The effects of hatchery and wild ancestry and experience on the relative ability of steelhead trout fry (*Oncorhynchus mykiss*) to avoid a benthic predator

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Abstract: Differences in selection regimes between hatchery and natural environments and environmental stimuli, among other factors, have the potential to cause differences in predator avoidance ability between hatchery and wild steelhead trout fry (*Oncorhynchus mykiss*). In two separate laboratory experiments, fry raised from eggs of wild Quinault River steelhead trout survived predation by prickly sculpin (*Cottus asper*) significantly better than size-matched offspring of a locally derived hatchery population, which were reared under similar conditions. Wild fry also survived predation better than hatchery fry in natural stream enclosures over a 3-day test period. Experience, in the form of 50-min visual exposure to sculpin predation on "sacrificial" steelhead trout, improved the ability of fry from both populations to avoid predation by sculpin. Wild-experienced fry were eaten in the fewest number of trials followed by wild-naive, hatchery-experienced, and hatchery-naive fry. The results of this study are consistent with the hypothesis that innate predator avoidance ability has been negatively altered through domestication and that attempts to condition hatchery-reared steelhead to avoid predators may be limited for domesticated populations.

Résumé : Les différences dans le régime de sélection selon l'origine artificielle et naturelle, et les stimuli environnementaux, entre autres facteurs, peuvent causer des différences dans la capacité d'éviter les prédateurs entre des alevins d'élevage et des alevins sauvages de saumon arc-en-ciel (*Oncorhynchus mykiss*). Dans deux expériences de laboratoire distinctes, des alevins provenant d'oeufs de saumons arc-en-ciel sauvages de la rivière Quinault ont nettement mieux survécu à la prédation par le chabot piquant (*Cottus asper*) que la progéniture de taille comparable d'une population d'élevage provenant de la région et élevée dans des conditions similaires. Les alevins sauvages ont aussi mieux survécu à la prédation que les alevins d'élevage en enclos, dans un ruisseau naturel, pendant un essai de 3 jours. L'expérience, par exposition visuelle de 50 min à la prédation par les chabots de saumons arc-en-ciel sacrifiés, a amélioré chez les alevins des deux populations la capacité d'échapper à la prédation par les chabots. Ce sont les alevins sauvages initiés qui ont été mangés dans le plus petit nombre de cas, suivis par les alevins sauvages novices, puis les alevins d'élevage initiés, puis les alevins d'élevage novices. Les résultats de l'étude confortent l'hypothèse selon laquelle l'aptitude innée à l'évitement des prédateurs est négativement affectée par la domestication, et les tentatives de conditionnement des saumons arc-en-ciel d'élevage pour qu'ils évitent les prédateurs semblent n'avoir que des effets limités dans les populations domestiquées.
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Introduction

Substantial research has demonstrated that domestication (Utter et al. 1993) of anadromous salmonid populations results in phenotypic divergence from wild founder populations for a host of biological characters (see Leider et al. 1990). For the case of steelhead trout (*Oncorhynchus mykiss*) in the Pacific Northwest, the phenotypic differences

attributable to domestication may reduce the reproductive success of hatchery populations. Empirical evidence exists that naturally produced progeny of wild steelhead populations survive better than offspring of locally derived domesticated populations during egg-to-fry, fry-to-smolt, and smolt-to-adult stages (Reisenbichler and McIntyre 1977; Chilcote et al. 1986; Leider et al. 1990).

In addition to evidence that environmental rearing conditions can strongly influence various behavioral characteristics of juvenile salmonids (Fenderson and Carpenter 1971; Dickson and MacCrimmon 1982; Bachman 1984), recent studies also demonstrate that several generations of hatchery propagation may alter innate behavioral characteristics such as aggression (Swain and Riddell 1990) and antipredation tactics (Johnsson and Abrahams 1991). These studies suggest there is a genetic basis for some behavioral differences between hatchery and wild fish, which may reduce the fitness of hatchery fish in natural environments. A direct link, however, between behavioral characteristics (e.g., antipredation responses) of hatchery fish and their reduced survival during juvenile stages has yet to be demonstrated.

