

The effects of domestication on the relative vulnerability of hatchery and wild origin spring Chinook salmon (*Oncorhynchus tshawytscha*) to predation

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Abstract: We tested whether one generation of state-of-the-art hatchery culture influenced the vulnerability of Chinook salmon (*Oncorhynchus tshawytscha*) fry to predators. Size-matched hatchery and wild origin spring Chinook salmon fry were exposed to rainbow trout (*Oncorhynchus mykiss*) and torrent sculpin (*Cottus rhotheus*) predators in 10.8 m³ net pens. The hatchery origin fry were the offspring of first generation hatchery-reared broodstock, and the wild origin fry had no history of hatchery culture; both originated from the same stock. Wild origin fry were found to have a 2.2% ($p = 0.016$) survival advantage over hatchery origin fry during 2 years of predation challenges. The most important findings of this study are (i) domestication can affect the susceptibility to predators after only one generation of state-of-the-art hatchery culture practices, and (ii) the domestication effect was very small.

Résumé : Nous vérifions si un élevage pendant une génération dans une pisciculture de pointe influence la vulnérabilité des alevins de saumon chinook (*Oncorhynchus tshawytscha*) aux prédateurs. Nous avons exposé des alevins de saumons chinook du printemps, de pisciculture et d'origine sauvage, appariés en fonction de la taille, à des prédateurs, des truites arc-en-ciel (*Oncorhynchus mykiss*) et des chabots de torrent (*Cottus rhotheus*), dans des enclos de filet de 10,8 m³. Les alevins de pisciculture étaient les rejetons d'un stock reproducteur de première génération d'élevage en pisciculture et les alevins sauvages n'avaient aucun antécédent d'élevage en pisciculture; les deux groupes provenaient d'un même stock. Les alevins d'origine sauvage ont eu un avantage de survie de 2,2 % ($p = 0,016$) sur les alevins d'élevage au cours des deux années de confrontation avec les prédateurs. Les résultats les plus importants de notre recherche sont que (i) la domestication affecte la vulnérabilité aux prédateurs après une seule génération d'élevage dans des conditions de pisciculture de pointe et (ii) l'effet de la domestication est très petit.

[Traduit par la Rédaction]

Introduction

Propagation of fish in hatcheries has the potential to unintentionally change the genetic composition of donor populations and subsequently contribute to reduced survival in natural environments. This is a particular concern for supplementation or conservation hatcheries because the objective of these hatcheries is to increase natural production (Mobrand et al. 2005). The mechanism of genetic change most likely to occur in conservation hatcheries is domestication (i.e., natural selection in artificial environments; Busack and Currens 1995; Campton 1995). Conservation hatcheries use methods such as representative broodstock selection, factorial mating, low rearing densities, and a high proportion of natural origin fish in the broodstock to control for other

sources of potential genetic change (Busack and Currens 1995).

Domestication selection may be most extreme when ecological conditions such as predation are dramatically different between natural and hatchery environments. Natural environments contain a diversity of predators such as sculpins (*Cottus* spp.) (Ricker 1941; Hunter 1959) and rainbow trout (*Oncorhynchus mykiss*) (Beauchamp 1995), and the mortality of young salmonids caused by predation can be substantial (Fresh and Schroder 1987; Rieman et al. 1991; Ruggerone and Rogers 1992). In contrast, predators, particularly fishes, are generally absent from the rearing environments of conservation hatcheries (Maynard et al. 1995). The relaxation of predator-induced mortality in hatcheries can result in the survival of genotypes that would be selected against in natural environments. This can result in genetic differences that are maladaptive in natural environments and ultimately result in reduced survival.

Various laboratory studies have demonstrated differences in predation mortality or predator avoidance behavior between hatchery and wild fish. Genetic differences between hatchery and wild origin steelhead trout (i.e., sea-run *O. mykiss*) increased the predation mortality of hatchery origin fish when exposed to a benthic predator (Berejikian 1995). Other researchers have found behavioral evidence

Received 10 April 2006. Accepted 5 March 2007.

