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Freshwater mussel assemblage structure in a regulated river in the Lower Mississippi River Alluvial Basin, USA†

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ABSTRACT

1. This paper documents a diverse, reproducing freshwater mussel community (20 species) in Lower Lake — an impounded, regulated portion of the Little Tallahatchie River below Sardis Dam in Panola Co., Mississippi, USA.

2. Despite being regulated and impounded, the lake has a heterogeneous array of habitats that differ markedly in mussel community attributes. Four distinct habitat types were identified based on current velocity and substrate characteristics, representing a gradient from habitats having lotic characteristics to lentic habitats. All four habitat types supported mussels, but habitats most resembling unimpounded, lotic situations (relatively higher current velocity and coarser substrate) had the highest mussel abundance and species density (10.1 mussels m^{-2}, 1.8 species m^{-2}, respectively). Lentic habitats (no flow, fine substrate) were characterized by lower abundance and species density (2.0 mussels m^{-2}, 0.8 species m^{-2}, respectively), but supported mussel assemblages distinctive from lotic habitats.

3. Evidence of strong recent recruitment was observed for most species in the lake and was observed in all four habitat types.

4. Although impounded and regulated, Lower Lake represents one of the few areas of stable large-stream habitat in the region. The presence of a diverse, healthy mussel community in this highly modified habitat suggests that a large component of the regional mussel fauna is relatively resilient and adaptable and is limited primarily by the absence of stable river reaches. Management actions that increase stream stability are likely to result in expansion of the mussel fauna and restoration of a valuable component of ecosystem function in this region.
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KEY WORDS: mussels; Unionidae; reservoir tailwaters; recruitment; habitat stability; impoundment; channel incision

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INTRODUCTION

The Lower Mississippi River Alluvial Basin supports one of the most diverse temperate freshwater faunas on Earth, but aquatic resources in this region are severely affected by recent human activities and the Basin is considered one of the most endangered ecosystems in the United States (Noss *et al.*, 1995). Stream habitat throughout much of this region is highly altered by channelization, impoundment, effects of intensive agriculture, and catastrophic stream channel erosion (Jackson and Jackson, 1989; Shankman, 1999; Shields *et al.*, 2000). Consequently, remnant freshwater mussel communities are few and scattered (Miller *et al.*, 1992; Hartfield, 1993) and often occur in regulated or highly modified stream reaches (Cooper and Johnson, 1980). In upland regions of eastern North America and Europe, the relationship of mussel distribution and abundance to physical habitat variables has received considerable attention in recent years (e.g. Holland-Bartels, 1990; Strayer and Ralley, 1993; DiMaio and Corkum, 1995; Hastie *et al.*, 2000; McRae *et al.*, 2004), and results of this work inform conservation strategies for mussels in these areas (Layzer and Madison, 1995; Heinricher and Layzer, 1999; Hastie *et al.*, 2003). Similar studies are lacking for lowland stream systems that harbour mussel communities distinct from upland streams. Effective conservation of mussel resources in the Lower Mississippi River Alluvial Basin requires knowledge of habitat affinities of mussels in lowland streams in this region.

The history and extent of stream degradation in the Little Tallahatchie River, Mississippi, USA, is typical of many stream systems in the Lower Mississippi River Alluvial Basin. Clearing of hillsides for row-crop production coupled with the highly erodible nature of soils in the basin initiated catastrophic soil erosion that resulted in the filling of stream channels with as much as 5 m of sediment (Schumm *et al.*, 1984). To relieve the resulting frequent flooding, nearly the full length of the upper mainstem and most major tributaries were channelized beginning in the 1930s. Channelization subsequently initiated a cycle of headcutting and channel destabilization as streams adjusted to the lowered base level (Shields *et al.*, 1994). Sardis Dam was constructed in 1940 on the mainstem in the central portion of the drainage, and at full capacity impounds approximately 119 km of the river. Downstream of Sardis Dam and Lower Lake the Little Tallahatchie River is unimpounded, but the seasonal hydrograph is altered substantially by dam release for flood control, resulting in high, scouring flows in late summer and fall as the reservoir is drawn down to accommodate winter floodwater storage. Approximately 32 km downstream of Sardis Dam, the river is diverted through the Panola Quitman Floodway, a large drainage canal, which dewaters the remainder of the lower Little Tallahatchie River. This type of cumulative, basin-wide destruction of stream habitat is common in the Lower Mississippi River Alluvial Basin (Jackson and Jackson, 1989). Consequently, stable, large-stream mussel habitat is currently rare within the Little Tallahatchie River system and elsewhere in the region.

This paper describes attributes of a diverse mussel community occurring in a short section of the Little Tallahatchie River, and discusses the applicability of the results to the conservation of freshwater mussels and other aquatic resources in the Lower Mississippi Alluvial Basin.

STUDY AREA

The study site is an area known as Lower Lake on the Little Tallahatchie River, immediately downstream of Sardis Reservoir in Panola County, Mississippi, USA (34° 24′ N, 89° 48′ W; Figure 1). Lower Lake encompasses a short reach (about 2–3 km) of the old river channel and a large borrow pit that was a source of material for Sardis Dam, the largest earth-fill dam in the world when constructed in 1940. River flow is impounded in Lower Lake by a low-head dam at the lake outlet, impounding *ca* 156 ha. Water enters Lower Lake from the Sardis Dam spillway on the east side of the lake and flows in a roughly westerly

