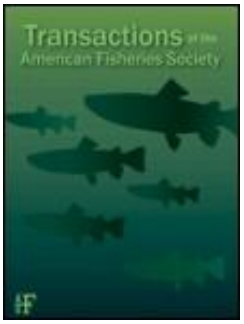

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[Article]

Survival, Development, and Growth of Fall Chinook Salmon Embryos, Alevins, and Fry Exposed to Variable Thermal and Dissolved Oxygen Regimes

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Abstract.—Some fall Chinook salmon *Oncorhynchus tshawytscha* initiate spawning in the Snake River downstream of Hells Canyon Dam at temperatures that exceed 13°C and at intergravel dissolved oxygen concentrations that are less than 8 mg O_2/L. Although water temperature declines and dissolved oxygen increases soon after spawning, the initial temperature and dissolved oxygen levels do not meet the water quality standards established by the states of Oregon and Idaho for salmonid spawning. Our objective was to determine whether temperatures from 13°C to 17°C and dissolved oxygen levels from 4 to more than 8 mg O_2/L during the first 40 d of incubation followed by declining temperature and rising dissolved oxygen affected survival, development, and growth of Snake River fall Chinook salmon embryos, alevins, and fry. During the first 40 d of incubation, temperatures were experimentally adjusted downward approximately 0.2°C/d and oxygen was increased in increments of 2 mg O_2/L to mimic the thermal and oxygen regime of the Snake River where these fish spawn. At 40 d postfertilization, embryos were moved to a common exposure regime that followed the thermal and dissolved oxygen profile of the Snake River through emergence. Mortality of fall Chinook salmon embryos increased markedly at initial incubation temperatures of 17°C or more, and a rapid decline in survival occurred between 16.5°C and 17°C; there were no significant differences in survival at temperatures up to 16.5°C. Initial dissolved oxygen levels as low as 4 mg O_2/L over a range of initial temperatures from 15°C to 16.5°C did not affect embryo survival to emergence. There were no significant differences in alevin and fry size at hatch and emergence across the range of initial temperature exposures. The number of days from fertilization to eyed egg, hatch, and emergence was highly related to temperature and dissolved oxygen; fish required from 6 to 10 d longer to reach hatch at 4 mg O_2/L than at saturation and up to 24 d longer to reach emergence. In contrast, within each dissolved oxygen treatment, fish required about 20 d longer to reach hatch at 13°C than at 16.5°C (no data were available for 17°C) and up to 41 d longer to reach emergence. Overall, this study indicates that exposure to water temperatures up to 16.5°C will not have deleterious effects on survival or growth from egg to emergence if temperatures decline at a rate of 0.2°C/d or more after spawning. Although fall Chinook salmon survived low initial dissolved oxygen levels, the delay in emergence could have significant long-term effects on their survival. Thus, an exemption to the state water quality standards for temperature—but not oxygen—may be warranted for the portions of the Snake River where fall Chinook salmon spawn.

The reproductive success of Pacific salmon *Oncorhynchus* spp. is intrinsically linked to intergravel water temperature and dissolved oxygen at the time adults spawn. For example, exposure of embryos early in development to water temperatures and dissolved oxygen levels near tolerance thresholds usually reduces survival (Donaldson 1955; Olson and Foster 1955; Seymour 1956, 1959; Combs and Burrows 1957; Smith 1957; Alderdice et al. 1958; Silver et al. 1963; Shumway et al. 1964; Combs 1965; Davis 1975). Hatching and emergence timing also depend on early incubation temperature and dissolved oxygen level (Seymour 1956; Alderdice et al. 1958; Alderdice and Velsen 1978; Murray and McPhail 1988). Emergence timing is of ecological significance because emergence at times of adequate food supply and habitat is a major selective force for species survival (Brannon 1987).

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Alevin and fry size also depend on temperature and dissolved oxygen early in the incubation period (Seymour 1956; Davis 1975; Heming 1982; Beacham and Murray 1985, 1990; Murray and Beacham 1986, 1987). Fry size at emergence can influence swimming ability (Bams 1967), downstream migration rate (Connor et al. 2003c), migration timing (Connor et al. 2002), and growth (Connor and Burge 2003). Further, fry survival after emergence may be low if oxygen levels result in metabolic compensation that reduces energy reserves for swimming, feeding, avoiding predators, and other activities (Warren 1971; Davis 1975).

Spawning of Snake River fall Chinook salmon *O. tshawytscha* in the 157 km of free-flowing Snake River downstream of Hells Canyon Dam (hereafter, the Snake River) begins during October at temperatures that can exceed 13°C (Groves and Chandler 1999). Oxygen levels as low as 4 mg O_2/L have been measured in the water column near Hells Canyon Dam (river kilometer [rkm] 399, measuring from its confluence with the Columbia River) at the onset of spawning, when water temperatures were above 16°C; oxygen levels increase progressively through natural aeration as one moves downstream from the dam. Measurements from simulated redds indicate that intergravel dissolved oxygen levels are less than 1.3 mg O_2/L lower than those in the water column 90% of the time immediately after redd construction (Idaho Power Company, unpublished data). These temperature and dissolved oxygen levels do not meet the water quality standards established by the states of Oregon and Idaho for salmonid spawning (Department of Environmental Quality [Oregon] 2006; Department of Environmental Quality [Idaho] 2006). For example, during the fall Chinook salmon spawning and incubation period (23 October to 15 April), the Oregon standard requires that the 7-d average maximum temperature not exceed 13°C and that the daily minimum dissolved oxygen concentration be greater than 11 mg O_2/L for the water column and 8 mg O_2/L in the intergravel environment (Department of Environmental Quality [Oregon] 2006). The state of Idaho requires that during the spawning and incubation period (not defined), the weekly maximum temperature not exceed 13°C and the daily minimum dissolved oxygen concentration be greater than 6 mg O_2/L in the water column and 5 mg O_2/L in the intergravel environment (with a 7-d average of 6 mg O_2/L in the latter; Department of Environmental Quality [Idaho] 2006).

State agencies set water quality standards based on studies in which eggs were exposed to constant temperature and dissolved oxygen regimes (see Davis 1975 and McCullough et al. 2001 for reviews). However, thermal regimes and dissolved oxygen concentrations in rivers where salmon spawn are rarely constant after spawning (Dauble and Watson 1997; Connor et al. 2003b). Few studies have evaluated how early life stages of Chinook salmon respond to elevated temperatures and reduced dissolved oxygen levels that are followed by a decline in temperature and an increase in dissolved oxygen level. Olson and Foster (1955) determined that survival to hatch exceeded 90% for Columbia River fall Chinook salmon embryos exposed to initial temperatures of 11.7–16.1°C when temperature was lowered at a rate of 0.2°C/d; only 21% survived an initial temperature of 18.4°C. Seymour (1956) exposed spring Chinook salmon eggs from four different rivers to initial temperatures of 7.2–18.3°C and then lowered the temperature approximately 0.11°C/d; survival from fertilization to hatch ranged from 94% to 99% for initial temperatures of 7.2–15.6°C and from 0% to 76% for an initial temperature of 18.3°C. While these two studies used a declining thermal regime to evaluate survival of Chinook salmon embryos, they did not alter dissolved oxygen concentrations, which remained at 100% air saturation. We conducted a laboratory study in 2004 to expand on the findings of Olson and Foster (1955) and Seymour (1956) and to evaluate the existing water quality standards for temperature and dissolved oxygen set by the states of Idaho and Oregon for the Snake River. Our objective was to determine whether temperatures from 13°C to 17°C and dissolved oxygen levels from 4 to more than 8 mg O_2/L during the first 40 d of incubation followed by declining temperature and rising dissolved oxygen affected survival, development, and growth of Snake River fall Chinook salmon embryos, alevins, and fry.

