

The influence of Pacific salmon decay products on near-field streambed sediment and organic matter dynamics: a flume simulation

John F. Rex,^{1,2,3*} Ellen L. Petticrew,^{1,3} Sam J. Albers³ and Neil D. Williams⁴

¹ Geography Program, University of Northern British Columbia, Prince George, British Columbia, Canada

² Ministry of Forests, Lands, and Natural Resource Operations, Prince George, British Columbia, Canada

³ Quesnel River Research Centre, University of Northern British Columbia, Likely, British Columbia, Canada

⁴ URS Infrastructure and Environment UK Ltd, Chesterfield, Derbyshire, UK

Received 31 May 2013; Revised 25 March 2014; Accepted 14 April 2014

*Correspondence to: John F. Rex, Ministry of Forests, Lands, and Natural Resource Operations, 1011 Fourth Avenue, Prince George, BC V3L 3H9, Canada.

E-mail: john.rex@gov.bc.ca

ESPL

Earth Surface Processes and Landforms

ABSTRACT: Pacific salmon are biogeomorphic agents shown to induce positive feedbacks on their natal watersheds. However, the literature documenting their ecological effects on in-stream natal environments is more divisive. The disturbance salmon create during redd construction has the potential to reduce stream productivity. The pulse of salmon organic matter (SOM) and marine derived nutrients (MDNs) released during carcass decay has been reported as either stimulating in-stream productivity or having no local effect. To evaluate the ecological costs and benefits of salmon spawning events, MDN delivery and storage processes need to be identified and quantified. A simulation was conducted in three flow-through flumes (2 m × 2 m × 30 m) over a 33-day period (consisting of 15 baseline, four MDN exposure, and 14 post-exposure days) to assess near-field sediment and organic matter dynamics during active and post-spawn simulations. The objective of the study was to measure changes in the amounts and particle sizes of suspended and gravel-stored fine sediment, in order to elucidate the process and significance of SOM recruitment to the gravel bed via sedimentation. Gravel beds in all flumes were enriched with SOM following treatments but the response was highest in the active spawn simulation. The more effective delivery in the active spawn simulation was attributed to its higher inorganic sediment concentration, which is known to enhance floc formation. Although the active spawn simulation delivered more SOM to the gravel bed, the post-spawn phase may be equally important to natural streams because its decay phase is longer than the active spawn and consequently can provide SOM to the streambed as long as carcasses remain in-stream. The delivery, and potential retention, of SOM to spawning streambeds and the intergravel environment may be particularly important for interior streams, which experience low flow conditions during the spawning phase and accordingly have the potential for hyporheic nutrient recruitment and storage. Copyright © 2014 John Wiley & Sons, Ltd.

KEYWORDS: Pacific salmon; marine-derived nutrients; organic matter; fine sediment; flocculation; flume simulation

Introduction

Spawning Pacific salmon initiate significant biophysical changes within natal streams through channel bed disturbance during redd construction and delivery of marine derived nutrients (MDNs) during streambed fertilization (DeVries, 2012). The stream response to channel bed disturbance and nutrient subsidy has been interpreted as having both positive and negative effects, which has led to contradictory perspectives about the ecological benefit of spawning salmon to their natal streams. Some research suggests a net-benefit to natal streams with increased nutrient levels and benthic productivity (Wipfli *et al.*, 1998; Johnston *et al.*, 2004) while others suggest a more variable response with nutrient export (via smolt outmigration) exceeding that imported by adult salmon (Moore *et al.*, 2007) as well as a decrease of primary productivity (Holtgrieve and Schindler, 2011). Therefore the

ecological impact of salmon spawning activities, as a stabilizing or destabilizing force, remains a topic of active discussion.

Disparate findings in the literature regarding the influence of salmon on their natal streams may be the result of measurable differences in biophysical condition of spawning environments (e.g. interior versus coastal) and/or confounding differences in spatial and temporal limits of the experiments. However, most studies have focused directly on the biota and water chemistry within the confines of the stream channel boundary (Janetski *et al.*, 2009) with fewer studies focusing on the streambed.

The gravel beds of salmon spawning streams potentially play an important role in the retardation of nutrient transport through the spawning reaches as they can act as a sink for nutrients, due to the porosity of gravels and their ability to capture and retain fine sediment. Specifically, the gravel bed can trap and store fine sediment and its associated nutrients which are moving as flocs that form from silt and clay-sized

inorganic sediment and available organic matter. Flocs have been shown to enhance delivery of MDN to gravel beds (Petticrew, 2005; Rex and Petticrew, 2008) and provide nutrients for localized biological activity, such as biofilm growth (Albers and Petticrew, 2012). Flocs are composite particles of inorganic sediment and organic material formed under favourable chemical, physical, or biological conditions (Droppo *et al.*, 1997). They can be an effective vector for streambed delivery of MDN because salmon organic matter (SOM) generated flocs are larger and have a higher settling rate than their component parts (Petticrew, 2005). Characterizing and quantifying the role of fine sediment interactions with SOM in MDN delivery, retention, and release within natal streambeds will result in better predictive ability regarding the economy and fate of MDNs in watersheds supporting salmon stocks.

