

# Spatial Distribution of Macroinvertebrates Inhabiting Hydrilla and Coontail Beds in the Atchafalaya Basin, Louisiana

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## ABSTRACT

Hydrilla [*Hydrilla verticillata* (L.f.) Royle] became established in the Atchafalaya River Basin (ARB) in south central Louisiana during the 1970s, and now dominates the submergent macrophyte community. We examined the potential effects of this shift in macrophyte composition on the distribution of phytomacrofauna by comparing water quality and macroinvertebrate assemblage structure in canopy and sub-canopy habitats at edge and interior locations within hydrilla and native coontail (*Ceratophyllum demersum* L.) beds during the latter stages of the 2001 flood pulse. Both plant species exhibited similar water quality characteristics during the study, with significantly higher temperature, dissolved oxygen, and pH levels in canopy habitats. Principal components analysis of log-transformed macroinvertebrate densities identified four assemblages that together accounted for 63.5% of the variation in the density data. The Gastropoda-Hydrachnida assemblage exhibited higher densities in coontail during May-June (declining river stages), and was more abundant at interior locations in both macrophyte beds during July (stable river stages). The Hemiptera-Amphipoda assemblage exhibited higher densities in the canopies of the two plants during both sampling periods, as did the Decapoda-Odonata assemblage in July. The Diptera-Coleoptera assemblage showed a similar trend in vertical distribution, as well as marginally higher densities in hydrilla beds. The continued spread of hydrilla throughout the ARB has reduced the diversity of macrophyte habitats available to phytophilous macroinvertebrates, and has resulted in pervasive hypoxia in the macrophyte sub-canopy over large portions of available littoral habitat, with significant impacts on the vertical distribution of littoral macroinvertebrates.

*Key words:* *Hydrilla verticillata*, *Ceratophyllum demersum*, hypoxia, invasive species.

## INTRODUCTION

The contribution of aquatic macrophytes to the structure and function of littoral freshwater habitats has long been recognized (Jeppesen et al. 1998, Grenouillet et al. 2002), and

numerous studies support the contention that shifts in the species composition of littoral macrophyte communities will likely have significant effects on the abundance and distribution of phytophilous macroinvertebrates. Many macroinvertebrate taxa exhibit preferences for specific macrophytes based on plant density and architecture (Dvořák and Best 1982, Cyr and Downing 1988) and associated differences in the composition and abundance of epiphytic forage (Rooke 1986, Dudley 1988, Cattaneo et al. 1998). Other macrophyte characteristics also have been cited as important factors influencing the phytomacrofauna, including seasonal patterns of macrophyte growth and senescence (Smock and Stoneburner 1980, Hargeby 1990), and plant-mediated shifts in water quality (Froge et al. 1990, Rose and Crumpton 1996, Unmuth et al. 2000) and invertebrate vulnerability to fish predation (Crowder and Cooper 1982, Diehl 1988, Diehl and Kornijów 1998). Most importantly, the diversities of littoral macroinvertebrates and macrophytes appear to be closely related (Brown et al. 1988), and the ability of aggressive exotic macrophytes to supplant native vegetation (Madsen et al. 1991) likely has significant effects on the structure of shallow-water invertebrate communities (Cattaneo et al. 1998, Cheruvilil et al. 2001, 2002) and their role in the trophic structure of lentic and lotic systems (Gotceitas 1990, Dionne and Folt 1991).

In the last four decades, the composition of many littoral macrophyte communities throughout the southeastern United States has changed significantly with the spread of exotic hydrilla (Colle and Shireman 1980, Keast 1984). Hydrilla arrived in the Atchafalaya River Basin (ARB) in south central Louisiana sometime during the mid-1970s, and along with water hyacinth [*Eichhornia crassipes* (Mart.) Solms] have replaced coontail and fanwort (*Cabomba caroliniana* Gray) as the dominant species of aquatic vegetation in the ARB. Although hydrilla provides shelter, breeding sites, and cover for numerous invertebrate and vertebrate species (Barnett and Schneider 1974, Balciunas and Minno 1984), high density hydrilla stands can significantly impact littoral water quality (Steward 1970, Pesacreta 1988) as well as invertebrate abundance and distribution (Scott and Osborne 1981).

