Highly variable physical and biological characteristics of hyporheic zones among young streams undergoing primary succession

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Abstract: Opportunities are rare to study ecological primary succession and physical channel development in brand-new streams. An exception exists in streams recently formed atop extensive pyroclastic materials deposited during the 1980 eruption of Mount St Helens (USA), an area known as the Pumice Plain. Recent work demonstrated unexpectedly high diversity of benthic invertebrates in Pumice Plain streams at <4 decades post eruption, both within and among streams. Given the ecological importance of the hyporheic zone (HZ), we asked if differential development of HZs, both physically and biologically, could help explain the among-stream variability in surface assemblages. In 2019 (39 y post eruption), we measured abiotic variables and collected hyporheic invertebrates with a modified Bou–Rouch method from 4 Pumice Plain streams already understood to vary substantially in terms of successional trajectory. The HZ was accessible to just ~30 cm below the stream beds because of a nearly impermeable layer of compacted ash overlain by alluvium. Hyporheic invertebrate assemblages were low-diversity subsets of the benthos, dominated by Chironomidae, and lacking true groundwater taxa. Hence, the benthic zone appears to influence the underdeveloped HZ assemblages in these young streams, more so than the reverse. Substantial among-stream variation in HZ assemblage structure also reflected previously documented spatial patterns of the benthos. Mean densities of hyporheic invertebrates varied by >2 orders of magnitude, and standing biomass varied by >4 orders of magnitude among streams. The stream with greatest density and richness had large median particle size, a stable bed, and dense riparian woody vegetation and was dominated hydraulically by downwelling. Streams occupying eastern vs western sides of the Pumice Plain were strongly differentiated abiotically and biotically, and snapshot water stable isotope data suggest hydrological sources drove these differences, with eastern streams likely fed by glacier melt and western streams fed by warmer groundwater sources. This survey provides novel insight into HZ development in newly formed streams and points to further avenues of research, including exploring the development of groundwater assemblages in Pumice Plain aquifers and evaluating the role of woody riparian plants in establishing surface-water/groundwater connections to develop the ecotone characteristic of mature hyporheic zones.

Key words: invertebrate communities, disturbance, Mount St Helens, hydrology, headwaters, hyporheos, primary succession, volcanic eruption, colonization, dispersal, geomorphology, glaciers

INTRODUCTION

Hyporheic zones are hotspots for ecosystem processes in streams and provide habitat for diverse assemblages of invertebrates (Boulton et al. 1998). A stream's hyporheic zone (HZ) typically represents an ecotone between true groundwater and stream surface water, with invertebrate assemblages constituting a blend of epibiont taxa generally associated with the benthic zone of streams and stygobiont taxa associated with true groundwater (Hutchins et al. 2020, Dole-Olivier et al. 2022). Several aquatic insect epibionts spend substantial proportions of their juvenile stages in the

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HZ (e.g., Stanford and Gaufin 1974, Dorff and Finn 2020, Negishi et al. 2022), and others enter the HZ temporarily as a behavioral response to physical disturbance (Palmer et al. 1992, Vander Vorste et al. 2016, Milner et al. 2022) or to biotic interactions in the surface stream (Robertson et al. 1995). Stygobionts include a few insects that lack a flying stage (e.g., Leys et al. 2010) but mainly comprise species from other taxa, with crustaceans particularly well represented. Although not well understood to date, invertebrates in the HZ likely influence ecosystem processes such as decomposition and nutrient cycling (e.g., Bärlocher and Murdoch 1989, Mermillod-Blondin et al. 2003).

Despite the ecological relevance of the HZ, little is known about how this habitat develops in association with new stream channels. Streams tend to be very old features on landscapes; therefore, opportunities are rare to study physical channel development and primary succession in new systems. The bulk of the ecological work done thus far on young streams experiencing primary succession has occurred in recently deglaciated streams draining into Glacier Bay, Alaska, USA (e.g., Milner et al. 2008, 2011). The Glacier Bay body of work includes 1 survey of HZ invertebrates in a single newly developing stream (McDermott et al. 2010) and reported assemblages with relatively low diversity that were nested subsets of the local benthic (epibiont) assemblage.

In addition to recently deglaciated landscapes, extensive areas of freshly deposited pyroclastic material (i.e., tephra) from volcanic eruptions provide another fruitful setting for studying stream channel development and primary succession at watershed scales (e.g., Claeson et al. 2021). The 1980 eruption of Mount St Helens (Lawetlat′la in the indigenous Cowlitz language) in the state of Washington, USA, was a massive lateral blast that deposited pyroclastic materials across ~15 km^2 and up to 100 m deep atop pre-existing forests and streams on the north side of the mountain (Lipman and Mullineaux 1981, Meyer and Martinson 1989). This area, now known as the Pumice Plain, has been a focal point for research on ecological primary succession (Dale et al. 2005, Service 2021), but this work has been primarily terrestrial. Although several new streams appeared shortly after the eruption, no stream-specific research was initiated until ~35 y post eruption, and nothing is known about the development of associated hyporheic zones.

Surveys of Pumice Plain streams undertaken during 2015 to 2016 showed that benthic macroinvertebrate and algal assemblages were diverse and varied substantially among streams (i.e., had high beta diversity; Claeson et al. 2021). The highest-level taxonomic differences were between 2 groups of streams distinguished by apparently contrasting water sources to the Pumice Plain. Streams in 1 group had colder water temperatures and relatively high NO_3^- concentrations but low conductivity, suggesting water sourced from glacier runoff (Ilg and Castella 2006, Saros et al. 2010). Streams in the 2nd group had higher water temperatures, low NO_3^-, and high conductivity, suggesting groundwater sources (Claeson et al. 2021). Riparian vegetation development was also highly variable among streams but did not appear to strongly influence benthic invertebrate assemblages, although canopy cover was associated with increased particulate organic matter and rates of organic matter processing (LeRoy et al. 2023).

Because the HZ plays an important role as habitat and refuge from disturbance, we speculated that differences in geomorphological development of the HZ among Pumice Plain streams might contribute to the observed differences in benthic assemblages. The physical structure of the HZ influences which invertebrates can colonize and use the space as habitat (Stubbington 2012, Mathers and Wood 2016). Substrate size and surface/subsurface hydraulics can affect habitat accessibility and quality. For example, larger particles provide more interstitial space, the permeability of which also influences O_2 saturation, organic material, and, hence, the types and sizes of invertebrates that can inhabit the HZ (Mathers et al. 2021). In addition, areas of downwelling (net water movement from surface to subsurface) are often associated with more epibiont taxa in the HZ, in contrast with areas of upwelling, which typically have more stygobiont taxa (Dole-Olivier et al. 2022).

The primary objective of this study was to assess the status of both the invertebrate assemblages and their physicochemical habitat in the HZ of young Pumice Plain streams. Our approach was observational and entailed biotic and abiotic data collection 39 y after the massive eruption that created the Pumice Plain. We addressed 3 major questions: Q1) Which abiotic factors are most strongly associated with HZ invertebrate assemblage structure in these young streams? Q2) Do HZ assemblages vary among streams in similar patterns as the corresponding benthic assemblages (Claeson et al. 2021)? Q3) Are taxa unique to the HZ present, or are HZ assemblages primarily nested subsets of their benthic counterparts?

METHODS

To address the study questions, we studied hyporheic invertebrate assemblages and physicochemical characteristics of 4 Pumice Plain streams during the growing season in 2019. We measured some physicochemical variables already shown to be associated with the benthic invertebrates of Pumice Plain streams (e.g., water temperature, chemistry; Claeson et al. 2021), and we collected additional geomorphological and hydrological data including upwelling/downwelling patterns and streambed aggradation/degradation, as well as stable isotope ratios of water to get a clearer picture of major hydrologic sources to the streams. The 4 study streams were distributed across the Pumice Plain and represented 2 streams hypothesized to be mainly glacier fed and 2 streams hypothesized to be mainly fed by groundwater (Claeson et al. 2021).

