12-2007

NEOCHETINA SPECIES AND ARTHROPOD COMMUNITIES IN WATER-HYACINTH RAFTS IN SOUTH CAROLINA

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Recommended Citation
Powell, Benjamin, "*NEOCHETINA* SPECIES AND ARTHROPOD COMMUNITIES IN WATER-HYACINTH RAFTS IN SOUTH CAROLINA" (2007). *All Theses*. 287.
https://tigerprints.clemson.edu/all_theses/287

NEOCHETINA SPECIES AND ARTHROPOD COMMUNITIES IN WATER-HYACINTH RAFTS IN SOUTH CAROLINA

A Thesis
Presented to
the Graduate School of
Clemson University

In Partial Fulfillment
of the Requirements for the Degree
Master of Science
Entomology

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by
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December 2007

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ABSTRACT

Arthropod communities inhabiting feral water-hyacinth rafts were surveyed monthly in South Carolina's Coastal Plain from March 2005 through February 2006. Special attention was given to the chevroned waterhyacinth weevil [*Neochetina bruchi* (Hustache)], the mottled waterhyacinth weevil [*N. eichhorniae* (Warner)] (both Coleoptera: Curculionidae), and the waterhyacinth moth [*Niphograpta albiguttalis* (Warren)] (Lepidoptera: Crambidae), which were imported into North America to control water-hyacinth. Communities of arthropods are compared among sites, flow regimes (lentic, lotic, and tidal), and months of the year. The arthropod communities in water-hyacinth rafts in South Carolina are more diverse than previously reported. Rafts in each of five freshwater systems contained numerous species that were unique to each ecosystem. Water-hyacinth rafts in lentic and lotic systems produced similar arthropod abundances and diversities and contained arthropod assemblages with similar feeding strategies. Rafts that were repeatedly stranded on river banks in tidal waterways contained fewer species than lentic and lotic sites. Tidally stranded plants contained different arthropod assemblages with reduced frequencies of collectors-gatherers, collectors-filterers, and shredders-detritivores and increased frequencies of predators and shredders-herbivores. Arthropod species richness and abundance remained relatively constant throughout the year at each site, with minor fluctuations that coincided with the emergences of Odonata and chironomid Diptera in late spring and early summer. Seven species of aquatic insects are reported as new records for South Carolina. Though none of the three imported biological control agents have ever been released in South Carolina, all were collected. *Niphograpta albiguttalis* was not collected at the regular study sites but was recorded during initial surveys in 2004. Both of the *Neochetina* weevil species were collected at all seven study sites during this study. Weevil abundances varied among sites and between species. *Neochetina eichhorniae* was significantly more abundant than *N. bruchi* at two sites, and the two species were about equally abundant at the five remaining sites. Weevil abundances were similar at lentic and lotic sites but were slightly reduced in tidally stranded rafts. An inverse, temporal relationship occurred between abundances of adult weevils and their larvae. In addition, descriptions and illustrations of the larvae of the water-hyacinth weevils are provided for discriminating between the two species.

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ACKNOWLEDGMENTS

Several people should receive credit for their assistance with this project.

I give thanks to Dr. John Morse (Clemson University) for his guidance through the development and implementation of this study and for his thoughtful review of this manuscript. He served as the primary advisor of this thesis, and his direction and advice were essential to the completion and validity of this project. I also thank Dr. Peter Adler and Jack Whetstone (both Clemson University) who served on the advisory committee for this thesis, provided direction during this study, and reviewed this manuscript. All three individuals have contributed greatly to my professional development and refinement.

I am grateful to the Division of Entomology at Clemson University for providing me with the facilities and materials necessary to conduct this study.

I appreciate the assistance of Dr. Steve de Kozlowski and Chris Page (South Carolina Department of Natural Resources) who provided me with background and literature concerning the history and management of water-hyacinth in South Carolina. I thank Dr. Ted Center (United States Department of Agriculture) for providing literature concerning biological control of aquatic weeds in North America. Also, I thank Dr. Dale Habeck (University of Florida) for his assistance with identifications of Lepidoptera larvae and Dr. Arnold Eversole (Clemson University) for his assistance with crustacean identification.

Finally, I thank the late Dr. J. C. Nettles for establishing a memorial grant with the Division of Entomology at Clemson University. Without the support of this fund, this I could not have completed this project.

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CHAPTER ONE

INTRODUCTION

Ever since it escaped Amazonia in the late 19th century, water-hyacinth, *Eichhornia crassipes* (Martius) Solms-Laubach, proliferated to become a conspicuous component of freshwater ecosystems around the tropical, subtropical, and warm-temperate world. Its subsequent domination of the freshwater ecosystems it invaded significantly impacted the ecology and practical uses of waterways throughout its newly expanded range. Numerous studies have demonstrated that the invasion of this aquatic macrophyte into non-native waters has dramatically altered the physical, chemical, and biological characteristics of the affected water systems (Gopal 1987). In response, most affected countries have instated aggressive management plans with significant budgets to eradicate or at least to control this weed (Gopal 1987, Drake *et al*. 1989, Luken and Thieret 1997). Though many of these initiatives have proven successful at limiting this plant's expansion and reducing its populations, water-hyacinth remains an influential species in most of the ecoregions to which it has been introduced.

The realization that water-hyacinth may be more of an enduring immigrant than a temporal transient has prompted numerous investigations of the ecological role that this plant serves. These studies focused on physical influences such as water temperature, evaporation/transpiration rates (Benton Jr. *et al.* 1978), hydrology (Gowanloch and Bajkov 1948), and sediment loading (Schmitz *et al.* 1993) as well as on chemical factors such as dissolved oxygen (Ultsch 1973), pH, conductivity, nutrient cycling (Reddy and DeBusk 1991), and pollutant sequestering (Penfound and Earle 1948, Gopal 1987, Martins and Pitelli 2005). To complement these investigations, biologists have explored the importance of water-hyacinth rafts to other freshwater biota and have examined water-hyacinth's influences on microbial populations (Gunasekera *et al*. 1982, Mishra and Dwivedi 1982), its associative and competitive interactions with other aquatic plants (Batanouny and El Fiky 1984, Denny 1984, Gay 1960, DeSilva *et al*. 1984, Morris 1974), and its importance to the ecology of wetland animals (Goin 1943, O'Hara 1967, Rzoska 1973, Ultsch 1973, Junk 1977, Achaval *et al*. 1979, Neiff and Carignan 1997, Toft *et al*. 2003).

Water-hyacinth can dramatically alter aquatic habitats both physically and chemically (Penfound and Earl 1948, Gopal 1984, 1987) and has been referred to as an "ecosystem engineer" (Simberloff *et al.* 1997, Toft *et al.* 2003). In turn, these physical and chemical changes to naive ecosystems affect the distributions and abundances of indigenous organisms, both directly and indirectly (Jones *et al.* 1994), and might influence the evolution of other freshwater species (Mooney and Cleland 2001). Water-hyacinth has been shown to alter freshwater ecosystems to such a degree as to prompt Holm *et al*. (1969) to label this problematic plant as "one of the world's worst weeds."

Several studies have recorded the complete exclusion of native freshwater species, following the introduction of water-hyacinth. Pelagic plankton communities have suffered as a result of shading and nutrient retention by water-hyacinth rafts (Abu Gidieri and Yousif 1974, Gopal *et al.* 1984, Scott *et al.* 1979, Ashton *et al.* 1979, McVea and Boyd 1975). Water-hyacinth also out-competes other macrophytes for light and nutrients (Gowanloch 1944). Brendonck *et al.* (2003) mentioned the loss of immersed and submerged macrophytes in Lake Chivero in Zimbabwe after the introduction of water-hyacinth and discussed the impacts of this loss to populations of plankton, macroinvertebrates, and fishes. Water-hyacinth excludes other floating macrophytes such as waterlettuce, *Pistia stratiodes* L., in East Africa (Gay 1960) and two of its congeners, *Eichhornia paniculata* (Spreng.) Solms in Jamaica (Baker 1965) and *E. azurea* (Sw.) Kunth in Central and South America (Bock 1966).

Water-hyacinth impacts animal communities. Midgley *et al.* (2006) recorded depletion of diversity and abundance of benthic invertebrates beneath water-hyacinth rafts in two impoundments in South Africa. Fish populations are reduced in areas overgrown by water-hyacinth due to the reduction of dissolved oxygen and photosynthetic activity (Dubois 1955, Bishai 1961, Timmer and Weldon 1967, Holm *et al.* 1969, McVea and Boyd 1975, Ahmad 1977, Sharma *et al*. 1978) and to the contamination of spawning grounds (Achmad 1971). Another report mentioned that water-hyacinth has impacted populations of some waterfowl by eliminating the aquatic macrophytes that the birds use for food (Tabita and Woods 1962). In light of this ability of water-hyacinth to exclude other freshwater species, some authors have considered this plant to be a serious threat to much of the world's freshwater biodiversity (Gopal 1987, Drake and Mooney 1989, Luken and Thieret 1997).

While there exists a concern for what organisms may be eliminated in water-hyacinth's presence, there also is concern for what organisms thrive where this plant occurs. Numerous bacteria and fungi have been isolated from various locations within water-hyacinth rafts, including the causative agent for human cholera, *Vibrio cholera*

Pacini (Iswaran *et al*. 1973, 1980, Nayak *et al*. 1979, Seshadri *et al*. 1982, Gunasekera *et al*. 1982, Mishra and Dwivedi 1982). Even though studies report that plankton communities are frequently depleted in the water column beneath water-hyacinth rafts, several planktonic species flourish in the interstitial spaces among plants (Monakov 1969, Abu Gidieri and Yousif 1974, El Moghraby 1975, McVea and Boyd 1975, Lenzi-Grillini 1982, Gopal *et al.* 1984, Scott *et al*. 1979, Ashton *et al*. 1979, Brendonck *et al*. 2003). Water-hyacinth competes with other aquatic macrophytes, but some vascular plants are able to take advantage of water-hyacinth's presence. These include some smaller, floating plants such as *Lemna* spp., *Azolla* spp., and *Salvinia* spp., a few immersed plants such as *Hydrilla* spp., *Ceratopogon* spp., *Potamogeton* spp., and *Egeria* spp., and several marshland emergents, such as *Cyperus* spp., *Scirpus* spp., *Ludwigia* spp., and *Phragmites* spp. (Gay 1960, Tur 1972, Trivedy *et al.* 1978, Batanouny and El Fiky 1984, Denny 1984). This dynamic assemblage of plants increases the rate of succession by forming floating islands, commonly referred to as sudds or tussocks. In many countries several of the plants that associate with water-hyacinth are themselves noxious species that exacerbate the problems. The formation of floating islands of water-hyacinth and its associates is a serious threat to navigation, stormwater management, water retrieval systems, and man-made structures.

In addition to the problems posed by the plant community, many nuisance animals inhabit water-hyacinth rafts. Several macroinvertebrates that are considered to be significant threats to human health multiply within water-hyacinth rafts. Populations of biting midges (Diptera: Ceratopogonidae) and mosquitoes (Diptera: Culicidae), groups which contain species that are vectors of several human pathogens, have been shown to surge and are increasingly difficult to manage in water-hyacinth rafts (Seabrook 1962). Some studies have reported that leeches (Annelida: Hirudinia) are common in water-hyacinth rafts (Monakev 1969, Costa and de Silva 1978, Achaval *et al* 1979). Also, the snail *Biomphalaria alexandrina* (Ehrenburg), which is an intermediate host for the causative agent of schistosomiasis, has been reported as reaching some of its greatest recorded abundances in water-hyacinth rafts (Seabrook 1962, Mitchell 1976). While water-hyacinth alone has contributed to the detriment of freshwater resources, it appears that this plant has the potential to augment populations of other noxious species by providing suitable habitat for establishment, a phenomenon reported in other organisms (Grosholz 2005).

As biologists have investigated the community dynamics of water-hyacinth rafts to determine the ecological role served by this problematic plant, they have reported consistently that water-hyacinth rafts harbor an extremely abundant and relatively diverse assemblage of macroinvertebrates. Michael (1968) estimated that the abundance of macroinvertebrates ranges from 9,000 to 11,000 individuals per liter of root volume. O’Hara (1967) observed abundances ranging from 3,446 to 84, 223 (mean 16,484) individuals per square meter, and Junk (1977) reported as many as 138,000 invertebrates per square meter. The community also is comprised of numerous species. Gopal (1987 pp. 120, 121) provided a table listing 82 species of annelids, arthropods, and mollusks that have been reported from water-hyacinth rafts in four previous investigations: Costa and de Silva (1978) in Sri Lanka, O’Hara (1967) in the United States, Achaval *et al.*

(1979) in Uruguay, and Michael (1968) in India. Other studies (Monakev 1969, Akhtar 1978, Achaval *et al.* 1979, Naidu *et al*. 1981, Toft *et al*. 2003, de Marco *et al.* 2001, Masifwa *et al.* 2001) could have added to this list, but most of these investigations have been limited either in their scope or taxonomic resolution, especially with regard to the insects. Most studies of macroinvertebrate communities in water-hyacinth rafts have pursued species identifications of the annelids and mollusks present but have determined only larger taxonomic groupings of the arthropods, especially in the North American studies of water-hyacinth faunas. This bias likely is a result of regional limitations in the taxonomy of arthropods, especially with regard to the insects, and the notion that individual insect species do not contribute greatly to the productivity of water-hyacinth rafts.

A few authors have sought to determine all of the species of macroinvertebrates inhabiting water-hyacinth rafts and have determined the arthropod species that occur there. Four publications (Costa and de Silva 1978, O'Hara 1967, Achaval *et al.* 1979, Michael 1968) contributed to the list of 82 macroinvertebrate species compiled by Gopal (1987). In this list, the arthropods represent 62% of the total species, and the insects account for only 39% (32 species). Junk (1977) performed a detailed investigation of the fauna of floating vegetation in the Bung Borapet Reservoir, Thailand. He reported 36 species of mollusks and arthropods. Five species (14%) were crustaceans, and nine species (25%) were insects. He also mentioned that there were representatives of several other insect families present but these species had not been determined because of taxonomic limitations. More recently, Neiff and Carignan (1997) provided the most complete list of macroinvertebrate species to be found in water-hyacinth rafts. Their study of two natural lakes in a floodplain of the Parana River (Argentina) produced a list of 77 species of annelids, arthropods, and mollusks. In this list, 63 species (82%) were arthropods, and 53 species (69%) were insects. If the list of Neiff and Carignan (1997) is compared with the lists compiled by Junk (1977) and Gopal (1987), we find that the arthropods appear to be under-represented in the earlier investigations of water-hyacinth fauna. Arthropods represent one of the most diverse groups of animals on the planet (Wilson 1988) and likely are the most diverse group of animals inhabiting floating vegetation such as water-hyacinth.

On occasion, researchers have observed that the invertebrate community in water-hyacinth rafts varies over time as environmental conditions change. Michael (1968) reported that certain macroinvertebrates, mainly oligochaete worms, were most abundant during winter months. Costa and de Silva (1978) also found a similar temporal differentiation and reported that the difference in the community assemblage was due to differing water characteristics among seasons. Neiff and Neiff (1978, 1980) corroborated the observation of seasonal variation. Achaval *et al.* (1979) collected different invertebrates in water-hyacinth rafts in the Parana River following floods during the rainy season. While all of these studies observed seasonal variation among invertebrate communities, they were conducted in the tropics where seasons are differentiated less by temperature than by the amount of rainfall. The seasonal variation observed is most likely a function of the amount of flow and the type of materials transported in that flow. This concept was supported by Neiff and Carignan (1997) who observed variation between hydrological periods (low and high water) but no correlation with seasonality.

The macroinvertebrate fauna of water-hyacinth rafts also varies in space. The phenotypic plasticity of water-hyacinth allows it to thrive in a wide array of environmental conditions (Cooley *et al*. 1979), and the multiple morphological forms discussed by Cooley provide habitats with different physical structures. Within water-hyacinth rafts, Masifwa *et al*. (2001) observed an invertebrate community at the periphery of the rafts that was quite different from the community several meters into the rafts. They attributed this change to the morphology of the vegetation and to the reduced concentration of dissolved oxygen recorded as little as five meters from the perimeter. Junk's (1977) study of the Bung Borapet reservoir reported that the invertebrate fauna was significantly different between water-hyacinth rafts near the reservoir's inflow than those near the outflow. He demonstrated that the community assemblage was dependent on the morphological characteristics of the vegetation as well as on the physicochemical properties of the water. Other authors also have noted variation among water-hyacinth rafts in a single freshwater system (O'Hara 1969, Neiff and Neiff 1980, Achaval *et al.* 1979, Toft *et al.* 2003, Ramirez *et al*. 2007). Neiff and Carignan (1997) recorded differences in two lakes that were isolated from each other only during periods of low water. Although many authors have observed varying arthropod communities within and among water-hyacinth rafts in a particular body of water, few have compared rafts in separate freshwater systems in a particular geographic region. Furthermore, no one has compared arthropod communities of water-hyacinth rafts in multiple freshwater systems in a temperate climate.

