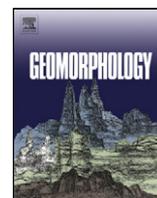




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Biogeomorphic impacts of migration and disturbance: Implications of salmon spawning and decay

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ABSTRACT

Geomorphologic processes often involve a biotic element that acts to regulate landform development. This biotic element can be plant or animal-based with a feedback that ultimately benefits the ecology of the organism. Pacific salmon (*Oncorhynchus* sp.) are an example of an animal biogeomorphic agent exhibiting such feedbacks and, because of long migrations from the sea to freshwater spawning grounds, are a species of interest that act on both local and regional scales. Upon returning to their natal streams, salmon generate a dual disturbance, resuspending large amounts of sediment as they construct nests while at the same time generating a substantial nutrient pulse through post-spawn die-off and decay. The retention and export of these nutrients are of importance to any hypothesized productivity boost driven by the marine derived nutrients (MDNs). Using experimental enclosures in the Horsefly River spawning channel in north-central British Columbia, our objectives for this study were to i) quantify the magnitude of organic and inorganic sediment export and retention from an active-spawning area and ii) determine the contribution of fine sediment MDN storage. Using a suspended sediment mass balance model, marine isotope enrichment and a time series of gravel bed sediment infiltration, we found strongly linear relationships between sediment infiltration and marine-derived nutrient enrichment. Elevated suspended sediment produced by salmon redd (nest) construction acted as an effective vector for MDN infiltration into the gravel bed. This study demonstrated that localized patterns of sediment deposition are regulated by salmon activity which in turn act to control MDN storage within, and release from, the gravel bed. Furthermore, this study demonstrates the ability of a biogeomorphic agent like salmon to establish a feedback mechanism that creates favorable conditions which ultimately benefit the organism.

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1. Introduction

Instances of solely abiotic processes driving landform dynamics are rare, occurring on Earth in only very extreme climates (Corenblit et al., 2011). Instead, the vast majority of geomorphic processes have some biotic element that helps to regulate landform change which in turn has an ecological feedback to the original biotic element (Corenblit et al., 2011). For example, Pollen-Bankhead and Simon (2010) found that riparian soil structure was stabilized by plant root networks thereby retaining local habitat for future plant colonization and providing stable bank conditions along rivers. Examples of these local feedbacks are not limited to plants because zoogeomorphic (animal driven) processes are also recognized as significant drivers of landform change (e.g. North American beaver dams Naiman et al., 1994). Such local zoogeomorphological feedbacks generated in conjunction with large migrations across landscapes and ecosystem boundaries suggest that

zoogeomorphic processes have the potential to alter and regulate regional and local nutrient flow (Vanni, 2002; Quinn, 2005; DeVries, 2011). For example, within their natal streams Pacific salmon cause seemingly opposing ecological forces of physical disturbance (via sediment resuspension) and nutrient subsidy (via post-spawn decay). These ecological forces have been demonstrated to impact abiotic and biotic elements (Rex and Petticrew, 2008; Albers and Petticrew, 2012) within spawning streams revising the role thought to be played by sediment and nutrients during the salmon's freshwater lifecycle.

Fine sediments, including clay and silt-sized particles, have been recognized as important delivery and storage vectors for nutrients and contaminants (Owens et al., 2005). In the case of Pacific salmon, ecologically important nutrients are transferred from marine environments to freshwater spawning habitats via the bodies of returning salmon (i.e. marine-derived nutrients (MDNs)). The coincident processes of fine sediment resuspension from redd (nest) construction and the pulse of nutrients to the water column from fish die-off result in salmon organic matter combining with inorganic silts and clays to provide a vector for the retention and storage of nutrients in the spawning gravels (Rex and Petticrew, 2008; Petticrew et al., 2011). In the water column the sediments form structures, known as flocs, that settle more quickly

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than their constituent particles (Petticrew et al., 2011). Once stored on, or in, the gravel bed, flocs increase the potential for localized biological production through longer period and greater amounts of intergravel retention allowing for organic matter processing (Wotton, 2007). Flocs, however, contribute an unknown amount to the overall MDN storage potential of spawning habitats.

The heavier inorganic (mineral) framework of flocs acts as a substrate for bacteria and salmon organic matter such that the resultant particles are more likely to settle out of the water column closer to the point of resuspension rather than be flushed downstream. Most studies have focused on MDN sequestration into benthic biofilms and periphyton (e.g. Moore and Schindler, 2008) but have remained largely silent on potential delivery vectors. The occurrence of this salmon–sediment floc generation and delivery mechanism has been clearly shown in the laboratory (Arkinstall, 2005), flumes (Rex and Petticrew, 2008) and the field (McConnachie and Petticrew, 2006) but the rate of exchange of MDN between the water column and gravel bed remains unclear. The temporal and spatial significance of these sediment vectors on gravel bed storage of MDN has not been quantified, thereby restricting our ability to estimate the impact of gravel bed storage of MDNs on biological productivity in these habitats. The objectives of this study are to i) quantify the magnitude of inorganic and organic sediment export and retention from an active-spawning area and ii) determine the contribution of fine sediment MDN storage and its effects on habitat conditions.

