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Cover Page Footnote

We thank Henrey Deese, Tess Ens, Caitlyn Lowry, Matt Moskowitz and the 2018 Methods in Field Biology class for assistance in the field and lab, and Chris Bowyer, Mark Nussbaum and Tony Swinehart for assistance with field and laboratory equipment. Special thanks to Chris Bowyer for taking temperature measurements every week throughout the study. Research costs supported by the Hillsdale College Biology Department. This is paper #33 of the G.H. Gordon BioStation Research Series.

Seasonal Changes of Benthic Macroinvertebrate Functional Feeding Group Biomass Within Forest and Meadow Habitats of a First-order Michigan (USA) Stream

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Abstract

Little is known about seasonal changes in stream benthic macroinvertebrate assemblages. We determined the ash-free dry mass of macroinvertebrates within a forested and a meadow reach of Fairbanks Creek in northern Lower Michigan throughout all seasons of 2018 and 2019. The macroinvertebrate assemblage of the forested reach was dominated by invertebrates in the shredder functional feeding group (FFG), whereas the meadow reach was composed primarily of scrapers and filtering collectors. Regardless of reach, the biomass of all FFGs was low during the winter and early spring, peaked in May or June, and gradually declined throughout the summer and fall. General trends in biomass were the same for both years of the study, although 2018 had overall higher biomass despite being a slightly cooler year.

Keywords: Functional, feeding, group, ash-free, dry mass, aquatic, season

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Understanding and quantifying the organic biomass of benthic macroinvertebrates is important for assessing and predicting the health of aquatic ecosystems. Because the abundance of different types of aquatic macroinvertebrate functional feeding groups (FFGs) depends on available sources of organic carbon, understanding how such organisms respond to natural and anthropogenic variables allows for rapid assessment of stream conditions (Vannote et al. 1980, Grubaugh et al. 1996, Rosi-Marshall and Wallace 2002, Greathouse and Pringle 2006, Rosi-Marshall et al. 2016, Houghton and DeWalt 2021). Since FFG differences between sites are due in large part to changes in the biomass of available food types and sources, the biomass of specimens should reflect these changes more accurately than will simple specimen counts (Houghton and Lardner 2020, Venarsky et al. 2020, Cummins et al. 2022).

Relatively few studies have compared differences in stream macroinvertebrate assemblages or secondary production over multiple seasons or multiple years (Nolte 1991, Lugthart and Wallace 1992, Huryn and Wallace 2000, Shearer er al. 2002, Bottazzi et al. 2011, Hill et al. 2016 Berlajolli et al. 2019, Kreiling et al. 2021). Understanding seasonal variation in the biomass of benthic assemblages is important to understanding the optimal time to sample them, as well as predicting changes in seasonal nutrient flux, prey choice variation among predators, and other community interactions (Uieda and Pinto 2011, Klecka and Boukal 2012, Anderson et al. 2016, Hill et al. 2016, Berlajolli et al. 2019, Kreiling et al. 2021). Thus, the objective of this study was to compare benthic macroinvertebrate FFG biomass in two distinct stream reaches throughout all seasons within a single stream over a two-year period.

Materials and Methods

Fairbanks Creek is a first-order stream located in northwestern Lower Michigan. Detailed descriptions of the stream can be found in Houghton and Wasson (2013) and Houghton (2015). The creek has both forest and meadow habitats within a 2 km reach (Fig. 1), offering an opportunity to test different habitats within an otherwise undisturbed watershed. Our meadow reach (44.0466° N, 85.6723° W) was ~1.4 km downstream of our forest reach (44.0481° N, 85.6586° W).

