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Macroinvertebrate abundance and distribution of hydrilla and ceratophyllum habitats in the Atchafalaya River Basin, Louisiana

Jose Checo Colon-Gaud
Louisiana State University and Agricultural and Mechanical College

MACROINVERTEBRATE ABUNDANCE AND DISTRIBUTION OF HYDRILLA AND CERATOPHYLLUM HABITATS IN THE ATCHAFALAYA RIVER BASIN, LOUISIANA

A Thesis

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Abstract

Submerged aquatic vegetation (SAV) plays an important role in aquatic systems, providing shelter, breeding habitat, and epiphytic forage for numerous fishes and aquatic macroinvertebrates. Since 1960, many lentic habitats in the southern U.S. have been invaded by *Hydrilla verticillata*, and in the last two decades this aggressive macrophyte has become the dominant species of SAV in the Atchafalaya River Basin in south central Louisiana. Because of its highly branched morphology and characteristically high densities, I found it difficult to quantitatively sample the macrofauna inhabiting hydrilla stands with traditional gears such as sweep nets, particularly under the canopy. As a consequence, I developed a suitcase trap that provided an efficient, quantitative method of sampling hydrilla-associated macroinvertebrates, and compared the abundance and taxonomic composition of samples collected with suitcase and sweep net samplers in dense hydrilla habitat. The suitcase trap is easy to deploy and retrieve, effective in all plant densities, permits estimation of macroinvertebrate densities by plant volume or dry weight, and is more effective than traditional sweep nets in describing the vertical distribution of macroinvertebrates inhabiting hydrilla-dominated littoral habitats.

To provide a better understanding of the effects of exotic macrophyte invasions on the ecology of epiphytic invertebrates, and to identify possible management alternatives to mitigate detrimental impacts associated with these invasions on littoral habitat quality, I measured the density of vegetation-dwelling macroinvertebrates on exotic *Hydrilla verticillata* and native *Ceratophyllum demersum* in the Atchafalaya Basin. I collected a total of 34,996 macroinvertebrates from hydrilla and coontail habitat from May to August 2001 to determine how exotic hydrilla compares to native macrophytes in terms of

macroinvertebrate habitat. Abundant macroinvertebrate taxa included Amphipoda, Decapoda, Diptera, Gastropoda, and Ephemeroptera. Overall, macroinvertebrate abundance between hydrilla and coontail was relatively similar. It is apparent from this study that, at least at the assemblage level, differences between abundance and distribution patterns of macroinvertebrates in different macrophyte species do exist. Principal component analysis displayed differences between macroinvertebrate assemblages, although the relative effects (and interactions) of declining or fluctuating water quality, macrophyte architecture, food resource quantity and quality, and predatory mortality on macroinvertebrate community composition remain to be identified.

Chapter 1.
Introduction

The purpose of this research was to provide information on the effects of exotic plants on water quality and the abundance of vegetation-dwelling organisms in the Atchafalaya River Basin (ARB) in south central Louisiana. My investigation focused on the effects of bed position and water quality on the abundance and distribution of invertebrates inhabiting hydrilla (*Hydrilla verticillata*) and coontail (*Ceratophyllum demersum*) dominated habitats in this large river floodplain system. The study was designed to provide a better understanding of the effects of exotic macrophyte invasions on the ecology of epiphytic invertebrates, and to identify possible management alternatives to mitigate detrimental impacts associated with exotic macrophyte invasion on littoral habitat quality.

The ARB, a floodplain of the Atchafalaya River, has evolved into a highly altered and regulated system managed by the U.S. Army Corps of Engineers as an emergency floodway for the lower Mississippi River. Since 1960, many lentic habitats in the southern U.S. have been invaded by hydrilla, and in the last two decades this aggressive macrophyte has become the dominant species of submerged aquatic vegetation (SAV) in the ARB, and has likely had substantial impacts on the abundance and species composition of the littoral macroinvertebrate community. The annual water regime of the ARB has historically been a winter-spring inundation followed by a summer-fall dewatering of the floodplain, with numerous dredged canals, bayous, and lakes maintaining water throughout the year. Gresham (1963) described this water fluctuation cycle as ideal for most forms of fish and animal life. However, hydrilla grows quickly throughout the spring flood pulse in the ARB, and as water levels decline in late spring,

the hydrilla collapses into an extremely dense canopy. Many studies have reported the important role of SAV in providing shelter, breeding habitat, and epiphytic forage for numerous fishes and aquatic macroinvertebrates (Killgore et al., 1989). However, high density SAV beds such as the hydrilla-dominated habitats in the ARB are not beneficial to a fishery (Martin and Shireman, 1976), and often displace native aquatic plant communities and interfere with angler access, fish foraging success, invertebrate abundance, and local water quality.

The aquatic macrophyte community in the ARB has changed considerably in the last 25 years. The expansion of exotics such as hydrilla has undoubtedly reduced the diversity and abundance of native aquatic plants, with unknown consequences for the invertebrate community. Vegetation-dwelling invertebrates are important food organisms for juvenile and adult fishes, particularly in lakes with a limited benthic community, and macroinvertebrate abundance and species composition is strongly influenced by habitat structure and water quality (Merritt and Cummins, 1996). Therefore, negative impacts on littoral habitat quality due to the invasion of an aggressive exotic macrophyte such as hydrilla could have significant consequences on the species composition and dynamics of shallow water invertebrates and fishes.

Because of its highly branched morphology and characteristically high densities, I found it difficult to quantitatively sample the macrofauna inhabiting hydrilla stands with traditional gears such as sweep nets, particularly under the canopy. As a consequence, I developed a suitcase trap that provided an efficient, quantitative method of sampling hydrilla-associated macroinvertebrates, and compared the abundance and taxonomic composition of samples collected with suitcase and sweep net samplers in dense hydrilla

habitat. The suitcase trap is easy to deploy and retrieve, can be used in all plant densities, permits estimation of macroinvertebrate densities by plant volume or dry weight, and is more effective than traditional sweep nets in describing the vertical distribution of macroinvertebrates inhabiting hydrilla-dominated littoral habitats.

The goal of this study was to compare the quality of hydrilla and coontail as macroinvertebrate habitat in the ARB. I used macroinvertebrates to assess hydrilla-related impacts on littoral habitat quality because they are the most frequently used taxa for water quality assessment (Hellawell, 1986) due to their: 1) ubiquitous presence in almost all aquatic systems; 2) susceptibility to many different environmental perturbations; 3) variability in responses to environmental pressures; 4) sedentary nature, relative to other aquatic organisms such as fishes, which permits effective determination of the spatial extent of perturbations; and 5) relatively long life cycles that allow temporal changes in relations to abundance and age structure (Rosenberg and Resh, 1993). Specifically, the objectives of my study were to: 1) determine the abundance and community composition of hydrilla-dwelling aquatic macroinvertebrates, 2) evaluate the effects of macrophyte-induced reductions in water quality on macroinvertebrate densities, and 3) compare the species composition and density of the macroinvertebrate community between exotic hydrilla and native coontail. These data provide a more thorough understanding of the relationships between habitat structure and the dynamics of littoral macroinvertebrates, and may help mitigation efforts aimed at reducing negative impacts associated with exotic macrophyte invasions.

Study Site

The ARB (Figure 1.1) in south central Louisiana is the largest contiguous freshwater swamp in the nation, encompassing approximately 1,806 square miles of unique wildlife habitat, and is well defined by a system of levees that surround it on the north, east, and west. The ARB is a large floodway designed to divert Mississippi River floodwaters to the Gulf of Mexico, with the Atchafalaya River regulated to carry about 30 percent of the combined discharge of the Red, Black, and Mississippi rivers on an annual basis. The ARB is predominantly wooded lowland and cypress-tupelo swamp with some freshwater marshes in the lower distributary area.

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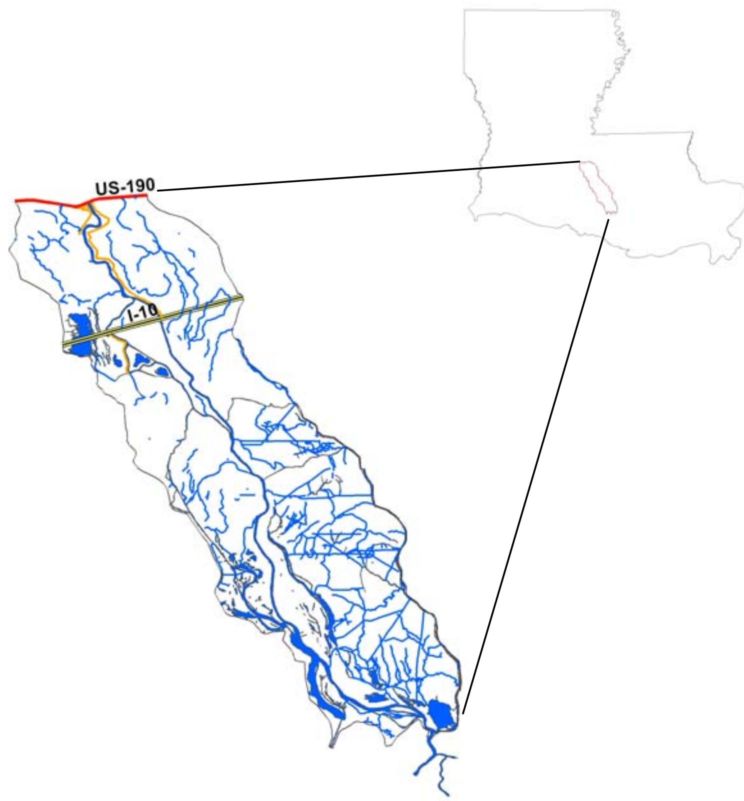

Figure 1.1. The Atchafalaya Basin, south central Louisiana.

Chapter 2.
A Suitcase Trap for Sampling Macroinvertebrates in Dense Submerged Aquatic Vegetation

Introduction

Dense stands of submersed aquatic vegetation (SAV) have become problematic in many freshwater systems throughout the world. Hydrilla *Hydrilla verticillata* is a widespread nuisance in lentic systems across the southeastern United States, often displacing native macrophytes and becoming the dominant species of littoral SAV (Colle and Shireman, 1980; Keast, 1984). Although hydrilla infestation typically reduces navigability, angler access, and sub-canopy water quality (Colle and Shireman, 1980; Langeland, 1996), dense stands of hydrilla do provide shelter, breeding sites, foraging habitat, and cover for numerous littoral invertebrates and vertebrates (Balciunas and Minno, 1985). Hydrilla grows quickly, and the density of well-established hydrilla stands precludes the use of sweep nets or similar gears for sampling the hydrilla-associated macrofauna, particularly below the surface canopy. Several collecting gears have been developed and evaluated to study macroinvertebrate abundance and distribution in vegetated habitats (Kajak, 1971; Martin and Shireman, 1976; Balciunas and Minno, 1985; Brinkman and Duffy, 1996; Turner and Trexler, 1997), but many of the "cutter" type gears (Gerking, 1957) are cumbersome, and the density of littoral *Hydrilla* stands makes rapid isolation of the sample difficult. As a consequence, I developed a suitcase-type trap that proved to be an effective method for collecting macroinvertebrates in high-density hydrilla stands. Unlike sweep netting, the suitcase trap requires the operator to be in the water. However, the suitcase trap offers several advantages, including operation at any depth, which allows examination of the vertical

distribution and abundance of epiphytic macrofauna in both canopy and understory habitats.

