

How Do You Measure a Year in the Life?
Examining Ecosystem-Wide Responses to Senescence of Invasive Hydrilla
in Upland Streams of the Cumberland Plateau, Tennessee

By
Sandra Bojić

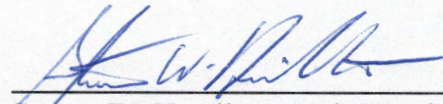
A Thesis
In Partial Fulfillment
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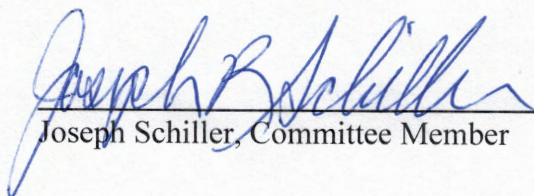
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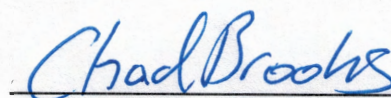

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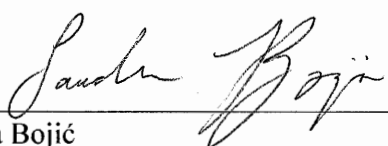
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ABSTRACT

Aquatic macrophytes provide structural complexity and regulate nutrient availability between periods of growth and senescence. Invasive macrophytes disrupt this process by altering both biotic and abiotic dynamics within streams. Hydrilla (*Hydrilla verticillata*) is an invasive submerged aquatic macrophyte whose quiescent propagules, low-light requirements, and fast growth rates allow it to dominate in any body of freshwater where it establishes. In 2004, monoecious hydrilla, which experiences seasonal dieback, was discovered in the Emory River Watershed (ERW), a high-elevation drainage characterized by high quality waters and notable diversity. Considering its high rate of biomass production, hydrilla has the potential to influence normal nutrient processes. Water chemistry, periphyton, and macroinvertebrates samples were collected from eight stream reaches, four with and four without hydrilla. Water samples were analyzed for concentrations of orthophosphate and nitrate/nitrite nitrogen, and abiotic parameters were measured via YSI. Periphyton were sampled from cobble, and chlorophyll *a* concentration was used as a proxy for algal biomass. Macroinvertebrates were subsampled and identified to allow analysis of diversity, function feeding groups, and similarity metrics. Orthophosphate and conductivity were higher during the growing season, while nitrate/nitrite was higher during the senescent season. Periphyton growth and proportions of grazer/scrapers and collector-filterers were greater at hydrilla sites during the growing season. Macroinvertebrate analyses showed no significant effects of hydrilla on diversity metrics. Analyses of community similarity indicated high similarity within hydrilla sites than within non-hydrilla sites during the growing season, suggesting that hydrilla may have a homogenizing effect on macroinvertebrate communities. I hypothesize that water level fluctuations may be causing hydrilla senescence during the growing

season when stream discharge declines, exposing and desiccating plants growing too close to the bank; nutrients from these decomposing plants are then returned to the water when water levels rise following rain events. Suggestions for future studies regarding hydrilla in the ERW would be to determine the physiological responses of hydrilla to water level fluctuations as well as evaluate effects on macroinvertebrates via secondary productivity rather than diversity and community metrics, as biomass data may be able to give greater insight into the metabolic outcomes of seasonal dieback.

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INTRODUCTION

Aquatic Macrophytes in Freshwater Environments

Aquatic vascular plants, otherwise known as aquatic macrophytes, are essential components to the structuring of freshwater environments. Considered to be ecosystem engineers, they create habitat complexity via bioconstruction and biostabilization, allowing for the dispersal, colonization, and establishment of various organisms (Corenblit et al. 2009). Macrophytes provide substrate for microflora, microfauna, and macroinvertebrates (Cummins and Klug 1979), which in turn create an abundance in food sources for macroinvertebrates and fishes (Chicharo et al. 2006, Dolph et al. 2011, Feio et al. 2017). Considering their importance to other organisms and their status as the largest sessile organisms in freshwater ecosystems (Carpenter and Lodge 1986), they have tremendous power to structure the biotic and abiotic conditions of both lentic and lotic systems.

In addition to contributing to habitat structure, macrophytes are energetically valuable to freshwater environments. While herbivory is largely limited as a result of highly indigestible proteins (Boyd 1970), aquatic plants are an important contribution to the river continuum upon decomposition (Kornijow et al. 1995). Macrophytes also influence the nutrient availability of surrounding waters between periods of growth and senescence. During periods of growth, macrophytes absorb and sequester carbon, nitrogen, and phosphorus from the water column and through the sediment, releasing these nutrients back into the water upon senescence (Kroger et al. 2007), at which point they act as a nutrient source readily absorbed by periphyton, phytoplankton, and other aquatic macrophytes (Howard-Williams 1981, Landers 1982). For annual or herbaceous perennial plants, this pattern of sequestering then releasing nutrients may

correspond with phenological shifts resulting from seasonal changes in light availability and temperature.

Direct effects of nutrient leaching during macrophyte senescence on the photosynthetic community are relatively established (Kistritz 1978, Lu et al. 2018). However, effects on the next trophic level, the macroinvertebrate community, are less known. It is known that macroinvertebrates characterized as scrapers are associated with increased periphyton (Rodriguez-Castillo et al. 2017), while macroinvertebrates characterized as clingers are considered intolerant to excessive levels of periphyton growth (Ashton and Morgan 2014). If senescence is thought to influence periphyton, one could hypothesize that an influence on periphyton-associated or periphyton-repelled macroinvertebrates would also be present. Also, macroinvertebrates feeding on detritus have been found to be the primary decomposers of macrophytes in riverine systems (Battle and Mihuc 2000), so senescence may result in an increase in shredders and detritivores. An association of collector-gatherers and collector-filterers with macrophyte beds has also been observed due to accumulations in fine particulate organic matter (Fowler 2012). All being said, there is a gap in the literature linking macroinvertebrates with detritus, nutrient concentrations, and periphytic growth resulting from senescing macrophytes, especially within the context of invasive macrophytes.

Biology of Hydrilla

Hydrilla (*Hydrilla verticillata*) is a submerged macrophyte native to the Eastern Hemisphere. First discovered in North America in 1960, it was likely transported in the aquarium plant trade as a result of misidentification. It is morphologically similar to native *Elodea canadensis* and invasive *Egeria densa* (Blackburn et al. 1969). Hydrilla can be differentiated from *Elodea* by having average leaf whorls greater than four (*Elodea* has four or fewer) and from *Egeria* by having serrate leaves with a toothed midrib (*Egeria* has serrulate leaves with no midrib teeth) (True-Meadows et al. 2016). Many advocate for molecular identification techniques as morphological identification is difficult and leads to misidentification (Rybicki et al. 2013). Hydrilla now co-occurs with these genera and dominates in oligotrophic and eutrophic waters worldwide, earning it the title of the “perfect aquatic weed” (Langeland 1996).

Hydrilla has many adaptations that allow it to invade almost any body of freshwater. The plant relies on the production of turions, axillary propagules, and tubers, subterranean turions, that detach and become dormant, allowing it to survive and reproduce after periods of unfavorable conditions including herbicide application (Netherland 1997). Compared to other macrophyte species, hydrilla requires the lowest amount of irradiance to produce the most photosynthate (Van et al. 1976), allowing it to begin photosynthesis earlier in the day and colonize deeper pools, both adaptations that enable hydrilla to compete with native plants for limited dissolved carbon in the water column (Langeland 1996). It also has a fast growth rate with stems reaching up to the surface of the water at which point they grow horizontally, thus limiting light penetration below by 95% (Haller and Sutton 1975). Fragmentation of the stems is a major mode of reproduction for the species alongside turion and tuber production and, to a

minor extent, seed production (Langeland 1996). These three survival strategies culminate in the creation of adverse conditions for photosynthetic life of the benthos.

There are several recognized “biotypes” of hydrilla that occur globally, many of which are suggested to be so distinct as to be considered different species. Biotypes are characterized by unique genetic, morphological, and phenological differences. North America has two biotypes, one monoecious and one dioecious, prompting speculation of two separate introductions (Langeland 1996). Phylogenetic analyses of the presumably monotypic species indicate three distinct lineages: an Indian/Nepalese/US dioecious lineage, a Japanese/Korean/European lineage, and an Indonesian/Malaysian/Australian lineage; North America monoecious biotype is hypothesized to be a hybrid of the Indian and Indonesian lineages (Benoit 2011). The dioecious type mostly occurs in subtropical climates while the monoecious type is found invading water bodies in both subtropical and cool-temperate climates.

The two biotypes occupy different regions likely due to separate introductions as well as differences in their growth properties. Monoecious hydrilla declines in biomass with reduced photoperiods while the dioecious remains the same; the monoecious type is the only one of the two with tubers that can germinate at low temperatures (Steward and Van 1987). Thus, the dioecious type persists throughout the year as a perennial, while the monoecious type grows as a semi-herbaceous perennial, meaning it persists below-ground via propagules but the above-ground shoots die back seasonally. While the dioecious type is mostly limited in North America to the subtropics and warm-temperate climates, and its spread is less of a concern. Due to the propagules, the monoecious hydrilla has considerably greater tolerance to harsh environmental conditions and its range on the continent is steadily expanding, threatening waterways

nationwide. This study involves an invasion of hydrilla experiencing seasonal senescence of above-ground biomass that is presumed to be the occurrence of the monoecious biotype.

Ecological Impacts of Hydrilla

Hydrilla has been found to impact aquatic communities, but based on the study organism chosen, these impacts can be negative, positive, or sometimes both. Native macrophytes experience entirely negative consequences from hydrilla invasion. Low light requirements and fast growth rates make hydrilla a superior competitor. Its invasive potential is inversely related to native macrophyte richness (Thomaz et al. 2009), suggesting that greater diversity fosters taxa that are able to more successfully compete with hydrilla. This is supported by the observation that most of its infestations are facilitated by preliminary infestations of reservoirs with low macrophyte richness, the setting of most invasion studies. Threat of displacement by hydrilla is high even for dominant macrophytes that have similar properties and are closely related to hydrilla such as *Vallisneria* (Haller and Sutton 1975) and *Egeria* (Bianchini et al. 2010), the latter itself being an exotic invader in North America.

The literature suggests that hydrilla invasion brings both gains and losses to aquatic vertebrates. Higher survival but lower body mass and slower growth are found for largemouth bass inhabiting hydrilla-infested waters (Brown and Maceina 2002), suggesting that the habitat complexity of the beds increases refugia from anglers and predators but decreases foraging efficiency by forcing individuals to ambush rather than search for prey (Savino and Stein 1989). The reduction in foraging success is so well documented that it is even suggested to be a line of

defense against alien crayfish predation on fishes in its native range of China (Huang et al. 2016). Unfortunately, there is also evidence suggesting it may facilitate the spread of non-native fishes in North America, which can use parts of the plant for nest building (Nico and Muench 2004).

Investigations into the effects of hydrilla invasion on macroinvertebrates have also yielded results both negative and positive. For instance, a reduction in dissolved oxygen in the sub-canopy of beds corresponds with a decline in gastropods (Colon-Gaud et al. 2004), which are important in maintaining periphyton levels and are important as prey. In contrast, some studies show higher macroinvertebrate abundance in hydrilla beds over mixed and diverse beds (Thorp et al. 1997). Other studies found no significant difference in macroinvertebrate richness, abundance, or biomass between diverse aquatic beds and hydrilla beds; Theel et al. (2008) suggest that the increased habitat complexity created by hydrilla may reduce fish foraging of macroinvertebrates, which are not necessarily increasing in number despite greater habitat.

A consideration of the study region is vital to making predictions about level of impact and, ultimately, management decisions. For a weed as successful as hydrilla, a well-rounded understanding of its behavior and consequences in various environments is critical. The current study stands in contrast to most of the literature, taking place in a high-gradient, high-quality riverine system.

Hydrilla in the Emory River Watershed

The Emory River Watershed (ERW) is located in eastern Tennessee on the Cumberland Plateau and harbors considerable biodiversity for the region. Monoecious hydrilla was first

documented in the ERW by Dr. Dwayne Estes in 2004. In 2010, he and other researchers conducted a detailed survey of the watershed to pinpoint the source, assess the extent of coverage, and identify risk to native freshwater species (Estes et al. 2011). They determined that hydrilla covered 26% of total river area surveyed at the time and concluded that risk to biota was high. In 2018, I discovered hydrilla growing upstream of its known origin and discontinuous with the reaches originally identified as impacted (Fig. 1). Its current distribution in the watershed may be much larger than previous estimates.

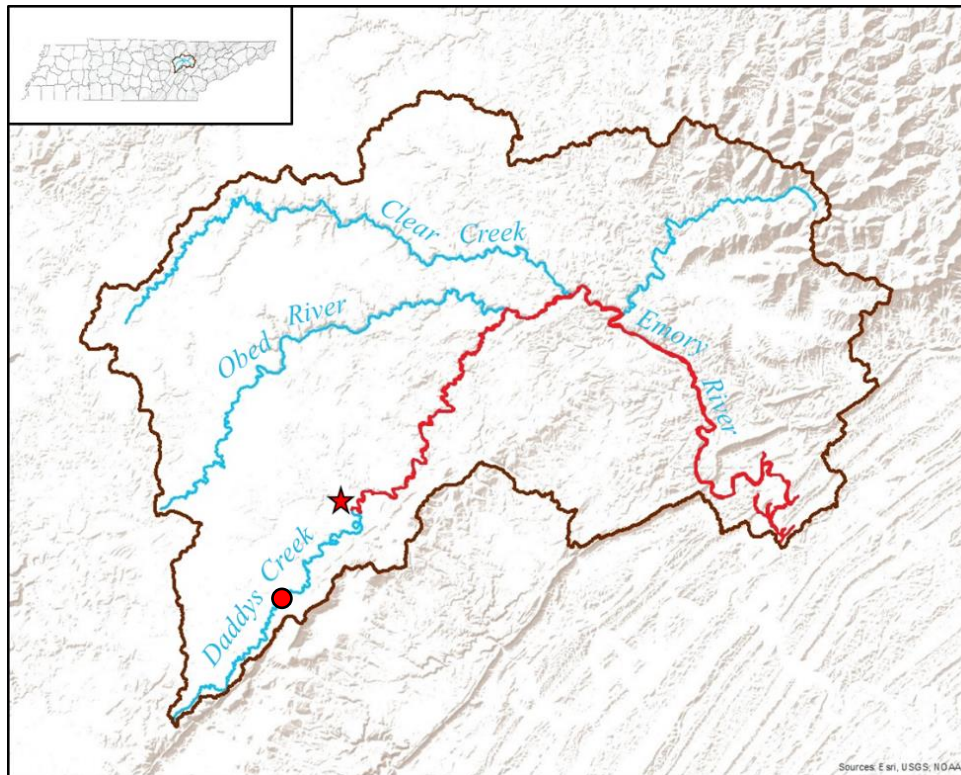


Figure 1. Terrain map of the Emory River Watershed (brown) with its three major tributaries: Daddys Creek, Obed River, and Clear Creek, Cumberland and Morgan counties, Tennessee. River highlighted in red indicates hydrilla infestation in the watershed and red star the point of origin as determined by Estes et al 2011. Red circle indicates Old Highway 28 dam site where we discovered hydrilla growing upstream of established origin. Produced in ArcMap.

Study Objectives

The aim of the current study was to examine monoecious hydrilla's temporal effects on the surrounding stream ecosystem. Specifically, my study asks the following questions:

1. Does the phenology of monoecious hydrilla alter nutrient availability and natural nutrient cycling patterns?
2. Do changes in the natural pattern of nutrient cycling have an upwards cascading effect on algal and invertebrate communities?

To address these questions, the following hypotheses were formulated and tested:

1. Presence of monoecious hydrilla influences the nutrient availability between periods of growth and senescence.
2. Changes in nutrient availability directly influence levels of periphytic algal growth between periods of growth and senescence.
3. Increases in particulate organic matter resulting from senescing hydrilla influence macroinvertebrate community structure.
4. Changes in periphytic algal growth influence macroinvertebrate community structure.

The following outcomes were predicted:

1. Nutrient concentrations of hydrilla sites will be higher during the senescent season rather than the growing season.
2. Periphytic algal growth at hydrilla sites will mimic nutrient concentrations; therefore, chlorophyll *a* concentrations will be higher during the senescent season rather than the growing season.

3. Macroinvertebrate communities at hydrilla sites will exhibit a greater shift in dominance towards detritus-associated taxa during hydrilla's senescence.
4. Proportions of periphyton-associated macroinvertebrate taxa will increase with increasing chlorophyll *a* concentrations.

Significance of Study

The occurrence of hydrilla in this watershed is one of very few documented records of an infestation in a high-quality mountain stream system (Estes et al. 2011). Most of the ERW is designated federally as Wild and Scenic River, meaning that it is free-flowing, largely lacking in impoundments, and harbors exceptional water quality (Wild and Scenic Rivers Act 1968). As a result, the ERW is characterized by high levels of diversity and endemism; this most notably includes vascular flora (Rodgers 2016, Schmalzer et al. 1985), as well as fishes (Kanno et al. 2012) and other aquatic organisms. Hydrilla being the aggressive competitor that the literature suggests poses a direct threat to this nearly natural stream system. Studies in this system are immensely important from a conservation standpoint, while investigations into the temporal effects of hydrilla invasion are largely lacking in the literature.

MATERIALS AND METHODS

Research Permit

A Scientific Research and Collecting Permit (ID: OBRI-2018-SCI-0001) was acquired from the National Park Service in January 2018 in order to make specimen-based collections. This allowed sampling within the boundaries of the Obed Wild and Scenic River for the entire calendar year.

Description of Study Area

This study took place in Cumberland and Morgan counties of eastern Tennessee in Ecoregion 68a, the Cumberland Plateau, a part of the Southwestern Appalachians. This elevated ecoregion is bordered on the west by the Interior Plateau and on the east by the Ridge and Valley. It has a modern landscape mosaic of forest and agriculture as well as some coal mining present (Griffith et al. 1997) but historically included extensive and diverse riverscours communities. Also known as river prairies, these riparian communities are endemic to the ecoregion and include grassland flora specifically adapted to floodwater disturbance (Murdock 2016). The geology of the region is characterized by Pennsylvanian-age sandstones, siltstones, conglomerates, and shales (Knight et al. 2014), with stream beds in the region predominantly conglomerate sandstone and shale (Hardeman et al. 1966). These rock layers have low permeability, causing flashy stream conditions that result in well-adapted riverine communities.

Site Selection

Sites were chosen based on status of infestation, availability of sampling habitat, and accessibility (Fig. 2). Four hydrilla-infested sites were identified on Daddys Creek: three localities downstream of the original source pond (I-40, Chestnut Hill, and Antioch Bridge) as well as Old Highway 28, an upstream site where hydrilla was newly established. Four hydrilla-absent sites were identified scattered throughout the watershed and include the following: one site upstream of the Old Highway 28 site on Daddys Creek (Rhea Road), one downstream of the Old Highway 28 site where hydrilla had not yet established (Highway 68), and two sites on Clear Creek, an adjacent tributary of the Obed River where no hydrilla occurs (Clear Creek and Barnett Bridge). Due to the geological context creating high levels of incision, sampling was further limited to accessible areas established by bridge crossings.

