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RESTORATION AND COLONIZATION OF FRESHWATER MUSSELS AND FISH IN A SOUTHEASTERN UNITED STATES TAILWATER†

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ABSTRACT

The French Broad River originates in North Carolina, flows west into Tennessee and at its confluence with the Holston River forms the Tennessee River. Douglas Dam, located on the French Broad River 52 km above its mouth, is operated primarily for peaking hydroelectric power and flood control. Prior to completion of the dam in 1943, the lower French Broad River contained about 53 species of freshwater mussels and 100 species of fish. By 1977, the fauna in the 52-km-long tailwater was reduced to 12 species of mussels and 42 native species of fish. Improvements in tailwater conditions occurred following initiation of minimum flows in 1987, and consistent reaeration of discharge in 1993. From 1988 to 2002, we sampled three sites (4, 28, and 39 km downstream of the dam) to monitor the fish assemblage. Each year since 1988, we have collected one or more additional species, indicating continued immigration. We collected 82 native and 9 exotic species of fish overall, but the maximum of 67 species in 1 year suggests that some species reside in the tailwater at low densities or all immigrants may not successfully colonize the tailwater. There is limited potential for most extirpated species of mussels to naturally recolonize the tailwater because source populations are isolated. Consequently, 19 754 adult mussels of 19 species were introduced between 1997 and 2000. Survival of translocated mussels has been high, and successful reproduction of at least one translocated species has occurred. Additionally, four mussel species are naturally colonizing the tailwater. Colonization and recruitment of additional mussel species is expected as populations of their host fishes increase. We believe that the improved conditions of the tailwater may allow for the re-establishment of sustaining populations of 30 mussel species of historic occurrence, but the continued operation of Douglas Dam as a peaking hydroelectric project will reduce the probability of successfully reintroducing some species. Published in 2006 by John Wiley & Sons, Ltd.

KEY WORDS: minimum flows; reaeration; dams; fish; mussels; recolonization; reintroduction

INTRODUCTION

The Tennessee River is one of the most regulated drainages in the southeastern United States; the Tennessee Valley Authority (TVA) operates 11 dams on the Tennessee River, and 27 dams on major tributaries. Gehrke *et al*. (1999) defined four zones in regulated streams: a reach upstream of the impoundment where flows are unmodified; an impounded reach inundating lotic habitat; the immediate tailwater where flow alterations are greatest; and a reach further downstream where flow alterations are attenuated due to the influx of tributary inflows. Only two of these zones (the impounded and tailwater zones) occur in much of the Tennessee River system because distances between dams and impoundments are relatively short, and reaches upstream of impoundments are the tailwaters of other dams. Most dams in the Tennessee Valley are operated primarily to supply electrical power during daily peak demands, and for flood control. Daily and seasonal hydrographs below peaking hydroelectric projects bare little resemblance to preimpoundment conditions (Gore *et al*., 1989). These altered hydrographs result in a state of constant flux in the amount and location of suitable habitat for aquatic biota in peaking project tailwaters (Nestler *et al*., 1989). Moreover, profound changes in physical and chemical conditions can occur in these tailwaters

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(Dortch and Martin, 1989; Gore *et al*., 1989). The biodiversity of streams in the Tennessee River Valley was among the richest anywhere in the North Temperate Zone; however, inundation of riverine habitat and decades of operating dams in a peaking mode have devastated the fauna.

In the Tennessee River drainage, many of the fish species extirpated from tailwater areas have the potential to recolonize these waters because of the existence of tributary populations. In contrast, most species of mussels extirpated from tailwaters do not have the potential for recolonization because tributary populations either have been extirpated or they are isolated by impoundments (Anderson *et al*., 1991; Layzer *et al*., 1993). Furthermore, most species of mussels have a complex life history that includes a larva (glochidium) that is an obligate parasite on fish. Glochidia of many mussel species are host specific and can metamorphose into juveniles only on one or a few species of fish. Because adults are relatively immobile, recolonization by mussels is inextricably linked to successfully parasitizing a host and the subsequent movements of the infested host. Thus, even when there is connectivity between tailwaters and a source population, recolonization is likely to take decades. Consequently, re-establishment of mussel populations necessitates translocating adult or juvenile mussels; however, unsuitable tailwater conditions must first be ameliorated. Despite increasing electrical demands and offstream uses of water, there is a growing interest in modifying discharge regimes and water quality to restore biodiversity. In 1987, TVA initiated a major program to improve tailwater conditions below 16 dams. In most tailwaters, this program resulted in improvements in the fish and benthic macroinvertebrate assemblages (Scott *et al*., 1996), suggesting that re-establishment of mussel populations might be successful.

Re-establishing mussel populations is critical because freshwater mussels are considered to be the most imperiled group of organisms in North America (Strayer *et al*., 2004). Moreover, the introduction of zebra mussels (*Dreissena polymorpha*) to North America in the 1980s confounded efforts to conserve remaining populations of unionids. Zebra mussels established dense populations soon after their introduction, and extirpated local populations of native unionids in the Laurentian Great Lakes (Gillis and Mackie, 1994; Schloesser and Nalepa, 1994). Their subsequent invasion of the Ohio River system, including the Tennessee River, was of particular concern because this drainage contains many critically endangered unionid species. Consequently, efforts were initiated to locate and evaluate potential refugia (Dunn and Layzer, 1997; Sickel *et al*., 1997; Nichols *et al*., 2000).

The improvements in discharge from Douglas Dam located on the lower French Broad River in eastern Tennessee provided a potential opportunity for re-colonization by fish and restoration of mussel populations in the tailwater. The tailwater also has a low potential for zebra mussel invasion via commercial and recreational boats. The goal of our study was to evaluate the 52-km-long tailwater of Douglas Dam for re-establishment of endangered species of mussels. Specific objectives were to document the historical fish and mussel assemblages, monitor fish recolonization, evaluate the present composition of the fish assemblage with respect to the presence of glochidial hosts, evaluate sites for reintroducing mussels, and determine the likelihood of establishing self-sustaining mussel populations.

STUDY AREA

The 351-km-long French Broad River originates near Rosman, North Carolina and at its confluence with the Holston River in Knoxville, Tennessee, forms the Tennessee River (Figure 1). Douglas Dam is the largest (61 m high, 519 m long) of the four dams on the mainstem of the French Broad River and is located 52 km upstream from its mouth. The dam, completed in 1943, created a 12 788 ha reservoir that inundated 69 km of the French Broad River. The dam and reservoir are operated primarily for hydroelectric peaking power and flood control. During peak generation, the powerhouse discharges 510 m^3/s. Prior to October 1987, there was no discharge during periods of nongeneration; thus, prolonged periods of nongeneration resulted in aerial exposure of shoals and increased water temperatures in the 52-km-long tailwater. Each of the four powerhouse turbines is fed by an individual penstock that draws from the hypolimnion. During periods of lake stratification, water discharged frequently contained <4 mg/L of dissolved oxygen (DO). In October 1987, discharge regime was modified to include pulsing one of the four turbines for 30–45 min every fourth hour to maintain a minimum flow of 16.6 m^3/s at Saffell Island located 4 km downstream (rkm 48). Various configurations of surface water pumps and injection of liquid oxygen were tested between 1987 and 1993. After reaeration techniques became fully operational in 1993, nearly all water discharged contained >4 mg DO/L (Scott, 1999).

