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Effects of Complete Redd Dewatering on Salmonid Egg-Hatching Success and Development of Juveniles

DUDLEY W. REISER[1] AND ROBERT G. WHITE[2]

Idaho Cooperative Fishery Research Unit, University of Idaho Moscow, Idaho 83843

Abstract

The effects of prolonged stream desiccation on development of salmonid eggs were simulated for steelhead *Salmo gairdneri* and spring chinook salmon *Oncorhynchus tshawytscha*. Recently fertilized eggs were placed in artificial redds and subjected to controlled water flows in outdoor laboratory channels. Control redds were continuously submerged. "Dewatered" redds were exposed to air; water flowed through the substrate 10 cm below the eggs. Eggs were dewatered 1–4 weeks (steelhead) or 1–5 weeks (chinook salmon) before they were returned to water in hatchery incubators, where hatching success and subsequent fry development were monitored. Several combinations of cobble, coarse sediment, and fine sediment used to cover eggs did not influence egg development, provided the mixtures retained at least 4% moisture by weight. Dewatered eggs hatched sooner than control eggs; faster hatch was associated with higher substrate temperature in exposed redds. Hatching success of dewatered eggs averaged 94% for steelhead (control: 88%) and 76% for chinook salmon (control: 56%) and was not affected by the time eggs had been dewatered. After 8 (chinook salmon) and 8.5 (steelhead) weeks of rearing, juveniles from dewatered and control eggs had grown equally well.

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Diversion of water for agricultural, industrial, and domestic purposes can reduce streamflow severely. When depleted streams have been used by salmonids for spawning, redds may become dewatered below the level of the eggs. Potential consequences include desiccated or frozen eggs (Neave 1953; McNeil 1966; Becker et al. 1982) and impaired embryonic development. In several laboratory studies (Borodin 1927; Domurant 1956; Reiser and White 1981a), the ability of salmonid embryos to develop in moist conditions without being submerged in water has been measured, but these results cannot be extrapolated to natural conditions. Our study addressed the effect of prolonged egg dewatering on hatching success and on development of larvae and juveniles. We also investigated the influence of sediment quality on egg survival.

[1] Present address: Bechtel Group, Incorporated, Environmental Services Department, Fifty Beale Street, Post Office Box 3965, San Francisco, California 94119.

[2] Present address: Montana Cooperative Fishery Research Unit, Montana State University, Bozeman, Montana 59717.

Methods

Our experiments with steelhead *Salmo gairdneri* and spring chinook salmon *Oncorhynchus tshawytscha* occurred at the Idaho Department of Fish and Game's Hayden Creek Research Station near Lemhi, Idaho. Our tests with newly fertilized eggs began on 22 May 1979 for steelhead and on 6 September 1979 for chinook salmon. Eggs used in both tests came from 2–3 females and were fertilized by 2–3 males. Steelhead eggs were obtained from Dworshak National Fish Hatchery, Idaho; chinook salmon eggs were from the Cowlitz River Hatchery, Washington.

To simulate salmonid spawning beds we used two 1.2 m wide × 2.4 m long channels each subdivided into eight 1.2 m long × 0.3 m wide × 0.3 m deep chambers in which flows could be controlled independently (Fig. 1). The channels were installed outside to allow environmental exposure and were plumbed with Hayden Creek water. Water-surface slope for the chambers was 2%. One channel was used for steelhead, two for chinook salmon.

Artificial redds were Whitlock–Vibert (W–V) boxes (Whitlock 1979) filled with 6.4–50.8 mm gravel. Four boxes were placed equidistantly in

