THE DELIVERY, SEASONAL STORAGE, AND TROPHIC TRANSFER OF MARINE-DERIVED NUTRIENTS WITHIN A STREAM-RIPARIAN ECOTONE

by

Leah M. Vanden Busch

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Abstract

The objectives of this study were to evaluate nutrient delivery, storage, and trophic transfer between the Horsefly River spawning channel and its riparian zone during the 2011 sockeye salmon run and subsequent 2012 spring. The hyporheic zone was investigated as a pathway for nutrient exchange, transformation, and storage by analyzing water movement and ammonium (NH_4^+) concentration. Using stable isotopic analysis, the assimilation and storage of marine-derived nutrients (MDN) were evaluated through multiple trophic levels. Results identified lateral hyporheic flow as a dominant pathway for MDN delivery to deep-rooted vegetation, specifically willow trees <7-m from the streambank. Amphipods and chironomids appeared to assimilate MDN in the fall and maintained high spring biomass, indicating an important nutrient linkage in the salmon feedback loop. Finally, a temporal reversal in NH_4^+ concentration across the stream-riparian interface and a seasonal shift in nutrient fluxes revealed reciprocal subsidies that highlight the interconnectedness of these adjacent systems.

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Chapter 1

Ecotones, Salmon, and Marine-Derived Nutrients: A Literature Review

1.1 Zone Ecology

1.1.1 Ecotones

An ecotone represents the boundary or transitional zone between adjacent ecosystems. The concept of ecotones has evolved greatly since the beginning of the 1900s when it first appeared in environmental literature as "edge habitats" or "zones of tension" (Decamps & Naiman 1990). Originally, ecotones were viewed as static boundaries where dominant ecological systems reached their limit and were notably important as areas of habitat, cover, and food for wildlife species. Now, they are widely recognized to have a much richer function (Decamps & Naiman 1990, Risser 1995, Clary & Medin 1999). Ecotones act as a connection between distinct ecosystems, providing a delicate balance that allows energy and matter to flow in a manner which supports and links the adjoining areas (Naiman et al. 1988, Gosz 1993, Naiman & Decamps 1997, Febria et al. 2011). These interfaces provide critical ecosystem services including buffering pollutants, attenuating and transforming nutrients, and providing refuge for prey and a source area for predators and pests (Evans 1956, Krause et al. 2011). As a result of their narrow spatial extent and steep ecological gradient, ecotones offer high species richness and unique genetic diversity (Risser 1993). When this biodiversity coincides with a high number of endemic or taxonomically unusual species, ecotones can be considered biodiversity hot spots, which are often areas of priority for conservation efforts (Myers et al. 2000). Ecotone boundaries are difficult to define, as their temporal and spatial characteristics are perpetually transitory. This indistinct framework emphasizes *flow* across three-dimensional boundaries (Pinay et al. 1990, Bretschko 1995, Kerne 2002, Febria et al. 2011). The processes that control energy and material flux are intricately connected to the biological activities that comprise an ecotone's structure and organization; therefore, both qualitative and quantitative attributes need to be described in order to understand an individual ecotone (Evans 1956).

Areas in proximity to waterbodies contain numerous aquatic-terrestrial interfaces, including riparian zones, hyporheic zones, aquatic marginal wetlands, and lake littoral zones. These areas are of particular interest due to their sensitivity, and reactivity, to environmental change and therefore, provide a primary landscape to observe and understand effects of local and global change (Naiman & Decamps 1990). They are considered indicators of change and can provide early warning signs for analogous regions (Risser 1993). Terrestrial-aquatic ecotones guide the principles of the river continuum concept, which does not treat rivers and streams as bounded systems, but as systems which are integrally linked to downstream, upstream, and adjacent environmental inputs and properties (Hynes 1974, Vannote et al. 1980, Naiman et al 1998, Bo et al. 2006).

1.1.2 Riparian Zone Ecology

The land that borders a river, the riparian zone, provides an essential connection to maintain ecological functions in these adjacent and connected habitats (Ward & Stanford 1995, Ward et al. 1999, Allan & Castillo 2007). Riparian zones are some of the most diverse, dynamic, and ecologically productive habitats of all terrestrial ecosystems (Naiman & Decamps 1997, Clary & Medin 1999). Exhibiting high moisture gradients, contrasting vegetation species, and a mosaic of habitats along a river corridor, riparian zones often contain high flora and fauna biomass, especially in arid regions (Clary & Medin 1999). As in all ecotones, riparian zones perform functions that drive ecological connections, such as filtering pollutants and trapping suspended particles (Peterjohn and Correll 1984) and mediating biogeochemical transformation (Carlyle and Hill 2001).

1.1.3 Hyporheic Zone Ecology

Water in rivers and streams passes between the channel bed surface and subsurface along discrete flow paths. This interstitial area of mixing, the hyporheic zone (Figure 1.1), regulates the exchange of nutrients and gases between groundwater and surface water (Triska et al. 1989, Valett et al. 1993, Fisher 1997, Malard et al. 2002). The hyporheic zone represents a hydrologic continuum between river water and groundwater and cannot be precisely separated (Alley et al. 2002, Plummer et al. 2013). The hyporheic zone provides a medium in which these two inherently different, but coupled ecosystems can interact.

Many critical functions are provided by the hyporheic zone: nutrient transformation (Ward et al. 1998, Hancock 2002), pollution attenuation (Wagner & Bretescko 2002), refuge during low flow events (Grimm et al. 1991, Boulton & Stanley 1995, Robertson & Wood 2010), habitat for salmonid embryo survival (Geist & Dauble 1998, Kondolf 2000, Robertson & Wood 2010), and post-disturbance stream recovery (Valett et al. 1994, Gardner et al. 1999, Hancock 2002). The hyporheic zone also acts as a transient storage area, where a portion of the water moving downstream is temporarily retained in regions of stagnant or slow moving water. Intense biogeochemical transformations occur in storage zones (Packman & Bencala 2000).

The hyporheic zone relies on surface water to supply crucial resources to hypogean fauna, such as food, nutrients, and dissolved gases (Wagner & Bretescko 2002). The subsurface environment has habitat limitations (permanent darkness and space restrictions) that typically support a lower biodiversity than the stream's surface water (Gilbert 1990, Ward et al. 1998, Hancock 2002). Hypogean fauna are often rare, niche organisms that act as bio-indicators for groundwater contamination and facilitate intense biogeochemical activity that supports the entire aquatic-terrestrial interface (Boulton & Stanley 1996, Hancock 2002).

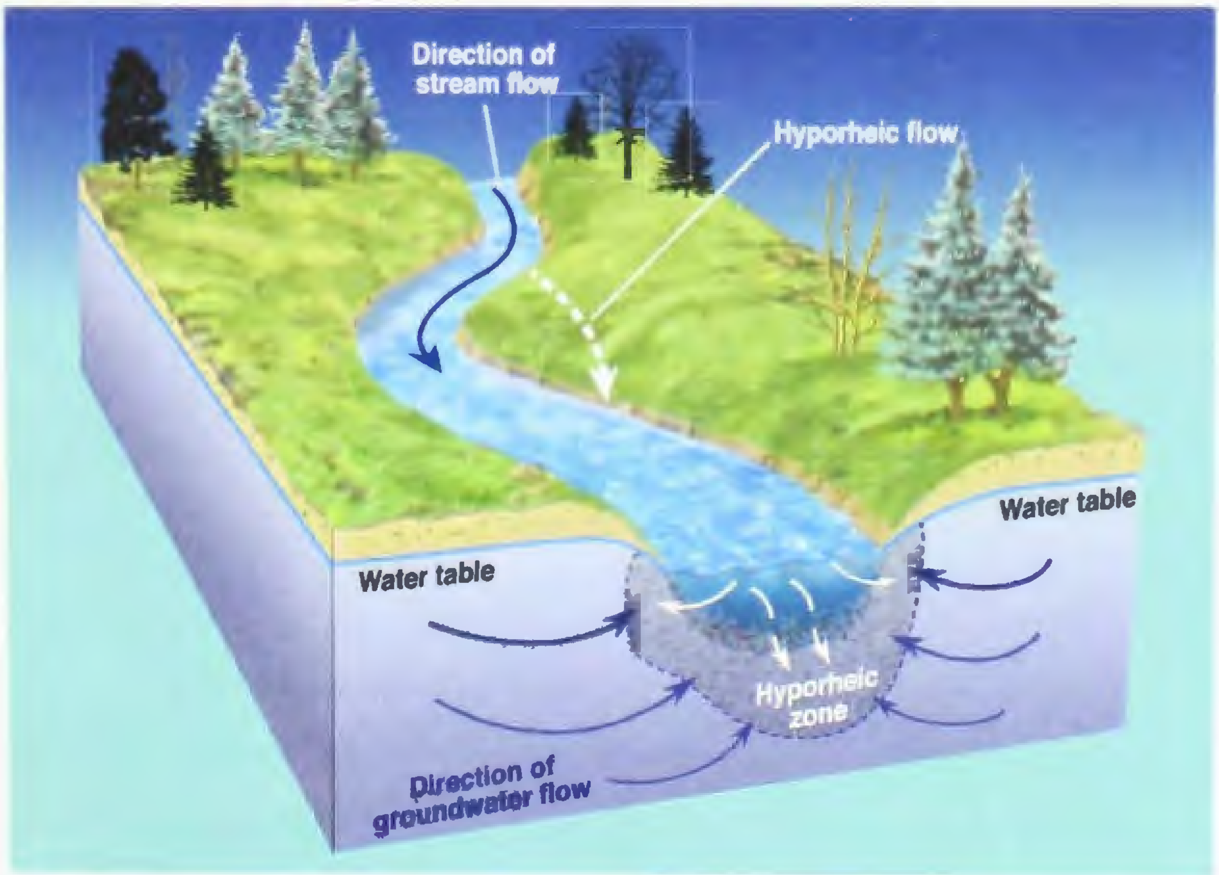


Figure 1.1. Diagram depicting the location of the hyporheic zone as an interstitial area between stream water and groundwater. Local geomorphic features, such as the meander bend pictured here, can form localized flow features within stream and banks. (From Alley et al. 2002.)

1.1.4 Interstitial Zone Overlap

Traditionally, streams and rivers were viewed as discrete systems within the bounds of the surface water and the riverbed that encapsulated this flow. We now know that lotic environments are some of the most dynamic and complex ecosystems on this planet. Streams are intricately connected to the land and water that immediately surround it and, especially, to the interfacing systems that join the land to the stream and the stream to the groundwater (Figure 1.2; Triska et al. 1993, Boulton et al. 1998). The hyporheic zone and riparian zone have dynamic, shifting boundaries that are controlled by surface stream direction and velocity overall. Investigating the biological, physical, and chemical processes in these overlapping and inherently difficult to define ecotones produces complicated questions. Processes, rather than discrete products, tend to be the focus when interpreting hydrologic and biogeochemical interactions within the hyporheic/riparian interface.

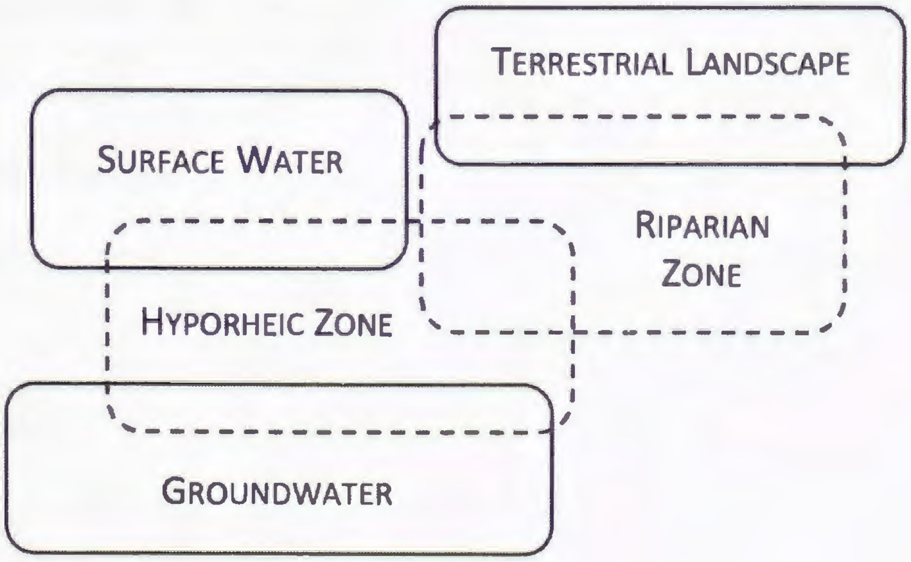


Figure 1.2. Schematic diagram showing the hydrological ecosystems and ecotones that can interact with the hyporheic zone and their relative location to the hyporheic zone (adapted from Boulton et al. 1998).

1.2 Pacific Salmon

Every year, millions of Pacific salmon (*Oncorhynchus spp.)* migrate hundreds of kilometers from the Pacific Ocean to their natal spawning grounds (Hobbs & Wolfe 2008). They gain about 95-99% of their biomass while at sea and deliver substantial quantities of marine-derived nutrients (MDN) to the nutrient-poor freshwater systems in which they spawn (Naiman et al. 2002). This annual event provides an important source of nutrients and energy to enhance fish and aquatic productivity, as well as terrestrial wildlife and plant species (Bilby et al. 1996, Willson et al. 1998, Helfield & Naiman 2001, Wipfli et al. 2003, Albers & Petticrew 2012).

Decreasing salmon abundance has been well documented in California, Idaho, Washington, and Oregon (Nehlsen et al. 1991, Brown et al. 1994). In one century, the average number of salmon returning to these rivers has declined from 45 million to less than 2 million (Naiman et al. 2002). These declines cannot be attributed a single cause, but instead are an outcome of many factors, including reduced ocean productivity, overfishing, freshwater and estuarine habitat loss, exotic species introduction, and unsustainable hatchery practices (Miller et al. 2014). Salmon stocks north of the United States-Canada border are also experiencing declines (Jacob et al. 2010, McDaniels et al. 2010, Peterman & Dorner 2011). Decreases in productivity have been rapid and consistent since the 1990s across a large geographical range, spanning from Washington and British Columbia to southeast and southern Alaska (Beamish et al. 2012, Peterman & Dorner 2012). The Canadian government-sanctioned Commission of Inquiry into the Decline of Sockeye Salmon in the Fraser River, the Cohen Commission, has investigated this issue due to poor returns and low biological productivity. British Columbia's Fraser River basin, the second most productive sockeye salmon (*O. nerka*) fishery in the world, is currently experiencing problems threatening the stability of salmon stocks (Cohen 2012). Mean summer water temperature has increased by ~1.5°C since 1950 and, recently, spawning salmon have encountered record high temperatures that have been associated with high levels of migration mortality (Martins et al. 2011). Lately, there has been extreme variability in Fraser River fish stocks and dramatic shifts in migration behavior, which indicates that ecological dynamics in interior watershed systems are under stress (Hague et al. 2011). This unpredictability raises concern because habitat degradation continues due to land-use activities that negatively alter salmon habitat and prevent their passage upstream (Baldwin et al. 2003, Ficke et al. 2007, Lohse et al. 2008, Jacob et al. 2010). Reduced salmon runs will result in a smaller MDN pool and may inhibit the ability of river systems to support current resident and anadromous fish populations (Bilby et al. 1996, Scheuerell et al. 2005). A more complete ecological picture of freshwater salmon habitats will aid restoration and management of both disappearing and thriving salmon streams.

1.2.1. Marine-Derived Nutrients

MDN are characterized as the nutrients released from salmon throughout their migration and spawn, such as waste products, eggs, sperm, and decomposing salmon carcasses (Naiman et al. 2002, Lessard & Merritt 2006). The upstream delivery of MDN by anadromous salmon goes against ordinary nutrient flow, which tends to favor downstream delivery (Murota 2003, Mitchell & Lamberti 2005). This nutrient pulse provides a significant nutrient subsidy to enhance primary and secondary productivity in oligotrophic, interior systems (Bilby et al. 1996). The post-spawn die-off leaves thousands of salmon to decay on the river bed and the riverine community metabolizes the flesh in several ways (Kline et al. 1997). Biofilms, the primary benthic producers, quickly remove nutrients from the water column through uptake and retention (Costerton et al. 1995, Reisinger et al. 2013). Aquatic macroinvertebrates and resident fish in the river obtain MDN through direct salmon consumption (Wipfli et al. 1998, 1999, 2003). Terrestrial animals and birds also take advantage of the salmon surplus by predation and scavenging of carcasses (Woodward et al. 2005, Obermeyer et al. 2006). Partially eaten fish that have been carried across the landscape and salmon-enriched waste products from predators/scavengers provide MDN to riparian vegetation (Helfield & Naiman 2006, Hocking & Reimchen 2009). Biota that do not directly consume salmon carcasses or eggs still benefit from the nutrient pulse because MDN are accumulated through higher trophic levels (Bilby et al. 1996). Salmon runs not only enrich the local biotic community, they drive a positive feedback loop that increases survivorship and reproduction to elevate their own populations (Schindler et al. 2003, Wipfli et al. 2003, Koyama et al. 2005).

1.2.2 Horsefly River in the Fraser River Watershed

British Columbia's Fraser River is utilized as a transportation corridor and spawning grounds for five types of Pacific Salmon. Some of these fish, such as Pink salmon (*O. gorbuscha*), will travel a very short distance from the mouth of the Fraser River to reach their spawning grounds, but the hardiest of salmon, the Chinook salmon (*O. tshawytscha*), will migrate over 1000 kilometers to the river's headwaters near Mount Robson (Benke & Cushing 2005). The entirety of the Fraser River main channel is undammed, allowing for natural fish passage along much of its' length (Evenden 2007). This is a rather unprecedented feature for large rivers in populated regions, and the Fraser River is ranked as the third largest undammed river in North America. However, this river and its’ salmon populations are not exempt from other damaging environmental challenges that hinder salmon and ecosystem resiliency, including warming water (Ficke et al. 2007, Jacob et al. 2010, McDaniels et al. 2010, Hauge et al. 2011, Martins et al. 2011), sea lice (*Lepeophtheirus salmonis)* (Krkošek et al. 2007), oceanic conditions (Worm et al. 2006 , Thomson & Hourston 2011), and agricultural and urban run-off (Baldwin et al. 2003, Smith et al. 2007, Lohse et al. 2008).

Sockeye salmon are prized as a valuable commercial fishery, a cultural necessity, and a superior food source in Canada. Therefore, much of the research on salmon is focused on monitoring sockeye populations (Cohen 2012). The International Union for the Conservation of Nature (IUCN) conducted an endangerment assessment on subpopulations of sockeye salmon in the North Pacific. This assessment categorized five of eleven Fraser River sockeye salmon stocks as threatened: one as Critically Endangered, three as Endangered, and one as Vulnerable. Out of the 22 subpopulations of sockeye on the Fraser River, seven were classified as "endangered" (IUCN-SSG 2013).

Sockeye salmon return to the Fraser River in relatively predictable 4-year cycles of abundance and decline, characterized by a dominant year with very large returns, followed by a sub-dominant year with approximately half of the dominant year's returns, and then two years of very low returns (Henderson & Graham 1998, Guill et al. 2012). Since the late 1970s, salmon escapement to the Horsefly River steadily increased, with a peak occurring in 2001 of over 1.5 million returning sockeye (Figure 1.3). This cyclical predictability was disrupted in 2009 when what was supposed to be a peak year had returns similar to a low sub-dominant year, with only a little over 80,000 returning. The Quesnel subpopulation, which includes Horsefly River, remains as "least concern" (IUCN-SSG 2013). However, when performing a three-generation nonparametric escapement calculation (*from* Geiger & Zhang 2002), salmon escapement on the Horsefly River has declined 5.3% per year between 1998-2013, which is judged as a biologically meaningful decline.

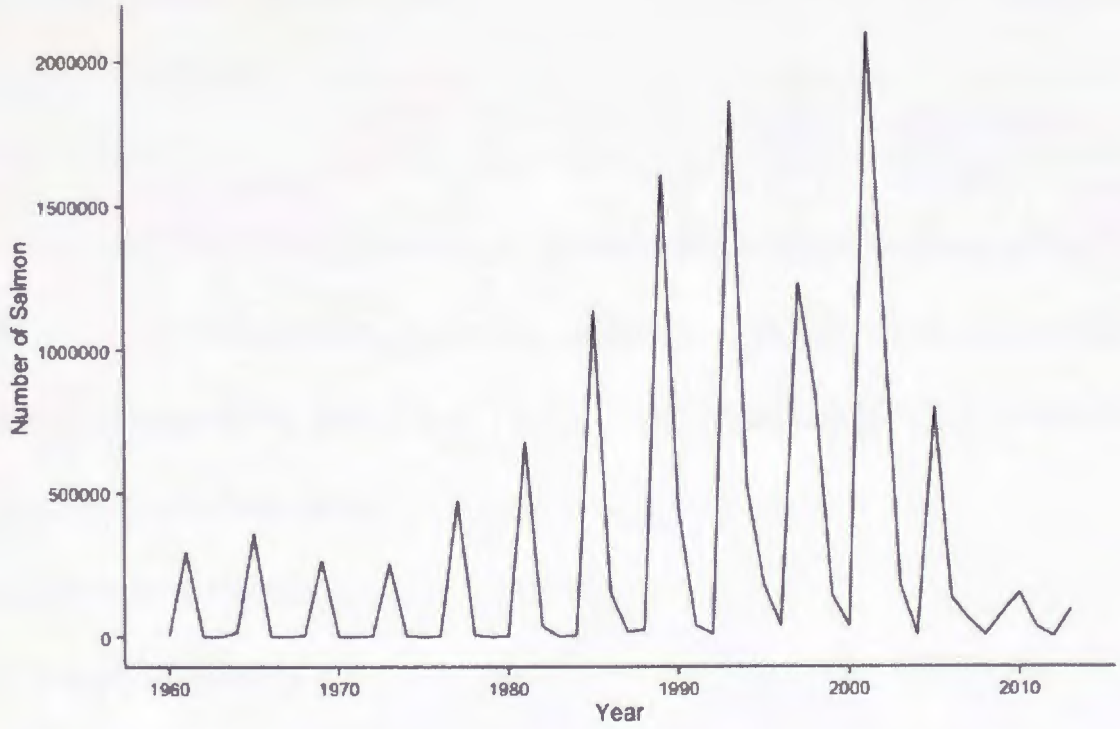


Figure 1.3. Sockeye salmon populations in the Horsefly River from 1960 to 2013. Note: 2013 data are preliminary and could change. Source: Dept. of Fisheries and Oceans Canada.

1.3 Nitrogen

1.3.1 The Nitrogen Cycle

Nitrogen, occurring in 78% of the Earth's atmosphere, is one of the most common elements in the natural world. However, nitrogen in its most abundant form, gaseous N_2, is not readily available for biological uptake (Chapin et al. 2011). In river ecosystems, particularly small streams, primary producers are of greatest significance in providing energy to consumers (Allan & Castillo 2007). Nitrogen-fixing organisms, typically located freely in soil organic matter or symbiotically-bonded to plant species, must first alter the state of nitrogen into the bioavailable forms of (mainly) ammonium (NH_4^+) and nitrate (NO_3^-), also known as dissolved or inorganic nitrogen (Vitousek et al. 1997, Ashkensas et al. 2004). The process of nitrification utilizes nitrifying organisms and partially decomposed organic matter to convert NH_4^+ to NO_3^- (Richey et al. 1984, Williams 2000). Certain environmental conditions help facilitate this conversion, including an aerobic environment, a soil pH between 7 and 9, and an approximate soil temperature of 25°C (Chapin et al. 2011). Denitrification, on the other hand, is the reduction of NO_3^- to gaseous forms of N (NO, N_2O, N_2) by denitrifying bacteria, which is typically facilitated by anaerobic environments (Payne 1973, Betlach & Tiedje 1981, Kaushal 2008). Nitrification favors the oxygen-rich hyporheic zone, whereas the riparian zone has high potential for denitrification due to its anoxic environment (Casey et al. 2001, Kaushal 2008). The hyporheic/riparian interface may provide a positive feedback loop whereby nitrogen can continuously cycle between its forms and support an even greater diversity of organisms and habitat.

1.3.2 Marine-Derived Nitrogen ($\delta^{15}N$)

There are two stable isotopes of nitrogen, $\delta^{14}N$ and $\delta^{15}N$, which differ from an ordinary nitrogen atom by the number of neutrons contained in the nuclei. $\delta^{14}N$ is significantly more abundant, comprising 99.634% of the available forms of nitrogen isotopes (Junk & Svec 1958). However, the marine nitrogen pool has a high ratio of $\delta^{15}N$ compared to freshwater ecosystems. The $\delta^{15}N$ composition of a spawning Pacific salmon ranges from 10 to 15‰ (Welch and Parsons 1993), while other available sources of nitrogen in rivers and streams tend to be closer to the 0‰ $\delta^{15}N$ composition of atmospheric nitrogen (Kendall 1998). The isotopic disparities between these nutrient pools offer a technique for measuring the assimilation of MDN by freshwater organisms, where isotopic enrichment corresponds to increased MDN assimilation (Kline et al. 1990, Bilby et al. 1996, Chaloner et al. 2002, Hicks et al. 2005, Scheuerell et al. 2007). The trophic position of a consumer is indicated by an increasingly positive enrichment value on the trophic food chain (Minigawa & Wada 1984). This occurs because $\delta^{15}N$ is not as readily excreted as a nitrogen waste product (Robinson 2001) and accumulates within the organism.

During the process of nitrogen-fixation, many soil microbes discriminate against using marine-derived nitrogen ($\delta^{15}N$), as this has a stronger nitrogen-oxygen bond than terrestrial nitrogen ($\delta^{14}N$) (Stevenson & Cole 1999). Consequently, the products of activities like decomposition, nitrification, and denitrification are less enriched with $\delta^{15}N$, leaving the original substance with higher enrichment (Templer et al. 2007).

Studies have shown that when salmon enter streams, NH_4^+ is the initial product of salmon carcass decay and surface water concentration increases rapidly (O'Keefe & Edwards 2002, Drake et al. 2006, Pinay et al. 2009, Kiernan et al. 2010). Ammonium values will be used as a substitute for stable isotopic concentrations when analyzing surface and hyporheic water samples.

1.4 Carbon

1.4.1. The Carbon Cycle

Some 3.5 billion years ago in the Precambrian period, cyanobacteria began to bind with sediments forming stromatolites, the most ancient records of life on Earth. Stromatolites are the pioneers of oxygenic photosynthesis, which radically transformed the atmosphere into an oxic environment and initiated the dominance of oxygen-requiring organisms (Des Marais 2000, Kopp et al. 2005). Organic carbon, the other byproduct of photosynthesis, is the structural building material for all of life, as we know it, and flows freely through the biosphere as decomposable organic matter (Pace 2001). When plants and animals die, shed, or excrete waste, the organic carbon material undergoes a microbial-mediated transformation to inorganic carbon, primarily carbon dioxide (CO_2). CO_2 is transported through interstices, or the gaps between matter (i.e. soil, surface water, groundwater, and air), until it is picked-up and utilized by another living organism (Fry 2006). Decomposition in a biotic community is incredibly efficient; a long-term study of mineral soils found relatively minor changes in total organic C content 40-years after reforestation (Billings & Richter 2006).

Photosynthesizing cyanobacteria and stromatolites created local oxygen-rich environments, which facilitated the colonization of other microorganisms (Kopp et al. 2005). These highly productive and energetic colonies of autotrophic and heterotrophic organisms, called biofilms, remain as primary producers across almost every ecosystem. In a salmon-bearing stream, a substantial amount of organic carbon is delivered by the annual inland salmon migration. Microbial biofilms mediate marine-derived nutrient assimilation from the water column into aquatic and terrestrial food webs (Cummins 1974, Hoellein et al. 2007).

1.4.2. Marine-Derived Carbon ($\delta^{13}C$)

As with marine-derived nitrogen, marine carbon isotopes are distinctly enriched compared to freshwater or terrestrial values. Marine $\delta^{13}C$ signatures are enriched relative to the atmosphere, whereas freshwater $\delta^{13}C$ signatures are derived from sources of dissolved carbon dioxide in the water (Fry 2006). The stable isotopic ratio of $^{13}C/^{12}C$ allows for the identification of important primary food sources, as these stable isotopes pass through the food chain relatively unchanged (Doucett et al. 1996). Salmon predominately possess a marine carbon signature because their life strategy shifts from feeding to reproduction as they enter freshwater. Animal tissues reflect the $\delta^{13}C$ of their assimilated food within about 1‰. In isotopic terms, the expression "You are what you eat" is quite accurate and provides the basis for studying trophic food chains (DeNiro & Epstein 1978, Rounick & Winterbourne 1986, Michener & Schell 1994, Fry 2006).

1.5 Stream-Riparian Ecosystem Response

The input of marine-derived nutrients to salmon-bearing freshwater ecosystems can be seen throughout all trophic levels of a food web. Major freshwater and terrestrial components of these food webs are outlined in this section (Figure 1.4).

1.5.1 Aquatic

1.5.1.1 Biofilms

In the presence of spawning salmon, biofilms become enriched with marine isotopes (Kline et al. 1990, Holtgrieve et al. 2010). Since they are primary producers, utilization and trapping of MDN at this level will aid increased accumulation in species occupying higher tropic levels (Lamberti 1996, Wipfli et al. 1998). Their growth rate varies between streams due to specific environmental conditions, such as temperature and timber harvest, and salmon legacy effects (Rex & Petticrew 2008, Ruëgg et al. 2011, Reisinger et al. 2013). Albers & Petticrew (2012) found that biofilm density decreased during the active-spawn period due to spawning disturbance, whereas during the post-spawn period, biofilm abundance increased to above pre-spawn values and utilization of marine-derived nutrients was observed.

1.5.1.2 Macroinvertebrates

Consumption of salmon carcasses and eggs by aquatic macroinvertebrates represents an important bottom-up uptake of MDN into the food web (Lessard & Merritt 2006, Kiernan et al. 2010). Current research has found that aquatic invertebrates respond both positively and negatively to the MDN pulse. Reduced invertebrate densities and altered community structure in streams with actively spawning salmon have been observed due to disturbances from particularly high salmon densities and redd construction (Peterson & Foote 2000, Minakawa & Gara 2003, Moore & Schindler 2008, Honea & Gara 2009). However, other studies have discovered increased macroinvertebrate density due to MDN (Bilby et al. 1996, Claeson et al. 2006). Wipfli et al. (1998) documented an increase in invertebrate densities by 8 to 25 times when adding salmon carcasses to an artificial flume. Lessard & Merritt (2006) discovered that only certain taxa responded positively to MDN enrichment, particularly chironomid midges and shredders. Macroinvertebrates encompass a diverse community of feeding groups and life cycle structures. The timing of spawning season within an insect's life cycle, as well as salmon nutrient legacy, will contribute to species and location-specific enrichment (Honea & Gara 2009, Guyette et al. 2014).

1.5.1.3 Fish

Marine stable isotope enrichment is evident in anadromous and resident fishes (Bilby et al. 1996, Wipfli et al. 2003). Increased growth rates of cutthroat trout (*O. clarki*), Dolly Varden (*Salvelinus malma*), and anadromous salmon (*Oncorhynchus* spp.) suggest a transfer of nutrients and energy from decaying salmon to subsequent fish populations (Wipfli et al. 2003). Salmon carcasses, eggs, and fry provide a rich food source for fish populations (Schindler et al. 2003), and also initiate a positive feedback effect that benefits the next generation of salmon by increasing primary food resources and juvenile salmon growth rate and energy density (Wipfli et al. 1998, Adkison 2010, Rinella et al. 2012).

1.5.2 Terrestrial

1.5.2.1 Riparian Vegetation

Several studies have recognized that $\delta^{15}N$ and $\delta^{13}C$ are incorporated into terrestrial vegetation adjacent to salmon spawning streams (Bilby et al. 1996, Ben-David et al. 1998, Bilby et al. 2003, Reimchen et al. 2003, Hocking & Reimchem 2009). On Chichagof Island in southeast Alaska, the trees and shrubs surrounding salmon streams derive ~22-24% of foliar nitrogen (N) from nitrogen stable isotopes (Helfield & Naiman 2001). MDN enrichment of vegetation has been observed to extend throughout a 200-m riparian zone (Ben-David et al. 1998) and at a distance of 800-m from the stream, presumably due to the displacement of salmon by bears (Hilderbrand et al. 1999a). An established, mature riparian forest is able to retain nutrients better than a small, young forest (Milner et al. 2008, DeVries 2012). Once MDN has been established in a population of trees, they may preserve MDN within the ecosystem for 30 or more years following declines in salmon population

(Koyama et al. 2005). Evidence exists that MDN are associated with increased growth rates of riparian vegetation (Gende et al. 2002). In southeast Alaska, the growth rate of Sitka spruce within 25-m of spawning streams were found to be triple that of trees in reference sites (Helfield & Naiman 2001).

The fertilization of riparian vegetation by spawning salmon initiates a positive feedback loop, in which vegetation growth and production benefits from the influx of salmon nutrients, and salmon spawning and rearing habitat is improved because of streamside vegetation (Helfield & Naiman 2001). The shading of streams by vegetation helps to moderate in-stream temperature, which influences developmental rates of young salmon by directing optimal timing of life history events and controlling embryo development. Riparian root systems help to stabilize banks and filter sediments to minimize siltation and erosion, thus providing well oxygenated redd conditions that are ideal for salmon production (Nakano & Murakami 2001). Terrestrial inputs of organic matter support the production of aquatic insects, which are a basic source of food for juvenile salmon (Helfield & Naiman 2001). Large woody debris, which accumulates in streams with riparian vegetation, plays an essential role in providing rearing habitat for salmonids (Fausch & Northcote 1992). Large wood also enhances hyporheic exchange (Hester & Gooseff 2010), which may influence the riparian-hyporheic interactions that are being investigated in this study.

1.5.2.2 Terrestrial Animals

Many studies have investigated the effect of salmon abundance in stream ecosystems on black and brown bear diet (Hilderbrand et al. 1999b, Weaver & Zammuto 2004, Helfield & Naiman 2006). Nitrogen stable isotope analysis from hair samples of grizzly bears in the Columbia River basin and from coastal brown bears in Alaska have documented, respectively, 33% to more than 90% of N in their diet from salmon-derived nutrients (Naiman et al. 2002). Grizzly bears living in areas with easy access to salmon streams also exhibit greater productivity and population density (Darimont et al. 2010).

Although bears are the prevailing animals associated with salmon consumption, many other terrestrial animals prey on spawning salmon and decaying carcasses. On the Olympic Peninsula of Washington, 14 mammals, primarily black bears, raccoons, and otters, were found consuming salmon carcasses. In the same study, eight species of birds, varying from winter wrens to bald eagles, were noted scavenging decaying salmon (Cedarholm et al. 1989). American dippers (*Cinclus mexicanus*) nesting along southeast Alaska streams have higher reproductive performance associated with their diet of salmonids (Obermeyer et al. 2006). It is feasible that all terrestrial animals feeding on salmon carcasses increase MDN enrichment around a spawning stream by physically moving salmon across the riparian and through excretion of waste products.

Figure 1.4. MDN transfer, assimilation, and trophic transport in a stream-riparian ecosystem is complex in nature and influential in several interacting ecosystems.

1.6 Research Objectives and Hypotheses

This study aims to describe nutrient delivery, seasonal storage and trophic transfer within a stream-riparian ecotone. Marine-derived nutrients transported by sockeye salmon during the 2011 salmon run will be analyzed to determine if these nutrients are being utilized by stream macroinvertebrates and riparian vegetation, and to determine if MDN are delivered by and stored in the hyporheic zone. Nutrients can be removed from the water column quickly from multiple trophic levels (Naiman et al. 2002), which is why several sources will be used to quantify nutrient storage. These observations will be made before and during the salmon spawn, during and after the salmon die-off, and the following spring. The Horsefly River spawning channel is a representative sample of other similar systems, particularly spawning channels in interior British Columbia.

1.6.1 Delivery and Storage of Ammonium in the Hyporheic Zone

The aim of the research described in Chapter 2 was to determine if ammonium (NH_4^+), presumably from spawning salmon, was being delivered to, transported through and/or stored within the hyporheic zone. MDN transport to the riparian zone through nutrient deposition by bears has been well documented (Hilderbrand et al. 1999, Helfeld & Naiman 2006), however, the delivery of salmon nutrients via the hyporheic zone and the potential for overwinter storage may also be a critical pathway for MDN to transfer to riparian vegetation (O'Keefe & Edwards 2002, Pinay et al. 2009). The following hypotheses were developed to evaluate the research aim described above.

Null Hypothesis I: NH_4^+ concentration of surface water will not be correlated with the number of spawning salmon in the HFC.

Null Hypothesis II: There will be no difference between NH_4^+ concentrations of surface and hyporheic water.

Null Hypothesis III: NH_4^+ concentration of hyporheic water will not be correlated with distance from the streambank.

Null Hypothesis IV: There will be no difference between the mean NH_4^+ concentration of surface and hyporheic water between fall and spring.

These hypotheses help to inform the following questions about the system:

Question One – What is the extent of the hyporheic zone at this site?

Question Two – Is NH_4^+ being retained in the hyporheic zone during the course of the salmon spawn?

Question Three - Is NH_4^+ stored in the hyporheic zone over the winter?

Question Four - Does NH_4^+ concentration change as hyporheic water moves further from the stream?

1.6.2 Storage and Trophic Transport of MDN in a the Stream-Riparian Ecosystem

The aim of the research presented in Chapter 3 was to investigate MDN assimilation, trophic transport, and storage in a stream-riparian food web by tracing $\delta^{13}C$ and $\delta^{15}N$ in stream macroinvertebrates and riparian vegetation and soil during the 2011 sockeye salmon spawn and subsequent spring. In British Columbia, salmon spawn occurs in the fall when many plants are senescing or becoming dormant. Despite an apparent contrast in run timing and plant growth, biological uptake of MDN can occur quickly and be stored within riparian soil and plants (Drake et al. 2006) and stream organisms (Bilby et al. 1996). There are still questions, however, especially in regard to the environmental factors that limit uptake and persistence of MDN in individual species and in the riparian forest as a whole (Drake et al. 2011, Devries 2012, Rinella et al. 2013).

For this study, macroinvertebrates were evaluated according to their functional feeding group (FFG) to determine if species type, abundance, and stable isotopic concentration changes during the MDN pulse and between seasons. Three riparian plant species with differing life strategies were also investigated to determine the pathway, uptake, and retention of MDN in the riparian zone adjacent to the salmon spawning channel. The following hypotheses were developed to evaluate the aim listed above:

Null Hypothesis V: There will be no difference between stable isotopic signatures ($\delta^{13}C$ and $\delta^{15}N$) of macroinvertebrate taxa throughout salmon spawn and between fall and spring.

Null Hypothesis VI: Macroinvertebrate $\delta^{15}N$ signatures will not be correlated with NH_4^+ concentration of surface and hyporheic water.

Null Hypothesis VII: There will be no difference between stable isotopic signatures ($\delta^{13}C$ and $\delta^{15}N$) of riparian vegetation between seasons.

Null Hypothesis VIII: Stable isotopic signatures ($\delta^{13}C$ and $\delta^{15}N$) of riparian vegetation and soil will not be correlated with distance from the streambank.

Null Hypothesis IX: Riparian vegetation $\delta^{15}N$ signatures will not be correlated with NH_4^+ concentration of riparian hyporheic water.

These hypotheses help supply information about the following research questions:

Question One – Is the MDN signal retained by macroinvertebrates and riparian vegetation?

Question Two – Do macroinvertebrate functional feeding groups show temporal differences to the MDN pulse?

Question Three – Does macroinvertebrate species type and abundance change throughout the salmon spawn and between fall and spring?

Question Four – Does rooting depth of vegetation have an effect on MDN concentration?

Chapter 2

Temporal and Spatial Aspects of Nitrogen Cycling in the Hyporheic Zone

2.1 Hyporheic Zone as Vector for Nutrient Transport

The upstream delivery of marine-derived nutrients (MDN) by salmon to their freshwater spawning grounds is evident within the water, organisms, and materials of the surrounding watershed (Allan & Castillo 2007). MDN signatures are found within terrestrial vegetation bordering salmon streams, as well as within nearly any animal that permanently or temporally occupies that area (Kline et al. 1990, Naiman et al. 2002). For example, MDN transport from the streambed to the riparian zone through MDN nutrient deposition by bears has been well documented (Hilderbrand et al. 1999, Helfield & Naiman 2006). The transfer of nutrients through the hyporheic zone has also been investigated as a critical pathway to promote this nutrient exchange (O'Keefe & Edwards 2002, Pinay et al. 2009). The hyporheic zone acts as a transient storage area by transporting and transforming essential nutrients. The rooting zone of riparian vegetation also can extend into hyporheic flow paths (Helfield & Naiman 2006) potentially explaining the MDN signal observed in this vegetation (Bilby et al. 1996, Ben-David et al. 1998, Reimchen et al. 2002, Bilby et al. 2003).

2.1.1 Defining the Hyporheic Zone

Water in rivers and streams passes between the channel bed surface and subsurface along discrete flow paths. Groundwater and surface water exchange is regulated in an interstitial mixing area known as the hyporheic zone. Rapid and frequent hydrologic exchange occurs allowing for the renewal of nutrients and oxygen (Hancock 2002). Often the extent is only a few meters beneath the streambed, but the hyporheic zone can be considerably large, extending several kilometers inland (Stanford & Ward 1988). The water table, or the boundary of saturated/unsaturated soils, is not easily delineated because it is spatially and temporally dynamic (Triska et al. 1989, Vervier et al. 1992, Boulton et al. 1998). The hyporheic zone is now thought to be an essential component of stream function, with the definition of streams expanding to not just what is above the streambed, but integrally related to what is below (Fisher 1997, Malard et al. 2002).

The hyporheic zone can be delineated using three primary components – biological, geochemical, and hydrologic.

2.1.1.1 Biological

The biological method for defining the hyporheic zone is the presence of organisms living in this region of mixed waters. Observations of stream organisms deep within the streambed gravels were used for preliminary studies in identifying the hyporheic zone (Coleman & Hynes 1970). The idea of organisms living below the streambed was criticized heavily at first, but continued discoveries of macroinvertebrates beneath the streambed confirmed its existence (Hynes 1974). When Stanford & Ward (1988) identified riverine invertebrates 2-km from the main channel of the Flathead River in Montana, the extent of the hyporheic zone expanded to include subsurface areas adjacent to rivers and across floodplains. The main objectives of hyporheic biological methods are to understand species type and habitat and to identify if species are either epigean (periodic users of the hyporheic) or hypogean (permanent residents of the hyporheic). When defining the hyporheic zone in this way, it is important to recognize that taxa composition and abundance can change between seasons, meaning that one-time sampling does not necessarily produce a representative sample (Hancock & Boulton 2009).

