

AN ABSTRACT OF THE THESIS OF

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A time series observation of two stream communities: disturbance, seasonal variation,
and macroinvertebrate assemblages

Abstract approved:

Kerry L. Yurewicz

Macroinvertebrate surveys offer a rapid and cost-effective approach for research linking hydrological indices with biological communities in streams. While macroinvertebrates have been successfully used to describe water quality, only recently has research demonstrated their use for describing flow regime. The intent of my research was to describe the response of benthic communities in headwater streams to seasonal and hydrological variation. In 2014, I sampled two streams biweekly in the Hubbard Brook Experimental Forest in New Hampshire from stream thaw in early April until streams froze in late December. I found changes in taxonomic and functional membership and assemblage rheophily in apparent response to hydrological disturbance. Assemblage response patterns to high flow were similar at both sites for a period of approximately five days. Beyond five days, the recovery was unique to each site, however, and emphasized the importance of considering both

the spatial and temporal nature of lotic environments when describing benthic communities. These findings become more important as effective policy-making in the face of a changing climate and continuing human impacts requires thorough understanding of abiotic influences on our aquatic communities.

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A time series observation of two stream communities: disturbance, seasonal variation,
and macroinvertebrate assemblages

By Donovan Nathaniel King

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The late Michele L. Pruyn, Associate Professor of Plant Biology, Plymouth State University, served on the committee through the thesis seminar and defense. Her contributions are gratefully acknowledged here.

I understand that my thesis will become part of the permanent collection of Plymouth State University, Lamson Library. My signature below authorizes release of my thesis to any reader upon request.

Donovan Nathaniel King, Author

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I: Introduction

Ecosystem health is the ability for a system to maintain both organization and functionality in the face of changing conditions (Costanza and Mageau, 1999; Meyer, 1997). A healthy ecosystem is regarded as one where the community as a whole, and the services it provides, has a high degree of resistance or resilience. Streams provide many important ecosystem services, including potable water, food, recreation, and aesthetics (Meyer, 1997). Flow conditions have long been considered to be important to stream health. By affecting flow, any alterations in either precipitation or runoff patterns within a given region are likely to have important consequences to the health of streams in that area. Altered flows may impact species of concern, as has happened for Idaho's white sturgeon (*Acipenser transmontanus*), an endangered fish species that is suffering low recruitment likely due to an impoundment and consequential change to hydrology (Paragamian et al., 2009). In New England, extensive efforts were made to restore Atlantic salmon (*Salmo salar*) to streams from which they had previously been extirpated. Stream discharge and temperature are strong determinants of the survival of this endangered fish (Hodgkins and Dudley, 2011; Rustad et al., 2012). As streams continue to be shaped by anthropogenic activities, it is becoming increasingly critical to study the impact of flows on biological communities (Tetzlaff et al., 2005).

Changing climate:

Climate change is altering New England's hydrological patterns with predictions for warmer, wetter winters and higher risks of summer drought (Rustad et al., 2012). This will alter both stream flow patterns and stream water temperatures, although the consequences of the former are likely to be more important than the

latter. This is because while stream temperature will be affected by the increase in average yearly temperature, it is unlikely to have a significant impact: warming is expected to make winters milder rather than increase summer highs. Because water has a lower temperature limit, the streams will still be reduced to this 0° C during winter. Additionally, ground water has a stable temperature close to the average temperature of a given region, thus the thermal properties of water may moderate the rising peak temperatures associated with global warming (Hodgkins and Dudley, 2011).

The impacts of changing flow regimes, on the other hand, are not expected to be so tempered. The amount of precipitation that leaves a forest as stream water depends on the type of precipitation, the type and seasonal condition of foliage, and the existing soil moisture, as well as the potential evapotranspiration, which can change greatly in a single day (Baker et al., 2004). Increases in precipitation have been observed over the last several decades (Groffman et al., 2012; Hodgkins and Dudley, 2011), though changes in annual precipitation and stream runoff do not demonstrate the clear and significant trends of temperature (Campbell et al., 2007). Climate predictions show more frequent heavy precipitation events occurring in New England, but precipitation models contain more uncertainty than temperature models (Rustad et al., 2012).

Previous research has shown that hydromorphology, the shape of water's course through a substrate, defines stream habitat type, distinguishing between high flow erosional zones and depositional areas of slower flow, or between pools, riffles,

and snags of woody debris (Garcia et al., 2012). Even within a single habitat type, there is complex variation as one scales down to the resolution of a stream insect or newly hatched fish fry because micro-eddies stirred by substrate irregularities facilitate or hinder the exchange of gases across the gill membranes (Biggs et al., 2005). Townsend (1989) argued that the temporal existence of a particular community within a specific site result from flow disturbance and chance as much as from predator/ prey dynamics and habitat factors.

The effects of changing climate on a system are slow and therefore more confounded by additional variables. However, urban catchments with high percentages of impermeable surfaces can provide observations for how altered flows might impact stream biota. For example, an examination of the effects of urbanization of stream systems highlighted flow regimes as one of the most significant driving forces of change among fish assemblages (Roy et al., 2005). They found that as the surrounding imperviousness increased, the stream was subjected to more frequent and more intense high flow events, similar to the predictions for how climate change might impact New England's hydrology. Roy et al. found that these altered flow regimes favored "lentic tolerants," or those species able to meet the energy efficiency demands of lower flows, as minimal discharge levels dominated the periods between precipitation events, and fish species associated with more rapid flows negatively correlated to increased flashiness (the magnitude and frequency of changes in flow).

Changes to community structure associated with stream flows are not limited to fish. Kennen et al. (2010) found a similar relationship with macroinvertebrates. In a

large study examining sites in New England and New York, Kennen et al. looked at both rural and urban gauged watersheds to test for ecological responses to alterations in flow regime from impermeable catchments, where watersheds have been paved. Changes in macroinvertebrate communities were found to correlate with the magnitude, frequency, duration, and flashiness of stream flow, all of which might also change with climate.

However, increasing flashiness is not by necessity detrimental to a stream system. While some assemblages may suffer reduced richness or functionality, Fisher et al. (1982) observed a desert stream following a flash flood and found rapid recolonization of invertebrates. Biodiversity quickly increased as new taxa took advantage of available niche space before species dominance reduced diversity in later successional periods. Fisher et al. suggested the disturbance acted to reset the communities within the stream preventing the dominance or indirect competition of various species, a finding supported later by Death (2002). This suggests that seasonally extreme weather events, such as floods or droughts, can contribute to the biodiversity of a stream system. Taxa less competitive in present stream conditions might persist indefinitely if disturbance events are frequent enough, improving the available pool of colonizers and strengthening the resilience of the system.

Research has also demonstrated that the invertebrate recolonization of stream beds following disturbance can be more related to the substrate type than the frequency of the disturbance. Gjerløv et al. (2003) placed traps of invertebrate-free substrate into streams and monitored their seven day recolonization rates. They found

that the more similar a trap's substrate was to the test site's substrate, the faster recolonization occurred. But interestingly, they also found disturbance frequency did not have a significant relationship with recolonization rates. Their research indicates that the rate of recovery for these communities was most strongly determined by the local substrate type. Large stones and woody debris offered refugia where invertebrates could seek shelter from disturbance while remaining in close proximity to the site. It is important to note that this finding was specific to the rates of, and not the cumulative success of recolonization. Higher rates of disturbance may depress the ecosystem services provided by an assemblage or could reduce the productivity of the community as individuals spend more energy in recolonizing than in growth and reproduction.

Thus, the role disturbance plays in an ecosystem is a topic of debate. Death (2002) observed that competition among lotic invertebrates was minimal, proposing that assemblages were determined primarily by the opposing variables of resource availability and flow-related disturbance. As resource availability increased, so did species richness, but as disturbance increased, richness declined. The intermediate disturbance hypothesis was unsupported as a predictive model, and in fact was counter to Death's observations (2002). Death's postulation was that potential species richness is determined by the available resources while the realization of that richness is determined by the disturbance regime.

Further studies will help to refine ecologists' understanding of how lotic communities respond to abiotic and biotic variables. However, disturbance (primarily

flow rate) is highlighted by most studies as the greatest observed determinant of community assemblage within a stream. Therefore, an intensive exploration of how hydromorphology influences stream organisms will allow future studies to include this fundamental variable in models to elucidate the finer effects of more subtle site variations.

Macroinvertebrate bioindicators:

Stream macroinvertebrates serve as ideal bioindicators of stream conditions. As early as 1907, German scientists began using aquatic macroinvertebrates as useful indicators of saprobity in lotic systems (Cairns and Pratt, 1993). In the U.S., stream ecology research in the middle of the 20th century confirmed the useful application of insects for quickly, inexpensively, and reliably determining the conditions of a stream (Gaufin and Tarzwell, 1952). By the end of 1980s, researchers had designed broadly accepted metrics for defining stream systems based on macroinvertebrate communities (Hilsenhoff, 1988; Lenat, 1988).

Research concerning the effects of extreme events on macroinvertebrates has begun to establish an understanding of how these organisms respond to various flow regimes. For example, caddisfly larvae (Trichoptera) were studied under laboratory and field conditions to assess their response to food availability, water temperature and stream flow (Gallepp, 1977). Most flow regimes elicited similar feeding behavior from the caddisflies, but the lowest flows saw a decrease in feeding and a commensurate increase in unattached, or mobile, behaviors. In lentic systems, filter feeders must actively pass water across the feeding structures. Lotic systems allow a passive

approach dependent on the flow of the stream. Low flows decreased feeding efficiency of these caddisflies (Gallepp, 1977), prompting them to seek more favorable conditions. This work demonstrated the importance of flow rates to species' success similar to the importance of water quality, suggesting that assemblages might be affected by direct effects of flow regimes upon the organisms themselves, even when the flows are not altered to the degree of disturbance.

While it is well-established that macroinvertebrate communities make useful bioindicators for water quality, it wasn't until recently that an attempt was made to relate invertebrate assemblages to flow regimes. Extence et al. (1999) addressed this question by constructing a metric called a LIFE score whereby communities can be defined by an average flow preference, similar to the way they had been assessed in the past for their saprobity tolerance. They were thus able to predict the community flow-type for several large rivers in England. Similarly, Monk et al. (2006, 2008) argued that the hydrology itself is insufficient to describe the health of a stream when detached from the community dynamics. Not only can macroinvertebrate community description serve as a potential analogue for more expensive, long-term direct hydrological measurements, but community description is also vital to assessing the real condition of a stream ecosystem. The LIFE score is not yet developed for North American invertebrates. Insect flow preferences that have been documented for North American genera (Merritt and Cummins, 1995) tend to agree with the findings for their European relatives, but further research is needed to ensure reliability. This

research has been started in Canada (Armanini et al., 2011) but has not yet gained traction in the U.S.

Still, much of the research on flow regimes and invertebrate communities focuses on large streams and multi-year time scales. This research enables better definitions of the biotic communities as they relate to the abiotic influences controlled by flow. However, many of the changes in watershed dynamics predicted by climate change models are expected to happen at a seasonal time scale. Recently published hydrological data showed insignificant increases in precipitation and stream discharge for the Hubbard Brook Experimental Forest (Campbell et al., 2007) despite evidence of an increase in stream discharge events at the 0.95th quantile (King, unpublished). This discrepancy is readily explained by the intra-annual hydrological variation. Increases in precipitation occurred in early spring and late autumn were compensated by decreases in late summer precipitation and stream discharge (Rustad et al., 2012) masking the disruption to stream flow regimes. Long term sampling at a fine temporal scale is needed to study potential impacts of shifting, intra-seasonal flow.

Research objectives

In order to better understand effects of flow variation at fine temporal scales, I observed benthic invertebrate communities at two specific sites over the course of a year in a location providing a high degree of stream discharge temporal resolution. The study was conducted on second order streams in the Hubbard Brook Experimental Forest. Resh and Rosenberg (1989) argued that first order streams drain watersheds too small to experience wide variations in discharge. Yet high order streams have

mostly homogenized stream beds and their responses to precipitation events are tempered by their size, so that a similar study would require much more extensive sampling over a longer period of precipitation events. I hypothesized that two locations on separate streams in close proximity observed simultaneously would demonstrate similar relationships for assemblage membership with increasing and decreasing discharge rates. I expected that periods with increased maximum flow rates would decrease biodiversity as assemblage members were subjected to extreme conditions.

II: Methods

Site Description:

The Hubbard Brook Experimental Forest (HBEF) (Figure 2.1) is a temperate forested valley in the White Mountain National Forest in central New Hampshire. It is operated by the United States Department of Agriculture's Forest Service and by the National Science Foundation as a Long Term Ecological Research (LTER) site. The forest has weather typical of northern New England, with long winters providing as much as a third of the annual precipitation as snow. The January average air temperature is -9°C . Summers usually remain cool, with average air temperatures for July in the forest at 18°C (Campbell et al., 2007).

Gauged weirs are used at HBEF to isolate watersheds for experiment and observation, providing stream flow measurements every 5 minutes for the duration of this study. The weir at watershed 4 was chosen to provide the most reliable record for 2014 stream flow for my study sites (Green, personal communication) and has been in continual use since 1960 (Campbell et al., 2007). Watershed 4 is situated centrally in the upslope catchment of both streams, but directly feeds only Paradise Brook. Staff at the HBEF gather additional information for each stream including stream temperature and water chemistry.