Study streams

All Pumice Plain streams originate at perennial springheads, immediately upstream of which surface water is not present. Streams then flow north into Spirit Lake (Fig. 1). On the eastern side of the Pumice Plain, springs feeding streams have been hypothesized to be associated with shallow aquifers with short residence times, given thermal and chemical proxies of glacier melt (Ilg and Castella 2006, Saros et al. 2010). The glacier source was speculated to be the Forsyth Glacier on the northeast side of the mountain, peripheral to the crater left by the 1980 eruption (Claeson et al. 2021; Fig. 1). Conversely, streams on the western side of the Pumice Plain have warmer temperatures, high conductivity, and lower NO_3^- than eastern streams, suggesting groundwater sources from deeper aquifers with longer residence times. Immediately following the eruption, the deep layer of pyroclastic materials of various sizes that formed the Pumice Plain was overlain by a thick crust of compacted and nearly impermeable tephra (mainly ash; Leavesley et al. 1989) that would have influenced the hydrological and geomorphological development of the new streams (Meyer and Martinson 1989). All streams have a winter-rain-type flow regime (Poff and Ward 1989), with higher flows in winter and spring, and baseflow conditions and occasional drying in summer and early autumn.

For this study, we selected a single 20 to 40-m reach on each of 4 focal streams at elevations of 1088 to 1102 m. We aimed for reach lengths of 20× the wetted width of each stream, but lengths varied slightly (shorter/longer) given accessibility of locations to install hyporheic sample wells (see following paragraph) in comparable reaches among the 4 streams. Each sample reach occupied a relatively low-gradient elevational band oriented between steeper upper slopes of the mountain and lower depositional reaches of streams approaching their confluence with Spirit Lake. Each of the reaches also had coarse alluvial material on the stream bed. In order from west to east across the Pumice Plain, the 4 streams were Geothermal-West (Geo-W), Clear, Willow, and Forsyth creeks. The western streams Geo-W and Clear had the groundwater signature, and eastern streams Forsyth and Willow had the glacier-melt signature detected in the earlier study (Claeson et al. 2021). Riparian vegetation was

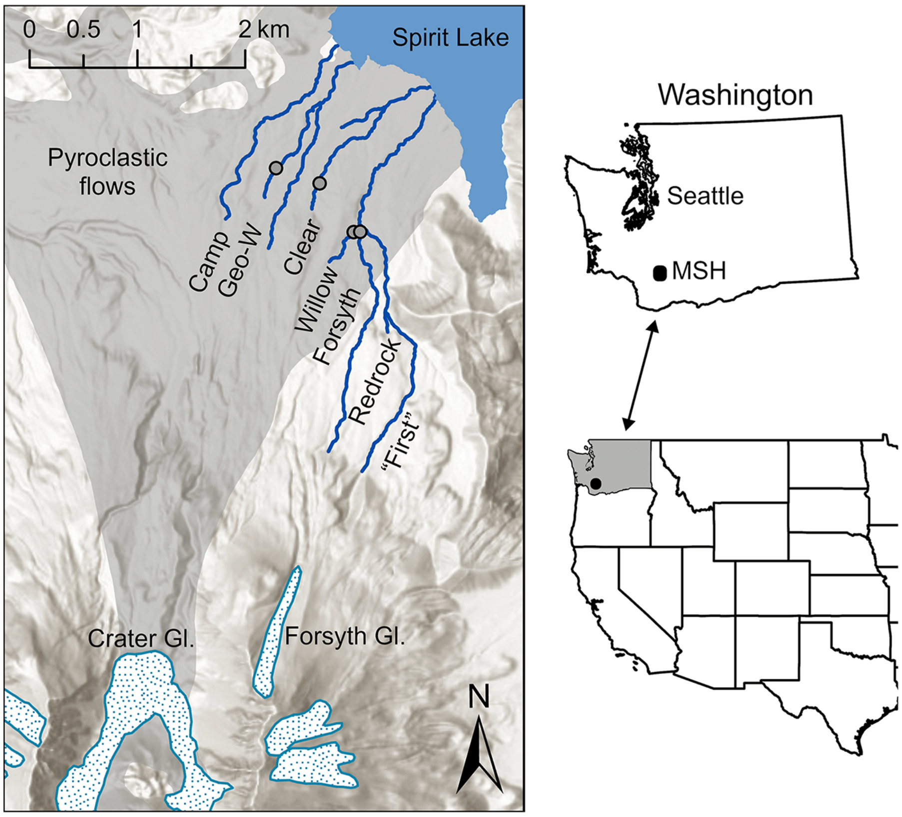

Figure 1. Study location. Maps at right show location of Mount St Helens (MSH) volcano in the state of Washington in the northwestern USA. Left panel shows the north-flowing stream channels present on the Pumice Plain in 2019, locations of study reaches in the 4 focal streams of the current study (gray dots), and contemporary locations of glaciers within and surrounding the crater produced by the 1980 eruption (stippled areas, with glacier names mentioned in the text ending in Gl.). Darker-shaded area labeled as pyroclastic flows indicates the location of the Pumice Plain. All other areas included in the left panel were also heavily disturbed by events associated with the eruption, including hot blast, debris avalanches, mudflows, or a combination.

minimal at 1 western (Clear) and 1 eastern (Willow) stream reach, and the other western (Geo-W) and eastern (Forsyth) reaches had substantial woody vegetation with a closed riparian canopy primarily consisting of the early successional species Sitka alder (*Alnus alnobetula* ssp. *sinuata* [Regel] Á. Löve & D. Löve) and Sitka willow (*Salix sitchensis* Sanson ex Bong.) (LeRoy et al. 2023).

Environmental data collection

Field data collection took place May to October 2019 (timeline in Fig. S1). Between 12 May and 10 June, we used a steel driver to install 4 schedule-40 PVC pipes (2.5-cm diameter, 1.2 m total length; henceforth wells), into the hyporheic zone midchannel in each of the 4 study reaches. Field access was limited early in the study period, hence the extended time span to complete well installation. Within reaches, wells were spaced at least 5 m apart and remained in place for the duration of the study period. Each well was capped at the bottom and had a 15-cm screen composed of 5-mm diameter holes, as described by Dorff and Finn (2020). We placed the wells such that the middle of each screen was ~30 cm deep into the HZ. We encountered an impermeable, concrete-like layer similar to the crust described by Leavesley et al. (1989) within ~30 to 40 cm below the surface of each of the young stream beds, which limited our sampling of the HZ to these relatively shallow depths. We used the wells throughout the study period to collect data on local upwelling/downwelling conditions, aggradation of the stream bed, HZ water chemistry, and HZ invertebrates. Other abiotic data were collected from stream surface water, as described below.

We installed a 3001 Levelogger® 5 (Solinst® Canada Ltd, Georgetown, Ontario, Canada) in each of the 4 stream reaches to record stage (m) and water temperature (°C) continuously at 1-h intervals from 12 May to 12 October 2019. Leveloggers were placed flush with the streambed surface and secured to a section of rebar hammered at least 30 cm into the stream bed. We used the stage data in combination with instantaneous discharge (Q) measured on 9 dates to produce rating curves for estimating continuous changes in discharge at each stream throughout the study period. Instantaneous Q was measured with an FH950 flow meter (Hach®, Loveland, Colorado) across a range of flow magnitudes. We used flow data estimated from the rating curves for each of the 4 streams to calculate mean discharge (L/s), number of days with zero flow, and CV of daily flow for each stream throughout the 5-mo study period. We also calculated mean surface-water temperatures for each stream from the hourly data recorded by the Leveloggers.

