

Evidence for Hyporheic Transfer and Removal of Marine-Derived Nutrients in a Sockeye Stream in Southwest Alaska

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Abstract.—Evidence for the importance of marine-derived nutrient (MDN) inputs from spawning salmon to terrestrial and freshwater ecosystems is rapidly accumulating, but the mechanisms by which MDN inputs are transferred and stored within spawning streams and their catchments are poorly understood. Presumed marine isotope signals have been found in riparian vegetation, suggesting that marine nutrients may impact terrestrial plant communities. Studies have suggested that MDN increases stream productivity both immediately after spawning and during the following spring. The peak of many spawning runs occurs at the end of the summer growing season, suggesting that overwinter storage of MDN must be occurring. A potential location for lateral nutrient transfers and overwinter MDN storage is the hyporheic zone within stream channels or in adjacent riparian floodplains. Within Lynx Creek, a sockeye-spawning stream in the Wood River Lake drainage in southwestern Alaska, extensive floodplain hyporheic zones occur along spawning reaches. Surface water moves into the floodplain hyporheic zone and flows downstream 70–80 m before returning to the stream. Ambient nutrient concentrations within the surface and hyporheic zone indicate that marine-derived nitrogen and phosphorus entered hyporheic flow paths, where they were rapidly removed from the water during the spawning run. Some marine-derived ammonium was remobilized as nitrate and continued to move, but marine-derived phosphorus was stored for at least the duration of the spawning run. Hyporheic sediments are not scoured by winter floods and contain active heterotrophic biological communities that are capable of storing and transforming various forms of MDN. Thus, it seems likely that hyporheic storage and re-release of marine-derived nutrients is an important mechanism by which salmon-derived nutrients are retained over winter within stream ecosystems and subsequently made available to primary producers the following growing season.

Introduction

Pacific salmon feeding in the nutrient-rich North Pacific Ocean incorporate carbon, nitrogen, and phosphorus into their body tissues along with other micronutrients that provide an important nutrient and energy subsidy to the oligotrophic streams where they spawn (Cederholm et al.

1999; Kline et al. 1997; Larkin and Slaney 1997). This nutrient subsidy can enhance insect and fish growth (Bilby et al. 1996; Chaloner and Wipfli 2002). Marine-derived nutrients are also an important source of energy for numerous riparian wildlife species (Ben-David 1997; Cederholm et al. 2000; Hilderbrand et al. 1999a, 1999b). Marine stable isotopes signatures have been found

within leaves of riparian vegetation, suggesting that salmon products can potentially influence terrestrial productivity and community composition (Ben-David et al. 1998; Helfield and Naiman 2001).

Although we have greatly expanded our understanding of the potential significance of these marine nutrients in recent years, many questions remain regarding the mechanisms of transport to the riparian zone and where nutrient inputs may be stored within the ecosystem. Animals are one potentially important transfer vector from stream to riparian zone. Where present, bears remove significant numbers of salmon from streams and transfer nutrients through their urine and deposition of carcass remains that they do not consume (Hilderbrand et al. 1999a; Reimchen 2000). Numerous other species of wildlife and birds (Ben-David 1997; Cederholm et al. 2000) as well as insects (Wipfli et al. 1998) feed on salmon carcasses and distribute the nutrients throughout the stream and adjoining riparian forest. Within the stream, aquatic biota incorporate salmon nutrients directly into their own tissue, retaining it within biota (Bilby et al. 1996; Kline et al. 1990, 1993; Mathisen et al. 1988). Physical processes such as accumulation in pools or entrainment on woody debris can retain carcasses in the stream beyond the spawning period (Cederholm and Peterson 1985). Whereas consumption of carcasses by biota is one mechanism for the transfer and storage of salmon-derived nutrients, we also know that salmon release inorganic nutrients through active metabolism while on the spawning grounds and through decomposition of carcasses that remain in the stream channel (Richey et al. 1975; Schuldt and Hershey 1995).