The diversity of invertebrates in water-hyacinth rafts is not just a function of environmental factors, because humans also have contributed. Resource managers from around the world have looked to phytophagus invertebrates as a method for biologically controlling water-hyacinth populations. In doing so, humans have transported invertebrate enemies of water-hyacinth from their native ranges to various regions of the world. Most notably, four arthropods: the chevroned water-hyacinth weevil [*Neochetina bruchi* (Hustache) (Coleoptera: Curculionidae)], mottled water-hyacinth weevil [*N. eichhorniae* (Warner) (Coleoptera: Curculionidae)], water-hyacinth moth [*Niphograpta albiguttalis* (Warner) (Lepidoptera: Pyralidae)], and water-hyacinth mite [*Orthogalumna terebrantis* Wallwork (Acarina: Galumnidae)], have been widely distributed around the world. In addition, 15 other arthropods are being tested or released in select countries (Center *et al*. 2002). Because the hunt for natural enemies continues, several more invertebrate species likely will have their ranges expanded by human hands.

In North America, the macroinvertebrate fauna of water-hyacinth rafts has been addressed twice. The first study was conducted by O'Hara (1967) in canals of southern Florida. His inspection was the first to investigate macroinvertebrates in water-hyacinth rafts, and his results have inspired similar investigations in other parts of the world. O'Hara claimed that more than 55 species were present, but taxonomic limitations, largely in the insects, prevented the determination of the exact number of species. As for the arthropods collected, five spiders, three crustaceans, two mayflies (Ephemeroptera), seven dragonflies (Odonata), two beetles (Coleoptera), and three true bugs (Hemiptera) were identified to genus level or better. The flies (Diptera) and several beetles were identified only to the family level. Three types of caddisfly (Trichoptera) cases were collected but not identified beyond order, and other aquatic insects such as moths (Lepidoptera) and dobsonflies/alderflies (Neuroptera) were not mentioned. Despite his taxonomic limitations, O'Hara (1967) determined that the arthropods are the most speciose group of macroinvertebrates that occur in water-hyacinth rafts in Florida and that the amphipod *Hyalella azteca* Saussure (Amphipoda: Hyalellidae) was the single-most abundant macroinvertebrate present.

The second North American study of water-hyacinth macroinvertebrates was conducted by Toft *et al*. (2003). They explored the fauna of water-hyacinth rafts in the Sacramento/San Joaquin River Delta in California and compared the productivity of the nonindigenous water-hyacinth to that of the native pennywort, *Hydrocotyle umbellate* L. (Ariaceae). Though they applied species names to the crustaceans collected, they referred to the insects only by their family groupings. Their study showed that water-hyacinth serves a different ecological role from pennywort by harboring a different community of macroinvertebrates; however, it did not provide species-level resolution to all of the macroinvertebrates present nor did it determine which insect species contribute most to the water-hyacinth community. Considering the taxonomic limitations of O'Hara (1969) and the restricted scope of Toft *et al*. (2003), the species of North American insects that occur in water-hyacinth rafts have yet to be determined completely.

In North America, water-hyacinth rafts can be found in California and the southern United States, including South Carolina. Although water-hyacinth has been present in South Carolina for nearly a century, no ecological studies concerning this plant have ever been conducted there. In South Carolina, water-hyacinth is considered to be a nuisance species but is no longer the primary aquatic weed. Periodic cold winters and the use of herbicides keep populations of this plant from becoming major threats; nevertheless, water-hyacinth persists and has the potential to develop serious infestations when left unchecked (SCDNR 2004).

The water-hyacinth rafts of South Carolina provide an excellent medium for addressing the ecology of this plant's macroinvertebrate community for four reasons. First, the aquatic macroinvertebrates of South Carolina have been well documented, and their taxonomy is highly developed relative to that of many regions in the rest of the world, allowing for the determination of most of the species in the region. Also, the aquatic fauna of this region is extremely diverse (Brigham *et al.* 1976), allowing for a high level of ecological resolution. Second, although water-hyacinth is limited to the mild climate of South Carolina's Atlantic Coastal Plain, it can be found in multiple watersheds characterized by a wide array of flow regimes. Water-hyacinth is present in lentic and lotic systems and also can be found in tidal, freshwater marshes near the coast. No studies have investigated the fauna of water-hyacinth rafts that are repeatedly stranded on shorelines in tidal systems; therefore, water-hyacinth rafts in South Carolina provide an opportunity to investigate how being stranded on land alters the arthropod community. Third, South Carolina has a temperate climate and lies near the northernmost extent of water-hyacinth’s range in eastern North America. In this region, water-hyacinth plants experience a dormant season when growth ceases and emergent portions of the plants are killed by freezing temperatures. Few faunistic studies of water-hyacinth rafts have been conducted in temperate locations, and this geographic circumstance provides an opportunity to investigate the water-hyacinth community outside of the tropics and subtropics. Finally, no biological control agents of water-hyacinth have ever been released in this state, although they have been released in nearby Florida. South Carolina’s water-hyacinth rafts provide a means of determining the ability of these agents to colonize plants in distant watersheds and of assessing their life histories in a temperate location.

My project investigates water-hyacinth rafts in South Carolina to determine which arthropods inhabit these plants in eastern North America and to address ecological questions concerning the arthropods that inhabit water-hyacinth rafts in multiple flow regimes in a temperate climate. I compare the species composition, species richnesses, and abundance of arthropod communities inhabiting water-hyacinth rafts 1) among five freshwater systems in two watersheds in the Atlantic Coastal Plain, 2) among lentic, lotic, and tidal habitats, and 3) among seasons for one year. To complement these comparisons, I determine the proportions of functional feeding groups among sites, flow regimes, and seasons. I also determine the distributions and abundances of imported biological control agents in South Carolina and compare their abundances among sites, flow regimes, and seasons of the year. To enable the correct determination of larvae of the water-hyacinth weevils, I also describe and illustrate the larvae of *N. bruchi* and *N. eichhorniae*.

CHAPTER TWO

MATERIALS AND METHODS

Rivers and reservoirs in the Atlantic Coastal Plain of South Carolina were surveyed in 2004 to assess the distribution of water-hyacinth and to locate perennial populations that would remain stable through the following year, 2005-2006. Seven sites were chosen for the arthropod surveys. Three of these sites, (1) Stumphole Swamp in Lake Marion (MAR) in Calhoun County, (2) Back River Reservoir (BRR) in Berkeley County, and (3) Goose Creek Reservoir (GCR) in Berkeley County, comprised the lentic collection sites. The lotic (W) and tidal (L) collections were taken from (4,5) Quinby Creek (QCW, QCL) on the Cooper River in Berkeley County and the (6,7) Samworth Wildlife Management Area along the Pee Dee River (PDW, PDL) in Georgetown County. Each lotic collection (QCW, PDW) was taken from a water-hyacinth raft that remained floating in the creek channel at ebb-low tide. Each tidal collection (QCL, PDL) was taken from a water-hyacinth raft that was stranded on the creek bank at ebb-low tide.

Description of Sites

(1) BRR: Back River Reservoir is located southeast of Monck’s Corner and lies west of the middle reach of the Cooper River. The reservoir was formed by the damming of one bifurcation of the Cooper River channel. The downstream end of the reservoir is separated from the river, but the upstream end still receives water from the Cooper River via a canal. The water level in Back River Reservoir fluctuates slightly each day with the tides, but the reservoir is essentially lentic. This reservoir contains the greatest

abundance of aquatic macrophytes of the study sites, and is dominated by *Ludwigia hexapetala* (Hook & Arn.) Zardini, Gu & Raven and *Hydrilla verticillata* (L.f.) Royle. Water-hyacinth rafts grow among and are held in place by stands of *L. hexapetala*. Because this reservoir provides water to a major electrical plant and to other industries, the vegetation is managed more heavily than at any of the other study sites. Water-hyacinth persists among the other aquatic plants, but its rafts are kept small and isolated by the frequent application of chemical herbicide.

(2) GCR: Goose Creek Reservoir is a 600 acre reservoir near the southernmost reach of the Cooper River between the towns of Goose Creek and North Charleston. Goose Creek Reservoir was formed in 1903 by the damming of Popperdant Creek. The littoral zone is heavily vegetated and contains the highest diversity of aquatic macrophytes of any of the sites in this study. Water-hyacinth rafts persist in the small tributaries and among the mats of other plants. In the location studied, water-hyacinth dominated a small tributary protected from wind by stunted maple trees, *Acer* sp., and willows, *Salix* spp. The depth beneath the raft studied was approximately 2 meters.

(3) MAR: Stumphole Swamp is located in the northernmost fourth of Lake Marion in what used to be the floodplain of the Congaree River. When the lake was first formed in 1942, the floodplain of the Congaree River and Stumphole Swamp were flooded. Stumphole Swamp is characterized by stands of large bald cypress trees in an average depth near 1.5 meters. Water-hyacinth grows among and is held in place by the trunks of the bald cypress trees. Numerous other floating macrophytes are present in the

same area. Stumphole swamp receives water from the Congaree River but is predominantly lentic.

(4,5) QCW, QCL: Quinby Creek is a tributary on the eastern side of the Cooper River and empties near the middle reach of the river. Historically, the marshes along this creek were modified for the rice industry, which no longer exists. Numerous canals and dykes remain, providing an excellent habitat for aquatic macrophytes. The creek is tidal, fluctuating up to two meters twice per day, and the current in the creek channel can be substantial. Water-hyacinth rafts riddle the banks of the main channel and the flats behind the dykes. Most of the rafts are held in place by the overgrowth of *Ludwigia hexapetala*. The raft used for the study of lotic plants (4, QCW) was held in place by the remnant pillars of an old rice-loading dock located at the confluence of Quinby Creek and Turkey Creek. This raft remained floating even at the lowest of low tides. The raft used for the study of tidally stranded plants (5, QCL) was located near the lotic study site, but was held close to the bank by *Ludwigia hexapetala* plants. This raft was always stranded on the bank at ebb-low tide.

(6,7) PDW, PDL: The Samworth Wildlife Management Area is situated in the freshwater marshes along the Pee Dee River. Like Quinby Creek, the hydrology of this area had been modified by the rice industry and is characterized by numerous canals and dykes. The rafts studied at this location were situated along a secondary channel of the Pee Dee River which is subject to intense flows driven by tidal fluctuations of up to two meters. The water-hyacinth raft used for the lotic plant study (6, PDW) was held in place by a fallen tree and spatterdock [*Nuphar luteum* (Small) E.O. Beal] and remained floating even at the lowest of low tides. The raft used for the study of tidally stranded plants (7, PDL) was held in place by the modified roots (knees) of bald cypress trees that protruded from the bank. These plants were always stranded out of the water at ebb-low tide.

Collection Procedures

Plants and animals were manually collected from all seven sites monthly, beginning in March 2005 and concluding in February 2006. Floating plants were collected using a 7-gallon (26.49 L) bucket with a sharply filed rim which served as a modified dipper. Three bucket thrusts were made at each collection event. Each thrust sampled a surface area of 900 cm^2 and a volume of approximately 20 L, so each collection event sampled 2,700 cm^2 of water-hyacinth raft and 60 L of water and plants. The first thrust was made at the perimeter of the water-hyacinth raft, the second at 1 meter into the raft, and the third at the center of the raft (usually 5 to 10 meters from perimeter). At each thrust, the bucket was forced into the water-hyacinth raft at a 45 degree angle and pressed horizontally below the water surface. As water flowed into the bucket, plants were raked by hand into the bucket. Once the bucket was 75% full, the bucket was lifted by its handle, trapping the water and plants inside. Individual plants then were shaken vigorously in the bucket to dislodge invertebrates into the bucket. Rinsed plants were removed from the bucket and placed in a large, plastic trash bag with a collection label. Once all plants had been thoroughly rinsed, the contents of the bucket were poured through a 500-micron sieve to capture dislodged animals. Sieve contents then were transferred to a large zip-lock bag and fixed in 100% ethanol.

Stranded plants were collected using a similar methodology. Stranded plants were scooped from the substrate using a 7-gallon (26.49 L) bucket, taking care not to dig deeply into the sediment. Three thrusts also were taken from the stranded raft, one at the raft perimeter, another at one meter into the raft, and the last from the center of the raft. Water was collected from the nearby channel, strained to remove unwanted macroinvertebrates, and poured into the bucket containing the plants collected from the bank. The plants then were processed in the same way as the plants collected from floating rafts.

Aquatic plants other than water-hyacinth were collected using this methodology because these plants were growing among water-hyacinth plants at the study sites. Additional plant species were recorded for each site.

Bags containing rinsed plants were transported to a greenhouse at the Clemson University Insectary. Rinsed plants from each site were segregated into large Berlese funnels, each constructed of two 5-gallon (18.92 L) buckets, a grated funnel, and a 100-watt flood lamp over a jar of 100% ethanol. Plants were dried in the funnel for up to one week, and any remaining animals were combined with the animals extracted by the on-site rinses.

Identification and Analysis

All macrofaunal arthropods, with a couple of exceptions, were sorted and identified from each sample. Amphipods, isopods, and Chironomidae larvae were sub-sampled to no more than 10, 10, and 50 individuals, respectively. Amphipods, isopods, and chironomids were sorted to determine species richness and not abundance; therefore, they were subsampled by picking representatives of each morphological variant rather than by a quantified method. Arachnids and Collembola were not sorted. Thysanoptera were identified to family, and Orthoptera were identified to subfamily. Although species names were not applied to Thysanoptera or Orthoptera, morphological variants were considered to be separate species and counted as such. Adult insects known to be active flyers (including adult Diptera, Ephemeroptera, Hymenoptera, Lepidoptera, Odonata, and Trichoptera) were not sorted or counted. All sorted arthropods were identified to species when possible.

All individuals, except for amphipods, isopods, and Chironomidae, were counted to determine abundances. When counting individuals, each species of amphipod, isopod, and chironomid was considered as a single individual. This study was concerned more with determining the species richness of these groups than their abundances. This was done to reduce workload, because other studies have already determined that these three groups are the most abundant arthropods in water-hyacinth rafts. Also, any species that was collected at a single sampling event and was represented by less than five individuals was considered a transient species that does not typically inhabit water-hyacinth rafts. These are included in the list of species collected but not considered in statistical analyses.

Larvae and adults of the same genus and species were collected in the same water-hyacinth raft. Many larvae cannot be determined beyond the genus level. When adults and larvae of a single genus were present, indeterminate larvae were considered to be one of the adult species and were not counted as additional species to prevent overestimating the species richness of arthropods present, even though some of the larvae actually might have been different from the adult species collected.

Arthropod communities were compared among sites, among flow regimes, and among months of the year. Species richness and abundance among sites and months were compared using Analysis of Variance (ANOVA), and individual sites, flow regimes, and months were grouped for likeness using Fisher's Least Significant Difference (LSD). Tables of pair-wise comparisons using paired t-Tests of Significance are provided for both species richnesses and abundances among sites. Sites, flow regimes, and months also were compared by the percent species unique to each and the percent functional feeding groups per site, regime, or month.

Special attention was paid to the insect species that have been imported into the United States for the biological control of water-hyacinth, including *Neochetina eichhorniae*, *N. bruchi*, and *Niphograpta albiguttalis*. The distributions of these insects in South Carolina were determined both by collection data and by observed evidence of feeding scars. Their abundances also were compared among sites, flow regimes, and months of the year using paired t-Tests of Significance.

All specimens were deposited in the Clemson University Arthropod Collection, 312 Long Hall, Department of Entomology, Soils, and Plant Sciences, Clemson University, Clemson, SC 29634.

CHAPTER THREE

RESULTS

Plant Community

Other than water-hyacinth, two plants were collected in every sample at every site: *Lemna* spp. and *Azolla caroliniana* Willd. Other aquatic plants also were encountered. *Ludwigia hexapetala* (Hook & Arn.) Zardini, Gu & Raven was present in every sample of every site except PDW and PDL. *Hydrilla verticillata* (L.f.) Royle was present in all samples at BRR and QCW, and was collected during the summer months at MAR, GCR, and QCL. *Potamogeton crispus* L. was collected three times at BRR. The summer samples (May through August) at GCR contained *Pistia stratiodes* L., *Myriophyllum aquaticum* (Vell.) Verdc., and *Hydrocotyle umbellata* L. *Hydrocotyle umbellata* was also collected at GCR in September.

Arthropod Community

The 84 samples produced 9,070 identified arthropods (Table 1, Figure 1.1). Ten species of crustaceans were collected. These species represent 9 genera from 8 families and 3 orders. A total of 246 insect species were collected. The insect species represent 179 genera from 74 families and 10 orders. Twenty-five species were ubiquitous among all sites. An additional 12 species were found at all but one of the five freshwater systems surveyed. A total of 129 species were collected at multiple sites and in multiple months. Each site contained species that were unique to that site. The total number of species that were collected at only a single site was 117. Of the 117 species that were unique to a particular site, 72 species were collected at a single sampling event and were represented by five or fewer individuals. These are considered transient species that do not regularly inhabit water-hyacinth rafts. Disregarding the transient species brings the total number of arthropod species that regularly inhabit water-hyacinth rafts in South Carolina to 184.

Comparison of Sites

Back River Reservoir (BRR): The total abundance of arthropods (Figure 2.1) collected at this site was 1,316 individuals (14.5% of the total for the study), and the average abundance per month (Figure 2.2) was 109.0 ± 30.5 (95% confidence interval [CI]) individuals, ranging from 51 (October 2005) to 229 (May 2005) individuals (Figure 2.3). The total species richness (Figure 3.1) was 108 species with an average (Figure 3.2) of 29.0 ± 3.8 (CI) species per collection. The highest richness was recorded in February 2006 with 39 species (Figure 3.3). The 108 species collected represent 93 genera in 48 families of 11 orders. Twenty-four species (22.2% of site, 9.3% of total) were unique to this site.

