Salmon as biogeomorphic agents: temporal and spatial effects on sediment quantity and quality in a northern British Columbia spawning channel

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Abstract Pacific salmon have a large biogeomorphic impact on their natal streams. An opportunity to utilize a regulated salmon spawning channel in the summer of 2009 allowed a temporal and spatial evaluation of the biologic and geomorphic effects of salmon spawning on fine sediment infiltration into gravel bed streams. These salmon transfer biologically valuable marine-derived nutrients upstream to their natal habitats, while at the same time imparting energy to the streambed via their spawning activity, thereby modifying the geomorphic conditions. Fine sediment infiltration rates were used to monitor the physical activity of redd construction, and the biological effects of die-off on the gravel bed. Infiltration bags and piezometers were used to determine the mass of sediment deposited on and in the streambed, and the oxygen content of the gravel bed, respectively. Sedimentation increased during the period of active redd construction while the proportion of organic matter in the gravel-stored sediment increased following the instream decay of carcasses. Results suggest that the response seen over a small spatial scale may be the result of flocs forming in the water column and infiltrating into the streambed. A response to both changes in quantity and quality of sediment was observed as reductions in inter-gravel oxygen values. Further work on nutrient and sediment loads in both the water column and the gravel bed will allow a rigorous mass balance model.

Key words salmon; gravel bed; nutrients; fine sediment; storage; biogeomorphology; geomorphic agent; flocculation; marine-derived nutrients

INTRODUCTION

Anadromous fish exert considerable influence on their natal habitats through yearly nutrient pulses and substantial habitat modification (Naiman *et al.*, 2002; Hassan *et al.*, 2008). Each year, millions of Pacific salmon (*Oncorhynchus* spp.) return from the ocean to their natal freshwater streams to spawn and die (Naiman *et al.*, 2002). Recent work in salmonid streams has identified the synergistic role these fish play in regulating the quality of these natal habitats (Hassan *et al.*, 2008; Rex & Petticrew, 2008). Salmon can construct redds 10–35 cm deep in the streambed (Schindler *et al.*, 2003). During this process, clay, silt and sand are re-suspended into the water column. Sediment re-suspension during active spawning is an important nutrient delivery pathway (Rex & Petticrew, 2008). Similarly, post-spawning die-off is an important nutrient source (Naiman *et al.*, 2002). The temporal overlap of these two processes creates ideal conditions for flocculated particles to settle out of the water column (Droppo *et al.*, 1997); this floc-mediated nutrient delivery impacts the quality of inter-gravel habitats (Rex & Petticrew, 2006). The reciprocal influence of redd construction by fish has a large impact on the natal stream ecosystem (Rex & Petticrew, 2008). However, whether redd construction has a net benefit on the stream remains uncertain. Moore & Schindler (2008) found that the disturbance of salmon spawning decreased biotic abundance and had no effect on the system's ability to retain nutrients. In contrast, Rex & Petticrew (2006, 2008) demonstrated the importance of fine sediment retention on inter-gravel habitat quality in an artificial flume environment. This paper represents a portion of a larger study which attempts to characterize the biogeomorphic influence of salmon on their natal habitats. The objectives of this paper are to: (a) test this influence in a semi-natural system, the Horsefly River spawning channel, using a spatial control; and (b) assess the quantity and quality of gravel-stored fine sediment over the length of a salmon spawning period, which temporally represents pre-spawning, active spawning, and the die-off periods.

METHODS

Study site

The Horsefly River spawning channel (HFC) is an artificial salmon stock enhancement stream located in Horsefly, British Columbia, Canada. Sockeye salmon (*O. nerka*) enter the HFC via the Horsefly River. Water flow into the channel is controlled by a large siphon supplying water from a settling pond connected to the Horsefly River. Upstream access to the Horsefly River for the salmon was restricted by a permanent gate at the upper portion of the channel. This confinement forced the salmon to spawn inside the channel. Control of discharge, salmon entry to the channel, and fish densities simulated natural spawning conditions. Prior to the sampling period, the channel bed was cleaned of sediment using a 30-cm rake mounted on a bulldozer that re-suspended the sediment, which was then flushed to a downstream settling pond via artificially-generated high discharge. The study site was located in the upper portion of the spawning channel. A 60-m section of the channel was divided into three sections using steel fences. Spatial treatments of varying salmon numbers were applied to each section (Fig 1(c)). The downstream and middle sections were used as areas to assess active salmon spawning. The upstream section was intended to remain free of fish as the spatial control on salmon redd construction. However, a small number of salmon escaped into the upstream section, diminishing the spatial control. Live salmon were removed from the upstream section when possible, minimizing spawning activity. Dead salmon were also taken out of the upstream section, removing any die-off effects from the spatial control.