Published on the NRC Research Press Web site at cjfas.nrc.ca on 14 June 2007.

J19267

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that hatchery origin steelhead trout and brown trout (*Salmo trutta*) were more vulnerable to predation than their wild origin counterparts (Johnsson and Abrahams 1991; Fernö and Järvi 1998; Álvarez and Nicieza 2003). Of the aforementioned studies, only Álvarez and Nicieza (2003) tested predation vulnerability after a single generation of hatchery rearing, and only Fernö and Järvi (1998) and Berejikian (1995) used fish that were from the same donor stock. It is important to test fish after limited exposure to hatchery environments because that is one of the strategies used in conservation hatcheries (at least one generation of natural spawning between hatchery culture) to limit domestication. Furthermore, using the same stock is important because genetic differences between stocks can confound results. In addition, none tested for direct evidence (actual consumption) of vulnerability using both a benthic and a midwater predator, both of which are potential predators to young salmonids. Sculpins are generally ambush type predators that live on the stream bottom and blend in with their surroundings, while trout are generally a cruising type predator that are more visible and tend to overtake their prey in short bursts of speed. Prey fish may use different tactics to avoid capture by predators with different foraging methods so it is important to challenge fish with different predators. Finally, none used yearling Chinook salmon (*Oncorhynchus tshawytscha*) as the prey species.

The purpose of this study was to determine if there are inherent differences in the survival of wild origin and first generation hatchery origin spring Chinook salmon fry when exposed to predators. We conducted a common garden experiment to control for nongenetic factors that could influence survival. These fry were produced at a state-of-the-art supplementation facility that is the centerpiece of the Yakima/Klickitat Fisheries Project (YKFP) to increase natural production of Chinook salmon.

Materials and methods

This work was conducted on stream-type (Healey 1983) spring Chinook salmon fry in the upper Yakima River in central Washington State, USA. The wild origin (hereafter termed wild) fry used in our study are the offspring of wild, naturally spawned spring Chinook salmon. The hatchery origin (hereafter termed hatchery) fry are the offspring of returning first generation hatchery-reared adults, which were derived from the same stock (population) as the wild adults. The adult broodstock were collected downstream of the spawning grounds at Roza Dam throughout the duration of the spring migration so that a representative sample of the population in terms of return timing, age, and size were obtained (Knudsen et al. 2006). Adult broodstock were held in a concrete raceway at the hatchery until spawning commenced in early September. For a detailed description of the supplementation program, see Knudsen et al. (2006).

During spawning, gametes were collected and fertilized according to a standard mating protocol of 3 × 3 factorial crosses to maintain genetic diversity. A sample of fertilized eggs (mean 199; range 169–275) from each parental cross were placed in individual incubation containers (10.2 cm diameter × 5 cm tall isolettes) and incubated in Heath trays

(Knudsen et al. 2005). To obtain the experimental fry, we randomly selected isolettes until nearly all of the adult broodstock used for the factorial crosses were represented at least once and we had enough fry to conduct our study. All surviving fish in the selected isolettes were used. This ensured that our sample of experimental fish represented the true reproductive effort expressed by each parental cross. During 2003, we selected approximately 12 000 fry of each origin: hatchery-by-hatchery parents (hatchery line) and wild-by-wild parents (wild line). This represented the progeny of 33 wild females, 25 wild males, 32 hatchery females, and 15 hatchery males. This accounted for 58 wild families and 59 hatchery families. During 2004, we selected approximately 8000 fry of each origin. This represented the progeny of 18 wild females, 18 wild males, 20 hatchery females, and 20 hatchery males. This accounted for 54 wild families and 58 hatchery families. These fish were transferred outside into two identical 1710 L polyethylene, conical-bottomed circular tanks on 17 April 2003 and 19 April 2004 as unfed fry.

