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Impact of Fine Sediment on Egg-To-Fry Survival of Pacific Salmon: A Meta-Analysis of Published Studies

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Egg-to-fry survival of salmonids is tempered by habitat degradation, including increased sediment in streams. To best manage multiple salmon species and prioritize scarce habitat restoration funds for the benefit of fish recovery, many studies have described and predicted the relationship between fine sediment deposited in spawning gravels and salmonid egg-to-fry survival. In this article, we used published studies, agency reports, and university theses ($N = 14$) to create predictive relationships between percent fine sediment and egg-to-fry survival of Chinook (Oncorhynchus tshawytscha), coho (O. kisutch) and chum (O. keta) salmon, and steelhead trout (O. mykiss). In our analysis, coho survival tended to decline more rapidly per unit sediment increase and chum survival least rapidly. Threshold effects were observed, with survival dropping rapidly when percent fines less than 0.85 mm was greater than 10%. For other size classes of fines, a threshold was primarily observed only for eyed egg survival when fines exceeded 25–30%. Our predictive models combine both field and laboratory data and take into account a variety of conditions; they include estimates of uncertainty in the impact of sediment on egg-to-fry survival. These models can be used to forecast effects of watershed management practices on salmonids and to make comparisons between predicted salmonid survival rates under alternative management strategies for conditions where fine sediment is the limiting factor for survival.

Keywords salmon incubation, salmon spawning, sediment deposition

INTRODUCTION

Since six species of Pacific salmonids were listed by the U.S. Endangered Species Act (ESA) as threatened or endangered (Knudsen et al., 2000), research and modeling has focused on factors that threaten the continued existence of these species. Habitat degradation is key among these factors (Nehlsen et al., 1991), including instream sedimentation resulting from human activities such as timber harvest, agriculture, urban and rural residential development, and road construction (e.g., Bjornn and Reiser, 1991; Waters, 1995). Increasing amounts of fine sediment (∼2 mm or smaller) in spawning gravels has been shown to decrease survival of salmonid eggs to emergence (Bjornn and Reiser, 1991; Everest et al., 1987; Greig et al., 2005a, 2007).

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Because of the importance of fine sediment deposition to early salmonid survival, a great deal of research effort has gone into modeling the processes by which fine sediment enters and moves through stream systems. Our ability to model mechanisms by which land use increases sediment delivery to streams (e.g., the WEPP model: Elliot et al., 1995; Elliot and Hall, 1997; the PSYCHIC model: Davison et al., 2008) as well as our ability to model the mechanisms of transport and storage through stream networks (e.g., NetStream, Miller, 2003; the EUROSEM-GRIDSEM model, Botterweg et al., 1998; LISEM, DeRoo and Wessling, 1996) has become more sophisticated. Additional research has focused on the empirical evaluation of these processes (e.g., Collins and Walling, 2004; Heywood and Walling, 2003; Walling et al., 2008; Cai et al., 2005). As a result, we are increasingly confident in our predictions of how land use affects sediment deposition in stream reaches (Nilsson et al., 2003; Opperman et al., 2005).

However, sediment modeling exercises are often conducted at coarse resolutions across large extents, whereas our

understanding of how sediment impacts salmonid egg-to-fry survival comes from laboratory experiments or observations at the scale of a habitat unit or redd. Extrapolating results of individual survival studies to the larger scales at which we can restore sediment processes may be inappropriate because of differences in experimental conditions (i.e., season, geomorphology of stream, water chemistry), methods (i.e., laboratory vs. *in situ* studies, genetic origin of fish), and response variables (i.e., life stage, sediment metric) considered. As well, there are many factors other than sediment, such as dissolved oxygen, incubation temperatures, and biological controls, that contribute to the complexity of the spawning environment at the redd scale, and therefore to salmon survival (Malcolm et al., 2003; Greig et al., 2005b). Yet, for successful management of watersheds and salmon populations, managers need a reliable way to link disparate types of survival analyses.

Managers often rely on complex models to select restoration projects that will have positive benefits for fish (e.g., EDT, Mobrand Biometrics Inc., 2004). If such models are used, then they must accurately predict not only which projects are likely to result in a decrease in fine sediment deposition but, ultimately, how survival of salmonids will respond to that reduced sediment deposition under a variety of conditions. While there are more detailed models that include several of the suite of factors present in the natural spawning environment (e.g., Alonso et al., 1996; Wu, 2000), calibration of these models is a large task and must be repeated for each new basin. Accurate prediction of fish response over large spatial extents requires models developed from studies conducted over a range of conditions. Since landscape scale studies are generally lacking, one way to address this gap is to pool results from multiple studies, thus incorporating the variability observed between individual studies into the modeled relationship. Incorporating known sources of variability is important whether the model has a narrow focus, e.g., the response of egg-to-fry survival to changes in sediment composition, or is an input to a more complex model of fish response to changes in multiple environmental factors.

Development of quantitative relationships linking sediment and survival that are robust to these differences in experimental conditions, methods, and response variables will improve our ability to link small-scale observations on fish survival to large-scale sediment input, routing, and storage models. We have compiled data from individual published studies relating egg survival to fine sediment composition, reanalyzed these data together, and developed models to predict species-specific mean survival as a function of sediment composition. In this modeling effort, we assume that it is the sediment quantity and to some extent the grain size that is primarily controlling survival. We do not account for the host of non-sediment factors, e.g., the potential impact of poor quality groundwater upwelling (Malcolm et al., 2003), on salmon survival.

We present a review of existing published data relating sediment to salmon egg-to-fry survival for steelhead trout (*Oncorhynchus mykiss*) and Chinook (*O. tshawytscha*) and chum (*O. keta*) and coho (*O. kisutch*) salmon. We explore multiple early life stages and sediment size classes in freshwater systems of the Pacific Northwest United States to provide a meta-analysis of these existing data. Our meta-analysis is unique in that it yields models that are robust to the details of particular experiments as well as provides improved quantitative estimates of model and parameter uncertainty. We compare these robust models to identify species-specific differences and gain insight into the structure of the mechanistic relationships involved. For example, we ask whether the relationships between sediment and survival are linear, or whether they include a threshold above which survival is improbable? These robust models not only increase our understanding of watershed and salmonid ecology, but also provide powerful management tools by enabling combinations of models and estimates of uncertainty.