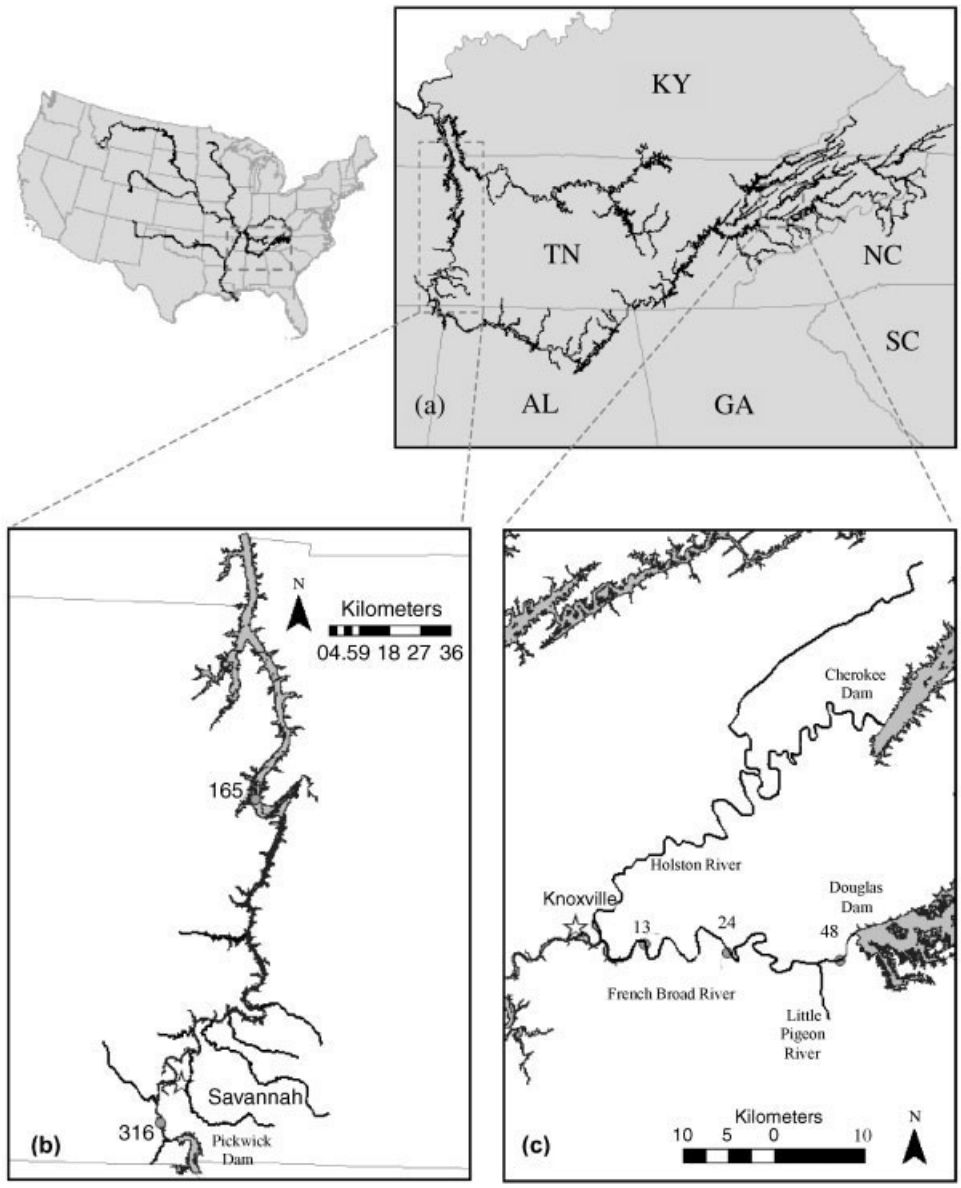

Figure 1. (a) Location map of the Tennessee and French Broad rivers. (b) Locations of mussel collection sites in the lower Tennessee River. (c) Map of the French Broad River below Douglas Dam showing fish sampling sites

HISTORICAL FAUNA

The historical fish fauna of the French Broad River is poorly known. Although Cope (1870) collected fish in several of its tributaries, there were no extensive surveys of the mainstem, particularly in the lower 52 km, prior to completion of Douglas Dam in 1943. To reconstruct the likely composition of the historical fish assemblage, we relied heavily on the synopsis of collection records provided in Etnier and Starnes (1993), reviewed unpublished fish collections of the mainstem made since the construction of Douglas Dam, examined records for the resident fish fauna in the lower portion of the Holston River, and augmented these data with our judgment based on extensive personal collecting in the upper Tennessee River system. In all, the historical fish fauna likely consisted of 100 species (Table I). Additionally, nine introduced species have been collected from the lower French Broad River.

Table I. Historical (pre-impoundment of the Tennessee River) and recent fish fauna of the lower French Broad River

Family species	Common name	Historical[a]	1977[b]	1988–1993[c]	1994–2002[c]
Petromyzontidae	Lampreys				
Ichthyomyzon bdellium	Ohio lamprey	X			X
Ichthyomyzon castaneus	Chestnut lamprey	X			X
Lampetra appendix	American brook lamprey	X			X
Acipenseridae	Sturgeons				
Acipenser fulvescens	Lake sturgeon	X			X*
Scaphirhynchus platorynchus	Shovelnose sturgeon	X			
Polyondontidae	Paddlefishes				
Polyodon spathula	Paddlefish	X			
Lepisosteidae	Gars				
Lepisosteus oculatus	Spotted gar	X	X	X	X
Lepisosteus osseus	Longnose gar	X	X	X	X
Clupeidae	Herring				
Alosa alabamae	Alabama shad	X			
Alosa chrysochloris	Skipjack herring	X		X	X
Dorosoma cepedianum	Gizzard shad	X	X	X	X
Dorosoma petenense	Threadfin shad	X	X	X	X
Hiodontidae	Mooneyes				
Hiodon tergisus	Mooneye	X	X	X	X
Anguillidae	Freshwater eels				
Anguilla rostrata	American eel	X			
Cyprinidae	Minnows				
Campostoma oligolepis	Largescale stoneroller	X	X	X	X
*Carassius auratus**	Goldfish				X
*Ctenopharyngodon idella**	Grass carp				X
*Cyprinus carpio**	Common carp		X	X	X
Cyprinella galactura	Whitetail shiner	X	X	X	X
Cyprinella spiloptera	Spotfin shiner	X	X	X	X
Cyprinella whipplei	Steelcolor shiner	X			
Erimonax monachus	Spotfin chub	X			
Erimystax insignis	Blotched chub	X			
Hybognathus nuchalis	Mississippi silvery minnow	X			
Hybopsis amblops	Bigeye chub	X	X	X	X
Luxilus chrysocephalus	Striped shiner	X			X
Luxilus coccogenis	Warpaint shiner	X			
Macrhybopsis aestivalis	Speckled chub	X	X	X	X
Macrhybopsis storeriana	Silver chub	X			X
Nocomis micropogon	River chub	X	X	X	X
Notemigonus crysoleucas	Golden shiner	X	X		X
Notropis atherinoides	Emerald shiner	X	X		X
Notropis leuciodus	Tennessee shiner	X	X		X
Notropis photogenis	Silver shiner	X	X		X
Notropis rubellus	Rosyface shiner	X		X	X
Notropis stramineus	Sand shiner	X			X
Notropis telescopus	Telescope shiner	X		X	
Notropis volucellus	Mimic shiner	X	X	X	X
Phenacobius uranops	Stargazing minnow	X			X
Pimephales notatus	Bluntnose minnow	X		X	X
Pimephales promelas	Fathead minnow				X
Pimephales vigilax	Bullhead minnow	X		X	
Catostomidae	Suckers				
Carpiodes carpio	River carpsucker	X		X	X
Carpiodes cyprinus	Quillback	X			X
Carpiodes velifer	Highfin carpsucker	X			
Catostomus commersoni	White sucker	X			X

