

Effects of American Water Willow Establishment on Density, Growth, Diet, and Condition of Age-0 Largemouth Bass in Kansas Reservoirs

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Abstract.—Many Kansas reservoirs are currently experiencing decreased sport fish production as a result of the typical aging processes that occur in impounded systems. American water willow *Justicia americana* was planted in three Kansas reservoirs (>1,800 ha) for littoral zone habitat enhancement to mitigate sport fish losses and increase the recruitment of age-0 largemouth bass *Micropterus salmoides*. We investigated whether the density, growth, condition, and diet of age-0 largemouth bass in coves with water willow differed from coves without water willow in these reservoirs. Samples of largemouth bass were collected from 2001 to 2004 in June, July, and August. We found a consistent pattern among reservoirs and sample years; coves with water willow had significantly greater densities of age-0 largemouth bass than control coves, but no significant differences were found in growth, condition, or diet. Water willow beds appeared to buffer wave action, trapping fine sediments and floating debris, which significantly increased the overall habitat complexity. The additional organic material may have augmented littoral productivity, supporting the higher densities without physiologically hindering the age-0 largemouth bass. Overall, our study suggests that water willow establishment is an effective means of enhancing littoral nursery habitat for age-0 largemouth bass.

Macrophytes can benefit largemouth bass *Micropterus salmoides* 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). 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. The structural complexity provided by

macrophytes is thought to increase 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 abundance of zooplankton (Quade 1969; Timms and Moss 1984; Moss et al. 1996), macroinvertebrates (Tolonen et al. 2003), and fish (Dibble et al. 1996; Smart et al. 1996) as well as more diverse fish assemblages (Killgore et al. 1989; Keiper et al. 1998; Pierce et al. 2001). 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; Strakosh et al. 2005). These reservoirs are ideal

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targets for macrophyte establishment to increase sport fish production and reduce shoreline erosion (Dick et al. 2004). Whereas successfully establishing aquatic macrophytes is often limited by the high abundances of herbivores and benthic feeding organisms (e.g., common carp *Cyprinus carpio*) that uproot them (Cox 1999; Dick et al. 2004; Smart et al. 2005), American water willow *Justicia americana* (hereafter, water willow) is resistant to these disturbances (Dick et al. 2004).

The introduction of water willow in reservoirs provides an opportunity to assess the effect of a large-scale habitat manipulation. Currently, the majority of the literature on the relationships between macrophytes and centrarchid fishes 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 (2006) found that areas with water willow had greater habitat complexity as well as a greater diversity and abundance of macroinvertebrates, zooplankton, and fishes than areas without water willow. Therefore, we tested the effects of water willow introduction on population dynamics of age-0 largemouth bass. We predicted the presence of water willow would be associated with higher abundance, growth rate, and condition of age-0 largemouth bass because of increased habitat complexity and diet quality (i.e., more macroinvertebrates and fishes) relative to habitats devoid of vegetation.

Methods

Study sites.—Littoral habitats of three Kansas impoundments (1,853–3,240 ha) were sampled during June, July, and August from 2001 to 2004. The three reservoirs were Hillsdale Reservoir (completed in 1982), Melvern Reservoir (1972), and El Dorado Reservoir (1981). All of the reservoirs were primarily built for flood control but also 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 sport fish production through water willow establishment. Before water willow establishment these reservoirs were mostly devoid of aquatic macrophytes.

Lakewide 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 our study. Cove area was 1.77 ± 1.14 ha (mean \pm SD). Coves were chosen as sampling units because age-0 largemouth bass exhibit limited movement patterns and usually do not migrate between

coves (Copeland and Noble 1994). In Hillsdale and Melvern reservoirs, three of the six coves were randomly selected for water willow establishment 1 year before sampling, and the other three coves served as controls. The water willow used for plantings were at least 0.5 m tall, exhibited no visible signs of stress (i.e., yellowing leaves, broken stalks, and insect infestations), and had the majority of the root system intact. Individuals were planted 0.4 m apart in rows parallel to their 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.—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. All sampling was conducted between 0800 and 2100 hours. At each sampling location a 36.7-m-long \times 2.0-m-high block net (3.2 mm bar mesh) was used to enclose a 149-m² (24.5 m \times 6.1 m) area parallel to and starting from the shore. Before setting up the block net, we measured dissolved oxygen (mg/L), conductivity (μ S/cm), temperature ($^{\circ}$ C), and turbidity (nephelometric turbidity units [NTU]) in the center of the sampling area using a YSI Model 85 meter (Yellow Springs Instruments, Yellow Springs, Ohio) and an Orbeco-Hellige turbidity meter. The block net was carefully maneuvered into position to minimize disturbance of fish, secured to the bottom using poles and weights, and then inspected for any gaps.

