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Do predator exclusion, position, and plant architecture influence hydrilla-dwelling macroinvertebrate communities?

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DO PREDATOR EXCLUSION, POSITION, AND PLANT ARCHITECTURE INFLUENCE
HYDRILLA-DWELLING MACROINVERTEBRATE COMMUNITIES?

A Thesis

Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree of
Master of Science

in

The School of Renewable Natural Resources

by
Jonathan C. Fisher
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TABLE OF CONTENTS

ACKNOWLEDGEMENTS.....	ii
ABSTRACT.....	iv
CHAPTER	
1 INTRODUCTORY MATERIAL.....	1
INTRODUCTORY METHODS.....	6
2 EFFECTIVENESS OF ARTIFICIAL PLANTS IN SUBSURFACE EXCLOSURES AS A SUBSTRATE FOR HYDRILLA-DWELLING MACROINVERTEBRATE COMMUNITIES.....	11
METHODS.....	11
RESULTS.....	15
DISCUSSION.....	19
3 THE EFFECTS OF PREDATOR EXCLUSION AND BED POSITION ON HYDRILLA-DWELLING MACROINVERTEBRATE COMMUNITIES.....	23
METHODS.....	23
RESULTS.....	26
DISCUSSION.....	29
4 THE EFFECTS OF PREDATOR EXCLUSION, POSITION, AND PLANT ARCHITECTURE ON HYDRILLA-DWELLING MACROFAUNAL COMMUNITIES.....	35
METHODS.....	35
RESULTS.....	38
DISCUSSION.....	42
5 DIETS OF FISHES INHABITING HYDRILLA BEDS.....	49
METHODS.....	49
RESULTS.....	52
DISCUSSION.....	56
6 SYNTHESIS AND CONCLUSIONS.....	59
LITERATURE CITED.....	64
VITA.....	76

ABSTRACT

Hydrilla verticillata invaded south central Louisiana during the 1970s subsequently becoming the dominant submerged macrophyte in floodplain habitats of the Atchafalaya River Basin. The effects of hydrilla on littoral habitat structure, water quality, fish, and macroinvertebrates have been pervasive, and I hypothesized that dense hydrilla stands would also impact vertebrate predation on resident macroinvertebrates, although predation effects would likely be mediated by bed position. During 2003 and 2004, I conducted exclosure experiments in the Atchafalaya River Basin with artificial substrates to test for variations in hydrilla bed macroinvertebrate communities caused by predation, plant architecture, and bed position. To determine invertebrates consumed by fishes, I also examined stomach contents of potentially invertivorous fishes inhabiting these beds. Results indicate that position and predation are important in structuring macroinvertebrate communities, whereas plant architecture had little effect. My diet analyses indicate that the fishes sampled fall into three categories: 1) those that do not feed on macroinvertebrates; 2) those that feed on small invertebrates (e.g., dipterans); and 3) those that feed on large invertebrates (e.g., decapods) and poeciliid fishes. Further, the diets of the invertivorous fishes coincide with the distributions found in the macroinvertebrate community and, in general, those macroinvertebrates most commonly found in fish diets occurred in greater densities within the bed interior.

CHAPTER 1: INTRODUCTORY MATERIAL

Over the past century, waterways in the United States have been invaded by numerous exotic flora and fauna (<http://www.invasivespecies.gov/>), many of which have proven to cause significant changes in the ecology of the invaded system (Townsend 1996; Valley and Bremigan 2002). In Louisiana, many freshwater habitats are congested with hydrilla (*Hydrilla verticillata*), common salvinia (*Salvinia minima*), and water hyacinth (*Eichhornia crassipes*), as well as other species that can impede recreational boaters and negatively affect water quality (Langeland 1996) and the distribution and abundance of resident faunal communities (Colon-Gaud et al. 2004).

Aquatic macrophytes modify hydrology and sequester sediments and nutrients (Howard-Williams 1983) and affect many physicochemical parameters in the surrounding water column. Dense beds can lower pH and light levels in the sub-canopy, which, in conjunction with day/night cycling of photosynthesis/respiration, can lead to significant modifications in dissolved oxygen dynamics (Buscemi 1958; Kollman and Wali 1976; Reddy 1981; Carpenter and Lodge 1986; Suthers and Gee 1986; Frodge et al. 1990; Carter et al. 1991; Rose and Crumpton 1996), especially among canopy-forming plant species (Haller and Sutton 1975; Wychera et al. 1993; Smart et al. 1994).

Interactions between macrophytes and phytoplankton can also affect turbidity levels and primary production. In the littoral zone, algal communities occur both as phytoplankton in the water column and epiphyton on macrophyte substrates. Littoral phytoplankton can shade aquatic plants and limit or prevent macrophyte growth

(Roberts et al. 2003). However, submerged aquatic plants such as hydrilla can also inhibit littoral phytoplankton densities by reducing nutrient concentrations (Jones 1990), and also trap suspended particles, decreasing turbidity (van den Berg et al. 1997; Pluntke and Kozerski 2003). Epiphytic algae benefit from increased surface areas in dense plant beds, and epiphytic primary production can exceed that of their macrophyte hosts by several-fold (Borum 1987). Host plants with complex architectures may harbor greater epiphyton biomass than more simply structured plants (Lalonde and Downing 1991), although high canopy densities in many submerged taxa (e.g., hydrilla, *Colon-Gaud* and Kelso 2004) may severely limit the photic zone (Langeland 1996). In nutrient enriched systems such as the Atchafalaya River Basin (ARB), the rate of respiration may more than double the rate of photosynthesis (Verduin 1987), and the physical and biological interactions among macrophytes and algae could have profound effects on littoral physicochemistry, including decreased pH and dissolved oxygen concentrations (Bryan et al. 1992; Sabo et al. 1999a, 1999b). These impacts on water quality could further affect the distribution and abundance of other biota, particularly ARB larval and adult fishes (Fontenot et al. 2001; Rutherford et al. 2001; Engel 2003).

In addition to their importance in littoral physicochemistry, macrophyte beds also provide habitat for numerous aquatic organisms. Macrophyte-associated communities can be more diverse and abundant than those found on any other aquatic substrate (Gerking 1957, 1962; Krull 1970). A key role of littoral macrophytes is providing cover, and a variety of macroinvertebrates and age-0 fishes use macrophyte beds as predation refugia (Moxley and Lanford 1982; Carpenter and Lodge 1986). Additionally, epiphyton (Kesler 1981; Lodge 1986) and other organic matter trapped on plant surfaces (Baer et

al. 2001) provide important forage for macroinvertebrates. Age-0 largemouth bass *Micropterus salmoides* abundance has been positively correlated with hydrilla coverage, possibly due to the refuge from piscivory and increased macroinvertebrate abundances found in macrophyte beds (Tate et al. 2003). As a result, plant-dwelling macroinvertebrate abundance, particularly for taxa such as trichopterans and amphipods, may be suppressed in the presence of predatory fishes (Wellborn and Robinson 1991).

Although both macroinvertebrates (Watkins et al. 1983) and fishes (Dibble et al. 1996; Chick and McIvor 1997) use macrophyte beds as a refuge from predation, bed density can significantly affect refuge quality. High density beds increase prey survival and reduce fish foraging success, intermediate density beds appear to be most advantageous for predators, and low density beds are sub-optimal for both predators and prey (Crowder and Cooper 1982; Keast 1984; Dibble et al. 1996; Cheruvilil et al. 2002). Young of the year bluegill *Lepomis macrochirus* have been shown to trade off foraging efficiency for cover in the presence of piscivorous fishes (Mittelbach 1981; Gotceitas 1990), such as age-0 largemouth bass, which show decreased foraging efficiency, growth, and abundance as well as delayed ontogenetic diet shifts in dense macrophyte canopies (Anderson 1984; Bettoli et al. 1992; Miranda and Pugh 1997; Pothoven et al. 1999; Valley and Bremigan 2002; Mason 2002). Young bluegills have also been shown to prefer dense macrophyte cover with small interstitial spaces, whereas largemouth bass prefer less dense cover with larger interstitial spacing (Dibble et al. 1996).

In addition to macrophyte density, macroinvertebrate communities are also affected by macrophyte type and architecture. Macrophytes of similar structural complexity often host similar macroinvertebrate communities, and the density and diversity of resident macroinvertebrate communities are usually positively associated with macrophyte complexity (Krecker 1939; Schramm et al. 1987; Cyr and Downing 1988; Chilton 1990; Thorp et al. 1997; Cheruvilil et al. 2002; Mihuc et al. 2002; Willis et al. 2005; but see Cattaneo et al. 1998). This relationship may be due not only to increased habitat, but also inhibition of foraging by invertivorous fishes such as pumpkinseed sunfish *Lepomis gibbosus*, which have reduced capture rates of cladoceran and damselfly prey in more complex macrophyte stands (Dionne and Folt 1991).

Hydrilla verticillata is an invasive, canopy-forming, submerged aquatic plant that was introduced to the ARB in the early 1970s (Sanders 1974). Hydrilla forms thick mats or beds in littoral areas of the ARB, resulting in reduced dissolved oxygen levels and increased physicochemical stratification of the water column (Colon-Gaud 2003). Hydrilla beds support large macroinvertebrate communities, although the composition of these communities differs substantially among bed positions, particularly between the normoxic canopy and the hypoxic sub-canopy (Colon-Gaud 2003). Although hydrilla beds may benefit ARB larval fishes by providing dissolved oxygen refugia during periods of hypoxia (Fontenot et al. 2001; Engel 2003), age-0 largemouth bass exhibit delayed ontogenetic diet shifts and reduced growth in areas supporting dense hydrilla stands (Mason 2002).

Predation by fishes can be an important structuring factor for macroinvertebrate communities, and top-down control of invertebrate community composition by vertebrate predators has been extensively demonstrated by exclusion experiments (Gilinsky 1984; Bronmark 1988; Bronmark et al. 1992; Diehl 1992; Batzer 1998; Johansson and Brodin 2003). Results indicate that exclusion of vertebrate predators can trophically release predaceous invertebrates, causing non-predaceous invertebrates to decline in abundance (Batzer et al. 2000). In some cases, fish predators can have greater impacts on the abundance of macroinvertebrates than macrophyte biomass (Johansson and Brodin 2003). Importantly, these experiments indicate that predaceous invertebrates can be just as important as vertebrates regarding their impacts on invertebrate community composition (Benke 1978; Andersson and Danell 1982; Kesler and Munns 1989). However, abiotic factors can also limit invertebrate communities, confounding the apparent effects of top-down control (Thorp and Bergey 1981; Chilton and Margaf 1990).

This project will explore the effects of predation by vertebrates on macroinvertebrate communities and the influence of hydrilla beds on trophic relationships among littoral organisms in the ARB. Specifically, the objectives of this study are to: 1) determine the effect of position within a hydrilla bed on macroinvertebrate community composition and abundance, 2) examine the effect of macrophyte architecture on macroinvertebrate community composition, and 3) assess the role of predation in determining macroinvertebrate diversity and abundance in ARB hydrilla beds.

INTRODUCTORY METHODS

The ARB is a large floodplain swamp ecosystem associated with the Atchafalaya River, the major distributary of the Mississippi River, which carries about one-third of the annual flow of the Mississippi River to the Gulf of Mexico. Various habitats within the ARB are chronically hypoxic (dissolved oxygen < 2.0 mg/L) and stratified during the latter stages of the flood pulse, which is related to water flow/turbulence and pH (Sabo et al. 1999a, 1999b).

This study consisted of three separate experiments and a field study conducted during the late summer of 2003 and 2004. A different site was used each year due to inter-annual variation in macrophyte bed formation. The sites were selected because each had a stable bed of hydrilla that exhibited consistent daytime canopy dissolved oxygen levels 3.0 mg/L or above (although nocturnal hypoxia was undoubtedly common; Colon-Gaud 2003). Open water areas adjacent to both study sites were used by recreational boaters, although the 2004 site had more traffic, possibly because of its proximity to the boat launch. The 2003 study site was located west of Plaquemines, Louisiana near Bayou Pigeon and the Intracoastal Canal (Figure 1.1). This site (UTM Zone 15 658085 3331520) is a bayou approximately 80 m wide, with water depth averaging 0.7 m. The bed was located on the east side of the bayou in water that averaged 0.5-m deep. The 2004 study site was located west of Pierre Part, Louisiana near Belle River and Intracoastal Canal (Figure 1.1). This site (UTM Zone 15 667331.9

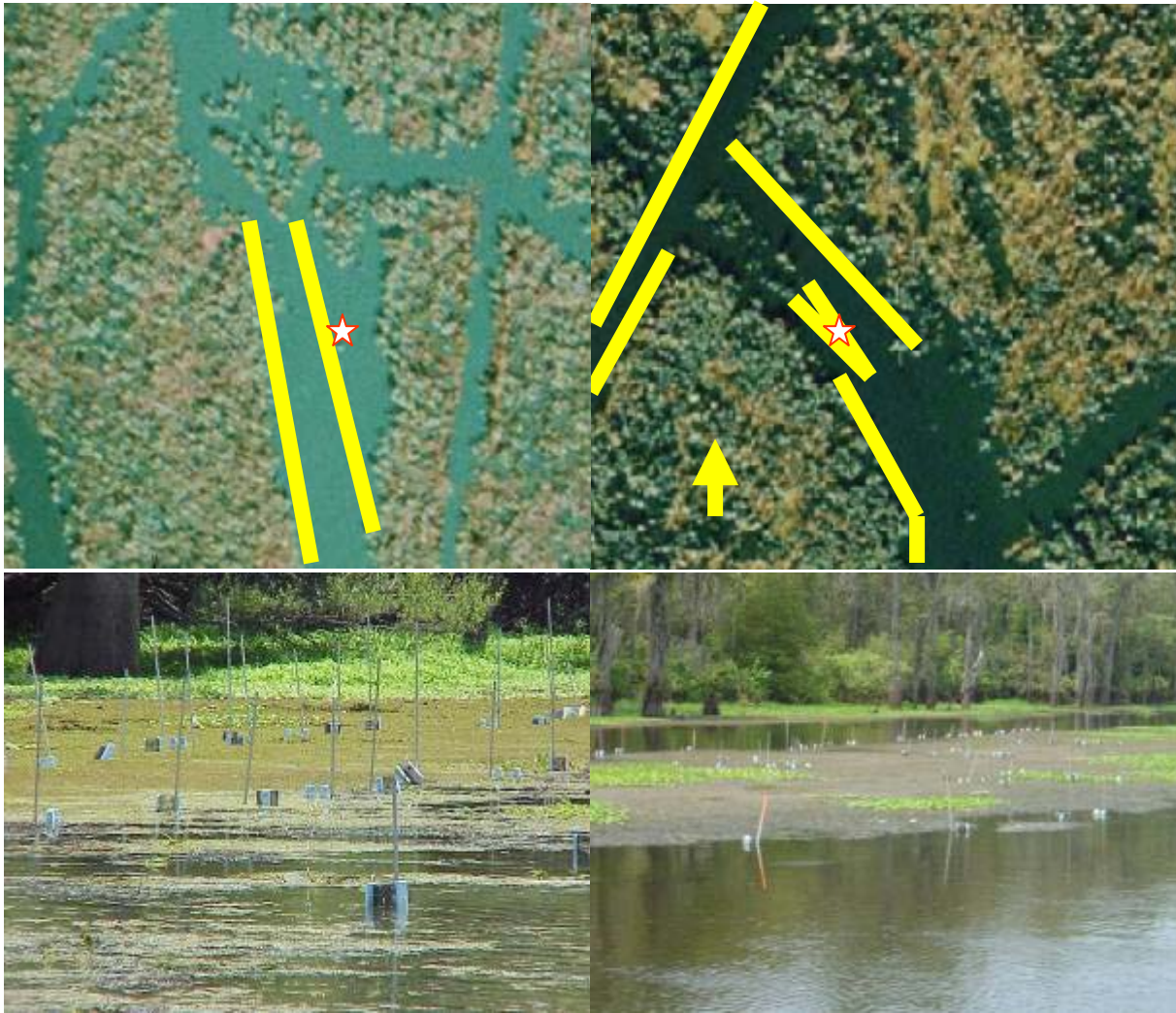


Figure 1.1—Aerial photographs of the 2003 (top left) and 2004 (top right) study sites. Yellow lines indicate approximate boundaries of hydrilla beds, white stars indicate actual study site location, and yellow arrows indicate north. Exclosures set up at the 2003 (bottom left) and 2004 (bottom right) study sites.

3309287) was a bayou approximately 90 m wide, with water depth reaching 2 m in the channel and 0.5-1.5 m in the hydrilla bed.

All experiments conducted in this project used a floating exclosure as the experimental unit. Each unit consisted of a cylindrical mesh exclosure extending about 36cm into the water column suspended under a foam float. Exclosures constructed of three different mesh sizes [small (3mm x 4mm), medium (10mm x 11mm), and large



Figure 1.2—Floating subsurface enclosures used in the experiments. Mesh sizes from left to right are small, medium, and large.

