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Changes in the Freshwater Mussel Community in the Kentucky Portion of Kentucky Lake, Tennessee River, since Impoundment by Kentucky Dam

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ABSTRACT

The unionid mussel fauna of Kentucky Lake has changed significantly over the past century. Prior to the completion of Kentucky Dam in 1944, 42 species had been reported from the mainstem Tennessee River now inundated by Kentucky Lake. After Kentucky Dam was completed, the tailwater fauna experienced minor change in species richness with 38 species being reported between 1978 and 1985. Currently, the Kentucky portion of Kentucky Lake supports 21 species. Four of these were not reported in the historical fauna prior to impoundment: *Anodonta suborbiculata, Plectomerus dombeyanus, Potamilus ohiensis,* and *Toxolasma parvus*; thus only 17 of the original species survived impoundment while four species invaded after Kentucky Dam was constructed. *Amblema plicata* is now the most abundant species. *Plectomerus dombeyanus,* first found in the Tennessee River in 1981, is the second most abundant mussel in the Kentucky portion of Kentucky Lake. *Quadrula quadrula* peaked in relative abundance at 51% in 1989 but subsequently declined to 10% by 2001. Few mussels survive in the deep channel where fine sediment continues to accumulate and anaerobic conditions sometimes occur. The faunal decline is typical following large dam construction, while the continuing change in the mussel fauna may reflect an aging reservoir and invasion of opportunistic species.

KEY WORDS: Unionidae, mussel, Tennessee River, Kentucky Lake, Kentucky Dam, reservoir

INTRODUCTION

Freshwater mussels (Bivalvia: Unionidae) are an important ecological component of many medium to large, flowing rivers, often constituting the predominant benthic biomass (Strayer et al. 1994) and contributing significantly to secondary production (Negus 1966; Vaughn et al. 2004). Mussels filter enormous volumes of water, removing large quantities of suspended material, and depositing large quantities of organic matter utilized by other benthic organisms (Sephton et al. 1980; Spooner and Vaughn 2006; Vaughn and Spooner 2006). Further, mussels serve as sentinels to the health of rivers and lakes. Their long lifespan, averaging 20 years or more and generally sessile existence, make them natural sentinels of water conditions (Maddox et al. 1990; Martel et al. 2003; Ravera et al. 2003; Strayer et al. 2004; Brown et al. 2005). Mussels may be both dense and diverse at a single location, e.g., in the continually flowing, dam tailwater reaches of the Tennessee River, mussels often occur at densities of over 100/m^2, with 20 or more species occurring together (Sickel 1985; Miller et al. 1992; Lewis and Sickel 2004). Mussels now, however, are among the most imperiled animals on the planet, with many species having become extinct in the past century, and many more on the federal endangered species list (Williams et al. 1993).

Mussels constitute an important natural resource in the Tennessee River and Kentucky Lake in western Kentucky. The larger, heavier shelled species were once harvested commercially for the pearl button industry, but this industry disappeared in the 1950s when plastics replaced mother-of-pearl as the material for buttons (Anthony and Downing 2001). Growth of the Japanese cultured pearl industry provided a new market for Tennessee Riv-

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er shells in the 1960s; and once again shells were harvested by the thousands of tons (Isom 1969). Although some harvest continues for the jewelry industry, in western Kentucky the shell industry has declined, and commercial shell harvest in the Kentucky portion of Kentucky Lake is scheduled to cease February 28, 2011 according to the Kentucky Department of Fish and Wildlife Resources regulation 301 KAR 1:085 (KDFWR 2006). Although the direct monetary value of shells may be declining because of market forces in the cultured pearl industry, the full ecological value of mussels remains to be evaluated. Reduced harvest of shells may allow mussels to reach their ecological potential.

There is increasing interest in ecological studies of spatial and temporal heterogeneity in freshwater mussel distributions. Mussels generally are found aggregated within a non-uniform benthic environment (Downing and Downing 1992), and aggregation may influence reproductive success (Downing et al. 1993; Lewis 2001). For resource managers, understanding heterogeneity and temporal changes in mussel populations is essential to regulating activities such as harvest, sand and gravel dredging, or other activities that impact the mussel resources and which could reduce densities of particular species below that needed to sustain reproductive success (Anthony and Downing 2001; Strayer et al. 2004). Periodic surveys, for example at five year intervals, are a way to monitor the mussel resources and determine if existing regulations are sufficient to maintain the mussel communities.

The great diversity of the mussels of North America was recognized in the early 1800s (Rafinesque 1820; Lea 1834), and later it became obvious that the geologically ancient Tennessee and Cumberland River valleys had contributed to the evolution of that diverse fauna (Ortmann 1925). With nearly 300 recognized species in North America, the lower Tennessee River contains about 15%, a number of which are on the federal endangered species list. In the upper Tennessee, Cumberland, and Duck Rivers, about twice that number once occurred (Parmalee and Bogan 1998).

