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Ecological Succession and Fragmentation in a Reservoir: Effects of Sedimentation on Habitats and Fish Communities

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Abstract.—While processes of depositional filling and ecological succession in natural lakes have been well described, these concepts are relatively new and seldom applied to reservoirs, especially at the landscape scale. However, ecological time has been sufficient to allow us to see successional processes in many reservoir systems. Illustrative of such processes, Lake Texoma is a 36,000-ha reservoir located in southern Oklahoma and northern Texas, and patterns of depositional filling and subsequent processes are apparent in the up-lake ends (there are two large-river tributaries) of this system. Completed in 1944, Lake Texoma has a drainage area of more than100,000 km^2, most of which is highly erodable agricultural lands. We used historic aerial photographs, geographic information systems technology, and field measurements to examine a variety of surface and habitat features and analyzed experimental gill-net samples using ordination techniques to characterize the fish communities in portions of the reservoir most affected by sedimentation. Extensive sedimentation and accretion of sediments above water level has effectively resulted in surface area reduction, cove isolation, fragmentation of lacustrine habitats, morphometric changes, and establishment of terrestrial vegetation on newly deposited lands. Most notably, sedimentation has led to the development of linear bars of deposition above normal pool elevation that have blocked mouths of coves, bisected large areas of the reservoir, and fragmented several pools. In our study site alone, 332 ha (surface area) of reservoir has experienced accretion of land above the water level. Reservoir fragments had lower shoreline development values (mean = 2.21) than comparable control sites (mean = 3.39). Depositional shorelines associated with sedimentation exhibited lower gradients than nondepositional shorelines (mean = 2.0% versus 4.2%, respectively), and habitat heterogeneity was lower along depositional shorelines than along nondepositional shorelines. Fish communities in isolated reservoir fragments appeared to be distinct from fish communities in nonfragmented habitats. This change in community structure may be driven by an appreciable reduction of pelagic species from fragmented sites, as these sites have limited or no connectivity to the main body of the reservoir. With respect to the newly deposited lands, ecological succession of vegetation followed a progression from mud flats to dense, nearly monotypic stands of black willow Salix nigra forests within a few years. These habitat changes had strong implications to the fish communities as well as to adjacent terrestrial wildlife communities and will likely pose many challenges, and perhaps opportunities, for natural resource managers.

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Introduction

Numerous processes lead to the formation of naturally occurring lakes in North America (Hutchinson 1957; Wetzel 2001) but, at northern latitudes, most exist as a result of glacial activities during the most recent Pleistocene event (e.g., glacial moraine lakes) and, at southern latitudes, most exist as a result of fluvial processes (e.g., oxbow lakes). Accordingly, these lakes are generally hundreds to thousands of years old. Over such ecological and geological time spans, numerous ontogenic changes occur, including biological, chemical, and physical effects. Ontogenic changes have been described in trophic state (Greeson 1969; Carpenter 1981, Whiteside 1983; Wetzel 2001), food webs and food-chain lengths (Kaunzinger and Morin 1998) and various physicochemical parameters (Wetzel 2001). With sufficient time, allochthonous input, and autochthonous production, many lakes experience sedimentation and filling. As bed accretion occurs, lakes may make the transition from a lentic system to more swamp-like or marsh-like habitats and, with sufficient time, to hydric and possibly mesic terrestrial habitats (Whittaker 1975; Klinger 1996; Wetzel 2001).

Compared to naturally occurring lakes, man-made reservoirs are a relatively new feature on the landscape. Large man-made impoundments only became commonplace in the United States within about the past century, and the number of dams worldwide is estimated to exceed 40,000 (Nilsson and Berggren 2000). Nevertheless, as with naturally occurring lakes, reservoirs also experience accretion of substrates due to sedimentation. While appreciable accretion may not be occurring reservoir-wide in most cases, it is likely occurring in at least the headwater regions of most reservoirs, as is apparent in such processes as delta formation at reservoir inlets (James and Barko 1990; Williams 1991) and isolation of backwaters that were formerly connected (Slipke and Maceina 2005; Slipke et al. 2005). However, in many systems, total reservoir volume has been reduced appreciably (Julien 1998), and this process has been reported for reservoir systems worldwide (Tejwani 1984; Annandale 1987; White 1988; Fan and Morris 1992; Hassanzadeh 1995; Tundisi et al. 1998). Sedimentation rates have exceeded those originally predicted in several reported instances; in a study of 21 reservoirs in India, Tejwani (1984) noted that annual sedimentation rates were 40–2,166% greater than was assumed at the time of project design. Einsele and Hinderer (1997) reported that human activities have increased sediment yield by a factor of 2 to more than 100 among lakes they studied in Europe. In a study of several Australian reservoirs, Chanson and James (1998, 1999) reported that numerous dams became fully silted, though it should be noted that the reservoirs they studied were relatively small. In the United States, Thornton et al. (1990) stated that among reservoirs constructed prior to 1953 in the Midwest, Great Plains, and southeastern and southwestern states, 33% have lost from one-half to three-quarters of their original volume, and about 10% have had all usable storage depleted by sediment deposition.

A review of the scientific literature reveals that the majority of the research associated with reservoir sedimentation lies within the fields of hydrology, water resources, civil engineering, and geology, as indicated by the journals in which the information is published. Less common are studies that address the ecological effects of reservoir sedimentation. Long-term patterns of ecological succession in natural lakes has been described with respect to several parameters, and the field of paleolimnology has revealed much about historic conditions, processes, and communities (Smol 1992; Wetzel 2001;

Cohen 2003). Ecological effects of reservoir succession may be similar to those of natural lake succession, but research is needed to ascertain this assertion.

It is clear that sedimentation is having a profound impact on reservoirs worldwide, but our knowledge of the landscape-scale effects of sedimentation on reservoirs is primarily restricted to the mechanics of deposition. There is a paucity of knowledge and information on ecological effects of this process. In this paper, we address issues related to sedimentation in Lake Texoma, a large reservoir on the eastern edge of the Great Plains. Our objectives were to describe (1) broad patterns of sediment deposition, (2) effects of deposition on selected littoral habitat characteristics, and (3) effects of sedimentation on the large-bodied fish community structure.

Study Area

Lake Texoma is a 36,000-ha reservoir on the Oklahoma–Texas border, impounding the Red and Washita rivers (Figure 1). The reservoir was formed by completion of the Denison Dam in 1944, and the reservoir was full by the late 1940s. The drainage area of the reservoir is 101,362 km^2, including 81,999 km^2 in the Red River drainage and 19,363 km^2 in the Washita River drainage (Matthews et al. 2004; Matthews and Marsh-Matthews 2007). The drainage area includes much of southwestern Oklahoma and north-central Texas, as well as much of the Texas panhandle and parts of eastern New Mexico. There is a strong aridity gradient within the drainage, with precipitation ranging from ca 45–94 cm in the east–west gradient. Vegetation patterns reflect the precipitation gradient, with aridity-tolerant short-grass and shrub ecosystems to the west and tall-grass prairie and cross timber ecosystems to the east. The vast majority of the drainage area is used for agricultural purposes, including primarily livestock grazing and hay and row-crop production.