METHODS

Existing Data on Salmonid Egg-to-Fry Survival

We surveyed the primary literature for studies on salmonids in the Pacific Northwest that investigated the effects of fine sediment deposition on egg-to-fry survival. Of the 96 papers identified, most discussed observed or implied effects, but did not provide data or experimental analysis. Fourteen of these studies provided data that we could reanalyze, including seven experiments with Chinook salmon, four with steelhead, six with coho, and three with chum (Table 1). Some of these investigated the effects of sediment on survival of wild fish eggs in streams (e.g., Cederholm and Lestelle, 1974; Hall and Lantz, 1969), while others (e.g., Reiser and White, 1988; Tappel and Bjornn, 1983) described laboratory experiments, often using hatchery fish reared at high densities. Because of a general lack of field studies (e.g., all studies on Chinook salmon were laboratory studies), and because the laboratory studies have been well cited, we reasoned that including them would strengthen our dataset. In addition, our methodology would test whether the conclusions from field studies differed from those in the lab, and hence whether combining them was justified statistically. The sieve size used to quantify the sediment composition varied between studies, but, within each of the four groups considered here, all were within 0.2 mm (0.8–0.85 mm, 3.327–3.4 mm, 4.6–4.8 mm, 6.35–6.4 mm). We reanalyzed the data using one or more of five measures of substrate composition: percent fines < 0.85 mm, percent fines < 3.4 mm, percent fines < 4.8 mm, percent fines < 6.4 mm, and geometric mean particle size. The Fredle index (Lotspeich and Everest, 1981) has been shown to produce higher correlations with survival than the geometric mean (Chapman, 1988, using Tappel and Bjornn's (1983) data); however, the calculation of the index requires additional sediment size data not available from all papers reporting geometric means. In fact, we could only add a single study to what Chapman (1988) had summarized, so we chose not to include this metric.

Table 1 Pacific salmonid studies evaluated, including whether the study was conducted in an artificial (lab) or natural (field) environment, the number of redds monitored in each experiment, the life stage at which monitoring began, the sediment metric(s) used, and the slope of the logistic regression line fit to the original data

Source	Type no. redds[a]	Species	Life stage	Sediment metric	Slope (linear, quadratic)[b]
Bennett et al., 2003	Lab 8	Chinook	Green egg-to-fry	% fines < 0.85 mm	0.0602, –0.0032
				% fines < 3.4 mm	0.0312, –0.0038
				% fines < 4.8 mm	0.0268, –0.0029
				% fines < 6.4 mm	0.0243, –0.0022
				Geometric mean	0.1527
Bjornn, 1968	Lab 32	Chinook	Green egg-to-fry	% fines < 6.4 mm	–0.1425
Bjornn, 1969	Lab 28	Chinook	Green egg-to-fry	% fines < 6.4 mm	–0.0066, –0.0018
		Steelhead	Green egg-to-fry	% fines < 6.4 mm	–0.0795
Cederholm and Lestelle, 1974	Field 11	Steelhead	Eyed egg-to-yolk absorption	% fines < 0.841 mm	—
				% fines < 3.36 mm	+
Cederholm and Salo, 1979	Lab 31	Coho	Green egg-to-fry	% fines < 0.85 mm	–0.1971
				% fines < 3.36 mm	–0.0886
Hall and Lantz, 1969	Field 20	Coho	Egg-to-fry[c]	% fines < 0.83 mm	–0.2166
Hall, 1986	Lab 6	Chinook	Eyed egg-to-fry	% fines < 0.8 mm	–0.1578, –0.0058
		Chum	Eyed egg-to-fry	% fines < 0.8 mm	–0.1458
		Coho	Eyed egg-to-fry	% fines < 0.8 mm	–0.3328, 0.0046
Koski, 1966	Field 22	Coho	Egg-to-fry[c]	% fines < 3.327 mm	–0.1203
Koski, 1975	Lab 35	Chum	Egg-to-fry[c]	% fines < 3.327 mm	0.2469, –0.0037
Reiser and White, 1988	Lab 15	Chinook	Green egg-to-fry	% fines < 0.84 mm	–0.1447
				% fines < 4.6 mm	–0.0738
		Steelhead	Eyed egg-to-fry	% fines < 0.84 mm	–0.1630
				% fines < 4.6 mm	+
		Steelhead	Green egg-to-fry	% fines < 0.84 mm	–0.1367
				% fines < 4.6 mm	–0.0550
Reiser and White, 1990	Lab 8	Chinook	Eyed egg-to-fry	% fines < 0.84 mm	—
				Geometric mean	–0.4870, 0.0119
		Chinook	Green egg-to-fry	% fines < 0.84 mm	–0.1458
				Geometric mean	0.0710
Scrivener and Brownlee, 1989	Field 13–14	Chum	Egg-to-fry[c]	Geometric mean	0.3347
		Coho	Egg-to-fry[c]	Geometric mean	0.2048
Tagart, 1984	Field 18	Coho	Egg-to-fry[c]	% fines < 0.85 mm	—
Tappel and Bjornn, 1983	Lab 15	Chinook	Eyed egg-to-fry	% fines < 0.85 mm	–0.2818
				% fines < 4.76 mm	0.0411, –0.0034
				% fines < 6.35 mm	0.0254, –0.0025
				Geometric mean	1.2135, –0.0382
		Steelhead	Eyed egg-to-fry	% fines < 0.85 mm	–0.2870
				% fines < 4.76 mm	–0.1165
				% fines < 6.35 mm	–0.0969
				Geometric mean	1.1284, –0.0363

[a] Number of redds (or artificial equivalent) is the same for each experiment unless indicated otherwise.
[b] All relationships shown are statistically significant (Wald test) at the 0.05 level. A – indicates the slope is not significant , + indicates the individual relationship is not statistically significant, but when combined with other observations within the same species and egg stage, a significant relationship emerges.
[c] Development stage not identified.