Henry van der Schalie (1939) predicted that Kentucky Dam would significantly alter the habitats of the Tennessee River resulting in the loss of many species. As Kentucky Dam was being constructed, van der Schalie stated, "If, after the impounding of waters, the reaction of the mussels now occupying that region is similar to that of mussels found in ponded areas elsewhere, we can predict safely that the proposed Gilbertsville Dam at Paducah will entirely change the fauna now found in the lower Tennessee. Records that give definitive information as to the ecology and distribution of the naiads of this area prior to the construction of such power dams will consequently be valuable for future studies of the taxonomy and zoogeography of these animals" (van der Schalie 1939). He listed 31 species occurring from Savannah, TN, (TRM 190) to Paducah, KY.

Whenever dams are placed across rivers, sediment accumulates upstream and often covers the natural gravel and sand substrates. Ellis (1936) had stated, "Experimental studies demonstrated that layers of fine silt from one fourth of an inch to one inch thick produced a very high mortality among fresh-water mussels living in gravel or sand beds, and in water which was otherwise favorable." These predictions of the loss of great faunas have been realized in recent years in a number of large reservoirs (Blalock and Sickel 1996; Vaughn and Taylor 1999). No one anticipated the adaptation of many species to the broad floodplains that were to be flooded by Kentucky Dam.

The objective of this paper was to compile data from earlier reports and collections such that the changes in the mussel fauna in the Kentucky portion of Kentucky Lake can be documented. Only two mussel surveys were conducted in the Kentucky portion of the lower Tennessee River prior to impoundment: one by Paul Bartsch in 1907 and one by Ellis in 1930. In each of these surveys only a few sites in Kentucky were investigated. Therefore we relied on other surveys from Tennessee, such as Ortmann (1925) and van der Schalie (1939), to infer what the pre-impoundment mussel fauna may have been. Their surveys extended farther up the Tennessee River indicating a faunal change occurring upstream from Savannah, Tennessee (TRM 190); therefore we used data only from downstream of that point. Because so few samples were made prior to impoundment, we included two extensive surveys of the Kentucky Dam tailwater, one by TVA in 1978 (Gooch et al. 1979) and one by Sickel (1985) to provide a more complete list of species we believe were present in the pre-impoundment fauna and to provide a comparison between the tailwater and impoundment fauna.

STUDY AREA

Kentucky Lake is the largest of the Tennessee Valley Authority (TVA) reservoirs on the Tennessee River and was formed by the construction of Kentucky Lock and Dam completed in 1944 at a point 36 km upstream from the Ohio River at Tennessee River Mile (TRM) 22.4 in Marshall and Livingston counties, Kentucky. Kentucky Lake extends upstream for 296.6 km to Pickwick Landing Lock and Dam (TRM 206.7) in Hardin County, Tennessee. Water storage in the reservoir first began 16 August 1944, with final closure of the dam on 30 August 1944 (Lowery et al. 1990). Minimum pool elevation of 107.9 m above mean sea level (MSL) was reached 7 April 1945, a height of 15.9 m above the original normal river elevation. The scheduled annual surface elevation fluctuation is 1.52 m. Since filling and inundation of the river floodplain and adjacent tributaries, a minimum elevation of 104.6 m occurred once on 11 March 1961 (Lowery et al. 1990). This drop of 3.3 m below minimum pool exposed large areas where mussels may have become established. The length of exposure and effect on any mussels is not known to the authors (Sickel and Burnett 2001).

For approximately half of the length of Kentucky Lake, from Pickwick Landing Dam to about TRM 110 at the mouth of the Duck River in Humphreys County, Tennessee, the reservoir essentially remains within its natural banks, and the sediment in the original channel remains swept clean of silt providing good mussel habitat similar to that of the river before impoundment (Isom 1969). Downstream from this region, sediment accumulates covering the original gravel substrate with varying amounts of fine silt and providing poor habitat for mussels within the main channel. Also, at times of low flow, the deeper areas may become depleted of dissolved oxygen. A TVA study in 1965 (Isom 1969) reported 1.2 m of sediment in the channel 15 km upstream from Kentucky Dam (TRM 31.7) and 0.61 m of sediment at TRM 41, just north of the Eggners Ferry Bridge (TRM 41.75). In reference to the inundated river channel, according to Isom (1969), "The first evidence of a 'flowing water' fauna: bryozoa, sponges, snails and caddisflies, was found above TRM 89.'' Thus between TRM 110 and 89 a transition from a riverine to a predominantly lacustrine environment occurs. The Kentucky/Tennessee boundary occurs at TRM 49.2 (USACE Navigation Chart No. 8) east of the center of the channel and TRM 62.5 (USACE Navigation Chart No. 10) west of the channel with the boundary extending along the channel line between these points (U.S. Army Corps of Engineers 2007). Therefore, the Kentucky portion of Kentucky Lake is in what we consider to be the lacustrine reach of Kentucky Lake. Within the lacustrine region, outside of the original river channel, broad areas of river floodplain and the lower reaches of tributaries became inundated. These areas now provide most of the habitat for mussels (Sickel and Chandler 1982).

