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ARTICLE

The effects of high rearing density on the potential for domestication selection in hatchery culture of steelhead (*Oncorhynchus mykiss*)

Neil F. Thompson and Michael S. Blouin

Abstract: Hatchery-reared steelhead (*Oncorhynchus mykiss*) often have lower fitness than natural-origin fish when spawning in the wild. Fitness loss in hatcheries is partly due to genetic adaptation to captivity (domestication), but the underlying selection pressures driving adaptation remain unknown. Circumstantial evidence suggests that adaptation to hatcheries is accelerated when fish are reared at high density. We hypothesized two mechanisms by which high rearing densities could accelerate adaptation to the hatchery. First, high density could increase the among-family component of variation in fork length, which could increase the opportunity for selection after release. Second, a growth trade-off in fork length among families could occur across densities (family-by-environment interaction). We raised the same set of families, in replicate, at each of two densities. We found main effects of density (high density reduced body size) and family (accounted for 33%–53% of variance in size at release) on juvenile fork length. However, high density did not increase the percentage of variance in fork length among families, and there was weak evidence for a family-by-environment interaction. We propose an alternate model of how increased density might exacerbate domestication selection. The relationship between size at release and probability of survival is strongly nonlinear (almost truncational) for steelhead. Because high density decreases the fork lengths of all families approximately equally, high density could simply reduce the number of families that are above a threshold for high survival, resulting in strong among-family selection after release from the hatchery.

Résumé : Les truites arc-en-ciel anadromes (*Oncorhynchus mykiss*) élevées en écloserie présentent souvent une moins bonne aptitude que leurs congénères provenant de milieux naturels quand elles frayent à l'état sauvage. Si la diminution de l'aptitude en écloserie est due en partie à une adaptation génétique à la captivité (domestication), les pressions de sélection sous-jacentes à cette adaptation demeurent inconnues. Des preuves circonstancielles donnent à penser que l'adaptation aux écloseries est accélérée quand les poissons sont élevés dans des conditions de forte densité. Nous examinons deux mécanismes qui pourraient expliquer comment de fortes densités durant l'élevage pourraient accélérer l'adaptation au milieu d'écloserie. Premièrement, une forte densité pourrait accroître la composante de la variation de la longueur à la fourche parmi les familles, ce qui pourrait accroître la possibilité de sélection après le lâcher. Deuxièmement, un compromis sur le plan de la croissance exprimé par la longueur à la fourche parmi les familles pourrait se produire à différentes densités (interaction famille-milieu). Nous avons élevé le même ensemble de familles, en double, à deux densités différentes. Nous avons constaté d'importants effets de la densité (une densité élevée réduisait la taille du corps) et de la famille (qui explique de 33 % à 53 % de la variance de la taille au moment du lâcher) sur la longueur à la fourche des juvéniles. Cependant, une densité élevée ne se traduisait pas par une augmentation du pourcentage de variance de la longueur à la fourche parmi les familles, et les indices d'une interaction famille-milieu étaient faibles. Nous proposons un autre modèle pour expliquer comment une densité élevée pourrait exacerber la sélection par domestication. Le lien entre la taille au lâcher et la probabilité de survie est fortement non linéaire (presque tronqué) pour la truite arc-en-ciel anadrome. Étant donné qu'une densité élevée réduit à peu près également les longueurs à la fourche de toutes les familles, une forte densité pourrait simplement réduire le nombre de familles qui dépassent le seuil requis pour une survie élevée, ce qui se traduirait par une forte sélection parmi les familles après le lâcher de l'écloserie. [Traduit par la Rédaction]

Introduction

Release of captively reared salmonids is a widely used tool to conserve threatened and endangered populations (Waples and Drake 2004). One issue with this conservation strategy is that hatchery-reared salmon (*Oncorhynchus* spp. and *Salmo* sp.) and steelhead (*Oncorhynchus mykiss*) often have lower fitness than natural-origin fish when spawning in the wild environment (for reviews, see Araki et al. 2008; Christie et al. 2014). Using data from six populations of four salmonid species, Christie et al. (2014) showed that early-generation hatchery fish (produced from wild or integrated broodstock) average half the fitness of their natural-origin counterparts. Strong evidence that the reduction in fitness resulted from genetic adaptation to captivity (domestication selection) is found in steelhead from the Hood River (Araki et al. 2007; Christie et al. 2012). Environmental effects also contribute to the fitness difference, as demonstrated in a population of Wenatchee River Chinook salmon (*Oncorhynchus tshawytscha*) (Williamson et al. 2010). However, the fact that fitness differences appear to increase with generations in the hatchery (reviewed in Araki et al. 2008) suggests that genetic adaptation to hatcheries is a general phenomenon.

