

Reduced hatchery rearing density increases social dominance, postrelease growth, and survival in brown trout (*Salmo trutta*)

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Abstract: Hatchery fish reared for conservation or supplementation often have difficulties adapting to natural conditions, resulting in poor performance in the wild. In a standard hatchery, fish are confined at high densities, which creates a social environment different from that experienced after release. Here we investigated how rearing density influences social dominance, postrelease growth, and survival in brown trout (*Salmo trutta*). Fish were reared at three density treatments: conventional hatchery density, half of conventional hatchery density, and natural density. Four months after hatching, dominance status was determined, and 36 fish from each treatment were released into an enclosed stream and recaptured after 36 days. Trout reared at natural density had higher dominance status and grew faster, both in the hatchery and in the natural stream, than trout from higher densities. Moreover, trout reared at natural density were twice as likely to survive in the stream as trout from higher densities. These novel results suggest that more natural rearing densities would facilitate the development of adaptive behaviour in hatchery salmonids and, thereby, their contribution to natural production.

Résumé : Les poissons élevés en pisciculture pour la conservation ou la supplémentation ont souvent de la difficulté à s'adapter aux conditions naturelles, ce qui entraîne une performance mitigée en nature. Dans une pisciculture ordinaire, les poissons sont confinés à des densités élevées, ce qui crée un environnement social différent de celui qu'ils connaissent après leur libération. Nous étudions comment la densité durant l'élevage influence la dominance sociale, la croissance après la libération et la survie chez la truite brune (*Salmo trutta*). Nous avons élevé des poissons dans trois conditions expérimentales, la densité habituelle de pisciculture, une densité de moitié de la densité habituelle de pisciculture et la densité naturelle. Quatre mois après l'éclosion, nous avons déterminé le statut de dominance et libéré 36 poissons de chacun des traitements dans un cours d'eau fermé pour les capturer 36 jours plus tard. Les truites élevées à des densités naturelles ont un statut de dominance supérieur et croissent plus rapidement, tant en pisciculture que dans le cours d'eau naturel, que les truites gardées aux densités plus élevées. De plus, les truites élevées aux densités naturelles sont deux fois plus susceptibles de survivre dans le cours d'eau que les truites élevées aux densités plus fortes. Ces résultats inédits indiquent que des densités d'élevage plus naturelles favoriseraient le développement d'un comportement adaptatif chez les salmonidés d'élevage et, par conséquent, amélioreraient leur contribution à la production naturelle.

[Traduit par la Rédaction]

Introduction

Hatchery-reared fish are released in large numbers to compensate for losses in natural production or to sustain valuable populations (Aprahamian et al. 2003). However, the efficiency of such hatchery programs is debated, and it has been questioned whether wild and hatchery fish are ecologically exchangeable (Waples 1999; Bisson et al. 2002; Brannon et al. 2004). As in many other animals, fish raised in captivity often have difficulties adapting to wild conditions, resulting in reduced growth, survival, and reproductive success compared with wild conspecifics (Araki et al. 2007).

Even if wild parent offspring from local populations are used to avoid disruption of local adaptation and other genetic effects (Gharrett and Smoker 1991), rearing in the homogenous high-density environment typical of a standard hatchery is inadequate to prepare fish for a life in the wild (see Brännäs and Johnsson 2008).

The general difficulties associated with transferring animals that are born and reared in captivity to the wild are linked to evolutionary questions concerning the limitation of phenotypic plasticity and the fitness consequences of the phenotypic response to differing environments encountered over an individual's life span (Stearns 1989; Relyea 2002; Ghalambor et al. 2007). Not least critical are conditions early in life. Growing evidence on a range of animal taxa suggests that early life events can exert long-lasting effects on the phenotype (Metcalf and Monaghan 2001), including alteration of behavioural traits. In Atlantic salmon (*Salmo salar*), for example, early experience is important for adequate homing to the natal river (Hansen et al. 1993) and for efficient reproductive behaviour (Fleming et al. 1997). The importance of early life experience is now starting to influence conservation and supplementation programs with the goal of maintaining the diversity of natural behaviour in

Received 17 March 2009. Accepted 6 October 2009. Published on the NRC Research Press Web site at cjfas.nrc.ca on 16 January 2010.
J21107

Paper handled by Associate Editor Bror Jonsson.

