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Family influence on length at release and size-biased survival post release in hatchery-reared steelhead: A mechanism to explain how genetic adaptation to captivity occurs

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ABSTRACT

Genetic adaptation to captivity influences the reproductive success of hatchery-reared steelhead (*Oncorhynchus mykiss*) spawning in the wild, but the mechanism by which adaptation occurs is not well understood. Because body size-at-release is positively correlated with post-release survival in hatchery-reared smolts, one hypothesis is that hatcheries select for physiological and/or behavioral traits that promote fast growth in captivity. If those juvenile growth traits are maladaptive for spawning or offspring survival in the wild, then that could explain why hatchery fish quickly evolve to have lower reproductive success than natural-origin fish in the wild environment. First-generation hatchery-reared steelhead from the Hood River, (Oregon) have lower reproductive success in the wild than do natural-origin fish, and substantial evidence suggests the fitness difference is genetically based and due to genetic adaptation to captivity. Here we ask whether the 'selection on size-at-release' hypothesis could explain the rapid genetic adaptation observed in this well-studied steelhead population. Using scale analysis, we back-calculated length at ocean entrance to test whether size-selective survival occurred in two cohorts (brood year [BY] 1997 and 2009). In BY 2009, we found evidence of weak size-selective survival (difference of 9 mm between pre-release average length and back-calculated length from surviving adults), but in BY 1997, strong (37 mm difference) size-selective survival was observed. Family identity explained 33% of the variance in fork length before release, and fork length was highly heritable in both BY cohorts. Thus, the requisite genetic variation for response to selection on size-at-release exists in this population. Our results support the hypothesis that size-selective survival does occur after release, and that selection for traits promoting fast growth in the hatchery could be a mechanism by which rapid adaptation to captivity has occurred in the Hood River winter steelhead hatchery program.

1. Introduction

Hatchery-reared steelhead (*Oncorhynchus mykiss*) often have lower reproductive success (fitness) than natural-origin fish when spawning in the wild (reviewed in Christie et al., 2014). Evidence for a genetic component to the fitness reduction has been found in steelhead from the Hood River, Oregon (Araki et al., 2007; Christie et al., 2012) and the Wenatchee River, Washington (Ford et al., 2016). In the Hood River population, a fitness tradeoff occurs in which first-generation hatchery fish have lower fitness than natural-origin fish when spawning in the wild, but the opposite is true in captivity. When hatchery-origin fish are used as broodstock they have higher fitness (return more adults) than natural-origin fish that are used as broodstock (Christie et al., 2012). There is also a second fitness tradeoff in the wild; the hatchery families that return in large numbers have lower per-capita fitness than hatchery families that return in small numbers (Christie et al., 2012). Thus, the traits that make a hatchery family perform well (have high survival to adult return) in the hatchery environment are maladaptive for successful adult spawning or offspring survival in the wild environment. The mechanism by which adaptation to captivity occurs in the Hood

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River population (i.e. the traits under selection and the environmental factors that cause selection) are poorly understood.

One hypothesis is that traits that drive fish to grow rapidly in the novel environment of a hatchery are favored by selection in the hatchery, but entail a survival cost in the wild (Reisenbichler et al., 2004; Araki et al., 2008; Berejikian et al., 2012). This is because body size-at-release is correlated with survival to adult return for hatchery-origin steelhead (Tipping, 1997; Reisenbichler et al., 2004; Bond et al., 2008; Clarke et al., 2014; Osterback et al., 2014). Most hatchery steelhead programs, including the Hood River winter steelhead program, rear fish for a single year from the egg to smolt stage. The single year rearing program is atypical from wild conditions in which natural-origin smolts typically emigrate at 2 years of age or older in Oregon (Reagan, 2011; Clemens, 2015). If size-selective survival occurs after release from the hatchery, then families that are larger-bodied at release would be expected to have higher survival to adult return. However, if the traits that favored rapid growth in the hatchery are maladaptive in the wild, then the families returning in highest numbers to spawn may produce offspring that are poorly adapted and have low survival in the wild environment, as reported in Christie et al. (2012). Such a tradeoff in juvenile performance in hatchery vs. semi-natural conditions was found in Atlantic salmon (*Salmo salar*) where individuals that grew quickly in the hatchery environment had poor survival and growth in a semi-natural stream channel and vice versa for individuals that grew slowly in the hatchery (Saikkonen et al., 2011). Additionally, survival tradeoffs in which offspring of natural-origin steelhead survive better in the wild compared to offspring of hatchery-origin steelhead and vice versa in hatchery conditions (hatchery-origin juveniles survive better than natural-origin juveniles) are known to occur (Reisenbichler and McIntyre, 1977; Reisenbichler et al., 2004). Such performance tradeoffs in survival and growth are what we would expect if rapid adaptation to captivity is occurring and that hatchery-origin adults possess traits that if passed on to their offspring lead to reduced survival in the wild environment.