Numerous studies have investigated the macrophyte specificity of phytophilous macroinvertebrates in both lentic (Hanson 1990, Peets et al. 1994, Dvořák 1996) and lotic (Rooke 1984, Iverson et al. 1985, Tokeshi and Pinder 1985) systems. Fewer investigations have focused on phytomacrofauna differences between native and invasive plants (Keast 1984, Chilton 1990, Cheruvilil et al. 2001), the spatial distribution of

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the phytomacrobenthos within littoral macrophyte beds, or the potential influence of sub-canopy water quality on macroinvertebrate abundance. Higler (1975) noted differences in macroinvertebrate community composition within a water soldier (*Stratiotes aloides* L.) bed that were related to a successional gradient of submerged versus floating plants. Junk (1977) reported substantial reductions in dissolved oxygen (DO) levels within water hyacinth and swamp millet [*Isachne globosa* (Thunb.) O. Ktze] beds in a Thailand reservoir that resulted in much lower densities of microcrustaceans, aquatic insects, and bivalves relative to samples collected near the bed edge. Similar results were reported for dense beds of exotic Eurasian milfoil (*Myriophyllum spicatum* L.), which supported a higher density, biomass, and richness of phytomacrobenthos in canopy and edge habitats due to differences in milfoil architecture and water quality (Sloey et al. 1997).

Because of the importance of macrophyte community composition to the dynamics of littoral macroinvertebrates, the reduction in native plant abundance may have significant consequences for the distribution and abundance of ARB phytomacrobenthos. In this study, we compared water quality and macroinvertebrate abundance and distribution (edge versus middle, surface versus bottom) between nearly monospecific stands of hydrilla and coontail to assess potential changes in the ARB littoral macroinvertebrate community related to the continued spread of hydrilla in this subtropical swamp habitat. Although coontail is not a rooted plant, modified leaves often anchor plants to the substrate (Godfrey and Wooten 1981). In the ARB, coontail beds were stationary throughout the year (often interspersed with large woody debris and cypress stumps) and occupied the entire water column, so this seemed an appropriate native species for ecological comparison to exotic hydrilla.

## MATERIALS AND METHODS

From May to August 2001, samples of hydrilla and coontail, approximately 10 to 40 g dry weight, were obtained from two field sites in the ARB. Collections were made with a specially-designed sampling device that consisted of a 60 by 45-cm suitcase constructed of 0.5-cm thick angle aluminum with 600- $\mu$  stainless steel mesh walls (Colon-Gaud and Kelso 2003). 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 (primarily stems) 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). At each collection location between 10 a.m. and 1:00 p.m., we measured water temperature, DO, and pH with a DataSond20 (Hydrolab® Inc., Denver, CO) portable water quality meter.

All plant material and associated macroinvertebrates from each sample were washed into a numbered plastic bag, Rose Bengal (a biological stain for animal tissue) was added to stain the sample, and the bag was transported on ice and then frozen in the laboratory. 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 included the total number and density (number per g of dry plant matter) of macroinvertebrates in each sample. Aquatic insects were identified according to Merritt and Cummins (1996), and other invertebrates were identified according to Pennak (1989) and Thorp and Covich (2000).

Samples were divided into two seasons prior to analyses; May-June samples were collected when macrophyte densities were lower and water levels were elevated due to a late stage increase from 17 May (2.4 m NGVD) to 15 June (3.6 m; Atchafalaya River gauge 03120, U.S. Army Corps of Engineers, New Orleans District). July samples were collected when macrophyte densities were high and water levels were declining or stable. All data were entered into a computer for statistical analyses with the SAS statistical package (SAS Institute, Inc. 2001). We log-transformed the temperature and DO data to improve normality prior to analysis, and then used general linear models with Tukey-Kramer tests of least-square mean differences to examine spatial and temporal trends in water quality between the two macrophyte species. The Dunn-Sidak method was used to adjust  $\alpha$ -levels for each of the three variables to maintain an overall alpha-level of 0.05 (Sokal and Rohlf 1995).