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captive-bred animals aimed for re-introduction (Rabin 2003).

Competitor density is an important factor influencing the development of behavioural and other phenotypic traits in many animal species (Milinski and Parker 1991; Cresswell 1998), including fish (Grant 1997; Bohlin et al. 2002). In intensive food fish farming, the effects of stocking density have been extensively studied for a number of traits, but with variable results, suggesting that many factors interact with density to affect performance in a farming situation (for a review, see Brännäs and Johnsson 2008). Still, density-dependent growth and associated traits have been demonstrated in several studies on farm fish (review by Ellis et al. 2002). For example, a study on Arctic char (*Salvelinus alpinus*) and rainbow trout (*Oncorhynchus mykiss*) in a self-feeding setup revealed that relative dominance rank remained unchanged with increasing competitor density, but the relative payoffs of high-ranking individuals decreased (Alanärä and Brännäs 1996).

In supplementation hatcheries, rearing densities are typically much higher than in the wild, which may result in development of behaviours that are inefficient in the wild (Weber and Fausch 2003; Jonsson and Jonsson 2006). However, most studies to date comparing the performance of wild and hatchery-reared fish have not allowed the effects of density per se to be separated from other typical effects of the hatchery environment, e.g., reduced structural complexity (Berejikian et al. 2000; Braithwaite and Salvanes 2005; Lee and Berejikian 2008), reduced variation in food supply and prey types (Brown et al. 2003), and absence of natural predators (Vilhunen et al. 2005). In addition, hatchery fish may perform poorly relative to wild-reared conspecifics simply because they have been protected from natural selection prior to release, i.e., first-generation selection (Einum and Fleming 2001). Most importantly, there is a shortness of studies evaluating the effects of hatchery density on postrelease performance. In a recent full-scale hatchery study, we showed that reduced density increases growth rate, enhances smoltification, and reduces fin damage in Atlantic salmon reared for supplementation. However, because of low recapture rates in the wild, we were not able to substantially evaluate effects of rearing density on postrelease growth and survival (Brockmark et al. 2007).

The aim of the present study was to investigate how hatchery rearing density early in life influences the development of social status in salmonids and, subsequently, post-release growth and survival in nature. As model species, we used anadromous (sea-run) brown trout (*Salmo trutta*), a species frequently reared in hatcheries to supplement natural populations. Wild brown trout spend their first 1–3 years in streams, where they establish feeding territories, or form hierarchical groups, depending on population density and habitat structure (Kalleberg 1958; Jenkins 1969). Resource-defence theory predicts that territorial behaviour should decrease at high competitor densities, which has been confirmed in several studies (Grant 1997). In addition, the maintenance of hierarchical social groups likely requires the development of familiarity through repeated encounters with, and recognition of, a limited number of individuals, (i.e., the “dear enemy” effect: Senar et al. 1990; Griffiths

and Magurran 1997), a social situation typical of low-density environments. We therefore hypothesized that development under reduced density conditions should facilitate the ability to cope with social interactions, including the ability to defend contested resources, with subsequent positive effects on growth and survival in the wild. To address this hypothesis, trout were hatchery-reared from the egg stage at three densities: (i) conventional hatchery density (H), (ii) half of conventional hatchery density (M), and (iii) natural density (L). Parr from the three treatment groups were then scored for dominance, released in an enclosed natural stream section, and recaptured after about a month, allowing estimation of density effects on postrelease growth and survival.