(48mm x 99mm)] were used to exclude different sized organisms. The mesh was attached to foam floats at the top, and to a six-inch PVC pipe cap at the bottom, which served as the anchor point for a plastic aquarium plant that mimicked hydrilla (complex architecture), or eelgrass (simple architecture; Gerrish and Bristow 1979; Figure 1.2). These plastic plants resemble natural plants (Pluntke and Kozerski 2003), and have been shown to support natural densities of epiphytes (Cattaneo 1978; Cattaneo and Kalff 1979, 1981; Cattaneo 1983; Fontaine and Nigh 1983; Gilinsky 1984) and macroinvertebrates (Gerrish and Bristow 1979; Rooke 1986; Wellborn and Robinson 1991). A short length of nylon rope held each enclosure to a pole driven into the

substrate beneath the macrophyte bed. This attachment allowed the unit to remain in place for the duration of the experiment, while also allowing the unit to float immediately below the water surface. The top of each exclosure remained open to the air above the water, which allowed colonization by adult aquatic insects, and minimized shading that could reduce periphyton growth on the artificial plants.

Exclosures were organized in a completely randomized block design and placed randomly within their bed position treatment. Invertebrates were allowed to colonize for five weeks before the exclosures were harvested, based on suggestions by Ofenbock and Moog (2001; a minimum of three weeks and a maximum of six weeks for artificial substrates) and Kaller et al. (2001; five weeks for a substrate replacement experiment); maximum epiphyton community development may occur after 10 to 14 d (Borum 1987). Water quality (temperature, pH, specific conductance, dissolved oxygen, and turbidity)

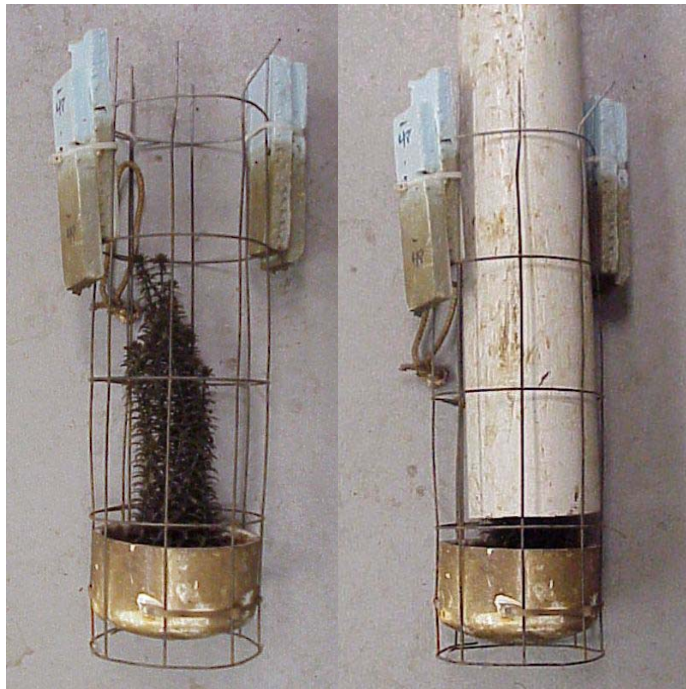


Figure 1.3—Simulated harvest of exclosures. Note that rapid insertion of the PVC tube excluded organisms on the exclosure mesh.

was measured inside the beds and in the adjacent channel each week the exclosures were deployed.

Exclosures were harvested by quickly placing a length of 15 cm PVC pipe down through the unit until it fitted snugly into the bottom cap (figure 1.3). This allowed for the collection of those organisms found on and around the artificial plant but not on the surrounding mesh. The entire

unit and enclosed water were removed from the water, and the contents poured through a sieve (mesh diameter < 0.5 mm). Material retained on the sieve (including the artificial plant) were placed in a plastic bag, preserved in 95% ethanol, and placed on ice until the samples could be frozen.

Water quality was measured after each unit was harvested, and although measurements made after collection of the exclosures may have influenced results, post-harvest measurement minimized pre-harvest exclosure disturbance, reducing the chance highly mobile organisms fled the exclosure before harvest. I felt it was important to measure water quality at each harvested exclosure because dissolved oxygen microhabitats occur within macrophyte beds (Miranda et al. 2000). This procedure was streamlined in 2004 to one measurement in the channel and five representative measurements within the macrophyte bed because of a lack of variability in the 2003 water quality data.

After the contents of each collection were thawed, organisms were separated by hand and identified to genus where possible. Insects, except chironomids (Diptera: Chironomidae), were identified with a dissecting microscope according to Merritt and Cummins (1996). Chironomids were mounted on slides and identified to subfamily with a compound light microscope according to Epler (2001). All other invertebrates were identified with a dissecting microscope to the lowest practical taxonomic level with the aid of Smith (2001). Lengths (mm) of all organisms collected for the second experiment in 2003 were measured with an ocular micrometer.

CHAPTER 2: EFFECTIVENESS OF ARTIFICIAL PLANTS IN SUBSURFACE EXCLOSURES AS A SUBSTRATE FOR HYDRILLA-DWELLING MACROINVERTEBRATE COMMUNITIES

Both aquarium plants and subsurface exclosures have been used successfully to sample macrophyte-dwelling macroinvertebrates (Chapter 1). However, these two types of sampling structures have not been used together to examine patterns of macroinvertebrate community structure. The purpose of this experiment was to determine whether macroinvertebrates colonizing artificial plants placed inside subsurface exclosures were representative of the hydrilla-dwelling macroinvertebrate community in the ARB.

METHODS

This study was conducted from September 2 to October 15, 2003 at the 2003 study site (Figure 1.1) in a hydrilla bed. Fifteen exclosures of each mesh type were randomly placed on the interior of the hydrilla bed. The primary intent of this experiment was not to show variation between mesh types (except for the final week of the experiment), but each mesh type was included in the study because mesh size was an integral part of the overall experimental design. Three exclosures of each mesh treatment were harvested at 10, 17, 24, 31, and 43 days, hereafter referred to as weeks one through five. Originally the experiment was to conclude at the end of five weeks with exclosures harvested once every week, but poor weather conditions caused a delay in week one sampling, so the remaining sampling dates were adjusted to maintain equal times between exclosure retrieval.

On each sampling date, exclosures were harvested, and water quality (temperature, dissolved oxygen, and pH) was then measured at each harvest location

with a Hydrolab Quanta (Hydrolab Corporation, Austin, TX). Dissolved oxygen (DO), temperature, and pH was compared between interior and exterior positions in the hydrilla bed with multivariate analysis of variance (MANOVA) and Tukey-Kramer adjusted least squared means post-tests, and between weeks on the bed interior with a MANOVA and Tukey-Kramer adjusted least squared means post-tests. Next, three samples of hydrilla-dwelling macroinvertebrates were taken near the surface in an undisturbed interior portion of the experimental bed with the suitcase-type vegetation sampler developed by Colon-Gaud and Kelso (2003) to test for experimental artifacts. Contents of the exclosures and the vegetation samples were washed over a sieve (mesh < 0.5 mm), preserved in 95% ethanol, sorted, and identified to genus where possible.

Plant matter collected in the vegetation samples was sorted into hydrilla and non-hydrilla groups. Morphological measurements on four subsamples of hydrilla stems between two and four meters long were taken from each vegetation sample. Total stem length (S_T), number of leaf whorls (W_N), and number of apical buds (B) were measured for subsampled hydrilla and five artificial plants. Averages of stem diameter (S_D), number of leaves per whorl (W_L), leaf width (L_W), and leaf length (L_L) were taken in centimeters for each vegetation sample and from the five artificial plants based on 10 separate measurements for each parameter (Figure 2.1).

I used the equation:

$$SA_{Total} = \text{stem surface area} + \text{leaf surface area} + \text{apical bud surface area} \quad (1)$$

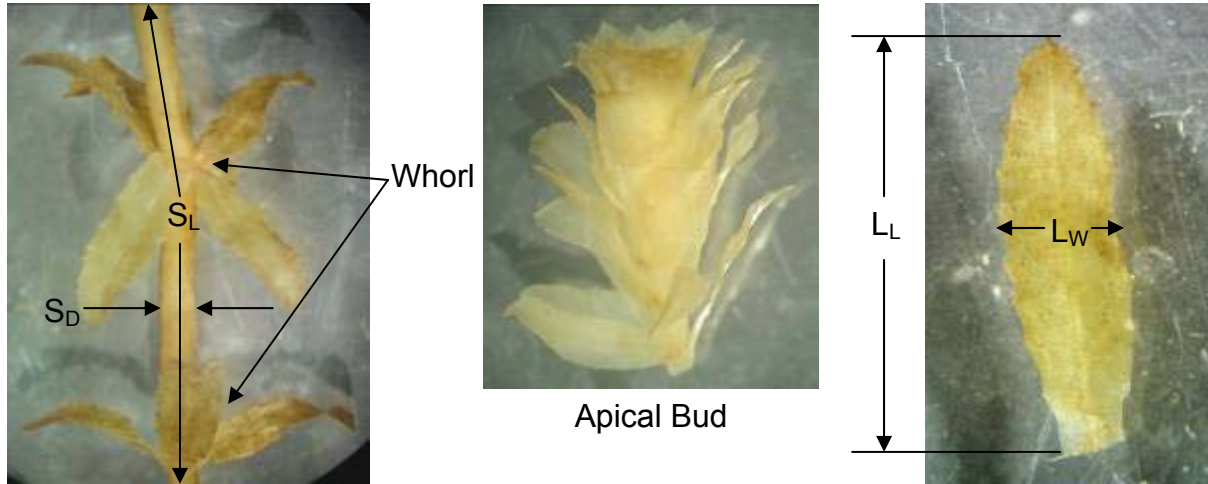


Figure 2.1—Morphological features used in surface area equation

to estimate surface areas of the hydrilla and artificial plants. The stems are approximately cylindrical, and surface area can be approximated with the equation ($\pi \times \text{diameter} \times \text{height}$), with the stem surface area described by:

$$SA_{\text{Stem}} = \pi S_D S_L \quad (2).$$

Hydrilla leaves are approximately elliptical in shape. The surface area of a hydrilla leaf was calculated as double the area of one side:

$$SA_{\text{Leaf}} = 2\pi L_L L_W \quad (3)$$

which assumes that leaf edges contribute a negligible amount to surface area. The total number of leaves can be approximated by multiplying equation 3 by the number of whorls (W_N) and the number of leaves per whorl (W_L). Apical buds (B) only occur at the end of actively growing stems (Langeland 1996) and likely contribute little to the overall colonizeable surface area. However, assigning apical buds as a constant number of leaf whorls yields:

$$SA_{\text{Leaves}} = 2\pi(W_N + 4B)W_L L_L L_W \quad (4).$$

Total surface area of hydrilla (equation 1) in each sample can then be calculated by adding equations 2 and 4:

$$SA_{\text{Total}} = \pi S_D S_L + 2\pi(W_N + 4B)W_L L_L L_W \quad (5).$$

The total colonizeable surface area was calculated for both the hydrilla subsamples and artificial plants with equation 5. Hydrilla subsamples and the remaining plant matter were dried to a constant weight and weighed to the nearest tenth of a gram. I used a power model to relate plant dry weight (independent variable) and surface area (dependent variable), and then used this model to estimate total hydrilla surface area (cm²) based on the total dry weight (g) of each vegetation sample. Surface area was used to standardize macroinvertebrate abundances between vegetation samples and artificial plants and allow for comparisons between the experimental units and the suitcase samples.

Only macroinvertebrates that were present in at least 10% of samples were used for analysis, and of those, only taxa approximating normality after a log + 1 transformation were considered for the MANOVAs. Macroinvertebrate density data was first analyzed with canonical discriminant function analysis to explore the data and test for separation of groups (Johnson and Wichern 2002). I then used a MANOVA with least squared means post-tests to test for macroinvertebrate community differences between exclosure harvest times and the vegetation sample control. I also used MANOVA and post-tests to examine differences in the macroinvertebrate community composition between the three mesh treatments on the final week and the suitcase samples. The remaining non-normal taxa were analyzed using logistic regression. All

macroinvertebrate contrasts were determined *a priori* and only contrasts between a treatment group and the control were considered for analysis.

RESULTS

Over the entire course of the field experiment dissolved oxygen was greater ($P <$

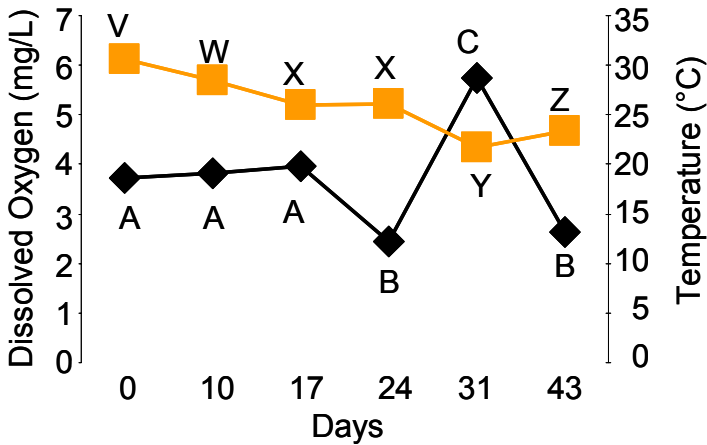


Figure 2.2—Dissolved oxygen concentration (black diamonds) and temperature (orange squares) during the experimental period. Letters (A through C) indicate significant differences in dissolved oxygen concentration and letters (V through Z) indicate significant differences in temperature.

0.0001) on the exterior of the hydrilla bed (mean = 4.62 mg/L) versus the interior (mean = 3.75 mg/L), whereas temperature and pH did not differ. Dissolved oxygen and temperature on the interior of the bed varied between weeks (Figure 2.2) with the highest mean DO on week five (DO = 5.74 mg/L) and

temperature (30.56°C) on week zero and the lowest mean DO on week four (DO = 2.45 mg/L) and temperature (21.68°C) on week five.

The averaged parameters for the hydrilla surface area yielded the following equation:

$$SA_{Total} = \pi * 0.16 * S_L + 2\pi(W_N + 4B) * 0.26 * 1.0 * 4.1$$

$$= 0.16 * \pi * S_L + 2.132 * \pi * (W_N + 4B) \quad (6).$$

and the power model equation for predicting surface area from dry weight was

$$SA = 2390.3618 * Weight^{0.83623} \quad (7)$$

with $r^2 = 0.9265$. Surface area of the artificial plants averaged 1276.62 cm². These surface area measurements were then used to standardize macroinvertebrate densities between artificial plants and vegetation samples.

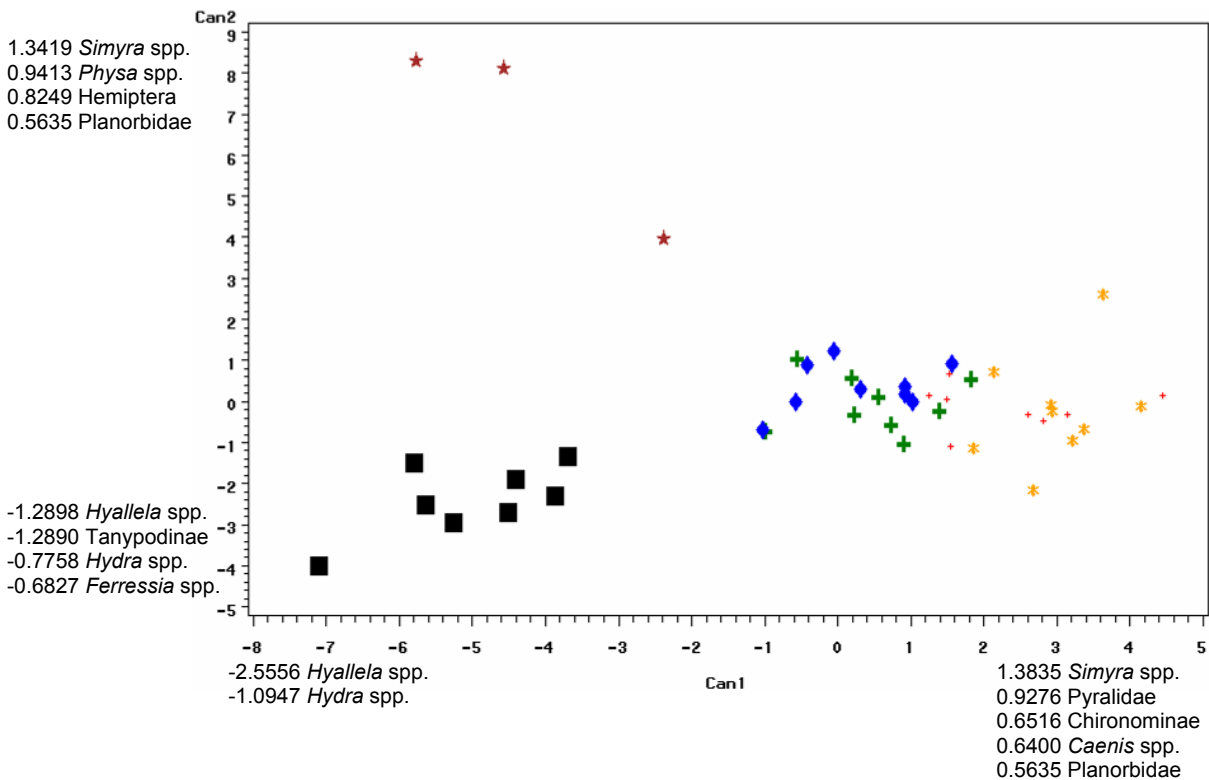


Figure 2.3. – Canonical discriminant function analysis of invertebrate data. Red plus signs indicate week 1, orange asterisks week 2, green plus signs week 3, blue diamonds week four, and black squares week five. Maroon stars indicate vegetation samples. Pooled coefficients for each canonical axis are shown.