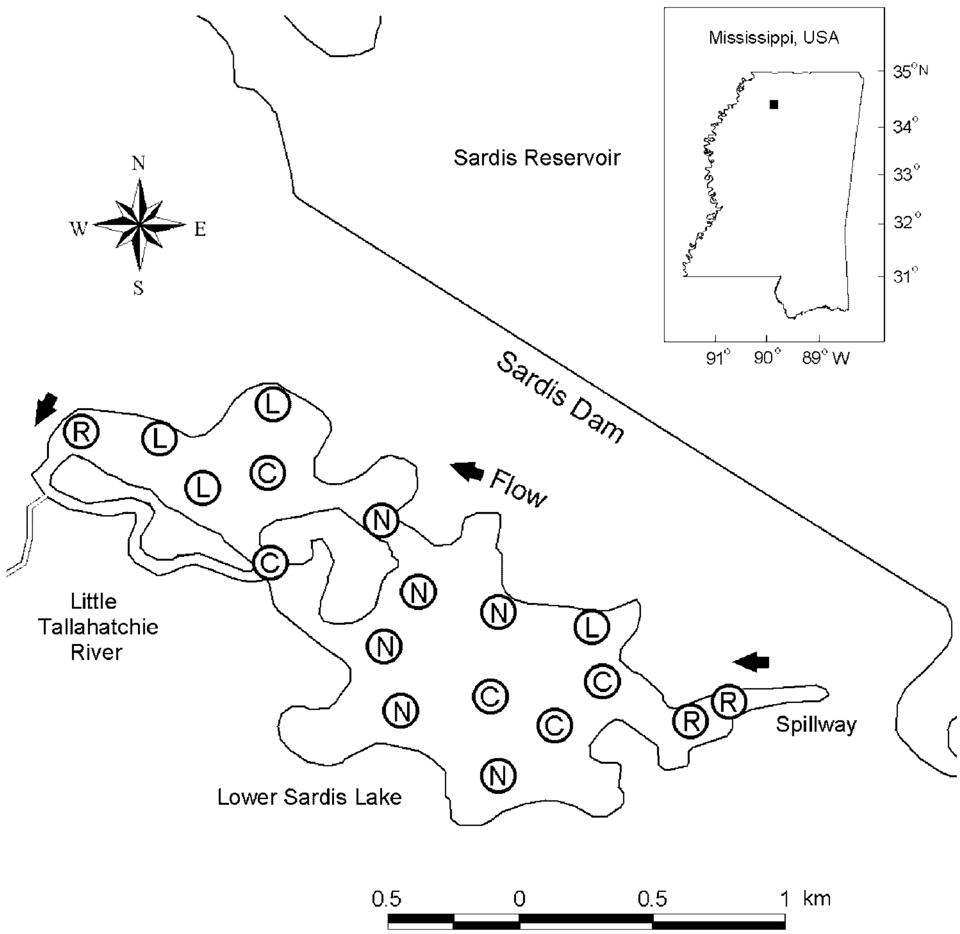

Figure 1. Map of Lower Lake, Sardis Reservoir, Little Tallahatchie River, Panola Co., MS. Circles indicate locations of paired, replicate subsamples from 18 sample points in the lake. Sample point abbreviations: R = riverine; C = open lake — current; N = open lake — no current; L = lentic backwaters. Arrows indicate general direction of flow in Lower Lake. Inset map shows location of Lower Lake and Sardis Dam in Mississippi.

direction to re-enter the unimpounded Little Tallahatchie River over the low-head dam at the lake outlet. Areas with higher current velocity resembling riverine conditions occur downstream of the spillway, immediately upstream of the lake outlet, and, to a lesser extent, in constricted areas adjacent to the large island in the centre of the lake. Because of the impounded nature of Lower Lake and the regulated input via Sardis Dam spillway, physical habitat conditions are relatively stable for most of the year. The primary deviations from habitat conditions described here occur during high release periods from Sardis Dam associated with gradual reservoir draw-down in fall to winter pool, and periodic closure of Sardis Dam for dam maintenance and inspection.

The Little Tallahatchie River system lies within the Mississippi Embayment section of the Gulf Coastal Plain physiographic province. Lower Lake is situated on Tertiary sediments of the North Central Hills, a few kilometres east of the Loess Bluffs that demarcate the eastern edge of the Mississippi Alluvial Plain.

METHODS

The mussel fauna of Lower Lake was sampled in August 1999. Sampling was conducted using a systematic sampling array developed by superimposing a grid of $180 \times 4\,km^2$ cells over a topographic map of the lake and designating sampling points at the centre of each cell (Figure 1). In the field, each sample point was located approximately using triangulation of landmarks evident on the map, and the boat was anchored at that point. In situations where the centre point of the cell fell on dry land or in shallow nearshore waters potentially exposed by low lake levels (less than *ca* 1 m depth), sample points were moved the minimal distance necessary to locate points in permanently inundated areas. At each sample point, depth was measured to the nearest 0.1 m and current velocity was characterized as: no perceptible current, slight current (0.02–$0.05\,m\,s^{-1}$), or strong current (0.08–$0.16\,m\,s^{-1}$) (Marsh McBirney Flo-Mate, model 2000 with wading staff extension rods, measurements taken at $0.4 \times$ depth; Gordon *et al*., 1992). Predominant substrate composition at each sample point was characterized visually as: silt, silty sand, clean sand, or sand-gravel. Gravel present in Lower Lake included fine to medium gravel (2–16 mm, Wentworth scale) as well as fine to medium-sized hard clay particles that resembled gravel.

Habitat at each sample point was classified *a posteriori* as one of four physical habitat types based on current velocity and substrate characteristics (e.g. Baker *et al*., 1991; Armantrout, 1998; Figure 1): (1) lentic backwaters (no current, silt substrate, $n = 4$), (2) open lake — no current (no current, silty sand substrate, $n = 6$), (3) open lake — current (slight current, clean sand substrate, $n = 5$), and (4) riverine (strong current, sand-gravel substrate, $n = 3$). Because depth was fairly uniform across the lake (mean depth = 3.0 m, range = 1.3–4.6), this variable was not used in later habitat classification. There was no difference in mean depth among the four habitat types (One-way ANOVA: $F = 1.097, P < 0.3831, \mathrm{df} = 3, 14$).

