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Comparative Performance of Genetically Similar Hatchery and Naturally Reared Juvenile Coho Salmon in Streams

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Abstract.—Hatchery-reared salmon have been reported to be inferior to wild fish in some studies and competitively superior in others. We examined the influence of early rearing environment (hatchery versus natural) on the summer survival, movement, and growth of genetically similar juvenile coho salmon *Oncorhynchus kisutch* in streams. In each of 2 years, 5,000–10,000 fry from a hatchery cohort were placed above barrier falls in each of two streams to rear naturally at low density. The rest were reared at high density in hatchery raceways. After 3 months (late spring), we electrofished the streams, marked the naturally reared salmon caught, and then added equal numbers of marked hatchery-reared salmon to the streams. The streams were electrofished again in the summer to monitor survival, movement, and growth. Hatchery-reared and naturally reared juveniles survived equally well (about 90% survived each summer), and few fish of either rearing type emigrated from the study streams. Hatchery fish were about 10% larger than naturally reared fish at the time of introduction, but there was no evidence for size-related survival in the streams. When adjusted for size, hatchery fish grew at faster rates than naturally reared fish. Our results suggest that hatchery-reared coho salmon perform similarly to naturally reared salmon when introduced into streams in low numbers and with a relatively small size advantage.

Wild salmon populations are declining in many areas of the world, and there is increasing pressure to develop management strategies to increase recruitment (Jonsson and Fleming 1993). There are mixed opinions in the scientific community about the efficacy of using hatchery fish to enhance (''supplement'') wild production (Lichatowich and McIntyre 1987; Meffe 1992; Cuenco et al. 1993). Many studies have concluded that hatchery fish perform poorly in streams (Miller 1954; Bachman 1984; Maynard et al. 1996). However, other studies indicate that hatchery-produced salmon outcompete and displace wild fish (Nickelson et al. 1986).

Nickelson et al. (1986) examined the effect of hatchery supplementation on the production of wild coho salmon *Oncorhynchus kisutch* in 15 Oregon coastal streams and concluded that hatchery fish displaced wild fish. Densities of wild coho salmon were 44% lower in streams stocked with hatchery-produced salmon than in unstocked streams; however, the relative frequencies of hatchery and wild fish displaced from the study streams were unknown. The streams were stocked at high densities and if levels exceeded carrying capacity, displacement of wild fish may have resulted primarily from large numbers of fish in the streams rather than from displacement by competitively superior hatchery fish (Berg and Jorgensen 1991).

The effect of a supplementation program on a wild population depends not only on the numbers of hatchery fish released but also on the relative performance of the hatchery and wild fish. Both genetics and early rearing experience influence the performance of hatchery fish after they are released in streams. For example, the survival and growth of hatchery fish depend on their size (Hume and Parkinson 1988) and behavior (White et al. 1995) when they are stocked and their genetic predisposition to survive and grow in a stream (Symons 1969). Likewise, the ability of hatchery fish to displace wild fish depends, in part, on relative size differences and competitive ability, both of which are genetically and environmentally controlled (Fenderson et al. 1968; Swain and Riddell 1990; Berejikian et al. 1996; Rhodes and Quinn 1998). Most of the literature seems to be consistent with the hypothesis that hatchery fish perform poorly relative to wild fish, but there are some exceptions. Symons (1969) found no differences in survival between hatchery and wild Atlantic salmon *Salmo salar*, and Mason et al. (1967) reported that hatchery brook trout *Salvelinus fontinalis* had higher survival rates than wild brook trout.

To predict how hatchery fish will perform relative

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to wild fish in streams, both the genetic and environmental components must be understood. Most studies comparing the survival and growth of hatchery and wild salmonids in the field have examined the genetic component by rearing genetically different populations under similar environmental conditions (Flick and Webster 1964; Mason et al. 1967; Reisenbichler and McIntyre 1977). However, rearing environment may influence performance independent of genetics and should be more thoroughly investigated (Olla et al. 1994).

In this study we simulated hatchery supplementation by releasing hatchery-reared coho salmon parr into two streams containing naturally rearing coho salmon. The two rearing groups were derived from the same group of parents so differences in survival, growth, and movement over the summer could be attributed to early rearing conditions, not genetics. Specifically, we tested the null hypotheses that the hatchery-reared and naturally reared salmon in the streams had equal rates of survival, growth, and patterns of movement.