Before fish sampling, we recorded the vegetation density, substrate, and water depth in each enclosure along two transects perpendicular to the 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 by placing a 0.5-m quadrant in the water and counting the stems within the quadrant (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, rootwads, and vegetation were visually estimated for the enclosure.

Age-0 largemouth bass were sampled with 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 each enclosure, one person electrofishing and

netting and the other person netting. Sampling effort was standardized by area of each enclosure (149 m²). Actual fishing time (i.e., duration of electric current application [s]) was used to ensure that consecutive runs within an enclosure were sampled with approximately equal effort. Multiple passes were conducted until an obvious depletion rate was achieved (i.e., each consecutive run consisted of less than one-half the number of fish found in the previous run), with a minimum of three and a maximum of six runs. The maximum likelihood (ML) method assuming constant probability of capture (Zippin 1956) was used to estimate the density (fish/m²) 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 can underestimate population size (Peterson et al. 2004); thus, enclosures with greater habitat complexity (i.e., water willow) may have higher densities than we report.

Age-0 largemouth bass were placed on ice and brought to the laboratory 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 the contents were then fixed in a 10% formalin solution, rinsed in water, and stored in 70% alcohol (Bowen 1996). Stomach contents were examined from three fish per 5-mm length-class from each cove from each month ($n = 924$). Diet items were identified (when possible) to species for fish and to family 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 \times 1-mm squares and recording the area occupied by each food item, which was used as a surrogate for mass (Hellowell and Abel 1971; Franssen and Gido 2006). Whereas this method only gives an approximation of biomass or volume, we choose this simpler method to increase the spatial and temporal extent of this analysis.

Daily growth rings from age-0 largemouth bass sagittal otoliths were used to test whether growth rates differed in fish from 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 (Isely et al. 1987; Secor et al. 1992). Daily growth rings were examined from five fish per 5-mm length-class from each cove for each month ($n = 1,133$; Tripe 2000). Approximate age was calculated by adding 5 d to the daily growth ring count to adjust for the period

between hatching and swim-up (Kramer and Smith 1962).

Following Sutton et al. (2000), the residualized dry weight (RDW) was used as an index of condition. Condition (RDW) was calculated by modeling dry weight as a function of the weight-length equation $W = aL^b$, where W is weight and L is length. The intercept (a) and the slope (b) were estimated based on the equation $\log_{10}(\text{dry weight}) = \log_{10}(a) + b \times \log_{10}(L) + \text{RDW}$. 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 (as does Fulton's condition factor, for example), 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 probably due to protein mass, which is a large component of fish dry weight and used for energy after lipid depletion. Condition was calculated for 10 fish per 5-mm length-class from each cove from each month ($n = 1,577$).

Data analyses.—Data from the two sampling sites within each cove for a given time period were pooled for all analyses. Thus, our sampling units were individual coves. Samples were not able to be collected from Melvern Reservoir in June of 2001, which reduced our total sample size to 210. 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 $\log_{10}(n + 1)$ transformed and percent composition data by area were arcsine-square-root transformed if necessary.

Split-plot, repeated-measures analyses of variance (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 subplots. 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 nonconstant 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

TABLE 1.—Results from the split-plot, repeated-measures analysis of variance comparing age-0 largemouth bass densities, growth (mm/d), and condition (residual dry weight [RDW]) among three reservoirs. The reservoirs were the blocks, the whole-plot treatments were water willow (WW) and control (nonvegetated), and the coves were the subplots. The repeated measures were years and months. Significant values derived from the false discovery rate ($P < 0.021$) are indicated by bold italics.

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

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. The false discovery rate (FDR) method of Benjamini and Hochberg (1995) was employed to control type I and type II error rates for the three SPRANOVAs. An FDR-controlled P -value of 0.024 was necessary for rejection of the null hypothesis.