We do not know the environmental conditions in hatcheries that exacerbate rapid adaptation to hatcheries or what specific

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N.F. Thompson and M.S. Blouin. Department of Integrative Biology, Oregon State University, 3029 Cordley Hall, Corvallis, OR 97331, USA.
Corresponding author: Neil F. Thompson (e-mail: thompsne@science.oregonstate.edu).

traits are under selection in the early stages of domestication. Several traits have been shown to differ between multigeneration hatchery stocks and wild source populations (Fleming and Gross 1993; Fleming et al. 1994, 2002; Berejikian 1995; Fleming and Einum 1997; Fritts et al. 2007), but no study has demonstrated a positive effect on fitness in captivity for those traits. Identifying the environmental conditions in hatcheries that drive domestication selection may point to a way to lessen the selection pressure in captivity and reduce fitness loss after release.

Evidence that rapid (1 year in captivity) genetic adaptation to the hatchery is occurring was observed in Hood River steelhead via two distinct trade-offs (Christie et al. 2012). First, a trade-off was found in which families (the progeny of one female mated with one male) that performed well in the hatchery (returned many adults) performed poorly when spawning in the wild, and vice versa. Second, first-generation hatchery fish outperformed wild fish when used as broodstock in the hatchery, but performed worse than wild fish in the wild environment.

Interestingly, the strength of the fitness trade-off across wild and hatchery environments in each cohort appears to be correlated with the rearing density experienced by the cohort in the hatchery (see online supplementary material, Fig. S1[1]; Christie et al. 2012). When a cohort was reared at a high density, the fitness trade-off appeared stronger than the trade-off in cohorts reared at low density. Hatcheries rear fish at high density to produce the largest number of juveniles possible that would produce the largest number of returning adults (Ewing and Ewing 1995; Flagg and Nash 1999). We hypothesize that rearing density influences the strength and ability for domestication selection to occur.

We propose two ways in which high rearing density could intensify domestication (genetic adaptation to captivity). First, if high density increases the proportion of variation in body size among families in the hatchery, then the opportunity for among-family selection would increase. Second, if high density substantially changes the rank order body size of families, then high density may favor families having traits that are less favorable in the wild (here we presume that low-density conditions are more natural than high-density conditions). Genotype (family)-by-environment (density) interactions are ubiquitous and can have strong effects on fitness in novel environments (Via and Lande 1985). We define fitness in the hatchery as body size, because size at release from the hatchery is a strong predictor of survival to return as an adult for hatchery-reared *O. mykiss* (Tipping 1997; Reisenbichler et al. 2004; Bond et al. 2008; Clarke et al. 2014; Osterback et al. 2014).

In this study, we reared steelhead (*O. mykiss*) under high- and low-density conditions to determine if (*i*) rearing at high density increases among-family variation in body size (increased opportunity for selection among families) and (*ii*) if a family-by-environment interaction occurs such that rank order family body size changes substantially. We expected the opportunity for among-family selection (i.e., percentage of variation in body size that is among families) to be larger at high density than at low density. We also predicted a significant family-by-density interaction would exist such that the largest families in high density would not be the largest families in low density. We chose to use steelhead as our study model because the strongest evidence for effects of domestication and adaptation to captivity is found in this species.

Materials and methods

Broodstock collection and spawning procedures

Mature winter steelhead were collected using a fish trap located at river kilometre 103.7 on the Siletz River by the Oregon Department of Fish and Wildlife (ODFW). Following standard ODFW procedures, broodstock were transported to the Alsea River hatchery and artificially spawned (ODFW 2013). All matings were 1 to 1 pairings with no individual being used in more than one mating. Winter steelhead return over the span of 2 calendar years (typical return is December to May) and spawn in the spring. For example, adults that returned in late 2011 and early 2012 are referred to as the 2011 run year, and their offspring that hatched in the spring of 2012 are referred to as the 2012 brood year (i.e., BY 2012). For simplicity, we here use brood year to identify each cohort of offspring and their parents.