Six measurements were made of physicochemical parameters at each reach on each day that we sampled benthic invertebrates. Specific conductance (ECTestr Low, www.eutechinst.com), pH (AccuMet AP61, www.fishersci.com), temperature (YSI-55, www.ysi.com), dissolved oxygen (YSI-55, www.ysi.com), and flow velocity (FloWatch FW 450, www.flowatch.com) measurements were all made on-reach. All measurements were made within 2 h of each other to minimize diel fluctuations. In addition, the tempera-

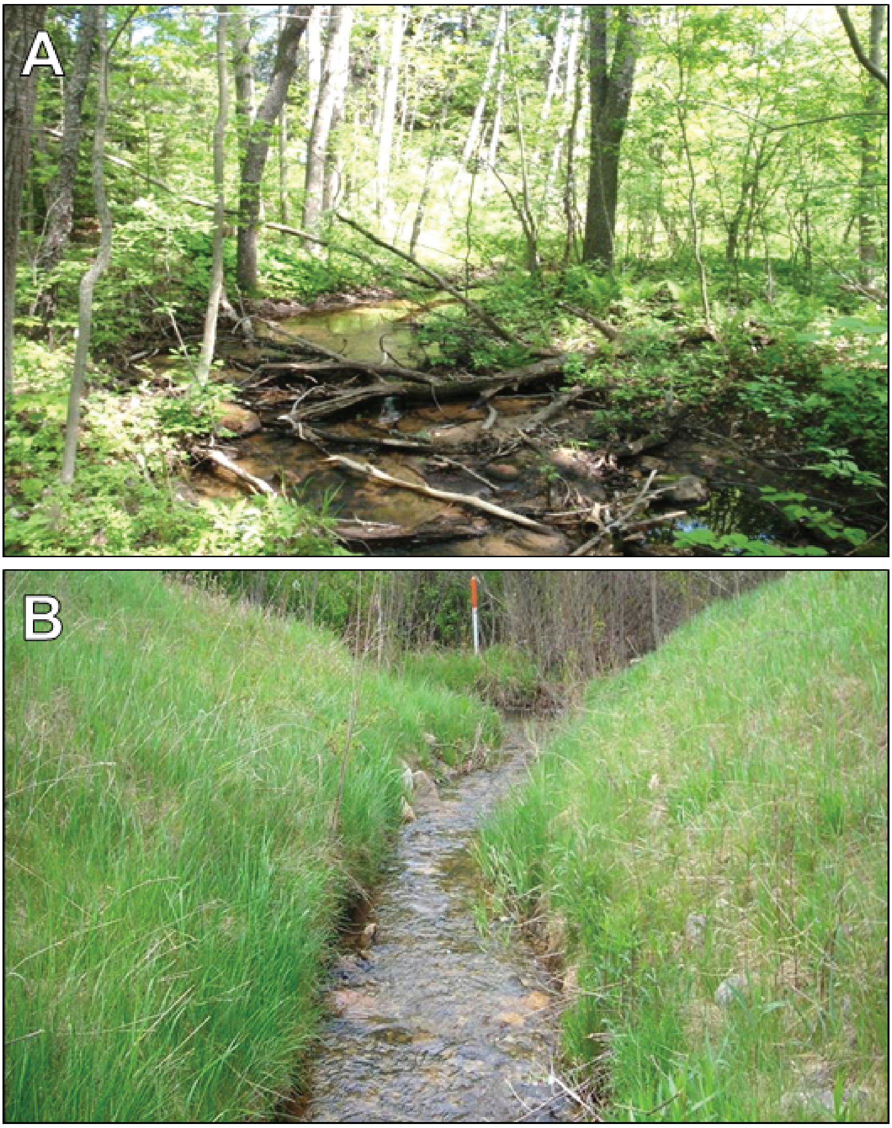

Figure 1. Photos of the forest reach (A) and meadow reach (B) of Fairbanks Creek.

ture of both stream reaches was taken each Friday afternoon for the 2 years of the study using a standard digital thermometer.

Benthic macroinvertebrates were sampled from both stream reaches using a Hess sampler on 24 occasions over the 2 years: 5 during winter, 9 during spring, 6 during summer, and 4 during fall. To maintain relatively consistent sampling intervals, we tried to sample during the first week of each month when possible. Sampling during winter 2018 was not possible due to the stream being frozen. Three Hess samples were collected from each reach on each date, for a total of 72 Hess samples and 24 composite samples from each of the two reaches. Specimens were identified to the lowest taxon possible, typically family or genus, using Hilsenhoff (1995), recorded, and then assigned to one of five FFGs: filtering collectors, gathering collectors, predators, scrapers, and shredders (Merritt et al. 2019).