Goose Creek Reservoir (GCR): The total abundance of arthropods (Figure 2.1) collected at this site was 2,826 (31.2% of total) individuals, and the average (Figure 2.2) was 235.5 ± 43.1 (CI) individuals per month and ranged from 89 (June 2005) to 367 (September 2005) individuals (Figure 2.3). The total species richness (Figure 3.1) was 102 species with an average (Figure 3.2) of 33.3 ± 5.0 (CI) species per collection. The highest richness was recorded in September with 49 species (Figure 3.3). The 102 species collected represent 86 genera in 46 families of 11 orders. Twenty-three species (22.6% of site, 9.0% of total) were unique to this site.

Lake Marion (MAR): The total abundance of arthropods (Figure 2.1) collected at this site was 1,605 (17.7% of total) individuals, and the average (Figure 2.2) was 113.8 ± 74.2 (CI) individuals per month and ranged from 33 (March 2005) to 417 (May 2005) individuals (Figure 2.3). A dramatic drop in abundance occurred between July 2005 (205 individuals) and August 2005 (63 individuals) and coincided with a bloom of the noxious alga, *Lynbya* sp. Abundances remained low until the alga retreated in December. The total species richness (Figure 3.1) was 103 species with an average (Figure 3.2) of 29.0 ± 4.7 (CI) species per collection. The highest richness was recorded in April 2005 with 44 species (Figure 3.3). The 103 species collected represent 82 genera in 50 families of 12 orders. Twenty-five species (24.3% of site, 9.7% of total) were unique to this site.

Quinby Creek Water (QCW): The total abundance of arthropods (Figure 2.1) collected at this site was 1,454 (16.0% of total) individuals, and the average (Figure 2.2) was 121.2 ± 33.4 (CI) individuals per month and ranged from 77 (February 2006) to 216 (August 2005) individuals (Figure 2.3). The total species richness (Figure 3.1) was 99 species with an average (Figure 3.2) of 25.6 ± 4.9 (CI) species per collection. The highest richness was recorded in November with 35 species (Figure 3.3). The 99 species collected represent 84 genera in 48 families of 12 orders. Twenty-two species (22.22% of site, 8.6% of total) were unique to this site.

Quinby Creek Land (QCL): The total abundance of arthropods (Figure 2.1) collected at this site was 187 (2.1% of total) individuals, and the average (Figure 2.2) was 15.6 ± 2.2 (CI) individuals per month and ranged from 10 (October) to 23 (May) individuals (Figure 2.3). The total species richness (Figure 3.1) was 38 species with an average (Figure 3.2) of 7.8 ± 1.5 (CI) species per collection. The highest richness was recorded in July, November, and February each with 11 species (Figure 3.3). The 38 species collected represent 36 genera in 23 families of 7 orders. Four species (10.5% of site, 1.6% of total) were unique to this site.

Pee Dee Water (PDW): The total abundance of arthropods (Figure 2.1) collected at this site was 1,277 (14.1% of total) individuals, and the average (Figure 2.2) was 106.4 ± 44.2 (CI) individuals per month and ranged from 48 (March 2005) to 312 (May 2005) individuals (Figure 2.3). The total species richness (Figure 3.1) was 92 species with an average (Figure 3.2) of 21.0 ± 5.6 (CI) species per collection. The highest richness was recorded in May 2005 with 48 species (Figure 3.3). The 92 species collected represent 77 genera in 40 families of 13 orders. Nineteen species (20.7% of site, 7.4% of total) were unique to this site.

Pee Dee Land (PDL): The total abundance of arthropods (Figure 2.1) collected at this site was 405 (4.5% of total) individuals, and the average (Figure 2.2) was 33.8 ± 16.8 (CI) individuals per month and ranged from 13 (May 2005) to 312 (February 2006) individuals (Figure 2.3). The total species richness (Figure 3.1) was 40 species with an average (Figure 3.2) of 8.5 ± 3.6 (CI) species per collection. The highest richness was recorded in Feb 2006 with 25 species (Figure 3.3). The 40 species represent 36 genera in

22 families of 7 orders. Ten species (25.0% of site, 3.9% of total) were unique to this site.

Tests of significance of arthropod abundance per site (Table 2, Figure 2.2) indicate that arthropod communities vary significantly among sites (ANOVA $p<0.0001$, df=6). Arthropods were more abundant at GCR than at all other sites. Abundances at BRR, MAR, QCW, and PDW were statistically identical. Abundances at QCL and PDL were statistically identical to each other and significantly lower than at all other sites (LSD=56.6).

Tests of significance of arthropod species richness per site (Table 3, Figure 5) indicate that arthropods vary significantly among sites (ANOVA $p<0.0001$, df=6). Fisher's Least Significant Difference groupings indicate overlap among BRR, GCR, MAR, PDW, and QCW. GCR contained more arthropods than PDW and QCW, and BRR, GCR, and MAR had greater abundances than PDW.   QCL and PDL were statistically identical to each other and significantly lower than all other sites (LSD=5.91).

Comparison of Flow Regimes

Statistical measures suggest that the abundances and species richnesses of arthropod communities are similar in both lentic and lotic sites. Though GCR appears to have a greater abundance of arthropods than all other sites (Figure 3), arthropod abundances at lentic sites, on a whole, are not significantly different from lotic sites (LSD=56.6, Table 2). Though lentic sites appear to contain slightly more species than lotic sites (Figure 5), there is considerable variation among lentic and lotic sites and groupings suggest that lentic and lotic sites overlap and are not significantly different (LSD=5.91, Table 3).

Lentic and lotic sites also had a similar species composition. Of the 129 species that were collected at multiple sites, only 13 species (10.1%) were uniquely common to either lentic or lotic sites. Only one species, *Sepedon* sp. (Diptera: Sciomyzidae), was common to all three lentic sites and absent at the lotic sites. Eleven other species, including one beetle (Coleoptera), two caddisflies (Trichoptera), and eight midges (Diptera: Chironomidae), were collected at two of the three lentic sites and none of the lotic sites (Table 1). On the other hand, *Sphaeroma* sp. (Isopoda: Sphaeromatidae) was the only species common to the lotic sites and absent from lentic sites. The presence of this isopod at the lotic sites is probably a result of the close proximity of these sites to the brackish water marshes along the coast, because this genus is reported as a group of marine or brackish water species that can often be found in low salinity habitats (Charmantier and Charmantier-Daures 2001). The distribution of *Sphaeroma* spp. likely depends more on access and proximity to saline habitats than on amount of flow.

The relative percentages of functional feeding groups were nearly the same for both lentic and lotic sites, with some variation among individual sites. Typically, predators comprise the most speciose group (33-42%), followed by collector-gatherers (26-36%), herbivores (23-32%), collector-filterers (0-7%), and detritivores (0-2%). Comparisons of the abundances of each feeding group could not be made because the abundances of amphipods and Chironomidae larvae were not determined. Because these two groups contain the majority of the collector-gatherer species present, any attempt to determine the relative abundances of the functional feeding groups would have been biased heavily against the collector-gatherers.

Tidally stranded plants harbored a different assemblage of arthropods from the lentic and lotic sites. Tidally stranded plants contained fewer arthropods than either lentic or lotic sites (LSD=56.6, Table 2) and contained significantly fewer species (mean LSD=5.91, Table 3). The percentages of functional feeding groups also differed in that the collector-gatherers comprised a much smaller proportion of the species and the collector-filterers and detritivores were completely absent (Table 1). Of the 65 species collected at tidal sites, 17 were unique to tidal sites, and many of the unique species were of terrestrial origin (Table 1).

Comparison of Months

The abundances of arthropods did not differ significantly from month to month through the sampling period (ANOVA $p<0.1357$, df=11). There was a slight increase in the number of individuals collected in April and May and a decrease recorded in June (Figure 4.1), but these fluctuations were not significantly different from the other months. The same trend was observed with regard to the richness of species recorded for each month (Figure 4.2). The decrease in abundance and species richnesses recorded in June was due largely to a reduction in the number of Odonata and Chironomidae (Diptera) larvae. While abundances and diversities of all arthropods did not vary significantly among months, some species were season-specific.

Imported Biological Control Agents

Of the three insect species that were introduced into the United States to control water-hyacinth, only the water-hyacinth weevils, *Neochetina bruchi* and *N. eichhorniae* (Coleoptera: Curculionidae), were collected at the study sites. *Niphograpta albiguttalis* (Lepidoptera: Crambidae) was never collected at the study sites but was observed at GCR during the initial surveys in 2004. Evidence of weevil feeding was recorded in every raft and in every month during the study. At least one of the two species was collected in every sample except MAR 2-iii-05, BRR 27-xi-05, and QCL 22-i-06. Though no weevils were collected in these three samples, evidence of their feeding was present. In most samples, both species were collected together with some variation among sites and months.

Across the entire study area, *Neochetina eichhorniae* was more common than *N. bruchi*. A total of 1,377 adults, larvae, and pupae of *N. eichhorniae* were collected as opposed to 779 individuals of *N. bruchi*. Although both weevils were collected at all seven sites at one time or another, *N. eichhorniae* was collected at more sampling events than *N. bruchi*.

The sampling methodology did not effectively collect all of the larvae and pupae in each sample. Even though the plants were shaken vigorously on site and dried in Berlese funnels, dissections of the processed plant material produced undetached puparia and dead larvae (mostly early instars) that had not been dislodged from the plants. The collection data also indicated a disparity between the number of larvae and adults collected, where the total number of larvae collected was 682 and the total of adults was

1,474 for both species. For this reason, comparisons of abundances can only be made for the adults with confidence. The total number of *N. eichhorniae* adults was 944, and the average collected in each sample was 11.2 ± 3.3 (CI). The total of *N. bruchi* adults was 530 with an average of 6.3 ± 1.9 (CI) per sample.

Weevil abundances varied among the collection sites (Figure 6). Goose Creek Reservoir (GCR) was the most productive with 440 adult weevils, followed by PDW (368), PDL (187), BRR (147), QCW (147), MAR (137), and QCL (48). Abundances of each species also varied among sites (Figure 7). The total number of *N. eichhorniae* adults was greater at all sites except for PDW and PDL. Although the monthly averages for *N. eichhorniae* were not significantly different from those of *N. bruchi* at BRR, MAR, QCL, and PDL, the averages for *N. eichhorniae* were significantly greater at GCR ($p = 0.0004$) and QCW ($p = 0.0029$) and significantly smaller at PDW ($p = 0.0097$).

Abundances of adult water-hyacinth weevils were not significantly different among flow regimes (Figures 8, 9). Both the total number of adults collected at each site and the average number recorded for each month indicate independence from flow regime. The three greatest totals and averages were observed at GCR, PDW, and PDL which represent all three flow regimes studied. Likewise, the three lowest totals and averages were recorded in each of the three flow regimes. On the other hand, if the weevil abundances are compared between PDW and PDL, there was a reduction in the number of weevils in tidally stranded rafts. The same relationship was also recorded for QCW and QCL, suggesting that the weevils might move out of tidally stranded plants to nearby plants that remain floating.

An interesting trend was observed when water-hyacinth weevil abundances were determined for each month (Figure 5.1). Although the sampling methodology did not collect all of the larvae that were present, larvae were collected in the same way at each sampling event, allowing for the comparison among abundances of larvae in different months. The data that were collected suggest that there was an inverse relationship between the abundance of adults and the abundance of larvae/pupae (Figure 5.1). Adults of both species were most abundant in the fall, winter, and spring months and declined during the summer months. Larvae were most abundant in the spring and summer months and declined during the fall and winter months. The abundances of larvae coincided with the growing and dormant seasons of the plant. Water-hyacinth began growth in March, but the leaves were small and barely protruded from the water surface. The plants grew through the following months until November when the first subfreezing temperatures occurred. Subfreezing air temperatures killed the emergent portions of the plants, leaving only the submerged portions (roots, stems, and petiole bases).

New State Records

Several species of arthropods were collected during this investigation that had not been recorded in South Carolina by previous studies. These include the three insects imported for the biological control of water-hyacinth, *Neochetina bruchi*, *Neochetina eichhorniae*, and *Niphograpta albiguttalis*. Other aquatic insects newly recorded for South Carolina were *Laccodytes pumilio* (LeConte) (Coleoptera: Dytiscidae), *Triaenodes* *baris* Ross (Trichoptera: Leptoceridae), *Onychylis alternans* LeConte (Coleoptera: Curculionidae), and *Hydrocanthus regius* Young (Coleoptera: Noteridae).

CHAPTER FOUR

DISCUSSION

Efficacy of Sampling Methodology

The method for sampling arthropods (i.e., dipping) that was used in this study had not been tested for use in water-hyacinth rafts before this investigation, although it has been used to sample pleustonic macroinvertebrates in other studies and has been used to collect *Lissorhoptrus oryzophilus* Kuschel weevils from rice plants. I learned that during this study a similar methodology was used in water-hyacinth rafts in Mexico by Ramirez *et* al. (2007), with success. The method was useful for collecting consistent quantities of plant matter and macroinvertebrates because the bucket provided a standardized volume that remained unchanged from sample to sample. The bucket, sieve, and containers were inexpensive, easily transported, and could be used from the deck of a small boat or the shore. This method proved to be effective at collecting sedentary animals in and on water-hyacinth rafts. Some species were aquatic arthropods (Table 1) and fish (not reported) that avoid capture by other methods, including strong swimmers such as species of Baetidae mayflies (Ephemeroptera), Belostomatidae and Naucoridae bugs (Hemiptera), along with Dytiscidae and Hydrophilidae beetles (Coleoptera). The abundance (9,070 individuals) and species richness (256 species) of captured arthropods are also testaments to the effectiveness of this method.

There were several deficiencies presented as well. This method was not effective for collecting adult insects that are active flyers. Frequently, adult Orthoptera, Hemiptera, Diptera, Lepidoptera, and Hymenoptera were observed fleeing water-hyacinth rafts as sampling commenced. These individuals would be collected best by quantitative sweeping or Malaise traps. Also, the use of a seven-gallon bucket was difficult to implement where plants were taller than 40 cm. Even with the rim sharpened, it was difficult to penetrate old growth that was highly entangled. Even with these disadvantages, this sampling method was useful for collecting arthropods in South Carolina’s water-hyacinth rafts.

The use of Berlese funnels for collecting boring insects and epiphytic macroinvertebrates was not as effective as was expected. Though some additional water-hyacinth weevil larvae and chironomid larvae were collected by using the funnels, several of the boring insects died before they were able to exit the plant material. The only way to remove boring insects effectively would be to perform dissections of the plants by hand. The funnels also did not dry the plant material consistently. Frequently, fungus developed in the funnels before the plants were fully dried, even with the high intensity 100-watt incandescent bulbs. The development of the fungus prevented the further analysis of plant matter by deteriorating the plants and affecting the weight of each sample. On two occasions, the plants were burned by the 100-watt bulb. If plants are to be processed to determine dry weight, they must be dried by another method.

Plant Community

The plant community of water-hyacinth rafts was never completely monocultural. Other floating plants such as *Lemna* spp., *Azolla* spp., and *Ludwigia* spp. were typically present, and water-hyacinth roots provided substrate for the growth of several other aquatic plants. The persistence of other aquatic macrophytes in water-hyacinth rafts was aided by the interruption of plant growth by two factors: the freezing air temperatures during the winter months and the use of spray herbicides. Both factors limit the growth of the water-hyacinth canopy and allow light to penetrate below the water surface. Submerged plants are not affected significantly by either factor and are able to proliferate as light is made available. Aided by wind and water currents, the floating plants move in and out of water-hyacinth rafts and rapidly re-colonize rafts with reduced canopies. Environmental and anthropogenic factors that limit water-hyacinth growth in South Carolina maintain a diversity of plants in water-hyacinth rafts.

The diversity of plants sustains the species richness of arthropods that inhabit water-hyacinth rafts in South Carolina. Several insect species were collected in water-hyacinth rafts even though they feed specifically on other aquatic plants. Most notably, the water primrose flea beetle *Lysathia ludoviciana* Fall was present in most samples from all sites except PDW and PDL, the only sites where water primrose (*Ludwigia* spp.) was not present. Likewise, the waterfern weevil, *Stenopelmus rufinasus* Gyllenhal, which is specific to *Azolla* spp., and the duckweed weevil, *Tanysphyrus lemnae* Fabricius, which is specific to *Lemna* spp., were typically present. Several other phytophagus insects that are host specific to other aquatic plants were also present, including *Parapoynx maculalis* Clemens, *Samea multiplicalis* (Guenee), *Neargyractis slossonalis* (Dyar), *Callibaetis* spp., *Perigaster cretura* (Herbst), *Onychylis nigrirostris* Boheman, *Lissorhoptrus* sp., *Pseudolampsis guttata* (LeConte), and many others (Driesche *et al*. 2002). The diversity of aquatic plants in South Carolina's water-hyacinth rafts helps explain why more than 25% of the species collected were herbivorous arthropods, even though water-hyacinth is not native to North America and does not have a large number of endemic species that feed on it specifically in this range.

The Arthropod Community

Many more arthropod species were recorded in this study than had been observed by any previous studies of water-hyacinth faunas. The 184 species (excluding the 72 transient species collected) that were typical of water-hyacinth rafts in South Carolina outnumber the species recorded by O'Hara (1967) by more than eight fold. Also, the species richness recorded was more than three times that of Neiff and Carignan (1997), which revealed the greatest species richness of arthropods in water-hyacinth rafts to date. The relatively large richness recorded here can be attributed mostly to two factors: the increased scope of this study and the environmental characteristics of the study area.

