

Effects of hatchery and wild ancestry and rearing environments on the development of agonistic behavior in steelhead trout (*Oncorhynchus mykiss*) fry

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Abstract: At emergence, fry from a wild steelhead trout (*Oncorhynchus mykiss*) population displayed higher levels of one type of mirror-elicited agonistic behavior (swimming against a mirror) than did fry from a locally derived hatchery (domesticated) population. Newly emerged wild fry also dominated hatchery fry in size-matched dyadic dominance challenges. However, given an approximately 3.0–4.5% size advantage, hatchery fry dominated smaller wild competitors in 68% of encounters, indicating that small size differences at emergence can strongly influence dominance. Hatchery fry reared in a natural stream channel for 105 days were more aggressive than those reared in hatchery tanks and than wild fry reared in either environment. In otherwise identical hatchery tanks, low density and low food rations were associated with elevated agonistic behavior by hatchery fry, but not by wild fry. This study suggests that four to seven generations of domestication has resulted in behavioral divergence of the hatchery population from its wild donor population. The extent to which such differences determine the outcomes of interactions between offspring of wild and hatchery steelhead spawning in streams will depend on the size differences and emergence dates of the populations as well as genetic bases of aggression.

Résumé : Chez les alevins récemment éclos d'une population sauvage de truites arc-en-ciel (*Onchorhynchus mykiss*) anadromes, on a observé qu'un type de comportement agonistique suscité par un miroir (les sujets attaquent le miroir en nageant) est plus marqué que chez des alevins provenant d'une écloserie locale (population domestiquée). Les jeunes alevins sauvages ont également dominé ceux de l'écloserie dans des provocations de domination dyadiques. Toutefois, compte tenu d'un avantage de taille d'environ 3,0 à 4,5%, les alevins de l'écloserie ont dominé les compétiteurs sauvages de plus petite taille dans 68% des rencontres, ce qui indique qu'une faible différence de taille à l'éclosion peut avoir une grande influence sur la dominance. Les alevins de l'écloserie qui ont été élevés dans un cours d'eau naturel pendant 105 jours étaient plus agressifs que ceux qui ont été élevés dans les bassins de l'écloserie et que les alevins sauvages élevés dans l'un ou l'autre de ces milieux. Dans des bassins semblables, on a observé que lorsque la densité et les rations alimentaires sont faibles, le comportement agonistique est marqué chez les alevins de l'écloserie, mais non chez les alevins sauvages. Cette étude indique qu'après quatre à sept générations de domestication, la population de l'écloserie présente une divergence de comportement par rapport à la population sauvage dont provenaient les géniteurs des sujets de l'écloserie. L'influence de ces différences sur l'issue des interactions entre les alevins de truites arc-en-ciel anadromes sauvages et les alevins élevés en écloserie lorsqu'ils fraient dans des cours d'eau dépend des différences de tailles et de l'époque de l'éclosion de même que des facteurs génétiques de l'agressivité.

[Traduit par la Rédaction]

Introduction

Hatchery programs for anadromous salmonids can supplement natural production but may have negative ecological consequences for wild populations (see Steward and Bjornn 1990 for a review). In particular, juvenile hatchery salmonids may have competitive advantages over wild conspecifics (Chandler and Bjornn 1988; Swain and Riddell 1990) that

could contribute to the displacement of wild fish (Nickelson et al. 1986). Stream-dwelling juvenile salmonids compete for resources such as food and cover through agonistic behavior (Chapman 1962; Hartman 1965). Levels of aggression have been positively associated with dominance ability (Egglishaw 1967; Fenderson and Carpenter 1971; Holtby et al. 1993), and winners of dominance encounters generally obtain the most energetically profitable stream positions (Fausch 1984; Metcalfe 1986).

Swain and Riddell (1990) demonstrated that newly emerged coho salmon (*Oncorhynchus kisutch*) fry from populations that had been cultured for several generations (i.e., domesticated) were more aggressive than fry from geographically proximate wild populations. Agonistic behavior has a heritable component in coho salmon (Riddell and Swain 1991), but differences in agonistic behavior among wild coho and chinook salmon (*Oncorhynchus tshawytscha*) populations

Received June 26, 1995. Accepted March 11, 1996.
J12971

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also exist and apparently have a genetic basis (Taylor and Larkin 1986; Rosenau and McPhail 1987). Thus, studies comparing the behavior of a wild population to that of hatchery-produced fish from another population may be confounded. The present study compares agonistic behavior of a wild steelhead population to a locally derived hatchery population, thereby minimizing the potential for interpopulation differences not related to domestication.

Variation in rearing environments can also affect agonistic behavior of juvenile salmonids. For example, food deprivation increased levels of agonistic behavior in juvenile chum salmon (*Oncorhynchus keta*; Olla et al. 1990) and Atlantic salmon (*Salmo salar*; Symons 1968). In other studies on Atlantic salmon, agonistic activity of naturally reared fry was less than that of hatchery-reared fry when both groups were held at high densities, but the reverse was true at the lowest densities (Fenderson et al. 1968; Fenderson and Carpenter 1971).

Relative body size has also been recognized as a strong determinant in the outcome of dominance encounters for over 30 years (Chapman 1962). The interplay, however, between body size and aggressiveness has been studied recently (Huntingford et al. 1990; Holtby et al. 1993) but remains unclear. We investigated the relationship between aggression, relative size, and dominance by first evaluating between-population differences in levels of aggression, and then evaluating contests between socially naive individuals of equal and unequal size from the different populations.

Behavioral characteristics at any developmental stage result from present and past interactions between an individual's genotype and external environmental factors (Alcock 1993). Genetically based and environmentally induced effects of hatcheries on aggressive behavior of salmonids have been investigated by controlling for either genotype or rearing environment, respectively. However, we have limited understanding of how environmental factors influence the development of agonistic behavior for hatchery and wild populations that have innate behavioral differences.