Site conditions

Discharge was measured through a combination of staff gauge readings and a pressure transducer (Unidata 8007 WPD) and applied to a calibrated rating curve. Rainfall was measured using three anchored buckets located near the study site. Rainfall values were calculated by averaging the volume of water in each bucket and normalizing it per unit area. Salmon densities were enumerated visually and with a digital camera. The salmon were visually counted by two individuals. In instances where the counts differed greatly (>10 salmon), the salmon were recounted until a similar count was reached. Where live salmon densities were too active to be counted visually (12–28 September) a digital photograph was taken of the reach and salmon were counted at a later date.

Gravel bed sampling

Gravel bed sediment storage was sampled using modified infiltration bags (Petticrew & Rex, 2006) which allow for vertical and horizontal sediment delivery to the gravel sample. Prior to the beginning of sampling, three 0.35-m holes were dug in each section. Plastic bucket frames covered with galvanized steel mesh (aperture 0.025 m) were placed in each hole. The plastic frames prevented outside gravels from filling the hole, while the steel mesh allowed for normal water flow through the gravels. Additionally, the plastic frames allowed for periodic removal of gravel-stored fine sediment samples and replacement of clean gravel in the same unaltered position. In each stream section three infiltration bags were placed at the base of the buckets and covered with gravel cleaned of sediment <2 mm. Bags were removed weekly, and replaced with new bags and cleaned gravel. For each sampling period, gravels were rinsed through a 2-mm sieve to remove all <2 mm sediment into a volumetrically calibrated bucket. The water and sediment was sub-sampled to determine the mass of fine sediment (<75 μm) by re-suspending all the material in a sample bucket, waiting 10 s and sub-sampling the top portion of water. This method allows for larger particles to settle out and ensures that only fine sediment is sampled (Petticrew & Rex, 2006). In this same manner, 300 mL was collected in bottles for determination of biological oxygen demand (BOD). The inorganic and organic concentrations of the fine sediment in each sample were determined gravimetrically after filtration, followed by ashing at 500°C. To determine a comparative mass of fines stored in the gravels, the inorganic and organic concentrations were standardized by correcting for the total weight of gravel removed by each bag. The remaining material (<2 mm) was dried, weighed and also standardized by the amount of gravel collected by each bag. BOD sample bottles were covered in aluminium foil and incubated in the HFC near the sampling area. Oxygen levels were taken daily, at regular intervals, for five days (note, BOD was not determined for 9 October as the bottles exploded due to extremely cold temperatures). To monitor inter-gravel dissolved oxygen (DO) levels, three piezometers were buried in each section at a depth of 28 cm in the bed prior to beginning the experiment. Piezometers were sampled daily, and analyzed for DO following an evacuation of the tubing to ensure residual water was not sampled.

Data analysis

Parameter estimates from nonlinear curve fitting were used as an indication of significant differences between sections for the three measures (<2 mm sediment, fine sediment and organic matter to fine sediment ratio) of sediment quantity and quality. Overlapping confidence intervals of the parameter estimates and the degree of model fit between sections were used as measures of statistical difference. A modified Gaussian function was used to describe both the <75 μm sediment and <2 mm sediment relationships. A modified sine function was used to describe the fine sediment ratio relationship. The rate of oxygen change in the BOD samples was also assessed by comparing parameter estimates. For each sampling period and for each section, a measure of oxygen change was estimated by fitting linear regressions for the five dates and three bottles (n = 15). The slope parameter estimate was used as a measure of oxygen change, and the confidence intervals around those estimates were used to test for a significant difference. All model fits and assumptions were assessed by examining residuals, significance of parameter estimates and q–q plots. All statistical analyses were done using R 2.8.1-1 (R, 2008).

