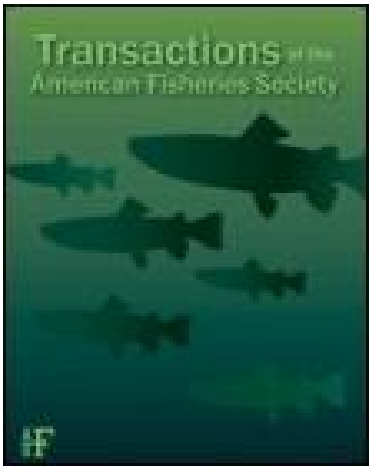

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Effects of Dewatering on Chinook Salmon Redds: Tolerance of Four Developmental Phases to Daily Dewaterings

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Effects of Dewatering on Chinook Salmon Redds: Tolerance of Four Developmental Phases to Daily Dewaterings

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Abstract

Four intergravel developmental phases of chinook salmon *Oncorhynchus tshawytscha* were dewatered experimentally in artificial redds. The redds consisted of aquaria containing a gravel mix and supplied with 4 liters of water per minute at 10 C. Cleavage eggs and embryos (the egg phases), and eleutheroembryos and pre-emergent alevins (the alevin phases) were dewatered 20 consecutive times in 22-day tests. The egg phases were considerably more tolerant than the alevins. Some cleavage eggs were killed by 12- and 16-hour daily dewaterings, but embryos survived up to 22-hour daily dewaterings. Embryos also tolerated extended, multiple dewaterings (over 60% survival for four consecutive 118-hour periods) and one-time, continuous dewatering for up to 12 consecutive days (over 80% survival). In contrast, about half the eleutheroembryos were killed by 4-hour daily dewaterings, and nearly all pre-emergent alevins were killed by 1-hour daily dewaterings. Intergravel temperatures were affected by insolation and air temperature. Intergravel temperatures increased to lethal levels during dewatering of cleavage eggs in early fall, and limited their survival. Growth of egg phases from some females was retarded by dewatering, but this phenomenon was not consistent for all egg groups. The size of surviving eleutheroembryos decreased as the length of daily dewatering periods increased.

Our research objective was to evaluate the effect of dewatering on survival and development of eggs and alevins of chinook salmon *Oncorhynchus tshawytscha* in artificial redds. In the experiments reported here, we studied the tolerances to daily dewaterings of four development phases: cleavage eggs, embryos, eleutheroembryos, and pre-emergent alevins. We also examined the effect of dewatering on growth of eggs and alevins during the intergravel period.

A power-peaking mode of hydroelectric generation requires frequent changes in the amount of water released through turbines at dams; these changes may result in short-term, often rapid, fluctuations in downstream flow. Present-day alterations in stream flow also are caused by consumptive uses of water such as irrigation, by pumped-storage projects, and by filling of new or drought-depleted reservoirs. As a result of flow manipulation, redds containing developing salmonid eggs and alevins in the gravel of stream beds may be dewatered for various periods. The problem gains importance in the Pacific northwest because of increasing legal and socioeconomic conflicts among intensified water-use projects and the need to enhance salmonid production.

Methods

Six dewatering tests were completed during the fall of 1979 and 1980 (Table 1). The tests involved 20 successive dewaterings in 22 days of four developmental phases incubated in artificial redds. The test period approximated the number of temperature units (Leitritz and Lewis 1976; Alderdice and Velsen 1978) required for normal development from one phase to the next at 10 C. One temperature unit (TU) equals one degree centigrade above freezing (0 C) for a period of 24 hours. One test (T-4) was subdivided and deployed longer dewaterings at less frequent intervals.

The artificial redds (Fig. 1) consisted of glass aquaria (68 cm long, 16 cm wide, and 30 cm deep) filled with a mix of rounded gravel graded to diameters of 2.5 to 3.2 cm (50%), 1.3 to 2.5 cm (25%), and 0.3 to 1.0 cm (25%). The mix simulated typical spawning bed composition (Burner 1951; McNeil and Ahnell 1964; Phillips et al. 1975), but lacked fine materials that might impede intergravel flow (Adams and

TABLE 1.—*Test designations and procedures for dewatering experiments with intergravel developmental phases of chinook salmon.*

Test[a]	Development phase[b]	Temperature units[c]	Dewatering procedure	
			Number of dewaterings	Dewatering periods
T-1	Cleavage eggs	17–211	20	0, 4, 8, 12, 16 hours
T-2	Embryos	242–428	20	0, 2, 4, 8, 12 hours
T-3	Embryos	293–461	20	0, 8, 12, 16, 22 hours
T-4.1	Embryos	282–461	1	0, 22, 46, 70, 118 hours
T-4.2	Embryos	282–461	Varied	0, 22, 46, 70, 118 hours
T-4.3	Embryos	282–461	1	0, 6, 8, 10, 12 days
T-5	Eleutheroembryos	468–648	20	0, 1, 2, 4, 8 hours
T-6	Pre-emergent alevins	691–894	20	0, 1, 2, 4, 8 hours

[a] Progeny from three females were used in T-2 and T-5. Progeny from two females were used in T-1, T-3, and T-6 because eggs from the third female showed "soft egg" syndrome. Progeny from only one female were used in T-4 for the same reason.

[b] All eggs were from the Klickitat Hatchery except those in T-4, which were from the Washougal Hatchery.

[c] Temperature units, accumulated from egg fertilization, are in centrigrade degree-days and are given for the incubator controls (no dewatering) to quantify normal intergravel development at 10 C.

