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Physical Factors Influencing Survival to Emergence and Time of Emergence of Shoreslope-Spawned Kokanee Salmon in Flaming Gorge Reservoir, Utah-Wyoming

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PHYSICAL FACTORS INFLUENCING SURVIVAL TO EMERGENCE AND TIME OF EMERGENCE OF SHORESLOPE-SPAWNED KOKANEE SALMON IN FLAMING GORGE RESERVOIR, UTAH-WYOMING

by

Randall J. Jeric

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ABSTRACT

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of Emergence of Shoreslope-Spawned Kokanee Salmon

in Flaming Gorge Reservoir, Utah-Wyoming

by

Randall J. Jeric, Master of Science

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Department: Fisheries and Wildlife

I used incubation baskets containing viable eggs and spawning substrate to estimate the survival to emergence and time of emergence of kokanee salmon *Oncorhynchus nerka* at depths to 20 m in Flaming Gorge Reservoir, Utah-Wyoming. Traps on the incubation baskets captured fry emerging from a known quantity of eggs. Water drawn into a syringe from an intragravel pipe buried near each incubation basket was used to determine intragravel dissolved oxygen concentrations throughout the intragravel period. Water from control baskets without eggs did not have significantly greater dissolved oxygen concentrations than adjacent water. A jar associated with each incubation basket collected sediment to determine absolute and organic sedimentation during the study. Temperatures at the substrate-

water interface were used to describe degree-days accumulated before emergence. Survival to emergence ranged from zero to 66% and was most significantly related to mean intragravel dissolved oxygen concentrations. Survival to emergence, mean intragravel dissolved oxygen concentrations, and organic sedimentation decreased with depth.

(71 pages)

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Randall J. Jeric

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CHAPTER 1

INTRODUCTION

Various physical factors of intragravel waters have been identified as influencing the development and survival of incubating salmonid embryos. Among these factors, intragravel dissolved oxygen concentrations, water temperature, and quantities of fine sediments have been repeatedly reported as important determinants of salmonid spawning success in lotic environments. During the intragravel period, dissolved oxygen concentrations and water temperatures may act independently or in combination to influence metabolic rates and exchange of wastes of salmonids developing in streams. Fine sediments in the intragravel matrix can affect rates of exchange between stream surface waters and the intragravel environment, altering dissolved oxygen concentrations in redds. Accumulations of fines on redds can impede intragravel water exchange and reduce the ability of salmonid fry to emerge from redds. The influence of water temperatures and dissolved oxygen concentrations on the condition of emerging fry (i.e., length, weight, and fat reserves) can affect the competitive abilities of salmonids during early life stages, ultimately affecting population recruitment.

Despite widespread distribution of shoreslope-spawning salmonid populations in lakes and reservoirs throughout North America, the influence of dissolved oxygen concentration, water temperature, and sediment deposition on the survival and development of salmonid embryos incubating in lacustrine waters has not been

defined. The reduced water velocities of lentic waters likely reduces exchange of intragravel flows and dissolved oxygen concentrations relative to lotic waters. Stratification of the water column within the range of spawning depths in lakes and reservoirs can result in dissolved oxygen and water temperature variations associated with depth that do not occur in streams. Knowledge of the relationship of salmonid survival to emergence and time of emergence relative to depth could influence management practices in reservoirs where water levels fluctuate during the period prior to emergence.

My research evaluated the influence of several factors identified as important to salmonid reproductive success in streams on the survival of salmonids spawned in lentic waters. Additionally, I considered the dimension of water depths to 20 m not associated with studies in lotic environs. Site-specific methods were developed to measure the influence of intragravel dissolved oxygen concentrations, temperatures at the substrate-water interface, and sediment accumulations on the survival to emergence and time of emergence of shoreline-spawned kokanees in Flaming Gorge Reservoir, Utah-Wyoming. I evaluated the validity of these methods and discussed the implications of the results relative to management of salmonid populations in lakes and reservoirs.

CHAPTER 2

EVALUATION OF A METHOD FOR MEASURING INTRAGRAVEL DISSOLVED OXYGEN CONCENTRATIONS AND SURVIVAL TO EMERGENCE IN SHORE-SPAWNED SALMONIDS[1]

Abstract.--I describe an incubation basket and a modified intragravel water sampling device used to quantify salmonid survival to emergence relative to dissolved oxygen concentrations in deep lacustrine habitats. Incubation baskets containing viable kokanee *Oncorhynchus nerka* eggs and shale substrate were set by divers in 2-20-m-deep spawning habitat in Flaming Gorge Reservoir, Utah-Wyoming. Water drawn into a syringe from an intragravel pipe buried near each incubation basket was used to determine intragravel dissolved oxygen concentrations throughout the incubation period. A trap on each incubation basket captured emergent fry in a holding bag. The bags were exchanged weekly to determine survival to emergence and time of emergence. Water in control baskets without eggs did not have significantly greater dissolved oxygen concentrations than adjacent water.

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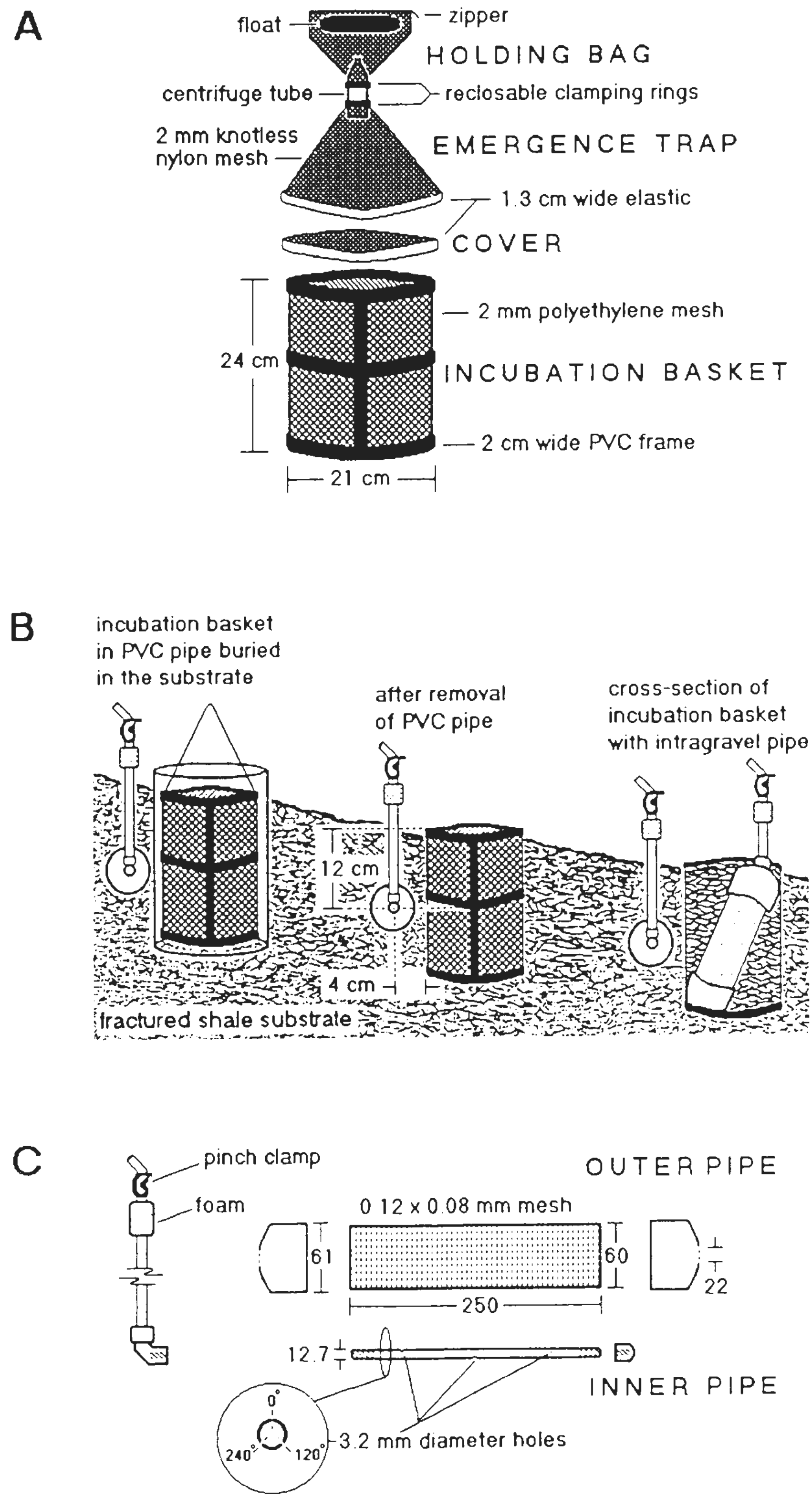
[1]The contents of this chapter were previously published as: Jeric, R. J., T. Modde, and J. M. Godfrey. 1995. Evaluation of a method for measuring intragravel dissolved oxygen concentrations and survival to emergence in shore-spawned salmonids. North American Journal of Fisheries Management 15:185-192.

Introduction

Intragravel dissolved oxygen concentrations influence survival of salmonids incubating in lotic waters (Wickett 1954; Coble 1961; Phillips and Campbell 1962; Bianchi 1963; Koski 1966, 1975; McNeil 1966; Sowden and Power 1985), but lack of adequate means of measuring intragravel dissolved oxygen in deep lentic environments has prevented evaluation of this relationship for lacustrine spawners. Previous attempts to relate intragravel survival of shore-spawned salmonids to dissolved oxygen concentrations were marginal or unsuccessful, and indicated need for a site-specific approach to measure associated variables. Dissolved oxygen concentrations sampled from the water column above kokanee *Oncorhynchus nerka* spawning habitat in Banks Lake, Washington, were at or near saturation throughout incubation and could not be used to detect differences in survival of alevins (Stober et al. 1979). Hassemer (1984) found no relation between survival of kokanee embryos and dissolved oxygen concentrations of intragravel water sampled through piezometers driven into the substrate at 1.5 and 6.0 m depths in Coeur d'Alene Lake, Idaho. Beattie et al. (1986) determined that groundwater high in dissolved oxygen flowing through shoreline redds of kokanees in Flathead Lake, Montana, increased egg survival relative to areas lacking groundwater discharge. I describe a method for measuring salmonid survival from egg-deposition to emergence relative to site-specific intragravel dissolved oxygen concentrations in deep water, without disrupting pre-emergent fish.

Methods

To monitor in situ survival to emergence and time of emergence, I adapted incubation baskets of Maret et al. (1993) by eliminating iron framing that might alter dissolved oxygen concentrations. The incubation basket frame was constructed from a 24-cm-long piece of 21-cm-diameter, schedule 80 polyvinyl chloride (PVC) pipe. Six equally spaced panels (20 x 9 cm) were removed with an electric jigsaw, leaving a 2-cm-wide frame (Figure 2-1A). I glued a rectangle (64 x 23 cm) of rigid polyethylene net (2-mm square mesh) inside the frame with PVC adhesive, aligning the seam along a vertical section of frame. To form a bottom for the incubation basket, I centered a piece (about 30 x 30 cm) of polyethylene net on a 17-cm diameter wood disk (2-cm thick), and pressed a 19.5-cm inside diameter section of PVC pipe (5-cm wide) over the net and around the disk. I heated the area of net between the disk and PVC pipe with an electric heat-gun, to shape vertical sides around the disk. Excess net overlapping the disk was trimmed, leaving a molded mesh bottom with 2-cm vertical sides. The bottom was fitted inside the base of the net-lined frame with sides turned upward. I fastened the bottom to the frame using a 1.5-cm-wide piece of PVC pipe (21-cm diameter) from which a section was cut to yield a band of 59-cm outside circumference. The band fit tightly inside the mesh bottom and was attached to the base of the incubation basket frame with seven equally spaced aluminum rivets. A twine harness was tied to the top of the frame.


A
float
zipper
HOLDING BAG
centrifuge tube
reclosable clamping rings
2 mm knotless nylon mesh
EMERGENCE TRAP
1.3 cm wide elastic
COVER
2 mm polyethylene mesh
24 cm
INCUBATION BASKET
2 cm wide PVC frame
21 cm
B
incubation basket in PVC pipe buried in the substrate
after removal of PVC pipe
cross-section of incubation basket with intragravel pipe
12 cm
4 cm
fractured shale substrate
C
pinch clamp
foam
OUTER PIPE
0 12 x 0.08 mm mesh
61
60
22
250
12.7
INNER PIPE
0°
240°
120°
3.2 mm diameter holes

Incubation baskets were filled with fractured shale substrate sorted from kokanee spawning habitat in Flaming Gorge Reservoir, Utah-Wyoming. The shale was rinsed under water in a plastic crate with 2-cm^2 openings to remove shale fragments and organic debris. Pieces longer than about 6 cm were removed and the remaining substrate was used in the incubation baskets. This sorting process resulted in a substrate size-composition similar to the spawning habitat used by kokanees observed at the study site. A three-stem funnel (each stem 2.5-cm diameter) was centered inside a half-filled incubation basket before filling the remainder with shale. The incubation basket was placed in 15-cm-deep water and 50 kokanee eggs (4-26 h after fertilization) were poured into the funnel, about one-third through each stem. The eggs were fertilized with sperm from kokanees collected in Flaming Gorge Reservoir by the Wyoming Game and Fish Department in 1990. Dead eggs were removed, and mortality for the pool of eggs was less than 1% during the handling period. After gently removing the funnel, a 2-mm-mesh knotless-nylon cover was fastened by an elastic band to the top of the incubation basket (Figure 2-1A). The incubation basket was placed in a water-filled plastic bag that was sealed to minimize disruption of eggs during transport.