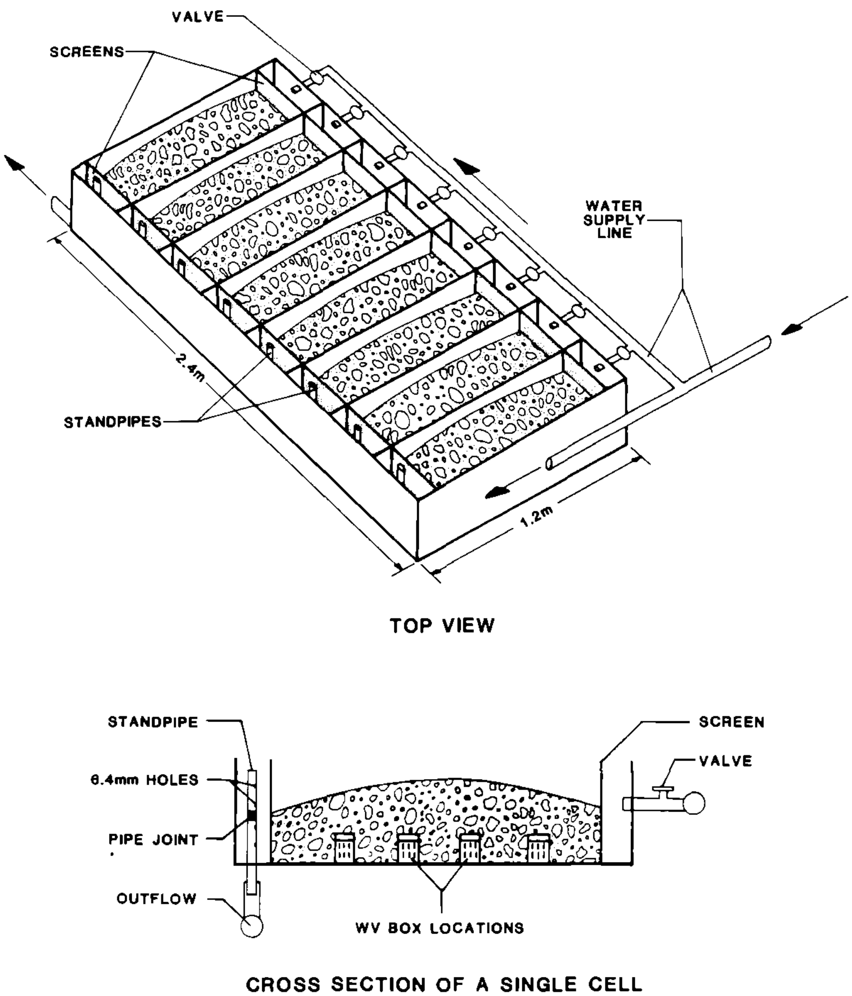

FIGURE 1.—*Top and cross-sectional views of experimental chambers used in dewatering tests with salmonid eggs. Water levels in dewatered chambers were about 10.0 cm below the eggs. WV = Whitlock–Vibert.*

each chamber. The boxes sat on a 2.5-cm-thick layer of cobble and were covered with one of four sediment mixtures chosen on the basis of previous tests (Reiser and White 1981b) to provide a range of sediment quality. The sediment ingredients were rounded river cobble (13–76 mm diameter), "coarse" particles (0.84–4.6 mm), and "fine" particles (less than 0.84 mm); particle size was determined with sieves. The volumetric contributions of each ingredient to the mixtures, determined by water displacement, were

Mix 1: 10% fine, 90% cobble;
Mix 2: 20% coarse, 80% cobble;
Mix 3: 10% fine, 20% coarse, 70% cobble;
Mix 4: 20% fine, 30% coarse, 50% cobble.

Mixtures 2 and 3 were used with chinook salmon; all four mixtures were used with steelhead. Sediments were not removed between the steelhead and chinook salmon tests. In the tests with chinook salmon, some chambers were shielded from rain and snow to determine the effect of precipitation on the results. Water-filled vials were inserted in the sediments during the chinook salmon tests to allow detection of freezing conditions (as indicated by any broken glass collected later).

To start a test, 100 eggs were placed in each W–V box within 24 hours of their fertilization. Flows through each chamber were established so that about 2.5 cm of water covered all sediment mixtures; this corresponded to inflows of 300 ml/second. After 3 days, water flows in half the chambers of each sediment or sediment–shelter treatment were reduced to a level approximately 10 cm below the eggs. Water flows were maintained below the eggs to simulate groundwater flows. At each of four weekly intervals thereafter, eggs were removed from one W–V box in each chamber, checked for survival, and transferred to a Heath stack tray incubator. Steelhead eggs were removed at weeks 1, 2, 3, and 4 (the last batch having been dewatered four consecutive weeks), but because mortality within the first sample was unusually high, a consequence, we felt, of handling during the "tender" (pre-eyed) phase of egg development, we delayed sampling chinook salmon eggs until week 2 and extended it through week 5.

For the steelhead tests, the channel contained four unreplicated experiments stratified by sediment mixtures. Within each experiment, the eggs in one chamber were dewatered, and those in a second chamber were kept inundated. Within each chamber, each W–V box represented one exposure duration. For chinook salmon, four experiments—two sediment mixtures, each with or without a precipitation shelter—were spread over two channels, but this time the experiments were repeated; chambers with duplicate treatments were side by side.