Materials and methods

In the autumn of 2004, sea-ranched brown trout originating from Dalälven on the east coast of Sweden were captured and artificially spawned. Fertilized eggs were incubated at the Swedish Board of Fisheries research station in Älvkarleby. On 16 February 2005, eggs were transported to the Swedish Board of Fisheries research station in Kälmarne where the experiment was conducted. The eggs were placed in conventional hatchery tanks ($1 \times 1 \text{ m}^2$) at the three densities described above: (i) H, 2500 fish; (ii) M, 1250 fish; and (iii) L, 120 fish. Conventional hatchery density was set according to the local hatchery practice at $1.56 \text{ kg}\cdot\text{m}^{-3}$. The natural density was based on high density levels for wild brown trout described by Elliot (1994). In total, 18 hatchery tanks, six replicates for each of the three density treatments, were used. The mortality rate in the hatchery was very low during the experiment (mean percent mortality \pm standard error (SE) = $0.97\% \pm 0.009\%$).

The fry started to feed on 15 April. Commercial fish food was provided at rates of 2% of fish mean body mass per day in all density treatments throughout the experiment. The water depth was kept at 17 cm until the end of June, when it was increased to 67 cm. On 21 June, 2 September, and 7 October 2005, 30 fish from each of the 18 replicate tanks (i.e., 540 fish per occasion) were anaesthetized with 2-phenoxyethanol ($0.5 \text{ mL}\cdot\text{L}^{-1}$) and individually measured for body mass ($\pm 0.1 \text{ g}$) and fork length ($\pm 1.0 \text{ mm}$).

Dominance ranking

The effect of density treatment on dominance rank was determined in replicate groups of six fish, using the removal method (modified after Metcalfe et al. 1989; Johnsson 1993). Thirty-six replicate groups of six fish (totally 216 individuals) were ranked for dominance between 19 August and 1 September. Each test fish was used only on one occasion. The test fish were sampled in a pseudo-randomized fashion to ensure equal representation from the 18 hatchery tanks (12 fish from each tank were used).

For each replicate group, two fish from each of the three density treatments were sampled from the hatchery tanks, anaesthetized, and measured for body mass and fork length. In addition, to enable identification in the dominance trials, fish were marked with coloured spangles mounted on a stainless steel wire inserted below the dorsal fin (modified from Johnsson 1993). Each group of six fish was placed in

one of 12 identical flow-through aquaria (57 × 28 cm) containing river water (20 cm depth) with a flow rate of approximately 4 L·s⁻¹. The bottom of each aquarium was covered with stones (2–5 cm in diameter). The fish were left to acclimatize over two nights before the observations started. To allow fish to adapt to the experimental feeding conditions, a live chironomid larva was provided on two occasions during the acclimatization day. The larva was released with a pulse of water through a plastic tube at the centre of the upstream end of the aquarium.

Observations and recordings started the next day when the following procedure was repeated during three trials, conducted at 0800, 1200, and 1600. The behaviour of the fish was observed for 6 min, 3 min before and 3 min after the delivery of food (a live chironomid larva, see above). We recorded the identity of the individual taking each chironomid and the outcome of overt aggressive interactions (circling, attack, nips, and chases; for definitions, see Johnsson and Åkerman 1998) for each individual. These behaviours were used to calculate a score to determine dominance rank as follows: +1 for acquiring the food without contest; +2 for acquiring the food in contest with other fish, and +1 for winning aggressive encounters (see Harwood et al. 2003). Most of the food (94%) was acquired without contest, and overt aggression levels were low; only 31% of the individuals showed any overt aggression during the trials. However, if fish had taken the same amount of food, or if no food was taken (6% of the ranks), dominance was based on the number of aggressive interactions won.

The individual with the highest calculated rank was then removed and the remaining fish were left overnight. Dominance determination, as described above, continued for two more days, allowing us to rank the three most dominant fish out of six. Dominance rank of the three remaining individuals was set to be equal, as a pilot study had shown that these fish were more or less inactive and, therefore, very difficult to rank.