2.1.1.2 Geochemical

Geochemical methods define the hyporheic zone as a volume of sediment that contains a certain proportion of surface water. This volume of water varies between stream reaches and microhabitats, and is defined by Triska et al. (1989) as being anywhere from greater than 10% to less than 98% channel water. For example, the hyporheic zone may be quite expansive in unconfined floodplains or may be small due to confining hillslopes around a river. Additionally, stream microhabitats can control hyporheic exchange, with some areas, such as riffles with high stream discharge, reducing the proportion of surface water infiltrating the hyporheic zone (Tonina & Buffington 2009). Many different geochemical methods can be used to identify hyporheic flow paths including the use of natural tracers (i.e. temperature, pH, and electrical conductivity) or injection of conservative tracers (e.g. NaCl or dye) (Malard et al. 2002).

2.1.1.3 Hydrologic

Hydrologic methods define the hyporheic zone by using groundwater flow models to describe the volume and magnitude of water moving through a medium. Physical parameters of groundwater level and soil characteristics are needed to describe hyporheic flow (McDonald & Harbaugh 1988, Wondzell 2006). Water levels are measured at a point-in-time, either occasionally using manual methods of measurement or continuously using a water level data logger, and typically describe hyporheic flow over a period of time (Dearden & Palumbo-Roe 2010).

For this study, geochemical methods were used to find hyporheic locations influenced by surface water, and hydrologic variables of groundwater level, hydraulic conductivity, and soil porosity were used to define hyporheic flow.

2.1.2 Physical Characteristics of Hyporheic Flow

2.1.2.1. Piezometers and Wells

Piezometers and monitoring wells are used to access water beneath the surface. They can be comprised of a variety of materials (e.g. plastic tubing, PVC, aluminum) and span a range of lengths and widths, depending on the application. Wells are perforated along the length of the pipe to capture the height of the water table. Piezometers are perforated only around the lower section of the pipe, which measures pore water pressure at the intake location. For this study, piezometers were used and functioned as perforated pipes fixed vertically in the ground to passively intercept groundwater (Sprecher 2000). Their function is to facilitate groundwater level measurements, water sampling, and tracer introductions (Tonina & Buffington 2009).

2.1.2.2 Hydraulic Head and Hydraulic Conductivity

Groundwater is always moving from high to low potential energy; therefore the distribution of hydraulic head throughout an area indicates where groundwater will flow. The hydraulic head at a particular location represents the total potential energy of subsurface water and is measured in units of length above a fixed datum (Jones & Holmes 1996). The relative rate of movement is described by the vertical hydraulic gradient (VHG, $m \cdot m^{-1}$) and horizontal hydraulic gradient (HHG, $m \cdot m^{-1}$) between two piezometers. Both measurements can be calculated with the following equation:

$$\text{VHG or HHG} = \Delta h / \Delta l \qquad \text{Eqn (2.1)}$$

where:
Δh = difference in height between two hydraulic heads; and,
Δl = flow path length between two piezometers (vertical distance for VHG and horizontal distance for HHG).

Hydraulic conductivity (*K*) describes the ease with which groundwater moves through pore spaces in the alluvium or soil, and is a measurement of distance traveled over time (with units $L \cdot T^{-1}$). The obtained values depend on sediment porosity and connectivity of these pore spaces, which are functions of the type and condition of sediments (Tonina & Buffington 2009). The simplest method to obtain hydraulic conductivity values is through a bail or slug test (Freeze & Cherry 1979). Water is either introduced to or removed from a piezometer and the water level is then monitored until it returns to quasi-equilibrium conditions. Many methods have been developed to calculate hydraulic conductivity for specific subsurface conditions; this study will use the Hvorslev Method which calculates the time it takes for the water level to rise to 37% of the initial maximum (Hvorslev 1951, Campbell et al. 1990). The equation is as follows:

$$K = r^2 \mathrm{Ln}(L/R) \ / \ [2LT_0] \qquad \text{Eqn (2.2)}$$

where:
K = hydraulic conductivity;
r = radius of well casing;
R = radius of well screen;
L = length of well screen; and,
T_0 = time require for the water level to rise to 37% of the initial change.

Within the channel, VHG measurements are used to determine if water is moving into the ground from the river (downwelling or groundwater recharge) or from the ground to the surface water (upwelling or groundwater discharge). These conditions may change temporally, such as during high water events where groundwater is recharged due to the downwelling of excess surface water (Mouw et al. 2009) or conditions may remain steady where upwelling water is constantly delivering limiting nutrients to the surface water and producing localized zones of productivity (Valett et al. 1994). By observing hyporheic and surface water data, areas of groundwater discharge and recharge can be identified. These "charged" zones exhibit particularly active hyporheic exchange that may alter water chemistry and redirect groundwater flow patterns (Janzen 2008).

Typically, a patchy matrix of bidirectional water exchange exists at the reach and segment scale and creates a variety of habitats for a diverse assemblage of organisms. Site specific characteristics, such as soil type, water inflow, and intruding vegetation, contribute to this variable matrix (Dent et al. 2001, Poole et al. 2008, Tonina & Buffington 2009). Localized zones around tree roots, for example, can cause disparate conditions that depend on specific spatial and temporal variables. In some locations, tree roots may cause upwelling by drawing water and nutrients from the hyporheic zone (Constantz et al. 1994). However, exactly the opposite process commonly occurs when plant roots transpire water directly from groundwater, resulting in a drawdown and localized depression of the water table (Winter 2000). Changes in the local water table could be a likely cause of this disparity.

2.1.2.3 Residence Time

The hyporheic zone acts as a storage site, which traps water and solutes and then releases them over time. Water may exchange between the stream and hyporheic zone in short increments many times along its flow path, transferring heat, oxygen, solutes, and biota. Increased water residence time occurs when stream water enters deeper into the alluvium or flows across riparian or floodplain soils before entering the stream again (Harvey & Wagner 2000, Boano et al. 2006, Hester & Gooseff 2010). Hyporheic exchange can regulate the biogeochemical transformations or release of essential nutrients to a stream, such as inorganic nitrogen. Where residence time is short, nitrogen is exported downstream at a greater rate. Increased residence time facilitates internal denitrification which removes inorganic nitrogen from the system (Triska et al. 1989, Wondzell & Swanson 1996b).

Zarnetske et al. (2011) performed a hyporheic residence time experiment to investigate the spatial and temporal physiochemical conditions that control nutrient transformation in a drainage dominated by agriculture and forestry. They discovered that short water residence times (<6.9 hours) were associated with biogeochemical processes of ammonification, nitrification, and rapid utilization of DO and DOC. Residence times beyond 6.9 hours resulted in denitrification and net removal of nitrate from the stream. Although every hyporheic location studied will yield different outcomes, shorter residence times prompting aerobic metabolic process and longer residence times facilitating anaerobic metabolic processes is a commonly agreed upon response (Triska et al. 1993, Peyrard et al. 2011, Binley et al. 2013).

2.1.3. Modeling Hyporheic Flow

The primary methods used to trace water flow paths in the hyporheic zone include water temperature differences, tracer tests, and groundwater level loggers. These methods can be used alone or in combination and may be incorporated into predictive hydrologic models. The USGS program MODPATH is commonly used to simulate particle tracking in groundwater transport and to calculate water residence time (Pollock 1994). The mapping and spatial analysis software ArcGIS has groundwater tools for advection-dispersion modeling of groundwater flow, particle tracking, and chemical dispersion (ESRI 2013). For this study, ArcGIS groundwater software was used to model hyporheic flow.

A geographic information system (GIS) groundwater model was used in this study because of its distinct spatial and visual advantages. By utilizing technology in ArcGIS, data management and tools for modeling are integrated into a single predictive working environment, from which results of a groundwater flow model can be seen directly in a presentable output. The ArcGIS groundwater analysis tool Darcy Flow models two-dimensional flow by utilizing variables of groundwater head elevation, porosity, saturated thickness, and transmissivity (defined partially by hydraulic conductivity). Local flow velocity and direction are defined for each cell in the grid, and Darcy's Law is applied to the cells adjacent to the center cell in order to generate a flow field (Tauxe 1994). Water that flows through the ground is governed by Darcy's Law, which states that flux rates are a direct function of hydraulic conductivity and hydraulic gradient (Freeze & Cherry 1979). A precursor to Darcy Flow is the Flow Direction function, which confines flow direction towards one of eight adjacent cells (Jenson & Domingue 1988).

2.1.4 Hypotheses

The aim of this study is to determine if the hyporheic zone acts as a delivery corridor and storage zone for ammonium (NH_4^+) that is delivered to the stream by spawning salmon. The concentration of NH_4^+ between stream and hyporheic water samples will be evaluated, as well as the spatial variables that control nutrient exchange. Over-winter storage of NH_4^+ will be assessed by sampling throughout the 2011 sockeye salmon spawn and the subsequent spring. The following hypotheses will be tested:

Null Hypothesis I: NH_4^+ concentration of surface water will not be correlated with the number of spawning salmon in the HFC.

Null Hypothesis II: There will be no difference between NH_4^+ concentrations of surface and hyporheic water.

Null Hypothesis III: NH_4^+ concentration of hyporheic water will not be correlated with distance from the streambank.

Null Hypothesis IV: There will be no difference between the mean NH_4^+ concentration of surface and hyporheic water between fall and spring.

2.2 Methods

2.2.1 Study Site

Fieldwork was performed in Horsefly, BC (52° 19′N, 121° 1′W) located in the Cariboo region of British Columbia (Figure 2.1). The 131-km long Horsefly River is the largest tributary of Quesnel Lake in the Fraser Basin of the Quesnel watershed. This river provides important spawning grounds for sockeye salmon (*Oncorhynchus nerka*) and, to a lesser degree, Chinook salmon (*O. tshawytscha*). Historically, the Horsefly River has supported large sockeye salmon populations; however, recent salmon spawning cycles have produced lower than average numbers (Albers 2010).

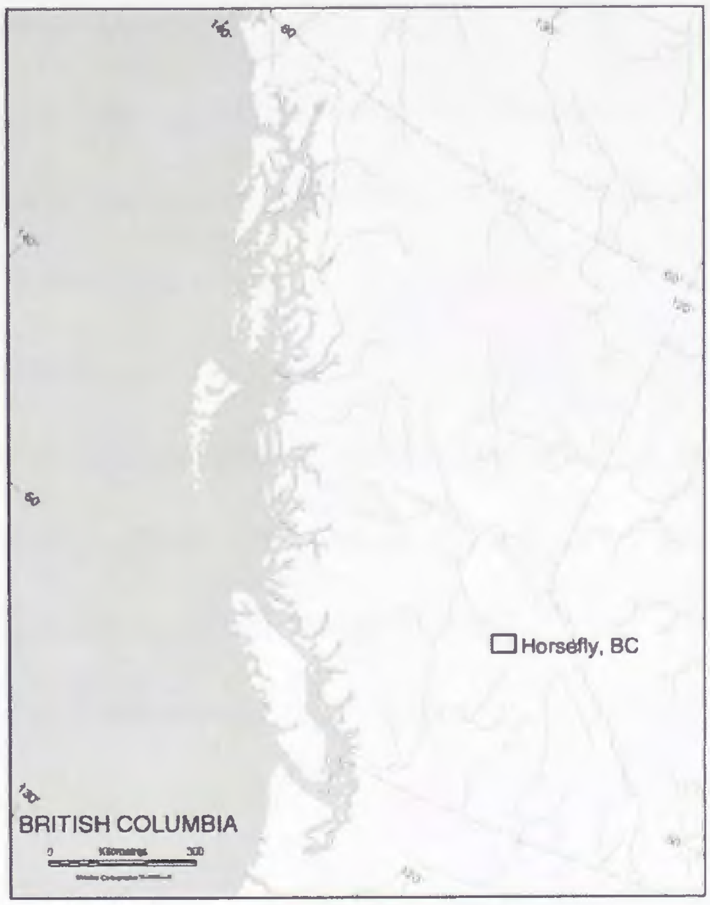


Figure 2.1. Map of British Columbia displaying the town of Horsefly, the location where this study was conducted.

2.2.1.1 Horsefly River Spawning Channel

The Horsefly River spawning channel (HFC) is an artificial channel managed by the Department of Fisheries and Oceans Canada (DFO) that was designed and constructed as part of a salmon enhancement program to improve salmon production and facilitate fisheries management by creating an optimal spawning environment for salmon (Figure 2.2). The channel is approximately 1.6 km in length and 10 m wide with a designed slope of 1%. Maximum salmon capacity in the channel is 23,000 adults (Holmes 2008). The approximately 1-m deep gravel layer lining the channel surface is relatively uniform in particle size and shape, and was designed for ideal spawning conditions. Additionally, the alluvium and soil surrounding this gravel layer may have an irregular development due to channel engineering. Water inflow is regulated by a large pump that siphons water from a settling pond, which is connected to the Horsefly River at the upstream end of the channel. At the start of the salmon run, a fence is installed in the Horsefly River directly upstream of the channel mouth to restrict upstream migration and allow a selected number of salmon to enter the HFC. The confined salmon then spawn in the channel. There are two salmon gates within the channel that restrict movement but also become temporary dams once the salmon spawn-out (Figure 2.1). Carcasses become lodged against the gates, increasing the water level and creating a reservoir that is released mid-day when the dead salmon are sampled, marked, and released into the main channel.

Figure 2.2. Aerial view of the Horsefly River spawning channel in Horsefly, BC. The Horsefly River is depicted with flow direction arrows.

In the summer and fall of 2011, in addition to regular DFO enhancement activities, a 900-m^2 area of the channel and adjacent riparian zone was converted into an experimental site. The average wetted width of the experimental channel in this reach is 12.3 m, with bankfull width being only 0.1 to 0.2 m wider due to the incised channel. The maximum water height at the channel's riparian edge is 1.4 m. The average of three measurements were taken prior to sampling events to define channel width and height using methods outlined by Leopold (1994). Vegetation composition resembles other riparian zones along the Horsefly River, consisting primarily of deciduous trees with a diameter at breast height (DBH) of less than 0.3 m. Predominant tree species include willows (*Salix sp.*) and Black cottonwood (*Populus trichocarpa*), and dominant shrub species are Red-osier dogwood (*Cornus sericea*) and Twin-berry (*Lonicera involucrata*). Other prevalent vegetation includes Mountain alder (*Alnus tenuifolia*), Saskatoons (*Amelanchier alnifolia*), Cow parsnip (*Heracleum maximum*), and Prickly rose (*Rosa acicularis*). The riparian zone upstream of the study site is composed mainly of smaller shrubs and grasses, with a dense riparian forest forming at the beginning of the meander bend (Figure 2.3). The reason for this difference in forest maturity is unknown, but is likely due to tree clearing during the construction of the channel.

Figure 2.3. The study site in June 2011, showing meander bend in spawning channel and adjacent riparian zone. Piezometers F and G are located upstream (right side in this photo) of the riparian forest and are located in the un-forested section.

Before the introduction of salmon, the top 30 cm of the channel bed gravels were mechanically cleaned to resuspend stored fine sediment and, subsequently, increase the flow of dissolved oxygen (DO) within the streambed. This was undertaken by the DFO and was accomplished using a rake mounted on a bulldozer, followed by a managed increase in water flow to flush out suspended solids. A temporary sandbag dam was constructed about 200 m upstream from the experimental site where mechanical cleaning ceased and the turbid water was pumped from the channel into an isolated settling pond adjacent to the channel. This was done in order to minimize the impact of fine sediment resuspension in the Horsefly River preceding the salmon run. Due to the location of this downstream settling pond, the final 250 m of the channel is not cleaned. The experimental site is located within this section where the streambed has not been disturbed (Figure 2.2).

Although the HFC was created to optimize salmon spawning habitat, the artificial construction and environmental manipulation of the channel results in underlying differences when compared to natural systems on the Horsefly River and the broader Pacific West Coast. Notably, the water in the channel is pumped from a settling pond. Although water in the settling pond originates in the Horsefly River, chemical and biological attributes of this water will be altered from being held in an environment that is more stagnant than the free-flowing river. Some of these changes may include reduced DO, increased dissolved nutrient concentration, and an altered aquatic plant and animal community. Channel bed cleaning prior to the introduction of salmon is an obvious, unnatural disturbance, which likely results in a mass export of macroinvertebrates, biofilms, and dissolved nutrients. While the cleaning promotes the flow of DO to benefit salmon eggs, it may unintentionally alter the ecology of the spawning habitat in undesirable ways (e.g. decrease food reserves for salmon fry). Also, the Horsefly River is characterized by annual spring flooding events that create large floodplains throughout the region. The HFC is protected from floods, which does create a safe haven for eggs and juvenile salmon (Holmes 2008). However, it results in a geomorphology that is different from the sandy substrate and wide, meandering gravel bars created by the floods.

2.2.2 Study Design

The experimental site was chosen at a meander bend 50 m from the mouth of the channel (Figure 2.4). Twenty-five piezometers were installed in a grid, comprising five instream piezometers and 20 piezometers located on the riparian zone adjacent to the channel. Each piezometer was spaced 1 to 2 m apart, with variability due to physical barriers, such as trees and boulders. Piezometers were constructed of 1-in (2.54-cm) inner diameter electrical metallic tubing (EMT) and were 10 ft (3.048 m) in length. Forty-four, ¼-inch diameter holes were drilled near the bottom of the pipe to allow for passive hyporheic water inflow. A pointed, steel tip was welded to the bottom in order to drive them into the ground (Figure 2.5). Riparian piezometers were all installed to approximately the same depth, 2.4 m below the ground surface. Instream piezometers were installed approximately 1 to 1.5 m below the streambed.

Figure 2.4. Map of the experimental study site on the Horsefly River spawning channel. Contours display 0.1-m changes in land elevation (NAD83).

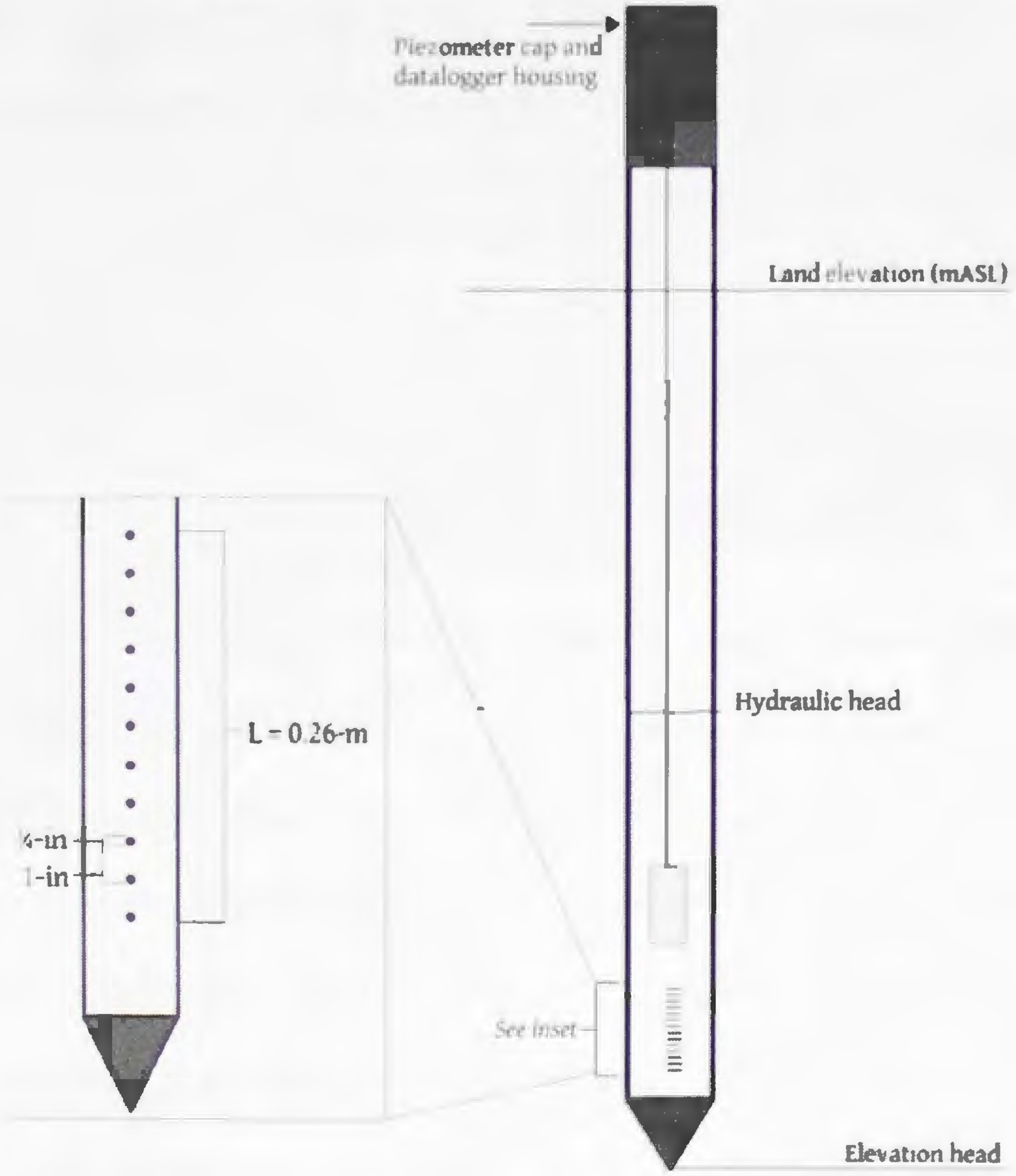


Figure 2.5. Diagram of piezometer marking levels of elevation used in the study. Measurements of piezometer holes are displayed in the inset diagram. The variable length of well screen (L) is described in the Hvorslov equation.

2.2.2.1 Rhodamine Tracer Test

In order to select a subset of hyporheic sampling locations for this study, a tracer experiment using a slug injection of a fluorometric dye tracer, Rhodamine-WT, was executed. Subsequent samples were collected to track the breakthrough curves of fluorescence concentration versus time throughout the study site. This fluorescent dye was chosen for its excellent detectability, use in low concentrations, and low potential for sorption (Harvey & Wagner 2000). Using methods adapted from Kilpatrick & Cobb (1985), the volume of Rhodamine-WT required for the tracer injection was determined by the following equation:

$$V_s = (3.79\times10^{-5}) * (QL/v) * C_p \qquad \text{Eqn (2.3)}$$

where:
C_p = peak concentration at the sampling site, in micrograms per liter;
L = length of the measurement reach, in meters;
Q = stream discharge, in cubic meters per second;
V_s = volume of Rhodamine-WT 20-percent dye, in milliliters; and,
v = mean stream velocity, in meters per second.

The peak concentration (C_p) at the sampling site was 1 μg/L, following Kilpatrick & Cobb (1985). A location 120-m upstream from the study site was chosen as the injection site (Figure 2.2). The length of the reach (L) was a uniform glide, with no obvious pools or back channel storage areas, to allow for uniform dispersion across the channel (Turner Designs 1995). To achieve the desired concentration of Rhodamine-WT (V_s), three serial dilutions were performed using stream water to obtain a 100 μg/L working solution.

On July 15, 2011, water samples were extracted from 24 piezometers to record background fluorescence prior to the tracer test. (One dry piezometer located in the northwest corner of the site was eliminated from the test.) The following day, 100 L of Rhodamine-WT working solution, comprised of five 20-L buckets, was released as a bulk slug into the thalweg at the injection site. To enable rapid water collection post-release and capture a representation of the entire study area, a subset of nine piezometers was selected from every 3-m^2 area of the study site (piezometers A, C, E, G, J, O, Y, V, R). Water sampling commenced once the dye plume reached the top of the study site and continued every half-hour for two hours, at which point we exhausted all the sterilized sample containers. All 24 piezometers were again sampled that evening and the next morning.

Water samples were analyzed for fluorescence (μg/dl) within 24 hours of collection using a desktop fluorometer (Turner Quantech Digital Filter Fluorometer Model FM109515, Barnstead | Thermolyne, Iowa, USA) equipped with a narrow band filter of 540 nm and a sharp-cut filter of 585 nm.

This dye tracer test was performed under the premise that it would be possible to sample all 25 of the piezometers at a frequency and length of time that allowed for concurrent analysis and detection of breakthrough curves throughout the study site. However, manual sampling with two people did not allow sufficient intervals or quantity of data to determine the precise path of Rhodamine-WT tracer. Consequently, this test only partially helped to define which piezometers to use for the study. Individual trends in fluorescence and location were examined to determine the subset of 10 study piezometers. One qualifier, as determined by the tracer test, was that the location must have displayed an increase in fluorescence, followed by a decrease (piezometers G, J, O, V). The second qualifier, location, was chosen to select piezometers that were positioned along a hypothetical path flowing across the meander bend (piezometers F, G, I, J, K, O), beneath the stream (piezometers C, D), or at an increment extending into the riparian forest adjacent from the top of the meander bend (piezometers G, I, V, W). Overall, dye attenuation was highest at instream piezometers and riparian sites located near the upstream bank.

2.2.2.2 Sampling Scheme

Sampling occurred during the 2011 sockeye salmon run and the subsequent spring of 2012. Seven sampling periods were timed to characterize varying delivery and biochemical activity of MDN. The fall period (August 23 to October 6) consisted of one pre-salmon spawn sampling week, three weeks during active salmon spawning, and a final post-spawn week once all salmon had spawned-out. There were two sampling periods in the spring, one before and one after spring break-up (Figure 2.6). Each sampling week consisted of 3 consecutive days in which water samples were collected.

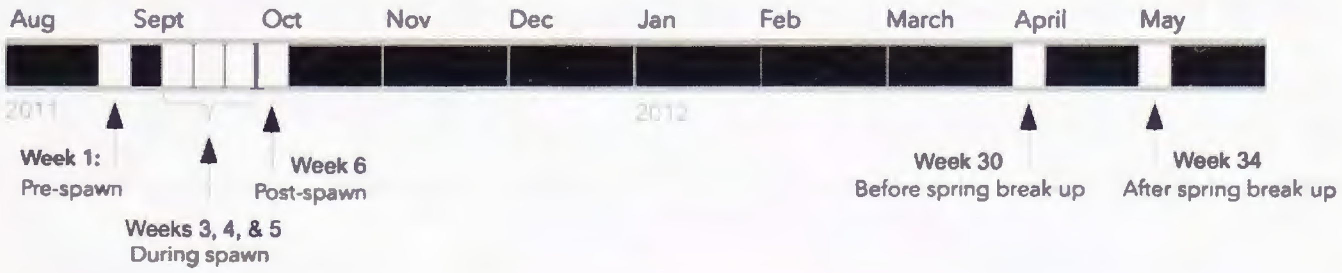


Figure 2.6. Sampling periods timed to characterize the temporal nutrient delivery and retention during the 2011 sockeye salmon run and the subsequent spring.

2.2.3 Site Characteristics and Aquifer Variables

Daily precipitation and air temperature measurements were recorded at an Environment Canada hydrometeorological station located next to Gruhs Lake, Horsefly, BC (52° 21′ 56″ N, 121° 21′ 19″ W, el. 777 m). Horsefly River hydrometric data was obtained from two Environment Canada discharge measurement sites on the Horsefly River: Horsefly River above McKinley Creek (52° 17′ 23″ N, 121° 3′ 37″ W) and Horsefly River above Quesnel Lake (52° 26′ 46″ N, 121° 25′ 7″ W). The McKinley Creek station is located about 30 km upstream from the study site and the Quesnel Lake station is approximately 20 km downstream.

A land survey was conducted to map sampling locations, piezometers and topography of the study site using an electronic theodolite survey station (Leica Flexline TS06 Total Station, Heerbrugg, Switzerland). Over 100 survey points were loaded into the geospatial processing program ArcMap (ArcGIS, Esri, California) to build a contour map of the study site (Figure 2.4).

A subset of ten piezometers, chosen to represent hyporheic flow paths, contained capacitance water level probes (Odyssey Capacitance Water Level Logger, Christchurch, NZ) that recorded water level in the piezometers at 15-minute intervals between August 22 - October 8, 2011 and at 5-minute intervals between March 30 – May 7, 2012. Surface water staff gauge readings were recorded at mid-day during each sampling day.

Two pressure transducers (HOBO Water Level Logger U20-001-04, Massachusetts, USA) were installed at the study site from March 30 – May 7, 2012 to measure surface water level during spring melt. The logger recorded absolute pressure (kPa) and temperature (°C) every 15 minutes. HOBOware Pro software was then used to convert pressure readings into surface water level readings by means of barometric pressure compensation.

Hydraulic conductivity (*K*) was measured on April 1, 2012 during baseflow conditions using a falling-head slug test (Bouwer 1989, Wondzell & Swanson 1996a). For this test, the time interval on all capacitance water level loggers was increased to 1-minute. Then, a known amount of water was withdrawn from each piezometer. After 3 hours, the recorded data for the slug test were downloaded and then the instruments were reset to 5-minute intervals to continue ongoing groundwater level data collection. Hydraulic conductivity was calculated according to the Hvorslev equation (Equation 2.2).

Porosity refers to the fraction of the soil's volume that is composed of pore space which can be filled by water and/or air (Flint & Flint 2002). In sandy substrates, porosity has an inferred proportional relationship with hydraulic conductivity. However, this relationship does not exist for all substrate types. For example, clay typically has very low hydraulic conductivity, yet high porosity due to its structure. Soil pits were dug to extract samples from hyporheic-influenced soils and porosity measurements of three samples, located ~777.8-778.0 mASL, were performed in the laboratory. To calculate porosity, samples were first oven dried at 75°C for at least 12-h. Then water was added to a known volume of soil (V_{total}) in a beaker until the water covered the top surface of the soil. The volume of water added, which can also be referred to as pore space (V_{void}), was determined by subtracting the water left in the beaker from the original total volume. The unit-less measurement of porosity is the ratio of volume of pore space in soils to the volume of material, with more porous substances closer to 1.0 or 100% saturation:

$$\text{Porosity} = V_{void}/V_{total} \qquad \text{Eqn (2.4)}$$

2.2.4 Groundwater Modeling

The water level inside the piezometers, presented as a height in meters above sea level (mASL), indicates the hydraulic head of sediments surrounding the piezometer opening. However, for hyporheic flow analysis, this study treats treats these measurements as water table elevations and are used to interpret the lateral flow direction, while assuming that vertical flow is negligible. Since there were no wells installed on the study site to directly measure the water table and determine the VHG of riparian piezometers, negligible VHG remains an underlying assumption of hyporheic flow analysis.

Water levels inside the piezometers exhibited natural temporal fluctuations, with some locations experiencing as much as a 1-m rise between late fall and spring break-up. Changes in channel surface water level occurred daily during peak spawn as a result of the build up and release of a "salmon dam" caused by carcasses becoming lodged against gates separating sections of the spawning channel (Figure 2.2). Hyporheic water levels changed as surface water fluctuated, which indicates that this riparian zone is hydrologically connected to the surface water. During the spring monitoring period, natural rises in water level were observed during snowmelt and two large precipitation events that initiated spring break-up in 2012. To better visualize the fluctuation in water level across the study site, ArcGIS 10.1 technology was used to create rasters that display hydraulic head at one point-in-time. These rasters were then compiled into separate movies during three peak water events in the spring of 2012: 1) A snowmelt event of 6-days between April 7 and April 13, in which the snowpack decreased from 23-cm to 0-cm; 2) A two-day period between April 26 and 28 after 27.4-mm of precipitation, initiating the start of spring freshet; 3) A 24-hour period on May 1 where surface water rose considerably after precipitation and in conjunction with the start of the spring break-up cycle.

Hyporheic flow path maps were generated to compare water movement at a point-in-time at midnight during each month of the study. The day of the month was chosen to reflect a steady state condition by eliminating outside influences of water level change, i.e. salmon dam or precipitation. Two different techniques were used to analyze and validate results of flow direction and magnitude in ArcGIS, one with and the other without the Darcy Flow function. However, due to limited sampling of aquifer properties, the Darcy Flow model did not produce realistic results. Consequently, this study will only describe the hyporheic flow analysis that did not use the Darcy Flow function.

To generate the flow path maps (Figure 2.7), a hydraulic head raster was created using thin plate spline interpolation. The Spline tool in ArcGIS uses an algorithm that minimizes surface curvature and generates a smooth surface that passes through the input points (DeMarsily 1986). From this hydraulic head raster, two new rasters were created to represent direction and magnitude, or relative speed, of flow. The Flow Direction function, located in the Spatial Analysis hydrology toolbox, was executed to determine direction by locating the steepest descent in hydraulic head from each cell (1.0-m^2 area) of the raster (Jenson & Domingue 1988). By using the percent rise in slope from the hydraulic head raster, a proxy for magnitude of flow was determined. Points from these new rasters were symbolized as arrows that depict the flow direction and magnitude of flow.

Utilizing ArcGIS technology to generate computed flow patterns can be a useful tool when modeling spatial environments; however, there are several sources of potential error in the models generated by this study. Particularly, the low number of sample data points (n=10 or 0.01 points per m^2) may result in errors during the interpolation routine. Although interpolation is a valid method for predicting values of an area when data points are limited (DeMarsily 1986), error is reduced with greater sampling density (Kennedy et al. 2008). Some uncertainty also exists in hydraulic head values because, in low permeable substrates, piezometers may produce a lagged response (Hvorslev 1951). Also, this study's assumption that

VHG of riparian piezometers is negligible may not be accurate. If strong vertical hydraulic gradients do exist in riparian piezometers, then the models will produce an unrealistic representation of groundwater level and flow (Jones & Holmes 1996).

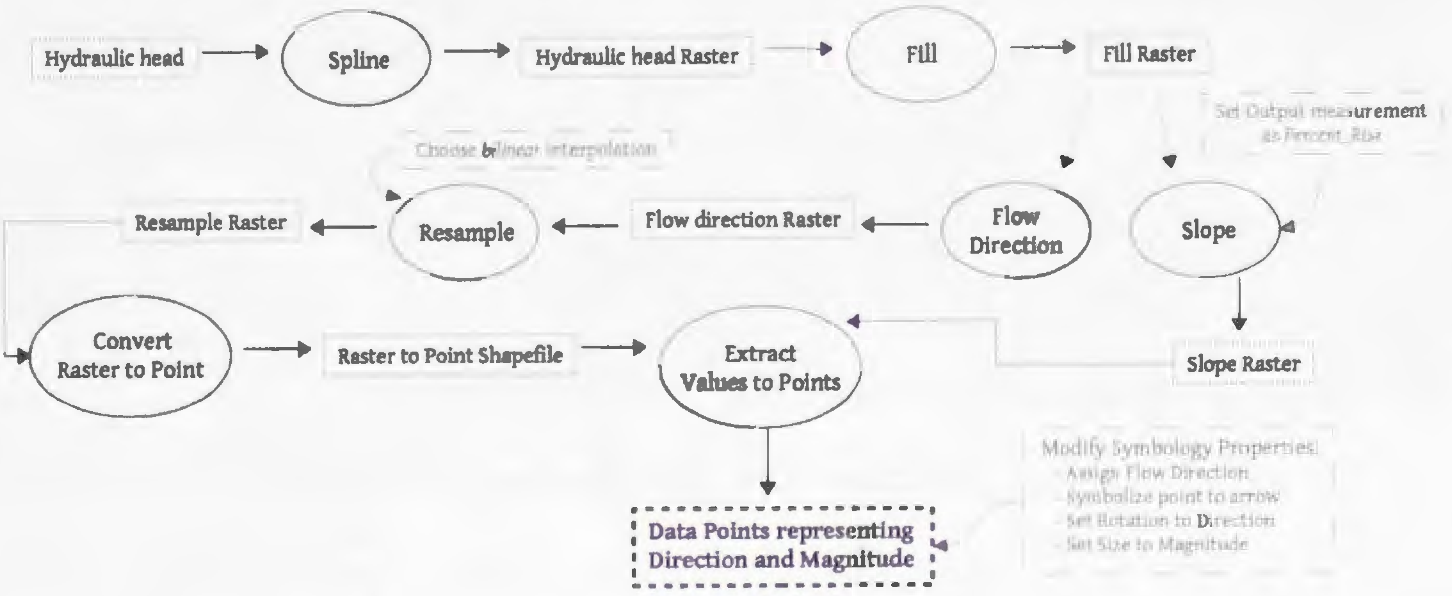


Figure 2.7. Workflow chart showing steps for hyporheic water flow analysis using Spatial Analysis tools in ArcGIS.

2.2.5 Water Chemistry

2.2.5.1 Field Sampling

Hyporheic water samples were collected from the chosen ten piezometers around mid-day for three consecutive days during each week of the sampling period. Water was extracted using a hand-operated vacuum pump with an attached food-grade silicon hose and collected into separate 125-ml Erlenmeyer flasks. Surface water samples were taken 5 m upstream, 5 m downstream, and at the midpoint of the study site using a 60-ml syringe with Luer-Lok tip. Samples were then filtered with 0.2-μm syringe filters. Approximately 12 to 15 ml of filtered water was collected in sterile plastic centrifuge tubes and placed immediately on ice. The samples were transferred to a freezer within 4 hours of collection and kept frozen until laboratory analysis. All water extraction materials that made contact with water were acid-washed in a 10% hydrochloric acid bath for a 2 hour minimum soak time and triple-rinsed with deionized water (DI).

2.2.5.2 Laboratory Analysis

At the University of Northern British Columbia's Central Equipment Laboratory, water samples were analyzed for ammonium (NH_4^+) concentration using an AutoAnalyzer (Bran+Luebbe AutoAnalyzer 3, Norderstedt, Germany). The method used is a modification of the Berthelot reaction, using salicylate reagents and a measurement of 660 nm (Rowland 1983). Before analysis of the samples, a calibration was performed using standards of 0, 10, 25, 100, and 1000 μg/L N. Two quality control samples of 0 and 100 μg/L N were inserted after every tenth sample. About 10% of the samples were re-analyzed the following day for quality assurance. Samples that exceeded 1000 μg/L N were diluted and re-analyzed to achieve results within the calibrated range.

2.2.6 Statistical Analysis

All statistical computations and graphs were conducted using the program R (R Core Team 2013), as well as the R packages "AICcmodavg", "car", "ggplot2", "gridExtra", "lattice", "mgcv", "plyr", and "scales". For each sampling week, the three observations from each site were averaged to obtain mean NH_4^+ concentration. To confirm statistical independence, temporal autocorrelation tests were conducted using R's built-in autocorrelation function [acf()] to determine if NH_4^+ displayed "persistence" between sampling weeks (Chatfield 2004). Ammonium concentration of three locational groupings (surface water, instream piezometers (C and D), and riparian piezometers) were averaged as a whole and between seasons, square-root transformed for normality, and regressed through linear modeling to determine statistical differences between locations and seasons. Pearson's product-moment correlations were also performed to test the relationship between the arrival of salmon and presence of NH_4^+. For all analyses, the confidence level for statistical significance was set to $p \leq 0.05$. Additionally, highly significant results were identified if $p \leq 0.001$.

Several site specific variables were chosen to be analyzed as predictors of NH_4^+ concentration. Spatial variables included *distance from streambank, distance from top of meander bend, withdrawal depth,* and *hydraulic conductivity.* The temporal variables used were *precipitation* and *staff gauge reading.* Before statistical analysis, all variables were standardized to eliminate discrepancies between units of measurement and enable direct interpretation (Schielzeth 2010). The following calculation was used to standardize variables:

$$\text{standardized parameter} = (x_i - \bar{x}) \,/\, \alpha \qquad \text{Eqn (2.5)}$$

where:
x_i = observation *i*;
$\bar{x}$ = mean of all observations; and,
α = standard deviation of all observations.

Hyporheic sites were separated into two groups for statistical analysis of NH_4^+: 1) all hyporheic samples (n=10) and 2) riparian hyporheic samples (n=8). Correlation between predictor variables, known as multicollinearity, was evaluated with variance inflation factors (VIF) using the vif() function in R. Lower VIF values indicate less correlation, thus increasing the strength of multiple regression analysis because the variables are more independent (O'Brien 2007). Linear and multiple regressions tested the relationships between mean NH_4^+ concentration and one or two predictor variables. The temporal variables *precipitation* and *staff gauge reading* were tested separately from spatial variables. Multiple regression analysis included the interaction term and was performed using variables with low or moderate correlation ($1 < VIF < 5$). Mean NH_4^+ concentrations were log-transformed for normality. An information theoretic approach, specifically Akaike's 'An Information Criterion (AIC)', was used to identify the most parsimonious models. AIC provides a means for selecting the model that is as simple as possible, but no simpler (Burnham & Anderson 2002). Second-order AIC (AIC_c), which is adjusted for small sample size, was used and has the following equation:

$$AIC_c = (2k * (n/(n-k-1)) - 2\ln(L) \qquad \text{Eqn (2.6)}$$

where:
k = number of predictors;
n = sample size, and;
L = maximized value of the likelihood function.

For the spatial analysis, two linear regressions and three multiple regressions with the lowest AIC values were retained as a candidate set to further rank these models according to Akaike weights (w_i). Akaike weights represent relative likelihoods, or probabilities, for each model in the candidate set (Mazerolle 2015). For the temporal analysis, the best linear and multiple regression were retained as a candidate set. Lastly, the resulting effect size from regression equations was analyzed to interpret the meaning of the best models.

In ArcGIS, exploratory statistics were analyzed for normality and volume balance residuals were analyzed for steady and constant field flow during spatial interpolation.

2.3 Results

2.3.1 Precipitation and Discharge

Throughout the fall sampling period, the Horsefly region experienced relatively little precipitation, with an average of 0.5 mm/day and 2 out of 3 rain-free days. Compared to long-term climate normals recorded by Environment Canada, the total rainfall was low during this season. Through the month of September, 15.9 mm of rain was recorded, compared to the long-term September average of 43.9 mm of rain. Horsefly River discharge, calculated from the McKinley Creek and Quesnel Lake stations, remained relatively constant, but decreased slightly as the fall progressed (Figure 2.8). The spawning channel is located approximately halfway between these two discharge stations. Although discharge at the spawning channel was not measured in the fall, it was likely very similar to measurements obtained during a study conducted in 2010 because water inflow at the channel is regulated by a siphon. Using Albers (2010)'s calculations, maximum (~3 m^3/s) and minimum (~1.5 m^3/s) discharge was much lower at the channel during salmon spawn than at the Horsefly River stations (McKinley Creek max: ~12 m^3/s, min: ~6 m^3/s; Quesnel Lake max: ~19 m^3/s , min: ~14 m^3/s).

During the spring, water levels in the Horsefly River and spawning channel were more variable due to snowmelt, precipitation events, and the onset of spring break-up (Figure 2.9). The largest precipitation event of the spring season occurred on April 26, 2012 with 27.4 mm of precipitation falling in a 24-hour period. A peak in discharge at McKinley Creek station was observed the next day. This rise in discharge and continuing rain carried downstream to the Quesnel Station when a peak in discharge was observed on May 3, 2012. As compared to Intensity-Duration-Frequency (IDF) curves provided by Environment Canada, no rare or large-scale rainfall events occurred during this study.