The incubation basket was taken by scuba divers to an incubation site that had been prepared by burying 22 cm of a 30-cm long PVC pipe (30-cm outside diameter) vertically into the kokanee spawning habitat. After tearing away the plastic bag, divers lowered the incubation basket by the harness into the pipe. The pipe was

extracted, surrounding the incubation basket with substrate (Figure 2-1B). Prior to emergence of fry, divers replaced the mesh cover on the incubation basket with an emergence trap made of 2-mm-mesh knotless-nylon cloth and a funnel cut from a plastic centrifuge tube (14-cm length of 2.7-cm diameter with tapered end cut to a 1-cm diameter opening; Figure 2-1A). A mesh cover was used prior to the emergence trap to eliminate intrusion of naturally spawned eggs while allowing an even distribution of sediments entering the incubation basket, and to prevent spawning kokanees or angler gear from becoming entangled in the traps. The holding bag on the emergence trap was exchanged weekly, and captured fry were counted to determine survival to emergence and time of emergence.

Intragravel water samples were drawn from a horizontal intragravel pipe modified from Hoffman (1986; Figure 2-1C). The outer pipe (250-mm length of 60-mm outside diameter 0.12 x 0.08-mm-mesh polypropylene filtration tube) had PVC end-caps (61-mm inside diameter) glued to each end. An inner pipe (254-mm length of 12.7-mm outside diameter PVC threaded nipple) was drilled with three equally spaced holes (3.2-mm diameter) circumferentially offset 120°. A threaded end-cap (12.7-mm inside diameter) on one end of the inner pipe was sealed with glue to a hole (22-mm diameter) in one outer end-cap. The other end of the inner pipe was threaded into a 90° polypropylene elbow (12.7-mm inside diameter threaded compression fitting) through a hole (22-mm diameter) in the outer end-cap. The elbow was sealed to the end-cap with silicone caulk. Water from within the pipe was drawn through

flexible tubing (about 50-cm length of 10-mm outside diameter x 2-mm wall) connected to the compression fitting. Foam pipe insulation (19-mm inside diameter) buoying the tubing was held by a pinch-clamp, which was opened during sampling. The intragravel pipe was buried parallel to the shoreline, 12 cm deep in the substrate, and about 4 cm from the shoreward-side of the incubation basket (Figure 2-1B).

Water was drawn from the intragravel pipe by scuba divers using a large syringe similar in volume (700 mL) to the filtration tubing. The syringe cylinder (Figure 2-2) was made from acrylic tubing (220-mm length of 70-mm outside diameter x 3-mm wall) squared at one end and beveled 60° at the other end. The cylinder face (75-mm diameter) was made from flat acrylic (10-mm thick) that was counter-sunk (5 mm deep to 63-mm diameter) to fit into the square end of the cylinder. A 3-mm diameter hole through the center of the cylinder face was counter-bored (5 mm deep to 6.5 mm-diameter) to hold a nipple (13-mm length of 6-mm outside diameter, 1.5-mm-wall acrylic tubing). The plunger plate (63-mm diameter) was made from 17-mm-thick flat acrylic with two channels (5 mm wide x 4 mm deep, separated by 3 mm) that held rubber piston seals (64-mm outside diameter x 55-mm inside diameter x 4.8-mm wide). The seals were set antagonistically so that as one seal evacuated, the other filled the syringe. A counter-bore (22-mm diameter x 7-mm deep) in the plunger plate centered an acrylic rod (21-mm diameter x 240-mm long) held by a bolt recessed in the opposite side of the plate. A threaded knob on the other end of the rod was used to pull the plunger through the cylinder. A removable guide-

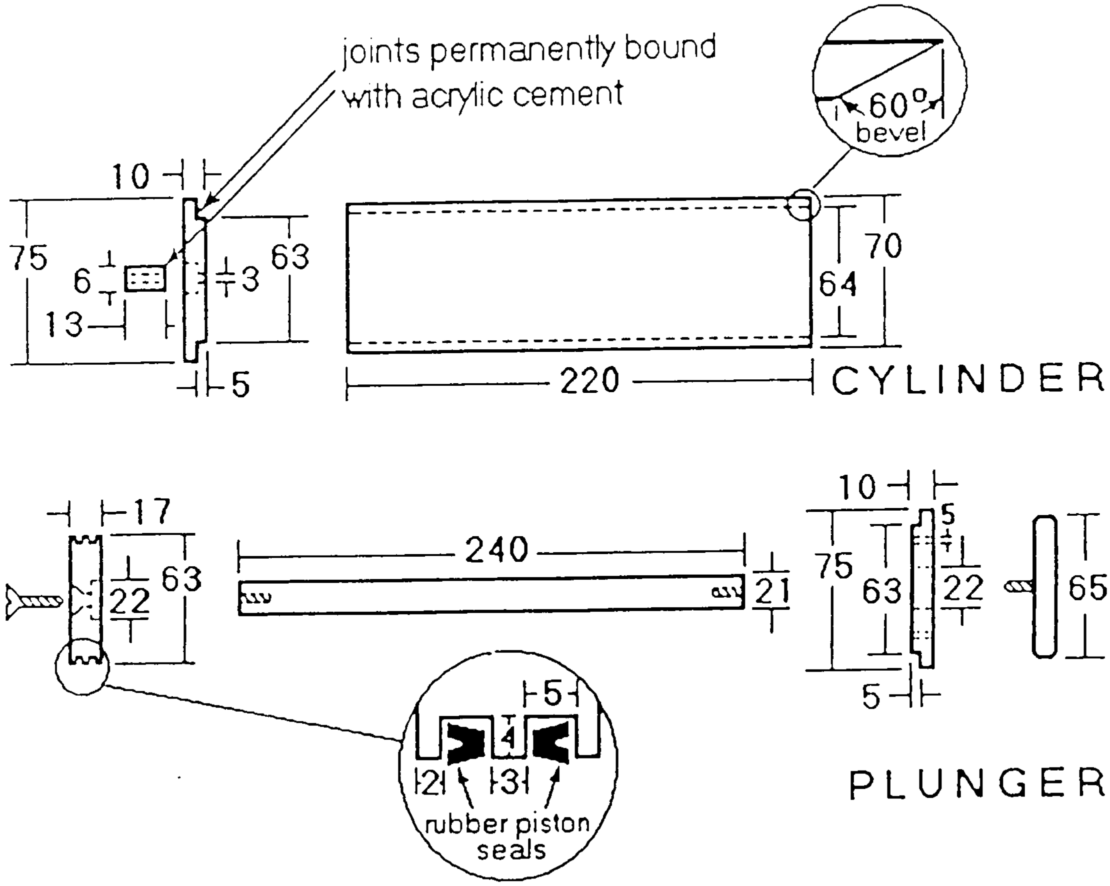


Figure 2-2.--Exploded view of syringe with measurements in mm.

plate (75-mm diameter) made from 10-mm-thick flat acrylic was counter-sunk (5 mm deep to 63-mm diameter) to fit into the beveled end of the cylinder. A hole (22-mm diameter) centered in the guide plate held the plunger plate square to the cylinder wall, and two holes (5-mm diameter) allowed water to evacuate from the rear of the cylinder as the plunger was drawn.

To eliminate air from the syringe, the plunger was inserted into the cylinder under water. Before connecting the syringe to the hose of the intragravel pipe, the plunger was depressed flush to the face plate, purging water from the cylinder. The plunger was retracted to fill the syringe in 40-45 s (about 1 L/min). At the surface the water sample was passed through latex tubing from the syringe nipple to a 300-mL BOD bottle, and fixed for dissolved oxygen determination by the Winkler Method using the azide modification for nitrate interference (APHA et al. 1985).

The equipment described was lightweight and durable. Materials for 58 incubation baskets cost US$278 (1990), and time of construction was 81 person-h. Materials for 50 incubation basket covers, 50 emergence traps, and 100 holding bags cost $216, and labor by a tailor was $296. Materials for the intragravel pipes cost $6.20 each, and 36 were built in about 18 person-h. Materials and machining of the acrylic syringe parts were about $42 each. Throughout two field-seasons the incubation baskets and intragravel pipes remained under water for more than 400 d with no apparent deterioration. The incubation baskets and intragravel pipes were easily cleaned with water from a pressure-sprayer. The emergence traps were cleaned

of algal growth in a washing-machine with a dilute bleach solution. The acrylic syringes are brittle and must be handled carefully, especially during subfreezing temperatures. All field work was completed by two scuba divers, except ice-diving and incubation basket installation, which required two additional people.

Field Evaluation

To test whether intragravel dissolved oxygen samples from the intragravel pipe represented water within the incubation basket, three independent control baskets were buried at 3-5-m depths within kokanee spawning habitat. Each control basket, containing an intragravel pipe and sorted substrate (but no kokanee eggs), was buried with an associated intragravel pipe as described for the other incubation basket (Figure 2-1B). The three control baskets and adjacent intragravel pipes were sampled six times during the incubation period. Repeated measures analysis determined no difference in dissolved oxygen concentrations between samples taken within and adjacent to the control baskets (SYSTAT, Inc. 1989; Table A-1 in the appendix). Dissolved oxygen concentrations within the intragravel pipes of the control baskets were highly correlated with the dissolved oxygen concentrations sampled from the adjacent intragravel pipes (Figure 2-3).

Dissolved oxygen concentrations of samples (each equal to the volume of the filtration-tube) from a single intragravel pipe varied 0.5 mg/L or less over four consecutive draws (6.1, 6.6, 6.5, and 6.6 mg/L), indicating water within the filtration

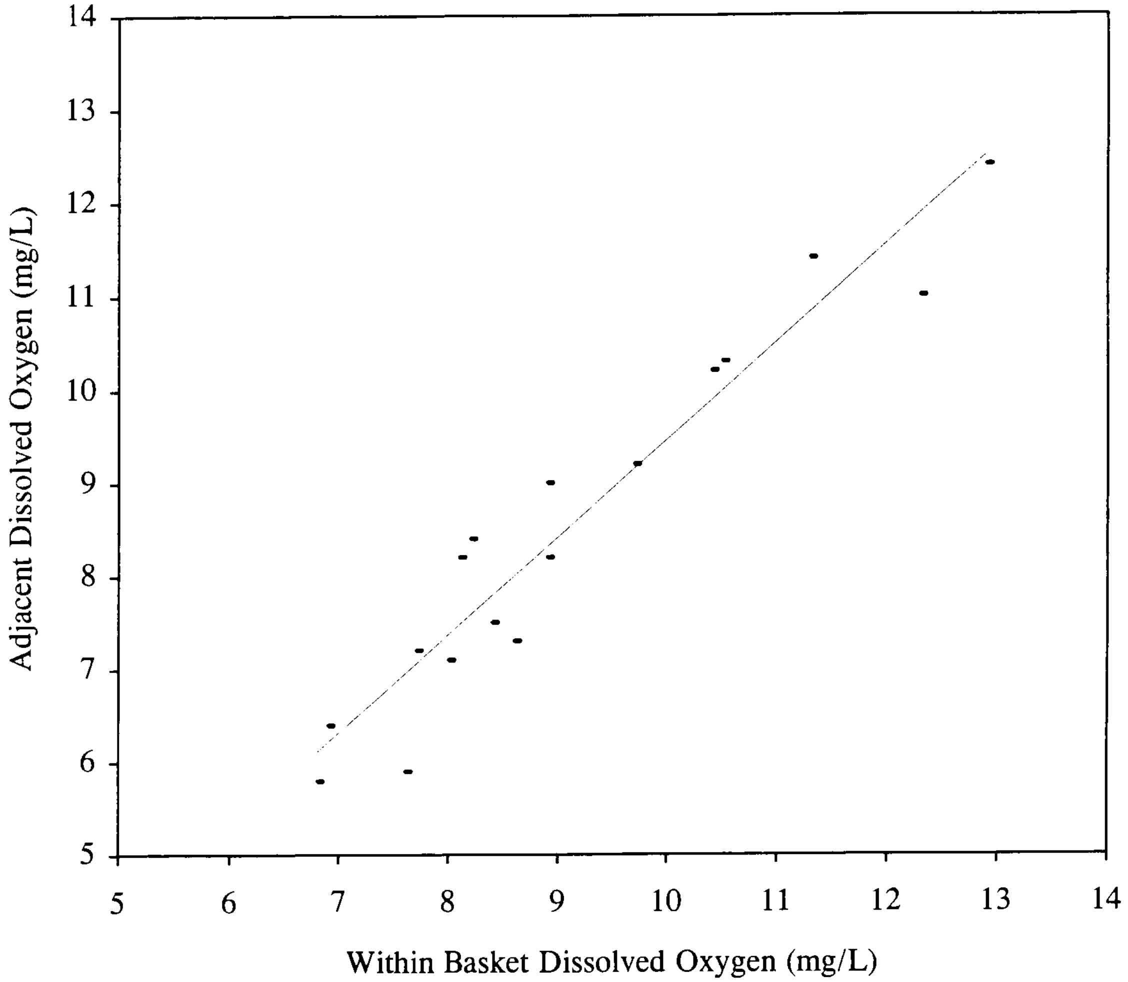


Figure 2-3.--Relation between dissolved oxygen concentrations of water within the control basket (Within DO) and the dissolved oxygen concentrations adjacent to the control basket (Adjacent DO).

tube represented surrounding intragravel water. The intragravel pipes were set horizontally to sample the width of the redd, and the off-set holes of the inner pipe drew water radially about the pipe. Dissolved oxygen sampled from the substrate-water interface above intragravel pipes was consistently higher than water from the associated intragravel pipes. During a 6-week period, three anoxic samples were drawn from an intragravel pipe while the associated substrate-water interface dissolved oxygen concentrations ranged from 12.2 to 14.5 mg/L, indicating that sampling caused no mixing of intragravel and water-column waters. These anoxic samples also indicated that potential residual air or water contamination in the syringe was not a concern for the volume of water sampled.

