

Predictability of littoral-zone fish communities through ontogeny in Lake Texoma, Oklahoma-Texas, USA

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Synopsis

We sampled larval, juvenile and adult fishes from littoral-zone areas of a large reservoir (Lake Texoma, Oklahoma-Texas) (1) to characterize environmental factors that influenced fish community structure, (2) to examine how consistent fish–environment relationships were through ontogeny (i.e., larval vs. juvenile and adult), and (3) to measure the concordance of larval communities sampled during spring to juvenile and adult communities sampled at the same sites later in the year. Larval, juvenile and adult fish communities were dominated by Atherinidae (mainly inland silverside, *Menidia beryllina*) and Moronidae (mainly juvenile striped bass, *Morone saxatilis*) and were consistently structured along a gradient of site exposure to prevailing winds and waves. Larval, juvenile and adult communities along this gradient varied from atherinids and moronids at highly exposed sites to mostly centrarchids (primarily *Lepomis* and *Micropterus* spp.) at protected sites. Secondly, zooplankton densities, water clarity, and land-use characteristics were related to fish community structure. Rank correlation analyses and Mantel tests indicated that the spatial consistency and predictability of fish communities was high as larval fishes sampled during spring were concordant with juvenile and adult fishes sampled at the same sites during summer and fall in terms of abundance, richness, and community structure. We propose that the high predictability and spatial consistency of littoral-zone fishes in Lake Texoma was a function of relatively simple communities (dominated by 1–2 species) that were structured by factors, such as site exposure to winds and waves, that varied little through time.

Introduction

For fishes, their 'environment' encompasses multiple factors that are both abiotic (e.g., hydrology, habitat, water quality) and biotic (e.g., presence of other species, levels of primary production; Matthews 1998). Different life-history stages (e.g., larval vs. juvenile or adult) may be influenced by different environmental factors. For instance, springtime hydrology and associated turbidity may be important determinants in the local distribution of larval fishes (e.g., Matthews 1984, Mitzner 1991), whereas the structures of juvenile or adult fish communities may be more related to site-specific environmental factors, habitat diversity, or interactions with predators (Tonn & Magnuson 1982, Lyons & Magnuson 1987, Benson & Magnuson 1994, Lienesch & Matthews 2000, Marsh-Matthews & Matthews 2000). Identifying which environmental factors are important in the structuring of fish communities and how they vary through ontogeny may increase understanding of fish community dynamics.

Reservoirs represent ideal systems to study fish–environment relationships. Reservoirs exhibit strong spatial gradients with uplake regions being more riverine and downlake regions near the dam being more similar to natural lakes (Thornton et al. 1990, Gido et al. 2002). As a result, many biotic (e.g., fish communities) and abiotic (e.g., water clarity or nutrients) characteristics in reservoirs vary predictably along these gradients. Fish abundance, biomass, and species composition often exhibit predictable patterns along these gradients (Gelwick & Matthews 1990, Gido & Matthews 2000, Lienesch & Matthews 2000, Gido et al. 2002), though previous studies have been restricted to adult fishes. However, in some cases, local factors relative to a particular reach of shoreline (e.g., Lienesch & Matthews 2000, Gido et al. 2002) or landscape-level factors associated with a particular drainage basin (e.g., Larsen et al. 1986, Schloesser 1991, Williams et al. 2002 reported from streams) may override gradient-type variables in structuring reservoir communities. The interplay of these mechanisms results in a diversity of environmental conditions, which makes reservoirs unique study systems for assessing fish–environment relationships.

Our objectives were (1) to characterize environmental factors that influenced fish community

structure, (2) to examine how consistent fish–environment relationships were through ontogeny, and (3) to measure the concordance of larval fish communities sampled during spring to juvenile and adult fish communities sampled at the same sites later in the year. We focused on littoral–zone communities because they are an important functional component of aquatic systems (Northcote 1988), but are much less studied in reservoirs because communities are dominated by smaller-bodied species of no commercial or recreational interest. We made assessments of larval, juvenile and adult fish communities over a 6-month period during 2001. Larval communities were assessed monthly from March through June; we assessed juvenile and adult communities in July and October. We expected that juvenile and adult fish communities would be structured mostly around local habitat features because of their more diverse life-history requirements. Unlike larval fishes, many of these fishes are reproductively active, feed on a wide variety of foods (e.g., algae, fish, zooplankton, and benthic invertebrates), and require habitats that afford protection from larger-bodied piscivores. As we are aware of no similar studies with larval fishes, we had no expectations about what types of factors might be associated with larval communities, or whether these factors would be similar to or different from juvenile and adult fish communities. Previous studies also have indicated that littoral–zone fish communities in Lake Texoma are structured along strong spatial gradients (e.g., water clarity) that exist in the reservoir (Gido et al. 2002). Understanding these fish–environment relationships and how they change through time or ontogeny is important in understanding the overall dynamics and structure of reservoir fish communities.

Materials and methods

Study area

Lake Texoma is a 35 200-ha impoundment at the confluence of the Red and Washita rivers in Oklahoma and Texas, USA. The U.S. Army Corps of Engineers constructed the reservoir in 1944 for flood control and hydroelectric power production. The watershed of the reservoir encompasses about 103 000 km²; land use is predominantly agriculture,

ranching, and forest with relatively low human population densities. Highly saline inflows from the Red River occur due to natural salt sources in the headwaters and tributaries. As a result, conductance values in Lake Texoma are high for freshwater ($700\text{--}1200\ \mu\text{S}\cdot\text{cm}^{-1}$ Gelwick & Matthews 1990) and distinctly different between river arms (Red River arm, usually $1000\text{--}2000\ \mu\text{S}\cdot\text{cm}^{-1}$; Washita River arm, usually $500\text{--}1000\ \mu\text{S}\cdot\text{cm}^{-1}$). Secchi depths in the reservoir typically range from 50 to 125 cm and are usually greater downlake; maximum reservoir depth is around 25 m (Matthews 1984). Reservoir stages fluctuate about 2 m per year on average, but may exceed 3 m in any given year (U.S. Army Corps of Engineers 2003¹). Extensive sedimentation is the major anthropogenic influence on Lake Texoma as recent estimates indicate the reservoir has lost up to 11% of its storage capacity since construction (Gido et al. 2000).