2. Materials and methods

2.1. Study site and preparation

We utilized an artificial salmon enhancement stream, the Horsefly River spawning channel (HFC), to examine the biogeomorphic impacts of salmon spawning. The HFC is in the Horsefly watershed (52° 19'N/121° 19'W), located within the Cariboo region of British Columbia, Canada (Fig. 1a). Further details on channel characteristics, in addition to the results of a separate portion of this same study can be found in Albers and Petticrew (2012). For the present paper, we utilized the HFC in an upstream–downstream paired treatment approach where a control enclosure (10 m × 20 m) was kept free of salmon and an active-spawn enclosure of the same size was loaded with salmon to

simulate natural spawning conditions. The gravel bed was cleaned of fine sediment and weed growth prior to the start of the experiment ensuring a consistent baseline. Cleaning was accomplished by raking the gravel bed to a depth of 30 cm using a large fork mounted on a bulldozer. This resuspended fine material and weed biomass were then flushed downstream and pumped out of the HFC. Water flow into the channel was controlled by a large siphon supplying water from an upstream settling pond which is connected via a side channel to the Horsefly River. Discharge in the HFC was monitored through a combination of staff gauge readings and a pressure transducer (Unidata 8007 WPD) and applied to a calibrated rating curve. The rating curve was estimated by measuring flow velocity at 0.6 of the depth at 1 m intervals across the channel and at a range of representative stage heights ($n = 4$).

The introduction of sockeye salmon (*Oncorhynchus nerka*) into the HFC was regulated by a downstream gate off the mainstem of the Horsefly River. Sockeye salmon were loaded into the active-spawn enclosure (Fig. 1b) by opening the portion of the downstream exclusion fence which separated the experimental area from the rest of the channel. The control enclosure, which was located immediately upstream of the active-spawn enclosure, was intended to remain free of fish as a spatial control although some live fish did escape into this enclosure. These fish were removed from the control enclosure to mitigate any upstream spawning influences. Salmon were counted in the field or, when densities were too high for this approach to be feasible, counts were made from photographs.

2.2. Suspended sediment

Two automatic water samplers (Teledyne ISCO, Inc.) were placed streamside with the sampling tube located in the thalweg of the HFC at 0.6 of the depth near the rear of both the control and the active-spawn enclosures (Fig. 1b) to sample for suspended sediment. Water was sampled from each enclosure every 3 h, eight times per day (except where noted) into two sample bottles to form two 12 h composite samples. Water samples were later filtered with glass fiber filters, dried at 60 °C for 12 h, weighed, ashed at 550 °C for 2 h and weighed again. Organic and inorganic estimates of suspended sediment concentration were derived from this process.

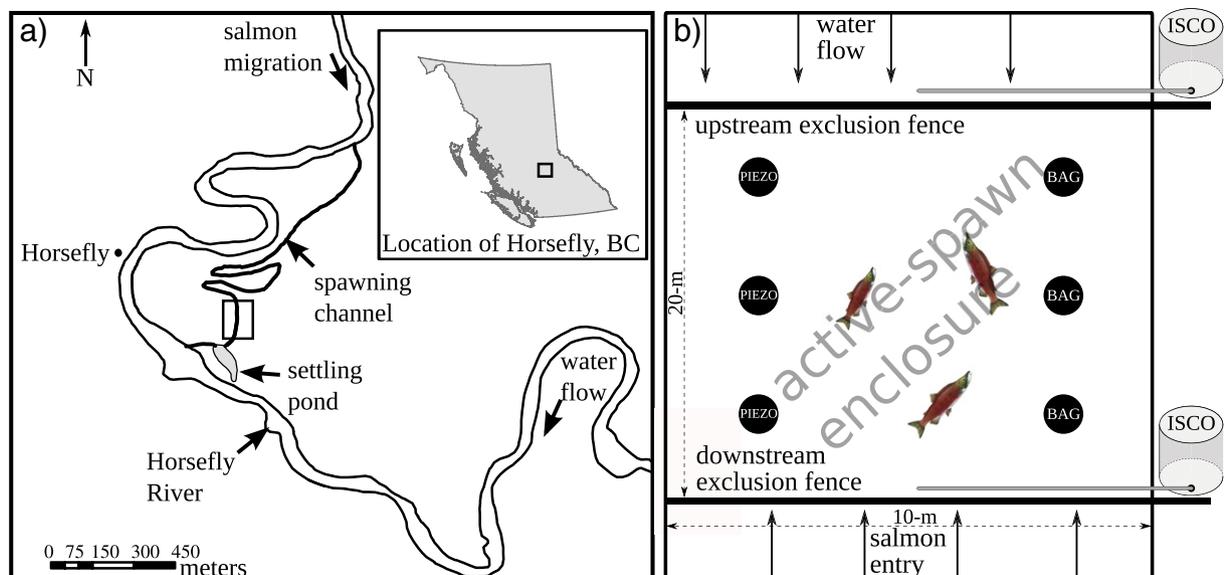


Fig. 1. a) Horsefly River, British Columbia. Experimental section of the HFC is indicated by the black box in the spawning channel. b) Schematic of fence, piezometer, ISCO and infiltration bag placement in the active-spawn enclosure. Figure is not drawn to scale.

2.3. Infiltration bags

Sediment and nutrient infiltration into the active-spawn enclosure were assessed weekly by sampling a column of gravels in the gravel bed using modified infiltration bags (Rex and Petticrew, 2006). Plastic frames cut from 20 l buckets were placed in pre-dug 0.35 m holes in the gravel bed to prevent gravels from backfilling the hole (Fig. 1b). A collapsed bag with a rigid rim was placed in the bottom of the frame. This bag was covered with gravels cleaned of sediment <2 mm. Three short lengths of rope attached to the collapsed bag extended from the bag through the gravel to the streambed surface. Following an exposure period of approximately one week, the column of gravel was removed by pulling the bag up through the frame by the attached ropes and transferring all sediment, water and gravel into a bucket. This material was then rinsed through a 2 mm sieve into a volumetrically calibrated sample bucket. This method allows for repetitive stationary sampling because the plastic frames remain buried at the same location over the experimental period. The frames were lined with galvanized steel mesh (opening = 2.5 cm) to maintain natural water flow conditions through the gravels. Gravels were sized for comparisons from each infiltration bag ($n = 10$) by measuring the major axes.

