

Dynamics of the Offshore Fish Assemblage in a Southwestern Reservoir (Lake Texoma, Oklahoma–Texas)

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Reservoirs are relatively new ecosystems with fish assemblages that include both native and introduced species. Spatial and temporal variability in such fish assemblages is difficult to predict from ecological theory. We characterized the dynamics of an offshore fish assemblage of Lake Texoma by sampling multiple fixed sites fortnightly with gill nets from 1981 to 1984 (402 net-nights). Univariate and multivariate analyses were used to quantify (1) variation of the fish assemblage in space and time, (2) spatial and temporal independence of samples, (3) persistence of species associations, and (4) correlations between the dynamics of the fish assemblage and environmental conditions. Overall, depth and season accounted for the greatest amount of variation in the fish assemblage in our study area. Much of this variation was the result of spatial and temporal fluctuation in the abundance of various age classes of *Dorosoma cepedianum* (Gizzard Shad), *Morone saxatilis* (Striped Bass), and *Aplodinotus grunniens* (Freshwater Drum). With the exception of a winter kill of the nonnative *Dorosoma petenense* (Threadfin Shad), the reservoir fish assemblage differed little among years. Species associations were constant across years during the warm season but not in cold seasons. Overall, the fish assemblage in our study area remained relatively consistent, in spite of considerable variability in reservoir volume, turbidity, and temperature.

RESERVOIR ecosystems are unique in that both native and introduced species are assembled in an environment that was engineered and is partially regulated by humans. Characterizing the spatial and temporal patterns of these assemblages helps determine factors (human and nonhuman) that regulate community structure. However, because of the artificial nature of reservoirs, conflicting predictions can be made about how local fish assemblages or entire faunas in reservoirs might vary across space and time.

At one extreme, fish assemblages could be quite variable because of frequent or extreme environmental fluctuations. For example, increases in turbidity reduce the efficiency of visual predators, potentially altering abundances of both predator and prey species (Kashuba and Matthews, 1984; Matthews, 1984; O'Brien, 1990). Increases in turbidity also limit primary productivity (Holz et al., 1997) and abundance of zooplankton (Dirnberger and Threlkeld, 1986), which could have strong effects in reservoir food webs. Fluctuations in water level can influence reproductive success of fishes by rap-

idly altering water depth at spawning sites or depositing sediment on eggs or larvae in nests (Miranda et al., 1984; Ploskey, 1986; Guy and Willis, 1995). In addition, biotic interactions in reservoirs are likely to be unpredictable because the community includes both native and introduced species lacking an evolutionary history of coexistence (Li and Moyle, 1981; Moyle, 1986; Noble, 1986). Thus, asymmetrical competition among species could lead to extirpation or stochastic fluctuations in species abundances (Wydoski and Bennett, 1981; McComas and Drenner, 1982).

Alternatively, reservoir fish assemblages could show little temporal variation if they consist of species tolerant of reservoir conditions or if biotic interactions are weakly linked because predator and prey species have broad resource requirements. For example, Stein et al. (1995) attribute the success of *Dorosoma cepedianum* (Gizzard Shad) in reservoirs to its ability to switch from a zooplankton to a detritus diet. Additionally, this species can grow sufficiently large to escape predation. Such uncoupling in food webs contrasts with the more tightly linked sit-

uation in many oligotrophic lakes in which changes in one trophic level may affect adjacent or more distant trophic levels (e.g., via cascading effects; Carpenter et al., 1985; McQueen et al., 1986).

A combination of the above responses is also possible. Composition of the fish fauna at the whole-reservoir scale may remain relatively unchanged across time, but local fish assemblages may differ markedly in response to variable environmental conditions within the reservoir, such as longitudinal chemical gradients (Matthews et al., 1989; Thornton et al., 1990). If this is true, we might predict that fish assemblages at fixed sites would change markedly over time but that the overall assemblage in the reservoir would remain relatively unchanged.

Numerous studies document nonrandom distribution of fishes within reservoirs (e.g., Dendy, 1946; Lambou, 1962; Nadirov and Malinin, 1997). Fish biomass is typically higher in riverine and inshore areas than in open-water sections of reservoirs (Vanderpuye, 1982; Nadirov and Malinin, 1997). Fernando and Holcik (1991) suggest higher fish abundances in these areas is because most reservoir fishes are native to the preimpounded river system and are better suited for more riverine conditions. Among environmental factors, temperature and dissolved oxygen are most often linked to distribution of reservoir fish species (Dendy, 1946; Coutant, 1985; Craig and Babaluk, 1993).

We characterized the dynamics of the offshore assemblage of relatively large-bodied fish species in the Red River Arm of Lake Texoma on the basis of gill net sampling at multiple fixed sites across 3.5 yr. Our primary goal was to describe variation in the fish assemblage in our study area across a fine temporal scale (every two weeks). However, because of marked differences in habitat use by individual species (Dowell, 1956; this study), we consider spatial and temporal variation simultaneously. Therefore, we assessed variation in species abundance and composition of the assemblage at three temporal (annual, seasonal, and fortnightly) and two spatial (individual sites or all sites pooled) scales. Specifically, we describe abundance patterns for all common species and also ask (1) How did samples vary across space and time? (2) Were samples spatially or temporally independent across sites and dates (i.e., spatially or temporally autocorrelated)? (3) Did species associations persist across time? and (4) How was the fish assemblage influenced by abiotic factors (e.g., changes in turbidity or reservoir volume)? To address these four objectives, multivariate techniques were used to summarize

variation in the fish assemblage. These techniques simplify the analyses of assemblage data, given the many potentially complex relationships that can occur with biotic and abiotic factors (Gauch, 1982).

MATERIALS AND METHODS

Study area.—Lake Texoma is a 36,000-ha impoundment of the Washita and Red Rivers on the Oklahoma–Texas border (Matthews, 1984). Reservoir releases and resulting fluctuations in water level are primarily for hydropower and flood control. Secchi depth transparency typically ranged from 100–125 cm during our study (Matthews, 1984) but was as little as 15 cm during turbid inflows. Conductivity ranged from 750–1200 micromhos/cm (WJM, unpubl. data), and reservoir elevation ranged from 611.7–632.1 m above sea level (U.S. Army Corps of Engineers, unpubl. data).