Released fish

On 2 September, 108 fish, 36 from each density treatment (six from each replicate hatchery tank), were sampled for release in the natural stream section. All individuals were anaesthetized, adipose fin clipped, measured for wet body mass and fork length, marked using a passive integrated transponder (PIT) tag inserted into the body cavity, and left overnight to recover from handling. On the following day, all 108 fish were released in the middle of a divided section of a natural stream, River Ansjöån. This section is 95 m in length and consists of three pool areas with riffles between them. The stream section is blocked with stainless-steel mesh in both ends, so no fish could escape from or invade the stream. Fish stocked in the stream only have access to naturally occurring food and are exposed to natural predation from American mink (*Mustela vison*) and grey heron (*Ardea cinerea*) (authors' personal observation).

Between 8 and 9 October (36–37 days after release), fish were recaptured using electric fishing. The stream section was fished until no remaining fish were caught on two consecutive fishing passes (i.e., in total seven passes).

Statistical analysis

To analyse treatment effects on growth rate in the hatchery, we used the following analysis of covariance (ANCOVA) model (see also Johnsson and Bohlin 2006):

$$L_t \text{ or } W_t = L_0 \text{ or } W_0 + \text{Tr}$$

where L_t and W_t are tanks means of fork length and body mass at the end of the growth period, respectively, L_0 and W_0 are tank means of initial fork length and body mass, respectively, and Tr is the density treatment with three levels (H, M, L). This analysis was conducted for two growth periods in the hatchery: 21 June – 2 September (74 days), and 2 September – 7 October (33 days). Growth rate in the stream, based on individual growth of the PIT-tagged fish during the second period above (2 September – 7 October, 33), was analysed using the corresponding ANCOVA model:

$$L_t \text{ or } W_t = L_0 \text{ or } W_0 + \text{Tr} + \text{Repl}(\text{Tr})$$

where Repl is replicate tank (random factor), nested in treatment, Tr.

We also analysed treatment effects on mean body size (mass or length) for all sampling occasions using the model

$$L_t \text{ or } W_t = \text{Tr} + \text{Repl}(\text{Tr})$$

with notation as above.

Treatment effects on the recapture probability of released fish in the stream were analysed using a logistic regression model:

$$\text{Recapture} = L_0 + \text{Tr} + \text{Repl}(\text{Tr})$$

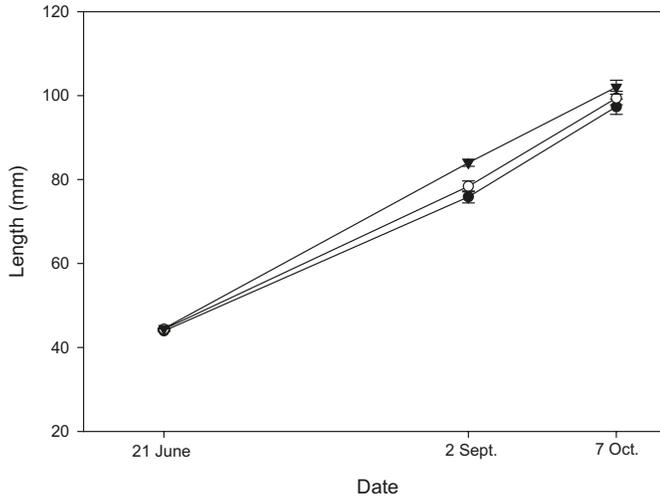
where Recapture is a binomial response variable with the values 0 or 1. Other notation is as above.

The random factor Repl(Tr) was nonsignificant in all initial analyses above and was therefore excluded from the final analyses to increase power. Growth and size data did not deviate from normal distribution (Kolmogorov–Smirnov tests) and showed homogenous variance (Levene's test). Alpha values were set to 0.05 for all analyses above.