The experiment was conducted twice, once per year for 2 years. In 2012, the broodstock were first-generation (F1) hatchery fish (i.e., they had natural-born parents, but spent their juvenile phase in the hatchery). We were unable to use natural-born broodstock because of a small run of natural-born steelhead in the Siletz River during BY 2012. In 2013, all broodstock were natural-born individuals, as determined by the presence of the adipose fin. A fin clip was taken from each broodstock fish and stored in 95% ethanol for parentage analysis.

After fertilization and water hardening, all embryos were transported to the Oregon Hatchery Research Center in Alsea, Oregon. In BY 2012, all families were spawned on 10 May. Three spawning events occurred during BY 2013. Six families were spawned on 10 April, three families on 24 April, and one family on 1 May. The 10 April spawning was reared on chilled water to slow development so all families would hatch and begin feeding exogenously on pelleted food at the same time. All embryos were kept in separate family groups until the density treatments were set up (89 days in BY 2012 and 75, 82, or 96 days owing to three spawning events in BY 2013). We could not pool families earlier because of potential losses during first feeding that would have compromised the study design. We measured fork length of each family when the density treatments were created to determine if early differences in size predicted final body size. No effects of initial body size were found in either year of our study (Table S1[1]).

Density treatments

Our goal for density treatments was to have 140 fish·m^{-3} in the high-density treatment and 20 fish·m^{-3} in the low-density treatment, which mirror the range of densities experienced by fish in the Hood River winter steelhead hatchery program. Fry were randomly chosen from each family and put into one of two density treatments. The high-density treatment was created in 1.8 m diameter tanks, while the low-density treatment was created in 3.6 m diameter tanks. All tanks were tan fiberglass with netting covering the surface to provide shade, cover, and protection from avian predation. Tanks were supplied with ambient temperature water from Fall Creek using a flow-through system.

We note that in this experiment we varied density by using approximately the same number of fish per tank and varying tank size, rather than by using a single tank size and varying the number of fish. We set up our treatment this way because only three 3.6 m tanks existed at the research center. The next largest available tank size was 1.8 m diameter, but those tanks were too small to have enough fish per family in the low-density treatment for an adequate family-level statistical analysis. To test whether the main effects of density on growth rate caused by our treatments mimicked those that would have occurred if we had varied only number of fish, we ran a side experiment in 2013. We created four 1.8 m diameter tanks at the same high and low densities as used in our treatments (two replicates per density) by varying only number of fish. The mean difference in fork length in this treatment was 19.5 mm, while our treatment that varied tank size produced an average 23 mm difference (Fig. S2[1]). Thus, we conclude that at least the main effect of density on body size that we produced in

[1]Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2015-0233.

our treatment was very similar to what would have been produced by using a single tank size and varying the number of fish.

In 2012, 35 juveniles per family from six families were pooled in each treatment tank (n = 210 per tank). The two treatments (high and low density) were replicated twice for a total of four tanks. All tanks were created on 7 August 2012. No marking of the fish was done prior to termination of the experiment.

In 2013, 10 families were used with each family contributing 20 fish to high-density tanks and 31 fish to low-density tanks. All treatment tanks were created on 15 July 2013. Three replicates of each density treatment were created. For high-density tanks the total number of fish in the tank was 200 individuals (10 families × 20 fish per family). For each low-density tank, 310 fish were present (10 families × 31 fish per family). All individuals had the adipose fin removed during January 2014 following ODFW procedures to mimic standard hatchery production as closely as possible (ODFW 2013).

The density treatments differed slightly between years because of loss of four families in 2012. A mechanical malfunction occurred in the hatchery during early rearing (when each family was being reared independently), which led to the loss of four families. We attempted to get as close to the target densities for our treatments as possible, but we do note a slight difference between years.

Fish husbandry

Individuals in all treatments were fed to satiation daily with Bio-Oregon (Longview, Washington) commercial fish feed. The satiation style feeding regime was used to mimic the production process for 1-year smolt hatchery programs as closely as possible. Fish were fed six to eight times per day until reaching 0.75 g, then fed four to six times per day until the fish were 3 g, then two to four feedings per day for the remainder of the experiment (R. Couture, ODFW, personal communication). High- and low-density groups were fed at the same rate receiving the same amount of food per gram of fish. Thus, any difference between densities should be due to increased metabolic or behavioral costs in one treatment rather than absolute food availability. Rearing procedures including tank cleaning and health monitoring followed the ODFW Alsea hatchery operations plan for Siletz stock winter steelhead (ODFW 2013). Monthly temperatures are reported in Table S2[1].