METHODS

To document the mussel fauna of the Tennessee River in the Kentucky portion of Kentucky Lake, data were gathered from published literature, museum records, and numerous unpublished technical reports of mussel surveys conducted by the Tennessee Valley Authority and by Murray State University. All records we could find for the pre-impoundment period were included; however, for the post-impoundment data, only records that added to the overall species list were included. Schuster (1988) compiled a list of mussels occurring in Kentucky from available literature and museum collections, and we depended heavily on this material for historical data and to provide entry points to museum collections now online. His report provided a good source to historical data because he gave museum catalogue numbers for specimens he examined. These numbers were checked and verified online at the Smithsonian National Museum of Natural History, Department of Invertebrate Zoology (http://www.nmnh.si.edu/iz/), the University of Michigan Museum of Zoology (http://www.ummz.umich.edu/

mollusk/databases/index.html), the Ohio State University Museum of Biological Diversity, Mollusks Division (http://www.biosci.ohiostate.edu/~molluscs/OSUM2/), and Carnegie Museum of Natural History (http://collections.carnegiemnh.org/mollusks/specimen/index.cfm). Schuster's (1988) report was summarized by Cicerello et al. (1991) but did not distinguish the mussels reported from Kentucky Lake from those reported elsewhere in the Tennessee River watershed in Kentucky including the Clarks River, so we depended on the original records for location data. Data from mussel surveys conducted at Murray State University were summarized from technical reports. For the Sickel 1989 and the Sickel et al. 1981, 1995, and 2001 surveys, many of the same 94 sites in the Kentucky portion of Kentucky Lake that were surveyed in 1981 were surveyed again in 1989 (56 sites), 1995 (86 sites), and 2001 (89 sites). At each site, 20 1-m^2 quadrats were searched by a diver (only 10 quadrats at each site in 1989). The diver followed an anchored transect line collecting 10 quadrats on each side of the line. The quadrat was a 1-m^2 frame divided by cross bars into quarters to help the diver orient hand sampling under poor visibility conditions. Sampling was accomplished by digging into the sediment and placing mussels in fine mesh bags. All mussels were later identified and counted. Percentage abundance of each mussel species from each of the four surveys was used to examine changes in species composition within Kentucky Lake between 1981 and 2001. We used the taxonomic nomenclature of Turgeon et al. (1998). Earlier reports often used different nomenclature. Synonyms can be found in Parmalee and Bogan (1998).

RESULTS AND DISCUSSION

From 1907 to 2001, 50 species of unionid mussels were reported from the mainstem lower Tennessee River from Savannah, TN, to Paducah, KY, including what is now Kentucky Lake in Kentucky and Tennessee and the Kentucky Dam tailwater but not including the Pickwick Dam tailwater upstream from Savannah where several additional species may occur that probably did not occur in Kentucky (Table 1). All of these species probably occurred in the Tennessee River in Kentucky, but because of the paucity of pre-impoundment data we could not be certain.

Prior to the construction of Kentucky Dam in 1944, only four mussel collections had been made from the region, and van der Schalie (1939) apparently had access to data from only three of these: part of a Bryant Walker/Calvin Goodrich collection now in the University of Michigan Museum of Zoology, Ortmann's 1924 collection in the Carnegie Museum (Ortmann 1925), and the 1930 survey by Ellis in the University of Michigan Museum of Zoology. The first record of the mussels of the lower Tennessee River in western Kentucky was the unpublished collection of Paul Bartsch at the Smithsonian National Museum of Natural History. Bartsch was an assistant curator at the Smithsonian in 1907 (later served as a curator in the Division of Mollusks from 1914–1946) when the U.S. Bureau of Fisheries sponsored the survey of the mussels of the Mississippi, Ohio, and Tennessee Rivers in response to the extensive harvest of shells by the pearl button industry. Smithsonian collection records indicated that on 12 July 1907, the Bartsch expedition began in St. Paul, MN, and followed the Mississippi River to the Ohio River and up the Tennessee River. They reached Paducah, KY, on 19 August 1907 where a collection was made on the Tennessee River at Stiles (probably Stiles Crossing, TRM 7). From there the expedition apparently traveled upstream, perhaps overland, and made several stops for collections as they traveled back downstream. On 27 August, they collected near Savannah, TN, (TRM 190) and then made several stops down the Tennessee River until they collected at Danville Landing (TRM 78) on 30 August 1907. On that same day they collected also at Panther Creek Island (TRM 59) and Birmingham, KY (TRM 31). The last collection of the expedition was made on that day below the "E.P. & S. Bridge" after which Bartsch left to catch the ship, Albatross, for an expedition to the South Pacific. The location marked as "Below E.P.& S.? Bridge" was thought to be near Birmingham, KY, because it was the last collecting station with Birmingham being the previous station, but its precise location remains unknown because no bridge today is called E.P. & S. We found the probable location of the "E.P. & S. Bridge" on an 1895

Table 1. The mussel fauna of the lower Tennessee River before and after impoundment by Kentucky Dam in 1944 at Tennessee River Mile (TRM) 22.4, with X indicating presence, and decimal numbers are percent abundance of each species. Sample locations are indicated by TRM from Savannah, TN to Paducah, KY. Abundance data for Kentucky Lake samples from 1981 through 2001 compare approximately the same 86 to 94 sites where 20 1-m² quadrat samples were collected at each site except in 1989 when only 10 1-m² quadrat samples were collected at 56 sites. Kentucky Dam tailwater samples from 1978 and 1985 are included to provide a more complete estimate of the species probably present in the original river fauna prior to impoundment and for comparison to the present lake fauna.