Methods

Experiments were conducted in two streams in southeastern Washington (Silver and Forks Creeks) during two consecutive years (1996 and 1997). Riparian zones of both streams consisted of red alder *Alnus rubra*, and second growth Douglas fir *Pseudotsuga menziesii* and Sitka spruce *Picea sitchensis.* Average stream temperatures ranged from 7°C in the winter to 14°C in the summer (Rhodes, unpublished data). Streams were approximately 4 m wide in the summer with average depths of about 0.5 m. Water falls on each stream (4 m, Silver Creek; 16 m, Forks Creek) are impassable barriers to anadromous salmon. Both streams have resident populations of cutthroat trout *O. clarki* and riffle sculpin *Cottus gulosus* and torrent *C. rhotheus* sculpin.

Coho salmon that returned to the Forks Creek Hatchery were artificially spawned in October and November, and their eggs were incubated at the hatchery. Spawners were a mixture of wild and hatchery strains. In 1995, 192 females and 111 males were spawned, and 373 females and 373 males in 1996. At emergence in February, fry composing the naturally reared group were planted above each falls: 5,000 in 1996 and 10,000 in 1997. Densities in 1996 were approximately 1.7 fry/m^2 in Forks Creek and approximately 1 fry/m^2 in Silver Creek; densities in 1997 were double those in 1996. The remaining fry, which composed the hatchery-reared group, were placed into 1-m deep raceways (6×25 m) at a density of approximately 3,000 fry/m^2 and were hand-fed a commercial diet daily.

In late spring, study streams were electrofished thoroughly by blocking off consecutive reaches (about every 15 m) with nets and sampling each reach repeatedly until few fish were caught. Naturally reared coho salmon were anesthetized with tricaine methanesulfonate, measured for weight (g) and fork length (mm), marked, and then released where they were found. In 1996 the fish were marked with a left ventral fin clip, and in 1997 they were marked by injecting an inert paint into the dorsal, anal, or caudal fins; the first 340 fish were individually marked, the rest were marked red on the anal fin. Traps were placed at the downstream ends of each stream above the falls to collect fish emigrating from the study reaches. Three days after the naturally reared fish were collected, a presumably random sample of the fry that had reared in the hatchery raceways were placed into the streams to match the numbers of naturally reared salmon caught in each area of the streams. These hatchery-reared fish were first subjected to electrofishing in a shallow raceway to control for the experience of the naturally reared fish. Fish were anesthetized, marked (right ventral fin, 1996; paint injection, 1997, the first 340 being individually marked, the rest orange on the anal fin) and measured for weight and length. Study streams were electrofished again later in the summer (late July 1996; mid-July and late September 1997) to compare the survival, growth, and movement of the two groups.

Survival.—To test the null hypothesis that hatchery-reared and naturally reared coho salmon survived at equal rates, the ratio of marked hatchery to naturally reared coho salmon recovered was compared to 1:1 using the binomial test or the chi-square goodness-of-fit test (depending on the sample size; Zar 1996). It was assumed that both groups were equally vulnerable to electrofishing. Data were analyzed separately for each stream and year and by pooling across years and streams. The 1997 data were further partitioned by habitat type (isolated pools and the main stream). Because hatchery-reared fish were approximately 10% larger than wild fish at the time of planting, we tested for possible size-related survival differences by comparing initial mean length (late spring) of individually marked fish that were recovered later in the summer to initial mean length of those that were not recovered.

In addition to testing the hypothesis that hatch-

TABLE 1.—Estimated number of juvenile coho salmon before hatchery fish were planted (at the beginning of the summer), catchability (number of fish caught/estimated abundance) and estimated summer survival.

Year and creek	Habitat type[a]	Estimated number of fish	Catch-ability (%)	Summer survival (%)
1996				
Forks	All	303	30	100
Silver	All	69	72	83
1997				
Forks	Isolated	108	75	42
	Main	1,189	65	88
Silver	Isolated	57	82	63
	Main	317	17	100

[a] Habitat types include isolated pools and the main stream.

TABLE 2.—Numbers (N) of juvenile coho salmon marked and recovered in Forks and Silver creeks in 1996. Percentages are relative to number marked in May.

Stream and rearing type	Marked in May	Recovered in July	
		N	%
Forks			
Natural	70	21	30
Hatchery	70	35	50
Silver			
Natural	49	22	45
Hatchery	49	9	18

ery-reared and naturally reared coho salmon survived at the same rate, we estimated the proportion of salmon that survived the summer by calculating a daily mortality rate from the total numbers of salmon caught at two sampling periods. When more fish were caught at the later sampling period, a survival rate of 100% is reported. Mark–recapture data were used to estimate the abundance of coho salmon in the streams at the beginning of the summer so that catchability could be estimated by dividing the number caught by the estimated abundance (Wootton 1990).