Predation trials were conducted in a 3 m × 30 m concrete raceway at the Cle Elum Supplementation and Research Facility in Cle Elum, Washington. Eight 3 mm nylon mesh net pens measuring 3 m long × 2.4 m wide × 1.5 m high were placed in the raceway to contain each group of trials. Net pens were totally enclosed with a zippered top. Each net pen included one 0.8 m and one 1.3 m diameter floating hoop covered with black plastic to provide overhead cover and a 1.2 m tall plastic evergreen tree to provide in-water cover.

Predators were collected by backpack electrofishing and angling in nearby Yakima Basin streams and were introduced into the net pens at least 1 day prior to the introduction of the fry. Each net pen received three rainbow trout and three torrent sculpin (*Cottus rhotheus*) during 2003. Two rainbow trout and two torrent sculpin were used per pen during 2004 to reduce the fry mortality to less than 50% and avoid density-dependent selection of the predators (i.e., switching to the consumption of less vulnerable prey as the more vulnerable individuals become scarce). Using fewer predators also made it easier to collect enough replacements for the predator assemblages periodically throughout the experiment to avoid the possibility of pseudoreplication (Hurlbert 1984). We therefore used a new assemblage of predators for every other week of trials during 2004 (Table 1), but used the same assemblage of predators throughout 2003 (Table 1).

Trials were conducted between 19 May and 23 June 2003 and between 3 May and 28 June 2004 (Table 1). Each weekly trial started on Monday with the introduction of 100 hatchery and 100 wild, size-matched fry. Before introduction into the net pens, all fry were anesthetized in a solution of tricaine methanesulfonate, measured to the nearest millimetre fork length (mm FL), and differentially marked by excising a small amount of fin tissue from the tip of either the upper caudal or lower caudal. These marks were alternated between net pens and origins to eliminate any possible introduced biases between clip types. A subsample (753 hatchery and 753 wild) was also weighed to the nearest milligram to compare the condition of the fry. All data was entered directly onto a microcomputer, and the mean lengths of the two stocks of fry were matched as closely as possible. The

Table 1. Dates the trials were performed, the predator sets used, and the mean (ranges in parentheses) fork lengths of rainbow trout (*Oncorhynchus mykiss*) (RBT) and total lengths of torrent sculpin (*Cottus rhotheus*) (TSC) at the time of stocking during 2003 and 2004.

Date fry stocked	Week no.	Predator set	RBT (mm)	TSC (mm)
19 May 2003	1	1	204.4 (178–252)	112.1 (92–143)
26 May 2003	2	1	—	—
9 June 2003	3	1	—	—
16 June 2003	4	1	—	—
3 May 2004	1	1	185.2 (161–229)	108.3 (95–124)
10 May 2004	2	1	—	—
24 May 2004	3	2	172.2 (161–204)	114.4 (103–141)
31 May 2004	4	2	—	—
7 June 2004	5	3	171.4 (153–209)	113.3 (96.5–134.5)
14 June 2004	6	3	—	—
21 June 2004	7	4	189.6 (150–249)	113.25 (102–133)

Note: A predator set is a group of three (2003) or two (2004) rainbow trout and three (2003) or two (2004) torrent sculpin.

fry were then allowed to recover from the anesthetic before being introduced simultaneously into the net pens. Food for the fry was introduced into each net pen from Tuesday through Thursday to ensure that weakening due to hunger did not influence survival. Feeding also introduced a situation where the fry had to choose whether to increase their exposure to predation to feed. Each weekly trial was terminated on Friday, when all surviving prey were removed, enumerated, measured to the nearest mm FL, and interrogated for marks to assign origin. Nets were also examined for the presence of dead fry. We assumed that all missing fry were consumed and did not die from causes other than predation. To evaluate this assumption, we gastrically lavaged the predators (Light et al. 1983) at the end of week 6 in 2004 and enumerated the number of fry contained in each predator by counting whole fish and paired diagnostic bones from partially digested fish (Hansel et al. 1988). We also compared the mortality of the two origins of fry in the circular holding tanks to determine if one origin was more likely to die in the absence of predators.