We measured 3 variables describing physical aspects of the streambed surface once each during the study period. We used a modified pebble count of 100 particles (Kaufmann et al. 1999) at each study reach on 13 July to calculate the median particle size of streambed sediments (D_{50}). On the same date at each reach, we calculated the bottom component of the Pfankuch index (Pfankuch 1975), higher scores of which indicate greater physical instability of the bed. We also measured the change in elevation (aggradation/degradation, in cm) of the stream bed at each reach over the duration of the study period as the difference in relative elevation of the bed surface at the start and end (12 October) of the study. We had marked bed elevations on the exterior of all sample wells and on the rebar securing Leveloggers at each site upon installation to serve as elevation references throughout the study period.

We also measured physical and chemical characteristics of water inside each installed well. To quantify degree of upwelling or downwelling at the local scale, we measured hydraulic head (HH) in all wells on 3 dates (11 July, 6 August, and 10 October) as the relative difference in water surface elevation inside vs outside of the wells (to the nearest 0.5 cm). Negative values indicate lower water levels inside a well compared with the stream surface (downwelling), and positive values indicate upwelling. We also measured dissolved O_2 (DO; % saturation) and specific conductance (µS/cm; standardized to 25°C) of hyporheic water with a YSI Pro2030 multisonde (Yellow Springs Instruments, Yellow Springs, Ohio), with probes dropped to the bottom of each well on a single date during baseflow conditions (11 August).

We also collected water samples from stream surface and potential hydrologic sources from which we measured stable isotope ratios of water (δ^2H and δ^{18}O; ‰). Water samples consisted of single collections on 14 to 15 July 2019 from each of the 4 focal streams, an additional 3 Pumice Plain streams from the western ($n = 1$) and eastern ($n = 2$) sides, and candidate baseflow-season water sources higher on the mountain (Claeson et al. 2021). The candidate sources included meltwater from the young Crater Glacier that has developed inside the crater left by the 1980 eruption, a spring inside the crater, and ice from the Forsyth Glacier (Fig. 1), which survived the eruption after being beheaded and losing ~90% of its total volume (Brugman and Post 1981). Each sample was collected, unfiltered, into a sterile 20-mL polypropylene vial and capped full, with no headspace. Samples were stored in the dark at room temperature until analyzed on an L2120-i analyzer (Picarro, Inc., Santa Clara, California) with results normalized to Vienna Standard Mean Ocean Water.

Invertebrate data collection

We collected hyporheic invertebrates from installed wells with a modified Bou–Rouch pumping method (Bou and Rouch 1967, Dorff and Finn 2020). Given the possible disturbance associated with installing wells, we did not collect invertebrate samples for at least 4 wk following their installation. All wells across the 4 study streams were pumped for invertebrate collections during midday hours on each of 2 dates: 12 July and 14 August 2019. Later dates in the study period had reduced flow that prevented successful sampling. We pumped hyporheic water at a standard rate (~1 pump/sec) from each well into a 20-L bucket until we had collected up to 8 L of water or the maximum possible before the connection was lost, which occurred frequently, likely because of the low-permeability layer in the subsurface of each stream. Pumping failed in 5 individual wells in August given reduced water volumes in Forsyth and Geo-W (more detail in "Data analysis" below). All other wells produced at least 0.5 L/sample (Table S1), which we deemed a minimum acceptable volume for invertebrates to be included in analysis because a substantial proportion of total abundance is expected in the first 0.5 L, regardless of total volume pumped (e.g., Hunt and Stanley 2000). We ran the collected water through a 125-μm sieve and preserved the retained invertebrates in 80% ethanol for short-term storage and transport. In the laboratory, invertebrates were sorted, identified to the greatest taxonomic resolution possible (Merritt et al. 2019), enumerated, and body lengths measured to estimate biomass from length/mass regressions (Benke et al. 1999) by Aquatic Biology Associates, Corvallis, Oregon.

As part of a concurrent but unrelated study, we collected benthic invertebrates from each of the 4 focal stream reaches on each of 10 dates throughout the study period (May–October 2019). Samples for each reach/date were a composite of 8 randomly distributed Surber samples (500-μm mesh size, 0.09-m^2 sample area). For the current study, which emphasizes the hyporheos, we pooled benthic invertebrates across sample dates for each stream, identified individuals at the same taxonomic resolution as the hyporheic samples, and considered only presence/absence of benthic taxa to address the question (Q3) of whether hyporheic assemblages were subsets of the corresponding benthos in each stream, or if, alternatively, the HZ had a distinct fauna. We addressed this question both with the entire benthic dataset and with the benthic data collected solely in July and August 2019 (same period as hyporheic invertebrates were collected), but we emphasize results from the full dataset because epibiont taxa often move between hyporheic and benthic zones during their life cycle (e.g., Dorff and Finn 2020). These benthic invertebrates were not involved in other components of the current study.

Data analysis

To assess differences among streams and sample dates in the abiotic variables sampled for the 1st time in the current study (compared with Claeson et al. 2021) and in hyporheic invertebrate community metrics, we used analysis of variance (ANOVA) with mixed effects for any variables for which replicates had been collected on multiple dates or simple 1-way fixed effects ANOVA if replicate samples had been collected on a single date. We then applied Tukey's honestly significant difference tests (with Holm method for multiple comparisons) for any ANOVA with a p-value <0.05 to assess pairwise differences among streams. We tested all response variables for normality and $\log_{10}(x + 1)$ transformed them if necessary to achieve normality, with zeros maintained. We also reviewed all residual plots for homoscedasticity. Abiotic variables included HH (4 replicates/stream on each of 3 dates except Forsyth in October because the HZ was dry) and aggradation/degradation of the stream bed over the span of the study period (5 replicates/stream, 1 sample date). Invertebrate metrics included taxa richness, density of individuals (no./L pumped), and total biomass (mg/L) from data collected on 2 dates, with 4 replicates/stream except when pumping failed in August in Forsyth ($n = 1$) and Geo-W ($n = 2$). HH and invertebrate richness, density, and biomass were tested for fixed-effect differences among streams and dates, with well replicates as a random effect. All simple and mixed-model analyses were performed in R (version 4.3.2; R Project for Statistical Computing, Vienna, Austria) with functions lm (package *stats*), lmer (package *lme4*, version 1.1-35.3; Bates et al. 2015), and glht (package *multcomp*, version 1.4-25; Hothorn et al. 2008).

Because volume pumped varied among wells and dates, and because no./L pumped is merely a semiquantitative measure of invertebrate numbers per unit volume of HZ sediment, we also ran ANOVAs on absolute abundance and total biomass/well, regardless of volume pumped. Similar outcomes of ANOVA between these 2 types of invertebrate input data provide stronger inference about invertebrate distribution patterns among streams. We also ran any additional assemblage-level quantitative analyses (following) using both no./L and total abundance of taxa collected per well.

We then evaluated aspects of the spatial distribution of hyporheic taxa. We first addressed the question of whether hyporheic assemblages were taxonomically unique or nested subsets of the associated benthos with a 1-tailed paired t-test (streams as groups) comparing the number of taxa solely found in the hyporheic samples in each stream with the number of taxa shared between the hyporheic and benthic samples in the same stream. To visualize distribution patterns of taxa both within streams (benthic vs hyporheic habitats) as well as among the hyporheic zones of the 4 streams, we produced Venn diagrams illustrating the proportion of taxa shared either between habitats or among streams compared with the proportion unique to a single habitat or stream. We used R functions ggVennDiagram (package *ggVennDiagram*, version 1.5.2; Gao et al. 2021) and plot.euler (package *eulerr*, version 7.0.2; Larsson 2018) to produce the Venn diagrams, which required presence/absence data only. We then used density (no./L) of each hyporheic taxon for indicator species analysis in PC-ORD (version 7; McCune et al. 2002) to determine if any hyporheic taxa were indicative of any of the 4 study streams. Indicator values range from 0 to 100. We tested each value for statistical significance using 4999 Monte Carlo randomizations.

