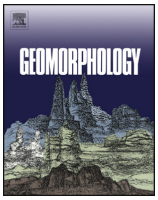
Geomorphology 305 (2018) 163–172

Contents lists available at ScienceDirect

Geomorphology

journal homepage: www.elsevier.com/locate/geomorph



Sex that moves mountains: The influence of spawning fish on river profiles over geologic timescales

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ARTICLE INFO

Article history:
Received 19 May 2017
Received in revised form 22 September 2017
Accepted 24 September 2017
Available online 28 September 2017

Keywords:
Biogeomorphology
Landscape evolution
Resilience
Salmon spawning

ABSTRACT

A key component of resilience is to understand feedbacks among components of biophysical systems, such as physical drivers, ecological responses and the subsequent feedbacks onto physical process. While physically based explanations of biological speciation are common (e.g., mountains separating a species can lead to speciation), less common is the inverse process examined: can a speciation event have significant influence on physical processes and patterns in a landscape? When such processes are considered, such as with 'ecosystem engineers', many studies have focused on the short-term physical and biological effects rather than the long-term impacts. Here, we formalized the physical influence of salmon spawning on stream beds into a model of channel profile evolution by altering the critical shear stress required to move stream bed particles. We then asked if spawning and an adaptive radiation event (similar to the one that occurred in Pacific salmon species) could have an effect on channel erosion processes and stream profiles over geological timescales. We found that spawning can profoundly influence the longitudinal profiles of stream beds and thereby the evolution of entire watersheds. The radiation of five Pacific salmon from a common ancestor, additionally, could also cause significant geomorphic change by altering a wider section of the profile for a given distribution of grain sizes. This modeling study suggests that biological evolution can impact landscape evolution by increasing the sediment transport and erosion efficiency of mountain streams. Moreover, the physical effects of a species on its environment might be a complementary explanation for rapid radiation events in species through the creation of new habitat types. This example provides an illustrative case for thinking about the long- and short-term coupling of biotic and abiotic systems.

1. Introduction

Organisms influence geomorphic process and form (Viles, 1988). Biologic activities are important for relatively short-term processes (Dietrich and Perron, 2006), such as vegetation impacts on turbulence (Nepf, 1999) and sedimentation (Yager and Schmeeckle, 2013), or biotic (plant and animal) effects on sediment transport and stabilization/destabilization of the stream bed by salmon (Statzner, 2012; Buxton et al., 2015), crayfish (Rice et al., 2016), invertebrates (Albertson et al., 2014), and biofilms (Grant et al., 1986). In some cases, the small-scale biotic feedback might lead to large-scale geomorphic shifts, such as the evolution of land plants that alter channel bank stability and that promote the river meander planform (Gibling and Davies, 2012) or woody debris trapping sediment that changes a bedrock river reach to an alluvial channel (Montgomery et al., 1996; Polvi and Wohl, 2013). These feedbacks can have important larger-scale ecological influences, such as the beaver species impoundment influence on watershed species richness (Jones et al., 1994; Wright et al., 2002), stickleback species diversification on ecosystem functioning in lakes (Harmon et al., 2009), or reciprocal feedbacks between vegetation and landform development (Corenblit et al., 2007). Geomorphologists have long recognized the importance of biotic feedbacks on physical process (Viles, 1988; Butler, 1995; Butler and Sawyer, 2012), particularly at the particle- or stream-reach scale; yet we have fewer examples of these reach-scale feedbacks having significant landscape-scale influence.

In North America, paleontological evidence suggests that coastal mountain building along the Pacific during the middle Miocene and early Pliocene caused a radiation (speciation of a single species into many) of Pacific salmon (*Onchcorhynchus* spp.) from a common ancestor with Atlantic salmon (*Salmo* spp.). Mountain building, it is argued, increased the types of environments for adaptive radiation to occur rather than biological isolation by glaciers (Montgomery, 2000). This radiative event was most likely caused adaption to novel environments and one that did not occur along the Atlantic coast where orogeny predated salmon (Stearley and Smith, 1993). Contrary to this inquiry, we ask: could the radiation of Pacific salmon, in turn, influence landscape evolution?

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https://doi.org/10.1016/j.geomorph.2017.09.033
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A wide range of physical conditions and processes control the erosion rate, slope, and relief of river channel profiles, such as climate, tectonics, and bedrock lithology. Climate is largely important because of its impact on the magnitudes and durations of river flow discharges, which in turn partly influence sediment transport rates. Tectonics drive rock uplift, which controls the rate of base-level fall. The rate of rock uplift ultimately effects the rate of sediment supply from hillslopes to the river systems. Sediment transport has multiple roles in channel evolution. Transported grains (i.e., tools) abrade exposed bedrock on riverbeds, but sediment can also cover bedrock and provide protection from erosion (Sklar and Dietrich, 2001; Gasparini et al., 2007; Turowski et al., 2007; Johnson et al., 2009; Turowski and Bloem, 2016). The balance between the upstream sediment supply and the transport capacity of a given river reach also controls the thickness and extent of alluvial cover as well as the channel slope (Lisle and Hilton, 1999; Yager et al., 2007; Madej et al., 2009; Nelson et al., 2009). In theory, channel slope, grain size, roughness and/or morphology will adjust to allow a river to carry the imposed upstream sediment load and erode at the rate of rock uplift (Dietrich et al., 1989; Madej et al., 2009; Yanites and Tucker, 2010). Lithology also controls channel profiles by partially dictating the relative strength of the tools and the eroding bedrock surface in a reach, which in turn partly control erosion rate (Sklar and Dietrich, 2001); and spatial changes in lithology can cause differences in channel morphology (e.g., width, slope) (Allen et al., 2013; Forte et al., 2016).

In addition to these physical processes that impact sediment transport and channel evolution, the act of salmon spawning, which involves creating a nest (called a 'redd') to incubate their eggs in streambeds, can alter streambed conditions and subsequent sediment transport rates and channel stability (Buffington et al., 2004; Gottesfeld et al., 2004). The act of spawning involves a female salmon undulating her tail fin against bed sediment to create pits in which she lays her eggs that are fertilized by males (Figs. 1 and 2). The eggs are then buried by the female with additional sediment that she excavates from upstream of the original pit. Bed areas that have undergone spawning often have lower amounts of fine sediments (Hassan et al., 2008), coarser and better-sorted grain sizes, and a looser bed structure (Montgomery, 2000; Buxton et al., 2015) (Figs 1 and 2).