To determine the ash-free dry mass (AFDM), specimens of each sample within each FFG were placed into pre-dried porcelain crucibles. Crucibles containing the specimens were dried for 2 h at 60 °C in a drying oven and then slowly cooled to room temperature before weighing. Crucibles and specimens were then transferred to a muffle furnace and incinerated at 500 °C for 3 h. After cooling to room temperature in the muffle furnace, the remaining material was transferred back to the drying oven, dried for 1 h at 60 °C, cooled to back room temperature, and weighed. AFDM was calculated as the final mass of material remaining after incineration subtracted from the mass of specimens before entering the muffle furnace. Total AFDM per FFG was determined per Hess sample, and the mean AFDM for each reach was determined from the 3 Hess samples taken on each of the 24 sampling dates.

Mean AFDM values per FFG from the three Hess samples were plotted per sampling date for both years and study reaches. Second-degree polynomial regression models were determined for each FFG for each reach and year using Excel for Windows with the Real Statistics add-in (https://www.real-statistics.com/). This analysis assessed the fit of biomass changes assuming a seasonal increase during the early months followed by a decrease during the later months.

Results

Both reaches exhibited predicted trends (Allan 2004) in water physicochemistry, with warming temperatures, decreasing dissolved oxygen and pH, and increasing specific conductance into the summer months, before reciprocal changes in the fall (Table 1, Fig. 2). Macroinvertebrate biomass from the forested reach was dominated by shredders (64%), whereas the meadow reach was composed primarily of filtering collectors (50%) and scrapers (33%) (Fig. 3). Biomass of gathering collectors (< 5%) and predators (10–12%) was similar between reaches. Total biomass and that of most FFGs was higher in 2018 than in 2019 (Fig. 4, 5). The biomass of all FFGs followed similar trends at both stream reaches and for both years, with low values during the winter and early spring, peaks in May or June, and gradual declines throughout the summer and fall (Fig. 4, 5). The decline of shredders at the forest reach in 2018 was particularly gradual, with similar biomass values between July and December. R^2 values for each second-degree polynomial fit model ranged from 0.12 to 0.61, with an overall mean of 0.37. There was no difference in mean R^2 values between years ($p = 0.30$) or between reaches ($p = 0.84$) (Two-sample T-test).

Specimens of most aquatic insect taxa varied notably between seasons, whereas non-emergent taxa were more consistent throughout the year (Table 2). We could not quantify the biomass of individual taxa, since weights of individual specimens were frequently below the detection limit of our balance. Specimen counts of non-emergent organisms, however, such as *Gammarus* (Amphipoda: Gammaridae), and several species of snails (Gastropoda) and segmented worms (Opisthopora: Lumbricidae) were consistent between seasons, whereas the immature stage of aquatic insects such as *Cheumatopsyche* and *Hydropsyche* (Trichoptera: Hydropsychidae), *Glossosoma* (Trichoptera: Glossosomatidae), *Stenonema* (Ephemeroptera: Heptageniidae), *Paragnetina* (Plecoptera: Perlidae), and several species of dragonfly (Odonata: Anisoptera) were 3 – 5x more abundant in spring and summer than in winter.

Discussion

Differences in FFG biomass between stream reaches were related to differences in riparian vegetation and its influence on available organic matter. The closed canopy of the forested reach decreased the available sunlight needed for periphyton growth, resulting in a lower biomass of scrapers relative to the open-canopied meadow reach. Conversely, the closed forest canopy increased the biomass of allochthonous coarse particulate organic matter such as wood and leaf debris that is consumed by shredders. Such trends have been documented frequently, both in Michigan streams and elsewhere (Vannote et al. 1980, Houghton and Wasson 2013, Houghton et al. 2018). The greater biomass of filtering collectors at the meadow reach was probably due to the higher stream velocity (Table 1) delivering a higher biomass of suspended seston over the same time period relative to the forest reach. Coarse particulate matter released from the upstream forested reach may have also increased the available of food for filtering collectors (Vannote et al. 1980).