Sampling

In the 2012 experiment, fish were raised in outdoor tanks for 122 days before sampling. In 2013, fish were reared outdoors for 274 days (to smolt size). At sampling, all fish were euthanized via overdose of MS-222 following procedures outlined by the American Veterinary Medical Association (Leary et al. 2013). Fork length was measured in millimetres for each individual, and a fin clip was taken for genetic parentage analysis. Fin clips were stored in 95% ethanol.

Genetic parentage analysis

Genotypes at six microsatellite loci were used to assign juveniles back to family groups. DNA was extracted using Chelex 100 following the protocols of Nelson et al. (1998). The SPAN B suite of loci (*Ogo4*, *Omm1046*, *Omy7*, *One102*, *Ots4*, *Ssa407MP*) were amplified using a PCR thermal cycling regime of 95 °C for 15 min, 35 cycles of 94 °C for 30 s, 57 °C for 90 s, 72 °C for 60 s, with a final extension of 60 °C for 30 min (Stephenson et al. 2009). All loci were multiplexed in a single reaction for each fish. Genotype scoring was performed on an ABI 3730 capillary electrophoresis system (Applied Biosystems, Foster City, California) at the Oregon State University Center for Genome Research and Biocomputing. GeneMapper version 4.1 (Applied Biosystems, Foster City, California) was used to analyze genotype data.

Parentage analysis was performed using the SOLOMON program with an exclusion method because broodstock pairings were known (Christie et al. 2013). Juveniles that mismatched at any locus were checked manually to determine the putative broodstock pairing they belonged to. All fish were eventually assigned back to a known broodstock pair.

Table 1. Intraclass correlations (ICC), variance components in each tank (by year and density treatment), and sample sizes (number of fish per tank).

Year	Density	ICC	V_W	V_A	Total no. of fish
2012	Low	0.14	49	8	182
		0.14	50	8	183
	High	0.17	47	10	183
		0.19	48	11	187
2013	Low	0.33	335	165	284
		0.43	334	254	276
		0.35	242	133	181
	High	0.40	190	126	186
		0.53	159	180	189
		0.37	159	94	189

Note: V_A and V_W are variance components for among and within families, respectively. No significant ($p < 0.05$) difference was found between high- and low-density ICC values in either year.

Statistical analysis

To assess if high-density rearing increased variation in among-family body size, we calculated the intraclass correlation (ICC) for final body size in each tank (Kempthorne 1957). The ICC is a ratio of variance in fork length among families to total variance in fork length within each tank (sum of variance among and within families). A large ICC value suggests that the opportunity for among-family selection to act is high because substantial differences in family fork length (fitness) are present. ICCest in R (version 2.15.1) was used to calculate ICC values and variance components (Wolak et al. 2012; R Core Development Team 2012). A Welch's t test (2012: n_{low} = 2, n_{high} = 2; 2013: n_{low} = 3, n_{high} = 3) was used to determine if the ICC values differed statistically between low- and high-density tanks. An alternate method to analyze the ICC data is via a two-way ANOVA with density treatment and year as factors. Because the ANOVA produced the same results as the Welch's t test, we only report and discuss the results from the latter.

A linear mixed effects model was used to determine if a significant family-by-environment (family-by-density) interaction occurred. Our response was mean family fork length. The model included fixed terms for family, density, and the interaction between family and density. A random tank term was included to account for the correlation between families within a tank, tank-to-tank variation, and replication. All mixed modeling was done following protocols of Zuur et al. (2009) using the nlme package in R version 2.15.1 (Pinheiro et al. 2012; R Development Core Team 2012).

