REGULATED RIVERS: RESEARCH & MANAGEMENT, VOL. 8, 63–71 (1993)

MUSSELS: THE FORGOTTEN FAUNA OF REGULATED RIVERS. A CASE STUDY OF THE CANEY FORK RIVER

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ABSTRACT

During the past century freshwater mussel populations have declined precipitously throughout North America. Much of this loss has resulted from the construction of dams. In the Cumberland River system, 23% (22 species) of the historic mussel fauna is extinct or listed as endangered. Several additional species have either been extirpated from the Cumberland River or exist only in small, non-reproducing populations. Mussels of headwater streams have been severely affected by coal mining and poor land use practices. An intensive survey was conducted in the Caney Fork River, a major tributary to the Cumberland River, to determine the historic and extant mussel fauna. The results indicate that at least 37 species of mussels have been extirpated from the Caney Fork River, mainly as a result of the construction and operation of the Center Hill Dam. Among the species extirpated, two are now extinct, five are endangered and five are candidates for listing as threatened or endangered. Effects associated with this dam include the inundation of 102 km of riverine habitat, the discharge of hypolimnetic water (which limits mussel reproduction) and an alternating pattern of stream bed scouring and dewatering. The recognition of mussel life history requirements during preconstruction could have reduced many of these effects.

KEY WORDS Mussels Dam construction Life history requirements

INTRODUCTION

Freshwater mussels are globally distributed, being absent only from Antarctica. They occur in a wide array of habitats ranging from first order streams to the largest rivers, as well as in lentic environments. Although mussels are found in most types of freshwater habitats, many species occur only over a relatively narrow range of a physical habitat gradient, such as water velocity. Indeed, the richest mussel assemblages typically occur in riffle or shoal areas, precisely those habitats most affected by dams.

Despite their widespread distribution, freshwater mussels have received little consideration in the planning, construction and operation of dams. Many factors have contributed to the neglect of this faunal group. In the United States, before the passage of various environmental laws beginning with the National Environmental Policy Act of 1969, most environmental concerns associated with dam construction were related to commercially or recreationally important resources. Although a few species of mussels were commercially harvested for manufacturing pearl buttons, this industry did not appear to be affected by the first dams constructed on the Tennessee River (Isom, 1969). Moreover, the vast majority of the mussel species had no economic value because of their small size, coloured nacre or thin shells.

Even though the standing crop of mussels may exceed by an order of magnitude the biomass of all other benthic organisms in a stream (Negus, 1966; Fisher and LaVoy, 1972), they are not important in the diets of most fish; consequently, they received little attention. The paucity of information on their life histories may also have contributed to their ecological requirements being overlooked in the planning of dams.

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0886-9375/93/010063-09$09.50

Received 1 October 1991
Accepted 5 June 1992

Larvae (glochidia) of most North American mussels are obligate parasites on fish. Although glochidia of some species, such as *Anodonta grandis*, are capable of metamorphosis to the juvenile state on at least 25 species of fish, transformation of other species, such as *Plethobasus cyphyus*, may only occur on a single fish species (see Gordon and Layzer, 1989). As the life histories of most mussels are inextricably tied to the presence and well being of their host fish, any efforts to conserve mussels must include sufficient protection for their hosts. Indeed, dams and other forms of habitat degradation may destroy mussel populations by affecting the host fish populations rather than directly affecting the mussels.

Passage of the Endangered Species Act in 1973 has afforded some protection for both rare and common species of mussels in the United States. Construction of Columbia Dam on the Duck River, Tennessee, ceased in 1977 because its completion would have affected two species of mussels (Jenkinson, 1980). Thus the abundant and diverse mussel fauna of the Duck River was protected but only because of the presence of endangered species.

We review the historic and present mussel fauna of the Cumberland River system based on published accounts and our own collecting efforts, and we delineate causes of the mussel declines, with particular emphasis on the Caney Fork River.