We used analysis of variance (ANOVA) to test whether the sizes of the predators used were similar between net pens. Two-tailed Student's *t* tests were used to test for differences in the mean lengths of the two stocks in each net pen. In addition to the *t* tests for the means, we used the *G* test of independence, with the null hypothesis that the sizes of fry had the same distribution at stocking. The length–weight relationships of the fry at stocking were compared using analysis of covariance (ANCOVA), with log-transformed weight as the dependent variable and log-transformed length as the covariate. To determine if replicates performed with the same predator assemblages were independent, we compared the differences in survival between the two origins of fry for each net pen replicate in the first exposure to a predator assemblage with the survival differences in subsequent exposures to those predators using the Pearson's correlation coefficient. If there were dependency among the predators, we expected to find a correlation that would indicate that subsequent exposures could not be used as true individual replicates. The 2003 and 2004 differences in survival of the

two origins for each replicate were tested using the Mann–Whitney *U* test. If no significant difference were found, it would indicate that it is appropriate to pool the 2 years of data. Wilcoxon matched pairs tests were used to test whether there were differences in survival between the two stock origins. The ANOVA and Student's *t* tests were calculated using Microsoft Excel, and all other tests were calculated using STATISTICA software (StatSoft, Inc. 2001). All tests were considered significant at $p < 0.05$.

Results

The mean lengths of the predators in all net pens were similar (Table 1), and the lengths of predators in each net pen did not differ significantly (ANOVA; $F = 0.125$, $df = 39$, $p = 1.0$). We found no significant differences between the mean fork lengths (*t* test, $p > 0.05$) of the hatchery and wild fry that were introduced into the net pens. The size distributions of the hatchery and wild fry at introduction differed significantly in 4 of the 84 replicates (*G* test, $p < 0.05$). The mean fork lengths of the two origins of fish at introduction never varied by more than 0.4 mm within a net pen trial. The condition (length–weight relationships) of the fry were the same at the time of stocking (ANCOVA; $F = 0.5$, $df = 1$, $p = 0.48$).

If a specific assemblage of predators in a net pen were prone to keying in on a certain physical or behavioral trait of one of the two origins of fry, then reusing that assemblage of predators would not constitute a true replicate and would skew the results. Using the Pearson's correlation coefficient, we found no indication of dependency among the predators between the first and second exposure ($r = 0.273$, $df = 30$, $p = 0.13$), the first and third exposure ($r = 0.263$, $df = 6$, $p = 0.53$), or the first and fourth exposure ($r = -0.506$, $df = 2$, $p = 0.49$). There was also no difference in the survival differences between years (Mann–Whitney *U*, $p = 0.54$). We therefore combined all trials during 2003 and 2004 to perform Wilcoxon matched pairs tests to increase the statistical power of our tests.

Virtually all of the mortalities were consumed fish. Only four hatchery fry and three wild fry out of 8400 stocked per origin were recovered as uningested mortalities. There was no evidence these mortalities were caused by predation, so they were not included as such in the statistical tests. We were able to recover direct evidence of 37% of the fry that were missing during week 6 of 2004 via gastric lavage. The remaining fry may have been completely digested if they were consumed within the first 2 or 3 days of a trial (Elliot 1991). It is also unlikely that the fry died from other causes before being eaten because the mortality of the fry in the circular holding tanks throughout the duration of our study was very low (<1%).

For all 84 trials combined, hatchery fry survival averaged 69.0% (standard deviation, SD = 18.68), and wild fry survival averaged 71.2% (SD = 17.31). Hatchery fry survival was higher in 32 of the trials, wild fry survival was higher in 46 of the trials, and survival was equal in six of the trials. We found significantly higher survival of the wild fish over the hatchery fish for both years combined using all of the predator exposures ($Z = 2.42$, $n = 84$, $p = 0.016$). We also tested only the first exposures, as a more conservative test, which resulted in the same conclusion as the pooled test ($Z = 1.98$, $n = 40$, $p = 0.047$).