Despite the differences in biomass of different FFGs between them, the trends in FFG seasonal biomass were consistent between the two reaches. Most abundant aquatic insects at the two reaches are known to be univoltine with a peak adult emergence in June or July (Houghton 2015), suggesting similar peaks in larval biomass in May or June, regardless of FFG. Our observation of consistent biomass in non-emergent benthic macroinvertebrates has been noted in previous studies (Aarefjord et al. 1973, Anderson et al. 2016, Berlajolli et al. 2019, Kreiling et al. 2021).

An important exception to the generalization of aquatic insect emergence in June and July was the shredder genus

Table 1. Mean (±SE) physicochemical values of the forested and meadow reaches of Fairbanks Creek, based on season, for combined 2018 and 2019 data. Physicochemical measurements were taken from the two reaches on the same dates as benthic invertebrate samples. *N* = 5 for winter, 9 for spring, 6 for summer, and 4 for fall for both reaches.

	Forest				Meadow			
	Winter	**Spring**	**Summer**	**Fall**	**Winter**	**Spring**	**Summer**	**Fall**
Temperature (°C)	2.1 (0.02)	10.4 (0.03)	13.2 (0.03)	7.1 (0.02)	2.1 (0.02)	11.4 (0.03)	17.7 (0.04)	7.4 (0.02)
D.O. (mg/L)	11.5 (0.03)	9.9 (0.05)	9.7 (0.05)	10.3 (0.07)	13.1 (0.10)	10.6 (0.07)	10.4 (0.06)	11.0 (0.08)
pH	9.2 (0.00)	9.1 (0.00)	8.6 (0.00)	8.8 (0.02)	9.2 (0.00)	9.0 (0.03)	8.2 (0.00)	8.3 (0.00)
Conductance (µS/cm)	235 (0.00)	270 (0.00)	310 (0.00)	300 (2.11)	225 (4.78)	300 (2.24)	330 (0.00)	310 (0.00)
Velocity (m/s)	0.09 (0.04)	0.14 (0.05)	0.12 (0.08)	0.10 (0.07)	0.26 (0.07)	0.32 (0.10)	0.23 (0.09)	0.21 (0.12)