CUMBERLAND RIVER SYSTEM: HISTORIC MUSSEL FAUNA

The 1160 km long Cumberland River and its tributaries once contained one of the most diverse assemblages of freshwater mussels in the world. Wilson and Clark (1914) conducted the first major study of this fauna and reported the distributions and relative abundances of 60 species, but did not provide any quantitative estimates of mussel densities. Nonetheless, their account of finding mussels to be very abundant on the same shoals where commercial musselers harvested 90 metric tonnes of shells the preceding year indicates that dense beds of mussels were common. The upper Cumberland River system was resurveyed between 1947 and 1949, before the closure of Wolf Creek Dam (Neel and Allen, 1964). The results of that study clearly indicated that the mussel fauna had undergone a substantial change. Although the species list recorded by Neel and Allen (1964) was nearly identical to the list reported by Wilson and Clark (1914), the distributions and relative abundances of species had changed. Neel and Allen (1964) reported that mussels were still abundant on shoals in the mainstem, but few occurred in the Big South Fork, where Wilson and Clark (1914) reported them to be common.

More recent studies of the mussel fauna in the Cumberland River system have been restricted to tributaries or short reaches of the mainstem. The results of these studies indicate continued changes in the mussel fauna of both the mainstem (Stansbery, 1969; Parmalee *et al.*, 1980; Miller *et al.*, 1984) and the tributaries (Thompson, 1985; Schmidt *et al.*, 1989; Anderson *et al.*, 1991). Our collecting efforts, along with an extensive review of the literature and examination of museum specimens, indicate that the Cumberland River system once contained at least 94 species of mussels (Gordon and Layzer, 1989). Ten of these species, all in the genus *Epioblasma*, are believed to be extinct, and 26 other species are either listed as endangered or are candidates for listing as threatened or endangered by the U.S. Fish and Wildlife Service. Moreover, some populations of endangered species, such as *Obovaria retusa*, consist of only a few old individuals, with no evidence of recent recruitment (Parmalee and Klippel, 1982). Thus 38% of the historic fauna of the Cumberland River system is either extinct or threatened with extinction.

Causes of mussel declines

Although all of the reasons for the changes in the distribution and abundance of mussels may never be known, impoundments and poor land use practices have greatly altered the Cumberland River system and have had major effects on mussels. In the upper watershed, extensive coal mining has severely degraded many streams (Harker *et al.*, 1980). Neel and Allen (1964) reported that acid mine drainage was responsible for some of the changes in mussel populations, particularly the drastic declines in *Epioblasma* spp. in the Big South Fork. Recent surface mining has resulted in the extirpation of mussels from several stream reaches in the upper Cumberland River system (Anderson, 1989). Pollution and siltation resulting from logging, agriculture and off-road vehicles have degraded aquatic habits and are probably contributing to the continued decline in mussels.

The Cumberland River is a highly regulated stream with five dams on the mainstem and six dams on major tributaries (Figure 1). The mainstem dams have inundated over 500 km of the river as well as many kilometres of the lower reaches of numerous tributaries. Only short reaches of free-flowing river remain between the lower four dams. Although nearly 200 km of unimpounded river remain between the fourth and fifth dams, flows and water temperatures in this reach are highly altered due to the operation of Wolf Creek Dam (Gordon and Ramachandran, 1986; Nestler *et al.*, 1988). Results of our studies on the Caney Fork River, a major tributary of the Cumberland River, illustrate many of the specific causes of the decline in mussel populations.