Salmon-based flocs, formed from fine sediment and SOM have been documented in the water column (McConnachie and Petticrew, 2006) and streambed (Petticrew and Arocena, 2003) of salmon streams during and after spawning events. Optimal conditions for floc formation occur in the water column during spawning due to the temporal overlap of suspended fine sediment and SOM. Higher in-stream concentrations of fine sediment are generated by suspension during streambed disturbance from redd construction at the same time that SOM from salmon carcasses and also SOM previously stored in the streambed are released. Suspended sediment concentrations decrease in the post-spawn period but the timeframe for SOM contribution is longer and can extend from fall through spring in interior streams, as carcasses not removed by predators can remain in slow-water areas such as behind large woody debris piles (Minakawa and Gara, 2005; Strobel *et al.*, 2009). The two processes of redd construction and carcass decay result in concomitant fine sediment re-suspension and SOM contributions to the water column that has been termed the salmon disturbance regime (Albers and Petticrew, 2012). The salmon disturbance regime can be quite extended in some regions as the spawning phase can take up to four weeks with considerable temporal overlap of active spawn and die-off. The role of the gravel bed in regulating the ecological benefit of MDN from spawning salmon depends upon the temporal and spatial relationships among MDN delivery to and retention in the bed during the salmon disturbance regime.

Previous re-circulating flume-based investigations have shown that flocs formed in the water column, settled on, and infiltrated into, the gravel-bed matrix within 20 m of where SOM and clay were added and elevated interstitial nitrogen concentrations for 14 days (Rex and Petticrew, 2008, 2010). Field-based investigations have identified elevated marine nitrogen signals in streambed surface biofilms (Albers and Petticrew, 2012), in the hyporheic zone below the stream and riparian areas following spawning periods (O'Keefe and Edwards 2003; Pinay *et al.*, 2008) and can be associated with substantial intergravel storage of fine sediment after the spawning phase (Albers and Petticrew, 2013).

With the aim of providing more information to elucidate the effects and benefits of the salmon disturbance regime on stream channel conditions this study was undertaken to investigate potential near-field recruitment (<20 m) of sediment and SOM to the streambed during active and post-spawning simulations. The study objectives were to: (1) simulate flow conditions and fine sediment and SOM concentrations observed in British Columbia interior natal streams; (2) measure the development and changing size of flocs; (3) quantify the role of flocs in enriching streambeds with SOM. These objectives were achieved using three flow-through flumes in an analogue

simulation of natural stream conditions during active and post-spawn phases. This study investigates near-field floc formation and sedimentation of SOM during active and post-spawn simulations to identify trends in streambed delivery and retention.

Methods

Study and flume characteristics

Three 30 m × 2 m × 2 m outdoor flumes at the University of Northern British Columbia's Quesnel River Research Centre (QRRC) in Likely, British Columbia were used from 28 July 2010 to 29 August 2010. The flumes are fed from a groundwater source with negligible particulate matter concentrations. Flume beds were composed of gravels having a grain size distribution between 1 and 25 cm (*b*-axis), which is similar to preferred spawning habitat (Bjorn and Reiser, 1991). Riffle bars (approximately 15 cm high) spanning the widths of the flumes were constructed to represent natural bed forms in spawning reaches. Riffle bars were sampled using infiltration bags (Rex and Petticrew, 2010). Prior to the experiment, each flume bed was cleaned by re-suspending fine particulate material and flushing it out by a combination of pressure washing and high flume discharges. Once cleaned, discharge was standardized across the flumes to represent water column depth and velocity levels typical of regional salmon spawning sites (less than 15 cm deep and 10 cm s⁻¹, respectively).

Experimental design

The three flume simulations were designated as an active spawn (SOM+clay concentration of 5 mg l⁻¹), post-spawn (SOM+clay concentration of 0.5 mg l⁻¹) and a SOM-only treatment that served as a clay control (Table I). Quantities of SOM added to each of the three flumes during this study were based on stream areal biomass estimates (100 g m⁻²) from O'Ne-eil Creek, British Columbia (Petticrew, 2005) which was the same stream system that defined this study's range of total suspended sediment concentrations (McConnachie and Petticrew, 2006).

Liquefied SOM and dispersed suspended clay were added to each flume via a constant flow from separate stock tanks. Approximately 23% less SOM was added to the active-spawn flume due to differences in delivery over the four day period (Table I). Stock solutions from tanks passed through Tygon tubing to two 60 µm Nitex screened funnels before entering the flume. Clay and salmon passed through separate 60 µm Nitex lined funnels first and then were combined in a larger, screened funnel before being added to the flume. This delivery system ensured that no particles greater than 60 µm were added to any flume.