Redd morphology is similar to that of a dune and can create locally higher shear stresses on the downstream end of a redd than would be experienced on a flat bed (Buxton et al., 2015). Although bed coarsening would be expected to increase the critical shear stress (stress needed to initiate sediment movement) and therefore decrease post-spawning sediment transport rates (Montgomery, 2000), larger bedload fluxes or increased bed scour have been observed with more spawning activity (Hassan et al., 2008). Bedload fluxes increase with spawning because bed coarsening is offset by the reduced packing of the streambed, which decreases grain resistance to motion, and by the higher applied shear stresses on redds (Buxton et al., 2015). The overall result is a lower critical Shields stress (dimensionless critical shear stress) and enhanced bed mobility (Buxton et al., 2015). Enhanced mobility and sediment transport could act to reduce the cover effect of sediment thereby increasing the ability of the river system to erode underlying bedrock.

Although salmon spawning has been observed to account for up to 55% of total sediment fluxes during floods (Hassan et al., 2008), the potential effect of salmon on landscape and channel profile evolution is not yet known. Here, we ask: (i) can salmon spawning significantly influence landscape evolution? And, if so, (ii) do the different species of salmon cause distinct patterns in landscape form, including changes in relief and topography? We ask the second question because the grain sizes that can be moved by female salmon varies with fish species (Kondolf and Wolman, 1993; Kondolf, 2000; Riebe et al., 2014). Therefore, the proportion of a watershed that contains redds will partly depend on salmon species, or set of species of different sizes, and bed grain size. To ask these questions, we generalized and formalized the geomorphic influence of salmon spawning on the critical shear stress required to move sediment from recent flume experiment results (Buxton et al., 2015) into a mechanism-based model of landscape evolution (Yanites et al., 2013). We use our results to initiate a search of landscapes that might illustrate evidence of a biotic control on landscape evolution.

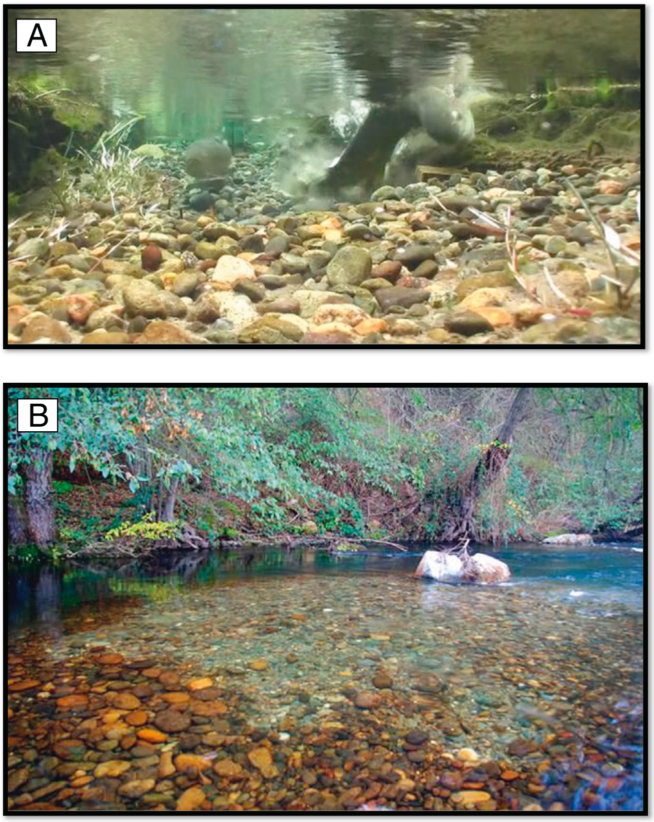

Fig. 1. Steelhead spawning in a small stream reach in the Methow basin in north central Washington State: (A) a female steelhead salmon species actively turning sideways to remove fine grain sediment and create a pit in the stream bed (photo credit John Jorgensen). (B) The light color gravels are evidence of a newly constructed Chinook redd on the Stanislaus River (CA) showing the extent and change of gravel size (photo credit JD Richey).

2. Methods

2.1. Landscape evolution model

We model the erosion of one dimensional river profiles and allow for mixed alluvial-bedrock behavior. To do this, we use a modified version of the equation outlined by Yanites et al. (2013) in which the change in bed elevation with time is given by

$$\begin{aligned} \frac{dz}{dt} &= U_r - E \text{ when h} = 0 \\ \frac{dz}{dt} &= U_r - \frac{dh}{dt} \text{ when h} > \end{aligned} \tag{1}$$

where z is the bed elevation, t is time, h is sediment thickness, E is the bedrock erosion rate, and U_r is the rock uplift rate, which is constant at 0.1 mm/y for all model runs. This formulation allows for either a thick sediment layer that prevents bedrock erosion from occurring or a thinner layer that can be scoured, allowing for bedrock erosion, during high flow events. Thus, our modeling approach is formulated to represent river systems that over long timescales erode bedrock but often have beds covered with alluvium.

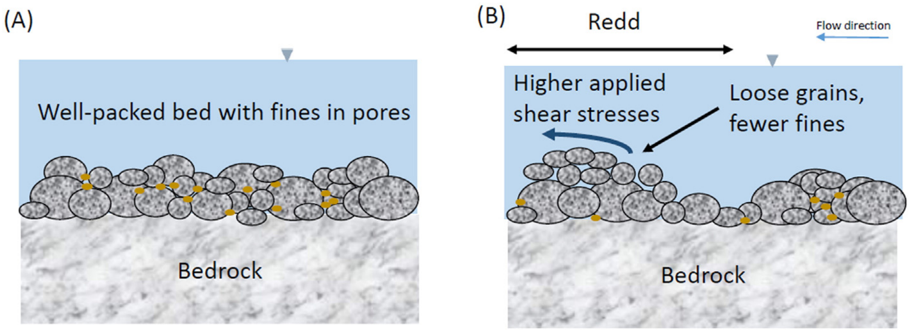

Fig. 2. Conceptual diagram of a salmon redd before (A) and after (B) spawning. Note that spawning evacuates fine grained sediment from the redd and that spawning unpacks and moves bed material downstream increases its potential for entrainment (Buxton et al., 2015).