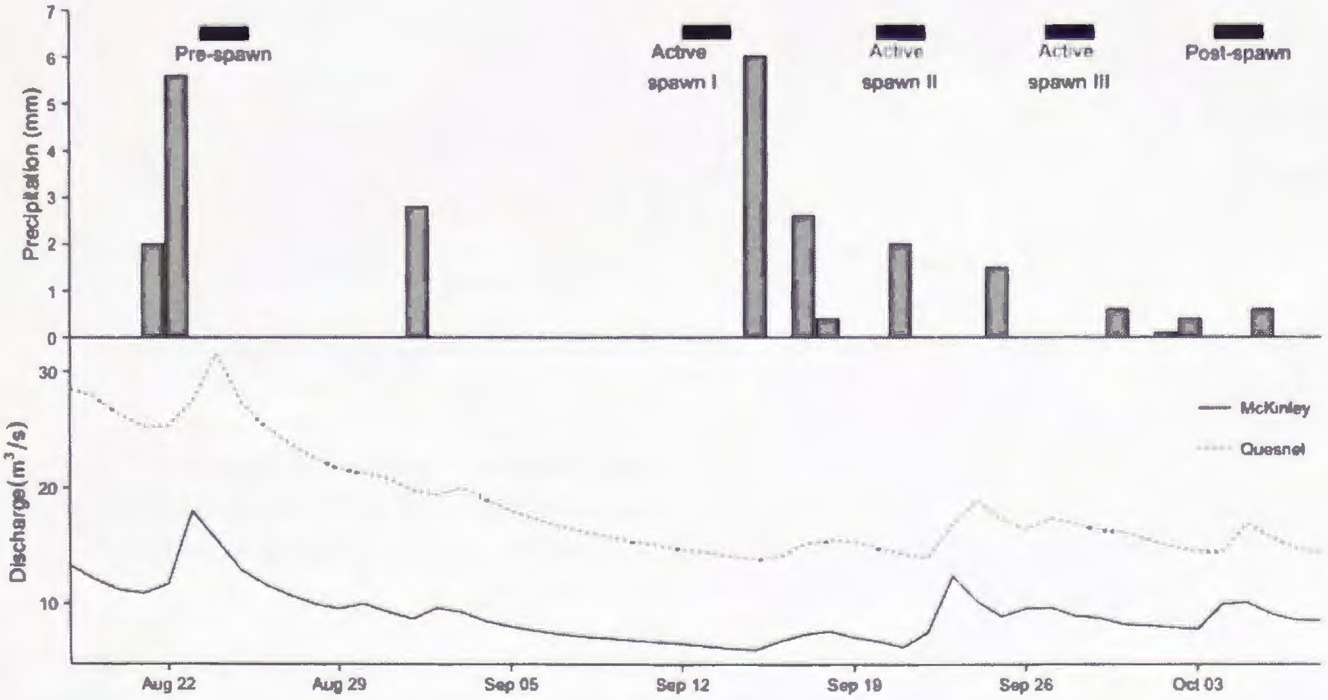


Figure 2.8. Characterization of stream conditions at the Horsefly River spawning channel in the fall of 2011. The top graph displays precipitation and the bottom graph displays Horsefly River discharge at two measuring sites.

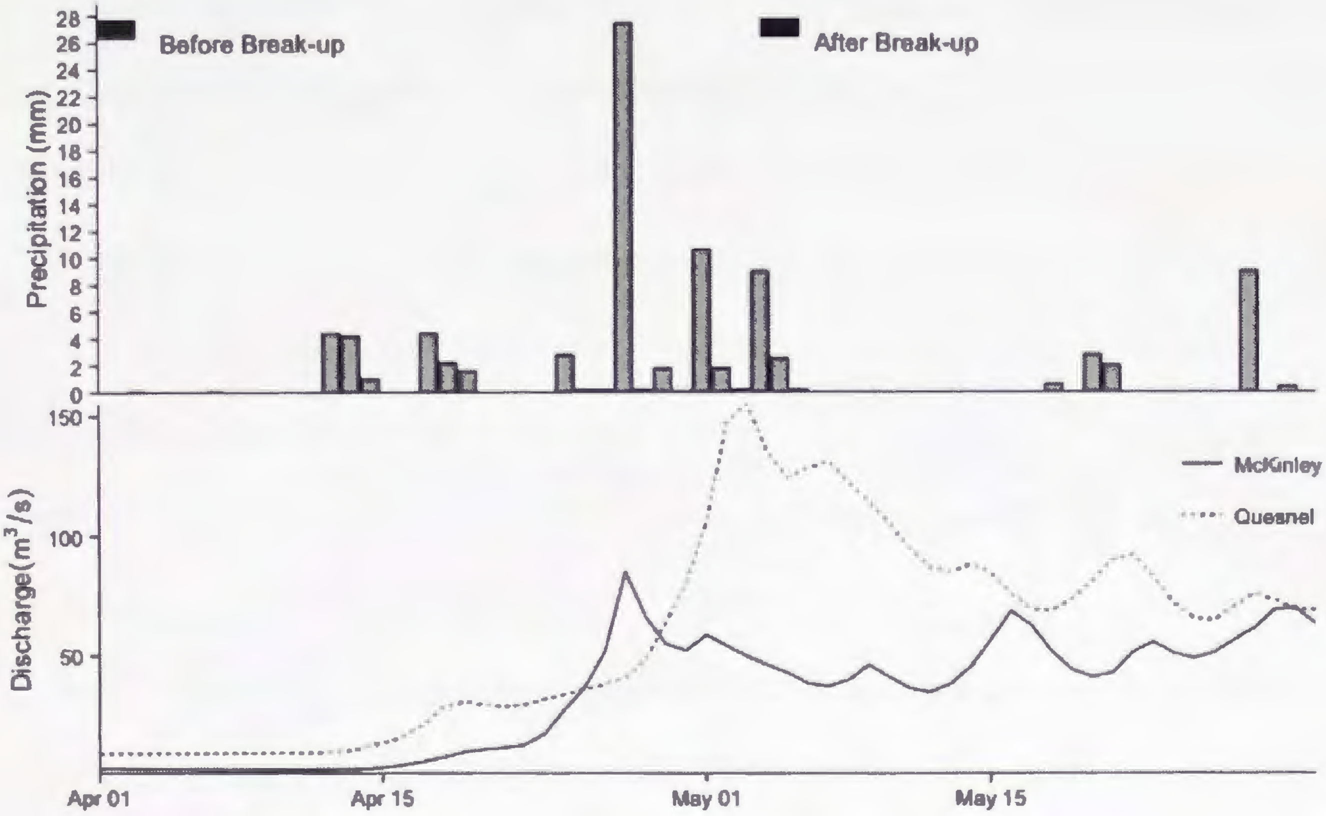


Figure 2.9. Characterization of stream conditions at the Horsefly River spawning channel in the spring of 2012. Precipitation is displayed on the top graph and the bottom graph displays discharge measurements from two sites on the Horsefly River.

2.3.2 Aquifer Variables

The substrate and soil material in which hyporheic water flowed was mostly comprised of "silt, sandy silts, clayey sands, and till" throughout the study site, as defined by common hydraulic conductivity values listed in Freeze & Cherry (1979) (Table 2.1). Piezometer D, located deepest in the substratum and beneath the spawning channel, displayed the highest conductivity and consisted of silty and fine sands.

Porosity values from hyporheic-influenced soil from the C horizon ranged from 0.30 total porosity at soil pit 1 to 0.62 and 0.65 at soil pits 2 and 3, respectively (Figure 2.10). These samples were all extracted within a depth of 20-cm from each other, or between ~777.8 and 778.0 mASL. Soil pits 2 and 3 displayed a greater occurrence of clay mottling, especially soil pit 3 which had a C horizon characterized by gley, or waterlogged, soils. During sampling, hyporheic water began to infiltrate soil pits 2 and 3, whereas the water table was not hit while digging soil pit 1. Overall, soil pits 2 and 3 were considerably sandier than the coarse material at soil pit 1. These porosity measurements and observations support representative porosity values of geologic material from Freeze & Cherry (1979), which states that the 0.30 value at soil pit 1 is comparable to course sand or gravel, and the porosity values at soil pit 2 and 3 are indicative of clay.

VHG at the instream piezometers, C and D, indicated downwelling flow throughout all sampling periods. There were three days in the fall (of a total of fifteen observations) at site D where water was slightly upwelling, but still nearly level with stream surface water (Figure 2.11a). Piezometer C consistently displayed a stronger downwelling gradient. In the spring, two sharp decreases in VHG mirror surface water level changes during peak flow events (see Figure 2.11b) indicating that groundwater recharge is greater during precipitation and break-up events.

Table 2.1. Hydraulic conductivity (*K*) measurements from each study piezometer on April 1, 2012. The soil material type, which is associated with standard *K* values, is adapted from Freeze & Cherry (1979).

Location	*K* (cm/s)	Category *K*	Material
C	0.000062	10 E -05	Silt, sandy silts, clayey sands, till
D	0.000831	10 E -04	Silty sands, fine sands
F	0.000111	10 E -04	Silt, sandy silts, clayey sands, till
G	0.000021	10 E -05	Silt, sandy silts, clayey sands, till
I	0.000066	10 E -05	Silt, sandy silts, clayey sands, till
J	0.000036	10 E -05	Silt, sandy silts, clayey sands, till
K	0.000026	10 E -05	Silt, sandy silts, clayey sands, till
O	0.000166	10 E -04	Silt, sandy silts, clayey sands, till
V	0.000083	10 E -05	Silt, sandy silts, clayey sands, till
W	0.000064	10 E -05	Silt, sandy silts, clayey sands, till

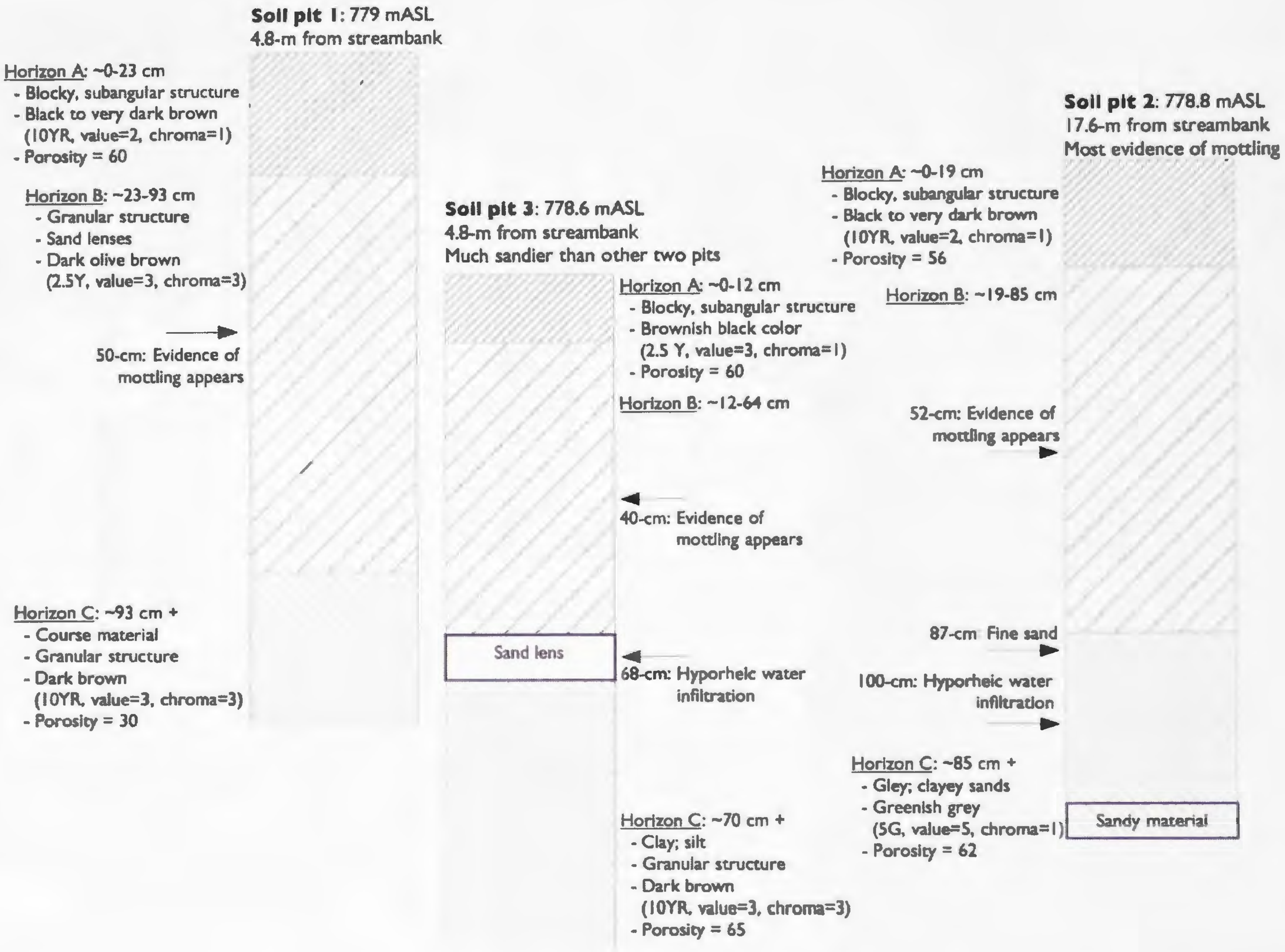


Figure 2.10. Description of three soil profiles from the riparian zone. The diagram depicts relative heights (mASL) and distances from the streambank for each soil pit, i.e. soil pit 1 and 3 were located closest to the streambank and soil pit 1 was highest in elevation. Soil structure and color are described from the Munsell Soil Color Book.

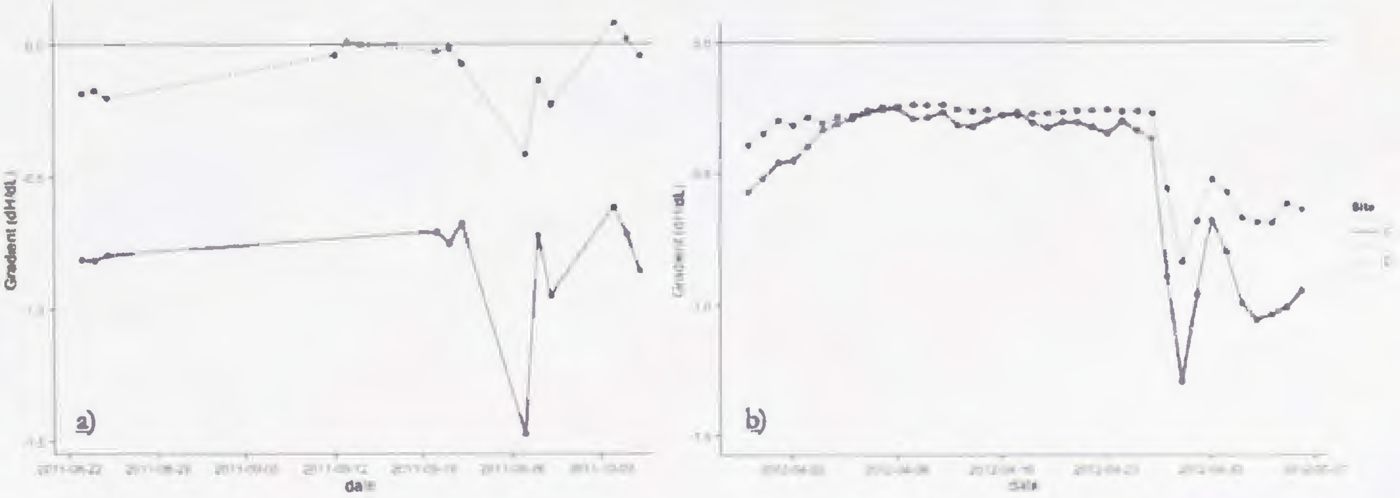


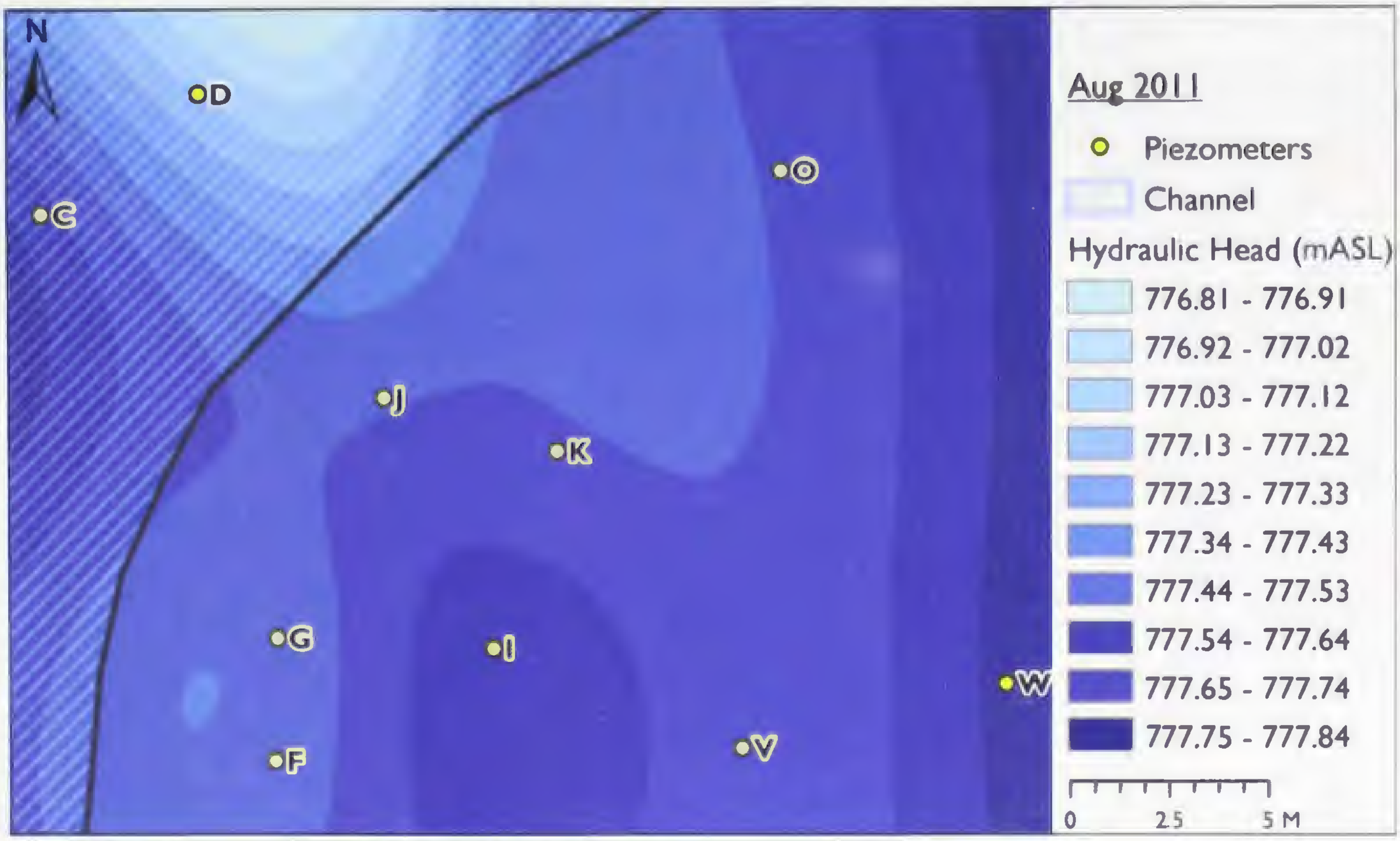
Figure 2.11. Vertical hydraulic gradient in the fall (a) and spring (b) at instream piezometers C and D. Fall data (a) were only collected on days for which data are displayed.

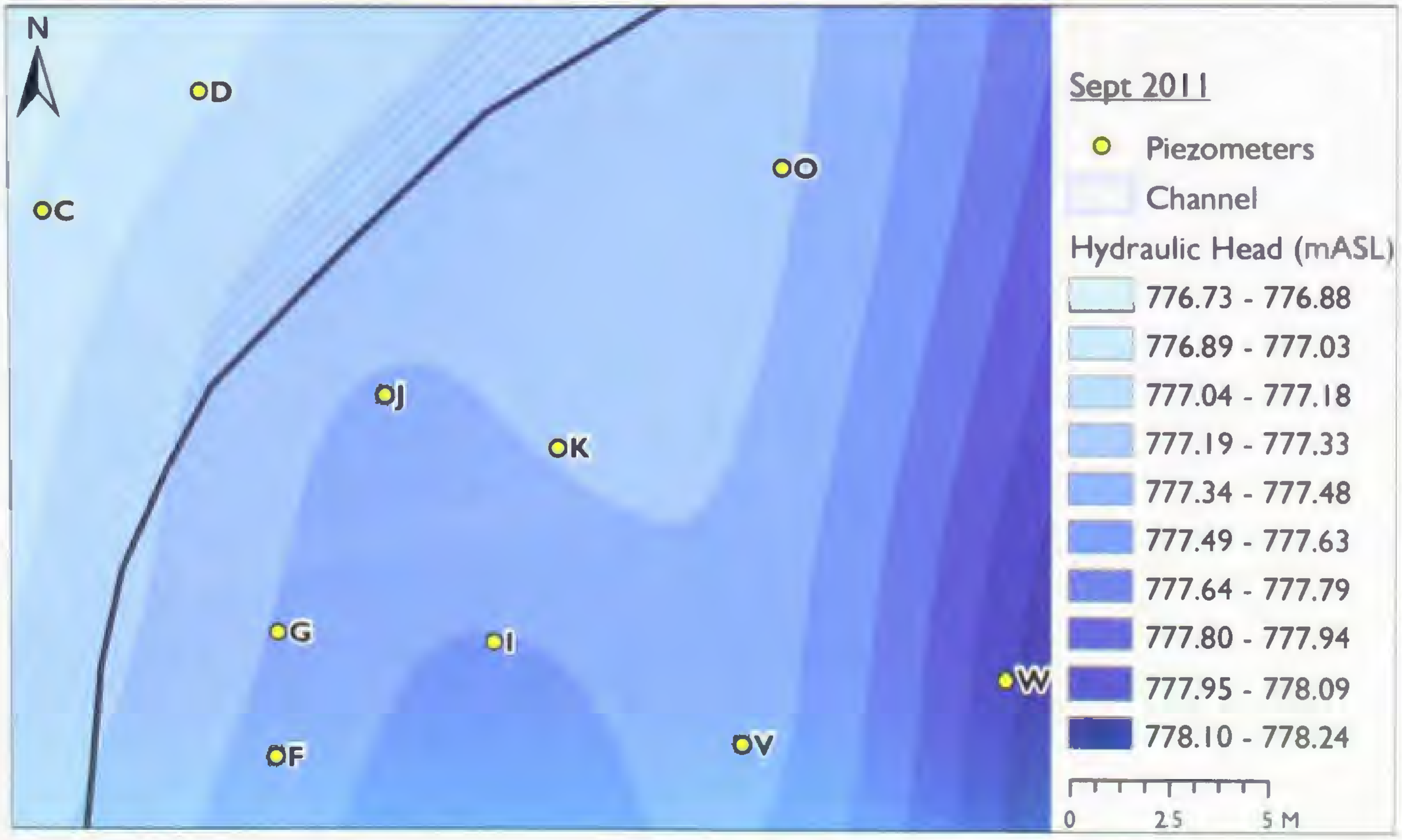
2.3.3 Geographic Information Systems (GIS)

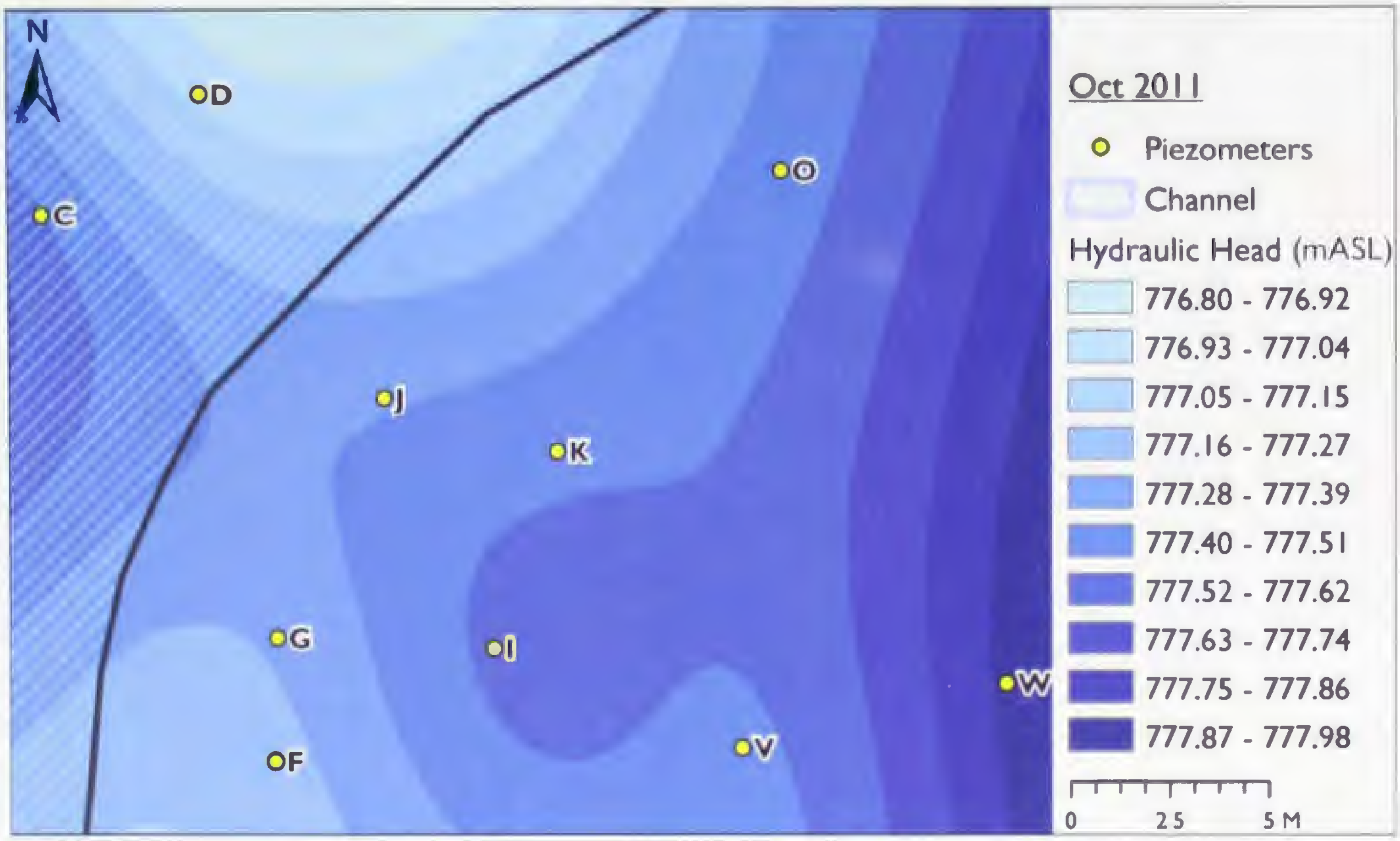
In order to visualize the spatial and temporal fluctuations of hyporheic water at the study site, hydraulic head and flow direction maps were created in ArcGIS 10.1 to observe reoccurring and unique patterns during each month included in the study.

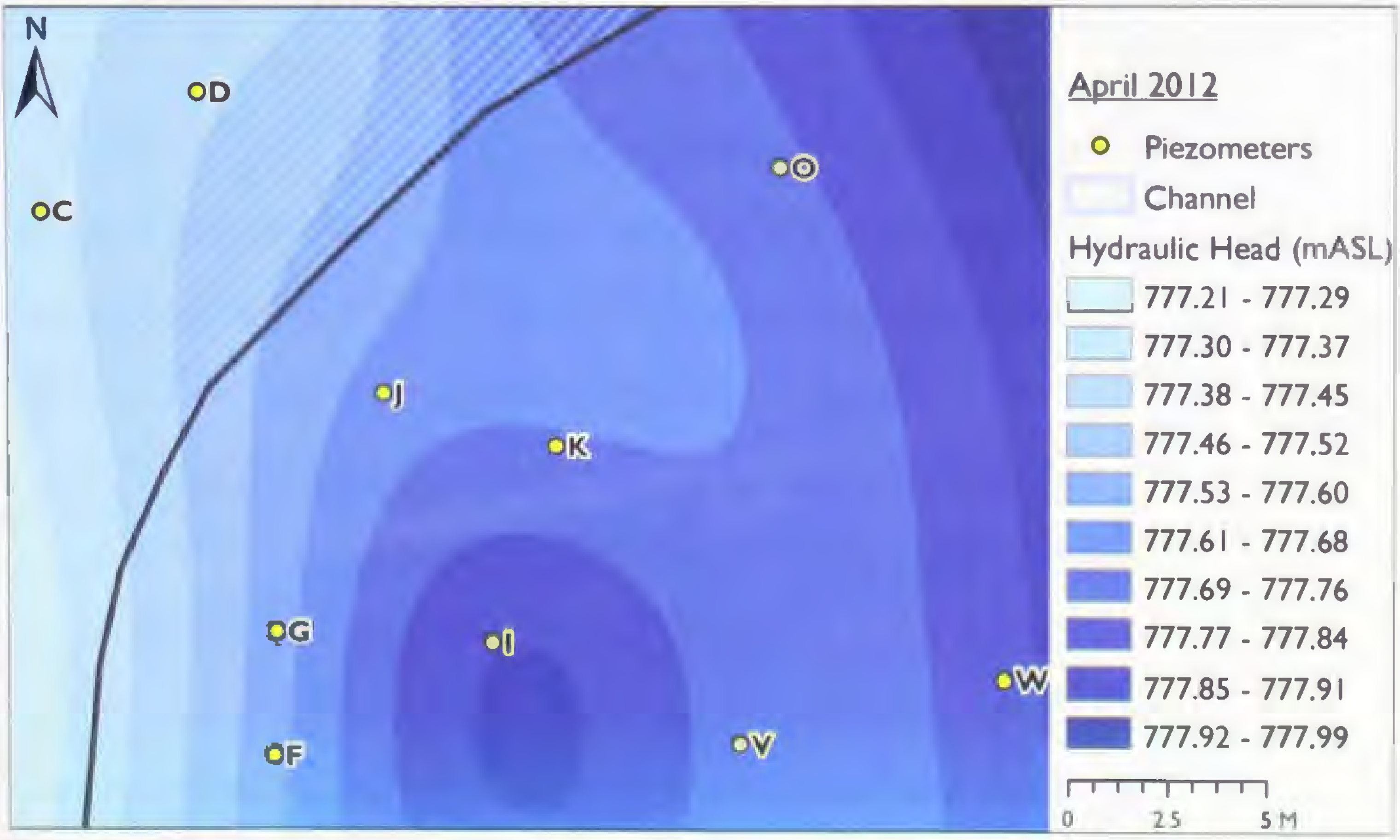
2.3.3.1 Hydraulic Head Contour Maps

Figure 2.12 shows variation in hydraulic head during each study month. Hydraulic head is consistently higher further away from the stream, and generally depicts a gradual, one-directional flow towards the surface stream. Note that each map has a unique scale, as hydraulic head changed as much as 1-m between seasons at some locations.


N
D
C
O
J
K
G
I
W
F
V
Aug 2011
Piezometers
Channel
Hydraulic Head (mASL)
776.81 - 776.91
776.92 - 777.02
777.03 - 777.12
777.13 - 777.22
777.23 - 777.33
777.34 - 777.43
777.44 - 777.53
777.54 - 777.64
777.65 - 777.74
777.75 - 777.84
0
2.5
5 M


N
D
C
O
J
K
G
I
W
F
V
Sept 2011
Piezometers
Channel
Hydraulic Head (mASL)
776.73 - 776.88
776.89 - 777.03
777.04 - 777.18
777.19 - 777.33
777.34 - 777.48
777.49 - 777.63
777.64 - 777.79
777.80 - 777.94
777.95 - 778.09
778.10 - 778.24
0
2.5
5 M


N
D
C
O
J
K
G
I
W
F
V
Oct 2011
Piezometers
Channel
Hydraulic Head (mASL)
776.80 - 776.92
776.93 - 777.04
777.05 - 777.15
777.16 - 777.27
777.28 - 777.39
777.40 - 777.51
777.52 - 777.62
777.63 - 777.74
777.75 - 777.86
777.87 - 777.98
0
2.5
5 M


N
D
C
O
J
K
G
I
W
F
V
April 2012
Piezometers
Channel
Hydraulic Head (mASL)
777.21 - 777.29
777.30 - 777.37
777.38 - 777.45
777.46 - 777.52
777.53 - 777.60
777.61 - 777.68
777.69 - 777.76
777.77 - 777.84
777.85 - 777.91
777.92 - 777.99
0
2.5
5 M

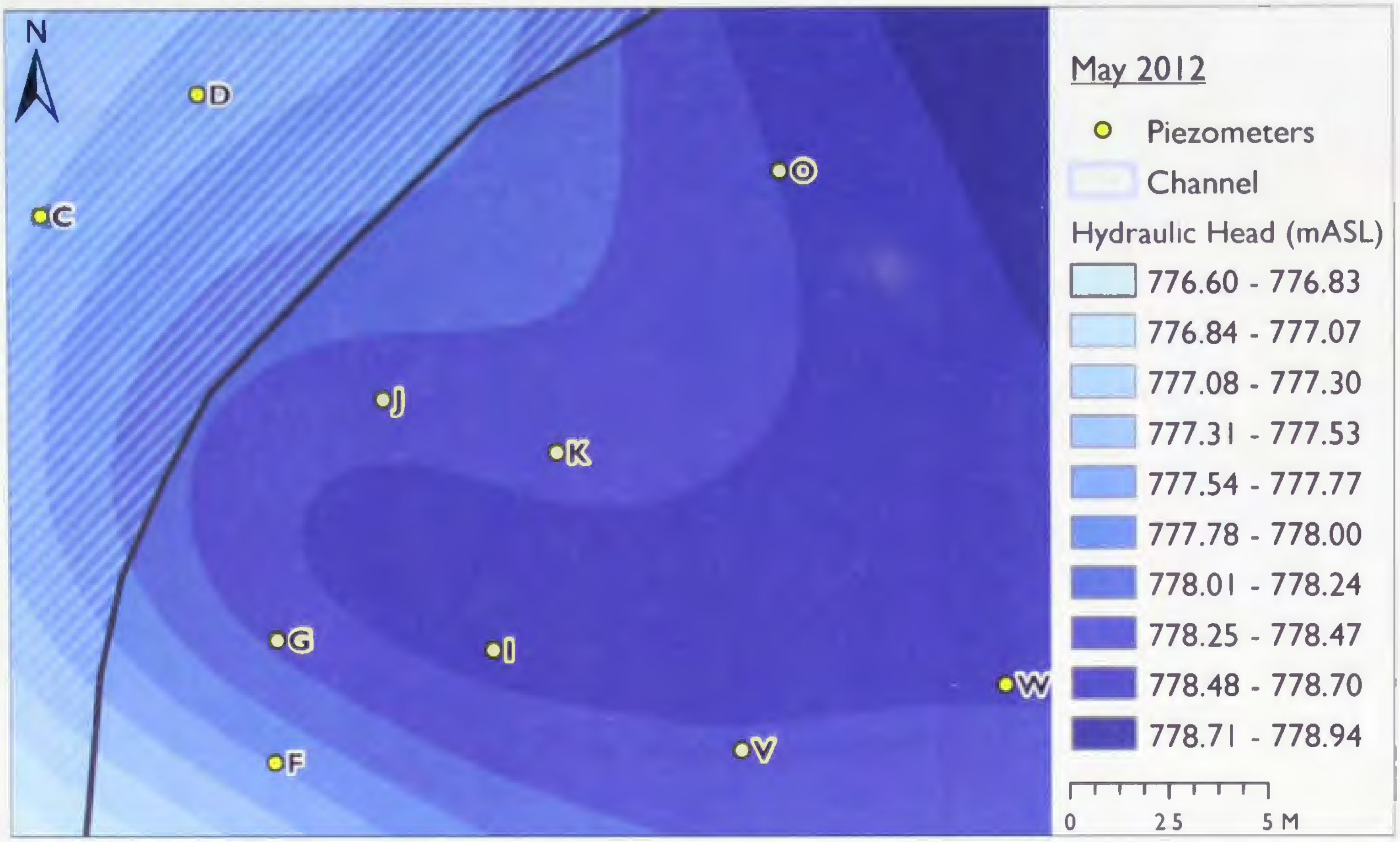


Figure 2.12. Hydraulic head (mASL) at the Horsefly River spawning channel during each month of the study. Note that each map has a unique scale.

Movies were created to illustrate patterns in hydraulic head fluctuations during three peak flow events in the spring of 2012 (Figure 2.13). These movies can be viewed online at YouTube by typing in the links below or searching with the keywords "horsefly river spawning channel":

Snowmelt, April 8-13 – http://youtu.be/zeOw7XueWVc
Spring break-up, April 26-28 – http://youtu.be/D0bVT9CvGZk
Spring break-up, May 1 - http://youtu.be/zP1SkxSKNRM

Each movie represents a different time interval and magnitude of change, but the overall pattern of water movement remains the same. Water level is highest and responds the quickest at piezometers W & I during all events. Piezometer K consistently shows a depression in the water table and has a slower response time. All locations were responsive to changes in surface water level indicating that the hyporheic zone is well connected to the channel and there is a high rate of groundwater recharge in the spring.

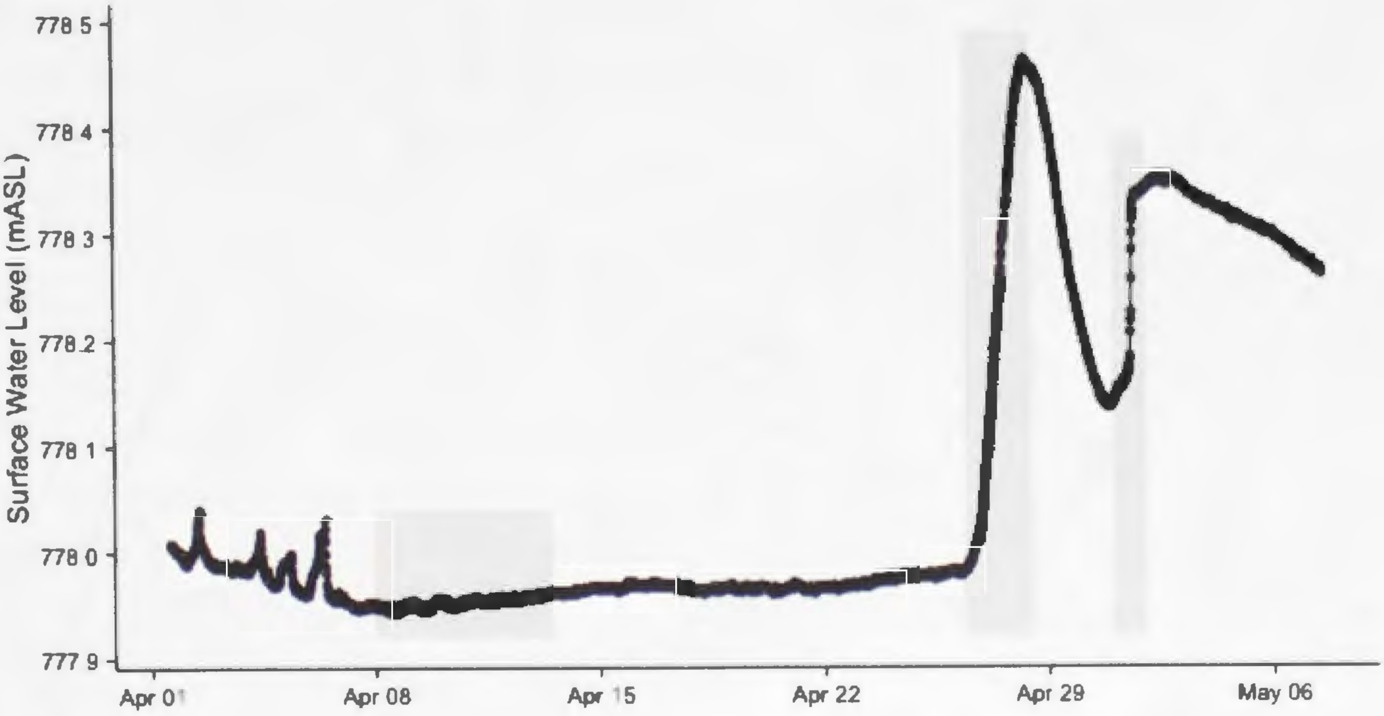
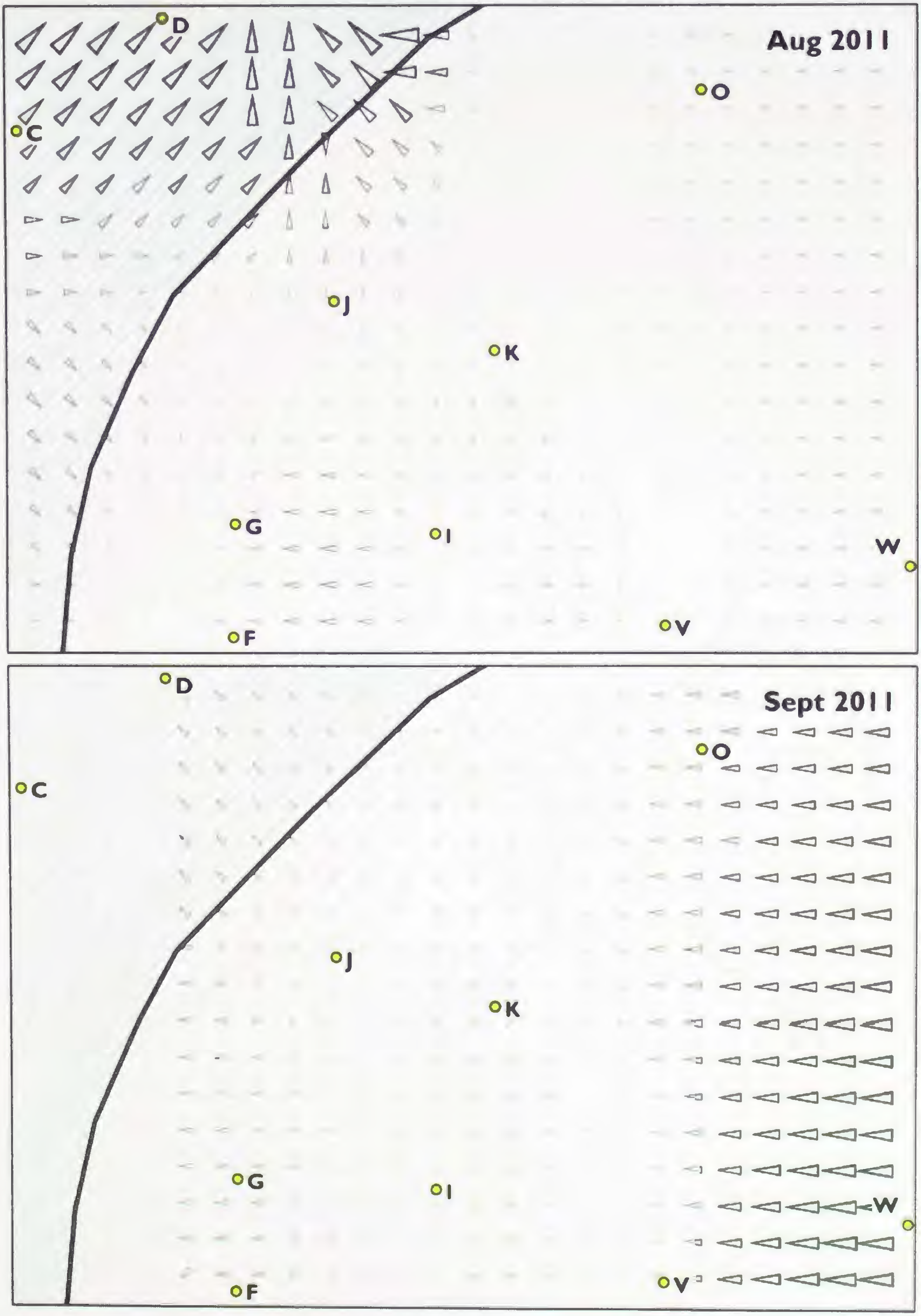
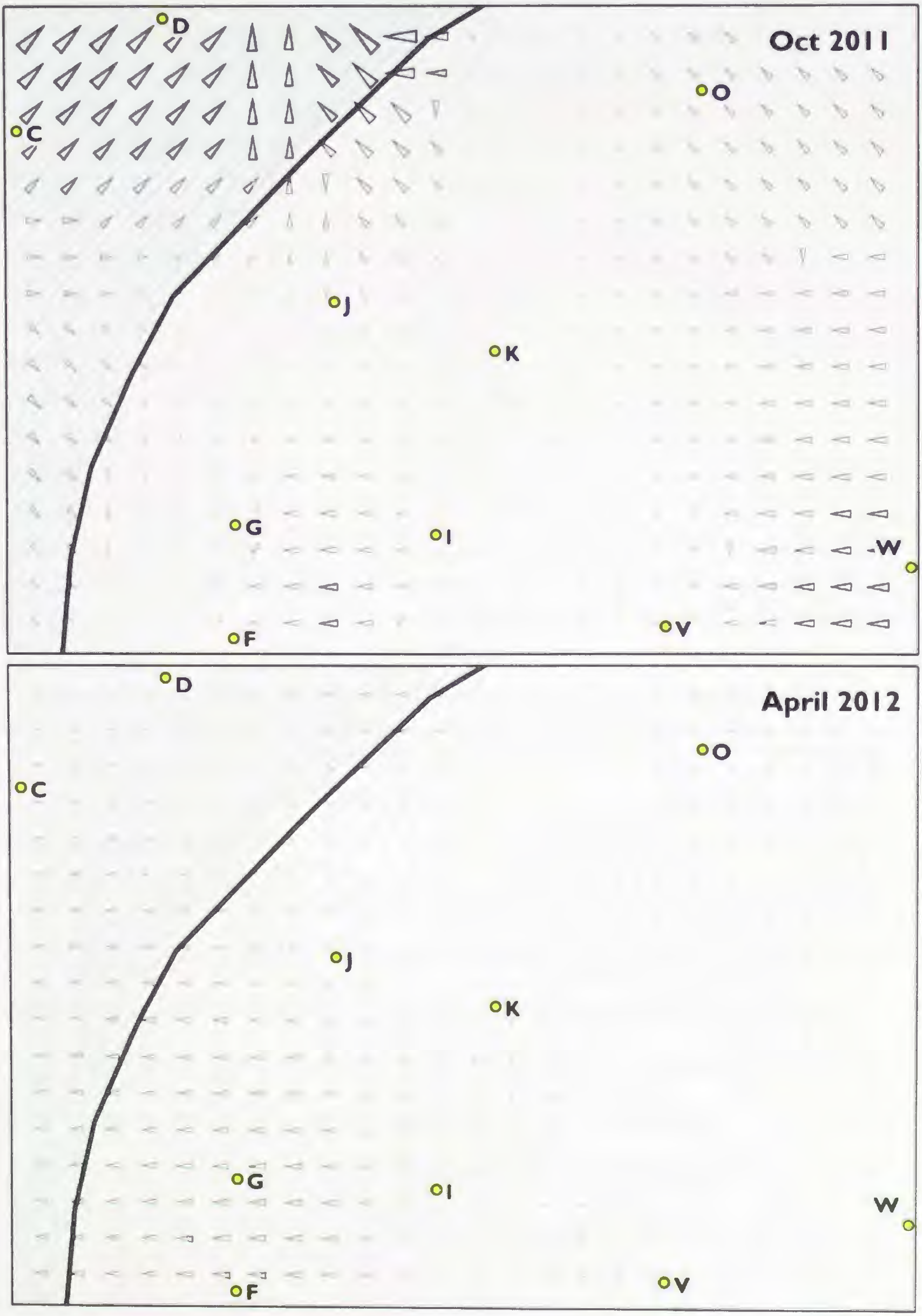


Figure 2.13. Surface water hydrograph between April 1 and May 8, 2012. Grey rectangles encompass the dates used for movies depicting hydraulic head fluctuations.

