

# Differences in juvenile phenotypes and survival between hatchery stocks and a natural population provide evidence for modified selection due to captive breeding

Kathryn E. Kostow

**Abstract:** Juvenile phenotypes and fitness as indicated by survival were compared for naturally produced steelhead (*Oncorhynchus mykiss*), a new local hatchery stock, and an old nonlocal hatchery stock on the Hood River, Oregon, U.S.A. Although the new hatchery stock and the naturally produced fish came from the same parent gene pool, they differed significantly at every phenotype measured except saltwater age. The characteristics of the new hatchery stock were similar to those of the old hatchery stock. Most of the phenotypic differences were probably environmentally caused. Although such character changes would not be inherited, they may influence the relative fitness of the hatchery and natural fish when they are in the same environment, as selection responds to phenotypic distributions. A difference in fitness between the new hatchery stock and naturally produced fish was indicated by significant survival differences. Acclimation of the new hatchery stock in a "seminatural" pond before release was associated with a further decrease in relative smolt-to-adult survival with little increase in phenotypic similarity between the natural and hatchery fish. These results suggest that modified selection begins immediately in the first generation of a new hatchery stock and may provide a mechanism for genetic change.

**Résumé :** Les phénotypes des jeunes et leur survie (comme mesure de fitness) ont pu être comparés chez des truites arc-en-ciel anadromes (*Oncorhynchus mykiss*) nées en nature, des truites d'un nouveau stock local de pisciculture et des truites d'un ancien stock non local de pisciculture dans la rivière Hood, Oregon, É.-U. Bien que le nouveau stock de pisciculture et le stock naturel proviennent du même pool génétique parental, ils diffèrent significativement par tous les caractères phénotypiques mesurés, sauf l'âge en eau salée. Les caractéristiques du nouveau stock de pisciculture ressemblent à celles de l'ancien stock de pisciculture. La plupart des différences phénotypiques sont probablement attribuables à l'environnement. Bien que de tels caractères ne soient pas transmis génétiquement, ils peuvent affecter le fitness relatif des poissons de pisciculture et des poissons sauvages quand ils cohabitent dans le même milieu, puisque la sélection réagit à la distribution des phénotypes. Il existe des différences significatives de survie, donc de fitness, entre le nouveau stock de pisciculture et le stock sauvage. L'acclimatation du nouveau stock de pisciculture dans un étang « semi-naturel » avant sa libération en nature entraîne une diminution additionnelle de la survie des saumoneaux jusqu'au stade adulte et augmente peu la ressemblance phénotypique entre les poissons de pisciculture et les poissons sauvages. Ces résultats indiquent que la sélection modifiée agit immédiatement dès la première génération dans un nouveau stock de pisciculture et qu'elle peut fournir un mécanisme pour le changement génétique.

[Traduit par la Rédaction]

## Introduction

Phenotypic and fitness differences between wild fish and hatchery fish that have been captive for several generations are well documented (e.g., Reisenbichler and McIntyre 1977; Fleming et al. 1996; Johnsson et al. 2001). Many of the differences are argued by the authors to have a genetic basis (e.g., Fleming et al. 1994; Berejikian 1995; Kallio-Nyberg and Koljonen 1997). The mechanisms that have been proposed to cause genetic divergence between hatchery and

wild fish include modified selection pressures caused by different survivals and mortalities in the artificial versus natural environments (Reisenbichler and Rubin 1999; Ford 2002). Other mechanisms include accumulation of genetic load caused by relaxed selection during captivity (Lynch and O'Hely 2001) and genetic changes caused by small broodstocks and other demographics that lower effective population sizes (Ryman and Laikre 1991; Ryman et al. 1995). These mechanisms may work concurrently to eventually erode the fitness of a captive population when it is returned to the wild (Woodworth et al. 2002).

The idea that modified selection pressures might cause hatchery and wild fish to diverge has been criticized by some resource managers in the northwestern United States because the survival of fish while in captivity can be very high, up to 90% for fish reared from eggs to smolts (ODFW and USFWS 1996). Given these high survivals, some managers argue that there appears to be little opportunity for se-

Received 13 February 2003. Accepted 19 December 2003.

Published on the NRC Research Press Web site at <http://cjfas.nrc.ca> on 18 May 2004.

J17339

**K. Kostow.** Oregon Department of Fish and Wildlife,  
17330 SE Evelyn Street, Clackamas, OR 97015, U.S.A.  
(e-mail: Kathryn.E.Kostow@state.or.us).

lection to occur either for or against particular individuals while they are captive (see, for example, the requirements for domestication selection presented by Doyle (1983)). However, it may be possible for modified selection to continue to affect the hatchery fish after they are released. In order for this to occur, the hatchery fish would have to continue to experience different selection pressures after release than those experienced by the wild fish. One way this might occur is if the hatchery and wild fish express significantly different phenotypes while they are in the same natural environment and experience different survivals under the same conditions.

It is a common practice in steelhead (*Oncorhynchus mykiss*) hatchery programs to accelerate growth rates and smoltification to produce large, yearling smolts (see examples of release criteria in ODFW and USFWS (1996)). Managers adopt this practice in an effort to optimize postrelease survival of the hatchery fish (Wagner et al. 1963; Wagner 1967) while reducing or eliminating residual hatchery fish (Jonasson et al. 1995; Bigelow 1995). It is generally recognized that this protocol could make hatchery steelhead juveniles larger and younger than wild fish (Berejikian et al. 1996). Many chinook (*Oncorhynchus tshawytscha*) and coho salmon (*Oncorhynchus kisutch*) hatchery programs also increase growth rate and size at release to produce vigorous smolts and to improve smolt-to-adult survival (Mahnken et al. 1982; Dickhoff et al. 1995).

The implications of intentionally manipulating juvenile phenotypes in a hatchery program are particularly important when the program is implemented for the purpose of increasing the size of a wild population. The current management perspective is that hatchery fish in a conservation hatchery program of this kind should be as "similar" to wild fish as possible to lower both genetic and ecological risks to wild fish (Independent Multidisciplinary Science Team 2000; McMichael et al. 2000). "Similarity" is most often viewed in a genetic or phenotypic context. One idea associated with this perspective is that if hatchery and wild fish were phenotypically "similar", then selection in the natural environment might affect the two groups in a "similar" way, decreasing the opportunity for genetic divergence.

However, manipulation of juvenile phenotypes is used in steelhead hatchery programs in the northwestern United States even when the program goal is to produce hatchery fish for conservation purposes with characteristics that are "similar" to those of wild fish (Phillips et al. 2000). Many managers propose that the environmentally caused differences that result from the manipulations are not genetically important because they are not inherited (Swain et al. 1991). However, selection differentials respond to phenotypic distributions and influence fitness regardless of the source of phenotypic variation. After the hatchery fish are released, they are exposed to the same natural environment as wild fish. If the hatchery and wild fish have substantially different phenotypes when they are in the same environment, natural selection may affect them differently. These different selection regimes could lead to eventual genetic divergence between the groups.

A comparison of wild fish that have never been in captivity and hatchery fish from the same parent gene pool may reveal phenotypic and fitness differences that provide the

opportunity for modified selection pressures to occur. In this paper, I compare several juvenile phenotypes and fitness as indicated by survival of naturally produced steelhead and hatchery steelhead from a newly founded conservation hatchery program. The evaluation site was the Hood River, a tributary of the lower Columbia River at river kilometre (rkm) 270 in Oregon, U.S.A., which has indigenous winter and summer steelhead populations. Juvenile out-migrants were evaluated over 5 years, from 1994 through 1998. During the evaluation period, two hatchery stocks were released into the Hood River. The "new" hatchery stock was founded starting in 1991 from wild winter steelhead adults captured at Powerdale Dam at rkm 6.4 on the mainstem Hood River. This hatchery program was implemented for the purpose of rapidly increasing the size of the wild winter steelhead population. The "old" hatchery program was implemented to provide a sports fishery in the Hood River and used a nonlocal summer steelhead hatchery stock that was founded in the 1950s.

One may expect significant phenotypic and fitness differences between the old hatchery stock and the native Hood River steelhead populations. The primary question for this paper was how hatchery juveniles from the new hatchery stock compared with naturally produced juveniles that had never been in captivity but came from the same parent gene pool as the hatchery fish. Fish from the new hatchery stock were also compared with fish from the old hatchery stock.

## Materials and methods

### Study populations

All adult steelhead have been captured and sorted at a trap at Powerdale Dam since 1992. The adult trap captured 100% of the adult steelhead destined to spawn in the Hood River and was located below 100% of the natural production area in the basin. The population sizes and composition of the naturally spawning parent populations that produced the out-migrants in 1994 through 1998 were therefore known. Broodstock for the new hatchery program was collected at the same trap, whereas the old hatchery stock smolts were imported from a different basin.

