EFFECTS OF WATER WILLOW ESTABLISHMENT ON LITTORAL ASSEMBLAGES IN KANSAS RESERVOIRS: FOCUS ON AGE-0 LARGEMOUTH BASS

By

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A.A.S, Paul Smith's College, 1994
B.S., Cornell University, 1996
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AN ABSTRACT OF A DISSERTATION

submitted in partial fulfillment of the

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ABSTRACT

A large scale habitat manipulation was conducted to assess the effects of establishing an emergent macrophyte, American water willow *Justicia americana*, on littoral reservoir communities. Coves in three large (>1,800 ha) Kansas impoundments were chosen and half planted with water willow. Sampling was conducted during the summer from 2001 to 2004. I found that water willow coves had more complex habitat as well as higher abundance and diversity of fishes, macroinvertebrates, and zooplankton than control coves. However, strong temporal variation in water levels influenced the amount of inundated water willow available in these systems. The effects of water willow on density, growth, condition, and diet of age-0 largemouth bass *Micropterus salmoides* were assessed. Significantly higher densities of age-0 largemouth bass were found in water willow coves, but growth, condition, and diet did not differ between water willow and control coves. Therefore, water willow was able to support higher abundances of age-0 largemouth bass than control coves without affecting growth, condition, or diet. Characteristics of age-0 largemouth bass from the water willow coves were compared to those from two small impoundments (<80 ha) with abundant macrophyte and healthy largemouth bass populations. Small impoundments had higher densities of age-0 largemouth bass than water willow coves in the three large impoundments, but individuals on average also had lower growth, condition, and fewer fish in their diet. Thus, largemouth bass populations in small impoundments may be more regulated by density dependent factors than populations in large impoundments. Overall, water willow is beneficial to littoral areas, supporting an increase in both abundance and diversity of assemblages. Finally, I used a field experiment to test the inundation and desiccation tolerance of water willow for different depths and durations. Water willow was susceptible to inundation, but resistant to desiccation. My findings provide information that can be used to select candidate reservoirs for water willow establishment based on expected water-level fluctuations.

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Major Professor
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TABLE OF CONTENTS

LIST OF FIGURES

CHAPTER TWO

CHAPTER THREE

CHAPTER FOUR

LIST OF TABLES

CHAPTER TWO

CHAPTER THREE

CHAPTER FOUR

APPENDICES

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CHAPTER 1

INTRODUCTION

Habitat manipulations are often used to enhance fish populations, but in large complex systems the outcome of such manipulations are unpredictable and the costs may outweigh the benefits (Summerfelt 1999). This is particularly true in reservoirs that are more dynamic than natural lakes (Wetzel 2001). For example, the trophic status of reservoirs can change drastically within 15 years after construction. Reservoirs typically go through a trophic upsurge, which is stimulated by nutrients released from newly inundated organic matter in the watershed followed by trophic depression, which occurs as that nutrient pool is processed through the system (Kimmel and Groeger 1986). During the upsurge phase, increased aquatic productivity and inundated vegetation provide abundant food and habitat for sport and bait fishes and other aquatic organisms (Kimmel and Groeger 1986; Ploskey 1986). However, as the system stabilizes during the subsequent trophic depression, littoral habitat complexity declines and fish assemblages are typically dominated by benthic omnivores such as common carp *Cyprinus carpio*, bigmouth buffalo *Ictiobus cyprinellus*, and freshwater drum *Aplodinotus grunniens* in Midwestern U.S. reservoirs (Kimmel and Groeger 1986; Ploskey 1986).

Many natural resource managers introduce aquatic macrophytes to improve sportfish production and control shoreline erosion in reservoirs devoid of aquatic vegetation. American water willow *Justicia americana* L. (Vahl.) has recently been planted in Kansas reservoirs (Marteney 1993) and elsewhere (Dick et al. 2004). My dissertation was aimed at understanding of the role of habitat in structuring reservoir fish assemblages, particularly how local assemblage may respond to water willow manipulations.

Organisms, such as macrophytes, that physically modify their environment can have both direct and indirect effects on local species assemblages (Jones et al. 1997; Crooks 2002). Macrophytes can buffer harsh environmental conditions by dampening hydrodynamic energy (Kahl 1993; Summerfelt 1999; Bouma et al. 2005) and by decreasing water temperatures by shading (Wetzel 2001) contributing to increased water quality and clarity by reducing shoreline erosion (Kahl 1993; Summerfelt 1999) and turbidity (Kahl 1993; Vestergaard and Sand-Jensen 2000). Shifts in microbial and algal assemblages can be caused by macrophytes decreasing nutrient and light availability (Boyd 1971; Brown 1986; Smart et al. 1996) simultaneously providing a substrate for epiphytic bacteria and algae (Dodds 2002), the principal food source of many benthic organisms (Baker and Orr 1986; Beckett et al. 1992). Senescence of macrophytes releases nutrients acquired from sediments, stimulating pelagic production (Carpenter 1980) and increasing organic substrate used by benthic organisms (Beckett et al. 1992). Shelter from predation and harsh environmental conditions coupled with an increase in food resources can lead to an increase in zooplankton (Quade 1969; Timms and Moss 1984; Moss et al. 1996), macroinvertebrate (Tolonen et al. 2003), and fish (Dibble et al 1996; Smart et al. 1996) abundance as well as an increase in their assemblage diversity (Killgore et al. 1989; Keiper et al. 1998; Pierce et al. 2001b).

The role of emergent macrophytes in structuring littoral assemblages will depend on timing of water level fluctuations in regards to life histories of littoral organisms.

Shallow habitats in reservoirs can be strongly influenced by wave action (Lienesch and Matthews 2000) and water level fluctuations. Declining water levels likely reduce availability of inundated water willow habitat, which could negatively impact littoral assemblages. For example, littoral fishes, macroinvertebrates, and zooplankton may be more vulnerable to predation if they are forced from the shelter of water willow to areas with less cover (Willis 1986). This may be especially important for juvenile fishes that are very susceptible to predation and whose densities peak in summer (June 1977; Hatzenbeler et al. 2000; Pierce et al. 2001a).

The primary goal of my dissertation was to characterize the effects of emergent macrophyte establishment on reservoir littoral assemblages. Experimental methods were used to achieve this goal, including a large-scale habitat manipulation conducted in three large impoundments over a four-year period. In Chapter 2, I characterized the role of water willow in structuring littoral assemblages in three large reservoirs. My objectives for this chapter were 1) investigate how water willow establishment might be altering the physiochemical characteristics in the littoral zone, 2) measure the effects of water willow establishment on littoral fish, macroinvertebrate, and zooplankton assemblage structure, and 3) explore the amount of variation explained by the presence of water willow in structuring littoral assemblage composition with respect to other environmental variables, including spatial and temporal factors. Chapter 3 focused on the juvenile stage of individual species, largemouth bass *Micropterus salmoides*, which has ecological and socio-economical importance in these systems. Specifically, I examined effects of water willow establishment on densities, growth rates, condition, and diets of age-0 largemouth bass in three large impoundments. I then compared my findings from water willow areas to two small, stable impoundments with abundant vegetation and healthy largemouth bass populations. In Chapter 4, I addressed the suitability of Kansas reservoirs for water willow establishment by quantifying the inundation and desiccation tolerance of water willow. The duration that water willow can be inundated or desiccated was then used to predict possible reservoirs for establishment based on historic water level data.

CHAPTER 2

THE ROLE OF EMERGENT VEGETATION IN STRUCTURING LITTORAL ASSEMBLAGES OF ZOOPLANKTON, MACROINVERTEBRATES, AND FISHES

ABSTRACT

Organisms that physically modify their environment can affect the structure of local species assemblages. My study tested the influence of an emergent macrophyte, water willow, on the structure of littoral assemblages of reservoirs. Specifically, I characterized 1) how water willow alters the physiochemical characteristics of the littoral zone; 2) its affect on littoral fish, macroinvertebrate, and zooplankton assemblage structure; and 3) its relative contribution to explaining variation in assemblages with respect to other environmental factors. Coves with and without water willow in three large Kansas impoundments were sampled monthly during each summer over a four-year period, 2001-2004. Physical habitat, water chemistry, fishes, macroinvertebrates, and zooplankton were quantified in replicate 149 m^2 enclosures in each cove. Multivariate analysis of covariance was used to test if measured variables differed between water willow and control coves and among months. A redundancy analysis was used to examine the association of environmental variation and water willow with fish assemblage structure. Water willow coves had significantly greater amounts of flooded riparian vegetation and woody debris. In general, coves with water willow had greater abundances and diversity of fishes, macroinvertebrates, and zooplankton than did coves without water willow. However, seasonal and spatial variation in habitat and environmental conditions were the primary drivers of assemblage dynamics. Thus,

understanding these spatial and temporal patterns is critical to understanding how water willow influences assemblage structure in reservoirs.

INTRODUCTION

Organisms that physically modify their environment can have extensive direct and indirect effects on their environment, leading to the restructuring of local species assemblages (Jones et al. 1997; Crooks 2002). Macrophytes, in particular, can influence both physiochemical and biological characteristics of aquatic systems. They buffer harsh environmental conditions by dampening hydrodynamic energy (Kahl 1993; Summerfelt 1999; Bouma et al. 2005), and decrease water temperatures by shading (Wetzel 2001). Macrophytes can cause a shift in microbial assemblages by decreasing nutrient and light availability to phytoplankton (Boyd 1971; Brown 1986; Smart et al. 1996) simultaneously providing a substrate for epiphytic bacteria and algae (Dodds 2002), the principal food source of many benthic organisms (Baker and Orr 1986; Beckett et al. 1992). Shelter from predation and harsh environmental conditions coupled with an increase in food resources can lead to an increase in zooplankton (Quade 1969; Timms and Moss 1984; Moss et al. 1996), macroinvertebrate (Tolonen et al. 2003), and fish (Dibble et al 1996; Smart et al. 1996) abundance as well as an increase in diversity (Killgore et al. 1989; Keiper et al. 1998; Pierce et al. 2001b).

Although introducing macrophytes to reservoirs can potentially increase sportfish production, many reservoirs remain unvegetated because of insufficient plant propagules and unsuitable conditions for seedling establishment (Smart et al. 1996). Moreover, reservoirs targeted for macrophyte establishment often have limited success because of high abundances of herbivores and benthic feeding organisms (e.g., common carp *Cyprinus carpio*) that uproot macrophytes (Cox 1999; Dick et al. 2004; Smart et al. 2005). American water willow *Justicia americana* L. (Vahl.; hereafter water willow), however, is resistant to biotic disturbances (Dick et al. 2004) and desiccation (Strakosh et al. 2005), and is currently being planted in many Kansas reservoirs (Marteney 1993). These efforts provide an excellent opportunity to evaluate the influence of emergent macrophytes on structuring littoral-zone assemblages across multiple systems.

Water willow is an emergent species with a native range from Quebec to Texas and from Kansas to the Atlantic coast (Gleason and Cronquist 1993; Niering and Olmstead 1997). It typically grows on the margins and shallow areas of lotic and lentic systems (Penfound 1940; Niering and Olmstead 1997) in areas exposed to ample sunlight (Fritz and Feminella 2003; Smart et al. 2005). As a colonial plant it forms dense stands by rhizomatous growth and can quickly spread along shorelines through fragmentation, growing in water up to 1.2 m in depth (Penfound 1940). A semi-rigid, but flexible fibrous stem enables water willow to withstand scouring floods in lotic systems (Fritz and Feminella 2003), and strong wave action in lentic systems (Penfound 1940). Water willow is also tolerant of moderate water-level fluctuations (including drought) and high turbidity (Niering and Olmstead 1997; Dick et al. 2004; Smart et al. 2005; Strakosh et al. 2005). These characteristics help water willow withstand the dynamic environmental conditions of reservoir littoral areas.

Unlike submergent macrophytes that have the ability to occupy a wider range of depths, water willow is restricted to depths $\leq$ 1.2 m (Penfound 1940) similar to other emergents (Wetzel 2001). These shallow habitats can be strongly influenced by wave action (Lienesch and Matthews 2000) and water level fluctuations in reservoirs, whether climatic or human induced, can dictate the availability of emergent macrophyte habitat (Strakosh et al. 2005). Annual and intra-annual patterns of precipitation in the Midwest are highly variable and can influence average water levels in reservoirs. However, most regions receive the bulk of their precipitation during the spring, causing an increase in water levels through the spring followed by a during through the summer months. Declining water levels likely reduce availability of inundated water willow habitat, which could negatively impact littoral assemblages (Ploskey 1986). For example, littoral fishes, macroinvertebrates, and zooplankton may be more vulnerable to predation if they are forced from the shelter of water willow to areas with less cover (Willis 1986). The reduction of water willow habitat may be especially important for juvenile fishes whose densities peak towards the end of summer (June 1977; Hatzenbeler et al. 2000; Pierce et al. 2001a).

The main goal of my study was to characterize the role of water willow in structuring littoral assemblages in three Kansas reservoirs. My first objective was to quantify habitat in water willow and control coves in order to investigate how water willow establishment might be altering the physiochemical characteristics in the littoral zone. The second objective was to measure the effects of water willow establishment on littoral fish, macroinvertebrate, and zooplankton assemblage structure. My third objective was to explore the amount of variation explained by the presence of water willow in structuring littoral assemblage composition with respect to other environmental factors, including spatial and temporal variation.

METHODS

Study Sites

Fishes, macroinvertebrates, and zooplankton were sampled in cove habitats of three impoundments to characterize the effects of water willow on assemblage structure. El Dorado Reservoir was filled in 1981 after impoundment of the Walnut River; Hillsdale Reservoir was filled in 1982 on Big Bull Creek, part of the Osage River system; and Melvern Reservoir was filled in 1972 on the Marais des Cygnes River (Table 1). All three reservoirs were primarily built for flood control, but support both recreation and wildlife areas. Prior to water willow establishment, the reservoirs had few, if any, aquatic macrophytes.

Coves were chosen because they are ecologically important habitats within reservoirs that are distinct from the main body of the reservoir because of a large influx of allochthonous material from shorelines and flooded riparian habitats, and less exposure to wind (Kimmel 1990; Matthews 1998). Coves also provide important spawning and nursery habitat for sport and non-game fishes (Meals and Miranda 1991).

Lake wide surveys were conducted to identify coves (based on visual inspection) that were similar in substrate, size, slope, and structural habitat characteristics. Of these, six coves per impoundment were randomly selected for my study. Mean cove area was

1.77 ha ± 1.14 (SD). In Hillsdale and Melvern reservoirs, three of the six coves were randomly selected for water willow establishment one year prior to sampling, the other three coves served as controls. Water willow used for plantings were ≥ 0.5 m tall, exhibited no visible signs of stress (i.e., yellowing leaves, broken stalks, insect infestations) and had the majority of the root system intact. Individuals were planted 0.4 m apart in rows parallel to shore every 1.8 m. In El Dorado Reservoir water willow establishment began in 1996 as part of a vegetation pilot study. Therefore, three coves were randomly chosen from a pool of coves with existing water willow stands, and control coves were randomly chosen from a pool of coves without vegetation.

Sampling

Physical and biological properties were sampled in all coves monthly during each summer (June, July, and August) from 2001 through 2004. Two sampling locations within each cove were randomly selected (without replacement within a given year) each month (420 total). All sampling was conducted between 08:00 and 21:00 hrs Central Standard Time. The methods were modified from Tripe (2000) and Maceina et al. (1993). At each sampling location a 30.6 m long by 2.0 m high block net (3.2 mm bar-mesh) was used to enclose a 149 m^2 (24.5 m by 6.1 m) area parallel to shore. Prior to setting up the block net, water quality variables were measured in the center of the sampling area. Dissolved oxygen, conductivity, and temperature were measured using an YSI model 85 (Yellow Springs Instruments, Yellow Springs, Ohio) and turbidity was measured using an Orbeco-Hellige turbidity meter. The block net was carefully maneuvered into position, so as not to disturb fishes, secured to the bottom using poles and anchors, and inspected for any gaps.

Zooplankton and macroinvertebrates were collected within the blocked area. Zooplankton were sampled using a 20 cm diameter, 63-µm mesh tow net and preserved in either a 70% ethyl alcohol or 10% formalin solution. Tow nets were pushed or pulled parallel to the bank for the length of the enclosure at 3.1 m and 6.1 m from the shore (Tripe 2000). Zooplankton were identified to family using Smith (2001), enumerated, and density (number of zooplankton per liter; *n/L*) was calculated. Macroinvertebrates were sampled using a 30 cm wide by 25 cm tall, 500-µm D-frame sweep net. The net was swiped along the substrate for 0.25 m (Rabeni 1996) at 2, 4, and 6 m from shore along two transects located at 6 and 18 m from the end of the block net. Macroinvertebrates were preserved in either a 70% ethyl alcohol or 10% formalin solution with Pheloxine B, identified to family using Merritt and Cummings (1999), enumerated, and abundances (expressed as the number of individuals/enclosure; *n/E*), were calculated.

Prior to fish sampling, vegetation density, substrate, and depth in each enclosure was recorded along two transects perpendicular to shore at 8 and 16 m from the left end (facing shore) of the block net. Measurements were taken 2, 4, and 6 m from shore. Vegetation density was measured using a 0.5 m quadrant placed in the water and stems within the quadrate were counted (Crowder and Cooper 1982). Substrate was classified using a modified Wentworth Scale (Bain et al. 1985). Mean slope was derived from the two depth profiles. Percent coverage (surface area) of large woody debris, small woody debris, root wads, and vegetation were visually estimated for the enclosure.

Fishes were sampled using the gas powered Smith-Root Model 15-C backpack electrofishing unit (Smith-Root, Vancouver, Washington; 200-300 V pulsed-DC). Sampling was conducted at frequency of 60 Hz and a 48% duty cycle. A two-person sampling crew with one person electrofishing and netting, and another person netting, thoroughly covered all habitats within each enclosure. Effort was standardized by area (149 m^2) and abundances are reported as number of fish captured per enclosure (*n/E*). All fishes were identified to species, enumerated, measured (total length) and held until completion of all electrofishing runs. Fishes that were unable to be identified in the field were preserved in 10% formalin and return to the lab for identification; all other fishes were released.

Data Analyses

Data from the two sampling sites within each cove for a given time period were pooled for all analyses. Fish, macroinvertebrate, and zooplankton abundances were $\log_{10}(x + 1)$ transformed to approximate a normal distribution. Physical, chemical, and habitat measurements were tested for normality using the Kolmogorov-Smirnov and Shapiro-Wilk statistics (SPSS 2001). Percent coverage measurements were square-root arcsine transformed (Krebs 1999). Environmental variables were tested for multicollinearity using product-moment correlations. If variables were highly correlated ($r > 0.70$), a single representative variable was chosen for inclusion in the analyses.

I employed a variety of multivariate techniques that emphasized different aspects of littoral assemblage structure to investigate the effects of water willow establishment. Three metrics were calculated to characterize the diversity of the fish, macroinvertebrate and zooplankton assemblages; species richness (S; total number of taxa in sample), Simpson's diversity index ($D = 1 / (\Sigma P_i^2)$, P_i = the proportion of an individual species abundance out of the total sample abundance), and Simpson's Evenness ($E = D / D_{max}$, D = Simpson's Index and $D_{max} = 1 / S$).

Multivariate analysis of covariance (MANCOVA) was used to test for differences in assemblage structure between water willow and control coves and among months, while controlling for variations among reservoirs and years. The MANCOVA was chosen because of its ability to handle multiple dependent variables and covariates, and rigorously test for differences while controlling for Type I error (Tabachnick and Fidell 1996; Green et al. 2000; Scheiner 2001). Additionally, testing several dependent variables simultaneously may reveal complex patterns missed by univariate tests (Scheiner 2001). Three separate MANCOVAs were conducted to investigate if habitat variables, organism abundance, and diversity metrics differed between water willow and control coves and among months. For all models, fixed effects were cove type (water willow or control coves) and month (three levels; June, July, or August). Reservoir and year were included as covariates in these models because I was primarily interested in the effects of water willow, and not differences among reservoirs or years. Only fishes, macroinvertebrates, and zooplankton that occurred in all reservoirs and that occupied > 5 % of the sampling sites within each reservoir were included in these analyses. Wilk's lambda was used to calculate the multivariate F-statistic (SPSS 2001). If the overall MANCOVA was significant, separate analyses of covariances (ANCOVAs) were conducted to investigate each dependent variable separately. The alpha level was set at 0.10 *a priori* and Bonferroni corrected for the separate MANCOVAs ($\alpha = 0.10 / 3 = 0.033$). The false discovery rate (Benjamini and Hochberg 1995) was employed to control Type I and Type II error rates for the multiple ANCOVAs at $\alpha = 0.033$. Similar to the sequential Bonferroni (Hochberg 1988), the *P*-values were ranked in ascending order ($P_{(1)} < P_{(2)} < \ldots P_{(m)}$) and compared to $(\alpha * i)/ m$, where i = rank of *P*-value and m is the total number of tests. The null hypothesis (H_i) was rejected when $P_i \leq (\alpha * i)/ m$ and all others with smaller *P*-values (Benjamini and Hochberg 1995; Verhoeven et al. 2005). Type III sums of square were used in all analyses. Tests were conducted in SPSS for Windows (SPSS Inc. 2001).

Redundancy analysis (RDA) was used to examine the association among environmental variation, presence of water willow, and fish assemblage structure. A linear method of gradient analysis was chosen because the samples were from a relatively narrow range of environmental conditions (i.e., coves) and minimal species turnover across sites (Jongman et al. 1995; Legendre and Legendre 1998). Data analyses only included fishes that occurred at ≥ 10 % of the sampling sites within each reservoir to eliminate the influence of rare species (ter Braak, C. J. 1995). Environmental variables for this study included physical, chemical, spatial, and temporal components. The RDA scaling focused on the inter-species correlations and data were centered by dividing species scores by their standard deviations (Legendre and Legendre 1998; ter Braak and

Simlauer 2002). Monte Carlo simulations were conducted (1000 permutations) to test if axes were significantly different ($P < 0.05$) from random (Legendre and Legendre 1998; ter Braak and Simlauer 2002). Triplots of species, environmental variables, and sites were used to characterize the effects of the environmental gradients on species abundances. Separate RDAs were used for each reservoir to control for variance associated with species turnover across reservoirs (beta-diversity; Gauch 1982). The statistical software CANOCO ver. 4.5 (ter Braak and Simlauer 2002) was used for the ordination analyses.

RESULTS

Habitat Characteristics

Habitat variables differed significantly between water willow and control coves, and among months (MANCOVA; Tables 2 and 3). Water willow coves had significantly (ANCOVAs; Table 3) more complex habitat (i.e., water willow, flooded vegetation, woody debris) and smaller mean substrate sizes than control coves. Almost a ten-fold decrease in water willow stem density occurred from June to August. June had significantly greater flooded riparian vegetation, large and small woody debris, water willow density, and turbidity than July or August, and July had significantly greater water temperatures than other months.

Animal abundance

The overall test combining abundances of common fishes, macroinvertebrates, and zooplankton showed significant differences between water willow and control coves, and among months (MANCOVA; Table 4). In general, water willow coves had greater mean abundances of littoral organisms than control coves.

Forty-two fish species were identified from the three reservoirs; 36 fish species were found in El Dorado, 26 in Hillsdale, and 30 in Melvern Reservoir (Table 5). Four fish species were found at > 70% of the sampling sites; bluntnose minnow *Pimephales notatus* (87%), red shiner *Cyprinella lutrensis* (81.2%), green sunfish *Lepomis cyanellus* (73.6%) and age-0 largemouth bass *Micropterus salmoides* (73.2%). Only 13 species were found in all reservoirs and collected from > 5 % of the enclosures. The three most numerically abundant fishes across reservoirs were red shiners, bluntnose minnows, and age-0 *Lepomis* spp. (Table 6). Mean total fish abundance (number per enclosure; minimum, maximum) increased throughout the summer and was, on average, greater for water willow coves (152; 0, 792; N = 210) than for control coves (97; 5, 429; N =210). Six of the 13 fishes had abundances that significantly differed between cove types (Figure 1). Bluntnose minnows and age-0 largemouth bass were twice as abundant in coves with water willow than control coves. Age-0 *Lepomis* spp. and orangethroat darters were four times more abundant, and channel catfish were eight times more abundant in water willow than control coves. In June, twice as many bluegill were caught in water willow than control coves, but the opposite pattern was found in August. Abundance of bluntnose minnows, channel catfish, and Age-0 *Lepomis* spp. were 8, 15, and 54 times greater, respectively, in August than June.

Fifty three macroinvertebrate taxa were collected, of which 17 occurred in ≥ 5% of collections from each reservoir (Table 7). Mean total macroinvertebrate abundance (number per enclosure; minimum, maximum) was 189 (1, 1528; N =210) for water willow coves and 124 (3, 2132; N =210) for control coves. Abundance of six macroinvertebrate taxa significantly differed between cove type and two macroinvertebrate taxa differed among months (Table 4; Figure 2). Five of the macroinvertebrates had significantly greater abundances in water willow coves. Caenidae (Ephemeroptera), Ephemeridae (Ephemeroptera), and Oligochaeta were twice as abundant in water willow than control coves. Coenagrionidae (Odonata) were three times and Corixidae (Hempitera) were ten times more abundant in water willow coves. In contrast, Heptageniidae (Ephemeroptera) were three times more abundant in control coves. Only two taxa exhibited significant temporal variation; Gastropoda were 17 times more abundant and Amphipoda were 9 times more abundant in June than August.

Zooplankton were classified into 9 taxa, 8 of which were common in all three reservoirs (Table 8). *Leptodora* sp. were commonly collected in El Dorado, but rarely in Hillsdale or Melvern. Mean total zooplankton density (number/L; minimum, maximum) was 10.3 (0.23, 69.7; N =210) for water willow coves and 9.6 (0.3, 76.1; N =210) for control coves. Overall zooplankton abundance peaked in July. Only Chydoridae was found to be significantly more abundant in water willow coves than controls (Table 4; Figure 3). Two zooplankton taxa were significantly different among months. Both Sididae and Rotifera abundances were two to three times greater in July than in June or August (Figure 3).

Assemblage Diversity

Diversity metrics exhibited similar patterns across reservoirs for water willow and control coves (Table 9). Results from MANCOVA for the diversity metrics found a significant interaction between water willow and month (Wilk's lambda= 0.836, $F_{18, 386}$ = 2.013, $P = 0.009$; Table 10). Water willow coves had significantly greater ($P \leq 0.009$) taxa richness (S_{fish}, S_{macro}, and S_{zoo}) and invertebrate diversity (D_{macro} and D_{zoo}) than control coves (Figure 4). In contrast, control coves had significantly ($P = 0.007$) greater fish assemblage evenness (E_{fish}) values than water willow coves (Figure 4). Significantly more fish species also were caught in August than in June or July. In contrast, the evenness of the assemblage was significantly lower in August that in June. The only temporal difference was in fish diversity, which was significantly greater in water willow than control coves in June. However, the opposite pattern was found in August resulting in a strong cove by month interaction (D_{fish}; Figure 4).

Fish Assemblage Structure

The overall contribution of water willow in structuring littoral fish assemblages was overshadowed by temporal and spatial variation. The combined variance in fish assemblage structure explained by the first two axes from the RDAs for El Dorado, Hillsdale, and Melvern reservoirs were 31.4%, 39.6%, and 31.5%, respectively. These axes all were significantly different than random (Monte Carlo simulations; 1000 permutations; $P < 0.01$). The environmental variables that accounted for a large portion of the variation were consistent across reservoirs (Figures 5-7). Sample month was strongly associated with the first RDA axis in all reservoirs and was driven by high abundances of age-0 *Lepomis* spp. and bluntnose minnow that were negatively related to June samples (Figures 5-7).

The gradient found along Axis 2 represented spatial and environmental differences, primarily related to sampling sites (i.e., coves). In all three reservoirs, red shiners were strongly associated with Axis 2, and consistently had an inverse relationship with enclosure depth, substrate size, and distance to nearest tributary. Water quality data also indicated that sites associated with red shiners had higher turbidity. Green sunfish in Melvern and Hillsdale also were strongly associated with Axis 2, but exhibited an opposing pattern to the red shiners, occurring in enclosures with larger substrates and greater depth (Figures 5-7).

Fishes occupying water willow coves in El Dorado varied along a strong up to down-lake gradient that was correlated with Axis 2. Sites with a negative Axis 1 score and positive Axis 2 score were sampled down-lake, and sites with a positive Axis 1 score and negative Axis 2 score are typically up-lake sites.

DISCUSSION

Although I do not have data prior to the introduction of water willow, my findings suggest that water willow alters environmental conditions of reservoir coves. Treatment coves had significantly greater amounts of flooded riparian vegetation and woody debris, which could be the result of water willow buffering wave action and reducing shoreline erosion (Summerfelt 1999). Smaller substrates in water willow coves may be attributable to trapping and accumulation of organic sediments, which has been observed for other littoral macrophytes (e.g., cattails *Typha angustifolia*; Burton et al. 2002). Therefore, water willow appears to effectively trap woody debris and other allochthonous materials providing increasing structural complexity.

The structural complexity provided by water willow is one of the key attributes that could augment abundance of littoral organisms. I found that approximately 40% of the common fish species found across the three reservoirs were significantly more abundant in water willow coves than controls. Several of these species (age-0 largemouth bass, age-0 *Lepomis* spp. and adult bluegills) are commonly associated with aquatic vegetation and can benefit from its establishment in littoral areas (Killgore et al. 1989; Annett et al. 1996; Dibble et al. 1996). Bluntnose minnow, orangethroat darter, and channel catfish all occur with water willow or other macrophytes in lotic systems (Orth and Jones 1980; Cross and Collins 1995; Pflieger 1997). Possible mechanisms responsible for the significant increase in abundance of fishes in water willow coves could be protection from predators or enhanced food supplies, such as macroinvertebrates. For example, Lyons and Magnuson (1987) found that in the absence of age-0 yellow perch, walleye predation resulted in an 80% adult darter mortality.

In my study, six of the macroinvertebrate taxa were significantly more abundant in water willow coves than in controls. As with fishes, this difference in abundance could be due to greater structural complexity and cover from predation. Similar to my results, Tolonen et al. (2003) also found greater abundances of Odonata, Corixidae, and Ephemeroptera in macrophytes and noted that these taxa were depleted by fish in areas with less cover. The greater amounts of woody debris in water willow coves also may attract additional macroinvertebrates because some species preferred woody debris over emergent macrophytes (Lewin et al. 2004). The combination of water willow and woody debris surfaces may further support greater amounts and varieties of epiphytic bacteria that are the principal food source of many invertebrates (Cummins and Klug 1979; Baker and Orr 1986). Finally, water willow could provide a refuge from predation and facilitate the occurrence of species vulnerable to predation. Diehl (1995) found that in the absence of megalopterans and odonates, yellow perch *Perca flavescens* significantly reduced abundance of chironomids. However, when aquatic macrophytes were present, megalopteran and odonate populations increased and reduced yellow perch predation pressure on chironomids by providing them with other prey options.

Although these studies indicate that macrophytes are used by zooplankton as a predation refuge, I found only one taxa (Chydoridae) to be significantly more abundant in water willow coves. Chydoridae are typically associated with vegetation (Smith 2001), and are typically more abundant in structurally complex habitats where macrophyte coverage is around 40% (Tremel et al. 2000). Lemke and Benke (2004) also found that a species of Chydoridae had significantly greater abundances, biomass, and production in vegetation than in areas devoid of vegetation. I also found high abundances of several fishes that can decimate zooplankton populations and can also cause zooplankton to avoid the area due to increased predation risk (Burks et al. 2001; Romare et al. 2004). For example, Lewin et al. (2004) reported that zooplankton biomass was three times greater in sites with no cover than those with cover and related to predation by fishes.