The SOM slurry was prepared by rotting pieces of pink salmon (*Oncorhynchus gorbuscha*) encased in 60 µm Nitex screen bag and water for three weeks in sealed plastic buckets. The resultant liquid fraction was added to each salmon tank (1.5 l per day). Kaolin clay was dispersed in distilled water by ultrasonication for five minutes and sieved through 60 µm Nitex screening prior to addition. Similarly, SOM was screened through 60 µm mesh prior to being added to the stock tanks.

Sampling included a baseline period that extended 15 days from 28 July 2010 to 11 August 2010 during which only groundwater was run through each flume. The exposure period began on 12 August 2010 and extended for four days, through to 15 August, after which the post-exposure period extended for 14 days until 29 August 2010.

Table 1. Experimental design, flume conditions, and summary findings for the near-field recruitment of SOM and fine sediment during active-spawn, post-spawn, and salmon-only treatments

Active-spawn	Post-spawn	Salmon-only
SOM + Clay (5.0 mg l ⁻¹) Masses: 597.3 g and 26,987.0 g	SOM + Clay (0.5 mg l ⁻¹) Masses: 772.9 g and 2,430.0 g	SOM no Clay Mass: 766.6 g
Baseline		
<i>Water column particle size distribution (PSD) measured</i>		
<i>Three intergravel sediment sample bags pulled 11 August</i>		
Baseline infiltrated inorganic matter range over all treatments 53.9 - 58.3 mg kg ⁻¹ Baseline infiltrated organic matter range over all treatments: 45.1 - 47.4 mg kg ⁻¹		
Exposure		
<i>Water column particle size distribution (PSD) measured</i>		
d ₅₀ = 17 µm % of particles > 60 µm = 32	d ₅₀ = 203 µm % of particles > 60 µm = 59	d ₅₀ = 250 µm % of particles > 60 µm = 72
<i>Three intergravel sediment sample bags pulled 16 August</i>		
Average inorganic concentration: 329.1 mg kg ⁻¹ Average organic concentration: 74.7 mg kg ⁻¹ Intergravel mass > other two treatments	Average inorganic concentration: 88.8 mg kg ⁻¹ Average organic concentration: 56.8 mg kg ⁻¹ Intergravel mass < active spawn = salmon-only	Average inorganic concentration: 66.6 mg kg ⁻¹ Average organic concentration: 45.5 mg kg ⁻¹ Intergravel mass < active spawn = post-pawn
Post-Exposure		
<i>Water column particle size distribution (PSD) measured</i>		
<i>Three intergravel sediment sample bags pulled 18, 20, 23, 29 August</i>		
390 µm particles concentration 434.0 µl kg ⁻¹ Inorganic mass > other two treatments	390 µm particles concentration 43.0 µl kg ⁻¹ Inorganic mass = Salmon-only	390 µm particles concentration 82.0 µl kg ⁻¹ Inorganic mass = Post-spawn

* Italicized titles indicate procedures for all treatment columns

Sampling

For each sample period, material was collected from both the water column and flume bed. Infiltration bags were installed in rows of three across each constructed riffle bar on 28 July 2010, after discharge levels were standardized in the flumes. One bag was buried in the centre of the riffle bar and the remaining two were buried approximately 40 cm from the flume walls. Bags were buried to a depth of 15 cm with cleaned gravels. Each flume was divided into three sampling areas consisting of two riffles. These were identified as the front, middle and rear sampling areas of the flume.

Three infiltration bags were removed on each sample date. One bag was randomly selected from each of the three sample areas, which were used to determine a mean value spatially representative of the flume. Infiltration bags were removed by holding the retrieval ropes in one hand, placing a plastic lid over the reference column of gravel with the other hand and then pulling the bag up in one motion to capture the gravel, fine sediment and water contained within that gravel column. The entire sample was sieved using a 2 mm screen and the filtrate was transferred to a volume calibrated bucket for further analysis. The total volume of filtrate material collected from each bag and the total weight of the gravels collected from each bag was measured. Fine sediment was sub-sampled from the infiltration bag sample by vigorously stirring the sample within a bucket, waiting 10 seconds to allow larger and dense particles such as sand to settle, and then sampling the top 10 cm of filtrate. This method of sub-sampling the finer sediment that passed through the 2 mm sieve has been shown to collect particles with constituent components $< 75 \mu\text{m}$ (i.e. larger aggregated and/or flocculated particles will be sampled in this portion of the water column but after disaggregation the constituent particles measured are all smaller than $75 \mu\text{m}$) (Petticrew *et al.*, 2007).