Naturally produced steelhead (*Oncorhynchus mykiss*) in the Pacific Northwest typically live in streams for 2 or 3 years prior to seaward migration, whereas hatchery-produced steelhead are most commonly released at age 1. To "push" hatchery-reared steelhead to reach a threshold smolt size (Wagner 1968; Seelbach 1987; Tipping et al. 1995) in 1 year, they are typically fed very high rations. They are also reared at high densities to maximize the production potential of hatcheries. The high rations and densities common in hatcheries contrast sharply with conditions encountered by wild steelhead in natural streams. Fry-to-smolt mortality is much greater for wild than for hatchery-reared fish, and wild fish may survive better at sea than hatchery fish. The different selection regimes encountered by wild and hatchery populations may cause adaptive, genetic changes over a few generations of culture.

The objectives of this study were to investigate the effects of hatchery ancestry, rearing environment, and their interaction on the development of agonistic behavior in juvenile steelhead and to determine the relative effects of aggression and size-at-emergence on the outcome of between-population dyadic dominance encounters. Specifically, we tested the following null hypotheses: (1) levels of agonistic behavior in newly emerged steelhead fry did not differ between hatchery

and wild populations; (2) population type, rearing environment, and their interaction had no effect on the development of agonistic behavior of age-0 fry; and (3) population type and body size had no effect on dominance interactions between newly emerged fry.

Materials and methods

Study populations

Fertilized eggs were obtained from one-to-one matings of wild Quinault River, Washington, steelhead on March 22, 1993 (six pairs), and March 31 to April 2, 1994 (seven pairs). Steelhead were collected in the southwest corner of Lake Quinault and were identified as wild by the absence of the fin damage ubiquitous in Quinault Tribal Hatchery steelhead (M. Figg, Quinault Indian Fisheries Division, Amanda Park, Wash., personal communication). Subsequent scale analysis indicated that these steelhead had migrated to sea after 2 years in freshwater and had narrowly spaced freshwater circuli, also indicating natural rearing (Leider et al. 1990). Scales of one male and one female spawned in 1993 could not be definitively analyzed because of scale regeneration, but both fish were used because their fin condition and run timing were similar to wild Quinault steelhead.

Fertilized eggs were also obtained from one-to-one matings of hatchery steelhead spawned at Quinault National Fish Hatchery on Cook Creek, a tributary to the lower Quinault River, on March 23, 1993 (8 pairs), and February 15 and 23, 1994 (10 pairs). The Cook Creek population was derived solely from wild adult steelhead captured in the mainstem of the lower Quinault River from 1972 to 1974. There is no evidence that steelhead were ever introduced to the Quinault National Fish Hatchery or Quinault River system from another river system. Cook Creek steelhead are released as 1-year-old smolts and spend from 2 to 4 years in the ocean. Hence, those spawned in 1993 and 1994 were as many as four to seven generations removed from their wild ancestors. Scale analysis showed that the Cook Creek brood fish had migrated to sea after 1 year in freshwater and had wide, uniform spacing of freshwater circuli. Both of those traits indicated that these fish were hatchery reared as juveniles.

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 along the Washington coast. They also found that Cook Creek steelhead had allozyme frequencies distinct from wild Quinault steelhead and other Washington coastal populations but concluded that these differences were an artifact of the hatchery program and did not necessarily indicate adaptive differences. We believe that the wild broodstock collected in Lake Quinault for this study are the closest to the donor wild population available, and that comparing Cook Creek hatchery and Quinault wild populations provides a valid evaluation of the effects of domestication on steelhead fry behavior.

Rearing environments

Eyed eggs were transported to the University of Washington's Big Beef Creek Research Facility, Kitsap County, Washington, and incubated on well water in Heath trays. In 1993, eyed eggs from both stocks were incubated at 10°C until emergence. In 1994 incubation temperatures were manipulated to synchronize emergence of both populations and to facilitate the sequence of mirror image stimulation experiments (MIS) and dominance challenges. In 1994, Cook Creek eggs were incubated at average temperatures ranging between 5.6°C and 7.2°C and wild Quinault eggs, between 8.3°C and 10.0°C, depending on whether they were to be placed into rearing tanks, or used in dominance challenges or MIS experiments.

With the exception of fry that would be tested at the button-up

stage of development (i.e., when the yolk sac was no longer externally exposed), fry from both populations were released into hatchery and natural environments in 1993. Four treatment combinations of population and rearing environment were created: CN, CH, QN, QH, where C is Cook Creek (hatchery) population, Q is Quinault (wild) population, H is hatchery environment, and N is natural environment.

The natural rearing environment consisted of seven consecutive 14.9-m² riffle-pool habitat units on each side of a wooden barrier (total of 14 units) in a side channel of Big Beef Creek. The units were separated from one another by wood-framed screens constructed of 8 mm square mesh galvanized screen, which prevented fry from moving between the units. The channel received a water flow of approximately 0.06 m³·s⁻¹ from the main channel of Big Beef Creek. Red alder (*Alnus rubra*), western cedar (*Thuja plicata*), and salmonberry (*Rubus spectabilis*) comprised the main canopy and streamside vegetation. Fish were exclusively dependent on natural production of terrestrial and aquatic invertebrates. Food production in the stream channel has been shown to be very similar between channels and among units (Spalding et al. 1995). Steelhead rearing in the stream channel were vulnerable to kingfishers (*Ceryle alcyon*), green-backed herons (*Butorides striatus*), and blue herons (*Ardea herodias*), but no piscivorous fish were present. Each unit contained one sunken Douglas fir tree top, approximately 1.5 m in height, for cover. One hundred thirty-eight newly emerged Cook Creek fry were stocked into each of seven randomly chosen riffle-pool units, and each of the remaining seven units were stocked with 138 Quinault fry. There was equal representation from each family within their respective population.

The hatchery environment consisted of dark green, square rearing tanks (1.8 × 1.8 m wide, 0.5 m deep), supplied with well water routed through a heat exchanger to induce diel temperature fluctuations similar to those in the stream channel. Fry were stocked at an initial density of 2839 fish·m⁻³ and were scatter-fed a semimoist crumble before being switched to a dry feed after 2 weeks. The fish were initially fed six times daily, which was gradually reduced to twice daily over the 105-day rearing period. The food ration was decreased from 4.5% to 3.0% of biomass over the course of the study, approximating the food manufacturer's guidelines for satiation feeding.

