Adaptations to Invasion: Macroinvertebrate Community Response to the Invasive Submersed Macrophyte, *Hydrilla verticillata*, in the Emory River Watershed, Tennessee

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Adaptations to Invasion:

Macroinvertebrate Community Response to the Invasive Submersed Macrophyte, *Hydrilla verticillata*, in the Emory River Watershed, Tennessee

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Angelina Dominique Fowler

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Date

DEDICATION

To my husband, Jerrod W. Manning. I love you, Makka-Makka.

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Abstract

ANGELINA DOMINIQUE FOWLER. Adaptations to Invasion: Macroinvertebrate Community Response to the Invasive Submersed Macrophyte, *Hydrilla verticillata*, in the Emory River Watershed, Tennessee (under the direction of DR. STEVEN W. HAMILTON).

The Emory River Watershed (ERW), flowing through the Cumberland Plateau of Tennessee, features a network of high-quality, fast-flowing, deeply incised streams. This area encompasses the Obed Wild and Scenic River (OWSR), managed by the U.S. National Park Service under the National Wild and Scenic River System (NWSRS). The invasive macrophyte *Hydrilla verticillata* (a.k.a. hydrilla) is established within this virtually pristine environment. Macroinvertebrates were sampled from hydrilla-infested and non-infested riffles and upstream in associated pools with significant submersed vegetation. Nine study sites consisted of areas both within and outside of the OWSR boundaries, with hydrilla-infested stream portions occurring along Daddy's Creek and Obed River, and comparative non-infested areas present along Clear Creek and upper Daddy's Creek. Analysis of macroinvertebrate taxa collected in September 2010 indicated no significant differences in mean Shannon-Weaver Diversity values between hydrilla-infested and non-infested riffle and pool habitats as determined by One-way Analysis of Variance (ANOVA). Macroinvertebrate functional feeding groups (FFG) were also evaluated for all riffle and pool communities via a Multi-Way Contingency

Analysis, demonstrating significant differences in the proportion of FFG's between all hydrilla-infested and non-infested habitats. There was a higher proportion of collector-filterers in hydrilla-infested riffles and higher proportion of collector-gatherers in hydrilla-infested pools. Additionally, Morisita's Index of Community Similarity (MICS), which was used to determine macroinvertebrate abundance similarities among hydrilla-infested and non-infested riffle and pool sites, respectively, indicated variability among similarity comparisons. One-way ANOVA identified significant differences between means of MICS among site comparisons, signifying further differences in taxa composition among hydrilla-infested and non-infested riffle and pools. Furthermore, Principal Component Analysis (PCA), a mutli-variate method used to distinguish relationships of macroinvertebrate taxa abundance between hydrilla-infested and non-infested sites, evaluated distinct differences between pool sites. Based on these results acquired from the duration of this study, hydrilla was found to be important in influencing the spatial arrangement and functioning of various macroinvertebrate communities within the ERW. This study also predicts the importance of hydrilla as a structural and nutritional resource for macroinvertebrates, as demonstrated by FFG analyses between hydrilla-infested and non-infested sites. It is anticipated that seasonal fluctuations in biomass associated with growth and senescence will be very important in ecosystem processing. Further research and long-term monitoring needs to be conducted to determine other possible impacts hydrilla may have on other freshwater biota while it persists in this high-quality stream environment.

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CHAPTER I

INTRODUCTION

In 1968, Congress passed the National Wild and Scenic River System Act for the protection of outstanding lotic systems. The National Wild and Scenic River System was established to support conservation of rivers and the surrounding environments while ensuring the free-flowing state of these rivers, the protection of water quality, and the fulfillment of other "national conservation purposes" (Wild and Scenic Rivers Act, 1968). Located within the Emory River Watershed (ERW) of east Tennessee, the Obed Wild and Scenic River (OWSR) was recognized by the National Wild and Scenic River System in 1976 to be administered by the U.S. National Park Service (Interagency Wild and Scenic Rivers Council, 2011). In 2004, the invasive submersed macrophyte, *Hydrilla verticillata* (i.e. hydrilla), was discovered in several stream reaches in the OWSR during a rare and endangered floristic survey of the Obed River Gorge (Estes and Fleming, 2008). Estes et al. (2010) performed a survey of the distribution, abundance, and habitat colonization of hydrilla in the majority of the ERW to determine the extent of the hydrilla infestation in an effort to preserve the virtually natural, free-flowing environment. Because the streams of the ERW provide high quality habitat for many aquatic organisms, this thesis research was conducted to begin efforts to identify potential impacts of hydrilla on the native freshwater biota.

Human Impacts on Ecosystems

The environment is not static, but rather involves an ever-changing system of biotic and abiotic factors that interact with the organisms in that environment. In fact, the dynamic nature of Earth, including its flora and fauna, is reflected by numerous environmental changes throughout geologic history (Sprugel, 1991; Cox, 1999). The ecosystem processes that occur within both terrestrial and aquatic environments largely depend on gradual changes that allow for the development of more diverse and stable conditions with time (Orians, 1974; Rapport et al., 1998). Ecosystem change presents opportunities for many organisms, where fundamental processes such as extinction, biological invasion and species succession can occur (Fraterrigo and Rusak, 2008). Although the environment is capable of recovering from change, coping with disturbance or resisting displacement in structure or function is an important aspect of ecosystem resilience (Westman, 1978). Hill (1987) defined resilience as "the ability to recover to the initial state after disturbance." Resilience allows for ecosystems to sustain damages by replenishing the pre-disturbance state and structure, therefore recovering the resources that inhabiting organisms depend on. This flexibility is linked to the reorganization of ecosystems, which is associated with the response of organisms to these changes. Biological diversity, or the variations in genes, organisms and ecosystems, plays a significant role in the sustainability of dynamic ecosystems. It is what drives productivity, stability and resilience, allowing these complex systems to remain sustainable and maintain the organization of ecosystem services (Cox, 1999; Elmqvist et al., 2003; Westman, 1978).

The origination of disturbance and the resulting changes made to the environment are extremely diverse. Both anthropogenic influences and natural phenomena are responsible for affecting ecosystem dynamics, resulting in a broad range in ecological response and reorganization (Fraterrigo and Rusak, 2008). Ecological interactions among organisms, including those with humans, have created and allowed for the persistence of ecosystems, which in turn has formed the foundation for evolutionary adaptations and ecological stability (Cox, 1999).

Although considered an integrated component of the environment, humans can be an unnatural, external, and often destructive force on natural ecosystems. Anthropogenic influences have significantly impacted nearly all ecosystems on Earth and therefore play an important role in ecosystem transformation (Hobbs et al., 2006; Jacobs, 1975; Vitousek et al., 1997). The environment is constantly changing with some degree of sustainability, yet humans magnify these changes through continuous modifications to the natural world. Exponential human population growth has increased demand for resources. Furthermore, advances in technology have allowed for the alteration of ecosystems for commercial, industrial, residential and agricultural purposes.

Human impacts result in disruption of ecosystem processes and modification of ecosystem composition (Chapin et al., 1997). As a result, the constancy of human activities has contributed to significant declines in biodiversity, reducing the capacity for ecosystems to buffer disturbance and to restore structure and function following disturbance (Elmqvist et al., 2003; Westman, 1978). The interactions between overexploitation, habitat destruction (including pollution), introduction of alien species and the diseases spread by alien species are contributing to the reduction of biodiversity around the world (Wilcove et al., 1998; Wilson, 1992).

A major concern in both terrestrial and aquatic environments is habitat alteration and degradation. Because the variety in habitat types is associated with species diversity, the elimination of these habitats drastically reduces the ability for many organisms to survive, contributing to the disappearance of species at an alarming rate. Although habitat destruction and landscape transformation is the primary threat to ecosystems worldwide, the second most critical threat, which often coincides with habitat degradation, is the establishment of invasive species (Chapin et al., 1997; Vitousek et al., 1997; Wilcove et al., 1998).

Invasive Species

Species exhibit distributions that are influenced by a variety of physical and chemical attributes and reflect their evolutionary history. Although some organisms have limited ranges, most respond to the changes or disturbances in their environment through some method of dispersal. Dispersal of organisms is a natural process whereby they shift distributions to alternative geographical location where conditions are favorable (Cox, 1999; Croteau, 2010). The mechanisms of dispersal are diverse and, therefore, vary in the nature and effectiveness. This process is significant and ecosystems depend on it for essential development of ecosystem functioning, gene flow and evolution (Gibbs et al., 2010; Sexton et al., 2009). Given a long span of time, many organisms are capable of long-distance dispersal, surmounting formidable barriers, if necessary (Cox, 1999).

Natural barriers, such as mountain ranges and water bodies, result in geographic isolation essential for species and ecosystems to evolve. However, global movements of humans has elevated the dispersal process, rendering these geographic barriers ineffective by expanding the dispersal distance of species into areas that naturally would not have occurred (Hobbs et al., 2006). Since species respond to changes in the environment where they thrive, it can be difficult to distinguish whether an organism has expanded or shifted its range due to natural or human-induced causes (Cox, 1999). Nevertheless, transportation technologies and global trade have provided new means of dispersal that do not occur in nature (Jenkins, 1996). Although biological dispersal is a critical process for ecosystem stability, the deletion or addition of one or more species, especially through human activities, can alter diversity and species interactions, resulting in major impacts to ecosystem functionality (Orians, 1974).

Human involvement is a crucial aspect of the invasion process where exotic flora and fauna are brought into regions outside of their native range, either intentionally or accidentally (Pyšek and Richardson, 2006). The first stage in exotic species establishment is introduction, which allows for the persistence of populations in a new geographical range (Richardson et al., 2000). Typically, after multiple introductions occur, exotic species have the potential to become invasive if conditions are favorable for them to proliferate (Jacobs, 1974). Exotic organisms are considered to be invasive when they establish themselves in regions outside of their native range, threatening native ecosystems or human health. Not all exotic species exhibit invasive characteristics, but those that do are capable of introducing and harboring exotic diseases, in addition to outcompeting and displacing analogous native species by encouraging homogenization of biodiversity (Chapin et al., 1997; Cox, 1999; Pyšek and Richardson, 2006). Invasive species are typically habitat generalists, having the potential to colonize in virtually any environment, yet most thrive in areas similar to their natural habitat. Many exotic species that become invasive are adapted for successful establishment and proliferation based on aggressive reproductive characteristics. These invasive alien species often become naturalized when they reproduce consistently and are capable of sustaining populations despite human efforts to prevent their establishment (Pyšek and Richardson, 2006; Richardson et al., 2000). For example, *Pueraria montana* (kudzu), a Japanese vine purposefully brought to North America as an ornamental in 1876, has become established and overgrown forests and roadsides in approximately 3 million acres in the southeastern United States. Its ability to fix nitrogen allows it to grow very quickly, hindering the growth of nearby native vegetation adapted to low-nitrogen soils and contributing to the eutrophication of aquatic environments though runoff. It has had a considerable impact on the economy, proven nearly impossible to manage, particularly in its current widespread distribution throughout the Southeast (Blaustein, 2001; Simberloff, 2011).

Inadvertent or deliberate introduction of exotic species has had dramatic effects on terrestrial and aquatic environments, causing catastrophic shifts to the environment and detrimental impacts on biodiversity worldwide (Pyšek and Richardson, 2006). Although many exotic species have become nuisances in the modern world, the influences that they have on natural ecosystems are not just a recent development. The year 1492 marked the "discovery" of the New World by Christopher Columbus, and thanks to the European exploration and colonization that followed, a phenomenon that has been called "the Columbian Exchange" began. This event is marked by the exchange of flora and fauna (including disease) between the eastern and western hemispheres (Crosby, 1972). While it is true humans have been an integrated component of the environment before the year1492, the Columbian Exchange is considered to have historically formed the foundation for the global impact of humans on the environment. Yet, this event provided an international exchange of "necessities" ranging from organisms to commodities that shaped modern civilization and culture throughout the world. Elton (1958) describes the Columbian Exchange as "one of the great historical convulsions of the world's flora and fauna" due to the significant impact that was made as a result of global species transference (Hobbs et al., 2006; Jenkins, 1996). Although humans have historically been aware of the international exotic species transference, the consequences these alien species present to ecosystems, until recent decades, have not been recognized as problematic.

Threats to Freshwater Ecosystems

Aquatic ecosystems are more at risk than many terrestrial ecosystems. In particular, freshwater environments, which make up only 0.01% of the world's water, directly support more than 6% of all described species on Earth. It is thought that biodiversity decline in freshwater ecosystems is much greater than terrestrial ecosystems due to the demand on freshwater as a resource for human consumption. Dudgeon et al. (2006) describes global freshwater biodiversity as threatened by five major interactive components: over-exploitation (primarily vertebrates), pollution, habitat degradation, alteration of flow in lotic environments, and invasive species establishment. Although the transformation of land and degradation of habitats is the primary driving force in the loss of biodiversity worldwide, invasive species are recognized as the most rapidly growing threat in both terrestrial and aquatic environments (Cox, 1999; Padilla and Williams, 2004; Vitousek et al., 1997; Wilcove et al., 1998).

Approximately one third of the world's most costly, uncontrollable and detrimental aquatic invasive organisms are aquarium or ornamental species (Padilla and Williams, 2004). The primary source of invasive aquatic species has previously been recognized as ship ballast water, yet the essentially unregulated aquarium trade and aesthetics (e.g., water garden plants) are increasingly recognized as significant contributors (Padilla and Williams, 2004). In many instances, these organisms are deliberately brought to a new area for commercial use or personal aesthetics where they are purposefully released or escape captivity. Others are inadvertently released, for example when aquatic "hitchhikers" are introduced through some sort of economically important activity via shipments of other plant or animal materials (Anderson, 2011).

Invasive aquatic plants, in particular, have had major impacts on biodiversity in freshwater ecosystems. Over 35 families of freshwater and riparian plants include species considered to be invasive. Several hundreds are considered nuisances to aquatic environments, threatening the structure, function and diversity of natural aquatic systems (Anderson, 2011). Habitats that are susceptible to invasive aquatic plants are diverse, ranging from natural lentic and lotic systems to man-made irrigation canals, reservoirs, hydroelectric power systems, and aquaculture facilities.

Role of Macrophytes in Freshwater Ecosystems

Lentic and lotic ecosystems are highly variable and distinctive in terms of physical, chemical and ecological characteristics, as are the many uses by humans. The characterization of aquatic plants is based on their ability to adapt to the physicochemical features of the aquatic habitat in which they live, acquiring the resources necessary for development and reproduction (Anderson, 2011). Macrophytes can either grow partially or completely in water, and are typically found in the littoral zone of lotic and lentic environments, where light penetrates to the substrate. Macrophytes can be categorized into four functional groups: free-floating, floating-leaved, emergent or submersed (Cook, 1990; Lacoul and Freedman, 2006). Free-floating plants are those that do not contact the sediments, hanging unanchored in the water column (Anderson, 2011; Lacoul and Freedman, 2006). Representative free-floating plants include invasive *Eichornia crassipes* (water hyacinth) and *Pistia stratiotes* (water lettuce). Floating-leaved plants have some leaves that float on the surface of the water, but are rooted in sediments (Lacoul and Freedman, 2006). Examples of floating-leaved plants include *Nymphaea odorata* (white water lily) and *Nelumbo* spp. (lotus). Emergent plants are rooted in the sediment, typically inhabiting the shallowest portions of the littoral zone where the majority of their aerial system extend above the surface of the water. Examples include invasive *Lythrurum salicaria* (purple loosestrife) and *Butomus umbellatus* (flowering rush). Those that are rooted in the sediment and grow completely underwater are submersed macrophytes. These plants grow in the deepest portion of the littoral zone where they are subjected to varying levels in light. Examples include *Myriophyllum* *spicatum* (Eurasian watermilfoil), *Potamogeton crisupus* (curlyleaf pondweed) and *Hydrilla verticillata* (hydrilla).

All macrophyte types play an important role in lentic and lotic systems worldwide, significantly influencing physical, chemical and biological parameters through their development and metabolic activities (Madsen et al., 2001). Because their growth habit reflects the physical and chemical features of an aquatic habitat, aquatic plants vary in their influences on productivity and ecosystem processes. In most freshwater environments, macrophytes are important in primary production, stabilizing chemical and physical characteristics, serving as a substrate for epiphytic algae, and providing food and habitat for aquatic and semiaquatic animals, vertebrates and invertebrates alike (Carpenter and Lodge, 1986; Kaenel et al., 1998).

Submersed macrophytes, in particular, have major effects on productivity and biogeochemical processing in freshwater, because they represent a living link between the sediment and water column in lentic and lotic systems (Carpenter and Lodge, 1986). These aquatic plants largely influence the physical environment by impeding water flow, increasing water depth, stabilizing sediment and retaining particles in substrate, mediating temperature, and reducing light penetration into the water column (Carpenter and Lodge, 1986; Gregg and Rose, 1982; Madsen et al., 2001). Additionally, macrophytes are important in dissolved oxygen and carbon dioxide flucuations, and in nutrient cycling, including the release of dissolved solids (Carpenter and Lodge, 1986; Marshall and Westlake, 1978). In general, submersed aquatic vegetation is important in the physical, chemical and biological processes of an aquatic habitat. The amount of macrophyte biomass can influence inhabiting organisms, particularly those dependent on it for habitat, including macroinvertebrates (Barko et al., 1991; Carpenter and Lodge, 1986; Madsen et al., 2001).

Macroinvertebrates are a large component of many freshwater ecosystems and are easily influenced by variability in the environment. Macrophytes play an important role as a substrate, refuge from predators, and indirect (i.e., epiphytic algae), and direct food source for macroinvertebrates (Newman, 1991; Parsons and Matthews, 1995). Due to their relatively sedentary nature and sensitivity to long and short-term changes, the structure and function of macroinvertebrates is important in community assessment and evaluation of impacts in freshwater environments and the overall habitat quality (Davis and Lathrop, 1992).

Both natural and anthropogenic disturbances can result in large ecosystem response to variations in submersed aquatic vegetation, in turn affecting biotic interactions of macroinvertebrates (Kaenel et al., 1998). Aquatic macrophytes are important in the structural and spatial distribution of macroinvertebrates, providing oviposition sites and shelter for many species (Ward, 1992). The ability of a macrophyte to support macroinvertebrates varies, where conditions such as surface area, leaf morphology, nutrient uptake and chemical secretions play a role in abundance and species richness (Krull, 1970). Macrophytes also affect trophic relationships and influence types of functional feeding groups present in a specific freshwater habitat, especially during plant senescence (Gregory, 1983; Kaenel et al., 1998; Newman, 1991). Shredders benefit from decaying (typically allochthonous) vegetation, grazers (scapers) from the consumption of epiphytic and epilithic algae and other microflora, and collector-gatherers from fine particulate organic matter that accumulates on and among the substrate materials, including macrophytes. Submersed macrophytes therefore support varying abundances, distribution and diversity of macroinvertebrates (Kaenel et al., 1998). Despite their ecological importance, excessive growth of aquatic macrophytes, particularly of those with invasive characteristics, has the potential to drastically influence aquatic communities (Bates and Hentges, 1976).

Biology of *Hydrilla verticillata*

Hydrilla verticillata (L.F.) Royle (also known as hydrilla or water thyme) is an invasive, submersed aquatic macrophyte thought to be native to Asia (Cook and Luönd, 1982). Since its discovery in the United States in the 1950's, hydrilla has altered freshwater ecosystems due to its many survival adaptations that allow it to persist and reproduce in nearly all aquatic habitats. Throughout portions of North America, hydrilla has established itself as one of the most devastating aquatic weeds, impacting chemical, physical, and biological aspects of freshwater environments, including lakes, wetlands and rivers (Langeland, 1996). Hydrilla has significantly impaired the natural state of the freshwater ecosystems it has colonized because its physiological characteristics, reproductive potential, and aggressive growth allow it to disperse rapidly (Bates and Hentges, 1976; Langeland, 1996).

The physiological adaptations of hydrilla include greater shade tolerance and low respiratory rates. Compared to other submersed macrophytes, hydrilla is adapted to very lower light intensities, exhibiting greater shade tolerance than most aquatic plant species, higher rates of photosynthesis, and low rates of dark respiration and photorespiration (Bowes et al., 1977; Cook and Lüönd, 1982; Jana and Chouduri, 1979).

One of the most significant aspects of hydrilla that allows it to successfully colonize many freshwater habitat types is its ability to reproduce with an assortment of asexual and sexual means. Hydrilla can reproduce from seeds, fragmentation, tubers and turions (Langeland, 1996). Fragmentation allows hydrilla to establish a new population from a single whorl of leaves. The production of turions in leaf axils and tubers (subterranean turions) that form terminally on rhizomes adds to the establishment of new populations, and allows hydrilla to over-winter and remain viable during non-growth periods (Steward and Van, 1987). Additionally, tubers are resistant to desiccation and can sustain for several days out of water. The multiple reproductive capabilities of hydrilla have allowed for proliferation in virtually every freshwater environment to which it is introduced (Cook and Lüönd, 1982).

Although *Hydrilla* is considered a monotypic genus with a single species, it demonstrates considerable genetic variation. *Hydrilla verticillata* is highly polymorphic, having several biotypes, two of which have established in North America, one monoecious and one dioecious (Cook and Lüönd, 1982; Netherland, 1997; Pieterse, 1981; Pieterse et al., 1985; Verkleij et al., 1983). Although both forms share similar characteristics that distinguish them from other submersed aquatic plants, they differ genetically, morphologically, and ecologically from one another (Steward and Van, 1987). For example, the monoecious form, which possesses both staminate (male) and pistillate (female) floral parts, has an annual growth habit and will first spread along the hydrosoil of an aquatic habitat before growing upward through the water column. In contrast, the dioecious form is either staminate or pistillate, has a perennial growth habit, and develops vertically in the water column before forming a dense canopy near the surface. Both also differ ecologically, genetically and morphologically as well as varying in reproductive capabilities and growth conditions, such as size and production of turions and tubers (Steward and Van, 1987).

Ecosystem-level Influences of Hydrilla

In addition to its multiple reproductive capabilities and aggressive growth patterns, hydrilla is capable of altering the abiotic and biotic factors of freshwater ecosystems (Langeland, 1996). Although submersed aquatic vegetation can be beneficial and necessary for the ecosystem functionality, *H. verticillata* can negatively affect ecosystem processes during and after aggressive growth and development (Bates and Hentges, 1976; Langeland, 1996). Once established in an aquatic environment, hydrilla is capable of physically shading and outcompeting native submersed aquatic vegetation due to its exponential proliferation, although interspecific competition among macrophyte species is poorly understood (Wetzel, 2001). This adds to the homogenization of macrophyte composition, potentially altering the balance of the ecosystem (Langeland, 1996). Other than aquatic plant biodiversity loss, however, hydrilla has not been observed to diminish the biodiversity of other aquatic communities, such as macroinvertebrates, epiphytic algae, fish, and waterfowl. In fact, increased aquatic vegetation may be ecologically beneficial to some communities and has been demonstrated to encourage the abundance and species richness of macroinvertebrates by increasing the amount of available habitats and food, which in turn increases populations of fish species (Moxley and Landford, 1982; Newman, 1991; Thorp et al., 1997).

Because submersed aquatic vegetation is also important in providing epiphytic algae with a substrate for growth, hydrilla is likely responsible for the support and productivity of epiphytic algae in aquatic habitats. Although hydrilla may support epiphytic algae, competition for similar resources such as available light and nutrients has been shown to prevent successful development of other macrophytes (Dunn et al., 2008). Takashi et al. (2004) demonstrated that epiphytic algae were responsible for low light penetration on the leaf surfaces of the submersed aquatic macrophyte, *Potamogeton perfoliatus*. Low light levels in turn reduced the amount of growth and production, and interrupted the physiological ability of *P. perfoliatus* to photosynthesize. Most submersed aquatic vegetation is dependent on high light levels for development, but hydrilla has been found to be capable of adapting to extremely low light levels by exhibiting greater shade tolerance and developing in deep water where limited light is available (Bowes et al., 1977). This demonstrates hydrilla's ability to compete with other aquatic plants for limited dissolved carbon in water and perhaps photosynthesize earlier in the daytime where high light levels are not sufficient (Langeland, 1996). Although epiphytic algae are likely to develop on the canopy of hydrilla, the low light levels that may occur from the growth of the algae will probably not have any effect on hydrilla's physiology. Additionally, since hydrilla is capable of developing under low light conditions (Bowes et al., 1977), epiphytic algae may not be able to develop due to the limited amount of light, especially in deeper waters or in the understory of the hydrilla canopy.

Johnson and Montalbano (1987) noted that hydrilla provides an ideal habitat for wintering waterfowl. Because waterfowl potentially feed upon hydrilla beds, there are concerns that waterfowl may in turn transport and disperse propagules. Joyce et al. (1980) demonstrated that tubers and turions are spread through the digestive tracts of some waterfowl and are able to survive ingestion and regurgitation. It is also possible that waterfowl may transport stem fragments from monoecious hydrilla or seeds from dioecious types via attachment to body parts (e.g., feet, feathers), but this has not yet been definitively established (Johnson and Montalbano, 1987). Langeland (1996) stated that the passing of viable seeds through waterfowl digestive tracts could be important in "natural, long distance dispersal."

Environmental factors such as light, water temperature, sediment composition, and the presence of carbon and other nutrients, play a key role in influencing the productivity and distribution of submersed aquatic vegetation (Barko et al., 1986). In addition to providing habitat for aquatic species, submersed aquatic vegetation is also important in the alteration or the stabiliziation of physical and chemical properties in freshwater ecosystems (Barko et al., 1991). Although submersed aquatic vegetation influences several aspects of freshwater environments during normal plant development and metabolic activity (Zimba et al., 2001), hydrilla may have adverse effects on the environmental factors of a balanced aquatic habitat. The aggressive growth and development exhibited by hydrilla, in which it densely colonizes aquatic habitats, may alter the natural chemical and physical environment.

Lentic and lotic environments may exhibit markedly different physical and chemical characteristics; therefore, the presence of specific types of macrophytes and its abundance and biomass will influence the ecosystems differently. The development of hydrilla may be similar in both types of habitats, although dispersal and propagation will vary. Additionally, its effects on the chemical and physical properties will differ between the two habitat types. For example, lentic water bodies exhibit limited water movement in terms of flow, but do experience some mixing when aquatic species such as fish and phytoplankton swim through the water column and more so when wind moves over the surface, forming waves and currents (Agrawal, 1999). Hydrilla is fairly limited as to what physical properties may be influenced in lentic habitats due to lack of constant flow in these systems, although lake circulation may be affected. It is clearly understood that increased beds of macrophytes impede water flow in both lentic and lotic systems, although the reliance of lake fluctuations on macrophyte biomass and canopy structure is not yet known (Carpenter and Lodge, 1996). Consequently, surface wind stress is reduced when it encounters aquatic vegetation, which reduces the mixing layer depth in lentic systems, particularly in the littoral zone (Coates and Folkard, 2009; Herb and Stefan, 2005). Hydrilla abundance throughout a lake may have significant effects on vertical mixing in lakes. Furthermore, in lotic systems where water is constantly moving, the flow of water will be impacted with increased macrophytic biomass (Carpenter and Lodge, 1996), whereby hydrilla can slow the velocity of downstream flow.

Barko and Smart (1981) demonstrated that hydrilla is capable of altering photosynthetic capacity over a large range of light availability and can remain metabolically active even at temperatures as high as 16°C. Because photosynthetic capacity positively correlates with light availability and temperature increases as light penetrates the surface of the aquatic environment, increased growth and development of the hydrilla canopy may also encourage increases in water surface temperatures. However, light is attenuated exponentially with depth within the macrophyte canopy and thermal gradients are eliminated with circulation of water, particularly in streams (Carpenter and Lodge, 1996), therefore, increased macrophyte growth may actually reduce temperatures due to shading of the water column.

Photosynthetic capacity and increased macrophytic growth is also correlated with dissolved oxygen (DO) and pH. Negative effects on fish and macroinvertebrates are likely to occur if DO levels fall well below 5mg/L (Caraco and Cole, 2002). During the day, beds of aquatic macrophytes release large amounts oxygen, increasing DO (Kaenal et al., 2000). However, during low light periods, typically at night, aquatic plants continue to respire, taking up large amounts of oxygen from the water. Because hydrilla develops densely throughout the water column, nighttime respiration lowers dissolved oxygen levels due to respiratory uptake of oxygen. Although hydrilla often significantly decreases oxygen levels in lakes, it may not do so in lotic systems due to the continuous flow and turbulence of water which entrains oxygen into the water (Wetzel 2001).

Submersed aquatic vegetation can modify varying levels of pH in freshwater ecosystems. Although inorganic carbon has a large impact on pH levels, free carbon dioxide is quickly used for photosynthesis (Raven, 1970; Van et al. 1976). Reddy and Busk (1985) demonstrated that increasing submersed vegetation may cause declines in nitrogen and phosphorus levels of nutrient enriched waters, where hydrogen ions are removed from the water column through assimilation, subsequently causing an increase in pH levels. Furthermore, metabolism of submersed macrophytes can remove inorganic carbon, in turn reducing the pH of the water. Because hydrilla grows prolifically, it can be expected to maximize carbon, nitrogen, and phosphorus uptake during periods of development. Conversely, during senescence of shoots, a large release of dissolved substances would occur, particularly organic carbon, which can cause an increase in ion concentration where pH levels can decrease (Carpenter and Lodge, 1996).

Physical properties within a freshwater ecosystem can change drastically with increases in aquatic vegetation. Submersed macrophytes significantly influence physical properties of the aquatic environment, including interactions between sedimentation rates and water movement. Because it is capable of rapid proliferation and dense growth, hydrilla can modify aquatic habitats by limiting movement of water and light in the water column (Crooks, 2002), reducing erosion and turbidity by stabilizing deposited sediments (Madsen et al., 2001), and decreasing phytoplankton populations by filtering nutrients, therefore promoting water clarity where established (Langeland, 1996).

Study Objective

The establishment of *Hydrilla verticillata* in the Emory River Watershed (ERW) of east Tennessee provides unique insight into the previously unstudied establishment of this species in cool, rugged, high-gradient streams that flow through this area. Furthermore, the ERW encompasses the Obed Wild and Scenic River (OWSR), an area containing relatively pristine, free-flowing streams that are protected under the National Wild and Scenic River System. Since hydrilla is characterized as an invasive species, its establishment in the OWSR can potentially have detrimental effects on the structure and function of macroinvertebrate communities. The objective of this project was to determine possible impacts of hydrilla on macroinvertebrate communities in the ERW by comparing macroinvertebrate communities collected from hydrilla-infested and non-infested stream reaches. Metrics of community structure and function such as diversity, eveness, community similarity, and functional feeding group composition were compared in riffle and pool habitats which are either infested with hydrilla or not infested. This study attempts to determine possible ecosystem-level consequences of hydrilla in this lotic environment. Thus, the null hypothesis of this thesis research is:

H_0: There is no difference in metrics of macroinvertebrate community structure and function between hydrilla-infested and non-infested riffle communities or hydrilla-infested and non-infested pool communities.

Significance of the Study

Understanding the community-level impacts of increased macrophyte biomass on macroinvertebrates in the ERW can provide additional information on biotic interactions that occur in lotic systems, specifically between macroinvertebrates and submersed macrophytes. Additionally, it will provide insight on the responses of macroinvertebrate communities to invasive aquatic plant species in stream ecosystems, which could facilitate the development of long-term monitoring protocols as an initial step in invasive species management. Furthermore, this study will aid in providing information to the National Park Service and other agencies for the protection of natural resources in a time of environmental and human-induced change, emphasizing the need for the conservation of biodiversity in stream ecosystems.

CHAPTER II

STUDY AREA

Location and Background

The Emory River Watershed (ERW) consists of a network of cool, clear, deeply incised streams in the Cumberland Plateau physiographic province of east Tennessee (Fig. 1). This river system includes several nearly pristine and undisturbed free-flowing streams administered by the U.S. National Park Service as the Obed Wild and Scenic River (OWSR). The OWSR has remained in free-flowing condition since the Wild and Scenic River System Act in 1968, which was established by Congress to maintain lotic systems of the United States that are "scenic and wild" with "outstandingly remarkable scenic, recreational, geologic, fish and wildlife, historic, cultural or other similar values (Wild and Scenic Rivers Act, 1968; Interagency Wild and Scenic Rivers Council, 1998)." Approximately 2078 ha of the ERW are protected within the OWSR, which covers 73 km of streams including portions of Daddy's Creek, Clear Creek, Obed River and Emory River in Cumberland, Morgan and Fentress Counties (TDEC, 2002; TVA, 1998; Fig. 1). The ERW also includes one designated state Natural Area (Frozen Head State Park) comprising 4806 ha of undisturbed forest located to the east of the OWSR. Additionally, the Catoosa Wildlife Management Area, located at the western and southern periphery of the OWSR, covers 32,374 ha of the ERW. Much of the surrounding landscape encompassing the ERW is deciduous forest (>72%), but includes some agriculture and coal mining activities, although only agriculture practices are conducted on private lands adjacent to the OWSR (TDEC, 2002; TDEC, 2008; TVA, 1998).

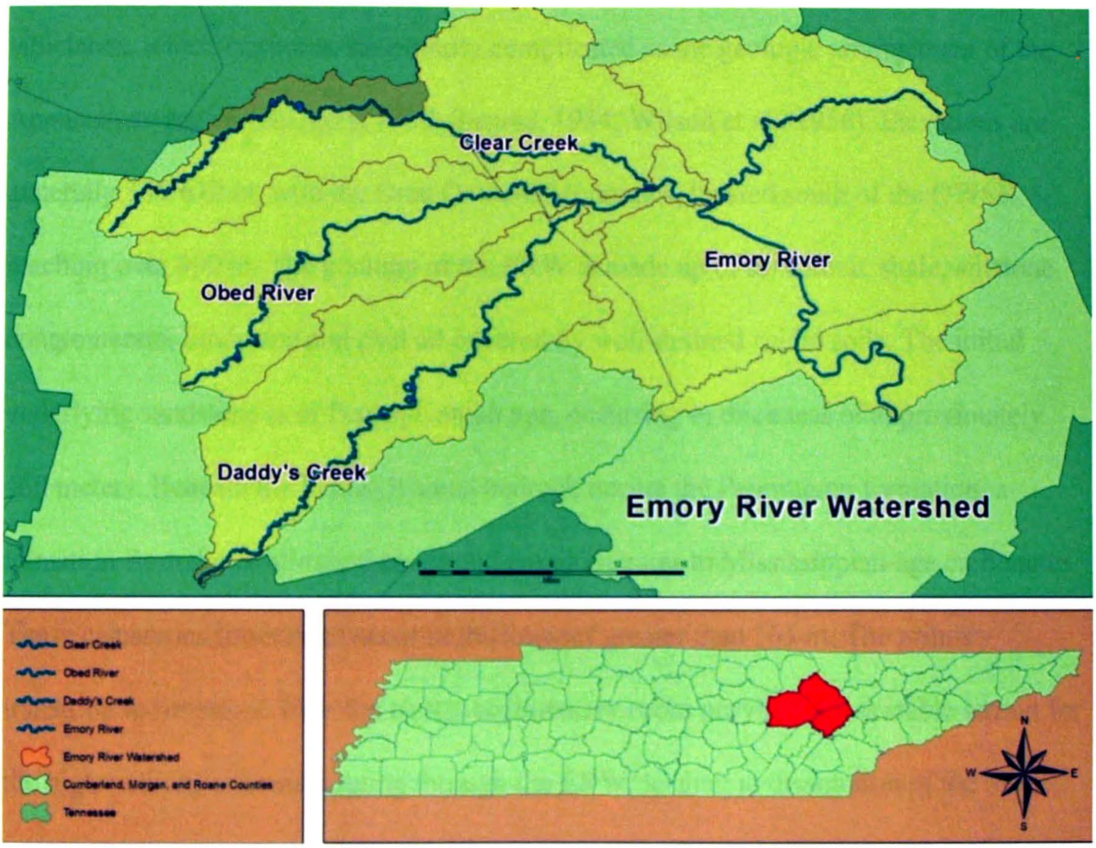

Figure 1. Tennessee map highlighting the location of the Emory River Watershed, the majority in Morgan, Cumberland and Roane counties (small portion of Fentress and Bledsoe counties also shaded), including the major tributaries of Daddy's Creek, Obed River, Clear Creek and Emory River. (Map courtesy of Jerrod W. Manning, 2011).