Our study area was approximately 35 km upstream from the dam, within the Red River Arm of Lake Texoma near the University of Oklahoma Biological Station. Three locations were chosen to represent major limnetic habitat types available to fish in this area of the reservoir: a shallow cove, a bay formed by a large tributary creek, and the main channel of the reservoir. Matthews et al. (1988) provide a detailed description and map of these locations. Within each location, we sampled surface and bottom waters. The cove had a maximum depth of about 6 m and was sheltered from prevailing south winds. The tributary creek formed a bay 6.4 km long, north of the main channel and partially open to prevailing winds, with an average depth of 11 m. The main channel site was in the middle of the Red River Arm of the reservoir directly south of the University of Oklahoma Biological Station and had an average depth of 18 m. Each major habitat was at least 1.1 km from the others. To be explicit about our spatial scale of investigation, we refer to the cove, tributary arm, and main channel locations as “habitats” and places where individual nets were set as “sites” (i.e., surface and bottom nets at each habitat are separate sites).

The fish assemblage in Lake Texoma has been described previously (Riggs and Bonn, 1959; Echelle et al., 1971; Matthews et al., 1985). Three of the dominant species in the assemblage are the result of introductions. Inland Silverside, *Menidia beryllina*, was first recorded in 1953 (Riggs and Bonn 1959); Threadfin Shad, *Dorosoma petenense*, appeared in 1957 (Riggs and Moore 1958); and Striped Bass, *Morone saxatilis*, were stocked from 1965 to 1974 (Harper and

Namminga 1986). Although threadfin shad can maintain their populations with natural reproduction, they were restocked in 1982 after a virtually complete winter kill. We included this species in our analysis although variation in its abundance obviously was partially regulated by stocking.

Field sampling.—We used experimental gill nets with multiple mesh sizes to estimate relative abundance of fishes at the six sample sites (Matthews et al., 1988). Each net was 61 m long and 1.83 m deep, with successive 7.6-m panels grading in mesh size from 19–102 mm bar measure. Although gill nets selectively catch certain species (Jensen, 1986; Weaver et al., 1993) or size classes (McCombie and Fry, 1960), they provide useful estimates of change in relative abundance (Hubert, 1983). Our gill netting did not sample small-bodied fishes such as minnows, young *Dorosoma* spp., or *M. beryllina* that were probably abundant in some areas. Thus all analyses are restricted to larger species and size classes.

Nets were set approximately every two weeks (fortnightly) from April 1981 to July 1984. Two nets (one surface and one bottom) were set at each habitat in the afternoon and retrieved the following day, beginning at approximately 0900 h and ending by early afternoon. There was a total of 67 sample dates and 402 net-nights. Bottom nets were set with the lead line directly on the substrate, and surface nets were set with the top line approximately 0.5 m below the surface. All fishes were identified to species, weighed, and measured.

As a general index of temporal changes in environmental conditions in our study area, water temperature and Secchi depth were recorded at the main channel site on each sampling date. Reservoir volume was taken from the U.S. Army Corps of Engineers at Denison Dam. Inflow from the Red River was estimated from the U.S. Geological Survey gauging station approximately 30 km upstream from the reservoir at Gainesville, Texas.

Data analysis.—To account for ontogenetic differences in abundance patterns of the most abundant large-bodied taxa (e.g., Polis, 1984; Matthews, 1998), we separated *M. saxatilis* (striped bass), *D. cepedianum*, *Ictalurus furcatus* (Blue Catfish), *Ictiobus bubalus* (Smallmouth Buffalo), and *Morone chrysops* (White Bass) into size classes (Table 1) based on length-frequency histograms. Small and medium size classes were assumed, on the basis of many dissections across seasons, to represent immature individuals (age-

TABLE 1. SIZE CLASSES AND SPECIES CODES FOR TAXA USED IN ANALYSIS OF THE FISH ASSEMBLAGE IN THE RED RIVER ARM OF LAKE TEXOMA. Small age classes (s) are assumed to represent age-1 individuals, medium age classes (m) age-2 or younger individuals, and large age classes (l) mature adults > age-2.

Species	Code	Length (mm)
<i>Morone saxatilis</i>	MORSAX-s	< 200
	MORSAX-m	200 to 300
	MORSAX-l	> 300
<i>Dorosoma cepedianum</i>	DORCEP-s	< 150
	DORCEP-m	150 to 250
	DORCEP-l	> 250
<i>Ictiobus bubalus</i>	ICTBUB-m	< 400
	ICTBUB-l	≥ 400
<i>Ictalurus furcatus</i>	ICTFUR-m	< 300
	ICTFUR-l	≥ 300
<i>Morone chrysops</i>	MORCHR-s	< 225
	MORCHR-l	≥ 225

1 or age-2), whereas the large size classes represented mature adults (over age-2). Henceforth, we use the term “species” to represent both individual size classes (where separated) and species not separable by size classes.

Fish assemblage variation across space and time.—

Correspondence analysis (CA) was used to summarize variation in the fish assemblage. CA is a multivariate ordination technique useful in analyzing a species × sample data matrix (Gauch, 1982). Axis gradient lengths provide a measure of faunal turnover: sample scores four standard deviations apart should have few species in common (i.e., a complete turnover in species composition; Gauch, 1982; ter Braak, 1995). Eigenvalues and sample scores for the CA were calculated using PC-ORD (vers. 2.0, B. McCune and M. J. Mefford, Glenden, OR, 1995, unpubl.). Although CA has been criticized for creating a spurious “arch” on the second and subsequent axes (Hill and Gauch, 1980), a similar analysis that corrects this arch (detrended correspondence analysis) yielded patterns almost identical to those from the CA. Because rare species can have a strong effect on these analyses (ter Braak, 1995), we only included those species that accounted for more than 1% of the total catch in our analyses. Rare species are more likely to occur randomly in samples and not represent true differences in assemblage structure across space or time. Because species abundances rarely exceeded 100 individuals per sample, no transformations were applied (Gauch, 1982).

To examine interannual variation in CA

scores, we defined a sample year as 1 April through 31 March of the next year. Because the fish assemblage showed marked seasonal variation (see below) each year was further divided into warm (April–Oct.) and cold (Nov.–March) seasons. Seasons were chosen to approximate changes in water temperature (warm > 15 C and cold ≤ 15 C) that coincided with changes in local abundance of some common fish species (WJM, pers. obs.). Thus, comparisons among years were made separately within warm and cold seasons.

Analysis of variance was used to partition variation in axes scores among the main effects of year (1981, 1982, 1983), season (warm, cold), habitat (main channel, tributary arm, cove), depth (surface, bottom), and their interactions. Warm season collections from 1984 were excluded from this analysis because sampling was incomplete for that season.