We assessed differences in overall community structure of hyporheic invertebrate assemblages among streams with nonmetric multidimensional scaling (NDMS) using Sørensen dissimilarity as the distance measure (PC-ORD, with 250 random starts and 500 iterations). Input values for each of 40 taxa were $\log_{10}(x + 1)$-transformed mean densities (across wells) for each stream/date, resulting in $n = 8$ total community samples (4 streams, 2 dates). We used stream/date means because densities were often low in individual wells, wells varied in total pumped volume, and sample sizes varied among streams in August. We also evaluated correlations of abiotic variables (Table 1) and standard invertebrate metrics (see Table S2 for the full list of variables tested) with NMDS ordination axes. We added any variables with Pearson correlations of $r > |0.50|$ as vectors on the resulting NMDS biplot indicating direction of correlation, with length scaled to correlation strength. The final 2-dimensional biplot was rotated +40° such that environmental factors with strongest correlations to community structure ran along axis 1. We then used multi-response permutation procedure (MRPP) in PC-ORD to test 2 null hypotheses that 1) invertebrate assemblages were the same between eastern and western streams and 2) invertebrate assemblages were the same between the 2 sample months. As in the NMDS, we used Sørensen dissimilarity as the distance measure, with number of permutations = 999. The test statistic for MRPP is A, which ranges from −1 to +1 and describes effect size of the grouping variable. MRPP results here are highly conservative, given the small sample sizes ($n = 4$ streams each).

RESULTS

Environment

Physicochemical conditions varied widely among the 4 Pumice Plain streams in both the surface and subsurface (Table 1), with many variables differentiating western (Geo-W, Clear) from eastern (Forsyth, Willow) streams. Median particle size on the stream bed (reach scale) varied from 6 mm at the westernmost stream (Geo-W) to 32 mm at the easternmost (Forsyth Creek). DO % saturation and specific conductivity of hyporheic water varied similarly, with eastern streams having substantially greater DO (79–83% saturation) than western streams (23–33.5% saturation), and eastern streams with much lower specific conductivity (70–78 µS/cm) than western streams (319–573 µS/cm). Mean surface-water temperature was also greater in western (7.2–7.8°C) than eastern streams (4.7–5.7°C). HH observations varied among streams ($F_{3,40} = 8.3$, $p < 0.0001$; see Appendix S2 for all statistical output tables), with mean upwelling in the 2 western streams and downwelling in the eastern streams (Fig. 2A), although there was high variability among wells, including some extreme individual data points. Maximum HH (upwelling) recorded was 36.5 cm at a well in Clear Creek in July, and minimum HH (downwelling) was −30.7 cm at a well in Forsyth Creek in August. There was no effect of sample date ($F_{2,41} = 1.5$, $p = 0.2$) on HH observations. All streams showed signs of streambed aggradation throughout the study period (Fig. 2B), but the magnitude of aggradation varied among streams ($F_{3,16} = 4.4$, $p = 0.02$). Clear Creek had the highest mean aggradation (8.6 cm), which was higher than aggradation

Table 1. Physical and chemical data from 4 study streams on the Pumice Plain formed by the 1980 eruption of Mount St Helens, Washington, USA, with 2 streams on the western side and 2 streams on the eastern side of the Pumice Plain. Single values in cells represent data collected once during the study period. For any variable with multiple replicates collected, values are mean (range). Data are organized into 2 categories representing variables measured in the surface habitat of each stream (surface) and variables measured in the hyporheic sample wells (hyporheic). Discharge values were estimated from rating curves (see Methods). D_{50} = median particle size on streambed surface. δ^{18}H and δ^{2}O are isotope ratios from snapshot surface-water samples in July 2019 (see also Fig. 3). Q = discharge, HZ = hyporheic zone, DO = dissolved O_2, Cond. = specific conductivity. Streambed aggradation and hydraulic head patterns are visually depicted in Fig. 2. See Claeson et al. (2021) and LeRoy et al. (2023) for additional environmental characteristics associated with these streams.

		Surface variables									Hyporheic variables		
Location	Stream	Q (L/s)	CV of Q	Zero-flow days (No.)	Pfankuch index	D_{50} (mm)	Aggradation (cm)	δ^{18}O (‰)	δ^{2}H (‰)	Water temperature (℃)	HZ DO (% sat.)	HZ cond. (µS/cm)	Hydraulic head (cm)
Western	Geo-W	2.5 (0–5.0)	0.34	24	23	6	4.5 (0–7)	−13.06	−90.10	7.2 (1.9–12.7)	23.0	573	0.3 (−4.0–3.1)
Western	Clear	11.3 (5.8–27.9)	0.13	0	38	9	8.6 (3–15)	−13.36	−89.30	7.8 (2.9–14.9)	33.5	319	6.2 (−8.4–36.5)
Eastern	Willow	45.3 (18.5–69.6)	0.10	0	30	18	2.2 (0–8)	−13.49	−93.80	4.7 (2.1–8.3)	83.1	78	−3.7 (−7.0–4.5)
Eastern	Forsyth	3.2 (0–8.2)	0.37	36	25	32	1.4 (0–4)	−14.05	−95.32	5.7 (3.5–8.9)	78.8	70	−6.4 (−30.7–2.0)

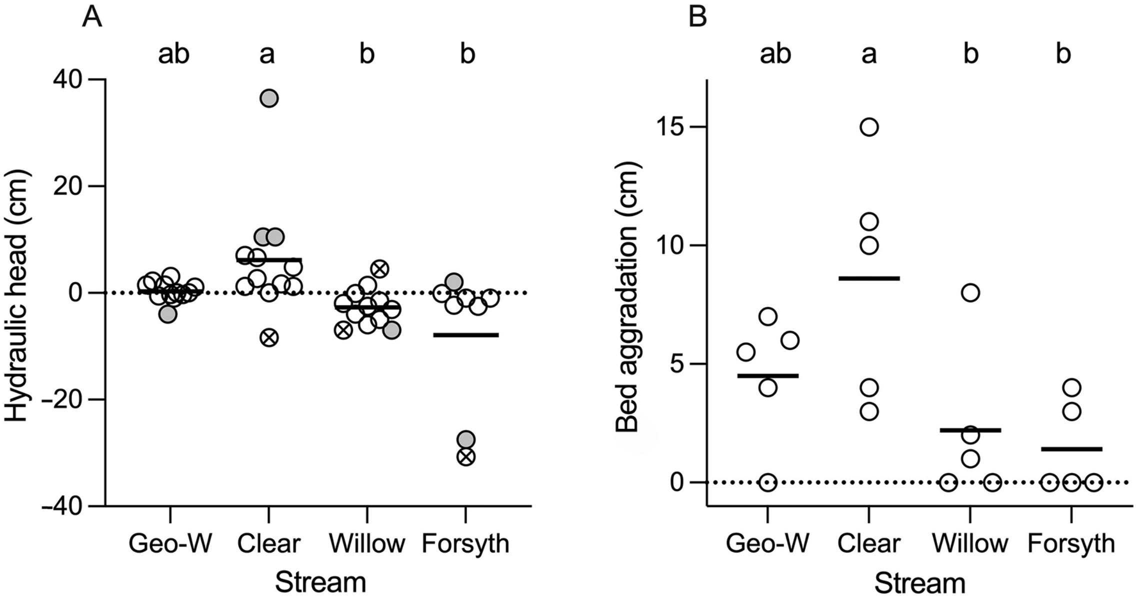

Figure 2. Hydraulic head (A) and streambed aggradation throughout the 5-mo study period (B) in each of the 4 study streams (data summarized in Table 1). Streams are organized along the *x*-axes from west to east on the Pumice Plain of Mount St Helens, Washington, USA. Each data point is a single replicate observation, black horizontal lines are means, and horizontal dotted lines indicate 0 on *y*-axes. In panel A, replicates representing highest and lowest readings for each stream are coded according to sample date, with grey shaded points indicating July and x-marked points indicating August. Other points are open, including all October samples (none of which had high or low extremes). Points in panel B are values recorded from a single date at the end of the study period. Lowercase letters along the top indicate differences between streams, based on Tukey's post-hoc tests (Holm method) with $p < 0.05$.

in the 2 eastern streams (Forsyth: 1.4 cm, Willow: 2.2 cm). Geo-W had intermediate aggradation (4.5 cm). A visual of the aggradation process in Clear Creek is in Fig. S2.

