

The biophysical ecology of salmon redds

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BACKGROUND AND MOTIVATION

Recent work [Martin *et al.*, 2017] suggests the thermal tolerance of salmon embryos is not fixed, but rather depends on the velocity of surrounding water within redds. Because the metabolic rate of embryos increases exponentially with temperature, supplying enough oxygen to meet demand becomes more difficult at elevated temperatures. Oxygen is supplied to embryos from the surrounding water by diffusion at a rate dependent on the concentration gradient at the egg's surface [Martin *et al.*, 2017]. Diffusion is slow in water, thus as embryos consume oxygen, they deplete dissolved oxygen in the surrounding water. This reduces the concentration gradient, and consequently limits the supply of oxygen to the embryos. Oxygen-rich stream water downwelling into the streambed sediment replenishes oxygen through convective transfer, and thereby increases oxygen supply [Tonina and Buffington, 2009]. Fisheries biologists have long known that the survival of salmon embryos can be impaired when there is insufficient interstitial flow within redds and that reduced flows are typically accompanied by reduced oxygen concentrations within the redd (Coble 1961). The “oxygen-limitation hypothesis” as the mechanistic basis underlying thermal tolerance in fish embryos provides a unifying framework to explain why embryos die when temperatures get too warm and when interstitial flows are too low; both outcomes result from a mismatch between oxygen supply and demand, where flow determines the supply of oxygen to developing embryos, and temperature determines oxygen demand.

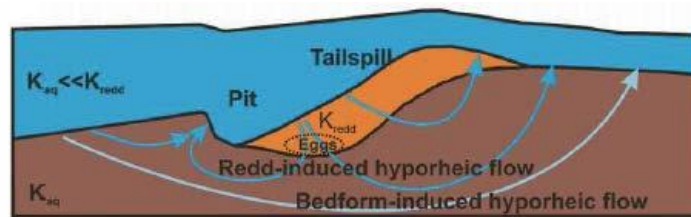


Figure 1: Idealized 2D redd shape and induced hyporheic flows due to flow-redd interaction. The hyporheic flow is the main mechanism for bringing oxygen rich stream water to the egg pocket and for removing waste products.

The flow-dependence of thermal tolerance has important water management implications. In drought years, the stock of cool water stored behind the Shasta dam is limited. In these years, the primary management tool is to reduce the discharge at Shasta to avoid running out of cool water before the end of the embryonic development period. However, it is equally important to ensure that benefits of maintaining low temperatures are not offset by reductions in flow-dependent oxygen supply to embryos (reduce hyporheic flows within the redd). Optimal water management therefore requires quantitatively assessing the tradeoffs between managing for temperature and flow. The biophysical model of Martin *et al.* [2017] is an ideal tool for considering these tradeoffs because it mechanistically predicts oxygen balance in response to both temperature and interstitial flow. However, the application of this model to water management in the Sacramento River is currently limited by a poor understanding of the factors affecting the relationship between river discharge and interstitial flow velocity.

Here, we propose a novel research program combining computational fluid dynamics, controlled egg survival experiments with high resolution dissolved oxygen mapping within eggs pockets, and novel flume experiments that will allow us to “see” how water flows through redds. The outcome of the proposed research will be an experimentally validated hydrodynamic model that predicts interstitial flow velocity as a function of river discharge, river bathymetry, and gravel characteristics. This hydrodynamic

model, when combined with the existing biophysical model of embryonic oxygen supply and demand, will allow managers to jointly assess the roles of flow and temperature on egg survival.

Oxygen supply to developing embryos is driven by processes that occur at three hierarchical scales. At the highest level, above ground flow conditions (discharge, stage) along with the local bathymetry set the potential for how much oxygen-rich stream water flows into the redd by generating a pressure gradient along its surface. Secondly, intra-redd structure (variation in gravel size and location of the egg pockets), determines how readily a given pressure gradient at the surface of the redd translates to convective oxygen supply to egg pockets. Finally, variation in pore-scale flow velocities within egg pockets combined with oxygen depletion as water flows through the egg pocket results in large variation in the oxygen conditions experienced by eggs even within the same egg pocket, which has important implications for egg to fry survival. Below we describe our proposed research program to understand factors affecting oxygen supply to eggs at each of these scales. Together, this modeling framework can address key questions about water management that cannot be addressed by temperature models alone. These include the impacts of very low flows (such that occur when there is concerns about redd de-watering), the advantages of increased flows within the same temperature range, and the impacts of different levels of sedimentation on redds.