Other aspects of the physical limnology of Lake Texoma differ from most reservoirs, and fish communities have been shown related to some of these characteristics. Water temperatures gradually decrease with increasing depth, but an abrupt thermocline is not observed (Matthews & Hill 1988). Rather, a distinct chemocline exists whereby a sharp decrease in dissolved oxygen and pH concurrent with an increase in specific conductance occurs between 4 and 10 m depth (Matthews & Hill 1988). Although the vertical position of the chemocline varied among stations and years, echolocator charts indicated that the summer distribution of many offshore fishes (especially those of schooling adult striped bass, *Morone saxatilis*) were typically greatest just above the chemocline regardless of its depth (Matthews et al. 1985). Analyses of inshore fish communities showed that juveniles of several species were related to levels of wave action associated with persistent southern winds common throughout summer (Lienesch & Matthews 2000) and reservoir water level changes (Gelwick & Matthews 1990). However, despite large annual differences in reservoir volume, temperature, and turbidity, fish communities have been relatively stable through time scales ranging from years to decades (Gido & Matthews 2000, Gido et al. 2000).

¹ U.S. Army Corps of Engineers, Tulsa District, Water Control Data Systems web site address: www.swt-wc.usace.army.mil/DENI.lakepage.html.

Field data collection

We collected larval fish samples monthly from March through June (March samples contained no fishes) at 41 sites on Lake Texoma (Figure 1) as part of a larger evaluation of anthropogenic influences on reservoir biota conducted during 1999–2001 (see Schnell et al. 2002, Eggleton et al. 2004 for more details). We collected samples at each site by making a 70-m tow with a 500- μm mesh net (diameter 0.5 m, opening area $0.2\ \text{m}^2$, net length 2 m) parallel to the shoreline in water 1.0–1.5 m deep. We took two replicates tows by two persons walking in tandem with the net between them; each person was less than 1 m from the net. Samples were preserved with 10% formalin, labeled, and returned to the laboratory for identification and enumeration. Because of high larval abundances in some tows, samples were subsampled as needed to produce more manageable numbers of fishes for identification. Subsampling consisted of pouring the collected sample into a gridded sorting pan, disentangling sample contents if necessary, and homogenizing the sample by repeated shaking. Following adequate mixing, 1/4, 1/8, or 1/16 of the sample (depending on total abundance of larvae) was sorted and identified. We conducted subsampling such that a minimum of 100 fishes was always identified. We identified larvae to family using

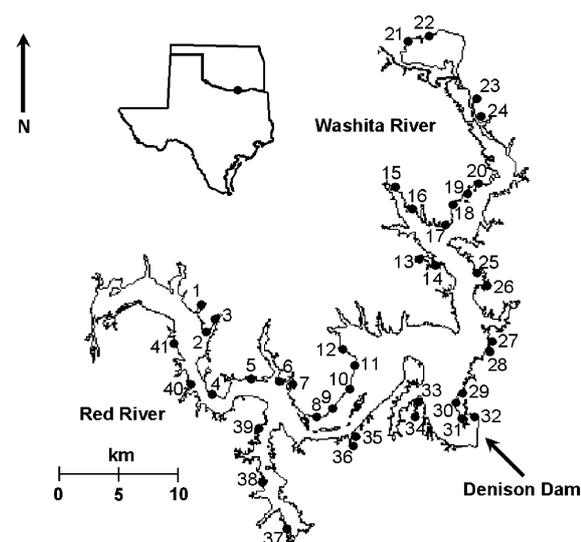


Figure 1. Location of the 41 study sites on Lake Texoma, Oklahoma-Texas.

standard keys (primarily TVA 1976 and Auer 1982, but also several unpublished government agency keys) and enumerated them with the aid of a stereoscope. We expressed larval abundances as number of larvae per tow based on extrapolation from the subsample.

We sampled juvenile and adult fishes at the same 41 sites during July and at 22 of the 41 sites during October. The sites sampled in October were a randomly selected subset of the 41 sites sampled in July and stratified by reservoir area (i.e., main reservoir vs. each river arm). Reservoir water levels were approximately 188 m above mean sea level during both periods; thus, shoreline habitat was essentially the same between sample periods. During both sampling periods, four replicate samples were taken at each site in adjacent 25-m reaches. For each reach, we took separate samples using a 7.62 m × 1.8 m bag seine (4.8-mm mesh, one offshore haul in water 1.0–1.5 m depth) and 4.6 m × 1.2 m (3.2-mm mesh, several inshore hauls) regular seine. We then pooled fishes from all inshore hauls and the offshore haul to depict the fish community for that 25-m reach; abundances were expressed as number of fishes per reach. Gido et al. (2002) indicated that four reaches per site were sufficient to depict fish community richness in littoral-zone areas of Lake Texoma, and provides additional details on sampling procedures. Following sorting and identification in the laboratory, we reclassified species to families for analysis to be consistent with the larval fish analyses.

We measured or estimated 24 environmental variables that encompassed physical, chemical, biotic, land-use, and hydrologic factors for each of the 41 sites (Appendix A). During a preliminary data analysis, we considered up to 20 additional variables because of their availability, but subsequently discarded them due to high correlation with one or more of the 24 variables used. Site exposure to winds and waves was ranked on a scale of 1 (low exposure) to 3 (high exposure). High-exposure sites contained an aspect of 120–240°, had fetches greater than 1 500 m, and were usually dominated by sand substrates. Low-exposure sites had variable aspects, short fetches usually < 500 m, and usually finer-particle substrates. Medium-exposure sites contained variable aspects and substrates and fetches of 500–1 500 m. Of the 41 sites, 20 were classified as high exposure, 10 as

medium, and 11 as low. Fisher's exact test indicated that sites of differing exposure level were homogeneously distributed across areas of the reservoir ($p = 0.54\text{--}0.75$ from pair-wise tests).

We estimated habitat diversity at each site as a function of substrate and cover complexity during July and October 2001 following Gido et al. (2002). We measured water chemistry variables at all sites in April, July and October. Because water chemistry varies through time and fish communities typically reflect recent environmental conditions, we used seasonal means for depicting site-specific water chemistry. For example, we used the site-specific average value for April and July in the July analyses, whereas the site-specific average value of July and October were used in October analyses. Water chemistry analyses were conducted in accordance with standard methods (APHA 1998) and performed through the U.S. Environmental Protection Agency laboratory in Ada, Oklahoma, USA. Land-use characteristics were determined for the drainage area of each site using geographic information system (GIS) in conjunction with the National Land Cover Dataset (Vogelmann et al. 2001). At sites without well-defined drainage areas, land use was characterized within a 500-m buffer surrounding the sites. Mean discharge was determined for each month and river arm with the monthly value assigned to each site in that river arm. Zero discharge was assigned for all 15 sites in the main reservoir during all months.

