Negative influences of predacious egg-eating worms, *Haplotaxis ichthyophagous*, and fine sediments on coho salmon, *Oncorhynchus kisutch*, in natural and artificial redds

by

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ABSTRACT

Measurements of emergence from natural coho salmon redds and field experiments with artificial redds were used to investigate redd production and survival in relation to biotic and abiotic intergravel variables. Coho salmon emerged from 64% of natural redds, number of individuals emerging from 15 trapped redds ranged from 0 to 2,671. Number of fry emerging from trapped redds was negatively related to fine sediments < 3.33 mm (g) and the presence of an egg-eating oligochaete worm, *Haplotaxis ichthyophagous*. Survival of eyed eggs in artificial redds declined over time, and was 70% at hatching and 52% at emergence. Survival to hatching was negatively related to fine sediments < 2.8 mm (g) that intruded into egg containers, and the presence of *H. ichthyophagous.* Worm infestation in egg containers increased over the sampling period, and survival to alevin and emergent fry stages was mostly controlled by presence of worms. Worms invaded all egg containers in some redds, and few to none in other redds. Egg survival in redds with worms averaged 9%, while in redds without worms survival averaged 78%. Fine sediments and worms had a significant negative influence on survival of eggs in redds.

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TABLE OF CONTENTS

Page

TABLE OF CONTENTS (cont'd)

Page

LIST OF TABLES

LIST OF TABLES (cont'd)

LIST OF FIGURES

Figure Page

INTRODUCTION

The negative influence of fine sediments on salmonid survival in natural and artificial redds has been widely reported (Koski 1966, Phillips et al. 1975, Cederholm et al. 1981, Tappel and Bjornn 1983, Tagart 1984, Chapman 1988, Meehan 1991, Weaver and Fraley 1993, Rinne 2001). The amount of fine sediment that enters a stream is attributable to a combination of land use, parent geology, and natural processes. In the stream, fine sediments are subject to transport, deposition, and gravel infiltration processes (Lisle 1989). Fine sediments smaller than pore spaces in redd gravels can intrude into egg pockets and decrease ova and embryo survival by direct asphyxiation. Fine sediments that intrude can also plug interstitial gravel spaces and change the redd environment by decreasing permeability, oxygen availability, and metabolite removal. Fine sediments that are larger than redd gravel pore spaces can lodge and form a seal (Beschta and Jackson 1979, Chapman 1988, Lisle 1989, and Bjornn and Reiser 1991). The seal can prevent further intrusion; however, the seal can also cause fry entrapment and eventual suffocation or starvation in the redd.

Relationships between fine sediments and survival in natural redds are difficult to measure. Female coho salmon may form multiple redds and may also have variable fecundity (Young et al. 1990). Several investigators have attributed weak relationships between redd survival and abiotic redd variables to the technical difficulties associated with locating and sampling egg pockets within redds (Chapman 1988, Meyer 2003); while another group contends the entire redd influences survival (Lisle and Lewis 1992, Weaver and Fraley 1993). In spite of these potential shortcomings, models relating coho salmon survival to fine sediments in natural redds have been constructed in Oregon and Washington (Koski 1966, Tagart 1984).

Controlled experiments have been conducted to reduce the uncertainty associated with egg survival and sediments (Clifford 1940, Coble 1961, Dill and Northcote 1970, Phillips et al. 1975, Cloern 1976, Cederholm et al. 1981, Rinne 2001). However, laboratory studies of egg survival cannot duplicate natural gravel compositions (Lisle 1989) or egg pocket structure (Chapman 1988). Some field studies have also been criticized for not adequately simulating natural egg pocket structure (Chapman 1988). In nature, however, there may be a variety of egg pocket configurations with no standard shape to simulate.

An oligochaete worm can also influence the survival of pre-emergent coho salmon. Described only in a few northern California coastal streams, the aquatic oligochaete worm, *Haplotaxis ichthyophagous*, consumes ova in salmonid redds. This worm can kill eggs with copious mucous secretions, but may have a preference for dying or decomposing ova (Williams 1996). Both natural (Briggs 1953) and artificial redd studies (Williams 1996, Coey 1998, Meyer 2003) have documented high coho salmon egg mortality attributable to *H. ichthyophagous*. Quantifying worms in redds can be difficult because of worm mobility (Briggs 1953, Meyer 2003).

In light of these potential limitations, I chose to study coho salmon egg to emergent fry survival using natural redds and artificial redds. The study was conducted in three streams: Prairie, Streelow, and Boyes Creeks. The three streams have experienced differing amounts of disturbance (e.g. relatively undisturbed, recovering from disturbance and recently disturbed), and therefore have varying habitat quality. The objectives of this study were to:

1. Determine production and survival of coho salmon from eyed egg to emergent fry in redds from three different streams.
2. Identify variables that influence coho salmon production in natural redds and survival in artificial redds.
3. Build models to explain coho salmon production and survival.

SITE DESCRIPTION

The Prairie Creek watershed lies within the Northern California coastal zone in Redwood National and State Parks, Humboldt County, California. Prairie Creek is a coastal stream that drains into Redwood Creek, which empties into the Pacific Ocean near Orick, California. The majority of the Prairie Creek basin is underlain by shallow marine and alluvial sedimentary rocks probably deposited by the ancestral Klamath River. During and after sediment deposition, the basin underwent folding, fracturing, and faulting. The lower portion of the basin consists of shallow marine sands (Gold Bluffs Beach Sands), whereas upper portions consist of coarse alluvial sequences, or Klamath rock (Cashman et al. 1995). The climate of the basin can be characterized as temperate. Annual air temperatures are moderated by proximity to the Pacific Ocean, and average 11 °C. Mean annual precipitation is 172 cm, and falls mostly from late fall through early spring. This precipitation pattern controls the streamflow regime that is low in summer and high in winter. Study areas included the upper 16 km of Prairie Creek, and the lower 2 km in Boyes and Streelow Creeks, which are tributaries to Prairie Creek (Figure 1).

Prairie Creek is a fourth order, low gradient stream (0.0032 m/m) that drains a 34.4 km^2 watershed (Lisle 1989). Mean annual discharge is about 1.49 m^3/s and bank full discharge is 5.6 m^3/s. In November 1998, Prairie Creek experienced a 5 yr flood with discharge reaching 8.8 m^3/s (Klein, Randy 2003, personal communication, Redwood National Park, Arcata, CA. 95521).

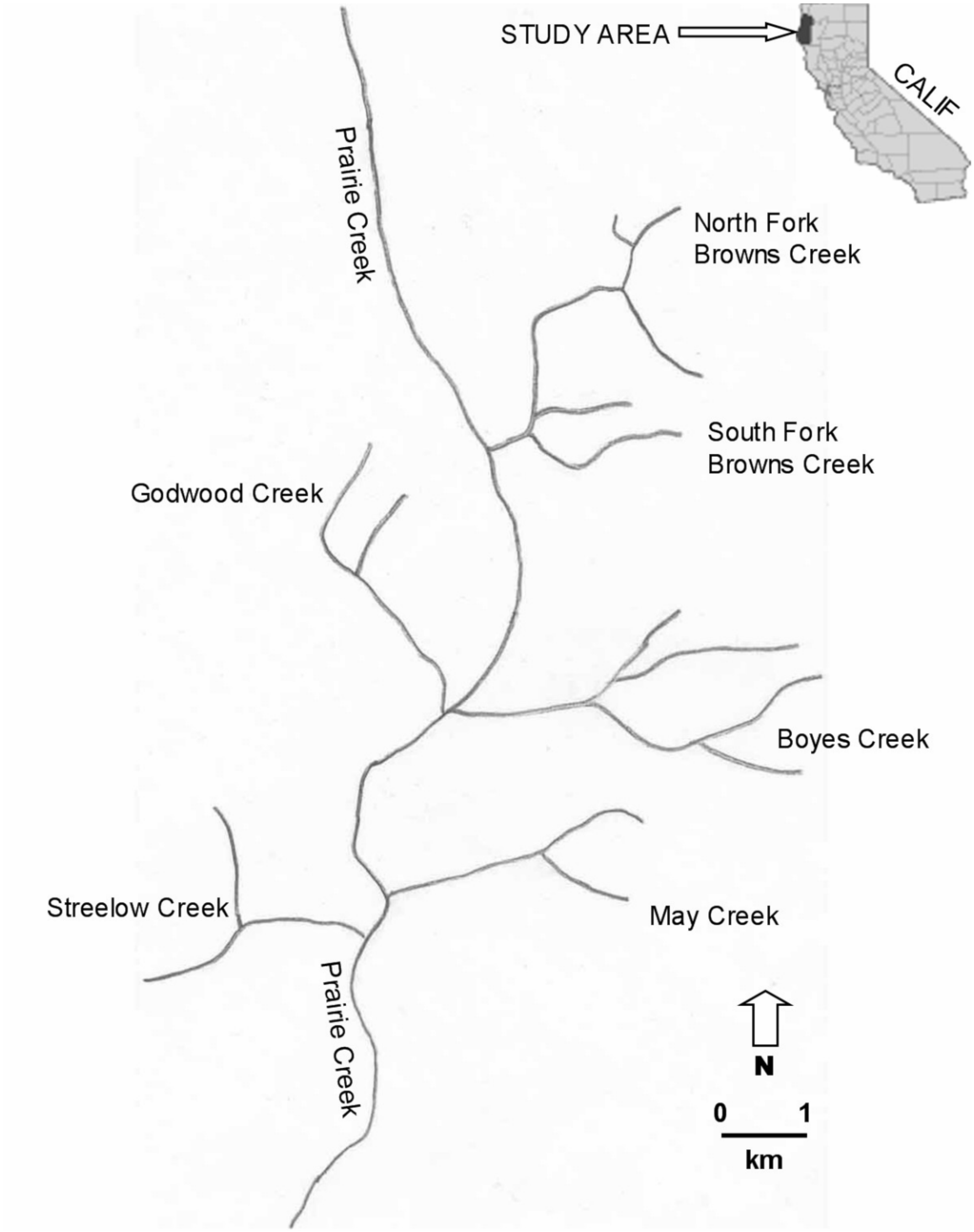

Figure 1. Prairie Creek, Boyes Creek, and Streelow Creek study reaches, Humboldt County, California (map made by William Hendrickson and Michael Sparkman).