Although many studies indicate that these biological and physical mechanisms are important, the role of the hyporheic zone in the transport and storage of salmon-derived nutrients has remained largely unexplored. Hyporheic zones are subsurface, saturated zones containing some proportion of water that previously ran within the surface stream channel (Edwards 1998; Harvey and Wagner 2000). For purposes of this study, we have focused on the floodplain hyporheic zone, which is an area of hydraulically conductive substrate beneath the overlying soil and vegetation of the riparian terrace. From studies in non-salmon streams, we know that nutrients entering the hyporheic zone from surface water can be rapidly taken up through physical sorption

and biological uptake by biofilm communities within the hyporheic zone and that the hyporheic zone can, thus, serve as a transient storage zone for these nutrients (Triska et al. 1989, 1994). Where hyporheic waters are near the soil surface, the roots of riparian vegetation may transfer nutrients from hyporheic water to their leaves. Our study objectives were to 1) delineate hyporheic flow-paths along a designated reach of Lynx Creek, southwestern Alaska; 2) determine whether the hyporheic zone could act as a vector for transfer of nutrients from spawning salmon to riparian vegetation; and 3) explore the likelihood that hyporheic storage of marine derived nitrogen (N) and phosphorus (P) could be occurring.

Methods

We conducted our study at the University of Washington's facilities in the Wood River Lakes System in southwestern Alaska (59°20'N latitude, 158°40'W longitude), where spawning sockeye salmon *Oncorhynchus nerka* have been studied since 1946 (Rogers and Rogers 1998). The Wood River system is a series of four interconnected lakes (425 km²) that drain into Bristol Bay, which in turn supports the world's largest commercial sockeye salmon fishery.

Our study took place on Lake Nerka (201 km²), which is the largest lake in the Wood River Lakes system. Lake Nerka is bordered by mountains (800-m elevation) at its western end and flat muskeg areas at its eastern end. The lake's watershed is characterized by a boreal forest association of white spruce *Picea glauca* interspersed with balsam poplar *Populus balsamifera* and willow *Salix* spp. along riparian zones, moist tundra communities at low elevations, and extensive stands of green alder *Alnus crispa* at higher elevations (J. Helfield and K. Bartz, unpublished data). Very little alder is found in riparian areas. In addition to Lake Nerka's primary inlet and outlet, approximately 60 surface water streams enter along its shores. Our study stream, Lynx Creek, has a summer base flow discharge of approximately 500 L/s. The stream supports runs of 600–18,000 sockeye salmon with a mean run size of 3,040 fish over the last 55 years (Rogers and Rogers 1998). The salmon run during the summer reported here (2000) was approximately 9,910 fish, the largest run over the past 20 years (Rogers and Rogers 1998).

We installed a rectilinear grid of 130 piezometers on a meander bend of Lynx Creek (Figure

1). For results presented here, we selected a subset of 15 wells that were located along discrete flow paths (determined by using NaCl as a conservative tracer and a conductivity meter to map the flow of water). Piezometers were 2.5 cm schedule 40 PVC pipe, open on the bottom end. These piezometers enabled us to measure water surface elevation and collect samples for water chemistry analysis. Hyporheic water was sampled with a battery driven peristaltic pump. A manifold holding sampling probes was fitted to the pump tubing, so that temperature, dissolved oxygen, and electrical conductance could be measured simultaneously with portable field meters (YSI). Because gravel hydraulic conductivities were high, it was impossible to empty the wells. Water was withdrawn from the pipe bottom until about 4 standing volumes were withdrawn; then, the pump rate was lowered to ensure that new water flowing into the pipe bottom was sampled. Temperature, electrical conductance, and oxygen concentrations in the sample stream were monitored to confirm that remaining standing water was not contaminating samples.

Surface water samples were collected at sites upstream from, adjacent to, and downstream from the piezometer grid. All samples for inorganic water chemistry were collected during mid-day and filtered in the field with syringe-mounted GF/F filters. Samples for dissolved inorganics were fixed with chloroform, and samples for both dissolved inorganics and total dissolved nutrients were frozen within 8 h of collection. These samples were collected through the summer field season (May to September) every 3–10 d, depending on the rate of change for parameters of interest (samples were generally measured within a few days of collection so that the sampling interval could be adjusted accordingly). Inorganic nitrate was measured by the cadmium reduction method (Mulvaney 1996) in the field laboratory with a Spectronic 20 Genesys and a 1-cm cell yielding a detection limit of $10 \mu\text{g NO}_3\text{-N/L}$. SRP was measured by the ascorbic acid method (Kuo 1996) in the field laboratory with a Spectronic 20 Genesys and a 5-cm cell yielding a detection limit of $8 \mu\text{g/L}$ soluble reactive phosphorus (SRP). The P-detection limits in the field laboratory were unusually high for