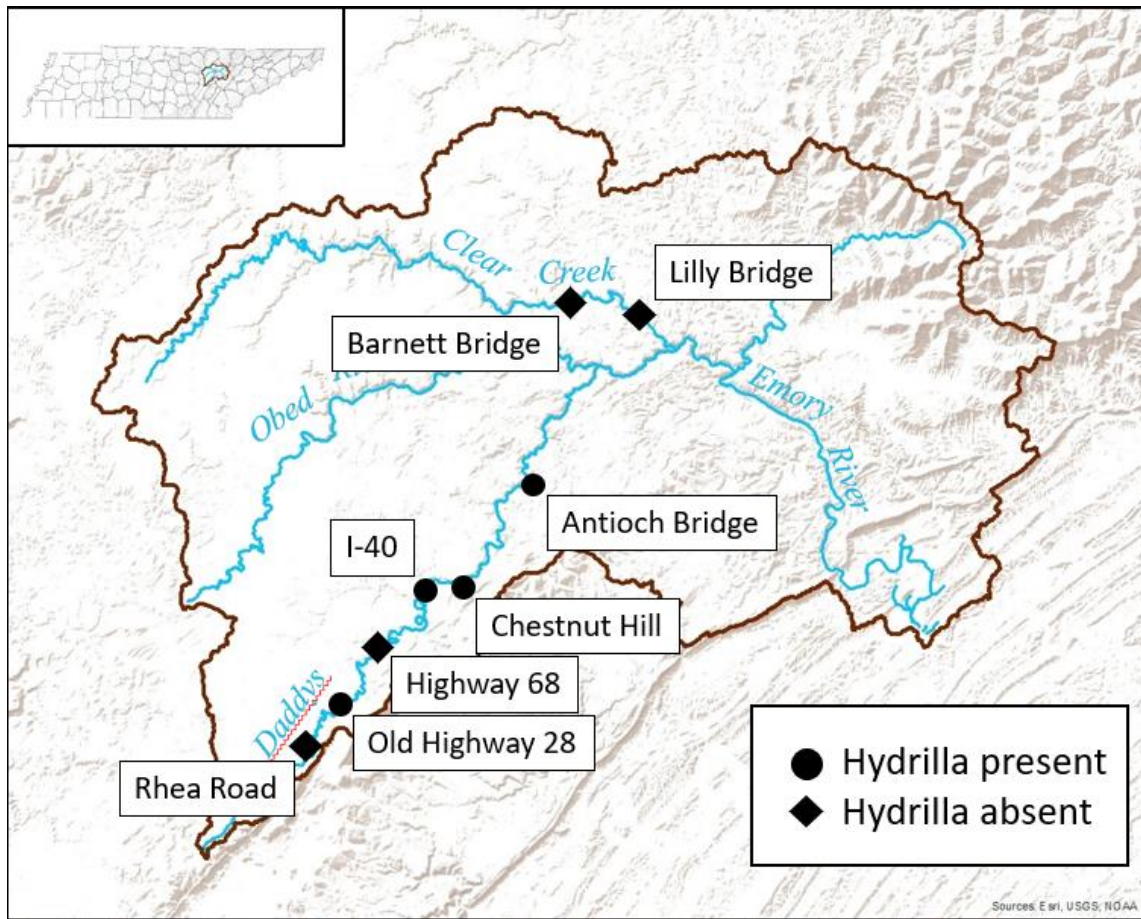


Figure 2. Map of study sites located in the Emory River Watershed among Morgan and Cumberland Counties, Tennessee. Hydrilla sites are represented by circles and non-hydrilla sites are represented by diamonds.

Sampling Design

Sampling took place during the periods of peak growth and senescence for hydrilla. The growing season was characterized by peak biomass production from August through October. After this, hydrilla above-substrate growth begins to break up, becoming negligible by late December (Harlan et al. 1985). Therefore, senescence samples were collected during dieback of above-substrate shoots from late October through December when the release of nutrients would

occur. Senescence season sampling was limited by an exceptionally wet 2018 winter causing streams to flood, making fieldwork difficult.

Sampling took place in 2018. Growing season samples were collected on August 14, 15, and 26, and September 8 and 9. Sampling for the senescent season occurred on November 21, 23, and December 7 and 19.

Assessment of the Physical Environment

Abiotic measurements including water temperature (°C), dissolved oxygen (mg/L, % saturation), pH, and specific conductivity (mS/cm) were collected using a YSI 600QS multiparameter meter (YSI Inc., Yellow Springs, OH). Prior to field collection, the instrument was calibrated in the lab. In most cases, it was calibrated every day before entering the field. The only times where the instrument was not calibrated immediately before fieldwork were when overnight lodging was necessary, in which case the instrument had been calibrated the day before. Canopy coverage was quantified via convex spherical densiometer (Forestry Suppliers, Inc., Jackson, MS).

Nutrient Analysis

Water samples were collected for each site and date from mid-depth of water column in 250 mL Nalgene bottles that were cleaned prior using non-phosphate soap. Samples were stored on ice in the field and frozen in the lab until delivered to Hancock Biological Station, Murray,

Kentucky, for nutrient analysis. Samples were analyzed for orthophosphate (i.e., soluble reactive phosphorus) and nitrate/nitrite concentrations (mg/L). These nutrients are the most readily assimilated by algae and most commonly measured in the literature (Lebkuecher et al 2015).

Orthophosphate concentrations were analyzed via QuikChem Method 10-115-01-1-B, "Determination of Orthophosphate by Flow Injection Analysis Colorimetry," which corresponds to EPA Method 365.1 (O'Dell 1993). Nitrate/nitrite concentrations were analyzed via QuikChem Method 10-107-04-1B, "Nitrate/Nitrite in Surface and Wastewaters," which corresponds to EPA Method 353.2 (Wendt 2000).

Periphyton Sampling

Periphyton samples were collected from natural substrate (i.e., cobble characterized by a particle size of 64–256 mm) at riffles and pools of each site. Pools were sampled because this is where most hydrilla growth occurs (Estes et al. 2011). Riffles were sampled because these habitats harbor the most diverse algal communities and could be more impacted by nutrient changes as more light penetrates in these shallower regions. Once chosen, the sample cobble were placed individually in Ziploc bags, labelled with locality information, and stored on ice and then in a cold room for 12-24 hours awaiting pigment analysis. Chlorophyll *a* remains viable for up to 48 hours (Lebkuecher et al. 2015), but it is optimal to conduct the analysis as soon after collection as possible to avoid pigment degradation.

Periphyton Processing

In order to make the connection between nutrient availability and uptake, I chose to isolate the photosynthetic community within the periphyton by quantifying fluorescence of chlorophyll *a* via fluorimetry, using that as a proxy for periphytic biomass. The upper surface of each sample cobble was scraped of periphyton into one liter of tap water using a razor blade. Scraped periphyton were suspended in the water via mixing of an AlgaeChek Ultra portable fluorimeter and nephelometer, model RS232 (ModernWater, Newcastle, DE). The fluorimeter connects to PC software TPlot8 to produce fluorescence values. Because the values are dynamic based on mixing speed and power, the average of the first three readings was taken once a relatively stable point was achieved. This resulting fluorescence value was recorded as µg/L of water, which was then converted to mg/L to work with standard formulas.

In order to correct for the specific size of the cobble, surface area of the cobble was measured using the foil weight method (Hauer and Lamberti 2006). In this protocol, foil is wrapped along the surface of the rock that was scraped and cut to match that area. The cut foil was then weighed and surface area determined via the following equation established in Hauer and Lamberti (2006):

$$\text{Stone surface area (m}^2\text{)} = \frac{\text{foil wt. in grams that covered stone surface}}{\text{foil wt. in grams of 1 m}^2\text{ of foil}}$$

Once both the concentration of chlorophyll *a* (mg/L) and the surface area of the rock (m²) were known, I was able to determine relative colonization of photosynthetic periphyton using the following equation in the foil weight method protocol:

$$\text{Relative colonization (mg/m}^2\text{)} = \frac{[\text{chl } a] \times 26.7 \times 1 \text{ L water}}{\text{rock surface area in m}^2}$$

where 26.7 is the absorption correction.

Sampling of Macroinvertebrates

At each site, riffle areas, characterized by shallow depth and fast flow, were identified and chosen for sampling of macroinvertebrates. Riffles feature optimal substrate for clinging, current velocity for food catchment, and dissolved oxygen, among other factors (Brown and Brown 1984), thus giving the greatest insight into the extent of diversity at a site.

Macroinvertebrates were collected in accordance with the state of Tennessee's Standard Operating Procedure for Macroinvertebrate Stream Surveys (TDEC 2017). This requires sampling from two riffles using a 1 m² kicknet and a two-person sampling team (Fig. 3); one member of the team holds the net in such a way that it impedes the downstream flow of water while the second member, standing upstream of the net, disrupts the substrate by dislodging gravel, cobble, and boulders, effectively dislodging any organisms present and allowing them to flow into the kicknet. The kicknet was then rinsed in a sieve bucket and the sample transferred into a 1000 mL Nalgene container with 70% isopropyl alcohol.



Figure 3. A characteristic riffle habitat sampled by a two-person kick team using a 1 m² kicknet.

Due to the unusually high rainfall during the winter of 2018, sampling efforts during senescence were limited to small windows between when the water levels retreated and the next rain event occurred. Because of this time constraint, we were unable to sample the Barnett Bridge site (hydrilla absent) for macroinvertebrates and periphyton during the senescent season. This site was, however, included in nutrient and abiotic analysis.

Processing of Macroinvertebrates

Macroinvertebrate samples were processed following the same protocols (Division of Water Resources 2017). Each site's sample bottle was emptied into a gridded pan for subsampling (Fig. 4). The sample material was removed from four randomly selected cells. The

contents of these four cells were hand-sorted to remove debris and isolate macroinvertebrates. If the cumulative number from these four cells is less than 160 (i.e., 200 minus 20%) additional cells are selected at random and picked until the target of $200 \pm 20\%$ is achieved. If the initial count exceeded 240 (i.e., 200 plus 20%), the macroinvertebrates were placed again in the gridded pan and the procedure for the rough sample (i.e., randomly chosen cells) was repeated until macroinvertebrates totaled fell within the 160-240 allotted total.

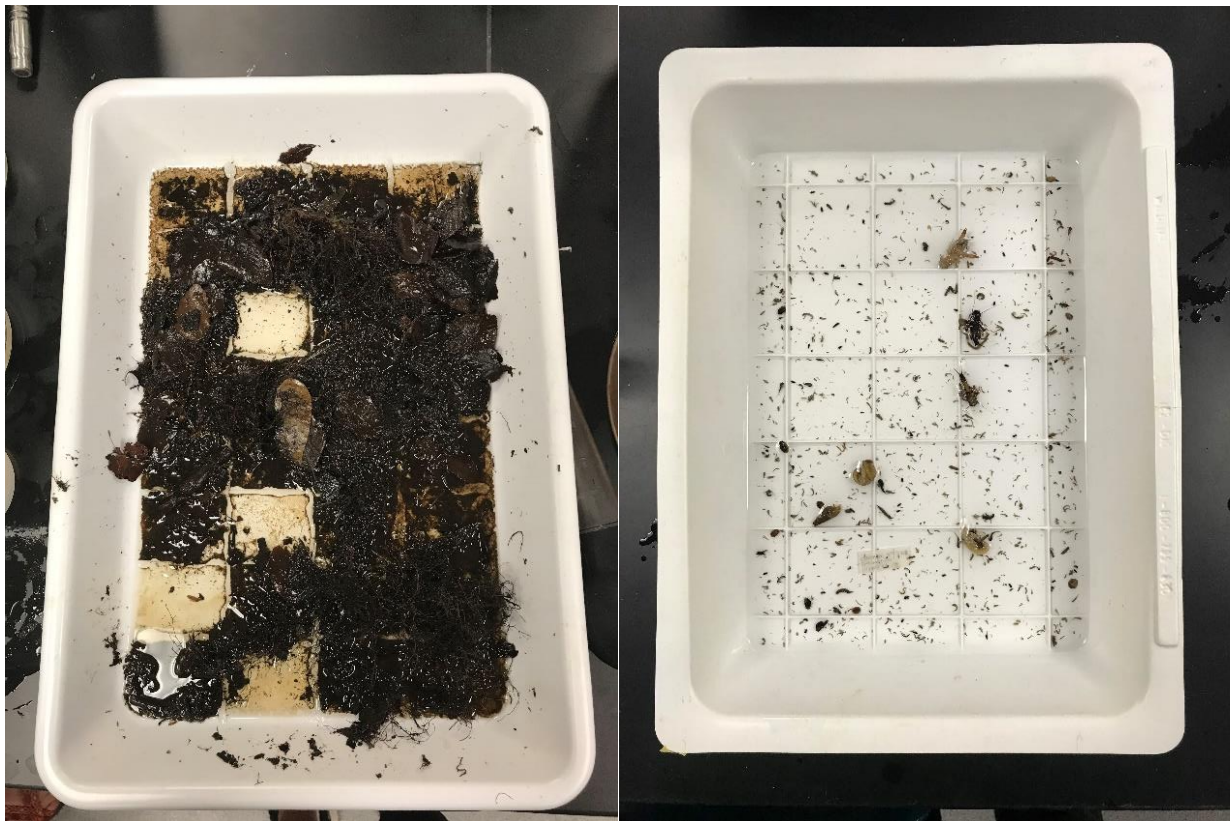


Figure 4. Initial rough sample emptied into gridded pan with four random cells chosen and removed for sorting (left); post-sort subsampling grid of macroinvertebrates for a $200 \pm 20\%$ pick (right).

Individuals from the subsample were identified to genus or lowest practical taxonomic unit. Diptera pupae were identified to order and Trichoptera pupae to family. Oligochaetes and snails were identified only to subclass and class levels, respectively. Taxonomic identification of non-biting midges, family Chironomidae (Diptera) required slide-mounting of larvae using CMC-10 mounting media (Masters Company, Inc., Wood Dale, IL).

Data Analyses

All statistical analyses including ANOVAs and contingency analyses were conducted using JMP® Pro 14® (SAS Institute Inc., Cary, NC). All other calculations were made in Microsoft Excel (Redmond, WA).

Abiotic measurements were analyzed via two-way ANOVA using a mixed-model approach to account for repeated measurements. Effects of season, status of hydrilla, or interaction between the two were tested. In order to rule out light availability by way of open canopy as a confounding factor influencing periphytic growth, I conducted linear regression of canopy coverage by periphytic biomass.

Orthophosphate, nitrate/nitrite, and relative colonization of periphyton (mg/m^2) were all analyzed by two-way ANOVA using the mixed model approach. Box plots were constructed to visualize effects of treatments, and bar graphs were created to associate values by site. Periphyton colonization of cobble in pools and riffles was analyzed separately.

Macroinvertebrates were identified to genus or lowest practical taxonomic unit using published taxonomic keys (Epler 2010, Merritt et al. 2008, Morse et al. 2017, Smith 2001, Wiederholm 1983). Identifying macroinvertebrates to taxonomic units allowed us to calculate the following seven metrics outlined in Protocol K, Data Reduction of Semi-Quantitative Samples (TDEC 2017): taxa richness (TR), EPT richness (EPT), EPT abundance minus *Cheumatopsyche* (%EPT-Cheum), percent clingers minus *Cheumatopsyche* (%Clingers-Cheum), percent oligochaetes and chironomids (%OC), percent nutrient-tolerant organisms (%Tnutol), and North Carolina Biotic Index (NCBI). TR is the total number of distinct taxa in a subsample, whereas EPT is the total number of distinct taxa that belong to the orders Ephemeroptera, Plecoptera, and Trichoptera, three groups that, as a whole, are relatively intolerant of low-quality stream conditions (Lenat 1993). The second metric, %EPT-Cheum, is the proportion of EPT individuals excluding *Cheumatopsyche*, a relatively tolerant trichopteran. The %Clingers-Cheum metric refers to the proportion of individuals in taxa that are characterized by their habit of clinging to substrata; low numbers of these individuals are an indicator of overgrowth of periphyton and/or sedimentation. Again, the more tolerant *Cheumatopsyche* are not included.

In contrast, %OC is the proportion of these more-tolerant individuals of annelid class Oligochaeta and dipteran family Chironomidae, and %Tnutol is the proportion of individuals in the following taxa considered to be tolerant of poor water quality (nutrient tolerant) conditions: *Cheumatopsyche*, *Stenelmis*, *Polypedilum*, *Cricotopus*, *Cricotopus/Orthocladius*, *Lirceus*, *Caenis*, Gastropoda, and Oligochaeta. Finally, NCBI is a calculation of the overall biotic condition of a sample based on taxa having various tolerance values to poor stream conditions. The NCBI represents the weighted average community tolerance.

These seven biometrics are scored from 0 (highly impacted conditions) to 6 (exceptional conditions) and culminate in a Tennessee Macroinvertebrate Index (TMI) for the stream segment where a score of 32 or greater indicates that the stream segment meets biocriteria established for Ecoregion 68A (TDEC 2017).

In order to further assess community structure, Shannon's Diversity Index and Pielou's evenness were calculated. Shannon's Diversity Index (H') is a measure of diversity in a sample that considers the number of taxa and the proportional representation of each taxon. It is calculated by the following formula (Shannon and Weaver 1949):

$$H' = -\sum[p_i \times \ln(p_i)]$$

where p_i is the proportion of individuals belonging to taxon i . The higher the H' value, the more diverse the sample. Value approaching zero indicates no diversity while highest diversity can be anywhere from 3.5 to greater than 4.

Pielou's evenness (J') is a measure of how evenly the individuals in a sample are distributed among the taxa. Once the abundance of each taxon present is known, evenness is calculated by the following formula (Pielou 1969):

$$J' = \frac{H'}{H'_{max}}$$

where H' is Shannon's Diversity Index and H'_{max} is the highest Shannon's Diversity Index value if each taxon observed was equally likely to be chosen. Richness, H' , and J' values were

averaged by treatment group and tested statistically via Two-Way ANOVA using the mixed-model approach.

To assess community function, taxa were categorized into trophic guilds known as functional feeding groups (FFGs) based on their mode of food acquisition; these categories include collector-filterer, collector-gatherer, grazer/scrapper, piercer-herbivore, predator, and shredder (Cummins 1995). A multi-way contingency analysis was conducted to assess differences in FFG proportions among the treatments. A mosaic plot was created to demonstrate the FFG make-up.

Morisita's Index of Community Similarity (I_m) and Analysis of Similarity (ANOSIM) were used to assess similarities in taxa composition among the study sites. Morisita's Index uses pair-wise comparisons to test how similar or different two datasets are; to calculate I_m , the following formula is used (Horn 1977, Morisita 1959):

$$I_m = \frac{2\sum x_i y_i}{(l_1 + l_2)XY}$$

Where x_i and y_i are the number of individuals of taxon i , l_1 and l_2 are the Simpson's dominance index values, and X and Y are the total number of individuals of all taxa in samples 1 and 2, respectively. Simpson's dominance for each sample is calculated using the following equation:

$$l_1 = \frac{\sum (x_i - 1)}{X(X - 1)}$$

Where x_i is the number of individuals in taxon i and X is the total number of individuals belonging to all taxa in a sample. An I_m value of 1 would indicate that samples 1 and 2 were

identical and share all the same taxa in equal proportions; a value of 0 would indicate that the samples were entirely different and share none of the same taxa. Differences in average pairwise comparisons were assessed by one-way ANOVA split by season to avoid violation of assumptions established by the statistical test.

Analysis of Similarity (ANOSIM) is a non-parametric test that analyzes whether two groups show greater similarity in taxa between one another as within one another; the null hypothesis would be that communities showed greater or equal similarity between groups than within groups (Clarke 1993). Communities were analyzed for three factors: sampling season, status of hydrilla, and site. ANOSIM was conducted using R Studio.

RESULTS

Table 1. Resulting averages and ANOVA output for abiotic data (pH, dissolved oxygen, temperature, and specific conductivity) for growing and senescent seasons and with or without hydrilla presence in the Emory River Watershed, Tennessee. Measurements collected using YSI 600QS multiparameter meter. Asterisk (*) indicates $p < 0.05$.

Variable	Season	Hydrilla status	Average	DF	Effect of season		Effect of status		Effect of season*status	
					F	P	F	P	F	P
pH	Growing	Present	7.45	1	0.024	0.885	0.129	0.728	2.058	0.177
		Absent	7.03							
	Senescent	Present	7.15							
		Absent	7.22							
Dissolved oxygen (% saturation)	Growing	Present	105.03	1	5.209	0.074	1.532	0.247	3.63	0.118
		Absent	95.50							
	Senescent	Present	97.35							
		Absent	94.41							
Temperature (°C)	Growing	Present	22.99	1	375.085	<0.0001*	1.252	0.293	0.574	0.467
		Absent	22.78							
	Senescent	Present	9.13							
		Absent	7.84							
Conductivity (mS/cm)	Growing	Present	0.17	1	10.912	0.0311*	2.903	0.141	2.135	0.220
		Absent	0.09							
	Senescent	Present	0.07							
		Absent	0.05							

Canopy coverage was higher at upstream sites than downstream sites and during the growing season than the senescent season (Table 2).

Table 2. Percent canopy coverage of sampling sites, listed from upstream to downstream, during the growing and senescent seasons in the Emory River Watershed, Tennessee. Measured via convex spherical densiometer. Asterisk (*) indicates hydrilla presence.

Site	Canopy coverage (%) during the growing season	Canopy coverage (%) during the senescent season
Rhea Road	96.7	62.8
Old Highway 28*	62.8	47.8
Highway 68	50.1	34.1
I-40*	51.7	48.2
Chestnut Hill*	41.0	40.0
Antioch Bridge*	23.7	38.5
Lilly Bridge	20.1	48.9
Barnett Bridge	26.7	N/A

Nutrient Concentrations

Two-Way ANOVA indicated no significant effect of hydrilla presence on orthophosphate concentrations ($F_{1,6}=1.821$, $p=0.226$). Season was also not a significant factor on orthophosphate concentrations ($F_{1,6}=4.706$, $p=0.073$), though we see a trend towards higher concentrations during the growing season (Fig. 5). The interaction between season and presence of hydrilla was not found to be a significant factor ($F_{1,6}=1.879$, $p=0.220$).