For this study, I chose two sites for macroinvertebrate sampling: Paradise Brook and Bear Brook (Figure 2.1). Both streams are on the south aspect in the northern half of the Hubbard Brook Valley and run through mixed canopy forest of

both deciduous and coniferous trees. Canopy cover for both streams was estimated in a concurrent study to be approximately 90% between spring leaf out and autumn abscission (Yurewicz, personal communication). The streams flowed free from ice and snow in early April of 2014 when this study began and they were blanketed again in snow and ice in early January 2015.

Macroinvertebrate Sampling:

Beginning April 6, 2014, I collected one sample from each stream every 14 days until December 28, 2014. An attempt was made to sample on January 11, 2015, but both streams had frozen over. I sampled the same location in each stream on every biweekly collection date, with the expectation that sampled substrate can be fully recolonized by macroinvertebrates in seven days (Resh, 1979). Occasionally, high flow events occurred between sampling dates. To observe the community responses to these events, I collected an additional sample immediately following high flow events from an area adjacent to the primary sample site in each stream, taking care to sample substrate that resembled that of the primary site and maintaining enough distance so as to minimize any disturbance to the primary site (Figure 2.2). This method gave me one long-term, consistent observational series to describe the local community at each site and a supplemental, post-disturbance set of samples adding to the resolution of the data set.

On most occasions, I used a Surber sampler (0.09 m² sampling area, 500 μ m mesh size) according to the typical protocol, disturbing the substrate in the defined area and allowing the stream flow to carry material into the net. I lifted large stones

from the bed, rinsed them in the flow, and set them to the side to be returned as found after sampling. I then emptied the sampling net into a small jar for transporting to the lab. I drained all water from the jar and added 70% ethanol to preserve the sample.

However, during especially low flows (most common in late summer and early autumn), I had to force the water from my sample area into the net by hand. During some rare high flow conditions, the stream washed a large volume of stones into the net. In these instances, I emptied the net into a bucket, rinsed the substrate, and poured the released material through the net again leaving the stones behind. I repeated this until I felt I had adequately matched the sampling intensity of previous dates. I added the stony substrate back to the brook just upstream of the sample site to allow the stream to wash the substrate back into a location approximating its origin.

On two specific occasions there were additional departures from my standard collection method. On September 21, 2014, the jar containing Paradise Brook's sample spilled back into the stream while I was placing the lid on. I did not take careful note the initial volume of the sample and have no estimate for the percentage of loss. On December 28, 2014, the high flow at Bear Brook prevented me from safely positioning the Surber sampler as desired: the strong flow velocity kept lifting the sampler. I compensated by lifting substrate into the path of the flow so that it could rinse into the sampler. Both samples appeared successful despite the anomaly and I maintained both of these samples in my data set.

I sorted each sample in the laboratory using a dissecting microscope at 40x magnification. I removed all visible macroinvertebrates and then sorted them into four taxonomic groups: Ephemeroptera, Plecoptera, Trichoptera, and Chironomidae &

others. I later processed the first three of these groups further as described in a later section.

Watershed Data:

I used stream discharge data collected at the weir situated at the outlet of watershed 4. Stream measurements were made using a 120° V-notch weir and stage height was recorded every five minutes. Committee member Mark Green used a sliding window to calculate the average seasonal flow, and this was then subtracted from the actual flow. Correlating macroinvertebrate assemblages with the resulting decomposed flow helped to emphasize flow events rather than seasonality.

The stream variables I extracted from this dataset were water temperature, stream flow maxima, minima, and median as well as the Richards-Baker flashiness index, or RBI (Baker et al., 2004).

$$RBI = \frac{\sum_{i=1}^n |q_i - q_{i-1}|}{\sum_{i=1}^n q_i}$$

equation 2.1

where q is any metric of stream flow. Discharge rates, as calculated by the USDA at the Hubbard Brook Experimental Forest, were used for q in this study.

Stream data were observed for windows of increasing temporal distance of $n + 1$ where the sum includes all days from one to nine. As assemblages are thought to fully recolonize following seven days (Resh, 1979), correlations beyond nine days were assumed to be influenced by additional and unknown variables and were not examined.

I used the HBEF data to sine transform the numerical day of the year to seasonal values so that the peak of the sine wave coincided with the peak mean water temperature on August 10. This gave me a variable to use for seasonal variation.

$$SV = -\cos \left[\left(\frac{2\pi}{365} \right) (DV + x) \right]$$

equation 2.2

where SV is the seasonal value, DV is the numerical day of the year, and x is the difference between the median DV and SV . August 10th was chosen as representing the solar season and June 10th was chosen to provide distance between two seasonal values, offering a way to test for the strength of correlations, while still serving as a plausible trend, coinciding with a potential Leptophlebiidae emergence observed in my data.

Community analysis:

I identified all Ephemeroptera, Plecoptera, and Trichoptera to family (Merritt and Cummins, 1995; Peckarsky et al., 1990). Because of a combination of factors – including various instar stages, individual sizes, and the condition of specimens in my samples – I did not attempt further taxonomic resolution. Family-level identification allowed me to classify taxa by functional groups and flow preference for analysis. Furthermore, Demars et al. (2012) suggested family-level resolution for sampling multiple streams. Lenat (1988) also found identification to family sufficient for water quality analysis; however, Monk (2012) found finer taxonomic resolution, to species, enhanced the description of site-specific communities and allowed for greater explanatory power.

Only Ephemeroptera and Plecoptera sustained enough of an abundance within my samples to warrant independent analysis. While the dipteran Chironomidae were abundant, previous research has found they are unreliable indicators of stream flow (Extence et al., 1999). My data concurred and also found no consistent trends with stream temperature nor with seasonal values; therefore, correlations between Chironomidae and flow were not analyzed further. However, all organisms were used to calculate the community metrics of Shannon's H , LIFE score, and percent EPT.

For each sample I calculated biodiversity. I chose to use Shannon's H over other diversity indices, as other calculations lessen the impact of rare taxa upon the score (Magurran, 1988). Because of my smaller sample sizes, it was important to give equal weight to all taxa.

$$H = - \sum_{i=1}^s p_i \ln p_i$$

equation 2.3

where s is the number of defined groups, and p is the proportion of s composed of group i . I also measured each individual for the orders Ephemeroptera, Plecoptera and Trichoptera, and the family Chironomidae to the nearest 0.1 mm using a micrometer mounted on a dissecting microscope. For the former two groups I measured total body length. Since Trichoptera and Chironomidae have non-sclerotized bodies, I estimated head capsule size for these groups. I then used published regressions (Benke, 1999) to obtain dry mass (M) estimates.

$$M = aL^b$$

equation 2.4

where L is the length of the body or head capsule, and a and b are constants specific to the taxon of concern. Biomass tends to follow an approximately cubed growth, so that an increase in body length l will increase body mass by l^3 , despite the sometimes complex body morphologies.

I assigned each family to a functional group or groups reflecting their diet and ecological role (Merritt and Cummins, 1995). When a family contained more than one functional group, I assigned partial representation to each possible classification (Table 2.1). For example, heptageniids both collect fine particulate matter from the substrate and scrape algal biofilm from the same, so I assigned equal proportions of heptageniids to each of these functional groups.

I also assigned a modified LIFE (Lotic Invertebrate Flow Evaluation) score to each community sample (Extence et al., 1999) in order to describe flow preference. To do this, each family in a sample was assigned a score based on rheophily, an organism's tolerance of increased flow, and the abundance of individuals, so that within rank I (rapid flow) increasing abundance increases the score assigned, while within rank V (drought tolerant) increasing abundance decreases the score (Table 2.2). The LIFE score for the community is then calculated as the average score for all taxa in the sample. Extence et al. (1999) assigned abundance categories by \log^{10} to describe large sample sizes from high order streams. In order to adjust for my smaller sample sizes, I increased my abundance scores logarithmically by three (Table 2.2). Not all organisms present in my sample had LIFE scores defined by Extance et al., but these comprised a minority proportion of the samples and were therefore left out of this

calculation. Chironomidae were also disregarded as Extence et al. determined this family does not reliably fit a LIFE score.

Percent EPT is an informal measure of stream quality developed for citizen science projects (Thompson, 2007). This metric was used here in support of more formal and rigorous metrics. To find the percent EPT, I used the method prescribed by Thompson (2007) as a method used in practice. I counted each taxon present in my sample in a binary fashion, so that the presence of a taxon, regardless of actual abundance, scored 1. Then the number of taxa belonging to Ephemeroptera, Plecoptera, or Trichoptera was divided by the total number of taxa.

Statistical analyses:

To find relationships between assemblage membership and flow variables I conducted Spearman rank correlation tests. Rank correlations were used to minimize the effect of small sample sizes and unavoidable changes in sampling efficiency that resulted from varying stream conditions. For assemblage membership, I examined absolute and relative abundance by order and family. I also examined absolute and relative biomass for the orders Ephemeroptera, Plecoptera, and Trichoptera, in addition to the family Chironomidae and I examined absolute biomass for families within Ephemeroptera and Plecoptera. Additionally, I examined LIFE scores, diversity, and total abundance. For flow variables, I tested minimum, median, and maximum discharge rates and flashiness to elucidate the disturbance type most associated with any observed assemblage change. The maximum, median, and minimum flows, as well as flashiness, agreed on general trends when correlated to

assemblages. All correlations are provided in the appendix. However, only the median flows are discussed in the Results section. I chose to use the median to as the most robust and consistent statistical measure of stream flow. Other metrics may strengthen or weaken the conclusion.

I also examined correlations between assemblage membership variables and seasonal values. While August 10th was determined to be the peak summer day using stream temperature, I analyzed these two metrics separately allowing water temperature to test for physiological responses in contrast to behavioral responses triggered by endogenous clocks or photoperiod.

I also completed Mann Kendall tests on family membership variables to look for strong increases or decreases in number over the sampling season.

I performed all statistical analyses using the software R (R Core Team, 2013).

Table 2.1: List of invertebrate taxa relevant to this study. Functional group assignment according to Merritt and Cummins (1995). Some families occupy more than one functional role. Numbers in parentheses indicate the proportion of that family assigned to that functional classification. Rheophily ranks assigned according to Extence et al. (1999) for the determination of LIFE scores (Table 2.2).

Order	Family	Functional Group(s)	Rheophily Score
Ephemeroptera	Heptageniidae	Collectors (0.5), Scrapers (0.5)	I
	Ephemerellidae	Collectors	II
	Leptophlebiidae	Collectors (0.5) Scrapers (0.5)	II
	Baetidae	Collectors (0.5), Scrapers (0.5)	II
Plecoptera	Leuctridae	Shredders	II
	Perlodidae	Predators	I
	Chloroperlidae	Predators	I
	Peltoperlidae	Shredders	
Trichoptera	Psychomyiidae	Collectors	II
	Brachycentridae	Filterers (0.33), Collectors (0.33), Shredders (0.33)	II
	Hydroptilidae	Scrapers (0.5), Collectors (0.5)	IV
	Lepidostomatidae	Shredders	II
Diptera	Chironomidae	Predators (0.5), Collectors (0.5)	
	Ceratopogonidae	Predators	
	Tipulidae	Shredders	IV
	Simuliidae	Filterers	II
	Dixidae	Collectors	
Coleoptera	Elmidae	Collectors (0.5), Scrapers (0.5)	II
Hexapoda	Collembola	Collectors	
Trombidiformes	Hydrachnidia	Parasites	
Oligochaeta	undetermined	Collectors	
Odonata	undetermined	Predators	

Table 2.2: *Modified LIFE score table (sensu Extence et al., 1999). Extence et al.'s original values were A (<10), B (<100), C (<1000), and D (>1000) for abundance rankings (1999).*

		Abundance			
		A (< 3)	B (< 9)	C (< 27)	D (>27)
Rheophily	I Rapid	9	10	11	12
	II Moderate	8	9	10	11
	III Slow	7	7	7	7
	IV Intermittent	6	5	4	3
	V Standing	5	4	3	2
	VI Drought	4	3	2	1

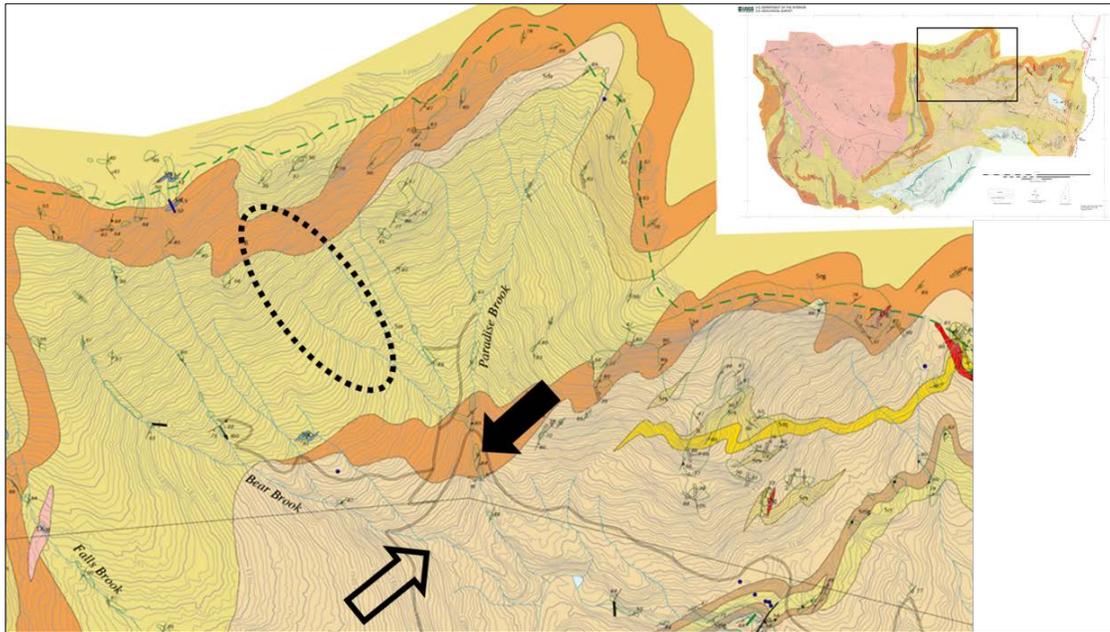


Figure 2.1: Sample sites within the HBEF. The dashed line highlights watershed four. The filled arrow indicates the Paradise Brook sample location, while the outlined arrow indicates the Bear Brook location. (Image credit: USGS)