Discharge (*Q*) patterns through the study period also varied among streams (Table 1, Fig. S3), with mean *Q* varying by more than an order of magnitude from lowest (Geo-W: 2.5 L/s) to highest (Willow: 45.3 L/s). As observed previously (Claeson et al. 2021, LeRoy et al. 2023), lower flows occurred in streams with more woody riparian vegetation, one (Geo-W) on the west side and the other (Forsyth) on the east side of the Pumice Plain. We also observed zero-flow days in these 2 streams (24 and 36 d, respectively), and the Pfankuch index indicated they had more stable beds than the 2 streams with greater mean *Q* (Table 1). Interestingly, CV of *Q* was also greater in these 2 streams with lower mean *Q*.

Water stable isotope ratios measured from single snapshot samples in July distinguished western vs eastern streams, including not just the 4 focal streams in this study but also 3 additional streams on the Pumice Plain (Fig. 3). Eastern streams showed more depleted signatures (lower $\delta^{18}O$ and $\delta^{2}H$) than western streams, similar to the signature of meltwater collected from the Forsyth Glacier. Interestingly, the 2 glaciers sampled showed the most contrasting values among all samples collected, with Forsyth Glacier most depleted in heavy isotopes (e.g., $\delta^{18}O = -14.05‰$) and Crater Glacier least depleted ($\delta^{18}O = -12.00‰$). The sample from the spring located inside the crater was similar ($\delta^{18}O = -12.03‰$) to the Crater Glacier sample.

Invertebrates

We collected a total of 40 hyporheic taxa from the combined sample dates and wells across the 4 streams (Appendix S1). Within streams, total richness varied from 2 taxa at Clear Creek to 24 at Forsyth, and richness of samples pumped from individual wells varied from 0 to 20 taxa (Fig. 4A). Chironomidae dominated in terms of both abundance and richness, representing 47.5% (19 of 40) of the total taxa and ranging from 40% of all taxa at Geo-W to 58% of all taxa at Willow Creek. Two other Diptera taxa were documented, both in the Tipuloidea, in addition to 4 mayflies, 6 stoneflies, 3 caddisflies, and 6 broader taxa of noninsect invertebrates.

Hyporheic taxa richness varied substantially among streams ($F_{3,24} = 17.1$; $p < 0.0001$). On average, Forsyth Creek had 2.6× greater richness than Willow Creek, 3.3× greater richness than Geo-W, and 26× greater richness than Clear Creek (Fig. 4A). Invertebrate densities (no./L) varied similarly ($F_{3,24} = 44.9$; $p < 0.0001$; Fig. 4B), with Clear Creek containing the lowest density and Forsyth Creek the greatest (280× greater than Clear Creek). Post-hoc tests identified differences in HZ invertebrate density among all pairs of streams, with the 2 western streams having lower densities than the 2 eastern streams. Total standing biomass

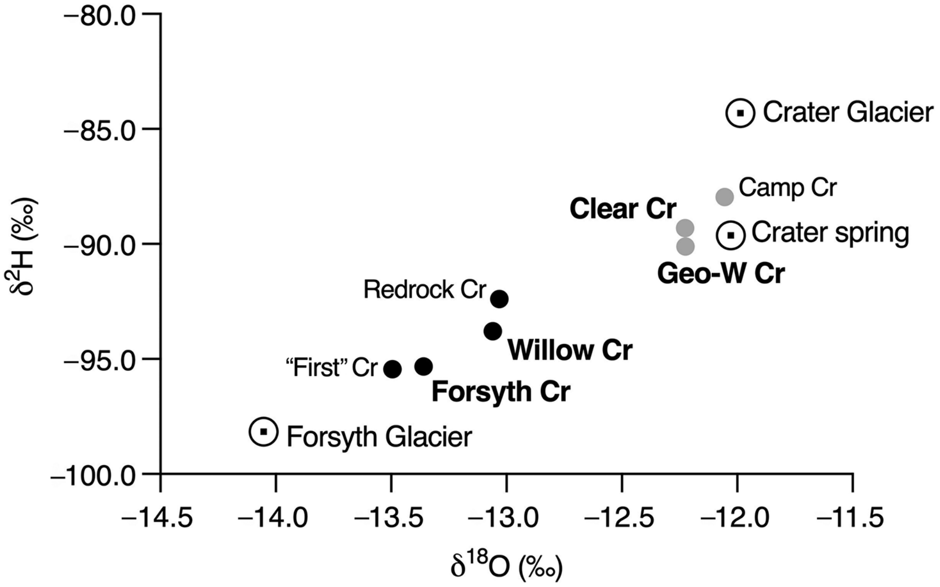

Figure 3. Stable isotope ratios of water (δ^2H and $\delta^{18}O$; ‰) from snapshot samples collected mid-July 2019 from 4 study streams on the Pumice Plain of Mount St Helens, Washington, USA. Filled smaller circles are samples from surface water of Pumice Plain streams, including the 4 study streams (labeled in bold font) plus 3 additional streams (see Fig. 1 for names and locations). Gray fill indicates streams on the western side, and black fill indicates streams on the eastern side of the Pumice Plain. Open bullseye circles indicate samples from potential sources higher on the mountain and include 2 glaciers labeled by name and a spring inside the crater. Cr = creek.

of HZ invertebrates again showed similar patterns ($F_{3,24} = 34.8$; $p < 0.0001$; Fig. 4C), with mean biomass varying by nearly 4 orders of magnitude between Clear Creek (lowest) and Forsyth Creek (highest). None of these 3 metrics varied between the 2 sample dates (all $p > 0.3$). Overall patterns and inference were the same for absolute abundance and total biomass per well (regardless of volume pumped) as ANOVA input (Fig. S4), hence we report here only the results using units/L as input.

The hyporheic invertebrate assemblages at each stream primarily included taxa present in their corresponding benthic zone (Fig. 5A). Taxonomic richness of the benthos collected

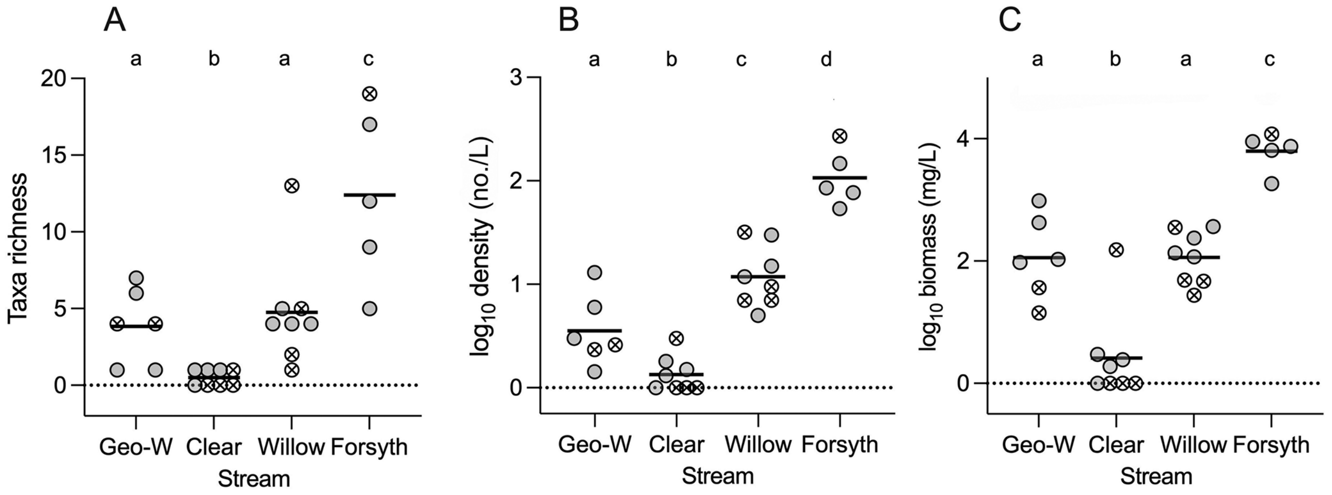

Figure 4. Variation in hyporheic invertebrate community metrics, including taxa richness (A), density of individuals (B), and standing biomass (C) among 4 streams on the Pumice Plain, Mount St Helens, Washington, USA. Streams are organized along the *x*-axis from west to east. In each panel, single points represent the invertebrate assemblage from 1 replicate well (units/L), black horizontal lines are means, and horizontal dotted lines indicate 0 on *y*-axes. Grey shaded points are samples from July, and x-marked points are from August. Note log scale (with zeros preserved) of *y*-axis in panels B and C given substantial variation among streams. Lowercase letters along the top indicate differences between streams, based on Tukey's post-hoc tests (Holm method) with $p < 0.05$.