The new hatchery stock, Hood River Winter Stock, was founded starting in 1991 from wild Hood River winter steelhead. Wild adults were distinguished from any hatchery fish that entered the trap by a lack of fin clips or other marks. Each year of this study, 10–25% of the wild population was taken for the broodstock, sampled throughout the wild run time distribution. The juvenile out-migrants in this study were produced by the 1993 through 1997 brood years. The broodstocks ranged in size from 43 to 82 fish and included from 0% to 48% hatchery fish. The hatchery fish that were used in the broodstock were adult returns from the first years' releases of the same stock. The hatchery protocols used to rear, acclimate, and release the new hatchery stock were those designed for the regular hatchery program, described in Olsen and French (2000) and O'Toole (1991), since the intent was to evaluate the products of the program as it was intended for normal implementation. The hatchery smolts were released directly into the East Fork of the Hood River in 1994 and 1995 but were acclimated for several weeks before release in 1996 through 1998 in a pond that

was supplied with some “enriched environmental features” (Flagg and Nash 1999). One hundred percent of the new hatchery stock juveniles were marked with fin and mandible clips.

The old hatchery stock, South Santiam Hatchery Skamania Summer Stock, originated from several tributaries in southwest Washington in the late 1950s (Reisenbichler et al. 1992). The broodstock was transferred to South Santiam Hatchery in Oregon in the 1970s and was released annually into several Oregon rivers, including Hood River, to provide a sports fishery. The total broodstock size during the 1990s was quite large, but only a small part of the production was released into the Hood. The number of parents that produced fish for the Hood ranged from 54 to 92 fish and was composed of 100% hatchery fish. Juveniles from the old hatchery stock were reared outside the Hood Basin then released as smolts directly into the West Fork of the Hood River. One hundred percent of the old hatchery stock juveniles were marked with fin clips.

The two wild steelhead populations in the Hood River were distinguished by adult run time and geographic spawning distribution. The winter steelhead population passed Powerdale Dam between January and June and immediately spawned in the East and Middle forks of the Hood River. The summer steelhead population passed Powerdale Dam between April and October and spawned the following spring in the West Fork of the Hood River, above a partial passage barrier that blocked winter steelhead. Resident rainbow trout were sympatric with the summer steelhead population (Kostow 1995).

Naturally produced juveniles ranged in age from 0 to 4 years so the 1994 through 1998 out-migrants were attributed to past parent-years proportional to their age distributions. The naturally spawning winter steelhead parent population ranged in size from 166 to 491 fish. No winter steelhead hatchery fish were intentionally passed above the dam in brood years 1992 through 1995. However, because of the presence of older smolts that had been produced from earlier brood years and the accidental release of a few adult hatchery fish above the dam, it was determined that 2–3% of the parents of the 1994 through 1996 out-migrants had been hatchery fish from other hatchery stocks outside the Hood Basin. Some hatchery adults from the new winter steelhead hatchery stock were intentionally passed above the dam starting in 1996. The 1997 and 1998 naturally produced out-migrants had 43% and 51% hatchery parents, respectively. Hatchery summer steelhead adults from the South Santiam/Skamania stock were passed above the dam during the study and potentially mingled with the wild summer steelhead in the West Fork. The naturally spawning summer steelhead parent population ranged in size from 652 to 2211 fish but included a much larger hatchery component, 78–88% hatchery fish.

### Juvenile phenotype data

Juvenile phenotypes of old hatchery stock juveniles, new hatchery stock juveniles, and naturally produced juveniles were measured during 5 years of juvenile out-migration from 1994 through 1998. The new hatchery stock juveniles were measured for length and weight before release as yearling smolts. Releases occurred between 1 April and 15 May

each year. The old hatchery stock juveniles were released as yearling smolts in April. A subsample of juveniles from both hatchery stocks were recaptured along with naturally produced juveniles in four rotary-screw (smolt) traps located in the West Fork at rkm 6.4, in the Middle Fork at rkm 2.1, in the East Fork at rkm 1.6, and in the lower mainstem Hood River at rkm 7.2. The traps were operated from about the first of April to about the end of October each year and were checked on most days. Further details about the field sampling protocols are described in Olsen (2003).

The origin of the juveniles captured in the smolt traps was identified as new hatchery stock, old hatchery stock, or naturally produced fish based on the fin and mandible marks or lack of marks. Phenotype data for the naturally produced winter and summer steelhead were combined, as individuals from these life histories could not be differentiated in the mainstem trap. The fish were measured for length (millimetres), weight (grams), date of capture, and age at capture determined from a juvenile scale sample. Juveniles passing the mainstem smolt trap were moving below all-natural rearing habitats in the basin and were believed to be leaving the Hood River, whereas those captured in the tributary smolt traps may have been moving within the basin. Therefore, the date of capture and the age at capture in the mainstem trap were considered to be the date of and age at out-migration from the Hood Basin. Out-migration from the Hood did not necessarily mean that the fish were smolting and moving into the ocean. Further phenotypic data were collected when the out-migrants returned as adults to the Powerdale trap in 1995 through 2002. Freshwater age, also considered to be the age at smolting, was determined by a saltwater entry mark on the adult scales (Borgerson 1992). Saltwater age and total age at spawning were also determined from the adult scales.

The dates of capture at the mainstem trap (dates of out-migration) and age data from adult scales were combined for all years within origin group: naturally produced, new hatchery stock, and old hatchery stock. However, the mean values and the distributions of the length and weight traits differed within the three origin groups depending on when and where they were measured; therefore, the data were distributed among several treatments. For naturally produced juveniles, two treatment groups were identified: captured in the tributaries (all three traps) and captured in the mainstem trap with data for all years combined. For the old hatchery stock, there were also two treatment groups: captured in the tributary trap (West Fork) and captured in the mainstem trap with data for all years combined. For the new hatchery stock, five treatment groups were analyzed to take into consideration the changes in release strategy part way through the study. For the two years of direct releases (1994–1995), there were two treatments: at release and captured in the mainstem trap. For the three years of acclimated releases (1996–1998), there were three treatments: at release, captured in the tributary trap (East Fork), and captured in the mainstem trap.

Over the 5 years, nearly 3000 juvenile fish were measured in the tributary traps, whereas over 5250 were measured in the mainstem trap. Most of the phenotype sample sizes were therefore large and most of the data sets were approximately normally distributed. Exceptional data sets included the date of out-migration for naturally produced juveniles and the

length and weight measurements for naturally produced juveniles in the tributaries, all of which had bimodal distributions. The length and weight data were analyzed among all treatment groups using pairwise *F* tests to compare phenotypic variances and pairwise *t* tests assuming either equal or unequal variances depending on the results of the *F* tests to compare mean phenotype values. Dates of out-migration were also compared by applying pairwise *t* tests and *F* tests to the dates of capture at the mainstem trap. Freshwater age (interpreted as age at smolting) and saltwater age were compared using *t* tests.

Further information about the behavior of the naturally produced fish was qualitatively described from the trapping data. Comparisons of age at capture and dates of capture in the mainstem and tributary smolt traps and comparisons of age at capture in the smolt traps and age at smolting determined from adult scales revealed life history complexity among the naturally produced fish that was not present among any hatchery treatments. Graphics were developed to demonstrate and compare the distribution of phenotypic variation for some of the more complex traits and the behavior patterns were described. The only comparison that could be made was that the life history complexity was present in the naturally produced fish but absent in the hatchery fish.

### Survival data

The following measures of survival were made as fitness indicators: egg-to-smolt survival, smolt-to-adult survival, egg-to-adult survival, parent per capita production of smolt offspring, and parent per capita production of adult offspring. Survival data were measured for each of the 5 out-migrant years from 1994 through 1998 for naturally produced winter steelhead, naturally produced summer steelhead, the new hatchery stock and the old hatchery stock.

For the two hatchery stocks, the survival data were computed from hatchery monitoring records, smolt release data, and adult return data. The parent populations were the broodstocks in brood years 1993 through 1997 that produced the smolts that were released into the Hood Basin. Egg production was determined from the number of females spawned and the average fecundities of the females. Egg-to-smolt survivals occurred during captivity for the hatchery stocks and were tracked while the fish were in the hatcheries from green eggs to smolt release. Only natural mortalities were considered; losses resulting from intentional culling were not counted. Smolt-to-adult survivals were determined for each out-migrant year from the number of smolts released into the Hood River and the number of adults returning for their first spawning measured at the mouth of the Hood River. Fish from the 1994 through 1998 release years returned for their first spawning from 1995 through 2002. The number of adults at the mouth of the Hood River was determined by the Powerdale Dam counts, where the adults were also aged and assigned to their out-migration year, and the annual harvest rate in the basin below the dam.