Methods

Temperature and dissolved oxygen treatments.—Two spawning reaches along the Snake River can be differentiated on the basis of temperature (Connor et al. 2002). The reach extending 94 km downstream from Hells Canyon Dam (rkm 397; hereafter, the upper reach) is the warmer of the two during spawning and was the reach of interest for this study. The water temperature of the upper reach was measured by means of four constant-recording thermographs that were placed and maintained at rkm 309, 325, 348, and 369. Data from these monitors were averaged to provide daily mean water temperatures for each year from 1991 to 2003 (Figure 1, top panel). For missing data, we developed a linear regression model that predicted daily mean water temperature in the upper reach based

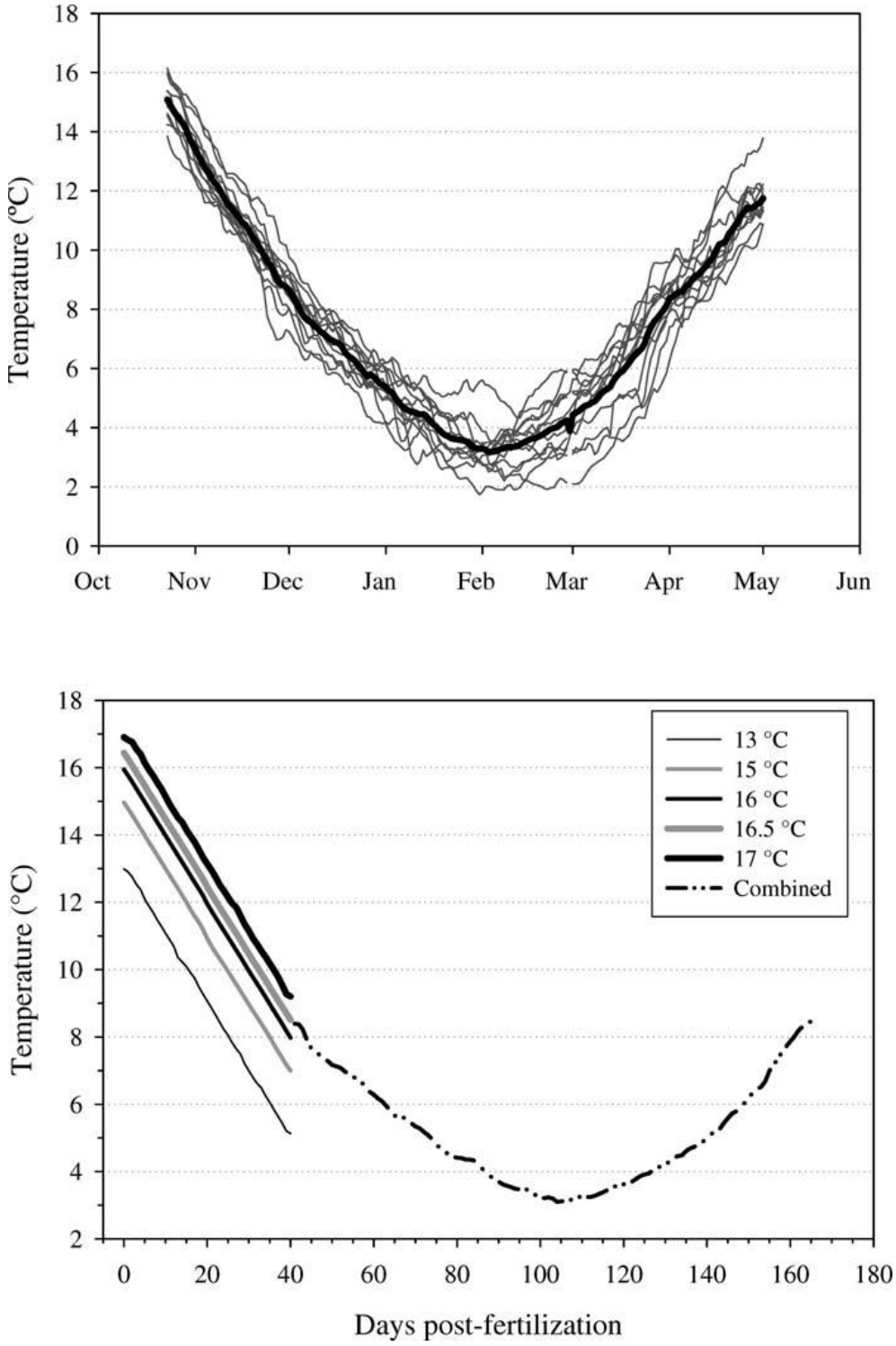

FIGURE 1.—The top panel shows the daily mean temperatures of the Snake River below Hells Canyon Dam (see text for location) for each of 12 years from 1991 to 2002 (gray lines) and the grand daily mean for all years (bold line). The bottom panel shows the temperature treatments used in the laboratory with Snake River fall Chinook salmon embryos, alevins, and fry during the entire incubation period. The combined line represents an average condition of the two Living Stream systems.

TABLE 1.—Experimental design and abbreviated names for each of the 14 initial temperature–dissolved oxygen treatments used in the laboratory experiment.

Initial (40-d average) incubation temperature (°C)	Initial (40-d average) dissolved oxygen level (mg/L)			
	4 (5.3)	6 (7.2)	8 (8.9)	100% air saturated (9.6–11.0)
13 (9.1)				13–S
15 (11.0)	15–4	15–6	15–8	15–S
16 (12.0)	16–4	16–6	16–8	16–S
16.5 (12.5)	16.5–4	16.5–6	16.5–8	16.5–S
17 (13.1)				17–S

on values available from Hells Canyon Dam ($R^2 = 0.99$; $P < 0.05$).

Water temperatures during laboratory exposure mimicked the 1991–2003 interannual mean thermal regime in the upper reach based on the recorded temperature data, that is, temperatures declined through early incubation and then increased through hatch and emergence (Figure 1, bottom panel). We selected five temperature treatments that differed in initial temperature (13, 15, 16, 16.5, and 17°C). We determined the duration of the early incubation period based on 2001 data that showed that warm temperatures and drought conditions persisted for approximately 40 d after spawning. The initial temperatures were allowed to decline at approximately 0.2°C/d over the first 40 d of incubation. Average temperatures over the first 40 d ranged from 9.1°C for the 13°C group to 13.1°C for the 17°C group (Table 1). We then developed a common incubation temperature regime that approximated the historic temperature pattern, starting at 8.5°C on day 41 of incubation, decreasing to 3.2°C by day 103, and thereafter increasing to 9.0°C at the end of the experiment on day 168.

The initial dissolved oxygen levels were based on periodic samples collected in 2003 by Idaho Power Company staff from a spawning site in the upper reach at rkm 392.7. Intergravel dissolved oxygen levels as low as 4 mg O_2/L have been recorded at this site. Using this as a lower limit, we set the laboratory treatments at 4, 6, and 8 mg O_2/L and 100% air saturated values (9.0 mg O_2/L at 15°C to 8.8 mg O_2/L at 16.5°C; Table 1). The initial dissolved oxygen levels were maintained for 16 d postfertilization and were then increased 2 mg O_2/L where possible (8 mg O_2/L was increased to a 100% air-saturated value; 100% air-saturated values remained unchanged; Figure 2). On day 39 of the experiment, the dissolved oxygen level was again increased 2 mg O_2/L. Average dissolved oxygen levels during the first 40 d ranged from 5.3 mg O_2/L in the 4-mg-O_2/L group to 11.0 mg O_2/L in the 100% air-saturated group (Table 1). Dissolved oxygen levels were maintained at 100% air-saturation values from day 40 to the end of the experiment.