Growth.—We compared the growth rates of individually marked hatchery-reared and naturally reared coho salmon recovered in Forks Creek in 1997 by transforming individual growth increments (in weight) into relative instantaneous growth rates using the equation (Ricker 1979):

$$G = \frac{\log_e w_2 - \log_e w_1}{t_2 - t_1},$$

where w_1 and w_2 are the weights of fish caught at times t_1 and t_2. To determine if there was a relationship between growth rate and size we regressed instantaneous growth rate on initial weight. Because hatchery-reared and naturally reared coho salmon differed in size at the time of planting, we used a t-test to compare instantaneous growth rates of fish within the weight range (4.0–7.9 g), where hatchery-reared and naturally reared fish overlapped. Analysis of covariance (ANCOVA), with initial weight as a covariate, could not be used to determine whether hatchery-reared and naturally reared salmon grew at different rates because the initial weight range for hatchery-reared fish (4.0–7.9 g) was much narrower than for naturally reared fish (2.5–8.7 g), and ANCOVA assumes equal covariances.

Movement.—To test the null hypothesis that hatchery-reared and naturally reared coho salmon moved in similar patterns, the ratios of fish that moved upstream and downstream in Forks Creek in 1997 were compared between the rearing groups by using the chi-square test of independence. The numbers of fish from each rearing group caught in the downstream traps were also compared.

Results

Survival

A large proportion of the coho salmon in the study streams survived the summer (range, 83–100%; Table 1). We found little evidence that hatchery-reared and naturally reared salmon survived at different rates in the study streams. Ratios of hatchery to naturally reared salmon recovered in the streams were indistinguishable from 1:1 when the data were pooled across years and streams (484:499, $\chi^2 = 0.23$, $P > 0.05$; Tables 2, 3) or partitioned by year, creek, recovery date, or habitat type ($P > 0.05$). Only in Silver Creek in July 1996 was the ratio of marked fish recovered different from 1:1 (22:9, binomial test, $P < 0.05$; Table 2).

Summer survival in isolated pools was lower than survival in the main stream, ranging from 42% to 63% (Table 1), yet we still found no difference in survival between rearing groups in isolated pools (Table 3). We believe estimates of summer survival were accurate (except for Silver Creek in 1997 and Forks Creek in 1996) because we caught more than 65% of the fish in the creeks (Table 1).

If size and summer survival were related, then size could have confounded the above analyses because hatchery-reared fish were larger than naturally reared fish (Figure 1). However, there was no evidence for size-selective mortality (e.g., Figure 2).

TABLE 3.—Numbers (*N*) of juvenile coho salmon marked and recovered in pools and in the main stream of Forks and Silver creeks in 1997. Percentages are relative to number marked in June.

Creek and habitat type	Rearing type	Marked in Jun	Recovered in Jul		Recovered in Sep	
			N	(%)	*N*	(%)
Forks						
Isolated pools	Natural	72	53	74	20	28
	Hatchery	72	41	57	27	38
Main stream	Natural	425	173	41	160	38
	Hatchery	425	187	44	157	37
Silver						
Isolated pools	Natural	50	17	34	9	18
	Hatchery	50	17	34	16	16
Main stream	Natural	40	9	23	0	0
	Hatchery	40	6	15	4	10