At each sample point two replicate mussel samples (subsamples) were taken, one on either side of the boat. Each subsample consisted of $2.5\,m^2$ of substrate excavated to a depth of 15 cm using a diver-operated gasoline-powered suction dredge. Mussels too large to enter the dredge hose (diameter = 80 mm) were hand-collected by the diver and combined with the dredge sample at the surface. During sample collection, other mussel species that were observed at each sample point but were outside of quantitative samples were recorded. Samples were transported to shore and mussels were retrieved by washing the substrate across a series of three sieves (smallest mesh size = 2.5 mm). This method allowed detection of all mussels in the sample including small juveniles and recent recruits. Each live mussel was identified and measured along the anterior–posterior axis to the nearest 0.1 mm with dial callipers. Mussels were preserved in 70% ethanol and voucher specimens were deposited at the Mississippi Museum of Natural Science, Jackson, MS.

Differences in overall mussel density (number of individuals m^{-2}, all species combined) and species density (number of species m^{-2}) among habitat types were tested using unbalanced, two-factor nested ANOVA (SAS Institute, 2000) with habitat type and sample points within habitat types considered fixed effects. Tukey's (HSD) multiple range test was used to perform multiple comparison tests among means. For ANOVA, mussel density and species density was $\log_{10}$-transformed to satisfy assumptions of normality and homogeneity of variance, and means and variance of these variables were reported for each habitat type using values re-transformed into linear scale. The total number of species found in each habitat type (presence/absence) was compiled using the results of quantitative sampling augmented by qualitative observations of species in particular habitat types. Species observed qualitatively but not found in quantitative samples were considered as present in that habitat but at densities below detectability by quantitative methods; these species were not included in any other analyses. Multi-response permutation procedures (MRPP; PC-ORD, McCune and Mefford, 1999) with Euclidean distances were used to test the hypothesis of no mussel assemblage differences among habitats (samples grouped by habitat). The MRPP is a nonparametric, randomization analogue of parametric procedures like discriminant analysis but has the advantage of not requiring distributional assumptions (Mielke and Berry, 2001). MRPP results are presented over all habitat types (34 subsamples $\times$ 17 species matrix grouped by habitat; two subsamples excluded because they had no mussels) and from all possible pairwise comparisons between habitat types. The chance-corrected within-group agreement statistic (A) was used to evaluate effect size. This statistic is independent of sample size and describes within-group homogeneity. A sequential Bonferroni procedure (Quinn and Keough, 2002) with a p-value of 0.05 was used to control for Type I error in the pairwise analyses. Assemblage evenness among habitat types was calculated using Hurlbert's (1971) probability of an interspecific encounter. The index gives the probability that two randomly sampled individuals from the assemblage represent two different species (Gotelli and Entsminger, 2001).

To evaluate evidence of recent recruitment in the community, length–frequency histograms based on 2 mm size classes were plotted for the three most abundant species in Lower Lake (*Amblema plicata*, *Obliquaria reflexa*, and *Quadrula pustulosa*). To evaluate evidence of recent recruitment for all species encountered in quantitative samples, the percentage of individuals less than 25 mm in length was calculated for each species. Although growth trajectories vary widely among mussel species, 25 mm was chosen as a conservative upper size limit that encompasses individuals recruited to the populations within the last 2–3 yr for most species. In other studies, this size range included recruits and juveniles for five species (Haag, 2002) and was at or below the minimum size at maturity for eight species, including three present in Lower Lake (Haag and Staton, 2003). To examine potential differences in recruitment among habitat types, the overall percentage of individuals less than 25 mm was calculated for all species combined in each habitat type, and tabular values were used to construct 95% confidence intervals around these percentages (Rohlf and Sokal, 1969).

RESULTS

Mean overall mussel density (all species combined) in Lower Lake over all habitat types was 5.2 individuals m^{-2} but differed significantly among habitats ($F = 12.40, p < 0.0001, \mathrm{df} = 3, 18, R^2 = 0.75$). Mussel density among habitats increased along a gradient corresponding to increasing current velocity and substrate particle size (Table 1). Mussel density did not differ among samples within habitat units ($F = 1.27, p < 0.3135, \mathrm{df} = 14, 18$).

Twenty species of native bivalves occurred in Lower Lake, and all but three were recorded in quantitative samples (Table 1). The number of species encountered in each habitat type ranged from 9 to 19, and habitats with discernible flow (riverine and open lake — current habitats) had the highest total species richness. Mean species density over the study area was 1.4 species m^{-2} but differed significantly among habitats ($F = 3.90, p < 0.0262, \mathrm{df} = 3, 18, R^2 = 0.58$). Species density among habitats increased similarly to mussel density, along a gradient corresponding to increasing current velocity and substrate particle size (Table 1). Species density did not differ among samples within habitat units ($F = 0.92, p < 0.5591, \mathrm{df} = 14, 18$). In addition to native bivalves, the introduced Asian clam (*Corbicula fluminea*) was found throughout Lower Lake in all habitat types.

Mussel assemblages were distinctive among the four habitat types. Within-habitat homogeneity of mussel assemblages was significantly greater than expected by chance (MRPP, $A = 0.183, p < 0.00044$). Pairwise comparisons between habitat assemblages were all significant except for riverine versus open lake — current and open lake — current versus open lake — no current (Table 2). Pairwise effect sizes indicated riverine *vs.* lentic backwater habitats had the greatest differences in assemblages (Table 2).