Meta-analysis includes a variety of statistical methods for synthesizing the results of individual studies (e.g., Hedges and Olkin, 1985). One requirement for meta-analysis is that there is a common summary statistic across studies, which is often a measure of a treatment effect in a series of experiments. Under certain assumptions, the analysis of the summary statistics is equivalent to the analysis of the original data (Olkin and Sampson, 1998; Mathew and Nordström, 1999). We chose to utilize the original data in our meta-analysis since it was generally available and the published summary statistics were not consistent across studies. Furthermore, we felt that a logistic model more accurately reflected the relationship between sediment and survival in that survival is constrained between zero and one. By using this novel approach, we hoped to improve on past analyses.

The individual datasets that were used to develop new models (based on combined datasets) are identified in Table 1. We only combined studies where either individual relationships with fine sediment substrate were significant or a significant relationship was found when combined with other data in the same species and egg stage class. We included all data that showed any evidence of a statistical relationship between fines and survival

and excluded the few datasets without a clear relationship (only 8%).

Statistical Analysis

We used logistic regression models to fit data from multiple sources. The logit of survival was regressed on the various measures of sediment composition, where $\text{logit(s)} = \log(\frac{s}{1-s})$, the log of the odds of survival. The relationship between the logit of survival and fines is linear, whereas the relationship between survival and fines is not. The transformation is survival $= \frac{1}{1+e^{\beta_0+\beta_1 * Sediment}}$. With a single independent variable that has only a linear component, the odds of survival, $(\frac{s}{1-s})$, has an intuitive interpretation, i.e., the proportional change in the mean odds of survival with a one-unit change in sediment.

The reasoning behind these models is that each egg has a specific probability of surviving to produce a fry, and that probability depends on sediment composition (at least in part; recall that we did not include other factors influencing survival in our models). Further, each observation of a group of eggs (e.g., an experimental tray or a redd in the stream) is considered a binomial experiment with N trials, where N is the number of eggs in the observational unit. We require an estimate of N, the number of eggs in the observational unit, in order to fit this model. In most of the studies, the number of observed eggs or the estimated number of eggs per female was reported. For studies without this information, we used species-specific average fecundity values. In a few of the studies, the reported data were means of two to six observational units; these data were pooled and treated as one observational unit, but weighted to compensate for the expected reduction in variability.

We first fit logistic regression models to the data from each experiment independently. This initial fitting indicated that nearly all of the data were over-dispersed, i.e., the observed variation exceeded that expected under a binomial model. Quasi-likelihood procedures (after McCullagh and Nelder, 1989) were used to fit the models to the data. We used Williams' method (Williams, 1982) to estimate the over-dispersion parameter, which was subsequently used to adjust the standard errors of the regression parameter estimates. We also checked for quadratic relationships between sediment metrics and egg-to-fry survival.

Next, we compared the slopes of the relationships between percent fines and survival among studies using Wald tests (see McCullagh and Nelder, 1989). If the slopes were significantly different, we did not try to combine the datasets. Otherwise, a parallel slopes model was fit to the combined dataset. This combined data model was used to estimate the change in the odds of egg-to-fry survival as a function of changes in the percentage of fines in the substrate. We tested whether models with a common slope shared a common intercept. If not, a weighted average of the intercepts was calculated.

To construct 95% Wald confidence intervals for the estimated mean survival when a weighted average was used for the intercept, we used a bootstrap procedure (Efron and Gong, 1983). A bootstrap sample was drawn from each of the groups having a common slope. We fit a parallel lines model to the bootstrap sample and used the slope of the lines as an offset in a subsequent model to estimate the intercept. We repeated this 5000 times and used the output to estimate the variances of the intercept and slope, as well as the covariance between them.

RESULTS

The datasets included in this meta-analysis are from studies that represent both lab and field experiments on coho, steelhead, Chinook, and chum salmon. In 34 out of 39 regressions, when the data were reanalyzed using our approach, there was a significant linear relationship between the proportion of fines and (logit) egg-to-fry survival. In 13 of these, a significant quadratic relationship was also detected, but there was no obvious pattern across species. Two of the five non-significant relationships were statistically significant when combined with data from other studies in the same species, even though the studies were initially modeled with separate regression lines, and, in two additional data sets, there was a second sediment metric that did produce a significant relationship with survival. Thus, only one dataset was completely eliminated from the analysis (Tables 1 and 2). The inclusion of non-significant datasets would not have contributed much to the estimation of the slope of the regression line, as they all had large 95% confidence intervals; though, by eliminating them, we have probably underestimated the confidence intervals of the final models for percent fines < 0.85 mm. There were several groups (e.g., chum salmon and steelhead vs. geometric mean) with only a single source dataset. These are included in the tables that follow, even though the parameters are the same as those in Table 1. The annual survival estimates reported by Scrivener and Brownlee (1989) were based on calculated egg deposition and enumeration of emergent fry for the entire study area. Since the other studies monitored individual redds or some laboratory equivalent, the Scrivener and Brownlee data were not included in the meta-analysis.

For the smallest sediment size class (percent fines < 0.85 mm), we were able to create a new, combined model for Chinook and coho salmon together based on five and three datasets, respectively; however, only one dataset was available for chum salmon (Table 2, Figure 1). The three steelhead datasets did not share a common slope.