	Bartsch: Sta. 134–135[1] Paducah, Stiles [Crossing]	Bartsch: Sta. 167 Birmingham and Sta. 168 E. P. & S. Bridge	Bartsch: Sta: 159 Johnsonville to Sta: 164 Panther Creek	Bartsch: Sta: 136 Savannah to Sta: 158 above Johnsonville	Walker/Goodrich Collection: Egner's Ferry	Ortmann: Dixie-Trotters Landing Walker/Goodrich: (*)	Ellis: Fort Henry and Paducah	Ellis: Savannah and Britt's Landing	TVA: Ky Dam Tailwater	Sickel: Ky Dam Tailwater	Sickel and Chandler: Kentucky Lake	Sickel: Kentucky Lake	Sickel, Herod, Blalock: Kentucky Lake	Sickel and Burnett: Kentucky Lake
YEAR	1907	1907	1907	1907	1919?	1924	1930	1930	1978	1985	1981	1989	1995	2001
Species	TRM 0–7	TRM 2231	TRM 59–100	TRM 102–190	TRM 42	TRM 102	TRM 0–61	TRM 122–190	TRM 5–22	TRM 7–22	TRM 23–62	TRM 23–62	TRM 23–62	TRM 23–62
Actinonaias ligamentina				X		X*				0.02				
Amblema plicata	X	X	X	X	X	X	1.04		7.78	11.92	17.08	20.31	38.74	36.60
Anodonta suborbiculata											0.95	2.39	0.71	0.36
Arcidens confragosus									0.03	0.01	0.73	2.56		0.06
Cyclonaias tuberculata	X	X	X	X	X	X	2.60	5.63	6.71	5.89				
Cyprogenia stegaria				X					0.03					
Dromus dromas				X										
Ellipsaria lineolata	X	X	X	X		X		0.70	4.64	4.91				
Elliptio crassidens	X	X	X	X	X	X	2.08	5.28	1.29	1.38				0.06
Elliptio dilatata	X		X	X		X	0.52	0.35	2.40	1.65				
Fusconaia ebena	X	X	X	X		X	21.35	3.52	40.39	35.36	0.80	1.71	1.97	2.86
Fusconaia flava							2.08		0.03	0.20	4.38	1.71	2.91	2.55
Fusconaia subrotunda		X	X	X		X	0.52		0.21	0.82				
Lampsilis abrupta	X[1]					X	0.52		0.03	0.07				
Lampisilis cardium	X			X		X								
Lampsilis fasciola				X										
Lampsilis ovata	X	X	X	X						0.09				
Lampsilis teres	X			X	X	X	0.52			0.02				
Lasmigona complanata									0.03	0.11				
Leptodea fragilis		X		X		X*				0.78	1.24		0.39	0.61
Lexingtonia dolabelloides				X										
Ligumia recta	X	X		X		X			0.18	0.24				
Megalonaias nervosa	X	X	X	X	X	X	11.46	10.92	3.89	4.11	9.27	8.02	4.65	4.01
Obliquaria reflexa				X		X	6.77	3.52	1.35	3.25	6.93	4.10	6.93	2.74
Obovaria olivaria		X		X		X	1.56	3.87		0.02				
Obovaria retusa	X		X	X		X		0.35		0.04				
Plectomerus dombeyanus											0.15	1.19	18.11	32.46
Plethobasus cooperianus				X		X	1.04	5.63		0.09				