Samples were filtered onto pre-ashed, pre-weighed glass fibre filters for gravimetric analysis. Suspended sediment concentration of these sub-samples was determined by weighing filters dried at 60°C for 24 hours. Filters were then ashed for two hours at 550°C and weighed again to determine the inorganic and organic sediment fractions. The calculated sediment concentration was used to determine the total weight of fine sediment present in each infiltration bag, and these values were normalized by the weight of gravels from each bag. Particle size of the fine sediment fraction ($< 75 \mu\text{m}$) was measured using a Laser In Situ Scattering and Transmissometry

probe (LISST-100) from Sequoia Scientific Inc. (Bellevue, WA). This probe is able to measure particle sizes between 2.5 and 500 microns following calibration with ultrapure water. Infiltration bag LISST samples were diluted with distilled water in a 1:3 ratio, to ensure samples were within the operational range of the instrument, and placed into the sample chamber. The LISST fires a laser into the sample and measures the scatter of laser light on to a series of 32 concentric ring detectors (Agrawal and Pottsmith, 2000). Each bag sample was measured three times and the average of those series was used as the mean particle size distribution for that bag sample. Following sample collection, data were processed using MS ExcelTM macros that verified proper probe functioning and calculated central tendency measures for each three second sample (Williams, 2006; Williams *et al.*, 2007). Similar to the gravimetric sediment measures, LISST infiltration bag volume concentration data was normalized by the volume of water used to rinse infiltration gravels and the mass of gravels sampled from each bag. This process resulted in an estimate of volume of particles (including flocs and aggregates with constituent particles $< 75 \mu\text{m}$) per gravel mass collected in each bag.

Statistical analysis and data manipulations

All analysis and plotting was completed using R 2.14.1 (R Development Core Team, 2011) with *ggplot2* package (Wickham, 2009). Water column particle size data were calculated as an average between measurements taken at the front and back of each flume. Kolmogorov–Smirnov (K-S) tests were performed to compare the cumulative particle size distribution during each treatment averaged over the exposure period. Locally weighted regression, or LOESS, curves were utilized as exploratory graphical tools to visualize temporal patterns of sediment infiltration. The curves were generated using the *stat_smooth* function in *ggplot2* with a spanning coefficient of 1.25 to prevent overfitting.

Results

Simulating natural flow conditions, fine sediment, and SOM concentrations in the flumes

Flow conditions similar to that observed in natal streams were maintained for the duration of the study. Clay was added to treatment flumes in concentrations representative of that

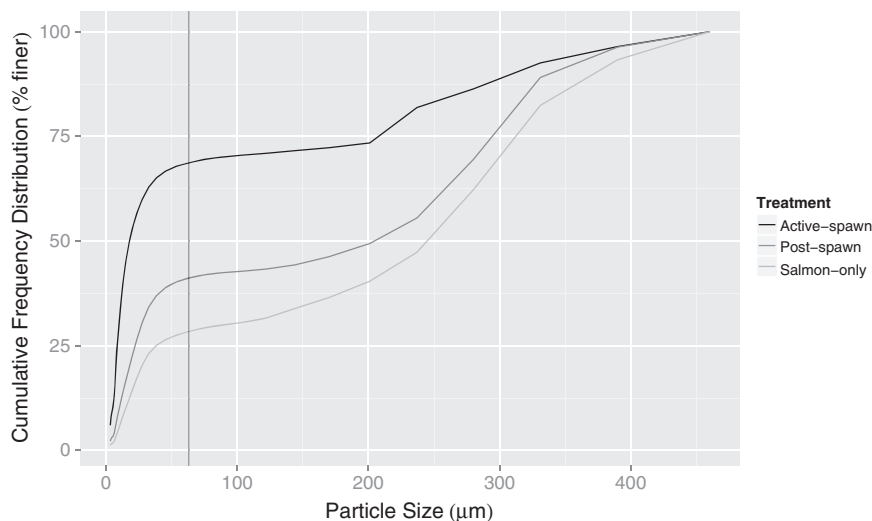


Figure 1. Average cumulative particle size distributions of suspended sediment during the exposure period. No particles larger than $60 \mu\text{m}$ were added to the flume, this threshold is indicated by the vertical line.

observed in natural studies (McConnachie and Petticrew, 2006) with clay added to the active-spawn simulation in a concentration that was approximately 10-fold more (5 mg l^{-1}) than that added to the post-spawn flume (0.5 mg l^{-1}). Although SOM delivery to each stock tank was set to a similar rate across all three flumes, the active-spawn simulation flume received ~23% less total SOM from its stock tank than the others (Table I).

Quantifying the development and changing size of flocs

Suspended sediment particle size changed following the addition of clay and/or SOM. Each treatment flume experienced floc formation as evidenced by the increase in suspended sediment particle size relative to the constituent materials added to the flume (Figure 1). The cumulative frequency distribution curves of particle size show 28, 41 and 68% of the suspended sediment for salmon-only, post-spawn and active spawn treatments respectively was finer than the screening threshold of $60 \mu\text{m}$, indicating that 72, 59 and 32% of the particles were flocs of larger sizes generated during the exposure phases in each respective treatment. The particle size pattern for each treatment was anticipated because the mass of kaolin clay particles (~25 000 g) added to the active spawn treatment overwhelms the signal at the lower end of that particle size distribution. In the post-spawn treatment only 2500 g of clay particles were combined with SOM whereas none was added in the SOM-only treatment.

