



Fish assemblages in a Mississippi reservoir mudflat with low structural complexity

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Abstract In shallow reservoirs, seasonal water drawdowns expose littoral areas and over time produce barren mudflats. When flooded, mudflats provide homogeneous substrates, turbid water, and eroding shorelines of limited ecological value. We hypothesized that in mudflats structurally complex habitats are occupied by more fish, smaller fish of a larger range in sizes, more species, and fish assemblages that are different from those in simpler habitats. We tested these hypotheses over two consecutive years with fish collections made in sites with varying structural complexity. Results indicated that structural complexity harbors more fish in transects and enclosures. Structural complexity did not influence median length, but length range increased with structural complexity. Average species richness increased with structural complexity. Fish assemblage composition changed as structural complexity increased. The

ability of cover to provide survival, growth, and carrying capacity benefits is fundamental to programs aimed at increasing structural complexity. Results suggest observed effects on fish assemblages can lead to such benefits. Considering mudflats are a major component of reservoirs, expand as reservoirs age, and there is a potential to exert meaningful change on fish assemblages of impounded rivers by managing mudflats, we suggest additional attention is needed to develop practical habitat restoration options.

Keywords Reservoir aging · Fish attractors · Littoral · Drawdown · Regulated zone · Habitat complexity

Introduction

Dictated by operational goals, water-level fluctuations are a universal and important characteristic of many lakes and reservoirs (Kennedy, 1999; Coops et al., 2003; Bao et al., 2015). This is particularly true of flood-control reservoirs that can experience seasonal drawdowns as low as 10–20% of typical capacity because of their requirement to store seasonally excessive runoff. By design, these reservoirs store flood waters during times of high runoff and release them gradually over extended periods. Thus, a more stable water level is achieved downstream from the dam at the expense of extreme water level fluctuations

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within the reservoir. The reservoir elevation contours affected by the water level fluctuation (i.e., the regulated zone) vary from terrestrial to aquatic seasonally. In reservoirs where shore slopes are steep, the regulated zone resembles bare bands (or rings). In reservoirs with more moderate shore slopes, regulated zones resemble barren landscapes, often called mudflats.

Reservoir mudflats are characterized by low structural complexity (Carmignani & Roy, 2017). They exhibit low gradients, uniform relief topography, and straight shorelines shaped by wave action and sediment deposition. Sediment distribution in mudflats follows predictable patterns as elevation contours exposed to wave action for the longest duration annually have the coarsest sediment, while the average grain size decreases with lessened wave exposure (i.e., in lower elevation contours; Furey et al., 2004). The interaction of wave action, soft sediment, and shallow depth in mudflats increases water turbidity (Bao et al., 2015). Turbidity decreases light penetration associated with clear water and may influence fauna assemblage diversity through competitive mechanisms linked to finding food, avoiding predation, and other processes related to visibility (Davies-Colley & Smith, 2001). Perhaps the most distinguishing feature in mudflats is the absence of vegetation. Most aquatic, wetland, or terrestrial vegetation is unable to endure the annual cycles of water level fluctuations (Wilson, 1973; New & Xie, 2008), and decay of woody vegetation is expedited by cycles of exposure and flooding.

Loss of structural complexity in reservoir shorelines is a major concern among water resources, conservation, and fish management interests worldwide (Gois et al., 2008; Santos et al., 2008; Kaufman et al., 2014). There is evidence from many studies that reduced structural complexity diminishes species diversity and carrying capacity (Yanovski et al., 2017). In freshwater systems it has been demonstrated that macrophyte complexity is positively correlated with faunal richness and abundance (Petr, 2000; Kovalenko et al., 2012). Low complexity habitats intensify predation and competition (Almany, 2004), altering the biotic community composition, population survival, and growth of key taxa (Smokorowski & Pratt, 2007). The ecological significance of structural complexity has been related to the availability of complex sheltered space (Almany, 2004) that can

support higher abundance and biodiversity (Bell et al., 1991), higher carrying capacity (Kostylev et al., 2005), and in some cases higher production than homogeneous space (Kovalenko et al., 2012). Habitats with greater structural complexity may support greater species richness through greater microhabitat availability and thus greater niche space (Willis et al., 2005), through reduced predation and prey depletion (Kovalenko et al., 2012), or both. Greater structural complexity may provide habitable space to organisms with a wider variety of body sizes, thereby also increasing species richness (Tokeshi & Arakaki, 2012).

The fish assemblages that develop in mudflats of reservoirs are poorly understood, despite the scope of mudflats in reservoirs and their increased impact on biotic communities as reservoirs age. Thus, our goal was to characterize the fish assemblage richness and composition associated with mudflats, the scarce cover that exists naturally in mudflats, and a gradient of structural complexity created by structures of diverse sizes installed by conservation organizations. We hypothesized that within mudflats, areas with increased structural complexity are occupied by (1) more fish; (2) smaller fish but a larger range in sizes across the assemblage; (3) more fish species; and (4) fish assemblages that are unlike those in simpler habitats.