Discussion

The incubation baskets and intragravel pipes have been used to identify positive relationships between salmonid survival to emergence and dissolved oxygen concentrations at 2-20-m depths. The incubation baskets may be removed through time to monitor embryonic survival and development relative to dissolved oxygen concentrations, and the holding bags on the emergence traps retain live fry for measuring length, weight, and condition factor. Use of substrate within the incubation baskets seemed to limit fungal growth often encountered among eggs in incubation boxes (Harshbarger and Porter 1979), and more closely simulates natural conditions. However, sorting of substrate sizes and depth of burial of eggs were

based on qualitative observations by divers, and may have affected dissolved oxygen concentrations and survival to emergence relative to natural conditions.

The water sampling method was simple and allowed scuba divers to collect samples under ice. The large volume of water drawn from intragravel pipes was sufficient for analyses of other chemical constituents such as pH and CO_2. By burying the PVC pipe sleeves and intragravel pipes before preparing the incubation baskets, intragravel waters and organics at the incubation sites were stabilized. Incubation site preparation enhanced experimental design by allowing installation of 45 incubation baskets in a 22-h period, and likely minimized bias in mortality by reducing the handling period of eggs.

References

APHA (American Public Health Association), American Water Works Association, and Water Pollution Control Federation. 1985. Standard methods for the examination of water and wastewater, 16th edition. APHA, Washington, D.C.

Beattie, W., P. Clancey, J. Decker-Hess, and J. Fraley. 1986. Impacts of water level fluctuations on kokanee reproduction in Flathead Lake. Montana Department of Fish, Wildlife, and Parks, Annual Report 1985, Kalispell.

Bianchi, D. R. 1963. The effects of sedimentation on egg survival of rainbow trout and cutthroat trout. Master's thesis. Montana State College, Bozeman.

Maret, T. R., T. A. Burton, G. W. Harvey, and W. H.Clark. 1993. Field testing of new monitoring protocols to assess brown trout spawning habitat in an Idaho stream. North American Journal of Fisheries Management 13:567-580.

Coble, D. W. 1961. Influence of water exchange and dissolved oxygen in redds on survival of steelhead trout embryos. Transactions of the American Fisheries Society 90:469-474.

Harshbarger, T. J., and P. E. Porter. 1979. Survival of brown trout eggs: two planting techniques compared. Progressive Fish-Culturist 41:206-209.

Hassemer, P. F. 1984. Spawning ecology and early life history of kokanee *Oncorhynchus nerka* in Coeur d'Alene and Pend Oreille Lakes, Idaho. Master's thesis. University of Idaho, Moscow.

Hoffman, R. J. 1986. A horizontal intragravel pipe for sampling water quality in salmonid spawning gravel. North American Journal of Fisheries Management 6:445-448.

Koski, K. V. 1966. The survival of coho salmon *Oncorhynchus kisutch* from egg deposition to emergence in three Oregon streams. Master's thesis. Oregon State University, Corvallis.

Koski, K. V. 1975. The survival and fitness of two stocks of chum salmon *Oncorhynchus keta* from egg deposition to emergence in a controlled stream environment at Big Beef Creek. Doctoral dissertation. University of Washington, Seattle.

McNeil, W. J. 1966. Effect of the spawning bed environment on reproduction of pink and chum salmon. U.S. Fish and Wildlife Service Fishery Bulletin 65:495-523.

Phillips, R. W., and H. J. Campbell. 1962. The embryonic survival of coho salmon and steelhead trout as influenced by some environmental conditions in gravel beds. Pacific Marine Fisheries Commission Annual Report 14:60-75.

Sowden, T. K., and G. Power. 1985. Prediction of rainbow trout embryo survival in relation to groundwater seepage and particle size of spawning substrates. Transactions of the American Fisheries Society 114:804-812.

Stober, Q. J., R. W. Tyler, C. F. Cowman, Jr., J. Wilcock, and S. Quinnell. 1979. Irrigation drawdown and kokanee salmon egg to fry survival in Banks Lake. University of Washington Fisheries Research Institute Final Report FRI-UW-7913, Seattle.

SYSTAT, Inc. 1989. SYSTAT: The system for statistics. Evanston, Illinois.

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

CHAPTER 3

INFLUENCE OF SOME INTRAGRAVEL CONDITIONS ON SURVIVAL TO EMERGENCE OF SHORESLOPE-SPAWNED KOKANEES IN FLAMING GORGE RESERVOIR, UTAH-WYOMING

Abstract.--Incubation baskets containing viable kokanee *Oncorhynchus nerka* eggs and shale substrate were set by divers in 2-20-m-deep shoreslope-spawning habitat in Flaming Gorge Reservoir, Utah-Wyoming. A trap on each incubation basket captured emergent fry to determine survival to emergence and time of emergence. Water from an intragravel pipe buried adjacent to each incubation basket was used to determine intragravel dissolved oxygen concentrations throughout the incubation period. A jar associated with each incubation basket collected sediment to determine absolute and organic sedimentation during the study. Temperatures at the substrate-water interface were used to describe degree-days accumulated before emergence. Survival to emergence ranged from 0 to 66% and was most significantly related to mean intragravel dissolved oxygen concentrations. Survival to emergence, mean intragravel dissolved oxygen concentrations, and organic sedimentation each decreased with depth.

Introduction

Dissolved oxygen concentrations in waters surrounding incubating salmonid embryos can be an important factor influencing their survival, development, time of

emergence, and post-emergent competitive abilities. Positive relations between intragravel dissolved oxygen concentrations and salmonid embryo survival have been determined in numerous stream and laboratory studies (e.g., Wickett 1954; Alderdice et al. 1958; Garside 1959, 1966; Coble 1961; Phillips and Campbell 1962; Silver et al. 1963; Shumway et al. 1964; Mason 1969; Wells and McNeil 1970; Koski 1975; Hamor and Garside 1976; Sowden and Power 1985). Time of emergence of salmonids incubated in laboratory streams varies in response to decreasing dissolved oxygen concentrations. Development of salmonid embryos may decrease directly with decreasing dissolved oxygen concentrations (Garside 1959, 1966; Silver et al. 1963; Shumway et al. 1964; Brannon 1965; Hamor and Garside 1976), but reduced oxygen availability at critical stages of development may induce hatching or hasten emergence (Alderdice et al. 1958; Bams 1969). Reduced oxygen availability throughout incubation may decrease the length and competitive abilities of emergent fry, reducing subsequent growth and survival (Mason 1969).

Salmonid survival to emergence, developmental rates, and emergence timing are influenced by water temperatures during the incubation period. Earlier times of emergence were associated with increased water temperatures both in situ (Holtby 1988; Murray et al. 1989) and in laboratory streams (Garside 1966; Hamor and Garside 1976). Relative to cooler waters, reduced survival to emergence, timing of emergence, and size at hatching were observed for salmonids incubated in controlled lotic water temperatures $\geq 10°C$ (Heming 1982; Murray et al. 1989). The effect of

temperature on emergence timing can influence competition among salmonids by altering feeding and swimming abilities (Thomas et al. 1969). Earlier emerging salmonids may assert territorial advantages over later emerging fish (Mason and Chapman 1965).

Accumulation of fines in redds can alter the intragravel environment of the redd, reducing survival to emergence of salmonids (Ringler and Hall 1975; Chapman 1988). Decreasing survival with increasing fine accumulations in salmonid redds can result from reduced intragravel water flow, which decreases dissolved oxygen available to incubating embryos (Phillips et al. 1975; Hausle and Coble 1976). Bianchi (1963) found that increased sedimentation reduced the apparent water velocity and dissolved oxygen concentrations in salmonid redds, resulting in greater mortality of eggs. The water exchange rate can be a significant factor affecting the concentration of oxygen supplied to incubating salmonids (Hamor and Garside 1976).

Despite numerous studies relating timing and survival to emergence to dissolved oxygen concentration, water temperature, and sedimentation in lotic systems, parallel investigations in lentic systems are scant. Hassemer and Rieman (1981) suggested that shoreslope-spawning kokanees in Coeur d'Alene Lake, Idaho, used angular substrate, which allowed excellent water exchange, presumably increasing oxygen available to eggs. Sly (1988) used intragravel dissolved oxygen concentrations measured from 2.0-6.0-m depths to distinguish between good and degraded lake trout *Salvelinus namaycush* spawning habitat among several lakes in

southern Ontario, and found that low dissolved oxygen concentrations occurred in gravel with high sediment deposition. Water column dissolved oxygen concentrations sampled from kokanee spawning grounds in Banks Lake, Washington, were at, or near, saturation throughout incubation and could not be used to detect differences in survival of embryos (Stober et al. 1979). Hassemer (1984) found no relationship between survival of kokanee embryos and dissolved oxygen concentrations of intragravel water sampled at 1.5 and 6.0-m depth in Coeur d'Alene Lake.

Relative to lotic systems, the reduced water current, thickness of ice-cover, and differences in pressure associated with depth of lentic waters could affect dissolved oxygen concentrations available to salmonid embryos incubating along shoreslopes. Lake or reservoir regulation may influence recruitment of shoreslope-spawning salmonids by altering the intragravel condition of redds within and below the range of water-level fluctuations (Fraley and Decker-Hess, 1987). Time of emergence of kokanees from several sites in Flathead Lake, Montana, was synchronous with minimum water-column dissolved oxygen concentrations during egg incubation (Woessner and Brick 1985).

In this study, I measured the in situ survival rate and emergence timing of kokanee embryos incubating in Flaming Gorge Reservoir, Utah-Wyoming. I then examined the relationship of survival and emergence to intragravel dissolved oxygen concentrations, depths, temperatures, and sedimentation rates observed on the spawning grounds during incubation in 1991-92.

Study Area

Flaming Gorge Reservoir is a large (145 km long, 17,000 ha surface area), high elevation (1841 m at full pool), complex reservoir in northeast Utah and southwest Wyoming (Schmidt and Brayton 1981). The long-axis of the reservoir is oriented primarily north-south. This study occurred along the northeastern slope of an east-shore bay, located south of Wildhorse Draw (Figure 3-1). Prevailing west winds create frequent wave activity along a shale talus-slope that extends to about 20-m depth near the opening of the bay. Spawning by kokanees in this bay peaked in late October in 1991. These kokanees used unconsolidated, angular shale substrate (<10-cm long) along steep (21-40°) slopes, and distributed eggs evenly among 1.5-15-m water depths (Gipson and Hubert 1993).

Methods

Survival from egg fertilization to emergence was determined using incubation baskets containing viable kokanee eggs (4-26 h after fertilization) and sorted spawning-habitat substrate. The eggs were fertilized from kokanees collected in Flaming Gorge Reservoir by the Wyoming Game and Fish Department in 1991. Thirty incubation baskets, each containing 50 eggs covered by a 12-cm deep layer of sorted substrate, were buried within the study area by divers on November 7 and 8, 1991. Three baskets were distributed within each 2-m depth interval, from 1-21-m, along a 25-m length of shore.

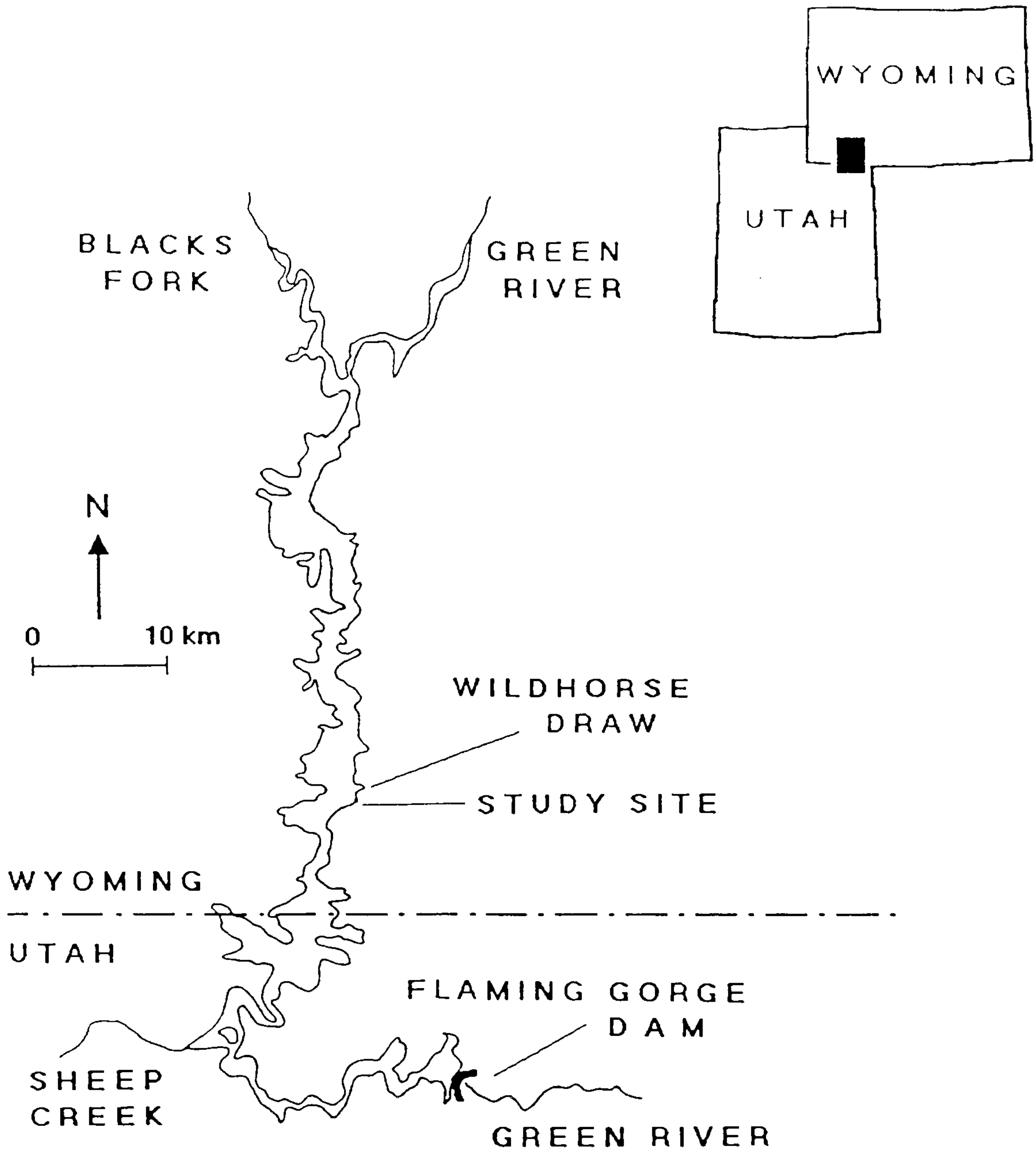


Figure 3-1.--Map of Flaming Gorge Reservoir showing location of study site.