The Prairie Creek watershed is forested with old growth redwood (*Sequoia sempervirens*) and Sitka spruce (*Picea sitchensis*), mixed with western hemlock (*Tsuga heterophylla*), bay laurel (*Umbellularia californica*), big leaf maple (*Acer macrophyllum*), and red alder (*Alnus rubra*). Stream substrate within the study area of Prairie Creek consists of well sorted cobbles and gravels.

Streelow Creek is a third order, low gradient stream (0.004 m/m) that drains a 5.7 km^2 watershed. Mean annual discharge is 0.25 m^3/s. Streelow Creek was extensively logged (clear-cut) from the 1950's to the 1960's for old growth redwood, and is considered to be in a recovering state. The watershed is forested with second growth redwood, mixed primarily with red alder. The streambed of Streelow Creek has cobbles mixed with sands.

Boyes Creek is a third order stream with a moderate channel gradient (0.089 m/m) that drains a 4.4 km^2 watershed. The gradient within the study reach is 0.013m/m. Boyes Creek has a mean annual discharge of 0.19 m^3/s. Boyes Creek is considered sediment impaired because of past clear cutting practices, unstable hill slopes, and road construction failure in 1989 which caused several hundred tons of fine sediments to enter the stream. Although the watershed contains some old growth redwood, the dominant age is second growth, mixed with big leaf maple, red alder, bay laurel, and western hemlock. Boyes Creek streambed consists of cobbles mixed with large amounts of fine sediments and silts.

METHODS AND MATERIALS

Spawning Surveys

The Institutional Animal Care and Use protocol (issue date December 1998, permit number 98/99.F.48C) was followed throughout the course of the study.

Adult coho salmon spawning surveys were conducted weekly in designated reaches of Prairie Creek, Boyes Creek, and Streelow Creek (Figure 1). Surveys were conducted from late November through early March in winters of 1998/99 and 1999/00 to measure the distribution of spawning fish. Prairie Creek contained five reaches which averaged 3.5 km in length. Boyes Creek and Streelow Creek were surveyed to stream distances of 2.0 and 2.2 km upstream of their confluence with Prairie Creek. Orange flagging noting stream distances every 100 m in Prairie Creek, and every 50 m in Boyes Creek and Streelow Creek, allowed observations to be referenced to discrete sections. One or two surveyors walked every reach weekly noting and assigning upstream distances (m) to live fish, redds, and carcasses present. Areas upstream of indexed reaches were also checked on occasion. Surveys were not conducted during high flows which muddied the water. Subsequent surveys commenced when the water cleared sufficiently to see fish and redds. Surveys were suspended when no coho salmon carcasses were found for a consecutive two week period.

All live fish observed were visually identified to species (e.g. Chinook salmon, coho salmon, steelhead trout). Sex, condition (e.g. fresh, dark, presence of fungus), and fork length (FL) (cm) were estimated when possible. Location in stream (e.g. pool, run, glide, riffle, riffle crest) and stream distance were also recorded on the field data form.

Coho salmon carcasses were identified to species, and FL, sex, and condition were recorded. The abdomens of female coho salmon carcasses were opened to expose and count any remaining unspawned eggs to give a general idea of egg retention.

I measured maximum length and width of each redd to the nearest decimeter (dm) using a stadia rod. The uppermost edge of digging (uncovered pot) was included in measurements to determine the physical space required for redd construction. The mound and tailspill of coho salmon redds that were candidates for natural fry emergence trapping were also measured for maximum length and width independent of the uncovered upstream pot to compare with fry emergence trap dimensions. All redd measurements were made after redd construction was completed to minimize disturbance to spawning fish, and discriminate true redds from test digs (Briggs 1953). In addition, test redds were considered to have a maximum length less than 1.5 m. Distance from the start of the study reach and location of the redd in the stream channel was recorded. When possible, species and sex of fish on redds were recorded and their size estimated. Fish adjacent to a redd were not considered to be on the redd because earlier surveys had shown that one species may temporarily reside near another species' redd. All redds were marked with florescent orange or pink flagging. The date of redd formation, a redd number, redd length (m) and width (m) were written on the flagging with an indelible marker. If a fish was on redd, the species, sex, and size (FL) were recorded. Flagging was tied to riparian vegetation parallel to the most upstream part of the redd (e.g.

uncovered pot). The location of the flagging and associated information allowed later surveyors to note if the redd had increased in size, or if superimposition by other spawning fish had taken place.

Fry Emergence Trapping

Natural fry emergence trapping and gravel quality indices were used to investigate the relationship between the redd environment and the number of coho salmon fry emerged in 1999. In each stream, coho salmon fry emerging from 5 natural redds were trapped using fry emergence traps. I considered redds suitable for trapping emergent fry if: 1) water depth over redd was less than 1.5 m, 2) the redd was readily distinguished from the surrounding bottom substrates, 3) redd dimensions did not exceed the size of the emergence traps, and 4) no superimposition of redds was apparent.

Fry emergence traps used were modified from Porter (1973) and Field-Dodgson (1983), similar to those used by Tagart (1984). The trap frames, constructed of 1.27 cm steel rod, were tear-drop in shape with a perimeter of 813 cm, total length of 323 cm, maximum width of 208 cm, and a maximum height of 31 cm. Large heavy duty zippers were sewn into the longitudinal midline of the trap netting to allow for standpipe access and determination of redd inflow rate and abiotic measurements over time. Netting was 3 mm aperture on the upstream facing section, and 1 mm aperture to the downstream (cod) end. The netting of the trap was fastened to the steel frame with 45 - 70 cable ties having 18 or 30 lb tensile strength. The trap netting extended beyond the trap frame, and the overhang served as a sub surface gravel apron which prevented fry from escaping laterally beyond the trap perimeter. The trap shape, low height, and method of setting (see below) allowed for continual trapping under relatively high flows.

Fry emergence traps were placed on redds in each stream during March-April 1999, 54 - 70 days after redd formation. Previous studies of coho salmon fry emergence within the Prairie Creek watershed have found 70 - 94 days from redd formation to first emergence, with an average of 85 days (n = 12) (Klatte and Roelofs 1998, Roelofs and Sparkman 1999). Setting the traps within this range of redd ages minimized negative impacts associated with installing the trap, reduced the amount of silt and debris that clogged the netting or settled onto the redd, and also insured that the traps were functioning before fry emerged from the gravel. Traps were placed over the mound (with standpipes installed) and tailspill of the redd to encompass the entire redd. The trap frame, complete with netting, was anchored to the streambed with 7 - 9 hooked rebar stakes that were 1.27 cm in diameter and 61 - 71 cm long. When driving rebar stakes, the hook or bent portion was fastened over the trap frame. A section of rope was tied from the upstream facing trap frame to a nearby tree or metal fencepost to prevent trap loss in high flows. The trap apron was buried to a depth of 15 - 25 cm and held in place with hand sized and larger cobbles to prevent lateral migration of emerging fry beyond the trap perimeter. Burying the trap apron also helped keep the trap secured to the streambed. A soft plastic hollow flex tube with a length of 162 cm attached the tube shaped livebox to the cod end of the trap frame. A cone within the livebox provided an area of reduced velocity, and refugia for captured emergent fry. One mm mesh screens on the sides of the livebox allowed water to exit, and a screw lid on the end was removed to empty the livebox contents. Elevating the cap end of the livebox above the stream greatly reduced turbulence during high flows. A metal fence post was driven alongside the livebox just upstream of the screw cap lid, and rope was fastened from the fence post to the downstream end of the livebox. By changing the attachment point of the rope to the fencepost, the position and angle of the livebox could be adjusted to ensure calm water areas within the livebox during changing stream flows. The time required to set a fry emergence trap ranged from 7 - 12 person hours, and averaged 8.7 person hours.

Fry traps were checked and cleaned every other day until emergence began. Then they were checked daily until no fry were captured for 10 consecutive days (Olson 1996, Klatte and Roelofs 1998, Roelofs and Sparkman 1999). If no fry were collected from a redd, trapping was terminated about 115 days after redd formation by removing the livebox screw cap end. Emergent fry collected in the trap livebox were transferred to 18 L buckets with fresh stream water for identification, counting, and measurements. All captured fry were identified to species, and daily random samples of $\leq$ 25 were measured for fork length ($\pm$ 1 mm) and weight ($\pm$ 0.1 g) using a measuring board and a portable electronic balance (model CT 600 Sz, Ohaus Inc., Pine Brook, New Jersey). Abnormalities in morphology, or presence of alevins were noted. Sub-samples of fry for measurements were anesthetized with tricaine methanesulfonate (MS-222), and after handling and recovery, were released into the stream margin.