To obtain an estimate of the mass of fine sediment infiltrating into the gravels a subsample of the <2 mm sample was taken following resuspension of all the materials in the calibrated bucket. Following a 10 s delay to allow for the settling of sands the top portion of the water column was sampled for fines. This method has been used accurately in the past to capture particles with constituents <75 μm in size (Petticrew et al., 2007). Fine sediment from the infiltration bags was filtered onto glass fiber filters, dried at 60 °C for 12 h, weighed, ashed at 550 °C for 2 h and weighed again. These values were then multiplied by the volume of rinse water for a total mass estimate. Response variables derived from this process were infiltrated organic and inorganic sediment.

2.4. Piezometers

To monitor intergravel changes and responses to stored fine sediment, dissolved oxygen was measured in three piezometers constructed of plastic tubing buried to a depth of 28 cm in the gravel bed in both enclosures prior to beginning the experiment. Piezometers were sampled daily, and analyzed for dissolved oxygen following an evacuation of the tubing to ensure residual water was not sampled. The oxygen meter was calibrated on each sampling date.

2.5. Mass balance

To determine a suspended sediment load for each 24 h period, for each enclosure, for each suspended sediment type (organic and inorganic) we used the following equation:

$$SS \text{ load} = 2 \times \frac{1}{n} \sum_{i=1}^n [SS.12h]_i \times Q.12h_i \quad (1)$$

where *SS load* represents the daily suspended sediment load, *n* represents the number of sample bottles filled in one day (either 1 or 2), *[SS.12 h]* is the suspended sediment concentration over a 12 h period and *Q.12h_i* is the total volume of water that passed through the channel in a 12 h period. Due to equipment malfunction with ISCO samplers, several sampling dates only had either one 12 h suspended sediment concentration or no suspended sediment data. Eq. (1) illustrates that for sampling dates that only had one 12 h concentration, the daily load was estimated by multiplying that single value by two. For dates with two 12 h sediment load estimates, Eq. (1) resulted in these values being summed to give a 24 h load estimate. From these daily suspended sediment loads, we estimated the mean suspended sediment load for each period that an infiltration bag was installed. Each estimate was

drawn from a sample size ranging from 1 to 5 depending on the availability of daily suspended sediment load data. The mean suspended load during an infiltration period was then multiplied by the number of days that the corresponding bag was receiving sediment in that period. The mass balance of suspended sediment in the active-spawn enclosure (i.e. the effect of spawning and dying fish on suspended sediment) was estimated by subtracting the suspended sediment load in the active-spawning enclosure from that entering it from the upstream control enclosure. Therefore the net load amount of suspended sediment in the active-spawn enclosure over a given bag deployment period is described by the following relationship:

$$M_{net \text{ load}} = B \times \frac{1}{d} \sum_{i=1}^d (SS \text{ load.}active_i - SS \text{ load.}control_i) \quad (2)$$

where *M_{net load}* is the mass difference of suspended sediment loads from the control enclosure to the active-spawn enclosure per infiltration bag period, *d* is the number of days for which daily suspended sediment data were available and *B* is the number of days that a bag was receiving sediment.

The infiltration bags were sampled approximately on a weekly basis. We used that deployment period to calculate the mean load values for the suspended sediment (Eq. (2)). To estimate the volume of gravels that the fine sediment could infiltrate into in the active-spawn enclosure we used a gravel depth of 0.20 m. Although the plastic frames were placed in 0.35 m holes, 0.20 m was the practical sampling depth as a layer of gravels formed on the bottom of the frames. We divided the gravel bed into three equal zones, in a downstream direction so that each zone included one infiltration bag and extrapolated fine sediment infiltration over the entire zone (Fig. 1b). We estimated the volume of the top 0.20 m of gravels for each zone of the enclosure (*V_{zone}*) to be 13.3 m³. Correspondingly, we expressed the total amount of fine sediment infiltrated in the active-spawn enclosure by the following:

$$V_{total \text{ sed}} = \sum_{i=front}^{back} \frac{SI_i}{V_i} \times V_{zone} \quad (3)$$

where *V_{total sed}* is the total estimated sediment in the gravel bed, *SI_i* is mass of infiltrated fine sediment at one of three positions (back of the enclosure to the front) in the gravel bed (*i*) and *V_i* is the volume of an infiltration bag ($\pi r^2 h$).

2.6. Nutrient addition estimates from salmon carcass decay

The mass of salmon decay products were modeled using estimated addition rates from the Takla River (Johnston et al., 2004) and daily fish counts from the Horsefly Channel in 2009. The amount of nutrients added into the water column was estimated using the same equations outlined by Johnston et al. (2004). The model outlined below, therefore, generates an estimated value for the mass of nutrients lost from salmon carcasses and added to the water column on a daily basis. The total new nutrient contribution of all salmon dying on a given day, *t*, is estimated by:

$$New_t = D_t \times \% \text{ Nutrient (Carbon or Nitrogen)} \quad (4)$$

where *D_t* is the number of dead salmon that died on day *t* and % *Nutrient* is the average percent composition of salmon flesh for either carbon and nitrogen. The total amount of salmon nutrients present in the stream on day *t* (*Nut_t*) is given by:

$$Nut_t = New_t - Nut_{t-1} e^k \quad (5)$$

where *New_t* is the new arrival of nutrients on day *t* (Eq. (4)) and *k* is the constant decay rate of sockeye salmon given by Johnston et al. (2004) from Takla River. The decay rate from Johnston et al. (2004) for carbon

was -0.0360 kg/day and -0.0460 kg/day for nitrogen and $Nut_{t-1}e^k$ is the total amount of nutrients remaining in the system on day t from all previous days. The daily mass addition of salmon (for both carbon and nitrogen) to the water column on day t is given by:

$$Addition_t = Nut_{t-1}(1 - e^k). \quad (6)$$

2.6.1. Carcass removal

Over the course of the experiment, some salmon were removed from the HFC system either via dead pitching or black bear (*Ursus americanus*) consumption. Dead pitching was done to reduce the number of decaying salmon down to a more natural representation of a spawning stream. If there was a net loss of fish on a given day (i.e. $D_t - D_{t-1} < 0$), the salmon nutrients removed on that day from the stream were estimated by using the average nutrient content of salmon from the previous day and multiplying that number by the total number of fish removed from the system. Total nutrient removal is therefore estimated by:

$$Total\ nutrient\ removal = \left(\frac{Ini_{t-1}}{D_{t-1}} \right) * Fish\ Removed_t. \quad (7)$$

Dead salmon (D_t) were enumerated visually by two individuals on a daily basis. In instances where the counts differed greatly (> 10 salmon), the salmon were recounted until a similar count was reached.

2.6.2. Assumptions

Several assumptions are made in the accounting of dead pitched and bear removed salmon carcasses. The first is that carcasses were removed randomly, such that all levels of decay have an equal chance of removal. Evidence of bear removal was seen throughout the channel not just on the banks. Moreover, bears removed fish from the HFC with evidently little preference for any particular decay stage of fish. Salmon in an advanced state of decay were consumed by bears just as readily as fresh carcasses. Dead pitching was done on one day (September 26th, 2009) such that all dead fish were removed from the system. As fish were non-selectively removed from the channel the use of an average fish mass was appropriate for the above analysis.

A second key assumption is that the calculated addition rate for each nutrient does not vary between the Takla River (Johnston et al., 2004) and the Horsefly River. Water temperature during the period of salmon decay would likely be the biggest difference between sample areas. To assess the differences, average temperature during the decay period from both streams were compared. The mean temperature in the active-spawn enclosure of the HFC during the post-spawn period was 9.63 °C (standard error of the mean = 0.116). The mean temperature for all streams was taken from Fig. 3 in Johnston et al. (2004) and was calculated using Engauge Digitizer (Mitchell, 2010). The mean value of all streams for every year during the post-spawn period was calculated to give a single value. This mean temperature was 9.88 °C (standard error of the mean = 0.121). These are comparable river temperatures to those observed in the HFC and this small difference indicates that the addition rate estimated from streams in the Takla system was an acceptable surrogate for the Horsefly system.

2.7. Isotope characterization

Migratory salmon gain approximately 95% of their body mass at sea (Groot and Margolis, 1991). As a result, the ratio of heavier isotopes of nitrogen and carbon in spawning salmon is more reflective of marine conditions. This difference is particularly stark in relation to isotope ratios characteristic of inland spawning ecosystems such as the Horsefly River, which has no other direct link to the marine ecosystem other than salmon. Therefore, isotope ratios can be utilized to trace the fate of MDNs. To determine the level of MDN enrichment,

we estimated enrichment for each sample date. The MDN enrichment was calculated as follows (Johnston et al., 1997):

$$MDN\ enrichment\ (\%) = \frac{(\delta X_{sed} - \delta X_c)}{(\delta X_s - \delta X_c)} \times 100 \quad (8)$$

where X refers to either N or C , δX_{sed} is the isotope ratio of infiltrated sediment in the active-spawn enclosure, δX_c is the isotope ratio of sediment in the control enclosure, and δX_s is the isotopic ratio of salmon tissue.

Isotope values were analyzed at Pacific Centre for Isotopic and Geochemical Research (University of British Columbia). The mean nutrient and isotope content of salmon were estimated by randomly sampling four freshly dead salmon from the study reach on October 5th, 2009. A small portion of somatic tissue was removed from the fish and immediately frozen. Samples were then freeze dried prior to analysis. Infiltrated sediment (< 75 μm) was also analyzed for $\delta^{15}N$ and percent N and C .

2.8. Statistical analysis

Linear regressions were used to evaluate the effect of infiltrated sediment and salmon activity on the enrichment of fine sediments with MDN. Linear model assumptions were evaluated by residual and qq plots and transformed as necessary (Quinn and Keough, 2002). An analysis of variance was used to determine if grain-size in gravel bags varied between section and date. Spearman's rank correlation coefficient was used to compare organic and inorganic sediment in both the infiltration bags and the suspended sediment. Dissolved oxygen was also compared to MDN enrichment. R (R 2.14.1, 2011) was used for all statistical analyses and ggplot2 (Wickham, 2009) was used to produce all plots. All p-values were assessed at an α level of 0.05.