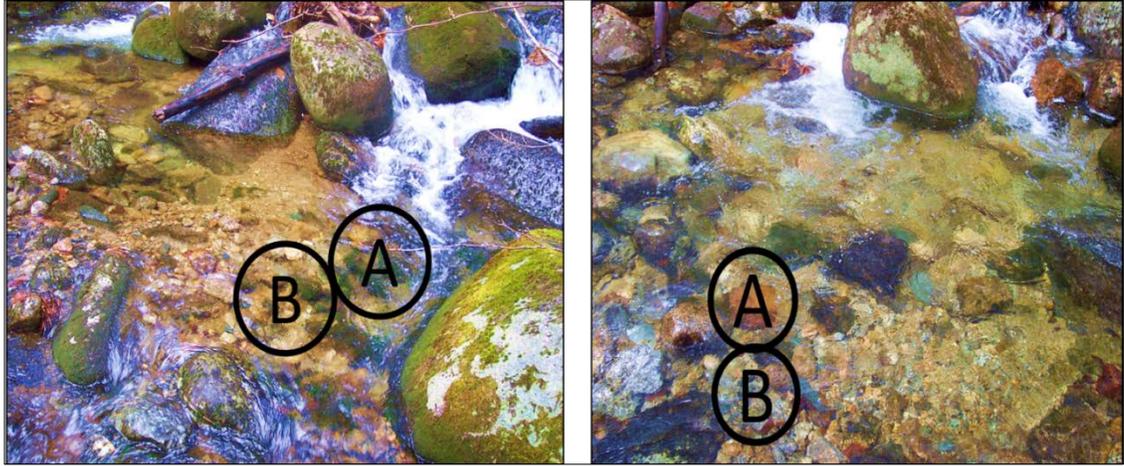


Figure 2.2: *Sample sites within the HBEF. Bear Brook is on the left and Paradise Brook is on the right. A designates primary sampling sites while B designates my secondary sampling site used after high flows that did not align with sampling dates.*

III: Results

Paradise Brook

Assemblage Description

In Paradise Brook the relative abundance of Plecoptera was 37% and Ephemeroptera was 19%. The relative abundances of the other taxonomic groups were Trichoptera at 11%; Chironomidae at 20% and taxa other than Ephemeroptera, Plecoptera, Trichoptera, and Chironomidae (hereafter referred to as EPTC) at 13% (Figure 3.1). Paradise Brook's biomass, assessed only for EPTC taxa, was dominated by Plecoptera (59%) and Ephemeroptera (29%). Trichoptera (9%) and Chironomidae (2%) had considerably less representation in biomass than they did in number (Figure 3.2).

Ephemeroptera (Figure 3.3) were distributed into four observed families: Leptophlebiidae (36% of individuals), Heptageniidae (26%), Ephemerellidae (21%), and Baetidae (18%). Paradise Brook's Ephemeroptera biomass was concentrated in two families, Heptageniidae (38%) and Leptophlebiidae (36%), with lesser representations among Ephemerellidae (15%) and Baetidae (11%).

Plecoptera consisted of the families Leuctridae (45% of individuals), Chloroperlidae (32%), Perlodidae (13%), and Peltoperlidae (10%) (Figure 3.4). Larger bodied Perlodidae comprised the largest percentage of biomass (38%), followed by Chloroperlidae (31%), Leuctridae (17%) and Peltoperlidae (14%).

Functional groups in Paradise Brook samples had a somewhat even distribution, with 33% predators, 29% gatherers, and 28% shredders. Scrapers and

parasites comprised a smaller proportion of the assemblage (8% and 2%, respectively, Figure 3.5).

Relationships to flow

The total abundance of macroinvertebrates per sample demonstrated increasingly negative correlations to the median decomposed flow as the days of discharge observed prior to sampling increased from one day ($\rho = -0.12$; $p = 0.577$) to five days ($\rho = -0.94$; $p < 0.001$). At six days prior to sampling, the correlation rapidly declined ($\rho = -0.03$; $p = 0.889$) before total abundance demonstrated a strong positive relationship to flow at seven days ($\rho = 0.62$; $p = 0.001$). This positive relationship remained to day nine (Figure 3.6 a).

Plecoptera abundance demonstrated relationships nearly indistinguishable from those described above for total abundance. The relative abundance of Plecoptera (Figure 3.7) presented similar correlations: the relationship for one day was weak ($\rho = 0.18$; $p = 0.400$) but rapidly changed to a significant negative relationship at four days ($\rho = -0.46$; $p = 0.026$). Like absolute abundance, strong positive significant relationships emerged at seven days ($\rho = 0.72$; $p < 0.001$).

Ephemeroptera's absolute abundance showed an earlier significant relationship to flow with one day ($\rho = -0.47$; $p = 0.038$), but reached a maximum correlation similar to the total and the Plecoptera at five days ($\rho = -0.94$; $p < 0.001$). However, Ephemeroptera did not show a positive correlation at seven days as was seen for total macroinvertebrate abundance and the Plecoptera. Instead, Ephemeroptera maintained a negative correlation ($\rho = 0.50$; $p = 0.013$). In contrast to Plecoptera, the relative

dominance of Ephemeroptera (Figure 3.7) demonstrated an increasing, positive significant correlation to flow at five days ($\rho = 0.54$; $p = 0.006$). The relative dominance then moved to a negative correlation for seven days ($\rho = 0.62$; $p = 0.001$).

For functional group relative abundance, predators reached a maximum negative correlation with flow at four days ($\rho = -0.60$; $p = 0.002$) and retained a negative relationship for the remainder of the nine days. Scrapers attained a maximum positive correlation ($\rho = 0.50$; $p = 0.013$) also with four days. Scrapers then moved to a negative correlation ($\rho = -0.87$; $p < 0.001$) by seven days. Gatherers had no significant relationship with flow, but showed trends similar to those of scrapers. Shredders showed no relationship to flow until six days ($\rho = 0.43$; $p = 0.037$).

Shannon's H (Figure 3.6 b) reached a strong negative correlation ($\rho = -0.77$; $p < 0.001$) by five days after an initially insignificant relationship ($\rho = 0.16$; $p = 0.455$). Diversity retained a negative relationship with flow for the remainder of the observed period. Percent EPT and the LIFE score (Figure 3.6 c, d) demonstrated similar trends. Percent EPT reached a significantly negative relationship ($\rho = -0.73$; $p < 0.001$) at four days, but showed a positive correlation ($\rho = 0.50$; $p = 0.013$) at seven days. The LIFE score attained significance with a strong negative correlation ($\rho = -0.93$; $p < 0.001$) at four days and then climbed to a positive relationship ($\rho = 0.50$; $p = 0.013$) at seven days.

Other notable relationships

Ephemeroptera biomass demonstrated a strong correlation to increasing stream temperature ($\rho = 0.60$; $p = 0.001$) and both early ($\rho = 0.63$; $p < 0.001$) and late summer ($\rho = 0.64$; $p < 0.001$) seasonal values. The relative abundance of predators (Figure 3.8) increased with increasing temperature ($\rho = 0.59$; $p = 0.002$), while shredders had a negative correlation ($\rho = -0.43$; $p = 0.028$).

Bear Brook

Assemblage Description

Ephemeroptera, Plecoptera, and Chironomidae made up the largest proportion of the Bear Brook community in numbers, comprising 37%, 23% and 20% of collected individuals, respectively. Non-EPTC taxa comprised 11% and Trichoptera represented the remaining 9% of the individuals sampled from this site (Figure 3.1). The biomass for Bear Brook was dominated by Plecoptera, at 43% across all samples, and Ephemeroptera, at 41%. The large bodied Trichoptera accounted for 13% and Chironomidae, while nearly as numerous as Ephemeroptera and Plecoptera, made up just 3% of total biomass (Figure 3.2).

Bear Brook's Ephemeroptera (Figure 3.3) were comprised of Leptophlebiidae (37% of individuals), Ephemerellidae (36%), Heptageniidae (15%), and Baetidae (12%). Biomass was concentrated in the two most abundant families, Leptophlebiidae (45%) and Ephemerellidae (41%). The remaining biomass belonged to Baetidae (8%) and Heptageniidae (6%).

On Bear Brook, Leuctridae (62%) numerically dominated the sampled Plecoptera, with Chloroperlidae (21%), Perlodidae (14%), and Peltoperlidae (3%) comprising the remainder of the order (Figure 3.4). Despite their lesser numbers, the larger bodied Perlodidae (32%) and Chloroperlidae (30%), represented a comparable amount of the sampled biomass as the slender Leuctridae (28%). Peltoperlidae (10%) showed a similar increase in representation for biomass.

By functional group, Bear Brook was dominated by gatherers (47%), followed in abundance by predators (23%) and shredders (20%). Scrapers accounted for the remaining 10%. As with Paradise Brook, filterers and parasites were present, but accounted for less than 1% of individuals (Figure 3.5).

Relationships to flow

The total abundance per sample demonstrated increasingly negative correlations to median decomposed stream flow as the days of discharge observed prior to sampling increased, beginning at one day ($\rho = -0.34$; $p = 0.104$) before peaking at six days (ρ of -0.77 ; $p < 0.001$). The negative relationship remained for the nine days observed (Figure 3.6 a).

Ephemeroptera abundance had a consistently negative relationship to increasing flow, with the strongest observed correlation at six days ($\rho = -0.89$; $p < 0.001$). However, the relative abundance of Ephemeroptera (Figure 3.7) showed an increasingly positive relationship with flow, from insignificant at one day ($\rho = -0.10$; $p = 0.642$) to strongly positive at five days ($\rho = 0.66$; $p < 0.001$). Day six presented a negative relationship ($\rho = -0.20$; $p = 0.349$) that continued to strengthen for the

remainder of the nine days observed. Ephemeropteran biomass was negatively correlated with flow for all days, increasing from one day ($\rho = -0.39$; $p = 0.060$) to the strongest relationship at day seven ($\rho = -0.82$; $p < 0.001$).

Plecoptera abundance had an increasingly negative relationship with flow beginning insignificant at day one ($\rho = -0.13$; $p = 0.54$) and reaching a maximum negative correlation at day four ($\rho = -0.79$; $p < 0.001$). This trend remained for the following five days, though the significance varied. The relative abundance of Plecoptera (Figure 3.7) had an increasingly negative relationship with flow from an insignificant correlation at one day ($\rho = 0.12$; $p = 0.577$) to significantly negative ($\rho = -0.69$; $p < 0.001$) at four days. However, by day six, a strong positive correlation ($\rho = 0.60$; $p = 0.002$) emerged, and this positive relationship persisted to day nine. Plecoptera biomass demonstrated a similar trend to Plecoptera relative abundance, though the significance was much lessened. At day five, biomass trended negative ($\rho = -0.31$; $p = 0.140$). Day seven showed a positive relationship ($\rho = 0.41$; $p = 0.047$) that persisted for the remainder of the nine days.

The predator functional group's relative abundance began with a highly insignificant relationship to flow ($\rho = 0.08$; $p = 0.710$) before becoming increasingly negative ($\rho = -0.77$; $p < 0.001$) by five days. Predators then trended positive by day six ($\rho = 0.20$; $p = 0.349$). The positive relationship strengthened until day nine ($\rho = 0.50$; $p = 0.013$). Shredders had a similar, if more pronounced, trend as predators, trending positive ($\rho = 0.25$; $p = 0.239$) at day one before moving toward a negative $\rho = -0.46$ ($p = 0.024$) by day four and then returning to a positive relationship ($\rho = 0.46$; $p = 0.015$) by day six. Gatherers began by trending negative ($\rho = -0.28$; $p =$

0.185) and then became significantly positive ($\rho = 0.46$; $p = 0.024$) by day five, before returning to a negative correlation ($\rho = -0.54$; $p = 0.007$) by day six. Scrapers presented no reliable trend and no significant correlations at the $p = 0.050$ level.

The Shannon Diversity Index (Figure 3.6 b) had a strong initial negative correlation to flow ($\rho = -0.79$; $p < 0.001$) by day two. However, by day six the relationship became insignificant ($\rho = 0.26$; $p = 0.220$) and remained so for the remaining days. The LIFE score had a strengthening negative correlation with flow, reaching significance ($\rho = -0.42$; $p = 0.041$) at four days and continuing to become more significant over the remaining days (Figure 3.6 d). Percent EPT had a more erratic pattern and showed no significant correlations with flow.