The first two axes generated by the canonical discriminant function analysis were significant ($P_1 < 0.0001$ and $P_2 = 0.0406$, Figure 2.3). Temporal changes in macroinvertebrate community composition were evident along the first canonical axis, reflecting decreasing abundances of *Simyra* spp. (Lepidoptera: Noctuidae), Pyralidae (Lepidoptera), Chironominae (Diptera: Chironomidae), *Caenis* spp. (Ephemeroptera: Caenidae), and Planorbidae (Gastropoda) as the experiment progressed. Week five samples and the vegetation samples collected with the suitcase sampler occupied

similar positions along the first axis. The second canonical axis reflected differences between the vegetation samples, which grouped towards higher densities of *Simyra* spp., *Physa* spp. (Gastropoda: Physidae), Hemiptera, and Planorbidae, and exclosure samples, which grouped towards *Hyallela* spp. (Amphipoda: Hyallelidae), Tanypodinae (Diptera: Chironomidae), *Hydra* spp. (Hydrazoa: Hydridae), and *Ferressia* spp. (Gastropoda: Ancyliidae).

Differences between weekly densities of eight of the most abundant macroinvertebrate taxa and the vegetation samples collected at the conclusion of the experiment (Figure 2.4) indicated that Coenagrionidae (Odonata), Chironominae, Anisoptera (Odonata), and Tanypodinae quickly achieved and maintained natural densities throughout the experiment. *Hyallela* spp. and *Physa* spp. were typically less abundant in the exclosures than in hydrilla samples, although densities increased to near-natural levels by the end of the experiment. *Caenis* spp. were able to quickly colonize the exclosures and attain relatively high densities, although by week four the density of these mayflies had also dropped to levels characteristic of the surrounding plant bed. Cladocerans were the only taxa that showed a continual trend of increasing abundance within the exclosures, exhibiting significantly higher densities than the hydrilla samples during the final sampling period.

Few differences were found in macroinvertebrate densities between mesh treatments and the hydrilla samples collected during the final week of the experiment. *Caenis* spp. had significantly greater densities in the medium ($P = 0.0450$) and large ($P = 0.0046$) meshes compared to the control. Conversely, Coenagrionidae was

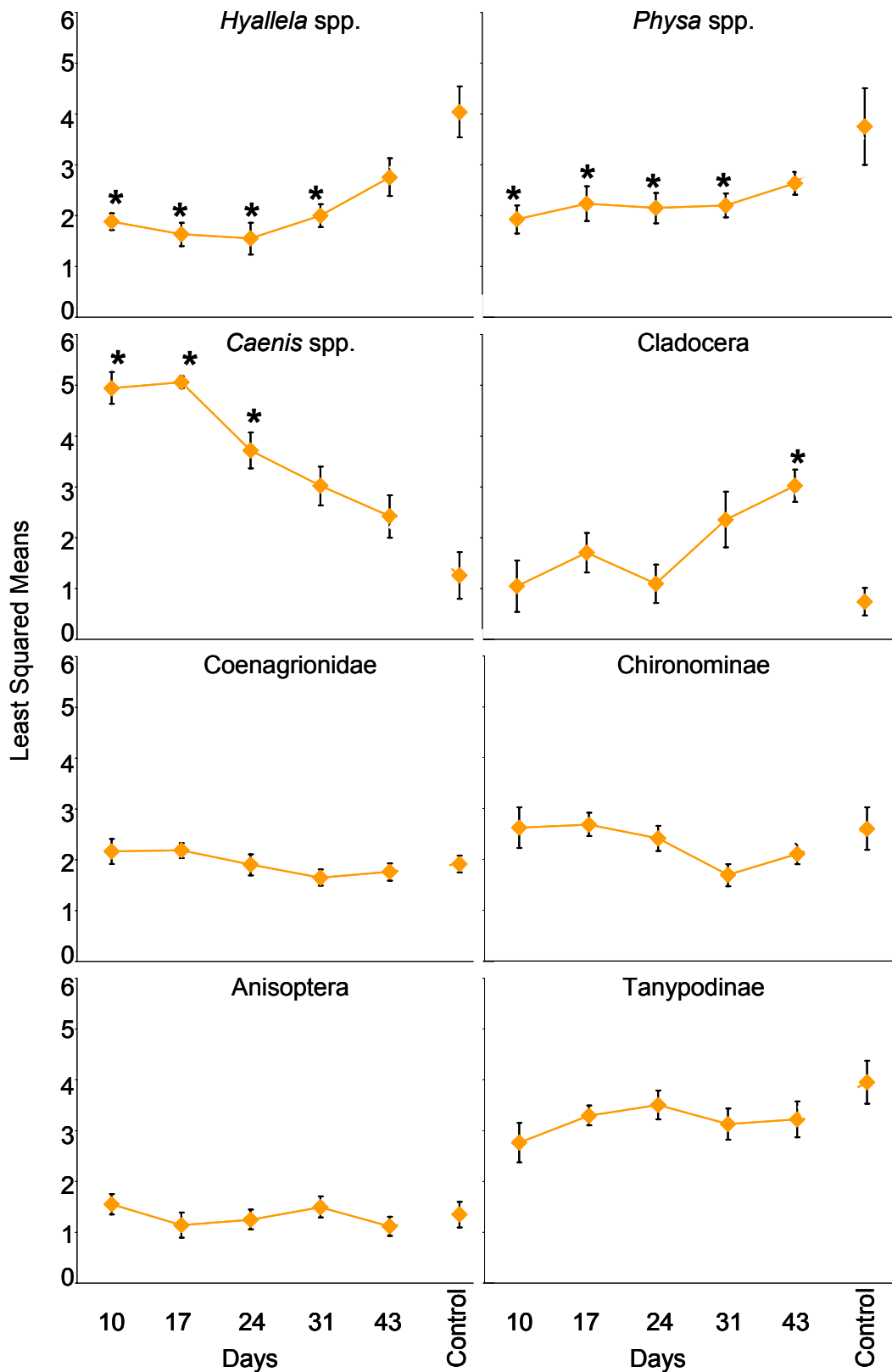


Figure 2.4—Least squared mean densities of macroinvertebrate taxa. Treatments significantly different from the control are indicated with asterisks.

significantly less abundant ($P = 0.0475$) in the medium mesh exclosures relative to the hydrilla samples, and Coenagrionidae ($P = 0.0475$), *Hyallela* spp. ($P = 0.0006$), and Tanypodinae ($P = 0.0049$) were significantly less abundant in the small mesh exclosures. Logistic regression did not reveal any significant differences between week treatments and the control after many taxa were removed from the analysis due to a preponderance of zeros.

DISCUSSION

Dissolved oxygen is considered an important factor in structuring hydrilla-dwelling ARB macroinvertebrate communities (Colon-Gaud 2003). In the ARB, DO is considered normal when concentrations are greater than 3.0 mg/L, potentially stressful between 2.0 and 3.0 mg/L and hypoxic at concentrations less than 2.0 mg/L (Sabo et al. 1999b; Rutherford et al. 2001). Dissolved oxygen concentrations were less than 3.0 mg/L during two weeks of the experiment, but diurnal DO levels did not reach hypoxic levels. Even though it is likely that nocturnal DO concentrations were hypoxic in the hydrilla canopy (Colon-Gaud 2003), it does not appear that DO patterns changed temporally during the course of the experiment, or spatially among the treatment sites, and did not affect the macroinvertebrate colonization patterns. While temperature did significantly decrease as time progressed, the temperatures measured are well within previously recorded temperature ranges for the ARB (Sabo et al. 1999a) and is likely not biologically significant.

It is important that the macroinvertebrate communities inhabiting the artificial plants in the exclosures be representative of the natural hydrilla-dwelling community to validate future experiments and analyses. Canonical discriminant function analysis

clearly shows exclosures from the final week of the experiment grouping with the vegetation samples and away from the other four weeks on the first axis (Figure 2.3). Although the macroinvertebrate communities inhabiting the exclosures harvested during the final week of the experiment did separate from the vegetation samples on the second canonical axis, these differences were not significant for seven of the eight individual taxa examined (Figure 2.4).

In my experiment, the large mesh treatment was designed to be most similar to the surrounding vegetation by permitting access of fishes and large invertebrates to the artificial plants. Results of comparisons between macroinvertebrate communities in the various mesh sizes and the suitcase samples indicated that in fact this was the case; only *Caenis* spp. exhibited a significantly different (higher) density in the large mesh exclosure compared to the hydrilla samples. Conversely, three taxa were less abundant in the small mesh exclosures, suggesting that restricted access of predators or competitors significantly altered the epiphytic macroinvertebrate community.

It is interesting to note that the examined taxa colonized the exclosures in three distinct ways. Coenagrionidae, Chironominae, Anisoptera, and Tanypodinae all maintained constant densities throughout the experiment that were indistinguishable from those found in the vegetation. This rapid and constant colonization suggests that these organisms require only an open space to colonize and the amount of open space may limit the distributions and densities of these organisms. *Caenis* spp. quickly colonized the exclosures, but decreased in density as the experiment progressed to densities similar to the surrounding vegetation. This rapid colonization and decline suggests that caenid mayflies rapidly colonize empty or newly available spaces, but that

predation, competition, or behavioral responses to changing periphyton densities result in declining densities to levels comparable to the surrounding hydrilla habitat. Finally, *Hyallolella* spp., *Physa* spp., and cladocerans slowly colonized the exclosures and increased in density during the course of the experiment to levels comparable to, or exceeding (cladocerans) those found in hydrilla. Increasing periphyton growth through time (Cattaneo and Kalff 1979; Cattaneo 1983) was likely responsible for late colonization of exclosures by these three herbivorous taxa (Smith 2001). Additionally, the pipe cap used as a base for the exclosures may have been responsible for the increased cladoceran densities by keeping those cladocerans that undergo daily vertical migrations within the exclosure during the day (Davidson et al. 2000).

The observed temporal abundance patterns do provide insights into the food habits of the two odonates that colonized the exclosures. Dragonfly nymphs (Anisoptera) and coenagrionid damselflies are voracious invertivorous odonates (Merritt and Cummins 1996), and both taxa remained similar in density throughout the study in all mesh treatments. The decline in caenid mayflies may be at least partially due to predation from these two odonates, which may have switched to a more diverse diet as mayflies declined and the relative density of other potential prey items, such as hyallelid amphipods and cladocerans, increased. As a consequence, natural densities of predaceous odonates present throughout the study may have caused prey organisms initially present in densities different from the surrounding vegetation to return to natural levels as the experiment progressed.

Results of this experiment demonstrate that artificial plants in subsurface exclosures can be effective sampling units for hydrilla-dwelling macroinvertebrates.

Macroinvertebrate densities were similar between exclosures harvested on the final week of the experiment and vegetation samples. Further, the large mesh was most similar among the three mesh treatments to macroinvertebrate densities found in vegetation samples. Therefore, it is reasonable to assume that further studies employing these exclosures with a minimum deployment of 5-6 weeks will yield results representative of natural macroinvertebrate community dynamics in ARB hydrilla beds.

CHAPTER 3: THE EFFECTS OF PREDATOR EXCLUSION AND BED POSITION ON HYDRILLA-DWELLING MACROINVERTEBRATE COMMUNITIES

The abundance and species composition of macroinvertebrate communities can be strongly influenced by predation pressure from both invertebrate and vertebrate predators (Chapter 1). Predatory mortality is a dynamic process in freshwater systems, varying temporally as the species and size distribution of the predatory community changes, and spatially among different habitat types. Hydrilla, due to its dense canopy, could inhibit predation on macroinvertebrates by visually-foraging fishes, and we would expect this inhibition to be most evident in the interior of a hydrilla bed (Colon-Gaud 2003). The purpose of this experiment was to test for the effects of predator exclusion and position within a hydrilla bed on hydrilla-dwelling macroinvertebrate communities.

METHODS

This study was conducted from September 2, 2003 to October 15, 2003 in a hydrilla bed west of Plaquemines, Louisiana near Bayou Pigeon and the Intracoastal Canal (Figure 1.1). Ten exclosures of each of the three mesh types were randomly placed within and on the outside edge of the hydrilla bed ($N = 10$ per treatment, total $N = 60$). The exclosures were harvested 43 days after the initiation of the experiment, a delay of eight days over the planned end date because of poor weather. Contents of the exclosures were preserved, sorted, and identified, and the total length of all organisms was measured to the nearest millimeter, except for chironomid (Diptera) larvae, which were not measured, and *Palaemonetes* spp. (Decapoda: Palaemonidae), for which carapace length was measured because of their curled body shape after preservation.

The 24 taxa analyzed in this study (Table 3.1) occurred in at least 10% of the samples and were identified to genera, with the exception of chironimids, which were identified to subfamily, some gastropods, which were identified to family, odonates in the family Libellulidae, which, due to their small size, could not confidently be identified to genus, and odonates in the family Coenagrionidae because the caudal gills of many were lost during sample processing, confounding further identification.

I employed three multivariate analyses of variance (MANOVA) that were used, similar to profile analysis, to test *a priori* contrasts. First, I tested for differences in macroinvertebrate abundances between position treatments, summing over the mesh treatments. Next, I examined differences between like meshes across the position treatments. Finally, I tested for differences between mesh treatments within each position treatment. Logistic regression was attempted on the 17 remaining non-normal taxa to examine spatial patterns in abundance. To assess abundance patterns by trophic group, taxa were placed into feeding groups (predator, collector, scraper, shredder, piercer, omnivore, or parasite) adapted from Merritt and Cumins (1996), with the normally-distributed log transformed abundances of predators, collectors, and scrapers analyzed with the same profile-type analysis as the individual taxa. Differences in length distributions among treatments for the 11 taxa included in the first MANOVA were analyzed with a log-linear regression separately for each taxon (Agresti 1996).

Table 3.1.—Macrofaunal taxa, frequency of occurrence (FO), mean number of organisms per plant, and the statistical analysis used.

Taxa	FO (%)	Mean	Analysis
Tanypodinae (Diptera: Chironomidae)	100	22.45	MANOVA
Chironominae (Diptera: Chironomidae)	98	22.10	MANOVA
<i>Caenis</i> spp. (Ephemeroptera: Caenidae)	97	28.66	MANOVA
Cladocera	97	50.52	MANOVA
Coenagrionidae (Odonata)	95	12.53	MANOVA
<i>Physa</i> spp. (Gastropoda: Physidae)	95	14.67	MANOVA
<i>Hyallela</i> spp. (Amphipoda: Hyallellidae)	93	22.20	MANOVA
Copepoda	67	4.02	MANOVA
Libellulidae (Odonata)	53	2.91	MANOVA
Orthocladinae (Diptera: Chironomidae)	52	4.32	MANOVA
Hydrobiidae (Gastropoda)	42	3.48	Logistic Regression
<i>Bezzia</i> spp. (Diptera: Ceratopogonidae)	33	2.40	Logistic Regression
<i>Hexagenia</i> spp. (Ephemeroptera: Ephemeridae)	33	2.05	Logistic Regression
<i>Palaemonetes</i> spp. (Decapoda: Palaemonidae)	33	3.50	MANOVA
<i>Simyra</i> spp. (Lepidoptera: Noctuidae)	32	3.00	Logistic Regression
Planorbidae (Gastropoda)	30	3.94	Logistic Regression
<i>Hydra</i> spp. (Hydrazoa: Hydridae)	28	4.24	Logistic Regression
<i>Ondontomyia</i> spp. (Diptera: Stratiomyidae)	27	1.37	Logistic Regression
<i>Placobdella</i> spp. (Rhynchobdella: Glossiphoniidae)	23	1.64	Logistic Regression
<i>Culicoides</i> spp. (Diptera: Ceratopogonidae)	22	3.69	Logistic Regression
Pyrilidae (Lepidoptera)	20	1.00	Logistic Regression
<i>Culex</i> spp. (Diptera: Culicidae)	18	1.73	Logistic Regression
<i>Gambusia affinis</i> (Cyprinodontiformes: Poeciliidae)	18	1.45	Logistic Regression
<i>Chaoborus</i> spp. (Diptera: Chaoboridae)	17	1.30	Logistic Regression
<i>Ferressia</i> spp. (Gastropoda: Ancyliidae)	17	1.70	Logistic Regression
Ostracoda	15	6.67	Logistic Regression
<i>Hydrocanthus</i> spp. (Coleoptera: Hydrophilidae)	13	1.25	Logistic Regression
<i>Uranotaenia</i> spp. (Diptera: Culicidae)	13	1.12	Logistic Regression

RESULTS

Artificial plants in the exclosures were colonized by a diversity of invertebrates, but most sample units were dominated by chironimids, caenid mayflies, cladocerans, odonates, physid snails, and amphipods (Table 3.1). Six taxa differed in abundance between position treatments (Figure 3.1) and no interactions were found between treatment groups. Coenagrionidae, Orthocladinae, and Chironominae were more abundant in the edge treatment, whereas *Caenis* spp., *Hyallela* spp. (Amphipoda: Hyallelidae), Cladocera, *Physa* spp., and Libellulidae (Odonata) were more abundant in the interior treatment. *Palaemonetes* spp., Tanypodinae, and Copepoda did not differ between position treatments (Figure 3.1).