Individual species differed in their distributions among habitats in Lower Lake. Assemblage evenness increased from flowing to non-flowing habitats (Table 1). Nine species occurred only in habitats with discernible flow (riverine and open lake — current habitats, Table 1), but riverine habitats and both open lake habitat types were dominated by *Q. pustulosa* and, to a lesser extent, by *A. plicata* and *O. reflexa*. Open lake — no current habitats were characterized further by prominence of *Lampsilis teres* which represented a high proportion of the assemblage only in this habitat type. Lentic backwaters were not dominated by any

Table 1. Distribution of freshwater mussel species among four habitat types in Lower Lake, Little Tallahatchie River, Panola Co., MS. 'P' denotes species that were present but not detected in quantitative sampling. For mean overall densities and mean species densities of each habitat type, values with the same superscripted number were not significantly different

Species	Proportion of mussel community			
	Habitat type			
	Riverine	Open lake with current	Open lake no current	Lentic backwaters
Arcidens confragosus	—	0.008	—	—
Amblema plicata	0.063	0.078	0.121	—
Anodonta suborbiculata	—	—	—	0.044
Fusconaia ebena	—	0.008	—	—
Lampsilis cardium	0.006	0.008	—	—
Lampsilis teres	0.038	0.023	0.187	0.044
Leptodea fragilis	0.031	0.008	0.066	0.130
Megalonaias nervosa	P	P	—	—
Obliquaria reflexa	0.151	0.141	0.121	0.087
Plectomerus dombeyanus	0.050	P	—	—
Potamilus ohiensis	P	P	—	—
Potamilus purpuratus	0.044	0.031	0.077	0.087
Pyganodon grandis	P	P	0.022	0.130
Quadrula pustulosa	0.597	0.609	0.396	0.130
Quadrula quadrula	P	0.047	0.011	0.044
Toxolasma parvus	—	P	—	—
Toxolasma texasensis	P	P	P	0.174
Tritogonia verrucosa	0.019	0.008	—	—
Truncilla donaciformis	P	0.016	—	—
Utterbackia imbecillis	P	0.016	—	0.130
Total number of mussels	159	128	91	23
Mean mussel density (no. m^{-2}, 95% c.i.)	10.1 (6.2–16.4)^{1}	5.1 (3.5–7.5)^{1,2}	3.5 (2.5–5.0)^{2,3}	2.0 (1.4–2.8)^{3}
Mean species density (no. m^{-2}, 95% c.i.)	1.8 (1.2–2.5)^{1}	1.6 (1.2–2.1)^{1}	1.2 (0.9–1.7)^{1,2}	0.8 (0.4–1.3)^{2}
Evenness (Hurlbert's PIE)	0.544	0.601	0.778	0.921

Table 2. Results of pairwise multi-response permutation procedure for mussel assemblages in four habitat types in the Little Tallahatchie River, Panola Co., MS. Effect size is the chance-corrected within-group agreement (A) that is independent of sample size. Observed p-values were compared with Bonferroni corrected p-values based on a significance level of $p<0.05$. Asterisks indicate significant differences and 'ns', no differences detected

	Open lake — current effect size (p-value)	Open lake — no current effect size (p-value)	Lentic effect size (p-value)
Riverine	0.072 (0.0773) ns	0.201 (0.00215)*	0.361 (0.00065)*
Open lake–current		0.020 (0.1591) ns	0.140 (0.00145)*
Open lake–no current			0.061 (0.00384)*

single species but were characterized by the prominence of several species that composed only a small percentage of assemblages elsewhere in Lower Lake (e.g. *Leptodea fragilis*, *Pyganodon grandis*, *Toxolasma texasensis* and *Utterbackia imbecillis*). In addition, *Anodonta suborbiculata* was found only in lentic backwaters. Eight species were found in all four habitats, but only five (*L. teres*, *L. fragilis*, *O. reflexa*, *Potamilus purpuratus*, and *Q. pustulosa*) occurred in all habitats in numbers detectable by quantitative sampling (Table 1).

There was evidence of strong recent recruitment for most species in Lower Lake. Length — frequency distributions for the three most abundant species in the lake (*A. plicata*, *O. reflexa*, and *Q. pustulosa*) revealed the presence of individuals in a wide range of size classes, including small individuals (< 12.0 mm) probably representing recent recruits (Figure 2). For 12 species, the percentage of individuals less than 25 mm in length ranged from 15% to 100%, and 10 of these had individuals less than or equal to 10.9 mm (Table 3). Five species had no individuals less than 25 mm length: *Arcidens confragosus*, *A. suborbiculata*, *Fusconaia ebena*, *Plectomerus dombeyanus*, and *Tritogonia verrucosa*.