The increased abundance of fishes in water willow areas may account for the similarities in zooplankton densities between water willow and control coves found in my study.

Fish, macroinvertebrate, and zooplankton assemblages in water willow coves had significantly higher measures of diversity than coves without water willow, which concurs with other studies that examined the effects of macrophytes on littoral assemblage structure (Killgore et al. 1989; Keiper et al. 1998; Pierce et al. 2001b). In control coves fish abundances were more even, likely because of the more homogeneous habitats. Thus, water willow coves not only sustain greater abundances of various taxa, but also provide suitable habitat for rare and less common species. Bettoli et al. (1993) also reported a decline in littoral fish species after vegetation removal and that the presence of vegetation facilitated the persistence of rare species by reducing competitive interactions.

The spatial component from the RDAs strongly associated with Axis 2 (Figures 5-7) was the experimental treatment of individual coves and thus, included differences in habitat complexity resulting from water willow establishment. Additionally, individual water willow coves with greater amounts of woody debris and inundated riparian vegetation may have heavily vegetated shorelines, abundant in trees and other woody vegetation. Some coves may also be more likely to receive floating debris from wind and wave action. The additional habitat may attract other fishes with preferences for specific habitat types and characteristics. For example, Lewin et al. (2004) found that some juvenile fishes preferred woody debris over reed beds. Killgore et al. (1989) found that fish preferred areas adjacent to vegetation, which in my study could expand the influence of water willow to areas near its edges. Similarly, Romare et al. (2003) also found that small fishes used the edges of macrophytes and preferred dense emergents over floating vegetation. Water willow stands provided fishes with complex and edge habitat, but also increased the availability of woody debris and riparian vegetation. Therefore, the overall increase in habitat diversity, including edge habitat, within water willow coves could partly account for spatial differences in assemblage structure.

Littoral communities of these reservoirs exhibited a strong degree of temporal variation. This was largely attributed to decreasing water levels from June to August, which significantly reduced availability of structural habitat. In contrast, Hatzenbeler et al. (2000) found that in Wisconsin lakes woody debris and emergent vegetation remained unchanged throughout the summer, and Pierce et al. (2001a) reported that peak aquatic macrophyte density in Spirit Lake, Iowa occurred in September. The receding water level in my study reservoirs most likely had negative impacts on small bodied and age-0 fishes by forcing them out of shallow cover and into deeper water were they are more vulnerable to predation (Willis 1986; Kohler et al. 1993). Although availability of complex habitat declined in both treatment and control coves, habitat availability was consistently higher in coves with water willow which might be critical to the survival of some species.

Strong temporal changes in fish abundance from June to August were partly because of recruitment of age-0 fish and seasonal movements related to food and cover availability. Spawning chronology of many reservoir fishes typically peak in spring or the end of summer, which is reflected in my findings (June 1977; Claramunt and Wahl

2000). Axis 1 from all RDAs of each reservoir indicated the influx age-0 *Lepomis* spp. and bluntnose minnows into coves in August. Hall and Werner (1977) reported that movements of several littoral zone fishes were significantly related to food and habitat availability.

The macroinvertebrates and zooplankton that exhibited temporal differences in my study were Amphipoda, Gastropoda, Rotifera, and Sididae. Both Amphipoda and Gastropoda abundance were highest in June and drastically dropped through August. In contrast, Rotifera and Sididae densities peaked in July. These patterns may be due to greater predation rates throughout the summer as fish abundances increase. Gilinsky (1984) also found that both macroinvertebrate richness and density decreased through the summer due to increasing fish predation. The July peak of Sididae I observed concurs with the findings of Post et al. (1997), who reported largemouth bass predation on large cladocerans corresponded to the peak in cladoceran densities. They also found that largemouth bass were able to effectively reduce the large bodied cladocerans by August. However, other studies did not find any differences in zooplankton biomass through time (Lewin et al. 2004) or that it was variable from site to site (Wolfinbarger 1999). Fish appeared to exert enough predation pressure to decrease macroinvertebrate abundance through the summer.

Overall, I found that areas with water willow increased abundance and diversity of littoral zooplankton, macroinvertebrates, and fish. I also found significantly higher amounts of riparian vegetation and woody debris in water willow areas. These findings coupled with its rapid spreading ability by fragmentation and rhizomatous growth could have compounding effects on littoral assemblages. For example, as a water willow bed expands, the more debris will be trapped and shoreline protected, increasing both the complex habitat and riparian vegetation. The amount of water willow coverage in my study was relatively low, 15.8% ± 18.1 (mean percent coverage ± 1 SD) in June to 10.7% ± 15.0 in August, many studies consider 10-40% as intermediate coverage, which promotes high species richness of fishes (Dibble et al. 1996). Although I found greater abundances and diversity of littoral organisms in water willow than control coves, my results may only be the initial restructuring of the littoral assemblage by water willow, and changes may continue occur until water willow expansion has stabilized.

Investigating the role of emergent macrophytes in structuring littoral assemblages is important part in understanding benefits of intentional plantings and for predicting potential negative impacts of anthropogenic activities, like water level management or shoreline modification. Near-shore littoral areas that would be vulnerable to these activities are often the most productive and species rich areas within lentic systems (Wetzel 2001), especially within cove habitats. My findings support the use of water willow for habitat enhancement. However, identifying temporal patterns of organisms and environmental factors is critical to understanding both how and when water willow influences the assemblage structure.

Table 1.—Characteristics of the three Kansas reservoirs used to investigate the relationship between fish assemblage structure and water willow (U. S. Army Corp of Engineers, Kansas City and Tulsa Districts).

	El Dorado	**Hillsdale**	**Melvern**
Dam construction (yr)	1981	1982	1972
Location	37° 50' 50" N	38° 28' 20" N	38° 30' 45" N
	96° 49' 22" W	94° 52' 45" W	95° 42' 40" W
Elevation above mean sea level (m)	408	280	315
Drainage area (km^2)	665	372	904
Surface area (ha)	3,240	1,853	2,804
Mean depth (m)	5.8	4.5	6.7
Shoreline development index	7.8	5.4	18.4
Storage ratio/drainage index	2.6	7.2	1.1

Table 2.—Summary of habitat variables for coves in Kansas reservoirs with (WW) and without (control) water willow pooled across reservoirs and years. Values are presented as the mean (minimum, maximum) from 420 total samples (210 for water willow coves and 210 from control coves).

	June		July		August	
Habitat Variable	**WW**	**Control**	**WW**	**Control**	**WW**	**Control**
% WW coverage	16 (0, 58)	3 (0, 42)	14 (0, 78)	1 (0, 17)	11 (0, 51)	2 (0, 19)
WW density (# stems/ m^2)	12 (0, 76)	1 (0, 10)	5 (0, 51)	0 (0, 2)	2 (0, 18)	0 (0, 2)
Mean temp. (^{o}C)	26 (22, 30)	26 (21, 32)	30 (26, 34)	30 (27, 34)	29 (23, 34)	28 (23, 33)
DO (mg/L)	8 (4, 11)	9 (5, 14)	6 (3, 10)	7 (1, 11)	7 (4, 9)	7 (4, 10)
Turbidity (NTU)	58 (8, 197)	41 (9, 97)	28 (5, 77)	22 (5, 62)	33 (0, 124)	21 (0, 96)
Conductivity (us/cm)	302 (183, 360)	299 (187, 363)	310 (235, 356)	307 (167, 385)	305 (253, 353)	311 (236, 363)
Mean depth (m)	0.5 (0.1, 0.8)	0.5 (0.2, 0.8)	0.4 (0.1, 0.8)	0.4 (0.1, 0.8)	0.4 (0.1, 0.7)	0.4 (0.2, 0.7)
Mean substrate class	1.7 (1, 4)	2.1 (1, 5)	1.9 (1, 4)	2.4 (1, 5)	1.8 (1, 5)	2.3 (1, 4)
% Large woody debris	13 (0, 70)	7 (0, 56)	4 (0, 36)	4 (0, 65)	4 (0, 30)	1 (0, 23)
% Small woody debris	12 (0, 65)	7 (0, 50)	8 (0, 56)	3 (0, 30)	8 (0, 79)	4 (0, 52)
% Root wad	1 (0, 12)	1 (0, 8)	1 (0, 10)	1 (0, 8)	2 (0, 26)	1 (0, 25)
% Riparian vegetation	36 (0, 100)	21 (0, 67)	22 (0, 100)	16 (0, 100)	10 (0, 75)	6 (0, 60)

Table 3.—Results from the multivariate analysis of covariance (MANCOVA) testing for differences in fixed effects (cove type and month), using reservoir and year as covariates and the habitat measurements as dependent variables. Degrees of freedom reported are hypothesis and error.

MANCOVA	Multivariate Wilk's Lambda	F	df	*P*-value
Cove Type	0.577	*11.679*	12, 191	0.000
Month	0.637	*9.073*	12, 191	0.000

ANCOVA	Univariate Dependent Variable	F	df	*P*-value
Cove Type	Percent WW coverage	62.507	1, 202	0.000
	WW density (# stems/ m^2)	12.527	1, 202	0.000
	Turbidity (NTU)	14.392	1, 202	0.000
	Mean substrate class	13.796	1, 202	0.000
	% Small woody debris	7.767	1, 202	0.006
	% Flooded riparian vegetation	7.477	1, 202	0.007
	% Large woody debris	6.902	1, 202	0.009
Month	WW density (# stems/ m^2)	10.376	2, 202	0.000
	Mean temp. (^{o}C)	59.936	2, 202	0.000
	Turbidity (NTU)	21.793	2, 202	0.000
	% Flooded riparian vegetation	19.473	2, 202	0.000
	DO (mg/L)	18.499	2, 202	0.000
	% Large woody debris	12.301	2, 202	0.000
	% Small woody debris	4.148	2, 202	0.017

Table 4.—Results from the multivariate analysis of covariance (MANCOVA) testing for differences in fish, macroinvertebrate, and zooplankton abundance between water willow and control coves and among months using reservoir and year as covariates. Degrees of freedom reported are hypothesis and error. Abundance values are the group mean (± 1 SE).

MANCOVA	**Wilk's Λ**	**F**	**df**	***P*-value**
Cove Type	0.482	4.817	37, 166	0.000

Abundance	**Fish (*N/e*)**	**Macroinvertebrate (*N/e*)**	**Zooplankton (*N/L*)**
Water willow	0.50 (0.02)	0.36 (0.01)	0.22 (0.01)
Control	0.39 (0.01)	0.27 (0.01)	0.19 (0.01)

MANCOVA	**Wilk's Λ**	**F**	**df**	***P*-value**
Month	0.157	6.825	74, 332	0.000

Abundance	**Fish (*N/e*)**	**Macroinvertebrate (*N/e*)**	**Zooplankton (*N/L*)**
June	0.37 (0.02)	0.34 (0.02)	0.19 (0.01)
July	0.42 (0.02)	0.32 (0.02)	0.25 (0.01)
August	0.54 (0.02)	0.29 (0.02)	0.19 (0.01)

ANCOVA		**Dependent Variable**	**F**	**df**	***P*-value**
Cove Type					
	Fishes	Age-0 *Lepomis* spp.	23.24	1, 202	0.000
		Etheostoma spectabile	23.369	1, 202	0.000
		Ictalurus punctatus	11.912	1, 202	0.001
		Age-0 *Micropterus salmoides*	11.581	1, 202	0.001
		Pimephales notatus	7.661	1, 202	0.006

Table 4.—Continued.

ANCOVA	Dependent Variable	F	df	*P*-value
Cove Type				
Macro	Ephemeroptera Heptageniidae	18.375	1, 202	0.000
	Ephemeroptera Caenidae	9.371	1, 202	0.003
	Ephemeroptera Ephemeridae	8.388	1, 202	0.004
	Hemiptera Corixidae	32.784	1, 202	0.000
	Odonata Coenagrionidae	8.12	1, 202	0.005
	Oligochaeta	7.87	1, 202	0.006
Zoo	Chydoridae	8.594	1, 202	0.004
Month				
Fishes	*Pimephales notatus*	27.314	2, 202	0.000
	Ictalurus punctatus	9.774	2, 202	0.000
	Age-0 *Lepomis* spp.	119.857	2, 202	0.000
Macro	Amphipoda	5.432	2, 202	0.005
	Gastropoda	5.31	2, 202	0.006
Zoo	Rotifera	12.31	2, 202	0.000
	Sididae	5.351	2, 202	0.005
Cove Type * Month				
Fishes	*Lepomis macrochirus*	6.407	2, 202	0.002

Table 5.—All fish species sampled during the study and the percentage of sites they occurred within El Dorado (ELD), Hillsdale (HSD), and Melvern (MEL) reservoirs. Species with an * occurred in all reservoirs and occupied > 5 % of the sampling sites within each reservoir.

	% Occurrence				% Occurrence		
Fish Species	**ELD**	**HSD**	**MEL**	**Fish Species**	**ELD**	**HSD**	**MEL**
Lepisosteus osseus	4.2	0.0	21.2	*Labidesthes sicculus*	45.8	0.0	34.8
*Dorosoma cepedianum**	56.9	38.9	33.3	*Fundulus notatus*	4.2	0.0	0.0
*Campostoma anomalum**	19.4	12.5	9.1	*Gambusia affinis*	29.2	19.4	0.0
*Cyprinella lutrensis**	80.6	88.9	74.2	*Morone chrysops*	15.3	0.0	10.6
Cyprinus carpio	16.7	11.1	1.5	*Lepomis cyanellus**	68.1	70.8	81.8
Luxilus cornutus	4.2	0.0	0.0	*Lepomis humilis**	72.2	47.2	54.5
Lythrurus umbratilis	1.4	0.0	0.0	*Lepomis macrochirus**	48.6	65.3	59.1
Notemigonus crysoleucas	2.8	38.9	3.0	*Lepomis microlophus*	0.0	4.2	3.0
Notropis buchanani	1.4	0.0	0.0	*Lepomis megalotis*	12.5	1.4	48.5
Notropis ludibundus	1.4	0.0	15.2	Age-0 *Lepomis* spp. *	65.3	55.6	43.9
Phenacobius mirabilis	13.9	4.2	6.1	*Micropterus dolomieu*	6.9	0.0	3.0
*Pimephales notatus**	76.4	90.3	93.9	*Micropterus salmoides**	59.7	90.3	69.7
Pimephales promelas	2.8	15.3	7.6	*Pomoxis annularis*	26.4	12.5	4.5
*Pimephales vigilax**	25.0	16.7	12.1	*Pomoxis nigromaculatus*	5.6	5.6	0.0
Semotilus atromaculatus	1.4	0.0	0.0	*Etheostoma spectabile**	31.9	31.9	74.2
Ictiobus bubalus	5.6	0.0	0.0	*Percina caprodes**	69.4	18.1	53.0
Ictiobus cyprinellus	4.2	2.8	4.5	*Percina phoxocephala*	68.1	1.4	25.8
Ameiurus natalis	0.0	1.4	0.0	*Sander vitreus*	9.7	4.2	12.1
*Ictalurus punctatus**	26.4	11.1	7.6	*Sander canadense*	0.0	0.0	1.5
Noturus exilis	0.0	0.0	21.2	*Aplodinotus grunniens*	12.5	8.3	1.5
Pylodictis olivaris	6.9	0.0	0.0				
				Total number of species	**36**	**26**	**30**

Table 6.—Mean number of fish captured per enclosure (minimum, maximum) in water willow coves compared to control coves for El Dorado (N = 144), Hillsdale (N = 144), and Melvern (N = 122) reservoirs. Fish with an asterisk were included in the MANCOVA analysis.

Taxa	**El Dorado**		**Hillsdale**		**Melvern**	
	WW	**Control**	**WW**	**Control**	**WW**	**Control**
Lepisosteus osseus	0.1 (0, 3)	0 (0, 0)	0 (0, 0)	0 (0, 0)	0.6 (0, 5)	0.3 (0, 5)
*Dorosoma cepedianum**	8.4 (0, 65)	4 (0, 21)	5.3 (0, 43)	8.6 (0, 129)	5.4 (0, 54)	2.4 (0, 42)
*Campostoma anomalum**	1.5 (0, 22)	0.8 (0, 8)	0.6 (0, 7)	0.1 (0, 1)	1 (0, 13)	0 (0, 1)
*Cyprinella lutrensis**	27.5 (0, 124)	16.1 (0, 90)	33.1 (0, 331)	80.5 (0, 255)	6.6 (0, 29)	9.9 (0, 159)
Cyprinus carpio	0.4 (0, 6)	0.1 (0, 2)	0.5 (0, 5)	0 (0, 1)	0 (0, 1)	0 (0, 0)
Luxilus cornutus	0 (0, 0)	0.1 (0, 1)	0 (0, 0)	0 (0, 0)	0 (0, 0)	0 (0, 0)
Lythrurus umbratilis	0 (0, 0)	0.1 (0, 3)	0 (0, 0)	0 (0, 0)	0 (0, 0)	0 (0, 0)
Notemigonus crysoleucas	0.1 (0, 2)	0 (0, 0)	1.1 (0, 11)	1 (0, 9)	0.1 (0, 1)	0 (0, 0)
Notropis buchanani	0 (0, 0)	0 (0, 1)	0 (0, 0)	0 (0, 0)	0 (0, 0)	0 (0, 0)
Notropis ludibundus	0 (0, 1)	0 (0, 0)	0 (0, 0)	0 (0, 0)	0.7 (0, 8)	1.2 (0, 20)
Phenacobius mirabilis	1.1 (0, 19)	0.3 (0, 6)	0.1 (0, 1)	0 (0, 0)	0.2 (0, 3)	0 (0, 0)
*Pimephales notatus**	14.1 (0, 92)	14.5 (0, 124)	42.5 (1, 491)	21.2 (0, 157)	52.4 (0, 432)	22.6 (0, 187)
P. promelas	0.1 (0, 2)	0 (0, 0)	1.3 (0, 19)	0 (0, 1)	0.8 (0, 15)	1.1 (0, 34)

Table 6.—Continued.

Taxa	El Dorado		Melvern		Hillsdale	
	WW	Control	WW	Control	WW	Control
*Pimephales vigilax**	1 (0, 12)	2.4 (0, 19)	5.4 (0, 62)	1.3 (0, 19)	0.6 (0, 14)	0.4 (0, 8)
Semotilus atromaculatus	0 (0, 1)	0 (0, 0)	0 (0, 0)	0 (0, 0)	0 (0, 0)	0 (0, 0)
Ictiobus bubalus	0.1 (0, 1)	0 (0, 1)	0 (0, 0)	0 (0, 0)	0 (0, 0)	0 (0, 0)
Ictiobus cyprinellus	0.2 (0, 3)	0 (0, 0)	0.5 (0, 10)	0 (0, 0)	0.9 (0, 28)	0 (0, 0)
Ameiurus natalis	0 (0, 0)	0 (0, 0)	0 (0, 0)	0 (0, 1)	0 (0, 0)	0 (0, 0)
*Ictalurus punctatus**	4.5 (0, 29)	0.1 (0, 2)	0.3 (0, 3)	0.1 (0, 2)	0 (0, 0)	0.4 (0, 6)
Noturus exilis	0 (0, 0)	0 (0, 0)	0 (0, 0)	0 (0, 0)	0.4 (0, 3)	0.2 (0, 2)
Pylodictis olivaris	0 (0, 1)	0.2 (0, 3)	0 (0, 0)	0 (0, 0)	0 (0, 0)	0 (0, 0)
Labidesthes sicculus	11.1 (0, 249)	2.1 (0, 23)	0 (0, 0)	0 (0, 0)	1.8 (0, 26)	2.1 (0, 29)
Fundulus notatus	0.1 (0, 1)	0.1 (0, 3)	0 (0, 0)	0 (0, 0)	0 (0, 0)	0 (0, 0)
Gambusia affinis	3.5 (0, 57)	0.9 (0, 6)	2.3 (0, 45)	0.1 (0, 3)	0 (0, 0)	0 (0, 0)
Morone chrysops	1.1 (0, 26)	0.1 (0, 1)	0 (0, 0)	0 (0, 0)	0.2 (0, 3)	0.2 (0, 4)
*Lepomis cyanellus**	3.7 (0, 22)	5.4 (0, 45)	8.5 (0, 50)	11.4 (0, 61)	8.5 (0, 42)	9.4 (0, 65)
*Lepomis humilis**	6.8 (0, 27)	4.1 (0, 21)	2 (0, 12)	0.9 (0, 5)	1.9 (0, 17)	1.5 (0, 10)
*Lepomis macrochirus**	2.3 (0, 24)	1.4 (0, 13)	4.9 (0, 28)	3.4 (0, 23)	1.8 (0, 15)	1.4 (0, 11)
Lepomis microlophus	0 (0, 0)	0 (0, 0)	0.1 (0, 1)	0.1 (0, 2)	0.1 (0, 1)	0 (0, 0)
Lepomis megalotis	0.1 (0, 2)	0.3 (0, 3)	0 (0, 0)	0 (0, 1)	1.8 (0, 20)	2.2 (0, 20)

Table 6.—Continued.

Taxa	**El Dorado**		**Melvern**		**Hillsdale**	
	WW	**Control**	**WW**	**Control**	**WW**	**Control**
Age-0						
Lepomis spp. *	68.7 (0, 424)	17.7 (0, 120)	38.9 (0, 325)	5.3 (0, 36)	8.1 (0, 83)	5.2 (0, 41)
Micropterus dolomieu	0 (0, 1)	0.1 (0, 2)	0 (0, 0)	0 (0, 0)	0.1 (0, 3)	0 (0, 0)
*Micropterus salmoides**	2.8 (0, 14)	1.8 (0, 10)	16.8 (0, 107)	8.3 (0, 56)	5.6 (0, 50)	1.2 (0, 5)
Pomoxis annularis	2.1 (0, 23)	0.2 (0, 3)	0.4 (0, 5)	0.1 (0, 1)	0.1 (0, 1)	0.1 (0, 2)
Pomoxis nigromaculatus	0.2 (0, 5)	0 (0, 1)	0.1 (0, 2)	0 (0, 1)	0 (0, 0)	0 (0, 0)
*Etheostoma spectabile**	0.6 (0, 6)	0.5 (0, 5)	0.9 (0, 7)	0.4 (0, 4)	9.5 (0, 50)	1.6 (0, 18)
*Percina caprodes**	6.3 (0, 93)	2 (0, 13)	0.3 (0, 3)	0.3 (0, 3)	1.5 (0, 9)	1.5 (0, 8)
Percina phoxocephala	4.9 (0, 61)	4.3 (0, 24)	0 (0, 1)	0 (0, 0)	0.4 (0, 4)	1 (0, 6)
Sander vitreus	0.2 (0, 2)	0.1 (0, 3)	0.1 (0, 2)	0 (0, 0)	0.2 (0, 2)	0.1 (0, 1)
Sander canadense	0 (0, 0)	0 (0, 0)	0 (0, 0)	0 (0, 0)	0.1 (0, 2)	0 (0, 0)
Aplodinotus grunniens	0.8 (0, 14)	0.1 (0, 2)	0.1 (0, 1)	0.3 (0, 6)	0 (0, 1)	0 (0, 0)

Table 7.—Mean macroinvertebrate abundances (number sampled per enclosure; minimum, maximum) in water willow coves compared to control coves for El Dorado (N = 144), Hillsdale (N = 144), and Melvern (N = 122) reservoirs. Macroinvertebrates with an asterisk were included in the MANCOVA analysis.

Taxa	El Dorado		Hillsdale		Melvern	
	WW	Control	WW	Control	WW	Control
Ephemeroptera						
Baetidae*	4.4 (0, 70)	2.4 (0, 64)	5.2 (0, 40)	7.3 (0, 100)	5.4 (0, 76)	2.2 (0, 18)
Caenidae*	4.7 (0, 40)	4.5 (0, 48)	10.6 (0, 70)	5.8 (0, 146)	6.9 (0, 46)	3.5 (0, 24)
Ephemeridae*	2.2 (0, 23)	0.4 (0, 8)	0.4 (0, 5)	0.2 (0, 3)	1.2 (0, 15)	1 (0, 27)
Heptageniidae*	1.2 (0, 12)	11.7 (0, 77)	0.3 (0, 4)	2.6 (0, 70)	1.2 (0, 17)	1.1 (0, 6)
Odonata						
Aeshnidae	0 (0, 0)	0 (0, 0)	0 (0, 0)	0 (0, 1)	0 (0, 0)	0 (0, 1)
Coenagrionidae*	0.6 (0, 6)	0.8 (0, 17)	3.1 (0, 32)	0.3 (0, 4)	1.3 (0, 20)	0.4 (0, 3)
Corduliidae	0 (0, 0)	0.6 (0, 19)	0 (0, 0)	0 (0, 1)	0.1 (0, 2)	0 (0, 0)
Gomphidae	0 (0, 1)	0 (0, 0)	0.1 (0, 1)	0 (0, 0)	0.1 (0, 1)	0 (0, 1)
Lestidae	0 (0, 1)	0 (0, 0)	0 (0, 0)	0 (0, 0)	0.1 (0, 1)	0 (0, 0)
Libellulidae	0 (0, 0)	0 (0, 0)	0.4 (0, 10)	0 (0, 1)	0.1 (0, 1)	0 (0, 0)
Macromiidae	0 (0, 0)	0 (0, 0)	0 (0, 0)	0 (0, 0)	0 (0, 1)	0 (0, 0)
Hemiptera						
Belostomatidae	0 (0, 0)	0 (0, 0)	0.1 (0, 2)	0 (0, 0)	0 (0, 0)	0 (0, 0)
Corixidae*	13.8 (0, 109)	0.5 (0, 4)	15.4 (0, 226)	1.3 (0, 24)	3.2 (0, 24)	1.7 (0, 18)
Gerridae	0.2 (0, 5)	0.1 (0, 2)	1 (0, 20)	0.4 (0, 10)	0 (0, 0)	0 (0, 0)
Hebridae	0 (0, 0)	0 (0, 0)	0 (0, 0)	0 (0, 0)	0 (0, 1)	0.1 (0, 1)
Mesoveliidae	0 (0, 0)	0 (0, 0)	0 (0, 0)	6.5 (0, 187)	0 (0, 0)	0 (0, 0)
Nepidae	0 (0, 0)	0 (0, 0)	0 (0, 0)	0 (0, 0)	0 (0, 1)	0 (0, 0)
Veliidae	0 (0, 1)	0 (0, 0)	0 (0, 0)	0 (0, 0)	0 (0, 0)	0 (0, 0)

Table 7.—Continued.

Taxa	**El Dorado**		**Hillsdale**		**Melvern**	
	WW	**Control**	**WW**	**Control**	**WW**	**Control**
Megaloptera						
Sialidae	0.1 (0, 3)	0 (0, 0)	0.1 (0, 1)	0 (0, 1)	0 (0, 1)	0 (0, 0)
Coleoptera						
Chrysomelidae	0 (0, 0)	0 (0, 0)	0 (0, 0)	0 (0, 0)	0 (0, 0)	0 (0, 0)
Dytiscidae	0.3 (0, 8)	0.2 (0, 8)	0 (0, 1)	0 (0, 1)	0.1 (0, 1)	0 (0, 0)
Elmidae	0.2 (0, 2)	1.2 (0, 14)	0 (0, 0)	0 (0, 0)	0 (0, 1)	0 (0, 1)
Gyrinidae	0 (0, 1)	0 (0, 0)	0.2 (0, 4)	0.1 (0, 1)	0.5 (0, 8)	0.1 (0, 3)
Haliplidae	0 (0, 0)	0 (0, 0)	1.7 (0, 20)	0 (0, 1)	0 (0, 0)	0 (0, 1)
Hydrophilidae*	0.1 (0, 1)	0.1 (0, 1)	0.1 (0, 1)	0.1 (0, 1)	0.1 (0, 1)	0.1 (0, 2)
Trichoptera						
Hydroptilidae*	0.7 (0, 17)	0.3 (0, 5)	2.9 (0, 48)	3.8 (0, 98)	0.3 (0, 3)	0.4 (0, 8)
Leptoceridae*	1.4 (0, 16)	0 (0, 1)	8.8 (0, 148)	2.7 (0, 23)	0.7 (0, 8)	0.5 (0, 4)
Limnephilidae	0 (0, 1)	0 (0, 0)	0 (0, 0)	0.1 (0, 2)	0 (0, 1)	0 (0, 1)
Polycentropodidae*	0.2 (0, 2)	0.4 (0, 4)	0.1 (0, 1)	0.1 (0, 2)	0.2 (0, 2)	0.1 (0, 1)
Trichoptera	0.1 (0, 3)	0 (0, 1)	0 (0, 0)	0 (0, 0)	0 (0, 1)	0 (0, 0)
Lepidoptera						
Pyralidae	0 (0, 0)	0 (0, 1)	0 (0, 0)	0 (0, 0)	0 (0, 0)	0 (0, 0)
Diptera						
Ceratopogonidae*	0.8 (0, 8)	0.1 (0, 2)	12.3 (0, 122)	2.1 (0, 16)	0.5 (0, 8)	0.6 (0, 6)
Chaoboridae	0.4 (0, 14)	0.4 (0, 16)	0 (0, 0)	0.4 (0, 12)	0.1 (0, 2)	0 (0, 0)
Chironomidae*	75 (1, 673)	35.7 (0, 230)	99.3 (0, 470)	97 (2, 1050)	63.3 (3, 426)	48.1 (4, 197)
Culicidae	0.1 (0, 2)	0.6 (0, 20)	0 (0, 1)	3.5 (0, 77)	0.1 (0, 4)	0 (0, 0)
Dixidae	0.1 (0, 1)	0 (0, 0)	0 (0, 1)	0 (0, 0)	0 (0, 0)	0 (0, 0)

Table 7.—Continued.

Taxa	El Dorado		Hillsdale		Melvern	
	WW	**Control**	**WW**	**Control**	**WW**	**Control**
Dolichopodidae	0 (0, 0)	0 (0, 0)	0.1 (0, 2)	0 (0, 0)	0 (0, 0)	0 (0, 0)
Empididae	0 (0, 0)	0 (0, 0)	0 (0, 0)	0 (0, 0)	0 (0, 0)	0 (0, 1)
Sciomyzidae	0 (0, 0)	0 (0, 0)	0 (0, 1)	0 (0, 1)	0 (0, 0)	0 (0, 0)
Tabanidae	0 (0, 1)	0 (0, 0)	0.1 (0, 1)	0 (0, 0)	0 (0, 0)	0 (0, 1)
Diptera	0 (0, 0)	0 (0, 1)	0.1 (0, 1)	0 (0, 1)	0 (0, 1)	0 (0, 1)
Other invertebrates						
Terrestrial*	0.6 (0, 11)	0.2 (0, 2)	1.9 (0, 40)	2.9 (0, 70)	0.3 (0, 2)	0.6 (0, 4)
Collembola	0.1 (0, 2)	0.3 (0, 8)	0.1 (0, 1)	0.4 (0, 8)	0 (0, 1)	0.2 (0, 6)
Amphipoda*	26.9 (0, 544)	2.7 (0, 43)	19.9 (0, 310)	26.9 (0, 510)	6.7 (0, 96)	2 (0, 44)
Decapoda	0 (0, 1)	0.1 (0, 2)	0.2 (0, 3)	0.5 (0, 12)	0 (0, 1)	0 (0, 0)
Copepoda	24.1 (0, 489)	8.1 (0, 126)	0 (0, 1)	0 (0, 1)	0 (0, 0)	0.1 (0, 1)
Hydrachnidia	0.3 (0, 3)	0.3 (0, 6)	3.8 (0, 60)	2.9 (0, 38)	1 (0, 7)	0.8 (0, 7)
Oligochaeta*	24.9 (0, 403)	4.3 (0, 52)	76.4 (0, 716)	50.2 (0, 790)	11.6 (0, 232)	4.2 (0, 80)
Gastropoda*	1.3 (0, 35)	0.2 (0, 4)	3.4 (0, 40)	2.3 (0, 60)	0.4 (0, 4)	0.6 (0, 9)
Hirudinea	0 (0, 0)	0.3 (0, 8)	0 (0, 1)	0.1 (0, 3)	0.1 (0, 2)	0.1 (0, 2)
Branchiura	0.9 (0, 20)	0.1 (0, 2)	0 (0, 0)	0 (0, 0)	0.4 (0, 6)	1 (0, 7)
Bivalve	0 (0, 0)	0.2 (0, 3)	0 (0, 0)	0 (0, 0)	0 (0, 0)	0.1 (0, 1)

Table 8.—Mean zooplankton densities (number/L; minimum, maximum) in water willow coves compared to control coves for El Dorado (N = 144), Hillsdale (N = 144), and Melvern (N = 122) reservoirs. Zooplankton with an asterisk were included in the MANCOVA analysis.