Table 1. Continued

	Bartsch: Sta. 134–135[1] Paducah, Stiles (Crossing)	Bartsch: Sta. 167 Birmingham and Sta. 168 E. P. & S. Bridge	Bartsch: Sta. 159 Johnsonville to Sta. 164 Panther Creek	Bartsch: Sta. 136 Savannah to Sta. 158 above Johnsonville	Walker/Goodrich Collection: Egner's Ferry	Ortmann: Dixie-Trotters Landin Walker/Goodrich: (*)	Ellis: Fort Henry and Paducah	Ellis: Savannah and Britt's Landing	TVA: Ky Dam Tailwater	Sickel: Ky Dam Tailwater	Sickel and Chandler: Kentucky Lake	Sickel: Kentucky Lake	Sickel, Herod, Blalock: Kentucky Lake	Sickel and Burnett: Kentucky Lake
Plethobasus cyphyus						X		0.35	0.03	0.07				
Pleurobema clava				X										
Pleurobema cordatum	X	X	X	X	X	X	12.50	30.63	10.69	6.96				
Pleurobema plenum						X[2]								
Pleurobema rubrum			X		X	X	5.21	3.52	0.03					
Pleurobema sintoxia								1.76						
Potamilus alatus	X		X	X	X	X			0.60	1.51	0.51	0.68	0.55	1.4
Potamilus ohiensis											0.80			
Ptychobranchus fasciolaris	X		X	X		X				0.04				
Pyganodon grandis										0.11	1.61	0.17	0.63	0.24
Quadrula apiculata										0.20			1.18	2.67
Quadmla cylindrica				X					0.06	0.44				
Quadrula fragosa						X[3]								
Quadrula metanevra	X	X	X	X		X	7.81	10.21	1.89	0.98				
Quadrula nodulata							5.21		0.15	0.49	7.37	6.48	5.83	2.67
Quadrula pustulosa	X	X	X	X	X	X	4.69	10.56	14.31	11.01	0.22		0.39	0.06
Quadrula quadrula	X					X*	9.38		3.05	3.89	47.15	50.68	17.01	10.15
Toxolasma parvus											0.15			0.06
Tritogonia verrucosa	X		X	X		X			0.09	0.58	0.36			
Tuncilla donaciformis							1.04	0.35	0.03	1.42	0.15			0.43
Tuncilla tuncata							2.08	2.46	0.09	1.16				
Utterbackia imbecillis								0.35		0.04	0.15			
Number of species	20	14	17	30	9	29	21	19	27	36	19	12	14	18
Total number collected							192	284	3340	4497	1370	586	1270	1645

Bartsch 1907. Data from the Smithsonian National Museum of Natural History, Department of Invertebrate Zoology

Walker & Goodrich 1919?. Data from University of Michigan Museum of Zoology with uncertain date, possibly 1919.

Ortmann 1924. Data partly from van der Schalie (1939) and partly from Ortmann (1925) and the collection at the Carnegie Museum.

Ellis 1930. Data from van der Schalie (1939) and the University of Michigan Museum of Zoology.

TVA 1978. Data from Gooch et al. (1979).

Sickel data from Sickel (1985), Sickel and Chandler (1981), Sickel (1989), Sickel et al. (1996), and Sickel and Burnett (2002).

1 In the Paul Bartsch collection at the Smithsonian, *L. abrupta* was reported from Station 135, Tennessee River near Paducah on 19 Aug 1907 but precise location not recorded. Station 134 was indicated as Stiles Paducah Turnpike and collected on the same date. Stiles Crossing is at Tennessee River Mile 7.

2. Ortmann (1925) reported these as *Pleurobema cordatum* plenum and indicated they were rare and found among the more common *Pleurobema cordatum* Two specimens are at the Carnegie Museum, Catalog No. 61.12006.

3. Ortmann (1925) reports all of these from Dixie as *Quadrula quadrula fragosa* and indicates this form to be common in the Cumberland River but rare in the Tennessee River He distinguishes a from Q *quadrula* that occurs elsewhere in the Tennessee River. Four specimens are at the Carnegie Museum, Catalog No. 61.11982.

Atlas as being the railroad bridge, Elizabethtown-Paducah-St. Louis RR, which crossed the Tennessee River at approximately the present location of Kentucky Dam, TRM 22.4. Apparently the shell collection was deposited at the Smithsonian and no record was ever published. Smithsonian staff recently has placed a portion of the collection records online.

The Bartsch collection includes 33 species of mussels collected from Savannah, TN, to Paducah, KY, which includes most of the region of the river now under Kentucky Lake and the tailwater downstream from Kentucky Dam. Four species he collected that were not characteristic of the Kentucky portion of the Tennessee River were *Dromus dromas* (I. Lea, 1834), *Lampsilis fasciola* Rafinesque, 1820, *Lexingtonia dolabelloides* (I. Lea, 1840), and *Pleurobema clava* (Lamarck, 1819). These species were characteristic of the Muscle Shoals of northern Alabama with *D. dromas* and *L. dolabelloides* belonging to the Cumberlandian fauna (Ortmann 1925) typically found in the middle and upper Tennessee, Cumberland, and Duck Rivers (van der Schalie 1939). The other twenty-nine species he collected were reported by others for the lower Tennessee River (Table 1). These species are the typical Interior Basin (or Ohioan) fauna of big rivers (Ortmann 1925).

The next report of lower Tennessee River mussels was that of Ortmann (1925). His only collection within what is now Kentucky Lake was made in 1924 at Dixie/Trotters Landing, which is in the vicinity of New Johnsonville, Tennessee at TRM 102. He reported 26 species, and much of that collection is at the Carnegie Museum. Three species in the collection were not recorded by Bartsch (*Plethobasus cyphyus* (Rafinesque, 1820), *Pleurobema plenum* (I. Lea, 1840) and *Quadrula fragosa* (Conrad, 1835)). All the species he collected at Dixie except *P. plenum* and *Q. fragosa* have been reported from the Kentucky portion of the Tennessee River post-impoundment, but most have been reported only from the Kentucky Dam tailwater and not from the reservoir. Ortmann was one of the authorities on mussels in the early twentieth century, so if he determined these two species to be *P. plenum* and *Q. fragosa,* they probably were; however, neither has been reported before or since from the lower Tennessee River. The specimens are at the Carnegie Museum, and could be examined: *P. plenum* (Cat. No. 61.12006) and *Q. fragosa* (Cat. No. 61.11982).