STUDY AREA

The Caney Fork River originates along the Cumberland Plateau of central Tennessee and flows north-west to its confluence with the Cumberland River (Figure 2). Great Falls, a natural barrier located at km 145, isolates the aquatic fauna of the upper basin. A dam constructed on top of Great Falls formed a 920 ha impoundment. In 1948, the U.S. Army Corps of Engineers completed the Center Hill Dam Project at km 43. The 76 m high dam formed a 9330 ha impoundment, inundating the river to the base of Great Falls. The dam is operated primarily for the production of peaking power and flood control. The peaking operation discharges water from the hypolimnion and normally results in flows ranging from $<2\ m^3\ s^{-1}$ to $350\ m^3\ s^{-1}$ in the tailwater (Layzer *et al.*, 1989). This fluctuation in discharge results in an alternating pattern of scouring and dewatering of much of the stream bed.

METHODS

We selected 47 sites within the Caney Fork River system to determine the present and historic mussel fauna. Several sites were located on most tributaries and five sites were located in the first 23 km of river below the Center Hill Dam. At each site the stream banks, exposed gravel bars and stream bottom were searched for mussel shells. Living mussels were located by snorkelling or by using a glass bottom viewing bucket.

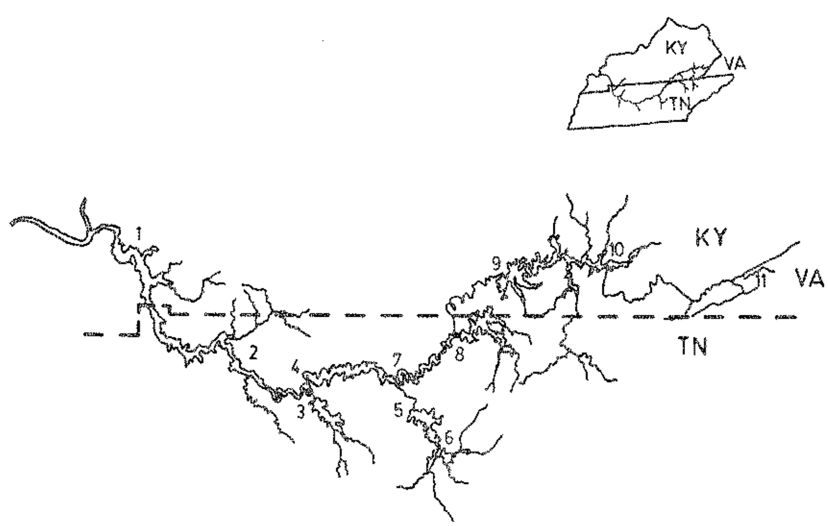

Figure 1. Map of the Cumberland River system with major dams. Numbers indicate locations of major dams: 1 = Barkley; 2 = Cheatham; 3 = J. Percy Priest; 4 = Old Hickory; 5 = Center Hill; 6 = Great Falls; 7 = Cordell Hull; 8 = Dale Hollow; 9 = Wolf Creek; 10 = Laurel Fork; 11 = Martins Fork

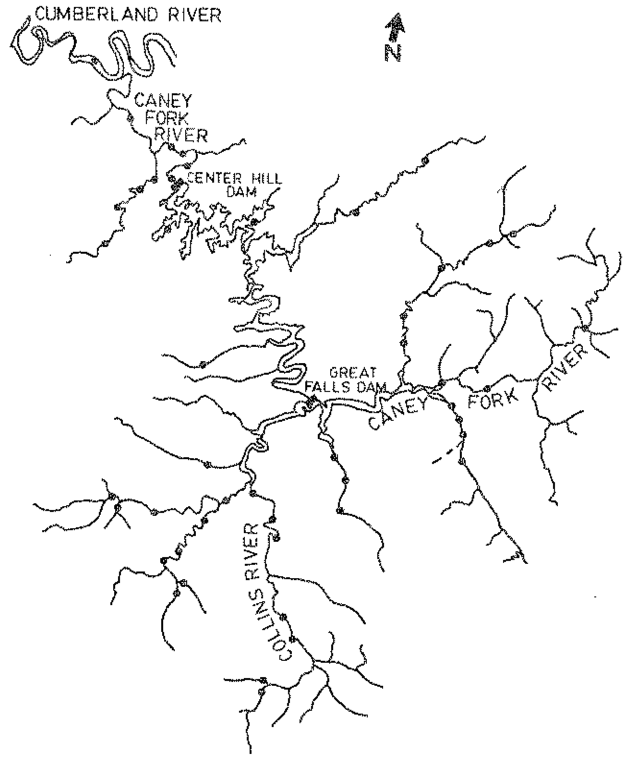

Figure 2. Map of the Caney Fork River system, Tennessee. Sampling sites indicated by dots

