2-5-2014

Optimal Reproduction in Salmon Spawning Substrates Linked to Grain Size and Fish Length

Clifford Riebe
University of Wyoming, criebe@uwyo.edu

Leonard S. Sklar
San Francisco State University

Brandon T. Overstreet
University of Wyoming

John K. Wooster
National Oceanic and Atmospheric Administration – Fisheries, Habitat Conservation Division, Santa Rosa, California

Follow this and additional works at: http://repository.uwyo.edu/geology_facpub

Publication Information

This Article is brought to you for free and open access by the Geology and Geophysics at Wyoming Scholars Repository. It has been accepted for inclusion in Geology and Geophysics Faculty Publications by an authorized administrator of Wyoming Scholars Repository. For more information, please contact scholcom@uwyo.edu.
Optimal reproduction in salmon spawning substrates linked to grain size and fish length

Clifford S. Riebe¹, Leonard S. Sklar², Brandon T. Overstreet³, and John K. Wooster⁴

¹Department of Geology and Geophysics, University of Wyoming, Laramie, Wyoming, USA; ²Department of Geosciences, San Francisco State University, San Francisco, California, USA; ³Department of Geography, University of Wyoming, Laramie, Wyoming, USA, ⁴National Oceanic and Atmospheric Administration – Fisheries, Habitat Conservation Division, Santa Rosa, California, USA

Abstract Millions of dollars are spent annually on revitalizing salmon spawning in riverbeds where redd building by female salmon is inhibited by sediment that is too big for fish to move. Yet the conditions necessary for productive spawning remain unclear. There is no gauge for quantifying how grain size influences the reproductive potential of coarse-bedded rivers. Hence, managers lack a quantitative basis for optimizing spawning habitat restoration for reproductive value. To overcome this limitation, we studied spawning by Chinook, sockeye, and pink salmon (Oncorhynchus tshawytscha, O. nerka, and O. gorbuscha) in creeks and rivers of California and the Pacific Northwest. Our analysis shows that coarse substrates have been substantially undervalued as spawning habitat in previous work. We present a field-calibrated approach for estimating the number of redds and eggs a substrate can accommodate from measurements of grain size and fish length. Bigger fish can move larger sediment and thus use more riverbed area for spawning. They also tend to have higher fecundity, and so can deposit more eggs per redd. However, because redd area increases with fish length, the number of eggs a substrate can accommodate is maximized for moderate-sized fish. This previously unrecognized tradeoff raises the possibility that differences in grain size help regulate river-to-river differences in salmon size. Thus, population diversity and species resilience may be linked to lithologic, geomorphic, and climatic factors that determine grain size in rivers. Our approach provides a tool for managing grain-size distributions in support of optimal reproductive potential and species resilience.

1. Motivation

The lives of salmon culminate in dramatic migrations to natal rivers and streams, where females build redds in riverbeds, spawn, and, in semelparous species, guard their eggs until they die [Rounsefell, 1958; Quinn and Myers, 2004]. These migrations are driven by olfactory homing common among the Oncorhynchus and Salmo genera [Dittman and Quinn, 1996]. This homing is so precise that fish often return to within meters of where they emerged from the substrate years before as fry [Quinn et al., 2006]. This promotes reproductive isolation [Taylor, 1991; Fraser et al., 2011], fosters genetic diversity [Hendry et al., 2000; Olsen et al., 2003; Carlson et al., 2011a] and thus may also enhance species resilience [Gustafson et al., 2007; Greene et al., 2010; Schindler et al., 2010]. Thus, successful spawning in reaches and rivers spanning a range of conditions may help reduce potential for wide fluctuations in salmon populations [Schindler et al., 2010]. Conversely, degradation or loss of spawning habitat may make populations prone to collapse [Nehlsen et al., 1991; Waples et al., 2009; Carlson et al., 2011b], thus threatening fisheries-based economies [Healey, 2009], the continuance of aboriginal traditions [Boas, 1966; Campbell and Butler, 2010], and the annual delivery of millions of tons of ecosystem-sustaining nutrients from oceans to riparian corridors [Willson and Halupka, 1995; Heifield and Naiman, 2001; Naiman et al., 2002; Moore et al., 2007].

Wild salmon are important enough to economies, cultures, and ecosystems that revitalizing and maintaining their spawning habitats have become major components of the $1.5 billion-per-year river restoration industry in the United States [Bernhardt et al., 2005]. Despite these investments, many salmon populations continue to struggle, in part because the factors that contribute to robust salmon populations are not fully understood and because many of the factors we do understand are not easy to control. For example, although millions of dollars are spent every year on spawning substrate restoration [Kondolf et al.,
2007], the role of grain size in regulating the number of salmon redds and eggs that substrates can accommodate has never been quantified. Here we explore these relationships using field observations of spawning by three species of salmon in coarse-bedded rivers and creeks of California and the Pacific Northwest. Our analysis provides the basis for a new tool for managing spawning habitat for optimal reproduction. We discuss how this tool might be used to enhance salmon population diversity and species resilience in reaches where other factors besides grain size are not limiting to successful spawning.

2. Grain-Size Distributions and Spawning Habitat

Grain size is a fundamental regulator of the quality of salmon spawning habitat [McNeil and Ahnell, 1964; Kondolf and Wolman, 1993]. To be suitable for salmon spawning, substrates need to be coarse enough that they resist fluvial scour [Montgomery et al., 1996] and permit through-flow of oxygen-rich water [Greig et al., 2007]. Yet they simultaneously need to be fine enough that female fish can move sediment and thus build redds and deposit their eggs within the riverbed [Kondolf and Wolman, 1993]. Spawning habitat quality is therefore sensitive to changes in flow regime and sediment loading [Goode et al., 2012] that influence bed-surface grain-size distributions. For example, logging, road building, and agriculture may increase fine sediment delivery to streams [Platts and Megahan, 1975; Lisle, 1989; Soulsby et al., 2001; Opperman et al., 2005], clogging interstices of spawning substrates [McNeil and Ahnell, 1964], reducing their permeability [Tappel and Bjornn, 1983], and suffocating eggs in salmon redds [Chapman, 1988; Greig et al., 2007]. Conversely, dams and gravel mines may deprive downstream reaches of sediment [Kondolf, 1997], leading to size-selective transport [Williams and Wolman, 1984; Kondolf, 1997] that coarsens riverbeds and hinders spawning [Ligon et al., 1995] if residual particles are too large for female salmon to move as they try to build redds [Burner, 1951].

To mitigate bed-surface coarsening and improve conditions for spawning, ecosystem managers often add sediment to rivers in so-called “gravel augmentation” projects [Bunte, 2004; Pasternack et al., 2004]. Yet there is no gauge for quantifying how substrate grain size influences the number of redds a riverbed can accommodate. Which rivers are likely to benefit most from gravel augmentation? What sediment sizes should be added to achieve the best balance between increased potential to accommodate redds and resistance to fluvial scour? How effective is gravel augmentation at providing sustained improvements in potential to accommodate redds and eggs in riverbeds? Answering these questions is crucial to optimizing restoration activities and expenditures. Yet there is little physical basis in the literature for doing so.

2.1. Empirical Insight From Data Compilations

In assessing spawning habitat and designing restoration projects, managers typically rely on grain-size data from reaches where salmon have constructed redds in the past. For example, median particle diameters ($D_{50}$) and fish lengths from a compilation of observations from various rivers [Kondolf, 1988; Kondolf and Wolman, 1993] have been widely interpreted to define an “envelope” that reflects a grain-size limitation on ability to build redds [Kondolf and Wolman, 1993; Kondolf, 2000; Quinn, 2005; Kondolf et al., 2008]. This envelope has been referred to as the 10% rule by some [Armstrong et al., 2003; Bunte, 2004] for its slope of 0.1 mm/mm on a plot of $D_{50}$ versus fish length (Figure 1a). It is often used to set goals in restoration management. Yet the 10% rule fails to predict spawning in coarse-bedded reaches where female salmon build redds [Quinn et al., 1995], as illustrated by new grain size and fish length data plotted in Figure 1a. This implies that suitable substrates may be overlooked or undervalued in spawning habitat studies that use the 10% rule. Moreover, by prescribing grain-size distributions that are unnecessarily fine, the 10% rule may make restored beds overly susceptible to fluvial scour. Thus, it may needlessly shorten the lifespan of benefits from gravel augmentation.