Data analysis

We used canonical correspondence analysis (CCA; ter Braak 1986) to assess relationships between fish communities and environmental variables. This technique is a direct gradient analysis that ordines a species × sample data matrix within the constraint that site and species scores be linear combinations of environmental variables (Palmer 1993). Although McCune & Grace (2002) warn that CCA may be inappropriate to describe community structure when environmental variables are not measured without error, their examples indicate minimal distortion of the resulting ordination when measurement error is less than 20%. Measurement error in most of our environmental variables, especially water chemistry, was suspected to be far less than 20%. Therefore, we

assumed that impacts of measurement error on environmental variables were negligible in our analyses. Significance of the fish–environment association was assessed by comparing observed eigenvalues from the first three ordination axes to those generated from randomization of the data (10 000 iterations). Rejection of this test meant that observed eigenvalues were greater than expected by chance (i.e., eigenvalues generated from randomized data), which indicated a significant association existed between fish communities and environmental variables. All CCA calculations were done using PC-ORD.²

To examine the spatial consistency between larval communities during the spring and juvenile and adult fish communities sampled from the same sites during the summer and fall, we calculated Spearman rank correlation coefficients (Zar 1999) between the abundance and richness of larval fish families in April, May, and June and the same measures for juvenile and adult fish families in July and October. All correlation analyses were performed using SAS.³ Additionally, we performed Mantel tests (Legendre & Legendre 1998) to assess the spatial concordance of larval communities during spring and juvenile and adult fish communities during summer and fall. Mantel tests were performed between family \times sample matrices (square-root transformed raw counts using the Sorensen dissimilarity measure) with PC-ORD. Significance for all analyses was declared at $\alpha = 0.05$. To account for multiple comparisons in correlation and Mantel analyses, sequential Bonferroni adjustment of alpha was done following Rice (1989) and Gelwick & Matthews (1992).

Results

Larval fishes

Broad spatial patterns in larval abundance were observed throughout sampling in that total abundances of larvae were consistently greater in the

river arms. Mean abundances from April through June were $313 \pm \text{SE of } 78$ and 275 ± 59 larvae tow^{-1} in the Red and Washita river arms, respectively, compared to 72 ± 19 larvae tow^{-1} in the main reservoir. Atherinidae, which in Lake Texoma included inland silverside, *Menidia beryllina*, and to a lesser extent, brook silverside, *Labidesthes sicculus* (Pratt et al. 2002), comprised 53% of the individuals sampled reservoir wide and were highly abundant in all areas of the reservoir. However, other families collected from larval fish communities differed among areas of the reservoir. Clupeid larvae were found almost exclusively in the river arms. Abundances of larval cyprinids were consistently greatest in the Red River arm (sites 1–7, 37–41; Figure 1), whereas larval centrarchids were most abundant in the Washita River arm (sites 13–26; Figure 1). Main reservoir sites (sites 8–12, 27–36; Figure 1) contained mostly atherinids and centrarchids (>95% of the individuals) throughout sampling. Mean familial richness also was consistently greater in the river arms than the main reservoir.

Three separate canonical correspondence analyses conducted in April, May, and June explained 45–61% of the variation in community structure on the first two CCA axes. Observed eigenvalues were significantly greater than randomly generated values during all 3 months on axis 1 ($p = 0.001$ – 0.007), and during two of three months on axis 2 (April, $p = 0.011$; May, $p = 0.027$; June, $p = 0.331$). Thus, more highly correlated variables with these axes were considered significant environmental gradients. During all 3 months, site exposure was the most highly correlated variable with axis 1 (Table 1), and thus, most associated with the structure of larval fish communities (Figure 2). Additionally, the structure of larval communities was related to zooplankton densities and variables associated with water clarity (Secchi depth and water-column chlorophyll-*a*). Structuring of larval fish communities also was weakly related to land-use characteristics (proportion of forest land and residential area within site drainages), but higher correlations for these variables were observed only in May and June (Table 1).

Relationships between larval fishes (classified to family) and environmental measures were relatively consistent through time. Larval communities varied along a gradient of site exposure, with

² McCune, B. & M.J. Mefford 1999. PC-ORD. Multivariate analysis of ecological data, Version 4.0. MJM Software, Gleneden Beach, Oregon, USA.

³ Statistical Analysis System (SAS) Institute, Inc., 2000. Statistical Analysis System, Version 8. SAS Institute, Inc., Cary, North Carolina.

Table 1. Most important site–environment correlations for first and second axes from canonical correspondence analysis (CCA) of fish (larval, juvenile and adult) and environmental variables in Lake Texoma, April–October 2001.

Variable	CCA axis-1	Variable	CCA axis-2
<i>April (larval)</i>			
Site exposure	−0.663	Zooplankton density	−0.443
Forest lands	0.452	Percent residential area	−0.376
Secchi depth	0.394	Percent crop land	−0.372
Total phosphorus	−0.389	Percent pasture/hay	−0.317
Water-col. chlorophyll- <i>a</i>	−0.353	Site slope	−0.304
<i>May (larval)</i>			
Site exposure	0.728	Benthic chlorophyll- <i>a</i>	−0.554
Zooplankton density	−0.440	Zooplankton density	−0.531
Water temperature	−0.428	Secchi depth	0.457
Percent residential area	−0.413	Site exposure	0.402
Water-col. chlorophyll- <i>a</i>	0.389	Mean May discharge	−0.358
<i>June (larval)</i>			
Site exposure	0.699	Secchi depth	0.672
Conductivity	0.463	Mean June discharge	−0.606
Habitat diversity	−0.393	Total suspended solids	−0.526
Percent residential area	−0.361	Percent grassland	−0.373
Site slope	−0.356	Total phosphorus	−0.368
<i>July (juvenile and adult)</i>			
Secchi depth	−0.702	Site exposure	−0.621
Total nitrogen	−0.672	Zooplankton density	0.588
Percent forest land	−0.428	Percent grassland	−0.582
Total suspended solids	0.424	Percent CIT ^a	0.457
Site exposure	−0.413	Percent residential area	0.414
<i>October (juvenile and adult)</i>			
Site exposure	−0.551	Percent forest land	0.509
Benthic chlorophyll- <i>a</i>	0.530	Percent grassland	−0.492
Invertebrate density	−0.448	Conductivity	0.448
Percent crop land	0.436	Percent residential area	−0.391
Habitat diversity	−0.358	Percent CIT ^a	0.376

^a CIT equals commercial-industrial-transportation land use.

differences mostly related to the abundances of atherinids and centrarchids (Figure 3). Fish–environment correlations were consistently greatest for these two families and always in opposite directions (Table 2). Atherinids tended towards the middle of family ordinations because they were found at most sites. However, a strong preference for high-exposure sites was exhibited in that mean abundance of larval atherinids at high-exposure sites exceeded that at low-exposure sites by 53 and 142% in April and May, respectively (June atherinid abundances were much lower overall and similar across levels of site exposure).