Other notable relationships

Overall abundance on Bear Brook increased as the sampling date approached August 10th, the late summer seasonal value ($\rho = 0.49$; $p = 0.011$), while the average individual biomass increased as June 10th drew closer ($\rho = 0.40$; $p = 0.044$). Ephemeroptera showed correlations to early summer seasonal values for abundance ($\rho = 0.43$; $p = 0.029$) and biomass ($\rho = 0.47$; $p = 0.015$). The relative abundance of the gatherer functional group (Figure 3.8) increased with late summer values ($\rho = 0.56$; $p = 0.003$) and increasing stream temperature ($\rho = 0.59$; $p = 0.002$), while scrapers decreased as early summer drew closer ($\rho = -0.45$; $p = 0.021$).

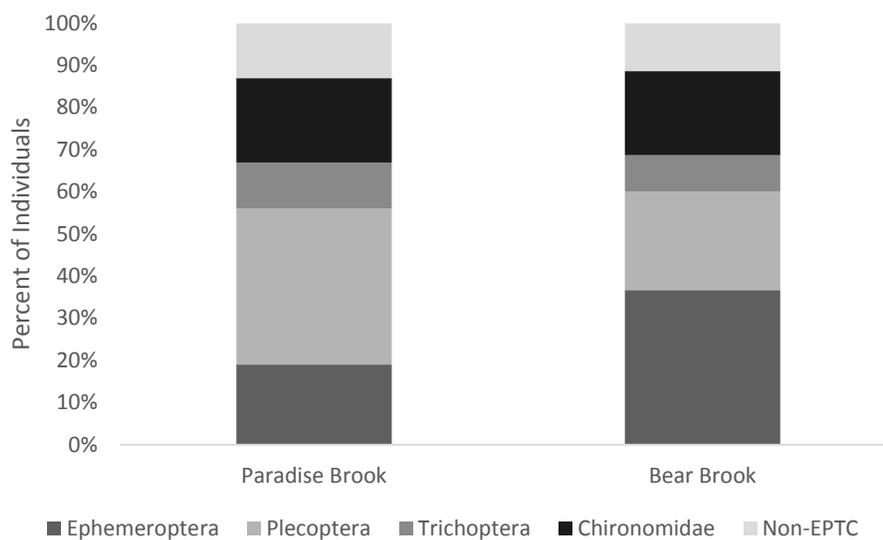


Figure 3.1: *Relative abundance of all taxa for Paradise Brook and Bear Brook. Of note is the lower abundance of Ephemeroptera in Paradise Brook samples versus Plecoptera, and the reverse pattern in Bear Brook.*

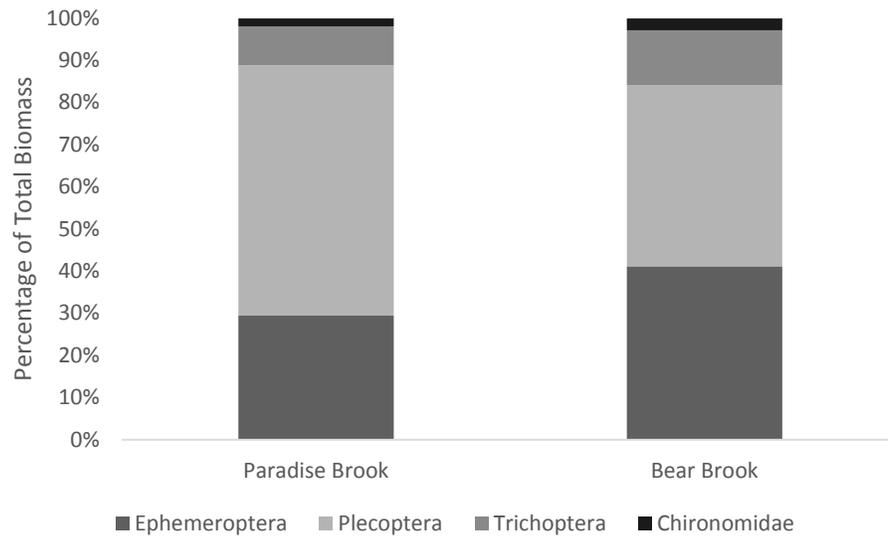


Figure 3.2: *Relative biomass of EPTC taxa for Paradise Brook and Bear Brook. Note that Ephemeroptera and Plecoptera were much more dominant for biomass than abundance indicating their larger size (Fig. 3.1).*

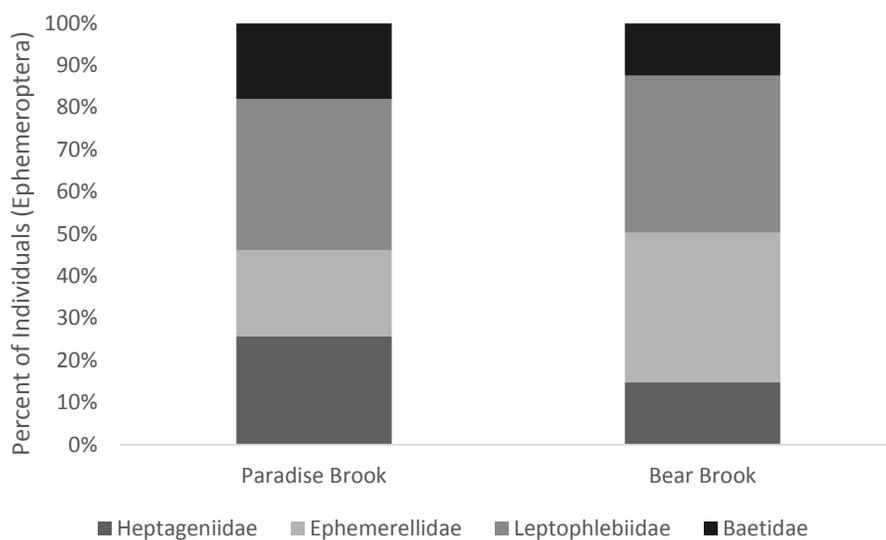


Figure 3.3: *Relative abundance of Ephemeroptera families for Paradise Brook and Bear Brook. Heptageniidae and Baetidae were less common in Bear Brook than in Paradise Brook.*

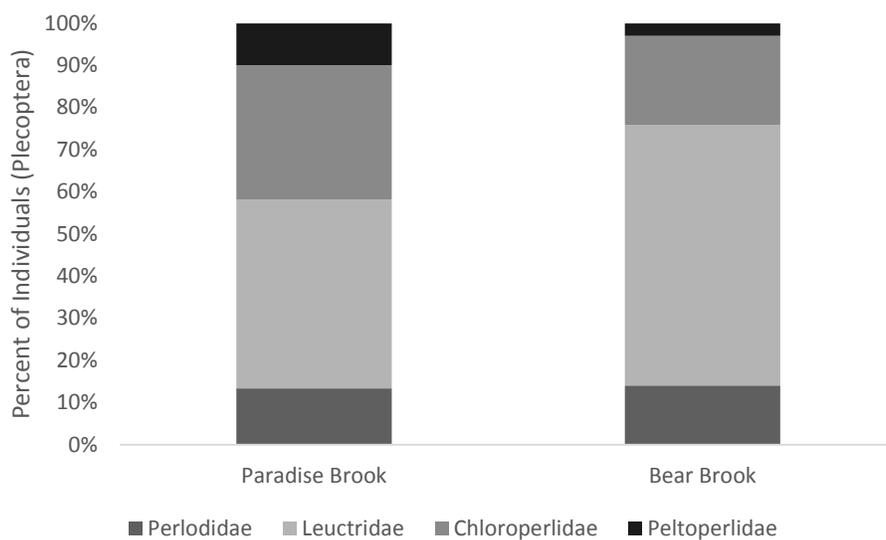


Figure 3.4: *Relative abundance of Plecoptera families for Paradise Brook and Bear Brook.*

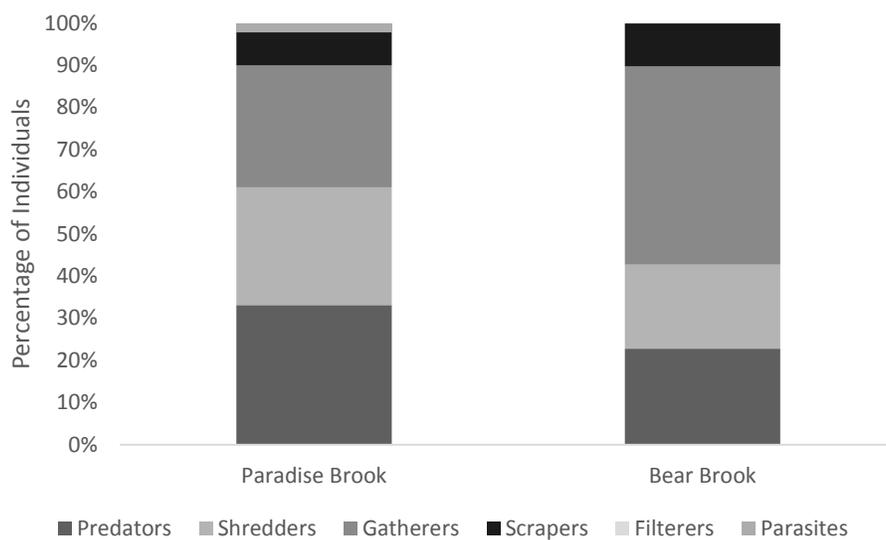


Figure 3.5: *Relative abundance of functional groups for Paradise Brook and Bear Brook. Predators, shredders, and gatherers were more evenly distributed in Paradise Brook samples than in Bear Brook, where gatherers comprised nearly half the of the assemblage.*

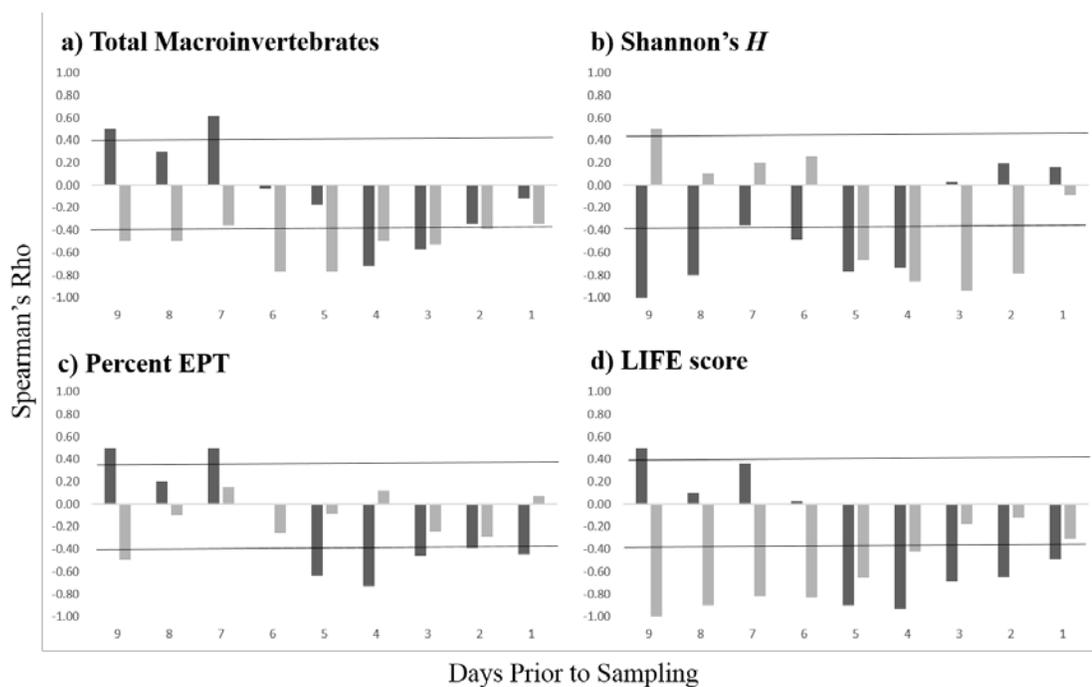


Figure 3.6: Degree of correlation for median decomposed flow over n days prior to sampling and a) total abundance, b) Shannon's H , c) percent EPT, and d) LIFE score at Paradise Brook (darker bars) and Bear Brook (lighter bars). Bars extending past the horizontal black lines indicate a statistically significant rho value ($p \leq 0.050$).

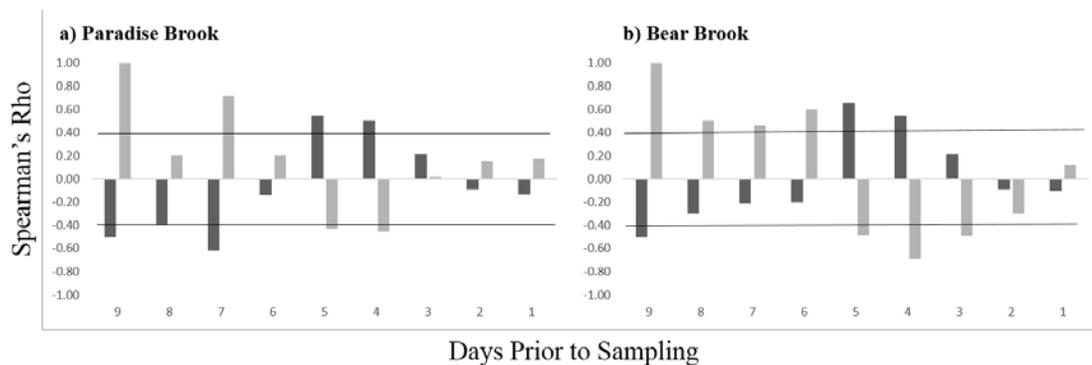


Figure 3.7: Degree of correlation for median decomposed flow over n days prior to sampling and the relative abundance of Ephemeroptera (darker bars) and Plecoptera (lighter bars) at a) Paradise Brook and b) Bear Brook. Bars extending past the horizontal black lines indicate a statistically significant rho value ($p \leq 0.050$).