Nylon mesh covers (1-mm bar) were placed on top of the incubation baskets to prevent intrusion of naturally spawned eggs, while allowing fine sediments to enter the basket. On March 28, 1992, the mesh covers were replaced with emergence traps to capture emergent fry. The holding bag on each emergence trap was exchanged every 7 d from April 25 to May 30, 1992, and captured fry were counted to determine survival to emergence. On May 30, all incubation baskets were removed to count the live fry that remained.

A horizontal intragravel pipe buried adjacent to each incubation basket was used to sample dissolved oxygen concentrations of intragravel water associated with each incubation basket. The pipes were centered at the depth of the eggs in the incubation basket. Intragravel dissolved oxygen concentrations were sampled every 28 d, beginning November 9, 1991. Extreme weather conditions altered this sampling schedule on January 11 and February 2, 1992. Dissolved oxygen concentrations were measured using the Winkler titration method with azide modification for nitrate interference (APHA et al. 1985). A detailed description of the construction, installation, and use of the incubation baskets and emergence traps, and extraction of intragravel water samples from the horizontal pipes can be found in Jeric et al. (1995).

Sediment deposition on redds during the incubation period was measured using sediment traps. Sediment was collected into 1-L polyethylene jars with 5.4-cm diameter openings. A jar was mounted upright on a stainless-steel rod driven into the substrate about 15 cm down-slope from each incubation basket, so that the

top of the jar was at the same depth as the top of the incubation basket. The jars were installed on December 7, 1991 and sediment samples were collected for three periods on February 2, March 28, and May 23, 1992. Solids from each jar were aspirated onto precombusted 0.45-micron glass-fiber (Whatman GF/C) filters, dried at 103°C for 24 h, and weighed to 0.1 mg. The dried samples and filters were combusted for 45 min at 550°C in a muffle furnace and reweighed to determine the organic weight.

Thermometers bound to stakes were set at the substrate-water interface every 2-m depth, from 2-20-m deep, along the midline of the study area. Divers recorded temperatures at the substrate-water interface from each thermometer on each sample date. Degree-days were calculated at each depth by linearly interpolating temperatures between sample intervals.

Results

Three of the 30 incubation baskets originally installed (2.1, 2.4 , and 18.0-m-depth) were dislocated by kokanee spawning activities. Data associated with these baskets are not included in the analyses.

Time of Emergence

Emergent fry were first captured the week ending May 2, and peak emergence occurred the week ending May 9 (Figure 3-2). Four of the 398 total fry

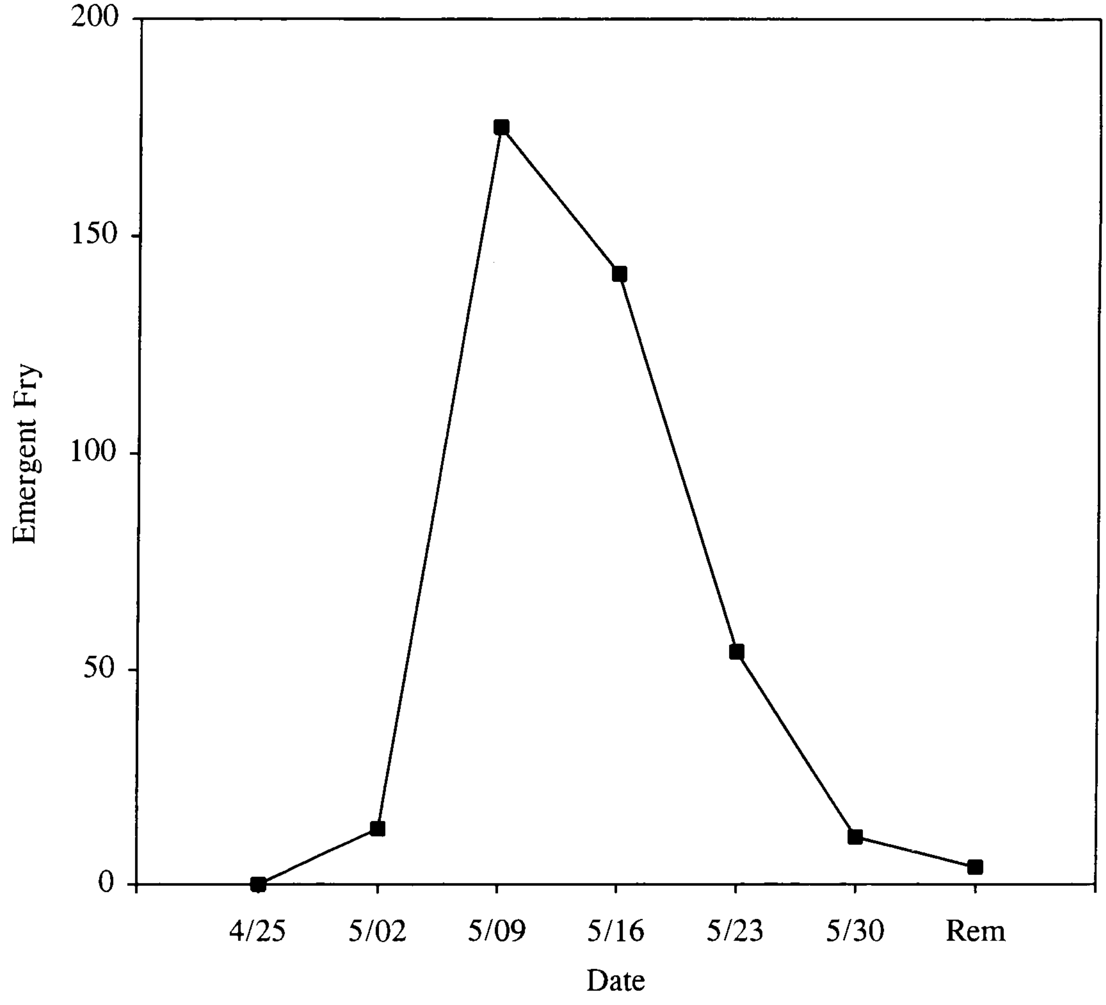


Figure 3-2.--Number of emergent fry captured weekly from all incubation baskets, Flaming Gorge Reservoir, 1992. Remnants (Rem) were live fry remaining in the incubation baskets on May 30.

captured (about 1%) had not emerged from the incubation baskets on May 30. First emergence of fry occurred at temperatures between 6.8 and 9.6°C, at 681 and 739 degree-days, respectively (Table 3-1). Peak emergence occurred between 714 and 842 degree-days at temperatures ranging from 6.8 to 11.1°C. Final emergence occurred between 970 and 1056 degree-days, and the greatest temperature at which emergence occurred ranged from 12.8 to 13.5°C.

Survival to Emergence

Survival to emergence ranged from zero to 66% (Table 3-2) and was inversely related to depth ($r^2 = 0.33$, $P < 0.0005$; Figure 3-3). Mean intragravel dissolved oxygen concentrations were inversely related to depth (Table 3-3; $r^2 = 0.78$, $P < 0.0005$; Figure 3-4). Survival to emergence was directly related to mean intragravel dissolved oxygen concentrations ($P < 0.0005$, $r^2 = 0.39$; Figure 3-5), and minimum intragravel dissolved oxygen during the incubation period ($r^2 = 0.32$, $P < 0.002$).

The total dry weight of sediments deposited increased with depth during periods 1 and 2 (test of slope = 0; $P < 0.0005$) but decreased with depth during period 3 ($P < 0.01$) when sedimentation was greatest (Table 3-4; Figure 3-6). The proportion of organic sediments deposited decreased with depth during each period ($P < 0.0005$ for periods 1 and 2, $P < 0.05$ for period 3). The log of the mean percent organic sediment (for all periods combined) decreased with depth ($r^2 = 0.89$, $P < 0.0005$; Figure 3-7).

Table 3-1.--Substrate-water interface temperatures (°C), degree-days by sampling interval, and cumulative degree-days by depth, Flaming Gorge Reservoir, 1991-92. Column headings refer to calendar date (top) and days after incubation basket installation (bottom).

Substrate-water interface temperature

Depth	11/09	12/07	01/11	02/02	02/29	03/28	04/25	05/02	05/09	05/16	05/23	05/30
(m)	2	30	65	86	114	142	170	177	184	191	198	205
2	9.0	5.5	0.7	0.8	1.8	6.3	7.0	9.6	10.9	13.3	14.3	15.5
4	8.7	5.2	0.8	1.0	1.8	5.8	6.8	9.3	10.9	13.1	13.6	15.4
6	8.8	5.5	1.5	1.5	2.3	3.9	6.7	9.3	11.1	12.8	13.5	14.8
8	8.8	5.5	1.7	2.0	2.1	3.7	6.9	8.6	10.6	12.8	13.2	13.0
10	8.8	5.5	2.2	2.8	2.5	3.0	6.7	8.6	10.0	12.5	12.1	12.9
12	8.9	5.5	2.9	2.9	2.7	3.2	6.7	8.6	8.2	11.3	9.7	12.5
14	8.8	5.5	2.8	2.7	2.8	3.3	6.6	7.8	7.9	8.5	8.8	10.9
16	8.8	5.5	2.9	2.8	2.8	3.0	6.3	7.2	7.7	8.1	8.2	8.0
18	9.0	5.5	3.2	2.8	3.5	3.2	5.9	7.0	7.5	7.8	8.1	7.4
20	9.0	5.5	3.1	2.9	3.1	3.2	5.5	6.8	6.5	7.2	7.9	6.8

Degree-days by sampling period

2	18	203	109	16	36	113	186	58	72	85	97	104
4	17	195	105	19	39	106	176	56	71	84	94	102
6	18	200	123	32	53	87	148	56	71	84	92	99
8	18	200	126	39	57	81	148	54	67	82	91	92
10	18	200	135	53	74	77	136	54	65	79	86	88
12	18	202	147	61	78	83	139	54	59	68	74	78
14	18	200	145	58	77	85	139	50	55	57	61	69
16	18	200	147	60	78	81	130	47	52	55	57	57
18	18	203	152	63	88	94	127	45	51	54	56	54
20	18	203	151	63	84	88	122	43	47	48	53	52

Cumulative degree-days

2	18	221	330	345	382	495	681	739	811	896	992	1097
4	17	212	317	336	375	482	658	714	785	869	962	1064
6	18	218	340	372	425	512	660	716	788	871	963	1062
8	18	218	344	383	440	521	670	724	791	873	964	1056
10	18	218	353	405	479	556	692	746	811	890	976	1063
12	18	219	366	427	506	588	727	781	839	908	981	1059
14	18	218	363	421	498	583	722	772	827	885	945	1014
16	18	218	365	425	503	584	715	762	814	869	926	983
18	18	221	373	436	525	618	746	791	842	895	951	1005
20	18	221	372	435	519	607	729	772	818	866	919	970

Table 3-2.--The emergence timing and survival rates of kokanee fry captured weekly from incubation baskets in Flaming Gorge Reservoir, 1992. Fifty eggs were placed in each incubation basket on November 7 and 8, 1991. Remnants are live fry remaining in incubation baskets on 5/30.