Egg and alevin incubation.—Gametes were collected from Snake River–origin fall Chinook salmon that had returned to the state of Washington salmon hatchery near Lyons Ferry. The Lyons Ferry hatchery stock has historically been used for culture, and the cultured fish are genetically similar to wild Snake River fall Chinook salmon (Bugert et al. 1995; Marshall et al. 2000). Before spawning, adults were held in raceways supplied with 12°C well water. Staff collected gametes from 10 males and 10 females during routine spawning on 22 November 2004. Individual males and females were verified as Lyons Ferry stock based on visible implant elastomer tags. On the collection day, eggs and milt were transported on ice to the Pacific Northwest National Laboratory in Richland, Washington. Gametes were combined the same day and separated into six replicates. Fertilized eggs from each replicate were then sequentially distributed to 14 initial temperature–dissolved oxygen groups (Table 1) and placed into egg tubes (~300 eggs/tube). Egg tubes were constructed of 15-cm sections of 10-cm-diameter white PVC pipe that was screened on the bottom and slotted on the sides (4 banks of 11 horizontal grooves, each 2.5 mm × 5 cm). A total of 84 egg tubes were used in this study (6 replicates over 14 treatment groups).

Egg tubes from the 15, 16, and 16.5°C groups were placed in one of four individual chambers (30 × 40 cm) within one of three troughs (30 × 305 × 15 cm), where initial temperature and dissolved oxygen were manipulated during the first 40 d of incubation. Water temperature was manipulated by means of a computer and data logger system that controlled the delivery of chilled and ambient well water; desired temperature varied little during the study (SD < 0.05°C). A computer and data logger system were also used to control dissolved oxygen levels in the troughs. Compressed nitrogen gas was used to lower the dissolved oxygen level to less than 4 mg O_2/L at the upstream end of each trough. Computer-controlled air stones then raised dissolved oxygen to the desired level in a mixing chamber (30 × 23 cm) upstream of each egg chamber. Water with the proper dissolved oxygen level flowed from the mixing chamber into the egg

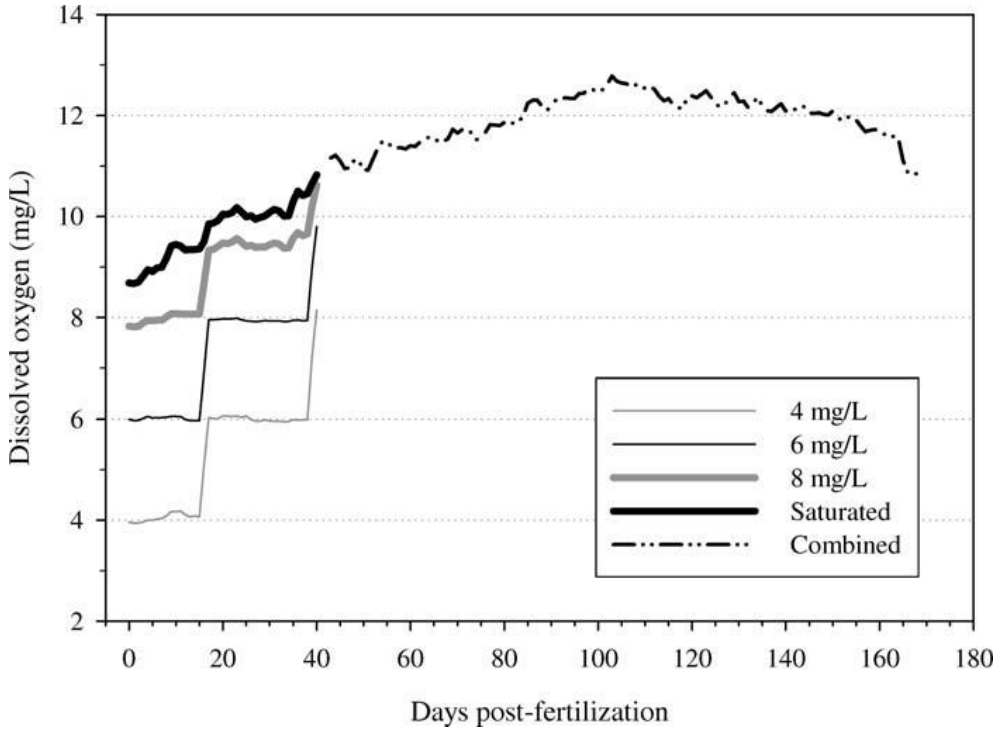

FIGURE 2.—Daily mean dissolved oxygen levels during the entire laboratory incubation period with Snake River fall Chinook salmon embryos, alevins, and fry, 2004. The combined line represents an average condition of the two Living Stream systems.

chamber. Daily variation in dissolved oxygen was low (the SD of the average daily values averaged 0.2 mg O_2/L and ranged from 0.04 to 0.50 mg O_2/L). Dissolved oxygen was recorded at 5-min intervals by the computer, and additional dissolved oxygen readings were taken daily with a dissolved oxygen meter (YSI, Inc., Yellow Springs, Ohio; Model 95). Weekly calibrations were made to the computer program to provide temperature compensation for the dissolved oxygen levels. Flow rate within the troughs averaged 6 L/min, and velocity through the egg tubes was calculated (based on cross-sectional area) at 0.18 cm/s.

Egg tubes in the 13°C and 17°C initial temperature groups were housed in separate large tubs (~150 L), each equipped with a mechanical chiller. Temperature was controlled by manually adjusting the mechanical chiller; desired temperature varied little during the study (SD $<$ 0.05°C). Dissolved oxygen levels for the 13°C and 17°C groups were maintained at 100% air-saturation values during the first 40 d of incubation.

On day 40, the egg tubes from all 14 groups were transferred to one of two Living Stream systems (60 $\times$ 274 $\times$ 55 cm; 700-L capacity). Temperature in the 13°C treatment was more than 2°C cooler than the 8.5°C in the Living Stream system on day 40 (Figure 1, bottom panel). We acclimated eggs from this treatment by raising the temperature of the eggs 2°C every 30 min until the temperatures of the eggs and the Living Stream system were the same. We used a data logger and computer-controlled chiller and aeration system to maintain temperature within 0.2°C of the target temperature and dissolved oxygen levels at 100% air-saturation values (range, 11.5–12.8 mg O_2/L).

When eggs reached 250 accumulated temperature units (ATUs), they were placed in a shallow, water-filled transparent container on a lighted table, counted, and scored as normally eyed, eyed but retarded or abnormal, or dead. Dead eggs were counted and removed. An embryo was considered normally eyed if eyes were obviously pigmented, the embryo encircled one-half or more of the circumference of the egg, and the yolk was strongly vascularized (Leitritz and Lewis 1976). Eggs scored as normally eyed or eyed but retarded or abnormal were counted and returned to their tubes for continued incubation.

The dates of first hatch, 50% hatch, and 100% hatch for each of the six replicates within each initial temperature–dissolved oxygen group were determined by counting and separating the hatched alevins from unhatched eggs and comparing that count with the total number in each replicate. Hatching counts were made daily from the onset to the completion of hatching.

Hatched alevins remained in egg tubes until they reached approximately 750 ATUs (~75% yolk absorption; Murray and McPhail 1988). At that time, they were transferred to a shallow, water-filled tray, where we recorded the number of alevins alive (abnormal or normal) or dead. For each replicate, 100 normal alevins (when available) were transferred to an emergence tube. Abnormal and extra alevins were removed and euthanized. Emergence tubes were constructed of 5-cm white PVC pipe (~17 cm long) capped at the bottom (volume, approximately 300 cm^3). This opaque PVC tube was connected at the surface with a 1-cm transparent PVC tube to a 6.5-cm transparent PVC pipe screened on the bottom. Approximately 750 mL of water/min was introduced into the bottom of the opaque side tube, which then overflowed into the top of the transparent tube. Approximately 50 cm^3 of pea gravel were added to the bottom of the opaque tube followed by several gravel cobbles (~2.5 cm in diameter) to create habitat with interstitial spaces for the developing alevins. As alevins were added to the tube, more cobble was added. When we were finished, the gravel extended to approximately 2.5 cm below the water line and tube leading to the transparent collection area; gravel occupied approximately 50% of the volume of the emergence tube. Any alevins that emerged during the first 24 h were discarded and their number subtracted from the original number placed in the tube. After 24 h, all emerging fry were counted and removed. Monitoring of emergence continued daily until all fry emerged or until 1,200 ATUs was reached. The dates of first, 50%, and 100% emergence were recorded for each tube.