Representative collections of shells were retained, while live mussels were returned to the stream after identification. Voucher specimens of many species were deposited in the Ohio State University Museum of Zoology, Columbus, Ohio.

RESULTS

We found 50 species of mussels in the Caney Fork River and its tributaries (Table I). Of the 17 species found alive, 10 only occurred in tributaries. No living mussels or shells were encountered in the mainstem upstream of the Great Falls Dam. The habitat in this section was obviously degraded by active gravel dredging and by the presence of 'yellow boy', a ferric precipitate often associated with coal mines, and silt. Many sites on tributaries in this area were also degraded by gravel dredging and silt accumulations. At the least affected sites we found seven species, including living specimens of two species (*Pegias fabula* and *Pleurobema gibberum*) that are on the federal endangered species list. Incidental collecting along Center Hill Lake indicated that at least two species were living in the lake (Table I).

Downstream of Center Hill Dam we found four species alive and relic shells of 31 other species. The relic shells included specimens of two extinct, five endangered and five candidate species. We did not find any living mussels in the first 12 km below the dam. This river reach was characterized by a well armoured channel near the dam and an aggraded channel further downstream. The partial recovery to pre-dam physical conditions corresponded with the first live mussels found 13 km downstream of the dam.

The size and condition of the single *Cumberlandia monodonta* found indicates that this species has probably reproduced, albeit limitedly, since closure of the dam. The large size and amount of shell erosion of the other live mussels in the Center Hill Dam tailwater indicated that these mussels may have been present since the dam was constructed.

Table I. Mussels (Unionidae) of the Caney Fork River system, Tennessee. R = relic shells; L = alive; X = present

Species	Present study: Caney Fork River	Present study: Tributaries	M*	SB†	MR‡	Status
Actinonaias ligamentina	L		L	X		
A. pectorosa			R	X		
Alasmidonta sp.§		L		X		
Amblema plicata	L	R	L			
Anodonta grandis		L				
A. imbecillis		L				
Cumberlandia monodonta	L		R	X		Candidate
Cyclonaias tuberculata	R		L			
Cyprogenia stegaria	R					Endangered
Dromus dromas	R		R			Endangered
Ellipsaria lineolata	R		R			
Elliptio crassidens	L		L			
E. dilatata	R		R			
Epioblasma brevidens	R			X		Candidate
E. capsaeformis	R			X		Candidate
E. haysiana	R					Extinct
E. lewisii	R					Extinct
E. obliquata	R			X		Endangered
E. triquetra	R					
Fusconaia subrotunda	R					
Lampsilis abrupta	R		L			Endangered
L. cardium	R					
L. fasciola	R	L				
L. ovata			R	X		
L. teres	R		L			
Lasmigona complanata				X		
L. costata	R	L	L	X		
L. sp.§		L				
Leptodea fragilis		R				
Lexingtonia dolabelloides	R					Candidate
Ligumia recta	R					
Medionidus conradicus		R				
Megalonaias nervosa	L		L			
Obliquaria reflexa	R		R	X		
Obovaria subrotunda			R			
Pegias fabula		L		X		Endangered
Plethobasus cicatricosus				X		Endangered
P. cyphyus	R					
Pleurobema clava	R					
P. coccineum	R		R			
P. cordatum	R		L			
P. gibberum		L		X		
P. pyramidatum	R		R			Candidate
Proptera alata	L¶	R	R			
Ptychobranchus fasciolaris	R		L			
P. subtentum				X		
Quadrula cylindrica	R		R			
Q. metanevra	R		R			
Q. pustulosa	L					
Q. quadrula					X	
Q. tuberosa					X	
Toxolasma lividus					X	