The number of naturally spawning parents that produced each out-migrant year was estimated from the juvenile age distribution and counts of adults past Powerdale Dam, corrected for a prespawning mortality of 5% for winter steelhead and 10% for summer steelhead. Naturally spawning

wild and hatchery fish were treated equally. Natural egg production was calculated from the number of females passed and an average fecundity of 3500 eggs per female. The egg-to-smolt and smolt-to-adult survivals of naturally produced winter and summer steelhead depended on an estimate of wild smolt production from the Hood River. An estimate of total smolt production from the basin was made from sampling of unmarked juveniles at the mainstem trap. The total production estimate was distributed among summer and winter steelhead using the data from the West Fork trap (summer steelhead) and the traps in the East and Middle forks (winter steelhead). Since it was evident from the size and age data that some of the out-migrants may not have been smolts, only fish larger than 165 mm were used to make the smolt production estimates. Trap efficiencies were regularly monitored and adjusted seasonally to account for variations in flows. A pooled Petersen mark-recapture estimate with Chapman's modification (Ricker 1975) was used to make the juvenile abundance estimates. Further details about the methods used to calculate the number of naturally produced winter and summer smolts are provided in Olsen (2003). The number of adult offspring was determined using the same method that was used for hatchery fish. Fish from the 1994 through 1998 out-migrants returned for their first year of spawning in 1995 through 2002. Age and lower Hood River sports harvest were again taken into consideration to calculate the adult returns to the river mouth for each out-migrant year.

The survival statistics, egg-to-smolt survival, smolt-to-adult survival, egg-to-adult survival, parent per capita production of smolt offspring, and parent per capita production of adult offspring, were computed for each of the out-migrant years for naturally produced winter steelhead, naturally produced summer steelhead, the new hatchery stock, and the old hatchery stock. The results averaged over the 5 years for each group were then compared using pairwise *t* tests. Within the new hatchery stock group, the two direct-release years (1994–1995) and the three acclimated-release years (1996–1998) were also broken out for comparison to take into consideration the change in release strategy that occurred during the study.

## Results

### Length and weight of juveniles

Naturally produced juveniles were significantly smaller ( $P < 0.001$ ) than all treatments of both the new and the old hatchery fish stocks measured both as length and as weight (Table 1). They were also more variable in length than hatchery fish, while they showed similar amounts of variation in weight, although in different distributions. Both the length and weight trait distributions of naturally produced fish measured in the tributaries were strongly bimodal (Fig. 1) and the fish were significantly smaller ( $P < 0.001$ ) than when measured in the mainstem trap.

The fish from the new hatchery stock differed in size depending on when and where the fish were measured. The new hatchery stock fish that were directly released were significantly bigger, both in length and weight and both at release and at recapture, than those that were acclimated ( $P <$

**Table 1.** Comparison of juvenile lengths and weights.

Group	<i>N</i> (lengths)	Average length (SD) (mm)	<i>N</i> (weights)	Average weight (SD) (g)
Natural (tributary)	2289	119.3 (48.5)	1690	28.4 (26.3)
Natural (mainstem)	919	171.3 (29.0)	722	53.6 (23.0)
New hatchery stock (direct release)	915	192.3 (22.8)	915	81.7 (27.9)
New hatchery stock (direct, mainstem)	391	208.0a (15.1)	382	89.3b (22.0e)
New hatchery stock (acclimated release)	1007	185.7 (24.6)	1007	75.2 (28.4)
New hatchery stock (acclimated, tributary)	413	196.6 (16.4c)	383	78.9 (19.9d)
New hatchery stock (acclimated, mainstem)	2535	199.4 (16.6c)	2437	78.0 (20.0d)
Old hatchery stock (tributary)	211	208.5a (21.1)	205	87.0b (26.5)
Old hatchery stock (mainstem)	1371	208.1a (18.0)	1345	88.1b (22.4e)

**Note:** The lengths of the old hatchery stock measured in the tributaries and in the mainstem were not significantly different from each other or from those of the new hatchery stock at the mainstem trap when the smolts were direct released (indicated by "a"). All other pairwise mean lengths analyzed with *t* tests were significant at  $P < 0.001$ . The mean weights of the two old hatchery stock samples and the direct-release new hatchery stock sample at the mainstem trap (indicated by "b") were not significantly different from each other. All other pairwise mean weights analyzed with *t* tests were significant at  $P < 0.001$ . Variances for two of the new hatchery stock lengths and weights (indicated by "c" and "d", respectively) and for the direct-release new hatchery stock and old hatchery stock at the mainstem trap (indicated by "e") were not significantly different. All other pairwise variances analyzed with *F* tests were significantly different at  $P < 0.001$ .

0.001). Within both the direct-release and the acclimated groups of the new hatchery stock, the fish became significantly longer and heavier as they progressed from release to recapture in the mainstem trap ( $P < 0.001$ ). The change in size was partially due to a loss of the smallest hatchery fish between release and recapture, although other changes in the distribution also occurred (Fig. 2a).

The old hatchery stock juveniles were significantly larger ( $P < 0.001$ ) than four of the treatments of the new hatchery stock juveniles measured by both length and weight, but the two stocks were not significantly different in either measurement at the mainstem trap when the new hatchery stock fish were directly released. The average size of old hatchery stock juveniles was uniform from release to out-migration in that neither length nor weight varied by sampling site. Even though the acclimated fish from the new hatchery stock were significantly smaller than fish from the old hatchery stock, they had a size distribution at the mainstem trap that was more similar to that of the old hatchery stock than to that of the naturally produced fish (Fig. 2b).

#### Age at smolting and age at first spawning

Fish from both hatchery stocks were significantly younger when they smolted, as determined by the age at which they entered salt water, than the naturally produced fish ( $P < 0.001$ ). The hatchery fish were also nearly uniform in age, whereas the naturally produced fish were highly variable (Table 2). The younger and lesser variation in freshwater age of the hatchery fish corresponded to younger and lesser variation in total adult age at first spawning. Another consequence of a younger total age was that the average generation time of the hatchery fish was shortened by 1 year, from 4 years for the naturally produced fish to 3 years for both hatchery stocks. The new and old hatchery stocks had nearly identical age distributions. Both stocks were intended to be yearling smolts and this objective was achieved in over 99% of the fish based on ages from adult scales. Both hatchery

stocks showed similar characteristics and diversity in saltwater age and were similar to wild fish in this trait.

#### Time of out-migration

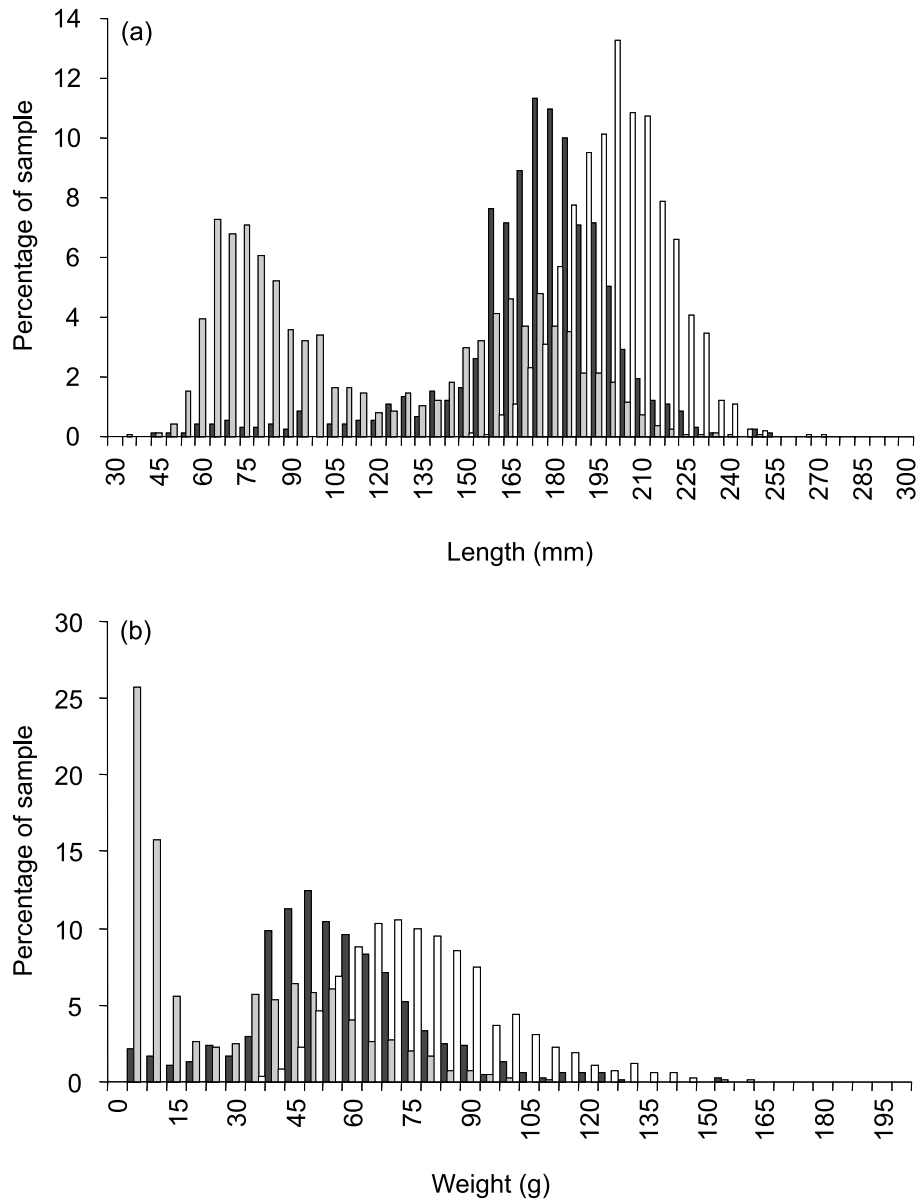
Time of out-migration was measured as the date at which fish were captured in the mainstem trap. This was a difficult trait to measure in this study with a complete lack of bias because two protocols affected sampling, which affected the character of the trait. First, hatchery fish could not out-migrate before they were released. Second, the Hood could not be sampled for out-migrating juveniles all year because the river experiences high flashy flows in the winter and smolt traps cannot safely operate.