As mentioned above, the most intuitive way to understand the impact of sediment on survival is through changes in the odds of survival. The odds of survival can be transformed into actual survival, but this relationship is nonlinear. Table 3 describes how a 1% increase in percent fines (for each size class) translates into a change in predicted odds of survival by species. For example, a 1% increase in fines < 0.85 mm will result in a 16.9% (13.3, 20.4) reduction in the odds of survival for Chinook salmon (Table 3). There was a somewhat more dramatic reduction in

Table 2 Results of comparisons within and across studies where metric is percent fines < 0.85 mm. Groups are based on species and egg stage at which monitoring began. Bold font indicates parameters of final models developed for this analysis

			Comparisons within groups of studies				
Species	Life stage	Source	Slope[a] (SE)	p-value[b]	Intercept[c] (SE)	p-value[b]	Intercept[d] (SE)
Chinook	Green egg-to-fry	Reiser and White, 1988	–0.1853 (0.0211)	>0.07	–0.1082	<0.0001	1.3418 (0.1940)
		Reiser and White, 1990			1.7497		
		Bennett et al., 2003			0.5698		
	Eyed egg-to-fry	Hall, 1986			0.9374		
		Tappel and Bjornn, 1983			2.6680		
		Reiser and White, 1990	Excluded	—	—	—	—
Steelhead	Green egg-to-fry	Reiser and White, 1988	–0.1502	>0.48	0.7547	<0.0001	NA
	Eyed egg-to-fry	Reiser and White, 1988			3.1604		
	Eyed egg-to-fry	Tappel and Bjornn, 1983	–0.2869		3.3137	NA	
	Eyed egg-to-yolk	Cederholm and Lestelle, 1974	Excluded	—	—	—	—
Coho	Green egg-to-fry	Hall and Lantz, 1969	–0.2024 (0.0345)	>0.97	2.2629	0.0002	2.7219 (0.5602)
	Green egg-to-fry	Cederholm and Salo, 1979			2.1563		
	Eyed egg-to-fry	Hall, 1986			0.4670		
	Green egg-to-fry	Tagart, 1984	Excluded	—	—	—	—
Chum	Eyed egg-to-fry	Hall, 1986	–0.1458 (0.0288)	NA	0.1436 (0.3156)	NA	NA
All species			–0.1846 (0.0125)	>0.18	—	<0.0001	1.9890 (0.1523)

[a]The same estimate within a group signifies that studies were not significantly different from one another ($p > 0.05$), and different estimates indicate significant differences within the group ($p < 0.05$). Standard error is from logistic regression if bootstrapping was unnecessary; otherwise, it was from bootstrap. Excluded studies were those with non-significant slopes (Table 1).
[b] p-value refers to the test of whether the parameter is the same for all group members.
[c]Intercept fit using logistic regression. Standard error was included if no bootstrapping was necessary.
[d]Intercept fit during bootstrap procedure with bootstrap standard error.

survival for coho salmon (18.3%), and a slightly less dramatic reduction for chum salmon (13.6%). By combining data for all species, we estimate that, on average, a 1% increase in percent fines < 0.85 mm will result in about a 17% reduction in the odds of survival over all species.

Similarly, we were able to provide combined models for percent fines < 3.3–4.8 mm for each species and for pairs of species with similar survival patterns (Table 4, Figure 2). The studies of Chinook used 4.8 mm as an upper bound on fine sediment, except for Bennett et al. (2003), who also included measurements of percent fines < 3.4 mm. We tested for a difference between the regression lines fit to each of these and found no statistical difference (slope: $p > 0.68$, intercept: $p > 0.45$); hence, only data on percent fines < 4.8 mm were used, since this size class corresponded to the other Chinook studies. Because we expect the mechanisms by which sediment affects egg-to-fry survival to be similar across species, we used these results for Chinook salmon to justify combining the two size classes in steelhead, where a direct test of differences was not possible.

The models for percent fines < 3.3–4.8 mm were based on three studies with Chinook salmon, four with steelhead, two with coho salmon, and one with chum. Changes in the odds of survival for a given increase in fine sediment are much less for this metric than when the metric is percent fines < 0.85 mm, with the exception of the eyed egg-to-fry survival in Chinook (Table 3). The pattern in the modeled odds of survival with each 1% increase in fine sediment was similar to that seen above, with a lower impact on chum (–6.0), and (with the exception of eyed Chinook eggs) the largest effect on coho (–9.2). The impact on green Chinook eggs and steelhead was intermediate. The large change in the odds of survival with increasing fines for eyed Chinook eggs (–14.2 per 1% increase in fines) appears anomalous, but the odds of survival is actually higher for eyed eggs at any level of percent fines, even though the rate of change is greater. When evaluating actual survival, this is reflected in the fact that the impact is constrained to levels of fines above 20%, whereas, in the other groups, there is a smaller change per sediment increment over a larger range of fines (Figure 1c and 1d). In general, survival at a particular level of fines is higher when the metric includes larger size classes (Figure 1).

We provide combined models for both Chinook and steelhead salmon for the largest size class (percent fines < 6.4 mm) and for a model based on the geometric mean of the sediment grain sizes (Table 5). Comparisons within and among the studies utilizing both sediment metrics indicate that the relationship between Chinook survival and sediment is not consistent. There is a moderate to strong quadratic component in three of the four studies for the largest sediment size class, but the evidence for a quadratic relationship in Bjornn's (1968) study is weak ($p > 0.09$). Similarly, only one of the four geometric mean datasets has a significant quadratic relationship. While a single slope could be fit to the three studies with a similar relationship, no common slope model could be fit to all four studies. A common quadratic model was fit to the steelhead data from both sediment metrics. The odds of survival is not constant across sediment composition because of the quadratic relationship, but ranges from a decrease of 4.1% (–12.0, 4.6), when fines < 6.4 increase from 10% to 11%, to a decrease of 15.7% (–30.1, 1.5), when

