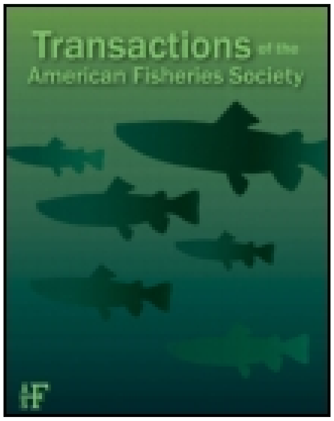
This article was downloaded by: [University of Idaho College of Law Lib]
On: 02 October 2014, At: 16:27
Publisher: Taylor & Francis
Informa Ltd Registered in England and Wales Registered Number: 1072954 Registered office: Mortimer House, 37-41 Mortimer Street, London W1T 3JH, UK



Transactions of the American Fisheries Society
Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/utaf20

Influence of Habitat Characteristics on Shore-Spawning Kokanee

Steven L. Whitlock[a], Michael C. Quist[b] & Andrew M. Dux[c]

[a] Idaho Cooperative Fish and Wildlife Research Unit, Department of Fish and Wildlife Sciences, University of Idaho, 875 Perimeter Drive, Mail Stop 1141, Moscow, Idaho 83844, USA

[b] U.S. Geological Survey, Idaho Cooperative Fish and Wildlife Research Unit, Department of Fish and Wildlife Sciences, 875 Perimeter Drive, Mail Stop 1141, Moscow, Idaho 83844, USA

[c] Idaho Department of Fish and Game, 2885 West Kathleen Avenue, Coeur d'Alene, Idaho, 83815, USA

Published online: 30 Sep 2014.

To cite this article: Steven L. Whitlock, Michael C. Quist & Andrew M. Dux (2014) Influence of Habitat Characteristics on Shore-Spawning Kokanee, Transactions of the American Fisheries Society, 143:6, 1404-1418, DOI: 10.1080/00028487.2014.931302

To link to this article: http://dx.doi.org/10.1080/00028487.2014.931302

PLEASE SCROLL DOWN FOR ARTICLE

Taylor & Francis makes every effort to ensure the accuracy of all the information (the "Content") contained in the publications on our platform. However, Taylor & Francis, our agents, and our licensors make no representations or warranties whatsoever as to the accuracy, completeness, or suitability for any purpose of the Content. Any opinions and views expressed in this publication are the opinions and views of the authors, and are not the views of or endorsed by Taylor & Francis. The accuracy of the Content should not be relied upon and should be independently verified with primary sources of information. Taylor and Francis shall not be liable for any losses, actions, claims, proceedings, demands, costs, expenses, damages, and other liabilities whatsoever or howsoever caused arising directly or indirectly in connection with, in relation to or arising out of the use of the Content.

This article may be used for research, teaching, and private study purposes. Any substantial or systematic reproduction, redistribution, reselling, loan, sub-licensing, systematic supply, or distribution in any form to anyone is expressly forbidden. Terms & Conditions of access and use can be found at http://www.tandfonline.com/page/terms-and-conditions

Transactions of the American Fisheries Society 143:1404–1418, 2014
© American Fisheries Society 2014
ISSN: 0002-8487 print / 1548-8659 online
DOI: 10.1080/00028487.2014.931302

ARTICLE

Influence of Habitat Characteristics on Shore-Spawning Kokanee

Steven L. Whitlock*
*Idaho Cooperative Fish and Wildlife Research Unit, Department of Fish and Wildlife Sciences,
University of Idaho, 875 Perimeter Drive, Mail Stop 1141, Moscow, Idaho 83844, USA*

Michael C. Quist
*U.S. Geological Survey, Idaho Cooperative Fish and Wildlife Research Unit,
Department of Fish and Wildlife Sciences, 875 Perimeter Drive, Mail Stop 1141, Moscow,
Idaho 83844, USA*

Andrew M. Dux
Idaho Department of Fish and Game, 2885 West Kathleen Avenue, Coeur d'Alene, Idaho, 83815, USA

Abstract
Sockeye Salmon *Oncorhynchus nerka* and kokanee (lacustrine Sockeye Salmon) commonly spawn in both lentic and lotic environments; however, the habitat requirements of shore spawners are virtually unknown relative to those of stream spawners. A laboratory experiment and an in situ incubation study were conducted to better understand the influence of habitat characteristics on the shoreline incubation success of kokanee. The laboratory experiment assessed kokanee intragravel survival, fry emergence, and fry condition in response to eight substrate treatments. The in situ study, conducted at three major shoreline spawning sites in Lake Pend Oreille, Idaho, evaluated the effect of depth, substrate composition, dissolved oxygen, shoreline slope, and groundwater on intragravel survival. Substrate size composition was generally a poor predictor of survival in both the laboratory experiment and in situ study; although, fry condition and counts of emerged fry in the laboratory were lowest for the substrate treatment that had the highest proportion of fine sediment. Results of the in situ study suggest that groundwater flow plays an important role in enhancing intragravel survival in habitats generally considered unsuitable for spawning.

The spawning habitat requirements of Pacific salmon *Oncorhynchus* spp. have been studied extensively in lotic systems (Bjornn and Reiser 1991; Kondolf et al. 2008; Sear and DeVries 2008). Decades of laboratory and field investigations have focused on describing the relationship between substrate composition and intragravel survival (Chapman 1988; Kondolf 2000; Jensen et al. 2009), and recent investigations have been concerned with interactions between hyporheic flows and redd morphology (Montgomery et al. 1996; Tonina and Buffington 2007; Malcolm et al. 2008). Although many advancements have been made towards understanding intragravel survival of salmonids in lotic systems, knowledge of habitat requirements for shore-spawning ecotypes is considerably less developed (Leonetti 1996). This is likely because Sockeye Salmon *O. nerka* and its landlocked form, kokanee (lacustrine Sockeye Salmon), is the only member of the genus that commonly spawns on shorelines as well as in streams (Foerster 1968; Burgner 1991). To date, most of the published work on shore-spawning *O. nerka* has been observational (Foerster 1968; Kerns and Donaldson 1968; Hassemer and Rieman 1981; Burgner 1991). No attempts have been made to simulate shore-spawning conditions in the laboratory and only a small

---

*Corresponding author: steven.whitlock@oregonstate.edu
Received January 7, 2014; accepted May 28, 2014

number of in situ incubation studies have been conducted (Hassemer 1984; Gipson and Hubert 1993; Fincel et al. 2009). A better understanding of shoreline intragravel survival is important for managing *O. nerka* populations because shore-spawning ecotypes contribute greatly to recruitment in many systems (Hassemer 1984; Blair et al. 1993; Jeric 1996). Furthermore, experimental knowledge about what constitutes favorable shoreline spawning habitat is essential for gauging the impacts of anthropogenic alterations to littoral habitats through shoreline development and water-level regulation (Smokorowski and Pratt 2007).

Intragravel survival is controlled by a suite of abiotic factors that act differently in streams and on shorelines (Leonetti 1996; Greig et al. 2007). Interrelated factors that influence survival are dissolved oxygen (DO), temperature, water flow, and substrate composition. Egg-to-fry survival and fry condition are dependent on the delivery of DO to the intragravel environment (Silver et al. 1963; Einum et al. 2002). Temperature determines the oxygen capacity of water and the developmental rate of eggs and sac-fry (Cooper 1965; Greig et al. 2007). Substrate composition influences the amount of water exchanged between surface water and the egg pocket (Greig et al. 2007; Malcolm et al. 2011). The proportion of particles less than 1 mm in diameter is considered to be a particularly important determinant of incubation success for salmonids (Chapman 1988; Jensen et al. 2009). Water flow provided by groundwater can negate the deleterious effect of fine sediments on survival (Sowden and Power 1985; Garrett et al. 1998). In streams, surface, hyporheic, and groundwater flows can supply oxygenated water to egg pockets (Malcolm et al. 2003, 2008; Gibbins et al. 2008). The absence of horizontal flow on shorelines changes the relationship between substrate composition and survival and influences where spawning takes place. Shore spawners often select habitats with alternative sources of water flow provided by wave action or groundwater (Woodey 1965; Foerster 1968; Lorenz and Eiler 1989; Burger et al. 1995). However, spawning also occurs in areas apparently lacking in supplemental water flow, such as deepwater habitats (Hassemer 1984; Jeric 1996).

Shoreline habitat selection and egg deposition behaviors also differ from those found in streams. Shoreline redds lack the flow-oriented structure of redds in streams (e.g., pit, tailspill; Crisp and Carling 1989; Jeric 1996). Shore spawners also select a wider array of substrates sizes than do *O. nerka* in streams (Hassemer 1984; Kondolf and Wolman 1993). The inability to displace larger particles in some areas has resulted in alternative egg deposition behaviors (Hassemer and Rieman 1981; Kondolf et al. 1993). In some cases, shore-spawned eggs are "broadcast" over large (50–300 mm) immovable substrate rather than buried (Foerster 1968; Kerns and Donaldson 1968; Hassemer and Rieman 1981; Burgner 1991). Lentic environments present additional habitat characteristics for *O. nerka* to select from in terms of depth and shoreline slope, and habitat selection is not uniform among lakes and reservoirs. Shore-spawning *O. nerka* select shallow, fine-sediment, beaches (Woodey 1965; Olsen 1968; Leonetti 1996), rocky island shores (Kerns and Donaldson 1968; Blair and Quinn 1991), and talus slopes with up to 60° angles (Stober et al. 1979; Hassemer 1984). In Lake Coeur d'Alene, Idaho, and Flaming Gorge Reservoir, Wyoming–Utah, shore spawning has been observed at depths down to 20 m (Hassemer and Rieman 1981; Gipson and Hubert 1993). The diversity of egg deposition behaviors and spawning environments used by *O. nerka* across systems makes habitat assessment challenging and necessitates the evaluation of shore spawning under a variety of conditions.

Understanding the influence of habitat characteristics on kokanee intragravel survival is of particular importance in Lake Pend Oreille (LPO), Idaho, because shore spawners are the most abundant kokanee ecotype and because they persistently select apparently unsuitable spawning habitat. In the mid-1990s, resource managers began raising the winter lake elevation in an effort to enhance kokanee recruitment by inundating wave-washed gravels in the nearshore area (Maiolie et al. 2002). Despite lakewide changes in nearshore habitat quality, kokanee continued to spawn primarily in depositional environments on the southern end of the lake. Shoreline redd counts from 1972 to 2012 suggested that the majority of shore spawning occurred in Scenic Bay (Wahl et al. 2011), which is highly developed and dominated by sand substrate (Fincel et al. 2009). Recent underwater videography has also discovered substantial deep-spawning aggregations in Scenic Bay and areas on the southwestern shore of the lake. Kokanee spawning behavior in LPO is puzzling to resource managers and raises important questions about the role that habitat characteristics, particularly substrate composition and depth, play in regulating intragravel survival of *O. nerka* on shorelines.