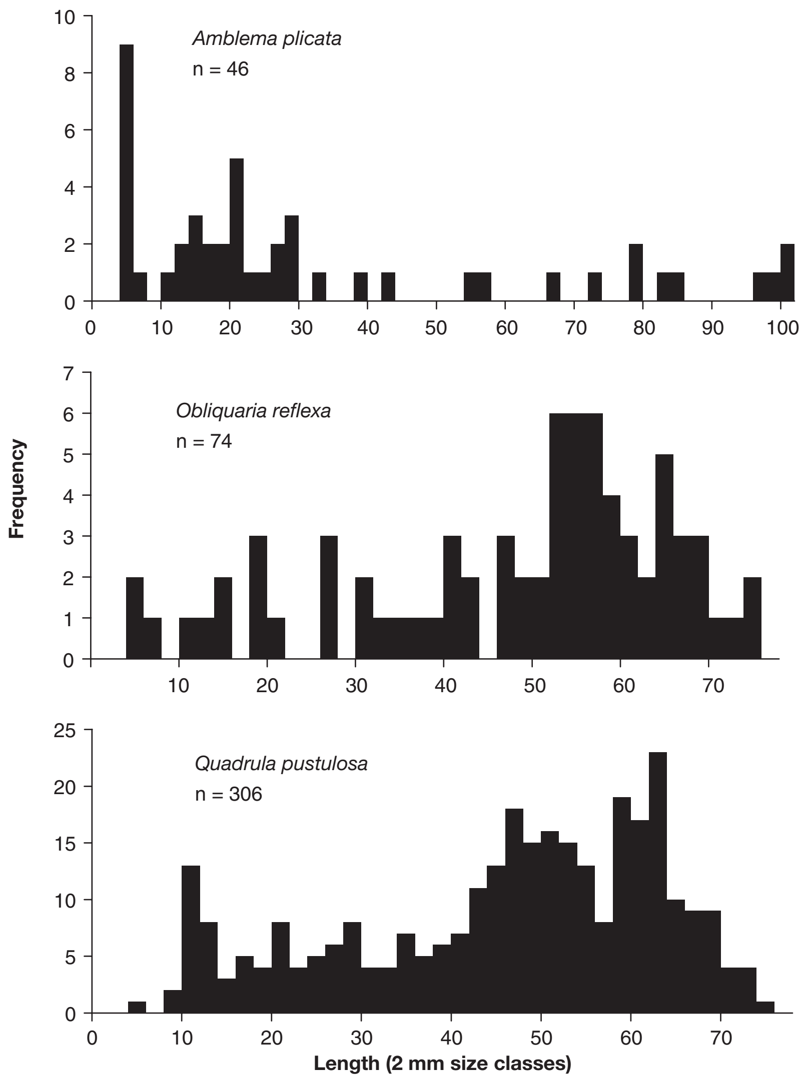

Figure 2. Length — frequency histograms for the three most abundant mussel species in Lower Lake, Little Tallahatchie River, Mississippi, in 1999.

Table 3. Evidence of recent recruitment for mussel species encountered in quantitative, whole-substrate samples from Lower Lake, Little Tallahatchie River, Panola Co., MS. Minimum size represents the smallest individual observed for a particular species

Species	*N*	Minimum length (mm)	% <25 mm	95% confidence interval
Arcidens confragosus	1	37.0	0	—
Amblema plicata	31	4.6	57	—
Anodonta suborbiculata	1	111.4	0	—
Fusconaia ebena	1	103.0	0	—
Lampsilis cardium	2	10.9	50	—
Lampsilis teres	27	5.6	71	—
Leptodea fragilis	15	8.0	65	—
Obliquaria reflexa	55	5.0	15	—
Plectomerus dombeyanus	8	26.5	0	—
Potamilus purpuratus	20	10.1	62	—
Pyganodon grandis	5	24.2	17	—
Quadrula pustulosa	212	5.7	16	—
Quadrula quadrula	8	4.2	20	—
Toxolasma texasensis	4	5.6	100	—
Tritogonia verrucosa	4	50.1	0	—
Truncilla donaciformis	2	8.7	100	—
Utterbackia imbecillis	5	20.5	40	—
Habitat type (all species)				
Riverine	159	—	19	14–24
Open lake — current	128	—	23	17–30
Open lake — no current	91	—	54	44–64
Lentic backwaters	23	—	44	21–61

Evidence of recent recruitment was observed in all four habitat types (Table 3). Percentage of individuals less than 25 mm in length was highest in habitats with no current (open lake — no current and lentic backwaters), but the 95% confidence interval for lentic backwaters overlapped with confidence intervals for both riverine and open lake — current habitats.

DISCUSSION

Even though regulated and impounded, Lower Lake supports a diverse, heterogeneous mussel community. Mussel abundance, species density, and assemblage composition differed markedly among different habitats in the lake; we interpret this result as evidence of strong spatial pattern given our coarse characterization of habitat. The habitat types identified fall along a gradient describing a transition from habitats having lotic characteristics to lentic habitats. Habitats most resembling unimpounded, lotic situations had the highest mussel abundance and species density. Lentic habitats were characterized by lower abundance and species density but supported mussel assemblages highly distinctive from lotic habitats. Similar differences in mussel community attributes among habitats occur in other large, impounded rivers. In the Tennessee and upper Mississippi rivers, the highest abundance and species richness occur in habitats which most resemble lotic habitats of unimpounded rivers (faster currents, coarser substrates) (Holland-Bartels, 1990; Ahlstedt and McDonough, 1993). In addition, species assemblages in lentic habitats in these rivers differ from those in lotic habitats but include many of the same species characteristic of lentic habitats in Lower Lake (e.g. *A. suborbiculata*, *L. fragilis*, *P. grandis*, and *U. imbecillis*). Predictable gradients of community organization

Table 4. Mussel diversity in unregulated Lower Mississippi River Alluvial Basin streams compared with Lower Lake, Little Tallahatchie River, Panola Co., MS

Stream, state	Number of mussel species	Source
Hatchie River, Tennessee	33	Manning, 1989
Big Black River, Mississippi	31	Hartfield and Rummel, 1985
Bayou Bartholomew, Louisiana	29	George and Vidrine, 1993
Wolf River, Tennessee	25	Kesler *et al*., 2001
Big Sunflower River, Mississippi	22	Miller *et al*., 1992
Lower Lake, Mississippi	20	this study

in large rivers across the central United States suggest the presence of strong, pervasive mechanisms of community structure that remain in effect even under the disrupting influences of impoundment.