The suspended sediment d_{50} increases from $17 \mu\text{m}$ in the active spawn treatment to $203 \mu\text{m}$ in the post-spawn and $250 \mu\text{m}$ in the salmon-only treatment. The salmon-only treatment had the highest proportion of particles $> 200 \mu\text{m}$ while the active spawn suspended sediment distribution was finer than both the salmon-only and post-spawn curves due to the large quantity of clay added during that treatment (K-S test $D=0.48$, $p\text{-value}=0.001$ and $D=0.55$, $p\text{-value} 0.001$, respectively). The salmon-only and post-spawn comparison was not significantly different (K-S test $D=0.32$, $p\text{-value}=0.08$) possibly reflecting the low clay concentration in these treatments compared to the active spawn simulation.

Floc enrichment of flume gravel beds with SOM

Flocs forming in the water column were sequestered to the streambed as shown by an increase in both the organic and inorganic sediment load of fine ($< 2 \text{ mm}$) sediment in flume gravels (Figure 2). LOESS curves using raw data rather than sample averages show a consistent and substantial increase in gravel-bed storage for both the organic and inorganic sediment fraction in the active spawn treatment compared to both the post-spawn and salmon-only. Neither the salmon-only nor post-spawn treatments experienced concentrations much higher than observed during the baseline period (Table I). The active spawn simulation exhibited the strongest response despite the addition of 23% less SOM to the channel compared to the salmon-only and post-spawn treatments. LOESS estimates indicate that while the post-spawn and salmon-only treatments did not exhibit a notable increase in either organic or inorganic sediment to the gravel bed, infiltrated inorganic and organic sediment was retained in the active-spawn gravel bed up to 13 days after the exposure period (Figure 2).

Particle size analysis of gravel-bed samples in the post-exposure period indicates that the stored fine sediment particle size and volume of material increased in each flume. The largest increases were measured in the active spawn channel. The post-spawn and salmon-only particle size analysis indicates that flocs retained similar distribution from the first to second week in the post-exposure period. In contrast, the active spawn distribution increased substantially, doubling from the first week post-exposure when it was similar to the other treatments (Figure 3). The increased volume of particles $> 300 \mu\text{m}$ in the active spawn simulation (Table I) infers that these larger flocs grew in the gravel bed after the finer suspended particles observed in Figure 1 settled onto the gravel bed.

Discussion

Study findings indicate that there are substantial differences in the efficiency of near-field sediment and SOM recruitment to gravel beds during simulated active and post-spawn phases. The higher clay concentration of the active spawn simulation increased organic matter delivery to the gravel bed despite the addition of considerably less SOM to this treatment. This is the result of increased flocculation due to higher

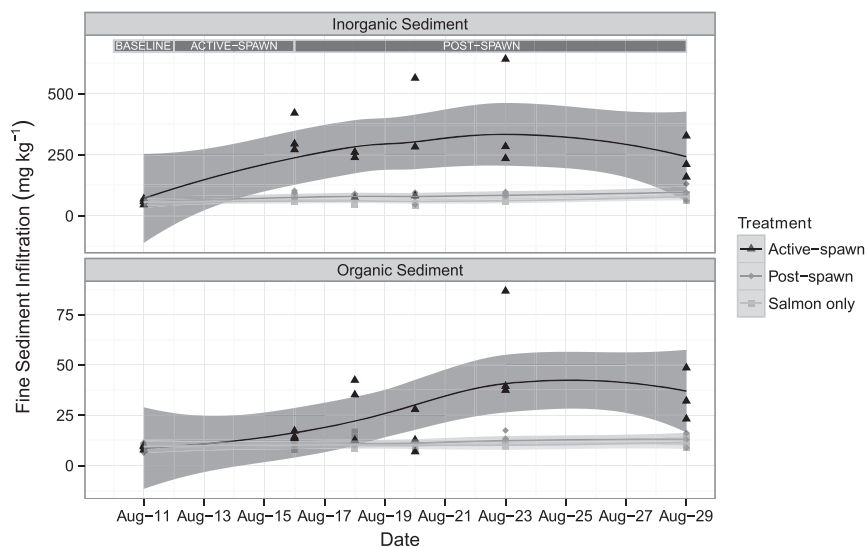


Figure 2. Infiltrated sediment normalized by the gravel mass in each infiltration bag. Each line denotes a LOESS smoother for each treatment. Bands indicate the standard error associated with the LOESS estimation. Points are raw data values.