The purpose of this research was to further our understanding of shoreline incubation requirements, and in so doing, begin to explain the spawning ecology of kokanee in LPO. Specific objectives for this research were to (1) develop a relationship between substrate composition and intragravel survival in a simulated shoreline environment and (2) elucidate habitat characteristics influencing shore-spawning kokanee incubation success in major spawning areas of LPO. The first objective was addressed by completing a kokanee egg incubation experiment designed to simulate shoreline intragravel conditions. The laboratory experiment was intended to describe the relationship between substrate composition and intragravel survival under shoreline water flow conditions. For the second objective, an in situ incubation study was conducted to evaluate how habitat conditions at multiple scales influence intragravel survival. The in situ study measured the influence of substrate composition on kokanee survival in LPO and investigated the viability of kokanee eggs deposited at depths greater than 5 m.

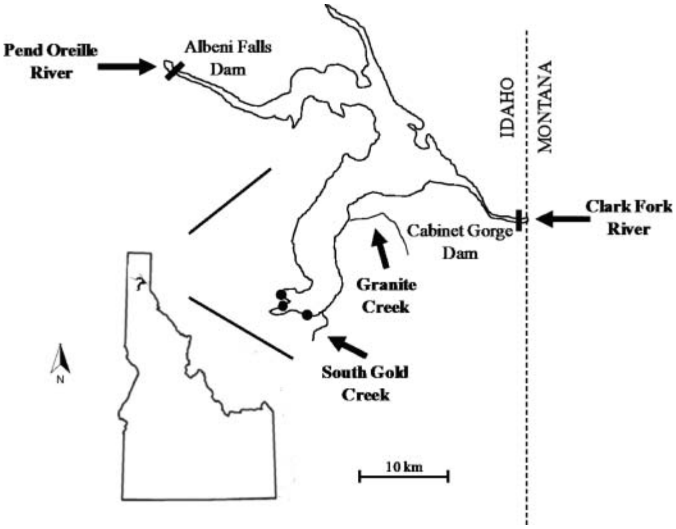


FIGURE 1. Lake Pend Oreille, Idaho, with study sites represented by solid circles (●).

METHODS

Study area.—Lake Pend Oreille is meso-oligotrophic with a surface area of 38,000 ha, a mean depth of 164 m, and 310 km of shoreline (Figure 1). The lake is affected by two dams constructed in 1952: Cabinet Gorge Dam located on the Clark Fork River and Albeni Falls Dam located on the lake's outlet. Other major tributaries in the system include the Pack River, Trestle Creek, South Gold Creek, and Granite Creek. In winter, the water column remains aerobic and the water temperature drops below 4°C, but the lake does not freeze (Stross 1954). Kokanee spawning occurs at two time periods during the year: late September (early run) and November–December (late run). Early-run kokanee consist of only the stream ecotype and spawn in Granite Creek, South Gold Creek, Trestle Creek, and the Clark Fork River. A portion of the late-run spawners use the same streams as the early run fish, but most of the late-run fish are thought to spawn in Scenic Bay and Idlewilde Bay, and on shelf-like beaches in the southern half of the lake (Maiolie 1994). The Idaho Department of Fish and Game operates a weir on Sullivan Springs, a tributary of Granite Creek, to supply eggs for annual stocking efforts in the lake.

Egg boxes.—Whitlock–Vibert egg boxes were used in both the laboratory experiment and in situ study to simulate kokanee redds (Whitlock 1979; Garrett and Bennett 1996). The boxes are artificial salmonid egg pockets composed of an upper incubation chamber and a lower nursery chamber (Whitlock 1979). Whitlock–Vibert boxes have been used in numerous laboratory and in situ kokanee incubation studies (Hassemer 1984; Garrett et al. 1998; Fincel et al. 2009). For this study, 50 fertilized kokanee eggs were loaded in the upper chamber along with 9.5-mm gravel (Irving and Bjornn 1984; Fincel et al. 2009). Egg boxes were retrieved at two points during incubation to evaluate survival to the eyed and preemergent stages of development (Garrett and Bennett 1996; Fincel et al. 2009).

Laboratory experiment.—The laboratory experiment was conducted in experimental incubation troughs located at the University of Idaho that simulated winter incubation conditions in LPO. Water was added to troughs via dribblers on the surface and drained from a standpipe on the surface rather than being directed horizontally through the gravel, as is common in many stream-based experiments (Tappel and Bjornn 1983; Reiser and White 1988). The intention of the trough design was to produce a gradient of surface and intragravel water exchange rates, produced by differing substrate permeabilities across treatments (Greig et al. 2007). Water was supplied to each of 24 experimental troughs via a 1.5-hp pump and drained to a reservoir containing a chiller and air stones, which recirculated water (Figure 2a). Chilled, dechlorinated make-up water was added to the reservoir through an aeration column at a rate of 5 L/min to maintain DO levels and reduce fungal growth (Waterstrat 1997). Dribblers (4.76 mm inner diameter) were distributed evenly across the length of the trough and were suspended approximately 3 cm above the water (Figure 2). Valves in the tubing network were adjusted so that 1.1 L/min of water was evenly distributed across

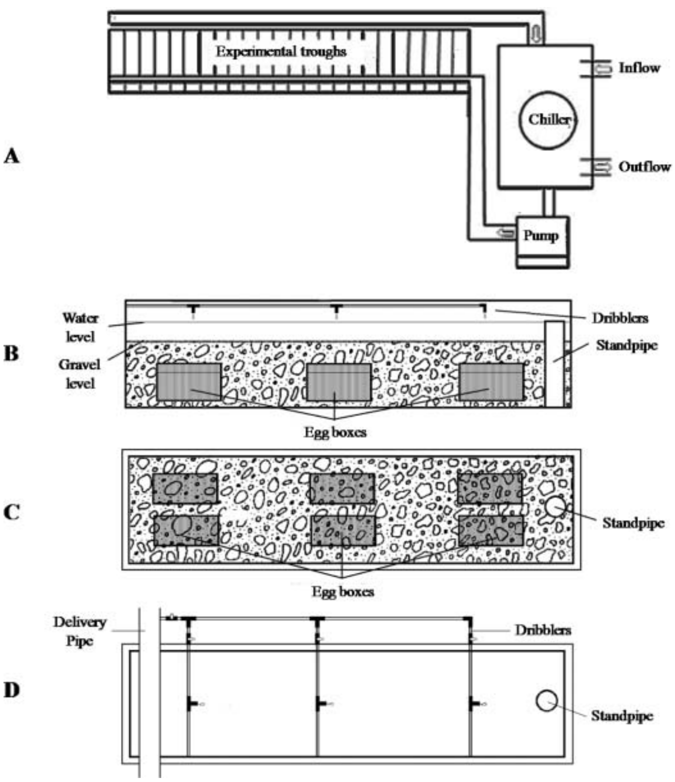


FIGURE 2. Design of an experimental trough used in a kokanee laboratory incubation experiment at the University of Idaho, 2011–2012, intended to simulate shoreline habitat conditions. (**A**) The quasi-recirculation system. Individual troughs are depicted by (**B**) a side view, (**C**) a plan view of egg box positions in gravel, and (**D**) a plan view of the water delivery system.

dribblers. Water depth was maintained at 25 cm, providing a distance of approximately 8 cm between the water and substrate surface. Water temperature in the system was also maintained at 4–8°C and surface water DO was at saturation (~9–12 mg/L) to match the overwinter conditions in LPO (Stross 1954; Hassemer 1984). A thermograph (Onset, Cape Cod, Massachusetts) was placed in the trough located the farthest away from the pump (i.e., warmest trough) to monitor temperature throughout the experiment.

Substrate treatments in this study consisted of a subset of those used in the only known stream-based kokanee laboratory incubation experiment (Irving and Bjornn 1984). Eight of the 16 gravel treatments used by Tappel and Bjornn (1983) and Irving and Bjornn (1984) were created by sifting commercially supplied rock. Substrate treatments were described in terms of the percentage of particles by weight that were less than 9.5 mm and less than 0.85 mm in diameter. For example, 50:20 is equal to a homogenous substrate mixture in which 50% of particles by weight were less than 9.5 mm and 20% by weight were less than 0.85 mm in diameter (Tappel and Bjornn 1983; Bennett et al. 2003). The eight substrate treatments randomly assigned to the 24 troughs in the laboratory experiment were 50:20, 40:16, 35:8, 30:12, 25:6, 20:8, 20:1, and 0:0.

"Green" (i.e., undeveloped) kokanee eggs were obtained from the Sullivan Springs spawning weir and transported to the University of Idaho where they were disinfected with iodophor (100 mg/L for 10 min: Piper et al. 1982). Fertilized eggs from multiple donors were mixed together. All handling was conducted within 48 h of fertilization to avoid handling during the period when salmonid eggs are most sensitive to physical shock (Piper et al. 1982; Crim and Glebe 1990). Gravel and green kokanee eggs were loosely placed in the incubation chamber of each egg box. Eggs were discarded if they appeared whitened, bloody, or not water hardened. Six egg boxes were assigned to each experimental trough. Boxes were buried in substrate to a depth of 5–10 cm, similar to stream-spawning kokanee egg burial depths (Scott and Crossman 1973; Steen and Quinn 1999). Of the six boxes placed in each trough, two were covered in 1-mm mesh and randomly positioned for measurement of preemergent survival. Egg survival was determined by counting the number of eyed eggs; opaque eggs were considered to be dead. Survival to later stages was determined by counting the number of living embryos present. A monitoring stake was placed in each experimental trough, enabling intragravel water samples to be drawn via a syringe. Monitoring stakes were modified from the design used by Leonetti (1996). One monitoring stake was placed in each trough between the pair of egg boxes in the center and the pair of boxes nearest the standpipe. Intragravel and surface DO was measured four times during incubation. Samples were drawn from monitoring stakes using a 70-mL syringe and DO concentration was measured to the nearest 0.1 mg/L by placing the probe of a calibrated electrode-based DO meter (YSI model Pro 2030, Yellow Springs Instruments, Yellow Springs, Ohio) inside each syringe and gently agitating. Surface water DO was measured along with intragravel DO over the course of the experiment. Kokanee eggs were treated with formalin once during the experiment to prevent fungal (*Saprolegnia* spp.) growth in egg boxes (Argent and Flebbe 1999; Bennett et al. 2003). Formalin was administered on January 27, 2012, in the form of a bath treatment of Parasite S (Western Chemical, Ferndale, Washington) brought to a concentration of 1,667 mg/L for 15 min.