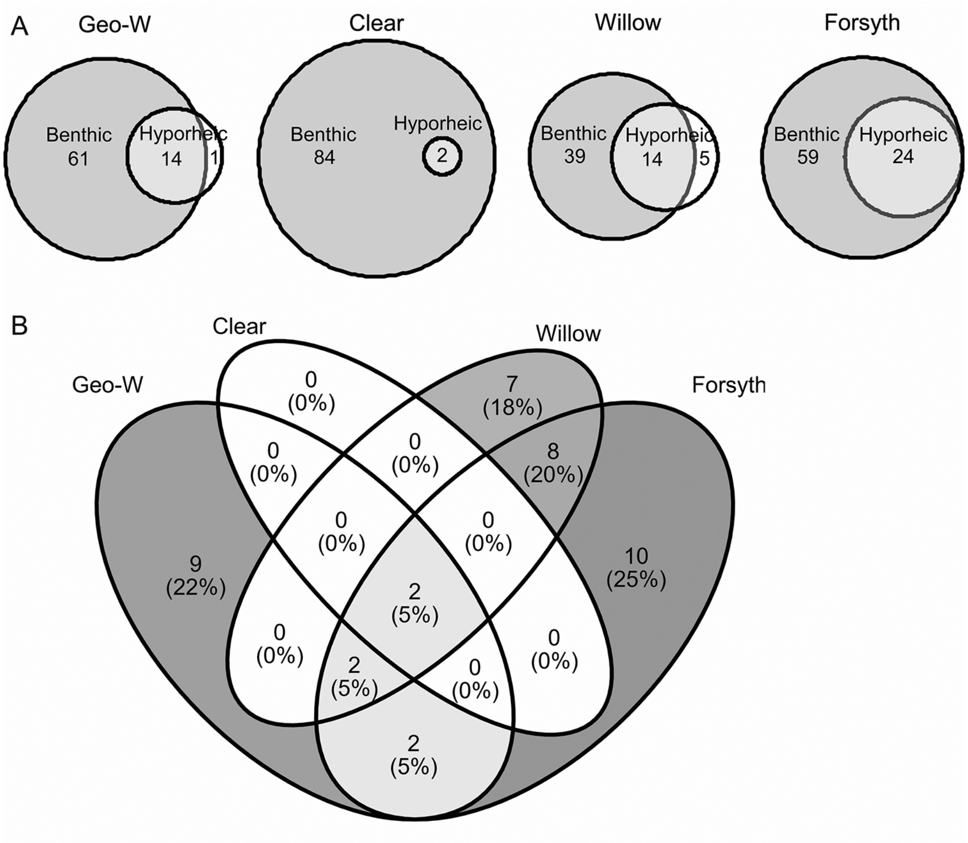

Figure 5. Venn diagrams illustrating presence/absence patterns of benthic and hyporheic taxa within each stream (A) and hyporheic taxa among the 4 study streams (B) on the Pumice Plain, Mount St Helens, Washington, USA. Numbers in each compartment are number of taxa either unique to 1 habitat/stream or shared among multiple habitats/streams. Greyscale shading in panel B is proportional to % (in parentheses) of the total number of taxa observed, with greater percentages indicated by darker shades. Lighter shades in central compartments indicate minimal numbers of shared taxa among streams, with most taxa either unique to single streams or unique to streams on the east side of the Pumice Plain (Willow and Forsyth). Grayscale shading patterns are interpreted similarly in Panel A, which was produced using benthic taxa presence/absence from 10 samples collected May to October 2019 (Appendix S3).

May through October 2019 was substantially greater than that of the HZ, totaling 118 taxa and ranging from 53 at Willow Creek to 86 at Clear Creek (Appendix S3). No taxa were unique to the corresponding HZ in 2 of the 4 streams: Forsyth and Clear. Geo-W had a single unique taxon in its corresponding HZ (*Cricotopus*, Chironomidae), and Willow Creek had the greatest number of taxa found uniquely in its corresponding HZ ($n = 5$), including 2 mayflies (*Ameletus* sp. and *Drunella coloradensis*), a leuctrid stonefly, a chironomid (*Boreochlus*), and a polychaete worm. However, the 5 insects are common benthic taxa, and although they were not collected in their corresponding benthic zones (in Geo-W and Willow creeks), they occurred in the benthos of other Pumice Plain streams (Appendix S3). The paired t-test comparing taxa unique to the HZ vs those shared with the benthic zone supported the qualitative observation that hyporheic taxa in each stream were predominantly subsets of the benthos ($t = 2.6$, df $= 3$, $p = 0.04$). Patterns were similar if solely the benthic invertebrates collected in July and August were included (Fig. S5), although total benthic richness for these 2 mo was, not surprisingly, smaller than total richness across the full study period (range of 38 taxa at Willow to 69 taxa at Clear). Therefore, slightly more taxa were identified as unique to the corresponding hyporheic zones when the limited sampling time frame was considered.

Indicator species analysis of the hyporheic assemblages identified most indicator taxa in Forsyth Creek, including 9 chironomids, 1 mayfly, 2 stoneflies, and harpacticoid copepods (Table 2). Just one taxon (Ostracoda) was an indicator in the Geo-W hyporheic assemblage, and there was weak evidence ($p = 0.09$) for a single chironomid (genus *Thienemanniella*) as an indicator at Willow. Clear Creek had no indicator taxa. These results are unsurprising, given that the Clear Creek hyporheic assemblage contained only taxa in common with all 3 of the other streams, whereas Forsyth contained 10 taxa solely found in that stream (Fig. 5B). Geo-W and Willow were intermediate, with 9 and 7 taxa solely found in those streams, respectively. Indeed, most taxa were either solely found in 1 of those 3 streams or were shared between the 2 eastern streams. Just 2 taxa, oligochaetes

Table 2. Hyporheic indicator taxa for 4 study streams on the Pumice Plain formed by the 1980 eruption of Mount St Helens, Washington, USA. Only taxa whose indicator values (IV) had *p*-values <0.10 from indicator species analysis are shown. No indicator taxa occurred in Clear Creek. Most indicators were for the easternmost Forsyth Creek, with single taxa from Willow and Geo-W creeks bolded. A dash (–) indicates where taxonomic ID was made only to a coarser level.