Continues

Table I. Continued

Family species	Common name	Historical[a]	1977[b]	1988–1993[c]	1994–2002[c]
Cycleptus elongatus	Blue sucker	X			X
Hypentelium nigricans	Northern hogsucker	X	X	X	X
Ictiobus bubalus	Smallmouth buffalo	X	X	X	X
Ictiobus cyprinellus	Bigmouth buffalo	X			
Ictiobus niger	Black buffalo	X		X	X
Lagochila lacera	Hairlip sucker	X			
Minytrema melanops	Spotted sucker	X			X
Moxostoma anisurum	Silver redhorse	X			X
Moxostoma carinatum	River redhorse	X	X	X	X
Moxostoma duquesnei	Black redhorse	X	X	X	X
Moxostoma erythrurum	Golden redhorse	X	X	X	X
Moxostoma macrolepidotum	Shorthead redhorse	X	X	X	X
Ictaluridae	Catfishes				
Ameiurus melas	Black bullhead	X			X
Ameiurus natalis	Yellow bullhead	X	X		X
Ameiurus nebulosus	Brown bullhead	X			X
Ictalurus furcatus	Blue catfish	X		X	
Ictalurus punctatus	Channel catfish	X	X	X	X
Noturus eleutherus	Mountain madtom	X		X	X
Noturus flavus	Stonecat	X			
Pylodictis olivaris	Flathead catfish	X	X	X	X
Esocidae	Pikes				
Esox masquinongy	Muskellunge	X			
Salmonidae	Trout				
*Oncorhynchus mykiss**	Rainbow trout				X
*Salmo trutta**	Brown trout				X
Fundulidae	Topminnows				
Fundulus catenatus	Northern studfish	X			X
Fundulus notatus	Blackstripe topminnow	X	X	X	X
Poeciliidae	Livebearers				
*Gambusia affinis**	Western mosquitofish	X	X	X	X
Atherinidae	Silversides				
Labidesthes sicculus	Brook silverside	X	X	X	X
Cottidae	Sculpins				
Cottus carolinae	Banded sculpin	X	X	X	X
Moronidae	Temperate basses				
Morone chrysops	White bass	X	X	X	X
Morone mississippiensis	Yellow bass	X		X	X
*Morone saxatilis**	Striped bass				X
Centrarchidae	Sunfishes				
Ambloplites rupestris	Rock bass	X	X	X	X
*Lepomis auritus**	Redbreast sunfish		X	X	X
Lepomis cyanellus	Green sunfish	X		X	X
Lepomis gulosus	Warmouth	X		X	X
Lepomis macrochirus	Bluegill	X	X	X	X
Lepomis megalotis	Longear sunfish	X		X	
Lepomis microlophus	Redear sunfish	X		X	X
Micropterus dolomieu	Smallmouth bass	X	X	X	X
Micropterus punctulatus	Spotted bass	X	X	X	X
Micropterus salmoides	Largemouth bass	X	X	X	X
Pomoxis annularis	White crappie	X	X	X	X
Pomoxis nigromaculatus	Black crappie	X		X	X
Percidae	Perches				
Etheostoma blennioides	Greenside darter	X	X	X	X
Etheostoma camurum	Bluebreast darter	X			X
Etheostoma jessiae	Blueside darter	X		X	X

Continues

Table I. Continued

Family species	Common name	Historical[a]	1977[b]	1988–1993[c]	1994–2002[c]
Etheostoma kennicotti	Stripetail darter	X			X
Etheostoma Rufilineatum	Redline darter	X	X	X	X
Etheostoma simoterum	Snubnose darter	X	X	X	X
Etheostoma vulneratum	Wounded darter	X			
Etheostoma zonale	Banded darter	X	X	X	X
*Perca flavescens**	Yellow perch			X	X
Percina aurantiaca	Tangerine darter	X			X
Percina burtoni	Blotchside logperch	X			
Percina caprodes	Logperch	X	X	X	X
Percina evides	Gilt darter	X			X
Percina sciera	Dusky darter	X		X	X
Percina shumardi	River darter	X			
Percina squamata	Olive darter	X			
Percina tanasi	Snail darter	X		X	X
Sander canadense	Sauger	X	X	X	X
Sander vitreus	Walleye	X		X	X
Sciaenidae	Drums				
Aplodinotus grunniens	Freshwater drum	X	X	X	X
Total native species		100	42	56	78
Introduced species			3	4	9

*Introduced species.
[a]Primarily based on Etnier and Starnes (1993).
[b]Data from Harned (1979).
[c]Our study.

The historical mussel fauna in the mainstem of the French Broad River, particularly in the lower 52 km, also is poorly known. To reconstruct the likely composition of this assemblage, we used taxonomic composition of shells from an aboriginal site (unpublished data, P. Parmalee), a collection of relic shells from a presumed muskrat midden (unpublished data, J.R. Shute and P. Rakes), reviewed pertinent literature, especially the extensive species distribution records in Parmalee and Bogan (1998), and our own collection records. We assumed that most species recorded from the Little Pigeon River (Parmalee, 1988), a major tributary to the lower French Broad River, also once occurred in the French Broad River. Boepple and Coker (1912) reported the occurrence of the ebonyshell (*Fusconaia ebena*) in the French Broad River, but Hughes and Parmalee (1999) found no evidence in their examination of aboriginal middens that this species occurred in the upper Tennessee River system prior to damming of the mainstem. Morrison (1942), however, suggested that the absence of ebonyshells in aboriginal middens was a result of the deeper habitat occupied by this species and therefore not collected for food. Due to the lack of unequivocal evidence of its occurrence, we conservatively choose not to include the ebonyshell as part of the historical fauna of the French Broad River. From the above records, we estimated that at least 53 species of mussels once occurred in the mainstem of the lower French Broad River (Table II). It is possible that additional species such as the deertoe (*Truncilla truncata*) which has been recorded both upstream (Ahlstedt, 1991) and downstream (Hughes and Parmalee, 1999) of the study area also occurred in the lower French Broad River.

