Ecological Engineering 36 (2010) 1167–1173

Contents lists available at ScienceDirect

Ecological Engineering

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

Salmon-derived nitrogen delivery and storage within a gravel bed: Sediment and water interactions

John F. Rex*, Ellen L. Petticrew

University of Northern British Columbia, Geography Program, 3333 University Way, Prince George, BC, Canada V2N 4Z9

ARTICLE INFO

Article history:
Received 13 August 2009
Received in revised form
21 December 2009
Accepted 2 February 2010

Keywords:
Pacific salmon
Flocculation
Gravel bed
Interstitial water
Nitrogen
Marine-derived nutrients

ABSTRACT

Post-spawning salmon carcasses are broadly recognized as a source of organic matter- and marine-derived nutrients (MDN) in Pacific salmon streams, but MDN delivery and retention processes are not well understood. Recent studies emphasize the interaction of inorganic particulate matter and salmon organic matter, through flocculation, as a delivery mechanism for MDN to the streambed. This study builds upon previous flocculation studies to look at nitrogen delivery and storage within the gravel bed of a re-circulating flume. Findings indicate that nitrogen storage in surface and interstitial water is lower than sediment-associated nitrogen. Flocculation of salmon organic matter and inorganic sediment is presented as a delivery mechanism in spawning and post-spawning periods that helps to maintain ecological productivity within Pacific salmon streams. Based on these findings it is recommended that salmon enhancement activities should include leaving post-spawn carcasses in-stream and that fertilization programs should consider flocculation processes to increase nutrient delivery to the streambed.

1. Introduction

Pacific salmon can play a significant role in the nutrient cycle of their natal watersheds because they deliver substantial quantities of marine-derived nutrients (MDN) during spawning events (Bilby et al., 1996; Naiman et al., 2002; Schindler et al., 2003). Pacific salmon gain upwards of 95% of their mass during their marine growth phase (Groot and Margolis, 1991; Naiman et al., 2002) and therefore represent a net input of nutrients to natal watersheds if carcasses are retained. For example, Finney et al. (2000) identified that spawning salmon contribute between 25 and 75% of the annual nitrogen load in southeastern Alaskan streams.

Although the MDN delivered by spawning Pacific salmon is annually variable due to the number of spawning salmon that return to their natal streams, these nutrients have been observed to support both terrestrial and aquatic plant and animal populations, including juvenile salmon (Naiman et al., 2002; Drake et al., 2006; Hocking and Reimchen, 2006). The loss of MDN returns to salmon-bearing watersheds may further exacerbate stock decline (Scheurell et al., 2005). Salmon stock enhancement programs recognize the importance of MDN returns as indicated by stream-fertilization programs that include salmon carcass drops or the addition of salmon carcass analogues. Fertilization programs are designed to enhance low-productivity watersheds or restore those with declining salmon populations by increasing overall stream productivity and salmon production (Kohler et al., 2008; Wipfli et al., 1998). To effectively manage Pacific salmon streams and maximize the efficacy of salmon enhancement activities, MDN cycling processes must be understood including delivery and storage mechanisms.

MDN are delivered to the riparian zone by animals feeding on salmon carcasses including the remains of post-feeding carcass and defecation of the salmon predator and subsequent scavengers (Naiman et al., 2002). In-stream processes are not as clearly understood, but it has recently been reported that salmon-derived MDN can be delivered to streambeds by flocs (Rex and Petticrew, 2008). Flocs composed of salmon organic matter and clay enriched the gravel bed of a flume when suspended sediment concentration was 5 mg l^{-1}, which is similar to that observed during active spawning as a result of redd creation (Petticrew, 2005).

Flocculation refers to the group of physical, chemical, and biological processes that joins inorganic sediments with organic materials in aquatic environments (Droppo et al., 1997). Spawning activities create an optimal environment for floc formation because organic matter levels are elevated due to the presence of spawning and decaying salmon at the same time that ambient suspended sediment levels are elevated due to redd creation. Spawning salmon remove fine sediments from the streambed at the redd site (Bjornn

* Corresponding author. Present address: Ministry of Forests & Range, Forest Science, 5th Flr. 1011 4th Avenue, Prince George, BC, Canada V2L 3H9.
Tel.: +1 250 565 6100; fax: +1 250 565 6671.
E-mail address: john.rex@gov.bc.ca (J.F. Rex).

0925-8574/$ – see front matter © 2010 Elsevier B.V. All rights reserved.
doi:10.1016/j.ecoleng.2010.02.001

and Reiser, 1991; Malcolm et al., 2005). Streambed excavation by the female salmon disturbs bed sediments, the finest of which (silts and clays) remain in suspension and flow downstream while the coarser sediments, such as sands and small gravels, settle out below the redd near the tailspill (Kondolf, 2000). The quantity of streambed material moved during spawning can be substantial, rivalling spring freshet when spawning populations are high (Poirier, 2004; Hassan et al., 2008).