Season was found to be a significant factor on nitrate/nitrite concentrations ($F_{1,6}=8.395$, $p=0.027$) with higher concentrations during the senescent season rather than the growing season (Fig. 6). Neither hydrilla presence ($F_{1,6}=0.422$, $p=0.540$) nor its interaction with season ($F_{1,6}=1.495$, $p=0.267$) were shown to be significant factors affecting nitrate/nitrite.

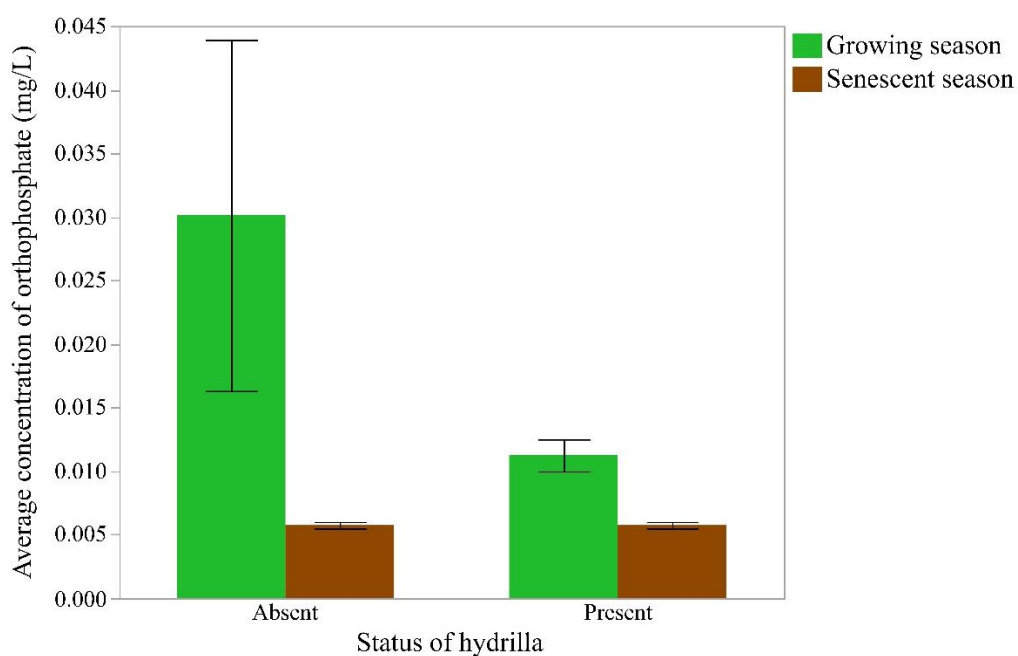


Figure 5. Concentrations of orthophosphate (mg/L) in stream water samples by status and season of hydrilla collected in the Emory River Watershed, Tennessee. Bars indicate standard error.

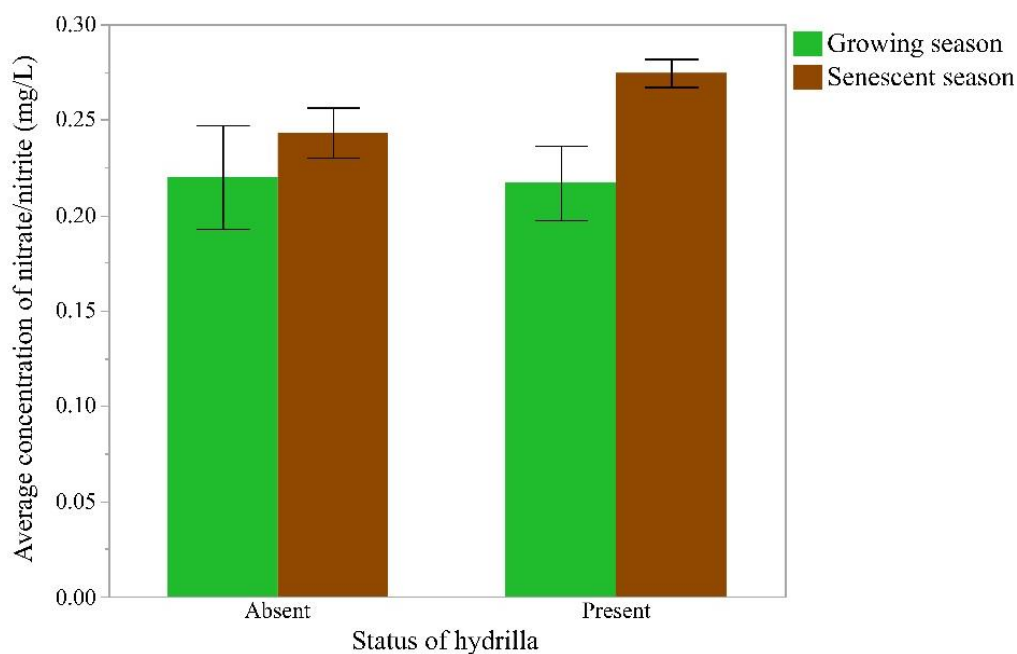


Figure 6. Concentrations of nitrate/nitrite (mg/L) in stream water samples by status and season of hydrilla collected in the Emory River Watershed, Tennessee. Bars indicate standard error.

Periphyton

There were no significant effects of season ($F_{1,5}=2.716$, $p=0.160$), hydrilla presence ($F_{1,5}=1.304$, $p=0.305$), nor an interaction between the two ($F_{1,5}=0.582$, $p=0.305$) on periphyton colonization of pool cobble (Fig. 7). However, season was a significant factor affecting periphyton colonization on riffle cobble ($F_{1,5}=24.234$, $p=0.004$); greater colonization was found on riffle cobble during the growing season. Hydrilla presence ($F_{1,5}=5.816$, $p=0.061$) and the interaction of the two ($F_{1,5}=5.240$, $p=0.071$) were not significant, but a trend towards greater periphyton colonization on riffle cobble at hydrilla sites during the growing season was observed (Fig. 8).

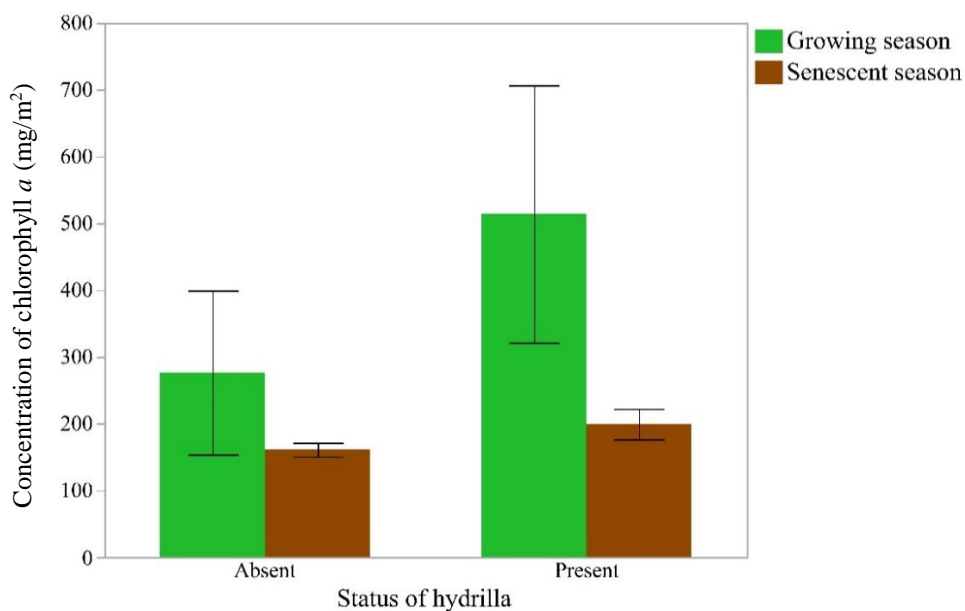


Figure 7. Concentrations of chlorophyll *a* (mg/m²) scraped from pool cobble by status and season of hydrilla. Collected in the Emory River Watershed, Tennessee and measured using digital fluorimeter with size corrections made using the foil weight method. Bars indicate standard error.

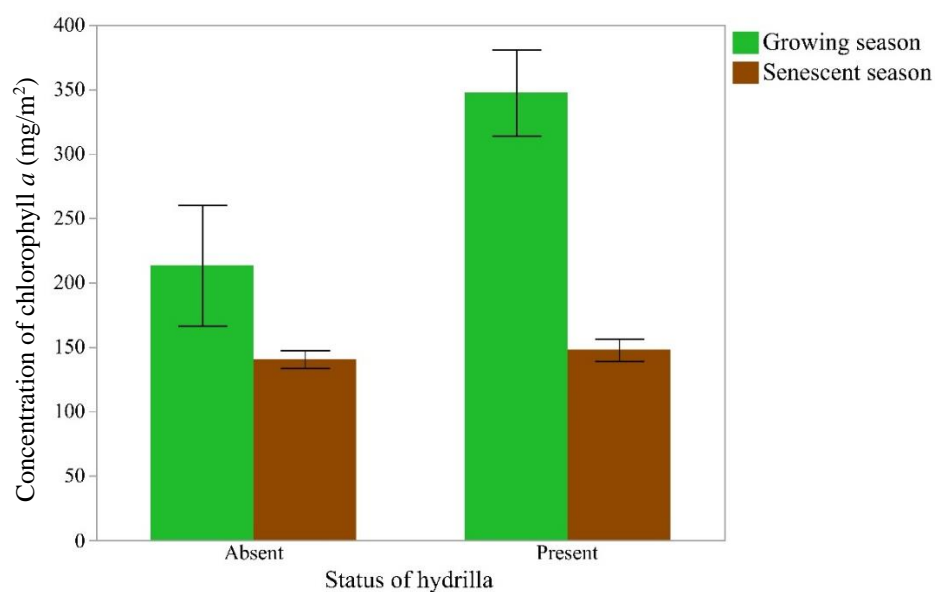


Figure 8. Concentrations of chlorophyll *a* (mg/m²) scraped from riffle cobble by status and season of hydrilla. Collected in the Emory River Watershed, Tennessee and measured using digital fluorimeter with size corrections made using the foil-weight method. Bars indicate standard error.

No significant relationship of chlorophyll *a* with canopy coverage was established for riffle (Fig. 9) or pool cobble (Fig. 10) when the two variables were regressed.

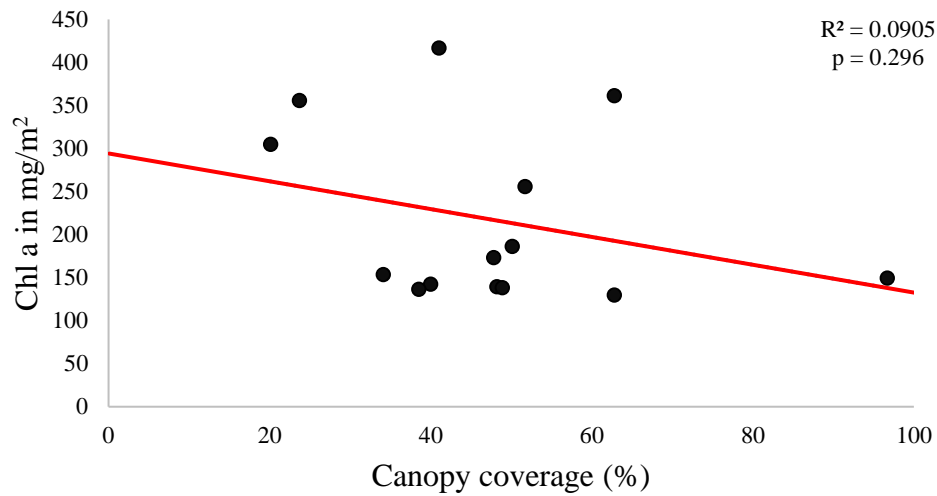


Figure 9. Scatterplot of the relationship between each sample site's canopy coverage and the resulting periphytic growth on riffle cobble. Growing and senescent seasons are plotted together.

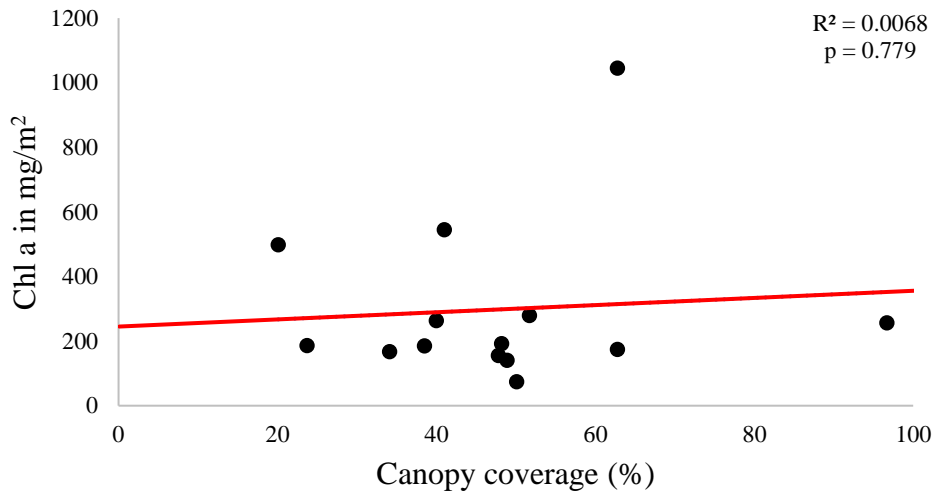


Figure 10. Scatterplot of the relationship between each sample site's canopy coverage and the resulting periphytic growth on pool cobble. Growing and senescent seasons are plotted together.

Macroinvertebrate Diversity

A total of 2,960 individuals comprising 89 taxonomic units were processed and identified. The site with the highest total richness during the growing and senescent seasons was Antioch Bridge, a hydrilla site, with a total of 39 unique taxa during either season (Fig. 11).

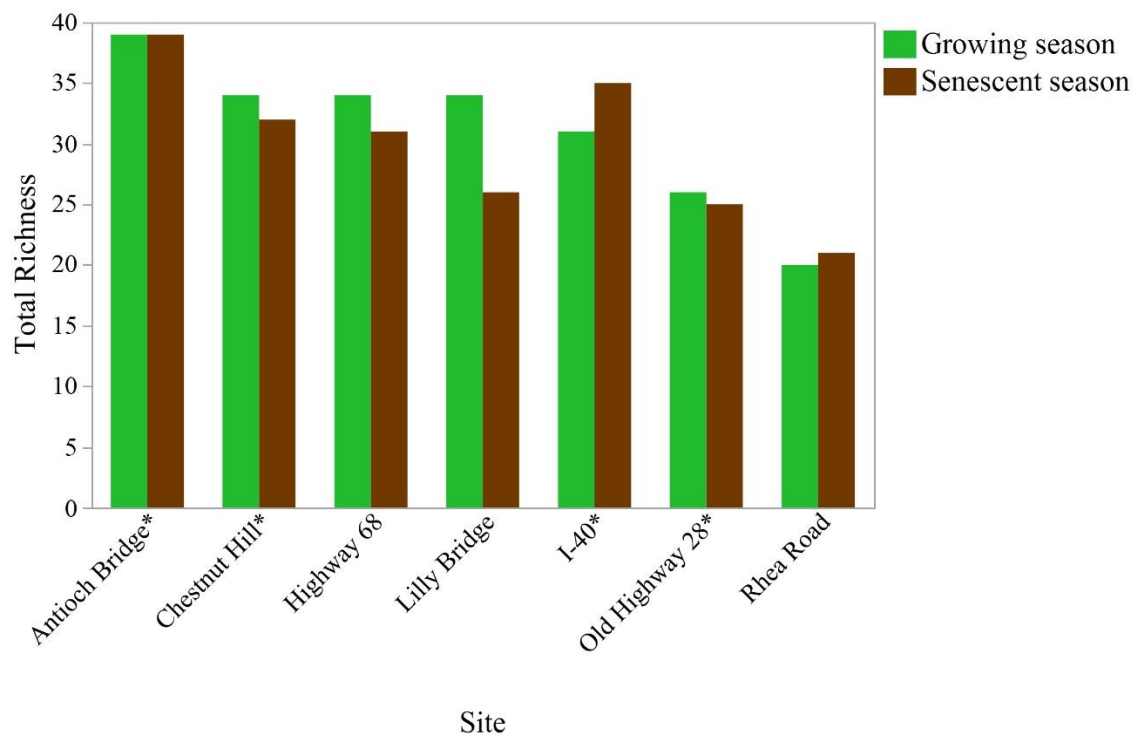


Figure 11. Total richness of macroinvertebrate taxa in subsamples sorted from samples collected at each field site in the Emory River Watershed, Tennessee during both growing and senescent seasons. Asterisk (*) indicates hydrilla presence.

Greater richness was observed during the growing season rather than the senescent and at hydrilla sites rather than at non-hydrilla sites. The highest mean richness was observed at hydrilla sites during the senescent season (Fig. 12). Despite these differences in means, neither

season ($F_{1,5}=1.327$, $p=0.302$), nor hydrilla presence ($F_{1,5}=1.226$, $p=0.319$), nor an interaction of both ($F_{1,5}=1.792$, $p=0.238$) were found to be significant factors.

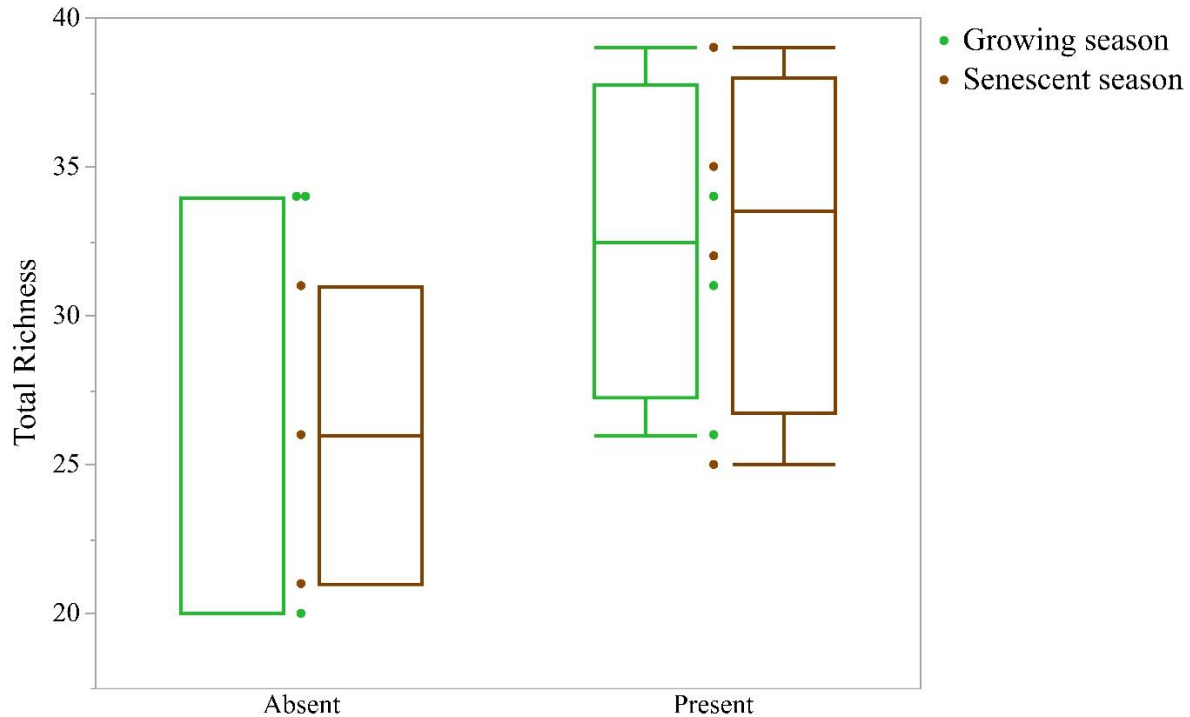


Figure 12. Total richness of macroinvertebrate community in the Emory River Watershed, Tennessee by status of hydrilla and season of collection. Box plots indicate minimum and maximum values, 25 and 75% quartiles, and the mean.

The site with the highest taxa evenness during the growing season was Chestnut Hill, a hydrilla site, with a value of 0.88 and during the senescent season was I-40, a hydrilla site, with a value of 0.86 (Fig. 13). Higher evenness was observed during the growing season rather than the senescent and with hydrilla presence rather than in hydrilla absence. The highest evenness was found at hydrilla sites during the growing season (Fig. 14).