METHODS

Fish sampling

We selected 3 of the 12 sites sampled by Harned (1979) to monitor the fish assemblage over time. The sites were located 4, 28, and 39 km below Douglas Dam (Figure 1). These sites were selected to evaluate possible changes in the fish assemblage with respect to distance from the dam; each site included riffle, run, and pool habitats. All fish

Table II. Historical and present mussel fauna of the lower French Broad River, and prognosis for re-establishing self-sustaining populations. Limiting factor: H, known hosts are mid-water column species or, if hosts are unknown, hosts for congeneric species are mid-water column species; P, potential donor populations are small, functionally extinct, or subspecies may be extinct

Species	Common name	Source[a]	Current status[b]	Prognosis (limiting factor)
Actinonaias ligamentina	Mucket	1, 2, 3	Extirpated	Good
Actinonaias pectorosa	Pheasantshell	2	Extirpated	Good
Alasmidonta marginata	Elktoe	1	Extirpated	Good
Amblema plicata	Threeridge	1, 3, 4, 5	Resident	Good
Cyclonaias tuberculata	Purple wartyback	1, 3, 4, 5	Resident	Good
*Cyprogenia stegaria**	Fanshell	1, 2, 3	Extirpated	Good
*Dromus dromas**	Dromedary pearlymussel	1, 2, 3	Extirpated	Good
Ellipsaria lineolata	Butterfly	5	Extirpated	Good
Elliptio crassidens	Elephantear	1, 3, 4, 5	Resident	Poor (H)
Elliptio dilatata	Spike	1, 3, 5	Extirpated	Good
Epioblasma arcaeformis	Sugarspoon	1, 3	Extinct	—
*Epioblasma brevidens**	Cumberlandian combshell	1	Extirpated	Good
*Epioblasma capsaeformis**	Oyster mussel	1, 3	Extirpated	Good
Epioblasma cf. *florentina**		1, 3	Extirpated	Poor (P)
Epioblasma haysiana	Acornshell	1, 3	Extinct	—
Epioblasma lewisii	Forkshell	3	Extinct	—
Epioblasma propinqua	Tennessee riffleshell	3	Extinct	—
Epioblasma stewardsoni	Cumberland leafshell	1, 3	Extinct	—
*Epioblasma torulosa gubernaculum**	Green blossom	1, 2	Extirpated	Poor (P)
Fusconaia barnesiana	Tennessee pigtoe	1, 3, 4	Resident	Poor (H)
Fusconaia subrotunda	Longsolid	1, 2, 3	Extirpated	Poor (H)
*Hemistena lata**	Crackling pearlymussel	1, 3	Extirpated	Poor (H)
*Lampsilis abrupta**	Pink mucket	4	Resident	Good
Lampsilis fasciola	Wavyrayed lampmussel	1, 3	Extirpated	Good
Lampsilis ovata	Pocketbook	1, 3, 4	Resident	Good
Lasmigona costata	Flutedshell	1, 3	Extirpated	Good
*Lemiox rimosus**	Birdwing pearlymussel	1, 3	Extirpated	Good
Leptodea fragilis	Fragile papershell	3, 4	Resident	Good
Lexingtonia dolabelloides	Slabside pearlymussel	1, 3, 4	Extirpated	Poor (H)
Ligumia recta	Black sandshell	1, 2, 4, 5	Resident	Good
Medionidus conradicus	Cumberland moccasinshell	1, 3	Extirpated	Good
*Obovaria retusa**	Ringpink	2	Extirpated	Poor (P)
Obovaria subrotunda	Round hickoryshell	1, 3	Extirpated	Unknown
*Plethobasus cooperianus**	Orangefoot pimpleback	1, 2, 3	Extirpated	Unknown
Plethobasus cyphyus	Sheepnose	1, 2, 3	Extirpated	Good
Pleurobema cordatum	Ohio pigtoe	2, 3, 4	Resident	Poor (H)
Pleurobema oviforme	Tennessee clubshell	1, 3	Extirpated	Poor (H)
*Pleurobema plenum**	Rough pigtoe	1, 2, 3	Extirpated	Poor (H)
Pleurobema rubrum	Pyramid pigtoe	1, 2, 3	Extirpated	Poor (H)
Pleurobema sintoxia	Round pigtoe	3	Extirpated	Poor (H)
Potamilus alatus	Pink heelsplitter	1, 3, 4, 5	Resident	Good
Ptychobranchus fasciolaris	Kidneyshell	1, 2, 3	Extirpated	Good
Ptychobranchus subtentum	Fluted kidneyshell	1, 3	Extirpated	Good
Pyganodon grandis	Giant floater	1, 3	Resident	Good
Quadrula cylindrica	Rabbitsfoot	1, 2, 3	Extirpated	Poor (H)
*Quadrula intermedia**	Cumberland monkeyface	3	Extirpated	Poor (H)
Quadrula metanevra	Monkeyface	2	Extirpated	Good
Quadrula pustulosa	Pimpleback	1, 2, 3, 4, 5	Resident	Good
*Quadrula sparsa**	Appalachian monkeyface	1, 3	Extirpated	Poor (H, P)

Continues

Table II. Continued

Species	Common name	Source[a]	Current status[b]	Prognosis (limiting factor)
Quadrula verrucosa	Pistolgrip	4	Nonindigenous	Not applicable
Toxolasma lividus	Purple lilliput	1	Extirpated	Good
Villosa iris	Rainbow	1, 3	Extirpated	Good
*Villosa trabalis** (or *V. perpurpurea**)	Cumberland bean (or purple bean)	1, 3	Extirpated	Good
Villosa vanuxemensis	Mountain creekshell	1, 3	Extirpated	Good

[a]Source of record of occurrence: 1, Parmalee (1988); 2, Shute and Rakes (unpublished data, 1998); 3, Parmalee (unpublished data, 1990); 4, this study; 5, Harned (1979).
[b]Excluding mussels translocated in this study.
* = Listed as endangered by the U.S. Fish and Wildlife Service.

samples were collected over a 3-day period during daylight hours in spring or summer while discharge from Douglas Dam was either zero or at minimum levels. In shallow water throughout the river channel and along the shorelines, a crew of five persons collected fish using a backpack electro-shocker, dip nets, and a 6.1-m-long seine with 4.8 mm mesh. The seine was routinely positioned perpendicular to the river's flow at a distance of 6 m downstream from the person operating the backpack shocker. As direct current (DC) was applied to an area approximately equal to the width of the seine, the operator moved downstream to the stationary seine. Fish stunned by the electric field were collected as they drifted into the stationary seine or were dip-netted. Each seine set and electrofishing pass constituted one unit of sampling effort. An effort was made to sample all habitat types with respect to depth, current velocity, and substrate. In areas of little or no current (e.g., backwaters), seine hauls were made. Additional backpack shocking along shorelines sampled brush, boulder, undercut bank, and tree root habitats; each 5-min-long sample was counted as one unit of effort. Sampling was repeated in each habitat until three successive passes produced no additional new species. We used boat electrofishing to sample along shorelines and channel sections of deep pools. Shocking runs, in a downstream direction, continued until two successive runs failed to collect any additional species in a given habitat. Each 10-min-long boat-shocking run was counted as two units of sampling effort. All captured fish, except young-of-the-year fishes were identified, counted, and examined for anomalies (parasites, deformities, etc.). Some fish were preserved in 10% formalin and kept as voucher specimens or for later laboratory verification. Temporal changes in the fish assemblage were assessed with the Tailwater Fish Index (TFI) (Scott, 1999). The TFI is a modification of the Index of Biotic Integrity (Karr *et al.*, 1986), and is composed of 12 metrics (Table III). Scores of all metrics are summed and the integrity of the fish assemblage is based on the total score (58–60 = excellent; 48–52 = good; 40–44 = fair; 28–34 = poor; ≤ 22 = very poor).