For the macroinvertebrate data, we transformed the densities (log number per gram dry weight of plant material), grouped the organisms into 12 taxonomic categories (including other), and examined differences in macroinvertebrate mean densities between the two plant species with a general linear model and Tukey-Kramer tests of least-square mean differences, again adjusting  $\alpha$ -levels for each of the 12 tests to maintain an overall alpha-level of 0.05 (Sokal and Rohlf 1995). We then used principal components analysis (PCA) to investigate differences in distribution among seasons and bed positions for the 12 taxonomic groups. By using the PCAs, we were able to avoid problems with non-independence of macroinvertebrate densities, and also identify principal components (hereafter referred to as assemblages) made up of macroinvertebrate groups that exhibited similar patterns in time or space. We used variables with loadings (correlations of each taxonomic group with the assemblage) greater than |0.35| to identify important taxonomic groups within each assemblage (0.35 represents a significant correlation at an  $\alpha$ -level of 0.01 for 50 degrees of freedom; each taxonomic group was represented in 54 collections). Scores were then calculated for each collection location for all assemblages with eigenvalues over 1.0 (these assemblages explained more variation in density than any one of the 12 taxonomic groups). High scores reflected higher densities of those taxonomic groups loading positively on that assemblage at that collection location (and low densities of groups loading negatively on that assemblage), and we used these location scores in a mixed-model analysis of variance to examine differences in macroinvertebrate communities between sites (hydrilla versus coontail), seasons (early summer versus late summer), locations (interior versus edge), and positions (canopy versus sub-canopy), with Tukey-Kramer tests of least-square mean differences.

## RESULTS

*Water Quality.* Overall trends in water quality were relatively consistent for similar positions in the hydrilla and coontail beds for both seasons (Table 1). Analyses of variance revealed no differences in temperature or DO between the macrophyte species ( $P > 0.46$ ), seasons ( $P > 0.10$ ) or bed locations (edge versus interior;  $P > 0.48$ ). However, pH was higher in hydrilla ( $6.94 \pm 0.03$  SE) than coontail ( $6.82 \pm 0.04$ ;  $F = 7.83$ ,  $P = 0.008$ ), and temperature, DO, and pH levels were significantly higher in the canopies of both plants (Table 2).

*Macroinvertebrate Abundance and Distribution.* We collected a total of 34,996 macroinvertebrates from hydrilla and coontail beds in the ARB from May to July 2001. Although mean densities were similar for most of the taxonomic groups in the two macrophytes (Table 3), gastropods were significantly more abundant in coontail beds, with a similar trend exhibited by rhyndobdellid leeches and hydracarine water mites. In contrast, decapods showed a trend of higher densities in ARB hydrilla beds.

Principal components analysis of the 12 taxonomic groups resulted in four assemblages with eigenvalues over 1.0 that together explained 63.5% of the variation in the data (Table 3). These assemblages (identified by the two taxa loading most highly on that assemblage) included Gastropoda-Hydrachnida (29.2% of the cumulative variance), Decapoda-Odonata (13.9%), Diptera-Coleoptera (10.7%), and Hemiptera-Amphipoda (9.7%).

Site scores for the Gastropoda-Hydrachnida assemblage were significantly higher in coontail ( $0.72 \pm 0.27$  SE) than hydrilla ( $-0.23 \pm 0.20$ ,  $P = 0.008$ ), reflecting higher overall densities of snails, leeches, water mites, and mayflies (positively

loading groups, Table 4), and lower densities of pyralid moth larvae (negative loading) in the native macrophyte (Figure 1). Further analysis based on a marginally insignificant species\*season interaction ( $P = 0.068$ ) revealed that this assemblage was more abundant in coontail ( $0.77 \pm 0.48$ ) than hydrilla ( $-0.82 \pm 0.34$ ) during May-June ( $P = 0.01$ ), but exhibited similar abundance in the two macrophytes in July (coontail  $0.67 \pm 0.26$ , hydrilla  $0.35 \pm 0.23$ ,  $P = 0.89$ ). This assemblage also showed significant differences in horizontal distribution within the macrophyte beds ( $P = 0.034$ ), but again there was a season\*location interaction ( $P = 0.002$ ) that reflected a more uniform spatial distribution for this assemblage during May-June ( $P = 0.40$  between edge and interior locations), but higher densities at interior ( $1.06 \pm 0.26$ ) than edge locations ( $-0.03 \pm 0.20$ ) during July ( $P = 0.0006$ ; Figure 1).