3. Results

3.1. Suspended sediment and nutrients

The difference in the magnitude of suspended sediment (i.e. $M_{net\ load}$) from the control enclosure to the active-spawn enclosure demonstrated a pattern, dependent on the sediment type, that varies with salmon activity and decay products (Fig. 2a and b). The inorganic portion of $M_{net\ load}$ was consistently negative indicating a pattern of weekly net retention of inorganic suspended sediment in the active-spawn enclosure. In general, inorganic $M_{net\ load}$ was greatest during the period when live salmon were present in the HFC (Fig. 2a). By the end of the experiment, net inorganic suspended sediment retention had returned to pre-spawn levels. In contrast, the organic portion of $M_{net\ load}$ demonstrated fluctuation between positive (export) and negative (retention). During the period of highest spawning salmon activity, estimates of organic $M_{net\ load}$ were mostly positive indicating a net export of organic matter from the spawning enclosure. (Fig. 2b). Another period of net export was also noted during the post-spawn phase of the salmon lifecycle when salmon numbers were low and most salmon were decaying. The nutrient estimates shown from Fig. 2a and b highlight the increasing C and N contribution from decaying carcasses to the water column. This period of salmon organic matter decay (seen in Fig. 2a and b as C or N additions) into the water column overlapped with the period of post-spawn organic suspended sediment export from the active-spawn enclosure, after September 28th, 2009.

3.2. Infiltration bags

The mean b-axis of gravels sampled from infiltration bags was not significantly different between zones over the course of the experiment ($p > 0.05$). This suggests that gravel porosity did not vary significantly and that physical flow and infiltration conditions did not vary spatially

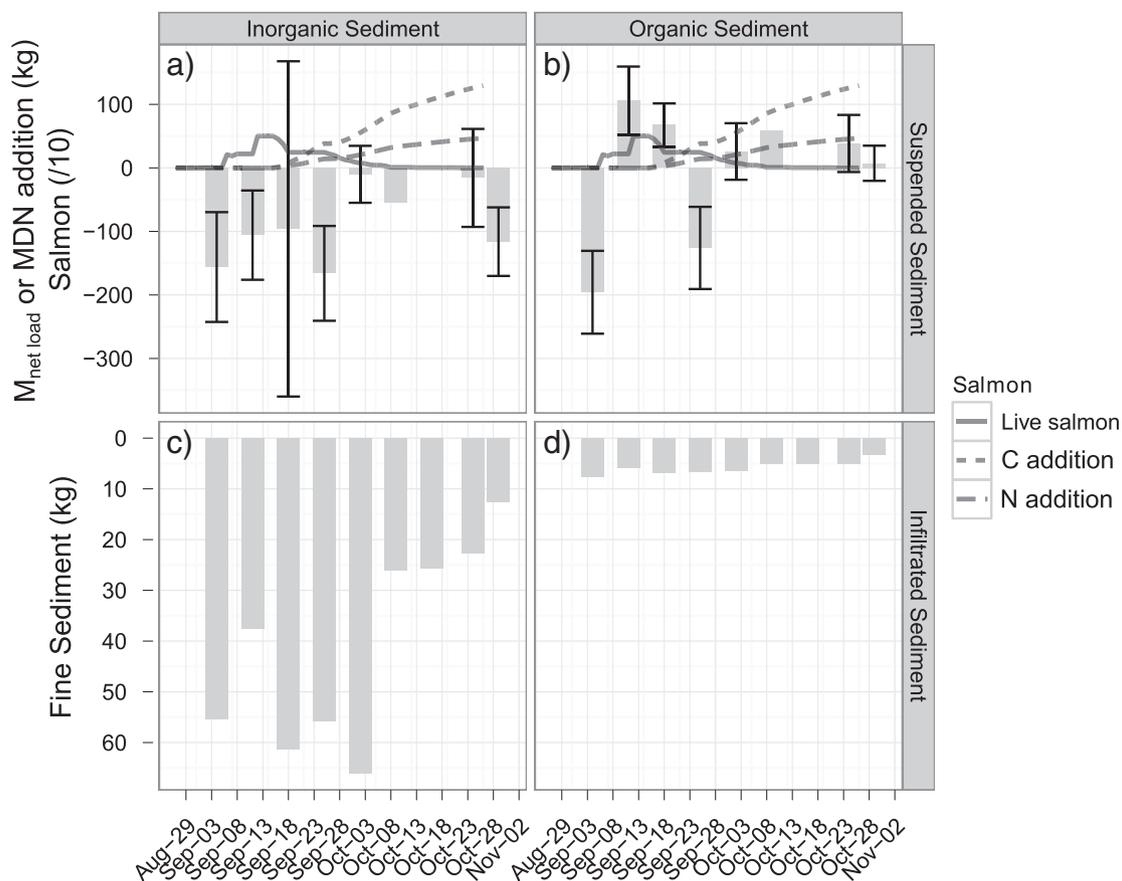


Fig. 2. Magnitude of sediment retention and export in the HFC experiment. Solid grey line indicates the pattern of live salmon. Dashed lines refer to the magnitude of nutrient (C or N) addition from salmon. Magnitude of suspended sediment ($M_{net\ load}$) is shown as grey bars in panels a) and b) with error bars representing one standard error of the mean. The number of live salmon was divided by 10 to accommodate varying scales. Note that the vertical axis for infiltrated sediment is reversed.

or temporally for the duration of bag sampling indicating that those parameters were not relevant for our result interpretation. Inorganic and organic fine sediment deposition into infiltrated bags were high during the peak of spawning activity and remained elevated until almost all salmon were dead (Fig. 2c and d). Ratios of organic sediment and inorganic sediment (Fig. 3a; ratio = 2:13) were maintained over the full period of observation as indicated by a strong correlation. Inorganic and organic infiltrated sediment were lower on the last day of sampling than pre-spawn levels indicating a potential return of the system to a pre-disturbance state.