Once eggs were transferred to Heath stack trays, we checked them daily for proportions hatched and preserved random samples of alevins in 10% formalin. After alevins absorbed their yolk sacs, we transferred samples of juveniles from each treatment group to separate rearing compartments within four parallel fiberglass troughs. Screens divided each trough into eight compartments, each 0.6 m long × 0.56 m wide × 0.30 m deep. Compartments were filled with the juveniles in the order that eggs had been retrieved from W–V boxes; the lower compartments contained fish from the first two weekly egg samples and the uppermost compartments contained those from the 4- (steelhead) or 5- (chinook salmon) week samplings. Within each trough, fish from dewatered or control eggs of the same sediment experiments occupied similar compartment positions. We used a programmed feeding schedule based on average fish weight throughout the rearing tests. Fish were inventoried and weighed weekly from 19 August to 18 October 1979 for steelheads and from 15 January to 12 March 1980 for chinook salmon. After the final inventories, random samples of juveniles were preserved in 10% formalin; these and the previously preserved fish were measured for total length to the nearest 0.5 mm and weighed to the nearest 0.1 mg.

During the outdoor phase of the experiments, temperatures of dewatered sediments in four chambers were measured with Pacific Transducer remote-bulb thermometers placed at egg level. Temperatures were recorded at 0800 hours (minimum temperatures), 1200 hours (increasing), and 1600 hours (maximum) and averaged. During the steelhead tests, temperatures of dewatered substrate in one chamber were continuously recorded with a Partlow thermograph, which confirmed that minimum and maximum temperatures were near 0800 and 1600 hours, respectively. Air and water temperatures were monitored with Taylor and Weathermeasure thermographs. When the W–V boxes were recovered each week, sediment samples were taken adjacent to those boxes that had been dewatered. These sediments were weighed, dried in a forced-air oven at 110 C for 24 hours, and reweighed; the weight losses corresponded to the moisture contents of the samples.

Results

Egg-Hatching Success

Most of the steelhead eggs sampled at week 1 failed to hatch (Table 1). We attribute this to handling, not to treatment effects. Dewatered eggs sampled later averaged 94% hatch versus 88% for watered controls. Over all treatments, hatching success of dewatered and control eggs differed neither with respect to sediment quality ($\chi^2 = 4.22$; 3 df; $P > 0.10$) nor with respect to sampling time ($\chi^2 = 0.04$; 3 df; $P > 0.10$). Thus, the length of the dewatering period did not influence egg-hatching success.

Dewatered eggs of chinook salmon averaged 76% hatch (Table 1) and, as for steelhead, hatching success was unrelated to the length of the dewatering period ($\chi^2 = 5.53$; 3 df; $P > 0.10$). The hatch of continuously watered chinook salmon eggs declined with time, however, and the effect was particularly evident for the treatment containing the mix of fine and coarse sediments. Thus, egg-hatching success was affected by both hydration and sediment mix ($\chi^2 = 6.53$; 1 df; $P < 0.05$). This may have been

TABLE 1.—*Percentage hatch of steelhead and chinook salmon eggs, based on 100 eggs per artificial redd, as functions of sediment quality, presence or absence of precipitation shelters, and weeks eggs were dewatered. "Watered" eggs were controls.*

Treatment: sediment mix;[a] precipitation shelter; dewatered or watered redds	Weeks redds were dewatered								Mean % hatch	
	Steelhead[b]				Chinook salmon[c]					
	1	2	3	4	2	3	4	5	Steel-head[d]	Chinook salmon[e]
10% fine										
Without shelter										
Dewatered	23	97	91	97					95	
Watered	13	93	82	54					76	
20% coarse										
Without shelter										
Dewatered	39	98	93	98	76	80	83	71	96	78
Watered	19	73	73	97	76	75	82	66	81	75
With shelter										
Dewatered					72	75	68	72		72
Watered					79	60	68	79		72
10% fine, 20% coarse										
Without shelter										
Dewatered	50	98	82	91	85	86	77	75	90	81
Watered	28	100	91	98	80	56	34	34	96	51
With shelter										
Dewatered					77	70	76	74		74
Watered					74	38	2	0		29
20% fine, 30% coarse										
Without shelter										
Dewatered	68	93	95	67					85	
Watered	72	100	97	98					98	
Mean										
Dewatered	45	97	90	88	78	78	76	73	92	76
Watered	33	92	86	87	77	57	47	45	88	57

[a] "Fine" particles had diameters <0.84 mm; "coarse" sediments were 0.84–4.6 mm in diameter. Percentages are volumetric contributions; the unstated difference comprised 13–76-mm cobble.
[b] Unreplicated values.
[c] Means of two replications.
[d] Weeks 2–4 only.
[e] Mean of replicate means.

due to additional fine sediments imparted with Hayden Creek water during the previous steelhead tests and deposited within the interstitial spaces of the watered substrate. Visual comparisons of dewatered and watered sediments during the chinook salmon tests indicated that extraneous fine material had accumulated in the latter; the effect would have been to reduce water flow through the substrate, and to impair the transport of oxygen to, and metabolites from, the eggs.