The 10% rule fails to capture the grain-size limitations on salmon spawning (Figure 1a). Moreover, its suitable-or-not assessment of habitat may be overly simplistic. It cannot, for instance, explain gradients in habitat use, such as decreases in area occupied by redds across reaches with increasing $D_{50}$ (e.g., Figure 1b). Evidently, 100% of the bed can be used when substrates are fine-grained, while little can be used when they are relatively coarse (Figure 1b). This suggests that substrates span a spectrum in spawning habitat suitability due to variations in grain-size distributions. If a riverbed’s place within the suitability spectrum could be accurately gauged, managers would have a powerful new tool for assessing spawning habitat and restoring substrates in a way that balances the needs of the fish against degradation due to inevitable
sediment transport. As a conceptual starting point for developing such a tool, we consider the redd-building process mechanistically.

### 2.2. Biophysical Limits on Redd Building

To construct redds, female salmon turn on their sides and swat or “cut” at the bed with their tails, thus inducing lift forces that excavate particles from the surface. The force required to move a particle should scale with particle size \([\text{Buffington and Montgomery}, 1997]\), but fish can only generate so much force with their tails. Hence, some particles may be too big for fish to move. This should set limits on the fraction of the riverbed surface that is available for spawning. In general, we expect that the fractional coverage of the bed by moveable particles \((F_M)\) should be equal to the fractional area that can accommodate redd building, assuming that hydraulic conditions are suitable for spawning everywhere in the reach of interest. Note that \(F_M\) represents substrate conditions that influence ability to build redds in isolation of the flow and depth criteria \([\text{Moir and Pasternack}, 2008]\) that define suitable hydraulic conditions for salmon spawning. In general, \(F_M\) should vary from one reach to the next according to differences in bed-surface grain-size distributions and the size of the largest particle that fish can move \((D_{95})\). We stress that \(F_M\) is a biophysical index of habitat suitability that is specific to the substrate and the fish that use it; any applications of \(F_M\) in spawning habitat assessment and management will require a separate assessment of hydraulic suitability, to confirm that areas that are suitable in terms of grain size are also suitable in terms of water flow and depth.

---

**Figure 1.** Relationships among fish lengths, bed-surface grain-size indices, and spawning use. (a) Previous and new compilations of data reveal broad scatter in the relationship between \(D_{50}\) of the riverbed surface and the lengths of spawning salmonids. Regression line through previous compilation (solid line; after \(\text{Kondolf and Wolman} [1993]\)) has a slope of \(-0.04\, \text{mm/mm} \, (\sim -4%)\). "Envelope" is a cap on previous data (dashed line, after \(\text{Kondolf and Wolman} [1993]\)). Its slope of \(-0.1\, \text{mm/mm} \, \text{is the basis of the "10% rule," a term used both here and elsewhere in the literature to describe it. New compilation is tabulated in the supporting information. (b) Spawning use, measured as the fraction of riverbed area occupied by redds, decreases with the 84th percentile of particle sizes on the bed \((D_{84})\) for three species of salmon studied here.
Figure 2 illustrates the relationship between FM, DT, and bed-surface grain-size distribution for two different riverbeds. Although the median particle size (D50) is the same in each case, one distribution is wider (with a bigger difference between D84 and D50). The extra width in the distribution means that a larger fraction of the bed is covered by particles with diameters bigger than DT (Figure 2); coverage by movable particles is lower when the grain-size distribution is wider, both for the specific case shown in Figures 2a and 2b and more generally when D50 < DT. Conversely, when DT < D50, as shown in Figure 2c, coverage by movable particles is greater when the spread is wider. Thus, variations in both the spread and central tendency of grain size are important in determining how much of the bed is movable for fish with a given DT. This helps explain why D50 alone is a poor predictor of which riverbeds can be used by different-sized fish (e.g., see Figure 1a).

Table 1. Study Site Locations and Characteristics of Spawning Female Salmon

<table>
<thead>
<tr>
<th>River or Creek</th>
<th>Location</th>
<th>Study Timing</th>
<th>Salmon Species</th>
<th>Escapement (10^3 fish)</th>
<th>Female Fish Length (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>South Prairie Creek, WA</td>
<td>47.12 122.07</td>
<td>September-October 2009</td>
<td>Pink</td>
<td>540.6</td>
<td>445 ± 2 (201)</td>
</tr>
<tr>
<td>Scotch Creek, BC</td>
<td>50.95 119.46</td>
<td>October 2010</td>
<td>Sockeye</td>
<td>522.4</td>
<td>569 ± 4 (38)</td>
</tr>
<tr>
<td>Shasta River, CA</td>
<td>41.82 122.60</td>
<td>October 2009</td>
<td>Chinook</td>
<td>6.1</td>
<td>721 ± 2 (456)</td>
</tr>
</tbody>
</table>

aData for Chinook salmon correspond to fall-run spawning.
Escapements (the number of returning fish) from Scotch Creek are available on request from Fisheries and Oceans Canada. No escapements are available for South Prairie Creek itself; here we report proxy data from the nearby White River counting facility (USACE, 2009). Available data suggest that escapements for both pink and sockeye salmon were near record levels during our study. Spawning returns of Chinook salmon were also relatively high, ranking in the 73rd percentile of 30 years of available escapement data for the Shasta River (California Department of Fish and Game, 2010).

Chinook salmon lengths are unpublished results from Shasta River carcass and trap surveys; data are available on request from California Department of Fish and Wildlife. Pink and sockeye salmon lengths are from carcass surveys conducted in this study. Values are reported as means ± s.e.m. (with number of measurements in parentheses). See supporting information for measurements of pink and sockeye salmon lengths.
3. Study Design

Knowing the threshold particle size ($D_T$) for the fish of interest is evidently crucial to quantifying how the usability of spawning substrates (as encapsulated in $F_{SSH}$) varies with grain size (Figure 2). However, to our knowledge, the relationship between $D_T$ and salmon size has never been quantified. To overcome this limitation, we studied redds built by pink, sockeye, and Chinook salmon in coarse-bedded rivers and creeks of California and the Pacific Northwest. Our goal was to explore how interspecific differences in salmon size influence redds building. We also sought to develop a predictive model for the potential of riverbeds to accommodate redds and eggs during spawning by different-sized fish.

3.1. Study Sites

We selected three study sites with coarse bedded reaches (Table 1) and made observations of redds during the latter half of fall-run spawning at each site. Both our 2009 study of pink salmon and our 2010 study of sockeye salmon coincided with high escapements (i.e., the number of returning fish) according to data available from nearby counting facilities (Table 1). This is consistent with first-hand evidence from the field; fish were congregating in great abundance in nearly every reach we visited during our studies of South Prairie Creek and Scotch Creek. Chinook salmon escapements were also high during our Shasta River study relative to historical records (Table 1).