The model is solved in a forward finite difference scheme and calculates the divergence of sediment flux to conserve sediment on the bed using the Exner equation:

$$\frac{dh}{dt} = -\frac{1}{1-\lambda}\frac{dq_s}{dx} \tag{2}$$

where λ is porosity, and q_s is the unit sediment flux in each reach. Sediment transport and bedrock erosion potential require the quantification of shear stress, τ:

$$\tau = \rho g H S \tag{3}$$

where ρ is the density of water, g is gravity, H is flow depth, and S is channel slope. Flow depth is calculated using Manning's equation for a rectangular channel:

$$H = \left(\frac{nQ_w}{W}\right)^{\frac{3}{5}} S^{-\frac{3}{10}} \tag{4}$$

where Q_w is water discharge, n is a friction factor, and W is channel width. Channel width is assumed to scale with drainage area (Montgomery and Gran, 2001):

$$W = k_w A^b \tag{5}$$

where k_w is a scaling coefficient, and b is an exponent that usually ranges between 0.3 and 0.6 for bedrock channels (Fig. 2). For equations here, b is 0.5 and k_w is 5×10^{-6}, which includes the conversion of kilometers (for A) to meters (for W). Drainage area varies with distance downstream according to Hack's Law:

$$A = c_h x^{\frac{1}{h}} \tag{6}$$

where c_h is a scaling coefficient (equal to 1 in this study), and h is an exponent that is ~0.5–0.7 for natural channels. We hold h equal to 0.54 for the modeled scenarios here.

The dimensionless sediment flux in each reach is determined using a modified Meyer-Peter and Mueller equation bedload transport equation (Wong and Parker, 2006):

$$q_s^* = 3.97\left(\tau^* - \tau_c^*\right)^{1.5} \tag{7}$$

where τ^* is the dimensionless boundary shear stress, and τ_c^* is the critical Shields stress needed to begin sediment transport. Eq. (7) was only used for model runs in which no salmon were present and is modified below to account for the presence of salmon. The dimensionless shear stress and sediment flux are defined using the following two equations:

$$\tau^* = \frac{\tau}{(\rho_s - \rho) g D_{50}} \tag{8}$$

$$q_s^* = \frac{q_s}{\sqrt{\left(\frac{\rho_s - \rho}{\rho}\right) g D_{50}^3}} \tag{9}$$

where τ and τ_c are the boundary shear stress and critical shear stress, respectively, and ρ_s is the sediment density. The median grain size of the bed (D_{50}) and the 84th percentile of the grain size (D_{84}) distribution (see salmon model below for its use) vary in the downstream direction according to Sternberg's law:

$$\begin{aligned} D_{50} &= D_{50o} e^{-ax} \\ D_{84} &= D_{84o} e^{-ax} \end{aligned} \tag{10}$$

where the subscript o denotes the grain size in channel headwaters, x is distance downstream, and a is an empirical parameter that describes the rate of downstream fining. A number of factors can influence the pattern of grain size along a river profiles including sediment supplied from hillslope processes (Dietrich et al., 1989; Sklar et al., 2017), tributary inputs (Rice, 1999), channel gradient, channel roughness, and variations in fluvial dynamics (Powell, 1998).

Our focus, however, is to understand how the presence of salmon influences geomorphic efficiency and river profile evolution in the absence of other complicating feedbacks. Because of this, grain size is held steady at each model node through the model run, without considering changing grain size in response to changes in channel hydraulics, slope, or sediment supply. The erosion rate is modeled using an equation that approximates the effects of bed sediment and erosion potential (τ):

$$E = K\left(1 - \frac{Q_s}{Q_c}\right)\tau \tag{11}$$

where K is an erodibility coefficient that partly depends on rock strength, Q_s is the sediment supply to each reach, and Q_c is the bedload transport capacity that is determined in each reach using either Eq. (9) or (12) for runs without or with salmon respectively. The part of the equation in the parentheses simulates the cover effect of river sediment (Sklar and Dietrich, 2004). Shear stress is assumed to represent a proxy for a myriad of bedrock erosion processes. Parameter Q_s is a function of the sediment transported from the upstream reach and the sediment added from tributary and local hillslope inputs, which is equal to the mean vertical river incision rate over the previous 10,000 years. We assumed that 30% of the sediment supplied by the hillslopes is in the bedload size fraction. Field-measured estimates of the portion of load transported via bedload are wide ranging and are dependent on a wide range of processes and local variables (e.g., Mueller et al., 2016). Values range for near zero to 70% (Dadson et al., 2003; Schlunegger and Hinderer, 2003). Given the topographic environments of interest here, we assume 30% of the total sediment eroded by upstream hillslope processes is moved via bedload.

The threshold nature of sediment transport and the influence of salmon on these thresholds require the use of a variable discharge to accurately quantify salmon effects over landscape evolution timescales and to capture the importance of thresholds in these systems (Tucker, 2004). We used an inverse γ distribution for discharge, which has been shown to simulate discharge distributions reasonably well (Lague et al., 2005; DiBiase and Whipple, 2011). Modeled timesteps were one year, and we assumed that active bedload transport only occurred for 10% of the time when shear stress exceeded the critical shear stress (sediment flux was zero otherwise). Discharge in each annual timestep was determined from the inverse γ distribution. In each model run (see details on runs below) we simulated 100-km-long river profiles in 1-km increments (i.e., dx) over 5 My to ensure that a steady-state (erosion rate equals the rate of tectonic rock uplift) profile is reached. To be clear, the approach only characterizes mainstem evolution, not the watershed-scale influence (e.g., tributaries). We assume mainstream elevational change will drive adjustments across the whole network.

2.2. Salmon model formulation

Although salmon spawning has many impacts on stream channels (e.g., higher sediment fluxes, change in grain sizes, and morphology), we assumed the dominant influence was a decrease in τ_c^* in spawned areas of the bed, which accounts for many of these effects. The critical Shields stress for spawned bed areas (τ_{cf}^*) was assumed to be 41% of τ_c^* based on a set of flume experiments of simulated salmon spawning effects on τ_c^* (Buxton et al., 2015). In undisturbed portions of the bed in reaches with spawning and in reaches that completely lack fish, τ_c^* was assumed to be 0.0495 (Wong and Parker, 2006). The persistence of this lower τ_{cf}^* in spawned bed areas will vary with the transport of fine sediment into the redd (increases packing) (Buxton et al., 2015) and with the timing and magnitudes of high (redd removal) (Gottesfeld et al., 2004) and low (reworking of the bed) water discharges. Field observations suggest that redd topography can be rapidly erased by subsequent floods (Peterson and Quinn, 1996) or can persist for over a year in other locations; it is hypothesized that persistence depends upon the relationship of stream and salmon size (Buffington et al., 2013). We assumed if a reach supports spawning (see below), redds will be created in that reach during each timestep and their effect on τ_{cf}^* will persist until the next timestep (one year), which is likely their maximum influence.

We then applied these two different critical Shields stresses to different parts of the bed in reaches with spawning. We assumed that within a given reach, salmon will only spawn in a certain fraction (A_f/A_t) of the total bed area (A_t) and the remaining bed area ($A_{nf} = A_t - A_f$) remains unaltered by salmon. We modified Eq. (5) to account for the spawned and unspawned portions of each reach

$$q_s^* = 3.97\left[\frac{A_f}{A_t}\left(\tau^* - \tau_{cf}^*\right)^{1.5} + \frac{A_{nf}}{A_t}\left(\tau^* - \tau_c^*\right)^{1.5}\right] \tag{12}$$

which reverts to Eq. (5) if A_f is zero (no spawning in a reach). Volumetric sediment flux (Q_s) equals the product of channel width (W) and dimensional unit flux (from Eqs. 9 and 12).