Two assemblages showed differences in abundance between canopy and sub-canopy habitats. Scores for the Hemiptera-Amphipoda assemblage were much higher (higher densities of hemipterans, amphipods, and leeches) in the canopy of both plants regardless of season (canopy =  $0.46 \pm 0.21$ , sub-canopy =  $-0.39 \pm 0.21$ ,  $P = 0.001$ ; Figure 2). The Decapoda-Odonata assemblage (which included positive associations with mayflies and other) exhibited the same overall trend of higher scores in the canopy ( $P = 0.02$ ), but there was a significant position\*season interaction ( $P = 0.006$ ), which indicated similar canopy and sub-canopy densities of these taxa during May-June ( $P = 0.98$ ), but higher densities in canopy ( $0.78 \pm 0.25$ ) relative to sub-canopy ( $-0.49 \pm 0.25$ ) habitats in July (particularly at interior hydrilla locations; Figure 2). The Diptera-Coleoptera assemblage did not exhibit any significant density patterns, although there was a trend of

TABLE 1. SEASONAL UNTRANSFORMED MEAN VALUES (STANDARD ERRORS ARE IN PARENTHESES) FOR PHYSICOCHEMICAL PARAMETERS IN HYDRILLA AND COONTAIL HABITATS IN THE ATCHAFALAYA BASIN, LOUISIANA DURING 2001.

Site	Position	Location	Dissolved Oxygen (mg/L)	Temperature	pH
May-June					
Hydrilla	Canopy	Interior	3.28 (0.07)	26.44 (0.38)	7.00 (0.03)
	Sub-canopy	Interior	1.79 (0.42)	25.79 (0.66)	6.94 (0.05)
	Canopy	Edge	2.87 (0.42)	26.22 (0.47)	6.98 (0.04)
	Sub-canopy	Edge	1.84 (0.48)	25.40 (0.68)	6.93 (0.05)
Coontail	Canopy	Interior	3.78 (0.06)	28.25 (0.40)	6.78 (0.00)
	Sub-canopy	Interior	0.65 (0.45)	25.60 (0.16)	6.77 (0.03)
July					
Hydrilla	Canopy	Edge	3.61 (0.17)	27.70 (0.11)	6.80 (0.00)
	Sub-canopy	Edge	0.65 (0.10)	25.59 (0.22)	6.75 (0.04)
	Canopy	Interior	2.58 (0.98)	28.13 (1.45)	7.01 (0.21)
	Sub-canopy	Interior	0.32 (0.07)	25.64 (0.03)	6.74 (0.00)
Coontail	Canopy	Edge	4.20 (0.85)	30.30 (1.25)	7.06 (0.07)
	Sub-canopy	Edge	1.36 (0.51)	28.76 (1.37)	6.90 (0.08)
	Canopy	Interior	4.00 (1.75)	28.61 (1.21)	7.11 (0.35)
	Sub-canopy	Interior	1.89 (2.06)	24.72 (0.50)	6.87 (0.18)
Hydrilla	Canopy	Edge	1.66 (0.75)	27.26 (0.63)	6.74 (0.06)
	Sub-canopy	Edge	0.84 (0.57)	25.27 (0.19)	6.72 (0.05)

TABLE 2. COMPARISONS OF TEMPERATURE, pH, AND DISSOLVED OXYGEN LEVELS BETWEEN CANOPY AND SUB-CANOPY HABITATS IN HYDRILLA AND COONTAIL HABITATS IN THE ATCHAFALAYA BASIN, LOUISIANA, FROM MAY-JULY 2001, WITH \* DENOTING A SIGNIFICANT DIFFERENCE BETWEEN HABITATS.

Parameter	Canopy	Sub-canopy	F-value	P
Temperature	27.90 ± 0.42	26.19 ± 0.42	14.79	0.0004*
pH	6.93 ± 0.03	6.83 ± 0.03	5.59	0.0233*
Dissolved oxygen	3.30 ± 0.28	1.36 ± 0.24	30.99	0.0001*

higher densities in hydrilla ( $0.26 \pm 0.46$ ) than coontail ( $-0.55 \pm 0.53$ ;  $P = 0.07$ ), and higher densities in canopy ( $0.05 \pm 0.46$ ) versus sub-canopy ( $-0.33 \pm 0.46$ ;  $P = 0.09$ ) habitats.