Physiography and Geology

The physiographic region of the Cumberland Plateau is a geologic setting in Tennessee that lies to the western margin of the southern Appalachians, extending southwestward across Virginia and Kentucky through Tennessee to northern Georgia and northern Alabama. The terrain is partially composed of large, rugged, flat-topped tablelands, which are not as structurally complicated as the geologic arrangement of the Appalachian region (Rodgers, 1953; Stearns, 1954; Wilson et al., 1956). Elevations are generally 366-610 m, with the Crab Orchard Mountains, located south of the OWSR, reaching over 900 m. The geology of the ERW is made up of sandstone, shale, siltstone, conglomerate, limestone and coal all covered by well-drained acidic soils. The initial underlying sandstone is of Pennsylvanian age, occurring in thickness of approximately 460 meters. Beneath the Pennsylvanian bedrock occurs the Pennington formation, a transition from the clastic sandstones and conglomerates to Mississippian-age carbonates. These calcareous limestones occur in thicknesses greater than 305 m. The primary transition to limestone from the clastic sedimentary rocks provides a less stable terrain for the high-velocity streams running through the ERW, leading to dissolution of the rock and the formation of karst and cave systems in the area (Miller, 1974). As the network of streams incised the Pennsylvanian cap rock, large angular slabs of sandstone eroded. This process resulted in a separation of deep, vertical slopes from the plateau forming canyons in which talus accumulates, contributing to the large boulder and cobble substrata that comprise the substrate of many stream reaches in the ERW (Miller, 1974; Rodgers, 1953; Stearns, 1954; TDEC, 2002; TDEC, 2008; TVA, 1998; Wilson et al., 1956).

Hydrology

The four major streams of the ERW drains approximately 1,593 km^2 include the Obed River, Clear Creek, Daddy's Creek, and the Emory River to its confluence with the Clinch River (TDEC, 2002; USGS, 2011). The steepest stream gradients are present in downstream-most reaches, with drops averaging 3.6 to 6.5 m per km. Some of the most rugged landscape found in the ERW is located in the headwaters of the Emory River in Morgan County, which drains an area of 3,236 km^2 (TVA, 1998). Only a short reach of the Emory River from its confluence with the Obed River to Nemo Bridge is included within the OWSR boundaries (TVA, 1998; Fig. 1).

The Obed River is the largest tributary of the Emory River, draining an approximate total area of 1,295 square km. Its headwaters are located outside of the OWSR boundaries a few kilometers northwest of Crossville, Tennessee. Daddy's Creek and Clear Creek are the major tributaries which join the Obed River only a few kilometers upstream of its confluence with the Emory River (Fig. 1). Clear Creek drains approximately 448 km^2 in the northwest portion of the ERW, flowing northeast from its source outside of the OWSR boundaries to its junction with Obed River, 6.4 km above the Obed River and Emory River confluence. The largest tributary of Obed River, Daddy's Creek, drains approximately 453 square km, flowing northeast to its junction with Obed River 14.5 km above the Obed River and Emory River confluence (TVA, 1998; Fig. 1).

The flow of water in the ERW is heavily influenced by seasonal precipitation, runoff patterns, groundwater recharge and flow alterations such that water levels and velocity can change quickly (TVA, 1998). Therefore, the stream conditions within the OWSR change dramatically with weather conditions and seasons. During the summer months when precipitation is generally lower, the streams reflect more of a discontinuous pattern, in which pools form with little or no surface flow between them. Both the winter and spring seasons tend to offer more precipitation to drive higher flow, where discharge has been measured up to 190,000 cfs in the Emory River (TVA, 1998; USGS, 2011).

CHAPTER III

METHODS & MATERIALS

National Park Service Research Permit

In compliance with the National Park Service (NPS), a research permit was acquired to conduct specimen and data collection in the Obed Wild and Scenic River (OWSR). Field work began in September 2010 when the permit was approved through the Research Permit and Reporting system for the OWSR.

Site Selection

Macroinvertebrates were collected from 9 sites on three major tributaries of the Emory River that flow into and through the OWSR, including Daddy's Creek, Clear Creek, and the Obed River. Four sites were infested with hydrilla and 5 were not infested with hydrilla, designated as "hydrilla-infested" or "non-infested," respectively. Due to the steep and rocky terrain that surrounds the deeply incised streams within the OWSR and the challenges this presents for carrying sampling equipment and instruments to remote stream sites, all areas sampled within the park were established at designated access points used to support recreational activities such as fishing, kayaking and hiking. Sampling sites outside the OWSR were established upstream of highway bridge crossings. Appendix A includes photos taken at the majority of sampled hydrilla infested and non-infested riffle and pool sites.

The 9 sampling sites included 2 that lie outside of the park boundary. Potter's Ford at Obed River, Obed Junction upstream of the confluence of Obed River and Daddy's Creek, Barnett Bridge at Clear Creek, and Lily Bridge at Clear Creek were all non-infested stream sites sampled within the OWSR. One additional site, U.S. Highway 68 bridge at Daddy's Creek, was 2.4 km upstream of the source pond for the hydrilla infestation, and therefore outside of the OWSR boundary (Fig. 2).

Hydrilla-infested stream sites included Devil's Breakfast Table at Daddy's Creek, Obed Junction downstream of the confluence of Obed River and Daddy's Creek, and upstream of Nemo Bridge at Obed River. One additional hydrilla-infested site, Antioch Bridge at Daddy's Creek, was outside of the OWSR boundary located upstream of Devil's Breakfast Table, approximately 24-32 km downstream of the source of the hydrilla infestation (Fig. 2).

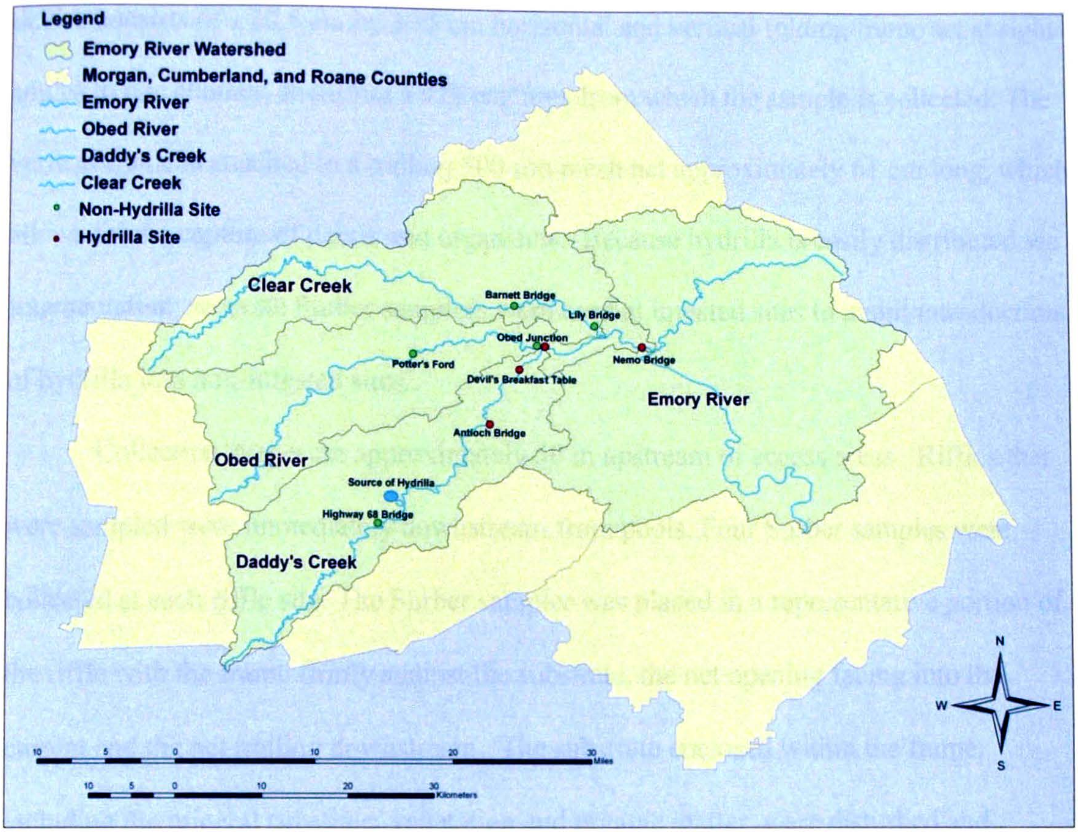

Figure 2. Sample sites within the Emory River Watershed, including the source pond of *Hydrilla verticillata*. Red dots indicate hydrilla-infested sites; green dots indicate non-infested sites. (Map courtesy of Jerrod W. Manning, 2011).

Macroinvertebrate Collections

Macroinvertebrates were collected from both riffle and pool habitats (Fig. 3) on September 18, 19 and 25, 2010. In addition to collection of riffle and pool samples, physical and descriptive data including physiocochemisty readings and substrate assessments were also taken.

The riffle habitats sampled at all sites were downstream of sampled pool habitats. Macroinvertebrates were collected from riffles using a Surber sampler (Fig. 4). This device consists of a 30.5 cm by 30.5 cm horizontal and vertical folding frame set at right angles to one another, enclosing a 929 cm^2 area from which the sample is collected. The vertical frame is attached to a trailing 500 µm mesh net approximately 61 cm long, which allows for the capture of debris and organisms. Because hydrilla is easily distributed via fragmentation, separate Surber samplers were used at infested sites to avoid introduction of hydrilla into non-infested sites.

Collection sites were approximately 50 m upstream of access areas. Riffles that were sampled were immediately downstream from pools. Four Surber samples were collected at each riffle site. The Surber sampler was placed in a representative portion of the riffle with the frame firmly against the substrate, the net opening facing into the current and the net trailing downstream. The substrate enclosed within the frame, including the mineral substrate, vegetation and organic matter, were disturbed and scrubbed with a coarse brush to loosen attached invertebrates which are carried by the current into the net (Fig. 5a). The substrate was agitated until it was likely that most of loose debris and organisms within the enclosed area had been dislodged. After collecting each riffle sample, the contents of the net were emptied into a 1 L Nalgene bottle over a white plastic pan (46 cm x 36 cm) and the net was inspected for clinging macroinvertebrates to ensure no macroinvertebrates were lost in the transfer process (Fig. 5b), Each of the four samples were kept separate, preserved in 10% formalin and labeled by site and sample type (e.g., Devil's Breakfast Table, riffle 1; Fig. 5c).

Macroinvertebrates were collected only from pools with sufficient submersed vegetation, i.e., native species in "non-infested" sites and hydrilla in the "infested" sites. All four infested sites where densely vegetated with hydrilla. However, only 2 of the 5 non-infested pool sites, Clear Creek at Barnett Bridge and Clear Creek at Lily Bridge, had presence of native submersed vegetation, *Najas guadalupensis*, in significant amounts. Pool sites that were intended for sampling in the Obed River at Potter's Ford and Obed Junction and Daddy's Creek at Highway 68 were not sampled due to absence of sufficient submersed vegetation in these areas. Pools were sampled utilizing a 30.5 cm wide triangle dip-net with 800/900 µm mesh size, an instrument designed for semi-quantitative and qualitative sampling of shallow ponds and streams and areas with heavy weeds (Wildlife Supply Company "Indestructible Net;" Fig. 6). Four dip-nets were used for pool collections; 2 were marked "hydrilla-infested" and the other 2 "non-infested" to avoid contamination of non-infested sites. At each of the 6 pool sites, a two-collector team sampled vegetation simultaneously with the dip-net for approximately ten 30.5 cm long "jabs," for a total of approximately 9300 cm^2 area of combined collected vegetation. A "jab" is a term to describe the net entering the stream, bumping or disrupting the bottom in the rooted area of vegetation to loosen the submersed macrophytes while avoiding bottom sediments, and swiftly bringing the net back up to the surface of the water (Fig. 7). At each pool site, all material collected by the two-collector team was combined and placed in one or more 1 L Nalgene container, preserved with 10% formalin and labeled by site and sample type (e.g., Devil's Breakfast Table, pool).

Figure 3. View of a typical pool (background) and riffle (foreground) encountered during sampling. Photo taken at Nemo Bridge, hydrilla-infested site.

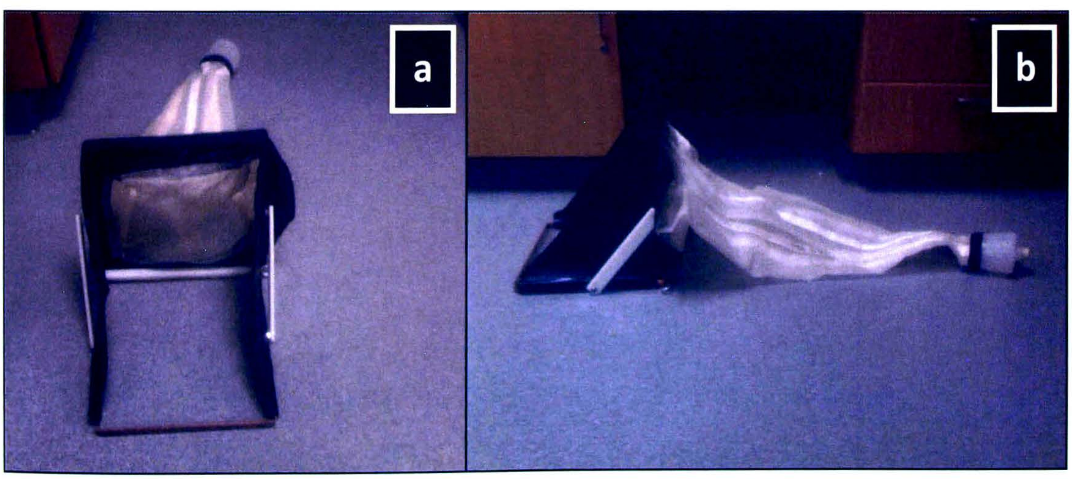

Figure 4. Photograph example of a Surber sampler used for sampling riffles. Front view (a); side view (b).

Figure 5. Example of Surber sampling (a) conducted within riffle habitats, (b) emptying of contents of net into Nalgene containers, and (c) rinsing pan into container.

Figure 6. Photograph example of a triangular dip-net used for sampling in pool habitats.

Figure 7. Example of a "two-collector team" sampling with triangle dip-nets in pools.

Macroinvertebrate Processing and Identification

Macroinvertebrate processing and identification was conducted in the Aquatic Macroinvertebrate Laboratory of the Center of Excellence for Field Biology at Austin Peay State University, with assistance from undergraduate and graduate laboratory assistants. Macroinvertebrates samples were removed from formalin in the laboratory under a fume hood, soaked in water for 24 hours, and then placed in 70% isopropanol (Fig. 8a).

Macroinvertebrates were removed from the debris obtained from both riffle and pool habitats, and sorted by order into site specific vials until further identification (Fig. 8b). Most specimens were identified to genus with the exception of a few invertebrate groups. Aquatic annelids (phylum Annelida), including leeches and aquatic earthworms, were not identified below classes Hirudinea and Oligochaeta, respectively. Aquatic mites were identified to suborder Hydracarina and flatworms to family Planariidae. Snails (class Gastropoda) and bivalves (class Bivalvia) were identified to family. Additionally, immature specimens or those in poor physical condition that prevented identification were identified to the lowest possible level. All identifiable macroinvertebrates except non-biting midges (Diptera: Chironomidae), were identified using published taxonomic keys (Thorp and Covich, 1991; Epler, 1996; and Merritt et al., 2008).

Chironomidae larvae were initially sorted by subfamily or tribe (Chironominae: Chironomini or Tanytarsini, Orthocladiinae, Tanypodinae). These were then mounted under glass cover slips on microscope slides with CMC-10 mounting media (Masters Company, Inc., Wood Dale, IL) for generic identification using taxonomic keys

(Wiederholm, 1983; Epler, 2001; and Ferrington et al., 2008). Meiji MZS and Olympus SZH and G10X stereo-zoom dissecting microscopes with magnification ranges of 7-64X were used for sorting and identifying of most macroinvertebrates. Slide mounted non-biting midges (Chironomidae) were identified to genus using Olympus BH2 and CH30 compound microscopes with a magnification range of 40-1000X. Identified taxa were entered into a Microsoft Excel spreadsheet for statistical analysis and evaluation. In compliance with the NPS permit, representative specimens were made available to park staff for use in interpretive programs upon request. After specimen identifications were confirmed and the project was deemed complete, rare or unique voucher specimens were cataloged and maintained in the Aquatic Macroinvertebrate Laboratoy as a repository.

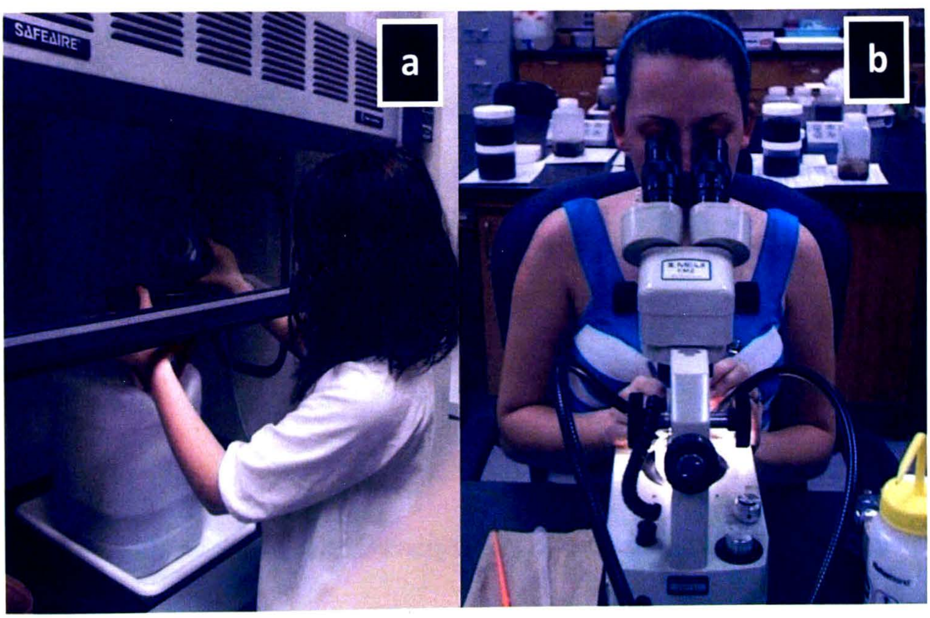

Figure 8. Sample processing including (a) removal of formalin for isopropanol replacement and (b) macroinvertebrate sorting.

Data Analysis

Metrics of macroinvertebrate community structure, the number of taxa and species distribution among taxa, obtained from the enumerated macroinvertebrtate samples included taxa richness, Shannon-Weaver Diversity Index, and Pielou's Evenness. Taxa richness is the number of taxa present in a sample, community, or taxonomic group (Brower et al., 1998). The Shannon-Weaver Diversity Index (H'), a measure of sample "heterogeneity," may range from 0 (no diversity) to approximately 3.5 (high diversity). The function describing H' is:

$$H' = - \Sigma (p_i \ln p_i),$$

where p_i is the proportion of the total number of individuals that belong to taxa *i*.

Pielou's Evenness (J') measures how equally distributed individuals are among taxonomic groups in the sample using Shannon-Weaver information (Pielou, 1966, Brower et al., 1998; Ludwig and Reynolds, 1988). The function describing J' is:

$$J' = H'/H_{max}',$$

where H' is the Shannon-Weaver Diversity Index of the sample and H_{max}' is the natural log (ln) of the sample taxa richness encountered within that site.

Both richness and evenness were calculated in a Microsoft Excel. Utilizing JMP® version 9.0, One-Way Analysis of Variance (ANOVA) was used to test if H' differed between hydrilla-infested and non-infested riffle and infested and non-infested pool habitats (SAS Institute, Inc., 2010).

Diversity and evenness indices are insensitive to community species composition; similar diversity and/or evenness indices could be obtained from samples sharing all the same species or not sharing any species. Therefore, Morisita's Index of Community Similarity (I_M) was used to determine taxa compositional similarities between hydrilla-infested and non-infested sites. This index estimates the probability of selecting a pair of individuals at random that will belong to same taxon relative to selecting a pair of the same taxon from another community (Brower et al., 1998). Morisita's Index of Community Similarity is:

$$I_M = \frac{2\Sigma x_i y_i}{(l_1 + l_2)N_1 N_2},$$

where l_1 and l_2 is the Simpson's dominance index (l) of the two samples being compared calculated as:

$$l_1 = \frac{\Sigma x_i(x_i-1)}{N_1(N_1-1)} \quad \text{and} \quad l_2 = \frac{\Sigma y_i(y_i-1)}{N_2(N_2-1)},$$

where x_i and N_1 are the number of individuals in taxa *i* and total number of individuals in community 1, respectively. Likewise, y_i is the abundances of taxa *i* in community 2 and N_2 is the sum of all individuals in that community. Morisita's index ranges from 0 (no similarity = no shared taxa) to 1 (identical = all taxa shared in equal proportions). A One-way ANOVA was used to determine if there was an overall difference between the means of I_M calculated among all non-infested and hydrilla-infested riffle sites and hydrilla-infested and non-infested pool sites.

The most abundant taxa per site were also evaluated. This was determined by identifying the 20 most abundant taxa found within each hydrilla-infested and non-infested riffle and pool site which were then displayed in bar graphs using Microsoft Excel. To evaluate relationships of taxa abundance among hydrilla-infested and non-infested riffle and among infested and non-infested pool communities, a principal components analysis (PCA) was executed on a correlation matrix using SYSTAT version 8.0 (SYSTAT, Inc). Principal components analysis is a method of reducing data into a few linear combinations (a.k.a., principal components) based on extraction of maximum variance from the data set (Tabachnick and Fidell, 2001). It provides a two-dimensional visualization of relationships among samples via components while capturing as much of the variability in the original variance as possible and allowing for complete structuring of the data set by also reducing the dimensionality of the data set. Excluded from this analysis were taxa that occurred in less than 3 samples or those represented by 5 or fewer organisms per riffle or pool sample.

Macroinvertebrate taxa were classified to functional feeding groups (FFG), a description of trophic strategy – collectors-gatherers, collectors-filterers, shredders, grazers/scrapers, predators or piercer-herbivores (Merritt et al, 2008). This was the only metric of community function evaluated. Functional feeding group composition of hydrilla-infested sites were compared to non-infested sites using a categorical Multi-way Contingency Analysis via JMP® version 9.0 to determine if there was a significant association in the distribution of FFG with respect to the presence of hydrilla in riffle and pool habitats (SAS Institute, Inc, 2010). Frequencies of functional feeding groups were displayed in a mosaic plot to compare proportions of FFG with respect to presence or absence of hydrilla. Probabilities of FFG for each hydrilla-infested and non-infested riffle and pool site were also displayed using pie-charts with Microsoft Excel.

Abiotic Data Collection and Analysis

Abiotic variables including water physicochemistry readings such as temperature (°C), dissolved oxygen (% saturation and mg/l), specific conductivity (mS/cm), total dissolved solids (mg/L) and pH (SU), were measured from each riffle and pool habitat before macroinvertebrate collections using a YSI 600QS multiparameter meter. Prior to entering the field, the YSI was calibrated following the manufacturer's instructions. Notes regarding environmental or physical conditions of riffle and pool habitats were recorded. Appendix B includes table comparisons of inorganic and organic substrate present in riffle and pool habitats, in addition to bar graphs of all abiotic data of variables measured at each sampling site.

CHAPTER IV

RESULTS

Evaluation of Macroinvertebrates

A total of 32,244 individual macroinvertebrates comprising 132 unique taxa were collected from riffle and pool communities in hydrilla-infested and non-infested sites, 122 different taxa from riffles and 84 from pools. Forty-four taxa were unique to riffles, whereas 11 were only collected in pool habitats. Total individuals from riffles and pools were 26,245 and 5,999, respectively.

Comparison of Macroinvertebrate Community Structure and Function between Hydrilla-infested and Non-infested Riffles and Pools

Taxa Richness

Taxa richness from hydrilla-infested and non-infested riffle and pool habitats varied among sites. For riffle habitats, richness ranged between a high of 72 taxa at Obed Junction (non-hydrilla site) to a low of 37 from Hwy 68 (non-hydrilla site), with richness at the remaining hydrilla-infested and non-infested sites above 50 taxa (Table 1). One-way ANOVA of taxa richness between hydrilla-infested and non-infested riffles yielded no significant difference in taxa richness as a result of hydrilla presence in pool habitats upstream from sampled riffles (p-value > 0.05, N.S.).

Within pool habitats, richness ranged between a high of 53 at Lily Bridge (non-hydrilla site) to a low of 23 taxa at Devil's Breakfast Table (hydrilla site, Table 2). There was no significant difference in the taxa richness between hydrilla-infested and non-infested pools, as determined with a one-way ANOVA (p-value > 0.05, N.S.)

Shannon-Weaver Diversity Index

Shannon-Weaver Diversity (H') of sampled riffle habitats ranged from a low 2.11 at Highway 68 (non-hydrilla site) to a high of 3.46 at Barnett Bridge (non-hydrilla site, Table 1). Figure 9 depicts "means diamonds" for the one-way ANOVA comparing H' values between hydrilla-infested and non-infested riffle samples. There was no significant difference in the means of the H' values between hydrilla and non-hydrilla riffle samples (p > 0.05, N.S.).

Shannon-Weaver Diversity of sampled pools ranged from a low of 2.08 at Obed Junction (hydrilla site) to a high of 3.07 at Lily Bridge (non-hydrilla site). "Means diamonds" for one-way ANOVA comparing H' values between hydrilla-infested and non-infested pool samples are depicted in Figure 10. There was no significant difference in the means of the H' valuies between hydrilla and non-hydrilla pool samples (p > 0.05, N.S.).

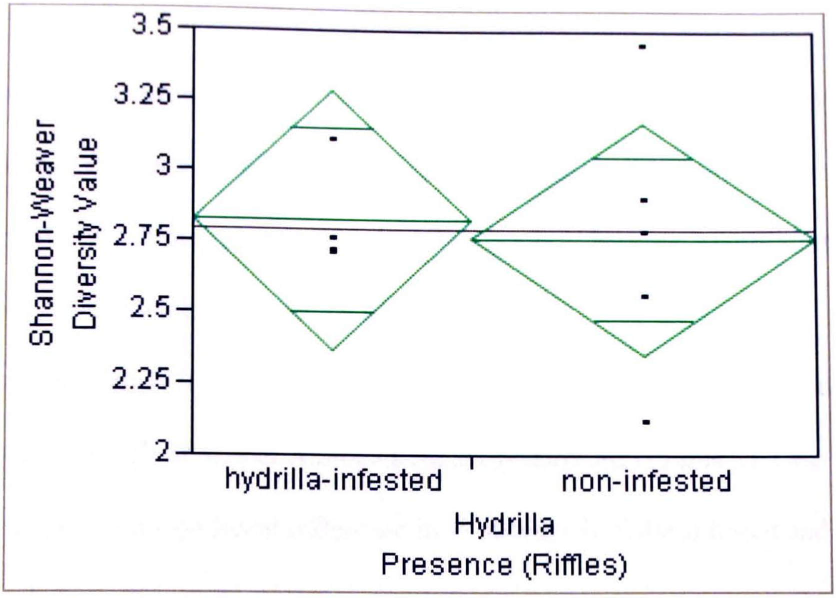

Figure 9. JMP® One-Way Analysis of Variance depicting Shannon-Weaver Diversity values and variable means between hydrilla-infested and non-infested riffle sites. Plotted diamonds indicate no significant difference between mean diversity values acquired from hydrilla-infested and non-infested riffle habitats (p-value: 0.82).

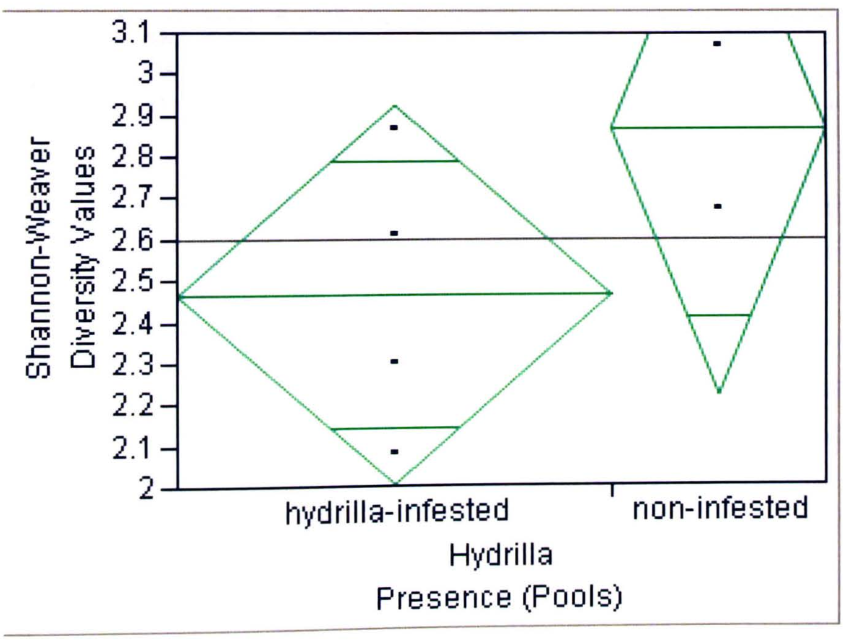

Figure 10. JMP® One-Way Analysis of Variance depicting Shannon-Weaver Diversity values and variable means between hydrilla-infested and non-infested pool sites. Plotted diamonds indicate no significant difference between mean diversity values acquired from hydrilla-infested and non-infested pool habitats (p-value: 0.23).

Evenness

Pielou's Evenness (J') ranged from a low of 0.50 at Highway 68 (non-hydrilla site) to a high of 0.84 at Barnett Bridge (non-hydrilla site) in riffle habitats (Table 1). One-way ANOVA indicated no significant difference in J' between hydrilla-infested and non-infested riffle habitats (p-value > 0.05, N.S.).

Evenness values in sampled pools ranged from a low of 0.56 at Obed Junction (hydrilla site) to a high of 0.79 at Antioch Bridge (hydrilla site) (Table 2). One-way ANOVA indicated no significant difference in J' between hydrilla-infested and non-infested pools (p-value > 0.05, N.S.).

Table 1. Shannon-Weaver Diversity, Pielou's Evenness, taxa richness and total number of individuals of riffle habitat samples from hydrilla-infested and non-infested sites. (DBT=Devil's Breakfast Table).

Sample Site	Shannon-Weaver Diversity (H')	Pielou's Evenness (J')	Taxa Richness (s)	Total # of Individuals (N)
Barnett Bridge	3.46	0.84	62	2269
Lily Bridge	2.90	0.70	62	4307
Obed Junction*	2.78	0.65	72	3417
Potter's Ford*	2.56	0.71	37	1695
Hwy 68*	2.12	0.50	71	2548
Obed Junction'	2.72	0.65	66	3862
Antioch Bridge'	2.76	0.70	51	1575
DBT'	3.11	0.76	60	1107
Nemo Bridge'	2.71	0.66	59	5465
Total				26245

' hydrilla-infested sites
*pools upstream from these riffles were not sampled due to lack of significant submersed vegetation

Table 2. Shannon-Weaver Diversity, Pielou's Evenness, taxa richness and total number of individuals of pool habitat samples from hydrilla-infested and non-infested sites. (DBT=Devil's Breakfast Table).

Sample Site	Shannon-Weaver Diversity (H')	Pielou's Evenness (J')	Taxa Richness (s)	Total # of Individuals (N)
Barnett Bridge	2.67	0.72	42	813
Lily Bridge	3.07	0.77	53	816
Obed Junction[+]	2.08	0.56	40	2390
Antioch Bridge[+]	2.87	0.79	38	545
DBT[+]	2.30	0.73	23	438
Nemo Bridge[+]	2.61	0.71	40	997
Total				5999

[+] hydrilla-infested sites

Morisita's Index of Community Overlap

Morisita's Index values were used to compare taxa similarity between hydrilla-infested and non-infested sites. This metric considers relative abundance or the proportions of shared taxa among the total number of individuals sampled. For riffle habitats, values ranges from a low of 0.42 in the comparison of Potter's Ford and Obed Junction (hydrilla site) to a high of 0.85 between Barnett Bridge and Devil's Breakfast Table. Comparing non-hydrilla infested riffle sites, values ranged from a low of 0.25 between Highway 68 and Barnett Bridge to a high of 0.81 between Lily Bridge and Obed Junction. Hydrilla-infested riffle sites ranged from a low of 0.74 between Antioch Bridge and Nemo Bridge, and a high of 0.82 between Devil's Breakfast Table and Antioch Bridge (Table 3). When comparing all sites, one-way ANOVA detected a significant difference between the means among all hydrilla-infested and non-infested riffle site comparisons (Fig. 11).

Table 3. Morisita's Index of Community Overlap for sampled non-infested vs. hydrilla-infested riffle sites indicating community similarity based on relative abundances of taxa.

	Barnett Bridge	Lily Bridge	Obed Junction	Potter's Ford	Hwy 68	Obed Junction^{+}	Antioch Bridge^{+}	D.B.T.$^{+}$	Nemo Bridge^{+}
Barnett Bridge									
Lily Bridge	0.74								
Obed Junction	0.73	0.81							
Potter's Ford	0.42	0.40	0.41						
Hwy 68	0.25	0.28	0.31	0.26					
Obed Junction^{+}	0.70	0.81	0.84	0.42	0.58				
Antioch Bridge^{+}	0.63	0.53	0.53	0.50	0.77	0.77			
D.B.T.$^{+}$	0.85	0.70	0.74	0.45	0.47	0.82	0.82		
Nemo Bridge^{+}	0.69	0.73	0.63	0.67	0.44	0.81	0.74	0.78	

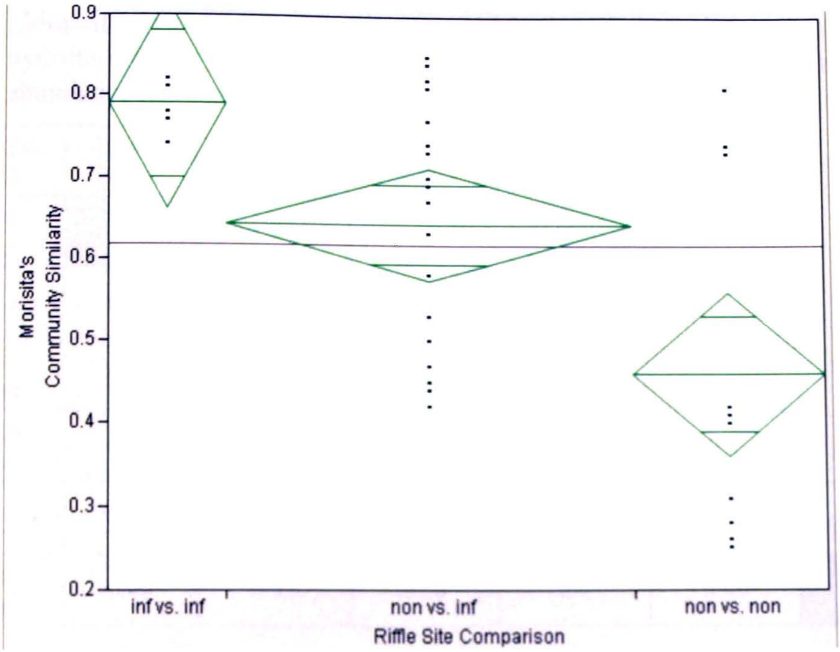

Figure 11. JMP® One-Way Analysis of Variance depicting Morisita's Community Similarity values between hydrilla-infested and non-infested riffle sites. Plotted diamonds indicate a significant difference between mean comparison values acquired from riffles. (p-value: 0.0007; inf= infested sites; non = non-infested sites).

