

Genetic Differences in Growth and Survival of Juvenile Hatchery and Wild Steelhead Trout, *Salmo gairdneri*

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Relative growth and survival of offspring from matings of hatchery and wild Deschutes River (Oregon) summer steelhead trout, *Salmo gairdneri*, were measured to determine if hatchery fish differ genetically from wild fish in traits that can affect the stock-recruitment relationship of wild populations. Sections of four natural streams and a hatchery pond were each stocked with genetically marked (lactate dehydrogenase genotypes) eyed eggs or unfed swim-up fry from each of three matings: hatchery × hatchery (HH), hatchery × wild (HW), and wild × wild (WW). In streams, WW fish had the highest survival and HW fish the highest growth rates when significant differences were found; in the hatchery pond, HH fish had the highest survival and growth rates. The hatchery fish were genetically different from wild fish and when they interbreed with wild fish may reduce the number of smolts produced. Hatchery procedures can be modified to reduce the genetic differences between hatchery and wild fish.

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Nous avons mesuré la croissance et la survie relatives de descendants issus de croisements entre des truites steelhead de pisciculture et des steelheads d'été sauvages, *Salmo gairdneri*, de la rivière Deschutes (Orégon), afin de déterminer si les poissons de pisciculture diffèrent génétiquement des poissons sauvages par des caractères susceptibles d'affecter la relation stock-recrutement des populations sauvages. Des sections de quatre cours d'eau naturels et un étang de pisciculture ont été ensemencés chacun avec des œufs embryonnés génétiquement marqués (génotypes lactate déshydrogénase) ou avec des alevins non nourris au stade de nage vers le haut résultant de chacun de trois croisements: pisciculture × pisciculture (HH), pisciculture × sauvage (HW) et sauvage × sauvage (WW). Dans les cours d'eau, les poissons WW ont le plus haut taux de survie, et les poissons HW le plus haut taux de croissance là où il y a des différences significatives; dans l'étang de pisciculture, les poissons HH ont les taux de survie et de croissance les plus élevés. Les poissons de pisciculture diffèrent génétiquement des poissons sauvages et, quand ils se croisent avec des poissons sauvages, peuvent causer une diminution du nombre de smolts produits. Les méthodes de pisciculture peuvent être modifiées de façon à réduire les différences génétiques entre les poissons de pisciculture et les poissons sauvages.

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INTRODUCTION of artificially propagated salmonids into natural stream systems may influence resident wild populations (Hochachka 1961). The hatchery-reared fish may affect the wild population through competition for food and space re-

sources (Needham and Slater 1944; Reimers 1957; Vincent 1972), or the genetic structure of the wild population may be affected by interbreeding of hatchery fish and wild fish on natural spawning grounds. A genetic effect is contingent upon there being a genetic difference between the wild fish and the hatchery fish spawning together in the wild. Results of studies with brook trout, *Salvelinus fontinalis* (Greene 1952; Flick and Webster 1964), and with Atlantic salmon, *Salmo salar* (Fenderson et al. 1968), indicated the existence of genetic differences between hatchery and wild fish.

For anadromous species on the Pacific coast, it

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is not known whether adults resulting from release of artificially propagated juveniles differ genetically from wild adults, especially in traits that may affect the stock-recruitment relationship of a wild population (Ricker 1975). This study was designed to test the hypothesis that there are no genetic differences in growth rate or survival between offspring from matings of hatchery \times hatchery (HH), hatchery \times wild (HW), and wild \times wild (WW) summer steelhead trout, *S. gairdneri*.

Materials and Methods

Summer steelhead trout were captured during their upstream migration in a trap at Pelton reregulating dam on the Deschutes River, a tributary of the Columbia River, during fall and winter 1974-75. They were held at the Oregon Department of Fish and Wildlife Round Butte Hatchery until sexually mature. Hatchery fish could be identified because they are flipped before release into the Deschutes River. As the terms are used in this paper, hatchery fish are reared in a hatchery for about 1 yr before their release, and wild fish result from natural reproduction.