## DISCUSSION

The physicochemical environments provided by the two aquatic plants were similar, with minimal differences in temperature or pH between plants, bed positions, or sampling periods. Although both plants exhibited significantly higher temperature and pH levels in canopy habitats, these differences were not likely to be biologically significant to resident organisms (Thorp and Covich 2000). In contrast, mean sub-canopy DO levels were typically below 2.0 mg/l, even during the flood pulse. Nocturnal declines in canopy DO levels and persistent hypoxia in sub-canopy habitats is a common phenomenon in submerged macrophyte beds (Carpenter and Lodge 1986, Froge et al. 1990) that likely selects for macroinvertebrate taxa such as chironimids and snails, which are highly tolerant of low DO conditions (McMahon 1983, Ward 1992), or mobile taxa such as amphipods and decapods that can locate normoxic refugia within dense macrophyte stands (Miranda et al. 2000). Percent saturation of DO was often below 30%, particularly in the sub-canopy, which has been shown to reduce respiration in a diversity of littoral and sublittoral macroinvertebrates (Jonasson 1978).

Prior to sampling, we developed several hypotheses concerning the distribution and abundance of phytophilous macroinvertebrates based on the habitat characteristics of these two macrophytes. Several studies have found that macroinvertebrate abundance is positively related to macrophyte

surface area and structural complexity (Kershner and Lodge 1990, Thorp et al. 1997). These two plants are qualitatively similar in architecture (relatively complex), but we predicted that macroinvertebrate densities would be greater in hydrilla because of higher stem and canopy densities and reduced fish predation (Savino and Stein 1982, Schramm et al. 1987) relative to coontail. We expected higher densities of macroinvertebrates during July relative to May-June due to more stable water levels and increased periphyton abundance later in the summer, as well as higher densities in the canopy due to persistent sub-canopy hypoxia in both plant species. Finally, based on the results of Sloey et al. (1997), we predicted that macroinvertebrate densities would be higher at the bed edge.

Differences in macroinvertebrate density between the two plants were evident for the Gastropoda-Hydrachnida assemblage, but contrary to our expectations, densities were higher in native coontail. This difference does not seem to be attributable to plant-related variation in water quality (both beds exhibited sub-canopy hypoxia), but may be related to variation in available periphyton food resources. Differences in periphyton density among plants of varying architecture have been reported for several macrophyte taxa (Cattaneo and Kalff 1980, Allen and Ocvetki 1981). Although coontail is more finely dissected than hydrilla, differences in architecture parallel those of *Elodea canadensis* Rich. and Eurasian watermilfoil, which were found to support similar densities of periphyton in Canadian lakes (LaLonde and Downing 1991). However, in the ARB, it may be the growth characteristics of these plants rather than plant architecture that has the greatest effect on the associated periphyton community.

TABLE 3. UNTRANSFORMED MEAN DENSITIES ( $\pm$  SE) OF MACROINVERTEBRATES FOUND IN HYDRILLA AND COONTAIL HABITATS IN THE ATCHAFALAYA BASIN, LOUISIANA, FROM MAY-JULY 2001. TESTS OF SIGNIFICANT DIFFERENCES WERE BASED ON LOG-TRANSFORMED DATA, WITH \* DENOTING A SIGNIFICANT DIFFERENCE BETWEEN PLANT SPECIES.

Taxa	Coontail	Hydrilla	Pvalue
Amphipoda	1.87 ± 0.30	1.52 ± 0.27	0.28
Coleoptera	0.18 ± 0.04	0.21 ± 0.67	0.76
Decapoda	1.01 ± 0.31	1.75 ± 0.38	0.07
Diptera	7.03 ± 1.26	5.24 ± 0.95	0.16
Ephemeroptera	1.49 ± 0.25	3.20 ± 0.71	0.58
Gastropoda	12.40 ± 2.61	3.00 ± 0.75	<0.0001*
Hemiptera	0.56 ± 0.09	0.56 ± 0.11	0.68
Lepidoptera	0.20 ± 0.09	0.12 ± 0.03	0.92
Odonata	0.75 ± 0.15	1.54 ± 0.32	0.28
Rhynchobdellida	0.28 ± 0.07	0.11 ± 0.02	0.07
Hydrachnida	0.65 ± 0.12	0.37 ± 0.06	0.04
Other	0.14 ± 0.06	0.21 ± 0.06	0.93

TABLE 4. MACROINVERTEBRATE ASSEMBLAGES DETERMINED FROM PRINCIPAL COMPONENTS ANALYSIS OF ORGANISMS COLLECTED FROM HYDRILLA AND COONTAIL HABITATS IN THE ATCHAFALAYA BASIN, LOUISIANA. ONLY LOADINGS GREATER THAN |0.35| ARE PRESENTED FOR EACH ASSEMBLAGE.