Between hydrilla-infested and non-infested pool sites, similarity values ranged from a low of 0.08 between Barnett Bridge and Obed Junction, and a high of 0.78 between Barnett Bridge and Devil's Breakfast Table, with Lily Bridge and Devil's Breakfast Table following closely with a similarity value of 0.77 (Table 4). When evaluating non-hydrilla infested pools from Barnett Bridge and Lily Bridge, Morisita's Index was high with a similarity value of 0.77. Hydrilla-infested sites, however, had very low values, ranging from a low of 0.11 between Devil's Breakfast Table and Obed Junction, and a high of 0.50 between Nemo Bridge and Antioch Bridge. One-way ANOVA detected a significant difference among similarity values acquired among all hydrilla-infested and non-infested pool sites (Fig. 12).

Table 4. Morisita's Index of Community Overlap for sampled non-infested vs. hydrilla-infested pool sites indicating community similarity based on relative abundances of taxa.

Sample Site (Pools)	Barnett Bridge					
Barnett Bridge		Lily Bridge				
Lily Bridge	0.77		Obed Junction+			
Obed Junction+	0.08	0.18		Antioch Bridge+		
Antioch Bridge+	0.37	0.45	0.12		D.B.T.+	
D.B.T.+	0.78	0.77	0.11	0.32		Nemo Bridge+
Nemo Bridge+	0.40	0.53	0.20	0.5	0.43	

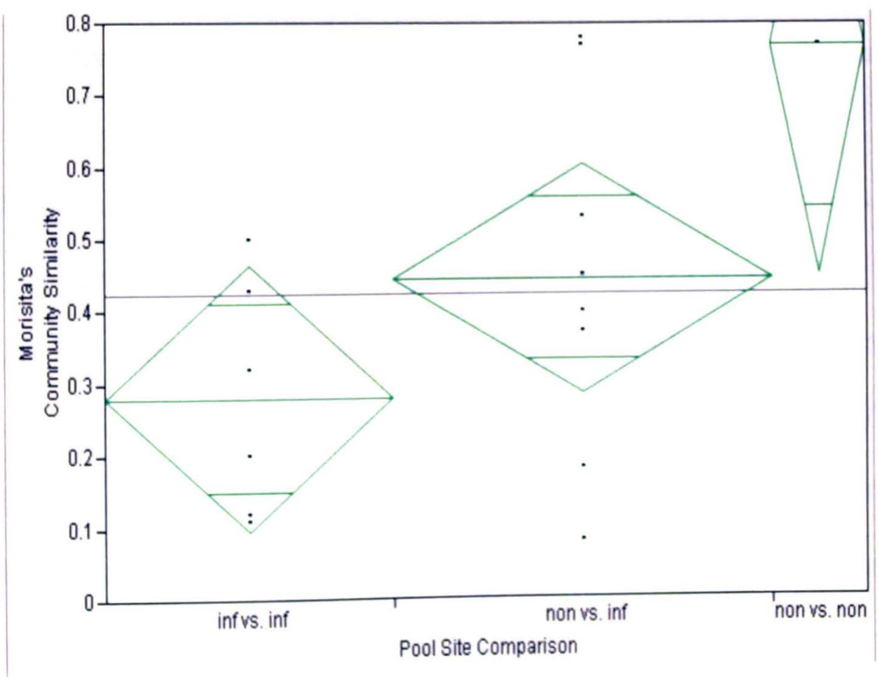

Figure 12. JMP® One-Way Analysis of Variance depicting Morisita's Community Similarity values between hydrilla-infested and non-infested pool sites. Plotted diamonds indicate a significant difference between mean comparison values acquired from pools. (p-value: 0.039; inf= infested sites; non = non-infested sites).

Contingency Analysis of Functional Feeding Group Relationships

Functional feeding group (FFG) distributions in hydrilla vs. non-hydrilla riffle habitats were evaluated using Contingency Analysis (Fig, 13). There was a significant association between frequencies of FFG and the presence of hydrilla (p-value <0.001).

Among non-infested sites proportions of FFG varied, although the majority of taxa were consistently collector-filterers and collector-gatherers (Fig. 14). Highway 68 riffle samples consisted of 65% collector-filterers and 18% collector-gatherers (Fig. 14). Obed Junction riffle samples were 46% collector-gatherers and 23% collector-filterers (Fig. 14). Lily Bridge riffle samples were 44% collector filterers and 33% collector-gatherers (Fig. 14). At Barnett Bridge 36% were collector-gatherers and 21% collector-filterers, while 27% were scrapers and grazers (Fig. 14). Individuals from Potter's Ford were 43% collector-filterers, 19% collector-gatherers, and 21% scraper and grazers (Fig. 14).

Individuals from hydrilla-infested sampled riffles were also mostly collector-gatherers and collector-filterers, although proportions varied between sites (Fig. 15). The majority of individuals at Nemo Bridge were represented by collector-filterers (60%) and collector-gatherers (27%; Fig. 15). Obed Junction followed with 47% collector-filterers and 34% collector-gatherers (Fig. 15). Antioch Bridge had 45% collector-filterers and 21% collector-gatherers, and Devil's Breakfast Table had 37% collector-gatherers and 34% collector-filterers (Fig. 15).

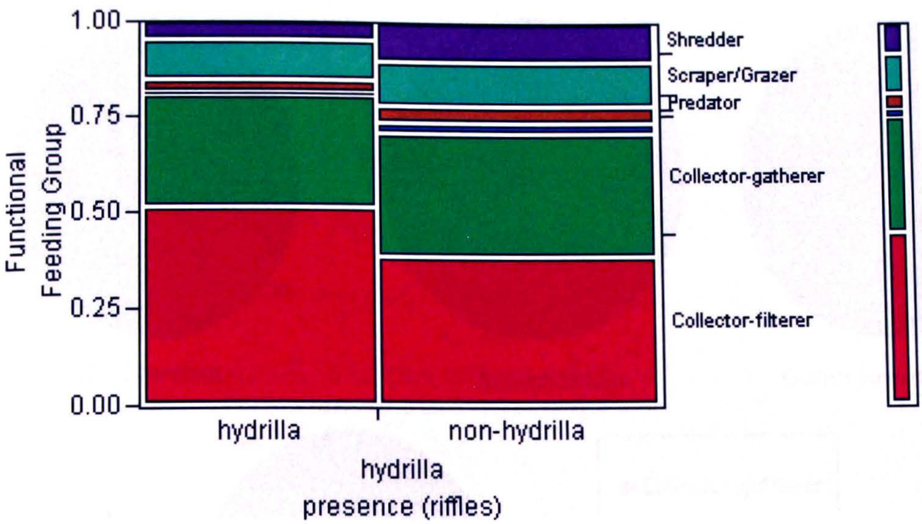

Figure 13. JMP® Multi-way Contingency Analysis depicting distributions of functional feeding groups evaluated from hydrilla-infested and non-infested riffle sites. Mosaic plot indicates a significant association between functional feeding groups and hydrilla presence in riffle communities (p-value < 0.001).

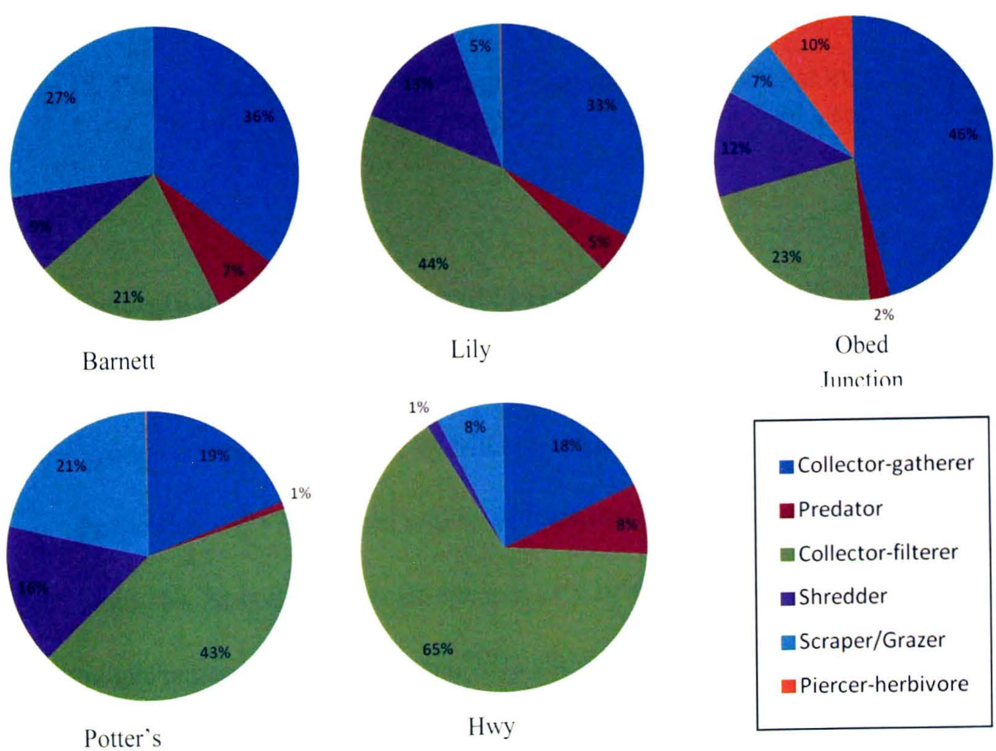

Figure 14. Proportion of functional feeding groups in riffle habitats at non-infested sites: Barnett Bridge, Lily Bridge, Obed Junction, Potter's Ford and Hwy 68.

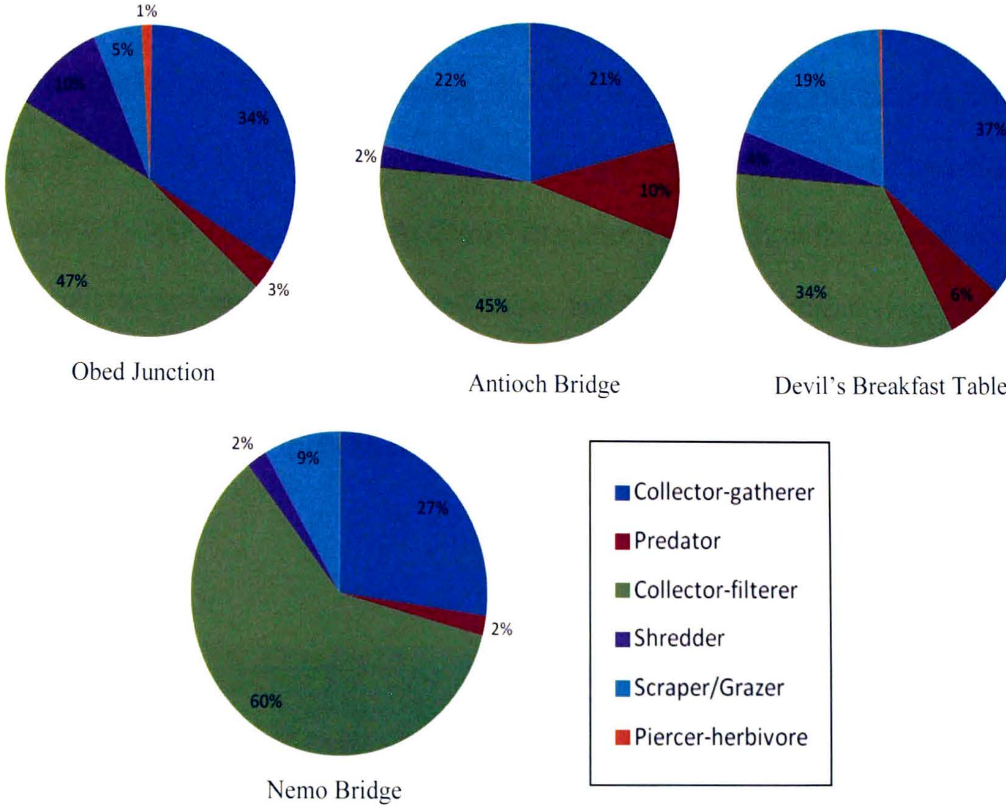

Figure 15. Proportion of functional feeding groups in riffle habitats at hydrilla-infested sites: Obed Junction, Antioch Bridge, Devil's Breakfast Table, and Nemo Bridge.

Figure 16 depicts a mosaic plot of FFG distributions in hydrilla vs. non-hydrilla pools habitats. There was a significant association between frequencies of functional feeding groups and the presence of hydrilla (p-value <0.001).

Proportions of FFG varied within all hydrilla-infested and non-infested pool sites (Figs.17 and 18). At both Barnett Bridge and Lily Bridge, non-hydrilla sites, the majority of individuals were-collector-gatherers, 27% and 43%, respectively. There were also a higher percentage of scrapers/grazers at Barnett Bridge than Lily Bridge with 34% and 17%, respectively (Fig. 17).

Obed Junction had highest percentage of collector-gatherers of any hydrilla-infested pool, with this FFG representing 77% of all individuals (Fig. 18). Antioch Bridge (Fig. 18) had 33% of all individuals were collector-gatherers, 17% collector-filterers, and an unusually high 25% predators. At Devil's Breakfast Table, 30% of the invertebrates were collector-gatherers, 24% collector-filterers, and 23% scrapers/grazers (Fig. 18). At Nemo Bridge, the macroinvertebrates were mostly collector-gatherers (49%), with another 20% as collector-filterers (Fig. 18).

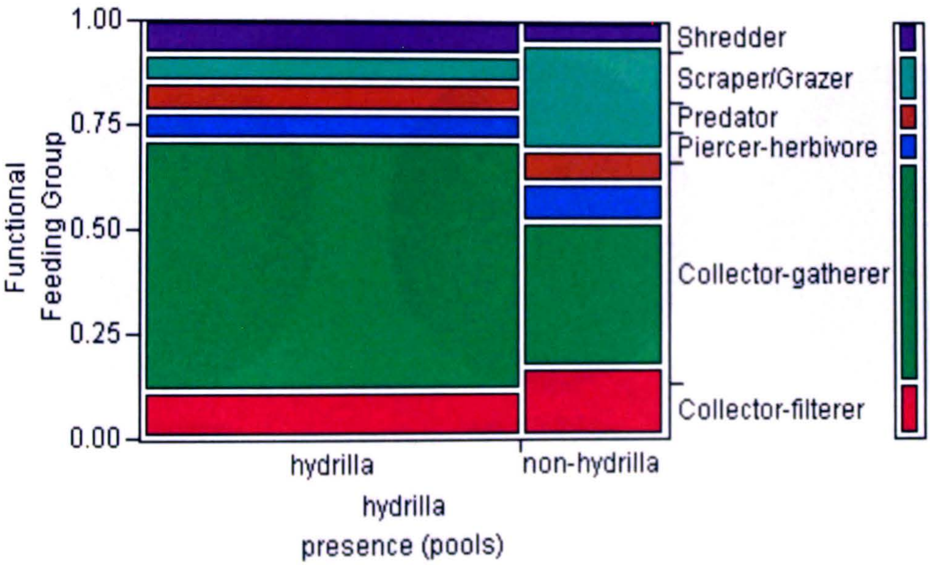

Figure 16. JMP® Multi-way Contingency Analysis depicting distributions of functional feeding groups evaluated from hydrilla-infested and non-infested pool sites. Mosaic plot indicates a significant association between functional feeding groups and hydrilla presence in pool communities (p-value < 0.001).

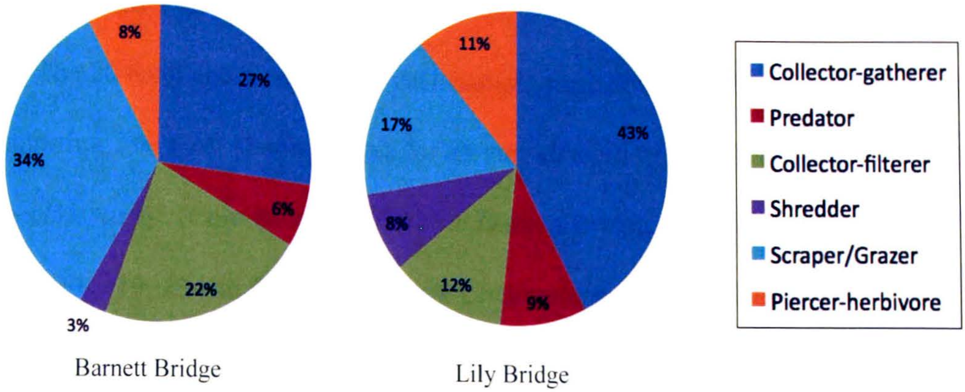

Figure 17. Proportion of functional feeding groups in pool habitats at non-hydrilla sites: Barnett Bridge and Lily Bridge.

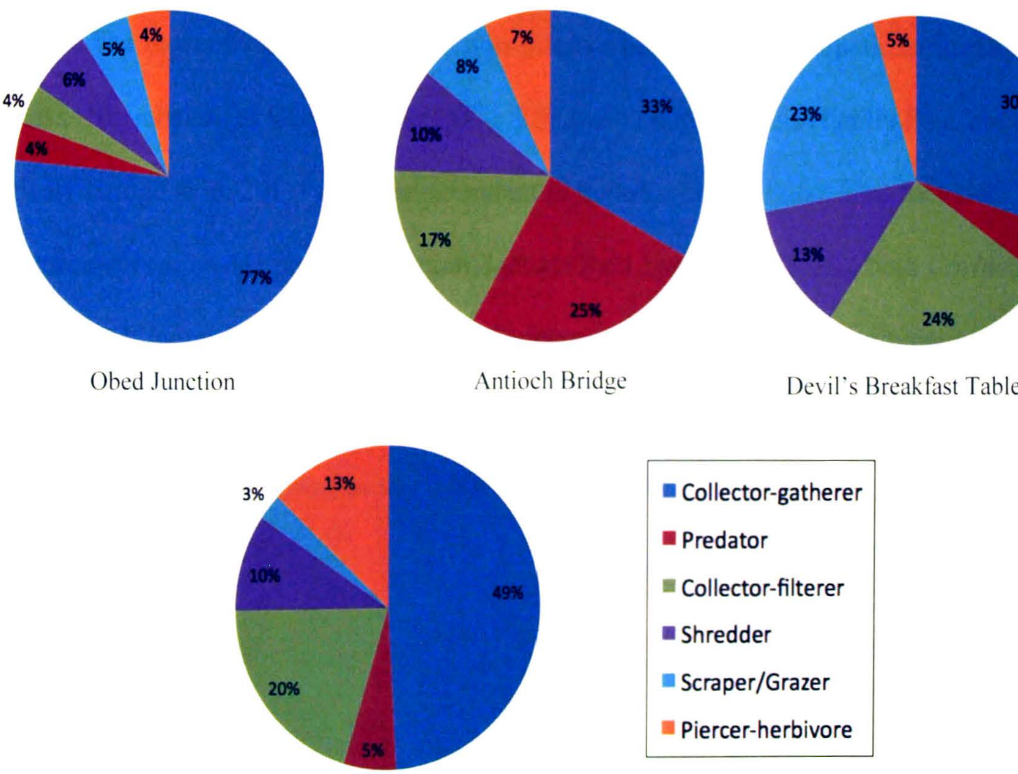

Figure 18. Proportion of functional feeding groups in pool habitats at hydrilla infested sites: Obed Junction, Antioch Bridge, Devil's Breakfast Table, and Nemo Bridge.

Most Abundant Taxa

The 20 most abundant taxa in each sample were determined for all riffle and pool communities. The most abundant taxa for all non-infested riffle sites included *Microcylloepus* sp. (Coleoptera: Elmidae) at Barnett Bridge, Lily Bridge and Obed Junction (Fig. 19, 20 and 21, respectively), *Cheumatopsyche* sp. (Trichoptera: Hydropsychidae) at Potter's Ford (Fig. 22), and *Rheotanytarsus* sp. (Diptera: Chironomidae) at Highway 68 Bridge (Fig. 23). Taxa most abundant in hydrilla-infested riffle sites included *Rheotanytarsus* sp. at Obed Junction, Antioch Bridge and Devil's Breakfast Table (Fig. 24, 25, and 26, respectively), and *Cheumatopsyche* sp. at Nemo Bridge (Fig. 27).

The most abundant taxa for all non-infested pool sites were aquatic earthworms (class Oligochaeta) at Barnett Bridge (Fig. 28) and planorbid snails (family Planorbidae) at Lily Bridge (Fig. 29). Taxa most abundant in hydrilla-infested pool sites included *Paratanytarsus* sp. (Diptera: Chironomidae) at Obed Junction (Fig. 30), both *Corbicula fluminea* (Veneroida: Corbiculidae) and *Tanytarsus* sp. (Diptera: Chironomidae) at Antioch Bridge (Fig. 31), planorbid snails and aquatic earthworms at Devil's Breakfast Table (Fig. 32) and *Tanytarsus* sp. at Nemo Bridge (Fig. 33).

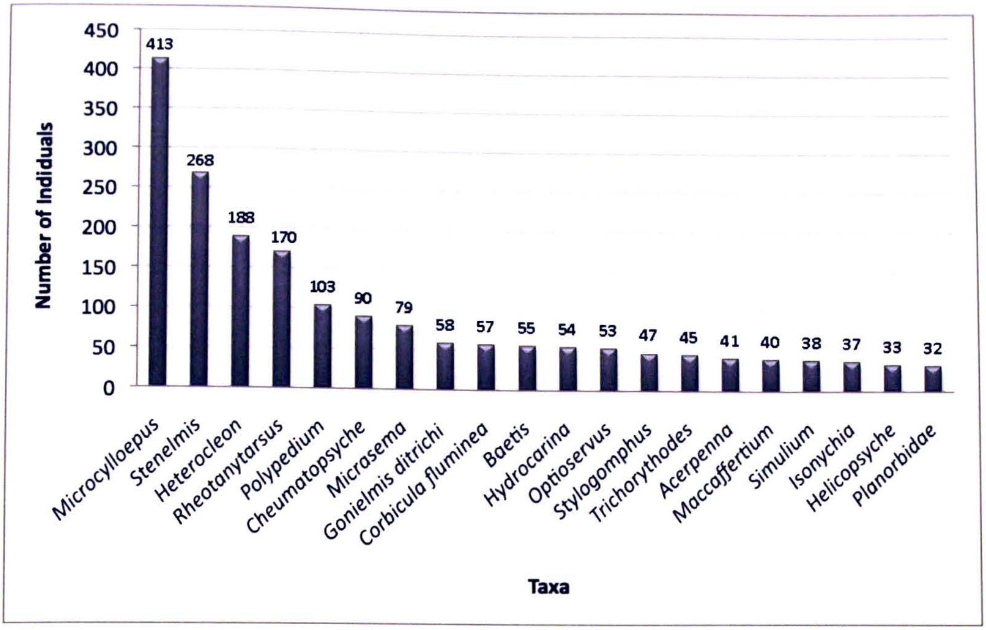

Figure 19. Bar graph depicting 20 most abundant taxa found within riffle habitats of Barnett Bridge (non-hydrilla site). Number above each bar indicates total number of taxa.

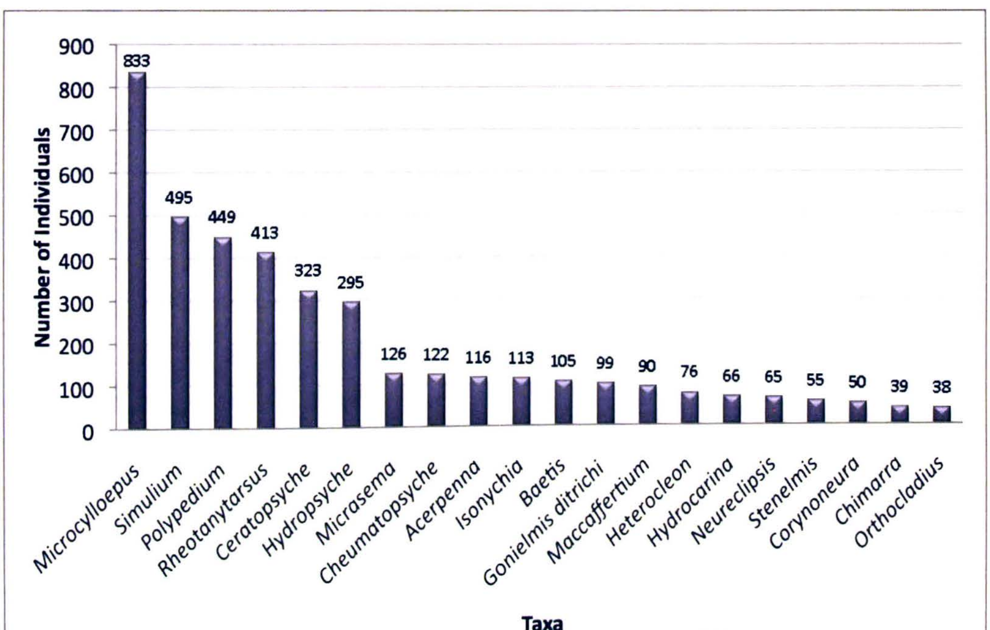

Figure 20. Bar graph depicting 20 most abundant taxa found within riffle habitats of Lily Bridge (non-hydrilla site). Number above each bar indicated total number of taxa.

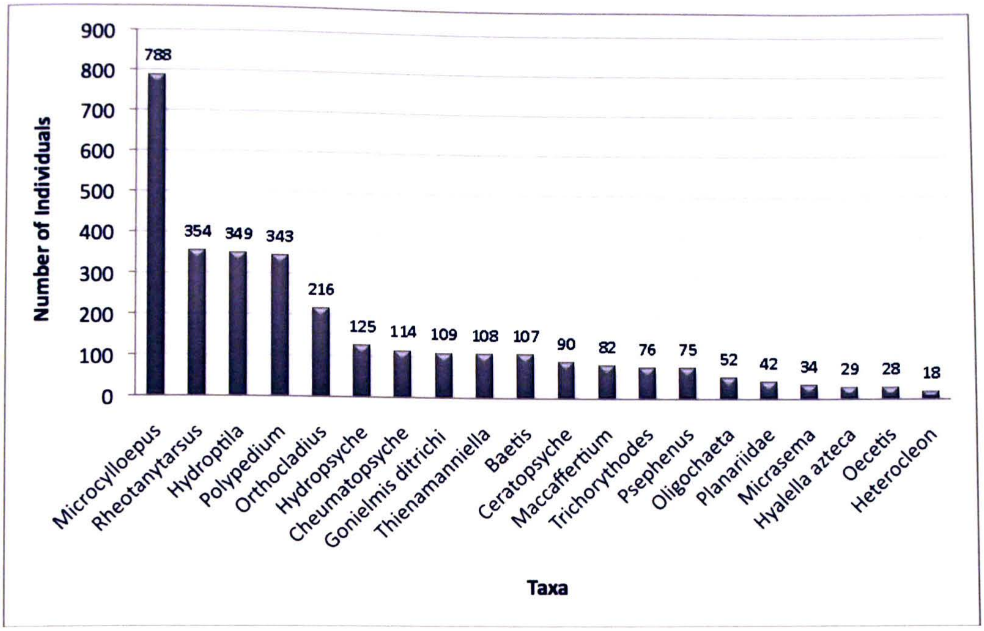

Figure 21. Bar graph depicting 20 most abundant taxa found within riffle habitats of Obed Junction (non-hydrilla site). Number above each bar indicated total number of taxa.

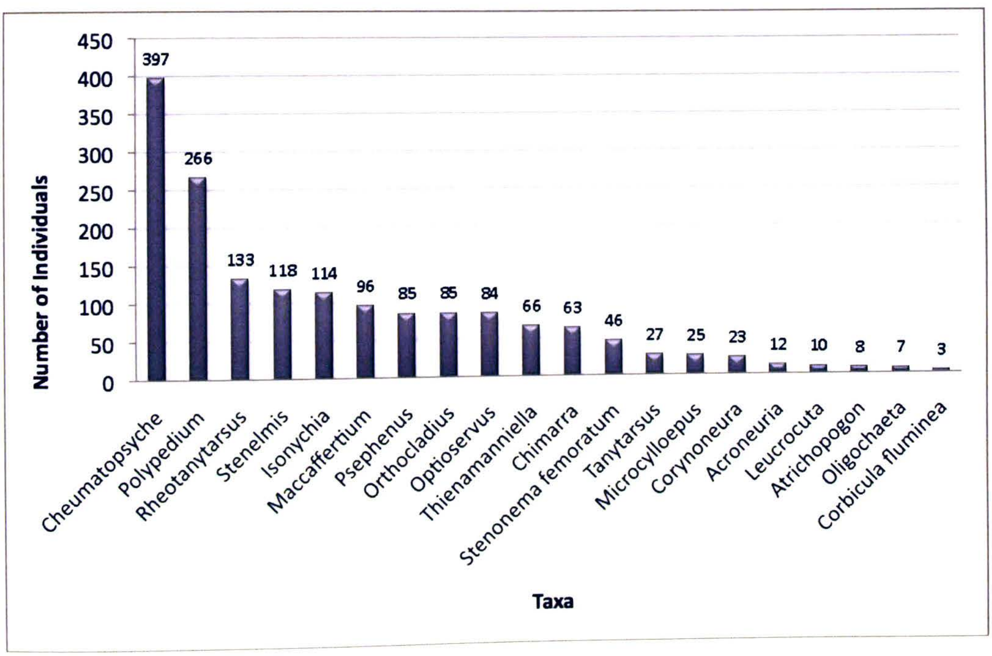

Figure 22. Bar graph depicting 20 most abundant taxa found within riffle habitats of Potter's Ford (non-hydrilla site). Number above each bar indicated total number of taxa.

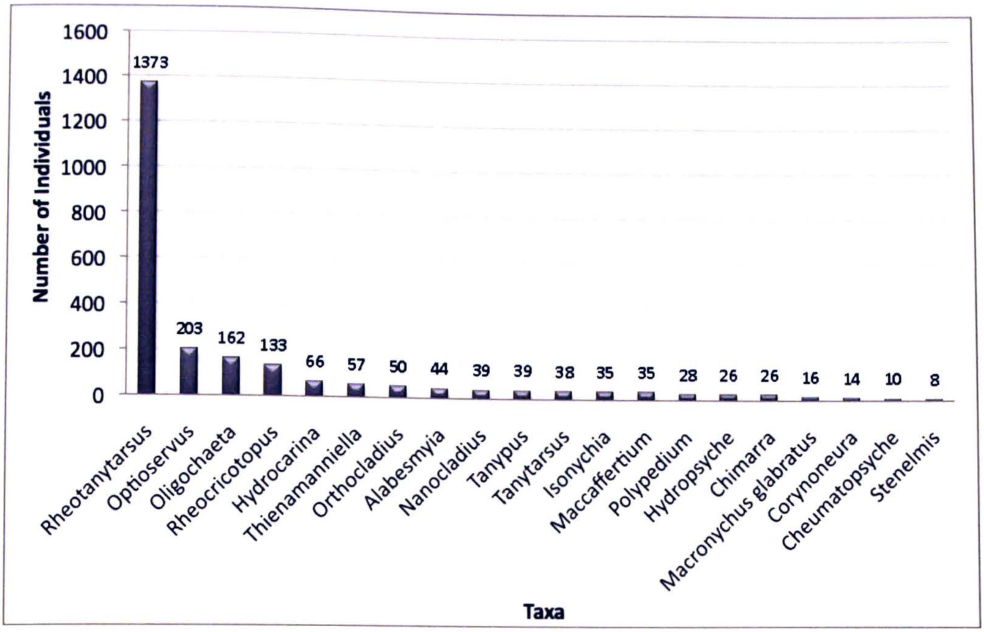

Figure 23. Bar graph depicting 20 most abundant taxa found within riffle habitats of Highway 68 (non-hydrilla site). Number above each bar indicated total number of taxa.

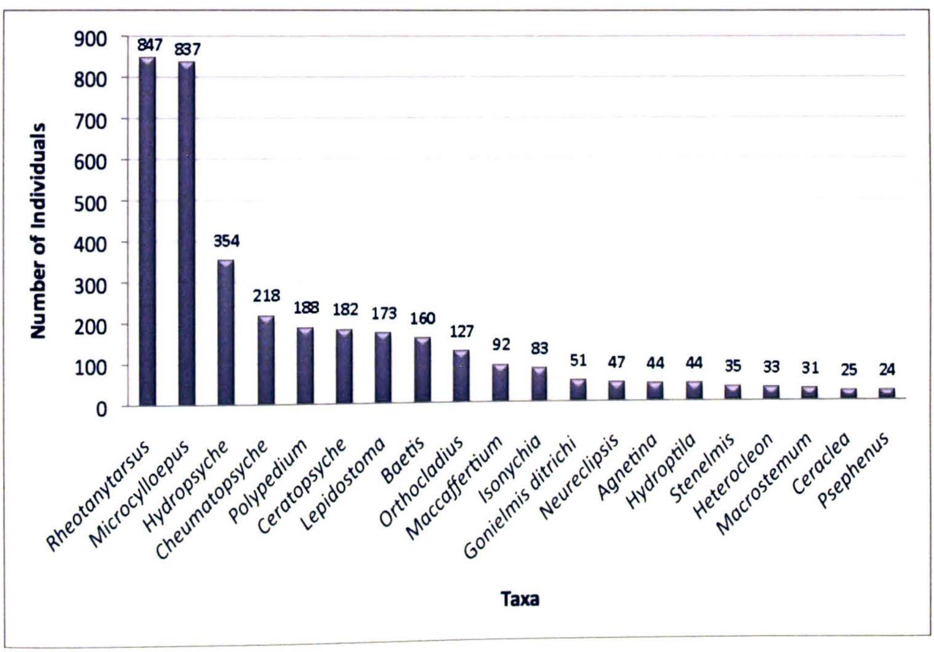

Figure 24. Bar graph depicting 20 most abundant taxa found within riffle habitats of Obed Junction (hydrilla site). Number above each bar indicated total number of taxa.

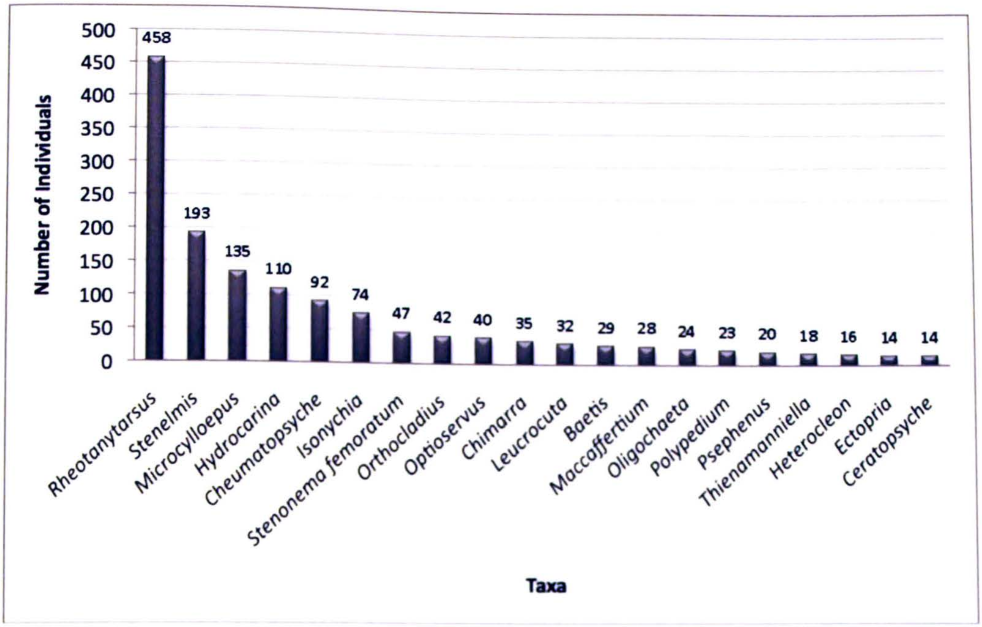

Figure 25. Bar graph depicting 20 most abundant taxa found within riffle habitats of Antioch Bridge (hydrilla site). Number above each bar indicated total number of taxa.