Species diversity in Lower Lake is comparable to some of the highest quality, unregulated large streams in the Lower Mississippi River Alluvial Basin (Table 4). The fauna of Lower Lake differs from these streams primarily in that it is composed mostly of common, widespread species. No federally endangered or threatened species are present, and only two species known from Lower Lake are considered of conservation concern regionally or range-wide: *A. confragosus*, imperilled in Mississippi (Mississippi Natural Heritage Program, 2002), and *Lampsilis cardium*, special concern range-wide (Williams *et al*., 1993). The paucity of species of conservation concern in Lower Lake probably reflects the inability of these species to adapt to or persist in impounded conditions (Pringle *et al*., 2000). Most eastern tributaries of the Lower Mississippi River Alluvial Basin are severely degraded, and their mussel faunas are greatly reduced (Hartfield, 1993). Therefore, the presence of a diverse, large-stream mussel fauna, even one composed of common, widespread species, is significant from a regional biodiversity perspective.

In addition to its high diversity, the mussel community in Lower Lake is significant because most species are reproducing. Today, many mussel populations are dominated by older individuals, and evidence of recent recruitment is often rare, presumably because of human-induced habitat changes that have made conditions unfavourable for juvenile survival (Miller *et al*., 1992; Ahlstedt and McDonough, 1993; Layzer *et al*., 1993; Warren and Haag, 2005). In contrast, in Lower Lake there was evidence of strong recent recruitment for 12 of the 17 species encountered in quantitative sampling. For the remaining five species as well as the three species not found in quantitative samples, we have subsequently encountered young individuals of all species except *F. ebena* (Haag and Warren, unpublished data). Only a single individual of *F. ebena* was found, estimated to be greater than 48 yr old on the basis of the number of putative annuli in a shell thin-section from the specimen (Haag and Warren, unpublished data). This species may be a non-reproducing, pre-impoundment relict that has not adapted to present conditions in Lower Lake.

Although there was evidence of recruitment in all habitat types, the percentage of small individuals in the population was higher in habitats with no current. Rather than suggesting that no-current habitats are more favourable for mussel recruitment, differences in recruitment strength among habitats are better explained by differences in life histories among species. Species with the highest percentage of small specimens (e.g. *L. teres*, *L. fragilis*, *P. purpuratus*, and *T. texasensis*) were most common in no-current habitats. These species typically have higher fecundity, higher growth rates, and shorter lifespans (e.g. 5–12 yr) than species that dominate in Lower Lake habitats with current (e.g. *Q. pustulosa*, lifespan to at least 50 yr) (Haag and Staton, 2003; Haag, unpublished data). Fast-growing, short-lived species are expected to invest more energy in reproduction on an annual basis than long-lived species (Stearns, 1992; Winemiller and Rose, 1992), explaining the relatively higher levels of recent recruitment seen in no-current habitats.

The age structure and abundance of most species in Lower Lake suggest that these populations are currently stable. Demographic modelling showed that the population of *Q. pustulosa* in Lower Lake is stable or increasing, based on observed rates of recruitment, growth, and survivorship from 1999 to 2001

(Haag, 2002). The percentage of young individuals for other species in Lower Lake is similar to or greater than *Q. pustulosa*, indicating that these populations also may be self-sustaining. However, Lower Lake is isolated from the upper Little Tallahatchie River basin by Sardis Dam, and at least partially isolated from the lower basin by the low-head dam at the lake outlet and from the remainder of the Yazoo River system by the extent of highly degraded habitat in the lower river (Jackson and Jackson, 1989). Despite the healthy attributes observed for most species, isolation renders these populations vulnerable to local extinction by demographic or environmental stochasticity (e.g. Hastie *et al*., 2001) and human-caused perturbations (e.g. Brown *et al*., 2005; Warren and Haag, 2005), particularly those species represented by small populations (e.g. *A. confragosus*, *Megalonaias nervosa*, *Toxolasma parva*, *Truncilla donaciformis*).

Lower Lake supports a rare example of a stable, diverse large-stream mussel assemblage in a region that has experienced widespread stream habitat degradation. The presence of this assemblage in Lower Lake is remarkable given the regulated, impounded, and isolated nature of the habitat. Moreover, most of the habitat in Lower Lake was created during construction of Sardis Dam and was colonized by this mussel assemblage over the past 60 years. These observations suggest that, with the exception of several sensitive species absent from Lower Lake, much of the large stream mussel fauna of the Lower Mississippi River Alluvial Basin is resilient and adaptable when stable habitat is available. In upland streams, the availability of stable flow refuges protected from scour is one of the most important predictors of mussel occurrence (Vannote and Minshall, 1982; Layzer and Madison, 1995; Strayer, 1999; Hastie *et al*., 2000; Arbuckle and Downing, 2002). In lowland streams of the Lower Mississippi River Alluvial Basin and other areas naturally lacking hard substrates, the absence of stable substrate may be one of the major factors limiting mussel abundance and diversity, particularly in streams destabilized by human activities. Accordingly, management actions that increase stream stability and integrity such as modification of dam releases to mimic natural hydrographs more closely, restoring at least minimum flows to historical stream channels dewatered by diversion channels, and restoring and protecting riparian vegetation (Poff *et al*., 1997, Morris and Corkum, 1999; Pringle *et al*., 2000) will have positive impacts on mussel resources.