The effects of density treatment on dominance rank, food acquisition, and overt aggression were analysed using the nonparametric Friedman two-way analysis of variance by ranks (Siegel and Castellan 1988). For each matched replicate group (total of 36), the mean dominance ranks of the two individuals from each of the three density treatments were compared. The effect of size (i.e., fork length) on dominance rank was analysed using Wilcoxon's signed ranks test (Siegel and Castellan 1988). To avoid confounding size and treatment effects on dominance rank, each density treatment was analysed separately (three tests in total). Within each replicate group of six fish, the size was compared between the more and less dominant individual from each density treatment. Alpha values were Bonferroni-adjusted to 0.017 to account for the three related tests. Effects of body mass on dominance rank were, as expected, similar as those of fork length. These analyses were therefore excluded to simplify presentation.

All statistical analyses were conducted using SPSS (version 15; SPSS Inc., Chicago, Illinois).

Fig. 1. Mean fork length in the hatchery for brown trout (*Salmo trutta*) reared at three densities: H, conventional hatchery density (●); M, half of conventional hatchery density (○); L, natural density (▼). Error bars denote standard error of means.



Results

Growth in the hatchery

Growth rate in length for three density treatment groups is illustrated (Fig. 1). On the first sampling occasion, on 21 June, mean body mass and length did not differ significantly between fish in the three density treatments (body mass, $F_{2,15} = 1.8$, $p = 0.20$; length, $F_{2,15} = 1.8$, $p = 0.20$). However, on 2 September (at the time of release into the stream), body size differed significantly (body mass, $F_{2,15} = 6.9$, $p = 0.007$; length, $F_{2,15} = 9.3$, $p = 0.002$), where fish from the low-density treatment (L) group were larger than fish from the other two treatment groups. This effect was no longer significant on 7 October (body mass, $F_{2,15} = 3.1$, $p = 0.07$; length, $F_{2,15} = 1.8$, $p = 0.20$).

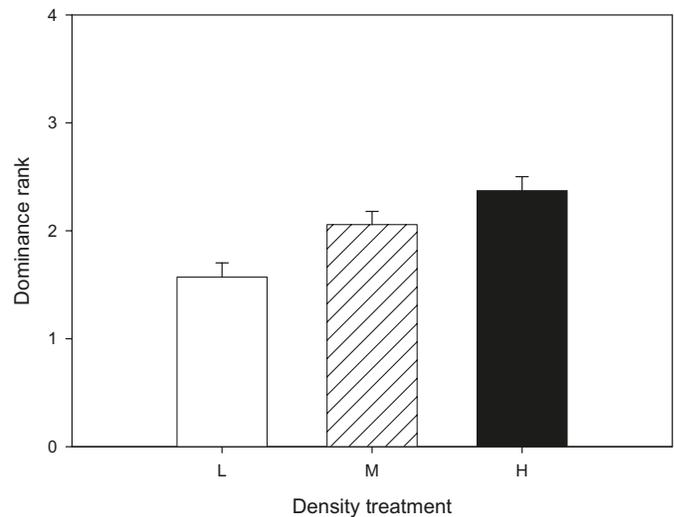
During growth period 1 (21 June – 2 September), fish from the low-density treatment (L) group grew faster than conspecifics from the other treatment groups (body mass, $F_{2,14} = 8.8$, $p = 0.003$; length, $F_{2,14} = 13.7$, $p = 0.001$). However, there was no significant effect of treatment during the second growth period (2 September – 7 October) (body mass, $F_{2,14} = 1.3$, $p = 0.30$; length, $F_{2,14} = 0.5$, $p = 0.60$).

Dominance

Fish from the low-density treatment (L) had significantly higher dominance rank than fish from the two higher densities (Friedman two-way analysis of variance; $\chi^2 = 11.37$, $df = 2$, $p = 0.003$; see Fig. 2). Body size (i.e., fork length) had no significant effect on dominance rank in any of the three treatment groups (Wilcoxon's signed ranks test; $t < 2.0$, $df = 34$, $p > 0.1$ in all cases; $\alpha = 0.017$). Mean fork lengths of the fish used in the dominance experiment were 69.2 ± 0.9 mm (mean \pm SE) in H, 68.0 ± 1.1 mm in M, and 72.0 ± 1.1 mm in L.