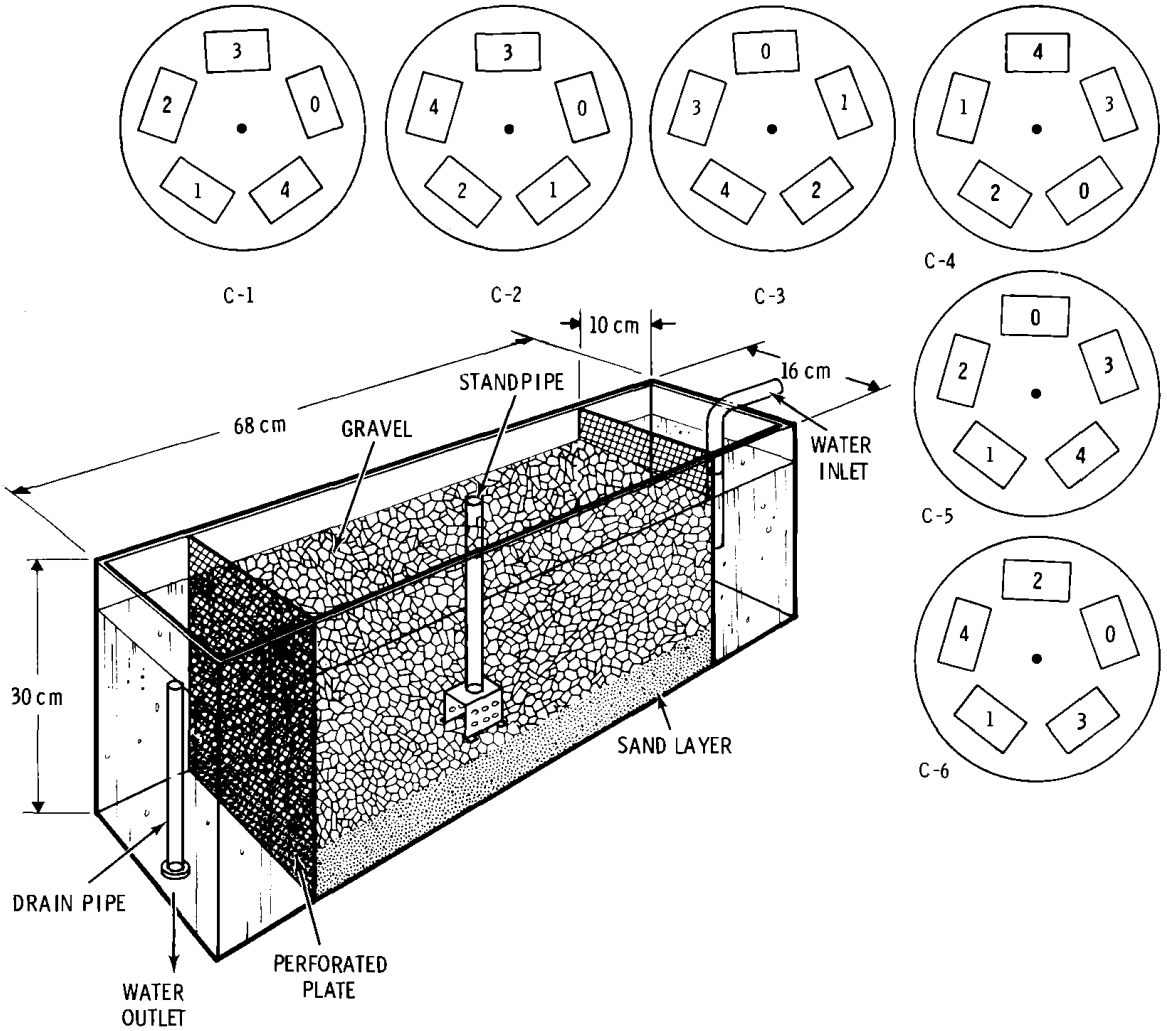

FIGURE 1.—*An artificial redd constructed from a glass aquarium filled with a gravel mix and provided with inlet and outlet chambers at opposite ends. One randomized arrangement of 30 aquaria within six circular (C-1 to C-6) tanks also is shown. Numbers in aquaria represent dewatering treatments. Progeny from one female salmon were placed in two circular tanks (10 aquaria) when healthy eggs were available from three females.*

Beschta 1980). The bottom of each aquarium had a 2.5-cm layer of sand to simulate the packed substrate that often underlies stream beds. All gravel was removed from aquaria, remixed, replaced, and disinfected with malachite green oxalate between tests.

Aquaria contained inflow and outflow chambers (≈10 cm deep) at each end, separated from the gravel mix by perforated (2.3-mm holes) aluminum alloy plates. Water flowed into the inlet, passed through one plate to enter the gravel mix, then exited through the second plate and a drainpipe. Aquaria were supported on concrete blocks placed in circular fiberglass tanks (183 cm diameter), located outdoors. Water leaving the aquaria was retained in the confinement tanks as a temperature-moderating water bath and allowed to reach over ¾ the aquarium height before being wasted.

Each artificial redd received Columbia River water at 4 liters/minute, and temperature was maintained at 10 C by mixing heated, chilled, or ambient water. Flow was deemed adequate to eliminate possible problems with dissolved oxygen or metabolic waste (Alderdice et al. 1958; Silver et al. 1963; Shumway et al. 1964; Davis 1975). To dewater each aquarium, the inflow hose was removed, the water bath emptied, the drainpipe removed to drain the gravel mix, a stopper inserted in the drainpipe hole, and the water bath refilled to its original level. The water bath simulated the thermal inertia of the gravel mass surrounding redds in streams during dewatering. Aquaria were rewatered by removing the stopper, which allowed water to enter from the water bath, and replacing the drainpipe and inflow hose. Complete dewatering or rewatering of a redd took less than 1 minute.

The four developmental phases tested extended from fertilized eggs to eyed eggs, eyed eggs to near hatch, 24 hours before hatch to advanced yolk-sac alevins, and advanced yolk-sac alevins to emergence from gravel. The phases were designated cleavage eggs, embryos, eleutheroembryos (yolk-sac alevins), and pre-emergent alevins, respectively (Balon 1975). Separation of developmental phases was based on an estimated 1,000 TUs from fertilization to initial emergence, about 250 TUs being alloted to each phase. Chinook salmon eggs incubated at 10 C normally require 51 days from fertilization to 50% hatch (Alderdice and Velsen 1978).

Chinook salmon eggs and sperm were obtained from state-operated hatcheries, placed on ice in sealed containers, and transported to our laboratory. Eggs were fertilized and reared in Heath® incubators until needed. Incubation temperatures were monitored, and accumulated TUs were calculated to quantify development. Eggs in incubators and artificial redds were treated weekly with malachite green. To start a test, cleavage eggs (after water-hardening) or embryos (collectively, the egg phases) were poured in a hand-excavated area of the gravel to within 2–3 cm of the sand layer. The gravel then was slowly replaced. Due to their susceptibility to crushing, eleutheroembryos and pre-emergent alevins (collectively, the alevin phases) were added to aquaria through a temporary standpipe leading to a perforated plastic chamber (open bottom, open ends), modified from Phillips et al. (1975). Water depth in artificial redds, controlled by length of the drainpipe, was maintained at or just below the gravel surface to ensure intergravel flow. For tests with pre-emergent alevins, the gravel surface was slanted so that the outlet end was covered by 5 cm of water, and the drainpipe was screened to retain emergents in the outlet chamber. Water flow was started to each redd at least 24 hours before each development phase was planted, and the first dewatering occurred 24 hours later.

The experimental design was developed for analysis of variance. Thirty artificial redds were used in each test, distributed in groups of five among six circular tanks (Fig. 1). One aquarium in each tank was a control (no dewatering), and the other four were assigned dewatering periods (treatments). Control and treatment positions were randomized for each test. Egg groups were obtained in early fall from three female chinook salmon, fertilized with mixed sperm from at least five males, and incubated separately. Progeny from each female were placed in aquaria of two circular tanks (total 10 artificial redds per female) to isolate possible differences in fertilization, vitality, or genetics of progeny. Fifty eggs or alevins were planted randomly in each artificial redd 24 hours before the first dewatering. Survivors were recovered 24 hours after the last dewatering. Recovery was at least 95% of all organisms planted.