Predation can be a major source of mortality for juvenile salmonids (Ruggerone and Rogers 1984; Fresh and Schroder 1987). In freshwater lakes and streams, sculpins (*Cottus* sp.) have been observed to prey heavily on age 0 salmonid fry (Ricker 1941; Hunter 1959). Patten (1975) suggested that because of certain innate behaviors such as vertical position in the water column and microhabitat use, steelhead fry were more vulnerable to predation by sculpins than any of the five species of North American Pacific salmon (*Oncorhynchus* spp.). Predation by sculpins on naturally produced steelhead fry in streams may induce selective pressures favoring antipredation responses. Hatchery-produced steelhead are too large to be vulnerable to sculpin when released as age 1 smolts. Natural selection against risk-averse phenotypes in streams may be relaxed on fry reared in predator-free hatcheries, which may increase the proportion of risk-taking individuals in hatchery populations over generations. If the differences in selection regimes between natural and hatchery environments are strong, innate antipredation responses of hatchery steelhead populations may differ from those of wild populations after a relatively few generations of culture.

In conjunction with possible genetic changes that may occur through domestication, typical hatchery-rearing environments possibly obscure the development of antipredation responses within an individual's lifetime because hatcheries lack sensory stimuli associated with predation. Predator avoidance ability of juvenile salmonids can significantly improve after prior exposure to predators (Thompson 1966; Ginetz and Larkin 1976; Patten 1977; Olla and Davis 1989). It is unknown, however, whether or not such experiences can fully compensate for potential deficits in predator avoidance ability that may exist for hatchery fry. For cases in which fry planting might be a reasonable supplementation option (see Steward and Bjornn 1990), it would be especially important to understand the combined influence of domestication and experience on the ability of steelhead fry to avoid naturally occurring freshwater predators.

The primary objective of this study was to assess the relative predator avoidance ability of F_1 steelhead fry from wild and hatchery populations of common ancestry. The second objective was to investigate the interactive effects of wild and hatchery ancestry and experience on the relative ability of steelhead fry to avoid predation by sculpins.

Materials and methods

Study populations

Eyed eggs from seven pairs (one to one matings) of wild Quinault River steelhead were collected at the Quinault Department of Natural Resources pen rearing facility on Lake Quinault, Washington, located approximately 120 km west of Seattle. Wild Quinault River steelhead were identified by the absence of any fin damage common to hatchery steelhead. Subsequent scale analysis confirmed that these steelhead had narrowly spaced freshwater circuli and migrated to sea after 2 years in fresh water, hence were produced naturally, not in a hatchery (cf. Leider et al. 1990).

Eyed eggs were also obtained from 10 pairs (one to one matings) of hatchery steelhead spawned at the Quinault National Fish Hatchery on Cook Creek, a tributary to the lower Quinault River. The Cook Creek population was derived solely from wild adult steelhead captured in the main stem of the lower Quinault River from 1972 to 1974. There is no evidence that any steelhead have ever been introduced to the Quinault National Fish Hatchery or Quinault River system from any other river system. Cook Creek spawners in 1994 were at least one generation removed from their wild ancestors, and given the ages of Cook Creek steelhead (ranging from ages 1.2 to 1.4), may have been as many as four to seven generations removed. Scale analysis showed that Cook Creek brood fish migrated to sea after 1 year of freshwater residence and had wide, uniform spacing of freshwater circuli, indicating that these fish were reared in the hatchery as juveniles.

Eyed eggs were transported to the University of Washington's Big Beef Creek Research Facility, Kitsap County, Washington, and incubated in Heath trays. At emergence, Cook Creek fry (placed in rearing tanks from May 26 to May 27, 1994) and wild Quinault fry (placed in rearing tanks from May 31 to June 1, 1994) were reared in separate, square rearing tanks (1.8 × 1.8 m wide by 0.5 m deep), supplied with 10–10.5°C well water at a rate of 23 L/min. Fry were stocked in the tanks at an initial stocking density of 2469 fish/m^3. Fry from both populations were scatter fed a semimoist crumble four times daily at a ration of 2% of biomass per day until they were removed for experiments.

Prickly sculpin were collected in minnow traps from Big Beef Creek, placed in a 400-L tank, and maintained on a daily ration of frozen thawed steelhead eggs for approximately 3 weeks before experiments were conducted. Sculpin ranged in size from 105 to 125 mm total length.