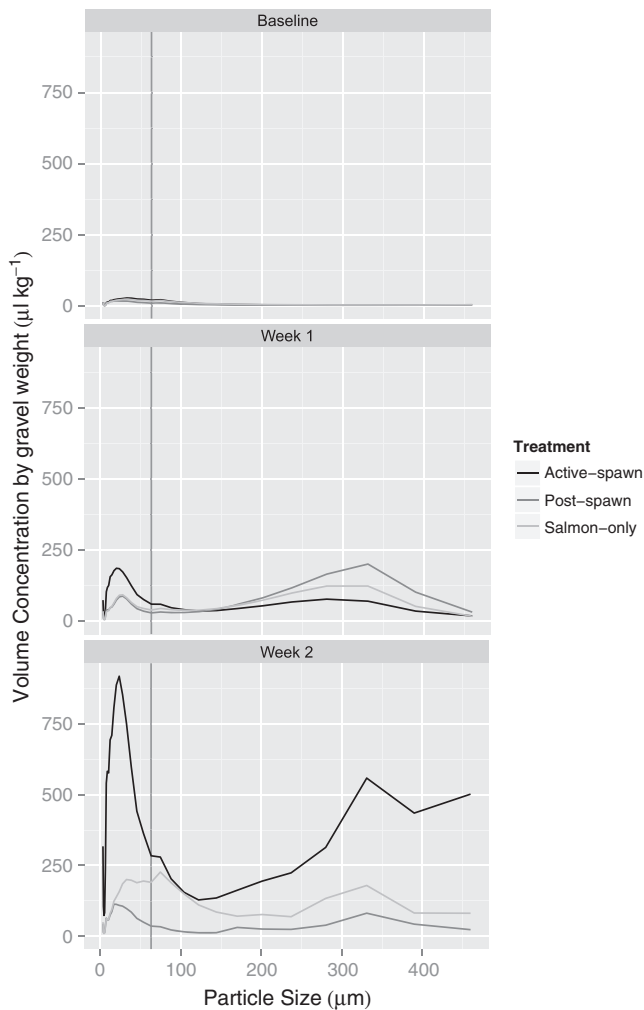


Figure 3. Average particle size spectra of infiltrated sediment. Baseline is defined as the period before the exposure treatment while weeks 1 and 2 represent samples from the post-exposure period. Vertical lines indicate the 60 μm screening threshold.

concentrations of clay. The clay provides increased surface area for attachment while the number of individual clay particles increases the probability of collisions and hence floc formation (Droppo *et al.*, 1997).

Flocculation was observed in each flume following the addition of SOM and/or SOM plus clay (Figure 1). The largest flocs suspended in the water column were observed in the salmon-only and post-spawn treatment conditions which is similar to the finding of Petticrew (2005) in the Stuart-Takla watershed of northern interior British Columbia. However, in the context of retention by the gravel bed, the active-spawn conditions yielded the greatest mass and volume of infiltrated material (Figures 2 and 3).

Representativeness of simulated experiments

The spatial scale of the flumes allows assessment of near-field sequestration of SOM, which was identified as occurring within 20 m in the spawning channel study by Albers and Petticrew (2012). Although devoid of actively spawning salmon, the simulation allows comparison of near-field floc recruitment associated with differing water column concentrations of suspended sediment that are representative of a spawning and post-spawn phase.

The SOM prepared for this investigation is somewhat different than can be expected under natural conditions and

the screening of SOM at 60 μm is likely to create smaller particles than the full range observed in a natural stream. SOM preparation in this study was artificial but the findings are relevant to natural systems because the flume conditions are more conservative than natural systems. The variety of SOM and inorganic sediment particle size and composition found in natural systems may magnify natural river floc formation and sedimentation. The SOM stock solution was screened to < 60 μm to test for flocculation and its contribution to SOM deposition and gravel-bed sequestration. It is likely that larger particles of the breakdown products would be intercepted by the bed in natural spawning conditions, but this effect was controlled in this study to investigate flocculation processes. The SOM decay product used in this study was generated in an artificial manner to allow a controlled testable event, this liquid SOM will also be generated in-stream and it represents a high quality MDN that can be used by organisms or moved to the gravel bed as flocs.

The experimental design consisted of three spawning simulations; one in each flume which allowed for monitoring of different sediment processes in parallel following a baseline period. This design provided the advantage of running all simulations in the same meteorological conditions over the 33 day experiment, representative of the local annual spawning environment. All flumes were seeded with similar gravel sizes, fed with identical water and subjected to similar external conditions, meaning that all potential hydro-morphological influences were controlled and the experimental treatments were the only variable. Consequently, there is high confidence that the varying response measured between the treatments is due to the treatments themselves rather than any systematic underlying difference in flumes.

SOM-floc dynamics

The trends in particle size documented during this study verify that: (1) flocs formed in the water column and settled onto the flume gravel bed within 20 m of the source material; (2) flocs were stored and grew after they settled and infiltrated into the gravel bed. Flocs that settle into intergravel pore spaces can consolidate or grow by both physical and biological processes which include particle collision and bacterial processing (Krishnappan, 2007; Areepitak and Ren, 2011). Specifically, microbial processing of nutrient-rich sediments results in bacterially exuded exopolysaccharides which act to 'glue' particles together (Wotton, 2007) generating larger denser flocs or aggregates which are stored on the streambed surface or within intergravel spaces. Over the course of the experiment, intergravel floc growth was observed to be most substantial in the active-spawn simulation (Figure 3), with aggregate sizes of ~20 and 325 μm representing the two main modes in the size distributions. While these mode sizes did not change much during the post-exposure period the volume of sediment in the active-spawn treatment did markedly increase over this time. Considering that no new material was added to the flumes after the exposure period this change in mass and volume suggests that microbial activity is the dominant influence on particle size growth.