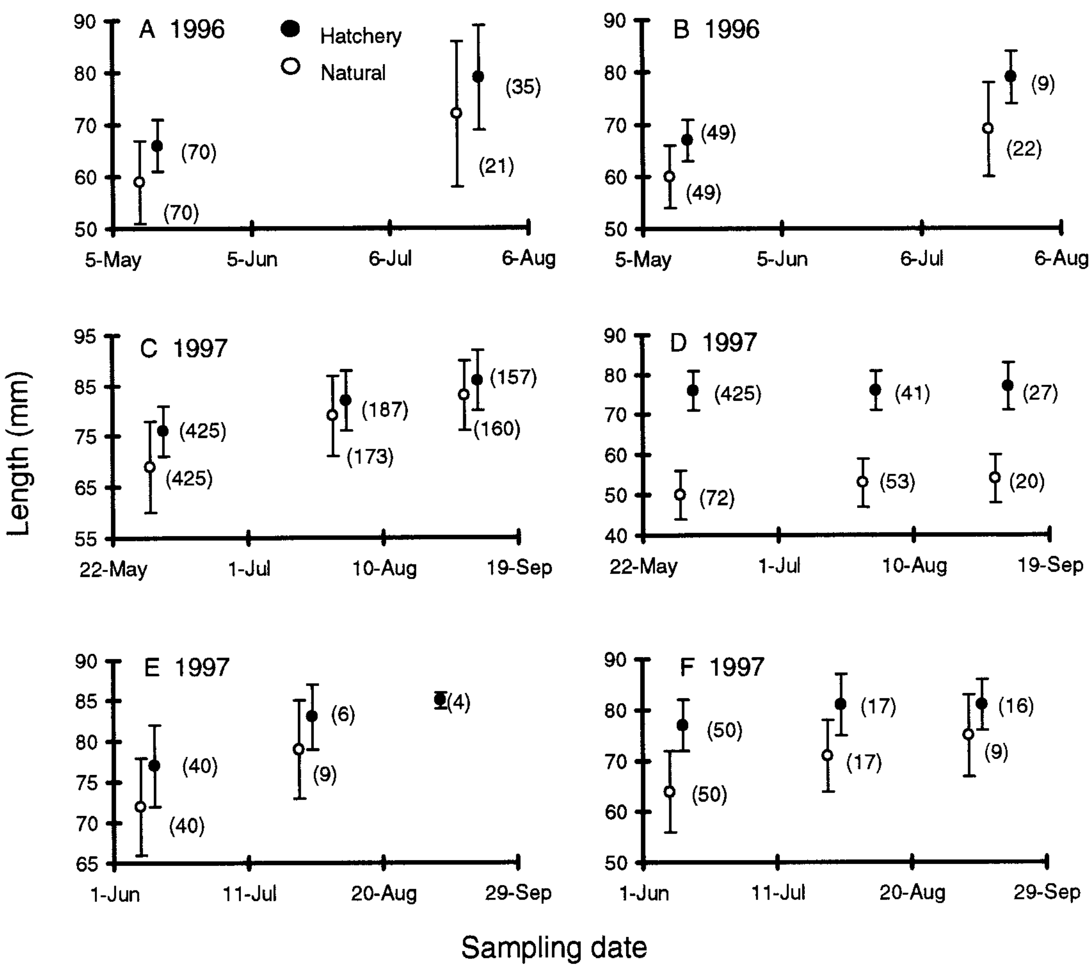

FIGURE 1.—Mean lengths (±SD) of hatchery-reared (solid circles) and naturally reared (open circles) coho salmon caught in **(A)** Forks Creek in 1996, **(B)** Silver Creek in 1996, **(C)** Forks Creek in the main stream in 1997, **(D)** Forks Creek in isolated pools in 1997, **(E)** Silver Creek in the main stream in 1997, **(F)** Silver Creek in isolated pools in 1997. Numbers in parentheses are sample sizes.

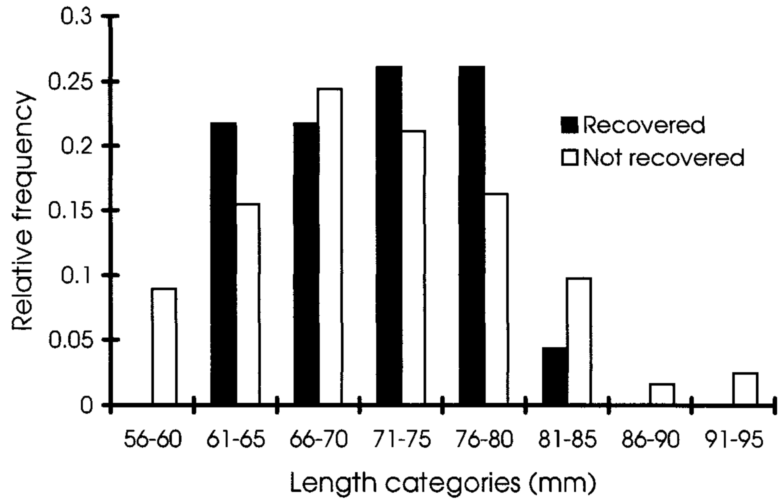

FIGURE 2.—Relative frequency of lengths of individually marked fish in June partitioned by those that were recovered ($N = 23$) and not recovered ($N = 123$) at the end of the summer in Forks Creek 1997.