Study area

The study was conducted in the mudflats of Enid Lake in northwest Mississippi, USA. This flood-control reservoir was impounded by the U.S. Army Corps of Engineers (USACE) in 1952 to protect agricultural interests downstream. During normal water years, the reservoir fluctuates 6.1 m (Fig. 1), which causes a change in surface area of approximately 4,000 ha, from 6,527 ha at summer pool to 2,476 ha at winter pool.

These extensive annual fluctuations repeated over 65 years have degraded the 4,000-ha regulated zone and turned it into barren mudflats. The mudflats are largely featureless but are recolonized by terrestrial plants when exposed in fall and winter, starting at higher contour elevations as water recedes. However, terrestrial vegetation grows slowly because of poor soil quality and a brief growing season after

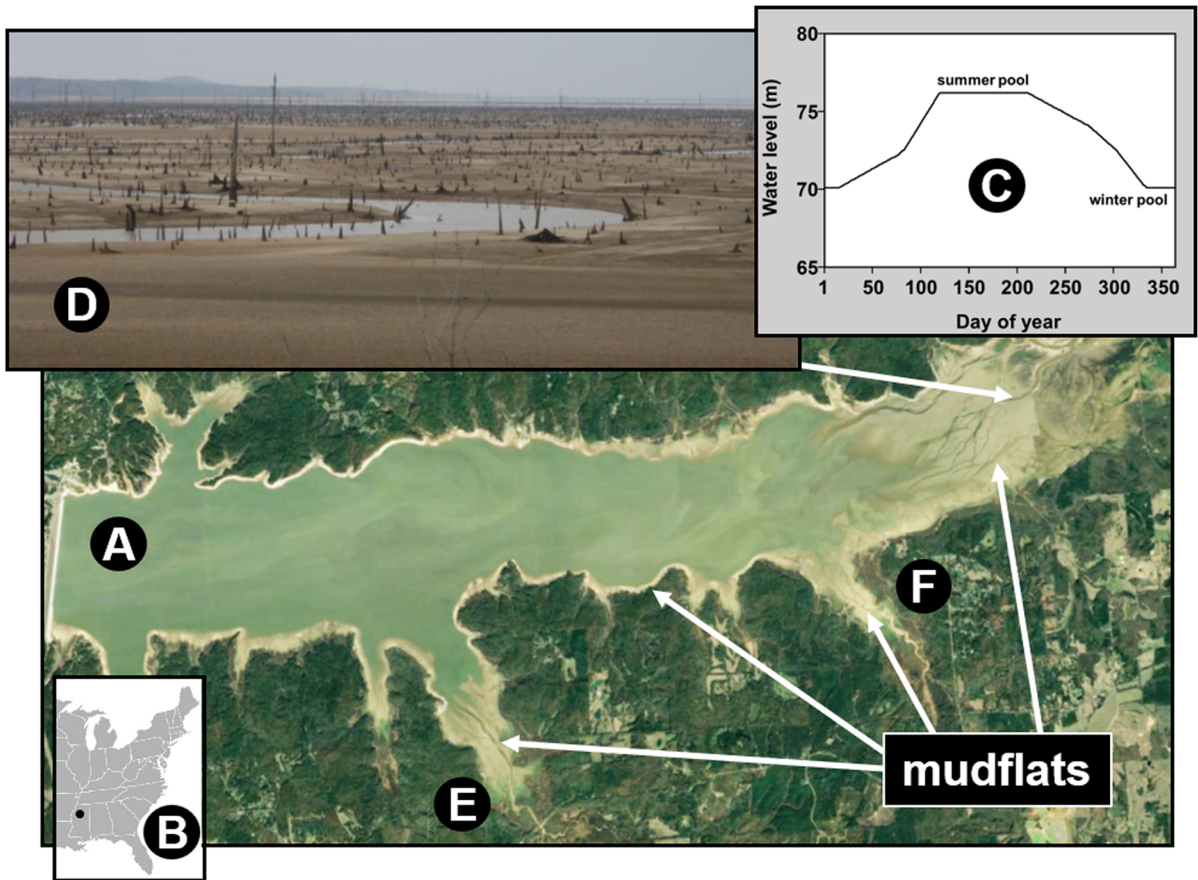


Fig. 1 Enid Lake (A) in northwest Mississippi, USA (B). The reservoir fluctuates 6.1 m annually exposing nearly 4,000 ha (C, D). Water level at the time of the aerial photo was 72.2 m

drawdown. Plants in mudflats degrade quickly after a few months of flooding the following spring and summer. A few creek channels traverse the mudflats, carved by water discharge in winter when the mudflats are exposed, but these channels are shallow, and their bank slopes are rarely steep. Substrates are mostly fine sediment originating from eroding shorelines and watersheds.