Juveniles from both hatchery stocks out-migrated significantly earlier than naturally produced juveniles based on mean date of out-migration ( $P < 0.001$ ). However, the primary difference between the groups was that the out-migration time distribution for natural fish was highly variable, whereas the out-migration time for hatchery fish was very narrow (variance for wild fish ( $\sigma_W$ ) = 3377 and variance for hatchery stock ( $\sigma_H$ ) = 317,  $P < 0.001$ , also compared in Fig. 3). A large number of naturally produced fish out-migrated during the spring and the new hatchery stock matched this peak time reasonably well. But less than 1% of either hatchery stock was captured in any smolt trap after the end of June. In contrast, naturally produced fish were captured throughout the season. Their lowest period of movement was during midsummer when river flows were at the lowest levels, and then out-migration increased again in September. Substantial numbers of fish continued to out-migrate through October and it is possible that some continued to out-migrate through the winter after sampling stopped.

#### Life history complexity

The size, age, and movement data also revealed information about natural juvenile behavior and life history patterns in the Hood Basin that were absent among the hatchery fish. Among the naturally produced fish, small age-0 and age-1

**Fig. 1.** (a) Length distributions of naturally produced fish measured in the tributaries (shaded bars) and in the mainstem trap (solid bars) compared with the acclimated new hatchery stock fish measured in the mainstem trap (open bars). (b) Weight distributions of naturally produced fish measured in the tributaries (shaded bars) and in the mainstem trap (solid bars) compared with the acclimated new hatchery stock fish measured in the mainstem trap (open bars).

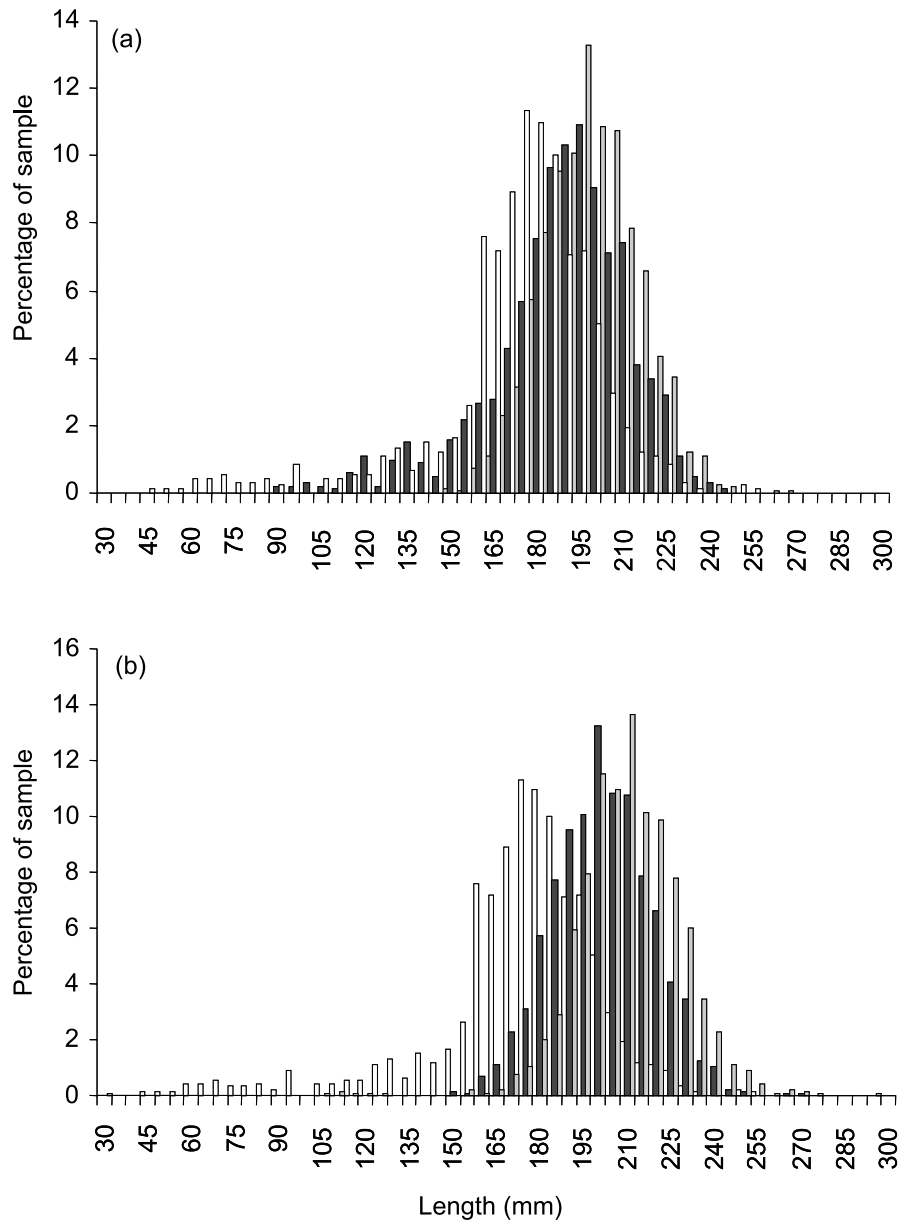


fish were more common in the tributary traps (Fig. 4). These results indicate that young presmolting fish were moving for several years among different rearing environments within the Hood Basin as they grew. Very young fish were also seen migrating past the mainstem trap, indicating that some of them were leaving the Hood Basin. However, age-0 smolts were absent, whereas age-1 smolts were rare among naturally produced fish based on the age at saltwater entry mark identified on adult scales. This result indicates that about 25% of the naturally produced fish out-migrated from the Hood Basin as presmolts. The nonsmolting juveniles that were leaving the Hood Basin may have died or they may have reared for another year or two in the Columbia before smolting. Larger, age-2 and age-3 juveniles, probably smolts, dominated the mainstem trap in the spring. However,

all ages of naturally produced fish, with highly variable sizes and both smolts and presmolts, were moving within the Hood Basin and out of the Hood Basin at all times that sampling occurred (Fig. 5).

These behavior patterns were absent among the hatchery fish (Figs. 4 and 5). They entered the mainstem trap from a few days to a few weeks after release and were large and relatively uniform sized. They were released at age 1 and less than 1% of them were older than age 1 when they entered salt water, as indicated by the entry mark on the adult scales (Fig. 4). Hatchery fish were not found lingering in the Hood Basin either. They were released between the first of April and the middle of May and over 99% of them were gone from the Hood Basin by the end of June based on sampling that continued through October (Fig. 5). Residual hatchery

**Fig. 2.** (a) Comparison of the length distributions of the acclimated new hatchery stock just before release (solid bars) and when captured at the mainstem trap (shaded bars). The distribution measured in the tributary trap was intermediate. The distribution of the naturally produced fish at the mainstem trap is also shown (open bars). (b) Comparison of the length distribution of the acclimated new hatchery stock (solid bars), the old hatchery stock (shaded bars), and the naturally produced fish (open bars), all measured in the mainstem trap.



steelhead, which never out-migrate and have been seen near release sites in other Columbia tributaries (e.g., Jonasson et al. 1995; McMichael et al. 2000), have not been observed in the Hood Basin after June, although their presence cannot be completely ruled out.