Conversely, centrarchids were found almost exclusively at low-exposure sites. Mean abundance exceeded 70 larvae tow^{-1} at low-exposure sites compared to <5 larvae tow^{-1} at high- and med-

ium-exposure sites. Larval catostomids and cyprinids showed some association with high- and medium-exposure sites (catostomids were not collected in June), but correlations were weaker (Table 2). In Lake Texoma, Cyprinidae included as many as 15 species from 9 genera, whereas catostomids have been documented as being primarily smallmouth buffalo, *Ictiobus bubalus*, and river carpsucker, *Carpionodes carpio* (Gido et al. 2002). Centrarchids abundant at low-exposure sites in marinas and off-lake coves (sites 13–14, 23–24, 26, 33–36) in Lake Texoma have been documented as bluegill, *Lepomis macrochirus*; longear sunfish, *L. megalotis*; and orangespotted sunfish, *L. humilis*; largemouth bass, *Micropterus salmoides*; and white crappie, *Pomoxis annularis* (Gido et al. 2002). Abundances of Clupeidae (documented as gizzard

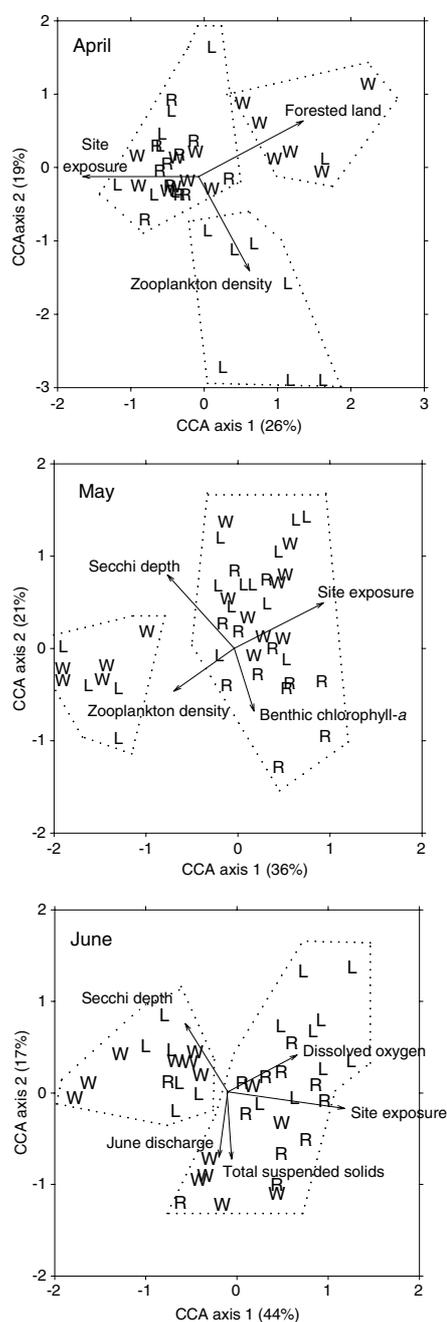


Figure 2. Scatterplot of site scores from canonical correspondence analysis of larval fish communities sampled at Lake Texoma, April–June 2001. Arrows (rescaled by factor of 2) represent relative directions and strengths of gradients. Sites identified by location in the reservoir as L = main reservoir, R = Red River arm, and W = Washita River arm (see Figure 1). Numbers in parentheses with axis labels represent percent variance explained. Dotted lines represent general groupings of sites referenced in Discussion.

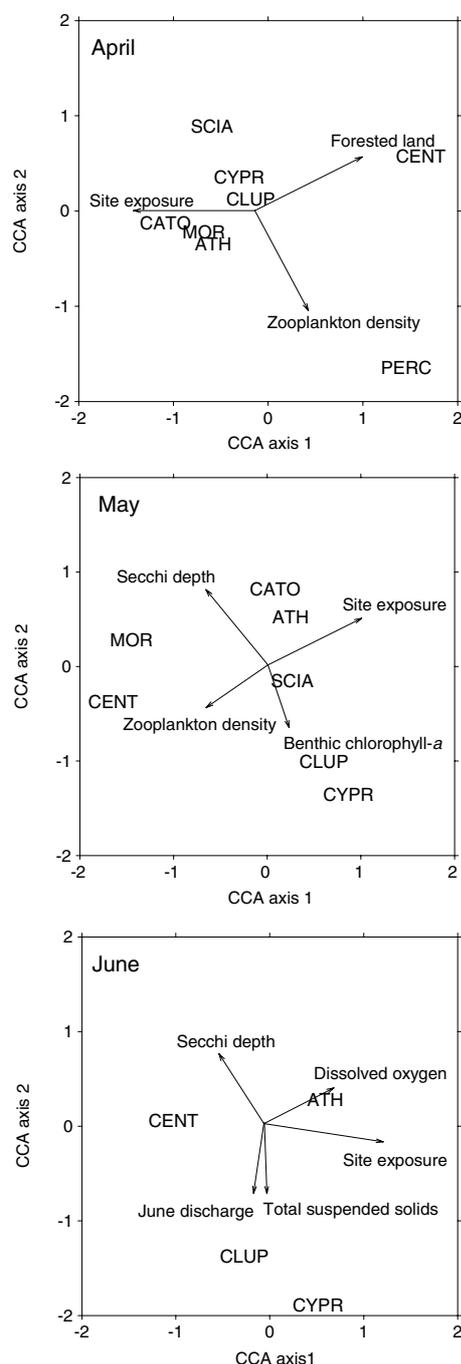


Figure 3. Scatterplot of family scores from canonical correspondence analysis of larval fish communities at Lake Texoma, April–June 2001. Arrows (rescaled by factor of 2) represent relative directions and strengths of gradients. Codes: ATH = Atherinidae, CATO = Catostomidae, CENT = Centrarchidae, CLUP = Clupeidae, CYPR = Cyprinidae, MOR = Moronidae, PERC = Percidae, SCIA = Scianidae.

Table 2. Most important fish–environment correlations for first and second axes from canonical correspondence analysis (CCA) of fish (larval, juvenile and adult) and environmental variables in Lake Texoma, April–October 2001.