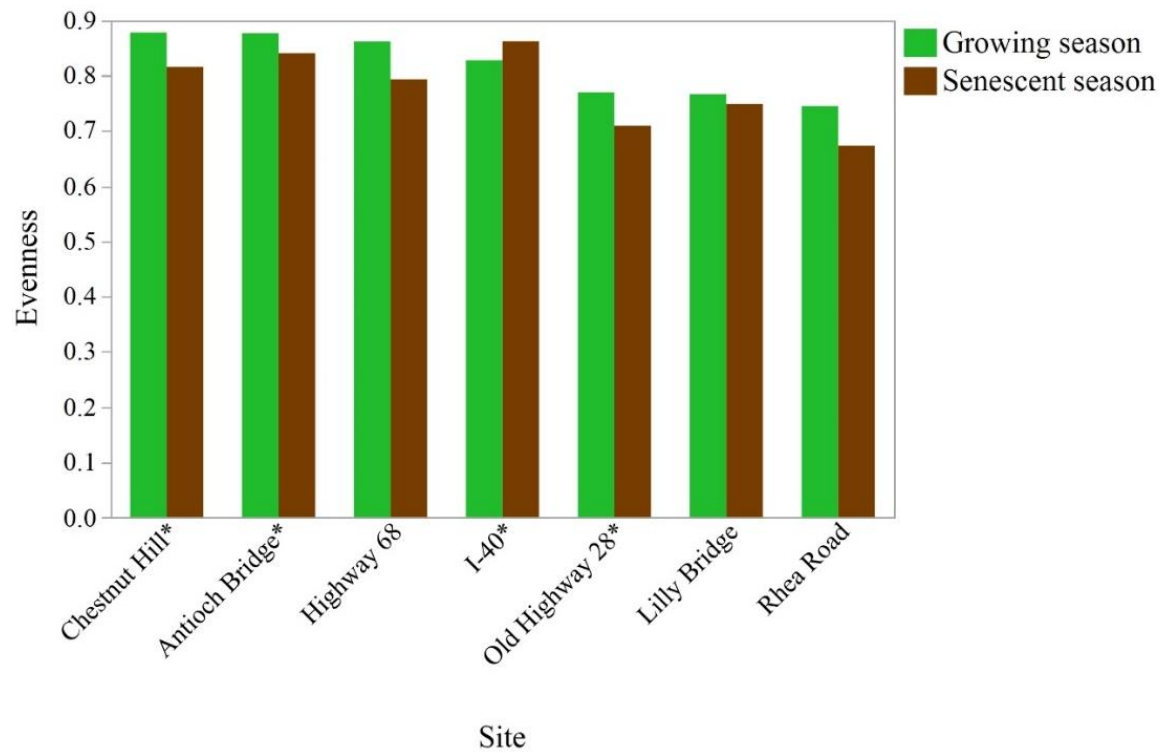


Figure 13. Evenness of macroinvertebrate community in subsamples sorted from samples collected at each field site in the Emory River Watershed, Tennessee during both growing and senescent seasons. Asterisk (*) indicates hydrilla presence.

When analyzed via Two-way ANOVA, season was a significant factor with higher evenness observed during the growing season ($F_{1,5}=7.535$, $p=0.041$). Neither hydrilla presence ($F_{1,5}=1.752$, $p=0.243$) nor its interaction with season ($F_{1,5}=0.494$, $p=0.514$) were found to be significantly different.

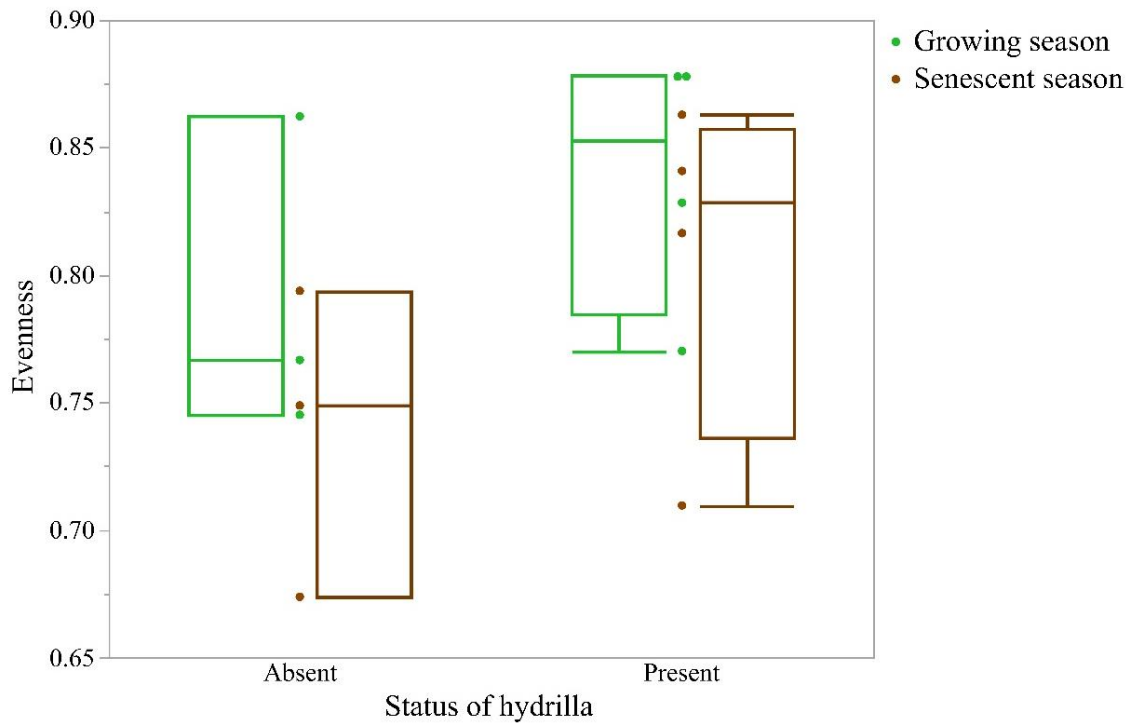


Figure 14. Evenness of macroinvertebrate community in the Emory River Watershed, Tennessee by status of hydrilla and season of collection. Box plots indicate minimum and maximum values, 25 and 75% quartiles, and the mean.

The site with the highest Shannon's Diversity (H') during both the growing and senescent seasons was Antioch Bridge, a hydrilla site, at 3.21 and 3.08, respectively (Fig. 15). There was higher diversity observed during the growing season rather than the senescent season and with hydrilla presence rather than without. The treatment with the highest average H' was hydrilla presence during the growing season (Fig. 16).

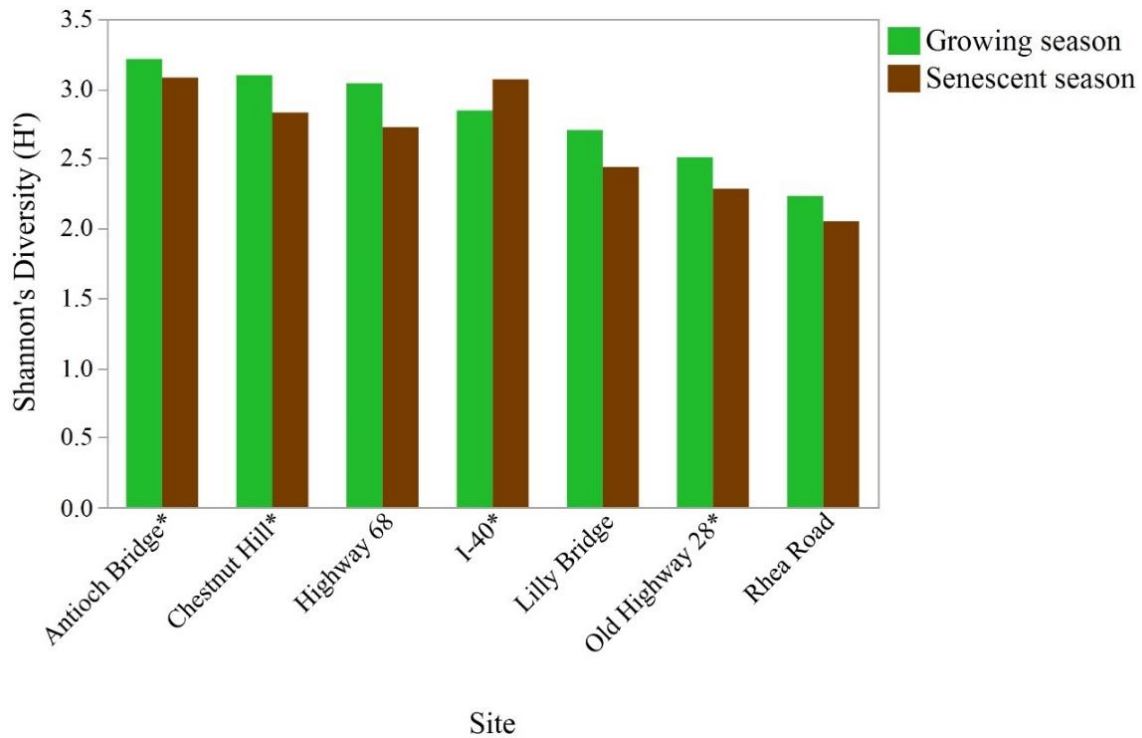


Figure 15. Shannon's Diversity (H') for macroinvertebrate community in subsamples sorted from samples collected at each field site in the Emory River Watershed, Tennessee during both growing and senescent seasons. Asterisk (*) indicates hydrilla presence.

Two-way ANOVA indicated a significant difference in season ($F_{1,5}=6.778$, $p=0.048$), with higher diversity observed during the growing season. Hydrilla presence ($F_{1,5}=1.607$, $p=0.261$) and the interaction ($F_{1,5}=1.252$, $p=0.314$) were not significant factors.

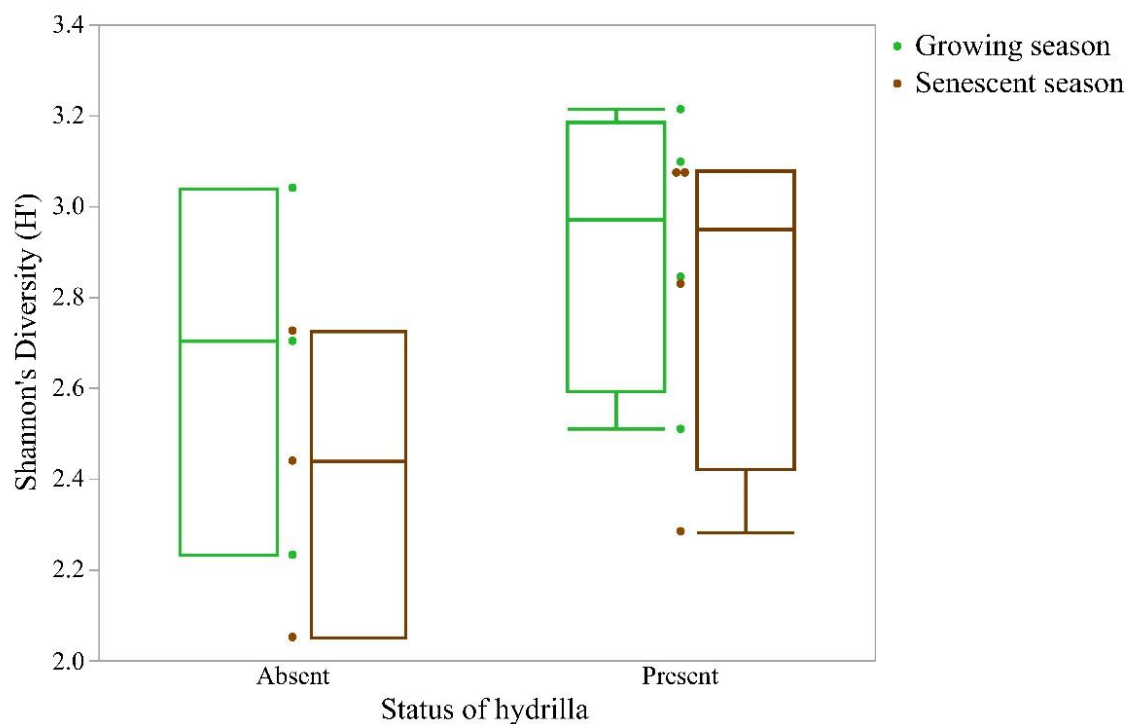


Figure 16. Shannon's Diversity (H') for macroinvertebrate community in the Emory River Watershed, Tennessee by status of hydrilla and season of collection. Box plots indicate minimum and maximum values, 25 and 75% quartiles, and the mean.

EPT Richness and Abundance

The highest EPT richness was observed at Lilly Bridge, a non-hydrilla site, at 21 taxa during the growing season and at Antioch Bridge, a hydrilla site, at 17 taxa during the senescent season (Fig. 17).

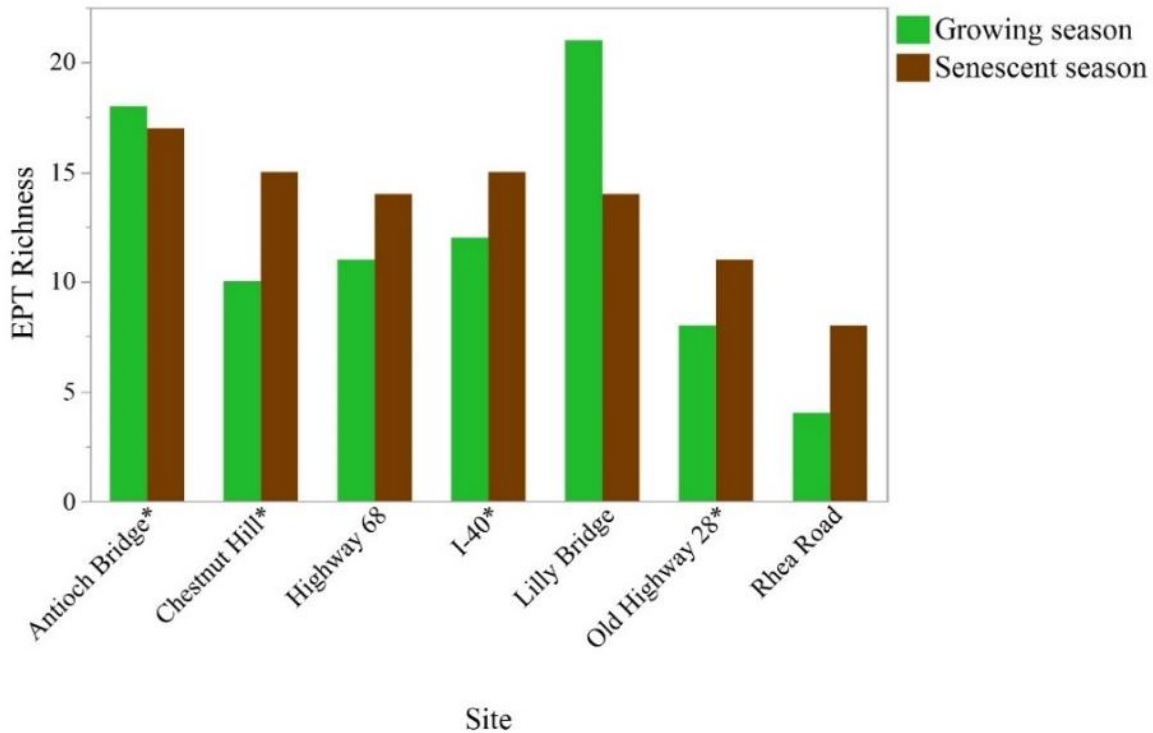


Figure 17. EPT richness of macroinvertebrate community in subsamples sorted from samples collected at each site in the Emory River Watershed, Tennessee during both growing and senescent seasons. Asterisk (*) indicates hydrilla presence.

On average, higher EPT richness was observed during the senescent season rather than the growing season and with hydrilla rather than without. The highest EPT richness was found at hydrilla sites during the senescent season (Fig. 18). Two-way ANOVA indicated no significant effects of season ($F_{1,5}=0.576$, $p=0.482$), hydrilla presence ($F_{1,5}=0.135$, $p=0.728$), nor an interaction between the two ($F_{1,5}=0.576$, $p=0.482$) on EPT richness.

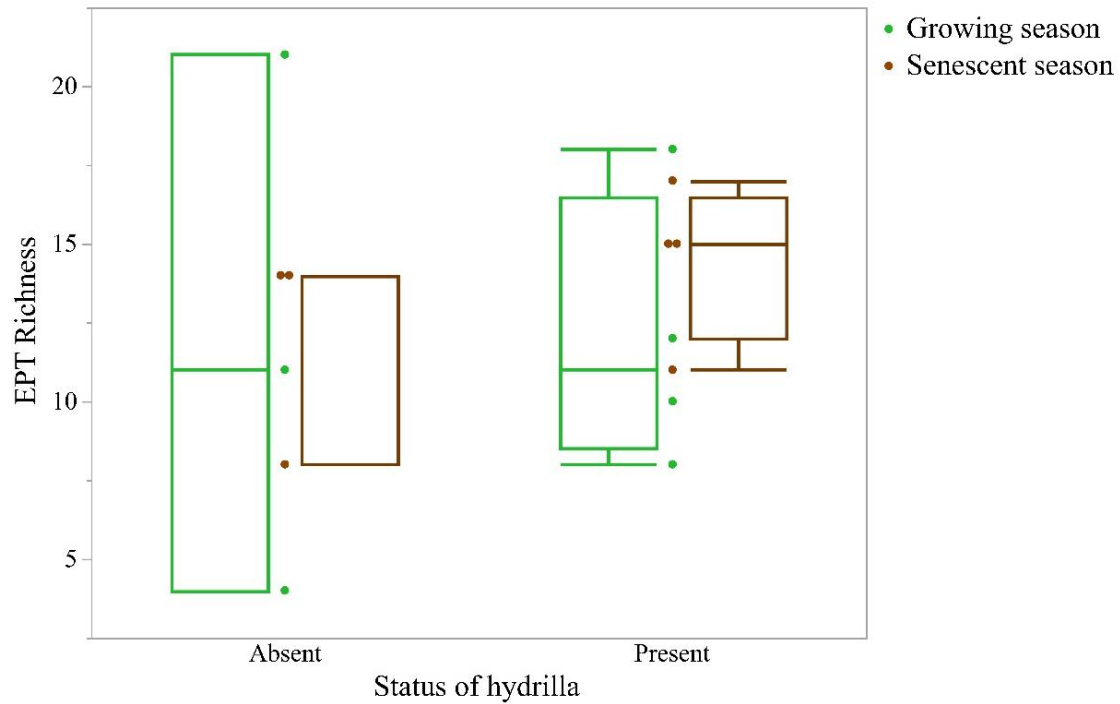


Figure 18. EPT richness of macroinvertebrate community in the Emory River Watershed, Tennessee by status of hydrilla and season of collection. Box plots indicate minimum and maximum values, 25 and 75% quartiles, and the mean.

The highest EPT abundance during the growing season was found at Old Highway 28, a hydrilla site, at 55%; the highest abundance during the senescent season was found at Lilly Bridge, a non-hydrilla site, at 71% (Fig. 19). EPT abundance was higher during the senescent season rather than during the growing season and at hydrilla sites rather than non-hydrilla sites. The treatment with the highest average EPT abundance was hydrilla absence during the senescent season (Fig. 20). Two-way ANOVA indicated no significant effects of season ($F_{1,5}=1.413$, $p=0.288$), presence of hydrilla ($F_{1,5}=0.029$, $p=0.870$), nor an interaction between the two ($F_{1,5}=1.028$, $p=0.357$) on EPT abundance.