3.3. Sediment characteristics

Ratios of inorganic and organic sediment patterns were plotted for both the water column and the infiltration bags and evaluated using correlation methods (Fig. 3). The strong linear relationship between the inorganic and organic infiltrated sediment values indicates nutrient rich sediment depositing on the gravel bed and a relatively stable relationship in a ratio of approximately 2:13 of organic to inorganic sediment entering the gravel bed. Conversely, the lack of a significant linear relationship between inorganic and organic measures in the water column suggests a different composition of particles in the water column. We evaluated the strength of organic and inorganic sediment-associated MDN deposition using the marine isotope $\delta^{15}\text{N}$ (Fig. 4). Enriched $\delta^{15}\text{N}$ was linearly related to the natural log of live salmon indicating that the number of live salmon present resulted in higher enrichment of sediment (Fig. 4a). In turn, the greatest $\delta^{15}\text{N}$ enrichment of the sediment was associated with the period of greatest sediment retention and decay (Sept. 19–Oct. 05). Enriched $\delta^{15}\text{N}$ values

were significantly predicted by infiltrated organic and inorganic sediment (Fig. 4b and c). Both inorganic and organic sediment significantly explained over 70% of the variation of $\delta^{15}\text{N}$ enrichment. In all panels in Fig. 4 the data point of least enrichment and in the lower range of the predictor variables corresponded to the last measurement taken during the experiment, reflecting low infiltrated sediment and no live salmon present. Enrichment of $\delta^{15}\text{N}$ was also significantly negatively correlated to dissolved oxygen of intergravel water (Fig. 5).

4. Discussion

This paper presents novel results showing a pattern of gravel bed fine sediment and MDN infiltration and release driven by a salmon disturbance regime. The salmon are acting as biogeomorphic agents in two ways: first by the physical act of digging redds and reintroducing sediment into the water column and second by providing a major source of nutrient-rich organic matter during their die-off. The results presented here suggest that a similar experimental approach should be undertaken at a larger scale such as replication over several natural rivers as the absence of replicated treatments limits our inference to the HFC. To our present knowledge, however, there have been no other attempts to trace sediment, MDNs and habitat conditions such as dissolved oxygen at this resolution for the full length of a spawning event. Moore et al. (2007) focused primarily on suspended sediments to demonstrate the net sediment export potential of spawning salmon. Similarly, Tiegis et al. (2009) demonstrated that the effects of salmon disturbance and salmon nutrient enrichment both play important roles in patterns of ecosystem response. The focus, however, has for the most part remained on biological components of stream ecosystems

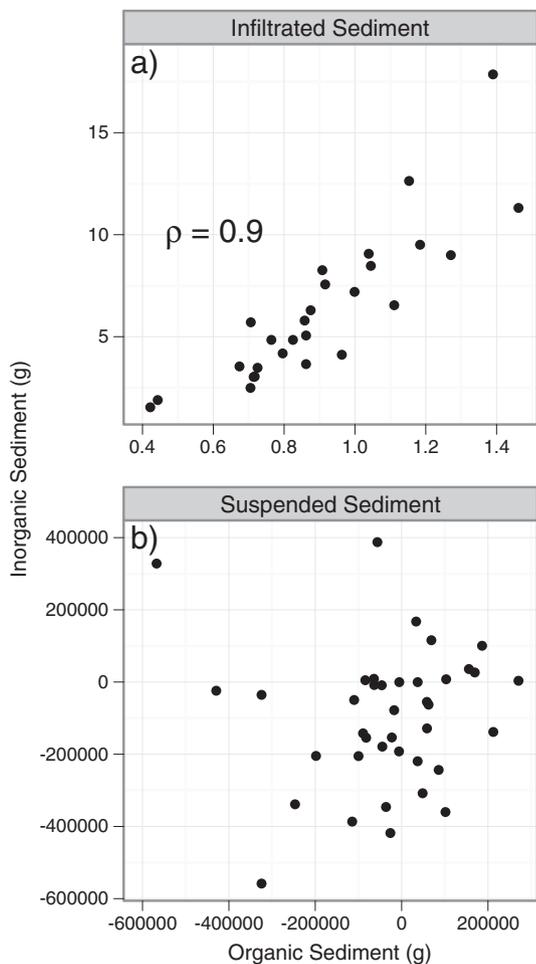


Fig. 3. Sediment comparisons between the water column and the gravel bed. Individual observations were used for this analysis rather than the population means (suspended sediment) or summed values (infiltrated sediment) from Fig. 2. Negative values present in the suspended sediment panel represent instances where the control section suspended sediment total exceeded the active-spawn total. Presence of a ρ value in the infiltration panel indicates a significant correlation at an α -level of 0.05 and indicates the strength of the correlation.

rather than biogeomorphic feedbacks associated with sediments infiltrating into the gravel bed and subsequently influencing the biological components. Similarly, biogeomorphic agents remain underappreciated drivers of landform change (but see DeVries, 2011) and important components of geomorphology. By utilizing infiltration bags that sampled fine sediment and were repeatedly replaced with cleaned gravels, we were able to examine the quality and quantity of sediments as they penetrated below the gravel bed surface. The replacement of loosely packed gravels would have closely simulated loosened redd gravels outside of the frame buckets. Replacement gravels, manually cleaned of sediment, also simulated salmon-cleaned gravels in the adjacent channel bed (Groot and Margolis, 1991) suggesting that gravels in the infiltration bags are similar to natural salmon-disturbed habitats.