2.3.3.2 Hyporheic Flow Maps

A synthesis of geospatial and temporal information was used to characterize subsurface flow direction and the magnitude, or relative speed, of water movement during each study month. Hyporheic flow path maps show groundwater generally flowing towards the stream, or from a position with higher hydraulic head to a lower one (Figure 2.14). In the fall months, the greatest relative speed of riparian hyporheic water is typically flowing from piezometer W to V, where the hydraulic gradient between these points was large. In the spring, the magnitude of flow is greatest between piezometers F, G, & I, where the land surface had the highest slope.


Aug 2011
D
O
C
J
K
G
I
W
V
F
Sept 2011
D
O
C
J
K
G
I
W
V
F


Oct 2011
D
C
O
J
K
G
I
W
F
V
April 2012
D
O
C
J
K
G
I
W
F
V

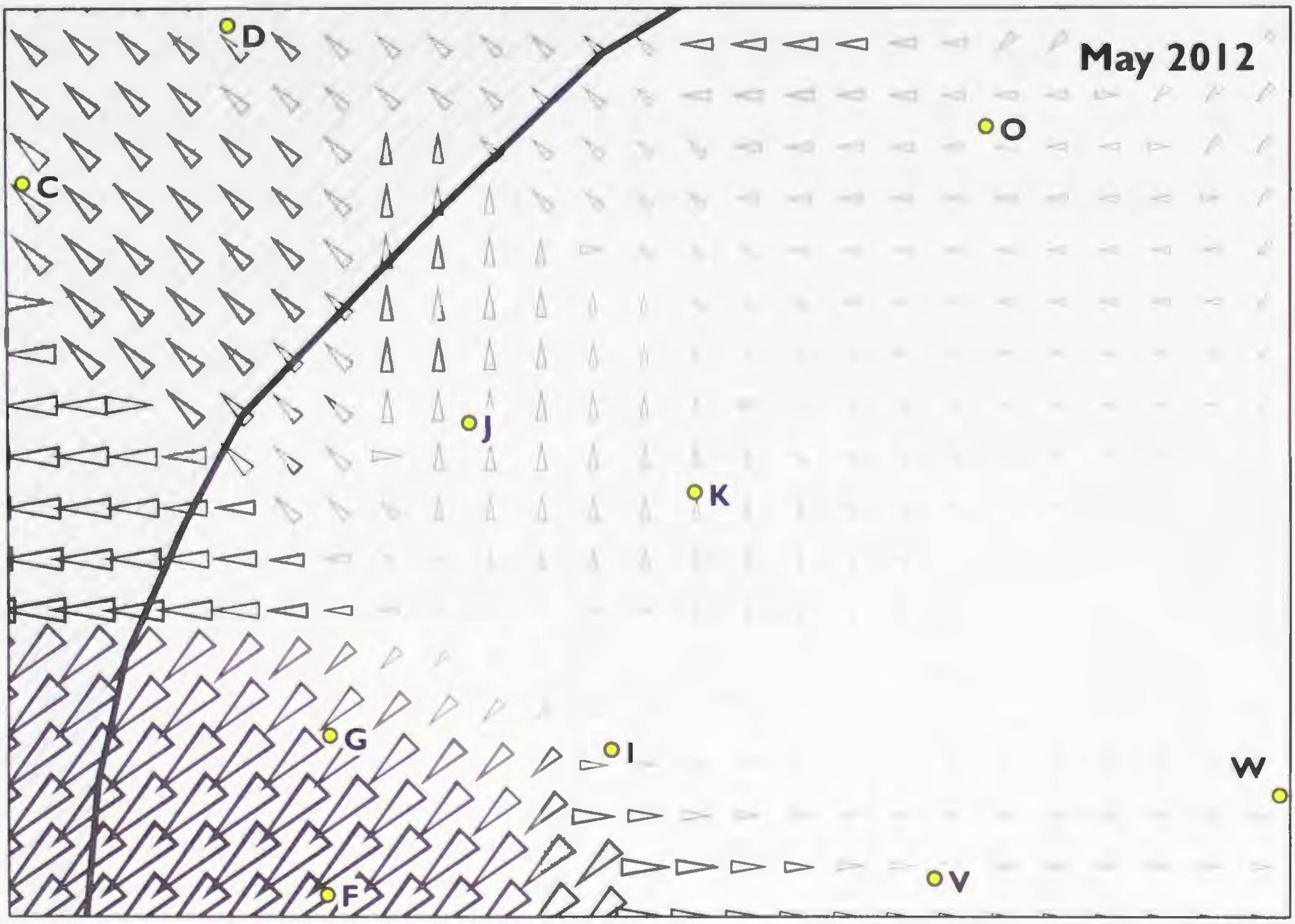


Figure 2.14. Hyporheic water flow direction and relative speed, represented by arrow direction and size, as modeled by spatial analysis of hydraulic head contours in ArcGIS during each month of the study. Land surface elevation is depicted by the contour lines (0.1-m intervals).

2.3.4 Ammonium

Wide variation in NH_4 concentration was observed both temporally over the period of study and spatially within the experimental site. Values ranged from <5 μg/L N at surface water sites to >500 μg/L N at hyporheic water sites near the spawning channel (Figure 2.15). Surface water samples ranged from < 5 to 80 μg/L N, with mean, median, and mode values of 12.5, 8.5, and 14.0 μg/L N, respectively. Ammonium concentration at hyporheic sites ranged from a low of 25 μg/L N at the site furthest from the streambank (site W) to a high of 606 μg/L N below the streambed (site D). The overall average value of hyporheic NH_4^+ was 160 μg/L N, with both median and mode values of 119 μg/L N (Figure 2.16). Surface water NH_4^+ concentration was found to be highly significantly different from hyporheic water ($p < 0.001$) throughout the study.

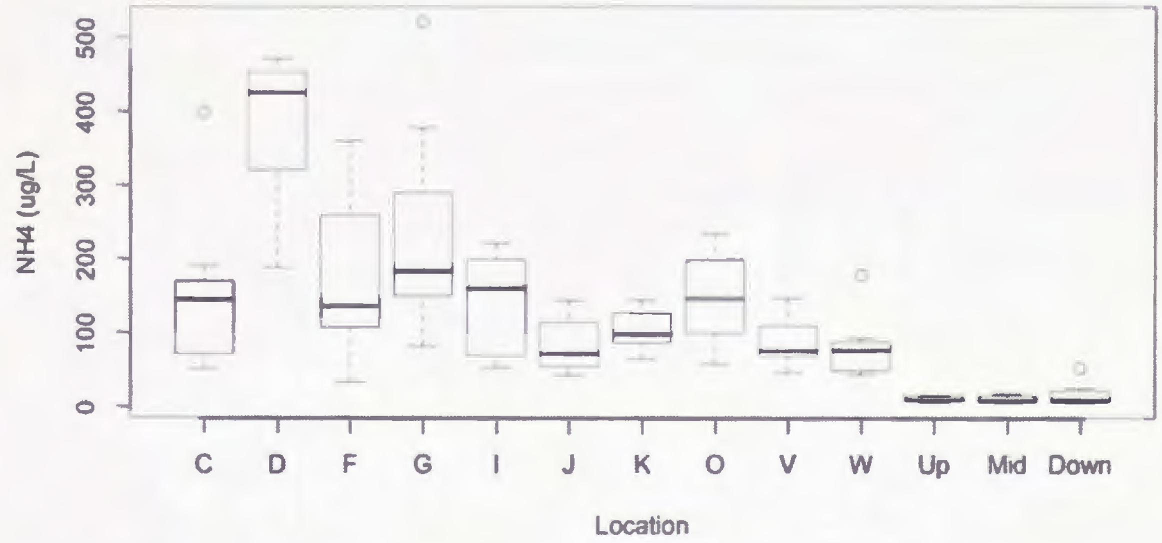


Figure 2.15. Box plots displaying all ammonium (NH4) concentration data at each sampling location. "Up," "Mid," and "Down" represent surface water samples.

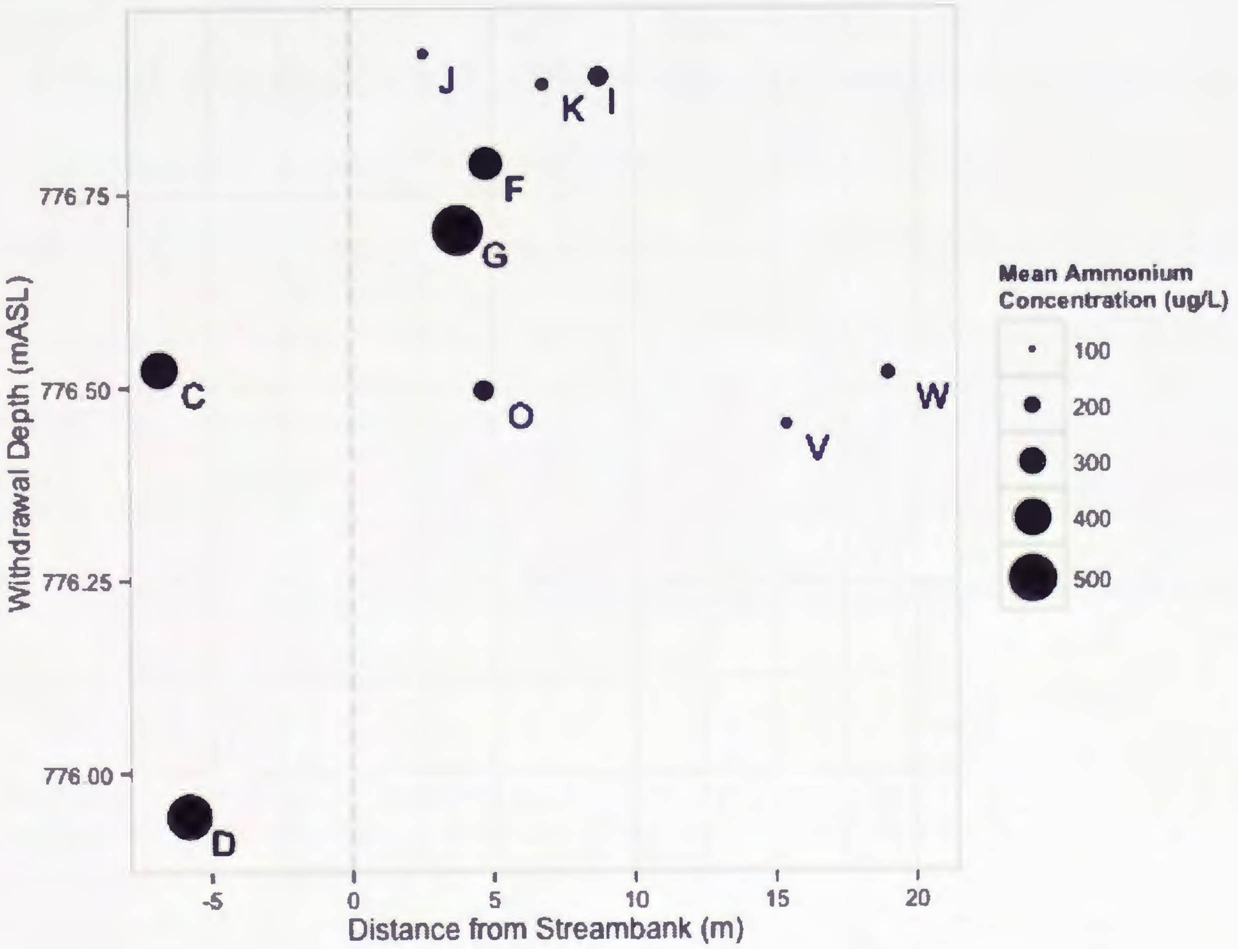


Figure 2.16. Mean ammonium (NH_4^+) concentration, represented by symbol size, of all sampling weeks at the hyporheic sampling locations. Withdrawal depth is measured as meters above sea level (mASL).

2.3.4.1 Seasonality of Ammonium

Ammonium was present in surface and hyporheic water during all sampling periods. Linear regressions evaluating the change in NH_4^+ concentration between Fall 2011 and Spring 2012 indicate that not only is NH_4^+ still present after the winter, but there is a statistically significant overall increase in NH_4^+ concentration in surface water ($p < 0.001$) and hyporheic water ($p < 0.05$) during the spring season (Table 2.2). The only sites exhibiting a decrease in spring NH_4^+ concentration are at instream piezometers C and D, which were drawing hyporheic water from below the streambed (Figure 2.17). In fact, a highly significant decrease from fall to spring values was identified at instream piezometers ($p < 0.001$).

A trend of decreasing NH_4^+ concentration is evident as the fall spawning season progresses (Figure 2.17). There were six water sampling days (during Active spawn I and Active spawn II) in which salmon were entering the spawning channel and correlations between salmon number and NH_4^+ could be analyzed (Table 2.3). The results display a statistically significant ($p < 0.05$) negative correlation between number of salmon and surface water NH_4^+ concentration (correlation coefficient of -0.919). This outcome is contrary to the hypothesis that more salmon will result in an increase of NH_4^+ in the water column.

Table 2.2. The change in ammonium (NH_4^+) concentration at each sampling location between Fall 2011 and Spring 2012 sampling periods. "Up," "Mid," and "Down" represent surface water samples.

Site	**Change in spring NH_4^+**	**p-value**	**Effect size**	**R-squared**
C	**Decrease**	2e-04	-1.23	0.53
D	**Decrease**	2.8e-06	-0.651	0.694
F	None			
G	**Increase**	7.3e-05	1.1	0.572
I	**Increase**	0.004	0.838	0.361
J	**Increase**	0.013	0.628	0.282
K	**Increase**	2.3e-04	0.554	0.504
O	None			
V	**Increase**	4.7e-05	0.708	0.591
W	None			
Up	**Increase**	0.008	0.58	0.319
Mid	**Increase**	0.006	0.631	0.339
Down	None			
All hyporheic water	**Increase**	0.045	0.228	0.019
All surface water	**Increase**	2.4e-04	0.613	0.2

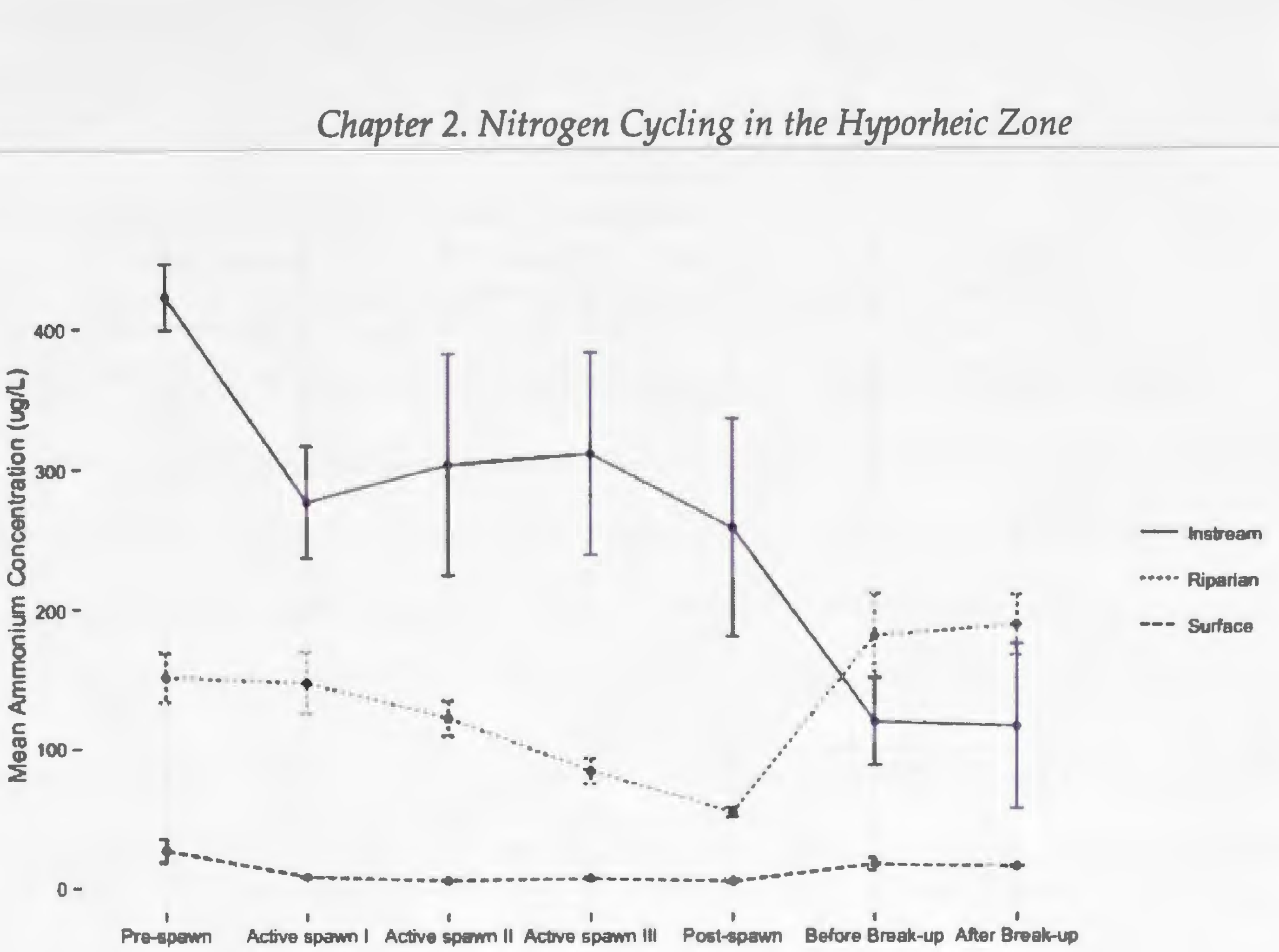


Figure 2.17. Mean ammonium concentration (µg/L N) at water sampling locations during each sampling period, with error bars showing standard error. The "Instream" group represents piezometers located in the stream (n=2); "Riparian" represents the riparian hyporheic piezometers (n=8); "Surface" represents the surface water sampling locations (n=3).

Table 2.3. Sockeye salmon (*O. nerka*) spawning escapement at the Horsefly River spawning channel and mean NH_4^+ concentration for surface water samples during Active Spawn I and II.

Date	Number of Salmon	Mean NH_4 (ug/L N)
Sept.12	2131	27.8
Sept.13	2243	24.8
Sept.14	2244	23.0
Sept.20	2339	14.7
Sept.21	2341	19.3
Sept.22	2346	19.0

2.3.4.2 Variables Affecting Hyporheic Ammonium

Predictor variables describing spatial and temporal attributes were used to assess NH_4^+ concentration for two groups: 1) all hyporheic sites (n=10) and 2) riparian hyporheic sites (n=8). For group 1, the variables *distance from streambank, withdrawal depth, hydraulic conductivity, precipitation,* and *staff gauge reading* were analyzed. Group 2 additionally considered the variable *distance from top of meander bend*. Variance inflation factors (VIF) of group 1 and group 2 variables were all low to moderate, meaning that each variable is reasonably independent of the other variables (Table 2.4). Therefore, all variables were considered for regression analysis.

Table 2.4. Variance inflation factors (VIF) used to describe multicollinearity for predictor variables used in multiple regression analyses

Variable	Type	Group 1 VIF	Group 2 VIF
distance from streambank	Spatial	1.54	2.09
distance from top of meander bend	Spatial	n/a	1.76
hydraulic conductivity	Spatial	4.61	1.80
withdrawal depth	Spatial	4.82	2.70
precipitation	Temporal	1.09	1.22
staff gauge reading	Temporal	1.04	1.22

Linear regressions were used to analyze the statistical significance between each variable and NH_4^+ concentration. For group 1, the variables *distance from streambank, withdrawal depth,* and *hydraulic conductivity* were considered statistically significant to predict NH_4^+ concentration ($p < 0.05$). The group 2 variables that were statistically significant ($p < 0.05$) included *distance from streambank, distance from top of meander bend,* and *precipitation*.

AIC_c values from linear and multiple regressions of spatial variables were analyzed to determine a candidate set of the most robust models, which included the two best linear regressions and three best multiple regressions (Table 2.5). The most effective spatial variables in predicting NH_4^+ concentration varied between groups, but multiple regressions were consistently stronger models than linear regressions. For all hyporheic samples (group 1), the predictor variables *distance from streambank*, *withdrawal depth*, and their interaction term produced the most robust regression with an Akaike weight (w_i) of 0.58, which describes the probability of this model being the best model in the candidate set. When analyzing the riparian hyporheic samples (group 2), the multiple regression of *distance from top of meander bend*, *hydraulic conductivity*, and their interaction term had the lowest AIC_c and $w_i =$ 0.62. The strongest singular spatial variables to predict NH_4^+ concentration were *hydraulic conductivity* for group 1 and *distance from streambank* for group 2.

The effect sizes associated with the regression results aid in understanding the real world application of these models (Table 2.5). The interpretation of group 1's best model explains that, independently, an increase in *distance from streambank* (effect size = -0.20) and *withdrawal depth* (effect size = -0.20) tend to result in lower NH_4^+ concentrations. However, when distance from streambank *and* withdrawal depth increase together (effect size = 0.36), this will cause NH_4^+ concentration to decrease less. The multiple regression of *distance from streambank* and *withdrawal depth* had similar results for both groups. The interpretation of this model for group 2 explains that when controlling for *withdrawal depth*, a 1-m increase in *distance from streambank* will cause NH_4^+ concentration to decrease by 0.27 μg/L N (effect size = -0.27).

Table 2.5. Model selection results of spatial variables for all hyporheic (group 1) and riparian hyporheic (group 2) models. The effect size is written in parenthesis after each predictor variable. The most parsimonious linear and multiple regressions are ranked by second-order Akaike's Information Criterion (AIC_c) scores. SB = streambank, TMB = top of meander bend, df = degrees of freedom, w_i = Akaike weights.

Group	Model variables (effect size)	df	AIC_c	ΔAIC_c	w_i
1	distance from SB (-0.20) + withdrawal depth (-0.20) + interaction term (0.36)	5	127.45	0.00	0.58
1	distance from SB (-0.18) + hydraulic conductivity (0.33)	4	129.29	1.83	0.23
1	distance from SB (-0.29) + withdrawal depth (-0.33)	4	130.01	2.56	0.16
1	hydraulic conductivity (0.36)	3	133.43	5.98	0.03
1	withdrawal depth (-0.27)	3	143.17	15.72	0.00
2	distance from TMB (-0.32) + hydraulic conductivity (0.06) + interaction term (0.20)	5	100.89	0.00	0.62
2	distance from SB (-0.08) + withdrawal depth (-0.07) + interaction term (0.25)	5	103.66	2.78	0.16
2	distance from SB (-0.04)	3	104.71	3.83	0.09
2	distance from SB (-0.27) + withdrawal depth (-0.12)	4	105.38	4.49	0.07
2	distance from TMB (-0.03)	3	105.54	4.65	0.06

When analyzing the temporal variables, AICc results demonstrated that, for both groups, the linear regression using *precipitation* was the strongest model, followed by the multiple regression of *precipitation* and *staff gauge reading* (Table 2.6). The results state that for each incremental increase in *precipitation*, NH_4^+ concentration will increase by 0.03 μg/L N (group 1) or 0.05 μg/L N (group 2). When controlling for *staff gauge reading*, each incremental increase in *precipitation* will cause an even greater increase in NH_4^+ concentration (0.20 μg/L N for group 1 and 0.27 μg/L N for group 2). However, when the stream channel level rises, as signified by a higher *staff gauge reading*, NH_4^+ concentration will decrease by 0.10 μg/L N (group 1) or 0.12 μg/L N (group 2) when controlling for *precipitation*.

Table 2.6. Model selection results of temporal variables for all hyporheic (group 1) and riparian hyporheic (group 2) regression models. The effect size is written in parenthesis after each predictor variable. The most parsimonious linear and multiple regressions are ranked by second-order Akaike's Information Criterion (AIC_c) scores. df = degrees of freedom, w_i = Akaike weights.

Group	Model variables (effect size)	df	AIC_c	ΔAIC_c	w_i
1	precipitation (0.03)	3	150.71	0.00	0.63
1	precipitation (0.20) + staff gauge reading (-0.10)	4	151.75	1.04	0.37
2	precipitation (0.05)	3	103.50	0.00	0.53
2	precipitation (0.27) + staff gauge reading (-0.12)	4	103.76	0.25	0.47

2.4 Discussion

2.4.1. Defining the Hyporheic Zone of the Horsefly River Spawning Channel

Hyporheic zones respond to changes in surface water levels and stream discharge (Valett et al. 1994), and this concept is substantiated by our study. The hypothesis that a hyporheic zone is present beneath the stream and below the riparian zone was confirmed through hydraulic head contour and flow mapping, as well as perceptible changes in hydraulic head that corresponded with surface water level fluctuations. Hydraulic head beneath the riparian zone varied between a lower limit of 80-cm and 164-cm deep during low flow in the fall and from an upper limit of 10-cm to 56-cm below the surface at the peak of spring break-up. Directly beneath the stream, the saturated thickness of the hyporheic zone extended from the streambed to at least 155-cm deep and possibly deeper, but this is unknown as 155 cm was the deepest point sampled. During specific times at particular study sites, hydrologic and chemical characteristics implied the presence of a boundary between saturated and unsaturated soils.

Hyporheic flow is controlled primarily by factors of sediment characteristics (grain size, type, and connectivity), groundwater and surface water discharge rates, and hydraulic conductivity (Valett et al. 1994, Dent et al. 2001, Tonina & Buffington 2009). The degree to which these variables exert control over hyporheic exchange depends upon scale, time, and place. Attributes of this aquifer were evaluated according to hydraulic head, hydraulic conductivity, and soil characteristics.

2.4.1.1. Aquifer Properties

Negative VHG at instream piezometers (C and D) affirm that the experimental site is a location of groundwater recharge. Slight upwelling and neutral VHG occurred infrequently at piezometer D during low flow (Figure 2.11a), suggesting that the upper limit of the hyporheic/groundwater boundary is around 155-cm below the streambed (or 775.943 mASL). High flow events had a discernible effect on groundwater recharge; for example, VHG dropped from -0.37 to -1.29 $m \cdot m^{-1}$ at C and -0.27 to -0.84 $m \cdot m^{-1}$ at D during a rain event on April 26, 2012.

Hydraulic conductivity (K) values were relatively consistent throughout the study site ($K \sim 10^{-4}$ to 10^{-5}), indicating a fairly homogeneous soil type of silt/clayey sands at lower K and silty/fine sands at higher K (Table 2.1; Freeze & Cherry 1979). The lowest K was observed at riparian site G and coincides with personal observations of slow-refilling and particulate-rich water. During low water events, piezometer G contained only enough water to fill one 12-ml sample, which suggests that the water table was occasionally situated just above the piezometer openings located 164 cm below the land surface (or 777.292 mASL).

During soil sampling, evidence of clay mottling was observed in the B horizon of all soil pits, which marks the perched height of the water table (specifically between 778.2 and 778.5 mASL). Gley and blue/green soils, which characterize a persistent water table, were identified in the C horizon of the soil pit located furthest from the streambank (soil pit 2).

Since hydraulic conductivity defines the ease of water movement in soil, it seems to infer that a location with high porosity will also exhibit high hydraulic conductivity. However, the resistance of water movement in soil depends on the size and connectivity of pore spaces. As sediment particle size decreases, the proportion between porosity and *K* fails because the actual correlation is between *K* and pore throat radii (Soil Survey Manual 1993). Clay, being the typical example of this, consists of ultra-fine grained minerals and displays a strong apparent cohesion due to electrostatic forces between ions of minerals and oxygen atoms. This structure is highly porous, and often supersaturated, but exhibits low hydraulic conductivity because the many pore spaces are not well connected (Barnes 1995).

2.4.1.2. *Hyporheic Flow Paths*

Elevated hydraulic head values at locations furthest from the stream indicate one-directional flow of groundwater toward the stream channel (Figure 2.12), which is an expected result and typical of both surface and groundwater flow direction (Triska et al. 1993, Chestnut & McDowell 2000). The flow maps suggest there was a greater opportunity for hyporheic flow through the riparian meander bend in the fall because of the variable flow directions and a small magnitude of flow toward the stream. In the spring, the pattern of flow was strongly one-directional toward the channel, indicating that hyporheic flow at this time was likely limited (Figure 2.14). Although water is generally flowing into the channel, hyporheic exchange between the stream and streambank still occur on a smaller scale (Duval & Hill 2007). Evidence of this exchange from the stream to riparian zone occurred during the

Rhodamine-WT tracer test when fluorescence of hyporheic water increased after the slug injection. Hyporheic exchange between the stream and streambed was confirmed from VHG measurements.

Although VHG indicated a dominantly downward flow of water into the streambed, the flow of riparian groundwater towards the stream is known to promote upwelling conditions (Hill et al. 1998). This discrepancy could be the result of a localized influence associated with bedforms and also the artificial construction of the channel (Kasahara & Wondzell 2003). The streambank at the HFC is relatively steep compared to natural meander bends on the Horsefly River, where there is a gradual transition between the stream and riparian zone. Perhaps there is a limited connection between the flow of water from the riparian zone and the flow of water into the streambed at this site. To improve on the interpretation of hyporheic flow across the riparian and beneath the stream, piezometers installed upstream of the meander bend may have resulted in hydraulic head values that inferred different flow directions and magnitudes.

2.4.2. Sources and Uptake of Ammonium in Surface Water

Contrary to other experiments of natural or artificial salmon additions (Minakawa & Gara 1999, O'Keefe & Edwards 2002, Johnston et al. 2004, Chaloner et al. 2004, Mitchell & Lamberti 2005, Claeson et al. 2006, Janetski et al. 2009, Levi et al. 2011), NH_4^+ concentration of surface water did not increase upon the arrival of salmon and, thus, this study fails to reject the null hypothesis (I). Average values decreased from 27 μg/L N before the arrival of salmon to post-spawn values of 5 μg/L N. In fact, a strong negative correlation ($r = 0.91$, $p < 0.05$) between salmon abundance and NH_4^+ concentration was calculated during active salmon spawn, which infers that the presence of salmon significantly reduced surface water NH_4^+ concentration (Table 2.3). Ammonium concentration naturally varies between rivers, and some examples of systems which gain NH_4^+ in the presence of salmon are listed in Table 2.7. In a Washington stream, NH_4^+ level remained unchanged during salmon spawn and this was attributed to the rapid removal of NH_4^+ from solution due to biological uptake (Bilby et al. 1996).

Table 2.7. Examples of streams with increased NH_4^+ concentration during salmon runs, as compared to the present study. Most values were estimated from published graphs.

Authors	Location	Species	NH_4^+ *with* salmon (μg/L)	NH_4^+ *without* salmon (μg/L)
Present study	Horsefly channel, BC	Sockeye	5	27
Minakawa & Gara 1999	Little Kennedy Creek, WA	Chum	~250	~50
O'Keefe & Edwards 2002	Lynx Creek, AK	Sockeye	147	2
	Peterson Creek, AK	Pink, Chinook, Coho	~15	~0
Chaloner et al. 2004	Salmon Creek, AK	Pink, Chinook, Coho	~12	~5
Mitchell & Lamberti 2005	Fish Creek, AK	Chum, Pink, Coho, Chinook	40-60	<5
Levi et al. 2011	Prince of Wales Island, AK	Pink, Chum	~160	~10

Certainly ammonia was delivered to the spawning channel by salmon (Mitchell & Lamberti 2005), but since we cannot attribute NH_4^+ concentration in water samples to salmon, a new question arose. Where is NH_4^+ coming from? Possibly the most influential local source was the resuspension of sediment and bacteria during the channel cleaning that occurred between August 8-12 and 15-18, 2011, ending 5 days prior to pre-spawn sampling. Over a 10-day cleaning period, a year's worth of accumulated streambed nutrients were released, potentially causing a dissolved nutrient spike which mostly attenuated before sampling commenced.

When N availability increases, microbes absorb, or mineralize, dissolved organic N (DON) as energy for growth and excess N is excreted as NH_4^+ in a process called ammonification. Nitrifying bacteria then absorb, or immobilize, this additional NH_4^+ and nitrification becomes the predominant transformation mechanism (Figure 2.18; Peterson et al. 2001, Chapin et al. 2011). This process of peak NH_4^+ attenuation followed by a decline has been observed in other salmon-bearing rivers (Johnston et al. 2004, Claeson et al. 2006, Rinella et al. 2013). Furthermore, 2011 was a weak year for Horsefly River sockeye returns and the spawning channel was filled to less than 10% of capacity. In contrast, the sub-dominant 2010 salmon escapement surpassed the total 2011 escapement on only the second day of spawning channel operation, and was eventually filled to 100% capacity. In another northern BC stream, Johnston et al. (2004) found that NH_4^+ concentrations exceeded NO_3^- during a year of high salmon abundance, but the reverse was true the following year during low salmon abundance. At the HFC, low spawner density in conjunction with resuspension of the previous year's dissolved nutrients likely overshadowed NH_4^+ delivery by 2011's spawners.

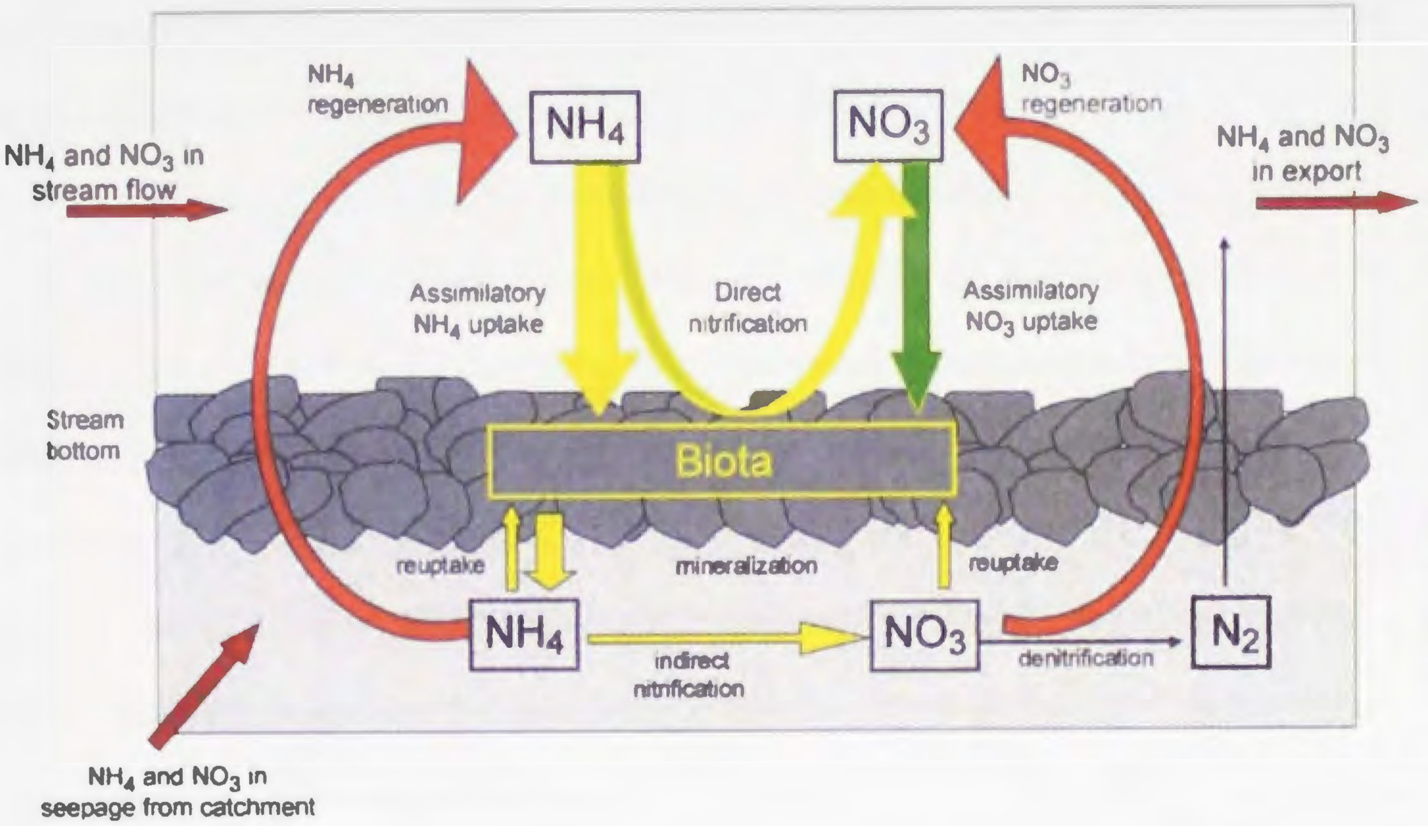


Figure 2.18. A conceptual model of the nitrogen cycle at the interface of surface and hyporheic water. (From Peterson et al. 2001. Reprinted with permission from AAAS.)

In N-limiting ecosystems, actinorhizal plants, such as alder (*Alnus spp.*), provide an important source of N to forested ecosystems through symbiotic nitrogen fixation. Alder-fixed nitrogen (AFN) can be transported to the stream by advection of water through the soil and direct leaf litterfall and, similar to MDN enrichment, is utilized by surrounding microbes and vegetation (Helfield & Naiman 2002, Compton et al. 2003). The N supplied by alders is transferred to riparian soils primarily through root secretions and leaf litter, and has been shown to increase soil NH_4 and NO_3^- concentrations (Shaftel et al. 2012). Alders commonly grow near water throughout the Cariboo region, which encompasses the Horsefly watershed (J. Holmes, pers. comm.), and Mountain alders (*A. tenuifolia*) were present in the riparian forest of our study site. In mature forests, AFN may be a more important contributor of soluble nutrients than MDN, perhaps, in part, because the timing of maximum stream N from alder occurs in both the spring and the fall (Wondzell & Swanson 1996b, Helfield & Naiman 2002, Shaftel et al. 2012).

Land-use activities in the Horsefly River watershed include mainly logging, agriculture, mining, and urbanization (Holmes 2008, Smith & Owens 2014), which all can deliver substantial amounts of N to the stream. Small to medium sized beef cattle and hay production farms border much of the river upstream from the spawning channel. Further upstream, logging has been active in the past and present. Paved and gravel roads run adjacent to and over the spawning channel within the 1000 person town of Horsefly. However, these anthropogenic activities appear to be a minor source of dissolved nutrients. Surface water samples from the Horsefly River, taken directly upstream of the spawning channel in March 2008, displayed concentrations of dissolved inorganic N (DIN; nitrite + nitrate + ammonia) at 99 μg/L and soluble reactive phosphorus (SRP; orthophosphate) at 3.3 μg/L (Holmes 2008). Concentrations at these levels are considered low (Meybeck 1982, Tank & Dodds 2003) and are an order of magnitude or more lower than studies from N-rich agricultural streams by Hill et al. 1998 (>1000 μg/L N) and Böhlke et al. 2009 (1400 – 14,000 μg/L N). However, DIN and SRP values during the summer and fall would provide a better picture of the effect of land-use activities.