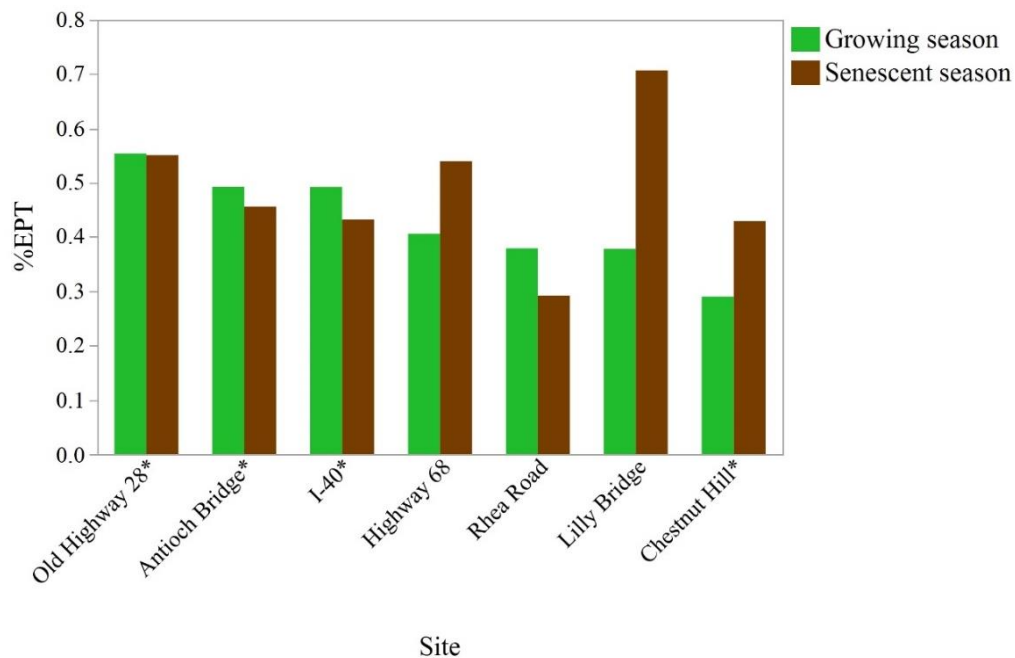


Figure 19. EPT abundance in macroinvertebrate community in subsamples sorted from samples collected at each field site in the Emory River Watershed, Tennessee during both growing and senescent seasons. Asterisk (*) indicates hydrilla presence.

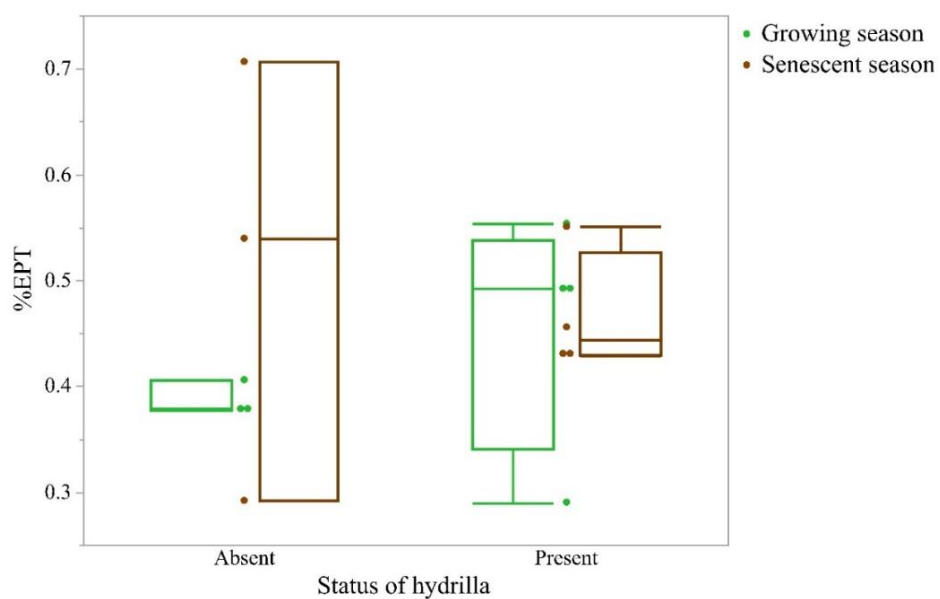


Figure 20. EPT abundance of macroinvertebrate community in the Emory River Watershed, Tennessee by status of hydrilla and season of collection. Box plots indicate minimum and maximum values, 25 and 75% quartiles, and the mean.

Biometric Scores and TMI

The stream segment with the lowest TMI during the growing and senescent seasons was Rhea Road at 16 and 26, respectively (Table 3). The site with the highest TMI was Antioch Bridge, a hydrilla site, during the growing season and I-40, a hydrilla site, during the senescent season, both having scores of 38. All sites met the biocriteria of the ecoregion except for Rhea Road (both seasons), Highway 68 (senescent season), and Chestnut Hill (growing season).

Table 3. Biometric scores resulting in a Tennessee Macroinvertebrate Index (TMI) for each site in the Emory River Watershed, Tennessee during the growing season and senescent seasons. Small numbers to the top left are raw values; large numbers centered are biometric scores. A TMI score of 32 or higher indicates that the site meets the biocriteria set for the ecoregion; red text indicates sites that did not met these requirements. Asterisk (*) indicates hydrilla presence.

Site	Season	TR	EPT	NCBI	%TnutoI	%Clingers- Cheum	%EPT- Cheum	%OC	TMI							
Rhea Road	Growing	20	2	4	5.19	4	56.0	2	25.8	2	12.6	0	27.5	6	16	
	Senescent	21	2	4	5.43	4	21.5	6	41.1	4	26.8	2	25.8	6	26	
Old Highway 28*	Growing	26	4	8	2	4.48	6	17.2	6	67.0	4	47.6	6	19.3	6	34
	Senescent	25	4	11	4	4.86	4	22.7	6	64.8	6	34.8	4	10.5	6	34
Highway 68	Growing	34	4	11	4	4.73	6	20.3	6	40.1	4	36.6	4	23.3	6	34
	Senescent	31	4	14	6	4.90	4	28.7	4	58.4	2	40.1	4	8.9	6	30
I-40*	Growing	31	4	12	4	4.29	6	24.9	6	52.3	4	41.5	4	11.4	6	34
	Senescent	35	6	15	6	5.42	4	25.2	6	49.1	6	36.5	4	21.2	6	38
Chestnut Hill*	Growing	34	4	10	4	4.96	6	34.9	4	57.4	4	28.7	2	23.7	6	30
	Senescent	32	4	15	6	5.00	4	25.2	6	61.0	6	34.6	4	17.7	6	36
Antioch Bridge*	Growing	39	6	18	6	5.12	4	30.2	6	71.4	6	43.7	4	14.6	6	38
	Senescent	39	6	17	6	5.45	4	27.9	6	44.1	4	42.6	4	21.6	6	36
Lilly Bridge	Growing	34	4	21	6	4.50	6	42.3	4	79.1	6	35.8	4	7.5	6	36
	Senescent	26	4	14	6	5.00	4	14.4	6	35.1	4	70.7	6	19.7	6	36

Functional Feeding Groups

Multi-way contingency analysis revealed significant differences in proportion of functional feeding groups with hydrilla presence and between seasons (Fig. 21; $X^2=477.506$, $p<0.0001$). Proportionally more collector-filterers and shredders were collected during the senescent season, while there were greater proportions of collector-gatherers, predators, and grazer/scrapers during the growing season. There were greater proportions of collector-filterers and grazer-scrapers at hydrilla sites during both seasons, with the greatest proportion of grazer/scrapers at hydrilla sites during the growing season. Predators and piercer-herbivores were proportionally equal on average between hydrilla and non-hydrilla sites.

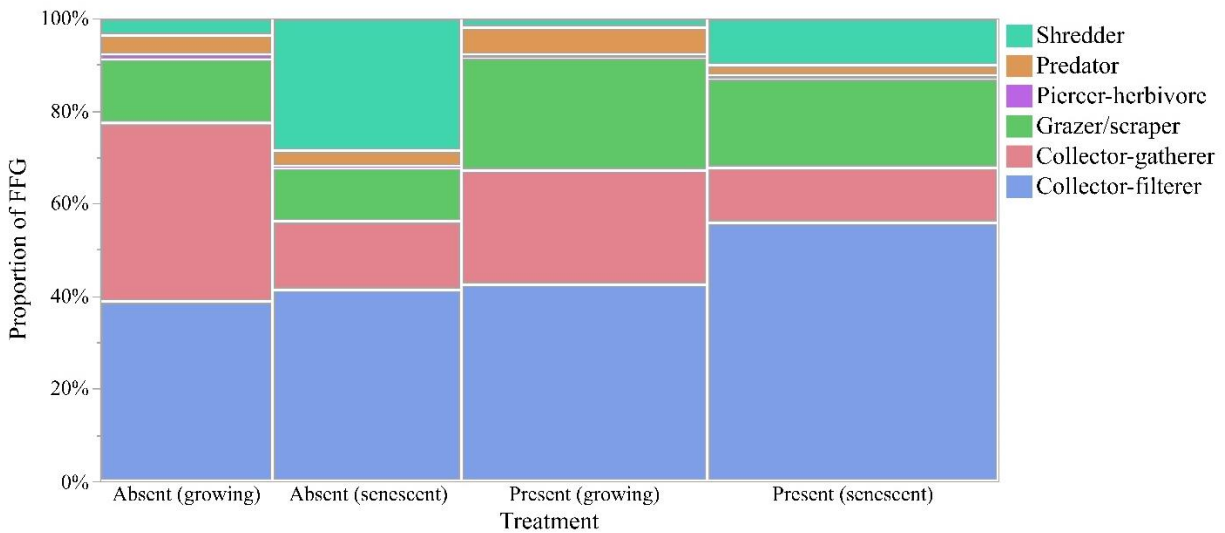


Figure 21. Mosaic plot depicting average proportions of FFGs characterizing macroinvertebrate communities in the Emory River Watershed, Tennessee by the following treatment groups: hydrilla-absent during the growing season, hydrilla-absent during the senescent season, hydrilla-present during the growing season, hydrilla-present during the senescent season.

Analysis of Community Similarity

The sites with the highest Morisita's Index (I_m) values indicating highest community overlap during the growing season were Chestnut Hill and I-40, both hydrilla sites, with an I_m value of 0.79 (Table 4). The sites with the lowest community overlap during the growing season were Highway 68 and Lilly Bridge, both non-hydrilla sites, with an I_m value of 0.11. The sites with the highest community overlap during the senescent season were Chestnut Hill and I-40, both hydrilla sites, and Antioch Bridge and I-40, both hydrilla sites, each pair-wise comparison having an I_m value of 0.93 (Table 5). The sites with the lowest community overlap during the senescent season were Old Highway 28, a hydrilla site, and Lilly Bridge, a non-hydrilla site, with an I_m value of 0.19. Hydrilla sites were more similar to each other than non-hydrilla sites were during both the growing and senescent seasons; hydrilla sites showed greater similarity to non-hydrilla sites during the senescent season than the growing season (Fig. 22).

Table 4. Pair-wise comparisons of sites in the Emory River Watershed, Tennessee showing Morisita's Index of Community Overlap (I_m) during the growing season. Asterisk (*) indicates hydrilla presence.

Site (Growing Season)	Rhea Road						
Rhea Road		Highway 68					
Highway 68	0.32		Lilly Bridge				
Lilly Bridge	0.16	0.11		Old Highway 28*			
Old Highway 28*	0.45	0.47	0.26		I-40*		
I-40*	0.39	0.71	0.12	0.62		Chestnut Hill*	
Chestnut Hill*	0.41	0.72	0.33	0.60	0.79		Antioch Bridge*
Antioch Bridge*	0.32	0.52	0.57	0.74	0.54	0.69	

Table 5. Pair-wise comparisons of sites in the Emory River Watershed, Tennessee showing Morisita's Index of Community Overlap (I_m) during the senescent season. Asterisk (*) indicates hydrilla presence.

Site (Senescent Season)	Rhea Road						
Rhea Road		Highway 68					
Highway 68	0.54		Lilly Bridge				
Lilly Bridge	0.65	0.33		Old Highway 28*			
Old Highway 28*	0.63	0.76	0.19		I-40*		
I-40*	0.68	0.81	0.57	0.61		Chestnut Hill*	
Chestnut Hill*	0.80	0.88	0.49	0.77	0.93		Antioch Bridge*
Antioch Bridge*	0.72	0.70	0.70	0.47	0.93	0.86	

One-way ANOVA of pairwise comparisons resulting in Morisita's Index of Community Similarity showed a significant effect of comparison on macroinvertebrate community similarity ($F_{2,18}=9.998$, $p=0.0012$) during the growing season; hydrilla sites showed greater within-site similarity (present vs. present) than non-hydrilla sites (absent vs. absent). No significant effect of comparison was found in the senescent season. ANOSIM revealed a significant effect of season ($R=0.4956$, $p=0.001$), but the effect of hydrilla presence ($R=0.1473$, $p=0.078$) was not significant, though a marginal p-value suggests a trend for hydrilla sites showing greater similarity than non-hydrilla sites.

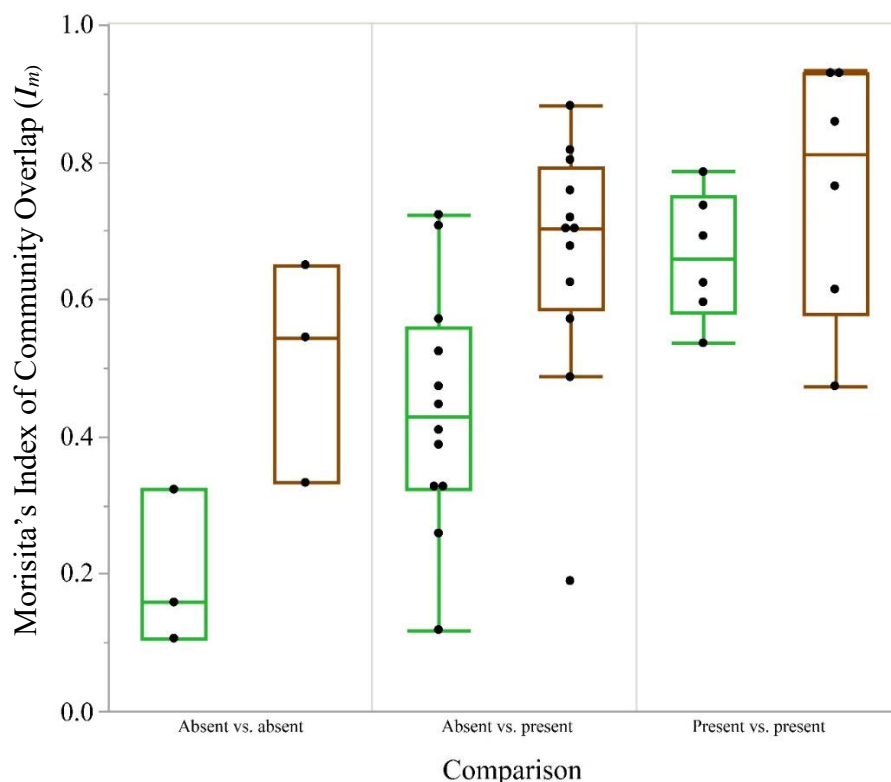


Figure 22. Morisita's Index of Community Similarity (I_m) values in the growing and senescent seasons for the following pairwise comparisons of the Emory River Watershed, Tennessee: hydrilla absent versus absent, hydrilla absent versus present, and hydrilla present versus present. Greater index values indicate greater similarity. Box plots indicate minimum and maximum values, 25 and 75% quartiles, and the mean.

DISCUSSION

For the study region, 2018 was a year of above-average rainfall (Table 6), which caused frequent fluctuations in discharge throughout the sampling seasons.

Table 6. Rainfall for Crossville, Tennessee in 2018 courtesy of U.S. Climate Data:

<<https://www.usclimatedata.com/climate/crossville/tennessee/united-states/ustn0122/2018/12>>
(Retrieved 18 Nov 2019).

Month	2018 precipitation (in)	Normal precipitation (in)
August	4.28	3.98
September	10.59	3.9
November	6.36	5.12
December	7.47	4.96

The summer growing season experienced moderate discharge peaks of 300-500 ft³/s and lows between 10-87.5 ft³/s (Fig. 23), while the fall senescent season experienced dramatic peaks of 967.6-2000 ft³/s and moderate low flows between 100-750 ft³/s (Fig. 24). Each sampling event occurred during a period of lowest flow immediately followed by storm-related high discharge. It is suspected that these water level fluctuations contributed to the results found in this study.

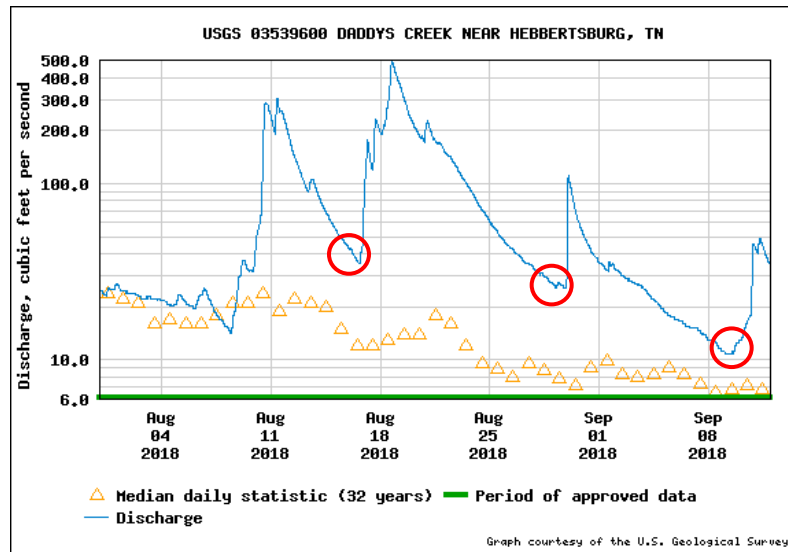


Figure 23. Hydrograph of water levels at Daddys Creek near Hebbertsburg, Tennessee, between July 31 and September 11 corresponding to the hydrilla growing season. Red circles indicate sample dates. Graph by U.S. Geological Survey:

https://waterdata.usgs.gov/nwis/uv?site_no=03539600 (Retrieved 20 Oct. 2019).

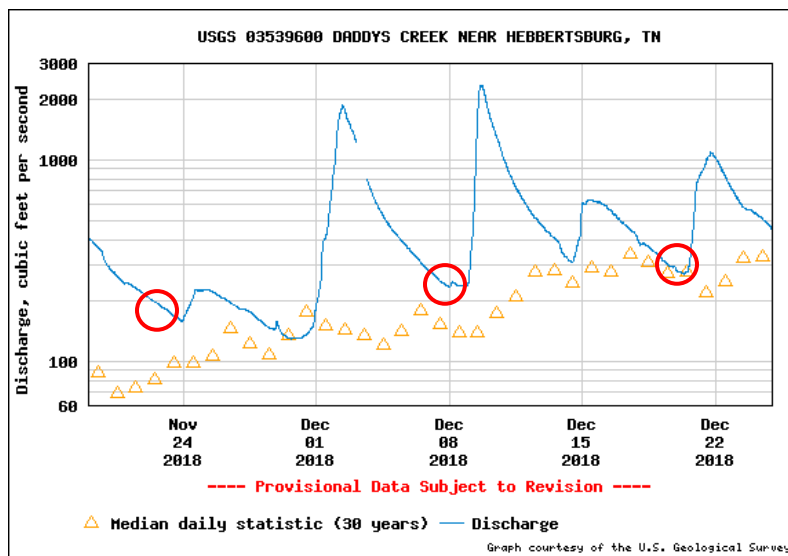


Figure 24. Hydrograph of water levels at Daddys Creek near Hebbertsburg, Tennessee, between November 19 and December 24 corresponding with the hydrilla senescent period. Red circles indicate sample dates. Graph by U.S. Geological Survey:

https://waterdata.usgs.gov/nwis/uv?site_no=03539600 (Retrieved 20 Oct. 2019).

The results of nutrient analysis did not show support for the first hypothesis, that nutrient concentrations at hydrilla sites would be products of the two phenological seasons. Specifically, the prediction was that concentrations of both orthophosphate and nitrate/nitrite would be higher during the senescent season due to senescing plant release of nutrients. Though effects of season on nutrient concentrations were observed, hydrilla sites did not differ significantly from non-hydrilla sites. There was a difference in how the two nutrients responded within each season; while nitrate/nitrite were significantly higher during the winter senescence as predicted, orthophosphate showed a trend towards higher concentration during the summer growing season. To interpret these inverse responses, the following hypotheses were formulated: the winter discharge/leaf fall hypothesis and the summer low-flow desiccation hypothesis.

Figure 25 depicts the discharge leaf fall hypothesis. Streams gain both allochthonous (riparian) input via leaf fall and autochthonous (in-stream) input via senescing macrophytes in the autumn and thus have decomposition occurring in the fall and winter. The higher nitrate/nitrite levels witnessed during the senescent season are likely the result of sustained nutrient release from decomposition of combined terrestrial and aquatic senescent vegetation (Berg and Staaf 1981). Phosphorus levels could be misrepresented in senescence samples due to faster assimilation rates (Landers 1982) coupled with dilution by greater flow in the winter brought on by stochastic and persistent weather occurrences. Though both summer and winter seasons in 2018 experienced water level fluctuations, only the winter season maintained high discharge rates that never dropped below 100 ft³/s (Fig. 24). The lowest flow period that allowed sampling in the winter season was at least ten times greater than the lowest flow during the summer sampling.