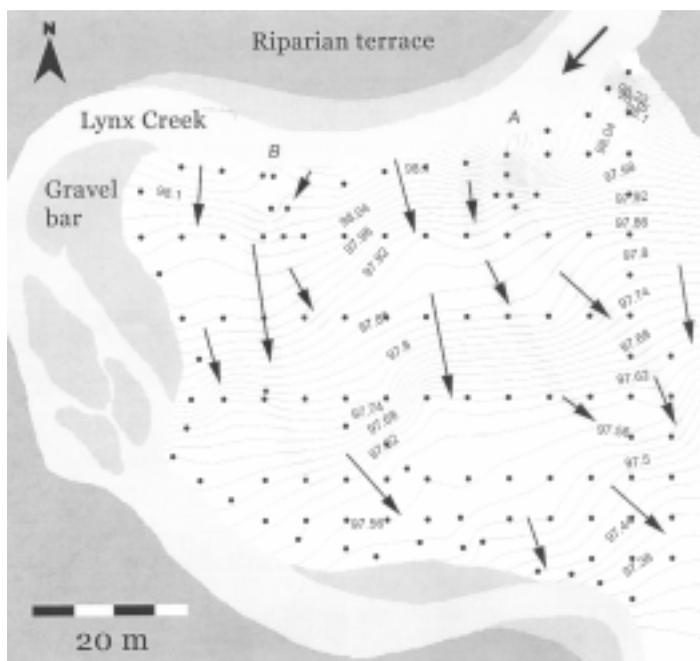


FIGURE 1. Map of Lynx Creek study site showing elevation (m) of groundwater above an arbitrary datum within the riparian hyporheic zone. Filled circles are piezometer locations. Water flow is across head contours. Shaded areas depict major flow paths delineated with salt tracer. Data from flow paths A and B are plotted in Figure 2. Arrows illustrate major flow directions. Contour interval is 2 cm.

SRP, and water samples checked by the analytical laboratory at the University of Washington, Seattle, confirmed that actual background concentrations were in the range of 1–3 $\mu\text{g/L}$. Ammonium samples were measured in the field laboratory by the fluorometric technique (Protocol A) in Holmes et al. (1999) with a detection limit of 1 $\mu\text{g NH}_4^+\text{-N/L}$. Samples for total dissolved nutrients were digested using the alkaline persulfate method (Valderrama 1981) and analyzed as described above for N nitrate and P.

To estimate the potential importance of spawning sockeye in the nutrient budget of Lynx Creek, nitrogen and phosphorus imported by returning adults was compared with estimates of total system losses (concentration \times discharge). Discharge from Lynx Creek was estimated by prorating discharge measured during the summer over the year using a hydrograph from Elva Creek (USGS station 15302840), which is located less than 15 km away and has a watershed area 10% smaller than Lynx Creek. To estimate input from fish, we assumed the average salmon contained 73 g N and 12 g P (Mathisen et al. 1988), and we multiplied this by the run size to calculate annual total fish N and P input to the system.

Results and Discussion

A hydraulic head contour plot (Figure 1) and tracer injections confirmed the existence of an extensive hyporheic zone that is 30–150 cm below the soil surface and, thus, potentially within the rooting zone of riparian vegetation. The total depth of the water mass actively exchanging with surface water is unknown but exceeds the 20–40 cm our piezometers penetrated the saturated zone. Temperature and electrical conductance values from piezometers were always similar to surface water values and showed little spatial variation that would indicate mixing with other water masses. Groundwater temperatures (4°C) were never detected within the grid, suggesting that the upper layer of the hyporheic zone that we sampled was derived entirely from advecting surface stream water. Dissolved oxygen concentrations within the grid varied from near saturation ($>11\text{ mg/L}$) at the head of the flow field to less than 1 mg/L further down the flow paths. Although concentrations decreased along the direction of flow, only a few anaerobic pockets were observed; most sites had DO concentrations greater than 3 mg/L .