Taxa	Assemblage			
	1	2	3	4
Amphipoda		0.49		0.64
Coleoptera			0.72	
Decapoda		0.88		
Diptera			0.75	
Ephemeroptera	0.49	0.37	0.47	
Gastropoda	0.83			
Hemiptera				0.84
Lepidoptera	-0.46		0.51	
Odonata		0.70		
Rhynchobdellida	0.61			0.47
Hydrachnida	0.71			
Other		0.58		

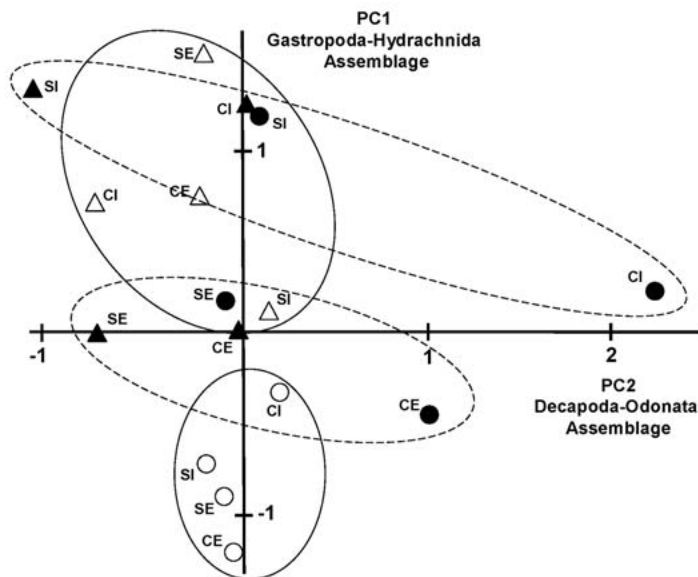


Figure 1. Bi-plot of mean sampling location scores for macroinvertebrate principal components PC1 (Gastropoda-Hydrachnida assemblage) and PC2 (Decapoda-Odonata assemblage) in Atchafalaya Basin coontail (triangles) and hydrilla (circles) beds during May-June (open symbols) and July (closed symbols). Samples were taken at canopy (C) and sub-canopy (S) locations at the edge (E) and interior (I) of the plant beds. Note differences in scores between coontail and hydrilla along PC1 in May-June (solid ellipses), and between interior and edge habitats in July (dashed ellipses).

Periphyton density declines with depth due to shading effects from phytoplankton (LaLonde and Downing 1991) and plant biomass in the upper water column (Cattaneo and Kalff 1980, Allen and Ocvski 1981, Cattaneo et al. 1998), but the latter effect is much more apparent in ARB hydrilla beds. Hydrilla grows rapidly during the spring flood pulse, and subsequently collapses into a dense surface canopy as flood waters recede. Coontail typically does not exhibit similar densities in the upper water column, and increased light penetration likely results in higher periphyton densities at greater depths in coontail beds. Such a relationship might be particularly evident for this assemblage, given the importance of periphyton food resources to the diet of aquatic snails (Lodge 1986, James et al. 2000, Pinowska 2002).

Although overall seasonal differences in macroinvertebrate density related to periods of increasing (May-June) and decreasing (July) stages in the Atchafalaya River were not apparent for any of the assemblages, the Gastropoda-Trombidiformes assemblage was much more abundant at interior bed locations in July. Sloey et al. (1997) reported a higher biomass of macroinvertebrates at the edges of Eurasian milfoil stands, and attributed the higher biomass to increased foliage densities, particularly at the shallow bed edge. A similar distribution pattern was reported for macroinvertebrates inhabiting a swamp millet stand in a Thailand reservoir, although lower densities in the central portion of the bed were attributed to poor water quality (Junk 1977). We did not quantify coontail and hydrilla foliage density, but there were no obvious trends in canopy structure between bed locations for either plant species. Greater canopy and sub-canopy hypoxia at the bed edge (at least for coontail; Table 1), increased predation by