Depth	Date						Rem-	- Survival -	
(m)	4/25	5/02	5/09	5/16	5/23	5/30	nants	Sum	%
2.5	0	7	18	1	0	0	0	26	52
3.9	0	2	26	1	0	0	0	29	58
3.9	0	2	28	0	0	0	0	30	60
4.0	0	1	6	0	0	0	0	7	14
4.6	0	0	16	0	0	0	0	16	32
6.0	0	0	19	14	0	0	0	33	66
6.7	0	0	6	19	1	0	0	26	52
7.2	0	0	12	8	0	0	0	20	40
7.3	0	0	17	0	0	0	0	17	34
8.3	0	0	4	7	0	0	0	11	22
8.7	0	0	8	21	3	1	0	33	66
9.2	0	0	0	0	0	0	0	0	0
10.9	0	0	2	8	2	0	0	12	24
11.6	0	0	3	10	0	0	0	13	26
12.1	0	0	0	0	0	1	0	1	2
12.5	0	0	0	0	14	0	0	14	28
12.9	0	0	6	16	2	0	0	24	48
13.3	0	0	1	20	0	0	0	21	42
14.3	0	0	0	0	0	0	0	0	0
14.4	0	0	2	2	5	0	0	9	18
16.1	0	0	0	1	4	3	2	10	20
16.5	0	0	0	7	9	1	0	17	34
17.4	0	0	0	0	11	2	2	15	30
18.1	0	0	0	0	0	0	0	0	0
18.6	0	0	0	0	0	0	0	0	0
19.1	0	0	0	0	0	0	0	0	0
19.4	0	1	1	6	3	3	0	14	28
Sum:	0	13	175	141	54	11	4	398	

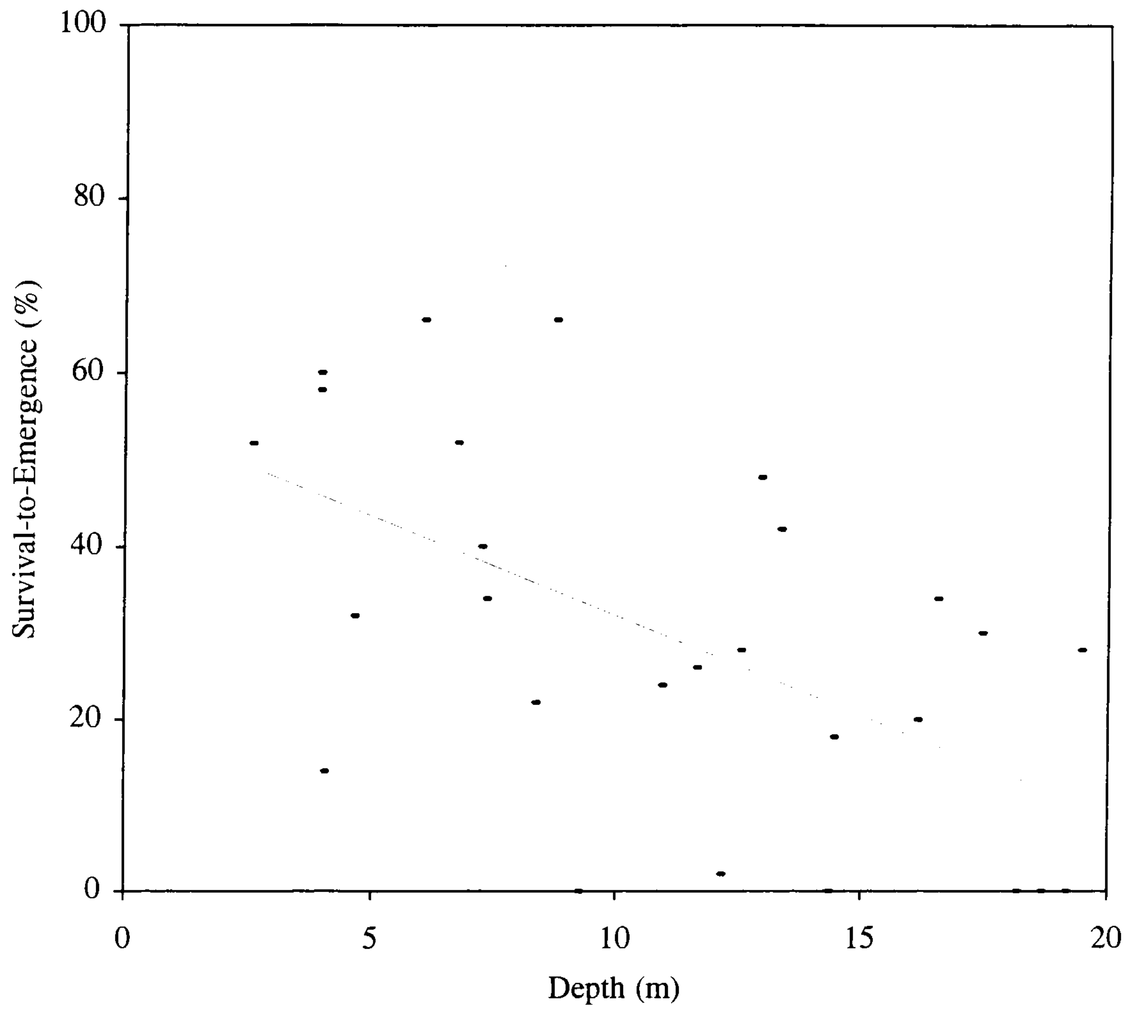


Figure 3-3.--The relation of survival to emergence to depth. The regression equation is: (Percent survival to emergence) = -2.306 x (Depth) + 55.059, r^2 = 0.33, N = 27.

Table 3-3.--Dissolved oxygen concentrations (mg/L) of water samples collected from intragravel dissolved oxygen pipes on eight dates, Flaming Gorge Reservoir, 1991-92. SD is standard deviation.

Depth	Date									
(m)	11/9	12/7	1/11	2/02	2/29	3/28	4/25	5/23	Mean	SD
2.5	7.0	7.3	4.8	8.3	9.6	10.9	8.2	6.9	7.9	1.8
3.9	7.5	6.0	7.7	7.5	8.2	10.4	8.4	7.3	7.9	1.2
3.9	7.1	5.8	8.7	8.4	8.3	10.8	8.0	7.3	8.1	1.4
4.0	6.2	6.0	8.1	8.6	8.4	10.4	8.7	8.0	8.1	1.4
4.6	6.7	7.1	7.4	8.0	7.5	11.1	8.2	8.4	8.1	1.4
6.0	6.3	6.5	7.9	7.6	7.2	9.7	6.7	5.9	7.2	1.2
6.7	7.5	5.6	7.9	7.6	7.6	9.7	6.2	6.2	7.3	1.3
7.2	5.9	6.9	7.0	6.7	6.5	8.9	8.3	6.2	7.1	1.0
7.3	5.8	6.2	6.6	5.3	5.8	7.9	6.9	6.1	6.3	0.8
8.3	4.9	1.8	5.8	5.9	5.2	6.6	6.2	5.7	5.3	1.5
8.7	6.4	6.3	7.9	7.6	7.3	8.4	7.9	5.7	7.2	1.0
9.2	6.6	5.7	6.0	6.1	7.3	7.5	5.8	6.7	6.5	0.7
10.9	7.0	7.0	7.1	6.0	6.8	8.2	8.5	8.0	7.3	0.8
11.6	7.2	5.7	3.7	4.7	6.5	5.8	5.8	7.1	5.8	1.2
12.1	7.0	7.4	6.7	5.8	5.2	8.0	7.4	7.3	6.9	0.9
12.5	7.8	6.5	4.6	3.4	4.2	3.5	5.0	3.6	4.8	1.6
12.9	7.9	6.5	5.3	6.6	5.2	8.2	8.1	7.1	6.9	1.2
13.3	7.1	7.1	6.7	6.0	5.3	8.4	8.0	7.4	7.0	1.0
14.3	7.2	7.4	3.0	1.2	2.4	3.1	4.6	5.5	4.3	2.3
14.4	5.9	6.7	5.3	5.0	5.0	6.0	6.6	6.2	5.8	0.7
16.1	6.9	6.9	3.2	2.7	2.4	2.1	3.3	2.6	3.8	2.0
16.5	6.8	7.1	3.3	4.1	2.2	4.4	5.6	5.7	4.9	1.7
17.4	7.7	6.9	3.6	4.3	3.3	3.9	3.9	2.8	4.6	1.8
18.1	7.7	7.3	7.5	1.5	1.3	2.6	1.2	1.5	3.8	3.1
18.6	6.2	6.4	2.4	1.6	1.3	0.3	1.0	1.0	2.5	2.4
19.1	7.7	7.5	1.1	1.1	0.9	0.4	1.2	0.9	2.6	3.1
19.4	3.0	3.7	1.8	3.8	4.7	5.2	4.6	3.4	3.8	1.1

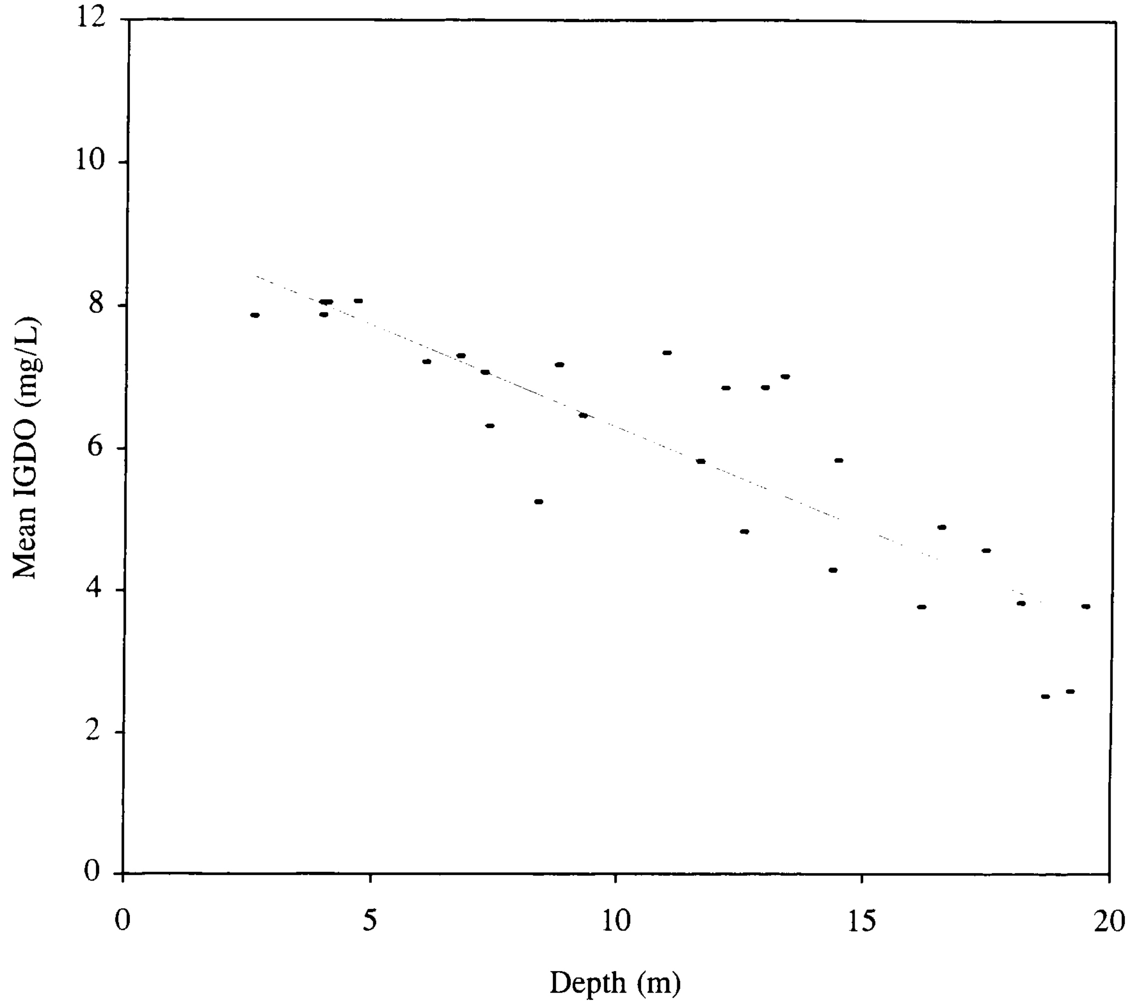


Figure 3-4.--The relation of mean intragravel dissolved oxygen (Mean IGDO) concentrations to depth. The regression equation is: (Mean IGDO) = -0.286 x (Depth) + 9.150, $r^2 = 0.78$, $N = 27$.