Eggs that had been dewatered hatched earlier (in the Heath stack incubator) than controls. This was most evident for steelhead eggs dewatered 3 and 4 weeks, for which median hatching dates were advanced as much as 11 days and an average of about 8 days (Table 2). We did not monitor hatching times for chinook salmon as closely as for steelheads; hatching dates for chinook salmon eggs dewatered 4–5 weeks were several days earlier than for controls, although differences were not as pronounced as in steelhead tests. Differences in hatching times between watered and dewatered eggs were probably the result of the higher temperatures in dewatered sediments, which exposed dewatered eggs to more temperature units (degree-days above 0 C) than control eggs (Table 2).

During steelhead tests, water temperatures began at 5.5 C on 23 May, reached a low of 3.3 C on 24 May, then moved irregularly upwards to a high of 8.5 C on 20 June. Temperatures of dewatered sediments were consistently

TABLE 2.—*Dates of median hatch (50% of eggs hatched) of steelhead eggs in relation to dehydration of sediments, length of dewatering period, and sediment type, plus temperature units accumulated during tests in watered and dewatered sediments.*

		Sediment mixture[a]			
Sampling period	Water	10% fine	20% coarse	10% fine + 20% coarse	20% fine + 30% coarse
		Date of median hatch			
1 week					
Dewatered eggs		6 Jul	5 Jul	5 Jul	4 Jul
Watered eggs		7 Jul	8 Jul	7 Jul	7 Jul
2 weeks					
Dewatered eggs		30 Jun	1 Jul	1 Jul	29 Jun
Watered eggs		3 Jul	3 Jul	3 Jul	3 Jul
3 weeks					
Dewatered eggs		25 Jun	25 Jun	25 Jun	25 Jun
Watered eggs		3 Jul	4 Jul	3 Jul	30 Jun
4 weeks					
Dewatered eggs		23 Jun	23 Jun	26 Jun	23 Jun
Watered eggs		4 Jul	2 Jul	3 Jul	29 Jun
		Accumulated temperature units, watered and dewatered sediments[b]			
1 week	36	69	53	61	50
2 weeks	76	138	117	127	109
3 weeks	125	234	196	213	183
4 weeks	179	322	263	279	258

[a] "Fine" particles had diameters <0.84 mm; "coarse" sediments were 0.84–4.6 mm in diameter. Percentages are volumetric contributions; the unstated difference comprised 13–76-mm cobble.

[b] One temperature unit (T.U.) equals 1 C above 0 C for 24 hours.

higher, ranging from 3.3 C on 29 May to 14.4 C on 12 June, after which they decreased an average of about 2 C. Overall, temperatures in the dewatered sediment with 10% fine particles (Mix 1) averaged higher than the others, possibly because this chamber was exposed longer to the sun than the others.

During chinook salmon tests, water temperatures trended downward from 11.4 C on 8 September to 5.0 C in mid-October; no freezing occurred in the sediments. Air temperatures dropped below water temperatures briefly in early October, but generally were 3–7 C warmer. As in the steelhead tests, temperatures of dewatered sediments typically stayed above those of watered sediments (Table 2), although unsheltered sediments sometimes were cooler than the water during October. Sheltered substrates remained some 2 C warmer than their unsheltered counterparts; sheltered sediments with 20% coarse particles (Mix 2) were the warmest over all, and unsheltered substrates with 10% fine and 20% coarse particles (Mix 3) were the coolest.

Moisture contents of dewatered sediments were 3.1–8.8% by weight in the steelhead tests, and 4.4–8.1% during the chinook salmon tests (Table 3). The length of the dewatering period had little (and no consistent) effect on these values. The highest moisture levels in the steelhead tests occurred in the sediment mixture containing 20% fine and 30% coarse particles (Mix 4); sediments with 10% fine and 20% coarse particles (Mix 3) had the greatest moisture during chinook salmon tests. In general, the mixtures with the least amount of total (noncobble) sediment (Mix 1 and Mix 2) had the smallest percentage of moisture. Over all, no differences in moisture content could be directly attributed to precipitation (rain or snow fell on 8 days during the steelhead tests, on only 1 day during the chinook salmon test) or shelters.