By investigating water-hyacinth rafts in five different freshwater systems, in two watersheds, and throughout the entire year, I acquired species that had not been recorded by previous studies. I found that more than one-third of the 184 species observed were unique to the site where each was collected. By surveying multiple freshwater systems, I demonstrated that many more arthropod species can inhabit water-hyacinth rafts than had been reported previously by investigations of a single body of water or of a region within a single watershed. Also, several species were present in water-hyacinth rafts only during certain times of the year. Although no differences occurred in the abundances and species richnesses of arthropods in different seasons, species were unique to either the growing or dormant seasons. In addition, improved taxonomy enabled the determination of most of the species collected. When attempting to determine all of the species that inhabit water-hyacinth rafts in a particular geographic region, one must account for all of the aquatic systems in the region and every distinct season, a need that is likely true for other floating and emergent plants, which share similar biologies and provide refuge for diverse faunas.

The environmental characteristics of South Carolina's freshwater ecosystems and anthropogenic factors that limit the size of water-hyacinth rafts in South Carolina also contribute greatly to the sustenance of a diverse arthropod community. The southeastern United States, including South Carolina, contains a large diversity of aquatic arthropods (Brigham *et al* 1978, Merritt and Cummins, 1996). Because freshwater systems in the Coastal Plain of this region are characterized by a great diversity and abundance of aquatic plants, and have been for a long time (Godfrey and Wooten, 1981), many species of aquatic arthropods endemic to this region are adapted for life in and among aquatic vegetation. In the historical record of the aquatic fauna of South Carolina, a great number of species are capable of surviving and thriving in water-hyacinth rafts, provided that water-hyacinth rafts do not completely dominate the system, exclude other plants, and deplete the oxygen concentration in the water column. Because water-hyacinth populations are kept in check by frequent freezes during cold winters and the application of chemical herbicides during the growing season, water-hyacinth is prevented from adversely affecting the faunas of the freshwater systems in this study.

A great deal of variation was observed in the arthropod communities of the five ecosystems investigated. Total abundance was much greater at Goose Creek Reservoir than at any other site. Although I cannot explain exactly why this site contained so many individuals, I can provide explanations as to why the other lentic sites, BRR and MAR, had diminished abundances. Back River Reservoir is managed heavily for its nuisance aquatic plants. During this study, the collection site was sprayed twice with chemical herbicides, once in June 2005 and again later that summer, which severely damaged the plants but did not kill them entirely. Roots of these plants remained viable but were stunted, meaning that the volume of the root matt was reduced dramatically. Coincident with the chemical treatment was a decline in arthropod abundance. The use of herbicides on rafts in BRR likely have contributed to reduced arthropod abundance at this site by reducing the habitat available, which is consistent with the observations of Michael (1968) and Toft *et al*. (2003) who demonstrated a positive correlation between the surface area of root matter to macroinvertebrate abundance. In Lake Marion, herbicides were never applied at the study site, yet arthropod abundance was comparable to that of BRR. Considering that the greatest abundance of any collection event was taken from Lake Marion in May of 2005 with 417 individuals, the decline in abundance was noteworthy. The decline Lake Marion also was a result of factors concerning the root matt. At MAR, the roots became inhospitable to aquatic arthropods by the presence of the noxious alga, *Lynbya* sp., which is known to produce secondary metabolites that are toxic to many animals, including invertebrates (Berry *et al.* 2004). *Lynbya* sp. was first observed at MAR in July of 2005, and a drop in arthropod abundance coincided with this event. Arthropod numbers remained low and *Lynbya* sp. remained present through December 2005. With colder water temperatures, the alga receded, and arthropod numbers resurged in January 2006.

Herbicide applications in Back River Reservoir did not appear to affect species richness of arthropods adversely. Even though arthropod abundance was reduced among the stunted roots, richness remained high (Figure 3.1). In fact, BRR produced more species than any other site. Arthropod species richness likely was enhanced by herbicide applications because water-hyacinth rafts were prevented from growing expansively and dominating the reservoir, displacing other macrophytes, and depleting oxygen from the water column.

Lentic and lotic sites contained similar arthropod abundances and diversities. Even though the community composition varied among all sites, most species collected were typical of lentic-littoral or lotic-depositional habitats, as indicated by Merritt *et al.* (2007). Also, the percent functional feeding groups of both flow regimes were similar, not changing in relative percentages from one flow regime to the other. In both situations, predators are the most speciose, followed by the collectors-gatherers, herbivores, and collectors-filterers respectively. This suggests that microhabitats within water-hyacinth rafts are similar in both lentic and lotic systems. In water-hyacinth rafts, flow rates are reduced, detritus and sediments are deposited, and oxygen concentrations are depressed. This combination of environmental conditions is consistent across water-hyacinth rafts despite the physical characteristics of the surrounding waterway. In turn, arthropods that live among water-hyacinth plants are suited for life in typically lentic conditions despite the physical characteristics of the surrounding waterway.

The physical conditions that tidal systems impose on water-hyacinth rafts directly affect the abundance and species richness of arthropods that live among these plants. Community assemblages were composed of fewer aquatic species and more terrestrial species, especially carabid and staphylinid beetles. Where rafts were frequently stranded above water by receding tides, aquatic arthropods abandoned the refuge of the roots. Some remained but they risked suffocation and dehydration and were exposed to terrestrial predators such as carabid and staphylinid beetles. On the other hand, the phytophagus arthropods that actually fed on water-hyacinth rafts or other plants contained therein were not affected by the tides to such a degree. These arthropods remained on the plants as long as the plants remained healthy, as evidenced by the increase in the percent herbivores, the retention of the same species, and the statistically similar abundances of water-hyacinth weevils in tidal rafts relative to lentic and lotic rafts.

Neochetina **spp. and Other Injurious Arthropods**

Water-hyacinth plants in South Carolina are fed on by several arthropods, as indicated by the variety of feeding scars observed. Pierce wounds were present, indicating that hemipteroid insects and mites were feeding on the plants. Also, leaves were shredded, skeletonized, and bored by the feeding of coleopterans, orthopterans, and lepidopterans. The following arthropods were observed actively feeding on water-hyacinth plants, *Orthogalumna terebrantis* Wallwork (Acari: Galumnidae), *Tetranychus tumidus* Banks (Acari: Tetranychidae), the aphid *Rhopalosiphum nympheae* (L.) (Hemiptera: Aphidae), one unidentified cicadellid (Hemiptera: Cicadellidae), and an unidentified katydid (Tettigoniidae: Conocephalinae). Two lepidopterans, the water-hyacinth moth *Niphograpta albiguttalis* and the pickerelweed moth *Bellura densa* (Walker), were found boring in water-hyacinth petioles, although neither of these caterpillars was collected at the sample locations. Another lepidopteran, the waterlilly leaf-cutter *Synclita obliteralis* Walker, used water-hyacinth leaves to build its portable case. Its activity formed numerous rectangular notches along the leaf margins. One other insect, the Japanese beetle *Popillia japonica* Newman, was not collected at the study sites but was observed shredding the leaves of adjacent plants. Two arthropods were feeding in water-hyacinth petioles below the water surface, including the amphipod *Hyalella azteca* and the midges *Glyptotendipes* spp. These species were feeding only in aged, dying leaves in galleries formed by the boring of *Neochetina* larvae. These arthropods were opportunistically feeding where damage had occurred previously. Although this study was not designed to determine the relative efficacy of the arthropods that feed on water-hyacinth, observations of the amount of feeding damage and the sheer number of individuals suggest that the water-hyacinth weevils, *Neochetina eichhorniae* and *N. bruchi*, were the most injurious arthropods feeding on water-hyacinth plants in South Carolina. Every raft studied contained these weevils, both larvae and adults were present, and almost every plant was scarred by their activity.

Although many *Neochetina* researchers have questioned the ability of the water-hyacinth weevils to disperse by flight, Center *et al.* (2002) have observed them flying to lights in southern Florida. Like the earliest studies, I never observed water-hyacinth weevils flying, or even separating their elytra. Most of the weevils were covered with a thick layer of waxy scales that sealed the elytral suture and prevented separation of the elytra. These weevils appeared incapable of flight. Nevertheless, the weevils in South Carolina likely fly at some point during their adult lives because they have successfully immigrated into South Carolina, colonized distant freshwater ecosystem throughout the Coastal Plain, and dispersed to every raft surveyed.

Water-hyacinth weevils were dispersed throughout the study area, but their population densities varied among sites. The abundances of water-hyacinth weevils were similar at all sites except for Goose Creek Reservoir, where it was significantly greater than at all other sites. At this site, the great abundance of weevils was mirrored by the relatively high abundance of all other arthropods at that site, suggesting that the condition(s) that contributed to the high numbers of weevils also contributed to the large quantity of arthropods in general. Center and Dray (1992) and Moran (2004) have shown that plant quality affects the population density and feeding activity of water-hyacinth weevils. Using population density of water-hyacinth weevils as a measure of plant vigor, I show that the factors that contribute to increased plant quality and high population densities of water-hyacinth weevils also contribute to increased population densities of other aquatic arthropods. Also, this trend is evidenced in Back River Reservoir where reduction of plant vigor by herbicide application resulted in reduced arthropod abundances. In other words, the abundance of arthropods in water-hyacinth rafts is influenced by the health of the plants themselves.

Water-hyacinth weevils overwinter primarily as adults in South Carolina's water-hyacinth rafts even though the portions of the plants (lamellae and petioles) where the adults normally feed and deposit eggs are killed by freezing air temperatures. To overcome the loss of their typical food source, the water-hyacinth weevils displayed behavior that enabled their survival through the coldest months of the year. During the winter months, I observed weevils feeding at the base of the petioles below the water surface where the plants remained alive. Often, many weevils congregated and remained below the water surface, only climbing above the surface during the warmest parts of the day. The weevils were able to survive long periods below the water surface. The weevils were lethargic in the winter months and moved little except when agitated. Also, the weevils halted egg-laying mainly because the petioles, where they normally deposit their eggs, had been killed by freezes. As a result, weevil larvae declined in number as the winter progressed. Only the oldest, last-instar larvae were collected in the winter months, and their numbers declined as the winter progressed. These eldest larvae were able to survive the winter freezes only because they had bored down to the petiole bases and mainstem below the water surface before freezing temperatures killed the emergent portions of the plants.

Conclusions

Water-hyacinth is a persistent invader of waterways in South Carolina’s Coastal Plain and will be an influential member of these ecosystems for years to come. While this plant is not native to South Carolina, it is inhabited by numerous arthropods and is consumed by native and imported species. Attributable to periodic winter freezes, advances in chemical control, and the feeding of the water-hyacinth weevils, water-hyacinth is prevented from negatively impacting the communities of aquatic arthropods in South Carolina waterways, and in its current state water-hyacinth serves as substrate for a diverse and abundant arthropod community. Considering that the community composition of aquatic arthropods is indicative of the general health of aquatic systems (Lenat 1993), water-hyacinth in its currently managed state does not appear to contribute greatly to the detriment of the water quality in these systems, as indicated by the large abundance and great species richness of invertebrates living therein, not withstanding the potential of water-hyacinth to impact these systems negatively. Rather, limited growth of this problematic weed in South Carolina has maintained the biological integrity of South Carolina’s waterways.

The arthropod communities that are resident to water-hyacinth rafts in South Carolina vary from site to site, but the communities in both lentic and lotic systems are similar. When the plant was removed from the water by receding tides, the arthropod community changed. Also, when water-hyacinth rafts were infiltrated by biological stressors such as *Lynbya* sp. or when plant vigor was reduced by the application of chemical herbicides, the arthropod community changed significantly.

In the mildly temperate climate of the Atlantic Coastal Plain in South Carolina, water-hyacinth persists as a perennial herb by the warmth of the water. Many aquatic and subaquatic arthropods take advantage of the year-round habitat provided, and the arthropods that live among the plant bases and roots are not greatly impacted by the physical stresses that freezing temperatures impart on the crown of the plant. Even the water-hyacinth weevils, *Neochetina eichhorniae* and *N. bruchi*, that were imported from the tropics in South America into the Unites States to control water-hyacinth have dispersed to and throughout South Carolina and have become established in water-hyacinth plants throughout the plant’s range in the state. The water-hyacinth weevils, like the plant and its arthropod community, survive the coldest part of the year by the warmth of the water and are established residents throughout the year even though their reproduction is interrupted by the death of the emergent parts of the plant each winter.

Water-hyacinth is a complex organism which has profound influences on the dynamics of freshwater ecosystems, not the least of which is the provision of suitable habitat to a great abundance and species richness of arthropods. Even outside of its native range, water-hyacinth rafts are home to animals endemic to the invaded waterway. Where plant populations are prevented from expanding and dominating freshwater ecosystems, arthropod communities thrive. By harboring so many arthropods, water-hyacinth has a profound influence on biological processes in freshwater ecosystems, even where water-hyacinth populations are prevented from dominating those systems.

CHAPTER FIVE

DESCRIPTIONS OF THE LAST INSTAR LARVAE OF *NEOCHETINA EICHHORNIAE* AND *N. BRUCHI* (COLEOPTERA: CURCULIONIDAE), WITH NOTES ON THEIR EARLIER INSTARS

Abstract

Larvae of the water-hyacinth weevils, *Neochetina eichhorniae* Warner and *N. bruchi* Hustache (Coleoptera: Curculionidae), are described and illustrated. Fifty larvae and twelve puparia of the water-hyacinth weevils were collected from water-hyacinth plants in Cooper and Pee Dee Rivers in the Coastal Plain of South Carolina, USA. Their cuticular morphology is described and illustrated for discrimination of these species. Illustrations are provided for the entire body, head capsule, mouthparts, spiracles, and cuticular microsculpture. The mouthparts and caudal spine-like spiracles, as well as microsculpture and chaetotaxy of the body, are specialized for boring through water-hyacinth petioles and stems. Chaetotaxy and overall shape and size are similar for the two species. Though the epipharynx is similar in both species, it is complex and likely provides characters for separating larvae of the water-hyacinth weevils from those of other *Neochetina* species and other Curculionidae. The larvae of the two water-hyacinth weevils are similar, but they can be distinguished from each other by the color of the head capsule, the presence or absence of ventral peg-like tubercles, and the relative sizes of the caudal spine-like spiracles.

Keywords

insect, beetle, invasive species, biocontrol, nonindigenous species, weed

Introduction

Water-hyacinth, *Eichhornia crassipes* (Mart.) Solms-Laub., rapidly became a problematic weed in the southern United States, following its importation from South America and its release in Louisiana in 1884. The plant continues to limit use of freshwater resources throughout the southern United States and in the tropics worldwide (Center *et al*. 2002). In an attempt to slow the plant's expansion, water-hyacinth weevils were imported from Argentina and released in the United States. The mottled water-hyacinth weevil, *Neochetina eichhorniae* Warner (Coleoptera: Curculionidae: Erirhininae), and its sister species, the chevronned water-hyacinth weevil, *N. bruchi* Hustache, were released first in 1972 in Florida and subsequently re-released in other states, including California, Louisiana, and Texas (Center *et al.* 2002). The weevils have dispersed (Powell, unpublished) and likely inhabit water-hyacinth populations throughout the United States. More recently, other countries in Africa, Asia, Australia, and Europe have imported one or both of the weevil species. A complete list of countries containing one or both species of water-hyacinth weevils was compiled by Julien (2000) and is restated in Appendix A. Because interest in using the weevils to control water-hyacinth continues to grow throughout the world and because the likelihood that the weevils will be spread by humans is increasing, these beetles could colonize water-hyacinth populations worldwide.

Though the number of species of adult Curculionidae described from North America exceeds 3,000 (Johnson & Triplehorn 2005), few larvae, mostly agricultural or forest pests, have been described (Burke and Anderson 1976, Stehr 1991). Except for the well-known rice water weevil, *Lissorhoptrus oryzophilus* Kuschel, a pest of rice, the weevil larvae that inhabit freshwater habitats remain undescribed (Stehr 1991). Merritt et al. (2007) briefly discussed the weevils associated with freshwater habitats in North America, including water-hyacinth weevils, and provided a diagnostic key to genera of adults of some aquatic or semiaquatic weevils, but they did not address larvae. No keys to the genera or species of larvae of aquatic weevils exist. Association of the larvae with the host plant and adults on the same plant allows for the tentative identification of the larvae (Merritt et al. 2007); however, this information does not help distinguish larvae of two or more species inhabiting the same host.

Water-hyacinth weevils belong to the family Curculionidae, subfamily Erirhininae, and genus *Neochetina*. Though systematic consensus now considers the Erirhininae to be a distinct family (Erirhinidae) in the superfamily Curculionoidea (ITIS 2007), the genus *Neochetina* is regarded herein as a member of the Erirhininae, a subfamily in the family Curculionidae. Like most Erirhininae weevils, the water-hyacinth weevils can be found in any life stage on their host plants, which are typically aquatic macrophytes. This specificity has made many of the Erirhininae weevils candidates for biological control of problematic aquatic plants.