Survival of kokanee to eyed and preemergent stages of development was measured by retrieving egg boxes at different times. On February 21, 2012, two uncovered egg boxes per trough were retrieved at random to determine egg survival to the eyed stage. Afterwards, experimental troughs were darkened with opaque polyethylene sheeting to prevent preemergent fry from expending energy to avoid light (Heard 1964; Bams 1969). Sheeting was removed and the two mesh-covered boxes were retrieved on April 1 to measure survival of embryos to the preemergent stage. Fry were allowed to emerge from residual boxes.

Troughs were surveyed for emergent fry nightly from April 20 until termination of the experiment on May 4, 2012. The number of fry visible on the surface water of each trough was enumerated with the aid of a flashlight. Troughs were surveyed in random order each night to reduce the effect of fry disturbance in adjacent troughs. Nightly counts after peak emergence were used as an index of abundance of emergent fry among treatment groups. Detectability of fry during counting was assumed to be constant across all substrate treatments. Emergent fry were collected from the surface water of each trough with a vacuum pump at the end of the experiment. Fry FL was measured to the nearest 0.1 mm using a stereoscope coupled with a camera and image analysis software (Image-Pro Plus 5.1, MediaCybernetics, Bethesda, Maryland). Dry weight was measured to the nearest milligram after desiccating the sample for 24 h at 60°C (Busacker et al. 1990; Steinhart and Wurtsbaugh 2003).

Eyed egg survival, preemergent survival, emergent fry count, and emergent fry condition were analyzed using a mixed-model approach (Pinheiro and Bates 2000). Substrate treatments were modeled as categorical fixed effects nested within a trough random variable. Intragravel survival proportion and fry counts were modeled using generalized linear mixed models (GLMMs), estimated using the Laplace approximation (Warton and Hui 2011; Hosmer et al. 2013). Minimum DO measured in each trough up until box retrieval was included as a variable in the survival models and its effect was described using the exponential function of the parameter value (i.e., odds ratio), interpreted as the estimated increase in the odds of survival associated with a one-unit change in the value of the predictor (McCullagh and Nelder 1989). Poisson regression was used to model emergent fry counts and counting events were considered independent replicates, under the assumption that all fry remained in the surface water after emergence, unless disturbed. The relative condition of emergent fry was summarized using a dry weight version of Fulton's fry condition factor (K_{DW} : Reiser and White 1988):

$$K_{DW} = \frac{\text{dry weight(mg)} \times 10^3}{[\text{wet fork length(mm)}]^3}.$$

Fry condition factor was modeled using a linear mixed model estimated with restricted maximum likelihood.

Model fit was assessed using deviance residual plots and the area under the receiver operating characteristic curve (ROC curve; Hosmer et al. 2013). Overdispersion of GLMMs was evaluated using a dispersion parameter ($\hat{c}$) calculated from deviance residuals (McCullagh and Nelder 1989). Likelihood ratio tests were used to test for fixed effects in logistic and Poisson regression models (Warton and Hui 2011). The effect of substrate on fry condition factor was assessed using an F-test (Pinheiro and Bates 2000). When treatment effects were detected, Tukey pairwise comparisons were used to test for differences among treatments (Zar 2009).

In situ study.—An in situ incubation study was conducted at three major shoreline spawning sites in LPO to identify relationships between habitat characteristics and survival. Egg boxes were buried in substrate and laid out using a double matrix design modified from the one used by Hassemer (1984) in Lake Coeur d'Alene. Matrices were placed in three current shoreline spawning sites, where kokanee spawn at relatively high densities. Spawning sites included in the current study were Eagle Marina, Bernard Mine, and Scenic Bay (Figure 1). The three shoreline sites were selected because they characterized dissimilar habitat types. The Scenic Bay site consisted primarily of sand substrate with larger particles at depth, the Eagle Marina site consisted of a mixture of cobble, gravel, and sand, and the Bernard Mine site was located on an active talus slope and was the steepest and most exposed of the three sites.

Egg boxes were laid out within each site in two 4 × 4 matrices at shallow (1–4 m) and deep (10–14 m) isobaths. Both matrices were arranged with 1-m spacing in the direction parallel to shore and 1.5-m spacing perpendicular (Hassemer 1984). The metered slope line and a 1 × 1.5-m PVC rectangular frame served as a guide for spacing egg boxes. The slope of matrices was estimated after boxes were placed by measuring the average difference in depth between the top and bottom row of boxes using a dive computer (Gipson and Hubert 1993).

Egg boxes were deployed using the same methods as those in the laboratory experiment. In total, 96 egg boxes were planted in the lake between December 8 and 12, 2011, among the three shoreline sites. Of the 16 egg boxes placed in each matrix, six were randomly assigned to measure eyed egg survival and 10 for preemergent survival. Four additional "handling mortality" boxes were buried adjacent to each matrix to estimate mortality resulting from the transport, loading, and burial of boxes (Hassemer 1984; Fincel et al. 2009). Handling boxes were retrieved within 3 d of placement. Egg boxes without mesh (i.e., eyed stage) were retrieved between February 28 and March 1, 2012, and egg boxes with mesh (i.e., preemergent stage) were retrieved between April 24 and April 26, 2012.

Temperature and intragravel DO were monitored during the in situ incubation study using methods similar to the laboratory experiment. Ambient temperature was monitored by four thermographs placed in the vicinity of egg box matrices. Thermograph data were used to calculate accumulated temperature units (ATUs) at sites. Intragravel DO concentration was measured at half of the egg box locations at four points during incubation. Monitoring stakes, described for the laboratory experiment, were randomly placed at two egg boxes per row (parallel to shore). Intragravel DO was measured by extracting water samples from monitoring stakes at depth by using 70-mL syringes. Filled syringes were capped immediately after sample collection and carried to a DO meter at the surface. Intragravel DO was first measured at each monitoring stake 2–3 d after egg boxes and stakes were installed and monthly thereafter. Dissolved oxygen could not be measured at every stake during every visit because some of the monitoring stakes became either clogged or kinked.

Substrate was sampled at every egg box location following completion of the study using an underwater bulk sampling device (Young et al. 1991; Kondolf 2000). The sampler used in this study was modified from the "cookie-cutter" design described by Klingeman and Emmett (1982). Divers pressed the sampler into the substrate and excavated encircled material to a depth of 8 cm using a cylinder (140 mm diameter × 165 mm height). Each sample was composed of three to four full cylinders of material from the same location that were placed in a 68-L plastic bag. The cylinder was capped during transfer from the sampler to the bag to minimize loss of fine sediment. Plastic bags were sealed at depth with cable ties and hoisted to the surface in sealed buckets (Marsden and Krueger 1991). Substrate samples were dried in an oven and sorted using the suite of sieves described by Tappel and Bjornn (1983).

An information theoretic approach was used to select parsimonious logistic regression models for the effect of box- and matrix-level habitat characteristics on kokanee intragravel survival (Burnham and Anderson 2002). Four model-selection procedures were performed in total using Akaike's information criterion (AIC) adjusted for small sample sizes (AIC_c). Separate model-selection procedures evaluated the effect of habitat variables on survival to eyed and preemergent stages.

Two procedures were performed for each developmental stage: one using all egg boxes and another using only egg boxes where intragravel DO was measured through time (DO subset). The goal of model-selection procedures that included all boxes was to evaluate the influence of habitat characteristics on survival. The DO subset model-selection procedures contained fewer observations; thus, the number of candidate models and their complexity was reduced (Table 1). The purpose of model selection for the DO subset was to assess whether inclusion of intragravel DO would improve fit or produce a different conclusion compared with procedures that included all available boxes.

Habitat variables included in this analysis were site, depth, slope, and substrate composition. Minimum DO was also included in DO subset candidate models. Depth was treated as a categorical variable indicating whether an egg box was placed in the shallow or deep isobath. Slope was included as a continuous matrix-level variable that described the plane angle of shoreline. There is no unifying statistic for describing substrate conditions; therefore, median particle diameter (D50) and percentage of particles by weight less than 0.85 mm (hereafter "fines") were included in model-selection procedures (Kondolf and Wolman 1993; Kondolf 2000). Median particle diameter and fines were examined separately due to their lack of independence. Minimum DO concentration observed at each egg box through time was included as a variable in the in situ analysis for the same reason as in the laboratory experiment. Correlation among explanatory variables was assessed prior to analysis and variable pairings with substantial correlations ($r^2 > 0.50$) were excluded.

TABLE 1. Candidate models for kokanee intragravel survival to eyed and preemergent stages of development for an in situ incubation study conducted at three shoreline spawning sites on Lake Pend Oreille, Idaho, 2011–2012. The left column indicates candidate models in which all egg boxes were used to assess survival. The right column shows candidate models that were evaluated using a subset of boxes for which minimum intragravel DO through time was measured. The variable "substrate" represents two substrate variables that were modeled separately: median particle diameter and the proportion of particles less than 0.85 mm.

All boxes	Dissolved oxygen subset
[Null]	[Null]
Site	Matrix
Depth	Slope
Substrate	Substrate
Slope	DO
Site, depth	Matrix, substrate
Site, substrate	Slope, substrate
Depth, substrate	Matrix, DO
Depth, slope	Substrate, DO
Substrate, slope	Slope, DO
Site, depth, slope	Matrix, substrate, DO
Site, depth, substrate	Slope, substrate, DO
Site, slope, substrate	
Site, depth, slope, substrate	
Site, depth, site × depth	
Site, substrate, site × substrate	
Depth, substrate, depth × substrate	
Site, depth, site × depth, substrate	

Candidate models consisted of additive models for all variables as well as several biologically plausible two-way interactions. Interactions were only included in candidate models when both main-effect terms were also present (Table 1). Models containing the site × depth interaction hypothesized that intragravel survival was related to the particular matrix containing an egg box. Candidate models for DO subset boxes were assembled differently because they possessed fewer observations and would have exceeded the recommended number of events per variable for model selection (Vittinghoff and McCulloch 2007). Site and depth main effects and their interaction were collapsed into a categorical variable with six levels named "matrix" (Table 1).

When initial fitting of candidate models indicated overdispersion ($\hat{c} > 1$) quasi-AIC adjusted for small samples (QAIC_c) was used to rank models, and an additional parameter was added to each model to account for the estimation of dispersion (Burnham and Anderson 2002). The variance inflation factor for QAIC_c was fixed using the lowest $\hat{c}$ value among candidate models because there was no global model (Burnham and Anderson 2002). Models were judged as those with AIC_c or QAIC_c scores within 2.0 of the model with the lowest score ($\Delta < 2$). Top models were evaluated using methods described in the laboratory section.