Taxa	**El Dorado**		**Hillsdale**		**Melvern**	
	WW	**Control**	**WW**	**Control**	**WW**	**Control**
Naplii*	2.6 (0, 18)	3.9 (0.1, 21)	4.6 (0.1, 20)	3.6 (0.1, 27)	2.1 (0, 8)	3.2 (0.1, 17)
Sididae*	1.1 (0, 13)	0.9 (0, 7)	0.9 (0, 8)	0.7 (0, 15)	0.4 (0, 4)	0.3 (0, 2.8)
Cyclopoida*	2 (0, 10)	2.1 (0, 14)	3.8 (0.1, 46)	1.5 (0, 11)	1.9 (0, 16)	1.3 (0, 6)
Calanoida*	1.1 (0, 24)	1.4 (0, 10)	1.5 (0, 16)	1.1 (0, 24)	0.1 (0, 1.6)	0.1 (0, 0.8)
Daphnia*	1.3 (0, 11)	1 (0, 7)	0.5 (0, 4)	0.7 (0, 21)	0.1 (0, 1.4)	0.1 (0, 0.8)
Rotifera*	0.6 (0, 4)	2 (0, 44)	1.9 (0, 37)	0.9 (0, 18)	0.7 (0, 6)	1.2 (0, 18)
Chydoridae*	0.2 (0, 6)	0.4 (0, 13)	0.8 (0, 3)	0.3 (0, 2.6)	0.3 (0, 5)	0.1 (0, 1)
Bosminidae*	0.1 (0, 1.7)	0.1 (0, 3)	1.5 (0, 10)	1.1 (0, 21)	0.3 (0, 5)	0.8 (0, 11)
Leptodora	0.1 (0, 0.7)	0 (0, 0.7)	0 (0, 0.1)	0 (0, 0.9)	0 (0, 0.2)	0 (0, 0)

Table 9.—Summary of littoral assemblage characteristics for water willow versus control coves for El Dorado (N = 144), Hillsdale (N = 144), and Melvern (N = 122) reservoirs across all sampling dates. Values are the mean + 1 SD.

	El Dorado		**Hillsdale**		**Melvern**	
	WW	**Control**	**WW**	**Control**	**WW**	**Control**
Fish Assemblage						
Species Richness (S)	11.00 (3.96)	9.06 (3.02)	8.89 (1.72)	6.50 (2.21)	9.48 (3.30)	8.39 (2.52)
Simpson's Diversity Index (D)	3.49 (1.94)	4.04 (1.56)	3.38 (1.13)	2.32 (0.91)	3.71 (1.49)	3.78 (1.21)
Evenness (E)	0.32 (0.17)	0.48 (0.18)	0.39 (0.13)	0.40 (0.19)	0.41 (0.15)	0.49 (0.20)
Macroinvertebrate						
Taxa Richness (S)	7.11 (2.72)	5.50 (2.08)	8.81 (4.68)	6.67 (3.74)	7.82 (2.71)	6.85 (2.65)
Simpson's Diversity Index (D)	3.04 (1.48)	2.64 (1.05)	3.29 (1.32)	2.49 (0.97)	2.69 (1.02)	2.29 (0.93)
Evenness (E)	0.47 (0.24)	0.51 (0.19)	0.40 (0.14)	0.44 (0.20)	0.37 (0.15)	0.38 (0.18)
Zooplankton						
Family Richness (S)	6.81 (1.83)	6.56 (1.13)	7.46 (0.68)	6.94 (1.24)	5.70 (1.29)	5.03 (1.42)
Simpson's Diversity Index (D)	2.95 (0.93)	2.94 (0.76)	3.56 (1.32)	2.75 (0.98)	2.74 (0.72)	2.42 (0.73)
Evenness (E)	0.46 (0.16)	0.46 (0.14)	0.47 (0.18)	0.40 (0.15)	0.49 (0.11)	0.49 (0.11)

Table 10.—Results from the multivariate analysis of covariance (MANCOVA) that testing for differences in fixed effects (cove type and month), using reservoir and year as covariates and the habitat measurements as dependent variables. Degrees of freedom reported are hypothesis and error.

MANCOVA	**Wilk's Λ**	**F**	**df**	***P*-value**
Cove Type*month	0.836	2.013	18, 386	0.009

ANCOVA	**Dependent Variable**	**F**	**df**	***P*-value**
Cove Type	Fish Richness (S_{fish})	21.545	1, 201	0.000
	Macro Richness (S_{macro})	14.682	1, 201	0.000
	Fish Evenness (E_{fish})	11.847	1, 201	0.001
	Macro Diversity (D_{macro})	11.392	1, 201	0.001
	Zoo Diversity (D_{zoo})	7.42	1, 201	0.007
	Zoo Richness (S_{zoo})	7.054	1, 201	0.009
Month	Fish Richness (S_{fish})	4.835	2, 201	0.009
	Fish Evenness (E_{fish})	4.849	2, 201	0.009
Cove Type*month	Fish Diversity (D_{fish})	6.359	2, 201	0.002

Figure 1.—Differences in abundance of six fish species between water willow and control coves and across months. The significant model effects and associated *P*-values are listed for each species. Water willow coves are represented with dashed lines and open circles, and control coves with solid lines and circles. Each circle denotes mean abundance (number per enclosure) and error bars indicate ± 1 SE.

Figure 2.—Differences in abundance of eight macroinvertebrates between water willow and control coves and across months. The significant model effects and associated *P*-values are listed for each macroinvertebrate. Water willow coves are represented with dashed lines and open circles, and control coves with solid lines and circles. Each circle denotes mean abundance (number per enclosure) and error bars indicate ± 1 SE.

Figure 3.—Differences in abundance of three zooplankton between water willow and control coves and across months. The significant model effects and associated *P*-values are listed for each zooplankton. Water willow coves are represented with dashed lines and open circles, and control coves with solid lines and circles. Each circle denotes mean density (number/L) and error bars indicate ± 1 SE.

Figure 4.—Differences in seven diversity metrics between water willow and control coves and across months. The significant effects and associated *P*-value are listed for each diversity metric. Water willow coves are represented with dashed lines and open circles, and control coves with solid lines and circles. Each circle denotes mean fish abundance and error bars indicate ± 1 SE.

Figure 5.—Redundancy analysis (RDA) for El Dorado Reservoir depicting relationships between sites, fishes, and environmental variables. Top panel (A) shows the axis loadings of environmental variables plotted with sampling sites. Bottom panel (B) indicates the associations of fish species with the environmental variables. Triangles represent sites in water willow coves and circles are in control coves. The length and direction of arrows indicate the strength of axis loadings. The solid arrows denote environmental variables labeled with abbreviations: PWW = percent water willow, WW = water willow present, COND = conductivity, DEPAVE = mean depth, SUBAVG = mean substrate class, PLWD =

percent large woody debris, PVEG = percent flooded riparian vegetation, WWC1-3 = individual water willow coves, CC1-3 = individual control coves, Lmacro = mean abundance of large macroinvertebrates, Smacro = mean abundance of small macroinvertebrates, Tzoo = total zooplankton density, Y02 = sampling year 2002. Fish species are represented with dashed arrows and are labeled with first three letters of the genus and specific epithets (Table 4).

Figure 6.—Redundancy analysis (RDA) for Hillsdale Reservoir depicting relationships between sites, fishes, and environmental variables. Top panel (A) shows the axis loadings of environmental variables plotted with sampling sites. Bottom panel (B) indicates the associations of fish species with the environmental variables. Triangles represent sites in water willow coves and circles are in control coves. The length and direction of arrows indicate the strength of axis loadings. The solid arrows denote environmental variables labeled with abbreviations: PWW = percent water willow, WW = water willow present, COND = conductivity, DEPAVE = mean depth, SUBAVG = mean substrate class, PLWD = percent large woody debris, PVEG = percent flooded riparian vegetation, WWC1-3 = individual water willow coves, CC1-3 = individual control coves, Lmacro = mean abundance of large macroinvertebrates, Smacro = mean abundance of small macroinvertebrates, Tzoo = total zooplankton density, Y02 = sampling year 2002. Fish species are represented with dashed arrows and are labeled with first three letters of the genus and specific epithets (Table 4).

Figure 7.—Redundancy analysis (RDA) for Melvern Reservoir depicting relationships between sites, fishes, and environmental variables. Top panel (A) shows the axis loadings of environmental variables plotted with sampling sites. Bottom panel (B) indicates the associations of fish species with the environmental variables. Triangles represent sites in water willow coves and circles are in control coves. The length and direction of arrows indicate the strength of axis loadings. The solid arrows denote environmental variables labeled with abbreviations: PWW = percent water willow, WW = water willow present, COND = conductivity, DEPAVE = mean depth, SUBAVG = mean substrate class, PLWD = percent large woody debris, PVEG = percent flooded riparian vegetation, WWC1-3 = individual water willow coves, CC1-3 = individual control coves, Lmacro = mean abundance of large macroinvertebrates,

Smacro = mean abundance of small macroinvertebrates, Tzoo = total zooplankton density, Y02 = sampling year 2002. Fish species are represented with dashed arrows and are labeled with first three letters of the genus and specific epithets (Table 4).

Figure 1.

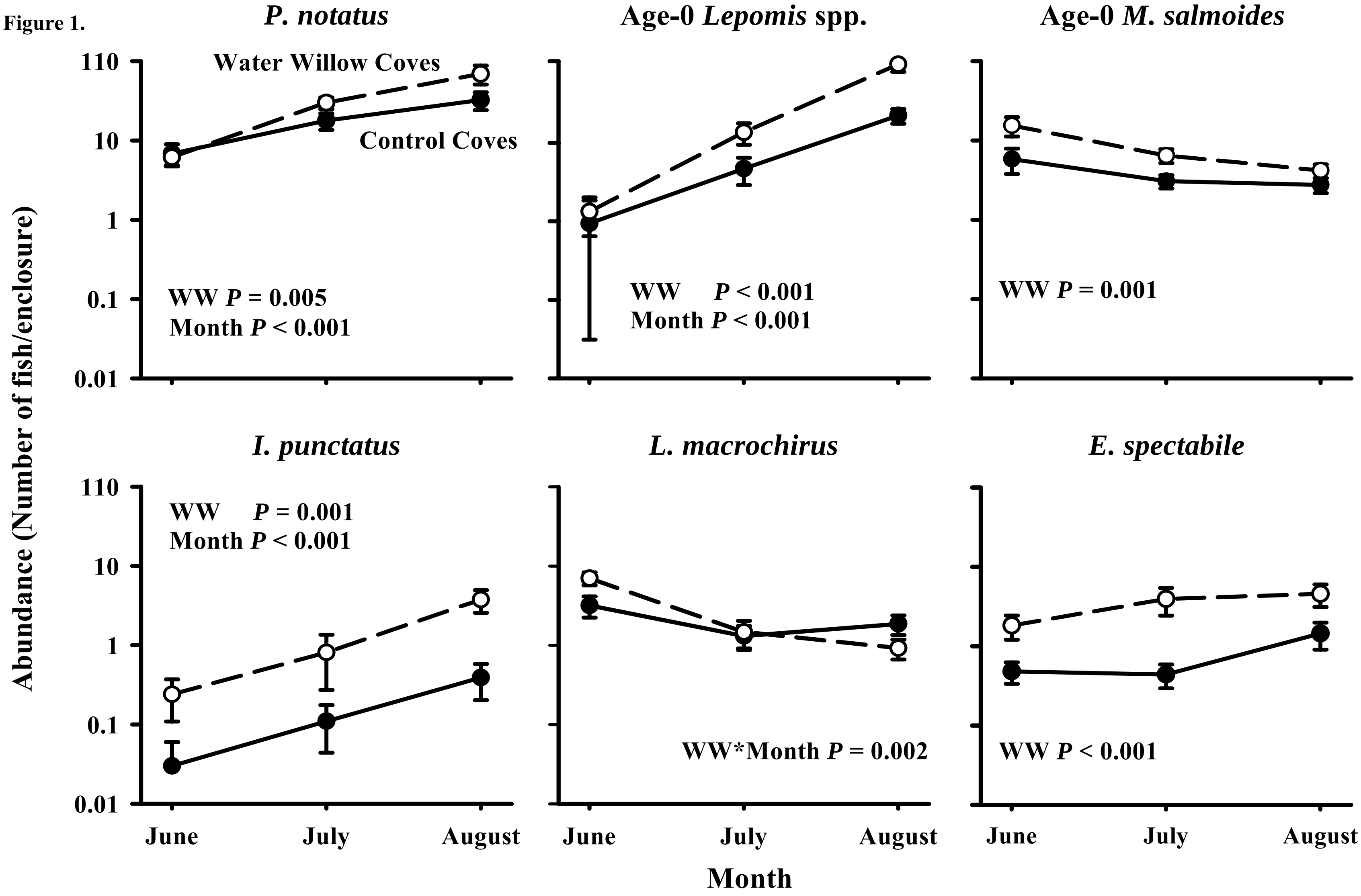

P. notatus
Age-0 Lepomis spp.
Age-0 M. salmoides
I. punctatus
L. macrochirus
E. spectabile
Water Willow Coves
Control Coves
WW P = 0.005
Month P < 0.001
WW P < 0.001
Month P < 0.001
WW P = 0.001
WW P = 0.001
Month P < 0.001
WW*Month P = 0.002
WW P < 0.001
110
10
1
0.1
0.01
Abundance (Number of fish/enclosure)
June
July
August
Month

Figure 2.

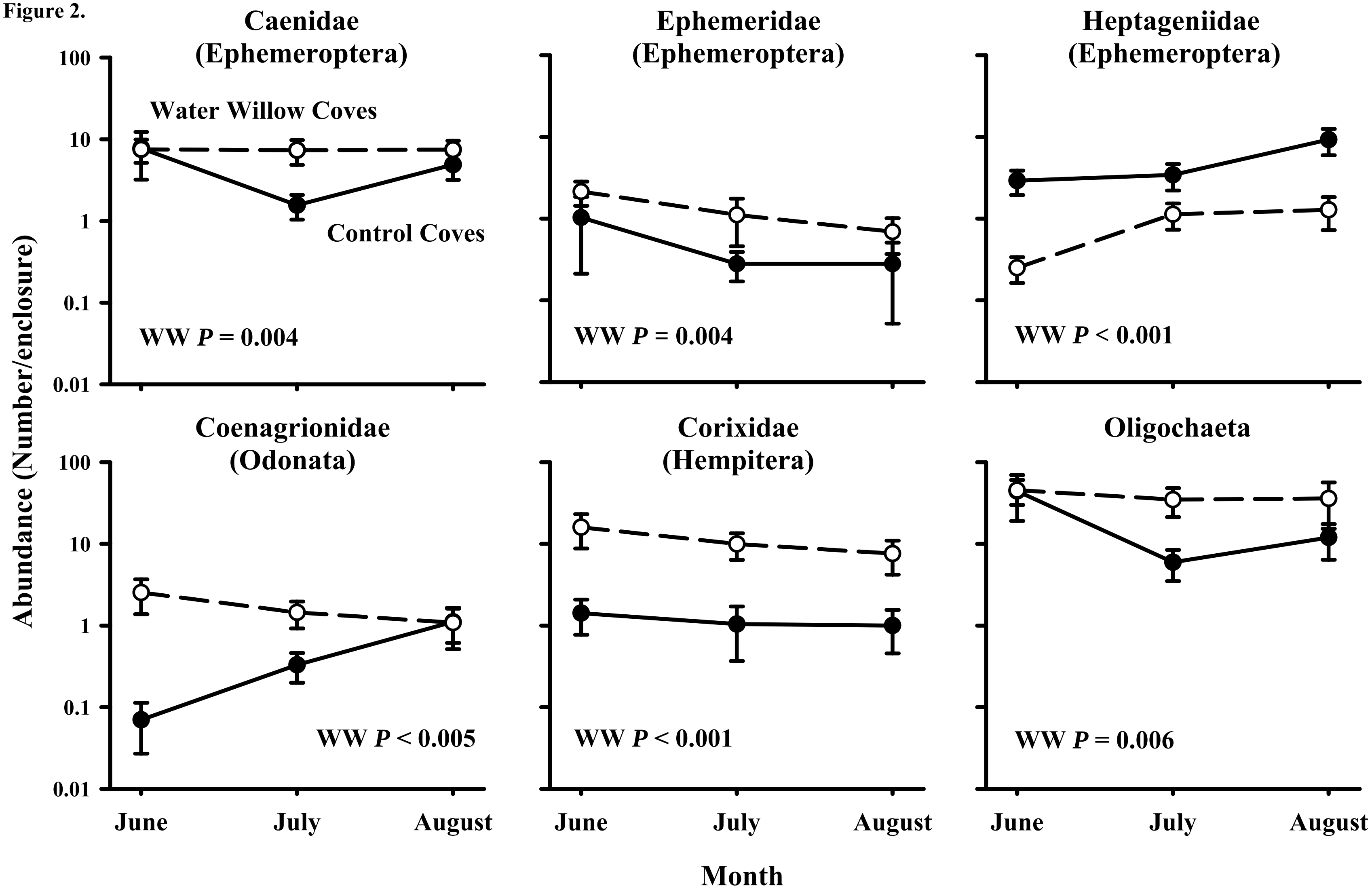

Caenidae
(Ephemeroptera)
Ephemeridae
(Ephemeroptera)
Heptageniidae
(Ephemeroptera)
Water Willow Coves
Control Coves
WW P = 0.004
WW P = 0.004
WW P < 0.001
Coenagrionidae
(Odonata)
Corixidae
(Hempitera)
Oligochaeta
WW P < 0.005
WW P < 0.001
WW P = 0.006
100
10
1
0.1
0.01
Abundance (Number/enclosure)
June
July
August
Month

Figure 2.—Continued.

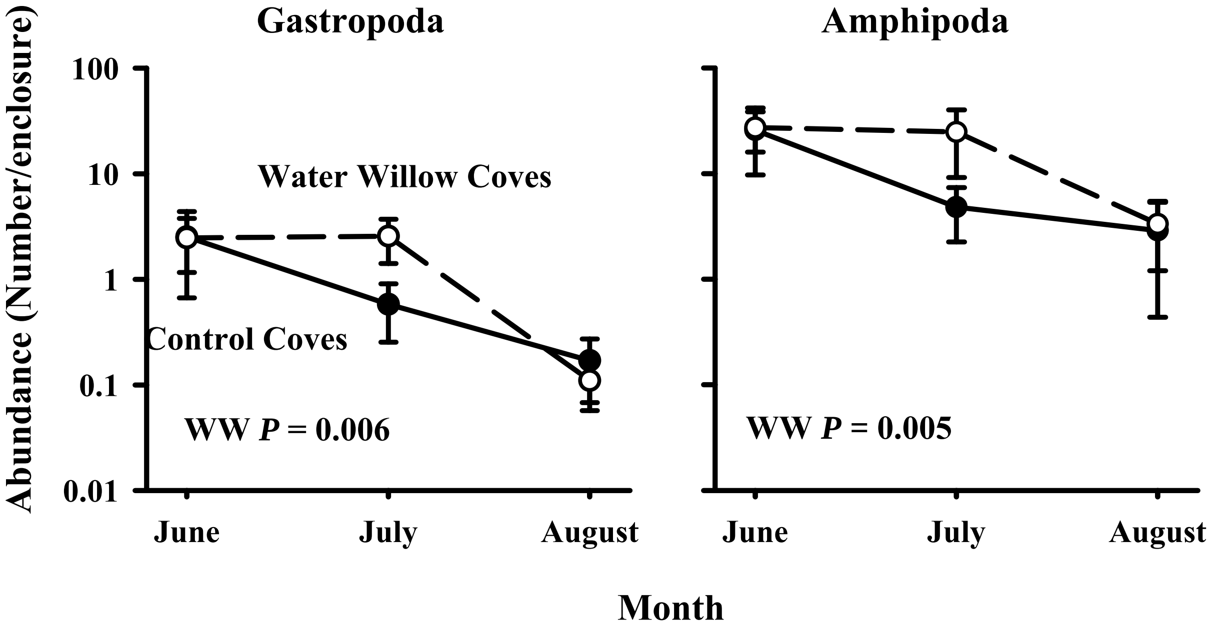


Figure 3.

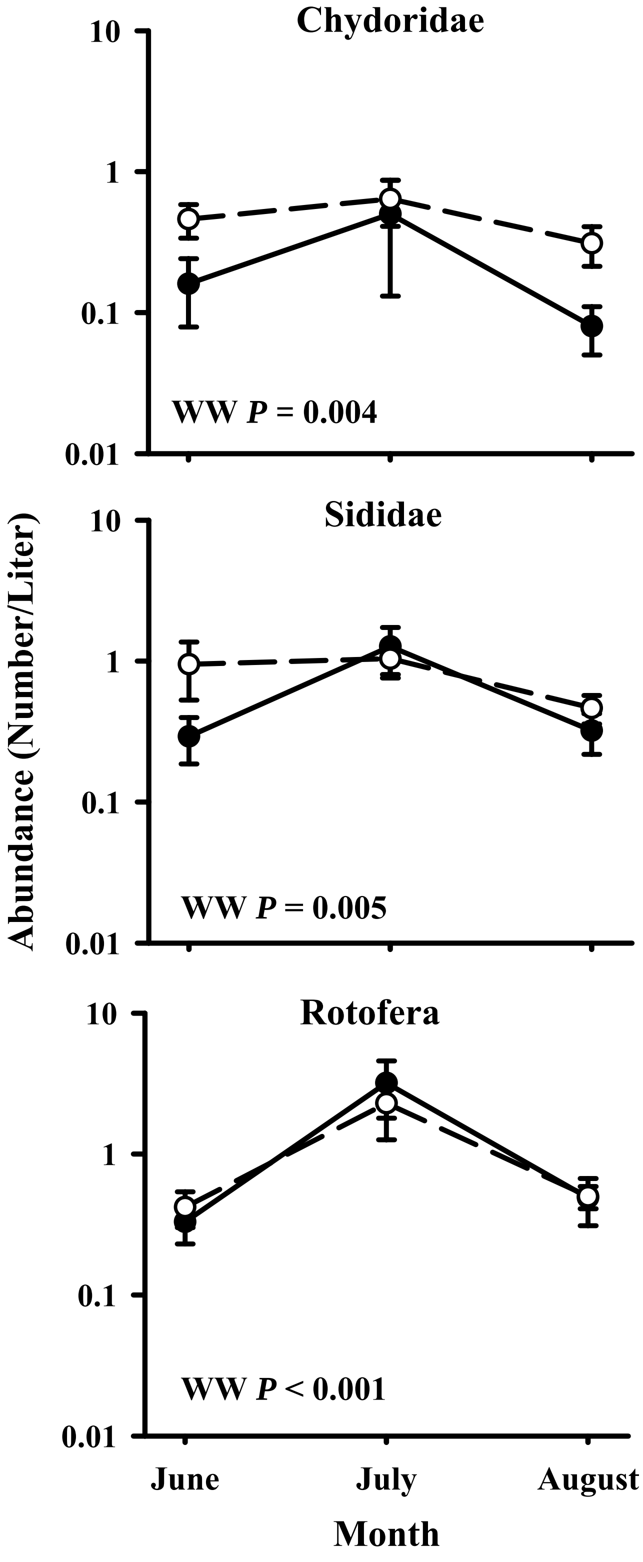

Chydoridae
10
1
0.1
0.01
WW P = 0.004
Sididae
10
1
0.1
0.01
WW P = 0.005
Rotofera
10
1
0.1
0.01
WW P < 0.001
Abundance (Number/Liter)
June
July
August
Month

Figure 4.

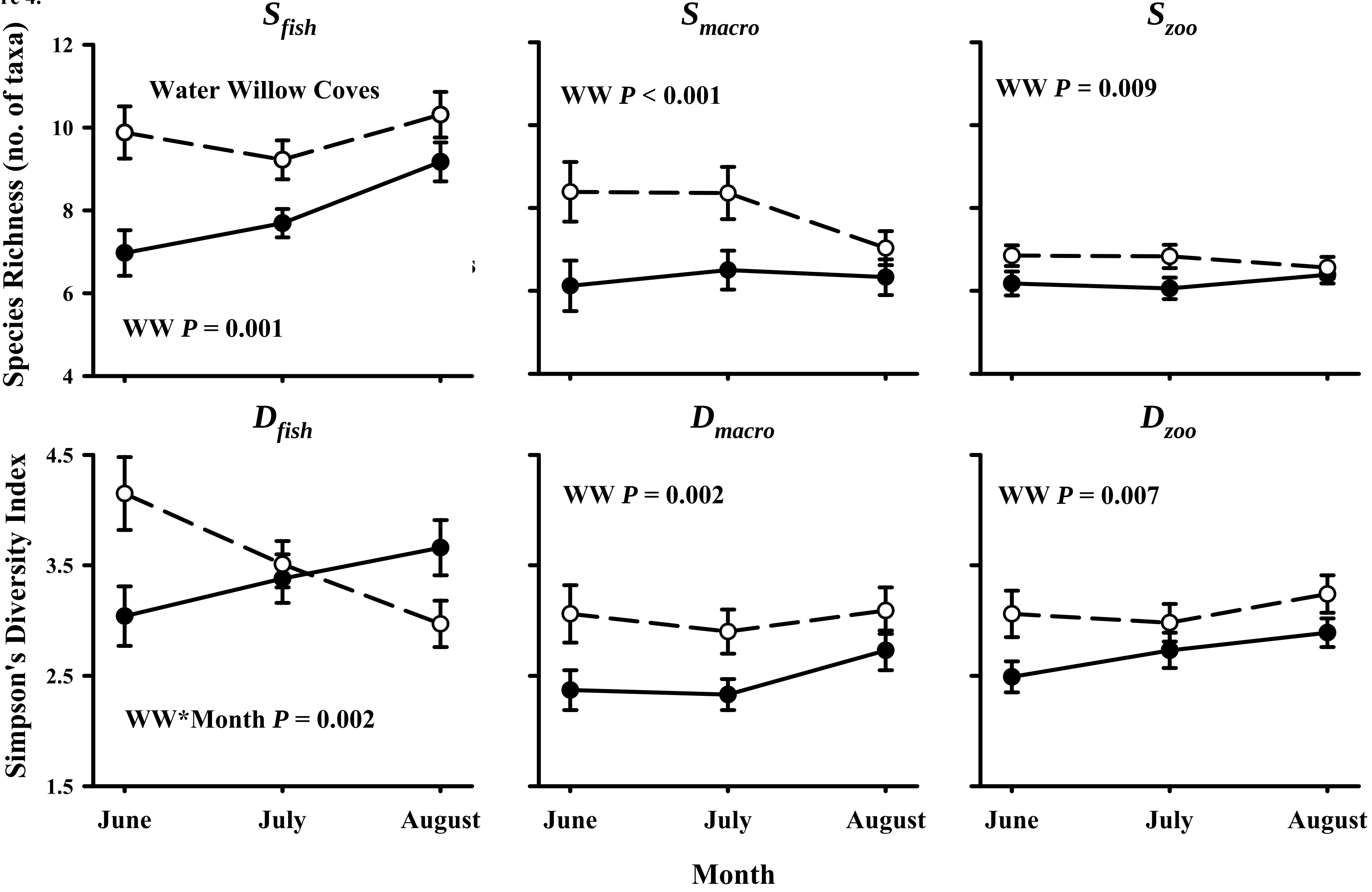

S fish
S macro
S zoo
Species Richness (no. of taxa)
12
10
8
6
4
Water Willow Coves
WW P = 0.001
WW P < 0.001
WW P = 0.009
D fish
D macro
D zoo
Simpson's Diversity Index
4.5
3.5
2.5
1.5
WW*Month P = 0.002
WW P = 0.002
WW P = 0.007
June
July
August
June
July
August
June
July
August
Month

Figure 4.—Continued

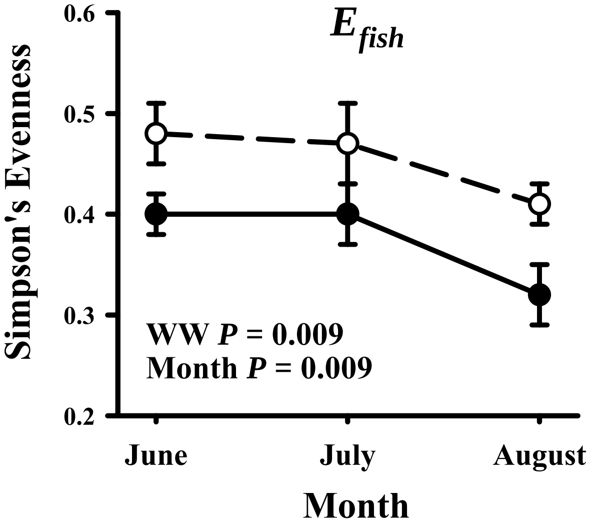
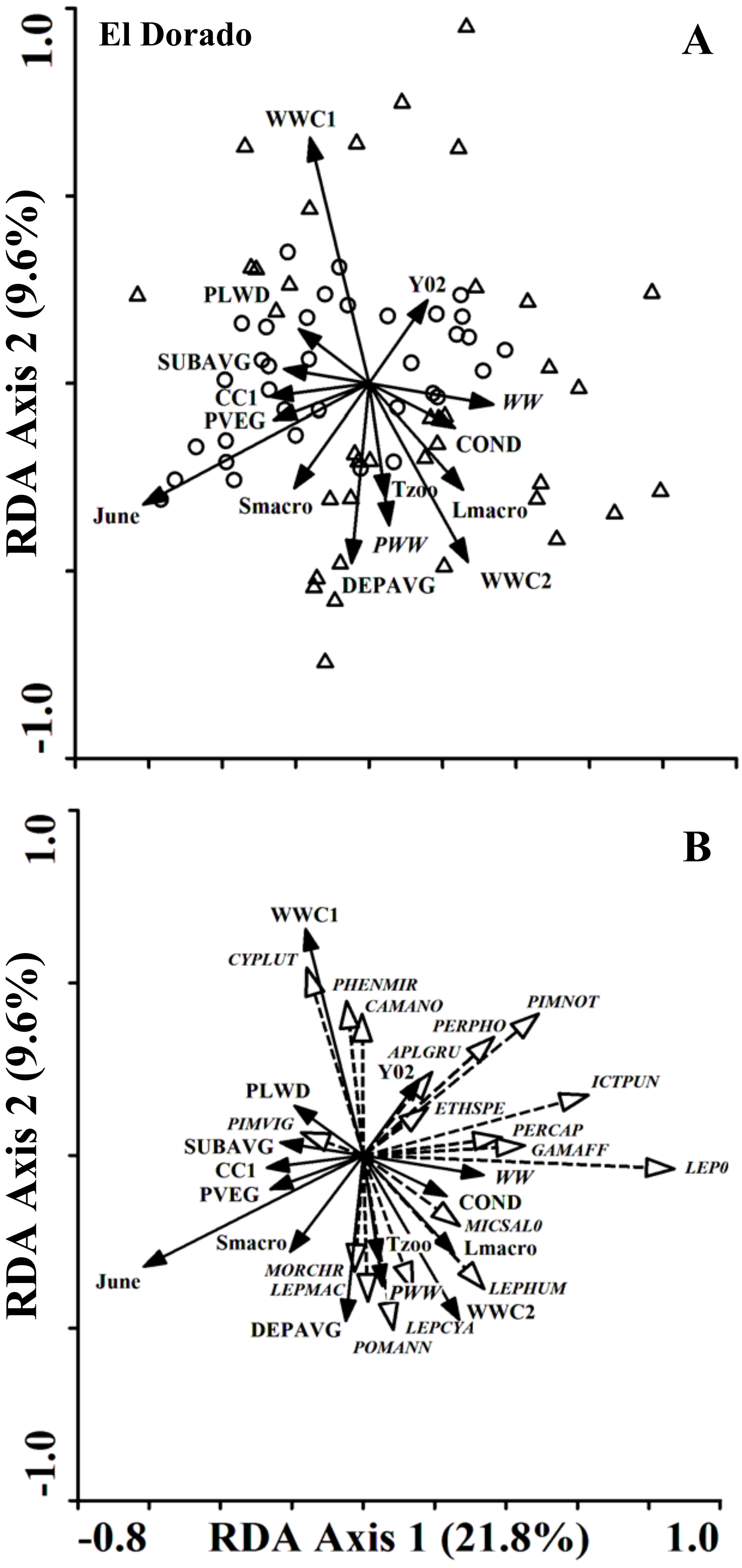


Figure 5.