Spawning fish were abundant enough at each site that fish appeared to be using substrates with diverse grain-size distributions, from relatively fine to very coarse (Figure 1b). This was a key aspect of our

Table 2. Reach-Scale Measurements of Particle-Size Distributions and Coverage by Movable Particles

<table>
<thead>
<tr>
<th>Reach</th>
<th>Coverage of Riverbed by Redds a (%)</th>
<th>$D_{50}$ (mm)</th>
<th>$D_{40}$ (mm)</th>
<th>$D_{30}$ (mm)</th>
<th>Coverage by Movable Particles b</th>
<th>$z$</th>
<th>Predicted Coverage by Movable Particles d</th>
<th>Spawning Use e (redds/m²)</th>
<th>Spawning Capacity f (redds/m²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>PS01</td>
<td>17.8</td>
<td>89</td>
<td>195</td>
<td>2.19</td>
<td>0.53</td>
<td>0.087</td>
<td>0.54</td>
<td>0.10 ± 0.01</td>
<td>0.32 ± 0.04</td>
</tr>
<tr>
<td>PS02</td>
<td>22.5</td>
<td>91</td>
<td>195</td>
<td>2.14</td>
<td>0.51</td>
<td>0.060</td>
<td>0.53</td>
<td>0.13 ± 0.02</td>
<td>0.31 ± 0.04</td>
</tr>
<tr>
<td>PS03</td>
<td>7.6</td>
<td>118</td>
<td>220</td>
<td>1.86</td>
<td>0.41</td>
<td>0.343</td>
<td>0.36</td>
<td>0.05 ± 0.01</td>
<td>0.21 ± 0.03</td>
</tr>
<tr>
<td>PS04</td>
<td>64.2</td>
<td>49</td>
<td>122</td>
<td>2.49</td>
<td>0.79</td>
<td>0.729</td>
<td>0.78</td>
<td>0.38 ± 0.05</td>
<td>0.46 ± 0.06</td>
</tr>
<tr>
<td>PS05</td>
<td>23.5</td>
<td>59</td>
<td>210</td>
<td>3.56</td>
<td>0.61</td>
<td>0.377</td>
<td>0.66</td>
<td>0.14 ± 0.02</td>
<td>0.39 ± 0.05</td>
</tr>
<tr>
<td>PS06</td>
<td>39.9</td>
<td>80</td>
<td>225</td>
<td>2.81</td>
<td>0.57</td>
<td>0.169</td>
<td>0.57</td>
<td>0.23 ± 0.03</td>
<td>0.34 ± 0.04</td>
</tr>
<tr>
<td>PS07</td>
<td>22.9</td>
<td>80</td>
<td>160</td>
<td>2.00</td>
<td>0.61</td>
<td>0.252</td>
<td>0.61</td>
<td>0.13 ± 0.02</td>
<td>0.36 ± 0.04</td>
</tr>
<tr>
<td>PS08</td>
<td>40.0</td>
<td>89</td>
<td>220</td>
<td>2.47</td>
<td>0.52</td>
<td>0.075</td>
<td>0.53</td>
<td>0.24 ± 0.03</td>
<td>0.31 ± 0.04</td>
</tr>
<tr>
<td>PS09</td>
<td>16.7</td>
<td>89</td>
<td>220</td>
<td>2.47</td>
<td>0.52</td>
<td>0.075</td>
<td>0.53</td>
<td>0.10 ± 0.01</td>
<td>0.31 ± 0.04</td>
</tr>
<tr>
<td>PS10</td>
<td>92.4</td>
<td>46</td>
<td>112</td>
<td>2.43</td>
<td>0.81</td>
<td>0.818</td>
<td>0.80</td>
<td>0.54 ± 0.07</td>
<td>0.47 ± 0.06</td>
</tr>
<tr>
<td>PS11</td>
<td>48.1</td>
<td>80</td>
<td>215</td>
<td>2.69</td>
<td>0.58</td>
<td>0.177</td>
<td>0.58</td>
<td>0.28 ± 0.03</td>
<td>0.34 ± 0.04</td>
</tr>
</tbody>
</table>

*Measured by surveying.
*Measured graphically (see Figure 5 and text).
$z$ is calculated from equation (8) using $D_{50}$, $D_{40}$, and $D_{30}$.
Predicted using $z$ in equation (7).
*Predicted using equations (6–9). $D_T$ is calculated from equation (6) using average fish lengths (see Table 1). Errors are s.e.m. propagated using uncertainties reported in Table 3.
Experimental design; by choosing rivers with healthy salmon populations, we sought conditions in which spawning habitat was the limiting factor on spawning habitat use. In some instances, grain sizes were so coarse that fish could only build a few scattered redds across the ∼100 m² reach of interest. In others, grain sizes were sufficiently fine that nearly 100% of the bed was covered by redds (Table 2). Thus, for each species, we were able to identify and study redds built in substrates spanning a range of conditions. By including sites in coarse-bedded reaches in particular, and by focusing on rivers with high densities of returning spawners, we can be reasonably certain that our analysis of particles from redds (described next) puts realistic constraints on threshold particle sizes ($D_T$) for the salmon runs studied here. This is important, because quantifying the relationship between $D_T$ and fish size was central to our analysis.

3.2. Methods

Our field measurements encompassed two spatial scales. Measurements of the dimensions of moved particles from a suite of individual redds permitted us to quantify $D_T$ for the salmon that built the redds. We then applied our measurements of $D_T$ to reach-scale measurements of bed-surface grain-size distributions to quantify the fractional coverage of moveable particles for the fish. In this way, we sought to develop an improved understanding of how the redd-building ability of individual fish translates into estimates of the amount of spawning that can be supported in reaches with hydraulic conditions amenable to salmon reproduction.

Figure 3. (a) Schematic cross section showing redd building [after Burner [1951]] and (b) plan-view image from our 2009 study showing a typical completed pink salmon redd in South Prairie Creek. Arrows show flow direction. (a) Females cut at the bed, inducing lift forces that excavate particles and create characteristic pit-and-tailspill topography. Periphyton on the undersides of particles in elevated positions in the tailspill provide clear evidence that female salmon have moved them there. The white shapes in the tailspill of the redd depicted in Figure 3b outline grains we sampled after marking their locations on the photo in the field. Redd boundaries in Figure 3b were readily identified based on absence of periphyton and pit-and-tailspill topography. We marked them with weighted flagging tape (as shown in Figure 3b) for measurements of redd dimensions. Flag in middle of tailspill marks its crest.
3.2.1. Measurements at Individual Redds
We visited each site during or immediately after the peak of spawning and selected redds that appeared to be recently completed, with fully formed pit-and-tailspill topography (Figure 3a) and an absence of periphyton (Figure 3b), which generally grows on moved particles and thus obscures redds within a few weeks after they are built. We focused on redds in coarse-bedded reaches, to make our measurements of DT as meaningful as possible. We photographed each redd from above (e.g., see Figure 3b), measured the flow depths and velocities in redd pits using a flow meter, and then examined tailspills in search of large particles with convincing evidence of movement by female salmon during redd building. For example, we judged the presence of periphyton on the undersides of grains to be a clear sign they had been flipped recently. Likewise, if a particle occupied an elevated position on the tailspill, we could be reasonably certain that it had been moved there by a female salmon during redd building. We extracted the largest of these clearly moved particles from each tailspill (e.g., Figure 3b) for measurements. Despite taking care not to disturb buried egg pockets, we are fairly certain we sampled the tailspills exhaustively enough that we measured the largest grains moved in each redd. Particle masses were measured with a spring scale and major-, intermediate-, and minor-axis diameters were measured with a ruler. We recorded dimensions for all particles we extracted from redds but only used the heaviest (and thus most difficult to move) particle from each redd in this analysis. We also estimated the area of disturbed substrate at each redd (A_REDD) from the dimensions of redd pits and tailspills (Figure 3b). Observations from individual redds are reported in supporting information.

3.2.2. Measurements at the Reach Scale
At each site, we selected a series of 10–11 reaches spanning a range in bed-surface grain-size distributions, from coarse to fine. All reaches encompassed the tailouts of pools or riffles immediately downstream of tailouts and moreover supported spawning by at least a few (and sometimes many) fish during our study. Reaches were at least 100 m² in area with particles scattered such that there was not any strong spatial sorting (i.e., patchiness) in bed-surface grain size. Thus, we chose reaches that were relatively uniform in substrate and that appeared to be hydraulically suitable for spawning at the time of our study. At each reach, we measured grain-size distributions using standard pebble counts [Wolman, 1954; Bunte and Abt, 2001] and quantified the fraction of area occupied by redds using a measuring tape that spanned multiple transects through the reach; we recorded observations of the fraction of the tape overlying redds as a proxy for the fractional coverage of redds in the reach. Results of these measurements are plotted against D₈₄ in Figure 1b and reported in Table 2.