The drainages of the Washita and Red rivers have a long history of extensive erosion, resulting in high turbidity and heavy silt loads in these rivers (Matthews 1988; Matthews et al. 2005). The upstream ends of both the Washita and Red River arms of Lake Texoma are visibly experiencing substantial sedimentation. Sedimentation is apparent from aerial photographs but is also easily detected while boating in the area. Many local fisherman, residents, marina operators, and biologists have provided anecdotal evidence of extensive sedimentation, and it is apparent that portions of the reservoir are rapidly filling and becoming impassable by boats during low-water periods. More notably, it is also apparent from aerial photographs and ground visitation that sedimentation has occurred to the point of accretion of new lands above the water level and that such depositions are occurring in a pattern that resulted in fragmentation of large areas of water from the main body of the reservoir. In much of the area, accretion of these new lands above the normal water level had taken place over a long enough time span that they had become forested by the onset of our research in 2004 (this paper).

While extensive deposition is visible in both of the two major arms of the reservoir, we selected a study area within the Washita River arm, as this area appeared to be experiencing a greater extent of sedimentation than the Red River arm. Prior to construction of the reservoir, the Washita River channel was dammed via the construction of two dikes, and the river was rerouted by the U.S. Army Corps of Engineers to avoid flooding an existing oil field. The old river channel was effectively contained between the two dikes, and the new river channel bypassed the oil field and became the inlet to the reservoir.

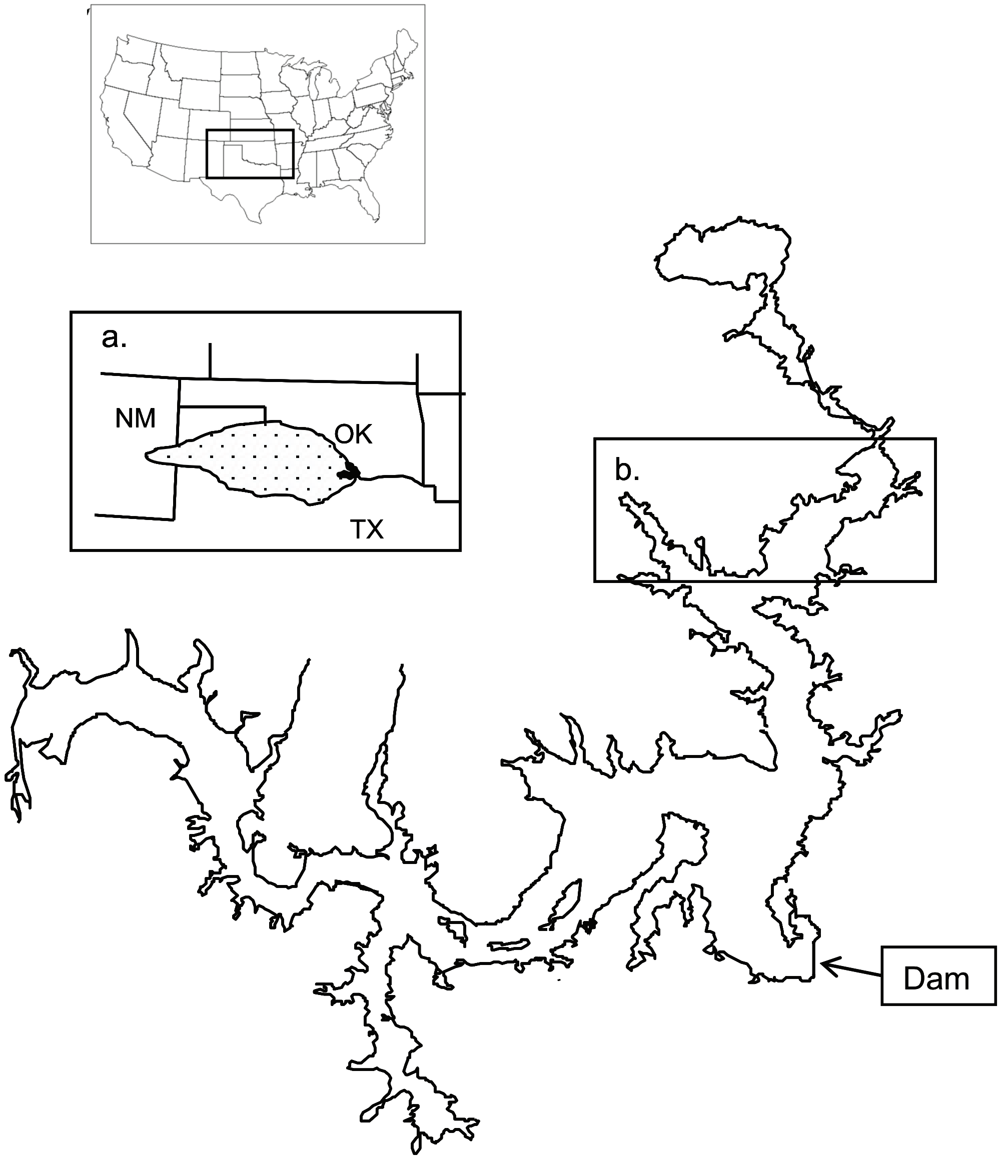

Figure 1. Lake Texoma, Oklahoma and Texas, including the 101,362 km^2 drainage area (inset a) in Oklahoma (OK), Texas, (TX), and New Mexico (NM), and the portion of the reservoir (inset b) for which we conducted geographic information systems analyses, habitat assessment, and fish sampling.

Our study site extended from the inlet of the new river channel to a distance approximately 10 km downstream (Figure 1). We selected this area because it appeared to contain the majority of the sedimentation and accretion of new lands above the normal water level.

Methods

Spatial Analyses

To assess patterns of sediment deposition, we obtained a time series of aerial photographs of the study site. We used photographs from 1969, 1983, 1991, and 2003 because these are the years for which such images were available. Information on exact dates, flight altitudes, and water levels at the times that photographs were taken was not available. Photographs were scanned and imported for spatial analyses using geographic information systems (GIS); all GIS analyses were completed using ArcView (ESRI 2001). All images were digitized to the 1-m pixel level, georeferenced, and orthorectified. On each of the four time-series photographs, we conducted queries for total area of water and total area of land that was previously water. Four relatively large (>100-ha) areas within the study site had become fragmented by sediment deposition. From the 2003 image, we determined surface area, total shoreline length, and proportion of depositional shoreline for each reservoir fragment (fragmented due to sediment deposition). Surface area and shoreline length values were used to calculate the shoreline development index of reservoir fragments. To serve as a basis of comparison, we conducted spatial analyses on two control sites; these sites were large coves that were nearby and of approximately the same surface area as the four reservoir fragments. We queried the two control sites for total area of water and shoreline length and calculated their shoreline development index. Because control sites were not fragmented from the main body of the reservoir, we drew a straight line across the mouth of each cove to make them polygons suitable for queries.

Habitat

We examined three littoral habitat attributes as they relate to sediment deposition: shoreline development, proportion of shorelines that are depositional, and bank slope values in depositional versus erosional shorelines. The shoreline development index provides an indication of shoreline irregularity and has implications towards littoral versus pelagic habitats (Wetzel 2001) and was calculated with values determined using GIS analyses. Shoreline development values were determined for each of four reservoir fragments that had formed by 2003 and for each of the two control sites.