Redd inflow rates and other abiotic measurements of the redd environment required semi-permanent standpipes to be placed in each redd of study prior to emergence trapping. Standpipes were modified versions (Mark VI) from Terhune (1958) and Barnard and McBain (1994). Thirty-six standpipes were fabricated from schedule 40 steel plumbers pipe (I.D. 2.54 cm) and cut to lengths of 32 - 45 cm. Pipes were cut in length to fit under the fry emergence trap netting. The lower ends of the standpipes were given 12 grooves 1 mm deep and 1.6 - 2.0 mm wide. Four 3.2 mm holes were drilled per groove, and spaced 19 mm apart. The vertical row of grooves minimized blockage of holes by small particles, and the large number of holes (n = 48) imitated a spherical sink allowing water to freely flow into the standpipe from adjacent substrates (Terhune 1958, Barnard and McBain 1994). Rolled round stock (3.17 cm diameter) was lathed to a point on one end for penetrating the stream substrates, and counter sunk with grooves on the opposite end for insertion into the pipe end with the grooves and holes. Adhesive was used to seal the round stock to pipe junction. Pipes were treated with a rust inhibitor, and then painted with several coats of rust inhibiting spray enamel. Two to three standpipes were driven into the mid line of the natural redd mound 35 - 47 days after redd formation to minimize any negative impacts to the developing embryos (i.e. eyed eggs are less sensitive to shock or disturbances than un-eyed eggs). Pipes were spaced about 0.5 m apart, with two pipes set in small redds, and three set in larger redds. A total of 36 standpipes were used in the study. A one inch steel driving rod was used to create a pilot hole in the redd for the standpipes. As the pilot hole driver was removed, the semi-permanent standpipe was inserted into the same hole. Standpipes were then gently tapped far enough to place the drilled holes 18 - 25 cm deep, which approximated the depth of coho salmon egg pockets (Briggs 1953, Koski 1966). Plastic caps were used to cover the water surface portion of the standpipe when not in use.

Sub-gravel inflow rates (ml/sec) for each natural redd were determined using methods of Klatte and Roelofs (1998), Klein (1999), and Roelofs and Sparkman (1999). Measurements consisted of three trials per pipe per redd every 2 - 4 weeks over the course of eyed egg development through emergent fry using an electric vacuum pump (model 130, Schuco Inc., Carle Place, New York). Measurements were made during varying hydrologic conditions with an aim to describe natural variation, and possible influences upon survival of emerging fry. One person performed the critical aspect of the technique over the course of the study to reduce between-observer variation in measurements (Young and Hubert 1989). A second person recorded data, and turned the pump on and off at specific times. A plastic standpipe extension was first attached to one of the steel standpipes within the redd. A 2.5 cm block of wood with a groove for the vacuum pump tubing was set on top of the plastic standpipe extension. The water surface elevation within the standpipe was found by gently lowering the vacuum pump tubing along the wooden block into the standpipe until a slurping noise was heard. Vise grips were then fastened to the tubing at a point flush with the top of the wood block. The block of wood was then removed, and the tube dropped 2.5 cm beneath the water surface. The vacuum pump then pumped intragravel water into the vacuum pump reservoir with decimeter markings. After the initial 2.5 cm of water was stored in the reservoir, the starting point in dm was recorded, and a stop watch was activated. Water was pumped into the reservoir until at least 1 dm was collected, then the tubing was pulled out of the standpipe at the same time the stop watch was stopped. Inflow rate was determined by subtracting the starting amount of water from the final amount of water, and dividing by time. Inflow rates in dm/s were then converted to volume (ml) by multiplying by 650 ml/dm to give inflow rate in ml/s. Inflow rates were not further converted to permeability (cm/hr) because standpipes were not calibrated to standpipes made by Barnard and McBain (1994) or Terhune (1958). Pipe inflow rate measurements for each redd were then averaged for each sampling date to determine a redd inflow rate. Redd inflow rates for each sampling date were then averaged to determine a redd value that encompassed the period of eyed egg incubation to fry emergence.

Intragravel dissolved oxygen (mg/l), specific conductance (µS/cm), and temperature (°C) were determined electrometrically (YSI Environmental Inc., Model Numbers 55 and 30, Yellow Springs, OH) every 2 - 4 weeks in each standpipe at a gravel depth of 18 - 25 cm. The removable plastic extension to the standpipe prevented direct mixing of stream water with intragravel water. Abiotic measurements for each sampling date were averaged to determine a redd value. Redd values per sample time were then averaged to determine a redd value that encompassed the entire period of measurements.

Stream values of the above parameters were also determined using hand held instruments. Stream specific conductance (µS/cm) was taken to compare with redd specific conductance to detect possible upwelling within redds. Continual stream temperature of each stream was determined using Optic temperature data loggers (Onset Computer Inc., Bourne, MA). Emergence could then be to be correlated with temperature units.

Redd gravel collection began after 10 d of zero catches in fry emergence traps, during a low stream flow. Methods were similar to previous substrate studies from 1996

- 1998 in Prairie Creek (Klatte and Roelofs 1998, Roelofs and Sparkman 1999), and included weight determination (g) and volume displacement (ml). A 30 cm wide hollow core grab sampler was used to collect redd substrates around each standpipe to a depth of 25 cm. This was sufficient to characterize the redd and egg pocket environment (Shirazi et al. 1979). Briggs (1953) found that coho salmon average egg depth was 25 cm in Prairie Creek. Samples were adequate for determining particle size distribution and averaged 49 kg, and ranged from 41 to 57 kg. Redd gravel samples (includes all standpipe samples within a given redd) averaged 126 kg, and ranged from 88 to 161 kg. A total of 1,765 kg of gravels and fine sediments were collected from 15 redds. After substrate collection, samples of suspended sediments within the gravel cavity were taken by stirring the water within the core sampler, and immersing a 1200 ml container into the core water column.

Redd substrates were sieved through geometrically decreasing stainless steel sieve sizes of 128, 64, 32, 16, 8, 4, 2.0, 1.0, 0.50, 0.25, 0.125, 0.0625 mm, and pan (< 0.0625 mm), with an additional sieve size of 0.85 mm inserted into the series. Particles $\geq$ 16 mm were wet sieved by hand, briefly drained and then weighed wet. Volume was determined for each particle size class by displacement (ml) in the field. The remainder of grab sample substrates (i.e. < 16 mm) was brought to Redwood National Park Southern Operations Center Sediment Laboratory in Orick, California, for further analysis. In the laboratory, particles $\geq$ 4 mm and < 16 mm were wet sieved, weighed (g), and volume determined by displacement (ml) for each particle size class. Particles < 4 mm were oven dried at 60 - 80 °C for 48 - 72 hrs, depending upon the amount of water present. After drying, the total sediment weight of particles < 4 mm was recorded. Sediments < 4 mm were then split four to six times using a Scientific Instruments Testing Equipment Laboratory Apparatus (Humboldt Mfg. Co., Norridge, IL.) to obtain representative sub-samples. Sub-samples were split to dry weights of 316.5 to 1,104.2 g, which allowed for proper sieving. Smaller amounts may not sieve correctly because of the number of sieves (< 4 mm) involved (n = 8, including the pan). Gravel sub-samples were mechanically shaken through sieves (e.g. < 4mm to pan) using a Central Scientific Sieve Shaker (Catalog #18480, Central Scientific Co., Inc., Chicago, IL.) for 5 - 6 minutes at 3.5 cycles per second. Sediments in each sieve fraction were then weighed (± 0.1 g) on an Ohaus CT 600-Sz portable electronic balance, and poured into a 250 ml graduated cylinder filled with sufficient water for volume displacement. Weight and volume displacement for each particle size class were highly correlated ($r = 0.99$, $p < 0.001$), therefore, cumulative percentage of fine sediments was expressed by weight. The sub-sample dry weight per sieve (e.g. > 2, > 1, > 0.85 mm, etc.) was expressed as a fraction of the total sub-sample weight. Fractions were then multiplied by the total dry weight < 4 mm to estimate the sample dry weight per sieve size for particles < 4 mm. Samples of the suspended sediments were oven dried at 60 - 80 °C for 8 - 12 hours. Dried sediments were weighed, and volume determined using volume displacement. The dry weight was then expressed as a fraction of the original sample volume, and multiplied by the core volume to estimate the suspended sediment component for the core sample. The estimated weight was then added to the extrapolated weight of the pan.

Sediment particle size distribution and gravel indices (e.g. cumulative percentage of fine sediments < 3.33 mm, geometric mean particle diameter [Dg] in mm) from samples were determined using methods described by Platts et al. (1983) and Shirazi et al. (1979). The values were calculated using custom software GRAVEL$^©$ (Goforth 1992, Klein 1999). GRAVEL$^©$ uses the 'method of moments' for calculating Dg, and expresses percent fine sediments on a cumulative basis by weight or volume. GRAVEL$^©$ was used to characterize the entire redd by pooling samples.

The response, or dependent variable in the natural redd study was the log (x+1) transformation of the number of coho salmon emergent fry captured (redd production) per fry emergence trap. Log (x+1) was used to transform the data to approximate normality. Data were not expressed as percent survival because the number of eggs deposited in any given redd was unknown. The original redd sample size of 15 was reduced to 14 because high flows scoured one of the coho salmon redds in Streelow Creek. *A priori* considerations were used for independent variable selection. Inflow rate, dissolved oxygen concentration, cumulative percentage of fine sediments < 3.33 mm in diameter, worm presence, and geometric mean particle diameter were chosen as independent variables. Evidence of worm presence consisted of worm capture or collection of eggs with observable puncture holes during periods of abiotic redd measurements and gravel extraction. The independent variable, worms (*Haplotaxis ichthyophagous*), was treated as a dummy variable and coded 0 for worm absence, and 1 for worm presence (Zar 1999). All possible subsets of independent variables were used in model selection, except for variables where significant correlations existed.