3.2.3. Measuring Fish Size
Quantifying the relationship between DT and fish size was a major goal of our work. To quantify fish size, we measured fork lengths of randomly sampled dead female salmon using a measuring tape. If fork length was difficult to measure due to decomposition, we measured hypural lengths (from the mideye to hypural bone) instead and used them to estimate fork length from the relationship between hypural and fork lengths (determined from measurements of both lengths on relatively fresh fish). This helped keep our samples random (i.e., not biased toward fresh fish) but was only necessary for 11 out of the 201 female pink salmon carcasses we measured and none of the sockeye salmon carcasses. Lengths of pink and sockeye salmon are reported in supporting information. For lengths of Chinook salmon, we use unpublished carcass and trap data for the fall 2009 run on the Shasta River. These data are available on request from the California Department of Fish and Wildlife. Average female fish lengths are reported in Table 1.

4. Results and Analysis
4.1. Threshold Particle Sizes
Our analysis of particles from redds shows that the mass of the largest particle moved increases with redd area (Figure 4a). The trend is well defined by the power-law regression expressed in equation (1).

\[ M_L = 0.40 A_{REDD}^{0.75} \]  

(1)

Here A_REDD is measured in m² and M_L is the mass in kg of the largest particle moved in the redd. The prefactor and exponent are regression parameters. These parameters are reported in Table 3, along with uncertainties and statistics for this and all other regressions in our analysis.
Table 3. Equations, Measured and Derived Parameters, and Regression Statistics

<table>
<thead>
<tr>
<th>Equation Number</th>
<th>Formula</th>
<th>Number of Observations</th>
<th>Regression Intercept (a)</th>
<th>Regression Slope (b)</th>
<th>Correlation Coefficient (r)</th>
<th>Statistical Significance (p &gt; F ratio)</th>
</tr>
</thead>
<tbody>
<tr>
<td>(1)</td>
<td>$M_r = aA_{REDD}^b$</td>
<td>67</td>
<td>0.40 ± 0.03</td>
<td>0.75 ± 0.06</td>
<td>0.85</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>(2)</td>
<td>$M_T = aA_{REDD}^b$</td>
<td>60</td>
<td>0.68 ± 0.05</td>
<td>0.75 ± 0.06</td>
<td>0.89</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>(3)</td>
<td>$A_{REDD} = aL/600^b$</td>
<td>60</td>
<td>3.3 ± 0.2</td>
<td>2.3 ± 0.2</td>
<td>0.89</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>(4)</td>
<td>$M_T = aL/600^b$</td>
<td>68</td>
<td>1.7 ± 0.2</td>
<td>1.7 ± 0.2</td>
<td>0.89</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>(5)</td>
<td>$D_T = aM^b$</td>
<td>68</td>
<td>95 ± 21</td>
<td>0.36 ± 0.04</td>
<td>0.73</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>(6)</td>
<td>$D_T = aL/600^b$</td>
<td>68</td>
<td>115 ± 13</td>
<td>0.62 ± 0.09</td>
<td>0.73</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>(11)</td>
<td>$E = a + b(L - 600)$</td>
<td>13</td>
<td>3410 ± 230</td>
<td>8.1 ± 1.6</td>
<td>0.84</td>
<td>0.0003</td>
</tr>
</tbody>
</table>

*Equations (2), (4), and (6) are derived from one or more regression equations and thus do not have comparable numbers of observations, coefficients of determination, or statistical significance. 600 mm is the common reference fish length in these equations; we use it to center the data around a value that is close to the average from our data set. Equation (11) reduces to $E = 8.1L - 1450$ but here is expressed in terms of centered fish length = 600 mm so that uncertainty in regression intercept is consistent with uncertainty in fecundity for a typical fish length.
Hereafter, we use the upper bound of the 95% prediction interval on equation (1) as an upper threshold on the mass of particles that fish are able to move during redd building ($M_T$).

$$M_T = 0.68 \ A_{REDD}^{0.75}$$

(2)

In using equation (2) to distinguish movable from immovable grains, we assume that the largest particles measured here are representative of the largest particles that fish moved during the spawning run. This should be reasonable given that we sampled redds in a range of substrates, including coarse-bedded reaches that salmon were not evidently able to completely use for redd building. If we used a lower threshold instead (e.g., the 75% prediction interval), it would lead to a more conservative estimate of the amount of substrate that salmon can exploit for redd building in a given reach. However doing so would require a justification for excluding many of the particles that appeared to have been moved according to our observations. We are not able to identify a clear rationale for excluding any particles except the extremes, which, according to statistical conventions, would be just 5% of the data.

Equations (1) and (2) and Figure 4a indicate that the fish that build bigger redds can also move bigger sediment grains. However, it is difficult to know which fish built which redd and thus moved each of the largest particles we measured. To definitively connect female fish size to the largest particles moved, we would have needed to watch the redd-building process around the clock, from start to finish. But because redd building can span many days [Burner, 1951; Chapman, 1988], only a few threshold particles could be linked to fish size in this way in any given spawning run. We overcame this limitation using an existing database of coupled measurements of fish lengths and redd dimensions [Crisp and Carling, 1989]. A power-law regression through the data (Figure 4b) shows that redd area increases with the 2.3 power of fish length, $L$ (in mm).

$$A_{REDD} = 3.3 \ [L/600]^{2.3}$$

(3)

The denominator of equation (3) (i.e., 600 mm) is a reference value that is close to the overall average fish length of pink, sockeye, and Chinook salmon in our study; when $L$ is equal to it, $A_{REDD}$ is equal to the power-law intercept (3.3 m$^2$). Thus, we employ the reference value to give the prefactor physical meaning as a value for a typical fish, both here, for redd area in equation (3), and for other variables of interest in regressions that follow.

Although equation (3) is specific to Atlantic salmon ($Salmo salar$) and trout ($S. trutta$ and $O. mykiss$), it is also consistent with averages and ranges of redd areas and fish lengths measured in our study of Pacific salmon, as shown in Figure 4b. Thus, it appears to be broadly suitable for linking salmonid fish lengths to threshold particle sizes. For example, by combining it with our mass-versus-area relationship from the pink, sockeye, and Chinook salmon redds (equation (2) and Figure 4a), we arrive at equation (4), which expresses the relationship between mass of the largest particle moved and fish length.

$$M_T = 1.7 \ [L/600]^{1.7}$$

(4)

This threshold relationship can be expressed in terms of particle diameter ($D_T$) by combining it with equation (5), the best-fit orthogonal regression between intermediate-axis length ($D_b$) and particle mass ($M$) from redds examined in our study (Figure 4c).

$$D_b = 94.8 M^{0.36}$$

(5)

Substituting equation (5) into (4) yields equation (6).

$$D_T = 115 [L/600]^{0.62}$$

(6)

Here the exponent and prefactor subsume the regression parameters of equations (2) through (5). Equations (4) and (6) define the threshold between movable and immovable grains as a function of fish length, as shown in Figure 4d.
The left side of equation (1) explains 73% of the variance in \( M_L \), implying that redd area (and thus fish size) is a dominant explanatory variable in the mass of the largest particle moved in redds. Adding our redd-specific estimates of flow velocity in a multiple regression analysis explains an additional 2% of the variance in \( M_L \).

Hence, although increases in flow velocity may contribute to increases in the mass of the largest particle moved in redds, the effect is evidently dwarfed by the effect of fish size. This may partly reflect covariation between flow velocity and fish length, which has been observed in previous studies [Rogers, 1987; Quinn et al., 2001] and was evident across our sites as well: velocity and redd area are positively correlated with a statistically significant coefficient of determination of 0.3 \((p < 0.001)\) across the redds we examined (see Figure 5).