In our experiment even during the most active-spawning period, inorganic suspended sediment concentrations in the downstream border of the active-spawn enclosure were not elevated relative to the incoming water from the control enclosure indicating near-field settling of salmon-resuspended fines. Inorganic suspended sediment was highly variable (i.e. large standard error of the mean) during the period of highest salmon activity with bursts of elevated sediment levels (e.g. Moore et al., 2007) from redd constructing salmon being the probable cause. An interesting observation evident in Fig. 2(c,d)

is the high rate of fine sediment infiltration during peak spawn when efforts by salmon to clean the gravels are in progress. The material is resuspended but settles back to the gravels over short distances (i.e. the 20 m reach used here). The modeling of enclosure sediment retention versus export shown in Fig. 2(a,b) supports this observation, in that all the fine inorganic sediment introduced into the water column by salmon is being retained while the flux of organic sediment alternates between export downstream and retention, depending on the activity of the fish. Organic export fluxes are associated with the most active-spawn period when maximum sediment resuspension via redd construction occurs and secondarily during maximum decay, as indicated by the C and N additions to the channel (Fig. 2b). Both of these responses show a clear impact of salmon on the water column conditions.

Organic suspended sediment export during the active-spawn is likely a combination of waste products released by salmon during spawning and as well as initial decay products beginning to form as suggested by Chaloner et al. (2002). Net organic matter export during this time period provides evidence that this waste and decay material is too light to settle on its own. Without sufficient fine sediment present in the water column from redd construction or upstream delivery, the organic matter remains too light to settle and will be exported downstream. The similar organic to inorganic ratio of 2:13 collected in the infiltration bags over the period of experiment (Fig. 3a) suggests suitable concentrations for floc generation which preferentially settle in or on the gravel bed. The fine inorganic sediment is acting as a vector for the salmon decay products. Infiltrated organic and inorganic sediment reflected the presence of live salmon with a >50% decrease in infiltration levels after salmon spawning (Fig. 2c) and a distinct salmon isotope sediment enrichment pattern (Fig. 4b and c). The strongly linear relationships between isotope enrichment and sediment infiltration into the gravel bed indicate that MDN-laden inorganic sediment is preferentially entering the gravel bed (Fig. 4). This is consistent with recent studies in a flume based environment (Rex and Petticrew, 2008, 2010) that found that MDN becomes bound to sediment in the water column as flocs, which increase infiltration of sediment and MDN into gravel bed.

Suspended organic matter returned to export conditions during the post-spawn period reflecting the release of decay products from salmon as well as potential gravel bed MDN release (Fig. 2b). This switch to exporting matter from the active-spawn enclosure may also be a function of there being lower concentrations of fine inorganic sediment in the water column, due to lack of spawning activity, thereby restricting flocculation, potential settling and nutrient delivery. By the end of the experiment, no live salmon were present in the system and infiltrated sediment levels were reduced accordingly. Decaying carcasses, however, remained in the stream providing a continuous source of MDNs as evidenced by isotopic ratios. Isotope enrichment of sediment, however, was not maintained (the last observation was the lowest value) indicating that nutrients were not being transferred to the gravel bed with the same efficiency during the post-spawn period (Fig. 4b and c). It is in this context that salmon can be considered biogeomorphic agents as their life history can dictate near-field patterns of nutrient enrichment. Without a delivery vector in the form of elevated suspended sediment levels, MDNs are evidently not as effectively transferred to the gravel bed.

Our results also indicate that salmon nutrients bound to sediment cause a drop in oxygen levels, impacting lotic biological and ecosystem conditions (Fig. 5). Fine sediment infiltration has long been associated with a drop in dissolved oxygen. Oxygen levels are important for salmon embryo development and fine sediment runoff from reduced tree cover and logging practices is often attributed as a significant cause of salmon embryo mortality (Peterson and Quinn, 1996). However, because we observed substantial organic matter infiltration into the gravel bed it seems more likely that the drop in dissolved oxygen is a result of benthic metabolism (Hargrave, 1969) of MDNs. If the

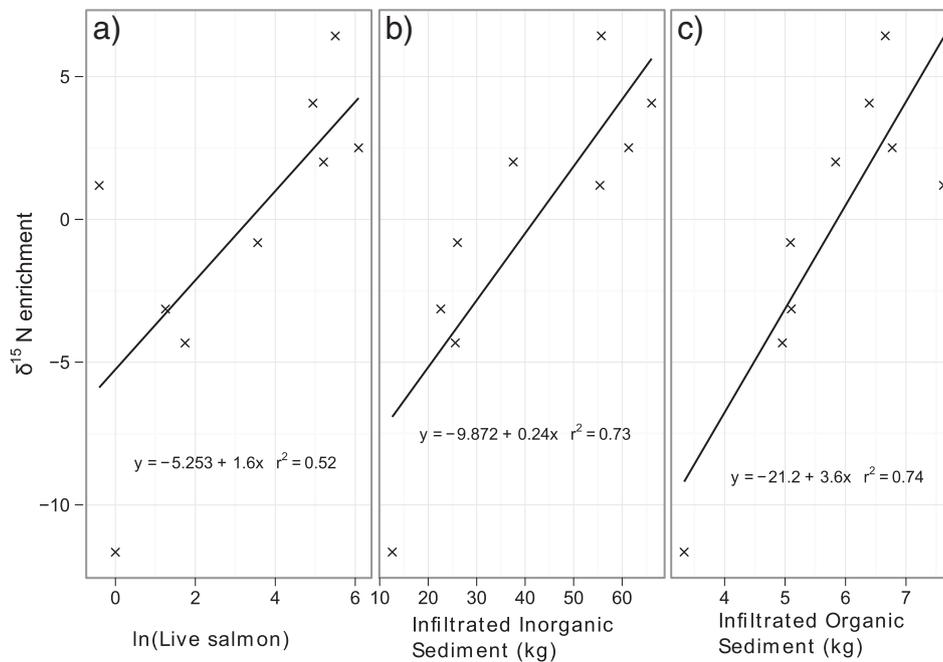


Fig. 4. Relationship between $\delta^{15}\text{N}$ enrichment and salmon activity and sediment infiltration. The data point on the far left near the origin in each panel represents observations taken on the last day of sampling.

dissolved oxygen levels were a result of reduced flow through intergravel spaces, we would not expect a significant relationship between dissolved oxygen and $\delta^{15}\text{N}$ enrichment (Fig. 5). Rather, the relationship is highly significant and provides further evidence of MDN infiltration contributing to an ecosystem response. Furthermore, the data provide an indication of the extremely fast processing time of organic material in salmon-bearing benthic systems.