When analysing the two components of the dominance rank separately, food acquisition yielded very similar treatment effects as dominance rank (Friedman two-way analysis of variance; $\chi^2 = 15.64$, $df = 2$, $p < 0.001$), whereas overt aggression levels did not differ significantly among treat-

Fig. 2. Mean dominance rank for brown trout (*Salmo trutta*) reared at three densities: L, natural density; M, half of conventional hatchery density; H, conventional hatchery density. Error bars denote standard error of means. 1, highest possible dominance rank; 3, lowest possible rank.



ments (Friedman two-way analysis of variance; $\chi^2 = 0.15$, $df = 2$, $p = 0.93$).

Performance in the stream

Overall, 35 of 108 (or 32.4%) of the released fish were recaptured. Trout from the low-density treatment had significantly higher recapture rates than fish from the higher rearing densities (Wald $\chi^2 = 6.41$, $p = 0.041$; Fig. 3). The initial length of the released fish had no significant effect on recapture rate (Wald $\chi^2 = 1.91$, $p = 0.17$). Growth rate in length in the semi-natural stream (over 33 days) was affected by density treatment, where fish from the L treatment grew faster than conspecifics from the other density treatments. Growth in body mass was not affected by treatment (body mass, $F_{2,31} = 0.17$, $p = 0.84$; length, $F_{2,31} = 7.24$, $p = 0.004$; Fig. 4).

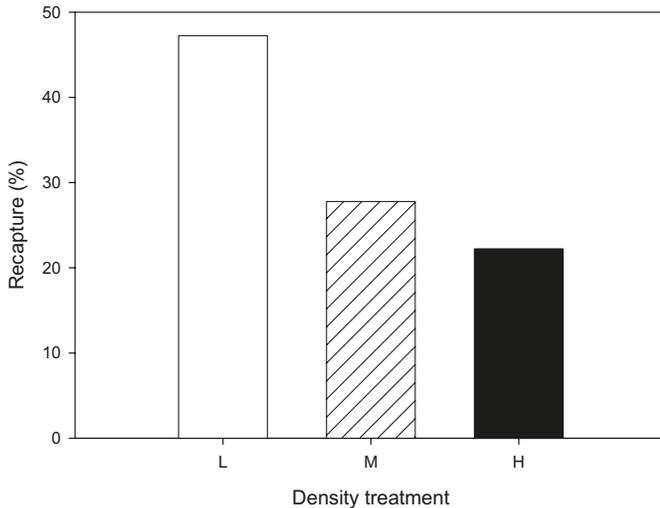
Discussion

Brown trout parr reared at natural densities were dominant in competition for food over conspecifics from higher density treatments. Furthermore, when the fish were released into nature, trout from the natural-density treatment grew faster and were twice as likely to survive compared with trout reared at higher densities. These results are consistent with our hypothesis that reduced density facilitates the development of competitive and dominant behaviour and suggest that short-term benefits of dominance and priority access to resources are translated into long-term benefits in terms of growth and survival in nature.

Growth rate in the hatchery

Although fish in all density treatments received the same feeding rate, trout reared at natural density grew faster than the other fish between June and September. Previous studies on farmed salmonids have generally found that high rearing densities have negative effects on growth rate and survival

Fig. 3. Recapture rate (%) in a natural stream section in October, 36 days after release, for brown trout (*Salmo trutta*) hatchery-reared at three densities: L, natural density; M, half of conventional hatchery density; H, conventional hatchery density.