Surface water ammonium concentrations increased dramatically when salmon entered Lynx Creek. Values that were less than 2 $\mu\text{g N/L}$ before the entrance of salmon began to increase immediately upon salmon entry and peaked at the height of the run at 147 $\mu\text{g N/L}$. The rapid increase in ammonium is likely due to excretion by nonfeeding salmon metabolizing body protein for energy (Hendry and Berg 1999). The proportion of total inorganic N as ammonium increased from less than 2% to more than 17% when fish were present. The increase began as salmon were holding in the stream and before individuals began to die. Upon death, which occurs approximately 1 week after entry to this stream, decomposition of salmon tissue in the stream further increased concentrations of ammonium. Increased ammonium concentrations were observed in other streams that we sampled within the area (a total of 23 additional streams). Ammonium increased from near zero in streams with salmon runs with no significant increase in those without salmon runs, supporting the interpretation that the ammonium increase is attributable to salmon inputs.

In Lynx Creek, this ammonium entered the hyporheic zone where we detected elevated levels up to 82 $\mu\text{g N/L}$ in piezometers in the upper section of the flow paths where surface water entered the hyporheic zone (Figure 2). This increase in hyporheic ammonium concentration began at the same time stream concentration increased. Ammonium concentrations along the flow paths declined to near zero background concentrations within 3–5 m along the transect from where surface water entered the hyporheic zone (Figure 2a). These results are consistent with experimental ammonium additions we performed in 1999 and previous work showing high uptake potential for ammonium within the hyporheic zone.

Stream surface water nitrate concentrations decreased from a high of 482 $\mu\text{g N/L}$ in June to a low of 290 $\mu\text{g N/L}$ just prior to the entry of fish. This reduction occurred as stream discharge progressively decreased through the summer and likely reflects the reduced movement of nitrate from valley wall alder forests as soil moisture in the watershed decreased. When spawners entered the stream, there was a small increase of about 50 $\mu\text{g N/L}$ in stream nitrate concentration, suggesting that some of the ammonium released by fish was nitrified within the channel. Within the hyporheic zone, nitrate concentrations in the