Alevin and Juvenile Development

Because sampling times varied, sizes of steelhead alevins (yolk-sac larvae) could not be compared statistically with respect to treatments they had received as eggs. We saw examples of Siamese-twin (two-bodied) and two-headed ale-

TABLE 3.—*Moisture conditions (% by weight) in dewatered sediments in relation to length of dewatering period during steelhead and chinook salmon tests.*

Duration of dewatering	Steelhead tests: sediment mixture[a]				Chinook salmon tests: sediment mixture[a]			
					20% coarse		10% fine + 20% coarse	
	10% fine	20% coarse	10% fine + 20% coarse	20% fine + 30% coarse	Sheltered	Unsheltered	Sheltered	Unsheltered
1 week	4.6	4.1	4.1	7.3				
2 weeks	4.2	3.1	3.7	6.9	4.4	4.9	8.1	6.0
3 weeks	4.7	4.5	4.9	8.8	5.7	5.8	7.8	7.0
4 weeks	3.5	3.9	5.2	8.7	5.7	5.4	7.7	4.9
5 weeks					4.4	5.4	7.5	7.7

[a] "Fine" particles had diameters <0.84 mm; "coarse" sediments were 0.84–4.6 mm in diameter. Percentages are volumetric contributions; the unstated difference comprised 13–76-mm cobble.

vins, but frequencies of these structural anomalies were no greater for groups that had been dewatered than for those that had not.

After 60 days rearing in the fiberglass troughs, steelheads from dewatered eggs did not differ significantly from controls in mean length ($P > 0.05$, Duncan's Multiple Range Test; Ott 1977) or mean weight ($P > 0.10$). Mean total length of juveniles ranged from 51.7 to 58.6 mm (watered eggs) and from 49.5 to 58.2 mm (dewatered eggs) (Table 4). Over all, we found no significant difference in final length ($P > 0.05$) or final weight ($P > 0.10$) among groups of steelhead with respect to the interaction of sediment type, watering regime, and sampling period. Significant differences in fish length and weight were found among sediment types. However, these were caused by unintentional differences in temperature of the rearing water; valves to two sources of water had been opened erroneously, resulting in two thermally different sources of rearing water. Growth rates of steelheads from dewatered eggs (0.014–0.026 g/day) did not differ significantly ($P > 0.05$) from those of controls (0.014–0.029 g/day).

Lengths of chinook salmon alevins from dewatered eggs significantly exceeded ($P < 0.05$) lengths of those from watered eggs, although weights did not ($P > 0.10$). Mean total lengths ranged from 22.0 to 24.6 mm for alevins from watered eggs and from 24.0 to 26.2 mm for those from dewatered eggs (Table 4). Mean weights were 295.0–327.0 mg and 290.0–331.0 mg for alevins from watered and dewatered eggs, respectively. Length differences probably were due to variations in intragravel temperatures. No significant differences ($P > 0.05$) in length or weight of alevins could be attributed to shelters, sediment type, or sampling period. As in the steelhead test, no increase in alevin anomalies resulted from dewatering of eggs.

After 57 days rearing, the lengths, weights, and growth rates of chinook salmon juveniles from dewatered eggs (51.7–56.2 mm; 1.36–1.81 g; 0.017–0.024 g/day) did not differ significantly ($P > 0.10$) from those of controls (46.9–57.5 mm; 1.25–1.85 g; 0.015–0.025 g/day) (Table 4).

Discussion

Fisheries and resource managers generally have believed that the dewatering of salmonid redds would result in the rapid desiccation of eggs. Dewatered redds were considered a total loss to recruitment. Our dewatering tests in experimental channels indicate that salmonid eggs can tolerate 1–5 weeks dewatering with essentially no effects on hatching success, or on development and growth rates of alevins and juveniles, provided sediment moisture content is at least 4% by weight and the sediments neither freeze nor reach temperatures that exceed incubation tolerances. In somewhat contrasting studies, Reiser (1981) and Reiser and White (1981b) found a significant increase in the mortality of newly fertilized eggs when streamflows were severely reduced over experimental redds. However, those tests were not designed to evaluate the effects of complete redd dewatering, but rather the effects of surface-flow reduction on the intragravel environment and the eggs harbored within. The reduction in flow associated with those tests resulted in the eggs being incubated in essentially stagnant water. Thus