Implications of SOM retention in gravel beds

Flocs that remain in storage can be suspended by salmon during subsequent nest construction or entrained back into the flow with higher water velocities. The period of intergravel

storage will depend upon local stream and intergravel conditions. The potential for stored flocs, comprised of SOM and inorganic sediment, to re-enter the water column and continue to move downstream is high during prolonged spawning events and periods of increased discharge such as spring melt and rainstorm events. This experiment was designed for the analysis of the near-field effects of flocculation, but it can be postulated that the material in natural channels would continue to move downstream as part of the sediment-nutrient load and be processed as part of the river continuum.

Flocculation mechanisms, both in the water column and the gravel bed, alter the size and the density of the particles enhancing the residence time of nutrients in these flumes and natural systems. In natural streams, retention can be further enhanced in storage areas such as pools including those created by large woody debris dams and backwater zones. Large particle formation in gravel-bed samples infers the retention of SOM and MDN, which can act to stimulate benthic algal and bacterial productivity. This indicates that flocs are an important connection between decaying SOM and re-incorporation of that organic matter into aquatic ecosystems.

The active spawn simulation was found to deliver more MDN to the gravel bed than the post-spawn or salmon-only treatment. In natural systems, however, the post-spawn phase may play an equally important role because the post-spawn salmon decay phase is longer than active spawn. The post-spawn phase extends from the time of salmon death until the carcasses leave the stream via predators, scavengers, or storm events which can extend from weeks to months. The delivery and retention potential of MDN may be particularly important for nutrient-poor interior natal streams. Interior streams with snow-melt dominated hydrological regimes experience low-flow conditions during and after the spawning phase whereas rain and mixed regime coastal watersheds can experience their highest flow after spawning (Eaton and Moore, 2010). The autumnal low-flow conditions of interior watersheds may provide better settling and gravel-bed entrainment conditions for flocs than high-flow conditions of rain dominated and mixed hydrology regime systems. In addition, the potential for increased settling during low-flow and relatively higher contribution of groundwater during this time enhances the potential for hyporheic exchange and recruitment. Current field investigations are underway to test these hypotheses and assess the importance of floc-mediated SOM delivery to natal streambeds and its role in MDN cycling within interior streams of British Columbia.

Conclusion

Findings from this study highlight a potentially important role for sediment-mediated feedback loops in freshwater ecosystems, specifically that MDN sedimentation and streambed retention may influence Pacific salmon stream productivity. The findings show the delivery of SOM coincident with floc sequestration and growth in the flume bed of each treatment, but with a more effective delivery and retention in the active-spawn simulation. Consequently, sediment processes (deposition and retention) influence biological processes (streambed nutrient retention and utilization) highlighting the ecological importance of both salmon and sediment-mediated mechanisms in the MDN cycle.

Acknowledgements—The authors would like to thank Alex Koiter for his contribution in the field to this project. The authors also extend their thanks to Laszlo Enyedy for technical and mechanical support. NSERC Discovery and FRBC Landscape Ecology grants to ELP funded this

research. The paper represents contribution number 15 in the University of Northern British Columbia's Quesnel River Research Centre (QRR) publication series.