### Survival

The annual survivals and the data from which they were calculated are presented for naturally produced winter and summer steelhead and for the new and old hatchery stocks (Table 3). Averages, standard deviations, and information about statistical significance for each measurement are also presented (Table 4).

Both the new and the old hatchery fish had high egg-to-smolt survivals while they were in captivity compared with

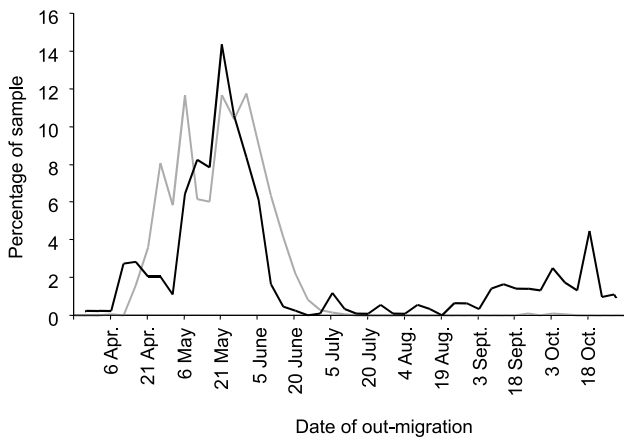
wild fish rearing in the natural environment (Tables 3 and 4). Both hatchery stocks had average egg-to-smolt survivals over 60% compared with less than 2% for the naturally produced winter steelhead and less than 1% for the naturally produced summer steelhead (differences between natural and hatchery fish significant at  $P < 0.001$ ). Both hatchery stocks therefore produced significantly more smolt offspring per parent ( $P < 0.001$ ) than did the naturally spawning parents (Table 4).

The survival superiority was reversed between the natural and hatchery groups for smolt-to-adult survivals, which occurred while all of the fish were in the same environment. Naturally produced smolts had average smolt-to-adult survivals of 5–6%, whereas both hatchery stocks had average survivals over the 5 years of about 1% (differences between

**Table 2.** Comparisons of freshwater and saltwater ages for naturally produced steelhead, the new hatchery stock, and the old hatchery stock.

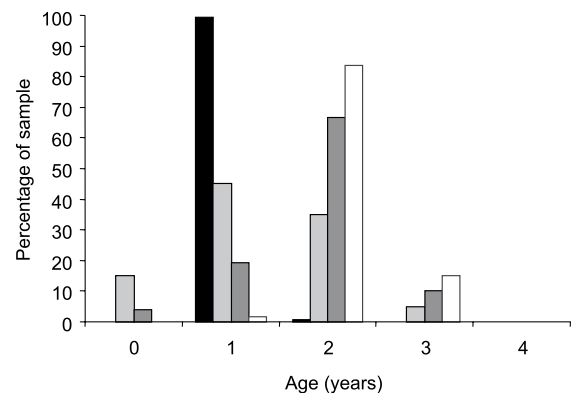
Freshwater age (years)	Saltwater age (years)	Natural winter steelhead (%)	Natural summer steelhead (%)	New winter hatchery (%)	Old summer hatchery (%)
1	1	—	0.8	1.5	2.9
	2	0.9	0.1	76.7	83.5
	3	0.8	—	19.8	12.6
	4	—	—	—	0.1
	Repeat	0.1	—	1.2	0.8
2	1	4.9	5.9	—	—
	2	59.5	57.4	0.6	0.1
	3	16.5	12.4	0.1	0.01
	4	—	0.2	—	—
	Repeat	5.2	2.9	—	—
3	1	0.5	1.3	—	—
	2	8.9	16.5	—	—
	3	2.4	1.4	—	—
	Repeat	0.1	0.9	—	—
4	2	0.1	0.1	—	—

**Note:** All measurements are from scales collected from returning adult fish at Powerdale Dam.

**Fig. 3.** Time of out-migration, measured as date of capture in the mainstem smolt trap averaged over all years of the study, comparing naturally produced fish (solid line) and the new hatchery stock (gray line).

natural and hatchery fish significant at  $P < 0.001$ ; Table 4). However, the survival superiority given the hatchery fish while they were captive continued through to return adults, as they had higher overall egg-to-adult survivals and produced many more adult offspring per parent than the naturally produced fish (both significant at  $P < 0.001$ ; Table 4).

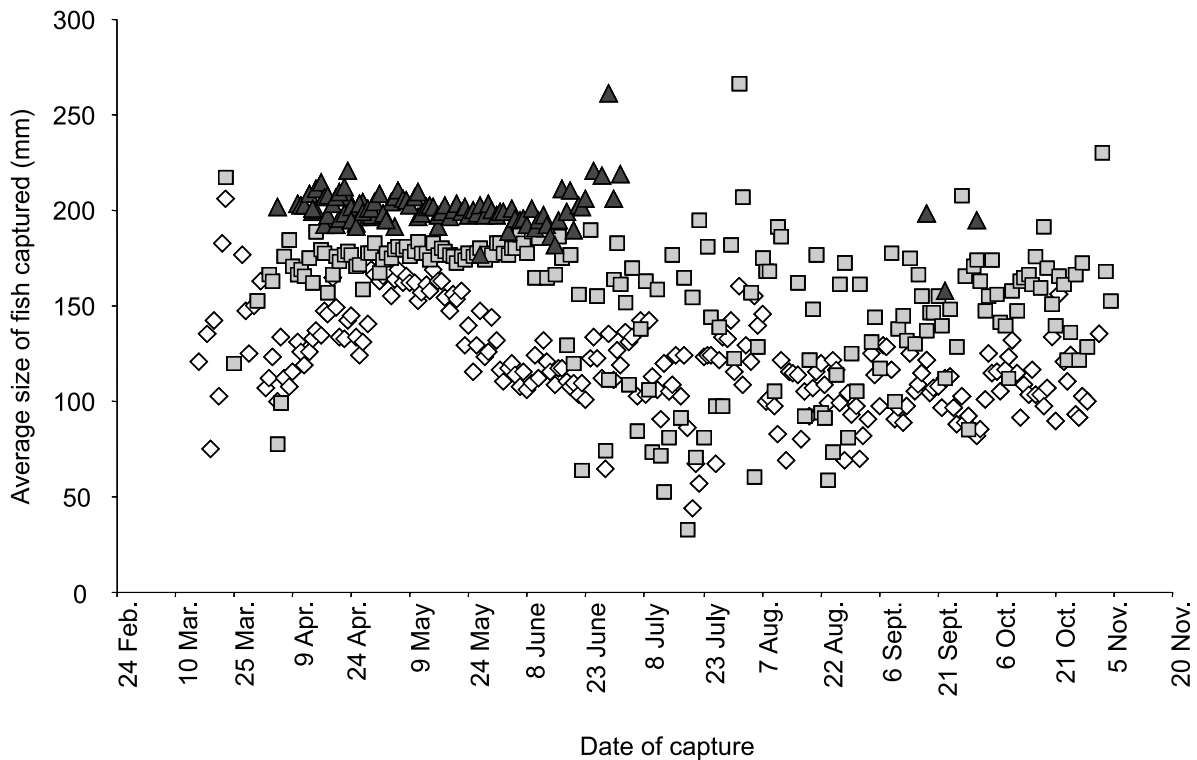
The naturally produced winter steelhead had significantly higher egg-to-smolt survivals, smolt offspring produced per parent, egg-to-adult survivals, and adult offspring produced per parent than the naturally produced summer steelhead (all significant at  $P < 0.01$  or greater; Table 4). For example, egg-to-smolt survivals were 10 times higher among the winter steelhead than among the summer steelhead. This difference in survivals was probably related to a difference in the proportion of hatchery parents and the origin of hatchery parents between the two naturally spawning populations. The winter steelhead population included 2–51% hatchery fish, primarily first-generation returns from the local

**Fig. 4.** Ages of juveniles comparing the data for the new hatchery stock measured from adult scales (solid bars) and the naturally produced fish measured in three different samples: tributary smolt traps (light shaded bars), mainstem smolt trap (dark shaded bars), and as adults (open bars). All three naturally produced samples included fish that were age 4 but at less than 1%.

broodstock included among the natural spawners in the last 2 years of the study, whereas the summer steelhead population included 78–88% hatchery fish each year of the study, all from the old hatchery stock (Table 3). The two natural populations had similar smolt-to-adult survivals (differences not significant; Table 4).