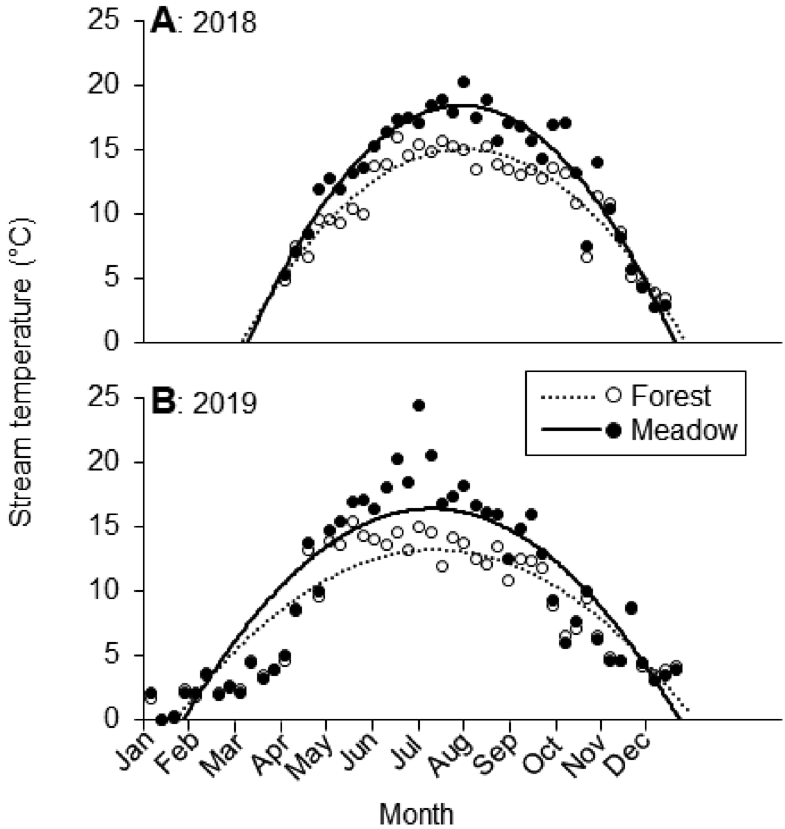

Figure 2. Temperatures of the forest and meadow reaches of Fairbanks Creek for 2018 (A) and 2019 (B), with a second-degree polynomial fit line for each year. Temperature readings were taken every week when the stream was open. Blank values represent weeks when the stream was frozen. X-axis labels correspond to the first day of each month.

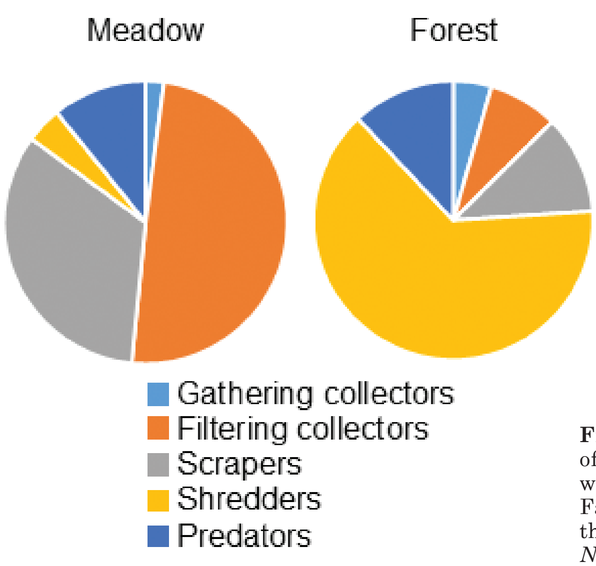

Figure 3. The relative ash-free dry mass of the five functional feeding groups within the meadow and forest reaches of Fairbanks Creek, reflecting collections throughout both years and all seasons. $N = 24$ for each reach.