In 1994, offspring from both populations were reared only in hatchery tanks to determine if the two most obvious differences between the stream channel and the hatchery tanks in 1993 (food availability and rearing density) would affect both populations equally. Emergent fry from each population were divided among four rearing tanks so that each tank received equal representation from all families. Two of the four tanks were stocked at a "high density" (D) of 2469 fish·m⁻³ and two at a "low density" (d) of 235 fish·m⁻³. One tank at each density was fed a "high ration" (R), reduced from 6% of biomass to 4% of biomass from emergence to 59 days post-emergence and the other a "low ration" (r), reduced from 2.5 to 1%. Fish biomass was estimated weekly by individually weighing a sample of 50 fry from each tank, and food rations (weighed daily to the nearest 0.1 g per tank) were adjusted accordingly. This procedure was followed for both populations, creating a total of eight tanks with all combinations of population (Quinault and Cook Creek), density (high and low), and ration (high and low). All tanks received 23 L·min⁻¹ of 10°C well water throughout the study.

Mirror image stimulation

Mirror image stimulation (MIS) experiments (Gallup 1968) were conducted to quantify agonistic behavior. MIS tests allow for adequate replication of subjects and have the advantage over dyadic or group encounters of matching a fish against an opponent of equal size and motivational state and eliminating bias from differential agonistic responses to kin and nonkin (Brown and Brown 1992,

1993). Agonistic responses of coho and chinook salmon fry to MIS correlated with responses to conspecifics (Taylor and Larkin 1986; Rosenau and McPhail 1987; Taylor 1988; Swain and Holtby 1989). Although there has been some debate as to the applicability of MIS experiments (Ruzzante 1992), they have been used successfully to differentiate levels of aggressiveness among populations (Holtby and Swain 1992). We used MIS to simultaneously evaluate population and rearing environment effects on agonistic behavior of steelhead.

Mirror-elicited behavior in salmonids has been categorized into three aggressive behaviors (swim against mirror (SAM), lateral display (LAT), and wigwag (WIG) and one submissive behavior (SUB). Definitions of these behaviors follow those described in MIS studies involving coho and chinook salmon (Taylor and Larkin 1986; Rosenau and McPhail 1987; Swain and Riddell 1990; Riddell and Swain 1991; Holtby et al. 1993). SAM was a swimming motion by a fish with its snout against the mirror, often involving a violent shaking of the head and snapping of the jaws. Lateral display included a range of threat displays with the fish parallel to the mirror, with dorsal and anal fins erect, mouth open, and body stiffened. The fish remained motionless or paddled forward with lowered pectoral fins. Lateral displays while swimming with exaggerated body motions were categorized as WIG displays. WIG and LAT were measured separately but were combined for analysis. Submissive displays met all of the following criteria: a fully depressed dorsal fin, depressed anal fin, and a partially folded caudal fin.

All MIS experiments, described below, were conducted in 19-L aquaria, situated in two, 10 × 1.2 m wooden flumes. Each flume was divided in half longitudinally, creating four channels with 10 Plexiglas viewing windows (41.0 cm wide × 30.5 cm high) per channel. The aquaria were placed inside the flumes so that one aquarium could be seen through each of the 40 observation windows. Water was recirculated through the flumes at a depth of 27 cm (just below the tops of the aquaria) to provide excellent visibility between the viewing windows and the aquaria. Each aquarium received 0.5 L·s⁻¹ of 10.5°C well water sprayed through a 3 mm mesh screen that covered the top. Gravel substrate was added to the aquaria to a depth of 3–4 cm.

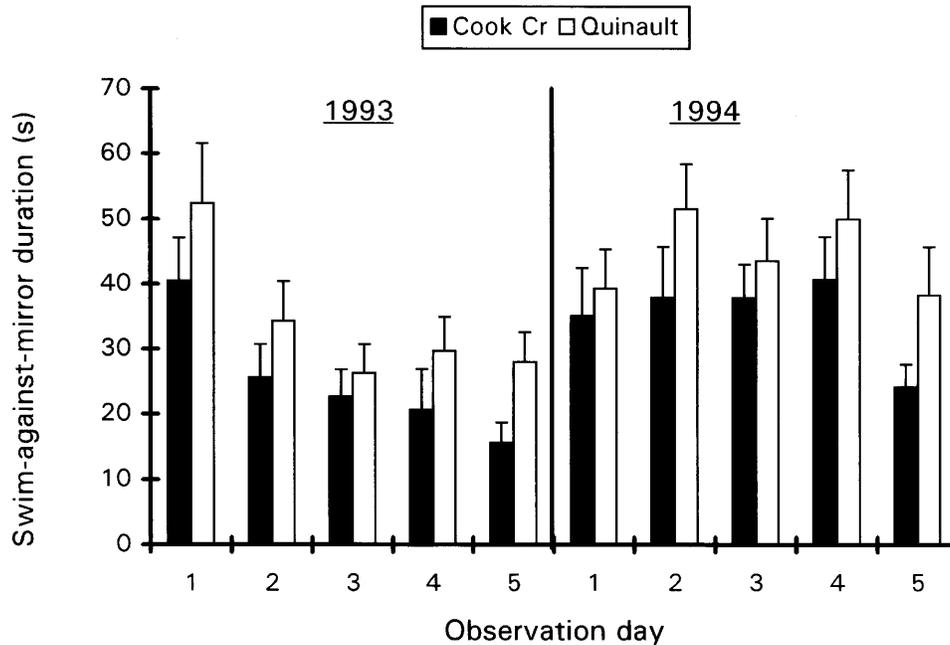
During daylight hours an intensity of 600 lux illumination at the water surface was provided by five pairs of wide-spectrum 40W fluorescent bulbs over each flume. Light intensity during nighttime was reduced to 30 lux, provided by fluorescent bulbs approximately 3.0 m from the sides of the flumes. The flumes were covered with black plastic sheets to avoid disturbing the fish during observation.