Bank slope measurements were done in May 2006. To examine the influence of deposition on bank slopes, we used GIS imagery to delineate depositional and nondepositional, or erosional, shoreline and compared the two. Depositional shorelines were defined as shorelines that exist as a result of sediment deposition and included those areas that were represented by new lands (lands and shorelines that were not present in the 1969 image). Erosional shorelines were defined as those that had not changed, or that had possibly receded, since 1969. We chose to call them erosional shorelines because virtually all of them showed patterns of erosion that are typical of reservoirs in which water levels fluctuate widely: banks lacked vegetation, active erosion was evident, and substrate particle sizes were large. Within each of three reservoir fragments that we identified via the spatial analyses, we selected five locations along depositional shorelines and five locations along erosional shorelines. The fourth reservoir fragment site was not examined due to difficulties with boat access to the area. Sites were selected using a systematic approach; once depositional and erosional shorelines were delineated and measured using GIS, the total length of each category within each of the three fragments was divided by 5. The first site was selected randomly between zero and the total length (m) of the shoreline within respective categories. For example, if there were 860 m of depositional shoreline, 860/5 = 172; the first site was randomly selected between 0 and 172, and each subsequent site was at 172-m intervals. We used these locations as beginning points for transects. Transects began at water's edge and extended 110 m into the body of water perpendicular to the shoreline, and we measured depth, to the nearest cm, at 10-m intervals (with the first point being 0 cm depth). Depth was measured using a depth rod where water was shallow enough to wade and using a depth finder mounted on a boat where water was excessively deep to wade. The depth finder was checked for accuracy at the beginning and end of each sampling period over a wide range of depths using a sounding weight attached to a line; the depth finder was always within 2% of the measured depths. Within each of three reservoir fragments, we compared the mean slope of depositional shoreline measurements to the mean slope of the erosional shoreline measurements. All slope comparisons were made from shoreline to 50 m and again from shoreline to 110 m. Finally, we compared the mean slope of all 15 depositional shoreline measurements to the mean slope of all 15 erosional shoreline measurements. All slope comparisons were done using single-tailed paired *t*-tests (Zar 1998), and we selected an alpha value of 0.05.

Fish Community Composition

We used experimental gill nets to assess the community structure of large-bodied fishes (large enough to be captured in a 1.27-cm-mesh, or greater, experimental gill net). Gill nets were 61 × 1.83 m and had a lead-core bottom line and foam-core float line; each net had eight panels, with mesh sizes ranging from 1.27 to 10.16 cm, at 1.27 cm-increments, among the eight panels. Three nets were set in each of the three reservoir fragments (as identified via GIS analyses), and in each of three control sites, for 3 nights (9 net-nights/site; total = 54 net nights). Control sites were selected as a basis for comparison of community structure, and all three control sites were attached to the main body of the reservoir. The control sites consisted of two large coves (the same two coves used as control sites for GIS analyses) and one main-reservoir pelagic site adjacent to the reservoir fragment sites. Each net-night included one littoral set, one surface pelagic set, and one benthic pelagic set. All gill netting was done in fall (September–November) 2005. A reservoir fragment site and a control site were sampled at adjacent times before sampling additional sites to ameliorate possible seasonal effects. Thus, if a seasonal effect occurred, we assumed that it would affect fragment sites and control sites approximately equally. Gill nets were checked after approximately each 24 h; all fish were removed, identified, enumerated, weighed, and measured, and any live fishes were released away from nets.

To address community structure, we constructed relative abundance tables, determined species richness, and calculated Shannon diversity (Pielou 1975). We used two-way analysis of variance (Zar 1998) to compare mean fish abundance (log10-transformed) among fragment and control sites. We used a one-tailed *t*-test (ZAR 1998) to look for differences in mean species richness and Shannon diversity between fragment and control sites. Last, we conducted correspondence analyses (CA), a multivariate ordination approach used to reveal similarities between communities based on species composition, and graphically display the extent of similarities on multidimensional space (Everitt and Dunn 2001). All CA analyses were conducted using NTSys software (Applied Biostatistics, Inc. 2001) and were conducted for sites and for species; site CAs indicate similarities among sites and species CAs provide insight on the species that have the greatest influence on the site scores. For all CAs, we log-transformed the abundance data and omitted extremely rare species (those occurring as < 1% of the total catch). This prevented rare species from driving the ordination, allowing us to base comparisons on the more abundant species comprising each community.

Results

Spatial Analyses

Total surface area of water in the designated study area was 3,710 ha (Figure 1, inset b.). Within this area, sedimentation resulted in extensive deposition and accretion of new lands above the surface of the water, and isolation or partial isolation of several reservoir fragments, since 1969 (Figure 2, Figure 3a). Total surface area of water within the area for which we were able to obtain the time series of photographs (1969, 1983, 1991, and 2003) was 810 ha, and ontogenic sedimentation patterns were apparent between each time period (Figure 3b.). From 1969 to 2003, total surface area of water in the entire study site was reduced by 332 ha, with this same amount of area now represented by depositional lands that had accreted above the surface of the water (Figures 2 and 3; Table 1). Loss of surface area of water and increase in new depositional lands was exponential over this time period (Figure 4; Table 1.)

Habitat

By 2003, four relatively large fragments (mean = 234 ha; range = 143–342 ha) and five smaller fragments (<10 ha) were apparent (Figure 3a; Table 2). Mean shoreline development values were 2.21 (range = 1.41–3.13) among reservoir fragments and 3.39 (range = 3.22–3.56) among control sites (Table 2), however, sample sizes were too small (three reservoir fragments and two control sites) to test for significance. Among fragmented sites, depositional shorelines accounted for 21–56% (mean = 39%) of total shoreline length (Table 2). Bank slopes were significantly less along depositional shorelines than along erosional shorelines in all three fragments and among pooled data (Table 3; Figure 5). This pattern was true from the shoreline out to 50 m and from the shoreline out to 110 m. A mean depth of 1 m was reached within 8–10 m of the shoreline along erosional banks; a mean depth of 1 m was not reached until 15–60 m from the shoreline along depositional banks (Figure 5).