Independent variables showing strong correlations (e.g. $P < 0.05$) were not included in multiple regression models together (e.g. inflow rate and dissolved oxygen concentration, geometric mean particle diameter and cumulative percentage of fine sediments < 3.33). Using this rationale, I included dissolved oxygen concentration and cumulative percentage of fine sediments < 3.33 in analyses and omitted inflow rate and geometric mean particle diameter because dissolved oxygen concentration and fine sediments < 3.33 were considered more important for fish survival. No correlation between worm presence or absence and fine sediments < 3.33 mm was detected. The number of regression models used in statistical analysis was limited to fourteen to reduce the risk of overfitting statistical models to a relatively small number of observations (e.g. Harvey et al. 2002). I used Akaike's Information Criterion (AIC_c) adjusted for small sample sizes, and estimates of posterior relative probabilities for each model to evaluate alternative models (Burnham and Anderson 1998). AIC_c is an information-theory-based approach for estimating the fit between candidate models and data. AIC_c allows the investigator to identify the model that minimizes information loss, and properly separates noise from structural information. Posterior relative probabilities, defined as the relative likelihood of model i versus model j, further determined which model was favored over other models using 'weight of evidence' expressed as probabilities. Finally, the probability of a particular independent variable being included in the best fitting model was determined by summing the probabilities of all candidate models that included that particular independent variable (Burnham and Anderson 1998).

Artificial Redds

Artificial redds were constructed and planted with eyed coho salmon eggs to estimate survival at three important life history stages (hatching, alevin, and emergent fry), and to determine specific relations of average egg container survival with average abiotic and biotic (worms) redd variables. In each stream, five artificial redds were dug with a McLeod shovel on 25 - 26 January, 2000. Redds were randomly located in likely coho salmon spawning areas across environmental gradients (e.g. inflow rates, sediment particle sizes) based upon natural redds, and built to reflect the size and shape of natural redds. The length, width, and depth of fifteen artificial redds averaged 2.25 x 0.95 x 0.25 m. As cobbles and gravels were removed and placed around the redd cavity, the stream current winnowed fine sediments downstream. Two permeability standpipes were placed in each redd, one 30 cm upstream of the first two egg containers (#1 and 2), and the other 30 cm downstream of the last two egg containers (#5 and 6). The pipes were placed far enough from the egg containers to minimize gravel disturbances while sampling any of the egg containers. The standpipes were set such that the holes ranged from 18 - 25 cm deep when covered with gravels.

Coho salmon eyed eggs from the California Department of Fish and Game Trinity River Hatchery were used in the experiment because the low number of returning adult wild coho salmon within the Prairie Creek watershed prohibited using their eggs. Trinity River Hatchery coho salmon are also within the same evolutionarily significant unit (ESU) as Prairie Creek stock (Southern Oregon/Northern California), and were certified as disease free by a California Department of Fish and Game fish pathologist. On 26

January 2000, 5,000 eyed eggs from the Trinity River Hatchery were placed in damp burlap bags and covered with crushed ice for delivery to the coastal streams. A total of 4,500 eyed coho salmon eggs were used in the experiment. A random sub-sample of 50 of the remaining 500 eggs were measured for diameter (mm) with a Vernier caliper (Mitutoyo CNR 91-008, PR 91-106, Aurora, IL) to the nearest 0.01 mm. Egg diameter averaged 7.17 mm (S.D. 0.23) and ranged from 6.72 - 7.82 mm. Eggs were then placed in a graduated cylinder pre-filled with water to determine volume displacement (ml). A second trial was conducted using another 50 randomly chosen eyed eggs. Both trials determined the volume displacement to be 12 ml's. Fifty eyed eggs were placed in each egg container, and a total of 90 egg containers were used in the experiment. Egg containers were made of styrene, which is similar to polyvinyl chloride (PVC), and were cylindrical in shape. Components to the egg containers included a screw in lid which had a set screw to insure that the lid did not loosen, a cylinder or body, and a bottom cap that was glued to the cylinder. Each egg container had 104 - 2.8 mm diameter holes drilled to ensure adequate water passage (Table 1).

Table 1. Dimensions for artificial redd egg containers used to estimate coho salmon survival at three early life history stages.

Diameter	78 mm
Height	95 mm
Volume	420 ml
Thickness of material	4 mm
No. of holes in screw lid	15
No. of holes in cylinder	75
No. of holes in bottom cap	14
Total No. of holes	104
Hole Diameter	2.8 mm

Six egg containers were placed in each redd in three pairs placed 0.3 m apart along the midline of the redd. Distances between paired egg pockets were great enough to minimize disturbance of gravels surrounding other egg containers during removal. Replicate containers were located laterally 8 cm apart. After the standpipes were set into position, egg containers were buried at a depth of 25 cm by pulling the previously removed and cleaned cobbles/gravels into the redd cavity with the McLeod shovel. Any remaining fine sediments were once again winnowed away, similar to the action of spawning salmon. Substrates immediately upstream of the completed artificial redds were removed to form the uppermost pot and mimic the natural redd form. Cords with labels on the end above the stream substrates were attached to each egg container before burial to aid in identifying and pulling the correct randomly selected egg container from the redd.

One - 2 days prior to pulling the egg containers, inflow rates (ml/sec) and abiotic measurements of dissolved oxygen concentration (mg/l), specific conductance (µS/cm), and temperature (°C) for each redd were determined using methods used in natural redds. Similar to the natural redd study, pipe measurements were averaged to give redd values. Stream dissolved oxygen concentration, specific conductance, and temperature were measured using the same methods. Stream specific conductance was measured to detect possible upwelling within redds**.** Stream temperatures (°C) were determined using Hobo temperature data loggers (Hobo Inc., Pocasse, MA), and allowed developmental stages to be correlated with temperature units. Unfortunately, temperature probes in Streelow Creek were dislodged during storms and lost.

Paired egg containers were randomly drawn without replacement for removal and counting of dead and surviving eggs, eleutheroembryos, alevins, and emergent fry at time intervals based upon egg ages of 55, 71, and 90 - 92 days. The time intervals corresponded to the hatching stage, the alevin stage, and the emergent fry stage, respectively. The hatching stage included eggs that were in a pre-hatch and post hatch (eleutheroembryo) stage. Each egg container was excavated and lifted from the redd substrate, and immediately placed in a 5 gallon bucket to prevent the escape of water and sediments. Egg container water and fine sediments < 2.8 mm that intruded into egg containers were then placed in individual containers for further analysis.

Eggs were considered dead if eye pigments (black and gold) were missing, or if the egg appeared opaque (Ramsden, Gary 1999, personal communication, Trinity River Hatchery, Lewiston, CA. 96052). Eluetheroembryos, alevins, and emergent fry were considered dead if they appeared opaque, not breathing, nor moving when placed in a small dish of water. The paired, egg container survival data were averaged to determine an average percentage of survival in egg containers. After collecting survival data, remaining eggs, eleutheroembryos, and fry were euthanized in a solution of 500 mg MS-222/L, and transported to the California Cooperative Fisheries Research Unit Laboratory for further analysis. Predacious oligochaete worms (*H. ichthyophagous*) were also counted and collected if present.

In the laboratory, 10 randomly drawn sub-samples of coho salmon eleutheroembryos, alevins, and emergent fry were taken from each egg container. Eleutheroembryos were measured for total length (mm), and alevins and emergent fry were measured for fork length (mm) using a Vernier Caliper to the nearest 0.01 mm. Larval and emergent fish were then patted dry and weighed on an analytical balance (model A5200, Ohaus Inc., Pine Brook, NJ) to the nearest 0.0001 g. Fine sediments that intruded into the egg containers were oven dried (oven model 17, Precision Scientific Co., Chicago, IL) at 60 - 80 °C for 8 - 10 hours, and weighed on an analytical balance to the nearest 0.0001 g. The amount of fine sediments in paired egg containers was then averaged for statistical analyses.

The dependent variable in the artificial redd study was the average egg survival in two containers retrieved from each redd each sampling date. Sample size at each sample period equaled 15. *A priori*, I determined that inflow rate, dissolved oxygen, fine sediments (< 2.8 mm), and worm presence were likely to be the most influential independent variables. No correlation between worm presence or absence, and the amount of fine sediments < 2.8 mm was detected. The independent variable predacious worms was once again treated as a dummy variable and coded 0 for worm absence, and 1 for worm presence. Multiple regression was used to identify significant relations of abiotic and biotic independent variables with survival. All possible subsets of independent variables were used in model selection. The number of regression models used in statistical analysis was limited to 15 to reduce the risk of overfitting statistical models to a relatively small number of observations. AIC_c adjusted for small sample sizes, estimates of posterior relative probabilities for each model, and the probability that the best fitting model contained a particular independent variable were once again used for model evaluation (Burnham and Anderson 1998).

RESULTS

Spawning Surveys 1998/99 and 1999/00

Coho salmon were present from December 1998 - February 1999, and from December 1999 - January 2000. Spawning occurred from mid December through January in both study years, however one coho salmon redd was also made in each stream during February 1999. Coho salmon spawning peaked in mid to late January. The average size of coho salmon redds was 6.1 m^2 (n = 19; S.D. 3.2) in 1998/99 and 11.9 m^2 (n = 8; S.D. 4.3) in 1999/00. One female coho salmon carcass found in Prairie Creek contained 650 eggs in the 1998/99 spawning survey.

Fry Emergence from Natural Redds

Coho salmon emerged from nine of 15 redds sampled for emergent fry (Table 2). The majority of coho salmon were emergent fry (99.8%), and the remaining 0.2% were alevins. Emergent fry trap catches ranged from 0 - 2,671 individuals, and totaled 9,987. Average emergent fry production per redd was 908 (S.D. 517) in Prairie Creek, 130 (S.D. 292) in Boyes Creek, and 959 (S.D. 1322) in Streelow Creek. Two redds in Streelow Creek contained *H. ichthyophagous*, and catches of emergent fry in each were less than 14 individuals.

Table 2. Coho salmon fry emergence from natural redds (calendar days in parentheses) in three northern California streams during 1999.