Water-flow rate and temperature in each artificial redd were monitored and adjusted as re-

quired during periodic daily checks that corresponded, generally, to dewatering and rewatering times. Because intergravel flow was high and water was uniformly diffused through the gravel mix (determined by malachite green as a disinfectant and dye before start of each test), dissolved oxygen concentrations were considered to remain at or near saturation after initial checks. Intergravel temperatures were monitored automatically with an Esterline-Angus Model 2064 Datalogger®, first with five channels (fall 1979) and later, as recorder capacity was expanded, with twelve channels (fall 1980). The unit was programmed to record temperatures every 20 minutes on direct printout and magnetic cassette tapes. A calibrated temperature probe was inserted near the center of a redd for monitoring. When only five channels were available, the five probes were assigned to all redds in one randomly selected circular tank. With twelve channels available, water bath temperatures in all circular tanks and the air temperature also were monitored. Computer programs were used to read data from the cassette tape, which produced printouts of corrected temperature data and cumulative TUs for each monitored treatment. Graphs illustrating superimposed daily temperature regimes, and graphs showing temperature means and ranges, also were plotted for each probe. Intergravel temperatures varied with air temperature, insolation, and dewatering treatment. Water bath temperatures remained near 10 C.

Developmental phases were hand-sorted from gravel in each redd at test termination. Live and dead eggs were identified by color (translucent or opaque), and preserved in Stockard's solution in coded vials. Live and dead alevins were identified by color and activity, and preserved in 10% formalin in coded jars. Intergravel growth and development were determined from preserved specimens. Examinations were "blind" by an observer unaware of previous treatment.

Four growth "interphases" were defined for egg stages, based on common recognition features (Knight 1963; Leitritz and Lewis 1976). The first interphase represented development as it was when eggs were planted; if it still was present when redds were opened, it indicated no further growth. The fourth interphase represented normal development under continuous watering (for example, controls) at 10 C, whereas the two interphases between represented some retardation. For alevin stages, comparisons were made of length, weight, and length–weight ratio from survivors of different treatments. Specimens preserved from incubator stocks supplemented comparisons with intergravel controls.

Results

Tests were conducted from September through January, a span corresponding to the normal spawning period for fall-run chinook salmon and the intergravel period of their progeny in the Columbia River system. Temperature changes occurred in dewatered redds despite the surrounding 10 C water bath. The direction and magnitude of change were related to air temperature and insolation. Air temperatures and solar radiation were high under cloudless skys in early fall, becoming cooler and sometimes dropping below freezing during winter. Intergravel temperatures in exposed redds varied accordingly, although the changes were not necessarily as great as in the air. Temperatures in dewatered redds also affected cumulative TUs at test termination for each treatment (Table 2).

Cleavage Eggs

Cleavage eggs from three females differed in tolerance to dewatering in test T-1, resulting in varied results among circular tanks and treatments. A "soft egg" syndrome (unknown pathology) developed in incubator trays containing eggs from one female after the redds were planted. Thus, data from the two circular tanks (10 redds) stocked with these eggs were not evaluated further.

Of the healthy cleavage eggs in four circular tanks, over 50% survived twenty successive 12-hour dewaterings and over 30% survived twenty 16-hour dewaterings (Fig. 2). However, mortality probably was not due entirely to dewatering, but also to high temperatures that resulted from insolation. This was unexpected because of the thermal-stabilization potential of the 10 C water bath. Maximum redd temperatures in the monitored circular tank were 17 C and 28.5 C under 12- and 16-hour dewatering regimes, respectively (Table 2, test T-1). Air temperatures in the shade reached 27.5 C.

Mean daily intergravel temperatures were

TABLE 2.—*Temperature units (centigrade degree-days) accumulated by developmental phases of chinook salmon in artificial redds during dewatering treatments (Tr), redd temperature ranges during treatments, and air temperature ranges during tests (maximum–minimum).*

Test and measure	Treatment					Air temperature
	Control Tr-0	Tr-1	Tr-2	Tr-3	Tr-4	
T-1						
TU	194	201	199	218	271	
C	12.5–6.7	17.5–7.1	13.7–7.2	17.0–7.3	28.5–8.1	27.5–6.9
T-2						
TU	186	184	182	176	169	
C	11.0–9.4	10.7–7.2	11.0–5.5	11.2–4.6	11.0–5.1	15.0–3.0
T-3						
TU	168	169	169	167	165	
C	11.2–7.7	11.7–7.1	12.0–6.9	11.4–7.1	11.4–6.9	19.9–1.9
T-4.2[a]						
TU	178	176	182	168	160	
C	10.8–6.4	10.3–6.2	11.5–6.8	10.7–5.4	10.7–8.6	9.0–1.7
T-5						
TU	180	178	179	175	177	
C	10.5–9.0	10.5–7.4	10.8–6.4	10.3–7.0	12.5–6.6	8.6–3.3
T-6						
TU	203	206	207	206	203	
C	10.0–7.3	10.4–6.8	10.5–6.7	10.7–6.6	10.6–6.7	15.9–1.0

[a] Test T-4.2 involved one dewatering, thus corresponding with other tabulated data.

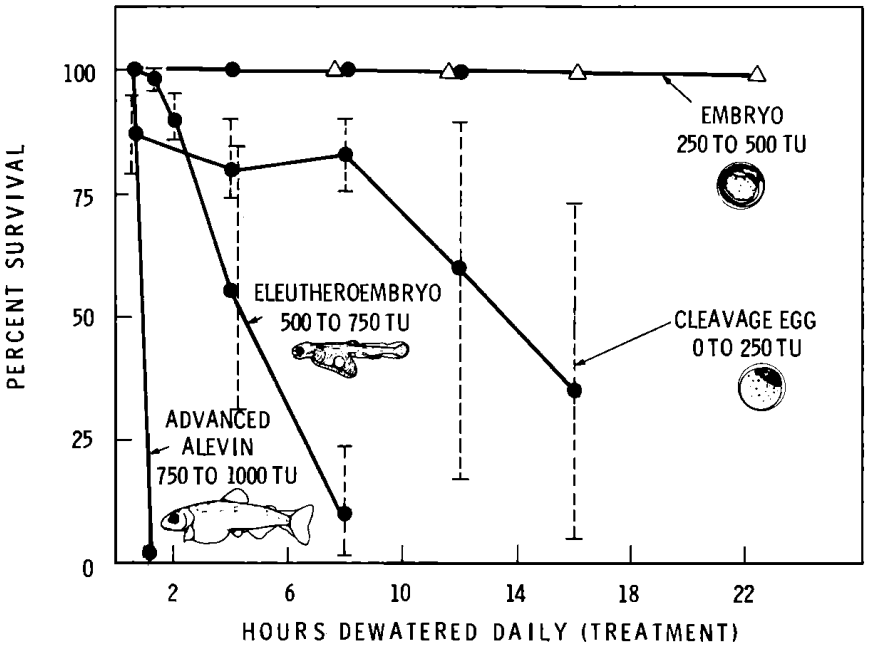

FIGURE 2.—*Comparative tolerance of four developmental phases of chinook salmon to dewatering, based on 20 consecutive daily dewaterings. The data points are averages from 6 artifical redds, except where noted in text. (● and △ indicate two tests with embryos; vertical broken lines are ranges; TU = temperature unit.)*