El Dorado
A
1.0
-1.0
RDA Axis 2 (9.6%)
WWC1
PLWD
Y02
SUBAVG
CC1
PVEG
WW
COND
Tzoo
Lmacro
Smacro
June
PWW
WWC2
DEPAVG
B
1.0
-1.0
RDA Axis 2 (9.6%)
WWC1
CYPLUT
PHENMIR
CAMANO
PIMNOT
PERPHO
APLGRU
Y02
ICTPUN
PLWD
ETHSPE
PIMVIG
PERCAP
GAMAFF
SUBAVG
LEP0
CC1
WW
PVEG
COND
MICSAL0
Smacro
Tzoo
Lmacro
June
MORCHR
LEPMAC
LEPHUM
PWW
WWC2
DEPAVG
LEPCYA
POMANN
-0.8
RDA Axis 1 (21.8%)
1.0

Figure 6.

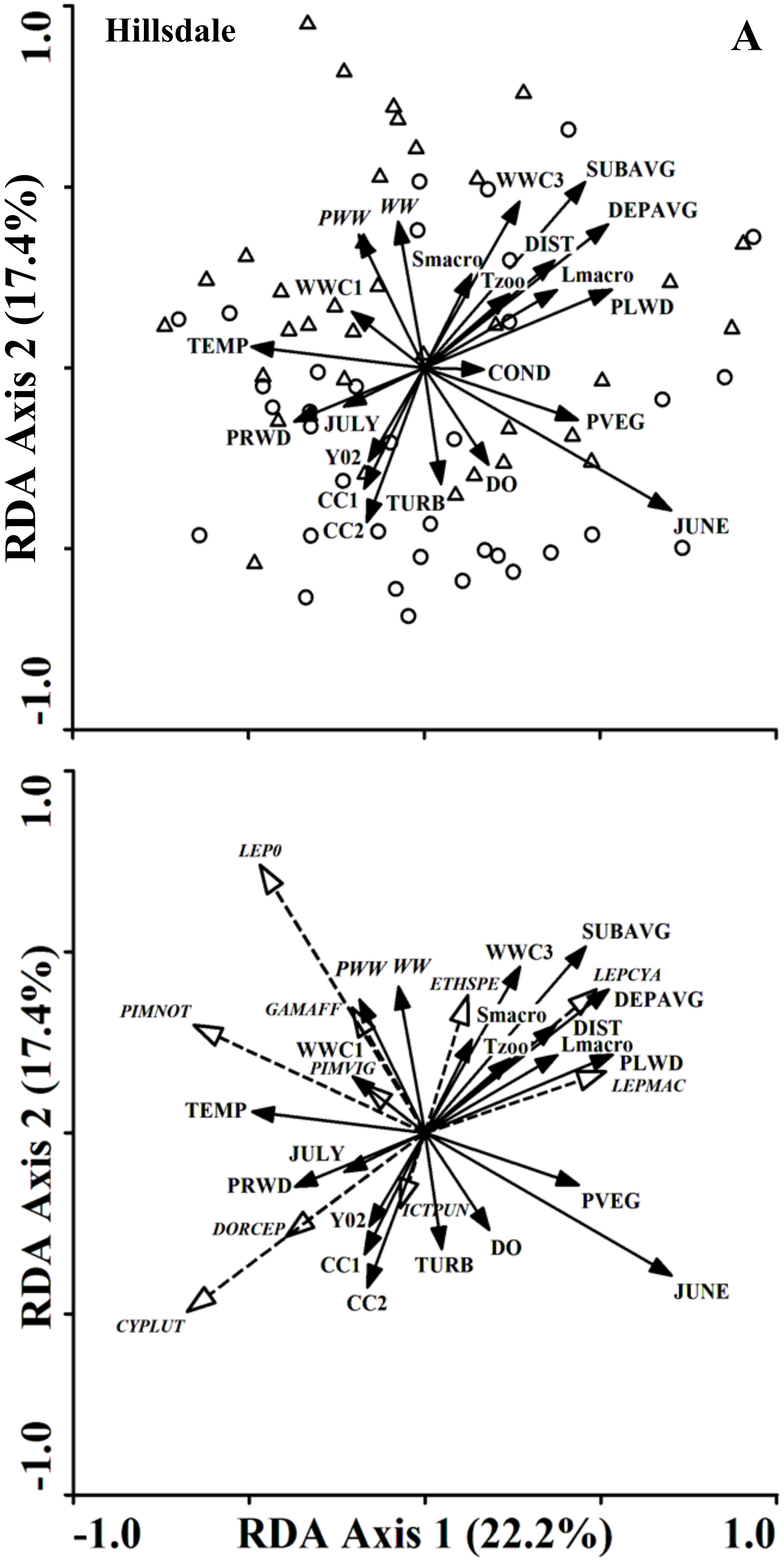
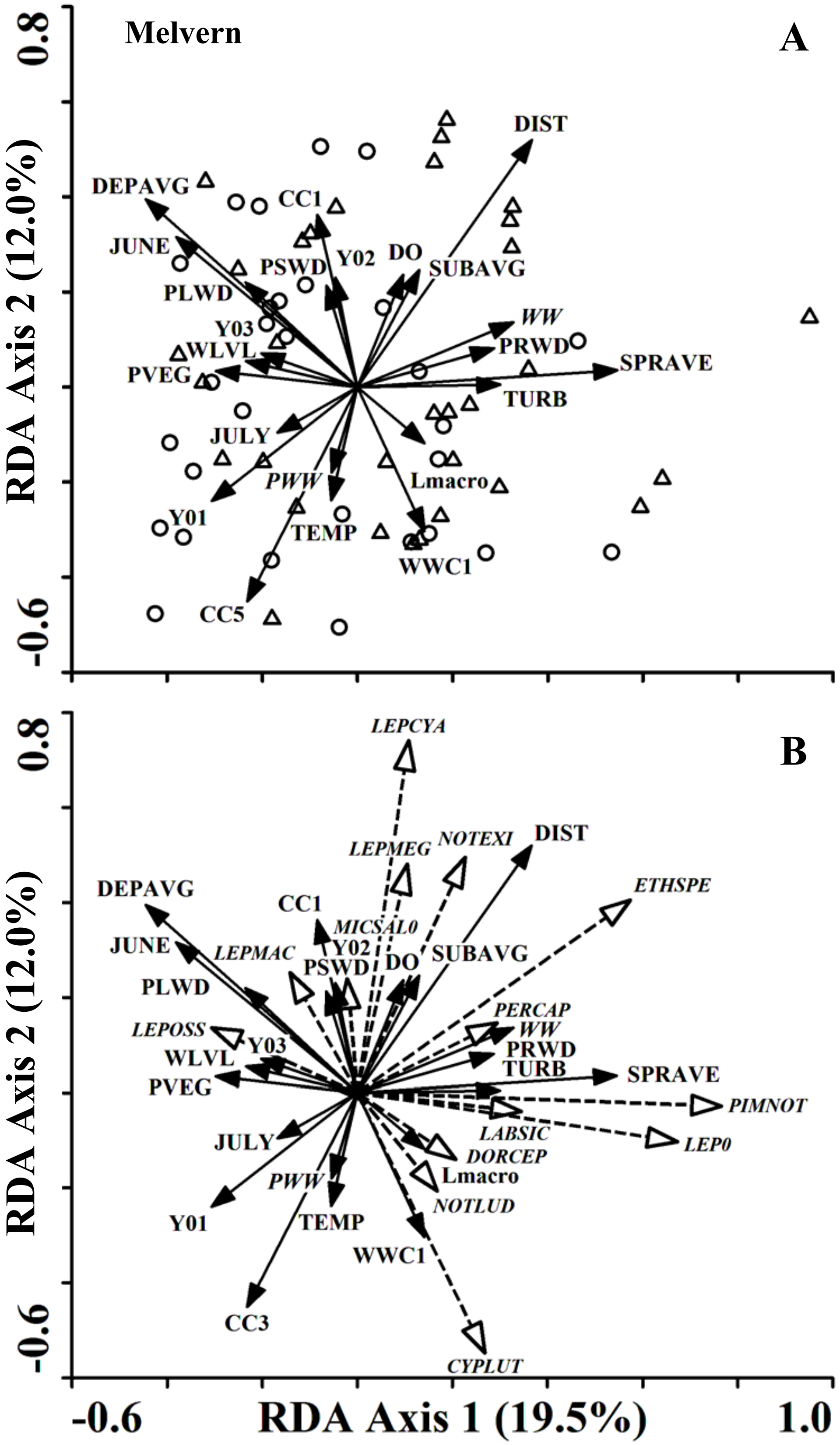

Hillsdale
A
RDA Axis 2 (17.4%)
RDA Axis 1 (22.2%)
1.0
-1.0
SUBAVG
WWC3
DEPAVG
DIST
Lmacro
PLWD
Smacro
Tzoo
PWW
WW
WWC1
TEMP
COND
JULY
PRWD
Y02
CC1
CC2
TURB
DO
PVEG
JUNE
LEP0
PIMNOT
GAMAFF
ETHSPE
LEPCYA
LEPMAC
PIMVIG
ICTPUN
DORCEP
CYPLUT

Figure 7.



Melvern
A
B
RDA Axis 2 (12.0%)
RDA Axis 1 (19.5%)
0.8
-0.6
-0.6
1.0
DIST
DEPAVG
CC1
JUNE
Y02
DO
SUBAVG
PSWD
PLWD
Y03
WLVL
PVEG
WW
PRWD
SPRAVE
TURB
JULY
PWW
Lmacro
Y01
TEMP
WWC1
CC5
CC3
LEPCYA
LEPMEG
NOTEXI
ETHSPE
MICSAL0
LEPMAC
LEPOSS
PERCAP
PIMNOT
LABSIC
LEP0
DORCEP
NOTLUD
CYPLUT

CHAPTER 3

EFFECTS OF AMERICAN WATER WILLOW ESTABLISHMENT ON AGE-0 LARGEMOUTH BASS IN KANSAS IMPOUNDMENTS

ABSTRACT

Many Kansas reservoirs are currently experiencing a decrease in sportfish production coincident with the typical aging processes that occurs in impounded systems. To mitigate these losses American water willow, *Justicia americana*, was planted for littoral zone habitat enhancement, and to increase the recruitment of age-0 largemouth bass *Micropterus salmoides*. I investigated whether density, growth, condition, and diet of age-0 largemouth bass in water willow coves in three large reservoirs (> 1,800 ha) differed from coves without water willow in three large impoundments. I then compared data from water willow coves to two small impoundments (< 90 ha) with dense macrophytes, abundant largemouth bass populations, and stable water levels to compare results from water willow coves to those from "model" systems. Samples were collected from 2001 to 2004 in June, July, and August to estimate age-0 largemouth bass density, growth, condition, and diet. Split plot repeated measures analysis of variances were conducted to test for differences in density, growth, and condition between water willow and control coves, and between large and small reservoirs. Multivariate analysis of variances were used to test for differences in proportions of diet items between water willow and control sites, and between large and small impoundments. Redundancy analysis was also conducted to explore patterns in the diet across treatments. Overall I found a consistent pattern among reservoirs and sample years; water willow coves had significantly greater densities of age-0 largemouth bass than control coves, but no differences were found in growth, condition, or diet. The small impoundments had significantly greater age-0 largemouth bass densities than water willow coves from large reservoirs, but also had lower growth, condition, and frequency of fish in their diet. Ordination revealed that age-0 largemouth bass in water willow coves had more fish in their diet, whereas in small impoundments, bass had a greater proportion of macroinvertebrates in their diet. I also found significant monthly and annual variation in diet that was attributed to age-0 largemouth bass life history traits (i.e., ontogenetic diet shift, natural mortality) and water level fluctuations. My study suggests water willow can be an effective means of enhancing littoral habitat and increasing age-0 largemouth bass densities in reservoirs.

INTRODUCTION

Soon after the initial impoundment, reservoirs undergo an increase in productivity fueled by the release of terrestrial nutrients leached from inundated soils and vegetation (Kimmel and Groeger 1986). Combined with abundant flooded terrestrial vegetation, this trophic upsurge can result in high standing stocks of age-0 (defined as hatch date to 1 January) largemouth bass (*Micropterus salmoides*) and their prey (Shelton et al. 1979). However, over time (5 – 20 yrs) the terrestrial nutrients are flushed from the system and submerged vegetation is reduced, leading to an eventual reduction in productivity. Thus, a negative relation between reservoir age and sportfish abundance is common throughout North America (Kimmel and Groeger 1986; Miranda and Durocher 1986; Ploskey 1986).

Since the 1950s, several manipulations have been tested to prolong the initial high-quality sportfisheries in U.S. reservoirs (Miranda 1996). Increasing water levels are often used to inundate terrestrial vegetation, which increases nutrients, food items and habitat, whereas decreasing water levels are used to concentrate predators and prey (Ploskey 1986; Willis 1986). Several studies have indicated that inundating terrestrial vegetation during spawning and post-spawning periods increased growth and survival of juvenile largemouth bass (Aggus and Elliot 1975; Jenkins 1975; Miranda et al. 1984). However, Kohler et al. (1993) found that fluctuating water levels during the period of largemouth bass spawning negatively impacted hatching success by desiccating eggs during draw downs, and possibly increasing nest predation and nest desertion by male largemouth bass during high water levels. Summer draw downs negatively impact age-0 largemouth bass by forcing them out of cover and into deeper water were they are more vulnerable to predation (Willis 1986; Kohler et al. 1993). Thus, water-level management in reservoirs can offer great potential to increase sportfish production, but the timing and magnitude of water withdraws will likely have a strong influence on littoral zone communities. Unfortunately, water levels in reservoirs are often not controlled by fisheries managers.

Another option to increase sportfish production is habitat enhancement. Brush piles, tire structures, stake beds, standing timber, and rock reefs can be installed to enhance littoral areas (Brown 1986) but are typically costly and only effective for a short duration. A more feasible and long term solution is the planting of aquatic macrophytes (Durocher et al. 1984; Smart et al. 1996; Dick et al. 2004). The establishment of aquatic vegetation can benefit largemouth bass and other littoral organisms, enhance nutrient recycling, and decrease bank erosion (Brown 1986; Dibble et al 1996; Smart et al. 1996;

Summerfelt 1999). However, the success of aquatic macrophytes in reservoirs is highly dependent on the magnitude and timing of water level fluctuations (Strakosh et al. 2005).

Macrophytes can benefit largemouth bass populations by providing cover, increasing foraging efficiency, and augmenting prey abundance, especially for age-0 largemouth bass (Dibble et al. 1996; Wrenn et al. 1996). Several studies have reported a positive association between largemouth bass abundance and abundance of aquatic macrophytes (Dibble et al. 1996; Parkos and Wahl 2002), and Durocher et al. (1984) reported that as submerged vegetation approached 20% of the total lake coverage there was an increase in largemouth bass standing stock (Durocher et al. 1984). The structural complexity provided by macrophytes is a likely mechanism that causes increased largemouth bass densities. For example, macrophytes provide colonizing surfaces for epiphytic bacteria and algae (Dodds 2002), the principal food source of many invertebrates (Baker and Orr 1986) that are consumed by young bass. Macrophyte decomposition also builds organic substrate used by benthic organisms (Beckett et al. 1992). Moreover, shelter from predation and harsh environmental conditions coupled with an increase in food resources can lead to an increase in zooplankton (Quade 1969; Timms and Moss 1984; Moss et al. 1996), macroinvertebrate (Tolonen et al. 2003), and fish (Dibble et al 1996; Smart et al. 1996) abundances and more diverse fish assemblages (Killgore et al. 1989; Keiper et al. 1998; Pierce et al. 2001b). Presumably, high densities of prey in littoral zones with macrophytes would benefit largemouth bass populations, assuming vegetation densities are not sufficiently high to inhibit their foraging success (Wiley et al. 1984).

Many reservoirs remain unvegetated because of insufficient native plant propagules and unsuitable conditions for seedling establishment (Smart et al. 1996). These reservoirs are ideal targets for macrophyte establishment to increase sportfish production and reduce shoreline erosion (Dick et al. 2004). The Kansas Department of Wildlife and Parks (KDWP) currently is evaluating the use of aquatic vegetation to improve largemouth bass production (Marteney 1993). Whereas successfully establishing aquatic macrophytes is often limited by high abundances of herbivores and benthic feeding organisms (e.g., common carp *Cyprinus carpio*) that uproot macrophytes (Cox 1999; Dick et al. 2004; Smart et al. 2005), American water willow *Justicia americana* L. (Vahl.; hereafter water willow), is resistant to these biotic disturbances (Dick et al. 2004).

The majority of the literature on the relations between macrophytes and centrarchids has been specific to submerged vegetation. The effects of water willow, an emergent macrophyte, on largemouth bass interactions, diets, densities, growth, or condition are lacking in the scientific literature. Strakosh (Chapter 2) found that areas with water willow had greater habitat complexity as well as greater diversity and abundance of macroinvertebrates, zooplankton, and fishes. Therefore, I predicted that age-0 largemouth bass in areas with water willow would have higher abundances, growth rates, and condition because of increased habitat complexity and food resources relative to habitats devoid of vegetation.

The introduction of water willow in reservoirs provides an opportunity to assess the impact of a large-scale habitat manipulation. However, the littoral zones in Kansas reservoirs are extremely dynamic, influenced by rapidly changing water levels. Annual and intra-annual variation in precipitation and anthropogenic water level management and can cause large fluctuations in water levels. Therefore, I also sampled two small, stable impoundments that had abundant vegetation and healthy largemouth bass populations, which allowed me to compare my results from water willow coves to those from "model" systems. I tested if age-0 largemouth bass in the small impoundments would have similar densities, growth, diets, and condition to those from water willow coves in large reservoirs.

METHODS

Study Sites

Littoral habitats of three large (1,853 - 3,240 ha) and two small (30 and 87 ha) Kansas impoundments were sampled during June, July, and August from 2001 to 2004 (Figure 1). The three large impoundments were Hillsdale Reservoir, which impounded Big Bull Creek, part of the Osage River system in 1982; Melvern Reservoir, which impounded the Marais des Cygnes River in 1972; and El Dorado Reservoir, which impounded the Walnut River in 1981. All three reservoirs were primarily built for flood control, but support important recreation and wildlife areas. These reservoirs were selected because they are part of the Kansas Department of Parks and Wildlife habitat enhancement project to stabilize shoreline erosion and increase sportfish production through water willow establishment. Prior to water willow establishment these reservoirs were mostly devoid of aquatic macrophytes.

In each reservoir, coves were identified based on visual inspection of field and aerial photographs. Of these, six coves that were similar in physical and habitat characteristics were randomly selected for my study in each reservoir. In Hillsdale and Melvern reservoirs, three of the six coves were randomly selected for water willow establishment one year prior to sampling, the remaining three coves served as controls. Water willow used for plantings were > 0.5 m tall, exhibited no visible signs of stress (i.e., yellowing leaves, broken stalks, insect infestations), and had the majority of the root system intact. Individuals were planted 0.4 m apart in rows parallel to shore every 1.8 m. In El Dorado Reservoir water willow establishment began in 1996 as part of a vegetation pilot study. Therefore, three coves were randomly chosen from a pool of coves with existing water willow stands, and control coves were randomly chosen from a pool of coves without vegetation.

The two small impoundments had > 20 % aquatic macrophyte coverage, stable water levels, and abundant largemouth bass populations (Strakosh, personal observation). Pottawatomie State Fishing Lake Number 2 (Pot2) was built in 1955 for recreation and wildlife habitat. Lake Wabaunsee was constructed as part of a water conservation project finished in 1939 and serves as a municipal water supply. Fish communities consisted primarily of centrarchids and ictalurids.

Sampling

All coves were sampled three times each summer (June, July, and August) from 2001 through 2004. Two sampling locations within each cove were randomly selected (without replacement within a given year) for sampling each month. Lake Wabaunsee and Pot2 were sampled at two randomly selected shoreline locations (without replacement within a given year) and sampled identically to the large impoundments. All sampling was conducted between 0800 and 2100 hrs.

Sampling methods followed Schoenebeck et al. (2005). At each sampling location a 30.6 m long by 2.0 m high block net (3.2 mm bar-mesh) was used to enclose a 149 m^2 (24.5 m by 6.1 m) area parallel to shore. Prior to setting up the block net dissolved oxygen (mg/L), conductivity (µs/cm), temperature (^oC), and turbidity (NTU) were measured in the center of the sampling area using a YSI model 85 (Yellow Springs Instruments, Yellow Springs, Ohio) and an Orbeco-Hellige turbidity meter. The block net was carefully maneuvered into position to minimize disturbance of fishes, secured to the bottom using poles and weights, and then inspected for any gaps.

Age-0 largemouth bass were sampled using a Smith-Root Model 15-C backpack electrofishing unit (Smith-Root, Vancouver, Washington; 200-300 V pulsed-DC). Sampling was conducted at frequency of 60 Hz and a 48% duty cycle. A two-person crew thoroughly covered all habitats within each enclosure with one person electrofishing and netting and another person netting. Sampling effort was standardized by area (149 m^2) and shock time (seconds; duration of electric current application) to ensure that consecutive runs within an enclosure were sampled with approximately equal effort. To match the sampling protocol by Tripe (2000) in El Dorado Reservoir, multiple passes were conducted until an obvious depletion rate (i.e. each consecutive run was < 1/2 the number of fish of the previous run) was achieved, with a minimum of 3 and a maximum of six runs. The maximum likelihood (ML) method assuming constant probability of capture (Zippin 1956) was used to density (fish/m^2) of age-0 largemouth bass. Only one run was performed if no age-0 largemouth bass were caught on the first pass. It is important to note that ML population estimates for complex habitats tend to underestimate population size (Peterson et al. 2004), thus enclosures with greater habitat complexity (i.e., water willow) may have higher densities than I report.

Age-0 largemouth bass were placed on ice and brought to the lab for analysis of diet, growth, and condition. Diet of age-0 largemouth bass was quantified to test for differences between water willow and control coves. Stomachs of age-0 largemouth bass were removed and contents fixed in 10% formalin solution, rinsed in water, and stored in 70% alcohol (Bowen 1996). Stomach contents were identified (when possible) to species for fish, and families for macroinvertebrates and zooplankton. Frequency of occurrence and percent composition by area were calculated for each fish to quantify food habits. Percent composition was obtained by separating food items on a grid of 1 mm by 1 mm squares and recording the area occupied by each food item, which was used as a surrogate for mass (Hellawell and Abel 1971).

Daily growth rings on sagittal otoliths from age-0 largemouth bass were used to test if growth rates differed between water willow and control coves. Otolith removal and preparation followed Secor et al. (1992). Otoliths were mounted on a glass slide with thermoplastic cement and polished if necessary (Isley et al. 1987; Secor et al. 1992). Daily growth rings were examined from five fish per 5 mm length class from each cove from each month (Tripe 2000). Approximate hatch date was calculated following Tripe (2000) as: Date of capture - (Age of fish at swim up + 5 days).

Residualized dry weight (RDW) was used as an index of condition following Sutton et al. (2000). Condition (RDW) was calculated by modeling dry weight as a function of the weight-length equation (weight = aL^b). The intercept (a) and the slope (b) were estimated based on the equation: $\log_{10}(DW) = \log_{10}(a) + b * \log_{10}(L) + RDW$.

Sutton et al. (2000) obtained the RDW from the fitted model residuals, which represents the variation in dry weight after controlling for variation in length. The RDW was chosen because it does not have growth rate assumptions (e.g., Fulton's condition factor), controls for length biases, is highly correlated with percent total fat ($r^2 = 0.58$; $P < 0.001$), and is less time consuming and costly than full lipid analysis (Sutton et al. 2000). Additionally, residual variation in the relationship between RDW and percent total fat is likely due to protein mass, which is a large component of fish dry weight and utilized for energy after lipid depletion.

Data Analyses

Data from the two sampling sites within each cove for a given time period were pooled for all analyses. All variables were tested for normality using the Kolmogorov-Smirnov and Shapiro-Wilk statistics and homogeneity of variances was examined using Levene's Statistic (SPSS 2001). Abundance data were $\log_{10}$ transformed and percent coverage measurements were square-root arcsine transformed if necessary.

Split plot/repeated measures analyses of variances (SPRANOVA) were used to test for overall differences between water willow and control coves for age-0 largemouth bass densities, growth rates, and RDW (dependent variables). The reservoirs were blocks, whole-plot treatments were water willow versus control coves, and individual coves were the sub-plots. The repeated measures were years and months. Analyses were performed using mixed model analysis (PROC MIXED) in the statistical software package SAS version 8.01 (SAS Institute 2000). Unlike the general linear models, PROC MIXED takes into account correlations among observations and non-constant variability (Littell et al. 1996). Tests of hypotheses were conducted with the Type III Tests of fixed effects, and fit statistics provided by SAS were used to choose the most appropriate covariance matrix structure for the analyses (Milliken and Johnson 1998). Correct degrees of freedom were calculated using the Satterthwaite method (Littell et al. 1996, Milliken and Johnson 1998). Contrast statements were set *a priori* and used to explore significant differences and interactions.

Multivariate analysis of variances (MANOVAs) were conducted to investigate if food habits of age-0 largemouth bass differed between water willow and control coves, and between water willow coves in the large reservoirs and littoral habitats of small impoundments. Diet items that occurred in < 5% of age-0 largemouth bass stomachs were pooled into higher taxonomic groups. A general macroinvertebrate category was created to incorporate infrequent macroinvertebrates and stomach contents that I was unable to be identified to a lower taxonomic level. This general category allowed me to contrast fish that generally foraged on invertebrates, and those foraging on zooplankton or fish, which I felt more accurately reflected ontogenetic changes in diet. A total of 8 categories were used in my diet analyses; zooplankton, fish, Ephemeroptera, Hemiptera, Corixidae (Hemiptera), Chironomidae (Diptera), Amphipoda, and general macroinvertebrates. The dependent variables were the arcsine transformed percent composition by area for each diet category. In the large impoundment models the fixed effects were year (four levels; 2001-2004), month (three levels; June, July August), reservoir (three levels; El Dorado, Hillsdale, and Melvern), and water willow (two levels; water willow and non-water willow coves). The MANOVA comparing large and small impoundments the fixed effects were year (four levels; 2001-2004), month (three levels; June, July August), and reservoir (two levels; El Dorado, Hillsdale, Melvern, Pot2, and

Lake Wabaunsee). Wilk's Lambda was used to calculate the multivariate F-statistic (SPSS 2001).

If the overall MANOVAs were significant, redundancy analyses (RDAs) were conducted to explore variation in food habits among samples within each reservoir. Environmental variables for this analysis included spatial (e.g., water willow or control cove, etc.) and temporal (year, month) components as well as the length of individual largemouth bass. The RDA scaling focused on the inter-species correlations and was centered by dividing species scores by their standard deviation (Legendre and Legendre 1998; ter Braak and Simlauer 2002). Monte Carlo simulations were conducted (1000 permutations) to test if axes were significantly different ($P < 0.05$) from random (Legendre and Legendre 1998; ter Braak and Simlauer 2002). Biplots of diet items and environmental variables were used to characterize the variation in age-0 largemouth bass food habits.

Alpha levels set at 0.10 a priori and Type III sums of square were used in all ANOVAs. The false discovery rate (Benjamini and Hochberg 1995) was employed to control Type I and Type II error rates for the multiple tests. Similar to the sequential Bonferroni (Hochberg 1988), the P-values were ranked in ascending order ($P_{(1)} < P_{(2)} <\ldots P_{(m)}$ and compared to $((\alpha * i)/ m)$, where i = rank of P-value and m is the total number of tests. Reject the null hypothesis (H_i) when $P_i < ((\alpha * i)/ m)$ and all others with smaller P-values (Benjamini and Hochberg 1995; Verhoeven et al. 2005). Type III sums of square were used in all analyses.

RESULTS

Water Willow versus Control Coves

Over all large impoundments, age-0 largemouth bass were twice as abundant in water willow (584 ± 1254 [number/ha; mean ± SD]; N = 210) than in control coves (232 ± 502; N = 210) ($P = 0.001$, Tables 1 and 4). This effect was consistent through time and space (Figure 2), as there were no interactions between cove type and other main effects. Growth (mm/day) of age-0 largemouth bass was highly variable between water willow and control coves (Figure 3), and although a significant year by water willow treatment interaction (Table 4) was found, the contrast statements indicated no significant difference between water willow and control coves when compared within years ($P > 0.07$). Control coves in 2004 had significantly ($P < 0.002$) higher growth rates than those found in other years. No significant differences were found in age-0 largemouth bass condition between water willow and control coves (Tables 3, 4; Figure 4).

All reservoirs had significant annual and monthly variation in age-0 largemouth bass density, growth, and condition. Hillsdale had the highest densities, up to an order of magnitude greater than other reservoirs (Table 1). The highest abundances generally were found in June and decreased through August, but this pattern varied among years. No consistent pattern was found for growth or condition (Tables 2, 3).

No significant differences in diet were found between water willow and control coves (MANOVA; Wilk's lambda= 0.554, $F_{8,71} = 0.8$, $P = 0.05$). However, diet differed significantly among reservoirs, years (MANOVA, Reservoir by Year; Wilk's lambda= 0.311, $F_{48,353} = 1.971$, $P < 0.001$) and months (MANOVA, Reservoir by Month; Wilk's lambda= 0.484, $F_{32,263} = 1.791$, $P = 0.007$).