Methods

The trap consisted of two 60-cm x 45-cm panels constructed of 0.5-mm thick, 50-mm angle aluminum, with 600-μ stainless steel mesh covering the panel openings (Figure 1.1). The two panels were attached at one end with two 75-mm x 38-mm aluminum hinges welded onto the frames, and at the other end by two 75-mm brass clasps that were bolted to the frame edges so that the trap could be closed securely to isolate the sample. Four 25-mm diameter x 12-mm wide aluminum rings were welded to the top of the sampler, and a rope threaded through these rings permitted a second operator on the boat to help with deployment and retrieval of the 9-kg sampler. My sampling methodology consisted of lowering the trap slowly into the water to the desired depth in the open position, quickly closing and latching the sampler to isolate the sample, and then trimming away any vegetation caught in the frame as it was retrieved. On the boat, I opened the trap, washed all vegetation and associated macroinvertebrates into a numbered plastic bag, added Rose Bengal stain to the sample, and placed the bag on ice for transport to the laboratory, where samples were frozen. The total elapsed time for setting and retrieving the trap and collecting the sample in the plastic bag was about 5 min.

I collected three paired sweep net and suitcase samples on 14 September and 26 October 2001 to compare the effectiveness of the two gears. All samples were collected approximately 5 m from each other in one hydrilla bed in the Atchafalaya River Basin (ARB) in south-central Louisiana. Sweep net samples were taken by lowering the

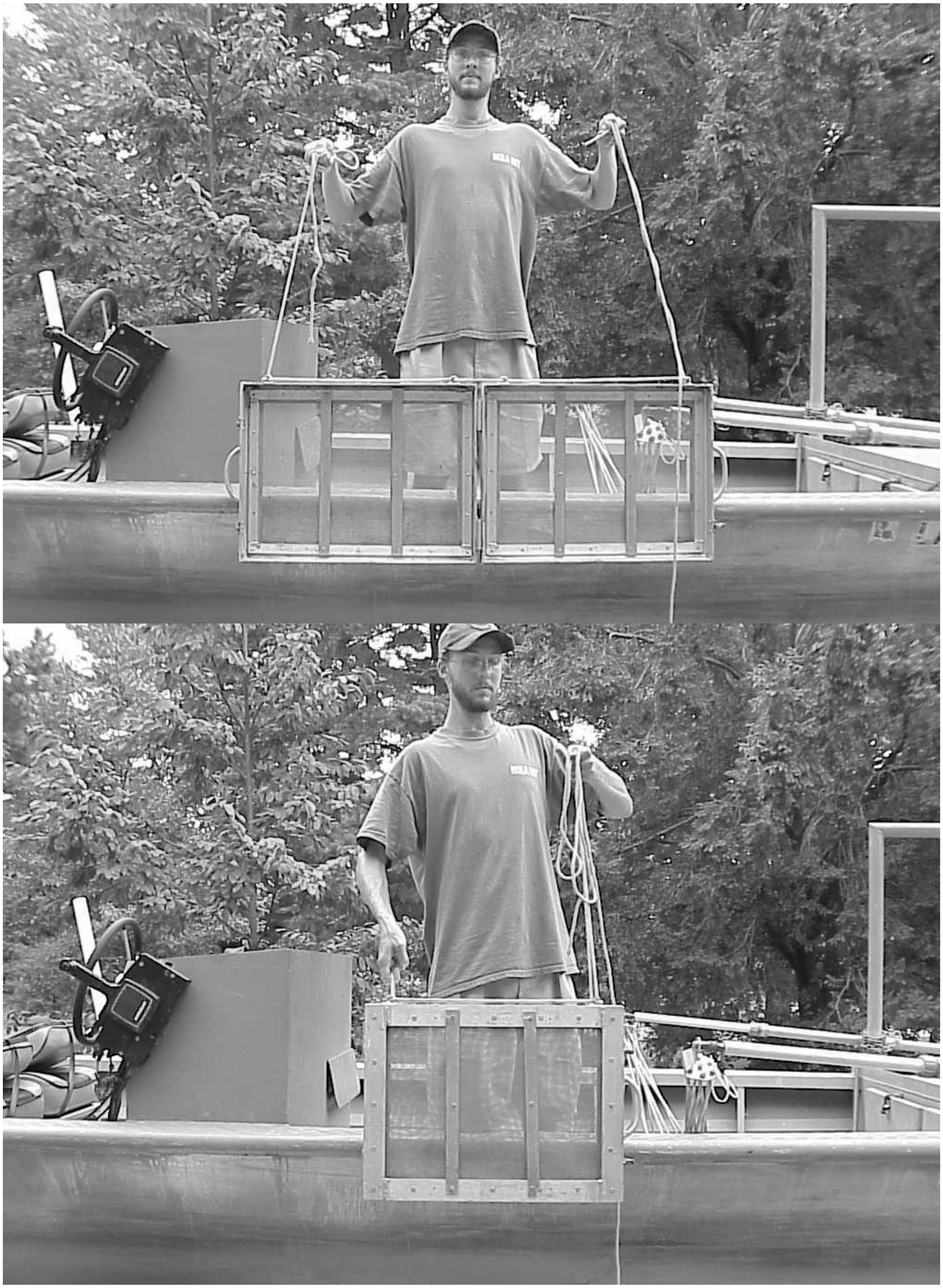

Figure 2.1. Suitcase trap in open position (top) and closed position (bottom).

net slowly until submerged, and moving it laterally away from the disturbed area. Swept areas approximated the area sampled with the suitcase trap, and vegetation hanging outside the sweep net frame was removed before the samples were washed into plastic bags, stained with rose Bengal, and transported to the laboratory for freezing. In the laboratory, samples were thawed, macroinvertebrates were removed and preserved in 95% ethyl alcohol, and the vegetation in each sample was drained of excess water, dried for 7 d at 32 °C, and weighed. Macroinvertebrates from each sample were subsequently sorted into groups, identified, and counted.

Data collected from each sample included the total number and density (number per g of dry plant matter) of individuals grouped into six (September) or seven (October) orders, plus a group of miscellaneous taxa. On each date, I calculated the percent composition by number for each taxonomic group in the two samplers (samples combined for each sampler), and used analysis of variance of log-transformed densities to assess differences in abundance estimates between the two gears on each sampling date. All statistical analyses were completed with the SAS statistical package (SAS Institute Inc., 2001).

Results

The abundance of macroinvertebrates collected with the two gears differed substantially in September samples, with the suitcase trap consistently yielding greater numbers and higher density estimates (log number per g of dry plant weight) for each taxonomic group (Table 1.1). Although variability in macroinvertebrate abundance among samples was characteristically high, the number of individuals per g of plant material was significantly greater for amphipods ($P = 0.02$), ephemeropterans ($P = 0.02$),

and odonates ($P = 0.04$) collected with the suitcase trap; density estimates for all other groups were not significantly different between the two gears. In the October samples, the suitcase trap collected more individuals of all groups except dipterans and other, although the total numbers of macroinvertebrates and log-density estimates for each group were similar for the two gears (Table 2.2).

Discussion

The suitcase trap has the advantage that the vegetation sample and its associated macrofauna can be quickly trapped even in the densest hydrilla habitat, with the unsampled vegetation outside the trap frame easily removed after the trap is closed. I found the suitcase trap provided density estimates that were greater than or comparable to those provided by sweep nets for a diversity of macroinvertebrates inhabiting hydrilla beds in the ARB. Although use of the trap required the operator to be in the water, the suitcase offered several advantages over traditional sweep netting when collecting macroinvertebrates in dense cover. Rapid closure of the sampler followed by the trimming of protruding vegetation provided a readily quantifiable mass of hydrilla and its associated macrofauna. In contrast, quantifying the amount of plant material sampled by the sweep net was difficult because the net did not typically collect all of the vegetation in the swept area. In these situations, collection of dislodged epiphytic organisms without the associated stems and leaves would make density estimation problematic. In addition, the suitcase sampler could be deployed and closed quickly and did not "hang up" on the vegetation as the sample was being collected. We caught several highly mobile organisms such as *Palaemonetes* spp., *Procambarus* spp., as well as several fishes, indicating that closure of the trap was rapid enough to provide reliable abundance

Table 2.1. Total number and density (mean number per gram of dry plant matter ± SE) of organisms collected from hydrilla beds with the suitcase trap and sweep net on 14 September 2001.

	Suitcase Trap		Sweep Net	
Taxa	Total	Mean Density	Total	Mean Density
Amphipoda*	221	3.84 ± 1.26	19	0.41 ± 0.12
Hyalella azteca				
Decapoda	135	1.75 ± 0.55	24	0.48 ± 0.28
Palaemonetes sp.				
Diptera	575	3.41 ± 1.73	134	1.09 ± 0.22
Chironomidae				
Ceratopogonidae				
Stratiomyidae				
Chaoboridae				
Ephemeroptera*	616	4.47 ± 1.89	68	0.8 ± 0.39
Baetidae				
Caenidae				
Gastropoda	10	0.17 ± 0.09	5	0.1 ± 0.01
Odonata*	59	1.04 ± 0.41	2	0.05 ± 0.01
Coenagrionidae				
Libellulidae				
Other	57	0.24 ± 0.12	44	0.12 ± 0.02

*Density is significantly different ($P < 0.05$).

Table 2.2. Total number and density (mean number per gram of dry plant matter ± SE) of organisms collected from hydrilla beds with the suitcase sampler and sweep net on 21 October 2001.

	Suitcase Trap		Sweep Net	
Taxa	Total	Mean Density	Total	Mean Density
Amphipoda	440	2.9 ± 1.68	223	1.93 ± 1.06
Hyalella azteca				
Decapoda	96	0.67 ± 0.57	22	0.27 ± 0.08
Palaemonetes sp.				
Diptera	960	2.74 ± 1.20	1666	10.23 ± 6.05
Chironomidae				
Ceratopogonidae				
Stratiomyidae				
Chaoboridae				
Ephemeroptera	52	0.25 ± 0.09	13	0.2 ± 0.06
Baetidae				
Caenidae				
Gastropoda	1060	9.63 ± 4.41	899	11.69 ± 3.30
Lepidoptera	252	1.89 ± 0.83	205	1.95 ± 0.67
Odonata	244	0.98 ± 0.42	198	1.15 ± 0.34
Coenagrionidae				
Libellulidae				
Other	156	0.35 ± 0.07	170	0.24 ± 0.08

estimates for all invertebrate taxa we encountered in ARB hydrilla beds. Finally, collecting sweep net samples below the upper canopy was essentially impossible. In contrast, the suitcase trap was able to sample vegetation in canopy and sub-canopy habitats, which has allowed us to further investigate the effects of depth, physicochemistry, and position (e.g., interior and edge) on macroinvertebrate abundance patterns.

The relatively high standard deviations associated with the mean macroinvertebrate densities reflected the typically overdispersed distribution of vegetation-dwelling organisms, and was due to spatial variability in vegetation density and distribution (Martin and Shireman, 1976), as well as the non-random distribution of macroinvertebrates throughout these structurally complex habitats (Minshall and Minshall, 1977; Lamberti and Resh, 1979; Resh, 1979). Use of the suitcase trap does not reduce the need to collect several samples to provide reasonably precise estimates of macroinvertebrate density, but the trap does provide an effective and easy to use method for collecting quantitative samples in high-density SAV habitats.

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Chapter 3.
Macroinvertebrate Abundance and Distribution of Exotic and Native Beds in the Atchafalaya Basin, Louisiana

Introduction

Hydrilla *Hydrilla verticillata* has become a problem in many freshwater systems throughout the southeastern United States, often displacing native macrophytes (Colle and Shireman, 1980; Keast, 1984) and significantly altering littoral habitat structure. Hydrilla arrived in the Atchafalaya River Basin (ARB) in south central Louisiana sometime during the mid-1970's, and has since become the dominant species of submerged aquatic vegetation (SAV) in the ARB. Hydrilla has several characteristics that have contributed to its successful colonization of the ARB, including rapid early spring growth during the Atchafalaya River flood pulse that results in thousands of acres of dense surface mats in excavated canals and natural bayous and lakes by late summer. Although SAV provides shelter, breeding sites, and cover for numerous invertebrate and vertebrate species (Balciunas and Minno, 1985), high density hydrilla stands can significantly impact littoral water quality (Steward, 1970), alter invertebrate abundance and distribution (Scott and Osborne, 1981), and interfere with fish foraging success (Martin and Shireman, 1976).