Salmon organic matter-based flocs are expected to form in the water column due to the collision of organic matter and suspended sediment, but also due to the presence of bacteria that bind organic matter and suspended sediment together with extra-cellular polymeric substances (Petticrew and Arocena, 2003; Droppo, 2004; Wotton, 2007). Once formed, floc capture in the streambed is enhanced by the increased settling rate as compared to the component particles as well as the increased surface and intergravel water exchange due to redd creation. Salmon redds increase streambed roughness and surface water down-welling (Malcolm et al., 2005; Tonina, 2005). Increased surface and intergravel water exchange enhances the probability of water-borne flocs entering the streambed where they can be retained in intergravel pores. This study expands upon previous work by investigating flocculation as an MDN delivery process in the post-spawn period. At that time, salmon organic matter is present from decaying carcasses and suspended concentrations are low (<1 mg l^{-1}) because redd construction has ceased. Further, the study assesses nitrogen storage time in the water column, channel bed material, and interstitial water of a re-circulating channel to identify the potential for each compartment to retain MDN.

2. Materials and methods

2.1. Study location and channel description

The study was completed between August 4 and 31, 2008 at the Quesnel River Research Center in a re-circulating channel. The re-circulating channel was constructed from a decommissioned Chinook salmon fry rearing channel that had dimensions of 30 m × 2 m × 2 m. It contained approximately 1 m of fine gravels, sands, and some clay which was topped with 30 cm of clean gravel and small cobble ranging in size between 1 and 10 cm. This size range was selected because it is similar to that from local salmon spawning streams and is often identified as preferred by spawning Pacific salmon (Bjornn and Reiser, 1991). This top-dressing was washed prior to its placement in the channel.

The channel was designed to replicate the general hydrologic conditions observed at O'Ne-eil Creek, a productive sockeye salmon stream 210 km northwest of Prince George, BC (McConnachie and Petticrew, 2006). Specifically, instead of replicating all channel morphologic conditions (i.e. riffle pool complexes with large woody debris placement etc.) it has a similar slope of approximately 0.01 m m^{-1}, a water depth of 20–25 cm and a velocity between 5 and 10 cm s^{-1}. The channel was filled with 18,000 l of groundwater that was devoid of background salmon organic matter and suspended sediments. Water was re-circulated using a Gould's centrifugal pump that moved approximately 1800 l min^{-1}.

2.2. Stock solution description

The stock solution of salmon was made by rotting 6 kg of Pink salmon (*Oncorhynchus gorbuscha*) for 3 weeks and then combining the decay product elutriate with lab-grade kaolin clay. The quantity of salmon tissue rotted represents the lower range of salmon tissue areal density (100 g m^{-2}) observed in O'Ne-eil Creek in 2001 (Petticrew and Rex, 2006). A total of 378 g of salmon organic matter was added to the flume. The stock solution of clay was made by adding 9 g of kaolin clay to 2 l of water and then disaggregating the solution using an ultrasonic probe (Misonix Inc., Sonicator, Ultrasonic Processor XL 2020, 10 min exposure at amplitude setting 4) prior to its addition to the stock bucket. Adding 9 g of clay to the flume resulted in a concentration of 0.5 mg l^{-1}.

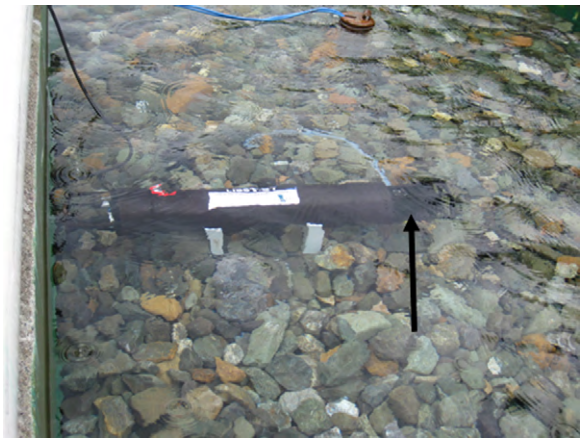

Fig. 1. Downstream view of the LISST-100 in the re-circulating channel. The arrow denotes location of the sample window for particle size analysis.

Stock solutions of clay and salmon were introduced at the same time to a stock bucket at the head of the channel that had a 200 cm^2 grid of sixteen 0.6 cm holes in the front and rear central portion of the container. The upstream grid was not screened but the downstream grid was screened with 200 μm Nitex to prevent large particles from entering the channel.

2.3. In situ suspended sediment particle sizing

Suspended sediment particle sizes were measured using the laser in situ scattering and transmissometry probe (LISST-100), from Sequoia Instruments. This probe measures suspended sediment size over 32 size classes ranging from 2 to 460 μm using laser scatter. It fires a laser into the water contained within a known sample volume and measures the scatter of laser light on to a series of 32 concentric ring detectors (Agrawal and Pottsmith, 2000). The LISST-100 was mounted on Perspex plastic blocks approximately halfway down the length of the flume (Fig. 1). It was positioned with the 5 cm sample orifice perpendicular to flow 12 cm off the channel bottom.

Prior to its placement in the channel, the LISST-100 probe was calibrated with ultrapure water to ensure that the background scatter of the instrument was within allowable factory calibration limits. This calibration file was then used to correct field data for background scatter. It was observed during the baseline period that the groundwater used in these flumes was indistinguishable from the laboratory and factory calibration traces with ultrapure water indicating very low particle content in the channel's water column before stock solutions were added. LISST-100 measurements for each exposure period commenced at the time stock solutions were introduced to the stock bucket at the head of the channel and continued for 60-min at a frequency of 3 s (n = 1200 samples).