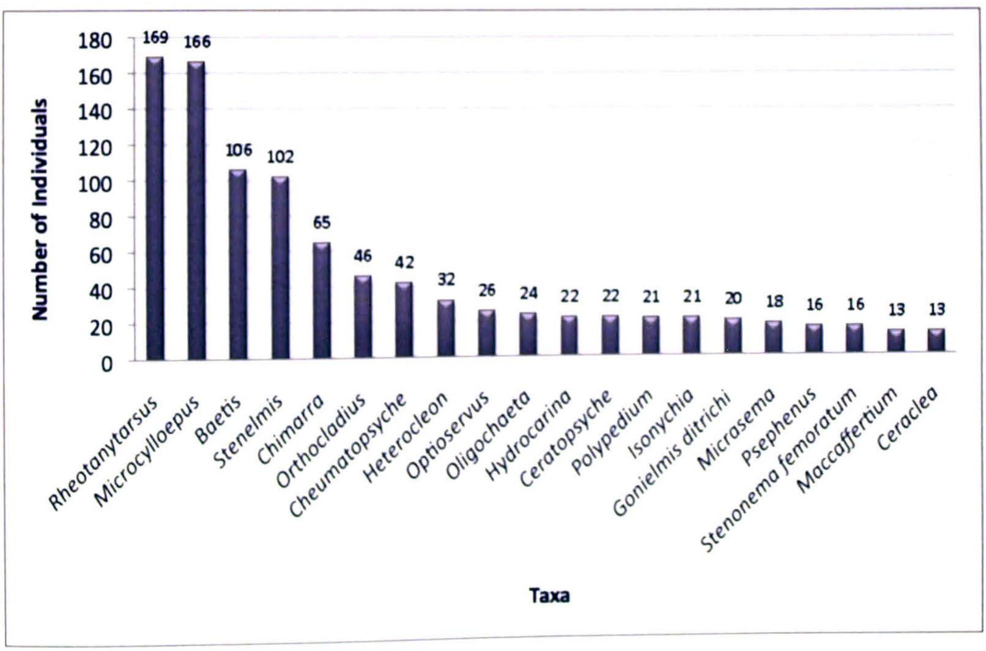

Figure 26. Bar graph depicting 20 most abundant taxa found within riffle habitats of Devil's Breakfast Table (hydrilla site). Number above each bar indicated total number of taxa.

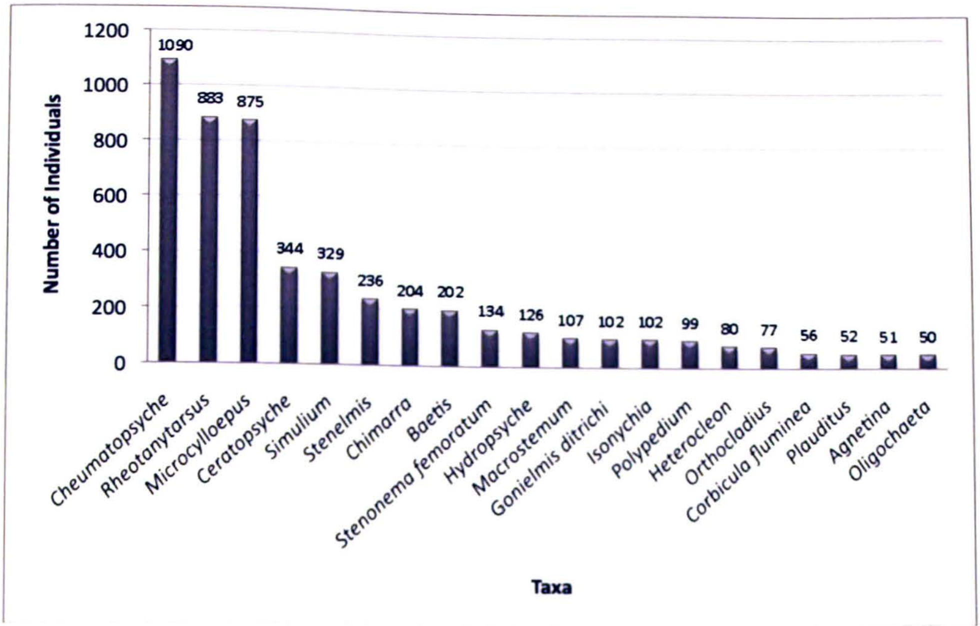

Figure 27. Bar graph depicting 20 most abundant taxa found within riffle habitats of Nemo Bridge (hydrilla site). Number above each bar indicated total number of taxa.

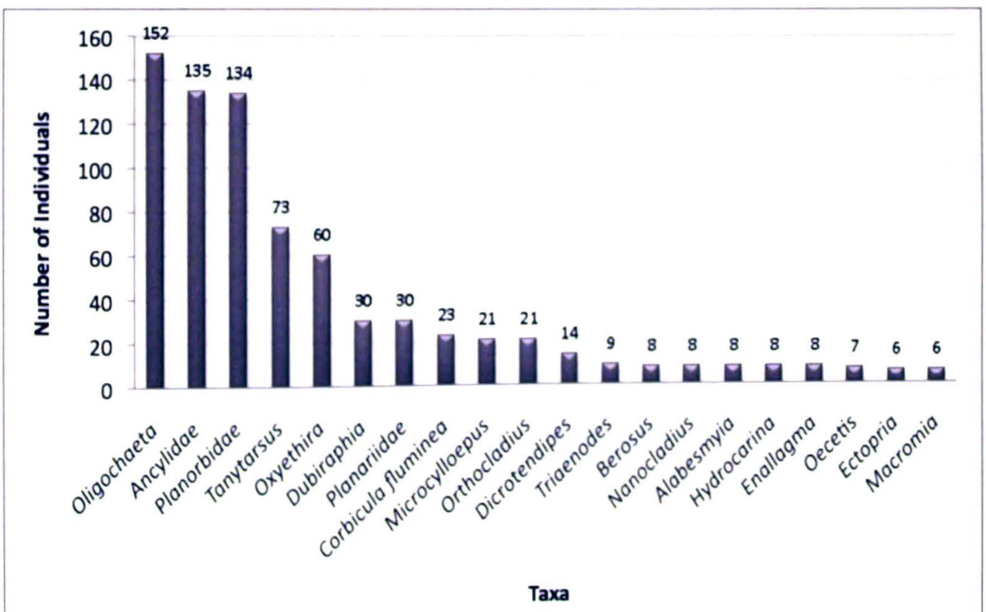

Figure 28. Bar graph depicting 20 most abundant taxa found within pool habitats of Barnett Bridge (non-hydrilla site). Number above each bar indicated total number of taxa.

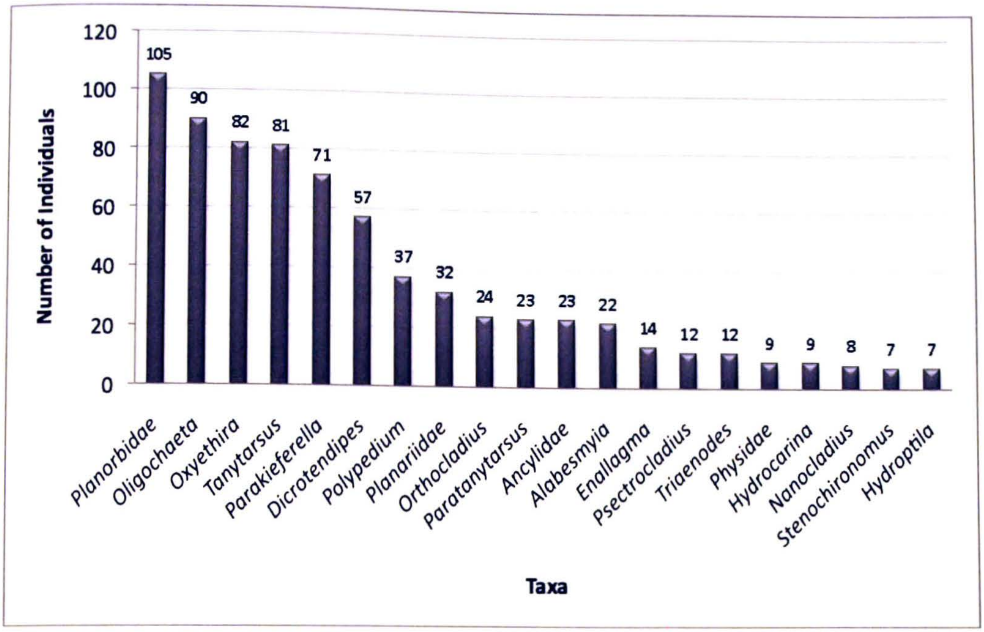

Figure 29. Bar graph depicting 20 most abundant taxa found within pool habitats of Lily Bridge (non-hydrilla site). Number above each bar indicated total number of taxa.

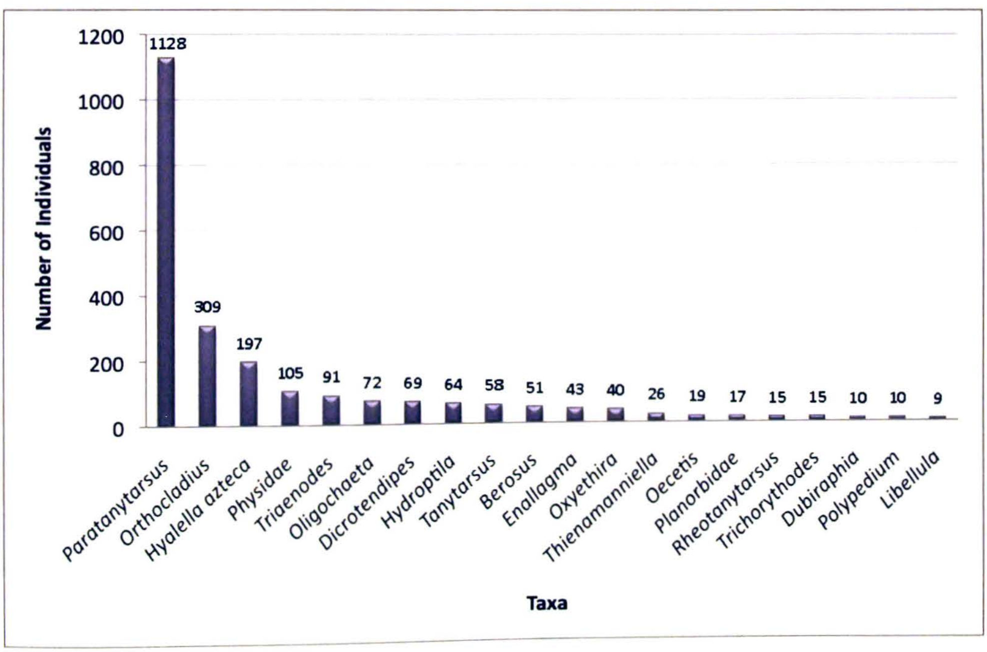

Figure 30. Bar graph depicting 20 most abundant taxa found within pool habitats at Obed Junction (hydrilla site). Number above each bar indicated total number of taxa.

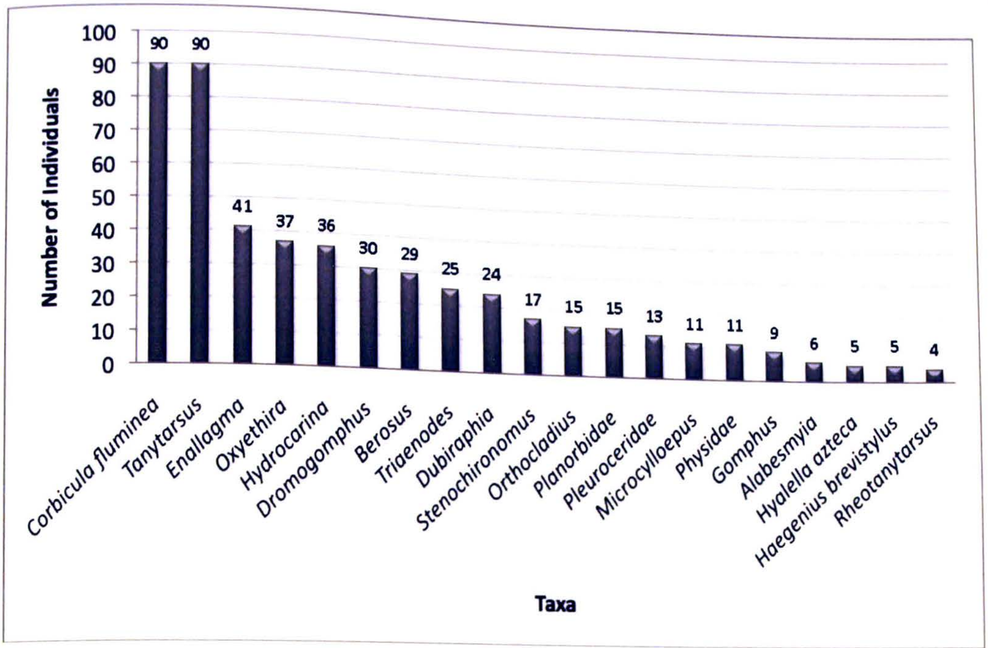

Figure 31. Bar graph depicting 20 most abundant taxa found within pool habitats at Antioch Bridge (hydrilla site). Number above each bar indicated total number of taxa.

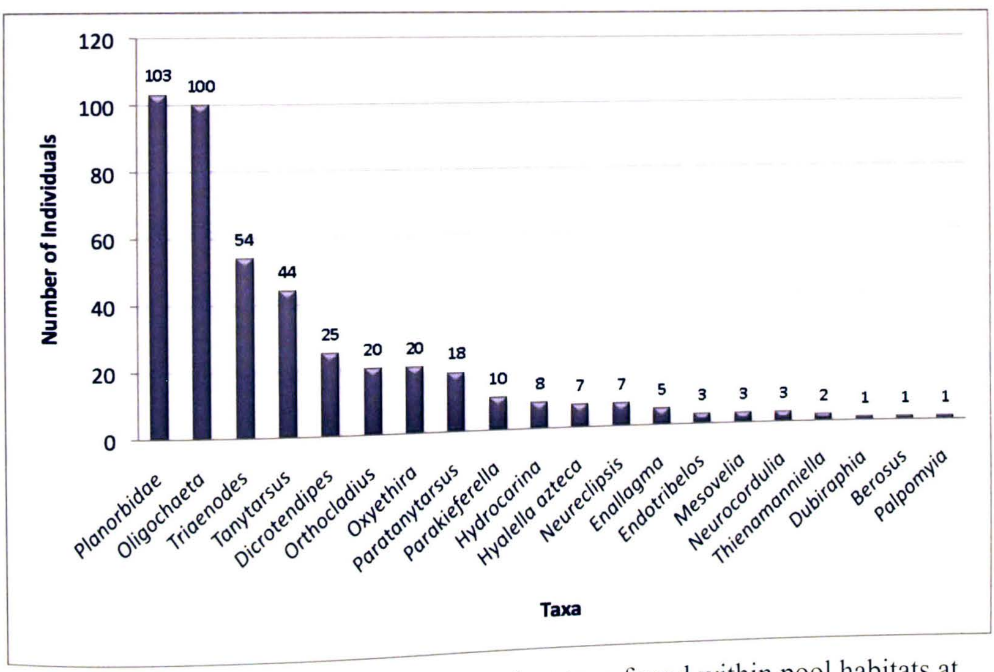

Figure 32. Bar graph depicting 20 most abundant taxa found within pool habitats at Devil's Breakfast Table (hydrilla site). Number above each bar indicated total number of taxa.

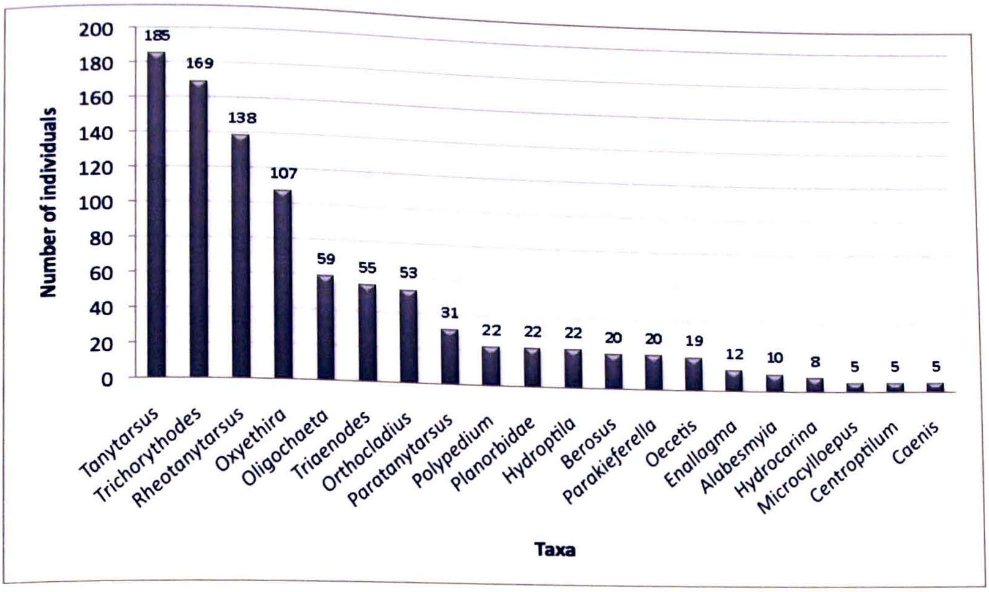

Figure 33. Bar graph depicting 20 most abundant taxa found within pool habitats at Nemo Bridge (hydrilla site). Number above each bar indicated total number of taxa.

Principal Components Analysis

Principal Components Analysis (PCA) revealed a relationship between taxa composition within sampled hydrilla-infested and non-infested riffles. There was no separation along component 1 or component 2 although component loadings varied (Fig. 34). Component 1 accounted for 23% of the total variation. Organisms with high positive loadings included *Gonielmis* sp., and *Microcylloepus* sp. (Coleoptera: Elmidae), followed by *Tvetenia* sp. (Diptera: Chironomidae) and *Ceratopsyche* sp. (Trichoptera; Hydropsychidae). Taxa with high negative loadings included *Optioservus* sp. (Coleptera: Elmidae) and *Alabesmyia* sp. (Diptera: Chironomidae). Component 2 accounted for approximately 19% of the total variation. Taxa with high positive loadings included

Nilotanypus sp. and *Thienamannimyia* sp. group (Diptera: Chironomidae). Organisms with high negative loadings included *Dicrotendipes* and *Orthocladius* (Diptera: Chironomidae) followed by *Psephenus herricki* (Coleoptera: Psephenidae) and *Hydroptila* sp. (Trichoptera: Hydroptilidae). Graphing of component 1 versus 2 revealed no distinction of taxa abundance among riffle communities although Highway 68 and Barnett Bridge had heaviest loadings. Hydrilla-infested sites clustered within non-infested sites indicating similarity in taxa abundance and composition between sites (Fig. 34).

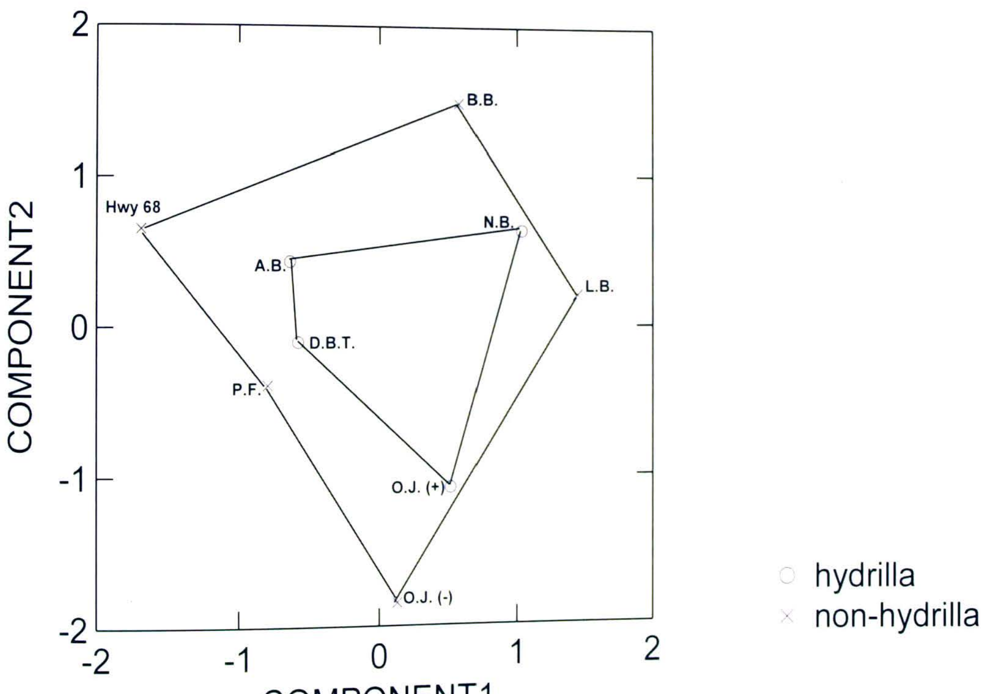

Figure 34. Principal components analysis correlation on abundances of macroinvertebrate taxa from hydrilla-infested and non-infested riffle sites (B.B. = Barnett Bridge; L.B. = Lily Bridge; O.J. (-) = Obed Junction, non-hydrilla; P.F. = Potter's Ford; O.J. (+) = Obed Junction, hydrilla; A.B. = Antioch Bridge; D.B.T. = Devil's Breakfast Table; N.B. = Nemo Bridge).

Although PCA among riffles was characterized by poor separation, for samples from hydrilla-infested and non-infested pools, separation did occur (Fig. 35). Component 1 accounted for nearly 31% of the total variation in pool samples. Organisms with high positive loadings included *Neurocordulia* sp. (Odonata: Corduliidae), *Parachironomus* sp. (Diptera: Chironomidae), and *Macronychus* sp. (Coleoptera: Elmidae). Taxa with high negative loadings were *Triaenodes* sp. (Trichoptera: Leptoceridae), *Hyalella azteca* (Amphipoda: Talitridae), *Berosus* sp. (Coleoptera: Hydrophilidae), *Hydroptila* sp., and *Orthocladius* sp. Component 2 accounted for 23% of the total variation in the analysis. High positive loadings were indicated by *Polypedilum* sp. and *Parakieferella* sp. (Diptera: Chironomidae). Taxa with high negative loadings included *Corbicula fluminea*, *Dromogomphus* sp. (Odonata: Gomphidae), and Hydracarina (water mites). Graphing of component 1 and 2 revealed a distinct separation between hydrilla-infested and non-infested pools, indicating no similarity between taxa abundances and composition (Fig. 35).

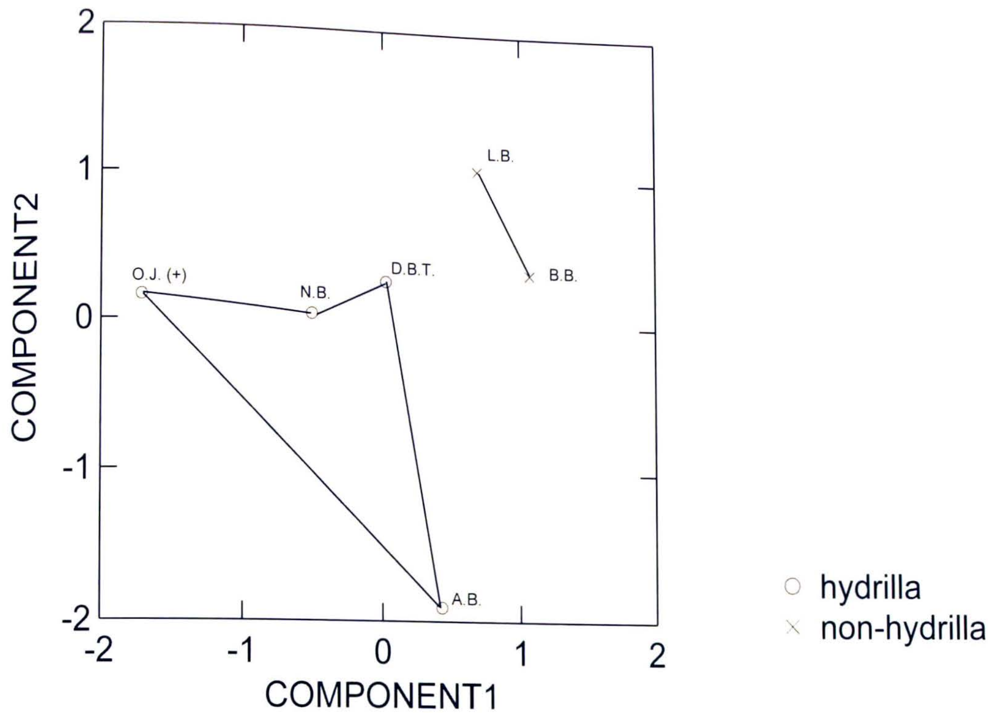

Figure 35. Principal components analysis correlation on abundances of macroinvertebrate taxa from hydrilla-infested and non-infested pool sites. (B.B. = Barnett Bridge; L.B. = Lily Bridge; O.J. (+) = Obed Junction, hydrilla; A.B. = Antioch Bridge; D.B.T. = Devil's Breakfast Table; N.B. = Nemo Bridge).

CHAPTER V

DISCUSSION

Macroinvertebrate and Macrophyte Assemblages in Streams

Streams are temporally and spatially variable environments, having major impacts on the structure and function of lotic communities that inhabit them (Minshall 1988). The River Continuum Concept (RCC) is a conceptual framework for characterizing the biological and chemical properties of lotic systems. The RCC hypothesis seeks to explain how the change in physical attributes of streams from the headwaters to the mouth, including sources of organic matter, relates to changes in structure and function of its biological communities (Vannote et al., 1980). According to this conceptual framework, macroinvertebrate functional feeding group (FFG) composition changes in response to stream size and geomorphology, which is correlated with various sources of organic matter that provide energy to the macroinvertebrate communities. Therefore, the structure, function and abundance of taxa may vary according to the limiting conditions presented within habitats based on the accumulation of both allochthonous and autochthonous material (Heino et al., 2005; Vannote et al., 1980).

Most small headwater streams in eastern deciduous biomes are heavily shaded and little autochthonous organic matter is generated in the stream as a result. The macroinvertebrate communities of these small headwater streams contain relatively few grazing species and are mostly dominated by shredder macroinvertebrates specialized for consuming allochthonous coarse particulate organic matter (CPOM) originating from the forested watershed and breaking it down to fine particulate organic matter (FPOM). The FPOM is consumed in turn by collector-gatherers and collector-filterers. Partially shaded and shallow mid-order streams have a large proportion of grazers specialized for feeding on periphyton that thrive on the surface of aquatic macrophytes and other substrates, where collector-filterers and collector-gatherers are also found in response to the input of FPOM from local and upstream reaches. Large (high-order) rivers, being deep and completely open to sunlight, are dominated by detritivores, mostly collector-gatherers, consuming FPOM; aquatic macrophytes and associated epiphytic organisms are restricted to the littoral zone. Overall, these morpho-behavioral adaptations of macroinvertebrates reflect shifts in structural and functional attributes of a stream based on input of organic matter and the availability of habitat along a physical gradient (Vannote et al., 1980; Wallace and Webster, 1996).

Macroinvertebrate distribution and abundance along a stream gradient is influenced by a large number of environmental factors within a stream's physical environment, including human-induced disturbances (Allan, 2004), naturally-induced disturbances (Lake, 2000), the accumulation of both allochthonous and autochthonous material, and habitat heterogeneity (Boyero, 2003; Erman and Erman, 1984; Vannote et al., 1980). Macrophytes play key roles in the physical environment by stabilizing sediment dynamics, adding to habitat heterogeneity, mediating dissolved oxygen levels, and serving as substrate for other organisms such as epiphytic algae, fish and hydrophyte-dwelling macroinvertebrates (Carpenter and Lodge, 1986; Riis and Biggs, 2003). They encourage a physically and chemically complex environment in aquatic ecosystems, including the addition of structural features of a habitat, which in turn influences macroinvertebrate diversity, density and distribution (Carpenter and Lodge, 1986). Macrophytes are generally found from the mid-reaches of mid-order streams to the margins of large rivers (Vannote et al., 1980), where factors such as flow variability (Riis and Biggs, 2003), degree of substrate availability (Barko and Smart, 1986), and light availability (Barko and Smart, 1981; Canfield and Hoyer Jr., 1988) support their colonization, which, in turn, can have significant impacts on spatial distribution of macroinvertebrates.

The objective of this study was to determine influences of the invasive aquatic macrophyte *Hydrilla verticillata* (hydrilla) on macroinvertebrate communities inhabiting riffle and pool habitats within the Emory River Watershed (ERW). As mentioned above, aquatic vegetation mediates important ecological processes of streams, producing autochthonous carbon and providing habitat and refugia for many aquatic organisms. The predictions incorporated in the structural framework of the RCC highlights habitat heterogeneity as a primary component in many freshwater environments. Habitat heterogeneity encourages macroinvertebrate abundance and diversity (Vannote et al., 1980), which in turn can improve the complexity of the ecosystem and food web interactions (Wallace and Webster, 1996). The importance of submersed macrophytes in biotic interactions depends on their biomass and productivity within a freshwater environment, which encourages habitat heterogeneity where present. Excessive macrophyte growth as demonstrated by invasive species such as hydrilla, however, can alter the stability of the river ecosystem by decreasing habitat heterogeneity, therefore possibly disrupting the fundamental predictions of the RCC (Theel et al., 2008; Vannot et al., 1980). Invasive plant species such as hydrilla have degraded lentic communities by lowering oxygen levels due to increased nighttime respiration and decompositional respiration of senescent biomass, resulting in mortality of fish and macroinvertebrates (Carpenter and Lodge, 1986). As a result of excessive macrophyte growth, changes in species abundances also have the potential to alter food webs and ecosystem processes in lotic environments.

Macroinvertebrate Analysis

Taxa Composition

Taxa richness, evenness and diversity values were metrics used to evaluate taxa composition and community structure within sampled hydrilla-infested and non-infested riffle and pool sites. On average, non-infested riffle sites had higher richness values than hydrilla-infested riffles, although values from hydrilla-infested areas did not deviate significantly from non-infested areas. The majority of riffle sites had greater than 50 different taxa, with the exception of Potter's Ford at Obed River, where only 37 taxa were collected (Fig. 9).

Pielou's evenness values also varied in riffles, where hydrilla-infested sites had higher evenness values on average than non-infested sites (Table 1). The lowest evenness occurred at Highway 68 with a value of 0.50, although it was second highest for total number of taxa collected. This is due to 1373 *Rheotanytarsus* (Chironomidae) in the sample, which exceeds by >6 times the second most abundant taxon (Coleoptera: Elmidae: *Optioservus*) and the total of the other 70 taxa combined (1175) from this site.

To account for both richness and distribution of individuals among the taxa (evenness) at each site, Shannon-Weaver Index (H') was calculated. Although H' values varied between sites, there was no overall significant difference observed between the means of H' between hydrilla-infested and non-infested riffle sites, as determined with one-way analysis of variance (ANOVA; Fig. 11).

Within pools, non-infested sites had higher taxa richness on average than hydrilla-infested sites, although the differences were not significant. The majority of sampled pools had over 40 taxa, with the exception of Antioch Bridge and Devil's Breakfast Table where only 23 and 38 taxa were collected, respectively (Fig. 10). Evenness values also varied between pool sites. Pools not infested with hydrilla had higher evenness on average than pools infested with hydrilla, although Antioch Bridge, a hydrilla-infested site, had the highest evenness with a value of 0.79 (Table 2). There was no significant difference in means of H' between hydrilla-infested and non-infested pool sites (Fig. 12).

Shannon-Weaver Index is a metric widely used in community ecology to measure community diversity. The metric was developed in information theory to measure the uncertainty of encountering a symbol in a message. Applied to community ecology, it is analogous to the uncertainty of sampling a given species occurring in a community. The uncertainty of encountering a given species in a community of low diversity is less than it would be in a community of high diversity (Ludwig and Reynolds, 1988). Shannon-Weaver Index is useful in summarizing both the taxa richness and the distribution of individuals among those taxa (evenness) in the community, reaching its maximum (H_{max}') when the individuals in the sample are evenly distributed among the taxa (Ludwig and Reynolds, 1988). Within both aquatic and terrestrial environments, species diversity in a community reflects habitat diversity; thus, H' can also be used as a proxy measure of habitat structure (Brower et al., 1997).

Although there was no significant difference in mean H' values between hydrilla-infested and non-infested riffle and between hydrilla-infested and non-infested pool sites, the variability in diversity patterns may still be attributed to the distinct physical and chemical attributes within habitats that influence the distribution and abundance of macroinvertebrates. Generally, riffle habitats are more diverse than pool habitats, although habitat diversity and suitability play a large role in macroinvertebrate colonization and community structure (Brown and Brussock, 1991; Resh et al., 1988). For example, upstream riffle sites including Potter's Ford at Obed River and Highway 68 at Daddy's Creek, exhibited the lowest riffle diversity values (Table 1), most likely due to differences in physical and chemical characteristics from riffle sites located further downstream. This not only demonstrates that perhaps the structured environment of riffle habitats in headwaters is less complex, but also reaffirms the concept associated with the RCC that diversity is associated with habitat complexity, typically increasing downstream. In addition, Daddy's Creek at Hwy 68 appears to be heavily impacted by anthropogenic disturbances such a cattle pasturing and row cropping on adjacent land. In some cases, diversity was higher at hydrilla-infested pool sites than most non-infested riffle sites. This may be due to the distinct habitat provided by the dense hydrilla beds, but this also may be attributable to minute differences in physical characteristics between sites, where the abundance of organic and inorganic material can vary. For instance, based on visual assessments, some sites had visually higher composition of inorganic substrate such as cobble and boulder, than organic substrate such as leaf litter and submersed vegetation (see Appendix B). When comparing pools, however, both non-infested sites including Lily Bridge and Barnett Bridge at Clear Creek exhibited higher diversity than most hydrilla-infested pools, although Antioch Bridge was second highest in diversity (Table 2).

Because macroinvertebrate assemblages are largely influenced by habitat availability, suitability and heterogeneity of streams (Brooks et al., 2005; Heino et al., 2005; Wallace and Webster, 1996), the differences in habitat composition among sampled sites may explain the variability in macroinvertebrate diversity. Hydrilla may be increasing structural complexity of habitats as reflected in the apparent higher diversity values in hydrilla-infested pools than in many non-infested habitats. Conversely, structural complexity may also be limited in other sites by the uniformity of structure in hydrilla beds in some of the infested pool habitats, which is represented by low diversity values. Although there is no significant difference in means of H' between non-infested and hydrilla-infested riffle and pool sites when this study was conducted, diversity may be affected during times of the year when periodic high flows remove large quantities of macrophyte biomass.

Seasonal effects can have major influences on both macroinvertebrate and macrophyte colonization. In streams with large seasonal amplitude in discharge in winter (such as in the ERW), low flow and high light availability during summer allows for extensive macrophyte growth (Sand-Jensen et al., 1989), whereas streams with constant discharge allow for the presence of macrophytes to persist year-round (Dawson, 1978; Sand-Jensen, 1998). Although *Hydrilla verticillata* is a perennial aquatic plant, the submersed shoots of the monoecious biotype die back in the winter, concurrently during the time in which flow within the ERW increases dramatically. This sudden change in macrophyte biomass may alter the community composition of macroinvertebrates, where different macroinvertebrate taxa are present before and after presence of shoots. In particular, the senescence of hydrilla shoots during its seasonal transition into becoming metabolically active only through its tubers may result in large ecosystem response to the decomposition of hydrilla, where trapped organic matter and dissolved substances can be released, resulting in high nutrient flux (Carpenter and Lodge, 1986). Alternatively, the increase in macrophytic biomass during the formation and growth of new shoots in spring may result in large macroinvertebrate community response, particularly from epiphytic organisms that depend on vegetation for habitat, as well as aquatic herbivores important to food web interactions (Carpenter and Lodge, 1986). Consequently, these fluctuations in biomass may trigger changes in macroinvertebrate diversity in response to shifts in food resources and the physical environment, which presumably did not occur or were not as large before the hydrilla introduction.