Alevin and fry size.—Within 1 d of 50% hatch and again at 50% emergence, a sample of 15 alevins from each replicate was euthanized. The alevins were preserved in a 10% solution of neutral-buffered formalin (NBF) for 80 d, after which all samples were removed from the NBF, blotted dry, and individually measured for length (nearest 0.5 mm) and mass (wet weight; nearest 1 mg). Body tissue and yolk were separated for each alevin, dried in an oven at 60°C for 2 d, and then weighed as a group to the nearest milligram (i.e., one combined dry tissue and one combined dry yolk weight were obtained for each replicate). Average (individual) weights for dry body tissue and dry yolk were calculated by dividing the combined dry weights by the number of individuals in each sample.

Data analysis.—Survival was calculated as the percentage of fertilized eggs or alevins that survived from one development period to the next—fertilization to eyed egg, eyed egg to hatch, and hatch to emergence. Survival from fertilization to emergence was calculated from the following multiplicative model:

$$\begin{aligned} P\ &(\text{survival from fertilization to emergence}) \\ &= P(\text{survival from fertilization to eyed egg}) \\ &\quad \times P(\text{survival from eyed egg to hatch} \mid \\ &\qquad \text{survival to eyed egg}) \\ &\quad \times P(\text{survival from hatch to 750 ATUs} \mid \\ &\qquad \text{survival to hatch}) \\ &\quad \times P(\text{survival from 750 ATUs to emergence} \mid \\ &\qquad \text{survival to 750 ATUs}). \end{aligned}$$

Analysis of variance (ANOVA) was conducted for each survival stage with respect to the initial incubation temperature–dissolved oxygen treatments (data were the arcsine square root transformations of proportion survival). A Tukey pairwise comparison was done when ANOVA showed significant differences in survival among temperature–dissolved oxygen treatments. Multiple regression analysis and ANOVA were used to evaluate the number of days to hatch and emergence as functions of treatment. The pattern of residuals and the lack of fit to the linear model were evaluated. For a subset of the data on the number of days to reach each stage, the effects of temperature and dissolved oxygen were analyzed further by a regression that fit separate intercepts for each temperature class and a common slope for dissolved oxygen. Differences in the size at hatch or emergence among the different temperature–dissolved oxygen treatments were evaluated with nonparametric Kruskal–Wallis H-tests.

Results

Survival

Fall Chinook salmon embryo survival from fertilization to eyed egg equaled or exceeded 88% for all temperature groups (Table 2), and there was no significant difference among temperature groups ($F = 1.40$; $P = 0.18$). Embryo survival from fertilization to hatch ranged from 2.5% to 96.6% (Table 2) and was statistically different among initial temperature groups ($F = 99.95$; $P < 0.0001$). The greatest variation in survival was observed in eggs in the 17–S and 13–S groups (Table 2). Based on Tukey pairwise comparisons at $\alpha = 0.05$, survival to hatch in the 17–S group was significantly lower than that in all other treatments, while survival to hatch in the 13–S group was significantly lower than that in all groups except 15–4, 16–4, 16.5–4, and 16.5–6. The survival to hatch among individual egg tubes within the 13–S group ranged from 78% to 91%. By contrast, survival within other temperature groups varied less than 6%. Overall survival from fertilization to emergence was significantly different among the treatment groups ($F = 10.27$; $P < 0.0001$). The lowest rates of survival to

TABLE 2.—The mean ± the SD survival percentages over various intervals of fall Chinook salmon embryos and alevins for each initial temperature–dissolved oxygen (DO) treatment group in a laboratory study, 2004 (e.g., 15–4 indicates exposure to 15°C and 4 mg O_2/L; the letter "S" denotes the DO level associated with 100% air saturation). Sample size is six replicates for each group. Survival rates from hatch to emergence and from fertilization to emergence are based on the multiplicative model (see text).

Initial temperature–DO group	Fertilization to eyed egg	Eyed egg to hatch	Fertilization to hatch	Hatch to emergence	Fertilization to emergence
13–S	96.7 ± 0.8	87.5 ± 5.4	84.4 ± 4.7	98.8 ± 1.7	83.4 ± 5.5
15–4	94.3 ± 4.9	98.7 ± 1.2	93.1 ± 5.8	99.8 ± 0.4	92.9 ± 6.1
15–6	96.6 ± 1.0	99.6 ± 0.6	96.1 ± 1.0	99.6 ± 0.5	95.7 ± 1.3
15–8	96.3 ± 1.3	99.8 ± 0.3	96.2 ± 1.3	99.8 ± 0.3	96.0 ± 1.4
15–S	96.7 ± 1.0	99.7 ± 0.5	96.4 ± 0.8	99.0 ± 0.6	95.5 ± 1.3
16–4	88.0 ± 14.6	98.1 ± 1.9	86.5 ± 15.7	99.6 ± 0.6	86.2 ± 15.7
16–6	95.5 ± 2.4	99.5 ± 0.5	95.1 ± 2.7	99.9 ± 0.1	95.0 ± 2.7
16–8	95.3 ± 1.1	99.8 ± 0.2	95.1 ± 1.2	99.2 ± 1.0	94.4 ± 2.0
16–S	96.9 ± 1.5	99.7 ± 0.3	96.6 ± 1.5	99.2 ± 0.8	95.8 ± 1.9
16.5–4	95.2 ± 2.3	97.0 ± 2.7	92.4 ± 3.8	99.0 ± 2.0	91.5 ± 4.1
16.5–6	94.2 ± 3.8	99.0 ± 1.1	93.3 ± 4.6	99.0 ± 1.4	92.3 ± 4.6
16.5–8	96.3 ± 1.3	99.2 ± 0.5	95.6 ± 1.3	99.0 ± 1.2	94.6 ± 1.5
16.5–S	95.6 ± 1.8	99.1 ± 0.7	94.8 ± 2.2	99.0 ± 1.6	93.8 ± 2.5
17–S	94.9 ± 3.0	2.5 ± 2.1	2.4 ± 2.1	70.6 ± 19.5	1.7 ± 1.6

emergence again occurred in the 17−S and 13−S groups, averaging 1.7% and 83.4%, respectively (Table 2). Survival to emergence in the 17−S group was significantly lower than that in all other treatment groups, while survival to emergence in the 13−S group was lower than that in all treatments except 15–4, 16–4, 16.5–4, and 16.5–6 (Tukey comparison with $\alpha = 0.05$). Survival rates to emergence among the individual egg tubes in the 13°C group ranged from 77% to 91%; differences in survival among the egg tubes in the other temperature groups were 3–6%.

Approximately 3–6% of the eggs initially exposed to dissolved oxygen levels of 4 mg O_2/L were scored as abnormal or retarded at the eyed egg stage; abnormal scores at that stage for all other treatments ranged from 0.8% to 3%. At 750 ATUs, approximately 1.1–2.2% of the live alevins that were initially exposed to dissolved oxygen levels of 4 mg O_2/L were classified as abnormal. This compares with less than 1% for all other groups except the 13−S group, where 1.2% were classified as abnormal.

Development Rate

Eggs in the 4- and 6-mg O_2/L treatment groups (all temperatures) took approximately 3–6 d longer to reach the eyed egg stage than eggs from the 8-mg O_2/L and 100% air-saturated groups. The eggs required more time to reach 50% hatch as temperature and dissolved oxygen decreased (Figure 3). For example, approximately 39 d were required to reach 50% hatch in the 16.5−S group, 50 d in the 16.5–4 group, and approximately 60 d in the 13−S group. The regression model that predicted the time to 50% hatch using temperature and dissolved oxygen was

$$\text{days to 50\% hatch} = 146.8 - 5.50(\text{initial temperature}) - 1.76(\text{initial dissolved oxygen}).$$

The model was significant ($F = 252.6$; $P < 0.0001$), as were the slope coefficients for temperature ($t = -20.84$; $P < 0.0001$) and dissolved oxygen ($t = -13.23$; $P < 0.0001$). Dissolved oxygen and temperature explained about 87% of the observed variability in the number of days to 50% hatch.