Figure 5. Grain-size distributions (solid lines), threshold particle sizes, and estimated fractional coverage by movable particles (circles) for pink, sockeye, and Chinook salmon. Inset maps show study site locations (stars). Average fish lengths are from carcass surveys and corresponding threshold particle sizes are from equation (6). Grain-size distributions were measured in pebble counts conducted in 100–200 m² facies spanning a range of conditions. Dotted lines show ranges in \( D_{50} \) and \( D_{84} \) (projected onto horizontal axes) and coverage by movable particles (projected onto vertical axes) for reaches studied here.
supporting information for data). Hence, the bigger fish that build the bigger redds evidently also spawn in faster water and thus may be aided in moving larger sediment grains by higher flow-related shear stresses on the bed. However, if this were the case we might expect to see a power law exponent \( > 1 \) in equation (6). Instead it is \( 0.62 \pm 0.09 \), implying that the largest particles moved by big fish are smaller, as a percentage of body size, than the largest particles moved by small fish. This does not preclude the possibility that bigger fish are aided by faster flow. Rather, it highlights the challenge of teasing apart the effects of different potentially confounding factors in the relationship between mass of the largest particle moved and fish length.

4.2. Coverage by Movable Particles

Equation (6) is readily compatible with our reach-scale pebble counts. In pebble counts, the frequency of each grain size represents its areal coverage on the bed [Bunte and Abt, 2001]. Hence, we can use them together with estimates of \( D_T \) (from equation (6)) to determine the fractional coverage by movable particles \( (F_M) \) for fish of a given size. The general approach is illustrated in Figure 2a. Figure 5 shows how we applied equation (6) to pebble count data from our study. Figure 5 also shows that our study reaches had diverse grain-size distributions, with \( D_{50} \) ranging from 39 to 118 mm and \( D_{84} \) ranging from 86 to 385 mm (see Table 2). \( D_T \) also varied considerably, from 95 mm for pink salmon in South Prairie Creek to 128 mm for Chinook salmon in the Shasta River. Together, the variations in grain-size distributions and threshold particle sizes contribute to a wide range in inferred coverage by movable particles, from as low as 0.44 to as high as 0.92 (Figure 5 and Table 2).

Some of the substrates were very coarse, with boulders \( (D_B > 256 \text{ mm}) \) covering >10% of the bed in 7 of 31 reaches (Figure 5). Yet all of the reaches studied here supported spawning to some degree (Table 2), substantiating our general observation from the field that fish appeared to be using much of the available spawning habitat, including the coarsest substrates that could plausibly support redd building. Coarser-grained beds supported less spawning (Figure 1b) and also had less coverage by movable particles (Figure 5). We suggest that \( F_M \) is a valuable indicator of a riverbed's physical potential to accommodate redd building; in principle, it should typically reflect the maximum area that can be used for spawning in a reach under the condition that other factors such as hydraulics are not limiting.

The graphical approach of quantifying \( F_M \), illustrated in Figure 5, uses a grain-size distribution measured in a pebble count together with \( D_T \) estimated from equation (6) using fish lengths measured in carcass surveys. Thus it captures interspecific differences in ability to move sediment and construct redds in substrates with different size distributions. \( F_M \) can also be quantified analytically by measuring the area under the grain-size distribution function from zero to \( D_T \). The concept is illustrated in Figures 2b and 2c; if the shape of the distribution is known, the area can be calculated precisely by numerical integration. Riverbed sediments commonly have lognormal grain-size distributions [Bunte and Abt, 2001]. When they do, the area under the curve can be estimated without integration using equations (7) and (8).

\[
F_M = \left[1 + e^{-1.702z}\right]^{-1}
\]  

(7)

The right side of equation (7) is a one-parameter logistic function that approximates the cumulative lognormal distribution (and thus the area under the curve in Figure 2b) to within 1% when \( z \) is calculated using equation (8) [Bowling et al., 2009].

\[
z = \frac{\log (D_T/D_{50})}{\log (D_{84}/D_{50})}
\]  

(8)

Here \( D_T \) is calculated from equation (6). The terms \( \log(D_{50}) \) and \( \log(D_{84}/D_{50}) \) are the mean and standard deviation of a lognormal grain-size distribution (measured in a pebble count). The statistic \( z \) expresses the difference between the threshold size and the mean size in terms of a number of standard deviations, consistent with conventional nomenclature in statistics.

Unlike the graphical approach to estimating \( F_M \) which requires plotting the entire grain-size distribution (Figure 5), the analytical approximation of equations (7) and (8) requires only the indices \( D_{50} \) and \( D_{84} \). Hence, it can be readily applied in assessing spawning substrates and monitoring changes over time, both in ongoing studies and from historical databases, even when they do not report complete grain-size
distributions, as is commonly the case. Equations (7) and (8) are limited, however, in that their lognormal formulation may not fully capture grain-size distributions of spawning substrates in rivers. Across the reaches studied here, there are clear departures from lognormal distributions; compare, for example, curves in Figure 5, which shows measured distributions, with curves in Figure 2, which shows exact lognormal distributions. Nevertheless, for our sites the analytical approximation closely predicts coverage by movable particles measured using the graphical approach; the overall Nash-Sutcliffe efficiency statistic indicates that 92% of the variance in $F_{M}$ is explained by equations (7) and (8). Moreover, predictions differ from measurements by <14% across the entire data set. Such close agreement across the wide range of conditions considered in our study implies that errors introduced by the lognormal approximation of equations (7) and (8) may often be small enough to ignore in the prediction of $F_{M}$.

Equations (7) and (8) enable straightforward analysis of the sensitivity of $F_{M}$ to variations in grain size and fish length. For example, coverage by movable particles can be readily mapped as a function of grain-size distributions, as is commonly the case. Equations (7) and (8) are limited, however, in that their lognormal formulation may not fully capture grain-size distributions of spawning substrates in rivers. Across the reaches studied here, there are clear departures from lognormal distributions; compare, for example, curves in Figure 5, which shows measured distributions, with curves in Figure 2, which shows exact lognormal distributions. Nevertheless, for our sites the analytical approximation closely predicts coverage by movable particles measured using the graphical approach; the overall Nash-Sutcliffe efficiency statistic indicates that 92% of the variance in $F_{M}$ is explained by equations (7) and (8). Moreover, predictions differ from measurements by <14% across the entire data set. Such close agreement across the wide range of conditions considered in our study implies that errors introduced by the lognormal approximation of equations (7) and (8) may often be small enough to ignore in the prediction of $F_{M}$.

Equations (7) and (8) enable straightforward analysis of the sensitivity of $F_{M}$ to variations in grain size and fish length. For example, coverage by movable particles can be readily mapped as a function of grain-size distributions, represented here by $D_{84}/D_{50}$ (a measure of the width of the grain-size distribution) and $D_{50}$ (the central tendency) for four fish lengths corresponding to different threshold particle sizes marked by vertical contour lines. (a–c) Open symbols show grain-size distributions from previous compilation of Figure 1a (after Kondolf and Wolman [1993]) for a range of fish sizes similar to the length listed in each label. Filled symbols mark substrates in reaches where we observed pink (Figure 6a), sockeye (Figure 6b), and Chinook salmon (Figure 6c) spawning in this study. (d) Open symbols are from the previous compilation. Filled symbols are from the new compilation of Chinook salmon data of Figure 1a as follows: red—Yuba River, $N = 71$ [Moir and Pasternack, 2010]; yellow—Feather River, $N = 47$ [California Department Water Resources, 2004]; brown—Sacramento River, $N = 27$ [The Nature Conservancy et al., 2008].