The amount of variation in age-0 largemouth bass diets explained by the first two axes of the RDAs was 16.4%, 17%, and 10.% for El Dorado, Hillsdale, and Melvern respectively (Figures 5-7), and axes were significantly different than random (P < 0.01; Monte Carlo simulations). Water willow explained relatively little variation in diet, which varied over months and years. In El Dorado (Figure 5) and Melvern (Figure 7), water willow was weakly associated with chironomids, zooplankton, and June, but this varied among years. A monthly pattern accounted for the greatest variation among individuals and was related to age-0 largemouth bass consuming zooplankton in June and consuming fish in August. Thus, Axis 1 for all the large reservoirs represents the intra-annual variation related to ontogenetic diet shifts for age-0 largemouth bass. The frequency of occurrence of zooplankton in largemouth bass stomachs supported this pattern, and was 59% in June, 19 % in July, and 7% in August, averaged across the three large impoundments. Conversely, frequency occurrence of fish in June was 6%, 23% in July, and 43% in August. In Melvern the separation along Axis 1 of zooplankton and macroinvertebrates was not as pronounced. Rather, Axis 2 showed inter-annual variation in diet, especially macroinvertebrates, indicated by the heavy year loadings along this axis. In El Dorado, general macroinvertebrates in diet contents were positively associated with 2003 and negatively related to 2002. In contrast, they were positively associated with 2002 for Hillsdale and Melvern. Zooplankton and chironomids were also commonly associated, and the frequency of occurrence of chironomids in largemouth bass diets followed the same pattern found for zooplankton decreasing throughout the summer; 47% (June), 18% (July), and 4% (August).

Large versus Small Impoundments

Overall, abundance of age-0 largemouth bass in Pot2 and Lake Wabaunsee were significantly higher compared to water willow coves in the large reservoirs (Figure 8), but this pattern varied among months and years (Tables 1 and 5). In contrast, age-0 largemouth bass growth rates, overall, were higher in large reservoirs (Figure 8), but significantly varied among years and reservoirs (Tables 2 and 5; Figure 8). Condition was often lower in small impoundments, but there was also considerable variation among reservoirs through time ($P < 0.0001$; Tables 3 and 5). Overall, small impoundments had higher amounts of vegetation (Table 7) than the large reservoirs (Strakosh Chapter 2).

Age-0 largemouth bass diets exhibited significant variation among reservoir type (small impoundment versus large reservoirs), years, and months (MANOVA, Reservoir by Year by Month; Wilk's lambda= 0.769, $F_{136, 6945} = 1.87$, $P < 0.0001$). The RDAs for Pot2 and Wabaunsee indicated similar patterns to the large reservoirs. Largemouth bass length and June were heavily loaded on Axis 1 in both RDAs. Also like the large impoundments annual variation was associated with Axis 2. However, macroinvertebrates were more closely associated with length than fish, and macroinvertebrates also had heavier loadings along Axis 1. The occurrence of fish in the diet of age-0 largemouth bass also exhibited higher annual variation in the small impoundments than in the large reservoirs. In addition, the frequency of occurrence of fish in the diet of largemouth bass in the small impoundments was 2% (June), 8% (July), and 5% (August) compared to 6% (June), 21% (July), and 42% (August) in the large impoundments.

DISCUSSION

Water Willow versus Control Coves

My data support the prediction that water willow coves would have greater densities than control coves, but did not show significant differences in growth, condition, or diet between cove treatments. The larger densities of age-0 largemouth bass in areas with water willow concurs with previous studies that found that age-0 largemouth bass abundance was positively related to habitat complexity and vegetation (Aggus and Elliot 1975; Annett et al. 1996; Dibble et al. 1996; Wrenn et al. 1996). Mechanisms associated with the increase age-0 largemouth bass abundance include predation refuge, increasing foraging efficiency, and augmenting prey abundance (Dibble et al. 1996; Wrenn et al. 1996). I not only found greater densities of prey items (fish and invertebrates) in water willow coves, but also significantly greater amounts of woody debris and riparian vegetation, increasing the overall availability of complex habitat (Strakosh Chapter 2).

Greater densities of age-0 largemouth bass in water willow coves did not correspond to changes in growth, condition, or diet. These results suggest that water willow is able to support greater densities of age-0 largemouth bass without a negative effect on growth or condition. Other studies have found both positive and negative effects of increased vegetation and age-0 largemouth bass abundance (Parkos and Wahl 2002). Miranda and Pugh (1997) found that growth was highest in coves with 10-20% vegetation coverage. In contrast, Wrenn et al. (1996) reported that age-0 largemouth bass in vegetated habitats had lower growth rates than those in areas without vegetation. They attributed this difference to an increase in competition in vegetated sites, less piscivory, and reduced feeding efficiency because of structural complexity. Schindler et al. (1997) also documented that largemouth bass condition was negatively related to population size, but did not find any differences in diet composition. Conflicting study results could be due to variation in quality and quantity of food resources among sites.

Water willow coves were found to have a greater abundance and diversity of zooplankton, macroinvertebrate, and fish than areas without water willow (Strakosh Chapter 2), and therefore may able to support greater densities of age-0 largemouth bass without negatively impacting growth or condition. Conversely, the increased diversity and abundance of other fishes in water willow areas may increase competitive interactions with age-0 largemouth bass. Largemouth bass are morphologically designed as a piscivore, and is a less efficient planktivore or insectivore relative to other fishes (Helfman et al. 1997). Because of this, age-0 largemouth bass are easily out competed when feeding on zooplankton or macroinvertebrates (Werner and Gilliam 1984). The potential increase in competition between age-0 largemouth bass and other fishes could have resulted in the similar growth rates between water willow and control coves in my study.

Age-0 largemouth bass in the large impoundments exhibited strong monthly and annual variation in densities, which are likely attributed to water level fluctuations and life history characteristics. Age-0 largemouth bass densities were usually highest in June, corresponding with the end of the spawning period. Differences between water willow and control coves were also greatest in June. These large differences are likely due to elevated spring water levels and the significantly greater amounts of inundated riparian vegetation in water willow than control coves (Strakosh et al. 2005). Several studies have found strong positive relationships between age-0 largemouth bass abundance and flooded terrestrial vegetation (Aggus and Elliot 1975; Jenkins 1975; Miranda et al. 1984), which provides increased food resources and nursery habitat. However, spawning success of largemouth bass populations is also vulnerable to water level fluctuations, which could effect densities of age-0 fish in these habitats. Low or falling water levels can negatively impact hatching success by desiccating eggs, possibly increase nest predation, and causing nest desertion by male largemouth bass (Kohler et al. 1993).

Data from Hillsdale Reservoir illustrate the strong effect of water level fluctuations and their interactions with water willow in regulating largemouth bass population dynamics. In June of 2003, Hillsdale had the lowest bass densities recorded for that reservoir, and this corresponded to low water levels (mean water level [± 1 SD] from March through June of 2003 was -1.0 m ± 0.14; US Army Corp of Engineers, Kansas City District). The water level remained below conservation pool from 1 July 2002 until March of 2004, allowing abundant riparian vegetation to establish along the shoreline of Hillsdale. The vegetation was inundated prior to the 2004 largemouth bass spawning period (late March through early June; Tripe 2000), resulting in the highest age-0 largemouth bass densities I recorded among large reservoirs. Additionally, water willow coves had densities five times greater than controls (Table 1; Figure 2). This difference may be due to water willow areas having greater structural complexity and organic material produced from consistent vegetative cover (Strakosh Chapter 2). Additionally, water willow probably suffered little or no mortality from water level decreases due to its desiccation tolerance (Strakosh et al. 2005). Paller (1997) found that inundated terrestrial vegetation coupled with pockets of aquatic macrophytes facilitated the recolonization of littoral areas by fishes. Therefore, water willow also may promote fish movement back into littoral areas after low water periods by providing cover and organic resources.

Water levels consistently and predictably declined throughout the summer, reducing the amount of inundated cover, which coincided with reduced densities of age-0 largemouth bass. Decreasing water levels can force age-0 largemouth bass out of shallow cover and into deeper water were they are more vulnerable to predation (Willis 1986; Kohler et al. 1993). Additionally, densities of other littoral fishes (e.g., *Lepomis* spp.) significantly increased from June to August. This increase in littoral fishes coupled with decreasing emergent macrophyte habitat could intensify organism interactions within littoral areas. These interactions may be more significant in the fall months when age-0 largemouth bass store lipids preparing for winter (Ludsin and DeVries 1997). However, if age-0 largemouth bass growth is sufficient to exceed gape limitations, they will become piscivorous by August and may benefit from concentrated forage fishes.

During the first year of life, largemouth bass go through ontogenetic changes in diet from planktivory to insectivory and finally to piscivory (Keast and Eadie 1985; Olson 1996). This pattern was also exhibited within the RDAs for the three large impoundments (Figure 5-7) and was further supported by the frequency of occurrence of fish in bass diets (Table 6). Despite the greater proportion of fish in the diet of age-0 largemouth bass from water willow coves in August no increases in growth or condition were observed. The first year of growth may be critical for largemouth bass because it has been linked to over winter survival (Ludsin and Devries 1997). Larger age-0 largemouth bass tend to have an increased chance of recruiting to age-1 (Isely et al. 1987;

Goodgame and Miranda 1993; Miranda and Hubbard 1994a, 1994b; Phillips et al. 1995). Increased survival of these larger bass is likely due to greater lipid reserves (Thompson et al. 1991; Miranda and Hubbard 1994a; Ludsin and DeVries 1997; Fullerton et al. 2000). Also, Miranda and Hubbard (1994b) found that in the presence of predators, age-0 largemouth bass > 126 mm had an 80% greater survival rate than bass < 126 mm. Because I found no difference in growth or condition between water willow and control coves, it does not appear that water willow will influence ontogenetic shifts in diet thereby effecting over winter survival.

Large versus Small Impoundments

I also predicted that age-0 largemouth bass in vegetated small impoundments would have similar densities, growth, diets, and condition as those in water willow coves in the large impoundments. Whereas largemouth bass were considerably more abundant in the small impoundments, they also had lower growth rates and condition than those in the large reservoirs. Bass in large impoundments were more piscivorous. High densities of age-0 largemouth bass in the small impoundments may be negatively effecting growth and condition, which could lead to decreased piscivory. Studies have found a negative relationship between age-0 largemouth bass density and growth (Miranda et al. 1984; Olson 1996; Garvey et al. 2000), as well as density and condition (Schindler et al. 1997;Wrenn et al. 1996; Parkos and Wahl 2002). In these cases the high densities delays the ontogenetic diet shift from macroinvertebrates to fish through competitive interactions, thereby decreasing growth (Olsen 1996; Garvey et al. 2000) and condition (Wrenn et al. 1996; Parkos and Wahl 2002). In contrast to the large reservoirs, age-0 largemouth bass in the small impoundments preyed mostly upon macroinvertebrates and few fish, even in August (Table 6). Age-0 largemouth bass have substantially greater growth rates feeding on fish than on invertebrates (Aggus and Elliot 1975; Miranda and Hubbard 1994a; Ludsin and Devries 1997). Olson (1996) did find that in Michigan lakes some largemouth bass grew rapidly during the invertebrate feeding stage. These fish were able to gain a size advantage over age-0 bluegill, shift to piscivory, and then utilize the age-0 bluegill for food. The lack of fish in the age-0 largemouth bass diet could be due intra-specific competition, but other studies have found that submergent macrophytes can also influence diet (Bettoli et al. 1992; Hayse and Wissing 1996).

Decreased growth and condition of largemouth bass in small impoundments could also be attributed to inhibited foraging efficiency in dense vegetation (Bettoli et al. 1992; Hayse and Wissing 1996). Wrenn et al. (1996) found that age-0 largemouth bass from vegetated sites were smaller and had reduced growth rates, which they attributed to high competition in vegetated sites, a diet low in fish, and reduced feeding efficiency because of structural complexity. They also reported density dependent effects when age-0 largemouth bass were > 300 fish/ha, considerably lower than Pot2 (5329 fish/ha) or Lake Wabaunsee (2287 fish/ha). The high densities of age-0 largemouth bass in the small impoundments negatively effected their growth and condition, thereby decreasing the chance of over winter survival and limiting the number that recruit to age-1 (Isely et al. 1987; Goodgame and Miranda 1993; Miranda and Hubbard 1994a, 1994b; Phillips et al. 1995).

Management Implications

Whereas the majority of research has been conducted on the effects of submergent macrophytes on age-0 largemouth bass, little work has been done on emergent vegetation. I found that water willow established in coves supported significantly greater abundances of age-0 largemouth bass without incurring negative impacts on growth or condition associated with density dependent mechanisms. This finding indicates that water willow increased the age-0 largemouth bass carrying capacity of the littoral zones where it was established. Additionally, because water willow is limited to a shallow depth distribution (< 1.2 m) it will not be able to colonize the entire lake, impacting the system like has been documented for submergent vegetation (Smart et al., 1996). However, due to its susceptibility to inundation its establishment should be limited to reservoirs with fairly stable water levels (Strakosh et al. 2005).

Table 1.—Age-0 largemouth bass densities (number/ha; mean [minimum, maximum]) for Kansas impoundments (N = 468 sites sampled). (*) Stocking of largemouth bass fingerlings occurred in late June of 2004.

Reservoir	**Year**	**June**		**July**		**August**	
		Water Willow	**Control**	**Water Willow**	**Control**	**Water Willow**	**Control**
El Dorado	**2001**	315 (0, 677)	0 (0, 0)	90 (0, 205)	112 (0, 336)	0 (0, 0)	11 (0, 67)
	2002	369 (0, 939)	45 (0, 268)	115 (0, 270)	251 (0, 603)	281 (0, 603)	136 (0, 342)
	2003	67 (0, 268)	78 (0, 335)	246 (0, 804)	134 (0, 335)	112 (0, 201)	78 (0, 335)
	2004*	45 (0, 134)	22 (0, 134)	78 (0, 201)	0 (0, 0)	123 (0, 268)	223 (0, 469)
Hillsdale	**2001**	1235 (0, 2243)	259 (0, 939)	575 (0, 1225)	413 (67, 1228)	375 (201, 738)	112 (0, 268)
	2002	1823 (0, 4496)	1937 (404, 3698)	1345 (134, 2619)	536 (134, 1609)	718 (134, 1156)	296 (103, 536)
	2003	0 (0, 0)	45 (0, 201)	994 (0, 2212)	559 (134, 1206)	168 (0, 469)	101 (0, 201)
	2004	5071 (1609, 11595)	1039 (0, 2882)	961 (469, 2145)	357 (67, 737)	525 (0, 1139)	570 (0, 1542)
Melvern	**2001**	NA	NA	321 (0, 941)	22 (0, 134)	250 (0, 692)	68 (0, 134)
	2002	850 (0, 2951)	168 (0, 469)	207 (67, 432)	148 (0, 351)	399 (206, 647)	197 (0, 336)
	2003	1139 (0, 4088)	89 (0, 268)	89 (0, 201)	11 (0, 67)	56 (0, 201)	34 (0, 67)
	2004	67 (0, 402)	11 (0, 67)	56 (0, 201)	0 (0, 0)	134 (0, 335)	56 (0, 134)

Table 1.—Continued.

Reservoir	**Year**	**June**		**July**		**August**	
		Water Willow	**Control**	**Water Willow**	**Control**	**Water Willow**	**Control**
Pot 2	**2001**	4591 (3016, 6166)	11059 (8177, 13941)	4725 (3686, 5764)	4591 (3016, 6166)	11059 (8177, 13941)	4725 (3686, 5764)
	2002	10523 (3820, 13874)	7138 (4625, 9651)	2882 (2480, 3284)	10523 (3820, 13874)	7138 (4625, 9651)	2882 (2480, 3284)
	2003	67 (0, 134)	1977 (1072, 2882)	670 (536, 804)	67 (0, 134)	1977 (1072, 2882)	670 (536, 804)
	2004	3820 (2480, 5161)	1810 (670, 2949)	134 (134, 134)	3820 (2480, 5161)	1810 (670, 2949)	134 (134, 134)
Wabaunsee	**2001**	1642 (1206, 2078)	4725 (4223, 5228)	1843 (1475, 2212)	1642 (1206, 2078)	4725 (4223, 5228)	1843 (1475, 2212)
	2002	2513 (1408, 3619)	871 (536, 1206)	402 (201, 603)	2513 (1408, 3619)	871 (536, 1206)	402 (201, 603)
	2003	1273 (1139, 1408)	1005 (938, 1072)	1206 (804, 1609)	1273 (1139, 1408)	1005 (938, 1072)	1206 (804, 1609)
	2004	3720 (268, 7172)	804 (536, 1072)	536 (536, 536)	3720 (268, 7172)	804 (536, 1072)	536 (536, 536)
Grand Mean							
El Dorado		199 (0, 939)	36 (0, 335)	132 (0, 804)	124 (0, 603)	129 (0, 603)	112 (0, 469)
Hillsdale		2032 (0, 11595)	820 (0, 3698)	969 (0, 2619)	466 (67, 1609)	447 (0, 1156)	270 (0, 1542)
Melvern		685 (0, 4088)	89 (0, 469)	168 (0, 941)	45 (0, 351)	210 (0, 692)	89 (0, 336)
Pot 2		5392 (0, 13874)	5496 (670, 13941)	2103 (134, 5764)	5392 (0, 13874)	5496 (670, 13941)	2103 (134, 5764)
Wabaunsee		2287 (268, 7172)	1852 (536, 5228)	997 (201, 2212)	2287 (268, 7172)	1852 (536, 5228)	997 (201, 2212)

Table 2.—Age-0 largemouth bass growth rates (mm/day) for Kansas impoundments. Values are the mean (minimum, maximum) from 1738 individuals.

Reservoir	**Year**	**June**		**July**		**August**	
		Water Willow	**Control**	**Water Willow**	**Control**	**Water Willow**	**Control**
El Dorado	**2001**	0.59 (0.49, 0.75)	0.76 (0.76, 0.76)	0.5 (0.43, 0.66)	0.6 (0.47, 0.73)	NA	NA
	2002	0.76 (0.56, 1.04)	0.75 (0.65, 0.85)	0.79 (0.61, 0.88)	0.79 (0.6, 0.95)	0.79 (0.6, 0.91)	0.79 (0.52, 0.94)
	2003	0.77 (0.57, 0.88)	0.79 (0.58, 0.9)	0.72 (0.56, 0.89)	0.73 (0.53, 1.08)	0.65 (0.59, 0.73)	0.71 (0.61, 0.84)
	2004	0.7 (0.54, 0.89)	0.77 (0.66, 0.84)	0.87 (0.87, 0.87)	NA	0.72 (0.6, 0.82)	0.86 (0.86, 0.86)
Hillsdale	**2001**	0.76 (0.57, 0.9)	0.76 (0.55, 0.89)	0.76 (0.59, 0.92)	0.75 (0.6, 0.92)	0.66 (0.53, 0.88)	0.69 (0.5, 0.91)
	2002	0.78 (0.62, 1)	0.79 (0.55, 1.06)	0.66 (0.46, 0.95)	0.72 (0.55, 0.89)	0.52 (0.38, 0.71)	0.56 (0.44, 0.76)
	2003	NA	0.88 (0.78, 1)	0.78 (0.54, 1.07)	0.82 (0.6, 1.03)	0.77 (0.63, 0.91)	0.87 (0.66, 1.02)
	2004	0.77 (0.6, 0.95)	1.05 (1.04, 1.05)	0.73 (0.53, 0.98)	NA	0.65 (0.51, 0.83)	0.7 (0.53, 0.9)
Melvern	**2001**	NA	NA	0.77 (0.62, 0.9)	NA	0.76 (0.54, 0.9)	0.76 (0.58, 0.87)
	2002	0.88 (0.74, 1.07)	0.85 (0.78, 0.97)	0.74 (0.57, 1.06)	0.78 (0.65, 0.91)	0.7 (0.47, 0.87)	0.68 (0.54, 0.82)
	2003	0.71 (0.58, 0.89)	0.69 (0.63, 0.74)	0.79 (0.58, 1.13)	0.84 (0.84, 0.84)	0.83 (0.75, 0.89)	0.77 (0.67, 0.85)
	2004	0.77 (0.77, 0.77)	NA	0.76 (0.59, 1.03)	NA	0.76 (0.59, 1.03)	0.73 (0.6, 0.85)

Table 2.—Continued

Reservoir	Year	June		July		August	
		Water Willow	**Control**	**Water Willow**	**Control**	**Water Willow**	**Control**
Pot 2	**2001**	0.66 (0.41, 0.9)		0.56 (0.39, 0.83)		0.52 (0.4, 0.67)	
	2002	0.81 (0.7, 1)		0.59 (0.43, 0.78)		0.53 (0.39, 0.63)	
	2003	0.75 (0.65, 0.84)		0.68 (0.49, 0.96)		0.53 (0.46, 0.61)	
	2004	0.72 (0.58, 0.94)		0.72 (0.51, 1.09)		0.83 (0.83, 0.83)	
Wabaunsee	**2001**	0.76 (0.55, 0.93)		0.7 (0.48, 0.92)		0.55 (0.41, 0.73)	
	2002	0.78 (0.6, 0.97)		0.62 (0.47, 0.8)		0.59 (0.53, 0.7)	
	2003	0.73 (0.62, 0.88)		0.6 (0.49, 0.77)		0.59 (0.49, 0.73)	
	2004	0.8 (0.67, 0.98)		0.75 (0.61, 0.88)		0.77 (0.65, 0.88)	
Grand Mean							
El Dorado		0.69 (0.49, 1.04)	0.77 (0.58, 0.9)	0.69 (0.43, 0.89)	0.73 (0.47, 1.08)	0.75 (0.59, 0.91)	0.77 (0.52, 0.94)
Hillsdale		0.77 (0.57, 1)	0.79 (0.55, 1.06)	0.73 (0.46, 1.07)	0.77 (0.55, 1.03)	0.6 (0.38, 0.91)	0.65 (0.44, 1.02)
Melvern		0.78 (0.58, 1.07)	0.76 (0.63, 0.97)	0.76 (0.57, 1.13)	0.79 (0.65, 0.91)	0.73 (0.47, 0.9)	0.71 (0.54, 0.87)
Pot 2		0.73 (0.41, 1)		0.62 (0.39, 1.09)		0.53 (0.39, 0.83)	
Wabaunsee		0.77 (0.55, 0.98)		0.67 (0.47, 0.92)		0.58 (0.41, 0.88)	

Table 3.—Age-0 largemouth condition (residual dry weight) for Kansas impoundments. Values are the mean (minimum, maximum) from 2644 individuals.

Reservoir	**Year**	**June**		**July**		**August**	
		Water Willow	**Control**	**Water Willow**	**Control**	**Water Willow**	**Control**
El Dorado	**2001**	0.009 (-0.05, 0.11)	0.032 (0.03, 0.03)	0.024 (-0.05, 0.06)	-0.023 (-0.18, 0.06)	NA	NA
	2002	-0.053 (-0.16, 0.06)	-0.067 (-0.09, -0.04)	0.04 (-0.01, 0.11)	0.022 (-0.18, 0.18)	-0.019 (-0.17, 0.06)	0.008 (-0.06, 0.04)
	2003	-0.026 (-0.1, 0.03)	-0.056 (-0.1, 0.01)	0.033 (-0.07, 0.11)	0.029 (-0.08, 0.11)	0.03 (-0.01, 0.07)	0.017 (-0.01, 0.04)
	2004	-0.036 (-0.07, 0.01)	-0.017 (-0.08, 0.04)	0.04 (-0.01, 0.11)	NA	0.021 (-0.02, 0.08)	0.01 (-0.03, 0.05)
Hillsdale	**2001**	0.025 (-0.13, 0.14)	0.037 (-0.05, 0.1)	-0.068 (-0.16, 0.01)	-0.061 (-0.16, 0.05)	-0.025 (-0.09, 0.07)	-0.009 (-0.06, 0.04)
	2002	-0.037 (-0.17, 0.12)	0.029 (-0.09, 0.11)	-0.018 (-0.18, 0.08)	-0.034 (-0.14, 0.06)	-0.006 (-0.13, 0.1)	0.033 (-0.11, 0.11)
	2003	NA	-0.05 (-0.12, 0.01)	0.001 (-0.08, 0.07)	0.01 (-0.09, 0.14)	0.002 (-0.03, 0.08)	-0.005 (-0.07, 0.03)
	2004	-0.016 (-0.11, 0.09)	-0.035 (-0.17, 0.07)	0.01 (-0.05, 0.09)	NA	-0.035 (-0.17, 0.03)	-0.021 (-0.17, 0.07)
Melvern	**2001**	NA	NA	0.065 (-0.04, 0.13)	NA	0.013 (-0.08, 0.1)	0.026 (-0.04, 0.09)
	2002	-0.073 (-0.15, 0.02)	-0.065 (-0.11, -0.02)	0.019 (-0.06, 0.18)	0.004 (-0.09, 0.06)	-0.035 (-0.13, 0.03)	-0.012 (-0.09, 0.06)
	2003	-0.032 (-0.13, 0.05)	-0.007 (-0.06, 0.04)	-0.017 (-0.06, 0.05)	0.066 (0.07, 0.07)	-0.058 (-0.12, -0.02)	-0.009 (-0.06, 0.04)
	2004	0.016 (0, 0.06)	NA	0.008 (-0.03, 0.04)	NA	0.013 (-0.05, 0.06)	0.039 (0.02, 0.06)

Table 3.— Continued.

Reservoir	**Year**	**June**		**July**		August	
		Water Willow	**Control**	**Water Willow**	**Control**	**Water Willow**	**Control**
Pot 2	**2001**	0.006 (-0.15, 0.17)	0.025 (-0.18, 0.16)	0.061 (-0.09, 0.16)	0.006 (-0.15, 0.17)	0.025 (-0.18, 0.16)	
	2002	-0.001 (-0.1, 0.08)	0.016 (-0.08, 0.13)	0.018 (-0.18, 0.1)	-0.001 (-0.1, 0.08)	0.016 (-0.08, 0.13)	
	2003	0.037 (-0.02, 0.1)	0.002 (-0.16, 0.09)	0.015 (-0.05, 0.07)	0.037 (-0.02, 0.1)	0.002 (-0.16, 0.09)	
	2004	-0.016 (-0.14, 0.06)	-0.052 (-0.09, 0.02)	0.004 (-0.04, 0.05)	-0.016 (-0.14, 0.06)	-0.052 (-0.09, 0.02)	
Wabaunsee	**2001**	0.016 (-0.04, 0.08)	-0.028 (-0.09, 0.04)	0.011 (-0.06, 0.08)	0.016 (-0.04, 0.08)	-0.028 (-0.09, 0.04)	
	2002	0.018 (-0.07, 0.1)	0.073 (-0.02, 0.14)	0.063 (0.02, 0.11)	0.018 (-0.07, 0.1)	0.073 (-0.02, 0.14)	
	2003	-0.021 (-0.06, 0.04)	0.008 (-0.08, 0.09)	-0.004 (-0.14, 0.09)	-0.021 (-0.06, 0.04)	0.008 (-0.08, 0.09)	
	2004	-0.041 (-0.11, 0.05)	0.024 (-0.06, 0.1)	0.033 (-0.02, 0.09)	-0.041 (-0.11, 0.05)	0.024 (-0.06, 0.1)	
Grand Mean							
El Dorado		-0.024 (-0.16, 0.11)	-0.04 (-0.1, 0.04)	0.034 (-0.07, 0.11)	0.011 (-0.18, 0.18)	0.003 (-0.17, 0.08)	0.01 (-0.06, 0.05)
Hillsdale		-0.01 (-0.17, 0.14)	0.001 (-0.17, 0.11)	-0.017 (-0.18, 0.09)	-0.019 (-0.16, 0.16)	-0.017 (-0.17, 0.1)	-0.006 (-0.17, 0.11)
Melvern		-0.044 (-0.15, 0.06)	-0.032 (-0.11, 0.04)	0.035 (-0.06, 0.18)	0.009 (-0.09, 0.07)	-0.015 (-0.13, 0.1)	0.003 (-0.09, 0.09)
Pot 2		-0.003 (-0.15, 0.17)	0.013 (-0.18, 0.16)	0.044 (-0.18, 0.16)	-0.003 (-0.15, 0.17)	0.013 (-0.18, 0.16)	
Wabaunsee		-0.006 (-0.11, 0.1)	0.004 (-0.09, 0.14)	0.016 (-0.14, 0.11)	-0.006 (-0.11, 0.1)	0.004 (-0.09, 0.14)	

Table 4.— Results from the split plot/repeated measures analysis of comparing age-0 largemouth bass densities, growth (mm/day), and condition (residual dry weight; RDW) among three large impoundments. The reservoirs were blocks, whole-plot treatments were water willow (vegetated) versus controls (non-vegetated), and coves were the sub-plots. The repeated measures were years and months. Significant values derived from the FDR (*P* < 0.021) are in bold.

Effect	Density	Growth	RDW
Year	$F_{3, 20.5}$ = 11.3; *P* = **0.0001**	$F_{3, 46}$ = 43.8; P < **0.0001**	$F_{3, 28}$ = 8.2; P = **0.0005**
Month	$F_{2, 18.5}$ = 11.3; *P* = 0.55	$F_{2, 48}$ = 4.9; P = **0.01**	$F_{2, 34}$ = 6; P = **0.0059**
Year*Month	$F_{6, 27}$ = 11.3; *P* = **0.002**	$F_{5, 37}$ = 7.1; P < **0.0001**	$F_{6, 28}$ = 11.3; P < **0.0001**
Reservoir	$F_{2, 28.9}$ = 29; *P* < **0.0001**	$F_{2, 49}$ = 2.7; P = 0.08	$F_{2, 30}$ = 5.4; P = **0.01**
Year*Reservoir	$F_{6, 20.8}$ = 9.2; *P* < **0.0001**	$F_{5, 51}$ = 9.9; P < **0.0001**	$F_{6, 28}$ = 11.8; P < **0.0001**
Month*Reservoir	$F_{4, 18.4}$ = 2.6; *P* = 0.07	$F_{4, 51}$ = 1.2; P = 0.33	$F_{4, 34}$ = 7.1; P = **0.0003**
Year*Month*Reservoir	$F_{11, 24.8}$ = 3.9; *P* = **0.002**	$F_{6, 54}$ = 7.1; P < **0.0001**	$F_{10, 34}$ = 3.7; P = **0.0021**
WW	$F_{1, 29}$ = 13; *P* = **0.001**	$F_{1, 42}$ = 16.6; P = **0.0002**	$F_{1, 30}$ = 1.2; P = 0.29
Year*WW	$F_{3, 20.5}$ = 2.2; *P* = 0.12	$F_{3, 36}$ = 11.4; P < **0.0001**	$F_{3, 27}$ = 0.4; P = 0.72
Month*WW	$F_{2, 18.6}$ = 1.1; *P* = 0.36	$F_{2, 49}$ = 0.1; P = 0.88	$F_{2, 34}$ = 0.9; P = 0.42
Reservoir*WW	$F_{2, 28.9}$ = 0.7; *P* = 0.49	$F_{4, 51}$ = 0.1; P = 0.97	$F_{6, 29}$ = 2.3; P = 0.06
Year*Reservoir*WW	$F_{6, 20.8}$ = 1.2; *P* = 0.36	$F_{2, 48}$ = 1.1; P = 0.33	$F_{2, 32}$ = 1.4; P = 0.27
Month*Reservoir*WW	$F_{4, 18.4}$ = 0.1; *P* = 0.98	$F_{4, 49}$ = 0.8; P = 0.53	$F_{6, 29}$ = 2.2; P = 0.07
Year*Month*Reservoir*WW	$F_{11, 24.8}$ = 1.7; *P* = 0.14	$F_{4, 52}$ = 0.8; P = 0.54	$F_{4, 28}$ = 0.2; P = 0.96

Table 5.— Results from the split plot/repeated measures analysis of comparing age-0 largemouth bass densities, growth (mm/day), and condition (residual dry weight; RDW) between two small and three large impoundments. The reservoirs were blocks and whole-plot treatments were coves. The repeated measures were years and months. Significant values derived from the FDR are in bold.