Predation on hatchery and wild fry in flume chambers

Apparatus

The first experiment was conducted to test the null hypothesis of no difference in the relative ability of Cook Creek

and Quinault steelhead fry to avoid predation by prickly sculpin. The experiment was conducted in two 10.0 × 1.2 m wide wooden flumes. The two flumes were divided in half longitudinally, creating four channels, each with 10 Plexiglas viewing windows measuring 41.0 cm wide by 30.5 cm high. During daylight hours an intensity of 600-lx illumination at the water surface was provided by five pairs of wide-spectrum 40-W fluorescent bulbs over each flume. The flumes were covered with black plastic sheets so that minimal light was able to escape to the observer area. This was sufficient to eliminate disturbance to the fish during observation. Light intensity during nighttime was reduced to 30 lx and was provided by fluorescent bulbs approximately 3.0 m from the flumes penetrating through the observation windows.

Trials were conducted from June 23 to July 1, 1994, in 12 nonadjacent chambers (64 cm long × 61 cm wide × 27 cm deep) situated in the flume channels. A total of 48 trials was conducted in four sets of 12 (i.e., the number of available chambers). The upstream and downstream barriers of each chamber were constructed of fine mesh nylon netting. A layer of gravel (0.5–2.0 cm in diameter) covered the bottom of each chamber to a depth of 5.0 cm. Water was recirculated through the flumes, creating a flow of 8.4 L/s through each chamber.

Procedures
A sample of fry from each population was removed from the rearing tanks without conscious selection, held separately, and anesthetized with tricane methanesulfonate (MS-222). For each trial, three fry were then specifically selected from each population such that the range in fork length within a population for a given trial was not more than 1.5 mm, and each individual from one population had a counterpart from the other population that did not differ by more than 0.5 mm (measurement error). The mean fork length of hatchery and wild fry in the rearing tanks did not differ at the time this experiment was conducted. The size-matching procedure was followed to minimize the confounding effects of size-selective predation (Parker 1971; Ware 1972; Patten 1977).

Adipose fins were clipped on all individuals from one or the other population in each trial, and this procedure was rotated between populations such that each population received fin clips in half of the 48 trials. There was no statistically significant effect of fin clipping on susceptibility to predation between any of the groups so treated in this experiment or in either of the following two experiments.

Each group of six fry was placed into a chamber and left to acclimate for 1.5 h before one sculpin was introduced into the downstream end of the chamber. The sculpin generally lay motionless and invariably took at least 2 h to acclimate and to begin stalking steelhead fry. Each trial was started at 16:00 on day 1. The chambers were then checked for survivors at 10:00 on day 2 (18-h exposure) for all 48 trials. The data (number of fry eaten from each population) were analyzed by a Wilcoxon signed-ranks test (Siegel and Castellan 1988) with the Z statistic corrected for ties. The first 15 trials were terminated after 18-h exposure of fry to sculpin, but the surviving fry were left exposed to the sculpin in 33 of the 48 trials for an additional 24 h (total of 42-h exposure) to observe whether differences in relative vulnerability to predation persisted after more prolonged exposure of fry from both populations to the sculpin.

Population and visual experience effects

Apparatus
A second experiment was conducted from June 28 to July 7, 1994, to test the null hypothesis that population of origin and prior visual experience have no effect on the ability of steelhead fry to avoid predation by prickly sculpin. Fry from both populations were presented with visual stimuli (i.e., experience) associated with predation by sculpin without actually being vulnerable, thereby eliminating the possibility that less fit individuals would be culled from the subject pool (Olla and Davis 1989).

Fry received experience in a Plexiglas aquarium (58 cm wide × 61 cm long × 40 cm deep) situated in one of the flume channels so it could be observed through one of the observation windows. The upstream and downstream ends of the aquarium were constructed of 8-mm square mesh galvanized screen to allow a unidirectional, 27 cm deep, laminar flow of water through the entire aquarium. A clear Plexiglas divider bisected the aquarium longitudinally from top to bottom. Six prickly sculpin were placed into the portion of the conditioning aquarium furthest from the observation window and were allowed to acclimate for at least 24 h prior to a conditioning session. The bottom of the aquarium was covered with approximately 5 cm of gravel 0.5–2.0 cm in diameter.