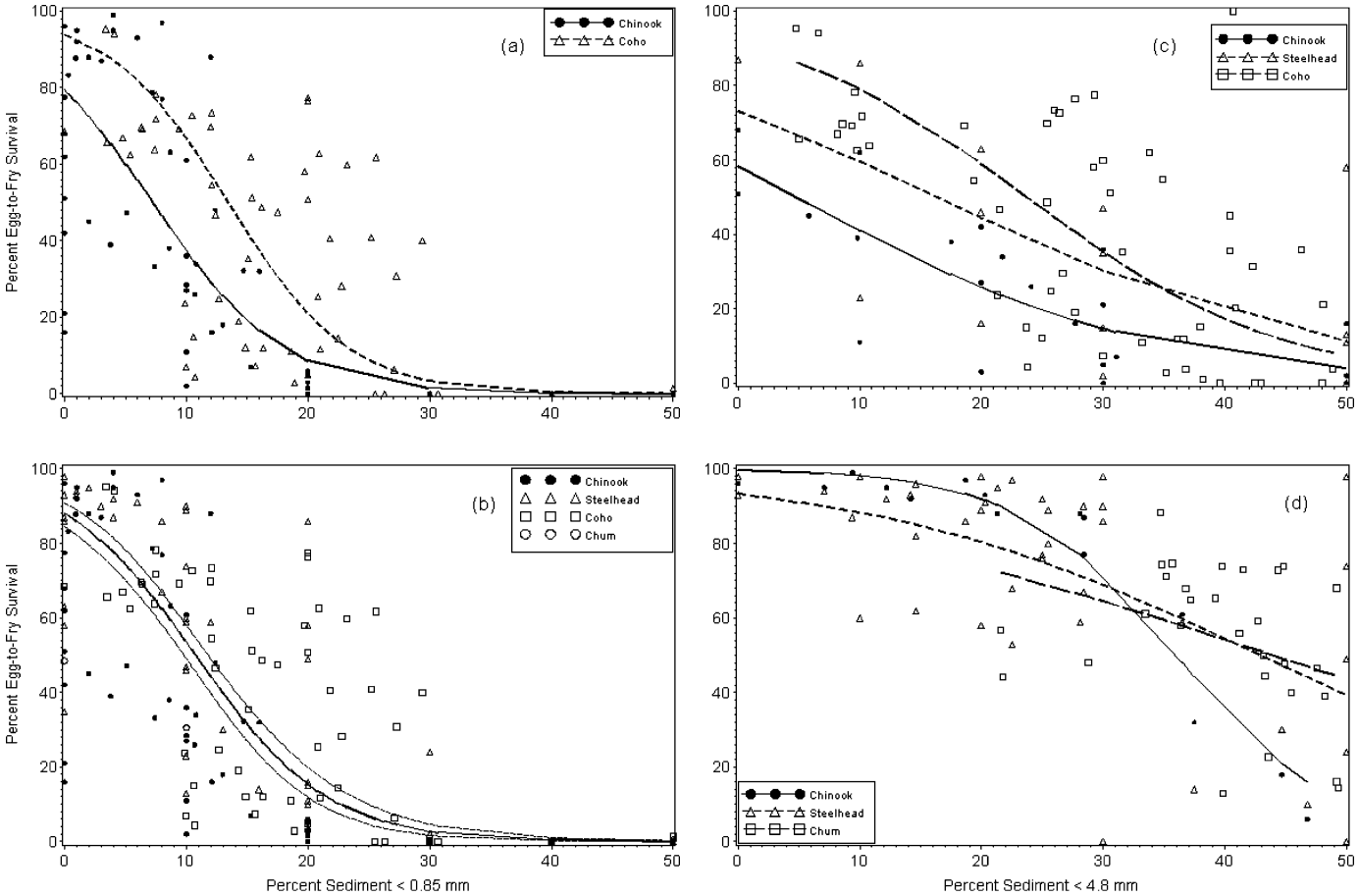

Figure 1 Relationship between egg-to-fry survival and percent sediment, showing data from the literature used in analysis. (a) Data and modeled egg-to-fry survival of Chinook and coho salmon vs. percent sediment < 0.85 mm.. (b) Egg-to-fry survival for Chinook, coho, and chum salmon vs. percent sediment < 0.85 mm. Line is the modeled mean survival based on data from all species and includes the 95% confidence interval. (c) Data and modeled green egg-to-fry survival for Chinook salmon, steelhead, and coho salmon vs. percent fines < 4.8 mm. (d) Data and modeled eyed egg-to-fry survival for Chinook salmon, steelhead, and chum salmon vs. percent fines < 4.8 mm.

fines increase from 50% to 51%. The odds of survival increase by 20.8% (9.2, 33.7) when the geometric mean of sediment size increases from 5 to 5.25 mm, and by 10.3% (–3.1, 25.6) when the mean increases from 10 to 10.25 mm.

Three field studies, two with coho salmon and one with steelhead, were included in the modeling and shared a common slope with the lab studies in their group. In both of the coho studies, the intercept from the field data was larger than those in the lab

Table 3 Comparison of the change in the odds of survival resulting from a 1% increase in fines

Species	Metric	Change in sediment	Egg stage	Change in odds of survival (%)	95% Confidence interval
Chinook	<0.85 mm	+1%	Green and eyed	−16.9	(–20.4,−13.3)
Coho		+1%	Green and eyed	−18.3	(–23.9,−12.3)
Chum		+1%	Eyed	−13.6	(–18.3,−8.6)
All species		+1%	Green and eyed	−16.9	(–19.1,−14.6)
Chinook	<3.4–4.6 mm	+1%	Green	−6.7	(–9.0,−4.4)
		+1%	Eyed	−14.2	(–18.3,−9.8)
Steelhead		+1%	Green and eyed	−6.0	(–8.3,−3.6)
Coho		+1%	Green and unidentified	−9.2	(–12.4,−5.9)
Chum		+1%		–4.2	(−7.3, −1.0)
All species		+1%	Green and eyed	−7.1	(–8.5,−5.7)
Steelhead	<6.4 mm	10–11%	Green and eyed	−4.1	(–12.0, 4.6)
		30–31%		−10.1	(–21.6, 3.0)
		50–51%		−15.7	(–30.1, 1.5)

Table 4 Results of comparisons within and across studies where metric is percent fines < 3.3–4.8 mm. Groups are based on species and egg stage at which monitoring began. Bold font indicates parameters of final models developed for this analysis