Class	Order	Family	Genus/species	Stream	IV	*p*
Insecta	Diptera	Chironomidae	*Micropsectra* spp.	Forsyth	97.5	0.0002
Insecta	Diptera	Chironomidae	*Pseudodiamesa* spp.	Forsyth	91.9	0.0002
Insecta	Diptera	Chironomidae	*Brillia* spp.	Forsyth	53.1	0.01
Insecta	Diptera	Chironomidae	*Corynoneura* spp.	Forsyth	42.5	0.06
Insecta	Diptera	Chironomidae	*Diplocladius* spp.	Forsyth	60.0	0.008
Insecta	Diptera	Chironomidae	*Eukiefferiella tirolensis* group	Forsyth	60.0	0.009
Insecta	Diptera	Chironomidae	*Orthocladius* spp.	Forsyth	58.2	0.0002
Insecta	**Diptera**	**Chironomidae**	***Thienemanniella* spp.**	**Willow**	**37.5**	**0.09**
Insecta	Diptera	Chironomidae	*Tvetenia bavarica* group	Forsyth	40.0	0.06
Insecta	Diptera	Chironomidae	*Parochlus* spp.	Forsyth	63.9	0.004
Insecta	Ephemeroptera	Baetidae	*Baetis* spp.	Forsyth	40.0	0.06
Insecta	Plecoptera	Capniidae	*Mesocapnia* sp.	Forsyth	72.0	0.002
Insecta	Plecoptera	Nemouridae	*Malenka* spp.	Forsyth	40.0	0.06
Copepoda	Harpacticoida	–	–	Forsyth	67.3	0.002
Ostracoda	–	–	–	**Geo-W**	**66.7**	**0.007**

and an orthoclad midge, were present in all 4 assemblages (Fig. 5B).

NMDS of the hyporheic assemblages in the 4 streams (Fig. 6) produced a stable 2-dimensional solution in which streams were arranged along axis 1 from westernmost to easternmost locations on the Pumice Plain (axis 1 $R^2 = 0.465$, axis 2 $R^2 = 0.397$; scree plot in Fig. S6). Total stress on a 0 to 1 scale was 0.015. Assemblages did not differ between the 2 sample months (MRPP $A = -0.03$, $p = 0.8$) but did differ between eastern and western sides of the Pumice Plain (MRPP $A = 0.1$, $p = 0.005$). Unsurprisingly, abiotic variables that distinguished eastern from western streams were correlated with NMDS axis 1, including water temperature, conductivity, hydrologic head, and aggradation of the stream bed throughout the study period (negative correlation with axis 1) and hyporheic DO and streambed D_{50} (positive correlation with axis 1). No flow-related variables predicted differences in the hyporheic invertebrate ordination, including number of zero-flow days (Table S2). Many of the invertebrate community metrics were also directly correlated with axis 1, and 2 metrics (% noninsects and % Chironomidae) had correlations with both axes (Table S2, Fig. 6). Results were nearly identical when absolute numbers collected per well were used as input, rather than no./L pumped (Fig. S7).

DISCUSSION

This study provides compelling results that increase our understanding of the abiotic and biotic development of hyporheic zones in young streams undergoing primary succession on the Pumice Plain of Mount St Helens. At the time of study, contrasting hydrologic sources and associated watershed characteristics had generated strongly contrasting physicochemical habitat conditions among the 4 study streams. Those abiotic differences appear to explain the bulk of the variability in hyporheic invertebrate assemblages (Q1), with additional variability likely influenced by presence/absence of woody riparian vegetation, which has developed at different rates among the young streams. The strong among-stream spatial variability of the hyporheic assemblages broadly mirrored patterns in benthic invertebrates reported previously (Q2; Claeson et al. 2021), in that the greatest differences were associated with the contrasting abiotic characteristics in streams occupying eastern vs western sections of the Pumice Plain. At this stage of development, 39 y following the 1980 eruption, the hyporheos of each stream was predominantly derived from the corresponding benthic (epibiont) community, with no evidence that stygobiont taxa had successfully colonized (Q3). It therefore appears unlikely that the relatively high diversity of benthic invertebrates at this stage of succession was influenced by availability of HZ habitat. The most relevant observation in support of this conclusion was that the stream with greatest benthic richness (Clear Creek) had the lowest hyporheic richness and showed very little evidence that HZ habitat suitable for invertebrates had even yet developed. Like the benthic assemblages, hyporheic assemblages showed high beta diversity, indicating strongly divergent successional trajectories among these young streams with similar geologic histories. Overall, eastern streams

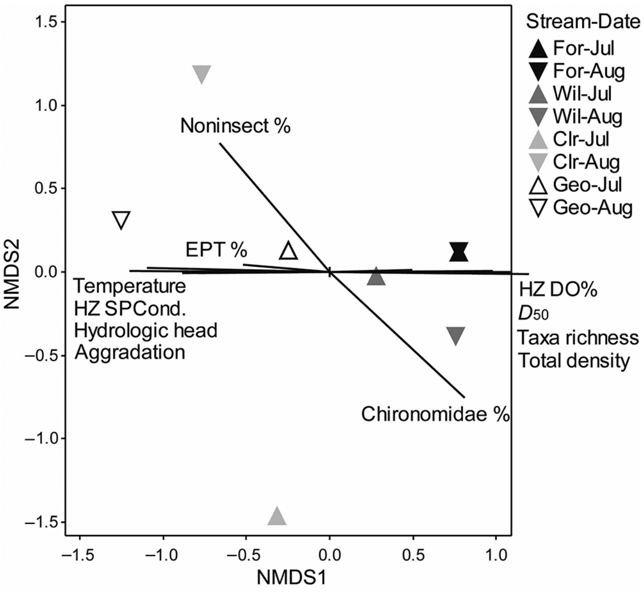

Figure 6. Nonmetric multidimensional scaling (NMDS) biplot of hyporheic invertebrate assemblages from the 4 study streams on the Pumice Plain, Mount St Helens, Washington, USA. Streams are coded per the legend, with increasing darkness of shading representing spatial positions west-to-east. Each point represents the mean assemblage, calculated as $\log_{10}$(no./L), among replicate sample wells at each stream/date. Vectors indicate abiotic and community-metric variables correlated with ordination axes, with length of vector proportional to correlation strength. Descriptors for vectors parallel to axis 1 are arranged top-to-bottom in order of decreasing Pearson's *r*. See Table S2 for additional details, including Pearson's *r* for all vectors. SPCond. = specific conductivity, HZ DO% = dissolved O_2 % saturation in hyporheic water, D_{50} = median particle size on the stream bed, EPT% = % of assemblage represented by Ephemeroptera, Plecoptera, and Trichoptera individuals.

had substantially greater invertebrate densities than western streams, with distinct taxonomic composition.

Despite strong biological differences among the 4 streams, they shared some physical features reflecting early stages of active channel development. Each of the streams had bed aggradation detectable during a 5-mo study period that included no major flood events, erratic patterns of upwelling and downwelling at the within-reach scale, and lack of the riffle–pool sequences expected in mountain streams of this region. Indeed, our overall observations were nearly identical to those observed by McDermott et al. (2010) in a stream of similar successional age that had formed following glacier recession in southeast Alaska. It is perhaps not surprising that streams in these 2 contrasting landscapes had similarly underdeveloped hyporheic assemblages derived from the corresponding benthos. McDermott et al. (2010) also observed a nearly impermeable layer of dense silt ~30 cm beneath the alluvium of the young Alaskan stream beds, much like the dense compacted ash layer that we encountered at similar depth beneath the beds of the Pumice Plain streams. These similarities point to a conclusion that relatively impermeable material is probably necessary for rapid development of surface-flowing streams on new landscapes. If this is the case then it would not be surprising that HZ habitat develops relatively slowly, at rates likely determined by an interaction of geomorphology (larger, steeper watersheds could provide more alluvial material at a faster rate), hydrology (floods of greater frequency and magnitude allow more frequent reworking of stream bed and channel), and the activities of riparian woody plants (roots of which loosen the dense subsurface layer and increase permeability and connections to groundwater). Burrowing and related activities of invertebrates also likely play a role in increasing interstitial space and permeability (Nogaro et al. 2006, Hose and Stumpp 2019). Oligochaetes, for example, were present in low numbers in all 4 streams, and we observed that many individuals had ash-filled guts.