Growth

Hatchery-reared coho salmon were longer than the naturally reared fish on all sampling dates (*t*-tests, $P < 0.05$), and their length distributions were narrower (*F*-tests, $P < 0.05$, Figure 1). ANCOVA of length–weight relationships for hatchery-reared and naturally reared fish indicated that hatchery-reared fish were lighter for their length than naturally reared fish. Nevertheless, comparisons of mean weights between hatchery-reared and naturally reared fish produced results similar to comparisons of mean lengths; i.e., hatchery-reared fish were heavier and weight distributions were narrower.

There was a significant negative relationship between instantaneous growth rate and initial weight among naturally reared coho salmon (Figure 3). Mean instantaneous growth rate was twice as high for hatchery-reared fish as for naturally reared fish within the overlapping weight range (4.0–7.9 g; 0.0030 versus 0.0015 in units $\Delta \log_e g/d$, two-tailed *t*-test, $P = 0.05$, df $= 21$; Figure 4).

Movement

Little downstream movement occurred among either wild or hatchery-reared coho salmon. In Forks Creek, only eight naturally reared salmon and seven hatchery-reared salmon were caught in

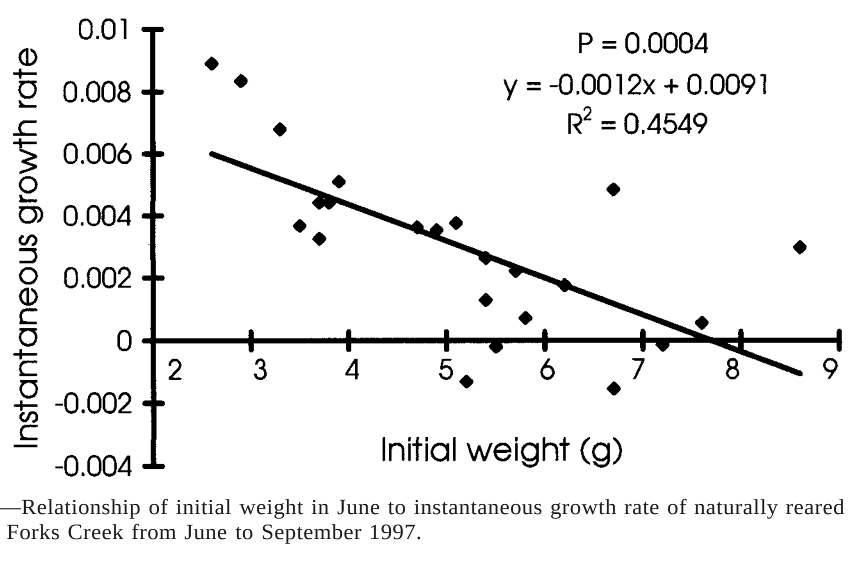

FIGURE 3.—Relationship of initial weight in June to instantaneous growth rate of naturally reared coho salmon that grew in Forks Creek from June to September 1997.