			Comparisons between groups of studies				
Species	Life stage	Source	Slope[a] (SE)	p-value[b]	Intercept[c] (SE)	p-value[b]	Intercept[d] (SE)
Chinook	Green egg-to-fry	Bennett et al., 2003	–0.0696 (0.0141)	>0.66	0.3336 (0.3096)	>0.89	NA
	Green egg-to-fry	Reiser & White, 1988					
	Eyed egg-to-fry	Tappel and Bjornn, 1983	–0.1528 (0.0265)		5.4962 (0.8859)	NA	NA
Steelhead	Green egg-to-fry	Reiser and White, 1988	–0.0615 (0.0126)	>0.26	1.0030 (0.4522)	NA	NA
	Eyed egg-to-yolk absorption	Cederholm and Lestelle, 1974			2.6359 (0.4184)	>0.75	NA
	Eyed egg-to-fry	Tappel and Bjornn, 1983					
	Eyed egg-to-fry	Reiser and White, 1988					
Coho	Green egg-to-fry	Cederholm and Salo, 1979	–0.0966 (0.0152)	>0.46	1.9393	0.0303	2.2911 (0.3860)
	Egg-to-fry	Koski, 1966			2.8783		
Chum	Egg-to-fry	Koski, 1975	–0.0428 (0.0168)	NA	1.8774 (0.7206)	NA	NA
Chinook + Steelhead			–0.0737 (0.0115)	>0.08	—	<0.0001	2.1132 (0.3009)
Coho + Chum			–0.0760 (0.0128)	>0.25	—	<0.0001	2.3753 (0.4512)
All species			–0.0746 (0.0087)	>0.06	—	<0.0001	2.2911 (0.2646)

[a]The same estimate within a group signifies that studies were not significantly different from one another ($p > 0.05$), different estimates indicate significant differences within a group ($p \leq 0.05$). Standard error is from logistic regression if bootstrapping was unnecessary; otherwise, it was from bootstrap.
[b] p-value refers to the test of whether the parameter is the same for all group members.
[c]Intercept fit with logistic regression. Standard error was included if no bootstrap was necessary.
[d]Intercept fit during bootstrap procedure with bootstrap standard error.

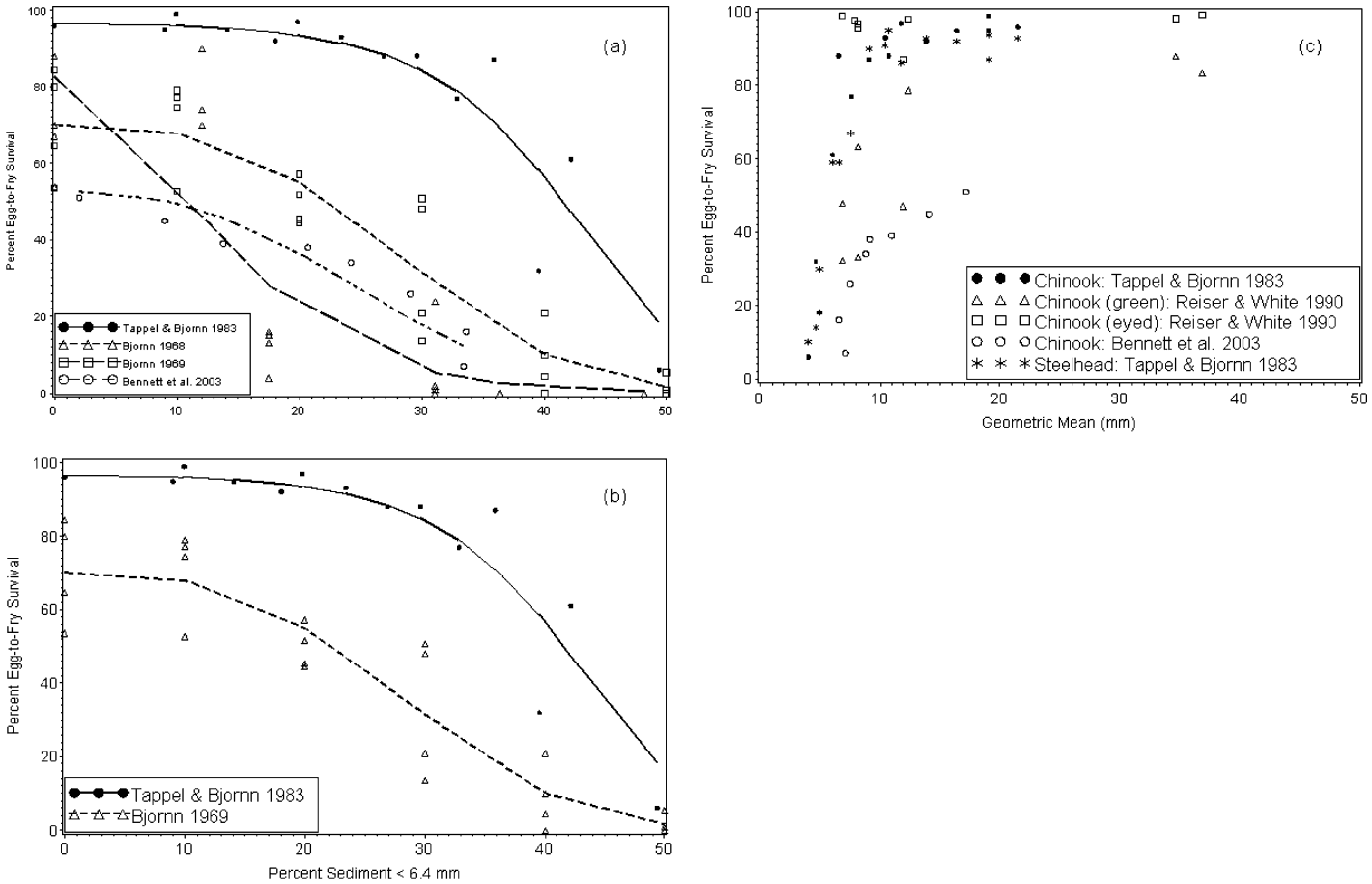

Figure 2 Relationship between egg-to-fry survival and sediment showing data from the literature used in analysis. (a) Chinook salmon data and modeled mean survival vs. percent sediment < 6.4 mm. (b) Steelhead data and modeled mean survival vs. percent sediment < 6.4 mm. (c) Chinook salmon and steelhead data vs. geometric mean of sediment size (mm).