In 1993 MIS experiments were conducted at successive developmental stages: emergence (i.e., at button-up; EM-93), 30 days post-emergence (PE30-93), and 105 days postemergence (PE105-93). In 1994, experiments were conducted at emergence (EM-94) and 51–59 days postemergence (PE51-94). Thus, during the 2 years there were five experiments. Socially naive fry tested at emergence (EM-93 and EM-94) were removed from the incubation trays, measured (fork length), and placed individually into the aquaria. Each family within a population was equally represented (± 1 fish) to avoid bias due to potential among-family differences in social behavior (Quinn et al. 1994). Fry used in the three experiments that involved a rearing phase were randomly selected from their respective rearing environments and placed individually into the aquaria.

For all experiments, fry were fed twice daily during a 4-day acclimation period, then once at least 1 h after testing on observation days. All fish had begun feeding by 48 h prior to each experiment. Fry were fed commercial salmon feed during EM-93, EM-94, and PE51-94. However, during PE30-93 and PE105-93 fry were fed frozen thawed bloodworms (*Tubifex* spp.) because half of these subjects were reared in the natural stream channel and preliminary revealed that they would not readily eat commercial pellets. Bloodworms appeared to be equally acceptable to all groups.

Experiments in 1993 involved 40 or fewer trials so all treatment

Fig. 1. Daily average (\pm SE) swim-against-mirror (SAM) durations for socially naive, newly emerged fry from the wild Quinault and Cook Creek hatchery populations in 1993 and 1994. The two populations differed significantly in levels of SAM ($n = 38$ per population, $p = 0.04$).



groups were tested simultaneously. Experiment PE51-94 involved more subjects than there were available tanks so observations had to be conducted in two sessions because only 40 aquaria were available. Two sets of trials were conducted such that 40 fry (5 from each of the 8 tanks) were tested beginning at 51 days postemergence and 32 fry (4 from each tank) were tested beginning at 59 days postemergence.

Each trial was initiated by placing a mirror over the entire back of the aquarium so that the fish could see its reflection from anywhere in the tank. After 45 elapsed, the 3-min observation period began. The observer was unaware of the fish's treatments group (with the exception of EM-94) to eliminate potential observer bias. The duration of each behavior pattern was recorded on a notebook computer. Each fish was observed once daily for 6 days in all 1993 experiments and 5 days in both 1994 experiments.

The dependent variable was the duration of each behavior (SAM, LAT, or SUB) during 3 min of observation. Data from all MIS experiments were first rank transformed to correct for heteroscedasticity, then analyzed by a nested-factorial ANOVA to incorporate the repeated measures on individual subjects over the course of each experiment (Hicks 1987; Tabachnick and Fidell 1989). Individual subjects were nested within populations and years for the combined analysis of EM-93 and EM-94. Subjects were nested within populations and rearing environments for PE30-93 and PE105-93 and within population, density, and ration for PE51-94. This design allowed us to test for (1) the main effects of population and year, (2) the effects of population and rearing environment (hatchery vs. natural) in 1993, (3) the effects of population, ration and density in 1994, and (4) all interactions. In addition, all main effects and interactions in each of the five experiments were crossed by observation day, which provided tests for the effect of observation day and observation day by other main effects interactions.

Dominance challenges

Dominance challenges were conducted in 12 nonadjacent chambers (64 cm long \times 61 cm wide \times 27 cm deep) situated in the flume channels. 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 $8.4 \text{ L}\cdot\text{s}^{-1}$ through each chamber. Sixteen trials were conducted at emergence where one socially naive fry from each population was paired with a fry of equal fork length (± 0.25 mm measurement error) from the other population. In subsequent trials, also conducted at emergence, fry from the “subordinate population” (determined by equal fork length trials 1 through 16) were given a 1.0 mm ($N = 14$) or 1.5 mm ($N = 14$) fork length advantage over a competitor from the dominant population. To identify the two fish in the chambers, adipose fins were clipped on one or the other fry so that each population received adipose clips in half of the trials. Fish that were not adipose clipped were handled in a similar manner including rubbing of scissors across the adipose fin to simulate a clip.

Each trial was begun by placing a pair of fry into a chamber and allowing them to acclimate overnight for approximately 16 h. On day 2 a small amount of commercial steelhead food was introduced into the upstream center of a chamber, and then again 30 s later. Agonistic behavior was then observed for 4 min. A second feeding and 4 min observation period was repeated 3–4 h later. This procedure was repeated on day 3 for a total of 16 min of observation over a 30-h period for each trial.

Dominance was assigned on the basis of total nips and chases delivered (Newman 1956; Abbott et al. 1985), the number of times a fish crossed the midline of the tank when not being chased, and the presence of a pale body coloration and prominent parr marks on the dominant fish and a dark lateral band on subordinates (Keenleyside and Yamamoto 1962). The sign test was used to test the null hypothesis that the number of both populations produced the same number of winners in both size-matched and size-mismatched trials.