As the initial dissolved oxygen and temperature declined, the time to 50% emergence increased (Figure 3). For example, fry from the 17−S group emerged 41 d earlier than those from the 13-S group and approximately 30 d earlier than those from the 16.5–4 group. The regression model that predicted the time to 50% emergence using temperature and dissolved oxygen was

$$\text{days to 50\% emergence} = 327 - 10.10(\text{initial temperature}) - 4.24(\text{initial dissolved oxygen}).$$

This model was significant ($F = 73.3$; $P < 0.0001$), as were the slope coefficients for temperature ($t = -9.91$; $P < 0.0001$) and dissolved oxygen ($t = -8.09$; $P < 0.0001$). Approximately 64% of the variability in time to emergence was explained by temperature and dissolved oxygen.

Across all treatments, embryos accumulated an average of 535 ATUs (range, 502–587 ATUs) at the time of 50% hatch and an average of 944 ATUs (range,

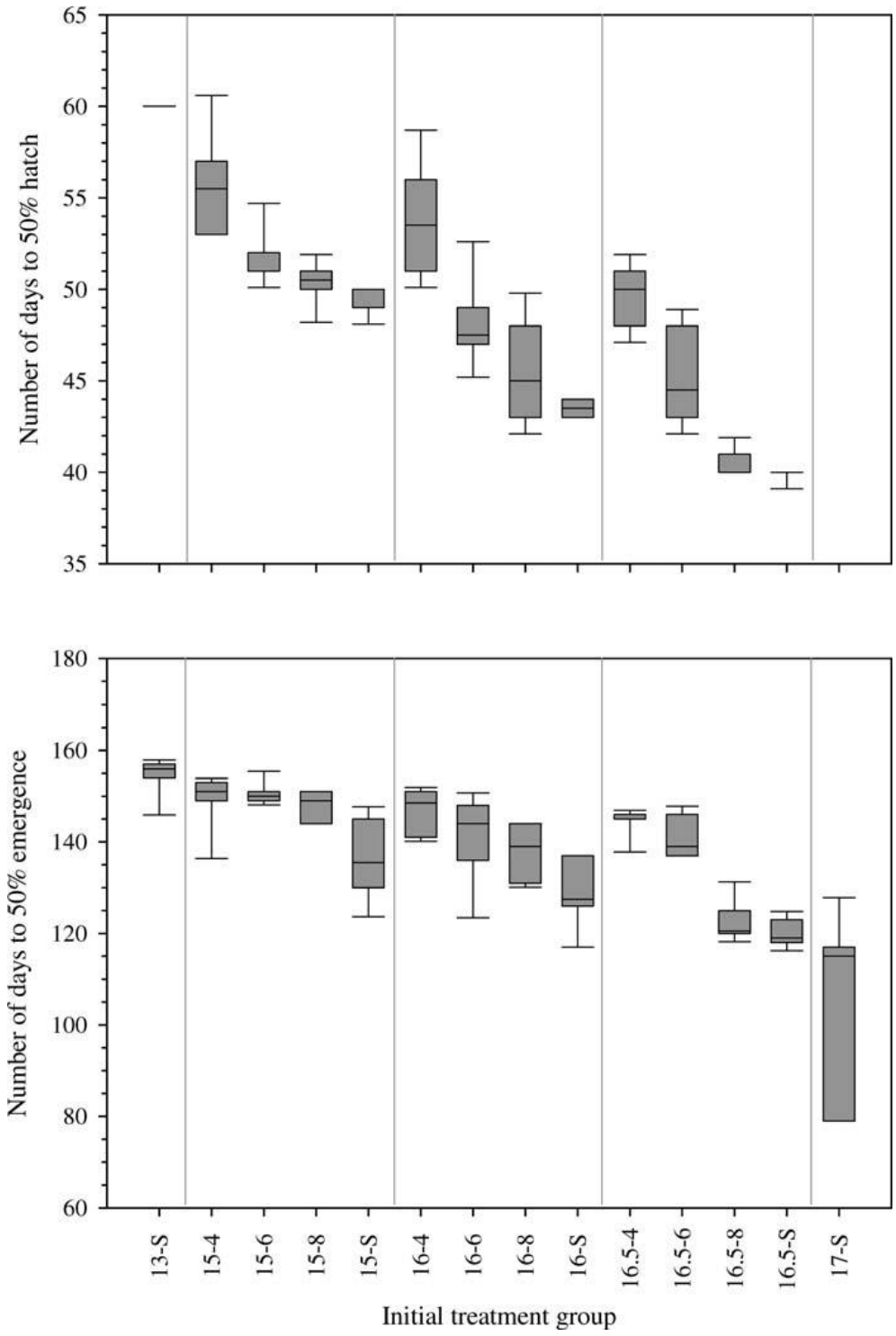

FIGURE 3.—Number of days from fertilization to 50% hatch (top panel) and 50% emergence (bottom panel) of Snake River fall Chinook salmon embryos and alevins in each initial temperature–dissolved oxygen group (e.g., 15–4 indicates exposure to 15°C and 4 mg O_2/L; the letter "S" denotes the dissolved oxygen level associated with 100% air saturation). The solid line inside each box represents the median. The upper and lower boundaries of each box show the 75th and 25th percentiles of the data, and the upper and lower whiskers show the 90th and 10th percentiles. Note there are no data at hatch for the 17–S group.

TABLE 3.—The mean ± SD accumulated temperature units from fertilization to 50% and 100% hatch and emergence, respectively, of fall Chinook salmon embryos and alevins for each initial temperature–dissolved oxygen (DO) group. See Table 2 for additional details.

Initial temperature–DO group	Fertilization to			
	50% hatch	100% hatch	50% emergence	100% emergence
13–S	511.4 ± 0.1	529.3 ± 0.1	930.8 ± 30.6	995.1 ± 30.9
15–4	559.6 ± 19.4	572.5 ± 19.6	970.4 ± 38.5	1,043.2 ± 31.8
15–6	533.9 ± 11.4	553.9 ± 23.9	980.0 ± 17.8	1,013.3 ± 20.3
15–8	522.3 ± 9.5	532.8 ± 13.4	963.3 ± 18.2	998.1 ± 21.9
15–S	516.4 ± 5.9	523.5 ± 5.8	901.9 ± 44.4	966.6 ± 21.8
16–4	586.6 ± 22.3	599.7 ± 26.7	997.4 ± 28.4	1,048.1 ± 37.5
16–6	547.1 ± 19.3	560.1 ± 23.7	966.9 ± 50.9	1,016.6 ± 24.5
16–8	527.4 ± 22.3	543.5 ± 17.6	948.7 ± 29.4	1,007.1 ± 23.8
16–S	512.6 ± 4.0	525.2 ± 3.3	906.4 ± 31.9	994.9 ± 58.7
16.5–4	577.7 ± 13.2	587.0 ± 17.0	1,001.0 ± 18.8	1,050.7 ± 27.8
16.5–6	544.6 ± 20.7	561.8 ± 25.3	984.3 ± 25.9	1,022.4 ± 19.5
16.5–8	508.1 ± 6.7	528.4 ± 8.5	901.6 ± 21.6	999.8 ± 14.3
16.5–S	502.1 ± 4.6	520.6 ± 0.6	891.1 ± 12.7	987.8 ± 12.3
17–S		458.8 ± 7.9	867.5 ± 75.7	907.0 ± 71.4

868–1,001 ATUs) at the time of 50% emergence (Table 3). No live alevins remained in the emergence tubes at the termination of the study (i.e., 1,200 ATUs).