Submerged structure is mostly lacking in mudflats because of removal during reservoir construction, degradation over time, or blanketing by sediment deposition. However, a limited amount of cover does exist. Most of the available cover is represented by occasional cypress trees *Taxodium* sp. and their broad root systems, established during years of drought when reservoir water level does not reach the higher contours of the mudflats. Other structures include cypress and willow *Salix* sp. saplings emerging

showing a contour of mudflats surrounding the reservoir. Fish assemblages in the mudflats of two embayments (E, F) were studied

annually near shore, occasional brush fish attractors < 10 m diameter, and stake beds < 2 m diameter. The latter two structures represent supplemental fish habitat installed periodically by organized angler groups in collaboration with the USACE and over time are usually at various levels of decomposition and partly blanketed by sediment. The structures described above commonly comprise < 1–3% of the total area of embayments in Enid Lake, with the remaining area comprised of featureless mudflats void of structural complexity.

Methods

Fish collections

We characterized mudflat fish assemblages in two successive seasons in 2016 (season 1) and 2017 (season 2) during months when water level was at or near summer pool elevation (approximately 76 m; Fig. 1). In season 1, we sampled transects in mudflat areas with and without natural cover. In season 2 we sampled enclosures that encircled various volumes of supplemental fish habitat installed on the mudflats at diverse depth contours. All fish collected were identified to species and measured for total length. For the purposes of analysis and commentary, the presence of cover or an increase in volume of cover will be assumed to be an indicator of increased structural complexity.

Season 1 transects

Fish were collected by boat electrofishing with two netters following methods outlined by Miranda and Boxrucker (2009). We sampled during early August 2016 (day of year 210–225), in two embayments, just as water level began to drop towards winter pool (Fig. 1). Both embayments have extensive mudflats (282 and 141 ha) and become entirely dewatered when reservoir water level drops to winter pool. We conducted a total of 60 boat electrofishing transects in the two embayments, with each transect extending 250–400 s of electrofishing time. Of the 60 transects, we randomly assigned 20 to areas with cover consisting mostly of a mixture of cypress and willow trees, with occasionally flooded terrestrial grasses next to shore or brush piles, hereafter collectively “cover” habitat. We randomly assigned the remaining 40 transects to shallow areas characterized by water that after inspection appeared to be void of cover, hereafter “open” habitat. Transects were divided evenly between each of the two embayments with a total of 30 transects, 10 cover and 20 open, allocated to each embayment. We selected unequal sample sizes because sites with cover were uncommon. Sampling sites were separated by a minimum of 100 m, length of transects were kept relatively short to allow for 100-m transect separation, cover was avoided by a minimum of 20 m in open water transects, and depth of transects averaged 1.0 m (min–max, 0.3–2.4 m). After

processing, most fish were released live, except for occasional voucher specimens.

Season 2 enclosures

In May–September 2017, we randomly selected and sampled 120 individual sites with ($N = 60$) and without ($N = 60$) cover within the larger of the two embayments. Six sampling events, each consisting of two consecutive days, were spaced approximately every 3 weeks over the study period. Each event included 20 samples representing varied levels of cover including no cover. The sites without cover were spaced at least 20 m away from any structures (e.g., shore, stream channel, brush piles). The sites with cover included a mixture of cypress and red cedar *Juniperus virginiana* Linnaeus structures held in place using cinder blocks that were installed during February 2017. Prior to flooding, the structures were measured for volume and geospatial coordinates were recorded. Each sampling site was encircled with a block net (30-m long, 2-m tall, 6.5-mm bar mesh), equipped with a lead line and float line, and deployed from a flat-bottom boat (Bettoli & Maceina, 1996) to enclose approximately 70 m². Immediately after the circle was closed, a depth measurement was taken to estimate volume of water encircled, and Prentox® Prenfish™ (5% rotenone emulsified in Naphthalene and 1,2,4-trimethylbenzene) was applied to achieve a concentration of 1–2 mg l⁻¹, in accordance with standard techniques (Bettoli & Maceina, 1996). Two netters equipped with 3 mm mesh dip nets collected fish within the net area for a minimum of 15 min or until all fish had been collected. Volume of the structures sampled varied from 0.8 to 157.4 m³ with a mean of 32.4 m³ and a median of 20.7 m³, and depth of sampling sites varied from 0.5 to 1.4 m with a mean and median of 0.9 m. Fish were stored on ice to transport to a laboratory for processing and disposal.

Data analysis

The four analyses that follow correspond to the four hypotheses listed earlier. To avoid statistical difficulties related to non-normality of our data, we used nonparametric, univariate, and multivariate permutation analysis of variance (Anderson, 2001). All count data were log_e + 1 transformed to meet the homogeneity of dispersion assumption.

Complex habitats are occupied by more fish

This univariate analysis was applied to Bray–Curtis dissimilarities to test if catch rates of fish of all species combined (dependent continuous variable) differed relative to cover (cover or open transects; independent class variable). Additionally, we applied a univariate permutation analysis of covariance to test if total fish counts in enclosures (dependent continuous variable) differed relative to structure volume (independent continuous variable), while controlling for site depth (independent continuous variable), and sampling week (independent class variable).