Stream/ Redd #	Redd Formation	Number of emergent fry	Temperature Units (Calendar Days) to First Emergence	Peak Emergence	50% Emergence	90% Emergence	Period of Emergence (days)
PCR1	1/25/99	1772	711 (91)	711 (91)	734 (94)	776 (99)	37
PCR2	1/25/99	996	711 (91)	767 (98)	793 (101)	815 (105)	29
PCR3	1/25/99	650	570 (74)*	872 (116)	872 (116)	880 (117)	54
PCR4	1/25/99	623	703 (90)	727 (93)	727 (93)	767 (98)	38
PCR5	1/16/99	498	702 (90)	737 (93)	737 (94)	780 (99)	22
BCR1	2/02/99	0	-	-	-	-	-
BCR2	1/27/99	652	682 (82)	749 (89)	783 (93)	877 (106)	57
BCR3	1/27/99	0	-	-	-	-	-
BCR4	1/29/99	0	-	-	-	-	-
BCR5	1/29/99	0	-	-	-	-	-
SCR1	1/23/99	2112	697 (86)	697 (86)	716 (88)	784 (96)	30
SCR2**	1/23/99	0	-	-	-	-	-
SCR3***	1/27/99	13	752 (88)	-	-	-	3
SCR4***	1/27/99	0	-	-	-	-	-
SCR5	2/17/99	2671	733 (89)	779 (94)	779 (94)	798 (96)	45

(PCR = Prairie Creek Redd; BCR = Boyes Creek Redd; SCR = Streelow Creek Redd)

* Early emergence of alevins.

** Streelow Creek redd #2 was scoured from high flows prior to trap placement.

*** Presence of oligochaete worm, *Haplotaxis ichthyophagous*.

Three patterns of emergence from natural redds were identified by catch distributions: normal (Figure 2), skewed to left (Figure 3), and bi-modal (Figure 4). Three of 15 coho salmon redds sampled (Prairie Creek redd #2 and redd #5, Streelow Creek redd #1) were superimposed on Chinook salmon redds, with Chinook salmon emergent fry catches equaling 2489, 1226, and 36. Coho salmon emergent fry fork lengths averaged 37.2 mm (S.D. 1.1) in Prairie Creek, 37.1 mm (S.D. 1.6) in Boyes Creek, and 36.8 mm (S.D. 0.6) in Streelow Creek. The average emergent fry fork length for Boyes Creek redds (n = 1) was considered unreliable because fry were observed under the trap netting for several days, and may have grown in the trap prior to capture. (Average fork lengths of coho salmon emergent fry are presented in Appendix A).

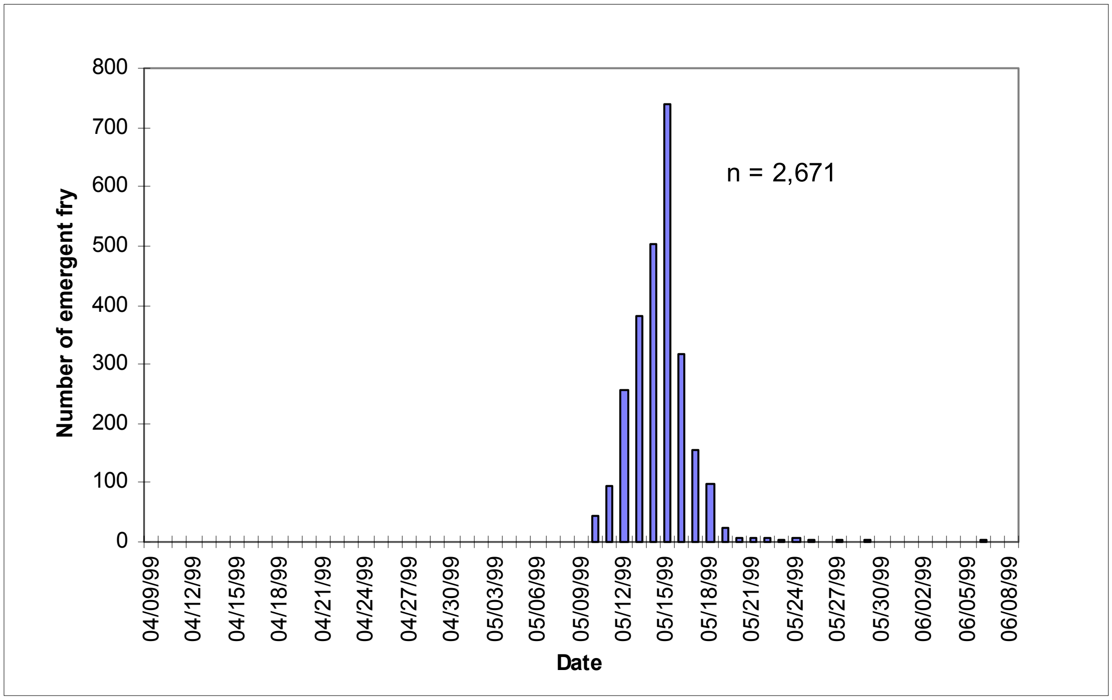

Figure 2. Coho salmon fry emergence pattern in redd #5, Streelow Creek, Humboldt County, California, 1999.

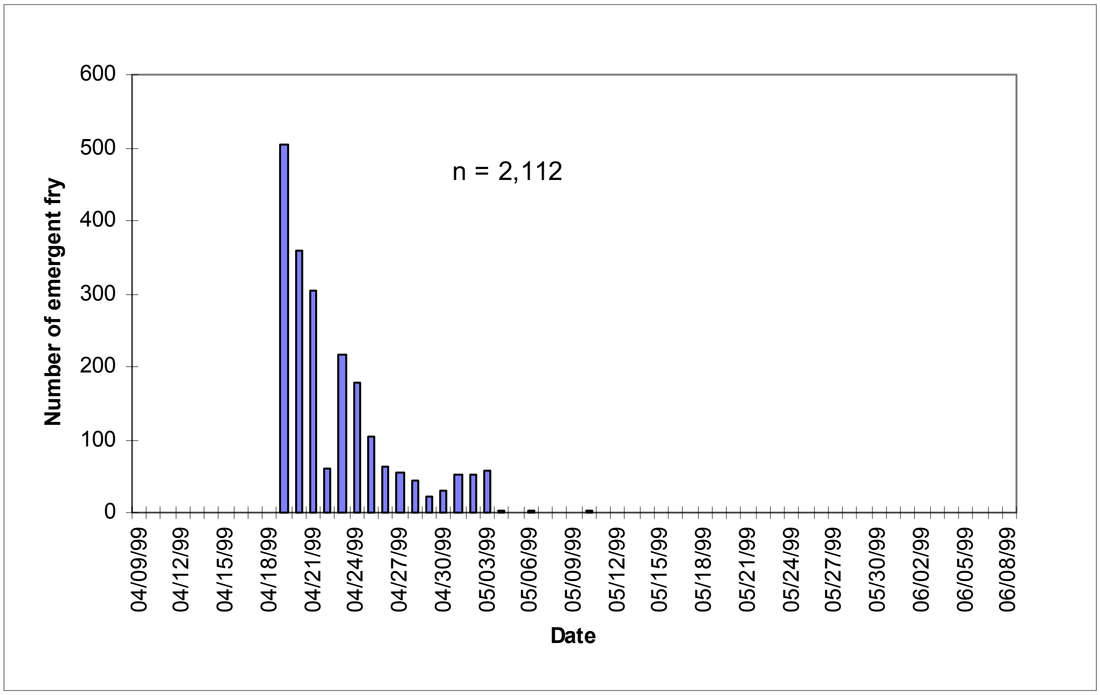

Figure 3. Coho salmon fry emergence pattern in redd #1, Streelow Creek, Humboldt County, California, 1999.

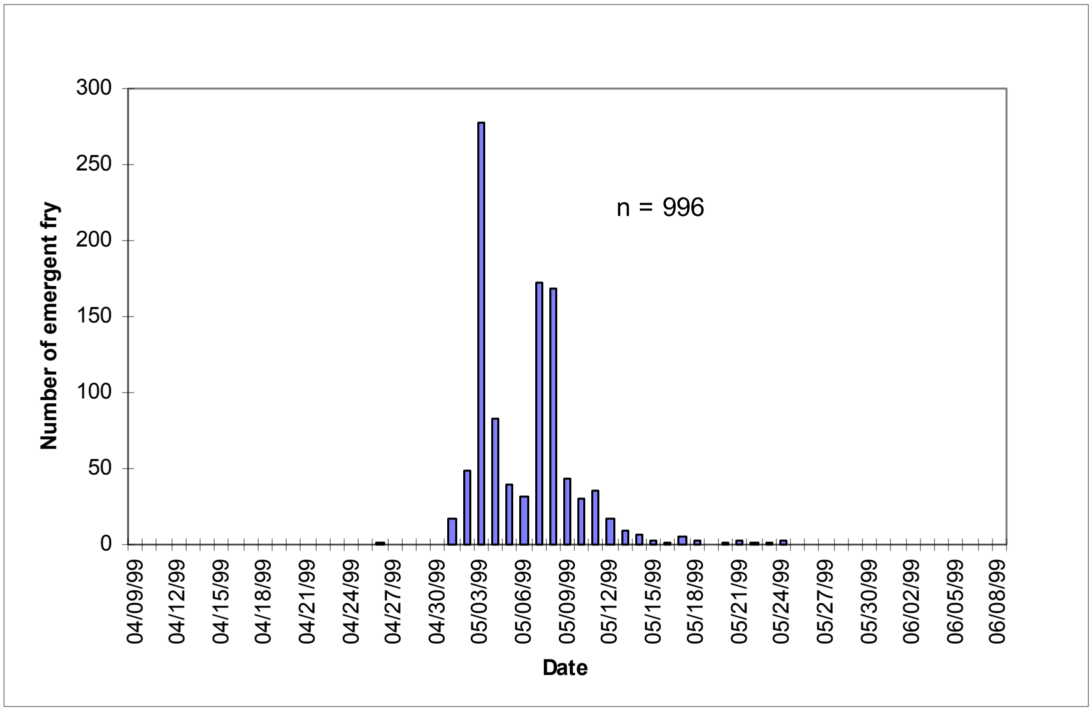

Figure 4. Coho salmon fry emergence pattern in redd #2, Prairie Creek, Humboldt County, California, 1999.