Water-hyacinth weevils have similar habits and typically feed and reproduce on the same plant. An adult female chews a hole in the leaf petiole and deposits a single egg (*N. eichhorniae*) or a cluster of eggs (*N. bruchi*). *Neochetina eichhorniae* tends to deposit eggs in the long, relatively narrow petioles of intermediate-aged leaves (Center 1987), whereas *N. bruchi* tends to deposit eggs in the inflated petioles of peripheral leaves (DeLoach and Cordo 1976). Larvae hatch in seven to ten days and begin burrowing to the meristematic tissue in the main stem. Larvae pass through three instars before pupating. Following the molt to the third-instar larva, approximately 30 days for *N. eichhorniae* and 45 days for *N. bruchi* after eclosion, each larva chews its way out of the plant and climbs down the rootstalks, below the water surface. It builds a silken puparium covered in secondary rootlets and attached to a primary rootstalk below the water surface. The adult emerges about one week later and climbs to the emergent portions of the plant to feed and reproduce (DeLoach and Cordo 1976).

Most larvae of the Curculionidae can be identified only by using a combination of morphological characters and host-plant information (Stehr 1991). Host-plant information is useful for the species identification of many weevil larvae because weevils tend to specialize on particular species or taxonomic groups of plants. For example, all *Neochetina* species feed only on plants in the family Pontederiaceae. Host-plant information is of little or no diagnostic value when two species occupy the same host plant and have similar life habits, as is the case with *N. eichhorniae* and *N. bruchi*. Because these weevils are economically important for their role in controlling water-hyacinth populations worldwide, researchers will need to distinguish the larvae of *N. eichhorniae* from those of *N. bruchi* and from each other and from the other *Neochetina* species. Morphological differences might provide means for rapid separation of the larvae of *N. eichhorniae* from *N. bruchi* and from the other *Neochetina* larvae. Along with general body form, the structure of the mouthparts (labrum, mandibles, maxillae, and labium) and the chaetotaxy of the head and body have been used to describe and identify larval Curculionidae (Barrett 1930, Anderson 1947, Stehr 1991).

The adult water-hyacinth weevils have been described in detail and can be distinguished by external and reproductive morphology. O'Brien (1976) provided detailed descriptions and a key to the adults of *Neochetina* species; however, there are no diagnostic characters published for distinguishing the species of *Neochetina* larvae.

The objective of my study is to describe the cuticular morphology of the larvae of the water-hyacinth weevils, *Neochetina eichhorniae* and *N. bruchi*, to determine and illustrate characters useful for consistent separation of these species.

Materials and Methods

Twelve puparia and fifty larvae were collected from the roots of water-hyacinth plants from the Samworth Wildlife Management Area on the Pee Dee River, Georgetown County, South Carolina, USA, on 28 May 2005 and from Goose Creek Reservoir, Berkeley County, South Carolina, USA, on 29 May 2005. The larvae and puparia were fixed in 80% ethanol, transported to Clemson University, and dissected. The pre-emergent adults and their shed larval cuticles were removed. The larvae were associated with the adults, using a method similar to the metamorphotype method described by Milne (1938), in which pharate adults inside pupal exuviae are collected in the same puparium as shed larval sclerites. Adults were identified using characters described by O’Brien (1976). The last larval cuticle was soaked in lactic acid at ambient temperature for ten minutes. The cuticle was then washed in 80% ethanol and dried in 100% ethanol. The cuticle was slide mounted ventral side up using PVA mounting medium. Illustrations were drawn for the head capsule, mouthparts, cuticular microsculpture, and spiracles. The fifty additional larvae were identified to species, using the tentative diagnostic characters from the dissected puparia. The characters were confirmed by their consistent correlation in these larvae, segregating the larvae into two groups unequivocally, without intermediates or other character combinations. The larvae in the two groups were then each measured and representatives were illustrated. In the following description, the terminology of Stehr (1991) is used. The puparia, pre-emergent adults, slide-mounted cuticles, and additional larvae are deposited in the Clemson University Arthropod Collection, Clemson University, Clemson, SC.

Results (Descriptions)

Neochetina eichhorniae **Warner** (third-instar larva)

Body (Fig. 1): Length 10.6 – 15.2 mm, max body diameter: 2.1 – 2.45 mm (N = 28).

Head (Fig. 3): hypognathous; elliptical to almost spherical; rugose, rufous, and well sclerotized; height (distance from clypeal margin to vertex) 0.72 - 0.74 mm; greatest width 0.73 - 0.75 mm; setae arranged in regular bilateral pattern; epicranial suture (ecs) as long as frontal sutures (frs); endocarina contiguous with base of epicranial suture; frons fused with clypeus; frontoclypeus (fcl) triangular; antennae short, one-segmented, projecting anterad from beneath lateral corners of frontoclypeus. Two pairs of stemmata present, larger pair located in antero-lateral corners of parietal sclerites, smaller pair more posterior and medial.

Labrum and *Epipharynx* (Fig. 4): labrum (lbr) limuloid and stalked basally with two pairs of submedian, hair-like dorsal setae (ds). Epipharyngeal apex bearing four, blunt anteromedian setae (ams) of subequal size and shape bordered by pair of longer, sharper, lateral anteromedian setae (lams); lateral margins of epipharynx each with three large, sickle-like lateral setae (ls) on each side; median epipharynx with dense, complex brush (epipharyngeal brush) of long and short spines directed anteromesad, epipharyngeal brush (epb) bordered by four large, blunt median setae (ms) directed anterad; labral rods obscured by epipharyngeal brush.

Mandibles (Fig. 6): Mandibles symmetrical, bifid, heavily sclerotized and subquadrate; apicoventral tooth truncate with two smaller, subapical accessory teeth (at) and concave, rugose cutting edge (cut); apicodorsal tooth (db) as long as apicoventral tooth, rounded apically; prostheca and mola absent; five sensory pegs ventrally, lateral setae absent.

Maxillae (Fig. 5): Each with cardo membranous, simple and subquadrate. Stipes well sclerotized, longer than wide, with one long seta on lateral margin and two long setae ventrally; Stipes expanded anteromedially into hemispherical lobe, medial margin with seven long, blade-like setae (ms), six aligned along margin, projecting apicomesad and one inserted slightly dorsally and projecting dorsomesad; apical mala small and blunt; palpus (pa) two-segmented and projecting beyond stipes by length of apical segment.

Labium (Fig. 7): Mostly membranous. Ligula absent. Premental sclerite (pms) trident-shaped but divided by membranous areas into median longitudinal, spatulate rod (mls) and two lateral longitudinal arches (lls). Base of prementum and apex of postmentum covered in fine asperities; apex of prementum entirely membranous with two longitudinal rows of four setae each. Palpi (pal) each two-segmented.

Thorax (Fig. 1): White, mostly membranous, and lacking articulated appendages. Pronotum (pn) transversely cribiform and well sclerotized; small, triangular sclerite present below prothoracic spiracle. Meso- and metathoraces each with dorsal and ventral, transverse creeping welts, each bearing row of hair-like setae and dense spinules (Fig. 11). Prothoracic spiracles (Fig. 10) present, meso- and metathoracic spiracles absent.

Abdomen (Fig. 1): Ten-segmented. Lateral spiracles (Fig 10, ls) present on first six segments and subequal in size and shape, spiracles absent from segment VII, spiracles of segment VIII modified into eversible spines (css), paired dorsally, frequently retracted in membranous fold. Segments I - VI each with three annulations, posterior annulation expanded into dorsal and ventral transverse creeping welts; welts each with row of hair-like setae and dense spinules (Fig. 11a-d), each ventral hair-like seta curved caudad at apex. Terminus truncate, composed of segments VIII, IX, and X; segments IX and X located below midline and reduced to rings around anus; anus margined by numerous, long hair-like setae; terminus with scattered hair-like setae and dense spinules (Fig. 11a,b).

Caudal Spine-like Spiracles (Fig. 8): Contiguous dorsally, projecting dorsocaudad from membranous fold at dorsum of terminus, eversible; total length 0.21 - 0.24 mm; two-segmented; apical segment shorter than base, length 0.090 - 0.096 mm; each pre-spiracular seta more than half as long as apical segment of its respective spine-like spiracle.

Neochetina bruchi **Hustache** (third instar larva)

Body (Fig. 2): Length 11.2 – 16.6 mm, max body diameter: 2.2 – 2.56 mm (N = 22).

Head (Fig. 3): As described for *N. eichhorniae* except color yellow; height 0.73 – 0.75 mm; greatest width 0.74 – 0.76 mm.

Labrum and *Epipharynx* (Fig. 4): As for *N. eichhorniae.*

Mandible (Fig. 6): As for *N. eichhorniae.*

Maxillae (Fig. 5): As for *N. eichhorniae.*

Labium (Fig. 7): As for *N. eichhorniae.*

Thorax (Fig. 2): As for *N. eichhorniae* except each segment with ventral creeping welt bearing two pairs of peg-like protuberances (*plp*, Fig. 2) from which ventral setae arise.

Abdomen (Fig. 2): As for *N. eichhorniae* except segments I - VI each with ventral creeping welt bearing two pairs of peg-like protuberances from which ventral setae arise. *Caudal Spine-like Spiracles* (Fig. 9): Contiguous dorsally, projecting dorsocaudad from membranous fold at dorsum of terminus; total length 0.29 - 0.31 mm; two-segmented; apical segment as long as or longer than base, length 0.15 - 0.16 mm; pre-spiracular setae each less than half as long as apical segment of its respective spiracle.

Notes on Earlier Instar Larvae

First- and second-instar larvae, though comparably smaller, resemble the third instar with a few distinct exceptions. For both *N. eichhorniae* and *N. bruchi*, the first two instars possess ventral hair-like setae that are extremely long relative to their respective body segments. While third-instar larvae have ventral setae that may be only as long as one-tenth the maximum diameter of their respective segments, first- and second- instar larvae have ventral setae that may be as long as one half the maximum diameter of their respective segments.

First and second instars also show a greater disparity in the relative lengths of their caudal spine-like spiracles. In *N. eichhorniae*, the apical segment of each caudal spine-like spiracle is longer relative to its base than in the third instar. Each apical segment may be as long as or slightly longer than its base. In *N. bruchi*, the disparity is even greater, with the apical segment of the caudal spine-like spiracle being four to seven times the length of its base. Although the caudal spine-like spiracles seem to change through successive instars, the head capsule tends to remain darker in *N. eichhorniae*, and the ventral peg-like protuberances remain present in *N. bruchi* and absent from *N. eichhorniae* through all instars, allowing for separation of the two species even in early instars.

(Material Examined) Twelve slide-mounted, sets of last instar larval cuticles collected from inhabited puparia. Fifty larvae representing all three larval instars fixed in 80% ethanol. The twelve puparia and 50 larvae were collected from water-hyacinth plants either in the Pee Dee River at the Samworth Wildlife Management Area, Georgetown County, South Carolina, USA, on 28 May 2004 or in Goose Creek Reservoir, Berkeley County, South Carolina, USA, on 29 May 2005. Twenty-eight larvae and six puparia were of *Neochetina eichhorniae*, while twenty-two larvae and six puparia were of *N. bruchi*. The slides, puparia, pre-emergent adults, and larvae are deposited in the Clemson University Arthropod Collection.

Diagnosis

Though the larvae of the water-hyacinth weevils *Neochetina eichhorniae* and *N. bruchi* have similar life habits, each possesses unique morphological characters. *Neochetina eichhorniae* larvae have head capsules that are slightly darker in color than those of *N. bruchi*; however, this character is variable and is of little use with larvae that have recently molted or are not side by side for comparison. *Neochetina bruchi* have two pairs of peg-like tubercles on each of the ventral creeping welts, a character that is lacking in *N. eichhorniae* larvae. This character is consistent through all larval instars but may be distorted or hidden from view by the method of fixation or the hydrostatic condition of each individual. The most consistent character for discriminating larvae of *N. eichhorniae* from those of *N. bruchi* is the relative sizes of the segments of the caudal spine-like spiracles. Each caudal spine-like spiracle of the *Neochetina eichhorniae* larva has an apical segment that is less than half the length of its basal segment (0.35-0.45x) and less than twice as long as each pre-spiracular seta. The caudal spine-like spiracles of *N. bruchi* larva are typically longer than those of *N. eichhorniae* and each possesses an apical segment that is equal to or longer than half the length of its basal segment (0.50-0.60x) and longer than twice the length of each pre-spiracular seta.

The difference in spiracular structure between *N. eichhorniae* and *N. bruchi* may be adaptive for the regions of the plant that each species inhabits. Because these boring insects puncture the air-filled vacuoles of adjacent plant cells to exchange gases, the length of the spines might depend on the size of the surrounding plant cells. *Neochetina eichhorniae* larvae begin development in intermediate-aged petioles where plant cells are narrower than the plant cells of the inflated petioles at the plant periphery where *N. bruchi* begins development. The inflated petioles provide buoyancy for the rest of the plant; thus inflated petioles are composed mostly of large cells filled with large, air-filled vacuoles. The longer spine-like spiracles of *N. bruchi* might be necessary for the larvae to puncture the larger cells of inflated petioles. This hypothesis is supported by the observation that early instars display an even greater disparity between the relative lengths of the spine-like spiracles than do the ultimate instars that are preparing to exit the plant for pupation.

Aside from this work, no diagnostic works have been published on the larvae of *Neochetina* weevils. No other larvae of Neochetina species have been described, preventing the accurate discrimination of *N. eichhorniae* or *N. bruchi* from their congeners without host data. The complexity of the epipharynx might provide key characters for distinguishing larvae of the water-hyacinth weevils from other *Neochetina* larvae and from those of other larval Curculionidae, as it has for many other weevil larvae (Anderson 1947). The shape of the tripartite premental sclerite (medial rod and lateral arches) might be useful for distinguishing *Neochetina* larvae from other Curculionidae larvae because most have an undivided, trident-shaped premental sclerite (Stehr, 1991). Although chaetotaxy provides little information for separating *N. eichhorniae* from *N. bruchi*, it may provide a means for separating the water-hyacinth weevils from their congeners and from other curculionid larvae. Another feature that might facilitate identification of *Neochetina* larvae to species and distinguish them from other erirhininae weevils is the structure of the spiracles, which appear to be highly modified in the Erirhininae weevils (Zhang *et al.* 2006). Until the other *Neochetina* larvae are described, a key cannot be produced for their segregation at the species level or from other genera.

Biogeographical Range

Endemic to South America (Argentina, Bolivia, Brazil, Ecuador, Guyana, Paraguay). Imported into Australia, Africa, Southeast Asia, Central America, and North America and Caribbean Islands. Full list of countries that have imported at least one of the water-hyacinth weevils is listed below with year first introduced (Julien *et al.* 2000). Australia (1971), Benin (1991), China (1996), Congo (1999), Cuba (1995), Egypt (2000), Fiji (1977), Ghana (1994), Honduras (1989), India (1983), Indonesia (1979), Kenya (1993), Malawi (1995), Malaysia (1983), Mexico (1972), Mozambique (1972), Myanmar (1980), Nigeria (1993), Panama (1977), Philippines (1992), PNG (1986), Rwanda (2000), Solomon Islands (1988), South Africa (1974), Sri Lanka (1988), Sudan (1978), Taiwan (1992), Tanzania (1995), Thailand (1979), Uganda (1993), USA (1972), Vietnam (1984), Zambia (1971), Zimbabwe (1971).

Acknowledgements

I give gratitude to Dr. John C. Morse, Clemson University, for his guidance through the preparation of this chapter and with insect taxonomy in general. I give thanks also to Dr. Peter Adler, Clemson University, and Dr. Alfred Wheeler, Clemson University, for reviewing this chapter and to Dr. Ted Center for providing me with literature.