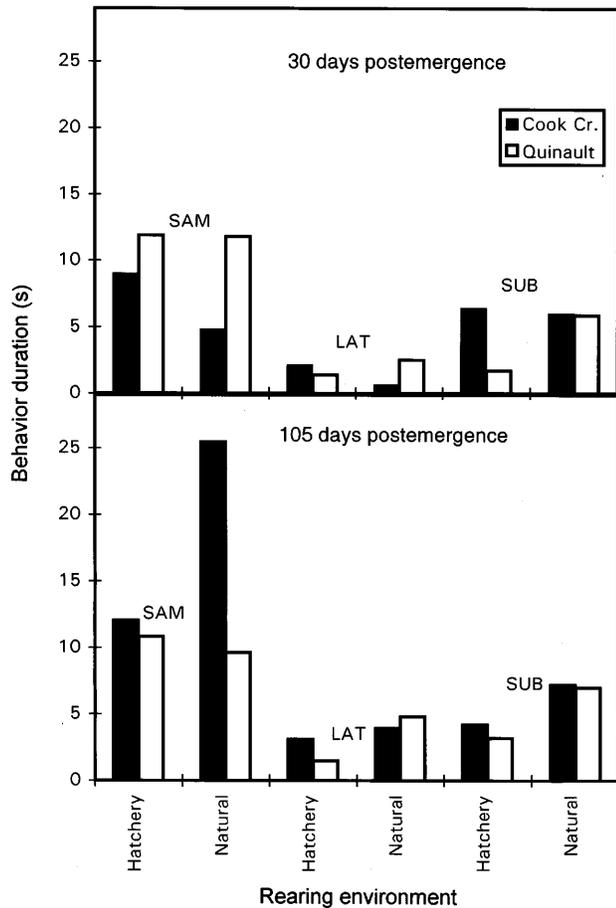
Results

Mirror image stimulation

Population comparison at emergence

At the button-up stage of development (i.e., emergence) wild

Fig. 2. Average swim-against-mirror (SAM), lateral display (LAT), and submissive (SUB) behavior durations by Cook Creek and Quinault fry reared in hatchery and natural environments for 30 or 105 days. No significant day, or day by main effects interactions existed, so each bar represents the average of six observation days. There was a significant ($p = 0.004$) population by rearing environment interaction for SAM at 105 days postemergence. Both graphs are shown on the same scale to demonstrate the differences between behavior durations at 30 and 105 days postemergence.



Quinault fry displayed greater levels of SAM than Cook Creek fry ($F_{1,72} = 4.30$, $p = 0.04$). Swim-against-mirror durations decreased over the 5-day experiment in 1993 for both populations, but levels of SAM showed no apparent trend in 1994 (Fig. 1). The observation day by year interaction was significant ($F_{4,288} = 5.96$, $p < 0.001$). The observation day by year interaction was also significant for lateral displays ($F_{4,288} = 3.43$, $p = 0.01$), and the trends were similar to those for SAM (i.e., decrease over days in 1993 and no apparent trend in 1994). The Quinault and Cook Creek populations did not differ significantly in the duration of LAT ($F_{1,72} = 0.13$, $p > 0.50$) and only slightly in SUB ($F_{1,72} = 3.73$, $p = 0.06$).

Population and rearing effects: 1993 results

At 30 days postemergence wild Quinault fry continued to display slightly greater, though not statistically significant, levels of SAM than Cook Creek hatchery fry ($F_{1,36} = 1.70$,

$p = 0.220$). There were also no significant differences between the populations or rearing environments in levels of LAT or SUB ($p > 0.05$ for all main effects and interactions).

The size distributions and mean sizes of fry from both populations in the stream channel were similar to those in the hatchery tanks at 30 days postemergence. By 105 days postemergence, however, stream-reared fish from both populations had greater variation in weight and fork length and were significantly smaller, on average, than those in the hatchery tanks, suggesting that the stream channel was a food-limited environment at 105 days postemergence but not at 30 days postemergence (Berejikian 1995).

At 105 days postemergence there was a significant interaction between population and rearing environment for SAM duration ($F_{1,180} = 7.17$, $p = 0.001$). Cook Creek fry reared in the natural stream channel (CN) displayed much greater levels of aggression than did the other three population-environment combinations (CH, QH, and QN). That is, the stream environment caused an increase in aggression for Cook Creek fry (Scheffe's multiple contrast, $p < 0.05$), but not for Quinault fry ($p > 0.05$). There was no day, or day by other main effects interaction so the data were pooled across observation days to display the nature of the population by rearing environment interaction (Fig. 2). Population type and rearing environment had no effect on LAT and SUB durations at 105 days postemergence ($p > 0.05$ for all main effects and interactions), and the overall durations of these behaviors were similar to those at 30 days postemergence.

Population, ration, and density: 1994 results

There was a significant highest order interaction: day by population by ration by density for SAM duration during PE51-94 ($F_{4,256} = 2.97$, $p = 0.022$). The decline in mean SAM duration for Cook Creek, high-density, low-ration fish (i.e., CDr) and concomitant increase for QDr after day 3 appeared to contribute to this interaction (Fig. 3). Possibly, fish adapted their behavior to the test environment after several days. After some period of time in the test environment, behaviour may be more strongly influenced by the test environment than by the pretest treatment. Because of this possibility, we believe that the results on the earlier test days of this experiment more accurately reflected the effects of the pretest environment. We, therefore, re-analyzed the data for the first 3 days of the experiment only.

Over the first 3 days there was no significant day by population by ration by density interaction ($F_{2,128} = 0.22$, $p > 0.50$). There was a significant population by ration by density interaction for SAM ($F_{1,64} = 7.45$, $p = 0.008$). Cook Creek fry reared under high ration and high density (CDR) displayed significantly lower levels of SAM than Cook Creek fry reared under low ration and low density. (Scheffe's multiple contrast $p < 0.05$; Fig. 4), and the levels of SAM displayed by CDR were very similar to those of Quinault fry reared under the same conditions (QDR). The combination of high density and high ration appears to have suppressed the development of aggression within the Cook Creek population. By contrast, levels of SAM for QDR did not differ significantly from those of Quinault fry reared under the other combinations of density and ration (Scheffe's multiple contrast, $p > 0.05$).

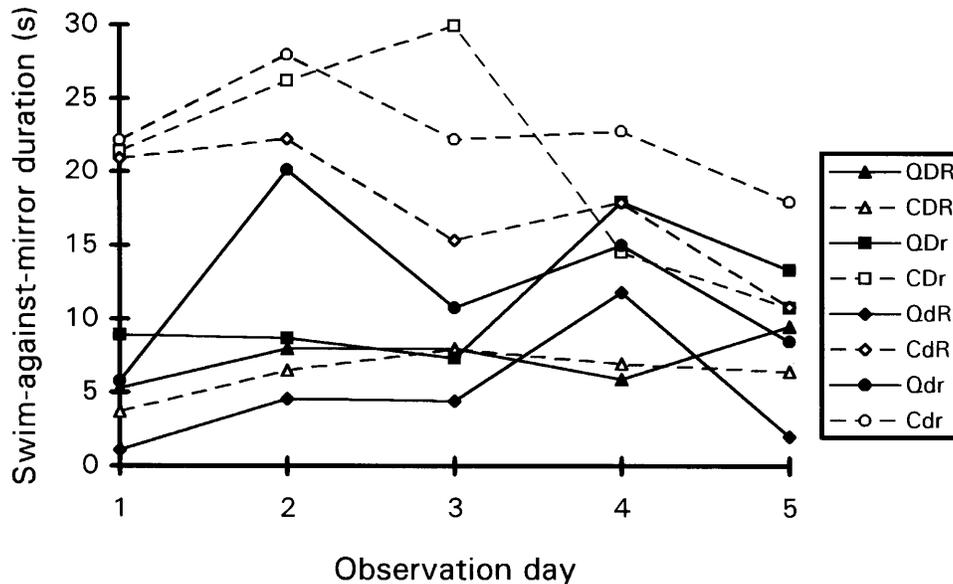
The population by ration by density interaction was marginally significant for LAT ($F_{1,64} = 4.05$, $p = 0.05$), and the

Table 1. ANOVA results (days 1 through 3 only) for mirror image stimulation experiment PE51-94 in which Quinault and Cook Creek fry were reared under high and low densities and rations in hatchery tanks to 51 to 59 days postemergence.