**Figure 6.** Coverage by movable particles mapped as a function of grain-size distribution, represented here by $D_{84}/D_{50}$ (a measure of the width of the grain-size distribution) and $D_{50}$ (the central tendency) for four fish lengths corresponding to different threshold particle sizes marked by vertical contour lines. (a–c) Open symbols show grain-size distributions from previous compilation of Figure 1a (after Kondolf and Wolman [1993]) for a range of fish sizes similar to the length listed in each label. Filled symbols mark substrates in reaches where we observed pink (Figure 6a), sockeye (Figure 6b), and Chinook salmon (Figure 6c) spawning in this study. (d) Open symbols are from the previous compilation. Filled symbols are from the new compilation of Chinook salmon data of Figure 1a as follows: red—Yuba River, $N = 71$ [Moir and Pasternack, 2010]; yellow—Feather River, $N = 47$ [California Department Water Resources, 2004]; brown—Sacramento River, $N = 27$ [The Nature Conservancy et al., 2008].
indices for different fish lengths (Figure 6). The spacing between contours on such a map shows the sensitivity directly; a given percent change in \( D_{50} \) or \( D_{84}/D_{50} \) induces a larger change in \( F_M \) where contours are closer together. For example, when \( D_{84}/D_{50} \) (the spread in the distribution) is big, changes in \( D_{50} \) lead to smaller changes in \( F_M \) than when \( D_{84}/D_{50} \) is small. Nevertheless, for all values of \( D_{84}/D_{50} \) and for all fish lengths, increases in \( D_{50} \) lead to decreases in \( F_M \). In contrast, increases in the width of the grain-size distribution (i.e., \( D_{84}/D_{50} \)) lead to increases, decreases, or no change at all in \( F_M \) depending on how \( D_{50} \) compares to \( D_F \). For example, when \( D_{50} = D_F \), half of the bed is movable (i.e., \( F_M \) equals 0.5) irrespective of the width of the distribution; this is illustrated by the vertical contour lines in Figure 6. Meanwhile, as fish length increases (from one plot to the next), \( D_F \) increases (equation (6)), shifting the entire surface of predicted \( F_M \) values to the right in the plots of \( D_{84}/D_{50} \) versus \( D_{50} \). Thus, for any combination of \( D_{50} \) and \( D_{84} \), \( F_M \) is higher when fish are longer; bigger fish can use more of a bed for spawning, because they can move larger particles than smaller fish.

Substrates used by salmon for spawning span a broad range in coverage by movable particles, as shown in Figure 6 by the scatter of measured grain-size indices over the mapped surfaces of \( F_M \). In contrast, the riverbeds used to define the 10% rule [Kondolf and Wolman, 1993] span a relatively narrow range, with \( F_M > 0.8 \) in all but one case. This suggests that spawning at the sites in the compilation of Kondolf [1988] was nearly unrestricted by coarse grain sizes on the bed. Yet our expanded compilation shows that female salmon can build redds even when coarse particles greatly reduce the area of usable substrate. For instance, predicted \( F_M \) is as low as \( \sim 0.2 \) for one case in Figure 6d. Clearly, the 10% rule would fail to predict spawning at such sites. In contrast, equations (7) and (8) explain spawning at all of the sites in our extended compilation in terms of differences in capacity to accommodate redd building, denoted as \( F_M \) in this analysis.

### 4.3. Substrate Spawning Capacity and Reproductive Potential

Coverage by movable particles is the fractional area (in \( \text{m}^2 \) per \( \text{m}^2 \)) of riverbed that female salmon can use for redd building. We can couple it with an estimate of the area of a typical redd (Figure 4b), to predict the riverbed’s “spawning capacity” \( (N_{\text{redds}}) \) which we define here as the number of redds per square meter that female fish can build in a reach, assuming hydraulic conditions are favorable.

\[
N_{\text{redds}} = F_M / A_{\text{redd}} 
\]  

(9)

Together, equations (6)–(9) predict that a hypothetical group of 600 mm long female salmon could build a maximum of 0.21 redds/\( \text{m}^2 \) in a substrate with \( D_{50} = 75 \text{ mm} \) and \( D_{84} = 200 \text{ mm} \). This corresponds to an estimated spawning capacity of 21 redds for a reach with 100 \( \text{m}^2 \) of riverbed area that is suitable in hydraulics and other factors that influence spawning besides grain size. To determine whether such predictions are realistic, we compared calculated spawning capacity with observations of spawning use for each of our study reaches, which were all hydraulically suitable for spawning (i.e., in tailouts and riffles where numerous fish were actively building redds). For these comparisons, spawning capacity was estimated from equations (6)–(9) using \( D_{50}, D_{84}, \) and \( L_{\text{fish}} \), while spawning use was based on the measured area and number of redds observed in each of the reaches (Table 2). Many of the observed values of spawning use plot close to a 1:1 line with spawning capacity (Figure 7). Spawning at or near capacity in hydraulically suitable reaches should be expected given that each of our sites boasted healthy populations of returning fish during the period of study (Table 1). This suggests that equation (9) may often yield realistic estimates of spawning capacity in rivers and creeks.

Taking the analysis a step farther, we use equation (10) to estimate the “reproductive
Figure 8. Functional relationships between salmon spawning and fish length. Fractional coverage by movable particles (after equations (7) and (8), with $D_{50} = 80$ mm and $D_{84} = 145$ mm) increases monotonically with fish length to up to nearly 0.9 (where ~90% of the bed surface is movable) for $L = 1000$ mm (a large Chinook salmon). The benefits of being bigger and thus able to move more sediment are partly offset by the need to build bigger redds (after Figure 4b). The production of more eggs per fish (i.e., higher fecundity) is another advantage of being bigger. The relationship between the number of eggs per unit area ($N_{Eggs}$) and $L$ reflects the tradeoff in a maximum in $N_{Eggs}$ at an intermediate, “optimum” fish length (denoted by arrows).

Figure 9. (a) Optimal reproductive potential and (b) corresponding fish lengths for different grain-size distributions. In each plot, the filled circle denotes grain-size distribution for circumstances shown in Figure 8 ($D_{50} = 80$ mm and $D_{84} = 145$ mm). Contours mark (a) equal numbers of eggs per m$^2$ and (b) fish lengths in mm. Dark and light shading show 50th and 90th percentile density regions, respectively, for all data plotted in Figure 6, thus highlighting a range of conditions in riverbeds where salmon commonly spawn.
potential" of a substrate, denoted $N_{\text{EGGS}}$, and defined as the number of eggs per unit area (e.g., eggs/m$^2$) that a hydraulically favorable riverbed can accommodate for fish of a given size.

$$N_{\text{EGGS}} = F_{\text{m}}E / A_{\text{REDD}}$$  \hspace{1cm} (10)

Here $E$ is fecundity, the number of eggs produced per fish. Pacific salmon almost never build more than one redd before they die [Quinn, 2005], so $E$ is also the maximum number of eggs deposited per redd (in units of eggs/redd). $E$ can be estimated from fecundity relationships. For example, equation (11) is a best-fit regression through average fecundity and fish length data for 13 species of salmon, trout, and char [Quinn, 2005].

$$E = 8.1L - 1450$$  \hspace{1cm} (11)

This equation explains 70% of the variance in the average fecundity data reported by Quinn [2005] (Table 3). Hence, it should be useful for generalized estimates of the reproductive potential of spawning substrates when the number of redds per unit area can be estimated from equations (6)–(9). However, it is important to recognize that substantial regional and intrapopulation differences in fecundity-length relationships have been reported in the literature [Healey and Heard, 1984; Beacham and Murray, 1993]. Such variability introduces potential for error in coupling equation (11) with equation (10). To minimize these errors we advise use of fecundity values that are specific to the population of interest. For simplicity in the present analysis, we retained equation (11) and combined it with equation (10). Together these equations predict that a hypothetical group of 600 mm long fish could place as many as 715 eggs/m$^2$ in a reach with $D_{50} = 75$ mm, $D_{84} = 200$ mm, and favorable hydraulic conditions. This would be a conservative estimate in reaches where superimposition during subsequent spawning allows multiple females to deposit eggs within the confines of a typical redd [McNeil, 1964; van den Berghe and Gross, 1984].