All of these sources (nutrient resuspension during channel cleaning, N-fixation by alder, and anthropogenic land-use activities) likely contributed DIN to the stream to varying degrees, but the fate of NH_4^+ still remains unclear due to its rapid immobilization from the water column. Peterson et al. (2001) compared long-term ammonium-^{15}N additions in 11 streams from varying biomes and found that on average 20-30% of NH_4^+ was removed by nitrifying bacteria, while 70-80% was assimilated by benthic organisms. Since discharge in the channel is relatively slow (~2 m^3/s), it can be assumed that the NH_4^+ uptake length is short (Peterson et al. 2001, Albers 2010) and that NH_4^+ was utilized directly in the stream by micro- and macro-organisms (Bilby et al. 1996, Webster et al. 2003, Levi et al. 2013). Desirable nitrification conditions of high dissolved oxygen (DO) and plentiful DON and/or NH_4^+ can contribute to the rapid uptake of NH_4^+ and low surface water NH_4^+ concentrations (Chapin et al. 2011, Levi et al. 2011). However, some streams, particularly oligotrophic streams, seem to have a fixed capacity for nitrification (Newbold et al. 1983). An N overload event was documented in other northern watersheds of the Fraser River basin by Johnson et al. (2004), when years of high salmon abundance and high NH_4^+ were followed by a year of low salmon and NH_4^+ abundance. In theory, a profusion of instantaneously immobilized NH_4^+ would remain mostly undetected in the spawning channel, until nitrifying bacteria and benthic organisms reached their N-uptake limit, at which point NH_4^+ concentration would begin to increase (Chapin et al. 2011).

2.4.3. Sources and Uptake of Ammonium in the Hyporheic Zone

Hyporheic water samples had significantly higher NH_4^+ concentrations compared to surface water values, both spatially and temporally, with an overall average enrichment of 1380% in the fall and 1035% in the spring. Therefore, this study rejects the null hypothesis (II) that there would be no difference between NH_4^+ concentration in surface and hyporheic water. This observation is supported by other studies in which hyporheic water was distinctly enriched in NH_4^+ compared to surface water (Valett et al. 1990, 1994, McClain et al. 1994, Fiebig 1995, Chestnut &

McDowell 2000, Greenwald et al. 2008). Riparian and hyporheic environments are known to be a net source of N to streams (Wondzell & Swanson 1996b, Shibata et al. 2004). Aerobic surface water is capable of rapidly removing NH_4^+ from solution through nitrification, whereas anaerobic subsurface environments facilitate denitrification (Peterson et al. 2001, Seitzinger et al. 2006). Advective transport of water through the hyporheic zone leads to longer contact time with sediments and associated microbes, increasing opportunities for biogeochemical transformation of N (Triska et al. 1990). These conditions complicate our ability to track the flux of NH_4^+ from salmon because the transformation of NH_4^+ to other forms of DIN or assimilation by organisms can occur both quickly and repeatedly.

2.4.3.1. Temporal Controls of NH_4^+

A major aim of this study was to determine if hyporheic storage of salmon-derived NH_4^+ occurred over the winter. Although NH_4^+ present in the hyporheic zone cannot be directly attributed to salmon, temporal trends of NH_4^+ concentration were observed, as well as a marked difference between instream and riparian hyporheic locations (Figure 2.17). Overall, the riparian zone displayed a significant increase in NH_4^+ concentration from fall to spring. Conversely, a significant decrease in NH_4^+ was observed in hyporheic water directly below the streambed (Table 2.2). Apparently these adjacent hyporheic systems have differing sources of N or disparate subsurface attributes that control biogeochemical processing. These results reject the null hypothesis (IV) that NH_4^+ concentration will not differ between seasons.

The riparian hyporheic zone may be N-limited in the fall and less limited in the spring when N becomes more available. From the regression analysis, it was found that precipitation was a strong predictor of riparian NH_4^+ concentration, indicating that NH_4^+ increases by 0.05 μg/L N with every millimeter of precipitation (Table 2.6). Past research has suggested that spring precipitation events induce lateral N inputs from the hill slope (Wondzell & Swanson 1996b, Shibata et al. 2004, Wondzell & Gooseff 2013), and that snowmelt and rain can aid N percolation from the overlying organic soil layers and leaf litter (Chafiq et al. 1999). Also, an interesting phenomenon of freeze-thaw in the spring bursts a multitude of microbial cells, releasing pulses of nutrients and inducing rapid accumulation of NH_4^+ and NO_3^- (Chapin et al. 2011). Triska et al. (1994) found riparian hyporheic locations to have lower NH_4^+ in the winter, *except* at sites with alders. During the anoxic winter months, alders may continue to fix N, thus contributing to the accumulation of NH_4^+. In the spring, the higher water table is capable of reaching the shallow rooting zone of alders.

Peak streamflow conditions in the spring induced strong downwelling gradients into the hyporheic zone beneath the streambed, which likely facilitated better nitrification conditions by delivering DO and lowering NH_4^+ (Wondzell & Swanson 1996b, Zarnetske et al. 2011). During the salmon spawn, leaf litter, biofilms, and streambed sediments continue to assimilate N from the surface water (Albers & Petticrew 2012). This storage and accumulation of nutrients and organic matter may have contributed to an increase in water residence time and decrease in DO, thereby increasing NH_4^+ concentrations beneath the streambed in the fall (Hinkle et al. 2001, Argerich et al. 2008, Heppell et al. 2014).

Flow direction maps provide evidence to a seasonal shift of nutrient exchanges between the channel and riparian zone (Figure 2.14). In the fall, weaker and more variable flows suggest that hyporheic water could be delivering NH_4^+ and other nutrients to the riparian zone. During the spring, break-up events (e.g. snowmelt and precipitation) promote strong subsurface flows toward the channel, resulting in a lateral flux of nutrients to the stream. The observed increase of surface water NH_4^+ concentration in the spring, alongside increased riparian hyporheic NH_4^+, substantiates this flow direction (Figure 2.17). Seasonally shifting nutrient flow between adjacent ecosystems is known as reciprocal subsidies. This interaction typically occurs when terrestrial and aquatic productivity peaks at different times of the year (Nakano & Murakami 2001). Temporally shifting hyporheic flow at the HFC may be evidence of another pathway for the exchange of reciprocal subsides in stream-riparian ecosystems.

2.4.3.2. Spatial Controls of NH_4^+

Ammonium content varied greatly between hyporheic locations, but statistical regressions confirmed a few spatial variables that can predict NH_4^+ concentration at this site. Distance from streambank continually ranked as a strong predictor of NH_4^+ in the hyporheic and riparian zones, demonstrating that NH_4^+ concentration decreased as distance from the streambank increased. This result supports the rejection of the null hypothesis (III) that the spatial variable, distance from the streambank, does not correlate with NH_4^+ concentration. While controlling for other variables, NH_4^+ has the potential to decrease between 0.20 and 0.29 $\mu g/L$ N with every meter further from the streambank (Table 2.5). Although some research has shown that anaerobic conditions conducive to denitrification result in more NH_4^+ with distance from streambank (Triska et al. 1993, Hinkle et al. 2001, Duval & Hill 2007), lateral distance from the stream is not always this straightforward.

Hidden beneath the surface are dominant patterns of hyporheic flow and micro-sites of accumulated organic matter, plant roots, and limited nutrients (McClain et al. 2003, Poole et al. 2004, Claret & Boulton 2009). Other studies also agree with our results of decreasing NH_4^+ with distance from the stream (Chestnut & McDowell 2000, O'Keefe & Edwards 2002). Since the hydraulic head maps indicate that subsurface water flow is generally toward the stream, it may be inferred that nutrients, sediment, and organic matter accumulate more readily in soils close to the streambank. Certain biogeochemical reactions may be occurring in these soils because of either increased N or C availability. Where N is not limiting, soil microbes will mineralize more DON as energy for growth and excrete excess NH_4^+ (Wondzell & Swanson 1996b, Chapin et al. 2011). Organically-rich subsurface sediments can induce a microbially-mediated reaction known as the dissimilatory reduction of nitrate to ammonium (DNRA). During this reaction, NH_4^+ availability increases in the absence of oxygen (Hill et al. 1998, Lewandowski & Nützmann 2010).

Hydraulic conductivity was the strongest singular predictor of NH_4^+ concentration when considering all hyporheic locations (group 1), indicating that as K increased, NH_4^+ also increased. This positive relationship conflicts with the assumption that higher K typically results in shorter water residence time, higher DO, and, therefore, a nitrification environment characterized by less NH_4^+ (Pinay et al. 1995, Chestnut & McDowell 2000). However, K values were only measured once in the spring, so interpretation of this variable would have been improved by conducting several K tests per study month and log averaging the values (U.S. Dept. of Agriculture 1993, Genereux et al. 2008, Hester 2008, Claret & Boulton 2009). In addition, slug tests themselves are a source of significant uncertainty when estimating *K* (Cardiff et al. 2011). Post-hoc reanalysis revealed that the significantly positive relationship between *K* and NH_4^+ occurred only during the fall sampling period. It is possible that soils around the piezometers settled during the winter and altered *K* of the sampling area. Also, when removing piezometer D from the analysis, which appears to be an outlier, the relationship between *K* and NH_4^+ weakens. Without piezometer D, the linear regression of distance from streambank becomes the most robust model (effect size = -0.02). However, if hyporheic water is well oxygenated, then a positive relationship between *K* and NH_4^+ may hold true. Past studies have demonstrated that NO_3^- concentrations can increase along a flow path, despite increased residence times, if there is enough DO and NH_4^+ available for nitrification to occur (Triska et al. 1990, Claret & Boulton 2009, Argerich et al. 2011).

The interaction of distance from streambank along with withdrawal depth was found to be a good predictor of NH_4^+ in the hyporheic zone (Table 2.5). Multiple regression results indicate that for every increase in withdrawal elevation at a given distance from the stream, there will be more NH_4^+ than if water was being drawn from a lower depth (Figure 2.19). However, this result contradicts the theory that deep hyporheic water is characterized by denitrifying anaerobic environments and higher NH_4^+ concentrations (Hill et al. 1998, Hinkle et al. 2001). By scrutinizing Figure 2.15, it appears that statistical significance may be an artifact of the positioning of these piezometers. When piezometer D, located about 0.5 m deeper than the next deepest location, is removed from multiple regression analyses, this interaction is no longer significant. However, without piezometer D, the only difference between the two groups is piezometer C. A better way to explore the effect of withdrawal depth on NH_4^+ concentration would have been to position piezometers in a nested design, where water would be extracted from three depths at approximately the same location.

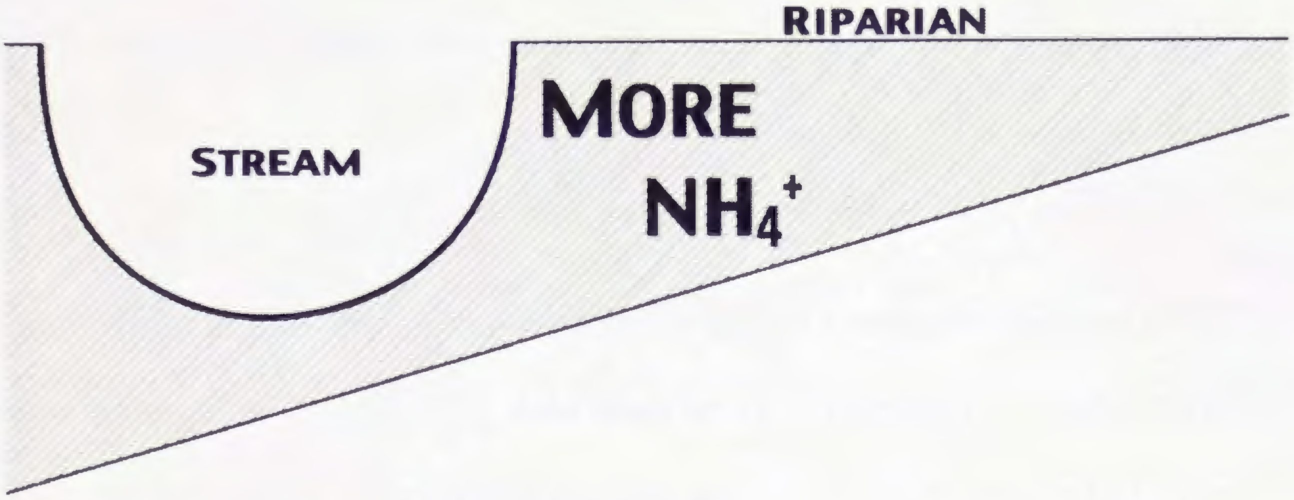


Figure 2.19. A profile of a stream and adjacent riparian zone displaying the subsurface zones that may have higher ammonium (NH_4^+) concentrations.

To better understand the fate of NH_4^+ at this meander bend, variables of DO and NO_3^- would have been advantageous. The presence or absence of oxygen controls the mechanisms behind subsurface N cycling (Argerich et al. 2011, Peyrard et al. 2011), so sufficient spatial and temporal density of DO values could have acted as a proxy for N concentration and transformation. For similar reasons, concentrations of NO_3^- would have been desirable. Since NH_4^+ additions from spawning salmon were likely rapidly converted to NO_3^-, knowing these values could address this assumption and, if confirmed, increased my ability to address N in terms of salmon input (Johnston et al. 2004). Nitrate values would have also helped discern the nutrient cycling relationship between NH_4^+ and NO_3^- in the hyporheic zone. The fate of most NO_3^- is assimilation and mineralization by primary producers, but NO_3^- can also be assimilated and stored for an extended period of time or denitrified to atmospheric N (Ashkenas et al. 2004, Hall et al. 2009). Nitrate assimilation is related to seasonal and diel availability of sunlight, with greater uptake and overall gross primary production during light hours (Mulholland et al. 2006). The relationship between values of NO_3^- and NH_4^+, as well as DO values, would help identify the subsurface mechanisms behind spatial and temporal N cycling.

2.4.4. Limitations and Lessons

Subsurface environments are inherently difficult to study because of the challenges involved with collecting data from an environment in which we have limited access. To compensate for this complication, averages, interpolation, and modeling are used to represent attributes of the many locations that cannot be examined directly. The present study was based on others that utilize an array of point measurements from which spatial variability for an entire study area is partially defined, particularly O'Keefe & Edwards (2002) and Pinay et al. (2009). Kennedy et al. (2008) explored the underlying question of error when averaging or interpolating spatial distribution of subsurface attributes. Their results indicate that a sampling density of 0.05 points per m^2 was sufficient to reduce error in reach-average values. To produce a realistic image of spatial distribution, sampling density of 0.08 to 0.09 points per m^2 was needed. Much of the uncertainty when answering our study questions arises from limited spatial resolution, as the sampling density for values of hydraulic head and conductivity were 0.011 points per m^2. Using Kennedy et al. (2008) as a guideline, 45 piezometers (0.05 points per m^2) would be needed at our study site to obtain enough values for reach-average estimates of subsurface properties and 72 piezometers (0.08 points per m^2) would be required to map a realistic image of hyporheic flow.

Consequently, the Rhodamine-WT tracer test, which had a sampling density of 0.028 points per m^2, only partially helped in designating the subset of study piezometers. To improve on this design, I would have first and foremost performed the topographic land survey and generated a contour map to identify likely subsurface flow paths, which can be estimated by subtle changes in the surface topography (Gordon et al. 1992, Hutchinson & Moore 2000). An in situ analysis of hydraulic conductivity and porosity would have been helpful in estimating the time required for the tracer to fall below detection limits. The temporal resolution is also an important consideration and the shortage of sample containers during this study's tracer test restricted the power of reliably detecting a breakthrough curve. The most ideal experiment would involve data loggers capable of continuously logging fluorescence.

The literature repeatedly reports "high variability" in describing the heterogeneity of streambed and soil properties (Chestnut & McDowell 2000, Hinkle et al. 2001, Malard et al. 2002, Saunders et al. 2006, Zhang 2007, Claret & Boulton 2009, Chapin et al. 2011, Wondzell & Gooseff 2013), and this site is no different. Johnson et al. (2014) points out that the residence time and removal of solutes in transient storage zones is still being debated, largely due to the spatial and temporal heterogeneity of hydraulic and biogeochemical processes in these storage zones. Therefore, it is crucial for any researcher undertaking a study of the hyporheic zone to design an experimental site with a high enough sampling density to reliably address the study questions.

The characterization of subsurface flows using hydraulic head measurements from piezometers is not strictly correct (Hutchinson & Moore 2000). Hydraulic head is a measure of pressure that varies with both horizontal location and vertical position. Whereas, water table elevation, which can be evaluated using wells, provides a more robust indicator of lateral flow direction (Jones & Holmes 1996). To improve on this design and produce a more accurate representation of subsurface flows, a well could be installed next to each sample piezometer to quantify both lateral and vertical hydraulic gradients.

Since the HFC was artificially-constructed, this site is an imperfect comparison to a meander bend on the Horsefly River. In particular, riparian zone flooding at the experimental site is uncommon, whereas flooding is an annual spring event throughout much of the Horsefly River floodplain (Clark 2013). Flood events cause the deposition of fine sediments, which would result in sandier substrates along the Horsefly River. Aquifer variables would likely be characterized with higher hydraulic conductivity and porosity when compared to the well-developed riparian soils of the HFC. Accordingly, salmon nutrients may exhibit longer hyporheic travel times and infiltrate to greater distances in the floodplain. However, due to the large number of variables and interactions that influence nutrient flow and transformation, this conclusion is merely speculation. For example, floodplains can store considerable amounts of sediment and dissolved nutrients (Smith & Owens 2014), so an influx of ammonium from salmon may be undetectable if the floodplains are not N-limited.

2.5. Conclusions

A hydraulically responsive hyporheic zone was discovered beneath the streambed and across a riparian meander bend at the Horsefly River spawning channel. This zone was well-connected, even during periods of low flow, and responded quickly to changes in surface water level. Although NH_4^+ was present in surface and hyporheic water samples throughout the study, we were unable to correlate NH_4^+ concentration with the arrival of spawning salmon. This outcome was likely the result of nutrient resuspension during channel cleaning, which occurred prior to the first sampling event and created a profuse export of inorganic N from the water column. Ammonium concentration in surface water samples were significantly lower than hyporheic water samples, with mean concentrations of 12.5 μg/L N and 160 μg/L N, respectively. This study also found that hyporheic NH_4^+ concentration decreased with increased distance from the streambank.

Overall, mean NH_4^+ concentration of surface and hyporheic water displayed a significant increase from fall to spring. However, a significant decrease was observed in the hyporheic water samples beneath the streambed. Ammonium appears to accumulate beneath the streambed during salmon spawn and/or throughout the summer, whereas NH_4^+ in the riparian hyporheic zone accumulates and stores over the winter. This reversal of NH_4^+ concentration between seasons could indicate reciprocal subsidies and the presence of a nitrification-denitrification coupling system on a larger time and spatial scale. During spring break-up, hydraulic head in the riparian to rose up to 10 cm beneath the land surface, providing water and nutrients to shallow-rooting plants at the onset of the growing season. This combination of snowmelt and precipitation coincided with greater riparian NH_4^+ concentration and a diffuse export of hyporheic water into the surface stream. These events occur around the time salmon fry emerge from the gravels, delivering a pulse of limiting nutrients and organic matter to activate stream microbial activity and supply energy for growth.

Anthropogenic sources of N from fertilizers and fossil fuel combustion persist and downstream eutrophication is an ever-growing global problem (Seitzinger et al. 2006), which has the potential to harm salmon at all life stages. The primary mechanism that permanently removes inorganic N is denitrification (Zarnetske et al. 2011). Since riparian and hyporheic zones are especially proficient at this process, understanding the diverse interaction of conditions that facilitate denitrification is critical to improving and protecting freshwater and marine environmental health.

Chapter 3

Uptake, Storage, and Trophic Transfer of Marine-Derived Nutrients in the Stream-Riparian Ecosystem

> *"When one tugs at a single thing in nature,*
> *he finds it attached to the rest of the world."* – *John Muir*

3.1 Stream-Riparian Food Webs

Salmon provide an isotopically-enriched marine-derived nutrient (MDN) signature when they migrate to freshwater rivers and lakes, which can be traced using stable isotopes of carbon and nitrogen ($\delta^{13}C$ and $\delta^{15}N$) (Mathisen et al. 1988, Kline et al. 1990, 1993, France 1994, 1995). Previous studies have estimated MDN incorporation in freshwater and terrestrial organisms to be as much as nearly 75% total N and over 50% total C (Bilby et al. 1996, Chaloner et al. 2002, Honea & Gara 2009). In interior British Columbia, this annual pulse of salmon nutrients occurs in the fall (Albers & Petticrew 2012), providing a significant nutrient subsidy to enhance stream productivity (Cedarholm et al. 1999, Gende et al. 2002, Naiman et al. 2002, Schindler et al. 2003, Janetski et al. 2009). However, certain types of organisms may have a better advantage to benefit from MDN because of their trophic role, the local ecology, and the timing of salmon spawn (Hicks et al. 2005, Lessard et al. 2009, Wipfli & Baxter 2010, Rinella et al. 2012, 2013). Additionally, nutrient pulses are carried through aquatic systems more quickly than terrestrial, so location within or proximity to a stream may affect nutrient assimilation and retention (Ben-David et al. 1998, Bilby et al. 2003, Nowlin et al. 2008).

At the base of a stream food web, primary producers (i.e. algae, diatoms, and microscopic phytoplankton) extract MDN from sediments and the water column (Fischer 2003, Foreman & Covert 2003, Tiegs et al. 2011). Bacteria and fungi colonize streambed substrates and salmon carcasses, and eventually entrap sediments and other primary producers, such as algae, to form a nutritious mass of biofilms (Figure 3.1; Costerton et al. 1995, Wipfli et al. 1998, Schindler et al. 2003). Consumers, including zooplankton and macroinvertebrates, obtain most of their energy from primary producers and biofilms, and some may incorporate MDN through direct consumption (Kline et al. 1997, Bilby et al. 1998, Minakawa & Gara 1999, Wipfli et al. 1999). Smaller consumers provide a rich and abundant food source for larger consumers, such as fish and aquatic, or semi-aquatic, mammals, which also may predate on spawning salmon or scavenge salmon carcasses (Cedarholm et al. 1989, Wipfli et al. 1998, Woodward et al. 2005). Stream food webs, however, exhibit even great complexity because they are imbedded within the surrounding terrestrial landscape (Cummins 1974, Vannote et al. 1980, Ward et al. 1998, Piccolo & Wipfli 2002). Soil, leaf litter, terrestrial insects, birds, and predacious mammals may either consume or be consumed by aquatic organisms (Nakano & Murakami 2001, Allan et al. 2003, Foreman & Covert 2003, Allan & Castillo 2007, Christie et al. 2008).

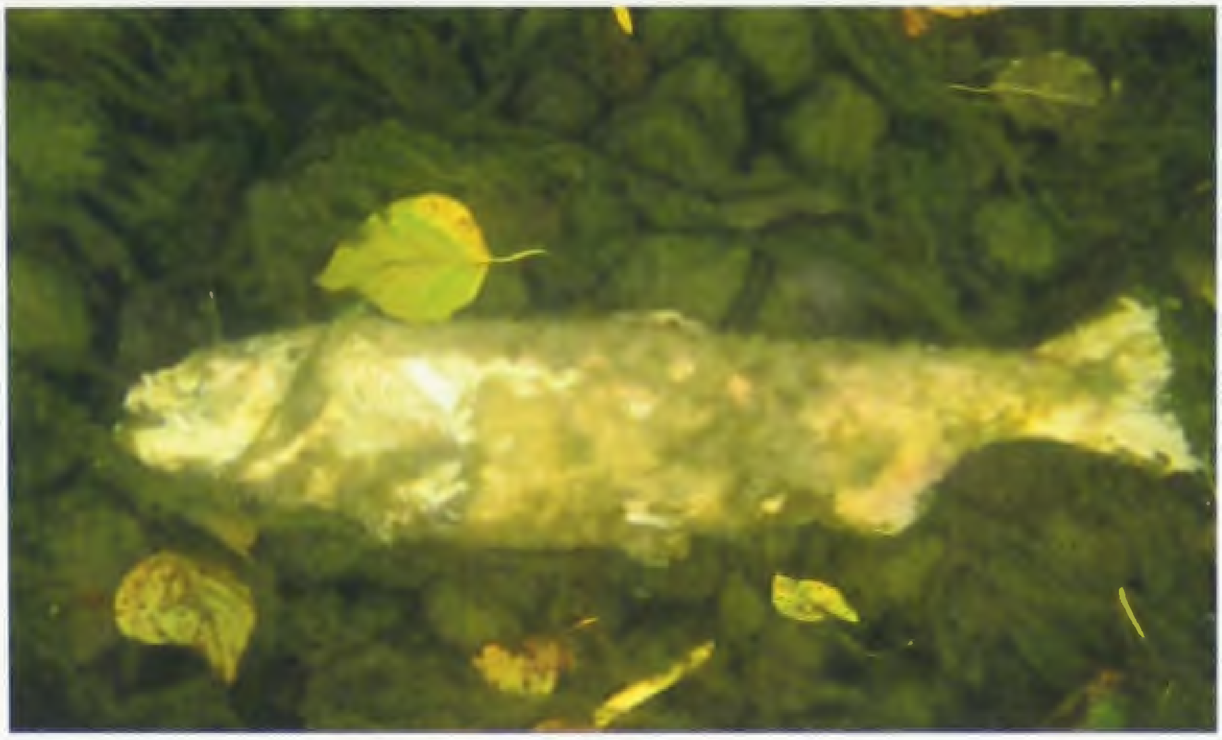


Figure 3.1. A decaying sockeye salmon (*O. nerka*) in the Horsefly River spawning channel. Biofilms, filamentous algae, and leaf litter can be seen on the surface substrate.

The interconnectivity of stream-riparian food webs can be observed through stable isotopic analysis of carbon and nitrogen, which is measured by the ratio of the heavy to light isotope (^{13}C:^{12}C and ^{15}N:^{14}N) and expressed as a δ-value in units of parts per thousand (‰). Stable nitrogen isotopes ($\delta^{15}N$) can indicate trophic position, as consuming organisms accumulate approximately 3-4‰ of the heavier isotope with each successive trophic transfer (DeNiro & Epstein 1981, Minagawa & Wada 1984). Since stable carbon isotopes ($\delta^{13}C$) change relatively little with movement through the food web, this ratio reflects an organism's diet and can be used to identify basal energy sources, including salmon (DeNiro & Epstein 1978, Staal et al. 2007). Although not used in this study, stable sulfur isotopes ($\delta^{34}S$) can also be used to track MDN assimilation in aquatic and riparian organisms. Sulfur isotopes can provide useful insight into MDN enrichment because they are a conservative diet tracer unaffected by confounding variations in trophic position (Hesslein et al. 1991, Barnes & Jennings 2007).

The annual resource pulse of salmon nutrients can help support macroinvertebrate populations (Minakawa et al. 2002, Lessard & Merritt 2006, Verspoor et al. 2011), enrich resident fish populations and increase juvenile salmon survivorship (Bilby et al. 1996, 1998, Wipfli et al. 2003, Rinella et al. 2012, Guyette et al. 2014), increase nutrient storage in basal resources, like biofilms (Albers 2010, Ruëgg et al. 2011, Reisinger et al. 2013), and promote terrestrial plant growth (Helfield & Naiman 2001, Koyama et al. 2005, Drake et al. 2006, Hocking & Reimchen 2009). Evidence of MDN enrichment may even persist in streamside vegetation and soils for years after salmon have left an area, known as a salmon legacy effect (Naiman et al. 2002, Schindler et al. 2003, Koyama et al. 2005, Reisinger et al. 2013).

3.1.1 Aquatic Food Webs

Macroinvertebrates, also referred to as aquatic insects or simply invertebrates throughout this chapter, are good indicators of the function and health of a stream ecosystem (Cummins 1974, Vannote et al. 1980). Each organism fulfills a particular ecological role and provides a crucial intermediate link that aids the flow of energy and nutrients between primary food sources and higher consumers (Malmqvist 2002, Woodward & Hildrew 2002). They are often categorized into the following functional feeding groups (FFG) based on their mechanism for obtaining food and the particle size of the food they consume: 1) shredders, 2) collector-gatherers, 3) collector-filterers, 4) scrapers, and 5) predators (Thorp & Covich 1991, Merritt & Cummins 1996). FFGs simplify the study of stream ecosystems by reducing a large number of taxa into a few collective groups; however, it must be recognized that most invertebrates feed opportunistically and cannot always be placed in a fixed

FFG (Anderson & Sedell 1979, Ward et al. 1998). Additionally, some food sources contribute directly to all consumers, particularly biofilms which are a ubiquitous assemblage of autotrophic and heterotrophic food sources (Allan & Castillo 2007, Allen et al. 2009). Detritus represents another ubiquitous food source in a stream that is composed of all non-living organic materials from terrestrial and aquatic origins (Flecker 1984).

3.1.1.1 Shredders

Shredders are the dominant FFG in low-order, headwater streams and in depositional microhabitats, such as pools, where the main food source is coarse particulate organic matter (CPOM) (Vannote et al. 1980, Honea & Gara 2009). Their functional significance is fundamental to freshwater food webs as they initiate nutrient cycling processes by breaking down, or shredding, CPOM (Graça 2001). Shredders are thought to preferentially consume terrestrial leaf litter (Vannote et al. 1980, Cummins et al. 1989, Bilby et al. 1996), and studies often report the highest abundance of shredders during fall (Hawkins & Sedell 1981, Reece & Richardson 1998, Thompson 2007). However, they will supplement their diet with other nutritious and available materials (Anderson & Sedell 1979, Graça 2001). Amphipods, which were abundant in the HFC, are versatile and omnivorous shredders that can adapt to seasonally shifting food sources, including terrestrial detritus, algae, biofilms, macrophytes, other invertebrates, fish, salmon roe, and carcasses (Brown & Diamond 1984, Mihuc & Mihuc 1995, MacNeil et al. 1997, Friberg & Jacobsen 1999, Thompson 2007).

3.1.1.2 Collectors

By converting CPOM to fine particulate organic matter (FPOM), shredders create a niche for collector-gatherers, which gather FPOM from the substrate, and collector-filterers, which filter FPOM from the water column (Short & Maslin 1977). As rivers grow larger and particles reduce in size, collecting organisms increasingly become the dominant macroinvertebrate groups (Vannote et al. 1980). Their precise diet is difficult to discern because they consume particles of everything that was once living, whether from terrestrial, aquatic, or marine origins (Allan & Castillo 2007).

3.1.1.3 Scrapers

Scrapers, also known as grazers, are adapted to shear or scrape algae from the surface of substrates and macrophytes (Lamberti et al. 1995). These organisms become more prevalent in mid-sized rivers where community consumption and respiration exceeds production via photosynthesis (Vannote et al. 1990). Due to their mechanism of feeding, scrapers consume primary producers and typically hold the lowest trophic position of macroinvertebrates (Anderson & Cabana 2007, Rinella et al. 2013). However, their food source is highly abundant and scraper populations can often coexist even though they have been known to consume over 90% of the plant biomass (Feminella & Resh 1991, Lamberti et al. 1995).

3.1.1.4 Predators

Predatory invertebrates derive their energy from live animal tissue and are often size selective, choosing prey smaller than themselves to consume (Hawkins & Sedell 1981, Graça 2001). The density of predators is not altered according to stream order, but instead is limited by prey availability (Vannote et al. 1990, Honea & Gara 2009).

3.1.2 Terrestrial Food Webs

In a stream-riparian ecosystem, allochthonous nutrient transfer to streams from the surrounding terrestrial environment has been well established (Vannote et al. 1980, Bilby & Bisson 1992, Polis & Hurd 1996, Naiman & Décamps 1997). However, nutrient fluxes also move in the opposite direction, from the stream to riparian, through flooding, advective hyporheic water transport, faunal delivery, and as emergent aquatic insects (Kennedy 1950, Cederholm et al. 1989, Kielland et al. 1997, O'Keefe & Edwards 2002, Ballinger & Lake 2006, Drake et al. 2006). The presence and ecological importance of nutrients transported from anadromous salmon to the riparian zone has been demonstrated through stable isotope anaysis of riparian biota (Bilby et al. 1996, Helfield & Naiman 2001, Naiman et al. 2002, Willson et al. 2004, Hicks et al. 2005, *and see* Chapter 1).

3.1.2.1 Willows

Willow trees, *Salix* sp., are common annual species in riparian zones, with deep roots that can penetrate the water table (Pinay et al. 2009). They rely mostly on groundwater during the growing season and are significantly limited by N availability (Menezes 2009). Their roots tend to exhibit increased growth toward the water table (Peter et al. 2012), with an average maximum rooting depth of 90 cm. Isotopic enrichment of *Salix* sp. is variable between studies, with some citing enrichment due to spawning salmon (Bartz & Naiman 2005, Koshino et al. 2013) and others documenting a lack of MDN assimilation (Hicks et al. 2005).

3.1.2.2 Horsetail

Horsetail, or *Equisetum* sp., has a lineage dating back to the 20-m tall Pseudobornia of the Triassic period, which also colonized streamside habitats, and may be the oldest living genus of vascular plants (Hauke 1963, Husby 2013). They have remained genetically isolated since the Jurassic period and retain ancient features of rhizomatous colonial growth and silicon-dependence (Channing et al. 2011). Today, horsetails have subsurface rhizomes that extend horizontally for long distances and can penetrate more than 1 m below the surface (Mitich 1992, Hodson et al. 2009). Marsh et al. (2000) found that the roots and rhizomes of *Equisetum* sp. concentrate in the upper soil C horizon, suggesting that this is where most of its nutrients are acquired. Their extensive rhizome system allows them to assimilate nutrients and sunlight from a wide-reaching area.

3.1.2.3 Dandelions

The common dandelion, *Taraxacum officinale*, has been a pervasive invasive species in North America for around 1000 years and colonizes a wide range of habitats, particularly wet, disturbed areas (Vavrek et al. 1997). They possess a highly-regenerative tap root that penetrates deep into the soil to reach moisture and nutrients beyond the limit of many other herbaceous species (Jackson 1982). Tap roots of 10 to 15 cm in length are common, but they are capable of growing up to 1 or 2 m (Stewart-Wade et al. 2002). *Taraxacum* sp. are commonly used in ecological studies due to their ubiquitous distribution across temperate climates. They possess an ability to concentrate a wide array of anthropogenic pollutants from the soil and are often utilized to monitor metal contamination in an area (Kabata-Pendias & Dudka 1991, Collier et al. 2010, Gworek et al. 2011, Maleci et al. 2014).

3.1.2.4 Soil

Hyporheic and riparian soil is a porous medium through which water can flow (Triska et al. 1989, Harvey & Wagner 2000). Surface water enters and moves through these soils, delivering nutrients, dissolved organic matter (DOM), and oxygen that have traveled downstream or have been laterally displaced from the surrounding land (Allan & Castillo 2007). This infiltration supports a diverse population of millions of microorganisms that live within soil, perpetually transforming organic and inorganic compounds (Lowell et al. 2009, Febria et al. 2011). Numerous combinations of sources, processes, and products makes understanding the mechanisms behind N and C cycling challenging, but large scale patterns exist among the variation (Foreman & Covert 2003, Billings & Richter 2006, Borch et al. 2010). Richter et al. (2000) conducted a 40-year forest development assessment and discovered two overwhelming conclusions about soil N and C budgets of an N-limiting system. First, there was a massive net transfer of N from mineral soils to the top organic soil layer and forest biomass, meanwhile N loss from the ecosystem was negligible. Second, total organic C content in mineral soils remained relatively unchanged, whereas the organic soil layer accumulated substantial amounts of C each year.

3.1.2. Hypotheses

This study aims to investigate MDN assimilation, trophic transport, and storage in a stream-riparian food web by tracing $\delta^{13}C$ and $\delta^{15}N$ in stream macroinvertebrates and riparian vegetation and soil during the 2011 sockeye salmon spawn and subsequent spring. In British Columbia, salmon spawn occurs in the fall when many plants are senescing or becoming dormant. Despite an apparent contrast in run timing and tree growth, biological uptake of MDN can occur quickly and be stored within riparian soil and plants (Drake et al. 2006) and streams (Bilby et al. 1996). There are still questions, however, especially in regard to the environmental factors that limit uptake and persistence of MDN in individual species and as the riparian forest as a whole (Drake et al. 2011, Devries 2012, Rinella et al. 2013).

For this study, macroinvertebrates were evaluated according to their functional feeding group to determine if species type, abundance, and stable isotopic concentration changes during the MDN pulse and between seasons. Three riparian plant species with differing life strategies were investigated to determine the pathway, uptake, and retention of MDN in the riparian zone adjacent to the salmon spawning channel. The following hypotheses were developed to evaluate the aim listed above:

Null Hypothesis V: There will be no difference between stable isotopic signatures ($\delta^{13}C$ and $\delta^{15}N$) of macroinvertebrate taxa throughout salmon spawn and between fall and spring.

Null Hypothesis VI: Macroinvertebrate $\delta^{15}N$ signatures will not be correlated with NH_4^+ concentration of surface and hyporheic water.

Null Hypothesis VII: There will be no difference between stable isotopic signatures ($\delta^{13}C$ and $\delta^{15}N$) of riparian vegetation between seasons.

Null Hypothesis VIII: Stable isotopic signatures ($\delta^{13}C$ and $\delta^{15}N$) of riparian vegetation and soil will not be correlated with distance from the streambank.

Null Hypothesis IX: Riparian vegetation $\delta^{15}N$ signatures will not be correlated with NH_4^+ concentration of riparian hyporheic water.

3.2 Methods

3.2.1 Field Sampling and Laboratory Analysis

Macroinvertebrates and salmon carcasses were sampled from the Horsefly River spawning channel (HFC) in Horsefly, British Columbia (Figure 2.1). Vegetation and soil were sampled from a riparian meander bend adjacent to the channel. The spawning channel was artificially constructed in 1989 to enhance salmon habitat; therefore, development of the channel bed and bank, as well as near-stream soil, is not natural. A meander bend located on the Horsefly River would likely be composed of sandier material. Still, the HFC remains hydrologically connected to the Horsefly River throughout the year, providing a year-round, off-channel habitat for stream and riparian organisms. The dominant microhabitat for most of the channel was a glide, with occasional pools representing the non-dominant habitat. The 625-m^2 experimental site encompasses the channel and riparian zone of a single meander bend (Figure 2.4). The stream habitat here was a uniform glide, with a fluctuating depth of approximately 0.5 to 1.0 m between low and high water events. The substrate consisted of a roughly 1-m deep gravel layer with uniform particle size and shape designed for ideal spawning conditions. The majority of the riparian zone was a forest comprised of predominantly deciduous trees and shrubs with a diameter at breast height of less than 0.3 m. At the upstream portion of the study site, the forest becomes a grassy area with small shrubs, which was likely disturbed by the building of a temporary road to the channel and is currently in an early successional stage. The sampling sites located within this grassy area were piezometers F and G, soil pit 1, and vegetation samples from 0 and

10 m on Transect 1 and 0 m on Transect 2. Terrestrial MDN deposits within the study site, as well as observed bear activity, were minimal; a total of five salmon carcasses and two piles of bear feces were recorded during the salmon spawn. Additional details about the study site and design can be found in Section 2.2.1.

3.2.1.1 Macroinvertebrates

Benthic macroinvertebrate samples were collected during each study week in Fall 2011 (n=5) and once after break-up in May 2012 (Figure 2.6) with a Surber sampler (500-μm mesh size). Sampling prior to spring break-up was not possible due to ice cover. While avoiding salmon redds, three random samples were taken at a cross-section about 5 m downstream from the study site at river right, mid-stream, and river left by disturbing a 0.093-m^2 area of the gravel bed for 1.5 minutes to a depth of 15 cm. Precise locations were not re-sampled between weeks; therefore recolonization of a sampling area was not measured. Sampling procedures were designed to quantify benthic macroinvertebrates residing on and within streambed gravels. The samples were preserved with 70% ethanol (Flecker 1984), and most extraneous materials (i.e. substrate, algae, leaf litter) were kept in the sample to avoid accidentally discarding invertebrates, besides for large rocks capable of crushing the sample. Although Surber samplers are designed for use in water <30 cm deep (Peckarsky 1984), the stream was shallow enough for the sampler to function as a kicknet for this study.

In the laboratory, macroinvertebrates were identified to the lowest practical taxonomical level (either genus or species) using *An Introduction to the Aquatic Insects of North America* (Merritt & Cummins 1996). Each taxon was assigned to one of the following functional feeding groups (FFG): collector-gatherers, collector-filters, scrapers, shredders, or predators. The family Chironomidae, however, includes species from two FFGs and was not identified further than family level because accurate identification required equipment and expertise unavailable for this study. Consequently, chironomid FFG assignment was generalized as 90% collector-gatherers and 10% predators, in accordance with Merritt & Cummins (1996).

After identification, individuals were sorted into taxa groups, dried to a constant mass (48 h at 75° C in a drying oven), and weighed on a microbalance (resolution of 10^{-7} g). The total mass of a group was used to calculate taxa biomass (g/m^3) per sampling week (Mason et al. 1983).

3.2.1.2 Riparian Vegetation

Vegetation samples were collected during three sampling weeks: pre-spawn (August 2011), post-spawn (October 2011), and after spring break-up (May 2012). This sampling schedule was selected to characterize nutrient uptake during the salmon spawn and after the winter. A total of six samples were taken along two transects at 0 m, 10 m, and 20 m. Transect 1 runs perpendicular to the stream at the top of the meander bend. Transect 2 runs parallel to the stream across the meander bend (Figure 2.4). From here on, locations at Transect 1 are referred to as T1-0, T1-10, and T1-20. Locations at Transect 2 are T2-0, T2-10, and T2-20. Three species were collected at each location: Common horsetail (*Equisetum arvense*), Pacific willow (*Salix lucida*), and Common dandelion (*Taraxacum officinale*). These species were chosen to represent different rooting depths and root structure. After collection, samples were transported to a freezer within 4 hours and remained frozen until laboratory analysis.

To obtain information of annual tree growth, three tree cores were extracted using an increment borer from a willow tree located centrally on the riparian meander bend. Cores were analyzed by UNBC's Tree Ring Lab following standard dendrochronological procedures. After mounting and sanding the tree cores, annual rings were measured to 0.001 mm using a Velmex measuring system (Stokes & Smiley 1968). Raw ring widths were averaged between cores and mean standardized chronologies were developed using the program ARSTAN to produce an index value (Veblen et al. 1991).

3.2.1.3 Additional Sampling

Soil samples were collected in May 2012 at three riparian locations at the study site (Figure 2.4). Soil pits were excavated to approximately 1-m deep and soil profiles were described by identifying horizons A, B, and C and measuring horizon widths (Figure 2.10). A soil horizon is a layer that is distinctly distinguishable from its adjacent layers. Certain soil characteristics, such as particle shape and color, were recorded using a Munsell® color chart. Porosity measurements performed in the laboratory also aided in describing the geologic material (refer to Section 2.2.3). Samples were extracted from each horizon, with additional samples collected where clay mottling was present, and frozen within 4 hours of collection. Soil sampling methods generally followed those of Schoeneberger et al. (2002).