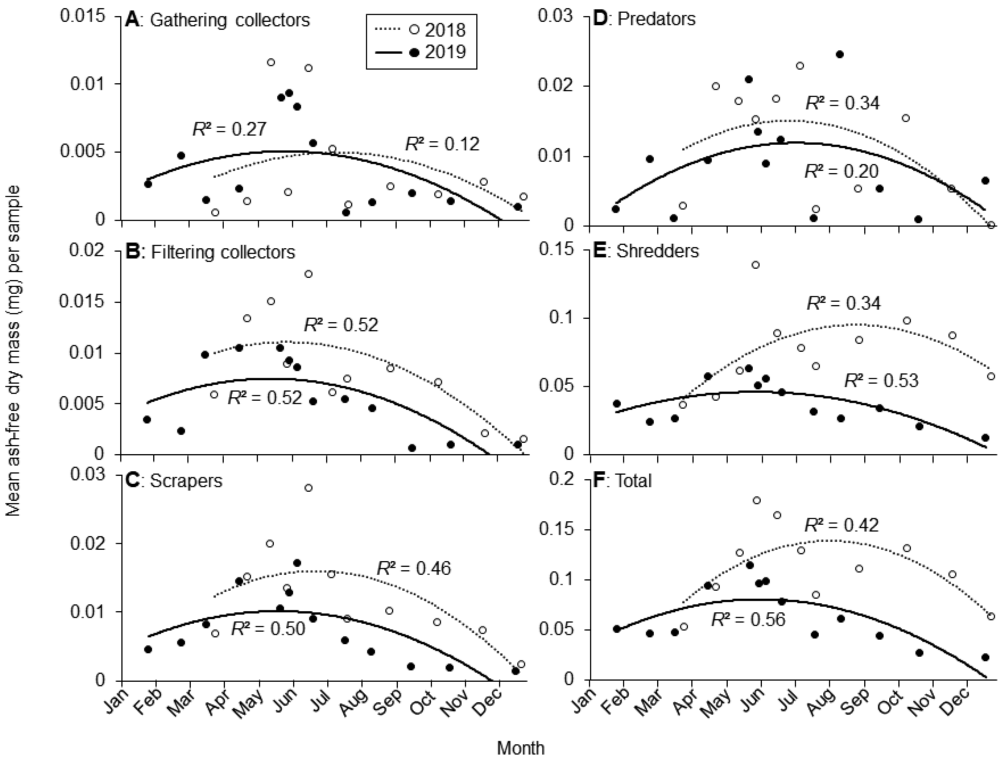

Figure 4. The mean ash-free dry mass of all specimens within gathering collector (A), filtering collector (B), scraper (C), predator (D), and shredder (E) functional feeding groups (FFGs), as well as the total for all FFGs (F) for the two years of the study at the forest reach. $N = 5$ for winter, 9 for spring, 6 for summer, and 4 for fall. Each marker represents 3 Hess samples taken on the same day. X-axis labels correspond to the first day of each month. Standard error bars omitted for readability.

Pycnopsyche (Trichoptera: Limnephilidae). *Pycnopsyche* species are known to reach terminal instar in May but not pupate until August or September, with emergence in September and fast growth during winter and spring (Cummins 1964, Mackay 1972). Thus, larval specimens of *Pycnopsyche* are abundant in streams throughout the year. In forested streams, *Pycnopsyche* species constitute a large portion of shredder biomass (Houghton 2021), which explains how the shredder biomass exhibited less of a decline after its May peak at our forested reach.

Overall patterns in biomass variation were consistent between the two years of the study. Since previous studies were of only a single year (Nolte 1991, Shearer et al. 2002, Bottazzi et al. 2011, Hill et al. 2016 Berlajolli et al. 2019, Kreiling et al. 2021), it is difficult to put this consistency in context of the literature. In a previous study of the adult caddisflies of Fairbanks Creek, Houghton (2015) found that adult specimen abundance periodicity of 27 common species varied very little within a 5-year period, despite this period encompassing both substantially colder and warmer than average seasonal temperatures.

The first year of our study (2018) had higher total biomass and higher biomass of nearly all FFGs than did the second year (2019). These higher biomass values are despite 2018 having a substantially colder winter and an overall lower temperature profile (Fig. 2). Indeed, we were unable to sample invertebrates or take temperature readings until April of 2018 due to the stream remaining frozen; whereas the stream was open throughout the entirety of 2019. Thus, we suspect that differences in benthic macroinvertebrate biomass were less dependent on temperature than they were on other factors. Several studies have suggested that differences in temperature are less important in small spring-fed streams like Fairbanks Creek than in other types of habitats (Williams 1983, Williams and Hogg 1988, Dobrin and Giberson 2003). It