Alevin and Fry Size

The mean wet weight of alevins at 50% hatch was 248 mg (range across treatments, 221–273 mg; Figure 4) and did not differ among treatments ($H = 12.5$; $P = 0.410$). The mean wet weight of fry at 50% emergence was 399 mg (range, 296–453 mg; Figure 4) and also did not differ among treatments ($H = 14.6$; $P = 0.335$). The mean fork length of alevins at hatch ranged from 20.6 to 21.6 mm across treatments (Figure 4); these differences were statistically significant ($H = 30.9$; $P = 0.002$). The average fork length of fry at 50% emergence was 35.2 mm (range, 31.5–36.9 mm) and did not differ among treatments ($H = 17.8$; $P = 0.167$).

The dry tissue weight of alevins at 50% hatch was slightly higher in the groups initially exposed to saturated conditions (mean = 14.5 mg) than in the groups exposed to other dissolved oxygen treatments (mean = 13.2 mg) (Figure 5). The differences among treatments were significant ($H = 41.0$; $P < 0.0001$). At the time of 50% emergence, the dry tissue weight of alevins averaged 59.9 mg (range, 31.5–69.4 mg; Figure 5). There was no significant difference in dry tissue weight among treatments at 50% emergence ($H = 13.5$; $P = 0.413$). The dry weight of yolk for alevins at 50% hatch averaged 83.0 mg (range, 72.0–95.0 mg) and did not differ among treatments ($H = 7.68$; $P = 0.810$; Figure 5). The mean dry yolk weight at 50% emergence ranged from 5.5 to 21.7 mg (Figure 5) and differed among treatments ($H = 31.3$; $P = 0.003$). Alevins had less yolk remaining at 50% emergence in the 4- to 8-mg O_2/L treatments (7.5 mg) than in the saturated levels (11.8 mg).

Discussion

Our results showed that the mortality of fall Chinook salmon embryos exposed to variable temperature and oxygen conditions was not affected by dissolved oxygen levels as low as 4 mg O_2/L over a range of temperatures from 15°C to 16.5°C. Embryo mortality increased markedly at initial incubation temperatures of 17°C or more. There was a rapid decline in survival between 16.5°C and 17°C and no significant difference in survival at temperatures up to 16.5°C. This upper thermal tolerance is similar to that reported in other studies that have used a declining thermal regime to evaluate survival in salmon embryos. Although they did not manipulate dissolved oxygen, Olson and Foster (1955) and Seymour (1956) found that exposure of Chinook salmon to water temperatures up to 16.1°C followed by declines of 0.1–0.2°C/d did not have deleterious impacts on embryo survival.

The temperature threshold of 16.5°C that we report here for Snake River fall Chinook salmon exceeds the 13°C threshold for Pacific salmon reported for constant incubation temperatures (reviewed in McCullough et al. 2001). Constant temperature regimes expose the embryos and alevins to elevated temperatures that might occur only at spawning. Further, they do not account for changes in temperature tolerance over time. Murray and Beacham (1987) concluded that egg sensitivity to elevated temperature rises after fertilization, reaches a peak, and begins to decline at a stage coincident with closure of the blastopore (epiboly; Vernier 1969). Hatching is another vulnerable period when temperature affects survival (Donaldson 1955).

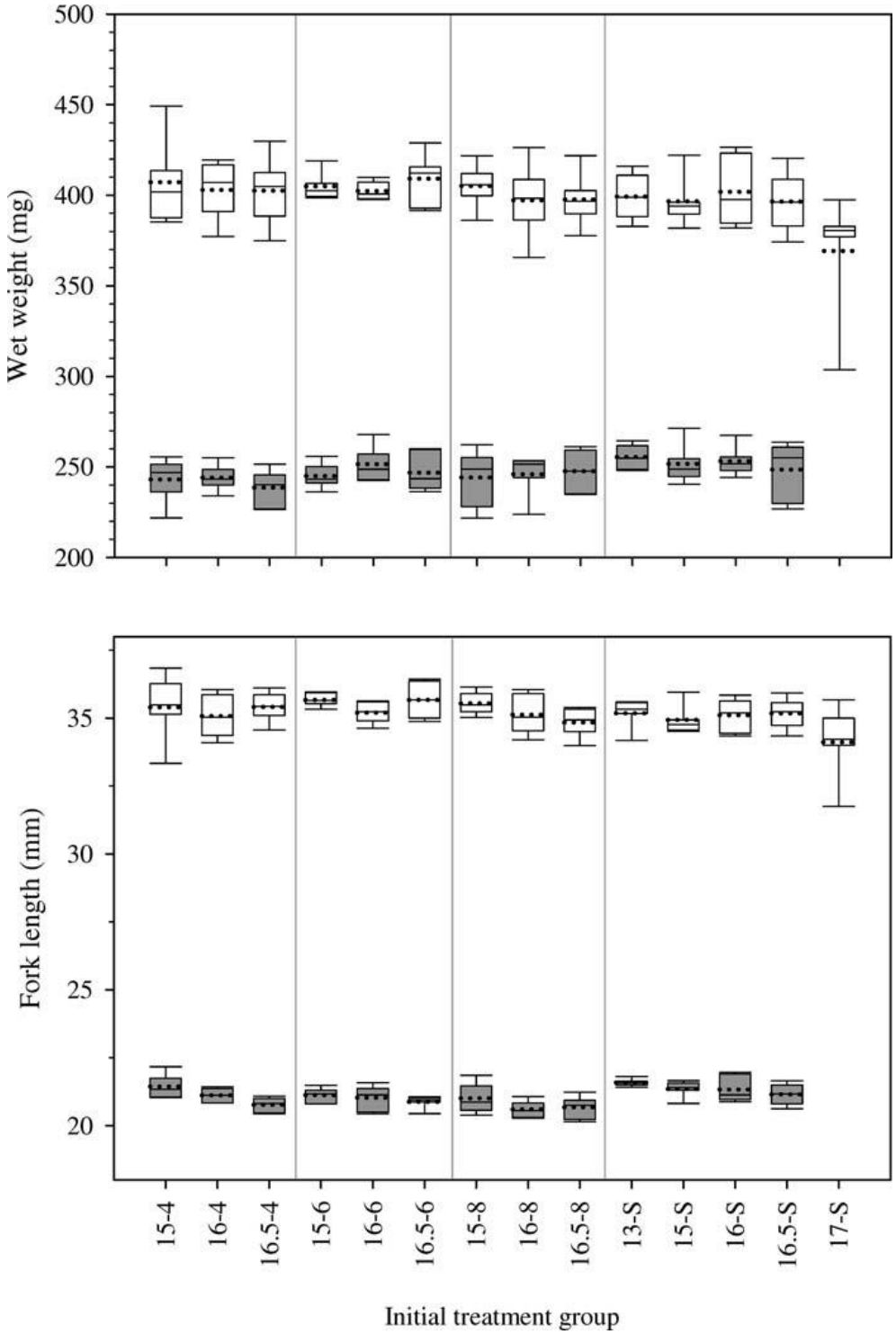

FIGURE 4.—Wet weight (top panel) and fork length (bottom panel) of Snake River fall Chinook salmon alevins at hatch (gray boxes) and emergence (white boxes) for each initial dissolved oxygen–temperature combination. The solid line inside each box represents the median; the dotted line represents the mean. See Figure 3 for additional details.