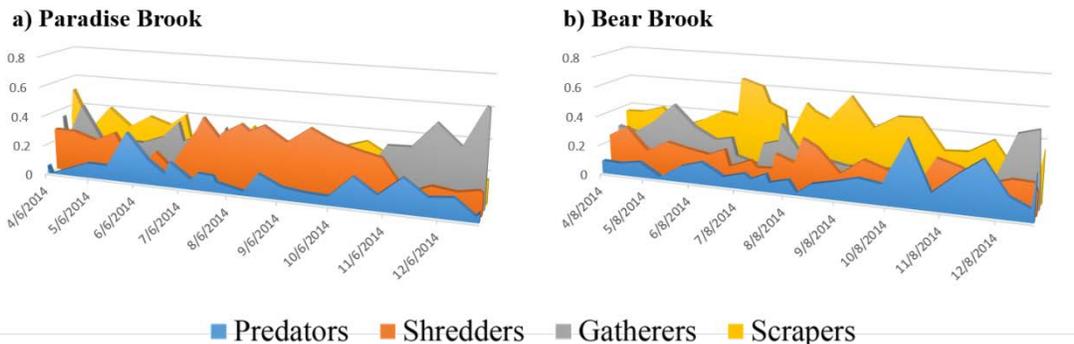


Figure 3.8: *Relative abundance of functional groups in Paradise Brook and Bear Brook. On a) Paradise Brook, note that shredders gain relative abundance following autumn leaf fall and share dominance with gatherers, the other detritivore group, before predators assume the highest relative abundance beginning in mid-summer. On b) Bear Brook, the shredders also gain relative abundance following autumn leaf fall and follow this through to spring. The dominance of shredders then gives way to the other detritivorous group, the gatherers.*

IV: Discussion

The intent of this study was to find the trends in community structure that correlate with stream flow. Following models established for saprobity (Hilsenhoff, 1987; Lenat, 1988), which use benthic macroinvertebrate community composition to determine stream conditions, as well as Extence et al.'s (1999) model for using macroinvertebrates to interpret large river flow regimes, I observed two specific second order benthic stream assemblages over the course of nine months. I then analyzed these assemblages using community trait indices to compare biotic responses to discharge rates. I hypothesized that increasing maximum flows would decrease biodiversity as only invertebrates capable of persisting through opposing extremes would survive within the system.

The data I collected were not sufficient to support my hypothesis. While I did find relationships between biotic metrics, including relative abundance and functional group composition, the two sites were not consistent on the direction and magnitude of trends. However, the findings did further the broader query in which my hypothesis was framed. My data showed a complicated response and recovery pattern in stream communities in response to changes in flow. These changes in membership demonstrate that even fine scale alterations to flow regimes, such as those predicted by some climate models (Rustad et al., 2012), have significant impacts on stream communities.

Seasonal observations

Over the course of the season, a pattern of shifting taxonomic and functional group membership fit with previous studies. For example, Ephemeroptera biomass steadily climbed and demonstrated greater variability as mature nymphs prepared for emergence (Brittain, 1982). Following this peak, the biomass and variability decreased as newly hatched nymphs with a more consistent size comprised a greater percentage of the assemblage. The late June timing of the event aligned well with the emergence observed by Fiance (1979) on streams located in the same valley as those used in the present study.

An increase in the relative abundance of the shredder functional group in early spring and late autumn followed a pattern in agreement with a previous study (Short et al., 1980) that suggested a high level of winter activity among stream invertebrates that feed on leaf litter. While my sampling was necessarily suspended when the streams froze, the data suggested that the relative abundance of shredders remained high throughout the winter. Different functional groups attained the highest relative dominance within each of the streams during summer – Bear Brook was dominated by gatherers while Paradise Brook had higher predators – but both streams showed a very similar pattern of seasonal shredder relative dominance.

The congruence of the seasonal patterns in my data points to the value of this study beyond the current research questions. The methods developed for this study uniquely captured the seasonality of a single assemblage. In the context of the stream

ecosystem as a whole, these observations may help track changes in the macroinvertebrate communities as the climate changes. Additionally, and importantly, the corroboration of my observations with other researchers suggests my methods successfully captured trends within the assemblage.

Initial response to flow events

Both Paradise Brook and Bear Brook were consistent in terms of the initial response of invertebrate abundance to increasing flows. A strengthening negative correlation indicated that the number of organisms within the site decreased as the velocity of the stream increased. As the stream became more rapid, rheophilic animals likely sought out refuge in larger or deeper substrate (Gjerløv et al., 2003) while the rest of the macroinvertebrates were washed downstream. Therefore, the assemblage abundance correlation with stream flow was resistant to change when animals entering the site from upstream replenished that abundance.

Supporting this conclusion was the decreasing LIFE score both as a function of increasing flow and as a function of time since peak flow. Animals with a high LIFE score are those most associated with high velocity streams (Extence et al., 1999). While Gjerløv et al. (2003) did not identify the taxa most likely to behaviorally seek refuge, they did indicate that the taxa were those most likely to have evolved in streams with a high level of flow-related disturbance. My own data support this since increasing flow rates led to decreased LIFE scores. This trend was most easily explained by refuge-seeking behavior among rheophiles. As invertebrates with high LIFE scores left the site, invertebrates with low LIFE scores remained, decreasing the

average score for the assemblage. Additionally, the percent EPT decreased with increasing flow for Paradise Brook, though it was insignificant for Bear Brook. Since the EPT taxa benefit from the longest aquatic evolutionary history (Hynes, 1984), they are the taxa with the highest average LIFE scores and the greatest abilities to seek refuge.

The above argues that LIFE scores and percent EPT should have had an initially strong negative correlation, as the rising stream washed a greater number of invertebrates from the bank into the stream (Fisher and Likens, 1973). My data show that, for Paradise Brook at least, LIFE scores and percent EPT both reached negative significance on the very first day of the event. The data from Bear Brook were less conclusive, potentially owing to site morphology (Biggs et al., 2005; Garcia et al., 2012; Townsend, 1989) and this was reflected in the erratic percent EPT correlations.

Ephemeroptera behaviorally use drift to escape sites with greater flow-induced threats (Hynes, 1984; Wiley and Kohler, 1984). As expected, their relative abundance increased with flow even while their absolute abundance declined. Plecoptera do not typically enter the drift as a behavioral response (Hynes, 1984) and did not share in this trend. As with total abundance, both Paradise Brook and Bear Brook agreed on these relationships.

Differences in site morphology (Biggs et al., 2005; Garcia et al., 2012; Townsend, 1989) may explain the difference in the functional group response to flow between the two sites. Paradise Brook's wider channel may have allowed different taxa to colonize and persist in high flow conditions than Bear Brook's narrower

channel. For instance, the gatherers appeared to be the sole functional group gaining in relative abundance on Bear Brook with increasing flow. Yet on Paradise Brook, an increase in relative dominance was more evenly distributed among all functional groups excepting, and at the expense of, predators.

When present assemblages were correlated to past flow conditions, my data showed that relationships strengthen as more time prior to the sample was considered, but only to about five days. Clustered around days four, five, and six there was a lessening or reversal of the correlation in almost all metrics. This was concurrent with Resh's (1979) assertion that seven days is sufficient time for macroinvertebrates to recolonize a site. It is important to note here that Resh, in context, was making the claim for sampling disturbance and not disturbance resulting from a rainfall event affecting the entire watershed.

Secondary response to flow events

Following the approximately five day initial response, there were additional correlations that extended through the nine days of prior stream conditions used in my analysis. The total abundance of macroinvertebrates in Paradise Brook samples showed a positive correlation to flow beyond six days prior to collection. This likely reflected an increase in the number of invertebrates in the days following an increase in flow, as the rising stream collected detritus from the banks and deposited it in the thalweg (Fisher and Likens, 1973). This abundant resource may have then supported a higher than average abundance of animals. Alternatively, a positive correlation may have been caused by a decrease in abundance as low flow conditions persisted.

If the positive correlation represented an increase in invertebrates in response to abundant allochthonous inputs, the shredder functional group – those organisms that feed primarily on leaf litter (Merritt and Cummins, 1995) – ought to have shown an increase in relative abundance similar to that of the total abundance. If the correlation results from a decrease in invertebrate abundance following decreases in flow, the functional representation should have been more evenly distributed in its response, lacking a mechanism for change in the assemblage functional make-up. Therefore, the observed positive correlation in the shredder relative abundance, at the expense of all other groups, supports the former interpretation. The most prevalent shredders, Plecoptera, also showed a positive correlation for their relative abundance in both streams.

The LIFE score further supported the interpretation of an increase in macroinvertebrates to take advantage of freshly deposited resources. If the positive relationship were the result of a decline in abundance following lessened flows, it would have been expected that the Paradise Brook LIFE score would show a negative relationship as invertebrates requiring flow for gas exchange, those with high LIFE scores, sought more hospitable conditions (Gallepp, 1977; Townsend, 1989; Wiley and Kohler, 1984), or an insignificant relationship if reduced flows did not force a change in assemblage. However, my data showed a positive correlation and indicated there was an increase in abundance concurrent with an increase in flow. Percent EPT in the Paradise Brook samples showed a nearly identical pattern and further supported the increased abundance interpretation.

Bear Brook also showed a secondary response, although it was distinctly different than Paradise Brook's. Following six days of strengthening negative relationships, similar to Paradise Brook, the relationship of Bear Brook's total abundance to flow remained significantly negative through day nine.

Bear Brook's site morphology was different than Paradise Brook's in an important way. Bear Brook's site was in a narrow channel within a cascade, while Paradise Brook's was in a wider channel within a pool. Therefore, while it was expected that Paradise Brook's LIFE score should decrease with decreasing flows, the Bear Brook site ought to maintain locally high flows, as the site was in the swiftest part of the local thalweg. However, Bear Brook's LIFE score showed a negative correlation to increasing flows. Furthermore, unlike the approximately five day correlation pattern displayed by other metrics, the LIFE score continually strengthened its negative correlation throughout the nine days analyzed in more of a linear pattern.

It was likely that the negative correlation reflected a site that had become depauperate following a high flow period. Increasing flow may have scoured resources from the site and the location's hydromorphology may have prevented substantial deposits of resources from accumulating (Biggs et al., 2005; Garcia et al., 2012). If the site collected only material likely to become trapped in large substrate – such as large leafy debris and less mobile invertebrates – then the data were consistent with the following interpretation.

While Paradise Brook's site allowed suspended material to settle out of the water column, Bear Brook's captured the material from the water column and the

force of the flow trapped it. The invertebrates with low LIFE scores, the non-EPT animals, were most easily caught (Wiley and Kohler, 1984) and reduced the average LIFE score of the sample. Importantly, the LIFE score decreased in a linear fashion as less rheophilic invertebrates continued to accumulate from upstream drift.

If this was the case, it is expected that the two functional groups with the greatest advantage were shredders, processing the leaf litter, and predators, taking the easy prey of trapped invertebrates. And indeed, following the five day initial response period, predators and shredders had a positive correlation with increasing flows, indicating an increase in their relative abundance within the assemblage. Additionally, the diversity showed a positive correlation and there were erratic and insignificant relationships with the percent EPT. This was likely the result of continuing drift immigration combined with the recolonization of predators and shredders.

Conclusion

The initial response of instream biota appeared generally consistent across two sites with different microhabitat conditions. Increases in stream flow removed invertebrates from the sampled stream bed, either by the force of the flow or by inducing a behavioral retreat. Not all organisms respond the same way to disturbance (Death, 2002; Death and Winterbourn, 1995; Wiley and Kohler, 1984) and not all habitats within a stream support the same recovery patterns (Death, 2002; Garcia et al., 2012; Townsend, 1989). Flow shapes stream communities more than any other typical variable (Armanini et al., 2011; Death, 2002; Extence et al., 1999; Monk et al.,

2008, 2006), so in the days more immediately following high flows, both Paradise Brook's and Bear Brook's sites showed similar patterns.

However, the differences between the sites remained important. The two stream sites that were the focus of this project were intended to act as replicate observations. If the percent EPT correlated negatively to the most recent high flow periods in both Paradise and Bear Brooks, for example, the interpretation of a causal linkage between these two variables would be strengthened. However, when data were analyzed at the end of the season, I found many contradicting trends between abiotic and biotic conditions: the two streams' sites were composed of different assemblages, showed different LIFE scores, and demonstrated different responses to flow.

Resh and Rosenberg (1989) suggested that the watershed for first order streams is insufficient to capture enough precipitation to raise the discharge rate beyond the threshold of invertebrate communities. I speculate that such was the case here, with the effects of meteorological variation unable to be extracted from those of spatial variation. LIFE scores have demonstrated usefulness on higher order streams and at longer time scales (Armanini et al., 2011; Extence et al., 1999; Monk et al., 2008, 2006), yet remained untested on streams of this order. However, Bear Brook's samples did have a significantly higher LIFE score than Paradise Brook's, and the possible reasons for this may help to explain the different responses to flow.