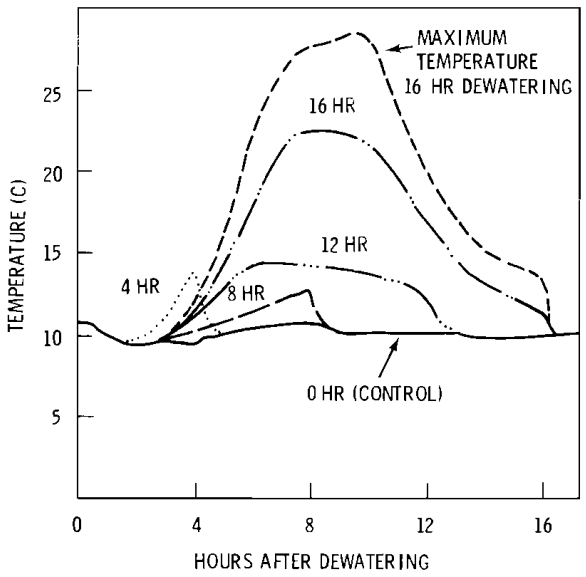

FIGURE 3.—*Mean daily intergravel temperatures in dewatered artificial redds containing cleavage eggs (test T-1), September 17–October 8. Zero (0) indicates temperatures in a control redd (no dewaterings), and other numbers indicate the hours (hr) redds were dewatered daily for other treatments beginning at 0600 hours. Temperatures were monitored from aquaria in only one circular tank. The dashed line shows maximum intergravel temperature for 16-hour dewaterings.*

highest in redds dewatered 16 hours (Fig. 3); these redds also showed the greatest mortality. All redds were dewatered daily at 0600 hours. Intergravel temperatures showed a midday rise corresponding to direct insolation. In the tank monitored for temperature, redd position (assigned randomly) caused some aquaria to receive sunlight sooner each morning than others. Thus, the earliest and steepest temperature rise occurred in the 4-hour dewatering treatment (Fig. 3). The next steepest temperature rise occurred in the 16-hour dewatering, which also showed the highest temperatures and longest duration of peak temperatures. Choice of midday dewatering period for test T-1 (conducted September 17 to October 8) and the warm, early fall weather made the temperature effect severe. Some redds were partially shaded at times during the day, and received less direct sunlight.

Monitored intergravel temperatures in the redd dewatered 16 hours daily exceeded 20 C on 17 days and 25 C on 5 days, and reached a maximum at 28.5 C. High intergravel temperatures persisted for 4 hours above 25 C, or 6 to 7 hours above 20 C, gradually declining after midday. Such temperature regimes must have contributed greatly to, or have been primarily responsible for, mortality during 16-hour daily dewaterings. Yet some cleavage eggs, possibly those in a cooler position in redds dewatered for 16-hours, survived.

Redds in other circular tanks positioned differently from those in the circular tank being monitored also experienced temperature rises during dewatering. Thus, high temperatures interacted with dewatering periods to produce the averaged mortality pattern (Fig. 2). Survival of cleavage eggs during dewatering probably would have been extended if intergravel temperatures had remained low.

Embryos

Tests with embryos were conducted three times with different dewatering regimes. High survival was obtained in all tests.

Redds in test T-2 (conducted November 16 to December 10) were dewatered daily at 0900 hours, and the maximum dewatered period was 12 hours. Air temperatures were cool (Table 2) but did not fall below freezing, corresponding to season. Intergravel temperatures of redds dewatered 8 and 12 hours declined as low as 6 C. Embryo recovery was greater than 99% at test termination. There were no mortalities due to dewatering.

Redds in test T-3 (conducted October 15 to November 6) were dewatered daily at 2200 hours, and the maximum dewatered period was 22 hours. Intergravel temperatures in dewatered redds did not decline below 6 C at night, but temperatures in redds dewatered 22 hours sometimes increased to 15 C during the day (Fig. 4). Embryo recovery was high at test termination. Again, no mortalities were attributable to dewatering.

The dewatering scheme in test T-4 (conducted December 30 to January 21) was modified because a dewatering period longer than 22 hours daily was required. Further, dewaterings longer than 24 hours require that the number of dewaterings be decreased, if each developmental phase is completed in a fixed 20 days, as assumed. To better define the tolerance of embryos to dewatering, and to examine the relationship between number and frequency of dewaterings, test T-4 was subdivided into three parts: dewaterings of 0, 22, 46, 70, and 118

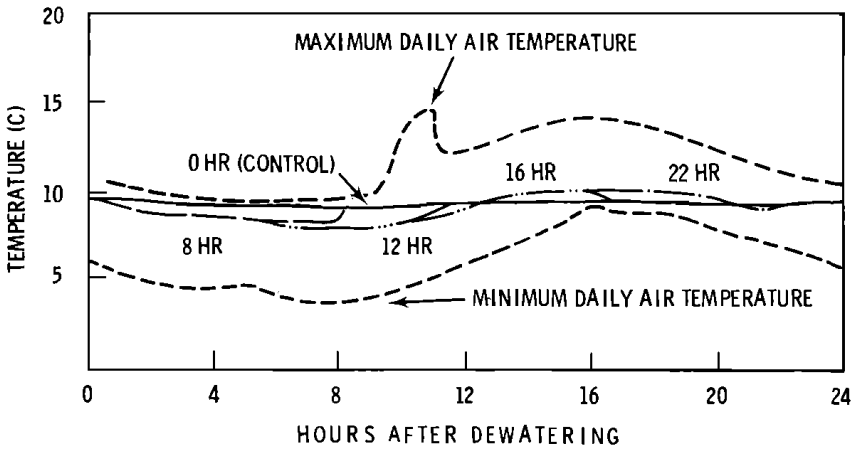

FIGURE 4.—*Mean daily intergravel temperatures in dewatered artificial redds containing embryos (test T-3), October 15–November 6. The numbers indicate the hours (hr) redds were dewatered daily beginning at 2200 hours. Intergravel temperatures in dewatered redds varied from night to day. Temperatures were monitored in only one circular tank. Dashed lines show averaged maximum–minimum daily air temperatures.*

hours duration conducted once (T-4.1); the same dewatering periods repeated 0, 20, 10, 7, and 4 successive times, respectively (T-4.2); and 0, 6, 8, 10, and 12-day dewaterings conducted once (T-4.3). Parts T-4.1 and T-4.3 each were done in two circular tanks (2 aquaria/treatment), whereas part T-4.2 was done in four circular tanks (4 aquaria/treatment). All embryos came from one female because the "soft egg" syndrome appeared in other egg lots.

Redds in T-4.1 were dewatered daily at 0900 hours. Air temperatures were cool but did not fall below freezing. Intergravel temperatures declined as low as 7 C in dewatered redds. There were no mortalities attributable to one-time dewatering for any period up to 118 hours.