The potential for widespread improvement in aquatic habitat conditions throughout the Lower Mississippi River Alluvial Basin is great at this time. Most major stream channelization projects in the region occurred between the 1930s and the 1960s, thus recovery from these insults has been under way for at least 40 years. Re-establishment of natural channel features such as meanders and point bars and recruitment of woody debris is evident for a number of streams, and biological communities have responded positively to these improvements (Jackson and Jackson, 1989; Shields *et al*., 1997, 1998). In western tributaries of the Mississippi River in Arkansas, drainage canals created from the 1940s to the late-1960s have been colonized by at least 23 species of freshwater mussels (Ahlstedt and Jenkinson, 1991). Many of the large-scale landscape problems, such as massive erosion from hillside farming, that resulted in the initial need for stream channelization have been abated successfully (USDA Forest Service, 1988). Further, a phalanx of conservation initiatives and landowner incentive programmes sponsored by federal and state agencies and non-governmental conservation organizations is encouraging catchment restoration and a shift away from destructive engineering approaches to flood control in the region (Stanturf *et al*., 2000). In the absence of additional perturbations, many streams can be expected to continue their trajectories of stabilization and recovery from channelization and other impacts. In the Lower Mississippi River Alluvial Basin, stabilized stream reaches would have high potential for colonization by a diverse assemblage of native mussel species, restoring a valuable component of ecosystem function to the region.

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REFERENCES

Ahlstedt SA, Jenkinson JJ. 1991. Distribution and abundance of *Potamilus capax* and other freshwater mussels in the St. Francis River system, Arkansas and Missouri, U.S.A. *Walkerana* **5**: 225–261.

Ahlstedt SA, McDonough TA. 1993. Quantitative evaluation of commercial mussel populations in the Tennessee River portion of Wheeler Reservoir, Alabama. In *Conservation and Management of Freshwater Mussels*, Cummings KS, Buchanan AC, Koch LM (eds). Proceedings of a UMRCC Symposium, Upper Mississippi River Conservation Committee: Rock Island, IL; 38–49.

Arbuckle KE, Downing JA. 2002. Freshwater mussel abundance and species richness: GIS relationships with watershed land use and geology. *Canadian Journal of Fisheries and Aquatic Sciences* **59**: 310–316.

Armantrout NB (compiler). 1998. Glossary of aquatic habitat inventory terminology. American Fisheries Society, Bethesda, MD.

Baker JA, Killgore KJ, Kasul RL. 1991. Aquatic habitats and fish communities in the lower Mississippi River. *Reviews in Aquatic Sciences* **3**: 313–356.

Brown ME, Kowalewski M, Neves RJ, Cherry DS, Schreiber ME. 2005. Freshwater mussel shells as environmental chronicles: geochemical and taphonomic signatures of mercury-related extirpations in the North Fork Holston River, Virginia. *Environmental Science and Technology* **39**: 1455–1462.

Cooper CM, Johnson VW. 1980. Bivalve mollusca of the Yalobusha River, Mississippi. *The Nautilus* **94**: 22–24.

DiMaio J, Corkum LD. 1995. Relationship between the spatial distribution of freshwater mussels (Bivalvia: Unionidae) and the hydrological variability of rivers. *Canadian Journal of Zoology* **73**: 663–671.

George SG, Vidrine MF. 1993. New Louisiana records for freshwater mussels (Unionidae) and a snail (Pleuroceridae). *Texas Journal of Science* **45**: 363–366.

Gordon ND, McMahon TA, Finlayson BL. 1992. *Stream Hydrology: An Introduction for Ecologists*. John Wiley: Chichester.

Gotelli NJ, Entsminger GL. 2001. *EcoSim*: *null models software for ecology*, *Version 7.0*. Acquired Intelligence Inc. & Kesey-Bear. http://homepages.together.net/~gentsim/ecosim.htm

Haag WR. 2002. Spatial, temporal, and taxonomic variation in population dynamics and community structure of freshwater mussels. PhD thesis, University of Mississippi, Oxford, MS.

Haag WR, Staton JL. 2003. Variation in fecundity and other reproductive traits in freshwater mussels. *Freshwater Biology* **48**: 2118–2130.

Hartfield P. 1993. Headcuts and their effect on freshwater mussels. In *Conservation and Management of Freshwater Mussels*, Cummings KS, Buchanan AC, Koch LM (eds). Proceedings of a UMRCC symposium, Upper Mississippi River Conservation Committee: Rock Island, IL; 131–141.

Hartfield PD, Rummel RG. 1985. Freshwater mussels of the Big Black River, Mississippi. *The Nautilus* **99**: 116–119.

Hastie LC, Boon PJ, Young MR. 2000. Physical microhabitat requirements of freshwater pearl mussels, *Margaritifera margaritifera* (L.). *Hydrobiologia* **429**: 59–71.

Hastie LC, Boon PJ, Young MR, Way S. 2001. Effects of a major flood on an endangered freshwater mussel population. *Biological Conservation* **98**: 107–115.

Hastie LC, Cooksley SL, Scougall F, Young MR, Boon PJ, Gaywood MJ. 2003. Characterization of freshwater pearl mussel (*Margaritifera margaritifera*) riverine habitat using river habitat survey data. *Aquatic Conservation*: *Marine and Freshwater Ecosystems* **13**: 213–224.

Heinricher JR, Layzer JB. 1999. Reproduction by individuals of a non-reproducing population of *Megalonaias nervosa* (Mollusca: Unionidae) following translocation. *American Midland Naturalist* **141**: 140–148.

Holland-Bartels LE. 1990. Physical factors and their influence on the mussel fauna of a main channel border habitat of the upper Mississippi River. *Journal of the North American Benthological Society* **9**: 327–335.

Hurlbert SH. 1971. The nonconcept of species diversity: a critique and alternative parameters. *Ecology* **52**: 577–585.

Jackson DC, Jackson JR. 1989. A glimmer of hope for stream fisheries in Mississippi. *Fisheries* **14**: 4–9.