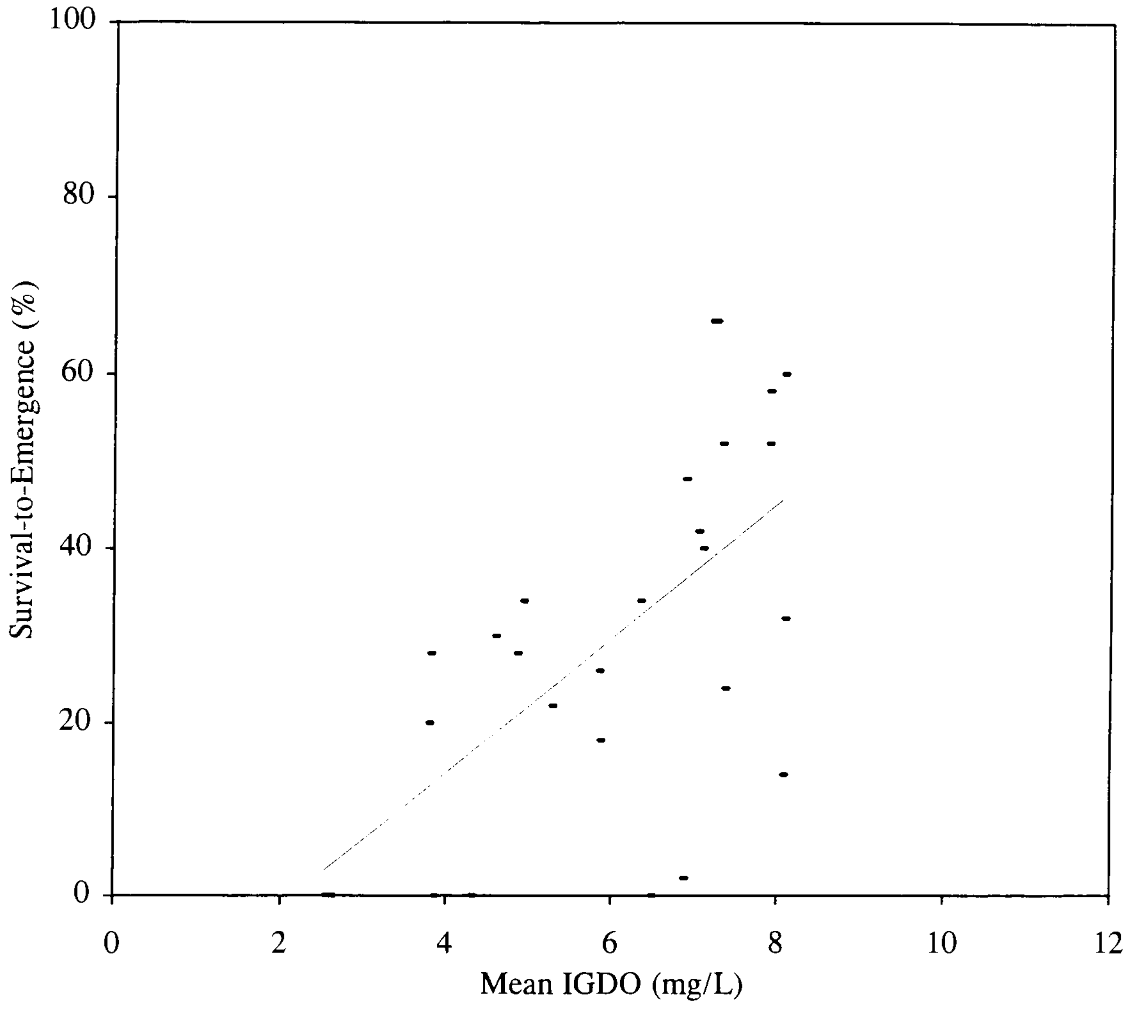


Figure 3-5.--The relation of percent survival to emergence to mean intragravel dissolved oxygen concentrations. The regression equation is: (Percent survival to emergence) = 7.728 x (Mean IGDO) - 16.945, r^2 = 0.39, N = 27.

Table 3-4.--Total dry (Total) and organic (Org) weight in grams, and percent organic (% Org) content of sediment samples collected for periods 1, 2, and 3 (November 9 to February 2, February 2 to March 28, and March 28 to May 23, respectively), Flaming Gorge Reservoir, 1991-92.

Depth	Period 1			Period 2			Period 3		
(m)	Total	Org	% Org	Total	Org	% Org	Total	Org	% Org
2.5	0.867	0.071	8.2	0.199	0.035	17.6	4.441	0.329	7.4
3.9	0.779	0.062	7.9	0.174	0.027	15.6	3.199	0.211	6.6
3.9	0.634	0.053	8.4	0.199	0.032	16.2	3.070	0.237	7.7
4.0	0.751	0.072	9.6	0.226	0.038	17.0	3.145	0.282	9.0
4.6	0.694	0.053	7.6	0.184	0.031	16.6	2.875	0.183	6.4
6.0	0.575	0.041	7.1	0.176	0.025	14.1	2.042	0.129	6.3
6.7	0.689	0.050	7.3	0.235	0.026	10.9	2.253	0.151	6.7
7.2	0.757	0.047	6.2	0.164	0.021	13.0	2.352	0.150	6.4
7.3	0.766	0.047	6.1	0.215	0.024	11.1	2.157	0.135	6.3
8.3	0.883	0.065	7.4	0.182	0.020	10.9	2.154	0.143	6.6
8.7	0.829	0.057	6.9	0.204	0.018	9.0	2.102	0.134	6.4
9.2	0.731	0.046	6.3	0.213	0.020	9.3	1.902	0.133	7.0
10.9	0.962	0.062	6.4	0.266	0.021	7.9	2.022	0.117	5.8
11.6	1.083	0.072	6.7	0.224	0.020	8.8	2.208	0.132	6.0
12.1	1.569	0.099	6.3	0.439	0.032	7.2	3.427	0.196	5.7
12.5	1.033	0.056	5.5	0.247	0.020	8.1	1.846	0.121	6.6
12.9	0.591	0.031	5.2	0.144	0.013	8.7	1.387	0.096	7.0
13.3	1.008	0.061	6.1	0.282	0.022	7.9	1.831	0.110	6.0
14.3	1.480	0.084	5.7	0.400	0.029	7.3	2.788	0.162	5.8
14.4	0.821	0.047	5.7	0.308	0.022	7.3	1.707	0.102	6.0
16.1	1.553	0.105	6.8	0.554	0.040	7.1	2.805	0.165	5.9
16.5	1.222	0.063	5.1	0.438	0.027	6.1	1.744	0.107	6.2
17.4	0.775	0.045	5.9	0.247	0.019	7.6	1.461	0.092	6.3
18.1	0.966	0.050	5.2	0.788	0.045	5.7	1.880	0.124	6.6
18.6	1.458	0.074	5.1	0.752	0.041	5.4	2.463	0.135	5.5
19.1	1.353	0.071	5.2	0.824	0.046	5.6	2.518	0.147	5.8
19.4	1.227	0.073	6.0	0.882	0.052	5.9	2.298	0.138	6.0

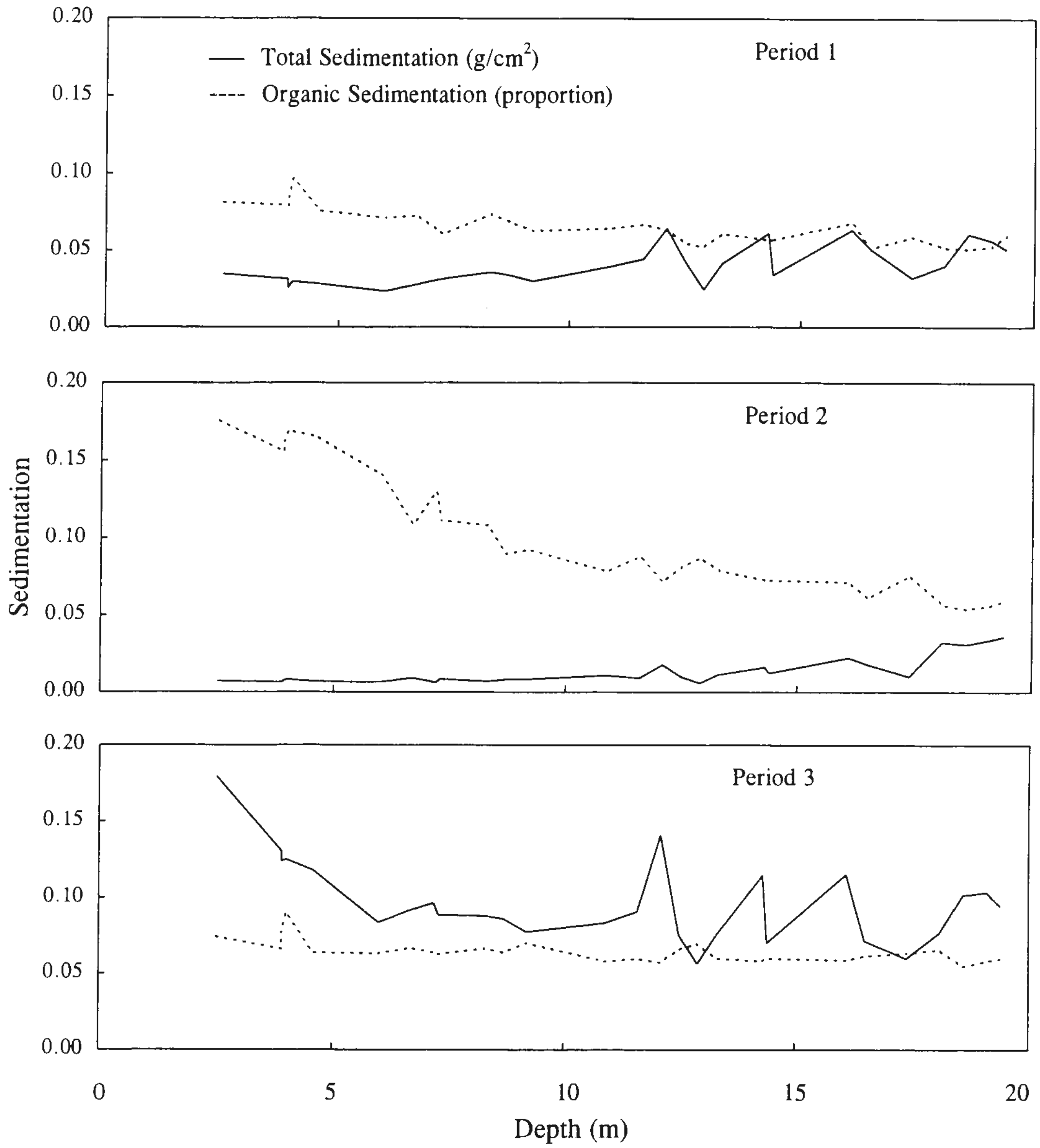


Figure 3-6.--Total dry (g/cm^2) and proportion organic sediment deposition by depth for periods 1, 2, and 3 (November 9-February 2, February 2-March 28, and March 28-May 23, respectively), Flaming Gorge Reservoir, 1991-92.

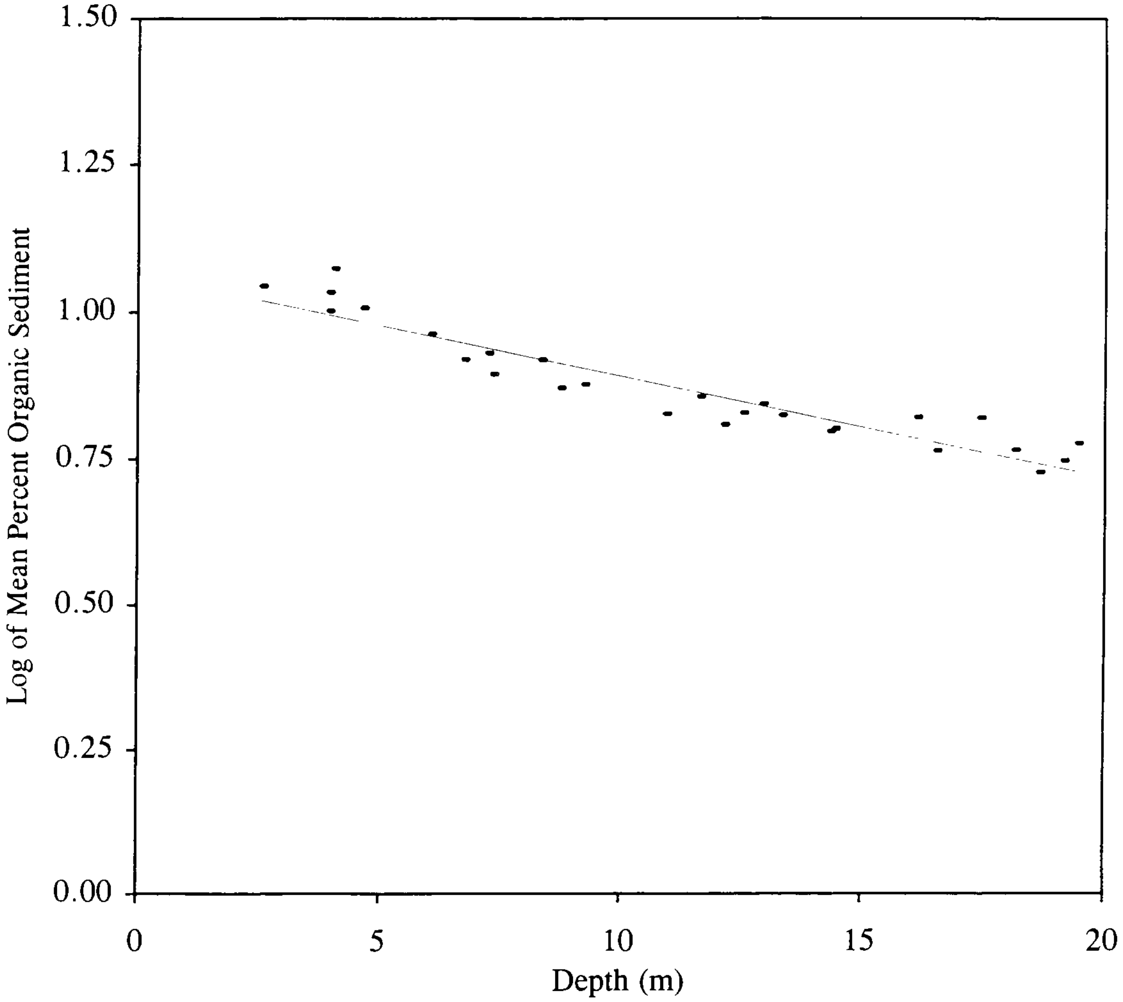


Figure 3-7.--The relation of the log of mean (for three periods) percent organic sediment to depth. The regression equation is: Log (mean percent organic sediment) = -0.017 x (Depth) + 1.063, r^2 = 0.89, N = 27.