The fine-scale hydromorphological features of the Paradise Brook collection site differed from those of Bear Brook's, even while the substrate, water depths, and

surrounding terrain were very similar. Paradise Brook's sampling site (Figure 4.1) was 2.00 m below the inlet to the pool, situated just upstream of the outlet. The site was located at the downstream boundary of the widest (3.82 m) part of the pool where the water column moves consistently in one direction. Paradise Brook tended to provide more sand and fine gravel in the sample than Bear Brook. Bear Brook was 0.73 m downstream of the inlet, a small cascade, but during higher flows was integrated into the cascade. The channel was much narrower (0.89 m) before widening into a riffle, abutted by a deeper side pool filled by an adjacent inlet. The flow here had greater variation in direction owing to the agitation of the cascading inlet. Research has found that the flow of water through a stream system at all resolutions impacts the biota that exist within that flow (Biggs et al., 2005). Thus the superficial similarity of the paired sites likely failed to distinguish between two ecologically distinct biotopes (*sensu* Demars et al., 2012). Differences in the assemblages of the two sites, both taxonomically and functionally, argue that they are best treated as distinct habitats, each with its own hydrological demands.

Townsend (1989) described a stream in terms of a patchwork of distinct habitats, both temporally and spatially. Refugia, depositional zones, macrophytes and other factors vary along the length of a stream. As well, flow rates vary with time. During high flows, a depositional zone might be scoured of both resources and animals. Alternatively, during low flows, an area with high scour might collect detritus. Research observing habitat (Biggs et al., 2005; Garcia et al., 2012; Hall et al., 2001) and flow (Death, 2002; Death and Winterbourn, 1995; Extence et al., 1999)

have helped to describe some aspects of this patchwork. The response and recovery patterns this study has begun to elucidate will further the understanding of the temporal dimension.

As our climate continues to change at an accelerated pace, an understanding of how stream flows shape benthic communities is essential. Predicted changes to seasonal rainfall promise more frequent extreme events, extending the total time my data show benthic macroinvertebrates spend in a response and recovery mode. Insects are well recognized as a fundamental part of all non-marine ecosystems, and changes to their community membership have the potential to cascade into profound changes for the system as a whole.

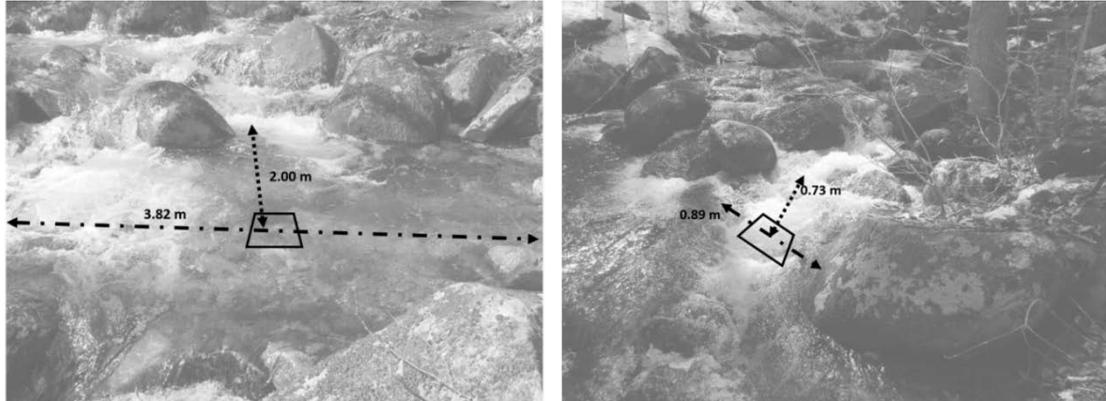


Figure 4.1: *The sample sites as they exist within the stream. The polygon denotes the primary sampling site within the stream. The dotted line (...) line measures the distance from the base of the cascade to the site and the dashed and dotted line (---) measures the width of the channelized flow. These photographs were taken during spring flow conditions. Note that the Paradise Brook site (left) is well downstream of the cascade and in a wide channel. The Bear Brook site (right) is within the cascade and in a narrow channel.*

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Appendix

These tables show the Spearman's rho values for assemblage variables versus decomposed flow values. The darker red color indicates a negative relationship while the darker green a positive relationship. However, significance of ≤ 0.05 is found only for rho values greater than 0.40 or less than -0.40. Because the stage height measuring device used in calculating flow often reported negative values as the minimum, the calculation for minimum flow regimes did not allow for correlations beyond two days and are here shown as NA.

Paradise Brook Median Flow

	1 Day	2 Days	3 Days	4 Days	5 Days	6 Days	7 Days	8 Days	9 Days
Absolute Abundance									
Total	-0.118	-0.346	-0.571	-0.719	-0.943	-0.029	0.616	0.300	0.500
Ephemeroptera	-0.426	-0.644	-0.616	-0.810	-0.943	-0.600	-0.205	-0.500	-0.500
Heptageniidae	-0.411	-0.588	-0.617	-0.031	-0.316	0.616	0.947	0.800	1.000
Ephemerellidae	0.241	0.356	0.530	-0.894	-0.866	-0.316	0.500	-0.632	1.000
Leptophlebiidae	-0.196	-0.505	-0.377	-0.205	0.000	-0.866	-1.000	-0.500	-1.000
Baetidae	-0.072	-0.019	-0.213	-0.359	-0.316	-1.000	-0.866	-0.800	-1.000
Plecoptera	-0.127	-0.252	-0.488	-0.807	-0.943	-0.029	0.616	0.359	0.500
Perlodidae	0.399	0.360	0.290	0.400	0.500	1.000	1.000	1.000	1.000
Leuctridae	-0.053	0.167	0.405	0.200	0.200	0.600	0.949	0.800	1.000
Chloroperlidae	0.124	0.068	-0.258	-0.655	-0.316	-0.700	-0.632	-0.900	-0.500
Peltoperlidae	0.334	-0.866	-0.866	NA	NA	NA	NA	NA	NA

Relative Abundance

Ephemeroptera	-0.135	-0.091	0.212	0.500	0.543	-0.143	-0.616	-0.400	-0.500
Heptageniidae	-0.244	0.059	0.443	0.638	0.800	0.300	0.051	0.600	0.500
Ephemerellidae	0.553	0.714	0.771	-0.900	-0.500	-0.400	-0.866	-0.800	-1.000
Leptophlebiidae	0.200	0.000	0.143	-0.100	0.500	-0.500	-1.000	-0.500	-1.000
Baetidae	-0.245	-0.109	0.087	0.205	0.400	-1.000	-0.866	-0.632	-1.000
Plecoptera	0.177	0.151	0.018	-0.455	-0.429	0.200	0.718	0.200	1.000
Perlodidae	0.255	0.487	0.754	0.200	1.000	0.866	1.000	0.500	1.000
Leuctridae	0.124	0.313	0.639	0.700	0.800	0.300	0.316	0.200	0.500
Chloroperlidae	-0.154	-0.033	-0.286	-0.429	0.000	-0.900	-0.949	-1.000	-1.000
Peltoperlidae	-0.086	-0.500	0.500	1.000	NA	NA	NA	NA	NA

Biomass

Ephemeroptera	-0.185	-0.282	-0.345	-0.333	-0.257	-0.314	-0.564	-0.700	-0.500
Heptageniidae	-0.221	-0.502	-0.563	-0.371	0.200	-0.300	-0.564	-0.700	-0.500
Ephemerellidae	0.517	0.786	0.771	-0.100	-1.000	0.200	0.000	-0.400	-1.000
Leptophlebiidae	-0.006	-0.286	-0.029	-0.100	0.500	0.500	1.000	0.500	1.000
Baetidae	-0.006	-0.607	-0.829	-0.900	-0.800	-1.000	-0.866	-0.800	-1.000
Plecoptera	-0.118	-0.227	-0.430	-0.833	-0.771	0.086	0.359	0.100	0.500
Perlodidae	0.345	0.607	0.486	0.400	0.500	1.000	1.000	0.500	1.000
Leuctridae	0.165	0.310	0.524	0.100	0.200	0.700	0.949	0.800	1.000
Chloroperlidae	-0.007	-0.233	-0.571	-0.607	-0.300	0.100	0.316	0.100	0.500
Peltoperlidae	0.200	-0.500	-1.000	-1.000	NA	NA	NA	NA	NA

Functional Group Relative Abundance

Predators	0.082	0.155	-0.030	-0.595	-0.486	-0.257	-0.359	-0.600	-0.500
Shredders	0.012	0.183	-0.037	0.310	0.029	0.429	0.821	0.600	1.000
Gatherers	-0.013	-0.096	0.127	0.132	-0.143	0.029	-0.263	-0.100	-0.500
Scrapers	-0.263	-0.296	0.079	0.500	0.486	-0.371	-0.872	-0.600	-1.000

Community Metrics

Shannon	0.159	0.200	0.030	-0.738	-0.771	-0.486	-0.359	-0.800	-1.000
Percent EPT	-0.445	-0.388	-0.462	-0.731	-0.638	0.000	0.500	0.205	0.500
LIFE	-0.492	-0.651	-0.687	-0.934	-0.899	0.029	0.359	0.100	0.500

Paradise Brook Maximum Flow

	1 Day	2 Days	3 Days	4 Days	5 Days	6 Days	7 Days	8 Days	9 Days
Absolute Abundance									
Total	-0.01	-0.22	-0.23	-0.23	-0.18	-0.17	-0.07	-0.07	-0.14
Ephemeroptera	-0.28	-0.32	-0.29	-0.35	-0.16	-0.12	-0.11	-0.11	-0.15
Heptageniidae	-0.53	-0.44	-0.34	-0.25	-0.01	0.02	-0.03	-0.01	-0.06
Ephemerellidae	0.47	0.48	0.39	0.29	0.32	0.33	0.35	0.35	0.33
Leptophlebiidae	-0.07	0.03	-0.18	-0.22	-0.02	-0.02	-0.05	-0.02	0.00
Baetidae	0.05	-0.22	-0.22	-0.02	0.24	0.35	0.18	0.18	0.09
Plecoptera	-0.18	-0.44	-0.43	-0.36	-0.24	-0.21	-0.14	-0.13	-0.20
Perlodidae	0.05	-0.20	-0.08	0.07	0.30	0.30	0.25	0.28	0.30
Leuctridae	0.00	-0.18	0.06	0.19	0.28	0.33	0.30	0.30	0.26
Chloroperlidae	0.04	-0.12	-0.15	-0.13	-0.21	-0.21	-0.11	-0.10	-0.20
Peltoperlidae	0.07	0.04	-0.11	-0.27	-0.27	-0.27	-0.27	-0.27	-0.27

Relative Abundance

Ephemeroptera	-0.15	0.11	0.19	0.12	0.18	0.20	0.09	0.09	0.11
Heptageniidae	-0.37	-0.05	-0.10	0.00	0.19	0.24	0.15	0.16	0.18
Ephemerellidae	0.54	0.61	0.57	0.43	0.36	0.35	0.31	0.31	0.31
Leptophlebiidae	0.25	0.36	0.21	0.09	0.11	0.11	0.09	0.11	0.15
Baetidae	-0.34	-0.37	-0.41	-0.23	-0.01	0.08	-0.06	-0.06	0.02
Plecoptera	-0.10	-0.39	-0.38	-0.27	-0.14	-0.10	-0.09	-0.08	-0.12
Perlodidae	0.07	-0.13	-0.05	0.05	0.20	0.20	0.09	0.13	0.14
Leuctridae	0.13	-0.02	0.00	0.19	0.34	0.40	0.35	0.35	0.39
Chloroperlidae	-0.32	-0.28	-0.32	-0.32	-0.42	-0.41	-0.34	-0.33	-0.39
Peltoperlidae	0.00	0.20	0.25	0.31	0.31	0.31	0.31	0.31	0.31

Biomass

Ephemeroptera	-0.26	-0.17	-0.02	-0.09	-0.11	-0.14	-0.10	-0.09	-0.16
Heptageniidae	-0.30	-0.35	-0.19	-0.08	-0.09	-0.11	-0.12	-0.11	-0.21
Ephemerellidae	0.30	0.49	0.43	0.23	0.17	0.11	0.10	0.12	0.11
Leptophlebiidae	-0.05	-0.04	0.01	0.04	0.24	0.24	0.20	0.24	0.19
Baetidae	0.19	-0.20	-0.22	-0.10	0.05	0.11	0.17	0.17	0.10
Plecoptera	-0.13	-0.42	-0.32	-0.30	-0.20	-0.21	-0.15	-0.14	-0.21
Perlodidae	0.20	0.00	0.02	0.05	0.25	0.25	0.29	0.33	0.34
Leuctridae	0.36	0.03	0.28	0.42	0.54	0.54	0.49	0.50	0.48
Chloroperlidae	-0.19	-0.35	-0.23	-0.08	-0.05	-0.03	-0.05	-0.04	-0.15
Peltoperlidae	-0.18	-0.29	-0.32	-0.64	-0.64	-0.64	-0.64	-0.64	-0.64

Functional Group Relative Abundance

Predators	-0.10	-0.25	-0.26	-0.29	-0.42	-0.45	-0.35	-0.35	-0.35
Shredders	-0.07	-0.14	-0.25	-0.07	0.19	0.24	0.21	0.22	0.21
Gatherers	0.32	0.45	0.58	0.35	0.11	0.06	0.04	0.03	0.01
Scrapers	-0.18	0.16	0.09	0.03	0.10	0.12	-0.02	-0.01	0.00

Community Metrics

Shannon	0.01	-0.11	-0.08	-0.22	-0.25	-0.28	-0.23	-0.22	-0.28
Percent EPT	-0.34	-0.56	-0.61	-0.55	-0.39	-0.32	-0.35	-0.35	-0.30
LIFE	-0.44	-0.72	-0.46	-0.46	-0.32	-0.33	-0.41	-0.39	-0.45