TABLE 4.—*Development of steelhead juveniles and chinook salmon alevins (yolk-sac larvae) and juveniles in relation to sediment, dewatering, and shelter treatments given to their egg stages.*

Egg treatment: sediment mix;[a] sheltered chambers or not; dewatered (D) or watered (W); weeks of dewatering or watering (2–5)	Steelhead juveniles (60 days posthatch)[b]				Chinook salmon alevins (1–2 days posthatch)			Chinook salmon juveniles (57 days posthatch)			
	N	Mean total length (mm) ± S.D.	Mean total wet weight[c] (g)	Growth rate (g/day)	*N*	Mean total length (mm) ± S.D.	Mean total wet weight[c] (mg)	*N*	Mean total length (mm) ± S.D.	Mean total wet weight[c] (g)	Growth rate (g/day)
10% fine											
Without shelter											
D-2	65	53.8 ± 5.8	1.72	0.018							
W-2	65	52.6 ± 6.2	1.82	0.021							
D-3	45	55.2 ± 6.2	1.81	0.019							
W-3	56	55.5 ± 6.5	1.95	0.023							
D-4	[d]	[d]	2.05	0.024							
W-4	34	57.9 ± 5.5	2.22	0.029							
20% coarse											
Without shelter											
D-2	48	55.6 ± 5.2	1.90	0.018	15	25.2 ± 0.88	319	20	53.5 ± 2.9	1.45	0.018
W-2	42	55.7 ± 7.7	1.75	0.021	15	24.0 ± 0.77	323	20	56.1 ± 3.2	1.60	0.021
D-3	35	57.0 ± 7.0	2.07	0.026	15	24.8 ± 0.90	322	20	55.1 ± 4.1	1.75	0.023
W-3	38	52.0 ± 7.5	1.56	0.019	15	23.9 ± 0.77	327	20	49.6 ± 5.0	1.39	0.017
D-4	42	58.2 ± 6.7	2.13	0.023	15	25.0 ± 0.91	322	20	54.3 ± 3.3	1.59	0.021
W-4	49	58.6 ± 5.2	2.20	0.027	15	24.6 ± 0.97	297	20	56.5 ± 2.7	1.69	0.022
D-5					15	24.7 ± 1.15	328	20	56.2 ± 2.9	1.81	0.024
W-5					15	23.6 ± 1.53	287	20	55.9 ± 4.1	1.68	0.022
With shelter											
D-2					15	24.1 ± 0.73	320	20	54.9 ± 3.8	1.72	0.023
W-2					15	23.5 ± 0.79	299	20	53.2 ± 3.7	1.35	0.016
D-3					15	25.9 ± 0.59	319	20	53.8 ± 3.5	1.39	0.017
W-3					15	23.2 ± 0.68	295	20	55.7 ± 2.1	1.71	0.024
D-4					15	26.2 ± 0.99	331	20	56.8 ± 3.2	1.75	0.023
W-4					15	22.8 ± 1.07	322	20	54.8 ± 3.5	1.47	0.019
D-5					15	24.6 ± 0.94	293	20	52.0 ± 2.4	1.42	0.018
W-5					15	22.8 ± 1.08	300	20	57.8 ± 2.5	1.85	0.025
10% fine, 20% coarse											
Without shelter											
D-2	74	52.5 ± 5.9	1.59	0.017	15	25.4 ± 0.89	310	20	54.8 ± 2.6	1.47	0.019
W-2	74	52.1 ± 4.8	1.51	0.016	15	24.4 ± 0.97	311	20	54.3 ± 3.3	1.38	0.017
D-3	79	49.5 ± 6.8	1.33	0.014	15	24.2 ± 1.11	310	20	52.7 ± 5.0	1.46	0.018
W-3	66	54.1 ± 4.1	1.72	0.020	15	22.1 ± 1.12	307	20	52.9 ± 3.8	1.37	0.017
D-4	79	54.1 ± 4.4	1.64	0.017	15	24.0 ± 1.04	327	20	53.3 ± 3.5	1.36	0.017
W-4	76	51.7 ± 6.0	1.49	0.015	15	23.3 ± 1.24	305	19	52.3 ± 3.3	1.25	0.015
D-5					15	24.1 ± 0.81	303	20	55.7 ± 3.6	1.57	0.020
W-5					15	22.3 ± 1.36	301	20	54.0 ± 2.8	1.45	0.018
With shelter											
D-2					15	25.0 ± 0.57	300	20	53.6 ± 3.3	1.41	0.017
W-2					15	23.9 ± 1.42	302	20	53.7 ± 4.5	1.53	0.020
D-3					15	24.3 ± 0.68	303	20	52.6 ± 5.5	1.46	0.018
W-3					14	24.0 ± 0.79	306	18	53.0 ± 3.9	1.50	0.019
D-4					15	24.5 ± 0.96	295	20	51.7 ± 4.2	1.39	0.017
W-4					4	22.0 ± 0.41	325	[d]	[d]	[d]	[d]
D-5					15	24.0 ± 0.58	290	20	54.6 ± 3.1	1.48	0.019
W-5					[d]		[d]	[d]	[d]	[d]	[d]
20% fine, 30% coarse											
Without shelter											
D-2	55	55.7 ± 4.2	1.87	0.019							
W-2	44	52.3 ± 6.0	1.42	0.014							
D-3	39	53.6 ± 5.9	1.59	0.016							
W-3	66	52.1 ± 6.2	1.54	0.018							
D-4	51	55.7 ± 4.2	1.74	0.018							
W-4	44	52.1 ± 6.4	1.48	0.016							