The new hatchery stock over the 5 years of the study had significantly fewer smolt and adult offspring per parent and lower smolt-to-adult survivals than the old hatchery stock (significant at  $P < 0.05$  or greater; Table 4). For example, over the 5 years, the new hatchery stock produced 35% fewer smolts and 60% fewer adult offspring per parent compared with the old hatchery stock. Comparisons of the direct-released new hatchery stock, the acclimated-released new hatchery stock, and the old hatchery stock demonstrated that the acclimated new hatchery stock had significantly lower smolt-to-adult, egg-to-adult, and adult offspring per parent than either of the other hatchery treatments ( $P < 0.05$

**Fig. 5.** Average length per day by date of out-migration for naturally produced fish in the tributaries (open diamonds) and in the mainstem (shaded squares) and for hatchery fish at the same locations (solid triangles) (both samples combined). Data are averaged over all years of the study. The hatchery fish were over 99% age-1 smolts. The naturally produced juvenile out-migrants ranged from age 0 to age 4 and included both smolts and nonsmolting migrants based on the differences between age at out-migration measured from juvenile scales and age at smolting measured from adult scales.



or greater; Table 4). For example, the average smolt-to-adult survival for the acclimated fish was only about half of what was observed for the direct-released fish and for the old hatchery stock. The direct-released fish and old hatchery stock had similar smolt-to-adult survivals.

## Discussion

The new hatchery stock juveniles differed significantly from the naturally produced juveniles in every phenotypic trait that was measured in this study, except saltwater age. The out-migrating new hatchery stock juveniles were larger and less variable in size, younger, and less variable in freshwater and total age, all smolts, whereas the out-migrating wild fish were either smolts or presmolts, out-migrated over a narrow spring window, whereas some wild fish out-migrated throughout the sampling season, and lacked the life history complexity that naturally produced juveniles expressed. The fish from the new hatchery stock more closely resembled the fish from the old hatchery stock, particularly by the time they reached the mainstem trap. The phenotypic differences were probably environmentally caused, since both the hatchery and naturally produced fish were from the same parent gene pool. However, large phenotypic responses by fish from the same parent gene pool to the differences between the captive and natural environments are consistent with the process of domestication (Kohane and Parsons 1989). After the hatchery fish were released, the phenotypic differences provided an opportunity for different responses

to selection by the two groups while they were in the same natural environment.

Some of the naturally produced juveniles may have had hatchery parents. Substantial numbers of the old hatchery stock summer steelhead were passed into natural spawning grounds each year and some first-generation winter steelhead adults from the new hatchery stock contributed to the 1997 and 1998 out-migrant years. It was not possible to determine whether the phenotypes of the offspring of naturally spawning hatchery fish differed from those of the offspring of wild fish, since the juveniles caught in the traps could not be assigned to either hatchery or wild parents. It is likely, however, that there were very few offspring of the naturally spawning old hatchery stock in the traps. Although the naturally spawning summer steelhead had very large proportions of old hatchery stock fish among them, their egg-to-smolt survivals were extremely low, only about 10% of what was observed for the naturally spawning winter steelhead. This result indicates reproductive failure by the old hatchery summer steelhead stock, which either did not deposit the eggs that were expected or did not produce juveniles that survived to be captured in the smolt traps. Once summer steelhead smolts reached the mainstem trap, their smolt-to-adult survival was not significantly different from that of the winter steelhead smolts, and the number of wild adult summer steelhead returning annually to the river was fairly constant since the early 1990s. Evidence of reproductive failure by the old hatchery stock in the Hood River is consistent with earlier studies of this same hatchery stock, which demon-

**Table 3.** Five years of survival data for naturally spawning winter and summer steelhead, the new hatchery stock, and the old hatchery stock in the Hood River.

Parent group	Smolt out-migration year	Number of parents	Hatchery fish among parents (%)	Number of eggs	Number of smolts	Egg-to-smolt survival (%)	Smolt offspring per parent	Number of adult offspring to river mouth	Smolt-to-adult survival (%)	Egg-to-adult survival (%)	Adult offspring per parent to river mouth
Naturally spawning winter steelhead	1994	355	3	751 450	5036	0.67	14.2	282	5.60	0.038	0.79
	1995	306	2	711 550	4672	0.66	15.3	263	5.63	0.037	0.86
	1996	166	3	279 300	7662	2.74	46.2	355	4.63	0.127	2.14
	1997	372	43	665 000	22 550	3.39	60.6	1212	5.37	0.182	3.26
	1998	491	51	1 000 800	14 024	1.40	28.6	1274	9.08	0.127	2.59
Naturally spawning summer steelhead	1994	2211	78	4 857 500	1347	0.03	0.6	156	11.60	0.003	0.07
	1995	1348	82	2 866 500	2883	0.10	2.1	144	4.99	0.004	0.11
	1996	1853	88	3 452 500	5661	0.16	3.1	112	1.98	0.003	0.06
	1997	652	80	1 238 000	3899	0.31	6.0	171	4.39	0.009	0.26
	1998	1493	88	2 936 000	8670	0.30	5.8	212	2.45	0.005	0.14
New winter steelhead hatchery stock	1994	75	0	62 200	38 034	61.20	507.1	354	0.93	0.569	4.72
	1995	43	2	95 000	42 898	45.14	997.6	579	1.35	0.610	13.48
	1996	82	28	63 800	50 904	79.80	620.8	381	0.75	0.598	4.65
	1997	68	46	85 500	59 837	70.01	880.0	323	0.54	0.378	4.75
	1998	58	48	102 500	62 136	60.64	1071.3	445	0.72	0.434	7.66
Old summer steelhead hatchery stock	1994	92	100	161 324	90 042	55.81	976.7	693	0.77	0.430	7.52
	1995	71	100	124 216	76 330	61.45	1075.4	1242	1.63	1.000	17.50
	1996	54	100	94 448	68 378	72.40	1267.0	622	0.91	0.658	11.52
	1997	54	100	94 624	60 993	64.46	1128.0	584	0.96	0.617	10.80
	1998	54	100	93 826	64 910	69.18	1210.7	588	0.91	0.627	10.97

**Note:** The naturally spawning fish were in the natural environment throughout their life cycle. The hatchery stocks were in a hatchery environment from eggs to smolts and then in the same natural environment as the naturally produced fish from smolts to adults. The proportions of previous-generation hatchery adults that were among the parents of each production year are also included. All data were corrected for age structure and harvest in the lower Hood River.

**Table 4.** Comparison of the average survivals for naturally spawning winter and summer steelhead, the new hatchery stock, and the old hatchery stock in the Hood River produced from the data in Table 3.

Group	Egg-to-smolt survival, average (SD) (%)	Smolt offspring leaving the river per parent, average (SD)	Smolt-to-adult survival, average (SD) (%)	Egg-to-adult survival, average (SD) (%)	Adult offspring to the river per parent, average (SD)
Naturally spawning winter steelhead	1.77 (1.24)	33.0 (20.1)	6.06a (1.74)	0.102 (0.063)	1.93 (1.08)
Naturally spawning summer steelhead	0.18 (0.12)	3.5 (2.3)	5.08a (3.86)	0.005 (0.003)	0.13 (0.08)
New winter steelhead hatchery (all years combined)	63.36b (12.83)	815.4 (243.8)	0.86 (0.31)	0.518d (0.105)	7.05 (3.81)
New winter steelhead hatchery (direct release)	53.17b (11.36)	752.4 (346.8)	1.14c (0.30)	0.590d (0.029)	9.10e (6.19)
New winter steelhead hatchery (acclimated release)	70.15b (7.82)	857.3 (226.1)	0.67 (0.11)	0.470 (0.114)	5.69 (1.71)
Old summer steelhead hatchery	64.66b (6.50)	1131.6 (113.7)	1.03c (0.34)	0.666d (0.207)	11.66e (3.62)

**Note:** All pairwise differences within each statistic are significantly different from each other at  $P < 0.05$  or greater except the following, which were not significant: natural winter versus natural summer smolt-to-adult (indicated by "a"); all new hatchery treatments versus old hatchery egg-to-smolt (indicated by "b"); new hatchery direct release versus old hatchery smolt-to-adult (indicated by "c"); new hatchery combined years and direct release versus old hatchery egg-to-adult (indicated by "d"); and new hatchery direct release versus old hatchery adult offspring per parent to the river (indicated by "e").

strated that it had low reproductive success in other basins (Chilcote et al. 1986; Leider et al. 1990; Kostow et al. 2003).