Prior to statistical analysis, LISST-100 data were processed using MS Excel™ macros that verified proper probe functioning and calculated central tendency measures for sample comparison (Williams, 2006). To determine change in the particle size distribution of suspended sediments between sample date, a two-way analysis of variance (ANOVA, SYSTAT 12) of arc-sin transformed

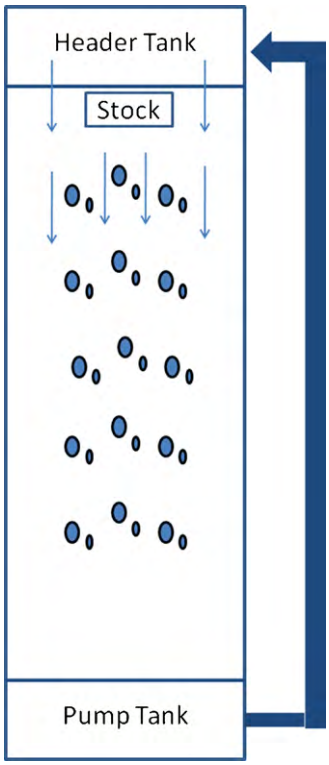

Fig. 2. Plan form of re-circulating channel showing the full 30 m channel length with infiltration bags (large circles) and piezometers (small circles) equally spaced within the central 20 m of the channel (not to scale). Arrows indicate direction of water movement.

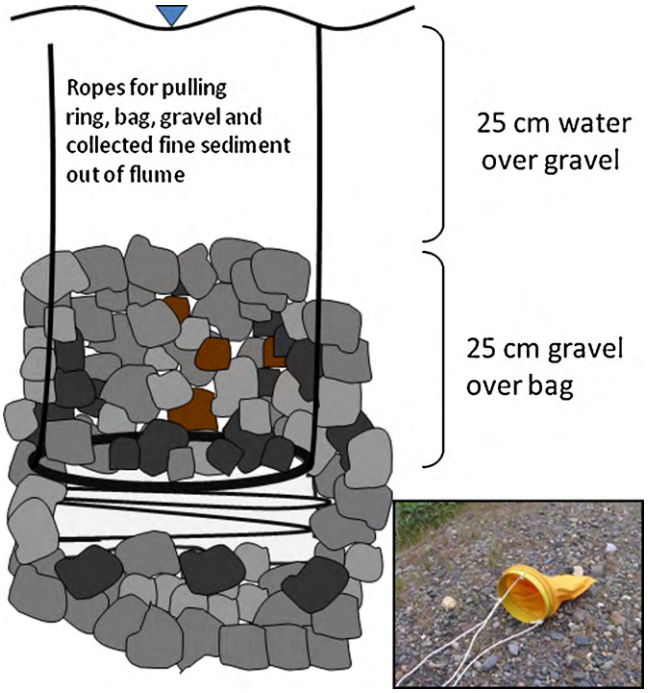

Fig. 3. Schematic of an infiltration bag deployed in the gravel bed of the re-circulating channel with an in-set photo of infiltration bag prior to its placement in the channel.

average grain size distributions (i.e. average from 1200 sample distributions) was used with date and grain-size as factors.

2.4. Nitrogen sampling

Nitrogen samples were collected from the re-circulating channel following a baseline period and then over a 2-week period after the addition of salmon + clay. Aqueous nitrogen samples were collected from three locations in the re-circulating channel including the (i) water column, (ii) intergravel water and sediment from infiltration bags and, (iii) intergravel water at 25-cm depth using piezometers (Fig. 2). Mid-depth water column samples were collected during the baseline period ($n = 1$) as well as 1, 2, 4, 6, 7, and 14 days ($n = 2$) after the addition of salmon + clay to the water column. Infiltration bag samples ($n = 3$) were collected during the baseline period as well as 2, 4, 7, and 14 days after the addition of salmon + clay to the channel. Piezometer samples ($n = 3$) were collected during the baseline period as well as 1, 2, 3, 5, 7, and 14 days after addition of the salmon + clay.

Surface water grab samples were collected from mid-depth in sterile 500 ml Nalgene™ bottles while facing in an upstream direction to prevent sample contamination. Infiltration bags collect sediment moving vertically and horizontally through a streambed (Lisle, 1991). They consist of a waterproof fabric bag 20 cm in diameter and 35 cm long attached with a hose clamp or large zip-tie to a brightly coloured steel ring buried 30 cm deep into the gravel bed and covered with a column of cleaned reference gravel. Reference gravel was washed and sieved to remove particles less than 2 mm. Infiltration bags were removed by lifting the ring through the reference gravel column, which includes the reference gravel and the sediment it captured during deployment (Fig. 3). Once the ring was lifted above the streambed surface, it was covered with a lid to prevent loss of captured sediments during retrieval through the water column. The sample was then transferred to a clean 20-l sample bucket. Nitrogen samples were collected from the sediment and water slurry collected by the infiltration bag in sterile 500 ml Nalgene™ bottles. Piezometers were driven into the gravel-bed at a 25-cm depth (Geist, 2000) and were screened with 200 μm Nitex to prevent sampling large particles from the streambed. Samples were drawn from piezometers using a Nalgene™ hand pump. The piezometer was emptied once and then a 500 ml sample was drawn into a sterile 500 ml Nalgene™ bottle.