RESULTS AND DISCUSSION

Conditions in the Horsefly channel from 28 August 2009 to 30 October 2009 are shown in Fig. 1, and are temporally characterized as pre-spawn, active spawn, and die-off periods. Inter-gravel DO was similar in all reaches until 18–26 September, coinciding with the most active spawning period. At this time the middle section exhibited decreases of up to 4 mg L^{-1} (Fig. 1(d)). However, during the same period, DO levels were relatively constant in the downstream section despite experiencing a similar level of spawning activity. A ~2 mg L^{-1} increase in inter-gravel O_2 concentrations in the middle section occurred following two days with rain events (Fig. 1(b)), but fluctuations over the next five days cannot be explained by the observed precipitation or discharge. The increase in inter-gravel sedimentation during this period (Fig. 2(a) and (b)) could be responsible for the diminished inter-gravel oxygen, in the form of capping the gravels, either by reducing inflows or blocking the gravel pores with sediment. Microbial use of oxygen is also a possibility and will be discussed later. To test for physical blockage, water infiltration rates of the gravels at the piezometer sites were measured once on 27 September and indicated a wide variation over the nine locations. Two of the downstream sites had infiltration rates of ~25 cm s^{-1} while two of the mid-section sites were lower at 6 and 12 cm s^{-1}, indicating faster inter-gravel flows in the downstream reach. Localized spatial variation of spawning activity, as noted by Hassan *et al.* (2008), probably contributes to this patchiness.

Sediment infiltration rates for the middle and downstream sections varied significantly from the upstream section based on model fit parameter estimates. Figures 2(a) and (b) show predominantly higher infiltration rates in the two reaches with fish spawning activity, with the highest rates measured during the period of active spawn. The temporal and spatial response to the physical disturbance of redd construction is apparent in this data set which identified increased quantities of <2 mm and <75 μm sediment infiltration. The model fit also indicated the ratio of fine sediment organic matter (OM) to inorganic sediment (Inorg) was significantly higher in the upstream reach as compared to the middle and downstream sections (Fig. 2(c)). The settling pond at the head of the HFC may be the cause of the elevated ratios of OM/Inorg as sands would be