Effect	SAM			LAT		SUB	
	df	F	p	F	p	F	p
Population	1,64	9.71	0.002	11.25	<0.001	0.03	—
Ration	1,64	6.14	0.017	4.87	0.032	4.77	0.034
Density	1,64	0.57	—*	1.88	—	0.23	—
Population × density	1,64	1.65	—	2.61	—	0.61	—
Population × ration	1,64	0.64	—	5.02	0.029	0.69	—
Ration × density	1,64	0.64	—	0.12	—	2.69	—
Population × ration × density	1,64	7.45	0.008	4.05	0.050	2.06	—
Day	2,256	1.69	—	0.30	—	2.49	—
Population × day	2,256	0.46	—	0.15	—	0.10	—
Density × day	2,256	1.28	—	0.31	—	0.35	—
Ration × day	2,256	0.79	—	0.02	—	0.38	—
Population × density × day	2,256	0.20	—	0.05	—	0.02	—
Population × ration × day	2,256	0.03	—	0.11	—	4.39	0.016
Density × ration × day	2,256	0.26	—	0.01	—	0.59	—
Population × ration × density × day	2,256	0.22	—	0.13	—	0.12	—

* $p > 0.10$

Fig. 3. Average daily swim-against-mirror (SAM) durations in experiment PE51-94 for each combination of population (Q, Quinault; C, Cook Creek), density (D, high; d, low), and ration (R, high; r, low). The day by population by density by ration interaction was significant ($p = 0.022$).



lower order population by ration interaction was significant ($F_{1,64} = 5.02, p = 0.03$; Table 1). Cook Creek fry reared under low ration, regardless of density, exhibited much higher levels of LAT than Quinault fry under the same conditions (Fig. 4). However, the Cook Creek low-density high-ration group (CdR) exhibited low levels of LAT, whereas this same group displayed high levels of SAM. Thus, for Cook Creek fry, low density may have had less effect on LAT than on SAM, whereas low ration was associated with high levels of both

behaviors. There was a significant population by ration by day interaction for SUB ($F_{1,256} = 4.39, p = 0.16$).

Dominance

Quinault fry won more dominance bouts (87.5%) than Cook Creek fry (12.5%) when there was no measurable difference in fork length (sign test, $n = 16, p = 0.004$; Table 2). In subsequent trials, Cook Creek fry were given a 1 or 1.5 mm (approximately 3.3–4.5%) fork length advantage over

Table 2. Outcomes of dominance challenges between Cook Creek and Quinault fry at emergence.

Cook Creek size advantage (mm)	N	Wins		df	p
		Cook Creek	Quinault		
None	16	2	14	1	0.004
1.0	14	9	5		
1.5	14	10	4		
Overall (1–1.5)	28	19	9	1	0.09

Note: Data from 1.0- and 1.5-mm size-mismatched trials were combined for analysis.

Quinault fry. The magnitude of the size difference had no significant effect on the outcomes of dominance bouts between the two populations (Chi-square test of homogeneity, $p > 0.50$) so the data from 1 and 1.5 mm size difference trials were combined. Larger Cook Creek fry won 68% of the bouts against smaller Quinault fry, which was a nonsignificant difference (sign test, $n = 28$, $p = 0.09$; Table 1). The frequencies of Quinault fry and Cook Creek fry winners, however, depended on whether the fry were size matched (Quinault fry won 87.5%) or size mismatched (Quinault fry won 32.5%). Therefore, the effect of body size was significant for these agonistic contests (Chi-square test of independence, $p < 0.001$). We were unable to detect any effect of adipose fin clips on the outcome of agonistic encounters (sign test, $n = 44$, $p > 0.25$).

Discussion

When paired at emergence, wild Quinault fry won significantly more dyadic dominance challenges than equalized Cook Creek hatchery fry, consistent with their higher levels of aggression at emergence. Huntingford et al. (1990) conducted within-population dominance experiments with Atlantic salmon and concluded that fighting ability, termed fierceness, may be the primary determinant of dominance and that size was more likely a consequence rather than a cause of dominance. Holtby et al. (1993) also suggested that body size may be a consequence of dominance and found that aggressiveness and lateral body profile were associated with dominance. Our results also suggest that aggressiveness may partly determine dominance because the Quinault population, which had higher levels of SAM, dominated equal sized Cook Creek fry in 87.5% of the contests. However, when given a slight (<5%) fork length advantage, Cook Creek fry dominated smaller Quinault fry in 68% of the contests, indicating that body size at emergence may also be a critical determinant of dominance for steelhead trout. Metcalfe et al. (1995) demonstrated that dominance in newly emerged Atlantic salmon was positively correlated with standard metabolic rate within full-sib groups; however, we did not collect metabolic data to test for such a relation in this study.