Among mesh treatments, Coenagrionidae, *Hyallela* spp., Libellulidae, Tanypodinae, Cladocera, and *Caenis* spp. exhibited a positive relationship between abundance and increasing exclosure mesh size (Figure 3.2). In contrast, Chironominae and *Palaemonetes* spp. were most abundant in the smallest meshes and decreased in abundance as mesh size increased. All three mesh treatments differed significantly across position in the Coenagrionidae and Chironominae. I detected no significant differences between mesh and position treatment groups for the remaining taxa analyzed with the logisitic regression.

Trophic group analysis revealed few differences not found by previous analyses (Figure 3.3). Collectors were the most abundant group followed by predators and scrapers. Predators did not differ between position treatments and were less abundant in the small meshes compared to the medium and large meshes. Collectors were less abundant in the small-mesh interior treatment relative to the other mesh- position

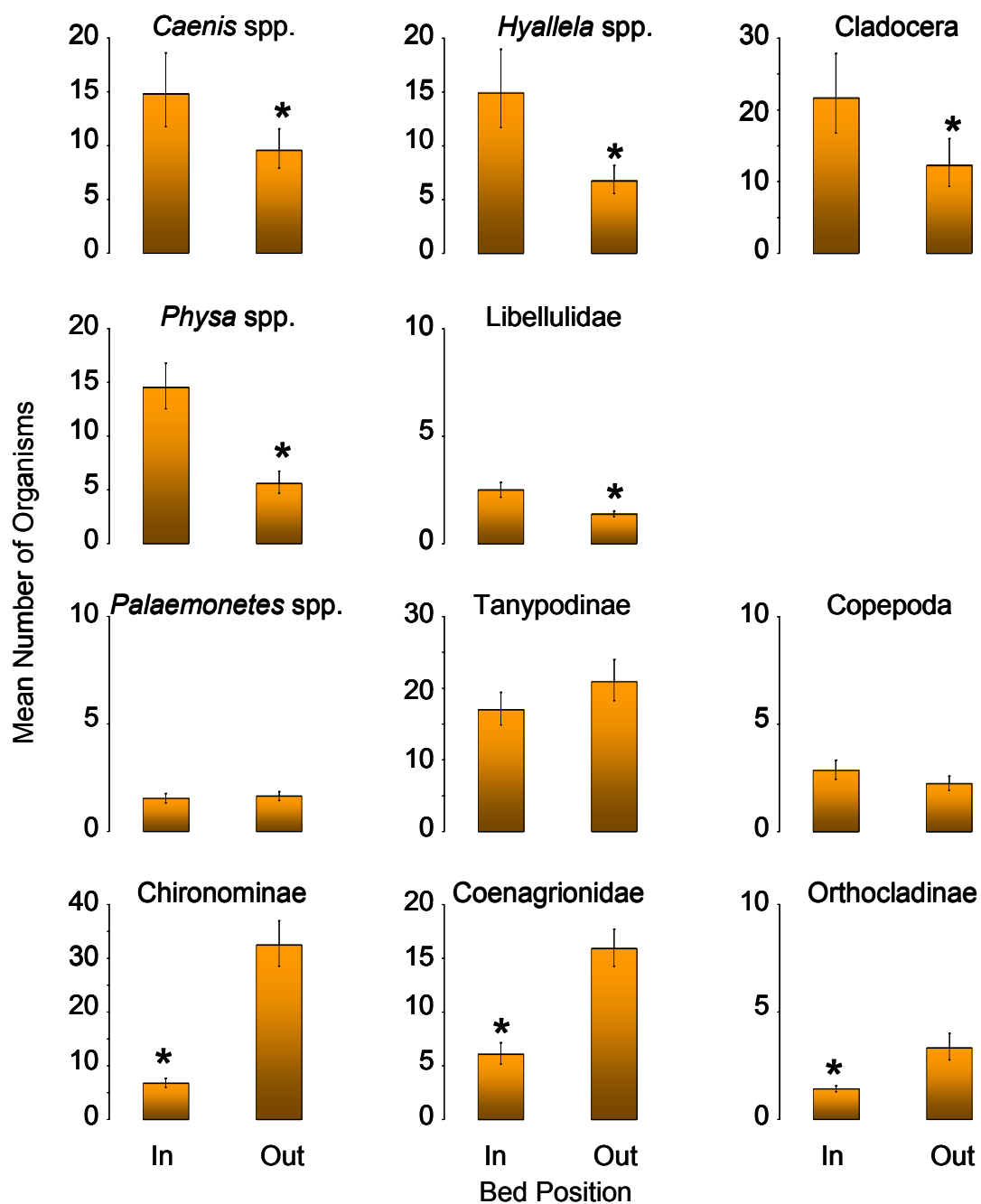


Figure 3.1—Untransformed means of normally distributed taxa for each position treatment. Error bars are standard error of the mean. Significant differences between positions for each taxon are indicated with an asterisk.

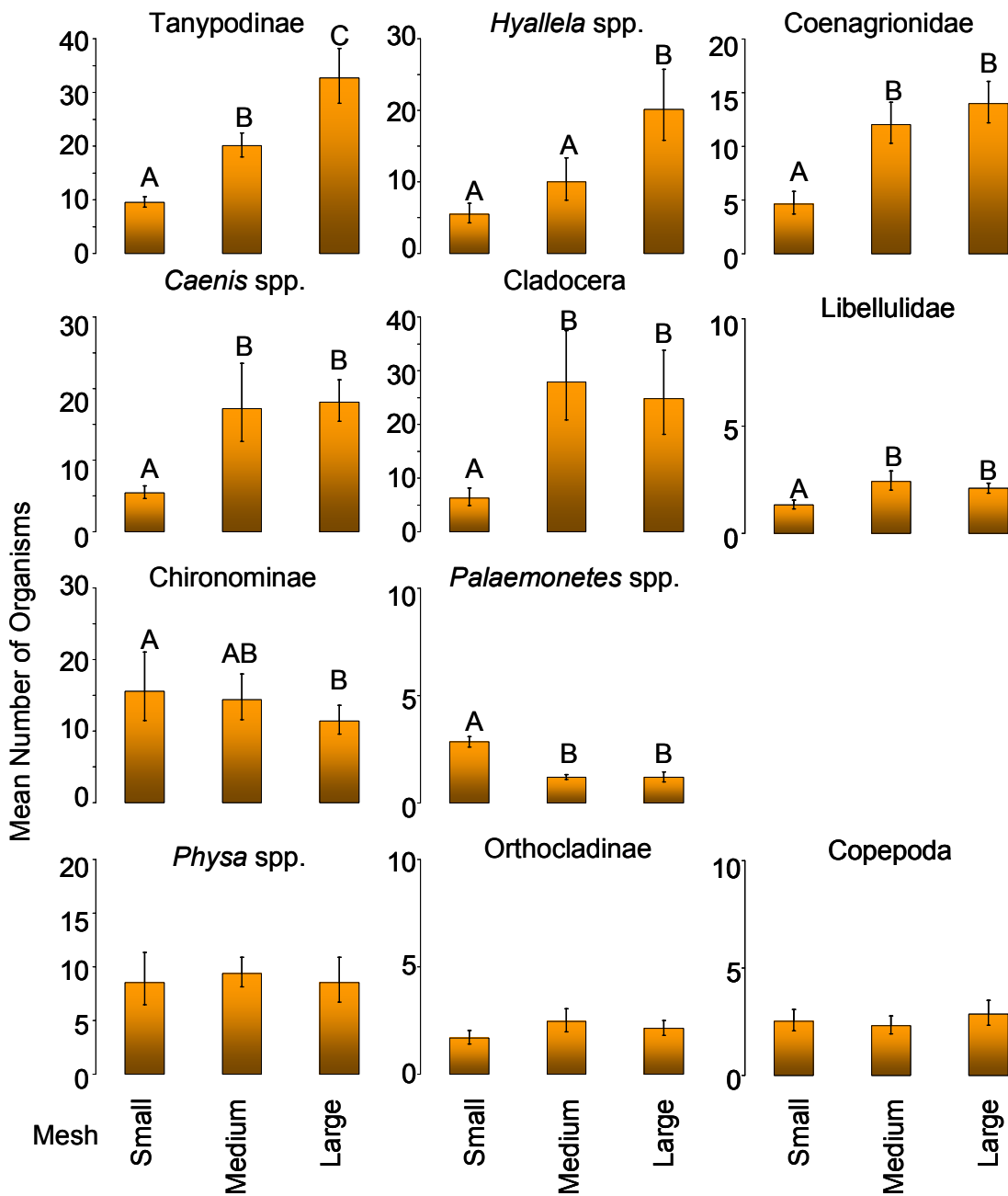


Figure 3.2—Untransformed means of normally distributed taxa for each mesh treatment. Error bars are standard error of the mean. Significance groupings within each taxon are indicated by letters where significant differences were present.

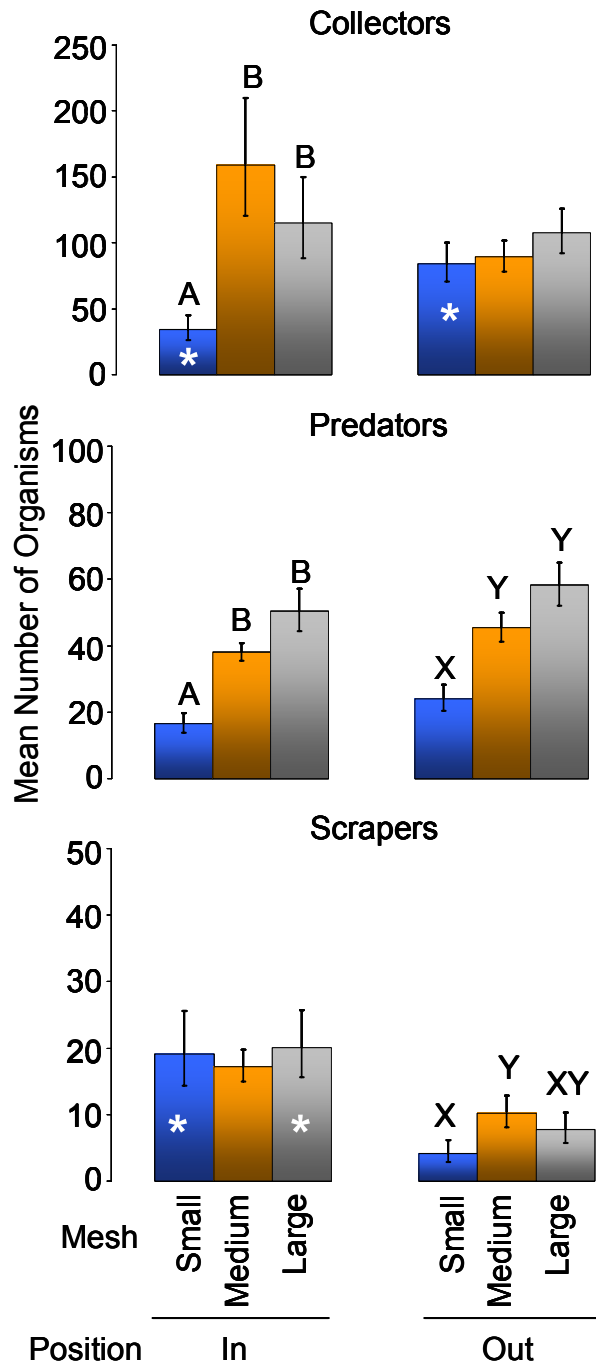


Figure 3.3—Mean number of organisms in each functional feeding group for each mesh and bed position combination. Error bars are standard error of the mean. Asterisks indicate significant within mesh between position differences. Letters indicate significant groups between meshes within each position treatment.

treatment combinations. Scrapers were more abundant in the bed interior than exterior, though this difference was only significant for the small and large meshed enclosures.

Significant differences in length were found between mesh and position treatment groups for four of the nine taxa that were measured (Figure 3.4). *Coenagrionidae* was 1.2 times more likely to be longer on the bed interior than in the corresponding enclosures placed at the bed edge. Mean lengths of *Palaemonetes* spp. were 2.5 times more likely to be longer in the small mesh treatment compared to the other mesh treatments, controlling for bed position.

DISCUSSION

Differences in predator abundances between mesh treatments across position treatments indicate that the mesh treatments did exclude

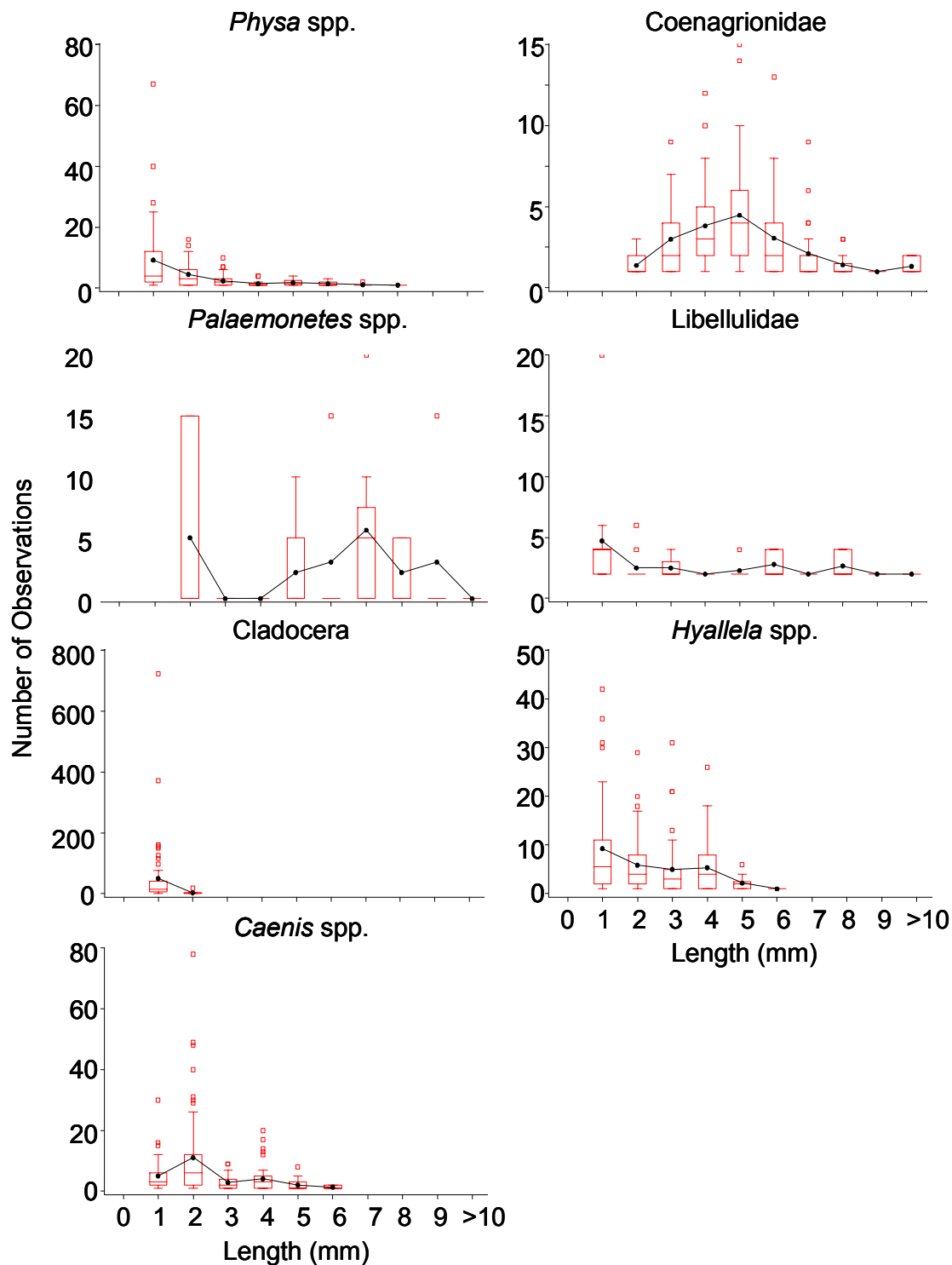


Figure 3.4– Length distributions (mm) for major taxa except Chironomidae (Diptera). Horizontal axes are constant, while vertical axes are different for each graph.

some predators, as expected. Further, predator abundance does not appear to be dependent on position within a hydrilla bed. Collectors were the most abundant feeding group, indicative of the eutrophic nature of the ARB. A possible explanation for fewer collectors in the small interior treatment is the hydrodynamic interaction between the small mesh treatment and the surrounding hydrilla bed, which may have reduced the amount of material available to collectors. Scrapers exhibited a trend similar to that of the most numerically abundant group member *Physa* spp., with greater abundances in the bed interior relative to the bed edge.