Changes in intragravel DO over the incubation period and across matrices were modeled using a linear mixed model fit with restricted maximum likelihood (Pinheiro and Bates 2000). An appropriate covariance structure for repeated measures was determined based on AIC ($\Delta < 2$) and an assessment of standardized residuals. Potential covariance structures included compound symmetric, autoregressive (lag 1), autoregressive heterogeneous, and general (Pinheiro and Bates 2000). This method was advantageous because it enabled egg box locations with incomplete DO records to be included in the analysis.

RESULTS

Laboratory Experiment

The experimental trough system remained within the range of temperature and DO for simulating winter conditions in LPO. Water temperature varied from 6.8°C to 7.6°C and surface DO was greater than 90% saturation over the course of the experiment. Surface water DO concentrations were between 9.2 and 11.5 mg/L and intragravel DO levels were between 8.4 and 11.3 mg/L. Intragravel DO differed significantly from surface water based on an asymptotic pairedcomparison permutation test ($P < 0.001$), indicating that a DO gradient was established between the intragravel area and surface water.

Fry emergence occurred over a 5-d period beginning on April 22, 2012. No fry were observed in one of the three troughs containing the 50:20 substrate treatment. Emerged fry remained below gravel during the day and moved into surface water at night. All fry emerged with fully absorbed yolk sacs. Fry counts peaked on April 26 and were relatively consistent until termination of the experiment on May 4, 2012. Between 8 and 28 fry were sampled from all experimental troughs that contained fry.

Substrate treatments and intragravel DO had only a small effect on intragravel survival. All model assumptions were met based on visual inspection of residual plots, GLMMs did not show evidence of overdispersion ($\hat{c} > 1$), and logistic regression models showed adequate discrimination (ROC > 0.7). Likelihood ratio tests indicated that survival of kokanee to the eyed stage was influenced by the minimum intragravel DO concentration, but not by substrate treatment (Table 2). Minimum intragravel DO had a significant positive effect on survival to the eyed stage but not to the preemergent stage. The odds ratio estimate for the eyed stage was 1.22 (1.03, 1.44 [lower and upper 95% profile likelihood confidence limits, respectively; LCL, UCL]) and 1.13 (0.96, 1.33) for the preemergent stage. Fry counts and condition were negatively affected by substrate treatments (Table 2). The Tukey pairwise comparisons indicated that the substrate treatment with the largest proportion of fine sediment (50:20) had a significantly lower fry count than all other treatments and a significantly lower condition factor (K_{DW}) than all others besides the 25:6 treatment (Figure 3).

TABLE 2. Likelihood ratio (LR) tests and *F*-tests of kokanee egg and fry survival in a laboratory incubation experiment conducted at the University of Idaho, 2011–2012. Likelihood ratio tests were used in global tests for the effect of eight substrate treatments and minimum intragravel dissolved oxygen on the proportion survival of embryos to the eyed and preemergent stages of development. Postemergence tests included a LR test to evaluate the effect of substrate treatments fry counts. An *F*-test was used to examine the effect of substrate treatments on Fulton's dry weight condition factor of fry.

Measurement	Statistical test	df	LR or *F*	*P*-value
Intragravel survival				
Eyed stage				
Dissolved oxygen	LR test	1	6.67	0.010
Treatment	LR test	7	10.64	0.155
Preemergent stage				
Dissolved oxygen	LR test	1	2.64	0.104
Treatment	LR test	7	8.50	0.291
Postemergence				
Fry count	LR test	7	25.57	<0.001
Fry condition	*F*-test	7, 15	3.69	0.016

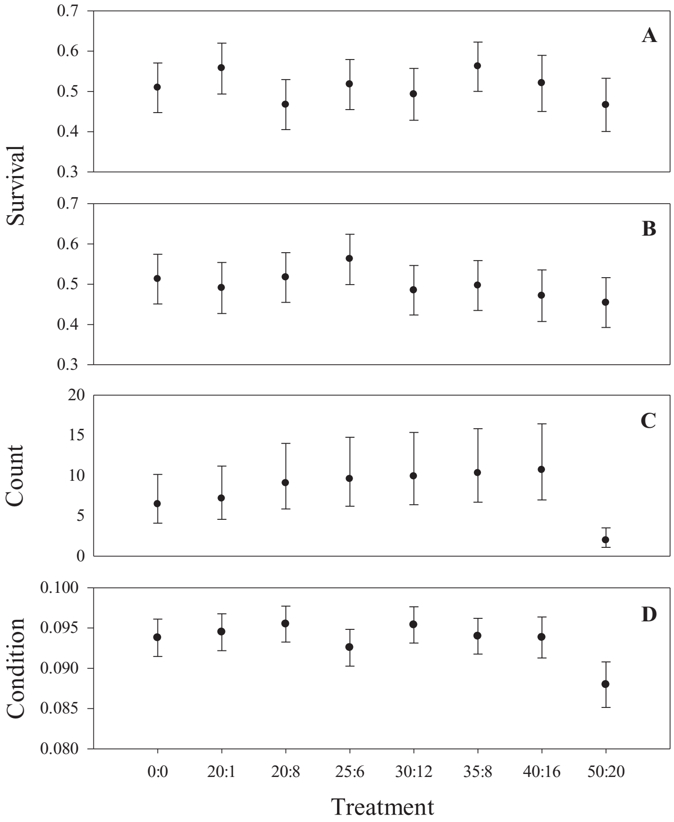


FIGURE 3. Mean survival of kokanee eggs to the (**A**) eyed and (**B**) preemergent developmental stages, (**C**) counts of emergent fry, and (**D**) condition of emergent fry from a laboratory incubation experiment conducted at the University of Idaho, 2011–2012. Error bars denote 95% profile likelihood CIs for proportions and counts and pivotal CIs for condition estimates. Mean fry counts are based on the average number of fry counted per experimental trough during nightly fry counts. Fry condition is based on fry collected from experimental troughs at termination of the experiment and calculated using the dry weight modification of Fulton's condition factor.

In Situ Study

Intragravel DO was measured at 2, 29, 76, and 113 d after placement of the last egg box matrix, eyed egg boxes were retrieved at days 82 and 83, preemergent egg boxes were retrieved between days 140 and 142, and substrate was sampled between days 149 and 155. The estimated shoreline slope of deep matrices was 22.9° for Eagle Marina, 24.0° for Scenic Bay, and 32.8° for Bernard Mine. The slopes of shallow matrices were more variable at 3.8° for Eagle Marina, 12.7° for Scenic Bay, and 28.3° for Bernard Mine. Although not quantified, periphyton cover increased throughout incubation at all matrices and was pronounced in shallow sites. The Scenic Bay site was dominated by filamentous green algae (e.g., *Cladophora* spp.); whereas, the Bernard Mine and Eagle Marina sites were dominated by stalked diatoms (e.g., *Cymbella* spp.). Survival in handling boxes averaged 97% among matrices indicating that the effect of handling mortality could be ignored. Several egg boxes were not recovered during the study including two eyed egg boxes at the deep matrix from the Bernard Mine, one preemergent egg box at the deep matrix from the Eagle Marina, and one preemergent egg box at the shallow matrix in Scenic Bay. Many of the egg boxes were not retrieved because they rolled down the slope in the process of unburying boxes. One monitoring stake failed at the Scenic Bay–deep matrix, and another at the Bernard Mine–deep matrix.

Temperature trends were relatively consistent across sites and depths, while trends in DO varied across matrices. Temperature remained between 3.1°C and 8.9°C during incubation and varied by less than 1°C across all locations until approximately March 20, 2012, when the shallow area of Scenic Bay began to warm. This pattern is reflected in ATUs among locations during incubation. At the time when eyed eggs were retrieved, the range of ATUs among the four thermograph locations was less than 6 ATUs. When preemergent boxes were retrieved, the shallow location in Scenic Bay was 12 ATUs ahead of the deep location in Scenic Bay, 17 ATUs ahead of the shallow location in Idlewilde Bay, and 32 ATUs ahead of the deep location in Idlewilde Bay. The top ranking, and also best fitting, repeated-measures DO model contained a general covariance structure where the maximum number of correlation parameters was estimated. Intragravel DO measurements of three egg box locations in the Bernard Mine–shallow matrix deviated from others by remaining at low levels. These egg boxes were dropped from the repeated-measures analysis in an attempt to conservatively describe patterns in declining DO (Figure 4). Intragravel DO declined through time at all matrices except Scenic Bay–shallow matrix and Eagle Marina–deep matrix, with the most rapid decline occurring at the Bernard Mine–shallow matrix (Table 3).

Substrate size distributions differed greatly among and within sites. Deep matrices in Bernard Mine and Scenic Bay were characterized by higher proportions of large cobbles at depth, while substrate composition at Eagle Marina was similar for both isobaths (Figure 5). Variability in substrate size distributions among egg boxes differed across matrices. Relatively homogenous substrate composition was observed at the shallow matrix in Scenic Bay and deep matrices of Bernard Mine and Eagle Marina (Figure 6). Substrate composition was heterogeneous at shallow matrices of Bernard Mine and Eagle Marina and the deep matrix of Scenic Bay.

Model selection procedures supported the hypothesis that intragravel survival was influenced by matrix and intragravel DO. Candidate models were overdispersed ($\hat{c} > 1$) in all model-selection procedures except the preemergent DO subset (Table 4). Top models showed adequate fit and discrimination (ROC > 0.7). Top models either had the lowest dispersion