Multivariate analysis of variance (MANOVA) was conducted to investigate whether the food habits (percent composition by area and total consumption by area) of age-0 largemouth bass differed between water willow and control coves. Diet items that occurred in less than 5% of age-0 largemouth bass stomachs were pooled into higher taxonomic groups and used as dependent variables in the MANOVA. A miscellaneous macroinvertebrate category was created to incorporate infrequent macroinvertebrates and stomach contents that we were unable to identify to a lower taxonomic level. This general category allowed us to contrast fish that generally foraged on invertebrates and those foraging on zooplankton or fish, which we felt more accurately reflected ontogenetic changes in diet. A total of eight categories (i.e., dependent variables) were used in our diet analyses; zooplankton, fish, Ephemeroptera, Hemiptera, Corixidae (Hemiptera), Chironomidae (Diptera), Amphipoda, and miscellaneous macroinvertebrates. We arcsine-transformed percent composition by area for each diet category. Fixed effects were year (four levels: 2001–2004), month (three levels: June, July, and August), reservoir (three levels: El Dorado, Hillsdale, and Melvern), and water willow (two levels: coves with and without water

willow). Wilk's lambda was used to calculate the multivariate F -statistic. If the overall MANOVA was significant, separate analyses of variances (ANOVAs) were conducted to investigate variation in each diet item separately. As above, FDR was used to control type I and type II error rates across the eight ANOVAs, and an FDR-controlled P -value of 0.029 was necessary for rejection of the null hypothesis.

Multivariate analysis of covariance was used to test for differences in habitat between water willow and control coves and among months, while controlling for variations among reservoirs and years. 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 we were primarily interested in the effects of water willow and not the differences among reservoirs or years. If the overall MANCOVA was significant, separate analyses of covariance (ANCOVAs) were conducted to investigate each dependent variable separately. An FDR-controlled P -value of 0.033 was necessary for rejection of the null hypothesis across the nine ANCOVAs.

Results

Water Willow versus Control Coves

Age-0 largemouth bass were approximately twice as abundant in water willow coves ($584 \pm 1,254$ fish/ha [mean \pm SD], $N = 210$) than in control coves (232 ± 502 fish/ha, $N = 210$) ($P = 0.001$; Table 1). Although there was considerable variability among reservoirs, years, and months in age-0 largemouth bass densities (Figure 1), these factors did not interact with cove type (i.e., presence of water willow). Growth (mm/d) of age-

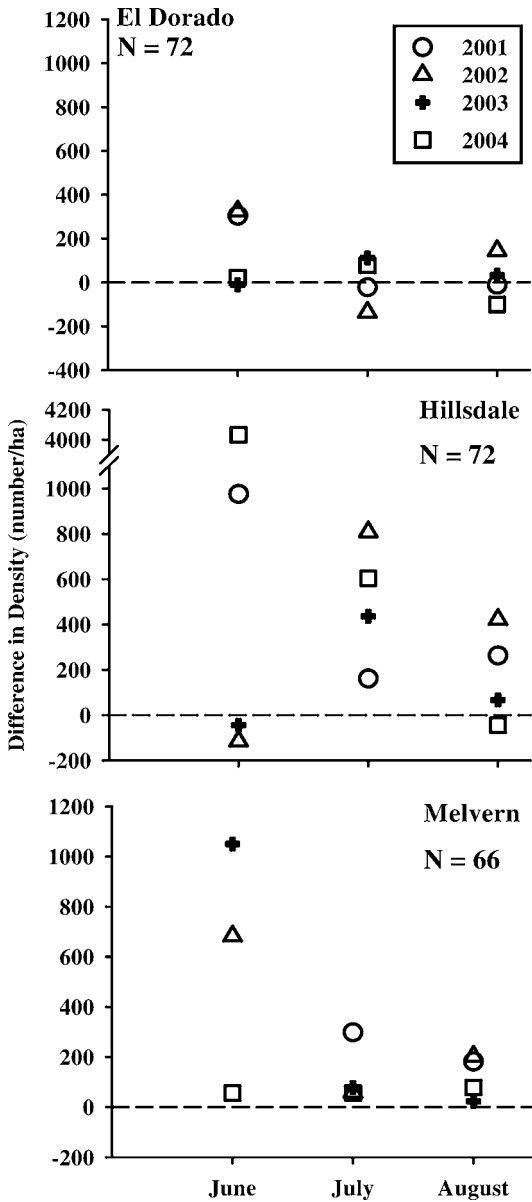


FIGURE 1.—Differences in age-0 largemouth bass density between water willow and control coves in El Dorado, Hillsdale, and Melvern reservoirs, 2001–2004.