Due to the relation of several habitat variables to depth, I examined the associations of the variables to each other in a correlation matrix (Table 3-5). I included the coefficient of variation (CV) of each variable, except depth, resulting in nine independent variables. The CV scales variation relative to the mean and incorporates measures of temporal habitat variability into the analyses. Nineteen of 36 associations in the correlation matrix were significant ($P < 0.05$). Survival to emergence versus these habitat variables was examined using step-wise multiple regression analysis (SAS Institute, Inc. 1982). A single independent variable, mean intragravel dissolved oxygen, produced the most significant regression model ($r^2 =$ 0.39). A principal components analysis (NCSS 1993) using normalized independent variables generated three factors. A second step-wise regression using these three factors explained less variation ($R^2 = 0.38$) in survival to emergence than mean intragravel dissolved oxygen alone.

Discussion

Time of emergence generally proceeded from shallow to deep water, following trends in water temperature during the period of emergence (Table 3-2). Throughout emergence, temperatures at the substrate-water interface decreased with depth, but cumulative degree-days did not decrease with depth until May 23 (Table 3-1). Due to inverse thermal stratification of the water column during the period of ice-cover, deep incubating kokanees accumulated more degree-days than those in

Table 3-5.--Correlation matrix of habitat variables associated with kokanee survival to emergence, Flaming Gorge Reservoir, 1991-92. Pearson correlation coefficients are listed (top) and *P*-values (bottom). CV is coefficient of variation of the mean, IGDO is intragravel dissolved oxygen, and Org is organic. Sediment related variables are indicated.

			Sediment					
	Mean IGDO	CV Mean IGDO	Mean Dry	Mean Org	Log (Mean % Org)	CV Mean Dry	CV Mean Org	CV Log (Mean % Org)
Depth	-0.894 0.001	0.554 0.003	0.049 0.807	-0.394 0.042	-0.918 0.001	0.094 0.641	-0.925 0.001	-0.913 0.001
Mean IGDO		-0.526 0.005	-0.235 0.237	0.195 0.330	0.779 0.001	-0.012 0.954	0.825 0.001	0.760 0.001
CV Mean IGDO			0.196 0.327	-0.043 0.831	-0.463 0.015	-0.366 0.061	-0.502 0.008	-0.421 0.029
Mean Dry Sediment				0.841 0.001	0.074 0.715	-0.310 0.116	-0.109 0.587	-0.081 0.689
Mean Org Sediment					0.565 0.002	-0.401 0.038	0.353 0.071	0.324 0.100
Log (Mean % Org Sediment)						-0.297 0.133	0.883 0.001	0.898 0.001
CV Mean Dry Sediment							-0.080 0.691	-0.208 0.298
CV Mean Org Sediment								0.881 0.001

shallow waters until about May 9. However, kokanees incubating in shallow waters were exposed to higher levels of dissolved oxygen. Despite the potential for differences in developmental rates of salmonid embryos associated with differences in dissolved oxygen and temperature before hatching (Alderdice 1958; Garside 1959, 1966; Brannon 1965; Hamor and Garside 1976; Burgner 1991), time of emergence seemed to be determined by water temperatures during the period prior to emergence.

Kokanee survival to emergence was related to depth and several of the habitat variables measured. Survival to emergence, mean intragravel dissolved oxygen, and organic sedimentation decreased with depth. Although mean intragravel dissolved oxygen explained the greatest amount of variation in survival, depth accounted for significant variation in the habitat variables. The study area was fairly homogeneous in slope and substrate composition, as indicated by the strong associations of most independent variables with depth. Gravel size in the incubation baskets was uniform to minimize bias associated with differences in substrate composition. Differences in survival by depth probably resulted from differences in associated habitat variables, and not from differences in pressure.

The position of the sediment jars above the substrate collected primarily particles falling from the water column, and not down-slope movement of sediments. While trends in dry sediment deposition at depth varied among periods, percent organic sedimentation decreased with depth in each period. Wave activity

suspending and concentrating organic materials near shore could potentially account for the greater organic sedimentation collected in shallow waters. However, percent organic sedimentation was highest during the period of ice-cover when turbulence was minimal.

The trends in organic sedimentation likely resulted from photosynthetic activity occurring throughout the incubation period. The second sediment collection period (February 2 to March 28; roughly concurrent with ice-cover) contained 67% of the maximum dissolved oxygen samples measured by site. At depths less than about 4 m, high concentrations of phytoplankton limited diver visibility under the ice to about 1-2 m on February 29. Visibility below this depth appeared limited only by light. Divers also observed bubbles (presumably oxygen at saturation) released by periphyton to about 2-m depth. Sufficient light penetrated reservoir ice (46-cm thick with negligible snow-cover) for photosynthesis to occur in shallow water. Snow melting into the bay and decomposition of kokanee carcasses in the study site could have provided nutrients adequate for growth of periphyton and phytoplankton (Richey et al. 1975; Minshall et al. 1991).

During kokanee incubation in Flaming Gorge Reservoir, net primary production may exceed net consumption of organic sediments, resulting in an adequate supply of oxygen available for egg survival. The amount of organic matter in aquatic sediment is not necessarily an indication of availability to reducers (Hargrave 1972) and hence not a good indication of potential oxygen reduction.

Under-ice circulation in the bay and diel water temperature fluctuations directly below the ice on sunny days (Kenney 1991) may enhance exchange of intragravel waters during the period of ice-cover. Natural convection (O'Brien et al. 1978; Johnson 1980) and fin movement by alevins (Bams 1969; Fast et al. 1982) may provide additional transport of dissolved oxygen to salmonids incubating under conditions of low water exchange. Prior studies in lotic waters examined effects of the quantitative composition of sediment (i.e., particle size-distributions, inorganic sediment) on the dissolved oxygen supply, survival to emergence, and time of emergence of incubating salmonids (Wickett 1954; Cordone and Kelley 1961; Bianchi 1963; Phillips et al. 1975; Ringler and Hall 1975; Hausle and Coble 1976; Meehan and Swantson 1977; Woods 1980; Tappel and Bjornn 1983; MacCrimmon and Gots 1986). These results indicated that the qualitative composition of sediment (i.e., percent organics) may influence the supply of dissolved oxygen to salmonids incubating in lacustrine habitats.

Prevailing west winds creating frequent waves along the shore of the study site may have increased exchange of shallower intragravel waters, providing a stable supply of dissolved oxygen to kokanee embryos. While mean intragravel dissolved oxygen was negatively correlated with depth, the CV of mean intragravel dissolved oxygen was positively correlated with depth, indicating greater temporal stability of dissolved oxygen in shallow waters. A stable supply of dissolved oxygen could have enhanced development and survival of shallower incubating kokanees. Lower

concentrations and greater variability in intragravel dissolved oxygen with depth may have contributed to the reduced survival to emergence observed. This supposition contrasts with Sly (1988), who suggested that increased wave activity increased organics in-filling substrate interstices, contributing to greater variability of dissolved oxygen within lake trout spawning substrates in Lake Ontario.

Developing salmonid embryos appear to exhibit greater tolerance to reduced dissolved oxygen concentrations and water flows at lower temperatures (Garside 1959; Silver et al. 1963; Hamor and Garside 1976; Chapman 1988). The low temperatures and concurrently high dissolved oxygen concentrations observed under the ice of Flaming Gorge Reservoir may reduce potential metabolic stresses encountered by incubating kokanees. During the ice-free periods, water temperatures and, presumably, metabolic demands of kokanee embryos are greatest. Wave activity may contribute to increased exchange of intragravel waters, increasing dissolved oxygen available to kokanee embryos. Developing sockeye salmon embryos from shore-spawning populations in Iliamna Lake, Alaska, are dependent upon wind-driven circulation for intragravel water exchange, and hatching occurs before ice-cover forms (Burgner 1991).

Consistency among several regression models supported the assumption of linear relationships within the range of variables measured. The depth at which predicted survival to emergence equaled zero was 23.9 m (Figure 3-3). The concentration of mean intragravel dissolved oxygen at which predicted survival to

emergence equaled zero was 2.2 mg/L (Figure 3-5). The predicted mean intragravel dissolved oxygen concentration at 23.9 m (the derived depth at which predicted survival was zero) was 2.3 mg/L (Figure 3-4), close to the predicted concentration at which no survival would occur.

These results provide novel information relevant to the ecology and management of shoreline-spawned salmonids. While shore-spawning by kokanees has been observed at depths near 20 m (Hassemer 1984; Gipson and Hubert 1993), estimates of survival to emergence relative to water depth have not been previously reported. In this study, in situ survival to emergence of 28% was observed from an incubation basket exceeding 19-m depth. Survival to hatching of 85% was observed for salmonids reared in aquaria at mean dissolved oxygen concentrations of 2.6 mg/L, with complete mortality occurring when dissolved oxygen was reduced to 1.6 mg/L after hatching (Silver et al. 1963). Survival to emergence in this study occurred under an instantaneous dissolved oxygen concentration of 1.8 mg/L, a mean dissolved oxygen concentration of 3.8 mg/L, and a maximum (for the incubation period) dissolved oxygen concentration of 5.2 mg/L. Survival rates for incubating kokanees have not previously been reported for water temperatures less than 1.7-2.0°C (Combs 1965; Murray and McPhail 1988; Beacham and Murray 1989). The lower initial temperature for "normal development" of sockeye salmon incubating in streams was reported as ranging from 4.4-5.8°C, with mortality of 80% when incubated at a constant 2°C (Combs 1965). Although substrate-water

interface temperatures measured during my study were interim values that varied widely throughout the intragravel developmental period, kokanee survival to emergence of 52% was observed from a site with an instantaneous substrate-water interface temperature minimum of 0.7°C.

Interior-spawning kokanee and sockeye populations may be better adapted to tolerate low mean incubation temperatures than coastal-spawning populations (Murray et al. 1989). Emergence of kokanees in my study occurred over a wide range of instantaneous temperatures (6.8-13.5°C) and developmental periods (681-1056 degree-days). However, mean temperatures at 50% emergence varied less than one degree, ranging from 5.3 to 6.1°C. Notwithstanding differences in dissolved oxygen, 50% emergence of kokanees in my investigation would have occurred from 122 to 136 days after fertilization, based on the relationship using mean water temperatures developed by Murray et al. (1989) for lotic-spawned interior kokanee populations. The days to 50% emergence derived from Murray et al. (1989) were less than the range observed for kokanees in Flaming Gorge Reservoir (184-198 days). These results support the contention that developmental times are considerably longer for kokanees in lakes or reservoirs versus streams (Murray et al. 1989).

These results indicated that several factors that varied with depth were critical to survival to emergence of kokanees in Flaming Gorge Reservoir. Investigations of the intragravel success of shore-spawning salmonids should

consider differences in intragravel dissolved oxygen concentrations, water temperatures, and rates of organic sedimentation that may occur with depth. The relation of survival to emergence to depth indicates that the distribution of spawning by depth may also be important to population recruitment in impoundments where water levels vary during the intragravel period.

References

Alderdice, D. F., W. P. Wickett, and J. R. Brett. 1958. Some effects of temporary exposure to low dissolved oxygen levels on Pacific salmon eggs. Journal of the Fisheries Research Board of Canada 15:229-250.

APHA (American Public Health Association), American Water Works Association, and Water Pollution Control Federation. 1985. Standard methods for the examination of water and wastewater, 16th edition. APHA, Washington, D.C.

Bams, R.A. 1969. Adaptations of sockeye salmon associated with incubation in stream gravel. Pages 71-87 *in* T.G. Northcote, editor. Salmon and trout in streams. H.R. MacMillan lectures in fisheries. University of British Columbia, Vancouver.

Beacham, T. D., and C. B. Murray. 1989. Variation in developmental biology of sockeye salmon (*Oncorhynchus nerka*) and chinook salmon (*O. tshawytscha*) in British Columbia. Canadian Journal of Zoology 67:2081-2089.

Bianchi, D. R. 1963. The effects of sedimentation on egg survival of rainbow trout and cutthroat trout. Master's thesis. Montana State College. Bozeman.

Brannon, E. L. 1965. The influence of physical factors on the development and weight of sockeye salmon embryos and alevins. International Pacific Salmon Fisheries Commission Progress Report 12:1-26.

Burgner, R. L. 1991. Life history of sockeye salmon (*Oncorhynchus nerka*). Pages 1-117 *in* C. Groot and L.Margolis, editors. Pacific salmon life histories. University of British Columbia Press, Vancouver.

Chapman, D. W. 1988. Critical review of variables used to define effects of fines in redds of large salmonids. Transactions of the American Fisheries Society 117:1-21.

Coble, D. W. 1961. Influence of water exchange and dissolved oxygen in redds of steelhead trout embryos. Transactions of the American Fisheries Society 90(4):469-474.

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

Cordone, A. J., and D. W. Kelley. 1961. The influences of inorganic sediment on the aquatic life of streams. California Fish and Game 47(2):189-228.

Fast, D. E., Q. J. Stober, S. C. Crumley, and E. S. Killebrew. 1982. Survival and movement of chinook and coho salmon alevins in hypoxic environments. Pages 51-60 *in* E. L. Brannon and E. O. Salo, editors. Salmon and Trout

Migratory Behavior Symposium, University of Washington, Seattle.

Fraley, J., and J. Decker-Hess. 1987. Effects of stream and lake regulation on reproductive success of kokanee in the Flathead River system, Montana, U.S.A. Regulated Rivers: Research and Management 1:257-265.