Research on hydrilla-dwelling macroinvertebrates has focused on their abundance in relation to the presence or absence of hydrilla (Balciunas and Minno,1984), but not on the associated effects of dense hydrilla beds on water quality and macroinvertebrate distribution. During summer, dense stands of hydrilla in the ARB exhibit nocturnal hypoxia [dissolved oxygen (DO) concentrations below 2.0 ppm] in the canopy and persistent hypoxia below the canopy (unpublished data), making these habitats of

marginal quality to organisms not adapted to hypoxic conditions. The goal of this study was to assess the effects of hydrilla habitat characteristics on littoral macroinvertebrates in this sub-tropical swamp habitat. Specifically, I focused on the effects of location within a hydrilla stand (edge, middle, surface, or bottom) and water quality on the composition and distribution of the hydrilla-dwelling macroinvertebrates in the ARB.

Numerous studies have reported that the diversity and abundance of vegetation-dwelling aquatic macroinvertebrates varies greatly among different macrophyte species (Macan, 1961; Schramm et al., 1987). The establishment of hydrilla in the ARB has likely had substantial impacts on the composition of the littoral macrophyte community as well as the abundances of associated epiphytic macroinvertebrates. Therefore, I designed this study to compare the macroinvertebrate assemblages found in hydrilla and native coontail *Ceratophyllum demersum* to assess potential hydrilla-related changes in the ARB littoral macroinvertebrate community.

Methods

From May to August 2001, samples of *Hydrilla verticillata* and *Ceratophyllum demersum*, approximately 10 to 40 g dry weight, were obtained from two sample sites in the Atchafalaya Basin. Collections were made with a specially constructed trap that consisted of a 60 x 45 cm suitcase constructed of 0.5-cm thick angle aluminum with 600-μ stainless steel mesh walls (Chapter 2). Macroinvertebrate densities were estimated from a total of 12 quantitative samples that were collected monthly from the macrophyte canopy (leaves and stems) and sub-canopy (stems and roots) at three locations in the middle (interior) of the plant bed and three locations in the edge of the plant bed (a total

of three canopy samples and three sub-canopy samples at both interior and edge locations).

All vegetation and associated macroinvertebrates were washed into a numbered plastic bag, Rose Bengal was added to stain the sample, and the bag was placed on ice for transport to the laboratory, where samples were frozen. The total elapsed time for setting and retrieving the trap and collecting the sample in the plastic bag was about 5 min. In the laboratory, samples were thawed, macroinvertebrates were removed and preserved in 95% ethyl alcohol, and the vegetation in each sample was drained of excess water, dried for 7 d at 32 °C, and weighed. Macroinvertebrates from each sample were subsequently sorted into groups, identified, and counted.

Data collected from each sample included the total number and density (number per g of dry plant matter) of individuals grouped into eleven orders, plus a group of miscellaneous taxa. Aquatic insects were identified according to Merrit and Cummins (1996). Other invertebrates were identified according to Pennak (1989) and Thorpe and Covich (2000).

Water depth, water temperature, dissolved oxygen, specific conductance, pH, and Secchi depth were measured at each collection location with a DataSond20 (Hydrolab® Incorporated, Denver, Colorado) portable water quality meter, and water clarity was measured with a Secchi disk. In addition, DO was measured at 30 min intervals over a 24-hour period with two DataSond3 (Hydrolab® Incorporated, Denver, Colorado) monitors on six occasions from July 2001 through July 2002 to assess diel DO fluctuations in canopy and sub-canopy habitats.

Samples were divided into two sampling seasons, early summer (May-June) when the macrophyte levels were low and the water levels were declining from the flood pulse, and late summer (July-August), when macrophyte levels were high and the water levels were low. All data were entered into a computer for statistical analyses with the SAS statistical package (SAS Institute Inc., 2001). I used principal components analysis (PCA) to group macroinvertebrate samples based on their taxonomic composition. Variable loadings over |0.35| were used to interpret each component, and I retained all components with eigenvalues over 1.0 for further analyses. For each of these components, I used the scores for each collection location in an analysis of variance to assess temporal and spatial differences in macroinvertebrate assemblage distributions between sites (hydrilla vs. coontail), seasons (early summer vs. late summer) and locations (interior vs. edge, canopy vs. sub-canopy).

Results

Water Quality

Overall trends in water quality were relatively consistent for similar positions in the hydrilla and coontail beds for both seasons (Table 3.1). Temperature and dissolved oxygen (DO) were significantly greater ($P < 0.0001$) in the canopies of both macrophytes compared to sub-canopy habitats, but no other significant differences in physicochemistry were observed. Principal component analysis of the four water quality variables resulted in two components with eigenvalues greater than one that accounted for 59% and 26% of the variance in the data, respectively. Principal component 1 was characterized by positive loadings for temperature, DO, and pH, whereas PC 2 showed positive loadings for specific conductance (Table 3.2). The plot of PC 1 versus PC 2

revealed substantial differences in physicochemistry between seasons, bed locations, and macrophytes (Figure 3.1). Seasonal differences were most evident along PC 2, as most sites exhibited higher specific conductance during the May-June compared to July-August. Bed location differences were evident in consistently higher scores along PC 1 for canopy locations relative to corresponding sub-canopy locations at interior and edge habitats for both macrophytes in July-August (e.g., hydrilla interior canopy versus hydrilla interior sub-canopy). During this period, however, differences were not consistent between locations and macrophyte types, i.e., for edge habitat, canopy and sub-canopy scores for hydrilla locations were much higher along PC 1 (higher temperature, DO, and pH) than corresponding scores for coontail locations. Conversely, for interior habitat, canopy and sub-canopy scores for coontail locations were consistently higher along PC 1 than corresponding scores for hydrilla locations. For both edge and interior habitats in July-August, all coontail locations scored lower on PC 2 than hydrilla locations, indicating a consistent pattern of lower specific conductance in the native macrophyte bed.

The influence of DO on hydrilla habitat quality was also evident in diel DO patterns in canopy and sub-canopy habitats (Figure 3.2). On most dates, canopy habitats exhibited pronounced diel DO fluctuations, whereas sub-canopy habitats had consistently low DO levels throughout the 24-hour period.

Macroinvertebrate Abundance Patterns

I collected a total of 34,996 macroinvertebrates from hydrilla and coontail habitats in the Basin from May to August 2001 (Table 3.3).

Table 3.1. Seasonal mean values (standard errors are in parentheses) for physicochemical parameters in hydrilla and coontail habitats in the Atchafalaya Basin, Louisiana from May-June (Season 1) and July-August (Season 2).

Site	Position	Location	Dissolved Oxygen (mg/L)	Temperature	Specific Conductance (µmhos/cm)	pH	Depth
				Season 1			
Hydrilla	Canopy	Interior	3.28 (0.07)	26.44 (0.38)	0.323 (0.020)	7.00 (0.03)	0.23 (0.05)
	Sub-canopy	Interior	1.79 (0.42)	25.79 (0.66)	0.325 (0.019)	6.94 (0.05)	0.68 (0.03)
	Canopy	Edge	2.87 (0.42)	26.22 (0.47)	0.316 (0.017)	6.98 (0.04)	0.26 (0.02)
	Sub-canopy	Edge	1.84 (0.48)	25.40 (0.68)	0.317 (0.016)	6.93 (0.05)	0.68 (0.04)
Ceratophyllum	Canopy	Interior	3.78 (0.06)	28.25 (0.40)	0.334 (0.007)	6.78 (0.00)	0.45 (0.05)
	Sub-canopy	Interior	0.65 (0.45)	25.60 (0.16)	0.288 (0.042)	6.77 (0.03)	1.40 (0.00)
	Canopy	Edge	3.61 (0.17)	27.70 (0.11)	0.327 (0.010)	6.80 (0.00)	0.47 (0.03)
	Sub-canopy	Edge	0.65 (0.10)	25.59 (0.22)	0.301 (0.034)	6.75 (0.04)	1.40 (0.00)
				Season 2			
Hydrilla	Canopy	Interior	2.58 (0.98)	28.13 (1.45)	0.298 (0.007)	7.01 (0.21)	0.05 (0.00)
	Sub-canopy	Interior	0.32 (0.07)	25.64 (0.03)	0.297 (0.009)	6.74 (0.00)	1.25 (0.05)
	Canopy	Edge	4.20 (0.85)	30.30 (1.25)	0.275 (0.010)	7.06 (0.07)	0.05 (0.00)
	Sub-canopy	Edge	1.36 (0.51)	28.76 (1.37)	0.270 (0.011)	6.90 (0.08)	1.00 (0.04)
Ceratophyllum	Canopy	Interior	4.00 (1.75)	28.61 (1.21)	0.223 (0.001)	7.11 (0.35)	0.45 (0.05)
	Sub-canopy	Interior	2.92 (2.32)	24.72 (0.50)	0.240 (0.018)	6.87 (0.18)	1.05 (0.05)
	Canopy	Edge	1.66 (0.75)	27.26 (0.63)	0.244 (0.007)	6.74 (0.06)	0.43 (0.03)
	Sub-canopy	Edge	0.84 (0.57)	25.27 (0.19)	0.249 (0.005)	6.72 (0.05)	1.20 (0.11)

Table 3.2. Principal Component Analysis of physicochemical parameters from hydrilla and coontail sites in the Atchafalaya Basin, Louisiana. Values presented are loadings for variables within each principal component. Values greater than |0.35| were used to interpret each component.

Physicochemical Parameters	Principal Component 1	Principal Component 2
Temperature	0.85	-0.24
Dissolved Oxygen	0.91	0.06
pH	0.90	0.10
Specific Conductance	-0.01	0.99

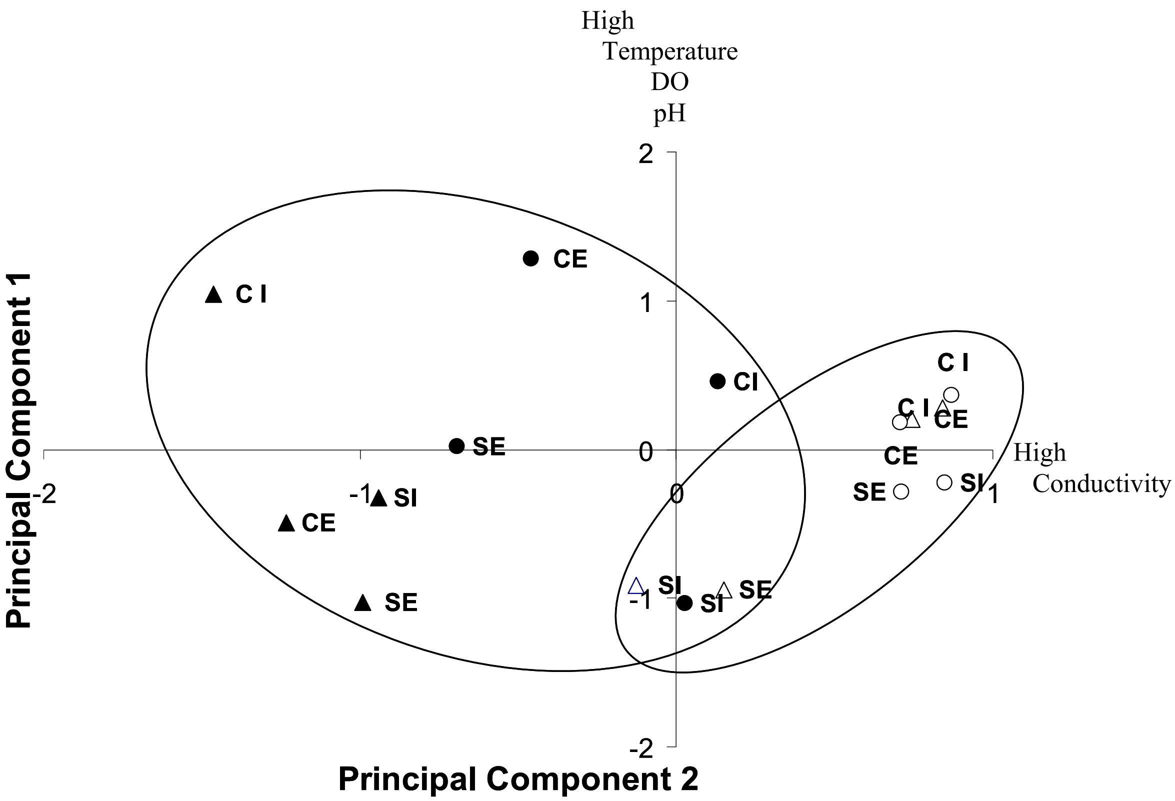

Figure 3.1. Principal component analysis of the physicochemical parameters affecting macroinvertebrate distribution in hydrilla and coontail. Open circles represent hydrilla during Season 1 (May-June), closed circles represent hydrilla during Season 2 (July-August), open triangles represent coontail during Season 1, and closed triangles represent coontail during Season 2, C = canopy, S = sub-canopy, I = interior, E = edge. Principal component 1 (temperature, DO, pH) and Principal component 2 (conductivity). Solid ellipse display seasonal differences within the macrophytes.