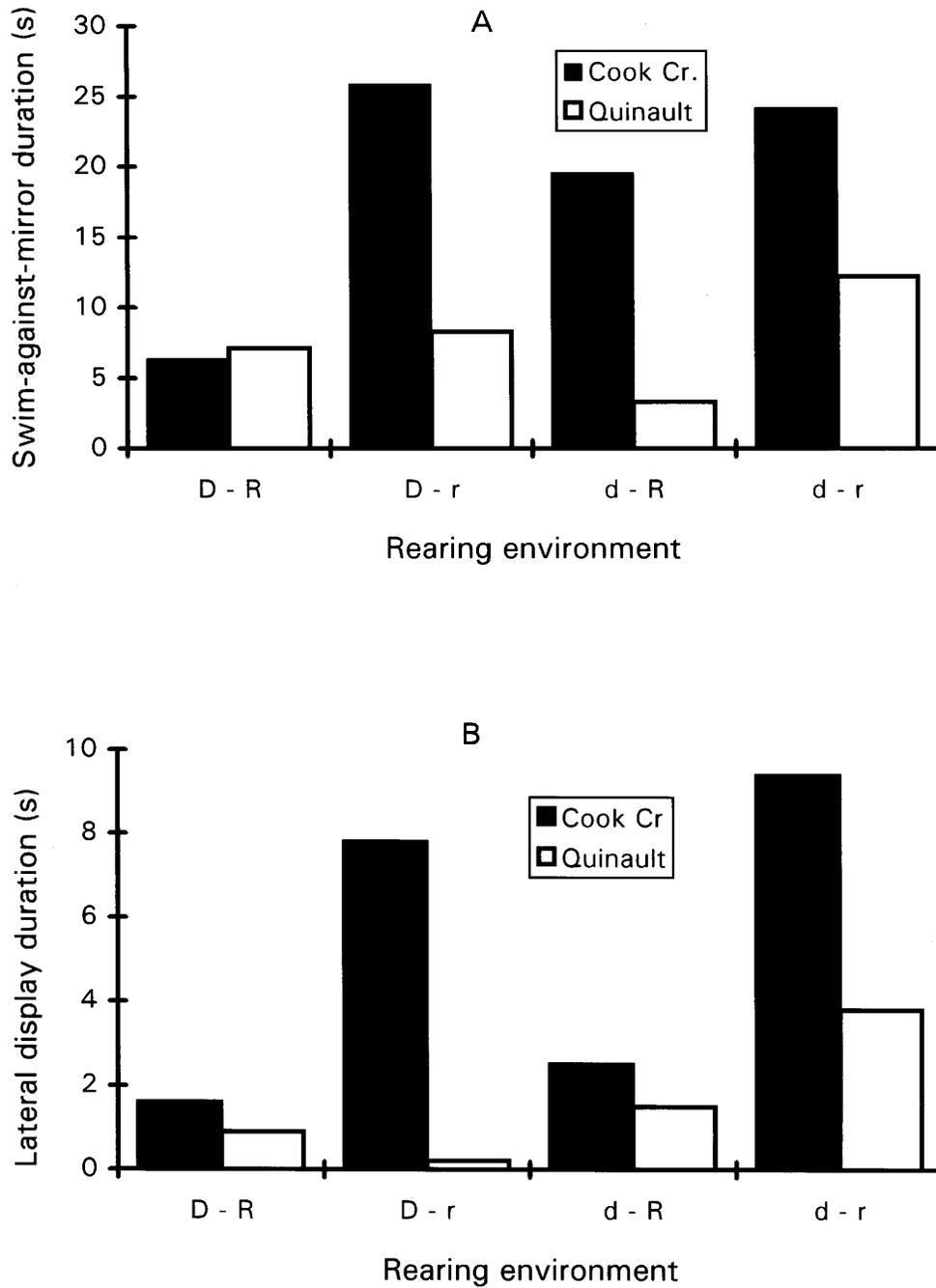
Declining SAM and LAT durations in 1993, and lack of a decline in 1994, might be explained by differences in the amount fed to individual fry between years. During acclimation and testing in 1993 emergent fry were fed slightly more than 10% of their biomass per day whereas in 1994 fry were fed at 7% of body weight (rations in 1994 were weighed individually for each fish to the nearest 0.001 g, much more precisely than in 1993). Fry from both populations tested in 1993 may have become satiated, reducing motivation to engage in agonistic behavior (cf. Symons 1968; Olla et al. 1990).

Cook Creek fry were more aggressive than Quinault fry in both years when reared under low densities and low food availability. At 105 days postemergence in 1993, Cook Creek fry reared at a relatively high ration and density in the hatchery tanks exhibited lower levels of aggression than Cook Creek fry reared under low ration and low density in the stream channel conditions. Similarly, Cook Creek fry reared under low ration and low density were more aggressive than Quinault fry reared under the same conditions. In fact, levels of SAM for Quinault fry were similar regardless of their rearing environment in both 1993 and 1994 (Figs. 2 and 4). Based on “socially naive” fry from the two populations at emergence, (2) the population by rearing environment interactions, and (3) the strong likelihood that the two populations are of common ancestry, we conclude that the observed differences in agonistic behavior between Cook Creek and wild Quinault steelhead have a genetic basis, probably created by four to seven generations of culture in the Quinault National Fish Hatchery.

The lifetime fitness of wild fry may depend more strongly on establishing dominance early in life (i.e., immediately following emergence) than it does for hatchery fry. Dominant individuals gain the most energetically profitable stream positions (Fausch 1984; Metcalfe 1986) and grow faster than subordinates (Newman 1956; Kalleberg 1958; Yamagishi 1962), possibly as a result of increased access to food (Metcalfe et al. 1988; Nielsen 1992). Dominance relationships in juvenile steelhead trout cannot be reversed through size reversals; hence, dominant fish tend to maintain their status (Abbott and Dill 1989), and as a result of their larger size, are probably better able to avoid natural predators than smaller, subordinate fry (Bams 1967; Patten 1977). In protected, food-rich hatcheries, fry are reared under high densities where “scramble competition” (Milinski and Parker 1991) predominates and territories cannot be defended (Grant and Kramer 1990). Although hatchery fry probably also benefit from rapid growth and large size at release (see below), optimal food acquisition strategies are likely to differ for hatchery-produced fry and wild fry emerging in natural streams (see also Doyle and Talbot 1986).