An unreported collection mentioned briefly by van der Schalie (1939) was a collection from Trotters Landing by Goodrich. We found a reference to this collection as the Bryant Walker and Calvin Goodrich collection online at the University of Michigan Museum of Zoology, but the date was uncertain—possibly 1919. This collection contained 23 species, adding three to the Ortmann list: *Actinonaias ligamentina, Leptodea fragilis* and *Quadrula quadrula.* We included these together in Table 1 because they came from the same location, TRM 102, in Tennessee. While searching the UMMZ database, we found nine entries in the Goodrich and Walker collection from Egners Ferry in Kentucky. There were no additional species that had not been reported by Bartsch, but we included it in Table 1 because it is the only pre-impoundment collection from that area. The date is uncertain because it was not included in the database, but because part of the Goodrich and Walker collection from Trotters Landing was dated 1919, we used this date. This needs to be verified if possible.

The final pre-impoundment collection was that of Ellis in 1930. He reported 26 species from the lower Tennessee River with 21 from Kentucky. His Kentucky sites were at Fort Henry, Stewart Co., TN/Calloway Co., KY, (TRM 61) and Paducah. These collections included six species that had not been reported by Bartsch or Ortmann (*Fusconaia flava* (Rafinesque, 1820), *Pleurobema sintoxia* (Rafinesque, 1820), *Quadrula nodulata* (Rafinesque, 1820), *Truncilla donaciformis* (I. Lea, 1829), *Truncilla truncata* Rafinesque, 1820, and *Utterbackia imbecillis* (Say, 1829)).

The Kentucky Dam tailwater mussel data of TVA in 1978 (Gooch et al. 1979) and Sickel (1985) (Table 1) represent the post-impoundment tailwater fauna that was similar to the pre-impoundment fauna with the addition of four species that had not been reported previously for the Kentucky section of the river: *Arcidens confragosus* (Say, 1829), *Lasmigona complanata* (Barnes, 1823), *Pyganodon grandis* (Say, 1829), and *Quadrula apiculata* (Say, 1829). This tailwater fauna closely resembles the pre-impoundment fauna. After impoundment, dramatic changes began to occur upstream from the dam, especially within the Kentucky portion of Kentucky Lake.

There is a large body of post-impoundment information on the mussels of Kentucky Lake starting with the investigation by Bates (1962) in which he pointed out that a number of species were adapting to the "mud shallows" as the deep main channel habitat was accumulating silt. Additional studies were conducted by Williams (1969) and Isom (1969), but they focused primarily on the main channel and did not record accurate sample locations. Bates (1962) reported the first occurrence of *Potamilus ohiensis* (Rafinesque, 1820), *Toxolasma parvus* (Barnes, 1823), and *Anodonta suborbiculata* Say, 1831. Isom (1969) reported two additional species from the riverine region between TRM 136–195.5: one valve of *Pleurobema oviforme* (Conrad, 1834) and *Cumberlandia monodonta* (Say, 1829). *Pleurobema oviforme* is considered a Cumberlandian species (Ortmann 1925) and probably did not occur in the Kentucky region. Although a weathered dead shell of *C. monodonta* was reported in 1991 at TRM 15.8 (Sickel 1991), we did not add it to the Kentucky Lake list because it had never been reported alive in the Kentucky region of the river.

Yokely (1972) conducted an extensive study of Kentucky Lake in Tennessee from Pickwick Landing Lock and Dam at TRM 206.7 downstream to mile (TRM) 93. Hubbs (2002) updated information on Kentucky Lake mussels within Tennessee. Bates (1975) conducted a reservoir wide survey of channel and overbanks, but relatively few samples were collected in Kentucky and they were collected with brail or PONAR grab, so they may not be representative of species composition. In his report few mussels were collected from the Kentucky section, and no additional species were reported.

The first systematic survey designed to establish accurately located sites for future monitoring in the Kentucky portion of Kentucky Lake was that of Sickel and Chandler (1982). In 1981 they collected at 94 locations within Kentucky from TRM 23–62. In this survey, divers utilized quadrat sampling to estimate mussel density, and sample sites were selected to represent four habitat types: old river levee, old river floodplain (referred to as overbank by Bates (1962)), main lake shoreline, and embayment. The surveys in 1989 (Sickel 1989), 1995 (Sickel et al. 1995), and 2001 (Sickel and Burnett 2001) resampled most of the same sites. Although those surveys were conducted by different divers who sometimes sampled 10 m^2 rather than 20 m^2 at some of the locations, the sampling was consistent enough that we believe they provide comparable data useful for documenting a progressive change in the mussel fauna.