Although length differences among treatments were evident for two taxa, some of these differences may have been due to the effects of outliers on mean length calculations when sample sizes were small. Coenagrionidae were longer in a treatment that yielded fewer individuals when the exclosures were harvested. Alternatively, there could have been an inverse relationship between density and mean length for these taxa in these treatments, reflecting size-related intraspecific interactions among individuals (Layman and Winemiller 2004), although this trend was not evident among all treatments. Greater mean lengths of palaemonetid shrimp in small-mesh exclosures in the bed interior relative to small-mesh exclosures at the bed edge did not seem to be due to small sample size.

The purpose of the various meshes used for the experimental units was to exclude invertivorous fishes, and I developed three hypotheses based on expected effects of exclosure mesh size and bed position on macroinvertebrates colonizing the exclosures. First, I hypothesized that as mesh size increased, predation from fishes on invertebrates would increase, reducing invertebrate abundances and average lengths.

Additionally, I hypothesized that predation from fishes would be greater on the edge of the hydrilla bed relative to the bed interior, resulting in relatively lower macroinvertebrate abundances in the medium and large-mesh exclosures placed near open water.

Finally, I hypothesized that macroinvertebrates should have been longest in the smaller mesh sizes inside the bed, theoretically receiving the lowest levels of fish predation.

The only measured taxon that matched abundance and length predictions was the omnivore *Palaemonetes* spp. Predation by fishes on various *Palaemonetes* species has been shown to affect both the size and abundance of these shrimp populations (Bass et al. 2001; Davis et al. 2003), and Mason (2002) showed that age-0 largemouth bass *Micropterus salmoides* consistently ate crustaceans (~30% of stomach contents by weight), including decapod shrimp, throughout the year in high density ARB hydrilla beds. Chironominae decreased in abundance as mesh size increased in the edge position treatment and bluegill *Lepomis macrochirus*, an abundant sunfish commonly associated with hydrilla in the ARB, is known to be a generalist browser and frequently consumes chironomids and other macroinvertebrates (Werner 1977; Desselle et al. 1978; Mittelbach 1981; Schramm and Jirka 1989; Olsen et al. 2003). In addition, many of the Chironominae found in the edge treatments were large (~10 mm) tube builders (personal observation), and these taxa may have partly mitigated their predation risk because of their tube building habits (O'Brien et al. 1976). *Hyallela* spp., *Physa* spp. and libellulid odonates increased in abundance on the interior of the bed. Numerous centrarchids, including redear sunfish *Lepomis microlophus*, a well-documented molluscivore (Desselle et al. 1978; Huckins 1997; McCollum et al. 1998), are abundant

in the ARB (Rutherford et al. 2001), which may partially explain the observed abundance patterns for these macroinvertebrates.

Overall, however, most taxa responded to the mesh and position treatments differently than predicted. Many taxa were either more abundant on the exterior of the bed or increased in abundance as mesh size increased. These results indicate a reduced or indirect role of fish predation in the determination of macroinvertebrate community structure in hydrilla beds. An alternative explanation could be that taxa that were more abundant in the small mesh exclosures were affecting the abundance of other macroinvertebrates. Chironominae are soft-bodied dipterans and most commonly feed as grazers and filter feeders (Epler 2001). Conversely, *Palaemonetes* spp. is a large, chitin covered omnivore (Posey and Hines 1991; Costantini and Rossi 2001; Smith 2001; Geddes and Trexler 2003). Different species of *Palaemonetes* spp. have been shown to prefer arthropod prey (Costantini and Rossi 2001) and can reduce abundances of benthic arthropods (Posey and Hines 1991). Most of the organisms found more commonly in the larger mesh sizes were either small (when compared to *Palaemonetes* spp., see figure 3.5), including Cladocera, *Caenis* spp. and *Hyallela* spp.; or soft bodied, including Coenagrionidae, Tanyptodinae, and Cladocera. The dragonflies of the family Libellulidae are not soft bodied, but were relatively small (most were < 5 mm total length) compared to *Palaemonetes* spp. (most were > 5 mm carapace length). These results suggest that smaller taxa in general are vulnerable to predation from *Palaemonetes* spp., which may exert a significant influence on macroinvertebrate community composition in ARB hydrilla beds.

Predation by fishes and the resulting trophic cascade appear to be important and detectable effects that shape hydrilla-dwelling macroinvertebrate communities in the ARB. *Palaemonetes* spp., although susceptible to predation by fishes both in and on the edge of hydrilla beds, may play a key role in determining macroinvertebrate community structure. When *Palaemonetes* spp. is absent or at low densities due to predation by fishes, other macroinvertebrates appear capable of increasing their densities. Although predation effects appear to be similar regardless of bed position for many macroinvertebrates, other taxa were more abundant on the bed interior. This varying abundance pattern between taxa suggests hydrilla may act as a barrier to predation on macroinvertebrates by some littoral fishes in the ARB, whereas other fishes may freely forage throughout a hydrilla bed.

CHAPTER 4: THE EFFECTS OF PREDATOR EXCLUSION, POSITION, AND PLANT ARCHITECTURE ON HYDRILLA-DWELLING MACROFAUNAL COMMUNITIES

I have demonstrated that predator exclusion and position within a hydrilla bed can influence the species composition of macroinvertebrate communities (chapter 3). Plant architecture and macrophyte structural complexity are factors that may also affect macroinvertebrate communities (Chapter 1). In this experiment I replicated the experiment analyzed in Chapter 3, while adding a new, possibly confounding variable, plant architecture, to the experiment. The purpose of this experiment was to determine whether, in addition to predator exclusion and position within a hydrilla bed, plant architecture had a discernible effect on macroinvertebrate community composition.

METHODS

This experiment was conducted from August 5 to September 8 2004 in an ARB hydrilla bed located west of Plaquemines, Louisiana, near Belle River and the Intracoastal Canal (Figure 1.1). Ten exclosures of each three mesh types containing either a hydrilla-like (complex) or *Vallisnaria*-like (simple) artificial plant were placed within and on the outside of the hydrilla bed (N = 10 per treatment, total N = 120). The exclosures were harvested 34 days after the initiation of the experiment. Contents of the exclosures were field preserved in 95% ethanol and later sorted and identified. Five exclosures were lost over the course of the experiment and seven samples were discarded due to mislabeling.

The 29 taxa analyzed in this study (Table 4.1) occurred in at least 10% of the samples and were identified and analyzed at the genus level, with the exception of

Table 3.1.—Macroinvertebrate taxa, frequency of occurrence (FO), mean number of organisms per plant, and the statistical analysis used.

Taxa	FO (%)	Mean	Analysis
<i>Caenis</i> spp. (Ephemeroptera: Caenidae)	100	18.83	MANCOVA
Tanypodinae (Diptera: Chironomidae)	95	10.43	MANCOVA
<i>Hyallela</i> spp. (Amphipoda: Hyallelidae)	94	19.28	MANCOVA
Chironominae (Diptera: Chironomidae)	93	12.49	MANCOVA
Hydrobiidae (Gastropoda)	93	15.16	MANCOVA
Planorbidae (Gastropoda)	91	20.60	MANCOVA
Coenagrionidae (Odonata)	76	3.06	MANCOVA
<i>Heterandria formosa</i> (Cyprinodontiformes: Poeciliidae)	71	7.19	MANCOVA
<i>Ferressia</i> spp. (Gastropoda: Ancyliidae)	69	9.41	MANCOVA
Cladocera	68	4.66	Logistic Regression
<i>Physa</i> spp. (Gastropoda: Physidae)	60	3.08	MANCOVA
<i>Callibaetis</i> spp. (Ephemeroptera: Baetidae)	57	4.35	Logistic Regression
<i>Ondontomyia</i> spp. (Diptera: Stratiomyidae)	56	4.73	Logistic Regression
Unionidae (Pelecypoda)	48	7.75	Logistic Regression
Platyhelminthes	40	2.65	Logistic Regression
<i>Palaemonetes</i> spp. (Decapoda: Palaemonidae)	38	2.41	Logistic Regression
<i>Bezzia</i> spp. (Diptera: Ceratopogonidae)	35	2.87	Logistic Regression
<i>Epitheca</i> spp. (Odonata: Corduliidae)	34	1.95	Logistic Regression
Pyalidae (Lepidoptera)	30	2.20	Logistic Regression
Culicidae (Diptera)	26	2.02	Logistic Regression
<i>Helobdella</i> spp. (Rynchobdellida: Glossiphoniidae)	25	2.63	Logistic Regression
Hydrachnida (Arachnida)	25	1.99	Logistic Regression
Copepoda	23	4.00	Logistic Regression
<i>Gambusia affinis</i> (Cyprinodontiformes: Poeciliidae)	22	2.16	Logistic Regression
<i>Pelocoris</i> spp. (Hemiptera: Naucoridae)	20	1.63	Logistic Regression
Belastomatidae (Hemiptera)	17	1.62	Logistic Regression
<i>Placobdella</i> spp. (Rynchobdellida: Glossiphoniidae)	16	2.80	Logistic Regression
Cambaridae (Decapoda)	15	1.29	Logistic Regression
<i>Hexagenia</i> spp. (Ephemeroptera: Ephemeridae)	12	1.61	Logistic Regression

chironomids, which were identified to subfamily, some gastropods, which were identified to family, and odonates in the family Coenagrionidae, due to the loss of caudal gills of during sample processing that limited further identification.

Macrofaunal abundances were standardized between plant treatments by plant surface area and were expressed as mean densities and frequency of occurrence (Table 4.1). Plants from the surrounding vegetation bed, such as *Hydrilla verticillata* and *Limnobium spongia*, intruded into many of the exclosures during the experiment. Plant matter found in exclosures was dried to a constant weight and included in the analysis as a covariate. I employed a multivariate analysis of covariance (MANCOVA) on the 10 approximately-normally distributed taxa to test *a priori* contrasts of mesh size, position, and plant type given the covariate intruded plant weight. Multinomial logistic regression was performed on the 19 remaining non-normally distributed taxa to examine spatial density patterns (Agresti 1996). Because of their abundances within the exclosures, least killifish *Heterandria formosa* and Western mosquitofish *Gambusia affinis* were included in the logistic regression. To assess density patterns by trophic group, taxa were placed into feeding groups (predator, collector, scraper, shredder, omnivore, and parasite) adapted from Merritt and Cumins (1996), with normally-distributed log-transformed densities of collectors, predators, scrapers, shredders, and omnivores analyzed with a MANCOVA that included intruded plant weight as the covariate. Invertebrate communities were compared at the order level (suborder for odonates) between years and sites of the study and between mesh and position treatments to test for consistent macroinvertebrate trends across years and sites with a MANOVA that incorporated linear contrasts.

RESULTS

Linear contrasts from the MANCOVA revealed varied responses of the macroinvertebrate taxa to position, plant, and mesh treatments given the covariate intruded plant weight. Bed position and plant architecture interacted significantly but mesh did not interact with the other treatments. Gastropods (Figure 4.1) were consistently denser inside the hydrilla bed compared to the outside edge and on simple plants, though this difference was not always significant due to the covariate. Of these snails, Hydrobiidae, *Ferressia* spp., and Planorbidae were significantly denser in simple plant treatments regardless of position treatments, and *Physa* spp was more abundant in the simple plant treatment but only on the bed exterior. Trends between treatments for the insects were not as uniform as the gastropods, though *Hyallela* spp. and *Ondontomyia* spp. also exhibited the highest densities in simple plants. Additionally, Coenagrionidae and Tanypodinae were denser in simple plants in the bed interior. Chironominae exhibited greater densities in the outside position treatment with complex plants, but was also denser on simple plants overall.

Few differences were found between mesh treatments (Figure 4.2). Chironominae and Coenagrionidae tended to increase in density as mesh size increased, whereas *Ondontomyia* spp. peaked in density in the medium mesh treatment.

Logistic regression revealed that the presence/absence of 17 of the 19 taxa analyzed was not affected by plant type ($P = 0.34$), but differed significantly among exclosures based on either position or mesh size (Table 4.2). Copepoda, Cambaridae, Hydrachnida and *Palaemonetes* spp. were more likely to be found in the small mesh

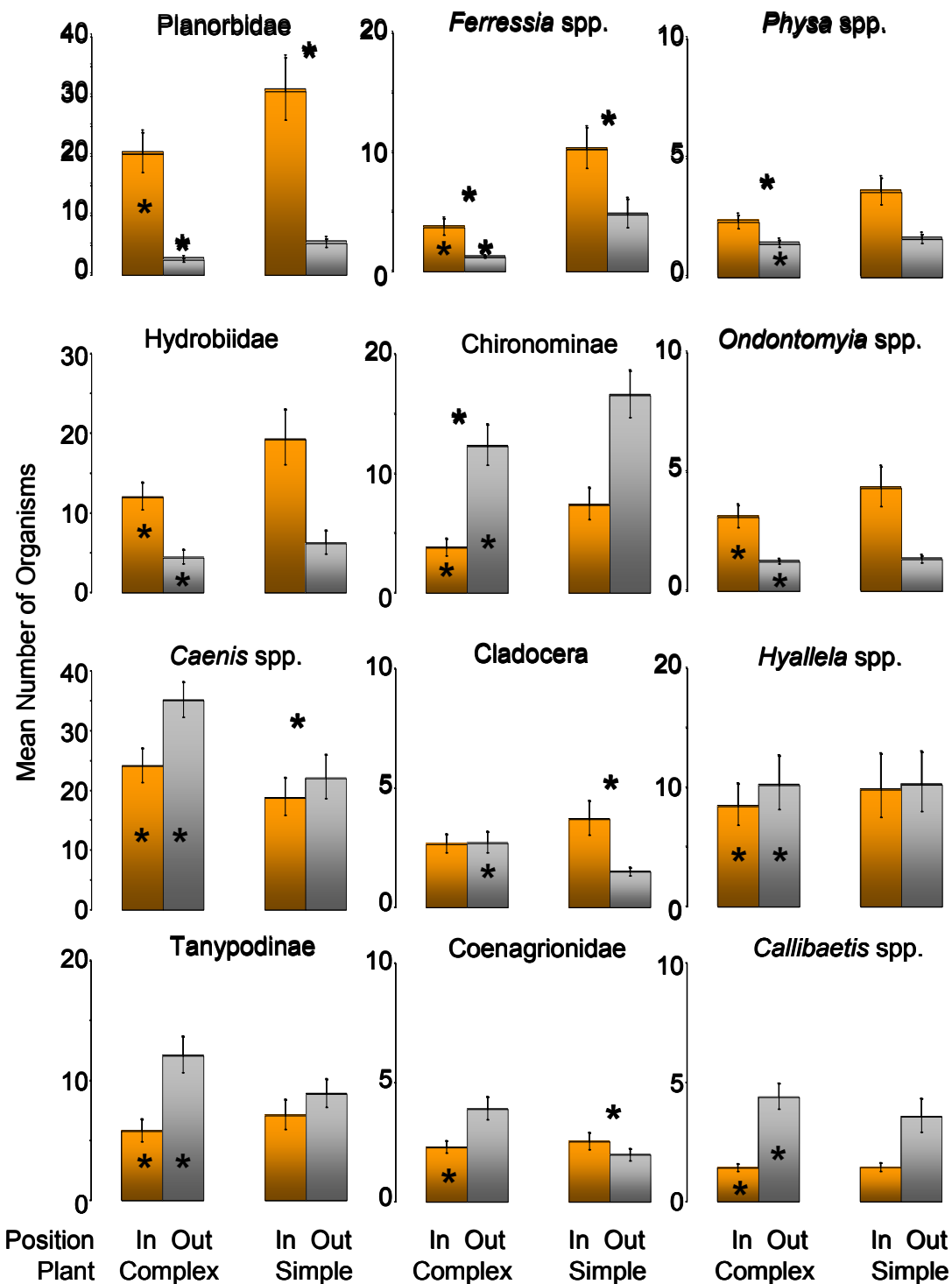


Figure 4.1—Untransformed means of normally distributed taxa for each position and plant treatment combination. Error bars are standard error of the mean. Significant differences within each taxon are indicated by asterisks above bar graph pairs for between position within plant comparisons and on the graphs for between plant within position comparisons where significant differences were present given the covariate intruded plant weight.