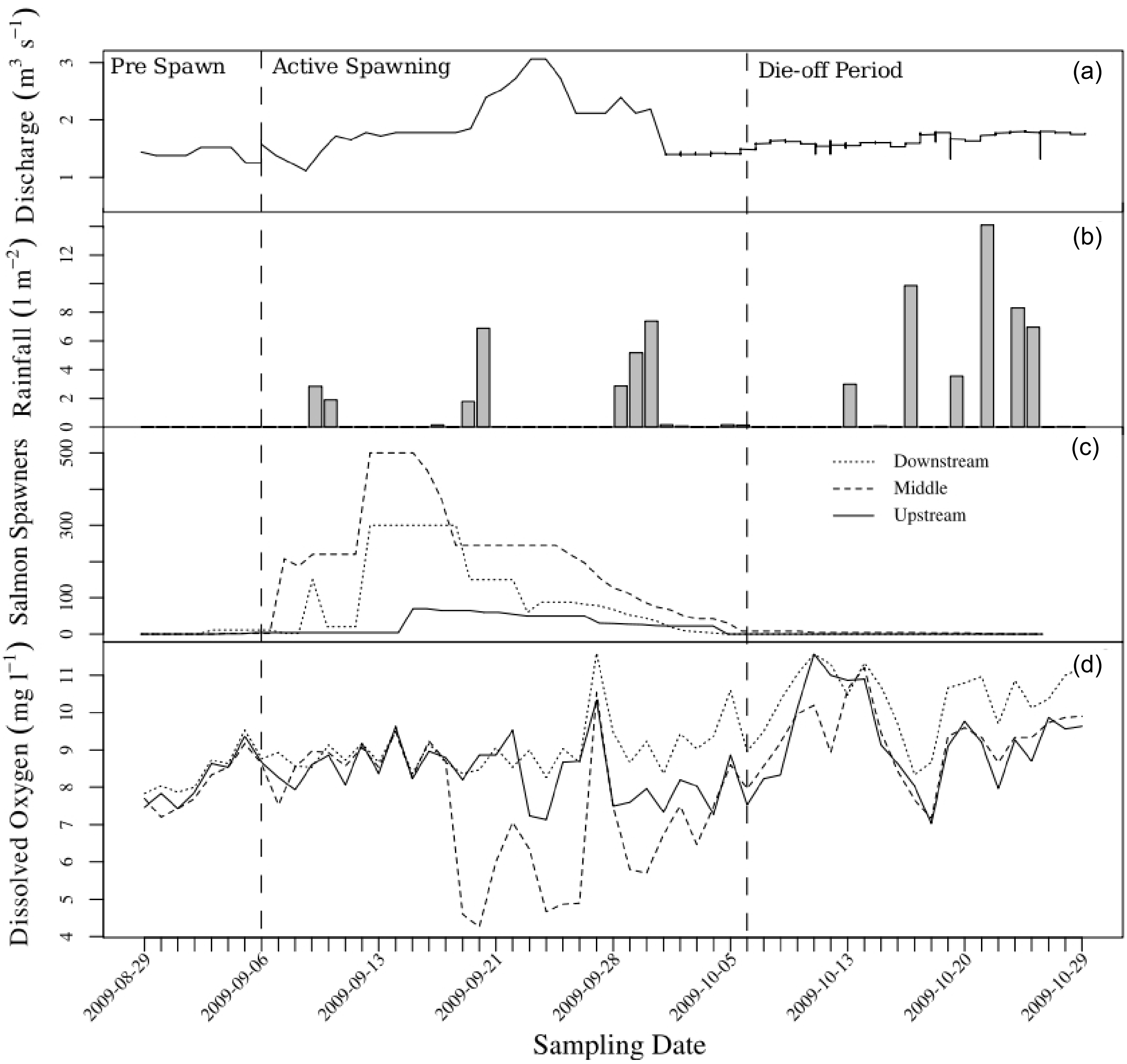

Fig. 1 Characterization of field conditions at the HFC. (a) discharge measurements; (b) rainstorm events; (c) number of salmon spawners present in each of the study reaches; (d) inter-gravel dissolved oxygen concentration: mean values of three replicates in each section.

removed from the water column prior to entering the channel, and the gravel bed in this section was not disturbed by fish as in the other two spawning reaches. During active spawn, the two reaches with spawners have significantly lower OM/Inorg ratios due to the digging, re-suspension and destruction of aggregates or flocs. These processes would favour the localized settling of inorganic particles reducing the OM/Inorg ratio. During the die-off period the ratios increase in the lower two reaches, supporting the findings of Rex & Petticrew (2008) that flocculation of particles is delivering a higher proportion of organic matter, while it is available, during carcass decay. The biological quality of the gravel-stored sediment, as reflected by the proportion of OM, increases in the two spawning reaches during the die-off period, reflecting the delivery of salmon nutrients. Future work, using stable isotopes, should quantify the amounts of retained marine-derived nutrients.

Rates of change of BOD were lowest prior to the entry of salmon into the system but similar across sections (Fig. 3). During the active salmon spawning period BOD decreased at a faster rate in all sections, with each of the sample dates being significantly different to the pre-spawn values.