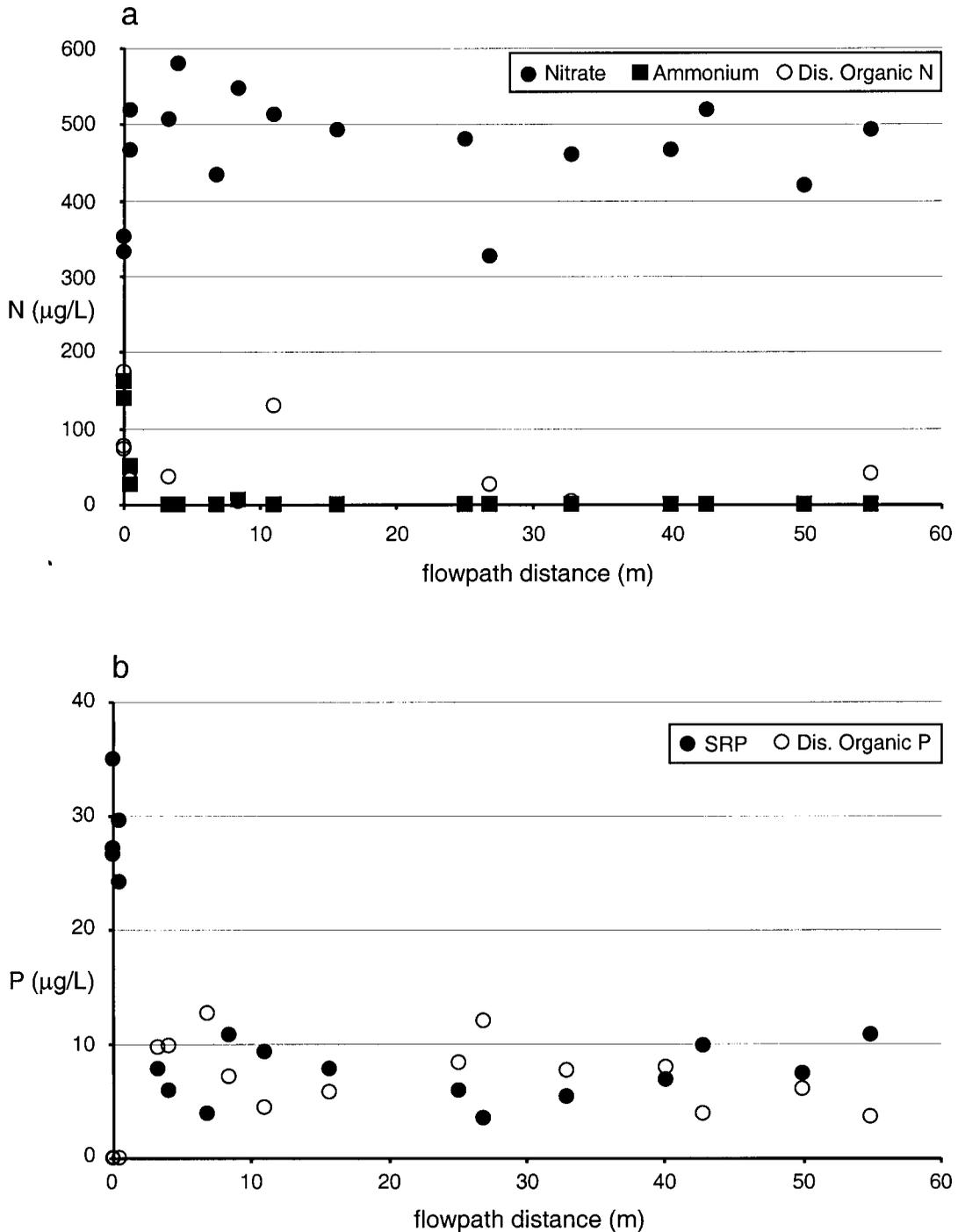


FIGURE 2. Longitudinal plots of dissolved inorganic and dissolved organic forms of N and P along flow paths A and B at the dates of maximum concentration within the upper flow path. a) ammonium, nitrate, and dissolved organic N from 21 August 2000. b) SRP and dissolved organic P from 3 September 2000. Distance 0 values are surface water concentrations at three sites adjacent to the location at which water enters the upper flow field.

first 3 m of the flow paths increased by 150–250 $\mu\text{g N/L}$ from the initiation of spawning to peak spawning densities. This increase is about the same magnitude as the increase in surface water ammonium concentration, suggesting that ammonium entering the hyporheic zone was nitrified. However, longitudinal plots of nitrate along the studied flow paths do not exhibit an obvious increase in nitrate that can be attributed to progressive nitrification (Figure 2a). Instead, nitrate values remained high throughout the flow paths, and any contribution by nitrification was undetectable in the high background variability. Conceivably, ammonium could have been incorporated into dissolved organic or particulate forms within the hyporheic zone and lost in those forms rather than being stored. However, 60 m of sand and gravel is an effective filter, and it is unlikely that particles move very far. Dissolved organic nitrogen values dropped from 31 to 37 $\mu\text{g/L}$ in the first few meters to below detection and remained low along the lower section; thus, we see no evidence for immediate loss in that form.

Soluble reactive phosphorus increased from background levels of less than 8 $\mu\text{g P/L}$ before salmon entered the stream to 45 $\mu\text{g P/L}$ by the end of August, just after the peak of the salmon run. Although phosphorus may also be released from living salmon through metabolism during spawning, the surface concentration increase began two weeks later than that of ammonium. As salmon began to die, SRP concentrations in the upstream section of the hyporheic zone increased from below detection limits to a peak of 33 $\mu\text{g P/L}$. Similar to ammonium, values decreased to background concentration 3–5 m along the flow paths (Figure 2b). For the duration of our sampling, we saw no indication that phosphorus was re-entering the flow stream as SRP. Likewise, dissolved organic P remained at detection limits in the lower flow path sections, indicating no immediate losses in that form (Figure 2b).

In reference to our study objectives, we conclude that hyporheic transport of salmon-derived nutrients to riparian vegetation is a feasible mechanism. Advecting surface water flowed up to 60 m into the riparian terrace, carrying N and P that appears to be derived from spawning salmon and lies within the rooting zone of riparian vegetation. Whether vegetation actually takes these nutrients up remains to be shown; however, actual uptake of salmon-derived products has not been documented for any known transport

vector; inference of uptake has been based solely on presence of presumed marine isotopic signatures. Our data suggest that the relative importance of N and P as a nutrient source from salmon to riparian vegetation differs in this catchment.