Continued

Table I. *Continued*

Species	Present study: Caney Fork River	Present study: Tributaries	M*	SB†	MR‡	Status
T. parvus	L¶					
Tritogonia verrucosa	R		L			
Truncilla truncata	R		R	X		
Venustaconcha sp.§		L				
Villosa iris§		L				
V. taeniata		R		X		
V. trabalis	R					Endangered
V. vanuxemii					X	

*Miller (1984).
†Starnes and Bogan (1988).
‡Museum records.
§Systematics presently being investigated.
¶Alive in Center Hill Lake.

DISCUSSION

The mussel fauna of the Caney Fork River has been one of the least studied faunas of any of the major tributaries to the Cumberland River. Starnes and Bogan (1988) listed a historic fauna of 17 species for the Caney Fork River. In addition to the 50 species we found, our review of other records indicates that the Caney Fork River once contained at least 60 species of mussels. As no mussel surveys were carried out before construction of Center Hill Dam, which inundated 102 km of river, it is possible that additional species once inhabited the Caney Fork River. Indeed, it is likely that some thin-shelled species (e.g. *Proptera ohiensis*) may also have occurred in the Caney Fork River, but their thin shells would have eroded in the 40 years following closure of the dam. We are unaware of any tributary to the Cumberland River that contained more species than the Caney Fork River. Our results, along with those of Miller (1984), indicate that only 23 species of mussels presently live in the Caney Fork River system. Included among the 37 extirpated species are two now-extinct species, five endangered species and five candidate species. Most of the species eliminated once occurred in the mainstem Caney Fork River below Great Falls.

Great Falls, a natural barrier to the upstream movement of fish and mussels, isolates the upper Caney Fork River. This isolation has resulted in a depauperate mussel fauna of only eight species. One species (*Medionidus conradicus*) apparently has been extirpated, and populations of the remaining seven species, including the endangered *Pegias fabula* and *Pleurobema gibberum*, have been greatly reduced or eliminated from some tributaries due to poor land use practices. Construction of a dam at Great Falls undoubtedly affected mussels inhabiting lotic areas that were inundated. As we did not locate any living mussels or relic shells in this area, we cannot assess the original effects of inundation; however, the impoundment continues to isolate tributaries and their mussel populations by acting as a barrier to interstream movement of headwater fishes. Thus recolonization by mussels of any tributary where they have been extirpated is improbable.

It is likely that the mussel fauna of the 102 km of river inundated by Center Hill Dam included most or all of the 39 species found below the dam. Isom (1969) reported that silt deposition affected the survival of juvenile mussels and was a major factor in the decline of mussels in the Tennessee River impoundments. Observed sedimentation in upstream tributaries suggests that sedimentation is also occurring in Center Hill Lake. Extirpation of mussels from impoundments may also be related to oxygen depletion in the hypolimnion (Isom, 1971). Near-anoxic conditions in the metalimnion and hypolimnion occur periodically in Center Hill Lake (Gordon *et al.*, 1986). Further, Center Hill Lake may fluctuate as much as 10 m annually

(U.S. Army Corps of Engineers, 1977). This fluctuation prevents colonization of shoreline habitat by any mussels that could tolerate lentic conditions. Inundation not only results in eliminating the lotic habitats required by many species of mussels but also destroys the habitats required by some host fish species. For example, all known hosts for *Epioblasma capsaeformis* are benthic fishes restricted to lotic environments (Hill, 1986).