The control aquarium had the same physical dimensions as the conditioning aquarium but contained no sculpin. Fry in the control aquarium (i.e., naive fry) were handled in the same manner as experienced fry.

Subsequently, predator avoidance challenges (described below) were conducted in 19-L aquaria situated on wooden frames inside the flumes so that each aquarium could be seen through an observation window. Water was recirculated through the flumes at a depth of 27 cm (just below the tops of the aquaria) to provide clear visibility of the aquaria. Each aquarium received 0.5 L/min of 10.5°C well water sprayed through a 3-mm mesh screen covering the top of each aquarium. Gravel substrate was added to the aquaria at a depth of 3–4 cm.

Procedures
Subjects from each population were removed without conscious selection from their respective rearing tanks. Twelve individuals from each population were then selected within a narrow size range (40 ± 0.5 mm) to minimize size-predation confounding effects, and half were adipose clipped to distinguish between individuals of the two populations. Six individuals from each population were then simultaneously placed into either the conditioning aquarium or the control aquarium to create four combinations of population and experience as follows: Cook Creek (hatchery), naive (CN); Cook Creek, experienced (CE); Quinault (wild), naive (QN); and Quinault, experienced (QE).

Each conditioning session (two sessions/day) was conducted as follows. Twelve steelhead fry, including 6 from

each population, were introduced into the near portion of the conditioning aquarium, separated from the sculpin by the Plexiglas divider. Quinault and Cook Creek fry were always conditioned together to ensure that fry from both populations received equal visual exposure to predation. The number of attacks by sculpin through the glass was recorded for 15 min. After 15 min, six sacrificial steelhead were added to the far side of the aquarium where they could be eaten by the sculpin, which could be observed by the 12 subjects. For the next 15 min the number of attacks by sculpin through the glass as well as failed and successful attacks on the six sacrificial steelhead were recorded. Subsequently, six additional sacrificial fry were placed in the far side of the aquarium and the same data were recorded for an additional 20 min (total conditioning time 50 min).

Solid Plexiglas flow barriers were placed at the upstream and downstream ends of the control and conditioning aquaria after the 50-min conditioning period, and the fish were administered a mild dose of MS-222 to limit their escape response while being netted. The subjects were removed from the two aquaria and placed into one of four 6.0-L holding containers depending on their treatment designation (CN, CE, QN, or QE). The entire conditioning process was repeated as necessary to conduct all of the predator avoidance trials described below.

Immediately after conditioning, one adipose-clipped fry was paired with one nonclipped fry and both fish were challenged to avoid predation by placing them into one of the 19-L aquaria with the sculpin, but the pair of steelhead were separated from the sculpin by a solid opaque plastic barrier for a 24-h acclimation period. After acclimation the dividers were removed and the tanks were observed at intervals of not more than 10 min until the first steelhead fry in each aquarium was eaten. The population and experience of the captured fish were identified by the presence or absence of an adipose clip on the surviving fish. The surviving fish was then removed. Trials were conducted until there were 10 cases where one fish was eaten within 3 h ($N = 60$) for each of the following six paired combinations: CE versus CN, CE versus QE, CE versus QN, CN versus QE, CN versus QN, and QE versus QN; thus, the experiment was balanced. Data were analyzed by a chi-square contingency table where the two rows were the outcomes (eaten or escaped) and the four columns were the treatments (QN, QE, CN, CE). Under the null hypothesis, half of the fry from each treatment would be eaten and half would escape (i.e., the expected frequency for each cell was 15). Significant deviations from expected frequencies would suggest that the four treatment groups were not equal in their ability to avoid predation, relative to fry from the other treatments.

Predation in a seminatural stream

A third experiment was conducted from July 16 to July 19, 1994, to test the null hypothesis that there was no difference in the relative ability of Cook Creek and Quinault steelhead fry to avoid predation by prickly sculpin in a seminatural stream environment. The experiment was conducted in a 34.2 m long × 6.2 m wide section of a side channel of Big Beef Creek. The stream channel provided natural