Eyed eggs or unfed swim-up fry from matings of these adults subsequently were placed in four small streams in the upper Trout Creek drainage which flows into the Deschutes River. Average weekly flows in these streams exceeded 28 ℓ /s only during periods of snowmelt or unusually wet weather. Water temperatures ranged from 0°C during winter and spring to 26°C during summer. Steelhead and resident rainbow trout and longnose dace, *Rhinichthys cataractae*, are known to occur in these streams. In January 1975 screens were installed in these streams to delineate four study sections (one each, 1.6 km long, in Opal, Dutchman, and Potlid creeks; and one, 0.8 km long, in Trout Creek) and to prevent steelhead and resident rainbow trout from entering the sections for spawning. Trout longer than 6.5 cm were removed from the sections by repeated electrofishing. Downstream traps were installed at each screen to capture out-migrating fish.

On February 24, 1975, each adult was killed, its eggs or sperm placed in a numbered container and stored at 4°C and a sample of liver tissue analyzed electrophoretically to determine the lactate dehydrogenase-4 (LDH-4) genotype of each fish (Utter et al. 1973). Preliminary analyses indicated the occurrence of three LDH genotypes, *BB*, *B'B*, and *B'B'*, which are known to exhibit simple Mendelian inheritance (Morrison and Wright 1966). After the genotypes were determined, the stored gametes were combined into three sets of fertilized eggs. Each set consisted of groups of eggs of each LDH genotype and each mating as follows:

Sets	Matings		
	HH	HW	WW
I	<i>B'B'</i>	<i>BB</i>	<i>B'B</i>
II	<i>BB</i>	<i>B'B</i>	<i>B'B'</i>
III	<i>B'B</i>	<i>B'B'</i>	<i>BB</i>

The numbers of adults used in these matings were:

Hatchery				Wild			
Males		Females		Males		Females	
<i>BB</i>	<i>B'B'</i>	<i>BB</i>	<i>B'B'</i>	<i>BB</i>	<i>B'B'</i>	<i>BB</i>	<i>B'B'</i>
13	14	13	16	4	4	4	4

Non-LDH genotypic variability was maximized in the offspring by dividing the eggs from each female into a number of subsamples equal to the number of males to be used in the mating. Each subsample of eggs was then fertilized by sperm from one male. Thus, a mating representing *m* males and *f* females consisted of *m* \times *f* individual matings.

It was necessary to repeat the spawning procedure on a second date (March 18) because of low survival in one mating of set III. Matings for sets II and III were repeated at this time. The numbers of adults used in these matings were:

Hatchery				Wild			
Males		Females		Males		Females	
<i>BB</i>	<i>B'B'</i>	<i>BB</i>	<i>B'B'</i>	<i>BB</i>	<i>B'B'</i>	<i>BB</i>	<i>B'B'</i>
13	14	13	20	5	12	4	6

Fertilization was delayed for < 12 h for all matings on both dates. The fertilized eggs were placed in Heath® incubator trays with a 23-27 ℓ /min flow of 10°C water. The eggs were left undisturbed until they reached the eyed stage; dead eggs were then removed.

Eggs from both spawning dates were used to stock the study sections (Table 1). Vibert® boxes, each containing 600 eggs, were marked to identify the eggs they contained, and three boxes of eggs (from each mating: HH, HW, WW) were placed in artificial redds excavated at regular intervals in the substrate of the study sections in Dutchman (15 redds), Potlid (15), and Trout (10) creeks. Each depression was then filled with gravel 1.5-7 cm in diameter. Potlid and Dutchman creeks were stocked with 9,000 eggs from each mating and Trout Creek with 6,000 from each. The Vibert® boxes were removed from the redds after fry emergence from the gravel was complete, and dead embryos were counted.

Opal Creek was stocked with 22,500 swim-up fry and a hatchery pond at Round Butte Hatchery with 18,000 (Table 1). The fry stocked in the hatchery pond were reared according to standard practices by personnel at Round Butte Hatchery.

Samples of juvenile fish were captured from the sections by electrofishing several times during the period from July 15, 1975 to April 8, 1976. These samples and the fish removed from the traps were frozen and taken to the laboratory where they were thawed and measured (fork length). The LDH genotype of each fish was determined from eye-tissue homogenates.