Effect	Density	Growth	RDW
Year	$F_{3, 90} = 7.4$; P = **0.0002**	$F_{3, 6} = 9$; P = **0.01**	$F_{3, 13} = 8$; P = **0.0028**
Month	$F_{2, 163} = 3.1$; P = 0.05	$F_{2, 3} = 9.2$; P = 0.06	$F_{2, 21} = 5.2$; P = **0.01**
Year*Month	$F_{6, 101} = 2.5$; P = 0.03	$F_{6, 6} = 2.8$; P = 0.12	$F_{6, 15} = 9.8$; P = **0.0002**
Reservoir	$F_{4, 166} = 63.2$; P < **0.0001**	$F_{4, 6} = 22$; P = **0.0011**	$F_{4, 13} = 3.6$; P = 0.04
Year*Reservoir	$F_{12, 94} = 4.6$; P < **0.0001**	$F_{11, 6} = 11$; P = **0.003**	$F_{12, 13} = 17.4$; P < **0.0001**
Month*Reservoir	$F_{8, 167} = 2$; P = 0.05	$F_{8, 3} = 4.7$; P = 0.09	$F_{8, 21} = 5.1$; P = **0.0013**
Year*Month*Reservoir	$F_{23, 100} = 2$; P = **0.0088**	$F_{16, 9} = 3$; P = 0.05	$F_{21, 18} = 9.1$; P < **0.0001**

Table 6.—Monthly patterns in diet items of age-0 largemouth bass for three large and two small impoundments. Large impoundments are El Dorado (ELD), Hillsdale (HSD), and Melvern (MEL) reservoirs. The two small impoundments are Pottawatomie State Fishing Lake Number 2 (POT2) and Lake Wabaunsee (LW). Values are the percentage of age-0 largemouth bass that contained that diet item out of the total number of stomachs examined for an individual reservoir within that month. Water willow and control coves in the large reservoirs were not significantly different and therefore combined.

	June					**July**					**August**				
Reservoir	**ELD**	**HSD**	**MEL**	**POT2**	**LW**	**ELD**	**HSD**	**MEL**	**POT2**	**LW**	**ELD**	**HSD**	**MEL**	**POT2**	**LW**
Diet Item															
Fish	5.8	4.8	11.7	5.5	0	31.1	21.7	13.8	10.9	5.8	54.5	43.2	35.9	5.1	6.1
Zooplankton	45.3	77.6	30	40	19.7	15.6	21.7	15.4	31.5	2.9	10.9	9.3	3.8	26.6	3
Macroinvertebrates															
Unidentified	30.2	23	40	25.5	29.5	38.9	45.9	46.2	45.7	39.1	34.5	35.6	46.2	62	53
Ephemeroptera															
Baetidae	0	4.2	0	3.6	1.6	0	1	4.6	1.1	0	0	0.8	0	1.3	0
Caenidae	0	0.6	0	0	4.9	1.1	0.5	0	0	0	1.8	0	0	3.8	1.5
Heptageniidae	0	1.2	0	0	0	13.3	0.5	0	0	0	0	0	0	3.8	0
Ephemeridae	0	0.6	0	0	0	2.2	0	0	0	0	1.8	0.8	0	0	0
Unidentified	0	0.6	0	1.8	0	22.2	2.9	4.6	7.6	10.1	1.8	0.8	2.6	6.3	3

Table 6.— Continued.

	June					**July**					**August**				
Reservoir	**ELD**	**HSD**	**MEL**	**POT2**	**LW**	**ELD**	**HSD**	**MEL**	**POT2**	**LW**	**ELD**	**HSD**	**MEL**	**POT2**	**LW**
Diet Item															
Odonata															
Unidentified	0	0	3.3	0	0	0	0.5	1.5	0	8.7	0	0	9	2.5	9.1
Zygoptera															
Coenagrionidae	0	10.3	0	5.5	6.6	0	1.9	3.1	1.1	2.9	1.8	0	5.1	1.3	13.6
Hemiptera															
Corixidae	19.8	17.6	1.7	7.3	6.6	35.6	10.6	24.6	2.2	4.3	36.4	11	5.1	1.3	19.7
Gerridae	0	0	0	0	0	0	2.4	0	0	0	1.8	2.5	0	5.1	0
Unidentified	2.3	1.8	20	5.5	4.9	0	5.8	10.8	3.3	0	0	0.8	3.8	1.3	3
Trichoptera	1.2	0	1.7	7.3	0	0	0	3.1	10.9	1.4	1.8	0	2.6	3.8	0
Coleoptera	0	3	1.7	10.9	1.6	1.1	2.9	3.1	10.9	17.4	0	5.9	5.1	15.2	1.5
Diptera															
Chironomidae	44.2	46.1	51.7	36.4	67.2	13.3	20.8	13.8	23.9	29	0	7.6	2.6	13.9	22.7
Unidentified	0	4.2	0	0	0	3.3	1	7.7	1.1	2.9	0	0	7.7	6.3	0

Table 6.— Continued.

	June					July					August				
Reservoir	**ELD**	**HSD**	**MEL**	**POT2**	**LW**	**ELD**	**HSD**	**MEL**	**POT2**	**LW**	**ELD**	**HSD**	**MEL**	**POT2**	**LW**
Diet Item															
Other Invertebrates															
Nematomorpha	0	0	0	0	0	3.3	0	0	0	1.4	7.3	0	0	8.9	3
Collembola	0	0	0	0	0	1.1	0	1.5	0	0	0	0	0	0	0
Amphipoda	10.5	18.2	16.7	23.6	62.3	4.4	7.2	3.1	18.5	69.6	0	0.8	6.4	12.7	33.3
Decapoda	0	0.6	0	0	0	0	0	0	2.2	0	0	0	0	1.3	0
Gastropoda	0	0	0	1.8	0	0	0	0	0	0	0	0	0	0	0
Arachnida															
Hydrachnidia	1.2	0	0	0	0	0	0	0	0	0	0	0	1.3	0	0
Araneae	0	0	0	1.8	0	1.1	0.5	0	1.1	0	0	0.8	0	0	0
Terrestrial	0	0	1.7	0	0	0	0.5	0	0	0	0	0	2.6	0	1.5
Empty	7	1.8	6.7	12.7	8.2	1.1	7.7	9.2	10.9	7.2	9.1	12.7	15.4	11.4	9.1

Table 7.—Summary of habitat variables for sampling sites in two small Kansas impoundments. Values are presented as the mean (minimum, maximum).

Habitat Variable	**June**		**July**		**August**	
	Pot2	**Wabaunsee**	**Pot2**	**Wabaunsee**	**Pot2**	**Wabaunsee**
% WW coverage	NA	60.1 (26, 92)	NA	48.3 (14, 100)	NA	52 (20, 85)
WW density (# stems/ m^2)	NA	116 (8, 287)	NA	120 (85, 191)	NA	107 (8, 255)
Mean temp. (^{o}C)	24.8 (21, 26.7)	26.1 (24, 28)	27.3 (24, 30)	27.6 (25, 28)	28.4 (24, 32)	28.4 (26, 32)
DO (mg/L)	7.6 (4.4, 9)	7.9 (7, 9)	5.9 (1.4, 7.7)	6.3 (3.2, 8.1)	6.1 (4, 8.3)	6.6 (3.7, 8.4)
Turbidity (NTU)	36 (6.6, 90)	24 (2.7, 83)	20.8 (8.9, 41)	15.9 (7.8, 35)	16.7 (6.3, 36)	11.2 (5.3, 14.5)
Conductivity (us/cm)	331.6 (318, 344)	376 (317, 547)	303.3 (296, 309)	349 (334, 363)	319 (318, 320)	336 (326, 352)
Mean depth (m)	0.47 (0.32, 0.53)	0.5 (0.33, 0.7)	0.5 (0.26, 0.74)	0.5 (0.26, 0.75)	0.57 (0.3, 0.7)	0.45 (0.24, 0.67)
Mean substrate class	1 (1, 1)	1.5 (1, 2.8)	1.35 (1, 2.5)	2.1 (1, 3.8)	1.63 (1, 2.8)	1.9 (1, 4.2)
Submergent density (# stems/ m^2)	119.2 (0, 553)	0.9 (0, 11)	198.8 (21, 504)	28.3 (0, 214)	54 (0, 172)	25.8 (0, 109)
% Large woody debris	9.2 (0, 35)	5.2 (0, 35)	0.5 (0, 1)	1.2 (0, 10)	3.2 (0, 15)	0.3 (0, 2)
% Small woody debris	0.7 (0, 5)	11 (0, 40)	0.7 (0, 5)	0	5 (0, 35)	12.5 (0, 100)
% Emergent Vegetation	49 (0, 95)	23.1 (0, 95)	25 (0, 100)	0	8.6 (0, 34)	12.63 (0, 86)
% Riparian vegetation	2 (0, 15)	0	4.7 (0, 20)	0	1.2 (0, 5)	0

Figure 1.—Sampling locations in Kansas. Large reservoirs for water willow experiment were El Dorado, Hillsdale, and Melvern. Lake Wabaunsee and Pot2 were small impoundments with stable water levels and abundant largemouth bass.

Figure 2.—Difference in age-0 largemouth bass density (fish/ha) between water willow and control coves in El Dorado, Hillsdale, and Melvern reservoirs from 2001 (circles), 2002 (triangles), 2003 (cross), and 2004 (square).

Figure 3.—Difference in age-0 largemouth bass growth (mm/day) between water willow and control coves in El Dorado, Hillsdale, and Melvern reservoirs from 2001 (circles), 2002 (triangles), 2003 (cross), and 2004 (square).

Figure 4.—Difference in age-0 largemouth bass condition (residual dry weight) between water willow and control coves in El Dorado, Hillsdale, and Melvern reservoirs from 2001 (circles), 2002 (triangles), 2003 (cross), and 2004 (square).

Figure 5.—Redundancy analysis (RDA) for El Dorado Reservoir depicting relationships between age-0 largemouth bass diet items and characterizing variables. The graph indicates the associations of diet items with the characterizing variables. Overall, the RDA was able to account for 28% of the variation in fish assemblage structure, and explained 16.2% with the first two axes. The length and direction of arrows indicate the strength of axis loadings. Diet items are represented with dashed arrows and are Ephemeroptera (*Ephem*), zooplankton (*Zoo*), Chironomidae (*Chiro*), and Corixidae (*Corix*). Solid lines are the environmental and dummy variables and are 2001-2003 (Y01-Y03), age-0 largemouth bass length (LNTH), June, July, and water willow cove (WW).

Figure 6.—Redundancy analysis (RDA) for Hillsdale Reservoir depicting relationships between age-0 largemouth bass diet items and characterizing variables. The graph indicates the associations of diet items with the characterizing variables. Overall, the RDA was able to account for 18% of the variation in fish

assemblage structure, and explained 17% with the first two axes. The length and direction of arrows indicate the strength of axis loadings. Diet items are represented with dashed arrows and are Amphipoda (*Amph*), general macroinvertebrates (*MacInv*), fish, zooplankton (*Zoo*), and Chironomidae (*Chiro*). Solid lines are the environmental and dummy variables and are 2001-2003 (Y01-Y03), age-0 largemouth bass length (LNTH), June and July.

Figure 7.—Redundancy analysis (RDA) for Melvern Reservoir depicting relationships between age-0 largemouth bass diet items and characterizing variables. The graph indicates the associations of diet items with the characterizing variables. Overall, the RDA was able to account for 18% of the variation in fish assemblage structure, and explained 10.2% with the first two axes. The length and direction of arrows indicate the strength of axis loadings. Diet items are represented with dashed arrows and are Amphipoda (*Amph*), general macroinvertebrates (*MacInv*), Hemiptera (*Hempt*), fish, zooplankton (*Zoo*), Chironomidae (*Chiro*), and Corixidae (*Corix*). Solid lines are the environmental and dummy variables and are 2001-2003 (Y01-Y03), age-0 largemouth bass length (LNTH), June, July, and water willow cove (WW).

Figure 8.—Difference in age-0 largemouth bass abundance (fish/ha), growth (mm/day), and condition (residual dry weight) between water willow coves in large impoundments (El Dorado, Hillsdale, and Melvern) and small impoundments (Pot2 and Lake Wabaunsee) from 2001 (circles), 2002 (triangles), 2003 (cross), and 2004 (square).

Figure 9.—Redundancy analysis (RDA) for Pot2 depicting relationships between age-0 largemouth bass diet items and characterizing variables. The graph indicates the associations of diet items with the characterizing variables. Overall, the RDA was able to account for 10% of the variation in fish assemblage structure, and explained 8.7% with the first two axes. The length and direction of arrows indicate the strength of axis loadings. Diet items are represented with dashed arrows and are general macroinvertebrates (*MacInv*), fish, zooplankton (*Zoo*), Chironomidae (*Chiro*), and Corixidae (*Corix*). Solid lines are the environmental and dummy variables and are 2001-2003 (Y01-Y03), age-0 largemouth bass length (LNTH), June, and July.

Figure 10.—Redundancy analysis (RDA) for Lake Wabaunsee depicting relationships between age-0 largemouth bass diet items and characterizing variables. The graph indicates the associations of diet items with the characterizing variables. Overall, the RDA was able to account for 14.4% of the variation in fish assemblage structure, and explained 11.4% with the first two axes. The length and direction of arrows indicate the strength of axis loadings. Diet items are represented with dashed arrows and are Amphipoda (*Amph*), general macroinvertebrates (*MacInv*), fish, zooplankton (*Zoo*), Chironomidae (*Chiro*), and Corixidae (*Corix*). Solid lines are the environmental and dummy variables and are 2001-2003 (Y01-Y03), age-0 largemouth bass length (LNTH), June, and July.

Figure 1.

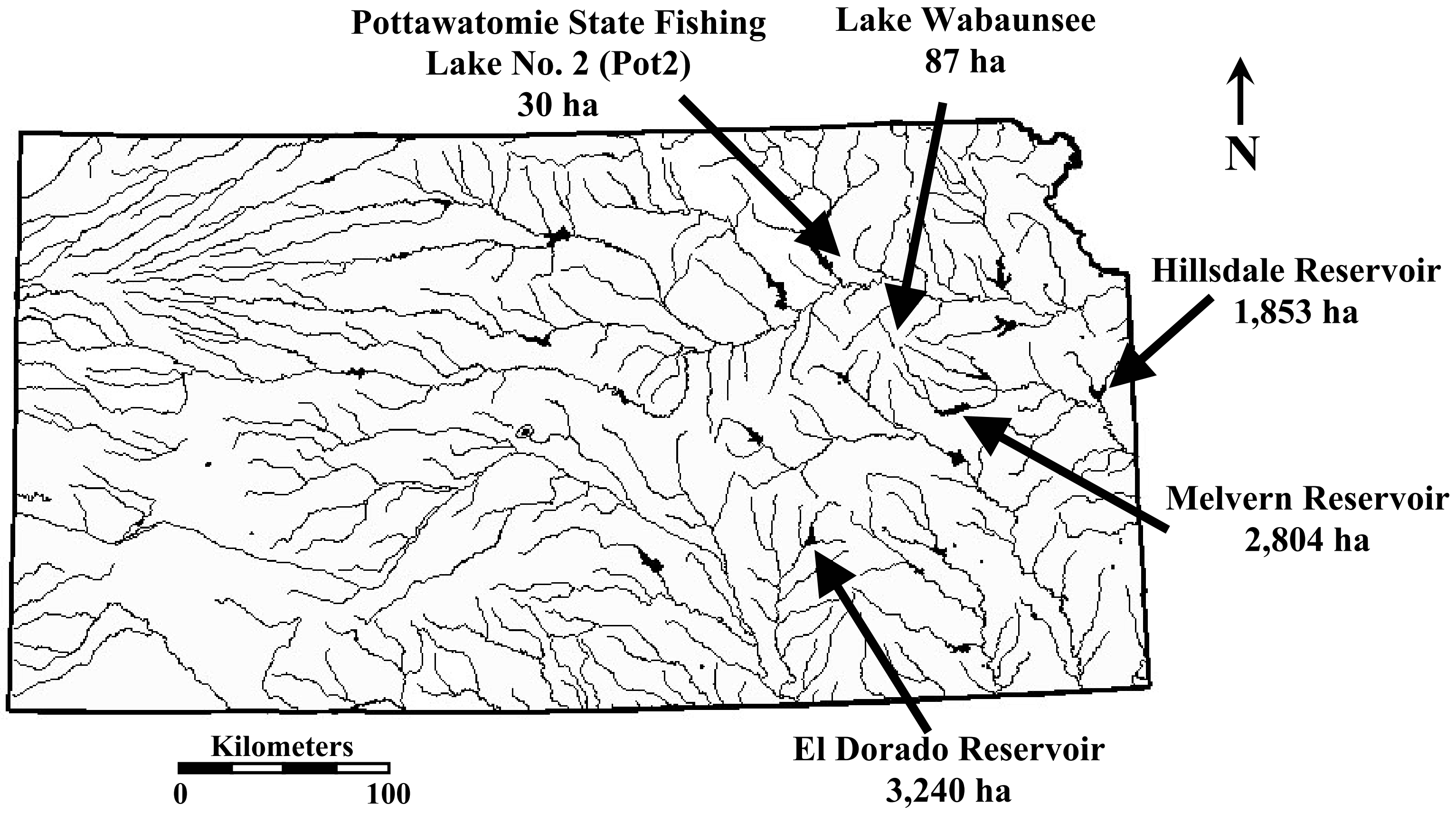

Pottawatomie State Fishing Lake No. 2 (Pot2)
30 ha
Lake Wabaunsee
87 ha
N
Hillsdale Reservoir
1,853 ha
Melvern Reservoir
2,804 ha
El Dorado Reservoir
3,240 ha
Kilometers
0
100

Figure 2.

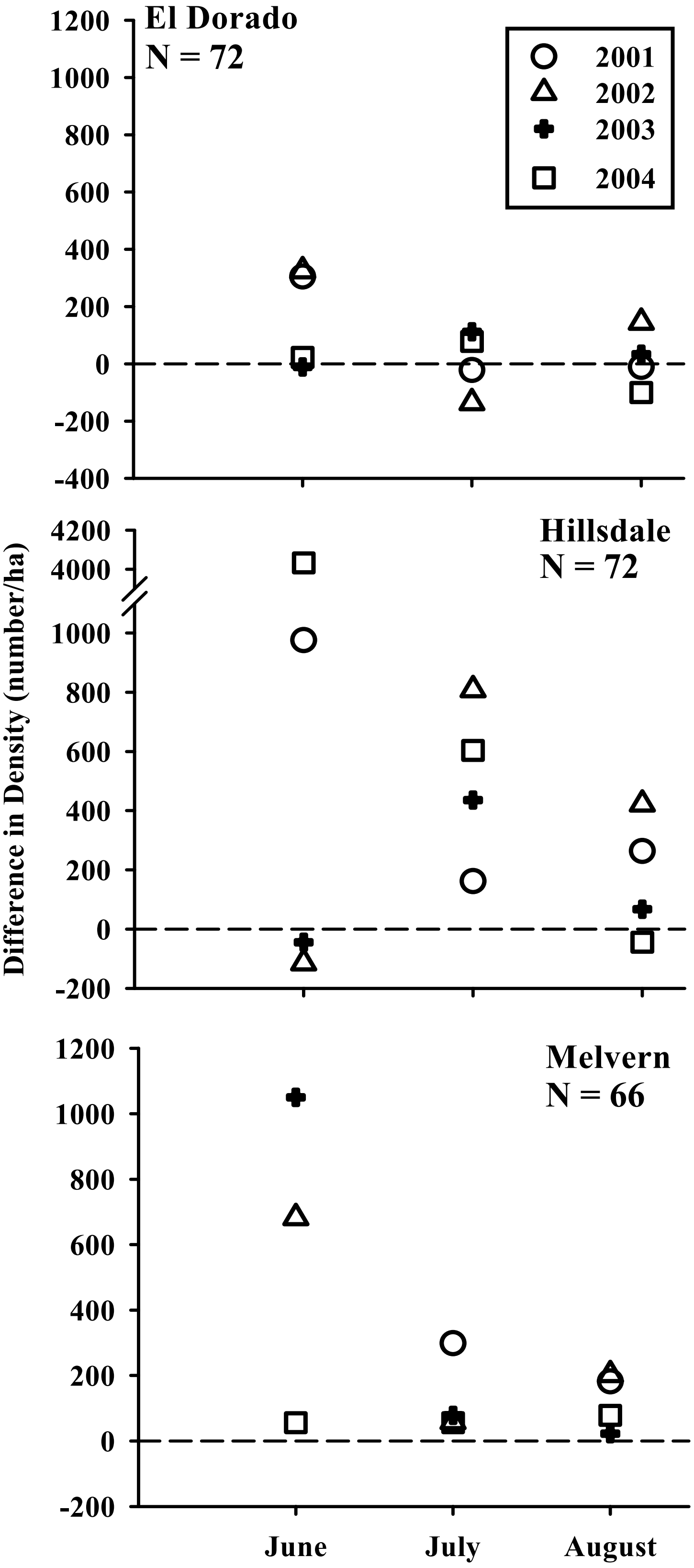

El Dorado
N = 72
1200
1000
800
600
400
200
0
-200
-400
○ 2001
△ 2002
✚ 2003
□ 2004
Hillsdale
N = 72
4200
4000
1000
800
600
400
200
0
-200
Difference in Density (number/ha)
Melvern
N = 66
1200
1000
800
600
400
200
0
-200
June
July
August

Figure 3.

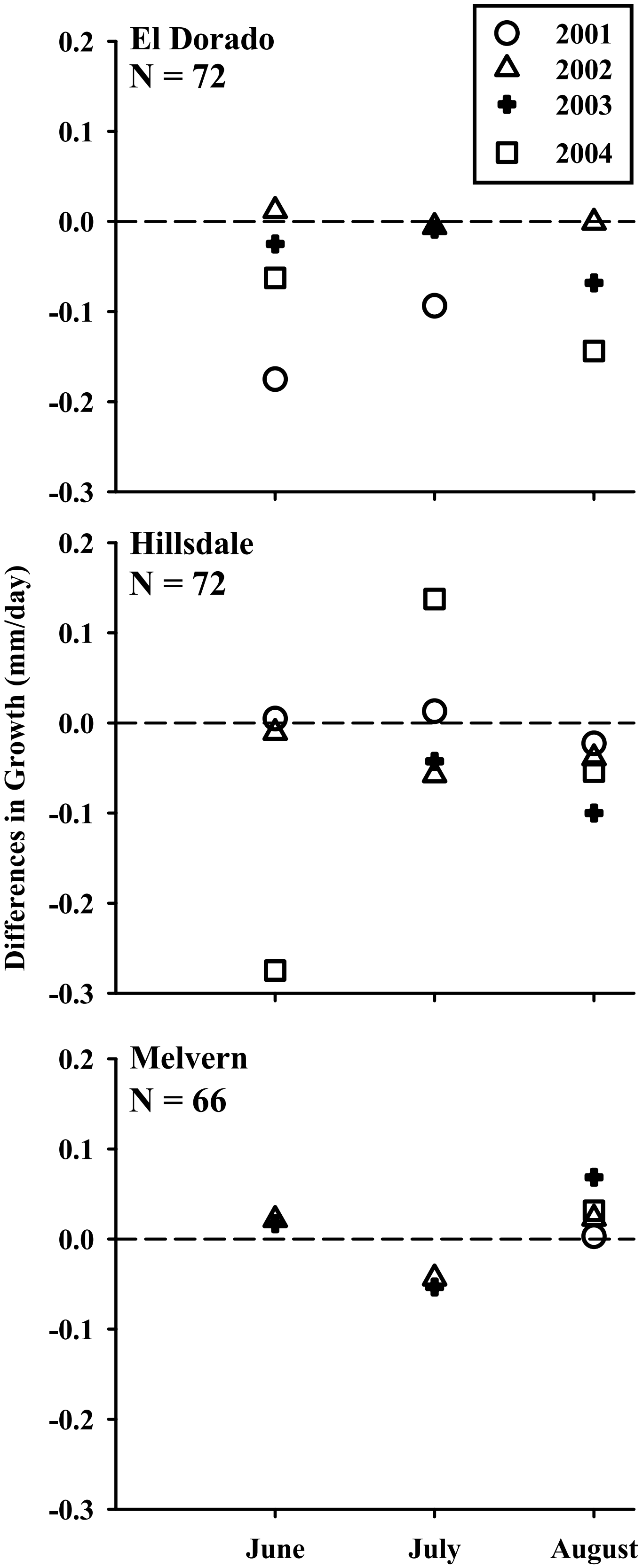

El Dorado
N = 72
Hillsdale
N = 72
Melvern
N = 66
2001
2002
2003
2004
0.2
0.1
0.0
-0.1
-0.2
-0.3
Differences in Growth (mm/day)
June
July
August

Figure 4.

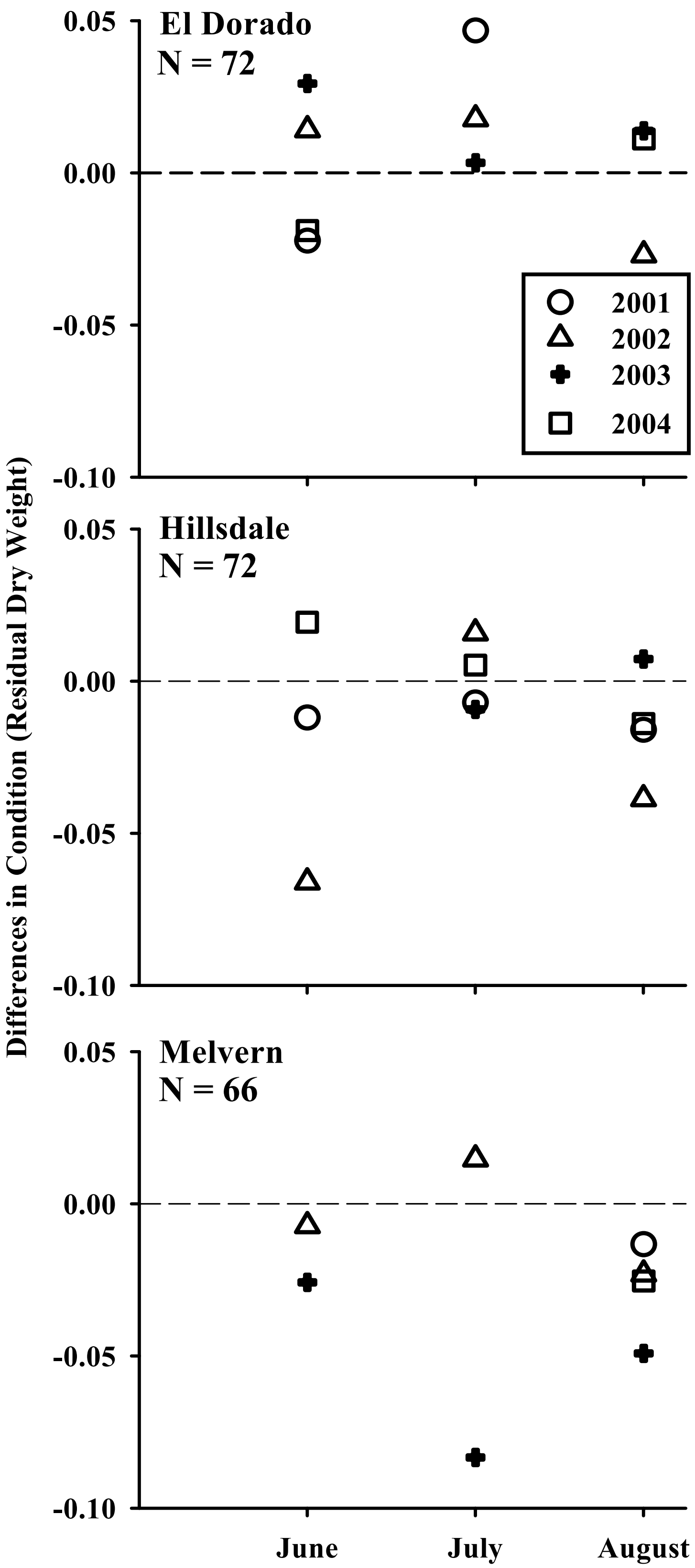

El Dorado
N = 72
Hillsdale
N = 72
Melvern
N = 66
0.05
0.00
-0.05
-0.10
Differences in Condition (Residual Dry Weight)
○ 2001
△ 2002
✚ 2003
□ 2004
June
July
August

Figure 5.

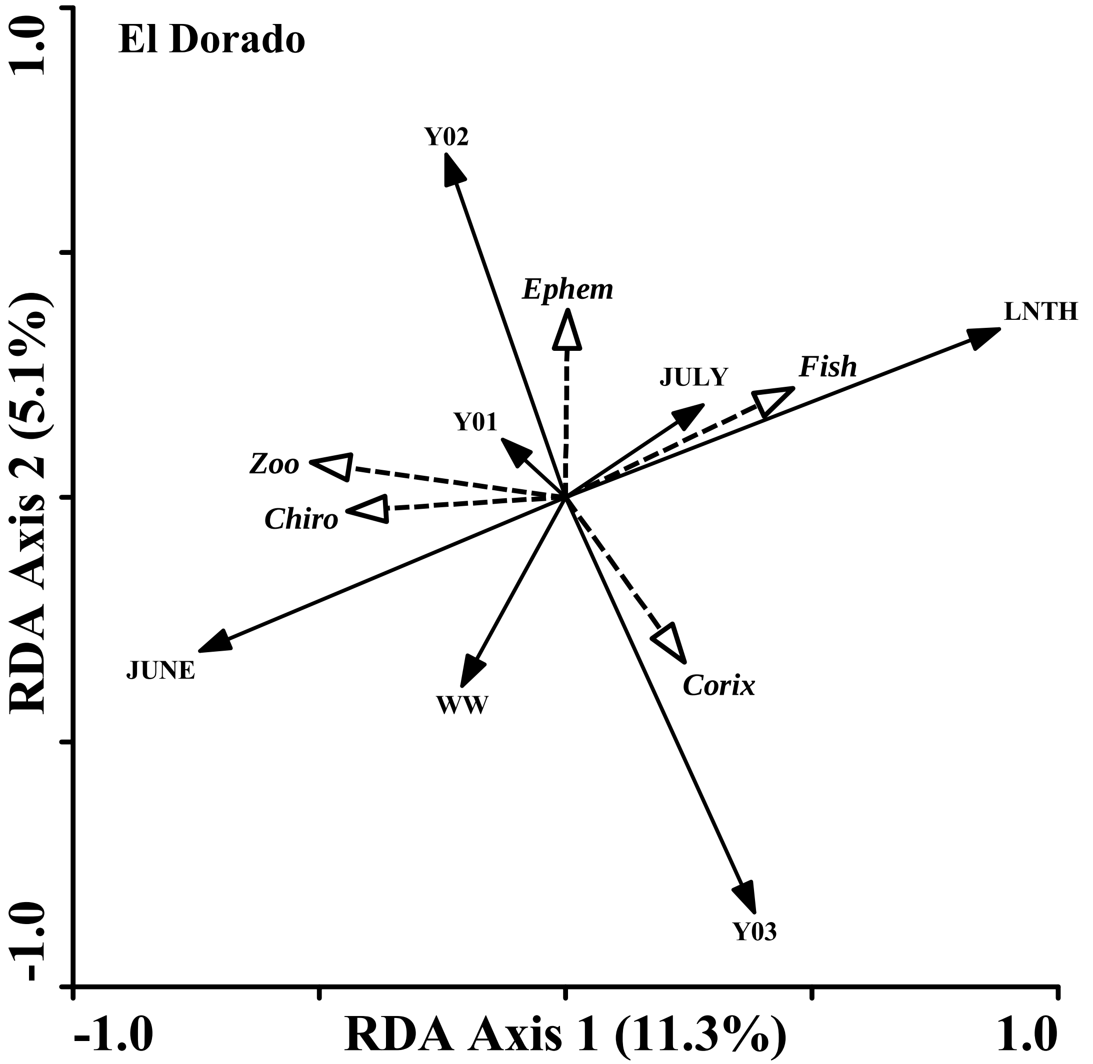

El Dorado
1.0
-1.0
RDA Axis 2 (5.1%)
-1.0
1.0
RDA Axis 1 (11.3%)
Y02
Ephem
LNTH
JULY
Fish
Y01
Zoo
Chiro
JUNE
WW
Corix
Y03

Figure 6.