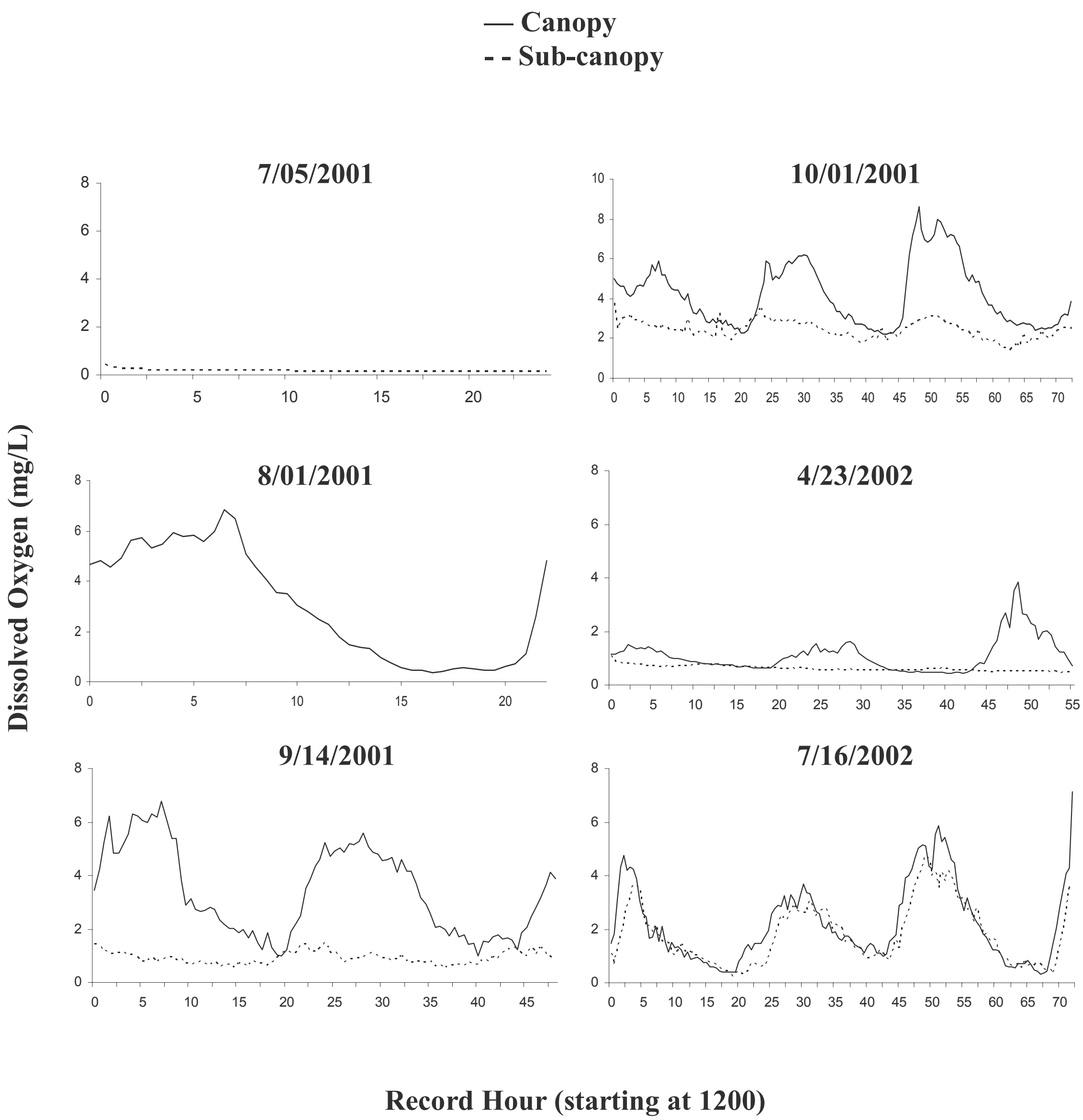

Figure 3.2. Diel dissolved oxygen patterns in canopy and sub-canopy habitats of hydrilla in the Atchafalaya Basin from July 2001 to July 2002. Data presented for 7/05/2001 does not include data for canopy habitat due to mechanical failures. Data presented for 8/01/2001 does not include data for sub-canopy habitat due to mechanical failures.

Table 3.3. Total and mean density (individuals per g dry weight of plant material) of macroinvertebrates found in hydrilla and coontail habitats in the Atchafalaya Basin, Louisiana from May-August 2001.

	Hydrilla		Coontail	
Taxa	Total	Mean Density	Total	Mean Density
Amphipoda				
Hyalella azteca	1184	34.82	828	41.40
Coleoptera				
Carabidae	0	0.00	1	0.05
Curculionidae	14	0.41	5	0.25
Dytiscidae	20	0.59	13	0.65
Gyrinidae	3	0.09	0	0.00
Haliplidae	125	3.68	10	0.50
Hydrophillidae	7	0.21	6	0.30
Noteridae	53	1.56	74	3.70
Decapoda				
Atyidae	5	0.15	0	0.00
Cambaridae	98	2.88	5	0.25
Palaemonidae	1194	35.12	254	12.70
Diptera				
Ceratopogonidae	634	18.65	1410	70.50
Chaoboridae	30	0.88	25	1.25
Chironomidae	9550	280.88	6999	349.95
Culicidae	36	1.06	8	0.40
Ephydridae	29	0.85	0	0.00
Stratiomyidae	88	2.59	52	2.60
Tabanidae	0	0.00	8	0.40
Ephemeroptera				
Baetidae	461	13.56	220	11.00
Caenidae	1315	38.68	1074	53.70
Ephemeridae	1	0.03	0	0.00
Leptophlebiidae	26	0.76	3	0.15
Neoephemeridae	3	0.09	6	0.30
unknown	6	0.18	0	0.00
Gastropoda	1319	38.79	3945	197.25
Hemiptera				
Belostomatidae	29	0.85	21	1.05
Corixidae	1040	30.59	263	13.15
Hebridae	53	1.56	68	3.40
Naucoridae	285	8.38	113	5.65
Nepidae	9	0.26	0	0.00
Pleidae	16	0.47	0	0.00
Veliidae	14	0.41	41	2.05
unknown	3	0.09	0	0.00
Lepidoptera				
Pyralidae	53	1.56	40	2.00
Odonata				
Aeshnidae	1	0.03	0	0.00
Coenagrionidae	538	15.82	331	16.55
Corduliidae	1	0.03	0	0.00

Table 3.3. Continued

Taxa	Hydrilla		Coontail	
	Total	Mean Density	Total	Mean Density
Lestidae	31	0.91	1	0.05
Libellulidae	26	0.76	51	2.55
Anisoptera unknown	1	0.03	1	0.05
Zygoptera unknown	4	0.12	3	0.15
Rhynchobdellida				
Glossiphoniidae	95	2.79	84	4.20
Trombidiformes				
Hydracarina	176	5.18	249	12.45
Other				
Arachnidae	4	0.12	0	0.00
Copepoda	6	0.18	10	0.50
Daphnidae	76	2.24	62	3.10
Hymenoptera				
Ichneumonidae	1	0.03	0	0.00
Isopoda	3	0.09	1	0.05
Trichoptera				
Leptoceridae	1	0.03	0	0.00
unknown	2	0.06	1	0.05
Mysidacea	34	1.00	7	0.35

Principal components analysis resulted in five components with eigenvalues over 1.0 that together explained 67% of the variation in the data (Table 3.4). Amphipods, decapods, odonates, and water mites loaded positively on PC 1, which accounted for 23% of the cumulative variance. Gastropods, leeches, and water mites loaded positively on PC 2, which accounted for 15% of the cumulative variance. Dipterans and ephemeropterans and Other (predominately microcrustaceans and Trichoptera) showed positive loadings for PC 3, which accounted for 11% of the cumulative variance. Coleopterans, dipterans, lepidopterans displayed positive loadings while water mites displayed negative loadings on PC 4 accounting for 10% of the cumulative variance. Amphipods, hemipterans, and rhynchobdellid leeches loaded positively on PC 5 which accounted for 9% of the cumulative variance.

There were few differences in macroinvertebrate assemblages between the two plant types among the five components with only PC 2, PC 3, and PC 4 consistently yielding greater densities ($P < 0.05$) in coontail (Figure 3.3, 3.4). Hydrilla sites scored lower than coontail sites during both seasons along PC 2 indicating reduced densities of gastropods, leeches, and water mites in hydrilla habitat (Figure 3.5). During Season 2, hydrilla sites scored higher than coontail sites along PC 3, indicating reduced densities of dipterans, ephemeropterans, and Other in coontail habitat. However, coontail sites scored higher than hydrilla sites along PC 4 during Season 2, indicating increased densities in coleopterans, dipterans, lepidopterans, and negative rhynchobdellid leeches for coontail habitat (Figure 3.6). During Season 2, there were considerable differences in interior canopy assemblages between macrophytes, with hydrilla exhibiting higher scores on PC 1 (higher amphipod, decapod, odonate, and water mite densities), and coontail exhibiting

Table 3.4. Principal component analysis of macroinvertebrates collected from hydrilla and coontail habitats in the Atchafalaya Basin, Louisiana. Values presented are loadings for variables within each principal component. Values greater than |0.35| were used to interpret each principal component (PC).