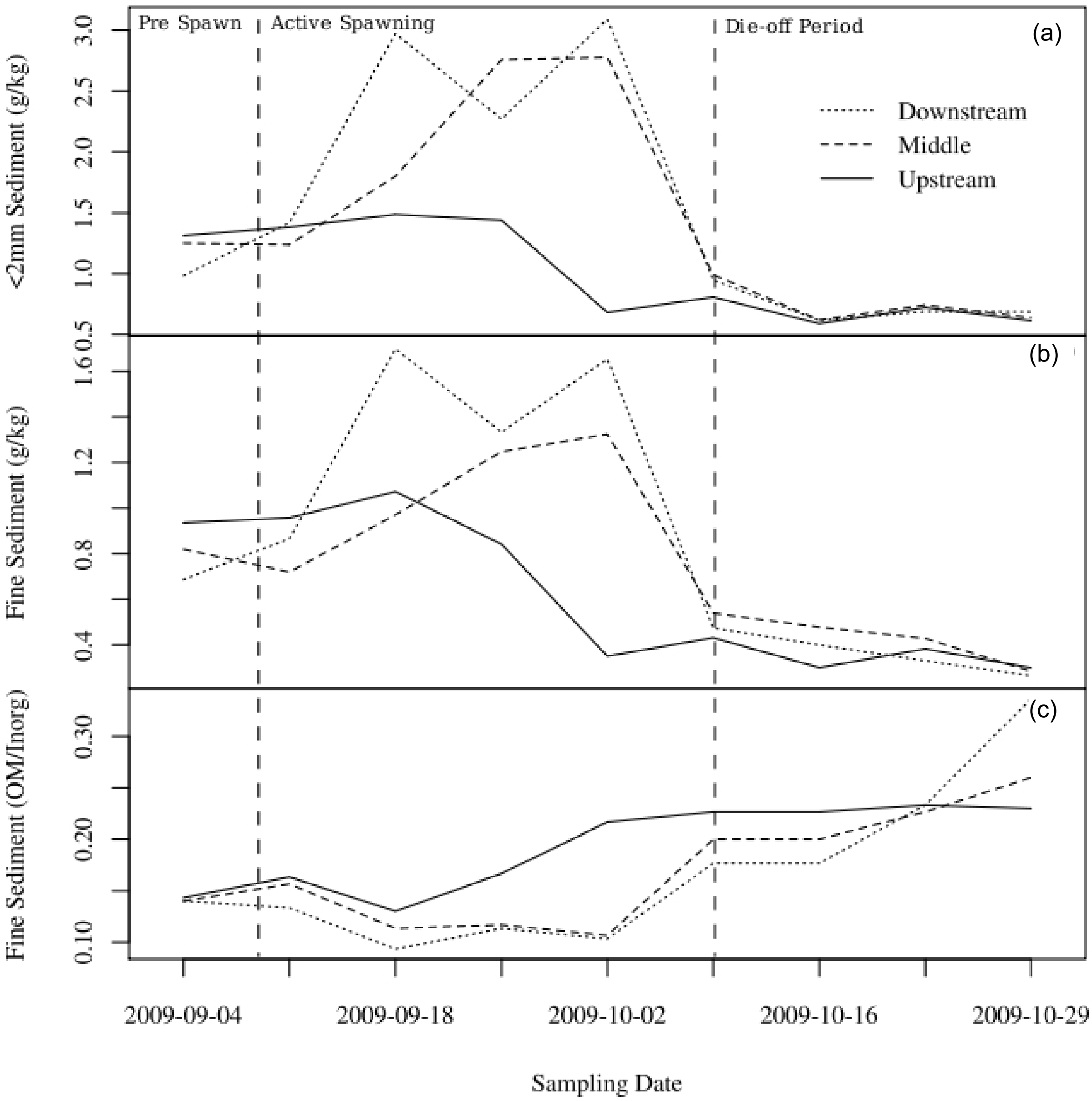

Fig. 2 Sedimentation into the gravel bed as collected by infiltration bags in the HFC study reaches during the course of the salmon spawning event of fall 2009. Values represent the mean of three replicate samples within a single treatment. Dashed vertical lines represent approximate segmentation of the spawning cycle. Significant overlap occurs between the active spawn and the die-off period which was operationally defined as <50 live salmon in the system. (a) Mass <2 mm sediment collected per mass of gravel in infiltration bags; (b) mass of fine sediment (<75 μm) collected per mass of gravel in infiltration bags; (c) ratio of <75 μm organic matter to inorganic sediment in gravel infiltration bags

During post-spawning die-off the rate of BOD remained significantly lower in all sections than during the active spawning period, but the last two dates have rates significantly higher than the pre-spawn values. Results of previous studies (Petticrew & Rex, 2006) would suggest a spatial difference in BOD should be seen between areas of active salmon spawning (middle and downstream) and areas where there were none (upstream). The lack of spatial separation is likely due to elevated amounts of organic matter in the infiltrated fine sediment in the upstream section (Fig. 2(c)). The temporal differences apparent in the three periods reflect a combination of the quantity of infiltrated sediment as well as the quality. The highest BOD rates, measured during the active spawn period, are generated by both the large quantity of sediment in the active spawn