Associating Functional Feeding Groups with Presence of Hydrilla

As a result of the heterogeneity of a stream's environment, macroinvertebrates have been presented with interacting constraints relative to finding food and acquiring food through specific "morpho-behavioural" feeding mechanisms relative to the physical environment in which they live (Wallace and Webster, 1996). Functional feeding groups (FFG) are categories of feeding strategies into which the various species that make up the stream community may be classified. Functional feeding groups are only categorizations of feeding mechanisms rather than type of food eaten because most methods of feeding can result in the consumption of all food type resources, which therefore means most macroinvertebrates are omnivorous (Cummins and Klug, 1979; Merritt et al., 2008; Wallace and Webster, 1996). Different FFG (i.e. predators, grazers [scraper], shredders, collector-gatherers, and collector-filterers) have important roles in ecosystem processes, particularly on energy flow and nutrient cycling through food web interactions. In turn, conditions within stream systems, including food resources such as detritus, periphyton, macrophytes, and animals influence FFG composition (Cummins and Klug, 1979; Merritt et al., 2008). Therefore, the amount of biomass produced by the hydrilla infestation in the ERW will most likely have a major influence to the food resources in streams, which should be reflected by the composition of FFG in hydrilla-infested sites.

Contingency analysis (CA) allows for the testing between two or more categorical variables to determine if one variable is "contingent" on the other, or tests for association between variables. Frequencies of different values of one categorical variable are displayed in contingency tables to see how they depend on the value of another categorical variable (Whitlock and Schluter, 2009). Multi-way contingency analysis (MCA), which tests for association between more than two categorical variables, was used to determine if frequencies of different FFG's were associated with the presence of hydrilla in sampled riffle and pool habitats. Proportions of FFG were also determined to visually identify the variability that occurred among hydrilla-infested and non-infested sites. For this analysis, there was a significant association that occurred between frequencies of FFG in hydrilla-infested and non-infested riffles (Fig. 13), in addition to corresponding sampled pools from each site (Fig. 24). These associations between proportions of FFG and the presence of hydrilla indicate a possible change in the macroinvertebrate community structure of infested riffle and pool habitats. Furthermore, the variability in proportions of FFG between hydrilla-infested and non-infested sites may also signify the unpredictability in stream dynamics relative to the differences in the physical and chemical characteristics of riffles and pools between sampled sites. Not only does the dependence of FFG on the presence of hydrilla indicate the divergence in habitat between infested and non-infested riffles and pools, but it also suggests that changes in food acquisition strategies of macroinvertebrates are a response to the hydrilla-driven habitat and nutrient cycling changes. For example, collector-gatherers, typically the most abundant FFG in streams of this size (Minshall et al., 1983; Wallace and Webster, 1996), were the largest proportion of FFGs encountered in both hydrilla-infested and non-infested pools. However, there was a higher percentage of collector-gatherer species in infested pools, which reflects the increase in fine particulate organic matter (FPOM) that may have accumulated in the dense beds of hydrilla. Not only does this signify that hydrilla plays an important role in accumulating and releasing particles in pool habitats, but also predicts that the ERW will experience increases in FPOM during the annual senescence of hydrilla shoots, resulting in a large ecosystem response by macroinvertebrates and other aquatic fauna.

Collector-filterers, which were the most abundant FFG present in hydrilla-infested riffle sites than non-infested riffles, reflect the abundant FPOM that is passing through riffle habitats as a result of the breakdown of hydrilla leaves and release of trapped FPOM from upstream pools. Collector-filterers, being important in hindering the transport of suspended particles further downstream, are removing the large amount of suspended FPOM not consumed by collector-gatherers in upstream reaches (Wallace and

Webster, 1996). Furthermore, collector-filterers are responding to animal drift from living and decomposing macroinvertebrates and other aquatic communities from adjacent upstream habitats. Besides significantly slowing downstream transport of nutrients and organic matter in hydrilla-infested riffles, collector-filterers are also contributing to downstream export of organic matter via drifting fecal particles, which will result in a considerable response from downstream deposit-feeding detritivores (Cummins and Klug, 1979; Merritt et al., 2008; Wallace and Webster, 1996).

The association of increase in collector-filterers and collector-gatherers with presence of hydrilla in riffle and pool habitats, respectively, reflects the alteration of energy sources caused by hydrilla. The differences in FFG proportions between hydrilla-infested and non-infested riffle and pool sites indicate the important interactions that occur between macrophytes and macroinvertebrates, such as the cycling of nutrients, on both a temporal and spatial scale. Furthermore, at the time the study was conducted, hydrilla beds were well developed, which implies that FFG composition will change when senescence occurs. Therefore, the changes caused by the seasonal fluctuations in hydrilla biomass may have major consequences on ecosystem processes within the ERW, including changes in functional feeding group compositions, food web functionality, nutrient cycling, and physiochemical conditions (Carpenter and Lodge, 1986).

Analyzing Macroinvertebrate Community Similarities

Morisita's Index of Community Similarity. Morisita's index of community similarity (MICS) is based on a measure of Simpson's dominance (D_s), or the concentration of the number of individuals among different taxa. This analysis makes pairwise comparison of communities, indicating the probability that a pair of individuals randomly sampled from both communities will belong to the same taxon (Brower et. al, 1998). This MICS was calculated to make pairwise comparisons between communities sampled from hydrilla-infested and non-infested sites, all non-infested sites, as well as all hydrilla-infested sites. Morisita's similarity among all pairs of hydrilla-infested riffles had a mean of 0.79 with all values higher than 0.73, indicating high community overlap between sites with hydrilla. Comparisons among pairs of hydrilla-infested and non-infested riffles indicated variability in community similarity between hydrilla-infested and non-infested riffles with mean similarity of 0.64 and probability values ranging from a low of 0.45 to a high of 0.85 (Table 3). In fact, many non-infested riffles shared higher community overlap with hydrilla-infested riffles than with other non-infested sites. Paired comparisons between non-infested sites had a mean similarity of only 0.46. This variation in community overlap among hydrilla-infested and non-infested sites not only implies possible differences in taxa distributions between compared riffles, but also that hydrilla may not be the only factor influencing the different distributions of macroinvertebrate communities. This can also be attributed to the significant differences between MICS in riffle comparisons when analyzing with one-way ANOVA (Fig. 11). Additionally, comparisons involving hydrilla-infested and non-infested pools demonstrated variability among sites, with a mean similarity of 0.44 and ranging from 0.08, near total dissimilarity, to 0.78. When comparing among hydrilla-infested pool sites, overlap values were low, ranging from 0.11 to 0.50 with a mean similarity of 0.28 (Table 4). Only one comparison could be made between non-infested pools due to lack of vegetation for sampling at other pool sites. The sites, Barnett Bridge and Lily Bridge, had a MICS value of 0.77. However, similar to riffle habitats, there was also a significant difference between MICS calculated in pool comparisons (ANOVA, Fig. 12). Perhaps this means that hydrilla-infested pools are different than non-infested pools, although, the sample size for comparing non-infested sites is much smaller than for hydrilla-infested sites. Nevertheless, hydrilla is contributing to a unique habitat structure in pools since the existing substrate (i.e. boulder/bedrock/cobble) does not typically support large beds of native submersed vegetation. Most likely, hydrilla may be extending habitat in some areas; likewise, it can be homogenizing habitat due to its invasive and pervasive character. As with riffle habitats, the variability in community similarity encountered between sites not only signifies differences in taxa distributions, but also that hydrilla may not be the only factor contributing to the inconsistency among sites. For example, inorganic substrate in infested pools ranged from predominance of sand and gravel in some to mostly cobble and boulders in others.

The physical environment of streams, especially fluctuations in hydraulic conditions, contributes significantly to macroinvertebrate distribution (Brooks et al., 2005). Distinct patterns of heterogeneity in streams are based primarily on the physical environment, including factors such as flow, depth, method of formation, and variability in substrate composition (Brown and Brussock, 1991). The abiotic environment of most streams can be characterized by natural disturbances such as flooding or drought, which in turn affects lotic inhabitants (Lake, 2000). Within the ERW, seasonal water movement and flow volume are largely influenced by precipitation patterns, groundwater recharge and flow alterations, which can drastically alter conditions of the stream system across a range of spatial to temporal scales (TWRA, 1998). This variability can also have a major impact on ecological structure and function in streams, where habitat patches can be altered during changeable flow conditions. Large volumes of rapidly moving water can alter the structure of inorganic and organic substrate in riffles, runs and pools by redistributing sediments and shifting detritus. The return of stable flow conditions following flow-generated disturbance can form new habitats that are colonized by inhabiting macroinvertebrates and other aquatic fauna (Lake, 2000; Merritt et al., 2008). The large and small-scale variability in the hydraulic environment of streams results in a "patchy" distribution of macroinvertebrates (Brooks et al., 2005) making it difficult to compare diversity, structure, and community structure among stream reaches. Additionally, the availability of suitable habitat is important when considering assemblages of macroinvertebrate communities because most habitat types are colonized and exploited in different ways due to differences in life history, trophic ecology and behavior (Brown and Brussock, 1991; Mackay, 1992; Merritt et al., 2008). Although important for some macroinvertebrates, the presence or lack of submersed vegetation (i.e., *Hydrilla verticillata* or *Najas guadalupensis*) in the ERW may not be the only factors affecting similarity comparisons among hydrilla-infested and non-infested sites. Because macroinvertebrates exploit diverse habitat types, their distribution in the ERW may be due to other physical, chemical or biological attributes.

Principal Components Analysis. Principal components analysis (PCA) based on correlation coefficient for data simplification was used to measure overall similarities in taxa abundance between hydrilla-infested and non-infested riffle and pool sites. Unfortunately, PCA based on correlation coefficient as a measure of similarity between samples has been considered inappropriate for ecological data. This is because distances between samples, or essentially the component loadings, are based on extractions of linear combinations of data, although based on maximum variance possible (Tabachnick and Fidell, 2001). In ecology, rarely do linear relationships exist, so the distances between taxa abundances of samples are often given disproportionate weight that can poorly represent the relationships among sampling units (Ludwig and Reynolds, 1988). This unsuitability, however, only applies to a broad range of environmental and compositional variation where linear relationships cannot exist. When seeking clusters, PCA has an advantage, although the components only highlight distances between natural groupings while sacrificing distances between samples within the groupings (Rosenberg and Resh, 1993). Other multi-variate methods have been proposed, including non-metric multidimensional scaling (NMDS), which seeks the rank order of dissimilarities between samples to identify similarities among groups. However, the dimension of the solution must be provided before the analysis is operated (even if the dimension may not be evident in the data set), indicating the need for several "trial runs" before the analysis is complete (Rosenberg and Resh, 1993). Noy-Meir and Whittaker (1977) discuss solutions to the increasing concerns raised by PCA users by suggesting the use of data obtained from a narrow range of environmental variables in which the linear model most likely would apply. For this study, PCA was applied to taxa abundances that were influenced by a narrow range of environmental variables (hydrilla-infested vs. non-infested sites), although this analysis may not have been the most appropriate to evaluate similarities. However, to aid in acquiring maximum variability, taxa that were in less than three samples and represented by five or fewer organisms were removed from the analysis.

Component loadings for riffle habitats varied due to differences in loadings of taxa abundances. Non-infested and infested riffles identified overlap in taxa abundance, in which all hydrilla-infested sites formed a narrower cluster within the non-infested sites. This overlap not only indicates similarity in overall taxa abundance and distribution among hydrilla-infested and non-infested riffles, but also that macroinvertebrates are assembling in a similar manner (Fig. 33). The analysis, however, detected heavier component loadings between non-infested sites Highway 68, Barnett Bridge and Obed Junction versus hydrilla-infested sites, which suggests that some taxa were more abundant and were distributed among the total number of individuals in a different way that separates them from clustering with the other sites. At Barnett Bridge and Obed Junction, *Microcylloepus* sp. (Fig. 17 and 19) was the most abundant taxa, whereas *Rheotanytarsus* sp. (Fig. 21) as the most abundant at Highway 68. Likewise, the majority of hydrilla-infested sites shared both *Microcylloepus* sp. and *Rheotanytarsus* sp. as the most abundant taxa, although many, including Obed Junction and Nemo Bridge, (Fig. 22 and Fig 25, respectively) had more representatives of these taxa than many of the non-infested sites. Principal components analysis not only recognized overall similarities among taxa in riffles, but also the slight variability in distributions among taxa between each sampling site.

Component loadings for pools were also variable. Principal components analysis for pool habitats detected a clear separation in overall taxa abundances between hydrilla-infested and non-infested sites (Fig. 33). This indicates that there are differences in taxa abundance and distribution, in addition to the assemblages of macroinvertebrates between the these sites. It is possible that these differences are because hydrilla is influencing the spatial arrangement of macroinvertebrates in infested pools and the much more homogenous substrate available in thick beds of hydrilla.

Macroinvertebrate colonization is both directly and indirectly influenced by habitat heterogeneity and complexity (Theel et al., 2008), therefore the more homogenous environment provided by dense beds of hydrilla may be contributing to alterations in the natural habitats structure within the ERW, particularly in pool habitats. In contrast, the native macrophyte *Najas guadalupensis* is most likely contributing to the heterogeneity of non-infested pools due to its patchy distribution, where abundant amounts of inorganic and organic substrate are more haphazardly distributed. The invasive character of *H. verticillata* means it has the potential to establish in all areas of the ERW downstream of its present distribution where it has the capacity to occupy all available habitats. Consequently, based on this data, hydrilla is most likely contributing to the homogeneity of pool habitats, which in turn is influencing the distribution and abundance of macroinvertebrates. Although macroinvertebrate diversity within hydrilla-infested sites did not differ significantly from non-infested sites, there should be concern. The shift from the natural, heterogeneous conditions previously existing in the ERW, to a more uniform and completely altered habitat caused by the establishment of hydrilla, may have reduced spatial complexity that is necessary for the more complex, balanced structuring and functioning of macroinvertebrate communities (Theel et al., 2008).

Comparison of Substrate Composition within Riffle and Pool Habitats

The composition of assorted inorganic and organic substrates throughout the high-gradient streams in the ERW offers a wide variety of microhabitats for many aquatic organisms. The unique physical environment within the ERW is attributed to the fundamental geologic processes that have influenced the hydrology by allowing for the formation of deeply incised streams (Stearns, 1954; TDEC 2002). During this study, visual assessments were made at each sampling site to evaluate the substrate types in the sampled reaches of the ERW. This evaluation was conducted to aid in understanding the substrate variability within the stream system as well as hydrilla's ability to colonize some stream portions with suitable substrate versus others where such substrate may be more limiting. Appendix A includes photographs of hydrilla-infested and non-infested riffle and pool sites sampled for this study. These images indicate the diverse substrate that composes the hydrosoil of the ERW, including the nearly homogenous composition in many pools that are now attributable to hydrilla.

At the majority of riffle sites there was an abundant mixture of substrate available including detritus, cobble and gravel, although exact composition at each site varied (Appendix B, Table B-3). Hydrilla-infested sites did not have any established populations of hydrilla within riffles, although there were drifted fragments from upstream pool habitats that composed much of the organic substrate. The majority of hydrilla-infested sites included both organic and inorganic substrate, dominated mainly by assorted allochthonous leaf debris, cobble and gravel, and sand, where hydrilla was present in sand-filled crevices between cobbles. Some hydrilla-infested sites, however, had large boulders surrounding the riffle habitats, although those were not present in areas that were sampled from. Non-infested stream sites, similar to the hydrilla-infested sites, had an abundant mixture of substrate available including detritus, cobble and gravel. Substrate types varied between all sites, but the most abundant at all sampled riffle habitats were detritus, gravel and cobble.

Substrate also varied between pool sites, but the majority composed of large, flat cobble slabs, fine gravel, and sand (Appendix B, Table B-4). Barnett Bridge had cobble and sand as the dominant substrate types, in which *Najas guadalupensis* was abundant, but patchy. Lily Bridge had extensive areas of bedrock and cobble, in which *N. guadalupensis* was growing from sand-filled crevices. Many of the hydrilla-infested pool sites had large cobble slabs with hydrilla in the sand-filled crevices. Nemo Bridge and Antioch Bridge also had a mixture of cobble with extensive areas of bedrock, in which hydrilla could only establish in the sand-filled interstices. Therefore, some of the hydrilla-infested pool sites more dense beds of hydrilla than others due to the variation in availability of finer substrates in which it can grow. The degree to which hydrilla can flourish in various portions of the ERW may explain some of the differences in macroinvertebrate community composition between non-infested and hydrilla-infested pools and riffles.

Future Considerations

Based on this study, it is difficult to judge if hydrilla is ecologically beneficial to the ERW or is exhibiting the negative impacts with which it is often associated. Regardless, its establishment provides insight on aquatic weed invasions in streams, as well as supplementary information on macroinvertebrate-macrophyte relationships in streams.

There is little information published about submerged invasive macrophytes in lotic environments. A more thorough understanding of aquatic plant invasions in lotic environments is needed, particularly on how an invasive submersed macrophyte can impact the macroinvertebrate communities as well as those of fish and other native biota. This understanding is essential when considering proper management approaches to controlling or eradicating invasive aquatic plant species and for protecting or restoring the natural freshwater ecosystem. Much attention has focused on *Hydrilla verticillata* in lentic systems or reservoirs because it is rarely found in fast flowing water (Cook and Lüönd, 1982; Langeland, 1996; Pieterse, 1981; Yeo et al., 1984). Long-term monitoring within the ERW is needed to understand the possible repercussions that could occur as hydrilla maintains its establishment and alters the natural flow patterns of the OWSR. Is it possible hydrilla is provoking "new" ecosystem properties within the ERW? To what extent will hydrilla maintain functional properties, such as ecosystem processing and nutrient turnover, for example, with respect to natural conditions within the ERW? There may be functional redundancy, in the case of the riffle habitats within the ERW, which do not seem to have changed with respect to macroinvertebrate diversity and distribution.

Hydrilla may also be enhancing or inhibiting existing properties to pool habitats, such as primary productivity and nutrient retention. On the other hand, it is possible hydrilla may also be adding new properties to these areas that have never experienced vegetation (since submersed macrophytes do not naturally exist in the lower stream reaches of the OWSR) by introducing a monotypic habitat or creating a new, distinctive habitat for macroinvertebrate assemblages. Although submersed aquatic vegetation may be ecologically beneficial, hydrilla may be producing an environment within the ERW that is stongly impacting the system during its annual senescence and contributing to the changes in spatial distribution of macroinvertebrates.

Because macroinvertebrate abundance and ecosystem functionality has been altered, this can have very large impacts on food web functionality, specifically on the several rare and endemic fish species that exist within the ERW that depend on macroinvertebrates as a food source. Microhabitats within the crevices of large cobble and bedrock substrate that support the distribution of the rare and endemic spotfin chub, *Erimonax monachus* (Kanno et al., 2012) are now occupied by hydrilla, which may have effects on seasonal migration patterns and habitat use by this fish species. Further investigations of the aquatic communities in conjunction with abiotic aspects of the ERW are needed to determine other possible influences that hydrilla may have on the ecology of this system. Nevertheless, the establishment of hydrilla has generated high macrophyte biomass in the ERW, and it is anticipated it will contribute to significant fluctuations in ecosystem processes.

It is important to keep in mind that these findings and assumptions only apply to the sampling period for this study. As mentioned above, hydrilla may have recurrent effects on the functionality of the ERW before and after senescence of shoots, resulting in ecosystem responses that were not assessed in this study. Furthermore, hydrilla may not be the only factor contributing to the functionality and spatial arrangement of macroinvertebrates within the ERW. This system is highly influenced by flow disturbances and varying hydraulic conditions that could impact the distribution and abundance of macroinvertebrates, which needs to be assessed in the future.

The establishment of *H. verticillata* in the ERW is unfortunate, yet unique. It has provided insight into the potential impacts of submersed invasive macrophytes in high-gradient stream ecosystems. Although the ERW is characterized by variable seasonal hydrology, these varying physical conditions have not prevented hydrilla from invading. This not only reveals that these physical conditions are undemanding to hydrilla, but also shows the ability and success that hydrilla has had in overcoming limitations in maintaining its dispersal and establishment since its introduction to North America. As demonstrated by its establishment in the ERW, it can be anticipated that no freshwater environment is safe from the establishment of *Hydrilla verticillata*, the ultimate aquatic weed.

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APPENDIX A

Photographs

Figure A-1. Riffle habitat sampled from Barnett Bridge at Clear Creek, Obed Wild and Scenic River, Morgan County, Tennessee.

Figure A-2. A pool sampled from Barnett Bridge at Clear Creek, Obed Wild and Scenic River, Morgan County, Tennessee.

Figure A-3. Photograph of *Najas guadalupensis* growing from the sandy substrate in a pool sampled from Barnett Bridge at Clear Creek, Obed Wild and Scenic River, Morgan County, Tennessee.

Figure A-4. Photograph of Clear Creek from Lily Bridge, Obed Wild and Scenic River, Morgan County, Tennessee.

Figure A-5. Riffle sampled from Lily Bridge at Clear Creek, Obed Wild and Scenic River, Morgan County, Tennessee.

Figure A-6. Photograph of *Najas guadalupensis* present within a pool sampled from Lily Bridge at Clear Creek, Obed Wild and Scenic River, Morgan County, Tennessee.

Figure A-7. Riffle sampled from Potter's Ford at Obed River, Obed Wild and Scenic River, Cumberland County, Tennessee.

Figure A-8. Riffle sampled from Highway 68 at Daddy's Creek, Emory River Watershed, Cumberland County, Tennessee.

Figure A-9. A view of Obed River at Obed Junction, Obed Wild and Scenic River, Morgan County, Tennessee.

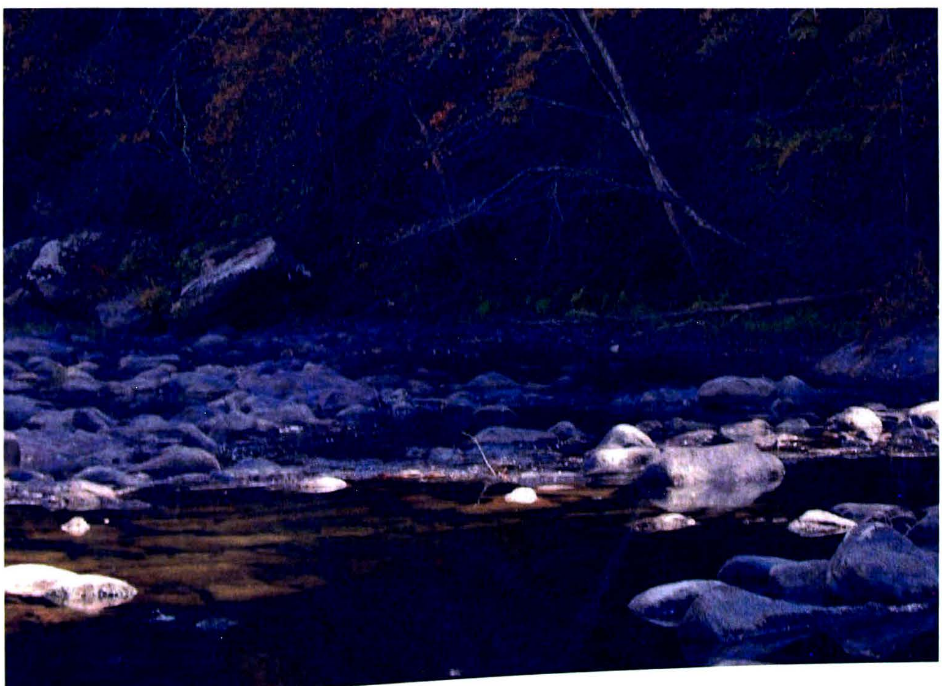

Figure A-10. Riffle sampled from Obed Junction (hydrilla site) at Obed Wild and Scenic River, Morgan County, Tennessee.

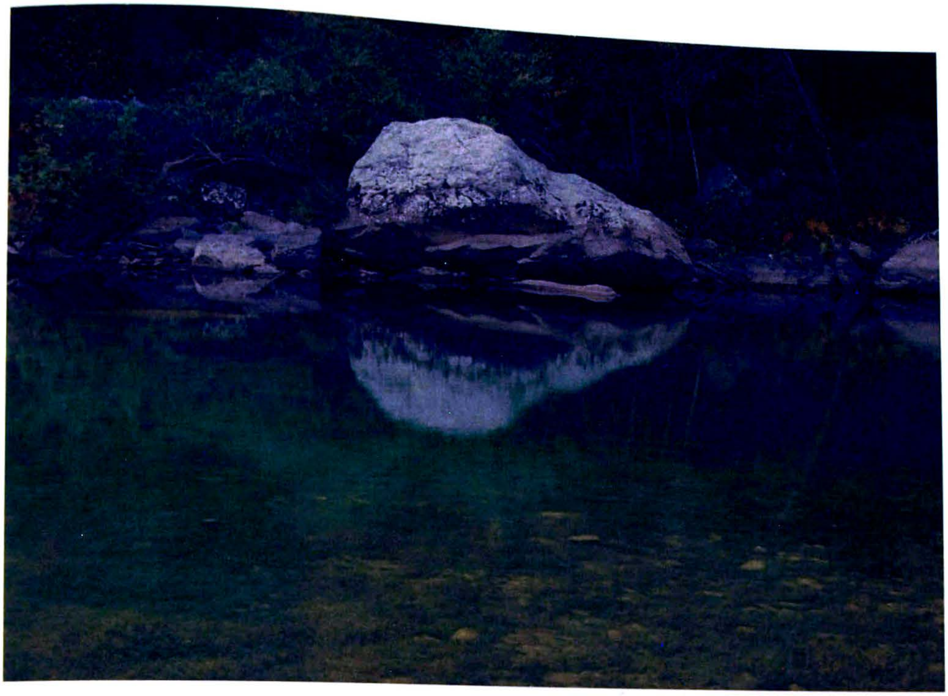

Figure A-11. A hydrilla-infested pool sampled at Obed Junction on Obed River, Obed Wild and Scenic River, Morgan County, Tennessee.

Figure A-12. Riffle sampled from Antioch Bridge located on Daddy's, Emory River Watershed, Cumberland County, Tennessee.

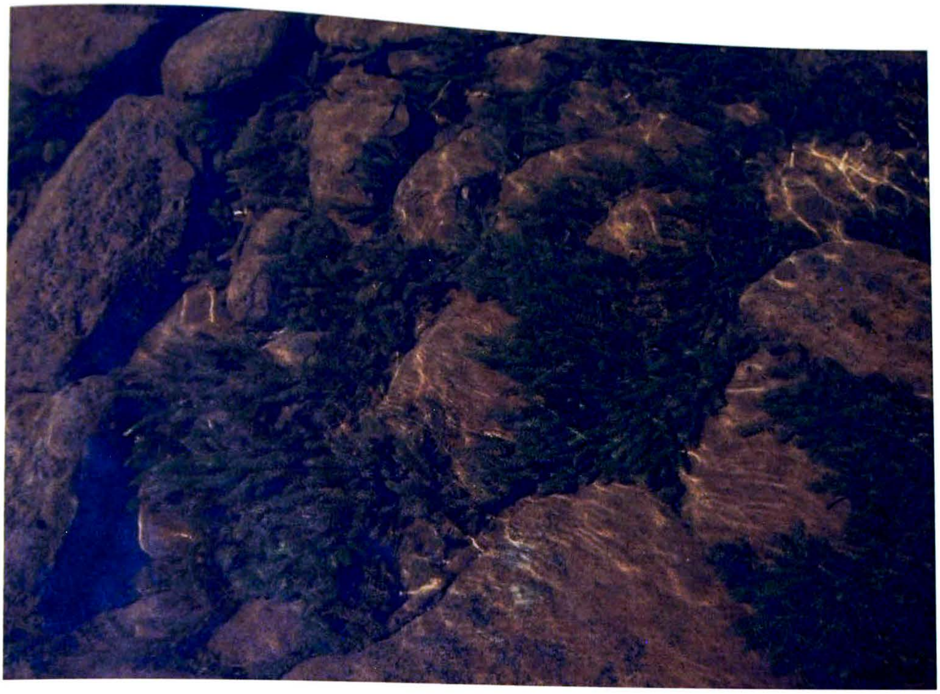

Figure A-13. Pool sampled from Antioch Bridge located on Daddy's Creek, Emory River Watershed, Cumberland County, Tennessee.

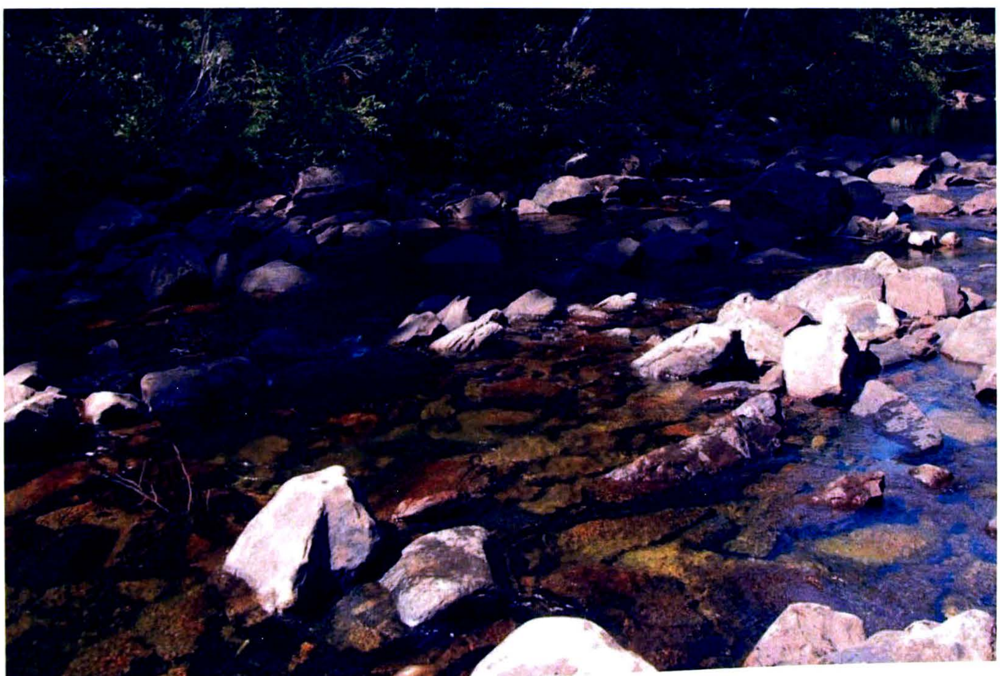

Figure A-14. Riffle sampled from Devil's Breakfast Table located on Daddy's Creek, Obed Wild and Scenic River, Cumberland County, Tennessee.

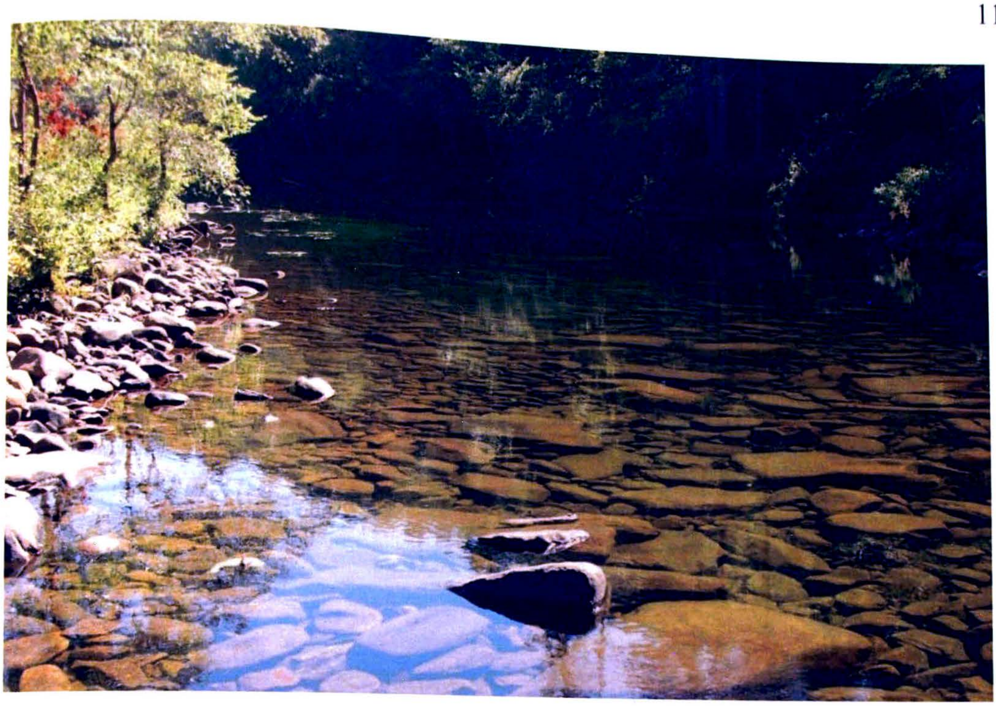

Figure A-15. Pool sampled from Devil's Breakfast Table located on Daddy's Creek, Obed Wild and Scenic River, Cumberland County, Tennessee.

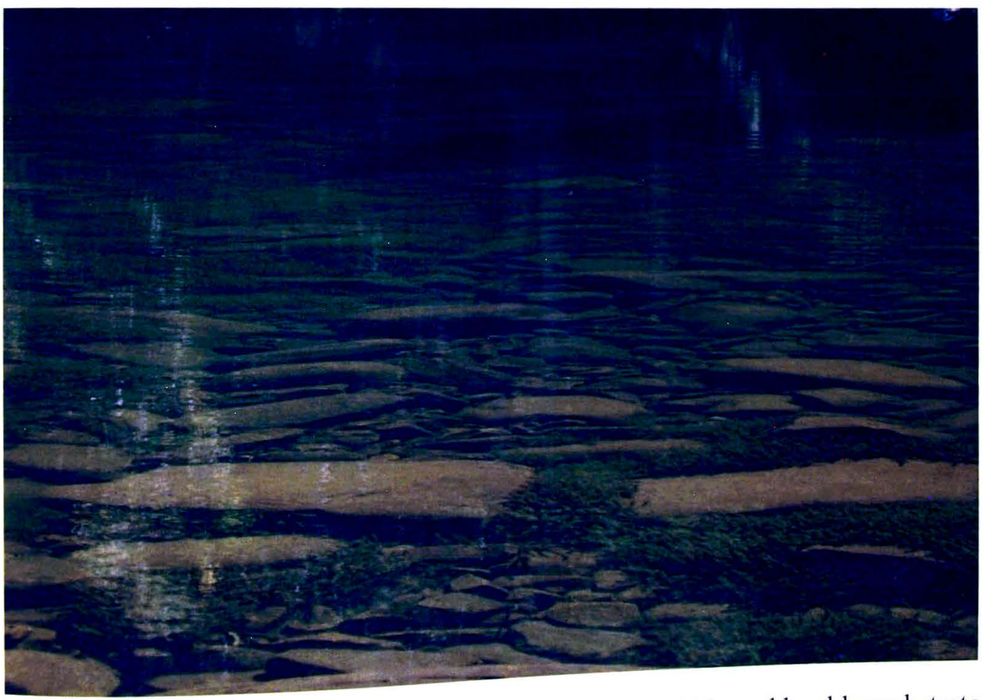

Figure A-16. *Hydrilla verticillata* growing between large cobble and boulder substrate at Devil's Breakfast Table, Daddy's Creek, Obed Wild and Scenic River, Cumberland County, Tennessee.

Figure A-17. Riffle sampled from Nemo Bridge located on Obed River, Obed Wild and Scenic River, Morgan County, Tennessee.

Figure A-18. *Hydrilla verticillata* growing from the interstices of the bedrock substrate from a pool sampled at Nemo Bridge, Obed Wild and Scenic River, Morgan County, Tennessee.

Figure A-19. *Triaenodes* sp. (Trichoptera: Leptoceridae) with a case constructed of hydrilla leaves

Figure A-19. *Oxyethira* sp. (Trichoptera: Hydroptilidae) and associated case attached to hydrilla leaves

APPENDIX B

Abiotic Data

Table B-1. Location and substrate assessment of riffle habitats at various sampling sites, Emory River Watershed, Cumberland and Morgan counties, Tennessee (CPOM= course particulate organic matter, DBT= Devil's Breakfast Table).