Fig. 1. The average number of fry (±SE) from each population (matched for size) eaten after 18 h of exposure to a single sculpin.
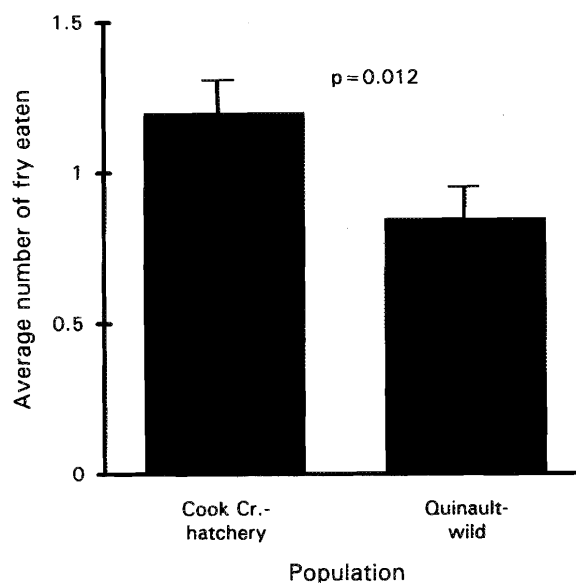
vegetation, photoperiod, food, gravel substrate, and temperature fluctuation (Spalding et al. 1995). The channel was bisected along its entire length by a vertical plywood divider and divided cross-sectionally into seven distinct habitat units (4.9 m long × 3.1 m wide) on each side of the longitudinal divider. The 14 units were alternating pool (mean velocity 4 cm/s, mean depth 19.8 cm) and riffle (mean velocity 11.5 cm/s, mean depth 10.1 cm) habitats, separated from each other by wood-framed, 8-mm mesh galvanized screens, which completely restricted both steelhead fry and sculpin from moving between units.
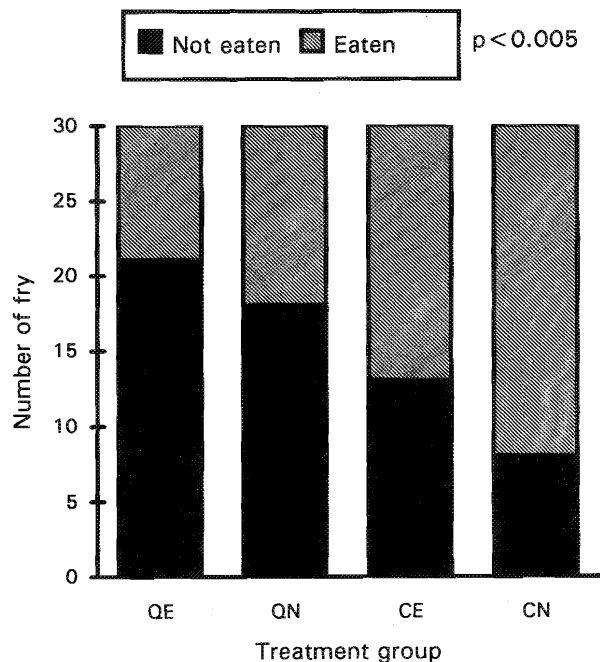
Thirteen fry from each population were introduced into each habitat unit followed by five sculpin, 2 h later. The fish were again selected so there was a one to one correspondence in length–frequency distributions between the two populations within each unit. Adipose clips were utilized to distinguish members of the two populations. The units were then sampled 3 days later with beach seines to enumerate survivors. At least six seine hauls were made through each unit, but hauls were continued until there were three consecutive hauls in which no fish were caught. The numbers of survivors per habitat unit from each population were compared by a Wilcoxon signed-ranks, Z statistic corrected for ties, and the number of survivors in pools and riffles was analyzed by a Mann–Whitney U test.

Results

Predation on hatchery and wild fry in flume chambers

Significantly more Cook Creek (hatchery) steelhead fry were eaten than Quinault (wild) fry after 18-h ($Z = -2.53$, $N = 48$, $p = 0.012$) exposure to a single sculpin in the flume chambers. Sculpin ate an average of 1.2 Cook Creek fry and 0.85 Quinault fry after 18 h (Fig. 1). For the 33 trials in which the surviving steelhead fry were left in the

Fig. 2. The number of fry that were eaten and not eaten in round-robin trials for each treatment group. Q, Quinault (wild) population; C, Cook Creek (hatchery) population; E, experienced; N, naive. Each treatment group was involved in 10 paired contests with each other group ($N = 60$).

Table 1. Mean number of steelhead fry from each population surviving (out of 13) after 3 days in pool and riffle units in the Big Beef Creek side channel.