We used ANOVA only to partition variance among the main effects and their interactions (i.e., we did not test significance) because we did not have replicate samples at each station and therefore could not derive an appropriate error sum of squares (L. Toothaker, pers. com.). Rather, we used ANOVA merely to analyze variance components and express the variation of each effect and their interactions as a percentage of the total variation in CA axis scores. Variance components were derived based on expected mean squares from a Model II (random effects) ANOVA (Sokal and Rohlf, 1995). In this analysis, we were able to evaluate whether the spatial (habitat or depth) or temporal (year or season) effects on assemblage structure were important alone or whether they interacted with other effects.

Independence of sample sites and dates.—We examined the similarity among sites and sampling periods to test the spatial and temporal independence of samples (i.e., spatial and temporal autocorrelation). We asked whether the species composition of a sample was better predicted by samples more proximal or more distant in space or time. However, because of the low statistical power of testing spatial independence across only six sites (i.e., with Mantel tests), we present only summary indices for these sites. For each site, we calculated mean number of species (size classes combined), total number of individuals, and mean CA axes scores.

These three indices (species richness, number of individuals, and CA axis scores) also were used to examine similarity of sample dates (with all six sites pooled) at different time intervals (lag) to examine potential patterns of temporal

autocorrelation. A Mantel test (Mantel, 1967) first was used to test for a significant association between a distance matrix of time between samples (days) and matrices representing the divergences in number of individuals, species richness and CA scores of our samples (e.g., Legendre and Fortin, 1989). The Mantel tests provide a correlation coefficient and test of significance between triangular matrices (Jackson and Somers, 1989; Legendre and Fortin, 1989). All calculations were made with the PC-Ord software package and 1000 random matrix simulations were used to assess significance levels (PC-Ord, vers. 2.0, B. McCune and M. J. Mefford, Glenden, OR, 1995, unpubl.). As an overview of the temporal autocorrelation, we plotted semivariograms (Legendre and Fortin, 1989; Burrough, 1995) to assay the point in time at which samples become independent (i.e., sill) or if there were periodic signals representing cyclic changes in the fish assemblage. In this analysis, semivariance is plotted on the ordinate and the lag period on the abscissa. Thus, an increase in semivariance with lag time would suggest samples close together in time (e.g., adjacent sample dates) were more similar than those far apart in time.

Persistence of species associations.—We examined persistence of species associations to suggest potential biotic interactions (e.g., predator-prey) or habitat associations. The identification of species associations also should improve our ability to predict how changes in the abundance of one species might affect other species. Product-moment correlations (Sokal and Rohlf, 1995) were used to examine correlations in mean abundance of species across all possible pairs of the six sample sites. The correlation coefficients between species pairs were used to construct matrices representing association among the 12 most common species within each season of each year. The warm season of 1984 was excluded from this analysis because we did not sample the complete season. All calculations were made with the PC-Ord software package, with 1000 random matrix simulations to assess significance levels (B. McCune and M. J. Mefford, Glenden, OR, 1995, unpubl.). Significant correlation between matrices indicated similar patterns of species associations in the years being compared. If there were overall significant effects among matrices, posthoc comparisons were assessed with Bonferonni corrected alpha levels (Sokal and Rohlf, 1995). Unweighted pair-group method using arithmetic averages (UPGMA) based on Euclidian distances was used to construct dendrograms from

each matrix to illustrate the community association patterns.

Influence of abiotic factors on the fish assemblage.—Canonical correspondence analysis (CCA) was used to detect relationships between environmental parameters (surface temperature, Secchi depth, and reservoir volume) and temporal variation in the fish assemblage. Because environmental variables were measured only at the main channel site (as an index of environmental conditions in our study area), the CCA was performed on species abundances pooled across sites on each date. CCA is a modification of CA that selects a linear combination of environmental variables to maximize the dispersion of species scores (ter Braak, 1995). This analysis produces a diagram that shows, by the length of vector arrows, the relative importance of environmental factors in describing variation in the fish assemblage. Monte Carlo simulations were used to test whether eigenvalues from the CCA were significantly greater than those generated from a randomized matrix. All analyses were conducted using PC-Ord (vers. 2.0, B. McCune and M. J. Mefford, Glenden, OR, 1995, unpubl.).

RESULTS

Field conditions and collections.—There was considerable variation in reservoir volume as a result of highly variable inflows from tributary rivers, with pronounced peaks in autumn 1981 and spring 1982 (Fig. 1). Reservoir volume fluctuated less, by comparison, in 1983 and 1984. Secchi depth, measured at the main channel site ranged from 0.15–1.80 m and was negatively correlated with discharge from the Red River ($r^2 = 0.17$, $df = 66$, $P < 0.001$) and reservoir volume ($r^2 = 0.22$, $df = 66$, $P < 0.001$). Surface water temperature in our study area ranged from 3–31 C and followed a similar pattern each year. The minimum temperature, however, was 2 C lower in winter 1981–1982 than in other years.

A total of 14,439 individuals, representing 25 taxonomic species, was captured. *Dorosoma cepedianum* was the most abundant species (34.1% of the total captures), followed by *M. saxatilis* (20.9%), *D. petenense* (9.5%), and *Aplodinotus grunniens* (Freshwater Drum, 9.5%). Other piscivorous fish common in our samples included *I. furcatus* and *M. chrysops*. Although the numerical abundance of *I. bubalus* (2.4%) and *Carpinus carpio* (River Carpsucker, 1.5%) was lower, they contributed substantially to the overall biomass.

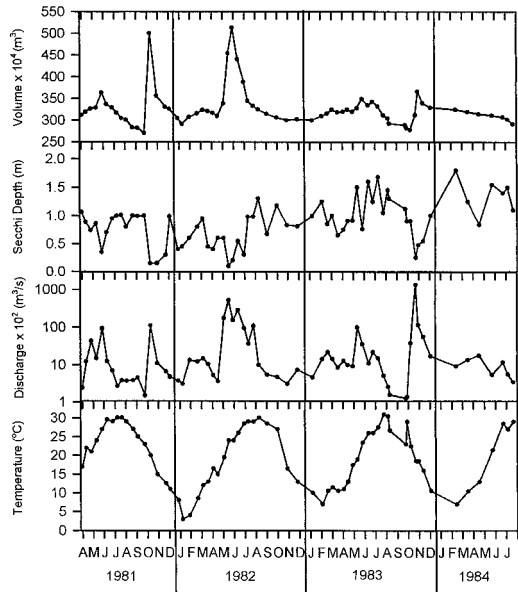


Fig. 1. Reservoir volume, Secchi depth, inflow from the Red River and surface water temperature from Lake Texoma for each sample date.