Complex habitats are occupied by smaller fish but a larger range in sizes

We used univariate permutation analysis of covariance applied to Euclidean similarities to test if median length (dependent continuous variable) of all species combined differed relative to structure volume (independent continuous variable), while controlling for site depth (independent continuous variable), and sampling week (independent class variable). This analysis was repeated with length range (i.e., max TL – min TL) as the independent class variable.

Complex habitats are occupied by more species

Species richness was estimated as the species counts in each of the season 1 transects and in each of the season 2 enclosures. For transects, we used a univariate permutation analysis of variance applied to Euclidean similarities to test if richness estimates (dependent continuous variable) differed between cover (cover or open transects; independent class variable). For enclosures, we used a univariate permutation analysis of covariance applied to Euclidean similarities to test if richness estimates (dependent continuous variable) changed with structure volume (independent continuous variable), while controlling for depth (independent continuous variable), and sampling week (independent class variable).

Fish assemblages in complex and simple habitats are different

We applied a multivariate permutation analysis of variance to Bray–Curtis dissimilarities to test if

species catch per effort (multiple species, dependent continuous variable) in transects differed between cover (cover or open transects; independent class variable). If they did ($P < 0.05$), we used indicator species analysis (Dufrêne & Legendre, 1997) to identify which species contributed most to the difference between cover and open transects. Additionally, we applied a multivariate permutation analysis of covariance to Bray–Curtis dissimilarities to test if counts by species in enclosures (multiple species, dependent continuous variable) differed relative to structure volume (independent continuous variable), while controlling for site depth (independent continuous variable), and sampling week (independent class variable). If significant effects were detected, the relationship between the fish assemblage and structure volume was further analyzed with canonical correlation analysis to inspect how individual species responded.

Data processing

Analyses of variance and covariance, univariate and multivariate, were performed with the *adonis* function from the *vegan* package, canonical correlation analyses with the *cancor* function from the *stats* package, and indicator species analysis with the *indval* function from the *labdsv* package. All analyses were done in program R (R Development Core Team, 2017).

Results

Overall, we collected 13,616 fish representing 22 species (Table 1). The most common species in transects were gizzard shad *Dorosoma cepedianum* (Lesueur, 1818) (23.1%), largemouth bass *Micropterus salmoides* (Lacepède, 1802) (16.6%), and bluegill *Lepomis macrochirus* Rafinesque, 1819 (13.2%). The most common species in enclosures were gizzard shad (37.8%), bluegill (25.9%), and common carp *Cyprinus carpio* Linnaeus, 1758 (15.6%). Size distribution of fish collected in transects and enclosures was log-normal (Fig. 2). Median total length was 79 mm (min–max: 22–742) in transects, and 46 mm (min–max: 15–785) in enclosures.

Table 1 List of species, counts, and percent composition (in parentheses) of fish collected in the mudflats of Enid Lake, Mississippi, USA

Common name	Scientific name	Transects ($N = 829$)	Enclosures ($N = 12,787$)
Spotted gar	<i>Lepisosteus oculatus</i>	18 (2.17)	13 (0.09)
Gizzard shad	<i>Dorosoma cepedianum</i>	192 (23.07)	4,827 (37.76)
Common carp	<i>Cyprinus carpio</i>	7 (0.85)	1,994 (15.60)
Emerald shiner	<i>Notropis atherinoides</i>	90 (10.87)	107 (0.84)
Blacktail shiner	<i>Cyprinella venusta</i>	74 (8.94)	368 (2.88)
Golden shiner	<i>Notemigonus crysoleucas</i>	0 (0.00)	54 (0.42)
Bullhead minnow	<i>Pimephales vigilax</i>	4 (0.48)	17 (0.13)
Spotted sucker	<i>Minytrema melanops</i>	1 (0.12)	40 (0.31)
Brook silverside	<i>Labidesthes sicculus</i>	95 (11.47)	136 (1.06)
Inland silverside	<i>Menidia beryllina</i>	59 (7.13)	267 (2.09)
Pirate perch	<i>Aphredoderus sayanus</i>	0 (0)	3 (0.02)
Blackspotted topminnow	<i>Fundulus olivaceus</i>	0 (0)	1 (0.01)
Channel catfish	<i>Ictalurus punctatus</i>	5 (0.60)	12 (0.09)
Flathead catfish	<i>Pylodictis olivaris</i>	0 (0)	1 (0.01)
White bass	<i>Morone chrysops</i>	0 (0)	23 (0.18)
Bluegill	<i>Lepomis macrochirus</i>	109 (13.16)	3,317 (25.94)
Green sunfish	<i>Lepomis cyanellus</i>	1 (0.12)	28 (0.22)
Orangespotted sunfish	<i>Lepomis humilis</i>	5 (0.60)	221 (1.73)
Largemouth bass	<i>Micropterus salmoides</i>	137 (16.55)	621 (4.86)
Black crappie	<i>Pomoxis nigromaculatus</i>	6 (0.72)	229 (1.79)
White crappie	<i>Pomoxis annularis</i>	23 (2.78)	378 (2.96)
Freshwater drum	<i>Aplodinotus grunniens</i>	3 (0.36)	130 (1.02)