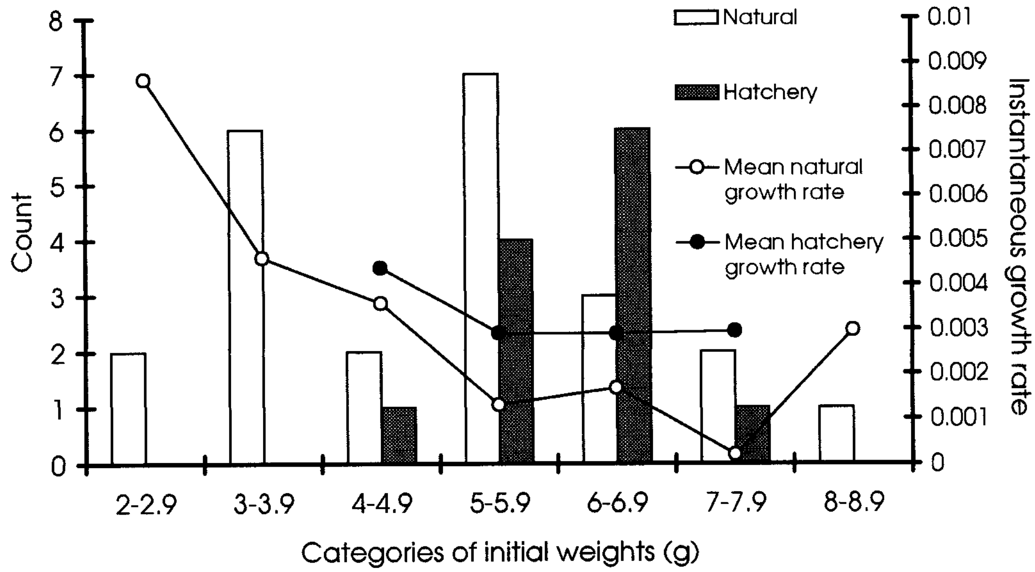

FIGURE 4.—Weight distributions in June of individually marked hatchery-reared and naturally reared coho salmon caught in Forks Creek, September 1997, and mean instantaneous growth rates.

the downstream traps over the summer of 1997. Further, the numbers of fish that moved upstream and downstream were independent of rearing type (chi-square contingency table analysis, $P > 0.05$).

Discussion

We detected few differences in performance between the hatchery-reared and naturally reared salmon in the streams. Hatchery-reared and naturally reared coho salmon survived equally well in both creeks and in both summers. Hatchery-reared fish were approximately 10% larger than naturally reared fish when they were planted in the creeks, and their larger size might have given them an advantage. However, both rearing groups survived the summer at high rates (about 90%), and there was no evidence of size-selective survival. In addition, we found no differences in movement between hatchery-reared and naturally reared salmon and few fish of either rearing type were displaced downstream. However, we did find evidence that the hatchery-reared fish grew faster than the naturally reared fish in the streams.

The high survival and low emigration that we observed might be expected if the streams were occupied below carrying capacity. The estimated density of coho salmon at the beginning of the summer in Forks Creek in 1997 was 0.5 fish/m^2. However, most fish (73%) were found in pools (contiguous with the main stream), and estimated densities in these pools were much higher (approximately 4 fish/m^2). Overcrowding (about 8 fish/m^2) could explain the lower survival (Table 1) and growth rates (Figure 1C–F) observed in isolated pools not contiguous with the main stream. Density in the entire reach was much lower in Forks Creek in 1996 (0.1 fish/m^2) and in Silver Creek in both years (0.02 fish/m^2 in 1996 and 0.1 fish/m^2 in 1997). The lower densities in 1996 might have resulted from movement of large numbers of unfed fry downstream (over the falls) soon after they were planted because the fry were released in high, turbid water. Lower densities in Silver Creek may have been caused by predation by cutthroat trout on fry (many more cutthroat trout were caught in Silver Creek than in Forks Creek) or early displacement after fry were planted.

Our findings suggest that the hatchery-reared fish were better competitors because their size-adjusted growth rates were higher than those of naturally reared fish. This is in agreement with Allee's (1974) results in an artificial stream channel. Hatchery-reared salmonids may be more aggressive than stream-reared fish (Fenderson et al. 1968; Mesa 1991), and high levels of aggression might enable hatchery-reared fish to acquire profitable foraging positions in streams (Fausch 1984). Results of laboratory experiments (Rhodes and Quinn 1998) are consistent with the conclusion that hatchery-reared coho salmon are successful competitors. Hatchery-reared coho salmon dominated size-matched stream-reared salmon, and a 10% size advantage of hatchery fish was sufficient to overcome a prior residence effect benefitting naturally reared fish.

Contrary to the findings of many studies in other salmonids (e.g., Miller 1954; Flick and Webster 1964; Wiley et al. 1993), we found that the hatchery phenotype was not inferior to the naturally reared phenotype in the stream environment. Olla et al. (1994) concluded that lack of predator avoidance experience would render hatchery fish vulnerable in a stream, but Dellefors and Johnsson (1995) found that hatchery-reared and naturally reared trout spent the same amount of time in a risky area containing a predator. Fenderson et al. (1968), Fenderson and Carpenter (1971), and Dickson and MacCrimmon (1982) concluded that behavioral anomalies exhibited by hatchery-reared Atlantic salmon were maladaptive, although the fitness consequences of the traits were not determined. Miller (1954) found that hatchery-reared cutthroat trout survived poorly in streams, but Symons (1969) found no difference in survival between hatchery-reared and naturally reared juvenile Atlantic salmon in streams.