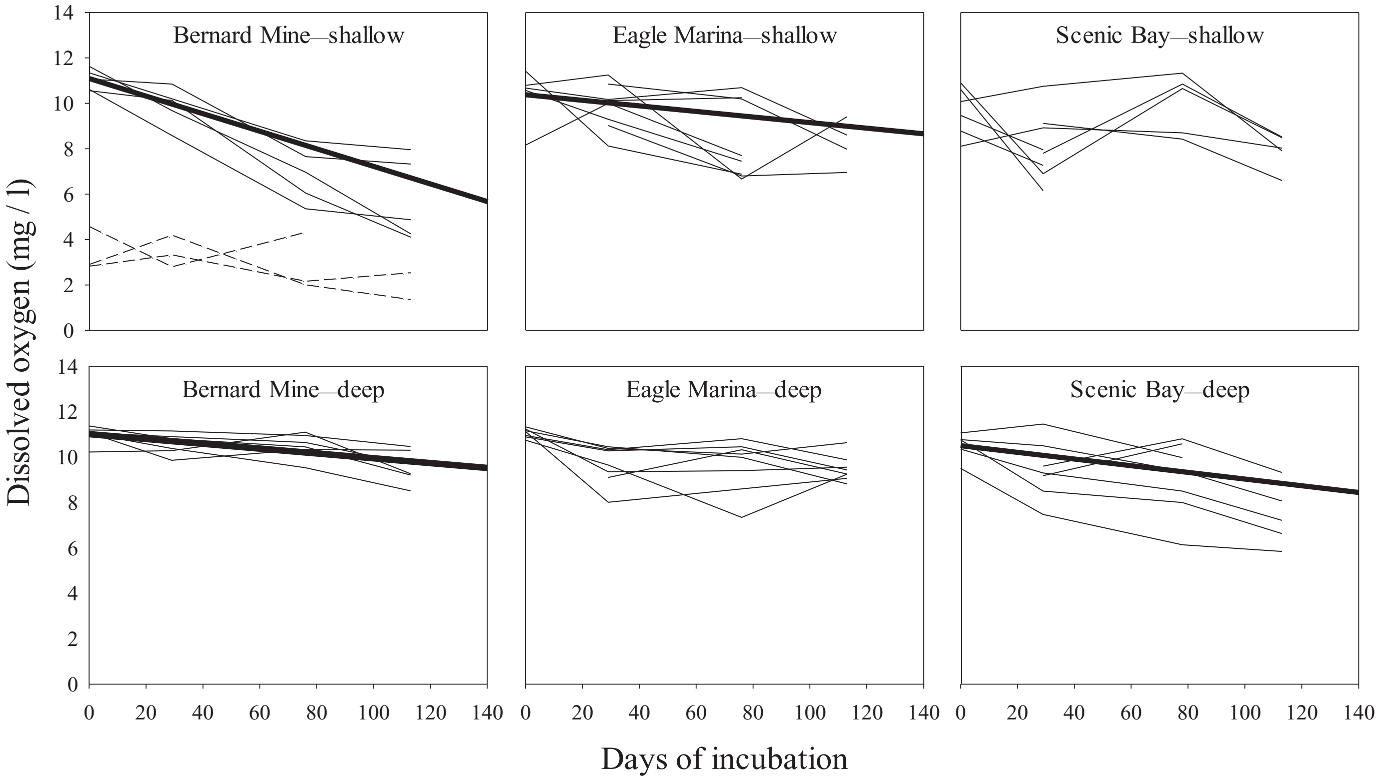


FIGURE 4. Intragravel dissolved oxygen measurements taken at four points from six egg box matrices during an in situ kokanee incubation study on Lake Pend Oreille, Idaho, 2011–2012. Thin lines represent measurements at individual egg box locations, thick lines represent the expected value for DO over the incubation period for matrices with nonzero slopes (<0.05), and dashed lines in the Bernard Mine–shallow matrix denote egg boxes that were excluded from the model (see text).

TABLE 3. Slope parameters for intragravel dissolved oxygen versus days of incubation at kokanee egg boxes located in shallow (1–4 m) and deep (10–14 m) isobaths at three shoreline spawning sites in Lake Pend Oreille, Idaho, 2011–2012.

Egg box matrix	Slope parameter	SE	*t*	df	*P*-value
Bernard Mine					
Shallow	−0.039	0.005	−7.2	148	<0.001
Deep	−0.011	0.003	−0.5	148	0.002
Eagle Marina					
Shallow	−0.012	0.006	−2.2	148	0.032
Deep	−0.003	0.005	−0.6	148	0.579
Scenic Bay					
Shallow	−0.004	0.005	−0.8	148	0.414
Deep	−0.015	0.006	−2.6	148	0.009

parameter estimate or were within 0.1 of the lowest. All top models demonstrated support for matrix-level effects on survival based on the presence of the "site × depth" interaction or "matrix" variable. Akaike weights of the top three models exceed 0.95 for all procedures. Model selection procedures that included the DO variable received support for matrix and DO variables. Substrate variables (D50, <0.85 mm) were included among top models for all eyed egg boxes. However, similar likelihood among the top three models and the error surrounding substrate odds ratios estimates demonstrated little to no effect of substrate size on survival.

Findings from model-selection procedures support the interpretation of intragravel survival data on a matrix-by-matrix basis. Therefore, the results presented here are based on interpretations of parameter estimates from the top-ranking models, none of which contained substrate variables. Survival to the eyed stage was generally higher than to the preemergent stage (Figure 7). Survival to both stages of development was higher at shallow than at deep matrices in Scenic Bay and Eagle Marina; the opposite was true at Bernard Mine. Survival to the eyed stage was highest at the shallow matrices of Eagle Marina (55 ± 3.8% [mean ± SE]) and Scenic Bay (48 ± 3.8%), followed by the deep matrices of Scenic Bay (38 ± 3.7%), Bernard Mine (37 ± 0.4.5%), Eagle Marina (19 ± 3.0%), and the shallow matrix at Bernard Mine (3 ± 1.1%). The Eagle Marina–shallow matrix had the highest survival to the preemergent stage (39 ± 2.9%), followed closely by the shallow matrix of Scenic Bay (33 ± 3.0%). Preemergent survival at all deep matrices was comparable. No fry survived to the preemergent stage at the Bernard Mine–shallow matrix. Complete mortality of eggs at the Bernard Mine–shallow matrix created issues in estimating parameters using regular maximum likelihood estimation. All candidate models for preemergent survival containing a "site × depth" interaction experienced quasi-complete separation of points where one of the parameter estimates diverged to infinity. Therefore, penalized maximum likelihood estimation was used to obtain parameter estimates and profile likelihood confidence intervals (Figure 7). Top models for the DO subset provided evidence of an effect of intragravel DO in addition to a matrix-specific effect. The estimated odds ratio for the effect of minimum DO on survival to the eyed stage was 1.24 (1.08, 1.45 [LCL,UCL]) and 1.34 (1.15, 1.57) for the preemergent stage. These estimates indicate that the DO concentration had a more pronounced effect on survival to the preemergent than to the eyed stage.

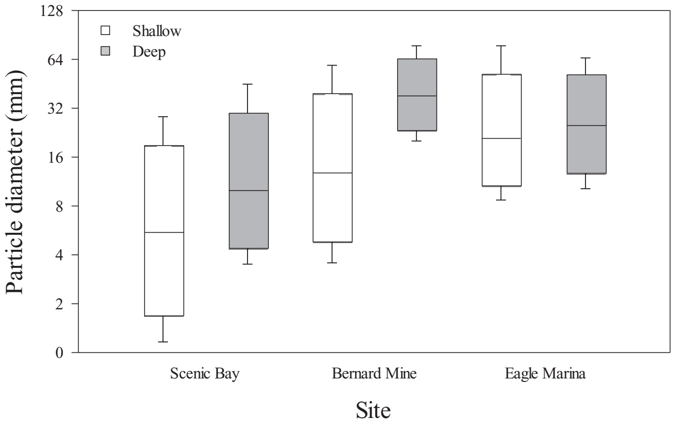


FIGURE 5. Particle size distributions for substrate sampled across six egg box matrices following an in situ kokanee incubation experiment on the shoreline of Lake Pend Oreille, Idaho, 2011–2012. Box plots were created by averaging the particle size distributions of 16 egg box locations per matrix. Particle diameter is shown on a $\log_2$ scale.

DISCUSSION

Survival responses were homogenous among treatments in the laboratory incubation experiment. It is uncommon for incubation studies to fail to detect a substrate treatment effect on survival; a meta-analysis by Jensen et al. (2009) found that substrate treatment did not significantly affect survival in 8% of previous laboratory and field incubation experiments involving Pacific salmon. Water flow rates are the most likely cause of similar intragravel survival among treatments. Although flow rates in the experiment were lower than those documented in the stream-based literature, guidance on water flow rates in shoreline environments is limited. Although the system succeeded in producing different DO concentrations between surface and intragravel water, this difference was not pronounced enough to produce variable responses among substrate treatments.

Subtle differences in surface and intragravel DO concentrations are unlikely to have influenced survival in the laboratory experiment. Minimum DO affected survival to the eyed but not the preemergent stage. However, considering the nearly uniform survival for eyed and preemergent embryos across all treatments, this finding does not appear to be biologically meaningful. Critical DO levels for salmonid eggs have been described as between 2 and 8 mg/L (Coble 1961; Silver et al. 1963; Davis 1975); intragravel DO was above these

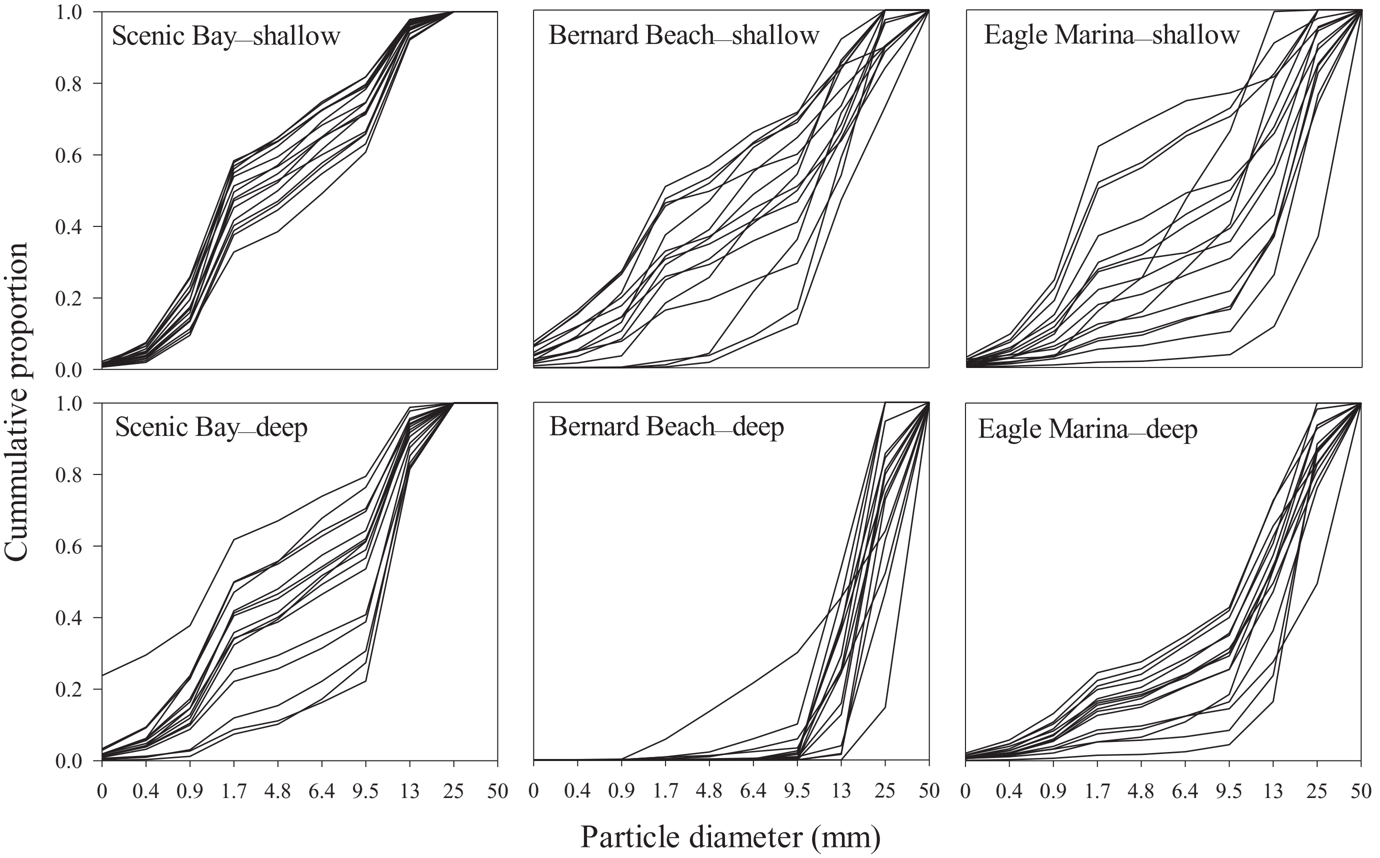


FIGURE 6. Cumulative particle size distributions for samples collected at 96 Whitlock–Vibert egg box locations in an in situ kokanee incubation study on Lake Pend Oreille, Idaho, 2011–2012. Greater separation among lines indicates greater substrate heterogeneity.

concentrations during the experiment. In addition, embryonic oxygen demand is initially low and increases as the embryo develops (Geist et al. 2006; Rombough 2007), so preemergent kokanee were more likely than eyed eggs to have been influenced by DO concentration.