Once collected, nitrogen samples including travel blanks were kept on ice (~4 °C) until they were analyzed. Spectrophotometric analysis occurred within 72–96 h of sample collection for total nitrogen (TN), dissolved organic nitrogen (DON), and ammonium (NH_4^+), dissolved nitrogen (DN), and nitrate + nitrite ($NO_3^- + NO_2^-$) (APHA, 1998). In addition to replicate samples and travel blanks, batch quality assurance and control (QA/QC) data including spike recovery samples were run to minimize analytical error. If spiked samples exceeded lab QA/QC limits or blank samples were three times larger than the detection limit, that set of samples was to be excluded from analysis. There were no surface water samples excluded from the dataset due to QA/QC protocols. A two-way ANOVA using nitrogen form and date was used to compare samples. Analysis of the salmon stock solution allowed calculation of nitrogen added to the channel (Table 1). Although this study was not designed as a mass balance investigation, these calculated nitrogen concentrations are useful to assess nitrogen compartmentalization in surface and interstitial water and the flume-bed.

Sediment bound nitrogen levels were determined by analysis of fine sediment collected from infiltration bags. A 220 ml liquid sample was collected from infiltration bag samples. It was centrifuged to concentrate the fine sediments into a plug that was then oven dried at 60 °C. Carbon to nitrogen ratios (C:N) were determined using the Dumas principle of complete and instantaneous oxidation of the sediment plug by flash combustion using a FISON

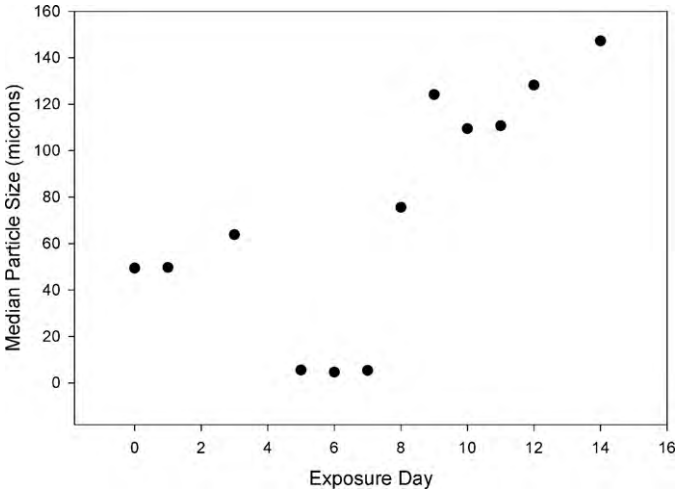

Fig. 4. Suspended sediment particle size distribution d_{50} values for each sample date during the 14-day monitoring period.

NA-1500 Elemental Analyzer (Milan, Italy) (Chikaraishi et al., 2005). To assess the C:N response to the single salmon + clay treatment over a 14-day period a repeated-measures ANOVA was applied (Manly, 2001).

3. Results and discussion

3.1. Suspended sediment particle size

Suspended sediment particle size distributions varied significantly over the 14-day period (Fig. 4, $F_{11,361} = 3.24$, $p < 0.01$). Following the addition of the salmon + clay, d_{50} values gradually increased until day 3. The gradual increase in d_{50} is a slower response than observed previously by Rex and Petticrew (2008) due to the concentration of clay. The previous study simulated active spawn conditions and used a higher clay concentration (5 mg l^{-1}) than the current post-spawn simulation (0.5 mg l^{-1}). As clay concentration increases so does the opportunity for particle collision and floc formation (Droppo et al., 1998).

An algal bloom extended from days 5 to 7, presumably in response to the addition of salmon nutrients. As a result of the bloom, d_{50} decreased due to the prominence of small algal cells in suspension. The bloom decreased after day 7 and the particle size distribution shifted to larger particle sizes quickly as identified by an increase in the d_{50} from less than 10 μm on day 7 to greater than 120 μm on day 9.

The rapid increase in the d_{50} after the algal bloom demonstrates that flocs formed in sizes similar to those observed in the previous 2007 experiments in the re-circulating channel (Rex and Petticrew, 2008), but the process is fundamentally different. Specifically, the previous investigation identified a significant increase in the proportion of particles >200 μm after the addition of salmon and salmon + clay when compared to baseline conditions because of floc formation. The higher clay concentration used in the previous study facilitated the formation of large flocs as has been noted in other floc-forming environments (Hill et al., 2000). The post-spawning simulation presented here shows smaller flocs formed after the addition of salmon + clay and then large flocs formed after the algae bloom die-off. Algal cell exopolymeric substances (EPS) enhance the formation of algal cell-based flocs (Wooton, 2004; Verspagen et al., 2006). This delay in floc formation (i.e. following the bloom) indicates the potential for flocs to form and be delivered to the streambed during low suspended sediment concentrations when carcasses are decaying in the stream.