Results

Among eyed eggs from the three streams, survival of WW embryos was significantly greater ($P < 0.05$) than that of HH and HW embryos

TABLE 1. Lactate dehydrogenase genotypes of eyed eggs (E) of steelhead trout (*Salmo gairdneri*) placed in artificial redds and unfed swim-up fry (F) stocked in experimental streams and a hatchery pond. HH = hatchery × hatchery; HW = hatchery × wild; WW = wild × wild.

Steelhead stocked		Matings		
Location	Life stage	HH	HW	WW
Potlid Creek ^a	E	B'B'	BB	B'B
Hatchery Pond ^a	F	BB	B'B	B'B'
Dutchman Creek ^b	E	BB	B'B	B'B'
Trout Creek ^{b,c}	E	B'B	B'B'	BB
Opal Creek ^{b,c}	F	B'B	B'B'	BB

^aEggs fertilized February 24, 1975.

^bEggs fertilized March 18, 1975.

^cOpal and Trout creeks stocked with fish from the same matings.

(Table 2). (These data did not include one Vibert® box of WW embryos from Potlid Creek and five boxes — two HH, two HW, and one WW — from Trout Creek that had been washed out of their redds.) The variance of the arc sine square root of percentage mortality for groups of eyed eggs was analyzed following the technique of least squares analysis of a linear model (Draper and Smith 1966) to overcome the problem of unequal sample sizes.

The traps at the lower ends of each study section were functional and assumed to have captured all downstream migrants during the period from their installation in April to November 8, 1975, except in Trout Creek where high water caused the trap to be inoperative during portions of May and June. The traps were not functional for most of the period after November 8, 1975. Less than 500 experimental fish from each stream were captured in the traps (Table 3).

In all streams where the numbers of juveniles from the experimental matings differed significantly, progeny of WW matings were most abundant (Table 4). In the hatchery pond, HH fish were the most abundant. Overwinter (October-

TABLE 2. Percent survival for different groups of eyed eggs stocked in three experimental streams (HH = hatchery × hatchery; HW = hatchery × wild; WW = wild × wild). *9,000/mating; **6,000/mating.

Creek	Total no. stocked	Matings		
		HH	HW	WW
Potlid	27,000*	89	83	93
Dutchman	27,000*	70	72	78
Trout	18,000**	75	84	86
Combined creeks	72,000	78.4	79.5	86.1

TABLE 3. Frequency of fish from three experimental matings that were recovered from traps before October 1975.

Creek	Matings			χ^2 ^a
	HH	HW	WW	
Opal	135	121	120	1.1
Potlid	52	228	105	141.1 ^b
Dutchman	122	99	190	23.4 ^b
Trout	75	88	81	2.4

^aExpected values for the chi-square calculations were derived by using data from Table 3 and assuming that eggs from dislocated Vibert® boxes made no contribution to the experimental populations.

^bStatistically significant at the 0.005 level.

March) shifts in relative abundance occurred in Opal Creek, where survival of WW fish was significantly greater than that of HH fish in the fall but not in the spring. In Potlid Creek, frequencies in the fall sample indicated no significant difference in relative abundance, and frequencies in the spring sample indicated significantly greater survival of WW than of HH fish.

Out-migration rates of 0% for HH, 31% for HW and 69% WW would have produced the observed frequency change between fall and spring in Opal Creek. The only trap sample obtained after September, which was from Opal Creek on December 1, 1975, consisted of only eight fish — two HW and six WW. Deschutes River summer steelhead trout fry from tributary streams (Fessler 1974) and summer steelhead and resident rainbow trout from several Idaho streams (Bjornn 1971) are known to migrate downstream during the fall and winter. A differential out-migration in Opal Creek but not in Trout Creek, both of which contained fish from the same matings, may have been due to the more extreme winter conditions in Opal Creek. Trout and Potlid creeks were covered with ice during most of the winter, but Opal Creek often was not. The recurrent absence of a protective covering of ice resulted in greater fluctuations in temperature in Opal Creek and ice frequently formed on the stream bottom.