By 1981 (Sickel and Chandler 1982) dramatic changes already had taken place in the mussel fauna in the Kentucky portion of Kentucky Lake compared with the pre-impoundment fauna. A number of pond or lake forms had appeared that were not found in the pre-impoundment, free flowing river, *Anodonta suborbiculata, Potamilus ohiensis,* and *Toxolasma parvus.* Also, a species new to the Tennessee River appeared, *Plectomerus dombeyanus* (Valenciennes, 1827). Two live individuals of *P. dombeyanus* were found at one of the sites sampled by Garry Pharris on 10 August 1981 while diving with Carol Chandler and accompanied by James Sickel, John Bates and Sally Dennis (Pharris et al. 1984). In 1989 only seven *P. dombeyanus* were found, and all occurred at the same site as in 1981. By 1995 their number had increased dramatically as the population was expanding up and down the lake from the original point of introduction. This same sample site had the highest mussel density in 1995 (113 mussels in 20 m^2, 33 *A. plicata,* and 54 *P. dombeyanus,* the largest number of that species found at any site in 1995). Again in 2001 this sample site had the greatest number of mussels (133 individuals in 20 m^2, 33 A. *plicata,* and 75 *P. dombeyanus).* The *P. dombeyanus* population continued to expand, and by 2001 it had become the second most abundant species within the sample area in Kentucky, making up 32% of the mussel community. Also in 2001, it was found for the first time below Kentucky Dam in the tailwater (Sickel and Burnett 2001).

Plectomerus dombeyanus is a Gulf coastal drainage species which had never been reported in the Tennessee River prior to 1981. However, its migration northward from Gulf tributaries had been noted as early as 1895 when Samuel N. Rhoads found it in Reelfoot Lake in west Tennessee, and Henry A. Pilsbry stated, "The species has not before been reported from so far north, east of the Mississippi, so far as I know" (Pilsbry and Rhoads 1896). Rhoads found two young specimens, identified as *Unio trapezoides* Lea (Academy of Natural Sciences of Philadelphia Cat. No. 69216 (http://data.acnatsci.org/biodiversity_databases/snails.php)), in Reelfoot Lake at Samburg, Obion County, Tennessee. This location is but 110 km from the Tennessee River, yet it took nearly a century for the species to appear in Kentucky Lake even though it obviously is well adapted to that habitat.

Anodonta suborbiculata was first reported in Kentucky Lake in Tennessee by Bates (1962), and its first appearance in Kentucky was reported by Morgan Sisk who collected three specimens on 14 August 1971. The Sisk specimens were identified by David Stansbery and reside in the Ohio State University Museum of Biological Diversity (Cat. No. 26528). Within Kentucky Lake, *A. suborbiculata* is never abundant and generally restricted to the back of bays in soft mud.

Potamilus ohiensis is a thin shelled species found predominantly in ponds and lakes in fine sediments or rivers in slow current (Parmalee and Bogan 1998). First reported in Kentucky Lake in Tennessee by Bates (1962) (as *Leptodea laevissima* (I. Lea, 1830)), we found it only in 1981 (Sickel and Chandler 1981); however, the shallow water in the back of bays where this species may occur were not sampled in later systematic surveys. It is commonly found along the shoreline as dead shells, probably brought up by muskrats or dying as the water recedes during late summer and fall drawdown. The lake form can be confused with small individuals of the lake form of *Leptodea fragilis* or very young *Potamilus alatus*.

Toxolasma parvus, first reported from Kentucky Lake by Bates (1962) (as *Carunculina parva* (Barnes, 1823)), is a small mussel generally found in bays and often overlooked because of its size. It can become abundant under conditions where it is protected from fish predation. We found only two specimens in 1981 and one in 2001. In a separate study (Berg et al. 1995) in which *Quadrula quadrula* were being held in mussel cages designed to protect them from muskrats, T. *parvus* became very abundant along with *Utterbackia imbecillis* after a period of two years. In the sediment outside the cages, none of either species were found. The cage mesh permitted small fish to enter but excluded larger fish, and small sunfish were seen in the cages. Both T. *parvus* and *U. imbecillis* utilize bluegill and green sunfish as hosts for their glochidia (Watters 1994). We believe they were brought in as glochidia on the gills of small sunfish. Larger sunfish and other predators that might have eaten the small mussels were excluded from the cages by the small mesh size. *Utterbackia imbecillis* was reported in the surveys only in 1981. It is found in mud substrate in the shallow water of bays.