0 largemouth bass was highly variable between water willow and control coves (Figure 2), and there was a significant year \times water willow treatment interaction (Table 1). Whereas control coves in 2004 had significantly ($P < 0.002$) higher growth rates than those found in other years, the contrast statements failed to show a significant difference between water willow and control coves when compared within years ($P > 0.07$). No significant differences were found in

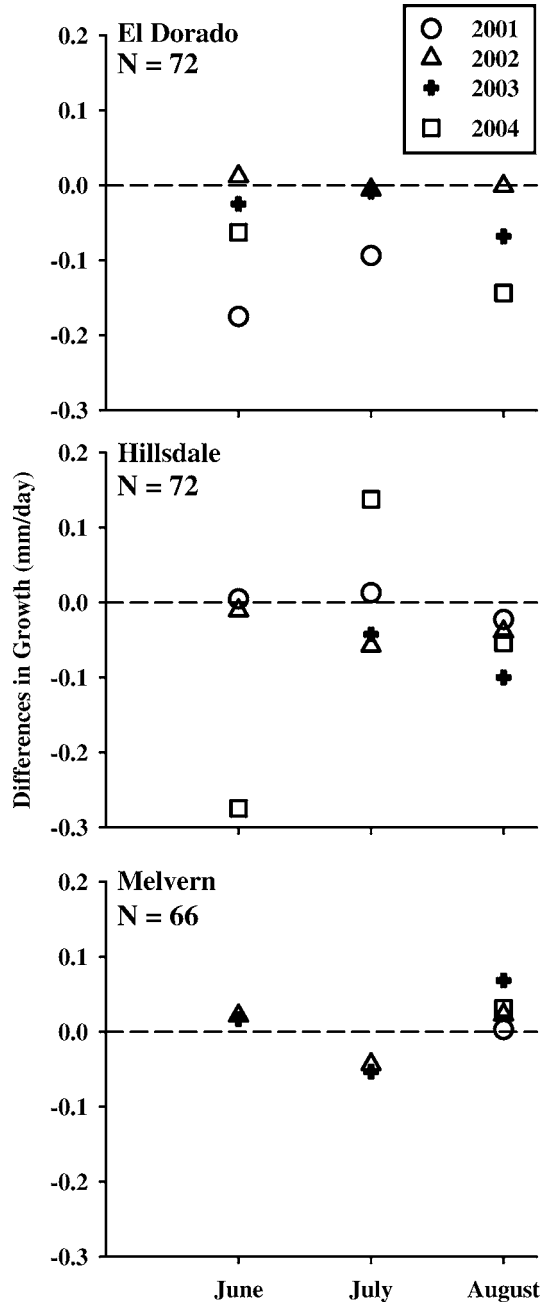


FIGURE 2.—Differences in age-0 largemouth bass growth between water willow and control coves in El Dorado, Hillsdale, and Melvern reservoirs, 2001–2004.

age-0 largemouth bass condition between water willow and control coves (Table 1; Figure 3).

All reservoirs had significant annual and monthly variation in age-0 largemouth bass density, growth, and condition (Table 1). Hillsdale Reservoir had the highest