Salmon seem to be a minor source of nitrogen in the Lynx Creek watershed, and most of the nitrogen entering the saturated riparian zone appears to be derived from other sources, most likely alder-dominated soils on the valley walls. A simple annual flux budget for nitrogen based on export of total dissolved nitrogen indicates that even in a year with a large fish run, as we observed in 2000, the salmon are still only supplying 6% of nitrogen discharged from the system, and the long term average is less than half that. Thus, although ammonium and nitrate from salmon are clearly present in the hyporheic zone during spawning, the bulk of nitrogen flowing beneath the riparian terrace enters before spawning and is unrelated to salmon. In contrast, salmon-derived phosphorus appears to be potentially much more important as a source for riparian vegetation. Summer-long SRP values are low, and the increase coinciding with spawning is much more pronounced. A flux budget for phosphorus export relative to potential input from salmon indicated that marine phosphorus made up 38% of the inorganic phosphorus discharged from the stream. Clearly, the rapid removal of SRP within the upper flow field may reduce the distance P penetrates into the riparian zone and thereby its availability to riparian vegetation throughout the flow field. Whether this P is subsequently released into the water and moved farther down the flow path requires further study. In regard to the question of storage of MDN within hyporheic zones, the differences between N and P must also be considered. Although ammonium, the dominant form of marine-derived N input into the hyporheic zone, is efficiently removed from solution (Triska et al. 1994), there is evidence that nitrification is converting some to nitrate, which continues to move down the flow paths. Denitrification is also occurring in the terrace soils (Gilles Pinay, personal communication), which could further reduce long-term storage of nitrogen. Nonetheless, advecting marine-derived N is physically retarded by entrainment within the hyporheic zone and is exposed to biological and physical uptake mechanisms that can retain it for periods exceeding the hydrologic residence time; so, overwinter storage of some proportion remains a possi-

bility. Definitive testing of overwinter nutrient retention will require research in a system that can be studied year round and some manipulative experiments. Phosphorus storage appears more likely because little export of SRP was observed during spawning, there are no pathways for gaseous loss, and conversion to more mobile forms is unlikely. However, how long the P is stored and how long it takes to work its way down the flow field and re-enter the surface stream remains to be demonstrated. The question is an important one for Lynx Creek because nutrient diffusing substrate studies indicate that benthic algae are strongly P-limited (R. T. Edwards, unpublished data).

The elevated nitrate concentrations we measured both before and during spawning likely result from extensive stands of nitrogen-fixing green alder that dominate the uplands of many of the watersheds. Our study site was characteristic of streams in southwestern Alaska where large stands of alder can dominate watersheds. This alder-derived nitrogen could be an important source of nutrients and must be considered when examining the flux of nutrients, especially N, in these systems. Alder covers approximately 44% of the Lynx Creek watershed, and in a survey of 23 additional watersheds in this area, dissolved nitrogen was highly correlated ($r^2 = 0.75$) with percent alder coverage (authors' unpublished data). This suggests that stream nitrogen budgets in this area are strongly influenced by alder coverage.

Summary

We have documented hyporheic flow beneath the riparian terrace in a sockeye spawning stream. Because the physical characteristics of the porous gravel substrate used by salmon for spawning also create ideal conditions for hyporheic flow, we believe that extensive subsurface flow is a characteristic feature of all salmon spawning streams. We have also documented elevated ammonium and SRP concentrations in surface water during the period of spawning and the intrusion of these nutrients into the hyporheic zone. These nutrients are rapidly removed from solution upon entering the metabolically active upstream edge of the hyporheic zone, demonstrating the potential for these areas to serve as storage areas for salmon-derived nutrients. In systems or years with few salmon relative to the capacity of wildlife to remove carcasses

from the stream, we predict that hyporheic transfer and storage will be relatively small. In contrast, during larger runs when animal consumption is saturated and many fish decompose within the stream, hyporheic transfer and storage may process an ecologically significant mass of N and P. The net effect of hyporheic processes on stream productivity depends upon the ultimate fate of N and P removed. If the bulk of ammonium is converted to mobile forms or lost via denitrification and if phosphorus is ultimately irreversibly bound to minerals, then hyporheic zones are a sink for MDN. If, on the other hand, nutrient spiraling within the saturated zone allows nutrients to slowly migrate down flow paths and re-enter the surface channel after some delay, hyporheic zones can function to buffer the seasonal pulse of limiting nutrients and increase stream productivity. Other sources of nutrients within the watershed, such as alder, need to be considered when interpreting the importance of salmon nutrients at any given location throughout the geographic range of salmon.

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