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APPENDICES

Appendix A

Tables

Table 1. Arthropod Master Inventory

Feed	Order	Family	Genus	Species	BRR	GCR	MAR	QCW	PDW	QCL	PDL	1° Collection
pred	Amphipoda	Corophiidae	*Corophium*	sp					+			PDW 27-xii-05
cg		Crangonyctidae	*Crangonyx*	*serratus* Embody	+	+	+	+	+			BRR 2-iii-05
cg		Gammaridae	*Gammarus*	*fasciatus* Say	+		+		+		+	PDW 2-iii-05
herb		Hyalellidae	*Hyalella*	*azteca* Saussure	+	+	+	+	+	+	+	GCR 18-iv-05
cg	Isopoda	Asellidae	*Caecidotea*	*communis* (Say)	+	+	+	+				GCR 18-iv-05
cg			*C.*	*racovitzai* (Williams)	+	+			+			PDW 4-xi-05
cg			*Lirceus*	*lineatus* (Say)	+		+		+			MAR 22-i-06
cg		Sphaeromatidae	*Sphaeroma*	sp				+	+			PDW 2-ix-05
cg	Decapoda	Cambaridae	*Procambarus*	*chacei Hobbs*		+	+	+	+			QCW 5-viii-05
cg		Palaemonidae	*Palaemonetes*	sp			+					MAR 12-v-05
?	Coleoptera	Anthicidae	*Ischyropalpus*	sp	+							BRR 2-iii-05
detr		Bostrichidae	*Lyctus*	sp		+						GCR 1-vi-05
pred		Cantharidae	gen	sp				+		+		QCL 15-x-05
pred		Carabidae	*Bradycellus*	*tantillus* Dejean							+	PDL 25-ii-06
pred			*Elaphropus*	*granarius* Dejean							+	PDL 25-ii-06
pred			*E.*	*xanthopus* Dejean							+	PDL 25-ii-06
pred			*Platynus*	*cincticollis* Say						+	+	QCL 26-xii-05
pred			*Polyderis*	*laevis* Say							+	PDL 22-i-06
pred			*Tachys*	*litoralis* Casey						+		QCL 2-xii-05
herb		Chrysomelidae	*Chaetocnema*	sp					+			PDW 1-vi-05
herb			*Glyptina*	sp							+	PDL 25-ii-06
herb			*Lysathia*	*ludoviciana* (Fall)	+	+	+	+		+		GCR 1-vi-05
herb			*Pseudolampsis*	*guttata* (LeConte)			+	+				MAR 12-v-05
pred		Coccinellidae	*Diomus*	sp							+	PDL 25-ii-06
pred			*Scymnus*	sp		+						GCR 8-x-05
?		Colydiidae	gen	sp				+				QCW 27-xii-05
herb		Curculionidae	*Lissorhoptrus*	sp						+		QCL 20-iv-05
herb			*Neochetina*	*bruchi* Hustache	+	+	+	+	+	+	+	GCR 2-iii-05
herb			*N.*	*eichhorniae* Warner	+	+	+	+	+	+	+	GCR 2-iii-05
herb			*Onychylis*	*alternans* LeConte	+			+	+	+	+	BRR 20-iv-05
herb			*O.*	*nigrirostris* Boheman		+	+		+	+	+	QCW 20-iv-05
herb			*Perigaster*	*cretura* (Herbst)	+					+		QCL 21-vi-05
herb			*Stenopelmis*	*rufinasus* Gyllenhal	+	+	+	+	+	+	+	PDW 19-iv-05
herb			*Tanysphyrus*	*lemnae* (Paykull)	+		+		+		+	BRR 20-iv-05
pred		Dytiscidae	*Bidessonotus*	*pulicarius* (Aube)				+				QCW 8-x-05

Feed	Order	Family	Genus	Species	BRR	GCR	MAR	QCW	PDW	QCL	PDL	1° Collection
pred			*Celina*	*imitatrix* Young					+			PDW 1-vi-05
pred			*Copelatus*	caelatipennis principes Young					+			PDW 1-vi-05
pred			*C.*	*glyphicus* (Say)				+				QCW 5-xi-05
pred			*C.*	*punctulatus* Aubé	+							BRR 22-i-06
pred			*Cybister*	*fimbriolatus* (Say)		+	+		+			GCR 18-iv-05
pred			*Desmopachria*	*convexa* (Aubé)	+							BRR 25-ii-06
pred			*Hydrovatus*	*pustulatus compressus* Sharp	+	+	+	+	+	+	+	GCR 2-iii-05
pred			*Laccodytes*	*pumilio* (LeConte)				+				QCW 21-i-06
pred			*Laccophilus*	*gentilis gentilis* LeConte				+				QCW 21-i-06
pred			*Liodessus*	*noviaffinis* Miller	+							BRR 25-ii-06
pred			*Neoporus*	*clypealis* (Sharp)			+					MAR 26-ii-06
herb		Elateridae	gen	sp				+				QCW 21-vi-05
cg		Elmidae	*Macronychus*	*glabratus* Say			+					MAR 2-iii-05
cg			*Stenelmis*	*antennalis* Sanderson			+					MAR 6-xi-05
cg			*S.*	*fuscata* Blatchley							+	PDL 25-ii-06
cg			*S.*	*lignicola* Schmude & Brown			+					MAR 31-v-05
herb		Haliplidae	*Haliplus*	*leopardus* Roberts					+			PDW 1-vi-05
herb			*H.*	*triopsis* Say					+			PDW 21-vi-05
herb			*Peltodytes*	*floridensis* Matheson	+							BRR 31-v-05
herb			*P.*	*sexmaculatus* Roberts	+							BRR 31-v-05
cg		Hydraenidae	*Hydraena*	*pennsylvanica* Kiessenwetter		+						GCR 27-xi-05
herb		Hydrochidae	*Hydrochus*	*simplex* LeConte	+	+						BRR 25-ii-06
cg		Hydrophilidae	*Berosus*	*exiguus* Say					+			PDW 1-vi-05
cg			*B.*	*infuscatus* LeConte	+			+	+			QCW 19-iv-05
cg			*Derallus*	*altus* (LeConte)		+	+				+	GCR 2-iii-05
cg			*Dibolocelus*	*ovatus* (Gemminger & Harold)					+			PDW 1-vi-05
herb			*Enochrus*	*blatchleyi* (Fall)			+					MAR 3-ix-05
herb			*E.*	*ochraceus* (Melsheimer)	+					+		QCW 21-vi-05
herb			*E.*	*pygmaeus* (Fabricius)	+	+	+	+	+			GCR 8-x-05
herb		Hydrophilidae (cont.)	*E.*	*sayi* Gunderson			+			+		QCL 15-x-05
cg			*Hydrobiomorpha*	*castus* (Say)	+							BRR 2-iii-05
cg			*Paracymus*	*nanus* (Fall)		+						GCR 21-i-06
cg			*Phaenonotum*	exstriatum (Say)	+					+	+	BRR 2-iii-05
cg			*Tropisternus*	*lateralis nimbatus* (Fabricius)					+			PDW 1-vi-05
cg			*T.*	*notator* Orchymont	+				+			BRR 20-iv-05
pred		Lampyridae	gen	sp	+	+		+		+		BRR 2-iii-05
pred		Noteridae	*Hydrocanthus*	*oblongus* Sharp	+	+		+			+	QCW 19-iv-05
pred			*H.*	*regius* Young	+	+	+	+	+		+	GCR 8-x-05
pred			*Suphis*	*inflatus* (LeConte)	+	+	+		+		+	GCR 2-iii-05

Feed	Order	Family	Genus	Species	BRR	GCR	MAR	QCW	PDW	QCL	PDL	1° Collection
pred			*Suphisellus*	*gibbulus* (Aube)	+	+	+	+	+		+	GCR 2-iii-05
herb		Scirtidae	*Scirtes*	*ovalis* Blatchley	+	+	+	+	+			MAR 12-v-05
pred		Staphylinidae	*Brachygluta*	sp							+	PDL 15-x-05
pred			*Diochus*	*schaumi* Kraatz							+	PDL 25-ii-06
pred			*Ischnosoma*	sp			+					MAR 22-i-06
pred			*Reichenbachia*	sp							+	PDL 25-ii-06
pred			*Stenus*	sp	+	+	+	+	+	+	+	QCW 2-iii-05
?	Diptera	Anthomyiidae	gen	sp	+							BRR 20-iv-05
herb		Anthomyzidae	gen	sp		+		+				GCR 2-iii-05
herb		Cecidomyiidae	gen	sp						+		QCL 2-ix-05
pred		Ceratopogonidae	*Bezzia/Palpomyia*	sp	+	+	+	+	+			GCR 2-iii-05
pred			*Ceratopogon*	sp		+						GCR 2-iii-05
pred			*Mallochohelia*	sp		+	+	+	+	+		GCR 2-iii-05
pred			*Probezzia*	sp	+							BRR 31-v-05
pred			*Sphaeromyia*	*longipennis* (Loew)	+		+		+			BRR 20-iv-05
cg		Chironomidae	*(Chironomini) gen 3*	sp				+				QCW 31-v-05
pred			*Ablabesmyia*	sp (A)				+				QCW 26-xi-05
pred			*A.*	*idei* (Walley)	+	+	+		+			BRR 6-viii-05
pred			*A.*	*mallochi* (Walley)				+				QCW 8-x-05
pred			*A.*	*peleensis* (Walley)	+	+	+	+	+			BRR 20-iv-05
pred			*A.*	(ramphe group)	+		+	+	+			MAR 31-v-05
cg			*Apedilum*	*elachistum* (Townes)				+				QCW 2-iii-05
cg			*Bryophaenocladius*	sp				+				QCW 26-xi-05
cg			*Chironomus*	*longipes* Staeger		+		+	+			PDW 19-iv-05
cg			*C.*	*ochreatus* (Townes)			+					MAR 12-v-05
cg			*C.*	*stigmaterus* Say					+			PDW 19-iv-05
cg			*C.*	sp					+			PDW 1-vi-05
pred			*Clinotanypus*	sp					+			PDW 25-ii-06
cg			*Corynoneura*	sp (H)		+	+	+				GCR 2-iii-05
cg			*Cricotopus*	*bicinctus* Meigen	+			+	+			BRR 20-iv-05
cg			*C.*	*politus* (Coquillet)			+					MAR 3-ix-05
herb			*C.*	(sylvestris group)		+	+		+			GCR 2-iii-05
cg			*C.*	sp			+					MAR 31-v-05
pred			*Cryptochironomus*	sp			+					MAR 2-iii-05
cg			*Dicrotendipes*	*modestus* (Say)	+		+	+	+			MAR 2-iii-05
cg			*D.*	*nervosus* (Staeger)				+				QCW 5-xi-05
cg			*D.*	*tritomus* (Kieffer)	+			+	+			BRR 20-iv-05
cg			*D.*	*simpsoni* Epler			+					MAR 12-v-05

Feed	Order	Family	Genus	Species	BRR	GCR	MAR	QCW	PDW	QCL	PDL	1° Collection
cg			*D.*	sp		+						GCR 18-iv-05
cg			*Endochironomus*	*nigricans* (Johannsen)		+	+		+			GCR 2-iii-05
cg			*E.*	*subtendens* (Townes)			+					MAR 31-v-05
herb			*Endotribelos*	*hesperium* (Sublette)	+			+				QCW 2-iii-05
herb			*Glyptotendipes*	sp (B)	+		+	+				BRR 2-iii-05
herb			*G.*	*meridionalis* Dendy & Sublette		+	+					MAR 2-iii-05
cg			*Goeldichironomus*	sp		+						GCR 2-iii-05
pred			*Guttipelopia*	*guttipennis* (Wulp)		+						GCR 2-iii-05
cg			*Gymnometriocnemus*	sp				+				QCW 2-ix-05
cg			*Kiefferulus*	*dux* (Johannsen)		+						GCR 18-iv-05
cg			*K.*	*pungens* (Townes)		+	+		+			GCR 1-vi-05
pred			*Labrundinia*	*becki* Roback		+		+				GCR 21-i-06
pred			*L.*	*johannseni* Beck & Beck				+				QCW 2-ix-05
pred			*L.*	*neopilosella* Beck & Beck	+	+		+				GCR 2-iii-05
pred			*L.*	sp (A)					+			PDW 1-vi-05
pred			*L.*	*virescense* Beck & Beck				+				QCW 26-xi-05
pred			*Larsia*	*decolorata* (Malloch)		+	+					GCR 18-iv-05
pred			*L.*	sp (B)					+			PDW 1-vi-05
cg			*Limnophyes*	sp	+			+	+	+	+	BRR 2-iii-05
cg			*Microtendipes*	(pedellus group)				+				QCW 2-iii-05
cg			*Nanocladius*	*alternantherae* Dendy&Sublette	+	+	+	+	+			MAR 2-iii-05
cg			*N.*	(crassicornus/rectinervis)	+		+					MAR 3-ix-05
pred			*Nilotanypus*	sp		+						GCR 1-vi-05
cg			*Orthocladius*	*oliveri* Soponis	+		+					MAR 2-iii-05
cg			*Parachironomus*	*carinatus* (Townes)	+		+	+	+			MAR 12-v-05
cg			*P.*	*directus* (Dendy&Sublette)		+	+		+			GCR 18-iv-05
cg			*P.*	(tenuicaudatus group)	+	+						GCR 18-iv-05
cg			*Parakiefferiella*	sp					+			PDW 26-xi-05
pred			*Paramerinas*	sp	+							BRR 6-xi-05
cg			*Paratanytarsus*	sp (D)	+		+					BRR 27-xii-05
cg			*P.*	*dissimilis* (Johannsen)	+							BRR 7-x-05
cg			*P.*	(quadratus group)	+	+	+		+			MAR 12-v-05
cg			*Phaenopsectra*	(punctipes group)	+							BRR 2-iii-05
cg			*Polypedilum*	*beckae* (Sublette)			+					MAR 31-v-05
cg			*P.*	(illinoiensis group)	+	+	+	+	+	+	+	GCR 2-iii-05
cg			*Procladius*	sp	+				+			BRR 27-xii-05
cg			*Tanypus*	*carinatus* Sublette					+			PDW 25-ii-06
cg			*Tanytarsus*	sp			+					MAR 2-iii-05

Feed	Order	Family	Genus	Species	BRR	GCR	MAR	QCW	PDW	QCL	PDL	1° Collection
cg			*T.*	sp (C)				+				QCW 5-xi-05
cg			*T.*	sp (G)					+			PDW 1-vi-05
cg			*T.*	sp (F)		+	+		+			PDW 1-vi-05
cg			*T.*	sp (L)				+				QCW 5-xi-05
cg			*T.*	sp (N)			+					MAR 3-ix-05
cg			*Thienemanniella*	*lobapodema* Hestenes & Saether	+		+					BRR 27-xii-05
cg			*Tribelos*	*fuscicorne* (Malloch)					+			PDW 19-iv-05
pred			*Xenochironomus*	sp			+					MAR 12-v-05
cg			*Zavreliella*	*marmorata* (Wulp)		+		+				GCR. 3-ix-05
herb		Chloropidae	gen	sp		+	+		+			PDW 2-ix-05
cf		Culicidae	*Anopheles*	*bradleyi* (King)	+	+			+			GCR 8-x-05
cf			*A.*	*punctipennis* (Say)		+						GCR 18-iv-05
cf			*A.*	*quadrimaculatus* (Say)			+		+			MAR 31-v-05
cf			*Culex*	*salinarius* Coquillett		+						GCR 8-x-05
cf			*C.*	*tarsalis* Coquillett		+	+					MAR 31-v-05
cf			*Uranotaenia*	*sapphirina* (Osten Sacken)		+						GCR 27-xi-05
cg		Ephydridae	*Ephydra/Notophila*	sp	+							BRR 2-iii-05
herb			*Setacera*	sp			+					MAR 2-iii-05
cg		Otitidae	gen	sp	+							BRR 3-ix-05
cg		Psychodidae	*Psychoda*	*alternata* Say			+					MAR 2-iii-05
herb		Scathophagidae	gen	sp			+					MAR 3-ix-05
pred		Sciomyzidae	*Sepedon*	sp	+	+	+					MAR 12-v-05
cg		Sphaeroceridae	gen	sp		+						GCR 2-iii-05
herb		Stratiomyiidae	*Hedriodiscus*	sp		+						GCR 2-iii-05
cg			*Myxosargus*	sp		+						GCR 2-iii-05
cg			*Odontomyia*	sp		+	+	+	+			GCR 18-iv-05
cg		Syrphidae	gen	sp	+	+		+		+		BRR 3-ix-05
pred		Tabanidae	*Tabanus*	sp					+		+	PDL 22-i-06
cg		Tipulidae	*Erioptera*	sp	+					+		QCL 2-iii-05
cg			*Helius*	*flavipes* Macquart		+						GCR 21-i-06
herb			*Limonia*	sp			+					MAR 3-ix-05
cg	Ephemeroptera	Baetidae	*Callibaetis*	*floridanus* Banks	+	+	+	+	+			BRR 20-iv-05
cg			*C.*	*pretiosus* Banks				+	+			BRR 31-v-05
cg		Caenidae	*Caenis*	sp	+		+	+	+			BRR 20-iv-05
cg		Heptageniidae	*Maccarffertium*	*integrum* (MacDunnough)				+				QCW 2-ix-05
cg		Leptophlebiidae	*Leptophlebia*	sp				+				QCW 27-xii-05
pred	Hemiptera	Anthocoridae	*Lasiochilus*	(near *pallidula*)				+		+		QCL 26-xii-05
herb		Aphididae	*Rhopalosiphum*	*nymphaeae* (L.)	+	+	+	+	+	+	+	MAR 12-v-05
pred		Belostomatidae	*Belostoma*	*lutarium* (Stâl)	+	+	+	+	+			GCR 2-iii-05