Fish Community Composition

Gill nets captured a total of 5,741 fish representing 20 species (Table 4). Mean fish abundance in fragment and control sites was 2,319 (range = 559–1,137) and 3,422 (range = 1,018–1,325), respectively, with no significance difference ($p = 0.37$) between these two habitat types. Mean species richness was 14.33 (range = 13–16) in fragment sites and 14.66 (range = 13–16) in control sites, with no significant difference ($p = 0.30$) between these two habitat types. Mean Shannon diversity values were 1.83 (range = 1.67–2.03) in fragment sites and 2.05 (range = 1.83–2.25) in control sites, with no significant difference (p = 0.125) between these two habitat types. At all sites, the first and second most abundant species were threadfin shad *Dorosoma petense* and gizzard shad *D. cepedianum*, respectively; all other species rankings varied among sites (Table 4). The three control sites clustered together in the CA site ordination; among the fragmented sites, two clustered together and the third was somewhat isolated but was closer to the control sites than to the fragmented sites (Figure 6). The CA ordination of species scores provided insight on which species had the greatest influence on similarities among sites. Among all three control sites, community structure was strongly influenced by striped bass *Morone saxatilis* and white bass *M. chrysops* (Figure 6). Community structure was influenced uniquely among fragmented sites; the three fragmented sites were influenced by freshwater drum *Aplodinotus grunniens* and blue catfish *Ictalurus furcatus*, white

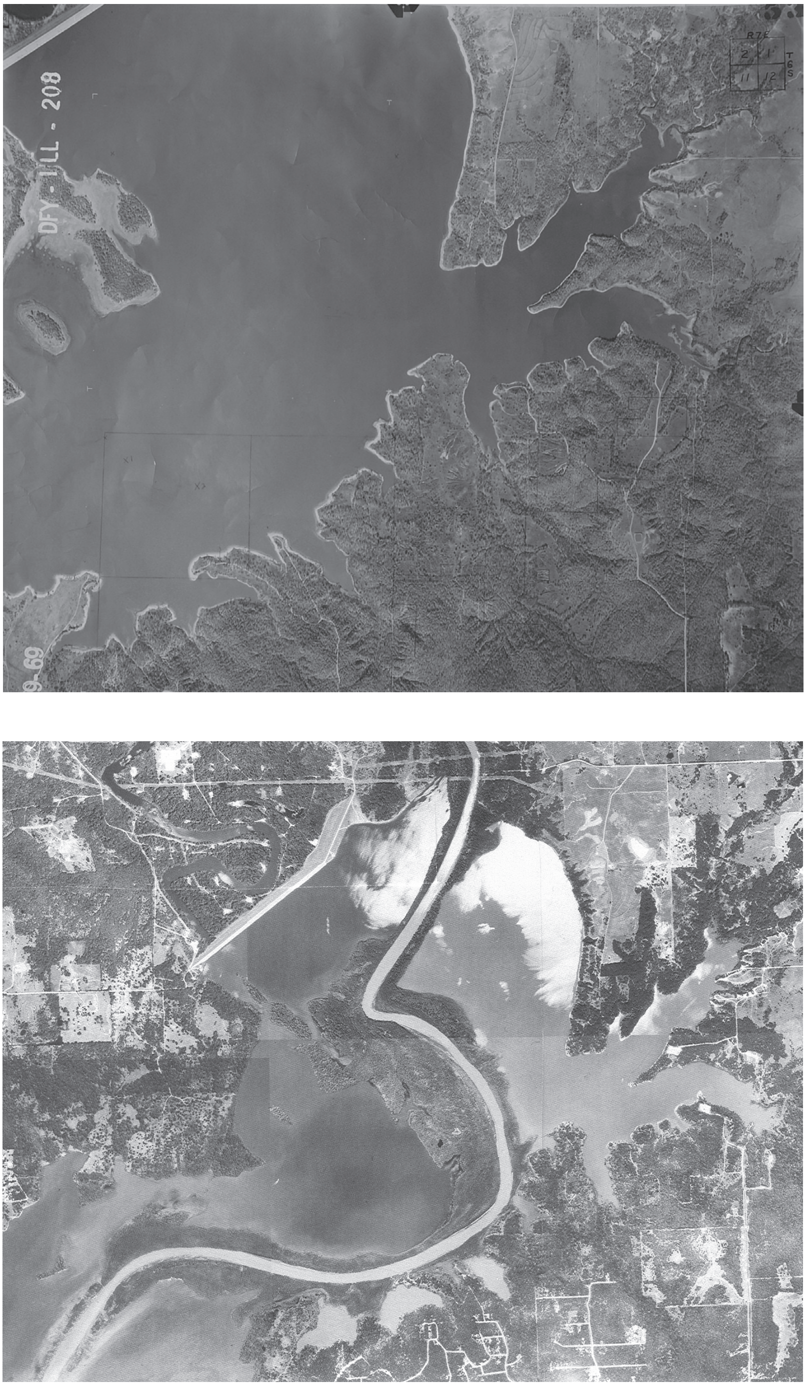

Figure 2. Aerial photographs of a portion of Lake Texoma, Oklahoma, taken in 1969 (top) and 2003 (bottom). 1969 image depicts lacustrine areas, and 2003 image depicts extent of sedimentation, formation of a new riverine channel within the boundaries of the reservoir, and fragmentation or partial fragmentation of several large (143–303-ha) areas and several smaller (<10-ha) areas, all of which were formerly one large pelagic area.