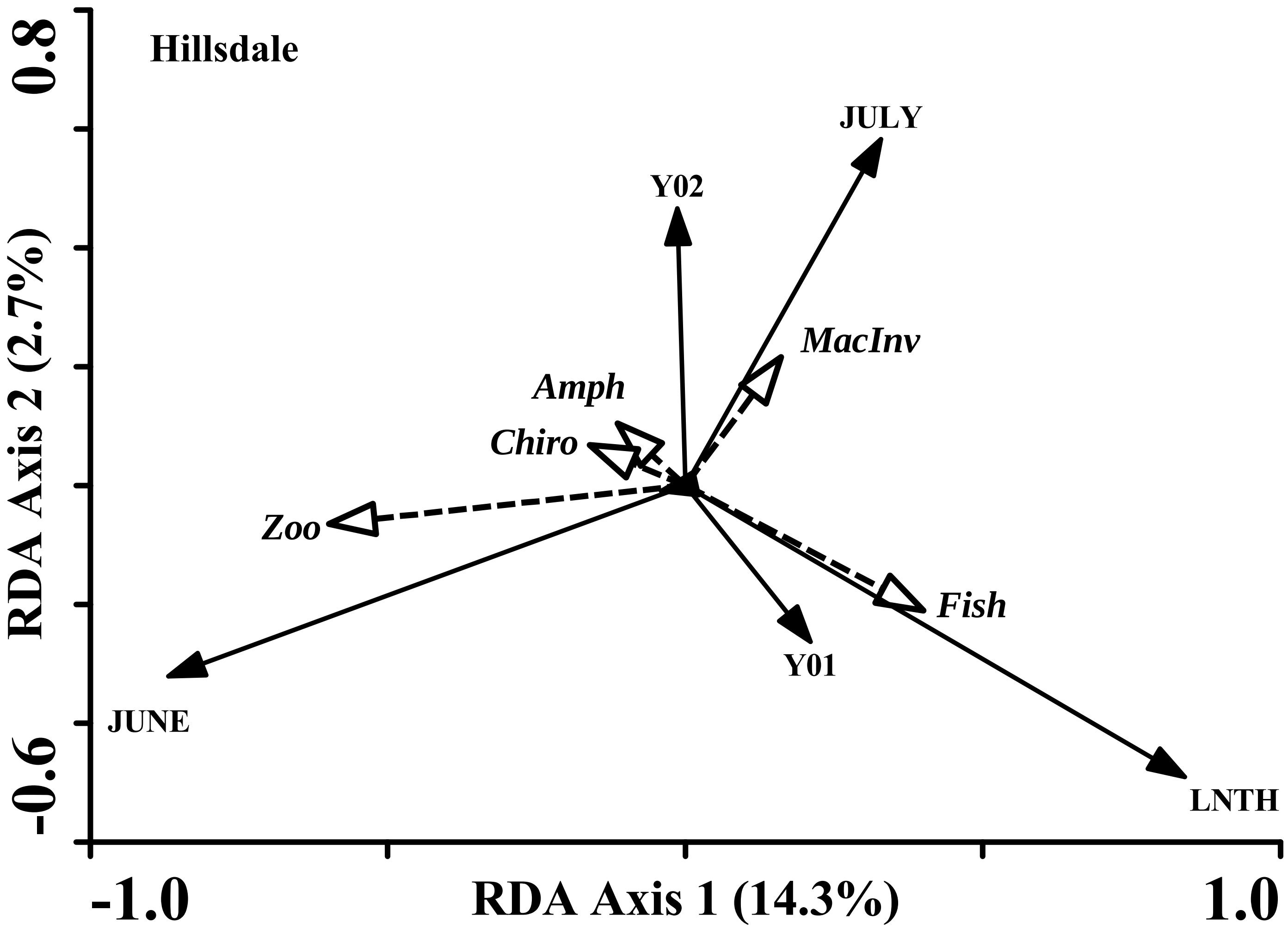
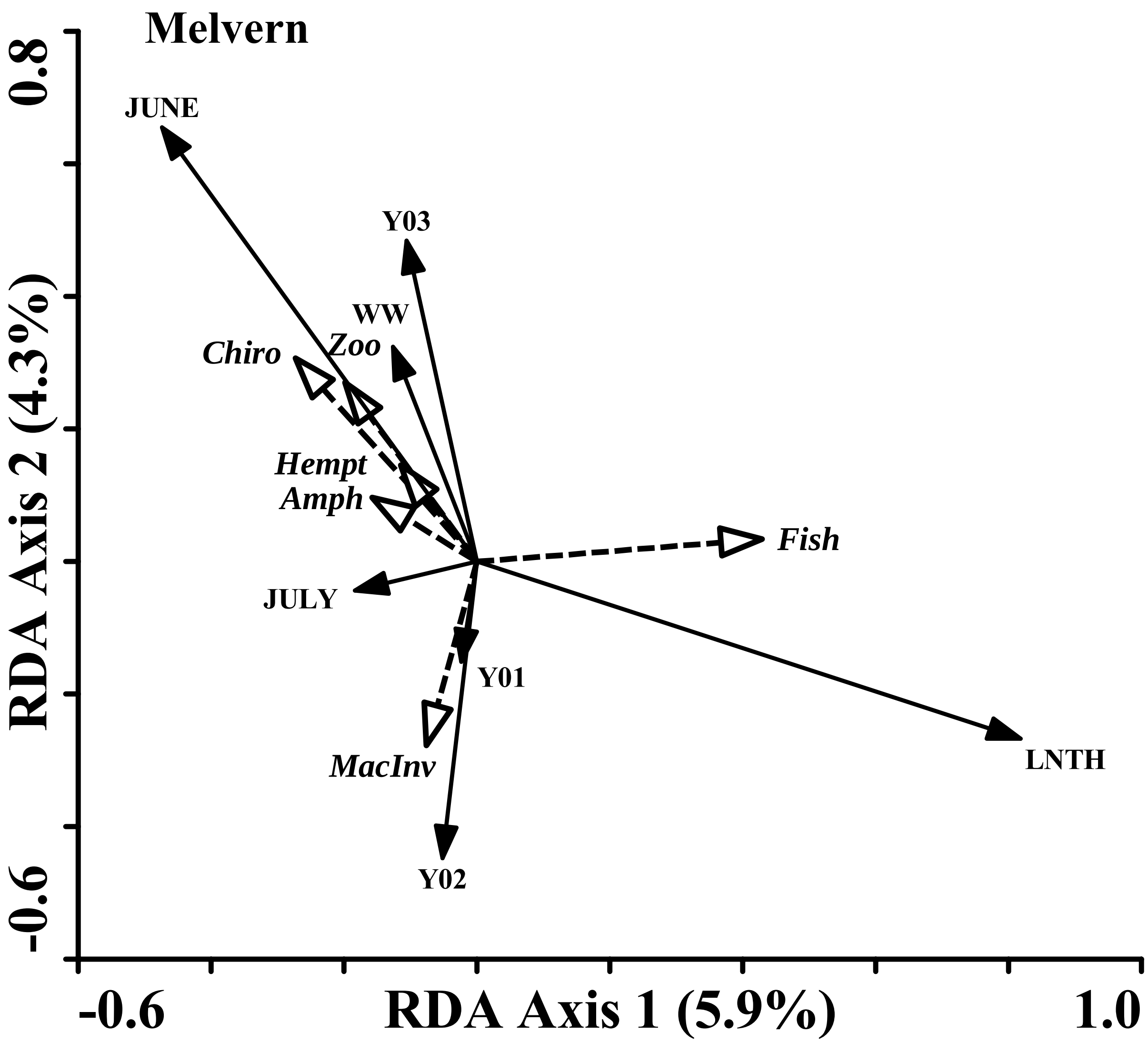

Hillsdale
RDA Axis 2 (2.7%)
0.8
-0.6
RDA Axis 1 (14.3%)
-1.0
1.0
JULY
Y02
MacInv
Amph
Chiro
Zoo
Fish
Y01
JUNE
LNTH

Figure 7.



Melvern
0.8
-0.6
RDA Axis 2 (4.3%)
-0.6
RDA Axis 1 (5.9%)
1.0
JUNE
Y03
WW
Zoo
Chiro
Hempt
Amph
Fish
JULY
Y01
MacInv
LNTH
Y02

Figure 8.

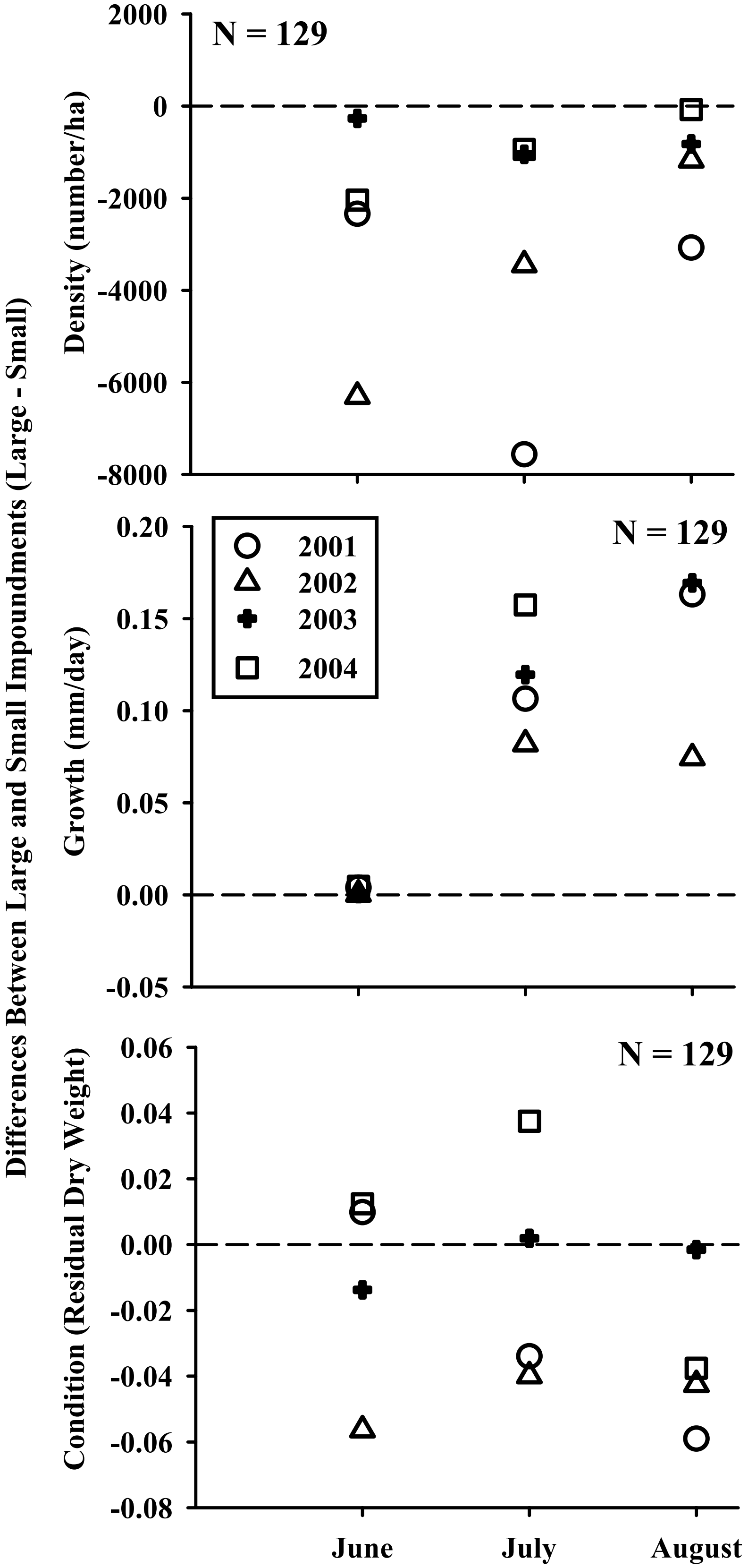
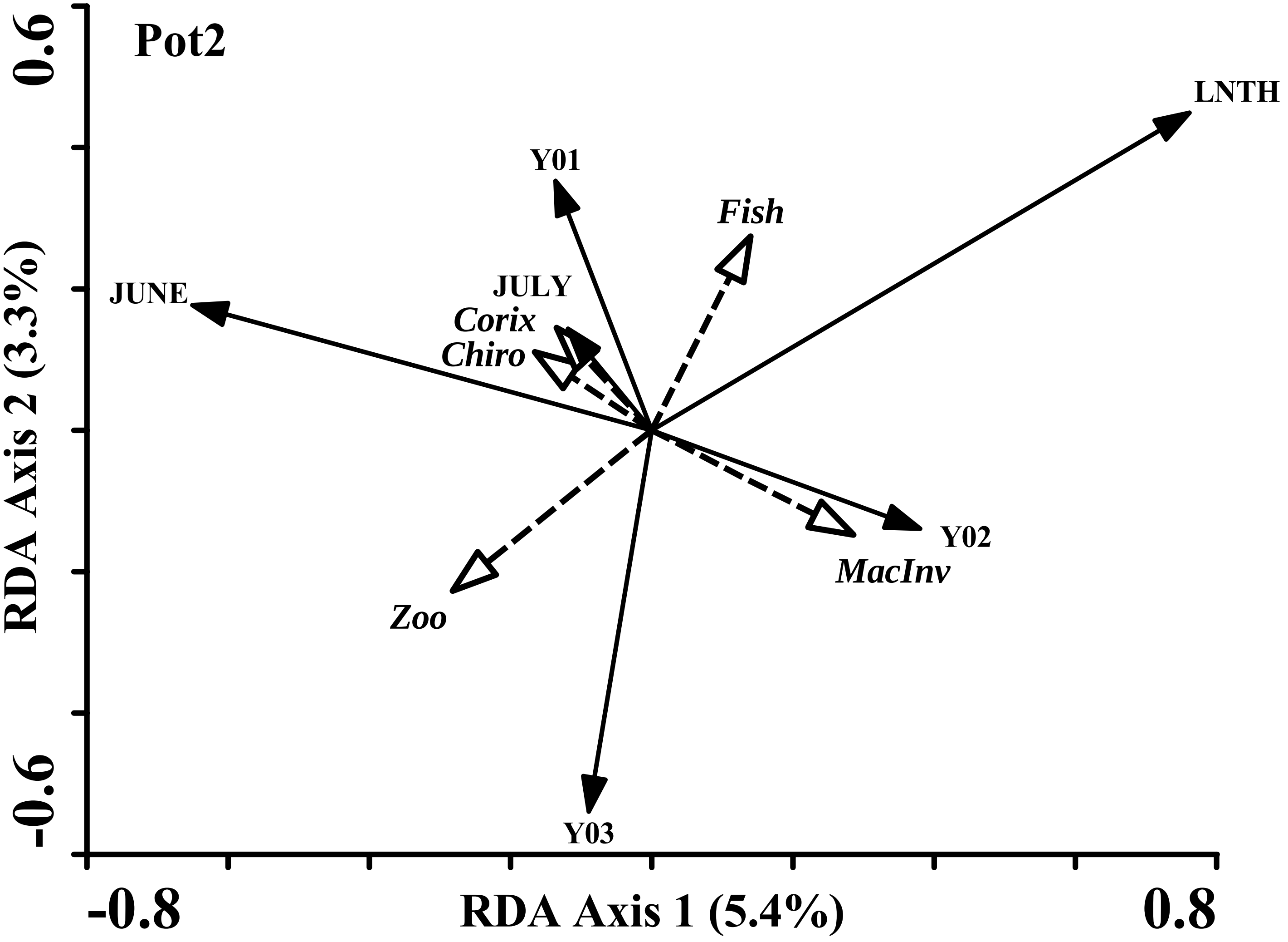
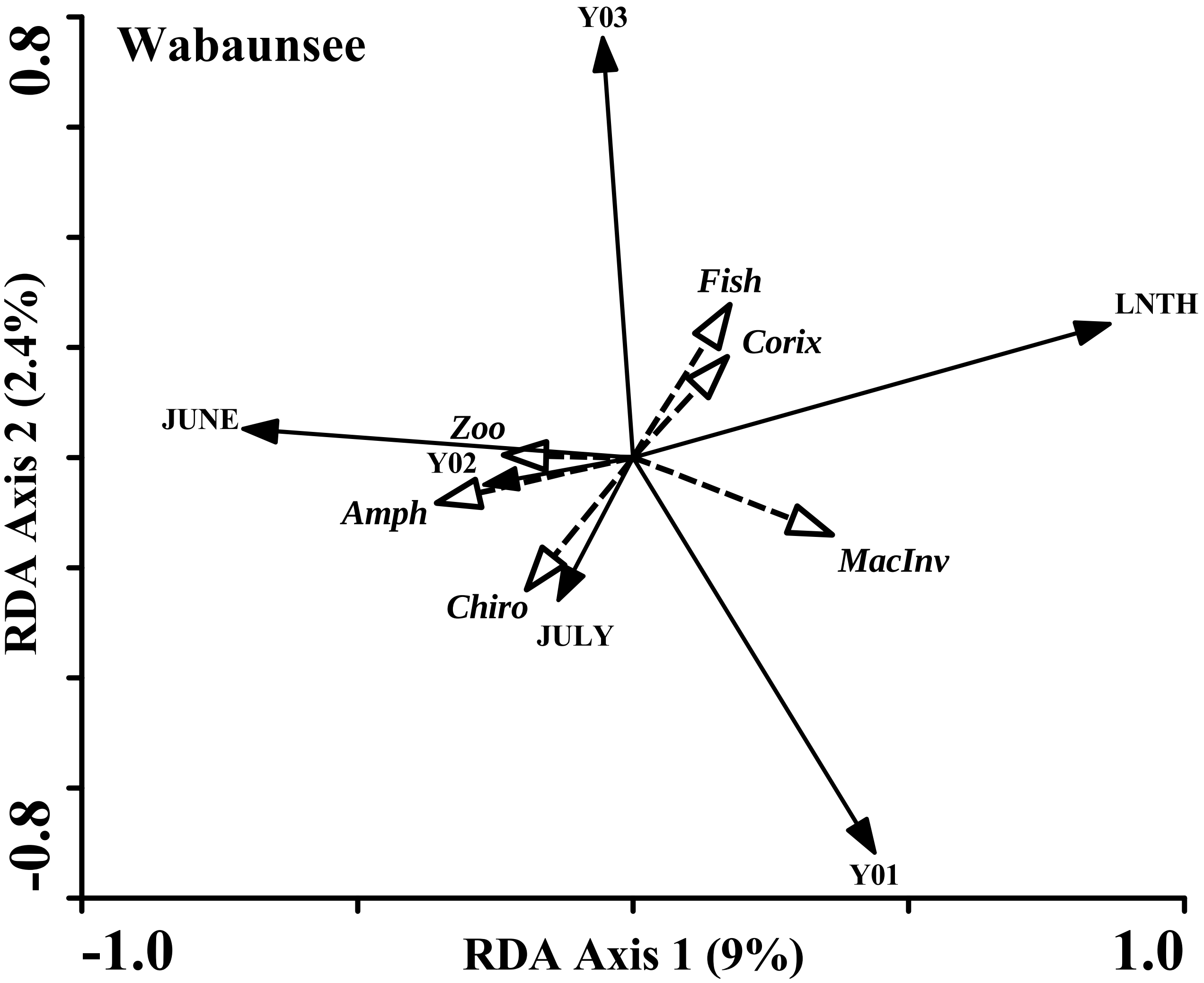

Differences Between Large and Small Impoundments (Large - Small)
Density (number/ha)
2000
0
-2000
-4000
-6000
-8000
N = 129
Growth (mm/day)
0.20
0.15
0.10
0.05
0.00
-0.05
N = 129
○ 2001
△ 2002
✚ 2003
□ 2004
Condition (Residual Dry Weight)
0.06
0.04
0.02
0.00
-0.02
-0.04
-0.06
-0.08
N = 129
June
July
August

Figure 9.



Pot2
0.6
-0.6
RDA Axis 2 (3.3%)
-0.8
0.8
RDA Axis 1 (5.4%)
LNTH
Y01
Fish
JUNE
JULY
Corix
Chiro
Y02
MacInv
Zoo
Y03

Figure 10.



Wabaunsee
Y03
Fish
LNTH
Corix
JUNE
Zoo
Y02
Amph
MacInv
Chiro
JULY
Y01
0.8
-0.8
RDA Axis 2 (2.4%)
-1.0
RDA Axis 1 (9%)
1.0

CHAPTER 4

THE RESPONSE OF WATER WILLOW, *JUSTICIA AMERICANA*, TO DIFFERENT WATER INUNDATION AND DESICCATION REGIMES

ABSTRACT

American water willow *Justicia americana* has been planted in reservoirs to provide important littoral habitat for fishes because of its ability to form dense stands, spread along shorelines, grow in water up to 1.2 m deep, and withstand harsh conditions. The response of water willow to periods of inundation or desiccation has not previously been quantified and is critical for evaluating its potential success in reservoirs. I tested the inundation response of plants at depths of 0.75, 1.50, and 2.25 m for 2, 4, 6, and 8 weeks. Response to desiccation was investigated using 2, 4, 6, and 8 week drying durations. In addition, 2 and 4 week drying periods were tested separately in June, July, and August. Number of leaves, total height, and total dry weight were measured as indicators of plant condition. Condition rapidly declined after being inundated for four weeks at all experimental depths and plants did not recover by the end of the experiment. A significant decrease in height and an increase in leaf number was observed after 8 weeks of desiccation. Condition also declined from June to August during the second desiccation experiment. Overall, water willow appeared to be more resistant to desiccation than to inundation. A 5% overall mortality was observed for the desiccation trials versus a 69% overall mortality from the inundation trials. Even the shortest inundation duration in this study (2 weeks) resulted in $\geq$ 40% mortality across all depth treatments, and was likely due to light limitation. My findings provide information that can be used to select candidate reservoirs for water willow establishment based on

expected water-level fluctuations. Additionally, this information could be used to manage water levels in reservoirs where water willow currently provides important habitat for fishes.

INTRODUCTION

Ecological processes that occur as reservoirs age are relatively well documented. In particular, reservoirs typically go through a trophic upsurge, which is stimulated by nutrients released from newly inundated organic matter in the watershed followed by trophic depression, which occurs as that nutrient pool is processed through the system (Kimmel and Groeger 1986). During the upsurge, increased aquatic productivity and inundated vegetation provide abundant food and habitat for sport and bait fishes and other aquatic organisms (Kimmel and Groeger 1986; Ploskey 1986). As the system stabilizes during the trophic depression the littoral habitat complexity declines and the fish assemblage is typically dominated by less desirable species such as common carp *Cyprinus carpio*, bigmouth buffalo *Ictiobus cyprinellus*, and freshwater drum *Aplodinotus grunniens* (Kimmel and Groeger 1986; Ploskey 1986). Thus, a negative relation between reservoir age and sportfish abundance is common throughout North America (Kimmel and Groeger 1986; Miranda and Durocher 1986; Ploskey 1986).

Since the 1950s, several biomanipulation techniques have been investigated and implemented to prolong the initial high quality sportfisheries in U.S. reservoirs (Miranda 1996). Reservoir water-level manipulations can be used to increase or sustain sportfish populations by inundating terrestrial vegetation to increase nutrients, food resources, and habitat, as well as to concentrate prey for predators (Ploskey 1986; Willis 1986).

However, this technique is limited to reservoirs with predictable inflows and regulations that support water-level fluctuations (Ploskey 1986; Willis 1986). Habitat enhancement is another technique used to mitigate the effects of trophic depression. Artificial and natural structures such as brush piles, tire structures, stake beds, standing timber, and rock reefs are placed in specific areas of reservoirs to benefit targeted fishes (Brown 1986). These structures can be cost and labor prohibitive, and are usually short term solutions. Another option that is often more feasible and long term is the planting of native aquatic macrophytes (Durocher et al. 1984; Smart et al. 1996; Dick et al. 2004).

Native aquatic macrophyte establishment can benefit fishes and a variety of other aquatic organisms (Brown 1986; Kahl 1993; Dibble et al 1996; Smart et al. 1996). Macrophytes provide refugia from predation and abundant food resources for many fish species (Wiley et al. 1984; Killgore et al. 1989). For example, large-bodied cladocerans, an important food source for age-0 fishes, use macrophytes for shelter from predation, leading to an increase in their overall abundance (Quade 1969; Timms and Moss 1984; Moss et al. 1996). Stems and leaves provide surfaces for colonizing by epiphytic bacteria and algae (Dodds 2002) that are the principal food source of many invertebrates (Baker and Orr 1986). Macrophyte decomposition releases nutrients that were taken from the sediments, which stimulates pelagic production (Carpenter 1980) and increases organic substrates used by benthic organisms (Beckett et al. 1992). Additionally, native aquatic macrophytes contribute to increased water quality and clarity by reducing shoreline erosion (Kahl 1993; Summerfelt 1999) and turbidity (Kahl 1993; Vestergaard and Sand-Jensen 2000).

Many reservoirs remain unvegetated because of insufficient native plant propagules and harsh conditions for seedling establishment (Smart et al. 1996). In an effort to increase sportfish production and control shoreline erosion, native aquatic macrophytes are being intensively planted in reservoir littoral areas (Marteney 1993; Dick et al. 2004). Unfortunately success has been limited by high abundances of herbivores and benthic feeding organisms (e.g., common carp) that uproot macrophytes (Cox 1999; Dick et al. 2004; Smart et al. 2005). American water willow *Justicia americana* L. (Vahl.; hereafter water willow) is resistant to these biotic disturbances and is now being extensively planted in reservoirs (Dick et al. 2004).

Water willow is an emergent species with a native range from Quebec to Texas and from Kansas to the Atlantic coast (Gleason and Cronquist 1993; Niering and Olmstead 1997). It typically grows on the margins and shallow areas of lotic and lentic systems (Penfound 1940; Niering and Olmstead 1997) in areas exposed to ample sunlight (Fritz and Feminella 2003; Smart et al. 2005). As a colonial plant it forms dense stands by rhizomatous growth and can quickly spread along shorelines through fragmentation growing in water up to 1.2 m (Penfound 1940). In some areas of the U.S. water willow is considered a pest species because of its dense vegetative patches and rapid spread (Penfound 1940; Couch 1976). A semi-rigid, but flexible fibrous stem enables it to withstand scouring floods in lotic systems (Fritz and Feminella 2003) and strong wave action in lentic systems (Penfound 1940). Water willow is also tolerant of moderate water-level fluctuations (including drought) and high turbidity (Niering and Olmstead 1997; Dick et al. 2004; Smart et al. 2005).

Water levels in many reservoirs can widely fluctuate within and among years. However, the amount of time that water willow could be either inundated or desiccated has not been quantified. This information is critical, particularly for newly established macrophytes (Dick et al. 2004), to evaluate the potential success of water willow for sportfish management in reservoirs that vary in magnitude and timing of water level fluctuations. Thus, the objectives of my study were to 1) investigate the response of water willow to different inundation periods and depths, and 2) examine the desiccation tolerance of water willow.

METHODS

Plant Collection and Establishment

Water willow was harvested from Lake Wabaunsee in Wabaunsee County, Kansas. Plants collected were $\geq$ 0.25 m tall, exhibited no visible signs of stress (i.e., yellowing leaves, broken stalks, insect infestations), and had the majority of the root system intact. Immediately after removal, individuals were placed upright in containers with water covering the entire root system. Plants were transported to a water supply pond of Milford Hatchery, Geary County, Kansas and individually planted in 19 L experimental plastic containers (cylindrical; 36.2 cm high and 29.2 cm in diameter) that were filled with 15-16 L of soil (silt loam) taken from nearby riparian areas. Containers were numbered and 1.3 cm holes were drilled around the bottom and sides to allow an exchange of water and organisms. All experimental plants were placed in the pond at a depth of 0.10 m (Penfound 1940) and allowed to acclimate three weeks prior to the start of experiments; this depth served as the control for all experiments. Plants grew approximately 3-4 cm during the acclimation period. Depth was defined as the distance from the top of the substrate in the experimental container to the water's surface.

Inundation Tolerance

I tested the response of water willow to inundation at three treatment depths and four durations. The number of leaves, total height (mm; distance from container substrate to end of longest stem), and total dry weight (g) were used as indicators of plant health (Kramer and Boyer 1995; Crawley 1997a; Stern et al. 2003). Twenty containers were randomly selected and placed at each of the three treatment depths: 0.75, 1.50, and 2.25 m. Ten randomly selected controls were retained at 0.10 m. Four simulated inundation durations were tested: 2, 4, 6, and 8 weeks. I derived experimental inundation depths and durations using water level data from eight Kansas reservoirs (Table 1; US Army Corp of Engineers, Tulsa District) that have or are under consideration for water willow plantings. Water levels from April through September (1995 - 2002) were used to correspond with the primary growing season of water willow (Penfound 1940), during which it would be most susceptible to inundation or desiccation (Smart and Dick 1999). [illegible]atment depths were based on the overall mean water level above conservation pool from the eight reservoirs, which was 0.76 m (± 0.02 SE) with a maximum of 10 m. The mean inundation duration was calculated for each reservoir by counting the number of consecutive days the water level was ≥ 0.75, 1.50, and 2.25 m above conservation pool (Table 1).

At the end of each inundation period, five containers were randomly selected from each depth treatment, moved to the control depth, and the height and number of leaves were recorded. After 11 weeks, water willow survival was recorded. Plants were removed from containers, thoroughly rinsed, and dried at 60^{o} C for a minimum of 4 days. Dry weight (g) of the whole plant was recorded and used as an index of final biomass. A multivariate analysis of variance (MANOVA) was used to investigate if number of leaves and total height (dependent variables) differed among inundation depths and durations (fixed effects). An analysis of variance (ANOVA) was used to test if the final dry weight (g) differed among the plants after the recovery period.

Desiccation Tolerance

The desiccation tolerance of water willow was tested with two experiments. The first experiment investigated the effects of 2, 4, 6, and 8 week drying durations, which represents typical periods of low water levels in Kansas reservoirs (Table 1). The mean duration (number of consecutive days) of water levels 0.6 m below conservation pool was 30 (± 13.9 SE) days and was 16 (± 11.5 SE) days for 1.2 m below conservation pool. Water levels were based on the maximum depth (1.2 m) at which water willow was reported to colonize (Penfound 1940). Two-week intervals were used for experimental durations. Drought/drawdown conditions were simulated by placing experimental containers on a dry, well-drained area on the shore of the pond with sparse to no vegetation. Both the drying and control areas received direct sunlight > 85 % of the day. Containers in the desiccation area were arranged in a square pattern approximately 5 cm apart. At the beginning of the experiment five containers were randomly assigned to each drying duration (2, 4, 6, and 8 weeks; n = 20 total) and moved from the control depth (0.10 m deep) to the drying area. Total height and number of leaves were recorded at the beginning of the experiment and when plants were returned to the control depth. Mortality was recorded at the end of 19 weeks. Plants were removed from containers, thoroughly rinsed, dried at 60^{o} C for a minimum of 4 days, and dry weight (g) of the whole plant was recorded. The percent change in plant height and leaf number that occurred over the drying duration was calculated for each plant. A MANOVA was used to test if percent change in height, percent change in leaf number, and dry weight differed among drought durations (2, 4, 6, and 8 weeks).