The suitability of each reach for spawning and A_f were determined by the available grain sizes on the bed (D_{50} and D_{84}). We acknowledge that this is a simplification of the factors salmon use to select spawning sites but assume that at scales of 10^3–10^6 years, many of these factors will average out and grain size will play a dominant role. Consistent with our assumption above about redd persistence, this approach may provide a liberal estimate of the extent of suitable spawning habitat. Other parameters, such as flow velocity and depth could be used to estimate spawning habitat suitability, but given that we are only modeling one discharge in each timestep, we could not obtain an estimate of the flow conditions that actually occur during spawning.

We estimated suitability for spawning for three species of Pacific salmon on the west coast of North America and for Atlantic salmon (*Salmo salar*) because of data availability and their range of grain sizes suitable for spawning. We selected Pink (*Oncorhynchus gorbuscha*), Sockeye (*O. nerka*), and Chinook salmon (*O. tshawytscha*). For each of the four species, we set a minimum grain size (D_{50min}) based on Kondolf and Wolman (1993), below which salmon spawning does not occur in a given reach because of site selection by females for incubating eggs (Table 1). This determines the first condition for spawning suitability:

$$if\ \mathrm{D}_{50} < D_{50\ \mathrm{min}},\ \mathrm{A_f} = 0 \tag{13}$$

Physiological constraints during redd construction also limit the maximum grain size that can be moved by each species and therefore A_f. To account for these effects, we used the equations developed by Bowling et al. (2009) and Riebe et al. (2014)

$$if\ \mathrm{D}_{50} > D_{50\ \mathrm{min}},\ \mathrm{A_f} = \left(1 + e^{-1.702r}\right)^{-1} \tag{14}$$

which is a one-parameter logistic function that approximates the cumulative lognormal distribution of grain sizes suitable for spawning. In Eq. (14), r is calculated from the grain sizes in reach and the maximum grain size that can be moved by each species (D_{max}) (Table 1):

$$r = \log\left(\frac{D_{\max}}{D_{50}}\right) / \log\left(\frac{D_{84}}{D_{50}}\right) \tag{15}$$

In the above formulation, we assume that if A_f can be used for spawning, the total area available for spawning will be subject to redd construction. Importantly, our formulation does not change the size or depth of the redd by species.

Suitability for spawning does not always imply full usage because ocean conditions may limit the number of salmon that are spawning each year and physical barriers (e.g., waterfalls) and human influences may limit salmon migration upstream (Quinn, 2005). We can ignore effect three because we are largely concerned with long-term salmon effects on river systems. Neglecting the first two effects implies that our predicted impacts of salmon spawning in a given reach are again maximum possible values. However, we indirectly account for limited spawning populations by only allowing spawning in 50% of the reaches (exact locations were randomly chosen) for which A_f is not equal to zero. This effectively means that salmon spawn in the maximum possible density in 50% of reaches for which spawning is possible but that they do not utilize the other 50% of the suitable reaches. We chose 50% as a middle value between 0 and 100 because the percent of reaches spawned in is highly variable by species, year-to-year, and over a network; additionally, this value will only impact the magnitude of the effect, not where geomorphic efficiency is increased relative to no fish.

Table 1
Modeling parameters for three Pacific salmon species and Atlantic salmon.

	Avg. length (mm)	D_{50min} (mm)	D_T (mm)[a]
Pink *Oncorhynchus gorbuscha*	445	6.5	95
Atlantic *Salmo salar*	510	15.0	100[b]
Sockeye *O. nerka*	569	14.5	111
Chinook *O. tshawytscha*	721	10.8	128

[a] D_T is the size of the largest particle the female can move during spawning for Pacific salmon (Riebe et al., 2014). Minimum D_{50} were reported in studies summarizes by Kondolf and Wolman (1993) for all species.

[b] The largest moveable particle size were limited ($n = 2$) for Atlantic salmon, so we used data from Louhi et al. (2008).

2.3. Model scenarios

Given that our results will be dependent on the choice of D_{50o}, D_{84o}, and a (the exponent in Eq. 10), we used a range of values for each parameter for each model scenario. For each species (or distribution of species) specific model scenario, we modeled headwater D_{50}/D_{84} pairs (i.e., D_o in Eq. 10) of 0.071/0.23, 0.142/0.23, 0.071/0.46, 0.0355/0.23, 0.071/0.115, 0.142/0.46, and 0.0355/0.115. For each of these grain size pairs, downstream fining occurred for seven different values of a in Eq. (10) ($a = [0.001, 0.005, 0.01, 0.05, 0.1, 0.5, \text{and } 1]$). These combinations resulted in 49 runs of different grain size distributions. We selected the range of a based on values reported in Rice (1999), which include either only the effects of particle abrasion (~0.0001–0.1 km^{-1}), which is a minimum, or the combined impacts of abrasion and selective transport on downstream fining (0.1–1 km^{-1}). The values of D_{50o} and D_{84o} were determined from a literature review (Marcus et al., 1992; Wohl and Wilcox, 2005; Mao et al., 2008; Nitsche et al., 2011; Yager et al., 2012) and from our unpublished measurements of grain sizes (D_{50o}: 25–640 mm; D_{84o}: 80–1190 mm) for channels with slopes between 0.05 and 0.15, which encompass the range of slopes observed for our modeled headwater channels. In this way, we encompass much of the natural variability in grain sizes and downstream fining in river profiles. Given that some of this variability is caused by lithology, we discuss the implications of salmon spawning in different lithologies in the Discussion section. In Fig. 3, we illustrate the importance of grain size distribution in controlling spawning location. We plot the distribution of D_{50} and D_{84} for two values of a and show where along the profile active spawning will occur based on a species maximum and minimum preferred grain size.

We first conducted a control scenario in which no spawning occurred to generate an expected profile for each D_{50o}, D_{84o}, and a parameter. Then, we conducted a run with the widest range of multiple salmon species (labeled 'Diverse' - lowest D_{50} [Pink] and highest D_{50} [Chinook]). In this scenario, we do not simulate individual species but change the range (max or min) of the spawnable D_{50}. This run simulates all salmon species present, without overlapping spawning (Figs. 3 and 4). Next, we ran a scenario for each of the four salmon species individually (Table 1). The results of individual species influence are summarized in Fig. 4, and individual runs across the range of densities are shown in supplemental figs. 1–3.