Analysis of emergence from natural redds

The best-fitting model for fry emergence contained two parameters, fine sediments < 3.33 mm and worm presence or absence:

(1) y = 5.729 - 2.218*worm presence or absence - 0.1662*<3.33 mm (g)

The model explained 41% of the variation in emergent fry catches. Models containing geometric mean particle diameter (Dg), fine sediments < 3.33 mm, and worm presence or absence and geometric mean particle diameter (Dg) also had considerable support (Table 3) (Burnham and Anderson 1998). The cumulative posterior probability that the actual best-fitting model included the cumulative percentage of fine sediments

< 3.33 mm and the presence or absence of worms was higher than for other variables (Table 4). (The cumulative percentage of fine sediments < 3.33 mm in each redd are presented in table format, Appendix B). Temperature and specific conductance among redds and stream water were nearly uniform, and demonstrated the lack of upwelling within redds (Appendix C).

Table 3. Models of transformed emergent fry catches in three streams in Humboldt County, California, 1999 using four physical variables and one biotic variable. Listed are the models used to test for best fit, as measured by the Akaike's information criterion (AIC_c). The symbol Δi indicates the difference in the AIC value of a given model and that of the best-fitting model. The plus and minus symbols indicate the influence of the physical or biotic variable on the number of emergent fry captures.

Independent variable(s)	Δi	p value	Adj. r^2 or r^2
Worms (-), < 3.33 (-)	0.00	0.021	0.41
Dg (+)	1.88	0.074	0.24
< 3.33 (-)	1.96	0.077	0.24
Worms (-), Dg (+)	2.38	0.054	0.30
Worms (-)	3.94	0.221	0.12
DO (+)	4.15	0.250	0.11
Worms (-), IR (-), < 3.33 (-)	4.96	0.060	0.36
Worms (-), DO (-), <3.33 (-)	5.02	0.062	0.36
IR (+)	5.68	0.795	0.01
DO (+), < 3.33 (-)	5.75	0.203	0.12
IR (+), Dg (+)	5.84	0.210	0.11
IR (-), < 3.33 (-)	6.00	0.224	0.10
Worms (-), DO (+)	6.56	0.278	0.06
Worms (-), IR (+)	7.92	0.477	0.00

Table 4. Summary of analyses by 14 models that were conducted to explain the variation in the number of emergent fry catches (transformed) in Prairie Creek, Boyes Creek, and Streelow Creek, Humboldt County, California, 1999.

Variable	Cumulative Probability
Worms	0.600
< 3.33	0.593
Dg	0.270
DO	0.108
Inflow rate	0.077

(< 3.33 = cumulative percentage of fine sediments < 3.33 mm in redds; Worms = worm presence or absence; DO = dissolved oxygen in mg/l; Dg = geometric mean particle diameter in mm; Inflow rate = average redd inflow rate in ml/sec)

Artificial Redd Experiments

Average percentage survival of coho salmon was 70% from eyed egg to hatching, 61% from eyed egg to alevin, and 52% from eyed egg to emergent fry (Table 5). Worm presence was lowest at the hatching stage, and increased with time. Temperature and specific conductance were similar in both redds (Appendix D) and stream water (Appendix E) during all sampling periods, suggesting a lack of upwelling within redds.

Table 5. Coho salmon artificial redd survival data (standard deviation in parentheses) in Prairie Creek, Boyes Creek, and Streelow Creek, Humboldt County, California, 2000.

Stream	Redd No.	Percent survival to Hatching	Alevin	Emergent fry
Prairie Creek	1	67 (1.4)	52 (2.8)	55 (35.4)
Prairie Creek	2	96 (5.7)	91 (9.9)	92 (2.8)
Prairie Creek	3	84 (2.8)	86 (11.3)	93 (9.9)
Prairie Creek	4	95 (1.4)	87 (12.7)	52 (2.8)
Prairie Creek	5	96 (0.0)	99 (1.4)	95 (1.4)
Boyes Creek	1	54 (25.5)	53 (55.1)	89 (7.1)
Boyes Creek	2	53 (18.4)	83 (12.7)	0 (0.0)a
Boyes Creek	3	43 (7.1)	22 (2.8)a	17 (21.2)a
Boyes Creek	4	42 (0.0)	72 (0.0)	40 (17.0)a
Boyes Creek	5	65 (7.1)	83 (4.2)	67 (41.0)
Streelow Creek	1	94 (2.8)	82 (19.8)	90 (5.7)
Streelow Creek	2	69 (38.2)	16 (22.6)a	0 (0.0)a
Streelow Creek	3	0 (0.0)a	0 (0.0)a	0 (0.0)a
Streelow Creek	4	93 (1.4)	89 (1.4)	84 (8.5)
Streelow Creek	5	94 (5.7)	0 (0.0)a	0 (0.0)a
Average:		70 (27.8)	61 (35.0)	52 (39.1)

a denotes worm presence

Survival to Hatching

The best model describing the variability in coho salmon survival from eyed egg to hatching contained two parameters, presence or absence of predacious egg-eating worms (*H. ichthyophagous*) and the amount of fine sediments < 2.8 mm that intruded into egg containers:

(2) $y = 0.9159 - 0.8079*\text{worm presence or absence} - 0.01057*<2.8\text{ mm (g)}$

The model explained 64% of the variation in coho salmon survival from eyed egg to hatching. Models with Δ*i* values greater than 3.0 had considerably less support in explaining the variation in survival from eyed egg to hatching (Table 6) (Burnham and Anderson 1998). The cumulative posterior probability that the actual best-fitting model included the presence or absence of worms and the amount of fine sediments < 2.8 mm was much higher than for other variables (Table 7). (Average amount of fine sediments < 2.8 mm that intruded into egg containers for three life history stages are presented in table format, Appendix F).

Table 6. Models of coho salmon survival from eyed egg to hatching in three streams in Humboldt County, California, 2000 using three physical variables and one biotic variable. Table headings are the same as in Table 3.

Independent variable(s)	Δ*i*	p value	Adj. r^2 or r^2
Worms (-), < 2.8 (-)	0.00	0.001	0.65
Worms (-), < 2.8 (-), DO (+)	3.25	0.002	0.64
Worms (-), DO (+)	3.88	0.004	0.54
Worms (-)	4.08	0.004	0.48
Worms (-), < 2.8 (-), IR (-)	4.23	0.003	0.62
Worms (-), IR (+)	6.90	0.013	0.43
Worms (-), IR (-), < 2.8 (-), DO (+)	7.66	0.005	0.64
Worms (-), DO (+), IR (+)	8.54	0.014	0.49
< 2.8 (-)	11.63	0.171	0.14
DO (+)	13.48	0.567	0.03
IR (+)	13.66	0.672	0.01
IR (-), < 2.8 (-)	15.22	0.371	0.01
< 2.8 (-), DO (-)	15.44	0.406	0.00
IR (+), DO (+)	17.27	0.844	0.00
IR (-), < 2.8 (-), DO (+)	19.86	0.591	0.00

Table 7. Summary of analyses by 15 models that were conducted to explain the variation in coho salmon hatching survival in Prairie Creek, Boyes Creek, and Streelow Creek, Humboldt County, California, 2000.

Variable	Cumulative Probability
Worms	0.99
< 2.8	0.81
DO	0.23
IR	0.11

(Worms = worm presence or absence; < 2.8 = fine sediments < 2.8 mm that intruded into egg containers; DO = dissolved oxygen in mg/l; IR = average redd inflow rate in ml/sec)

Predacious worms were found in 1 out of 15 redds sampled during the hatching stage. In the laboratory, 462 and 684 worms were counted in each egg container for Streelow Creek redd #3. The worms were long and thin, and pinkish to opaque in color. The worms clumped together, and excreted copious amounts of mucous. Total length of 20 specimens ranged from 46 - 330 mm and averaged 245.3 mm (S.D. 74.4). Weight ranged from 0.03 - 0.63 g, and averaged 0.42 g (S.D. 0.15). Orange egg matter was observed through the faint skin of numerous individuals, and offered strong evidence that the worms were indeed predators at the eyed egg to hatching and eleutheroembryo stage. Ingested egg matter was 1 - 13 mm long, and located primarily in distal segments of the worms. No eggs survived in the artificial redd with worms, while 75% (S.D. 20.8) of eggs survived in redds without worms.

Survival to Alevin

The best model describing the variability in coho salmon survival from eyed egg to alevin contained only one parameter, worm presence or absence:

(3) $y = 0.797 - 0.7022 *$worm presence or absence

The model explained 85% of the variation in coho salmon survival from eyed egg to alevin. However, the model containing worm presence or absence and average redd inflow rate (ml/sec) had a Δi of < 3.0, indicating it had some support (Table 8) (Burnham and Anderson 1998). The cumulative posterior probability that worms were the most important variable was readily apparent (Table 9).

Table 8. Models of coho salmon survival from eyed egg to alevin in three streams in Humboldt County, California, 2000 using three physical variables and one biotic variable. Table headings are the same as in table 3.