Chironomidae and, secondarily, other insects with flying adult stages dominated the invertebrate fauna of the young hyporheic zones in terms of both taxa richness and total abundance. Noninsects tended to constitute greater proportions of the assemblages in the more depauperate western streams (Clear and Geo-W) but notably included neither amphipods nor isopods, which are typically common in hyporheic assemblages (e.g., Hutchins et al. 2020, Dole-Olivier et al. 2022). A combination of unsuitable habitat and dispersal limitation might explain this observation because the nearest sources of colonists to Pumice Plain streams have been estimated to be ~5 km distant (Claeson et al. 2021). Spirit Lake, at the downstream terminus of each study stream, experienced toxic and anoxic conditions, as well as temperatures reaching at least 35°C following the eruption (Larson 1993), so the lake is unlikely to have provided colonist sources. Flying insects and small noninsects dispersing via other means, such as wind (Sugg and Edwards 1998, Cáceres and Soluk 2002) and zoochory (Maguire 1963), would have been the most likely early colonists. However, meiofauna were also notably rare despite our use of a fine-meshed sieve (125 μm) for HZ samples. Indeed, the observation that hyporheic assemblages were highly nested subsets of their corresponding benthos becomes even more noteworthy given the differences in mesh size between the hyporheic (125 μm) and benthic (500 μm) collections because one would expect the finer mesh to have retained smaller taxa distinctive of the HZ.

The most dominant factor driving among-stream assemblage differences on the Pumice Plain appears to be contrasting hydrologic sources of the streams (although geomorphological covariates are also likely influential). An earlier study (Claeson et al. 2021) hypothesized water-source differences based on among-stream variation of simple indicators of glacier melt, including relatively cold water temperature, low conductivity, and high nitrate concentrations. Here we provide additional evidence of source differences, including water stable isotopes that suggest a glacier-melt signature can vary quite strongly between individual glaciers. Our snapshot midsummer isotope data indicated that all surface streams sampled on the Pumice Plain were arrayed between isotopic endpoints represented by the 2 sampled glaciers, with eastern streams reflecting the signature of the Forsyth Glacier and western streams reflecting the Crater Glacier signature. Hence, it is probable that meltwater from the young Crater Glacier ultimately supports baseflow in streams on the western side of the Pumice Plain but is retained as groundwater that has a long enough residence time to result in higher water temperature, high dissolved solids, and other characteristics of groundwater-fed streams. We are unaware of water stable isotope studies associated with newly developed glaciers like the Crater Glacier, but our results suggest that this young ice had relatively less depletion of heavy isotopes (^{18}O and ^{2}H) than glaciers that have been on the landscape for longer time periods (e.g., Fellman et al. 2014). Following its decapitation during the 1980 eruption, the Forsyth Glacier retained some of its original ice mass, but its signature was also less depleted than expected relative to other glaciers in western North America (e.g., Fellman et al. 2014, Carling et al. 2017). Because these conclusions are based solely on snapshot samples, they should be interpreted with caution, but they clearly point to interesting avenues of future hydrologic research on Mount St Helens.

In addition to the varying water sources, covariates likely also play a role in differentiating hyporheic invertebrate communities between the eastern and western streams. For example, the contrasting patterns of upwelling vs downwelling in western vs eastern streams, respectively, probably reflect differences in size and slope of the catchment areas. Western streams were formed on materials deposited directly in the path of the pyroclastic flows and, hence, directly downslope of the concavity associated with the crater (see Fig. 1), whereas eastern streams are peripheral and sourced from higher, steeper areas that include glaciers that existed prior to the 1980 eruption. Indeed, it is possible that western streams are in earlier stages of channel development than eastern streams. Glaciers peripheral to the crater may have provided both water and sediment sources to the eastern streams immediately following the eruption, but the presumably larger and deeper aquifer(s) feeding the western streams may have taken longer to develop following the decimation of this section of the mountain and the gradual expansion of the new Crater Glacier. According to standard models (Schumm et al. 1984), the increased bed aggradation we observed in western compared with eastern streams could also point to earlier stages of channel evolution in the western streams. A combination of potentially earlier stages of channel development plus predominantly upwelling conditions in the western streams could help explain their poorly developed hyporheic zones and very low invertebrate densities relative to the eastern streams. These hypotheses could be tested with more detailed hydrological studies in the future.

Streambed stability, which was associated with riparian vegetation, appeared to play a secondary but meaningful role in the physical and biological development of the hyporheic zone that was unrelated to the broader-scale processes differentiating eastern vs western streams. The 2 streams with well-developed riparian vegetation and more stable stream beds had relatively high hyporheic taxa richness. These include 1 eastern (Forsyth) and 1 western (Geo-W) stream. Woody riparian vegetation stabilizes channels and supplies energy to invertebrates in the form of organic material (Corenblit et al. 2009). Although we did not measure organic material as part of this study, we have recorded substantially greater amounts of particulate organic material in stream reaches with greater densities of woody riparian vegetation (DSF, unpublished data). Of our 2 study reaches with minimal riparian vegetation, Willow Creek (eastern) had the highest discharge, associated with low bed stability, and had the lowest benthic richness but also the greatest number of taxa unique to the HZ compared with its corresponding benthos. This observation provides some support for the hyporheic refuge hypothesis (e.g., Palmer et al. 1992, Crossman et al. 2013), which states that benthic invertebrates use the HZ to escape flow-related disturbance in surface habitats. For this hypothesis to apply, however, hyporheic habitat must exist and be permeable to moving animals (e.g., Stubbington 2012). These conditions do not appear to be met in Clear Creek, which had the greatest bed instability and 2nd-highest flow of the 4 streams sampled but provided very little evidence that HZ habitat had yet developed that could function as a refuge from surface disturbance. The unique hyporheic fauna in Willow Creek, meanwhile, included epibiont taxa such as leuctrids and other stonefly taxa that are common occupants of HZ habitats in general (Puig et al. 1990, Dorff and Finn 2020, Stanford et al. 2024). An interesting general implication of these observations is that hyporheic zones of other cold, physically dynamic streams probably support substantially greater invertebrate diversity than what can be observed in the surface habitats alone (Malard et al. 2003).

The high beta diversity and substantial variation in physical habitat among these Pumice Plain streams and their developing HZs point to exciting avenues of future research associated with primary succession and channel development in newly formed streams. Indeed, the absence of obvious stygobiont fauna begs the question of when the subsurface habitats in young streams become true HZs. Ultimately, the answer depends on a definition of the HZ as either simply the wetted area beneath the stream bed or, more specifically, an ecotone in which surface and groundwater biota and materials are mixing (e.g., Peralta-Maraver et al. 2018).

Peralta-Maraver et al. (2018) showed that invertebrate assemblages in mature HZs are distinct from their corresponding benthic assemblages and, therefore, can be considered separate ecological communities. That is not the case in these young Pumice Plain streams, where the benthos + hyporheos together appeared to be a single community. A question worth pursuing is whether a groundwater fauna has yet developed in association with the Pumice Plain, which should be readily answerable with strategic sampling of spring sources (e.g., Nissen et al. 2018). A related question is when and what mechanisms will eventually result in direct connections between groundwater and stream surface water. Woody riparian plants will probably be key players in increasing subsurface porosity (Corenblit et al. 2007), particularly through the concrete-like layer of compacted ash underlying the alluvial materials deposited during the first few decades following stream formation. Given the striking similarities between young streams of similar age in 2 contrasting environments—glacier recession (McDermott et al. 2010) and pyroclastic deposits (the current study)—a space-for-time HZ sampling strategy along the well-understood chronosequence of Glacier Bay streams (Milner et al. 2000, 2024) might produce testable predictions about timelines of physical development and successional trajectories in the Pumice Plain streams.

Overall, the striking biotic and abiotic differences among these neighboring Pumice Plain streams point to a conclusion that seemingly minor differences in landscape position can have strong ecological effects on species sorting and successional trajectories. The proximity of these streams to one another makes them a practical natural laboratory for continued observation to build on our understanding of the key drivers of primary succession and channel development, assuming their continued protection from direct anthropogenic disturbance (Service 2021).

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