Forty years of operating the Center Hill Dam project for the generation of peaking hydroelectric power has greatly altered the morphology of the river channel for 12 km downstream. Exactly when mussels were extirpated from this reach is unknown; however, present conditions are obviously not conducive to maintaining mussel populations. The stream channel near the dam is degraded and well armoured due to the scouring effects of the hydroelectric discharges (Gore *et al.*, 1990). Moreover, the dam prevents replenishment of sand and gravel from upstream areas. Adult mussels, especially smaller species, may have been dislodged from the substrate and transported downstream into unfavourable habitats. Few, if any, recently metamorphosed juvenile mussels would find refuge from this scouring and downstream transport. Results of modelling the hydraulics of the river 2 km from Center Hill Dam indicate large areas of moderate velocities; however, these areas are dewatered during periods of no power generation (Gore *et al.*, 1989). Mussels cannot tolerate prolonged and frequent periods of dewatering below hydroelectric projects (Fisher and LaVoy, 1972).

About 8 km downstream the river is braided and the channel has aggraded (Gore *et al.*, 1989). There is also evidence that the low flow channels are unstable; consequently, mussels that occurred here would have been either covered by sediments or exposed as low flow channels shifted. About 13 km below the dam the stream channel recovers from the hydraulic effects of the peaking discharges. This recovery coincides with the first mussels we found alive.

Further downstream, we and Miller (1984) found more live mussels but at low densities, which indicates that additional factors were affecting the mussels. In addition to altering flow patterns, the Center Hill Project discharges water from the hypolimnion and water temperatures throughout the entire 43 km tailwater remain below 20°C (usually <12°C), except during prolonged periods of no discharge (Gordon and Ramachandran, 1986). On such occasions, Gordon and Ramachandran (1986) noted an 11°C decrease in water temperature within three hours of a resumption of discharge. The release of cold water has undoubtedly eliminated many warm water species of fish, including host species, from the tailwater. The disappearance of host fish has been correlated with the disappearance of *Anodonta implicata* in other waters (Davenport and Warmuth, 1965). Nonetheless, several warm water species, including known hosts (e.g. *Aplodinotus grunniens*), are common (but few darters and minnows are present) in the middle and lower reaches of the tailwater (Odenkirk, 1987). Moreover, the banded sculpin (*Cottus carolinae*), a known host for three species of *Epioblasma* extirpated from the tailwater, is abundant and occurs throughout the tailwater (Hunt, 1989).

Hence the extirpation of many mussels from the Caney Fork River does not appear to be related to the disappearance of their host fish. Instead, the altered temperature regime may have directly inhibited mussel reproduction. Coker *et al.* (1921) indicated that increasing water temperatures induce the reproductive activities of some mussels. For some species there is a temperature threshold that must be exceeded before development to the glochidial stage can be completed (Yokley, 1972). Moreover, the rapid and extreme temperature changes observed by Gordon and Ramachandran (1986) could induce abortion of developing larvae (Matteson, 1948).

In conclusion, the construction and operation of the Center Hill Dam project have devastated the once rich mussel assemblage of the Caney Fork River. The project contributed directly to the extinction of two species and placed in jeopardy the continued existence of at least five others.

Some of the major effects could have been eliminated, by installing a multilevel intake to regulate the temperature of the discharge, or reduced, by operating the project for baseload rather than peaking power. With closure of the dam, the loss of lotic habitat and associated mussels was inevitable, but the amount of this loss could have been decreased, albeit with a concomitant loss of hydroelectric generation capacity from a smaller dam. If mussels are not 'remembered' during the planning stages of future dams, many more species will become extinct.

ACKNOWLEDGEMENTS

We thank Lesa M. Madison for her assistance in the field and for drafting the illustrations, and Kevin S. Cummings for his constructive criticism of the manuscript. Funding for portions of this study were provided by the National Ecology Research Center of the U.S. Fish and Wildlife Service, Tennessee Wildlife Resources Agency, Kentucky Department of Fish and Wildlife Resources, and Tennessee Technological University Center for the Management, Utilization, and Protection of Water Resources.

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