Feed	Order	Family	Genus	Species	BRR	GCR	MAR	QCW	PDW	QCL	PDL	1˚ Collection
pred			*B.*	*testaceum* (Leidy)				+				QCW 19-iv-05
pred			*Lethocerus*	*uhleri* (Montandon)					+			PDW 1-vi-05
herb		Berytidae	*Jalysus*	sp			+					MAR 6-xi-05
herb		Cicadellidae	gen	sp 1	+	+	+	+	+	+	+	QCW 21-vi-05
herb			gen	sp 2						+		QCL 2-ix-05
herb			gen	sp 3						+		QCL 21-vi-05
pred		Corixidae	*Trichocorixa*	*calva* (Say)					+			PDW 1-vi-05
pred			*T.*	*sexcincta* (Champion)	+	+		+	+			BRR 20-iv-05
herb		Cydnidae	*Amnestus*	*pallidus* Zimmer			+					MAR 2-iii-05
herb		Delphacidae	*Megamelus*	sp	+	+	+	+	+	+	+	QCW 5-viii-05
pred		Gerridae	*Limnoporus*	*canaliculatus* (Say)			+	+				MAR 31-v-05
pred		Hebridae	*Hebrus*	*consolidus* Uhler		+						GCR 26-xii-05
pred			*Merragata*	*brunnea* Drake	+	+	+		+		+	PDW 1-vi-05
pred		Hydrometridae	*Hydrometra*	*martini* Kirkaldy	+		+	+				BRR 27-xi-05
pred		Mesoveliidae	*Mesovelia*	*mulsanti* White	+	+	+	+	+		+	PDW 19-v-05
pred		Naucoridae	*Pelocoris*	*balius* La Rivers	+			+				BRR 2-ii-05
pred			*P.*	*femoratus* (Palisot)	+	+	+	+	+			PDW 2-iii-05
pred		Nepidae	*Ranatra*	*australis* Hungerford			+	+	+			PDW 19-iv-05
herb		Ortheziidae	gen	sp	+							BRR 6-viii-05
pred		Pleidae	*Neoplea*	*striola* (Fieber)	+	+	+	+	+			GCR 2-iii-05
herb		Rhyparochromidae	*Pachybrachius*	*albocinctus* Barber	+					+		BRR 6-viii-05
herb			*Paromias*	sp						+		QCL 2-ix-05
herb			*Ptochiomera*	*nodosa* Say			+					MAR 2-iii-05
pred		Veliidae	*Microvelia*	*hinei* Drake		+						GCR 2-iii-05
pred			*M.*	*pulchella* Westwood			+		+		+	MAR 31-v-05
pred			*Platyvelia*	*brachialis* Stâl	+	+	+	+	+	+		QCW 19-iv-05
herb	Lepidoptera	Crambidae	*Munroessa*	*icciusalis* (Walker)	+							BRR 27-xii-05
herb			*Neargyractis*	*slossonalis* Dyar	+			+	+	+		QCW 2-iii-05
herb			*Parapoynx*	*maculalis* (Clemens)	+			+				QCW 31-v-05
herb			*Samea*	*multiplicalis* (Guenee)		+						GCR 3-ix-05
herb			*Synclita*	*obliteralis* (Walker)	+	+	+	+	+	+	+	GCR 2-iii-05
herb			*S.*	*tinealis* Munroe		+						GCR 18-iv-05
pred	Neuroptera	Corydalidae	*Chauliodes*	*pectinicornis* (L.)	+							BRR 25-ii-06
pred			*C.*	*rastricornis* Rambur			+		+			MAR 2-iii-05
pred		Sisyridae	*Climacia*	*areolaris* (Hagen)			+					MAR 4-viii-05
pred	Odonata	Aeshnidae	*Anax*	*junius* (Drury)	+	+		+				GCR 27-xi-05
pred			*Boyeria*	*grafiana* Williamson			+					MAR 4-viii-05
pred			*Coryphaeshna*	*ingens* (Rambur)	+	+		+				QCW 5-viii-05
pred		Coenagrionidae	*Enallagma*	*signatum* (Hagen)	+	+	+	+	+	+		GCR 2-iii-05

Feed	Order	Family	Genus	Species	BRR	GCR	MAR	QCW	PDW	QCL	PDL	1° Collection
pred			*E.*	*vesperum* Calvert	+							BRR 20-iv-05
pred			*Ischnura*	*posita* (Hagen)	+	+	+	+	+		+	GCR 2-iii-05
pred			*I.*	*ramburii* (Selys)	+	+						BRR 31-v-05
pred			*Nehalennia*	*irene* (Hagen)		+						GCR 2-iii-05
pred			*Telebasis*	*byersi* Westfall	+	+						BRR 20-iv-05
pred			*T.*	(near vulnerata)		+						GCR 6-viii-05
pred		Lestidae	*Lestes*	*inaequalis* Walsh				+				QCW 27-xii-05
pred			*L.*	*vigilax* Hagen		+						GCR 26-xii-05
pred		Libellulidae	*Epicordulia*	*princips* (Hagen)	+							BRR 27-xii-05
pred			*Erythemis*	*simplicocollis* (Say)	+	+	+	+	+	+	+	GCR 2-iii-05
pred			*Pachydiplax*	*longipennis* (Burmeister)	+	+	+	+	+	+		GCR 2-iii-05
pred			*Perithemis*	*tenera* (Say)		+						GCR 1-vi-05
pred			*Tetragoneuria*	*cynosura* (Say)	+			+				QCW 2-iii-05
herb	Orthoptera	Gryllidae (Trigoniinae)	*gen*	sp		+					+	GCR 1-vi-05
herb		Tettigoniidae (Conocephalinae)	*gen*	sp	+	+	+	+	+	+	+	GCR 1-vi-05
herb	Thysanoptera	Aeolothripidae	gen	sp					+			PDW 26-xi-05
herb		Phleothripidae	gen	sp				+				QCW 26-xi-05
herb		Thripidae	gen	sp				+				QCW 26-xi-05
herb	Trichoptera	Hydroptilidae	*Orthotrichia*	sp	+		+					BRR 6-xi-05
herb		Leptoceridae	*Leptocerus*	*americanus* (Banks)	+							BRR 3-ix-05
herb			*Oecetis*	*avara* (Banks)	+	+	+	+	+			QCW 19-iv-05
herb			*O.*	*cinarescens* (Hagen)	+							BRR 20-iv-05
herb			*O.*	(inconspicua *complex*)				+				QCW 8-x-05
herb			*Triaenodes*	*baris* Ross	+							BRR 2-iii-05
herb			*T.*	*ochraceus* (Betten & Mosely)	+			+				BRR 6-viii-05
detr		Limephilidae	*Hydatophylax*	*argus* (Harris)				+				QCW 27-xii-05
detr			*Ironoquia*	sp				+				QCW 27-xii-05
pred		Polycentropidae	*Cernotina*	*spicata* Ross	+		+					BRR 20-iv-05

Table 2. Pair-wise t-Tests of significance of arthropod abundances in water-hyacinth rafts and Fisher's Least Significant Difference among sites; BRR, Back River Reservoir; GCR, Goose Creek Reservoir; MAR, Lake Marion; PDW Pee Dee River lotic; QCW, Quinby Creek lotic; PDL, Pee Dee River tidal; QCL, Quinby Creek tidal;

	BRR	**GCR**	**MAR**	**PDW**	**QCW**	**PDL**	**QCL**	
BRR	1	<0.0001	0.3986	0.9091	0.6863	0.0093	0.0015	**Fisher's LSD**
GCR		1	0.0006	<0.0001	0.0001	<0.0001	<0.0001	56.6
MAR			1	0.3384	0.6586	0.0008	<0.0001	
PDW				1	0.6046	0.0126	0.0021	
QCW					1	0.0030	0.0004	
PDL						1	0.5238	
QCL							1	

Table 3. Pair-wise t-Tests of significance of arthropod species richnesses in water-hyacinth rafts and Fisher's Least Significant Difference among sites; BRR, Back River Reservoir; GCR, Goose Creek Reservoir; MAR, Lake Marion; PDW Pee Dee River lotic; QCW, Quinby Creek lotic; PDL, Pee Dee River tidal; QCL, Quinby Creek tidal

	BRR	**GCR**	**MAR**	**PDW**	**QCW**	**PDL**	**QCL**	
BRR	1	0.1555	1	0.0087	0.2523	<0.0001	<0.0001	**Fisher's LSD**
GCR		1	0.1555	0.0001	0.0117	<0.0001	<0.0001	5.91
MAR			1	0.0087	0.2523	<0.0001	<0.0001	
PDW				1	0.1261	<0.0001	<0.0001	
QCW					1	<0.0001	<0.0001	
PDL						1	0.8224	
QCL							1	

Appendix B

Figures (Graphs)

Figure 1.1: TAXA RICHNESS BY ORDER OF ARTHROPODS IN WATER-HYACINTH RAFTS

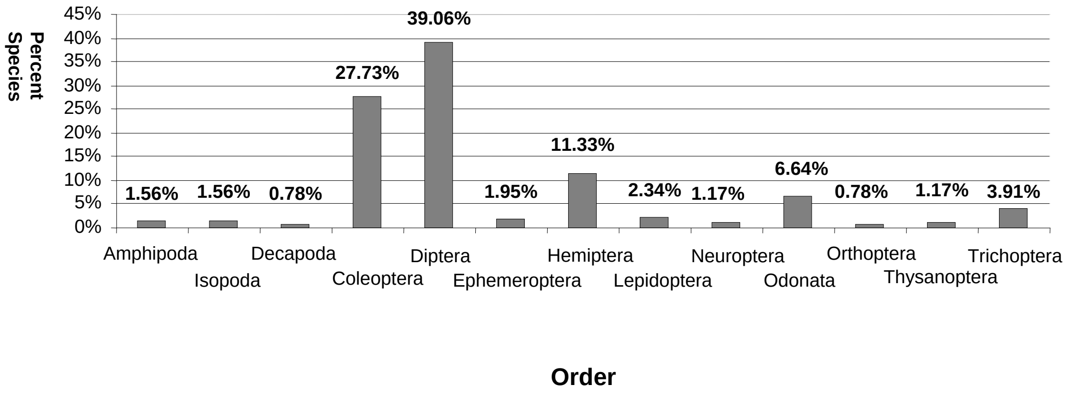


Figure 2.1: TOTAL ABUNDANCES OF ARTHROPODS IN WATER-HYACINTH RAFTS PER SITE, (black) lentic sites, (gray) lotic sites, (white) tidal sites

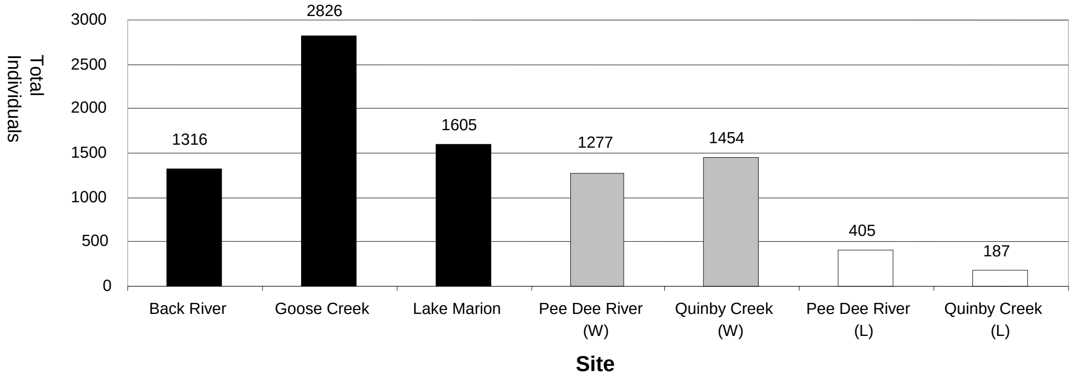


Figure 2.2: AVERAGE ABUNDANCES OF ARTHROPODS IN WATER-HYACINTH RAFTS PER SITE; error bars are 95% confidence intervals; (black) lentic sites (gray) lotic sites, (white) tidal sites

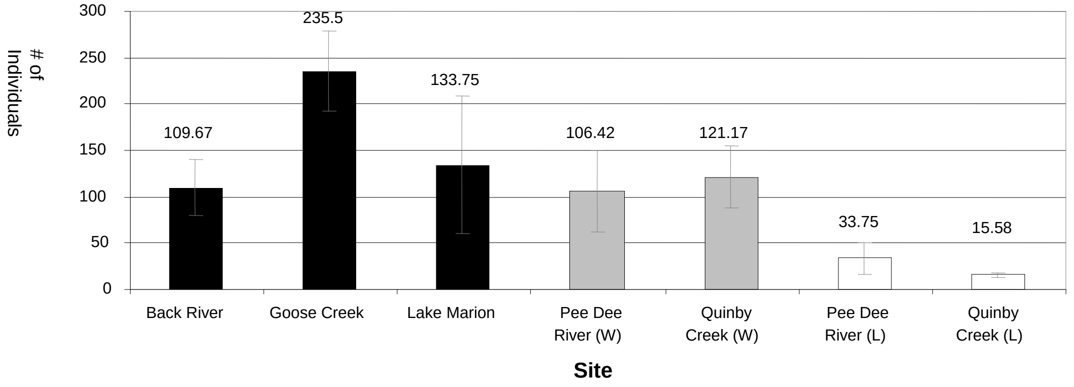


Figure 2.3: ABUNDANCES OF ARTHROPODS IN WATER-HYACINTH RAFTS PER SITE AND MONTH, March 2005 – February 2006

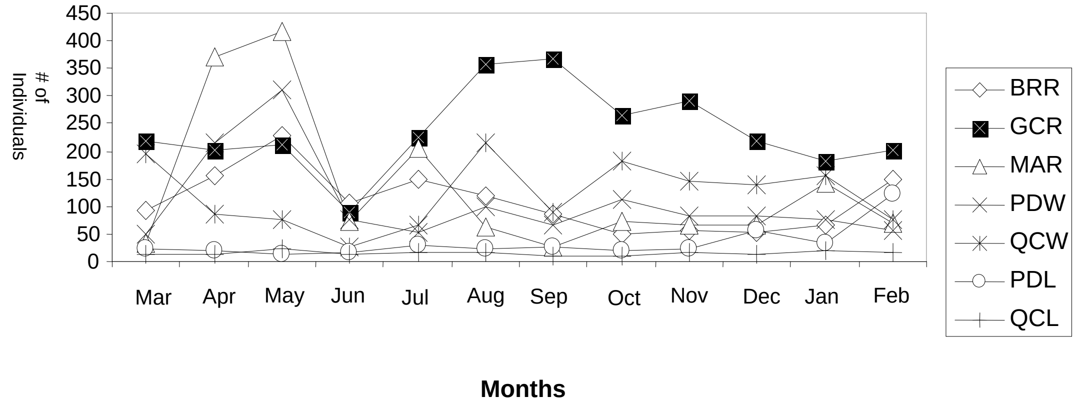


Figure 3.1: TOTAL NUMBER OF ARTHROPOD SPECIES IN WATER-HYACINTH RAFTS PER SITE, (black) lentic sites, (gray) lotic sites, (white) tidal sites

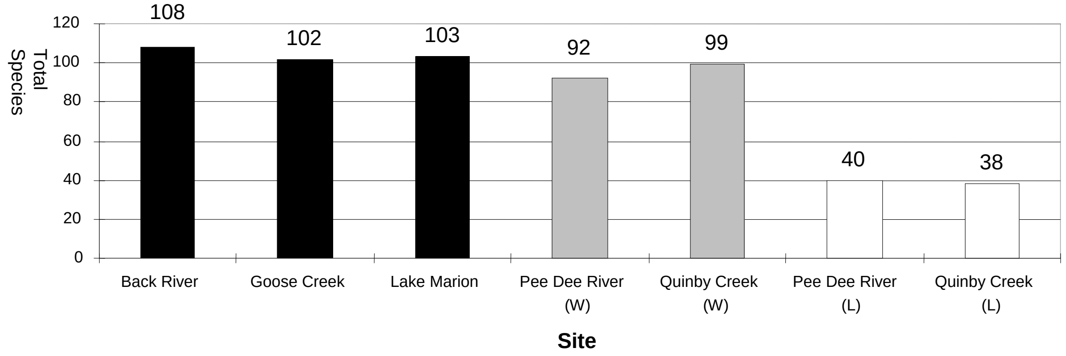


Figure 3.2: AVERAGE NUMBER OF ARTHROPOD SPECIES IN WATER-HYACINTH RAFTS PER SITE; error bars are 95% confidence intervals; (black) lentic sites, (gray) lotic sites, (white) tidal sites

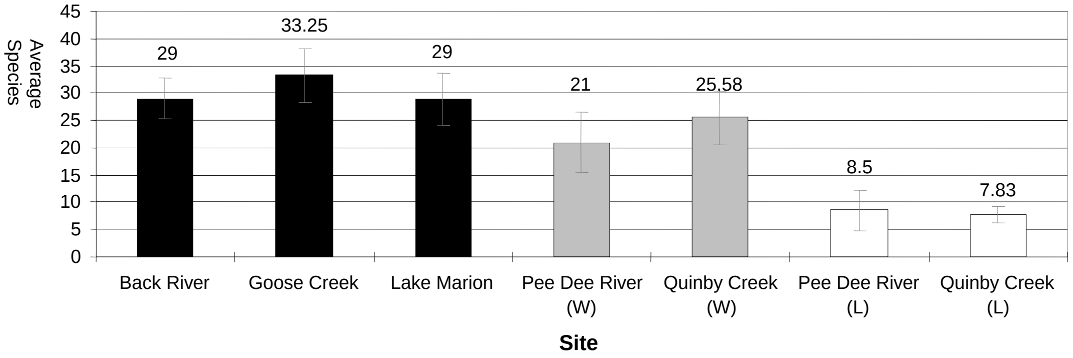


Figure 3.3: TOTAL NUMBER OF ARTHROPOD SPECIES IN WATER-HYACINTH RAFTS PER SITE AND MONTH, March 2005 – February 2006

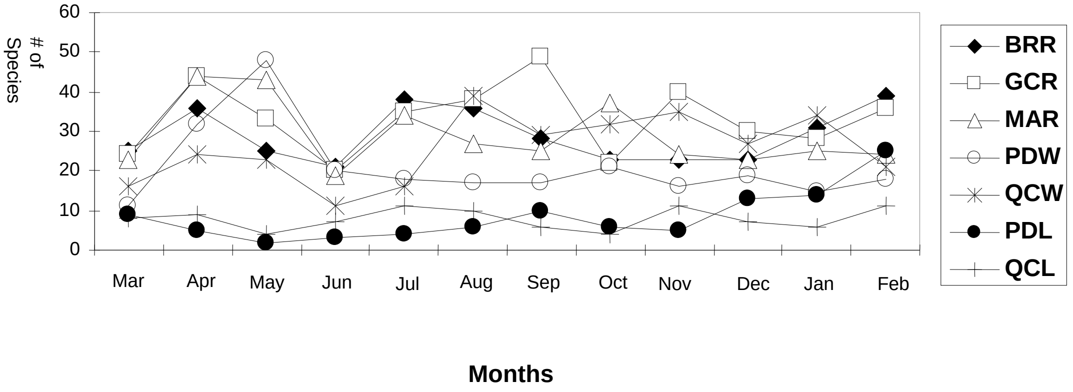


Figure 4.1: AVERAGE ABUNDANCES OF ARTHROPODS IN WATER-HYACINTH RAFTS PER MONTH, March 2005 – February 2006; error bars are 95% confidence intervals.