Paradise Brook Minimum Flow

	1 Day	2 Days	3 Days	4 Days	5 Days	6 Days	7 Days	8 Days	9 Days
Absolute Abundance									
Total	-0.43	-0.20	-1.00	NA	NA	NA	NA	NA	NA
Ephemeroptera	-0.55	-0.31	-1.00	NA	NA	NA	NA	NA	NA
Heptageniidae	-0.81	-0.89	NA						

Ephemerellidae	-0.03	-0.87	NA	NA	NA	NA	NA	NA	NA
Leptophlebiidae	-0.50	-0.32	NA	NA	NA	NA	NA	NA	NA
Baetidae	-0.15	-0.50	NA	NA	NA	NA	NA	NA	NA
Plecoptera	-0.27	-0.20	-1.00	NA	NA	NA	NA	NA	NA
Perlodidae	0.40	1.00	NA	NA	NA	NA	NA	NA	NA
Leuctridae	0.21	0.40	NA	NA	NA	NA	NA	NA	NA
Chloroperlidae	-0.14	-0.21	NA	NA	NA	NA	NA	NA	NA
Peltoperlidae	-0.87	NA	NA	NA	NA	NA	NA	NA	NA

Relative Abundance

Ephemeroptera	-0.07	-0.14	1.00	NA	NA	NA	NA	NA	NA
Heptageniidae	0.01	-0.40	NA	NA	NA	NA	NA	NA	NA
Ephemerellidae	0.54	-0.50	NA	NA	NA	NA	NA	NA	NA
Leptophlebiidae	0.00	-0.20	NA	NA	NA	NA	NA	NA	NA
Baetidae	0.09	0.50	NA	NA	NA	NA	NA	NA	NA
Plecoptera	0.30	0.03	-1.00	NA	NA	NA	NA	NA	NA
Perlodidae	0.65	0.50	NA	NA	NA	NA	NA	NA	NA
Leuctridae	0.56	0.40	NA	NA	NA	NA	NA	NA	NA
Chloroperlidae	-0.10	-0.10	NA	NA	NA	NA	NA	NA	NA
Peltoperlidae	-0.50	-1.00	NA	NA	NA	NA	NA	NA	NA

Biomass

Ephemeroptera	-0.55	-0.20	1.00	NA	NA	NA	NA	NA	NA
Heptageniidae	-0.67	-0.60	NA	NA	NA	NA	NA	NA	NA
Ephemerellidae	0.66	1.00	NA	NA	NA	NA	NA	NA	NA
Leptophlebiidae	-0.29	-0.20	NA	NA	NA	NA	NA	NA	NA
Baetidae	-1.00	-1.00	NA	NA	NA	NA	NA	NA	NA
Plecoptera	-0.31	-0.37	-1.00	NA	NA	NA	NA	NA	NA
Perlodidae	0.64	1.00	NA	NA	NA	NA	NA	NA	NA
Leuctridae	0.32	0.40	NA	NA	NA	NA	NA	NA	NA
Chloroperlidae	-0.52	-0.60	NA	NA	NA	NA	NA	NA	NA
Peltoperlidae	-0.50	1.00	NA	NA	NA	NA	NA	NA	NA

Functional Group Relative Abundance

Predators	0.12	-0.03	-1.00	NA	NA	NA	NA	NA	NA
Shredders	0.26	0.43	1.00	NA	NA	NA	NA	NA	NA
Gatherers	0.02	0.14	-1.00	NA	NA	NA	NA	NA	NA
Scrapers	-0.28	0.03	1.00	NA	NA	NA	NA	NA	NA

Community Metrics

Shannon	0.20	-0.09	-1.00	NA	NA	NA	NA	NA	NA
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Percent EPT	-0.26	-0.20	-1.00	NA	NA	NA	NA	NA	NA
LIFE	-0.63	-0.58	-1.00	NA	NA	NA	NA	NA	NA

Paradise Brook Flashiness

	1 Day	2 Days	3 Days	4 Days	5 Days	6 Days	7 Days	8 Days	9 Days
Absolute Abundance									
Total	0.28	0.35	0.30	-0.09	-0.19	-0.15	-0.05	0.17	0.12
Ephemeroptera	0.04	-0.11	0.02	-0.39	-0.62	-0.57	-0.42	-0.14	-0.10
Heptageniidae	0.57	0.12	-0.16	-0.10	-0.42	-0.44	-0.26	-0.13	0.06
Ephemerellidae	-0.24	-0.38	-0.40	-0.31	-0.23	-0.05	0.07	-0.08	0.30
Leptophlebiidae	-0.15	-0.41	-0.03	-0.23	-0.33	0.00	0.05	0.21	-0.10
Baetidae	-0.19	-0.18	0.15	0.26	-0.16	-0.41	-0.43	-0.44	0.06
Plecoptera	0.39	0.34	0.11	-0.12	-0.31	-0.32	-0.20	-0.15	-0.03
Perlodidae	0.00	-0.14	-0.22	-0.16	-0.17	-0.39	-0.34	-0.52	-0.35
Leuctridae	0.31	-0.03	-0.09	-0.16	-0.35	-0.16	-0.02	0.01	0.22
Chloroperlidae	0.23	0.49	0.24	0.31	0.25	0.06	-0.08	-0.14	0.04
Peltoperlidae	0.43	0.30	0.30	0.28	0.18	0.18	0.18	0.14	0.20

Relative Abundance

Ephemeroptera	-0.38	-0.54	-0.19	-0.15	-0.23	-0.17	-0.22	-0.14	-0.12
Heptageniidae	0.08	-0.29	-0.29	0.20	-0.02	-0.02	0.06	-0.06	0.09
Ephemerellidae	-0.30	-0.32	-0.47	-0.28	-0.19	-0.12	-0.19	-0.32	0.07
Leptophlebiidae	-0.06	-0.35	-0.02	-0.12	-0.23	0.16	0.13	0.24	0.03
Baetidae	-0.15	-0.36	-0.07	0.32	0.10	-0.14	-0.24	-0.49	-0.35
Plecoptera	0.40	0.42	0.02	0.05	-0.16	-0.17	-0.25	-0.34	-0.25
Perlodidae	-0.20	-0.13	-0.21	-0.01	-0.05	-0.13	-0.31	-0.51	-0.31
Leuctridae	0.28	-0.10	-0.28	-0.13	-0.35	-0.23	-0.17	-0.30	-0.17
Chloroperlidae	0.22	0.57	0.37	0.46	0.42	0.25	0.02	-0.17	-0.12
Peltoperlidae	-0.32	-0.39	-0.39	0.22	0.13	-0.04	-0.04	-0.08	-0.05

Biomass

Ephemeroptera	-0.22	-0.09	0.13	-0.11	-0.01	0.09	0.05	0.22	0.09
Heptageniidae	0.18	0.25	0.07	0.13	0.19	0.19	0.14	0.14	0.28
Ephemerellidae	-0.20	-0.01	-0.17	-0.01	0.24	0.38	0.31	0.07	0.38
Leptophlebiidae	0.15	-0.20	0.10	-0.15	-0.11	0.24	0.27	0.48	0.21
Baetidae	-0.60	-0.38	0.10	-0.15	-0.55	-0.61	-0.61	-0.25	-0.24
Plecoptera	0.34	0.25	0.11	-0.29	-0.24	-0.29	-0.15	-0.08	0.06
Perlodidae	0.13	-0.09	-0.08	-0.06	-0.14	-0.27	-0.06	-0.25	-0.10
Leuctridae	-0.06	-0.16	-0.04	-0.24	-0.19	-0.04	0.07	0.10	0.22
Chloroperlidae	0.19	0.46	0.25	0.14	0.09	-0.16	-0.32	-0.19	-0.05

Peltoperlidae	0.32	0.29	0.29	-0.05	-0.05	0.05	0.02	0.14	0.24
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Functional Group Relative Abundance

Predators	0.00	0.24	0.14	0.02	0.18	0.05	0.00	-0.17	-0.15
Shredders	0.47	0.40	-0.01	0.11	-0.07	-0.06	-0.01	-0.10	-0.13
Gatherers	0.10	-0.02	0.16	-0.20	0.05	0.17	0.24	0.45	0.51
Scrapers	-0.58	-0.80	-0.30	-0.17	-0.35	-0.28	-0.31	-0.17	-0.14

Community Metrics

Shannon	0.21	0.32	0.00	-0.21	-0.09	-0.03	-0.12	-0.15	0.00
Percent EPT	0.22	0.17	0.29	0.02	-0.13	-0.31	-0.25	-0.19	-0.37
LIFE	0.17	0.03	0.20	-0.37	-0.29	-0.29	-0.20	0.02	0.08

Bear Brook Median Flow

	1 Day	2 Days	3 Days	4 Days	5 Days	6 Days	7 Days	8 Days	9 Days
Absolute Abundance									
Total	-0.34	-0.39	-0.53	-0.50	-0.77	-0.77	-0.36	-0.50	-0.50
Ephemeroptera	-0.36	-0.39	-0.23	-0.20	-0.66	-0.89	-0.41	-0.60	-0.50
Heptageniidae	-0.18	-0.16	0.12	0.34	0.63	-1.00	NA	0.00	NA
Ephemerellidae	-0.36	-0.56	-0.67	-0.40	-0.56	-0.40	-1.00	-0.87	-1.00
Leptophlebiidae	-0.49	-0.33	-0.20	-0.15	-0.80	-1.00	-1.00	-1.00	-1.00
Baetidae	-0.31	0.32	0.63	0.87	0.87	-0.63	-0.50	-0.63	-0.87
Plecoptera	-0.13	-0.45	-0.58	-0.79	-0.66	-0.43	-0.21	-0.30	-0.50
Perlodidae	0.10	0.07	-0.07	0.41	-0.32	0.05	0.74	0.50	1.00
Leuctridae	-0.07	-0.39	-0.49	-0.71	-0.60	-0.31	-0.36	-0.56	-0.50
Chloroperlidae	-0.06	-0.21	-0.65	-0.73	-0.95	-0.30	-0.32	-0.40	-0.50
Peltoperlidae	-0.65	-0.77	-0.77	-0.87	-0.87	-0.77	-0.82	-0.87	-1.00

Relative Abundance

Ephemeroptera	-0.10	-0.09	0.21	0.55	0.66	-0.20	-0.21	-0.30	-0.50
Heptageniidae	-0.12	-0.28	0.07	0.50	1.00	-0.50	NA	0.50	NA
Ephemerellidae	-0.01	-0.19	-0.42	-0.14	0.00	0.60	0.50	0.50	1.00
Leptophlebiidae	-0.42	-0.14	0.17	-0.21	-0.63	-0.95	-1.00	-1.00	-1.00
Baetidae	-0.13	0.40	0.80	1.00	1.00	0.20	0.32	0.20	0.50
Plecoptera	0.12	-0.30	-0.49	-0.69	-0.49	0.60	0.46	0.50	1.00
Perlodidae	0.76	0.74	0.72	0.90	0.40	0.20	0.80	0.50	1.00
Leuctridae	0.15	-0.20	-0.24	-0.67	-0.54	0.43	0.46	0.20	1.00
Chloroperlidae	0.05	-0.02	-0.34	-0.57	-0.45	0.16	0.00	-0.22	0.00
Peltoperlidae	-0.50	0.21	0.74	0.50	0.50	0.80	0.11	0.50	1.00

Biomass

Ephemeroptera	-0.39	-0.48	-0.35	-0.38	-0.71	-0.77	-0.82	-0.50	-0.50
Heptageniidae	-0.05	-0.29	-0.02	-0.31	-0.60	-1.00	NA	-0.50	NA
Ephemerellidae	-0.50	-0.55	-0.70	-0.36	-0.40	-0.40	-1.00	-0.50	-1.00
Leptophlebiidae	-0.43	0.00	0.26	0.60	0.20	-0.40	-0.50	-0.50	-1.00
Baetidae	-0.39	0.20	0.40	0.50	0.50	-0.60	-0.32	-0.60	-0.50
Plecoptera	0.00	-0.08	-0.07	-0.29	-0.31	-0.20	0.41	0.30	0.50
Perlodidae	0.38	0.39	0.71	0.40	0.80	0.30	0.40	0.50	1.00
Leuctridae	0.20	-0.17	-0.26	-0.50	-0.29	0.14	0.15	-0.20	0.50
Chloroperlidae	-0.09	0.00	-0.07	-0.43	-0.30	0.30	0.32	0.10	0.50
Peltoperlidae	-0.14	-0.80	-0.40	-0.50	-0.50	0.40	0.74	1.00	1.00

Functional Group Relative Abundance

Predators	0.08	-0.02	-0.43	-0.45	-0.77	0.20	0.36	0.40	0.50
Shredders	0.25	-0.19	-0.27	-0.46	-0.37	0.49	0.31	0.46	0.50
Gatherers	-0.28	0.19	0.35	0.20	0.46	-0.54	-0.72	-0.80	-0.50
Scrapers	-0.35	-0.33	0.12	0.30	-0.03	-0.31	0.15	0.10	-0.50

Community Metrics

Shannon	-0.09	-0.79	-0.94	-0.85	-0.67	0.26	0.21	0.10	0.50
Percent EPT	0.07	-0.29	-0.24	0.12	-0.09	-0.26	0.15	-0.10	-0.50
LIFE	-0.31	-0.12	-0.18	-0.42	-0.66	-0.83	-0.82	-0.90	-1.00