To illustrate landscape change, we calculated the following for each run in each scenario: (i) steady-state profile shape (with and without spawning), (ii) total relief in the profile (i.e., maximum elevation minus base level), and (iii) mean profile elevation; the combination of which provides an integrated metric of the effects of salmon on river profiles. We define steady-state as when maximum elevation change over 10,000 years was <0.1% of total relief change. For each run in each scenario with salmon, we then determined the fractional change in total relief as the ratio of maximum elevations spawned and nonspawned model runs (minimum elevations were set at 0 as a model boundary condition). Any small bumps in the profiles on Figs. 6 and 7 are a result of the random distribution of spawned reaches. The mean fractional elevation change is the ratio of the average elevation of each profile, with the no spawning condition divided by the spawning condition; thus, the ratios in Figs. 3 and 5 and supplement figs. 1–3 are erosional efficiencies with lower numbers meaning higher erosional efficiency. Lower ratios also mean a lower profile elevation or relief relative to the control or no spawning condition. For example, a value of 1 means that there is no difference between spawning and no spawning, and a value of 0.5 means that the total relief or mean elevation was reduced by half from spawning activity. In these calculations, D_{50o}, D_{84o}, and a were held constant between the runs with and without spawning.

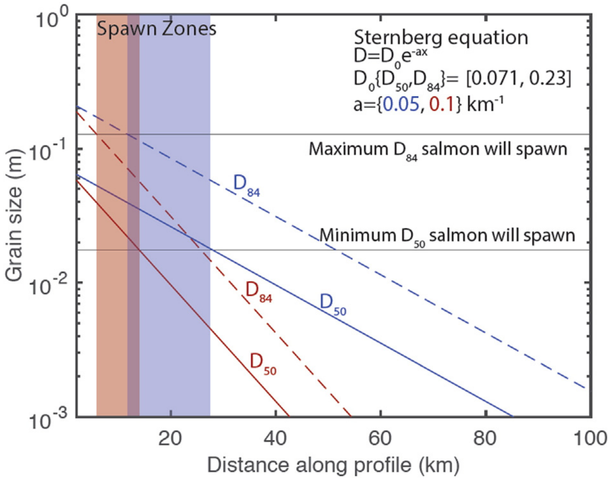

Fig. 3. Illustration of the grain size changes with distance along the stream profile based on Sternberg's equation. We analyzed the influence the Sternberg equations exponent (0.05, 0.1) on the influence of spawning. The position of suitable grain sizes for spawning (D_{50} and D_{84}) for Pacific salmon are indicated.

3. Results

Figs. 4–7 show the influence of salmon spawning on river profile evolution. We note that the absolute elevation of river profiles will scale with rock uplift and rock erodibility; therefore our focus is on the relative change in elevation/relief, the location in which spawning occurs, and changes in shape of the profile. Fig. 4 and supplementary figs. show the influence of different species of Pacific salmon on mean elevation and total relief (maximum elevation) change compared to the no spawned condition.

For a given value of percent of profile that is spawnable, variation in the impact on geomorphic effectiveness exists among individual species runs as well as between species. We illustrate this by plotting the results for Chinook and coloring the points according to D_{50} and D_{84} values in the headwaters (Fig. 4). Fig. 4 shows the profile change for Chinook; the profiles for the other species were similar (see supplementary figs.). We observed no relationship between grain size and relief change due to salmon spawning, other than grain size's direct impact on the location where salmon are able to spawn on the river profile. In general, when fish are not present, a larger D_{50} will require greater slopes to entrain the particle (for a given flow discharge) and to generate enough excess shear stress to expose bedrock to erosion processes. As grain sizes become larger, the river is driven closer to a threshold-dominated system (Yanites and Tucker, 2010). The entrainment of a particular size of grain becomes a relatively stronger control on channel slope than the excess shear stress. This is because of the use of a bedrock exposure term in Eq. (11). The product of the three terms (K, exposure, and τ) on the right hand side must equal the rate of rock uplift set in Eq. (1). When the entrainment threshold for grain size is negligible (i.e., $\tau^* \gg \tau^*_C$ in Eq. 7 or $\tau^* \gg \tau^*_{Cf}$ in Eq. 12), any change in slope has a large impact on erosion because the exposure term and the shear stress are significantly impacted. It is also true that in this scenario, any change in τ^*_C, such as from spawning, will have a negligible impact on erosional efficiency because it is much smaller than τ^*. As grain size becomes larger and τ^*_C becomes significant in Eqs. 7 and 12, changes in the entrainment threshold will have a significant impact on erosion. So, by reducing the critical threshold for entrainment, the introduction of salmon will have a greater impact on entrainment-threshold-dominated systems, which tend to emerge when grain sizes are larger. This effect also explains why there is a slight species-specific control as well (Fig. 5), but only in the cases when the range of grain sizes available for spawning is increased.

In Fig. 5, colors illustrate the different species' effects in the different model runs. Regardless of species, salmon spawning causes an increase in erosional efficiency, the magnitude of which depends on the percent