Variable	CCA axis-1	Variable	CCA axis-2
<i>April (larval)</i>			
Centrarchidae	0.634	Percidae	−0.709
Atherinidae	−0.399	Centrarchidae	0.308
Percidae	0.383	Clupeidae	0.243
Catostomidae	−0.362		
<i>May (larval)</i>			
Centrarchidae	−0.637	Clupeidae	−0.566
Atherinidae	0.486	Cyprinidae	−0.501
Clupeidae	0.338	Centrarchidae	−0.331
Cyprinidae	0.318		
<i>June (larval)</i>			
Centrarchidae	−0.715	Cyprinidae	−0.576
Atherinidae	0.490	Clupeidae	−0.336
<i>July (juvenile and adult)</i>			
Moronidae	−0.810	Centrarchidae	0.610
Catostomidae	0.460	Atherinidae	−0.541
Centrarchidae	0.428	Cyprinidae	−0.507
Scianidae	0.423		
Cyprinidae	0.373		
<i>October (juvenile and adult)</i>			
Centrarchidae	−0.564	Clupeidae	−0.596
Percidae	−0.554	Catostomidae	−0.442
Moronidae	0.454		

shad, *Dorosoma cepedianum*, and threadfin shad, *D. petenense*; Gido et al. 2002) did not appear related to site exposure but were associated more with water clarity, at least during May and June. Clupeid abundances were consistently greatest at turbid, uplake sites in the shallower, upstream sections of both river arms (sites 1–3, 15, 20, 24, 37–38, and 40).

Juvenile and adult fishes

The spatial distribution of juvenile and adult fish communities was different than that observed for larval fishes. For instance, total abundances of juvenile and adult fishes were consistently greater in the main reservoir than in the river arms. Mean abundances were 313 ± 40 fishes reach^{−1} in the main reservoir compared to 237 ± 78 fishes reach^{−1} in Washita River arm and 138 ± 26 fishes reach^{−1} in the Red River arm, opposite the pattern observed by Gido et al. (2002). Juvenile striped bass were 4–20 times more abundant in the main reservoir than the river arms, especially

at clearer sites downlake, and abundances from our sampling in 2001 were 10-fold greater than those observed by Gido et al. (2002) during 1999–2000. Cyprinids were three-fold more abundant in the river arms compared to the main reservoir. Unlike larval communities, centrarchids were found in relatively high abundances throughout the reservoir, although the particular species composing communities differed among areas. Generally, the river arms contained more bluegill, orangespotted sunfish, longear sunfish, and white crappie, whereas the main reservoir contained more black basses, *Micropterus* spp. (three species.)

Canonical correspondence analysis of juvenile and adult communities sampled in July and October suggested structuring similar to that observed for larval fishes. Observed eigenvalues were significantly different ($p = 0.001$ – 0.010) than randomly generated values on the first two axes. Thus, all variables highly correlated with either axis 1 or axis 2 were considered important gradients. In October, sites 15 and 36 skewed the ordination

substantially and were eliminated from the analysis. Site 15 contained high numbers of clupeids and little else, while site 36 contained only centrarchids.

The CCA for July explained 61% of the variance (44% on axis 1, 17% of axis 2) in juvenile and adult fish communities on the first two axes. Similarly, CCA explained 64% of the variance (42% on axis 1, 22% on axis 2) in October communities (Figure 4). In July, juvenile and adult communities were structured mainly along gradients of water clarity, total nitrogen, and proportion of grassland within site drainages (Figure 4). Site exposure, zooplankton density, and land-use gradients also were important, but were weaker, secondary gradients in July. By October, communities were again structured along gradients of site exposure and benthic chlorophyll-*a*, and secondarily along a land-use gradient that included proportion of forest and grassland within site drainages. As with larval fishes, site exposure and water clarity-related variables (Secchi depth and benthic chlorophyll-*a*) were consistently the strongest environmental gradients with juvenile and adult communities (Table 1).

Fish-environment relationships with juvenile and adult communities were similar to those observed with larval fishes. In July, the water clarity gradient was mostly related to the presence or absence of moronids (principally striped bass), a visual predator (Pfleiger 1997; Figure 5). Clearer sites located downlake (sites 9–11, 29–32) consistently contained greater abundances of striped bass whereas more turbid sites uplake did not. Fish-environment correlations supported this observation (Table 2), as did mean abundances. In July, mean abundance of juvenile striped bass was 191 ± 61 fishes reach⁻¹ in the main reservoir compared to <40 fishes reach⁻¹ in the river arms. Secondly, juvenile and adult fish communities differed along a site exposure gradient. As with larval fishes, structural differences along this gradient were mostly related to abundances of atherinids and centrarchids, as fish-environment correlations were always in opposite directions for these two families (Table 2). Mean abundance of atherinids was 126 ± 47 fishes reach⁻¹, 96 ± 31 fishes reach⁻¹, and 55 ± 22 fishes reach⁻¹ at high-, medium- and low-exposure sites, respectively, whereas mean abundance of juvenile and adult

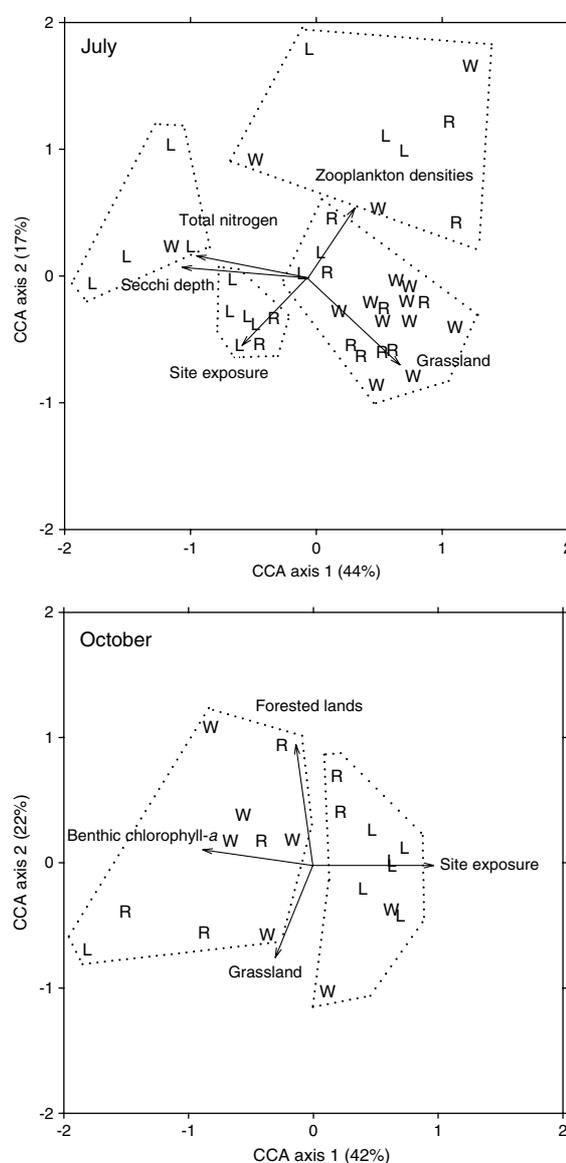


Figure 4. Scatterplot of site scores from canonical correspondence analysis of juvenile and adult fish communities sampled at Lake Texoma, July and October 2001. Arrows (rescaled by factor of 2) represent relative directions and strengths of gradients. Sites identified by location in the reservoir as L = main reservoir, R = Red River arm, and W = Washita River arm (see Figure 1). Numbers in parentheses with axis labels represent percent variance explained. Dotted lines represent general groupings of sites referenced in Discussion.