We were unable to determine whether the performance of naturally reared fish was reduced as a result of the addition of hatchery-reared fish. Nickelson et al. (1986) concluded that hatchery coho salmon released into streams displaced wild coho salmon. Nickelson et al. (1986) stocked hatchery fish at higher densities than we did. Also, the hatchery fish they used were 59% larger than the wild coho salmon, whereas in our study hatchery coho salmon when released were only 10% larger than the naturally reared salmon. It was unclear whether high stocking levels or large size differences were primarily responsible for the displacement of wild fish reported by Nickelson et al. (1986). However, our results of higher growth of relatively similar-sized hatchery-reared and naturally reared fish suggest that superior performance may also have played a role. Results of Nickelson et al. (1986) and our study suggest that hatchery fish can perform well in streams. Few naturally reared salmon may have been displaced in our study because hatchery salmon were released in relatively low numbers at sizes similar to the naturally reared fish. However, hatchery supplementation should be used cautiously because large numbers of hatchery fish that perform well in streams may displace naturally occurring salmon. Vincent (1987), Berg and Jorgensen (1991), and White et al. (1995) came to a similar conclusion, though Petrosky and Bjornn (1988) did not reach that conclusion in studies conducted on rainbow trout *O. mykiss* and cutthroat trout.

The magnitude and direction of fitness differences between hatchery-reared and wild fish and the cause of the differences (genotype or environment) will influence the outcome of hatchery supplementation (White et al. 1995). If the natural population is genetically similar to the hatchery population, supplementation may be an effective production tool because the fitness of hatchery-reared fish and naturally reared fish may be equivalent and genetic introgression is not a concern. However, if hatchery fish outcompete, displace or significantly reduce the performance of the naturally rearing fish, then supplementation may be self-defeating (White et al. 1995). To predict the outcome of a specific supplementation program, the factors that influence the outcome of territorial competition need to be evaluated, along with the effects of density on downstream emigration.

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References

Allee, B. J. 1974. Spatial requirements and behavioral interactions of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Salmo gairdneri*). Doctoral thesis. University of Washington, Seattle.

Bachman, R. A. 1984. Foraging behavior of free-ranging wild and hatchery brown trout in a stream. Transactions of the American Fisheries Society 113: 1–32.

Berejikian, B. A., S. B. Mathews, and T. P. Quinn. 1996. Effects of hatchery and wild ancestry and rearing environments on the development of agonistic behavior in steelhead trout (*Oncorhynchus mykiss*) fry. Canadian Journal of Fisheries and Aquatic Sciences 53:2004–2014.

Berg, S., and J. Jorgensen. 1991. Stocking experiments with 0+ and 1+ trout parr, *Salmo trutta* L., of wild and hatchery origin. 1. Post-stocking mortality and smolt yield. Journal of Fish Biology 39:151–169.

Cuenco, M. L., T. W. H. Backman, and P. R. Mundy. 1993. The use of supplementation to aid in natural stock restoration. Pages 269–293 *in* J. G. Cloud and G. H. Thorgaard, editors. Genetic conservation of salmonid fishes. Plenum, New York.

Dellefors, C., and J. I. Johnsson. 1995. Foraging under risk of predation in wild and hatchery-reared juvenile sea trout (*Salmo trutta* L.). Nordic Journal of Freshwater Research 70:31–37.

Dickson, T. A., and H. R. MacCrimmon. 1982. Influence of hatchery experience on growth and behavior of juvenile Atlantic salmon (*Salmo salar*) within allopatric and sympatric stream populations. Canadian Journal of Fisheries and Aquatic Sciences 39: 1453–1458.

Fausch, K. D. 1984. Profitable stream positions for salmonids: relating specific growth rate to net energy gain. Canadian Journal of Zoology 62:441–451.

Fenderson, O. C., and M. R. Carpenter. 1971. Effects of crowding on the behaviour of juvenile hatchery and wild landlocked Atlantic salmon (*Salmo salar* L.). Animal Behaviour 19:439–447.

Fenderson, O. C., W. H. Everhart, and K. M. Muth. 1968. Comparative agonistic and feeding behavior of hatchery reared and wild salmon in aquaria. Journal of the Fisheries Research Board of Canada 25:1–14.

Flick, W. A., and D. A. Webster. 1964. Comparative first year survival and production in wild and domestic strains of brook trout (*Salvelinus fontinalis*). Transactions of the American Fisheries Society 93: 58–69.

Hume, J. M. B., and E. A. Parkinson. 1988. Effects of size and time of release on the survival and growth of steelhead fry stocked in streams. North American Journal of Fisheries Management 8:50–57.