Quadrula quadrula is widely distributed in Kentucky Lake. In 1981 it was the most abundant species (47%) and was one of the most sought after commercial species. By 2001, it had declined to 10% as both *P. dombeyanus* and *Quadrula apiculata* began to be found in the same habitat. *Quadrula quadrula* and *Q. apiculata* appear to intergrade and may experience more intense competition. *Quadrula apiculata* was not reported until 1995, although it was present but had been confused with *Q. quadrula.* Wendell Haag pointed out the distinction between the two morphs while working at the Hancock Biological Station with David Berg on mantle biopsies, and later they were shown to be distinct populations (Berg et al. 1995, 1998). Although overall the percent of *Q. apiculata* was only 3% in 2001, relative to Q. *quadrula* it is increasing as *Q. quadrula* declined in abundance from 51% in 1989 to 10% in 2001. Some of the decline of *Q. quadrula* may be attributed to commercial harvest in the 1990s, but Lewis (2001) showed that *Q. quadrula* was experiencing low fertilization success compared with *Amblema plicata* and *Megalonaias newosa.*

Amblema plicata has become the most abundant species in the Kentucky portion of Kentucky Lake, increasing from 17% relative abundance in 1981 to 37% in 2001. It is found in all habitats sampled. In the shallow waters and sandy-mud substrate in the back of some shallow bays, juvenile *A. plicata* often can be seen moving toward deeper water in the fall as the drawdown is occurring. This species grows rapidly, has a thick pearly shell, and is a valuable commercial species. *Megalonaias nervosa* is found with *A. plicata,* but its abundance declined from 9% to 4% from 1981 to 2001.

The most abundant species in the Kentucky Dam tailwater, *Fusconaia ebena,* was found only rarely (0.8%) in the Kentucky portion of the reservoir in 1981; however, it increased to an abundance of 3% in 2001. It is mostly restricted to the levees along the river channel where there is still some current when discharge is occurring at the dam. The levee habitat contained the most species, probably because it is a habitat where sediment is not accumulating. Although the levee substrates generally consist of firm clay and the original river bank soils, in some areas there is gravel mixed in with the clay. This is not like the original gravel bottom of the channel but may provide a habitat most similar to the flowing water habitat where most of these mussels evolved.

Most mussel species with low abundance in the reservoir in this study are generally found on the levees. These include *Arcidens confragosus, Elliptio crassidens* (found only once), *Fusconaia flava, Quadrula nodulata, Quadrula pustulosa, Tritogonia verrucosa,* and *Truncilla donaciformis.* The other three species found in the reservoir, *Leptodea fragilis, Potamilus alatus,* and *Pyganodon grandis,* generally occur near shore or in bays and at low abundance. This gives a total of 21 species that have been found in the Kentucky portion of Kentucky Lake post-impoundment, with four of these new to the fauna. The other 25 species that once occurred in the Tennessee River in western Kentucky and Tennessee (Table 1) apparently were not able to adapt to the conditions found in the lower, lacustrine region of the reservoir or their fish hosts do not occupy these areas. Many of these species still occur in the tailwater of Kentucky Dam and also the Pickwick Dam tailwater at the upper end of the reservoir, but they do not persist in the lacustrine environment.

Why some species thrive in the reservoir environment and others do not is not understood at this time. Numerous factors probably determine mussel success or failure. The most obvious might be the occurrence and behavior of the host fish. The most common mussel in the Kentucky Dam tailwater is *Fusconaia ebena* yet it is rare in the reservoir. Its primary host is the skipjack herring (Watters 1994) which is very abundant below dams in the spring when F. *ebena* is gravid. The skipjack is primarily a plankton feeder in schools near the surface. In the deep water of the reservoir it would not be on the bottom where the mussels are located. The most abundant mussel in the reservoir is *Amblema plicata* which can utilize many hosts, e.g., black and white crappie, largemouth bass, sauger, sunfish and yellow perch (Watters 1994) all of which are abundant along the bottom of the reservoir. Once transformed, juvenile mussels drop from their host fish, and they encounter many dangers as they settle into the sediment and begin feeding. Swift current moving large gravel can crush the juveniles while fine silt in slack water may cover the juveniles and prevent access to food and oxygen (Isely 1911). At that stage there are many predators such as turbellarians that feed on the tiny mussels, and as the mussels grow, larger predators such as mollusk eating fish, drum and shell crackers, become important. In shallow water muskrats and otters may prey on larger mussels. Obviously, changing the environment from a shallow flowing river to a deep lacustrine reservoir favors some mussels while being detrimental to a larger number of species. While mussel densities in the reservoir seldom exceed $5/m^2$ compared with $100/m^2$ sometimes seen in the Kentucky Dam tailwater, overall the mussel community appears to be thriving although at a lower species richness in the reservoir compared with the tailwater (Sickel and Burnett 2002).

CONCLUSIONS

The unionid mussel fauna in the Kentucky portion of Kentucky Lake has undergone major changes over the past century and continues to change in species composition and abundance today. Of the original 42 species that had been reported in the Kentucky Lake reach of the Tennessee River before impoundment, only 17 species now survive in the Kentucky portion of the reservoir. Four additional species that were not reported prior to impoundment have invaded and survive bringing the present total to 21 species. One of these, *Plectomerus dombeyanus,* which first appeared in 1981, has become the second most abundant species. The most abundant species (47% relative abundance) in 1981 was *Quadrula quadrula,* but it declined to 10% of the community in 2001 while *Amblema plicata,* which made up 17% of the community in 1981, increased to 37% and is the most abundant mussel. As the reservoir ages, we predict continued changes in the mussel community as opportunistic species invade and as habitats change.

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