Increased sediment resuspension and bedload transport are often the physical variables associated with the salmon disturbance (Moore et al., 2007; Macdonald et al., 2010). Patterns of infiltration and $\delta^{15}\text{N}$

indicate that infiltrated fine sediment was enriched in organic matter and MDNs, such that infiltration should also be considered an additional important physical variable in this disturbance regime. Increased suspended organic sediment in the salmon enclosure during the most active-spawn period indicated salmon-mediated sediment organic matter contribution. A gravel bed response to this water column disturbance was detected via increased fine sediment infiltration during salmon spawning. Indeed, the physical impact of salmon is primarily felt through redd construction and substrate disturbance (DeVries, 2011) but when combined with abundant organic matter in the water

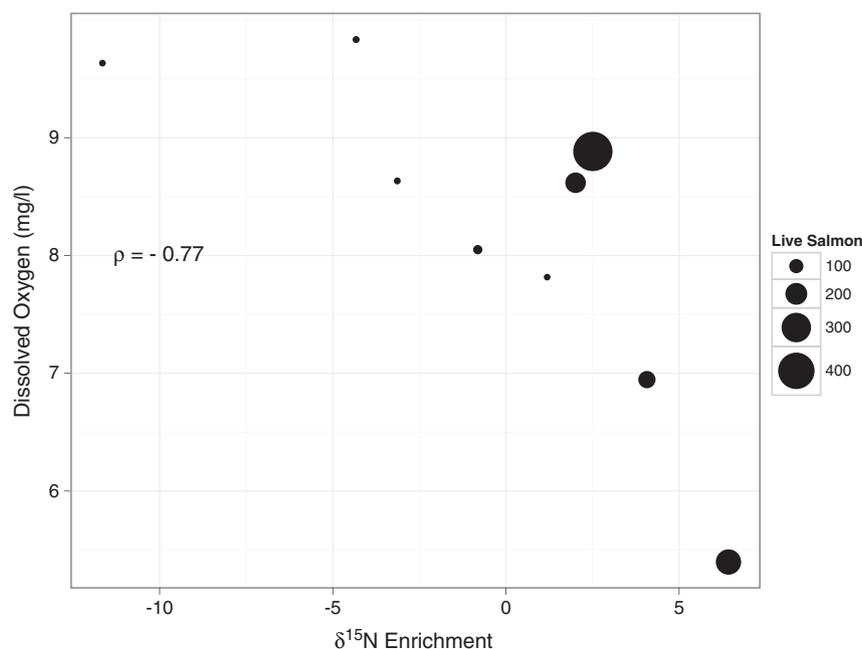


Fig. 5. Impact of $\delta^{15}\text{N}$ enrichment on gravel bed oxygen levels. Number of live salmon is denoted by the size of the data point.

column localized fine sediment and nutrient storage occurs. This process is particularly enhanced during the period of overlap between spawning and decay.

5. Conclusions

This study demonstrated that localized patterns of sediment deposition are regulated by salmon activity which in turn act to regulate MDN storage within, and release from, the gravel bed. In this experiment, which simulates natural conditions, the inorganic suspended sediment source, enriched with salmon organic matter, infiltrated into and was retained in the gravel bed. This retained material is sediment and salmon bound together as aggregates or flocs as evidenced by the high infiltrated inorganic and organic sediment correlation (Fig. 3a) and the relationship between $\delta^{15}\text{N}$ and infiltrated sediment (Fig. 4b and c). The short period and small distance over which sediment entered the gravel bed suggest that the fine sediment composite particles (flocs or aggregates) are behaving like saltating sand particles, in that they are physically resuspended and move only small distances along the river bed.

The resulting pattern of decreasing dissolved oxygen in the gravel bed further supports the premise of inorganic mediated delivery of organic matter to the gravels, and has implications for post-spawn ecological conditions. In our experiment the density of spawners generated moderate amounts of suspended sediment but the resultant intergravel oxygen depletion was not critical for egg survival (Alderdice et al., 1958) whereas in a disturbed system with higher external inorganic sediment loads but equivalent spawners the effects could be lethal. In this study the ratio of organic to inorganic matter (2:13) of the infiltrating sediment was such that it was sufficient to generate flocs and deliver it to the gravel bed yet not so rich to deplete gravel bed oxygen levels and inhibit egg growth. Patterns of dissolved oxygen do suggest some metabolic activity within the gravel bed indicating possible microbial activity driven by infiltrated salmon organic matter. Resuspended inorganic sediment which binds as flocs with organic particulate matter represents the key element in this regulated flow of MDNs. It is, however, the initial animal driven disturbance of nest construction that resuspended the inorganic sediment emphasizing the important organismal component of this biogeomorphic system. The particular case of Pacific salmon is an example of zoogeomorphological changes setting the conditions and feeding back to affect freshwater salmon habitat functioning. More generally, this study demonstrates that the linkage between abiotic (inorganically resuspended sediment) and biotic (spawning Pacific salmon) elements of a geomorphic system ultimately interact in a way that drive feedback loops within their associated habitats.

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