Postemergent fry counts and condition reflected a survival bottleneck prior to emergence and sublethal effects of substrate composition. Although emergence timing was similar among treatments, postemergent counts and condition were lower for the substrate treatment containing the highest proportion of fine sediment. The nearly spontaneous emergence of fry in this experiment is contrary to previous experiments involving *O. nerka*, which have reported sac-fry emerging prematurely from troughs containing large proportions of fine sediment (Bams 1969; Irving and Bjornn 1984). Emergent fry counts suggest that kokanee in the treatment with the highest proportion of fine sediment had the lowest survival to emergence, despite comparable survival to eyed and preemergent stages.

Emergent fry counts may have underestimated the relative abundance of fry in the poorest treatments because finer substrate offered better concealment. Fry in treatments with the largest proportions of fine sediment were often observed plunging into substrate when disturbed by observers. Differences in emergent fry condition indicate a sublethal effect of substrate composition. Fry condition is an important component in determining recruitment because smaller fry are less competitive for food resources and can experience growth depensation (Mason 1969; Einum and Fleming 2000). Fry condition in this experiment was not related to intragravel DO measured during the experiment, similar to other studies (e.g., Maccrimmon and Gots 1986). Diminished condition of fry could be the result of added energy expenditure of escaping from substrate with a large proportion of fine particles (Koski 1966). If the act of escaping from fine sediment decreases fitness or causes additional mortality, then fry emerging from areas with fine sediment are potentially less viable regardless of their survival to previous stages. Postemergent fry were not included in the in situ study due to logistic constraints, so the effect of escaping from the gravel could not be assessed.

Models provided evidence of intragravel DO and matrix-level effects on survival in the in situ study but little effect of substrate composition. Substrate composition varied greatly within several sites, yet variability in survival and intragravel DO was low. The discovery of matrix-specific effects is informative for understanding the scale necessary for assessing

TABLE 4. Top three ranked models for the effect of habitat variables on kokanee egg survival (S) to eyed and preemergent stages of development during an in situ incubation study conducted at three shoreline spawning sites in Lake Pend Oreille, Idaho, 2011–2012. Akaike's information criterion adjusted for small sample sizes (AIC$_c$) was used to rank candidates that were not overdispersed (i.e., $\hat{c} < 1$), and quasi-AIC$_c$ (QAIC$_c$) was used to rank models when overdispersion was present among candidate models ($\hat{c} > 1$). "All boxes" are models that included all egg boxes. "Dissolved oxygen subset" are models that only used a subset for which intragravel DO was measured. The number of egg boxes included in the model selection procedure (n), number of parameters in the model (K), Akaike model weights (w_i), Log likelihood and quasi-log likelihood of each model [Log$_e$ (L)], and variance inflation factor ($\hat{c}$) incorporated into model selection with QAIC$_c$ are all shown. The minimum intragravel DO measured at a given egg box over the course of incubation, median particle diameter (D50), and the proportion of substrate particles less than 0.85 mm (fines) collected at egg box locations were important covariates in the models.

Data set	n	K	ΔAIC$_c$ / QAIC$_c$	w_i	Log$_e$ (L)	$\hat{c}$
Eyed egg survival						
All boxes						
$S_{(\text{site, depth, site} \times \text{depth})}$	34	7	0	0.48	−53.75	1.62
$S_{(\text{site, depth, site} \times \text{depth, D50})}$	34	8	1.03	0.29	−52.54	1.62
$S_{(\text{site, depth, site} \times \text{depth, fines})}$	34	8	1.61	0.22	−52.82	1.62
Dissolved oxygen subset						
$S_{(\text{matrix, DO})}$	21	8	0	0.86	−35.82	1.30
$S_{(\text{matrix, DO, D50})}$	21	9	5.61	0.05	−35.44	1.30
$S_{(\text{matrix, DO, fines})}$	21	9	6.10	0.04	−35.69	1.30
Preemergent survival						
All boxes						
$S_{(\text{site, depth, site} \times \text{depth})}$	58	7	0	0.62	−75.14	1.77
$S_{(\text{site, depth, site} \times \text{depth, D50})}$	58	8	2.46	0.18	−75.02	1.77
$S_{(\text{site, depth, site} \times \text{depth, fines})}$	58	8	2.69	0.16	−75.13	1.77
Dissolved oxygen subset						
$S_{(\text{matrix, DO})}$	25	7	0	0.79	−49.43	<1
$S_{(\text{matrix, DO, fines})}$	25	8	4.13	0.10	−49.29	<1
$S_{(\text{matrix, DO, D50})}$	25	8	4.21	0.10	−49.33	<1

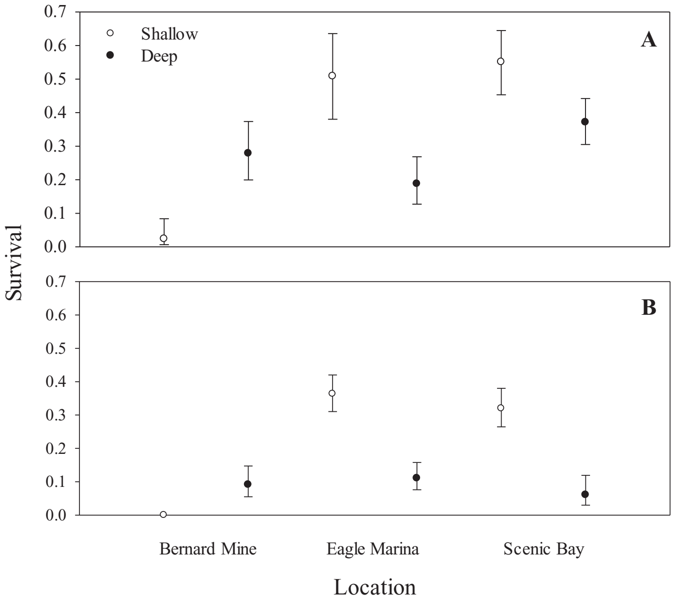


FIGURE 7. Mean survival of kokanee embryos to the (**A**) eyed and (**B**) preemergent developmental stages in Lake Pend Oreille, Idaho, 2011–2012. Estimated embryo survival for egg boxes located at shallow isobaths (1–4 m) are symbolized with open circles and deep isobaths (10–15 m) with solid circles; error bars denote 95% profile likelihood CIs.

shoreline habitat. It appears that patches of habitat large enough to contain multiple redds may be more useful for predicting shoreline incubation success than substrate composition at individual redd locations. These findings were similar to other incubation studies in LPO. Fincel et al. (2009) found site-specific effects on survival of kokanee among three areas in Scenic Bay, which were attributed to differences in substrate composition between sites. Hassemer (1984) reported 43% survival of kokanee to the preemergent stage in Scenic Bay, which was similar to the 33% survival observed in the in situ study. In addition, egg boxes removed from some areas of Scenic Bay were filled with silt, yet had between 24% and 60% survival (Hassemer 1984). The pattern of high survival despite high proportions of fine sediment present was also observed at the shallow matrix of the Scenic Bay site in this study.

The contrast between shallow matrices at Scenic Bay and Bernard Mine stands out in the analysis of matrix-specific substrate, DO, and survival. The substrate distribution in the Scenic Bay–shallow matrix contained the highest proportion of fine sediment of any matrix. On average, 50% of the particle size distribution was less than 5.5 mm in diameter, and 20% was less than 2.0 mm. Despite having the finest substrate, the Scenic Bay–shallow matrix also had high intragravel DO throughout the study and embryos had the second highest survival to the preemergent stage. On the other hand, the Bernard Mine–shallow matrix had a higher proportion of larger particles than both matrices in Scenic Bay. However, the Bernard Mine–shallow matrix had the lowest intragravel DO concentrations and no fish survived to the preemergent stage. Either the Bernard Mine–shallow matrix had exceptionally low survival or the Scenic Bay–shallow matrix had exceptionally high survival. Bernard Mine was the most exposed of the three sites and wave disturbance might explain the low survival in shallow water. However, the fact that egg boxes at the Bernard Mine–shallow matrix site were not dislodged or unburied seems to contradict this contention. Furthermore, low intragravel DO was routinely measured at the shallow matrix, although wave action is generally associated with higher intragravel flow and DO (Leonetti 1996; Leonetti 1997).

High survival of eggs and fry at the Scenic Bay–shallow matrix may have been due to a supplemental source of water flow provided by groundwater. Groundwater influence was a reasonable explanation because Scenic Bay and Eagle Marina are situated on a recharge area of the Spokane Valley Rathdrum Prairie Aquifer (Drost and Seitz 1978; Hsieh et al. 2007). Groundwater can enhance survival (Sowden and Power 1985; Garrett et al. 1998) and influence spawning site selection for a variety of species, including kokanee (Foerster 1968; Lorenz and Eiler 1989; Burgner 1991; Geist 2000). Garrett et al. (1998) found that stream-spawning kokanee redds in areas of upwelling had higher hatching success, despite having a higher proportion of fine sediment, than redds in nonupwelling areas. In a study of Sockeye Salmon redd site selection in off-channel habitats, Hall and Wissmar (2004) demonstrated that not only did spawners select redd sites in upwelling areas, but they were also less selective of substrate quality in areas of upwelling. The hypothesis that groundwater enhances kokanee survival in Scenic Bay led to a post hoc investigation of groundwater dynamics at egg box matrices.