In Opal and Potlid creeks, HW fish were larger ($P < 0.005$) than HH and WW fish (Table 4). Mean lengths of fish from Dutchman and from Trout creeks were not significantly different. In the hatchery pond, the HH fish were significantly larger than the HW and WW fish ($P < 0.01$).

Differences in the environmental conditions from stream to stream and sampling error resulting from the relatively small numbers of wild adults used in the matings were possible causes for the lack of consistency observed in the relative

TABLE 4. Frequencies (percent) and mean lengths (millimeters) in parentheses, of fish from experimental matings in samples from streams and a hatchery pond. χ^2 compares numbers of fish from each mating.

Location and collection date	No. fish	Matings			χ^{2a}
		HH	HW	WW	
Opal Creek					
July 14, 1975	222	34(46)	29(46)	37(45)	2.0
September 9, 1975	159 ^b	26(59)	32(62)	42(59)	5.6 ^c
October 25, 1975	464	26(60)	30(63)	44(61)	27.5 ^c
March 3, 1976	528	33(63)	32(65)	35(63)	0.8
Potlid Creek					
September 9, 1975	130	31(54)	37(57)	32(55)	0.7
November 4, 1975	316	39(59)	31(60)	30(60)	2.6
March 3, 1976	296	28(62)	33(65)	39(63)	7.2 ^c
Dutchman Creek					
August 17, 1975	453	33(55)	33(54)	34(54)	0.1
November 7, 1975	422	32(62)	36(63)	32(61)	2.7
February 29, 1976	234	29(70)	37(68)	34(70)	2.6
Trout Creek					
November 4, 1975	435	23(51)	29(52)	48(51)	27.4 ^c
April 8, 1976	115	22(54)	36(52)	42(52)	7.8 ^c
Hatchery Pond					
August 16, 1975	497	40(60)	31(56)	29(56)	10.8 ^c

^aExpected values were calculated by assuming that embryos from dislocated boxes made no contribution to the experimental populations.

^bMeasured lengths of 158 fish.

^cStatistically significant at the 0.05 level.

lengths and abundances of fish in the different study sections. Analysis of the variance in length for fish obtained in the fall and spring from all streams and inspection of the relative frequency data suggested that there was no selective advantage associated with individual LDH genotypes of fish that were stocked in the streams.

Discussion

There were genetic differences in growth rate and survival between the offspring of hatchery and wild steelhead. Differences in the numbers of fish recovered from the traps, although not consistent, suggested that there were behavioral differences between offspring of hatchery and wild fish; however, the effect of migration differences on the relative growth and survival of fish from these matings was not clear.

The observed differences in survival suggested that the short-term effect of hatchery adults spawning in the wild is the production of fewer smolts and ultimately, fewer returning adults than are produced from the same number of only wild spawners. This effect depends on the particular limiting factors and environmental conditions in a given stream system and on the total number of spawners. In some stream systems, the same total

number of smolts may be obtained simply by allowing more hatchery adults to spawn (Fig. 1A), whereas in other systems, numbers of smolts may be reduced regardless of how many hatchery adults spawn (Fig. 1B).

The length data for fish from Potlid and Opal creeks indicated that there were genetic differences between offspring from the different matings surviving after 1 full yr of exposure to natural selection in the stream environment. If these and other genetic differences persist until the offspring of hatchery and wild fish return as adults, there will be an additional effect on the wild population. The expected result is a reduction in the overall reproductive success of the wild population (long-term effect in Fig. 2). The relative magnitude of short-term and long-term effects would be expected to vary through time. In years in which the environment is unusually favorable for survival of fish, the short-term effect would be expected to be reduced, but this reduction in turn would increase the long-term effect in later years when the "mild year offspring" returned as adults and spawned in the stream. Conversely, in years in which the environment is unusually harsh, the short-term effect would be expected to be high, and the long-term effect low.