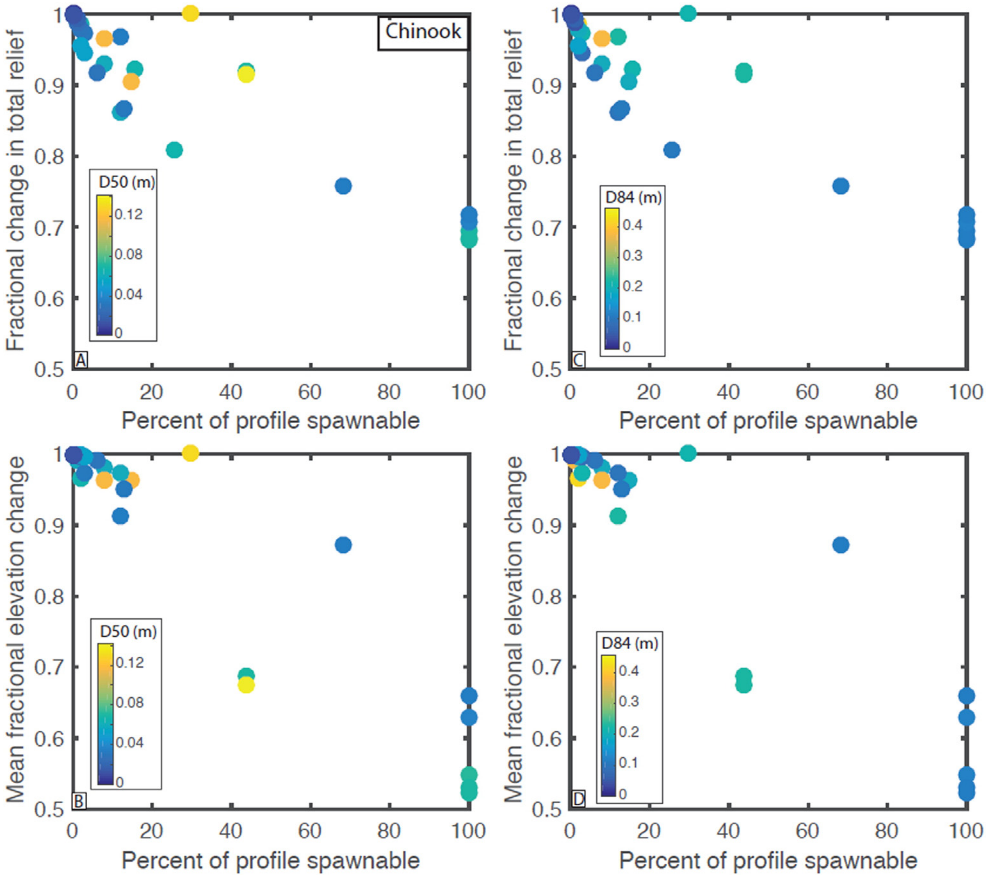

Fig. 4. Model results depicting relief and elevational changes caused by Chinook spawning over a range of Sternberg parameter estimates and percent of profile spawnable. Note: fractional relief and elevational changes of 1 means that spawning had no effect on the profile (and by extension, geomorphic efficiency). Lower values mean greater erosion by spawning (and a larger increase in geomorphic efficiency).

of profile in which spawning can occur. Recall that the locations of spawning are set by the grain size distribution along the profile and the species-specific grain size range. This is why when we plot all Pacific species (black squares in Fig. 5), more model runs resulted in a higher percentage of the profile that was spawned; this is caused by the assumption that more species equal a wider range of spawnable grain sizes. The geomorphic effect of spawning is thereby determined by the availability of suitable gravels for spawning and that range is wider in the presence of multiple species, particularly, Pink salmon are able to spawn in the smallest grain sizes and Chinook the largest.

Fig. 6 shows changes in channel profiles over four initial conditions to illustrate the influence of the location of available spawning grain sizes on profile evolution. The availability of spawning-sized gravels and the position of the gravels on the profile influence the magnitude of elevation change and the shape of the profile. For example, run 3 has spawnable gravels lower in the profile, which increases geomorphic efficiency at low elevations resulting in relatively lower slopes in the spawnable reaches. Additionally, spawning-induced changes lower profile lead to an increase in profile concavity because the lower slopes in the downstream reaches provide a lower base level to the upstream, unspawned reaches. However, when the spawning effects are limited to the headwaters, such as in run 34 (Fig. 6), concavity is reduced because the elevations of headwater streams are lowered, but the rest of the profile is not impacted. Therefore, runs 3 and 34 have reduced total relief because of salmon spawning, but run 3 has a much broader overall landscape impact because spawning affects the lower section of the profile. When the entire profile is spawned (e.g., run 22), channel slopes are reduced along the entire river and maximum relief and elevation change occur, including the small knickpoint in Fig. 6.

For each species run and the Diverse run, we ran 49 river profile models, each with a different grain size distribution (varying D_{50}, D_{84}, and the Sternberg exponent). Out of the 49 different grain size patterns considered here, Chinook resulted in 28 river profiles that had suitable grain sizes (and 21 where no spawning occurred because no suitable gravels were present); Pink salmon spawned in 32 of the profiles; Sockeye spawned in 30; Atlantic spawned in 25 different scenarios; and when considering the full diversity of Pacific salmon considered here, spawning occurred in 35 model scenarios. For clarity, our figures only included cases in which spawning occurred as there would be no profile change to compare against. Interestingly, out of all of the individual species, Pink had the greatest number of grain size scenarios that allowed spawning (because of the fine spawnable grain size). But, its narrow spawning range limited its geomorphic impact in the scenarios in which spawning occurred (such as in run 18 in Fig. 6). Chinook had a wide range of spawnable grain sizes, so when the appropriate spawnable grain size distribution was present, Chinook had the greatest net geomorphic impact.

In Fig. 7 we illustrate the differences in the channel profile between a species with a restricted range of spawning (right panel, Atlantic) and a river with the diverse population represented by the range of Pacific species considered here (left panel). We show two model runs to illustrate the impact of species diversification on channel evolution. The main difference in the model are the range of grain sizes suitable for spawning, that leads to more runs with different Sternberg parameters having grain sizes suitable for spawning. In the right panel, there was essentially no difference between the no spawning and spawning by Atlantic salmon (except for a very small reach where spawning occurred), but differences emerged with the diverse run because Chinook can move larger bed material and Pink can move finer bed material than

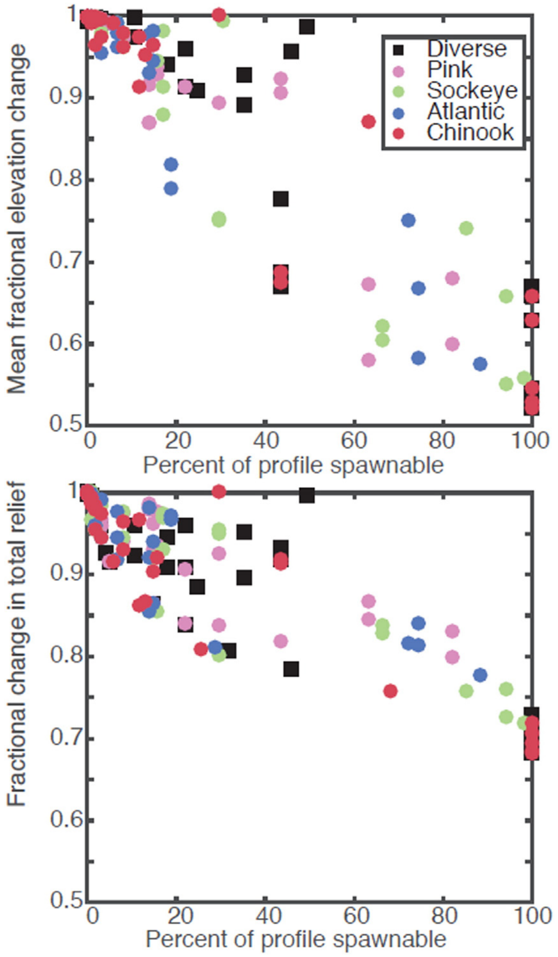

Fig. 5. Fractional profile changes for each species including the diverse combination of Pacific salmon. In general, the results show that the higher the proportion of the profile that is spawned, the greater the geomorphic impact though some variability exists. Part of this variability is caused by different species, denoted by different colors, spawning in different grain sizes (see text for explanation). Differences between mean elevation and relief change (i.e., some runs have a large relief change but relatively low mean elevation change) can be explained by considering where on the profile spawning occurs (e.g., see Fig. 6).

other species. This allowed spawning effects to impact a larger portion of the profile. The second panel shows the influence of spawning for Atlantic salmon and for the diverse model run compared to no spawning. The geomorphic effect of a higher functional diversity of spawners was greater than with only Atlantic salmon runs. We make this comparison to illustrate the potential influence of the biological radiation of Pacific salmon from the common ancestor, *Salmo* spp. Modern Atlantic salmon are presumably not the same size as the common ancestor, but it might approximate the geomorphic impact of salmon prior to their diversification.