Variation in the fish assemblage across space and time.—Of the 18 most common species or size classes, several showed noteworthy seasonal or annual variation (Fig. 2). *Dorosoma petenense* showed the most obvious differences across time, occurring in large numbers only in the warm season of 1981. Conversely, *Hiodon alosoides* (Goldeye), although highly variable in abundance, was least abundant during this time. Small and medium *M. saxatilis* and small *D. cepedianum* showed annual trends opposite those of *D. petenense*. Small *D. cepedianum* were present in high numbers in 1982 when small and medium size classes of *M. saxatilis* were in low numbers or absent. Both large *M. saxatilis* and *A. grunniens* showed marked seasonal abundance patterns, because the latter peaked in abundance in cold seasons and the former during warm seasons. *Pomoxis annularis* (White Crappie) also was notably more abundant in 1983 than in other years.

Spatial and temporal variation among samples was revealed when the 402 individual samples were analyzed with CA (Fig. 3). The first axis accounted for 16.2% of the variation in assemblage structure and had a gradient length of 4.6 standard deviations, indicating an almost complete turnover in species composition between samples at opposite ends of the ordination (Gauch, 1982). Low Axis I scores represented individual samples with high abundance of small *D. cepedianum* and all size classes of *M.*

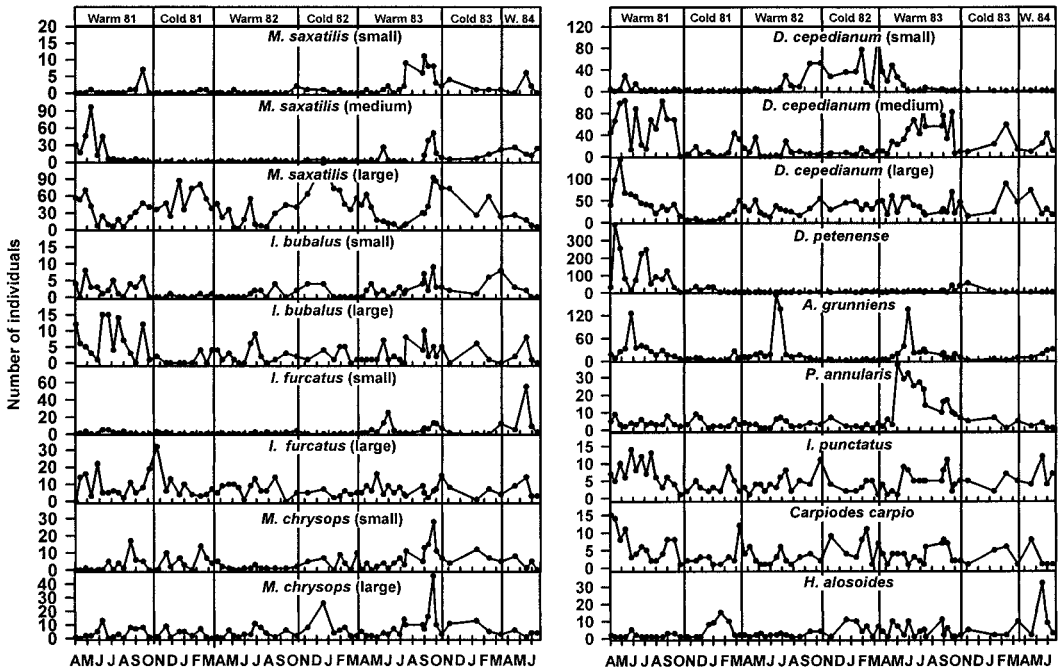


Fig. 2. Abundance of 18 common species and age classes caught in gill nets in Lake Texoma across the 67 sample dates. Number of individuals was pooled across sample sites for each given date. Note, scale of the y-axis varies among species.

saxatilis, *M. chrysops*, and *D. petenense*. High Axis I scores represented samples with high abundance of *A. grunniens* and *I. furcatus*. The second axis accounted for 14.8% of the variation in assemblage structure and had a gradient length of 4.3 standard deviations. The greatest variation on Axis II was from samples with high abundance of *D. petenense* versus those with high abundance of small *D. cepedianum*.

Greatest percent of variation in axis I scores, as revealed by partitioning of variance components (Table 2), was accounted for by depth (25.3%). The interactions of depth \times location and season \times year also accounted for a notable proportion of the overall variation in axis scores (10.4% and 12.8%, respectively). Year and season accounted for the greatest percent of variation on axis II scores (26.6 and 22.1%, respectively). However, these effects are not independent of each other as revealed by the interaction of season \times year that accounted for 15.9% of the total variation in axis scores.

Because depth and season accounted for much of the variation in samples, we plotted warm and cold seasons separately for each year and bottom and surface samples separately for each site (Fig. 4). Overlap in axis scores between surface and bottom sets was greatest in the shallow cove and least in the main channel

although, several outliers were apparent. Whereas there was much overlap in axis scores at the tributary arm location, there were generally higher axis scores at the bottom site. Although polygons drawn around points from warm and cold seasons showed much overlap, warm season samples clearly had higher axis scores than cold season samples on axis II during 1981. Conversely, cold season scores were slightly higher than warm season scores in 1983, suggesting a notable interaction between season and year on this axis.

Independence of samples among sites and dates.—Total number of individuals captured and species richness were greater during warm than cold season samples (Table 3). Overall, there were more fish in surface nets (mean = 41.2 individuals) than in bottom nets (mean = 30.8 individuals). However, this difference was less pronounced between surface and bottom nets in the shallow cove. CA axis I scores were greatest for surface samples in the main channel and tributary arm than other sites during both seasons, indicating greater abundances of *A. grunniens* and *I. furcatus* at these sites. CA axis II scores were greater in surface nets than bottom nets and slightly higher in the warm than in

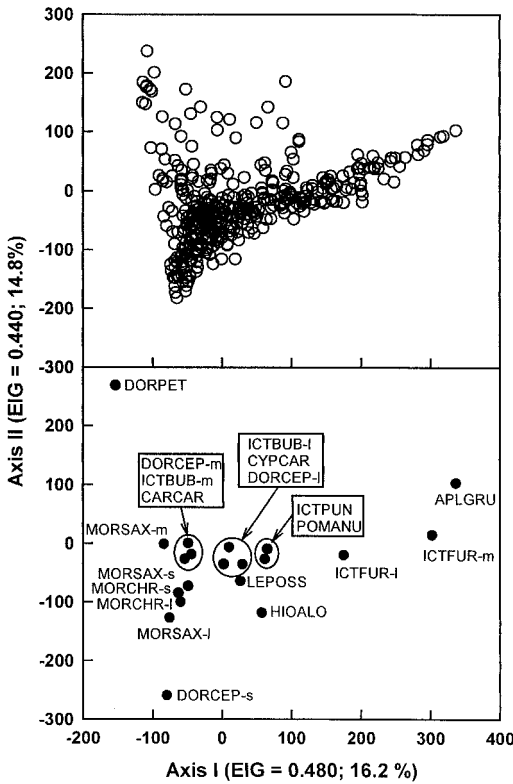


Fig. 3. Correspondence Analysis of the gill net samples from Lake Texoma. Top graph, sample scores; bottom graph, species scores. Species codes represent the first three letters from the genus and specific epithet. Suffixes -s, -m, and -l represent small, medium, and large size classes, respectively.