Taxa	PC 1	PC 2	PC 3	PC 4	PC 5
Amphipoda	0.39	0.05	0.22	-0.11	0.65
Coleoptera	0.13	0.17	0.18	0.73	-0.09
Decapoda	0.91	0.01	0.07	-0.02	-0.02
Diptera	-0.03	0.09	0.77	0.45	0.04
Ephemeroptera	0.08	0.09	0.83	0.01	-0.04
Gastropoda	-0.03	0.87	0.05	-0.07	0.12
Hemiptera	-0.10	-0.09	-0.23	0.19	0.71
Lepidoptera	-0.17	-0.23	-0.09	0.66	0.11
Odonata	0.80	0.20	0.13	0.01	0.09
Other	0.25	0.00	0.46	-0.25	-0.01
Rhynchobdellida	-0.08	0.38	0.10	-0.44	0.55
Trombidiformes	0.36	0.83	0.10	0.05	-0.13

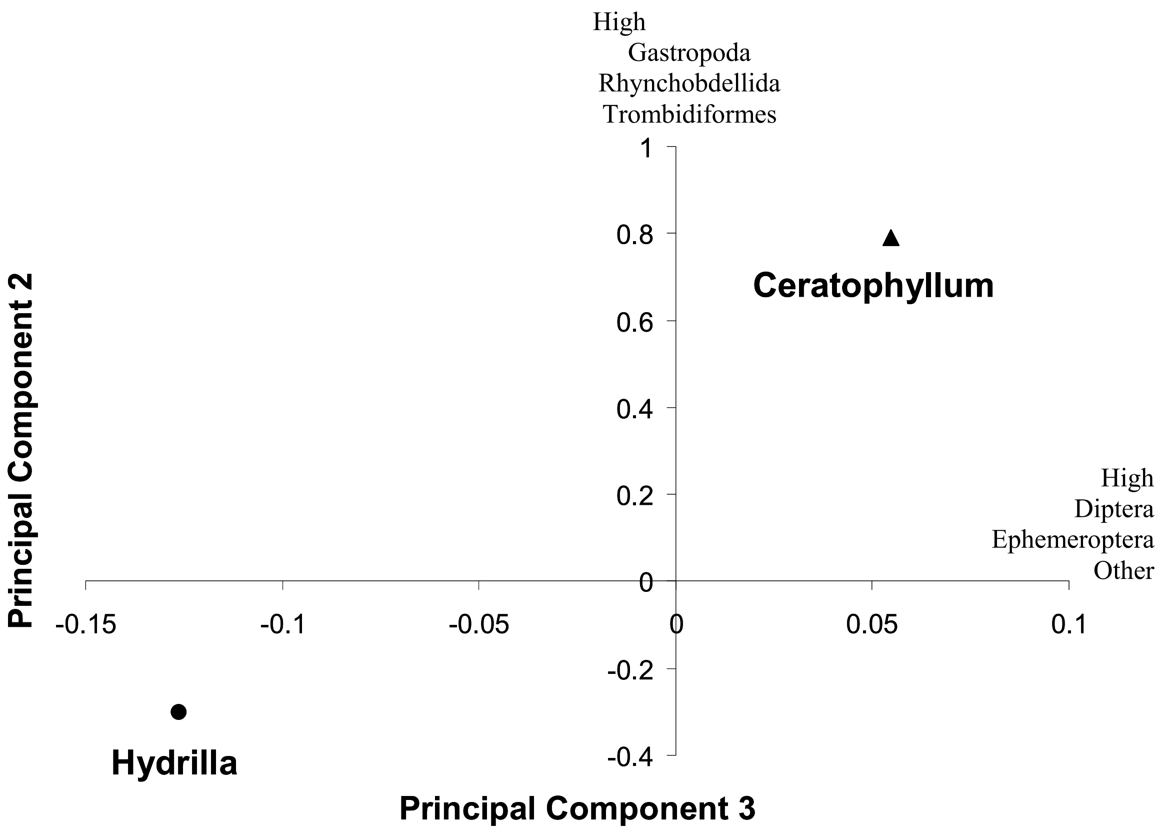

Figure 3.3. Principal components analysis of the macroinvertebrate assemblages and their distribution in hydrilla and coontail. Principal component 2 (Gastropoda, Rhynchobdellida, Trombidiformes) and Principal component 3 (Diptera, Ephemeroptera, Other).

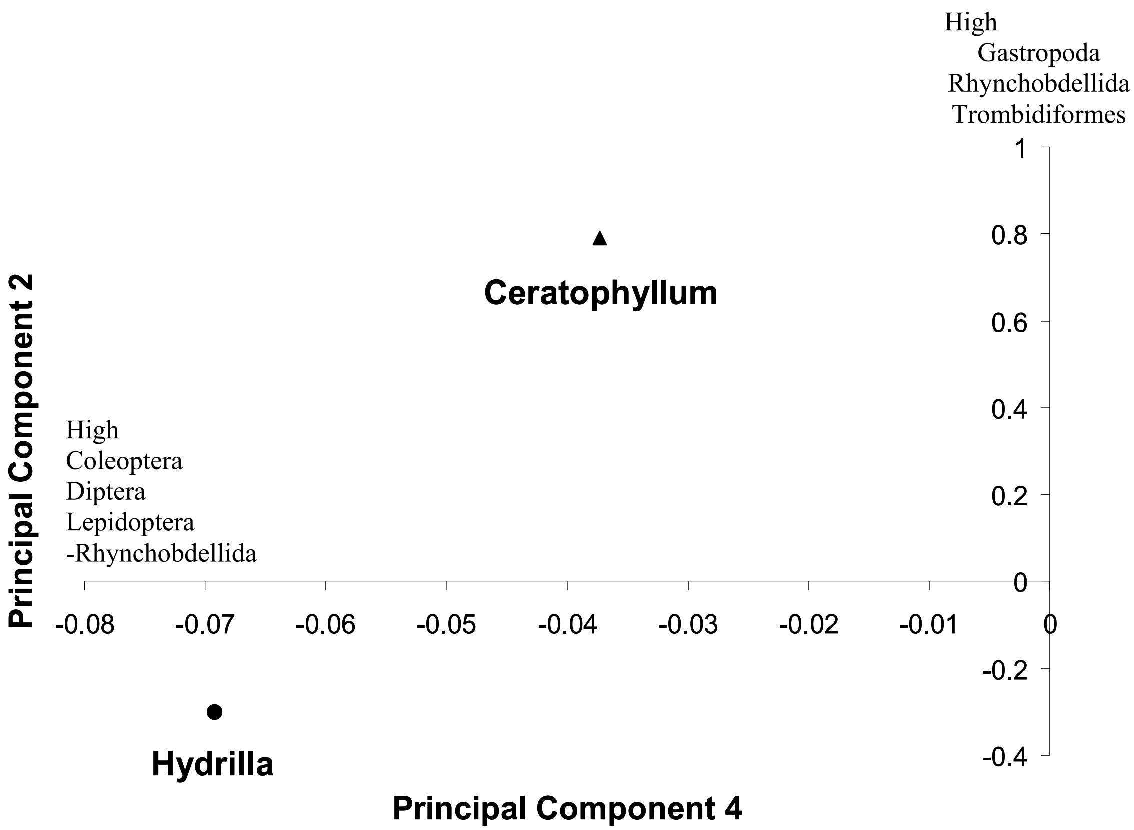

Figure 3.4. Principal components analysis of the macroinvertebrate assemblages and their distribution in hydrilla and coontail. Principal component 2 (Gastropoda, Rhynchobdellida, Trombidiformes) and Principal component 4 (Coleoptera, Diptera, Lepidoptera, -Rhynchobdellida).

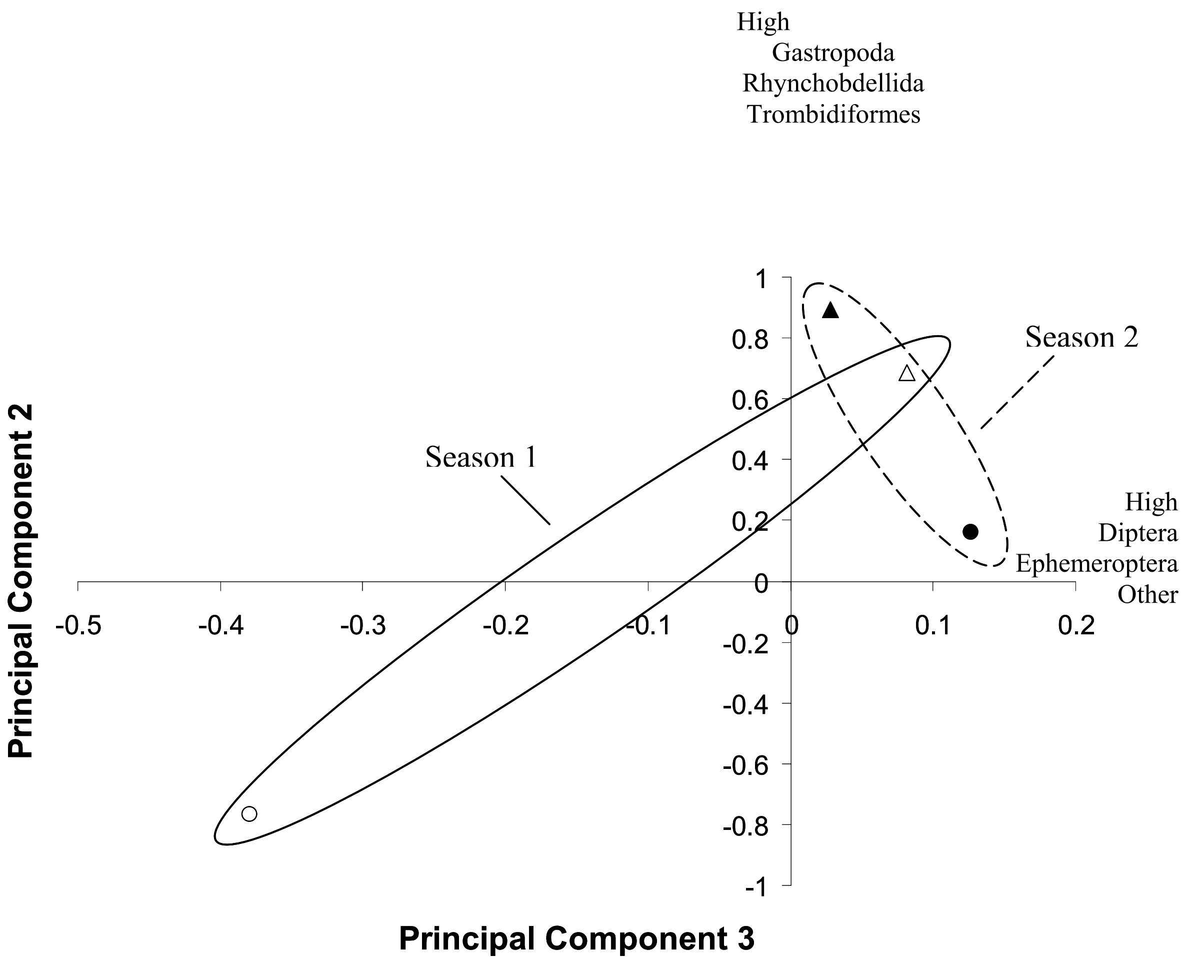

Figure 3.5. Principal components analysis of the macroinvertebrate assemblages and their distribution in hydrilla and coontail. Open circles represent hydrilla during Season 1 (May-June), closed circles represent hydrilla during Season 2 (July-August), open triangles represent coontail during Season 1, and closed triangles represent coontail during Season 2. Principal component 2 (Gastropoda, Rhynchobdellida, Trombidiformes) and Principal component 3 (Diptera, Ephemeroptera, Other).