[a] "Fine particles had diameters <0.84 mm; "coarse" sediments were 0.84–4.6 mm in diameter. Percentages are volumetric contributions; the unstated difference comprised 13–76-mm cobble.

[b] Steelheads from the 10% fine and 20% coarse mixtures were reared in spring water (constant temperature, 11–12 C). Those from the 10/20% and 20/30% mixtures were reared in Hayden Creek water (variable temperature, 5–9 C).

[c] Mean weight was recorded during last inventory period of rearing tests.

[d] Missing value.

the supply of oxygen to, and transport of metabolites from, the developing eggs would have been greatly reduced.

Other studies have shown the resilience of salmonid eggs to periods of dewatering. Hobbs (1937) found several redds of brown trout *Salmo trutta* that had been dewatered for about 5 weeks but still contained 83% viable eggs. Similar findings of healthy brown trout eggs within dewatered redds were reported by Hardy (1963). Hawke (1978) found viable chinook salmon eggs within stranded redds in a New Zealand river over which water had not flowed for about 3 weeks. In laboratory studies, Becker et al. (1982) reported chinook salmon egg survivals of over 80% after 12 days of incubation in dewatered conditions. The accepted hatchery practice of shipping eyed salmonid eggs in containers with no water further illustrates resistance to dewatering.

The most obvious effect of long-term dewatering on steelhead and spring chinook salmon eggs was accelerated embryogenesis. The ecological significance of accelerated egg development and earlier hatching dates is not known at this time, but would depend on both density-dependent (for example, food supply) and density-independent (such as water temperature and streamflow) factors, as well as behavioral mechanisms such as territoriality.

Although salmonid embryos may withstand extended periods of dewatering, newly hatched alevins are less tolerant. Reiser and White (1981a) estimated that chinook salmon alevins could withstand less than 10 hours of dewatering, even when kept moist in cotton cloth. Becker et al. (1982) reported about 50% mortality of newly hatched alevins that had been continuously dewatered for 4 hours, and almost 100% mortality of pre-emergent alevins dewatered for 1 hour. Apparently, as noted by Becker et al. (1982), the tolerance to dewatering by alevins decreases with the formation of functional gills.

Silver et al. (1963), Shumway et al. (1964), and Brannon (1965) showed that alevins resulting from eggs incubated at low oxygen concentrations are generally smaller than yolk-sac larvae from eggs incubated at high oxygen concentrations. Low oxygen concentrations in early stages of development may delay hatching and increase the number of anomalies (Alderdice et al. 1958). The lack of treatment effects on fish size and frequency of structural anomalies in our study indicates that dewatered eggs had adequate oxygen supply and metabolite disposal. Oxygen transport to embryos in dewatered redds probably occurs via the influx of air into gravel interstitial spaces, the dissolving of oxygen into the thin layer of water surrounding the egg, and the subsequent diffusion of oxygen through the egg capsule.