Differences in survival measurements for the naturally produced and new hatchery stock juveniles were also significant over all juvenile life stages, indicating that selection was different for the two groups. The naturally produced fish had relatively low egg-to-smolt survivals compared with the high survivals that the hatchery fish experienced while they were in captivity. This difference reflects a relaxation of natural selection on the hatchery fish while the fish were captive so that more fish reached smolting than would naturally do so (Lynch and O'Hely 2001). However, over the 5 years, the elevated egg-to-smolt survivals of the hatchery fish in captivity ranged from only 45% to 80%, which was lower than the 90–95% that is often reported for hatchery programs (ODFW and USFWS 1996). Survival also differed between the groups after the new hatchery fish were released into Hood River, with the advantage going to the naturally produced fish. Average smolt-to-adult survivals for the naturally produced winter and summer steelhead were five to six times higher than for the new hatchery stock.

Based on these two measures of survival, there were two opportunities for modified selection to affect the new hatchery stock. The first occurred while the hatchery fish were under artificial conditions, where selection was relaxed compared with the naturally produced fish but also 20–55% of the hatchery fish were lost each year. The second opportunity occurred after the fish were released when the new hatchery stock had very low smolt-to-adult survivals relative to the naturally produced fish while the two groups were in the same environment.

A third opportunity for modified selection is indicated by the change in length and weight of the new hatchery stock fish from their release to their recapture in the mainstem trap. The smolt traps readily captured very small, young wild fish throughout the sampling season, so it is unlikely that the small hatchery fish were simply not caught in the

traps. It is not known whether the smaller hatchery fish grew or died between sample sites. However, substantial growth between sample sites seems unlikely, since the time between release and recapture was only a few days to a few weeks. The old hatchery stock fish took a similar time to reach the mainstem trap but showed no evidence of growth. Further, over 99% of the hatchery fish that returned as adults had out-migrated and entered saltwater as yearling smolts rather than lingering somewhere to grow to an older age. On one hand, the loss of the small fish may be expected. Bigger body size in juvenile fish is generally thought to be advantageous when fish are placed in competition (Abbott and Dill 1989; McMichael et al. 1999). Most studies of steelhead hatchery fish performance have demonstrated that small hatchery steelhead, including any that do not smolt as yearlings, have very poor survival to adults (Wagner et al. 1963; Wagner 1967). Also, the size distributions of the new hatchery stock fish became progressively more similar to those of the old hatchery stock fish as they progressed from release to the mainstem trap. Finally, the treatment that produced the smallest hatchery fish was the acclimated releases of the new hatchery stock and it had the lowest smolt-to-adult survivals observed in this study. The earlier studies, along with the results presented here, suggest that the smaller hatchery fish had a survival disadvantage.

However, although the smallest hatchery fish were not observed after release, the naturally produced out-migrating juveniles were even smaller, yet they were readily captured in the traps throughout the monitoring season and had far higher survival to adults than either hatchery stock. Size of hatchery steelhead may be less important as a direct indication of survival potential than it is an easy to measure consequence of more complicated behaviors and physiological traits. Berejikian et al. (1996) proposed that larger size was a result of greater aggressiveness, which was advantageous in captivity but disadvantageous in the natural environment (also see Huntingford et al. 1990). Perhaps the smaller hatchery fish were lost soon after release because they were

poorer competitors during captivity and therefore were in relatively poor condition at release. Larger size, or more specifically rapid growth rate, is associated with the physiological changes that accompany smolting (Mahnken et al. 1982; Dickhoff et al. 1995). It is not natural for all Hood River steelhead to smolt as yearlings, so it was likely that some individuals responded poorly to the manipulations that accelerated smolting.

Modified selection pressures and demographic characteristics of a population may work together to contribute to genetic change in a captive population (Lynch and O'Hely 2001). The characteristics of a hatchery program may cause one mechanism or the other to be more important (Woodworth et al. 2002). Characteristics of the new hatchery stock in the Hood River may have increased the importance of small population effects. The census sizes of both the broodstock and the wild winter steelhead population were small during the 1990s. But also the modified age distribution of the hatchery fish decreased the length of their average generation by 1 year compared with the natural population, which should decrease their effective population size for comparable annual census sizes (Waples 1990). Other studies are currently underway in the Hood River to measure the effective sizes of these population components.

Comparisons of fish from the various hatchery treatments also revealed some differences between the two hatchery stocks and between the different release protocols. The new hatchery stock had very similar phenotypes and survivals when compared with the old hatchery stock, particularly when it was released directly into the Hood River without acclimation. The protocol of acclimating the new hatchery stock in a pond provided with some "enriched environmental features" (Flagg and Nash 1999) was associated with smaller juveniles and with juveniles that had smolt-to-adult survivals that were about half of those observed in the old hatchery stock and in the new hatchery stock when it was released directly. This result is contrary to some expectations (Maynard et al. 1995). The acclimated new hatchery stock juveniles were closer to the average size of the naturally produced fish when they were released, although they were still significantly much larger. However, the changes in their size distributions that occurred from release to recapture in the mainstem trap made them more closely resemble the old hatchery stock by the time they out-migrated, and their smolt-to-adult survivals also deviated further from those of the natural fish.

It appears that the most successful fish in the new hatchery stock generally resembled the old hatchery stock, following the homogenous life history strategy of being large yearling smolts that promptly entered the ocean during a narrow window after release. The complex strategies of wild steelhead juveniles to move from natal areas through a variety of rearing environments over 2 or 3 years with wide individual variation were indicated by our data and are also known to occur in other basins (e.g., Everest 1973) but were not present among the hatchery juveniles. It would be possible to artificially produce some of the variation, for example by releasing 2-year-old hatchery smolts, or smaller smolts, or a mix of smolts and presmolts. But as demonstrated by the apparent consequences for the smaller acclimated hatchery fish released in this study, hatchery fish may be made to

"look more like" wild fish without behaving like them or surviving like them.

Further, it is not desirable to remove all survival differences between the hatchery and wild fish. The survival advantage that occurs in the hatchery is necessary for a successful hatchery program regardless of potential consequences. In order for a hatchery program to have any value, it has to be able to produce more adult fish from the parents taken into captivity than would occur in the wild. This requires that egg-to-adult survivals and per capita offspring production be greater for hatchery fish than for wild fish. In spite of some shortcomings, the new hatchery stock evaluated in this study was successful by egg-to-adult survival and per capita offspring measures, as both measures were much higher for new hatchery stock fish compared with naturally produced fish.

In conclusion, this study demonstrated large average phenotype and survival differences between hatchery-produced and naturally produced fish from the same parent gene pool. These results indicate that a different selection regime was affecting each of the groups. The processes indicated by these results can be expected to lead to eventual genetic divergence between the new hatchery stock and its wild source population, thus limiting the usefulness of the stock for conservation purposes to only the first few generations.

## Acknowledgments

Funding for this project was provided by the Bonneville Power Administration. Huge thanks are due to Erik Olsen and his staff on the Hood River and to Mark Lewis.

## References

- Abbott, J.C., and Dill, L.M. 1989. The relative growth of dominant and subordinate juvenile steelhead trout (*Salmo gairdneri*) fed equal rations. *Behaviour*, **108**: 104–113.
- Berejikian, B. 1995. The effect of hatchery and wild ancestry and experience on the relative ability of steelhead trout fry (*Oncorhynchus mykiss*) to avoid a benthic predator. *Can. J. Fish. Aquat. Sci.* **52**: 2476–2482.
- Berejikian, B.A., Mathews, S.B., and Quinn, T.P. 1996. Effects of hatchery and wild ancestry and rearing environments on the development of agonistic behavior in steelhead trout (*Oncorhynchus mykiss*) fry. *Can. J. Fish. Aquat. Sci.* **53**: 2004–2014.
- Bigelow, P.A. 1995. Survival to Lower Granite Dam of wild and straying and non-straying Dworshak National Fish Hatchery steelhead. *In* Interactions of hatchery and wild steelhead in the Clearwater River of Idaho. *Edited by* U.S. Fish and Wildlife Service and Nez Perce Tribe. 1994 Progress Report. U.S. Fish and Wildlife Service, Ahsahka, Idaho.
- Borgerson, L.A. 1992. Scale analysis. U.S. Fish. Wildl. Serv. Prog. Rep. No. F-144-R-4. Oregon Department of Fish and Wildlife, Portland, Oreg.
- Chilcote, M.W., Leider, S.A., and Loch, J.J. 1986. Differential reproductive success of hatchery and wild summer-run steelhead under natural conditions. *Trans. Am. Fish. Soc.* **115**: 726–735.
- Dickhoff, W.W., Beckman, B.R., Larson, D.A., Mahnken, C., Schreck, C.B., Sharp, C., and Zaugg, W.S. 1995. Quality assessment of hatchery-reared spring chinook smolts in the Columbia River basin. *Am. Fish. Soc. Symp.* **15**: 292–302.
- Doyle, R.W. 1983. An approach to the quantitative analysis of domestication selection in aquaculture. *Aquaculture*, **33**: 167–185.