Sample Site	**Stream Name**	**Latitude; Longitude**	**Inorganic Substrate**	**% Organic Substrate (CPOM)[2]**
Barnett Bridge	Clear Creek	36.12281°N; 84.79482°W	Boulder-cobble-gravel	< 20%
Lily Bridge	Clear Creek	36.10198°N; 84.71728°W	Boulder-bedrock-cobble	~ 30%
Obed Junction[*]	Obed River	36.079766°N; 84.766989°W	Boulder-gravel-sand	~30%
Potter's Ford[*]	Obed River	36.07288°N; 84.90265°W	Cobble-bolder-gravel	~ 40%
Highway 68[1*]	Daddy's Creek	35.89025°N; 84.93800°W	Cobble-gravel-sand	~ 70%
Obed Junction[+]	Obed River	36.07916°N; 84.76288°W	Boulder-cobble-gravel	~ 30%
Antioch Bridge[1+]	Daddy's Creek	35.99786°N; 84.82331°W	Boulder-cobble-gravel	~ 30%
DBT[+]	Daddy's Creek	36.05865°N; 84.79289°W	Boulder-cobble-gravel	< 20%
Nemo Bridge[+]	Obed River	36.06865°N; 84.66230°W	Boulder-cobble-gravel	~ 30%

[1] Found outside of OWSR boundary
[2] Includes un-rooted organic material, i.e. leaf litter
[*] Pools not sampled due to lack of vegetation
[+] hydrilla-infested site

Table B-2. Location and substrate assessment of pool habitats at various sampling sites, Emory River Watershed, Cumberland and Morgan counties, Tennessee (CPOM= course particulate organic matter, DBT= Devil's Breakfast Table).

Sample Site	**Stream Name**	**Latitude; Longitude**	**Inorganic Substrate**	**% Organic Substrate (CPOM)**
Barnett Bridge	Clear Creek	36.12281°N; 84.79482°W	Cobble-sand	>50% (*N. guadalupensis*)
Lily Bridge	Clear Creek	36.10198°N; 84.71728°W	Bedrock-boulder-cobble	>70% (*N. guadalupensis*
Obed Junction[+]	Obed River	36.07916°N; 84.76288°W	Boulder-cobble-sand	>75% hydrilla
Antioch Bridge[1+]	Daddy's Creek	35.99786 °N; 84.82331°W	Boulder-bedrock-cobble	>75% hydrilla
DBT	Daddy's Creek	36.05865°N; 84.79289°W	Boulder-cobble-sand	>80% hydrilla
Nemo Bridge[+]	Obed River	36.06865°N; 84.66230°W	Boulder-bedrock-cobble	>50% hydrilla

[1] Found outside of OWSR boundary
[+] hydrilla-infested site

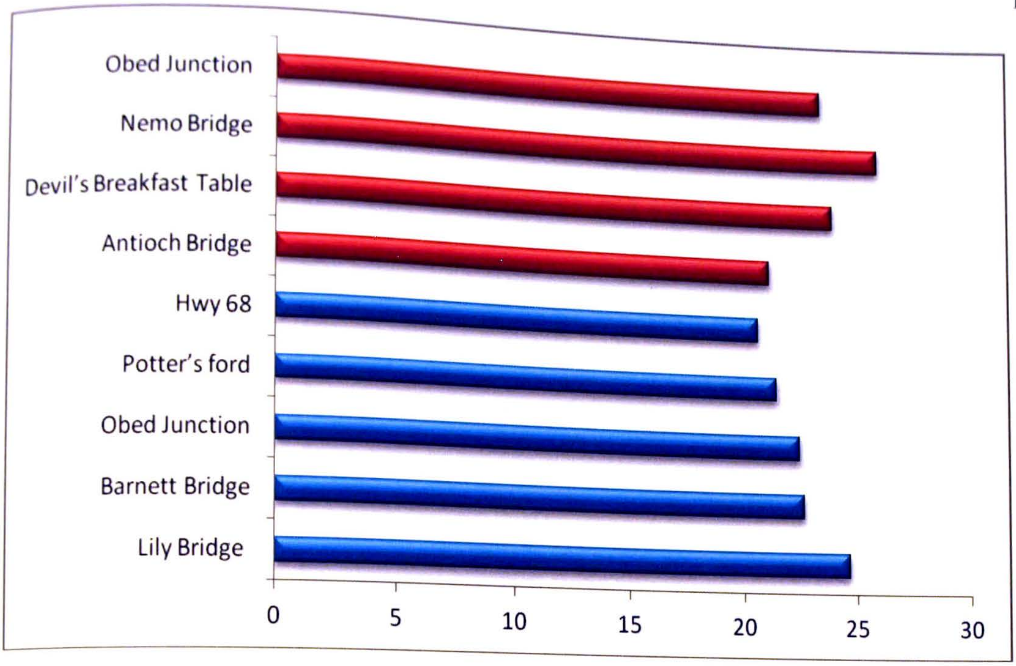

Figure B-19. Water temperatures (°C) of riffles at each sampling site, Emory River Watershed, Cumberland and Morgan counties, Tennessee. Red bars indicate hydrilla-infested site.

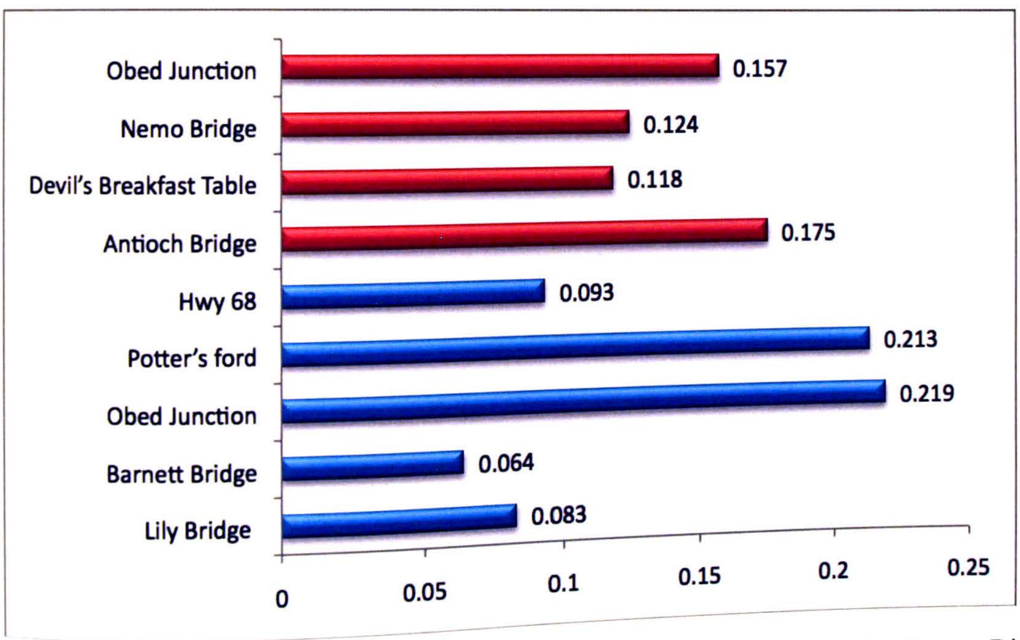

Figure B-20. Specific conductivity (mS/cm) of riffles at each sampling site, Emory River Watershed, Cumberland and Morgan counties, Tennessee. Red bars indicate hydrilla-infested sites.

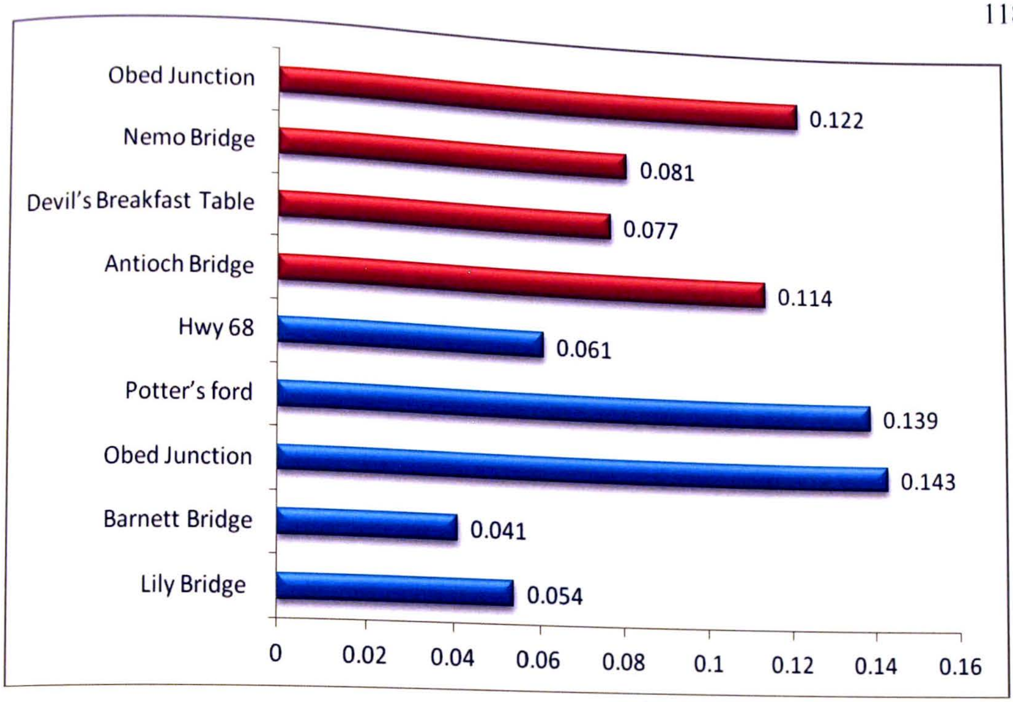

Figure B-21. Total dissolved solids (mg/L) of riffles at each sampling site, Emory River Watershed, Cumberland and Morgan counties, Tennessee. Red bars indicate hydrilla-infested sites.

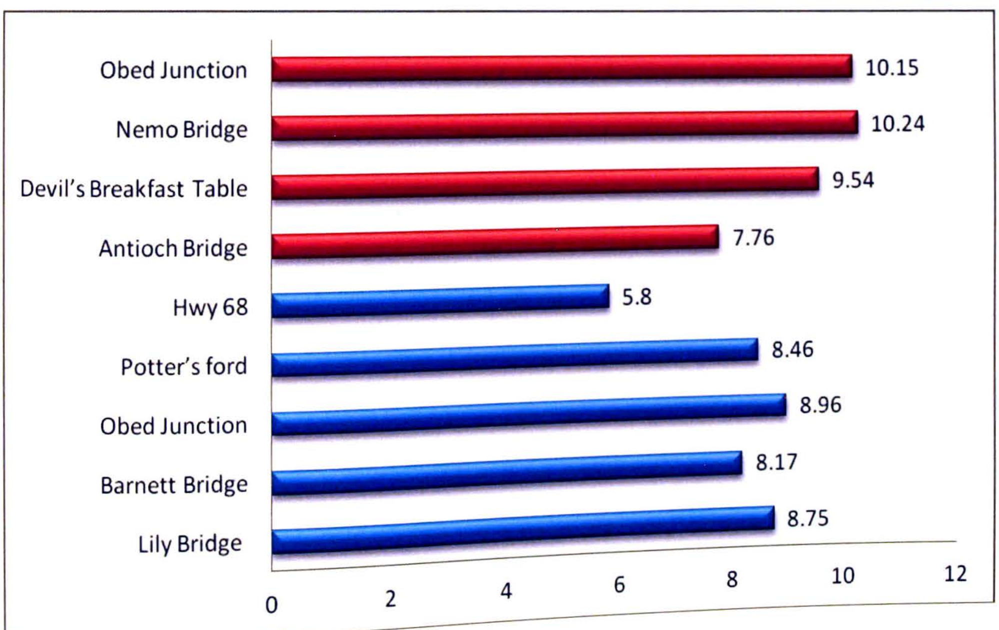

Figure B-22. Dissolved oxygen (mg/L) of riffles at each sampling site, Emory River Watershed, Cumberland and Morgan counties, Tennessee. Red bars indicate hydrilla-infested sites.

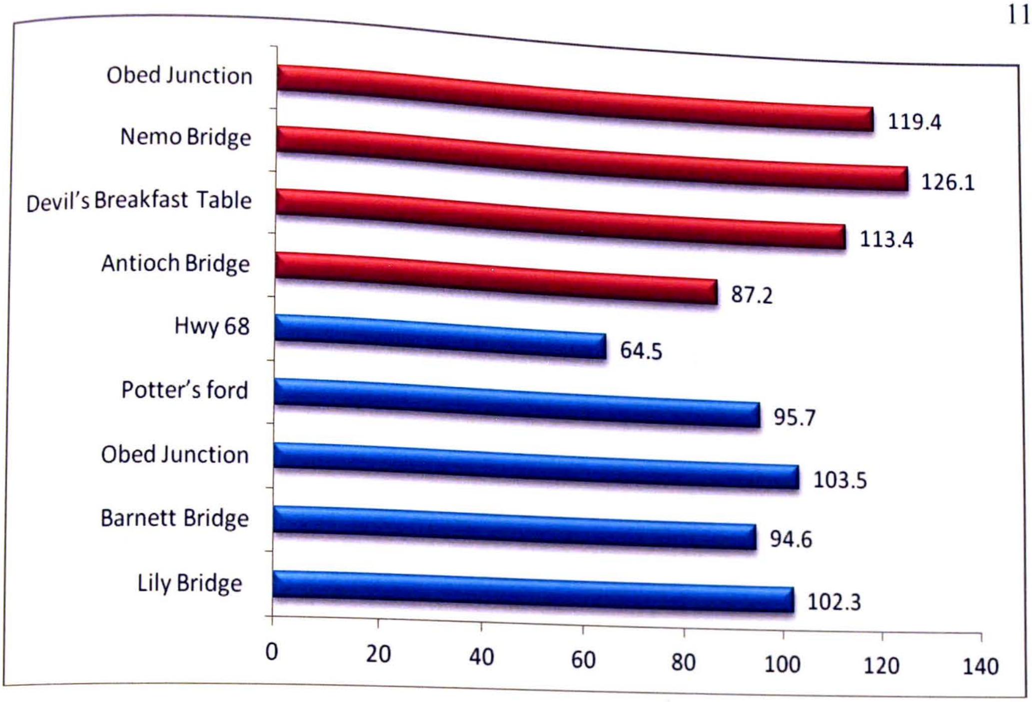

Figure B-23. Percent saturation of riffle dissolved oxygen percent saturation at sampling site, Emory River Watershed, Cumberland and Morgan counties, Tennessee. Red bars indicate hydrilla-infested sites.

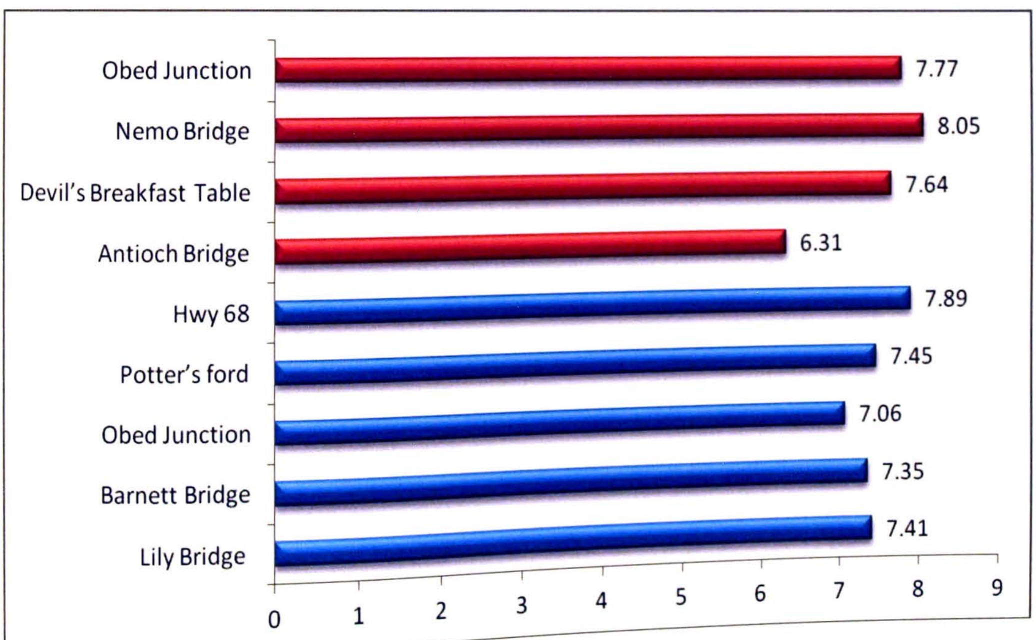

Figure B-24. The pH levels (SU's) of riffles at each sampling site in the Emory River Watershed, Cumberland and Morgan counties, Tennessee. Red bars indicate hydrilla-infested sites.

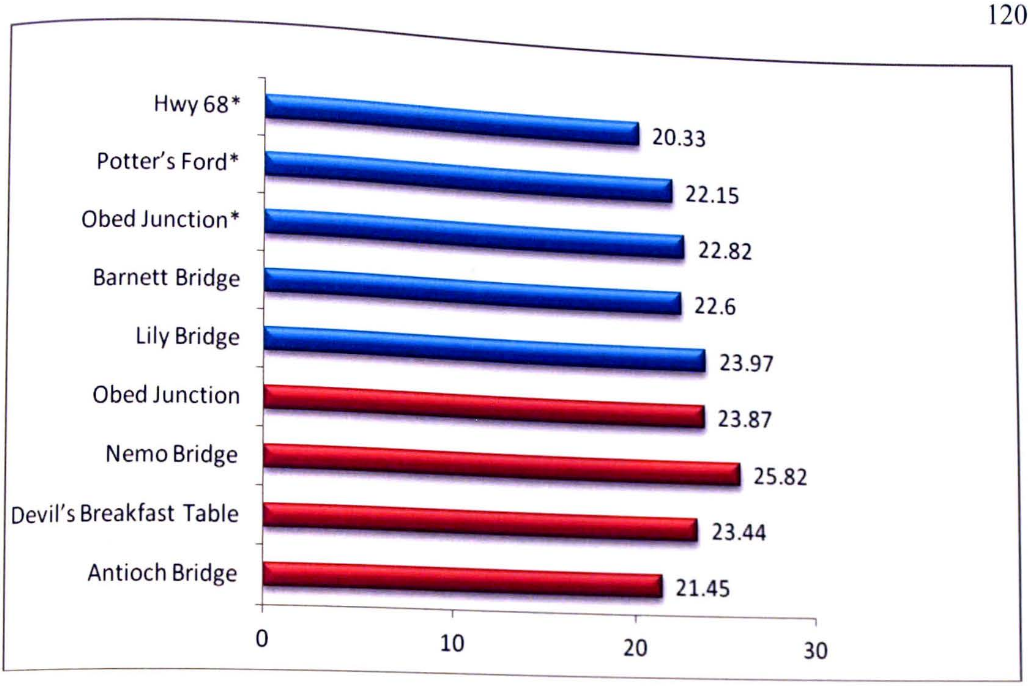

Figure B-25. Temperature (°C) of pools at each sampling site, Emory River Watershed, Cumberland and Morgan counties, Tennessee. Red bars indicate hydrilla-infested sites (* indicates pools not sampled).

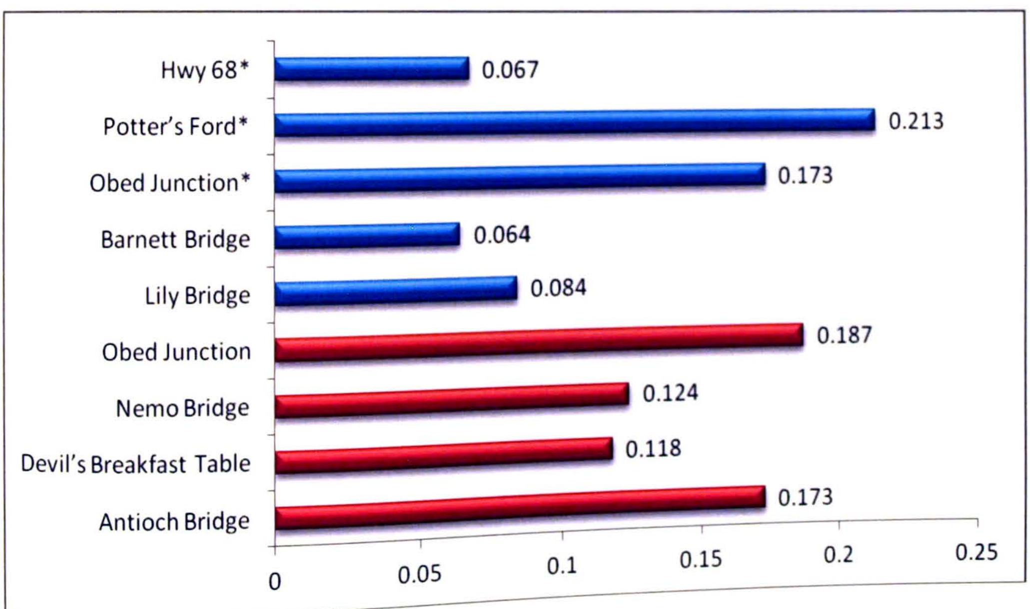

Figure B-26. Specific conductivity (mS/cm) of pools at each sampling site, Emory River Watershed, Cumberland and Morgan counties, Tennessee. Red bars indicate hydrilla-infested sites (* indicates pools not sampled).

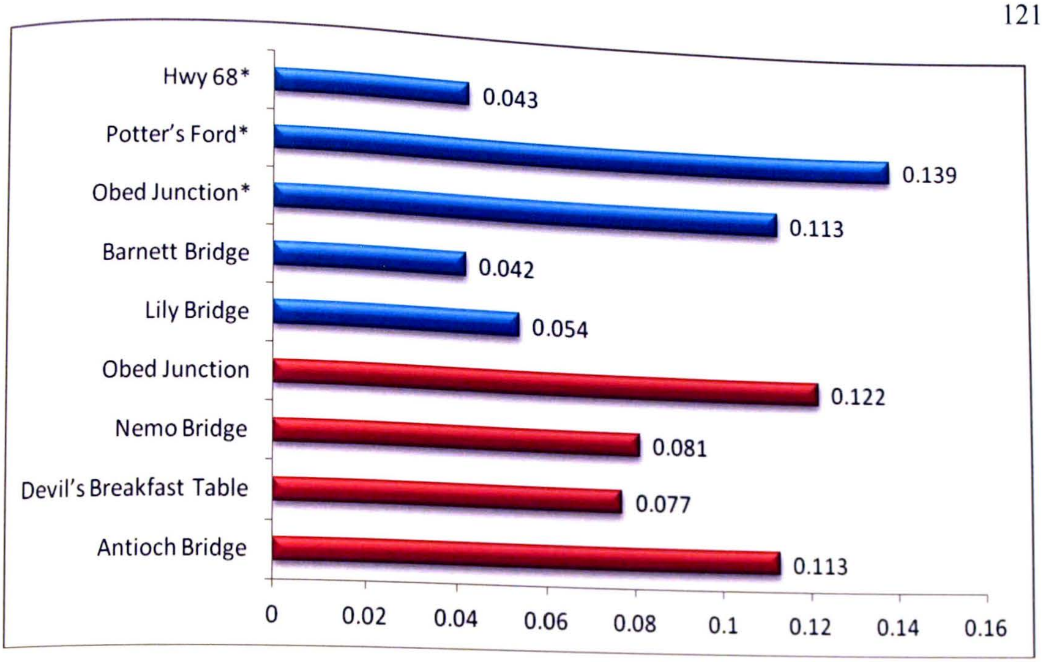

Figure B-27. Total dissolved solids (mg/L) of pools at each sampling site, Emory River Watershed, Cumberland and Morgan counties, Tennessee. Red bars indicate hydrilla-infested sites (* indicates pools not sampled).

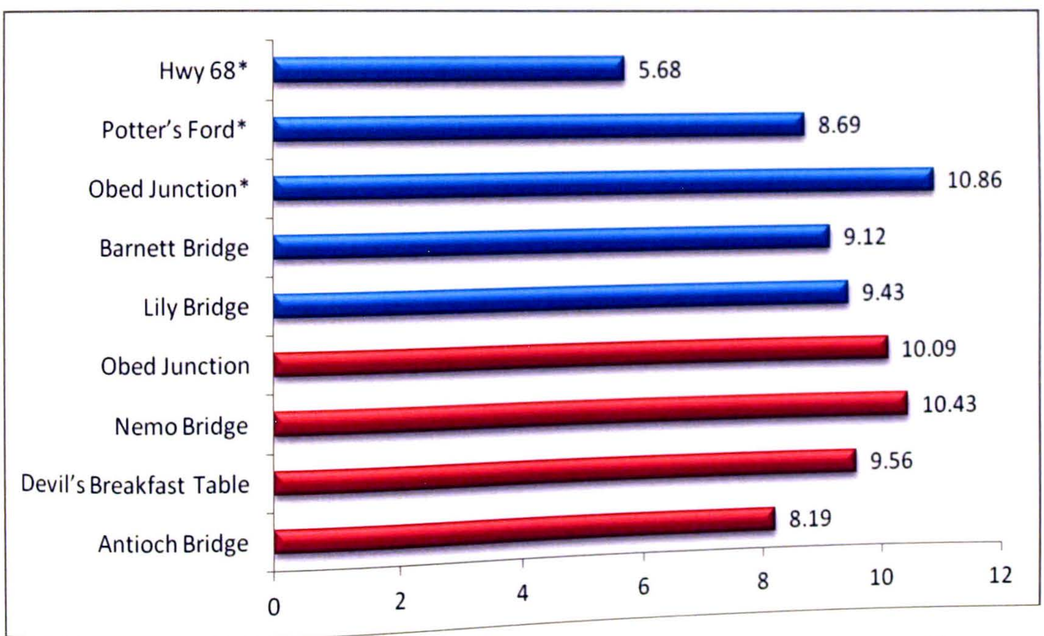

Figure B-28. Dissolved oxygen (mg/L) of pools at each sampling site, Emory River Watershed, Cumberland and Morgan counties, Tennessee. Red bars indicate hydrilla-infested sites (* indicates pools not sampled).

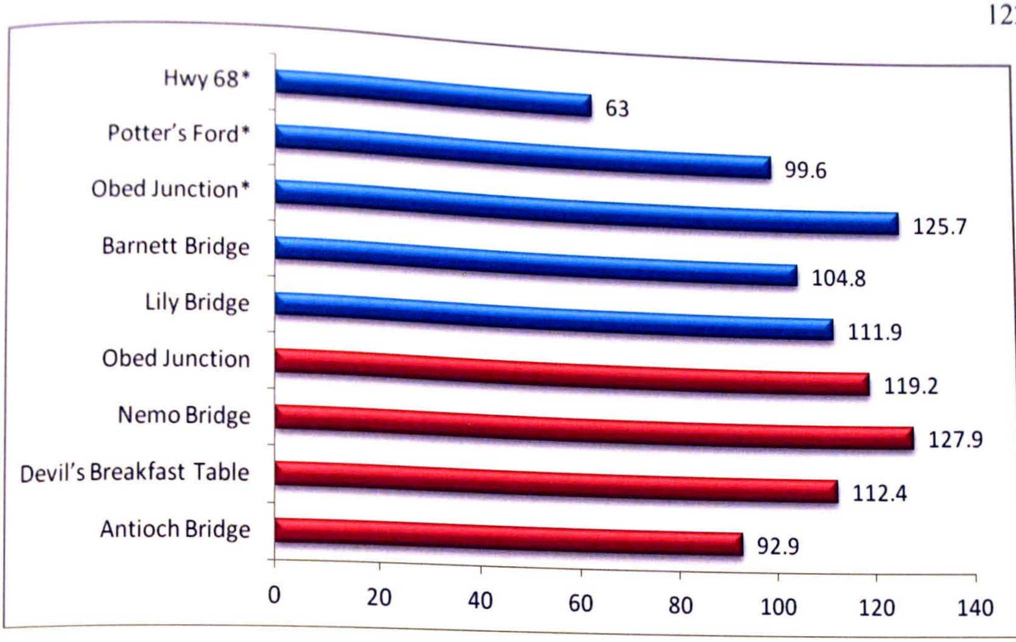

Figure B-29. Percent saturation of pool dissolved oxygen levels at each sampling site, Emory River Watershed, Cumberland and Morgan counties, Tennessee. Red bars indicate hydrilla-infested sites (* indicates pools not sampled).

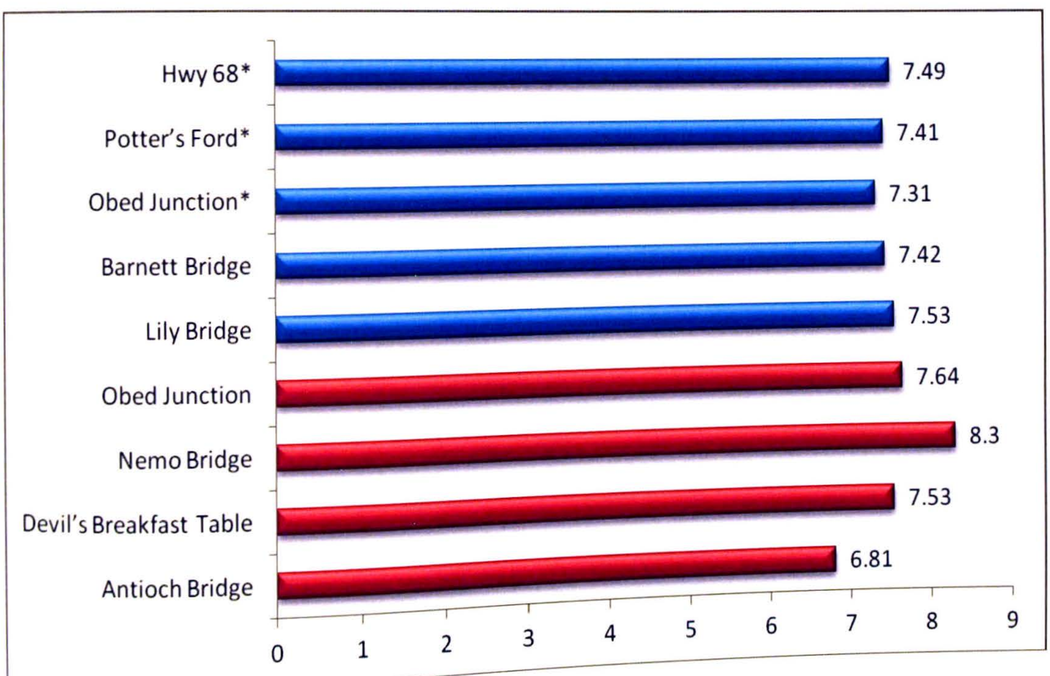

Figure B-30. The pH levels (SU's) of pools at each sampling site, Emory River Watershed, Cumberland and Morgan counties, Tennessee. Red bars indicate hydrilla-infested sites (* indicates pools not sampled).

APPENDIX C

Taxonomic Data Sheets and Functional Feeding Group Characterizations

TAXA	Functional Feeding Group	Barnett Bridge (Clear Creek)					
		Riffle 1	Riffle 2	Riffle 3	Riffle 4	Riffle Total	Pool
AMPHIPODA							
Gammaridae							
Gammarus	collector-gatherer						
Hyalellidae							
Hyalella azteca	collector-gatherer						
BIVALVIA							
Corbiculidae							
Corbicula fluminea	filter-feeder	4	19	32	2	57	23
COLEOPTERA							
Psephenidae							
Psephenus	scraper						
Ectopria	scraper	1	10	10	10	31	6
Dryopidae							
Helichus	scraper						
Elmidae							
pupae							
Ancrynonyx variegatus(adult)	collector-gatherer						5
Dubiraphia (adult)	collector-gatherer						1
Macronychus glabratus (adult)	collector-gatherer						2
Microcylloepus (adult)	collector-gatherer		38	9	4	51	
Optioservus (adult)	collector-gatherer	1				1	
Oulimnius (adult)	collector-gatherer	1		1		2	
Promoresia (adult)	collector-gatherer	2	1	2		5	
Stenelmis (adult)	collector-gatherer	6	41	9	4	60	
Ancyronyx variegatus (larvae)	collector-gatherer						
Dubiraphia (larvae)	collector-gatherer						29
Gonielmis ditrichi (larvae)	collector-gatherer	1	21	25	11	58	1
Macronychus glabratus(larvae)	collector-gatherer	12	1	3		16	2
Microcylloepus (larvae)	collector-gatherer	17	219	83	43	362	21
Optioservus (larvae)	scraper	5	22	18	7	52	
Promoresia (larvae)	collector-gatherer						
Stenelmis (larvae)	scraper	23	110	63	12	208	
Haliplidae							
Haliplus	shredder						
Hydrophilidae							
Berosus (adult)	collector-gatherer						8
Berosus (larvae)	shredder						

Barnett Bridge, cont'd		Riffle 1	Riffle 2	Riffle 3	Riffle 4	Riffle Total	Pool
Enochrus (larvae)	predator						
Scirtidae							
Scirtes (larvae)	shredder						
DECAPODA							
Cambaridae							
Cambarus	collector-gatherer (omnivorous)						
DIPTERA							
pupae			12	8	5		17
Athericidae							
Atherix	predator						
Ceratopogonidae							
Atrichopogon	collector-gatherer		1			1	
Culicoides	predator						
Dasyhelea	collector-gatherer						
Forcipomyia	collector-gatherer						
Monohelea	predator						
Palpomyia	predator						
Chironomidae							
(Chironominae)							
Dicrotendipes	collector-gatherer						14
Endochironomus	shredder						2
Endotribelos	collector-gatherer						1
Microtendipes	collector-filterer						
Nilothauna	collector-gatherer						
Parachironomus	predator						3
Paratendipes	collector-gatherer						
Polypedium	shredder	2	54	42	5	103	1
Pseudochironomus	collector-gatherer						
Stenochironomus	collector-gatherer		2		1	3	
(Orthocladiinae)							
Corynoneura	collector-gatherer	5	1	2	2	10	
Lopescladius	collector-gatherer						
Nanocladius	collector-gatherer		2	1		3	8
Orthocladius	collector-gatherer	5	2	1		8	21
Parakieferella	collector-gatherer						5
Psectrocladius	collector-gatherer						1
Rheocricotopus	collector-gatherer		19	3		22	
Synorthocladius	collector-gatherer	2		1	1	4	
Thienamanniella	collector-gatherer	7	4		1	12	

Barnett Bridge, cont'd		Riffle 1	Riffle 2	Riffle 3	Riffle 4	Riffle Total	Pool
Tvetenia	collector-gatherer		4	1		5	
(Tanypodinae)							
Alabesmyia	predator		1			1	8
Labrundinia	predator						
Nilotanypus	predator			3	2	5	
Pentaneura	predator		2	3	2	7	
Procladius	predator						1
Thinemannimyia group sp.	predator		2	2	1	5	
Tanypus	predator						
(Tanytarsini)							
Cladotanytarsus	collector-gatherer		1		1	2	
Neozavrelia	collector-gatherer						
Paratanytarsus	collector-gatherer						
Rheotanytarsus	collector-filterer	24	83	47	16	170	
Tanytarsus	collector-gatherer	1	3	7		11	73
Culicidae							
Anopheles	collector-filterer						
Ephydridae							
Hydrellia	shredder						
Empididae							
Chelifera	predator						
Hemerodromia	predator	3	4		2	9	
Simulidae							
Simulium	collector-filterer	7	10	19	2	38	
Tipulidae							
Antocha	collector-gatherer						
Erioptera	colector-gatherer						
Tipula	shredder						
EPHEMEROPTERA							
Baetidae							
Acerpenna	collector-gatherer	1	23	17		41	
Baetis	collector-gatherer	27		11	17	55	
Centroptilum	collector-gatherer				1	1	
Heterocleon	scraper	5	82	77	24	188	
Plauditus	collector-gatherer	1	5	14	4	24	
Caenidae							
Caenis	collector-gatherer			2		2	
Ephemerellidae							
Eurylophella	collector-gatherer						