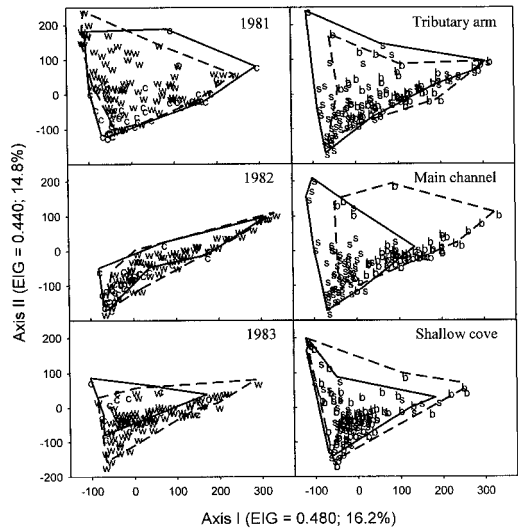


Fig. 4. Plots of the first two axes of the correspondence analysis in Figure 3, separated by year and season (left column; c = cold, w = warm), and habitat and depth (right column; b = bottom, s = surface).

cold seasons, indicating greater abundance of *D. petenense* at these sites and times.

Mantel tests revealed significant associations of time between samples (i.e., lag time) and the different community metrics (number of species, number of individuals, and CA axes). However, lag time was only weakly associated with species richness and number of individuals ($r = 0.212, P = 0.041$ and $r = 0.254, P = 0.022$, re-

TABLE 2. ANALYSIS OF THE FOUR MAIN EFFECTS AND THEIR INTERACTIONS OBTAINED FROM AN ANALYSIS OF VARIANCE OF CA AXIS SCORES. Percent variance for treatments and their interactions were derived from expected mean squares based on a Model II (Random effects) ANOVA following Sokal and Rohlf (1995).

Source	df	Axis I		Axis II	
		MS	% Variance	MS	% Variance
Axis I					
Depth (D)	1	424,163	25.3	53,510	10.9
Location (L)	2	83,642	11.9	2,588	3.1
Season (S)	1	123,270	11.8	118,092	22.1
Year (Y)	2	23,979	11.6	98,595	26.6
D × L	2	84,580	10.4	13,371	5.1
D × S	1	10,921	1.6	2,430	1.9
D × Y	2	7,150	6.6	1,645	3.2
L × S	2	29,428	3.6	7,247	2.4
L × Y	4	3,309	<0.1	3,375	<0.1
S × Y	2	89,396	12.8	45,126	15.9
D × L × S	2	2,419	<0.1	8,952	3.9
D × L × Y	4	2,388	<0.1	2,591	<0.1
D × S × Y	2	15,005	3.1	7,392	2.7
L × S × Y	4	3,101	<0.1	1,321	<0.1
D × L × S × Y	4	3,384	2.7	3,727	8.3

TABLE 3. MEAN NUMBER OF INDIVIDUALS, NUMBER OF SPECIES, AND CORRESPONDENCE AXIS SCORES (STANDARD DEVIATION) AVERAGED ACROSS WARM AND COLD SEASONS FOR THE SIX GILL NET SITES ON LAKE TEXOMA.

Site	Depth	Number of individuals	Number of species	Axis 1	Axis 2
Warm season					
Tributary arm	Surface	51.5 (37.1)	7.5 (2.7)	106.5 (87.7)	17.0 (52.1)
	Bottom	47.0 (33.5)	7.5 (2.0)	45.8 (111.9)	-9.6 (79.9)
Main channel	Surface	65.4 (41.1)	7.8 (2.4)	105.7 (83.4)	-5.7 (49.5)
	Bottom	26.0 (25.5)	5.2 (2.0)	-16.1 (60.2)	-30.2 (77.9)
Shallow cove	Surface	62.3 (71.9)	8.8 (3.3)	10.2 (79.3)	-8.7 (63.7)
	Bottom	66.4 (52.9)	10.1 (3.2)	-12.3 (60.7)	-24.7 (63.5)
Cold season					
Tributary arm	Surface	42.7 (24.4)	6.3 (2.2)	48.5 (69.4)	-39.5 (42.4)
	Bottom	30.8 (26.3)	6.9 (3.1)	-38.9 (36.1)	-70.0 (45.3)
Main channel	Surface	34.6 (17.6)	5.7 (2.0)	110.3 (87.9)	-8.9 (61.3)
	Bottom	10.1 (9.9)	3.8 (2.0)	-50.0 (25.5)	-92.3 (46.5)
Shallow cove	Surface	53.0 (28.5)	10.0 (2.4)	-10.7 (62.3)	-53.0 (58.7)
	Bottom	40.4 (26.2)	8.3 (3.0)	-38.0 (30.0)	-42.4 (75.5)

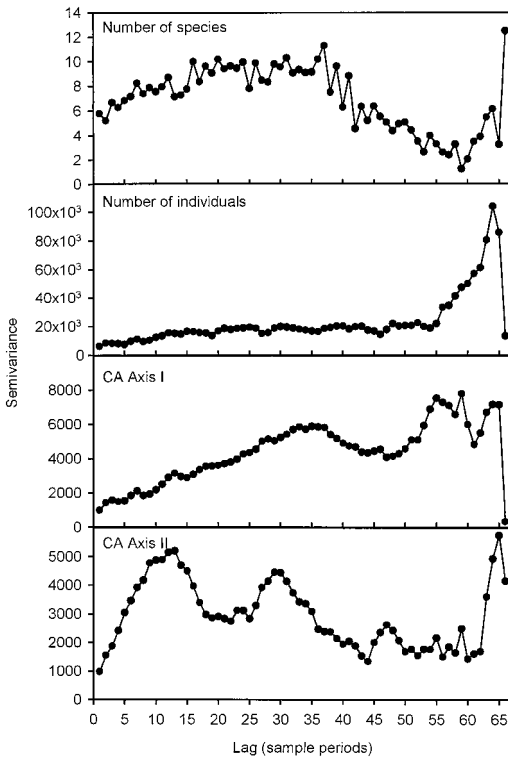


Fig. 5. Semivariograms representing the divergence (semivariance) of the fish assemblage in Lake Texoma at different sample intervals apart, based on the three community indices [species richness, number of individuals, and correspondence analysis (CA) axis scores].

spectively). There were strong associations between divergence in CA axis scores and time lag ($r > 0.437$, $P = 0.001$), and there was a marked increase in semivariance with lag time. In addition, the semivariogram for CA axis II (Fig. 5) showed a cyclic pattern in which distinct peaks in semivariance occurred at about 10 and 30 sample intervals. This pattern indicated a seasonal trend in the divergence of samples across time, because those samples that were 10 intervals apart corresponded to a lag of approximately six months (i.e., samples half a year apart were most different from each other on average).