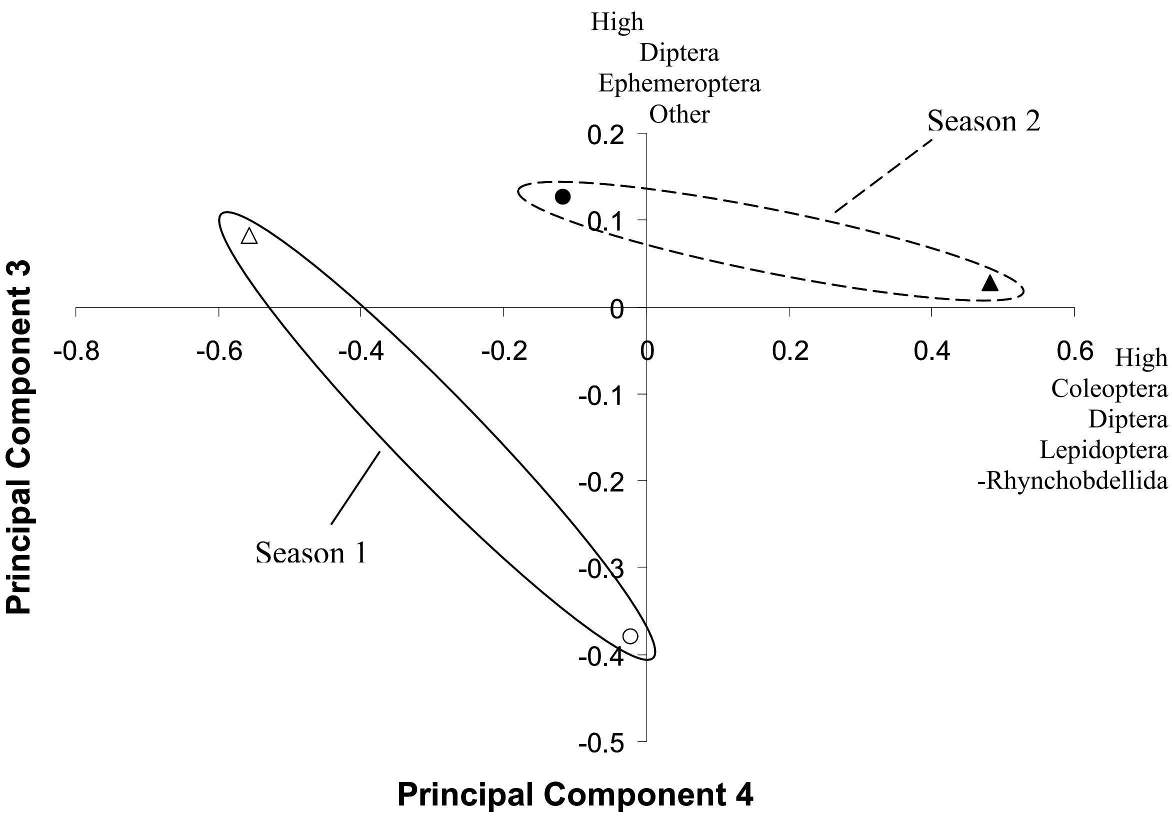

Figure 3.6. Principal components analysis of the macroinvertebrate assemblages and their distribution in hydrilla and coontail. Open circles represent hydrilla during Season 1 (May-June), closed circles represent hydrilla during Season 2 (July-August), open triangles represent coontail during Season 1, and closed triangles represent coontail during Season 2. Principal component 3 (Diptera, Ephemeroptera, Other) and Principal component 4 (Coleoptera, Diptera, Lepidoptera, -Rhynchobdellida).

higher scores on PC 1 (higher amphipod, decapod, odonate, and water mite densities), and coontail exhibiting higher scores on PC 2 (Figure 3.7). Season 1 scores along PC 3 were similar between the macrophytes, with the exception of outside canopy and sub-canopy sites in coontail, which appeared to support higher densities of dipterans, ephemeropterans, and other miscellaneous taxa (Figure 3.8). PCA also revealed differences in macroinvertebrate assemblages within macrophyte species related to bed position (Table 3.5). In hydrilla beds, seasonal trends in abundance were evidenced by higher site scores along PC 2 (higher gastropod, leech, and water mite densities) during Season 2 (Figure 3.7). During this time, lower sites scores along PC 1 for sub-canopy sites indicated substantially higher densities of amphipods, decapods, odonates, and trombidiform water mites in the interior hydrilla canopy, but not in the edge canopy. A seasonal effect on macroinvertebrate community structure was less evident in the coontail bed, although during Season 2, canopy and sub-canopy habitats at interior locations scored more positively along PC 2, indicating lower densities of gastropods, leeches, and water mites at the bed edge. Scores along PC 3 revealed additional differences in macroinvertebrate assemblages at the various bed locations, although patterns were different between the two macrophytes (Figure 3.8). For hydrilla-dwelling macroinvertebrates, interior canopy locations scored higher than edge canopy locations during Season 1 (higher densities of dipterans, ephemeropterans, and other taxa), but this pattern was reversed during Season 2. For coontail, canopy and sub-canopy locations exhibited higher scores along PC 3 during Season 1. During Season 2, these edge locations became quite dissimilar, with the edge canopy supporting more dipterans, ephemeropterans, and other taxa than the edge sub-canopy.

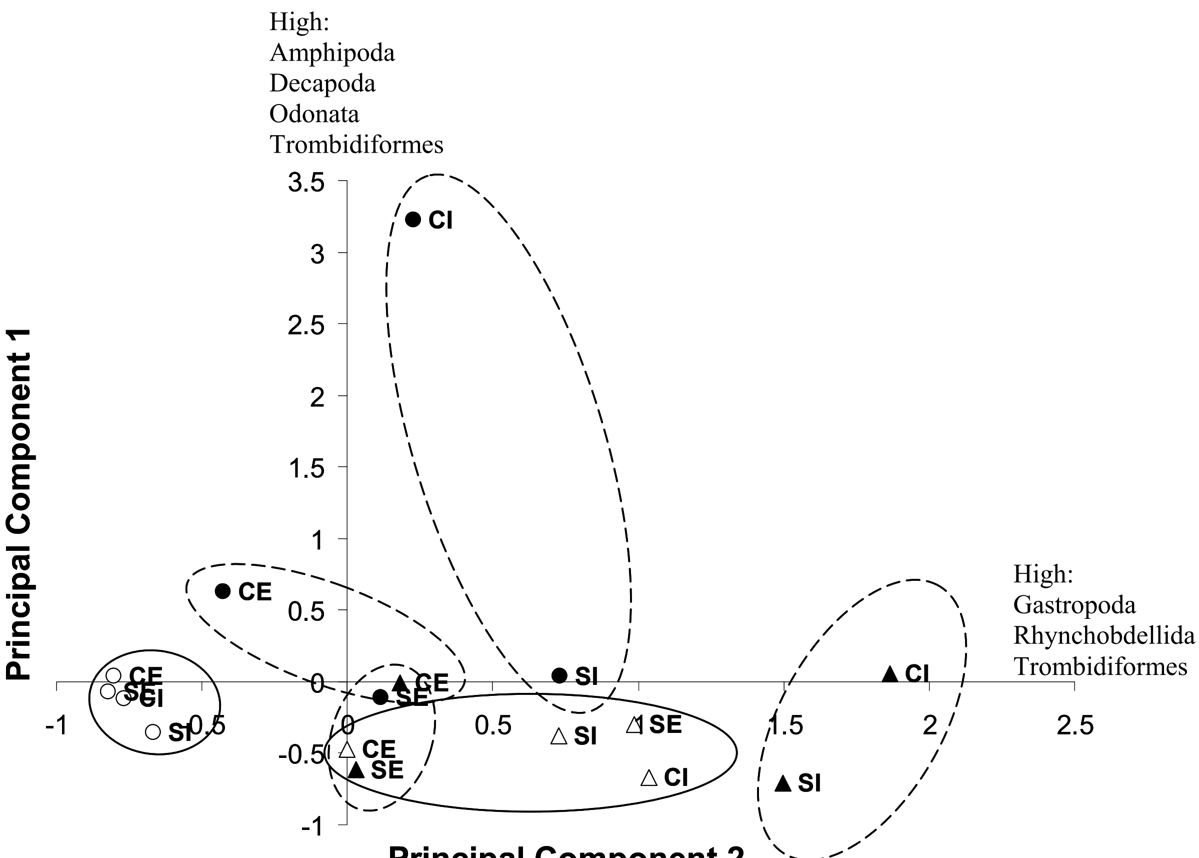

Figure 3.7. Principal components analysis of the macroinvertebrate assemblages and their distribution in hydrilla and coontail. Open circles represent hydrilla during Season 1 (May-June), closed circles represent hydrilla during Season 2 (July-August), open triangles represent coontail during Season 1, and closed triangles represent coontail during Season 2, C = canopy, S = sub-canopy, I = interior, E = edge. See text for interpretation of each principal component. Solid ellipse display differences within macrophyte type for Season 1. Dashed ellipse display differences in locations within the macrophyte.

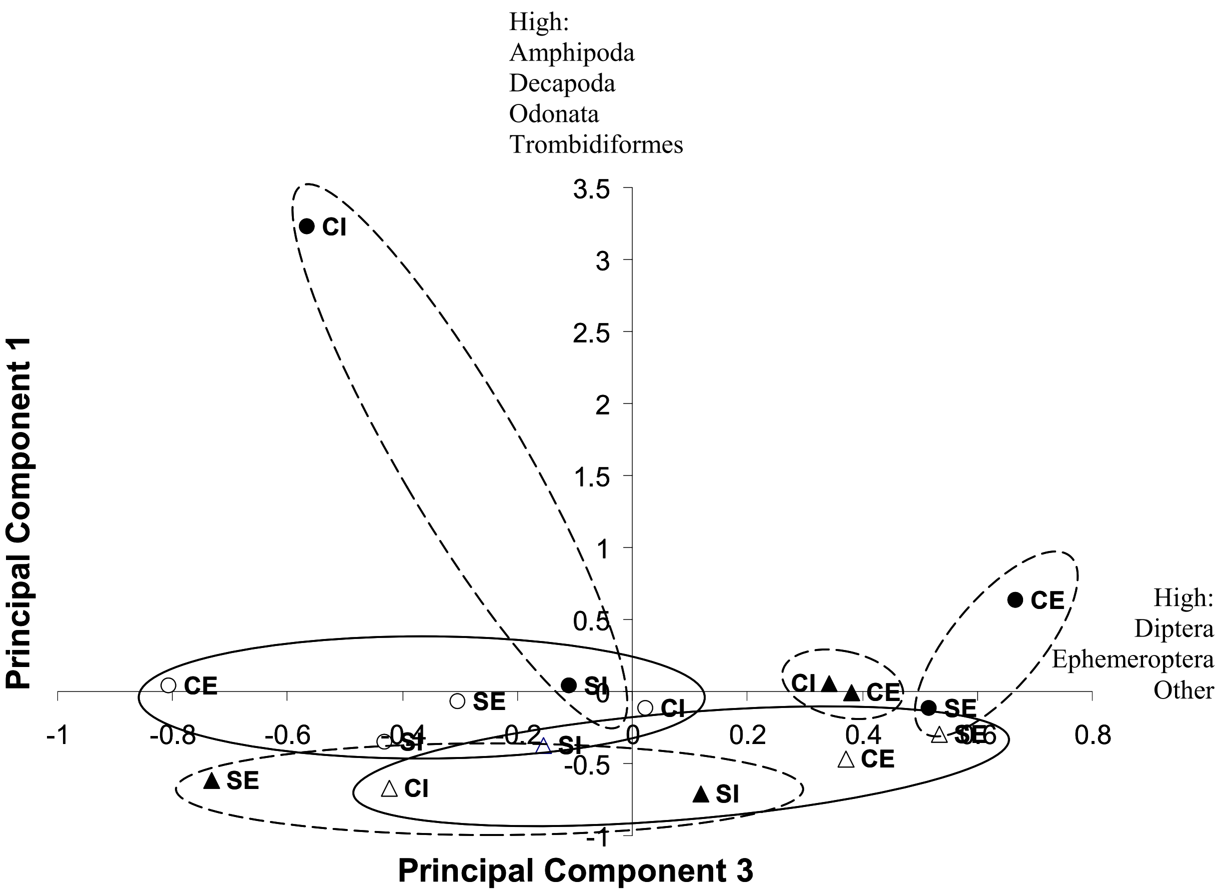

Figure 3.8. Principal components analysis of the macroinvertebrate assemblages and their distribution in hydrilla and coontail. Open circles represent hydrilla during Season 1 (May-June), closed circles represent hydrilla during Season 2 (July-August), open triangles represent coontail during Season 1, and closed triangles represent coontail during Season 2, C = canopy, S = sub-canopy, I = interior, E = edge. See text for interpretation of each principal component. Solid ellipse display differences within macrophyte type for Season 1. Dashed ellipse display differences in locations within the macrophyte.