The greater levels of aggression demonstrated by Cook Creek fry under natural conditions (i.e., low rations and densities) may be an indirect result of asymmetrical food and territory requirements of fry from the two populations. As mentioned, hatchery-reared steelhead are fed very high rations to reach smolt size in 1 year. Fish that do not grow large enough to smolt in 1 year are unlikely to emigrate to sea (Tipping et al. 1995) and may reside in freshwater for an additional year or more. Nonmigrating fish are far more likely to die or spawn in the stream rather than return to the hatchery outflow (Wagner 1969; Cramer 1981) and, hence, would not

Fig. 4. Average durations of (A) swim-against-mirror (SAM), and (B) lateral displays (LAT) for PE51-94. Data were pooled across observation days 1–3 to display the nature of the population by ration (R, high; r, low) by density (D, high; d, low) interactions, which were significant for SAM ($p = 0.008$) and LAT ($p = 0.05$).



contribute to the next generation of hatchery fish. Recent data provided no evidence of 2-year freshwater age hatchery-produced steelhead returning to the Quinault National Fish Hatchery (D. Zajac, U.S. Fish and Wildlife Service, Olympia, Wash.). Two-year freshwater age hatchery-reared steelhead were also absent in adult hatchery returns over a 6-year period in the Kalama River, Washington (Loch et al. 1985). Therefore, natural selection should, favor fast-growing fish,

which may include those fish that maximize food intake through high levels of aggression but suffer no consequences (e.g., increased vulnerability to predation) in a protected hatchery environment (see Swain and Riddell 1990). If selection for rapid growth is concomitant with increased systemic demand, hatchery steelhead may experience greater levels of hunger than wild fish when provided with limited rations. Hunger is positively associated with aggression (Symons

1968; Olla et al. 1990); thus, the higher levels of aggression displayed by Cook Creek fry under low rations compared with Quinault fry under the same conditions may also reflect differences in food requirements of individuals from the two populations.

Rearing density did not appear to affect levels of agonistic behavior as strongly as ration. Cook Creek fry reared at low density and high ration displayed levels of SAM more than three times as high as those reared under high density and high ration, whereas levels of LAT showed less of a rearing density effect (Fig 4). Grant and Kramer (1990) surveyed existing literature and determined that territorial behavior of several salmonid species breaks down at high densities. Our results suggest that rearing fish at high densities from emergence may also hinder the development of aggression, when food is plentiful.

The consequences of hatchery steelhead straying to spawn with wild steelhead are still unclear. Nickelson et al. (1986) provided evidence that hatchery coho salmon presmolts outplanted along several Oregon coastal streams replaced wild coho but produced no increase in overall adult populations. The concern that hatchery populations may displace wild populations through superior competitive ability has been supported by Swain and Riddell (1990), who found that newly emerged fry of two domesticated coho salmon populations were more aggressive than those of geographically proximate wild populations. Their results suggested a genetic basis for the population differences. Our results support this concern in the following respect. Cook Creek steelhead displayed elevated levels of aggression when reared in two different food-limited environments (a natural stream channel in 1993 and hatchery tanks receiving reduced ration in 1994). Offspring of domestic steelhead that reproduce in the wild would experience even lower food availability than was provided in our experiments and consequently should be more aggressive than offspring of wild spawners by 2 months postemergence, or sooner. The association of aggression with dominance ability for anything but socially naive fry is difficult to demonstrate because prior experience affects success in subsequent agonistic encounters (Francis 1983; Abbott et al. 1985; Beacham 1988). However, in general, levels of aggression are correlated with dominance (Egglisshaw 1967; Fenderson et al. 1971), and in particular, SAM can predict dominance status in coho salmon (Holby et al. 1993). In addition to aggression advantages, offspring of naturally spawning domestic steelhead might have the competitive advantages of prior residence and body size (Chapman 1962; Mason and Chapman 1965; Abbott et al. 1985; Chandler and Bjornn 1988) over offspring of wild steelhead because hatchery fish typically spawn earlier and, therefore, probably hatch earlier.

Although domesticated steelhead may have some competitive advantages over wild steelhead, empirical evidence demonstrates that naturally spawned offspring of domesticated steelhead may suffer greater mortality throughout all life-history stages than offspring of wild steelhead (Reisenbichler and McIntyre 1977; Chilcote et al. 1986; Leider et al. 1990). In addition to the potential fitness benefits of early social dominance, which wild fry demonstrated in this study, genetically based predator-avoidance behaviors may be partly responsible for the poor fry-to-smolt fitness of domesticated

populations. For example, Johnsson and Abrahams (1991) found that offspring of wild steelhead × domestic rainbow trout hybrids were more willing than offspring of pure wild steelhead to risk exposure to predation, but hybrids were no better able to survive brief exposure to predation. Cook Creek steelhead fry were less able to survive predation by prickly sculpin (*Cottus asper*) than were wild Quinault fry in two laboratory experiments and one field experiment (Berejikian 1995). Observations made during the laboratory experiments suggest that predator recognition and vigilance may have been important mechanisms.

Finally, the timing of spawning and emergence is an important consideration in determining the relative success of wild and hatchery-origin salmonids in streams. Early timing may facilitate acquisition of territories and provide a size advantage, but selective predation on early emerging fry may reduce this advantage (Brännäs 1995). The combination of potentially superior competitive ability (i.e., high aggression 2–3 months after emergence), and inferior predator avoidance ability of hatchery fry suggests that caution should be exercised in designing hatchery programs to supplement wild populations (see also Reisenbichler and McIntyre 1986; Hindar et al. 1991; Waples 1991).

Acknowledgements

We thank M. Figg, R. Rhodes, and S. Chitwood from the Quinault Department of Natural Resources, M. Park and A. Jensen from the Quinault National Fish Hatchery (QNFH) for their cooperation in obtaining steelhead broodstock and D. Zajac for providing background information on the QNFH. We thank G. George and S. Tezak for their technical assistance at Big Beef Creek and R. Reisenbichler and three anonymous reviewers for providing helpful comments on earlier versions of this manuscript. C. Sandkam, M. Kinnison, C. Rosendahl, and H. Sloan assisted with maintaining fish and setting up experiments. Funding was provided by the H. Mason Keeler Endowment, Roy S. Jensen Fellowship, Lauren R. Donaldson research grant, and the U.S. National Marine Fisheries Service (Northwest Fisheries Science Center) – University of Washington School of Fisheries CERP Cooperative.

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