Barnett Bridge, cont'd		Riffle 1	Riffle 2	Riffle 3	Riffle 4	Riffle Total	Pool
Leptohyphidae							
Trichorythodes	collector-gatherer	1	11	32	1	45	4
Isonychiidae							
Isonychia	collector-filterer	6	26	3	2	37	
Heptageniidae							
Leucrocuta	collector-gatherer						
Maccaffertium	scraper	1	28		11	40	
Stenacron	scraper						
Stenonema femoratum	scraper			7		7	
GASTROPODA							
Ancylidae	grazer		2	4	3	9	135
Planorbidae	grazer		21	9	2	32	134
Physidae	grazer		18	2	1	21	
Pleuroceridae	grazer						
Lymnaeidae	grazer						
HEMIPTERA							
Mesoveliidae							
Mesovelia	predator						
Saldidae							
Pentacora	predator						
Hydrocarina	predator	3	25	15	11	54	8
ISOPODA							
Asellidae							
Lirceus	collector-gatherer						
LEPIDOPTERA							
Crambidae							
Elophila	shredder						
Petrophila	shredder						1
MEGALOPTERA							
Corydalidae							
Corydalus cornutus	predator	2	4	1	1	8	
Nigronia	predator				1	1	
ODONATA							
Aeshnidae							
Boyeria vinosa	predator			1		1	1
Coenagionidae							
Argia	predator		1			1	
Enallagma	predator						8
Calopterygidae							

Barnett Bridge, cont'd		Riffle 1	Riffle 2	Riffle 3	Riffle 4	Riffle Total	Pool
Calopteryx dimidiata	predator						
Calopteryx maculata	predator						
Hetaerina americana	predator		1			1	
Corduliidae							
Epitheca	predator						
Neurocordulia	predator						2
Somatochlora	predator						
Gomphidae							
Dromogomphus	predator						5
Gomphus	predator						
Haegenius brevistylus	predator			1		1	2
Stylogomphus	predator	4	20	11	12	47	
Libellulidae							
Erythemis	predator						1
Libellula	predator						
Macromiidae							
Macromia	predator						6
Oligochaeta	collector-filterer	7	5	11	6	29	152
PLATYHELMINTHES							
Planaridae	omnivorous						30
PLECOPTERA							
Perlidae							
Acroneuria	predator				2	2	
Agnetina	predator		1			1	
Neoperla	predator						
TRICHOPTERA							
pupae					2	2	
Brachycentridae							
Micrasema	shredder		47	30	2	79	3
Helicopsychidae							
Helicopsyche	scraper		6	9	18	33	1
Hydropsychidae							
Cheumatopsyche	collector-filterer	11	63	14	2	90	
Ceratopsyche	collector-filterer	1		2		3	
Hydropsyche	collector-filterer	2	20			22	
Macrostemum	collector-filterer						
Hydroptilidae							
Hydroptila	piercer-herbivore						3
Oxyethira	piercer-herbivore						60
Orthotrichia	piercer-herbivore						

Barnett Bridge, cont'd		Riffle 1	Riffle 2	Riffle 3	Riffle 4	Riffle Total	Pool
Lepidostomatidae							
Lepidostoma	shredder		2	14		16	
Leptoceridae							
Ceraclea	collector-gatherer			1		1	
Mystacides	collector-gatherer						2
Nectopsyche	shredder						
Oecetis	predator		13	3	5	21	7
Triaenodes	shredder						9
Limnephilidae							
Pycnopsyche	shredder						
Philopotamidae							
Chimarra	collector-filterer	1	23	6		30	
Phryganeidae							
Ptilostomis	shredder						
Polycentropodidae							
Neureclipsis	collector-filterer		3		1	4	3
Nyctiophylax	predator						
Polycentropus	predator						

TAXA	Functional Feeding Group	Lily Bridge (Clear Creek)					
		Riffle 1	Riffle 2	Riffle 3	Riffle 4	Riffle Total	Pool
AMPHIPODA							
Gammaridae							
Gammarus	collector-gatherer						
Hyallelidae							
Hyalella azteca	collector-gatherer						
BIVALVIA							1
Corbiculidae							
Corbicula fluminea	filter-feeder						
COLEOPTERA				1	1	2	6
Psephenidae							
Psephenus	scraper						
Ectopria	scraper		2	10		12	
Dryopidae							
Helichus	scraper						
Elmidae							
pupae		1					6
Ancrynonyx variegatus(adult)	collector-gatherer						1
Dubiraphia (adult)	collector-gatherer		1			1	2
Macronychus glabratus (adult)	collector-gatherer	1				1	2
Microcylloepus (adult)	collector-gatherer	95	192	33	11	331	1
Optioservus (adult)	collector-gatherer						
Oulimnius (adult)	collector-gatherer	3				3	
Promoresia (adult)	collector-gatherer	4	7	4		15	
Stenelmis (adult)	collector-gatherer	5	9	3	10	27	4
Ancyronyx variegatus (larvae)	collector-gatherer						
Dubiraphia (larvae)	collector-gatherer						1
Gonielmis ditrichi (larvae)	collector-gatherer	26	38	35		99	
Macronychus glabratus(larvae)	collector-gatherer						
Microcylloepus (larvae)	collector-gatherer	179	154	88	81	502	1
Optioservus (larvae)	scraper	1				1	
Promoresia (larvae)	collector-gatherer		1			1	
Stenelmis (larvae)	scraper	13	2	1	12	28	1
Haliplidae							
Haliplus	shredder						6
Hydrophilidae							
Berosus (adult)	collector-gatherer						

Lily Bridge, cont'd		Riffle 1	Riffle 2	Riffle 3	Riffle 4	Riffle Total	Pool
Berosus (larvae)	shredder						5
Enochrus (larvae)	predator						
Scirtidae							
Scirtes (larvae)	shredder						1
DECAPODA							
Cambaridae							
Cambarus	collector-gatherer (omnivorous)						
DIPTERA							
pupae		14		7	14	35	14
Athericidae							
Atherix	predator						
Ceratopogonidae							
Atrichopogon	collector-gatherer						1
Culicoides	predator						
Dasyhelea	collector-gatherer						
Forcipomyia	collector-gatherer						
Monohelea	predator						
Palpomyia	predator	1				1	
Chironomidae							
(Chironominae)							
Dicrotendipes	collector-gatherer		1			1	57
Endochironomus	shredder						
Endotribelos	collector-gatherer						
Microtendipes	collector-filterer						1
Nilothauna	collector-gatherer						1
Parachironomus	predator						2
Paratendipes	collector-gatherer						2
Polypedium	shredder	182	144	67	56	449	37
Pseudochironomus	collector-gatherer						
Stenochironomus	collector-gatherer	18	9	4		31	7
(Orthocladiinae)							
Corynoneura	collector-gatherer	28	20	1	1	50	5
Lopescladius	collector-gatherer						
Nanocladius	collector-gatherer	1	1			2	8
Orthocladius	collector-gatherer	4	5	22	7	38	24
Parakieferella	collector-gatherer						71
Psectrocladius	collector-gatherer						12
Rheocricotopus	collector-gatherer	1		1	1	3	
Synorthocladius	collector-gatherer						

Lily Bridge, cont'd		Riffle 1	Riffle 2	Riffle 3	Riffle 4	Riffle Total	Pool
Thienamanniella	collector-gatherer	14	5	12	5	36	4
Tvetenia	collector-gatherer	3		1	2	6	
(Tanypodinae)							
Alabesmyia	predator						22
Labrundinia	predator						
Nilotanypus	predator	2		1		3	5
Pentaneura	predator						
Procladius	predator						2
Thinemannimyia group sp.	predator			2	2	4	
Tanypus	predator						
(Tanytarsini)							
Cladotanytarsus	collector-gatherer						
Neozavrelia	collector-gatherer				6	6	
Paratanytarsus	collector-gatherer						23
Rheotanytarsus	collector-filterer	76	164	67	106	413	
Tanytarsus	collector-gatherer		2		1	3	81
Culicidae							
Anopheles	collector-filterer						
Ephydridae							
Hydrellia	shredder						
Empididae							
Chelifera	predator						
Hemerodromia	predator	9	1		2	12	
Simulidae							
Simulium	collector-filterer	207	93	57	138	495	
Tipulidae							
Antocha	collector-gatherer						
Erioptera	colector-gatherer						
Tipula	shredder						
EPHEMEROPTERA							
Baetidae							
Acerpenna	collector-gatherer	10	21	84	1	116	
Baetis	collector-gatherer	14	39	24	28	105	
Centroptilum	collector-gatherer						3
Heterocleon	scraper	8	15	11	42	76	
Plauditus	collector-gatherer						
Caenidae							
Caenis	collector-gatherer						
Ephemerellidae							

Lily Bridge, cont'd		Riffle 1	Riffle 2	Riffle 3	Riffle 4	Riffle Total	Pool
Eurylophella	collector-gatherer			1		1	
Leptohyphidae							
Trichorythodes	collector-gatherer	20	6	3		29	2
Isonychiidae							
Isonychia	collector-filterer	31	61	17	4	113	
Heptageniidae							
Leucrocuta	collector-gatherer	6	9			15	
Maccaffertium	scraper	24	43	7	16	90	
Stenacron	scraper						
Stenonema femoratum	scraper			9		9	
GASTROPODA							
Ancylidae	grazer			2	5	7	23
Planorbidae	grazer	1				1	105
Physidae	grazer			1		1	9
Pleuroceridae	grazer						
Lymnaeidae	grazer						
HEMIPTERA							
Mesoveliidae							
Mesovelia	predator						
Saldidae							
Pentacora	predator						
HYDROCARINA	predator	34	7	17	8	66	9
ISOPODA							
Asellidae							
Lirceus	collector-gatherer (scavenger)						
LEPIDOPTERA							
Crambidae							
Elophila	shredder						1
Petrophila	shredder						
MEGALOPTERA							
Corydalidae							
Corydalus cornutus	predator	4	4		3	11	
Nigronia	predator						
ODONATA							
Aeshnidae							
Boyeria vinosa	predator		1			1	
Coenagionidae							
Argia	predator			2		2	
Enallagma	predator						14

Lily Bridge, cont'd		Riffle 1	Riffle 2	Riffle 3	Riffle 4	Riffle Total	Pool
Calopterygidae							
Calopteryx dimidiata	predator						
Calopteryx maculata	predator						
Hetaerina americana	predator						
Corduliidae			1			1	
Epitheca	predator						
Neurocordulia	predator						2
Somatochlora	predator			2		2	4
Gomphidae							
Dromogomphus	predator						
Gomphus	predator			1		1	
Haegenius brevistylus	predator						4
Stylogomphus	predator	3		3	1	7	2
Libellulidae							
Erythemis	predator						
Libellula	predator						
Macromiidae							
Macromia	predator						
Oligochaeta	collector-filterer				6	6	90
PLATYHELMINTHES							
Planariidae	omnivorous						32
PLECOPTERA							
Perlidae							
Acroneuria	predator	5	3			8	
Agnetina	predator	20	14	3	1	38	
Neoperla	predator						
TRICHOPTERA							
pupae							
Brachycentridae							
Micrasema	shredder	28	31	61	6	126	3
Helicopsychidae							
Helicopsyche	scraper			6		6	2
Hydropsychidae							
Cheumatopsyche	collector-filterer	49	33	15	25	122	
Ceratopsyche	collector-filterer	71	159	46	47	323	
Hydropsyche	collector-filterer	55	169	27	44	295	
Macrostemum	collector-filterer						
Hydroptilidae							
Hydroptila	piercer-herbivore		4	1		5	7
Oxyethira	piercer-herbivore						82

Lily Bridge, cont'd		Riffle 1	Riffle 2	Riffle 3	Riffle 4	Riffle Total	Pool
Orthotrichia	piercer-herbivore						
Lepidostomatidae							
Lepidostoma	shredder						
Leptoceridae							
Ceraclea	collector-gatherer	2		1		3	
Mystacides	collector-gatherer						1
Nectopsyche	shredder						
Oecetis	predator	9	12	14	1	36	7
Triaenodes	shredder						12
Limnephilidae							
Pycnopsyche	shredder						
Philopotamidae							
Chimarra	collector-filterer	17	18	1	3	39	
Phryganeidae							
Ptilostomis	shredder						1
Polycentropodidae							
Neureclipsis	collector-filterer	7	37	14	7	65	2
Nyctiophylax	predator	2		3		5	
Polycentropus	predator						2

TAXA	Functional Feeding Group	Obed Junction (Obed River)*				
		Riffle 1	Riffle 2	Riffle 3	Riffle 4	Riffle Total
AMPHIPODA						
Gammaridae						
Gammarus	collector-gatherer					
Hyalellidae						
Hyalella azteca	collector-gatherer	2		17	10	29
BIVALVIA						
Corbiculidae						
Corbicula fluminea	filter-feeder	2		7	3	12
COLEOPTERA						
Psephenidae						
Psephenus	scraper	17	12	44	2	75
Ectopria	scraper	2			2	4
Dryopidae						
Helichus	scraper					
Elmidae						
pupae						
Ancrynonyx variegatus(adult)	collector-gatherer					
Dubiraphia (adult)	collector-gatherer					
Macronychus glabratus (adult)	collector-gatherer					
Microcylloepus (adult)	collector-gatherer	8	21	6	18	53
Optioservus (adult)	collector-gatherer	3			1	4
Oulimnius (adult)	collector-gatherer					
Promoresia (adult)	collector-gatherer	5	1	5	2	13
Stenelmis (adult)	collector-gatherer				1	1
Ancyronyx variegatus (larvae)	collector-gatherer					
Dubiraphia (larvae)	collector-gatherer		1			1
Gonielmis ditrichi (larvae)	collector-gatherer	31	36	15	27	109
Macronychus glabratus(larvae)	collector-gatherer	2	2		2	6
Microcylloepus (larvae)	collector-gatherer	161	174	189	211	735
Optioservus (larvae)	scraper			7	6	13
Promoresia (larvae)	collector-gatherer					
Stenelmis (larvae)	scraper		1	4	1	6
Haliplidae						
Haliplus	shredder					
Hydrophilidae						
Berosus (adult)	collector-gatherer					

Obed Junction, cont'd		Riffle 1	Riffle 2	Riffle 3	Riffle 4	Riffle Total
Berosus (larvae)	shredder	1	1		1	3
Enochrus (larvae)	predator	1				1
Scirtidae						
Scirtes (larvae)	shredder					
DECAPODA						
Cambaridae						
Cambarus	collector-gatherer (omnivorous)					
DIPTERA						
pupae		9	11	9	12	41
Athericidae						
Atherix	predator					
Ceratopogonidae						
Atrichopogon	collector-gatherer					
Culicoides	predator					
Dasyhelea	collector-gatherer					
Forcipomyia	collector-gatherer					
Monohelea	predator					
Palpomyia	predator					
Chironomidae						
(Chironominae)						
Dicrotendipes	collector-gatherer			1	2	3
Endochironomus	shredder					
Endotribelos	collector-gatherer					
Microtendipes	collector-filterer		1			1
Nilothauna	collector-gatherer					
Parachironomus	predator					
Paratendipes	collector-gatherer					
Polypedium	shredder	66	61	108	108	343
Pseudochironomus	collector-gatherer					
Stenochironomus	collector-gatherer	1	5	1		7
(Orthocladiinae)						
Corynoneura	collector-gatherer	3	2			5
Lopescladius	collector-gatherer					
Nanocladius	collector-gatherer					
Orthocladius	collector-gatherer	58	52	68	38	216
Parakieferella	collector-gatherer					
Psectrocladius	collector-gatherer			1		1
Rheocricotopus	collector-gatherer					

Obed Junction, cont'd		Riffle 1	Riffle 2	Riffle 3	Riffle 4	Riffle Total
Synorthocladius	collector-gatherer	1	3	1	3	8
Thienamanniella	collector-gatherer	47	20	9	32	108
Tvetenia	collector-gatherer					
(Tanypodinae)						
Alabesmyia	predator	2				2
Labrundinia	predator					
Nilotanypus	predator					
Pentaneura	predator	2	1	1	2	6
Procladius	predator					
Thinemannimyia group sp.	predator					
Tanypus	predator					
(Tanytarsini)						
Cladotanytarsus	collector-gatherer					
Neozavrelia	collector-gatherer					
Paratanytarsus	collector-gatherer					
Rheotanytarsus	collector-filterer	69	127	36	122	354
Tanytarsus	collector-gatherer		4	1	2	7
Culicidae						
Anopheles	collector-filterer					
Ephydridae						
Hydrellia	shredder					
Empididae						
Chelifera	predator	1				1
Hemerodromia	predator		2			2
Simulidae						
Simulium	collector-filterer			5		5
Tipulidae						
Antocha	collector-gatherer		2			2
Erioptera	collector-gatherer	1				1
Tipula	shredder					
EPHEMEROPTERA						
Baetidae						
Acerpenna	collector-gatherer	1	2	5		8
Baetis	collector-gatherer	14	39	26	28	107
Centroptilum	collector-gatherer					
Heterocleon	scraper	3	6	7	2	18
Caenis	collector-gatherer					
Plauditus	collector-gatherer	1	10		1	12
Caenidae						

Obed Junction, cont'd		Riffle 1	Riffle 2	Riffle 3	Riffle 4	Riffle Total
Ephemerellidae						
Eurylophella	collector-gatherer				1	1
Leptohyphidae						
Trichorythodes	collector-gatherer	14	49	7	6	76
Isonychiidae						
Isonychia	collector-filterer	1			2	3
Heptageniidae						
Leucrocuta	collector-gatherer	1				1
Maccaffertium	scraper	18	8	16	40	82
Stenacron	scraper	14			2	16
Stenonema femoratum	scraper					
GASTROPODA						
Ancylidae	grazer	3				3
Planorbidae	grazer			2	2	4
Physidae	grazer			2	2	4
Pleuroceridae	grazer				1	1
Lymnaeidae	grazer					
HEMIPTERA						
Mesoveliidae						
Mesovelia	predator					
Saldidae						
Pentacora	predator			2		2
Hydrocarina	predator	1	9	2		12
ISOPODA						
Asellidae						
Lirceus	collector-gatherer (scavenger)					
LEPIDOPTERA						
Crambidae						
Elophila	shredder	1				1
Petrophila	shredder					
MEGALOPTERA						
Corydalidae					1	1
Corydalus cornutus	predator					
Nigronia	predator					

Obed Junction, cont'd		Riffle 1	Riffle 2	Riffle 3	Riffle 4	Riffle Total
ODONATA						
Aeshnidae						
Boyeria vinosa	predator					
Coenagionidae						
Argia	predator	1	1			2
Enallagma	predator					
Calopterygidae						
Calopteryx dimidiata	predator			1		1
Calopteryx maculata	predator					
Hetaerina americana	predator			2	1	3
Corduliidae						
Epitheca	predator					
Neurocordulia	predator		3			3
Somatochlora	predator					
Gomphidae						
Dromogomphus	predator	1				1
Gomphus	predator					
Hagenius brevistylus	predator					
Stylogomphus	predator					
Libellulidae						
Erythemis	predator		1	1		2
Libellula	predator					
Macromiidae						
Macromia	predator					
Oligochaeta	collector-filterer	9		23	20	52
PLATYHELMINTHES						
Planariidae	omnivorous	4		24	14	42
PLECOPTERA						
Perlidae						
Acroneuria	predator				1	1
Agnetina	predator	4	2	2	4	12
Neoperla	predator					
TRICHOPTERA						
pupae				2		2
Brachycentridae						
Micrasema	shredder	13	8	8	5	34
Helicopsychidae						

Obed Junction, cont'd		**Riffle 1**	**Riffle 2**	**Riffle 3**	**Riffle 4**	**Riffle Total**
Helicopsyche	scraper	2	7	1		10
Hydropsychidae						
Cheumatopsyche	collector-filterer	37	10	7	60	114
Ceratopsyche	collector-filterer	3	7	39	41	90
Hydropsyche	collector-filterer	4	17	68	36	125
Macrostemum	collector-filterer					
Hydroptilidae						
Hydroptila	piercer-herbivore	47	50	131	121	349
Oxyethira	piercer-herbivore					
Orthotrichia	piercer-herbivore					
unsure?	piercer-herbivore					
Lepidostomatidae						
Lepidostoma	shredder	4	8		3	15
Leptoceridae						
Ceraclea	collector-gatherer	9	7			16
Mystacides	collector-gatherer			2		2
Nectopsyche	shredder		16		1	17
Oecetis	predator	3	20	2	3	28
Triaenodes	shredder					
Limnephilidae						
Pycnopsyche	shredder					
Philopotamidae						
Chimarra	collector-filterer			3	1	4
Phryganeidae						
Ptilostomis	shredder					
Polycentropodidae						
Neureclipsis	collector-filterer	1	1	3		5
Nyctiophylax	predator					
Polycentropus	predator					

*pool not sampled due to lack of significant submersed vegetation

TAXA	Functional Feeding Group	Potter's Ford (Obed River)*				
		Riffle 1	Riffle 2	Riffle 3	Riffle 4	Riffle Total
AMPHIPODA						
Gammaridae						
Gammarus	collector-gatherer					
Hyalellidae						
Hyalella azteca	collector-gatherer					
BIVALVIA						
Corbiculidae						
Corbicula fluminea	filter-feeder	2	1			3
COLEOPTERA						
Psephenidae						
Psephenus	scraper	26	6	12	41	85
Ectopria	scraper					
Dryopidae						
Helichus	scraper					
Elmidae						
pupae						
Ancrynonyx variegatus(adult)	collector-gatherer					
Dubiraphia (adult)	collector-gatherer					
Macronychus glabratus (adult)	collector-gatherer					
Microcylloepus (adult)	collector-gatherer	5				5
Optioservus (adult)	collector-gatherer	3	1	1	3	8
Oulimnius (adult)	collector-gatherer	2				2
Promoresia (adult)	collector-gatherer					
Stenelmis (adult)	collector-gatherer	31	9	6	15	61
Ancyronyx variegatus (larvae)	collector-gatherer					
Dubiraphia (larvae)	collector-gatherer					
Gonielmis ditrichi (larvae)	collector-gatherer					
Macronychus glabratus(larvae)	collector-gatherer		1	2		3
Microcylloepus (larvae)	collector-gatherer	20				20
Optioservus (larvae)	scraper	36	18	22		76
Promoresia (larvae)	collector-gatherer	1				1
Stenelmis (larvae)	scraper	33	15	6	3	57

Potter's Ford, cont'd		Riffle 1	Riffle 2	Riffle 3	Riffle 4	Riffle Total
Haliplidae						
Haliplus	shredder					
Hydrophilidae						
Berosus (adult)	collector-gatherer					
Berosus (larvae)	shredder					
Enochrus (larvae)	predator					
Scirtidae						
Scirtes (larvae)	shredder					
DECAPODA						
Cambaridae						
Cambarus	collector-gatherer (omnivorous)				1	1
DIPTERA						
pupae		18	8	4		30
Athericidae						
Atherix	predator					
Ceratopogonidae						
Atrichopogon	collector-gatherer	5	1		2	8
Culicoides	predator					
Dasyhelea	collector-gatherer					
Forcipomyia	collector-gatherer					
Monohelea	predator			1		1
Palpomyia	predator					
Chironomidae						
(Chironominae)						
Dicrotendipes	collector-gatherer	1				1
Endochironomus	shredder					
Endotribelos	collector-gatherer					
Microtendipes	collector-filterer			1		1
Nilothauna	collector-gatherer					
Parachironomus	predator					
Paratendipes	collector-gatherer					
Polypedium	shredder	187	48	15	16	266
Pseudochironomus	collector-gatherer					
Stenochironomus	collector-gatherer					
(Orthocladiinae)						
Corynoneura	collector-gatherer	4	6	1	12	23
Lopescladius	collector-gatherer					
Nanocladius	collector-gatherer					

Potter's Ford, cont'd		Riffle 1	Riffle 2	Riffle 3	Riffle 4	Riffle Total
Orthocladius	collector-gatherer	45	15	19	6	85
Parakieferella	collector-gatherer					
Psectrocladius	collector-gatherer					
Rheocricotopus	collector-gatherer					
Synorthocladius	collector-gatherer					
Thienamanniella	collector-gatherer	12	22	19	13	66
Tvetenia	collector-gatherer					
(Tanypodinae)						
Alabesmyia	predator		1			1
Labrundinia	predator					
Nilotanypus	predator					
Pentaneura	predator					
Procladius	predator					
Thinemannimyia group sp.	predator					
Tanypus	predator					
(Tanytarsini)						
Cladotanytarsus	collector-gatherer					
Neozavrelia	collector-gatherer					
Paratanytarsus	collector-gatherer					
Rheotanytarsus	collector-filterer	79	35	15	4	133
Tanytarsus	collector-gatherer	2	6	14	5	27
Culicidae						
Anopheles	collector-filterer			1		1
Ephydridae						
Hydrellia	shredder					
Empididae						
Chelifera	predator					
Hemerodromia	predator					
Simulidae						
Simulium	collector-filterer	1	1			2
Tipulidae						
Antocha	collector-gatherer					
Erioptera	colector-gatherer					
Tipula	shredder					
EPHEMEROPTERA						
Baetidae						
Acerpenna	collector-gatherer					
Baetis	collector-gatherer					
Centroptilum	collector-gatherer					

Potter's Ford, cont'd		Riffle 1	Riffle 2	Riffle 3	Riffle 4	Riffle Total
Heterocleon	scraper					
Plauditus	collector-gatherer					
Caenidae						
Caenis	collector-gatherer					
Ephemerellidae						
Eurylophella	collector-gatherer			1		1
Leptohyphidae						
Trichorythodes	collector-gatherer					
Isonychiidae						
Isonychia	collector-filterer	81	22	11		114
Heptageniidae						
Leucrocuta	collector-gatherer	5	3	2		10
Maccaffertium	scraper	48	21	27		96
Stenacron	scraper		1			1
Stenonema femoratum	scraper	14	32			46
GASTROPODA						
Ancylidae	grazer			3		3
Planorbidae	grazer					
Physidae	grazer					
Pleuroceridae	grazer					
Lymnaeidae	grazer					
HEMIPTERA						
Mesoveliidae						
Mesovelia	predator					
Saldidae						
Pentacora	predator					
Hydrocarina	predator					
ISOPODA						
Asellidae						
Lirceus	collector-gatherer (scavenger)					
LEPIDOPTERA						
Crambidae						
Elophila	shredder					
Petrophila	shredder					
MEGALOPTERA						
Corydalidae						

Potter's Ford, cont'd		Riffle 1	Riffle 2	Riffle 3	Riffle 4	Riffle Total
Corydalus cornutus	predator					
Nigronia	predator					
ODONATA						
Aeshnidae						
Boyeria vinosa	predator					
Coenagionidae						
Argia	predator					
Enallagma	predator					
Calopterygidae						
Calopteryx dimidiata	predator					
Calopteryx maculata	predator					
Hetaerina americana	predator					
Corduliidae						
Epitheca	predator					
Neurocordulia	predator					
Somatochlora	predator					
Gomphidae						
Dromogomphus	predator					
Gomphus	predator					
Haegenius brevistylus	predator					
Stylogomphus	predator					
Libellulidae						
Erythemis	predator					
Libellula	predator					
Macromiidae						
Macromia	predator					
Oligochaeta	collector-filterer	2	5			7
PLATYHELMINTHES						
Planariidae	omnivorous			3		3
PLECOPTERA						
Perlidae						
Acroneuria	predator	8	3	1		12
Agnetina	predator					
Neoperla	predator					
TRICHOPTERA						
Trichoptera pupae		4				4
Brachycentridae						

Potter's Ford, cont'd		Riffle 1	Riffle 2	Riffle 3	Riffle 4	Riffle Total
Micrasema	shredder					
Helicopsychidae						
Helicopsyche	scraper					
Hydropsychidae						
Cheumatopsyche	collector-filterer	325	53	19		397
Ceratopsyche	collector-filterer	1	1			2
Hydropsyche	collector-filterer	1				1
Macrostemum	collector-filterer					
Hydroptilidae						
Hydroptila	piercer-herbivore	1	1			2
Oxyethira	piercer-herbivore					
Orthotrichia	piercer-herbivore					
Lepidostomatidae						
Lepidostoma	shredder					
Leptoceridae						
Ceraclea	collector-gatherer					
Mystacides	collector-gatherer					
Nectopsyche	shredder					
Oecetis	predator					
Triaenodes	shredder					
Limnephilidae						
Pycnopsyche	shredder					
Philopotamidae						
Chimarra	collector-filterer	54	8	1		63
Phryganeidae						
Ptilostomis	shredder					
Polycentropodidae						
Neureclipsis	collector-filterer					
Nyctiophylax	predator					
Polycentropus	predator					

*pool not sampled due to lack of significant submersed vegetation

TAXA	Functional Feeding Group	Highway 68 (Daddy's Creek)*				
		Riffle 1	Riffle 2	Riffle 3	Riffle 4	Riffle Total
AMPHIPODA						
Gammaridae						
Gammarus	collector-gatherer					
Hyalellidae						
Hyalella azteca	collector-gatherer					
BIVALVIA						
Corbiculidae						
Corbicula fluminea	filter-feeder					
COLEOPTERA					6	6
Psephenidae						
Psephenus	scraper					
Ectopria	scraper			1		1
Dryopidae						
Helichus	scraper			2		2
Elmidae						
pupae				5		5
Ancrynonyx variegatus(adult)	collector-gatherer				1	1
Dubiraphia (adult)	collector-gatherer					
Macronychus glabratus (adult)	collector-gatherer					
Microcylloepus (adult)	collector-gatherer					
Optioservus (adult)	collector-gatherer	5	51	2		58
Oulimnius (adult)	collector-gatherer			1		1
Promoresia (adult)	collector-gatherer					
Stenelmis (adult)	collector-gatherer	2				2
Ancyronyx variegatus (larvae)	collector-gatherer		1			1
Dubiraphia (larvae)	collector-gatherer	1			2	3
Gonielmis ditrichi (larvae)	collector-gatherer					
Macronychus glabratus(larvae)	collector-gatherer	12	2	1	1	16
Microcylloepus (larvae)	collector-gatherer					
Optioservus (larvae)	scraper	112		25	8	145
Promoresia (larvae)	collector-gatherer		2	4		6
Stenelmis (larvae)	scraper					
Haliplidae						
Haliplus	shredder					
Hydrophilidae						

Highway 68, cont'd		Riffle 1	Riffle 2	Riffle 3	Riffle 4	Riffle Total
Berosus (adult)	collector-gatherer					
Berosus (larvae)	shredder					
Enochrus (larvae)	predator					
Scirtidae						
Scirtes (larvae)	shredder					
DECAPODA						
Cambaridae						
Cambarus	collector-gatherer (omnivorous)					
DIPTERA						
pupae		22	22	4	5	53
Athericidae						
Atherix	predator					
Ceratopogonidae						
Atrichopogon	collector-gatherer					
Culicoides	predator					
Dasyhelea	collector-gatherer			1		1
Forcipomyia	collector-gatherer		1			1
Monohelea	predator					
Palpomyia	predator				1	1
Chironomidae						
(Chironominae)						
Dicrotendipes	collector-gatherer				1	1
Endochironomus	shredder		1			1
Endotribelos	collector-gatherer					
Microtendipes	collector-filterer	1	1			2
Nilothauma	collector-gatherer					
Parachironomus	predator					
Paratendipes	collector-gatherer				4	4
Polypedium	shredder	6	10	10	2	28
Pseudochironomus	collector-gatherer					
Stenochironomus	collector-gatherer	1	2	1		4
(Orthocladiinae)						
Corynoneura	collector-gatherer	1	10	1	2	14
Lopescladius	collector-gatherer			2		2
Nanocladius	collector-gatherer	4	31	4		39
Orthocladius	collector-gatherer	18	9	22	1	50
Parakieferella	collector-gatherer	2	2	2		6
Psectrocladius	collector-gatherer					

Highway 68, cont'd		**Riffle 1**	**Riffle 2**	**Riffle 3**	**Riffle 4**	**Riffle Total**
Rheocricotopus	collector-gatherer	11	17	95	10	133
Synorthocladius	collector-gatherer	3	1	3		7
Thienamanniella	collector-gatherer	18	19	20		57
Tvetenia	collector-gatherer					
(Tanypodinae)						
Alabesmyia	predator					
Labrundinia	predator		42		2	44
Nilotanypus	predator		1			1
Pentaneura	predator			1	1	2
Procladius	predator				3	3
Thinemannimyia group sp.	predator	1		3	1	5
Tanypus	predator		39			39
(Tanytarsini)						
Cladotanytarsus	collector-gatherer	1	5			6
Neozavrelia	collector-gatherer		2			2
Paratanytarsus	collector-gatherer					
Rheotanytarsus	collector-filterer	1006	219	146	2	1373
Tanytarsus	collector-gatherer	19	12	4	3	38
Culicidae						
Anopheles	collector-filterer			2		2
Ephydridae						
Hydrellia	shredder					
Empididae						
Chelifera	predator					
Hemerodromia	predator	6	1		1	8
Simulidae						
Simulium	collector-filterer		3			3
Tipulidae						
Antocha	collector-gatherer		3		2	5
Erioptera	colector-gatherer		1			1
Tipula	shredder					
EPHEMEROPTERA						
Baetidae						
Acerpenna	collector-gatherer	2	5	1		8
Baetis	collector-gatherer					
Centroptilum	collector-gatherer		1			1
Heterocleon	scraper					
Plauditus	collector-gatherer					
Caenidae						

Highway 68, cont'd		Riffle 1	Riffle 2	Riffle 3	Riffle 4	Riffle Total
Caenis	collector-gatherer	1				1
Ephemerellidae						
Eurylophella	collector-gatherer	1			1	2
Leptohyphidae						
Trichorythodes	collector-gatherer					
Isonychiidae						
Isonychia	collector-filterer	5	2	28		35
Heptageniidae						
Leucrocuta	collector-gatherer					
Maccaffertium	scraper	4	4	27		35
Stenacron	scraper					
Stenonema femoratum	scraper					
Gastropoda						
Ancylidae	grazer					
Planorbidae	grazer		1			1
Physidae	grazer					
Pleuroceridae	grazer					
Lymnaeidae	grazer					
HEMIPTERA						
Mesoveliidae						
Mesovelia	predator					
Saldidae						
Pentacora	predator					
Hydrocarina	predator	51	11	4		66
ISOPODA						
Asellidae						
Lirceus	collector-gatherer (scavenger)			2		2
LEPIDOPTERA						
Crambidae						
Elophila	shredder					
Petrophila	shredder					
MEGALOPTERA						
Corydalidae						2
Corydalus cornutus	predator	2				4
Nigronia	predator			4		
ODONATA						

Highway 68, cont'd		Riffle 1	Riffle 2	Riffle 3	Riffle 4	Riffle Total
Aeshnidae						
Boyeria vinosa	predator					
Coenagionidae						
Argia	predator					
Enallagma	predator			1		1
Calopterygidae						
Calopteryx dimidiata	predator					
Calopteryx maculata	predator					
Hetaerina americana	predator		1			1
Corduliidae						
Epitheca	predator					
Neurocordulia	predator					
Somatochlora	predator					
Gomphidae						
Dromogomphus	predator				3	3
Gomphus	predator				3	3
Haegenius brevistylus	predator				3	3
Stylogomphus	predator		1	3	4	8
Libellulidae						
Erythemis	predator					
Libellula	predator					
Macromiidae						
Macromia	predator				1	1
Oligochaeta	collector-filterer	73	76	5	8	162
PLATYHELMINTHES						
Planariidae	omnivorous					
PLECOPTERA						
Perlidae						
Acroneuria	predator	1	1			2
Agnetina	predator					
Neoperla	predator					
TRICHOPTERA						
pupae						
Brachycentridae						
Micrasema	shredder					
Helicopsychidae						
Helicopsyche	scraper					
Hydropsychidae						

Highway 68, cont'd		Riffle 1	Riffle 2	Riffle 3	Riffle 4	Riffle Total
Cheumatopsyche	collector-filterer	3		6	1	10
Ceratopsyche	collector-filterer	7				7
Hydropsyche	collector-filterer	17	3	6		26
Macrostemum	collector-filterer					
Hydroptilidae						
Hydroptila	piercer-herbivore					
Oxyethira	piercer-herbivore		1			1
Orthotrichia	piercer-herbivore					
Lepidostomatidae						
Lepidostoma	shredder					
Leptoceridae						
Ceraclea	collector-gatherer					
Mystacides	collector-gatherer					
Nectopsyche	shredder					
Oecetis	predator		4			4
Triaenodes	shredder		2			2
Limnephilidae						
Pycnopsyche	shredder				1	1
Philopotamidae						
Chimarra	collector-filterer	3		23		26
Phryganeidae						
Ptilostomis	shredder					
Polycentropodidae						
Neureclipsis	collector-filterer	1	3	1		5
Nyctiophylax	predator					
Polycentropus	predator					