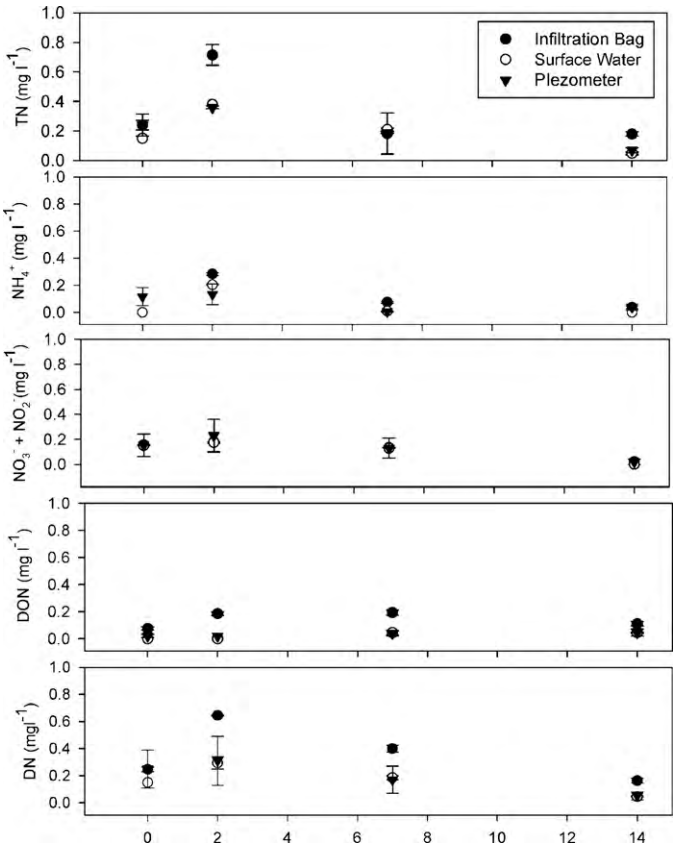

Fig. 5. Average concentration and standard error for total nitrogen (TN), ammonium (NH_4^+), nitrate and nitrite ($NO_3^- + NO_2^-$), dissolved organic nitrogen (DON), and dissolved nitrogen (DN) in infiltration bag, surface water and piezometer samples from baseline to day 14 after the addition of salmon + clay.

3.2. Nitrogen

Nitrogen concentrations increased following the addition of salmon organic matter (Fig. 5) but there were noticeable differences between nitrogen forms and pools. For ease of comparison between compartments (i.e. surface water, infiltration bags, or piezometers) sample data for baseline (day 0), day 2, day 7, and day 14 are pre-

Table 1
Nitrogen composition of salmon stock solution and calculated concentration in the flume based upon a volume of 18,000 l.

Nitrogen form	Lab analysis (mg l^{-1}) (1:250 dilution)	Total addition (mg)	Calculated flume concentration (mg l^{-1})
Dissolved organic	22	7,346	0.4
Ammonium	34	11,523	0.6
Nitrate + nitrite	<0.02	N/A	N/A
Dissolved	56	18,699	1.0
Total	59	19,701	1.1

sented graphically because samples were collected from each pool on those sample dates.

3.2.1. Surface water nitrogen concentrations

Surface water concentrations of ammonia and total nitrogen showed an immediate response to the addition of salmon + clay (Fig. 5). Water column TN concentrations increased threefold from baseline concentrations of approximately 0.15 to 0.44 mg l^{-1} on day 1 (day 2 data in Fig. 5 is 0.38 mg l^{-1}). The concentration of water column NH4$^+$ increased 12-fold from a baseline concentration that was less than detectable at 0.02 mg l^{-1} to more than 0.24 mg l^{-1} on day 1 (day 2 data in Fig. 5 is 0.21 mg l^{-1}). Nitrate and nitrite ($NO_3^- + NO_2^-$) concentrations along with DON exhibited minimal response while dissolved nitrogen (DN) increased following the trend of NH_4^+. These observations indicate the need for further controlled study because the anticipated nitrification of NH_4^+ to $NO_3^- + NO_2^-$ did not lead to increased $NO_3^- + NO_2^-$ concentrations in substantial quantities within the water column or elsewhere. Alternatively, the absence of increases in $NO_3^- + NO_2^-$ concentrations may reflect bacterial uptake (Pinay et al., 2009), storage within areas of the channel not sampled, or loss to the atmosphere through denitrification.

Surface water TN and NH_4^+ concentrations decreased to day 0 conditions by day 7, which also marked the end of the algal bloom. The surface water concentrations of all nitrogen forms are much less than anticipated after the addition of salmon + clay based calculated values (e.g. TN 0.44 mg l^{-1} vs. 1.1 mg l^{-1}). The difference between observed and expected levels may be due to nitrogen sequestration to the gravel bed or biological uptake that supported the later algal bloom Cak et al. (2008) identified that water column NH_4^+ levels due to the addition of salmon organic matter decreased rapidly from adherence to clay particles.

3.3. Interstitial water nitrogen concentrations

Interstitial water showed a response to the salmon + clay addition in both the infiltration bag and piezometer samples but the magnitude of the effect was substantially higher for infiltration bag samples (Fig. 5). This difference may reflect the higher sediment content in infiltration bag samples, which include both interstitial water as well as trapped sediments while piezometer samples are pumped from a deeper point in the gravel bed through 200 μm Nitex and were visually low in suspended sediments.