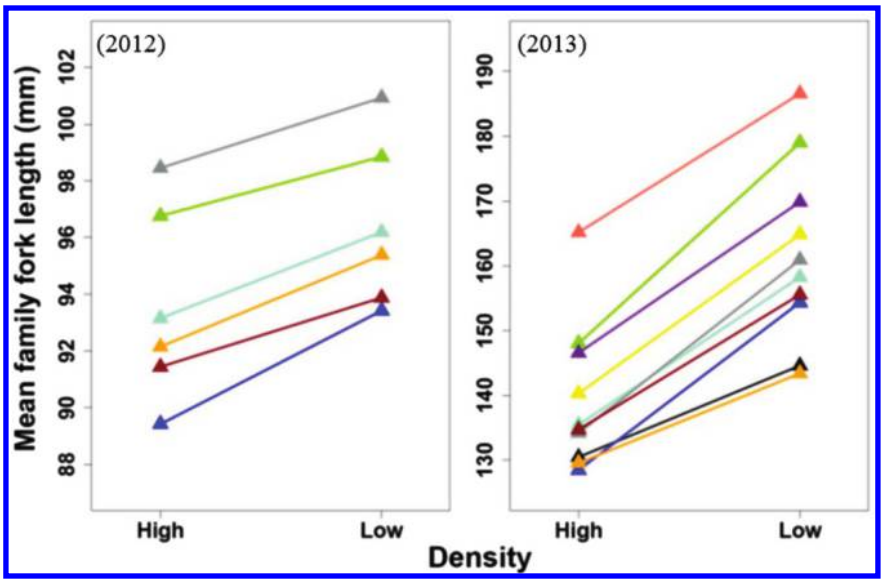
Results

Survival rates were 87% or greater in both years except for one low-density tank in BY 2013 (58% survival; Fig. S2[1]). The results of the ICC and family-by-density analyses were not substantially affected by including this tank. Therefore, we report the results from using all tanks in BY 2013.

Opportunity for among-family selection

ICC values and sample sizes for 2012 and 2013 can be found in Table 1. No significant difference in ICC values was found between high and low density in 2012 (Welch's t test, t = –3.9, p = 0.16) or in 2013 (t = –1.1, p = 0.35). Sample size was small for this test, and the effect of density on ICC values would need to be large to be statistically significant (de Winter 2013). The difference in ICC values would have needed to be 0.06 and 0.22 for 2012 and 2013, respectively, given the variation present in our data to result in

Fig. 1. Mean family fork length of families in 2012 and 2013 in high- and low-density rearing treatments. Each color represents one family. (For the coloured version of this figure, refer to the Web site at http://www.nrcresearchpress.com/doi/full/10.1139/cjfas-2015-0233.) No significant family-by-density interaction was found in 2012. In 2013, a statistically significant family-by-density interaction was found, but explains only 2% of the total variation. The interaction effect is weak compared with the main effects of density and family (which explain 90% of the total variation combined).



statistical significance at 80% power. The proportion of variance among families in body size increased with time in captivity, as 33%–56% of total variation in 2013 was due to differences between families compared with 14%–19% for the shorter 2012 experiment (Table 1). The 2013 experiment mimicked a 1-year smolt production program rearing fish outdoors for 274 days.

Family-by-environment interaction

In 2012 significant effects of density ($F_{[1,2]} = 37.7$, $p = 0.02$) and family ($F_{[5,10]} = 43.1$, $p \leq 0.0001$) were present on juvenile body size. Low density increased mean family fork length for all families (Table S3[1]). However, the interaction between family and density was not significant ($F_{[5,10]} = 0.5$, $p = 0.76$), suggesting that the effect of density did not vary substantially across families.

Significant effects of density ($F_{[1,4]} = 38.3$, $p = 0.004$) and family ($F_{[9,36]} = 67.9$, $p \leq 0.0001$) were again observed in 2013. Low density increased mean family fork length for all families (Table S3[1]). A significant family-by-density interaction ($F_{[9,36]} = 2.9$, $p = 0.01$) was observed in 2013. The significant interaction result indicates that the effect of density was not consistent across families, with some exhibiting larger changes in mean body size compared with others (Fig. 1). However, the magnitude of the interaction effect is small relative to the main effects of family and density (Fig. 1). The family-by-density interaction accounted for 2% of the total variance, whereas density and family accounted for 43% and 47%, respectively. Furthermore, when the rank order body size of families is compared across density treatments, the correlations are high, ranging from 0.82 to 0.95 (nine pairwise Spearman rank correlation coefficient between each pair of high- and low-density tanks; Table 2). The high correlation of rank order body size between density treatments suggests that rank order changed very little across densities.

Table 2. Spearman rank correlation coefficients of family rank order body size for all pairwise comparisons of high- and low-density tanks within a brood year.