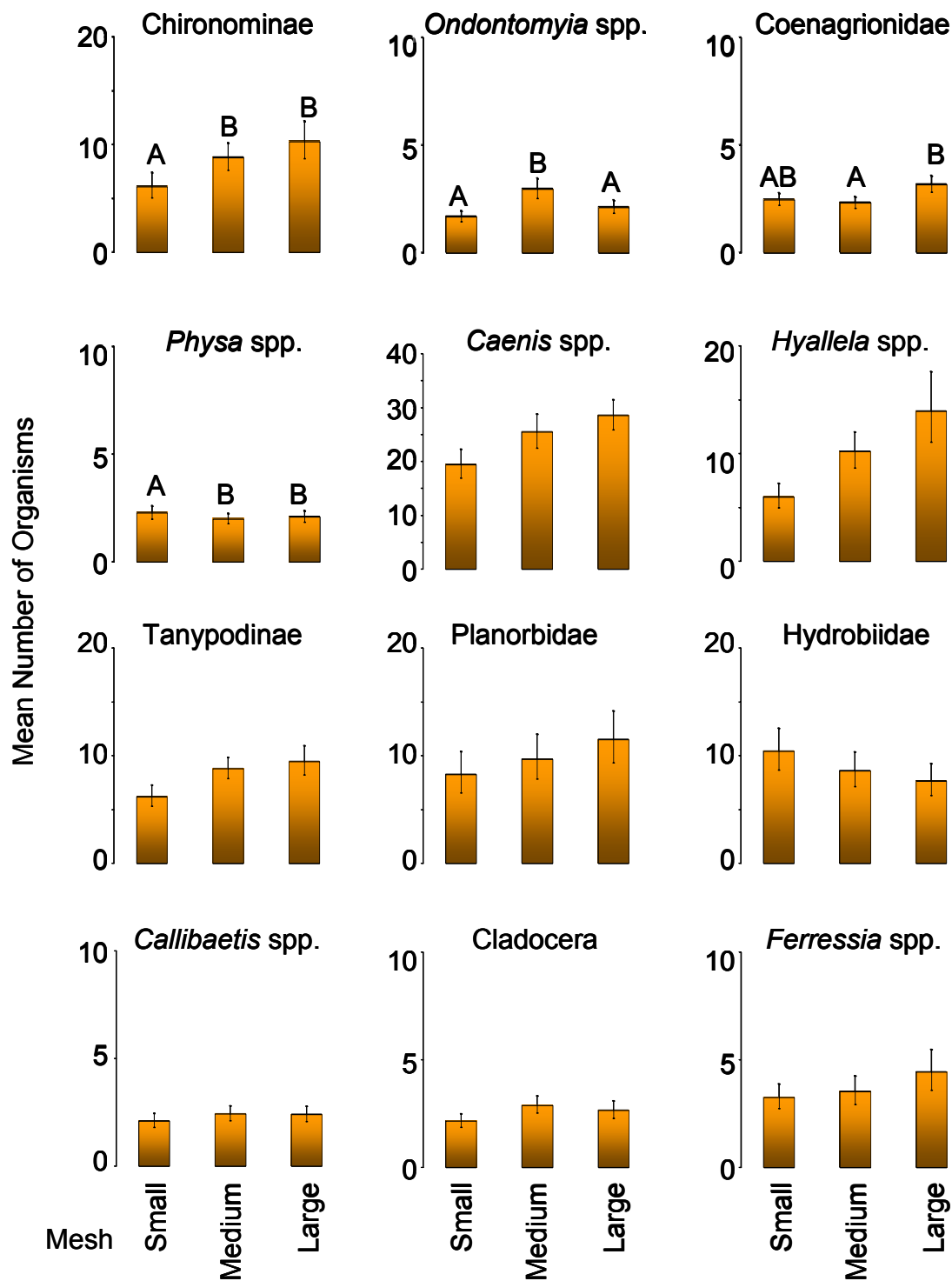


Figure 4.2—Untransformed means of normally distributed taxa for each mesh treatment. Error bars are standard error of the mean. Significance groupings within each taxon are indicated by letters where significant differences were present given the covariate intruded plant weight.

Table 4.2--Significant comparisons from the logistic regression. Taxa, significant treatment comparisons, and odds of presence in first listed treatment group compared to the second treatment are shown.

Taxon	Treatment	Comparison	Odds of Presence
Belastomatidae	Position	In vs. Out	72.92
<i>Callibaetis</i> spp.	Position	In vs. Out	0.21
Cambaridae	Mesh	Large vs. Medium	0.20
Cladocera	Position	In vs. Out	8.25
Copepoda	Position	In vs. Out	4.08
	Mesh	Large vs. Small	0.17
Culicidae	Position	In vs. Out	29.78
<i>Epithea</i> spp.	Mesh	Medium vs. Small	6.80
<i>Gambusia affinis</i>	Position	In vs. Out	8.76
	Mesh	Large vs. Small	0.06
	Mesh	Medium vs. Small	0.07
<i>Helobdella</i> spp.	Position	In vs. Out	24.92
<i>Hexagenia</i> spp.	Position	In vs. Out	4.63
Hydrachnida	Position	In vs. Out	21.33
	Mesh	Large vs. Medium	0.22
<i>Ondontomyia</i> spp.	Position	In vs. Out	52.61
	Mesh	Medium vs. Small	8.14
<i>Palaemonetes</i> spp.	Mesh	Large vs. Small	0.18
<i>Pelocoris</i> spp.	Position	In vs. Out	9.47
<i>Placobdella</i> spp.	Mesh	Large vs. Small	11.00
Platyhelminthes	Position	In vs. Out	3.90
Pyralidae	Position	In vs. Out	20.55

compared to the large mesh exclosures, whereas Western mosquitofish were more likely to be found the small-mesh exclosures compared to either of the other mesh sizes. In contrast, *Epitheca* spp. and *Ondontomyia* spp. had a greater probability of inhabiting the medium-mesh treatment compared to the small mesh, and *Placobdella* spp. had greater odds of inhabiting the large mesh compared to the small mesh exclosures. *Callibaetis* spp. was the only organism that was more likely to be found at the edge of the hydrilla bed, whereas Belostomatidae, Cladocera, Copepoda, Culicidae, Western mosquitofish, *Helobdella* spp., *Hexagenia* spp., Hydrachnida, *Ondontomyia* spp., *Pelocoris* spp., Platyhelminthes, and Pyralidae were all more likely to occur in the bed interior.

Among feeding groups, there was a significant interaction between mesh and position. Collectors were less abundant on the bed interior, regardless of mesh type, given the covariate intruded plant weight (Figure 4.3). Predator abundance did not differ in any of the treatment combinations. The greatest densities of scrapers were found in the bed interior on simple plants, regardless of mesh (Figure 4.4). Shredders and omnivores occurred in greater densities in the medium mesh on the bed interior compared with bed exterior.

The triple interaction between year, mesh, and position was significant in the across years comparison but further interpretation and analysis could not be performed.

DISCUSSION

The purpose of this study was to determine the effects of predator exclusion, position within a hydrilla bed, and plant architecture on hydrilla-dwelling macroinvertebrate communities. I developed several hypotheses about how the

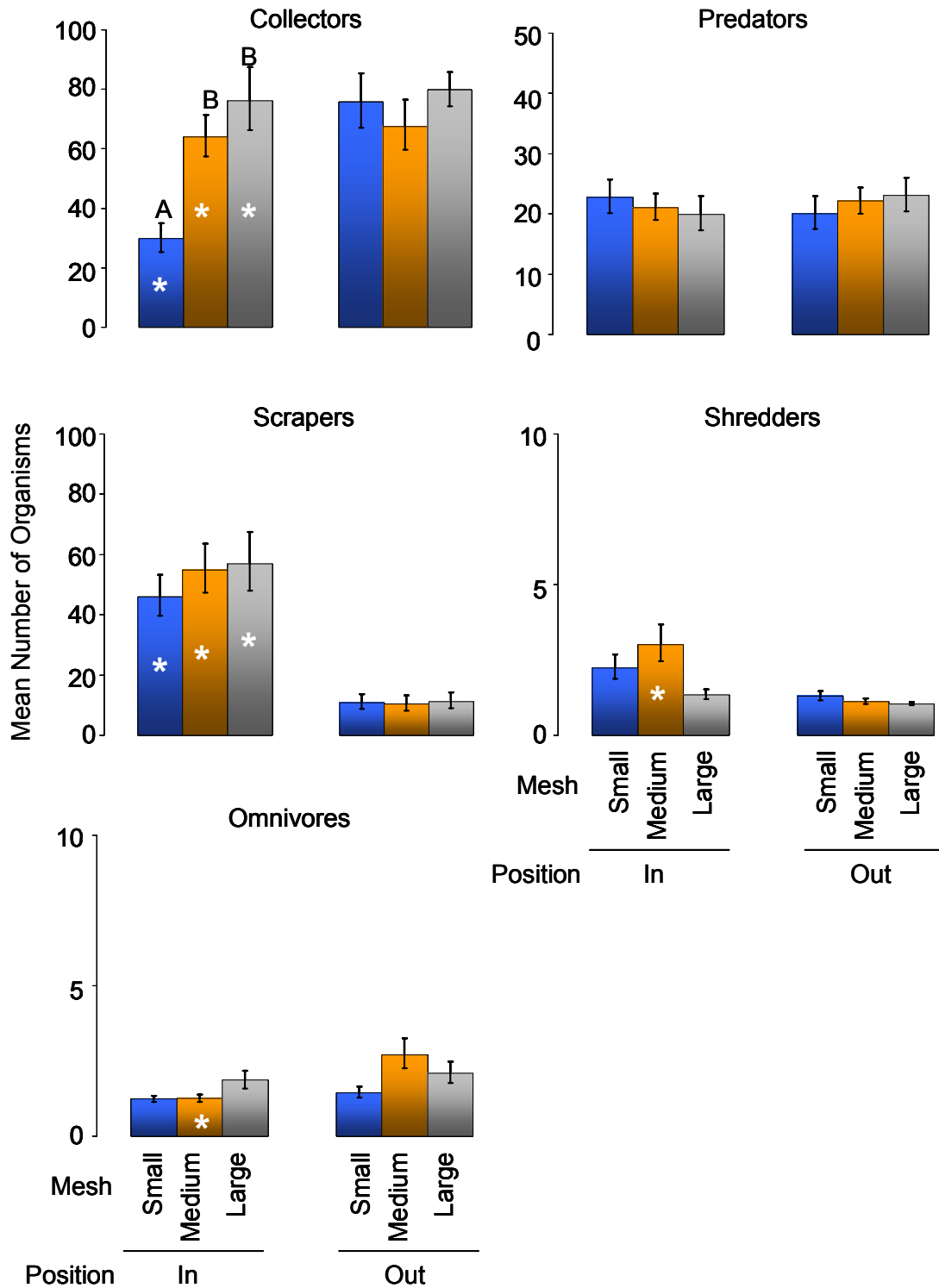


Figure 4.3—Mean number of organisms in each functional feeding group for each mesh and bed position combination. Error bars are standard error of the mean. Asterisks indicate significant within mesh between position differences. Letters indicate significant groups between meshes within each position treatment.

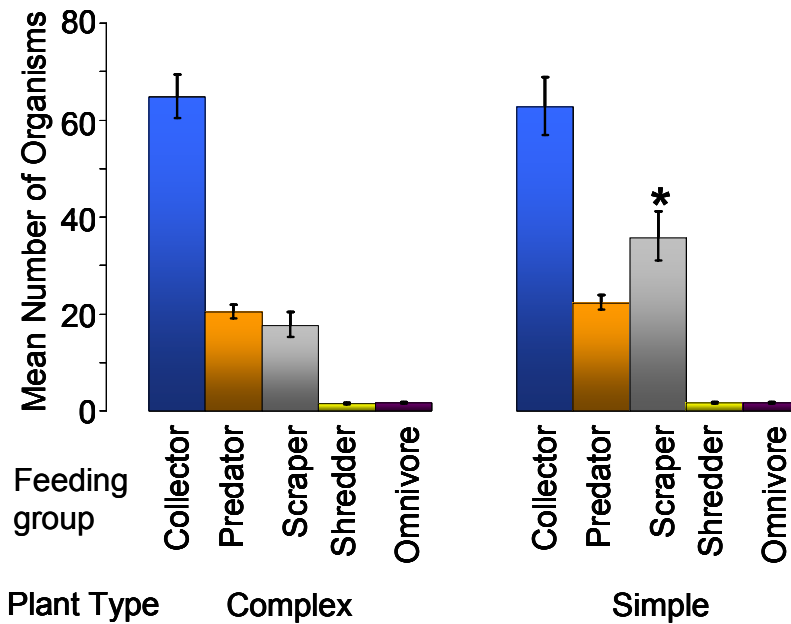


Figure 4.4—Mean number of organisms found from each feeding group within each plant architecture treatment. Error bars are standard error of the mean. An asterisk indicates a significant within feeding group between plant difference.

macroinvertebrate community would react based on these treatments. In general, macroinvertebrate density should be lowest in treatments with highest rates of predation. Assuming that fishes are the dominant littoral predators in the ARB, I

expected to find the lowest macroinvertebrate densities at the bed edge in exclosures constructed of the largest mesh, with increasing densities observed as mesh size decreased and exclosure position moved to the bed interior. I used artificial plants of simple and complex architecture in this study and expected that the more structurally-complex plants would harbor increased densities of macroinvertebrates (Chapter 1), which has been attributed to greater surface area, decreased predatory foraging success by fishes, and increased prey survival (Crowder and Cooper 1982).

Gastropods, both taxonomically and as the dominant plant bed scrapers, typically occurred in greater densities on the inside of the hydrilla bed across mesh and plant treatments. Redear sunfish *Lepomis microlophus* are abundant in the ARB (Rutherford et al. 2001), and are well known for preying extensively on mollusks (Desselle et al.

1978; Huckins 1997; McCollum et al. 1998), which may partially explain the observed abundance patterns for these macroinvertebrates. Redear sunfish may depress gastropod densities by grazing, which would have been evident in the large mesh exclosures, and may also reduce the densities of juvenile gastropods able to recruit to the plant beds, which may explain why decreased gastropod densities at the bed edge were observed irrespective of mesh treatment. All four taxa of gastropods were found to have greater densities in at least one position treatment on the simple plants when compared with the complex plants. The ribbon-like structure of the simple plants may have reduced self-shading by the artificial plant. Light reaching a greater proportion of the artificial plant surface may have in turn increased periphyton abundance, the dominant food of littoral gastropods (Rooke 1984, 1986).

In addition to gastropods, several other organisms were also more likely to be found on the inside of the hydrilla bed, particularly predators like the belostomatids, Western mosquitofish, *Helobdella* spp. and *Pelocoris* spp., though many apparent increases in density relative to bed position were confounded by the intruded plant weight covariate. Respiration activities of some of these organisms (e.g., culicids, belostomatids, and *Ondontomyia* spp.) involves constant or frequent contact with the water surface (Merritt and Cumins 1996), which may incur greater risk of predation at the bed edge, resulting in greater abundances within the confines of the hydrilla bed. In contrast to previous studies (Colon-Gaud and Kelso 2004), shredders in the family Pyralidae were more likely to be found on the bed interior, which may have been related to the availability of plant matter, though this relationship was not as strong at the feeding group level. Finally, many of these taxa, including crawfish, zooplankton,

mosquito larvae, Western mosquitofish, and grass shrimp are common prey of ARB fishes such as Western mosquitofish (Hayes and Rutledge 1991; Gophen et al. 1998; Mansfield and Mcardle 1998), bluegill *Lepomis macrochirus* (Walton et al. 1992; Harrel and Dibble 2001; Olsen et al. 2003), warmouth *Lepomis gulosus* (Hunt 1952; Guillory 1978; Henry 1979), and largemouth bass *Micropterus salmoides* (Pelham et al. 2001; Brenden and Murphy 2002; Garcia-Berthou 2002; Mason 2002). In addition to direct predation in the large-mesh exclosures, invertivorous fishes along the outer edge of the hydrilla bed may have also hampered recruitment of these macrofauna to the smaller-mesh exclosures.

In contrast to gastropods and some of the other invertebrates, some of the more commonly collected organisms that differed in abundance between positions exhibited greater densities on the outside edge of the hydrilla bed. Some of the insects analyzed with the MANCOVA (Figure 4.1) appeared to follow this pattern in the complex plant treatment, and Chironominae and *Caenis* spp. appeared to follow this pattern regardless of plant treatment, though many differences were confounded by the plant weight covariate. Some of the organisms that exhibited this trend (*Caenis* spp., Chironominae, and *Callibaetis* spp.) were collectors (see Figure 4.3), and the outside edge of the hydrilla bed may have provided more food particles from the adjacent water column. Although the complex plants likely provided some structural protection from predation, this trend runs contrary to my hypothesis, particularly for the large-mesh exclosures, and suggests that predation does not significantly affect the abundance and distribution of these hydrilla-dwelling taxa. In fact, a majority of the organisms analyzed

did not exhibit density changes as a result of mesh size, suggesting factors other than fish predation were more important in determining macroinvertebrate distribution.