Table 3.5. Associations between macroinvertebrate principal components and macrophyte habitats in the Atchafalaya Basin, Louisiana. Each main effect (Plant, Horizontal Location, Vertical Location) significance is reported by p -values under effect with greater scores.

	Plant		Horizontal Location		Vertical Location	
PC	Hydrilla	Coontail	Interior	Edge	Canopy	Sub-canopy
1					0.0156	
2		0.0103	0.0185			
3		0.0080				
4		0.0144				
5					0.0052	

Discussion

Macroinvertebrate taxa in ARB hydrilla and coontail beds were similar to communities found in two Florida lakes, which were dominated by dipterans, gastropods, caddisflies, dragonflies, and leeches (Schramm et al., 1987). Few other studies have compared macroinvertebrate communities in hydrilla and coontail habitats, although other studies in Florida have reported that dipterans, gastropods, ephemeropterans, amphipods, and caddisflies are abundant in hydrilla habitat (Martin and Shireman, 1976). Although a considerably different environment, a study in small lake in northern Italy (Cattaneo et al., 1998) found that coontail communities were dominated by gastropods and chironomid (Diptera) larvae.

Although macroinvertebrate densities were relatively similar for both macrophytes, gastropods were substantially more abundant in coontail beds. Overall physicochemistry appeared to be similar among plant types within seasons (although differences among bed positions were evident, particularly during Season 2), and gastropods tend to be tolerant of low DO conditions (McMahon, 1983), indicating that differences in abundance between macrophyte types were not likely due to poor water quality. Perhaps the architecture of coontail is more conducive to gastropod activity, or provides better foraging habitat or higher densities of periphyton or other epiphytic food resources. A similar study in a Wisconsin lake found that beds of coontail and watermilfoil (*Myriophyllum spicatum*) supported greater macroinvertebrate densities than plants with less structurally complex leaves like wild celery (*Vallisneria americana*), although differences in macroinvertebrate abundance among were not consistent across time (Chilton, 1990).

The lack of substantial increases in macroinvertebrate densities from Season 1 to Season 2 indicates that both macrophytes provide quality habitat during the summer in the ARB. Several studies have found that abundance of phytophilous macroinvertebrates is positively related to the surface area and structural complexity of the macrophytes they inhabit (Schramm et al., 1987; Kershner and Lodge, 1990; Thorp et al. 1997), and that macrophytes provide important refugia from predation (Balciunas and Minno, 1985; Schramm et al., 1987). In these respects, hydrilla and coontail both provide quality habitat for phytophilous organisms in the ARB.

Differences in the abundance of the macroinvertebrate taxa in relation to their positions in the macrophyte beds were likely related to sub-canopy reductions in DO concentrations. DO levels were always lower in the sub-canopy of each macrophyte, reducing the abundance and diversity of resident macroinvertebrates to those taxa adapted to low or highly fluctuating DO levels. Analyses of individual taxa revealed that significant differences between locations within the two macrophytes were most evident in hydrilla, where amphipods, decapods, and hemipterans were all more abundant in the canopy. Percent saturation of DO, particularly in the sub-canopy, was often below 30%, which has been shown to reduce respiration in a diversity of littoral and sub-littoral macroinvertebrates (Jonasson, 1978)

Principal component analysis provided additional evidence that macroinvertebrate abundance and species richness differed between seasons (Scott and Osborne, 1981), bed locations, and macrophyte species (Macan, 1961; Schramm et al., 1987). During Season 2, amphipods, decapods, and odonates were clearly more characteristic of the interior hydrilla canopy, although this trend was not evident during Season 1. Interestingly, this

abundance pattern did not seem to be related to diurnal DO levels, as canopy edge sites averaged 4.2 mg/l, whereas DO levels in the interior canopy averaged 2.6 mg/l. Although little is known about the effects of macrophyte bed position on the relative vulnerability of macroinvertebrates to littoral predators (particularly fishes), this abundance pattern could reflect increased predation on these taxa at the bed edge. A concurrent study showed that these three taxa made up 52.4% by number and 49.4% by weight of the diet of age-0 largemouth bass inhabiting dense hydrilla beds (Mason, 2002), and few bass were ever encountered in interior locations in high-density hydrilla beds (personal observation). Positional differences in macroinvertebrate assemblages were also evident for coontail during Season 2, as interior sites appeared to support higher densities of gastropods, leeches and water mites than edge sites. Interior sites did exhibit higher DO levels at this time relative to edge sites, but these taxa are relatively tolerant of hypoxic conditions, and it could be that, similar to hydrilla, edge positions resulted in higher levels of predation on these taxa.

The PCA also indicated that within seasons, macroinvertebrate assemblages in hydrilla and coontail beds were different, particularly in regards to abundance patterns of gastropods, leeches, and water mites (PC 2), and dipterans, ephemeropterans and other taxa (PC 3). During Season 1, all coontail sites supported higher densities of gastropods, leeches, and water mites than hydrilla sites, a trend that was also apparent during Season 2 at interior coontail locations. This pattern does not seem to be related to water quality differences between the two macrophyte types (Figures 1 and 2), and may be related more to plant architecture and the relative suitability of foraging habitats provided by hydrilla (high stem density, closed canopy, broader leaves) and coontail (lower stem

density, more open canopy, more threadlike leaves). During Season 2, edge positions in both hydrilla and coontail beds showed similarly high abundances of gastropods, leeches, and water mites, with the exception of sub-canopy edge sites in coontail. Again, this pattern did not appear to be related to water quality, and causes of these abundance differences are unknown.

Few studies have addressed differences in abundance and distribution patterns of macroinvertebrates in different macrophyte species. It is apparent from this study that, at least at the assemblage level, differences do exist, although the relative effects (and interactions) of declining or fluctuating water quality, macrophyte architecture, food resource quantity and quality, and predatory mortality on macroinvertebrate community composition remain to be identified. Both macrophytes in this study appeared to provide excellent habitat for a diversity of macroinvertebrates, and future studies should address their relative value (as well as other macrophyte species) as fish foraging habitat to better define the links between invertebrate and fish production, and the effects of exotic macrophyte invasions on the ecology of native invertebrate and fish assemblages.

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Chapter 4.
Summary

Macroinvertebrate abundance and distribution in hydrilla *Hydrilla verticillata* and coontail *Ceratophyllum demersum* habitats were assessed from May to July of 2001 in the Atchafalaya Basin in south central Louisiana. I collected a total of 34,996 macroinvertebrates from the two macrophytes using a specially constructed suitcase trap sampler that provided an efficient, quantitative method of sampling vegetation-associated macroinvertebrates. The suitcase trap proved to be easy to deploy and retrieve, effective in all plant densities, and allowed for estimation of macroinvertebrate densities by plant volume or dry weight of plant material. It also allowed for more effective methods of describing the vertical distribution of macroinvertebrates inhabiting macrophyte dominated littoral habitats when compared to traditional methods.

This study provided a description of the macroinvertebrate communities that inhabit the macrophytes of the Atchafalaya Basin that will help us better understand the relationships between littoral macrophytes and their resident macroinvertebrate communities, and perhaps better manage these plant beds as essential habitats for fishes and invertebrates. It also provided a comparison of macroinvertebrate communities and their assemblages between exotic hydrilla and native coontail as an assessment of potential impacts of hydrilla invasion on macroinvertebrate community composition. Several studied have addressed the relation of different plant species and their impacts on macroinvertebrate abundance and species diversity (Macan, 1961; Scott and Osborne, 1981; Schramm et al., 1987; Cyr and Downing, 1988). My study supported the assumption that different macrophyte species will yield differences in community structure and abundance of phytophilous macroinvertebrates (Krecker, 1939; Voigts,

1976). The negative impacts produced by dense stands of aquatic vegetation in the ecosystem dynamics and physicochemical parameters were a clear cause of differences in macroinvertebrate community distribution within the macrophyte beds. The fact that both habitats accounted for similar macroinvertebrate taxa provides evidence of both macrophytes serve as essential habitat. However, macrophyte growth conditions and highly fluctuating physicochemical parameters proved detrimental to some macroinvertebrate taxa as they displayed preference for certain locations within the macrophyte beds. Native coontail which is characteristically less dense (Savino and Stein, 1982) showed fewer macroinvertebrate variations for locations within the macrophyte bed.

Temporal variation has been addressed in previous studies as the abundance of macrophyte-related macroinvertebrates increases in relation to the amount of plant cover, surface area, and enhanced structural complexity of the macrophytes (Schramm et al., 1987; Keshner and Lodge, 1990; Thorp et al., 1997). However, the lack of substantial increases in macroinvertebrate densities from Season 1 to Season 2 indicates that both macrophytes provide quality habitat during the summer in the Basin. Macrophytes are considered to provide refuge from predation for aquatic macroinvertebrates (Balciunas and Minno, 1985; Schramm et al., 1987).

Although macroinvertebrate densities were relatively similar for both macrophytes, differences in macroinvertebrate assemblages between habitats suggest a distinction of macroinvertebrates towards certain macrophytes. Overall physicochemistry appeared to be similar among plant types within seasons indicating that differences in abundance between macrophyte types were not likely due to poor water quality. Macroinvertebrate

life cycles may play an important role in the abundance of certain taxa in relation to the macrophytes they inhabit. In addition, differences in macroinvertebrate assemblages and their distribution may be set by the physicochemical tolerance of individuals to the environmental factors posted by the macrophyte (Merrit and Cummins, 1996). However, habitat selection and local distribution patterns of macroinvertebrate communities may be significantly influenced by the competitors and predators present in such habitat (Hart and Resh, 1980; Peckarsky, 1980; Peckarsky and Dobson, 1980; Allan, 1982; Power et al., 1988).

In summary, the organisms collected from this study may represent the abundance and distribution of the macroinvertebrate community of the Atchafalaya Basin in Louisiana. Due to the known variability of invertebrate communities it would be incorrect to assume that the macroinvertebrate assemblages of this hydrilla and coontail habitats will be exactly similar to all exotic and native communities of submersed aquatic vegetation. It is possible that other not described environmental factors may have been at least partially responsible for the differences in macroinvertebrate abundance and distribution of hydrilla and coontail habitats. However, it would be safe to assume that the factors affecting macroinvertebrate assemblages would be the same in all macrophyte habitats, where macroinvertebrate abundance and community composition will be dictated by fluctuations of physicochemical parameters and the availability of plant cover.