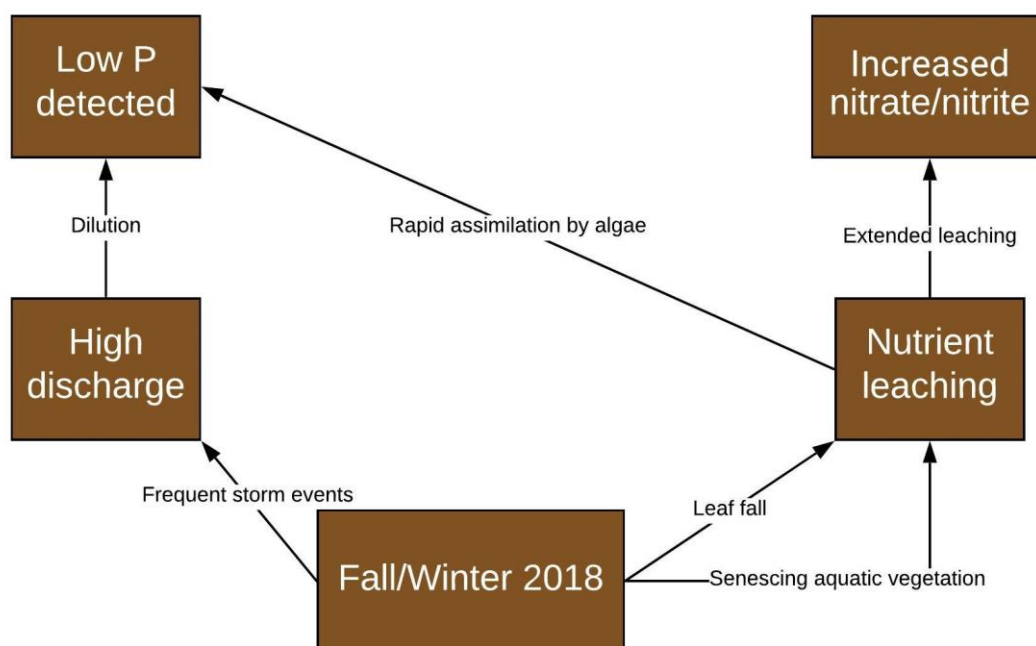


Figure 25. Discharge leaf fall hypothesis.

The low-flow desiccation hypothesis (Fig. 26) is an explanation that works with or without the discharge leaf fall hypothesis. Breakdown of plant matter, whether via allochthonous or autochthonous input, occurs in three phases: leaching of soluble materials followed by microbial decomposition and lastly mechanical breakdown via invertebrates (Webster and Benfield 1986). During the initial phase of leaching, nutrients differ in their release and assimilation rates. Phosphorus is released rapidly and mostly as orthophosphate (Carpenter 1980), which is quickly assimilated by algae (Landers 1982). Nitrogen, in contrast, is released more slowly (Nichols and Keeney 1973) and mostly as ammonium (Landers 1982), which is converted into nitrate and nitrite via nitrification. It is possible that the greater biologically-available phosphorus detected in the growing season is a product of several short-term nutrient-release events brought on by water level fluctuations.

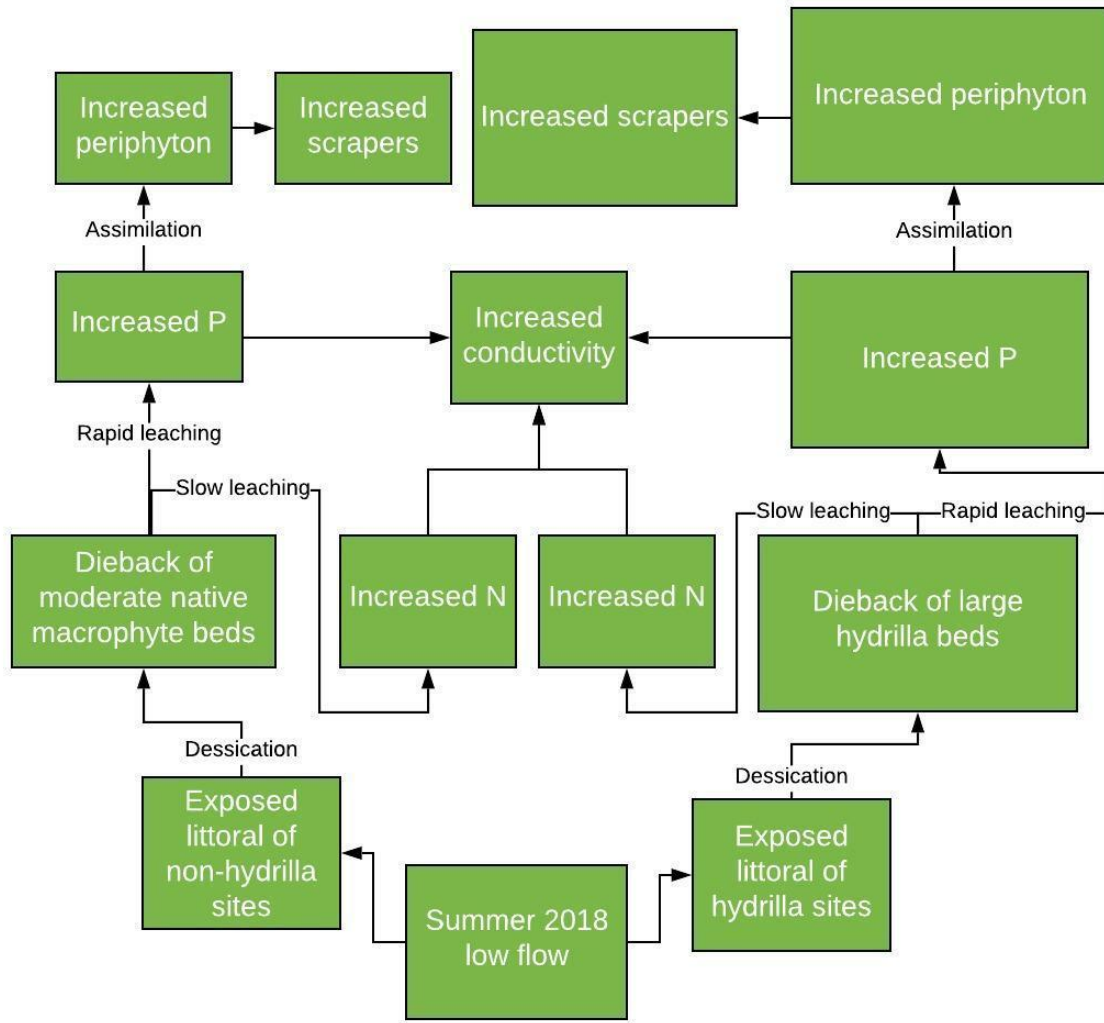


Figure 26. Low-flow desiccation hypothesis.

Greater periphyton growth and conductivity in the summer growing season support the low-flow desiccation hypothesis. Not only were both variables greater during the growing season, but a positive association with hydrilla was also observed. Riffle cobble at hydrilla sites had greater periphytic growth than non-hydrilla sites despite no relationship with light availability in the tree canopy. High conductivity is the result of increased total dissolve solids (TDS), which include phosphates and nitrates; increased nutrients, rooted macrophyte presence,

and macrophyte decay have all been observed to increase conductivity (Li et al. 2018, Lu et al. 2018, Stefanidis and Papastergiadou 2019). The results suggest that rather than a reduction in nutrient availability, nutrients may be more available in areas when and where hydrilla is actively growing. Hydrilla sites during the growing season exhibited the highest proportion of scrapers (Fig. 21), an invertebrate group closely associated with periphyton. These results suggest possible nutrient release during the growing season brought on by desiccation of hydrilla stems during low flow periods.

Unlike in the winter senescence season, discharge rates in the summer growing season were not maintained, but rather, dropped very low. While high flows result in bankfull and lateral dispersal of organisms, later low flows can expose the littoral region causing mortality in rooted macrophytes or portions of the stem exposed in those areas. Following a rain event, macrophytes stranded by low flow can, when rewetted, release nutrients that will now be available to other stream organisms. Therefore, greater phosphorus levels during the growing season could be a product of littoral macrophyte senescence, with hydrilla sites experiencing higher phosphorus release due to greater vegetative biomass, while increased assimilation by periphyton reduced the biologically available phosphorus that was sampled. Higher specific conductivity in the growing season also supports a hypothesis of periods of extreme low flow in the summer, as TDS become more concentrated and groundwater contribution increases with decreased flow.

Mesocosm experiments reveal that senescing hydrilla can have a direct impact on nutrient availability as well as the photosynthetic response of photoautotrophs. Those studies demonstrate that hydrilla decomposition results in a significant increase of total phosphorus and nitrogen in

the surrounding water, air, and sediment (Li et al. 2014). Studies on water drawdown regimes in reservoirs show that significantly more phosphorus is released than nitrogen during periods of rewetting following drawdown and that these nutrient releases correlate to increases in phytoplankton biomass (Lu et al. 2018). The results for the lotic system in this study suggest a similar trend to that found in the literature but for periphyton rather than phytoplankton. Littoral-growing hydrilla in the ERW may be susceptible to desiccation due to fluctuations in discharge; high discharge following rain events could be returning these nutrients to the water and sediment, making them available to periphyton and other stream organisms.

Differences in the mode of nutrient assimilation also support this hypothesis of littoral hydrilla senescence. Many submerged macrophytes including hydrilla have been found to assimilate nutrients, especially phosphorus, more efficiently through the sediment rather than directly from the water column (Carignan and Kalf 1980, Lu et al. 2018), so if the nutrient release is primarily in the water column, hydrilla plants and fragments downstream or in the immediate surrounding of the release would re-assimilate poorly if at all. Since periphyton colonizing rock cannot derive nutrients from this substrate (Burkholder 1996), it can be inferred that periphyton sampled for this study assimilate nutrients from the water column and that increased periphyton growth in the ERW is due to newly available nutrients in the surrounding water. Further experimentation is needed to support this hypothesis as the results of the current study cannot demonstrate with certainty that assimilation of nutrients by periphyton is a direct result of hydrilla senescence.

Though hydrilla sites on average exhibited higher-quality macroinvertebrate communities, hydrilla sites were not significantly more diverse than non-hydrilla sites. These

results agree with some literature (Theel et al. 2008) but disagree with others (Thorp et al. 1997). Considering the high level of complexity of hydrilla beds, the fact that diversity is not higher in the stream segments with hydrilla is an interesting find. However, Antioch Bridge (hydrilla site) seemed to host the highest macroinvertebrate diversity in this study. The predicted functional response of macroinvertebrates to increased periphyton and detritus is an increase in scrapers and shredders which are associated with periphyton and coarse particulate organic matter, respectively. Though shredders did not respond as predicted, hydrilla had a significant influence on FFG composition, and there were greater grazer/scrapers at hydrilla sites during the growing season. Therefore, these results support the hypothesis that increasing periphyton and particulate matter via senescing hydrilla influence macroinvertebrate community structure.

When evaluating similarity in macroinvertebrate communities among the treatments, it was discovered that these communities during the growing season were more similar to each other than to those during the senescent season. ANOSIM suggested a difference in similarity between seasons, while analysis of pairwise comparisons of Morisita's Index of Community Similarity suggested higher within-site similarity of hydrilla sites than within-site similarity of non-hydrilla sites. This may be due to the location of sampling sites in the watershed where hydrilla sites are closer to one another than non-hydrilla sites. However, since this phenomenon was not observed during the senescent season, we propose the alternative possibility that hydrilla may have a homogenizing effect on the macroinvertebrate community where variability in taxa is reduced; Fowler (2012) found this to be the case in macroinvertebrates found in pools of the ERW. Unfortunately, current studies in the ERW may not be able to answer this question as truly comparable replicate sites for hydrilla presence and absence are extremely limited to three mid-

order streams (Clear Creek, upper Obed River, and Daddys Creek), the latter being the only one invaded by hydrilla.

The results of this study suggest that water level fluctuations may lead to shoot senescence and consequent nutrient availability during the growing season. This finding is interesting because water level fluctuations have been used as a hydrilla management technique in reservoirs. Rewetting following a drawdown stimulates the germination of subterranean tubers, which can be killed by a second drawdown (Miller et al. 1976). Hydrilla tuber survival is directly linked to moisture level making them prone to desiccation, and repeated regimes of drawdown followed by rewetting have been found to significantly diminish tuber banks (Doyle and Smart 2001).

Parallels to past literature aside, the benefits of water level fluctuations in the ERW are less clear, though this study may give greater insight into optimum periods for selective herbicide application. The difficulty with using herbicide for hydrilla management is that though they are efficient at reducing above-substrate shoots, they may not be effective at eradicating subterranean propagules (Netherland 1997). Post-rain event application, on one hand, may be a useful strategy for depleting tuber banks via chemical control, though it's unclear if the water level fluctuations in the ERW are extreme, prolonged, or reliable enough to stimulate tuber germination. On the other hand, fluridone has been found to be an effective herbicide for controlling hydrilla when applied early in its growing season as well as during low discharge, at which point the concentration and exposure of the herbicide is at its maximum potential (Fox et al. 1994). Regardless, hydrilla control in the ERW will require consideration of water level fluctuations for optimal results.

An unexpected finding from this investigation was discovering *Dibusa angata*, an elusive caddisfly, occurring at Chestnut Hill on Daddys Creek in December 2018. To our knowledge, this is the first record of the species in Cumberland County, Tennessee (Etnier et al. 1998) or the Obed Wild and Scenic River (Jason Robinson, pers. comm.). *Dibusa angata*, the only species in the genus, is widespread but not commonly collected (Wiggins 1996). First instars occur in early winter but are indistinguishable from other hydroptilid genera (notably, *Ochrotrichia* and *Hydroptila*, with which it often co-occurs) until the fifth instar (Resh and Houp 1986). At this stage, the caddisfly exclusively feeds and creates its case from the freshwater red alga *Lemanea australis* (Fig. 27). The highest densities of fifth instars occur in December and January (Resh and Houp 1986), which coincided with our senescence sampling. Interestingly, this individual was found at a hydrilla site that did not meet the biocriteria for the ecoregion.



Figure 27. *Dibusa angata* 5th instar larva (right) and case made of *Lemanea australis* (left) viewed through a dissecting microscope. Individual collected in December 2018 from Chestnut Hill on Daddys Creek, Cumberland County, Tennessee.

Conclusions

This study observed differences in ecosystem response to hydrilla presence within two seasons of a year that experience atypical precipitation resulting in periods of exceptionally high and low discharge. Greater orthophosphate was observed in the growing season rather than the senescent season. Within the growing season, increases in periphyton and scraper/grazers were found at hydrilla sites. The growing season experienced repeated stream-level drops following by storm discharges that, coupled with our findings, prompt speculation of hydrilla senescence as a product of water level fluctuations. Low flow may result in senescence by desiccation, resulting in leached nutrients returned to the water column upon rewetting. Support for hydrilla as a homogenizer of macroinvertebrate communities was found, though distances between sites may be a confounding factor.

Future Studies

As most scientific endeavors go, this study resulted in more questions than answers.

Sampling was simplified to two general periods of year (summer growing and winter senescence) that ultimately experienced substantial within-season variation not accounted for in the study design. In order to determine validity of the low-flow desiccation or discharge leaf fall hypotheses, the following questions need resolving:

- How does hydrilla in the ERW respond to periods of high or low flow?
 - Does desiccation occur at low flow?
 - Is there a nutrient release when low flow is followed by high flow?

- Do rain events following low-flow periods stimulate tuber germination?

Once these are known, investigation into changes in the concentration of dissolved nutrients and periphyton in the context of these water level fluctuations would better indicate whether the presence of hydrilla significantly alters normal assimilation pathways. Alternatively, phytoplankton may be a more suitable study group. Though many studies focusing on assimilation by phytoplankton take place in lentic systems, hydrilla in the ERW mostly occupies slower moving pool areas where phytoplankton could be more abundant. Moreover, interactions between periphyton and phytoplankton in medium-order rivers are understudied, so this question in and of itself would provide useful information for tackling nutrient studies.

A resolved phenology for hydrilla in the ERW would also be a vital contribution to both invasion studies and management strategies. Were the results of this study a product of hydrilla senescence, or was senescence much earlier than sampling and, thus, unaccounted for in the findings? Considering that the leaching process occurs early in the decomposition process, understanding when hydrilla in the ERW senesces may aid in determining whether nutrient release and assimilation occurred.

Finally, diversity and function of the macroinvertebrate community may not have been as effective response variables as secondary productivity. Abundance of rapidly reproducing macroinvertebrates associated with periphyton and detritus consumption may give a more direct link to algal assimilation of nutrient pathways newly paved by one of freshwater biology's most notorious species.

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APPENDIX: Macroinvertebrate Taxonomic Data and Functional Feeding Groups

Rhea Road (hydrilla absent)			
Taxon	FFG	Growing season count	Senescent season count
AMPHIPODA			
Gammaridae			
<i>Gammarus</i>	collector-gatherer	1	
BIVALVIA			
Corbiculidae			
<i>Corbicula fluminea</i>	collector-filterer		
COLEOPTERA			
Dryopidae			
<i>Helichus</i>	scraper	2	
Elmidae			
<i>Ancyronyx (adult)</i>	collector-gatherer		
<i>Ancyronyx (larvae)</i>	collector-gatherer		
<i>Dubiraphia (larvae)</i>	collector-gatherer		
<i>Macronychus (larvae)</i>	collector-gatherer		
<i>Microcylloepus (adult)</i>	collector-gatherer		
<i>Microcylloepus (larvae)</i>	collector-gatherer		
<i>Optioservus (larvae)</i>	scraper		
<i>Oulimnius (larvae)</i>	collector-gatherer		
<i>Promoresia (adult)</i>	collector-gatherer		
<i>Promoresia (larvae)</i>	collector-gatherer		1
<i>Stenelmis (adults)</i>	collector-gatherer	3	
<i>Stenelmis (larvae)</i>	scraper	10	
Gyrinidae			
<i>Dineutus (larvae)</i>	predator		
Hydrophilidae			
<i>Berosus (larvae)</i>	shredder		
Psephenidae			
<i>Ectopria</i>	scraper		
<i>Psephenus (larvae)</i>	scraper		
<i>Psephenus (adult)</i>	nonfeeding		
DECAPODA			
Cambaridae			
<i>Cambarus</i>	collector-gatherer (omnivorous)		
DIPTERA			
Pupae		7	6
Ceratopogonidae			

<i>Atrichopogon</i>	collector-gatherer		
Chironomidae			
Chironomini			
<i>Microtendipes</i>	collector-filterer		
<i>Paratendipes</i>	collector-gatherer		
<i>Polypedilum</i>	shredder	5	2
Orthoclaadiinae			
<i>Corynoneura</i>	collector-gatherer		
<i>Cricotopus/Orthocladus</i>	collector-gatherer	1	1
<i>Diplocladius</i>	collector-gatherer		1
<i>Eukiefferiella</i>	collector-gatherer		
<i>Lopescladius</i>	collector-gatherer		
<i>Nanocladius</i>	collector-gatherer		
<i>Parakiefferella</i>	collector-gatherer		
<i>Rheocricotopus</i>	collector-gatherer	2	
<i>Thienamanniella</i>	collector-gatherer		
<i>Tvetenia</i>	collector-gatherer		1
Tanypodinae			
<i>Alabesmyia</i>	predator		
<i>Thienemannimyia</i> group sp.	predator		1
Tanytarsini			
<i>Cladotanytarsus</i>	collector-gatherer		
<i>Paratanytarsus</i>	collector-gatherer		4
<i>Rheotanytarsus</i>	collector-filterer	6	9
<i>Sublettea</i>	collector-filterer		
<i>Tanytarsus</i>	collector-gatherer	3	3
Empididae			
<i>Hemerodromia</i>	predator		
Simuliidae			
<i>Simulium</i>	collector-filterer	5	71
Tipulidae			
<i>Antocha</i>	collector-gatherer	1	
<i>Tipula</i>	shredder		
EPHEMEROPTERA			
Baetidae			
<i>Acerpenna</i>	collector-gatherer	9	3
<i>Baetis</i>	collector-gatherer		
<i>Heterocloeon</i>	scraper		
<i>Procloeon</i>	collector-gatherer		