4. Discussion

Biological evolution can influence landscape evolution. Our modeling suggests that adaptive radiation events, such as the one that occurred in the Pacific Northwest, can have profound effects on landscapes. Through this modeling exercise, we illustrate how the fine-scale process of salmon spawning can increase the local erosion efficiency of a stream reach and have coarse-scale implications for channel profile adjustments over geologic timescales. In particular, this illustrates how physical and biological systems can be coupled, with physical forces creating a template for biological processes, such as speciation, to occur, and, importantly, biological forces changing the outcome of the original physical template. These couplings are known in multiple systems (e.g., ecosystem engineers); yet, here, our example shows coupling over the large and long-term scales of biological and landscape evolution.

Our modeling results have implications for understanding biophysically coupled systems and adaptive radiation events. Our results suggest that the presence of species with a behavioral trait that can geomorphically alter a landscape can have long-term and large-scale effects on landscape erosion and shape. Additionally, the radiation of the species or more specifically, the diversification of the trait, can have further physical influence by altering a larger proportion of the landscape. That is, it is not just spawning of one species but that of many species over multiple grain sizes that increases the geomorphic change. Our comparison between the diversity of spawners (Pinks to Chinook) compared to Atlantic salmon (Fig. 7) illustrates the potential influence of the salmonid radiation; that is, we used modern Atlantic salmon as a preradiation proxy for the common ancestor (*Salmo* spp.). Although this assumption is large, the effect of multiple species is still apparent in the modeling, and this is a more conservative comparison than the spawners versus no spawners comparison.

These finding have implications for our view of observed adaption radiation events across multiple taxa. Speciation is common; radiation into multiple taxa over short time periods is less common. Adaptive radiation events are important for understanding biodiversity (Schluter, 1996). Potentially, the physical effect of spawning is a mechanism by which new spawning habitat arises and speciation can continue. That is, the radiation of the species was most likely initiated by mountain building and the increase in habitat types for spawning; in turn, this effect of the organisms on their environment through 'ecosystem engineering' (sensu Jones et al., 1994) could provide a complementary explanation for the pattern of some taxa to radiate 'explosively' (Harmon et al., 2009). The process of organism-driven environmental modification has implications on natural selection and therefore feedbacks on the dynamics of evolutionary biology. This is termed *niche construction* in evolutionary biology, which is a more evolution-based treatment of ecosystem engineers (Odling-Smee et al., 2003). Meaning, through their physical influence, ecosystem engineering species might create novel habitats that further stimulate speciation. Our modeling results encourage further investigation into the mechanics of how salmon spawning might influence speciation through the creation of new habitat types and their notable evolutionary implications.

Spawning influences the erosion efficiency along the profile at the location where the size of the sediment allows for spawning (Table 1). In most cases, the entire profile is not suitable for spawning, which creates transition points along the profile. One outcome of this longitudinal transition in erosion efficiency are changes in slope that might be significant enough to create knickpoints (Fig. 6). Knickpoint generation and migration upstream is typically associated with changes in base level (rise or fall) and are thought of as exogenous forces controlling the sediment routing system (Grimaud et al., 2016) or endogenous controls such as network structure and tributaries (Benda et al., 2004). One potential outcome of heterogeneous spawning through a profile is creation of endogenously created knickpoints.

Patterns in river concavity provide a potential landscape metric to test the impacts of salmon spawning. If different rivers exhibit variable spawning habitat along their profiles, then their concavities might be impacted differently. For example, rivers with habitat that tends to the higher elevations should exhibit lower concavities than rivers where the habitat is closer to base level. Of course, testing this would require accounting for other impacts (such as gradients in rock uplift, climate, network structure, or lithology), but it does provide a conceptual framework for thinking about what controls the observed variability in river concavity in locations that contain salmon species.

We stress that these results should be viewed as an indicator of the potential impact of salmon on bedrock river erosion and not necessarily the actual change in elevation one could expect from salmon. There are

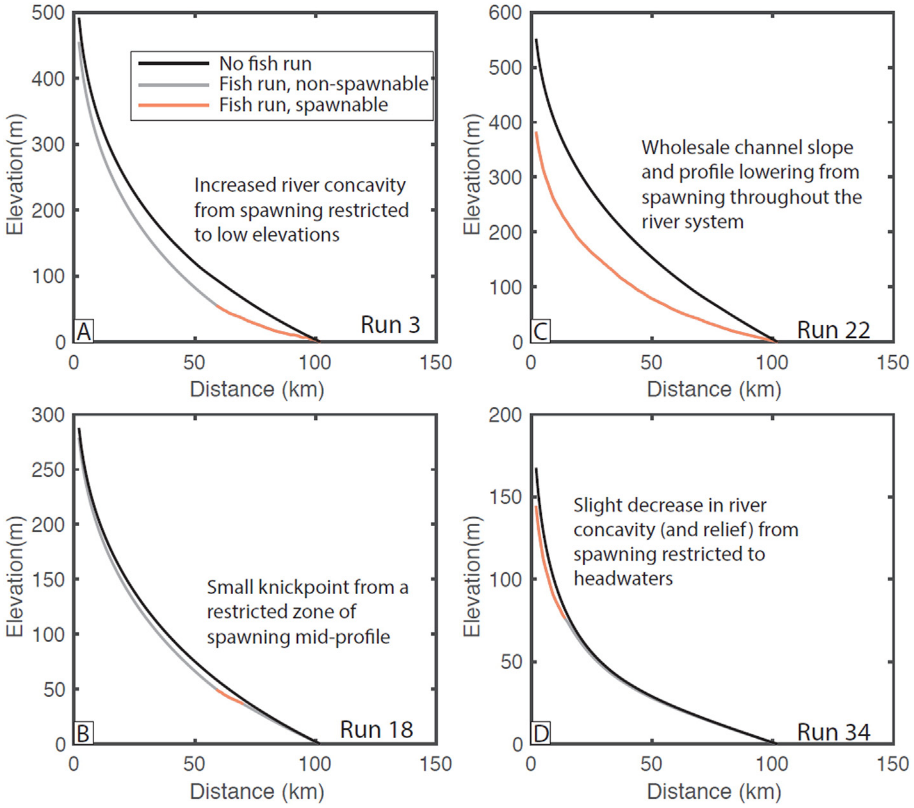

Fig. 6. Four example runs of different fish and Sternberg parameter estimates illustrating magnitude and concavity changes resulting from spawning on available gravels. Note changes in concavity caused by position of spawnable gravel and potential knickpoint initiation.