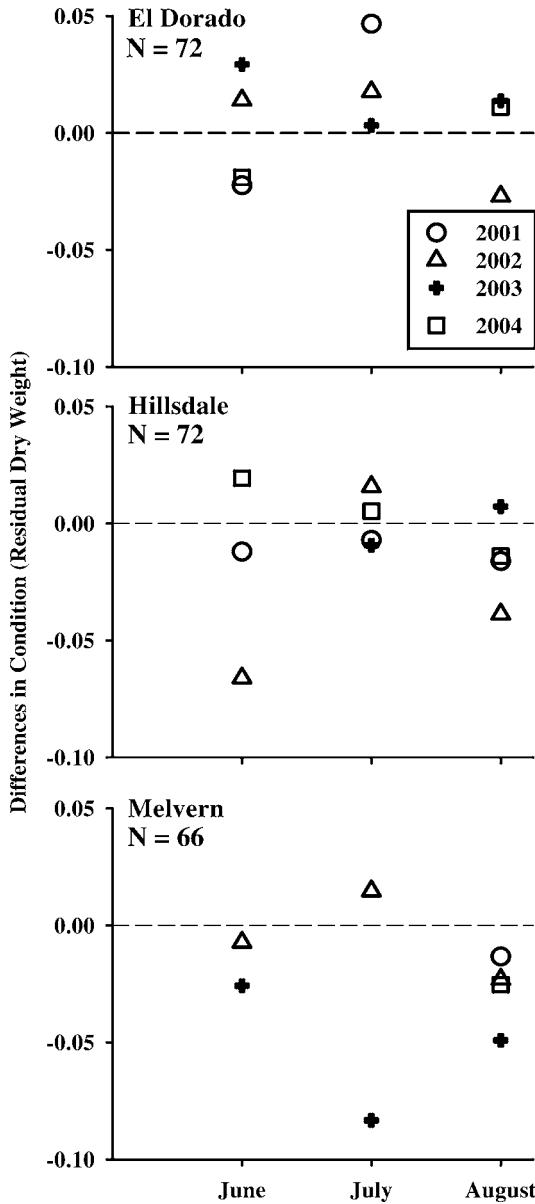


FIGURE 3.—Differences in age-0 largemouth bass condition (residual dry weight [see text]) between water willow and control coves in El Dorado, Hillsdale, and Melvern reservoirs, 2001–2004.

densities, up to an order of magnitude greater than in other reservoirs (Figure 1). Monthly abundances varied among years. No consistent pattern was found for growth or condition (Figures 2, 3). No significant differences (after controlling for false discovery rates) were found between water willow and control coves for diet composition (MANOVA: Wilk’s lambda = 0.554, $F_{8,71} = 0.8, P = 0.05$) or consumption (MANOVA:

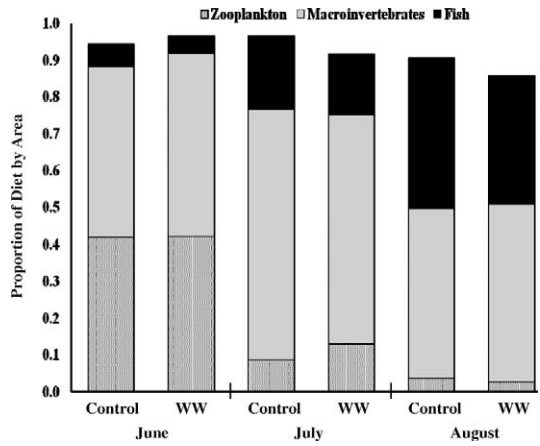


FIGURE 4.—Composition of age-0 largemouth bass diets in June, July, and August 2001–2004 in water willow (WW) and control coves. Values are the mean proportions of the different diet items in stomachs.

Wilk’s lambda = 0.985, $F_{8, 858} = 1.7, P = 0.105$) (Figure 4).

Habitat Characteristics

Habitat variables differed significantly between water willow and control coves and among months (MANCOVA; Tables 2, 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. An almost 10-fold decrease in water willow stem density occurred from June to August. Flooded riparian vegetation, large and small woody debris, water willow density, and turbidity were significantly greater in June than in July or August, and water temperatures were significantly higher in July than in the other two months.

Discussion

Our data support the prediction that treatment coves containing water willow would have greater densities of age-0 largemouth bass than control coves, but they did not show significant differences in growth, condition, or diet between cove treatments. Higher densities of age-0 largemouth bass in areas with water willow were consistent 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). The mechanisms associated with the increase in age-0 largemouth bass abundance probably include the vegetated coves’ offering a refuge from predators and augmenting prey abundance

TABLE 2.—Summary of habitat variables for coves in Kansas reservoirs with (WW) and without (control) water willow, pooled across reservoirs and years. Each value is the mean (minimum, maximum) from 420 samples (210 from water willow coves and 210 from control coves).

Habitat variable	Jun		Jul		Aug	
	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 (no. stems/m ²)	12 (0, 76)	1 (0, 10)	5 (0, 51)	0 (0, 2)	2 (0, 18)	0 (0, 2)
Mean temperature (°C)	26 (22, 30)	26 (21, 32)	30 (26, 34)	30 (27, 34)	29 (23, 34)	28 (23, 33)
Dissolved oxygen (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 (µs/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)

(Dibble et al. 1996; Wrenn et al. 1996). Not only were there 30% higher densities of prey items (fish and invertebrates) in water willow coves (Strakosh 2006), there were also significantly greater amounts of woody debris and riparian vegetation, increasing the overall availability of complex habitat.