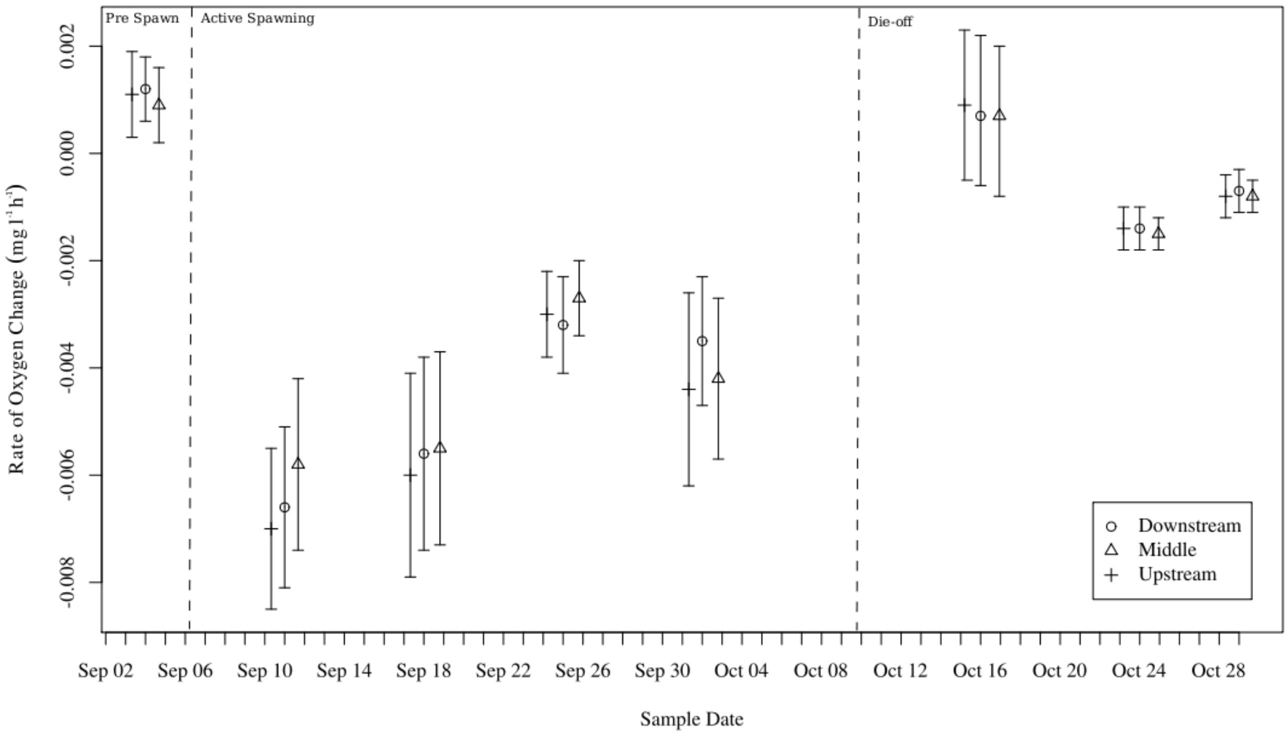

Fig. 3 The rate of BOD change over the course of a salmon spawning event. Points are the slope parameter estimate from a linear regression on three BOD bottles from the same section, over a five day period (n = 15). Error bars represent 95% confidence intervals. The middle points in each group of three represents the date sampled, and the points on either side are from the same sample date and were offset for clarity.

reaches (Fig. 2(a) and (b)) as well as the higher OM content of the upstream section (Fig 2(c)). In contrast, during the die-off period, BOD rates decreased relative to the active-spawn period, but samples from the final two weeks exhibit BOD rates which are significantly greater than the pre-spawn values. This period exhibited smaller quantities of gravel-stored sediment, but in the lower two reaches, the proportion of OM increased to match or exceed that in the upstream section, resulting in higher oxygen demands. This indicates that both the quantity and quality of gravel-stored fines are important for habitat maintenance.

Increased sedimentation in areas of active salmon spawning suggests that re-suspended sediment and flocculated material have settled out of the water column and infiltrated into the gravel bags over these small spatial scales. Claeson *et al.* (2006) demonstrated nutrient enrichment at sites 10–50 m downstream from salmon spawning grounds. Flocculated material has been shown to be an important delivery mechanism for salmon nutrients (Rex & Petticrew, 2008) and these results suggest that a settling response may be seen over a scale of 20 m. The drop in dissolved oxygen levels in the middle reach during active spawn (Fig.1(d)) could be a combination of physical trapping of sediments and an elevated aerobic microbial response to the presence of salmon nutrients as identified by Yoder *et al.* (2006), as both the quantities of sediment, and the BOD of those sediments were high. A second drop of ~3 mg L^{-1} of inter-gravel oxygen measured in the piezometers of all sections during the die-off (14–18 October, Fig. 1(d)) supports Claeson's *et al.* (2006) observation that nutrients are incorporated into the stream over a very small scale. The microbial response to the low quantity of infiltrated sediment with a high ratio of OM/Inorg, as indicated by the large drop in inter-gravel oxygen, suggests the delivery of salmon nutrients to the streambed at this small spatial scale.

These results represent a preliminary analysis of the biogeomorphic effect that spawning salmon have on streambeds and associated benthic communities. Subsequent work will incorporate further measures to establish a mass balance model involving marine-derived nutrients associated with sediment and biofilm. Particle size will be measured to test the hypothesis that flocculated material has been deposited over the streambed over small spatial scales. These results and future analyses will allow an estimate of the magnitude of biogeomorphic habitat modification by salmon.

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