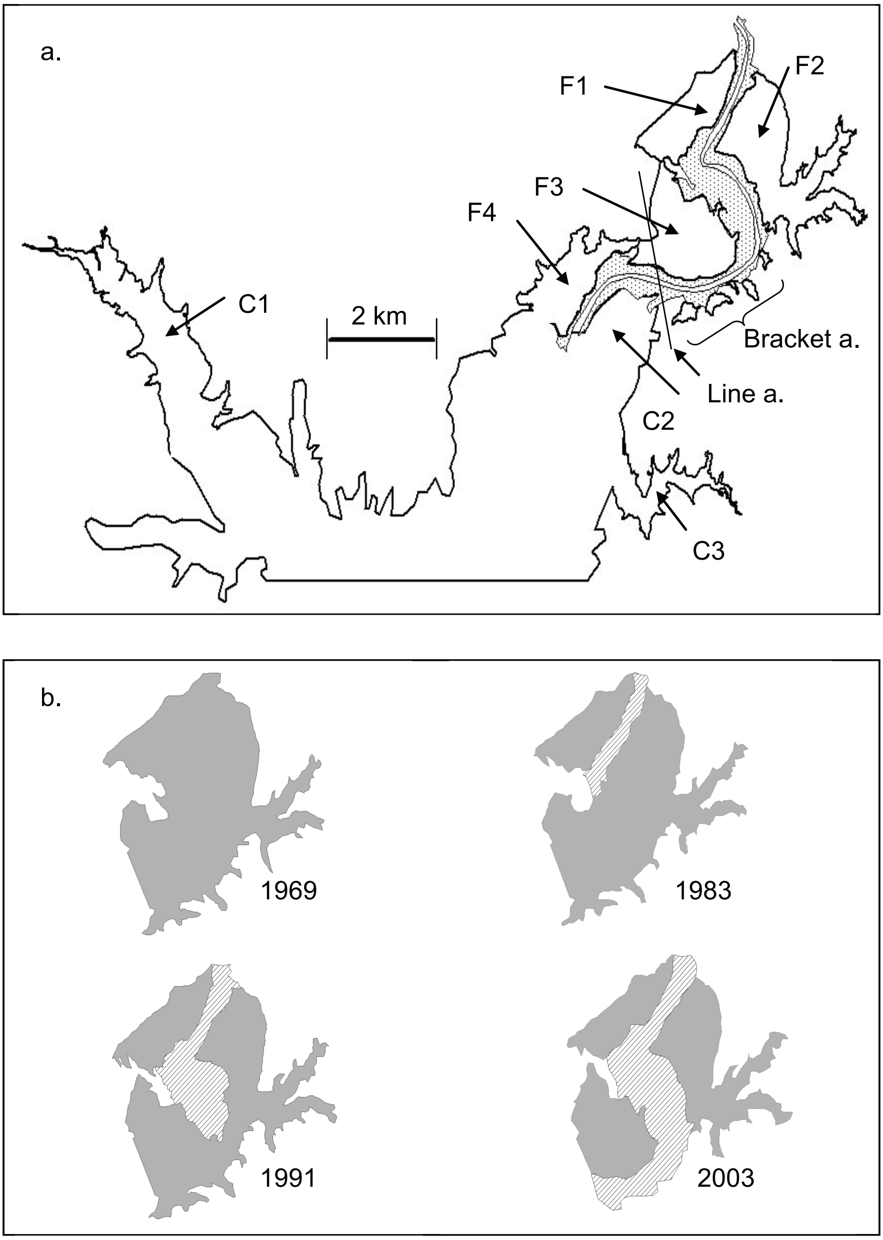

Figure 3. Study site in area of extensive sedimentation in a 4,042-ha portion of Lake Texoma, Oklahoma, as depicted by geographic information systems imagery. (a) Dotted area depicts 332 ha of land deposited in what was lacustrine as recently as 1969. F1–F4 depict large areas (143–303 ha) of water fragmented or partially fragmented by sediment deposition. Bracket a. denotes five small areas (<10 ha) fragmented by sediment deposition. C1–C3 depict control areas. F1, F2, F4, and C1–C3 also represent areas sampled for fishes via gill nets. Line a. denotes border of area depicted in lower figure. (b) Geographic information systems imagery of time-series depicting pattern of sediment deposition from 1969 to 2003 in a 850-ha area of Lake Texoma. Hashed area depicts land deposition from 1969 to 2003.

Table 1. Surface area of water lost, and mean rate of surface area of water lost, at four time periods for a selected portion of Lake Texoma, Oklahoma. Differences between years are due to extensive sedimentation and accretion of deposition of new lands above the water surface, as determined via global information systems analyses of scanned aerial photographs available for the time periods indicated. Patterns of land deposition can be seen in Figures 2 and 3.

Year	Surface area of water lost (i.e., land gained; ha)	Mean rate of surface area of water lost (ha/year)
1969	0	0.0
1983	40	2.9
1991	128	11.0
2003	332	20.3

crappie *Pomoxis annularis* and channel catfish *I. punctatus*, and river carpsucker and channel catfish, respectively (Figure 6).

Discussion

Fluvial transport of sediment is a natural process, and it can be expected that these sediments will deposit as water loses its velocity upon entering a reservoir. The accepted practice has been to design and operate reservoirs to fill with sediment (Palmieri et al. 2001), and extensive filling of reservoirs has occurred worldwide (Tejwani 1984; Annandale 1987; White 1988; Fan and Morris 1992; Hassanzadeh 1995; Tundisi et al. 1998). Whereas resource managers may not be able to stop siltation, we should be aware of the patterns and processes so that the appropriate management decisions can be made. In

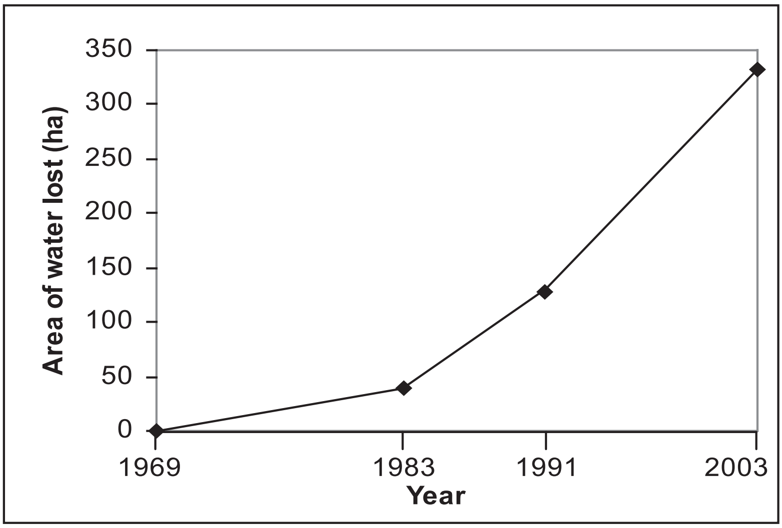

Figure 4. Area of reservoir surface lost due to extensive sedimentation in Lake Texoma, Oklahoma. Surface area loss was determined via geographic information systems analyses of aerial photographs taken in 1969, 1983, 1991, and 2003.

Table 2. Surface characteristics of three reservoir fragment sites and two control sites in Lake Texoma, Oklahoma. Fragment (F) sites are isolated or partially isolated from the main body of the reservoir by sediment deposition. Control (C) sites are nearby coves, are not fragmented from the main body of the reservoir and are of similar to fragment sites. All sites correspond to those in Figure 3A. Characteristics include area of water (Area), total shoreline length (*L*), length of depositional and erosional shorelines, percent (%) of total shoreline length that is depositional and erosional, and shoreline development (DL) values.

			Depositional		Erosional		
Site	Area (ha)	*L* (m)	*L* (m)	%	*L* (m)	%	DL
F1	143	598	336	56	262	44	1.41
F2	303	1,930	405	21	1,525	79	3.13
F3	342	–	–	–	–	–	–
F4	149	912	371	41	541	59	2.11
C1	218	2,106	0	0	2,106	100	3.22
C3	110	1,325	0	0	1,325	100	3.56

the Second National Reservoir Symposium sponsored by the American Fisheries Society, Kimmel and Groeger (1986) noted that future trends in reservoirs will depend more on our ability to conduct coordinated terrestrial and aquatic resources planning and management on a whole watershed scale than on the consequences of reservoir aging, per se. In river systems throughout North America, reservoir construction has resulted in fragmentation of riverine systems and flood plain dynamics (Allan and Benke 2005). Our findings suggest that the process of sedimentation in Lake Texoma has led to fragmentation of habitats, a notable pattern of sediment deposition, an increase in the amount of littoral habitats, a decrease in the quality of those littoral habitats, and

Table 3. Bank slope values for three reservoir fragments in Lake Texoma, Oklahoma. Fragment sites (F1–F4; data were not collected in site F3) were isolated or partially isolated from the main body of the reservoir by sediment deposition. Depositional shorelines were those that have been deposited since 1969. Erosional shorelines were those that have been in existence since impoundment of the reservoir in the late 1940s. Site numbers (F1–F4) correspond to those in Figure 3a.