Caenidae			
<i>Caenis</i>	collector-gatherer		
Ephemerellidae			
<i>Ephemerella</i>	collector-gatherer		
<i>Eurylophella</i>	collector-gatherer		1
Heptageniidae			
<i>Epeorus</i>	scraper		
<i>Leucrocuta</i>	collector-gatherer		
<i>Maccaffertium</i>	scraper		
<i>Stenacron</i>	scraper		
<i>Stenonema femoratum</i>	scraper		
Isonychiidae			
<i>Isonychia</i>	collector-filterer		
Leptohyphidae			
<i>Tricorythodes</i>	collector-gatherer		
GASTROPODA	grazer	4	4
ISOPODA			
Asellidae			
<i>Liricius</i>	collector-gatherer		1
MEGALOPTERA			
Corydalidae			
<i>Corydalus cornutus</i>	predator	2	
<i>Nigronia</i>	predator	4	
ODONATA			
Aeshnidae			
<i>Boyeria vinosa</i>	predator		
Calopterygidae			
<i>Calopteryx</i>	predator		
<i>Hetaerina</i>	predator	1	
Corduliidae			
<i>Neurocordulia</i>	predator	1	
Coenagrionidae	predator		
Gomphidae			
<i>Gomphus</i>	predator		
OLIGOCHAETA	collector-filterer	33	32
PLATYHELMINTHES	omnivorous		
PLECOPTERA			
Capniidae			
<i>Allocapnia</i>	shredder		
Perlidae			

<i>Acroneuria</i>	predator		
<i>Agnetina</i>	predator		
<i>Neoperla</i>	predator		
<i>Perlesta</i>	predator		
Perlodidae			
<i>Isoperla</i>	predator		
Taeniopterygidae			
<i>Taeniopteryx</i>	shredder		30
<i>Oemopteryx</i>	shredder		19
TRICHOPTERA			
Pupae		1	
Brachycentridae			
<i>Micrasema</i>	shredder		
Helicopsychidae			
<i>Helicopsyche</i>	scraper		
Hydropsychidae			
<i>Cheumatopsyche</i>	collector-filterer	46	5
<i>Hydropsyche</i>	collector-filterer	1	
Hydroptilidae			
<i>Dibusa angata</i>	scraper		
<i>Hydroptila</i>	piercer-herbivore		1
<i>Ochrotrichia</i>	piercer-herbivore		
<i>Oxyethira</i>	piercer-herbivore		
Lepidostomatidae			
<i>Lepidostoma</i>	shredder		
Leptoceridae			
<i>Ceraclea</i>	collector-gatherer		
<i>Oecetis</i>	predator		
Limnephilidae			
<i>Hydatophylax argus</i>	shredder		
Philopotamidae			
<i>Chimarra</i>	collector-filterer	12	1
Polycentropodidae			
<i>Nyctiophylax</i>	predator		
Rhyacophilidae			
<i>Rhyacophila</i>	predator		1
Thremmatidae			
<i>Neophylax</i>	scraper		

Old Highway 28 (hydrilla present)			
Taxon	FFG	Growing season count	Senescent season count
AMPHIPODA			
Gammaridae			
<i>Gammarus</i>	collector-gatherer		
BIVALVIA			
Corbiculidae			
<i>Corbicula fluminea</i>	collector-filterer		10
COLEOPTERA			
Dryopidae			
<i>Helichus</i>	scraper		
Elmidae			
<i>Ancyronyx (adult)</i>	collector-gatherer		
<i>Ancyronyx (larvae)</i>	collector-gatherer		
<i>Dubiraphia (larvae)</i>	collector-gatherer		
<i>Macronychus (larvae)</i>	collector-gatherer		
<i>Microcylloepus (adult)</i>	collector-gatherer		
<i>Microcylloepus (larvae)</i>	collector-gatherer		
<i>Optioservus (larvae)</i>	scraper		4
<i>Oulimnius (larvae)</i>	collector-gatherer		
<i>Promoresia (adult)</i>	collector-gatherer		
<i>Promoresia (larvae)</i>	collector-gatherer		
<i>Stenelmis (adults)</i>	collector-gatherer	1	1
<i>Stenelmis (larvae)</i>	scraper		
Gyrinidae			
<i>Dineutus (larvae)</i>	predator	1	
Hydrophilidae			
<i>Berosus (larvae)</i>	shredder		
Psephenidae			
<i>Ectopria</i>	scraper	1	1
<i>Psephenus (larvae)</i>	scraper		
<i>Psephenus (adult)</i>	nonfeeding		
DECAPODA			
Cambaridae			
<i>Cambarus</i>	collector-gatherer (omnivorous)		
DIPTERA			
Pupae			1
Ceratopogonidae			

<i>Atrichopogon</i>	collector-gatherer		
Chironomidae			
Chironomini			
<i>Microtendipes</i>	collector-filterer		
<i>Paratendipes</i>	collector-gatherer		
<i>Polypedilum</i>	shredder	3	2
Orthoclaadiinae			
<i>Corynoneura</i>	collector-gatherer	1	
<i>Cricotopus/Orthocladus</i>	collector-gatherer	10	1
<i>Diplocladius</i>	collector-gatherer		
<i>Eukiefferiella</i>	collector-gatherer		
<i>Lopescladius</i>	collector-gatherer		
<i>Nanocladius</i>	collector-gatherer		
<i>Parakiefferella</i>	collector-gatherer		1
<i>Rheocricotopus</i>	collector-gatherer	1	
<i>Thienamanniella</i>	collector-gatherer	1	
<i>Tvetenia</i>	collector-gatherer		3
Tanypodinae			
<i>Alabesmyia</i>	predator		
<i>Thienemannimyia</i> group sp.	predator		
Tanytarsini			
<i>Cladotanytarsus</i>	collector-gatherer		
<i>Paratanytarsus</i>	collector-gatherer		
<i>Rheotanytarsus</i>	collector-filterer	21	16
<i>Sublettea</i>	collector-filterer		
<i>Tanytarsus</i>	collector-gatherer		2
Empididae			
<i>Hemerodromia</i>	predator		
Simuliidae			
<i>Simulium</i>	collector-filterer	15	64
Tipulidae			
<i>Antocha</i>	collector-gatherer		
<i>Tipula</i>	shredder		
EPHEMEROPTERA			
Baetidae			
<i>Acerpenna</i>	collector-gatherer	1	
<i>Baetis</i>	collector-gatherer	11	
<i>Heterocloeon</i>	scraper	1	1
<i>Procloeon</i>	collector-gatherer		

Caenidae			
<i>Caenis</i>	collector-gatherer		
Ephemerellidae			
<i>Ephemerella</i>	collector-gatherer		
<i>Eurylophella</i>	collector-gatherer		1
Heptageniidae			
<i>Epeorus</i>	scraper		
<i>Leucrocuta</i>	collector-gatherer		
<i>Maccaffertium</i>	scraper	20	23
<i>Stenacron</i>	scraper		
<i>Stenonema femoratum</i>	scraper		
Isonychiidae			
<i>Isonychia</i>	collector-filterer	7	5
Leptohyphidae			
<i>Tricorythodes</i>	collector-gatherer		
GASTROPODA	grazer		
ISOPODA			
Asellidae			
<i>Lircius</i>	collector-gatherer		
MEGALOPTERA			
Corydalidae			
<i>Corydalis</i>	predator	18	2
<i>Nigronia</i>	predator		
ODONATA			
Aeshnidae			
<i>Boyeria vinosa</i>	predator		
Calopterygidae			
<i>Calopteryx</i>	predator		
<i>Hetaerina</i>	predator	2	
Corduliidae			
<i>Neurocordulia</i>	predator		
Coenagrionidae	predator	1	
Gomphidae			
<i>Gomphus</i>	predator		2
OLIGOCHAETA	collector-filterer	8	2
PLATYHELMINTHES	omnivorous	1	
PLECOPTERA			
Capniidae			
<i>Allocapnia</i>	shredder		
Perlidae			

<i>Acroneuria</i>	predator		
<i>Agnetina</i>	predator		
<i>Neoperla</i>	predator		
<i>Perlesta</i>	predator		
Perlodidae			
<i>Isoperla</i>	predator		
Taeniopterygidae			
<i>Taeniopteryx</i>	shredder		3
<i>Oemopteryx</i>	shredder		3
TRICHOPTERA			
Pupae		1	
Brachycentridae			
<i>Micrasema</i>	shredder	6	1
Helicopsychidae			
<i>Helicopsyche</i>	scraper		
Hydropsychidae			
<i>Cheumatopsyche</i>	collector-filterer	18	52
<i>Hydropsyche</i>	collector-filterer	37	9
Hydroptilidae			
<i>Dibusa angata</i>	scraper		
<i>Hydroptila</i>	piercer-herbivore		
<i>Ochrotrichia</i>	piercer-herbivore		1
<i>Oxyethira</i>	piercer-herbivore		
Lepidostomatidae			
<i>Lepidostoma</i>	shredder		
Leptoceridae			
<i>Ceraclea</i>	collector-gatherer		
<i>Oecetis</i>	predator	1	
Limnephilidae			
<i>Hydatophylax argus</i>	shredder		
Philopotamidae			
<i>Chimarra</i>	collector-filterer	26	42
Polycentropodidae			
<i>Nyctiophylax</i>	predator		
Rhyacophilidae			
<i>Rhyacophila</i>	predator		
Thremmatidae			
<i>Neophylax</i>	scraper		

Highway 68 (hydrilla absent)			
Taxon	FFG	Growing season count	Senescent season count
AMPHIPODA			
Gammaridae			
<i>Gammarus</i>	collector-gatherer		
BIVALVIA			
Corbiculidae			
<i>Corbicula fluminea</i>	collector-filterer	26	9
COLEOPTERA			
Dryopidae			
<i>Helichus</i>	scraper		
Elmidae			
<i>Ancyronyx (adult)</i>	collector-gatherer		
<i>Ancyronyx (larvae)</i>	collector-gatherer	1	
<i>Dubiraphia (larvae)</i>	collector-gatherer		
<i>Macronychus (larvae)</i>	collector-gatherer	2	1
<i>Microcylloepus (adult)</i>	collector-gatherer	5	
<i>Microcylloepus (larvae)</i>	collector-gatherer		
<i>Optioservus (larvae)</i>	scraper	7	7
<i>Oulimnius (larvae)</i>	collector-gatherer	5	2
<i>Promoresia (adult)</i>	collector-gatherer		
<i>Promoresia (larvae)</i>	collector-gatherer	5	
<i>Stenelmis (adults)</i>	collector-gatherer		
<i>Stenelmis (larvae)</i>	scraper		
Gyrinidae			
<i>Dineutus (larvae)</i>	predator		
Hydrophilidae			
<i>Berosus (larvae)</i>	shredder		
Psephenidae			
<i>Ectopria</i>	scraper		1
<i>Psephenus (larvae)</i>	scraper	1	1
<i>Psephenus (adult)</i>	nonfeeding		
DECAPODA			
Cambaridae			
<i>Cambarus</i>	collector-gatherer (omnivorous)		
DIPTERA			
Pupae		2	2
Ceratopogonidae			

<i>Atrichopogon</i>	collector-gatherer	4	
Chironomidae			
Chironomini			
<i>Microtendipes</i>	collector-filterer		
<i>Paratendipes</i>	collector-gatherer		
<i>Polypedilum</i>	shredder	3	5
Orthoclaadiinae			
<i>Corynoneura</i>	collector-gatherer		
<i>Cricotopus/Orthocladus</i>	collector-gatherer		4
<i>Diplocladius</i>	collector-gatherer		
<i>Eukiefferiella</i>	collector-gatherer		
<i>Lopescladius</i>	collector-gatherer	10	
<i>Nanocladius</i>	collector-gatherer		
<i>Parakiefferella</i>	collector-gatherer		
<i>Rheocricotopus</i>	collector-gatherer	1	
<i>Thienamanniella</i>	collector-gatherer	1	
<i>Tvetenia</i>	collector-gatherer	1	
Tanypodinae			
<i>Alabesmyia</i>	predator		
<i>Thienemannimyia</i> group sp.	predator	2	
Tanytarsini			
<i>Cladotanytarsus</i>	collector-gatherer	1	
<i>Paratanytarsus</i>	collector-gatherer		
<i>Rheotanytarsus</i>	collector-filterer	10	
<i>Sublettea</i>	collector-filterer	3	
<i>Tanytarsus</i>	collector-gatherer	1	1
Empididae			
<i>Hemerodromia</i>	predator	3	2
Simuliidae			
<i>Simulium</i>	collector-filterer	5	32
Tipulidae			
<i>Antocha</i>	collector-gatherer		
<i>Tipula</i>	shredder		1
EPHEMEROPTERA			
Baetidae			
<i>Acerpenna</i>	collector-gatherer		
<i>Baetis</i>	collector-gatherer	13	
<i>Heterocloeon</i>	scraper	4	2
<i>Procloeon</i>	collector-gatherer		

Caenidae			
<i>Caenis</i>	collector-gatherer	16	
Ephemerellidae			
<i>Ephemerella</i>	collector-gatherer		12
<i>Eurylophella</i>	collector-gatherer		1
Heptageniidae			
<i>Epeorus</i>	scraper		
<i>Leucrocuta</i>	collector-gatherer		
<i>Maccaffertium</i>	scraper	27	36
<i>Stenacron</i>	scraper		
<i>Stenonema femoratum</i>	scraper		10
Isonychiidae			
<i>Isonychia</i>	collector-filterer	3	1
Leptohyphidae			
<i>Tricorythodes</i>	collector-gatherer		
GASTROPODA	grazer		1
ISOPODA			
Asellidae			
<i>Lircius</i>	collector-gatherer		12
MEGALOPTERA			
Corydalidae			
<i>Corydalus</i>	predator		
<i>Nigronia</i>	predator	3	1
ODONATA			
Aeshnidae			
<i>Boyeria vinosa</i>	predator		
Calopterygidae			
<i>Calopteryx</i>	predator		
<i>Hetaerina</i>	predator		
Corduliidae			
<i>Neurocordulia</i>	predator		
Coenagrionidae	predator		
Gomphidae			
<i>Gomphus</i>	predator		1
OLIGOCHAETA	collector-filterer	14	8
PLATYHELMINTHES	omnivorous		
PLECOPTERA			
Capniidae			
<i>Allocapnia</i>	shredder		1
Perlidae			

<i>Acroneuria</i>	predator	1	5
<i>Agnetina</i>	predator		
<i>Neoperla</i>	predator		
<i>Perlesta</i>	predator		
Perlodidae			
<i>Isoperla</i>	predator		
Taeniopterygidae			
<i>Taeniopteryx</i>	shredder		8
<i>Oemopteryx</i>	shredder		1
TRICHOPTERA			
Pupae		1	
Brachycentridae			
<i>Micrasema</i>	shredder		
Helicopsychidae			
<i>Helicopsyche</i>	scraper		
Hydropsychidae			
<i>Cheumatopsyche</i>	collector-filterer	8	28
<i>Hydropsyche</i>	collector-filterer	4	2
Hydroptilidae			
<i>Dibusa angata</i>	scraper		
<i>Hydroptila</i>	piercer-herbivore	1	
<i>Ochrotrichia</i>	piercer-herbivore	2	
<i>Oxyethira</i>	piercer-herbivore		
Lepidostomatidae			
<i>Lepidostoma</i>	shredder		
Leptoceridae			
<i>Ceraclea</i>	collector-gatherer		
<i>Oecetis</i>	predator		
Limnephilidae			
<i>Hydatophylax argus</i>	shredder		
Philopotamidae			
<i>Chimarra</i>	collector-filterer	2	1
Rhyacophilidae			
<i>Rhyacophila</i>	predator		
Polycentropodidae			
<i>Nyctiophylax</i>	predator		
Thremmatidae			
<i>Neophylax</i>	scraper		1

I-40 (hydrilla present)			
Taxon	FFG	Growing season count	Senescent season count
AMPHIPODA			
Gammaridae			
<i>Gammarus</i>	collector-gatherer		
BIVALVIA			
Corbiculidae			
<i>Corbicula fluminea</i>	collector-filterer	3	15
COLEOPTERA			
Dryopidae			
<i>Helichus</i>	scraper		
Elmidae			
<i>Ancyronyx (adult)</i>	collector-gatherer		
<i>Ancyronyx (larvae)</i>	collector-gatherer		
<i>Dubiraphia (larvae)</i>	collector-gatherer		
<i>Macronychus (larvae)</i>	collector-gatherer	1	5
<i>Microcylloepus (adult)</i>	collector-gatherer	4	
<i>Microcylloepus (larvae)</i>	collector-gatherer		
<i>Optioservus (larvae)</i>	scraper	6	11
<i>Oulimnius (larvae)</i>	collector-gatherer	5	
<i>Promoresia (adult)</i>	collector-gatherer		
<i>Promoresia (larvae)</i>	collector-gatherer		
<i>Stenelmis (adults)</i>	collector-gatherer	1	
<i>Stenelmis (larvae)</i>	scraper		
Gyrinidae			
<i>Dineutus (larvae)</i>	predator		
Hydrophilidae			
<i>Berosus (larvae)</i>	shredder		
Psephenidae			
<i>Ectopria (larvae)</i>	scraper	2	
<i>Psephenus (larvae)</i>	scraper	11	4
<i>Psephenus (adult)</i>	nonfeeding	2	
DECAPODA			
Cambaridae			
<i>Cambarus</i>	collector-gatherer (omnivorous)		
DIPTERA			
Pupae		5	1
Ceratopogonidae			

<i>Atrichopogon</i>	collector-gatherer	1	
Chironomidae			
Chironomini			
<i>Microtendipes</i>	collector-filterer		
<i>Paratendipes</i>	collector-gatherer		
<i>Polypedilum</i>	shredder		3
Orthoclaadiinae			
<i>Corynoneura</i>	collector-gatherer		
<i>Cricotopus/Orthocladus</i>	collector-gatherer	2	2
<i>Diplocladius</i>	collector-gatherer		
<i>Eukiefferiella</i>	collector-gatherer		
<i>Lopescladius</i>	collector-gatherer		1
<i>Nanocladius</i>	collector-gatherer		1
<i>Parakiefferella</i>	collector-gatherer		
<i>Rheocricotopus</i>	collector-gatherer		
<i>Thienamanniella</i>	collector-gatherer		
<i>Tvetenia</i>	collector-gatherer		
Tanypodinae			
<i>Alabesmyia</i>	predator		1
<i>Thienemannimyia</i> group sp.	predator		
Tanytarsini			
<i>Cladotanytarsus</i>	collector-gatherer		
<i>Paratanytarsus</i>	collector-gatherer	2	2
<i>Rheotanytarsus</i>	collector-filterer	10	11
<i>Sublettea</i>	collector-filterer	1	1
<i>Tanytarsus</i>	collector-gatherer		
Empididae			
<i>Hemerodromia</i>	predator		
Simuliidae			
<i>Simulium</i>	collector-filterer		26
Tipulidae			
<i>Antocha</i>	collector-gatherer	1	1
<i>Tipula</i>	shredder		
EPHEMEROPTERA			
Baetidae			
<i>Acerpenna</i>	collector-gatherer		
<i>Baetis</i>	collector-gatherer	11	
<i>Heterocloeon</i>	scraper	3	2
<i>Procloeon</i>	collector-gatherer		

Caenidae			
<i>Caenis</i>	collector-gatherer	1	
Ephemerellidae			
<i>Ephemerella</i>	collector-gatherer		4
<i>Eurylophella</i>	collector-gatherer		4
Heptageniidae			
<i>Epeorus</i>	scraper		
<i>Leucrocuta</i>	collector-gatherer	1	
<i>Maccaffertium</i>	scraper	35	16
<i>Stenacron</i>	scraper		4
<i>Stenonema femoratum</i>	scraper		14
Isonychiidae			
<i>Isonychia</i>	collector-filterer	8	4
Leptohyphidae			
<i>Tricorythodes</i>	collector-gatherer		
GASTROPODA	grazer	3	7
ISOPODA			
Asellidae			
<i>Lircius</i>	collector-gatherer	19	4
MEGALOPTERA			
Corydalidae			
<i>Corydalus</i>	predator		
<i>Nigronia</i>	predator		1
ODONATA			
Aeshnidae			
<i>Boyeria vinosa</i>	predator	2	3
Calopterygidae			
<i>Calopteryx</i>	predator		
<i>Hetaerina</i>	predator		
Corduliidae			
<i>Neurocordulia</i>	predator		
Coenagrionidae	predator		
Gomphidae			
<i>Gomphus</i>	predator		1
OLIGOCHAETA	collector-filterer	7	25
PLATYHELMINTHES	omnivorous		
PLECOPTERA			
Capniidae			
<i>Allocapnia</i>	shredder		
Perlidae			