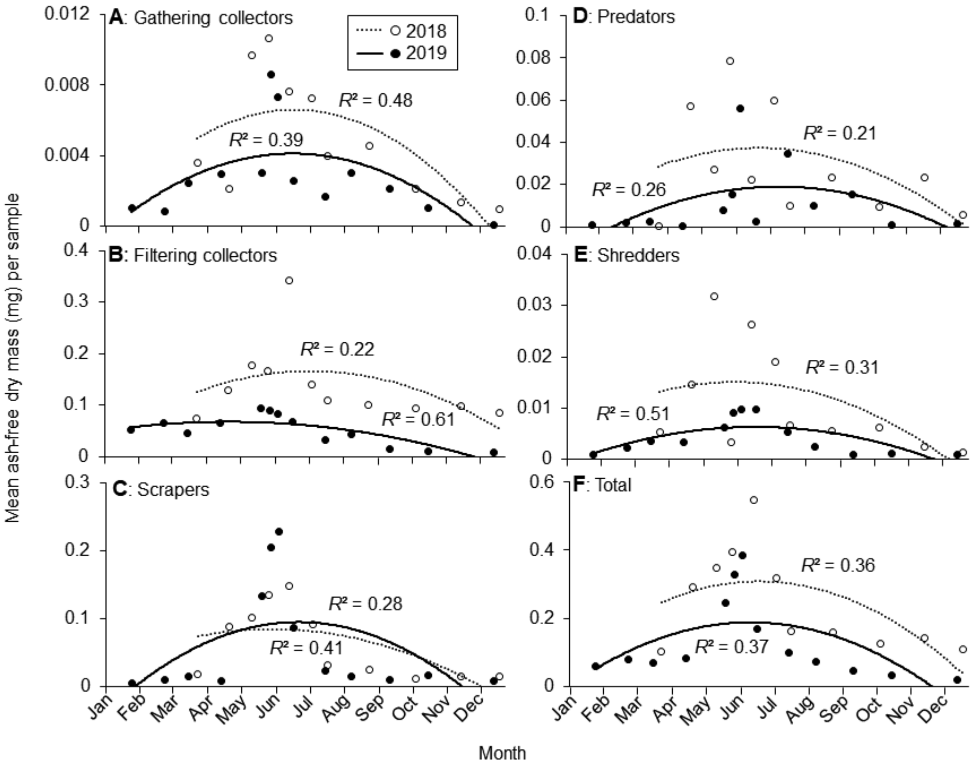

Figure 5. The mean ash-free dry mass of all specimens within gathering collector (A), filtering collector (B), scraper (C), predator (D), and shredder (E) functional feeding groups (FFGs), as well as the total for all FFGs (F) for the two years of the study at the meadow reach. $N = 5$ for winter, 9 for spring, 6 for summer, and 4 for fall. Each marker represents 3 Hess samples taken on the same day. Standard error bars omitted for readability.

is also possible that the cooler temperatures may have allowed individual specimens to accumulate greater biomass due to their lowered basal metabolic rate (Bouchard and Ferrington 2009).

Many future questions remain on this topic. For example, does higher biomass correspond to higher richness or diversity of the assemblage and, if so, does highest biomass represent the optimal benthic sampling period? Second, what factors (e.g., temperature, precipitation, innate life cycle) are most important for affecting biomass seasonally or annually? And, third, how does sampling strategy affect results? For example, taxa that are known to be highly abundant as adults at these two reaches, such as *Oecetis* (Trichoptera: Leptoceridae), *Lepidostoma* (Trichoptera: Lepidostomatidae), *Goera* (Trichoptera: Goeridae), *Banksiola* (Trichoptera: Phryganeidae), and many smaller species (Trichoptera: Hydroptilidae, Psychomyiidae) (Houghton 2015) were not located as larvae during this study, suggesting that quantifying the complete biomass of a benthic assemblage will require multiple sampling methods to capture the entire community (Cao and Hawkins 2011). Ultimately, being able to determine assemblage biomass will allow for more comparable sampling between different reaches and a greater understanding of food web dynamics and other benthic interactions.

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Table 2. The mean (±SE) number of specimens collected per Hess sample for the four seasons of 2018 and 2019 combined for both the forested and meadow reaches. All taxa arranged alphabetically. No distinction made for instar of specimens. *N* = 10 for winter, 18 for spring, 12 for summer, and 8 for fall. FFG = primary functional feeding group. FC = filtering collectors, GC = gathering collectors, Pr = predators, Sc = scrapers, Sh = shredders.