Fish length influences fecundity (equation (11)), redd area (equation (3)), and the fractional coverage by movable particles (equations (6)–(8)). These relationships can be combined to evaluate the net effect of fish length on reproductive potential for a bed with a given grain-size distribution, as shown in Figure 8 for $D_{50} = 80$ mm and $D_{84} = 145$ mm. Here $N_{\text{EGGS}}$ increases monotonically up to a maximum (at $L \approx 470$ mm) and then decreases with additional increases in length. This reflects a previously unrecognized tradeoff in the reproductive potential of spawning substrates. As fish length increases, the benefits of carrying more eggs and moving larger grains are partly offset by the need to build bigger redds. Bigger fish generally use more of a riverbed for spawning and can deposit more eggs per redd than smaller fish. Yet they do not necessarily deposit more eggs per unit area across a given reach, because they also tend to require bigger redds, leaving less space for other fish in the reach. Our model captures this tradeoff as a peak in reproductive potential at an optimum, intermediate fish length.

4.4. Optimal Reproduction

The optimum in reproductive potential should differ from one substrate to the next, due to variations in coverage by movable particles. For insight on how, we solved equation (10) for the maximum in $N_{\text{EGGS}}$ (Figure 9a) and the corresponding optimum fish length (Figure 9b) for the same combinations of $D_{84}/D_{50}$ and $D_{50}$ that we considered in Figure 6. For any given value on the vertical axis, increases in $D_{50}$ correspond to decreases in the predicted maximum number of eggs a reach can support. They also correspond to increases in the predicted length of fish that can deposit the most eggs per unit area (i.e., the fish with the optimum length). Likewise, except in the coarsest beds (on the far right of Figures 9a and 9b), increases in the width of the distribution (i.e., the ratio $D_{84}/D_{50}$) reduce the predicted maximum reproductive potential and increase the corresponding optimum fish length.

5. Discussion

5.1. Model Limitations

The development of equations (1), (2), (4), and (5) incorporates data from spawning fish and substrates with a broad but not exhaustive range of plausible sizes (Table 2). Can it be extrapolated to predict spawning by
smaller and larger fish in coarser and finer substrates? One premise of extrapolating our approach is that $F_M$ can generally be estimated from grain-size distributions and threshold particle sizes using graphical (Figures 2 and 5) or analytical methods (equations (7) and (8)). We suggest this should be true for salmonids that build redds by cutting at particles on the bed. Hence, we expect that our model’s estimates of reproductive potential will be broadly useful both in river ecosystem management and salmonid population modeling. Nevertheless, the model does have a number of limitations.

One limitation is that the model does not account for survival-to-emergence, which can be reduced by bed scour [Montgomery et al., 1996] and entrainment of pore-clogging fine sediment into the bed [McNeil and Ahnell, 1964; Chapman, 1988]. It also does not account for effects of size-related differences in egg-burial depths; bigger fish tend to dig deeper redds, which may put their eggs at a disadvantage in fine substrates if they are buried so deeply that they cannot receive adequate through-flow of oxygenated water [Holtby and Healey, 1986]. More generally, our model does not address differences in reproductive success of females, which can vary with fish size and arrival time at spawning grounds [Dickerson et al., 2005; Anderson et al., 2010]. Reproductive success may also depend on grain size if, for example, redds built in coarser substrates are shallower and thus more prone to scour. Our model does not address this possibility but rather accounts solely for the accommodation space provided by the substrate for spawning by fish of different sizes. Future work could add refinements that incorporate the influence of these factors on survival to emergence as a correction factor on our estimates of reproductive potential from equation (10).

An additional limitation of our model—and one which it shares with the 10% rule for assessing spawning habitat [Kondoff and Wolman, 1993]—is that the riverbed must be suitable in other aspects of spawning habitat, including flow depth, velocity, and water temperature [Knapp and Preisler, 1999; Allen, 2008; Moir et al., 2009; Moir and Pasterneck, 2010]. To fully account for the effects of these other factors that influence spawning use and success, it would be necessary to either model them or measure them directly and thus determine the fraction of each reach that is both thermally and hydraulically suitable for redd building. The grain-size model expressed in equations (6)–(9) could then be used to estimate the spawning capacity and reproductive potential of the otherwise suitable fractions of the reach.

In our analysis of salmon spawning of rivers and creeks in California and the Pacific Northwest, application of the model expressed in equations (6)–(10) to diverse reaches. As an outgrowth of this work, it should be possible to apply it to individual fish as well using equation (12), which simply combines equations (6) and (8) explicitly.

$$
Z = \frac{\log \left( \frac{115 (L/600)^{0.62}}{D_{50}} \right)}{\log (D_{84}/D_{50})}
$$

(12)

For example, equation (12) could be used in a Monte Carlo analysis of individual fish to determine uncertainties in $F_M$ (equation (7)) for fish populations with different distributions of fish sizes. This would help in evaluating the sensitivity of spawning capacity (equation (8)) and reproductive potential (equation (10)) to differences in the body-size distributions of different salmon populations.

5.2. Assessing Salmon Spawning Substrates

Our framework for quantifying the reproductive potential of salmon spawning substrates in rivers improves the scientific basis for aquatic habitat assessment. Biologists and ecosystem managers can now estimate the number of redds and eggs a reach can accommodate for a given species or size of fish (Figure 8). Alternatively, they can predict which-sized fish can spawn most productively in a given riverbed (Figure 9b). Or they can use our model to quantify changes in reproductive potential over time from historical records of grain size. This could help improve estimates of how much spawning habitat has been lost due to human activities such as gravel mining and dam construction [Yoshiyama et al., 1998]. It may also help clarify the role of spawning habitat loss in historical collapses of salmon populations [Nehlsen et al., 1991]. As dams are increasingly removed from rivers in California and the Pacific Northwest [Pess et al., 2008; Major et al., 2012; U.S. Department of the Interior et al., 2012], it would be helpful to have tools to predict and monitor changes in salmon carrying capacity that result from reopening habitat upstream and changing...
habitat downstream of removed dams [Pess et al., 2008]. Our model provides such a tool; it can be used to predict maximum carrying capacity of upstream reaches and provide a baseline for tracking changes in downstream reaches as sediment is released and as flow regimes revert from regulated to natural.

5.3. Managing for Optimal Reproductive Potential
In addition to improving habitat assessment, our framework for quantifying reproductive potential could also change how spawning substrates are managed. For example, our methods can help make restoration efforts more cost-effective by predicting how specific changes in $D_{50}$ and $D_{84}$ will increase reproductive potential. For the first time, the value of substrate restoration can be expressed quantitatively, in terms of added reproductive potential (i.e., number of eggs/m$^2$) per unit cost. Our framework can also be used in cost-benefit analyses of alternate restoration strategies. For example, it can help managers determine whether reproductive potential can be improved without gravel augmentation, via selective removal of coarse sediment. Where gravel augmentation is warranted, managers can determine if minor adjustments in grain-size distribution will suffice in place of the common practice of burying the bed in sediment of a specified size [Bunte, 2004]. Thus, decisions about restoration can be informed with a quantitative analysis of the benefits of habitat restoration.

Once a bed is restored, best practices call for any subsequent deterioration to be tracked over time to evaluate the sustainability of habitat improvements [Kondolf and Micheli, 1995; Wohl et al., 2005; Kondolf et al., 2007]. One potential source of deterioration is fluvial scour that transports added sediment away from the restoration site. In addition, salmon themselves can coarsen the bed during spawning [Montgomery et al., 1996] via size-selective transport [Kondolf et al., 1993] at rates that sometimes exceed transport by annual floods [Hassan et al., 2008]. Our model can be used to inexpensively track how these and other factors modulate reproductive potential over time. All that is needed is periodic repeat measurement of bed-surface grain-size distributions.