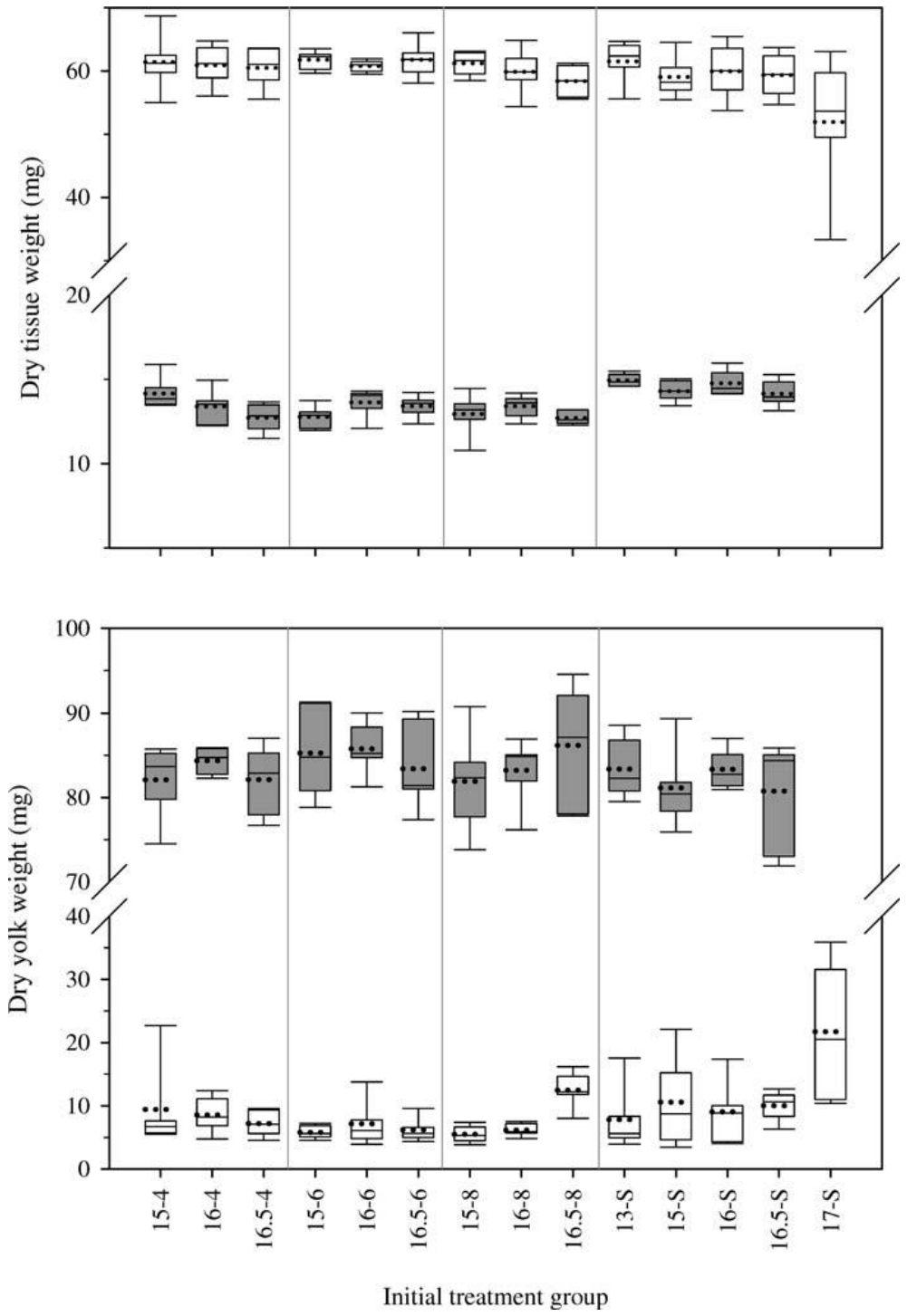

FIGURE 5.—Dry tissue weight (top panel) and dry yolk weight (bottom panel) of Snake River fall Chinook salmon alevins at hatch (gray boxes) and emergence (white boxes) for each initial dissolved oxygen–temperature combination. The solid line inside each box represents the median; the dotted line represents the mean. See Figure 3 for additional details.

The declining thermal regime that we used mimicked the river temperatures where study fish spawn and reduced the impact of elevated temperature at spawning by decreasing the amount of time embryos were exposed to upper temperature tolerance thresholds during critical periods of development.

The declining thermal regime after fertilization also resulted in high survival rates at oxygen levels that

were lower than the Idaho and Oregon standards. These high survival rates occurred because the critical oxygen level that affects salmonid embryo survival, growth, and development depends on temperature. Owing to reduced solubility, the oxygen content of water drops as temperature increases. For example, a sample of freshwater at sea level has 11.33 mg O_2/L at 10°C and 9.95 mg O_2/L at 16°C (Table 2 in Davis 1975). The metabolic needs of the developing embryo increase as temperature increases (Fry 1957; Smith 1957). Consequently, embryos developing in warm water must pass more water over the gills than those developing in cold water to deliver a given volume of oxygen per unit time (Davis 1975). Eggs of Atlantic salmon *Salmo salar* at 17°C used 29 cm^3 $O_2 \cdot kg^{-1} \cdot h^{-1}$, and the minimum required dissolved oxygen level was 8.7 mg O_2/L. As temperature was decreased to 5°C, the metabolism of the eggs slowed to 16 cm^3 $O_2 \cdot kg^{-1} \cdot h^{-1}$, and the minimum critical dissolved oxygen level was 5.7 mg O_2/L (reviewed by Smith 1957).

In this study, the date of 50% hatch for all groups occurred when the dissolved oxygen level exceeded 4 mg O_2/L and, in most cases, was near saturation. Using a computer model called WinSIRP (McLean et al. 1991; Fisheries and Oceans Canada 2006), we determined that the embryos in the 15.0–16.5°C temperature groups were exposed to dissolved oxygen levels less than the critical oxygen concentration P_c (Rombough 1986) for only a short time period early in incubation. Exposure of the embryos to ambient dissolved oxygen levels at or below the P_c value did not last long enough to reduce embryo survival, although the rate of development was slowed. Embryos have a variable oxygen requirement that depends on their stage of development (Davis 1975). The intergravel development of salmonid embryos encompasses four phases that are centered on the critical hatching period (Balon 1975): cleavage eggs and embryos (the prehatch phases) and eleutheroembryos and preemergent alevins (the posthatch phases). Experimental studies show that prehatch phases are more tolerant of low dissolved oxygen than are posthatch phases (Becker et al. 1983; Neitzel and Becker 1985). Uptake of oxygen by prehatch phases is a passive-diffusion process, whereas uptake of oxygen by posthatch phases is an active process that occurs through the circulatory system (Davis 1975). Consequently, early eggs may require less than 2 mg O_2/L, while hatching embryos may require up to 10 mg O_2/L (Alderdice et al. 1958). Atlantic salmon eggs used more oxygen just before hatching than at earlier stages (Smith 1957). The declining temperature regime in this study (at least 0.2°C/d) ameliorated the effects on fall Chinook salmon embryo survival from the low dissolved oxygen levels.

Although survival rates were high at low dissolved oxygen levels, there was an increase in embryo abnormalities at such levels. We documented that abnormal embryo development to the eyed egg (250-ATU) and advanced alevin (750-ATU) stages was related to low dissolved oxygen; nearly twice as many embryos exhibited abnormalities in the 4-mg O_2/L group as in the other groups. Silver et al. (1963) reported that up to 24.4% of the steelhead *O. mykiss* embryos reared at 2.6 mg O_2/L and nearly all Chinook salmon embryos reared at 1.6 mg O_2/L under a range of water velocities experienced abnormal development; most of the deformed steelhead embryos reared at 2.6 mg O_2/L survived through the hatching stage. In the laboratory, these abnormal embryos survived and were counted in our estimates of survival. However, abnormal alevins emerging from redds exposed to 4-mg O_2/L oxygen concentrations would probably not survive under natural conditions. Thus, our estimates of survival at low oxygen levels are probably slightly greater than would be expected in nature.

It is also possible that temperatures of prespawning adults increased our survival rates over those that would be expected in nature. The gametes for our study were collected from adults at Lyons Ferry Hatchery that had been held in 12°C well water before spawning. This temperature is cooler than the water temperatures experienced by adult salmon that arrive in the Snake River before the spawning period. Fall Chinook salmon can reach spawning areas as early as mid-August, when water temperatures are in excess of 20°C (Keefer et al. 2004). Exposure of female fish to elevated water temperature can adversely affect egg viability. For example, eggs taken from mature fall-run Chinook salmon held in hatcheries at water temperatures greater than 15.5°C had poor viability (Hinze 1959, as cited in California Department of Water Resources 1988). To our knowledge, however, the effect of elevated temperature on egg viability has not been studied in wild Chinook salmon.