Redds in T-4.2 were dewatered at 0900 hours for varied intervals and frequencies according to plan. Redds were rewatered 2 hours between dewaterings. Air temperatures ranged from 1.7 to 9 C during the test. Intergravel temperatures during prolonged dewatering followed a diel cycle. For example, the 118-hour dewatering, repeated four times, showed daily peaks near 10 C with nocturnal temperatures reaching 9 to 6.5 C. Control and water-bath temperatures remained near 10 C (±1.5 C). Cumulative dewatered times during the test were 0, 440, 460, 490, and 472 hours for the control, 22-, 46-, 70-, and 118-hour treatments, respectively.

Mean embryo survival in T-4.2 (Fig. 5) was 70% for the 70-hour dewaterings (7 repeats) and 64% for the 118-hour dewaterings (4 repeats). However, there was considerable variation among redds dewatered similarly in different circular tanks. The low survival in circular tank 4 (C-4) during 70-hour dewatering (36%), but high survival during 118-hour dewatering (92%), was puzzling. Many embryos recovered at test termination were near hatching or hatched. Control embryos were within 2–3 days of hatching. Dewatering stress may have caused premature hatch among treatment groups. Accordingly, the more susceptible advanced developmental phases (alevins, in T-5 and T-6) arising from premature hatch were lost. It also is possible that microbial activity was contagious among dead and live embryos in dewatered redds if the eggs had been clustered inadvertently when planted.

Embryos in T-4.3 had developed 1 week longer at 10 C than those in T-4.1 before being planted. Air temperatures remained cool but did not fall below freezing. Intergravel temperatures declined as low as 7 C in dewatered redds. Survival was 97, 83, 87, and 80% for embryos dewatered continuously for 6, 8, 10, and 12 days, respectively. Survival of controls was 95%. Such remarkable survival rates for embryos were associated with cool intergravel temperatures and intergravel moisture retention during dewatering in winter (December and January).

Comparison of T-4.1 (one-time dewaterings) with T-4.2 (multiple dewaterings) suggests that embryos were less tolerant when subject to a

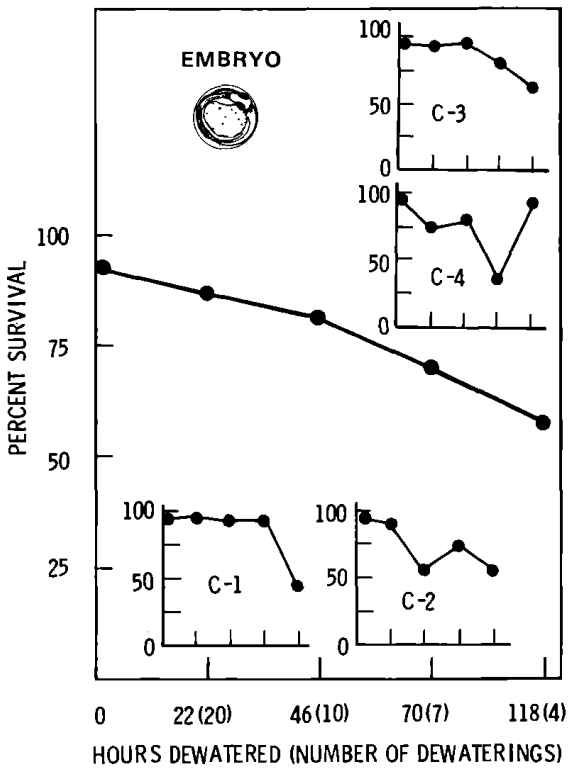

FIGURE 5.—*Mean tolerance of embryos to multiple dewatering periods (test T-4.2). The numbers of dewaterings used in the test are indicated in parentheses. Variable results among treatments in different artificial redds contained in four circular tanks (C-1 to C-4) are shown by the inserts.*

series of dewaterings than to one prolonged dewatering, at least during winter when air temperatures were low. This assessment is supported by the relatively high survival of embryos in T-4.3 (over 80%) that were continuously dewatered up to 12 days.

Eleutheroembryos

Redds in test T-5 (conducted December 12 to January 2) were dewatered daily at 0800 hours, and the maximum dewatering period was 8 hours. Air temperatures were cold, sometimes declining below freezing, corresponding to season. Intergravel temperatures rapidly dropped from 10 C to 6 C during dewatering, but fell no lower.

Survival of eleutheroembryos among controls and the 1-hour daily dewaterings was near 98%. Survival declined to 90, 56, and 11% for the 2-, 4-, and 8-hour daily dewaterings, respectively. Eleutheroembryos were considerably less tolerant of dewatering than were embryos (Fig. 2).

Pre-Emergent Alevins

Redds in test T-6 (conducted December 2 to December 23) were dewatered daily at 0800 hours, and the maximum dewatering period was 8 hours. Air temperatures remained low but usually above freezing (1 to 4 C) except for a 1-day warm wind (a "chinook") that rapidly increased air temperatures to 16 C. Intergravel temperatures declined as low as 6.6 C during dewatering, but increased to 11 C during the warm wind.

Pre-emergent alevins were the least tolerant of the developmental phases tested (Fig. 2). Less than 4% survived 1-hour daily dewaterings. All were killed at longer dewaterings. Recovery of controls was near 99%. A few control fish emerged, and most were distributed throughout the gravel of control aquaria at test termination. In contrast, dead individuals in dewatered redds were confined mainly to perforated-chamber areas and were decomposed. Most pre-emergent alevins, therefore, were killed during initial dewaterings.

Dewatering and Development

Contingency tables were used to analyze intergravel development of the two egg phases, the null hypothesis being no association between dewatering period and growth rate. A chi-square statistic (χ^2) was calculated for each table. If the χ^2 was significantly large ($P \leq 0.05$), the null hypothesis was rejected. Assessment was done on the basis of survivors at test termination, and results from each female usually were combined.

Assessment of dewatering effects on cleavage eggs in test T-1 was complicated by high temperatures from insolation when redds were dewatered. Accumulated TUs at test termination were higher for each treatment than for the control (Table 2), particularly for eggs exposed to 12- and 16-hour dewaterings, in the circular tank being monitored. High temperatures during 16-hour dewatering contributed to mortality, and 50% kill occurred between 12- and 16-hour dewaterings (Fig. 2).