Discussion

The data indicate that domestication can affect predation vulnerability in spring Chinook salmon populations after only one generation of state-of-the-art hatchery culture. The hatchery fish used in our study were cultured using practices typical of conservation hatcheries such as collecting broodstock that are representative of the wild population, random mating to avoid conscious or unconscious selection for certain traits, mating using factorial crosses to increase genetic diversity, and their parents were reared at low densities as juveniles (Busack and Currens 1995; Fast 2002). We know of no other studies that tested predation survival differences after only one generation of hatchery culture. Other studies that have found survival or behavioral differences between cultured salmonids and wild salmonids used fish that were artificially cultured for more than one generation (Vincent 1960; Berejikian 1995; Fernö and Järvi 1998) or under intentional selection for traits such as faster growth for farming operations (Johnsson and Abrahams 1991; Fleming and Einum 1997; Yamamoto and Reinhardt 2003). The only study of predation and domestication during the early stages of hatchery culture that we know of (Álvarez and Nicieza 2003) tested behavioral responses to a predator rather than directly testing survival.

Even though we detected a difference in survival after only one generation of hatchery culture, the difference was very small. The hatchery fry used in our study were only 2.2% more vulnerable to predation than the wild fry. In a companion study using the same Chinook salmon populations, Pearsons et al. (2007) observed a small difference in competitive dominance, although the difference was not statistically significant. Other studies have reported larger differences in survival. For example, Berejikian (1995) found nearly a 12% difference in survival between hatchery and wild origin steelhead fry. It is likely that the bigger differences in

survival were due to length of hatchery culture (one to seven generations) and fish culture practices. Hatcheries that continually use returning hatchery-reared fish as broodstock can compound the effects of domestication over generations because the genetic traits that lead to higher vulnerability to predators will not be selected against in the protected hatchery environments. Undergoing at least one generation of natural selection in the natural river environment between hatchery culture is theorized to reduce domesticating effects (Busack and Currens 1995) in hatchery fish. Unfortunately, few empirical data exist to examine this phenomenon.

We attempted to control for nongenetic differences in predation vulnerability, such as fish size, condition, and handling, by ensuring our fish were size-matched within a net pen and received the same amount and type of handling. Smaller fish may not be able to evade predators as well as larger fish because they are not able to swim as fast (Taylor and McPhail 1985). Studies have shown that smaller salmonids are more vulnerable to predators than larger salmonids (Patten 1977; Hargreaves and LeBrasseur 1986; Fritts and Pearsons 2004). Because our fish were size-matched and the condition (fatness) of the fish was the same, this would not explain the survival difference that we observed. The sizes of the predators in each net pen were also similar, which reduces the possibility of size-selective predation. Alternating the marks between upper and lower caudal fins ensured that both origins of fry were treated equally. Mortality in the circular tanks holding the experimental fry during the period of the predation trials was very low (0.88% hatchery and 0.87% wild), suggesting that differential mortality from sources other than predation could not explain the differences we observed. In addition, size-matching the fry made it less likely that environmentally based maternal effects (Heath and Blouw 1998) could have caused the difference that we observed. Furthermore, our tests were conducted at least 1 month after the fry began feeding. Heath and Blouw (1998) reported that a maternal effect of female body size to offspring size disappeared soon after the fry began feeding.