Infiltration bag nitrogen levels increased significantly ($F_{4,40} = 95.3$, $p < 0.01$) after the addition of salmon + clay. Further, there was a temporal response ($F_{3,40} = 119.7$, $p < 0.01$) with the increase in all nitrogen forms being greatest on day 2 after the addition of salmon + clay after which it decreased to baseline concentrations by day 14 (Fig. 5). Infiltration bag nitrogen level increases were highest for TN, NH_4^+, DON, and DN while $NO_3 + NO_2$ exhibited a similar trend to surface water concentrations. Nitrification of ammonia does not appear to be occurring in measurable quantities in the surface water or the flume bed. DON levels in infiltration bags remain elevated from days 2 to 7 but return to baseline conditions by day 14.

Piezometer data show a similar trend to surface water and are at lower concentrations than the infiltration bag samples. As a result, there is no difference between treatment periods but the trend observed is consistent with surface water for TN and DN increasing after the addition salmon + clay, which disappears by day 7. Piezometer NH_4^+ levels did not show the same increase following the addition of salmon + clay that surface water or infiltration bag samples demonstrate.

Infiltration bag water samples include both interstitial water as well as fine sediments (i.e. silt and clay) trapped and stored in the top 25 cm of the gravel bed. Enriched nitrogen levels in the bag samples between days 2 and 7 indicate that nitrogen is associated with fine sediment in the gravel matrix. Further, comparing the bag and piezometer samples, it is evident that these nitrogen enriched fine sediments are close to the gravel bed surface because piezometer water samples at 25 cm depth had lower concentrations than the bag samples.

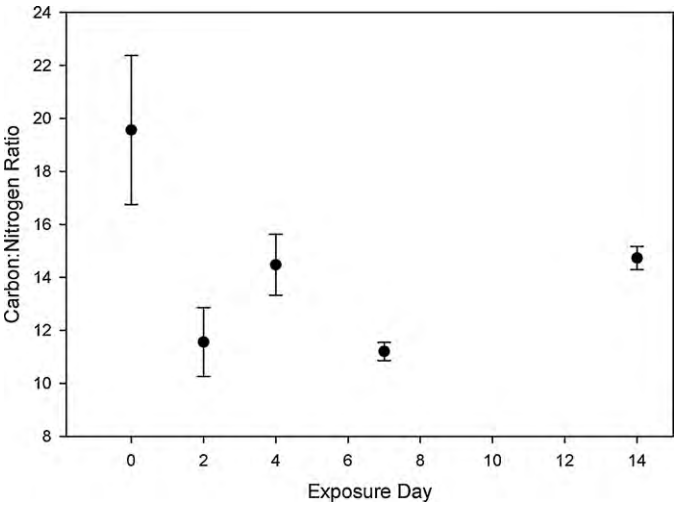

Fig. 6. Average carbon to nitrogen ratio for infiltration bag samples collected from the re-circulating channel ($n = 3$, error bars represent one standard error of the mean).

3.4. Intergravel fine sediment carbon to nitrogen ratios

Carbon to nitrogen ratios for fine sediment (<75 μm) collected in the infiltration bags significantly decreased ($F_{1,13} = 13.6$, $p < 0.05$) following the addition of salmon + clay to the re-circulating channel. The C:N ratios of fine sediment centrifuged from the infiltration bag samples shows that N is elevated from days 2 to 14 indicating the association of N with the particulate sediment. This sediment trapped by the gravels over the 14-day period is comprised of kaolin, salmon organic matter and bacteria delivered to the gravel bed via flocculation (Rex and Petticrew, 2008). This gravel bed enrichment has a longer retention period than observed for surface or interstitial water, extending throughout the 14-day study period (Fig. 6). There is some variability between the C:N ratios from days 2 to 14 likely due to spatial variability of hydrologic conditions over the flume-bed sampling area which is approximately 30 m^2. Despite this variability, it is important to recognize that mean values after the addition of salmon + clay are lower than the baseline condition indicating nitrogen enrichment of the flume-bed sediments.

Salmon organic matter-based flocs can deliver and enhance intergravel retention of sediment-bound MDN (Rex and Petticrew, 2008). We have evidence from this study that MDN, specifically nitrogen can be retained in gravel beds for several days, which may benefit hyporheic productivity. In a natural system, the signal observed here may be temporally reduced by N transformation and uptake as suggested by O'Keefe and Edwards (2002). They note that N retention in the hyporheic zone provides the opportunity for both physical and biological uptake, which may increase residence time. Similarly, Pinay et al. (2009) identified peak NO_3^- uptake in riparian hyporheic areas within 1 h of addition due to microbial and plant uptake. The flume-bed intergravel environment is different than the riparian hyporheic soils assessed in these two studies being free of surface vegetation and possibly its microbial

community. These differences may account for the residence time differences associated with N movement through the gravel bed. In addition, it points to the need for further investigation of nitrogen cycling in post-spawning streambed environments to determine if streambeds are significant storehouses of MDN delivered to natal streams by spawning salmon.

Although further investigation is required to clarify the interaction of MDN and natural streambeds, the findings presented identify that leaving salmon carcasses in streams can increase nutrient delivery and that adding a flocculent to stream-fertilization programs can enhance nutrient delivery to the streambed. Correspondingly, the removal of salmon carcasses during salmon counts by dead-pitch may lower MDN cycling in natal streams.