The moisture content of the surrounding sediment–substrate mixture is crucial to survival of dewatered eggs, because eggs must be kept moist to prevent their dehydration. Moisture retention depends, to a large degree, on the amount and texture of sediment present in the redd; finer materials retain more moisture. In our tests, the highest moisture levels (9%) were found in the sediment mixture containing the highest percentage of fine particles. In general, moisture levels of about 4% or more maintained viable eggs and allowed normal development and hatching. Moisture retention alone cannot explain the relatively constant moisture levels present over 5 weeks of continuous dewatering. If precipitation is discounted as a source of moisture replacement, two mechanisms acting within the gravel may help sustain high moisture levels. The first, capillary action, entails the upward movement of water from the water table through the sediment interstices (Buckman and Brady 1972). This process is impeded by trapped air and large soil pores and, for this reason, probably only operates in substrate mixtures containing abundant fines or at locations where the water table is close to the eggs. The second mechanism, water-vapor transfer, results from a vapor-pressure gradient between two adjoining areas; this mechanism is likely responsible for moisture replenishment in the coarse textured gravels characteristic of salmonid redds. Thus, if groundwater levels remain close to dewatered eggs, the eggs should remain moist. However, the specific distances from eggs to groundwater within which these moisture-replenishing mechanisms operate are unknown. In our tests, water levels were approximately 10 cm below the dewatered eggs.

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References

ALDERDICE, D. F., W. P. WICKETT, AND J. R. BRETT. 1958. Some effects of temporary exposure to low dissolved oxygen levels on Pacific salmon eggs. Journal of the Fisheries Research Board of Canada 15:229–250.

BECKER, C. D., D. A. NEITZEL, AND D. H. FICKEISEN. 1982. Effects of dewatering on chinook salmon redds: tolerance of four developmental phases to daily dewaterings. Transactions of the American Fisheries Society 111:624–637.

BORODIN, N. 1927. Hatching without running water. Transactions of the American Fisheries Society 57:162–164.

BRANNON, E. L. 1965. The influence of physical factors on the development and weight of sockeye salmon embryos and alevins. International Pacific Salmon Fisheries Commission Progress Report 12.

BUCKMAN, H. O., AND N. C. BRADY. 1972. The nature and properties of soils, seventh edition. MacMillan, New York, New York, USA.

DOMURANT, J. 1956. Embryonic development of trout (*Salmo trutta* L.), pike (*Esox lucius* L.), and roach (*Rutilus rutilus* L.) in waterless environment. Polskie Archiwum Hydrobiologii 3(16): 166–173.

HARDY, C. J. 1963. An examination of eleven stranded redds of brown trout (*Salmo trutta*) excavated in the Selwyn River during July and August 1960. New Zealand Journal of Science 6: 106–119.

HAWKE, S. P. 1978. Stranded redds of quinnant salmon in the Mathias River, South Island, New Zealand. New Zealand Journal of Marine and Freshwater Research 12:167–171.

HOBBS, D. F. 1937. Natural reproduction of quinnant salmon, brown, and rainbow trout in certain New Zealand waters. New Zealand Marine Department Fisheries Bulletin 6.

MCNEIL, W. J. 1966. Effect of the spawning bed environment on reproduction of pink and chum salmon. United States Fish and Wildlife Service Fishery Bulletin 65:495–523.

NEAVE, F. 1953. Principles affecting the size of pink and chum salmon populations in British Columbia. Journal of the Fisheries Research Board of Canada 9:450–490.

OTT, L. 1977. An introduction to statistical methods and data analysis. Duxbury Press, North Scituate, Massachusetts, USA.

REISER, D. W. 1981. Effects of streamflow reduction, flow fluctuation and flow cessation on salmonid embryo incubation and fry quality. Doctoral dissertation. University of Idaho, Moscow, Idaho, USA.

REISER, D. W., AND R. G. WHITE. 1981a. Incubation of steelhead trout and spring chinook salmon eggs in a moist environment. Progressive Fish-Culturist 43:131–134.

REISER, D. W., AND R. G. WHITE. 1981b. Influence of streamflow reductions on salmonid embryo development and fry quality. Idaho Water and Energy Resources Research Institute, Research Technical Completion Report, Moscow, Idaho, USA.

SHUMWAY, D. L., C. E. WARREN, AND P. DOUDOROFF. 1964. Influence of oxygen concentration and water movement on the growth of steelhead trout and coho salmon embryos. Transactions of the American Fisheries Society 93:342–356.

SILVER, S. T., C. E. WARREN, AND P. DOUDOROFF. 1963. Dissolved oxygen requirements of developing steelhead trout and chinook salmon embryos at different water velocities. Transactions of the American Fisheries Society 92:327–343.

Whitlock, D. 1979. The Whitlock-Vibert box handbook. Federation of Fly Fisherman, El Segundo, California, USA.