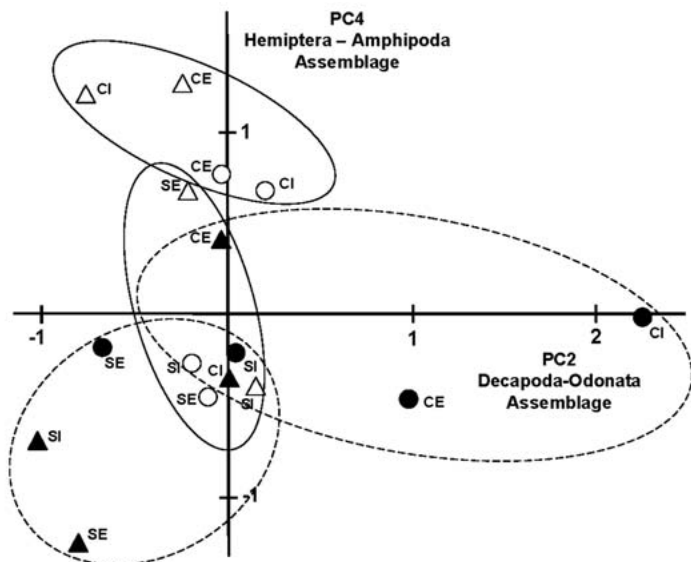


Figure 2. Bi-plot of mean sampling location scores for macroinvertebrate principal components PC2 and PC4 (Hemiptera-Amphipoda assemblage) in Atchafalaya Basin coontail and hydrilla beds. See Figure 1 for symbols. Note the consistently higher scores for canopy habitats along PC4 during May-June (solid ellipses) and July (dashed ellipses). Note similar scores along PC2 during May-June, with higher canopy scores during July, particularly for hydrilla.

fishes at the bed edge (Gotceitas 1990), or more favorable food resources on older plants in the bed interior (Beckett et al. 1992) might account for these density differences in July samples. However, if these factors were important, it is unclear why the other macroinvertebrate assemblages would not also have exhibited this spatial abundance pattern.

Temporal differences in macroinvertebrate distribution also were evidenced by increased densities of the Decapoda-Odonata assemblage in the bed canopies during July, but not in May-June. By July, water levels had stabilized after the spring flood pulse, with essentially no input of normoxic water into the plant beds. Both beds had experienced sub-canopy hypoxia for at least 1.5 months, which apparently restricted movements of these taxa below the normoxic canopy. The Hemiptera-Amphipoda assemblage exhibited this distribution pattern during both sampling periods, suggesting taxa-specific tolerance to declining water quality in the plant beds. The Gastropoda-Hydrachnida and Diptera-Coleoptera assemblages showed no vertical distribution patterns within the plant beds regardless of sampling period, but these assemblages were dominated by taxa such as snails, leeches, and chironimids that are tolerant of hypoxic conditions (Jonasson 1978, McMahon 1983, Pinder 1995).

The dynamics of phytophilous macroinvertebrate communities in lowland river systems is strongly influenced by season, macrophyte type, and changes in depth associated with flooding from the annual flood pulse (Humphries 1996). In addition to macrophyte architecture and seasonal flooding, we believe that macroinvertebrate distributions in ARB hydrilla and coontail beds illustrate the pivotal role of dense, architecturally complex macrophytes in mediating littoral DO dynamics and macroinvertebrate habitat quality. Phytophil-

ous macroinvertebrates in the ARB did not exhibit strikingly different abundance patterns in the native and exotic macrophytes. Sub-canopy DO levels were already low in both plant beds by the latter stages of the flood pulse, and remained low through early fall. However, native taxa such as coontail and fanwort that were historically common in the ARB have experienced substantial declines in abundance as hydrilla distribution and density have increased along the margins of ARB lakes, canals, and bayous. The ARB floodplain typically experiences a 2-3 m depth increase during the April-May flood pulse in the Atchafalaya River, resulting in extremely high canopy densities in hydrilla beds as floodwaters recede and the hydrilla plants collapse. Hydrilla now dominates virtually all vegetated littoral areas in the ARB not covered by water hyacinth, and provides marginal habitat value for most macroinvertebrate taxa in the sub-canopy. Prior to 1970, native macrophytes such as coontail and fanwort occurred in isolated, relatively sparse beds that contributed to the overall diversity of littoral habitats in the ARB. The arrival and spread of hydrilla throughout the southern ARB, however, has resulted in large expanses of dense littoral vegetation and a pervasive decline in habitat diversity for phytophilous macroinvertebrates. Unquestionably, the impact of this aggressive exotic macrophyte on water quality, invertebrates, and fishes (Maceina and Shireman 1982, Schmitz et al. 1993) over the last three decades has resulted in significant changes in the biotic structure and dynamics in the ARB littoral zone.

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