Q1: What is the relationship between river discharge and interstitial flow in the Sacramento River?

At the largest scale, differences in pressure across the redd surface causes river water to flow down through the redd in high pressure zones and then back up in low pressure zones [Figure 1, *Cardenas et al.*, 2016; *Cooper*, 1965; *Tonina and Buffington*, 2009]. These pressure gradients are driven by the complex interplay between river discharge, depth, and local bathymetry. Researchers have previously developed models to predict the pressure gradients across a redd as a function of these variables (Elliot and Brooks 1997a, Elliot and Brooks 1997b), however, these models were developed and parameterized exclusively for shallow streams, where pressure gradients across the redd are driven primarily by “static heads” due to differences in relative submergence across the redd. In deep rivers, such as the Sacramento River where Chinook salmon spawn, differences in relative submergence across the redd is negligible, and thus pressure gradients are primarily driven by dynamic heads caused by flow detachment shown by the presence of an eddy or recirculation in the pit and downstream of the redd (Figure 2). Thus, it is currently unknown how decreasing discharge in large rivers, such as the Sacramento River affects interstitial flows and consequently oxygen supply in salmon redds.

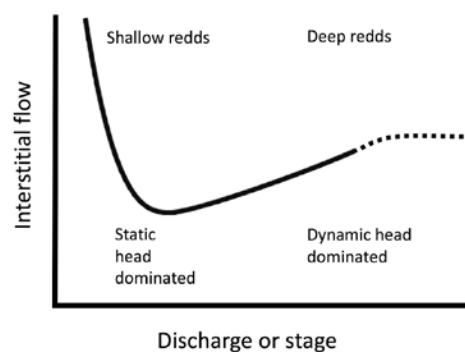


Figure 2: Hypothesized relationship between interstitial mean flow and river stage or discharge. At low discharge, the static head is dominant and (with the exception of redds that are almost exposed) interstitial flow decreases with increasing flow. At higher discharges the dynamic head is dominant, and interstitial flow increases with discharge. The increase in interstitial flow with increasing discharge and stage likely flattens above a critical threshold value (dotted black line), however theory and data are lacking to predict where the threshold should occur.

We propose to address this uncertainty by simplifying the redd as a two dimensional feature [Cardenas *et al.*, 2016b] (a conservative simplification) and study the pressure change due to the interaction between flow and redd via numerical modeling and selected flume experiments. We plan to model the surface water with the simulation software, Ansys Fluent CFD [Fluent Inc., 2003] from low (0.5) to high (30) relative submergence of a redd. Ansys Fluent has been shown to predict the near bed flow field and pressure with very high accuracy [Cardenas and Wilson, 2007]. We will solve the Reynolds Averaged Navier-Stokes equations with k-omega turbulence closure. The near bed pressure information from the 2D surface model will then be used as boundary condition for the 2D groundwater model. We plan to use MODFLOW as subsurface model. We will then quantify the mean downwelling flow over the bedform and the averaged interstitial flow for the portion of the redd where eggs are typically located. These two indices will be then correlated to discharge and relative submergence to quantify the dependence and provide quantitative information for Figure 2. In this task, we will use a uniform hydraulic conductivity for the redd and one for the undisturbed material as typically done. We will test the performance of the surface model by comparing near-bed pressure distribution predicted by the model with values measured at one flume experiment from Task 2. Similarly, the groundwater model will be tested by comparing predicted and measured residence time distribution.

Q2: How do gravel redd characteristics, fish-arranged grain size distribution, and sedimentation, affect interstitial flow experienced by eggs?