centrarchids was 27 ± 4 fishes reach⁻¹ at low-exposure sites, 25 ± 18 fishes reach⁻¹ at medium-exposure sites, and 5 ± 2 fishes reach⁻¹ at high-exposure sites. Juvenile and adult percids

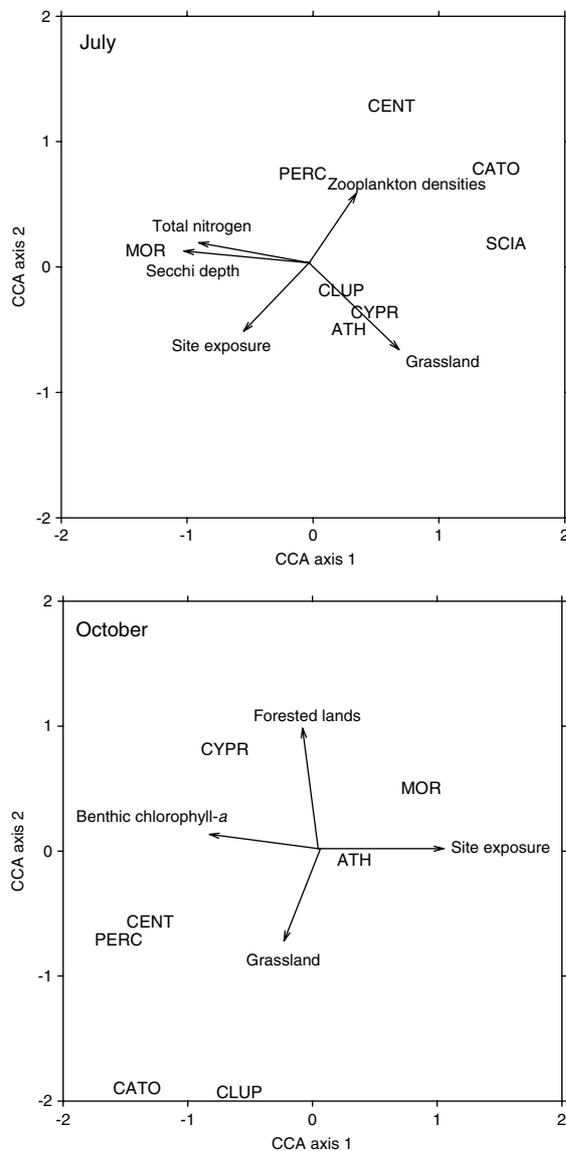


Figure 5. Scatterplot of family scores from canonical correspondence analysis of juvenile and adult fish communities at Lake Texoma, July and October 2001. Arrows (rescaled by factor of 2) represent relative directions and strengths of gradients. Codes: ATH = Atherinidae, CATO = Catostomidae, CENT = Centrarchidae, CLUP = Clupeidae, CYPR = Cyprinidae, MOR = Moronidae, PERC = Percidae, SCIA = Scianidae.

(darters), juvenile catostomids (suckers), and juvenile sciaenids (freshwater drum) also showed some association with lower-exposure sites, but correlations were weaker and not consistent for these groups (Table 2).

Concordance of larval, juvenile and adult fish communities through time

For all 41 sites, we averaged mean larval abundance over April, May, and June as a measure of general larval abundance for each family during spring. Concordance between larval communities sampled during spring and juvenile and adult communities sampled in July and October were significant for several families. In terms of abundances, rank correlation analyses indicated significant positive relationships for Atherinidae, Centrarchidae, Cyprinidae, and Percidae in July, and Clupeidae and Centrarchidae in October (Table 3). A negative correlation detected for Moronidae was significant in July, but larvae of this family were found in only 7 of 123 samples from April through June compared to 28 of 41 samples in July. We believe the high incidence of zero abundances in the spring larval data likely produced a spurious correlation. When July and October abundances were compared to observed larval abundances during individual months (i.e., April, May, and June separately), correlations were usually in the same direction but not always significant. We expected that correlations analyzed

Table 3. Spearman rank correlations (r_s) and associated p -values between spring abundances of larval fishes and July and October abundances of juvenile and adult fishes (classified to family) in Lake Texoma, 2001.

Family	r_s	p
<i>July (juvenile and adult)</i>		
Atherinidae	0.302	0.050
Clupeidae	0.209	0.190
Centrarchidae	0.605	<0.001
Cyprinidae	0.341	0.029
Moronidae	-0.372	0.017
Scianidae	-0.016	0.920
Catostomidae	0.276	0.081
Percidae	0.341	0.029
<i>October (juvenile and adult)^a</i>		
Atherinidae	0.173	0.440
Clupeidae	0.530	0.010
Centrarchidae	0.454	0.034
Cyprinidae	0.407	0.060
Moronidae	-0.316	0.152

^a Scianidae, Catostomidae, and Percidae not collected during October.

Significance declared at $\alpha = 0.05$. Bold type indicates result significant following Bonferroni adjustment.

Table 4. Standardized Mantel statistics (r_m) and p -values (in parentheses) of Sorensen dissimilarity measures between spring larval fish communities and July and October juvenile and adult fish communities in Lake Texoma, 2001.

Larval fish community sampling period	Juvenile and adult fish community sampling periods	
	July	October
April	0.305 (0.001)	0.253 (0.023)
May	0.251 (0.001)	0.261 (0.023)
June	0.144 (0.019)	0.347 (0.003)

Significance declared at $\alpha = 0.05$. Bold type indicates result significant following Bonferroni adjustment.

in this manner would be weaker because of disjunct hatching times of different families and different species within the same family. Cyprinidae and Centrarchidae are both large families that contain numerous species in Lake Texoma, whose hatching times range from early April throughout summer in the south-central United States (Pfleiger 1997). Similarly, some species (e.g., bluegill) will spawn multiple times during the same year. Following Bonferroni correction of alpha, correlations were significant only for Centrarchidae in July and Clupeidae in October (Table 4).

Larval, juvenile and adult community compositions also were similar. Standardized Mantel statistics generated from comparisons of larval and juvenile and adult community compositions were positive and significant (Table 4), which indicated concordance between the structures of April, May, and June larval fish communities and July and October juvenile and adult communities. When Bonferroni corrections of alpha were applied to Mantel tests, four of six comparisons remained significant, with larval–juvenile and adult comparisons for June–July and April–October becoming non-significant (Table 5).