Persistence of species associations.—Mantel tests showed significant concordance among years in warm season species associations (Table 4). The dendrograms showed that two groups were

TABLE 4. MANTEL CORRELATIONS AND PVALUES FROM COMPARISONS OF SIMILARITY MATRICES OF SPECIES ASSOCIATIONS ACROSS SIX GILL NET SITES IN LAKE TEXOMA. Comparisons were made among sample years for each season separately. P value < 0.008 was necessary to reject null hypotheses based on Bonferroni corrected alpha level.

Season	Year	r	P value
Warm	1981–1982	0.372	0.007
	1981–1983	0.577	0.001
	1982–1983	0.468	0.001
Cold	1981–1982	0.066	0.223
	1981–1983	0.035	0.329
	1982–1983	0.035	0.313

closely associated in warm seasons of all years (Fig. 6). Large and medium *D. cepedianum* typically occurred with large *M. saxatilis*. *Carpiodes carpio*, *I. bubalus*, and *I. punctatus* also consistently occurred together in warm seasons. Species associations in the cold season showed less consistency across years (Fig. 6), and Mantel tests showed no significant concordance among years (Table 4). Although *D. cepedianum* and *M. saxatilis* were often associated during cold seasons, the size classes of those species that were associated varied across years.

Influence of abiotic factors on the fish assemblage.—

A large proportion of the variation in the fish assemblage could not be explained by the environmental variables. Although eigenvalues from the first two axes of the CCA (Fig. 7) were significantly different from those from randomized matrices ($P < 0.001$), axis I and II only explained 13.8% and 6.0% of the variance in the fish assemblage, respectively (Table 5). The first axis showed the strongest association between assemblage composition and environment factors based on Pearson and Kendall (rank) correlations of sample scores with environmental parameters (Table 5). This axis was highly correlated with temperature ($r = 0.636$) and likely reflected seasonal changes in the fish assemblage (Fig. 7). The second axis had a much weaker species-environment association but suggested a correlation with reservoir volume ($r = 0.539$). Both large *I. furcatus* and *A. grunniens* increased in relative abundance during increased periods of reservoir volume, while small *M. saxatilis* declined in abundance in gill net samples at those times.

DISCUSSION

Variation in the fish assemblage across space and time.—Fortnightly gill net sampling for 3.5 yr allowed characterization of the spatial and temporal dynamics of fishes in the limnetic waters of Lake Texoma at the scale of our study sites. Under this sampling regime, the fish assemblage showed the greatest variation across sample sites (surface vs bottom) and seasons (warm vs cold). Similarly, species associations during the warm season were similar among years and appeared to be a consequence of habitat use. Thus, at least for the common species, the assemblage at our six sites remained relatively consistent at the time scale of our study (Fig. 8).

The most notable annual variation in our samples occurred because the fish assemblage in summer 1981 differed from subsequent

years. This difference was primarily the result of a winter kill of *D. petenense* in 1981–1982 and its extremely low abundance thereafter. Only because of a restocking effort did this species occur in our samples in 1983 (Harper and Nanninga, 1986). Variability in *D. petenense* abundance may have had pervasive effects in the reservoir fish assemblage. For example, Matthews et al. (1988) showed that the cold winter of 1981–1982 coincided with poor condition of adult *M. saxatilis* the next summer, likely due to low abundance of prey. In this study, we also showed that abundance of small and medium *M. saxatilis* was relatively low in 1982 (after the winter kill) compared to other years, suggesting low prey abundance also may have limited recruitment of small and medium age classes of *M. saxatilis* into the population. In addition, abundance of small *D. cepedianum* was highest during 1982. This may have been the result of a combination of the absence of a potential competitor (*D. petenense*) and reduced abundance of predators (small and medium *M. saxatilis*).

Abundance of individual species showed a wide range of variation across years and seasons. Some species varied little over time (e.g., *I. punctatus* and *Carpiodes carpio*), whereas for other species (e.g., *D. cepedianum* and *M. saxatilis*), adults varied little, but smaller size classes showed marked interannual variation. Two species other than *D. petenense* that showed relatively high interannual variation were *H. alosoides* and *P. annularis*. Based on our limited environmental data, it was not clear what attributed to the variable success of either species during our sampling. However, *H. alosoides* is known to vary markedly in abundance across years in reservoirs (Shelton, 1968) and river deltas (Donald, 1997).

Although much of the seasonal variation in the fish assemblage was dependent on year of sampling, there were general trends in the fish assemblage that appeared consistent across years. There was a decrease in abundance of adult *M. saxatilis* during summer because of down-reservoir migrations to cooler, deeper areas of the reservoir (Matthews et al., 1985; Coutant, 1985; Matthews et al., 1989). In addition, abundance of juvenile *A. grunniens* (< 200 mm SL) increased during summer. *Ictiobus bubalus* also showed a more localized seasonal shift in habitat use from littoral habitats during early summer to offshore habitats in late summer. This movement coincides with higher abundance of their preferred prey, copepods, in these habitats (Gido, in press). Overall, a large proportion of the local variability in the off-