Note we are not saying that large size at release is favored only in hatchery smolts, and not in wild smolts. Large size at ocean entrance is adaptive for *both* hatchery and natural-origin smolts, as we see size-selective survival in natural-origin smolts as well (Ward et al., 1989; Bond et al., 2008). Our hypothesis is that traits that promote high growth rate in juveniles can be selectively neutral in the high-food, predator free environment of the hatchery, but have a survival cost in the wild (e.g. Biro et al., 2006). This situation would explain the tradeoff we observe in adaptation to the two environments.

Several studies have shown that large body size-at-release is correlated with survival and can be under selection in hatchery-reared steelhead. Longer length at release was positively correlated with detection rates of PIT tagged hatchery-reared smolts from the Clearwater River (Idaho, USA) that emigrated through the Snake and Columbia rivers (Reisenbichler et al., 2004). Larger body size was also positively correlated with survival in one-year old hatchery steelhead smolts that were subjected to multi-week saltwater challenges (Beakes et al., 2010; Berejikian et al., 2017). Using back-calculation methods to estimate size-at-age from scale analysis, size-selective survival occurred in hatchery-reared steelhead from Scott Creek, California (USA; Bond et al., 2008). Returning hatchery-reared adults from the Scott Creek population were on average 23 mm larger as smolts than the average hatchery-reared smolt at release.

Response to selection requires that the trait under selection be heritable in the environment in which it is expressed. It is well established that growth rate in *O. mykiss* is highly heritable in commercial aquaculture and artificial selection programs (for a review: Gjedrem, 1983; Gjerde and Schaeffer, 1989; Elvingson and Johansson, 1993). Smaller scale experiments that mimic hatchery supplementation programs have found strong family effects on body size (Thompson and Blouin, 2015; Berejikian et al., 2017), and that body size-at-release is heritable (Berejikian et al., 2017). Thus, it is very likely that the genetic variation necessary for response to selection on traits related to growth rate exists in the Hood River and other steelhead programs. However, no study, to our knowledge, has estimated heritability or measured family effects on body size-at-release in a production cohort of steelhead smolts reared in a large hatchery program. So, this remains an open question.

To summarize, we hypothesize that genetic adaptation to captivity in Hood River steelhead has involved selection on traits that favor rapid growth in the novel hatchery environment, and that those traits lead to reduced fitness in the wild environment. Therefore, in this study we asked two questions in order to determine if the "selection on size-at-release" hypothesis is a plausible explanation for how adaptation to captivity has occurred in Hood River steelhead; (i) is there evidence of natural selection on size-at-release in two cohorts of hatchery-reared Hood River steelhead? (ii) is there substantial genetic variation for size-at-release in this hatchery population, as would be required for response to selection?

2. Methods

2.1. Population information and hatchery rearing practices

The Hood River in Oregon, (USA) supports a run of winter steelhead that is comprised of natural and hatchery-origin fish. A hatchery program using broodstock from the Hood River began releasing smolts in 1993 and continues to release approximately 50,000 smolts per year. The hatchery program previously operated as a supplementation program, but has recently changed its mission to provide tribal and sport harvest opportunities while minimizing risk to natural-origin fish (ODFW, 2016).

Maturing adult steelhead are captured in the Hood River and spawned artificially at the Parkdale Fish Hatchery (Parkdale, OR) operated by the Confederated Tribes of the Warm Springs (CTWS). Each female broodstock is typically mated with two males, but a 1-to-1 pairing sometimes occurs. Predominantly natural-origin adults are used as broodstock, but in some years hatchery-origin adults are incorporated due to low run size of natural-origin fish. In the two years of this study 100% natural-origin fish were used in brood year (BY) 2009 and 60% natural-origin fish were used in BY 2015. Scales or fin tissue were collected from all broodstock for genetic analysis by the Oregon Department of Fish and Wildlife (ODFW) and preserved with 95% ethanol (fin tissue) or dehydrated (scales).

After fertilized eggs were disinfected and water hardened in an iodophor solution at the Parkdale Fish Hatchery, they were transported on the same day to the ODFW Oak Springs Hatchery on the Deschutes River in Maupin, Oregon. Fertilized eggs were placed in heath tray incubators and developed until the entire egg yolk was absorbed. Water temperatures were manipulated while the embryos developed in the heath trays so that all fish begin exogenously feeding on the same date. After complete yolk absorption, the juveniles were placed into Canadian troughs where feeding with commercial fish food began. The juveniles were reared indoors for a few months and then transferred outdoors to larger tanks where the fish remained until liberation from the hatchery. The current size goal for the Hood River winter steelhead program is 90.8 g per fish at release (ODFW, 2016). The adipose fin was removed from each fish before release to mark it as a hatchery-origin fish.

2.2. Pre-release sampling and smolt release

Approximately one to two weeks prior to release from the hatchery, ODFW biologists sampled the cohort to measure fork length (mm) and weight (g). Approximately 400 fish were sampled from the production cohort each year. In addition to standard sampling for length and weight, for BY 2009 and BY 2015, a small piece of caudal fin tissue was taken from each fish and preserved in 95% ethanol or dried using