During the 2011 salmon spawn, samples of freshly dead salmon tissue and bear feces were collected from the study site as baseline salmon nutrient data. Samples were placed in a freezer within 4-hours of collection.

3.2.1.4 Stable Isotope Analysis

In preparation for stable isotope analysis, macroinvertebrates, vegetation, and soil samples were dried to a constant mass in a drying oven (for 48 hours at 75°C) and samples of salmon tissue and bear feces were freeze-dried for 48 hours. Dried samples were crushed using a mortar and pestle and weighed into tin capsules (at a resolution of 10^{-7} g) at the University of Northern British Columbia's Central Equipment Laboratory. These samples were then shipped to the University of California-Davis Stable Isotope Facility for analysis of carbon and nitrogen stable isotopic signatures ($\delta^{13}C$ and $\delta^{15}N$) using a continuous flow-isotope ratio mass spectrometer (dual-inlet Europa 20/20, PDZ Europa, Sercon Ltd., Cheshire, UK.). Isotope enrichment (reported in parts per thousand ‰) was determined as follows (McConnachie & Petticrew 2006):

$$\text{‰}\ \delta^{13}C \text{ or } \delta^{15}N = [\ (R_{sample} - R_{standard})\ /\ R_{standard}\ ]\ *\ 1000 \qquad \text{Eqn (3.1)}$$

where R is the ratio of the heavy isotope to the light isotope. A more positive δ value is isotopically enriched, which means that the sample contains proportionally more of the heavy stable isotope. Final values are expressed relative to internationally accepted standards of V-PDB (Vienna PeeDee Belemnite) for carbon and Air for nitrogen (Bilby et al. 1996). For quality assurance and control, about 10% of the samples were randomly split into duplicates prior to submission to UC-Davis. The mean relative percent difference (RPD) in molar C:N ratios of duplicated invertebrate and vegetation samples was 1.9%. Mean RPD for duplicated soil samples was 29.3%. This significant difference highlights the high variability of soil over short spaces (Freeze & Cherry 1979). Consequently, all samples were retained for data analysis and values from duplicate samples were averaged.

3.2.2 Statistical Analysis

Dual isotope plots were created to visualize mean $\delta^{13}C$ and $\delta^{15}N$ signatures of sampled organisms and materials for Fall 2011 and Spring 2012 by using the package "ggplot2" in R (Wickham 2009). The following statistical analyses were performed in R using the packages "stats", "nlme", and/or "base".

3.2.2.1 *Aquatic Samples*

In order to examine temporal trends in macroinvertebrate isotopic signatures, autocorrelation tests were conducted using R's built-in autocorrelation function [acf()] to determine if $\delta^{13}C$ and $\delta^{15}N$ concentration of each species was statistically independent between location (river right, mid-stream, and river left) and sampling week (Chatfield 2004). Dependence was discovered between sampling locations, so the three locations were averaged by taxa per week. All data were evaluated for a normal distribution by observing the histogram and quantile-quantile plot (Q-Q plot).

Only three insect orders (Amphipoda, Diptera, and Ephemeroptera) had sufficient biomass during both seasons to perform temporal analysis on stable isotopic signatures of $\delta^{13}C$ and $\delta^{15}N$. Chironomidae was the only family present in the order Diptera, so this group will simply be referred to as chironomids from here on. Linear regressions were conducted to analyze MDN concentration between sampling week and season. Multiple and linear regressions of MDN were analyzed against predictor variables of mean surface water NH_4^+ concentration, mean hyporheic water NH_4^+ concentration (from piezometers C and D), number of salmon, insect biomass, number of individuals per order, and surface water level that corresponded with each sampling period. Before analysis, all variables were standardized using Equation 2.5 to eliminate discrepancies between units of measurement and enable direct interpretation. Regression output results of p-value, R-squared, and effect size were used to interpret the significance, goodness-of-fit, and strength of a particular model. The confidence level for statistical significance was set to $p \leq 0.05$. Additionally, highly significant results were identified if $p \leq 0.001$.

3.2.2.2 *Diversity and Evenness of Macroinvertebrate Communities*

To better understand how the macroinvertebrate community of the HFC compares to that of the natural river, diversity and evenness calculations were evaluated with samples from the Horsefly River, taken by the B.C. Ministry of Environment on Oct. 4, 2011. These indices are helpful in understanding environmental health because a community that is highly uneven or has low biological diversity is less resistant to environmental stress (Peet 1974, Wittebolle et al. 2009). To assess community diversity, two well-known heterogeneity indices were computed: Shannon Diversity Index and Simpson Index. These measurements are based upon a combination of species richness and heterogeneity (Peet 1974). The Shannon Index equation, which is more sensitive to community changes in rare species, is computed as follows:

$$= -\sum_i \left(\frac{n_i}{N} * \ln\left(\frac{n_i}{N}\right)\right)$$

Eqn (3.2)

The Simpson Index, which is more sensitive to changes in the most abundant species, is calculated as:

$$= \frac{\sum_i n_i(n_i - 1)}{N(N-1)}$$

Eqn (3.3)

where:
n_i = individuals of one species; and,
N = total number of individuals.

In order to define these diversity indices in terms of number of species, the effective number of species (ENS) was computed. This measurement describes communities as the number of equally-common species which would produce the same heterogeneity as the sample (Peet 1974, Jost 2006).

$$\mathrm{ENS} = exp(\mathrm{H}) \qquad \text{Eqn (3.4)}$$

where:
H = Shannon Index.

Finally, a Lorenz curve was graphed to visualize population evenness of a community. The Lorenz graph, originally developed to measure income inequality (Lorenz 1905), displays a straight 45 degree line to represent perfect equality in a population and the Lorenz curve, which shows population evenness, or inequality (Figure 3.2). The Gini coefficient was calculated from the Lorenz graph, which is a single value (ranging from zero to one) used to describe evenness (Wittebolle et al. 2009).

The sampling methods employed by the Ministry of Environment (J. McLeod, pers. comm.) differed from this study in several ways, and, therefore, the results can only be used as a broad comparison between the two environments. They performed two kick samples for a 6-min duration by walking from one bank to the other. Since our method was designed to capture invertebrates residing in the hyporheic zone, samples were collected at three locations for 1.5 minutes each to allow for collection 15 cm beneath the sediment surface. The microhabitat they sampled was a riffle, whereas our location was a glide. However, since these indices are only based on the number of individuals and species, and do not factor common species among locations, the microhabitat type is not a variable that affects individual diversity and evenness values. The Ministry used a net with a mesh size of 400 μm, as compared to ours at 500 μm, so our results may not include invertebrates between 400 and 500 μm. Due to these differences, I would expect samples from the Horsefly River to contain a larger total number of invertebrates because of a longer sampling duration and smaller mesh size. I would also expect the spawning channel samples to include a greater abundance of chironomids, as the study design aimed to capture deeper-residing organisms.

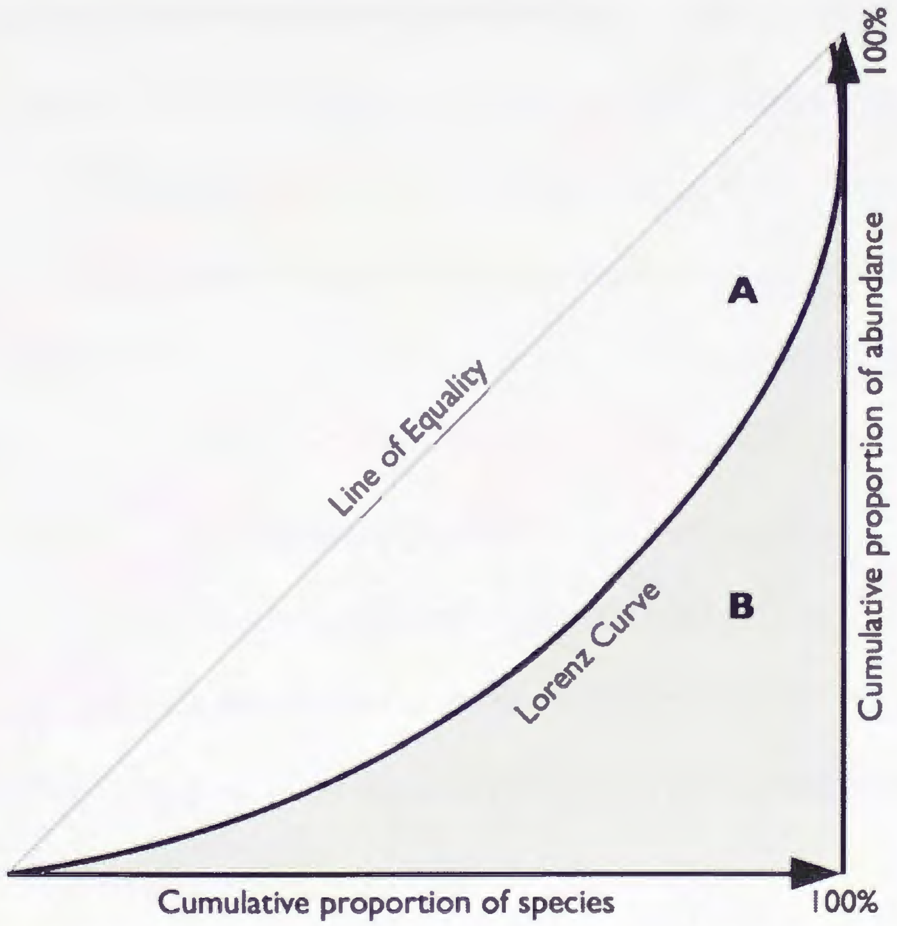


Figure 3.2. A typical Lorenz curve which graphically represents the inequality in a population. The areas above and below the Lorenz curve, marked A and B, respectively, simplifies the Gini coefficient equation, which is A/(A+B).

3.2.2.3 Riparian Samples

In order to examine temporal trends in vegetation isotopic signatures, autocorrelation tests were conducted using R's built-in autocorrelation function [acf()] to determine if $\delta^{13}C$ and $\delta^{15}N$ concentration of each species was statistically independent between the three sampling periods (Chatfield 2004). Since independence was identified, the $\delta^{13}C$ and $\delta^{15}N$ signatures across the six sampling locations were averaged between each species within a sampling period. All data were evaluated for a normal distribution by observing the histogram and quantile-quantile plot (Q-Q plot).

Linear least squares regressions were performed to test the hypothesis that vegetation isotope ratios will be higher with proximity to the stream. Model output results of p-value, R-squared, and effect size were used to interpret the significance, goodness-of-fit, and strength of a particular model. Additional predictor variables, including distance along transect, sample location, elevation, and rooting depth, were also applied to linear regression models in order to analyze other factors that may affect $\delta^{13}C$ and $\delta^{15}N$ signatures.

Stable isotopic signatures of soil samples were also analyzed for a normal distribution. Subsequent linear least squares regressions of $\delta^{13}C$ and $\delta^{15}N$ signatures against predictor variables of depth and distance from streambank were performed. Since the surface elevation varied at each soil pit, depth measurements were standardized to meters above sea level (mASL).

To test the relationship between vegetation isotopic signatures and NH_4^+ concentration of hyporheic water, linear regressions were performed for the Pre-spawn, Post-spawn, and Spring periods. Isotopic signatures from Transect 2 were paired with NH_4^+ concentration from nearby piezometers. Vegetation samples from T2-0 were tested against the average of NH_4^+ concentrations from sites F and G, which were both within 2 m of the vegetation samples. T2-10 isotopes were paired with NH_4^+ from K, which was also 2 m away. T2-20 isotopic signatures were matched with hyporheic site O, at a distance of 3 m from the vegetation samples. Stable isotopic signatures and NH_4^+ concentration were standardized before statistical analysis (Equation 2.5).

Statistical significance between spring vegetation and soil isotopes was tested through Pearson's product-moment correlations and linear regressions. The confidence level for statistical significance was set to $p \leq 0.05$. Additionally, highly significant results were identified if $p \leq 0.001$. For each soil pit, isotopic signatures from horizon A, B, and C were tested against vegetation isotopic signatures, with the notion that *S. lucida* isotopes will most closely correlate with horizon C and *E. arvense* and *T. officinale* isotopic signatures may reflect horizon A or B because of their shallower rooting depth. Each soil pit was paired with the closest vegetation transect: Soil 1 and T2-0, Soil 2 and T1-20, and Soil 3 and T2-20. The relationship between soil isotopes and hyporheic water NH_4^+ concentration could not be tested because there were not enough replicate soil observations collected.

3.3 Results

3.3.1 Temporal Trends of MDN

Dual isotope plots of $\delta^{13}C$ and $\delta^{15}N$ visually display the stream-riparian food web components at this site and provide an estimate of trophic levels (Figures 3.3 and 3.4). Predacious organisms of higher trophic level are located in the upper right corner of the graph (higher $\delta^{13}C$ and $\delta^{15}N$) and autotrophs are located in the lower left (lower $\delta^{13}C$ and $\delta^{15}N$). In the fall, the predacious subclass Hirudinea were the most enriched with $\delta^{15}N$ compared to all macroinvertebrate species. Riparian vegetation displays a lower (more negative) $\delta^{13}C$ value than the invertebrate groups. Vegetation $\delta^{15}N$ signatures vary widely between species, with *E. arvense* (Equisetum) exhibiting levels of $\delta^{15}N$ closer associated to those of invertebrates and salmon tissue. In the spring, macroinvertebrates remain enriched in $\delta^{13}C$ relative to riparian vegetation.

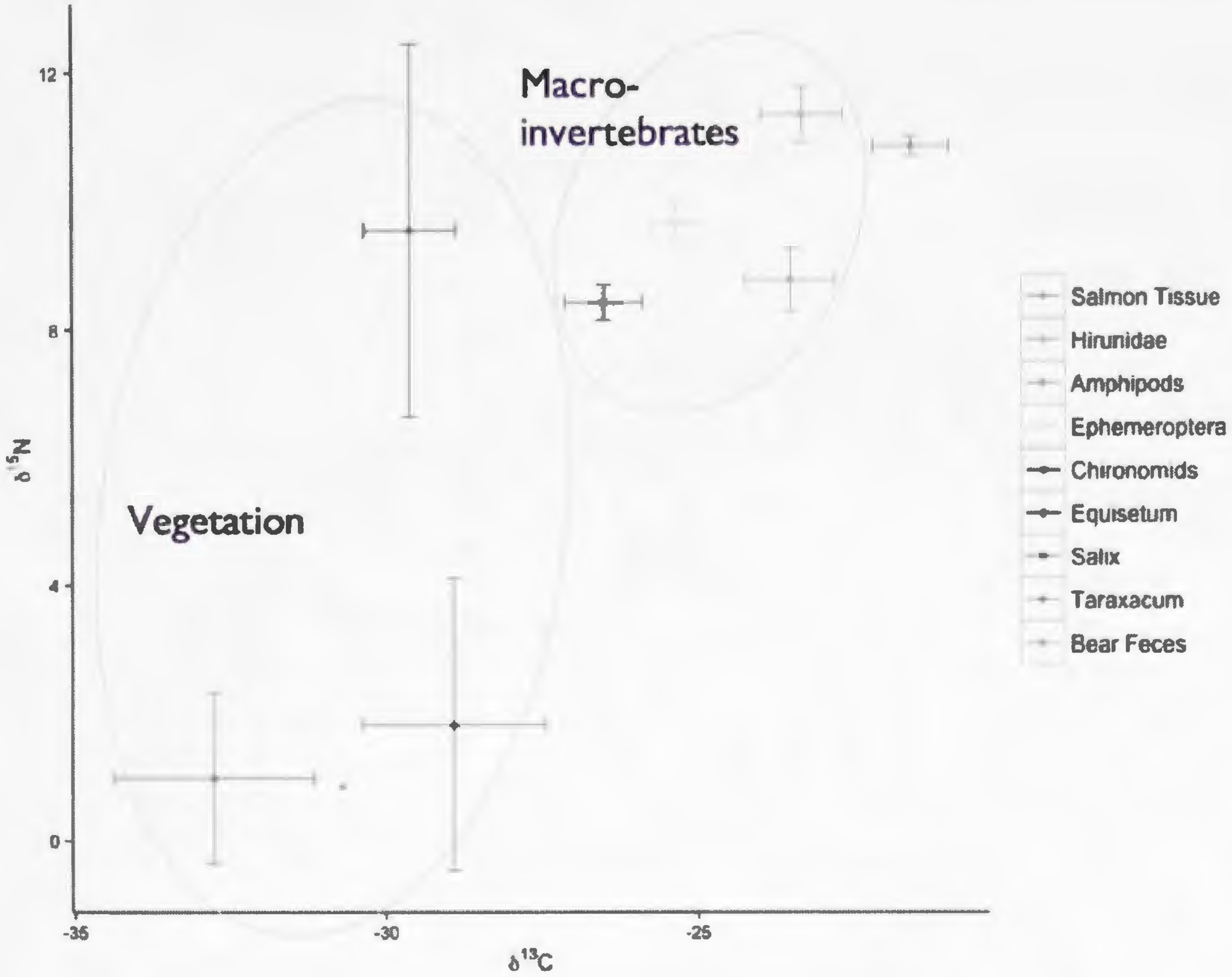


Figure 3.3. Dual isotope plot ($\delta^{13}C$ ‰ and $\delta^{15}N$ ‰) from all organisms and materials collected during the Fall 2011 salmon run. Isotopically enriched species are located in the upper right corner. Mean ± 1 SEM.

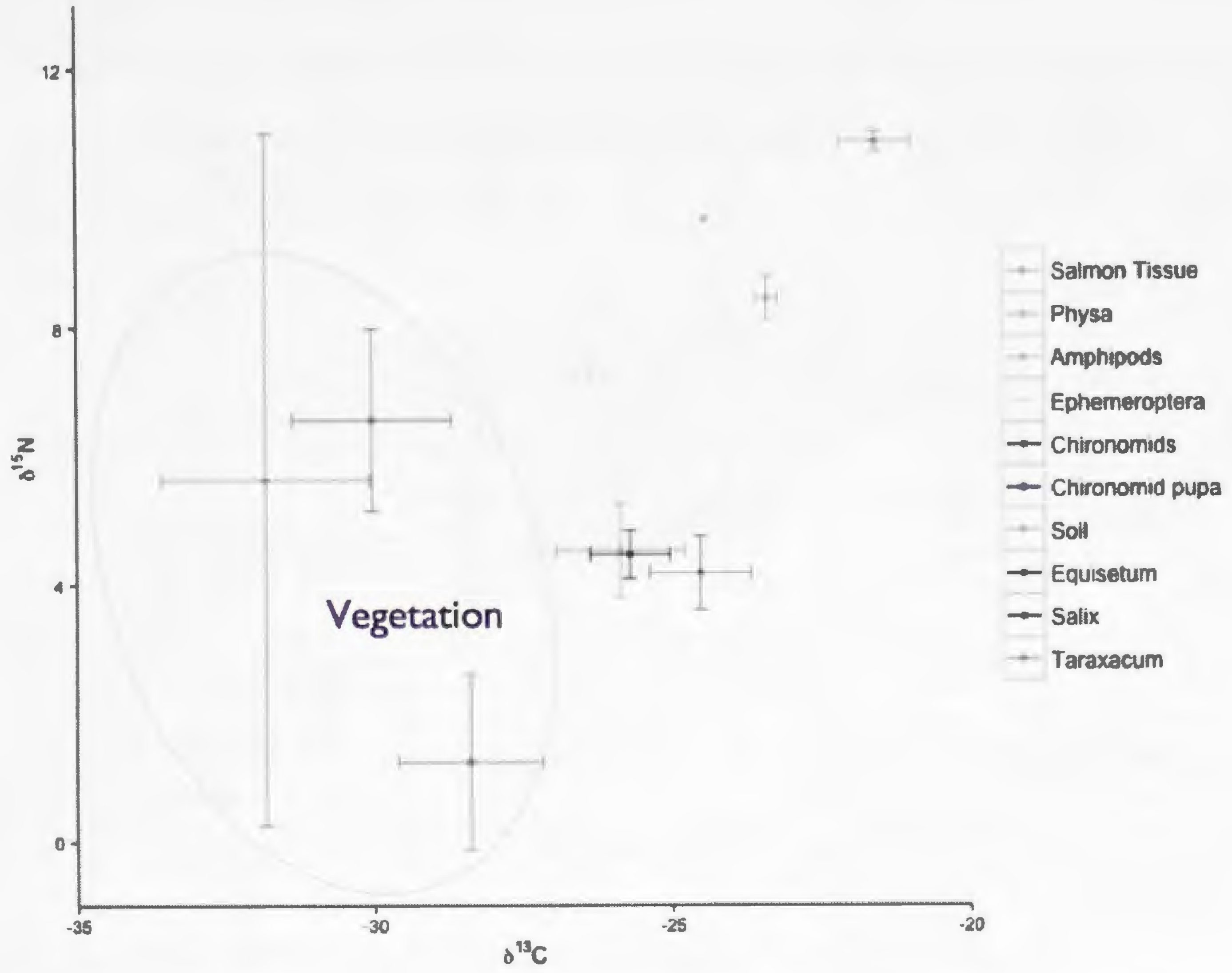


Figure 3.4. Dual isotope plot ($\delta^{13}C$ ‰ and $\delta^{15}N$ ‰) from all organisms and materials collected in Spring 2012, besides for salmon tissue, collected in Fall 2011, which is included as reference point. Mean ± 1 SEM.

The isotopic signatures of species that were collected in both the fall and spring are displayed in Figure 3.5. The invertebrates Ephemeroptera and Chironomids exhibited clear differences in $\delta^{15}N$ and $\delta^{13}C$ concentrations between seasons, with both groups displaying a significant decrease in spring $\delta^{15}N$ signatures. *T. officinale* (Taraxacum) was the only group with a higher overall $\delta^{15}N$ signature in the spring.

Regression analyses determined significant changes in isotopic signatures between seasons. Spring $\delta^{15}N$ signatures were significantly lower for Equisetum ($p <$

0.05), Chironomids ($p < 0.001$), and Ephemeroptera ($p < 0.001$). Conversely, spring $\delta^{15}N$ signatures for Taraxacum were significantly higher ($p < 0.05$). Signatures of $\delta^{13}C$ were significantly lower in spring for Ephemeroptera ($p < 0.05$), but higher for Chironomids ($p < 0.001$; Table 3.1).

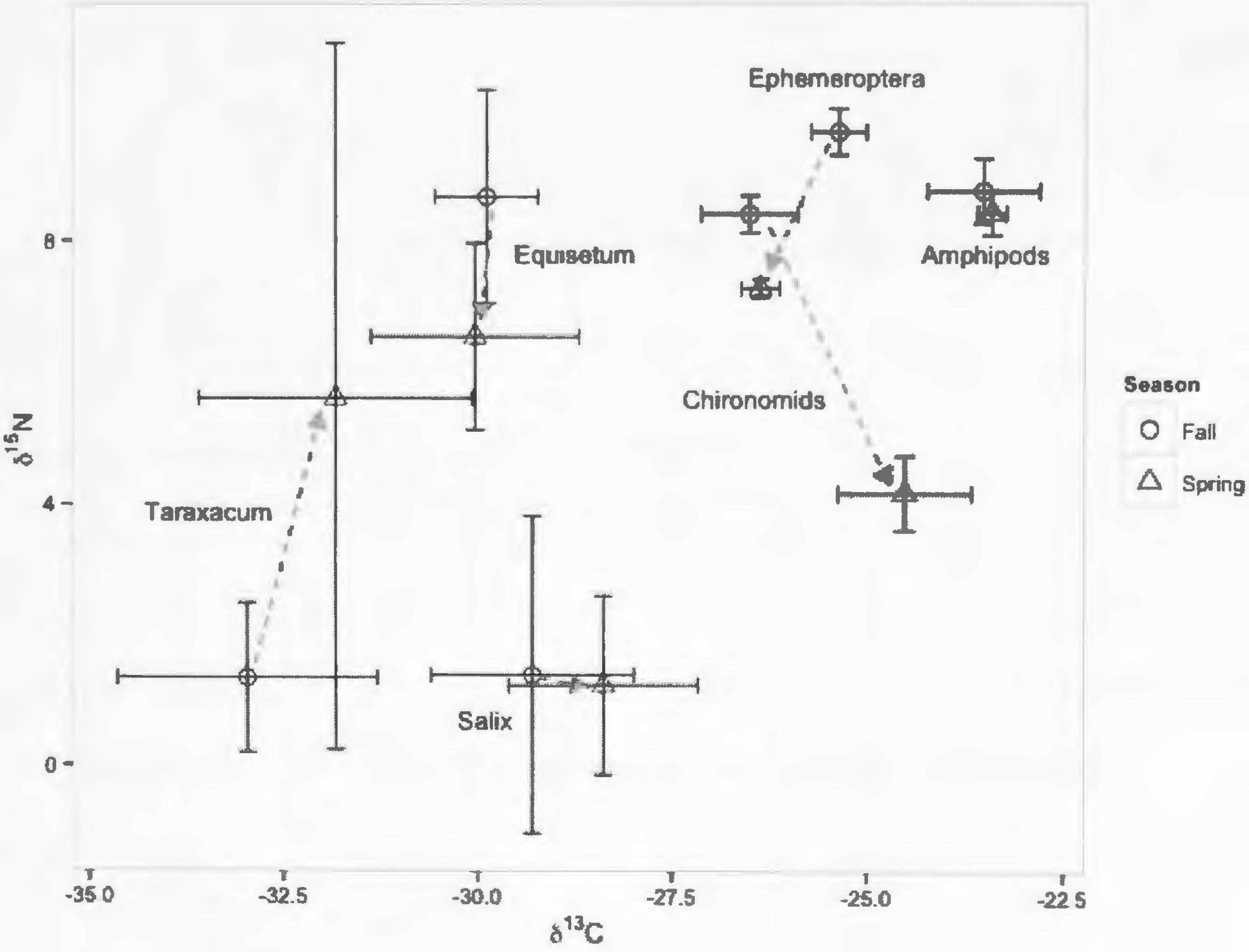


Figure 3.5. Temporal differences of vegetation and macroinvertebrate species collected in the fall and spring sampling periods. Units of $\delta^{13}C$ and $\delta^{15}N$ are parts per thousand (‰). Mean ± 1 SEM.

Table 3.1. Statistically significant differences observed in organisms between the fall and spring sampling periods.

Isotope	Group	p-value	Effect size	R-squared
$\delta^{15}N$	Equisetum	0.041	-3.843	0.284
$\delta^{15}N$	**Taraxacum**	**0.015**	**5.083**	**0.329**
$\delta^{15}N$	Chironomidae	7.2e-09	-4.242	0.969
$\delta^{15}N$	Ephemeroptera	1.2e-04	-2.377	0.959
$\delta^{13}C$	**Chironomidae**	**0.001**	**1.987**	**0.663**
$\delta^{13}C$	Ephemeroptera	0.009	-1.003	0.775

***Bold** indicates an increase in isotope value from fall to spring

3.3.2 Macroinvertebrate Assimilation of MDN

Macroinvertebrate groups Chironomidae and Ephemeroptera had a highly statistically significant association between $\delta^{15}N$ signatures and both surface water NH_4^+ and hyporheic water NH_4^+. Regression analysis showed that hyporheic NH_4^+ concentration increased with $\delta^{15}N$ signatures for both groups ($p < 0.001$). Simultaneously, $\delta^{15}N$ concentration of these species decreased when surface NH_4^+ increased ($p < 0.001$). There were no significant relationships detected between invertebrate isotopic signatures and the other tested predictor variables.

3.3.3 Macroinvertebrate Diversity and Abundance

Throughout the study, 13 different taxa from four phyla (Annelida, Arthropoda, Cnidaria, and Mollusca) were identified (Table 3.2). A cumulative total of 3,213 individual macroinvertebrates were enumerated and grouped into one of five functional feeding groups (FFG). Graphs of invertebrate biomass show that the majority of the community's biomass during every sampling week were shredders

(Figure 3.6). The shredder FFG was entirely composed of the species *Hyalella azteca* (referred to as amphipods for convenience). Biomass data are based on the mass of invertebrate groups; therefore the graphs of relative abundance (number of individuals in a group/total number of individuals) demonstrate a different ratio (Figure 3.7). These graphs show shredders as a dominant group, but they are outnumbered by collector-gatherers during some weeks, particularly in the fall. The collector-gatherers group contained taxa from the family Chironomidae, the subclass Oligochaeta, and the orders Ephemeroptera and Tricoptera, but consisted primarily of Chironomidae. When observing the taxon most commonly identified throughout the study, amphipods and chironomids were discernibly the most abundant species (Figure 3.8).

According to the Shannon Index and its related function, effective number of species (ENS), the Horsefly River has a greater diversity of species than the spawning channel (Table 3.3). However, results from the Simpson's Index and Gini coefficient indicate that the community in the spawning channel has greater species equality, or a similar number of individuals per species group (Table 3.3).

Table 3.2. Taxonomic identification and enumeration of macroinvertebrates in the Horsefly River spawning channel during the 2011 salmon spawn and the subsequent spring (labeled as Post-winter). The scientific classification of major taxonomic groups are identified in parentheses. Functional feeding group (FFG) classifications are as follows: CF (collector-filterers), CG (collector-gatherers), P (predators), SC (scrapers), and SH (shredders).

Taxon	FFG	Pre-spawn	Active spawn I	Active spawn II	Active spawn III	Post-spawn	Post-winter
Amphipoda (order)							
Hyalella azteca	SH	30	181	135	365	452	72
Diptera (order)							
Chironomidae	CG	13	43	169	259	405	304
Chironomidae pupa	CG		2	4	5	8	61
Pupa casing							215
Clitellata (class)							
Oligochaeta	CG	1	89	56	123	63	79
Hirudinea	P	2	16	20	28	11	2
Ephemeroptera (order)							
Leptophlebiidae paraleptophlebia sp.	CG	3	3	18	22	23	15
Baetidae	CG			1	1		8
unidentifiable		1	3	6	8	7	12
Plecoptera (order)	P					1	1
Tricoptera (order)							
Hydroptilidae oxyethira sp.	CG					2	
Hydropsychidae arctopsyche sp.	CF				2		
Gastropoda (class)							
Physa sp.	SC	4	10	1	8	7	4
Promenetus umbilicatellus	SC		11	10	16	7	12
unidentifiable		4	14	10	11	6	5
Bivalvia (class)							
Sphaeriidae	CF				7	1	
Hydrozoa (class)							
Hydra sp.	P	1	1				
Total		59	373	430	855	993	790

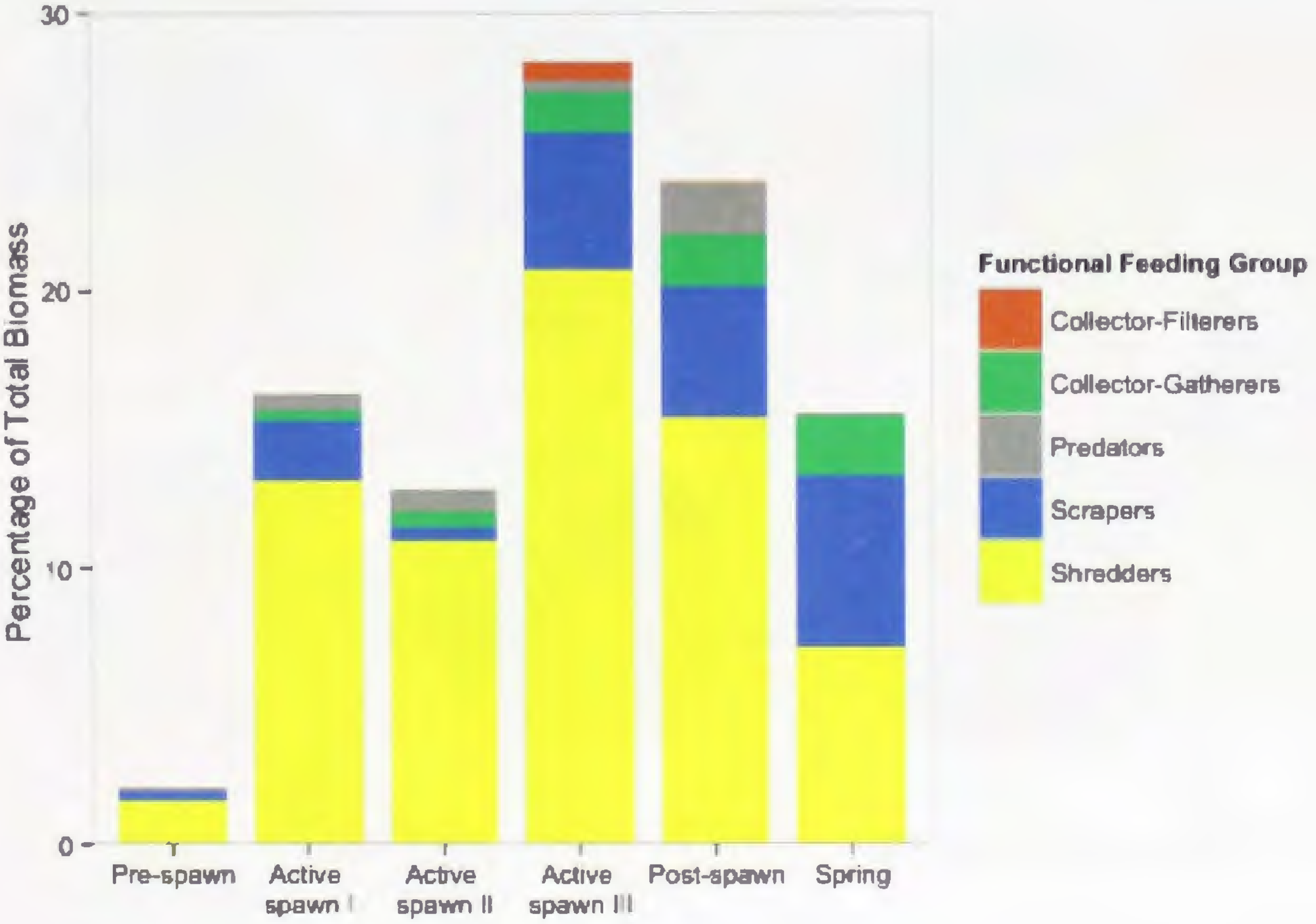


Figure 3.6. Bars displaying the percent biomass of each FFG during each sampling period. The height of the bars represents weekly biomass as a percentage of the total biomass. The actual weight of amphipods varied from a minimum of 50.2 mg during Pre-spawn and a maximum of 682.9 mg during Active Spawn III.

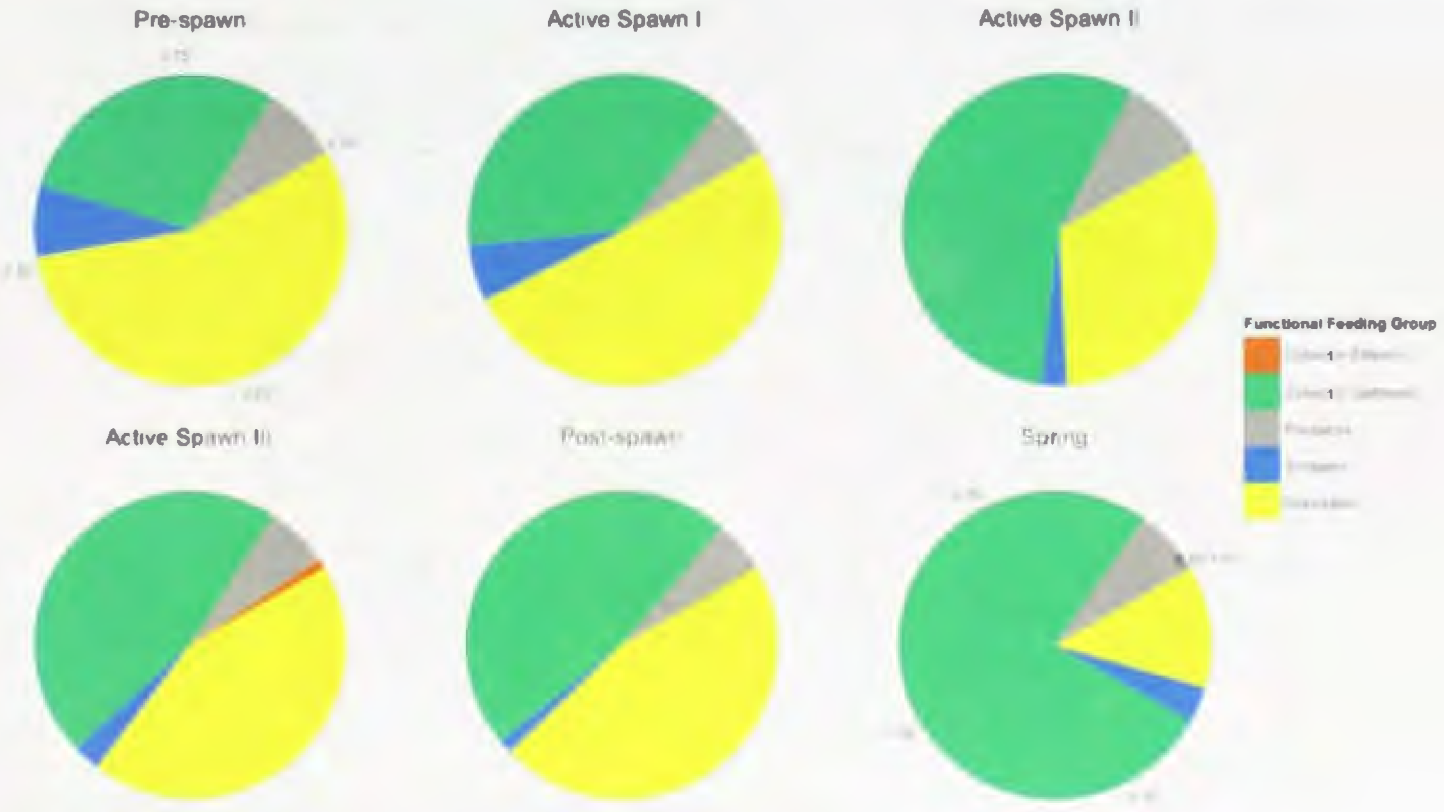


Figure 3.7. Pie charts displaying the relative abundance (as a percentage) of each FFG during each sampling period.

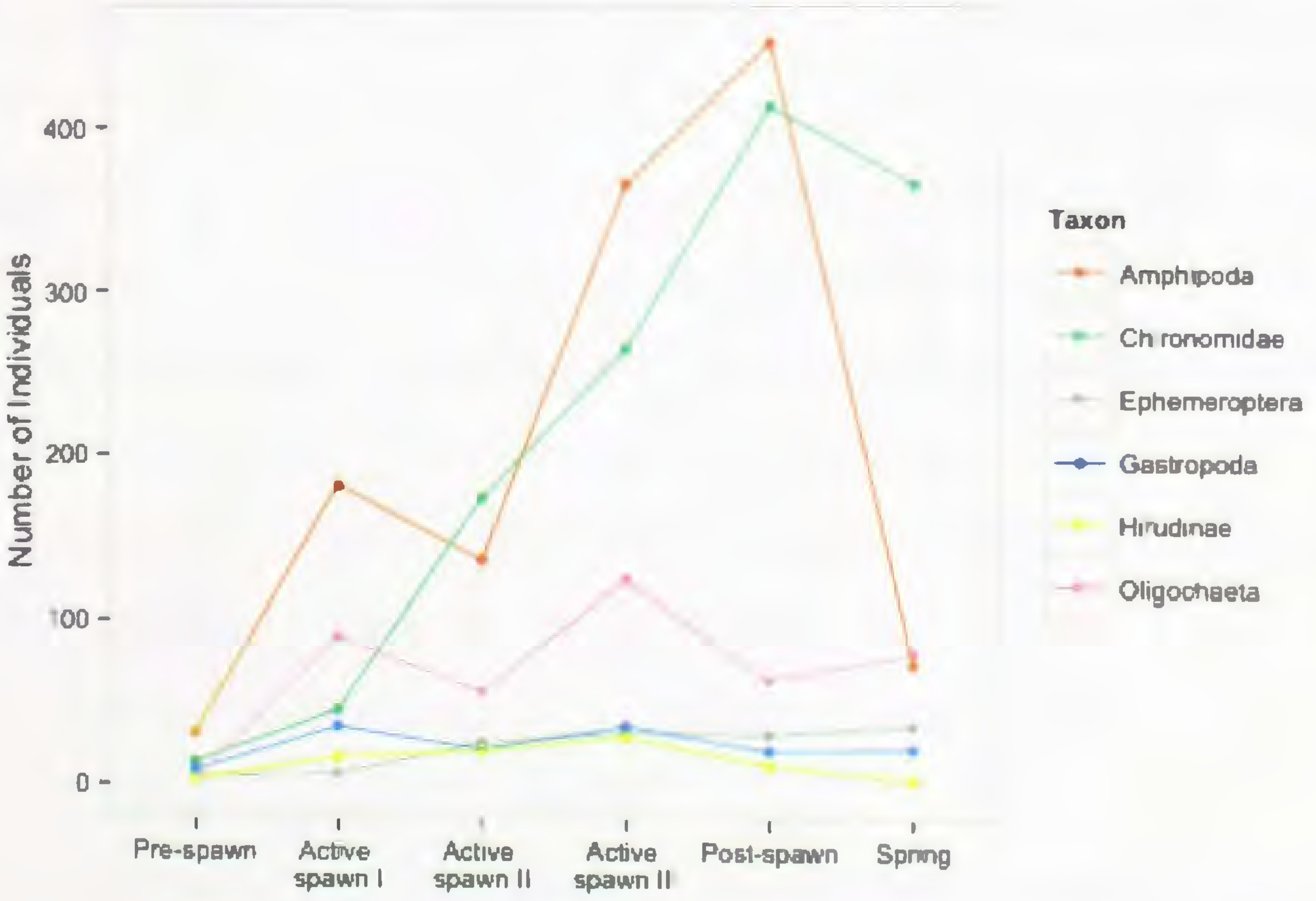


Figure 3.8. The number of individuals during each sampling week for commonly identified taxa at the HFC.

Table 3.3. Shannon Index and Effective Number of Species (ENS) diversity values, along with Simpson's Index and Gini coefficient evenness values for the Horsefly River spawning channel and the Horsefly River.

	Diversity		Evenness	
	Shannon Index	ENS	Simpson's Index	Gini coefficient
Spawning channel Post-spawn	1.133	3.1	0.789	0.745
Spawning channel Fall & Spring	1.364	3.9	0.646	0.763
Horsefly River Post-spawn	1.938	6.9	0.562	0.794

3.3.4 Spatial Trends of MDN in the Riparian Zone

S. lucida (Salix) isotopic signatures of both δ^{13}C and δ^{15}N displayed a highly significant decrease as the distance from the streambank increased ($p < 0.001$; Table 3.4). According to linear regression analysis, with every 1-m increment further away from the stream, δ^{13}C signatures decreased by 0.177‰ and δ^{15}N signatures decreased by 0.242‰ (Figure 3.9). Transect distance also displayed significance ($p < 0.001$ (δ^{13}C) and $p < 0.05$ (δ^{15}N)). When transects T1 and T2 were tested separately there was no significance detected between δ^{15}N and T2, indicating that distance from streambank is the primary variable when determining δ^{15}N concentration.