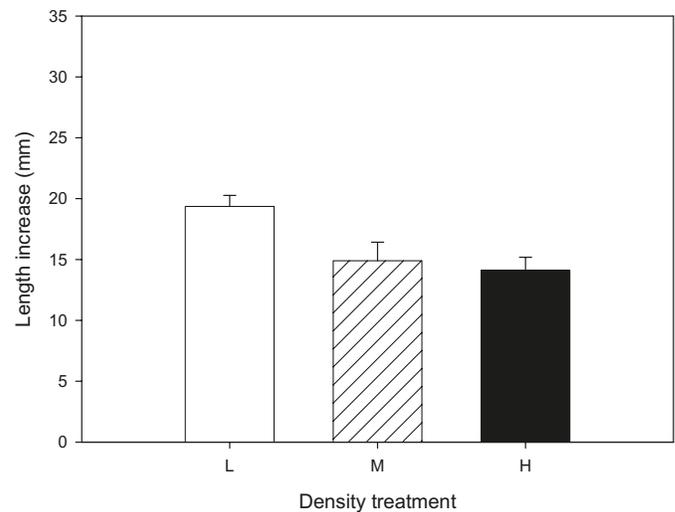


(Ellis et al. 2002). However, effects are species-specific; for example, Arctic char respond with increased growth rate to rearing densities up to $100 \text{ kg}\cdot\text{m}^{-3}$ (Jørgensen et al. 1993). Several studies have also reported negative effects of low rearing densities on growth rate. In rainbow trout, for example, low stocking densities can lead to increased size variation (North et al. 2006). There are several possible mechanisms that may explain the density effect on growth in the present study. For example, increased density can induce scramble competition where individuals simply are getting in each other's way, causing losses of a larger proportion of the food from the hatchery tank (Ruxton 1995). Related to this is the phenomenon of shadow interference where some individuals may experience reduced food intake from being "shadowed" by competitors (Elliott 2002; Krause and Ruxton 2002).

Dominance

Our study revealed strong effects of early rearing density on social dominance where fish from the natural-density treatment were dominant in competition for food relative to conspecifics from the higher-density treatments. Size is an important predictor of dominance status in fish (Johnsson et al. 2006). However, size variation was relatively small and we found no significant effects of size on dominance status in the present study, suggesting that the density effects on dominance were mainly due to other factors. The cost of territorial defence is expected to increase with competitor density up to a point at which resources are not economically defensible and, hence, territorial behaviour is expected to break down (Grant 1997). Thus, in a standard high-density hatchery environment, salmonids are unlikely to be able to express territorial behaviour. This does not necessarily mean that aggression levels decrease in the hatchery. Nipping and fin damage associated with scramble competition is common in high-density hatchery situations (MacLean et al. 2000; Ellis et al. 2002). However, several recent experiments suggest that hatchery-reared salmonids are less effi-

Fig. 4. Mean growth (increase in fork length) in a natural stream, during 36 days after release (2 September – 7 October), for brown trout (*Salmo trutta*) hatchery-reared at three densities: L, natural density; M, half of conventional hatchery density; H, conventional hatchery density. Error bars denote standard error of means.



cient in settling competitive interactions than wild conspecifics (Metcalf et al. 2003). For example, hatchery-reared brown trout spend more time in territorial contests than wild-reared trout without increased probability of winning (Deverill et al. 1999; Sundström et al. 2003), which may suggest that the hatchery environment impairs the efficiency of contest assessment (Leimar and Enquist 1984), perhaps due to environmental effects on neural development (Kihlslinger and Nevitt 2006).

Density effects on social behaviour may also be mediated through other cognitive mechanisms, as limited attention abilities constrain the amount of environmental information that can be processed by animals (Desimone and Duncan 1995). Social behaviour is likely facilitated by the development of familiarity with other individuals over time, which in turn is limited by (i) the number of individual identities that can be learned, and (ii) the opportunity for learning, i.e., how frequently a specific individual is encountered. Thus, in a high-density environment, there is little scope to develop social relations with specific individuals, which may impair the development of social behaviour. Previous studies have shown that familiarity can increase food intake, reduce aggression, and increase vigilance towards predation threat in brown trout groups, suggesting a link between social competence and fitness under natural conditions (Höjesjö et al. 1998; Griffiths et al. 2004).