- Everest, F.H. 1973. Ecology and management of summer steelhead in the Rogue River. *Oreg. Game Comm. Fish. Res. Rep. No. 7*. Oregon Game Commission, Corvallis, Oreg.
- Flagg, T.A., and Nash, C.E. 1999. A conceptual framework for conservation hatchery strategies for Pacific salmonids. NOAA-NWFSC Tech. Memo. No. 38.
- Fleming, I.A., Jonsson, B., and Gross, M.R. 1994. Phenotypic divergence of sea-ranched, farmed and wild salmon. *Can. J. Fish. Aquat. Sci.* **51**: 2808–2824.
- Fleming, I.A., Jonsson, B., Gross, M.R., and Lamberg, A. 1996. An experimental study of the reproductive behaviour and success of farmed and wild Atlantic salmon (*Salmo salar*). *J. Appl. Ecol.* **33**: 893–905.
- Ford, M. 2002. Selection in captivity during supportive breeding may reduce fitness in the wild. *Conserv. Biol.* **16**: 815–925.
- Huntingford, F.A., Metcalfe, N.B., Thorpe, J.E., Graham, W.D., and Adams, C.E. 1990. Social dominance and body size in Atlantic salmon parr, *Salmo salar*. *J. Fish Biol.* **36**: 877–881.
- Independent Multidisciplinary Science Team. 2000. Conservation hatcheries and supplementation strategies for recovery of wild stocks of salmonids. *Oreg. Plan Tech. Rep. 2000-1*. Oreg. Watershed Enhancement Board, Salem, Oreg.
- Jonsson, J.I., Hojesjo, J., and Fleming, I.A. 2001. Behavioral and heart rate responses to predation risk in wild and domesticated Atlantic salmon. *Can. J. Fish. Aquat. Sci.* **58**: 788–794.
- Jonasson, B.C., Carmichael, R.W., and Whitesel, T.A. 1995. Residual hatchery steelhead: characteristics and potential interactions with spring chinook salmon in northeast Oregon. *U.S. Fish. Wildl. Serv.-LSCP Annu. Prog. Rep. No. 14-48-0001-93538*. Oregon Department of Fish and Wildlife, Portland, Oreg.
- Kallio-Nyberg, I., and Koljonen, M.L. 1997. The genetic consequence of hatchery-rearing on life-history traits of the Atlantic salmon (*Salmo salar* L.): a comparative analysis of sea-ranched salmon with wild and reared parents. *Aquaculture*, **153**: 207–224.
- Kohane, M.J., and Parsons, P.A. 1989. Domestication: evolutionary change under stress. *Evol. Biol.* **23**: 31–48.
- Kostow, K. 1995. Biennial report on the status of wild fish in Oregon. Oregon Department of Fish and Wildlife, Portland, Oreg.
- Kostow, K.E., Marshall, A.R., and Phelps, S.R. 2003. Natural spawning hatchery steelhead contribute to smolt production but experience low reproductive success. *Trans. Am. Fish. Soc.* **132**: 780–790.
- Leider, S.A., Hulett, P.L., Loch, J.J., and Chilcote, M.W. 1990. Electrophoretic comparison of the reproductive success of naturally spawning transplanted and wild steelhead trout through the returning adult stage. *Aquaculture*, **88**: 239–252.
- Lynch, M., and O’Hely, M. 2001. Captive breeding and the genetic fitness of natural populations. *Conserv. Genet.* **2**: 363–378.
- Mahnken, C., Prentice, E., Waknitz, W., Sims, M.G., and Williams, J. 1982. The application of recent smoltification research to public hatchery releases: an assessment of size/time requirements for Columbia River hatchery coho (*Oncorhynchus kisutch*). *Aquaculture*, **28**: 251–268.
- Maynard, D.J., Flagg, T.A., and Mahnken, C. 1995. A review of seminatural culture strategies for enhancing the post-release survival of anadromous salmonids. *Am. Fish. Soc. Symp.* **15**: 307–314.
- McMichael, G.A., Pearsons, T.N., and Leider, S.A. 1999. Behavioral interactions among hatchery-reared steelhead smolts and wild *Oncorhynchus mykiss* in natural streams. *N. Am. J. Fish. Manag.* **19**: 948–956.
- McMichael, G.A., Pearsons, T.N., and Leider, S.A. 2000. Minimizing ecological impacts of hatchery-reared juvenile steelhead trout on wild salmonids in a Yakima Basin watershed. *In Sustainable fisheries management: Pacific salmon. Edited by E.E. Knudsen, C.R. Steward, D.D. MacDonald, J.E. Williams, and D.W. Reiser*. Lewis Publishers, New York. pp. 365–380.
- Olsen, E.A. 2003. Hood River and Pelton Ladder evaluation studies. *BPA Annu. Proj. No. 1988-053-04*, Bonneville Power Administration, Portland, Oreg.
- Olsen, E.A., and French, R.A. 2000. Hood River and Pelton Ladder evaluation studies. *BPA Annu. Proj. No. 1988-053-04*, Bonneville Power Administration, Portland, Oreg.
- Oregon Department of Fish and Wildlife (ODFW) and U.S. Fish and Wildlife Service (USFWS). 1996. Integrated Hatchery Operations Team — operation plans for anadromous fish production facilities in the Columbia River Basin. Vol. II. Oregon. *BPA Proj. No. 92-043*, Bonneville Power Administration, Portland, Oreg.
- O’Toole, P. 1991. Hood River Production Master Plan. *BPA Proj. No. 88-053*, Bonneville Power Administration, Portland, Oreg.
- Phillips, J.L., Ory, J., and Talbot, A. 2000. Anadromous salmonid recovery in the Umatilla River Basin, Oregon: a case study. *J. Am. Water Res. Assoc.* **36**: 1287–1308.
- Reisenbichler, R.R., and McIntyre, J.D. 1977. Genetic differences in growth and survival of juvenile hatchery and wild steelhead trout, *Salmo gairdneri*. *J. Fish. Res. Board Can.* **34**: 123–128.
- Reisenbichler, R.R., and Rubin, S.P. 1999. Genetic changes from artificial propagation of Pacific salmon affect the productivity and viability of supplemented populations. *ICES J. Mar. Sci.* **56**: 459–466.
- Reisenbichler, R.R., McIntyre, J.D., Solazzi, M.F., and Landino, S.W. 1992. Genetic variation in steelhead of Oregon and northern California. *Trans. Am. Fish. Soc.* **121**: 158–169.
- Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. *Bull. Fish. Res. Board Can.* No. 191.
- Ryman, N., and Laikre, L. 1991. Effects of supportive breeding on the genetically effective population size. *Conserv. Biol.* **5**: 325–329.
- Ryman, N., Jorde, P.E., and Laikre, L. 1995. Supportive breeding and variance effective population size. *Conserv. Biol.* **9**: 1619–1628.
- Swain, D.P., Riddell, B.E., and Murray, C.B. 1991. Morphological differences between hatchery and wild populations of coho salmon (*Oncorhynchus kisutch*): environmental versus genetic origin. *Can. J. Fish. Aquat. Sci.* **48**: 1783–1791.
- Wagner, H.H. 1967. A summary of investigations of the use of hatchery-reared steelhead in the management of a sports fishery. *Oreg. Game Comm. Fish. Res. Rep. No. 5*. Oregon Game Commission, Corvallis, Oreg.
- Wagner, H.H., Wallace, R.L., and Campbell, H.J. 1963. The seaward migration and return of hatchery-reared steelhead trout *Salmo gairdneri* Richardson, in the Alsea River, Oregon. *Trans. Am. Fish. Soc.* **92**: 202–210.
- Waples, R. 1990. Conservation of Pacific salmon. II. Effective population size and the rate of loss of genetic variability. *J. Hered.* **81**: 267–276.
- Woodworth, L.M., Montgomery, M.E., Brisco, D.A., and Frankham, R. 2002. Rapid genetic deterioration in captive populations: causes and conservation implications. *Conserv. Genet.* **3**: 277–288.