Regardless of season, *E. arvense* δ^{15}N signatures were found to be uniform across the study site. However, statiscially significant δ^{13}C trends from linear regressions detected that with every 1-m increase from the streambank values decreased by 0.085‰ ($p < 0.05$; Table 3.4).

T. officinale isotopes were generally consistent throughout the study site and no clear trends in isotope concentration were noted with distance from the stream.

Rooting depth was not a significant variable in predicting isotope concentration of vegetation species, nor were corresponding soil isotopes or hyporheic NH_4^+ concentration. Therefore, this study fails to reject the null hypothesis (IX) that there is not a correlation between riparian vegetation $\delta^{15}N$ signatures and riparian hyporheic NH_4^+ concentration

Overall, vegetation $\delta^{13}C$ signatures were highest at site T1-0, which was located directly on the streambank (Table 3.5). T1-0 exhibited significantly greater $\delta^{13}C$ signatures than sites T2-10 and T2-20 for all species. *S. lucida* $\delta^{13}C$ at T1-0 was significantly higher than all sites (except T2-0), and *E. arvense* $\delta^{13}C$ was greater than all locations (besides T1-10).

Table 3.4. Variables that display statistical significance in relation to terrestrial isotopic signatures.

Isotope	Group	Variable	p-value	Effect size	R-squared
$\delta^{15}N$	Salix	Distance from Streambank	0.001	-0.242	0.457
$\delta^{13}C$	Salix	Distance from Streambank	1.0e-04	-0.178	0.529
$\delta^{13}C$	Equisetum	Distance from Streambank	0.013	-0.085	0.369
$\delta^{13}C$	Soil	Depth	0.003	-1.834	0.544

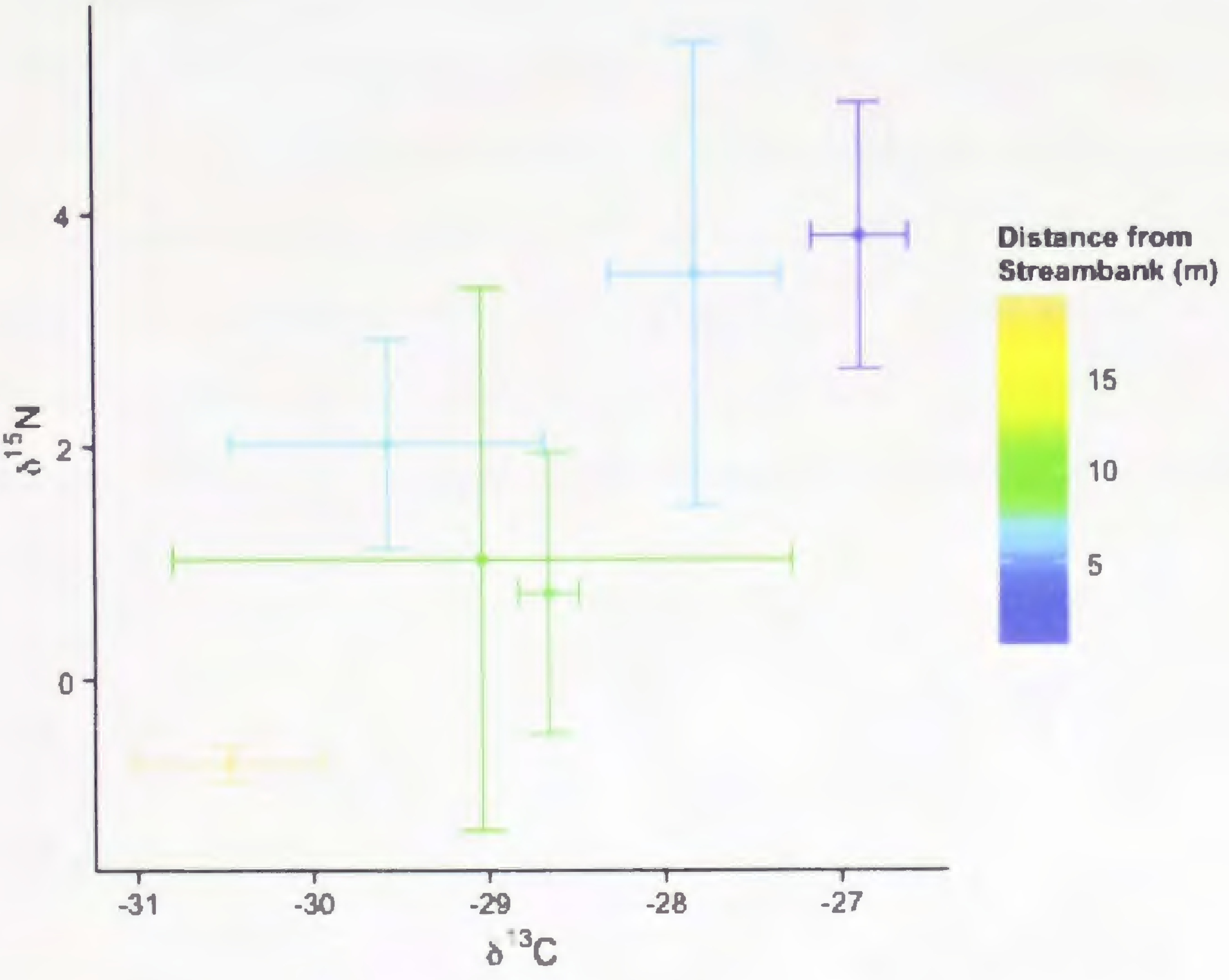


Figure 3.9. Dual isotope plot of willow (*S. lucida*) leaves. Each cross represents the average of all sampling periods at each sampling location. Units of $\delta^{13}C$ and $\delta^{15}N$ are parts per thousand (‰). Mean ± 1 SEM.

Table 3.5. P-values displaying significant differences in $\delta^{13}C$ at all vegetation sites compared to site T1-0, which was located directly on the streambank. Isotopic signatures were averaged between each sampling period.

	All species	Salix	Equisetum	Taraxacum
T1-10		<0.05		
T1-20	<0.05	<0.001	<0.05	
T2-0			<0.05	
T2-10	<0.05	<0.05	<0.05	<0.001
T2-20	<0.05	<0.05	<0.05	<0.001

There was a significant interaction between soil signatures of $\delta^{13}C$ and depth, with $\delta^{13}C$ increasing by 1.834‰ for every meter deeper below the surface (Figure 3.10, Table 3.4). Isotopic signatures of soil $\delta^{15}N$ were statistically uniform throughout the study site regardless of depth, but a closer look at soil pit 1, which was located closest to the streambank, reveals a positive trend with depth and both $\delta^{13}C$ and $\delta^{15}N$ (Figure 3.11). There was no statistical significance detected with soil $\delta^{15}N$ and distance from streambank thereby supporting a failure to reject this component of the null hypothesis (VIII).

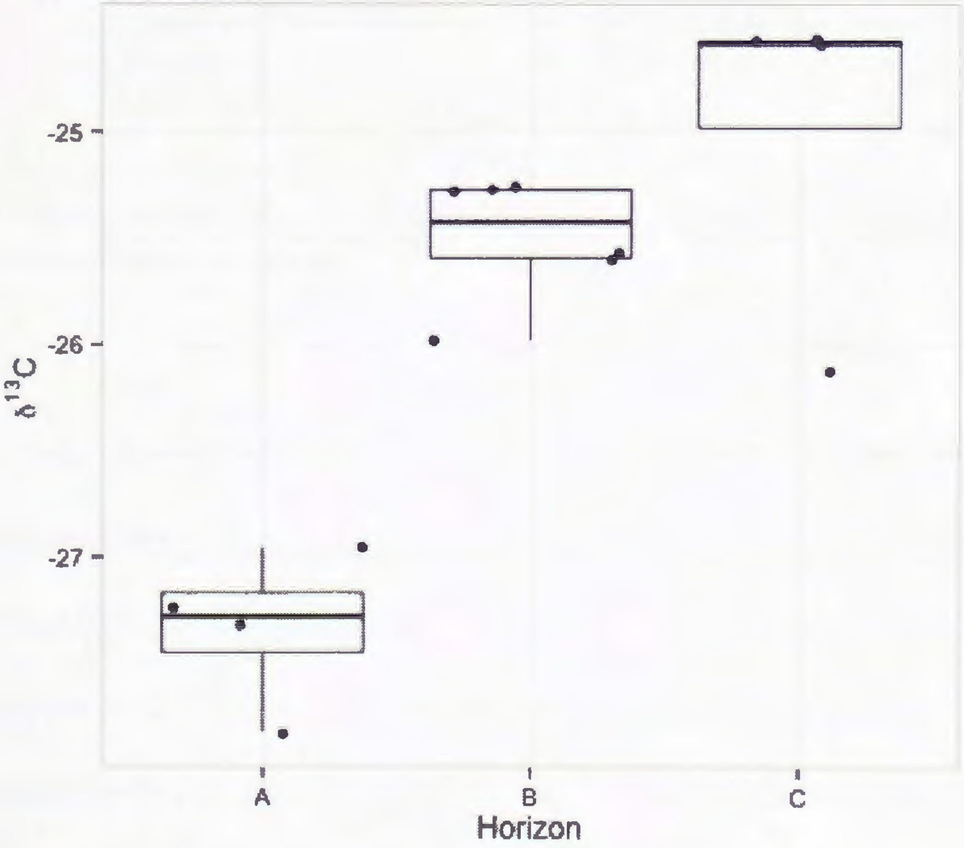


Figure 3.10. Box plots displaying $\delta^{13}C$ (‰) of soil horizons from three soil pits across the study site. Black dots represent actual $\delta^{13}C$ signatures.

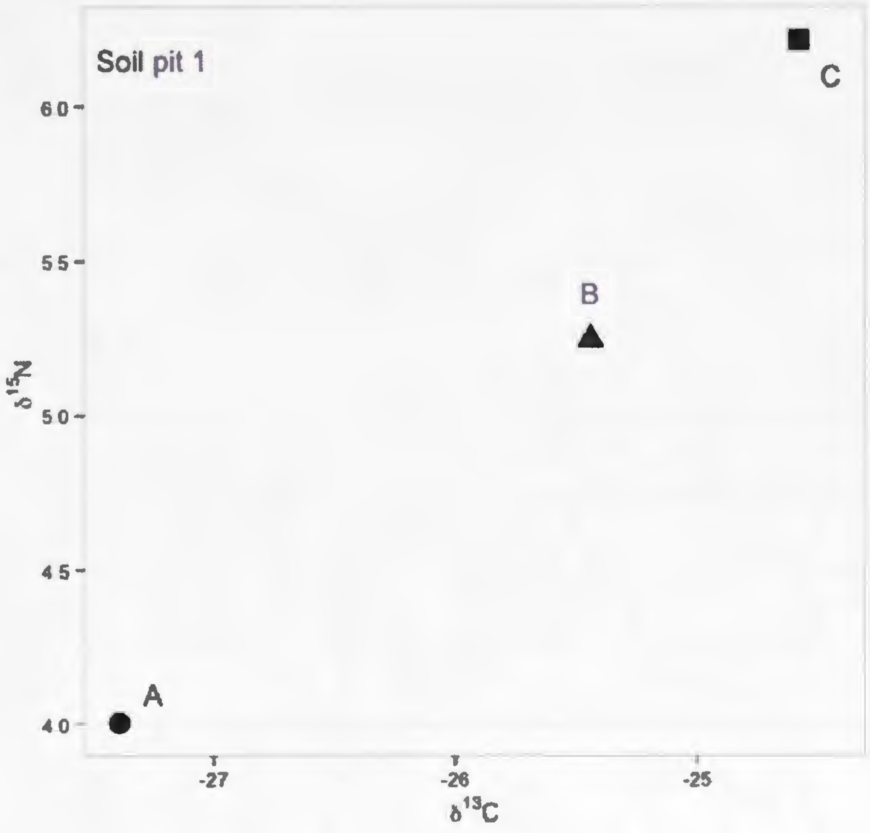


Figure 3.11. Stable isotopic signatures of $\delta^{13}C$ (‰) and $\delta^{15}N$ (‰) at soil pit 1, which was located closest to the streambank.

3.3.5 Tree Cores

Salix sp. tree cores were dated back to the year 1956. The spawning channel was constructed in 1989 and ring width analysis indicates that substantial tree growth began in 1996, with a record growth year in 1998 (Figure 3.12). A multiple regression analysis of ring width indices against salmon escapement in the spawning channel and total annual precipitation revealed that escapement and precipitation on their own do not predict ring width; however the interaction between these terms produces a significant regression ($p < 0.05$). When graphing standardized ring widths and salmon abundance (Figure 3.13), a particularly synchronous relationship is evident between 1997-2000, when salmon population was zero in 1997 and escalates to ~25,000 the next year. Another distinct peak in ring width and escapement occurred in 2006, when salmon return was nearly 20,000 individuals.

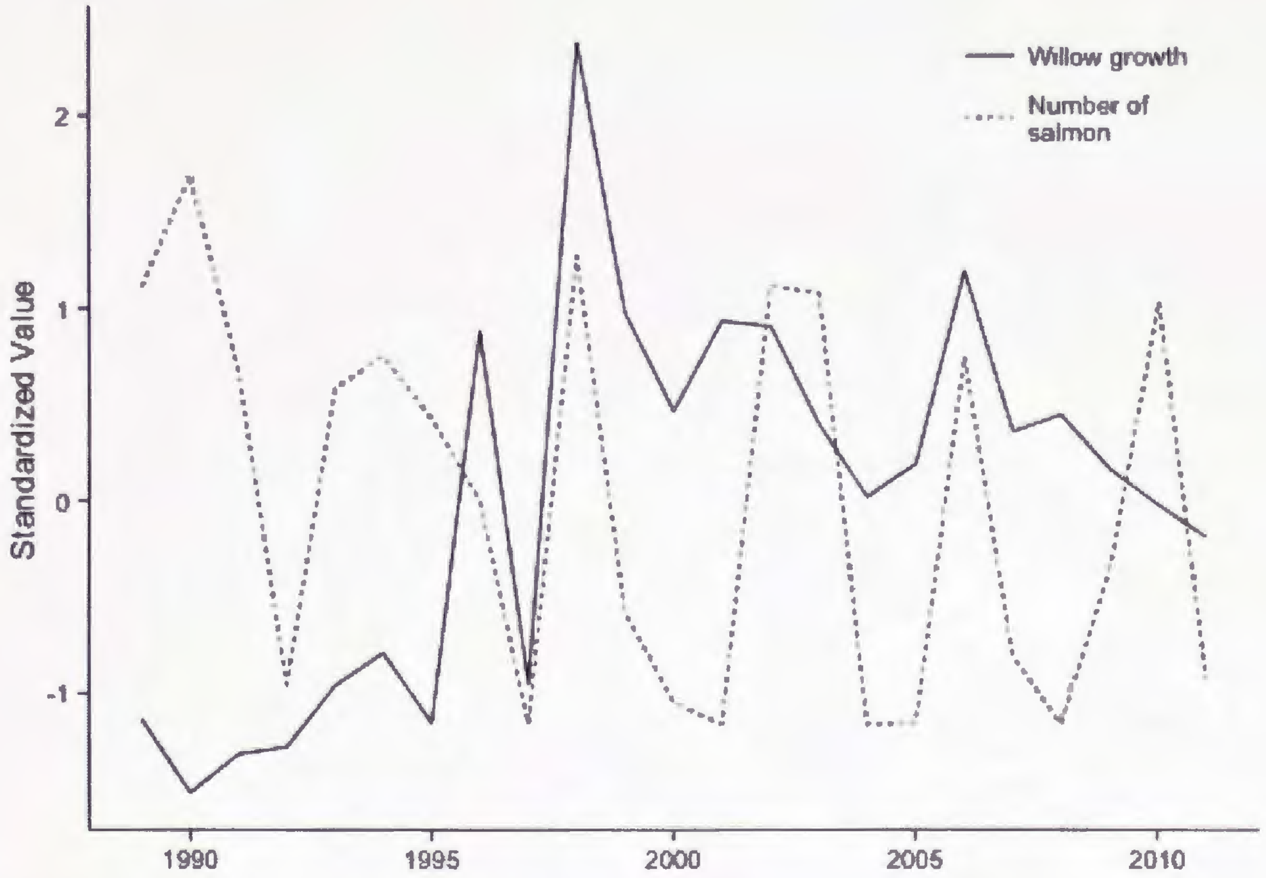


Figure 3.12. Annual ring width indices for a willow tree (*Salix* sp.) located centrally on the study site between the years 1956 and 2011. The vertical red dotted line delineates the year the spawning channel was built, 1989.

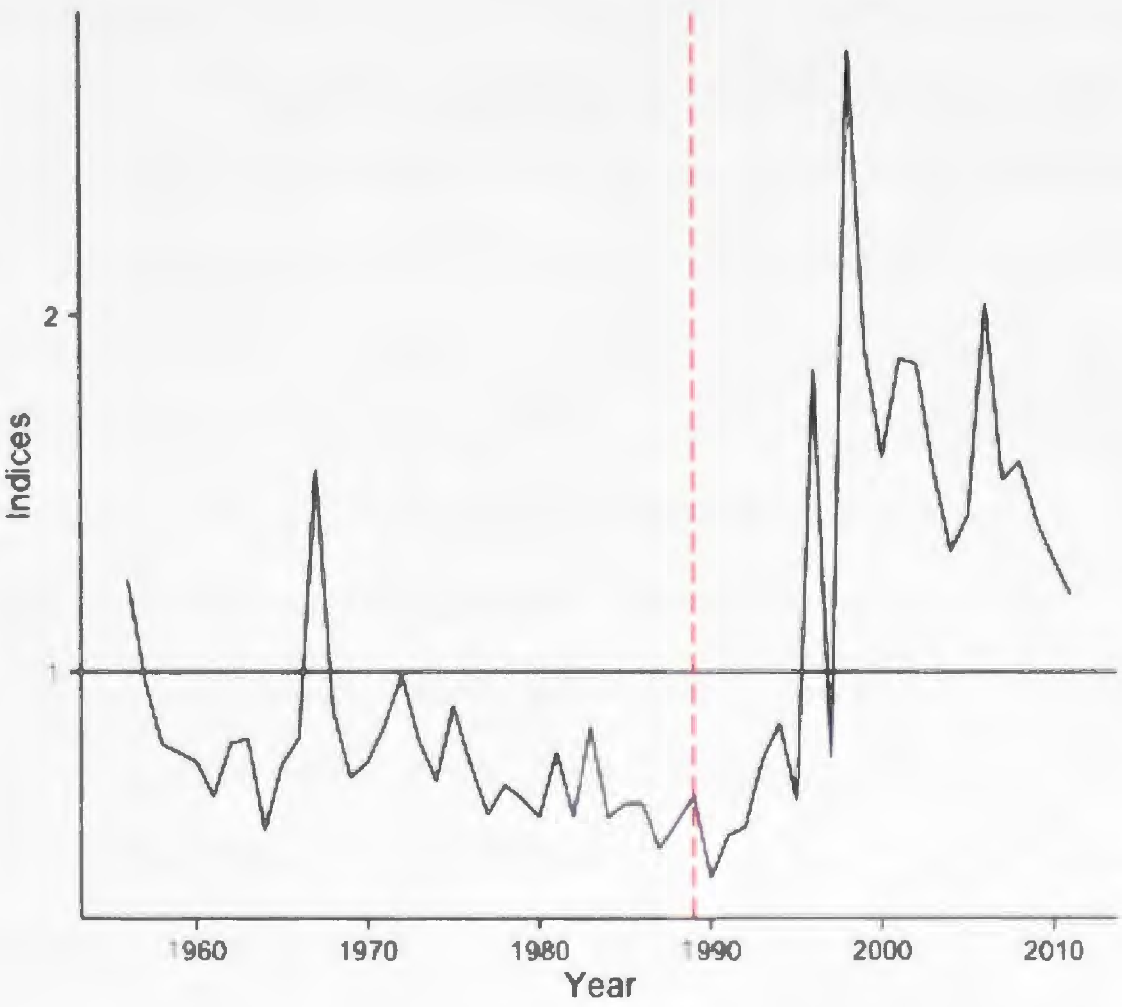


Figure 3.13. Standardized values of annual willow tree growth, measured by ring widths, and salmon escapement in the Horsefly River spawning channel since its establishment in 1989.

3.4 Discussion

3.4.1. Macroinvertebrate Community of the Horsefly River

The invertebrate community of the spawning channel is consistent with the theorized structure of low order, headwater streams described in the River Continuum Concept (Vannote et al. 1990). Shredders and collector-gatherers constitute the dominant, year-round FFGs, which are fueled by terrestrial-inputs provided by the bordering riparian forest (Doucett et al. 1996). Species richness is relatively low at this site, with only 13 taxa identified, although richness would likely increase slightly if some groups had been identified further, such as invertebrates from the family Chironomidae. In comparison, the community of the Horsefly River contained invertebrates from 41 taxa, which decreases to 34 total taxa when combining species from the Chironomidae family and the genus *Baetis*. Species diversity, according to the Shannon Index, is higher in the Horsefly River, although the spawning channel has greater evenness, according to the Lorenz curve and Gini coefficient, because fewer rare taxa were identified (Table 3.3). Theoretically, the healthiest communities are those with a large number of species and a nearly even distribution. Uneven communities are less resistant to environmental stress because each FFG provides a critical role to whole ecosystem function (Peet 1974, Wittebolle et al. 2009).

The richness and composition of an invertebrate community is highly dependent on the specific site, as well as sampling techniques. Temperature, substrate, surface flow, and microhabitat type are important variables that regulate species distribution (Hill & Hawkins 2014, Pingram et al. 2014, Silva et al. 2014, Dohet et al. 2015). The high abundance of amphipods (*Hyalella azteca*) defines this site as being more pond-like compared to the Horsefly River, which largely reflects the glide microhabitat of the spawning channel compared to the riffle that was sampled in the Horsefly River (France 1992). Insect drift from the settling pond at the top end of the channel may also have contributed to high amphipod abundance downstream. Although amphipods are widespread shredders commonly found throughout freshwater and marine environments (Strong 1972, Lowry & Springthorpe 2001), they were not observed in the Horsefly River samples and are not prevalent in the MDN literature. Shredders documented in other MDN studies typically are from the orders Plecoptera and Tricoptera, but the only shredders at the spawning channel were amphipods. Most of these studies are conducted in riffle habitats (Honea & Gara 2009), thus examining MDN dynamics of a glide habitat contributes new information to a limited area of study (*see* Thompson 2007). Investigating glide and pool environments may be especially important for sockeye salmon conservation because they supply early habitat and nourishment for eggs and fry, as well as potential rearing habitat for juveniles (Fillatre Miller et al 2011).

In the six week period between pre-spawn and post-spawn the total number of invertebrates increased markedly from 59 to 993 individuals, confirming the hypothesis that population would increase upon the arrival of salmon. The largest jump in community abundance and biomass occurred between weeks active spawn II and active spawn III (increase of 425 individuals), by which point the channel was at its maximum salmon capacity for this year (Figure 3.6). Abundance increased for all taxonomic and FFGs during this period, including the first appearance of collector-filtering organisms, specifically bivalves from the Sphaeriidae family and *Arctopsyche* sp., a Tricoptera species (Figure 3.14). Although MDN may play a role in increased abundance, the life history of most macroinvertebrates displays population growth during the summer (Hynes 1970). The daily build-up and release of the salmon dams was also most apparent between these weeks, with surface water levels fluctuating about 1 m during a day (*see* Section 2.2.1.1). The dams were composed of anything in the water column that could float downstream, from FPOM to salmon carcasses and tree branches, and constituted a dense, nutrient-rich food source for invertebrates and fishes to colonize and congregate. Total invertebrate abundance increased slightly between active spawn III and post-spawn, but this increase was only observed for amphipods and chironomids. In the spring, most species declined in number except for chironomids, which retained high abundance over the winter (Figure 3.8). Significantly more chironomid pupae were identified in the spring, as well as over 200 pupae casings. Chironomids remain in their pupal stage for a short period of time, indicating that chironomid morphing and emergence began at the onset of spring break-up and/or when channel ice thawed (Danell & Sjöberg 1977).

The study design aimed to capture pre-spawn abundance and isotopic signatures of macroinvertebrates as temporal control baseline conditions. However, preparatory cleaning of the spawning channel, which occurred between August 8-12 and 15-18, ending five days prior to invertebrate sampling, likely altered water chemistry (*see* Section 2.4.2) and may have affected pre-spawn taxa abundance. This activity ceased approximately 200-m upstream from my study site, where a temporary barrier inhibited the downstream flow of CPOM and a siphon pumped water and materials into an isolated settling pond (*see* Figure 2.2). Although the substrate at my study site was physically undisturbed by channel cleaning, the removal of upstream food sources and insect drift through siphoning may have displaced invertebrates, leading to initial low abundance. A high sediment to food ratio may also have adversely affected invertebrate density (Pingram et al. 2014). It is also plausible that with practice I became more effective at kick sampling during the sampling period, reflecting a lower abundance of invertebrates in Pre-spawn samples.

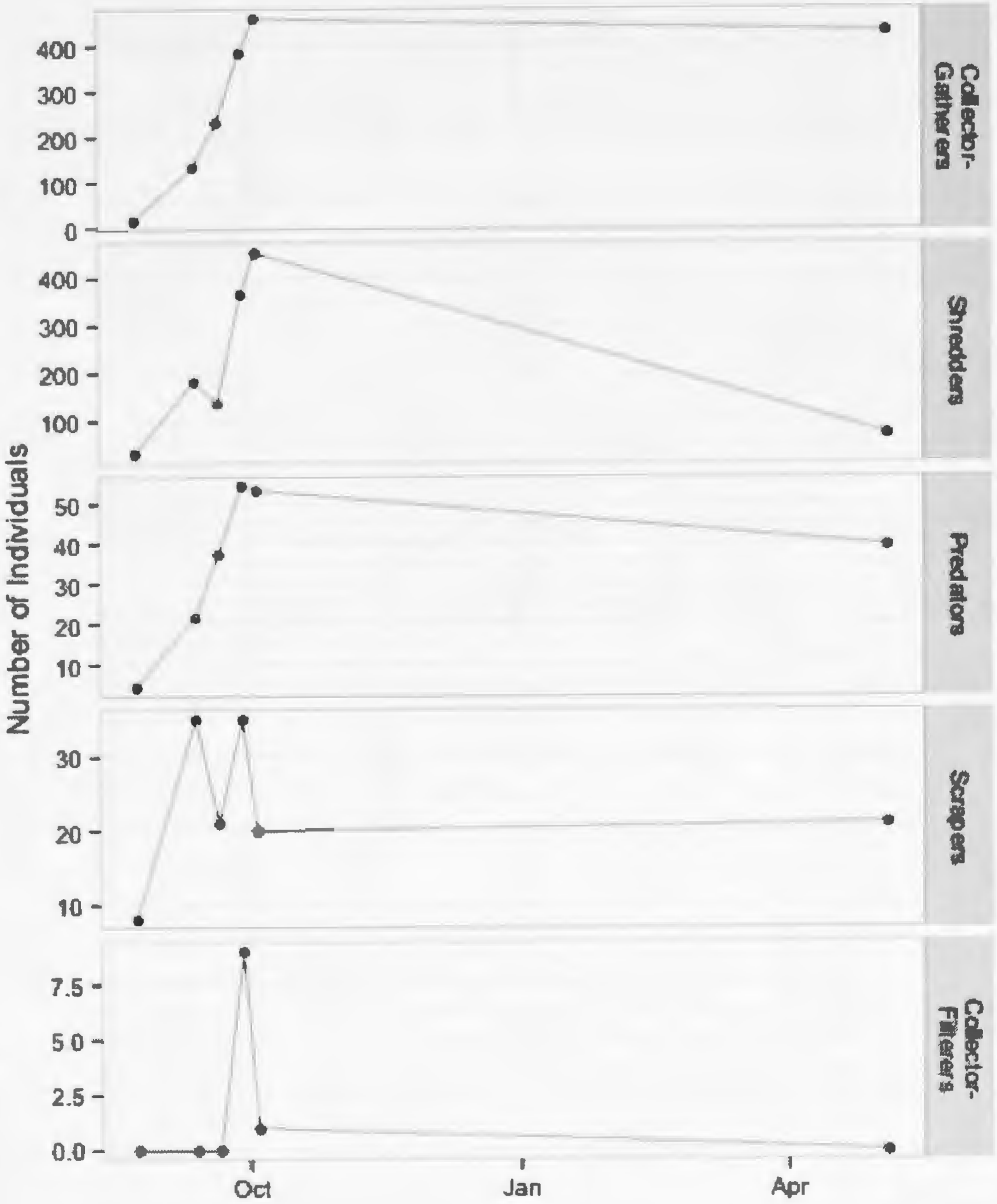


Figure 3.14. Number of individuals counted for each functional feeding group (FFG) during each of six sampling periods, beginning in August 2011 and ending in May 2012.

3.4.1.1 Macroinvertebrate Assimilation of MDN

An increase in species richness was directly attributable to the presence of salmon at this site; however, macroinvertebrate assimilation of MDN was variable between species. As detailed in Chapter 2, NH_4^+ enrichment of stream water could not be directly connected to the presence or abundance of salmon, a likely result of rapid nitrification of surface water NH_4^+ (*see* Section 2.4.2). However, NH_4^+ values of hyporheic water were significantly reduced during the post-spawn period, suggesting that salmon did contribute measurable nutrients to the stream (Figure 3.15). Accordingly, $\delta^{15}N$ signatures of macroinvertebrate groups Chironomidae and Ephemeroptera increased alongside hyporheic NH_4^+ concentration, which may signify MDN assimilation. This outcome results in a rejection of the null hypothesis (VI) that $\delta^{15}N$ signatures of these taxa will not be correlated with NH_4^+ concentration of hyporheic water. As well, the statistically significant negative correlation between Chironomidae and Ephemeroptera $\delta^{15}N$ signatures and surface water NH_4^+ results in a rejection of that component of the null hypothesis (VI). The relationship between salmon and each FFG is described in greater detail below.

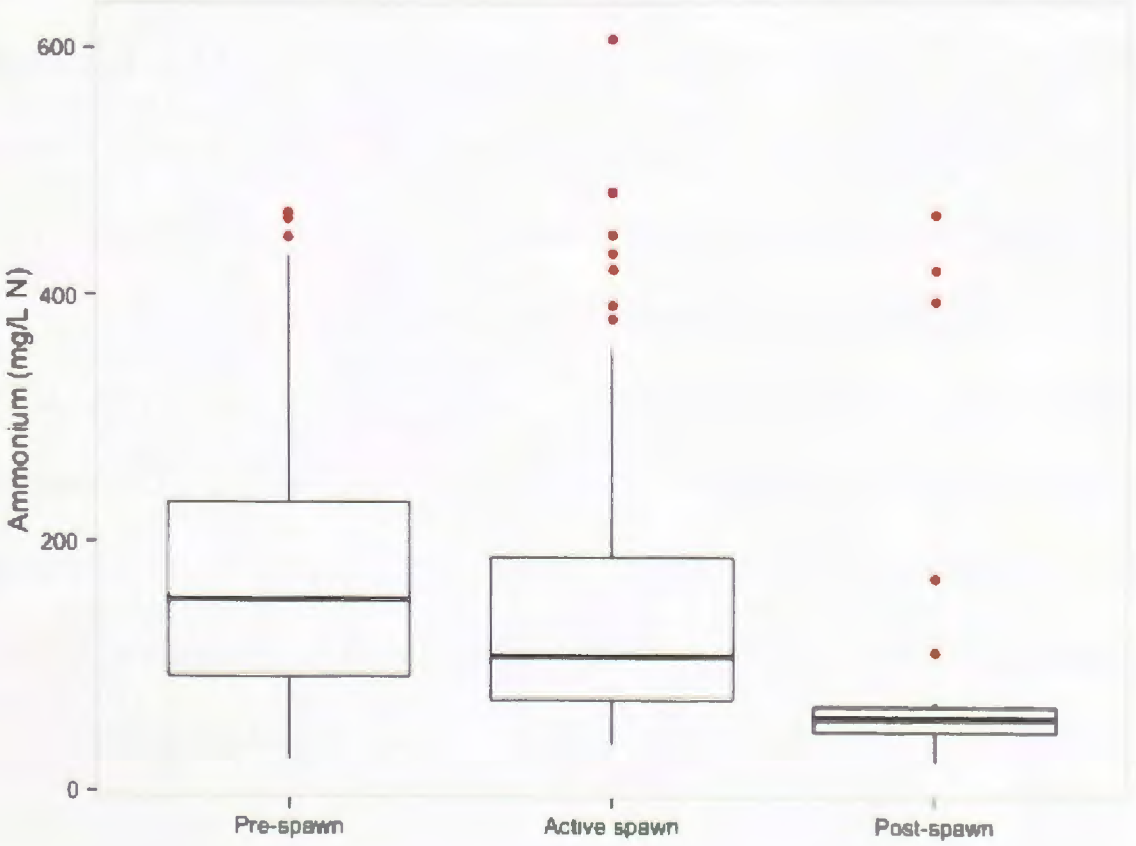


Figure 3.15. Boxplots displaying ammonium (NH_4^+) concentration of all hyporheic water samples. Active spawn includes data from three sampling weeks, Active spawn I, II, and III. Outliers are denoted by red dots.

Shredders:

High shredder density has been reported to coincide with leaf fall in autumn (Hawkins & Sedell 1981, Reece & Richardson 1998), which supports this study's finding of increasing amphipod abundance throughout the fall and lower abundance in the spring. The concurrent timing of salmon spawn and vegetation senescence enhances microbial activity on leaves and generates a bioenergetic advantage for shredders by promoting rapid growth rates (Minakawa et al. 2002, Ito 2003, Honea & Gara 2009). A trend of gradually increasing mean amphipod growth from Pre-spawn (7.97 mm) to Post-spawn (10.58 mm) was observed at this site. However, increased growth was not statistically significant, likely due to size variability within each sampling period (SD = 3.2-4.3 mm).

Weekly shredder $\delta^{15}N$ signatures also increased during the fall while salmon were actively spawning in the channel (Figure 3.16). Additions of nitrogen and phosphorus to a stream stimulates microbial activity on leaf litter, and shredders will preferentially feed on microbially-conditioned leaves (Ito 2003). The addition of MDN to the stream may be indirectly reflected in increased $\delta^{15}N$ of amphipods, as microbes colonizing leaves can quickly assimilate salmon-derived nutrients (Peterson et al. 2001). However, $\delta^{13}C$ continually decreases throughout salmon spawn, which is contrary to the expected $\delta^{13}C$ enrichment during conditioning of detrital matter (Rounick & Winterbourn 1986). This finding resembles Albers (2010)'s results of decreased $\delta^{13}C$ in post-spawn biofilms at the spawning channel. Thus, amphipods may also be feeding on another food source, such as biofilms or algae. Amphipods can exhibit plasticity when different food sources become available and have also been found to consume fish, macroinvertebrates, and other amphipods (MacNeil et al. 1997). Throughout the study, many amphipods were found residing within clumps of filamentous algae attached to the substrate, which may also be an important year-round food source.

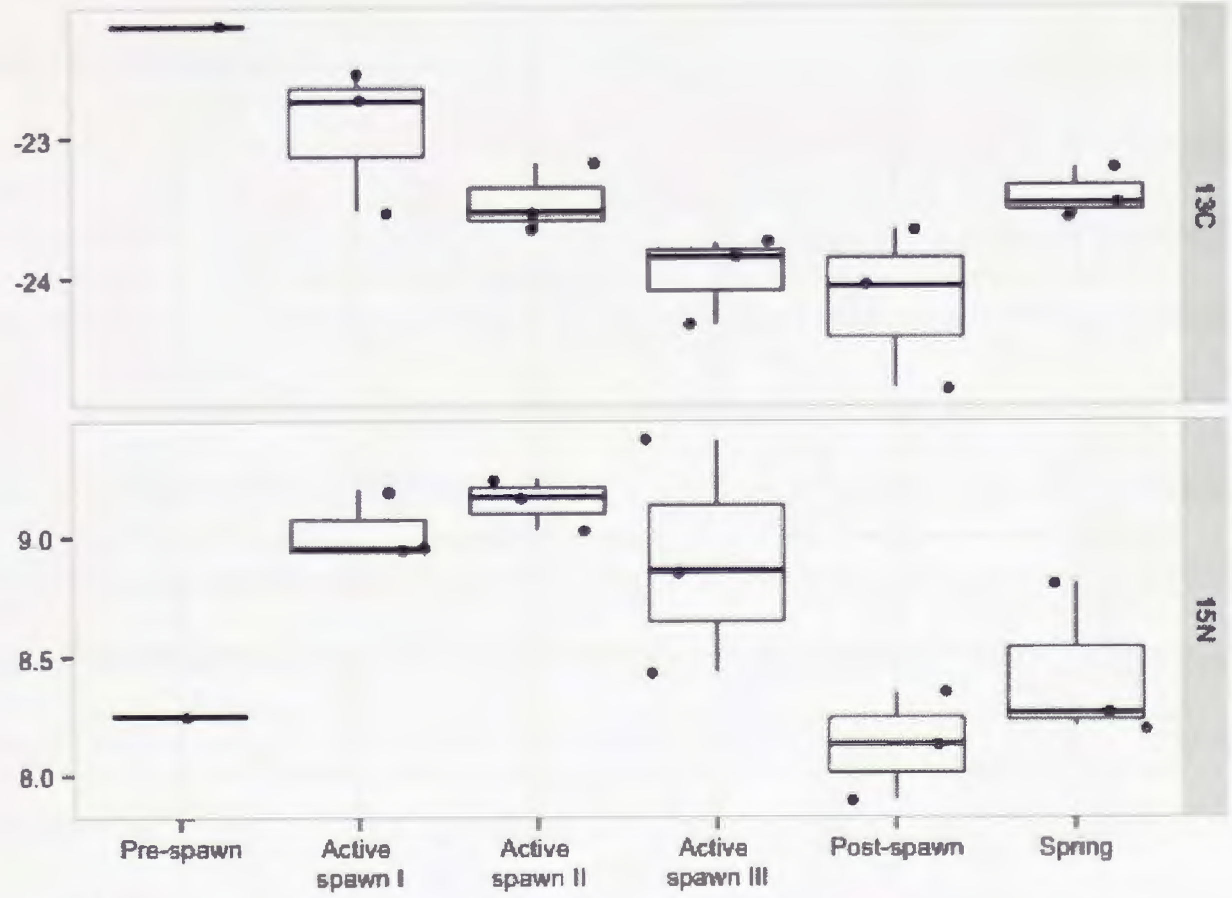


Figure 3.16. Boxplots displaying all $\delta^{13}C$ ‰ (top) and $\delta^{15}N$ ‰ (bottom) signatures from the shredder functional feeding group (FFG) during each sampling week. Black dots denote actual values.

Contrary to the other invertebrates, amphipod mean isotopic signatures remained consistent between seasons, likely because the brood sampled in the fall was identical to the spring (Menon 1966) and possibly because their primary food source also remained isotopically-enriched. Therefore, amphipods fail to reject the null hypothesis (V) that $\delta^{13}C$ and $\delta^{15}N$ will remain the same between seasons. Terrestrial leaves are thought to be the preferred food source of amphipods (Hawkins & Sedell 1981) and at this site isotopic ratios of fresh willow leaves are stable between seasons. The presence of N-fixing alders at the spawning channel likely provides a year-round contribution of N to forest soils (Johnson & Lindberg 1992), which may stabilize δ^{15}N in willow. Helfield & Naiman (2002) found that at spawning sites bordered by alder, spruce δ^{15}N was similar to alder δ^{15}N and decreased significantly at sites without alder.

Amphipods are not often referred to in MDN literature; however, in brown-water streams of Western Kamchatka, amphipods were found to be an essential element of the salmon feedback loop. They comprised more than 88% of invertebrate biomass, were observed feeding directly on salmon carcasses, and composed 68-88% of juvenile salmonid diets (Thompson 2007). Our results of isotopically-enriched amphipods in the spring support the notion that they may play an important role in the salmon feedback loop by linking MDN from spawners to their progeny. Since amphipods will migrate to find the highest quality food source (Cothran et al. 2014), it is possible that they move to spawning grounds in the fall to locate conditioned leaves and then relocate to the lakes and ponds they primarily occupy (Clifford 1991). Juvenile sockeye salmon preferentially rear in lakes (Eggers 1978), so an amphipod migration that mimics salmon movement may indicate an amplified response of the importance of amphipods to perpetuating the feedback loop.

Collector-Gatherers:

Chironomids were the most abundant taxa in the collector-gatherers FFG, comprising on average 67% of total group abundance. Aquatic earthworms, commonly called oligochaetes, were the second most abundant collector-gatherers, followed by two mayfly taxa, *Paraleptophlebia* sp. and Baetidae. Tricopteran, or caddisfly, collector-gatherers made an appearance during post-spawn sampling.

Stable isotopic signatures were obtained for the taxa Chironomidae and Ephemeroptera (mayflies). Due to the small mass of these organisms, duplicate samples were not always possible. Therefore, taxa analysis for some sampling weeks is based upon only one data point. Conclusions based upon singular data have a high likelihood for error and must be interpreted cautiously. There were no clear trends in isotopic composition for these invertebrates during the salmon spawn, although pre-spawn values were not obtained (Figure 3.17). Nitrogen isotopes for both taxa were very similar, suggesting similar trophic enrichment from a common food source. However, fall $\delta^{13}C$ signatures were slightly enriched for Ephemeroptera, which could be an indication of differing lipid content between the taxa, as proteins and carbohydrates are enriched in $\delta^{13}C$ relative to lipids (Post et al. 2007).

In the fall, chironomids had the least enriched $\delta^{13}C$ and $\delta^{15}N$ signatures of all the invertebrates, indicating that these chironomids are likely not predacious and are mostly or entirely collector-gatherers (Figure 3.3). Chironomidae and Ephemeroptera $\delta^{15}N$ signatures in the fall were significantly enriched ($p < 0.05$) over spring values, suggesting that they benefitted from assimilation of salmon nutrients into the food web (Figure 3.5). This outcome results in a rejection of the null hypothesis (V). Peterson et al. (2001) found that after NH_4^+-^{15}N injections around 70-80% of the NH_4^+ was directly assimilated by benthic organisms, with the rest removed by nitrifying bacteria. The quick removal of NH_4^+ from surface water could be a result of direct assimilation by collector-gathering organisms or indirect assimilation through the consumption of bacteria located among the streambed gravels (Bilby et al. 1996, Webster et al. 2003).