Richness of larval fishes was correlated to that observed for juvenile and adult communities sampled later in the year. Significant positive correlations resulted between family-level richness of larval fishes in April and family-level richness (reclassified from species) of juvenile and adult fishes sampled in July and October (Table 5). Significant correlations did not result when May or June larval communities were compared to July and October juvenile and adult communities. When alpha was Bonferroni-corrected, correlation was significant only between April larval and July juvenile and adult communities.

Discussion

Fish–environment relationships

Littoral–zone fish communities in Lake Texoma were spatially consistent and predictable through ontogeny in terms of abundance, richness, and structure. Fish communities could be classified into distinct categories associated primarily with area of the reservoir. Larval communities could be grouped into two or three categories depending on the month they were sampled. In April, three communities were identified based primarily on degree of site exposure and zooplankton densities. One community type was characteristic of well-protected, low-exposure sites in marinas and off-lake coves (termed ‘sheltered downlake coves’ for juvenile and adult fishes by Gido et al. 2002) and was characterized by high abundances of centrarchids. Most centrarchid species are nest-builders and require relatively stable, structurally complex habitats (Etnier & Starnes 1993) that are common in protected or otherwise less-exposed areas in reservoirs. Another community type was found at

Table 5. Spearman rank correlation coefficients (r_s) and p -values (in parentheses) between richness of spring larval fish communities and July and October juvenile and adult fish communities (classified to family) during 2001.

Juvenile and adult fish community sampling periods	Larval fish community sampling periods		
	April	May	June
July	0.470 (0.002)	0.112 (0.484)	−0.001 (0.995)
October	0.453 (0.034)	0.229 (0.306)	0.068 (0.762)

Significance declared at $\alpha = 0.05$. Bold type indicates result significant following Bonferroni adjustment.

mostly uplake sites, all of which were located in the middle section of the reservoir or the river arms. These sites were moderately to highly turbid, medium- or high-exposure sites with low to intermediate zooplankton densities; atherinids and clupeids were typically the most common fishes at these sites. The third community type was more difficult to generalize. Sites were mostly clear, high-exposure, sandy-shoreline sites located in the lower reservoir (sites 27–29, 32), but also contained three sheltered downlake sites in nearby marinas (sites 33, 34, and 36; Figure 1). Generally, sites in this category had low larval abundances, moderate to high zooplankton densities, and no characteristic taxa (i.e., low abundances of all families). Larval percids (most likely bigscale logperch, *Percina macrolepida*, based on July sampling) were associated with these sites, but catches were restricted to sites 33 and 34, both marina locations. We do not know whether this category represented a biologically relevant community type or an artificial collection of outlying sites unlike all others.

During May and June, site exposure continued to be an important gradient in larval communities; however, water clarity also became more important, similar to juvenile and adult fishes in July. Water clarity generally exists as a longitudinal gradient in Lake Texoma, being higher in the river arms and lower downlake (Gido et al. 2002). Two main larval community types were identified along gradients of site exposure and water clarity. One community type was found at clearer, sheltered, low-exposure sites and associated mostly with centrarchids. The other community type existed at turbid, medium- and high-exposure sites and was associated mostly with atherinids and clupeids.

Analysis of juvenile and adult fish communities (by families) identified four main types of communities. Three community types included: (1) well-protected, low-exposure sites in marinas and off-lake coves dominated by centrarchids; (2) clear, sand-bottomed shorelines located downlake and associated with juvenile striped bass; and (3) turbid, medium- to high-exposure shorelines located uplake and dominated by atherinids, and to a lesser extent, cyprinids and clupeids. These community types were similar to those discussed by Gido et al. (2002). The fourth category contained mostly sand-bottomed, medium- and

high-exposure sites with low zooplankton densities and moderate water clarities located in the middle section of the reservoir. These sites (sites 4, 8–12, and 39) were dominated by both inland silverside and juvenile striped bass and represented a transitional zone from turbid, uplake sites dominated by inland silverside to clearer, downlake sites dominated by striped bass. October communities contained a weak pattern of exposed vs. sheltered sites, but much overlap existed. These samples were dominated by inland silversides (89% of the composite catch), which may have made patterns more difficult to observe. We performed additional analyses that included only non-atherinids, but no pattern in communities emerged.

Consistency of fish–environment relationships

Because roughly similar community types were identified for larval, juvenile and adult fishes, it is not surprising that similar variables would be involved in the structuring of communities. Consistent in all larval, juvenile and adult analyses was the role of site exposure in structuring littoral-zone fish communities. Site exposure was among the most highly correlated CCA axis variables from larval stages in April through juvenile or adult stages in July and October; zooplankton densities, water clarity and water-clarity-related variables also were consistently important. Thus, our expectation that juvenile and adult communities would be structured more with local variables than larval communities because of reproductive activities and diverse feeding and habitat requirements was not realized in littoral-zone areas of Lake Texoma.

The structural consistency of larval, juvenile and adult fish communities might be commonplace in reservoirs like Lake Texoma. Previous studies in Lake Texoma indicated that wind velocity and wave height were strongly related to the structure of littoral-zone fish communities (Lienesch & Matthews 2000), although others have indicated that annual water level changes also were important (Gelwick & Matthews 1990). Persistent southern winds in Lake Texoma coupled with relatively flat terrain may influence littoral-zone communities by direct mechanical stress to fishes, erosion of the habitat within a particular reach of shoreline, or alteration of ambient food levels (e.g.,

zooplankton or benthic invertebrates; Lienesch & Matthews 2000, Gido et al. 2002). Gido et al. (2002) did not use site exposure as we did in their assessment (they used site aspect converted to eastness and northness; Roberts 1986), but exposure level of sites to wind and waves was a major feature of the habitat groupings they discussed. Site exposure may be of such importance in Lake Texoma that it overrides the effects of other variables that commonly influence fishes (e.g., nutrients, chlorophyll-*a*) which vary at larger scales. This is further supported by the fact that littoral-zone communities were simple and composed mostly of inland silversides and striped bass, both of which are limnetic, habitat generalists (Etnier & Starnes 1993) that appear to thrive in the types of unstable environments common along the shorelines of reservoirs (Lienesch & Matthews 2000).