Table III. Metrics and scoring criteria used to calculate the Tailwater Fish Index (TFI)

Metric	Score		
	1	3	5
1. Total number of species	<19	19–37	>37
2. Number of darter species	<4	4–6	>6
3. Number of sunfish species	<3	3–4	>4
4. Number of sucker species	<3	3–5	>5
5. Number of intolerant species	<4	4–8	>8
6. Tolerant species (%)	>40	20–40	<20
7. Omnivores + generalists (%)	>50	25–50	<25
8. Specialist insectivores (%)	<15	15–30	>30
9. Piscivores (%)	<2	2–5	>5
10. Catch-per-unit-effort	<6	6–11	>11
11. Hybrids (%)	>1	0.5–1	<0.5
12. Anomalies (%)	>5	2–5	<2

Mussel translocations and sampling

All species selected for translocation occur in the Tennessee River system; most species were historically found in the lower French Broad River, but a few species were not part of the historic fauna. Historically, ecological barriers (but not geomorphic or physical) existed in the Tennessee River that limited the upstream distribution of these species; following impoundment of the Tennessee River, these barriers no longer seem to exist as several species (including those we translocated) originally restricted to the lower Tennessee River have established populations several hundred kilometers upstream of their historical occurrence (Hughes and Parmalee, 1999). At least one of these species, the pistolgrip (*Quadrula verrucosa*), had colonized the French Broad River prior to our study. After consultation with state and federal agencies, a joint decision was made to translocate the few species not historically found in the French Broad River because of their ongoing upstream movement within the Tennessee River and because of the threat posed by the invasion of zebra mussels in the Tennessee River System. The French Broad River will likely remain a refuge for mussels from the zebra mussel invasion because barge traffic, a primary vector for upstream movement of zebra mussels in the Tennessee River, is restricted to the lower 3 km of the French Broad River.

Prior to translocating mussels and periodically thereafter, we conducted qualitative searches by snorkeling to determine species composition of the resident mussel fauna. To establish populations of unlisted mussel species and evaluate conditions for reintroducing endangered mussels, we collected mussels periodically from the lower Tennessee River in western Tennessee (Figure 1) while wading in shallow water or by SCUBA diving in deeper areas. Mussels were placed in coolers, covered with wet burlap, and transported to the laboratory where they were hand-scrubbed with wire brushes to remove any zebra mussels, and then quarantined for 30 days. In 1997, we translocated mussels that had been quarantined for 30 days in 1136 L tanks under static conditions, and then maintained in long-term holding facilities for $\geq$1 year as part of another study (Quinn, 2002). Subsequently, mussels translocated were quarantined for 30 days in a re-circulating system consisting of two 1136 L tanks, a sump, a biofilter, and pump. About 2 weeks before quarantining mussels, we inoculated the biofilter with filter material from a similar recirculating system used for maintaining fish. At the same time, we introduced about 50 fish (mixed species) into the quarantine tanks to maintain the bacterial culture; all fish were removed from the system when mussels were introduced. Mussels were fed live algae (*Bracteococcus grandis)* at an average rate of 1.4 mg (dry weight) per mussel every 2–3 days. Following quarantine, mussels were visually examined for zebra mussels before they were translocated to the French Broad River. Subsamples were moved to Center Hill Lake in central Tennessee where they were held in pocket nets for 12–17 months to monitor post-quarantine survival. Prior to translocation, mussels were marked with a power rotary tool (Morgan *et al*., 1997), or shellfish tags were attached with cyanoacrylate glue (Lemarié *et al*., 2000).

In 1997, we established two rectangular plots (250 m^2 and 120 m^2) located adjacent to Campbell Island (rkm 13). Corners of each plot were marked for the duration of the study by concrete blocks. Prior to translocating mussels, we drove steel rods into the substrate adjacent to the blocks, attached tape measures, and then delineated a grid consisting of 1-m^2. We inserted mussels into the substrate in nearly equal numbers into each 1 m^2 within each plot.

From 1998 through 2000, mussels were translocated to five rectangular plots established at the head of Seven Islands (rkm 24). Plot sizes varied from 170 to 250 m^2 and were determined by the number of mussels available and our desire to achieve a density of 10–12 mussels/m^2. We marked out 1-m-wide lanes the length of each plot and translocated nearly an equal number of mussels throughout each lane. In 1999, we used these same methods to translocate mussels to one plot (180 m^2) at Johnson Island (rkm 18) where plot size was limited by accessibility to suitable habitat.

We evaluated mussel survival at 1-year intervals following translocation with a stratified random sampling design. We drove steel rods into the substrate adjacent to each of the concrete blocks marking the plot corners and attached tape measures. A random numbers table was used to generate sampling points. At each point, a quadrat (1 m^2 for plots 1 and 2; 0.25 m^2 for plots 3–8) was laid on the substrate by snorkelers, the substrate was hand-excavated, and all mussels were identified and examined for marks before returning them to the river; unmarked individuals were considered to be resident mussels. On several occasions, we qualitatively searched the substrate downstream of each plot for dead and live mussels.

Between 1999 and 2003, we attempted to introduce three species of mussels by stream-side infestations of their glochidia on host fishes. Gravid pheasantshell (*Actinonaias pectorosa*), Cumberland moccasinshell (*Medionidus conradicus*), and fluted kidneyshell (*Ptychobranchus subtentum*) were collected from the Clinch River, Tennessee, and transported in coolers to the French Broad River. A hypodermic syringe filled with water was inserted into the marsupial gills and glochidia were flushed out (Waller *et al*., 1985). Host fishes were collected by electrofishing at Seven Islands on the French Broad River. Glochidia were then poured into a bucket containing the fish and about 4 L of river water. Fish were exposed to the glochidia for 30–45 min, and then released at the collection site. Each year after the initial infestations, we searched for juveniles at the site by snorkeling and hand-digging the substrate to a depth of 2–3 cm.

RESULTS

Fish assemblage

The construction and operation of Douglas Dam devastated the fish assemblage of the lower French Broad River. In 1977, only 42 of the original 100 species were collected at 12 sites (Harned, 1979; Table I). Lampreys, sturgeon, and paddlefish were not collected, and relatively few species of cyprinids, catostomids, and percids were collected in 1977. Following initiation of minimum flows and testing of aeration techniques (1988–1993), species richness increased; during this time, 14 species of fish colonized the tailwater (Figure 2). After 1993 when the aeration techniques became fully operational, native fish diversity continued to increase. Between 1994 and 2002, we collected 78 native species (78% of the historical fauna), and 9 introduced species in the tailwater (Table I). Although sampling effort varied among years, effort was not correlated with species richness ($r = 0.24$; $p = 0.17$); however, species richness was positively correlated with year ($r = 0.97$; $p < 0.0001$). Many of the species colonizing the tailwater during this period included those that we considered to be relatively intolerant of low DO and zero minimum flows such as lampreys, catostomids, and percids. Re-colonization of darters (*Etheostoma* spp. and *Percina* spp.) at the site closest to the dam (rkm 48) was slow. At this site, no darters were collected in 1988, and only one species was found in 1992; however, seven darter species were collected in 2002. Although we collected many of