		2012		2013		
Year	Density	High 1	High 2	High 1	High 2	High 3
2012	Low 1	1	1			
	Low 2	0.83	0.83			
2013	Low 1			0.85	0.87	0.94
	Low 2			0.82	0.95	0.95
	Low 3			0.85	0.87	0.94

Discussion

Reducing density did not reduce the percentage of variance in body size that was among families and thus was unlikely to reduce the ability for selection to act on traits that result in large body size in the novel hatchery environment. We also saw no evidence for strong family-by-density interactions. We note that density was confounded with tank size in our study and cannot rule out that using a single tank size and varying fish number might have produced a different outcome. However, our treatment produced strong main effects on mean fork length, and these were very similar to those observed in the side experiment that varied only fish number.

A statistically significant family-by-density interaction (i.e., a body size trade-off) was found in BY 2013, but the effect was small relative to the large main effects of family and density. The interaction effect accounted for 2% of the variance in fork length, while family and density effects accounted for 90% of the variance in fork length. Spearman rank correlations between mean family fork lengths among treatments were high (range of 0.82–0.95), demonstrating that the rank order body size changed very little from low to high densities. Families that were best adapted to captivity performed at a high level irrespective of the rearing density, while those families with maladaptive traits for attaining large body size in the hatchery did poorly regardless of the rearing density.

There are two possible caveats to our results that are worth mentioning. First, the 2013 fish were smaller than are typical for production hatchery releases of the Siletz River stock. This resulted because of an unusually cold water year, which caused production hatcheries to release smaller smolts as well. The facility rearing the Siletz River winter steelhead production class released fish on 9 May 2014 (24 days after our experiment ended) that were 19.3 fish per kilogram, when their release goal was 13.3 fish per kilogram (ODFW 2015). How slower growth could have affected our results is not obvious, but it is worth mentioning. Although, Fishback et al. (2002) found no genotype-by-temperature effect on growth in early rearing

of *O. mykiss*. This result suggests that the rank order body size of each genotype (family) is not significantly altered by water temperature effects on growth.

A second caveat is that because we used a full-sib mating design, we cannot conclude that all of the strong family effects seen in our study were completely genetically based. Nongenetic maternal effects and effects of common environment before families were mixed could contribute as well. In particular, spawn date could add an environmental effect in 2013 because earlier-spawned families are chilled as standard practice to ensure all families begin exogenous feeding simultaneously. On the other hand, mean family fork length at ponding was uncorrelated with mean final family fork length (Table S1[1]), so any environmental or maternal effect on final size would have to have occurred via another mechanism. Furthermore, growth rate in salmonids raised in captivity is known to be highly heritable (Gjedrem 1983; Gjerde and Schaeffer 1989; Hu et al. 2013). Thus, it seems reasonable to assume that a large proportion of the variance in fork length in our experiment was genetically based.

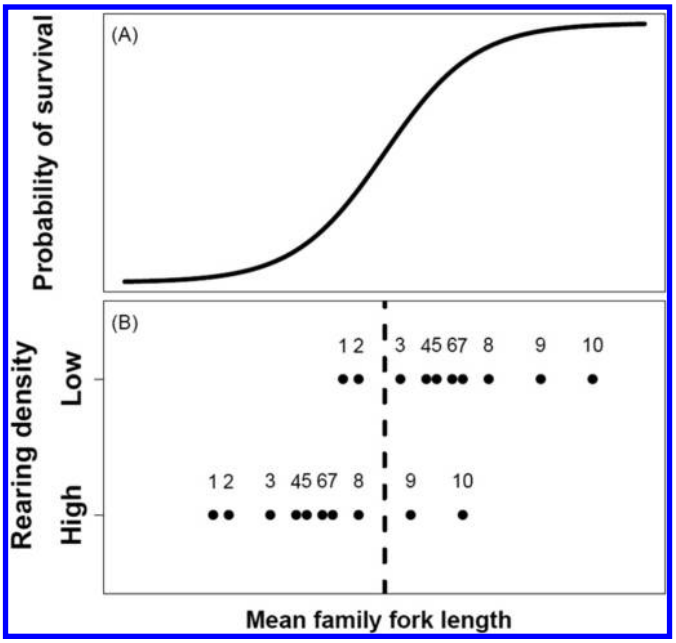
In the data from Christie et al. (2012), there appears to be a correlation between rearing density of Hood River steelhead cohorts and an indicator of domestication in each cohort (the trade-off between family fitness in the hatchery versus in the wild) (Fig. S1[1]). Yet, we saw no evidence that increased density increases the opportunity for among-family selection based on fork length while in captivity. Nor does reducing density appreciably influence which families perform best while in captivity (i.e., little change in family rank order based on body size). So, if increased density does enhance domestication selection, how might that occur?