The presence or absence of groundwater influence at egg box matrices was assessed by measuring the vertical hydraulic gradient of the intragravel zone beneath egg box locations using a PushPoint sampler (M.H.E. Products, East Tawas, Michigan) equipped with 6.35-mm-inner-diameter vinyl tubing (Rosenberry and LaBaugh 2008). The probe was inserted approximately 20 cm into the substrate at previous egg box locations. Clear vinyl tubing was attached to the opening at the top of the probe and extended above the water's surface. Upwelling or downwelling was determined by whether the water level in the tubing was situated above or below the surface water, respectively (Sowden and Power 1985; Geist and Dauble 1998; Mull and Wilzbach 2007). Groundwater was assessed at deep matrices by divers and an observer floating on the surface. Water level displacement was then measured to the nearest centimeter. To ensure accuracy of groundwater detection, air bubbles were removed from the tubing before sampling each site and the tubing was encircled by a life ring to dampen wave action around the tubing. Groundwater was not considered detected unless the tubing water-level showed a stable deviation from the surface water level of at least 3 cm. The groundwater assessment described here was not fully integrated with the in situ study (e.g., inclusion of groundwater covariates) because the bottom two rows of egg boxes at the Eagle Marina–deep site could not be identified and thus precluded complete groundwater assessment at every matrix.

The groundwater assessment detected downwelling at two of the six egg box matrices and helped to address unanswered questions from the in situ study. Downwelling groundwater was detected at 9 of the 16 egg box locations at the Scenic Bay–shallow matrix and at one of the egg boxes in the Eagle Marina–deep matrix. Downwelling may have existed at additional egg boxes at that site had the bottom two rows of the matrix been located. These findings are unique in that downwelling is seldom reported in the spawning habitat literature compared with upwelling (Geist and Dauble 1998; Lapointe 2012). Because downwelling carries surface water into intragravel habitats, it has several advantages over upwelling. Downwelling does not expose eggs to harmful groundwater that may be outside optimal incubation temperatures, contaminated, or anoxic due to long residence times (Youngson et al. 2004; Lapointe 2012). Results of the groundwater assessment suggest that downwelling plays a key role in enhancing the survival of embryos in LPO and might explain why so many kokanee spawn in what appears to be suboptimal habitat in Scenic Bay.

Although downwelling may explain the higher and more consistent intragravel DO at the Scenic Bay–shallow matrix, the reason for the decline in intragravel DO at the Bernard Mine–shallow matrix remains unclear. Temperature does not appear to be a significant driver of DO concentration during incubation. The shallow matrix in Scenic Bay warmed the most rapidly during incubation, yet the intragravel DO remained relatively constant. Another explanation is that diminished intragravel DO at Bernard Mine was associated with accumulation of organic matter or periphyton. Periphytonic biomass increased at all three sites during the study, but the Bernard Mine–shallow matrix had the largest accumulation of stalked diatoms. Accumulated organic matter can increase biological oxygen demand in the intragravel area and reduce egg-to-fry survival (Greig et al. 2007; Pattison et al. 2012). Alternatively, filamentous green algae may have improved incubation success in Scenic Bay. In either case, periphyton biomass or composition should be considered in future shore-spawning incubation studies as a potential predictor of intragravel survival.

The research presented here deviated from typical salmonid incubation experiments and in situ studies, both in the incubation environment that was investigated and in the estimated effects of habitat variables (Chapman 1988; Jensen et al. 2009). The laboratory experiment was the first known attempt to simulate the shoreline incubation environment of Pacific salmon, and the in situ study was one of few studies to examine the effects of habitat characteristics on intragravel survival at multiple depths and in multiple habitat types. Surprisingly, neither the laboratory experiment nor the in situ study found evidence that substrate composition greatly affects intragravel survival in shoreline environments, although survival was related to DO. Despite the poor survival–substrate relationship, several insights were gained from this research. Intragravel survival appeared to be better explained by habitat patches than by redd-scale substrate composition, regardless of depth. In addition, downwelling appears to have enhanced the survival of shoreline-spawned embryos and provides a compelling explanation for why the majority of kokanee spawn in apparently suboptimal habitat in southern LPO.

ACKNOWLEDGMENTS

The authors thank William Ament, William Harryman, Kelly Carter-Lynn, and Nicholas Wahl for assistance with the in situ study, and Jarrod Yates, Amy Long, Christine Moffitt, and many others for assistance with the laboratory experiment. The authors also thank Michelle Wiest for statistical support. Helpful comments on a previous version of the manuscript were provided by David Beauchamp, Daniel Schill, Michelle Wiest, Frank Wilhelm, and three anonymous reviewers. Funding for this project was provided by Idaho Department of Fish and Game and the Bonneville Power Administration. The Idaho Cooperative Fish and Wildlife Research Unit is jointly sponsored by the University of Idaho, U.S. Geological Survey, Idaho Department of Fish and Game, and Wildlife Management Institute. This project was conducted under the University of Idaho Institutional Animal Care and Use Committee Protocol 2012-7. The use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

REFERENCES

Argent, D. G., and P. A. Flebbe. 1999. Fine sediment effects on Brook Trout eggs in laboratory streams. Fisheries Research 39:253–262.

Bams, R. A. 1969. Adaptations of Sockeye Salmon associated with incubation in stream gravels. Pages 71–87 *in* T. G. Northcote, editor. Symposium on salmon and trout in streams. University of British Columbia, H.R. MacMillan Lecture Series in Fisheries, Vancouver.

Bennett, D. H., W. P. Connor, and C. A. Eaton. 2003. Substrate composition and emergence success of fall Chinook Salmon in the Snake River. Northwest Science 77:93–99.

Bjornn, T. C., and D. W. Reiser. 1991. Habitat requirements of salmonids in streams. Pages 83–138 *in* W. R. Meehan, editor. Influences of forest and rangeland management on salmonid fishes and their habitats. American Fisheries Society, Bethesda, Maryland.

Blair, G. R., and T. P. Quinn. 1991. Homing and spawning site selection by Sockeye Salmon (*Oncorhynchus nerka*) in Iliamna Lake, Alaska. Canadian Journal of Zoology 69:176–181.

Blair, G. R., D. E. Rogers, and T. P. Quinn. 1993. Variation in life history characteristics and morphology of Sockeye Salmon in the Kvichak River system, Bristol Bay, Alaska. Transactions of the American Fisheries Society 122:550–559.

Burger, C. V., J. E. Finn, and L. Holland-Bartels. 1995. Pattern of shoreline spawning by Sockeye Salmon in a glacially turbid lake: evidence for subpopulation differentiation. Transactions of the American Fisheries Society 124:1–15.

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.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical infromation-theoretic approach, 2nd edition. Springer-Verlag, New York.

Busacker, G. P., I. R. Adelman, and E. M. Goolish. 1990. Growth. Pages 363–387 *in* C. B. Shreck and P. B. Moyle, editors. Methods for fish biology. American Fisheries Society, Bethesda, Maryland.

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 on survival of steelhead trout embryos. Transactions of the American Fisheries Society 90:469–474.

Cooper, A. C. 1965. The effect of transported stream sediments on the survival of Sockeye and Pink salmon eggs and alevins. International Pacific Salmon Commission Bulletin 18.

Crim, L. W., and B. D. Glebe. 1990. Reproduction. Pages 547–559 *in* C. B. Schreck and P. B. Moyle, editors. Methods for fish biology. American Fisheries Society, Bethesheda, Maryland.

Crisp, D. T., and P. A. Carling. 1989. Observations on siting, dimensions, and structure of salmonid redds. Journal of Fish Biology 34:119–134.

Davis, J. C. 1975. Minimal dissolved oxygen requirements of aquatic life with emphasis on Canadian species, a review. Canadian Journal of Fisheries and Aquatic Sciences 32:2295–2332.

Drost, B. W., and H. R. Seitz. 1978. Spokane Valley–Rathdrum Prairie Aquifer, Washington and Idaho. U.S. Geological Survey, Open-File Report77-829, Tacoma, Washington.

Einum, S., and I. A. Fleming. 2000. Selection against late emergence and small offspring in Atlantic Salmon (*Salmo salar*). Evolution 54:628–639.

Einum, S., A. P. Hendry, and I. A. Fleming. 2002. Egg-size evolution in aquatic environments: does oxygen availability constrain size? Proceedings of the Royal Society Biological Sciences 269: 2325–30.

Fincel, M. J., S. R. Chipps, and D. H. Bennett. 2009. Composition and location of simulated lake-shore redds influence incubation success in kokanee, *Oncorhynchus nerka*. Fisheries Management and Ecology 16:395–398.

Foerster, R. E. 1968. The Sockeye Salmon. *Oncorhynchus nerka*. Fisheries Research Board of Canada Bulletin 162.

Garrett, J. W., and D. H. Bennett. 1996. Evaluation of fine sediment intrusion into Whitlock–Vibert boxes. North American Journal of Fisheries Management 16:448–452.

Garrett, J., D. H. Bennett, F. O. Frost, and R. F. Thurow. 1998. Enhanced incubation success for kokanee spawning in groundwater upwelling sites in a small Idaho stream. North American Journal of Fisheries Management 18:925–930.

Geist, D. R. 2000. Hyporheic discharge of river water into fall Chinook Salmon (*Oncorhynchus tshawytscha*) spawning areas in the Hanford Reach, Columbia River. Canadian Journal of Fisheries and Aquatic Sciences 57:1647–1656.

Geist, D. R., C. S. Abernethy, K. D. Hand, V. I Cullinan, J. A. Chandler, and P. A. Groves. 2006. Survival, development, and growth of fall Chinook Salmon embryos, alevins, and fry exposed to variable thermal and dissolved oxygen regimes. Transactions of the American Fisheries Society 135:1462–1477.

Geist, D. R., and D. D. Dauble. 1998. Redd site selection and spawning habitat use by fall Chinook Salmon: the importance of geomorphic features in large rivers. Environmental Management 22:655–669.

Gibbins, C., J. Shellberg, H. Moir, and C. Soulsby. 2008. Hydrological influences on adult salmonid migration, spawning, and embryo survival. Pages 195–223 *in* D. Sear and P. DeVries, editors. Salmonid spawning habitat in rivers: physical controls, biological responses, and approaches to remediation. American Fisheries Society, Symposium 65, Bethesda, Maryland.

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

Greig, S. M., D. A. Sear, and P. A. Carling. 2007. A review of factors influencing the availability of dissolved oxygen to incubating salmonid embryos. Hydrological Processes 21:323–334.

Hall, J. L., and R. C. Wissmar. 2004. Habitat factors affecting Sockeye Salmon redd site selection in off-channel ponds of a river floodplain. Transactions of the American Fisheries Society 133:1480–1496.