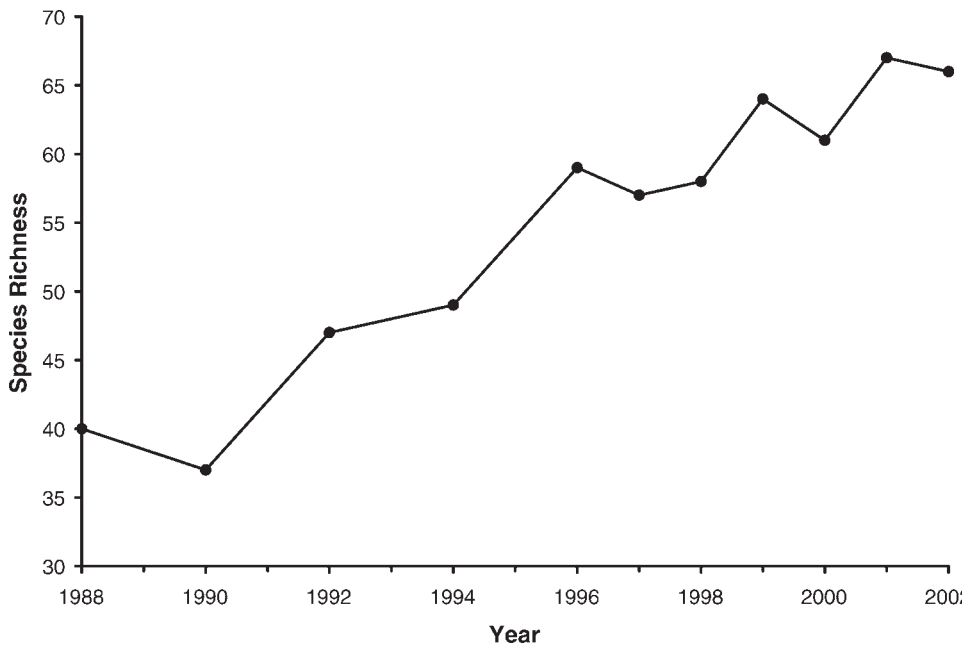

Figure 2. Changes in fish species richness in the lower French Broad River following institution of a minimum flow and oxygenation of the discharge from Douglas Dam

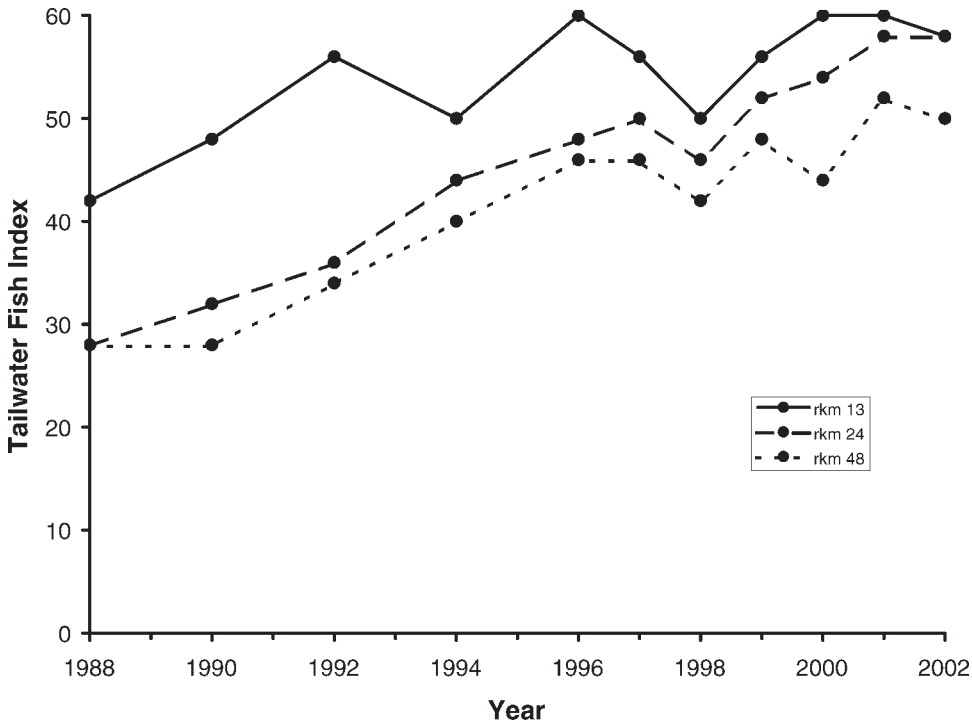

Figure 3. Tailwater Fish Index (TFI) scores for three sites on the lower French Broad River downstream of Douglas Dam following institution of a minimum flow and oxygenation of the discharge

the cyprinid species that occurred historically in the French Broad River, only a few individuals represented several of these species.

The TFI showed a dramatic improvement in the overall fish assemblage at our three permanent sampling sites (Figure 3). Increases in TFI values were temporally associated with distance from Douglas Dam. At the site farthest from the dam (rkm 13), TFI values improved from 42 (fair) in 1988 to 60 (excellent) in 8 years and have remained in the excellent range. At rkm 24, TFI values increased from poor in 1988 to excellent in 2001. At rkm 48, improvements in the fish assemblage increased from poor to good.

Resident mussel fauna

During qualitative searches and in our quadrat sampling for translocated mussels, we found 12 species of mussels alive, including the federally-listed endangered pink mucket (*Lampsilis abrupta*), and a fresh-dead shell of an additional species, the Tennessee pigtoe (*Fusconaia barnesiana*) (Table II). At Campbell Island (rkm 13), few live or dead indigenous mussels were found. In contrast, extensive mussel beds occurred over a 2.5 km stretch of river at Seven Islands (rkm 28). These extant mussel beds consisted primarily of very large (121–170 mm long) elephantears (*Elliptio crassidens*). The size and eroded condition of the elephantears and most other species found suggest they were living when Douglas Dam was constructed; however, recent (<5 years) recruitment was evident for the fragile papershell (*Leptodea fragilis*), pink heelsplitter (*Potamilus alatus*), pimpleback (*Quadrula pustulosa*), and the nonindigenous pistolgrip. Additionally, we judged the single fresh-dead Tennessee pigtoe that we collected to be about 5 years old. Throughout our study we did not see any evidence that zebra mussels had colonized the river.