	Shoreline to 50 m			Shoreline to 100 m		
Site	Mean	Range	*p*-value	Mean	Range	*p*-value
F1 depositional	0.04	0.032–0.064		0.030	0.007–0.064	
F1 erosional	0.065	0.054–0.098	0.016	0.044	0.015–0.098	0.024
F2 depositional	0.021	0.015–0.030		0.020	0.015–0.0300	
F2 erosional	0.081	0.020–0.159	0.003	0.040	0.003–0.1590	0.029
F4 depositional	0.012	0.080–0.018		0.011	0.004–0.018	
F4 erosional	0.062	0.041–0.109	0.001	0.042	0.016–0.1090	0.006
Pooled depositional	0.024	0.015–0.080		0.020	0.004–0.034	
Pooled erosional	0.069	0.020–0.159	0.025	0.042	0.003–0.159	0.025

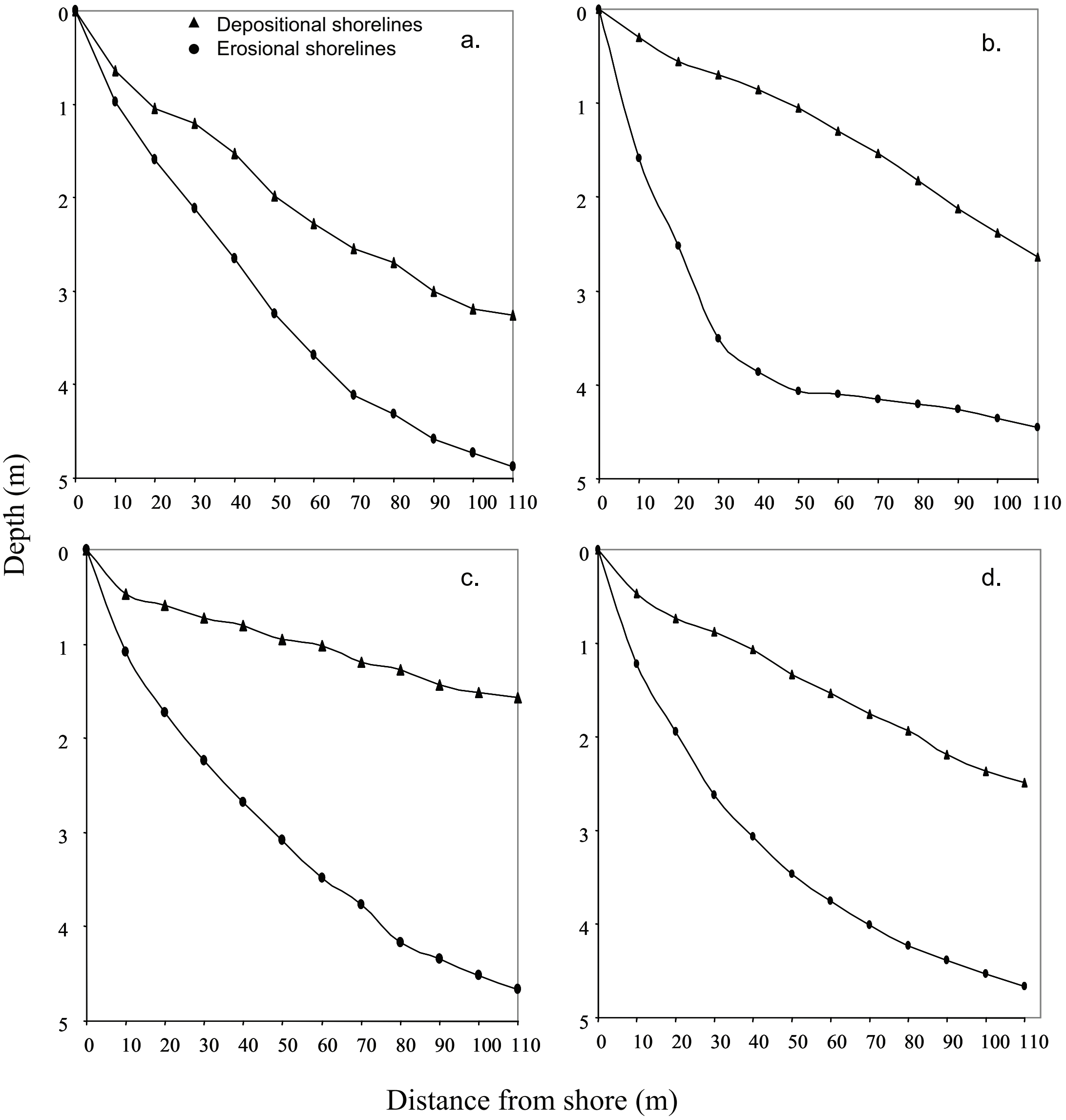

Figure 5. Mean bank slopes for each of three reservoir fragments (a–c) and combined mean bank slopes (d) for all three reservoir fragments in Lake Texoma, Oklahoma, 2006. Sites were fragmented or partially fragmented by sediment deposition since 1969. Values (in a–c) represent the mean of five bank slopes measured along depositional shorelines compared to the mean of five bank slopes measured along erosional shorelines. Bank slopes in a–c correspond to sites F1, F2, and F4, respectively, in Figure 3.

somewhat distinct fish communities among reservoir fragments.

The pattern of reservoir sedimentation and accretion of new lands in Lake Texoma was similar to patterns of deposition that can be seen in fluvial systems. As water has entered the reservoir, it has formed a channel by depositing sediment adjacent to and

Table 4. Abundance and diversity values of fish species captured in experimental gill nets from six locations in Lake Texoma, Oklahoma, fall 2004. Sites include reservoir fragments (F) isolated or partially isolated from the main body of the reservoir by sediment deposition and control (C) sites (not fragmented) in the main reservoir body. Sites correspond to Figure 3a.

Species name		F1	F2	F4	C1	C2	C3
Threadfin shad	*Dorosoma petenense*	650	328	433	589	572	868
Gizzard shad	*D. cepedianum*	305	79	91	94	291	175
Smallmouth buffalo	*Ictiobus bubulas*	31	28	21	101	49	50
White crappie	*Pomoxis annularis*	77	72	9	48	11	9
Striped bass	*Morone saxatilis*	8	0	5	36	57	100
River carpsucker	*Carpiodes carpio*	20	13	0	39	13	49
Channel catfish	*Ictularus punctatus*	23	17	4	28	17	27
White bass	*M. chrysops*	10	3	9	18	26	21
Blue catfish	*I. furcatus*	1	7	13	40	11	3
Freshwater drum	*Aplodinotus grunniens*	2	2	24	17	13	11
Longnose gar	*Lepistosteus osseus*	5	1	1	1	11	0
Goldeye	*Hiodon alosoides*	0	0	10	0	1	1
Flathead catfish	*Pylodictus olivarus*	0	2	1	0	2	6
Common carp	*Cyprinus carpio*	4	1	0	1	2	0
Spotted gar	*L. oculatus*	0	1	1	6	0	0
Spotted sucker	*Minytrema melanops*	0	3	0	0	0	2
Shortnose gar	*L. platostomus*	1	0	1	0	2	0
Silver chub	*Macrhybopsis storeriana*	0	0	0	0	1	2
Largemouth bass	*Micropterus salmoides*	0	1	0	0	0	1
Redear sunfish	*Lepomis microlophus*	0	1	0	0	0	0
Total		1,137	559	623	1,018	1,079	1,325
Species richness		13	16	14	13	16	15
Shannon Diversity		1.80	2.03	1.67	2.25	2.07	1.83

on both sides of the line of flow. This process is similar to the formation of a natural river levee. In rivers, as water levels exceed the elevation of the banks, water spills into the flood plain, losing much of its energy and allowing sediment to fall out of the water column and deposit adjacent to the river (Nienhuis and Leuven 2001). In Lake Texoma, it appears that this process occurs during high water levels, and as water levels drop to normal, the elevation of the new "levees" exceeds the surface water elevation. Additionally, we observed that numerous forbs and small tree seedlings, especially smartweed *Polygonum* spp. and black willows *Salix nigra*, quickly became established on these newly deposited lands. Establishment of vegetation likely enhances sediment deposition and accretion, as the vegetation increases roughness and decreases water velocity, allowing the sediment to drop out of suspension more easily and accumulate in the vegetation (Nienhuis and Leuven 2001). In Lake Texoma, the time series of photographs indicate the new channel and adjacent newly deposited land continued to form linearly in a down-lake direction until it came in contact with, or nearly in contact with, a shoreline. Contact with a shoreline caused the direction of water and sediment to turn and proceed in a new tangent until it reached another shoreline and so on, re-