Surviving cleavage eggs showed significant differences ($P \leq 0.05$) in growth between the three female parents, which was due partially to "soft egg" syndrome from progeny of one

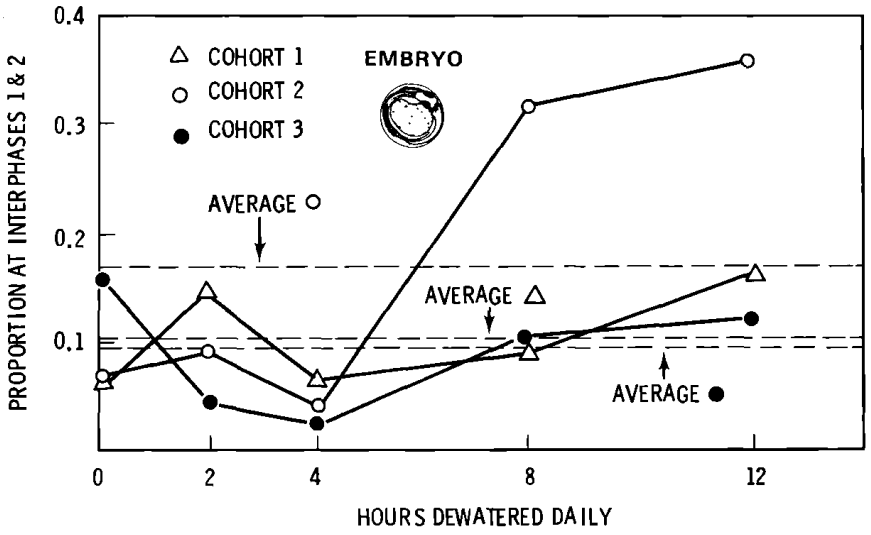

FIGURE 6.—*Effect of dewatering on development of three embryo cohorts (from three females) dewatered 20 consecutive times (test T-2). A high proportion of embryos that remained at interphases 1 and 2 at test termination indicates growth retardation. Response varied among embryos from three females (cohorts 1, 2, and 3).*

female. (Data on these eggs were omitted from mortality results.) Proportions of cleavage eggs reaching interphase 4 at test termination revealed high variability among progeny from each female and from one dewatering treatment to another. There was no clear trend indicating growth retardation of cleavage eggs from dewatering in test T-1.

Assessment of effects on embryos in tests T-2, T-3, and T-4 was not complicated by high temperatures, although accumulated TUs did vary with dewatering treatment. At termination of T-2 (up to 12-hour daily dewaterings), the proportion of embryos remaining at interphases 1 and 2 was determined for each treatment (Fig. 6). Embryos from female one (cohort 1) showed some negative association with dewatering period and those of cohort 3 showed no association with dewatering period, but neither displayed any consistent trend. However, embryos of cohort 2 revealed a highly significant association ($P \leq 0.01$) with dewatering period, and displayed an obvious trend. Thus, there was a pronounced decrease in growth when cohort 2 was dewatered 8 and 12 hours daily. Lower total TUs were involved in this relationship.

At termination of test T-3 (up to 22-hour daily dewaterings), effects on embryos varied between the two cohorts (Fig. 7). Embryos from cohort 1 had a highly significant association ($P \leq 0.01$) with dewatering period, while those from cohort 2 showed no association. Accumulated TUs were similar among dewatering treatments (Table 2). The significant association for cohort 1 was due largely to variation from one treatment to another. Thus, no consistent trend was apparent for retardation of development with dewatering period.

At termination of test T-4.2 (multiple dewa-

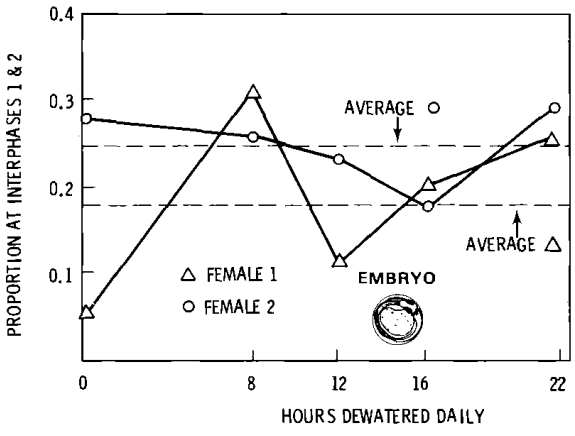

FIGURE 7.—*Effect of dewatering on development of two embryo cohorts (from two females) dewatered 20 consecutive times (test T-3). An increasing proportion of embryos remaining at interphases 1 and 2 at test termination indicates retardation. Response varied between embryos from two females, particularly noticeable in retarded development of eggs from female 2 (cohort 2) at control level.*

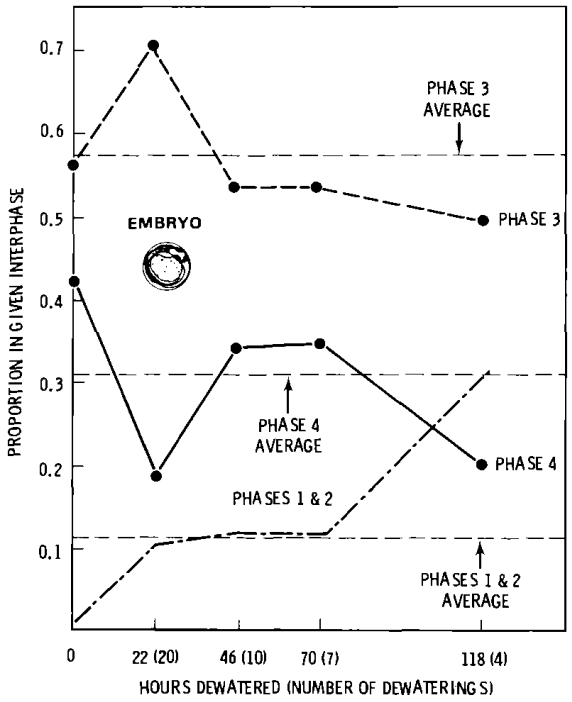

FIGURE 8.—*Effect of dewatering on development of embryos (from one female) with multiple number of dewaterings (test T-4.2). An increasing proportion of embryos remaining in interphases 1 and 2 at test termination, and a declining portion of embryos in interphases 3 and 4, indicate growth retardation.*

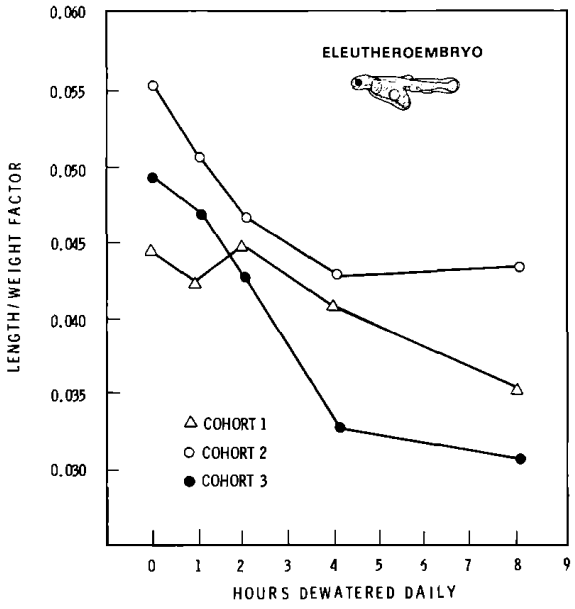

FIGURE 9.—*Effect of dewatering on development of eleutheroembryos (from three females) dewatered 20 consecutive times (test T-5). Decreasing values with increasing exposure periods indicates significant growth retardation. Responses differed among progeny from three females.*

terings), growth of embryos from the one female varied with dewatering treatment (Fig. 8). The proportion of eggs retained at interphases 1 and 2 showed a highly significant association ($P \leq 0.01$) with dewatering period, suggesting that growth was retarded as the dewatering period lengthened. Further, the proportion of embryos advancing to interphases 3 and 4 was generally highest among the control and the shorter, 22- and 46-hour dewatering treatments. Over half of the chi-square statistic was contributed by interphases 1 and 2, and by 0- and 118-hour treatments. Much of the other contribution to the chi-square issued from the "odd" fluctuation for interphases 3 and 4 in the 22-hour treatment. Part of this variation may have been caused by premature hatch. Note that accumulated TUs for the 118-hour treatment were considerably less than those of the other treatments (Table 2), which would retard embryo growth.