Independent variable(s)	Δi	p value	Adj. r^2 or r^2
Worms (-)	0.00	0.001	0.85
Worms (-), IR (-)	2.47	0.001	0.84
Worms (-), < 2.8 (+)	3.09	0.001	0.83
Worms (-), DO (+)	3.76	0.001	0.82
Worms (-), IR (-), DO (+)	5.27	0.001	0.84
Worms (-), IR (-), < 2.8 (+)	6.86	0.001	0.82
Worms (-), < 2.8 (+), DO (+)	7.28	0.001	0.82
Worms (-), IR (-), < 2.8 (+), DO (+)	9.95	0.001	0.84
< 2.8 (-)	24.03	0.065	0.24
DO (+)	26.27	0.216	0.11
IR (-), < 2.8 (-)	27.54	0.174	0.13
< 2.8 (-), DO (+)	27.68	0.183	0.12
IR (+)	28.04	0.819	0.00
DO (+), IR (-)	29.29	0.349	0.02
IR (-), < 2.8 (-), DO (+)	31.31	0.258	0.10

Table 9. Summary of analyses by 15 models that were conducted to explain the variation in coho salmon alevin survival in Prairie Creek, Boyes Creek, and Streelow Creek, Humboldt County, California, 2000.

Variable	Cumulative Probability
Worms	1.00
IR	0.22
< 2.8	0.16
DO	0.14

(Variable definitions are the same as in table 7)

The percentage of redds with worms at the alevin stage was greater than the percentage of redds with worms at the hatching stage. Four out of 15 redds contained worms at the alevin stage, however, the number of worms counted was markedly less than at the hatching stage. The range in counts of worms at the alevin stage was one to nine individuals. Streelow Creek redd #3, which had 1,146 worms at the hatching stage, contained only one worm at the alevin stage. Other evidence of worm presence included clear egg shells with observable puncture holes that were about 2 mm in diameter. Survival to alevin stage in redds with worms averaged 9.5% (S.D. 11.2), compared with 79.7% (S.D. 15.0) in redds without worms. The most dramatic decrease in survival occurred in Streelow Creek redd #5, where eyed egg to hatching survival with no worm presence was 94%, and eyed egg to alevin survival was 0% when worms were present.

Survival to Emergent Fry

The variation in coho salmon survival from eyed egg to emergent fry was also explained very well by the presence of worms:

(4) y = 0.7967 - 0.7017*worm presence or absence

The presence or absence of worms explained 83% of the variation in emergent fry survival. (Table 10). Models with Δi values greater than 3.0 were considered to have less support in explaining the variation in survival from eyed egg to emergent fry (Table 10) (Burnham and Anderson 1998). The cumulative posterior probability that worms were the most important variable was easily detected (Table 11).

Table 10. Models of coho salmon survival from eyed egg to emergent fry in three streams in Humboldt County, California, 2000 using three physical variables and one biotic variable. Table headings are the same as in table 3.

Independent variable(s)	Δi	p value	Adj. r^2 or r^2
Worms (-)	0.00	0.001	0.83
Worms (-), IR (-)	3.57	0.001	0.80
Worms (-), DO (+)	3.81	0.001	0.80
Worms (-), < 2.8 (-)	3.82	0.001	0.80
Worms (-), IR (-), DO (+)	8.15	0.001	0.79
Worms (-), IR (-), < 2.8 (-)	8.20	0.001	0.79
Worms (-), < 2.8 (-), DO (+)	8.47	0.001	0.78
Worms (-), IR (-), < 2.8 (-), DO (+)	13.96	0.001	0.77
DO (+)	20.03	0.020	0.35
DO (+), IR (-)	22.90	0.052	0.29
< 2.8 (-), DO (+)	23.34	0.062	0.27
< 2.8 (-)	23.57	0.119	0.18
IR (+)	25.43	0.348	0.07
IR (-), < 2.8 (-), DO (+)	26.91	0.104	0.26
IR (+), < 2.8 (-)	27.18	0.287	0.05

Table 11. Summary of analyses by 15 models that were conducted to explain the variation in coho salmon emergent fry survival in Prairie Creek, Boyes Creek, and Streelow Creek, Humboldt County, California, 2000.

Variable	Cumulative Probability
Worms	1.00
IR	0.13
D.O.	0.12
< 2.8	0.12

(Variable definitions are the same as in table 7)

Worm infestation was more prevalent at the emergent fry stage compared to the alevin and hatching stages. Six out of 15 redds contained worms at the emergent fry stage, with worm counts ranging from 1 - 32 per redd. One paired egg container with low counts of worms (n = 13) contained egg shells with observable puncture holes. Survival to emergent fry in redds with worms averaged 9.5% (S.D. 16.4), compared with 79.4% (S.D. 17.4) for redds without worms. The most dramatic decrease in emergent fry survival due to worms occurred in Boyes Creek redd #2, where eyed egg to alevin survival with no worm presence was 83%, and eyed egg to emergent fry survival was zero percent when worms were present.

DISCUSSION

Natural Redds

The transformed number of coho salmon fry emerging from natural redds was negatively related to the presence of predacious worms and cumulative percentage of fine sediments < 3.33 mm. These results agree with Briggs (1953) and Koski (1966). Briggs (1953) studied natural coho salmon redds in Prairie Creek during 1948 to 1951, and found an average of 56% mortality in coho salmon redds with worms, compared with 15% mortality without worms. Briggs (1953) attributed all variation in redd survival between coho salmon, Chinook salmon, and steelhead trout to predacious worms. Two natural redds I trapped that contained worms had less than 14 fry emerge, and support Briggs' (1953) findings of reduced survival in redds with predacious, egg-eating worms.

Of the two variables used in my model, sediments accounted for more of the variation than worm presence or absence. The redds I trapped in Boyes Creek had elevated levels of fine sediments < 3.33 mm (average = 27.6%) with no worms present, and only one in five redds produced emergent fry. Koski (1966) found that fine sediments < 3.33 mm decreased survival of coho salmon during the egg-emergent fry stage in natural redds from three Oregon coastal streams. Tagart (1984) also demonstrated a negative relationship between survival of coho salmon emergent fry and increasing amounts of fine sediments (< 0.85 mm) in his studies of natural redds in Washington. The best model of emergence from natural redds left considerable variation unexplained. This variation may have been due to: 1) multiple redd formation and partial egg deposition (Shirazi et al. 1979, Young et. al. 1990), 2) natural variation among females in fecundity, 3) my inability to describe conditions within discrete egg pockets (Chapman 1988, Meyer 2003), and 4) possible failure to detect worms in redds (Briggs 1953, Meyer 2003).

I was not able to discern whether a given redd contained all or a portion of eggs from a single female. It is possible that some sampled redds within Prairie Creek (Prairie Creek redd #2, Prairie Creek redd #5) did not have a female's complete egg deposition because gravel conditions were near optimal, and catches were lower than expected (i.e. < 1,000 individuals).

Salmonid redds can be made up of four layers: undisturbed bottom, egg pocket, bridge, and cover (Peterson and Quinn 1996). I could not measure abiotic variables within specific egg pockets, and hence, variables I measured in and adjacent to egg pockets were used to describe the redd environment. It is quite possible that by describing the redd environment (which included egg pockets), I may not have detected localized egg pocket conditions. However, the material surrounding egg pockets must also influence emergence success (Lisle and Lewis 1992, Weaver and Fraley 1993) because intergravel water must pass through the interstices of redd gravels before entering and leaving egg pockets. Additionally, emerging fry must move through the bridge and cover of the redd (Koski 1966, Phillips et al. 1975, Bjornn and Reiser 1991) prior to stream occupancy.

I may have underestimated worm presence in some redds because I could only detect worms during abiotic measurements (e.g. inflow rates) and gravel extraction.

Redds that produced no fry in Boyes Creek may have contained worms that were not detected due to worm mobility (Briggs 1953, Williams 1996, Meyer 2003). However, the percentage of fine sediments < 3.33 mm in Boyes Creek redds was high enough to cause asphyxiation or entrapment. The adjusted R^2 value for my model was 0.41, and was close to the R^2 value (0.47) for a linear model relating survival to emergence of coho salmon and fine sediments < 3.33 mm reported by Koski (1966).

Artificial Redd Experiments

In the artificial redd component of the study I was able to control variation associated with uncertainties in egg deposition and egg pocket locations. This also allowed me to estimate survival at three early life history stages: hatching, alevin, and emergent fry.

Survival from eyed egg to hatching was negatively affected by worm presence and the amount of fine sediments < 2.8 mm that intruded into egg containers. Most of the variation in hatching survival explained by this model was attributed to the presence of predacious worms. The digesting egg matter observed in worms was orange and indicated worms can consume live eggs because dead eggs quickly become white in color. Survival in a redd with worms (0%) and in redds without worms (75%) demonstrated the negative influence of worms. Fine sediments that intruded at the hatching stage probably negatively affected survival by coating the outer chorion layer of the egg, thereby decreasing available oxygen to developing eggs (Bams 1969). Young embryos are also thought to metabolize oxygen less efficiently than more advanced embryos (Bjornn and Reiser 1991).

The best models describing survival from eyed egg to alevin and to emergent fry stage included worm presence or absence. Additional models had higher AIC_c values and according to Burnham and Anderson (1998), showed considerably less statistical support. The cumulative probability (1.00) that worms were the best variable describing alevin and emergent fry survival was apparent using *a posteriori* techniques.

Fine sediments that intruded into egg containers at alevin and emergent fry stages probably had negligible effects on survival because: 1) the strong relationship of worms on survival overwhelmed the relationship between fine sediments and survival, 2) alevins and emergent fry can tolerate moderate amounts of fine sediments by ventilation swimming and gill mucous secretions that can cleanse the gills of fine sediments (Bams 1969), and 3) fry were manually removed from egg containers and did not have to physically move through the substrate.