Population	Pools		Riffles	
	Mean ± SE	N	Mean ± SE	N
Quinault, wild	10.4±0.9	7	9.0±0.9	7
Cook creek, hatchery	8.7±0.6	7	6.4±0.8	7

Predation in a seminatural stream

Of the 26 fish initially placed in each unit, an average of 7.6 (58%) Cook Creek and 9.7 (75%) Quinault fry survived after 3 days, which was a significant difference between the two populations ($Z = -2.24$, $N = 14$, $p = 0.025$). There was also a significant difference between pools and riffles in the total number (both populations combined) of fry recovered ($Z = -2.26$, $N = 7$, $p = 0.023$). An average of 15.5 fry remained in riffles and 19.1 fry remained in pools after 3 days. Fry from both populations survived better in pools than in riffles (Table 1).

Seven of the 28 sculpin recovered at the same time fry were removed on July 19 contained an average of 1.5 fry in their stomachs. Some fry may have been eaten by avian predators (e.g., belted kingfishers, *Ceryle alcyon*, green-backed herons, *Butorides striatus*, and blue herons, *Ardea herodias*), but avian predation has been shown to be minimal in the Big Beef Creek side channel in several previous studies (Spalding et al. 1995; Quinn et al. 1995; B.A. Berejikian, unpublished data).

Discussion

Poor fry-to-smolt survival of domesticated steelhead such as that observed by Chilcote et al. (1986) and Reisenbichler and McIntyre (1977) may be partly a result of inadequate predator avoidance ability by offspring of domesticated steelhead fry. My results clearly demonstrate that the relative ability of hatchery steelhead fry to avoid a benthic freshwater predator was significantly less than that of wild fry in two separate laboratory experiments. The relevance of these results to a natural situation was demonstrated by the third experiment, in which wild fry survived better than hatchery steelhead in 14.9-m^2 natural stream enclosures over a 3-day test period. Fry from the two populations were reared under identical conditions prior to the experiments, which suggests that the differences in predator avoidance ability were genetically determined. Johnsson and Abrahams (1991) found that domesticated rainbow trout × wild steelhead hybrids were more willing to forage in the presence of a predator than wild steelhead fry, suggesting that domestication may increase risk-taking behavior and increase susceptibility to predation. When individually challenged to survive 15 s of exposure to a piscine predator, however, domestic × wild hybrids were no better able to survive predation than wild steelhead. Increased risk-taking behavior without a concomitant increase in predator avoidance ability may increase vulnerability to predation.

enclosures with the sculpin for an additional 24 h, an average of 0.60 Cook Creek and 0.45 Quinault fry were eaten by sculpin during the 24-h period, even though more wild Quinault fry than Cook Creek fry were available to sculpin after 18 h. The average number of fry (both populations combined) eaten by individual sculpin increased from 2.08 (35%) after 18 h to 3.16 (53%) after 42 h.

Population and experience effects

During the 50-min conditioning periods, steelhead fry from both populations were equally subjected to an average of 4.4 attacks by sculpin attempting to capture the test fry through the glass divider in the conditioning aquarium. Sculpin also made an average of 6.0 failed attacks and 2.2 successful attacks on sacrificial steelhead.

Quinault experienced (QE) fry were captured least often, followed by QN, CE, and CN fry (Fig. 2). The differences in the relative abilities of the four treatment groups to survive predation were significant ($\chi^2 = 13.07$, df = 3, $p < 0.005$). An a posteriori analysis of the adjusted standardized residuals in each cell revealed that the significance of the overall test was primarily accounted for by deviations from expected frequencies under the null hypothesis for CN and QE fry. Cook Creek naive fish were eaten in 22 out of 30 trials, which was more often than expected ($Z = 3.0$, $p = 0.003$), while only nine QE fish were eaten, which was fewer than expected ($Z = 2.5$, $p = 0.012$). Thus, both population and experience factors affected relative vulnerability to predation.