References

- Agrawal YC, Pottsmith HC. 2000. Instruments for particle size and settling velocity observations in sediment transport. *Marine Geology* **168**: 89–114. DOI: 10.1016/S0025-3227(00)00044-X
- Albers SJ, Petticrew EL. 2012. Ecosystem response to a salmon disturbance regime: implications for downstream nutrient fluxes in aquatic systems. *Limnology and Oceanography* **57**: 113–123. DOI: 10.4319/lo.2012.57.1.0113
- Albers SJ, Petticrew EL. 2013. Biogeomorphic impacts of migration and disturbance: implications of salmon spawning and decay. *Geomorphology* **202**: 43–50. DOI: 10.1016/j.geomorph.2013.02.002
- Areepitak T, Ren J. 2011. Model simulations of particle aggregation effect on colloid exchange between streams and streambeds. *Environmental Science & Technology* **45**(13): 5614–5621.
- Bjornn TC, Reiser DW. 1991. Habitat requirements of salmonids in streams. *American Fisheries Society Special Publication* **19**: 83–138.
- DeVries P. 2012. Salmonid influences on rivers: a geomorphic fish tail. *Geomorphology* **157**: 66–74.
- Droppo IG, Leppard GG, Flannigan DT, Liss SN. 1997. The freshwater floc: a functional relationship of water and organic and inorganic floc constituents affecting suspended sediment properties. *Water, Air, and Soil Pollution* **99**: 43–53. DOI: 10.1007/BF02406843
- Eaton B, Moore RD. 2010. Regional hydrology. In *Compendium of Forest Hydrology and Geomorphology in British Columbia*, Pike RG, et al. (eds). British Columbia Land Management Handbook 66. Integrated Land Management Bureau: Prince, George, BC; 85–105.
- Holtgrieve GW, Schindler DE. 2011. Marine-derived nutrients, bioturbation, and ecosystem metabolism: reconsidering the role of salmon in streams. *Ecology* **92**: 373–385. DOI: 10.1890/09-1694.1
- Janetski DJ, Chaloner DT, Tiegs SD, Lamberti GA. 2009. Pacific salmon effects on stream ecosystems: a quantitative synthesis. *Oecologia* **159**: 583–595. DOI: 10.1007/s00442-008-1249-x
- Johnston NT, MacIsaac EA, Tschaplinski PJ, Hall KJ. 2004. Effects of the abundance of spawning sockeye salmon (*Oncorhynchus nerka*) on nutrients and algal biomass in forested streams. *Canadian Journal of Fisheries and Aquatic Sciences* **61**(3): 384–403.
- Krishnappan BG. 2007. recent advance in basic and applied research in cohesive sediment transport in aquatic systems. *Canadian Journal of Civil Engineering* **34**: 731–743.
- McConnachie JL, Petticrew EL. 2006. Tracing organic matter sources in riverine suspended sediment: implications for fine sediment transfers. *Geomorphology* **79**: 13–26. DOI: 10.1016/j.geomorph.2005.09.011
- Minakawa N, Gara RI. 2005. Spatial and temporal distribution of coho salmon carcasses in a stream in the Pacific Northwest, USA. *Hydrobiologia* **539**: 163–166.
- Moore JW, Schindler DE, Carter JL, Fox J, Griffiths J, Holtgrieve GW. 2007. Biotic control of stream fluxes: spawning salmon drive nutrient and matter export. *Ecology* **88**: 1278–1291.
- O'Keefe TC, Edwards RT. 2003. Evidence for hyporheic transfer and removal of marine-derived nutrients in a sockeye stream in southwest Alaska. *American Fisheries Society Symposium* **34**: 99–110.
- Petticrew EL. 2005. The composite nature of suspended and gravel stored fine sediment in streams: a case study of O'Neil Creek, British Columbia, Canada. In *Flocculation in Natural and Engineered Environmental Systems*, Droppo IG, et al. (eds). CRC Press: Boca Raton, FL; 71–94.
- Petticrew EL, Arocena JM. 2003. Organic matter composition of gravel-stored sediments from salmon-bearing streams. *Hydrobiologia* **494**: 17–24. DOI: 10.1023/A:1025416904982
- Petticrew EL, Krein A, Walling DE. 2007. Evaluating fine sediment mobilization and storage in a gravel-bed river using controlled reservoir releases. *Hydrological Processes* **21**: 198–210. DOI: 10.1002/hyp.6183
- Pinay G, O'Keefe TC, Edwards RT, Naiman RJ. 2008. Nitrate removal in the hyporheic zone of a salmon river in Alaska. *River Research Applications* **25**: 367–375.

- R Development Core Team. 2011. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing: Vienna. <http://www.R-project.org> [11 January 2012].
- Rex JF, Petticrew EL. 2008. Delivery of marine-derived nutrients to streambeds to Pacific salmon. *Nature Geoscience* **1**: 840–843. DOI: 10.1038/ngeo364
- Rex JF, Petticrew EL. 2010. Salmon-derived nitrogen delivery and storage within a gravel bed: sediment and water interactions. *Ecological Engineering* **36**: 1167–1173. DOI: 10.1016/j.ecoleng.2010.02.001
- Strobel B, Shivley DR, Roper BB. 2009. Salmon carcass movements in forest streams. *North American Journal of Fisheries Management* **29**: 702–714.
- Wickham H. 2009. *ggplot2: Elegant Graphics for Data Analysis*. Springer: Berlin. <http://had.co.nz/ggplot2/book> [11 January 2012].
- Williams ND. 2006. LISST Manuals. University of Plymouth: Plymouth; 50 pp.
- Williams ND, Walling DE, Leeks GJL. 2007. High temporal resolution in-situ measurement of the effective particle size characteristics of fluvial suspended sediment. *Water Research* **41**: 1081–1093.
- Wipfli MS, Hudson J, Caouette J. 1998. Influence of salmon carcasses on stream productivity: response of biofilm and benthic macroinvertebrates in southeastern Alaska, USA. *Canadian Journal of Fisheries and Aquatic Sciences* **55**: 1503–1511. DOI: 10.1139/f98-031
- Wotton RS. 2007. Do benthic ecologists pay enough attention to aggregates formed in the water column of streams and rivers? *Journal of the North American Benthological Society* **26**: 1–11.