Hassemer, P. F. 1984. Spawning ecology and early life history of kokanee (*Oncorhynchus nerka*) in Couer 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.

Heard, W. R. 1964. Phototactic behaviour of emerging Sockeye Salmon fry. Animal Behavior 12:382–388.

Hosmer, D. W., S. Lemeshow, and R. X. Sturdivant. 2013. Applied logistic regression, 3rd edition. Wiley, Hoboken, New Jersey.

Hsieh, P. A., M. E. Barber, B. A. Contor, M. A. Hossain, G. S. Johnson, J. L. Jones, and A. H. Wylie. 2007. Ground-water flow model for the Spokane Valley–Rathdrum Prairie Aquifer, Spokane County, Washington, and Bonner and Kootenai counties, Idaho. U.S. Geological Survey Scientific Investigations Report 2007–5044.

Irving, J. S., and T. C. Bjornn. 1984. Effects of substrate size composition on survival of kokanee salmon and Cutthroat and Rainbow trout. Idaho Cooperative Fisheries Research Unit, University of Idaho, Technical Report 84-6, Moscow.

Jensen, D. W., E. A. Steel, A. H. Fullerton, and G. R. Pess. 2009. Impact of fine sediment on egg-to-fry survival of Pacific salmon: a meta-analysis of published studies. Reviews in Fisheries Science 17:348–359.

Jeric, R. J. 1996. Physical factors influencing survival to emergence and time of emergence of shoreslope-spawned kokanee salmon in Flaming Gorge Reservoir, Utah–Wyoming. Master's thesis. Utah State University, Logan.

Kerns, O. E., and J. R. Donaldson. 1968. Behavior and distribution of spawning Sockeye Salmon on island beaches in Iliamna Lake, Alaska, 1965. Journal of the Fisheries Research Board of Canada 25:485–494.

Klingeman, P. C., and W. W. Emmett. 1982. Gravel bedload transport processes. Pages 141–179 *in* R. D. Hey, J. C. Bathurst, and C. R. Thorne, editors. Gravel-bed rivers. Wiley, New York.

Kondolf, G. M. 2000. Assessing salmonid spawning gravel quality. Transactions of the American Fisheries Society 129:262–281.

Kondolf, G. M., M. J. Sale, and M. G. Wolman. 1993. Modification of fluvial gravel size by spawning salmonids. Water Resources Research 29:2265–2274.

Kondolf, G. M., J. G. Williams, T. C. Horner, and D. Milan. 2008. Assessing physical quality of spawning habitat. Pages 249–274 *in* D. A. Sear and P. DeVries, editors. Salmonid spawning habitat in rivers: physical controls, biological responses and approaches to remediation. American Fisheries Society, Symposium 65, Bethesda, Maryland.

Kondolf, G. M., and M. G. Wolman. 1993. The size of salmonid spawning gravels. Water Resources Research 29:2275–2285.

Koski, K. V. 1966. The survival of Coho Salmon (*Oncorhynchus kisutch*) from egg deposition to emergence in three Oregon coastal streams. Master's thesis. Oregon State University, Corvalis.

Lapointe, M. 2012. River geomorphology and salmon habitat: some examples illustrating their complex association from redd to riverscape scales. Pages 193–215 *in* M. Church, P. Biron, and A. Roy, editors. Gravel bed rivers: processes, tools, environments. Wiley-Blackwell Scientific Publications, Hoboken.

Leonetti, F. E. 1996. Habitat attributes, Sockeye Salmon spawning behavior, and redd site characteristics at island beachers, Iliamna Lake, Alaska. Master's thesis. University of Washington, Tacoma.

Leonetti, F. E. 1997. Estimation of surface and intragravel water flow at Sockeye Salmon spawning beaches in Iliamna Lake, Alaska. North American Journal of Fisheries Management 17:194–201.

Lorenz, J. M., and J. H. Eiler. 1989. Spawning habitat and redd characteristics of Sockeye Salmon in the glacial Taku River, British Columbia and Alaska. Transactions of the American Fisheries Society 118:495–502.

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.

Maiolie, M. 1994. Studies for the recovery of the fisheries in Lake Pend Oreille, Idaho: study scope of work. Northwest Power Planning Council, 94–15, Portland, Oregon.

Maiolie, M., K. Harding, W. Ament, and W. Harryman. 2002. Lake Pend Oreille fishery recovery project. Idaho Department of Fish and Game, Completion Report 02-56, Boise.

Malcolm, I. A., S. M. Greig, A. F. Youngson, and C. Soulsby. 2008. Hyporheic influences on salmon embryo survival and performance. Pages 225–248 *in* D. A. Sear and P. DeVries, editors. Salmonid spawning habitat in rivers: physical controls, biological responses and approaches to remediation. American Fisheries Society, Symposium 65, Bethesda, Maryland.

Malcolm, I. A., A. F. Youngson, and C. Soulsby. 2003. Survival of salmonid eggs in a degraded gravel-bed stream: effects of groundwater–surface water interactions. River Research and Applications 19:303–316.

Malcolm, I. A., A. F. Youngson, C. Soulsby, C. Imholt, and R. J. Fryer. 2011. Is interstitial velocity a good predictor of salmonid embryo survival? Transactions of the American Fisheries Society 140:898–904.

Marsden, E., and C. C. Krueger. 1991. Spawning by hatchery-origin Lake Trout (*Salvelinus namaycush*) in Lake Ontario: data from egg collections, substrate analysis, and diver observations. Canadian Journal of Fisheries and Aquatic Sciences 48.

Mason, J. C. 1969. Hypoxial stress prior to emergence and competition among Coho Salmon fry. Journal of the Fisheries Research Board of Canada 26:63–91.

McCullagh, P., and J. A. Nelder. 1989. Generalized linear models, 2nd edition. Chapman and Hall, London.

Montgomery, D. R., J. M. Buffington, P. P. Peterson, D. Schuett-Hames, and T. P. Quinn. 1996. Stream-bed scour, egg burial depths, and the influence of salmonid spawning on bed surface mobility and embryo survival. Canadian Journal of Fisheries and Aquatic Sciences 53:1061–1070.

Mull, K. E., and M. A. Wilzbach. 2007. Selection of spawning sites by Coho Salmon in a northern California stream. North American Journal of Fisheries Management 27:1343–1354.

Olsen, J. C. 1968. Physical environment and egg development in a mainland beach area and an island beach area of Lliamma Lake. Pages 169–198 *in* R. L. Burgner, editor Further studies of Alaska salmon. University of Washington, Seattle.

Pattison, I., D. A. Sear, P. Carling, and A. L. Collins. 2012. Assessing the effect of fine sediment upon salmonid egg incubation using a modelling approach: SIDO-UK. Pages 1–6 *in* BHS Eleventh national symposium: hydrology for a changing world. British Hydrological Society, London.

Pinheiro, J. C., and D. M. Bates. 2000. Mixed-effects models in S and S-PLUS. Springer, New York.

Piper, R. G., I. B. McElwain, L. E. Orme, J. P. McCraren, L. G. Fowler, and J. R. Leonard. 1982. Fish hatchery management. U.S. Fish and Wildlife Service, Washington, D. C.

Reiser, D., and R. G. White. 1988. Effects of two sediment size-classes on survival of steelhead and Chinook Salmon eggs. North American Journal of Fisheries Management 8:432–437.

Rombough, P. J. 2007. Oxygen as a constraining factor in egg size evolution in salmonids. Canadian Journal of Fisheries and Aquatic Sciences 64:692–699.

Rosenberry, D. O., and J. W. LaBaugh. 2008. Field techniques for estimating water fluxes between surface water and ground water. U.S. Geological Survey, Survey Techniques and Methods 4-D2, Reston, Virginia.

Scott, W. B., and E. J. Crossman. 1973. Freshwater fishes of Canada. Fisheries Research Board of Canada Bulletin 184.

Sear, D., and P. DeVries, editors. 2008. Salmonid spawning habitat in rivers: physical controls, biological responses, and approaches to remediation. American Fisheries Society, Symposium 65, Bethesda, Maryland.

Silver, S., C. 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.

Smokorowski, K. E., and T. C. Pratt. 2007. Effect of a change in physical structure and cover on fish and fish habitat in freshwater ecosystems– a review and meta-analysis. Environmental Reviews 15:15–41.

Sowden, T., 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.

Steen, R. P., and T. P. Quinn. 1999. Egg burial depth by Sockeye Salmon (*Oncorhynchus nerka*): implications for survival of embryos and natural selection on female body size. Canadian Journal of Zoology 77:836–841.

Steinhart, G. B., and W. A. Wurtsbaugh. 2003. Winter ecology of kokanee: implications for salmon management. Transactions of the American Fisheries Society 132:1076–1088.

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

Stross, R. D. 1954. A limnological study of Lake Pend Oreille, Idaho, with special consideration of the ecology of the kokanee. Master's thesis. University of Idaho, Moscow.

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.

Tonina, D., and J. M. Buffington. 2007. Hyporheic exchange in gravel bed rivers with pool-riffle morphology: laboratory experiments and three-dimensional modeling. Water Resources Research [online serial] 43:W01421.

Vittinghoff, E., and C. E. McCulloch. 2007. Relaxing the rule of ten events per variable in logistic and Cox regression. American Journal of Epidemiology 165:710–8.

Wahl, N. C., A. M. Dux, W. J. Ament, and W. Harryman. 2011. Lake Pend Oreille fishery recovery project annual progress report: March 1, 2010—February 28, 2011. Idaho Department of Fish and Game, Report 11-22, Boise.

Warton, D. I., and F. K. C. Hui. 2011. The arcsine is asinine: the analysis of proportions in ecology. Ecology 92:3–10.

Waterstrat, P. R. 1997. Distribution and abundance of *Saprolegnia* in the water system of a Chinook Salmon hatchery. Journal of Aquatic Animal Health 9:58–63.

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

Woodey, J. C. 1965. Sockeye Salmon spawning grounds and adult returns in the Lake Washington watershed. Master's thesis. University of Washington, Seattle.

Young, M. K., W. A. Hubert, and T. A. Wesche. 1991. Biases associated with four stream substrate samplers. Canadian Journal of Fisheries and Aquatic Sciences 48:1882–1886.

Youngson, A. F., I. A. Malcolm, J. L. Thorley, P. J. Bacon, and C. Soulsby. 2004. Long-residence groundwater effects on incubating salmonid eggs: low hyporheic oxygen impairs embryo development. Canadian Journal of Fisheries and Aquatic Sciences 61:2278–2287.

Zar, J. H. 2009. Biostatistical analysis, 5th edition. Prentice-Hall, Englewood Cliffs, New Jersey.