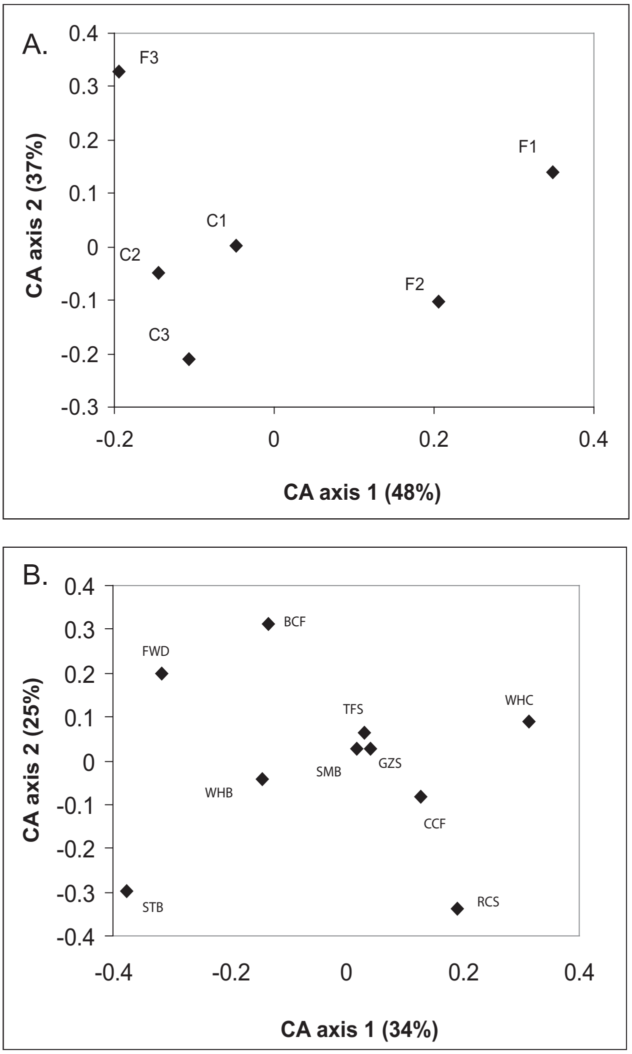

Figure 6. Correspondence analysis (CA) ordinations for fish communities sampled via experimental gill nets in each of three reservoir fragments (F1–F3) and each of three reservoir control sites (C1–C3). (A) Represents CA scores for sites. (B) Represents CA scores for species. Percent of variability explained by each axis is noted in axis labels. Three-letter codes for fish species are blue catfish (BCF), channel catfish (CCF), freshwater drum (FWD), gizzard shad (GZS), river carpsucker (RCS), smallmouth buffalo (SMB), striped bass (STB), threadfin shad (TFS), white bass (WHB), and white crappie (WHC).

sulting in a meandering pattern of the new channel and adjacent land. As these meanders occur, fragments of reservoir are isolated or partially isolated, either within the insides of meander bends or between the channel and the pre-existing adjacent landscapes.

The rate of accumulation of new land and subsequent loss of reservoir surface area was not linear; it increased rapidly since 1983. Because reservoirs become deeper and generally wider in the downstream direction, making for a greater volume to fill, an increasing rate of accretion above the water surface is counterintuitive. We offer two potential explanations, which may be working in combination: (1) the rate of sedimentation has increased since construction of Lake Texoma, and (2) sediment has continued to accumulate under the surface of the water at a nearly constant rate, such that once it exceeds the surface elevation of water, additional accretion occurs rapidly. Binford et al. (1983) and Wetzel (2001) note that accumulation of sediments in natural lakes, especially organic matter, show a sigmoid accumulation over time and that the sigmoid pattern may repeat after a major disturbance in the watershed. However, the process they describe spans geologic time, and if a comparable accumulation curve applies to reservoirs, it would be difficult to say where any given reservoir is on such a curve. Furthermore, Carline (1986) noted that environmental stability strongly influences fish community persistence and that reservoirs encompass a wide range of environmental stability. Using sediment deposition rates as a measure of environmental stability, Lake Texoma does not appear to be very stable, and it may be expected that fish community persistence may respond accordingly. Additional research in the areas of fluvial sediment load, sediment transport rates, deposition patterns, and bathymetry are needed to further address this phenomenon in Lake Texoma. Our data indicate that we may continue to see an increasing rate of loss of surface area of water and continued fragmentation of reservoir habitats.

Based on the measures of habitat we examined, a general decrease in habitat quality is associated with sediment deposition. Shoreline development values were lower in reservoir fragments than they were in control sites, indicating less littoral habitat per area of water. Bank slopes, and therefore water depth in littoral habitats, were significantly less along depositional shorelines than along erosional shorelines. These shallow, low-gradient littoral areas respond dramatically to water level fluctuations; a relatively small reduction of surface water level translates to loss of a large amount of surface area. Additionally, the length and proportion of these shallow depositional shorelines continues to increase in this area of Lake Texoma. And while we did not quantify substrate characteristics, we observed that substrates in depositional shorelines were virtually 100% silt. Littoral areas have been shown to be an important component of habitat in Lake Texoma. Fish biomass was shown to increase from offshore to inshore habitats in Lake Texoma (Gido and Matthews 2000), and littoral fish community in the up-lake region of Lake Texoma and other reservoirs has been shown to be more diverse and more like native riverine fish communities than those in downlake littoral zones (Fernando and Holcik 1991; Gido et al. 2002). While littoral habitats are generally considered good for a variety of species, including many sport fishes, the shorelines that are being developed as a result of sedimentation are monotypic and of low quality for all but a few species of fish, and their shallow nature makes them especially susceptible to drying as a result of even minor water level reduction. Furthermore, loss of pelagic habitats and reservoir fragmentation are likely detrimental to pelagic species. Lake Texoma is renowned for its striped bass and black bass fisheries. Striped bass generally prefer large, pelagic systems with abundant deep water (Matthews at al. 1985), and black bass tend to seasonally use littoral habitats with coarse substrates, moderate depths, and various sources of cover (Annett et al. 1996; Rogers and Bergersen 1996). Decreased water depths, fragmentation of habitats, shallow and monotypic littoral areas, silt substrates, and even reduced boat access as a result of habitat fragmentation may all have a negative affect on the pelagic, as well as the littoral fisheries and fishing opportunities.