In a second experiment, I tested if desiccation response differed across months. I tested 2 and 4 week drying durations in the months of June, July, and August. The same protocols were used as for the first experiment. I tested for differences in percent change in height, percent change in leaf number, and dry weight among months (June, July, and August), drying durations (2 and 4 week), and the interaction between month and drying duration with a MANOVA.

For all MANOVAs, Wilk's Lambda was used to calculate the multivariate F-statistic (SPSS 2001). If an overall MANOVA was significant ($P < 0.05$), separate ANOVAs were conducted to investigate each variable separately. Alpha levels were set at 0.05 a priori and Type III sums of square were used in all ANOVAs. Post hoc comparisons were conducted using the Bonferroni correction to control Type 1 error rate for multiple tests.

RESULTS

The results from the inundation experiment revealed that water willow condition rapidly declined after four weeks for all experimental depths (Figure 1) and did not recover by the end of the experiment (Table 1). A significant depth by week interaction was found for both leaf number and plant height (MANOVA $P < 0.001$; subsequent

ANOVAs $P < 0.001$). The post hoc comparisons for leaf number indicate that plants at the control depth had significantly ($P < 0.001$) more leaves than all the treatment depths after 4 weeks and the number of leaves had significantly ($P < 0.001$) increased by week 8. In contrast, no significant increase in height occurred for the control plants over the duration of the experiment. The ANOVA testing for differences in final dry weight revealed a significant week effect ($P = 0.002$). In general, control plants had significantly greater dry weights ($P < 0.01$) than those from the 2.25 m treatment and all plants inundated for more than 4 weeks (Table 2).

The overall mortality rate for the desiccation experiments was low (5%). The MANOVA for the duration of drying experiment found a significant week effect ($P = 0.003$) for the dependent variables dry weight, percent change in height, and percent change in leaf number. Separate ANOVAs for dry weight, percent change in height, and percent change in leaf number all showed a significant effect of drying duration ($P \leq 0.032$). The post hoc tests found a significant decrease ($P = 0.035$) in height between weeks 2 and 4 (Figure 2), and a significant increase ($P = 0.025$) in leaf number between week 2 versus week 8.

A significant month by week interaction effect ($P = 0.009$) was found when testing the effects of desiccation across different months. Individual ANOVAs revealed that dry weight significantly differed ($P < 0.001$) among months, as plants in the June trials were significantly heavier ($P \leq 0.046$) than those tested in August (Figure 3). Total height significantly decreased in the 4 versus the 2 week duration ($P = 0.005$), and during August compared to June or July ($P = 0.007$; Figure 3). The ANOVA testing the percent change in leaf number indicated a significant interaction ($P = 0.008$) between week and month. In June and July there was a greater number of leaves in the 4 week trial than the 2 week trial (Figure 3). In contrast, the number of leaves in August declined from 2 to 4 weeks (Figure 3). Mean temperatures for June, July, and August were similar (21.7°C , 23.8 °C, and 22.4 °C, respectively [National Weather Service Data]), but the precipitation totals differed across months (15.0, 14.0, and 2.8 cm for June, July, and August, respectively [National Weather Service Data]).

DISCUSSION

In general, water willow appears to be more resistant to desiccation than to inundation. A 5% overall mortality was observed in the desiccation trials versus a 69% overall mortality during the inundation trials. Even the shortest inundation duration in this study (2 weeks) resulted in $\geq$ 40% mortality across all depth treatments. My results concur with Dick et al. (2004) who also found that water willow was resistant to drought, but perished in depths > 1.2 m over an extended period of time. The cause of the susceptibility to inundation could be light limitation. In an inundation study conducted on three species of riparian plants (*Rumex* spp.), Nabben et al. (1999) reported that mortality rates of juvenile plants were greater when flooded with all light blocked, than for plants in conditions were light was provided (70% versus 0% mortality). They also found a decrease in dry weight for plants exposed to longer inundation durations. The average turbidity in the pond used in this study was 19 NTUs, and several cyanobacteria blooms were observed during the trial period, thus light was limiting to inundated plants. An additional indication of light limitation was the longer stems of the plants at 0.75 m during the 2 and 4 week trials (Figure 3). These plants were most likely receiving small but inadequate amounts of sunlight triggering a stem elongation response (Stern et al. 2003). The susceptibility to light limitation is consistent with Fritz and Feminella (2003), who noted water willow was confined to areas exposed to direct sunlight. Additionally, it commonly inhabits areas in and around lotic systems that typically are prone to flooding in late winter and spring when most river macrophytes are still dormant (Haslam 1978).

Water willow in the desiccation experiments lost height and increased the total number of leaves. This response also was observed in an alder species *Alnus maritime*, which responded to drought by maintaining a high rate of photosynthesis, increased leaf specific weight, and increased the root:shoot ratio (Schrader et al. in press). The large root and rhizomes of water willow (Penfound 1940) probably facilitate its ability to extract water from the soil and store ample amounts of food, thereby increasing resistance to drying conditions (Stern et al. 2003, Schrader et al. in press). The decrease in height that occurred in both desiccation trials could be a response of the plant to reallocate energy to leaves to produce more food, rather than upward growth (Figure 4). However, the increase in lateral growth also occurs when the apical meristem is removed, which could be the result of herbivory (Crawley 1997b) or the death of the upper stem. Plants in the monthly desiccation trial also showed a decrease in dry weight throughout the experiment. Typically, decreases in precipitation are coupled with increases in temperature from June through August in the Midwestern United States, which could result in both water and heat stress for plants (Crawley 1997a). Despite having similar temperatures for June, July, and August during my desiccation experiment, I still detected differences between treatments, which could indicate that warmer and dryer conditions could have more of an effect on water willow.

My findings provide information that can be used to select candidate reservoirs for water willow establishment based on historical water level fluctuations. For example, based on my results I recommend a 4 week time limit for water level increases of 0.75 m and 1.5 m, and 2 week limit for 2.25 m increases (longer durations result in about 100% mortality). Applying these limits to the reservoirs listed in Table 1, only Big Hill, El Dorado, and Marion reservoirs would be good candidates to successfully support water willow populations. This assessment is further supported by the fact that large populations of water willow successfully established in El Dorado and Big Hill reservoirs (D. D. Nygren, Kansas Department of Wildlife and Parks, personal communication). Additionally, this information could be used to mitigate magnitude and timing of water levels in reservoirs where water willow is established.

My general recommendation for future research would be to quantify minimum light and moisture requirements for growth and survival. Future inundation research should investigate a range of water clarities and depths, testing the effects of inundation and light limitation in combination and independently. Future desiccation experiments should investigate how soil type and plant interactions (e.g., shading, competition, etc.) may affect growth and survival during periods of drought.

Table 1.—Mean duration of increased or decreased water levels in respect to the conservation pool level from April to September for 1995 through 2002. Data are reported as the mean duration in days ± 1 SE (maximum). Durations were calculated by counting the number of consecutive days the water level was a certain elevation above or below conservation pool.

	Water level in respect to conservation pool				
Reservoir	**≥ 0.75 m**	**≥ 1.50 m**	**≥ 2.25 m**	**≤ 0.60 m**	**≤ 1.20 m**
Big Hill	2 ± 0.7 (3)	2	0	6 ± 3.3 (30)	0
Council Grove	14 ± 6.1 (48)	13 ± 5.6 (37)	13 ± 7.1 (34)	65 ± 26.8 (183)	39 ± 13.3 (74)
El Dorado	9 ± 5.1 (28)	9 ± 5.0 (14)	5	65 ± 26.8 (183)	89
Elk City	16 ± 4.2 (55)	17 ± 4.3 (45)	16 ± 4.4 (41)	11 ± 6.3 (28)	0
Fall River	15 ± 4.4 (78)	20 ± 6.4 (76)	17 ± 5.6 (66)	0	0
John Redmond	15 ± 4.7 (74)	23 ± 8.7 (68)	36 ± 12.8 (62)	21 ± 7.7 (77)	0
Marion	29	5 ± 3.5 (9)	0	24 ± 15.8 (71)	0
Toronto	17 ± 5.1 (75)	14 ± 4.9 (70)	12 ± 3.4 (36)	0	0
Overall	**14 ± 2.7 (78)**	**13 ± 2.6 (76)**	**12 ± 4.1 (66)**	**30 ± 13.9 (183)**	**16 ± 11.5 (89)**

Table 2.—Final water willow survival and dry weight for the inundation trials. Like superscript capital letters indicate no significant differences ($P \geq 0.05$).

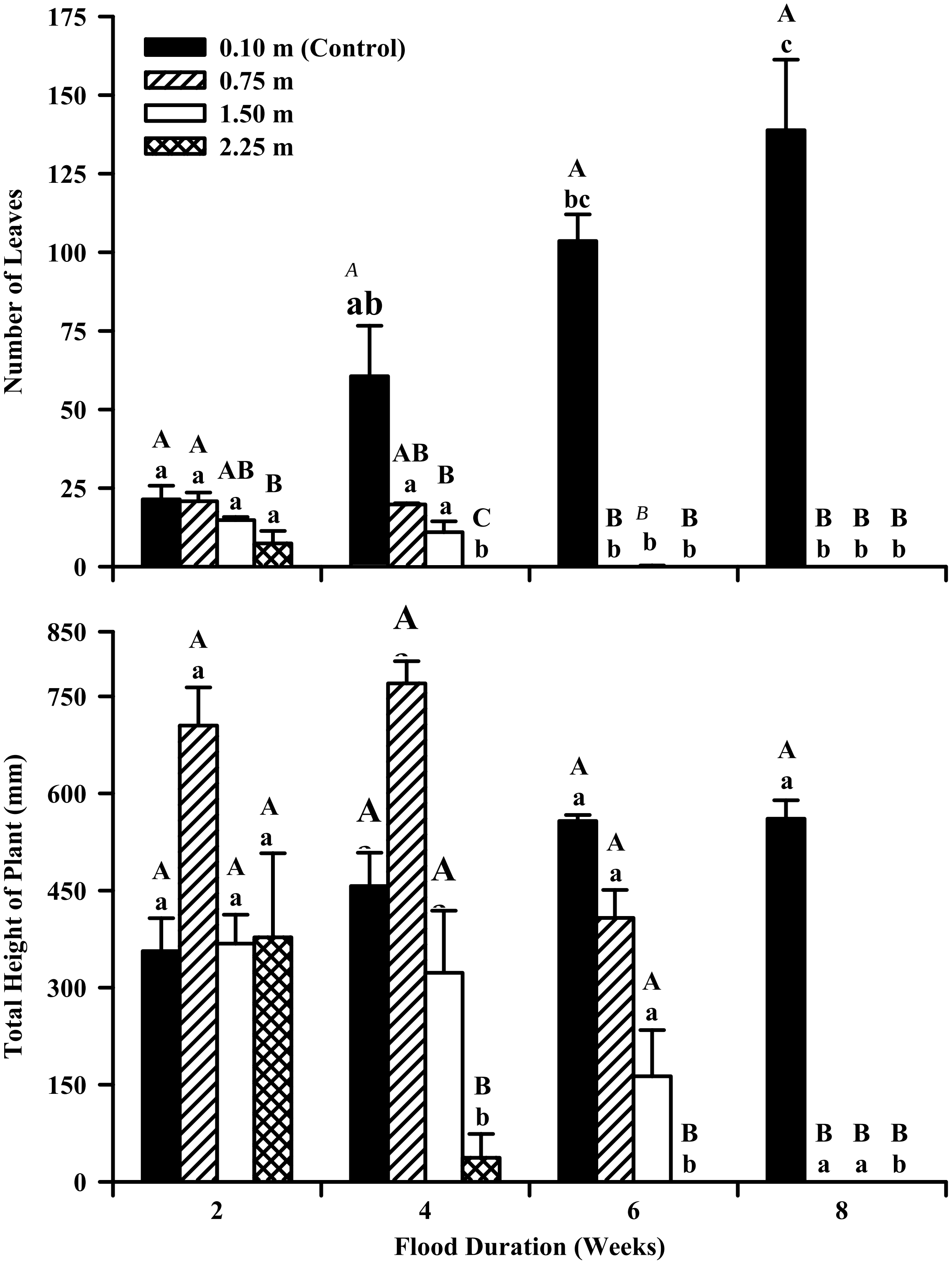
Inundation Duration	Experimental Depth (m)	% Mortality	Dry Weight (g)
0	0.10 Control	0	48.9 (10.1) ^{A}
2	0.75	40	48.6 (32.0) ^{AB}
	1.50	60	5.8 (3.6) ^{B}
	2.25	80	7.7 (7.7) ^{B}
4	0.75	40	20.8 (10.3) ^{AB}
	1.50	60	10.3 (8.3) ^{AB}
	2.25	100	0 ^{B}
6	0.75	100	0 ^{B}
	1.50	80	0.26 (0.26) ^{B}
	2.25	100	0 ^{B}
8	0.75	100	0 ^{B}
	1.50	100	0 ^{B}
	2.25	100	0 ^{B}

Figure 1.—The results from the inundation experiment testing water willow's inundation tolerance to progressively longer durations at three depths. Simulated inundation durations were 2, 4, 6, and 8 weeks at depths of 0.75 m, 1.50 m, and 2.25 m. The control depth was 0.10 m. Bars represent the mean ± 1 standard error. The bars with same capital letters are not significantly different ($P \geq 0.05$) for that week. Within each depth the bars with lower case letters are not significantly different ($P \geq 0.05$) across inundation durations.

Figure 2.—The results from water willow exposed to 2, 4, 6, and 8 week drying durations. Bars represent the mean ± 1 standard error, and those with same capital letter are not significantly different ($P \geq 0.05$).

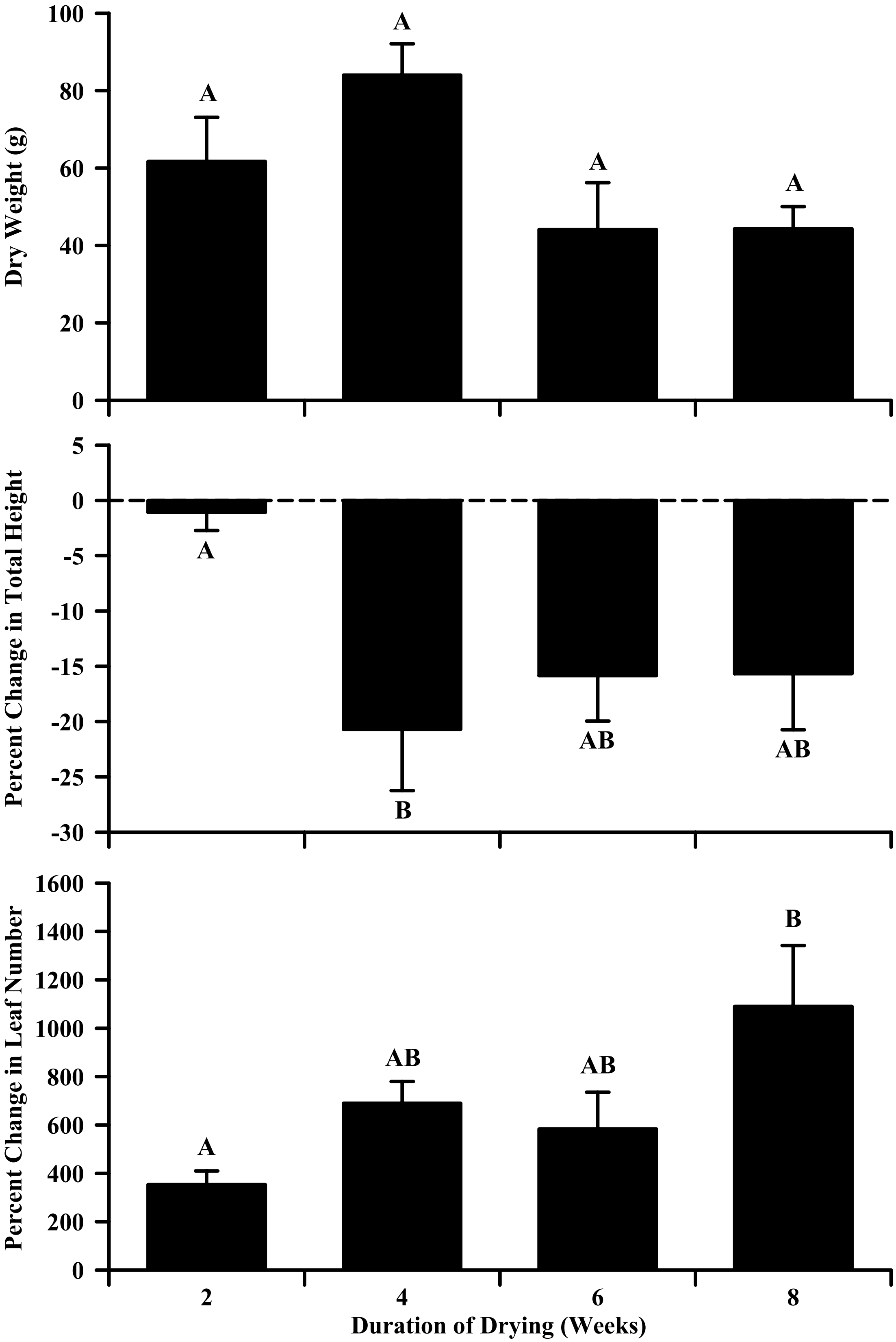
Figure 3.—The results from the experiment investigating if water willow response to drying differed among months. Two and 4 week duration were conducted within each month. Bars represent the mean ± 1 standard error, and those with same capital letters are not significantly different ($P \geq 0.05$).

Figure 1.



0.10 m (Control)
0.75 m
1.50 m
2.25 m
Number of Leaves
0
25
50
75
100
125
150
175
A a
A a
AB a
B a
A ab
AB a
B a
C b
A bc
B b
B b
B b
A c
B b
B b
B b
Total Height of Plant (mm)
0
150
300
450
600
750
850
A a
A a
A a
A a
A
A
A
B b
A a
A a
A a
B b
A a
B a
B a
B b
2
4
6
8
Flood Duration (Weeks)

Figure 2.



Dry Weight (g)
100
80
60
40
20
0
A
A
A
A
Percent Change in Total Height
5
0
-5
-10
-15
-20
-25
-30
A
B
AB
AB
Percent Change in Leaf Number
1600
1400
1200
1000
800
600
400
200
0
A
AB
AB
B
2
4
6
8
Duration of Drying (Weeks)

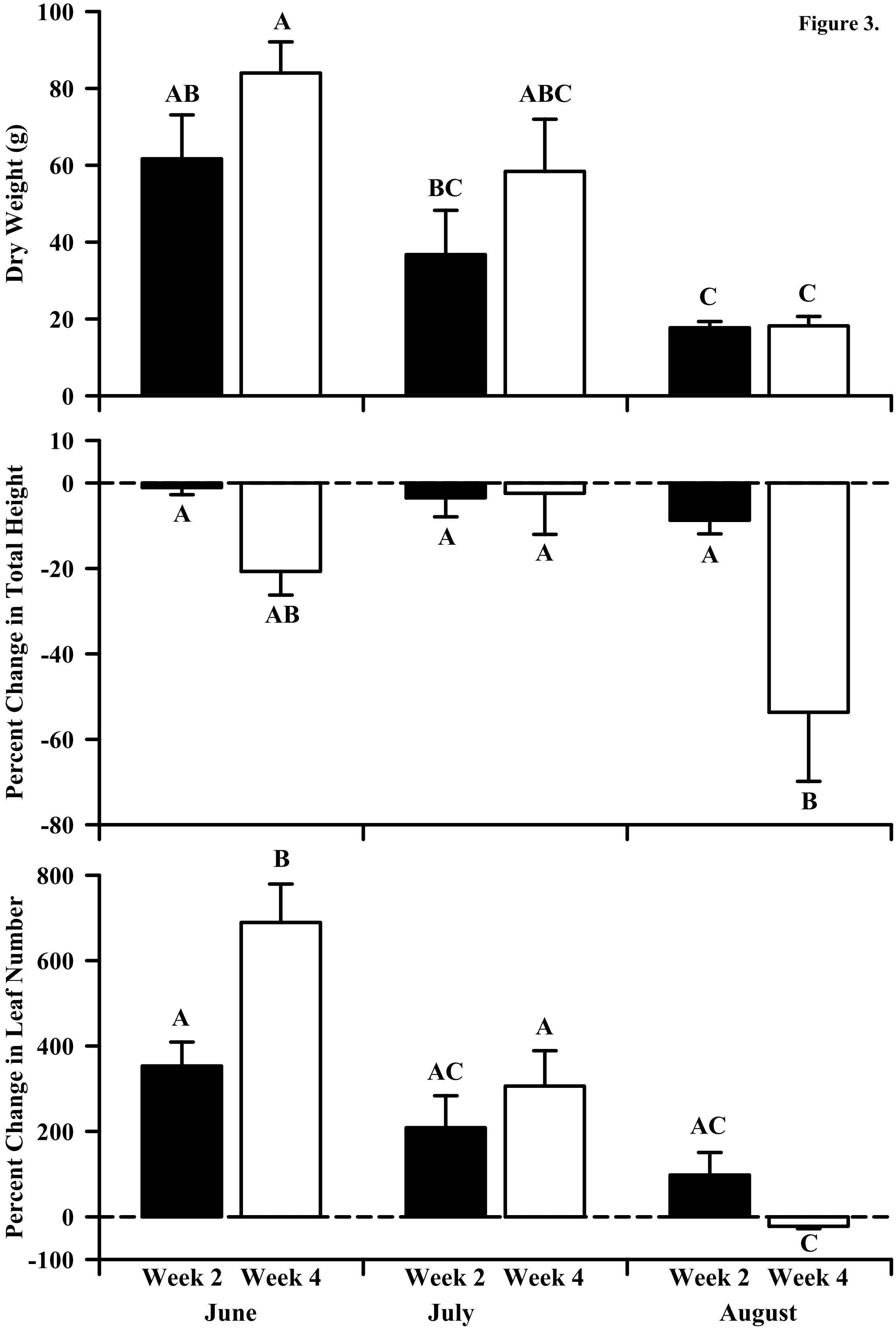


Figure 3.
Dry Weight (g)
100
80
60
40
20
0
AB
A
BC
ABC
C
C
Percent Change in Total Height
10
0
-20
-40
-60
-80
A
AB
A
A
A
B
Percent Change in Leaf Number
800
600
400
200
0
-100
A
B
AC
A
AC
C
Week 2
Week 4
Week 2
Week 4
Week 2
Week 4
June
July
August

CHAPTER 5

SUMMARY AND CONCLUSIONS

The primary goal of my research was to characterize the effects of an emergent macrophyte on littoral assemblages in reservoirs. Overall, I found that water willow establishment increased abundance and diversity of littoral zooplankton, macroinvertebrates, and fishes. This increase in diversity was coincident with increased habitat diversity and complexity in coves with water willow. However, temporal variability in water levels also influenced structural complexity in these reservoirs. In particular, decreasing water levels from June to August significantly reduced availability of structural habitat. Whereas the receding water level may have negative impacts on littoral assemblages by increasing competition and predation risk, abundance of some species also increased from June to August because of recruitment of age-0 fish and potentially seasonal movements related to food and cover availability. These temporal and spatial patterns of variation were the primary drivers of assemblage dynamics.

Water willow coves had greater densities of age-0 largemouth bass than control coves, but no differences were found in growth, condition, or diet. This pattern was generally consistent among reservoirs and sample years. In contrast, the small impoundments had significantly greater densities but lower growth and condition than water willow coves in large reservoirs. Poorer condition of age-0 largemouth bass and a lower frequency of fish in the diet suggest that density depend factors were likely more important in small impoundments.

Water willow may have facilitated an increase in abundance and diversity of consumers by increasing littoral zone productivity. Unlike other habitat enhancement structures that simply concentrate organisms without changing the productivity of the system (Gowan and Fausch 1996), emergent macrophytes are productive primary producers (Wetzel 2001) that may increase energy availability in littoral areas. Senescence of macrophytes releases nutrients acquired from sediments, stimulating pelagic production (Carpenter 1980) and increasing organic substrate used by benthic organisms (Beckett et al. 1992). Future studies that evaluate the contribution of water willow to system productivity will help managers evaluate its potential for increasing reservoir carrying capacity for sport fisheries.

The findings from Chapters 2 and 3 both support the use of water willow for habitat enhancement, but results from Chapter 4 suggests its use is restricted to reservoirs with relatively stable water levels. Water willow appeared to be more resistant to desiccation than to inundation. A 5% overall mortality was observed for the desiccation trials versus a 69% overall mortality from the inundation trials. Even the shortest inundation duration in this study (2 weeks) resulted in $\geq$ 40% mortality across all depth treatments, and was likely due to light limitation. My findings provide information that can be used to select candidate reservoirs for water willow establishment based on expected water-level fluctuations. Additionally, this information could be used to manage water levels in reservoirs where water willow currently provides important habitat for fishes.

Dynamic relationships exist within and among organisms and their environment. Using a large scale habitat manipulation across three large impoundments and investigating its effects across months and years provided valuable insight into the role of emergent macrophytes in structuring littoral assemblages. Expanding research to incorporate larger spatial and temporal scales is necessary to fully understand how aquatic systems function (Fausch et al. 2002). All three reservoirs exhibited seasonal patterns of decreasing water levels from June to August, which reduced the availability of structural habitat while fish abundances were increasing. This reduction in habitat could increase competitive interactions among fishes.

I did not investigate the role of water willow throughout the rest of the year. Water willow establishment may facilitate littoral recolonization after periods of extended drought (Chapter 3). This could be due to water willows desiccation tolerance, coupled with increases in riparian vegetation and thereby providing cover and organic resources. If water willow consistently supports greater diversity and abundance of littoral organisms throughout the year and facilitates their survival through drought events may result in system-wide effects. Increasing a top predator like the largemouth bass could have a cascading effect into pelagic areas where they will also forage, especially in spring and fall, competing with other pelagic piscivores (Raborn et al. 2004).

Spatial variation in effects of water willow within these reservoirs was consistent across the three study reservoirs that occupied separate river basins. Thus, my results are indicative of general patterns and processes that occur across reservoirs in the Midwest. Future research should concentrate on mechanisms responsible for changes in assemblage structure and how those changes are mediated by stochastic environmental conditions.

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APPENDICES

Table 1.—Results from the multivariate analysis of covariance (MANCOVA) for El Dorado Reservoir testing differences in fish, macroinvertebrate, and zooplankton abundance between water willow and control coves and among months using year as a covariate. Organisms that occurred at > 10% of the sampling sites were included in the analysis. Degrees of freedom are reported as hypothesis, error.

MANCOVA	**Wilk's Λ**	**F**	**df**	***P*-value**
WW*Month	0.026	1.811	98, 34	0.026

ANCOVA	**Dependent Variable**	**F**	**df**	***P*-value**
WW				
Fishes	Age-0 *Lepomis* spp.	1, 65	12.026	0.001
	Pomoxis annularis	1, 65	12.541	0.001
Macro	Ephemeroptera Heptageniidae	1, 65	27.217	0.000
	Hemiptera Corixidae	1, 65	21.533	0.000
	Trichoptera Leptoceridae	1, 65	12.905	0.001
	Ephemeroptera Ephemeridae	1, 65	7.914	0.006
Month				
Fishes	*Pimephales notatus*	12.14	2, 65	0.000
	Age-0 *Lepomis* spp.	38.44	2, 65	0.000
	Percina phoxocephala	8.4	2, 65	0.001
	Gambusia affinis	6.85	2, 65	0.002
	Pomoxis annularis	6.57	2, 65	0.003

Table 1.—Continued.

	Labidesthes sicculus	5.05	2, 65	0.009
Macro	Diptera Chironomidae	9.35	2, 65	0.000
	Ephemeroptera Baetidae	5.39	2, 65	0.007
Zoo	Rotifera	4.46	2, 65	0.015
	Leptodora	3.72	2, 65	0.029
Cove Type * Month				
Fishes	*Ictalurus punctatus*	18.19	1, 65	0.000

Table 2.—Results from the multivariate analysis of covariance (MANCOVA) for Hillsdale Reservoir testing differences in fish, macroinvertebrate, and zooplankton abundance between water willow and control coves and among months using year as a covariate. Organisms that occurred at > 10% of the sampling sites were included in the analysis. Degrees of freedom are reported as hypothesis, error.

MANCOVA	**Wilk's Λ**	**F**	**df**	***P*-value**
WW	0.12	2.95	47, 19	0.006
Month	0.008	4.09	94, 38	0.000

ANCOVA		**Dependent Variable**	**F**	**df**	***P*-value**
WW					
	Fishes	*Pimephales promelas*	8.711	1, 65	0.004
		Gambusia affinis	7.105	1, 65	0.010
		Pimephales notatus	6.574	1, 65	0.013
	Macro	Hemiptera Corixidae	13.005	1, 65	0.001
		Odonata Coenagrionidae	10.346	1, 65	0.002
		Coleoptera Haliplidae	7.609	1, 65	0.008
		Ephemeroptera Caenidae	6.699	1, 65	0.012
		Diptera Culicidae	6.418	1, 65	0.014
	Zoo	Chydoridae	12.104	1, 65	0.001
Month					
	Fishes	*Pimephales notatus*	17.921	2, 65	0.000
		Lepomis macrochirus	7.202	2, 65	0.001
	Macro	Gastropoda	5.782	2, 65	0.005

Table 2.—Continued.

	Hemiptera Corixidae	4.621	2, 65	0.013
Zoo	Sididae	6.627	2, 65	0.002
	Naplii	6.135	2, 65	0.004
	Rotifera	5.998	2, 65	0.004
	Calanoida	5.671	2, 65	0.005
Cove Type * Month				
Fishes	Age-0 *Lepomis* spp.	6.692	2, 65	0.002

Table 3.—Results from the multivariate analysis of covariance (MANCOVA) for Melvern Reservoir testing differences in fish, macroinvertebrate, and zooplankton abundance between water willow and control coves and among months using year as a covariate. Organisms that occurred at > 10% of the sampling sites were included in the analysis. Degrees of freedom are reported as hypothesis, error.

MANCOVA	**Wilk's Λ**	**F**	**df**	***P*-value**
WW	0.011	2.473	46, 14	0.034
Month	0.006	3.631	92, 28	0.000

ANCOVA	**Dependent Variable**	**F**	**df**	***P*-value**
WW				
Fishes	*Etheostoma spectabile*	1, 59	30.759	0.000
	Age-0 *Micropterus salmoides*	1, 59	13.88	0.000
Month				
Fishes	*Lepomis macrochirus*	2, 59	9.906	0.000
	Lepomis megalotis	2, 59	9.196	0.000
	Age-0 *Lepomis* spp.	2, 59	42.309	0.000
	Pimephales notatus	2, 59	7.518	0.001
	Lepisosteus osseus	2, 59	7.451	0.001
	Lepomis humilis	2, 59	4.686	0.013
Macro	Branchiura	2, 59	10.671	0.000
	Ephemeroptera Ephemeridae	2, 59	5.898	0.005
Zoo	Cyclopoida	2, 59	8.31	0.001
	Bosminidae	2, 59	4.769	0.012