as shallows at stream edges or in close proximity to physical objects. Recently emerged steelhead trout fry, observed adjacent to my study area in the Cedar River in 1965-66, were rarely found along sandy shore areas but were commonly seen among rocks at depths of 1 to 5 cm—when disturbed they hid under the rocks. The use of extreme shallows by steelhead trout fry may in part be an innate response to predators since this type of habitat in streams is relatively barren of other fish.

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HERITABLE RESISTANCE TO GAS BUBBLE DISEASE IN FALL CHINOOK SALMON, *ONCORHYNCHUS TSHAWYTSCHA*[1]

Construction of a series of dams on the Columbia River has resulted in air-supersaturation of the river during spring and early summer. Air-supersaturation is caused by the entrainment of air in water at depths as great as about 15 m in the plunge basins of the spillways below each dam. The level of air-supersaturation varies according to the amount of water-flow over the spillways (Ebel 1969). Supersaturation levels which are known to be fatal to salmonid fishes (Rucker and Hodgeboom 1953; Westgard 1964; Ebel 1969; and Blahm et al. 1975) are often sustained in the Columbia River from April through July, the period when many juvenile salmonids emigrate to the ocean.

Salmonids vary greatly in their tolerance for supersaturation (Ebel 1969). If a portion of this variability is related to additive genetic factors, an increase in the average tolerance of salmon populations to air-supersaturation can be expected as a result of selection. The purpose of this study was to estimate the influence of genetic factors on resistance to gas bubble disease for fall chinook salmon, *Oncorhynchus tshawytscha*. Specifically, the objectives were: 1) To determine the heritability of resistance to death from gas bubble disease for a stock of Columbia River fall chinook salmon, and 2) to determine the inherent level of resistance to gas bubble disease for several fall chinook salmon stocks.

Methods

Estimation of Heritability

Juvenile fall chinook salmon representing 80 families were reared at the Abernathy Salmon Cultural Development Center, near Longview, Wash. The families were produced by mating 20 males to 80 females, 4 females per male, in a nested breeding experiment. One hundred fish from each family were marked by cold-branding (Everest and Edmundson 1967) when they were 4 mo old and their weights averaged 2 g. Each group of 100 fish received a unique mark.

Thirty marked fish from each family were put into each of three tanks (1.8 m in diameter and 0.3 m deep) at the Abernathy Center. These groups of 30 fish will be referred to as tank-families. The remaining 10 fish from each family were put into a similar tank as a control. The test tanks were supplied with 18.9 liter/min of water which was air-supersaturated to 130 $\pm$ 1.5%.

Two variables, time to death for each fish after exposure to air-supersaturated water and the percentage survival for each family after 36 h of exposure, were examined.

Water to be air-supersaturated was directed into a pump to create a line pressure of 1.4 kg/cm^2. A controlled amount of air was injected into the line through an air stone inserted at a joint in the line. Aeration occurred under pressure in a 1.5-m vertical section of line. The test water then entered a pressurized tank where excess air was vented. Air-supersaturated water from the pressure tank was then jetted below the surface into the test tanks.

Stock Comparisons

Since differences between stocks of fish in their resistance to gas-bubble disease arise from both genetic and environmental factors, the fish used in the present experiments were reared in one location under controlled conditions to minimize differences related to environment. Differences in the groups of fish tested then were assumed to have a genetic basis.

Locations on or near the Columbia River that are discussed in this report are the following approximate distances (kilometers) upstream from the Pacific Ocean: Abernathy Salmon Cultural Development Center, 72; Kalama Hatchery, 105; Bonneville Dam, 234; Little White Salmon Hatchery, 265; Little Goose Dam, 635.

Experiment I.—In the fall of 1972, eggs were taken from mature fall chinook at Little Goose Dam on the Snake River, and at Trask River Salmon Hatchery. Smolts migrating downstream from Little Goose Dam must pass over seven dams and swim through water which may be air-supersaturated up to 130% (Beiningen and Ebel 1971). The Trask River enters the Pacific Ocean about 80 km south of the Columbia River and has never been known to contain lethal levels of air-supersaturated water. Eggs obtained at the Trask River Salmon Hatchery were taken from a large number of crosses, and eggs obtained at Little Goose Dam were from crosses between two males and two females.

Fertilized eggs from each source were transported to Oregon State University where they were incubated at 9.5°C. The fry were fed for 2 mo before being exposed to 127% air-supersaturated water. At the time of testing, the fish weighed between 1.3 and 1.5 g.