N total counts

Complex habitats are occupied by more fish

The median catch rate (fish per 5 min) was 22.5 in transects with cover and 9.0 in open transects. The permutation analysis of variance indicated these catch rates were different (pseudo- $F = 20.3$, $P < 0.01$). The permutation analysis of covariance applied to the enclosure samples indicated that total fish counts increased relative to structure volume (pseudo- $F = 4.4$, $P = 0.04$), but did not differ among weeks (pseudo- $F = 1.9$, $P = 0.10$), and there was no effect of depth (pseudo- $F = 0.4$, $P = 0.53$) or any of the interactions ($P \geq 0.07$).

Complex habitats are occupied by smaller fish but a larger range in sizes

For enclosures, the median total length varied from 25 to 192 mm, and the median range in total length from

19 to 765 mm. The analysis of covariance applied to median length indicated length did not differ relative to structure volume (pseudo- $F = 0.4$, $P = 0.49$) or depth at the structure (pseudo- $F = 0.0$, $P = 0.89$), but differed among weeks (pseudo- $F = 4.7$, $P < 0.01$). The analysis of covariance applied to length range indicated range increased relative to structure volume (pseudo- $F = 4.5$, $P = 0.04$; Fig. 3), that there was a volume \times week interaction (pseudo- $F = 2.4$, $P = 0.05$), and a depth effect (pseudo- $F = 4.2$, $P = 0.05$). Inspection of the interaction suggested that range in fish size increased with structure volume, but the range was largest in intermediate weeks and declined in early and late weeks. The effect of depth denoted increased length range in structure located in deeper water.

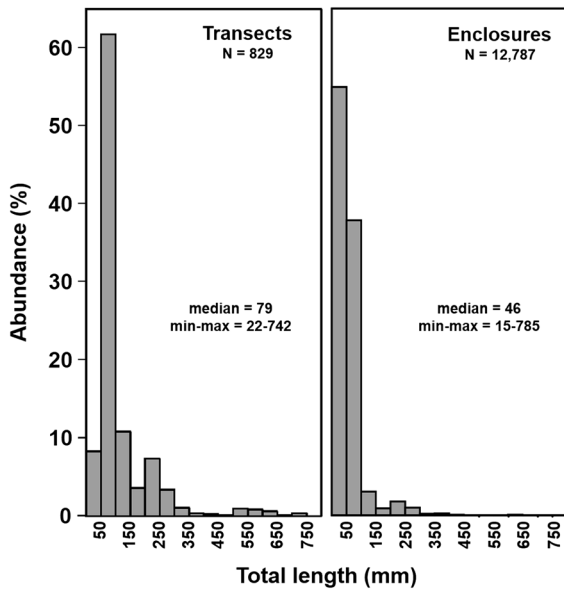


Fig. 2 Size distribution of fish collected in transects and enclosures in the mudflats of Enid Lake. *N* number of fish

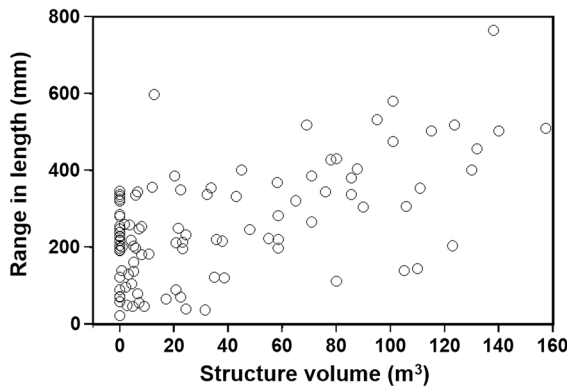


Fig. 3 Relationship between structure volume and length range of fish collected in enclosures in the mudflats of Enid Lake. Length range represents the residuals (i.e., deviation from the mean length range) after removing the effect of depth and week

Complex habitats are occupied by more species

For transects, the permutation analysis of variance indicated species counts differed between cover and open transects (pseudo- $F = 2.9$, $P = 0.03$). Median species counts were 7.5 in open transects and 9.5 in cover transects. In enclosures, the permutation analysis of covariance indicated species counts changed with structure volume (pseudo- $F = 14.7$, $P < 0.01$), but that there was an interaction between volume and week (pseudo- $F = 3.0$, $P = 0.01$). The interaction

suggested that species counts increased with structure volume, but the increase was highest in intermediate weeks and declined in early and late weeks. The effect of depth was not statistically significant (pseudo- $F = 3.1$, $P = 0.06$). All species collected in open sites were also collected in cover sites.