Although we did not have data before the introduction of water willow, our experimental design allowed us to infer that water willow alters the 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). This finding concurs with that of Fritz and Feminella (2003) and Fritz et al. (2004), who reported that water willow in lotic systems slowed current velocity and promoted substrate stabilization. Smaller substrate sizes in water willow coves may be attributable to trapping and accumulation of organic sediments, which also occurred

in lotic water willow patches (Fritz and Feminella 2003; Fritz et al. 2004) and 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 increasing structural complexity.

Greater densities of age-0 largemouth bass in water willow coves did not correspond to changes in growth, condition, or diet, suggesting that coves with water willow are 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 cover. 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

TABLE 3.—Results from a multivariate analysis of covariance testing for differences in fixed effects (cove type and month) with reservoir and year as covariates and the habitat measurements as dependent variables. The multivariate Wilk's lambda = 0.577 ($F = 11.679$; $df = 12, 191$; $P = 0.000$) for cove type and 0.637 ($F = 9.073$; $df = 12, 191$; $P = 0.000$) for month.

Fixed effect	Univariate dependent Variable	F	df	P
Cove type	% 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 temperature (°C)	59.936	2, 202	0.000
	Turbidity (NTU)	21.793	2, 202	0.000
	% Flooded riparian vegetation	19.473	2, 202	0.000
	Dissolved oxygen (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

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 among systems in quality and quantity of food resources.

In a concurrent study, Strakosh (2006) found that water willow was associated with greater abundance and diversity of zooplankton, macroinvertebrates, and fish. The mean abundance of fish species other than largemouth bass in water willow coves was 152 (compared with 91 in the control coves), and assemblages were generally dominated by opportunistic minnow species (red shiner *Cyprinella lutrensis* and bluntnose minnow *Pimephales notatus*) and sunfishes *Lepomis* spp. Increased abundance of other fishes in water willow areas could increase competitive interactions with age-0 largemouth bass, as largemouth bass are morphologically designed as a piscivore (Helfman et al. 1997) and can be easily out-competed when feeding on zooplankton or macroinvertebrates (Werner and Gilliam 1984). It is possible that interactions with other fishes resulted in the similar growth rates of age-0 largemouth bass between water willow and control coves despite the higher prey densities in the willow coves.

The age-0 largemouth bass in the reservoirs exhibited strong monthly and annual variation in density, which is probably attributable to water-level fluctuations and spawning chronology. Age-0 largemouth bass densities were usually highest in June, corresponding with the end of the spawning period. We also found the greatest differences in age-0 largemouth bass densities between water willow and control coves in June. These large differences were probably due to elevated spring water levels and the significantly greater amounts of inundated riparian vegetation in water willow coves than in 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.

Data from Hillsdale Reservoir highlight the importance of water-level fluctuations and their interactions with water willow in regulating largemouth bass population dynamics. In June of 2003, Hillsdale Reservoir had the lowest largemouth bass densities recorded for that reservoir, and this corresponded to low water levels (the mean \pm SD water level from March through June of 2003 was -1.0 ± 0.14 m; U.S. Army Corp of Engineers, Kansas City District,

unpublished data). The water level remained below the that of the conservation pool from 1 July 2002 until March of 2004, allowing abundant riparian vegetation to establish along the shoreline. The vegetation was inundated before the 2004 largemouth bass spawning period (late March through early June; Tripe 2000), resulting in the highest age-0 largemouth bass densities recorded among the reservoirs. Additionally, water willow coves had densities five times greater than for control coves. This difference may be due to water willow areas having greater structural complexity and organic material produced from consistent vegetative cover (Strakosh 2006). Additionally, water willow probably suffered little or no mortality from water level decreases owing 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 where 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 (Strakosh 2006). This increase in littoral fishes, coupled with decreasing emergent macrophyte habitat, could intensify the interactions among organisms within littoral areas. These interactions may be more significant in the fall months when age-0 largemouth bass store lipids in preparation 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 fish populations.

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) that may be critical for overwinter 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), probably 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 longer than 126 mm had an 80% greater survival rate than those less than 126 mm. Because we found no difference in largemouth bass growth or condition between water willow and control coves, it does not appear that water willow will influence ontogenetic shifts in diet or overwinter survival.

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. We found that water willow established in coves supported significantly greater abundances of age-0 largemouth bass without giving rise to the negative effects on growth or condition associated with density-dependent mechanisms. Thus, given the stability of water levels is adequate to sustain water willow (Strakosh et al. 2005), this appears to be a viable approach to offsetting the effects of habitat loss in reservoirs.

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