The small mesh treatment was designed to exclude all predaceous fishes, which I believed would lead to increased macroinvertebrate densities. However, some macroinvertebrates, such as *Placobdella* spp. Chironominae, and collectors, were found to be less dense in small-mesh exclosures. This abundance pattern may in fact have been related to the abundances of three other taxa that were found more often (Copepoda, Western mosquitofish, and *Palaemonetes* spp.) in small-mesh exclosures, which may have provided a refuge for these organisms from larger fish predators. Given their feeding habits, it is certainly plausible that grass shrimp and the Western mosquitofish were responsible for declines in the density of smaller macroinvertebrates in the small-mesh exclosures. Predatory fishes are abundant in littoral macrophyte beds in the ARB (Troutman 1997), and may be responsible for a trophic cascade that was reflected in these macroinvertebrate abundance patterns.

Many macroinvertebrate communities and distributions differed from those found during the 2003 study (Chapter 3), likely resulting the significant interactions that confounded more quantitative analyses. Coenagrionid damselflies, Chironominae, and gastropods (or scrapers) followed similar distribution patterns across the two studies. Orthocladinae was not found in sufficient numbers during this study to allow for meaningful statistical analyses, whereas this taxon was one of the primary taxa analyzed in 2003. Additionally, the dragonfly nymph assemblage changed between the sites with libellulids most abundant in 2003 and the corduliid *Epitheca* spp. being most numerous in 2004. During 2003 physid snails dominated the gastropod assemblage,

whereas in 2004 a suite of gastropods from four families accounted for most of the snails collected in the exclosures. Finally, hyallelid amphipods and caenid mayflies showed very different trends between sites and years.

Hydrilla-dwelling macrofaunal communities are structured by a wide range of biotic and abiotic factors. Plant architecture, except in the case of scrapers, does not appear to have a significant effect on macroinvertebrate densities. Distributions of some organisms, including scrapers and some collectors, appear to be based on food availability. Spatial patterns of many organisms appear to be related to direct predation by fishes, and hydrilla may prevent some fishes from effectively preying on these invertebrates in the bed interior. However, trophic cascades may also play an important role in structuring epiphytic macroinvertebrate communities, as the effects of fish predators on predaceous invertebrates and smaller fishes alter distributions of herbivorous or detritivorous macroinvertebrates.

CHAPTER 5: DIETS OF FISHES INHABITING HYDRILLA BEDS

Fishes and invertebrates use vegetation beds for both cover and as productive foraging habitat (Chapter 1). The basis of my field experiments was a hypothesis that hydrilla may act as a barrier to predation by fishes on macrophyte-dwelling macroinvertebrates, based on previous research that showed considerable differences in the diets of age-0 largemouth bass from low and high density hydrilla beds (Mason 2002). I previously explored the effects of predator exclusion, position within a hydrilla bed, and plant architecture on macroinvertebrate communities with field experiments. The purpose of this field study was to describe the diets of potentially invertivorous fishes inhabiting hydrilla beds near the 2004 experimental site to assess whether these fishes could be expected to exert significant predation pressure on the hydrilla-dwelling macroinvertebrate community.

METHODS

Collection of fishes occurred in late summer 2004 concurrent with the second enclosure experiment. Fishes were collected on August 11, September 1, and September 23, 2004. I collected fishes in the canals south of the sampling site on the first day, southwest on the second day, and at the sample site on the third day (Figure 5.1). Sampling could not be conducted north of the site on any day without interfering with recreational fishers.

Nine species of fishes were collected based on their perceived consumption of macroinvertebrates, the abundance of identifiable stomach contents (i.e. no gizzard), and potential association with vegetation (Ross 2001). I chose 50 as the minimum

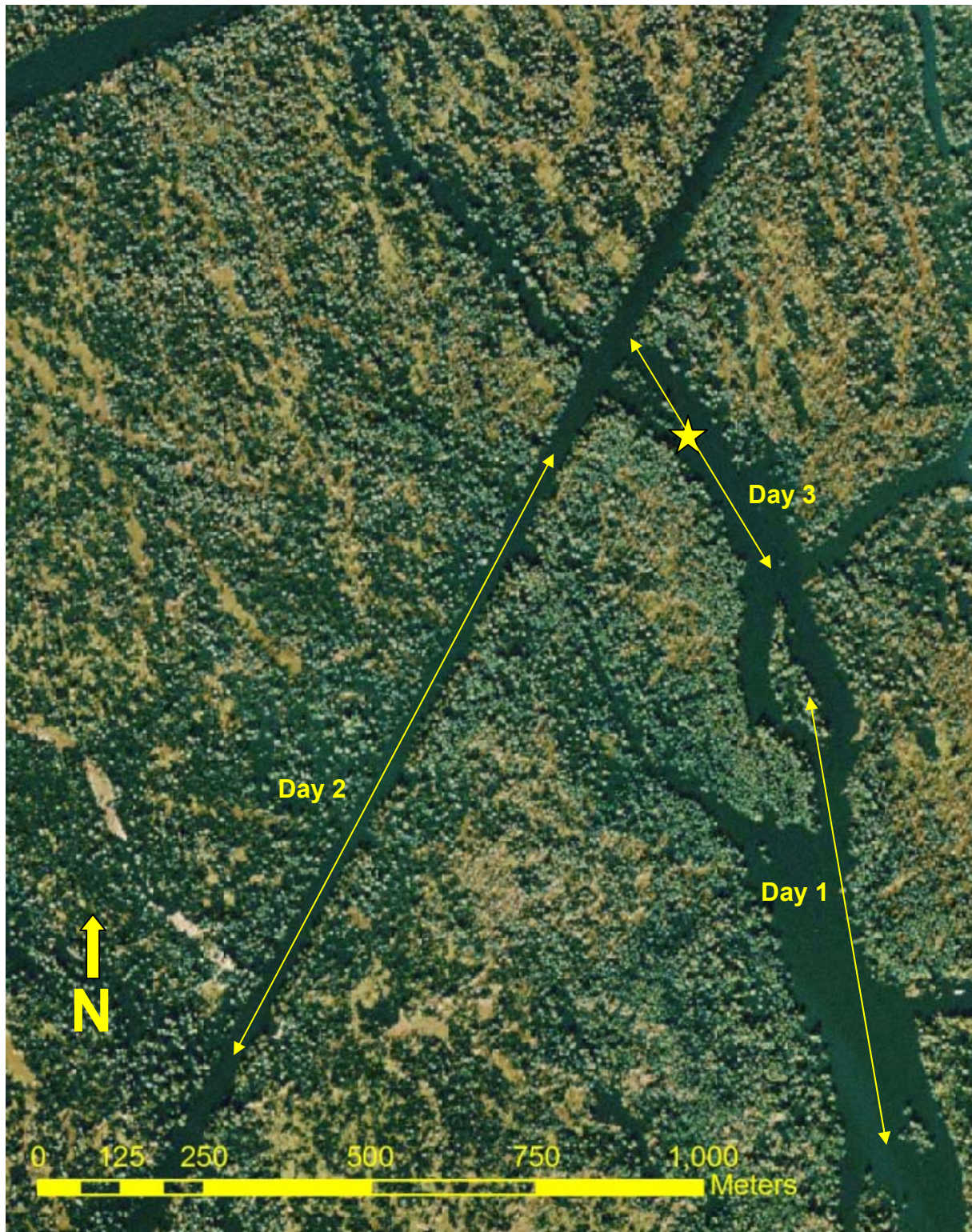


Figure 5.1—Locations of electrofishing runs on August 11 (Day 1), September 1 (Day 2), and September 23 (Day 3). The enclosure experiment site is marked with a star.

number of fishes collected for each species considered in the study, which allowed for an adequate analyzable sample size even with a high proportion of empty fish stomachs. Fishes that I analyzed included redear sunfish *Lepomis microlophus* (N = 54), warmouth *Lepomis gulosus* (N = 57), bluegill (N = 101), spotted sunfish *Lepomis punctatus* (N = 98), golden topminnow *Fundulus chrysotus* (N = 119), sailfin molly *Poecilia latipinna* (N = 74), Western mosquitofish *Gambusia affinis* (N = 68), least killifish *Heterandria formosa* (N = 50), and age-0 largemouth bass under 100 mm in length (N = 78), based on previous research of feeding ontogeny in ARB largemouth bass (Mason 2002).

I used boat electrofishing along the edges of hydrilla beds that lined the bayous and canals adjacent to the sample site. Collected fishes were immediately placed on ice (Bowen 1996), and stomachs were later removed and preserved in ethanol, except for fishes under approximately 90 mm in total length, which were preserved whole.

Fishes in the order Cyprinodontiformes do not have discernable stomachs (Wootton 1990), so contents of the first 5 to 10 mm of the alimentary canals of sailfin molly, Western mosquitofish, and least killifish were analyzed. Gut contents were examined with the aid of a dissecting microscope and identified to family when possible (Merritt and Cummins 1996; Smith 2001). Ingested plant matter was recorded as present or absent, as were prey items in the guts of sailfin molly, which were severely degraded and difficult to identify. Length of the gut was measured in ten randomly selected individuals from each of the cyprinodontiform fishes. Gut lengths were standardized by total length and were compared between species to assess the feeding ecology of these taxa (Wootton 1990).

Analysis of fish diets included comparisons of frequency of occurrence, and a principal components analysis of fish diets that yielded a biplot summarizing mean abundance of each prey item from each fish species (except sailfin molly and least killifish) to examine diet-based groupings of fishes. Principal component axes and scores were modified with a constant so that observations and variables were equally emphasized in the resulting plot (Friendly 1991; Johnson and Wichern 2002). This biplot allowed fish species and prey items to be graphed together, and vectors representing the loading of each prey item were drawn in the graphed space. Differences in gut length to fish total length ratios among the three cyprinodontiform fishes were assessed with analysis of variance (ANOVA) and Tukey-adjusted least square mean comparisons.

RESULTS

In order of decreasing length (Figure 5.2), I found empty stomachs in 28% of redear sunfish, 47% of warmouth, 24% of bluegill, 24% of spotted sunfish, 6% of largemouth bass, 10% of golden topminnow, 14% of sailfin molly, 6% of Western mosquitofish, and 2% of least killifish. Frequency of occurrence of prey items revealed that redear sunfish consumed mostly molluscs and plant matter (Figure 5.3), whereas decapods comprised over 50% of the identifiable prey in warmouth stomachs. Plant matter, chironimids, and hemipterans were important prey for bluegill and spotted sunfishes, although both species exhibited very broad diets. Unlike the other two sunfishes, largemouth bass predominantly preyed on fishes (mostly livebearers), but also consumed decapods (grass shrimp) and ephemeropterans (all in the family

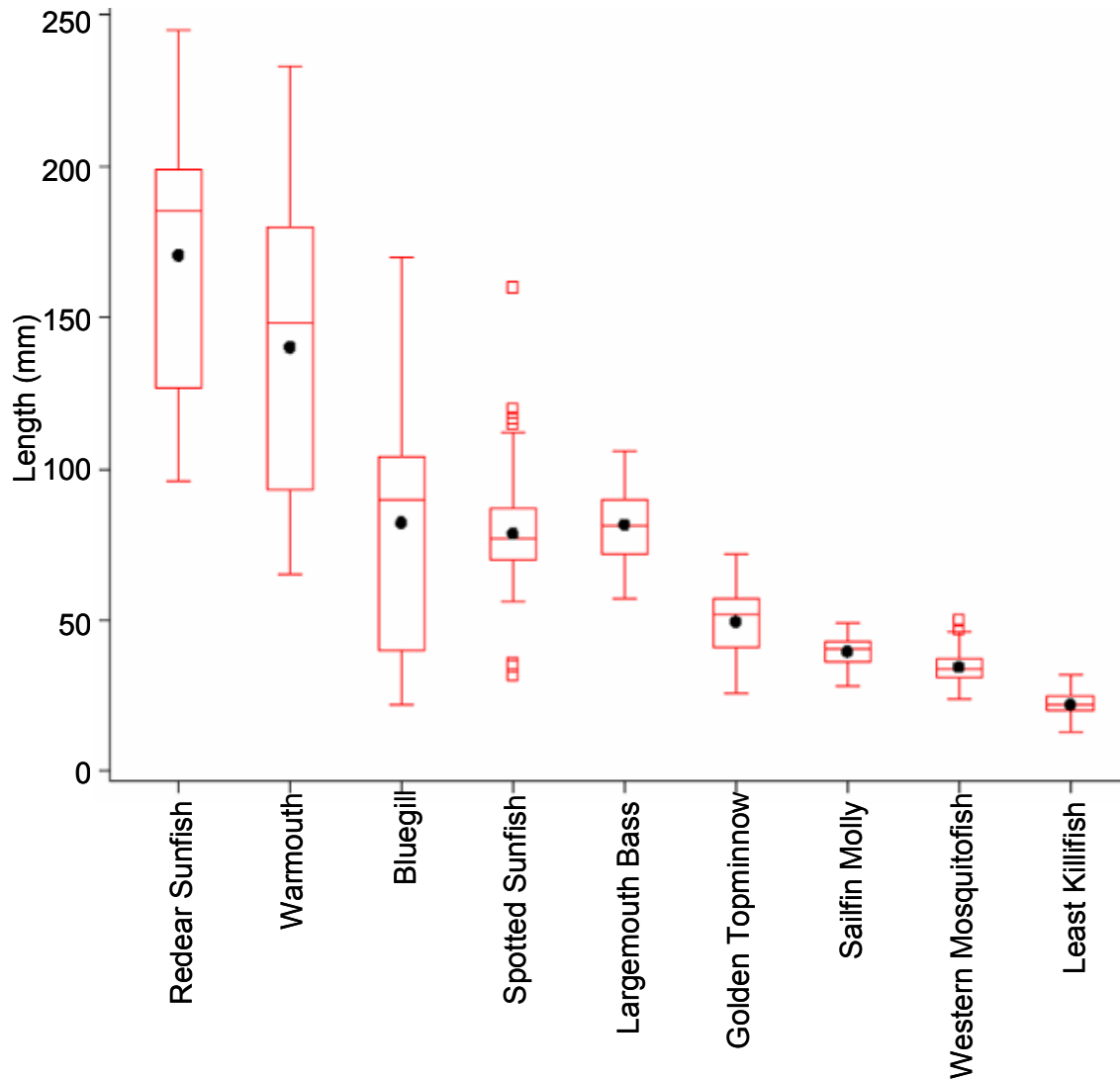


Figure 5.2—Length distributions of fishes collected.

Baetidae). Golden topminnow stomachs contained mostly plant matter, stratiomyids (Diptera: stratiomyidae), hemipterans, chironomids, other dipterans, and some fishes. Plant matter and zooplankton dominated the stomach contents of sailfin molly and Western mosquitofish, whereas least killifish guts were filled almost entirely with plant matter.