A possible model for how high density might increase the strength of domestication selection

An alternate model for how increased density could exacerbate domestication selection follows from four observations. (1) The effects of family identity on body size at release are substantial. For example, in our study 33%–53% of the total variance in fork length can be explained by family identity in 1-year-old fish. Thus, selection has a large amount of variation in fork length to act on when steelhead are reared in hatcheries. Growth rate in hatchery-reared salmonids is heritable, with estimates of h^2 ranging from 0.16 to 0.6 (Gjedrem 1983; Gjerde and Schaeffer 1989; Hu et al. 2013). Therefore, we expect that a large proportion of the among-family variation is additive and would respond to selection. (2) The distribution of hatchery family size (number of fish returning per family as spawning adults) tends to be highly skewed, suggesting strong selection among hatchery families (Christie et al. 2012; Abadía-Cardoso et al. 2013). (3) The main effect of increased density is to simply reduce the mean body size of all families (Refstie 1977; Banks 1992; Kavanagh and Olson 2014) and by an approximately uniform amount (this study's results). (4) Strong size-selective mortality postrelease has been demonstrated for numerous steelhead populations (Tipping 1997; Reisenbichler et al. 2004; Bond et al. 2008; Clarke et al. 2014; Osterback et al. 2014), although the potential effects of family identity on size-selective mortality have not been incorporated into a published model. Viability selection on body size postrelease is strongly nonlinear (almost truncational) in steelhead, as seen in the Clearwater River (Idaho, USA), Scott Creek (California, USA), and the Cowlitz River (Washington, USA) (Tipping 1997; Reisenbichler et al. 2004; Bond et al. 2008; Osterback et al. 2014). Thus, there appears to be a threshold size at release, below which fish have low probability of surviving to return as adults.

Given these observations, we suggest the following model by which increased density causes accelerated adaptation to the hatchery and reduced fitness in the wild. In a genetically variable population, some families are, by chance, better adapted to the hatchery environment than others. However, the traits that allow families to grow quickly in the novel hatchery environment put them at a disadvantage in the wild. That is, the traits that create fast growth in the hatchery do not have high fitness when expressed in the wild environment (Saikkonen et al. 2011). At high density only a small subset of families can achieve the threshold fork length for high postrelease survival from the hatchery, resulting in strong among-family selection after release (this model is illustrated using hypothetical data in Fig. 2). At low density, more families exceed the threshold for high probability of survival, causing reduced among-family selection (Fig. 2). Thus, a cohort of families raised at low density would show less adaptation to the hatchery and, presumably, higher average fitness in the wild.

Fig. 2. (A) A hypothetical survival curve to adult return with a nonlinear shape, as is seen in Reisenbichler et al. (2004), Tipping (1997), and Osterback et al. (2014). (B) Mean family fork lengths for hypothetical families reared in a hatchery. Note that the only effect of increased density is to decrease the mean fork length of all families by a constant amount. Families are labelled 1–10. Hypothetically, with truncation selection acting at the dashed vertical line, only 2 out of 10 families in high density survive at a high rate and return a large proportion of the hatchery adults. In low density, 8 of 10 families survive at a high rate. This would increase the number of returns for 6 out of the 10 families, leading to a less skewed distribution of number of returning adults per family and weaker selection on traits that influence the ability to grow large in the hatchery.



The potential for viability selection postrelease from the hatchery has been hypothesized previously to contribute to fitness loss (Reisenbichler et al. 2004; Araki et al. 2008; Berejikian et al. 2012). Our study and model advances this hypothesis by integrating differences in body size based on family identity that includes a heritable component. The traits under selection by domestication in the hatchery are likely selectively neutral in captivity because of high survival rates (87% or greater in this study). Postrelease those traits (we hypothesize body size) are no longer selectively neutral, as viability selection acts strongly against small-bodied families that did not grow to a large size while in captivity.

In summary, we do not see strong evidence in support of our original hypothesis that increased rearing density exacerbates the opportunity for among-family selection by increasing the among-family component of variation in size at release. Nor does it cause a fitness trade-off via large changes in rank order body size of families. In light of our findings, we propose an alternate model

by which increased density could enhance domestication selection by simply reducing the mean fork length of all families in the face of strong selection on fork length after release from captivity.

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