rearing techniques.

In conclusion, although low recapture rates weakened the evidence provided by postrelease data, the results for fin damage, seawater mortality, and growth in the rearing tanks suggest that density reduction improves welfare, postrelease growth, and survival of Atlantic salmon. Hence, improved growth and survival of released smolts reared at a reduced density can compensate for a decreased number of smolts produced per unit volume, which should be considered in commercial cost-benefit analyses of sea ranching and ocean fisheries programs for Atlantic salmon. Currently, welfare of fish in aquaculture is gaining attention of legislators, regulatory bodies, and consumer groups, signaling that the choice of rearing methods should be based on ethical guidelines to ensure animal welfare.

Acknowledgments

We thank Johan P. Persson and staff at E.on's fish farm for fish care during rearing and Hatem Abradabo, Stefan Lindberg, Barbro Egnér, and Claes Dellefors for helpful assistance in the field and during the hatchery sampling. The research was carried out as part of the Swedish research and development program, "Hydro-

power – environmental impact, remedial measures, and costs in existing regulated waters," financed by Elforsk, the Swedish Energy Agency, and the National Board of Fisheries and the Swedish Environmental Protection Agency. The experimental work was approved by the Ethical Committee for Animal Research at Göteborg University (license 199/2002). Financing for J.I.J and B.T.B. was provided by the Swedish Council for Agricultural and Forestry Research.

References

Ágústsson, T., K. Sundell, T. Sakamoto, V. Johansson, M. Ando, and B. T. Björnsson. 2001. Growth hormone endocrinology of Atlantic salmon (*Salmo salar*): pituitary gene expression, hormone storage, secretion and plasma levels during parr–smolt transformation. Journal of Endocrinology 170:227–234.

Alanärä, A., and E. Brännäs. 1996. Dominance in demand-feeding behaviour in Arctic char and rainbow trout: the effect of stocking density. Journal of Fish Biology 48:242–254.

Álvarez, D., and A. G. Nicieza. 2005. Compensatory response 'defends' energy levels but not growth trajectories in brown trout, *Salmo trutta* L. Proceedings of the Royal Society of London, Series B: Biological Sciences 272:601–607.

Basquill, S. P., and J. W. A. Grant. 1998. An increase in habitat complexity reduces aggression and monopolization of food by zebra fish (*Danio rerio*). Canadian Journal of Zoology 76:770–772.

Beckman, B. R., and W. W. Dickhoff. 1998. Plasticity of smolting in spring Chinook salmon: relation to growth and insulin growth factor-I. Journal of Fish Biology 53:808–826.

Beckman, B. R., D. A. Larsen, C. Sharpe, B. Lee-Pawlak, C. B. Schreck, and W. W. Dickhoff. 2000. Physiological status of naturally reared juvenile spring Chinook salmon in the Yakima River: seasonal dynamics and changes associated with smolting. Transactions of the American Fisheries Society 129:727–731.

Berejikian, B. A., R. J. F. Smith, E. P. Tezak, S. L. Schroder, and C. M. Knudsen. 1999. Chemical alarm signals and complex hatchery rearing habitats affect anti-predator behaviour and survival of Chinook salmon (*Oncorhynchus tshawytscha*) juveniles. Canadian Journal of Fisheries and Aquatic Sciences 56:830–838.

Berejikian, B. A., and S. L. Tezak. 2005. Rearing in enriched hatchery tanks improves dorsal fin quality of juvenile steelhead. North American Journal of Aquaculture 67:289–293.

Berejikian, B. A., E. P. Tezak, A. L. LaRae, T. A. Flagg, E. Kummerow, and C. V. W. Mahnken. 2000. Social dominance, growth and habitat use of age-0 steelhead (*Oncorhynchus mykiss*) grown in enriched and conventional hatchery rearing environments. Canadian Journal of Fisheries and Aquatic Sciences 57:628–636.

Berejikian, B. A., E. P. Tezak, S. C. Riley, and A. L. LaRae. 2001. Competitive ability and social behaviour of juvenile steelhead reared in enriched and conventional hatchery tanks and a stream environment. Journal of Fish Biology 59:1600–1613.

Blackburn, J., and W. C. Clarke. 1987. Revised procedure for the 24 hour seawater challenge test to measure seawater adaptability of juvenile salmonids. Canadian Technical Report of Fisheries and Aquatic Sciences 1515.