The results may provide only a conservative

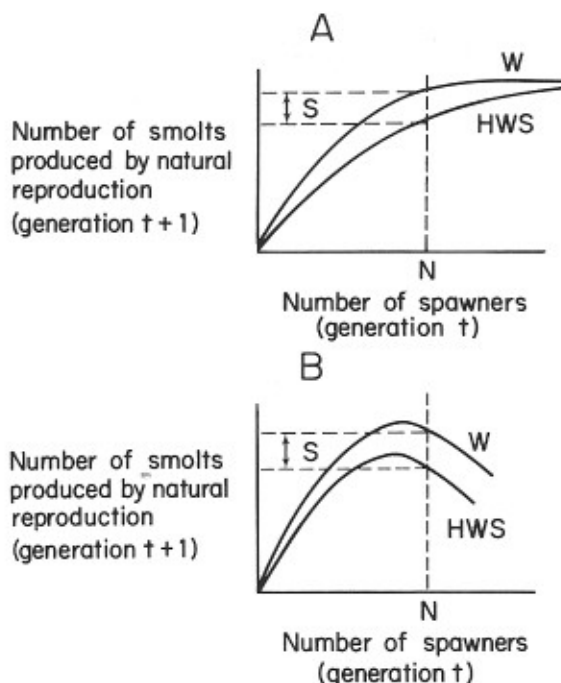


FIG. 1. Hypothetical stock-recruitment relationships. Numbers of smolts produced at high spawner densities are equivalent (A); never equivalent (B). See text for explanation. Short-term effect at an escapement of N spawners is S . W = the relationship for all wild spawners with no previous hatchery introductions. HWS = the relationship due to hatchery adults interbreeding with wild adults. HWS varies with the proportion of the total spawners that are hatchery fish; this proportion increases the distance between HWS and W . Available spawning area not limited (A); limited (B).

estimate of the effects of interbreeding between hatchery and wild fish. Most of the adult hatchery fish captured in the 1974-75 winter were no more than two generations removed from wild steelhead trout parents. As a stock of fish is subject to the selective forces of the hatchery environment over more generations, the genetic difference between the hatchery fish and the original wild stock will probably increase. In addition, a large number of adult hatchery fish spawn in the river immediately below the Pelton reregulating dam; consequently, some of the wild fish used for this experiment are likely to have had a hatchery fish for a parent. Finally, making all matings for each stream in the hatchery on the same day eliminated any potential effects due to differences in adult behavior. Differences in spawning time and other adult behavior may have a considerable effect on the relative performance of offspring of hatchery and wild adults. Hatchery steelhead from the

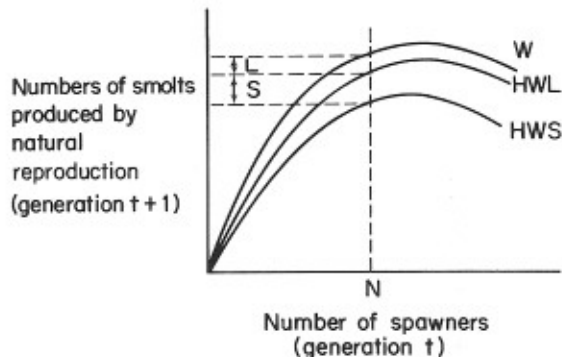


FIG. 2. Suggested effects of interbreeding between hatchery and wild fish and a hypothetical stock-recruitment relationship for naturally reproducing fish. Total effect at an escapement of N spawners is $L + S$. W = the relationship for all wild spawners with no previous hatchery introductions; HWL = the relationship resulting from genetic differences between wild adults that are offspring of hatchery and wild fish; HWS = the relationship resulting from interbreeding of hatchery wild adults. S = short-term effect and L = long-term effect (see text for explanation).

Deschutes River tend to spawn earlier than the wild fish. If natural selection in the stream system is regulating spawning time for optimal survival, then in most years poorer survival would be expected from fish spawning earlier than wild fish.

The smaller the genetic difference between the hatchery fish and wild fish the smaller the expected effect on the wild population. The genetic difference can be reduced by using native wild fish which are adapted to that particular stream system for brood stock to initiate the hatchery program and in subsequent generations. Hatchery practices could be modified to reduce artificial selective pressures such as selection for early time-of-return and rapid growth in the hatchery. These modifications extend the period of egg collection and prevent destruction of slow-growing individuals (grade-outs). This decrease in efficiency represents the cost of reducing the genetic differences between hatchery and wild fish.

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