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Appendix A.
Physicochemical Parameters Measured at Each Collection Locality and Date

Plant Type	ID#	Vertical Location	Horizontal Location	Season	Date	Temperature	Dissolved Oxygen	Depth	Specific Conductance	pH	Dry Weight (g)
HYDRILLA	1	CANOPY	EDGE	season1	5/17/2001	24.88	1.76	0.3	0.289	6.87	18.1
HYDRILLA	3	SUBCANOPY	EDGE	season1	5/17/2001	24.21	0.86	0.7	0.290	6.87	12.5
HYDRILLA	4	CANOPY	EDGE	season1	5/17/2001	25.31	2.19	0.3	0.289	6.89	36.9
HYDRILLA	5	SUBCANOPY	EDGE	season1	5/17/2001	24.18	0.67	0.8	0.291	6.83	7.2
HYDRILLA	6	CANOPY	INTERIOR	season1	5/17/2001	25.97	3.19	0.3	0.289	6.97	33.5
HYDRILLA	7	SUBCANOPY	INTERIOR	season1	5/17/2001	24.79	0.95	0.7	0.292	6.85	24.5
HYDRILLA	8	CANOPY	INTERIOR	season1	5/17/2001	25.62	3.14	0.3	0.288	6.93	9.2
HYDRILLA	9	SUBCANOPY	INTERIOR	season1	5/17/2001	24.52	1.22	0.7	0.290	6.86	20.6
HYDRILLA	10	CANOPY	EDGE	season1	5/17/2001	26.69	4.14	0.3	0.287	7.00	34.0
HYDRILLA	11	SUBCANOPY	EDGE	season1	5/17/2001	24.50	1.82	0.7	0.289	6.87	32.3
HYDRILLA	12	CANOPY	EDGE	season1	5/31/2001	27.20	2.99	0.2	0.358	7.04	20.7
HYDRILLA	13	SUBCANOPY	EDGE	season1	5/31/2001	27.22	3.03	0.6	0.357	7.00	19.3
HYDRILLA	14	CANOPY	INTERIOR	season1	5/31/2001	27.08	3.33	0.2	0.357	7.03	21.7
HYDRILLA	15	SUBCANOPY	INTERIOR	season1	5/31/2001	26.84	2.25	0.7	0.358	6.95	30.8
HYDRILLA	16	CANOPY	INTERIOR	season1	5/31/2001	27.08	3.46	0.1	0.357	7.06	34.9
HYDRILLA	17	SUBCANOPY	INTERIOR	season1	5/31/2001	27.00	2.73	0.6	0.358	7.08	42.9
HYDRILLA	18	CANOPY	EDGE	season1	5/31/2001	27.01	3.25	0.2	0.358	7.08	27.5
HYDRILLA	19	SUBCANOPY	EDGE	season1	5/31/2001	26.89	2.80	0.6	0.357	7.09	15.6
COONTAIL	20	CANOPY	EDGE	season1	6/15/2001	27.66	3.91	0.5	0.324	6.80	7.1
COONTAIL	21	SUBCANOPY	EDGE	season1	6/15/2001	25.22	0.46	1.4	0.234	6.68	10.6
COONTAIL	22	CANOPY	INTERIOR	season1	6/15/2001	28.64	3.83	0.5	0.341	6.78	32.2
COONTAIL	23	SUBCANOPY	INTERIOR	season1	6/15/2001	25.44	0.20	1.4	0.246	6.74	4.6
COONTAIL	24	CANOPY	EDGE	season1	6/15/2001	27.90	3.33	0.4	0.346	6.80	6.4
COONTAIL	25	SUBCANOPY	EDGE	season1	6/15/2001	25.97	0.76	1.4	0.340	6.81	15.3
COONTAIL	26	CANOPY	INTERIOR	season1	6/15/2001	27.85	3.72	0.4	0.327	6.78	18.3
COONTAIL	27	SUBCANOPY	INTERIOR	season1	6/15/2001	25.75	1.10	1.4	0.330	6.79	12.6
COONTAIL	29	CANOPY	EDGE	season1	6/15/2001	27.53	3.58	0.5	0.312	6.80	6.1

Appendix A. Continued

Plant Type	ID#	Vertical Location	Horizontal Location	Season	Date	Temperature	Dissolved Oxygen	Depth	Specific Conductance	pH	Dry Weight (g)
COONTAIL	30	SUBCANOPY	EDGE	season1	6/15/2001	25.59	0.73	1.4	0.328	6.76	6.6
HYDRILLA	31	CANOPY	EDGE	season2	7/5/2001	26.66	1.80	0.5	0.304	6.81	19.3
HYDRILLA	32	SUBCANOPY	EDGE	season2	7/5/2001	25.75	0.48	1.1	0.305	6.74	9.7
HYDRILLA	33	CANOPY	INTERIOR	season2	7/5/2001	26.68	1.60	0.5	0.305	6.80	17.1
HYDRILLA	34	SUBCANOPY	INTERIOR	season2	7/5/2001	25.66	0.25	1.3	0.305	6.74	23.8
HYDRILLA	35	CANOPY	EDGE	season2	7/5/2001	26.88	1.68	0.5	0.295	6.90	17.9
HYDRILLA	36	SUBCANOPY	EDGE	season2	7/5/2001	25.59	0.15	1.1	0.293	6.72	10.4
HYDRILLA	37	CANOPY	INTERIOR	season2	7/5/2001	29.57	3.56	0.5	0.291	7.21	11.8
HYDRILLA	38	SUBCANOPY	INTERIOR	season2	7/5/2001	25.61	0.38	1.2	0.288	6.74	19.4
HYDRILLA	39	CANOPY	EDGE	season2	7/5/2001	29.43	4.86	0.5	0.279	7.22	14.6
HYDRILLA	40	SUBCANOPY	EDGE	season2	7/5/2001	25.75	0.14	1.1	0.285	6.73	7.4
COONTAIL	41	CANOPY	EDGE	season2	7/6/2001	26.00	0.57	0.4	0.245	6.69	15.5
COONTAIL	42	SUBCANOPY	EDGE	season2	7/6/2001	25.61	0.35	1.4	0.240	6.66	10.9
COONTAIL	43	CANOPY	INTERIOR	season2	7/6/2001	27.40	2.25	0.5	0.222	6.76	49.8
COONTAIL	44	SUBCANOPY	INTERIOR	season2	7/6/2001	25.22	5.23	1.1	0.222	7.04	49.9
COONTAIL	45	CANOPY	EDGE	season2	7/6/2001	27.93	3.10	0.4	0.231	6.67	35.5
COONTAIL	46	SUBCANOPY	EDGE	season2	7/6/2001	24.95	0.18	1.2	0.251	6.68	33.1
COONTAIL	47	CANOPY	INTERIOR	season2	7/6/2001	29.81	5.75	0.4	0.223	7.45	22.8
COONTAIL	48	SUBCANOPY	INTERIOR	season2	7/6/2001	24.22	0.60	1.0	0.258	6.69	24.1
COONTAIL	49	CANOPY	EDGE	season2	7/6/2001	27.84	1.30	0.5	0.255	6.87	14.4
COONTAIL	50	SUBCANOPY	EDGE	season2	7/6/2001	25.26	1.98	1.0	0.256	6.83	5.3
HYDRILLA	51	CANOPY	EDGE	season2	7/6/2001	32.34	4.74	0.5	0.244	7.08	15.4
HYDRILLA	52	SUBCANOPY	EDGE	season2	7/6/2001	31.59	1.93	0.9	0.244	6.98	18.9
HYDRILLA	54	CANOPY	EDGE	season2	7/24/2001	33.35	7.03	0.5	0.283	7.17	17.7
HYDRILLA	55	SUBCANOPY	EDGE	season2	7/24/2001	31.78	2.60	0.9	0.245	7.05	14.4
HYDRILLA	58	CANOPY	EDGE	season2	7/24/2001	33.11	5.09	0.5	0.244	7.18	10.6
HYDRILLA	59	SUBCANOPY	EDGE	season2	7/24/2001	32.09	2.86	0.9	0.246	7.18	27.1

Appendix B.
Total Number of Macroinvertebrates Collected for Each Sample Bag

Plant Type	ID#	Vertical Location	Horizontal Location	Invert	Fish	Crawfish	Total
HYDRILLA	1	CANOPY	EDGE	150	0	2	152
HYDRILLA	3	SUBCANOPY	EDGE	199	0	1	200
HYDRILLA	4	CANOPY	EDGE	295	0	13	308
HYDRILLA	5	SUBCANOPY	EDGE	14	0	1	15
HYDRILLA	6	CANOPY	INTERIOR	211	3	4	218
HYDRILLA	7	SUBCANOPY	INTERIOR	48	0	4	52
HYDRILLA	8	CANOPY	INTERIOR	146	4	1	151
HYDRILLA	9	SUBCANOPY	INTERIOR	291	0	6	297
HYDRILLA	10	CANOPY	EDGE	597	22	0	619
HYDRILLA	11	SUBCANOPY	EDGE	76	5	4	85
HYDRILLA	12	CANOPY	EDGE	551	64	16	631
HYDRILLA	13	SUBCANOPY	EDGE	437	21	3	461
HYDRILLA	14	CANOPY	INTERIOR	504	20	10	534
HYDRILLA	15	SUBCANOPY	INTERIOR	436	24	0	460
HYDRILLA	16	CANOPY	INTERIOR	3236	37	7	3280
HYDRILLA	17	SUBCANOPY	INTERIOR	448	20	12	480
HYDRILLA	18	CANOPY	EDGE	576	36	8	620
HYDRILLA	19	SUBCANOPY	EDGE	362	1	1	364
COONTAIL	20	CANOPY	EDGE	168	1	0	169
COONTAIL	21	SUBCANOPY	EDGE	418	0	0	418
COONTAIL	22	CANOPY	INTERIOR	1096	8	0	1104
COONTAIL	23	SUBCANOPY	INTERIOR	18	0	0	18
COONTAIL	24	CANOPY	EDGE	114	0	0	114
COONTAIL	25	SUBCANOPY	EDGE	869	1	1	871
COONTAIL	26	CANOPY	INTERIOR	781	1	0	782
COONTAIL	27	SUBCANOPY	INTERIOR	548	1	0	549
COONTAIL	29	CANOPY	EDGE	97	1	0	98
COONTAIL	30	SUBCANOPY	EDGE	107	0	0	107
HYDRILLA	31	CANOPY	EDGE	436	6	1	443
HYDRILLA	32	SUBCANOPY	EDGE	192	1	0	193
HYDRILLA	33	CANOPY	INTERIOR	444	9	2	455
HYDRILLA	34	SUBCANOPY	INTERIOR	607	0	1	608
HYDRILLA	35	CANOPY	EDGE	587	4	0	591
HYDRILLA	36	SUBCANOPY	EDGE	76	1	0	77
HYDRILLA	37	CANOPY	INTERIOR	372	24	0	396
HYDRILLA	38	SUBCANOPY	INTERIOR	309	4	0	313
HYDRILLA	39	CANOPY	EDGE	77	3	1	81
HYDRILLA	40	SUBCANOPY	EDGE	84	0	0	84
COONTAIL	41	CANOPY	EDGE	980	8	0	988
COONTAIL	42	SUBCANOPY	EDGE	214	0	0	214
COONTAIL	43	CANOPY	INTERIOR	3616	20	4	3640
COONTAIL	44	SUBCANOPY	INTERIOR	2885	5	1	2891
COONTAIL	45	CANOPY	EDGE	1652	20	0	1672
COONTAIL	46	SUBCANOPY	EDGE	118	2	0	120
COONTAIL	47	CANOPY	INTERIOR	936	12	0	948

Appendix B. Continued

Plant Type	ID#	Vertical Location	Horizontal Location	Invert	Fish	Crawfish	Total
COONTAIL	48	SUBCANOPY	INTERIOR	892	16	0	908
COONTAIL	49	CANOPY	EDGE	752	0	0	752
COONTAIL	50	SUBCANOPY	EDGE	67	0	0	67
HYDRILLA	51	CANOPY	EDGE	1157	2	0	1159
HYDRILLA	52	SUBCANOPY	EDGE	1140	0	0	1140
HYDRILLA	54	CANOPY	EDGE	1507	2	0	1509
HYDRILLA	55	SUBCANOPY	EDGE	1208	0	0	1208
HYDRILLA	58	CANOPY	EDGE	929	34	0	963
HYDRILLA	59	SUBCANOPY	EDGE	1216	4	0	1220

Vita

José Checo Colón-Gaud was born in Mayagüez, Puerto Rico, on September 27, 1978. His parents are Víctor B. Colón and Marta I. Gaud. He attended private school at The Immaculate Conception Academy, Mayagüez, Puerto Rico, and was graduated in 1996.

He attended The University of Puerto Rico, Mayagüez, Puerto Rico, for a year before transferring to The University of Texas at El Paso, where he received a Bachelor of Science degree in biology with a minor in chemistry in May of 2000.

In June of 2000 he entered the Graduate School of Louisiana State University and is currently a candidate for the degree of Master of Science in fisheries from the School of Renewable Natural Resources under Dr. William E. Kelso.