Kesler DH, Manning D, Van Tol N, Smith L, Sepanski B. 2001. Freshwater mussels (Unionidae) of the Wolf River in western Tennessee and Mississippi. *Journal of the Tennessee Academy of Science* **76**: 38–46.

Layzer JB, Madison LM. 1995. Microhabitat use by freshwater mussels and recommendations for determining their instream flow needs. *Regulated Rivers*: *Research and Management* **10**: 329–345.

Layzer JB, Gordon ME, Anderson RM. 1993. Mussels: the forgotten fauna of regulated rivers. A case study of the Caney Fork River. *Regulated Rivers*: *Research and Management* **8**: 63–71.

Manning D. 1989. Freshwater mussels (Unionidae) of the Hatchie River, a tributary of the Mississippi River, in West Tennessee. *Sterkiana* **72**: 11–18.

McCune B, Mefford MJ. 1999. *PC-ORD*. *Multivariate Analysis of Ecological Data*. MjM Software Design: Gleneden Beach, OR.

McRae SE, Allan JD, Burch JB. 2004. Reach- and catchment-scale determinants of the distribution of freshwater mussels (Bivalvia: Unionidae) in south-eastern Michigan, U.S.A. *Freshwater Biology* **49**: 127–142.

Mielke PW, Berry KJ. 2001. *Permutation Methods: A Distance Function Approach*. Springer Series in Statistics, Springer-Verlag: New York.

Miller AC, Payne BS, Hartfield PD. 1992. Characterization of a freshwater mussel (Unionidae) community in the Big Sunflower River, Sharkey County, Mississippi. *Journal of the Mississippi Academy of Sciences* **37**: 8–11.

Mississippi Natural Heritage Program. 2002. *Endangered Species of Mississippi*. Museum of Natural Science, Mississippi Department of Wildlife, Fisheries, and Parks: Jackson, MS.

Morris TJ, Corkum LD. 1999. Unionid growth patterns in rivers differing in riparian vegetation. *Freshwater Biology* **42**: 59–68.

Noss RF, Laroe ET, Scott JM. 1995. Endangered ecosystems of the United States: a preliminary assessment of loss and degradation. Biological Report 28, US Department of the Interior, National Biological Survey, Washington, DC.

Poff NL, Allan JD, Bain MB, Karr JR, Presegaard KL, Richter BD, Sparks RE, Stromberg JC. 1997. The natural flow regime: a paradigm for river conservation and restoration. *BioScience* **47**: 769–784.

Pringle CM, Freeman MC, Freeman BJ. 2000. Regional effects of hydrologic alterations in the New World: tropical-temperate comparisons. *BioScience* **50**: 807–823.

Quinn GP, Keough MJ. 2002. *Experimental Design and Data Analysis for Biologists*. Cambridge University Press: Cambridge.

Rohlf FJ, Sokal RR. 1969. *Statistical Tables*. W.H. Freeman: San Francisco, CA.

SAS Institute. 2000. *SAS*, *8.01*. SAS Institute: Cary, NC.

Schumm SA, Harvey MD, Watson CC. 1984. *Incised Channels: Morphology, Dynamics and Control*. Water Resources Publications: Littleton, CO.

Shankman D. 1999. The loss of free-flowing streams in the Gulf Coastal Plain. *Bulletin Alabama Museum of Natural History* **20**: 1–10.

Shields FD, Knight SS, Cooper CM. 1994. Effects of channel incision on base flow stream habitats and fishes. *Environmental Management* **18**: 43–57.

Shields FD, Knight SS, Cooper CM. 1997. Rehabilitation of warmwater stream ecosystems following channel incision. *Ecological Engineering* **8**: 93–116.

Shields FD, Knight SS, Cooper CM. 1998. Rehabilitation of aquatic habitats in warmwater streams damaged by channel incision in Mississippi. *Hydrobiologia* **382**: 63–86.

Shields FD, Knight SS, Cooper CM. 2000. Cyclic perturbation of lowland river channels and ecological response. *Regulated Rivers: Research and Management* **16**: 307–325.

Stanturf JA, Gardiner ES, Hamel PB, Devall MS, Leininger TD, Warren ML. 2000. Restoring bottomland hardwood ecosystems in the Lower Mississippi Alluvial Valley. *Journal of Forestry* **98**: 10–16.

Stearns SC. 1992. *The Evolution of Life Histories*. Oxford University Press: Oxford.

Strayer DL. 1999. Use of flow refuges by unionid mussels in rivers. *Journal of the North American Benthological Society* **18**: 468–476.

Strayer DL, Ralley J. 1993. Microhabitat use by an assemblage of stream-dwelling unionaceans (Bivalvia), including two rare species of *Alasmidonta*. *Journal of the North American Benthological Society* **12**: 247–258.

USDA Forest Service. 1988. The Yazoo–Little Tallahatchie flood prevention project: a history of the Forest Service's role. Forestry Report R8-FR8. US Department of Agriculture Forest Service, Southern Region, Atlanta, GA.

Vannote RL, Minshall GW. 1982. Fluvial processes and local lithology controlling abundance, structure, and composition of mussel beds. *Proceedings of the National Academy of Sciences of the United States of America* **79**: 4103–4107.

Warren ML, Haag WR. 2005. Spatio-temporal patterns of the decline of freshwater mussels in the Little South Fork Cumberland River, USA. *Biodiversity and Conservation* **14**: 1383–1400.

Williams JD, Warren ML, Cummings KS, Harris JL, Neves RJ. 1993. Conservation status of freshwater mussels of the United States and Canada. *Fisheries* **18**: 6–22.

Winemiller KO, Rose KA 1992. Patterns of life history diversification in North American fishes: implications for population regulation. *Canadian Journal of Fisheries and Aquatic Sciences* **49**: 2196–2218.