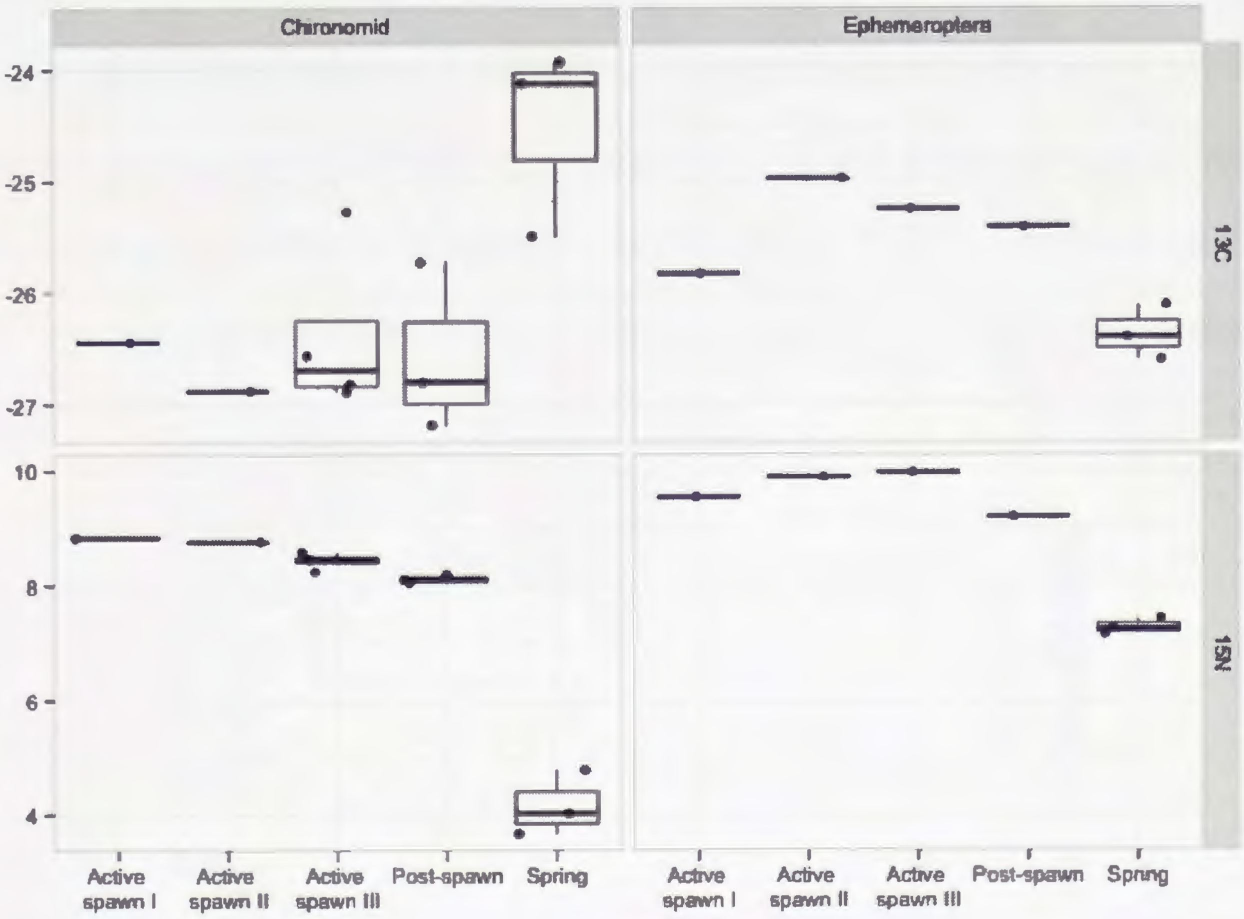


Figure 3.17. Boxplots displaying $\delta^{13}C$ ‰ (top) and $\delta^{15}N$ ‰ (bottom) signatures from two species of the collector-gatherer functional feeding group (FFG). Plots on the left show chironomid isotopic signatures and ephemeroptera are displayed on the right. Pre-spawn isotopic signatures are missing for these species. Black dots denote actual values.

A major difference between these species was the significant depletion of $\delta^{13}C$ in the spring for Ephemeroptera and a significant $\delta^{13}C$ enrichment for chironomids. Both of these results reject the null hypothesis (V) that $\delta^{13}C$ signatures will remain unchanged between seasons. This result, along with relatively enriched spring $\delta^{15}N$ signatures of Ephemeroptera, indicates that they are consuming distinctly different food sources or that their specific life histories alter tissue nutrient composition. During times of starvation, chironomid $\delta^{13}C$ signatures become significantly more enriched and, since chironomids hibernate during the winter, enriched spring $\delta^{13}C$

concurs with hibernation and subsequent starvation (Doi et al. 2007). Isotopic signatures also change during chironomid metamorphosis, with results of enriched $\delta^{13}C$ and decreased $\delta^{15}N$ in larvae, which could explain significantly lower $\delta^{15}N$ signatures in the spring. The slight enrichment of $\delta^{15}N$ and depletion of $\delta^{13}C$ in chironomid pupae relative to chironomid larvae (Figure 3.18) demonstrates the isotope turnover that is occurring during metamorphosis from the larval to adult stage (Doi et al. 2007).

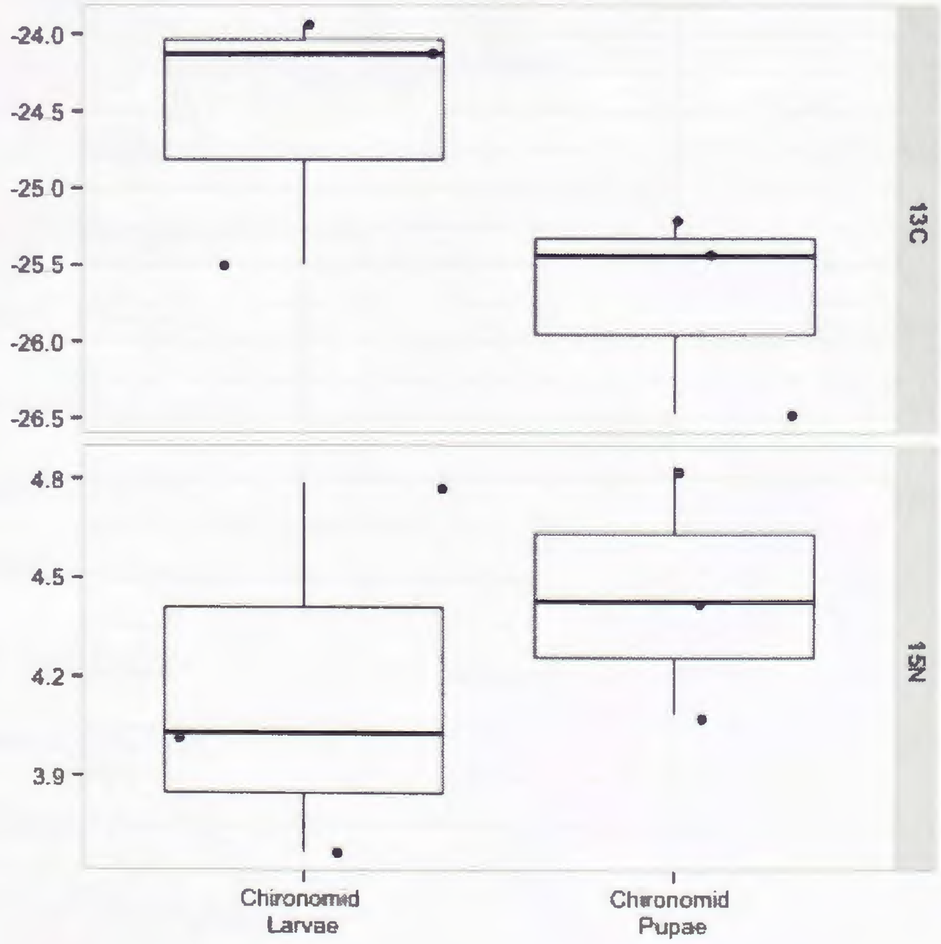


Figure 3.18. Chironomid larvae and pupae isotopic signatures collected in May 2012. Increased $\delta^{15}N$ (‰) and decreased $\delta^{13}C$ (‰) in pupae are demonstrating nutrient changes due to metamorphosis. Black dots denote actual isotope values.

In the spring, snowmelt, rain, and freshet induce lateral inputs from the riparian zone and elevates stream DOC (Holmes et al. 1996, Duff & Triska 2000, Harvey et al. 2013). Lower carbon and nitrogen isotopic signatures in the spring for Ephemeroptera could be reflecting a greater reliance on relatively depleted terrestrial food sources compared to enriched autumnal MDN assimilation. Spring freshet also may have contributed to lower collector-gatherer $\delta^{15}N$ signatures, as high water levels initiated downwelling hyporheic conditions and supplied DOC, N, and DO creating a nitrifying environment (Chapin et al. 2011, Zarnetske et al. 2011, Heppell et al. 2014). Nitrification creates $\delta^{15}N$-depleted NO_3^- (Chapin et al. 2011), which may partially be the reason for decreased invertebrate $\delta^{15}N$.

Chironomids are a fairly common benthic invertebrate identified in MDN studies and appear to benefit from salmon nutrients during the salmon spawn and retain high abundance after the winter (Hicks et al. 2005, Lessard & Merritt 2006, Lessard et al. 2009, Verspoor et al. 2011, Campbell et al. 2012). They are classified as hyporheos, or hyporheic-dwelling organisms, and are able to avoid spawning mortality by retreating deeper into the substratum during redd building disturbances that causes some invertebrates to decrease in abundance (Lessard & Merritt 2006, Honea & Gara 2009). Also, chironomids have been observed feeding on salmon carcasses (Chaloner & Wipfli 2002), so although isotopic signatures did not reflect salmon predation, this taxa could have altered its feeding habits to carcass consumption after fall conditions reduced primary productivity (Lessard & Merritt 2006). This study supports research that identifies chironomids as important organisms to the aquatic food web integration of MDN and their effect in providing source nutrients to future salmon stocks by maintaining high abundance (Chaloner et al. 2002b, Lessard & Merritt 2006).

Collector-Filterers:

Collector-filterer abundance has been found to increase after additions of coarse detritus, particularly leaf litter, as a response to increased FPOM from shredding organisms (Richarson 1992). They also may display enriched isotopic signatures coinciding with salmon spawn, indicating direct or indirect MDN incorporation (Honea & Gara 2009). The appearance of collector-filterers during active spawn at the HFC could be due to the cumulative effects of nutrient sources from both leaf senescence and salmon spawn.

Scrapers:

Gastropods constituted the entire scraper FFG and were represented by two species, *Physa* sp. and *Promenetus umbilicatellus.* Scraper abundance remained relatively uniform throughout the study, with total post-spawn abundance (n=21) nearly matching spring (n=20), showing persistence of scrapers in this stream. The response of scrapers to spawning salmon produces a variable response between regions, including reports of no discernible response (Lessard & Merritt 2006). Some studies have found a lack of MDN assimilation in scrapers (Rinella et al. 2013), while others have observed an accumulation of MDN and increased biomass in spawning locations (Bilby et al. 1996, Honea & Gara 2009).

Scraper isotopic signatures in the spring were δ^{15}N-enriched relative to all other taxa (Figure 3.4). Biofilms are the primary food source of these low-trophic order species (Anderson & Cabana 2007), which infers that either the gastropods and/or their food source remained enriched in MDN throughout the winter season. Adult *Physa* sp. likely spawn after spring break-up, so the brood sampled in the fall would be identical to the spring, which supports the assumption of $\delta^{15}N$ accumulation (Clampitt 1974). Additionally, winter can induce nutritional stress, illustrated by an increasing C:N ratio of source materials, which is known to cause $\delta^{15}N$ enrichment (Dekar et al. 2009).

Predators:

The relative abundance of predatory invertebrates was greatly influenced by the high number of chironomids of which 10% were classified as predators (Figures 3.7, 3.14). The next most prevalent predator group from the subclass Hirudinae, commonly known as leeches, continually increased upon the arrival of salmon and decreased after spawning. Predatory invertebrates are limited by their available prey (Richardson 1993, Honea & Gara 2009, Verspoor et al. 2011), thus, leech abundance may have fluctuated with resident fish and juvenile salmonid populations. Many riverine fish species will follow spawning salmon to gorge on salmon eggs and flesh (Cederholm et al. 1999, Moore & Semmens 2008), which likely were important nutrient sources for leeches.

The weekly isotopic signatures of leeches were represented by only one data point, so it is difficult to conclusively discuss trends (Figure 3.19). Carbon and nitrogen isotopic signatures generally decreased from active spawn to post-spawn, which may correspond to a reduction in live salmon, as well as a reduced number of resident fish following the spawners. Other fishes observed in the channel during the fall were Redside shiners (R*ichardsonius balteatus*), Rainbow trout (*O. mykiss*), and Kokanee salmon (*O. nerka*).

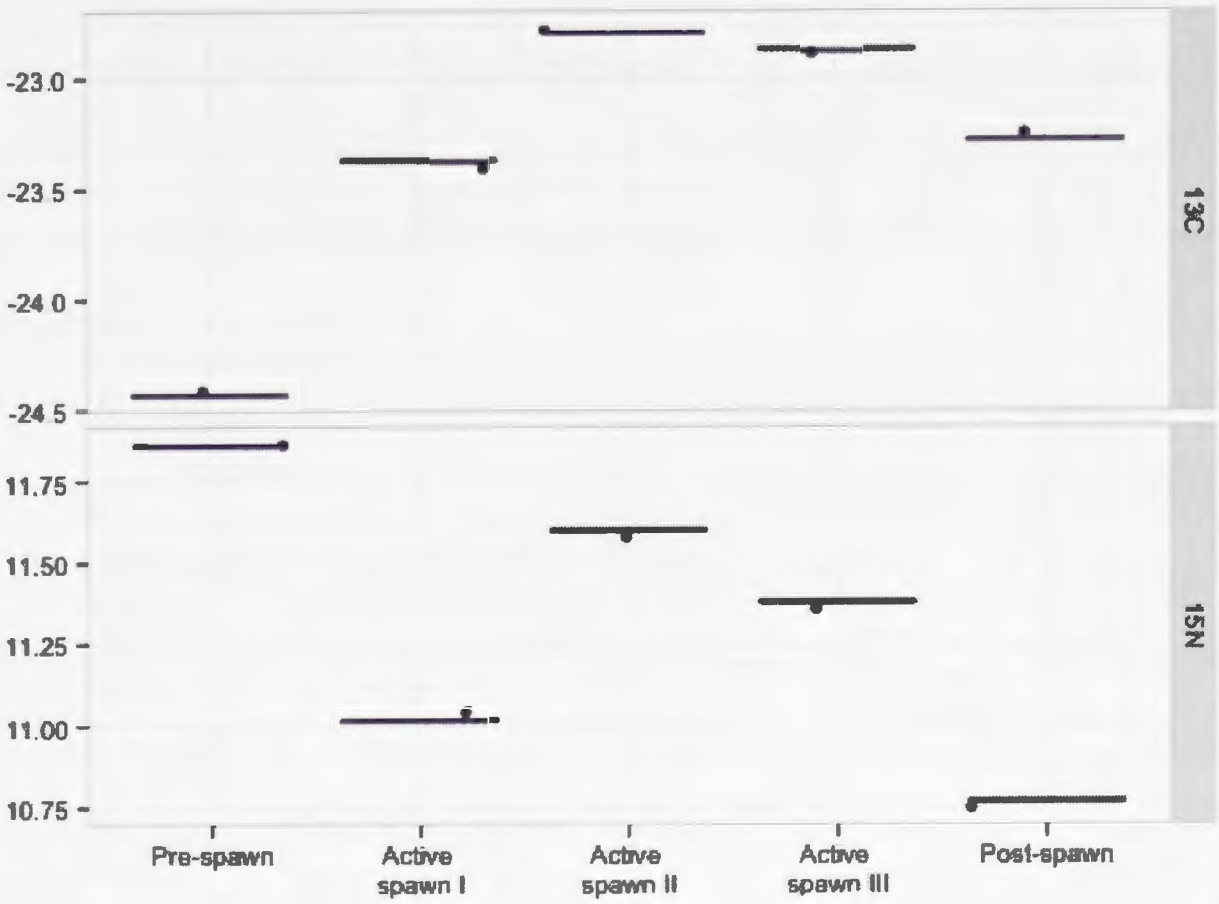


Figure 3.19. Boxplots displaying $\delta^{13}C$ ‰ (top) and $\delta^{15}N$ ‰ (bottom) signatures of Hirudinae (leeches) from the predator functional feeding group (FFG) during the fall sampling weeks. Spring isotope values were not obtained due to low abundance and mass. Black dots denote actual values.

3.4.1.2 Nutrient Sources in Aquatic Systems

The uptake and retention of salmon nutrients (MDN) were the focus of this study. However, they represent only one of many resource pulses to a stream that can enhance population productivity and growth (Richardson et al. 2010). Terrestrial leaf litter inputs, particularly in the fall, are an important food source to invertebrates with low trophic position (Wallace et al. 1999). Additionally, leaf leachate provides dissolved nutrients to aquatic primary producers and has been found to contribute 30% of total dissolved organic carbon (DOC) to a stream (Richardson et al. 2010). Lateral flows of groundwater can deliver DOC and dissolved inorganic nitrogen (DIN) to the stream from organic soil horizons, especially during high precipitation, flooding, and spring break-up events (Wondzell & Swanson 1996b, Mei et al. 2014). Nutrients are also transported from upstream sources (Wipfli et al. 2007) and, in this case, water in the spawning channel originates in the upstream settling pond, which is rich with macrophytes and algae.

The rationale in tracing MDN using stable isotopic analysis was that salmon are often migrating to oligotrophic streams and, therefore, contribute detectable amounts of N exceeding that of atmospheric N deposition (<5 kg ha^{-1} year^{-1}), in conjunction with the natural 10-15‰ $\delta^{15}N$ enrichment of marine sources relative to terrestrial sources (Welch & Parsons 1993). However, organisms and food sources can appear enriched in stable isotopes regardless of MDN presence (e.g. due to isotopic discrimination; Marshall et al. 2007, Staal et al. 2007), and substantial nutrient inputs can come from sources other than salmon (Triska et al. 1993, Helfield & Naiman 2002). When N is not the limiting nutrient in a system, the ability to trace marine-derived nitrogen can be significantly reduced owing to confounding effects of isotopic fractionation (Naiman et al. 2002). A nitrogen fractionation, a.k.a. enrichment, factor of approximately 3-4‰ occurs with each successive trophic position (Minagawa & Wada 1984), so an organism that utilizes many N sources will have a $\delta^{15}N$ value that incorporates multiple sources. In most systems, however, N sources are limited and demand exceeds supply (Aber et al. 1989). While this narrows the possible N options, it remains difficult to discriminate between relative source contributions when there is more than one N-rich source (Marshall et al. 2007). Since $\delta^{13}C$ signatures of a consumer reflects its' source with a smaller fractionation (~0.4‰), they can be helpful to determine primary nutrient sources

(DeNiro & Epstein 1978). Although this study did not aim to identify the food sources of invertebrates, isotopic signatures of possible sources (e.g. aquatic autotrophs, detritus, leaf litter, bed sediments, and resident fish) would have greatly helped discern patterns of enrichment and the specific impact of MDN.

3.4.2 Nutrient Uptake and Assimilation in the Riparian Zone

Riparian plants at this site possessed distinctly different $\delta^{13}C$ and $\delta^{15}N$ signatures, which lends to insights of plant function and overall nutrient availability (Menezes 2009, Chapin et al. 2011). For instance, *E. arvense* typically were enriched in $\delta^{15}N$ compared to other species, which could be the result of a preference for NH_4^+ (Chapin et al. 2011). Variations in isotopic fractionation are mostly due to N transformations, such as nitrification, denitrification, and volatilization (Finlay & Kendall 2007); plants that prefer NH_4^+ will be isotopically enriched relative to NO_3^- absorbing plants because nitrification has a fairly large fractionation effect (Chapin et al. 2011). *E. arvense* may also display enrichment because horsetail is especially effective at accumulating and retaining nutrients (Husby 2013). They even act as a nutrient pump by delivering nutrients from the soil C horizon to its shoots above-ground (Marsh et al. 2000).

All terrestrial plants obtain carbon from a well-mixed atmospheric reservoir in the form of CO_2 (Ben-David et al. 1998), thus $\delta^{13}C$ variation due to the source is insignificant and the presence or absence of MDN should not be a factor. Variation occurs from fractionation during CO_2 assimilation, which is primarily related to water use and plant growth rate (Finlay & Kendall 2007, Marshall et al. 2007). *S. lucida* consistently displayed $\delta^{13}C$ enrichment relative to *T. officinale* and *E. arvense* leaves, which is an expected result when comparing long-lived perennial species and annual or herbaceous species (Marshall et al. 2007). Seasonal variation in $\delta^{13}C$ was not detected, but there was a significant $\delta^{13}C$ enrichment in plants located directly on the streambank (Table 3.5). Plants that experience water stress discriminate against $\delta^{13}C$, so stream-side vegetation with a reliable supply of water will exhibit higher (less negative) $\delta^{13}C$ signatures (Wang et al. 2010). More available sunlight, resulting in a greater rate of photosynthesis, may also be contributing to $\delta^{13}C$ enrichment at this location (Leavitt & Long 1986), as the vegetation sampled here was not shaded by the riparian forest.

The nutritional value (C:N) of all sampled vegetation species decreased as fall progressed and were most nutritionally rich in the spring (Table 3.6). Prior to senescence trees will reabsorb N from the leaves, so a decrease in total N and an increased C:N is to be expected (Drake et al. 2006). *S. lucida* reabsorbed about 35% ± 10.6% of leaf N between August and September 2011, whereas *E. arvense* absorbed slightly less (30% ± 12.8%) and *T. officinale* reabsorbed the least N (15% ± 14.1%). The %C in *S. lucida* samples remained steady throughout seasons averaging around 46%, while the perennial *T. officinale* and *E. arvense* species had substantial reductions in %C from spring to fall, especially for *E. arvense*. This decreased nutritional value of senescent leaves amplifies the importance of the microbial-conditioning of leaf litter that coincides with salmon spawn for amphipod growth in the fall and winter energy storage.

Table 3.6. Stable isotopic signatures, percent of total carbon (C) and nitrogen (N), and the C:N ratio of sampled riparian vegetation at the Horsefly River spawning channel during Fall 2011 and Spring 2012.

Species	Date	$\delta^{13}C$	$\delta^{15}N$	%C	%N	C:N
Salix lucida	Aug 2011	-28.40	2.37	46.76%	2.45%	19.01
Salix lucida	Sept 2011	-29.23	1.87	46.60%	1.60%	29.15
Salix lucida	May 2012	-28.38	1.23	46.86%	3.88%	12.01
Equisetum arvense	Aug 2011	-29.34	10.39	30.33%	1.82%	16.84
Equisetum arvense	Sept 2011	-29.88	8.67	29.81%	1.26%	23.68
Equisetum arvense	May 2012	-30.03	6.55	39.22%	3.49%	11.17
Taraxacum officinale	Aug 2011	-32.53	0.54	37.87%	2.52%	14.93
Taraxacum officinale	Sept 2011	-33.24	1.09	38.00%	2.15%	17.52
Taraxacum officinale	May 2012	-31.64	5.28	43.67%	4.32%	10.05

Salix lucida (Pacific willow):

S. lucida were the only plants sampled that displayed a statistically significant spatial trend in $\delta^{15}N$, specifically decreasing $\delta^{15}N$ signatures with distance from streambank (Table 3.4). Similar results have been used to prove the influence of spawning salmon on riparian vegetation (Bilby et al. 1996, Ben-David et al. 1998, Helfield & Naiman 2002, Hicks et al. 2005, Drake et al. 2006, Hocking & Reimchen 2009). The reduction of $\delta^{15}N$ in inland willows suggests that less marine N reached these locations and potentially all $\delta^{15}N$ came from microbial denitrification. Inland willows had $\delta^{15}N$ signatures between -1 and 0‰, which represent standard values of atmospheric N assimilation (Kohl & Shearer 1980). At our site, the willow tree directly on the streambank had an average $\delta^{15}N$ enrichment of 5‰ relative to the willows 20-m inland in the fall, and 3‰ in the spring. This result confirms the hypothesis that near-stream vegetation will retain MDN over the winter. Similarly, the near-stream willows exhibited an average $\delta^{13}C$ enrichment of nearly 4‰ in the fall and greater than 3‰ in the spring. This could be due to high water and sunlight availability (Leavitt & Long 1986, Marshall et al. 2007, Wang et al. 2010), as well as MDN enrichment.

The roots of *Salix* sp. protrude into the hyporheic zone and have been found to rely on groundwater throughout their growing season (Menezes 2009). Since a trend of decreasing $\delta^{15}N$ with distance from the streambank is only apparent in deep-rooted willow trees, this infers that substantial quantities of MDN is transferred to the near-stream riparian zone by advective hyporheic water. This corresponds with results reported in Chapter 2, where NH_4^+ concentration in hyporheic water also decreased with distance from the streambank and did not appear to infiltrate inland locations during active salmon spawn. These data support the rejection of the null hypothesis (VIII) that stable isotopic signatures of *S. lucida* will not be correlated with distance from the streambank. Nitrogen isotope enrichment in riparian vegetation by $^{15}N\text{-}NH_4^+$ is substantiated by a study from Drake et al. (2006), where they discovered that tree roots began to absorb $\delta^{15}N$ within 7 days and that 37% of the $^{15}N\text{-}NH_4^+$ tracer was contained within tree tissues after six months.

From the tree ring analysis it appears that seven years after the construction of the spawning channel, this particular willow tree began exhibiting increased annual growth (Figure 3.12). Trees are capable of developing a physiological legacy effect that allows them to efficiently assimilate nutrients when they can depend on resource pulses (Drake et al. 2006), which seems to be occurring at this site. The standardized values of ring width and salmon abundance also display a synchronized relationship during certain years, particularly between 1997-2000, when salmon population was zero in 1997 and escalates to ~25,000 the next year, and in the year 2006 when salmon return was nearly 20,000 individuals (Figure 3.12). Recent studies have linked salmon abundance and tree ring growth (Drake & Naiman 2007, Reimchen & Fox 2013), however high precipitation, temperature, or other climate variables could also lead to increased growth (Garfinkel & Brubaker 1980). At this site, multiple variables plausibly acted together to increase tree growth, as evidenced by a significant multiple regression with the interaction of precipitation and salmon abundance. The construction of the spawning channel may also have created a higher local water table, thus promoting tree growth. Lastly, the strength of this analysis is questionable because only one willow tree was sampled; however, these preliminary results provide justification to continue tree ring research at this site.

Equisetum arvense (Common horsetail):

E. arvense showed a statistically significant $\delta^{15}N$ depletion in the spring which could be attributed to a decrease in available N, in conjunction with greater reliance on associated mycorrhizal fungi. As much as 70-80% of *E. arvense* roots are colonized by arbuscular mycorrhizal fungi (Hodson et al. 2009), which supply an alternative source of N; plants may rely more heavily on this symbiotic relationship when N availability is low, thus leading to relatively depleted $\delta^{15}N$ of *E. arvense* in the spring (Chapin et al. 2011). Rinella et al. (2013) also reported lower $\delta^{15}N$ signatures of horsetail in the spring, as well as an apparent $\delta^{15}N$ enrichment in the fall that did not vary with spawner density. Horsetail is known to be especially effective at accumulating and retaining nutrients (Marsh et al. 2000), which could account for its persistent $\delta^{15}N$ enrichment over the other plant species and may infer an accumulated salmon legacy effect. Carbon isotopic signatures remained the same between seasons, resulting in a failure to reject the null hypothesis for $\delta^{13}C$ and a rejection of the null hypothesis for $\delta^{15}N$ (VII).

Taraxacum officinale (Common dandelion):

A significant increase in $\delta^{15}N$ signatures of *T. officinale* in the spring demonstrates that herbaceous annual plants in the same area can exhibit vastly different nutrient assimilation techniques and that large spatial variations in nutrient concentration can occur in relatively close proximity (Chapin et al. 2011). This result supports the rejection of the null hypothesis (VII) that $\delta^{15}N$ signatures will remain the same between seasons. Half of the *T. officinale* sampling locations (3 out of 6) exhibited a sharp $\delta^{15}N$ increase in the spring (average of 8.21‰ ± 3.51), while the other locations remained similar to September signatures (average increase of 0.17‰ ± 0.93). Although $\delta^{15}N$ of a single herbaceous species has been documented to vary by >1‰ even when grown hydroponically on a known source (Robinson 2001), differences of this magnitude are probably due to microhabitat variation of the N pool. Dandelions flourish best in moist loam (Stewart-Wade et al. 2002) where conditions of high water content would limit DO and create denitrification conditions. These factors promote $\delta^{13}C$ depletion along with NH_4^+-$\delta^{15}N$ enrichment of the N pool (Marshall et al. 2007, Pinay et al. 2009). Low $\delta^{13}C$ and high $\delta^{15}N$ are present at three locations in the spring (T1-0, T2-10, and T2-20), which supports this theory. Also, arbuscular mycorrhizal fungi is common on dandelion roots (Hodson et al. 2009), so the $\delta^{15}N$ depleted plants could have been in locations where N was low and their reliance on N from the fungi was increased.

Soil:

Soil isotopic signatures of $\delta^{13}C$ followed a pattern of increasing enrichment with depth that is commonly found across ecosystems due to microbial preference for the lighter isotope and subsequent accumulation of the heavy isotope in older soils (Figure 3.9; Ehleringer et al. 2000, Garten et al. 2007). Patterns of $\delta^{15}N$ in soil were less obvious because nutrient pooling and mechanisms of N uptake and transformations all factor into $\delta^{15}N$ signatures (Garten et al. 2007). For example, as with $\delta^{13}C$, soil microbes tend to discriminate against the heavier N isotope in processes such as denitrification, resulting in a nitrate pool that is $\delta^{15}N$-enriched (Mariotti et al. 1981). $\delta^{15}N$ enrichment can occur at localized sites, such as floodplains, where moisture saturation leads to low oxygen levels and higher denitrification rates, or near plant roots because vegetation is often preferential to the lighter N isotope (Nadelhoffer & Fry 1994, Naiman et al. 2002).

A distinct variation in soil $\delta^{15}N$ signatures was observed in the deepest location sampled (horizon C), which was within the zone of hyporheic water inundation. Soil pit 1, located closest to the streambank on the upstream side of the meander bend, had a considerably high $\delta^{15}N$ value of 6.21‰, compared to soil pit 2 (3.76‰), located furthest from the streambank, and soil pit 3 (4.09‰), located on the downstream side of the meander bend (Figure 3.10). Given samples were taken at similar depths, enriched soil $\delta^{15}N$ could indicate a persistence of MDN infiltration in this location close to the stream's edge.

Carbon isotopic signatures across horizon C were nearly identical (-24.58‰ ± 0.02‰), but the rate of change in $\delta^{13}C$ of vertical organic matter decomposition differed between sites. The regression coefficient between $\delta^{13}C$ abundance and the log C concentration were used to define rate of change (Garten et al. 2007). Soil pit 1 $\delta^{13}C$ signatures changed at a rate of 0.64‰ along the depth continuum, whereas soil pit 2 and 3 displayed slower changes with $\delta^{13}C$ change rates of 0.46‰ and 0.53‰, respectively. This greater rate of change at soil pit 1 could indicate the presence of MDN-enriched hyporheic water inundating deep soil horizons located near to the stream's edge.

3.5 Conclusions

The broad sample design of this study captured a few primary nutrient pathways linking MDN to aquatic and terrestrial food webs at the Horsefly River spawning channel. All macroinvertebrate FFGs displayed characteristics that could be positively associated with the presence of salmon and MDN, including an increase in community biomass, species richness, and species diversity during the spawning period. Amphipods (shredders) and chironomids (primarily collector-gatherers) were the most abundant taxa, with both groups combined comprising between 55% of total abundance in the spring and 88% during post-spawn. Chironomids appeared to assimilate MDN during salmon spawn, as evidenced by enriched $\delta^{15}N$ signatures in association with increased NH_4^+ concentration of hyporheic water beneath the streambed, which may have provided energy to help them maintain elevated biomass in the spring. Juvenile salmon are highly dependent on chironomid larvae as a food source (Lessard & Merritt 2006) and this study further suggests that they provide a critical link between the MDN pulse in the fall and salmon fry emergence in the spring. Past studies have reported shredders as a group that maintains an elevated biomass throughout salmon spawn (Minakawa et al. 2002, Lessard & Merritt 2006, Honea & Gara 2009), but, to my knowledge, this is the first study in North America that identifies freshwater amphipods (in particular, *H. azteca*) as the only shredding invertebrate located in a spawning area. Since amphipods are known to migrate to find the highest quality food source (Cothran et al. 2014), it is possible that they travel to the spawning channel in the fall to locate microbially-conditioned leaf litter, which facilitates growth prior to winter (Ito 2003). Then they potentially relocate to ponds and lakes sometime after the salmon decomposition period, while maintaining an isotopically-enriched signature over the winter. This study suggests that amphipods, as well as chironomids, may be particularly connected to the sockeye salmon feedback loop, as their seasonal migration evidently delivers an abundant, MDN-enriched food source from spawning grounds to the lakes where juvenile sockeye rear.

Patterns of isotopic enrichment were variable between riparian plant species, which is likely the result of differing morphologies and mechanisms of N-fixation. The shallower rooting species of *E. arvense* and *T. officinale* did not exhibit decreasing $\delta^{15}N$ with distance from the streambank, nor a common temporal isotope change, suggesting a lack of MDN assimilation from the fall nutrient pulse. However, *S. lucida* displayed a clear trend of decreasing $\delta^{13}C$ and $\delta^{15}N$ concentration with increased distance from the stream, as well as persistent isotopic enrichment between seasons, indicating that this deeper rooted species is assimilating MDN.

Since riparian deposits of salmon carcasses and bear feces were not abundant at the experimental site, the lateral transfer of MDN through hyporheic flow appears to be the prominent delivery pathway and is most evident in willows <7-m from the streambank. This conclusion is further supported by enriched $\delta^{15}N$ found in deep, hyporheic-influenced soil samples located near the stream's edge. Nevertheless, riparian and hyporheic ecotones are boundaries, by definition, comprised of a mosaic of redox gradients that vary spatially and temporally (Naiman & Decamps 1997, Boulton et al. 2010, Febria et al. 2011). Markedly different N pools can exist within close proximity, thus, this pattern of near-stream MDN enrichment would be more conclusive with greater spatial and temporal resolution. Continued research of the mechanisms that facilitate nutrient transfer and storage within the salmon feedback loop will require a greater focus into the life histories and physiology of species that appear to provide critical linkages between salmon generations.

Chapter 4

Conclusions and Management Implications

4.1 Conclusions

The results of this thesis demonstrate that marine-derived nutrients from spawning salmon are delivered to the riparian zone of an interior British Columbia stream via lateral hyporheic transport. Previous studies have demonstrated hyporheic transport of MDN (O'Keefe & Edwards 2002, Pinay et al. 2009), but this thesis expands on preceding knowledge by providing a seasonal component that identifies the assimilation and storage of MDN through multiple trophic levels within the stream-riparian ecosystem. The primary aims of this thesis were to: 1) identify the hyporheic zone at this site, 2) determine if NH_4^+, presumably from spawning salmon, was retained in the hyporheic zone during salmon spawn and after the winter, 3) identify how macroinvertebrate FFGs responded to the MDN pulse and salmon spawn, and 4) determine if the rooting depth and distance from the stream of riparian vegetation had an effect on MDN concentration. Chapter 2 of this thesis defines the hyporheic zone at this location and discusses the biogeochemical factors which influence subsurface nitrogen retention and transformation. Chapter 3 identifies willow trees, amphipods, and chironomids as species which particularly benefit from spawning salmon and MDN. By examining the temporal effect of MDN, this thesis provides evidence of an asynchronous exchange of nutrient subsidies between the stream and riparian zone.

Results from Chapter 2 indicate that NH_4^+ concentration in riparian hyporheic water decreased with distance from the streambank and was not delivered to inland locations during the salmon spawn. This outcome corroborates results from Chapter 3 where the reduction in $\delta^{15}N$ of *S. lucida* with distance from the streambank suggests that less marine N reached these inland locations and potentially all of the $\delta^{15}N$ that was detected in inland willows came from microbial denitrification. Shallow-rooted plants did not display a trend of decreasing $\delta^{15}N$ with distance from the streambank, which further confirms that the hyporheic zone is a dominant pathway in transferring nutrients from the stream to riparian zone. However, the extent of this nutrient delivery is limited at the Horsefly River spawning channel because hyporheic water is generally flowing toward the channel. Accordingly, hyporheic nutrient delivery in any system will be controlled by the variables which drive hyporheic flow, particularly hydraulic head gradients and hydraulic conductivity (Wondzell & Gooseff 2013). Although this study was unable to correlate NH_4^+ concentration with the arrival of spawning salmon, the corroborating evidence of $\delta^{15}N$ in near-stream willows suggests that salmon provide a substantial amount of MDN to this system.

The vertical movement of MDN from salmon carcasses and enriched metabolic wastes deposited on the riparian zone and subsequently transferred to terrestrial vegetation has been well established (Ben-David et al. 1998, Hilderbrand et al. 1999, Gende et al. 2001, Klinka & Reimchen 2002, Helfield & Naiman 2006). However, much of this research has been performed around densely-populated bear habitat and in coastal forests where precipitation and nutrient leaching rates are high (Reimchen et al. 2002, Drake et al. 2006). Whereas, the Horsefly River is located in an interior sub-alpine zone, with an average annual precipitation of 517 mm (Burford et al. 2009). Approximately 35 mm of rain was recorded during the two month sampling period in the fall of 2011. Bear activity in the experimental site was minimal and riparian deposits of salmon carcasses (n=5) and bear feces (n=2) were low in number. With these considerations, it appears that drier, interior climates may be less influenced by vertical nutrient leaching and more reliant on lateral hyporheic delivery.

Hyporheic NH_4^+ concentrations beneath the streambed were also positively correlated with chironomid $\delta^{15}N$ signatures, which suggests that these hyporheic-dwelling macroinvertebrates can rapidly assimilate MDN. This nutrient subsidy in the fall is apparently beneficial to chironomids because their high abundance was retained after the winter. Previous studies have confirmed the particular ability of chironomids to utilize MDN and avoid spawning mortality (Hicks et al. 2005, Lessard & Merritt 2006, Lessard et al. 2009, Verspoor et al. 2011, Campbell et al. 2012), however, this study presents a dominant assimilation pathway in the form of $\delta^{15}N\text{-}NH_4^+$ that may also be facilitated by hyporheic flow.

Although shredding invertebrates commonly appear in MDN literature, the high occurrence of amphipods at this site provides a unique perspective. Amphipod biomass and abundance exhibits a rapid increase in the fall, presumably due to the consumption of leaf litter that has been microbially-conditioned with the aid of salmon nutrients, and amphipods also maintain high $\delta^{15}N$ concentration in the spring. Analogous to the preferred rearing habitat of sockeye salmon, amphipods are typically associated with lentic environments. These results, in conjunction with evidence of high amphipod predation by juvenile salmon (Thompson 2007), allow inference that amphipods may be particularly important to the feedback loop of sockeye salmon.

The seasonal measurements of nutrients associated with salmon in this study reveal reciprocal subsidies between the stream and riparian zone (Nakano & Murakami 2001). In the fall, an upstream delivery of MDN from spawning salmon was observed to increase macroinvertebrate community biomass, species richness, and species diversity. Simultaneously, terrestrial leaf litter fall contributed a compounding nutrient source to shredders, which are known to initiate nutrient cycling processes in the stream food web (Graça 2001). Hyporheic pathways delivered MDN from the stream to the riparian zone, which could then be assimilated by near-stream vegetation. Nutrient storage is evident in the riparian zone over the winter, but these nutrients eventually return to the stream during spring freshet. This seasonal shift in nutrient fluxes is further demonstrated by the reversal between increased hyporheic NH_4^+ concentration beneath the stream in the fall and higher riparian hyporheic NH_4^+ in the spring.

Boundaries between oxic and anoxic environments create redox gradients at the intersections of ecotones, root micro-sites, pockets of organic matter, and hotspots of bacterial assemblages (Stanford & Ward 1993, McClain et al. 2003, Claret & Boulton 2009, Borch et al. 2010). Redox, or electron transfer, reactions provide energy for biological growth, and strong redox gradients enhance biogeochemical activity and microbial processing (Borch et al. 2010, Rezanezhad et al. 2014). Nitrification and denitrification represent a tightly coupled oxidation-reduction (redox) reaction that facilitates rapid organic matter decomposition and an overall loss of nitrate from the aquatic environment (Zarnetske et al. 2011). The seasonal reversal of hyporheic NH_4^+ concentration beneath the stream and below the riparian could indicate the presence of a nitrification-denitrification coupling system on a larger time and spatial scale. This discovery highlights the importance of considering the entire stream-riparian ecosystem when implementing plans for salmon conservation and management.

4.2 Management Implications

Pacific salmon populations in the United States and Canada are displaying signs of stress, such as decreasing returns and inconsistent cycles. Continued research of these populations in their marine and terrestrial environments is required, as well as the implementation of conservation action plans (Nehlsen et al. 1991, Beamish et al. 2012, Peterman & Dorner 2012, Sharma et al. 2013). Salmon are tough and resilient species, and can immediately return to areas that have been blocked by dams for decades (Anderson et al. 2014). However, their physiology is sensitive in regards to climate change pressure, particularly warming water (Hague et al. 2011, Martins et al. 2011). Therefore, it is critical that we understand what makes a salmon's spawning and rearing habitat persistent and stable, so we may recognize changes in these ecosystems and implement meaningful conservation solutions.

Results from this study identified that MDN support the whole macroinvertebrate community and provide energy for growth to deep-rooted riparian vegetation bordering the stream. In turn, riparian vegetation provides shade for spawning salmon (Naiman et al. 2002), woody debris for juvenile salmon habitat (Fausch & Northcote 1992), and leaf litter to support the macroinvertebrate population (Vannote et al. 1980, Ito 2003). MDN stored in the riparian zone over the winter are delivered back to the stream in the spring, activating microbial activity and supplying energy for salmon fry (Nakano & Murakami 2001). These nutrients are recycled throughout the stream-riparian ecosystem (Wipfli et al. 2010), thus maintaining strong salmon returns is crucial for healthy salmon habitat. Doing this involves a more complete understanding of the biogeochemical interactions that link and support these ecosystems, as well as identifying the key reactions, elements, and species that are particularly critical elements of the salmon feedback loop.

The Horsefly River spawning channel offers a unique opportunity to study stream-riparian food web dynamics of an interior sockeye salmon system. Gates along the channel and a water pump dictating flow allow for experimental control and manipulation. The macroinvertebrate community is relatively simple, with dozens, as opposed to hundreds, of specific taxa, including some FFGs that are represented by only one species or family. The present study, in conjunction with studies from Albers (2010) and Albers & Petticrew (2012, 2013), present a useful baseline understanding of the biogeochemical nutrient dynamics that occur because of salmon spawn. From this simplified framework, strong food web models can be developed and interpreted with the intention of discovering critical linkages that elucidate the resilience of salmon populations. Nitrate removal experiments could also be implemented (e.g. Peter et al. 2012) and the microbial assemblages that facilitate denitrification could potentially be identified. The results presented in this thesis illustrate the innate connectivity of the stream-riparian ecotone, as well as the resilient salmon feedback loops embedded within this landscape.

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