Taxon	FFG	Winter	Spring	Summer	Fall
ANNELIDA					
Lumbricus	Sh	4.5 (1.2)	4.2 (1.4)	3.7 (2.2)	4.1 (2.0)
CRUSTACEA					
Gammarus	Sh	8.2 (3.5)	9.0 (6.2)	8.5 (4.1)	8.1 (4.3)
INSECTA					
COLEOPTERA					
Elmidae adults	Sc	5.0 (4.2)	28.9 (12.5)	15.7 (10.5)	6.2 (4.5)
Elmidae larvae	Sc	2.5 (1.9)	11.6 (5.8)	5.7 (4.6)	1.6 (0.9)
DIPTERA					
Chironomidae	GC	4.9 (3.4)	29.1 (15.2)	17.2 (11.7)	3.7 (2.9)
Simuliidae	FC	3.9 (3.0)	41.8 (22.2)	21.8 (16.4)	11.6 (8.5)
Tabanidae	Pr	0.0 (0.0)	0.5 (0.5)	0.0 (0.0)	0.0 (0.0)
Tipulidae	Sh	0.2 (0.1)	0.5 (0.4)	0.3 (0.2)	0.2 (0.1)
EPHEMEROPTERA					
Baetidae					
Baetis	GC	2.8 (1.4)	9.8 (6.2)	8.2 (7.0)	4.6 (3.2)
Acentrella	GC	0.0 (0.0)	0.2 (0.1)	0.0 (0.0)	0.0 (0.0)
Caenidae					
Caenis	GC	0.0 (0.0)	0.0 (0.0)	0.1 (0.1)	0.0 (0.0)
Heptageniidae					
Stenonema	Sc	5.1 (2.2)	15.8 (9.9)	13.7 (8.6)	6.2 (4.0)
Leptophlebiidae					
Paraleptophlebia	GC	1.5 (0.9)	1.0 (0.5)	2.1 (1.2)	1.8 (1.2)
ODONATA					
Aeshnidae	Pr	0.5 (0.4)	2.7 (1.6)	1.1 (0.8)	0.6 (0.3)
Corduliidae	Pr	0.4 (0.2)	3.1 (1.7)	1.6 (0.5)	0.1 (0.0)
Libellulidae	Pr	0.1 (0.1)	2.5 (1.4)	0.8 (0.6)	0.5 (0.3)
PLECOPTERA					
Perlidae					
Paragnetina	Pr	2.2 (0.5)	5.9 (1.2)	4.2 (3.0)	1.8 (1.4)
Perlodidae					
Isoperla	Pr	3.5 (2.3)	2.2 (1.6)	4.7 (3.6)	2.3 (1.8)
TRICHOPTERA					
Glossosomatidae					
Glossosoma	Sc	3.4 (2.0)	11.9 (7.6)	9.2 (4.1)	4.6 (3.0)
Protoptila	Sc	0.0 (0.0)	0.3 (0.1)	0.0 (0.0)	0.0(0.0)
Hydropsychidae					
Cheumatopsyche	FC	6.5 (2.9)	45.8 (16.4)	31.1 (22.8)	9.8 (6.7)
Diplectrona	FC	0.0 (0.0)	0.4 (0.3)	0.2 (0.2)	0.1 (0.0)
Hydropsyche	FC	9.8 (6.9)	51.2 (27.2)	22.8 (9.9)	10.9 (6.3)
Lepidostomatidae					
Lepidostoma	Sh	0.5 (0.3)	1.2 (0.9)	1.8 (1.1)	0.6 (0.4)
Leptoceridae					
Oecetis	Pr	0.0 (0.0)	0.2 (0.1)	0.3 (0.1)	0.1 (0.1)
Limnephilidae					
Pycnopsyche	Sh	3.5 (0.8)	4.2 (0.6)	3.6 (1.1)	2.9 (0.8)
Philopotamidae					
Chimarra	FC	1.5 (0.8)	3.5 (2.0)	2.9 (1.7)	1.6 (1.6)
Dolophilodes	FC	0.2 (0.1)	1.2 (0.7)	1.9 (1.1)	0.5 (0.3)
Polycentropodidae					
Polycentropus	Pr	0.2 (0.1)	0.0 (0.0)	0.5 (0.3)	0.0 (0.0)
Rhyacophilidae					
Rhyacophila	Pr	0.2 (0.1)	3.5 (2.2)	1.9 (1.0)	0.4 (0.3)
Thremmatidae					
Neophylax	Sc	0.4 (0.3)	1.6 (1.1)	0.8 (0.5)	0.7 (0.4)
MOLLUSCA					
GASTROPODA	Sc	3.5 (3.0)	3.4 (2.2)	2.9 (1.9)	3.8 (2.9)

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