Air-supersaturated water was produced by aerating water under a hydrostatic head of 3 m in a vertical column of 15.2-cm pipe. A regulated amount of air was injected into the lower portion of the column through four air stones. Water drawn from the bottom of the column was 123% air-supersaturated. This water was then heated to 13.5°C to attain the test level of 127 $\pm$ 2% supersaturation.

Experiment II.—In 1973, fall chinook eggs were obtained from Abernathy Salmon Cultural Development Center, Little White Salmon Hatchery, and Kalama Hatchery—all on the Columbia River—and from the coastal Trask River Salmon Hatchery. Eggs from fish at Columbia River hatcheries were taken on 2 October, and those from fish at Trask River Hatchery on 28 November. All eggs were taken to Oregon State University for incubation, rearing, and testing.

Because of differences in ages, the experimental groups had to be tested at different times. We held the test fish in a constant environment at equal densities during the rearing period. The fingerlings were reared at 13.5°C in a 5.2 m × 0.3 m × 0.3 m Plexiglas[2] tank which was divided into 16 sections. The sections were divided into four blocks of four tanks each. Fifty fish from each of the four stocks were put into one section in each of the four blocks establishing a randomized block design. Fish were reared for 50 days, at the end of which time they weighed from 1.0 to 1.7 g. Seven days before testing, each group of fish was marked with a group-specific cold brand.

The fish were exposed to 127 $\pm$ 2% air-supersaturated water at 11°C in a 16.5-liter tank. Time to 50% mortality, proportion dead in 96 h, and proportion dead in 150 h were determined. An apparatus similar to that described above for tests at the Abernathy Center was used in this experiment. In all tests, we measured the total

uncompensated hyperbaric dissolved gas pressure with a Weiss saturometer.

Results

Estimation of Heritability

Initial mortalities occurred 3 h after the test fish were placed in 130% air-supersaturated water. All fish were dead after 132 h. The grand means of time to death (hours) in the three tanks were 22.62, 24.66, and 25.04. Two fish died in the control tank.

Because of counting errors at time of marking, individuals per tank-family ranged from 5 to 54. Few tank-families varied greatly from the expected number per family (28.4) as was indicated by the harmonic mean (26.8). Because of the unequal numbers of individuals per tank-family and the large number of observations, an unweighted means analysis of variance was used (Kempthorne 1957). First, the unweighted means of each family in each tank were subjected to an analysis of variance (Table 1). Second, all observations were used in a one-way analysis of variance to compute the within tank-families (error) sum of squares. Because the distribution of time to death for fish in each tank followed a poisson distribution, a square root transformation of time to death was applied before the analysis of variance was carried out. The square root transformation is the most appropriate for poisson data (Bartlett 1936).

Variance components were estimated as:

$$\sigma_M^2 = (MS_M - MS_F)/tf = 0.027$$

$$\sigma_F^2 = (MS_F - MS_{MFT})/t = 0.041$$

$$\sigma_{MFT}^2 = (MS_{MFT} - (1/\bar{n}_h)MS_W) = 0.024$$

$$\sigma_W^2 = MS_W = 2.800.$$

The additive genetic variance, V_A, was estimated as $4\sigma_M^2$, and the total phenotypic variance, V_P, as $\sigma_M^2 + \sigma_F^2 + \sigma_{MFT}^2 + \sigma_W^2$. Heritability, h^2, or V_A/V_P, was $4(0.027)/2.892 = 0.037$. The standard error was 0.022 (Dickerson 1959).

Survival for each tank-family after 36 h of exposure to the test conditions ranged from 53.8 to 0%. The angular transformation was applied to these data before the analysis of variance described above was performed. The theoretical binomial variance, 821, was then used as an estimate of error variance. Heritability of resistance to gas bubble disease estimated in this analysis was: $V_A/V_P = 30.68/840.87 = 0.036$.

Stock Comparisons

Resistance to gas bubble disease by offspring of fall chinook salmon from Little Goose Dam and Trask River Salmon Hatchery exposed to 127% supersaturation in Experiment I differed markedly. Time to 50% mortality, averaged from two replicates, was 73.5 h for Trask River fish and 154 h for fish from Little Goose Dam; the difference of 80.5 (SE = 3.39) was highly significant.