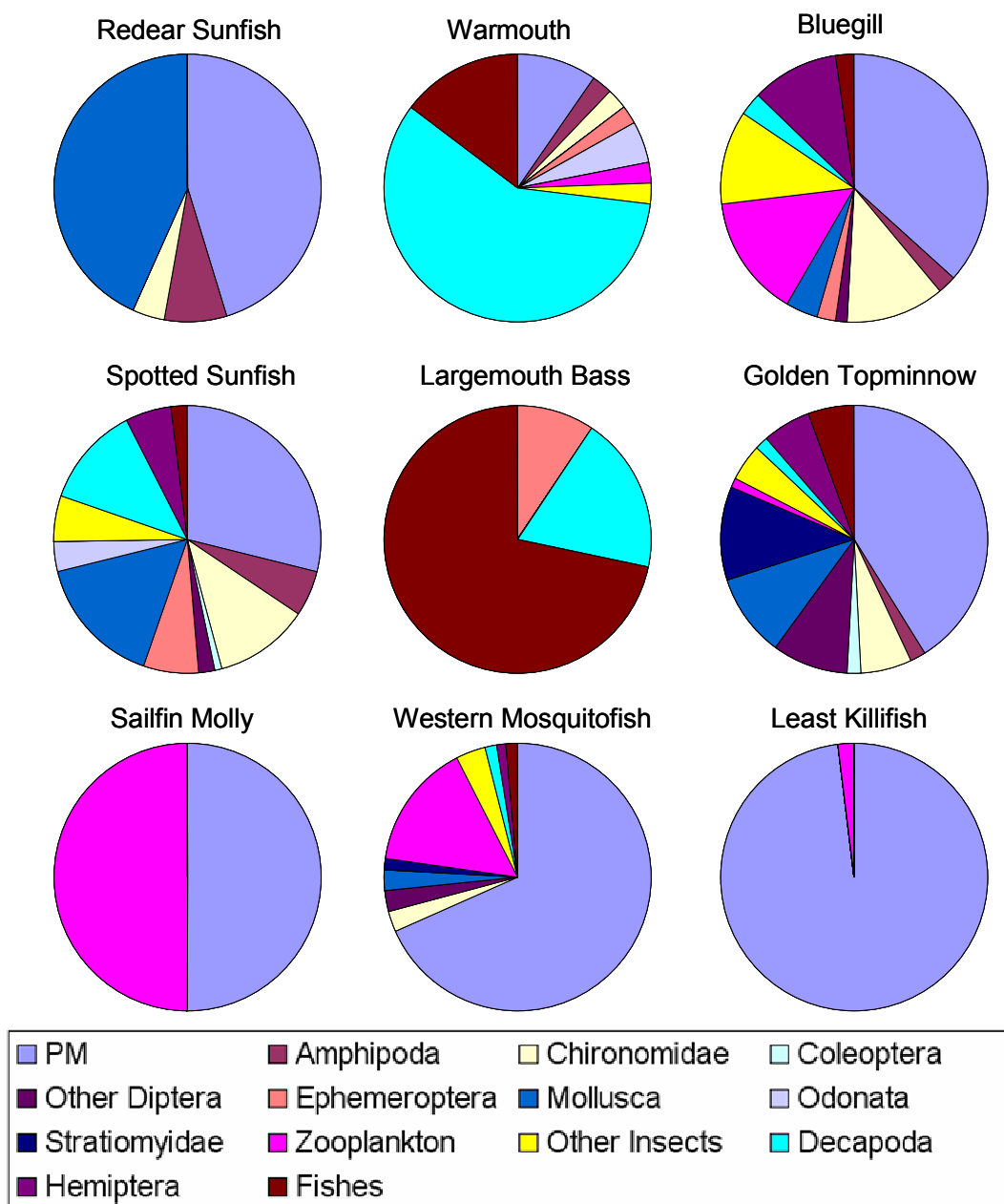


Figure 5.3—Frequency of occurrence for each prey item in each fish.

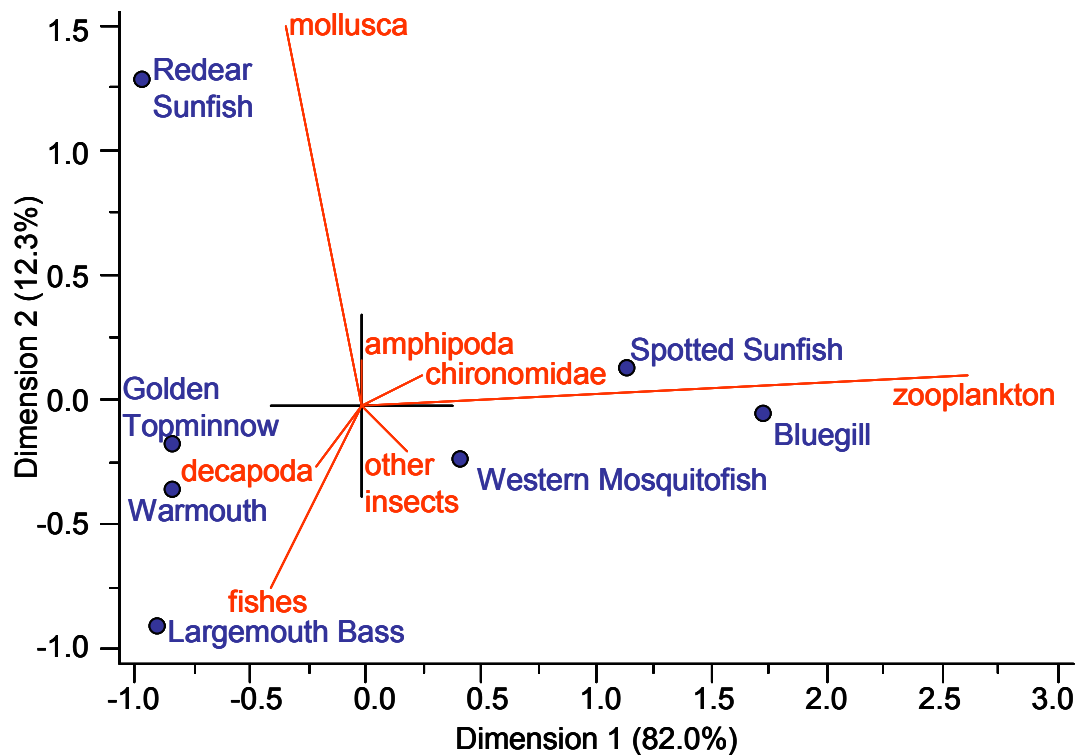


Figure 5.4—Symmetric Biplot of fishes (in blue) and prey items (in red).

Sailfin molly and least killifish gut content data were not included in the symmetric biplot (Figure 5.4) because most of the food items for these fishes were recorded as present or absent. In the symmetric biplot, redear sunfish were positively correlated with increasing dietary importance of molluscs. The positions of Western mosquitofish, spotted sunfish, and bluegill reflected relatively high predation on zooplankton, chironomids and other insects. Largemouth bass, and to a lesser extent golden topminnow and warmouth were positively correlated with increasing proportions of fish and decapod crustaceans in the diet, and negatively correlated with zooplankton and chironomids. Gut length ratios differed significantly between the four fishes, with sailfin mollies exhibiting a relatively longer gastrointestinal tract (gut ratio of 3.0) than least killifish (1.0; $P < 0.0001$), Western mosquitofish (0.68; $P < 0.0001$), or golden topminnow (0.74; $P < 0.0001$) the latter two were also shorter than least killifish ($P =$

0.0029, $P = 0.0176$ respectively). Western mosquitofish and golden topminnow gut ratios did not significantly differ ($P = 0.9081$).

DISCUSSION

Diets of the nine littoral fishes in the ARB were similar to previous reports from a diversity of lentic and lotic habitats. The dietary importance of mollusks in ARB redear sunfish is consistent with previous reports, as this sunfish is a specialized molluscivore and frequently feeds on gastropods and bivalves (Huckins 1997; McCollum et al. 1998). Warmouth typically prey on crawfish, freshwater shrimp, and other insects, but tend to forage more on decapods as fish size increases (Hunt 1952; Guillory 1978; Henry 1979) a trend that was clear in ARB fish. Bluegill are generalists and range from being primarily insectivorous to planktivorous depending on resource availability, although they generally prefer larger prey (Werner 1974; O'Brien et al. 1976; Werner 1977; Werner and Hall 1977; Mittelbach 1981; Werner et al. 1983; Mittelbach 1984; Keast 1985; Li et al. 1985; Williamson and Keast 1988; Schramm and Jirka 1989; Walton et al. 1992; Harrel and Dibble 2001; Olsen et al. 2003). Limited studies suggest spotted sunfish are also generalists (Hunt 1952; Henry 1979), which is consistent with their gut contents in the ARB. Largemouth bass consume zooplankton, amphipods, ephemeropterans, odonates, and decapods until reaching a total length of approximately 100 mm, at which point they become primarily piscivorous (McLane 1949; Werner 1977; Cochran and Aldelman 1982; Keast and Eadie 1985; Traxler and Murphy 1995; Cailteux et al. 1996; Olson 1996; Pelham et al. 2001; Brenden and Murphy 2002; Garcia-Berthou 2002; Mason 2002). Golden topminnows have been reported to consume coleopterans, chironomids, and other invertebrates (Hunt 1952),

whereas sailfin mollies feed almost exclusively on periphyton with some meiofauna, zooplankton, and mosquito larva (Hunt 1952; Harrington and Harrington 1961).

Western mosquitofish, a common bio-control for mosquitoes, have been shown to be omnivorous, feeding on algae, zooplankton, dipterans, and grass shrimp (Krumholz 1948; Hayes and Rutledge 1991; Gophen et al. 1998; Mansfield and Mcardle 1998).

Least killifish are omnivorous, feeding on algae, zooplankton, chironomids, and other invertebrates (Hunt 1952; Reimer 1970; Schaefer et al. 1994).

The symmetric biplot demonstrates three distinct feeding groups among the ARB fishes that I studied. The first group was composed of redear sunfish, which is the dominant littoral molluscivore in the ARB, although pumpkinseed sunfish *Lepomis gibbosus* may compete for this role in other systems (Huckins 1997). The next group included those fishes that fed primarily on large macroinvertebrates (i.e. decapods) and small fishes, and included primarily piscivorous age-0 largemouth bass, and the primarily invertivorous warmouth and golden topminnow. This group was negatively correlated with the redear sunfish, probably reflecting well-developed resource partitioning among these fishes (Huckins 1997). The third group was composed of fishes that fed on small and soft bodied macroinvertebrates, including bluegill, spotted sunfish, and Western mosquitofish. This group was uncorrelated with the other groups, suggesting little or no trophic overlap with the other littoral ARB fishes. Although not plotted, sailfin molly and least killifish would likely fit into the third group as zooplankton comprised the entirety of their diet that was not plant matter.

Wootton (1990) suggested that the ratio between gut length and total length was correlated to diet composition, based on a study that indicated that carnivores tended to

have ratios around or less than 1.0, omnivores ranged from just under 1.0 to 3.0, and herbivore ratios went from approximately 1.6 up to 8.0. This ratio provided a useful index to assess the diet of the cyprinodontiform fishes, as dominant gut contents from these taxa could not be measured as quantitatively as the other fishes in this study due to their typically degraded condition. Gut ratio analysis suggests that least killifish and sailfin molly are both omnivores, though the sailfin molly is better adapted for ingesting plant matter than the least killifish. Despite previous studies suggesting the Western mosquitofish is omnivorous, gut ratio analysis in this study suggested instead that this fish and the golden topminnow are better adapted for carnivory. Although the sailfin molly and least killifish may derive nutrition from the plant matter they ingest, it is doubtful Western mosquitofish or golden topminnows are true herbivores. Instead, Western mosquitofish and golden topminnow likely ingest large amounts of plant matter as a byproduct of feeding on phytophilic macroinvertebrates.

Though the fishes collected in this study were collected along the edges of hydrilla beds, it is apparent from analysis of invertebrate collections that all of the fishes fed on hydrilla-dwelling organisms. Many of the prey that were consumed, including molluscs, decapods, other crustaceans, and a diversity of insect taxa were commonly found in hydrilla beds (see previous chapters). In addition, the fact that plant matter was found in large proportions in the stomachs of all fishes except largemouth bass, and apparently provides little nutritive value (Wootton 1990) indicates that the fishes in this study were feeding on invertebrate taxa that were closely associated with the epiphyton on the hydrilla plants.

CHAPTER 6: SYNTHESIS AND CONCLUSIONS

The goal of this project was to explore the structuring forces that shape the species composition and spatial distribution of hydrilla-dwelling macroinvertebrate communities. Specific objectives were to: 1) determine the effectiveness of using artificial plants in floating subsurface exclosures to quantitatively sample hydrilla-dwelling macroinvertebrate communities, and to explore the roles of 2) bed position, 3) plant architecture or complexity, and 4) predation by fishes from the surrounding littoral environment on the abundance and bed location of hydrilla-dwelling macroinvertebrates.

I demonstrated that the exclosures and artificial plants used in these experiments were effective for obtaining representative samples of hydrilla-dwelling macroinvertebrate communities, and that the large mesh treatment most closely resembled the natural community (Chapter 2). I also explored some of the complex ecological interactions in this system, i.e., herbivorous organisms such as hyalleid amphipods and physid snails appeared to distribute themselves in the hydrilla bed based on periphyton availability, whereas the distribution of caenid mayflies appeared to be controlled by predaceous invertebrates (odonates). With the exception of scraping taxa (gastropods), the macroinvertebrates did not differ in density (number per unit surface area) between the simple and complex plant structures tested. However, because complex plants like hydrilla have much greater surface areas per plant, or per unit weight, one can infer that organisms would likely be more abundant, per plant, on architecturally-complex macrophytes.

Based on these experiments, it appears that hydrilla-dwelling macroinvertebrates are distributed primarily in relation to resource availability and predation. Some collectors were more abundant on the outside edge of hydrilla beds where, although predation was greatest (especially for baetid mayflies, which were frequently found in the stomachs of largemouth bass, or chironimids, which were commonly found in the stomach of all of the generalist fishes), the influx of food particles from the surrounding water column was likely also greatest. Scraper abundance was positively associated with the presumed increase in periphyton growth on simply structured plants, despite predation risk being lower on more structurally complex plants. Overall, the majority of taxa exhibited greater densities or odds of presence on the bed interior, where fish predation on macrofauna was presumed to be less, relative to the bed edge, regardless of other treatments. Fishes are not the only predators in these littoral plant beds, however, and predaceous invertebrates may also play a significant role in the distribution of these organisms. In particular, the interactions of predaceous invertebrates and invertivorous fishes may be important in the complex distributional patterns that were evident in the exclosure treatments, especially for those taxa that were least abundant in the smallest meshes in the bed interior, presumably the “safest” exclosure provided.

Fishes associated with hydrilla beds feed on many of the macrofauna found in this study, and organisms common in the stomachs of collected fishes were often distributed towards the bed interior. For example, gastropods, which are the primary prey item of redear sunfish, mosquitofish and amphipods, which comprised a significant portion of the largemouth bass diet, and hemipterans, stratiomyids, zooplankton, and

poeciliids, which were commonly consumed by bluegill, spotted sunfish, and golden topminnow were all more common on the bed interior. Chironomids, a common diet item for bluegill, spotted sunfish, and golden topminnow, exhibited the opposite distributional pattern, apparently trading protection from predation for food resources. Grass shrimp and Western mosquitofish, common diet items of largemouth bass and warmouth, were found predominantly in the small meshes regardless of bed position. The diets of the poeciliids were mainly composed of plant matter and zooplankton and did not contain, except Western mosquitofish to a small extent, the macrofauna collected. Of the organisms found in greater density on the bed edge (baetid mayflies, chironomids, caenid mayflies, and coenagrionid odonates) only caenid mayflies and coenagrionid odonates did not appear in the stomachs of fishes. These two macroinvertebrates may have behavioral traits that make them less vulnerable to fish predation, which would allow them access to the abundant food resources at the bed edge.

This study has shown that a hydrilla bed is likely separated into ecologically distinct zones of predation. The first zone is the bed interior, where macroinvertebrates and poeciliid fishes live with little predation from larger fishes due to high plant densities (i.e., interior bed treatments). Some predaceous fishes such as warmouth, as evidenced by declines in grass shrimp across positions but not in small meshes, and small young of the year fishes may persist in the bed interior. The next zone is the bed edge, where invertivorous fish densities are highest (i.e., bed edge treatments). In these habitats, it appears that macroinvertebrates that are vulnerable to predation (gastropods) exhibit depressed densities, whereas those that are apparently less

vulnerable (e.g., coenagrionid odonates) are flourishing. The third and final zone is the littoral zone adjacent to the bed, which is important habitat for piscivorous fishes (Mason 2002) such as largemouth bass and spotted gar *Lepisosteus oculatus*. During fish collections for the diet study, spotted gar were frequently observed near the edges of hydrilla bed, but the invertivorous fishes were collected only at the edge of hydrilla beds or within submerged structures such as tree stumps. The boundary between the first two zones would be a gradient depending on fish size and bed density, with fish density decreasing as distance from the bed edge increases, whereas the boundary between the second and third zones would be abrupt, with fishes inhabiting the bed edge apparently making few (and probably short) forays into the open water.

Further quantification of these zones would allow aquatic systems managers to take better advantage of resident macrophyte beds, exotic or native, and improve recreational fish stocks. In general, managers should focus aquatic plant control efforts on increasing edge habitat rather than complete eradication. Selective use of mechanical methods such as shredders and bottom barriers could achieve this goal. Future research into the optimal sizes of the various zones necessary to maximize objectives related to the abundance, diversity, growth, etc., of fishes found in either of the two outer zones would dictate the application of control methods and the resultant dimensions of the vegetation bed.

The dynamics of hydrilla-dwelling macrofauna community are complex and difficult to study. I have attempted to provide a framework for examining the factors that determine the spatial distribution of hydrilla-dwelling organisms, but many questions remain. Species-specific vulnerability to predation, both by invertivorous fishes and

predaceous invertebrates, of the hydrilla-dwelling macroinvertebrates in this study is poorly known and is in need of further study. The dynamics of collector food resource availability and how this resource changes with bed position is also unknown. The extent to which fishes utilized the hydrilla beds for foraging and cover is also unresolved, and there is little information available about how factors other than predation and dissolved oxygen influenced differences in macroinvertebrate community composition that were evident between the two years of this study. Perhaps most importantly, we need to understand the factors that determine macrophyte distributions, especially hydrilla, in the ARB, and the overall role of this exotic macrophyte on the biotic structure of the ARB littoral zone.

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VITA

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