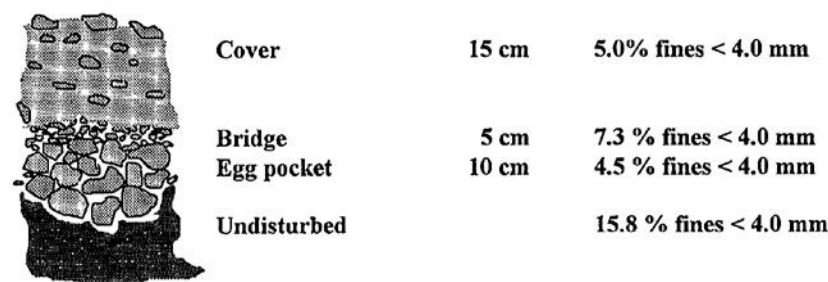


Figure 3: Stratigraphy of a typical chum salmon egg pocket indicating the approximate depth and gravel composition from Peterson and Quinn [1996]. This is considerate a typical redd internal architecture

Whether a given pressure gradient at the surface of the redd leads to sufficient water and oxygen supply to the egg pockets depends on the hydraulic properties of redds. During the construction of redds, salmon disturb the gravel bed, typically removing small gravel and fines. This disturbance increases the hydraulic conductivity within the redd and can increase interstitial flow by one order of magnitude compared to the undisturbed topography [Tonina and Buffington, 2009]. However, these studies did not consider the effects of within-redd variation in hydraulic conductivity [Cardenas *et al.*, 2016; Tonina and Buffington, 2009], and field studies of internal grain size distribution suggest this variation can be quite very strong [Peterson and Quinn, 1996; Rennie and Millar, 2000]. Zones of higher hydraulic conductivity within the redd, such as those typically occurring near egg pockets, cause flow lines to converge into those zones, such that more water flows in those areas. This effect could have a very important impact on egg development because it focuses oxygen rich flows to the eggs at a higher velocity than other areas. However, no study has yet addressed the effect of redd hydraulic heterogeneity. This is in part due to a dearth of information of redd internal architecture and the inherent difficulty to monitor flows within a heterogeneous porous media.

We propose to address this research gap by first, making detailed measurements of redd architecture by taking frozen core samples of Chinook redds from a non-threatened population (e.g. fall run) to map heterogeneity in hydraulic conductivity throughout the redd [Evenson, 2001]. Based on these measurements and literature information on redd architecture, we will construct artificial redds in a set of flume experiments to measure interstitial flow for different above ground flow velocities. To isolate the

contribution of internal redd heterogeneity on oxygen supply to eggs, we will then compare the intra-redd flow dynamics in redds constructed with realistic heterogeneous gravel compositions against those with homogenous gravel distributions. To allow us to see how water flows through redds, we will construct redds with artificial gravel made of material (fluoroplastic granules THV 221GZ) with index refraction matching that of the water. By seeding water with tiny, neutrally buoyant particles, and filming these particles as they move through the interstitial spaces in the porous media (a technique referred to as Stereoscopic Particle Image Velocimetry, S-PIV), we can reconstruct high resolution velocity maps of how water flows through redds and to the egg pockets embedded within them (Figure 4). This will allow understanding the effect of preferential flows caused by the fish rearranging the gravel around the eggs. Furthermore, S-PIV will allow us to observe the process sedimentation in redds in unprecedented detail, by allowing us to see through gravel and thus see where fines accumulate over time in redds. This will allow us to develop a more mechanistic understanding of how sedimentation occurs, and furthermore give insights into ways to prevent it (e.g. flushing flows, optimal gravel sizes, etc.).