Mussel translocations

Prior to quarantine, infestations of zebra mussels on native mussels collected from the lower Tennessee River were rare ($\sim$1 zebra mussel/1000 unionids). Mean survival during quarantine varied from 87% to 100% among species (Table IV). Following quarantine, no zebra mussels were found on any unionid. Long-term (12–17 months)

Table IV. Numbers and percent survival of mussels following quarantine in recirculating systems

Species	Number quarantined	Mean percent survival (±SE)	
		30 days	12–17 months
Amblema plicata	1433	98.0 ± 1.5	88.0 ± 0.0
Cyclonaias tuberculata	2188	98.7 ± 0.4	96.3 ± 1.8
Ellipsaria lineolata	45	87.5 ± 12.5	50.0 ± 0.0
Elliptio crassidens	1	100	100
Fusconaia ebena	2916	92.0 ± 5.0	77.0 ± 0.2
Fusconaia flava	173	99.0 ± 0.0	—
Megalonaias nervosa	192	100	100
Obliquaria reflexa	168	91.3 ± 6.3	40.5 ± 15.5
Quadrula metanevra	1422	99.7 ± 0.2	97.3 ± 1.2
Quadrula pustulosa	3308	89.5 ± 2.6	82.0 ± 4.6
Quadrula verrucosa	11	100	100
Truncilla truncata	9	89.0 ± 0.0	—

survival of mussels held at Center Hill Reservoir ranged from 77% to 100% for eight species, but was ≤ 50% for two species. In all, we translocated 19 754 adult mussels of 18 species into the 8 plots (Table V). At rkm 13, 12 mussels were introduced into every 1 m^2 of plot 1, and either 11 or 12 individuals were translocated into each 1 m^2 in plot 2. One year after translocation, estimated densities of live mussels within these plots were 55% (plot 1) and 52% (plot 2) of the densities translocated (Table VI). Mean density (±SE) of dead mussels in plot 1 was $0.76 \pm (0.18)/m^2$, and $1.00\ (\pm 0.25)/m^2$ in plot 2. Thus, recovery of translocated mussels averaged 61% for both plots.

In contrast to the initial equal distribution of mussels ($12/m^2$) translocated into plot 1, the distribution of mussels in 1 m^2 quadrats samples was highly contagious; samples contained 0–19 individuals, indicating active or passive movement. Moreover, the distribution of mussels in quadrat samples continued to change in subsequent years (χ^2, $p < 0.05$), indicating that mussels continued to move after the first year. This movement was not confined to the translocation plots. Four years after translocation, we found 76 live and 62 dead mussels in qualitative searches immediately downstream of plots 1 and 2. In both plots, estimated densities of live resident mussels were $\leq 0.01/m^2$.

Table V. Numbers of each species of mussel translocated to plots on the lower French Broad River

Species	Plot and number of mussels							
	1	2	3	4	5	6	7	8
Amblema plicata	410	140	293	134	—	1354	18	329
Cyclonaias tuberculata	550	155	542	687	419	16	592	365
Ellipsaria lineolata	—	—	—	—	—	21	—	201
Fusconaia ebena	771	40	687	432	1568	—	970	570
Fusconaia flava	—	—	72	—	—	165	—	20
Megalonaias nervosa	—	—	—	—	—	186	—	107
Obliquaria reflexa	—	265	—	—	—	94	—	45
Quadrula metanevra	400	295	277	473	157	2	438	247
Quadrula pustulosa	871	465	1009	934	302	171	945	275
Other species[1]	—	—	30	7	70	12	8	87
Total	3002	1360	2910	2667	2516	2023	2971	2246
Plot size (m^2)	250	120	250	250	250	170	180	200

[1]Includes: 2 *Arcidens confragosus*; 85 *Elliptio crassidens*; 70 *Lampsilis fasciola*; 1 *Leptodea fragilis*; 5 *Ligumia recta*; 7 *Pleurobema cordatum*; 30 *Potamilus alatus*; 7 *Quadrula verrucosa*; 7 *Truncilla truncata*. Additionally, 59 *Ligumia recta* were introduced outside the borders of plot 4, and therefore are not included in total.

Table VI. Density of mussels translocated to each plot on the lower French Broad River and estimated mean density with 95% CIs following translocation. Lower recoveries are due both to mortality and to mussel emigration

Translocation			Year and estimated mean density (95% CI)				
Plot	Year	Density (mussels/m^2)	1998	1999	2000	2001	2002
1	1997	12.00	6.60 (4.47–8.73)	6.52 (4.39–8.65)	6.16 (4.64–7.68)	4.12 (3.00–5.24)	—
2	1997	11.33	5.92 (4.67–7.16)	4.58 (3.32–5.85)	3.75 (2.35–5.15)	2.50 (1.50–3.50)	—
3	1998	11.64	—	7.60 (5.83–9.37)	10.24 (8.07–12.41)	12.96 (10.87–15.05)	9.20 (6.80–11.60)
4	1999	10.67	—	—	11.57 (9.15–14.00)	11.17 (9.25–13.09)	—
5	1999	10.06	—	—	—	9.70 (7.17–12.23)	3.20 (2.01–4.39)
6	2000	11.90	—	—	11.29* (8.03–14.56)	8.73 (6.38–11.07)	—
7	1999	16.51	—	—	11.33 (7.68–14.99)	9.11 (6.78–11.44)	—
8	2000	11.23	—	—	—	7.69 (5.73–9.65)	4.10 (2.87–5.33)

*Mussels were translocated in May and sampled 5 months later.

At Seven Islands (plots 3–6, and 8), densities of live mussels estimated 1 year after translocation varied from 65% to 108% of the densities translocated into each plot (Table VI). Densities of dead translocated mussels were ≤ 0.5 individuals/m^2 in all plots at Seven Islands. Estimated densities of live resident mussels varied from 0.05 to 2.5/m^2 among the five plots at Seven Islands. Retention (mean density) of live mussels on all sites 2 years after translocation was positively correlated with density of live resident mussels ($r = 0.84$; $p < 0.05$). This relationship seemed to persist throughout the study. In three plots sampled for 4 years, retention of live translocated mussels was 22% and 34% in two plots where densities of resident mussels were ≤ 0.01/m^2 but retention was 79% in plot 3 where the density of resident mussels was 2.5/m^2.

From 1999 to 2002, we infested 202 banded sculpins (*Cottus carolinae*) with glochidia of pheasantshells, 581 redline darters (*Etheostoma rufilineatum*) with glochidia of Cumberland moccasainshells, and 18 redline darters with glochidia of fluted kidneyshells. In 2002, no juveniles of these three species were found during a search of the substrate in the area where infested fish were released.

DISCUSSION

Prior to instituting a minimum flow release, operation of Douglas Dam as a peaking hydroelectric project resulted in dewatering of riffles and shallow shoreline areas during periods of no generation, and bank-full flows during peak generation. Daily peaking operations result in the amount and location of suitable fish habitat to be in a state of constant flux (Gore *et al*., 1989). Operating Douglas Dam as a peaking project for 35 years resulted in an impoverished fish fauna. Harned (1979) sampled 12 sites below Douglas Dam by a variety of methods, including rotenone, and collected only 42% of the historic fish assemblage in 1977. Species composition was similar 11 years later when we collected 40% of the historical fauna.

The establishment of a minimum flow and oxygenation of the discharge from Douglas Dam did much to restore the fish fauna to the lower French Broad River. Since 1988, we have collected 82% of the fish species historically occurring in the lower French Broad River. This twofold increase in species richness over a 14-year-long period clearly demonstrates that if there is connectivity between source populations and improved tailwater conditions, natural fish recolonization is possible and most of the historical fauna will re-colonize the tailwater in a relatively short time.