We did not manipulate flow rates within the egg tubes at the time we were manipulating water temperature and dissolved oxygen. Flow rate within the redd pocket influences embryo survival to emergence (Wickett 1954; Silver et al. 1963; Shumway et al. 1964; Ringler and Hall 1975). As oxygen concentration and flow rate were reduced, steelhead and Chinook salmon embryos required longer to hatch, were smaller at hatch, died more frequently both before and after hatch, and showed an increase in structural anomalies and deformities (Silver et al. 1963). Dissolved oxygen and flow rate were found to

influence the size of coho salmon *O. kisutch* and the time required to reach hatch (Shumway et al. 1964). Because we did not alter the flow rate, we cannot assess whether the dissolved oxygen levels we employed, combined with variations in flow rate, would alter our findings. This is a topic deserving further study.

There were greater discrepancies in survival rate in the groups exposed to 13°C and either saturated dissolved oxygen (i.e., the 13–S group) or a dissolved oxygen concentrations of 4 mg O_2/L. The results showed that survival in the group exposed to 16°C and 4 mg O_2/L (i.e., the 16–4 group) from fertilization to eyed egg had a very high standard deviation among individual egg tubes because of the position of the tubes within the treatment chamber. The results were similar in the treatment chamber in which eggs were exposed to 15°C and 4 mg O_2/L (i.e., the 15–4 group), where survival was 84% at one position and 95–97% at the other positions. More structural deformities at the eyed egg stage were also recorded in one egg tube position within the chambers exposed to 4 mg O_2/L. For example, the abnormal eyed egg counts in egg tubes 1–6 in the 15–4 group were 10, 19, 1, 6, 70, and 3, respectively. Similar findings of egg abnormalities were noted in the 16–4 group according to position in the treatment chamber. Position effects did not appear to be important in the treatments in which dissolved oxygen was greater than 6 mg O_2/L. Our only explanation for these anomalous results is that low dissolved oxygen conditions developed in some of the egg tubes. Delivery of oxygen across the egg capsule membrane (i.e., the chorion) at the time of hatch is critical for successful development (Smith 1957; Alderdice et al. 1958). Hatching mortality due to low dissolved oxygen has been observed in Chinook salmon (Silver et al. 1963), and premature hatch of alevins was noted in chum salmon *O. keta* exposed to hypoxia just before hatch (Alderdice et al. 1958).

Alevin fork length at emergence and wet weight at both hatch and emergence were not affected by dissolved oxygen level or temperature. The fork lengths of hatchlings were significantly different among treatments, but the differences were small (0.8 mm) and near the precision of our measurement technique (0.5 mm). Tissue weights were slightly higher at hatch in the groups exposed to saturated dissolved oxygen than in other dissolved oxygen groups, but the differences (1.3 mg) were again close to the measurement accuracy (1 mg). Other studies of Pacific salmon show that growth is affected at low dissolved oxygen levels and in declining temperature regimes. Declining temperature regimes have tended to increase alevin and fry size of Chinook salmon (Olson and Foster 1955; Murray and Beacham 1987). Steelhead embryos increased in length with increasing dissolved oxygen concentration; the differences in length at hatch were approximately 2–3 mm at concentrations from 3 to 11 mg O_2/L. The mean hatch length of Chinook salmon reared at 2.5 mg O_2/L was 19.7 mm, compared with 21.2 mm at 3.9 mg O_2/L and 24.8 mm at 11.7 mg O_2/L (Silver et al. 1963). Coho salmon embryos reared at dissolved oxygen levels of 2.3–3.9 mg O_2/L weighed about 39 mg less at hatch than other fry reared at the same temperature but at saturated dissolved oxygen levels (Shumway et al. 1964). Growth of steelhead embryos was restricted by the 14th day in units supplied with water that was less than saturated, and coho salmon showed reduction in growth by day 7 at dissolved oxygen levels of 6 mg O_2/L (Silver et al. 1963).

Although both initial dissolved oxygen and temperature were related to development time, temperature appeared to influence development time slightly more than dissolved oxygen. For example, within each temperature treatment, fish required 6–10 d more to reach hatch at 4 mg O_2/L than at saturation and up to 24 d more to reach emergence. In contrast, within each dissolved oxygen treatment, fish required about 20 d more to reach hatch at 13°C than at 16.5°C (there were no data for 17°C) and up to 41 d more to reach emergence. The inverse relationship between temperature and development time observed in this study is common to all salmon species (studies reviewed in Weatherley and Gill 1995). The variable thermal regime used in our study (i.e., declining followed by increasing temperatures) resulted in a longer time to hatch and emergence than reported in studies that used constant temperature regimes. Using a constant exposure at 14°C, Murray and McPhail (1988) discovered that Chinook salmon required 38 and 63 d to reach 50% hatch and 50% emergence, respectively. Subjecting eggs to an increasing temperature regime immediately after fertilization appears to delay hatch time more than subjecting them to a decreasing temperature regime (Murray and Beacham 1986, 1987).

Significantly more yolk remained at emergence in embryos initially exposed to saturated oxygen levels than in those exposed to lower oxygen levels. The exposure of our embryos early in their development to critical dissolved oxygen levels (P_c-values) that were less than ambient dissolved oxygen levels delayed development and slowed yolk adsorption. Oxygen uptake across the egg capsule membrane is restricted at low dissolved oxygen levels and warm temperatures and retards development (Fry 1957). Exposure of chum salmon eggs to 0.3 mg O_2/L starting on day 12 for 7 d delayed hatch by about 10–11 d (Alderdice et al. 1958). Alderdice et al. (1958) found that the developmental

delay was greatest in eggs exposed to hypoxic conditions for 7 d just before the eyed stage and that premature hatching occurred if eggs were subjected to low dissolved oxygen just before hatch. The time to median hatch of steelhead embryos reared at a constant temperature of 9.5°C and a dissolved oxygen level of 2.6 mg O_2/L was 5–8 d longer than the time for fry reared at the same temperature at 11.2 mg O_2/L (Silver et al. 1963). The time to median hatch of Chinook salmon was delayed approximately 2 d at 3.9 mg O_2/L relative to the time at 8.0 mg O_2/L (Silver et al. 1963). Coho salmon reared at dissolved oxygen concentrations ranging from 2.3 to 3.9 mg O_2/L at 10.2°C required about 7 d more to reach 50% hatch than embryos reared at dissolved oxygen levels approaching saturation (Shumway et al. 1964).

The findings from this study have implications for the management of fall Chinook salmon in the Snake River. It is likely that the three dams constituting the Hells Canyon complex (Hells Canyon, Brownlee, and Oxbow dams) have caused temperatures during fall Chinook salmon spawning to exceed the states' water quality standard of 13°C by delaying the natural cooling trends until later in the autumn. In our study, fall Chinook salmon embryos, alevins, and fry tolerated early incubation temperatures patterned after those observed in the Snake River after dam construction. Consequently, their long-term survival would not appear to be affected by the elevated temperatures. However, dissolved oxygen levels less than 5–8 mg O_2/L may affect the success of Snake River fall Chinook salmon populations by increasing the incidence of structural deformities and by delaying hatch and emergence. Migration delays could place the migrants within downstream reservoirs when water temperature and other environmental conditions are not conducive to their survival (Connor et al. 2002). Subyearling fall Chinook salmon that migrate downstream the first week of July (after flows begin to decline and downstream reservoirs heat up) survive at rates of only 5–20%, whereas those that initiate movement in late May survive at rates of 65–90% (Connor et al. 2003a; Smith et al. 2003). Although the fall Chinook salmon in our study survived low initial dissolved oxygen levels, such a delay in emergence timing could have significant long-term effects on their survival. Thus, an exemption to the state water quality standards for temperature—but not oxygen—may be warranted for the portions of the Snake River where fall Chinook salmon spawn.

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