Distance

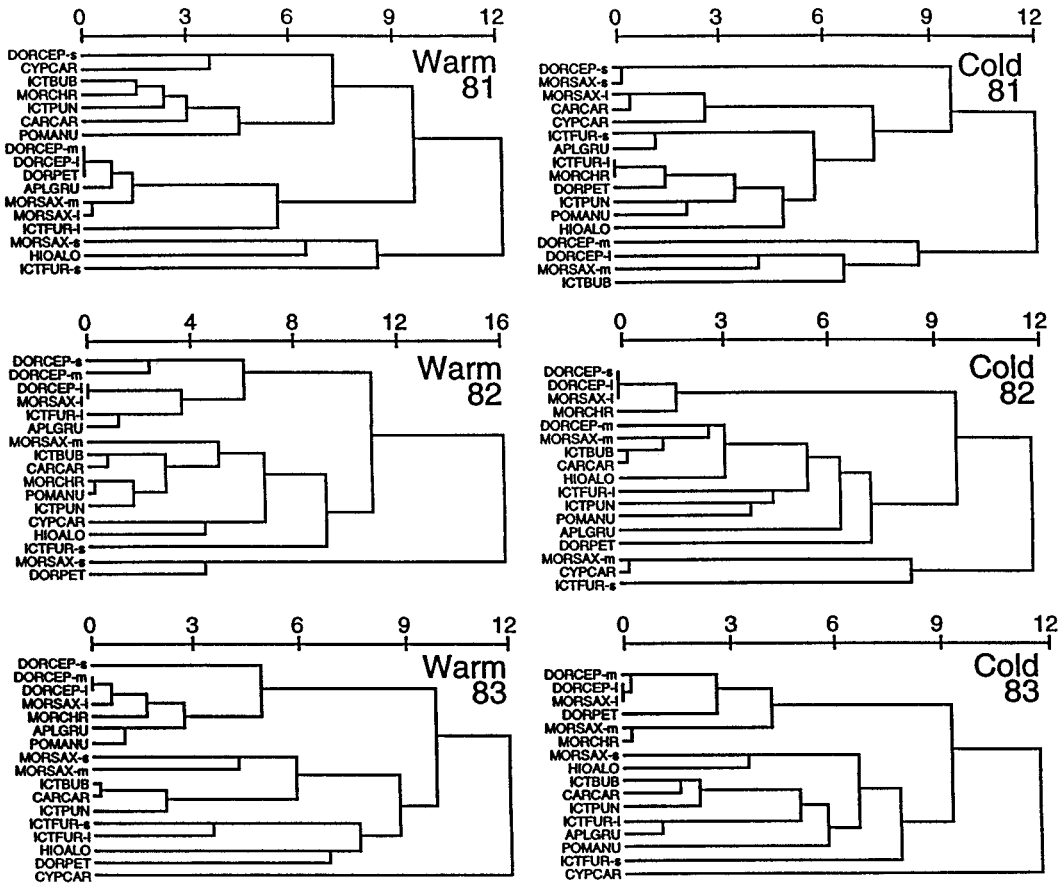


Fig. 6. Dendrograms from UPGMA clustering of species associations across the six gill net sites on Lake Texoma. Each dendrogram represents the associations for a given year and season. Species codes are as in Figure 3.

shore Lake Texoma fish assemblage likely was caused by patterns of seasonal migrations and reproduction, not absolute changes in population size at the scale of the whole reservoir.

Much of the variation in the Lake Texoma fish assemblage across sites was the result of depth (surface vs bottom; Table 2). In previous studies of Lake Texoma, most fish were reported to avoid reduced dissolved oxygen in benthic zones of Lake Texoma (Matthews et al., 1985; Matthews et al., in press). However, difference in physical conditions between surface and bottom varied across locations and was less pronounced in the shallow cove (WJM, unpubl. data). Presumably, the greater similarity in catch between the surface and bottom nets in the shallow cove occurred because the depth of the two nets differed by only a few meters in com-

parison to their vertical dispersion in the two deeper habitats.

Vertical distribution of fishes in lakes and reservoirs has been correlated with gradients of temperature and oxygen (Brandt et al., 1981; Rudstam and Magnuson, 1985; Moyle and Cech, 1999). In the main body of Lake Texoma, Matthews et al. (1985) showed that most fishes avoided low oxygen levels in the hypolimnion in late summer. Additionally, Schael et al. (1995) reported that depth distribution of *D. petenense* was influenced by seasonal differences in temperature and oxygen concentration. Measurements of these parameters in previous studies at the surface and bottom in each habitat demonstrated that this area of the reservoir stratifies in summer (Matthews et al., in press). However, because of frequent mixing of the wa-

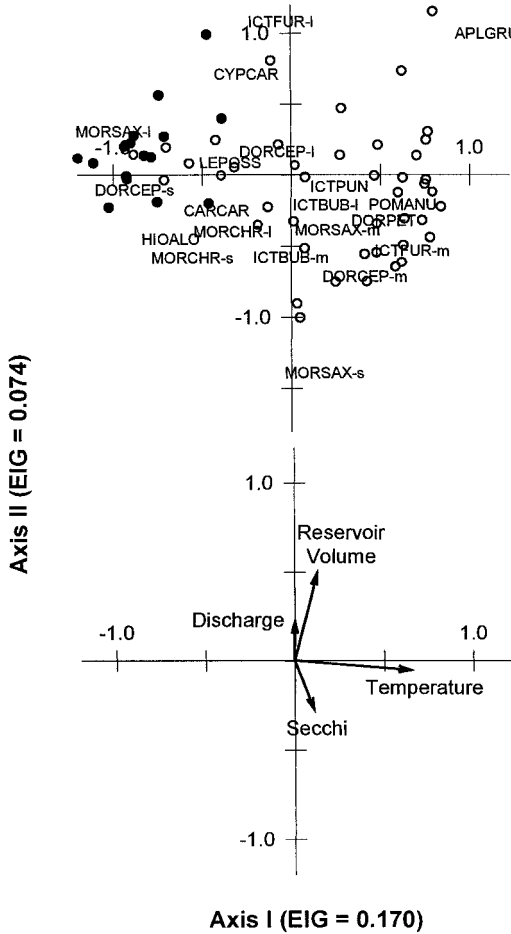


Fig. 7. Canonical correspondence analysis used to describe correlation of environmental factors with the variation in the fish assemblage of Lake Texoma. Each point is derived from pooled species abundances across sites for a given sample date. Top graph, sample and species scores with season in which samples were taken delineated by open (cold) and closed (warm) circles. Bottom graph, vector arrows representing the correlation of environmental factors with variation in fish assemblage. Species codes as in Figure 3.

ter column by wind, stratification in the Red River arm of Lake Texoma is weaker than in the deeper areas of the reservoir. Thus, benthic zones in our study area did not remain anoxic for long periods of time and still provide suitable habitat for several species.

Our spatial and temporal scales of sampling did not allow assessment of sources of variation that operate at larger scales, such as uplake-downlake environmental gradients or predator-prey cycles involving long-lived species. In fact, the younger size classes of *M. saxatilis* and *D. cepedianum* both showed notable annual varia-

TABLE 5. EIGENVALUES, VARIANCE EXPLAINED, PEARSON CORRELATIONS AND KENDALL CORRELATIONS FOR THE CCA ON LAKE TEXOMA GILL NET SAMPLES. Pearson and Kendall coefficients represent correlations between sample scores for an axis derived from the species data and the sample scores that are linear combinations of the environmental variables (B. McCune and M. J. Mefford, 1995, unpubl.).