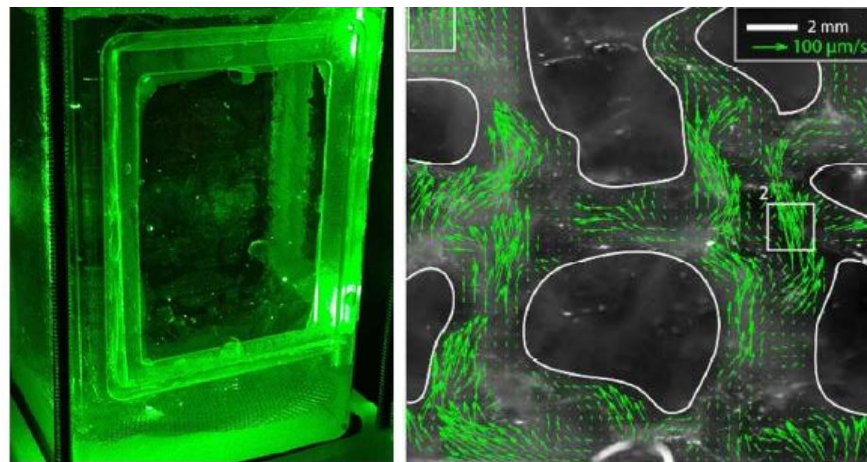


Figure 4: Example of MIR-couple PIV to measure interstitial flows within a granular matrix. On the left panel, the artificial gravel is packed within a 5 cm wide, 5 cm deep and 10 cm long flow through cell, but is not visible as it has the same refractive index as water. The right panel shows the interstitial flow vectors measured by the PIV.

Q3: How do oxygen dynamics within egg pockets affect variation in oxygen supply to individual eggs within egg pockets, and how does this variation affect aggregate survival rates?

Chinook salmon lay their eggs in four to six discrete clusters within a redd, with each ‘egg pocket’ containing roughly a thousand eggs. At first glance, clusters of similarly-sized spherical eggs appear to be a simple and relatively homogenous environment. However, experimental studies have demonstrated extreme variability in inter-pore flow velocities in these homogenous environments, such that up to 40% of water flows through 10% of the pore spaces, and conversely 50% of pore spaces may only receive 10% of the flow (Mantle et al. 2001). When combined with the fact that the embryos are consuming oxygen, this variability in inter-pore velocities leads to substantial variation in the local oxygen environments experienced by individual eggs even within the same egg pocket (Figure 5). Because survival is a highly non-linear function of oxygen supply, intra-redd variability in oxygen conditions has important consequences for relating mean flow and oxygen conditions within the egg pocket and the fraction of eggs within the pocket that survive. For example, due to the intra-redd variability in oxygen supply, a substantial fraction of eggs may die even if mean flow and oxygen conditions within the egg pocket are sufficient for egg survival.

We propose to explore how intra-egg pocket oxygen dynamics affect survival by developing the first high resolution 3D computational fluid dynamics model coupled with a mass transfer model for oxygen of an egg pocket. We will use this model to explore how the distribution of flows and local oxygen conditions experienced by individual eggs in an egg pocket varies with mean flow conditions and temperature.