The percentage of redds considered impacted by worms increased from hatching to alevin and emergent fry stages even though counts of worms were less than those found at the hatching stage. Worms were able to invade redds and leave shortly thereafter (as evidenced by Streelow Creek redd #3) which confirmed findings of Briggs (1953) that predacious worms were mobile. I found that invasion of worms within redds is variable (Streelow Creek redd #5, Boyes Creek redd #2) because worm presence was documented in some egg containers, and not others. Additionally, worms can invade a redd and kill all eggs within multiple egg containers.

In this study, survival decreased substantially in redds that did not have worm infestation at one stage, but did at other stages. For example, in Streelow Creek redd #5, survival at hatching was 94% but was reduced to 0% at the alevin stage after worms invaded. Likewise, Boyes Creek redd #2 alevin survival (83%) was reduced to 0% emergent fry survival due to worms. Survival in redds with worms at alevin and emergent fry stages was markedly and consistently lower than survival in redds without worms. For example, the average survival at the alevin and emergent fry stages in redds with worms was 9.5%, while in redds without worms survival to alevin and emergent fry was 80 and 79%, respectively.

CONCLUSIONS

These results clearly show the presence of egg-eating worms and the amount of fine sediments < 3.33 mm significantly reduced the number of coho salmon fry emerging from natural redds. In artificial redds, worms and fine sediments < 2.8 mm significantly reduced survival to the hatching stage, whereas survival from eyed egg to alevin and emergent fry stages was mostly controlled by the presence of worms.

The general distribution of these worms outside of the Prairie Creek watershed is unknown, and merits scientific inquiry. Although worms have been correlated with increasing amounts of fine sediments (Meyer 2003), factors controlling worm abundance are unknown. Clearly, scientific studies aimed at describing the distribution of predacious egg-eating worms and factors which control worm abundance are needed.

Egg-eating worms may set upper limits to emergent fry production. However, for at least the past decade Prairie Creek has supported sub-populations of adult Chinook and coho salmon.

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APPENDICES

Appendix A. Average coho salmon emergent fry fork lengths from natural redds in three northern California streams, Humboldt County, California 1999.

Stream	Redd No.	Sample Size	Average Fork Length (mm)	Standard Deviation
Prairie Creek	1	180	37.1	0.67
Prairie Creek	2	174	36.1	0.72
Prairie Creek	3	106	37.5	1.51
Prairie Creek	4	162	38.3	0.65
Prairie Creek	5	142	37.0	0.69
Boyes Creek	1	-	-	-
Boyes Creek	2	166	37.1	1.58
Boyes Creek	3	-	-	-
Boyes Creek	4	-	-	-
Boyes Creek	5	-	-	-
Streelow Creek	1	168	36.7	0.67
Streelow Creek	2	-	-	-
Streelow Creek	3	-	-	-
Streelow Creek	4	-	-	-
Streelow Creek	5	231	36.9	0.56

Appendix B. Cumulative percentage by weight (g) of fine sediments < 3.33 mm in 14 natural coho salmon redds in three northern California streams, Humboldt County, California 1999.

Stream	Redd No.	Cumulative percentage of fine sediments less than 3.33 mm (g)
Prairie Creek	1	18.61
Prairie Creek	2	14.03
Prairie Creek	3	25.18
Prairie Creek	4	17.25
Prairie Creek	5	17.52
Boyes Creek	1	26.89
Boyes Creek	2	26.84
Boyes Creek	3	31.05
Boyes Creek	4	20.37
Boyes Creek	5	32.99
Streelow Creek	1	18.48
Streelow Creek	2	--
Streelow Creek	3	18.69
Streelow Creek	4	16.66
Streelow Creek	5	19.30

Appendix C. Mean values (standard deviation in parentheses) for abiotic variables measured in natural coho salmon redds in three streams, and stream values over the course of eyed egg to emergent fry development.

Stream/abiotic variable	Mean redd value measured during eyed egg through emergent fry	Stream value
Prairie Creek		
Temperature (°C)	8.54 (0.36)	8.58 (0.35)
Specific Conductance (µS/cm)	62.73 (1.43)	61.37 (1.18)
< 3.33 mm (g)*	18.52 (4.10)	-
Dg* (mm)	11.21 (1.90)	-
Inflow rate (ml/sec)	30.75 (19.52)	-
D.O. (mg/l)	8.32 (1.55)	-
Boyes Creek		
Temperature (°C)	9.08 (0.20)	9.26 (0.19)
Specific Conductance (µS/cm)	82.44 (2.43)	80.24 (3.54)
< 3.33 mm (g)*	27.63 (4.86)	-
Dg* (mm)	7.29 (1.63)	-
Inflow rate (ml/sec)	27.46 (14.29)	-
D.O. (mg/l)	6.80 (0.47)	-
Streelow Creek		
Temperature (°C)	8.81 (0.22)	9.00 (0.29)
Specific Conductance (µS/cm)	72.55 (2.09)	71.22 (2.30)
< 3.33 mm (g)*	18.28 (1.14)	-
Dg* (mm)	10.75 (1.87)	-
Inflow rate (ml/sec)	33.76 (21.27)	-
D.O. (mg/l)	6.93 (0.54)	-

* denotes post-emergent fry measurement.

Appendix D. Mean values (standard deviation in parentheses) for abiotic variables measured in artificial redds in three streams during each of three developmental periods.

	Developmental Period		
Stream/redd variable	Hatching	Alevin	Emergent fry
Prairie Creek			
Temperature (°C)	9.15 (0.09)	8.85 (0.21)	9.10 (0.23)
Specific Conductance*	63.39 (2.09)	61.40 (1.51)	68.75 (1.06)
< 2.8 mm (g)	6.12 (4.19)	6.99 (6.91)	9.72 (10.97)
Inflow rate (ml/sec)	89.27 (33.89)	71.79 (36.19)	74.69 (44.58)
D.O. (mg/l)	9.02 (0.58)	10.13 (0.62)	9.97 (1.26)
Boyes Creek			
Temperature (°C)	9.81 (0.02)	9.43 (0.06)	8.95 (0.12)
Specific Conductance*	80.68 (1.65)	79.01 (3.27)	92.18 (0.52)
< 2.8 mm (g)	28.71 (11.46)	20.58 (9.89)	45.94 (42.20)
Inflow rate (ml/sec)	50.68 (31.28)	43.37 (24.12)	30.66 (17.24)
D.O. (mg/l)	7.75 (0.66)	7.84 (0.41)	7.33 (0.66)
Streelow Creek			
Temperature (°C)	9.51 (0.07)	9.25 (0.08)	8.86 (0.05)
Specific Conductance*	66.36 (3.12)	68.97 (1.43)	78.61 (2.01)
< 2.8 mm (g)	12.11 (5.81)	18.39 (22.19)	12.02 (8.66)
Inflow rate (ml/sec)	56.08 (24.59)	40.97 (17.74)	43.10 (13.82)
D.O. (mg/l)	8.09 (0.95)	8.67 (0.93)	9.18 (1.26)

* Units are microSemens per centimeter (μS/cm)

Appendix E. Mean values (standard deviation in parentheses) for abiotic variables measured in three streams during each of three developmental periods.

	Developmental Period		
Stream/variable	Hatching	Alevin	Emergent fry
Prairie Creek			
Temperature (°C)	9.18 (0.08)	8.92 (0.19)	9.14 (0.21)
Specific Conductance*	61.26 (1.62)	59.58 (0.99)	66.40 (1.05)
Boyes Creek			
Temperature (°C)	9.88 (0.04)	9.50 (0.00)	9.02 (0.09)
Specific Conductance*	76.78 (1.94)	72.52 (1.60)	87.22 (1.08)
Streelow Creek			
Temperature (°C)	9.58 (0.11)	9.36 (0.09)	8.86 (0.05)
Specific Conductance*	62.28 (2.09)	66.44 (0.48)	74.44 (1.69)

* Units are microSemens per centimeter (μS/cm)

Appendix F. Average fine sediments < 2.8 mm g (standard deviation in parentheses) in artificial egg containers sampled at hatching, alevin, and emergent fry stages in three northern California streams, Humboldt County, California, 2000.

Stream	Redd No.	Fine sediment < 2.8 mm (g) Hatching	Alevin	Emergent fry
Prairie Creek	1	3.26 (0.05)	5.27 (0.92)	9.71 (0.13)
Prairie Creek	2	2.74 (1.30)	0.91 (0.65)	1.18 (0.99)
Prairie Creek	3	3.18 (0.82)	0.69 (0.04)	0.60 (0.26)
Prairie Creek	4	10.56 (3.50)	16.49 (10.17)	27.75 (0.71)
Prairie Creek	5	10.84 (4.81)	11.58 (1.51)	9.37 (5.08)
Boyes Creek	1	16.29 (5.39)	16.16 (5.22)	13.49 (5.74)
Boyes Creek	2	17.56 (1.73)	19.24 (6.73)	46.34 (1.03)
Boyes Creek	3	37.00 (17.78)	37.73 (14.95)	118.42 (49.78)
Boyes Creek	4	30.79 (8.76)	12.52 (0.00)	25.05 (6.03)
Boyes Creek	5	41.89 (0.78)	17.25 (3.77)	26.39 (14.40)
Streelow Creek	1	20.80 (6.79)	4.47 (3.98)	14.65 (1.46)
Streelow Creek	2	14.65 (4.74)	57.50 (19.96)	25.65 (1.68)
Streelow Creek	3	10.22 (0.33)	14.68 (0.27)	4.85 (1.27)
Streelow Creek	4	9.27 (1.88)	6.50 (2.18)	4.76 (1.75)
Streelow Creek	5	5.65 (0.58)	8.82 (1.36)	10.18 (5.26)
Average:		15.65 (12.25)	15.32 (14.84)	22.56 (29.30)