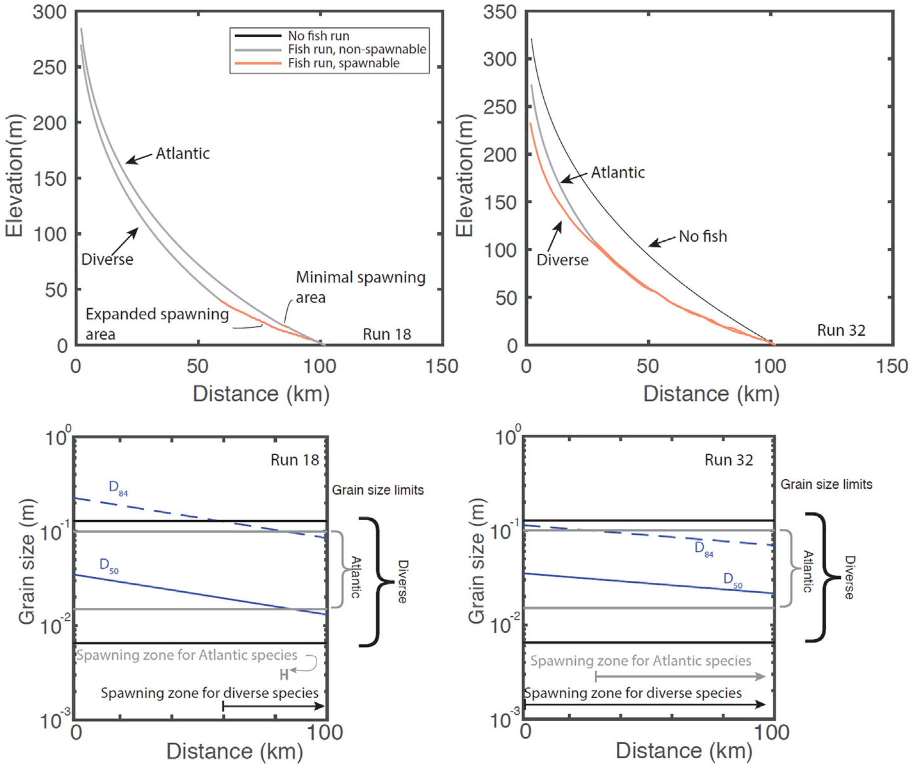

Fig. 7. Two example runs comparing Atlantic salmon do the diverse (all salmon) runs to illustrate the potential geomorphic influence of the radiation of Pacific salmon compared to their closest taxa.

a number of assumptions and parameters that we have taken liberty with that impact real systems. In addition to the assumptions outlined in the methods, we have also ignored how glacial-interglacial cycles would impact salmon habitat and water discharge. We have assumed a bedrock erodibility, which can vary widely across different rock types (Stock and Montgomery, 1999). Rock uplift was held constant and applied uniformly over the river profile. Grain size was only influenced by distance downstream and did not evolve with changes in shear stress. Rock type also influences the size of particles delivered from hillslopes to streams (Huddart, 1994). Given the importance of grain size to salmon spawning, variations in rock type along a river pathway has the potential to influence the impact of salmon spawning on erosion efficiency in negative and positive ways (i.e., generating grain sizes that limit or promote salmon spawning). More local impacts such as discrete tributary inputs, large woody debris, and sediment connectivity (e.g., sediment patches) could also expand or constrict habitat availability beyond what the simplified Sternberg model would predict (Rice, 2017). Feedbacks among salmon impacts and these different factors would be fruitful future research for understanding the interaction of salmon and landscape evolution. For example, changes in grain size caused by spawning activity and geomorphic change could propagate upstream and downstream, potentially allowing an expansion of spawnable habitat and a positive feedback on the impacts of salmon on landscape evolution. Moreover, the interaction between mainstem channel evolution and tributary inputs could impact the network structure (e.g., Benda et al., 2004) if these feedbacks develop over long timescales.

Nonetheless, the quantifiable impacts of salmon spawning on river dynamics shown in this modeling study provide a framework for considering how such impacts might translate into highly variable natural systems. For instance, we found that the location of spawnability has a large impact on the landscape response. Any natural processes that enhance salmon spawning in lower reaches of rivers will have a propagating effect across the landscape. Likewise, any scenarios that expand the geographical extent of spawnability – such as drainage capture, climate change, or tectonics – can also enhance the impact of salmon spawning on topography. Or, the intriguing case of escaped farmed salmon (e.g., *O. tshawytscha*) and trout (*O. mykiss*) invading into the freshwater systems of Patagonia (Pascual et al., 2009). Conversely, the large-scale extirpation or reduction of salmon in many rivers because of human activities (e.g., dams, loss of in-stream habitat, overfishing) could have geologic timescale consequences for channel profile and landscape evolution. River profiles that have evolved to be in dynamic equilibrium with salmon spawning may need to significantly adjust to the lack of salmon, particularly those watersheds with a diverse range of species.

5. Conclusion

The results of this study underline the importance of understanding drivers and feedbacks among components in biophysical systems over short- and long-term timescales as well as understanding biological controls on landscape evolution. Specifically, mountain building most likely fostered radiation of Pacific salmon and, in turn, that radiation might have significant influence on the erosion of those same mountains. Our main finding illustrates that the increase in sediment transport efficiency caused by salmon spawning allows for more frequent bedrock erosion; therefore steady-state channel slopes where fish are present will be lower than if those fish never reproduced in those reaches. This organism-driven influence has biological evolutionary implications, as well as implications for our understanding of landscape evolution.

Acknowledgements

AK, BY, and EY were funded by their respective universities, but not funded directly by a grant. We thank the organizers of the special issue and the Binghamton Conference for the invitation to participate. The modeling portion of this work was supported in part by Lilly Endowment, Inc., through its support for the Indiana University Pervasive Technology Institute, and in part by the Indiana METACyt Initiative. The Indiana METACyt Initiative at IU was also supported in part by Lilly Endowment, Inc.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.geomorph.2017.09.033.

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