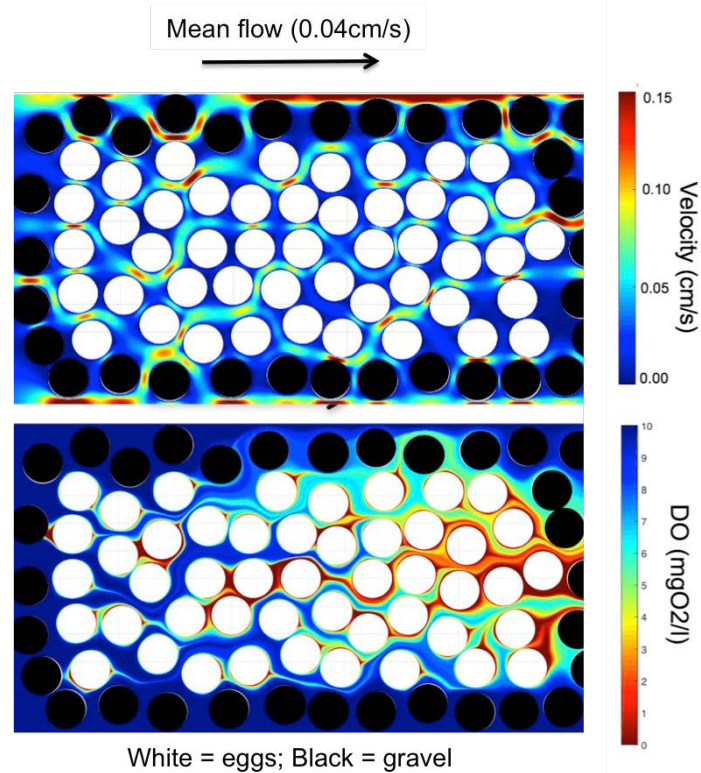


Figure 5: Example of flow velocity and dissolved oxygen concentration maps within a 2D egg pocket. Results were generated with a 2D computational fluid dynamics model coupled with a simulation of oxygen mass transfer.

We will use RIM-PIV of egg pockets embedded within gravel to test the 3D CFD model predictions with respect to flow. To test the model predictions regarding variation in DO and how this translates to mean egg pocket survival, we will conduct experiments with realistic egg pockets embedded within gravel in PVC pipes at reared at various temperatures and flow velocities (Figure 6). In addition, we will conduct experiments exposing embryos at different stages of development to low DO and elevated temperature for various length of time to develop a predictive model that relates oxygen imbalance with survival based on exposure and developmental stage.

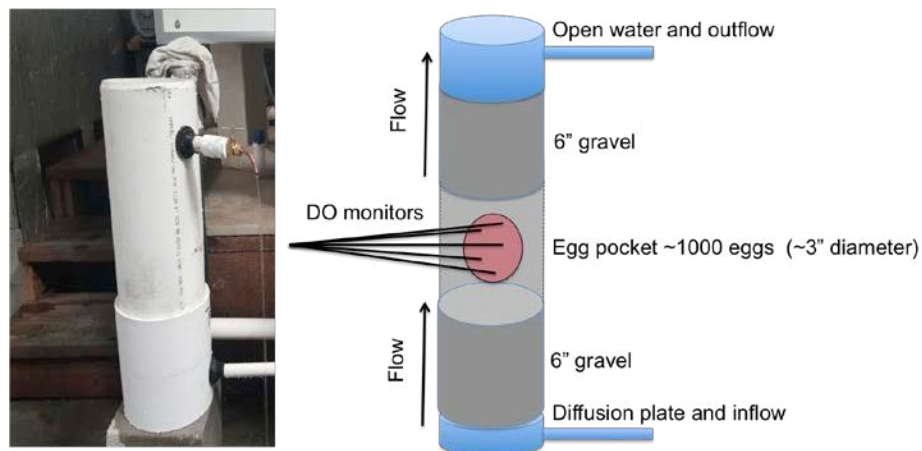


Figure 6: PVC pipe experimental chambers to examine oxygen dynamics and survival in realistic egg pockets embedded within gravel at a range of flow velocities and temperatures.

BUDGET

University of Idaho		
Category	Notes	Cost (USD)
PI (Daniele Tonina) expertise: Ecohydrology	2 weeks/year for 3 years	22,000
PI (Ralph Budwig) expertise: MIR, S-PIV	2 weeks/year for 3 years	22,000
PI (Tao Xing) expertise: CFD	2 weeks/year for 3 years	22,000
Postdoc (flume experiments, MIR, S-PIV)	3 year (1/3 time)	72,000
PhD student (flume experiments)	3 years full time	72,500
PhD student (CFD)	3 years full time	72,500
Undergraduate research assistant		11,000
Lab manager	6 weeks	10,000
Travel		15,000
Material for flume experiments		26,000
Software		2,750
Publication fees		9,000
Computers to run simulations		3,000
Tuition and fee for the students		75,000
Pre-overhead total		434,750
Overhead (18% if CESU otherwise 47.5%)		76,081
U Idaho Total		510,832
UC Santa Cruz		
Lab technician	3 years (2/3 time)	140,000
Undergrad research assistants		30,000
Lab material/heating cost for egg experiments		30,000
Travel		7,000
Publication Fees		6,000
Pre-overhead total		213,000
Overhead (26%)		55,380
UC Santa Cruz Total		268,380
Joint total		777,038

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