It is possible that we did not collect all rare fish species present; however, Howard (2000) sampled 14 sites every other month in 1999 and failed to collect any species that we did not collect. The 18% of the historical fauna that has not re-colonized the lower French Broad River consists primarily of two groups of fishes. One group consists of those species (e.g., Alabama shad, *Alosa alabamae*) that have either been extirpated from the entire Tennessee River system or are isolated from the lower French Broad River. The second group includes cyprinids such as the warpaint shiner (*Luxilus coccogenis*) that inhabit the mid-water column. Although we did collect several

mid-water cyprinid species, they were uncommon in our samples. The minimum flow release during periods of no generation has been effective in providing diverse habitats and suitable conditions for many of the 36 fish species that have re-colonized the river. Nonetheless, the continued operation of Douglas Dam as a peaking hydroelectric facility continues to impact the fish fauna. During full generation, there are few velocity refugia, a likely limiting factor for mid-water column species. Furthermore, the bank-full flows eliminate most shallow water habitats that are important as nursery areas (Holland, 1986; Scheidegger and Bain, 1995). In the French Broad River, loss of these nursery areas or nest destruction during peak generation may limit recruitment of many species (Farmer, 2001).

The historically rich mussel fauna of the lower French Broad River was also drastically reduced by the construction and operation of Douglas Dam; however, poor land-use practices starting with clearing of the forested watershed were a contributing factor (Hughes and Parmalee, 1999). Only 12 of the original 53 species remain in the tailwater. The effects of construction and operation of dams on mussel populations have been well documented (Williams *et al*., 1992; Layzer *et al*., 1993; Heinricher and Layzer, 1999; Vaughn and Taylor, 1999). Hydroelectric peaking operations are particularly harmful to mussels because of the alternate aerial exposure of shoals at low discharge and the scouring action of high flows during periods of electric power generation (Layzer *et al*., 1993). Discharge of anoxic water from Douglas Dam likely exacerbated the stress of aerial exposure on mussels.

Retention of translocated mussels varied greatly among plots, and downstream dispersal was evident. Downstream movement of mussels has been common in other translocation studies (e.g., Layzer and Gordon, 1993; Dunn, 1993; Morgan *et al*., 1997). Selection of sites to re-establish mussel populations is problematic. There are no widely accepted criteria for selecting sites to re-establish mussel populations. Microhabitat variables such as water depth and velocity tend to be poor predictors of natural mussel distributions (Strayer, 1981; Holland-Bartels, 1990; Strayer and Ralley, 1993), whereas complex hydraulic variables such as shear stress are better predictors (Layzer and Madison, 1995; Hardison and Layzer, 2001). Moreover, Strayer (1999) demonstrated that mussel beds occur in areas of hydraulic refuge with substrates that are stable during flood events; immediately adjacent to these beds, few mussels occur.

In the French Broad River, the size and eroded condition of most resident mussels suggest that they were present when Douglas Dam was constructed in 1943. Consequently, their distribution, particularly at Seven Islands (rkm 24) where densities reached $2.52/m^2$, probably reflect the location of existing hydraulic refugia, and perhaps the locations of some of the original mussel beds. While we did not measure microhabitat variables, substrate composition appeared to be composed primarily of gravel and rubble in all translocation plots, and during minimum flow there were no observable differences in water depths or velocities. Nonetheless, densities of resident mussels varied greatly among plots. Moreover, the positive correlation between resident mussel densities and retention of translocated mussels suggests differences in habitat (presumably hydraulic conditions) among plots. The scope of our study did not include determining specific habitat criteria for identifying sites for re-establishing mussel beds in other rivers. Nevertheless, based on the results of our study, we believe that future attempts to re-establish mussels in other streams will be most successful if translocations occur at sites of existing or historical beds.

PROGNOSIS FOR RE-ESTABLISHING THE HISTORICAL FAUNA

Re-establishment of fish and mussel populations requires suitable water quality, and habitat conditions that are temporally stable. Although the established minimum flow and increased DO concentrations released from Douglas Dam maintain good habitat conditions in shoal and riffle areas during periods of nongeneration, the continued operation of Douglas Dam as a peaking hydroelectric project remains a formidable obstacle to restoring viable populations of some fish and many mussel species that historically occurred in the lower French Broad River. During our study, the number of fish species in the lower French Broad River doubled since inception of minimum flows and oxygenation of the discharge; however, there remains an under-representation of some habitat guilds. In particular, the occurrence and abundance of mid-water column cyprinids is limited. While slow-moving pools, backwaters, and quiescent stream margins are prevalent during minimum flow conditions, these areas largely disappear during peaking flows, leaving little suitable habitat for mid-water cyprinids. Restoration of abundant populations of these cyprinids is unlikely to occur unless the discharge regime of Douglas Dam is changed to a run-of-the-river operation.

Clearly, mussel species relying on cyprinids that occupy the mid-water column, as hosts for their larvae (glochidia), cannot be re-established unless their hosts are present; however, the effects of hydroelectric peaking operations on mussels are more insidious. The large volume of water discharged during peaking operations dilutes mussel sperm concentrations in the water column, and may reduce egg fertilization rates. The glochidia of all extirpated mussel species are obligate parasites on fish, and many are host specific. During peak discharge, host fishes may move into hydraulic refugia that contain few mussels. Thus, glochidia released into the water column may have a reduced probability of contacting and infesting these fishes. Conversely, host fishes that become infested during minimum flows may move into hydraulic refugia during peak discharge where juveniles excyst, but these areas may not be suitable mussel habitat. Furthermore, juveniles excysting over suitable habitat during peak discharge may not be able to settle because of high shear stress (Layzer and Madison, 1995). Since velocity refugia for small, benthic fishes may exist in habitat suitable for mussels during peak discharges (see Gore *et al*., 1989), the re-establishment of mussel species that use benthic fishes as hosts may be most likely.

In the absence of empirical data on reproductive success of specific mussel species in peaking hydroelectric tailwaters, we based our judgment of the likelihood of re-establishing extirpated mussel species and maintaining resident species based on the occurrence, abundance, and habitat of their known (or in some cases suspected) host fishes, and availability of potential donor populations for translocation or propagation. For instance, we assigned a prognosis of 'good' for the probability of re-establishing mussel species such as the endangered oyster mussel (*Epioblasma capsaeformis*) and birdwing pearlymussel (*Lemiox rimosus*) that utilize as hosts, some of the most abundant benthic fishes (i.e., banded sculpin and banded darter, *Etheostoma zonale*) present in the lower French Broad River (Table II). Moreover, sizable populations of these two mussel species exist within the Tennessee River drainage. We assigned a prognosis of 'poor' to those mussel species where the availability of a donor population is limited or their glochidial hosts occupy the mid-water column. For instance, we consider the probability of re-establishing a population of the endangered ringpink (*Obovaria retusa*) to be poor because the last known population is in the Green River, Kentucky, where it seemingly is on the brink of extinction. In all, we judged that 30 species of mussels can be re-established, but it is unlikely that 16 species can be re-established under the existing discharge regime (Table II). Furthermore, the future composition of the mussel fauna will likely include some species that were not part of the original fauna; the nonnative pistolgrip has already colonized the lower French Broad River. Other species such as the washboard (*Megalonaias nervosa*) have moved >600 km up the Tennessee River since impoundment (Scruggs, 1960), and may continue their upstream movement into the French Broad River. Additional species listed by Hughes and Parmalee (1999) as recent invaders of the Tennessee River may also colonize the French Broad River. Thus, whether or not species of historical occurrence are introduced, the future composition of the mussel assemblage will differ markedly from the historical one because of invading, nonindigenous species and the previous global extinction of others.

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