<i>Acroneuria</i>	predator	1	
<i>Agnetina</i>	predator		
<i>Neoperla</i>	predator		
<i>Perlesta</i>	predator		
Perlodidae			
<i>Isoperla</i>	predator		
Taeniopterygidae			
<i>Taeniopteryx</i>	shredder		19
<i>Oemopteryx</i>	shredder		6
TRICHOPTERA			
Pupae		1	
Brachycentridae			
<i>Micrasema</i>	shredder		1
Helicopsychidae			
<i>Helicopsyche</i>	scraper		
Hydropsychidae			
<i>Cheumatopsyche</i>	collector-filterer	15	15
<i>Hydropsyche</i>	collector-filterer	5	1
Hydroptilidae			
<i>Dibusa angata</i>	scraper		
<i>Hydroptila</i>	piercer-herbivore		
<i>Ochrotrichia</i>	piercer-herbivore	1	
<i>Oxyethira</i>	piercer-herbivore		1
Lepidostomatidae			
<i>Lepidostoma</i>	shredder		
Leptoceridae			
<i>Ceraclea</i>	collector-gatherer		
<i>Oecetis</i>	predator		
Limnephilidae			
<i>Hydatophylax argus</i>	shredder		
Philopotamidae			
<i>Chimarra</i>	collector-filterer	12	4
Polycentropodidae			1
<i>Nyctiophylax</i>	predator	1	
Rhyacophilidae			
<i>Rhyacophila</i>	predator		
Thremmatidae			
<i>Neophylax</i>	scraper		

Chestnut Hill (hydrilla present)			
Taxon	FFG	Growing season count	Senescent season count
AMPHIPODA			
Gammaridae			
<i>Gammarus</i>	collector-gatherer		
BIVALVIA			
Corbiculidae			
<i>Corbicula fluminea</i>	collector-filterer	5	6
COLEOPTERA			
Dryopidae			
<i>Helichus</i>	scraper		
Elmidae			
<i>Ancyronyx (adult)</i>	collector-gatherer		1
<i>Ancyronyx (larvae)</i>	collector-gatherer	1	1
<i>Dubiraphia (larvae)</i>	collector-gatherer		
<i>Macronychus (larvae)</i>	collector-gatherer		
<i>Microcylloepus (adult)</i>	collector-gatherer		
<i>Microcylloepus (larvae)</i>	collector-gatherer		
<i>Optioservus (larvae)</i>	scraper	9	13
<i>Oulimnius (larvae)</i>	collector-gatherer	1	
<i>Promoresia (adult)</i>	collector-gatherer		
<i>Promoresia (larvae)</i>	collector-gatherer		1
<i>Stenelmis (adult)</i>	collector-gatherer	11	1
<i>Stenelmis (larvae)</i>	scraper	16	
Gyrinidae			
<i>Dineutus (larvae)</i>	predator		
Hydrophilidae			
<i>Berosus (larvae)</i>	shredder		
Psephenidae			
<i>Ectopria</i>	scraper	2	
<i>Psephenus (larvae)</i>	scraper	4	2
<i>Psephenus (adult)</i>	nonfeeding		
DECAPODA			
Cambaridae			
<i>Cambarus</i>	collector-gatherer (omnivorous)		
DIPTERA			
Pupae			5
Ceratopogonidae			

<i>Atrichopogon</i>	collector-gatherer		
Chironomidae			
Chironomini			
<i>Microtendipes</i>	collector-filterer		
<i>Paratendipes</i>	collector-gatherer	1	
<i>Polypedilum</i>	shredder	3	1
Orthoclaadiinae			
<i>Corynoneura</i>	collector-gatherer	2	
<i>Cricotopus/Orthocladus</i>	collector-gatherer	4	5
<i>Diplocadius</i>	collector-gatherer		
<i>Eukiefferiella</i>	collector-gatherer		3
<i>Lopescladius</i>	collector-gatherer		
<i>Nanocladus</i>	collector-gatherer		
<i>Parakiefferella</i>	collector-gatherer		
<i>Rheocricotopus</i>	collector-gatherer		
<i>Thienamanniella</i>	collector-gatherer		
<i>Tvetenia</i>	collector-gatherer		2
Tanypodinae			
<i>Alabesmyia</i>	predator		
<i>Thienemannimyia</i> group sp.	predator		
Tanytarsini			
<i>Cladotanytarsus</i>	collector-gatherer		
<i>Paratanytarsus</i>	collector-gatherer	3	2
<i>Rheotanytarsus</i>	collector-filterer	20	6
<i>Sublettea</i>	collector-filterer	9	
<i>Tanytarsus</i>	collector-gatherer	1	
Empididae			
<i>Hemerodromia</i>	predator		
Simuliidae			
<i>Simulium</i>	collector-filterer	1	53
Tipulidae			
<i>Antocha</i>	collector-gatherer	2	
<i>Tipula</i>	shredder		
EPHEMEROPTERA			
Baetidae			
<i>Acerpenna</i>	collector-gatherer		
<i>Baetis</i>	collector-gatherer	5	
<i>Heterocloeon</i>	scraper	3	
<i>Procloeon</i>	collector-gatherer		

Caenidae			
<i>Caenis</i>	collector-gatherer	5	
Ephemerellidae			
<i>Ephemerella</i>	collector-gatherer		10
<i>Eurylophella</i>	collector-gatherer		
Heptageniidae			
<i>Epeorus</i>	scraper		
<i>Leucrocuta</i>	collector-gatherer	1	1
<i>Maccaffertium</i>	scraper	24	18
<i>Stenacron</i>	scraper	3	1
<i>Stenonema femoratum</i>	scraper		18
Isonychiidae			
<i>Isonychia</i>	collector-filterer	6	
Leptohyphidae			
<i>Tricorythodes</i>	collector-gatherer		
GASTROPODA	grazer	5	4
ISOPODA			
Asellidae			
<i>Lircius</i>	collector-gatherer	5	6
MEGALOPTERA			
Corydalidae			
<i>Corydalus</i>	predator	2	
<i>Nigronia</i>	predator	3	
ODONATA			
Aeshnidae			
<i>Boyeria vinosa</i>	predator		
Calopterygidae			
<i>Calopteryx</i>			
<i>Hetaerina</i>	predator		
Corduliidae			
<i>Neurocordulia</i>	predator		
Coenagrionidae	predator		
Gomphidae			
<i>Gomphus</i>	predator	4	
OLIGOCHAETA	collector-filterer	10	26
PLATYHELMINTHES	omnivorous		
PLECOPTERA			
Capniidae			
<i>Allocapnia</i>	shredder		6
Perlidae			

<i>Acroneuria</i>	predator		1
<i>Agnetina</i>	predator		
<i>Neoperla</i>	predator		
<i>Perlesta</i>	predator		
Perlodidae			
<i>Isoperla</i>	predator		
Taeniopterygidae			
<i>Taeniopteryx</i>	shredder		15
<i>Oemopteryx</i>	shredder		1
TRICHOPTERA			
Pupae		1	
Brachycentridae			
<i>Micrasema</i>	shredder		
Helicopsychidae			
<i>Helicopsyche</i>			
Hydropsychidae			
<i>Cheumatopsyche</i>	collector-filterer	9	21
<i>Hydropsyche</i>	collector-filterer	7	5
Hydroptilidae			
<i>Dibusa angata</i>	scraper		1
<i>Hydroptila</i>	piercer-herbivore		1
<i>Ochrotrichia</i>	piercer-herbivore		
<i>Oxyethira</i>	piercer-herbivore		
<i>Lepidostomatidae</i>			
<i>Lepidostoma</i>	shredder		
Leptoceridae			
<i>Ceraclea</i>	collector-gatherer		
<i>Oecetis</i>	predator		
Limnephilidae			
<i>Hydatophylax argus</i>	shredder		
Philopotamidae			
<i>Chimarra</i>	collector-filterer	1	7
Polycentropodidae			
<i>Nyctiophylax</i>	predator		
Rhyacophilidae			
<i>Rhyacophila</i>	predator		3
Thremmatidae			
<i>Neophylax</i>	scraper		

Antioch Bridge (hydrilla present)			
Taxon	FFG	Growing Season count	Senescent season count
AMPHIPODA			
Gammaridae			
<i>Gammarus</i>	collector-gatherer		4
BIVALVIA			
Corbiculidae			
<i>Corbicula fluminea</i>	collector-filterer	5	7
COLEOPTERA			
Dryopidae			
<i>Helichus</i>	scraper		1
Elmidae			
<i>Ancyronyx (adult)</i>	collector-gatherer		
<i>Ancyronyx (larvae)</i>	collector-gatherer		
<i>Dubiraphia (larvae)</i>	collector-gatherer		2
<i>Macronychus (larvae)</i>	collector-gatherer	6	
<i>Microcylloepus (adult)</i>	collector-gatherer	12	
<i>Microcylloepus (larvae)</i>	collector-gatherer		4
<i>Optioservus (larvae)</i>	scraper	2	2
<i>Oulimnius (larvae)</i>	collector-gatherer		
<i>Promoresia (adult)</i>	collector-gatherer		
<i>Promoresia (larvae)</i>	collector-gatherer		1
<i>Stenelmis (adults)</i>	collector-gatherer	17	
<i>Stenelmis (larvae)</i>	scraper	8	
Gyrinidae			
<i>Dineutus (larvae)</i>	predator		
Hydrophilidae			
<i>Berosus (larvae)</i>	shredder		2
Psephenidae			
<i>Ectopria</i>	scraper	1	
<i>Psephenus (larvae)</i>	scraper		
<i>Psephenus (adult)</i>	nonfeeding		
DECAPODA			
Cambaridae			
<i>Cambarus</i>	collector-gatherer (omnivorous)		
DIPTERA			
Pupae		1	
Ceratopogonidae			

<i>Atrichopogon</i>	collector-gatherer		
Chironomidae			
Chironomini			
<i>Microtendipes</i>	collector-filterer		
<i>Paratendipes</i>	collector-gatherer		
<i>Polypedilum</i>	shredder	2	1
Orthocladiinae			
<i>Corynoneura</i>	collector-gatherer		
<i>Cricotopus/Orthocladius</i>	collector-gatherer	13	3
<i>Diplocladius</i>	collector-gatherer		1
<i>Eukiefferiella</i>	collector-gatherer		
<i>Lopescladius</i>	collector-gatherer		
<i>Nanocladius</i>	collector-gatherer		2
<i>Parakiefferella</i>	collector-gatherer		
<i>Rheocricotopus</i>	collector-gatherer		1
<i>Thienamanniella</i>	collector-gatherer	1	1
<i>Tvetenia</i>	collector-gatherer		
Tanypodinae			
<i>Alabesmyia</i>	predator		
<i>Thienemannimyia</i> group sp.	predator	1	
Tanytarsini			
<i>Cladotanytarsus</i>	collector-gatherer		
<i>Paratanytarsus</i>	collector-gatherer	1	1
<i>Rheotanytarsus</i>	collector-filterer	9	3
<i>Sublettea</i>	collector-filterer	1	
<i>Tanytarsus</i>	collector-gatherer		1
Empididae			
<i>Hemerodromia</i>	predator		
Simuliidae			
<i>Simulium</i>	collector-filterer	11	24
Tipulidae			
<i>Antocha</i>	collector-gatherer	2	
<i>Tipula</i>	shredder		
EPHEMEROPTERA			
Baetidae			
<i>Acerpenna</i>	collector-gatherer		
<i>Baetis</i>	collector-gatherer	12	
<i>Heterocloeon</i>	scraper	5	3
<i>Procloeon</i>	collector-gatherer	1	

Caenidae			
<i>Caenis</i>	collector-gatherer	4	
Ephemerellidae			
<i>Ephemerella</i>	collector-gatherer		9
<i>Eurylophella</i>	collector-gatherer		2
Heptageniidae			
<i>Epeorus</i>	scraper		
<i>Leucrocuta</i>	collector-gatherer	1	4
<i>Maccaffertium</i>	scraper	10	12
<i>Stenacron</i>	scraper		
<i>Stenonema femoratum</i>	scraper	11	3
Isonychiidae			
<i>Isonychia</i>	collector-filterer	4	6
Leptohyphidae			
<i>Tricorythodes</i>	collector-gatherer		
GASTROPODA	grazer	2	9
ISOPODA			
Asellidae			
<i>Lircius</i>	collector-gatherer	2	8
MEGALOPTERA			
Corydalidae			
<i>Corydalus</i>	predator	1	
<i>Nigronia</i>	predator		1
ODONATA			
Aeshnidae			
<i>Boyeria vinosa</i>	predator		
Calopterygidae			
<i>Calopteryx</i>	predator		
<i>Hetaerina</i>	predator		
Corduliidae			
<i>Neurocordulia</i>	predator		
Coenagrionidae	predator		
Gomphidae			
<i>Gomphus</i>	predator	1	
OLIGOCHAETA	collector-filterer	1	30
PLATYHELMINTHES	omnivorous		
PLECOPTERA			
Capniidae			
<i>Allocapnia</i>	shredder		3
Perlidae			

<i>Acroneuria</i>	predator	2	6
<i>Agnetina</i>	predator		
<i>Neoperla</i>	predator	3	
<i>Perlesta</i>	predator	1	
Perlodidae			
<i>Isoperla</i>	predator		
Taeniopterygidae			
<i>Taeniopteryx</i>	shredder		24
<i>Oemopteryx</i>	shredder		2
TRICHOPTERA			
Pupae			
Brachycentridae			
<i>Micrasema</i>	shredder		
Helicopsychidae			
<i>Helicopsyche</i>	scraper		
Hydropsychidae			
<i>Cheumatopsyche</i>	collector-filterer	11	6
<i>Hydropsyche</i>	collector-filterer	22	8
Hydroptilidae			
<i>Dibusa angata</i>	scraper		
<i>Hydroptila</i>	piercer-herbivore	1	1
<i>Ochrotrichia</i>	piercer-herbivore	3	
<i>Oxyethira</i>	piercer-herbivore		2
Lepidostomatidae			
<i>Lepidostoma</i>	shredder		
Leptoceridae			
<i>Ceraclea</i>	collector-gatherer	1	
<i>Oecetis</i>	predator	1	
Limnephilidae			
<i>Hydatophylax argus</i>	shredder		1
Philopotamidae			
<i>Chimarra</i>	collector-filterer	5	1
Polycentropodidae			
<i>Nyctiophylax</i>	predator		
Rhyacophilidae			
<i>Rhyacophila</i>	predator		
Thremmatidae			
<i>Neophylax</i>	scraper		

Lilly Bridge (hydrilla absent)			
Taxon	FFG	Growing season count	Senescent season count
AMPHIPODA			
Gammaridae			
<i>Gammarus</i>	collector-gatherer		
BIVALVIA			
Corbiculidae			
<i>Corbicula fluminea</i>	collector-filterer		1
COLEOPTERA			
Dryopidae			
<i>Helichus</i>	scraper		
Elmidae			
<i>Ancyronyx (adult)</i>	collector-gatherer		
<i>Ancyronyx (larvae)</i>	collector-gatherer		
<i>Dubiraphia (larvae)</i>	collector-gatherer		
<i>Macronychus (larvae)</i>	collector-gatherer	23	
<i>Microcylloepus (adult)</i>	collector-gatherer		
<i>Microcylloepus (larvae)</i>	collector-gatherer		1
<i>Optioservus (larvae)</i>	scraper		
<i>Oulimnius (larvae)</i>	collector-gatherer		
<i>Promoresia (adult)</i>	collector-gatherer	3	
<i>Promoresia (larvae)</i>	collector-gatherer	10	
<i>Stenelmis (adults)</i>	collector-gatherer	62	
<i>Stenelmis (larvae)</i>	scraper	6	1
Gyrinidae			
<i>Dineutus (larvae)</i>	predator		
Hydrophilidae			
<i>Berosus (larvae)</i>	shredder		
Psephenidae			
<i>Ectopria</i>	scraper	1	
<i>Psephenus (larvae)</i>	scraper		
<i>Psephenus (adult)</i>	nonfeeding		
DECAPODA			
Cambaridae			
<i>Cambarus</i>	collector-gatherer (omnivorous)		
DIPTERA			
Pupae			1
Ceratopogonidae			

<i>Atrichopogon</i>	collector-gatherer		
Chironomidae			
Chironomini			
<i>Microtendipes</i>	collector-filterer		3
<i>Paratendipes</i>	collector-gatherer		
<i>Polypedilum</i>	shredder	5	1
Orthocladiinae			
<i>Corynoneura</i>	collector-gatherer		
<i>Cricotopus/Orthocladius</i>	collector-gatherer	5	2
<i>Diplocladius</i>	collector-gatherer		
<i>Eukiefferiella</i>	collector-gatherer		2
<i>Lopescladius</i>	collector-gatherer		
<i>Nanocladius</i>	collector-gatherer		
<i>Parakiefferella</i>	collector-gatherer		
<i>Rheocricotopus</i>	collector-gatherer		
<i>Thienamanniella</i>	collector-gatherer		
<i>Tvetenia</i>	collector-gatherer		2
Tanypodinae			
<i>Alabesmyia</i>	predator		
<i>Thienemannimyia</i> group sp.	predator		
Tanytarsini			
<i>Cladotanytarsus</i>	collector-gatherer		
<i>Paratanytarsus</i>	collector-gatherer		
<i>Rheotanytarsus</i>	collector-filterer	2	1
<i>Sublettea</i>	collector-filterer		
<i>Tanytarsus</i>	collector-gatherer		4
Empididae			
<i>Hemerodromia</i>	predator		
Simuliidae			
<i>Simulium</i>	collector-filterer	2	15
Tipulidae			
<i>Antocha</i>	collector-gatherer		
<i>Tipula</i>	shredder		
EPHEMEROPTERA			
Baetidae			
<i>Acerpenna</i>	collector-gatherer	3	
<i>Baetis</i>	collector-gatherer	3	
<i>Heterocloeon</i>	scraper	6	3
<i>Procloeon</i>	collector-gatherer		

Caenidae			
<i>Caenis</i>	collector-gatherer		
Ephemerellidae			
<i>Ephemerella</i>	collector-gatherer	4	23
<i>Eurylophella</i>	collector-gatherer		5
Heptageniidae			
<i>Epeorus</i>	scraper		1
<i>Leucrocuta</i>	collector-gatherer	1	
<i>Maccaffertium</i>	scraper	1	1
<i>Stenacron</i>	scraper	1	
<i>Stenonema femoratum</i>	scraper	3	
Isonychiidae			
<i>Isonychia</i>	collector-filterer	1	3
Leptohyphidae			
<i>Tricorythodes</i>	collector-gatherer	10	
GASTROPODA	grazer		
ISOPODA			
Asellidae			
<i>Lircius</i>	collector-gatherer		
MEGALOPTERA			
Corydalidae			
<i>Corydalus</i>	predator		
<i>Nigronia</i>	predator		
ODONATA			
Aeshnidae			
<i>Boyeria vinosa</i>	predator		
Calopterygidae			
<i>Calopteryx</i>	predator		
<i>Hetaerina</i>	predator	1	
Corduliidae			
<i>Neurocordulia</i>	predator		
Coenagrionidae	predator		
Gomphidae			
<i>Gomphus</i>	predator	1	
OLIGOCHAETA	collector-filterer	3	26
PLATYHELMINTHES	omnivorous		
PLECOPTERA			
Capniidae			
<i>Allocaupnia</i>	shredder		9
Perlidae			

<i>Acroneuria</i>	predator		
<i>Agnetina</i>	predator	4	
<i>Neoperla</i>	predator		
<i>Perlesta</i>	predator		
Perlodidae			
<i>Isoperla</i>	predator		8
Taeniopterygidae			
<i>Taeniopteryx</i>	shredder		55
<i>Oemopteryx</i>	shredder		32
TRICHOPTERA			
Pupae			
Brachycentridae			
<i>Micrasema</i>	shredder	4	
Helicopsychidae			
<i>Helicopsyche</i>	scraper	2	
Hydropsychidae			
<i>Cheumatopsyche</i>	collector-filterer	4	
<i>Hydropsyche</i>	collector-filterer	19	1
Hydroptilidae			
<i>Dibusa angata</i>	scraper		
<i>Hydroptila</i>	piercer-herbivore	1	
<i>Ochrotrichia</i>	piercer-herbivore		
<i>Oxyethira</i>	piercer-herbivore	1	
Lepidostomatidae			
<i>Lepidostoma</i>	shredder	2	3
Leptoceridae			
<i>Ceraclea</i>	collector-gatherer	1	
<i>Oecetis</i>	predator		
Limnephilidae			
<i>Hydatophylax argus</i>	shredder		1
Philopotamidae			
<i>Chimarra</i>	collector-filterer	4	
Polycentropodidae			
<i>Nyctiophylax</i>	predator		
Rhyacophilidae			
<i>Rhyacophila</i>	predator	1	2
Thremmatidae			
<i>Neophylax</i>	scraper		