Table 5 Results of comparisons within and across studies where sediment metric is % fines < 6.4 mm or geometric mean (mm). Groups are based on species and egg stage at which monitoring began. Bold indicates parameters of final models developed for this analysis

			Comparisons between groups of studies						
Species	Life stage	Source	Quadratic slope[a] (SE)	p-value[b]	Linear slope[a] (SE)	p-value[b]	Intercept[c] (SE)	p-value[b]	Intercept[d] (SE)
			Sediment metric: Percent fines < 6.4 mm						
Chinook	Green egg-to-fry	Bjornn, 1968	ns	—	–0.1425 (0.0219)	NA	1.5557 (0.3755)	NA	NA
	Green egg-to-fry	Bennett et al., 2003	–0.0022 (0.0005)		–0.0110 (0.0213)	>0.68	0.0932 (0.2875)	<0.0001	NA
	Green egg-to-fry	Bjornn, 1969					0.8530 (0.2294)		
	Eyed egg-to-fry	Tappel and Bjornn, 1983					3.3068 (0.3329)		
Steelhead	Green egg-to-fry	Bjornn, 1969	–0.0016 (0.0006)	>0.75	–0.0077 (0.0308)	>0.57	0.2376 (0.3126)	<0.0001	NA
	Eyed egg-to-fry	Tappel and Bjornn, 1983					2.8925 (0.4648)		
			Sediment metric: Geometric mean (mm)						
Chinook	Green egg-to-fry	Bennett et al., 2003	ns	—	0.0775 (0.0191)	>0.16	–1.6037 (0.2750)	<0.0001	NA
	Green egg-to-fry	Reiser and White, 1990					–0.7847 (0.3020)		
	Eyed egg-to-fry	Reiser and White, 1990					6.6880 (0.5132)		
	Eyed egg-to-fry	Tappel and Bjornn, 1983	–0.0382 (0.0091)	NA	1.2135 (0.2236)	NA	–5.8271 (1.0609)	NA	NA
Steelhead	Eyed egg-to-fry	Tappel and Bjornn, 1983	–0.0363 (0.0058)	NA	1.1284 (0.1471)	NA	–5.6557 (0.7317)	NA	NA

[a] The same estimate within a group signifies that studies were not significantly different from one another ($p > 0.05$), different estimates indicate significant differences within a group ($p < 0.05$). Standard error was from logistic regression if bootstrapping was unnecessary; otherwise, it was from bootstrap.
[b] p-value refers to the test of whether the parameter is the same for all group members.
[c] Intercept fit with logistic regression. Standard error was included if no bootstrapping was necessary.
[d] Intercept fit during bootstrap procedure with bootstrap standard error.

studies, while there was no difference between the intercepts in the steelhead raised from eyed eggs (Tables 2 and 3).

DISCUSSION

We found evidence in the literature that increasing amounts of fine sediments in stream substrates reduces egg-to-fry survival for salmonids (see Table 1; all regression equations have a negative slope or, if quadratic, are generally concave down; the relationships with the geometric mean are reversed). Using data from published studies, we were able to construct models that predict the odds of survival for Chinook, chum, and coho salmon and steelhead for three fine sediment size classes. Fewer data were available for chum salmon than the other species analyzed, and we found no studies that investigated egg-to-fry survival of pink or sockeye salmon. When the sediment metric was percent fines < 0.85, 3.4, or 4.8 mm, the relationship with the odds of survival was generally linear, but when the metric was percent fines < 6.4 mm or the geometric mean, the relationship was often quadratic. The fact that the slopes of the modeled relationships were similar within most species and egg stage groups, despite the differences in intercept, suggests that the change in the odds of survival is constant and that differences in the environments for specific studies is reflected in the intercepts, i.e., the survival curve is simply shifted one way or the other. Adding more datasets for those groups with few sources of data would likely help establish a more robust estimate of the survival curve.

Greig et al. (2005a) identified oxygen availability as an important factor in the survival of salmon eggs, but the relationships between the sediment composition and oxygen levels were complex and varied from site to site as well as within sites. They found low correlations between various measures of sediment composition and survival. In groundwater-fed streams, survival may not be related to substrate composition, as the oxygen content of groundwater can vary independently of substrate characteristics (Sowden and Power, 1985); yet, there is a clear relationship between survival and dissolved oxygen in these systems (Sowden and Power, 1985; Malcolm et al., 2003). In addition, the amount of organic matter in the substrate and adjacent water column influences the amount of dissolved oxygen available to developing embryos (Greig et al., 2005a). We did, however, find significant relationships between sediment composition and egg-to-fry survival in nearly all of the studies we were able to locate. Perhaps these factors explain some of the variability we saw in these data. The models incorporated into this analysis are nonlinear (on the survival scale), and thus it is possible that the low linear correlations reported by Greig et al. (2005a) reflect the nonlinearity of the relationship between sediment and survival. The inter-site variability noted by Greig et al. (2005a) may correspond to the variability in the intercept of the regression line found here. The high intra-site variation in survival found by Greig et al., as well as regional differences in stream conditions (e.g., their study rivers had higher fine silts, clays, and organic matter than are typical in Pacific Northwest streams) highlight the complexity of the spawning environment and therefore the need to exercise caution when applying models such as ours to any one particular site.

The act of spawning cleans fine sediment from the gravel in redds; thus, it is sediment deposited after eggs are laid that could decrease survival (Chapman, 1988). Multiple mechanisms have been proposed to explain the negative impacts of this fine sediment deposition on egg-to-fry survival. First, fine sediment may impede the flow of oxygenated water through gravel in the

egg pocket (Chapman, 1988; Lisle 1989), causing suffocation of eggs or reducing the removal rate of toxic metabolic wastes (Bennett et al., 2003). These reduced dissolved oxygen levels may delay embryo development, lead to early emergence (before yolk sac absorption is complete), and/or decrease emergent fry size (Chapman, 1988). Second, a layer of fine sediment may reduce interstitial spaces and physically prevent fry emergence (Beschta and Jackson, 1979).