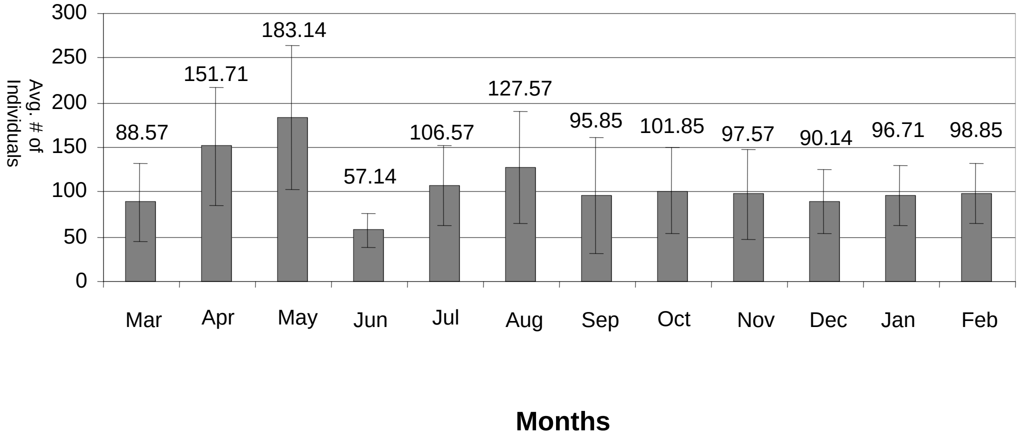


Figure 4.2: AVERAGE NUMBER OF ARTHROPOD SPECIES PER MONTH, March 2005 – February 2006; error bars are 95% confidence intervals.

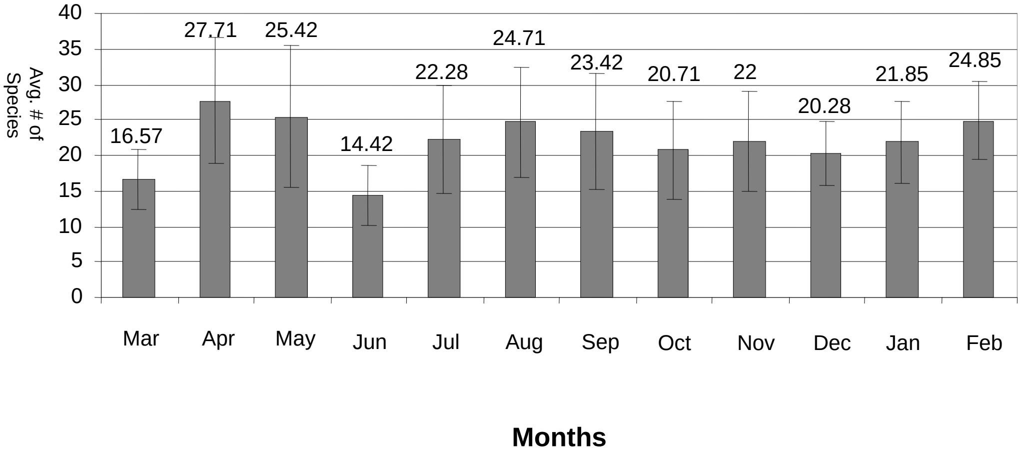


Figure 5.1: TOTAL ABUNDANCES OF NEOCHETINA SPP. IN WATER-HYACINTH RAFTS PER MONTH, March 2005 – February 2006

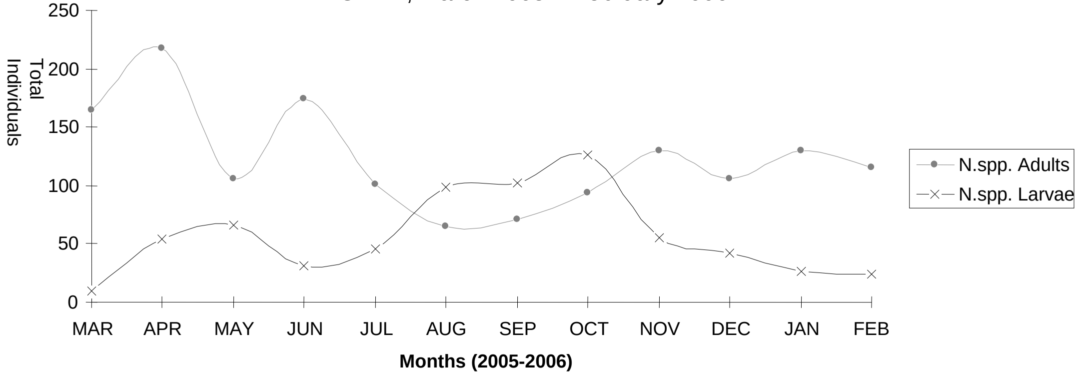
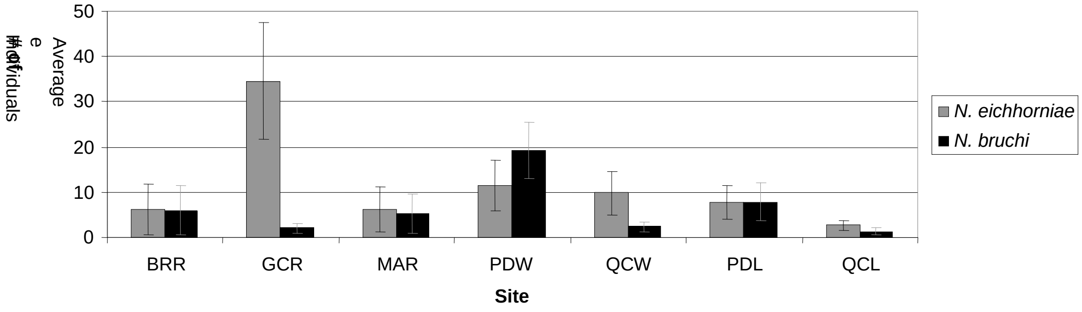
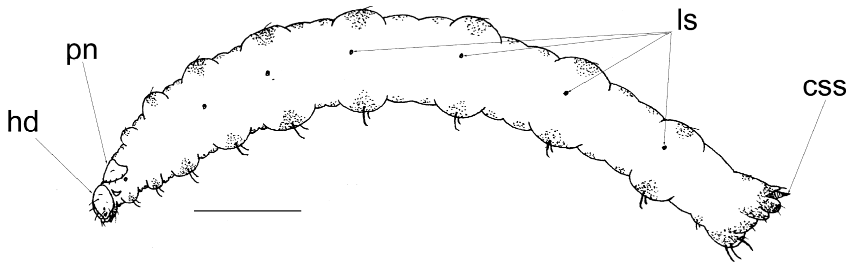


Figure 5.2: NEOCHETINA spp. ADULT ABUNDANCE IN WATER-HYACINTH RAFTS PER SITE; error bars are 95% confidence intervals.



Appendix C

Figures (Illustrations)



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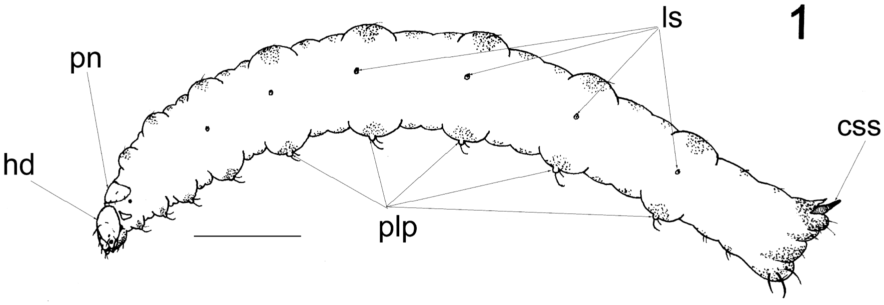

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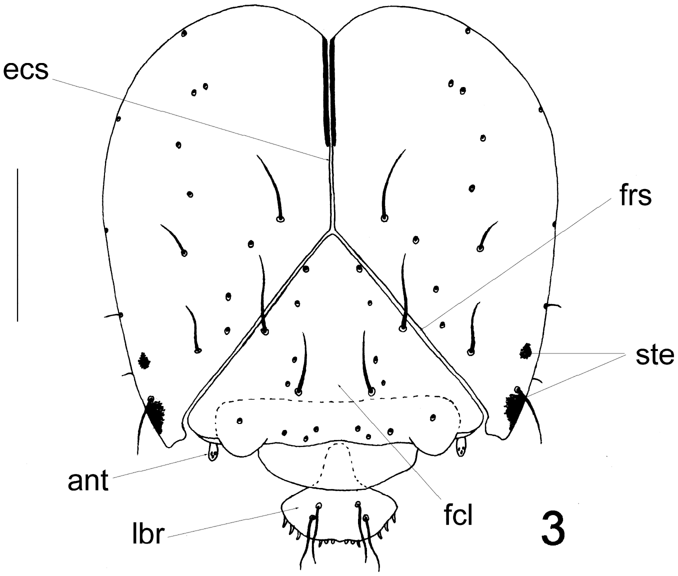

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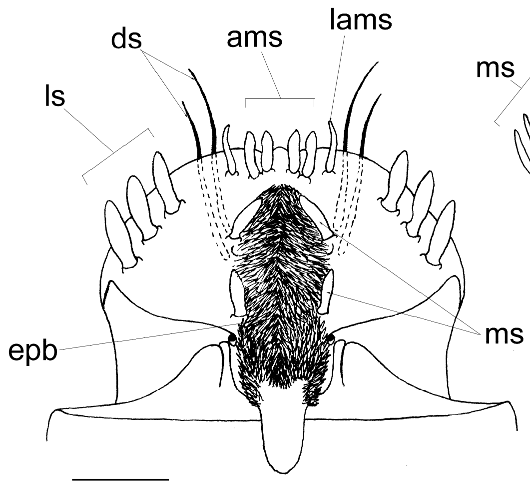
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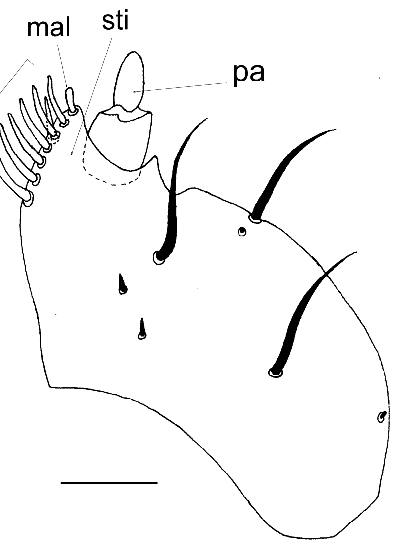
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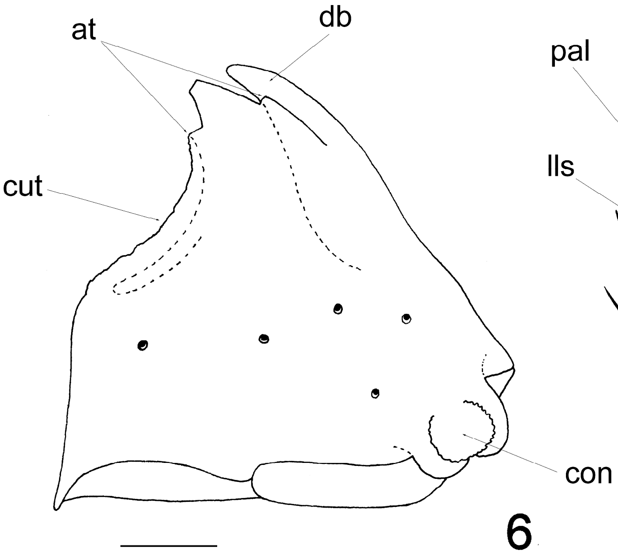
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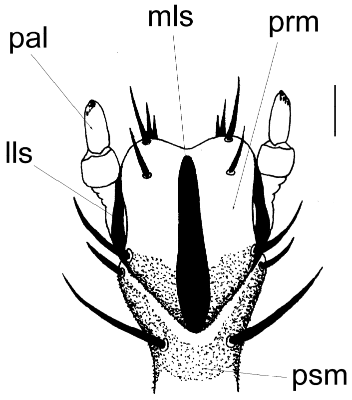
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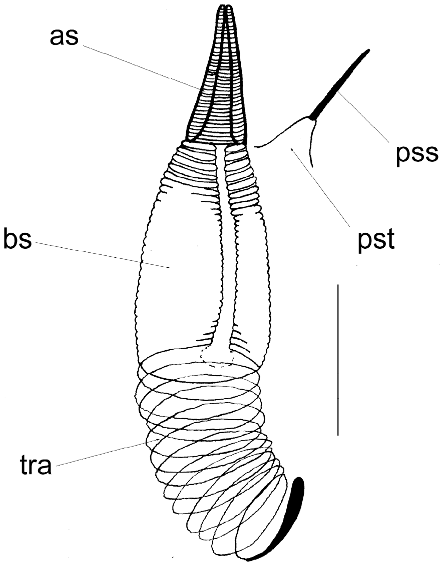

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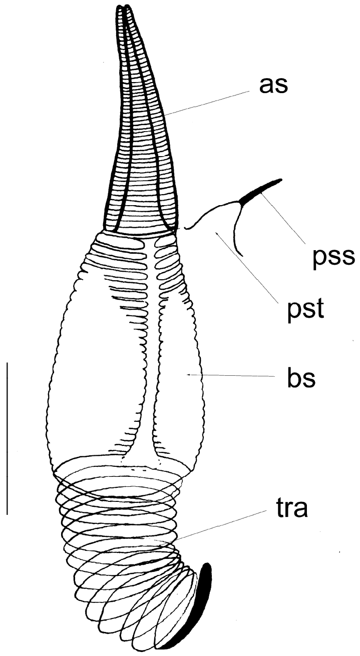

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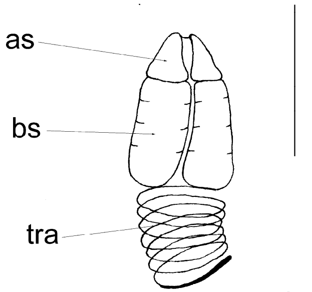

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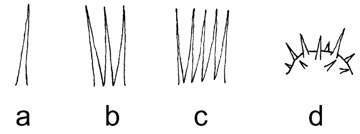

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<u>Figure Legends (Illustrations)</u>

Figures 1-3: Larvae of *Neochetina eichhorniae* Warner and *N. bruchi* Hustache. 1, *N. eichhorniae*, entire body, left lateral; *hd*, head; *pn*, pronotum; *ls*, lateral spiracles; *css*, caudal spine-like spiracles. Scale bar = 2 mm. 2, *N. bruchi*, entire body, left lateral; *hd*, head; *pn*, pronotum; *ls*, lateral spiracles; *css*, caudal spine-like spiracles; *plp*, peg-like protuberances. Scale bar = 2 mm. 3, Head capsule, anterior; *ant*, antenna; *ecs*, ecdysial suture; *fcl*, frontoclypeus; *frs*, frontal suture; *lbr*, labrum; *ste*, stemmata. Scale bar = 0.25 mm.

Figure 4-7: Mouthparts of larvae of *Neochetina eichhorniae* Warner and *N. bruchi* Hustache. 4, Epipharynx, ventral; *ams*, anteromedian setae; *ds*, dorsal setae; *epb*, epipharyngeal brush; *lams*, lateral anteromedian seta; *ls*, anterolateral setae; *ms*, median setae. Scale bar = 0.05 mm. 5, Left maxilla, ventral; *mal*, mala; *ms*, median setae; *pa*, palpus; *sti*, stipes. Scale bar = 0.05 mm. 6, Left mandible, ventral; *at*, accessory teeth; *con*, condyle; *cut*, cutting edge; *db*, dorsal bifurcation. Scale bar = 0.05 mm. 7, Labium, ventral; *lls*, lateral longitudinal sclerite; *mls*, median longitudinal sclerite; *pal*, palpus; *prm*, prementum; *psm*, postmentum. Scale bar = 0.05 mm.

Figure 8-11: Spiracles and cuticular microsculpture of *Neochetina eichhorniae* Warner and *N. bruchi* Hustache. 8, *N. eichhorniae*, left caudal spine-like spiracle and pre-spiracular seta, dorsal; *as*, apical segment; *bs*, basal segment; *pss*, pre-spiracular seta;

pst, pre-spiracular tubercle; *tra*, tracheal taenidia. Scale bar = 0.1 mm. 9, *N. bruchi*, left caudal spine-like spiracle and pre-spiracular seta, dorsal; *as*, apical segment; *bs*, basal segment; *pss*, pre-spiracular seta; *pst*, pre-spiracular tubercle; *tra*, tracheal taenidia. Scale bar = 0.1 mm. 10, *N. bruchi*, left spiracle of abdominal segment VI, left lateral; *as*, apical segment; *bs*, basal segment; *tra*, tracheal taenidia. Scale bar = 0.1 mm. 11, *N. bruchi*, examples of cuticular microsculpture on creeping welts; *a*, single spinule; *b* and *c*, trichomous spinules; *d*, mound with asperities.

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