The difference in time to 50% mortality in Experiment II (Table 2) between Columbia River and Trask River stocks (22.25 h; SE = 6.37) was

TABLE 1.—Analysis of variance of the square root of time to death for juvenile fall chinook salmon exposed to air-supersaturated water.

Source of variation	Degrees of freedom	Mean squares	Expectation of mean square
Tanks (T)	(t-1) = 2		
Males (M)	(m-1) = 19	0.575	$\sigma_{MFT}^2 + \frac{1}{\bar{n}_h}\sigma_W^2 + t\sigma_F^2 + tf\sigma_M^2$
Females within males (F)	m(f-1) = 60	0.250	$\sigma_{MFT}^2 + \frac{1}{\bar{n}_h}\sigma_W^2 + t\sigma_F^2$
Male-females by tanks (MFT)	(mf-1)(t-1) = 158	0.128	$\sigma_{MFT}^2 + \frac{1}{\bar{n}_h}\sigma_W^2$
Error (E)[1]	N . . .-mft = 6,566	2.800	σ_W^2

where: m = number of males
f = number of females per male
t = number of tanks (replicates)
$N . . .$ = total number of individuals
$\bar{n}_h$ = harmonic mean number of individuals per tank family = 26.82

[1]Error mean square obtained in separate analysis (see Kempthorne 1957:459).

TABLE 2.—Hours to 50% mortality (ET_{50}), and percentages dead in 96 h (P96) and 150 h (P150) for juvenile chinook salmon exposed to air-supersaturated water in Experiment II. Each value represents an average of four replicates; ranges are shown in parentheses.

Stock	ET_{50}	P96	P150
Abernathy	92.5 (70-116)	53 (43-64)	68.5 (63-80)
Little White Salmon	86.5 (82-94)	61 (57-67)	77.0 (75-80)
Kalama	73.8 (64-79)	64 (60-70)	86.0 (73-95)
Trask	62.0 (48-75)	70 (64-82)	86.8 (75-96)

TABLE 3.—Analysis of variance in time to 50% mortality for Trask and Columbia River chinook salmon (Experiment II).

Source of variation	Degrees of freedom	Mean squares	F
Total	15		
Blocks	3	367.7	3.02
Between stocks	3	739.5	6.07*
Columbia vs. Trask	1	1,485.2	12.19**
Within Columbia	2	366.6	3.01
Error	9	121.8	

*, **, statistical significance at the 0.05 and 0.01 levels, respectively.

significant (Table 3). Variation between the three Columbia River stocks was not significant.

Similar comparisons were made from data summarized after 96 and 150 h of exposure (Table 2). On the average, differences between Columbia and Trask stocks remained significant, but variation between Columbia River stocks became significant only after 150 h of exposure ($F = 5.01$). This difference was between the Kalama stock and other lower Columbia River stocks, suggesting that a difference in resistance to gas bubble disease exists even between stocks separated by relatively short distances. The reason for the similarity of resistances between lower Columbia River stocks probably was their common origin: Abernathy brood stock were originally taken from Spring Creek and Willard hatcheries, both of which are located upstream from Bonneville Dam.

The much greater difference in time to 50% mortality between fish taken from Little Goose Dam and fish from the Trask River (80.5 ± 3.39 h) than between combined lower Columbia stocks and the Trask stock (22.25 ± 6.37 h) indicates that fall chinook salmon migrating as far as Little Goose Dam are more resistant to gas bubble disease than are lower Columbia River stocks. This conclusion could be made only by comparing results from Experiments I and II, and by assuming that the results were not biased by the small number of crosses made at Little Goose Dam.

Discussion

Differences between stocks indicated that selection for phenotypes with greatest resistances to gas bubble disease has occurred in the Columbia River. This conclusion was supported by the observation that stocks with the longest histories of exposure to air-supersaturated water were most resistant to gas bubble disease.

Because additive genetic variance contributing to the observed differences probably has been reduced, and reduced at an unknown rate, it is impossible to estimate accurately the selection intensities that must have occurred in the past to produce the differences in resistance observed between Trask and Columbia River stocks. The low heritability for resistance to gas bubble disease in fall chinook salmon indicates that no great increases in resistance can be expected even at relatively high selection intensities.

The results further indicate that stocks transferred from coastal streams to hatcheries within the Columbia River drainage may experience high levels of mortality from gas bubble disease. On the other hand, Columbia River stocks may provide a source of brood fish that are resistant to gas bubble disease for stocking in other waterways.

Acknowledgments

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