Concordance of larval, juvenile and adult fishes

High concordance of larval, juvenile and adult fish communities classified at the family level occurred in terms of community structure (from Mantel tests), richness (from rank correlations), and abundance (from rank correlations). Correlation results indicated that high abundances of particular larvae at certain sites were positively associated with high abundances of juveniles and adults at these same sites 3–6 months later. This provides additional evidence that spatial patterns in fish community structure were consistent through time, and thus, ontogeny in Lake Texoma. Using multiple regression and CCA, Gido et al. (2002) also suggested that littoral-zone fish community structures in Lake Texoma were predictable, principally because the primary environmental gradients involved in structuring were temporally stable. Further, Gido et al. (2000) also reported notable consistency of offshore fish communities in Lake Texoma over time scales ranging up to 43 years, although they used indirect gradient analyses and drew no conclusions as to which variables were involved in the structuring of fish communities. Results here generally support this conclusion given that variables associated with fish community structure were constant (site exposure) or fluctuated little throughout the year (water clarity). Fishes exhibiting strong spatial patterns in their occurrence among littoral-zone habitat types

are common in natural lake communities (Keast et al. 1978, Hosn & Downing 1994, Hatzembeler et al. 2000), but such fish–habitat relationships may be weaker in artificial reservoir systems (Gelwick & Matthews 1990). However, we might expect reservoirs with strong temporally stable, spatial gradients such as Lake Texoma to have predictable community structures as observed here despite the mix of native and non-native species as well as riverine and lacustrine species.

This trend of temporal stability evidenced by the strong concordance of larval, juvenile and adult fish communities also may have other implications. Larval communities sampled in April (which showed the strongest correlations to July and October communities) may provide a useful index of juvenile and adult communities later in the year. Research with several sport fishes has indicated that year-class strength can be set very early in life (DeVries et al. 1991, Sammons & Bettoli 1998). In other words, once a particular life-history stage is survived (e.g., larvae through the first few weeks or juveniles through the first winter), sources and rates of mortality can be relatively constant and predictable during later life-history stages. Adams & DeAngelis (1987) demonstrated that the October abundance of largemouth bass >160 mm in a Tennessee reservoir was highly correlated to strong year classes of largemouth bass observed several years later. Thus, abundances of age-0 largemouth bass during fall served as an early indicator of future largemouth bass year-class strength in that system. This idea has never been extended to entire fish communities, but may be applicable in systems like Lake Texoma, where littoral-zone communities are less complex and structured by physical variables that vary little from year to year (e.g., site exposure or water clarity). Furthermore, many littoral-zone fishes serve as prey for many larger-bodied sport fishes; thus, consistency or lack thereof in communities may have major implications for resident piscivores (mostly sport fishes) or the stocking success of fingerling piscivores (Pierce et al. 2001).

Understanding the underlying factors that determine the structure of biotic communities is vital to the management of reservoirs. Our findings suggest that littoral-zone fish communities in Lake Texoma were predictable across space and through time with respect to larval, juvenile and adult

Appendix A. Environmental variables used in canonical correspondence analyses of larval and juvenile/adult fish assemblages in Lake Texoma.

Variable	Units	Measurement frequency	Technique
<i>Physical</i>			
Site exposure	Unitless – see text	Fixed for each site during all samples	Based on aspect, fetches, and substrate content; estimated from maps and site visits
Site slope	Percent	Fixed for each site during all samples	Estimated from site mapping to the nearest meter
Habitat diversity	Unitless – see text	Measured at each site during each sample	Estimated from site mapping (see Gido et al. 2002 for details)
Sub-basin drainage area	Ha	Fixed for all sites during all samples	Determined via geographic information systems and National Land Cover data set (Vogelmann et al. 2001)
Secchi depth	M	Measured at each site during each sample	Measured with Secchi disk
Water temperature	°C	Measured at each site during each sample	Measured with YSI Model 650 MDS field meter
<i>Chemical</i>			
Dissolved oxygen	mg l ⁻¹	Measured at each site during each sample	Measured with YSI Model 650 MDS field meter
Conductivity	µS cm ⁻¹	Measured at each site during each sample	Measured with YSI Model 650 MDS field meter
Total phosphorus	mg l ⁻¹	April and July average used for July analyses, July and October averages used for October analyses	Determined in EPA laboratory using standard methods (APHA 1998)
Total nitrogen	mg l ⁻¹	April and July average used for July analyses, July and October averages used for October analyses April and July average	Determined in EPA laboratory using standard methods (APHA 1998)
Total suspended solids	mg l ⁻¹	April and July average used for July analyses, July and October averages used for October analyses April and July average	Determined in EPA laboratory using standard methods (APHA 1998)
<i>Biotic</i>			
Water-column chlorophyll- <i>a</i>	µg l ⁻¹	Measured at each site during each sample	Measured with YSI Model 6890 field fluorometer
Benthic chlorophyll- <i>a</i>	µg l ⁻¹ d ⁻¹	May–June and June–July averages	Estimated in situ following Gido et al. (2002)
Total zooplankton density	Number l ⁻¹	Measured at each site during each sample	One (1) vertical tow with 63-µm mesh Wisconsin-style net
Benthic invertebrate density ^a	Number dredge ⁻¹	Measured during June at each site	Average of three (3) replicate Ponar dredge samples
<i>Land use</i> ^b	Percent drainage area	Fixed for each site during all samples	Determined via geographic information systems and National Land Cover data set
<i>Hydrologic</i>			
Mean monthly discharge	m ³ s ⁻¹	Estimated each month for each river arm ^{c,d}	Average of daily discharges for particular month
Mean seasonal discharge	m ³ s ⁻¹	Estimated for each river arm ^{d,e}	Average of March–May (spring analyses) or June–September (summer analyses) daily discharges

^a Used in juvenile/adult analyses only.

^b Estimated as proportion of total drainage surface area; classified as residential, commercial/industrial/transportation (CIT), forest land, grassland, pasture/hay, cropland, or wetland.

^c Value for each river arm were used for all sites in that river arm; main reservoir sites designated as zero discharge.

^d Average daily discharge during sample month; used in larval fish analyses only.

^e Average monthly discharge from March–May (for July samples) and June–September (for October samples); used in juvenile/adult analyses only.

community measures. Site exposure and, to lesser extent, water clarity and zooplankton densities were judged to be the most important structural variables determining community composition. Land-use factors did appear to be more important in the structuring of juvenile and adult than larval communities. However, the overall influence of these variables on fish communities appeared to be less important than site exposure or water clarity. The relative consistency of the structural variables through ontogeny suggests that the degree of site exposure may be of such magnitude in Lake Texoma that it has an overriding effect on fish communities compared to other environmental variables. This also may be a partial explanation of why littoral-zone fish communities are relatively simple in Lake Texoma, and dominated by a few species of habitat generalists. Generally, our findings were consistent with previous studies of similar scope in Lake Texoma (e.g., Lienesch & Matthews 2000, Gido et al. 2002). Given the prominence of reservoirs in river systems around the world, resource managers might need to consider aspects of community ecology such as those discussed here when making management decisions.

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