Bear Brook Maximum Flow

	1 Day	2 Days	3 Days	4 Days	5 Days	6 Days	7 Days	8 Days	9 Days
Absolute Abundance									
Total	-0.39	-0.35	-0.39	-0.46	-0.52	-0.51	-0.50	-0.51	-0.57
Ephemeroptera	-0.49	-0.41	-0.37	-0.40	-0.43	-0.38	-0.42	-0.42	-0.49
Heptageniidae	0.05	0.01	-0.13	-0.11	-0.01	0.15	0.07	0.07	0.05
Ephemerellidae	-0.52	-0.44	-0.52	-0.43	-0.45	-0.45	-0.48	-0.49	-0.46
Leptophlebiidae	-0.61	-0.39	-0.55	-0.68	-0.69	-0.69	-0.69	-0.69	-0.68
Baetidae	-0.20	-0.03	-0.19	-0.10	-0.13	0.04	0.03	-0.01	0.07
Plecoptera	-0.17	-0.17	-0.31	-0.35	-0.44	-0.44	-0.48	-0.48	-0.48
Perlodidae	-0.24	-0.03	-0.13	-0.24	0.02	0.09	-0.03	0.00	-0.08
Leuctridae	0.04	0.03	-0.12	-0.14	-0.29	-0.33	-0.32	-0.33	-0.30
Chloroperlidae	-0.23	-0.28	-0.28	-0.36	-0.21	-0.24	-0.31	-0.28	-0.28
Peltoperlidae	-0.65	-0.65	-0.41	-0.58	-0.72	-0.72	-0.72	-0.72	-0.72

Relative Abundance

Ephemeroptera	-0.36	-0.34	-0.23	-0.12	-0.06	-0.01	-0.11	-0.11	-0.14
Heptageniidae	0.13	0.09	-0.09	-0.02	0.06	0.21	0.10	0.10	0.12
Ephemerellidae	-0.05	-0.18	-0.22	0.01	0.08	0.08	0.05	0.04	0.07
Leptophlebiidae	-0.68	-0.54	-0.61	-0.71	-0.62	-0.62	-0.65	-0.62	-0.66
Baetidae	-0.02	0.06	0.02	0.12	0.22	0.34	0.28	0.26	0.36
Plecoptera	0.14	0.03	-0.08	0.00	0.05	0.02	-0.06	-0.06	0.02
Perlodidae	0.46	0.40	0.19	0.29	0.52	0.60	0.46	0.47	0.51
Leuctridae	0.28	0.18	0.05	0.07	-0.03	-0.08	-0.09	-0.10	-0.03
Chloroperlidae	-0.02	-0.13	-0.12	-0.06	0.11	0.07	-0.03	-0.01	0.07
Peltoperlidae	-0.50	-0.03	0.47	0.40	0.26	0.08	0.08	0.08	0.08

Biomass

Ephemeroptera	-0.53	-0.39	-0.31	-0.38	-0.42	-0.40	-0.33	-0.32	-0.40
Heptageniidae	-0.11	-0.18	-0.19	-0.20	-0.14	-0.04	-0.08	-0.08	-0.13
Ephemerellidae	-0.69	-0.51	-0.58	-0.58	-0.55	-0.55	-0.58	-0.57	-0.58
Leptophlebiidae	-0.60	-0.34	-0.34	-0.49	-0.47	-0.47	-0.48	-0.47	-0.48
Baetidae	-0.05	0.22	0.01	0.01	0.01	0.19	0.32	0.29	0.29
Plecoptera	0.03	0.06	-0.17	-0.11	0.02	0.08	0.08	0.09	0.09
Perlodidae	0.25	0.36	0.20	0.18	0.35	0.42	0.37	0.39	0.36
Leuctridae	0.32	0.23	0.16	0.19	0.07	0.02	0.05	0.04	0.06
Chloroperlidae	-0.05	-0.12	-0.07	-0.05	0.10	0.12	0.09	0.11	0.13
Peltoperlidae	-0.14	-0.14	-0.38	-0.38	-0.23	-0.20	-0.20	-0.20	-0.20

Functional Group Relative Abundance

Predators	0.09	0.03	-0.10	-0.11	-0.05	-0.07	-0.07	-0.06	-0.01
Shredders	0.29	0.31	0.27	0.20	0.10	0.04	0.02	0.02	0.04
Gatherers	-0.16	-0.17	0.02	0.03	-0.09	-0.09	-0.01	-0.02	-0.07
Scrapers	-0.54	-0.46	-0.41	-0.44	-0.36	-0.31	-0.39	-0.38	-0.41

Community Metrics

Shannon	-0.03	-0.23	-0.19	-0.18	-0.19	-0.24	-0.18	-0.18	-0.17
Percent EPT	-0.18	-0.11	-0.16	-0.20	-0.14	-0.10	-0.15	-0.14	-0.11
LIFE	-0.34	-0.19	-0.26	-0.44	-0.49	-0.52	-0.52	-0.51	-0.58

Bear Brook Minimum Flows

	1 Day	2 Days	3 Days	4 Days	5 Days	6 Days	7 Days	8 Days	9 Days
Absolute Abundance									
Total	-0.68	-0.60	-1.00	NA	NA	NA	NA	NA	NA
Ephemeroptera	-0.56	-0.37	-1.00	NA	NA	NA	NA	NA	NA
Heptageniidae	-0.26	-0.21	NA						

Ephemerellidae	-0.58	-0.52	1.00	NA	NA	NA	NA	NA	NA
Leptophlebiidae	-0.33	0.20	-1.00	NA	NA	NA	NA	NA	NA
Baetidae	0.50	1.00	NA	NA	NA	NA	NA	NA	NA
Plecoptera	-0.64	-0.66	-1.00	NA	NA	NA	NA	NA	NA
Perlodidae	0.07	0.82	1.00	NA	NA	NA	NA	NA	NA
Leuctridae	-0.56	-0.49	-1.00	NA	NA	NA	NA	NA	NA
Chloroperlidae	-0.46	-0.36	NA	NA	NA	NA	NA	NA	NA
Peltoperlidae	-0.87	-1.00	NA	NA	NA	NA	NA	NA	NA

Relative Abundance

Ephemeroptera	-0.12	0.03	1.00	NA	NA	NA	NA	NA	NA
Heptageniidae	-0.18	-0.21	NA	NA	NA	NA	NA	NA	NA
Ephemerellidae	-0.18	-0.03	1.00	NA	NA	NA	NA	NA	NA
Leptophlebiidae	-0.04	0.32	-1.00	NA	NA	NA	NA	NA	NA
Baetidae	0.50	1.00	NA	NA	NA	NA	NA	NA	NA
Plecoptera	-0.28	-0.54	-1.00	NA	NA	NA	NA	NA	NA
Perlodidae	0.74	0.60	1.00	NA	NA	NA	NA	NA	NA
Leuctridae	-0.19	-0.58	-1.00	NA	NA	NA	NA	NA	NA
Chloroperlidae	-0.02	-0.22	NA	NA	NA	NA	NA	NA	NA
Peltoperlidae	0.87	1.00	NA	NA	NA	NA	NA	NA	NA

Biomass

Ephemeroptera	-0.71	-0.66	-1.00	NA	NA	NA	NA	NA	NA
Heptageniidae	-0.59	-1.00	NA	NA	NA	NA	NA	NA	NA
Ephemerellidae	-0.61	-0.54	1.00	NA	NA	NA	NA	NA	NA
Leptophlebiidae	-0.14	0.80	-1.00	NA	NA	NA	NA	NA	NA
Baetidae	0.50	1.00	NA	NA	NA	NA	NA	NA	NA
Plecoptera	-0.16	-0.54	-1.00	NA	NA	NA	NA	NA	NA
Perlodidae	0.39	-0.10	1.00	NA	NA	NA	NA	NA	NA
Leuctridae	-0.37	-0.09	-1.00	NA	NA	NA	NA	NA	NA
Chloroperlidae	-0.24	-0.50	NA	NA	NA	NA	NA	NA	NA
Peltoperlidae	-1.00	-1.00	NA	NA	NA	NA	NA	NA	NA

Functional Group Relative Abundance

Predators	-0.01	0.03	-1.00	NA	NA	NA	NA	NA	NA
Shredders	-0.10	-0.49	-1.00	NA	NA	NA	NA	NA	NA
Gatherers	0.12	0.32	1.00	NA	NA	NA	NA	NA	NA
Scrapers	-0.32	-0.03	-1.00	NA	NA	NA	NA	NA	NA

Community Metrics

Shannon	-0.84	-0.82	-1.00	NA	NA	NA	NA	NA	NA
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Percent EPT	-0.13	0.20	-1.00	NA	NA	NA	NA	NA	NA
LIFE	-0.33	-0.26	-1.00	NA	NA	NA	NA	NA	NA

Bear Brook Flashiness

	1 Day	2 Days	3 Days	4 Days	5 Days	6 Days	7 Days	8 Days	9 Days
Absolute Abundance									
Total	-0.13	0.08	0.30	0.02	-0.04	0.14	0.10	0.35	0.23
Ephemeroptera	-0.30	-0.19	0.27	0.13	-0.12	0.08	0.01	0.21	0.14
Heptageniidae	0.17	0.02	0.58	0.66	0.29	0.37	0.40	0.40	0.34
Ephemerellidae	-0.25	-0.07	-0.10	-0.19	-0.13	-0.06	-0.15	-0.06	-0.40
Leptophlebiidae	-0.29	-0.20	0.08	-0.33	-0.36	0.01	0.01	0.23	0.07
Baetidae	-0.37	-0.73	-0.34	-0.06	-0.36	-0.33	-0.33	-0.41	-0.26
Plecoptera	-0.32	-0.09	0.00	-0.25	-0.22	-0.08	-0.13	0.08	-0.01
Perlodidae	0.31	0.56	0.77	0.50	0.04	0.16	0.10	0.28	0.13
Leuctridae	-0.43	-0.21	-0.12	-0.42	-0.26	-0.17	-0.19	0.00	-0.15
Chloroperlidae	0.00	0.28	0.19	0.04	0.18	0.04	-0.01	-0.01	-0.04
Peltoperlidae	-0.39	-0.39	-0.13	-0.41	-0.20	-0.61	-0.61	-0.61	-0.61

Relative Abundance

Ephemeroptera	-0.16	-0.30	0.01	0.17	-0.08	-0.02	-0.08	-0.13	-0.03
Heptageniidae	0.33	-0.04	0.06	0.44	0.14	0.07	0.15	-0.04	0.17
Ephemerellidae	-0.02	0.07	-0.27	-0.03	0.02	-0.17	-0.21	-0.37	-0.40
Leptophlebiidae	-0.07	-0.01	0.17	-0.17	-0.18	0.10	0.10	0.22	0.07
Baetidae	-0.32	-0.76	-0.46	-0.17	-0.41	-0.35	-0.35	-0.41	-0.31
Plecoptera	-0.16	-0.20	-0.51	-0.46	-0.32	-0.39	-0.41	-0.44	-0.41
Perlodidae	0.32	0.40	0.22	0.51	0.12	0.00	-0.07	-0.22	-0.06
Leuctridae	-0.28	-0.32	-0.45	-0.54	-0.33	-0.33	-0.33	-0.25	-0.28
Chloroperlidae	0.22	0.25	-0.21	-0.08	0.10	-0.22	-0.20	-0.43	-0.29
Peltoperlidae	-0.09	-0.77	-0.97	-0.69	-0.17	-0.51	-0.51	-0.51	-0.51

Biomass

Ephemeroptera	-0.13	-0.04	0.30	0.09	0.00	0.13	0.04	0.29	0.12
Heptageniidae	0.48	0.31	0.46	0.46	0.08	0.26	0.23	0.44	0.53
Ephemerellidae	0.11	0.26	0.14	0.11	0.13	0.14	-0.01	0.08	-0.14
Leptophlebiidae	-0.27	-0.22	0.06	-0.19	-0.14	0.19	0.19	0.41	0.24
Baetidae	-0.62	-0.83	-0.48	-0.15	-0.45	-0.45	-0.45	-0.43	-0.43
Plecoptera	-0.08	-0.05	-0.01	0.06	-0.22	-0.11	-0.09	0.07	0.01
Perlodidae	-0.01	-0.30	-0.22	0.24	-0.10	0.03	-0.02	0.05	0.12
Leuctridae	-0.51	-0.31	-0.18	-0.47	-0.28	-0.20	-0.22	-0.02	-0.11
Chloroperlidae	0.30	0.25	0.30	0.31	0.44	0.30	0.33	0.31	0.38

Peltoperlidae	0.77	0.54	0.26	0.14	-0.18	-0.04	-0.04	-0.04	-0.04
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Functional Group Relative Abundance

Predators	0.42	0.60	0.28	0.10	0.16	0.04	0.13	0.07	-0.05
Shredders	0.12	0.08	-0.25	-0.41	-0.20	-0.20	-0.24	-0.10	-0.15
Gatherers	-0.37	-0.27	-0.08	0.00	0.14	0.17	0.19	0.13	0.23
Scrapers	0.11	-0.10	0.17	0.18	-0.06	0.14	0.10	0.13	0.05

Community Metrics

Shannon	0.38	0.56	0.35	0.11	0.36	0.22	0.16	0.21	-0.10
Percent EPT	0.11	-0.12	-0.09	-0.10	-0.46	-0.43	-0.41	-0.40	-0.29
LIFE	-0.05	0.06	0.34	0.05	0.08	0.34	0.41	0.59	0.52