Our fish abundance, species richness, and Shannon diversity values did not differ significantly between reservoir fragment sites and control sites that were not fragmented from the main body of the reservoir. These are similar to results reported by Slipke and Maceina (2005) in Demopolis Reservoir, Alabama, where sediment deposition has isolated some backwaters. Several indices of diversity were very similar between open-access and closed-access habitats, although species richness of species with more than one individual captured was higher in open-access habitats. However, even though fish abundance, species richness, and Shannon diversity values did not differ significantly between fragment and control sites, CA indicated that community composition differed among sites. In Lake Texoma, threadfin shad, gizzard shad, and smallmouth buffalo were present and generally abundant at all sites; this observation is supported by the CA in that these three species clustered together near the center of the ordination. Control sites grouped together in the CA site ordination, indicating that these sites were similar with respect to species composition, and the CA species ordination indicated that striped bass and white bass strongly influenced these site scores. Control sites were not fragmented from the main reservoir body and are accessible to pelagic species such as striped bass and white bass. While striped bass and white bass were present in all sites, their abundance and influence on community structure was considerably lower in fragment sites than in control sites. Fragment sites F1 and F2 grouped only somewhat together, indicating that they have somewhat similar species composition. CA site ordination indicated that white crappie and channel catfish abundance had a strong influence on site F1 and river carpsucker and channel catfish abundance had a strong influence on site F2. While site F3 did not cluster with the other fragment sites or the control sites, it was more similar to the control sites, perhaps reflecting its greater level of connectivity to the main reservoir than either of the other fragmented sites. Site F3 was strongly influenced by freshwater drum and blue catfish.

Thus, the CA analyses indicated several things: (1) sites with a large degree of connectivity (control sites not fragmented from the main body of the reservoir) had community compositions that were similar to each other but quite dissimilar to fragmented sites, (2) availability of open water, and extent of connectivity to open water, may have had a strong influence on species composition, (3) pelagic species became less abundant and less important in terms of community composition in fragmented sites, and (4) fragmented sites vary widely with respect to community composition and may or may not be similar to each other or to sites with a high level of connectivity to the main body of the reservoir. Community composition among fragmented sites may be strongly influenced by the extent and periodicity of connectivity (which may include both spatial and temporal patterns of connectivity; temporal patterns of connectivity may include length of time a particular area has been fragmented, length of time it is connected during high-water events, frequency of connectivity, etc.) and habitat conditions that are unique to each individual fragment. For example, site F3 is only partially fragmented from the main body of the reservoir and has been influenced by fragmentation for a lesser period of time. This site was strongly influenced by freshwater drum and blue catfish, both of which are more associated with larger, pelagic bodies of water than smaller, more isolated, reservoir fragments (Robison and Buchanan 1988; Graham 1999). Site F2 was strongly influenced by white crappie;

this site had generally less turbid water and abundant standing dead trees, both of which are desirable for crappie habitat (Markham et al. 1991; Spier and Heidinger 2002).

The future patterns of ecological succession and reservoir fragmentation are uncertain; however, we can speculate based on observations from existing patterns. In Lake Texoma, current patterns of deposition and accretion above the surface level of the water indicate that the river will continue to form a new channel that is separated from the main body of the reservoir by adjacent sediment-deposition levees. If current processes and patterns continue, channels and associated levees may extend downlake over ecological time in a meandering pattern and, in the process, continue to leave isolated or partially isolated reservoir fragments. In the future, Lake Texoma and similar reservoirs that receive large sediment loads may resemble a series of reservoir fragments, bisected by a riverine channel. Once reservoir fragmentation occurs, physicochemical and biological factors within fragments may become influenced by both allochthonous and autochthonous sources (Adams et al. 1983; James et al. 1987; Kimmel et al. 1990; Jones and Knowlton 2005). Furthermore, fragments may be influenced by one of two allochthonous sources (or an interaction of the two): their own smaller watersheds and the larger, original watershed to which they have become disconnected. Among fragmented coves associated with tributary streams, stochastic and deterministic events within the smaller watershed of the tributary may play a strong ecological role (Grossman et al. 1982; Rahel et al. 1983; Strange et al. 1993). Among reservoir fragments that are not associated with tributary coves, interaction with the larger, main channel watershed may be more important. In Lake Texoma and in other reservoirs with relatively flat topography at their uplake ends, reservoir fragments may interact with the riverine channel in much the same manner as a large river interacts with adjacent floodplain lakes (Junk et al. 1989; Bayley 1995; Rodriguez and Lewis 1997; Ward et al. 1999), and the extent of connectivity may play an important role in community structure (Slipke and Maceina 2005; Slipke et al. 2005; Thomaz et al. 2007.). The flood pulse concept (FPC; Junk et al. 1989) was developed to describe the importance of seasonal flooding and the ensuing lateral connection between a river and its floodplain and may be an applicable construct for understanding the interaction between newly reforming riverine channels and adjacent reservoir fragments. Under the FPC, seasonal flooding plays an important role in nutrient distribution, primary production, movement of organisms, decomposition, and a variety of other ecological functions. Further, a flood is viewed as a disturbance (Junk et al. 1989; Wootton et al. 1996; Junk and Wantzen 2004) and, in that regard, leads to setback of an ecological community. While the FPC was developed to describe the interaction between a river and its floodplain, the concept applies to similar interactions between rivers and adjacent floodplain lakes (Bayley 1995; Borcherding et al. 2002; Junk and Wantzen 2004). Reservoir fragments in Lake Texoma are likely influenced by these processes, especially since both the Washita and Red rivers have no upstream dams or other flood control structures and are therefore subject to frequent flooding. However, additional research in this system is needed to understand the influence of periodic flooding and connectivity.

As the morphometry and community structure of reservoirs change, so may the challenges and opportunities faced by resource managers. For example, if large portions of reservoirs become a series of fragments interacting with a riverine channel, challenges may include issues such as selecting appropriate fish species to manage, managing reservoirs fragments that are highly variable and prone to flooding, providing access to fragments for anglers and other users, and management of new terrestrial landscapes and species that were not present in the immediate area just a few decades before. As fragments continue to fill in with sediment and undergo ecological succession, habitats that are intermediate between aquatic and terrestrial environments may exist. Such environments may pose additional natural resource and recreational opportunities. Many of the reservoir fragments in Lake Texoma provided extensive mud flats and marsh-like conditions, as well as relatively mesic terrestrial habitats that have become forested. Accordingly, opportunities for bird watching, waterfowl hunting, and deer and feral hog hunting have arisen, and many local residents have taken advantage of these opportunities.

While Lake Texoma serves as one example of reservoir succession, this process is not unique to this study site. The Red River Arm of Lake Texoma exhibits similar depositional patterns, and various Internet satellite imagery sites (e.g., http://earth.google.com) reveal that similar depositional patterns can be found on reservoirs throughout the world. Reservoir habitats and characteristics are not static. Physical and ecological processes will continue to change over ecological time. Such changes will likely be beneficial to some species and communities and detrimental to others, but changes are inevitable and natural resource managers should be ready for the challenges and capable of recognizing the opportunities.

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