Performance in the wild

The strong density effects on competitive behaviour measured in the hatchery were apparently translated into fitness-related performance upon release into the natural stream, where fish from the low-density treatment grew faster and survived better than conspecifics from the two higher-density groups. Interestingly, dominance, stream growth, and survival did not change continuously with density over the three levels, suggesting that threshold rearing densities may exist under which behaviour changes and sub-

sequent fitness in the wild increases dramatically. A speculative hypothesis is that this threshold density is related to the limiting density for territorial behaviour and (or) for developing interacting social groups, as discussed above. These ideas are of potential importance also for hatchery management and warrant further investigation.

There are several possible explanations for the strong density effects on growth and survival in the natural stream. The behavioural experiments indicated that natural-density fish were superior in contests over food. The fact that they also grew faster in the wild suggests that the results of the behavioural experiments were not artefacts, or short-time effects due to differential acclimatisation to the experimental setup among the treatment groups. Variable results from previous studies have shown that measurements of dominance in salmonids do not always reflect their growth in nature (Nakano 1995; Höjesjö et al. 2002; Martin-Smith and Armstrong 2002). In the present study, however, the density-related dominance effects on food intake appeared to be maintained in the natural stream. In turn, this suggests the possibility that the higher mortality of the higher-density groups was an indirect consequence of subordination, although recapture probability was not affected by body size. Dominant individuals are known to restrict subordinates access to food, which may reduce their energy status, thereby increasing risk-taking during foraging (de Laet 1985; Morgan 1988). In addition, brown trout parr have been shown to defend protective territories harder when predation risk increases in the habitat (Johnsson et al. 2004), which may further increase predation mortality for subordinates when protective cover is limited. Similar mechanisms have been proposed to reduce subordinate fitness in groups of overwintering tits (see also Ekman 1987). The mortality in the stream was likely caused by predation from mink and heron, which are common in the area. Starvation mortality is less likely to have occurred over the limited time span of the field experiment (36 days; see Johnsson and Bohlin 2006). Electric fishing was repeated to ensure that few if any individuals escaped recapture and migration was prevented by up- and down-stream fences (see Materials and methods).

Implications for hatchery rearing

To our knowledge, this is the first study showing clear effects of reduced hatchery density on postrelease growth and survival of salmonids. It should be pointed out that a considerable reduction of trout density down to high natural levels (Elliot 1994) was required to produce this effect, whereas reducing the density to half of standard hatchery levels had limited effects. In addition, it is not clear to what extent these results are species-specific, although it seems reasonable to assume that other territorial stream-living salmonids should respond similarly. Reducing density is a simple method to practice in supplementation and (or) conservation hatcheries. However, a density reduction down to natural levels may be challenging economically unless increased adult returns will compensate the reduction in numbers of released juveniles. In this context, two points are important to make. First, the present study only measured postrelease performance for 36 days. Thus, long-term cumulative effects on growth and return rates could not be evaluated. Second, consumers and other stakeholders are becoming increasingly

concerned with ethical issues, demanding the right for captive animals to express their natural behaviour (Shumway 1999; Huntingford et al. 2006; Ashley 2007). Although it is clear that hatcheries will never be able to produce fish that are ecologically equivalent to wild counterparts (Waples 1999), our results suggest that there is room for improvement. Considering that only one of many interacting factors in the hatchery environment was manipulated in the present study, the scope for modifying the rearing methods of supplementation hatcheries to increase their contribution to natural production may be considerable.

Acknowledgements

We thank Torleif Andersson and staff at the Swedish Board of Fisheries Research Station in Kälmarne for caring for the fish, Frida Laursen and Elin Brockmark for valuable assistance during the experiment, and Torgny Bohlin for helpful comments on the manuscript. The research was carried out as part of the Swedish R&D programme “Hydropower — Environmental impact, remedial measures and costs in existing regulated waters”, which was financed by Elforsk, the Swedish Energy Agency, the National Board of Fisheries, and the Swedish Environmental Protection Agency. J.I.J. was financed by the Swedish Research Council for Environment, Agricultural Sciences and Spatial Planning. The experiment was approved by the Ethical Committee for Animal Research in Göteborg (license 132/2005) and complies with current laws in Sweden.

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