	Axis I	Axis II	Axis III
Eigenvalue	0.170	0.074	0.010
Variance in species data	13.8	6.0	3.7
% of variance explained			
Pearson Correlation	0.817	0.499	0.542
Kendall (rank) Correlation	0.639	0.327	0.362

tion. Variation in recruitment of these longer-lived species could dramatically affect size structure of the population in subsequent years. Only long-term monitoring could address this issue.

Independence of sample sites and dates.—Characterization of spatial and temporal independence of samples is an important first step in determining how assemblages are structured. In addi-

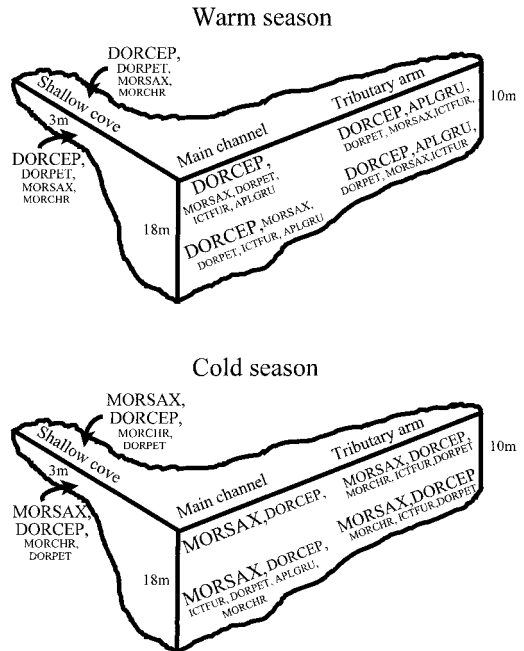


Fig. 8. General distribution patterns of fishes across the six gill net sites on the Red River arm of Lake Texoma for summer and winter months. Letter font represents the relative abundance of that species at a site for the given season.

tion, the composition of fishes captured at one period of time from a particular depth and habitat could be used to predict assemblage composition, at the same depth and habitat, on a future date. This information can be helpful in designing sampling efforts by allowing researchers to distribute their sampling effort in a way to adequately characterize the fish assemblage and minimize the redundancy of samples. In Lake Texoma, variation in assemblage structure was greatest among depths and seasons. Species composition differed the most between surface and bottom sites in the deeper habitats (main channel and tributary arm) and the shallow cove tended to support the highest numbers of individuals and species richness. These spatial differences suggest that sampling of a variety of habitats and depths is necessary to characterize the fish assemblage of Lake Texoma. Temporally, variation in species composition on proximal sample dates was much lower, on average, than samples more distant in time, as inferred by semivariograms (Fig. 5). However, the weak associations of species richness and number of individuals with lag time suggests changes in the assemblage over time were primarily due to species turnover. Because fortnightly sampling is somewhat redundant, characterizing the fish assemblage could be done over larger temporal scales that still account for seasonal variation in the assemblage. Overall, this relatively high degree of spatial and temporal autocorrelation implies the reservoir fish assemblage is localized, at least within short time periods (i.e., less than six months) and suggests a highly structured assemblage (e.g., see Fig. 6).

Persistence of species associations.—Species associations were concordant across years in warm seasons but not in cold seasons. The latter agrees with Gelwick and Matthews (1990), who found species associations in the littoral zone of Lake Texoma to be weak. The lack of consistency among years during the cold season, however, appeared to be the result of changes in abundance of younger life stages of common species. When a similar analysis (not shown) was performed with all life stages combined within species, there was significant concordance among all years for both warm and cold seasons [Mantel statistic (r) 0.223–0.566, $P < 0.035$]. Thus, in spite of changes in environmental conditions during our study (e.g., water level), species associations appeared to remain relatively consistent. The open water assemblage might be expected to show more concordant species associations than littoral zones because changes in reservoir level are less likely to change habitat

characteristics in offshore habitats (e.g., inundated vegetation).

A number of factors can influence the spatial and temporal distribution of reservoir fishes (e.g., Dendy, 1946; Vanderpuye, 1982; Fernando and Holcik, 1991) and, thus, associations of species across habitats. Higher productivity in the shallow cove resulting from greater light penetration to benthic surfaces may have concentrated foraging fishes in these habitats. Fernando and Holcik (1991) suggested that pelagic zones in reservoirs are often underutilized by fishes unless pelagic species are introduced into the system. They further suggested introduced pelagic species should have minimal associations with native littoral species because of little spatial overlap. Although this appears to be partially true in Lake Texoma, it is important to note the close association between the introduced *M. saxatilis* and the native *D. cepedianum* (Fig. 6). Overall, it appears that the distribution of resources in concert with differential habitat use by native and introduced species results in a structured fish assemblage. Field experiments would be necessary to determine the exact nature of these associations (e.g., biotic vs abiotic).

Influence of abiotic factors on the fish assemblage.—Seasonal changes in temperature explained the greatest amount of variation in the fish assemblage using CCA (Fig. 7). However, eigenvalues of the CCA were small, suggesting much of the variation in the fish assemblage could not be explained by environmental factors. Because we only sampled abiotic factors in the main channel, it is likely that site specific differences in water chemistry accounted for some of this unexplained variation. Regardless, it seems clear that patterns of species distribution or activity are strongly affected by temperature. For example, temperature is known to influence reproductive success (Irwin and Bettoli, 1995), survivorship (Harper and Namminga, 1986), and habitat use (Coutant, 1985, Matthews et al., 1985, Gido, in press) of reservoir fishes.

The second axis of the CCA suggests that changes in reservoir volume and turbidity also have some effects on the fish assemblage. *Ictalurus furcatus* and *A. grunniens* increased in relative abundance in nets during turbid inflow events, but it is unclear whether this was the result of (1) increased movement of these species or decreased movement of other species (e.g., Heimstra et al., 1969) or (2) avoidance of gill nets by these species in less turbid water. Although turbidity is known to lower the feeding efficiency of visual predators (O'Brien, 1990), effects of relatively short episodes of in-

creased turbidity on long-term fish assemblage structure are unclear.

Conclusions.—Multivariate techniques allowed us to quantify how the fish assemblage of Lake Texoma varied over a relatively fine-grained temporal scale. We were able to demonstrate marked seasonal changes in the fish assemblage that corresponded to seasonal changes in temperature. However, within seasons, samples were shown to have a high degree of temporal autocorrelation. Spatially, the fish assemblages varied primarily by depth, and species associations were relatively consistent across habitats. Thus, the fish assemblage at our study sites appeared to be highly structured and most species showed little annual variation in relative abundance. This occurred notwithstanding considerable annual variability in lake volume and turbidity.

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