Fish assemblages in complex and simple habitats are different

Fish assemblage composition in mudflats differed between open and cover transects (pseudo- $F = 3.6$, $P = 0.02$). Indicator species analysis showed largemouth bass (median TL of fish in the sample = 91 mm), bluegill (59 mm), orangespotted sunfish *Lepomis humilis* (Girard, 1858) (61 mm), blacktail shiner *Cyprinella venusta* Girard, 1856 (74 mm), and spotted gar *Lepisosteus oculatus* Winchell, 1864 (551 mm) occurred in association

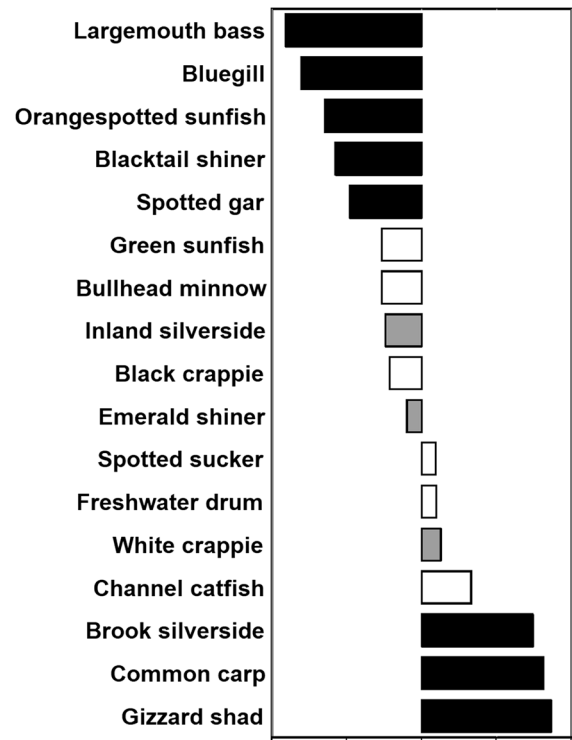


Fig. 4 Indicator species analysis of fish collected in transects with cover or with no cover in the mudflats of Enid Lake. Black bars indicate significant ($P < 0.05$) association with either cover or no cover; gray bars indicate no association; white bars indicate no association but low sample sizes and thus with uncertain indicator usefulness

with cover (Fig. 4). Conversely, gizzard shad (100 mm), common carp (635 mm), and brook silverside *Labidesthes sicculus* (Cope, 1865) (63 mm) occurred in association with open habitats. The remaining species showed no clear association with either cover or open habitats. This latter set of species that showed no association with cover includes some with low sample sizes and thus with uncertain indicator usefulness, and some with larger sample sizes whose low indicator scores signify they occupy both cover and open habitats indiscriminately.

In enclosures, partitioning the variance of fish assemblage showed that the temporal effect was strongest, with site depth and structure volume also contributing components of variation (Table 2). There was no evidence of interactions among the predictor variables. For most species the temporal changes reflected the seasonal dynamics of age-0 fish, which generally recruit to the sampling gear early in the season, peak, and then decrease in abundance as they shift to different habitats in the reservoir, perish, or both. Nevertheless, there were multiple versions of this pattern as some species peaked early in the sampling season (most species), some peaked later in the season (e.g., bluegill, brook silverside), and some showed more than one peak (e.g., gizzard shad, emerald shiner *Notropis atherinoides* Rafinesque, 1818).

The canonical correlation analyses distinguished species potentially influenced by structure volume. To avoid the ambiguities associated with small sample sizes, this analysis was restricted to 12 species with sample sizes ≥ 100 fish in enclosures (Table 1). The canonical correlation between structure volume and the latent variable representing the set of 12 species was 0.76 (Fig. 5). Individual species correlations with

the latent variables suggested black crappie *Pomoxis nigromaculatus* (Lesueur, 1829) (median TL of fish in the sample = 50 mm), bluegill (40 mm), blacktail shiner (60 mm), common carp (30 mm), emerald shiner (42 mm), largemouth bass (45 mm), orangespotted sunfish (47 mm), and white crappie *Pomoxis annularis* Rafinesque, 1818 (44 mm) showed affinity for cover; freshwater drum *Aplodinotus grunniens* Rafinesque, 1819 (177 mm) and inland silverside *Menidia beryllina* (Cope, 1867) (49 mm) showed affinity for no or low cover; and brook silverside (60 mm) and gizzard shad (56 mm) were about equally distributed through all levels of cover (Fig. 5).