Garside, E. T. 1959. Some effects of oxygen in relation to temperature on the development of lake trout embryos. Canadian Journal of Zoology 37:689-698.

Garside, E. T. 1966. Effects of oxygen in relation to temperature on the development of embryos of brook trout and rainbow trout. Journal of the Fisheries Research Board of Canada 23(8):1121-1134.

Gipson, R. D., and W. A. Hubert. 1993. Spawning-site selection by kokanee along the shoreline of Flaming Gorge Reservoir, Utah-Wyoming. North American Journal of Fisheries Management 13:475-482.

Hamor, T., and E. T. Garside. 1976. Developmental rates of Atlantic salmon *Salmo salar* L., in response to various levels of temperature, dissolved oxygen, and water exchange. Canadian Journal of Zoology 54:1912-1917.

Hargrave, B. T. 1972. Aerobic decomposition of sediment and detritus as a function of particle surface area and organic content. Limnology and Oceanography 17(4):583-596.

Hassemer, P. F. 1984. Spawning ecology and early life history of kokanee in Coeur d'Alene and Pend Oreille Lakes, Idaho. Master's thesis. University of Idaho,

Moscow.

Hassemer, P. F., and B. E. Rieman. 1981. Observations of deep-spawning kokanee on artificially created spawning habitat. North American Journal of Fisheries Management 1:173-176.

Hausle, D. A., and D. W. Coble. 1976. Influence of sand in redds on survival and emergence of brook trout *Salvelinus fontinalis*. Transactions of the American Fisheries Society 1:57-63.

Heming, T. A. 1982. Effects of temperature on utilization of yolk by chinook salmon (*Oncorhynchus tshawytscha*) eggs and alevins. Canadian Journal of Fisheries and Aquatic Sciences 39:184-190.

Holtby, L. B. 1988. Effects of logging on stream temperatures in Carnation Creek, British Columbia, and associated impacts on the coho salmon *Oncorhynchus kisutch*. Canadian Journal of Fisheries and Aquatic Sciences 45:502-515.

Jeric, R. J., T. Modde, and J. M. Godfrey. 1995. Evaluation of a method for measuring intragravel dissolved oxygen concentrations and survival to emergence of shore-spawned salmonids. North American Journal of Fisheries Management 15:185-192.

Johnson, R. A. 1980. Oxygen transport in salmon spawning gravel. Canadian Journal of Fisheries and Aquatic Sciences 37:155-162.

Kenney, B. C. 1991. Under-ice circulation and the residence time of a shallow bay. Canadian Journal of Fisheries and Aquatic Sciences 48:152-162.

Koski, K. V. 1975. The survival and fitness of two stocks of chum salmon *Oncorhynchus keta* from egg deposition to emergence in a controlled-stream environment at Big Beef Creek. Ph.D. thesis. University of Washington, Seattle.

MacCrimmon, H. R., and B. L. Gots. 1986. Laboratory observations on emergent patterns of juvenile Atlantic salmon *Salmo salar* relative to sediment loadings of test substrate. Canadian Journal of Zoology 64:1331-1336.

Mason, C. J. 1969. Hypoxial stress prior to emergence and competition among coho salmon fry. Journal of the Fisheries Research Board of Canada 26(1):63-91.

Mason, C. J., and D. W. Chapman. 1965. Significance of early emergence, environmental rearing capacity and behavioural ecology of juvenile coho salmon in stream channels. Journal of the Fisheries Research Board of Canada 22:173-190.

Meehan, W. R., and D. N. Swantson. 1977. Effects of gravel morphology on fine sediment accumulation and survival of incubating salmon eggs. USDA Forest Service Research Paper. PNW-220. Pacific Northwest Forest and Range Experiment Station, Portland, Oregon.

Minshall, W. E., E. Hitchcock, and J. R. Barnes. 1991. Decomposition of rainbow trout *Oncorhynchus mykiss* in a forest ecosystem inhabited only by non-anadromous fish populations. Canadian Journal of Fisheries and Aquatic Sciences 48:191-195.

Murray, C. B., and J. D. McPhail. 1988. Effect of incubation temperature on the development of five species of Pacific salmon (*Oncorhynchus*) embryos and alevins. Canadian Journal of Zoology 66:266-273.

Murray, C. B., J. D. McPhail, and M. L. Rosenau. 1989. Reproductive and developmental biology of kokanee from Upper Arrow Lake, British Columbia. Transactions of the American Fisheries Society 118:503-509.

NCSS (Number Cruncher Statistical Systems).1993. Statistics manual. Number Cruncher Statistical Systems. Kaysville, Utah.

O'Brien, R. N., S. Visaisouk, R. Raise, and D. F. Alderdice. 1978. Natural convection: a mechanism for transporting oxygen to incubating salmon eggs. Journal of the Fisheries Research Board of Canada 35:1316-1321.

Phillips, R. W., and H. J. Campbell. 1962. The embryonic survival of coho salmon and steelhead trout as influenced by some environmental conditions in gravel beds. Pacific Marine Fisheries Commission Report 14:60-73.

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 3:461-466.

Richey, J. E., M. A. Perkins, and C. R. Goldman. 1975. Effects of kokanee salmon *Oncorhynchus nerka* on the ecology of a subalpine stream. Journal of the Fisheries Research Board of Canada 32:817-820.

Ringler, N. H., and J. D. Hall. 1975. Effects of logging on water temperature and

dissolved oxygen in spawning beds. Transactions of the American Fisheries Society 1:111-121.

SAS Institute. 1982. SAS user's guide: statistics. SAS Institute, Inc. Cary, North Carolina.

Schmidt, B. R., and S. Brayton. 1981. Flaming Gorge Reservoir fisheries investigations. Utah Division of Wildlife Resources Publication 80-12, Salt Lake City.

Shumway, D. L., C.E. Warren, and P. Doudoroff. 1964. Influence of oxygen concentrations 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.

Sly, P. G. 1988. Interstitial water quality of lake trout spawning habitat. Journal of Great Lakes Research 14(3):301-315.

Sowden, T. K., and G. Power. 1985. Prediction of rainbow trout embryo survival in relation to groundwater seepage and particle size of spawning substrates. Transactions of the American Fisheries Society 114:804-812.

Stober, Q. J., R. W. Tyler, C. F. Cowman, Jr., J. Wilcock, and S. Quinnell. 1979.

Irrigation drawdown and kokanee salmon egg to fry survival in Banks Lake. University of Washington Fisheries Research Institute Final Report FRI-UW-7913, Seattle.

Tappel, P. D., and T. C. Bjornn. 1983. A new method of relating size of spawning gravel to salmonid embryo survival. North American Journal of Fisheries Management 3:123-135.

Thomas, A. E., J. L. Banks, and D. C. Greenland. 1969. Effect of yolk sac absorption on the swimming abilities of fall chinook salmon. Transactions of the American Fisheries Society 98:406-410.

Wells, R. A., and W. J. McNeil. 1970. Effect of quality of the spawning bed on the growth and development of pink salmon alevins. U.S. Fish and Wildlife Service Special Scientific Report-Fisheries 616, Washington D.C.

Wickett, P. 1954. The oxygen supply to salmon eggs in spawning beds. Journal of the Fisheries Research Board of Canada 11(6):933-953.

Woessner, W. W., and C. M. Brick. 1985. Hydrogeologic conditions during kokanee spawning, egg incubation and fry emergence at selected sites, Flathead Lake, Montana. Project Report Prepared for Montana Fish, Wildlife and Parks. Kalispell, Montana. University of Montana, Bozeman.

Woods, P. F. 1980. Dissolved oxygen in intragravel water of three tributaries to Redwood Creek, Humboldt County, California. Water Resources Bulletin 16(1):105-111.

CHAPTER 4

MANAGEMENT IMPLICATIONS

Researchers have recommended that studies of salmonid survival to emergence in streams focus on conditions within the egg pocket of redds (Chapman 1988; Young et al. 1989; 1990). King and Thurow (1991) suggested intragravel pipes be placed in the egg pocket to accurately measure dissolved oxygen concentrations within artificial redds used in streams. Structures typically associated with redds in streams (e.g., pit, tailspill) by definition require orientation to current (Burner 1951; Grost and Hubert 1990; Thurow and King 1994) and cannot be applied directly to redds of lacustrine spawners. Distinct redds or egg pockets are not necessarily established by shoreslope spawners. Individual redds were seldom apparent within the spawning habitat observed in Flaming Gorge Reservoir, due to successive kokanee spawning activity that resulted in movement of substrate down slopes. Hassemer and Rieman (1981) described deep, shoreslope spawning by kokanees in Lake Coeur d'Alene, Idaho, as "broadcasted" over large substrate, rather than confined to a redd. When using incubation baskets to measure survival to emergence of shore-spawned salmonids relative to intragravel conditions, a focus on egg-density and substrate composition representative of the spawning habitat may be more critical than attention to individual egg pockets.

Shore-spawning is common for salmonids, but factors such as depth of spawning, water-level fluctuations, reservoir ice-cover, and highly variable egg

deposition complicate direct assessment of total fry production for these populations compared to tributary-spawning stocks. Alternative methods that multiply estimates of survival to emergence, female spawner abundance, and fecundity provide a more feasible estimate of fry recruitment for lacustrine spawning populations. Estimates of fecundity and spawner abundance are frequently available, but survival to emergence estimates are rare. The method described here will allow more frequent measurement of survival to emergence and emergence timing than has been previously possible for shore-spawned salmonids.

As a forage and sport fish, often with self-sustaining populations, kokanees are a valuable component of many lakes and reservoirs in the western United States (Wydoski and Bennett 1981). Water-level fluctuations during incubation may increase egg mortality and reduce kokanee recruitment. Models predicting mortality of kokanees have been established for several reservoirs and lakes where irrigation or hydroelectric demands alter water levels during incubation (Stober et al. 1979; Stober and Tyler 1982; Fraley et al. 1986, 1989; Fraley and Decker-Hess 1987). Knowledge of survival at depth and time of emergence of shoreslope-spawned kokanees may help reservoir managers more accurately predict mortality under various drawdown regimes. Because the spawning kokanees observed distributed redds regularly with depth along the shoreslope of Flaming Gorge Reservoir, findings of greater survival in shallow waters indicated that reducing reservoir water levels during incubation would have reduced the number of emerging kokanees.

References

Burner, C. J. 1951. Characteristics of spawning nests of Columbia River salmon. U.S. Fish and Wildlife Service Fishery Bulletin 52:97-110.

Chapman, D. W. 1988. Critical review of variables used to define effects of fines in redds of large salmonids. Transactions of the American Fisheries Society 117:1-21.

Fraley, J., and J. Decker-Hess. 1987. Effects of stream and lake regulation on reproductive success of kokanee in the Flathead River system, Montana, U.S.A. Regulated Rivers: Research and Management 1:257-265.

Fraley, J., S. McMullin, and P. Graham. 1986. Effects of hydroelectric operations on the kokanee population in the Flathead River system, Montana. North American Journal of Fisheries Management 6:560-568.

Fraley, J., B. Marotz, J. Decker-Hess, W. Beattie, and R. Zubik. 1989. Mitigation, compensation, and future protection for fish populations affected by hydropower development in the Upper Columbia system, U.S.A. Regulated Rivers: Research and Management 3:3-18.

Grost, R. T., and W. A. Hubert. 1990. Redd site selection by brown trout in Douglas Creek, Wyoming. Journal of Freshwater Ecology 5:365-371.

Hassemer, P. F., and B. E. Rieman. 1981. Observations of deep-spawning kokanee on artificially created spawning habitat. North American Journal of Fisheries Management 1:173-176.

King, J. G., and R. F. Thurow. 1991. Sediment monitoring techniques validation. Idaho Department of Health and Welfare, Water Quality Bureau, Progress Report Year 2, Boise.

Stober, Q. J., and R. W. Tyler. 1982. Rule curves for irrigation drawdown and kokanee salmon egg to fry survival. Fisheries Research 1:195-218.

Stober, Q. J., R. W. Tyler, C. F. Cowman, Jr., J. Wilcock, and S. Quinnell. 1979. Irrigation drawdown and kokanee salmon egg to fry survival in Banks Lake. University of Washington Fisheries Research Institute Final Report FRI-UW-7913, Seattle.

Thurow, R. F., and J. G. King. 1994. Attributes of Yellowstone cutthroat trout redds in a tributary of the Snake River, Idaho. Transactions of the American Fisheries Society 123:37-50.

Wydoski, R. S., and D. H. Bennett. 1981. Forage species in lakes and reservoirs of the western United States. Transactions of the American Fisheries Society 110:764-77.

Young, M. K., W. A. Hubert, and T. A. Wesche. 1989. Substrate alteration by spawning brook trout in a southwestern Wyoming stream. Transactions of the American Fisheries Society 118:379-385.

Young, M. K., W. A. Hubert, and T. A. Wesche. 1990. Fines in redds of large salmonids. Transactions of the American Fisheries Society 119:156-160.

APPENDICES

APPENDIX A

ANOVA TABLE

Table A-1.--Repeated measures analysis of variance of differences in intragravel dissolved oxygen concentrations within and adjacent to control baskets.

Source	Sum of Squares	Degrees of Freedom	Mean Squares	F-statistic	P-value
Hypothesis	3.004	1	3.004	1.563	0.279
Error	7.688	4	1.922		

APPENDIX B
LETTERS OF PERMISSION

R2 Resource Consultants, Inc.

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Vernal, UT 84078

March 5, 1996

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March 5, 1996

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