*pool not sampled due to lack of significant submersed vegetation

TAXA	Functional Feeding Group	Obed Junction (Obed River)					
		Riffle 1	Riffle 2	Riffle 3	Riffle 4	Riffle Total	Pool
AMPHIPODA							
Gammaridae							
Gammarus	collector-gatherer		5			5	
Hyalellidae							
Hyalella azteca	collector-gatherer						197
BIVALVIA							
Corbiculidae							
Corbicula fluminea	filter-feeder			4	3	7	
COLEOPTERA							
Psephenidae							
Psephenus	scraper		4	13	7	24	
Ectopria	scraper	1		1	1	3	
Dryopidae							
Helichus	scraper						
Elmidae							
pupae							
Ancrynonyx variegatus(adult)	collector-gatherer						
Dubiraphia (adult)	collector-gatherer						9
Macronychus glabratus (adult)	collector-gatherer						
Microcylloepus (adult)	collector-gatherer	43	17	55	50	165	
Optioservus (adult)	collector-gatherer						
Oulimnius (adult)	collector-gatherer				4	4	
Promoresia (adult)	collector-gatherer	1				1	
Stenelmis (adult)	collector-gatherer	2	3	2	7	14	
Ancyronyx variegatus (larvae)	collector-gatherer						
Dubiraphia (larvae)	collector-gatherer						1
Gonielmis ditrichi (larvae)	collector-gatherer	15	2	27	7	51	3
Macronychus glabratus(larvae)	collector-gatherer				1	1	
Microcylloepus (larvae)	collector-gatherer	210	35	273	154	672	1
Optioservus (larvae)	scraper		2		3	5	
Promoresia (larvae)	collector-gatherer		1			1	
Stenelmis (larvae)	scraper	1	7	2	11	21	
Haliplidae							
Haliplus	shredder						
Hydrophilidae							

Obed Junction, cont'd		Riffle 1	Riffle 2	Riffle 3	Riffle 4	Riffle Total	Pool
Berosus (adult)	collector-gatherer						1
Berosus (larvae)	shredder	2	1		1	4	51
Enochrus (larvae)	predator						
Scirtidae							
Scirtes (larvae)	shredder						
DECAPODA							
Cambaridae							
Cambarus	collector-gatherer (omnivorous)						
DIPTERA							
pupae		9		22	9		31
Athericidae							
Atherix	predator						
Ceratopogonidae							
Atrichopogon	collector-gatherer						
Culicoides	predator						2
Dasyhelea	collector-gatherer						
Forcipomyia	collector-gatherer						
Monohelea	predator						
Palpomyia	predator						
Chironomidae							
(Chironominae)							
Dicrotendipes	collector-gatherer	1		2		3	69
Endochironomus	shredder						
Endotribelos	collector-gatherer						
Microtendipes	collector-filterer						
Nilothauna	collector-gatherer						1
Parachironomus	predator						
Paratendipes	collector-gatherer						
Polypedium	shredder	61	7	101	19	188	10
Pseudochironomus	collector-gatherer						
Stenochironomus	collector-gatherer	7		1	1	9	
(Orthocladiinae)							
Corynoneura	collector-gatherer	1			3	4	
Lopescladius	collector-gatherer						
Nanocladius	collector-gatherer						5
Orthocladius	collector-gatherer	35	8	37	47	127	309
Parakieferella	collector-gatherer						1

Obed Junction, cont'd		Riffle 1	Riffle 2	Riffle 3	Riffle 4	Riffle Total	Pool
Psectrocladius	collector-gatherer						2
Rheocricotopus	collector-gatherer	1				1	
Synorthocladius	collector-gatherer	1		1		2	2
Thienamanniella	collector-gatherer	9	1	6	7	23	26
Tvetenia	collector-gatherer	1			1	2	
(Tanypodinae)							
Alabesmyia	predator	2		1		3	5
Labrundinia	predator						
Nilotanypus	predator						
Pentaneura	predator	1		2		3	1
Procladius	predator						
Thinemannimyia group sp.	predator						
Tanypus	predator						
(Tanytarsini)							
Cladotanytarsus	collector-gatherer						
Neozavrelia	collector-gatherer						
Paratanytarsus	collector-gatherer			2		2	1128
Rheotanytarsus	collector-filterer	158	34	548	107	847	15
Tanytarsus	collector-gatherer	2				2	58
Culicidae							
Anopheles	collector-filterer						
Ephydridae							
Hydrellia	shredder						
Empididae							
Chelifera	predator						
Hemerodromia	predator						
Simulidae							
Simulium	collector-filterer	3	1	3	4	11	
Tipulidae							
Antocha	collector-gatherer						
Erioptera	colector-gatherer						
Tipula	shredder						
EPHEMEROPTERA							
Baetidae							
Acerpenna	collector-gatherer	10				10	
Baetis	collector-gatherer	37	23	37	63	160	
Centroptilum	collector-gatherer						1
Heterocleon	scraper	4	11	10	8	33	
Plauditus	collector-gatherer						

Obed Junction, cont'd		Riffle 1	Riffle 2	Riffle 3	Riffle 4	Riffle Total	Pool
Caenidae							
Caenis	collector-gatherer	1				1	
Ephemerellidae							
Eurylophella	collector-gatherer						1
Leptohyphidae							
Trichorythodes	collector-gatherer			5	2	7	15
Isonychiidae							
Isonychia	collector-filterer	28	9	41	5	83	
Heptageniidae							
Leucrocuta	collector-gatherer		1	3		4	
Maccaffertium	scraper	11	17	53	11	92	
Stenacron	scraper						
Stenonema femoratum	scraper						
GASTROPODA							
Ancylidae	grazer	1		2	1	4	
Planorbidae	grazer			1	1	2	17
Physidae	grazer	3		1		4	105
Pleuroceridae	grazer	1	6	2		9	
Lymnaeidae	grazer			9		9	
HEMIPTERA							
Mesoveliidae							
Mesovelia	predator						
Saldidae							
Pentacora	predator						
Hydrocarina	predator	3		9	12	24	6
ISOPODA							
Asellidae							
Lirceus	collector-gatherer (scavenger)						
LEPIDOPTERA							
Crambidae							
Elophila	shredder				8	8	
Petrophila	shredder						
MEGALOPTERA							
Corydalidae							
Corydalus cornutus	predator		2	7		9	
Nigronia	predator						
ODONATA							
Aeshnidae							

Obed Junction, cont'd		Riffle 1	Riffle 2	Riffle 3	Riffle 4	Riffle Total	Pool
Boyeria vinosa	predator						
Coenagionidae							
Argia	predator						
Enallagma	predator						
Calopterygidae							43
Calopteryx dimidiata	predator						
Calopteryx maculata	predator						1
Hetaerina americana	predator						
Corduliidae				3		3	
Epitheca	predator						
Neurocordulia	predator						2
Somatochlora	predator						
Gomphidae							
Dromogomphus	predator						
Gomphus	predator						
Haegenius brevistylus	predator						
Stylogomphus	predator				4	4	
Libellulidae							
Erythemis	predator						
Libellula	predator						9
Macromiidae							
Macromia	predator						
Oligochaeta	collector-filterer		7			7	72
PLATYHELMINTHES							
Planariidae	omnivorous	4		2		6	
PLECOPTERA							
Perlidae							
Acroneuria	predator			5	3	8	1
Agnetina	predator	8	6	14	16	44	
Neoperla	predator			1		1	
TRICHOPTERA							
pupae			1	1		2	
Brachycentridae							
Micrasema	shredder	3	1	1	8	13	2
Helicopsychidae							
Helicopsyche	scraper	2			1	3	1
Hydropsychidae							
Cheumatopsyche	collector-filterer	77	36	65	40	218	

Obed Junction, cont'd		Riffle 1	Riffle 2	Riffle 3	Riffle 4	Riffle Total	Pool
Ceratopsyche	collector-filterer	36	57	12	77	182	
Hydropsyche	collector-filterer	58	102	79	115	354	
Macrostemum	collector-filterer		14	9	8	31	
Hydroptilidae							
Hydroptila	piercer-herbivore	25	1	12	6	44	64
Oxyethira	piercer-herbivore						40
Orthotrichia	piercer-herbivore						1
Lepidostomatidae							
Lepidostoma	shredder	4	2	114	53	173	
Leptoceridae							
Ceraclea	collector-gatherer	2	1	17	5	25	
Mystacides	collector-gatherer	2				2	
Nectopsyche	shredder			5		5	
Oecetis	predator	6		9		15	19
Triaenodes	shredder						91
Limnephilidae							
Pycnopsyche	shredder						
Philopotamidae							
Chimarra	collector-filterer	2	5	1	2	10	
Phryganeidae							
Ptilostomis	shredder						
Polycentropodidae							
Neureclipsis	collector-filterer	5		40	2	47	3
Nyctiophylax	predator			1	1	2	
Polycentropus	predator	1				1	

TAXA	Functional Feeding Group	Antioch Bridge (Daddy's Creek)					
		Riffle 1	Riffle 2	Riffle 3	Riffle 4	Riffle Total	Pool
AMPHIPODA							
Gammaridae							
Gammarus	collector-gatherer						
Hyalellidae							
Hyalella azteca	collector-gatherer						
BIVALVIA							5
Corbiculidae							
Corbicula fluminea	filter-feeder						
COLEOPTERA							90
Psephenidae							
Psephenus	scraper	2	9	1	8	20	
Ectopria	scraper		3	3	8	14	1
Dryopidae							
Helichus	scraper						
Elmidae							
pupae			1			1	
Ancrynonyx variegatus(adult)	collector-gatherer						
Dubiraphia (adult)	collector-gatherer						9
Macronychus glabratus (adult)	collector-gatherer						2
Microcylloepus (adult)	collector-gatherer	9	18		2	29	
Optioservus (adult)	collector-gatherer						
Oulimnius (adult)	collector-gatherer		2			2	
Promoresia (adult)	collector-gatherer	1				1	
Stenelmis (adult)	collector-gatherer	2	21	1	1	25	1
Ancyronyx variegatus (larvae)	collector-gatherer						
Dubiraphia (larvae)	collector-gatherer						15
Gonielmis ditrichi (larvae)	collector-gatherer						
Macronychus glabratus(larvae)	collector-gatherer		2			2	
Microcylloepus (larvae)	collector-gatherer	8	75	12	11	106	11
Optioservus (larvae)	scraper	5	26	2	7	40	
Promoresia (larvae)	collector-gatherer						
Stenelmis (larvae)	scraper	30	112	9	17	168	
Haliplidae							

Antioch Bridge, cont'd		Riffle 1	Riffle 2	Riffle 3	Riffle 4	Riffle Total	Pool
Haliplus	shredder						
Hydrophilidae							
Berosus (adult)	collector-gatherer						
Berosus (larvae)	shredder						29
Enochrus (larvae)	predator						
Scirtidae							
Scirtes (larvae)	shredder						
DECAPODA							
Cambaridae							
Cambarus	collector-gatherer (omnivorous)						
DIPTERA							
pupae			13			13	46
Athericidae							
Atherix	predator						
Ceratopogonidae							
Atrichopogon	collector-gatherer		2			2	
Culicoides	predator						
Dasyhelea	collector-gatherer						
Forcipomyia	collector-gatherer						
Monohelea	predator						
Palpomyia	predator						
Chironomidae							
(Chironominae)							
Dicrotendipes	collector-gatherer						3
Endochironomus	shredder						
Endotribelos?	collector-gatherer						
Microtendipes	collector-filterer						
Nilothauma	collector-gatherer						
Parachironomus	predator						
Paratendipes	collector-gatherer						
Polypedium	shredder	3	15	1	4	23	
Pseudochironomus	collector-gatherer			1		1	
Stenochironomus	collector-gatherer						17
(Orthocladiinae)							
Corynoneura	collector-gatherer	2	4	2	1	9	
Lopescladius	collector-gatherer						
Nanocladius	collector-gatherer						1
Orthocladius	collector-gatherer		17	13	12	42	15
Parakieferella	collector-gatherer						

Antioch Bridge, cont'd		**Riffle 1**	**Riffle 2**	**Riffle 3**	**Riffle 4**	**Riffle Total**	**Pool**
Psectrocladius	collector-gatherer						1
Rheocricotopus	collector-gatherer						
Synorthocladius	collector-gatherer	2	5		1	8	
Thienamanniella	collector-gatherer	1	6	4	7	18	1
Tvetenia	collector-gatherer						
(Tanypodinae)							
Alabesmyia	predator						6
Labrundinia	predator						
Nilotanypus	predator		1		2	3	
Pentaneura	predator	1				1	
Procladius	predator						
Thinemannimyia group sp.	predator		1			1	
Tanypus	predator						
(Tanytarsini)							
Cladotanytarsus	collector-gatherer						
Neozavrelia	collector-gatherer		3	2		5	
Paratanytarsus	collector-gatherer						3
Rheotanytarsus	collector-filterer	22	301	70	65	458	4
Tanytarsus	collector-gatherer			1		1	90
Culicidae							
Anopheles	collector-filterer						
Ephydridae							
Hydrellia	shredder						
Empididae							
Chelifera	predator						
Hemerodromia	predator		3			3	
Simulidae							
Simulium	collector-filterer		2			2	
Tipulidae							
Antocha	collector-gatherer						
Erioptera	colector-gatherer						
Tipula	shredder						
EPHEMEROPTERA							
Baetidae							
Acerpenna	collector-gatherer						
Baetis	collector-gatherer	3	19	2	5	29	1
Centroptilum	collector-gatherer						2
Heterocleon	scraper	5	6	2	3	16	
Plauditus	collector-gatherer						
Caenidae							

Antioch Bridge, cont'd		Riffle 1	Riffle 2	Riffle 3	Riffle 4	Riffle Total	Pool
Caenis	collector-gatherer		1		1	2	
Ephemerellidae							
Eurylophella	collector-gatherer						
Leptohyphidae							
Trichorythodes	collector-gatherer		1		2	3	2
Isonychiidae							
Isonychia	collector-filterer	19	47	8		74	
Heptageniidae							
Leucrocuta	collector-gatherer	13	10	5	4	32	
Maccaffertium	scraper	10	11	2	5	28	
Stenacron	scraper			1		1	
Stenonema femoratum	scraper	10	21	10	6	47	
GASTROPODA							
Ancylidae	grazer						1
Planorbidae	grazer						15
Physidae	grazer						11
Pleuroceridae	grazer	1			3	4	13
Lymnaeidae	grazer						
HEMIPTERA							
Mesoveliidae							
Mesovelia	predator						
Saldidae							
Pentacora	predator						
Hydrocarina	predator	7	48	45	10	110	36
ISOPODA							
Asellidae							
Lirceus	collector-gatherer (scavenger)		3			3	
LEPIDOPTERA							
Crambidae							
Elophila	shredder						
Petrophila	shredder	1	1			2	
MEGALOPTERA							
Corydalidae							
Corydalus cornutus	predator		4	2		6	
Nigronia	predator		1			1	
ODONATA							
Aeshnidae							
Boyeria vinosa	predator						
Coenagionidae							

Antioch Bridge, cont'd		Riffle 1	Riffle 2	Riffle 3	Riffle 4	Riffle Total	Pool
Argia	predator			1		1	2
Enallagma	predator						41
Calopterygidae							
Calopteryx dimidiata	predator						
Calopteryx maculata	predator						
Hetaerina americana	predator						
Corduliidae							
Epitheca	predator						
Neurocordulia	predator						
Somatochlora	predator						3
Gomphidae							
Dromogomphus	predator						
Gomphus	predator						30
Haegenius brevistylus	predator						9
Stylogomphus	predator	6	1		3	10	5
Libellulidae							
Erythemis	predator						
Libellula	predator						
Macromiidae							
Macromia	predator						3
Oligochaeta	collector-filterer	1	20	2	1	24	
PLATYHELMINTHES							
Planariidae	omnivorous						1
PLECOPTERA							
Perlidae							
Acroneuria	predator	3	3	2		8	
Agnetina	predator						
Neoperla	predator	2	6			8	
TRICHOPTERA							
pupae							
Brachycentridae							
Micrasema	shredder		4	3	4	11	1
Helicopsychidae							
Helicopsyche	scraper				1	1	
Hydropsychidae							
Cheumatopsyche	collector-filterer	34	44	5	9	92	
Ceratopsyche	collector-filterer	6	5	2	1	14	
Hydropsyche	collector-filterer		12			12	
Macrostemum	collector-filterer						
Hydroptilidae							

Antioch Bridge, cont'd		Riffle 1	Riffle 2	Riffle 3	Riffle 4	Riffle Total	Pool
Hydroptila	piercer-herbivore				1	1	1
Oxyethira	piercer-herbivore						37
Orthotrichia	piercer-herbivore						
Lepidostomatidae							
Lepidostoma	shredder						
Leptoceridae							
Ceraclea	collector-gatherer	1	2	8		11	
Mystacides	collector-gatherer						
Nectopsyche	shredder						
Oecetis	predator						4
Triaenodes	shredder						25
Limnephilidae							
Pycnopsyche	shredder						
Philopotamidae							
Chimarra	collector-filterer	12	23			35	
Phryganeidae							
Ptilostomis	shredder						
Polycentropodidae							
Neureclipsis	collector-filterer	1	1	2		4	
Nyctiophylax	predator				1	1	
Polycentropus	predator						

TAXA	Functional Feeding Group	Devil's Breakfast Table (Daddy's Creek)					
		Riffle 1	Riffle 2	Riffle 3	Riffle 4	Riffle Total	Pool
AMPHIPODA							
Gammaridae							
Gammarus	collector-gatherer						
Hyalellidae							
Hyalella azteca	collector-gatherer						7
BIVALVIA							
Corbiculidae							
Corbicula fluminea	filter-feeder	1			7	8	
COLEOPTERA							
Psephenidae							
Psephenus	scraper	1	6	2	7	16	
Ectopria	scraper				6	6	
Dryopidae							
Helichus	scraper						
Elmidae							
pupae		1	4			5	
Ancrynonyx variegatus(adult)	collector-gatherer						
Dubiraphia (adult)	collector-gatherer						1
Macronychus glabratus (adult)	collector-gatherer						
Microcylloepus (adult)	collector-gatherer		6		5	11	
Optioservus (adult)	collector-gatherer		1			1	
Oulimnius (adult)	collector-gatherer		1	1		2	
Promoresia (adult)	collector-gatherer				6	6	
Stenelmis (adult)	collector-gatherer	2	9		1	12	
Ancyronyx variegatus (larvae)	collector-gatherer						
Dubiraphia (larvae)	collector-gatherer						
Gonielmis ditrichi (larvae)	collector-gatherer	5	9	6		20	
Macronychus glabratus(larvae)	collector-gatherer						
Microcylloepus (larvae)	collector-gatherer	39	27	11	78	155	
Optioservus (larvae)	scraper	3	10	2	10	25	
Promoresia (larvae)	collector-gatherer				7	90	
Stenelmis (larvae)	scraper		83				
Haliplidae							
Haliplus	shredder						

Devil's Breakfast Table, cont'd		Riffle 1	Riffle 2	Riffle 3	Riffle 4	Riffle Total	Pool
Hydrophilidae							
Berosus (adult)	collector-gatherer						
Berosus (larvae)	shredder						
Enochrus (larvae)	predator						1
Scirtidae							
Scirtes (larvae)	shredder						
DECAPODA							
Cambaridae							
Cambarus	collector-gatherer (omnivorous)						
DIPTERA							
pupae			7		6	13	7
Athericidae							
Atherix	predator	1				1	
Ceratopogonidae							
Atrichopogon	collector-gatherer						
Culicoides	predator						
Dasyhelea	collector-gatherer						
Forcipomyia	collector-gatherer						
Monohelea	predator						
Palpomyia	predator						1
Chironomidae							
(Chironominae)							
Dicrotendipes	collector-gatherer			2	1	3	25
Endochironomus	shredder						
Endotribelos	collector-gatherer						3
Microtendipes	collector-filterer						
Nilothauma	collector-gatherer						
Parachironomus	predator						1
Paratendipes	collector-gatherer						
Polypedium	shredder		17	2	2	21	
Pseudochironomus	collector-gatherer						
Stenochironomus	collector-gatherer						
(Orthocladiinae)							
Corynoneura	collector-gatherer		1			1	1
Lopescladius	collector-gatherer						
Nanocladius	collector-gatherer		1		2	3	
Orthocladius	collector-gatherer	2	16	8	20	46	20

Devil's Breakfast Table, cont'd		Riffle 1	Riffle 2	Riffle 3	Riffle 4	Riffle Total	Pool
Parakieferella	collector-gatherer						10
Psectrocladius	collector-gatherer						
Rheocricotopus	collector-gatherer						
Synorthocladius	collector-gatherer	1		1	1	3	
Thienamanniella	collector-gatherer	1	2	1	1	5	2
Tvetenia	collector-gatherer		1			1	
(Tanypodinae)							
Alabesmyia	predator						
Labrundinia	predator						
Nilotanypus	predator						
Pentaneura	predator	2				2	
Procladius	predator						
Thinemannimyia group sp.	predator		1		3	4	
Tanypus	predator						
(Tanytarsini)							
Cladotanytarsus	collector-gatherer						
Neozavrelia	collector-gatherer						
Paratanytarsus	collector-gatherer						18
Rheotanytarsus	collector-filterer	10	83	58	18	169	
Tanytarsus	collector-gatherer		1	3	2	6	44
Culicidae							
Anopheles	collector-filterer						
Ephydridae							
Hydrellia	shredder						
Empididae							
Chelifera	predator						
Hemerodromia	predator						
Simulidae							
Simulium	collector-filterer		2	3	1	6	
Tipulidae							
Antocha	collector-gatherer						
Erioptera	colector-gatherer						
Tipula	shredder						
EPHEMOPTERA							
Baetidae							
Acerpenna	collector-gatherer						
Baetis	collector-gatherer	13	54	21	18	106	
Centroptilum	collector-gatherer						
Heterocleon	scraper	1	21	6	4	32	

Devil's Breakfast Table, cont'd		Riffle 1	Riffle 2	Riffle 3	Riffle 4	Riffle Total	Pool
Plauditus	collector-gatherer						
Caenidae							
Caenis	collector-gatherer				2	2	
Ephemerellidae							
Eurylophella	collector-gatherer	1				1	
Leptohyphidae							
Trichorythodes	collector-gatherer	3				3	
Isonychiidae							
Isonychia	collector-filterer	7	13	1		21	
Heptageniidae							
Leucrocuta	collector-gatherer	1				1	
Maccaffertium	scraper		7	1	5	13	
Stenacron	scraper				3	3	
Stenonema femoratum	scraper	1	5		10	16	
GASTROPODA							
Ancylidae	grazer						
Planorbidae	grazer	1				1	103
Physidae	grazer						
Pleuroceridae	grazer	1	2		2	5	
Lymnaeidae	grazer						
HEMIPTERA							
Mesoveliidae							
Mesovelia	predator	1				1	3
Saldidae							
Pentacora	predator						
Hydrocarina	predator	5	7	5	5	22	8
ISOPODA							
Asellidae							
Lirceus	collector-gatherer (scavenger)	5				5	
LEPIDOPTERA							
Crambidae							
Elophila	shredder		5	4		9	
Petrophila	shredder						
MEGALOPTERA							
Corydalidae							
Corydalus cornutus	predator	1	2		2	5	

Devil's Breakfast Table, cont'd		Riffle 1	Riffle 2	Riffle 3	Riffle 4	Riffle Total	Pool
Nigronia	predator						
ODONATA							
Aeshnidae							
Boyeria vinosa	predator						
Coenagionidae							
Argia	predator						
Enallagma	predator				4	4	
Calopterygidae							5
Calopteryx dimidiata	predator						
Calopteryx maculata	predator						
Hetaerina americana	predator						
Corduliidae							
Epitheca	predator						
Neurocordulia	predator						3
Somatochlora	predator			1		1	
Gomphidae							
Dromogomphus	predator				1	1	
Gomphus	predator						
Haegenius brevistylus	predator				1	1	
Stylogomphus	predator		3		2	5	
Libellulidae							
Erythemis	predator						
Libellula	predator						
Macromiidae							
Macromia	predator						
Oligochaeta	collector-filterer		16		8	24	100
PLATYHELMINTHES							
Planariidae	omnivorous						
PLECOPTERA							
Perlidae							
Acroneuria	predator	1	2	3	3	9	
Agnetina	predator			1		1	
Neoperla	predator						
TRICHOPTERA							
Trichoptera pupae			2			2	
Brachycentridae							

Devil's Breakfast Table, cont'd		Riffle 1	Riffle 2	Riffle 3	Riffle 4	Riffle Total	Pool
Micrasema	shredder			10	8	18	
Helicopsychidae							
Helicopsyche	scraper			2	1	3	
Hydropsychidae							
Cheumatopsyche	collector-filterer	5	31	2	4	42	
Ceratopsyche	collector-filterer	1	13	3	5	22	
Hydropsyche	collector-filterer		9	1	2	12	
Macrostemum	collector-filterer						
Hydroptilidae							
Hydroptila	piercer-herbivore		2	1		3	
Oxyethira	piercer-herbivore						20
Orthotrichia	piercer-herbivore						
Lepidostomatidae							
Lepidostoma	shredder						
Leptoceridae							
Ceraclea	collector-gatherer		2	10	1	13	
Mystacides	collector-gatherer						
Nectopsyche	shredder						
Oecetis	predator			2	3	5	1
Triaenodes	shredder						54
Limnephilidae							
Pycnopsyche	shredder						
Philopotamidae							
Chimarra	collector-filterer	3	51	8	3	65	
Phryganeidae							
Ptilostomis	shredder						
Polycentropodidae							
Neureclipsis	collector-filterer		1	2		3	7
Nyctiophylax	predator	1	1	2	1	5	
Polycentropus	predator						

TAXA	Functional Feeding Group	Nemo Bridge (Obed River)					
		Riffle 1	Riffle 2	Riffle 3	Riffle 4	Riffle Total	Pool
AMPHIPODA							
Gammaridae							
Gammarus	collector-gatherer						
Hyalellidae							
Hyalella azteca	collector-gatherer						
BIVALVIA							
Corbiculidae							
Corbicula fluminea	filter-feeder	38	13	2	3	56	
COLEOPTERA							
Psephenidae							
Psephenus	scraper			1		1	
Ectopria	scraper	1				1	
Dryopidae							
Helichus	scraper						
Elmidae							
pupae							
Ancrynonyx variegatus(adult)	collector-gatherer						
Dubiraphia (adult)	collector-gatherer						1
Macronychus glabratus (adult)	collector-gatherer						1
Microcylloepus (adult)	collector-gatherer	129	15	35	56	235	
Optioservus (adult)	collector-gatherer	2				2	
Oulimnius (adult)	collector-gatherer						
Promoresia (adult)	collector-gatherer	1	1			2	1
Stenelmis (adult)	collector-gatherer	7	3	5	8	23	1
Ancyronyx variegatus (larvae)	collector-gatherer			1		1	
Dubiraphia (larvae)	collector-gatherer						
Gonielmis ditrichi (larvae)	collector-gatherer	34	46	9	13	102	2
Macronychus glabratus(larvae)	collector-gatherer						
Microcylloepus (larvae)	collector-gatherer	372	156	36	76	640	5
Optioservus (larvae)	scraper	3	4		4	11	
Promoresia (larvae)	collector-gatherer	51	24	61	77	213	
Stenelmis (larvae)	scraper						
Haliplidae							
Haliplus	shredder						

Nemo Bridge, cont'd		Riffle 1	Riffle 2	Riffle 3	Riffle 4	Riffle Total	Pool
Hydrophilidae							
Berosus (adult)	collector-gatherer						2
Berosus (larvae)	shredder	1				1	18
Enochrus (larvae)	predator						
Scirtidae							
Scirtes (larvae)	shredder						
DECAPODA							
Cambaridae							
Cambarus	collector-gatherer (omnivorous)						
DIPTERA							
pupae		24	5	3	4	36	69
Athericidae							
Atherix	predator						
Ceratopogonidae							
Atrichopogon	collector-gatherer						
Culicoides	predator						
Dasyhelea	collector-gatherer						
Forcipomyia	collector-gatherer						
Monohelea	predator						
Palpomyia	predator						
Chironomidae							
(Chironominae)							
Dicrotendipes	collector-gatherer						3
Endochironomus	shredder						
Endotribelos	collector-gatherer						
Microtendipes	collector-filterer						
Nilothauna	collector-gatherer						1
Parachironomus	predator						
Paratendipes	collector-gatherer						
Polypedium	shredder	51	12	27	9	99	22
Pseudochironomus	collector-gatherer			2		2	
Stenochironomus	collector-gatherer	19	1	1	3	24	
(Orthocladiinae)							
Corynoneura	collector-gatherer	2	4	4		10	1
Lopescladius	collector-gatherer			3		3	1
Nanocladius	collector-gatherer	4	64	9		77	53
Orthocladius	collector-gatherer						20
Parakieferella	collector-gatherer						

Nemo Bridge, cont'd		Riffle 1	Riffle 2	Riffle 3	Riffle 4	Riffle Total	Pool
Psectrocladius	collector-gatherer						
Rheocricotopus	collector-gatherer	2				2	
Synorthocladius	collector-gatherer	2				2	
Thienamanniella	collector-gatherer	3	6		1	10	1
Tvetenia	collector-gatherer	3	1		2	6	
(Tanypodinae)							
Alabesmyia	predator						10
Labrundinia	predator						
Nilotanypus	predator						
Pentaneura	predator	1				1	
Procladius	predator						
Thinemannimyia group sp.	predator	6	2			8	
Tanypus	predator						
(Tanytarsini)							
Cladotanytarsus	collector-gatherer						1
Neozavrelia	collector-gatherer				1	1	
Paratanytarsus	collector-gatherer						31
Rheotanytarsus	collector-filterer	580	85	139	79	883	138
Tanytarsus	collector-gatherer	13	6			19	185
Culicidae							
Anopheles	collector-filterer						
Ephydridae							
Hydrellia	shredder						1
Empididae							
Chelifera	predator						
Hemerodromia	predator		1			1	
Simulidae							
Simulium	collector-filterer	65	6	90	168	329	
Tipulidae							
Antocha	collector-gatherer						
Erioptera	colector-gatherer						
Tipula	shredder						
EPHEMEROPTERA							
Baetidae							
Acerpenna	collector-gatherer	7	6		1	14	
Baetis	collector-gatherer	55	42	43	62	202	
Centroptilum	collector-gatherer						5
Heterocleon	scraper	23	4	22	31	80	

Nemo Bridge, cont'd		Riffle 1	Riffle 2	Riffle 3	Riffle 4	Riffle Total	Pool
Plauditus	collector-gatherer	28	22		2	52	1
Caenidae							
Caenis	collector-gatherer	2				2	5
Ephemerellidae							
Eurylophella	collector-gatherer						
Leptohyphidae							
Trichorythodes	collector-gatherer	21	7	12	2	42	169
Isonychiidae							
Isonychia	collector-filterer	53		33	16	102	
Heptageniidae							
Leucrocuta	collector-gatherer						
Maccaffertium	scraper	8	5		3	16	
Stenacron	scraper						
Stenonema femoratum	scraper	17	12	79	26	134	
GASTROPODA							
Ancylidae	grazer						
Planorbidae	grazer		1			1	22
Physidae	grazer						
Pleuroceridae	grazer		1			1	4
Lymnaeidae	grazer						
HEMIPTERA							
Mesoveliidae							
Mesovelia	predator						
Saldidae							
Pentacora	predator						
Hydrocarina	predator	10	8	2		20	8
ISOPODA							
Asellidae							
Lirceus	collector-gatherer (scavenger)						
LEPIDOPTERA							
Crambidae							
Elophila	shredder			4		4	
Petrophila	shredder						
MEGALOPTERA							
Corydalidae							
Corydalus cornutus	predator	4	1	3		8	

Nemo Bridge, cont'd		Riffle 1	Riffle 2	Riffle 3	Riffle 4	Riffle Total	Pool
Nigronia	predator						
ODONATA							
Aeshnidae							
Boyeria vinosa	predator						
Coenagionidae							
Argia	predator	4	1			5	3
Enallagma	predator						12
Calopterygidae							
Calopteryx dimidiata	predator						
Calopteryx maculata	predator						
Hetaerina americana	predator	2				2	1
Corduliidae							
Epitheca	predator						
Neurocordulia	predator						1
Somatochlora	predator						
Gomphidae							
Dromogomphus	predator						
Gomphus	predator						
Haegenius brevistylus	predator						
Stylogomphus	predator	3				3	
Libellulidae							
Erythemis	predator						
Libellula	predator						
Macromiidae							
Macromia	predator						1
Oligochaeta	collector-filterer	13	12	13	12	50	59
PLATYHELMINTHES							
Planariidae	omnivorous		7			7	
PLECOPTERA							
Perlidae							
Acroneuria	predator		1		1	2	
Agnetina	predator	6	7	9	29	51	
Neoperla	predator						
TRICHOPTERA							
pupae		1				1	
Brachycentridae							
Micrasema	shredder	8	6		1	15	

Nemo Bridge, cont'd		Riffle 1	Riffle 2	Riffle 3	Riffle 4	Riffle Total	Pool
Helicopsychidae							
Helicopsyche	scraper						
Hydropsychidae							
Cheumatopsyche	collector-filterer	616	72	228	174	1090	2
Ceratopsyche	collector-filterer	93	19	77	155	344	2
Hydropsyche	collector-filterer	34	7	14	71	126	
Macrostemum	collector-filterer	26		40	41	107	
Hydroptilidae							
Hydroptila	piercer-herbivore						22
Oxyethira	piercer-herbivore						107
Orthotrichia	piercer-herbivore	3				3	6
Lepidostomatidae							
Lepidostoma	shredder	2				2	4
Leptoceridae							
Ceraclea	collector-gatherer	1		2		3	6
Mystacides	collector-gatherer						
Nectopsyche	shredder						
Oecetis	predator	2			4	6	19
Triaenodes	shredder	2				2	55
Limnephilidae							
Pycnopsyche	shredder						
Philopotamidae							
Chimarra	collector-filterer	27		74	103	204	408
Phryganeidae							
Ptilostomis	shredder						
Polycentropodidae							
Neureclipsis	collector-filterer						
Nyctiophylax	predator						
Polycentropus	predator						

VITA

Angelina Dominique "Angel" Fowler was born in Kileen, Texas to parents Richard C. Fowler and Susanne Gilbert-Fowler. She has three younger brothers, one of which was born to the same mother, Benjamin Carl Fowler, and two half-brothers, Caleb Richard Fowler and Travis John Fowler, born to their late mother Teresa Marie Fowler. Angel was a member of a military family where she traveled to various destinations, but raised most of her life in Oak Grove, Kentucky where her mother resides. She attended Christian County High School in Hopkinsville, Kentucky, graduating in 2003 where she shortly began Austin Peay State University (APSU). Throughout college, she was a server at the local Red Lobster, providing people with a smile and fantastic service every time she worked. She also interned at the Nashville Zoo where she had a chance to work with giraffes and other hoofstock. Once her undergraduate degree in Biology was conferred in summer 2009, Angel began graduate school that fall at APSU under the direction of Steven W. Hamilton, concurrently beginning her position as a Research Assistant for the Center of Excellence for Field Biology.

During graduate school, Angel presented at various mettings including Tennessee Academy of Science, Tennessee Entomological Society and Society for Freshwater Science (formerly North American Benthological Society). She has won a few awards for presenting, was apart of an APSU commercial, and had the opportunity to present her research at the 2011-2012 Provost Lecture Series. She also helped her fellow graduate students on numerous projects as a field technician to gain well-rounded knowledge of Biology. Angel hopes to be a part of conserving freshwater biodiversity by continuing her education researching invasive macrophytes in freshwater ecosystems. Depending on what opportunities arise, however, will ultimately determine her future.

Angel is married to Jerrod W. Manning and they have 5 cats: Conan, Roxy, Doodles, Peter and Mitzi, and one dog: Whiskey. The couple anticipates continuing their journey through life fossil hunting, nature treasure collecting, and frolicking in the wilderness with love in their hearts and smiles on their faces.