Two-way analysis of variance with interaction was used to analyze growth of eleutheroembryos in test T-5. The statistical design consisted of cohorts from three females and five dewatering treatments as the main effects. Analysis was performed on three different response variables: length, weight, and weight–length ratio. For all three response variables, highly significant effects ($P \leq 0.01$) were due to cohort, dewatering period, and the interaction between cohort and dewatering period.

Tukey's Q-test, a Studentized multiple range test (Snedecor and Cochran 1967), was applied for further analysis. At the 95% confidence level, the mean responses for both length and weight of eleutheroembryos of each cohort significantly differed ($P \leq 0.05$) from those of all other cohorts. For the weight–length response, eleutheroembryos from cohort 1 and cohort 3 were not significantly different from each other, whereas eleutheroembryos from cohort 2 were significantly larger than those from both other cohorts (Fig. 9). For all three responses, the length of dewatering showed the same significant differences. As the length of dewatering increased, the response measured decreased. Responses at 1- and 2-hour dewaterings differed significantly from those of the controls but not from each other; responses for all other dewatering periods did differ significantly from each other (Table 3).

TABLE 3.—*Results of Tukey's Q-test applied to assessment of development of eleutheroembryos (test T-5) at different dewatering treatments. Values not connected by an underline are significantly different from each other ($P \leq 0.05$). Values are means for eleutheroembryos from three female fish.*

Response	Dewatering treatment				
	0 hour	1 hour	2 hours	4 hours	8 hours
Length (cm)	2.849	2.736	2.707	2.634	2.564
Weight (g)	0.141	0.127	0.122	0.100	0.090
Length/weight ratio	0.049	0.047	0.045	0.038	0.347

The data clearly show that dewatering retarded the growth of eleutheroembryos, and that this effect increased in severity as the dewatering period increased. Growth retardation was accompanied by high mortality in 4- and 8-hour dewaterings (Fig. 2). Compared to the continuously watered controls, growth was also retarded at briefer 1- and 2-hour dewaterings. Eleutheroembryos from cohort 1 showed a positive response at 2-hour daily dewaterings (90% survival), which differed from responses of cohort 2 and cohort 3.

High mortality of pre-emergent alevins made growth analysis meaningless.

Discussion

In this study, we examined the relationships between intergravel dewatering and mortality of four salmonid development phases. The operation of many dams and reservoirs in the Pacific northwest for power production and irrigation causes extensive and rapid changes in downstream flow. If adult salmonids spawn during a sustained high discharge, subsequent reduction of flow may expose spawning beds and dewater redds. Effects of such drawdowns usually have been examined belatedly in field situations (Witty and Thompson 1974; Stillwell et al. 1977; Bauersfeld 1978). We used eggs and alevins of chinook salmon. The response of this species to dewatering does not necessarily reflect the response of any other species of salmon or trout.

Our artificial redds were designed to simulate the intergravel environment of salmonid spawning beds. Other variables that might influence survival and growth (for example, intergravel flow rate, seepage from bank storage, dissolved oxygen, and accumulation of metabolic products) largely were eliminated or standardized. Accordingly, fine materials were omitted from gravel composition (Phillips et al. 1975; Witzel and MacCrimmon 1981), intergravel flow of water was maintained at 4 liters/minute (Davis 1975), and dewatering and rewatering was rapid (<1 minute each). A water bath was used to simulate the thermally inert gravel mass that surrounds redds in stream beds. Yet we found that, in spite of our precautions, air temperature and insolation strongly influenced intergravel temperatures during dewatering. In particular, direct solar radiation rapidly raised temperatures in the depth of a redd during warm days of September and early October, and these temperatures reached lethal levels when a redd was dewatered 16 hours. When air temperatures were low during winter, intergravel temperatures during dewatering usually declined but did not fall below 6 C. Therefore, the 10 C water bath did not prevent high intergravel temperatures from insolation on exposed gravel surfaces, but it did moderate penetration of low temperatures from a freezing air mass.

There is little information in the literature on the upper thermal tolerance of salmonid eggs. A range of 5.8 to 14.2 C has been suggested for normal development of chinook salmon eggs at constant tempertures, but long periods of very low temperatures can be tolerated if the initial incubation temperature is above 5.6 C for 1 month (Combs and Burrows 1957; Combs 1965). A compilation of available incubation data (Alderdice and Velsen 1978) indicates that the lower and upper temperatures for chinook salmon eggs are about 2.5–3.0 and 16 C, respectively. But the effect of high but brief temperature rises on incubating chinook salmon eggs apparently has not been reported. We found, in brief experiments, that embryos and eleutheroembryos can survive thermal shock when transferred directly from 10 to 22 C and exposed up to 8 hours, but exposure to 26 C is lethal (unpublished data). In the dewatering test with cleavage eggs (T-1), intergravel temperatures exceeded 25 C five times in redds exposed 16 hours daily, and probably caused most of the mortality.

The four developmental phases varied in tolerance to dewatering. The order, from least to most tolerant, was pre-emergent alevins,

eleutheroembryos, cleavage eggs, and embryos. The first two developmental phases in this order have "hatched." Nearly all pre-emergent alevins (>725 TU) were killed by 1-hour daily dewaterings, and most probably died during initial exposures. Heavy mortality of eleutheroembryos (>465 TU) occurred at 4-hour daily dewaterings, and losses were associated with hatching and posthatch development. Tolerance of the alevin phases probably decreases with the formation of functional gills and a vascular system for uptake of dissolved oxygen from water.

Chinook salmon eggs (prehatch phases) were more tolerant of dewatering than were alevins (posthatch phases). Cleavage eggs were killed by 12- and 16-hour dewaterings due to insolation on exposed gravel in early fall. Fertilization of salmonid eggs is followed by water hardening (when eggs were planted in test T-1) and a "tender period" involving early cell division (when eggs were susceptible to shock) that extends to the eyed stage (Leitritz and Lewis 1976). Thus, cleavage eggs were tender when dewatered. Even so, maintaining cooler intergravel temperatures during dewatering likely would prolong the survival of cleavage eggs, possibly to a considerable extent. Embryos, the phase extending from the time eye spots become visible until hatching, tolerated daily dewaterings up to 22 hours for 20 consecutive days. Further, survival exceeded 80% for embryos dewatered continuously for 8-, 10-, and 12-day periods.