Discussion

A positive correlation between structural complexity and species richness has been reported for a wide variety of biota (Kovalenko et al., 2012). Habitats with high structural complexity have also been reported to support more fish than neighboring habitats that are less complex (Lingo & Szedlmayer, 2006; Moore & Hovel, 2010). Given that numerical density and species richness increase in tandem, it is also possible that the effect on species richness may sometimes be a sampling artifact, as higher numerical densities tend to include more species (Gotelli & Colwell, 2011). However, the mechanism commonly used to explain the effect of structural complexity on species richness is that high complexity provides additional food and shelter, and thus lessens competition and predation and allows more species to coexist (Hixon & Menge, 1991; Eklöv, 1997; Grenouillet et al., 2002; Almany, 2004). Complex habitat reduces encounter rates between prey and predators, and prey have often been

Table 2 Permutation analysis of covariance partitioning and analysis of mudflats fish assemblages (22 species) from Enid Lake, based on $\log_e + 1$ transformed counts and Bray–Curtis dissimilarities

Source	df	SS	MS	Pseudo- <i>F</i>	<i>P</i>
Week	5	81,394	16,279	11.44	< 0.01
Structure volume	1	8,526	8,526	5.99	< 0.01
Site depth	1	6,540	6,540	4.60	< 0.01
Week \times structure volume	5	8,975	1,795	1.26	0.17
Week \times depth	5	8,801	1,760	1.23	0.24
Structure volume \times depth	1	1,604	1,604	1.13	0.31
Week \times structure volume \times depth	5	6,354	1,271	0.89	0.62
Residual	95	135,180			
Total	118	257,374			

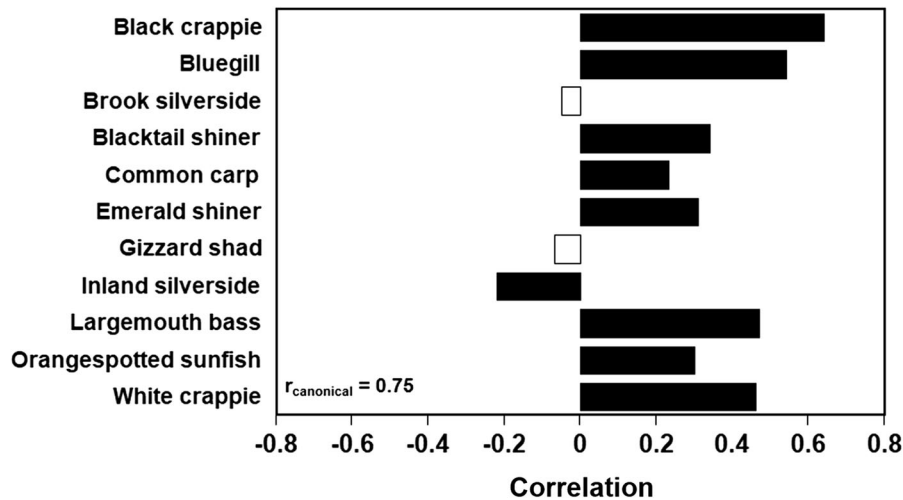


Fig. 5 Canonical correlation ($r_{\text{canonical}}$) between structure volume and a latent variable representing a set of 12 fish species with sample sizes > 100 fish in enclosures (Table 1). Black bars indicate significant ($P < 0.05$) species correlations

with the latent variable; white bars indicate no correlation. Higher positive correlations indicate an association with larger structure volumes, whereas higher negative correlations indicate an association with open water

reported to seek structural complexity in the presence of predators (Savino & Stein, 1989; Beukers & Jones, 1998). Food and shelter influence available niche space, and thus complex habitat can harbor additional species. However, while on average complex habitats supported higher species richness in the study mudflat, they did not harbor species that did not already occur in less complex habitat, and thus may not have attracted new species to the mudflat. Perhaps because of the influence of the barren mudflat habitats in the reservoir, or the limiting influence of reduction of volume to winter pool, species richness throughout Enid Lake is low ($N = 28$). Species richness is higher in neighboring reservoirs in the Tombigbee River ($N = 38$ –53 species; USFWS, 1988) and Tennessee River ($N = 46$ –70 species; Miranda & Dembkowski, 2016).

Altered fish assemblage composition in reservoir mudflats void of cover may also be associated with the temporal dewatering patterns that require annual recolonization. Species richness reductions have been reported in other environments that are dewatered periodically, such as marine mudflats exposed to daily dewatering cycles (Whitlatch, 1982; UK BRIG, 2008; Gerwing et al., 2016). Within Mississippi reservoirs, distinct fish assemblage composition has also been documented between distinct habitat types such as floodplains with natural vegetation and embayments which consist mostly of mudflats (Miranda et al.,

2014). During drawdown the Enid Lake fish assemblage vacates embayments and resides in a mostly featureless habitat provided by winter pool in the mainstem. Rising reservoir water levels during spring make mudflats available for colonization. The fish that colonize mudflats consist of species capable of overwintering in the conditions provided by winter pool and then quickly expanding and reproducing in the newly flooded areas available in spring and summer. These species are proficient colonizers, many are r-strategists, and are a subset of a lowland river fish assemblage adapted to seasonally expand into floodplains. The assemblage is convened over several weeks as species migrate at different rates into the newly flooded areas. Species present in the reservoir basin but often incapable of rapid colonization (e.g., flathead catfish *Pylodictus olivaris* (Rafinesque, 1818), small percids) or not well adapted to mudflat habitats (e.g., bowfin *Amia calva* Linnaeus, 1766, dollar sunfish *Lepomis marginatus* (Holbrook, 1855), longear sunfish *Lepomis megalotis* (Rafinesque, 1820)) are generally not well represented in the mudflats or the reservoir.