4. Conclusions

The controlled study presented here identifies the potential for MDN delivery and storage in the gravel bed during the post-spawning period. In addition, it emphasizes the need for further consideration of sedimentation and intergravel environments in the investigation of MDN cycling in Pacific salmon streams. Investigations of MDN cycling in Pacific salmon streambeds will complement previous water column-based investigations because it will clarify the complex water, sediment, and organic matter interactions that occur during and after spawning events.

Water column-based investigations of MDN dynamics in Pacific salmon streams identify moderate net gains in nutrients once the material exported during redd creation is considered (Tiegs et al., 2009; Moore et al., 2007). Although considerable quantities of nutrients are exported downstream during the short-term spawning event, streambed nutrient recruitment levels have not been identified during and after spawning. Flocs forming in the water column can settle downstream and enrich the streambed with MDN (Rex and Petticrew, 2008). O'Keefe and Edwards (2002) and Pinay et al. (2009) found that hyporheic concentrations of nitrogen increase as does microbial productivity during salmon runs. Based on the nitrogen delivery by flocs and the storage potential of gravel beds identified here we suggest that sediment–bound nitrogen delivery by flocs is an important component of MDN cycling and the sustainability of salmon streams that requires further investigation.

Acknowledgements

This project was assisted by Rick Holmes and Bill Best at the Quesnel River Research Centre. Field and lab support was provided by Sam Albers while Allen Esler completed the carbon to nitrogen combustion analysis. Funding to ELP was granted from the Canadian Natural Science and Engineering Research Council and Forest Renewal BC. This paper is contribution 6 in the Quesnel River Research Centre publication series.

References

Agrawal, Y.C., Pottsmith, Y.C.H., 2000. Instrument for particle size and settling velocity observations in sediment transport. Mar. Geol. 168 (1–4), 89–114.

APHA, 1998. Standard Methods for Examination of Water and Wastewater, 20th ed. American Public Health Association, p. 1325.

Bilby, R.E., Fransen, B.R., Bisson, P.A., 1996. Incorporation of nitrogen and carbon from spawning coho salmon into the trophic system of small streams: evidence from stable isotopes. Can. J. Fish. Aquat. Sci. 53, 164–173.

Bjornn, T.C., Reiser, D.W., 1991. Habitat requirements of salmonids in streams. In: Megahan, W. (Ed.), Influences of Forestry and Rangeland Management on Salmonid Fishes and their Habitats, vol. 19. American Fisheries Society Publication, pp. 83–138.

Cak, A.D., Chaloner, D.T., Lamberti, G.A., 2008. Effects of spawning salmon on dissolved nutrients and epilithon in coupled stream–estuary systems of southeastern Alaska. Aquat. Sci. 70 (2008), 169–178.

Chikaraishi, Y., Yarada, Y., Naoka, H., 2005. Carbon and hydrogen isotopic composition of sterols from riverine and sediments. Limnol. Oceanogr. 50 (6), 1763–1770.

Drake, D.C., Naiman, R.J., Bechtold, J.S., 2006. Fate of nitrogen in riparian forest soils and trees: an ^{15}N tracer study simulating salmon decay. Ecology 87 (5), 1256–1266.

Droppo, I.G., 2004. Structural controls of floc strength and transport. Can. J. Civ. Eng. 31, 569–578.

Droppo, I.G., Leppard, G.G., Flannagan, D.T., Liss, S.N., 1997. The freshwater floc: a functional relationship of water and organic and inorganic constituents affecting suspended sediment properties. Wat. Air Soil Poll. 99, 43–54.

Droppo, I.G., Jeffries, D., Jaskot, C., Backus, S., 1998. The prevalence of freshwater flocculation in cold regions: a case study from the Mackenzie River Delta, Northwest Territories, Canada. Arctic 51 (2), 155–164.

Finney, B.P., Gregory-Eaves, I., Sweetman, J., Marianne, S.V., Smol, J.P., 2000. Impacts of climatic change and fishing on Pacific salmon abundance over the past 300 years. Science 290, 795–797.

Geist, D.R., 2000. Hyporheic discharge of river water into fall chinook salmon (*Oncorhynchus tshawytscha*) spawning areas in the Hanford Reach, Columbia River. Can. J. Fish. Aquat. Sci. 57, 1647–1656.

Groot, C., Margolis, L., 1991. Pacific Salmon Life Histories. UBC Press, Vancouver, BC, p. 564.

Hassan, M.A., Gottesfeld, A.S., Montgomery, D.R., Tunnicliffe, J.F., Clarke, G.K.C., Wynn, G., Jones-Cox, H., Poirier, R., MacIsaac, E., Herunter, H., Macdonald, S.J., 2008. Salmon-driven bed load transport and bed morphology in mountain streams. Geophys. Res. Lett. 35, L04405, doi:10.1029/GL032997.

Hill, P.S., Milligan, T.G., Geyer, W.R., 2000. Controls on effective settling velocity of suspended sediment in the Eel River flood plume. Continent. Shelf Res. 20, 2095–2111.

Hocking, M.D., Reimchen, T.E., 2006. Consumption and distribution of salmon (*Oncorhynchus* spp.) nutrients and energy by terrestrial flies. Can. J. Fish. Aquat. Sci. 63, 2076–2086.