Braithwaite, V. A., and A. G. V. Salvanes. 2005. Environmental variability in early rearing environment generates behaviourally flexible cod: implications for rehabilitating wild populations. Proceedings of the Royal Society of London, Series B: Biological Sciences 272:1107–1113.

Brown, C., T. Davidson, and K. Laland. 2003. Environmental enrichment and prior experience of live prey improve foraging behaviour in hatchery-reared Atlantic salmon. Journal of Fish Biology 63(Supplement A):187–196.

Brown, C., and K. L. Laland. 2001. Social learning and life-skills training for hatchery-reared fish. Journal of Fish Biology 59:471–493.

Duan, C. 1997. The insulin-like growth factor system and its biological actions in fish. American Zoologist 37:491–503.

Elliott, J. M. 1994. Quantitative ecology and the brown trout. Oxford University Press, Oxford, UK.

Ellis, T., B. North, A. P. Scott, N. R. Bromage, M. Porter, and D. Gadd. 2002. The relationships between stocking density and welfare in farmed rainbow trout. Journal of Fish Biology 61:493–531.

Evans, D. H., editor. 1998. The physiology of fishes. CRC Press, New York.

Holtby, L. B., B. C. Andersen, and R. K. Kadowaki. 1990. Importance of smolt size and early ocean growth to interannual variability in marine survival of coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Fisheries and Aquatic Sciences 47:2181–2194.

Huntingford, F. A. 2004. Implications of domestications and rearing conditions for the behaviour of cultivated fishes. Journal of Fish Biology 65(Supplement A):122–142.

Huntingford, F. A., C. Adams, V. A. Braithwaite, S. Kadri, T. G. Pottinger, P. Sandøe, and J. F. Turnbull. 2006. Review paper: current issues of fish welfare. Journal of Fish Biology 68:332–372.

Imre, I., J. W. A. Grant, and E. R. Keeley. 2002. The effect of visual isolation on territory size and population density of juvenile rainbow trout (*Oncorhynchus mykiss*). Canadian Journal of Fisheries and Aquatic Sciences 59:303–309.

IUBMB (International Union of Biochemistry and Molecular Biology). 1992. Enzyme nomenclature 1992. Academic Press, San Diego, California.

Johnsson, J. I., and T. Bohlin. 2005. Compensatory growth for free? A field experiment on brown trout, *Salmo trutta*. Oikos 111:31–38.

Johnsson, J. I., J. Höjesjö, and I. A. Fleming. 2001. Behavioural and heart rate responses to predation risk in wild and domesticated Atlantic salmon. Canadian Journal of Fisheries and Aquatic Sciences 58:788–794.

Johnsson, J. I., E. Petersson, E. Jönsson, B. T. Björnsson, and T. Järvi. 1996. Domestication and growth hormone alter antipredator behaviour and growth patterns in juvenile brown trout, *Salmo trutta*. Canadian Journal of Fisheries and Aquatic Sciences 53:1546–1554.

Kalleberg, H. 1958. Observations in a stream tank of territoriality and competition in juvenile salmon and

trout (*Salmo salar* L. and *S. trutta* L.). Institute of Freshwater Research Drottningholm Report 39:55–98.

Kelley, J. L., A. E. Magurran, and M. G. Constantino. 2005. The influence of rearing experience on the behaviour of endangered Mexican fish, *Skiffia multipunctata*. Biological Conservation 122:223–230.

Kihslinger, R. L., and G. A. Nevitt. 2006. Early rearing environment impacts cerebellar growth in juvenile salmon. Journal of Experimental Biology 209:504–509.

Kohane, M. J., and P. A. Parsons. 1988. Domestication: evolutionary change under stress. Evolutionary Biology 23:31–48.

Kristiansen, T. S., A. Fernö, J. C. Holm, L. Privitera, S. Bakke, and J. E. Fosseidengen. 2004. Swimming behaviour as an indicator of low growth rate and impaired welfare in Atlantic halibut (*Hippoglossus hippoglossus* L.) reared at three stocking densities. Aquaculture 230:137–151.

Lema, S. C., M. J. Hodges, M. P. Marchetti, and G. A. Nevitt. 2005. Proliferation zones in the salmon telencephalon and evidence for environmental influence on proliferation rate. Comparative Biochemistry and Physiology 141A:327–335.

Maynard, D. J., T. A. Flagg, and C. V. W. Mahnken. 1996. A review of seminatural culture strategies for enhancing the postrelease survival of anadromous salmonids. Pages 307–314 *in* H. L. Schramm, Jr., and R. G. Piper, editors. Uses and effects of cultured fishes in aquatic ecosystems. American Fisheries Society, Symposium 15, Bethesda, Maryland.