It is possible that the comparison of hatchery and wild populations in my study may have been confounded by the existence of genetically distinct subpopulations of winter steelhead within the Quinault River system. Wild spawners were collected for this study in Lake Quinault and were probably destined to spawn in small tributaries to Lake Quinault or in the upper Quinault River system. Initial brood stock for the Quinault National Fish Hatchery (i.e., the Cook Creek population) was collected below Lake Quinault so their eventual spawning destination may have been the lower river, Lake Quinault tributaries, or the upper river. Reisenbichler and Phelps (1989) suggested that Lake Quinault may serve as a partial barrier to gene flow between the upper and lower river that allowed the upper Quinault population to genetically differentiate from the lower Quinault and other populations. However, Reisenbichler and Phelps (1989) also concluded that genetic differences detected by electrophoresis between Cook Creek steelhead and wild Quinault steelhead and other Washington coastal populations were an artifact of the hatchery program. I believe that the wild brood stock collected in Lake Quinault for this study were the closest to the donor wild population available and provide for a valid comparison between the Cook Creek hatchery and Quinault wild populations.

Theoretically, selection regimes for cultured and wild populations inevitably differ, even when the hatchery environment represents only a portion (usually egg to smolt) of the life cycle (Waples 1991). Gotceitas and Godin (1993) reported and reviewed evidence for strong responses by various salmonid species to sympatric predators (Metcalfe et al. 1987; Huntingford et al. 1988; Dill and Fraser 1984), but found only weak responses by juvenile salmon to an allopatric species, brook trout (*Salvelinus fontinalis*). Cook Creek hatchery fry in this study were descendants of steelhead that have been isolated as potential prey for sculpins, probably for several generations. In fact, by the nature of the hatchery program, hatchery steelhead would only encounter sculpin during seaward migration as smolts or returning adults and might be likely predators on sculpin, but certainly not prey for them. Thus, my results are consistent with the hypothesis that relaxation of benthic predation pressure during the juvenile stages, over several generations, may have increased the frequency of predator-susceptible phenotypes in the Cook Creek population relative to the wild Quinault population. Johnsson (1993) suggested that the combination of selection for rapid growth (which may have occurred in the Cook Creek population) and relaxed predation pressures in hatcheries will favor phenotypes that increase risk-taking behavior to maximize energy gain. Such a strategy would likely increase vulnerability of steelhead to predation in natural streams.

Qualitative observations of sculpin (lie-in-wait predators) and steelhead fry behavior provided some insight as to possible behavioral mechanisms that may have been responsible for the observed differences in predator avoidance ability. Most attacks by sculpin were preceded by the sculpin either making short abrupt movements when stalking a steelhead or quick flinches made during false, incomplete, or interrupted attacks. Steelhead appeared to be unaware of the threat posed by completely motionless

sculpin and were only able to detect the presence of sculpin by this movement. Fry that did not overtly respond to these cues were eaten much more often than those that responded by darting away, suggesting that differences in the ability of fry to detect and (or) recognize short, quick, preattack movements of sculpin were important. In addition, data from the conditioning trials revealed that sculpin failed on a high percentage (63%) of attacks on naive sacrificial steelhead. The ability of steelhead fry to avoid sculpin, therefore, may also depend upon interrelated factors such as morphology and swimming speed (see Webb 1977, 1978; Taylor and McPhail 1985), although I have no evidence suggesting that differences in such factors existed between the two populations.

Experience can significantly improve the predator avoidance ability of juvenile salmonids (Thompson 1966; Ginetz and Larkin 1976; Patten 1977; Olla and Davis 1989), but the benefits gained by experience may be limited by genetically determined predator-avoidance capabilities. In this study, population type and experience were both factors affecting the ability of size-matched steelhead fry to avoid predation by sculpin. Wild fry with 50 min of visual exposure to predation suffered the lowest number of mortalities whereas hatchery-reared naive fry suffered the greatest mortality. Exposing hatchery-reared juveniles to predation probably provides the stimuli necessary to trigger innate avoidance responses. Consequently, conditioning juvenile salmonids to avoid predators may be a useful tool for hatchery managers attempting to improve postrelease survival in fry supplementation programs. With the exception of Thompson (1966), however, no published studies have investigated the effectiveness or the feasibility of training fish to avoid predators on a production scale. Such practices might improve postrelease survival and could be particularly beneficial for supplementation programs involving wild brood stock. However, the potential for training offspring of domesticated salmonid populations to avoid predators may be limited when innate responses have been altered through domestication and are inappropriate in natural environments.

Acknowledgements

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