Jonsson, B., and I. A. Fleming. 1993. Enhancement of wild salmon populations. Pages 209–242 *in* B. B. Hemmingsen and G. Sundnes, editors. Human impact on self-recruiting populations. Tapir Press, Trondheim, Norway.

Lichatowich, J. A., and J. D. McIntyre. 1987. Use of hatcheries in the management of Pacific anadromous salmonids. Pages 131–136 *in* M. J. Dadswell and five coeditors. Common strategies of anadromous and catadromous fishes. American Fisheries Society, Symposium 1, Bethesda, Maryland.

Mason, J. W., O. M. Brynidson, and P. E. Degurse. 1967. Comparative survival of wild and domestic strains of brook trout in streams. Transactions of the American Fisheries Society 96:313–319.

Maynard, D. J., T. A. Flagg, C. V. W. Mahnken, and S. L. Schroder. 1996. Natural rearing technologies for increasing postrelease survival of hatchery-reared salmon. Bulletin of the National Research Institute of Aquaculture (Supplement 2):71–77.

Meffe, G. K. 1992. Techno-arrogance and halfway technologies: salmon hatcheries on the Pacific coast of North America. Conservation Biology 6:350–354.

Mesa, M. G. 1991. Variation in feeding, aggression, and position choice between hatchery and wild cutthroat trout in an artificial stream. Transactions of the American Fisheries Society 120:723–727.

Miller, R. B. 1954. Comparative survival of wild and hatchery-reared cutthroat trout in a stream. Transactions of the American Fisheries Society 83:120–130.

Nickelson, T. E., M. F. Solazzi, and S. L. Johnson. 1986. Use of hatchery coho salmon (*Oncorhynchus kisutch*) presmolts to rebuild wild populations in Oregon coastal streams. Canadian Journal of Fisheries and Aquatic Sciences 43:2443–2449.

Olla, B. L., M. W. Davis, and C. H. Ryer. 1994. Behavioral deficits in hatchery-reared fish: potential effects on survival following release. Aquaculture and Fisheries Management 25(Supplement 1):19–34.

Petrosky, C. E., and T. C. Bjornn. 1988. Response of wild rainbow (*Salmo gairdneri*) and cutthroat trout (*S. clarki*) to stocked rainbow trout in fertile and infertile streams. Canadian Journal of Fisheries and Aquatic Sciences 45:2087–2105.

Reisenbichler, R. R., and J. D. McIntyre. 1977. Genetic differences in growth and survival of juvenile hatchery and wild steelhead trout *Salmo gairdneri*. Journal of the Fisheries Research Board of Canada 34:123–128.

Rhodes, J. S., and T. P. Quinn. 1998. Factors affecting the outcome of territorial contests between hatchery and naturally reared coho salmon parr in the laboratory. Journal of Fish Biology 53:1220–1230.

Ricker, W. E. 1979. Growth rates and models. Pages 677–743 *in* W. S. Hoar, D. J. Randall, and J. R. Brett, editors. Fish physiology, volume 8. Academic Press, New York.

Swain, D. P., and B. E. Riddell. 1990. Variation in agonistic behavior between newly emerged juveniles from hatchery and wild populations of coho salmon, *Oncorhynchus kisutch.* Canadian Journal of Fisheries and Aquatic Sciences 47:566–571.

Symons, P. E. K. 1969. Greater dispersal of wild compared with hatchery-reared juvenile Atlantic salmon released in streams. Journal of the Fisheries Research Board of Canada 26:1867–1876.

Vincent, E. R. 1987. Effects of stocking catchable-size hatchery rainbow trout on two wild trout species in the Madison River and O'Dell Creek, Montana. North American Journal of Fisheries Management 7:91–105.

White, R. J., J. R. Karr, and W. Nehlsen. 1995. Better roles for fish stocking in aquatic resource management. Pages 527–547 *in* H. L. Schramm, Jr., and R. G. Piper, editors. Uses and effects of cultured fishes in aquatic ecosystems. American Fisheries Society, Symposium 15, Bethesda, Maryland.

Wiley, R. W., R. A. Whaley, J. B. Satake, and M. Fowden. 1993. An evaluation of the potential for training trout in hatcheries to increase poststocking survival in streams. North American Journal of Fisheries Management 13:171–177.

Wootton, R. J. 1990. Ecology of teleost fishes. Chapman and Hall, London.

Zar, J. H. 1996. Biostatistical analysis. Prentice-Hall, Englewood Cliffs, New Jersey.