The cause of the survival difference that we observed is uncertain. A greater proportion of hatchery fish may have exhibited behaviors that made them more conspicuous, attractive, or less wary and less able to elude predators. Because we did not perform rigorous behavioral observations during the trials, we do not have data to adequately explain why the hatchery fish were more vulnerable to predation than wild fish. However, we did observe that the fry generally formed a single-mixed origin school when introduced into the net pens, and no obvious differences in behavior between the two origins were observed. Because the survival difference between the two origins was small, any behavioral differences would probably be small as well. Behavioral differences of this magnitude are very difficult to detect even in a carefully controlled experiment. Pearsons et al. (2007) reported that 534 replicates were necessary to detect a significant difference in competitive dominance experiments between these same two populations because the actual difference was very small after one generation of hatchery culture. Many studies attribute the willingness of fish to risk exposure to predators as an effort to obtain more food (Johnsson and Abrahams 1991; Yamamoto and Reinhardt 2003). Hatchery origin fish are

sometimes selected for higher growth hormone levels (Fleming et al. 2002) and would therefore need to take more risks to maintain their higher rate of growth. This seems unlikely for our population because Pearsons et al. (2007) performed experimental trials to assess growth using the same two study populations and found no difference in growth.

To control for environmental effects and measure differences caused by genetic divergence, we performed this study entirely in an artificial environment in a common garden setting. This makes it difficult to quantify how the relative differences that we found would manifest in the natural environment on naturally produced fish. When predation is substantial in the natural environment, the genetic difference that we measured will likely contribute to a difference in survival. Although we included in-water and overhead cover, the natural environment is much more complex than our test arena, with a much wider array of cover, such as rocky substrate, woody debris, aquatic macrophytes, shallow margins, and turbidity. This higher complexity of the natural environment could either amplify or mute the relative difference in predation vulnerability that we measured. Even though we do not know how the magnitude of the difference that we measured would manifest in the natural environment, a genetic difference after only one generation of carefully conducted hatchery culture is an important finding that will likely have ramifications to the natural population.

The number of families that we used (over 50-origin⁻¹. year⁻¹) is far greater than other studies of predation and domestication (e.g., 4–11 families). If only a few families were tested, one family with attributes that made them exceptionally good or poor at avoiding predators could have driven the conclusions of the study. Our results are more likely to be reflective of the whole population rather than just the individuals that were tested. Using two kinds of predators also sets our study apart from others. Fry generally formed a single school and swam along the bottom of the net pens during short observations immediately after their introduction to the pens. It was not uncommon to witness two or three predatory attacks by the sculpins during those first 5 min. Upon fry recovery on the last day, fry were generally higher in the water column underneath the overhead cover where the sculpins were not able to attack them. Qualitative examinations of the gut contents revealed that both predator species consumed many fry and that the timing of predation was different between species. The appearance of the sculpin stomach contents indicated that most of their fry consumption occurred early in the experiment, because the fry were mostly in the advanced stages of digestion, while the rainbow trout stomachs included fry in various stages of digestion (from only bones remaining to freshly ingested).

In summary, we found that small changes in predation vulnerability occurred after only one generation of state-of-the-art hatchery culture. It is uncertain what genetic manifestation caused these fish to survive at different rates and what magnitude of impact this will have to offspring of fish that spawn in the natural environment. Additional studies will be required to understand why differences occurred and to evaluate changes compared with a wild control population and a production hatchery population over several generations so that the long-term fitness of the supplemented population can be measured. The goal of the YKFP is to address these

issues in the Yakima Basin so they can be applied to supplementation programs in other basins.

Acknowledgements

This work would not be possible without the assistance and coordination of the Yakama Nation Fisheries staff at the Cle Elum Supplementation and Research Facility. Craig Busack, Curt Knudsen, and Steve Schroder were instrumental in the initial design of this experiment. Michael Hamlin, Germaine Hart, Charity Davidson, Bryan Johnson, Christopher Johnson, Keith Pitts, Natalia Pitts, Gabriel Temple, and Timothy Webster all assisted with the implementation and collection of data. Two anonymous reviewers provided comments that improved the presentation of this work. This work was funded by the Bonneville Power Administration (BPA) as part of the YKFP. Special thanks are owed to David Byrnes and Patty Smith of the BPA for helping to administer the funding for this work.

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