High survival of embryos may be related to the relatively impermeable chorion, especially when the intergravel environment remains cool and moist. Embryos apparently can obtain sufficient oxygen under these conditions, when aided by periodic rewaterings, to survive. According to the literature (Davis 1975), inadequate dissolved oxygen concentrations can result in reduced growth and retarded development of salmonid eggs incubated in streambeds; further, the dissolved oxygen requirements of salmonid eggs gradually increase as development progresses, and mortality from hypoxia may occur at the point the circulatory system develops. Recent evidence suggests that salmonid eggs can develop normally without being submerged in water if they remain moist, for example, by being incubated in wet cotton cloth (Reiser and White 1981). Presumably, moisture permits adequate oxygen uptake and passage of metabolic products through the chorion.

We examined growth among survivors subjected to dewatering because sublethal effects are often ecologically important. Some embryos remained in early interphases as dewatering periods lengthened, indicating that growth may have been retarded. Because this phenomenon was not consistent for embryos from all females, the trends detected were not statistically significant. However, we suspect that additional experiments will demonstrate retardation of egg development from dewatering. We also suspect a complex relationship between growth rate and several other factors of the intergravel environment, including temperature, size composition of gravel, dewatering period, egg vitality, and oxygen. For example, a heavily silted section of stream may have a large temperature gradient between the surface and the deeper gravel (Wickett 1954), whereas a highly porous stream bed may have a maximum gradient of 1.1 C between the surface and 20 cm depth (Brown 1972). Thus, the amount of silt present will affect the extent of temperature change during dewatering. The amount of intergravel moisture retained during sequential dewaterings, another function of particle size, also may affect temperature and dissolved oxygen uptake. Also, fines can help keep eggs moist during dewatering by capillary action.

Growth retardation of alevins was more consistent than that of eggs. Dewatering eleutheroembryos up to 8 hours daily for 20 consecutive days resulted in high mortality in 4- and 8-hour treatments (44 and 89%, respectively). Survivors showed significant reductions in growth that intensified as the dewatering periods lengthened. Growth responses at 1- and 2-hour daily dewaterings differed from those at all other treatments, including the controls, but not from each other. Responses at 4- and 8-hour daily dewaterings differed from those at all other treatments, reflecting the stress that resulted in high exposure mortality.

Sequential daily dewaterings of 20 times in 22 days (the basic procedure applied in our present experiments, except T-4) may not reflect all field situations. Conceivably, eggs or alevins would be exposed daily from a power peaking mode of operation, especially if water flows were sufficiently high during fall spawn-

ing to permit redd construction in near-shore areas. However, one intentional drawdown also might expose salmonid eggs and alevins for an extended period of several days. We hope to establish the relationship between brief, consecutive dewaterings (measured in hours) and long, continuous dewaterings (measured in days) in further studies.

Our data may be extreme if extrapolated to field situations. Salmonid redds in streams are not likely to dewater abruptly, but to retain pockets of still water and to receive flowing water from bank storage. Further, fine materials in the gravel mix will provide some protection from desiccation and insolation. Nevertheless, alevin phases will remain more susceptible to dewatering than will egg phases because of morphological and physiological changes that accompany hatching. The problems of field assessment and resource protection become complex if, because of a prolonged spawning period, a spawning area contains an asynchronous mix of developing eggs and alevins.

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References

ADAMS, J. N., AND R. L. BESCHTA. 1980. Gravel bed composition in Oregon coastal streams. Canadian Journal of Fisheries and Aquatic Sciences 37: 1514–1521.

ALDERDICE, D. F., AND F. P. J. VELSEN. 1978. Relationship between temperature and incubation time for eggs of chinook salmon (*Oncorhynchus tshawytscha*). Journal of the Fisheries Research Board of Canada 35:69–75.

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 15:229–249.

BALON, E. K. 1975. Terminology of intervals in fish development. Journal of the Fisheries Research Board of Canada 32:1663–1670.

BAUERSFELD, K. 1978. The effect of daily flow fluctuations on spawning fall chinook in the Columbia River. Washington Department of Fisheries Technical Report 38.

BROWN, G. W. 1972. An improved temperature prediction model for small streams. Water Resources Research Institute, WRRI-16, Oregon State University, Corvallis, Oregon, USA.

BURNER, C. J. 1951. Characteristics of spawning nests of Columbia River salmon. United States Fish and Wildlife Service Fisheries Bulletin 61:97–110.

COMBS, B. D. 1965. Effect of temperature on the development of salmon eggs. Progressive Fish-Culturist 27:134–137.

COMBS, B. D., AND R. E. BURROWS. 1957. Threshold temperatures for the normal development of chinook salmon eggs. Progressive Fish-Culturist 19:3–6.

DAVIS, D. C. 1975. Minimal dissolved oxygen requirements of aquatic life with emphasis on Canadian species: a review. Journal of the Fisheries Research Board of Canada 32:2295–2332.

KNIGHT, A. E. 1963. The embryonic and larval development of the rainbow trout. Transactions of the American Fisheries Society 92:344–356.

LEITRITZ, E., AND R. C. LEWIS. 1976. Trout and salmon culture. California Department of Fish and Game Fish Bulletin 164.

MCNEIL, W. J., AND W. H. AHNELL. 1964. Success of pink salmon spawning relative to size of spawning bed materials. United States Fish and Wildlife Service Special Scientific Report Fisheries 469.

PHILLIPS, R. W., R. L. LANTZ, E. W. CLAIRE, AND J. R. MORING. 1975. Some effects of gravel mixtures on emergence of coho salmon and steelhead trout fry. Transactions of the American Fisheries Society 104:461–466.

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

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. J., 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.

SNEDECOR, G. W., AND W. G. COCHRAN. 1967. Statistical methods. Iowa State University Press, Ames, Iowa, USA.

STILLWELL, F. P., J. K. ATKINS, M. D. EVENSON, R. D. EWING, AND J. J. MARTIN. 1977. Determination of salmonid egg mortality resulting from closure of Lost Creen Dam, September 1, 1976–April 30, 1977. Oregon Department of Fish and Wildlife, Research Section, Information Report Series, Fisheries 77-9, Corvallis, Oregon, USA.

WICKETT, W. P. 1954. The oxygen supply to salmon eggs in spawning beds. Journal of the Fisheries Research Board of Canada 11:933–953.

WITTY, K., AND K. THOMPSON. 1974. Fish stranding surveys. Pages 113–120 *in* K. Bayha and C. Koski, editors. Anatomy of a river. Pacific Northwest River Basins Commission, Vancouver, Washington, USA.

WITZEL, L. D., AND H. R. MACCRIMMON. 1981. Role of gravel substrate on ova survival and alevin emergence of rainbow trout, *Salmo gairdneri*. Canadian Journal of Zoology 59:629–636.