Based on proposed mechanisms of how sediment affects survival (i.e., suffocation or entrapment), conventional wisdom suggests that relationships should be strongest when sediment size classes are smallest. Our analyses confirmed this assumption, where the odds of survival were lower and decreased faster when fines were < 0.85 mm than at larger size classes (Table 3). Note, however, that we did not have data to evaluate possible relationships with finer size classes such as silt, clay, or organic matter. Work by Greig et al. (2005b, 2007) suggests that these smaller classes are indeed important in some rivers, and therefore our models may not be applicable in all cases.

Using size classes available to us, we found four general patterns in the survival curves (Figures 1 and 2). At the smallest sediment size, percent fines < 0.85 mm, we saw evidence of a threshold in egg-to-fry survival of Chinook salmon and steelhead. There was a steep decrease in survival, leveling out at less than 10% when fines were greater than 25%. We found a similar relationship for eyed eggs when fine sediment was < 4.8 or 6.4 mm, but the threshold occurred at a much higher level of fines (above 50% for each). Mean survival for eyed eggs of Chinook or steelhead was generally greater than 90% until the percentage of fines increased beyond 20–25, at which point survival decreased rapidly. There was less of a threshold effect for green eggs of Chinook and steelhead for the same fine sediment class. For green eggs, survival was initially lower than for eyed eggs, and decreased steadily before leveling off at very low survival when fines were >30–40%. For the largest sediment size class (percent fines < 6.4 mm), the relationship with odds of survival was quadratic. When fine sediment was $<10\%$, survival was less affected than for other sediment size classes.

While in common use, size class thresholds of, for example, <0.85 mm are relatively arbitrary. A larger or smaller threshold might just as well have been used, and the choice of threshold might impact results and, in particular, perceived differences in percent fine sediment across regions. The use of the geometric mean of particle size as the sediment metric was suggested by Platts et al. (1979) and removes reliance on arbitrary thresholds. However, in our survey, we found only four studies for which we could extract the geometric mean. Of those, the sediment size mixture was not comparable, and survival was highly variable, especially when the geometric mean was between 7 and 13 mm. This is a level at which egg survival is expected to decrease, but the sharp increase is difficult to model due to the variability in the survival data. We were able to construct some relationships using these studies; but, before we can develop any meaningful predictive relationships, more studies are needed that record geometric mean particle size, particularly in the 7- to 13-mm range. If the geometric mean can be precisely and accurately determined, then use of this metric could decrease the variability in survival among studies because sediment sizes could more easily be classified on a similar scale.

There were several limitations of the data on our ability to construct predictive relationships. First, for many of the sediment metrics, we had too few datasets from which to build representative models. The sparse number of studies could not represent all (or even most) possible conditions encountered by fish in natural systems. Furthermore, there was a high amount of variability among studies. Much of the data we used were from laboratory studies, where experimental conditions were highly controlled, yet less realistic than field studies, where other factors (e.g., temperature, discharge) may interact to reduce egg-to-fry survival. Many of the laboratory studies used hatchery fish raised at much higher densities than found under natural conditions. Even within studies, estimates of the intercept were often not consistently precise, reflecting the inherent variability in survival. Another limitation was that to transform the predictions from odds of survival to actual survival, the intercept must be estimated even though there is little statistical justification.

Despite these limitations, our statistical approach complements existing mechanistic modeling (e.g., Alonso et al., 1996; Wu, 2000) and empirical (e.g., Lisle, 1989) approaches. Such approaches often cannot be used for conditions other than those for which they were created due to their complexity and lack of local empirical data for parameterization. A statistical meta-analysis approach, using data from a wide variety of sources, overcomes some of these limitations. In cases where researchers can appropriately match the experimental conditions of individual studies, statistical relationships can be used to estimate salmonid survival given the amount of fine sediment present in streams. Environmental conditions are variable within individual studies (e.g., Greig et al., 2005a; Sear, 1993) and our approach, which includes explicit consideration and calculation of confidence intervals can provide some estimate of the range of likely responses as well as the probability of particular responses. Across sites, conditions are even more variable. Land use management decisions and recovery planning decisions for these ESA-listed species are made over very large scales and across geographically diverse regions. Predictions from our models are averages with wide confidence intervals, and they can provide useful estimates of the changes expected in salmon survival given large-scale changes in land management or suites of proposed watershed restoration actions. For example, Steel et al. (2008) used earlier versions of these models to compare fisheries' impacts given six different watershed restoration strategies. Because they were able to model spatial variations in expected sediment deposition, they were also able to predict spatial patterns in salmon survival.

There are significant strengths of our approach. We synthesized information from available studies into simple predictive relationships that reflect underlying uncertainties in the original datasets. Due to a paucity of comparable rigorous studies,

our predictive relationships may not be robust to all conditions experienced by Pacific salmon species. However, because we combined data from various sources, the predictive relationships we have developed in this meta-analysis are more robust to the variables that often plague extrapolation of ecological relationships from small-scale studies to large-scale models. As well, they are more robust to geographical or ecological conditions than the relationships from individual studies of the relationship between fines and survival. The bootstrapped confidence intervals provide realistic ranges of predicted changes in salmon survival with changes in in-stream fine sediment. Like all models, the models presented here are best used with strong consideration, not just for the point estimate of the most likely model output, but also for the confidence intervals, the range of potential modeled outcomes. Like all models, the models presented here are also best used without extrapolating beyond the range of the data used to build the model. Our meta-analysis approach has increased the range of data used for any one relationship, but, as pointed out already, there are clearly stream types and ecological conditions for which no data are available, and extreme caution should be used if one must make estimates for stream types and conditions not represented in the original data.

Given known or modeled levels of fine sediment deposition associated with different types of land use (e.g., fines in streams can be much higher in agricultural and developed watersheds; Opperman et al., 2005), managers can use these predictive relationships to begin to identify areas where salmonid egg-to-fry survival may be limited. Moreover, our predictive relationships can be used to forecast potential effects of watershed management practices on salmonids and to make comparisons of relative predicted survivals under alternative management strategies to see what set of restoration actions is most likely to improve egg-to-fry survival (e.g., Steel et al., 2008). These predictive models should improve our ability to link large-scale models that predict how much sediment is, or will be, entering streams, to small-scale observations on fish survival and to more efficiently managing landscapes that contribute to fine sediment entering streams.

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