Volume of the structure installed in the mudflats enhanced numerical density, species richness, and size range, and changed fish assemblage composition in the structure. Large structures tend to be occupied by more fish, and more diverse fish assemblages than do small structures (Gladfelter et al., 1980; Rountree,

1989; Mellin et al., 2010). Small structures or patches of natural cover offer relatively more edge habitat than large patches, and large patches offer more protective interior habitat. A large plant patch or a brush pile structure may be detectable from a greater distance, but dispersing fauna may have a better chance of locating several small patches than one large patch (Bohnsack, 1991). We suspect that preference for size of the patch, and detectability of the patch are species, life stage, and site specific. Thus, a strategy for deployment of structure targeted at increasing structural complexity may be to provide a diversity of structure sizes to promote a variety of species across a range of life history stages.

An underlying principle motivating managers to increase structural complexity in mudflats is the production hypothesis, i.e., structural complexity provides additional habitat that increases the environmental carrying capacity and eventually the abundance and biomass of fish in the entire system (Fisher et al., 2006). Thus, barren mudflats may hypothetically be transformed into more productive environments by promoting vegetation growth or by adding structures such as brush piles. Various mechanisms have been suggested for this transformation (reviewed by Smokorowski & Pratt, 2007; Kovalenko et al., 2012), including supporting additional food, mediating predator–prey interactions, promoting recruitment, and providing shelter from predation to individuals that would otherwise have been lost. Published reports have documented many of these mechanisms. Added substrate contributed by woody structure reportedly provides additional periphyton and associated biota (Van Dam et al., 2002), supports similarly high macroinvertebrate densities as aquatic macrophytes (Bowen et al., 1998), and has a greater invertebrate biomass than open sediment (Smokorowski et al., 2006). Experiments have demonstrated that habitat structure can influence multiple predator behaviors and support the mechanism of increased prey refuge in more structurally complex habitats (Warfe & Barmuta, 2004). Controlled testing has also shown that supplemental brush structure improves recruitment of some fish species by providing spawning habitat to increase natural reproduction (e.g., Vogeley & Rainwater, 1975; Hoff, 1991; Hunt & Annett, 2002), and survival of juveniles (Miranda & Hubbard, 1994). Our results concur that increasing structural complexity in mudflats may promote

carrying capacity benefits and the restructuring of fish assemblages.

Nevertheless, increased abundance and species richness in structural complexity can also be attributed to behavioral attraction. An increase in fish abundance and diversity may represent aggregation of fish attracted from neighboring areas near the structure, with no benefits to increased production or carrying capacity (Pickering & Whitmarsh, 1997). However, attraction and production are not mutually exclusive (Brickhill et al., 2005) and can be considered opposite extremes along a gradient. While structure patches in mudflats may merely attract and concentrate some fishes and life stages, they may promote the growth and survival of others. Most fishes probably are somewhere between these two extremes. Thus, existence of attraction mechanisms does not refute the possibility of increased production. Attraction behavior of fish to structure presumably evolved because of a selective advantage such as faster growth and increased survival, both of which promote production.

Various measures for cover enhancement have been investigated in mudflats, but none has been completely satisfactory. Terraced ponds in the regulated zone enhanced diversity of flora and fauna in the Three Gorges Reservoir (Li et al., 2011). Seeding of mudflats has been attempted in the USA principally with agricultural crop (grasses and forbs) using various techniques that address local access conditions (Fowler & Hammer, 1976). Revegetation by transplanting plants has also been successful in small areas (Hellsten et al., 1996; Abrahams, 2006; Li et al., 2016). Enhancement has been attempted with reefs constructed of woody, stone, and synthetic materials (Santos et al., 2008; Miranda, 2017). Although success stories exist, enhancing mudflats by introducing natural or artificial cover has been constrained by the enormous amount of labor required to add cover in a sustained basis. Considering the broad extent of the problem, the worsening effect as reservoirs age, and the potential to exert meaningful changes, we suggest additional attention is needed to develop practical restoration options in mudflats. Specifically, future research should focus on the magnitude of change required with respect to percent coverage of natural or artificial cover to facilitate changes in fish assemblages which meet specific management objectives in a cost and time effective manner. However, we caution that in reservoirs with extensive water level

fluctuations and mudflats, improving structural complexity alone may not restructure fish assemblages—attention may also need to be given to the habitat-limiting conditions that exist at winter pool, which may present a bottleneck for assemblages that develop at summer pool.

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