McCormick, S. D. 1993. Methods for nonlethal gill biopsy and measurement of Na^+, K^+-ATPase activity. Canadian Journal of Fisheries and Aquatic Sciences 50:656–658.

McCormick, S. D., and B. T. Björnsson. 1994. Physiological and hormonal differences among Atlantic salmon parr and smolts reared in the wild, and hatchery smolts. Aquaculture 121:235–244.

McCormick, S. D., M. F. O'Dea, A. M. Moeckel, and B. T. Björnsson. 2003. Endocrine and physiological changes in Atlantic salmon smolts following hatchery release. Aquaculture 222:45–57.

McLean, A., N. B. Metcalfe, and D. Mitchell. 2000. Alternative competitive strategies in juvenile Atlantic salmon (*Salmo salar*): evidence from fin damage. Aquaculture 184:291–302.

Metcalfe, N. B., S. K. Valdimarsson, and I. J. Morgan. 2003. The relative roles of domestication, rearing environment, prior residence and body size in deciding territorial contests between hatchery and wild juvenile salmon. Journal of Applied Ecology 40:535–544.

Moriyama, S., S. Swanson, M. Nishi, A. Takahashi, H. Kawauchi, W. W. Dickhoff, and E. M. Plisetskaya. 1994. Development of homologous radioimmunoassay for coho salmon insulin-like growth factor-I. General and Comparative Endocrinology 96:149–161.

Munakata, A., B. T. Björnsson, E. Jönsson, M. Amano, K. Ikuta, S. Kitamura, T. Kurokawa, and K. Aida. 2000. Post-release adaptation processes of hatchery-reared honmasu salmon parr. Journal of Fish Biology 56:163–172.

Odling-Smee, L., and V. A. Braithwaite. 2003. The influence of habitat stability on landmark use during spatial learning in the three-spined stickleback. Animal Behaviour 65:701–707.

Olla, B. L., M. W. Davis, and C. H. Ryer. 1998. Understanding how the hatchery environment represses or promotes the development of behavioural survival skills. Bulletin of Marine Science 62:531–550.

Price, E. O. 1999. Behavioural development in animals undergoing domestication. Applied Animal Behaviour Science 65:245–271.

Quinn, T. P., and N. P. Peterson. 1996. The influence of habitat complexity and fish size on over-winter survival and growth of individually marked juvenile coho salmon (*Oncorhynchus kisutch*) in Big Beef Creek, Washington. Canadian Journal of Fisheries and Aquatic Sciences 53:1555–1564.

Staurnes, M., G. Lysfjord, L. P. Hansen, and T. G. Heggberget. 1993. Recapture rates of hatchery-reared Atlantic salmon (*Salmo salar*) related to smolt development and time of release. Aquaculture 118:327–337.

Sundell, K., C. Dellefors, and B. T. Björnsson. 1998. Wild and hatchery-reared brown trout, *Salmo trutta*, differ in smolt related characteristics during parr–smolt transformation. Aquaculture 167:53–65.

Sundström, L. F., M. Löhmus, and J. I. Johnsson. 2003. Investment in territorial defence depends on rearing environment in brown trout (*Salmo trutta*). Behavioral Ecology and Sociobiology 54:249–255.

Sundström, L. F., E. Petersson, J. I. Johnsson, J. Dannewitz, J. Höjesjö, and T. Järvi. 2004. Heart rate and behavioural responses to predation risk in brown trout (*Salmo trutta* L.) are affected by rearing environment. Journal of Fish Biology 67:1280–1286.

Virtanen, E., L. Soderholmtana, A. Soivio, L. Forsman, and M. Muona. 1991. Effects of physiological condition and smoltification status at smolt release on subsequent catches of adult salmon. Aquaculture 97:231–257.

Weber, E. D., and K. D. Fausch. 2003. Interactions between hatchery and wild salmonids in streams: differences in biology and evidence for competition. Canadian Journal of Fisheries and Aquatic Sciences 60:1018–1036.

Zydlewski, G. B., S. J. Foot, K. Nichols, S. Hamelberg, J. Zydlewski, and B. T. Björnsson. 2003. Enhanced smolt characteristics of steelhead trout exposed to alternative hatchery conditions during the final months of rearing. Aquaculture 222:101–117.