5.4. Biophysics of Coarse Particle Excavation
Our analysis of particles moved by female salmon in redds (Figure 4) raises new questions about the biophysics of redd building. Foremost, we lack a physical basis for explaining the 1.7 power-law exponent in equation (4). When coupled with well-established cube-law allometry between fish mass and length [Froese, 2006], equation (4) implies that $M_T$ scales with fish mass to the 0.6 power. Thus, heavier fish move heavier particles, but not in direct proportion to their larger mass. What drives the apparent decrease in efficiency with size in ability to generate forces that excavate particles and move them downstream? Decades of studies of fish locomotion offer some clues. A similar decline in efficiency, relative to size, is evident in salmon sprinting speeds; bigger fish swim faster overall during bursts, but travel fewer fish lengths per second than their smaller counterparts [Webb, 1975]. Redd building is like sprint swimming in that fish move sediment particles in bursts of cutting motions. Are size-related decreases in efficiency of sprint swimming and redd building outcomes of the same biophysical limitation? If so, does the limitation reflect the energetics and physics of burst swimming [Brett and Glass, 1973]? Could it partly reflect an adaptation to redd building in coarse substrates? Answering these questions would shed new light on salmon energetics and evolutionary adaptations of redd building and locomotion. As a first step for future studies of these relationships, it should be possible to use available data on burst speeds from the literature to estimate the critical shear stress associated with the largest moved particle in redds.

5.5. Grain-Size Distributions and Species Resilience
Salmon can spawn in substrates with a remarkably wide range in grain-size distributions, from fine to coarse (Figure 6), often working around the largest grains [Quinn et al., 1995] and commonly moving particles that are on par with their own body mass (Figure 4a). Yet they evidently build the most redds and thus thrive best in substrates that are relatively fine-grained (Figure 1b). This raises the question of why they use coarse riverbeds at all. They could be driven to them by a paucity of finer-grained substrates with suitable flow depths, velocities, and water temperatures. This is implicitly assumed in gravel augmentation projects that seek to install movable sediment at sites where hydraulic conditions are ideal. Yet our finding that reproductive potential is coupled to fish size (the optima in Figures 8 and 9), implies there may be advantages to spawning in coarse substrates beyond their use as a last resort when finer substrates are not available. For example, if fish size is strongly selected by substrate grain size (Figure 9b), the availability of...
diverse grain-size distributions, including coarse-bedded reaches, would tend to strengthen the portfolio effect for salmon [Greene et al., 2010; Schindler et al., 2010] by promoting diversity in populations from reach to reach and river to river. This would help buffer against wide fluctuations in salmon populations and the ecosystem services they provide [Hilborn et al., 2003; Greene et al., 2010]. Thus, species resilience may depend in part on access to habitats with a diverse array of grain-size distributions; this is corroborated by observations that bigger fish spawn in reaches with coarser substrates in well-studied sockeye salmon spawning habitat in Alaska [Quinn et al., 2001]. Our approach provides a way to determine how diversity in grain size translates into diversity in reproductive potential. It also provides managers with a tool for optimizing restoration investments for enhanced diversity and thus possibly for improved species resilience.

The importance of substrate diversity points to an underappreciated aspect of dam-related declines in salmon populations in the 20th Century. The biased loss of access to relatively coarse substrates in steep reaches upstream of dams reduced both the diversity and the amount of spawning habitat in many rivers. The loss of substrate diversity in particular may have contributed to a loss in resilience through a weakened portfolio effect, thus amplifying the well-studied impacts of severing salmon from their ancestral spawning grounds. Meanwhile, in reaches downstream of dams, systematic coarsening and narrowing in grain-size distributions [Ligon et al., 1995; Kondolf, 1997] likely reduced substrate reproductive potential for locally adapted populations (moving from left to right and top to bottom in the plots of Figures 6 and 9), even as interbreeding [Mackey et al., 2011] and competition [Harvey and Nakamoto, 1997; Ward et al., 2006] contributed to losses in diversity among previously isolated stocks. Thus, losses in substrate diversity both upstream and downstream of dams likely contributed to observed population declines [Nehlsen et al., 1991] and weakening in the portfolio effect [Carlson et al., 2011b] in the years following the peak of dam building in California [Yoshiyama et al., 1998] and the Pacific Northwest.

5.6. Spatial Distribution of Salmon by Size

If substrate grain size influences fish size as our analysis suggests (Figure 9), then it points to an underappreciated evolutionary connection between salmon and their spawning grounds. Namely, spawning site selection by different-sized fish may reflect an optimization related to the lithologic, geomorphic, and climatic factors that influence grain-size distributions in rivers [Sklar et al., 2006; Marshall and Sklar, 2012]. If so, it might help explain the distribution of salmon stocks and species from reach to reach and from river to river. Thus, substrate grain-size distribution is one of many factors, including reproductive success and the timing of arrival at spawning grounds [Holtby and Healey, 1986; Dickerson et al., 2005; Anderson et al., 2010], that might influence the distribution of salmon sizes across different rivers.

6. Conclusions

We showed that the existing framework for assessing salmon spawning substrates substantially undervalues the reproductive potential of coarse riverbeds. We presented a new mechanistic framework for estimating the number of redds and eggs a substrate can accommodate when other conditions such as flow velocity and depth are not limiting. This field-calibrated approach captures interspecific differences in ability to move sediment and build redds. It is easy to apply in the assessment of spawning habitat in creeks and rivers, only requiring estimates of $D_{50}$, $D_{90}$, and the length of the fish of interest. As might be expected, we found that bigger fish moved larger sediment. Thus, we infer that they can also use more of a given riverbed for spawning. Because they typically have higher fecundity (based on data from previous studies), they can also generally deposit more eggs per redd. Yet, despite the apparent advantages of being bigger, the biggest fish may be at a disadvantage in terms of reproductive potential, relative to their smaller counterparts; in a previously unrecognized tradeoff, our results suggest that the number of eggs a substrate can accommodate (i.e., its reproductive potential) is maximized for fish of intermediate length due to increases in redd area with increasing fish size. More work is needed to test this hypothesis and determine the extent to which the effect is moderated by differences in survival to emergence of offspring (i.e., reproductive success) of different-sized female salmon. Our observation that a riverbed’s grain-size distribution may be optimal for fish of a particular size raises the possibility that differences in grain size play a role in setting river-to-river differences in salmon size and species. This further implies that salmon...
population diversity and species resilience may be linked to the lithologic, geomorphic, and climatic factors that determine grain-size distributions in rivers. Our approach permits future researchers to quantify this linkage in greater detail and provides a tool for managing substrates in support of optimal substrate reproductive potential and species resilience.

**Notation**

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>$A_{REDD}$</td>
<td>Map area of redd, m$^2$.</td>
</tr>
<tr>
<td>$D_{50}, D_{84}$</td>
<td>50th and 84th percentiles of grain diameters on riverbed, mm.</td>
</tr>
<tr>
<td>$D_i$</td>
<td>Intermediate-axis diameter of a sediment grain, mm.</td>
</tr>
<tr>
<td>$D_T$</td>
<td>Intermediate-axis diameter of largest sediment grain that salmon of a particular size can move during redd building, mm.</td>
</tr>
<tr>
<td>$E$</td>
<td>Fecundity, which is the number of eggs female salmon produce (eggs/fish) and thus also the maximum number they can deposit within an individual redd, eggs/redd.</td>
</tr>
<tr>
<td>$F_M$</td>
<td>Fractional coverage of bed by particles that female salmon can move during redd building.</td>
</tr>
<tr>
<td>$L$</td>
<td>Fork length of female salmon, mm.</td>
</tr>
<tr>
<td>$M$</td>
<td>Mass of particle sampled from redd, kg.</td>
</tr>
<tr>
<td>$M_l$</td>
<td>Mass of largest particle moved in redd, kg.</td>
</tr>
<tr>
<td>$M_T$</td>
<td>Mass of largest particle that salmon of a particular size can move during redd building, kg.</td>
</tr>
<tr>
<td>$N_{REDDS}$</td>
<td>Maximum number of redds that can be built per unit area in a given reach, redds/m$^2$.</td>
</tr>
<tr>
<td>$N_{EGGS}$</td>
<td>Substrate reproductive potential, defined as the maximum number of eggs that can be deposited per unit area in a given reach, eggs/m$^2$.</td>
</tr>
<tr>
<td>$z$</td>
<td>Dimensionless exponent in one-parameter logistic-function approximation of the cumulative normal distribution.</td>
</tr>
</tbody>
</table>

**References**


Quinn, T. P. (2005), Behavior and Ecology of Pacific Salmon and Trout, UBC Press, Vancouver, B. C.