Kohler, A.E., Rugenski, A., Taki, D., 2008. Stream food web response to salmon carcass analogue addition in two central Idaho, USA streams. Freshw. Biol. 53, 446–460.

Kondolf, G.M., 2000. Assessing salmonid spawning gravel quality. Trans. Am. Fish. Soc. 129, 262–281.

Lisle, T.E., Eads, R.E., 1991. Methods to Measure Sedimentation of Spawning Gravels. Forest Service Research Note, PSW-411, Berkeley, CA.

Malcolm, I.A., Soulsby, C., Youngson, A.F., Hannah, D.M., 2005. Catchment-scale control on groundwater–surface water interactions in the hyporheic zone: implications for salmon embryo survival. River Res. Appl. 21, 977–989.

Manly, B.F.J., 2001. Statistics for Environmental Science and Management. Chapman & Hall/CRC Press, p. 336.

McConnachie, J.L., Petticrew, E.L., 2006. Tracing organic matter sources in riverine suspended sediment: implications for fine sediment transfers. Geomorphology 79, 13–26.

Moore, J.W., Schindler, D.E., Carter, J.L., Fox, J., Griffiths, J., Holtgrieve, G.W., 2007. Biotic control of stream fluxes: spawning salmon drive nutrient and matter export. Ecology 88 (5), 1278–1291.

Naiman, R.J., Bilby, R.E., Schindler, D.E., Helfield, J.M., 2002. Pacific salmon, nutrients, and the dynamics of freshwater and riparian ecosystems. Ecosystems 5, 399–417.

O'Keefe, T.C., Edwards, R.T., 2002. Evidence for hyporheic transfer and removal of marine-derived nutrients in a sockeye stream in southwest Alaska. Am. Fish. Soc. Symp. 33, 99–107.

Petticrew, E.L., 2005. Flocculation and aggregation of suspended and gravel-stored fine sediment in productive headwater streams—a case study of O'Ne-eil Creek, British Columbia, Canada. In: Droppo, I.G., Leppard, G.G., Liss, S.N., Milligan, T.G. (Eds.), Flocculation in Natural and Engineered Environmental Systems. CRC Press, Boca Raton, FL, pp. 71–93.

Petticrew, E.L., Arocena, J.M., 2003. Organic matter composition of gravel-stored sediments from salmon-bearing streams. Hydrobiologia 494, 17–24.

Petticrew, E.L., Rex, J.F., 2006. The importance of temporal changes in gravel-stored fine sediment on habitat conditions in a salmon spawning stream. In: Rowan, J.S., Duck, R.W., Werritty, A. (Eds.), Sediment Dynamics and the Hydromorphology of Fluvial Systems, vol. 306. International Association of Hydrological Sciences Press, pp. 434–441.

Pinay, G., O'Keefe, T.C., Edwards, R.T., Naiman, R.J., 2009. Nitrate removal in the hyporheic zone of a salmon river in Alaska. River Res. Appl. 25, 375–376.

Poirier, R., 2004. The effects of floods and sockeye salmon on streambed morphology. M.Sc. Thesis. University of Northern British Columbia, p. 137.

Rex, J.F., Petticrew, E.L., 2008. Delivery of marine derived nutrients to streambeds by Pacific salmon. Nat. Geosci. 1, 840–843.

Scheurell, M.D., Levin, P.S., Zabel, R.W., Williams, J.G., Sanderson, B.L., 2005. A new perspective on the importance of marine derived nutrients to threatened stocks of Pacific salmon (*Oncorhynchus* spp.). Can. J. Fish. Aquat. Sci. 62, 961–964.

Schindler, D.E., Scheurell, M.D., Moore, J.W., Gende, S.M., Francis, T.B., Palen, W.J., 2003. Pacific salmon and the ecology of coastal ecosystems. Front. Ecol. Environ. 1, 31–37.

Tiegs, S.D., Campbell, E.Y., Levi, P.S., Rüegg, J., Benbow, M.E., Chaloner, D.T., Merritt, R.W., Tank, J.L., Lamberti, G.A., 2009. Separating physical disturbance and nutrient enrichment caused by Pacific salmon in stream ecosystems. Freshw. Biol. 54, 1864–1875.

Tonina, D., 2005. Interaction between river morphology and intra-gravel flow paths within the hyporheic zone. Ph.D. Thesis. University of Idaho, p. 129.

Verspagen, J.M.H., Visser, P.M., Huisma, J., 2006. Aggregation with clay causes sedimentation of the buoyant cyanobacteria *Microcystis* spp. Aquat. Microb. Ecol. 44, 165–174.
Williams, N.D., 2006. LISST Manuals. University of Plymouth, p. 50.
Wipfli, M.S., Hudson, J., Caouette, J., 1998. Influence of salmon carcasses on stream productivity: response of biofilm and benthic macroinvertebrates in southeastern Alaska, USA. Can. J. Fish. Aquat. Sci. 55, 1503–1511.
Wooton, R.S., 2004. The ubiquity and many roles of exoploymers (EPS) in aquatic systems. Sci. Mar. 68 (Suppl. 1), 13–21.
Wotton, R.S., 2007. Do benthic biologists pay enough attention to aggregates formed in the water column of streams and rivers? J. N. Am. Benthol. Soc. 26, 1–11.